Edward A. Ueckermann

Editor

Eriophyoid Mites: Progress and Prognoses

Eriophyoid Mites: Progress and Prognoses

Edward A. Ueckermann

Editor

Eriophyoid Mites: Progress and Prognoses

Springer

Editor
Edward A. Ueckermann
ARC-Plant Protection Research Institute
Private Bag X134
Queenswood
0121 Pretoria
South Africa
UeckermannE@arc.agric.za

Cover Illustration: The tomato rust mite, Aculops lycopersici, photo taken by Dr. Ron Ochoa of the USDA, Beltsville, Maryland, USA.

Printed on acid-free paper

Contents

Preface

E. A. Ueckermann

The first reference to eriophyoids was apparently made by Reaumur (1737) who referred to galls and erinea caused by arthropods. He described them as maggots which was more correct than subsequent taxonomists who considered them fungi. The first genera were described in the middle of the nineteenth century, namely *Eriophyes* by Siebold and *Phytoptus* by Dujardin. Studies of the morphology of these mites were introduced by the remarkable work of Nalepa (1887) with his astounding accuracy in view of the optical equipment then available. During the twentieth century Keifer made a considerable contribution to the knowledge of eriophyoids, which established a firm foundation for future research. Mainly single species were described then and this resulted in many loose entities. Due to the lack of keys, thoughts to establish order gradually took shape and resulted in a series of books, namely *Mites Injurious to Economic Plants* by Jeppson et al. (1975), *Catalog of the Eriophyoidea of the world* by Amrine and Stasny (1994) and *World Crop Pests. Eriophyoid mites. Their Biology, Natural Enemies and Control* edited by Lindquist et al. (1996).

The need to continue with the ordering of the Eriophyoidea house, remained in the minds of eriophyoid specialists and was recently triggered by a series of e-mail conversations between Enrico de Lillo and Anna Skoracka. With the support of the world eriophydologists, they proposed a special eriophyoid session to the organizers of the 6th EURAAC symposium (Montpellier, July 2008). In the meantime they started by sending questionnaires to all eriophyoid specialists for their comments and the reaction was overwhelming. Unfortunately, financial, personal and health restrains have limited the presence of specialists like Jim Amrine, Jan Boczek, Evert Lindquist, George Oldfield and Valery Shevtchenko. In spite of this, about 30 specialists took part in this special session during which they took stock of the progress in a selected pool of eriophyoid research projects, since the red book of the *world crop pest* series on eriophyoid mites (Lindquist et al. 1996). Another aim of this session was to establish closer collaborations between all eriophyoidologists. It was also decided during this symposium to combine all the presented

E. A. Ueckermann (✉)
ARC Plant Protection Res. Inst., Private Bag X134, Pretoria 0001, South Africa
e-mail: ueckermannE@arc.agric.za

papers and more in a special Proceedings publication. Jan Bruin, the co-Editor-in-Chief of *Experimental and Applied Acarology*, was approached and immediately reacted positively.

Fourteen informative papers dealing with eriophyoids, their DNA, species interactions, quarantine importance, host specificity, potential as bio-control agents of weeds, chemical control, behaviour, their role in fungal pathogen epidemiology, influence in forests and on ornamentals, collecting and mounting techniques and their interaction with crops are presented here. This is an extensive and valuable update to eriophyoid science and a must for present and future researchers in this field.

Sincere thanks to all the contributors and *Experimental and Applied Acarology* for their important role in this milestone in eriophyoid research.

References

Amrine JW, Stasny TA (1994) Catalog of the Eriophyoidea (Acarina: Prostigmata) of the world. Indira Publishing House, West Bloomfield, 798 pp

de Reaumur RAF (1737) Des galles des plantes et des arbres, et des productions qui leur sont analogues; des insects qui habitant ces galles, & qui en occasionnent la formation & l'accroissement. In: Mémoires pour server a l'histoire des insects. Acad Roy Sci Paris 3(12):413–532

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. University of California, USA, 614 pp

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites. Their biology, natural enemies and control. World Crop Pests. 6. Elsevier, Amsterdam, 790 pp

Nalepa A (1887) Die Anatomie der Phytopten. Sitz. Kais. Akad. Wiss., Math.-natur. Kl. Wien Abt 96(4):115–165

What's "cool" on eriophyoid mites?

Enrico de Lillo · Anna Skoracka

Abstract Fundamental knowledge on the morphology, biology, ecology, and economic importance of Eriophyoidea has been exhaustively compiled by Lindquist et al. (Eriophyoid mites—their biology, natural enemies and control; Elsevier, 1996). Since that time, the number of recognized species and the economic importance of the taxon have increased substantially. The aim of this paper is to analyze and briefly review new findings from eriophyoid mites' literature after Lindquist et al. book, stressing persistent gaps and needs. Much recent attention has been given to sampling and detection, taxonomy and systematics, faunistic surveys, internal morphology, rearing techniques, biological and ecological aspects, biomolecular studies, and virus vectoring. Recommendations are made for integrating research and promoting broader dissemination of data among specialists and non-specialists.

Keywords Plant parasites · Pests · Quarantine organisms · Weed control agents · Pathogen vectors · Eriophyoidea

Introduction

The morphological, biological, behavioural, and ecological peculiarities of eriophyoid mites have been widely emphasized in the acarological literature since the late nineteenth century (Nalepa 1886–1929; Keifer 1938–1991; Lindquist 2001). After more than 150 years of investigations, about 4,000 eriophyoid species have been described from a vast array of host plants, and a huge number of species remains undiscovered (Amrine

E. de Lillo (✉)
Department of Biology and Chemistry of Agro-Forestry and Environment (Di.B.C.A.), Entomological and Zoological Section, Faculty of Agriculture, University of Bari, via Amendola, 165/A, 70126 Bari, Italy
e-mail: delillo@agr.uniba.it

A. Skoracka
Department of Animal Taxonomy and Ecology, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznan, Poland
e-mail: Anna.Skoracka@amu.edu.pl

et al. 2003). The great diversity of these tiny plant feeders is related to their extreme host specificity and intimate host relationships (Oldfield 2002). Their impact as specialized phytophagous mites is well known and strongly accented in each of their involvements as direct plant pests, plant pathogen vectors, agents of control of weeds, and food sources for predators (Hong and Cheng 1999; Oldfield 2002; Zhang 2003; Gamliel-Atinsky et al. 2009; Smith et al. 2009).

The last comprehensive compilation of information of the four-legged mites was *Eriophyoid Mites—Their Biology, Natural Enemies and Control* (Lindquist et al. 1996) which has been lauded as a milestone in basic and applied acarology by Norton (1997). This book contains fundamental knowledge on the morphology, biology, ecology, and importance of the taxon, and highlights paths for future research. Since then, the number of new eriophyoid taxa and their economic importance has grown worldwide.

Therefore, the need to update the state of knowledge of this important taxon is largely required (de Lillo and Skoracka 2008). The idea of a session devoted to eriophyoid mites met great interest among researchers and resulted in extensive talks on a few selected topics at the 6th Symposium of the European Association of Acarologists held in Montpellier, France, 2008. Owing to time and space constraints many significant subjects were not discussed at the session, and many questions previously outlined at the 10th International Congress of Entomology (Nuzzaci and de Lillo 1996) as well as by the authors of *Eriophyoid Mites—Their Biology, Natural Enemies and Control* (Lindquist et al. 1996) remain unanswered. The aim of the present paper is to analyze and briefly review the eriophyoid literature since 1996, stressing gaps in knowledge that still need to be investigated.

Literature before and after Lindquist et al. (1996)

Eriophyoids were recognized as a taxon in the Acari by Siebold (1850). The number of additions to eriophyoid literature stayed more or less constant for most of the next century until H. H. Keifer began publishing several taxonomic papers per year starting in the late 1930s and ending over 30 years later. Keifer's works constituted a considerable increase in the rate of publication on eriophyoids and this trend seems to be still increasing (Fig. 1). More than 60% of the total literature on Eriophyoidea was published after Keifer's involvement in *Mites injurious to economic plants* (1975), and about 25% of papers have appeared since 1996 (Fig. 1), confirming the scientific significance of the volume edited by Lindquist et al. (1996).

About 2,250 papers were published per year on the Acari during 1997–2007 as shown by an examination conducted on the CAB abstracts on-line database, herein used as standard abstracts review. Among plant associated mites, publications naming eriophyoids ranked third in number after those involving spider mites as plant feeders, and phytoseiids as predators (Fig. 2). They represented about the 7.5% of all contributions on plant mites in that range of time. The decreasing trend in 2007 may be explained by a common delayed indexing of papers published in that year (for the same reason, papers published in 2008 have not been considered).

A further analysis of the papers published during 1997–2007 showed that the most investigated topic, with about 53% of total papers (Fig. 3) was eriophyoids as pests of agricultural crops. Numbers of papers devoted to: (1) biological, chemical, and other strategies for mite control, (2) taxonomy, systematics, surveys, or to (3) ecological and biological investigations, each accounted for 28–30% of the total papers. Other topics, such
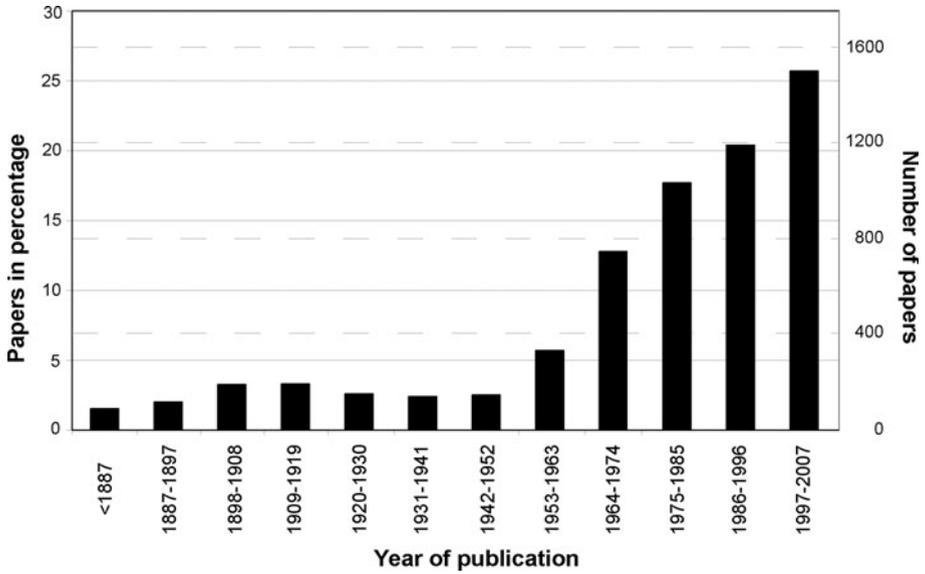
Fig. 1 Distribution of papers, in percentages (*on the left*) and absolute value (*on the right*), naming Eriophyoidea, published since 1850 and grouped in periods of 11 years (source: de Lillo's database)
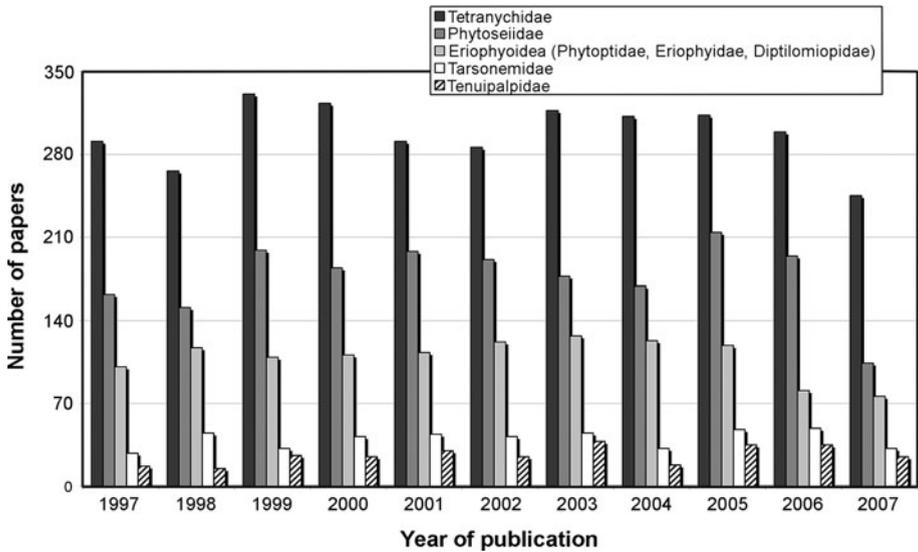
Fig. 2 Number of papers published on the main mite taxa of agricultural interest from 1997 to 2007 (source: CAB Abstracts on-line database)

as cladistics, internal morphology, rearing techniques, and molecular biology were treated in less than 1% of the contributions, probably because of the strongly specialized nature of the research.
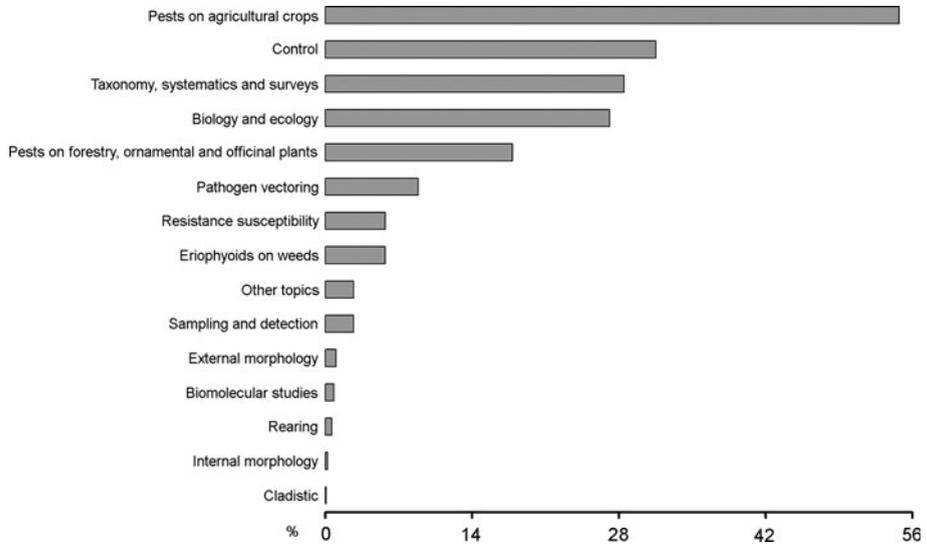
Fig. 3 Distribution of topics treated in papers naming Eriophyoidea published from 1997 to 2007 expressed in percentages in respect to the total number of Eriophyoidea papers published during the selected period (source: de Lillo's database). The sum of the percentages is higher than 100% because some papers treated more than one topic and they were counted more than once

State of research and tasks

Sampling and detection

The spatial and temporal distribution of eriophyoids in the field and on plants should be taken account into sampling. Several factors can affect these distributions: colonization and dispersal ability, mite population dynamics, mite-host relationships, plant phenology, host pruning, environmental factors, control strategies, and so forth (e.g. Pérez-Moreno and Moraza Zorilla 1998; Castagnoli and Simoni 2000; Arbabi et al. 2006; Ishihara et al. 2007; Lewandowski and Kozak 2008). An aggregated and uneven distribution of eriophyoids has been widely studied within plants and their organs (intraplant distribution) often indicating some site preferences (e.g. Davies et al. 2001a; Fernando et al. 2003; Kawai and Haque 2004; de Lillo et al. 2005a; Kuczyński and Skoracka 2005; Aghajanzadeh and Mallik 2007; Walton et al. 2007; Bertoldo et al. 2008; Monfreda et al. 2009).

In most cases, especially when the host is a tree or a bush, the whole plant cannot be sampled. Moreover, eriophyoids often tend to move and infest young tissues. But, young organs cannot be regarded as representative for the whole plant since mite density on different parts of the plant changes throughout the year (Skoracka et al. 2003; Fournier et al. 2004; Ferla et al. 2007). Also, different eriophyoid species show different intraplant distributions. Thus, it is obvious that sampling schemes should be planned with extreme care and should consider: time required for sampling, degree of accuracy, and both field and laboratory measurements. Such a scheme should include choosing appropriate sampling parameters, such as plant allocation in the field, organs to be sampled, their exposure and orientation, timing, and sample and subsample size.

Currently, destructive sampling is the most commonly used method. Attempts to apply more efficient and non-destructive samplings of infested parts of plants have been performed (Fournier et al. 2004), especially on plant organs with high economic value such as fruits (de Lillo et al. 2005a; Aghajanzadeh and Mallik 2007). An experimental effort to optimize the sample size during destructive sampling has been recently carried out for *Phyllocoptruta oleivora* (Ashmead) (Hall et al. 2005) showing a possible reduction in resource input. Sequential sampling was employed by Manzur (1989) in a study of *P. oleivora* and recently on *Dichopelmus notus* Keifer (Vieira-Neto et al. 2007). Conversely, infestation evaluation by symptom assessment, although easily and quickly applied, may not reflect actual mite density (Fernando et al. 2003). This appraisal technique must be weighted according to the purpose of the study. Efforts to develop efficient and accurate methods of estimating the population density of eriophyoid mites have been undertaken by several investigators (e.g. Hall et al. 1997; Pérez-Moreno and Moraza Zorilla 1998; Gabi and Mészáros 2001; 2003; Davies et al. 2002; Siriwardena et al. 2005; Bertoldo et al. 2008).

The strong interest in detection of these tiny mites points out that finding them and accurately assessing populations on different plant organs remains a critical step for any kind of investigations. Extensive efforts have been made during the last decade and many investigations have contributed to developing simpler and easier ways of detecting and collecting mites other than direct counts of mites on samples of plants. Each of these procedures is intended to increase efficiency and confidence in estimating and assessing populations, in counting specimens, and in saving time (reviewed by Monfreda et al. 2009). Of particular relevance is the application of a surfactant (e.g. polysorbate 80) which can wash mites from plants while keeping them alive, allowing a careful assessment of the population vitality, the concentration of large numbers of specimens, and the management of them for biological assays (de Lillo and Monfreda, unpublished data). Similarly, mite population assessment can be carried out in the laboratory by counting mites caught on adhesive tape traps previously applied on plant organs in the field (Bernard et al. 2005; Aghajanzadeh and Mallik 2007).

Ultimately, sampling procedures should be decided on a case-by-case basis and they should be first selected in view of the level of precision required either for management control decisions or for mite survey and biological investigations. In addition, comparisons among different sampling methods for eriophyoid mites are lacking and appear to be strongly needed.

Taxonomy and systematics

From 1996 to 2007, about 70 eriophyoids have been described as new species each year (Fig. 4). More than 50% of them have been found in China and this trend seems to have remained stable. In particular, the tropics remain the least explored regions, and a huge number of previously undescribed taxa is expected to be found there (Amrine et al. 2003). Merely keeping the current annual rate, discovering new eriophyoid species and genera would require from at least three centuries to a couple of millennia (Lindquist 2001). It should also be considered, that future findings of new taxa, especially in the tropics and on ancient hosts, could rectify, at least in part, the current systematics of Eriophyoidea. Issues addressed could include arrangement or simplification of prodorsum, leg and body setation, leg segmentation, and remnants of other structures (Lindquist 2001). It is relevant to note that recently a new genus and species have been described from the Cephalotaxaceae in China, as the first report for this family (Xue et al. 2007); two new genera and three new
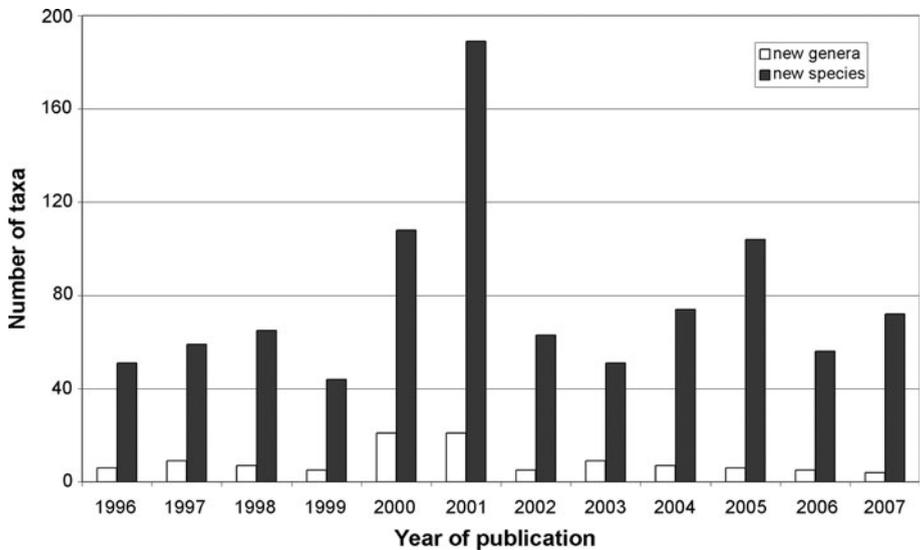
Fig. 4 Distribution of newly described eriophyoid species and genera since 1996 (source: de Lillo's database)

species have been found on *Araucaria angustifolia* (Bertol.) O. Kunze in Brazil (Flecht-mann 2000); as well as one new genus and two new species reported on ferns (Flechtmann 2002; Knihinicki and Boczek 2002). However, the special search for archaic forms of Eriophyoidea has been languishing.

Considering the extreme delicacy of the specimens mounted on slides and their fate over time, accurate morphometric descriptions of taxa (de Lillo et al. 2009) are essential for making identifications possible and revisions in the future, for example, to support phylogenetic relatedness within the Eriophyoidea as well as between them and other Prostigmata. Taxonomists world-wide have successfully adopted Lindquist's (1996a) system for notation of setae and other external structures, allowing the achievement of a standardized morphometric description to find homologies within the Acari. However, a careful reconsideration of traits for species characterization (Amrine et al. 1994) is needed to evaluate the importance of characters to systematics of Eriophyoidea. The present system is thought to be artificial (Lindquist 1996b; Lindquist and Amrine 1996). At this regard, Hong and Zhang (1996a, c, 1997) undertook cladistic analyses to test the mono-phyly of groupings within the present eriophyoid classification. However, their results need independent testing, though future phylogenetic studies need more correct, complete and detailed morphological studies (C. Craemer, personal communication). In addition, mor-phometric analyses should be widely applied, since these can help in distinguishing intraspecific variation, including host-adapted strains or even cryptic species (Amrine et al. 1994; Skoracka et al. 2002; Navia et al. 2006a; Skoracka and Kuczyński 2006; Magud et al. 2007; Vidović et al. 2008).

The morphometric characterization of species described by Nalepa and others using microscopy available a hundred or more years ago, the redescription of those inadequately described, and the revision of taxonomically problematic species belonging to the genus *Aceria*, and a few other genera, are urgently required at this time. Similarly, taxa to which

Nalepa assigned trinomials and tetranomials occurring on related host plants await careful revision. The difficulties in recovering the original material and managing it efficiently surely represent an important restriction in this task (Amrine et al. 2003; Knihinicki et al. 2009) that might be overcome by collection and designation of neotype.

Scanning electron microscopy (SEM) has revealed morphological characteristics useful in distinguishing different genera and, in a few cases, has added supplementary descriptive information. The recent enhancement of this technology has facilitated the study of the external morphology of these tiny mites (Duffner et al. 1998; Wergin et al. 2000; Achor et al. 2001), but SEM micrographs remain infrequently used in eriophyoid systematics studies. Some aspects need to be improved, such as optimizing specimen preparation to obtain the most real and natural view of a mite. The application of SEM technologies could be profitably exploited in comparative studies related to specific structures which require high resolution (empodial arrangements, minute details of the gnathosoma, legs, coxal and genital area, etc.). In spite of the considerable advantages offered by SEM, eriophyoidologists recommend avoiding the use of SEM images in place of drawings in descriptions of new taxa.

Faunistic surveys

Our current awareness of eriophyoid geographical diversity is largely restricted to temperate regions of the world, and a few tropical/subtropical countries such as India, Thailand, Brazil and Australia, where more than 90% of known species have been found. There is no doubt that faunistic investigations and available checklists are dependent on the involvement of native scientists and research institutions, as well as funding. Eriophyoids in tropical areas are particularly underrepresented and a huge number of eriophyoid taxa is expected to occur there (Lindquist 2001; Amrine et al. 2003). Moreover, a comprehensive survey of native and alien species has never been seriously carried out on any continent.

Since the last catalogue by Amrine and Stasny (1994) which included a world eriophyoid fauna list, a few local or regional checklists have been published or updated for the Palaearctic (Bernini et al. 1995; Petanović and Stanković 1999; Redfern et al. 2002; Skoracka et al. 2005; Erman et al. 2007; Ripka 2007; Mifsud et al. 2008), Indomalaya (Kuang 1995; Hong and Zhang 1996b; Kuang et al. 2005), Nearctic (Baker et al. 1996), and Australasian (Halliday 1998) regions. Recently, a European checklist has been published on-line within the Fauna Europaea project (de Lillo 2004). It was affected by a restricted availability of local bibliographic sources that resulted in many missed reports. Thus, after only 5 years from its publication, it requires significant updating.

The impressive economic development of China has been reflected in a surge of papers describing the Chinese eriophyoid fauna in the last 10 years. This trend may lead to the development of a new catalogue of Chinese eriophyoids, possibly making more data available to non-Chinese speaking scientists and updating the previous catalogue (Hong and Zhang 1996b).

Finally, a comprehensive survey of geographical distribution of eriophyoid species could provide a way to evaluate the role of the physical aspects of the environment on their success, the potential risk of some species as pests in new environments, and their modes of dispersal (Navia et al. 2006a). Whereas surveys of eriophyoids on weeds and invasive plants can contribute to searches for weed biological control candidates (Petanović and Rector 2007; Knihinicki et al. 2009).

Internal morphology

Despite its relevance for comparative arachnology (Lindquist 2001), since 1996 a decline of investigations on internal morphology of four-legged mites has been evident. Only five papers on this topic have been published; three of them reviewed the cheliceral arrangement, the sensorial structures and the secretive organs, respectively (de Lillo et al. 2002, 2005b; Nuzzaci et al. 2008), while the others considered mouthparts and legs (Vaneckova-Skuhrava 1996; de Lillo and Aldini 2001). Information regarding anatomy of eriophyoid mites relevant to all Acari was included in the treatise by Alberti and Coons (1999). Nuzzaci and de Lillo (1996) carefully examined the state of knowledge of eriophyoid morphology and, since then, the only new examinations have been of the leg sensilla (de Lillo and Aldini 2001). Undoubtedly, further morphological explorations (Lindquist 2001) are warranted to support functional interpretations of body structures and explain the astonishing miniaturization of structures in this taxon. Unfortunately, internal and structural morphology of eriophyoids is not easily funded. Moreover, the extreme minuteness of these mites makes all the phases of mite preparation and examination for fine morphology highly time-consuming and laborious.

Rearing techniques

Their intimate relationships with their hosts, their tiny size and structures, obscure life style, and high growth requirements cause serious restrictions for rearing of eriophyoid mites. Some of the most critical issues involved in rearing eriophyoids include: specimen transfer, reproduction in artificial micro-environments, durability of stock colonies over a long period, maintenance of host plants, contamination by other arthropods, stage identification, and direct observation during experiments. Few recent studies focused specifically on rearing methods and techniques including those of Gispert et al. (1997); Haq (2001); Wickramananda et al. (2005); De Silva and Fernando (2008). The procedure developed by De Silva and Fernando (2008) to successfully mass rear *Aceria guerreronis* Keifer on embryo culture seedlings for up to 5 weeks offers promise for rearing of species strictly associated with young and meristematic tissues. Rearing was also indirectly handled in a few others studies (Courtin et al. 2000; Schwoebel and Beiderbeck 2000; Gondim and de Moraes 2003; Skare et al. 2003; Ansaloni and Perring 2004; Skoracka and Kuczyński 2004; Witt 2004; Britto et al. 2008), resulting in successful multiplication of eriophyoids dedicated to various subsequent biological investigations.

Molecular biology studies

Since the end of the twentieth century, DNA analyses have been successfully used to study population genetics, taxonomy, systematics, and evolutionary relatedness of many Acari, although only a few of these have been eriophyoid mites among them (Navajas and Fenton 2000; Lindquist 2001). This can be demonstrated by the fact that of the 1,521,570 DNA sequences in the GenBank database originating from Acari, only 207 regard eriophyoid mites (from ca. 20 species in the family Eriophyidae) (http://www.ncbi.nlm.nih.gov/ accessed 27-March-09). In recent years, DNA barcoding (employing typical mitochondrial DNA sequences) has found increasing use as a powerful tool to assist species identification in many animal taxa (e.g. Hebert et al. 2003) but is not common for Eriophyoidea.

Nonetheless, a few studies of eriophyoid mites have been successfully addressed by applications of molecular methods. The geographical origin, ancestral host associations and colonization history of *A. guerreronis* have been largely explained using mitochondrial and nuclear markers (Navia et al. 2005b). The phylogenetic tree of *Cecidophyopsis* mites associated with *Ribes* spp. hosts has been built on the basis of rDNA regions, illustrating the monophyly of this group (Fenton et al. 2000). Genetic relationships between geographically dispersed populations of the biological control agent *Floracarus perrepae* Knihinicki and Boczek and its fern host were screened in order to choose the most effective mite population to release against the invasive fern (Goolsby et al. 2006). DNA sequences have been also used for assessing inter- and intra-specific variations and, thus, for discrimination between eriophyoid species (Fenton et al. 1996, 1997; Kumar et al. 1999, 2001; Carew et al. 2004; Lemmetty et al. 2004). Recently, it has been indicated on the base of molecular markers that *Aceria tosichella* Keifer and *Abacarus hystrix* (Nalepa) represent species complexes (Carew et al. 2009; Skoracka and Dabert 2009).

Molecular markers could also be used to elucidate the origin and relationships of Eriophyoidea with other major taxa of trombidiform mites, and for possible revision of families, subfamilies, and lower taxonomic groups. A sister relationship has been suggested between Eriophyoidea and Pachygnathoidea (Lindquist 1998), and between Eriophyoidea and Tydeoidea (Lindquist 1996b). Although no molecular data explaining the relationships of Eriophyoidea with other Prostigmata have been published yet, such investigations are currently continuing. Preliminary results based on molecular markers imply that the closest relative of Eriophyoidea is Tydeoidea (Lekveishvili, personal communication).

Broader application of genetic data to eriophyoid mite studies and combining molecular and morphological traits could make species identifications easier and quicker, and in some cases explain problems which are unresolved with traditional methods, e.g. conspecificity, cryptic complexes, population structures, and intra- and inter-specific variability.

Virus vectoring

Up to 1996, about a dozen economically important diseases of plants were known to be caused by agents which were transmitted by eriophyoid mites. The nature of most of these pathogens (particularly those infecting dicots) was uncertain (Oldfield and Proeseler 1996). More recent virological investigations have shown that most of these pathogens are viruses of the genus *Rymovirus*, *Tritimovirus* (family Potyviridae) or *Alexivirus*, with the exception of Blackcurrant Reversion Virus, which belongs to *Nepovirus* (family Comoviridae) (e.g. Jones 2000; Kumar et al. 2003, 2005; Kang et al. 2007). During the last 12 years, considerable research attention has been paid to 12 pathogens transmitted by nine eriophyoid vectors, although only scarce concern has been paid to understanding the intimate mechanisms of virus transmission (Young et al. 2007) and virus detection within the mite body (Latha and Doraiswamy 2008).

The most extensive studies of eriophyoid virus vectoring have concerned the Wheat Streak Mosaic Virus (WSMV), which is transmitted by *A. tosichella* (WCM). It causes one of the most destructive viral diseases of wheat and its occurrence is increasing in many wheat producing areas of the world (Sánchez-Sánchez et al. 2001; Navia et al. 2006b). It has been shown that acaricide treatments, control of volunteer wheats, tillage and environmental factors can affect mite survival and incidence of virus infection

(Harvey et al. 1998; Thomas and Hein 2003; Jiang et al. 2005; Coutts et al. 2008). In addition, biomolecular methods changing the virus region can effectively reduce the efficiency of vector transmission (Stenger et al. 2006; Young et al. 2007). Great attention has been also paid to the discovery and breeding of WSMV- and WCM-resistant wheat varieties as a promising methods for controlling this mite-vectored disease (e.g. Chen et al. 2003; Malik et al. 2003; Thomas et al. 2004; Harvey et al. 2005; Li et al. 2005, 2007). *Aceria tosichella* has been identified as a vector of three other plant disease viruses, namely Brome Streak Mosaic Virus (Stephan et al. 2008), Triticum Mosaic Virus (Seifers et al. 2009), and High Plain Disease (Mahmood et al. 1998; Seifers et al 2002; Skare et al. 2003, 2006). The latter agent causes serious economic damage on wheat and corn (Jensen et al. 1996).

The ability of one mite species to transmit three different viruses is unusual. Most reports suggest a high degree of specificity between virus and vector mite (Oldfield and Proeseler 1996). The ability to transmit more than one virus has also been observed in *A. hystrix*, which vectors Ryegrass Mosaic Virus (RMV) and Agropyron Mosaic Virus (AMV) (Oldfield and Proeseler 1996). However, recent host preference and performance assays, and genetic compatibility observations have shown that *A. hystrix* populations infesting *Lolium*-related grasses may be reproductively separate with respect to conspecific populations infesting *Elymus*-related grasses (Skoracka 2008 and references therein). Conversely, the possibility that different *Cecidophyopsis* spp. can function as vectors of one virus—Blackcurrant Reversion Virus (BRV) has been suggested (Lemmetty et al. 2004). In addition, it has been demonstrated that different host strains of single eriophyoid species can differ in vectoring ability and transmission biology of the pathogen agents (Kumar et al. 2001; Harvey et al. 2005).

During the last decade *Aceria cajani* Channabasavanna was confirmed as the only vector of the agent of the Sterility Mosaic Disease (SMD), whose viral nature has been documented (Kumar et al. 2001, 2003; Latha et al. 2007). Sterility mosaic virus causes the most devastating disease of pigeon pea and is an increasing problem in Asia (Dharmaraj et al. 2004; Jones et al. 2004). The transmission biology and relationships between this virus and its mite vector have been elucidated by Kulkarni et al. (2002) and by Latha and Doraiswamy (2004, 2008). Management of SMD by acaricides (Kandulna et al. 2005) and pigeon pea varieties resistant to mite and virus have been developed (e.g. Lakshmikantha and Prabhuswamy 2003; Kumar et al. 2005).

Attention has also been paid to epidemiology and control of vector and pathogen combination such as *Cecidophyopsis ribis* (Westwood) and BRV (e.g. Jones 2000; Lemmetty et al. 2004; Susi 2004), *Aceria ficus* (Cotte) and Fig Mosaic Virus (FMV) (e.g. Serrano et al. 2004), *Eriophyes insidiosus* Keifer et Wilson and Peach Mosaic Virus (PMV) (Gispert et al. 1998), *Acalitus essigi* (Hassan) and Readberry Disease (Davies et al. 2001b), and *Aceria tulipae* (Keifer) and GarV-B1 (Kang et al. 2007).

Phyllocoptes fructiphilus Keifer vectors an ilarvirus, designated Rose virus 1 (RSV-1) (Jesse et al. 2006; Tzanetakis et al. 2006), which causes Rose Rosette Disease (RRD) on the weed *Rosa multiflora* Thunb. and on ornamental roses, among which many varieties are resistant (Amrine 1996). This appears to be a unique example of an eriophyoid mite controlling a weed indirectly by means of a plant pathogen.

Thanks in large part to biomolecular methods, the identification of new sources of crop resistance to pathogens and their vectors is among the most important agricultural achievements of the past decade and remains the best strategy to control viral diseases (e.g. Marçon et al. 1999; Conner and Chen 2003).

Ecological and biological aspects

Phenology and developmental biology

Data on the phenology of eriophyoid mites are necessary to establish the timing for management strategies, especially for the control of refuge-seeking and gall-inducing species, since they are well protected in plant structures for most of their life cycle. Many studies in recent years have focused on detecting hibernation strategies of eriophyoid mites, to monitor the emergence period and the mite's period of environmental exposure (Pérez-Moreno and Moraza Zorilla 1998; Davies et al. 2001a, b; Gabi and Mészáros 2001, 2003; Ashihara et al. 2004; Walton et al. 2007). Consideration of air temperatures to which they are exposed and the developmental stages of host plants has provided a satisfactory prediction in modelling the emergence time for eriophyoids (Jarvis and Collier 2002; Cross and Harris 2003; Balaji and Hemavathy 2007; Webber et al. 2008). Thus, it seems to have the potential for wider use within agricultural systems and should be promoted for more species. Diapausing mites were found most frequently within buds of their deciduous host plants. In addition, live fruits, young paracladial shoots, and leaf rosettes of young plants can act as other overwintering sites (Davies et al. 2001a; Zemek et al. 2005). It has been also shown that *Cecidophyopsis psilaspis* (Nalepa), which infests evergreen hosts, does not seek hibernation sites, and has all stages present throughout the year (Marshall and Clayton 2004).

The emergence of *P. oleivora* adults showed a diel periodicity that was synchronous with the daily pattern of aerial dispersal of adult females. This phenomenon has been interpreted as an adaptive response of the mite to environmental factors, possibly including sunrise and drying of the plant, which could induce stress (Bergh 2001; Bergh et al. 2002). Patterns of diel activity have been reported for *Acalitus hibisci* Mondal et Chakrabarti (Chakrabarti and Chakrabarti 2005), *A. guerreronis* (Haq et al. 2002; Sumangala and Haq 2005), and *C. ribis* (Cross and Ridout 2001).

When arrhenotokous parthenogenesis in eriophyoid mites was experimentally demonstrated, the female-biased sex ratio could be explained (rev. Helle and Wysoki 1996). Thereafter, the outnumbering of males by females has often been observed for various eriophyoid species (e.g. Skoracka and Kuczyński 2004; Ozman and Goolsby 2005). Strikingly, Marshall and Clayton (2004) concluded that no evidence of arrhenotoky exists in *C. psilaspis* since females consisted 54–100% of the adult population. However, seasonal fluctuations in sex ratio may be common in eriophyoid mites and does not indicate that arrhenotoky is non-existent (Helle and Wysoki 1996). Other studies have shown that uninseminated females laid eggs resulting only in male offspring, indicating arrhenotoky in *P. oleivora*, *A. guerreronis*, and *A. hystrix* (Bergh and Smith 2001; Ansaloni and Perring 2004; Skoracka 2008).

Navia et al. (2005a) reported cases of ovoviviparity or viviparity in *A. guerreronis* and ovoviviparity was reported earlier for several other eriophyoid species (rev. Navia et al. 2005a). The conditions influencing this strategy are still not known. The authors suggest considering such results with caution since the typical life style of eriophyoids contains eggs.

Recently, Britto et al. (2008) discovered a new species, *Aceria inusitata* Britto and Navia with two forms of males, one resembling the protogyne and the other the deutogyne. This is the second example of a deuterogynous eriophyoid mite with dimorphic males. The first was reported by Shevchenko and De-Millo (1968) in *Trisetacus kirghisorum* Shev.

These reports offer evidence of the undiscovered life strategies that may await elucidation by future eriophyoidologists.

Such examples indicate a continuing strong need for experimental research to better understand the various life cycles of eriophyoid mites and the mechanisms governing their seasonal fluctuations. Also, a better awareness of how eriophyoid mites respond to changing environmental conditions will require further examination and biological comparisons between eriophyoid species in different climates.

Physiology

The fascinating and unusual phenomenon of secretion by eriophyoid mites has been summarized by Manson and Gerson (1996) and by Lindquist and Oldfield (1996). The ability of eriophyoids to spin, silk, and secrete wax and liquids has been recorded for several species by these authors. Wax-producing eriophyoids have been recorded most commonly. Since these reports, few additional cases have been reported.

Web-spinning is thought to be rather unusual for eriophyoids and only eight spinning species were mentioned by Manson and Gerson (1996). A new species showing "nest building" behaviour, A. inusitata was described recently (Britto et al. 2008). Deutogynes of A. inusitata, which have paired glandular structures in the opisthosoma that secrete a wax-like substance, build wax "nests" prior to the appearance of protogynes in the colony.

Wax secretion by adults and immatures has been recorded for Retracrus johnstoni Keifer (Gondim and de Moraes 2003). Frost (1997) showed that changes in the rate of wax production by grass-feeding A. hystrix had genetic and environmental components. It has been shown that wax filaments play a role in the regulation of water-loss and in maximizing wind drag when airborne. Filaments appear to be advantageous during summer mite migrations by increasing wind-shear stress on the mites, enhancing drifting on wind current, and reducing the rate of desiccation-induced mortality.

Eriophyoid secretory systems constitute a challenging field of investigation. Anatomical and biochemical observations as well as explanation of functions of these phenomena are needed.

Life-history parameters

Sabelis and Bruin (1996) reviewed available data on developmental and reproductive parameters for 25 eriophyoid species and discussed their roles in population increase. They emphasized the paucity of knowledge on life-history parameters of eriophyoids and, unfortunately, this deficit still exists. Since then, life-table parameters of only a few eriophyoid species have been investigated in detail. On the basis of several estimates, including generation time and intrinsic rate of increase, it has been shown that species attacking crop plants [e.g. A. hystrix, Aceria oleae (Nalepa), Tegolophus hassani (Keifer), Aculops lycopersici (Tryon), and A. guerreronis), as well as species attacking weeds [F. perrepae] are capable of rapid population increase under optimal environmental conditions (Ramarethinam and Loganathan 2000; Haque and Kawai 2003; Skoracka and Kuczyński 2004; Abou-Awad et al. 2005; Ozman and Goolsby 2005). In addition, temperature and humidity requirements for development and reproduction of A. lycopersici, A tulipae, and A. guerreronis have been carried out (Courtin et al. 2000; Haque and Kawai 2003; Ansaloni and Perring 2004; Xu et al. 2006). Information on life-history parameters is essential for understanding the population dynamics of species. Thus, the strong need of the investigation of life table parameters for other eriophyoid species is obvious.

14

Developmental times, reproduction and survival rates have been used as appropriate measurements in testing the host specificity of species evaluated as potential biological control agents for weeds.

Population density, fluctuation, distribution, and dispersal

Population dynamics and seasonal changes in infestation levels have been presented for several eriophyoid species (e.g. Gillespie et al. 1997; Gabi and Mészáros 2001; Zhang et al. 2001; Kasai et al. 2002; Fournier et al. 2004; Daud and Feres 2007). Many factors have been found to affect population dynamics of Eriophyoidea, including temperature, relative humidity, predation, rainfall, site and plant condition, habitat, and height of canopy (Quiros-Gonzalez 2000; Leite et al. 2003; Thomas and Hein 2003; Marshall and Clayton 2004; Abou-Awad et al. 2005; Chakrabarti and Chakrabarti 2005; Ozman and Goolsby 2005; De Gouvea et al. 2006; Jesse et al. 2006; Demite and Feres 2007; Lawson-Balagbo et al. 2007; Kula et al. 2008). Other studies have demonstrated that mite population densities are not influenced by weather factors, host- and site-specific effects, or air pollution (Varadarajan and David 2002; Skoracka and Kuczyński 2003; Buchta et al. 2006; Kula et al. 2008; Reis et al. 2008). Since data on factors affecting population dynamics are essential to predict fluctuations in densities of phytophagous invertebrates and in developing pest management strategies, long-term observations and experimental tests involving more eriophyoid species will certainly be required.

One long-term study has demonstrated that plant genotype and hybridization influence the population dynamics of *Aceria parapopuli* (Keifer) (McIntyre and Whitham 2003). Since mite population growth and extinction can be closely tied to rare host genotypes, these findings have important conservation implications. Such ecological studies are also relevant to the use of eriophyoids in biological control of weeds in relation to the assessment and selection of eriophyid strains based on host specificity.

Eriophyoid mites often display high levels of specificity to particular sites on their host plant (e.g. Leite et al. 2003; Fournier et al. 2004; De Gouvea et al. 2006; Ishihara et al. 2007). Studies of the distribution of eriophyoid mites, both within the field and within-plant have revealed mite aggregation and distribution patterns (Davies et al. 2001a; Kuczyński and Skoracka 2005; Ferla et al. 2007; Bertoldo et al. 2008). Both biotic and abiotic factors have been found to be responsible for the distribution of eriophyoid mites (e.g. plant and tissue age, level of canopy, microhabitat morphology, limited ambulatory dispersal capabilities, host-plant size and reproductive status, climate) (Davies et al. 2001a; Kuczyński and Skoracka 2005; Ishihara et al. 2007; Lewandowski and Kozak 2008). Other factors have been recognized as not influencing mite density and distribution in certain studies (e.g. shoot length, altitude, study site) (Kuczyński and Skoracka 2005; Ishihara et al. 2007). Density-dependent within-plant distributions (e.g. seasonal changes in population densities that are correlated with changes in mite distribution) have been described for a few species (Skoracka et al. 2003; Thomas and Hein 2003; Fournier et al. 2004; Bertoldo et al. 2008).

Eriophyoid mites dispersal activity has an important effect on within- and inter-plant distribution. Most dispersal studies have indicated primarily passive aerial dispersal of eriophyoids. Such studies suggest the possibility of long-distance dispersal (Duffner et al. 2001), considerable resistance to the rigorous environmental conditions during dispersal (Zhao and Amrine 1997), and a diel periodicity of dispersal (Bergh and Smith 2001). Among abiotic factors, solar radiation, time of day, and leaf wetness have been found to be factors that best explain aerial dispersal of the citrus rust mite; whereas wind speed,

humidity, temperature and rainfall appeared to have minimal effect (Bergh and Smith 2001). The density of the source population has been identified as a major influence on the aerial movement of the wheat curl mite (Thomas and Hein 2003). However, Davies et al. (2001b), while not discounting the possibility of low levels of aerial dispersal, have concluded that non-aerial movement (i.e. crawling) via the fruit pedicel is the dominant mode of blackberry fruit infestation by A. essigi. The impact of human activity on dispersal of eriophyoids was documented for the first time by Duffner et al. (2001) when they reported spread by adherence of mites to cloths and hands of workers. An important role of rain or phoretic transport by arthropods in eriophyoid dispersal has been suggested (Grahl and Leuprecht 1998; Waite 1999; Duffner et al. 2001; Tanaka and Shibao 2003), although not yet experimentally proven. Undoubtedly, further investigations of dispersal of eriophyoid mites are needed in relation to their distribution and population dynamics, and to current trends in management practises.

Behavioural ecology

Investigations into eriophyoid behaviour can be affected by their extreme small size, rearing problems and management difficulties of direct observation. Although so small and morphologically simple, eriophyoids have evolved observable and successful behavioural strategies. Data illustrating some details of mating and other aspects of sexual biology (such as male interest towards quiescent female nymphs, influence of conspecifics on spermatophore deposition, and diel patterns in spermatophore deposition) are valuable contributions to the understanding of sexual selection (Michalska 1999, 2000, 2005). Climbing leaf trichomes to pass through the quiescent nymphal stages enables the quiescent nymph of some species to better avoid detection by predators (Michalska 2003). The existence of social behaviours within mite colonies has been suggested by Britto et al. (2008). Finally, variations in female behaviour between host and non-host plants have indicated that females can quickly distinguish between hosts and promptly make foraging decisions (Skoracka et al. 2007). Studies of the role of behaviours such as sensorial interactions that enable eriophyoid mites to adapt to their environments should be promoted.

Inter-specific associations

Studies of the role played by eriophyoids in the plant ecosystem is mainly that of specialised herbivory, even though they are exposed to an array of other organisms with which they must interact to survive. Mite-host relationships are still scarcely known, although first attempts have been performed to elucidate the role of salivary components in inducing the myriad effects of feeding by eriophyoids on their hosts (de Lillo and Monfreda 2004; Monfreda and de Lillo 2006). Eriophyoid mites can interact with other plant herbivores by affecting the host plant (Moura et al. 2008) and can compete with fungal pathogens (Fournier et al. 2006; Gamliel-Atinsky et al. 2009). A leaf-rolling eriophyoid species had an indirect effect in structuring a terrestrial community of arthropods, by influencing the distribution and abundance of predators and other herbivores (Fournier et al. 2003). A mutualistic system encompassing prey-predator interactions has been discovered between eriophyoid mites and predators on *Cinnamomum camphora* (Kasai et al. 2005; Nishida et al. 2005). In addition, the host plants can favour predatory mites as "protection" against eriophyoids after their infestation, i.e. feeding by these mites causes host tissues to become more attractive or accessible to predators (Aratchige et al. 2004, 2007; Lawson-Balagbo

et al. 2007; Sabelis et al. 2008). The antagonistic relationships between eriophyoid and predatory mites have frequently been studied, which is understandable in view of the potential role of predators as biological control agents although no example of such application is known (e.g. Walde et al. 1997; Slone and Croft 2001; Fernando et al. 2003; De Vis et al. 2006; De Gouvea et al. 2007; Ferragut et al. 2008; Lawson-Balagbo et al. 2008). Nevertheless, eriophyoid mites represent a valuable alternative food source for predatory mites (Phytoseiidae, Ascidae, Stigmaeidae, Tydeidae, Anystidae) and insects (Heteroptera, Lepidoptera, and Diptera) that may be used as biological control agents against other targets (e.g. Brodeur et al. 1997; El-Laithy 1998; Kondo and Hiramatsu 1999; Wearing and Colhoun 1999; Abou-Awad et al. 2001; Momen 2001; Cuthbertson et al. 2003; Rasmy et al. 2003; Momen et al. 2004; Villanueva et al. 2005, 2006; Ozman-Sullivan 2006; Toyoshima and Amano 2006; Villanueva and Childers 2007; Negloh et al. 2008).

The so-called "social parasitic" association between gall-forming eriophyoids and certain tarsonemid mites, which are small enough to invade the galls and, perhaps, replace or consume the eriophyoid occupants, has been suggested by Beer (1963) and Lindquist (1986). Prischmann et al. (2005) have found phytoseiid *Neoseiulus hanselli* (Chant and Yoshida-Shaul) inside willow galls caused by *Aculus tetanothrix* (Nalepa). Phytoseiids have also been found in galls induced by *Acalitus* sp. on *Carpinus tschonoskii* Maxim. They were observed preying on *Acalitus* sp. and reproducing in galls. These results suggest that the galls made by eriophyoids may provide beneficial habitats for phytoseiid mites (Kawashima and Amano 2004). Undoubtedly, further research is needed to clarify this interesting phenomenon.

Pests on agricultural crops

Agriculturally important eriophyoids receive the widest interest among researches. The available literature of the taxon indicates, not surprisingly, that research has dealt with a wide range of topics, particularly bionomics and management.

Among the most investigated species, are those which have been recently introduced into new countries (e.g. *A. guerreronis*), are not efficiently controlled by predatory mites (*A. lycopersici*), are not easily controlled by chemicals because of their existence in protected areas of their hosts (e.g. *A. tulipae*), and are strictly involved in vectoring plant disease agents (e.g. *A. hystrix*, *Aceria cajani*, *A. ficus*, *Aceria mangiferae* [Sayed], *A. tosichella*, *C. ribis*) (Sabelis et al. 2007). Widespread temperate zone pests including *Aculus schlechtendali* (Nalepa), *P. oleivora*, *Calepitrimerus vitis* (Nalepa) and *Colomerus vitis* (Pagenstecher) have, deservedly, received the most attention.

Population dynamics, ecological relationships, and control strategies, mainly with the predatory fauna, have been largely treated. Numerous studies have been conducted on the specific needs of predators when preying on eriophyoids (Sabelis et al. 2007). Other studies have focused on highly virulent strains of acaropathogenic fungi, mainly *Hirsutella* spp. (e.g. Alves et al. 2005; Aghajanzadeh et al. 2007; Paz et al. 2007), and evaluated promising active ingredients for commercial mycoacaricides (de Faria and Wraight 2007).

The coconut rust mite *A. guerreronis* has been the most studied eriophyoid species since 1996 for its impressive economical and social impact, its sudden outbreak, and the menace it presents in possibly South-East Asian countries outside its present known range (Fernando et al. 2000; Haq 2007). It is the key pest of coconut in tropics and subtropics, and it has recently invaded Malaysia, India, the Philippines and Sri Lanka (Muthiah et al. 2001; Navia et al. 2006a). Studies on the molecular and morphological diversity, geographical range and expansion history of the coconut rust mite may help to limit further spread of this

species (Navia et al. 2005a, 2006b). Because chemical control of *A. guerreronis* seems to be scarcely effective (de Moraes and Flechtmann 2007) and detrimental to predators, the current emphasis of research is to identify and develop mite-resistant coconut varieties, and to survey for promising predators (e.g. Lawson-Balagbo et al. 2008) and for acaropatho-genic fungi as prospective mycoacaricides (e.g. Rosas Acevedo and Sampedro Rosas 2006; Shalini et al. 2007; Edgington et al. 2008). Other management efforts include a program to develop and popularize an eco-friendly nutrient management, organic manuring, and botanical pesticides (e.g. Moore 2000; Pushpa and Nandihalli 2008).

Despite numerous studies on eriophyoid mite pests of agricultural crops, several research areas demand further attention. Researchers are aware that the control of erio-phyoids by predatory mites usually fails without a complete knowledge of the biology and ecology of both prey and predator. To increase the effectiveness of this strategy, it is suggested to investigate the predator-prey relationships at a tri-trophic level to evaluate the host-plant changes induced by the pest attack which can provide advantages for the predatory action (Sabelis et al. 2007). Moreover, the presence of mite strains resistant to pesticides has scarcely been investigated (Qu et al. 1997). An accurate assessment of crop losses attributable to the mite infestations should also be promoted (Bernard et al. 2005; Walton et al. 2007) to avoid searches for unnecessary control measures.

Web sources

The internet era has completely transformed the communication processes among scientists, and the storage of knowledge. Thanks to the widespread availability of advanced computer facilities, the integration of research and sharing of information across international borders is cheaper, easier and faster than it has ever been, allowing greater dissemination of biodata among specialists and non-specialists alike (Behan-Pelletier and Newton 1999; Lindquist 2001; Magowski 2005).

The portals developed by the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org/welcome.htm) and Ecoport™ (http://ecoport.org/) share the goal of making biodiversity data readily and universally available, albeit according to different rules. Unfortunately, at present eriophyoids are only partially covered by Ecoport and are almost completely absent in GBIF. No bio-informatics or literature databases on eriophyoids are currently available on line, although digitalized, searchable, and dynamic databases (de Lillo and Amrine 1998) are often cited in the literature and confidentially used by some researchers. A static database of Eriophyoidea is also available on-line (Amrine et al. 2003). The Fauna Europaea project has provided an on-line inventory of the Eriophyoidea in Europe (de Lillo 2004; Magowski 2005), but updating of this project has not been planned.

The international scientific community is involved in a wide discussion on the fair use and copyright restrictions of scientific literature (Suber 2002), especially in recognition of the fact that progress in science is largely dependent on derivative works. With respect to rules (e.g. copyright expiration time, permission from editors, restricted users access, and so forth), eriophyoid sources should be collected and made available to research community, with particular regard to old and rare papers. An excellent example of such a source is the free access to "Eriophyoid Studies" by Keifer's: http://www.cdfa.ca.gov/phpps/ppd/publications/eriophyid_studies.html. Similar emphasis should be placed on making English translations of non-English papers, which eriophyoidologists badly need and which can be shared from their personal collections.

It is noteworthy that the last key to the world genera of eriophyoids was published in 2003 by Amrine et al., and since then many new genera have been described, and newly described species have not always been assigned to the correct genus; thus the key needs to be revised. An interactive, illustrated and dynamic key available on web could be planned following the example of the Interactive Diagnostic Key to Plant Parasitic, Free Living and Predaceous Nematodes, University of Nebraska-Lincoln (http://nematode.unl.edu/key/nemakey.htm), as well as other interactive identification resources on mites, for example the North American Bee-Associated Mites (http://insects.ummz.lsa.umich.edu/beemites/vk_bees/vk_bees.htm) and Invasive Mite Identification: tools for quarantine and plant protection (http://keys.lucidcentral.org/keys/v3/mites/Invasive_Mite_Identification/key/Whole_site/Home_whole_key.html), and others.

Considering other internet facilities, the Acarology discussing list (http://www.nhm.ac.uk/hosted_sites/acarology/) seems to not have been used widely enough to favour a sufficient exchange of information, topic discussions and project aggregations among researchers. An Erio-community should be officially established as a sort of permanent working group, and it should be aimed at guarantying that all the aspects related to the studies of eriophyoids be included in web sources. Probably, a selected chairman's office (or a moderator/s) and solicitations could attend the discussions and help to improve the community activities. The experience of the questionnaires submitted to a selected group of acarologists before the session on Eriophyoidea at Montpellier, 2008 has indicated that specialists are interested in participating in a such task.

Another web source is the *Voice over Internet Protocol (VoIP)*, which encodes speech and allows voice communications over IP networks, such as Internet or other packet-switched networks. It is becoming more familiar to the scientific community. Software using this protocol are user-friendly, and can allow users to apply instant messaging, transfer large files (unlike via e-mail), and host video conferences. VoIP appears to be a very cheap tool for fast, informal communications and its use should be promoted in the scientific community. Second Life™ platform could be the new frontier to be used.

Finally, all the internet aspects listed above, i.e. the development of databases and keys, web publication and access, scientific authority and responsibility, updating, and other "vital functions", should be included in eriophyoidologist projects that might be guaranteed, promoted, supported and maintained with the help of institutions, education centres, foundations, associations and scientific and non-profit consortia.

Who knows about eriophyoid mites outside the science community?

Lindquist (2001) has discussed the topic of *Public awareness and support* in Acarology underlining that the public's general lack of awareness of our science is one of the most serious weaknesses in attracting support for the study of Acari, and eriophyoid mites do not escape from this rule. Looking through the largest available web source, Wikipedia (http://en.wikipedia.org/wiki/Main_Page), a short string can be found at the query Eriophyoidea, and a page with some links is available for Eriophyidae. A few other websites show relevant information (e.g. http://www.sel.barc.usda.gov/acari/content/eriophyoidea.html). Recently the French edition of National Geographic (Fig. 5) published a magazine page dedicated to a newly described Chinese species. Several decades ago, the movie "Invisible enemies" (1968) was overseen by Shevchenko (personal communication), but it was only released in Russian.

An effort to emphasize and enhance the public awareness of eriophyoids has never been done and should involve specialists and others who are interested in this area, such as
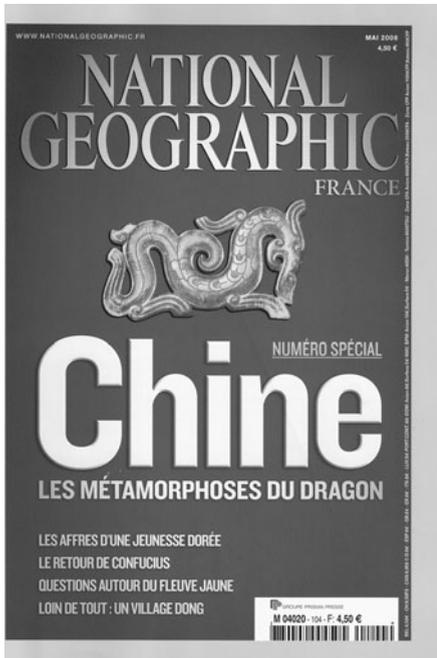
QUOI DE NEUF, MONSIEUR NOÉ ?

45 µm
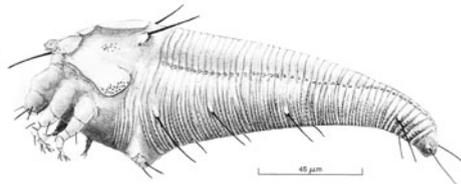
Un acarien au pays du Milieu Ils sont des milliards, ils sont partout. Souvent invisibles à l'œil nu, les acariens restent méconnus du grand public. Et généralement redoutés. Calpentaconvexus eyrei n'y changera probablement rien. Il vient d'être découvert dans la région autonome du Guangxi, dans le sud de la Chine. Microscopique (moins de 0,18 mm de long), C. eyrei vit sur les feuilles d'un châtaignier local. Cette espèce nouvelle appartient aux Ériophyides, l'une des 475 familles d'acariens. Car sous le terme d'acarien se cache un pan immense de la biodiversité : plus de 50 000 espèces connues, et probablement plusieurs centaines de milliers d'autres à découvrir ! Certains acariens – comme les aoûtats et les tiques – sont parasites d'animaux, d'autres vivent « libres », dans le sol, les eaux ou la poussière (ces derniers provoquent des allergies chez certains asthmatiques). Calpentaconvexus eyrei, lui, fait partie des parasites de végétaux. La plupart d'entre eux piquent les feuilles et déclenchent la formation de galles qui, selon les espèces, abîment plus ou moins sévèrement les parties touchées. D'après les premières observations, C. eyrei, lui, n'endommage pas son hôte. D'ailleurs, les acariens peuvent aussi nous être bénéfiques. La famille des Phytoseiides, par exemple, est utilisée dans la lutte biologique contre d'autres acariens, ravageurs eux. D'autres encore sont prédateurs des acariens responsables des crises d'asthme. L'homme en « domestique » même certains pour les saupoudrer sur la croûte de fromages artisanaux. Indirectement, les acariens participent aussi à la décomposition des végétaux, la dissémination des spores de champignons et le contrôle des insectes. On décrit chaque année une centaine d'acariens, mais aucune de ces découvertes n'est à minimiser.— Céline Lison et Benoît Fontaine

NATIONAL GEOGRAPHIC • MAI 2008

Castanopsis eyrei (châtaignier)

Calpentaconvexus eyrei, Chine
■ **Auteurs de l'espèce :** De-Wei Li (Institut de recherche forestière du Guangxi, Chine), Guo-Quan Wang et Sui-Gai Wei (université du Guangxi, Chine).
■ **Hôte :** En général, les acariens de la famille de C. eyrei sont spécifiques de leur hôte (ici, Castanopsis eyrei, un châtaignier). On ne les trouve pas sur une autre espèce.
■ **Publication scientifique :** Description publiée dans la revue Zootaxa.

ILLUSTRATION DE GILBERT HODEBERT

Fig. 5 Issue of France National Geographic printed in May 2008 with a special report on China, referring about *Calpentaconvex eyrei* (Li et al. 2007)

cecidologists, teachers, museum scientists, local and international scientific magazines and networks that promote science. The morphological, biological, and ecological features of eriophyoids make them attractive, enjoyable, impressive, educative and stimulating (Lindquist 2001).

References

Abou-Awad BA, Korayema AM, Hassanb MF, Abou-Elela MA (2001) Life history of the predatory mite *Lasioseius athiasae* (Acari, Ascidae) on various kinds of food substances: a polypeptide analysis of prey consideration. J Appl Entomol 125(3):125–130

Abou-Awad BA, Metwally AM, Al-Azzazy MM (2005) Environmental management and biological aspects of two eriophyid olive mites in Egypt: *Aceria oleae* and *Tegolophus hassani*. Z Pflanzenk Pflanzen 112(3):287–303

Achor DS, Ochoa R, Erbe EF, Aguilar H, Wergin WP, Childers CC (2001) Relative advantages of low temperature versus ambient temperature scanning electron microscopy in the study of mite morphology. Int J Acarol 27(1):3–12

Aghajanzadeh S, Mallik B (2007) Sampling and distribution pattern of citrus rust mite, *Phyllocoptruta oleivora* Ashmead (Acari, Eriophyidae), using adhesive tape method. Int J Agric Biol 9(2):329–332

Aghajanzadeh S, Prasad DT, Mallik B (2007) Genetic diversity in *Hirsutella thompsonii* isolates based on random amplified polymorphic DNA analysis. Biocontrol 52(3):375–383

Alberti G, Coons LB (1999) Acari-Mites. In: Harrison FW (ed) Microscopic anatomy of invertebrates, vol 8C. Wiley-Liss, New York, pp 515–1265

Alves SB, Tamai MA, Rossi LS, Castiglioni E (2005) *Beauveria bassiana* pathogenicity to the citrus rust mite *Phyllocoptruta oleivora*. Exp Appl Acarol 37(1–2):117–122

Amrine JW Jr (1996) *Phyllocoptes fructiphilus* and biological control of multiflora rose. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—Their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 741–749

Amrine JW Jr (2003) Catalog of the Eriophyoidea. A working catalog of the Eriophyoidea of the world. Ver. 1.0. http://insects.tamu.edu/research/collection/hallan/acari/eriophyidae

Amrine JW Jr, Stasny TA (1994) Catalog of the Eriophyoidea (Acarina: Prostigmata) of the world. Indira Publishing House, West Bloomfield

Amrine JW Jr, Duncan GH, Jones AT, Gordon SC, Roberts IM (1994) *Cecidophyopsis* mites (Acari: Eriophyidae) on *Ribes* spp. (Grossulariaceae). Int J Acarol 20:139–168

Amrine JW Jr, Stasny TAH, Flechtmann CHW (2003) Revised keys to the world genera of the Eriophyoidea (Acari: Prostigmata). Indira Publishing House, West Bloomfield

Ansaloni T, Perring TM (2004) Biology of *Aceria guerreronis* (Acari: Eriophyidae) on queen palm *Syagrus romanzoffiana* (Arecaceae). Int J Acarol 30:63–70

Aratchige NS, Lesna I, Sabelis MW (2004) Below-ground plant parts emit herbivore-induced volatiles: olfactory responses of a predatory mite to tulip bulbs infested by rust mites. Exp Appl Acarol 33:21–30

Aratchige NS, Sabelis MW, Lesna I (2007) Plant structural changes due to herbivory: do changes in *Aceria*-infested coconut fruits allow predatory mites to move under the perianth? Exp Appl Acarol 43:97–107

Arbabi M, Baradaran P, Ranjbar V (2006) Effect of different fig pruning methods on population of *Eriophyes ficus* Cotte in Saveh region. Appl Ent Phytopath 73(2):37–51

Ashihara W, Kondo A, Shibao M, Tanaka H, Hiehata K, Izumi K (2004) Ecology and control of eriophyid mites injurious to fruit trees in Japan. Jap Agric Res Quart 38(1):31–41

Baker EW, Kono T, Amrine JW Jr, Delfinado-Baker M, Stasny TA (1996) Eriophyoid mites of the United States. Indira Publishing House, West Bloomfield

Balaji K, Hemavathy AT (2007) Studies on the seasonal incidence of coconut eriophyid mite *Aceria guerreronis* Keifer (Acari: Eriophyidae). Asian J Bio-Science 2(1/2):88–91

Beer RE (1963) Social parasitism in the Tarsonemidae, with description of a new species of tarsonemid mite involved. Ann Entomol Soc Amer 56:153–160

Behan-Pelletier V, Newton G (1999) Computers in biology: linking soil biodiversity and ecosystem function—the taxonomic dilemma. Bioscience 49:149–153

Bergh JC (2001) The ecology and aerobiology of dispersing citrus rust mites in central Florida. Environ Entomol 30:318–326

Bergh JC, Smith AH Jr (2001) Ecology and aerobiology of dispersing citrus rust mites (Acari: Eriophyidae) in central Florida. Environ Entomol 30(2):318–326

Bergh JC, McCoy CW, Otieno BS (2002) Diel periodicity of emergence of adult citrus rust mites in central Florida. Exp Appl Acarol 26(3–4):169–185

Bernard MB, Horne PA, Hoffmann AA (2005) Eriophyoid mite damage in *Vitis vinifera* (grapevine) in Australia: *Calepitrimerus vitis* and *Colomerus vitis* (Acari: Eriophyidae) as the common cause of the widespread 'Restricted Spring Growth' syndrome. Exp Appl Acarol 35(1/2):83–109

Bernini F, Castagnoli M, Nannelli R (1995) Arachnida Acari. In: Minelli A, Ruffo S, La Posta S (eds) Checklist delle specie della fauna italiana, vol 24. Calderini, Bologna, p 131

Bertoldo G, de Gouvea A, Alves LFA (2008) Plano de amostragem para *Dichopelmus notus* (Eriophyidae) na cultura da erva-mate. Ciencia Rural 38(3):601–606

Britto EPJ, Gondim MGC Jr, Navia D, Flechtmann CHW (2008) A new deuterogynous eriophyid mite (Acari: Eriophyidae) with dimorphic males. Description and biological observations from *Caesalpinia echinata* (Caesalpiniaceae) from Brazil. Int J Acarol 34(3):307–316

Brodeur J, Bouchard A, Turcotte G (1997) Potential of four species of predatory mites as biological control agents of the tomato russet mite, *Aculops lycopersici* (Massee) (Eriophyidae). Can Entomol 129(1):1–6

Buchta I, Kula E, Kresťanpolová M (2006) Occurrence variations and spatial distribution patterns of *Eriophyes tiliae* (Pgst.) (Acari, Eriophyidae) subspecies in the urban environment. J Forest Sci 52(12):547–555

Carew ME, Goodisman MAD, Hoffmann AA (2004) Species status and population genetic structure of grapevine eriophyoid mites. Entomol Exp Appl 111(2):87–96

Carew M, Schiffer M, Umina P, Weeks A, Hoffmann A (2009) Molecular markers indicate that the wheat curl mite, *Aceria tosichella* Keifer, may be a species complex in Australia. Bull Entomol Res:1–8. doi: 10.1017/S0007485308006512

Castagnoli M, Simoni S (2000) Observations on intraplant distribution and life history of eriophyoid mites (Acari: Eriophyidae, Phytoptidae) inhabiting evergreen cypress, *Cupressus sempervirens* L. Int J Acarol 26(1):93–99

Chakrabarti S, Chakrabarti S (2005) Population dynamics and diurnal activity of *Acalitus hibisci* Mondal and Chakrabarti (Acari: Eriophyoidea). Acarologia 45(2–3):183–188

Chen Q, Conner RL, Li HJ, Graf R, Laroche A, Li HY, Ahmad F (2003) Genomic characterization of new sources of resistance to both wheat streak mosaic virus and wheat curl mite in wheat-*Thinopyrum* partial amphiploids. J Genet Breed 57(2):155–164

Conner RL, Chen Q (2003) Breeding for resistance to wheat streak mosaic virus and its mite vector. Adv Plant Dis Manag 37:3–389

Courtin O, Fauvel G, Leclant F (2000) Temperature and relative humidity effects on egg and nymphal development of *Aceria tulipae* (K.) (Acari: Eriophyidae) on garlic leaves (*Allium sativum* L.). Ann Appl Biol 137:207–211

Coutts BA, Strickland GR, Kehoe MA, Severtson DL, Jones RAC (2008) The epidemiology of wheat streak mosaic virus in Australia: case histories, gradients, mite vectors, and alternative hosts. Austr J Agric Res 59(9):844–853

Cross JV, Harris A (2003) Development of integrated pest management approaches for blackcurrant crops. Bull OILB/SROP 26(2):11–18

Cross JV, Ridout MS (2001) Emergence of blackcurrant gall mite (*Cecidophyopsis ribis*) from galls in spring. J Hort Sci Biotechnol 76(3):311–319

Cuthbertson AGS, Bell AC, Murchie AK (2003) Impact of the predatory mite *Anystis baccarum* (Prostigmata: Anystidae) on apple rust mite *Aculus schlechtendali* (Prostigmata: Eriophyidae) populations in Northern Ireland Bramley orchards. Ann Appl Biol 142(1):107–114

Daud RD, Feres RJF (2007) Population dynamics of phytophagous mites (Acari, Eriophyidae, Tenuipalpidae) on six rubber trees clones in southern Mato Grosso State. Rev Brasil Entomol 51(3):377–381

Davies JT, Allen GR, Williams MA (2001a) Intraplant distribution of *Acalitus essigi* (Acari: Eriophyoidea) on blackberries (*Rubus fruticosus* agg.). Exp Appl Acarol 25(8):625–639

Davies JT, Allen GR, Williams MA (2001b) Dispersal of *Acalitus essigi* to blackberry (*Rubus fruticosus* agg.) fruit. Entomol Exp Appl 101(1):19–23

Davies JT, Williams MA, Allen GR (2002) A new method for sampling eriophyoid mites from architecturally complex plant structures. J Appl Entomol 126(6):303–305

de Faria MR, Wraight SP (2007) Mycoinsecticides and mycoacaricides: a comprehensive list with worldwide coverage and international classification of formulation types. Biol Control 43(3):237–256

De Gouvea A, Boaretto LC, Zanella CF, Alves LFA (2006) Population dynamics of mites (Acari) in the mate-tea tree (*Ilex paraguariensis* St. Hil.: Aquifoliaceae). Neotrop Entomol 35((1):101–111

De Gouvea A, Zanella CF, Mazaro SM, Donazzolo J, Alves LFA (2007) Association and populational density of mites predators in the mate-tea tree *Ilex paraguariensis* St. Hil. (Aquifoliaceae) with or without the presence of phytophagous mites. Ciencia Rural 37(1):1–6

de Lillo E (2004) Fauna Europaea: Eriophyoidea. In: Magowski WŁ (ed) Fauna Europaea: Acariformes. Fauna Europaea version 1.1, http://www.faunaeur.org

de Lillo E, Craemer C, Amrine JW Jr, Nuzzaci G (2009) Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata). Exp Appl Acarol. doi:10.1007/s10493-009-9311-x

de Lillo E, Aldini P (2001) Functional morphology of some leg sense organs in *Pediculaster mesembrinae* (Acari: Siteroptidae) and *Phytoptus avellanae* (Acari: Phytoptidae). In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds), Acarology. Proc X Internat Congr, CSIRO Publ, pp 217–225

de Lillo E, Amrine JW Jr (1998) Eriophyoidea (Acari) on a computer database. Entomologica 31:137–146

de Lillo E, Monfreda R (2004) Salivary secretions of eriophyoids (Acari: Eriophyoidea): first results of an experimental model. Exp Appl Acarol 34(3–4):291–306

de Lillo E, Skoracka A (2008) Why should we talk about Eriophyoid Mites? In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier M-S, Vial L (eds) Integrative acarology. Proceedings of VI EurAAc Symposium, Montpellier, July 2008, pp 288–290

de Lillo E, Di Palma A, Nuzzaci G (2002) Morphological adaptations of mite chelicerae to different trophic activities (Acari). Entomologica 35(2001):125–180

de Lillo E, Bari G, Monfreda R (2005a) Preliminary study on the distribution of *Calepitrimerus vitis* (Nalepa) on tendone trained vineyards in Apulia, Southern Italy. Phytophaga XIV(2004):605–610

de Lillo E, Nuzzaci G, Di Palma A (2005b) Sensorial structures in mites and perspectives of research. Phytophaga XIV(2004):59–81

de Moraes GJ, Flechtmann CHW (2007) Phytophagous mites of tropical crops in eastern South America. In: Morales-Malacara JB, Behan-Pelletier V, Ueckermann E, Perez TM, Estrada-Venegas EG, Badii M (eds) Acarology XI. Proc XI Int Congress, Merida, Mexico 2002, pp 279–288

De Silva PHPR, Fernando LCP (2008) Rearing of coconut mite *Aceria guerreronis* and the predatory mite *Neoseiulus baraki* in the laboratory. Exp Appl Acarol 44:37–42

De Vis RMJ, De Moraes GJ, Bellini MR (2006) Mites (Acari) of rubber trees (*Hevea brasiliensis* Muell. Arg., Euphorbiaceae) in Piracicaba, State of São Paulo, Brazil. Neotrop Entomol 35(1):112–120

Demite PR, Feres RJF (2007) Occurrence and fluctuation of mite populations associated with rubber tree crop neighbor of fragments of Cerrado. Neotrop Entomol 36(1):117–127

Dharmaraj PS, Narayana YD, Kumar PL, Waliyar F, Jones AT (2004) Pigeonpea sterility mosaic disease: an emerging problem in Northern Karnataka, India. Int Chickpea Pigeonpea Newslet 11:47–49

Duffner K, Schruft G, Duggelin M, Mathys D, Wirtz S, Guggenheim R (1998) Low-temperature SEM studies on genital structures and spermatophores of the grape rust mite *Calepitrimerus vitis* Nalepa, 1905 (Acari, Eriophyoidea). Entomol Mitt Zool Mus Hamburg 12(157):277–288

Duffner K, Schruft G, Guggenheim R (2001) Passive dispersal of the grape rust mite *Calepitrimerus vitis* Nalepa 1905 (Acari, Eriophyoidea) in vineyards. Anz Schadl 74(1):1–6

Edgington S, Fernando LCP, Jones K (2008) Natural incidence and environmental profiling of the mite-pathogenic fungus *Hirsutella thompsonii* Fisher for control of the coconut mite in Sri Lanka. Int J Pest Manag 54(2):123–127

El-Laithy AYM (1998) Laboratory studies on growth parameters of three predatory mites associated with eriophyid mites in olive nurseries. Z Pflanzenk Pflanzen 105(1):78–83

Erman O, Özkan M, Ayyildiz N, Doğan S (2007) Check list of mites (Arachnida: Acari) of Turkey. Second supplement. Zootaxa 1532:1–21

Fenton B, Jones AT, Malloch G, Thomas WP (1996) Molecular ecology of some *Cecidophyopsis* mites (Acari: Eriophyidae) on *Ribes* species and evidence for their natural cross colonisation of blackcurrant (*R. nigrum*). Ann Appl Biol 128(3):405–414

Fenton B, Malloch G, Moxey E (1997) Analysis of eriophyid mite rDNA internal transcribed spacer sequences reveals variable simple sequence repeats. Insect Mol Biol 6(1):23–32

Fenton B, Birch ANE, Malloch G, Lanham PG, Brennan RM (2000) Gall mite molecular phylogeny and its relationship to the evolution of plant host specificity. Exp Appl Acarol 24(10–11):831–861

Ferla NJ, de Moraes GJ, Bonato O (2007) Distribuicao espacial e plano de amostragem de *Calacarus heveae* (Acari) em seringueira. Iheringia, Ser Zoologia 97(4):447–451

Fernando LCP, de Moraes GJ, Wickramananda IR (eds) (2000) Proc. Internat. Workshop on Coconut mite *Aceria guerreronis*, Coconut Research Institute, Sri Lanka, 6–8 January 2000, pp 117

Fernando LCP, Aratchige NS, Peiris TSG (2003) Distribution patterns of coconut mite, *Aceria guerreronis*, and its predator *Neoseiulus* aff. *paspalivorus* in coconut palms. Exp Appl Acarol 31(1/2):71–78

Ferragut F, Gallardo A, Ocete R, López MA (2008) Natural predatory enemies of the erineum strain of *Colomerus vitis* (Pagenstecher) (Acari, Eriophyidae) found on wild grapevine populations from southern Spain (Andalusia). Vitis—J Grapevine Res 47(1):51–54

Flechtmann CHW (2000) Two new genera and three new species of Eriophyidae (Acari) from the Brazilian pine, *Araucaria angustifolia* (Araucariaceae). Int J Acarol 26(2):137–144

Flechtmann CHW (2002) *Esalquia centennaria*, a new genus and a new species of Eriophyidae (Acari) from ferns in Brazil. Int J Acarol 28(1):41–44

Fournier V, Rosenheim JA, Brodeur J, Laney LO, Johnson MW (2003) Herbivorous mites as ecological engineers: indirect effects on arthropods inhabiting papaya foliage. Oecologia 135(3):442–450

Fournier V, Rosenheim JA, Brodeur J, Johnson MW (2004) Population dynamics and within-plant distribution of the mite *Calacarus flagelliseta* (Acari: Eriophyidae) on papaya in Hawaii. J Econ Entomol 97(5):1563–1569

Fournier V, Rosenheim JA, Brodeur J, Diez JM, Johnson MW (2006) Multiple plant exploiters on a shared host: testing for nonadditive effects on plant performance. Ecol Appl 16(6):2382–2398

Frost WE (1997) Polyphenic wax production in *Abacarus hystrix* (Acari, Eriophyidae), and implications for migratory fitness. Physiol Entomol 22:37–46

Gabi G, Mészáros Z (2001) New data to the knowledge of *Calepitrimerus vitis* Nalepa in the vine-growing region of Szekszárd, Hungary (Acari: Eriophyidae). Acta Phytopath Entomol Hung 36(1–2):193–200

Gabi G, Mészáros Z (2003) Examination of the development of the deutogynes of *Calepitrimerus vitis* Nalepa in the vine-growing region of Szekszárd, Hungary (Acari: Eriophyidae). Acta Phytopath Entomol Hung 38(3–4):369–376

Gamliel-Atinsky E, Freeman S, Maymon M, Belausov E, Ochoa R, Skoracka A, Peña J, Palevsky E (2009) The role of eriophyoids in fungal pathogen epidemiology, mere association or true interaction? Exp Appl Acarol. doi:10.1007/s10493-009-9302-y

Gillespie RL, Roberts DE, Bentley EM (1997) Population dynamics and dispersal of wheat curl mites (Acari: Eriophyidae) in north central Washington. J Kansas Entomol Soc 70(4):361–364

Gispert C, Perring TM, Oldfield GN (1997) Rearing Eriophyes insidiosus Keifer and Wilson (Acari: Eriophyoidea), a fastidiosus bud mite. Int J Acarol 23:227–231

Gispert C, Oldfield GN, Perring TM, Craemer R (1998) Biology of the transmission of peach mosaic virus by Eriophyes insidiosus (Acari: Eriophyidae). Plant Dis 82(12):1371–1374

Gondim MGC Jr, de Moraes GJ (2003) Life cycle of Retracrus johnstoni Keifer (Acari: Phytoptidae). Neotrop Entomol 32:197–201

Goolsby JA, de Barro PJ, Makinson JR, Pemberton RW, Hartley DM, Frohlich DR (2006) Matching the origin of an invasive weed for selection of a herbivore haplotype for a biological control programme. Mol Ecol 15(1):287–297

Grahl A, Leuprecht B (1998) Untersuchungen zur Biologie der Tomatenrostmilbe Aculus lycopersici und ihrer biologischen Bekämpfung. Mitt Dt Phytomed Ges 28(1):41–42

Hall DG, Childers CC, Eger JE, Allen JC (1997) Citrus rust mite (Acari: Eriophyidae) counts on fruit and the negative binomial distribution. Flo Entomol 80(1):1–10

Hall DG, Childers CC, Eger JE (2005) Effects of reducing sample size on density estimates of citrus rust mite (Acari: Eriophyidae) on citrus fruit: simulated sampling. J Econ Entomol 98(3):1048–1057

Halliday RB (1998) Mites of Australia: a checklist and bibliography. CSIRO Publ, Melbourne

Haq MA (2001) Culture and rearing of Aceria guerreronis and its predators. Entomon 26:297–302

Haq MA (2007) Coconut mite tragedy in peninsular India. In: Morales-Malacara JB, Behan-Pelletier V, Ueckermann E, Perez TM, Estrada-Venegas EG, Badii M (eds) Acarology XI. Proc XI Int Congress, Merida, Mexico 2002, pp 427–432

Haq MA, Sumangala K, Ramani N (2002) Coconut mite invasion, injury and distribution. In: Fernando LCP, de Moraes GJ, Wickramananda IR (eds) Proc. Internat. Workshop on Coconut mite Aceria guerreronis, Coconut Research Institute, Sri Lanka, 6–8 January 2000, pp 41–49

Haque MM, Kawai A (2003) Effect of temperature on development and reproduction of the tomato russet mite, Aculops lycopersici (Massee) (Acari: Eriophyidae). Appl Entomol Zool 38(1):97–101

Harvey TL, Seifers DL, Martin TJ (1998) Effect of imidacloprid seed treatment on infestations of wheat curl mite (Acari: Eriophyidae) and the incidence of wheat streak mosaic virus. J Agric Urban Entomol 15(1):75–81

Harvey TL, Seifers DL, Martin TJ, Michaud JP (2005) Effect of resistance to wheat streak mosaic virus on transmission efficiency of wheat curl mites. J Agric Urban Entomol 22(1):1–6

Hebert PDN, Ratnasingham S, de Waard JR (2003) Barcoding animal life: cytochrome c oxidase subunit I divergences among closely related species. Proc R Soc London B 270:S96–S99

Helle W, Wysoki M (1996) Arrhenotokus partenogenesis. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—Their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 169–172

Hong X-Y, Cheng N-H (1999) Review of virus diseases transmitted by eriophyid mites. Acta Phytopath Sin 26:177–184

Hong X-Y, Zhang Z-Q (1996a) A cladistic analysis of the Eriophyoidea (Acari: Prostigmata): tests of monophyly of families. Syst Appl Acarol 1:107–122

Hong X-Y, Zhang Z-Q (1996b) A phylogenetic study of the tribe Cecidophyini Keifer (Acari: Eriophyidae). Or Ins 30:279–300

Hong X-Y, Zhang Z-Q (1996c) The eriophyoid mites of China: an illustrated catalog and identification keys. (Acari: Prostigmata: Eriophyoidea). Mem Entomol, Internat 7:318

Hong X-Y, Zhang Z-Q (1997) Systematics and generic relationships of the mites in the subfamily Diptilomiopinae (Acari: Eriophyoidea: Diptilomiopidae). Syst Entomol 22:313–331

Ishihara MI, Yamasaki M, Yoshikawa J (2007) Spatial distribution and abundance of bud galls caused by eriophyoid mites among host trees Carpinus tschonoskii. J Appl Entomol 131(8):585–587

Jarvis CH, Collier RH (2002) Evaluating an interpolation approach for modelling spatial variability in pest development. Bull Entomol Res 92(3):219–231

Jensen SG, Lane LC, Seifers DLA (1996) New disease of maize and wheat in the high plains. Plant Dis 80(12):1387–1390

Jesse LC, Moloney KA, Obrycki JJ (2006) Abundance of arthropods on the branch tips of the invasive plant, Rosa multiflora (Rosaceae). Weed Biol Manag 6(4):204–211

Jiang W, Garrett KA, Peterson DE, Harvey TL, Bowden RL, Fang L (2005) The window of risk for emigration of wheat streak mosaic virus varies with host eradication method. Plant Dis 89(8):853–858

Jones AT (2000) Black currant reversion disease—the probable causal agent, eriophyid mite vectors, epidemiology and prospects for control. Virus Res 71(1–2):71–84

Jones AT, Kumar PL, Saxena KB, Kulkarni NK, Muniyappa V, Waliyar F (2004) Sterility mosaic disease - the "green plague" of pigeonpea: advances in understanding the etiology, transmission and control of a major virus disease. Plant Dis 88(5):436–445

Kandulna A, Singh J, Prasad R (2005) Management of eriophyid mite Aceria cajani, as transmitting agent of sterility mosaic disease of pigeonpea. Shashpa 12(1):51–53

Kang SG, Koo BJ, Lee ET, Chang MU (2007) Allexivirus transmitted by eriophyid mites in garlic plants. J Microbiol Biotechnol 17(11):1833–1840

Kasai A, Yano S, Nishida T, Kadono F, Takafuji A (2002) Spatial distribution pattern of domatia and seasonal occurrence of the eriophyid mite in relation to the foliation phenology of Cinnamomum camphora. Jap J Appl Entomol Zool 46(3):159–162

Kasai A, Yano S, Takafuji A (2005) Prey-predator mutualism in a tritrophic system on a camphor tree. Ecol Res 20(2):163–166

Kawai A, Haque MM (2004) Distribution pattern of Aculops lycopersici (Massee) (Acari: Eriophyidae) in tomato leaf and estimation method for the population density on leaf. J Acarol Soc Japan 13(1):31–39

Kawashima M, Amano H (2004) Seasonal occurrence and association of a gall-forming eriophyid mite and predacious phytoseiid mites (Acari: Eriophyidae, Phytoseiidae) in Japan. Int J Acarol 30:9–15

Keifer HH (1975) Eriophyoidea Nalepa. Injurious eriophyoid mites. In: Jeppson LR, Keifer HH, Baker EW (eds) Mites injurious to economic plants. University of California Press, Berkeley, pp 327–533

Knihinicki D, Boczek J (2002) New eriophyoid mites (Acari: Eriophyoidea) from Australia. Int J Acarol 28(3):241–249

Knihinicki DK, McCarren KL, Scott JK (2009) A new species of Aceria (Acari: Eriophyidae) damaging sowthistles, Sonchus spp. (Asteraceae), in Australia with notes on Aceria sonchi (Nalepa, 1902). Zootaxa 2119(2):3–38

Kondo A, Hiramatsu T (1999) Predatory ability of two species of phytoseiid mites (Acari: Phytoseiidae) on the peach silver mite, Aculus fockeui (Nalepa et Trouessart) (Acari: Eriophyidae). Appl Entomol Zool 34(4):485–487

Kuang H-Y (1995) Economic Insect Fauna of China. Acari: Eriophyoidea (1). Fasc. 44. Science Press, Beijing

Kuang H-Y, Luo G-H, Wang A-W (2005) Fauna of eriophyid mites from China (II) (Acari: Eriophyoidea). China Forestry Publ. House, Beijing

Kuczyński L, Skoracka A (2005) Spatial distribution of galls caused by Aculus tetanothrix (Acari: Eriophyoidea) on arctic willows. Exp Appl Acarol 36(4):277–289

Kula E, Buchta I, Hadaš P (2008) Effects of site conditions on the occurrence of Acalitus rudis (Canestrini) and Eriophyes leionotus (Nalepa) (Acari: Eriophyidae) in Czech Republic. Int J Acarol 34(2):155–166

Kulkarni NK, Kumar PL, Muniyappa V, Jones AT, Reddy DVR (2002) Transmission of Pigeon pea sterility mosaic virus by the eriophyid mite, Aceria cajani (Acari: Arthropoda). Plant Dis 86(12):1297–1302

Kumar PL, Fenton B, Jones AT (1999) Identification of Cecidophyopsis mites (Acari: Eriophyidae) based on variable simple sequence repeats of ribosomal DNA internal transcribed spacer-1 sequences via multiplex PCR. Insect Mol Biol 8(3):347–357

Kumar PL, Fenton B, Duncan GH, Jones AT, Sreenivasulu P, Reddy DVR (2001) Assessment of variation in Aceria cajani using analysis of rDNA ITS regions and scanning electron microscopy: implications for the variability observed in host plant resistance to pigeonpea sterility mosaic disease. Ann Appl Biol 139(1):61–73

Kumar PL, Jones AT, Reddy DVR (2003) A novel mite-transmitted virus with a divided RNA genome closely associated with pigeonpea sterility mosaic disease. Phytopathology 93(1):71–81

Kumar PL, Latha TKS, Kulkarni NK, Raghavendra N, Saxena KB, Waliyar F, Rangaswamy KT, Muniyappa V, Doriswamy S, Jones AT (2005) Broad-based resistance to pigeonpea sterility mosaic disease in wild relatives of pigeonpea (Cajanus: Phaseoleae). Ann Appl Biol 146(3):371–379

Lakshmikantha BP, Prabhuswamy HP (2003) Reaction of pigeon pea varieties to mite (Aceria cajani Channabasavanna) transmitting sterility mosaic disease. Pl Prot Bull (Faridabad) 54(3/4):6–7

Latha TKS, Doraiswamy S (2004) Interaction studies between pigeonpea sterility mosaic virus and mite vector. Indian J Plant Prot 32(2):105–110

Latha TKS, Doraiswamy S (2008) Detection of pigeonpea sterility mosaic virus, the causal agent of sterility mosaic disease of pigeonpea in viruliferous mite vector by DAS-ELISA and DIBA. Arch Phytopath Plant Prot 41(7):537–541

Latha TKS, Kumar PL, Doraiswamy S, Waliyar F (2007) Biodiversity of mite vector of Pigeonpea sterility mosaic virus in Tamil Nadu, India. Indian J Plant Prot 35(1):138–139

Lawson-Balagbo LM, Gondim MGC Jr, de Moraes GJ, Hanna R, Schausberger P (2007) Refuge use by the coconut mite *Aceria guerreronis*: fine scale distribution and association with other mites under the perianth. Biol Control 43(1):102–110

Lawson-Balagbo LM, Gondim MGC Jr, de Moraes GJ, Hanna R, Schausberger P (2008) Exploration of the acarine fauna on coconut palm in Brazil with emphasis on *Aceria guerreronis* (Acari: Eriophyidae) and its natural enemies. Bull Entomol Res 98(1):83–96

Leite GLD, Picanc'o M, Zanuncio JC, Marquini F (2003) Factors affecting mite herbivory on eggplants in Brazil. Exp Appl Acarol 31(3–4):243–252

Lemmetty A, Tikkanen M, Tuovinen T, Lehto K (2004) Identification of different *Cecidophyopsis* mites on *Ribes* in Finland. Acta Horticult 656:115–118

Lewandowski M, Kozak M (2008) Distribution of eriophyoid mites (Acari: Eriophyoidea) on coniferous trees. Exp Appl Acarol 44:89–99

Li H, Conner RL, Chen Q, Graf RJ, Laroche A, Ahmad F, Kuzyk AD (2005) Promising genetic resources for resistance to wheat streak mosaic virus and the wheat curl mite in wheat-*Thinopyrum* partial amphiploids and their derivatives. Genet Res Crop Evol 51(8):827–835

Li H, Conner RL, Liu Z, Li Y, Chen Y, Zhou Y, Duan X, Shen T, Chen Q, Graf RJ, Jia X (2007) Characterization of wheat-triticale lines resistant to powdery mildew, stem rust, stripe rust, wheat curl mite, and limitation on spread of WSMV. Plant Dis 91(4):368–374

Lindquist EE (1986) The world genera of Tarsonemidae (Acari: Heterostigmata): a morphological, phylogenetic, and systematic revision, with a reclassification of family-group taxa in the Heterostigmata. Memoirs Entomol Soc Canada 136:517

Lindquist EE (1996) External anatomy and notation of structures. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 1–30

Lindquist EE (1996) Phylogenetic relatioships. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 301–327

Lindquist EE (1998) Evolution of phytophagy in trombidiform mites. Exp Appl Acarol 22:81–100

Lindquist EE (2001) Poising for a new century in Acarology. In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds) In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds) Acarology. Proc X Internat Congr, CSIRO Publ, pp 17–34

Lindquist EE, Amrine JW Jr (1996) Systematics, diagnoses for major taxa, and keys to families and genera with species on plant of economic importance. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 33–87

Lindquist EE, Oldfield GN (1996) Evolution of eriophyoid mites in relation to their host plants. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 277–300

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites their biology, natural enemies and control. Elsevier. World Crop Pests vol 6

Magowski WŁ (2005) Online biodiversity databases as a nucleus of integration for contemporary acarology: lessons from fauna europaea database project. Phytophaga 14(2004):747–751

Magud B, Stanisavljević LZ, Petanović R (2007) Morphological variation in different populations of *Aceria anthocoptes* (Acari: Eriophyoidea) associated with the Canada thistle, *Cirsium arvense*, in Serbia. Exp Appl Acarol 42:173–183

Mahmood T, Hein GL, Jensen SG (1998) Mixed infection of hard red winter wheat with high plains virus and wheat streak mosaic virus from wheat curl mites in Nebraska. Plant Dis 82(3):311–315

Malik R, Smith CM, Brown-Guedira GL, Harvey TL, Gill BS (2003) Assessment of *Aegilops tauschii* for resistance to biotypes of wheat curl mite (Acari: Eriophyidae). J Econ Entomol 96(4):1329–1333

Manson DCM, Gerson U (1996) Web spinning, wax secretion and liquid secretion by eriophyoid mites. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 251–258

Manzur BE (1989) Plan de muestreo secuencial para acaro del tostado *Phyllocoptruta oleivora* (Ashm.) (Acari: Eriophyidae), en citricos. Revista de Information—Centro de Informaciones para la Regulacion de Poblaciones de Organismos Nacivos 7(1–43):55–63

Marçon A, Kaeppler SM, Jensen SG, Stuber C Sr (1999) Loci controlling resistance to high plains virus and wheat streak mosaic virus in a B73 × Mo17 population of maize. Crop Sci 39(4):1171–1177

Marshall VG, Clayton MR (2004) Biology and phenology of *Cecidophyopsis psilaspis* (Acari: Eriophyidae) on Pacific yew (Taxaceae). Can Entomol 136(5):695–710

McIntyre PJ, Whitham TG (2003) Plant genotype affects long-term herbivore population dynamics and extinction: conservation implications. Ecology 84(2):311–322

Michalska K (1999) Guarding and spermatophore deposition in the free-living eriophyid mite *Vasates robiniae* Nalepa. Behaviour 136:899–918

Michalska K (2000) The influence of conspecific males on spermatophore deposition in the eriophyid mite *Aculus fockeui*. Exp Appl Acarol 24:905–911

Michalska K (2003) Climbing of leaf trichomes by eriophyid mites impedes their location by predators. J Insect Behav 16:833–844

Michalska K (2005) Spermatophore deposition throughout the day by the plum rust mite, *Aculus fockeui*. Exp Appl Acarol 35:111–116

Mifsud D, Monfreda R, de Lillo E (2008) Eriophyoid mites (Acari: Prostigmata: Eriophyoidea) from the Maltese Islands (Central Mediterranean): new reports and a preliminary check-list. Entomologica 40(2006–2007):117–138

Momen FM (2001) Biology of *Euseius yousefi* (Acari: Phytoseiidae) life tables and feeding behaviour on different diets. Acta Phytopath Entomol Hung 36(3–4):411–417

Momen FM, Rasmy AH, Zaher MA, Nawar MS, Abou-Elella GM (2004) Dietary effect on the development, reproduction and sex ratio of the predatory mite *Amblyseius denmarki* Zaher & El-Borolosy (Acari: Phytoseiidae). Int J Trop Ins Sci 24(2):192–195

Monfreda R, de Lillo E (2006) Attuali conoscenze sulle secrezioni salivari negli Acari Eriophyoidea. Atti dell'Accademia Nazionale Italiana di Entomologia. Rendiconti 53(2005):379–388

Monfreda et al (2009) Collection and detection of eriophyoid mites. Exp Appl Acarol. doi: 10.1007/s10493-009-9315-6

Moore D (2000) Non-chemical control of *Aceria guerreronis* on coconuts. In: Fernando LCP, de Moraes GJ, Wickramananda IR (eds) Proc. Internat. Workshop on Coconut mite *Aceria guerreronis*, Coconut Research Institute, Sri Lanka, 6–8 January 2000, pp 63–70

Moura MZD, Soares GLG, Isaias RMDS (2008) Species-specific changes in tissue morphogenesis induced by two arthropod leaf gallers in *Lantana camara* L. (Verbenaceae). Austr J Bot 56(2):153–160

Muthiah C, Bhaskaran R, Kannaiyan S (2001) Bio-ecology and control of eriophyid mite of coconut—an Indian experience. Planter 77(902):255–263

Navajas M, Fenton B (2000) The application of molecular markers in the study of diversity in acarology: a review. Exp Appl Acarol 24(10–11):751–774

Navia D, Flechtmann CHW, Amrine JW Jr (2005a) Supposed ovoviviparity and viviparity in the coconut mite, *Aceria guerreronis* Keifer (Prostigmata: Eriophyidae), as a result of female senility. Int J Acarol 31(1):63–65

Navia D, de Moraes GJ, Roderick G, Navajas M (2005b) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyidae): origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. Bull Entomol Res 95(6):505–516

Navia D, de Moraes GJ, Querino RB (2006a) Geographic variation in the coconut mite, *Aceria guerreronis* Keifer (Acari: Eriophyidae): a geometric morphometric analysis. Int J Acarol 32(3):301–314

Navia D, Truol G, Mendonca RS, Sagadin M (2006b) *Aceria tosichella* Keifer (Acari: Eriophyidae) from wheat streak mosaic virus-infected wheat plants in Argentina. Int J Acarol 32(2):189–193

Negloh K, Hanna R, Schausberger P (2008) Comparative demography and diet breadth of Brazilian and African populations of the predatory mite *Neoseiulus baraki*, a candidate for biological control of coconut mite. Biol Control 46(3):523–531

Nishida S, Naiki A, Nishida T (2005) Morphological variation in leaf domatia enables coexistence of antagonistic mites in *Cinnamomum camphora*. Can J Bot 83(1):93–101

Norton RA (1997) Book review. Integr Pest Manag Rev 2:109–218

Nuzzaci G, de Lillo E (1996) Perspectives on eriophyoid mite research. Entomologica 30:73–91

Nuzzaci G, de Lillo E, Di Palma A (2008) Aspetti di morfologia funzionale negli Acari: le secrezioni "salivari". Atti dell'Accademia Nazionale Italiana di Entomologia. Rendiconti 55(2007):103–106

Oldfield G (2002) Biology, ecology, and evolution of gall-inducing arthropods. Science Publishers, Inc., Endfield (NH), USA

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vectors of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 259–273

Ozman SK, Goolsby JA (2005) Biology and phenology of the eriophyid mite, *Floracarus perrepae*, on its native host in Australia, Old World climbing fern, *Lygodium microphyllum*. Exp Appl Acarol 35(3):197–213

Ozman-Sullivan SK (2006) Life history of *Kampimodromus aberrans* as a predator of *Phytoptus avellanae* (Acari: Phytoseiidae, Phytoptidae). Exp Appl Acarol 38(1):15–23

Paz Z, Gerson U, Sztejnberg A (2007) Assaying three new fungi against citrus mites in the laboratory, and a field trial. Biocontrol 52(6):855–862

Pérez-Moreno I, Moraza Zorilla ML (1998) Population dynamics and hibernation shelters of *Calepitrimerus vitis* in the vineyards of Rioja, Spain, with a description of a new eriophyoid extraction technique (Acari, Eriophyidae). Exp Appl Acarol 22(4):215–226

Petanović R, Rector BG (2007) A new species of *Leipothrix* Keifer, 1966 (Acari: Eriophyidae) on *Dipsacus* spp. in Europe and reassignment of two *Epitrimerus* spp. (Acari: Eriophyidae) to the genus *Leipothrix*. Ann Entomol Soc Am 100(2):157–163

Petanović R, Stanković S (1999) Catalog of the Eriophyoidea (Acari: Prostigmata) of Serbia and Montenegro. Acta Ent Serb (special issue):1–143

Prischmann DA, James DG, McMurtry JA (2005) Occurrence of a predatory mite (Acari: Phytoseiidae) within willow galls caused by eriophyid mites. Int J Acarol 31:433–436

Pushpa V, Nandihalli BS (2008) Bioefficacy of botanicals in the management of coconut eriophyid mite, *Aceria guerreronis* Keifer. J Plant Prot Environ 5(1):90–94

Qu SC, Tashiro N, Etoh T, Sadamatsu M (1997) Occurrence of dithiocarbamate resistant strain and its susceptibilities to several chemicals in the pink citrus rust mite, *Aculops pelekassi* (Keifer), in Saga Prefecture. Proc Assoc Pl Prot Kyushu 43:125–129

Quiros-Gonzalez M (2000) Phytophagous mite populations on Tahiti lime, *Citrus latifolia*, under induced drought conditions. Exp Appl Acarol 24(12):897–904

Ramarethinam S, Loganathan S (2000) Biology of *Aceria (Eriophyes) guerreronis* (K.) (Acari: Eriophyoidea: Eriophyidae)—a perianth mite infesting coconut groves in India. Pestology 24(6):6–9

Rasmy AH, Momen FM, Zaher MA, Abou-Elella GM (2003) Influence of diet on life history and predatory capacity of *Amblyseius zaheri* Yousef & El-Brolossy (Acari: Phytoseiidae). Ins Sci Applicat 23(1):31–34

Redfern M, Shirley P, Bloxham M (2002) British plant galls. Identification of galls on plants and fungi. Field Stud 10:207–531

Reis AC, Gondim MGC Jr, De Moraes GJ, Hanna R, Schausberger P, Lawson-Balagbo LE, Barros R (2008) Population dynamics of *Aceria guerreronis* Keifer (Acari: Eriophyidae) and associated predators on coconut fruits in northeastern Brazil. Neotrop Entomol 37(4):457–462

Ripka G (2007) Checklist of the eriophyoid mite fauna of Hungary (Acari: Prostigmata: Eriophyoidea). Acta Phytopaht Entomol Hung 42(1):59–142

Rosas Acevedo JL, Sampedro Rosas L (2006) Variabilidad de cepas de *Hirsutella thompsonii*, a partir de acaros fitofagos en tres sistemas terrestres del estado de Colima, Mexico. Rev Mex Biodiver 77(1):7–16

Sabelis MW, Bruin J (1996) Evolutionary ecology: life history patterns, food plant choice and dispersal. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, pp 329–366

Sabelis MW, Lesna I, Aratchige NS (2007) A tritrophic perspective to the biological control of eriophyoid mites. IOBC/WPRS Bull 30(5):91–93

Sabelis MW, Janssen A, Lesna I, Aratchige NS, Nomikou M, van Rijn PCJ (2008) Developments in the use of predatory mites for biological pest control. IOBC/WPRS Bull 32:187–200

Sánchez-Sánchez H, Henry M, Cárdenas-Soriano E, Alvizo-Villasana HF (2001) Identification of Wheat streak mosaic virus and its vector *Aceria tosichella* in Mexico. Plant Dis 85(1):13–17

Schwoebel G, Beiderbeck R (2000) In vitro Gallbildung an Blattern von *Salix alba* durch *Aceria tetanothrix* Nal. Mitt Deut Ges all ang Ent 12:179–181

Seifers DL, Harvey TL, Louie R, Gordon DT, Martin TJ (2002) Differential transmission of isolates of the high plains virus by different sources of wheat curl mites. Plant Dis 86(2):138–142

Seifers DL, Martin TJ, Harvey TL, Fellers JP, Michaud JP (2009) Identification of the wheat curl mite as the vector of *Triticum* mosaic virus. Plant Dis 93(1):25–29

Serrano L, Ramon J, Segarra J, Medina V, Achón MA, López M, Juárez M (2004) New approach in the identification of the causal agent of fig mosaic disease. Acta Horticult 657:559–566

Shalini KV, Manjunatha S, Lebrun P, Berger A, Baudouin L, Pirany N, Ranganath RM, Prasad DT (2007) Identification of molecular markers associated with mite resistance in coconut (*Cocos nucifera* L.). Genome 50:35–42

Shevchenko VG, De-Millo AP (1968) Life-cycle of *Trisetacus kirghisorum* (Acarina: Tetrapodili)—pest of *Juniperus semiglobosa* Rgl. Vestnik LGU 3:60–67

Siebold CTH (1850) Über Eriophyes. Arachniden. Jahresber. schles. Ges. Kultur (Breslan) 28:88–89

Siriwardena PHAP, Fernando LCP, Peiris TSG (2005) A new method to estimate the population size of coconut mite, *Aceria guerreronis*, on a coconut. Exp Appl Acarol 37(1–2):123–129

Skare JM, Wijkamp I, Rezende J, Michels G, Rush C, Scholthof K-BG, Scholthof HB (2003) Colony establishment and maintenance of the eriophyid wheat curl mite *Aceria tosichella* for controlled transmission studies on a new virus-like pathogen. J Virol Meth 108(1):133–137

Skare JM, Wijkamp I, Denham I, Rezende JAM, Kitajima EW, Park J-W, Desvoyes B, Rush CM, Michels G, Scholthof K-BG, Scholthof HB (2006) A new eriophyid mite-borne membrane-enveloped virus-like complex isolated from plants. Virology 347(2):343–353

Skoracka A (2008) Reproductive barriers between populations of the cereal rust mite *Abacarus hystrix* confirm their host specialization. Evol Ecol 22:607–616

Skoracka A, Dabert M (2009) The cereal rust mite *Abacarus hystrix* (Acari: Eriophyoidea) is a complex of species: evidence from mitochondrial and nuclear DNA sequences. Bull Entomol Res:1–10. doi:10.1017/S0007485309990216

Skoracka A, Kuczyński L (2003) Population dynamics of eriophyoid mites (Acari: Eriophyoidea) living on grasses in Poland. Biological Lett 40(2):75–84

Skoracka A, Kuczyński L (2004) Demography of the cereal rust mite *Abacarus hystrix* (Acari: Eriophyoidea) on quack grass. Exp Appl Acarol 32(4):231–242

Skoracka A, Kuczyński L (2006) Infestation parameters and morphological variation of the wheat curl mite *Aceria tosichella* Keifer (Acari: Eriophyoidea). In: Gabryś G, Ignatowicz S (eds) Advances in Polish acarology. SGGW, Warszawa, pp 330–339

Skoracka A, Kuczyński L, Magowski WŁ (2002) Morphological variation in different host populations of *Abacarus hystrix* (Acari: Prostigmata: Eriophyoidea). Exp Appl Acarol 26(3–4):187–193

Skoracka A, Magowski WŁ, Kuczyński L (2003) Spatial and temporal distribution of cereal rust mite *Abacarus hystrix* (Acari: Eriophyoidea) on *Agropyron repens*. Biologia, Bratislava 58((5):913–917

Skoracka A, Lewandowski M, Boczek J (2005) A catalogue of eriophyoid mites (Acari: Eriophyoidea) of Poland. Catalogus faunae Poloniae, Muzeum i Instytut Zoologii PAN, Warszawa

Skoracka A, Kuczyński L, Rector BG (2007) Divergent host acceptance behavior suggests host specialization in populations of the polyphagous mite *Abacarus hystrix* (Acari: Prostigmata: Eriophyidae). Environ Entomol 36(4):899–909

Slone DH, Croft BA (2001) Species association among predaceous and phytophagous apple mites (Acari: Eriophyidae, Phytoseiidae, Stigmaeidae, Tetranychidae). Exp Appl Acarol 25(2):109–126

Smith L, de Lillo E, Amrine JW Jr (2009) Effectiveness of eriophyid mites for biological control of weedy plants and challenges for future research. Exp Appl Acarol. doi:10.1007/s10493-009-9299-2

Stenger DC, Hein GL, French R (2006) Nested deletion analysis of wheat streak mosaic virus HC-Pro: mapping of domains affecting polyprotein processing and eriophyid mite transmission. Virology 350(2):465–474

Stephan D, Moeller I, Skoracka A, Ehrig F, Maiss E (2008) Eriophyid mite transmission and host range of a brome streak mosaic virus isolate derived from a full-length cDNA clone. Arch Virol 153(1):181–185

Suber P (2002) Comment open access to the scientific journal literature. J Biol http://jbiol.com/content/1/1/3

Sumangala K, Haq MA (2005) Diurnal periodicity and dispersal of coconut mite, *Aceria guerreronis* Keifer. J Entomol Res 29(4):303–307

Susi P (2004) Black currant reversion virus, a mite-transmitted nepovirus. Mol Pl Pathol 5(3):167–173

Tanaka H, Shibao M (2003) A pattern of occurrence and dispersal of the tomato russet mite, *Aculops lycopersici* (Massee) in a tomato greenhouse. Proc Kansai Pl Prot Soc 45:23–27

Thomas JA, Hein GL (2003) Influence of volunteer wheat plant condition on movement of the wheat curl mite, *Aceria tosichella*, in winter wheat. Exp Appl Acarol 31(3–4):253–268

Thomas JB, Conner RL, Graf RJ (2004) Comparison of different sources of vector resistance for controlling wheat streak mosaic in winter wheat. Crop Sci 44(1):125–130

Toyoshima S, Amano H (2006) Diversity and abundance of phytoseiid mites on *Magnolia hypoleuca* Siebold et Zuccarini, a candidate source of natural enemies in natural vegetation. Appl Entomol Zool 41(2):349–355

Tzanetakis IE, Gergerich RC, Martin RR (2006) A new Ilarvirus found in rose. Plant Pathol 55(4):568

Vaneckova-Skuhrava I (1996) Life cycles of five eriophyid mite species (Eriophyoidea, Acari) developing on trees and shrubs. J Appl Entomol 120(9):513–517

Varadarajan MK, David PMM (2002) Population dynamics of the coconut mite *Aceria guerreronis* Keifer (Acari: Eriophyidae) and associated arthropods in Tamil Nadu, India. Ins Sci Applicat 22(1):47–59

Vidović B, Petanović R, Stanisavljević LJ (2008) Morphological variation of *Aceria* spp. (Acari: Eriophyoidea) inhabiting *Cirsium* species (Asteraceae) in Serbia. In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier M-S, Vial L (eds) Integrative Acarology. Proc. 6th Eur.A.Ac. Symposium, Montpellier, July 2008, pp 288–290

Vieira-Neto J, Lucio AD, Chiaradia LA (2007) Selecao de modelos para amostragem sequencial do acaro-do-bronzeado *Dichopelmus notus* Keifer (Acari, Eriophyidae) em erva-mate. Cerne 13(3):339–346

Villanueva RT, Childers CC (2007) Development of *Iphiseiodes quadripilis* (Banks) (Acari: Phytoseiidae) on pollen or mite diets and predation on *Aculops pelekassi* (Keifer) (Acari: Eriophyidae) in the laboratory. Environ Entomol 36(1):9–14

Villanueva RT, Rodrigues JCV, Childers CC (2005) Larval *Cryptothelea gloverii* (Lepidoptera: Psycidae), an arthropod predator and herbivore on Florida citrus. Exp Appl Acarol 36(1):83–92

Villanueva RT, Gagné R, Childers CC (2006) Two species of Cecidomyiidae predacious on citrus rust mite, *Phyllocoptruta oleivora*, on Florida citrus. Fla Entomol 89(2):161–167

Waite GK (1999) New evidence further incriminates honey-bees as vectors of lychee erinose mite *Aceria litchii* (Acari: Eriophyidae). Exp Appl Acarol 23(2):145–147

Walde SJ, Hardman JM, Magagula CN (1997) Direct and indirect species interactions influencing within-season dynamics of apple rust mite, *Aculus schlechtendali* (Acari: Eriophyidae). Exp Appl Acarol 21(9):587–614

Walton VM, Dreves AJ, Gent DH, James DG, Martin RR, Chambers U, Skinkis PA (2007) Relationship between rust mites *Calepitrimerus vitis* (Nalepa), bud mites *Colomerus vitis* (Pagenstecher) (Acari: Eriophyidae) and short shoot syndrome in Oregon vineyards. Int J Acarol 33(4):307–318

Wearing CH, Colhoun K (1999) Development of *Orius vicinus* (Ribaut) (Heteroptera: Anthocoridae) on different prey. Biocontrol Sci Technol 9(3):327–334

Webber J, Bruce Chapman R, Worner SP (2008) Forecasting emergence and movement of overwintering hazelnut big bud mites from big buds. Exp Appl Acarol 45(1–2):39–51

Wergin WP, Ochoa R, Erbe EF, Craemer C, Raina AK (2000) Use of low-temperature field emission scanning electron microscopy to examine mites. Scanning 22(3):145–155

Wickramananda IR, de Silva PHPR, Sarathchandra SR, Kumara ADNT, Rajapaksha RHS (2005) A method for *in vitro* culture of coconut mite, *Aceria guerreronis* Keifer (Acari: Eriophyidae) in immature leaf tissues of coconut (*Cocos nucifera*). In: Peiris TSG, Ranasinghe CS (eds) Proc int conf Coconut Research Institute of Sri Lanka, Part 2, pp 229–236

Witt ABR (2004) *Aceria liopeltus* Meyer (Acari: Eriophyidae) and *Asterolecanium conspicuum* Brain (Hemiptera: Asterolecaniidae), two potential biological control agents for *Acacia nilotica* ssp. *indica* (Mimosaceae) in Queensland, Australia. Afr Entomol 12:142–146

Xu X, Li L-Y, Wang D-S, Hong X-Y, Wu J, Yuan Y-D, Xie X-C (2006) Effect of temperature and relative humidity on development and reproduction of the tomato russet mite, *Aculops lycopersici* (Massee) (Acarina, Eriophyidae). Acta Entomol Sin 49(5):816–821

Xue X-F, Song Z-W, Amrine JW Jr, Hong X-Y (2007) Eriophyoid mites on coniferous plants in China with descriptions of a new genus and five new species (Acari: Eriophyoidea). Int J Acarol 33(4):333–345

Young BA, Hein GL, French R, Stenger DC (2007) Substitution of conserved cysteine residues in wheat streak mosaic virus HC-Pro abolishes virus transmission by the wheat curl mite. Arch Virol 152(11):2107–2111

Zemek R, Kurowská M, Kameníková L, Rovenská GZ, Havel J, Reindl F (2005) Studies on phenology and harmfulness of *Aceria carvi* Nal. (Acari: Eriophyidae) on caraway, *Carum carvi* L., in the Czech Republic. J Pest Sci 78(2):115–116

Zhang Z-Q (2003) Mites of greenhouses. Identification, biology and control. CABI Publishing, Wallingford

Zhang Y-X, Zhang Z-Q, Zhang X-J, Liu Q-Y, Ji J (2001) Population dynamics of phytophagous and predatory mites (Acari: Tetranychidae, Eriophyidae, Phytoseiidae) on bamboo plants in Fujian, China. Exp Appl Acarol 25(5):383–391

Zhao S, Amrine JW Jr (1997) Investigation of snowborne mites (Acari) and relevance to dispersal. Int J Acarol 23:209–213

Behavioural studies on eriophyoid mites: an overview

**Katarzyna Michalska · Anna Skoracka · Denise Navia ·
James W. Amrine**

Abstract Eriophyoid mites are excellent candidates for ethological research using the approaches of behavioural ecology and sociobiology. These tiny haplodiploid mites are highly specialized plant parasites, producing galls, forming nests, inhabiting refuges or living freely on plants. They reproduce via spermatophores deposited on a substrate and without pairing, which is a fascinating, though still poorly understood, mode of reproduction widespread in some groups of arthropods. Eriophyoid males can be involved in external sperm competition. In some species they also guard pre-emergent females and deposit spermatophores beside them. Although slow-walking, the minute eriophyoid mites can disperse for long distances on air currents or specific animal carriers. After landing on a plant they can distinguish between suitable and unsuitable hosts. Biological observations on a deuterogynous species indicate that parasociality could occur among eriophyoid mites. Many eriophyoids are of economic importance. Knowledge of their behaviour may promote understanding their ecology, may resolve problems in their phylogeny and may help developing methods for their control. In this paper, attention is directed to dispersal modes of eriophyoid mites, their feeding and host acceptance, spermatophore deposition and mating, defence against predators, and social behaviour.

K. Michalska (✉)
Department of Applied Entomology, Warsaw University of Life Sciences, Nowoursynowska 159,
02-776 Warsaw, Poland
e-mail: katarzyna_michalska@sggw.pl

A. Skoracka
Department of Animal Taxonomy and Ecology, Institute of Environmental Biology,
Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland

D. Navia
Laboratory of Plant Quarantine, Embrapa Genetic Resources and Biotechnology,
CP 02372, Brasília, DF 70.770-900, Brazil

J. W. Amrine
West Virginia University, Morgantown, WV, USA

Introduction

Although eriophyoid mites were first noted in the literature about 270 years ago and have
been thoroughly investigated since the mid-19th century, aspects of their behaviour have
only been studied for a few decades, and rather sparsely. Microscopic size of eriophyoids
and their tendency to hide within plant structures (Lindquist 1996) make direct observa-
tions of these mites difficult. These factors, together with difficulties in handling and
rearing them (e.g. within galls) probably was the reason preventing significant research in
behavioural investigations.

In the past century only a few topics on eriophyoid behaviour have been examined.
Several fundamental publications describing their ability to discriminate between different
host plants, describing feeding mechanisms, spermatophore deposition and picking up
sperm by females, and the possibility of the existence of different dispersal strategies have
emerged. All have been reviewed by Oldfield and Michalska (1996), Sabelis and Bruin
(1996), and Westphal and Manson (1996). Additionally, the effect of temperature and
photoperiod, and different wavelengths of light on the behaviour of eriophyoid mites have
been studied (Smith 1959; Sternlicht 1969).

Eriophyoidea are an economically important group due to the direct damage they can
cause to their hosts, their ability to transmit serious plant diseases, and also due to the
possibility of using them as biological agents for weed control (Lindquist et al. 1996).
Information on the behaviour of these tiny plant parasites could be of great practical
importance, e.g. to monitor pest populations or to develop better control methods. In
addition, such features like high host specialization, sex dissociation and social behaviors
(Oldfield 1996; Oldfield and Michalska 1996; Britto et al. 2008) make eriophyoid mites
suitable candidates for both ethological research as well as investigations using the
approach of behavioural ecology. By dint of technological advances in microscopy and
photography and in rearing methods, behavioural observations of these minute mites have
become more routine in recent years.

The aim of this paper is to review and update the information on the behaviour of
eriophyoid mites, indicating some so far unexplored avenues of their behaviour and
evolution.

Foraging behaviour

The evolutionary success of eriophyoid mites, as for any animal, depends on reproductive
success which in turn depends on effective foraging behaviour. Animals behave in such a
way as to find, capture and consume food containing adequate nutrition while spending the
least amount of time and energy possible in doing so (MacArthur and Pianka 1966). The
overall survival of phytophagous arthropods depends on dispersal to suitable host plants,
whether close by or far away. For eriophyoid mites, which are not adapted for active
dispersal between plants, both abandoning a plant and finding a new one is especially
difficult and risky. Thus, the mode of dispersal is a key component of the foraging strategy
for these mites, and influences their subsequent host acceptance and feeding behaviour.

Dispersal modes

For eriophyoid mites the proper host plant is a crucial factor for survival and reproduction. However, a portion of the mites actively disperse when conditions are suitable—high temperatures and humidity, approaching low pressure area, significant wind, etc.—independent of the condition of the host. Thus, in fact, eriophyoid mites can choose one of two things: stay on the plant and continue to increase the size of population, or disperse and take a chance on finding and colonizing a new habitat. But the problem is that tiny eriophyoid mites cannot actively seek new hosts. The only active mode of eriophyoid dispersal is by walking within one plant or from one plant to another if they touch one another. Except for this, only passive methods of dispersal have been observed for eriophyoid mites, i.e. (1) transferrance by air currents, (2) phoresy on animal carriers, or (3) dispersal by rain (Jeppson et al. 1975; Schliesske 1990).

Examples of all four modes can be found in the literature. However, among them aerial dispersal was considered the most important (Lindquist and Oldfield 1996; Zhao and Amrine 1997a, b). Many authors reported eriophyoids in the air on evidence from catches on sticky traps or on plates (e.g. Nault and Styer 1969; Lindquist and Oldfield 1996 and references therein, see also Table 1). Moreover, authors have observed different behavioural adaptations which were interpreted as facilitating aerial dispersal: initiating the take-off for dispersal by moving to the plant tips and standing up on their anal lobes (Fig. 1), moving the legs rapidly, arching bodies and leaping into the air, raising the hind part of the body while standing on their forelegs, forming swarms of thousands of individuals at leaf tips (Sabelis and Bruin 1996), and jumping so as to allow the mite to become airborne (Ozman and Golsby 2005). Although considered the most important, aerial dispersal has been regarded as the most risky mode of dispersal (Sabelis and Bruin 1996). When highly specialized animals move by wind, the probability of landing on a suitable host is very low. That is why Sabelis and Bruin (1996) proposed that aerial dispersal is advantageous for species with wide host ranges, giving *Abacarus hystrix* (Nalepa) as an example. However, recent studies have shown that this aerially dispersed grass-inhabiting ostensible generalist is in fact a complex of highly specialized species (Skoracka and Kuczyński 2006; Skoracka 2008). Furthermore, special behaviours interpreted as adaptations for aerial dispersal can be regarded not only as behaviours increasing the probability of launching into the atmosphere but also as increasing the probability of attaching to a passing object, such as an insect, a larger mite, or even a human (e.g. Gibson and Painter 1957; Duffner et al. 2001).

Eriophyoid mites attaching to other animals have been reported by several authors and this phenomenon was often interpreted as phoresy (e.g. Massee 1928; Gibson and Painter 1957; Shvanderov 1975; Waite and McAlpine 1992; see also Table 1). According to Lindquist and Oldfield (1996) eriophyoid mites do not show clear phoretic morphological adaptations, such as the pedicels or claws which can be found in other phoretic mites. Also, no specific adaptations for selectivity toward a more favourable carrier have been observed for eriophyoid mites. Thus, Lindquist and Oldfield (1996) concluded that the use of carriers by eriophyoid mites is an accidental behaviour. Even if accidental, transport by host-specific carriers would seem to be more efficient than aerial dispersal, and it would guarantee a greater possibility of finding a specific host (Sabelis and Bruin 1996), provided that eriophyoids can distinguish host-specific carriers from non-host-specific carriers that could take them even further away from a host-plant than the wind.

Wind and carriers have been the dispersal modes most often discussed in the literature for eriophyoids (Lindquist and Oldfield 1996, Sabelis and Bruin 1996, Lindquist 1998).

Table 1 Studies on eriophyoid mites dispersal

Species	Mode of dispersal				References
	Ambulatory	Wind	Rain	Carriers	
Abacarus hystrix (Nalepa)		X			Nault and Styer (1969); Frost (1997)
Acalitus essigi (Hassan)	X	X			Hanson (1933); Davies et al. (2001)
Acalitus hibisci Mondal et Chakrabarti	X				Chakrabarti and Chakrabarti (2005)
Acalitus phloeocoptes (Nalepa)		X			Sternlicht et al. (1973)
Aceria chibaensis (Kadono)		X			Kadono et al. (1982)
Aceria spp.				Leafhoppers	Painter and Schesser (1954)
Aceria cynodoniensis Sayed				Mole crickets	Cromroy (1983)
Aceria guerreronis Keifer	X	X		Bees, ants, and other insects, bats	Julia and Mariau (1979), Griffith (1984), Moore and Alexander (1987), Schliesske (1990), Sumangala and Haq (2005)
Aceria litchii (Keifer)	X	X		Honey bees, Phytoseiids	Mishra (1912), Lall and Rahman (1975), Waite and McAlpine (1992), Waite (1999), G.K. Waite unpubl.
Aceria loewi (Nalepa)				Spiders, dipterans, aphids, coleopterans	Shvanderov (1975)
Aceria tosichella Keifer		X		Aphis, trips, greenbugs	Slykhuis and Andrews (1953), Pady (1955), Slykhuis (1955), Staples and Allington (1956, 1959), Gibson and Painter (1957), Nault and Styer (1969), Harvey and Martin (1980, 1988), Harvey et al. (1990), Brey (1998), Thomas and Hein (2003), Liu et al. (2005)
Aculodes mckenziei (Keifer)		X			Nault and Styer (1969)
Aculodes dubius (Nalepa)		X			Nault and Styer (1969)
Aculops lycopersici (Tryon)				Aphids, human	Grahl and Leuprecht (1998), Tanaka and Shibao (2003)
Aculus comatus (Nalepa)		X			Krantz (1973), Duffner et al. (2001)

Table 1 continued

Species	Mode of dispersal				References
	Ambulatory	Wind	Rain	Carriers	
Aculus fockeui (Nalepa et Trouessart)		X	X	Human	Barke et al. (1972), Schliesske (1977)
Aculus schlechtendali (Nalepa)		X			Duffner et al. (2001)
Calepitrimerus vitis (Nalepa)	X	X		Human	Duffner et al. (2001), Gabi and Mészáros (2003)
Cecidophyopsis ribis (Westwood)		X	X	Aphids, ladybeetles, honey bees, spiders, dipterans, aphids, coleopterans	Massee (1928), Smith (1960), Behrens (1964), van de Vrie (1967), Shvanderov (1975), Duffner et al. (2001)
Cecidophyopsis vermiformis (Nalepa)	X				Burgess and Thompson (1985)
Davisella breitlowi (Davis)		X			Davis (1964)
Diptacus gigantorhynchus (Nalepa)		X	X	Human	Schliesske (1977)
Epitrimerus pyri (Nalepa)	X	X			Easterbrook (1978, 1979), Herbert (1979), Bergh (1992), Bergh and Judd (1993), Duffner et al. (2001)
Eriophyes armeniacus Bagdasarian	X				Oganezova and Pogosova (1994)
Eriophyes emarginatae Keifer	X				Oldfield (1969)
Eriophyes laevis (Nalepa)	X				Vuorisalo et al. (1989)
Eriophyes pyri (Pagenstecher)		X			Duffner et al. (2001)
Notostrix jamaicae Keifer		X	X	X	Schliesske (1990)
Phyllocoptes abaenus Keifer		X	X	Human	Schliesske (1977)
Phyllocoptes gracilis (Nalepa)	X				van Dinther (1951)
Phyllocoptruta oleivora (Ashmead)	X	X			McCoy (1979), Bergh and McCoy (1997), Bergh (2001), Bergh and Smith (2001)
Phytoptus avellanae Nalepa	X				Burgess and Thompson (1985)
Retracrus elaeis Keifer		X	X	X	Schliesske (1990)
Tegonotus acutilobus (Nalepa)		X			Duffner et al. (2001)
Floracarus perreperae Knihinicki et Boczek		X			Ozman and Goolsby (2005)

Table 1 continued

Species	Mode of dispersal				References
	Ambulatory	Wind	Rain	Carriers	
Different species		X			Mumcuoglu and Six (1974), Schliesske (1979), Somchoudhury et al. (1985), Zhao and Amrine (1997a, b)
Different species				Aphids	Batchelor (1952)

Fig. 1 *Aceria tulipae* (Keifer) standing erect on the caudal sucker
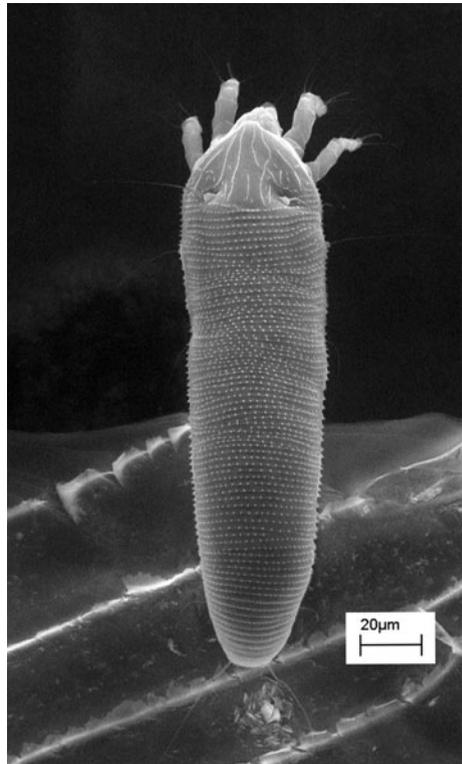
Authors have debated which mode is most often used and the most beneficial for eriophyoid mites. They have analyzed different factors (e.g. host availability, degree of mite-host specificity, mite adaptations) and tried to detect patterns in eriophyoid dispersal. Sabelis and Bruin (1996), however, have cautioned against such interpretations due to the lack of support by empirical data. Thus, the difficulty with finding clear answers results from the scarcity of studies regarding this topic.

Since these last significant reviews regarding eriophyoid dispersal, not much new information has been provided (see Table 1). In spite of the fact that dispersal is the key trait of eriophyoid foraging success, the mode of dispersal has been observed or recorded for only about 2.5% of approximately 4,000 described species. Considering the scarcity of

Fig. 2 The number of species versus mode of dispersal derived from search of the literature, from 1912 to 2008. Please note that several authors indicated two or more dispersal modes for the same species, sometimes in the same study
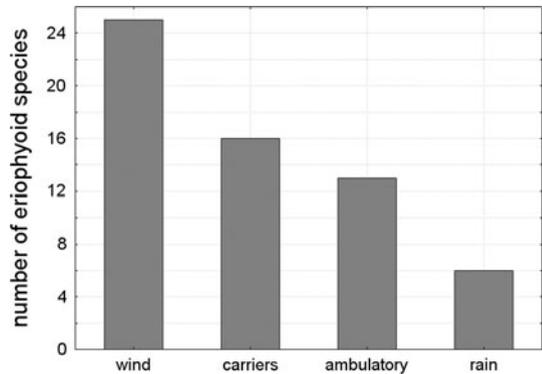
experimental data, it is difficult to draw general conclusions and definitely answer the question of which form of dispersal mode plays the more significant role in eriophyoid mites, if any. Table 1 provides a summary of present knowledge of cases of eriophyoid dispersal. These data have shown that dispersal by wind was reported the most frequently (Fig. 2). Also, Zhao and Amrine (1997a), who collected 10,000 mites in one small container of water in daily collections over just one year and captured more mites on windy days compared to calm ones, have proved that this way was clearly dominant over any other mode of dispersal. Two other modes, i.e. by carriers and ambulatory, occurred rarely when compared to wind, and dispersal by rain had the lowest frequency. Ambulatory movement is, however, very important within a plant or a tree, or in hedges, pastures, forests or other habitats, where branches or leaves of suitable plants contact one another or are close together.

Host acceptance and feeding

Host acceptance is thought to reflect the suitability of hosts for herbivore survival (Courtney et al. 1989; Singer et al. 1989). Irrespective of the method of transport (wind or carrier) when the eriophyoid mite ends up on a non-host, it losses time finding a new suitable host. Thus, an ability to quickly discriminate between host and non-host may well confer selective advantage.

It has been shown that few eriophyoid species can apparently distinguish between acceptable and unacceptable hosts. Differences in host acceptance can be measured as differences in reproduction and development on various hosts (Bergh and Weiss 1993; Chen et al. 2000; Skoracka and Kuczyński 2006) or directly by behavioural observations. For example, *Aceria tosichella* Keifer behaved differently according to the quality of their grass host plant, i.e., it stayed on hosts during periods of active plant growth and dispersed when host plant quality was deteriorating because of heavy feeding damage (Nault and Styer 1969). Thus, non-preference of the host can be exhibited by initiating new dispersal behaviour.

Kozłowski and Boczek (1987) and Kozłowski (1995) showed that feeding behaviour (i.e. time of probing and feeding) of *Aculus schlechtendali* (Nalepa) was different on various apple varieties. According to Gibson (1974), *A. hystrix* fed only on three among 11 grass species tested. Other studies have demonstrated that overall activity and the part of the plant occupied by *A. hystrix* differed among selected grass species (Skoracka et al. 2007). On familiar hosts, females of *A. hystrix* were not very active and showed little tendency to move. They spent most of their time resting in furrows on the upper leaf

surface. In contrast, females on non-hosts were generally more active and mobile, spending more time walking, running, and climbing over the whole plant surface including sites that are not typical for them, such as leaf margins, ligules, bases, and stems. In addition, they showed a high tendency toward dispersal. The behavioural reaction to non-hosts by *A. hystrix* was consistent with reduced individual fitness observed previously for the same populations on the same novel hosts, whereas behaviourally accepted hosts were the same ones on which these populations survived better and had higher fecundity (Skoracka and Kuczyński 2006). Thus, because the mites gain in fitness by discriminating between hosts, their behaviour was interpreted as adaptive discrimination.

Finally, after landing on the host and discriminating whether it is a proper one, the eriophyoid mite can start to feed. After probing, which takes several seconds, the mite takes a typical feeding stance, i.e. it slightly bends its body and anchors the rostrum to the host surface and contracts the telescopic palpal segments, which allows protrusion of the cheliceral stylets for a short distance into the plant tissues (Krantz 1973; Gibson 1974; McCoy and Albrigo 1975; Nuzzaci 1976). Information concerning the feeding behaviour of eriophyoid mites was summarized by Westphal and Manson (1996) and no new detailed data have been provided since.

Future directions

As indicated above, data regarding the foraging of eriophyoid mites are available only for a small number of species. It is obvious that knowledge of the mechanisms and factors influencing dispersal, host acceptance and feeding behaviour may help in defining strategies on management and estimating the risk posed by pest species to new areas. This topic requires more research. Some suggestions are given below.

Dispersal

Investigations into longevity of dispersing mites, tolerance of extreme conditions (low temperatures and pressures at high altitudes) and the potential for multiple launches from undesirable host plants should be made as these characteristics may help to ensure successful aerial dispersal.

Females are regarded as the dispersing stage in eriophyoid mites (Lindquist and Oldfield 1996). However, males and nymphs are found dispersing as well. Theoretically, a single eriophyoid female may be able to give rise to an entire population. Thus, a newly founded population may be genetically distinct from the source population. How often the founder effect occurs in nature and whether it influences the genetic differentiation among eriophyoid mite species should be studied.

To be successful in finding a proper host, eriophyoid mites may attach to specific carriers for dispersal. Research should try to determine which potential carriers can serve as specific vectors and guarantee eriophyoid success, and which are accidental and attachment to them may have no more success than aerial dispersal. Also, survival ability of eriophyoid mites on carriers, and the carriers' reactions to the presence of eriophyoid mites should be studied.

Generally, eriophyoid mites may use different means of dispersal. There is a question about the factors influencing each of these modes; or perhaps choosing a mode of dispersal

is accidental? It should also be determined whether particular species may use a combination of different dispersal techniques.

Host acceptance and feeding

It is important to recognize the decision process that leads mites to either accept or reject a given host. Suitability of the host plant can depend upon a number of factors such as a plant's chemical composition, nutritional quality and toxicity, the plant's physical characteristics, stage of growth, structure, prevalence of natural enemies or microenvironment (Thompson and Pellmyr 1991; Bernays and Chapman 1994). Which of them play a role in host plant discrimination in specific eriophyoid mites should be tested. Great attention should be paid to the mite solenidion, which is the sensory organ informing the mite about the chemical composition of the substrate. The host plant's chemical interaction with the solenidion, especially the ability of eriophyoid mites to discriminate among thousands of volatile compounds on plant surfaces and being attracted to only a very few of them, would be a very interesting area of study.

For phytophagous arthropods, host acceptance behaviour is a key character responsible for host plant specialization (Jaenike 1990). Thus, using behavioural data, host specificity of eriophyoids can be tested. Testing host acceptance is especially important with respect to invasive species which may be able to extend their host range and become a problem in ecosystems. An example of such an invasive species is *Aceria guerreronis* Keifer which has recently spread to most coconut production areas worldwide. Moore and Howard (1996) hypothesised that the original host of this mite is a non-coconut palm from which the mite switched to coconut palm when it became more extensive in the Americas or Africa. This hypothesis was supported by Navia et al. (2005) on the basis of molecular studies of American, African and Asian populations. However, recent information on the occurrence of *A. guerreronis* from coconut unproductive hybrids, possibly ancestral stock in Queensland, Australia (Ochoa personal comm. 2008) may lead to a change in this scenario. It may be possible that the mite originated from the coconut native region, the Indo-Pacific, and from there dispersed to the Americas and Africa. Both hypotheses indicate that the mite has extended its host range along its invasion routes. In addition to coconut, *A. guerreronis* has also been found infesting *Borassus flabellifer* L. in Asia (India and Sri Lanka), and *Syagrus romanzoffiana* (Cham.) Glassman in North America (California, USA).

Another example of expansion of host range seems to be *Aculops lycopersici* (Tryon). It has been suggested that the original host plant of this mite was a wild solanaceous plant somewhere in the Americas, and its association with tomato is recent (Oldfield 1996). Possibly, the original small and unproductive plant may have been resistant to *A. lycopersici*. Breeding productive tomatoes probably resulted in loss of resistance to the mite (a similar situation may have happened with the coconut palm tree). Host acceptance tests could help to verify this hypothesis.

It would be very important to investigate genetic and environmental causes influencing host acceptance behaviour in eriophyoid mites and to detect factors affecting mite transfer to new hosts. Also, finding genes responsible for resistance in original hosts to eriophyoid mites could be helpful in developing future mite control on cultivated plants.

Many other issues, e.g. responses and sequences associated with feeding, rhythmic patterns of feeding, and time intervals of probing and cell penetration should be tested among other eriophyoid species, especially species able to transmit plant viruses.

Sexual behaviour

Mating of eriophyoids was a puzzle until the publication by Oldfield et al. (1970) reporting that sperm transfer by these mites is indirect and takes place via minute, stalked spermatophores (8–25 μm long; head diameter 9–19 μm) deposited on the plant surface. The authors described the spermatophores of several species representing all three families of the superfamily Eriophyoidea. Behavioural observations on *Aculus fockeui* (Nalepa and Trouessart) [syn. *Aculus cornutus* (Banks)] and *Phyllocoptruta oleivora* (Ashmead) have revealed that eriophyoid males can deposit spermatophores in the absence of females. Also, females of *A. fockeui* did not require any assistance from males in picking up sperm from a spermatophore. Sexual 'independence' of males and females has been confirmed in the following eriophyoid species: *Aceria sheldoni* (Ewing) (Sternlicht and Goldenberg 1971; Sternlicht and Griffiths 1974), *Epitrimerus pyri* (Nalepa), *A. schlechtendali* (Oldfield 1988), *Acalitus essigi* (Hassan), *Aculops allotrichus* (Nalepa) (syn. *Vasates robiniae* Nalepa) (Michalska and Boczek 1991; Michalska 1999), *Cecidophyopsis hendersoni* (Keifer) (Michalska and Shi 2004), and *Abacarus hystrix* (Skoracka, unpubl.). This so called 'sex dissociation' (syn. mate dissociation or non-pairing) is widespread in several groups of arthropods including Arachnida (mites and pseudoscorpions), Hexapoda (collembolans and diplurans), Pauropoda, Symphyla and Diplopoda (polyxenids) (for review see Alexander 1964; Schaller 1971; Thomas and Zeh 1984; Proctor 1998). In mites, apart from eriophyoids, many other prostigmatic mites (rev. Thomas and Zeh 1984; 1984; Witte 1991; Proctor 1992, 1998; Witte and Döring 1999) and most oribatids (rev. Schaller 1971) are also dissociated. Most non-pairing organisms are aquatic or terrestrial often inhabiting soil or leaf-litter. The eriophyoids are the only known group of obligatory herbivores exhibiting this mode of reproduction.

Sex dissociation can be complete or incomplete. If it is incomplete, as in some water mites, spermatophore deposition is triggered only by previous contact with females or their odours (Proctor 1992). In eriophyoid mites, however, as can be inferred from the observations on *A. fockeui*, *A. allotrichus* and *C. hendersoni*, males can deposit spermatophores in total isolation from both conspecifics and their odours (Oldfield et al. 1970; Michalska and Boczek 1991; Michalska and Shi 2004; Michalska unpubl.).

It is commonly acknowledged that the high density of a population may favour sex dissociation, as it also increases the availability of receptive females and thereby the probability that spermatophores will be visited by females (Alexander 1964; Schaller 1971; Thomas and Zeh 1984; Proctor 1998). It also appears to be true for eriophyoid mites, as they live gregariously on plants and often develop in high population densities (Sabelis and Bruin 1996). By contrast, in sparse populations, males should produce numerous spermatophores in order to increase female-spermatophore encounter rate, which seems to be effective only in extremely mesic habitats with long-lasting viability of spermatophores (Thomas and Zeh 1984; Proctor 1998). As shown by the tests with *A. fockeui*, eriophyoid spermatophores can be viable for a relatively long time, up to 3 days after deposition on a leaf (Oldfield et al. 1970; Oldfield and Newell 1973), what could additionally favour sexual 'independence' of eriophyoid males.

Spermatophores of sex dissociated arthropods are small structures often difficult to be found by females in the vast volume of water or spatially intricate soil, litter and vegetation (Witte 1991; Proctor 1992, 1998). Furthermore, they are exposed to external sperm competition which may additionally diminish the chances that a female picks up a spermatophore of a particular male (Proctor 1992, 1998). Thus, non-pairing males are known to use the whole range of signaling devices (pheromone plume, signaling threads, zigzag

secretions) and behavioural tactics aimed at increasing the probability of visiting their spermatophores by females (Witte 1991; Proctor 1992; Proctor 1998). In this paper we focus on these issues putting stress on factors influencing spermatophore deposition by males, picking up sperm from spermatophores by females, contacts between sexes and avoidance of external sperm competition.

Attraction to spermatophores

Although some females of *A. fockeui* must have bumped into spermatophores to pick up sperm, others clearly changed their behaviour (they walked slower, on stiffened legs) when approaching a spermatophore, which may indicate its recognition via an emitted attractant (Oldfield et al. 1972). Also, as in other non-pairing arthropods, there is a gradual loss of the attractiveness of aging spermatophores to the females (Oldfield et al. 1970; Oldfield and Newell 1973; see also Proctor 1998) implying probably the simultaneous decrease of pheromone concentration in eriophyoid spermatophores.

It is a common view that the placement of spermatophores into groups by indirect sperm transferring arthropods helps to increase the pheromone-mediated attraction to sperm (Proctor 1998; Witte and Döring 1999). Males form rows or fields of their own spermatophores or, 'stealing' the pheromonal plume, they add spermatophores to those previously deposited by other males. Also, in eriophyoid mites, both free-living *A. hystrix* (Skoracka unpubl.), *Anthocoptes ribis* Massee, *A. shlechtendali*, *A. allotrichus*, *A. fockeui*, *Rhyncaphytoptus ulmivagrans* Keifer, and gall makers *A. essigi*, *Aceria brevipunctata* (Nalepa) (Michalska 1997) and *E. sheldoni* (Sternlicht and Giffiths 1974), spermatophores have been found in groups. In vagrants, spermatophore aggregations were most numerous along the midvein and near the junction of lateral veins with the midvein of leaves (i.e. in sites preferably occupied by the eriophyoids) and consisted of spermatophores deposited by different males (Oldfield et al. 1970; Michalska 1997; Michalska unpubl.)

Observations on interspecific attraction of spermatophores (Oldfield 1988) have revealed that females of *A. fockeui* and *A. schlechtendali* put on each other's hosts, readily accomplished self-insemination from spermatophores of congeneric males. By contrast, females of *E. pyri*, *P. oleivora*, *A. fockeui* and *A. schlechtendali* did not visit spermatophores deposited by males of the different genera. Interestingly, *E. pyri* (whose host plant, similar to *A. fockeui* and *A. schelchtendali*, belongs to Rosaceae) showed some interest in spermatophores of the *Aculus* species.

Spermatophore deposition rate and strategic ejaculation

Exempt from costly mating behaviours, males of sex-dissociated species need to produce numerous spermatophores to increase their presence for random, 'independent' females (Thomas and Zeh 1984; Proctor 1998). Indeed, in many sex-dissociated arthropods the rate of spermatophore deposition can be high (Proctor 1998). The extreme examples are water mites, in which hundreds of spermatophores per day can be produced. In eriophyoids, such as in other terrestrial prostigmatic mites, the spermatophore production is much lower. In isolation, *A. fockeui* males deposited on average 30 spermatophores per day, males of *P. oleivora* deposited 16 spermatophores per day (Oldfield et al. 1970) while *A. sheldoni* (Sternlicht and Goldenberg 1971) and *A. allotrichus* (Michalska, unpubl.) deposited only a few spermatophores per day.

Several factors can influence spermatophore deposition by eriophyoids. In *A. fockeui,* the rate of spermatophore placement depended on male age (Oldfield and Newell 1973) and time of the day (Michalska 2005).

In *C. hendersoni*, the host plant and its quality influenced the output of spermatophores. Males deposited much less spermatophores on an older, more lignified yucca leaf than on a young one (Michalska and Shi 2004). Similar inhibition of spermatophore deposition rate has been observed in males placed on young but mechanically injured leaves. Interestingly, on the leaves previously injured by conspecifics the rate of spermatophore deposition increased in comparison with the uninjured and mature (1–3 apical) leaves. This phenomenon may be a result of greater availability of nutrients in injured leaves due to communal feeding of eriophyoids. Moreover, one cannot exclude that the mite injury and/ or substances left by conspecifics on the leaf surface are cues signaling the availability of potential mates, thereby stimulating males to deposit spermatophores (Michalska and Shi 2004).

Sperm competition takes place when two or more ejaculates of different males compete over the fertilization of a given set of eggs. It is regarded as a major selective force that shapes both the ejaculate expenditures across species as well as the strategic ejaculation within species (Parker 1998; Wedell et al. 2002). Pairing males are known to strategically conserve sperm or invest in it depending on the availability of females, their mating status, quality, as well as the presence of rivals. Similarly, in sex dissociated species, e. g. some water mites, males increase or decrease spermatophore deposition rate in the presence of rival males and/or spermatophores, or increase it when they are accompanied by females. In others, however, conspecifics did not affect spermatophore deposition (Witte 1991; Proctor 1992).

Stimulation of spermatophore placement by eriophyoid males in the presence of females was observed in *C. hendersoni* (Michalska and Shi 2004). On the yucca leaves previously injured by eriophyoids, a male accompanied by six virgins deposited significantly more spermatophores than a male kept alone. However, on uninjured and mature leaves (on which, as was mentioned above, males of this species are generally reluctant to deposit spermatophores) such a stimulatory effect of virgins was not observed.

In the tests made so far on the effect of rival males on eriophyoid spermatophore deposition, no response or impediment of spermatophore placement in the presence of competitors was noted. *C. hendersoni* males, randomly chosen from a population and put on injured, mite-free yucca leaves did not change the deposition rate either in the presence of other males or their spermatophores (Michalska and Shi 2004). Random males of *A. fockeui* that were grouped on fresh, uninjured peach leaves behaved similarly (Michalska 2005). However, young males of this eriophyoid, tested in similar conditions, clearly diminished the deposition rate in the presence of rivals (Michalska 2000).

Several factors can be responsible for such interspecific differences in male behaviour. As predicted and confirmed by tests in several pairing species, ejaculate expenditures can depend on the species-specific level of sperm competition, male information about the actual level of sperm competition or alternative mating tactics (Parker 1998; Wedell et al. 2002). In eriophyoid mites, however, male decision about spermatophore deposition on a particular patch may also rely on the probability that any receptive female will seek spermatophores within that patch. On uninjured leaves (such as in the test with *A. fockeui*), with numerous rivals but without females and without cues left by conspecifics that could indicate the presence of receptive "mates", male chances for female fertilization could be especially low, which might force eriophyoids to conserve sperm (Michalska 2000). The differences in response between populations of mixed-age males and vigorous young males

of *A. fockeui* may be connected with the more intensive sperm competition occurring in the latter (Michalska 2005). To clarify this point, however, more studies on the strategic ejaculation of eriophyoid mites including experiments with varying number of rivals and the presence of receptive females are needed.

Male attendance of pre-emergent females and avoidance of external sperm competition

In many insect and mites, males search for females at their emergence sites in order to be the first to mate with them (Walter and Proctor 1999; Thornhill and Alcock 1983). A similar phenomenon has been observed in the eriophyoid mites *A. fockeui* (Putman 1939; Michalska and Boczek 1991), *A. allotrichus*, *A. essigi* (Michalska and Boczek 1991; Michalska and Mańkowski 2006), *A. hystrix* (Skoracka unpubl.), and *Cecidophyopsis ribis* (Westwood) (Fenton unpubl.) (after Michalska and Mańkowski 2006). Among them, only *A. allotrichus* and *A. hystrix* males exhibited solitary or joint guarding of quiescent female nymphs (QFNs). *Aculops allotrichus* males attended QFNs for many hours until female emergence, encircling them with spermatophores (Michalska 1999). By contrast, in non-guarding *A. fockeui* and *A. essigi*, male visits of pre-emergent females were usually short and only rarely males deposited spermatophores next to a QFN (Oldfield and Michalska 1996; Michalska and Mańkowski 2006).

Interest of eriophyoid males in QFNs seems to be connected with a single or at most few inseminations in a female's life (Michalska and Mańkowski 2006). In *A. fockeui,* both young and old virgins pick up sperm from only a single spermatophore (Oldfield and Newell 1973) and always store it asymmetrically in just one of the paired spermathecae (Oldfield 1973). Volumetric comparisons of a sperm-filled spermatheca and a sperm drop of spermatophores of *A. fockeui* and several other eriophyoids from dicots revealed a possible close relationship between the asymmetrical sperm storage and single insemination in these mites (Oldfield 1973).

Interestingly, most species currently known to store sperm asymmetrically originate from dicots, with only one exception of *A. hystrix* from a monocot (Oldfield 1999). It implies the predominance of male attendance of pre-emergent females on dicotyledonous plants. By contrast, symmetrical sperm storage (in both spermathecae) and multiple inseminations by females appears to be a rule for phytoptids inhabiting all gymnosperm, monocots and dicots as well as eriophyids from monocots (Oldfield 1999). This relationship supports recent observations on multiple visits to spermatophores and symmetrical sperm storage in *C. hendersoni* from yucca, which belongs to monocots (Michalska and Mańkowski 2006).

The asymmetrical sperm storage was also confirmed in guarding *A. allotrichus* and *A. hystrix* (Oldfield 1999*)*. As shown by Michalska and Mańkowski (2006), a majority of *A. allotrichus* females visited just one spermatophore in their lives. Nonetheless, some females mounted two spermatophores suggesting 'incomplete' monoandry in this species. As the presence of sperm in spermathecae was not examined in this study, further investigations are needed to determine whether *A. allotrichus* females replenish sperm supplies in the sperm sac during the second visit or require a second spermatophore due to unsuccessful insemination from the first spermatophore mounted.

As shown by the observations on *A. allotrichus* (Michalska 1999) eriophyoid guarding has some special features that make it very different from that of species in which males and females copulate. Firstly, sperm release is shifted to the period of female quiescence, which enables eriophyoid males to monopolize females before their emergence. It may explain why in the absence of rivals, some guarding males of *A. allotrichus* left QFNs prior

to their moult, a pattern rarely observed in species that exhibit male–female copulation (Michalska 1999). Secondly, eriophyoid females remain independent of males in picking up sperm from spermatophores deposited nearby. Perhaps, as a consequence, *A. allotrichus* males did not occupy any special resting position (e.g. on the top of a pre-emergent female as the males that copulate with females, as seen in *Tetranychus urticae* Koch), which could facilitate quick insemination of the mate (Michalska 1999). However, they spent 30–50% of the resting time tightly clinging to QFNs, which could reduce rival access to the QFN and spermatophore deposition nearby.

There is a common agreement that in insects, precopulatory guarding is an adaptation to securing a partner for mating rather than to reducing sperm competition after mating (Parker 1970; Simmons 2001). Similarly in non-guarding eriophyoids, deposition of a single spermatophore close to a QFN only increases the chances for its encounter with the emerging female. However, if males defend the nymph and its vicinity they could also avoid external sperm competition. In such a way, defense of spermatophore fields reduces spermatophore competition in some sex-dissociated arthropods (Proctor 1998).

In *A. allotrichus*, the fierce fighting between solitary guarders and intruders can be seen rarely, mostly at low densities (Michalska 1997). At high densities, it often happens that the guarders do not respond to intrusions, remain motionless or only move closer the QFN body. As a result, males frequently guard QFNs jointly, i.e. up to several males around a single nymph (Michalska and Boczek 1991; Michalska 1997). The avoidance of agonistic interactions at male crowding and joint guarding was reported by Potter (1981) for the spider mite, *T. urticae*. There are also numerous examples of other invertebrates as well as vertebrates in which at high densities of populations, males become less aggressive or non-territorial (rev. Potter 1981, see also Suhonen et al. 2008). According to Potter (1981), at high densities, the avoidance of aggressive interactions could be evolutionary advantageous for guarding males. Under such conditions, the intensity of rival invasions is increased as well as the probability that a guarder will be defeated. Moreover, if the guarder engages in fighting with an intruder he also risks that at the same time a female (or a preferable position on or close to her) would be 'taken over' by another intruding male.

In *A. allotrichus*, the activity of joint-guarders is quite different from that of males guarding solitarily. Isolated from the harassment of intruders single males alternately rested, deposited spermatophores, explored the close vicinity of QFNs or fed (Michalska 1999). They did not alter their activity as females approached moulting. On the contrary, males in a group of five spent most of their time being motionless and clumped close to the QFNs (Michalska 1997). The situation changed, however, a few hours before female emergence. During that time, co-guarders intensively explored the vicinity and often engaged themselves in pushing and wrestling with each other. Although the vicinity around QFNs was not blocked, yet spermatophore deposition appeared to be reduced due to more or less aggressive interactions between males (Michalska 1997).

Crushing spermatophores of rivals, breaking them, trampling to the ground or eating them is the method of reducing sperm competition characteristic for non-pairing males of other arthropods (Proctor 1998; Stam et al. 2002). In eriophyoid mites, however, such destructive behaviour has never been noted (Michalska unpubl.).

According to Witte and Döring (1999) destructive behaviour is less expected to occur in species with males that are unable to recognize rival spermatophores and to prevail in species that do not return to places where they previously deposited spermatophores. Also in eriophyoids, destructive behavior might have not evolved because for some reasons these mites are unable to distinguish between spermatophores. One cannot exclude however, other traits of eriophyoids, such as high density of population and relatively low

spermatophore production (see the section, *Spermatophore deposition rate and strategic ejaculation*) acting against destructive behaviour as well. In species exhibiting destructive behaviour the greater the density of competitor males is the higher should be the risk that the spermatophore will be found by a rival and destroyed. In a hypothetical, extreme situation, all male's spermatophores could be destroyed before females have a chance to pick up sperm from them. The losses from such destructive behaviour, may be greater at low spermatophore production (at the same rate of spermatophore destruction by rivals a male depositing more spermatophores would have the smaller portion of its spermatophores destroyed at any given time than a male with the lower deposition rate). Thus, at the specific level of population density and spermatophore production, even in species in which males perfectly distinguish between their own and rival spermatophores, destructive behaviour may not be beneficial and selected against.

Eriophyoid mating systems

The concept of mating systems refers to how males and females of a population can gain access to mates, how many mates they have, how long their bonds last, whether parental care is provided, and if so, by which sex (Shuster and Wade 2003; Danchin et al. 2008). In the sex dissociated arthropods, males and females can interact indirectly, via spermatophores, which can make their mating systems much more complex than in species where males and females pair to mate. For example, Proctor (1998) pointed out that analogous to lekking males that congregate in small arenas and are visited by females for copulation, aggregations of spermatophores can function as leks in sexually dissociated species. Similarly, in eriophyoids, placement of spermatophores into groups with spermatophores of other males (see the section *Attraction to spermatophores*) can be regarded as lek-like behaviour.

Considering that eriophyoid males produce numerous spermatophores while females pick up sperm from either single (or, in some species at the most two spermatophores) or several spermatophores in their life time (see the section *Male attendance of pre-emergent females and avoidance of external sperm competition*) two preliminary categories of eriophyoid mating systems could be taken into account: (1) the polygynous mating system (males mate many times and females only once in their lifetime) with female attendance polygyny (males attend individual females, abandon them shortly after mating and continue seeking mates) in one case, and (2) the polygamous mating system (both males and females mate many times) in the alternate case (see Shuster and Wade 2003). Spatiotemporal availability of females, male–male competition and external sperm competition may determine to what degree eriophyoid males will attend pre-emergent females, whether they will deposit spermatophores beside them or form 'leks' of spermatophores. Several species-specific traits can be crucial in respect to this, e.g. the number of self-inseminations by females, sex ratios (Michalska 1999; Michalska and Mańkowski 2006), population density, longevity of sperm in spermatophores, number of spermatophores produced in a male lifetime, and so forth.

Future directions

As shown above, some important issues concerning sexual behaviour of eriophyoid mites still remain to be elucidated, or studies on them are very preliminary. These concern especially, communication between sexes, female choice, external spermatophore competition and eriophyoid mating systems.

Knowledge of sex pheromones may have great practical importance for the control of eriophyoid pests in agricultural crops. Behaviour of *A. fockeui* females towards sperma-tophores, stimulation of spermatophore deposition by *C. hendersoni* virgins and male interest in quiescent female nymphs observed in several species strongly suggest the presence of sex attractants in both eriophyoid spermatophores and in females or quiescent female nymphs. However, only the isolation of such chemicals and their experimental bioassay will confirm sex attractants unambiguously. It would be necessary to determine whether the placement of spermatophores in groups indeed increases their attraction to females; what is the 'calling' distance of eriophyoid attractants; and what other factors may help eriophyoids to find spermatophores (e.g. electrostatic forces) or distinguish the sex of the individual (e.g. differences in size between males and females)?

Female choice by non-pairing females was uncertain (Proctor 1998) until the study by Gols et al. (2004) on the springtail, *Orchesella cincta* (L.). In the experiment, females were given a choice between spermatophores deposited by two different males. Paternity analysis based on the variation in a microsatellite locus showed that females were selective and picked up sperm from spermatophores of one male only. Previous observations by Hedlund et al. (1990) revealed that the smell of a spermatophore may play a role in *O. cincta* female choice. Do eriophyoid females choose similarly, on the basis of sper-matophore odour, or, other spermatophore traits such as contact chemicals, size of a spermatophore and the size of the sperm drop contained in it? In non-choice tests (Oldfield 1988) females picked up sperm from spermatophores of congeneric males of each other's host while they did not visit spermatophores produced by males of different genera. It suggests that eriophyoids are not able to distinguish between spermatophores of their own and closely related species. To verify this hypothesis, pair choice tests performed on the host plant of a female are needed, as well as experiments explaining how relatedness of a host plant of a male to the host plant of the female may interfere in the 'proper' choice of a spermatophore. Such knowledge could be very useful for better understanding of specia-tion mechanisms in this group of mites.

Sperm competition is one of the fundamental components of sexual selection that for years has been intensively investigated both theoretically and empirically (Danchin et al. 2008). Proctor (1998) pointed out that similar to sperm of external inseminators, the sperm contained in spermatophores of sex dissociated arthropods may compete outside the female's reproductive track. In spite of many reports that support this hypothesis, external spermatophore competition was not investigated in detail. As for eriophyoid mites, we already know that species can differ significantly in spermatophore deposition rates and there is flexibility of spermatophore deposition in the presence of rival males and females. Moreover, there are marked differences among eriophyoids in the degree of female attendance by males. It makes them very suitable objects for comparative studies on external sperm competition and spermatophore expenditures both within and across species.

There are still too few behavioural observations to allow a thorough classification of mating systems of eriophyoid mites. In the future, emphasis should be given to the number of matings by females and males, distribution of females and spermatophores as well as the interactions between and within sexes.

The observations on sperm storage and the number of self-inseminations by females (Oldfield 1999) imply the prevalence of eriophyoid polygyny on dicotyledonous host plants and polygamy on monocots and gymnosperms. It also suggests an impact of a host plant on the evolution of eriophyoid mating systems. In gymnosperms and some angio-sperms, including monocotyledonous Poaceae, a gregarious life habit appears to be one of

the plant adaptations to wind pollination (Culley et al. 2002). Such gregarious life habit of a host plant seems to have a beneficial effect on the aerial dispersal of eriophyids especially for those species with multiple insemination. As was observed in *C. hendersoni* (Michalska unpublished), polyandrous females visit many spermatophores in their lifetime and have to replenish sperm supplies virtually every day. It means that sooner or later after landing on a new plant such females would be faced with the necessity of finding a spermatophore. However, the more scattered a host there are less chances for females not only to find a host plant but also a host plant with spermatophores on it. Thus, if a host plant is scattered, such as in case of many dicotyledonous plants, it could be more advantageous for erio-phyoid females to pick up sperm just once in their lifetime and before migration to a new plant. Obviously, such a strategy also entails the cost of picking up sperm of a bad quality male for the entire female's life. As a consequence, on a gregarious host plant a female performing single insemination could achieve a much lower reproductive success than the polyandrous one and may be selected against. As is shown in the example of *A. hystrix* from grasses (Oldfield 1973), however, the secondary invasion of a gregarious plant species by an eriophyid in which females accomplish single insemination cannot be excluded. Therefore, to elucidate the possible role of a host plant in the evolution of eriophyoid mating systems more data on mating systems and phylogeny of eriophyoids as well as the ecology of a host plant needs to be collected.

Defence against predators

Many predaceous insects (dipterans, coleopterans, neuropterans, hemipterans, thysanopterans) and mites (Phytoseiidae, Stigmaeidae, Cheyletidae, Cunaxidae, Tarsonemidae, Tydeidae) have been reported to feed on eriophyoid mites (Perring and Mcmurtry 1996). Among them, phytoseiid and stigmaeid mites are considered the most important enemies of eriophyoids (Sabelis 1996; Thistlewood et al. 1996). In contrast to stigmaeids, phytoseiids are much larger and faster predators and are able to detect eriophyoid mites from a long distance via volatiles emitted by infested plants (Dicke 1988; Dicke et al. 1988; Aratchige et al. 2004). For many of them, however, eriophyoids are an alternative food only (Sabelis 1996; Sabelis and van Rijn 1996) while stigmaeids, in the vast majority, preferably prey upon these mites (Thistlewood et al. 1996). Moreover, being smaller, stigmaeids can more effectively seek eriophyoids within short distances and penetrate their hiding places that may be inaccessible for phytoseiids.

Prey organisms exhibit a variety of morphological, physiological, life-historical and behavioural adaptations that enable them to reduce the chances of being eaten (Sih 1987). Eriophyoid mites are much smaller and slower than insect and mite predators which significantly constrain their fleeing or physical defense upon attack (Sabelis and Bruin 1996). The probable consequence of this is the common use of refuges by these tiny mites. These refuges not only serve as a shelter against predators but can also play an important role in the protection of eriophyoids against adverse abiotic conditions. Refuge-forming eriophyoids induce the growth of galls out of plant tissue or spin web strands on a plant surface and live socially under webbing (Sabelis and Bruin 1996; Sabelis 1996; see also the section on "Social Behaviour"). Others inhabit very narrow spaces, e. g. acarodomatia of leaves or spaces under scales pressed against leaf petioles, sheaths, buds, fruits or bulbs (Sabelis and Bruin 1996; O'Down and Willson 1997; Kasai et al. 2002; Leśna et al. 2004; Romero and Benson 2005; Aratchige et al. 2007; Lawson-Balagbo et al. 2007). Others occupy habitats that are adverse for natural enemies such as *A. lycopersici* on the tomato

leaves covered by sticky and toxic trichomes (Sabelis 1996; Koller et al. 2007), or *Leipothrix darlingtoniae* Fashing hiding inside the pitchers of the insectivorous plant, cobra lily *Darlingtonia californica* Torr. (Fashing 1994; Fashing NJ, personal communication).

Many observations confirm that refuges of eriophyoid mites are not perfect hiding places from predatory mites. Phytoseiids can creep inside the pouch galls at the time of eriophyoid dispersal, when the galls are drying up and their entrances are opening. Also erinea, felt-like galls, are frequently visited by predatory mites (Sabelis 1996) as well as the 'narrow spaces' used by refuge seekers (Leśna et al. 2004; Aratchige et al. 2007; Lawson-Balagbo et al. 2007). *Aceria guerreronis* lives under the perianth of the coconut fruit. The eriophyoid invades the very young, 1–3 month old fruit when the perianth-fruit gap is too tight for predatory mites. Due to mite damage, however, the gap increases in size and within a month can be entered by phytoseiids (Aratchige et al. 2007; Lawson-Balagbo et al. 2007). It is very likely that such a 'gate opening' for predators is not only a by-product of the damage of plant tissue but may also be an induced plant defense against eriophyoids (Aratchige et al. 2007). This hypothesis is supported by the observations on *Aceria tulipae* (Keifer) inhabiting the inside of the tulip bulbs. First, the bulbs infested by eriophyoids produce volatiles that attract phytoseiids to them (Aratchige et al. 2004). Second bulb damage triggers the production of ethylene, which causes the widening of the space between scales at the apex of the bulb to such an extent that it becomes penetrable for predatory mites (Leśna et al. 2004).

Vagrants are generally much more vulnerable to predation than the refuge-forming or refuge-seeking eriophyoids. Although they can balance the higher risk of predation by better opportunities to produce offspring on the unconfined and usually, more nutritious plant parts (Sabelis and Bruin 1996) they have also developed various adaptations that can serve as anti-predatory defenses. Hiding in shafts of leaf trichomes by the quiescent stages of *Rhinophytoptus concinnus* Liro, and *Macrotuberculatus bagdasariani* (Shevtchenko and Pogosova) on elm (Michalska 2003) and *Aculus comatus* (Nalepa) on filbert (Krantz 1973) are good examples of this behavioural adaptation. The playback experiment with hungry females of the phytoseiid mite *Typhloctonus tiliarum* (Qud.) [synonym: *Neoseiulella tiliarum* (Quademans) (Chant and McMurtry 2007)] and the quiescent nymphs *R. concinnus* proved that by 'perching' on the tips of leaf hairs, the vagrants can avoid phytoseiid attack (Michalska 2003). The predatory females needed much more time to find and consume the nymphs on leaf hairs than the nymphs placed on a leaf blade. The hiding of quiescent stages can be advantageous for eriophyoid mites mainly for two reasons. First, being motionless the mites are unable to escape from predators. Second, by restricting the use of the refuges to only the quiescent period, the vagrant mites have not resigned from or limited their feeding and reproductive activities (Michalska, 2003). Apparently, hiding on leaf trichomes is not solely an eriophyoid 'invention'. In the tetranychid mite, *Yezonychus sapporensis* Ehara on the dwarf bamboo, quiescent juveniles rest and females lay eggs on tips of hairs (Saito 1985). An experiment with eight species of phytoseiid mites confirmed that the egg-lying behaviour of *Y. sapporensis* has a function of avoiding predation (Yanagida et al. 2001). Interestingly, for another mite, *Tetranychus kanzawai* Kishida constructing a web over the leaf, it has been proven that juveniles enter the quiescent stage on a leaf or hide in the web according to the actual presence or absence of predatory mites (Oku et al. 2003).

Climbing up a trichome by *R. conncinnus* resulted from a fixed chain of behaviours including: (1) the attachment of the anal sucker to the tip of a hair, (2) pushing back from a leaf or the basal part of a trichome and finally, (3) lifting the body up to become motionless (Fig. 3a). This quite bizarre mode of climbing was preceded by the equally curious
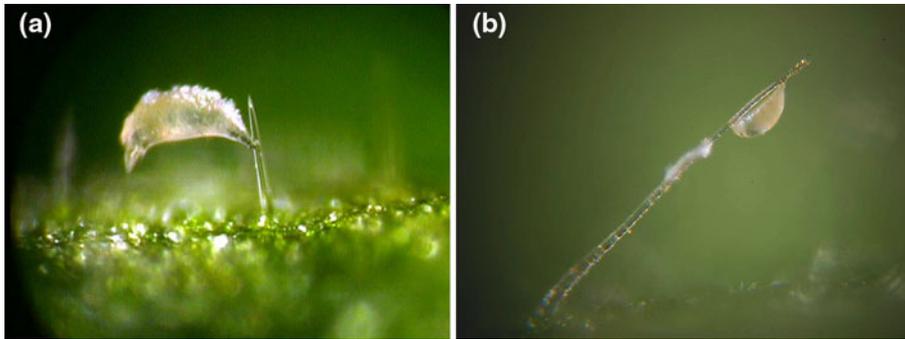
Fig. 3 Quiescent nymphs secured to tips of leaf trichomes: on **a** *Rhinophytoptus concinnus* Liro on elm and **b** *Aculus comatus* (Nalepa) on filbert (on a trichome, beneath a nymph can be seen the shed exuvium of the previous eriophyid that spent quiescent period and molted on the trichome)

searching behaviour of eriophyoids in a "hand stand" position. The pre-quiescent mites raised the caudal end of their bodies (becoming stiffened prior to the eriophyoid quiescence) and circled in both directions around the leaf blade until they found a suitable hair and attached to it with their anal sucker (Michalska 2003). By contrast, the juveniles of *A. comatus* went straight up the hair, made a turn on its tip and became motionless attached upside down along the longer axis of the trichome (Fig. 3b) (Krantz 1973; Michalska unpubl.).

These behavioural observations as well as the survey of resting sites of quiescent stages on leaves strongly suggest that hiding upon trichomes by all of the above mentioned eriophyoid species is fixed, i.e. takes place independently of the actual presence of predators (Krantz 1973; Michalska 2003; Michalska unpubl.). It is worth noting that both elm and filbert leaves are rich in domatia, plant structures frequently used by phytoseiids as shelters (Walter 1996; Kreiter et al. 2002; Romero and Benson 2005). The presence of domatia generally favours the occurrence of phytoseiids on leaves. Thus, the threat of predation on elms and filbert should be relatively high and constant which might be an important selective force in the evolution of eriophyoid climbing behaviour and its fixation. Curiously enough, on elms, another leaf vagrant, *R. ulmivagrans* lays eggs and spends the quiescent period exclusively inside domatia (Michalska 2003). As a rule, on leaves inhabited by this mite, the domatia are full of resting stages. It is likely that the eriophyoids inside domatia are preyed upon by phytoseiids. However, the dead bodies of the companions situated close to the entrance of a domatium may hinder predation on individuals lying deeper inside. For comparison, an eriophyoid (unidentified species) inhabiting the domatia of the tropical tree *Cupania vernalis* Cambess, clogs the entrances of domatia with the "tufts" made of the shed exuvia and a sort of silky material (Romero and Benson 2005). Whether such behaviours of eriophyoid mites could favour their avoidance of predation should be further investigated.

It must be stressed that as in many other communal animals, the tendency of eriophyoid vagrants to aggregate on leaves can be beneficial for them not only to enhance reproduction (see the section "Sexual Behaviour") or resource exploitation but also to enhance escape from predators (e.g. Danchin et al. 2008). In aggregations, an individual can be protected through (1) dilution effect (companions that are alternative prey), (2) selfish herd effect (an individual can hide behind companions), and (3) confusion effect (predators cannot concentrate on a single prey when other prey are moving).

In eriophyoid vagrants, one cannot exclude physiological adaptations against predators, such as prey toxicity or unpalatability (Sabelis 1996). Waxy or liquid coatings produced by some eriophyoids (Manson and Gerson 1996) may protect them against desiccation only, or they also make them less detectable or distasteful for predators; this question remains to be resolved and can be a subject for future research. And finally, do eriophyoids accumulate toxins from their host plants? The phytoseiid *Amblyseius victoriensis* (Womersley) [synonym: *Euseius victoriensis* (Womersley) (Chant and McMurtry 2007)] drastically diminished the rate of prey attacks when fed on the eriophyoid mite *A. lycopersici* from tomato in the comparison with other eriophyoid species (James 1989). Although its contact with toxic glandular trichomes of tomato leaves could negatively affect the hunting efficacy of this predator and also be responsible for its high mortality during the experiment (Sabelis 1996), the distastefulness and toxicity of *A. lycopersici* as a prey cannot be excluded. The accumulation of toxic plant compounds was recently found in another herbivorous mite from tomato, *Tetranychus evansi* Baker and Pritchard. The consumption of this herbivore by the phytoseiid *Neoseiulus californicus* (McGregor) negatively affected the developmental time and oviposition rate of the predator, to the similar extent as the adverse effect of the tomato plants. Interestingly, neither the plant nor the prey had any impact causing an increase in the mortality of this phytoseiid (Koller et al. 2007).

Future directions

The data are still lacking on the flexibility of antipredatory behaviour in eriophyoid mites. It is urgently needed to examine whether these mites, perhaps similar to tetranychids (Grostal and Dicke 2000) could assess the risk of predation using direct (dead bodies of companions) or indirect cues (faeces of predators fed on eriophyoids or other herbivores). Do the eriophyoids make a decision about refuge use or dispersal in relation to the presence of predators or their cues? How does the threat of predation affect the eriophyoid activities such as feeding or reproduction?

The observations on the genus *Stigmaeopsis* Banks (Mori and Saito 2004), living socially under a web have revealed that tetranychid mites can effectively defend the nest against the youngest stages of predatory mites through counterattack. Moreover, the more individuals per nest the better effect of 'nest defense' in this spider mite genus. Undoubtedly, solitary eriophyoids would lose in the confrontation with the much bigger and faster predatory mites. However, are eriophyoids equally defenseless in social groups? Social web-nests of *Aceria inusitata* Britto and Navia, for example, can contain more than one hundred individuals (Britto et al. 2008, see also the section on "Social Behaviour"). Could this eriophyoid adopt an anti-intruder strategy such as mass counterattack?

Social behaviour

Social organization among invertebrates is classified, according to its complexity, into eusociality or presociality (Wilson 1971). Eusocial organisms exhibit: division of labour, possibly with some sterile castes; overlapping of generations, such that different generations live in the same colony; and cooperation of individuals to care for immature forms. Presocial organisms can display some of these behaviours, but they do not display all three essential traits of eusociality. Presocial organisms can be further categorized into "sub-social", in which parents interact with immature forms, and "parasocial", in which

individuals of the same generation live in a cooperative system. Mites, for all presently known examples of social behaviour, can be classified as subsocial (Saito 1997).

Among phytophagous mites sociality has been reported and detailed for the woven nest-building mites of the genus *Stigmaeopsis*. These mites build dense oval woven roofs (web-nests) over depressions on the lower surfaces of host leaves and have been considered as subsocial or communal species (Saito 1995; Mori and Saito 2006). *Stigmaeopsis celarius* Banks exhibits biparental care, in a way that adult males and females can defend their nest and offspring from phytoseiid predators (Saito 1986). *Stigmaeopsis longus* (Saito) females share reproduction and labour evenly with their nest mates (Mori and Saito 2006). It has also been observed in *Stigmaeopsis miscanthi* (Saito) that members cooperate in nest building and sanitation activities (Sato et al. 2003). Saito (1997) listed six main factors affecting social organization in Acari: (1) male-haploidy and thelytoky, (2) low mobility, with 1 and 2 both favouring high relatedness; (3) continuous iteroparity and rapid development, allowing generation overlapping; (4) aggregation, increasing probability of sib interactions; (5) prevention of predation and nest building, requiring cooperative labour; (6) spatiotemporally stable environment, that can allow a longer lifetime, aggregation and also generation overlap. One of the ecological prerequisites of social organization of mites is a stable habitat with sufficient resources to enable mites to overlap generations. It is enhanced in some groups, such as spider mite species, under stable environmental conditions that allow them to survive longer in a given place (Saito 1986, 1997). The degree of aggregation is also important for social organization. Nest formation by webs probably evolved as a refuge from predators and shelter from adverse climatic conditions in a stable habitat, and it has simultaneously enhanced aggregation of individuals in a narrow space. Moreover, the period of time that a nest remains functional may be related to the number of individuals living on it and the amount of enclosed resources. Another factor that appears to be responsible for the extent of mite social evolution is the existence of labour that can be shared among individuals. In spider mites there is little labour that can be engaged in by different individuals, so there appears to be little opportunity for selection for division of labour in this group (Saito 1997).

Considerations concerning evolution of sociality in spider mites certainly could be extended to other phytophagous mites, such as eriophyoids. Regarding the conditions or factors affecting social behaviour presented by Saito (1997), it may be possible to show that some eriophyoid species exhibit or develop under conditions that promote sociality. The possibility of sociality in eriophyoid mites was first mentioned by Saito (1997) who suggested that the highly communal way of life of some species, especially gall eriophyoids, combined with male haploidy should have led to social interactions between individuals, if there were a possibility for selection for division of labour. However, so far, no behavioural studies have been conducted on eriophyoid social behaviour.

Searching for the occurrence of social behaviour in eriophyoids should be undertaken, especially considering that communal aggregation is an important factor. Signs of social behaviour should first be investigated in web spinning eriophyoid mites that build colonies under webs, similar to *Stigmaeopsis* social mites. In this way evidence for social behaviour in eriophyoids can be sought for *A. inusitata*, a deuterogynous species associated with *Caesalpinia echinata* Lam. from Brazil, colonies of which develop under "patches of webbing" (Fig. 4). For the most part, deuterogyny is primarily an evolutionary adaptation of eriophyoid mites for survival on deciduous plants in regions with well-defined winters, thus presenting alternation of life forms to survive different seasons. However, there are some reports of deuterogynous species in tropical areas; so far all examples belong to the genus *Aceria* (Britto et al. 2008). Among studied deuterogynous species occurring in
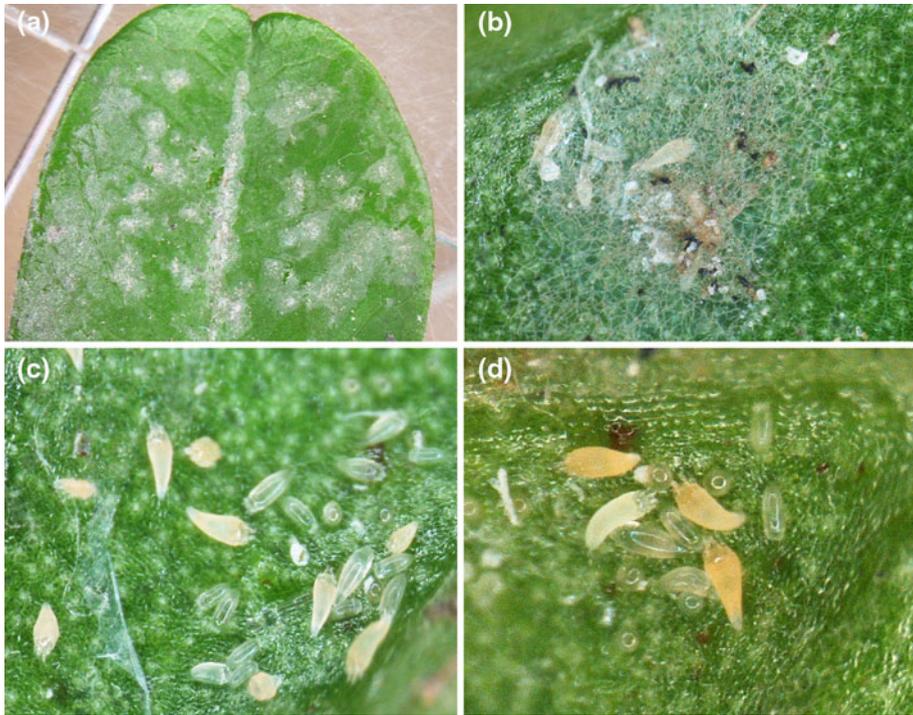
Fig. 4 Colonies of the deuterogynous web spinning eriophyoid mite, *Aceria inusitata* Britto and Navia, on *Caesalpinia echinata* leaves; **a** general aspect of "patches of webbing" on the upper leaf surface; **b** small colony isolated under a "nest-web"; **c** group of individuals after web removal; **d** coexisting protogynes and deutogynes (in the photograph, *whitish* and *yellowish* individuals, respectively) (photos by E. Britto and D. Navia 2007)

tropical areas, *A. inusitata* is a rare case, with a complex life cycle. This species presents two forms of females and two of males coexisting and developing in the same colony and in the same "nest" (Britto et al. 2008). Biological observations on *A. inusitata* suggested that more than one generation cohabit in the same "nest". Only deutogynes built the "nests" and afterwards the protogynes appeared in the colony. Large colonies, reaching 3.2 mm², can harbour more than 150 individuals. When the nests were removed, 100% mortality of protogynes and 25% of deutogynes was observed, and the surviving deutogynes rebuilt the "nest". This suggests that deutogynes are the dispersal form of the species and the "nest" makers; this conclusion is supported by the absence of glandular structures in the protogyne opisthosoma. Biological observations on *A. inusitata* indicate that the species presents overlapping generations and a division of labour. Thus it could be classified as a "parasocial" species. Behavioural studies should be conduced to better understand sociality in this species.

Future directions

Social behaviour of eriophyoid mites is an unexploited field that may be useful to better understand their phylogeny and evolution. Genetic, biological and ecological

characteristics of some groups of eriophyoid mites are extremely favourable for the development of sociality, and include male-haploidy, low mobility, iteroparity, gregarious life style, overlap of generations and development under a stable environment. Evidence of social behaviour in the deuterogynous web spinning species *A. inusitata* should be studied in greater detail. In the same way, sociality among other gregarious species, especially gall or erinea-making species, should be investigated.

Other perspectives for behavioural studies on eriophyoid mites

In addition to the needs and directions indicated in the sections above, there are several important behavioural issues that still need investigation in eriophyoid mites. Parental care, a fundamental issue in behavioural ecology which is indispensable for the recognition of mating systems and social behaviour, is an almost untouched topic. Caring for offspring is the rule for refuge-forming eriophyoids. A fertile female inducing gall growth or building a nest provides a shelter not only for herself but also for her progeny. Do vagrant species care for their progeny? Does the laying of eggs in communal batches by *C. hendersoni* (Michalska and Shi 2004) or concealing eggs in domatia by *R. ulmivagrans* (Michalska 2003) represent a form of parental care? If so, how common are such behaviours among the free-living species? Also, it may be worthwhile to inquire into how the evolution of these behaviours was influenced by the respective host plants and the presence of some specific plant structures (e.g. domatia, leaf trichomes).

Internal mechanisms responsible for how eriophyoid behaviour is elicited and coordinated still await recognition and investigation. It should include studies on (1) sensory and central nervous systems as well as neural processes expressing different behaviours of eriophyoids; (2) chemicals which control processes such as moulting, mating, aggregating and dispersal; (3) genetic basis of eriophyoid behavior. Only the knowledge on the internal mechanisms enables us to fully understand the effect of external factors on the behaviour and its evolution (Alcock 2001).

References

Alcock J (2001) Animal behavior. An evolutionary approach, 7th edn. Sinauer Associates, Sunderland, Massachusetts, p 543

Alexander RD (1964) The evolution of mating behaviour in arthropods. Symp Royal Entomol Soc Lond 2:78–94

Aratchige NS, Leśna I, Sabelis MW (2004) Below-ground plant parts emit herbivore-induced volatiles: olfactory responses of a predatory mite to tulip bulbs infested by rust mite. Exp Appl Acarol 43:97–107

Aratchige NS, Sabelis MW, Leśna I (2007) Plant structural changes due to herbivory: do changes in *Aceria*-infested coconut fruits allow predatory mites to move under the perianth? Exp Appl Acarol 43:97–107

Barke HE, Davis R, Hunter PE (1972) Studies on peach silvermite, *Aculus cornutus* (Acarina:Eriophyoidea). J Georgia Ent Soc 7:171–178

Batchelor GS (1952) The eriophyoid mites of the state of Washington. Wash Agr Exp Sta Tech Bull 6:1–32

Behrens E (1964) Zur biologie und okologie der johannisbeergallmilbe *Eriophyes ribis* Nal. Sowie ihrer bekampfung in johannisbeerenaubaugebiet perleberg. Bez Schwerin Wiss Z Univ Rostock, Math-Nat 13:279–288

Bergh JC (1992) Monitoring the emergence and behaviour of pear rust mite (Acarina: Eriophyidae) deutogynes using sticky-band traps. J Econ Entomol 85:1754–1761

Bergh JC (2001) Ecology and aerobiology of dispersing citrus rust mites (Acari: Eriophyidae) in central Florida. Environ Entomol 30:318–326

Bergh JC, Judd GJR (1993) Degree-day model for predicting emergence of pear rust mite (Acari: Eriophyidae) deutogynes from overwintering sites. Environ Entomol 22:1325–1332

Bergh JC, McCoy CW (1997) Aerial dispersal of citrus rust mite (Acari: Eriophyidae) from Florida citrus groves. Environ Entomol 26:256–264

Bergh JC, Smith AH Jr (2001) Ecology and aerobiology of dispersing citrus rust mites (Acari: Eriophyidae) in central Florida. Environ Entomol 30(2):318–326

Bergh JC, Weiss CR (1993) Pear rust mite, *Epitrimerus pyri* (Acari: Eriophyidae) oviposition and nymphal development on *Pyrus* and non-*Pyrus* hosts. Exp Appl Acarol 17:215–224

Bernays EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Chapman & Hall, New York

Brey CW (1998) Epidemiology of wheat curl mite (*Aceria tosichella* K.) and wheat streak mosaic virus on feral grass species and effect of glyphosate on wheat curl mite dispersal. Ph.D. Dissertation, Montana State University, Bozeman, 139pp

Britto EPJ, Gondim MG Jr, Navia D, Flechtmann CHW (2008) A new deuterogynous mite (Acari: Eriophyoidae) with dimorphic males from *Caesalpinia echinata* (Caesalpiniaceae) from Brazil: description and biological observations. Int J Acarol 34(3):307–316

Burgess JE, Thompson MM (1985) Shoot development and bud mite infestation in hazelnut (*Corylus avellana*). Ann Appl Biol 107:397–408

Chakrabarti S, Chakrabarti S (2005) Population dynamics and diurnal activity of *Acalitus hibisci* Mondal and Chakrabarti (Acari: Eriophyoidea). Acarologia 45:183–188

Chant DA, McMurtry JA (2007) Illustrated keys and diagnoses for the genera and subgenera of the Phytoseiidae of the world (Acari: Mesostigmata). Indira Publishing House

Chen H, Xu N, Chen Z (2000) On the relationship between content of free amino acid in tea shoot and resistance of tea tree to tea pink mite *Acaphylla theae* Watt. Acta Phytoph Sin 27:338–342

Courtney SP, Chen GK, Gardner A (1989) A general model for individual host selection. Oikos 55:55–65

Cromroy HL (1983) Potential use of mites in biological control of terrestial and aquatic weeds. In: Hoy MA, Cunningham G, Knutson L (eds) Biological control of pests by mites. Div. Agriculture and natural Resources. University of California, Berkeley, California, USA, pp 61–66

Culley TM, Weller SG, Sakai KA (2002) The evolution of wind pollination in angiosperms. Trends Ecol Evol 17:361–369

Danchin E, Giraldeau LA, Cézilly F (2008) Behavioural ecology. Oxford University Press, Oxford, p 874

Davies JT, Allen GR, Williams MA (2001) Intraplant distribution of *Acalitus essigi* (Acari: Eriophyoidea) on blackberries (*Rubus fruticosus* agg.). Exp Appl Acarol 25:625–639

Davis R (1964) Autoecological studies of *Rhynacus breitlowi* Davis (Acarina: Eriophyoidae). Fla Entomol 47:113–121

Dicke M (1988) Prey preference of the phytoseid mite *Typhlodromus pyri*: 1. Response to volatile kairomone. Exp Appl Acarol 4:1–13

Dicke M, Sabelis MW, de Jong M (1988) Analysis of prey preference in phytoseid mites using an olfactometer, predation models and electrophoresis. Exp Appl Acarol 5:225–241

Duffner K, Schruft G, Guggenheim R (2001) Passive dispersal of the grape rust mite *Calepitrimerus vitis* Nalepa 1905 (Acari: Eriophyoidea) in vineyards. J Pest Sci 74:1–6

Easterbrook MA (1978) The life history and bionomics of *Epitrimerus pyri* (Acarina: Eriophyoidae) on pear. Ann Appl Biol 88:13–22

Easterbrook MA (1979) The life history of the eriophyoid mite *Aculus schlechtendali* on apple in southeast England. Ann Appl Biol 91:287–296

Fashing NJ (1994) A new species of *Leipothrix* (Prostigmata: Eriophyoidae) form the cobra lily, *Darlingtonia californica* (Sarraceniaceae). Int J Acarol 20:99–101

Frost WE (1997) Polyphenic wax production in *Abaracus hystrix* (Acari: Eriophyoidae), and implications for migratory fitness. Physiol Entomol 22:37–46

Gabi G, Mészáros Z (2003) Examination of the development of the deutogynes of *Calepitrimerus vitis* Nalepa in the vine-growing region of Szekszárd, Hungary (Acari: Eriophyoidae). Acta Phytop Entomol Hung 38:369–376

Gibson RW (1974) Studies on the feeding behaviour of the eriophyoid mite *Abacarus hystrix*, a vector of grass viruses. Ann Appl Biol 78:213–217

Gibson WW, Painter RH (1957) Transportation by aphids of the wheat curl mite, *Aceria tulipae* (K.), a vector of the wheat streak mosaic virus. J Kansas Entomol Soc 30:147–153

Gols R, Ernsting G, van Straalen NM (2004) Paternity analysis in a hexapod (*Orchesella cincta*; Collembola) with indirect sperm transfer. J Insect Behav 17:317–328

Grahl A, Leuprecht B (1998) Untersuchungen zur Biologie der Tomatenrostmilbe *Aculus lycopersici* und ihrer biologischen Bekämpfung. Mitt. Dt Phytomed Ges 28:41–42

Griffith R (1984) The problem of the coconut mite, *Eriophyes guerreronis* (Keifer), in the coconut groves of Trinidad and Tobago. In: Webb R, Knausenberger W, Yntema L (eds) Proceedings of the 20th annual meeting of the Caribbean food crops society, St. Croix, U.S. Virgin Islands, Oct 21–26 1984. East. Caribbean Cent., Coll. Virgin Islands & Caribbean Food Crops Soc., pp 128–132

Grostal P, Dicke M (2000) Recognising one's enemies: a functional approach to risk assessment by prey. Behav Ecol Sociobiol 47:258–264

Hanson AJ (1933) The blackberry mite and its control. State College of Washington Agricultural Experiment Station Bulletin, vol 279, 20pp

Harvey TL, Martin TJ (1980) Effects of wheat pubescence on infestations of wheat curl mite and incidence of wheat streak mosaic. J Econ Entomol 73:225–227

Harvey TL, Martin TJ (1988) Sticky tape method to measure cultivar effect on wheat curl mite population in wheat spikes. J Econ Entomol 81:731–734

Harvey TL, Martin TJ, Seifers DL (1990) Wheat curl mite and wheat streak mosaic in moderate trichome density wheat cultivars. Crop Sci 30:534–536

Hedlund K, Ek H, Gunarsson T, Svegborn C (1990) Mate choice and male competition in *Orchesella cincta* (Collembolla). Experientia 46:524–526

Herbert HJ (1979) Population trends and behaviour of the pear rust mite, *Epitrimerus pyri* (Prostigmata: Eriophyoidea), on pears in Nova Scotia. Can Entomol 111:955–957

Jaenike J (1990) Host specialization in phytophagous insects. Annu Rev Ecol Syst 21:237–243

James DG (1989) Influence of diet on the development, survival and oviposition in an Australian phytoseiid, *Amblyseius victoriensis* (Acari: Phytoseiidae). Exp Appl Acarol 6:1–10

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. University of California press, Berkeley, Los Angeles, London, p 528

Julia JF, Mariau D (1979) Nouvelles recherché en Cote d'Ivoire sur *Eriophyes guerreronis* K., acarien ravageur des noix du cocotier. Oleagineux 34:181–189

Kadono F, Fujishiro H, Shiina M, Fujiie A (1982) Seasonal population trends of the Japanese pear rust mite, *Eriophyes chibaensis* Kadono (Acarina: Eriophyoidae) on pear trees in Chiba. Jap J Appl Entomol Zool 26:213–217

Kasai A, Yano S, Takafuji A (2002) Density of the eriophyoid mites inhabiting the domatia of *Cinnamomum camphora* Linn. affects the density of the predatory mite, *Ambyseius sojaensis* Ehara (Acari; Phytoseiidae), not inhabiting the domatia. Appl Entomol Zool 37:617–619

Koller M, Knapp M, Schausberger P (2007) Direct and indirect adverse effects of tomato on the predatory mite *Neoseiulus californicus* feeding on the spider mite *Tetranychus evansi*. Entomol Exp Appl 125:297–305

Kozłowski J (1995) The acceptance of leaves of various apple varieties by the apple rust mite—*Aculus schlechtendali* (Nal.). Rocz Nauk Rol E, Ochr Rośl 24:39–44

Kozłowski J, Boczek J (1987) Density and host plants of the apple rust mite—*Aculus schlechtendali* (Nal.) (Acarina: Eriophyoidea). Pr Nauk Inst Ochr Rośl 29:39–50

Krantz GW (1973) Observation on the morphology and behaviour of the filbert rust mite *Aculus comatus* (Prostigmata: Eriophyoidea) in Oregon. Ann Entomol Soc Am 66:706–717

Kreiter S, Tixter MS, Croft BA, Auger P, Barret D (2002) Plants and leaf characteristics influencing the predaceous mite *Kampimodromus aberrans* (Acari: Phytoseiidae) in habitats surrounding vineyards. Environ Entomol 31:648–660

Lall BS, Rahman MF (1975) Studies on the bionomics and control of the erinose mite *Eriophyes litchi* Keifer (Acarina: Eriophyiidae). Pesticides 9:49–54

Lawson-Balagbo LM, Gondim MGC Jr, de Moraes GJ, Hanna R, Schausberger P (2007) Refuge use by the coconut mite *Aceria guerreronis*: fine scale distribution and association with other mites under perianth. Biol Control 43:102–110

Leśna I, Conijn CGM, Sabelis MW (2004) From biological control to biological insight: rust-mite induced change in bulb morphology, a new mode of indirect plant defense? Phytophaga 14:285–291

Lindquist EE (1996) External anatomy and notation of structures. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 1–30

Lindquist E (1998) Evolution of phytophagy in trombidiform mites. Exp Appl Acarol 22:81–100

Lindquist EE, Oldfield GN (1996) Evolution of eriophyoid mites in relation to their host plants. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 277–300

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites their biology, natural enemies and control. Elsevier. World Crop Pests, 6, 822pp

Liu J, Lee EA, Sears MK, Schaafsma AW (2005) Wheat curl mite (Acari: Eriophyoidae) dispersal and its relationship with kernel red streaking in maize. J Econ Entomol 98:1580–1586

MacArthur RH, Pianka ER (1966) On the optimal use of a patchy environment. Am Nat 100:603–609

Manson DCM, Gerson U (1996) Web spinning, wax secretion and liquid secretion by eriophyoid mites. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 251–258

Massee AM (1928) The life history of the black currant gall mite, *Eriophyes ribis* (Westwood). Nat Bull Entomol Res 18:277–307

McCoy CW (1979) Migration and development of citrus rust mite on the spring flush of Valencia orange. Proc Fla State Hortic Soc 92:48–51

McCoy CW, Albrigo LG (1975) Feeding injury to the orange caused by the citrus rust mite, *Phyllocoptruta oleivora* (Prostigmata: Eriophyoidea). Ann Entomol Soc Am 68:289–297

Michalska K (1997) Reproductive behaviour of some species of eriophyoid mites. Ph.D. Thesis, Warsaw University of Life Sciences, p 85

Michalska K (1999) Spermatophore deposition and guarding in the free-living eriophyid mite *Vasates robiniae* (Acari). Behaviour 136:899–918

Michalska K (2000) The influence of conspecific males on spermatophore deposition in the eriophyoid mite *Aculus fockeui*. Exp Appl Acarol 24:905–911

Michalska K (2003) Climbing of leaf trichomes by eriophyoid mites impedes their location by predators. J Insect Behav 16:833–844

Michalska K (2005) Spermatophore deposition throughout the day by the plum rust mite, *Aculus fockeui*. Exp Appl Acarol 35:111–116

Michalska K, Boczek J (1991) Sexual behaviour of males attracted to quiescent deutonymphs in the Eriophyoidea (Acari). In: Dusbabek F, Bukva V (eds) Modern acarology, vol 2. Academia, Prague, pp 549–553

Michalska K, Mańkowski DR (2006) Population sex ratio in three species of eriophyoid mites differing in degree of sex dissociation. Biological Lett 43:197–207

Michalska K, Shi A (2004) A first view on factors influencing spermatophore deposition by the eriophyoid mite *Cecidophyopsis hendersoni* (Keifer). Phytophaga 14:141–148

Mishra CS (1912) Litchi leafcurl. Agric J India 7:286–923

Moore D, Alexander L (1987) Aspects of migration and colonization of the coconut palm by the coconut mite, *Eriophyes guerreronis* (Keifer) (Acari: Eriophyoidae). Bull Ent Res 77:641–650

Moore D, Howard FW (1996) Coconuts. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 561–570

Mori K, Saito Y (2004) Variation in social behaviour within a spider mite genus, *Stigmaeopsis* (Acari: Tetranychidae). Behav Ecol 16:232–238

Mori K, Saito K (2006) Communal relationship in a social spider mite, *Stigmaeopsis longus* (Acari: Tetranychidae): an equal share of labor and reproduction between nest mates. Ethology 112:134–142

Mumcuoglu Y, Six E (1974) Milben in der luft. Rev Suisse Zool 81:673–677

Nault LR, Styer WE (1969) The dispersal of *Aceria tulipae* and three other grass-infesting eriophyoid mites in Ohio. Ann Entomol Soc Am 62:1446–1455

Navia D, De Moraes GJ, Roderick G, Navajas M (2005) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyoidae): origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. Bull Entomol Res 95(6):505–516

Nuzzaci G (1976) [Behaviour of eriophyoid mites during the uptake of food]. Entomologica, Bari 12:75–80 (in Italian)

O'Down JD, Willson MF (1997) Leaf domatia and the distribution and abundance of foliar mites in broadleaf deciduous forest in Wisconsin. Am Midl Nat 137:337–348

Oganezova GG, Pogosova AR (1994) On the ecology of *Eriophyes armeniacus* (Acariformes, Tetrapodili) on *Prunus divaricata*. Zool Zh 73:28–32

Oku K, Yano S, Takfuji A (2003) Spider mite's use of refuges during the quiescent stage in the presence of a predator. Entomol Exp Appl 108:71–74

Oldfield GN (1969) The biology and morphology of *Eriophyes emarginatae*, a *prunus* finger gall mite and notes on *A. prunidemissae*. Ann Entomol Soc Am 62:269–277

Oldfield GN (1973) Sperm storage in female Eriophyidae (Acarina). Ann Entomol Soc Am 66:1089–1092

Oldfield GN (1988) Observations on intraspecific attraction to spermathophores by species of Eriophyoidae. In: Channa-Basavanna GP CA, Viraktamath CA (eds) Progress in acalogy. Oxford & IBH Publ, New Delhi, India, pp 249–253

Oldfield GN (1996) Diversity and host plant specifity. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 199–216

Oldfield GN (1999) Distribution of asymmetrical and symmetrical sperm storage in the Eriophyoidea and its phylogenetic implications. In: Bruin J, Geest LPS, Sabelis MW (eds) Ecology and evolution of the Acari. Kluwer Academic Publishers, Dordrecht, pp 157–161

Oldfield GN, Michalska K (1996) Spermatophore deposition, mating behaviour and population mating structure. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 185–198

Oldfield GN, Newell IM (1973) The role of the spermatophore in the reproductive biology of protogynes of Aculus cornutus (Acarina : Eriophyoidae). Ann Entomol Soc Am 66:160–163

Oldfield GN, Hobza RF, Wilson NS (1970) Discovery and characterization of spermatophores in the Eriophyoidea (Acari). Ann Entomol Soc Am 63:520–526

Oldfield GN, Newell IM, Reed DK (1972) Insemination of protogynes of Aculus cornutus from spermatophores and description of the sperm cell. Ann Entomol Soc Am 65:1080–1084

Ozman SK, Goolsby JA (2005) Biology and phenology of the eriophyoid mite, Floracarus perrepae, on its native host in Australia, old world climbing fern, Lygodium microphyllum. Exp Appl Acarol 35(3):197–213

Pady SM (1955) The occurrence of the vector of the wheat streak mosaic, Aceria tulipae, on slides exposed in the air. Plant Dis Rep 39:296–297

Painter RH, Schesser JH (1954) Western wheat grass, an oversummering host of Aceria tulipae (K.), vector of streak-mosaic of wheat. J Kansas Entomol Soc 27:118–119

Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. Biol Rev 45:525–567

Parker GA (1998) Sperm competition and the evolution of ejaculates: towards a theory base. In: Birkhead TR, Moller AP (eds) Sperm competition and sexual selection. Academic Press, San Diego, California, pp 3–54

Perring TM, McMurtry J (1996) Other predatory arthropods. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 471–479

Proctor HC (1992) Mating and spermatophore morphology of water mites (Acari: Parasitengona). Zool J Linnean Soc 106:341–384

Proctor HC (1998) Indirect sperm transfer in arthropods: behavioural and evolutionary trends. Annu Rev Entomol 43:153–174

Putman WL (1939) The plum nursery mite (Phyllocoptes fockeui Nal. And Trt.). Ann Rev Entomol Soc Am 55:431–435

Romero GQ, Benson WW (2005) Biotic interactions of mites, plants and leaf domatia. Curr Opin Plant Biol 8:436–440

Sabelis MW (1996) Phytoseiidae. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 427–456

Sabelis MW, Bruin J (1996) Evolutionary ecology: life history patterns, food plant choice and dispersal. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 329–366

Sabelis MW, van Rijn PCJ (1996) Eriophyoid mites as alternative prey. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 757–764

Saito Y (1985) Life types of spider mites. In: Helle W, Sabelis MW (eds) Spider mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol1A, pp 253–264

Saito Y (1986) Biparental defence in a spider mite (Acari: Tetranychidae) infesting Sasa bamboo. Behav Ecol Sociobiol 18:377–386

Saito Y (1995) Sociobiological aspects of spider mite life types. J Acarol Soc Jap 4:55–67

Saito Y (1997) Sociality and kin selection in Acari. In: Choe JC, Crespi BJ (eds) The evolution of social behaviour in insects and arachnids. Cambridge University Press, Cambridge, pp 443–457

Sato Y, Saito Y, Sakagami T (2003) Rules for nest sanitation in a social spider mite, *Schizotetranychus miscanthi* Saito (Acari: Tetranychidae). Ethology 109:713–724

Schaller F (1971) Indirect sperm transfer by soil arthropods. Annu Rev Entomol 16:407–446

Schliesske J (1977) Dispersal and food-plant range of *Aculus fockeui* Nal. & Trt. (Acari: Eriophyoidae) and of the species associated with it. Meded Fac Landbouwwet Rijksuniv Gent 42:1343–1351

Schliesske J (1979) Vorkommen und arten der verbreitung freilebender gallmilben (Acari: Eriophyoidea) an *Prunus* spp. in Niedersachsen. Zool Beitr 25:1–12

Schliesske J (1990) On the gall mite fauna (Acari: Eriophyoidea) of *Cocos nucifera* L. in Costa Rica. Plant Res Dev 31:74–81

Shuster SM, Wade MJ (2003) Mating systems and strategies. Princeton University Press, Princeton and Oxford, p 533

Shvanderov FA (1975) Role of phoresy in the migration of Eriophyoidea. Zool Zh 54:458–461

Sih A (1987) Predators and prey lifestyles: an evolutionary and ecological overview. In: WCh Kerfoot, Sih A (eds) Predation. Direct and indirect impacts on aquatic communities. University Press of New England, Hanover and London, pp 203–224

Simmons LW (2001) Sperm competition and its evolutionary consequences in insects. Princeton University Press, Princeton, NJ, p 434

Singer MC, Thomas CD, Billinton HL, Parmesan C (1989) Variation among conspecific insect populations on the mechanistic basis of diet breadth. Anim Behav 37:751–759

Skoracka A (2008) Reproductive barriers between populations of the cereal rust mite *Abacarus hystrix* confirm their host specialization. Evol Ecol 22:607–616

Skoracka A, Kuczyński L (2006) Is the cereal rust mite, *Abacarus hystrix* really a generalist?—testing colonization performance on novel hosts. Exp Appl Acarol 38:1–13

Skoracka A, Kuczyński L, Rector BG (2007) Divergent host acceptance behaviour suggests host specialization in populations of the polyphagous mite *Abacarus hystrix* (Acari: Prostigmata: Eriophyoidae). Environ Entomol 36(4):899–909

Slykhuis JT (1955) *Aceria tulipae* Keifer (Acarina, Eriophyoidae) in relation to the spread of wheat streak mosaic. Phytopathology 45:116–128

Slykhuis JT, Andrews JE (1953) Wheat streak mosaic in Alberta and its control. Mimeographed unnumbered publications. Canadian Dept. Agric. Sci. Exper. Farms Services, Lethbridge, Alberta, August

Smith BD (1959) Effects of temperature and photoperiod on black currants and on the behaviour of the gall mite (*Phytoptus ribis* Nal.). A. R. Long Ashton agric, hort. Res Stat 13:7–138

Smith BD (1960) The behaviour of the black currant gall mite (*Phytoptus ribis* Nal.) during the free living phase of its life cycle. A. R. Long Ashton agric, hort. Res. Stat 13:130–136

Somchoudhury AK, Choudhury AK, Mukherjee AB (1985) Mite vectors and their trapping. In: Mukhopadhyay S, Ghosh MR (eds) Use of traps of pest/vector research and control. Proc. nat. seminar, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, West Bengal, Kalyani, India, March 10–11, 1984:41–50

Stam E, Isaaks A, Ernsting G (2002) Distant lovers: spermatophore deposition and destruction behaviour by male springtails. J Insect Behav 15:253–268

Staples R, Allington WB (1956) Streak mosaic of wheat in Nebraska and its control. Univ Nebr Agric Exp Stn Res Bull 178:41

Staples R, Allington WB (1959) The efficiency of sticky traps in sampling epidemic populations of the eriophyoid mite *Aceria tulipae* (K.), vector of wheat streak mosaic virus. Ann Entomol Soc Am 52:159–164

Sternlicht M (1969) Effect of different wave lengths of light on the behaviour of an Eriophyoid bud mite, *Aceria sheldoni*. Entomol Exp Appl 12:377–382

Sternlicht M, Goldenberg S (1971) Fertilisation, sex ratio and post embryonic stages of the citrus bud mite *Aceria sheldoni* (Ewing) (Acarina: Eriophyoidae). Bull Entomol Res 60:391–397

Sternlicht M, Griffiths DA (1974) The emission and form of spermatophores and the fine structure of adult *Eriophyes sheldoni* (Ewing) (Acarina: Eriophyoidae). Bull Entomol Res 63:561–565

Sternlicht M, Goldenberg S, Cohen M (1973) Development of the plum gall and trials to control its mites *Acalitus phloeocoptes* (Eriophyoidae, Acarina). Ann Zool Ecol Anim 5:365–377

Suhonen J, Rentala MJ, Henkavaara J (2008) Territoriality in odonates. In: Córdoba-Aguilar A (ed) Dragonflies and damselflies: model organisms for ecological and evolutionary research. Oxford University Press, Oxford, New York, pp 203–219

Sumangala K, Haq MA (2005) Diurnal periodicity and dispersal of coconut mite, *Aceria guerreronis* Keifer. J Entomol Res 29:303–307

Tanaka H, Shibao M (2003) A pattern of occurrence and dispersal of the tomato russet mite, *Aculops lycopersici* (Massee) in a tomato greenhouse. Proc Kansai Pl Prot Soc 45:23–27

Thistlewood HMA, Clements DR, Harmsen R (1996) Stigmaeidae. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 457–470

Thomas JA, Hein GL (2003) Influence of volunteer wheat plant condition on movement of the wheat curl mite, *Aceria tosichella*, in winter wheat. Exp Appl Acarol 31(3–4):253–268

Thomas RH, Zeh DW (1984) Sperm transfer and utilization strategies in arachnids: ecological and morphological constrains. In: Smith RL (ed) Sperm competition and the evolution of animal mating systems. Academic Press, Orlando, Fla. (USA), pp 179–221

Thompson JN, Pellmyr O (1991) Evolution of oviposition behaviour and host preference in Lepidoptera. Annu Rev Entomol 36:65–89

Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge, p 547

Van Dinther JBM (1951) [*Phyllocoptes gracilis* as a cause of yellow leaf spots on Raspberry] Tijdschrift over Plantenziekten 57:81–94 (In German)

Vuorisalo T, Walls M, Niemel P, Kuitinen H (1989) Factors affecting mosaic distribution of galls of an eriophyoid mite, *Eriophyes laevis*, in alder, *Alnus glutinosa*. Oikos 55:370–374

Waite GK (1999) New evidence further incriminates honey-bees as vectors of lychee erinose mite *Aceria litchii* (Acari: Eriophyiidae). Exp Appl Acarol 23(2):145–147

Waite GK, McAlpine JD (1992) Honey bees as carriers of lychee erinose mite *Eriophyes litchi* (Acari: Eriophyiidae). Exp Appl Acarol 15:299–302

Walter DA (1996) Living on leaves: mites tomentia and leaf domatia. Annu Rev Entomol 41:101–114

Walter D, Proctor H (1999) Mitesecology, evolution and behaviour. UNSW Press, CABI Publishing

Wedell N, Gage MJG, Parker GA (2002) Sperm competition, male prudence and sperm-limited females. Trends Ecol Evol 17:313–320

Westphal E, Manson DCM (1996) Feeding effects on host plants: gall formation and other distortions. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, The Netherlands, World Crop Pests, vol 6, pp 231–242

Wilson EO (1971) The insect societies. Belknap Press, Cambridge, p 548

Witte H (1991) Indirect sperm transfer in prostigmatic mites from phylogenetic viewpoint. In: Schuster R, Murphy PW (eds) The Acari. Chapman and Hall, London, pp 137–176

Witte H, Döring D (1999) Canalized pathway of change and constraints in evolution of reproductive modes of microarthropods. In: Bruin J, Geest LPS, Sabelis MW (eds) Ecology and evolution of the Acari. Kluwer Academic Publishers, Dordrecht, pp 15–43

Yanagida H, Saito Y, Mori K, Chittenden AR (2001) Egg-depositing behaviour as a predator avoidance tactic of *Yezonychus sapporensis* Ehara (Acari, Tetranychidae). J Ethol 19:63–66

Zhao S, Amrine JW Jr (1997a) A new method for studying aerial dispersal behaviour of eriophyoid mites (Acari: Eriophyoidea). Syst Appl Acarol 2:107–110

Zhao S, Amrine JW Jr (1997b) Investigation of snowborne mites (Acari) and relevance to dispersal. Int J Acarol 23:209–213

Plant–eriophyoid mite interactions: cellular biochemistry and metabolic responses induced in mite-injured plants. Part I

Radmila Petanović · Malgorzata Kielkiewicz

Abstract This review is a comprehensive study of recent advances related to cytological, biochemical and physiological changes induced in plants in response to eriophyoid mite attack. It has been shown that responses of host plants to eriophyoids are variable. Most of the variability is due to individual eriophyoid mite–plant interactions. Usually, the direction and intensity of changes in eriophyoid-infested plant organs depend on mite genotype, density, or the feeding period, and are strongly differentiated relative to host plant species, cultivar, age and location. Although the mechanisms of changes elicited by eriophyoid mites within plants are not fully understood, in many cases the qualitative and quantitative biochemical status of mite-infested plants are known to affect the performance of consecutive herbivorous arthropods. In future, elucidation of the pathways from eriophyoid mite damage to plant gene activation will be necessary to clarify plant responses and to explain variation in plant tissue damage at the feeding and adjacent sites.

Keywords Vagrants · Mite gall formers · Sap-sucking feeders · Compatible and incompatible interactions

Introduction

Among phytophagous mites, the eriophyoid mites (Acari: Prostigmata: Eriophyoidea) are the most diverse group and many of eriophyoid species are economically important (Van Leeuwen et al. 2010). Around 3,700 species are currently recognised (Amrine et al. 2003) on angiosperms, coniferous plants and ferns throughout the world. Exceptional morphological, physiological and behavioral traits of eriophyoids (Nuzzaci and Alberti 1996)

R. Petanović (✉)
Department of Entomology and Agricultural Zoology, Faculty of Agriculture,
University of Belgrade, Nemanjina 6, Belgrade-Zemun 11081, Serbia
e-mail: rpetanov@agrif.bg.ac.rs

M. Kielkiewicz
Department of Applied Entomology, Faculty of Horticulture and Landscape Architecture,
Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

allow them to specialize in feeding on particular plant genotypes, and even on a single vegetative and/or generative plant organ (Jeppson et al. 1975; Boczek and Griffiths 1994; Westphal and Manson 1996). Therefore, most of them are highly host specific (Keifer et al. 1982; Boczek and Griffiths 1994; Oldfield 2005). However, a few species are known to inhabit a wide range of host plants (Jeppson et al. 1975; Westphal 1980; Meyer 1987; Oldfield 1996a). Meristems and young, soft tissues of all aboveground plant organs are preferred by eriophyoids presumably because of their high nutritional value. Interaction of host plant genotype, mite species and environmental factors result in the final form of plant/organ symptoms (Weis et al. 1988; Easterbrook and Palmer 1996; Rančić et al. 2006; Royalty and Perring 1996; Westphal and Manson 1996; Duso et al. 2008; Rančić and Petanović 2008). The consequences of eriophyoid mite feeding can range from symptomless to toxemias, and non-distortive effects such as russeting, silvering, bronzing etc., and formation of galls, distortions or other abnormalities and formation of a rapid necrotic lesion (hypersensitive reaction, HR) (Oldfield 1996b; Royalty and Perring 1996; Westphal and Manson 1996; Westphal et al. 1996). Although great progress has been achieved in research on plant–mite relationships in the second part of the twentieth century (Boczek and Griffiths 1994; Nuzzaci and Alberti 1996; Oldfield 1996a, b; Royalty and Perring 1996; Westphal and Manson 1996; Westphal et al. 1996; Duso et al. 2008), the limited knowledge we have on many aspects of eriophyoid mite–host plant interactions merit further investigation.

The present review related to plant–eriophyoid mite interactions consists of two parts. Types of morphological alterations of host plant organs with respect to eriophyoid life styles, as well as the variety of plant symptoms characteristic of eriophyoid damage are analysed in the second part of the review (Petanović and Kielkiewicz 2010). The aim of this review (Part I) is to present the new synthesis of results concerning plant–eriophyoid mite interactions with respect to cytological, biochemical and physiological effects achieved to date. Our intention was to compare results obtained by 1996 with those published within the last 15 years. In the light of new data, we tried to find possible explanations to previously presented results or raise the same unanswered questions, and finally suggest how future studies could answer our long-standing queries.

From eriophyoid mite stylet penetration to cell injury

The morphology of eriophyoid gnathosoma, its function and movement have been studied in detail by several authors (Keifer 1959; Shevtchenko and Silvere 1968; Jeppson et al. 1975; Silvere and Shtein-Margolina 1976) and reviewed by others (Krantz and Lindquist 1979; Lindquist 1996; Westphal and Manson 1996). Although the involvement of gnathosoma structures in the feeding process has been shown, not all phases are fully known (McCoy and Albrigo 1975; Hislop and Jeppson 1976; Nuzzaci 1979; Nuzzaci and Alberti 1996). The stylets of eriophyoid mouthparts are inserted into the cell wall mechanically (Keifer 1959; Shevtchenko and Silvere 1968; Krantz 1973; McCoy and Albrigo 1975; Hislop and Jeppson 1976; Nuzzaci 1976), where they cut and drill, and three glands (paired and unpaired) produce secretions (Nuzzaci and Alberti 1996). The paired glands presumably function as true salivary glands (Thomsen 1988; Nuzzaci and Alberti 1996), whereas the function of the unpaired one is still to be elucidated.

Eriophyoid saliva injected from the mouthparts enters the plant cells. As indicated by the review of Nuzzaci and Alberti (1996), the saliva travels between cheliceral stylets and labrum into the plant cell, whereas plant cell content moves through a canal formed by the

infracapitular stylets and the labrum. Some consider that cheliceral stylets are inserted into the cell during mite feeding (Jeppson et al. 1975; Nuzzaci 1979) or that the mite withdraws its cheliceral stylets from the cell wall after its perforation and then fixes the labrum to the hole in the cell wall to actively uptake the cell content (Westphal and Manson 1996). According to Thomsen's (1988) hypothesis, first the eriophyoid mite ejects saliva onto the surface of the leaf in order to digest the cuticle and cellulose of the cell wall enzymatically. Then, the marked site on the cell wall is located and punctured by the mite's chelicerae which then sucks out the cell content, taking 10–20 min. Contrary to Thomsen's (1988) model of eriophyoid mite feeding behaviour, Westphal and Manson (1996) are of the opinion that eriophyoids need only a few seconds for probing and cell penetration. Therefore, the saliva deposited on the plant surface may have no action on the cell wall before the mite inserts its chelicerae.

So far, it has been shown that aphid's polygalacturonases, pectinoesterases and celullases digest the components of the middle lamella and the primary cell wall to enable the stylet to penetrate between cells in order to reach the phloem tissue (Miles and Peng 1989; Ma et al. 1990). Amongst many other functions, it is already known that insect's polygalacturonases can produce oligosaccharides (for example, oligogalacturonic acid, OGA) from pectic components of plant cell wall that probably recognize plasma membrane receptors or depolarize plasma membranes and further induce the plant defensive responses (Ryan 1990, 2000; Walling 2000; Gatehouse 2002). Another oligosaccharide known as elicitor of defences in plants infected by fungal pathogens is chitosan (CHT, β-1,4-linked D-glucosamine), a deacetylated derivative of chitin. Recently, polygalacturonase activity was assessed in salivary secretions of *Aceria caulobia* (Nalepa), which suggests a putative role of this enzyme in eriophyoid-feeding signal release (Monfreda and Spagnuolo 2004). Lipophobic substances secreted by mouthparts of *A. caulobia* also consist of indole-3 acetic acid (IAA) and cytokinin-like compounds with plant growth regulatory effects (De Lillo and Monfreda 2002, 2004). Together with the earlier assumption related to the presence of hormonal substances in eriophyoid mite saliva (Jeppson et al. 1975; Westphal 1992; Boczek and Griffiths 1994), this finding affirms the statement that phytohormones of saliva can be secreted into epidermal cells and initiate further abnormal growth and the development of plant tissues.

Cellular biochemistry within plant organs in relation to eriophyoid mite feeding

There is much evidence showing that eriophyoid mite feeding strongly influences the host plant at a cellular level (Ishaaya and Sternlicht 1969; Westphal 1974, 1977, 1982; McCoy and Albrigo 1975; Thomsen 1975, 1988; Westphal et al. 1981, 1990a, b, 1991; Larew 1982; Royalty and Perring 1988; Baker and Chandrapatya 1989; Bronner et al. 1989; McCoy 1996; Westphal and Manson 1996; Kane et al. 1997; Kozlowski and Zielinska 1997; Kozlowski 1998; Rancic and Petanovic 2002a, b; Soika and Kielkiewicz 2004; Rančić et al. 2006; Pećinar et al. 2007, 2008). Generally, three types of eriophyoid mite–plant interactions have been distinguished: two types of compatible interactions (toxemias and other non-distortive effects together with gall forming) and one type of incompatible interaction (HR) (Westphal and Manson 1996). However, there are other eriophyoid-plant interactions that do not necessarily fit into this category (reviewed by McCoy 1996; Oldfield 1996b). Here, in the light of new research findings, we analyse some of the most familiar eriophyoid–plant interactions.

Free-living mites and the susceptible host plant

Compatible interactions between susceptible host plants and both free-living and gall mites are similar when it comes to injured cells and differ in responses of uninjured cells adjacent to the injured ones. Commonly, within the first 10–20 min of mechanical penetration of the epidermal cell wall by cheliceral stylets, the appearance of callosic (1,3-ß-glucan) disc-like feeding punctures (*syn.* cone-shaped feeding punctures) on the cell wall and deoxyribo-nucleic acid (DNA)-modification, associated with the accumulation of CHT within nucleus and suction cone, have been described (Bronner and Westphal 1987; Bronner et al. 1989).

In the case of free-living rust mites (e.g., *Thamnacus solani* Boczek and Michalska; the citrus russet mite, *Phyllocoptruta oleivora* (Ashmead); the grain rust mite, *Abacarus hystrix* (Nalepa); the tomato russet mite, *Aculops lycopersici* (Massee); and the apple russet mite, *Aculus schlechtendali* (Nalepa)), injuries are limited to the directly punctured epidermal cells which rapidly collapse and die (Gibson 1974; Royalty and Perring 1988; McCoy 1996; Westphal and Manson 1996). Rust mites move away from the injured site and attack other cells, which causes a massive destruction of the epidermis leaf surface visible as russeting, bronzing, silvering or discoloration. According to Royalty and Perring (1996), the oxidation processes within the mite-injured layer probably result in symptoms typical for damage caused by eriophyoid leaf vagrants. It is believed that adjacent cells do not undergo any damage. However, there are certain examples showing that changes in the rust-mite-infested leaf exceed the directly mite-injured area. Responses can vary among vagrants and host plant species (reviewed by Royalty and Perring 1996). For example, the lignification of thickened cell walls was observed in the regions adjacent to the epidermal cells destroyed by extensive feeding of *P. oleivora* on orange fruits, *A. schlechtendali* on apple leaves and fruits, and *A. lycopersici* on tomato leaves (McCoy and Albrigo 1975; Easterbrook and Fuller 1986; Royalty and Perring 1988; Kozlowski 1998). Apart from lignin formation, phellogen or 'cork cambium' was detected within apple tissues penetrated by *A. schlechtendali* (Easterbrook and Fuller 1986). Cytological analyses presented by Kozlowski and Zielinska (1997) and Kozlowski (1998) demonstrated that extensive feeding of *A. schlechtendali* on the lower apple leaf surface, apart from epidermal cell collapse caused the rupture of cell walls and plasmalemma, leading to the process of degeneration of the cells of spongy parenchyma accompanied by the thickening of cell walls and intercellular deposition of lignin-like compounds.

Recently, destructions of epidermal cells of the upper and lower surface of *Gallium mollugo* L. leaves was documented (Rančić and Petanović 2002a) as a consequence of *Aculus anthobius* (Nalepa) feeding. The study of some conspicuous structural malformations of *Dipsacus laciniatus* L. caused by infestation of *Leipothrix dipsacivagus* Pet. et Rector showed that the curled flower-stem leaves manifested not only significant cellular injuries, but also changes in mesophyll organization. Mesophyll of infested leaves consisted of 2–3 layers of palisade parenchyma and several layers of non-specifically differentiated spongy parenchyma. In addition, the epidermal cells of such leaves were enlarged (hypertrophied) comparing to those of non-infested leaves (Pećinar et al. 2007). The developmental stage of the host plant as well as the genotype of host plant and mite could be the main reasons why some vagrant species affect deeper cell layers as well as the epidermal ones. Injury of mature leaves of field-collected plants of *Cirsium arvense* (L.) Scop. caused by *Aceria anthocoptes* (Nalepa) was demonstrated to be limited to the epidermis of the lower surface. However, on young leaves of experimentally infested plants, rust mite injuries extended to the epidermal cells of both leaf surfaces and to those

of the deeper mesophyll layers. On these leaves, lesions on the lower leaf surface also affected the phloem of the vascular bundles (Rančić et al. 2006).

Accumulation of defence-related proteins (proteinase inhibitors (PIs), phenylalanine ammonia lyase (PAL), chalcone synthase (CHS), polyphenol oxidase (PPO), lipoxygenase (LOX)) and pathogenesis-related proteins (PR) (for example, β-1,3-glucanase (BGL2), PR-3- basic chitinase, PR-9 family with peroxidase properties) as a result of herbivore–host plant interaction has been frequently observed (Bowles 1990; Felton et al. 1989; Ryan 1990; Bronner et al. 1991a, b; Duffey and Felton 1991; Stout et al. 1994, 1996; Duffey and Stout 1996; Kielkiewicz 1996, 1998, 2002, 2003; Mayer et al. 1996; Bi et al. 1997; Inbar et al. 1998, 2003; Arimura et al. 2000; Walling 2000; Thaler et al. 2001, 2002; Forslund et al. 2000; Moran and Thompson 2001; Gatehouse 2002; Kant et al. 2004; Grinberg et al. 2005; Spence et al. 2007). Simultanously, it has been proved that infested host plants respond differently to chewing and sap-sucking pests (Stout et al. 1994, 1996; Jimenez et al. 1995; Mayer et al. 1996; Walling 2000).

Data on defence-related proteins in host plant–vagrant interactions are limited. However, Stout et al. (1996) presented evidence for several enzymatic proteins to be not only locally but also systemically induced in the leaves of tomato plants (Solanum lycopersicum L.), in response to A. lycopersici short-term feeding. Local induction of total peroxidases (POX, hydrogen peroxide (H_2O_2) oxidoreductase) activity was much more evident than the induction of PPO or LOX. More precisely, POX activity of mite-injured leaflets was over eight times higher than in undamaged leaflets of the 3rd leaf, and less than two-fold for PPO and LOX. It is worth noting, that POX and PPO induction was host plant systemic, whereas LOX was only leaf-systemic. Also, the systemic induction of POX was much stronger than the induction of PPO or LOX. The authors speculate that the high activity of POX within A. lycopersici-induced tomato plant should induce lignin formation shortly after mite feeding. Whether the changes affect mite performance and how the enzyme induction affects resistance of the plant itself needs to be elucidated. Earlier results of Royalty and Perring (1988) have shown the relationship between tomato leaf-epidermal cell damage by A. lycopersici and feeding rate of the individual mite. It has been proposed that the increased number of cells damaged during a given period of time resulted in gas exchange decrease (Royalty and Perring 1989), thereby causing the temperature and deficit of vapor-pressure of mite-infested leaves to increase, stimulating mite feeding. Thus, the defence reactions of an already infested tomato plant are more likely to be overcome.

Mite gall inducers and the susceptible host plant

The process of cecidogenesis has been documented (Westphal 1972, 1977; Westphal et al. 1990a) within the compatible interaction between a gall mite (Aceria cladophthirus Nalepa) and its susceptible host plant, the woody nightshade (Solanum dulcamara L.). The process begins with cell puncturing leading to the appearance of feeding punctures on the cell wall of the upper epidermis and follows by the increase of base property of the vacuoles (pH >8), modifications of cell membrane permeability, enlargement of the nucleus, dispersion of chromatin, increase of cytoplasm density and vacuolar fragmentation (Westphal 1982). The accumulation of CHT within nucleus and feeding punctures on the walls of mite-injured cells putatively induce the activity of adjacent cells (Bronner et al. 1989). These observations correlate with data reporting the high affinity of CHT for DNA molecules and polygalacturonate in plant–pathogen interactions (Hadwiger 1999). Since the cuticle of arthropods contains chitin, Bronner et al. (1989) assumed that it is introduced into the host cell wall during the process of penetration by chitinous mite chelicerae and initiates

nuclear DNA changes visible as chromatin dispersion. Furthermore, CHT could also be an important factor at the initiation of gall mite–plant compatible interaction, i.e. during the formation of the callosic disc-like feeding punctures. Selective staining with resorcinol blue for callose demonstrated that the 'suction truck' within cell walls is filled with grainy callose (Thomsen 1988). Callose is presumably used to regenerate the pierced plasmalemma of mite-injured cells. Presently, it is known that callose biosynthesis is controlled by a combination of glucan synthase-like (*GSL*) genes (Voigt et al. 2008), and the intensity and speed of callose deposition is regulated by abscisic acid (ABA) and non-protein amino acid-β-aminobutyric acid (BABA) (Cohen et al. 1999; Ton and Mauch-Mani 2004; Flors et al. 2005; Mauch-Mani and Mauch 2005; Adie et al. 2007; Asselbergh et al. 2008). Callose is known to be induced by mechanical wounding, pathogen infection and various abiotic stresses, therefore the deposition of callose is a non-specific rather than a specific response to gall mite attack (Stone and Clarke 1992; Kauss 1996; Jacobs et al. 2003). Since CHT acts on the nucleus, cytosol, plasma membranes and cell walls inducing initial events leading to the rapid synthesis and deposition of callose in pathogen infected plant tissues (Hadwiger 1999), we could imply that the appearance of CHT in eriophyoid mite-attacked plants can also elicit similar metabolic responses. This assumption seems to be consistent with recent results of molecular studies concerning the role of CHT and other oligosaccharides as elicitors of activating signalling pathways in plant defence against pests/pathogens or wound responses (Hadwiger 1999; Ryan 2000; Walling 2000; Gatehouse 2002). For example, it is well-documented that CHT locally induces responses through enhanced transcription/translation of genes encoding chitinase, RNAse, β-glucanase, thionis, defensins, PIs, and POXs capable of generating phenolics such as lignin. In the light of finding that CHT is able to trigger a systemic acquired resistance (SAR), by binding to the plant recognized receptors (PRR) (Iriti and Faoro 2007), it is not surprising that CHT could cause death of the cells directly punctured by eriophyoids as well as the division of adjacent cells.

Mitotic activity leads to the formation of the first and deeper layers of nutritive tissues from which gall mites suck nutritive compounds (Thomsen 1975; Westphal et al. 1981; Bronner and Westphal 1987; Bronner et al. 1989). If nutritive cells are punctured, they undergo the process described earlier for injured epidermal cells and soon die. However, continuous puncturing is necessary for the maintenance of the nutritive tissue (Mani 1964; Westphal and Manson 1996) and for the formation of an obvious gall. Experiments have shown that when the gall-former is artificially removed, the nutritive tissue recovers and turns into regular parenchyma cells (Rohfritsch 1975). Mayer (1952) observed that the fundatrix female of *Eriophyes macrorhynchus* (Nalepa), whilst feeding on the leaves of *Acer pseudoplatanus* L. caused the plant to produce a nutritive epidermis. However, between the death of female and beginning egg hatching, the nutritive tissue loses its typical appearance and dies off. Once the eggs hatch and the progeny begins to feed, the cells under the former nutritive epidermis revert once more to nutritive tissue (Larew 1982). It correspond with the earlier observation of Thomsen (1975) who shows that when *Eriphyes tiliae* (Pgst.) stops affecting gall formation on the leaves of *Tilia platyphylla* Scop., gall cells transform into epidermal cells with stomata and mesophyll cells with chloroplasts.

Further detailed investigations of longitudinal sections of a fully differentiated pouch gall on *T. platyphylla* Scop., caused by *E. tiliae*, show the presence of anthocyanins in the epidermal cells. A mature gall consists of hypertrophied parenchyma cells and nutritive tissue that comes mainly from anticlinal division and accumulates starch and proteins, but not lipids. The vascular bundles in the gall are connected to those in the healthy leaf area. However, no direct connection between the bundles and the nutritive tissue have been

observed. Fibres and tannins are found in gall phloem and lignified vascular bundle sheaths, respectively. Many unicellular, cylindrical hairs grow on the surface of the gall. Wcislo (1977) described the hypertrophy and hyperplasia of epidermal and mesophyll cells caused by *E. tiliae* (Pgst.) feeding on *Tilia cordata* Mill., and is of the opinion that disturbed mitoses (or rather endomitoses) are the reason for the process of polyploidization in the cell nuclei of the inner gall surface. Polyploidization has also been reported both in the cells of white alder (*Alnus rhombifolia* Nutt.) damaged by the alder-leaf bead gall mite *Eriophyes laevis* Nalepa (Hesse 1971), and in the cells of *Prunus padus* L. damaged by *Eriophyes padi* Nalepa (Westphal 1974). Fragmentation of vacuoles, increased density of endoplasmatic reticulum and ribosomes, and increased number of mitochondria and chloroplast alteration were found as a response to the feeding of *Aceria ulmicola* (Nalepa) on leaves of European elm (*Ulmus campestris* L.) (Westphal 1977). Analyses of several abnormalities induced by gall mites (*Eriophyes litchi* Keifer, *Abacarus euphoriae* Keifer, *Eriophyes striatus* Nalepa, *Eriophyes sandorici* Nalepa and *Eriophyes phylloperthus* Nalepa) on plant species of *Litchii chinensis* Sonn., *Euphoria longana* (Laur.), *Eupatorium odoratum* L., *Sandoricum koetjape* (Burm. F.) and *Acacia pennata* (L.), respectively, growing in Thailand (Baker and Chandrapatya 1989) have shown certain features in common, such as the absence or very few stomata on the surface of erinea, lignified cells close to vascular bundles, collenchyma and thick cuticle on the outer cell wall of epidermal cells. Mostly, the enlarged nuclei and dense cytoplasm were clearly visible within undifferentiated and hypertrophied densely packed cells.

Previously, only one example of different gall types induced by the same gall mite species (*Eriophyes goniothorax* (Nalepa)) has been reported (Boczek and Griffiths 1994). Recent assessment (Soika and Kielkiewicz 2004) showed that the same mite species—*Phytoptus tetratrichus* (Nalepa) induces galls that differ in external structure depending on the linden genotype. Edgerollings are induced on the small-leaf linden (*T. cordata*), whereas warty galls are formed on the upper side and erineum on the underside of the leaves of silver linden (*T. tomentosa* Moench.). Histochemical analysis shows that extensive thickening of whirled upward roll galls results in both upper epidermal and mesophyll cell differentiation. Repeated anticlinal and periclinal divisions of the upper epidermis leads to the formation of hypodermis consisting of numerous layers. The cells of the hypodermis are closely packed and filled with clearly visible nuclei. The epidermal cells lining the chambers consist of enlarged and divided cells, probably forming the nutritive tissue. Within the chambers, thin long papillae originating from upper epidermal cells are filled with clearly visible starch grains. Transverse sections through the erineum show papillar masses (composed of both simple and compound papillae) on the underside and a thick layer of compactly arranged cells occur under the lower and upper epidermis. Numerous proliferations are the result of non-synchronized periclinal and anticlinal divisions of cells of both upper and lower epidermis.

Within each gall type apart from the nutritive tissue layers, there are numerous cells filled with the material strongly stained with safranin. This staining procedure, locating compounds with phenolic hydroxyl group (Stafford 1988) reveals the accumulation of *o*-dihydroxyphenols in the galls inhabited by mites. Further studies (Kielkiewicz et al. in preparation) show that the abundance of *P. tetratrichus* is markedly lower when mites feed on the leaves of *T. cordata* with a significantly higher level of anthocyanins and condensed tannins than in leaves of *T. tomentosa* and further due to mite infestation, the concentration of both flavonoids and condensed tannins increases strongly in galled leaves of *T. cordata*, whereas condensed tannins are the only compounds which elevate in galled leaves of *T. tomentosa*. In an earlier study, Kane et al. (1997) proved, using both safranin and

phloroglucinol staining procedure, that young (1 week old) pouch galls caused by *E. laevis* on the leaves of European alder, *Alnus glutinosa* Gaertn., are very similar in structural architecture to the galls on leaves of *Alnus incana* (L.) Moench., except for the presence of tannins in the vascular bundle sheaths located in undifferentiated cell layers. Tannin deposits did not appear within bundle sheaths and cells derived from mesophyll until galls of *A. incana* were 3 weeks old. Comparison of internal structure of 3-week-old galls showed that galls of *A. incana* are more differentiated and have more tannin deposits than galls of *A. glutinosa*. Condensed tannins are commonly considered as plant defence compounds. Their deterrent, antifeedant or toxic effects on many arthropod herbivores are well-known (Feeny 1968; Haukioja et al. 1985; Harborne 1993; Bernays and Chapman 1994; Thompson 1994; Smith 2005). Therefore, it is concluded that differences in tannin content between alder genotypes at early stages of gall formation can significantly delay gall development and differentiation of the defensive response. Another known function of tannins and phenolic compounds, especially those located in the outer layer of the galls, is protection of gall-formers from parasitoids, predators and pathogenic infections (Cornell 1983; Taper et al. 1986; Taper and Case 1987; Mound 1994; Hartley 1998).

The presence of tannins in tissues have been reported in several other types of galls (Larew 1982). However, the eriophyoid mite galls that were stained (Johansen 1940) for the presence of tannins gave varying results. Gall and leaflet tissues of ash caused by *Aceria fraxini* Garm. stain poorly for tannins, whereas galls of willow (*Eriophyes aenigma* Walsh.) and filbert (*Phytopus avellanae* Nalepa) show many tanniferous cells in their walls, but their nutritive tissues stain poorly for tannins. The nutritive cells of very young alder galls (caused by *E. laevis*) contain compounds staining positively for tannins. The nutritive tissue accumulates more tannins as the alder gall matures. These observations point to the dynamic nature of the nutritive tissue and are in agreement with data presented by Kane et al. (1997).

Previous results show that the increase of the number and concentration of *o*-dihydroxyphenols is accompanied by the increase of the IAA level within galled leaves of *Pongamia globra* Vent and *Zizyphus jujube* Lamk. in response to mite-gall inducers— *Eriophyes cherianii* Massee and *E. cernuus*, respectively (Balasubramanian and Purushothaman 1972a, b; Tandon and Arya 1980; Tandon 1985). In both cases, the formation of galls is presumably the result of altered hormonal balance. This hypothesis is supported by the fact that phenolic compounds affect plant growth and development by regulating the rate of enzymatic oxidation of IAA and IAA polar transport (Lee et al. 1982; Hutangura et al. 1999). It has been proved that monophenols, POXs and IAA-oxidase enzymes promote IAA oxidation, while di- and polyphenols mostly inhibit the process. Therefore, condensed tannins and other *o*-dihydroxyphenols accumulated within galled leaves infested by the gall mite species might protect auxin from oxidation. Unlike previous studies, other possible mechanisms of auxin metabolism have been proposed for buds of lemon (*Citrus limona* L.) infested by the citrus bud mite (*Aceria sheldoni* (Ewing)) (Ishaaya and Sternlicht 1969). The auxin activity in lemon buds is decreased and phenolics level increased due to mite feeding. Results of further study (Ishaaya and Sternlicht 1971) reveal that in lemon buds infested by *A. sheldoni* the increase of phenolics concentration is related to a twofold increase of PPO activity and conversion of polyphenolics to the quinones that can easily react with proteins to form melanins responsible for the bronzing of lemon buds. Simultaneously, POX activity in mite-infested buds increases threefold, so the rapid oxidation of auxin could inhibit the growth of buds documented earlier (Ishaaya and Sternlicht 1969). Moreover, a decrease of the level of auxin in mite-infested lemon buds is accompanied by an increase in the ribonuclease (RNAase, an enzyme affecting the

build-up of polysomal and ribosomal RNA (ribonucleic acid)) activity, which suggests a relationship between RNAase and auxin. Injured or strongly infested citrus buds are not suitable to be a host for *A. sheldoni*.

The majority of recent cytological and histochemical studies are consistent with previous results concerning biochemistry and the structure of galled tissues (the small parenchyma cells with enlarged nuclei and dense cytoplasm rich in nutritive compounds—starch and proteins). For example, in the leaves of *Convolvulus arvensis* L. infested by *Aceria malherbae* Nuzz., the tissue hypertrophy and hyperplasia are observed in the zone of the main vein including epidermal cells of lower leaf surface (Rancic and Petanovic 2002b), whereas the epidermal cells of upper surface of leaves appear unchanged. Within palisade parenchyma, small cells with dense cytoplasm and prominent nuclei are considered to be nutritive tissue. Similarly, epidermal cells of the fern (*Lygodium microphyllum* subpinnae) respond to the feeding of *Floracarus perrepae* Knichinicki and Boczek by a great increase in size, cytoplasmatic density and division activity to eventually form well developed nutritive tissue within the roll galls (Freeman et al. 2005). The list of gall mite–host plant interactions expanded owing to the recent description and quantification of anatomical alterations a single host plant, sycamore maple (Rančić and Petanović 2008), and *A. erinea* (Nalepa) and *A. tristriata* (Nalepa) on common walnut leaves (Dulić-Stojanović et al. 2001) in which the macro-morphology of the gall is specific for the mite species. In each case, micro-morphology of galls is very similar and begins with the repeated anticlinal and periclinal divisions of lower epidermal cells, which leads to the formation of both the nutritive and mesophyll tissue not differentiating into palisade and spongy tissue.

Mite gall inducers and the resistant host plant

Only one case of unquestionable incompatible eriophyoid–host plant interaction between *Aceria lycopersici* (syn. *A. cladophthirus*) and resistant *S. dulcamara* plant has been documented (Bronner et al. 1991a; Westphal et al. 1981, 1990b) and clearly separated from compatible interaction (Westphal and Manson 1996). However, feeding of the blackberry gall mite (*Cecidophyopsis ribis* Westwood) that induces local HR within bud of red currant instead of gall (typical for blackcurrant plants) may be treated as a further example of an incompatible eriophyoid–host fix interaction (Westphal et al. 1996).

According to Walling (2000), compatible and incompatible interactions are distinguished by the rate of recognition and the presence/absence of HR. In the case of *A. lycopersici* and a resistant genotype of *S. dulcamara*, the mite begins feeding by puncturing the epidermal cell. Injured cells then collapse, next plasmolysis and shrinkage of the nucleus in the adjacent cells appear within 10 min, leading to cell death and the development of a local HR that prevents further development of mites. The lack of callose and lignin and the presence of polyphenol oxidation compounds are found within mite-injured cells (Westphal et al. 1981). The lack of lignin (Westphal et al. 1981; Bronner et al. 1991a), deposition of callose on the cell walls (Westphal et al. 1996), accumulation of phytoalexin and high activity of hydrolytic (Bronner et al. 1991a) and oxidative enzymes (Bronner et al. 1991b) can be determined in cells bordering the HR area. A detailed study by Bronner et al. (1991a) reports the accumulation of chitinase and β-1,3-glucanase as a response of *S. dulcamara* caused by the feeding of *A. cladophthirus*. This indicates that hydrolytic enzymes may contribute to the defence response of resistant plants by damaging mite peritrophic membranes (Mayer et al. 1996). However, it is still unknown if the chitinases or glucanases negatively affect mite fitness via toxin production or if they directly affect them. Enhanced activity of POXs in leaves of genotypes of *S. dulcamara*,
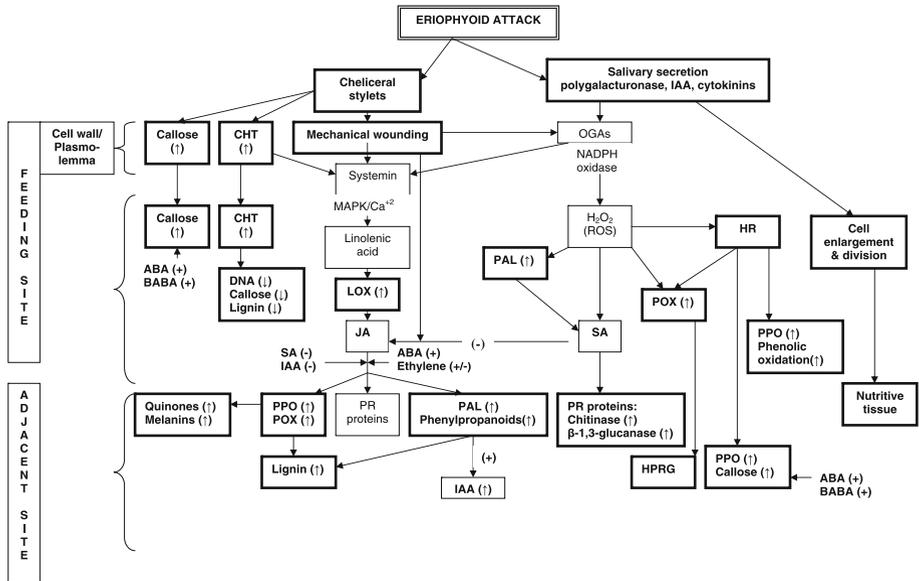
Fig. 1 Documented and putative compounds/events of pathways regulating host plant responses to eriophyoid attack (adopted from the text and references therein). Abbreviations: *MAPK* the mitogen-activated protein kinases, *NADPH oxidase* nicotinamide adenine dinucleotide phosphate oxidase, *ROS* reactive oxygen species, the remaining abbreviations are in the text. *Upward arrow* and *downward arrow* refer to increase and decrease, respectively; '+' and '−' refer to positive and negative modulation; *bold lettering* and *thicker frame* of rectangles refer to known component/event in the plant–eriophyoid interaction, *non-bold lettering* and *thin frame* of *rectangles* refer to unknown component/event in the plant–eriophyoid interaction

resistant to *A. cladophthirus*, is related to the enhancement of three major POX isozymes with molecular mass ranging from 33 to 35 KDa (Bronner et al. 1991b). The highest activity is found for POXs extracted from intercellular spaces. Histochemical detection methods with chlorine sulfite or phloroglucinol specific for syringyl propane units and coniferyl aldehyde groups, respectively documented the lack of lignification of tissues around the *A. cladophthirus*-induced HR in resistant genotypes of *S. dulcamara* (Westphal et al. 1981; Bronner et al. 1991b). Therefore, it is concluded that the increased activation of POXs during the HR formation is more involved in the hydroxyproline-rich glycoproteins (HPRG) than lignin biosynthesis (Bronner et al. 1991b). Several other abiotic and biotic stresses (e.g. pathogen infection, mechanical wounding) trigger HR accompanied or not by HPRG formation. Therefore, the response of a resistant plant genotype to *A. lycopersici* feeding cannot be considered as a specific defence reaction (Westphal et al. 1996).

An overview of documented and putative host plant responses initiated by vagrants and gall-formers in compatible and incompatible interactions is presented in Fig. 1.

Selected metabolic responses in host plants in relation to eriophyoid mite feeding: recent and neglected studies

The effects of both vagrant and non-vagrant eriophyoid mites on the metabolism of attacked host plants are extremely variable. While in some eriophyoid-infested plants or

plant organs, the rate of photosynthesis, photorespiration, respiration, transpiration, the concentration of chlorophylls and other pigments, carbohydrates, proteins, amino acids, and mineral nutrition increase, in other cases the rate of physiological processes and the concentration of primary and secondary plant compounds decrease (Rajagopal et al. 1970; Boczek 1974; Czeczuga 1975; Zawadzki 1975; Royalty and Perring 1989; Wilson and O'Dowd 1990; Flechtmann and Berti-Filho 1994; Easterbrook and Palmer 1996; Vaneckova-Skuhrava 1996; Kozlowski and Zielinska 1997; Kozlowski 1998; Larson 1998; Spieser et al. 1998; Kondo and Hiramatsu 1999; Shi and Tomczyk 2001; Haque and Kawai 2002; Tomczyk and Boczek 2006; Duso et al. 2008). Generally, the consequences of eriophyoid mite feeding depends on the eriophyoid genotype (or even race), density and period of feeding, and strongly differs depending on the host plant species, cultivar, organ age and environmental conditions.

Recent and neglected studies focus on the differences in the composition, concentration and the relation between primary and secondary compounds not only in mite-infested organs but also in the entire shoot. For example, it was shown (Kozlowski 1998) that at a density of 22–27 A. schlechtendali specimens per 1 cm^2 of a leaf, the ratio of the total phenolic compounds to carbohydrates increase from 3:1 in control to 5:1 in infested leaves in a susceptible apple cultivar (Pionier), which finally decreases the palatability of injured host plant to mites. Similarly, the results obtained for field grown blackberry cultivars infested by blackberry rust mite, Epitrimerus gibbosus (Nalepa), show that 3 weeks of mite feeding (at a density of 600–1,000 specimens/leaf) changed the nutritional value and palatability of infested leaves (Shi and Tomczyk 2001). In leaves of a thornfree cultivar, the increase in phenolic concentration is accompanied by the decreases in carbohydrate concentration, whereas in leaves of a thornless evergreen cultivar an increase in soluble protein concentration was noticed. Since the appropriate balance between feeding inhibitors and stimulators is a very important factor in eriophyoid–plant interaction, it is believed that the rise in the value of the ratio of total phenolics to total carbohydrates/proteins in infested blackberry leaves results in a decrease of successful mite feeding.

It is also documented that other gall-forming species—the walnut erineum mite, Aceria tristriatus (Nalepa); the apple leaf blister mite, Eriophyes mali (Nalepa); and the pear leaf blister mite, Eriophyes pyri (Pgst.)—induce different changes in the metabolism of galled leaves of walnut, apple, and pear trees, respectively (Tomczyk and Boczek 2006). Three types of responses that can change food resource quality to advantage of eriophyoids and/or other herbivorous arthropods feeding are distinguished. The first type of response, found in mite-infested walnut leaves, shows no changes in soluble proteins and a strong decrease in carbohydrate concentrations and a slight decrease of carbohydrate content in morphologically unaltered leaf tissues adjacent to the mite erinea. This suggests that erinea formed by A. tristriatus can act as a sink for carbohydrates which compete for assimilates with the adjacent ungalled leaf area. Additionally, the concentration of phenolics remains almost unchanged in relation to the uninjured control leaves. However, a slight increase in the concentration of these compounds occurs within the leaf tissue between galls. Although mite erinea occupied not more than 15–20% of the total leaf area, a strong reduction in the rate of photosynthesis (more than fivefold) is observed in galled leaves of walnuts. The second type of response, found in mite-infested apple leaves, shows a gradual increase in soluble protein concentrations related to the severity of damage, which is accompanied by a lack of changes in total carbohydrate content and rise of the concentration of phenolics. The third type of response, found in mite-infested pear leaves, first shows a strong increase then a rapid decrease in soluble proteins, for slightly and strongly galled leaves,

respectively. Simultaneously, the phenolic compounds decrease probably as a result of their oxidation, as it was suggested by Ishaaya and Sternlicht (1971).

The recent, abovementioned results are consistent with previous data regarding differences in metabolic capacity of linden leaves (*T. cordata*) galled by *E. tiliae* (Boczek 1974; Czeczuga 1975). Boczek (1974) showed a distinct decrease in the content of carbohydrates in *E. tiliae*-infested leaves. However, the distribution of ^{14}C assimilates among the leaf blade, midribs and galls was not uniform. The accumulation of ^{14}C assimilates in growing galls and their lower level in the blade and midrib was documented. This is in line with the nutrition hypothesis postulating that the gall is a sink of nutritive compounds, which determines the high performance of gall formers. Additionally, when a part of the blades of a healthy linden leaf was treated with kinetin (a chemical analogue of cytokinin), a higher retention of ^{14}C assimilates was observed in the treated leaf area than in the untreated one. Therefore, it was concluded that this class of plant growth regulators promoting cell division is involved in the metabolism of eriophyoid-infested leaves. A diverse metabolic capacity of *T. cordata* galls and leaf blade due to *E. tiliae* var. *rudis* Nal. was also reported by Czeczuga (1975) who analysed the composition of carotenoids. The analyses show that seven of them occur in the leaf blade and are absent in the galls, whereas three carotenoids are located specifically within galls. It is concluded that the feeding of *E. tiliae* accelerates the biosynthesis of some carotenoids and inhibits the biosynthesis of others.

In one of the later studies (Wilson and O'Dowd 1990) it was shown that galled leaves within a heavy galled portion of shoots of wild plum (*Prunus americana* Marsh.) infested by the plum fingergall mite, *Phytoptus emarginatae* (Keifer) strongly reduced the size of the photosynthetic area of the neighbouring leaves in comparison to leaves that did not develop near galls. This suggests the reallocation of resources within the mite-attacked shoot. Similarly, Larson (1998) showed that the presence of galls formed by *Phytoptus cerasicrumena* Walsh reduced not only the photosynthetic rate of galled leaves of naturally grown wild cherry plants (*Prunus scrotina* Poit. & Turpin) (by 47% compared to ungalled leaves in ungalled areas of plant), but also the photosynthesis of neighbouring ungalled leaves within the same shoot (by 24% compared to ungalled leaves on gall-free shoots). It is concluded that sink competition for nutrients between developing leaves and growing gall tissue might account for the negative impacts of sink-inducing galls on photosynthesis. Moreover, galled leaves significantly increased stomatal conductance and internal CO_2 compared to ungalled leaves, and ungalled leaves neighbouring galled leaves had a slightly lower stomatal conductance compared to ungalled leaves on ungalled control shoots. In this case, there is a low probability that *P. cerasierumena* could reduce the photosynthesis intensity by reducing gas exchange through stomatal damage, which was suggested in the case of the free living mite, *A. cornutus* (Andersen and Mizell 1987), or *A. lycopersici* (Royalty and Perring 1996).

Spieser et al. (1998) presented evidence that a high number of *A. schlechtendali* (4–5,000 individuals/leaf) directly damaging the leaf epidermis and indirectly inducing changes in mesophyll cells of leaves of young apple trees grown in Switzerland reduced the net CO_2 exchange by as much as 65%. Simultaneously, the transpiration process is affected due to partially open stomata, and decrease of guard cell turgor, as well as the desiccation of epiderma and parenchyma cells. Depending on the cultivar, *A. schlechtendali* infestation affects flower formation and the quality of apple yield in different ways. For example, fresh fruit weight, soluble carbohydrate content and skin colour intensity showed a stronger decrease in Jonagold compared to Golden Delicious, suggesting that the latter cultivar is relatively resistant to *A. schlechtendali* infestation. However, in contrast,

observations of workers in Trentino (North-Eastern Italy), showed that the trees of Golden Delicious were more susceptible to moderate and high mite densities in summer (Angeli et al. 2007; Duso et al. 2008). At densities of 14,523 and 31,750 mite-days/leaf, the size, weight and colour intensity of fruits decreased. It is concluded that environmental and agricultural factors could affect the final response of Golden Delicious apple trees to eriophyoids, as it was suggested earlier by Easterbrook and Palmer (1996).

Competition mediated by eriophyoid-induced plant responses

Eriophyoid mites can markedly alter the quality of directly infested plant tissues, as well as of tissues located far from the site of mite-feeding. Consequently, mites can influence the behaviour and feeding of other herbivorous arthropods. One of the first examples was documented by Croft and Hoying (1977), who stated that infestation of apple trees by large *A. schlechtendali* populations, early in the season, inhibits the development of the red spider mite (*Panonychus ulmi* (Koch)) population. A recent study has shown that a previous infestation of willow (*Salix viminalis* L.) genotypes by gall mite, *Aculops* spp. had no significant effect on the larval survival of *Dasineura marginemtorquens* Bremi. (Diptera: Cecidomyiidae) (Ollerstam 2002). In other compatible interactions, for example between *T. solani*, *P. oleivora*, *A. lycopersici* and susceptible host plants, food resource quality within infested organs favours further development of mites (Royalty and Perring 1996; Westphal and Manson 1996; Westphal et al. 1996). It seems that the incompatible interaction such as between *A. cladophthirus* and resistant plants of *S. dulcamara* may have ecological significance. The attack of *A. cladophthirus* triggers the true HR in resistant *S. dulcamara* plants, which causes the death of *A. cladophthirus* and increases the mortality of the next attacker, *T. solani* (Westphal et al. 1991). The HR allows the mite-infested plants to continue growing normally, but does not protect *S. dulcamara* plants from the subsequent attack of the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) (Westphal et al. 1990b). In this case, there appears to be a strong stimulation of *T. urticae* female fecundity and acceleration of *T. urticae* development on leaves previously infested by *A. cladophthirus*.

Comparing the effect of *Yucca* spp. leaf damage by previous *Cecidophyopsis hendersoni* (Keifer) infestation and carborundum powder treatment on the mite behaviour, Michalska and Shi (2004) showed that males deposit significantly more spermatophores on mite-infested than on non-infested leaves. In contrast, mechanically damaged leaves elicit inhibition of spermatophore deposition by *C. hendersoni* males. It is concluded that only mite-infested leaves produce a specific signal(s) informing that the infested plant is still suitable for colonization. The nature of the signal is yet to be elucidated. It has recently been determined that in the plant response to mechanical wounding ABA and ethylene are involved in transducing wound signals (oligopeptide systemin, jasmonic acid (JA)) (O'Donnell et al. 1996; Walling 2000; Gatehouse 2002). McCoy and Albrigo (1975) showed that leaves and fruits of citrus trees visibly injured by *P. oleivora* emitted ethylene in such amounts that the acceleration of organ degreening is visible. Recently, the emission of ethylene by tulip bulbs (*Tulipa gesneriana* L., cv. Yokohama) in response to the dry bulb mite, *Aceria tulipae* (Keifer) indicates the occurrence of wound response (Lesna et al. 2004). In this case, ethylene may be a putative factor mediating changes in bulb metabolism, which most probably affects the success of *A. tulipae* control with predatory mites. A detailed study on the involvement of signalling molecules in the plant defence response to eriophyoid is needed to elucidate the mechanism.

Concluding remarks and recommendation for future studies

Over the last 15 years, evidence permits us to present an updated review of induced plant response to eriophyoid mite attack related to cytological, biochemical and physiological changes. However, the data presented here show that the mechanisms of both susceptible and resistant plant responses to vagrant or gall-former attack are very speculative (Fig. 1). To improve understanding of plant–eriophyoid interaction with particular emphasis on signalling events, molecular and genetic methods should be applied. DNA microarray technology, which allows thorough analysis of the gene expression on the mRNA level, should be used to explore the complex (compatible and incompatible) interactions between eriophyoids and plants. We predict that the comparison of changes of mRNA abundance associated with HR necrosis or gall formation/maintenance would point out those transcripts, which are involved in each of the processes. This approach should also allow to assign a putative function to genes that show differential expression in response to eriophyoid infestation. Furthermore, molecular analysis will lead to a better understanding of the data on plant modifications upon eriophyoid attack documented to date. Future studies should also consider, at the gene level, the mechanisms of plant recovery after eriophyoid damage. Finally, attempts should be made to identify and characterize, at a molecular level, proteins that are secreted by eriophyoids during the process of feeding.

References

Adie BAT, Pérez-Pérez J, Pérez-Pérez MM, Godoy M, Sánchez-Serrano J-J, Schmelz EA, Solano R (2007) ABA is a signal for plant resistance to pathogens affecting JA biosynthesis and the activation of defences in *Arabidopsis*. Plant Cell 19:1665–1681

Amrine JW Jr, Stasny TAH, Flechtmann CHW (2003) Revised keys to world genera of the Eriophyoidea (Acari: Prostigmata). Indira Publishing House, Michigan

Andersen PC, Mizell RF III (1987) Impact of the peach silver mite, *Aculus cornutus* (Acari: Eriophyoidea), on leaf gas exchange of 'Flordaking' and 'June Gold' peach trees. Environ Entomol 16:660–663

Angeli G, Rizzi C, Dorigoni A, Ioriatti C (2007) Population injury levels of the apple rust mite *Aculus schlechtendali* (Nal.) on Golden Delicious and Red Delicious apple fruits. Bull OILB/SROP 30(4):255–260

Arimura G, Tashiro K, Kuhara S, Nishioka T, Ozawa R, Takabayashi J (2000) Gene responses in bean leaves induced by herbivoy and by herbivore-induced volatiles. Biochem Biophys Res Commun 277:305–310

Asselbergh B, De Vleesschauwer D, Höfte M (2008) Global switches and fine-tuning-ABA modulates plant pathogen defense. Mol Plant Microbe Interact 21:709–719

Baker GT, Chandrapatya A (1989) Plant abnormalites induced by eriophyid mites on several species of plants in Thailand. J Electron Microsc Soc Thail 3(2):39–47

Balasubramanian M, Purushothaman D (1972a) Indole acetic acid in the eriophyid mite gall on *Pongamia glabra* Vent. caused by *Eriophyes cheriani* Massee (Eriophyidae: Acarina). Labdev J Sci Tech 10-B(3–4):172–173

Balasubramanian M, Purushothaman D (1972b) Phenols in healthy and galled leaves of *Pongamia glabra* Vent. caused by an eriophyid mite, *Eriophyes cheriani* Massee (Eriophyidae: Acarina). Ind J Exp Biol 10:394–395

Bernays EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Chapman & Hall, New York

Bi JL, Murphy JB, Felton GW (1997) Antinutritive and oxidative components as mechanisms of induced resistance in cotton to *Helicoverpa zea*. J Chem Ecol 23:97–117

Boczek J (1974) Ecology of eriophyid mites on economic crops. Final report E21-ENT-24/FG-Po-245

Boczek J, Griffiths DA (1994) Structure and systematic of eriophyid mites (Acari: Eriophyoidea) and their relationship to host plants. In: Williams MAJ (ed) Plant galls, systematics association special volume 49. Calerdon Press, Oxford, pp 119–129

Bowles DJ (1990) Defense-related proteins in higher plants. Ann Rev Biochem 59:873–907

Bronner R, Westphal E (1987) Modifications des noyaux des cellules epidermiques foliaires de Solanacees soumises a l'action parasitaire d'un acerien cecidogene, *Eriophyes cladophthirus*. Premier Congres de la Societe Francaise de Phytopathologie, Rennes, Reumes:39

Bronner R, Westphal E, Dreger F (1989) Chitosan, a component of the compatible interaction between *Solanum dulcamara* L. and the gall mite *Eriophyes cladophthirus* Nal. Physiol Mol Plant Pathol 34:117–130

Bronner R, Westphal E, Dreger F (1991a) Pathogenesis-related proteins in *Solnum dulcamara* L. resistant to the gall mite *Aceria cladophthirus* Nalepa (syn. *Eriophyes cladophthirus* Nal.). Physiol Mol Plant Pathol 38(2):93–104

Bronner R, Westphal E, Dreger F (1991b) Enhanced peroxidase activity associated with hypersensitive response of *Solnum dulcamara* L. to the gall mite *Aceria cladophthirus* (Acari: Eriophyoidea). Can J Bot 69:2192–2196

Cohen Y, Reuveni M, Baider A (1999) Local and systemic activity of BABA (DL-3-aminobutyric acid) against *Plasmopora viticola* in grapevines. Eur J Plant Pathol 105:351–361

Cornell HV (1983) The secondary chemistry and complex morphology of galls formed by the Cynipinae (Hymenoptera): why and how? Am Midland Naturalist 110:225–234

Croft BA, Hoying SA (1977) Competitive displacement of *Panonychus ulmi* (Koch) by *Aculus schlechtendali* Nalepa in apple orchards. Can Entomol 109:1025–1034

Czeczuga B (1975) The carotenoid content of galls produced by *Eriophyes tiliae* var. Rudis Nal. (Acarina) on *Tilia cordata* Mill., leaves. Marcellia 38:223–225

De Lillo ER, Monfreda R (2002) La 'saliva' degli acari Eriophyoidea: messa a punto di un di indagine e risultati preliminari. Atti XiX Congresso nazionale italiano di Entomologia, catania 10–15 giugno 2002, pp 1365–1370

De Lillo ER, Monfreda R (2004) 'Salivary secretions' of eriophyoids (Acari: Eriophyoidea): first results of an experimental model. Exp Appl Acarol 34(3–4):291–306

Duffey SS, Felton GW (1991) Enzymatic anti nutritive defenses of the tomato plant against insects. In: Hedin PA (ed) Naturally occurring pest bioregulators. American chemical society symposium series 449, Dallas. American Chemical Society, Washington, DC, pp 166–197

Duffey SS, Stout MJ (1996) Anti nutritive and toxic compounds of plant defense against insects. Arch Insect Biochem Physiol 32(1):3–37

Dulić-Stojanović Z, Stevanović B, Petanović R (2001) Morfo-anatomske promene listova oraha izazvane eriofidama *Aceria erinea* (Nal.) i *A. tristriata* (Nal.). Zaštita bilja 52 (2) 236:99–114

Duso C, Castagnoli M, Simoni S, Angeli G (2008) The impact of eriophyoids on crops: new and old case studies. In: Bertrand M, Kreiter S, McCoy K, Migeon A, Navajas M, Tixter MS, Vial L (eds) Integrative acarology. Proceedings of the 6th Congress of the European Association of Acarologists, Montpellier, 21–25 July 2008, pp 317–324

Easterbrook MA, Fuller MM (1986) Russeting of apples caused by apple rust mite *Aculus schlechtendali* (Acarina: Eriophyidae). Ann Appl Biol 109:1–9

Easterbrook MA, Palmer JW (1996) The relationship between early-season leaf feeding by apple rust mite, *Aculus schlechtendali* (Nal.), and fruit set and photosynthesis of apple. J Hort Res 71(6):939–944

Feeny P (1968) Effect of oak leaf tannins on larval growth of the winter moth, *Operophtera brumata*. J Insect Physiol 14:805–817

Felton GW, Donato K, Delvecchio RJ, Duffey SS (1989) Activation of plant foliar oxidases by insect feeding reduces nutritive quality of foliage for noctuid herbivores. J Chem Ecol 15:2667–2694

Flechtmann CHW, Berti-Filho E (1994) Effect of feeding by two species of eriophyid mites (Acari, Eriophyidae) on the mineral content of their host plants. Internat J Acarol 20(1):61–65

Flors V, Ton J, Jakab G, Mauch-Mani B (2005) Abscisic acid and callose: team players in defence against pathogens? J Phytopathol 153:377–383

Forslund K, Pettersson J, Bryngelsson T, Jonsson L (2000) Aphid infestation induces PR-proteins differently in barley susceptible or resistant to the bird-cherry-oat aphid (*Rhapalosiphum padi*). Physiol Plant 110:496–502

Freeman TP, Goolsby JA, Ozman SK, Nelson DR (2005) An ultrastructural study of the relationship between the mite *Floracarus perrepae* Knihinicki & Boczek (Acariformes: Eriophyidae) and the fern *Lygodium microphyllum* (Lygodiaceae). Aust J Entomol 44:54–61

Gatehouse JA (2002) Plant resistance towards insect herbivores: a dynamic interaction. New Phytol 156:145–169

Gibson RW (1974) Studies of the feeding behavior of the eriophyid mite *Abacarus hystrix*, a vector of grass viruses. Ann Appl Biol 78:213–217

Grinberg M, Perl-Treves R, Palevsky E, Shomer I, Soroker V (2005) Interaction between cucumber plants and the broad mite, *Polyphagotarsonemus latus*: from damage to defense gene expression. Entomol Exp Appl 115:135–144

Hadwiger LA (1999) Host-parasite interactions: elicitation of defense responses in plants with chitosan. In: Jolles P, Muzarelli RAA (eds) Chitin and Chitinases. Birkhauser Verlag, Basel, pp 185–200

Haque MM, Kawai A (2002) Population growth of tomato russet mite, *Aculops lycopersici* (Acari: Eriophyidae) and its injury effect on growth of tomato plants. J Acarol Soc Jpn 11(1):1–10

Harborne JB (1993) Introduction to ecological biochemistry. Academic Press Limited, London

Hartley SE (1998) The chemical composition of plant galls: are levels of nutrients and secondary compounds controlled by the gall-former? Oecologia 113:492–501

Haukioja E, Niemela P, Siren S (1985) Foliage phenols and nitrogen in relation to growth, insect damage and ability to recover after defoliationin the mountain birch *Betula pubescens* ssp. tortosa. Oecologia 65:214–222

Hesse M (1971) Über Mehrkernigkeit und Polyploidisierung der Nahrgewebe einiger Milbengallen. Österr Bot Z 119:74–93

Hislop RG, Jeppson LR (1976) Morphology of mouthparts of several species of phytophagous mites. J Econ Entomol 69:1125–1135

Hutangura P, Mathesius U, Jones MGK, Rolfe B (1999) Auxin induction is a trigger for root gall caused by root-knot nematodes in white clover and is associated with the activation of the flavonoid pathway. Aust J Plant Physiol 26:221–231

Inbar M, Doostdar H, Sonoda RM, Leibee GL, Mayer RT (1998) Elicitors of plant defensive systems reduce insect densities and disease incidence. J Chem Ecol 24(1):135–149

Inbar M, Mayer R, Doostdar H (2003) Induced activity of pathogenesis related (PR) proteins in aphid galls. Symbiosis 34:293–300

Iriti M, Faoro F (2007) Review of innate and specific immunity in plants and animals. Mycopathologia 164:57–64

Ishaaya I, Sternlicht M (1969) Growth accelerators and inhibitors in lemon buds infested by *Aceria sheldoni* (Ewing) (Acarina: Eriophyidae). J Exp Bot 20(4):796–804

Ishaaya I, Sternlicht M (1971) Oxidative enzymes, ribonuclease, and amylase in lemon buds infested with *Aceria sheldoni* (Ewing) (Acarina: Eriophyidae). J Exp Bot 22(70):146–152

Jacobs AK, Lipka V, Burton RA, Panstruga R, Strizhov N, Schulze-Lefert P, Fincher GB (2003) An *Arabidopsis* callose synthase, GSL5, is required for wound and papillary callose formation. Plant Cell 15:2503–2513

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. Univ. Calif. Press, Berkeley, pp 327–614

Jimenez DR, Yokomi RK, Mayer RT, Shapiro JP (1995) Cytology and physiology of silverleaf white-fly induced squash silverleaf. Physiol Mol Plant Path 46:227–242

Johansen DA (1940) Plant microtechnique. Mc Grow-Hill, New York

Kane NA, Jones CS, Vuorisalo T (1997) Development of galls of *Alnus glutinosa* and *Alnus incana* (Betulaceae) caused by the eriophyid mite *Eriophyes laevis* (Nalepa). Int J Plant Sci 158(1):13–23

Kant MR, Ament K, Sabelis MW, Haring MA, Scuurink RC (2004) Differential timing of spider mite-induced direct and indirect defenses in tomato plants. Plant Physiol 135:483–495

Kauss H (1996) Callose synthesis. In: Smallwood M, Knox JP, Bowles DJ (eds) Membranes: specialized functions in plants. Bios Sci Publ, Guildford, pp 77–92

Keifer HH (1959) Eriophyid studies XXVI. Bull Calif Dept Agric 47:271–281

Keifer H, Baker E, Kono T, Delfinado M, Styer W (1982) An illustrated guide to plant abnormalities caused by Eriophyid mites in North America. USDA Agriculture Handbook Number 573

Kielkiewicz M (1996) Hypersensitive response of tomato leaf tissues towards *Tetranychus cinnabarinus* Boisd. (Tetranychidae) feeding. In: Mitchell R, Horn DJ, Needham GR, Welbourn VC (eds) Acarology IX. Ohio Biological Survey, Columbus, pp 47–50

Kielkiewicz M (1998) Concentration of some phenylpropanoid compounds and the activity of oxidative enzymes within tomato plant (*Lycopersicon esculentum* Mill.) locally infested by the carmine spider mite (*Tetranychus cinnabarinus* Boisd.). Zesz Nauk Ochr Srod 214:41–47

Kielkiewicz M (2002) Influence of carmine spider mite, *Tetranychus cinnabarinus* Boisd. (Acarina: Tetranychidae) feeding on ethylene production and the activity of oxidative enzymes in damaged tomato

plants. In: Bernini F, Nannelli R, Nuzzaci G, de Lillo E (eds) Acari: phylogeny and evolution, adaptations in mites and ticks. Kluwer Academic Publishers, Dordrecht, pp 389–392

Kielkiewicz M (2003) Defensive strategies of glasshouse tomato (*Lycopersicon esculentum* Mill.) plants against the carmine spider mite (*Tetranychus cinnabarinus* Boisd., Acari: Tetranychidae) infestation. Treatises and Monographs. Publications of Warsaw Agricultural University, Warsaw

Kondo A, Hiramatsu T (1999) Analysis of peach tree damage caused by peach silver mite, *Aculus fockeui* (Nalepa et Trouessart) (Acari: Eriophyidae). Jpn J Appl Entomol Zool 43(4):189–193

Kozlowski J (1998) Factors determining susceptibility and response of apple tree cultivars to the applerust mite *Aculus schlechtendali* (Nalepa). Rozprawy Naukowe IOR, Zeszyt 2, Poznan

Kozlowski J, Zielinska L (1997) Cytological changes in apple leaves infested with the apple rust mite– Aculus schlechtendali (Nal.) (Acarina: Eriophyidea). J Plant Prot Res 37(1/1):72–84

Krantz GW (1973) Observations on the morphology and behavior of the Filbert Rust Mite, *Aculus comatus* (Prostigmata: Eriophyoidea) in Oregon. Ann Entomol Soc Am 66:709–717

Krantz GW, Lindquist EE (1979) Evolution of phytophagous mites (Acari). Ann Rev Entomol 24:121–158

Larew HG (1982) A comparative anatomical study of galls caused by the major cecidogenic groups, with special emphasis on nutritive tissue. Dissertation, Oregon State Univ., Cornvallis

Larson KC (1998) The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. Oecologia 115(1/2):161–166

Lee TT, Starratt AN, Jevnikar JJ (1982) Regulation of enzymatic oxidation of indol-3-accetic acid by phenols: structure activity relationships. Phytochemistry 21(3):517–523

Lesna I, Conijn CGM, Sabelis MW (2004) From biological control to biological insight: rust-mite induced change in bulb morphology, a new mode of indirect plant defence? Phytophaga XIV:285–291

Lindquist EE (1996) External anatomy and systematics. External anatomy and notation of structures. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—their biology natural enemies and control. Elsevier, Amsterdam, pp 3–31

Ma RZ, Reeze JC, Black LV, Bramel-Cox PJ (1990) Detection of pectinesterase and polygalacturonase from salivary secretions of living greenbugs *Schizaphis graminum* (Homoptera: Aphididae). J Insect Physiol 36:507–512

Mani MS (1964) Ecology of plant galls. W Junk Publisher, The Hague

Mauch-Mani B, Mauch F (2005) The role of abscisic acid in plant–pathogen interactions. Curr Opin Plant Biol 8:409–414

Mayer J (1952) Rapports entre l'evolution cytologiques du tissue nourticier D'*Eriophyes macrorhynchus* Nal. et la biologique de l' Acarien. CR Soc Biol 233:1545–1547

Mayer RT, McCollum TG, McDonald RE, Polston JE, Doostdar H (1996) *Bemisia* feeding induces pathogenesis-related proteins in tomato. In: Gerling D, Mayer RT (eds) Taxonomy, biology, damage control and management. Intercept, Andover, pp 179–188

McCoy CW (1996) Stylar feeding injury and control of Eriophyoid mites in citrus. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 513–526

McCoy CW, Albrigo LG (1975) Feeding injury to the orange caused by the citrus rust mite, *Phyllocoptruta oleivora* (Prostigmata: Eriophyoidea). Ann Entomol Soc Am 68:289–297

Meyer J (1987) Plant galls and gall inducers. Gebruder Borntraeger, Berlin

Michalska K, Shi A (2004) A first view on factors influencing spermatophore deposition by the eriophyid mite *Cecidophyopsis hendersoni* (Keifer). Phytophaga XIV:141–148

Miles PW, Peng Z (1989) Studies on the salivary physiology of plant bugs: detoxification of phytochemicals by the salivary peroxidase of aphids. J Insect Physiol 35:865–872

Monfreda R, Spagnuolo M (2004) Enzyme activity of an eriophyoid 'salivary' secretion: preliminary report of polygalacturonase. Phytophaga 14:611–614

Moran PJ, Thompson GA (2001) Molecular responses to aphid feeding in *Arabidopsis* in relation to plant defense pathways. Plant Physiol 125:1074–1085

Mound LA (1994) Plant galls. In: Williams MAJ (ed) Systematics association special volume no. 49. Clarendon Press, Oxford, pp 131–149

Nuzzaci G (1976) Feeding behavior of eriophyid mites. Entomologica (Bari) 12:75–80

Nuzzaci G (1979) Contributo alla conoscenza dello gnathosoma degli Eriofidi. Entomologica 15:73–101

Nuzzaci G, Alberti G (1996) Internal anatomy and physiology. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites their biology natural enemies and control. Elsevier, Amsterdam, pp 101–150

O'Donnell PJ, Calvert C, Atzorn R, Wasternack C, Leyser HMO, Bowles DJ (1996) Ethylene as a signal mediating the wound response of tomato plants. Science 274(5294):1914–1917

Oldfield GN (1996a) Diversity and host plant specificity. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 195–216

Oldfield GN (1996b) Toxemias and other non-distortive feeding effects. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 243–250

Oldfield GN (2005) Biology of Gall-inducing Acari. In: Raman A, Schaefer CW, Withers TM (eds) Biology, ecology and evolution of gall-inducing arthropods. Science, Portland, pp 35–57

Ollerstam O (2002) Induced resistance in basket willow against a gall midge. Dissertation. Swedish University of Agricultural Science, Uppsala

Pećinar IB, Stevanović B, Rector G, Petanović R (2007) Anatomical injuries caused by *Leipothrix dipsacivagus* Petanovic & Rector on cut-leaf teasel, *Dipsacus laciniatus* L. (Dipsacaceae). Arch Biol Sci 59(4):363–367

Pećinar IB, Stevanović B, Rector G, Petanović R (2008) Morphological injury of cut-leaf teasel, *Dipsacus laciniatus* L. (Dipsacaceae) induced by the eriophyid mite *Leipothrix dipsacivagus* Petanovic et Rector (Acari: Eriophyoidea). J Plant Int 4(1):1–6

Petanović R, Kielkiewicz M (2010) Plant–eriophyoid mite interactions: specific and unspecific morphological alterations. Part II. Exp Appl Acarol. doi: 10.1007/s10493-009-9328-1

Rajagopal K, Jayaraj S, Subramanium TR (1970) Physiological mechanism of resistance in jasmine to blister mite *Aceria jasminii* C. (Eriophyidae: Acarina). Indian J Exp Biol 8:44–47

Rančić D, Petanović R (2002a) Anatomical alternations of *Galium mollugo* L. leaves caused by eriophyoid mite *Aculus anthobius* (Nal.). Acta Entomol Serb 7(1/2):119–128

Rančić D, Petanović R (2002b) Anatomical alternations of *Convolvulus arvensis* L. leaves caused by eriophyoid mite *Aceria malherbae* Nuzz. Acta Entomol Serb 7(1/2):129–136

Rančić D, Petanović R. (2008) Differences in the leaf morphology of sycamore maple infested by two congeneric eriophyid species at Tara National Park in western Serbia. In: Bertrand M, Kreiter S, McCoy K, Migeon A, Navajas M, Tixter M-S, Vial L (eds) Integrative Acarology. Proceedings of the 6th congress of the european association of acarologists, Montpellier, 21–25 July, 2008, pp 326–330

Rančić D, Stevanović B, Petanović R, Magud B, Toševski I, Gassmann A (2006) Anatomical injury induced by eriophyid mite *Aceria anthocoptes* on the leaves of *Cirsium arvense*. Exp Appl Acarol 38:243–253

Rohfritsch O (1975) Etude comparative de cellules du tissue naurricier de la jeune galle de l'*Aulax glechomae* L. sur le Glechoma hederaceum L. et de cellules du tissue naurricier abandone par le parasite. Marcellia 38:185–196

Royalty RN, Perring TM (1988) Morphological analysis of damage to tomato leaflets by tomato russet mite (Acari: Eriophyidae). J Econ Entomol 81(3):816–820

Royalty RN, Perring TM (1989) Reduction of photosynthesis of tomato leaflets by tomato russet mite (Acari: Eriophyidae). Environ Entomol 18:256–260

Royalty RN, Perring TM (1996) Nature of damage and its assessment. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 493–512

Ryan CA (1990) Protease inhibitors in plants: genes for improving defenses against insects and pathogens. Ann Rev Phytopathol 2:425–449

Ryan CA (2000) The systemin signalling pathway: differential activation of plant defensive genes. Bioch Bioph Acta 1477:112–121

Shevtchenko VG, Silvere AP (1968) Rotovoi aparat chetyrekhnogikh kleshchei (Acarina: Eriophyoidea). Esti NSV Tead Akad Tiom Biol 17:248–263

Shi A, Tomczyk A (2001) Impact of feeding of eriophyid mite *Epitrimerus gibbosus* (Nalepa) (Acari: Eriophyoidea) on some biochemical components of blackberry (*Rubus* spp.). Bull Polish Acad Sci, Biol Sci 49(1):41–47

Silvere A.P, Shtein-Margolina V (1976) Tetrapodili- Chetyrekhnogie Kleshchi. Inst Exp Biol Akad. Nauk Tallin, Estonia

Smith CM (2005) Plant resistance to arthropods. Molecular and conventional approaches. Springer, Dordrecht

Soika G, Kielkiewicz M (2004) Occurrence of *Phytoptus tetratrichus* (Nalepa) (Acari: Eriophyoidea) and differences in morphology of leaf galls on two linden species. Phytophaga XIV:615–622

Spence KO, Bicocca VT, Rosenheim JA (2007) Friend or foe? Plant's induced response to an omnivore. Environ Entomol 36(3):623–630

Spieser F, Graf B, Walther P, Noesberger J (1998) Impact of apple rust mite (Acari: Eriophyidae) feeding on apple leaf gas exchange and leaf color associated with changes in leaf tissue. Environ Entomol 27(5):1149–1156

Stafford H (1988) Proanthocyanidins and the lignin connection. Phytochemistry 27(1):1–6

Stone BA, Clarke AE (1992) Chemistry and physiology of higher plant 1, 3-β-glucans (callose). In: Stone BA, Clarke AE (eds) Chemistry and biology of (1, 3)-β-Glucans. La Trobe University Press, Bundoora, pp 365–429

Stout MJ, Workman J, Duffey SS (1994) Differential induction of tomato foliar proteins by arthropod herbivores. J Chem Ecol 20:2575–2594

Stout MJ, Workman KV, Duffey SS (1996) Identity, spatial distribution, and variability of induced chemical responses in tomato plants. Entomol Exp Appl 79:255–271

Tandon P (1985) Peroxidase-catalyzed IAA-oxidation in presence of cofactors and auxin protectors isolated from *Eriophyes* incited *Zizyphus* gall tissue. Cecid Int VI(1-3):69–81

Tandon P, Arya HC (1980) Presence of auxin protectors in *Eriophyes* induced *Zizyphus* stem galls. Experientia 36(8):958–959

Taper ML, Case TJ (1987) Interaction between oak tannins and parasite community structure: unexpected benefits of tannins to cynipid gall-wasps. Oecologia 71:254–261

Taper ML, Zimmerman EM, Case TJ (1986) Source of mortality for a cynipid gall-wasps (*Dryocosmus dubiosus* (Hymenoptera: Cynipidae)): The importance of tannin/fungus interaction. Oecologia 68:437–445

Thaler JS, Stout MJ, Karban R, Duffey SS (2001) Jasmonate-mediated induced plant resistance affects a community of herbivores. Ecol Entomol 26:312–324

Thaler JS, Fidantsef AL, Bostock RM (2002) Antagonism between jasmonate- and salicylate-mediated induced plant resistance: effects of concentration and timing of elicitation on defense-related proteins, herbivore, and pathogen performance in tomato. J Chem Ecol 28:1131–1159

Thompson J (1994) The coevolutionary process. University of Chicago, Chicago, p 376

Thomsen J (1975) Development and histology of galls on *Tilia platyphylla* caused by *Eriophyes tiliae tiliae*. Bot Tidsskr 69(4):262–270

Thomsen J (1988) Feeding behavior of *Eriophyes tiliae tiliae* Pgst. and suction track in the nutritive cells of the galls caused by mites. Ent Meddr 56(2):73–78

Tomczyk A, Boczek J (2006) Physiological and biochemical changes in tree leaves infested by some Eriophyoid mites (Acari: Eriophyoidea). In: Gabrys G, Ignatowicz S (eds) Advances in polish acarology. Warsaw, Poland, pp 413–419

Ton J, Mauch-Mani B (2004) β-amino-butyric acid-induced resistance against necrotrophic pathogens is based on ABA-dependent priming for callose. Plant J 38:119–130

Van Leeuwen T, Witters J, Nauen R, Duso C, Tirry L (2010) The control of eriophyoid mites: state of the art and future challenges. Exp Appl Acarol. doi: 10.1007/s10493-009-9312-9

Vaneckova-Skuhrava I (1996) Harmfulness of eriophyid mites (Eriophyoidea, Acari) causing galls on trees and shrubs in the Czech Republic. J Pest Sci 69:81–83

Voigt CA, Schafer W, Salomon S (2008) A comprehensive view on organ-specific synthesis in wheat (*Triticum aestivum* L.): glucan synthase-like gene expression, callose synthase activity, callose quantification and deposition. Plant Physiol Bioch 44:242–247

Walling LL (2000) The myriad plant responses to herbivores. J Plant Growth Regul 19:195–216

Wcislo H (1977) Observations on leaves galls of *Tilia cordata* Mill. induced by Eriophyes tiliae. Acta Biol Crac Ser Bot 20:147–152

Weis A, Walton R, Crego C (1988) Reactive plant tissue sites and the population biology of gall makers. Ann Rev Entomol 33:467–486

Westphal E (1972) Traces de succion parasitaires par quelques eriophyides cecidogenes. Aspects histochimiques et observations ultrastructurales. Marcellia 37:53–69

Westphal E (1974) Cécidogenèse et aspects structuraux de la galle en bourse de l'*Eriophyes padi* Nal. Sur la feuille de *Prunus padus* L. Marcellia 38:77–93

Westphal E (1977) Morphogenese, ultrastructure et etiologie de quelque galles d'Eriophyes (Acariens). Marcellia 39:193–375

Westphal E (1980) Responses of some Solanaceae to attack by the gall mite *Eriophyes cladophthyrus*. Plant Dis 64:406–409

Westphal E (1982) Modification du pH vacuolaires des cellules épidermiques foliaires de *Solanum dulcamara* soumises à l'action d'un acarien cécidogène. Can J Bot 60:2882–2888

Westphal E (1992) Cecidogenesis and resistance phenomena in mite-induced galls. In: Shorthouse J, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 141–156

Westphal E, Manson DCM (1996) Feeding effects on host plants: gall formation and other distorsions. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites–their biology, natural enemies and control. Elsevier, Amsterdam, pp 231–250

Westphal E, Bronner R, Le Ret M (1981) Changes in leaves of susceptible and resistant *Solnum dulcamara* infested by the gall mite *Eriophyes cladophthirus* (Acarina: Eriophyoidea). Can J Bot 59:875–882

Westphal E, Dreger F, Bronner R (1990a) The gall mite *Aceria cladophthirus*. I. Life- cycle, survival outside the gall and symptoms' expression on susceptible and resistant *Solnum dulcamara* plants. Exp Appl Acarol 9:183–200

Westphal E, Minnot MJP, Kreiter S, Gutierrez J (1990b) Hypersensitive reaction of *Solanum dulcamara* to the gall mite *Aceria cladophthirus* causes an increased susceptibility to *Tetranychus urticae*. Exp Appl Acarol 15:15–26

Westphal E, Dreger F, Bronner R (1991) Induced resistance in *Solanum dulcamara* triggered by the gall mite *Aceria cladophthirus* (Acari: Eriophyoidea). Exp Appl Acarol 12:111–118

Westphal E, Bronner R, Dreger F (1996) Host plant resistance. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 681–688

Wilson MF, O'Dowd DJ (1990) The relationship of leaf size and shoot length in *Prunus americana* to leaf-galling by mites. Am Midl Nat 123:408–413

Zawadzki W (1975) The preliminary observations on injuriousness of *Aculus fockeui* (Nal & Trt.). Zesz Probl Post Nauk Roln 171:157–166 (in Polish)

Plant–eriophyoid mite interactions: specific and unspecific morphological alterations. Part II

Radmila Petanović · Malgorzata Kielkiewicz

Abstract   The paper presents recent advances related to both specific and unspecific morphological alterations of plant organs caused by eriophyoid mites. Based on old and new case studies, the diversity of plant malformations, such as galls, non-distortive feeding effects and complex symptoms induced by eriophyoids and/or pathogens vectored by them, is analysed and summarised.

Introduction

Eriophyoid mites (Acari: Eriophyoidea) form galls or live freely on various host-plants (reviewed by Oldfield 1996a, b, 2005; Royalty and Perring 1996; Westphal and Manson 1996). In both cases, their stylet mouthparts cause only a small mechanical wounding. The wounding and injecting of specific salivary secretions into host-cells, by both cheliceral stylets of eriophyoid mites, result in a specific response of the affected leaf, stem, or bud tissues such as gall differentiation, hypersensitive reaction, or non-distortive feeding effects and in some cases complex symptoms, considered as syndromes.

Despite the improvement of our knowledge and the accumulation of new data during the last two decades, a detailed study of the great diversity of eriophyoid mite–host plant interactions with respect to morphological, histological, biochemical and physiological effect is still necessary.

R. Petanović (✉)
Department of Entomology and Agricultural Zoology, Faculty of Agriculture, University of Belgrade, Nemanjina 6, 11081 Belgrade-Zemun, Serbia
e-mail: rpetanov@agrif.bg.ac.rs

M. Kielkiewicz
Department of Applied Entomology, Faculty of Horticulture and Landscape Architecture, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

This update presents a new synthesis and advances related to plant–eriophyoid mite interactions. The results related to the formation of specific or universal compounds and physiological changes in mite-injured plant tissue/organs, which in many cases affect the performance of eriophyoid mites, are synthesized in the first part of the review (Petanović and Kielkiewicz 2009). Types of morphological alterations of host plant organs with respect to eriophyoid life styles, as well as the plant symptoms characteristic of eriophyoid damage are analysed in this part of the review. Besides the great variety of specific morphological alterations, we also present many cases of so-called unspecific alterations, which could be caused by the presence of at least two agents.

Macro-morphological host-plant symptoms with respect to eriophyoid mite life styles

Evolutionary ecology, i.e. life history patterns, food plant choice and dispersal of erio-phyoid mites were elaborated by Sabelis and Bruin (1996). It was discussed that the minuteness of eriophyoid mites have consequences for their impact on the host plant, their interactions with predators, and the ability to disperse. Being so small, eriophyoid mites are limited in their capacity for ambulatory movement (Oldfield 2005). They either hide in existing shelters—such as needles and leaf sheets, within buds and between bulb scales, or they induce the plant to create growth abnormalities that can then be used as shelters (leaf edge curls, erinea, galls). Nevertheless, other species of eriophyoid mites do not have such a typical refuge-seeking or refuge-creating life style. They can be found over the whole leaf surface, despite their vulnerability to predator attack and despite the opportunity to hide in narrow refuge places. They are considered as vagrants or free living eriophyoids. According to Amrine (unpublished data) in Huang (2008), it was calculated that the percentage of vagrants make up 43.6% of all species (1,618 vagrants compared to total of 3,708) of eriophyoid mites, which is higher than those of gall mites (15.8%), erineum mites (11.4%) and bud mites (8.9%). As gall, erineum and bud mites can be assumed as refuge creating mites, the percentage of this category is almost near to vagrants (36.1%), and the rest are probably the refuge seeking. Recently, Skoracka et al. (2009) calculated that Eriophyoidea are comprised mostly of vagrants (2,263 vagrants, 462 refuge-seeking and 941 refuge-inducing). However, they emphasised that we should be cautious about the conclusion as it is based on a simple records data. Generally, it could be concluded that at least a half of all eriophyoid mite species follow the vagrant life strategy and another half follow the refuge creating or seeking strategy and that both strategies might be advanta-geous to these mites.

Diversity of macro morphological alterations (symptoms) on plants, as the consequence of eriophyoid infestation, depends on eriophyoid mite–plant interactions, mite species, its life style, host plant species and its genotype. Vagrant species usually cause less diverse and superficially less specific symptoms than gall inducing species. On the other hand, refuge-seeking eriophyoids may sequester themselves in leaf axils, in leaf glands, or even squeeze through leaf stomata to feed and reproduce in the mesophyll layer, as in recently described species, *Schizoempodium mesophyllincola* Oldfield, Hunt and Gispert (Oldfield 2005). An interesting case is refuge-seeking mite, *Novophytoptus rostratae* Roivainen, investigated by Tchetverikov (2004). Colonies of mites were found within air cavities of the leaves, leaf sheaves, and under the epidermis of the stalks of plants of the family Cyperaceae and Juncaceae. The mites were found to feed on cells of chlorenchyma and cause "brownish striae".

Plant galls are abnormal structures caused by many gall-forming (*syn.* ceceidogenic) organisms belonging to different systematic groups. Gall induction is common only among the eriophyoid acarines; however a few tropical species of the family Tenuiplapidae induce poorly defined galls on their hosts (Oldfield 2005). Galls induced by eriophyoids are extremely diversified in shape, size, colours, etc. Eriophyoids that induce galls are usually highly site-specific, typically inducing galls of a specific form on a specific part of the green portion of the plant. They develop on all soft parts of their host plant: stems, leaves, petioles, buds, flowers, and even fruits and seeds, except for the roots, which are apparently not suitable for mite attack (Westphal 1992).

One of the oldest classifications (Küster 1911) is based on gall morphology. According to this system, galls are divided into two major classes: organoid galls characterized as abnormal modifications of plant organs, and histoid galls, characterized by complex and sometimes novel types and arrangements of internal tissues. Histoid galls are further subdivided according to their structure into kataplasmas, usually with less differentiated tissues, and prosoplasmas, structurally more complex. Detailed descriptions of these types is presented by Larew (1982). According to this classification, eriophyoid galls may be assumed as simple or complex kataplasmas.

A comparative study of the anatomy of *Salix piperi* Bebb. leaf gall, *Alnus rubra* Bang. bead gall, *Tilia europea* L. leaf gall, erineum on *Quercus garryana* Dougl., *Fraxinus latifolia* Benth. leaflet gall, *Rhus diversiloba* T. and G. leaflet gall, leaf gall on *Populus tremuloides* Michx., leaf gall of *Prunus virginiana* L., and big bud of *Corylus avellana* L., caused by 9 gall making species, allowed Larew (1982) to distinguish two different categories of galls. The galls which possess no distinctive nutritive layer (oak erineum, trembling aspen gall) and those that remain in the structure of the healthy leaf (oak erineum, poison oak gall and trembling aspen gall) belong to the category -'simple kataplasmas'. In these cases eriophyoid mite causes relatively little tissue disruption. The remaining galls possess a distinctive nutritive layer at least during the early stage of gall development. Additionally, the disruption (homogenization) of the mesophyll layers was seen in all of them. These two characteristics indicated that the mites influenced the host plant tissue to a significant extent, and thus their galls were categorized as 'complex kataplasmas'. Within this group, it is possible to sub-categorize the galls based on the thickness of the nutritive layer at gall maturity or alignment of nutritive cells and general type of nutritive cells. For example, the mature willow leaf gall has a nutritive layer which is 2–5 cells thick, while all other galls generally possess a one-cell-thick nutritive layer. A palisade arrangement of nutritive cells is seen in the willow gall and the filbert bud gall. A more random arrangement of globular nutritive cells is observed in the alder bead gall and choke cherry gall. The ash leaflet gall has a few nutritive cells arranged as a palisade, but most are small and randomly arranged. The mature gall of linden is an interesting case—both cytoplasmatically rich palisade-like nutritive cells and vacuolated randomly arranged cells lining the gall cavity.

Additionally, the position of the mite was used as one of the criteria for the classification of galls, and according to this, two major types of acarocecidia can be recognized. The first type includes galls with eriophyoid mites exposed externally on the epidermis, whereas the second one includes galls with eriophyoid mites inside the plant tissue (Mani 1964). Westphal (1992) and Westphal and Manson (1996) classified galls according to the nature of the plant organ attacked and the damage complexity degree into five major classes: (1) leaf galls, (2) stem galls, (3) bud galls, (4) fruit galls and (5) other distortions (other distortive, toxemias and non-distortive alterations are included here as well).

Examples of different plant galls caused by eriophyoid mites listed and described briefly or in detail in different monographs/reviews mentioned above (Mani 1964; Jeppson et al.

1975; Larew 1982; Westphal 1992; Boczek and Griffiths 1994; Westphal and Manson 1996) will not be repeated here.

Several researchers have suggested that the gall morphology is largely determined by the phytophagous mite rather than the host plant (Kane et al. 1997). For example, different species living on the same host plant can produce strikingly different effects (Boczek and Griffiths 1994). However, different congeneric species (*Cecidophyopsis* spp.), inhabiting different congeneric plant species (*Ribes* spp.), can provoke the same type of galls, i.e. bud galls (Amrine et al. 1994). Similarly, Rančić and Petanović (2008) concluded that anatomy of galls on different maple leaves, caused by three *Aceria* spp., was similar in spite of the fact that different species were the causative agents. In the same study, two different *Aceria* spp. were simultaneously observed to induce galls or erinea on the same individual sycamore maple. On the other hand, the same eriophyoid mite species can induce different symptoms to different plant species or to different developmental stages of the same host plant (Westphal 1980; Oldfield 1984; Soika and Kielkiewicz 2004). Weis et al. (1988) proposed in their review the hypothesis regarding the genes important in determining plant reactivity that have other functions in normal development and metabolism. They also recommended the methods which could be available to explore gene expression in the gall in relation to that in the rest of the plant. The host plant genotype, environment, and parasite genotype interact to determine the gall phenotype. They stated that evolution of plant–gall maker interaction is complicated by the fact that galls are phenotypic entities that develop under the influence of both plant and plant—gall maker genotypes. Development of molecular markers for eriophyoid mites provided insight into systematic position and even phylogenetic relationships of economically important species of currants, gooseberries, and grapevine (Fenton et al. 1996; Fenton 2002; Carew et al. 2004). Molecular and microarray techniques are still not used enough in eriophyoidology. We are expecting that accumulation of such results in the future will also help resolve many problems regarding the origin and the nature of specific host plant–eriophyoid mite relationships.

Apart from the category of gall makers (*sensu lato*), almost a half of eriophyoid species belong to leaf vagrants which predominantly cause so-called non-distortive changes to the host plants. Oldfield (1996b) summarized toxemias and other non-distortive feeding effects of eriophyoids considering them as specific separate type of alterations. They are related to changes in the appearance of the epidermis of green leaves, immature fruit, young stems or even bud bracts, which are variously referred to as rust, russeting, browning, bronzing, silvering, chlorotic spots, reddening etc. Symptoms could be primarily described as discolouration of plant organs, but are frequently associated with brown scarification and necrosis of infested buds, mortality of buds, witches broom or multiple branching owing to the death of primary growing points, distortion of veins, chlorotic spots, concentric ring blotch, mottle effects, hairless spots on the lower surfaces of attacked leaves, hardening and late ripening, irregular streaks, defoliation (if the collapse of lower leaf mesophyll follows extensive epidermal damage), lignifications, yellowish white areas, stunting, twisting, curling, desiccation of terminal buds or whole terminal shoots, distorted fruits, and premature drop.

Of the three families of Eriophyoidea, the Phytoptidae and Eriophyidae, among their assemblages, include many species that alter the development of plant cells upon which they feed. In many such instances, this results in the development of galls, the form of which is specific to the particular inducing species. The third family, Diptilomiopidae, consists of vagrant species. Among the largest of the three families, the Eriophyidae, the subfamily Eriophyinae consists of 66% of genera with gall-mite species, although the

Phyllocoptinae subfamily predominantly (80%) includes genera with vagrants (Oldfield 2005). It should be emphasized that non-distortive changes to plants have not been recorded in all cases of vagrant species. It is probably due to the lack of knowledge. Most of the data on the eriophyoid species life style originates from single records from literature, most often from descriptions of new species. If the population density had been low, the damage to the plant should usually be neglected. However, in the case of pest species that reproduce fast, symptoms, i.e. damages to plant organs are usually observed.

For instance, Phyllocoptinae mites *Rhombacus* sp. and *Acalox ptychocarpi* Keifer have been investigated in a case study as the recently-emerged pests of commercial eucalypt plantations in subtropical Australia (Nahrung and Waugh 2009). They cause blistering, necrosis and leaf loss to *Corymbia citriodora* subsp. *variegate* (F. Muell.) K.D. Hill & L.A.S. Johnson. Damage symptoms associated with eriophyoid mite feeding manifest as "spot type" and "patch type" of chlorotic or anthocyanic tissue discoloration.

Although the members of the subfamily Phyllocoptinae of the Eriophyidae include an especially large number of leaf vagrant mite species that cause various "rust" symptoms on deciduous and evergreen broad-leafed perennials, annual broad-leafed plants, grasses, and monocots, many species of the family Phytoptidae cause abortion of buds and stunting of needles (Boczek and Shevchenko 1996). Even whole conifer seedlings may turn yellow, desiccate and die as a result of feeding of some phytoptid mites (Löyttyniemi 1969). *Nalepella* spp. and some *Trisetacus* spp. are needle vagrants causing discolouring, i.e. chlorosis and browning of needles and their drop off (Castagnoli 1996). Diptilomiopids are assumed as less harmful to plants (Jeppson et al. 1975) although some species are causative agents of serious leaf deformation and premature leaf dropping, like *Rhyncaphytoptus platani* Keifer of *Platanus* in Europe (Schliesske 1989; Castagnoli 1996). It is most probable that diptilomiopids rarely reach high population levels on plants, which could be the reason for their harmlessness. The "paradox" of this family still remains to be explained.

Complex and mixed symptoms induced by eriophyoid mite feeding and/or pathogen transmission

Apart from galls and rust (*sensu lato*), eriophyoid mites have been considered to be the causative agents of the so called non-distortive feeding effects and complex symptoms which are difficult to separate from the symptoms of pathogens transmitted by them or by mixed infestation and/or infection. Symptoms like chlorosis, phyllody, flower virescence, internode shortening, enations, fasciation, axillary bud growth, necrotic spots, wart-like structures, blastomania, "witches broom", stunting, multiple inflorescences, and vegetative and floral malformations may be confused with other causative agents like thrips, fungi, viruses and phytoplasmas, or microelement deficiency. Most toxaemias and non-distortive feeding effects are only known from descriptions of the syndrome of macroscopic visual changes in the host which accompany the presence of the mite. In many cases, eriophyoid mites are either vectors important in disease epidemiology or they prefer infested/infected plants. However, many such symptoms have been proved to be caused exclusively by eriophyoid mites (Oldfield 1996b; Duso et al. 2008). A few cases of so called mixed and/or dubious symptoms, as well as syndromes, are presented below.

Aceria parapopuli (K.) and *A. populi* (Nal.) initiate a woody bud gall on species of *Populus* in North America and in Europe respectively, consisting of a solid mass of swelling, which can continue to grow for several years. Many buds along the same twig

can be attacked, with consequent retarded growth and deformation of the twig. *A. neoessigi* (K.) is the probable cause of catkin deformation of some species of poplar in North America. The inflorescences form clusters and hang like bunches of woody grapes about 10 cm in diameter and 20 cm long, which remain on the plant all summer (Castagnoli 1996).

Stenacis triradiatus (Nal.) and other eriophyoid taxa are probably the cause of a similar deformation known as "Wirrzopfe", found on species of *Salix* in Europe. Male and female catkins appear greatly modified, buds grow abnormally and internodes become shortened. However, viruses are probably also involved (Rack 1958; Westphal 1977). *Aceria fraxinivora* (Nal.), a widespread species, attacks the inflorescence of *Fraxinus* spp. Pedicels of individual flowers appear swollen, fused and distorted. These inflorescences remain on the tree for some time where they become brown and gradually form a shapeless mass (Castagnoli 1996). *Trisetacus juniperinus* (Nal.) induces a range of different, enormously severe types of symptoms in *Cupressus sempervirens* L.—enlarged deformed buds, irregular proliferations of axillary buds, blastomania, witches brooms, and deformed cones producing few seeds (Duso et al. 2008). A similar symptom of irregular proliferations of axillary buds of forsythia plants has been connected with *Aceria forsythiae* Domes (Petanović 2004). Recently, Australian vineyards have been affected by a syndrome called "Restricted Spring Growth" (RSG) which has not been associated with a clear cause yet. Bernard et al. (2005) showed that most of these symptoms were due to early *Calepitrimerus vitis* (Nal.) infestations. Severe leaf distortion and shoot length reduction depended on the mite density. Another syndrome, the so-called "Short Shoot Syndrome" (SSS), similar to the previous one, was reported in the Pacific Northwest of the USA. Symptoms were represented by bunch necrosis during early season, malformed leaves, short and angled shoots in spring, scar tissue, and bronzed leaves in summer. Walton et al. (2007) showed that SSS was associated with high *C. vitis* (Nal.) population densities (see also Duso et al. 2008). Detailed descriptions of the symptoms caused by the grape rust mite, recently investigated and called RSG or SSS have been made in the second part of the last century (Duso and de Lillo 1996 and references therein).

A complex of symptoms, which should also be concerned as a syndrome, was observed on invasive cut-leaf teasel, *Dipsacus laciniatus* L. in Serbia (Petanović and Rector 2007), and was later analyzed in more detail (Pećinar et al. 2009). The most discernible effects, observed on bolted plants under field conditions were the stunted growth, shortened internodes, smaller leaves, and abnormal proliferation of deformed flower heads. Statistical analysis revealed that nine morphometric traits out of 13 were significantly different between 'healthy' and infested plants. Results of the experiments conducted under laboratory conditions demonstrated the impact of mite feeding as a slowdown in plant development and a reduction in average length and width of the leaves.

Some of the symptoms previously attributed to eriophyoid mites were proved or suspected to be induced by phytoplasmas. Multiple inflorescences on *Cirsium arvense* (L.) Scop. has always been attributed to the presence of *Aceria anthocoptes* (Nal.), since their first report in 1892 (Petanovic et al. 1997). Affected plants lately recorded in Serbia showed irregular growth, atypical branching with small leaves, shortened internodes, hardening of the green inflorescence, and reduced vigour, as well as chlorosis or reddish brown discoloration of the leaves and stems, and multiple inflorescence. In this plant 16SrIII-B subgroup phytoplasma was reported for the first time (Rancic et al. 2005). Similarly, an interesting relationship between the feeding of *Paraphytoptus chrysanthemi* K. and phyllody, changes of floral organs into vegetative ones and stunted internodes of chrysanthemum plants, was registered decades ago (Breakey and Batchelor 1950). Damage

includes the stunting and curling of apical leaves, as well as bronzing, while leaves become brittle and bud clustering results in brooming. Recently, chrysanthemum plants showing flower proliferation, virescence, and stunting have been observed in Serbia. Phytoplasmas belonging to 16SrXII-A ribosomal subgroup (stolbur) were identified in symptomatic plants (Duduk et al. 2006). *Aceria spartii* (Can.), recorded in Italy and South Africa (Castagnoli 1978; Craemer et al. 1996), attack young apical shoots of *Spartium junceum* L. and cause excessive hairiness, thickening of the axis, shortening of internodes, and finally "witches broom" or cladode. Marcone et al. (1996) and Torres et al. (2002) reported that Spartium witches broom disease is associated with phytoplasma 16SrX group strain in Italy and Catalonia, Spain, respectively. X-disease-related phytoplasmas have been identified in ornamental trees and shrubs (forsythia, spirea, cypress and willow), with "witches broom", stunting, and fasciation symptoms (Paltrinieri et al.1998). Interaction of *Aceria bezzii* (Corti) and phytoplasmas of hackberry trees was reported together with the effect of drought in Italy (Mittempergher et al. (1999). As it was summarized by Oldfield and Proeseler (1996), the diameter of the oral opening and foregut of eriophyoid mites (the latter about 500 nm in an adult) may preclude ingestion of larger plant pathogens, many of which require circulation through the body of their vectors before they can be transmitted. The same authors stressed that "pleomorphic phytoplasmas may be an exception in that their limiting membrane allows them to assume a shape that might allow them to be ingested by an eriophyoid".

The transmission of phytoplasmas by eriophyoid mites has not been proven yet, so the incidence of common appearance of both causative agents of plant malformations should be studied comprehensively in the future in order to resolve their relationship, especially in many dubious cases in which symptoms are attributed to one of the causative agents.

Eriophyoid mites have been proven as vectors of plant viruses. Some symptoms were attributed to viruses, and some were attributed only to mites. For instance, feeding of the most intensively studied wheat curl mite (WCM), *Aceria tosichella* K., causes characteristic symptoms on wheat, a syndrome of curled, looped and trapped leaves. The same species causes kernel red streak of corn. Symptoms of wheat streak mosaic virus (WSMV), transmitted by *A. tosichella*, are light green to yellow streaks and dashes, followed by general chlorosis, stunting and, depending upon the degree of severity, poorly filled seed heads and shrivelled kernels. Symptoms of wheat spot mosaic virus (WSpMV) transmitted by this mite consist of an initial chlorotic spotting or ring spot, general chlorosis, stunting, and sometimes plant death (Styer and Nault 1996). Onion mite, *Aceria tulipae* (K.) physically damages the host by feeding upon the epidermal cells of the bulb, causing the cells to collapse and resulting in scarification. The foliage produced from infested bulb can be stunted, twisted and discoloured, symptoms reported to be similar to those caused by viral infections. In addition, *A. tulipae* is a vector of onion mite-borne latent virus (OMbLV), the causal agent of onion mosaic disease, and shallot mite-borne latent virus (ShMbLV). Infection by both viruses can be asymptomatic (Ostoja-Strazewski and Mattews 2009, and references therein). Black currant reversion disease and the vector of its causal agent, the black currant gall mite *Cecidophyopsis ribis* (Westwood), have been recognised for at least 100 years. At first, damage of this pest, done by causing galling buds and distortion of leaves, was confused with the symptoms of reversion disease. Later the symptoms of reversion were distinguished and it was shown that these mites transmit the causal agent of the disease. The symptom of the mite injury is enlargement and change of form, from conical to a spherical shape, of the gall mite infested bud. Most prominent reversion disease symptoms are expressed in leaves usually fewer in number and decreased in size, with a decrease in marginal serrations and number of main veins, and with a less

clearly defined sinus at the petiole. Besides this, a marked decrease in the density of hairs on the flower buds and an increased intensity of colour in the buds are observed early in the spring. Despite much research over several decades, the causal agent has been characterised as the black currant reversion associated virus (BRAV) only recently (Jones 2000).

Only a few studies described interaction of eriophyoid species and fungi as well as the possible role of eriophyoids as vectors of these pathogens. Lakshmanan and Jagadeesan (2004) reported the presence of eriophyid mite *Aceria guerreronis* Keifer and fungus *Botryodiplodia theobromae* Pat. in malformed nuts of coconut palms in India. The fungus produced typical symptoms, such as malformation and cracking in the presence of eriophyoid mite infestation. Normal-sized nuts with cracking symptoms were recorded in eriophyid mite-infested nuts.

The combined impact of *Aceria mangiferae* Sayed and *Fusarium subglutinans* (Wollenow and Reinking) on in vitro mango seedlings was investigated by Otero-Colina et al. (2007). Two types of malformations were recognized. Growth abnormalities attributed to *A. mangiferae* were named "atrophy of apical leaves". The apex of such seedlings showed a series of short internodes, the associated leaves were atrophic and dry, and the epidermis of leaves, stems and petioles were brown and coarse. Growth abnormalities attributed to *F. subglutinans* were named "bunchy top". Axillary buds of such plants develop as short and thick shoots with small epinastic leaves. It was proved that the mite can act as a vector of the etiological agent of the bunchy top. Another case study of the role of mango bud mite *Aceria mangiferae* Sayed in mango malformation epidemiology, caused by the fungus *Fusarium mangiferae* Britz, Wingfield and Marasas, showed that *A. mangiferae* can vector the pathogen, assist in fungal penetration, but does not appear to have a role in aerial dissemination of conidia. The authors proposed that future research should take into consideration potential eriophyoid mites–fungi interactions (Gamliel-Atinsky et al. 2008).

If the transmission of an etiological agent by eriophyoid mites is proven, symptoms should be attributed to eriophyoid mites and pathogen, both of them being important in aetiology and epidemiology.

Conclusions and future research

Recent studies showed that different life styles (vagrant vs. refuge-creating and -seeking) are represented almost equally between eriophyoids and are hypothesized as advantageous for these mites. However, the necessity of a detailed recognition of specific symptoms and an extensive study of the great diversity of host plant interactions, with respect to morphological, histological, biochemical, and physiological effects, still exists. The great diversity of specific eriophyoid mites–host plant relationships should be recognized at different levels of complexity of plant organs, tissues, and cells. Eriophyoid mites interactions with other organisms related to their host plants, as well as food resources and habitats, enlarge this complexity. Collection, recognition, adequate description, and classification of the great many malformations of plant tissues and organs must be continued. At the same time, elucidation of eriophyoid mites–host plant specific interactions at the gene level (through microarrays) is needed and should be the future task and challenge.

References

Amrine JW Jr, Duncan GH, Jones AT, Gordon SC, Roberts IM (1994) *Cecidophyopsis* mites (Acari: Eriophyidae) on *Ribes* spp. (Grossulariaceae). Internat J Acarol 20(3):139–168

Bernard MB, Horne PA, Hoffmann AA (2005) Eriophyoid mite damage in *Vitis vinifera* (grapevine) in Australia: *Calepitrimerus vitis* and *Colomerus vitis* (Acari: Eriophyidae) as the common cause of the widespread 'Restricted Spring Growth' syndrome. Exp Appl Acarol 35:83–109

Boczek J, Griffiths DA (1994) Structure and systematics of eriophyid mites (Acari: Eriophyoidea) and their relationship to host plants. In: Williams MAJ (ed) Plant galls, systematics association special volume, 49. Calerdon Press, Oxford, pp 119–129

Boczek J, Shevchenko VG (1996) Ancient associations: eriophyiid mites on gymnosperms. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 217–225

Breakey EP, Batchelor GS (1950) Phyllody of chrysanthemum and eriophyid mite *Paraphytoptus chrysanthemi* Keifer. Ann Ent Soc Am 43:492–494

Carew ME, Goodisman MAD, Hoffmann AA (2004) Species status and population genetic structure of grapevine eriophyoid mites. Ent Exp Appl 111:87–96

Castagnoli M (1978) Ricerche sulle cause di deperimento e moria dello *Spartium junceum* L. *Eriophyes genistae* (Nal.) e *E. spartii* (G.Can.) (Acarina: Eriophyoidea): ridescrizione, cenni di biologia e Danni in Italian. Redia 61:539–550

Castagnoli M (1996) Ornamental coniferous and shade trees. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 661–671

Craemer C, Neser S, Smith Meyer MKP (1996) Eriophyid-myte (Acari: Eriophyoide: Eriophyidae) as moontlike beheeragente van ongewenste uithemse plante in Suid—Africa. SA Tydskrif vir Natuurwetenskap en Tegnologie. In Afrikaans 15:99–109

Duduk B, Dukić N, Bulajić A, Krstić B, Bertaccini A (2006) Stolbus phytoplasmas infecting chrysanthemum plants in Serbia. Pest Phytomed (Belgrade) 21:107–111

Duso C, de Lillo E (1996) Grape. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 571–582

Duso C, Castagnoli M, Simoni S, Angeli G (2008) The impact of eriophyoids on crops: new and old case studies. In: Bertrand M, Kreiter S, McCoy K, Migeon A, Navajas M, Tixter MS, Vial L (eds) Integrative acarology. Proceedings of the 6th congress of the European association of acarologists, Montpellier, 21–25 July 2008, pp 317–324

Fenton B (2002) Speciation and biogeography in eriophyid mites: a review. In: Bernini F, Nanneli R, Nuzzaci G, de Lillo E (eds) Acarid phylogeny and evolution. Adaptation in mites and ticks. Kluwer, The Netherlands, pp 27–34

Fenton B, Malloch G, Jones AT, Thomas WP (1996) Molecular ecology of some *Cecidophyopsis* mites (Acari: Eriophyidae) on *Ribes* species and evidence for their natural cross colonisation of blackcurrant (*R. nigrum*). Ann Appl Biol 128:405–414

Gamliel-Atinsky E, Freeman S, Sztejnberg A, Maymon M, Belausov E, Ochoa R, Pena J, Palevsky E (2008) Eriophyoid and transmitted pathogens: the role of the mango bud mite in mango malformation epidemiology, presented in a case study. In: Bertrand M, Kreiter S, McCoy K, Migeon A, Navajas M, Tixter MS, Vial L (eds) Integrative acarology. Proceedings of the 6th congress of the European association of acarologists, Montpellier, 21–25 July 2008, pp 306–311

Huang K-W (2008) *Aceria* (Acarina:Eriophyoidea) in Taiwan: five new species and plant abnormalities caused by sixteen species. Zootaxa 1829:1–30

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. University of California Press, Berkeley

Jones AT (2000) Black currant reversion disease-the probable causal agent, eriophyid mite vectors, epidemiology and prospects for control. Virus Res 71:71–84

Kane NA, Jones CS, Vuorisalo T (1997) Development of galls of *Alnus glutinosa* and *Alnus incana* (Betulaceae) caused by the eriophyid mite *Eriophyes laevis* (Nalepa). Int J Plant Sci 158(1):13–23

Küster E (1911) Die Gallen der Pflanzen. Ein Lehrbuch der Botaniker und Entomologen. Hirzel, Leipzig

Lakshmanan P, Jagadeesan R (2004) Malformation and cracking of nuts in coconut palms (*Cocos nucifera*) due to the interaction of the eriophyoid mite *Aceria guerreronis* and *Botryodiplodia theobromae* in Tamil Nadu, India. Zeitschrift-für-Pflanzenkrankheiten-und-Pflanzenschutz. 111:206–207

Larew HG (1982) A comparative anatomical study of galls caused by the major cecidogenic groups, with special emphasis on nutritive tissue. Dissertation, Oregon State University

Löyttyniemi K (1969) A *Nalepella* species (Acarina: Eriophyidae) damaging needles of spruce (*Picea abies* (L.) Karst.). Ann Ent Fenn 35:123–124

Mani MS (1964) Ecology of plant galls. W. Junk, The Hague

Marcone C, Ragozzino A, Schneider B, Lauer U, Smart CD, Seemüller E (1996) Genetic characterization and classification of two phytoplasmas associated with Spartium witches' broom disease. Plant Dis 80:365–371

Mittempergher L, Sfalanga A, Vibio M, Bertaccini A (1999) Phytoplasmas, *Aceria bezzii* and drought in declining European hackberry (*Celtis australis* L.). In: International Symposium of Urban Tree Health Paris, France. Acta Hort 496:87–91

Nahrung HF, Waugh R (2009) Local dispersion and damage of *Corymbia citriodora* subsp.*variegata* (Myrtaceae) regrowth by eriophyid mites (Acari: Eriopyoidea). Systematic & Applied Acarology 14:19–29

Oldfield G (1984) Evidence for conspecificity of *Aculus cornutus* and *A. fockeui* (Acari: Eriophyidae), rust mites of Prunus fruit trees. Ann Entomol Soc Am 77:564–567

Oldfield GN (1996a) Diversity and host plant specificity. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 199–216

Oldfield GN (1996b) Toxemias and other non-distortive feeding effects. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 243–250

Oldfield GN (2005) Biology of gall-inducing acari. In: Raman A, Schaefer CW, Withers TM (eds) Biology, ecology and evolution of gall-inducing arthropods. Science Publishers, Inc, Portland, pp 35–57

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vectors of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 259–275

Ostoja-Strazewski JC, Mattews L (2009) *Aceria tulipae* (Keifer) (Acari:Eriophyoidea) on imported onion sets, and present status in Britain. Entomologist's Monthly Magazine 145:61–68

Otero-Colina G, Acosta MC, Santillán MT (2007) Malformation induced by *Aceria mangiferae* (Trombidiformes: Eriophyidae) and *Fusarium subglutinans* (Fungi: Deuteromycetes) to in vitro mango seedlings. In: Morales-Malacara JB, Behan-Pelletier V, Ueckermann E, Perez TM, Estrada-Venegas EG, Badii M (eds) Acarology XI: proceedings of the international congress, Merida, Mexico 2002, pp 455–458

Paltrinieri S, Martini M, Pondrelli M, Bertaccini A (1998) X-disease-related phytoplasmas in ornamental trees and shrubs with witches' broom and malformation symptoms. J Plant Pathol 80(3):261

Pećinar I, Stevanović BG, Rector B, Petanović R (2009) Morphological injury of cut-leaf teasel, *Dipsacus laciniatus* L. (Dipsacaceae) induced by the eriophyid mite *Leipothrix dipsacivagus* Petanovic et Rector (Acari: Eriophyoidea). J Plant Inter 4:1–6

Petanović R (2004) Štetne grinje ukrasnih biljaka—atlas, priručnik, (Mite pests of ornamental plants—atlas) in Serbian Beografik. Beografik, Beograd

Petanović R, Boczek J, Stojnić B (1997) Taxonomy and bioecology of eriophyids (Acari: Eriophyoidea) associated with Canada Thistle, *Cirsium arvense* (L.) Scop. Acarologia XXXVIII:181–191

Petanović R, Kielkiewicz M (2009) Plant–eriophyoid mite interactions: cellular biochemistry and metabolic responses induced in mite-injured plant. Part I. Exp Appl Acarol (this issue)

Petanović R, Rector BG (2007) A new species of *Leipothrix* (Acari: Prostigmata: Eriophyidae) on *Dipsacus* spp. in Europe and reassignment of two *Epitrimerus* spp. (Acari: Prostigmata: Eriophyidae) to the genus *Leipothrix*. Ann Entomol Soc Am 100:157–163

Rack G (1958) Eriophyiden als Bewohner der Wirzöpfe zweier Weidenarten. Mitt Hamburg Zool Mus Inst 56:31–80

Rančić D, Petanović R. (2008) Differences in the leaf morphology of sycamore maple infested by two congeneric eriophyid species at Tara National Park in western Serbia. In: Bertrand M, Kreiter S, McCoy K, Migeon A, Navajas M, Tixter M-S, Vial L (eds) Integrative acarology. Proceedings of the 6th congress of the European association of acarologists, Montpellier, 21–25 July 2008, pp 326–330

Rančić D, Paltrinieri S, Toševski I, Petanović R, Stevenović B, Bertaccini A (2005) First report of multiple inflorescence disease of *Cirsium arvense* and its association with a 16SrIII-B subgroup of phytoplasmas in Serbia. Plant Pathol 54:561

Royalty RN, Perring TM (1996) Nature of damage and its assessment. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 493–512

Sabelis MW, Bruin J (1996) Evolutionary ecology: life history patterns, food plant choice and dispersal. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 329–365

Schliesske J (1989) Zum Schadauftreten der Gallmilbe *Rhyncaphytoptus platani* Keifer (Acari:Eriophyoidea) an Platanen. Gesunde Pflanzen 41:325–326

Skoracka A, Smith L, Oldfield G, Cristofaro M, Amrine JW (2009) Host-plant specificity and specialization in eriophyoid mites and their importance for the use of eriophyoid mites as biocontrol agents of weeds. Exp Appl Acarol. doi:10.1007/s10493-009-9323-6

Soika G, Kielkiewicz M (2004) Occurrence of *Phytoptus tetratrichus* (Nalepa) (Acari: Eriophyoidea) and differences in morphology of leaf galls on two linden species. Phytophaga XIV:615–622

Styer WE, Nault LR (1996) Corn and grain plants. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 611–618

Tchetverikov FE (2004) Some features of biology and morphology of eriophyoid mite *Novophytoptus rostratae* Roivainen 1947 Vestnik SPbGU, pp 8–17

Torres E, Botti S, Paltrinieri S, Martin MP, Bertaccini A (2002) First report of Spartium witches' broom disease in Spain BPPS, New Disease Reports, 5: Feb 2002 to July 2002 http://www.bspp.org.uk/publications/new-disease-reports/reports.php?id=5

Walton VM, Dreves AJ, Gent DH, James DG, Martin RR, Chambers U, Skinkis PA (2007) Relationship between rust mites *Calepitrimerus vitis* (Nalepa) bud mites *Colomerus vitis* (Pagenstecher) (Acari: Eriophyidae) and short shoot syndrome in Oregon vineyards. Int J Acarol 33:307–318

Weis A, Walton R, Crego C (1988) Reactive plant tissue sites and the population biology of gall makers. Ann Rev Entomol 33:467–486

Westphal E (1977) Morphogenèse, ultrastructure et étiologie de quelque galles d'eriophyes (Acariens). Marcellia 39:193–375

Westphal E (1980) Responses of Some Solanaceae to attack by the gall mite *Eriophyes cladophthyrus*. Plant Dis 64:406–409

Westphal E (1992) Cecidogenesis and resistance phenomena in mite-induced galls. In: Shorthouse J, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 141–156

Westphal E, Manson DCM (1996) Feeding effects on host plants: gall formation and other distortion. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 231–241

Springer

Host-plant specificity and specialization in eriophyoid mites and their importance for the use of eriophyoid mites as biocontrol agents of weeds

Anna Skoracka · Lincoln Smith · George Oldfield · Massimo Cristofaro · James W. Amrine

Abstract Eriophyoid mites, which are among the smallest plant feeders, are characterized by the intimate relationships they have with their hosts and the restricted range of plants upon which they can reproduce. The knowledge of their true host ranges and mechanisms causing host specificity is fundamental to understanding mite-host interactions, potential mite-host coevolution, and diversity of this group, as well as to apply effective control strategies or to use them as effective biological control agents. The aim of this paper is to review current knowledge on host specificity and specialization in eriophyoid mites, and to point out knowledge gaps and doubts. Using available data on described species and recorded hosts we showed that: (1) 80% of eriophyoids have been reported on only one host species, 95% on one host genus, and 99% on one host family; (2) Diptilomiopidae has the highest proportion of monophagous species and Phytoptidae has the fewest; (3) non-monophagous eriophyoids show the tendency to infest closely related hosts; 4) vagrant eriophyoids have a higher proportion of monophagous species than refuge-seeking and refuge-inducing species; (5) the proportions of monophagous species infesting annual and perennial hosts are similar; however, many species infesting annual hosts have wider host ranges than those infesting perennial hosts; (6) the proportions of species that are monophagous infesting evergreen and deciduous plants are similar;

A. Skoracka (✉)
Department of Animal Taxonomy and Ecology, Institute of Environmental Biology,
Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland
e-mail: anna.skoracka@amu.edu.pl; skoracka@amu.edu.pl

L. Smith
Exotic and Invasive Weeds Research Unit, US Department of Agriculture, Agricultural Research
Service, 800 Buchanan Street, Albany, CA 94710, USA

G. Oldfield
US Department of Agriculture, Agricultural Research Service, Riverside, CA 92521, USA

M. Cristofaro
BBCAonlus/ENEA C. R. Casaccia, BAS BIOTEC SIC, via Anguillarese 301, 00123 Rome, Italy

J. W. Amrine
West Virginia University, Morgantown, WV, USA

(7) non-monophagous eriophyoid species have wider geographic distribution than monophagous species. Field and laboratory host-specificity tests for several eriophyoid species and their importance for biological control of weeds are described. Testing the actual host range of a given eriophyoid species, searching for ecological data, genetic differentiation analysis, and recognizing factors and mechanisms that contribute to host specificity of eriophyoid mites are suggested as future directions for research.

Introduction

Host specificity is a key property of plant parasites and is significant in the study of their evolutionary and applied ecology. The role of host plants in the differentiation and diversity of herbivores is real, and is a clue to understanding their global biodiversity (e.g., Ehrlich and Raven 1964; Strong et al. 1984; Farrell 1998). Within plant-feeding arthropod species, variation in host specificity can be observed. Some are highly specialized and feed on a single host species, whereas others extend their ranges to a wide array of hosts (e.g., Futuyma 1983; Jaenike 1990; Mitter and Farrell 1991; R'Kha et al. 1991; Novotny et al. 2002a, b; Dyer et al. 2007). However, the preponderance of narrow host specificity has been often observed, and herbivores species tend to be specialized in their use of particular plant taxa (Strong et al. 1984; Bernays and Chapman 1994; Bernays 1998; Funk et al. 2002). Even those that are relatively polyphagous commonly show a preference for some plant species above others (Fox and Morrow 1981; Yano et al. 1998; R'Kha et al. 1991; Drés and Mallet 2002; Bolnick et al. 2003; Ferrari et al. 2006; Magalhães et al. 2007). Such bias toward high host specificity has often been explained in terms of cost of adaptation (Kassen 2002). A higher performance on one host can be achieved at the expense of adaptation to other host species. Given that different host species have different defense systems, investing in many counter-adaptations should have a fitness cost for the parasite (Becerra 1997; Nosil et al. 2005). On the other hand, high specialization on fewer host species can make highly host-specific parasites more prone to local extinction (Poulin 2007). Generally, both strategies, specialization and generalization, can have advantages and ensure efficiency due to a great diversity of mechanisms leading to different patterns of host use (Fox and Morrow 1981). Factors that contribute to the host specificity of phytophagous arthropods are discussed in the next section of this paper.

Eriophyoid mites are among the smallest plant feeders. Their importance as direct crop pests, vectors of plant viruses and agents for biological control of weeds in indisputable (Oldfield 2005). Thus, determination of true host ranges of eriophyoid species and the mechanisms leading to particular host specificity is fundamental to understanding mite-host interactions, coevolution of mites and hosts, and the great species diversity of this group (Lillo and Sobhian 1994; Cullen and Briese 2001). Since the review *Diversity and Host Plant Specificity* by Oldfield (1996) no facts disclaiming the belief that most eriophyoid species are highly host specific have been revealed. However, since then, new data have been obtained regarding mite-host relationships, host-specificity testing, and factors that may influence mite specialization. The aim of this paper is to review the current knowledge of host specificity and specialization in eriophyoid mites and point to knowledge gaps and doubts. First, we review factors that have been suggested by researchers as

affecting host specificity of phytophagous arthropods with special attention to eriophyoid mites. Second, using available data on described species and recorded hosts we test whether any general trends exist in the host specificity of eriophyoid mites. Third, we present the importance of the knowledge on eriophyoid host specificity in biological control of weeds. Finally, we point and suggest future directions for research.

Factors influencing host specialization and specificity

Patterns of association between herbivores and their hosts may evolve as a result of parallel cladogenesis (i.e., the cospeciation of herbivore lineages with their hosts), or host switching and the colonization of new host species. Many physiological and ecological characteristics of both hosts and herbivores can facilitate host switching and subsequent decreases in host specificity, or in contrast, support higher specialization on fewer host species (Poulin 2007 and references herein).

Host-plant specificity can be mediated by plant chemical cues (Harborne 1982; Musser et al. 2002). Host shifts can be facilitated by plant chemical similarity, such as when a phytophagous species adopts a new host whose secondary compounds are similar to those of its old host (Ehrlich and Raven 1964; Becerra 1997; Becerra and Venable 1999; Wheat et al. 2007). On the other hand, host defence may reduce the probability of host switching. Under this scenario, phytophagous species dispersing to novel hosts suffer reduced fitness compared to those remaining on the native host (Clayton et al. 2003). Related plant taxa often have similar chemistry (e.g., Mathews et al. 2000). It has been shown for many herbivorous insects species that they feed on closely related congeneric plant species (Janzen 1980; Novotny et al. 2002a, b). Host shifts can be also limited to hosts that are geographically available. Becerra and Venable (1999) tested a model that a shift to a novel host species is more likely to evolve if its geographical range is coincident with the geographic distribution of the old host. They showed that polyphagous species in their host use have responded more strongly to geographic distribution of host plant, whereas monophagous species have responded more strongly to plant chemistry. Regardless, it should be noticed that there might be correlations between host phylogeny, chemistry and geography. None of these characteristics of host plants have been directly tested as influenced host specificity of Eriophyoidea. Eriophyoid species are characterized by very intimate relationships with their hosts, most of them are restricted to single host species. Among these which infest few host species the tendency that they feed on related host plants is expected (Oldfield 1996). Among polyphagous eriophyoid species, many attack cultivated plants which are distributed world-wide. Thus, wider geographic distribution for generalist eriophyoid species is expected.

The importance of host availability as a factor that influences the evolution of host use is well supported by many ecological studies (Strong et al. 1984; Bernays and Chapman 1994). It is expected that when hosts are short-lived, infrequent, unpredictable, and therefore hard to find, parasites should generalize, whereas for hosts that are long-lived, or abundant, predictable, and therefore easy to find, parasites should specialize (Jaenike 1990). It has been shown that host race formation (thus, host specialization) is more likely to evolve for phytophagous mite species exploiting perennials than for species exploiting annual crops or herbaceous plants (Magalhães et al. 2007).

Host availability, however, depends on dispersal capacities of parasites and their success in finding and establishing on a new host (Ward et al. 1998). Eriophyoid mites are almost totally dependent on wind currents to disperse (e.g., Nault and Styer 1969). The

probability of finding a particular host during air dispersal is very low (except when the host is very common), because mites have no control of wind direction, and cannot control where they land (Sabelis and Bruin 1996). Eriophyoids inhabiting hosts that are transient in space and time must disperse more frequently than if their hosts were more permanent. So, for eriophyoids on transient hosts, a generalist strategy is more likely to evolve. Thus, for wind-dispersed species living on short-lived, ephemeral, scarce, or unpredictable hosts (e.g., annuals) low host specificity is expected. *Aceria tosichella* Keifer can be an example of such a species. It is a monocot-infesting species which has a wide range of grass hosts (ca. 120 species), and for which air dispersal has been proven (Nault and Styer 1969).

Since the majority of eriophyoid mites have narrow host ranges, dispersal by phoresy on host-specific animal carriers, which may increase the possibility of finding a specific host, has been suggested (Sabelis and Bruin 1996). However, it is stressed that although phoresy happens for eriophyoids, it is rather rare and accidental, and wind is the dominant way of interplant dispersal for these mites (Zhao and Amrine 1997; Zhao 2000). Another way to avoid the risk of high mortality during wind dispersal is to evolve strategies which allow mites to persist during phenological changes in their hosts that make them unsuitable, so that they can resume development on the same long-lived host plant later. The formation of the diapausing form of adult female (deuterogyny), which survives on the plant during mite dormancy, is a widespread and successful strategy (Manson and Oldfield 1996). Due to the presence of such strategies, species inhabiting long-lived, stable and predictable hosts have been suggested to be highly host specific (Lindquist and Oldfield 1996). Most eriophyoids develop on perennials (Oldfield 1996). If they develop on annuals, then, the plant either (1) has habitable stages of development throughout the year, so that the mite always has a place to live (e.g., *A. tosichella* on wheat [summer wheat, winter wheat]), or (2) the mite develops on several hosts, which include both annuals and perennials, thus some hosts are available at all times [e.g., *A. tosichella*, *Aculops lycopersici* (Tryon)], or (3) the mite is able to survive within the overwintering fruit or on the seed of its only host (*Paraphytoptus pannolus* Keifer). Thus, mites developing on annuals can theoretically have either wide or narrow host ranges.

Another characteristic that can influence the pattern of parasite's host use is the degree of intimacy with the host environment. Weak associations of parasites with their host (e.g., in soft ticks, external herbivore feeders) may select for lower host specificity by avoiding specific host immune responses. Whereas, strong and intimate associations (e.g., in internal herbivore feeders, also gall-inducing eriophyoid mites) may select for higher host specificity by evolving complex processes enabling avoidance of host defences (Janzen 1970, 1980; Musser et al. 2002; Magalhães et al. 2007). High host specificity is, thus, expected for the gall-inducing and refuge-seeking eriophyoids, first because they are physiologically more intimately related with their hosts than vagrants are (Lindquist 1996; Lindquist and Oldfield 1996). Second, species living in shelters are better protected and hence less subject to predation (Sabelis 1996). Predators do not strongly influence the densities of mites living in shelters, so reproductive success of these mites is mainly limited by intra- and interspecific competition for food. This should lead to specialization on particular host species. Only a very few of the several thousand described Eriophyoidea species are known as generalists, and most of these few are vagrant species limited to either monocot or dicot hosts (Oldfield 1996). For example, a notable generalist, *Calacarus citrifolii* Keifer, a leaf vagrant species on citrus in South Africa, has been collected from plants in 21 dicot families. *Aculus schlechtendali* (Nalepa), another leaf vagrant species, can reproduce on some members of three related

genera according to Kozłowski and Boczek (1987). A non-vagrant mite, *Floracarus perrepae* Knihinicki and Boczek, induces galls only on hosts within the genus *Lygodium* (Goolsby et al. 2005).

Passive philopatry (i.e., preference to remain at the natal site) and host-associated mating (which often arises as a by-product of philopatry) were suggested as promoting the evolution of host specialization in the Acari (Magalhães et al. 2007). Passive philopatry is common and strong in gall-inducing eriophyoid species, which reproduce in the natal site within a host for many generations (Oldfield 2005). Thus, these characteristics also suggest that we should expect higher host specificity in gall-inducing eriophyoid species when compare to vagrant species.

While, the above hypotheses can be supported by some examples of particular eriophyoid species, it must be noted we know of no experiments that have been performed to test the above factors as determinants of eriophyoid host specificity. Therefore, we have collected all available records on eriophyoid mites and their hosts to determine if the known data support some of the hypotheses. Specifically, we test the following hypotheses:

(1) Most species belonging to Eriophyoidea are monophagous.
(2) The degree of host specificity in members of the three families: Eriophyidae, Phytoptidae, and Diptilomiopidae is similar (according to Oldfield 1996).
(3) Non-monophagous eriophyoid species infest closely related hosts.
(4) Host ranges of refuge-inducing eriophyoid species are more restricted than those of refuge-seeking and vagrant species.
(5) Host ranges of eriophyoid species developing on annual hosts are wider than species developing on perennial hosts.
(6) Host ranges of eriophyoid species developing on evergreen hosts (as representatives of more steady and constant habitat) are more restricted than these of species developing on deciduous hosts (as representatives of more unsteady and unstable habitat).
(7) Non-monophagous eriophyoid species have wider geographic distribution than monophagous species.

Materials and methods

For analyses a personal database developed by Jim Amrine and Enrico de Lillo containing records, including 3,957 eriophyoid species and 7,699 host plant species was used. The database was created from all available papers regarding eriophyoids published between 1830 to 2007. Details regarding sampling methods can be found in the respective papers. Each mite species was classified by the number of host plants (as species, genus, family) it is associated with. Any uncertain records were removed from analyses; therefore, sample sizes varied between particular analyses.

To test hypotheses no. (1) and (2), proportions of species that were monophagous vs. non-monophagous belonging to the whole superfamily Eriophyoidea, and each of the families were presented using the frequency distributions for the number of host species, host genera, and host families.

To test the hypothesis no. (3) only non-monophagous species ($N = 781$) were included into the analysis. The regression analysis of the number of host species per eriophyoid species and the number of host genera, and host families, respectively was performed.

To test the hypothesis no. (4) we compared host ranges of mites belonging to three groups differing in the degree of intimacy with the host plant: (1) "vagrant"—mites that are free living on any part of the plant, do not seek for refuges and are not able to create refuges; (2) "refuge-seeking"—mites that are not able to create refuges, but seek natural refuges offered by plants and live within them, (e.g., buds, leaf sheaths); (3) "refuge-inducing"—mites that are able to induce refuges (any types of galls and other distortions) and live within them (according to Sabelis and Bruin 1996; Westphal and Manson 1996). Proportions of monophagous species belonging to each of the groups were shown. The frequency distributions of eriophyoid species as a function of the number of host species for each of the groups were presented.

To test hypotheses no. (5) and (6) we compared host ranges of mites infesting (1) two types of hosts: annual (as representatives of short-lived hosts) and perennial (as representatives of long-lived hosts), and (2) two types of perennial hosts: evergreen (as representatives of more steady and constant habitat) and deciduous (as representatives of more unsteady and unstable habitat). Proportions of monophagous species belonging to each of the groups and the frequency distributions for the number of host species among eriophyoid species belonging to the each of the groups were presented.

To test the hypothesis no. (7) an attempt was made to correlate the geographic distribution ranges of eriophyoid species (measured as the number of ecozones where a given species has been recorded) with host range. The proportions of eriophyoids that are monophagous were presented in four classes of geographic distribution: class 1—containing eriophyoid species recorded in one ecozone, class 2—containing eriophyoid species recorded in two ecozones, class 3—containing eriophyoid species recorded in three ecozones, and class 4—containing eriophyoid species recorded in four and more ecozones. The grouping was done due to the low number of observations in 4, 5, 6 or 7 ecozones (to avoid expected values less than 5). Ecozones were applied according to the biogeographic realms of Udvardy (1975): Palearctic, Nearctic, Afrotropical [Ethiopian], Indomalaya [Oriental], Neotropic, Australasia [Australian], Oceania [Pacific]. Antarctic was not included since no eriophyoid species have been recorded there.

Differences between proportions were tested by chi-square with Bonferroni correction. The 95% confidence intervals for proportions were calculated using the binomial distribution. For computations Statistic and S-Plus software were used.

It must be noted that there is some uncertainty regarding the numbers of eriophyoid species due to nomenclatural problems. Some eriophyoid species names in the database are suspected of being synonyms, and there is a need for their taxonomic verification. Also, botanical taxonomic names require thorough verification due to the fact that botanical classification (especially for monocots) has undergone considerable revision in recent years, and many genera have been assigned to different families based on genetic sequence similarity. Data are used to illustrate general rules and support earlier beliefs, and to summarize all data available till now.

Results: patterns of host specificity in eriophyoid mites

Plant families of the greatest interest, i.e., those with the highest number of eriophyoid species (ES) recorded are: Rosaceae (ca. 300 ES), Fabaceae (ca. 250 ES), and Asteraceae (ca. 200 ES), as well as Aceraceae, Euphorbiaceae, Moraceae, Rubiaceae, Pinaceae, Salicaceae, Fagaceae, Poaceae (>100 ES each). All of these plant families are large in terms of number of species and geographical range, and many are of economic importance.

Table 1 Descriptive statistics for host ranges of superfamily Eriophyoidea and its three families

|	Phytoptidae	Diptilomiopidae	Eriophyidae	Eriophyoidea
N	169	374	3,331	3,874
No. host species				
Mean (95% CI)	2.2 (1.8–2.8)	1.4 (1.2–1.6)	1.7 (1.6–1.8)	1.7 (1.6–1.8)
Range	1–24	1–28	1–120	1–120
Percentage monophagous (95% CI)	69 (61–75) a	86 (82–89) b	80 (78–81) c	80 (79–91)
No. host genera				
Mean (95% CI)	1.2 (1.1–1.4)	1.1 (1.0–1.2)	1.1 (1.1–1.2)	1.1 (1.1–1.2)
Range	1–6	1–9	1–55	1–55
Percentage monophagous (95% CI)	88 (82–91) a	95 (93–97) b	95 (94–96) b	95 (94–95)
No. host families				
Mean (95% CI)	1.0 (0.1–1.0)	1.0 (1.0–1.1)	1.0 (1.0–1.1)	1.0 (1.0–1.1)
Range	1–2	1–5	1–21	1–21
Percentage monophagous (95% CI)	99 (96–100) a	98 (97–99) a	99 (99–100) a	99 (98–99)

Percentages in the same row followed by the same letter are not significantly different (chi-square tests, $P < 0.05$ with Bonferroni adjustment)

Hypothesis (1) For the analyzed Eriophyoidea species ($N = 3,874$) the number of reported host-plant species ranged from 1 to 120, with a mean number of host species of 1.67 ± 0.05 SE, a modal value of 1, and frequency of modal value 80% (Table 1; Fig. 1). The mean number of host genera and families recorded per one eriophyoid, as well as ranges and modal values, are given in Table 1. The frequency distributions for the number of host species, host genera, and host families were strongly skewed, with most eriophyoid species being found on one host species (80%), one host genus (95%), or one host family (99%) (Figs. 1, 2, 3).

Hypothesis (2) The frequency distributions for the numbers of host species for each family of Eriophyoidea analyzed separately were also strongly skewed, with most Phytoptidae, Eriophyidae, and Diptilomiopidae species been recorded from one host species (69, 80 and 86% respectively). All three percentages are significantly different (chi-square tests, $P < 0.0001$), indicating that Diptilomiopidae has the highest proportion of monophagous species and Phytoptidae has the fewest monophages (Table 1).

The maximum number of host species recorded per mite species was: 24 for the phytoptid *Trisetacus ehmanni* Keifer, 28 for the diptilomiopid *Diptacus gigantorhynchus* (Nalepa), and 120 for the eriophyid *A. tosichella*. Regarding specificity at the generic level, fewer Phytoptidae species (88%) were associated with hosts within one genus than Diptilomiopidae (95%) or Eriophyidae (95%). The percentage of eriophyoid species associated with plants within one family was similar for all three eriophyoid families (99, 98 and 99% for Phytoptidae, Diptilomiopidae and Eriophyidae, respectively) (Table 1). Oldfield (1996) concluded that the degree of host specificity in members of the three families is similar. However, our results show that this is true only at the family level of host specificity. Considering the proportions of species with the highest host specificity (i.e., monophagous) Phytoptidae seems to be the least host-specific, whereas Diptilomiopidae was the most.

Hypothesis (3) Non-monophagous eriophyoid mites showed a tendency to infest hosts belonging to the same family or to the same genus (thus, to closely related hosts). They
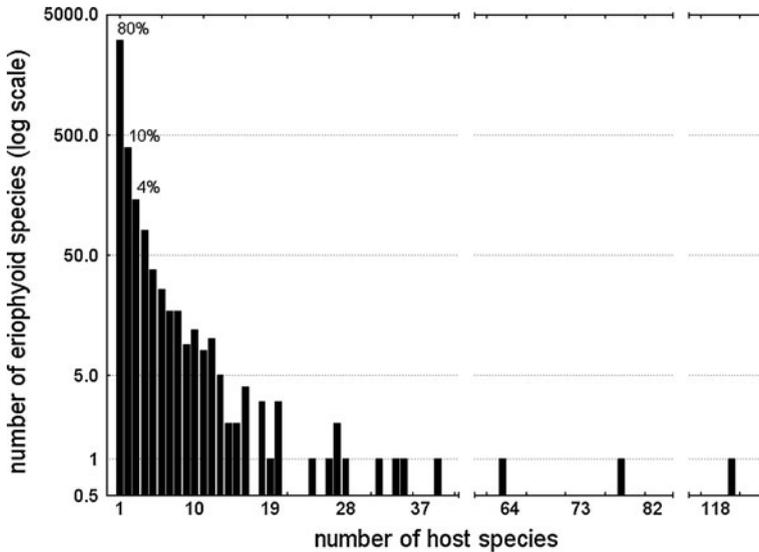
Fig. 1 Distribution of host species among eriophyoid species. Most eriophyoid species have been recorded from one host species (80%)
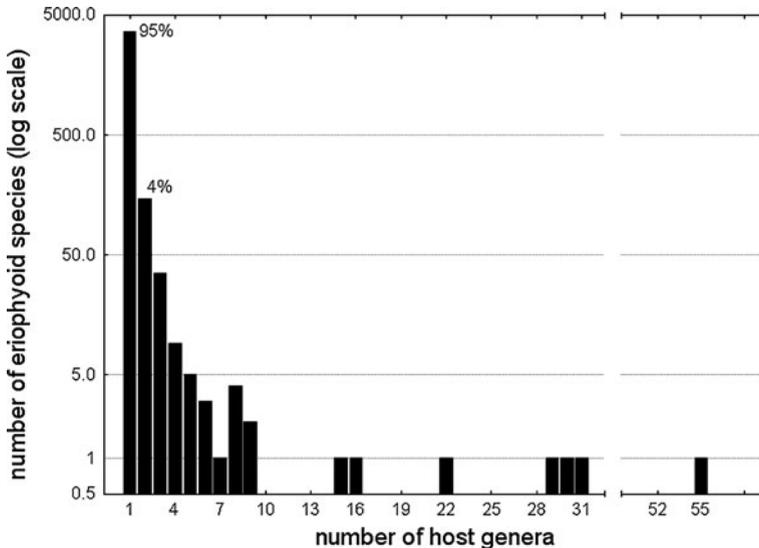
Fig. 2 Distribution of host genera among eriophyoid species. Most eriophyoid species have been recorded from one host genus (95%)

predominantly attack plants in only one genus (73%), and one family (96%). An example of a species with a wide host range is *Phyllocoptes fructiphilus* Keifer which can develop on nearly every species in the genus *Rosa* (except for *Rosa bracteata* J.C. Wendl.) but does not develop on any other genus of Rosaceae (Amrine 2002; James W. Amrine's results of
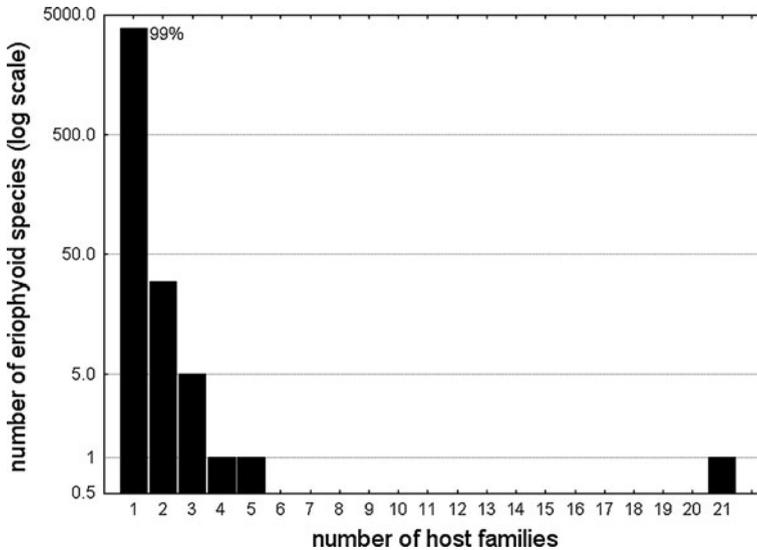
Fig. 3 Distribution of host families among eriophyoid species. Most eriophyoid species have been recorded from one host family (99%)

testing all of the common plants of Rosaceae in West Virginia). *Aceria tosichella* appears to be one of the most polyphagous eriophyoid species and has been reported from at least 120 host species in 55 genera, all in the family Poaceae. Other polyphagous mites are *Aceria tenuis* (Keifer) and *Abacarus hystrix* (Nalepa) also reported on many grass host species belonging to different genera. However, *Calacarus citrifolii* Keifer, which has been recorded from 35 host species belonging to 29 genera from 21 families, can be considered even more polyphagous because of the wider phylogenetic range of its hosts (Fig 4a, b). *Calacarus citrifolii* is unusual in attacking hosts in so many different families; however, host specificity of individual populations has never been experimentally tested.

Hypothesis (4) The frequency distributions of mite species as a function of the number of host plant species for each of the three groups of the degree of intimacy between eriophyoid mites and their hosts were skewed, with most vagrant, refuge-seeking, and refuge-inducing species being monophagous. The vagrants have a significantly higher percentage of monophagous species (84%) when compared to either refuge-seeking (76%) or refuge-inducing species (72%) (chi-square tests, $P < 0.0001$; Table 2; Fig. 5). Contrary to expectation (Lindquist 1996; Sabelis and Bruin 1996), host specificity seems to be the highest for vagrants, compared to either refuge-seeking or refuge-inducing mites. However, we should be cautious about this conclusion as it is based on a simple analysis of records data, not on controlled host-range testing experiments.

Hypothesis (5) The percentages of species that were monophagous of those infesting annual (71%) vs. perennial (68%) hosts were not significantly different (chi-square tests, $P = 0.64$) (Table 3; Fig. 6). This suggests that the longevity of the host plant does not influence host specificity of eriophyoid species, and that most species infesting either annual or perennial hosts are highly host specific. However, among eriophyoid species infesting annuals there are many which have evidently low host specificity than among
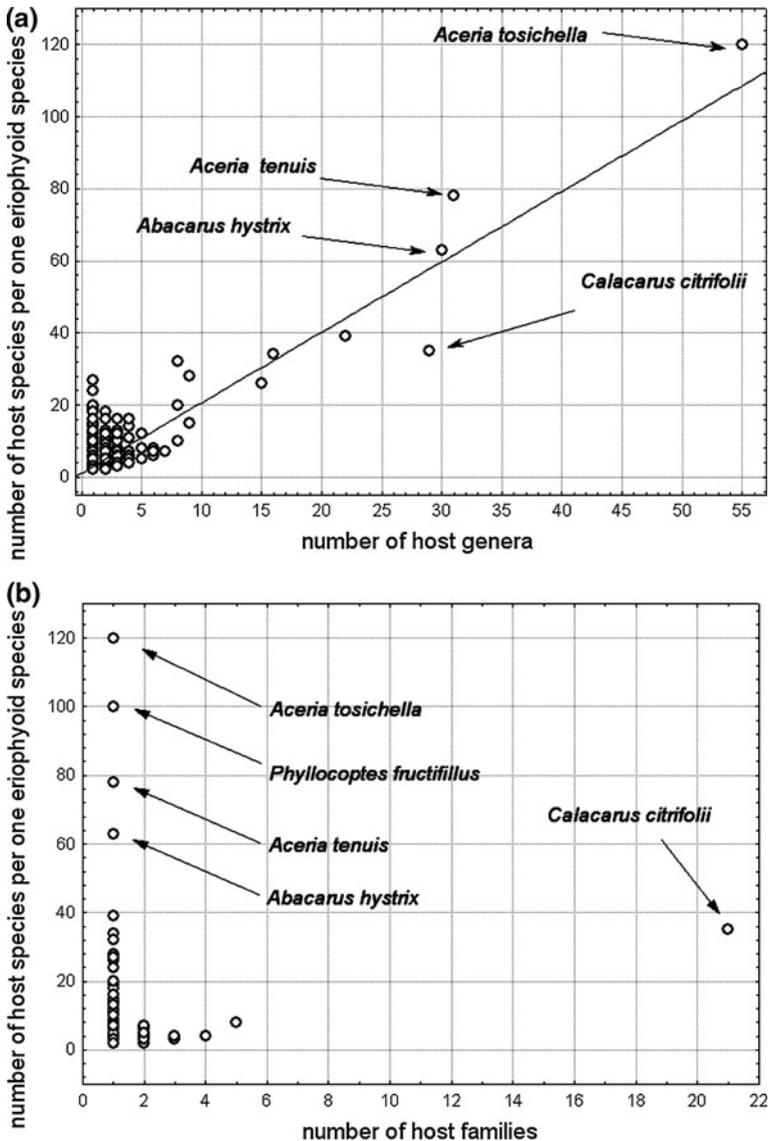
Fig. 4 Relation between number of host genera (**a**) and host families (**b**) and number of host species per eriophyoid species for non-monophagous eriophyoids

species infesting perennials (see the number of host species on Fig. 6). Thus, there is a higher tendency to have wide host ranges for eriophyoid species infesting short-lived hosts than among species infesting long-lived hosts.

Hypothesis (6) The percentages of species that were monophagous of those infesting deciduous (72%) vs. evergreen (75%) hosts were not significantly different (chi-square tests, $P = 0.48$) (Table 4; Fig. 7). This suggests that eriophyoids infesting evergreen species have similar host ranges to those infesting deciduous species. Thus, different host

Table 2 Descriptive statistics for host ranges (the number of host plant species per eriophyoid species) of three groups of eriophyoid mites

	Vagrant	Refuge-seeking	Refuge-inducing
N	2,263	462	941
Mean (95% CI)	1.5 (1.4–1.6)	2.2 (1.8–3.4)	1.8 (1.7–2.0)
Range	1–63	1–120	1–27
Percentage monophagous (95% CI)	84 (82–85) a	76 (72–80) b	72 (69–75) b

Percentages in the same row followed by the same letter are not significantly different (chi-square tests, $P < 0.05$ with Bonferroni adjustment)

strategies expressed as losing green foliage for part of the year or having persistent green foliage year round apparently do not affect eriophyoid host specificity.

Hypothesis (7) The proportion of species that are monophagous is significantly higher among species restricted to one ecozone compared to those in two and more ecozones (chi-square tests, $P < 0.0001$; Table 5). Among non-monophagous species recorded in many ecozones many are associated with cultivated plants, e.g., *A. lycopersici*—tomato; *Aculus fockeui* (Nalepa et Trouessart)—peach, plum; *Phyllocoptruta oleivora* (Ashmead)—citrus; *Eriophyes pyri* (Pagenstecher)—pear; *A. schlechtendali*—apple. It is likely that their widespread occurrence represents human distribution. Poorly studied species (i.e., those with only a species description) are reported for only one ecozone, but may have wider distributions if fully studied, which may bias the results.

Testing of host specificity in eriophyoid mites and its importance for biological control of weeds

Biological control of weeds

Biological control of weeds is the deliberate use of natural enemies to reduce the density of a particular weed to a tolerable level (Driesche et al. 2008). This usually involves the importation of natural enemies, such as an eriophyoid mite, from the land of origin of the plant, to control it in an adventive region where it is invasive (Smith et al. 2009b [in this issue]). In order to avoid causing environmental harm, it is important to use natural enemies that will not attack nontarget plant species. Therefore, considerable host-specificity testing is done prior to the release of biological control agents (Murdoch et al. 1985; McEvoy 1996; Sheppard et al. 2003; Delfosse 2004). Due to increasing regulatory requirements and decreasing tolerance of risk to native species, host specificity tests are undergoing continual improvement (Briese 2005; Carruthers and D'Antonio 2005; Sheppard et al. 2005).

The results of host specificity tests conducted under laboratory conditions may differ from what is expected under natural field conditions, because of the "artificial" environmental conditions of the bioassay (Marohasy 1996, 1998). During the past 20 years, use of field experiments has increased, because they provide results more predictive of the risk to nontarget species under natural conditions (Clement and Cristofaro 1995; Briese 1999). In cases where quarantine tests indicate damage to non-target plants, open field tests can demonstrate whether this is a realistic host plant, or a laboratory artifact ("false positive"). However, because open field tests must be conducted in the country of origin, often in
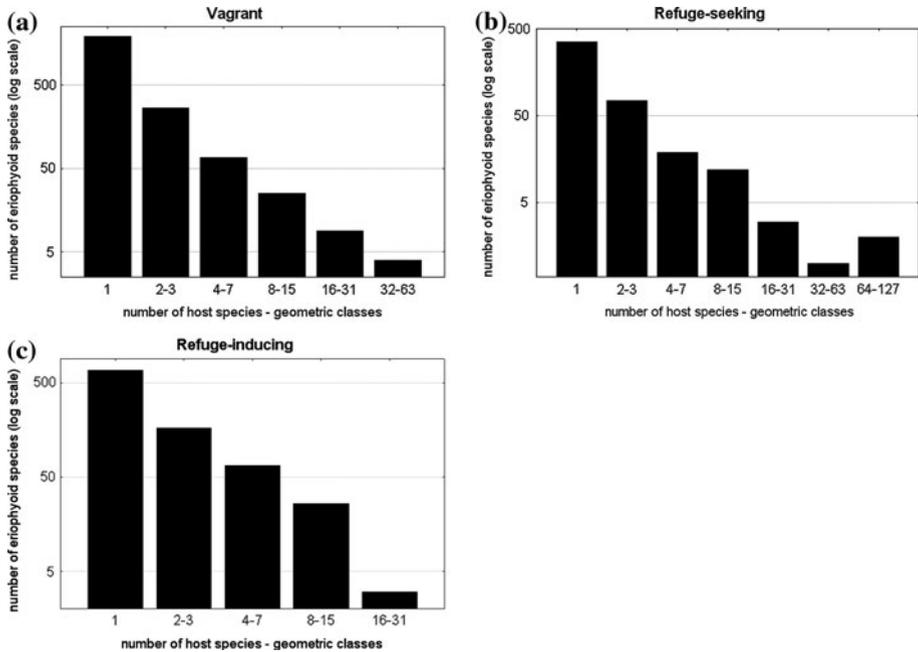
Fig. 5 Distribution of host species among eriophyoid species for three groups of eriophyoid mites: **a** vagrant, **b** refuge-seeking, **c** refuge-inducing

Table 3 Descriptive statistics for host ranges of two groups of eriophyoid mites inhabiting annual and perennial hosts

	Annual	Perennial
N	177	177
Mean (95% CI)	3.8 (1.2–5.6)	2.0 (1.6–2.3)
Range	1–120	1–15
Percentage monophagous (95% CI)	71 (63–77) a	68 (61–75) a

Percentages in the same row followed by the same letter are not significantly different (chi-square tests, $P < 0.05$ with Bonferroni adjustment)

remote areas and uncontrollable natural conditions, they are difficult to do well (Clement and Cristofaro 1995; Briese 1999).

Host specificity testing of eriophyoid mites

Laboratory experiments typically are conducted to test the ability of the classic biological control agent to develop on and damage nontarget plants. Emphasis is on the plant species thought to be most at risk, i.e., those most closely related to the known host plant (phylocentric approach) (Wapshere 1974). For insects, both choice and no-choice experiments are usually conducted to provide a measure of the "physiological" or "fundamental" host range (widest possible range corresponding to no-choice results) and "ecological" or "field" host range (more realistic range corresponding to choice results) (Sheppard et al. 2005).
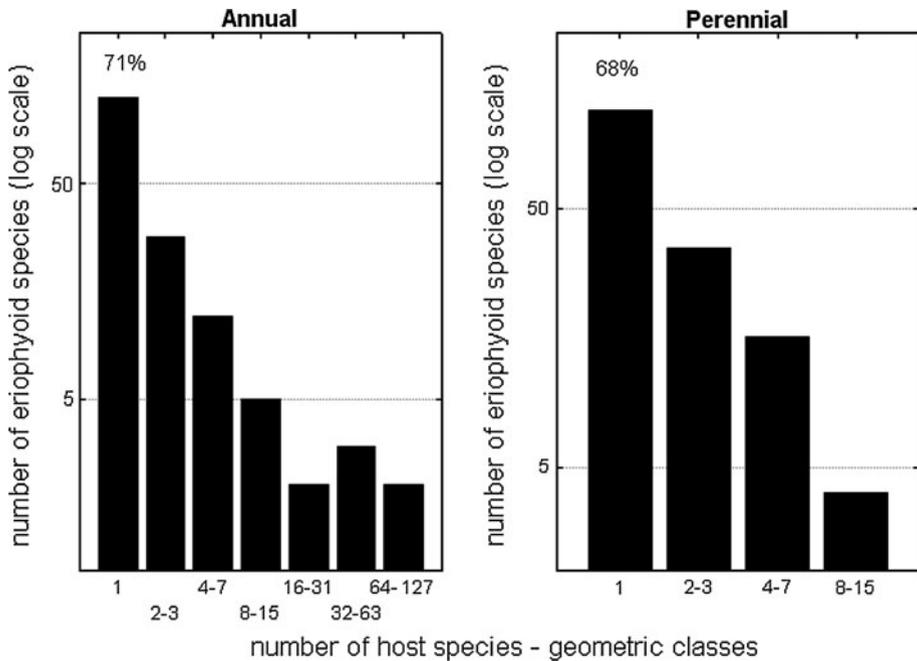
Fig. 6 Distribution of host species among eriophyoid species infesting annual and perennial hosts

Table 4 Descriptive statistics for host ranges of two groups of eriophyoid mites inhabiting deciduous and evergreen hosts

	Deciduous	Evergreen
N	250	250
Mean (95% CI)	1.8 (1.6–2.1)	1.9 (1.6–2.3)
Range	1–19	1–120
Percentage monophagous (95% CI)	72 (66–77) a	75 (70–80) a

Percentages in the same row followed by the same letter are not significantly different (chi-square tests, $P < 0.05$ with Bonferroni adjustment)

However, for eriophyoid mites, generally no-choice experiments have been conducted. This is probably partially a matter of convenience (because it is easy to infest each test plant, but difficult to allow mites to disperse by wind among test plants) and partially because scientists expect the mites to have extremely narrow physiological host range, therefore not necessitating follow-up with choice experiments. It has been argued that no-choice experiments are most relevant for "inactive, small, passively dispersed" organisms (Hill 1999); however this theory is untested. Because eriophyoid mites disperse primarily by wind, deprivation of wind may be expected to increase the tendency of mites to feed on a nontarget plant because they are not able to depart. Therefore, no-choice tests may produce "false positives". To our knowledge, choice experiments that permit mites to disperse by wind have not been done under laboratory conditions. Stoeva et al. (2008) conducted a choice experiment in which test plants touched an infested host plant, so the mites could disperse by crawling. However, their results did not differ greatly from those of a parallel
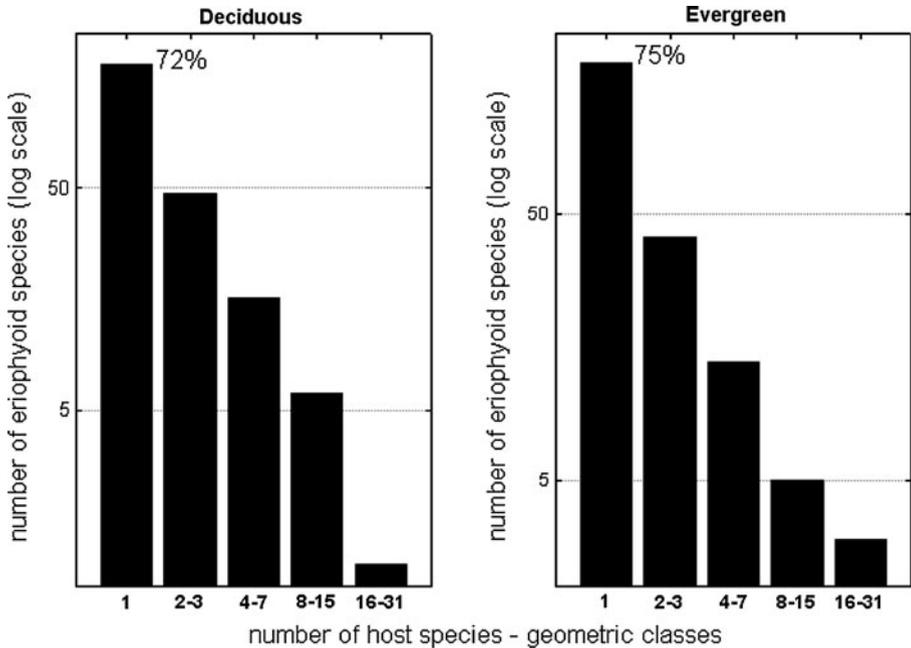
Fig. 7 Distribution of host species among eriophyoid species infesting deciduous and evergreen hosts

Table 5 Statistics for host ranges (the number of host plant species per eriophyoid species) of eriophyoid mites in the respective number of ecozones where the mites have been recorded

Class of geographic distribution	No. of eriophyoid species	Mean of host species per mite species (95% CI)	Range	Median value	Percentage monophagous (95% CI)	
1	3,569	1.4 (1.4–1.5)	1–78	1	83 (82–84) a	
2	236	3.9 (3.1–4.6)	1–39	2	41 (35–47) b	
3	35	5.9 (1.9–12.8)	1–120	1	51 (35–67) b	
4	14	9.8 (1.5–19.7)	1–63	1	57 (33–79)	
5	7	2.3 (0.5–4.0)	1–6	1	57 (25–85)	45 (31–62) b[a]
6	4	8.8 (1.3–14.3)	1–32	1	75 (33–97)	
7	8	12.2 (4.6–20.0)	3–27	9	25 (5–57)	

[a] This value includes classes 4–7

Percentages in the same column followed by the same letter are not significantly different (chi-square tests, $P < 0.05$ with Bonferroni adjustment)

Classes of geographic distribution are the following: 1—eriophyoids recorded in one ecozone, 2—eriophyoids recorded in two ecozones, etc.

no-choice experiment. For insects, in cases where the laboratory results indicated possible damage to nontarget plants, sometimes field experiments have been able to demonstrate that this does not occur under natural conditions (e.g., Medal et al. 1999; Smith et al. 2006; Bredow et al. 2007). Such field experiments have rarely been done with eriophyoid mites before obtaining approval for release (McClay et al. 1999; Littlefield and Sobhian 2000;

Sobhian et al. 2004; Smith et al. 2008, 2009a), but this may be the most practical way to resolve such uncertainty. Post-release experiments can be useful for better measuring risk to nontarget plants (Willis et al. 2003); however, this is not an acceptable approach for evaluating new agents before they are approved for release.

In order for host specificity experiments to produce results that accurately predict risk of damage to nontarget plants in the field, they must be designed based on knowledge of the life history of the eriophyoid mites and the plants. Plants must be at a suitable developmental stage to provide the plant structures that are vulnerable to the mites. Environmental conditions should be optimal for the mites, but it is possible that some stresses on the plants may make them more vulnerable to attack (Willis et al. 1995, 2003). The duration of experiments is an open question because generally little is known about the longevity, development rate, oviposition period, diapause requirements and dispersal behavior of the species being evaluated. For example, Stoeva et al. (2008) monitored test plants at 10, 20, 30, 40, 60 and 90 days and found that eriophyoid mites did not colonize one of the nontarget plant species until day 60. More knowledge of the basic life history of the mites would greatly help inform the appropriate design of host specificity experiments. The effect of plant quality is another potentially important variable. Plants that do not have tissue at the right stage for induction of galls will mask susceptibility (e.g., Goolsby et al. 2005), whereas those that have unusually soft tissue resulting from artificial growing conditions could be more susceptible than normal. However, data on these effects is generally lacking.

One of the main constraints to the efficacy of eriophyoid mites as biological control agents is that they may encounter genotypes of the target weed that are resistant to the mite (Sobhian and Andres 1978; Cullen and Moore 1983; Hufbauer and Roderick 2005; Goolsby et al. 2006; Hrusa and Gaskin 2008). On the other hand, eriophyoid mites that are capable of attacking several closely related plant species may be less likely to encounter resistant genotypes (Smith 2005). Clearly, eriophyoid mites vary in the level of host plant specificity (Cullen 1990). However, the physiological factors that control host plant specificity of eriophyoid mites are often unknown, as are the factors that provide resistance in some genotypes of host plant (Westphal and Manson 1996; Westphal et al. 1996; Freeman et al. 2005).

Conclusions and future directions

In its most basic sense, the host specificity of a parasite is determined by the number of host species it can exploit successfully (i.e., 'host range' sensu Lymbery 1989). Our analyses show that most eriophyoid species are monophagous. This result was consistent for each taxonomical level (superfamily or family) and various ecological groups (in terms of the degree of mites intimacy with hosts, and of the longevity and stability of infested hosts) tested. Among non-monophagous species a tendency to infest related hosts was detected. Thus, our investigations confirmed the hypotheses that species belonging to Eriophyoidea are indeed highly host specific. Generalist species are exceptional.

However, most of the mite-host relationships analyzed here were from single records from the literature, most often from the descriptions of new species. Thus, it is possible that the number of monophagous species is overestimated due to lack of knowledge. When the classification of herbivores as specialists and generalists is dependent on the number of plant species studied, it is likely that studies focusing on a small part of the local fauna may not detect all plants species which are actually infested by herbivores. With an increasing sampling the proportion of specialist species can decrease (Novotny et al. 2002b). On the

other hand, the number of generalists species might also be overestimated if the occurrence of species listed as the generalist is accidental on many of the recorded host plants, or due to not distinguishing host races or cryptic species of mite.

Indeed, many phytophagous arthropods regarded as host generalists have, on closer inspection, been actually shown to consist of groups of host specialists that differ in their host utilization (Drés and Mallet 2002). When such differences in host utilization are genetically based they may represent different host races (if there is a partial differentiation of the gene pools between host specialized populations) or even different species (total separation of gene pools) (e.g., Drés and Mallet 2002; Blair et al. 2005; Stireman et al. 2005; Magalhães et al. 2007). Host races that are an intermediate stage along the speciation continuum (Drés and Mallet 2002) can not be detected in such databases such as the one used here. Therefore, our analysis may underestimate host specialization.

Among non-monophagous eriophyoid mites *A. hystrix* can be an example of a such situation. Since a wide host range (ca. 60 grass species) is recognized for *A. hystrix*, it has been long considered as a host generalist (Sabelis and Bruin 1996). However, host specialization between some host-populations of *A. hystrix* has been demonstrated. When exchanged to each other's host *A. hystrix* females collected from different host plants showed no acceptance of and failed to colonize the novel host plant (Skoracka and Kuczyński 2006; Skoracka et al. 2007). Crossing experiments have revealed that in addition to host fidelity, which acts as a pre-zygotic barrier, post-zygotic barriers between *A. hystrix* host populations also exist (Skoracka 2008). A molecular genetic study has demonstrated that host populations of this mite exhibit more than 20% sequence divergence in the cytochrome oxidase subunit I (COI) gene (Skoracka and Dabert 2009). Thus, we can expect that over its huge host range *A. hystrix*, an ostensible generalist may comprise many specialized species. Other generalist eriophyoids, such as *A. tenuis*, *A. tosichella*, and *C. citrifolli*, may also represent species complexes. Recently, it has been indicated on the base of molecular markers that *A. toscihella* may be a species complex in Australia (Carew et al. 2009). The "outliers" in Fig. 4a and b should be examined to reveal if they are indeed single species with broad host ranges or if they in fact consist of many morphologically cryptic species or at least host races. Thus, we should be aware that results based on published records of eriophyoid occurrence may in fact reflect a limited knowledge of their host ranges.

Host specificity is one of the most fundamental properties of any parasite species (Adamson and Caira 1994). The successful adaptation to new hosts and to new geographical areas is correlated with the level of host specificity of a parasite (Poulin and Mouillot 2003). Thus, host specificity reflects the breadth of a parasite's ecological niche and its position and role in the biosphere. The need for a thorough knowledge of host specificity for important groups such as eriophyoid mites is evident. However, aside from a few potential agents in biological control of weeds for which host specificity tests have been performed, actual host specificity of the majority of eriophyoid species is unknown since it is based on field collection rather than on experimentation. There is a strong need to change our approach to the study of host specificity of eriophyoid mites and to challenge present knowledge. The following issues certainly warrant future attention.

1. To establish the actual host range of a given eriophyoid species host-specificity tests are required. They should include experimental evaluation of host-specific fitness, i.e., survival and reproduction of parental and successive progeny generations on various hosts, and host-specific preferences (e.g., Johnson et al. 1996; Drés and Mallet 2002). Testing of apparently monophagous eriophyoid species should consider both phylogeny and sympatry in choosing plant species as potential hosts. Testing of

eriophyoid species known to have wide host ranges should include all plant species recorded for these eriophyoids to determine which represent incidental hosts that cannot sustain reproduction.

2. The question of whether there is any host-dependent genetic differentiation within morphological eriophyoid species deserves particular attention. Reciprocal crosses between host populations infesting various plant species within the host range of a given eriophyoid species as well as using molecular genetics might help to determine whether these populations are actually the same species or whether they are host races or even cryptic species.

3. Ecological data such as prevalence or abundance of eriophyoid species on each of its host species would be valuable information on mite-host relationships. As such, all future records of eriophyoid mites on plant species should incorporate as much ecological information as possible.

4. Mechanisms that contribute to host specificity at three levels should be studied in detail, viz.

   (a) what influences host finding, i.e., how do different modes of dispersal affect host location,

   (b) what influences host selection, i.e., what cues make plants acceptable to eriophyoids (e.g., chemical, morphological),

   (c) what influences growth and reproduction on the established host, and does this also restrict the host range (e.g., essential nutrients, any specific nutritional requirements).

   It is also important to understand how different factors interact under different ecological conditions to affect selection pressure, instead of focusing on one factor as the major determinant of host range (Thompson 1988).

5. Parasites can coevolve with their hosts or they can speciate by changing host specificity (i.e., host-shifting). Although, it has been shown that speciation of seven *Cecidophyopsis* species did not closely follow speciation events in their *Ribes* host plant (Fenton et al. 2000), no general conclusions regarding causes of speciation of eriophyoid mites can be drawn at present. Too little is known about either host-switching events or coevolution with plants in regards to speciation of eriophyoids. Undoubtedly, there is a strong demand for more phylogenetic comparisons of eriophyoids and their hosts and new molecular tools developed in recent years have great potential to facilitate such studies, although analysis is not always straightforward (Vienne et al. 2007).

References

Adamson ML, Caira JN (1994) Evolutionary factors influencing the nature of parasite specificity. Parasitology 109:85–95

Amrine JW Jr (2002) Multiflora rose. In: Van Driesche R, Lyon S, Blossey B, Hoddle M, Reardon R (eds) Biological control of invasive plants in the eastern United States, USDA forest service publication FHTET-2002-04, pp 265–292

Becerra JX (1997) Insects on plants: macroevolutionary chemical trends in host use. Science 276:253–256

Becerra JX, Venable DL (1999) Macroevolution of insect-plant associations: the relevance of host biogeography to host affiliation. PNAS 96:12626–12631

Bernays EA (1998) Evolution of feeding behaviour in insect herbivores. Bioscience 48:35–44

Bernays E, Chapman RF (1994) Host-plant selection by phytophagous insects. Chapman and Hall, 328 pp

Blair CP, Abrahamson WG, Jackman TA, Tyrrell L (2005) Cryptic speciation and host-race formation in a purportedly generalist tumbling flower beetle. Evolution 59:304–316

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual speciation. Am Nat 161:1–28

Bredow E, Pedrosa-Macedo JH, Medal JC, Cuda JP (2007) Open field host specificity tests in Brazil for risk assessment of *Metriona elatior* (Coleoptera: Chrysomelidae), a potential biological control agent of *Solanum viarium* (Solanaceae) in Florida. Flo Entomol 90:559–564

Briese DT (1999) Open field host-specificity tests: is 'natural' good enough for risk assessment? In: Withers TM, Barton L, Stanley J (eds) Host specificity testing in Australasia towards improved assays for biological control. CRC for Tropical Pest Management, Brisbane, pp 44–59

Briese DT (2005) Translating host-specificity test results into the real world: the need to harmonise the yin and yang of current testing procedures. Biol Control 35:208–214

Carew M, Schiffer M, Umina P, Weeks A, Hoffmann A (2009) Molecular markers indicate that the wheat curl mite, *Aceria tosichella* Keifer, may be a species complex in Australia. Bull Entomol Res 99:479–486

Carruthers RI, D'Antonio CM (2005) Science and decision making in biological control of weeds: benefits and risks of biological control. Biol Control 35:181–182

Clayton DH, Bush SE, Goates BM, Johnson KP (2003) Host defense reinforces host-parasite cospeciation. PNAS 100:15694–15699

Clement SL, Cristofaro M (1995) Open-field tests in host- specificity determination of insects for biological control of weeds. Biocontrol Sci Technol 5:395–406

Cullen JM (1990) Current problems in host-specificity screening. In: Delfosse ES (ed) Proceedings of the VII international symposium on biological control of weeds, Rome, Italy, 1988, Istituto Sperimentale per la Patologia Vegetale, Rome, pp 27–36

Cullen JM, Briese DT (2001) Host plant susceptibility to eriophyid mites used for weed biological control. In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds) Acarology: Proceedings of the 10th international congress, CSIRO publishing, Melbourne, pp 342–348

Cullen JM, Moore AD (1983) The influence of three populations of *Aceria chondrillae* on three forms of *Chondrilla juncea*. J Appl Ecol 20:235–243

de Lillo E, Sobhian R (1994) Taxonomy, distribution and host specificity of a gall-making mite *Aceria tamaricis* (Trotter) (Acari—Eriophyoidea) asociated with *Tamarix gallica* L. (Parietales: Tamaricaceae) in southern France. Entomologica (Bari) 28:5–16

de Vienne DM, Giraud T, Shykoff JA (2007) When can host shifts produce congruent host and parasite phylogenies? A simulation approach. J Evol Biol 20:1428–1438

Delfosse ES (2004) Introduction. In: Coombs EM, Clatk JK, Piper GL, Cofrancesco AF (eds) Biological control of invasive plants in the United States. Oregon State University Press, Corvallis, pp 1–11

Drés M, Mallet J (2002) Host races in plant-feeding insects and their importance in sympatric speciation. Philos Trans R Soc Lond B 357:471–492

Dyer LA, Singer MS, Lill JT, Stireman JO, Gentry GL, Marquis RJ et al (2007) Host specificity of Lepidoptera in tropical and temperate forests. Nature 448:696–699

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18:586–608

Farrell BD (1998) 'Inordinate fondness' explained: why are there so many beetles? Science 281:555–559

Fenton B, Birch ANE, Malloch G, Lanham PG, Brennan RM (2000) Gall mite molecular phylogeny and its relationship to the evolution of plant host specificity. Exp Appl Acarol 24:831–861

Ferrari J, Goodfray HCJ, Faulconbridge AS, Prior K, Via S (2006) Population differentiation and genetic variation in host choice among pea aphids from eight host plant genera. Evolution 60:1574–1584

Fox LR, Morrow PA (1981) Specialization: species property or local phenomenon? Science 211:887–893

Freeman TP, Goolsby JA, Ozman SK, Nelson DR (2005) An ultrastructural study of the relationship between the mite *Floracarus perrepae* Knihinicki & Boczek (Acariformes: Eriophyidae) and the fern *Lygodium microphyllum* (Lygodiaceae). Aust J Entomol 44:57–61

Funk DJ, Filchak KE, Feder JL (2002) Herbivorous insects: model systems for the comparative study of speciation ecology. Genetica 116:251–267

Futuyma DJ (1983) Evolutionary interactions among herbivorous insects and plants. In: Futuyma DJ, Slatkin M (eds) Coevolution. Sinauer, Sunderland, pp 207–231

Goolsby JA, Zonneveld R, Makinson JR, Pemberton RW (2005) Host-range and cold temperature tolerance of *Floracarus perrepae* Knihinicki & Boczek (Acari: Eriophyidae), a potential biological-control agent of *Lygodium microphyllum* (Pteridophyta: Lygodiaceae). Aust J Entomol 44:321–330

Goolsby JA, DeBarro PJ, Makinson JK, Pemberton RW, Hartley DM, Frohlich DR (2006) Matching origin of an invasive weed for selection of a herbivore haplotype for a biological control programme. Mol Ecol 15:287–297

Harborne JB (1982) Introduction to ecological biochemistry. Academic Press, London, p 278

Hill RL (1999) Minimising uncertainty—in support of no-choice tests. In: Withers TM, Browne LB, Stanley J (eds) Host specificity testing in Australasia: towards improved assays for biological control. Scientific Publishing Indooroopilly, Queensland, pp 1–10

Hrusa GF, Gaskin JF (2008) The *Salsola tragus* complex in California (Chenopodiaceae): characterization and status of *Salsola australis* and the autochthonous allopolyploid *Salsola ryanii* sp. nov. Madrono 55:113–131

Hufbauer RA, Roderick GK (2005) Microevolution in biological control: mechanisms, patterns, and processes. Biol Control 35:227–239

Jaenike J (1990) Host specialization in phytophagous insects. Annu Rev Ecol Syst 21:243–273

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528

Janzen DH (1980) Specificity of seed-attacking beetles in a Costa Rican deciduous forest. J Ecol 68:929–952

Johnson PA, Hoppensteadt FC, Smith JJ, Bush GL (1996) Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortative mating. Evol Ecol 10:187–205

Kassen R (2002) The experimental evolution of specialists, generalists, and the maintenance of diversity. J Evol Biol 15:173–190

Kozłowski J, Boczek J (1987) Density and host plants of the apple rust mite, *Aculus schlectendali* (Nalepa) Acarina: Eriophyoidea). Prace Nauk IOR 29:39–50

Lindquist EE (1996) External anatomy and notation of structures. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 1–30)

Lindquist EE, Oldfield GN (1996) Evolution of eriophyoid mites in relation to their host plants. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 277–300)

Littlefield JL, Sobhian R (2000) The host specificity of *Phyllocoptes nevadensis* Roivainen (Acari: Eriophyidae), a candidate for the biological control of leafy and cypress spurges. In: Spencer NR (ed) Proceedings of the X international symposium on biological control of weeds, Bozeman, Montana, USA. Montana State University, Bozeman, pp 621–626

Lymbery AJ (1989) Host specificity, host range and host preference. Parasitol Today 5:298

Magalhães S, Forbes MR, Skoracka A, Osakabe M, Chevillon C, McCoy K (2007) Host race formation in Acari. Exp Appl Acarol 42:225–238

Manson DCM, Oldfield GN (1996) Life forms, deuterogyny, diapause and seasonal development. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 173–183)

Marohasy J (1996) Host shifts in biological weed control: real problems, semantic difficulties or poor science? Int J Pest Manag 42:71–75

Marohasy J (1998) The design and interpretation of host-specificity tests for weed biological control with particular reference to insect behaviour. Biocontrol News Infor 19:13–20

Mathews S, Tsai RC, Kellogg E (2000) Phylogenetic structure in the grass family (Poaceae): evidence from the nuclear gene phytochrome B. Am J Bot 87:96–107

McClay AS, Littlefield JS, Kashefi J (1999) Establishment of *Aceria malherbae* (Acari: Eriophyidae) as a biological control agent for field bindweed (Convolvulaceae) in the northern great plains. Can Entomol 131:541–548

McEvoy PB (1996) Host specificity and biological pest control. Bio Sci 46:401–405

Medal JC, Pitelli RA, Santana A, Gandolfo D, Gravena R, Habeck DH (1999) Host specificity of *Metriona elatior*, a potential biological control agent of tropical soda apple, *Solanum viarum*, in the USA. Biocontrol 44:421–436

Mitter C, Farrell B (1991) Macroevolutionary aspects of insect-plants relationships. In: Bernays EA (ed) Insect-plant interactions, vol 2. CRC Press, Boca Raton, pp 35–78

Murdoch WW, Chesson J, Chesson P (1985) Biological control in theory and practice. Am Nat 125:344–366

Musser RO, Hum-Musser SM, Eichenseer H, Peiffer M, Ervin G, Murphy JB, Felton GW (2002) Caterpillar saliva beats plant defences. Nature 416:599–600

Nault LR, Styer WE (1969) The dispersal of *Aceria tulipae* and three other grass-infesting eriophyid mites in Ohio. Ann Entomol Soc Am 62:1446–1455

Nosil P, Vines TH, Funk DJ (2005) Perspective: reproductive isolation caused by natural selection against immigrants from divergent habitats. Evolution 59:705–719

Novotny V, Basset Y, Miller SE, Drozd P, Cizek L (2002a) Host specialization of leaf-chewing insects in a New Guinea rainforest. J Anim Ecol 71:400–412

Novotny V, Basset Y, Miller SE, Weiblen GD, Bremer B, Cizek L, Drozd P (2002b) Low host specificity of herbivorous insects in a tropical forest. Nature 416:841–844

Oldfield GN (1996) Diversity and host plant specifity. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 199–216)

Oldfield G (2005) Biology of Gall-inducing *Acari*. In: Raman A, Schaefer CW, Withers TM (eds) Biology, ecology and evolution of gall-inducing arthropods. Science Publishers, Inc., Enfield (NH), USA, pp 35–57

Poulin R (2007) Evolutionary ecology of parasites, 2nd edn. Princeton University Press, Princeton, 332 pp

Poulin R, Mouillot D (2003) Parasite specialization from a phylogenetic perspective: a new index of host specificity. Parasitol 126:473–480

R'Kha S, Capy P, David JR (1991) Host-plant specialization in the *Drosophila melanogaster* species complex: a physiological, behavioural, and genetical analysis. Proc Natl Acad Sci USA 88:1835–1839

Sabelis MW (1996) Phytoseiidae. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 427–456)

Sabelis MW, Bruin J (1996) Evolutionary ecology: life history patterns, food plant choice and dispersal. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 329–366)

Sheppard AW, Hill R, DeClerck-Floate RA, McClay A, Olckers T, Quimby PC Jr, Zimmermann HG (2003) A global review of risk-benefit-cost analysis for the introduction of classical biological control agents against weeds: a crisis in the making? Biocontrol News Info 24:91N–108N

Sheppard AW, van Klinken RD, Heard TA (2005) Scientific advances in the analysis of direct risks of weed biological control agents to nontarget plants. Biol Control 35:215–226

Skoracka A (2008) Reproductive barriers between populations of the cereal rust mite *Abacarus hystrix* confirm their host specialization. Evol Ecol 22:607–616

Skoracka A, Dabert M (2009) The cereal rust mite *Abacarus hystrix* (Acari: Eriophyoidea) is a complex of species: evidence from mitochondrial and nuclear DNA sequences. Bull Entomol Res. doi:10.1017/S0007485309990216

Skoracka A, Kuczyński L (2006) Is the cereal rust mite, *Abacarus hystrix* really a generalist?—testing colonization performance on novel hosts. Exp Appl Acarol 38:1–13

Skoracka A, Kuczyński L, Rector BG (2007) Divergent host acceptance behavior suggests host specialization in populations of the polyphagous mite *Abacarus hystrix* (Acari: Prostigmata: Eriophyidae). Environ Entomol 36:899–909

Smith L (2005) Host plant specificity and potential impact of *Aceria salsolae* (Acari: Eriophyidae), an agent proposed for biological control of Russian thistle (*Salsola tragus*). Biol Control 34:83–92

Smith L, Hayat R, Cristofaro M, Tronci C, Tozlu G, Lecce F (2006) Assessment of risk of attack to safflower by *Ceratapion basicorne* (Coleoptera: Apionidae), a prospective biological control agent of *Centaurea solstitialis* (Asteraceae). Biol Control 36:337–344

Smith L, de Lillo E, Stoeva A, Cristofaro M, Rector B (2008) Challenges to evaluation of eriophyid mites for biological control of invasive plants. In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier M-S, Vial L (eds) Integrative acarology. Proceedings of the 6th European congress, European Association of Acarologists, Montpellier France, 21–25 July, European Association of Acarologists, pp 312–316

Smith L, Cristofaro M, de Lillo E, Monfreda R, Paolini A (2009a) Field assessment of host plant specificity and potential effectiveness of a prospective biological control agent, *Aceria salsolae*, of Russian thistle, *Salsola tragus*. Biol Control 48:237–243

Smith L, de Lillo E, Amrine JW Jr (2009b) Effectiveness of eriophyid mites for biological control of weedy plants and challenges for future research. Exp Appl Acarol. doi:10.1007/s10493-009-9299-2

Sobhian R, Andres LA (1978) The response of the skeletonweed gall midge, *Cystiphora schmidti* (Diptera: Cecidomyiidae), and gall mite, *Aceria chondrillae* (Eriophyidae) to North American strains of rush skeletonweed (*Chondrilla juncea*). Environ Entomol 7:506–508

Sobhian R, McClay A, Hasan S, Peterschmitt M, Hughes RB (2004) Safety assessment and potential of *Cecidophyes rouhollahi* (Acari, Eriophyidae) for biological control of *Galium spurium* (Rubiaceae) in north America. J Appl Entomol 128:258–266

Stireman JO, Nason JD, Heard S (2005) Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. Evolution 59:2573–2587

Strong DR, Lawton JH, Southwood TRE (1984) Insects on plants: community patterns and mechanisms. Blackwell Scientific, Oxford p 313

Thompson JN (1988) Variation in preference and specificity in monophagous and oligophagous swallowtail butterflies. Evolution 42:118–128

Udvardy MDF (1975) A classification of the biogeographical provinces of the world. IUCN occasional paper no. 18. Morges, Switzerland: IUCN, 49 pp

Van Driesche R, Hoddle M, Center T (2008) Control of pests and weeds by natural enemies: an introduction to biological control. Wiley-Blackwell, Malden p 484

Wapshere AJ (1974) A strategy for evaluating the safety of organisms for biological weed control. Ann Appl Biol 77:201–211

Ward SA, Leather SR, Pickup J, Harrington R (1998) Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? J Anim Ecol 67:763–773

Westphal E, Manson DCM (1996) Feeding effects on host plants: gall formation and other distortions. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 231–242)

Westphal E, Bronner R, Dreger F (1996) Host plant resistance. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam (World Crop Pests, vol 6, pp 681–688)

Wheat CW, Vogel H, Wittstock U, Braby MF, Underwood D, Mitchell-Olds T (2007) The genetic basis of a plant-insect coevolutionary hey innovation. PNAS 104:20427–20431

Willis AJ, Ash JE, Groves RH (1995) The Effects of herbivory by a mite, *Aculus hyperici*, and nutrient deficiency on growth in *Hypericum* species. Aust J Bot 43:305–316

Willis AJ, Berentson PR, Ash JE (2003) Impacts of a weed biocontrol agent on recovery from water stress in a target and a non-target *Hypericum* species. J Appl Ecol 40:320–333

Stoeva A, Rector BG, Harizanova V (2008) Host-specificity testing on *Leipothrix dipsacivagus* (Acari: Eriophyidae), a candidate for biological control of *Dipsacus* spp. In: Julien MH, Sforza R, Bon MC, Evans HC, Hatcher PE, Hinz HL, Rector BG (eds) Proceedings of the XII international symposium on biological control of weeds. CAB International Wallingford, pp 328–332

Yano S, Wakabayashi M, Takabayashi J, Takafuji A (1998) Factors determining the host plant range of the phytophagous mite, *Tetranychus urticae* (Acari: Tetranychidae): a method for quantifying host plant acceptance. Exp Appl Acarol 22:595–601

Zhao S (2000) Study of the dispersal and diversity of eriophyoid mites (Acari: Eriophyoidea). PhD. dissertation, West Virginia University, Morgantown, 141 pp

Zhao S, Amrine JW Jr (1997) A new method for studying aerial dispersal behavior of eriophyoid mites (Acari: Eriophyoidea). Syst Appl Acarol 2:107–110

Effectiveness of eriophyid mites for biological control of weedy plants and challenges for future research

L. Smith · E. de Lillo · J. W. Amrine Jr.

Abstract Eriophyid mites have been considered to have a high potential for use as classical biological control agents of weeds. We reviewed known examples of the use of eriophyid mites to control weedy plants to learn how effective they have been. In the past 13 years, since Rosenthal's 1996 review, 13 species have undergone some degree of pre-release evaluation (*Aceria genistae*, *A. lantanae*, *Aceria* sp. [boneseed leaf buckle mite (BLBM)], *A. salsolae*, *A. sobhiani*, *A. solstitialis*, *A. tamaricis*, *A. thalgi*, *A. thessalonicae*, *Cecidophyes rouhollahi*, *Floracarus perrepae*, *Leipothrix dipsacivagus* and *L. knautiae*), but only four (*A. genistae*, *Aceria* sp. [BLBM], *C. rouhollahi* and *F. perrepae*) have been authorized for introduction. Prior to this, three species (*Aceria chondrillae*, *A. malherbae* and *Aculus hyperici*) were introduced and have become established. Although these three species impact the fitness of their host plant, it is not clear how much they have contributed to reduction of the population of the target weed. In some cases, natural enemies, resistant plant genotypes, and adverse abiotic conditions have reduced the ability of eriophyid mites to control target weed populations. Some eriophyid mites that are highly coevolved with their host plant may be poor prospects for biological control because of host plant resistance or tolerance of the plant to the mite. Susceptibility of eriophyids to predators and pathogens may also prevent them from achieving population densities necessary to reduce host plant populations. Short generation time, high intrinsic rate of increase and high mobility by aerial dispersal imply that eriophyids should have rapid rates of evolution. This raises concerns that eriophyids may be more likely to lose efficacy over time due to coevolution with the target weed or that they may be more likely to adapt to nontarget host plants compared to insects, which have a longer generation time and slower population

L. Smith (✉)
USDA-ARS Western Regional Research Center, 800 Buchanan Street, Albany, CA 94710, USA
e-mail: link.smith@ars.usda.gov

E. de Lillo
Dipartimento di Biologia e Chimica Agroforestale e Ambientale, Facoltà di Agraria, Università Bari, Italy, via Amendola, 165/A, 70126 Bari, Italy

J. W. Amrine Jr.
Department of Biology, West Virginia University, 53 Campus Dr., Morgantown, WV 26506, USA

growth rate. Critical areas for future research include life history, foraging and dispersal behavior, mechanisms controlling host plant specificity, and evolutionary stability of eriophyid mites. This knowledge is critical for designing and interpreting laboratory and field experiments to measure host plant specificity and potential impact on target and nontarget plants, which must be known before they can be approved for release. One of the more successful examples of an eriophyid mite controlling an invasive alien weed is *Phyllo-coptes fructiphilus*, whose impact is primarily due to transmission of a virus pathogenic to the target, *Rosa multiflora*. Neither the mite nor the virus originated from the target weed, which suggests that using "novel enemies" may sometimes be an effective strategy for using eriophyid mites.

Keywords   Biocontrol · Invasive plant · Weed · Host plant specificity · Efficacy

Introduction

Classical biological control involves the importation and release of host-specific natural enemies to help regulate pest populations (Goeden and Andres 1999; van Driesche et al. 2008). This strategy is generally applied against invasive alien species that lack effective natural enemies in the adventive region. In order to avoid direct damage to nontarget species, biological control agents must be highly host specific. About 80% of currently known species of eriophyoid mites have been recorded in association with a single species of host plant (Skoracka et al. (2009) in this issue). There are about 4,000 recognized species, 25% of which were named in the last 12 years, suggesting that many more remain to be discovered (de Lillo and Skoracka (2009) in this issue). Thus, there should be a large number of prospective agents available to discover. In order to be effective and to mini-mize indirect nontarget impacts, biological control agents must significantly reduce fitness of the target weed (McClay and Balciunas 2005; Smith 2006). Eriophyoid mites can substantially damage vegetative and reproductive plant parts, have high reproductive rates, and disperse widely by wind, which all favor their potential to be effective biological control agents (Rosen and Huffaker 1983; Lindquist et al. 1996; Briese and Cullen 2001). Thus, eriophyoid mites have long been thought to have a high potential as a source for biological control agents of weeds, and many review papers have promoted their prospects (Cromroy 1977, 1983; Andres 1983; Boczek 1995; Boczek and Petanović 1996; Petanović 1996; Rosenthal 1996; Briese and Cullen 2001; Cullen and Briese 2001; Gerson et al. 2003). On the other hand, relatively few species of eriophyoids are considered economic pests (Lindquist et al. 1996; Hong et al. 2001), which suggests that the impact of most species is limited by factors such as host plant resistance or tolerance, natural enemies, and adverse abiotic conditions, which are the same factors that limit efficacy of biological control agents (Smith 2004).

At present, relatively few eriophyoid species actually have undergone evaluation, governmental approval and introduction to new regions, and few of these have significantly reduced populations of the target weed. In her 1996 review, Rosenthal discussed eight species of eriophyids with high potential. Briese and Cullen (2001) listed 29 species of eriophyid mites considered to have potential as biological control agents. However, today we find that only three of these species have been successfully intentionally introduced to other countries for classical biological control: *Aceria malherbae* Nuzzaci, *Aceria chondrillae* (Canestrini) and *Aculus hyperici* (Liro), all of which had been used before

1996. Briese and Cullen (2001) reported that all three of these mites had measurable impact on the target plant, but that only *A. chondrillae* had been a major contributor to control. Since Briese and Cullen's (2001) review, at least 13 other species have undergone pre-release evaluations, but only *Aceria genistae* (Nalepa), the boneseed leaf buckle mite (*Aceria* sp., which needs taxonomical evaluation), *A. lantanae* (Cook), *Cecidophyes rouhollahi* Craemer and *Floracarus perrepae* Knihinicki and Boczek, have been approved for release. Are eriophyid mites proving to be less useful than previously thought, and if so, what can be done to improve our ability to use them?

The purpose of this paper is to review the status of eriophyid mites as safe, effective biological control agents and to consider what areas of research are needed to improve our ability to evaluate and use these organisms for classical biological control of weeds. Here we present a more detailed treatment of some of the information and ideas in Smith et al. (2008).

Status of introduced eriophyids

In this section we discuss species that have been officially approved for release as classical biological control agents. *Aceria chondrillae, A. malherbae* and *Aculus hyperici* are the oldest cases of attempts to use eriophyid mites for biological control. More information on these projects can be found summarized in Rosenthal (1996), Briese and Cullen (2001) and Gerson et al. (2003).

Aceria chondrillae is native to Europe and has been introduced to control *Chondrilla juncea* L. (rush skeletonweed, Asteraceae) in Australia, the USA and Argentina (Cullen et al. 1982; Piper and Andres 1995; Cordo 1996; Cullen and Briese 2001). The plant has at least four different genotypes that vary in resistance to the mite, so it was necessary to find strains of the mite suitable for the various "forms" of the plant (Sobhian and Andres 1978; Cullen and Moore 1983). A Greek strain induced galls on two of the three Australian plant forms, but not on accessions from North America. The Vieste, Italy strain of the mite induced galls on all three N. American plant accessions tested, but not on the Australian narrow-leaf form. In California, the introduced mite is widespread and densities can be high in Sacramento and Eldorado counties (B. Villegas pers. comm.), but its effectiveness may be limited by the predatory mite, *Typhlodromus pyri* Scheuten (Phytoseiidae) (Piper and Andres 1995). In Idaho, *A. chondrillae* is widespread and appears to be limited by the cold winter weather which causes high mortality and by lack of rosettes in the fall on north-facing slopes (Milan et al. 2006; T. Prather pers. comm.). The mite is widespread in Oregon and Washington, and in some areas it may reduce flowering and seed production by 50–90%, depending on plant size and environmental conditions (E. Coombs pers. comm.). It does best in dry areas and where deer do not graze the early growth of the host plant. In Washington State, the weed has been successfully controlled in some areas, and *A. chondrillae* is considered to be the most effective of the three biological control agents that were released (Piper 1985; Piper et al. 2004). In Montana, rush skeletonweed is under eradication; however, the mite has been observed in several isolated *C. juncea* infestations in northwestern portions of the state (J. Littlefield pers. comm.). The mite is established in the Okanagan and Kootanay valleys of British Columbia, Canada, but the weed populations are persisting (R. De Clerck-Floate pers. comm.). In late September at Vernon, only about 10% of flower heads were distorted, a few plants were stunted, and it generally appears that the mite only establishes at sites where it has been released (P. Harris pers. comm.). In Australia, Greek strains of the mite helped reduce populations of the

susceptible narrow-leaf form of the weed, especially at drier locations; however, the presence of resistant forms has prevented further reduction of the weed (Burdon et al. 1981; Briese and Cullen 2001). The introduced rust fungus, *Puccinia chondrillina* Bubák and Syd., generally had more impact than *A. chondrillae* on *C. juncea* populations in Australia, California and Europe (Supkoff et al. 1988; Piper and Andres 1995; Briese and Cullen 2001). In Australia, the presence of genotypes resistant to the introduced strains of the mite and rust has prevented the achievement of complete control, but the weed is currently much less abundant because the resistant forms are less competitive and less widespread (J. Cullen pers. comm.).

Aculus hyperici is native to Europe and was introduced in 1991 to control *Hypericum perforatum* L. (St. Johnswort, Clusiaceae) in Australia (Briese and Cullen 2001). Establishment success varied greatly among sites, and plants collected from sites where establishment failed were resistant to mite attack in controlled experiments (Jupp et al. 1997, Mayo and Roush 1997, Mahr et al. 2000). Although the mite could significantly impact the target weed in the field, reducing shoot and root biomass, it has not significantly reduced weed populations (Mahr et al. 2000, Briese and Cullen 2001). Nevertheless, it is perceived to help reduce reproduction and dispersal of the weed. *Aculus hyperici* reproduces fastest on *H. perforatum*, but it can multiply well on at least four other *Hypericum* species, including a native nontarget species, *H. gramineum* Forst. (Cullen and Briese 2001). Mite populations persist longest on *H. perforatum* and *H. gramineum*; however, densities are lower on the latter species, damage is less, and they do not appear to significantly affect the plant's population in the field (Willis et al. 2003). In the USA, this weed was successfully controlled over most of its range by several species of introduced beetles (McCaffrey et al. 1995), and the mite was never introduced.

Aceria malherbae is native to Europe and forms galls on developing leaves and stems of *Convolvulus arvensis* L. (field bindweed, Convolvulaceae) (Boldt and Sobhian 1993; Rosenthal 1996; Littlefield 2004). This species was initially mistaken to be *Eriophyes convolvuli* Nalepa (Rosenthal 1983, Nuzzaci et al. 1985), and should not be confused with *Aculus convolvoli* (Nalepa) (which was previously assigned to the genus *Phyllocoptes*). *Aceria malherbae* was first released in the USA in 1989 (Boldt and Sobhian 1993; Rosenthal 1996), in Canada in 1989 (McClay and De Clerck-Floate 2002) and in South Africa in 1995 (Craemer 1995). In Texas, the mite appeared to increase very little for several years until a field site was accidentally mowed (G. J. Michels pers. comm.). This led to the discovery that mowing was useful both for dispersing the mite and for multiplying it. The mite has been redistributed widely during the past 10 years, and it is now difficult to find sites in Texas where field bindweed is not infested (Britten et al. 2003; G. J. Michels pers. comm.). Bindweed biomass has been reduced by over 95% in many areas, primarily on roadsides, highway medians, and yards. However, there has been much less success in cultivated row crops. In New Mexico, the mite alone can damage the bindweed sufficiently in unmanaged nonirrigated sites to allow encroachment by other weeds (L. Lauriault pers. comm.). Mite symptoms are more prominent in drier years and in unirrigated environments. If a late freeze, snow, or standing hail occurs after the mites emerge in the spring, it takes the rest of the year for populations to recover to levels that cause noticeable symptoms. In Colorado, the mite has also been widely distributed, but impact is highly variable (R. Hansen and G. J. Michels pers. comm.). However, it is so effective in western Colorado that it is difficult to collect enough plant material from infested plants for further distribution of the mite (D. Bean pers. comm.). The severity of *A. malherbae* galling may be highest at sites where field bindweed is significantly drought-stressed, which limits plant size and regrowth, hence producing greater impacts in western

than eastern Colorado; however, this remains to be demonstrated experimentally. In Fremont county Wyoming, the mite has been widely distributed and appears to be dispersing by itself (J. L. Baker pers. comm.). So far, it is most successful in pastures and alfalfa fields, galling up to 90% of bindweed plants. At some sites bindweed populations have decreased to innocuous levels in 4–5 years after release. The mite is widely distributed (largely by natural dispersal) in the eastern half of Montana, but infestations are patchy within and among sites (Littlefield 2004, pers. comm.). The populations do not appear to be correlated to habitat type, so patchiness may reflect low levels of survival during dormant periods or variation in suitability of the host plant. Variation in susceptibility to infestation has been experimentally demonstrated with some populations of the plant (Rosenthal and Platts 1990), but this factor has not been investigated regarding establishment and impact in the field. The weed population has not declined at a site in central Montana during the 8 years since the mite was first released. During this period, the percentage of plants infested ranged from 22 to 49% (mean 29%), although up to 100% of plants were infested in individual plots (J. Littlefield pers. comm.). In Oregon, the mite is established and is spreading in a dry rangeland area in Tygh Valley, where it is reducing bindweed biomass by 90% (E. Coombs pers. comm.). In eastern Washington, 10 years after establishment, *C. arvensis* plants with no mite symptoms are often found growing next to plants with extensive mite damage, so the mite has not achieved a economically acceptable level of control (R. Boydston pers. comm.). In Canada, *A. malherbae* has survived for at least 5 years at some sites in southern Alberta, and damage ranged from slight to extensive, depending on the site (McClay et al. 1999; McClay and De Clerck-Floate 2002). It is established in southern Alberta, where most releases occurred, but not in British Columbia, Manitoba or Saskatchewan (A. McClay and P. Harris pers. comm.). The most successful establishments have been around Medicine Hat near the Saskatchewan River and on irrigated land. Low population densities and extinctions at nonirrigated, drier upland sites suggest that the mites are more successful in habitats with the higher moisture levels in this region. This may be because moist habitats allow the plant to produce young tissue, which the mite colonizes, for longer during the summer, thus allowing for greater population increase. In South Africa, the mite was permitted in 1994 and has been released, but it has not been widely distributed nor monitored (Craemer 1995). Moreover, there is interest to introduce the mite in Mexico (Rodríguez-Navarro et al. 2008).

In laboratory climate chamber experiments, *A. malherbae* reduced shoot biomass by 37% and root biomass by 50% (Boydston and Williams 2004). However, variation in establishment and impact at field sites suggests the need to study the effects of climate and genetic variation in host plant resistance, both of which may limit mite efficacy. Methods using mowing and herbicides to complement use of the mite have been developed to improve management of the weed (Boydston and Williams 2004; Lauriault et al. 2004).

In host plant specificity tests conducted in laboratories and screen houses, *A. malherbae* caused galling on 3 *Convolvulus* and 12 *Calystegia* species (Clement et al. 1984; Rosenthal and Platts 1990; Craemer 1995). Despite this, the mite was approved for release in the USA. However, it is not permitted for release in California because of concern about risk to the 11 *Calystegia* species native to the state. Although Craemer (1995) observed galling on two nontarget species of *Convolvulus*, mites reproduced only on *C. arvensis*, suggesting that requirements for reproduction are more selective than for gall initiation. McClay similarly observed some galling on *Calystegia sepium* (L.) R. Br. that had been inoculated inside a cage, but found no evidence of reproduction (McClay and De Clerck-Floate 2002). The other previously mentioned host specificity studies reported only damage (gall presence) (Clement et al. 1984), or percentage of plants infested (not distinguishing between

live mites or damage) (Rosenthal and Platts 1990). In the latter experiment, test plants were in direct contact with each other, so mites could probably move between plants, increasing the risk of observing mites or galling on plants that they did not develop on. So, some of these results may overestimate the amount of damage likely to occur under field conditions. Recently conducted field experiments in Colorado demonstrated that the mite could form galls on the native nontarget species *Calystegia macrostegia* (Greene) Brummitt, *C. occidentalis* (A. Gray) Brummitt, and *C. purpurata* (Greene) Brummitt when inoculated with infested plant tissue (R. Hansen pers. comm.). However, the severity and frequency of galling was much less on the nontarget plants than on *C. arvensis*. When field plants were infested in the summer and examined the following summer, no galls were found on *Convolvulus equitans* Benth., *Calystegia macrostegia* or *C. occidentalis*, whereas 47% of the *C. arvensis* plants had galls. This suggests that the mite did not successfully overwinter on these nontarget plants and/or that aerially dispersing mites did not infest these plants. If aerially dispersing mites tend not to colonize nontarget plants, then there may be less risk of damage to them than suggested by experiments using direct inoculation methods (Smith et al. 2009). However, this remains to be demonstrated for *A. malherbae*. In any case, environmental conditions in Colorado are drier, and winter temperatures are colder, than the coastal regions where many native *Calystegia* plants occur in California, and the effects of these environmental differences on the ability of the mite to infest and damage plants are not known.

Cecidophyes rouhollahi was evaluated and approved for introduction to western Canada from southern France in 2003 to control *Galium aparine* L. and *G. spurium* L. (false cleavers, Rubiaceae) (McClay et al. 2002; Sobhian et al. 2004). In field experiments near Edmonton in Alberta, Canada, mites caused approximately 30% reduction in seed yield and biomass of false cleavers, growing either alone or with canola (McClay 2005). Galling and biomass reduction were greater when inoculating young plants compared to older plants. Although some wind-borne dispersal appeared to occur within the study site, mite populations tended to remain localized and patchy. Uninfested stems were often seen next to heavily galled stems. Despite several years of releasing the mite, it consistently failed to survive the winter (McClay 2005, pers. comm.). Southern Alberta is at a much higher latitude (50°N) than southern France (44°N), the origin of the mites, and winter temperatures are much lower (mean monthly minimum of about −20°C vs. +2°C), so it may be worth searching for a population of the mite in a region that has a climate more similar to that of central and southern Alberta, such as in southwestern Russia or eastern Turkey.

Floracarus perrepae Knihinicki and Boczek forms leaf-roll galls on *Lygodium microphyllum* (Cav.) R. Br. (Old World climbing fern, Lygodiaceae) and was recently approved for release in Florida. In general it has been relatively easy to establish eriophyid mites in the field by transferring infested plant parts, but in the case of *F. perrepae*, the regulatory permit prohibits removal of infested plant material from quarantine. This made it more difficult to move the mite out of quarantine, but the mite is now established on potted plants outside of quarantine and field releases began in June 2008 (R. Pemberton pers. comm.). During foreign exploration for natural enemies in Southeast Asia and Australia it was discovered that there was a high degree of genetic variability of the target plant between field sites (Goolsby et al. 2006). Furthermore, mites from a given location were best able to infest plants from the same location, whereas other plant accessions showed various degrees of resistance to infestation. Plants that genetically matched those occurring in Florida were found in only one location (Cape York, Australia), and mites from this region were chosen for introduction (Goolsby et al. 2006). Experimental and climate matching studies indicated that the mite should be climatically adapted to the target region

in Florida (Goolsby et al. 2005a, b). Pre-release field experiments showed that the mite could significantly reduce biomass of stems, leaves, roots and rhizomes (Goolsby et al. 2004). Although predators and the fungal pathogen, *Hirsutella thompsonii* Fisher, were observed to impact mite populations, they did not significantly reduce impact of the mite on the weed during a pre-release field experiment (Goolsby et al. 2004; Ozman and Goolsby 2005).

Aceria genistae (Nalepa) is native to Europe where it is associated with species of *Cytisus*, *Genista* and *Ulex* (brooms and gorse, Fabaceae). Given that the mite on *Spartium junceum* L. (Spanish broom) has been confirmed to be a distinct species, *A. spartii* (Canestrini) (Castagnoli 1978), it is possible that there is a complex of cryptic mite species or host-specific biotypes associated with the brooms and gorse. Mite specimens from the different host plants are currently being examined for taxonomic differences (Z.-Q. Zhang pers. comm.). A strain of *A. genistae* collected on *Cytisus scoparius* (L.) Link (Scotch broom) in France was released in New Zealand in November 2007 (R. Hill pers. comm.). It is now established at one site, and further distribution is underway. In Australia, the Scotch broom strain of the mite was released in 2008 in Victoria to control *C. scoparius* (Sheppard et al. 2006; Sagliocco 2008, pers. comm.). In the USA, *A. genistae* has been accidentally introduced, and is fairly widespread, between Mount Vernon, Washington and Portland, Oregon on *C. scoparius* (E. Coombs and J. Andreas pers. comm.). The mite appears to damage *C. scoparius* in the field, reducing flowering and plant biomass, although this has not been quantified. Predatory mites have been observed associated with its galls, but their impact is not known. Host specificity is currently being evaluated using the mite from *Cytisus* in Washington State, and so far this strain has not formed galls on *Ulex europaeus* L. (gorse) or *Genista monspessulana* (L.) L. A. S. Johnson (French broom) in transfer experiments (J. Andreas pers. comm.). Possibly a different strain of this mite species was reported on *U. europaeus* and *G. monspessulana* in California (Chan and Turner 1998). Infested plants in the field had little or no symptoms; however, when gorse seedlings were brought into a greenhouse, they developed stunted shoot tips and reduced, thickened scale leaves which were attributed to mite infestation. This suggests that natural enemies, cooler outdoor temperatures or some other factor may be preventing mite populations from damaging gorse in the field. In New Zealand, the same nominal species causes galling on *U. europaeus* but does not infest *C. scoparius* (Manson 1989; R. Hill pers. comm.). So, it appears that there are different host-specific *A. genistae* biotypes or cryptic species associated with *C. scoparius* and *U. europaeus*.

The boneseed leaf buckle mite (BLBM) is an *Aceria* sp. native to South Africa that induces erinea on *Chrysanthemoides monilifera* ssp. *monilifera* (L.) Norlindh (boneseed, Asteraceae) (Morley 2004a; Morley and Morin 2008). This mite was originally believed to be *A. neseri* Meyer; however, specimens collected from the type locality do not conform to the morphological description for this species (Morley 2004b). The holotype is no longer useable, but BLBM matches the paratypes. Apparently, either Meyer (1981) mistakenly described a different species of mite, or the description and illustration are otherwise in error (C. Craemer pers. comm.). Consequently, either the description for *A. neseri* needs to be corrected or BLBM must be described as a new species. BLBM was approved for release in Australia in July 2008, and the first releases were made later that year in the southern hemisphere spring (T. Morley pers. comm.). It has since been released at 42 sites, and signs of BLBM infestation have been observed at 12 of 27 sites that have been monitored. Drought conditions at some of the sites appear to be associated with lack of signs of the mite. Another biotype of this mite is associated with *Chrysanthemoides monilifera* ssp. *rotundata* (DC.) Norlindh (bitou bush) (Morley 2004a) in South Africa.

Bitou bush is also an invasive weed in Australia, so this biotype may be useful for biological control of this weed.

Accidental introductions

Aceria anthocoptes (Nalepa) is primarily associated with *Cirsium arvense* (L.) Scop. (Canada thistle, Asteraceae), a plant native to Eurasia (Ochoa et al. 2001). Previous records of host plants in Europe include the Cardueae *C. heterophyllum* (L.) Hill. (junior synonym of *C. helenioides* (L.) Hill.) and *C. vulgare* (Savi) Tenore (senior synonym of *C. lanceolatum* (L.) Scop.), and the Lactuceae *Crepis paludosa* (L.) Moench and *Leontodon autumnalis* L. (Nalepa 1892; Redfern et al. 2002; de Lillo and Amrine unpublished database). Recent attempts to find the mite on Cardueae in eastern Europe suggest that plants other than *C. arvense* are not typical hosts (Gassmann et al. 2004; R. Petanović pers. comm.). The report of *Crepis paludosa* appears to be erroneous, and no specimens of *A. anthocoptes* actually have been collected in Britain (J. Ostoja-Strazewsk pers. comm.). The eriophyid mite collected on *L. autumnalis* was previously recognized as a separate species, *Aceria leontodontis* (Lindroth) (Lindroth 1904; Roivainen 1950); however, it is now recognized to be a deutogyne form of *A. anthocoptes* (Petanović et al. 1997). Occurrence of *A. anthocoptes* deutogynes on *L. autumnalis* may indicate that this is an "accidental" host, which may not be capable of supporting reproduction (R. Petanović pers. comm.). Populations of *Aceria* spp. collected from four *Cirsium* spp. differed significantly in morphology, confirming differences between previously recognized species, *A. anthocoptes* and *A. cirsii* Petanović et al., but suggesting that *Aceria* from *C. eriophorum* (L.) Scop., *C. arvense* and *C. heterophyllum* represent three different species or biotypes (Vidović et al. 2008). However, it is not known if these populations are reproductively isolated or if they differ in host plant preference. Populations of *A. anthocoptes* collected on *C. arvense* from two different locations in Serbia differed in morphology, which indicates significant phenotypic, and possibility genetic, geographical heterogeneity within the species (Magud et al. 2007). In host range experiments, *A. anthocoptes* collected from *C. arvense* multiplied well only on *C. arvense* (Gassmann et al. 2006). However, *A. anthocoptes* or a close relative has sometimes been collected on *C. vulgare* in the field, and some mites collected on *C. arvense* have developed on *C. vulgare* in laboratory experiments (Gassmann et al. 2005, 2006).

Aceria anthocoptes has been accidentally introduced to the USA, and is apparently widespread on *C. arvense*, having been observed in Colorado, Delaware, Kansas, Maryland, Minnesota, Montana, Nebraska, North Dakota, Pennsylvania, South Dakota, Virginia, West Virginia and Wyoming (Ochoa et al. 2001; Hansen 2008; Michels et al. 2008; J. Littlefield and R. Hansen pers. comm.). In Colorado, it also has been collected from *Cirsium barnebyi* S. L. Welsch & Neese, *C. calcareum* (M. E. Jones) Woot. & Standl., *C. centaureae* (Rydb.) K. Schum., *C. ochrocentrum* A. Gary, *C. scariosum* Nutt., *C. scopulorum* (Greene) Cockerell ex Daniels, *C. tracyi* (Rydb.) Petr. and *C. undulatum* (Nutt.) Spreng., which are all native to North America, but it has not been collected on *C. vulgare* (Hansen 2008, pers. comm.). Phylogenetic relationships in Kelch and Baldwin (2003) indicate that *C. arvense* is more closely related to *C. vulgare* than to the North American *Cirsium* species, so it is surprising that *A. anthocoptes* occurs more on the North American species than on *C. vulgare*. The mite has not been observed in California despite repeated efforts to find it (B. Villegas pers. comm.), nor in Washington, although intensive surveys have not been conducted (G. L. Piper pers. comm.). Evaluation of this mite in

Europe as a prospective biological control agent has paused pending taxonomic comparison of specimens from North America and Europe (Rancic et al. 2006; Vidović et al. 2008).

Experiments confirm that *A. anthocoptes* causes russeting, bronzing, folding and distortion of the leaf blade and curling of leaf edge when feeding on *C. arvense* (Rancic et al. 2006). In Colorado, these symptoms appeared when mite populations reached high densities in laboratory or greenhouse environments, but they have not been seen in the field on either *C. arvense* or the other *Cirsium* species from which the mite has been collected (R. Hansen pers. comm.). In Montana, mite populations are very low in the spring and do not reach relatively high densities until autumn (J. Littlefield pers. comm.). No controlled field experiments have been conducted to measure the impact of *A. anthocoptes* on populations of *C. arvense*; however, there is an anecdotal observation of a decrease in the weed's population at a site in Colorado from 2000 to 2007 (Michels et al. 2008). Considering the widespread distribution of the mite, the lack of widespread signs of damage suggests that natural enemies, abiotic factors or host plant resistance may be limiting effectiveness of the mite. A phytoplasm has been shown to be associated with abnormal formation of multiple inflorescences on *C. arvense* (Rancic et al. 2005), which had previously been attributed to the presence of *A. anthocoptes* since its first record in 1892 (Petanović et al. 1997). However, the ability of the mite to transmit the phytoplasm has not yet been demonstrated (Gassmann et al. 2004).

Phyllocoptes fructiphilus is not an "approved" biological control agent in the sense that it was never officially authorized for release; rather this is an example of an invasive alien plant coming into contact with a novel eriophyid mite. The mite transmits an unidentified virus that causes rose rosette disease (RRD) of *Rosa multiflora* Thunb. (multiflora rose, Rosaceae) (Amrine 1996, 2002; Epstein and Hill 1999; Tzanetakis et al. 2006). *Rosa multiflora* was introduced to the eastern USA from Asia starting in the early 1800s, by the 1950s it was invading pastures and other unforested land, and by the 1980s it had become one of the most damaging invasive plants in the central USA. Both the mite and virus appear to be native to the USA, and neither is known to occur in Asia. The mite was first observed on *R. californica* Cham. and Schlecht. in California in 1940, and RRD was first observed in a native rose, *R. woodsii* Lindl., in California, Wyoming and Manitoba, Canada in 1941. By 1959, RRD appeared in Nebraska on *R. woodsii*, *R. multiflora* and cultivated roses, and the mite was later found to be abundant on all these plants. RRD can be transmitted by grafting infected plant tissue or by infestation by *P. fructiphilus*, but not by *P. adalius* Keifer, a leaf vagrant found on many kinds of roses in eastern USA, or by other insects associated with roses. Rose species and varieties differ in susceptibility to RRD and to *P. fructiphilus*, and plants that are resistant to one may or may not be resistant to the other (Amrine 2002). RRD takes about 2–4 years to kill *R. multiflora*. Mites can only effectively transmit the disease when feeding on rapidly growing plants, which only occurs in the spring or after abundant rainfall. Otherwise, plants are not very easily infected. Dispersing mites do not infect many plants that are greater than about 100 m from heavily infested plants, so geographic spread of RRD is relatively slow except within densely populated patches. During a field study in Indiana, the population density of *R. multiflora* decreased 36% from 1987 to 1994, while RRD infection rate steadily rose from 30 to 95% (Amrine et al. 1990; Amrine 2002). Plant mortality rose to 98%, but the rate of population decline was moderated by annual recruitment of seedlings, which took several years to become infected. Today, the weed is less common in many areas of Indiana, Maryland, Ohio, Pennsylvania and West Virginia that previously had high densities of the plant, and there are fewer invasions of roadsides, pastures, and other open land (J. Amrine pers.

comm.). This appears to be the most successful example of an eriophyid mite controlling an invasive alien weed. It is also the only eriophyid biological control example in which a plant pathogen was involved, and the pathogen appears to be the principal agent damaging the weed. Considering the ability of eriophyid mites to transmit viruses (Oldfield and Proeseler 1996; Nault 1997), more effort should be made to determine their potential use for biological control.

Although ornamental roses can be severely damaged by RRD, many varieties are not susceptible (Amrine 2002). However, public concern over risk of damage to ornamental plants has prevented efforts to further distribute the disease or mite (Amrine 1996, 2002; Epstein and Hill 1999). Given this concern, it is not likely that *P. fructiphilus* and the rose rosette virus would ever be approved for release as classical biological control agents. It is possible that public perception of risk to ornamental roses may be overestimated because residual damage caused by herbicides such as glyphosate has often been mistaken for RRD (B. Villegas pers. comm.); however, lack of methods to determine presence of the pathogen prevent resolving this question. Nevertheless, this example is interesting because it shows that an eriophyid adapted to a different host plant species than that targeted for control can be an effective agent ["new association" hypothesis of Hokkanen and Pimentel (1989)]. Although biological control projects generally look for highly adapted agents that co-evolved with the target weed, there are several examples in which a "new association" has proven to be effective (van Driesche et al. 2008).

Acalitus odoratus Keifer forms erinea on leaves of *Chromolaena odorata* (L.) R. M. King & H. Robinson (previously named *Eupatorium odorata* L., Siam weed, Asteraceae), which is a neotropical plant that has spread throughout the humid tropical parts of Africa, Asia, Micronesia and a small area in northern Australia (Cruttwell McFadyen 1995; Muniappan and Bamba 2000; Muniappan et al. 2005; Zachariades et al. 2009). *Acalitus odoratus* was emended from *adoratus* by Amrine and Stasny (1994) and should not be confused with *Aceria odorata* Crom., which is associated with *Pluchea odorata* [L.] Cass.). *Chromolaena odorata* is a major invasive weed in grasslands and plantation crops. A biological control program began in 1966, and studies in Trinidad indicated that the mite was host specific (Cock 1984; Cruttwell 1977). Although the mite was never deliberately introduced anywhere, it accidentally arrived in Malaysia around 1971 (possibly on plant material imported with weevils for biological control of *C. odorata* [Cruttwell McFadyen 1995]), and then rapidly spread throughout South and Southeast Asia (Ooi 1992; Waterhouse 1994; Cruttwell McFadyen 1995, 2002; Muniappan and Bamba 2000; Orapa et al. 2002b). It is not known how the mite spread over such a large region, although it is suspected by some that the common use of fresh cromolaena leaves as packing material for fresh produce shipped by boat may have played a role. The mite has also spread to Pacific islands including Indonesia, the Philippines, Papua New Guinea, and the Caroline and Mariana Island chains (Muniappan et al. 2005, 2006). It is most abundant in hot exposed sites but does not appear to significantly impact the weed (Ooi 1992; Cruttwell McFadyen 2002; Orapa et al. 2002a). The mite has not been reported from West or South Africa where the weed is also invasive (Muniappan et al. 2005).

Other eriophyid species being evaluated

Aceria lantanae (Cook) is associated primarily with *Lantana camara* L. (Verbenaceae) in the neotropics (Cook 1909; Flechtmann 1973; Flechtmann and Harley 1974; Keifer and Denmark 1976; Cromroy 1977, 1979, 1983; Craemer and Neser 1990; Neser and Cilliers

1990; Amrine and Stasny 1994; Rosenthal 1996). However, it has also been collected on three other species in the *Lantana* section *Lantana* (= section *Camara*) (Palmer and Pullen 1995; Day et al. 2003b; Sanders 2006). Although most of the literature on this weed has used the name "*L. camara*", weedy bush lantana [excluding the weedy "creeping lantana", *L. montevidensis* (Spreng.)] is now recognized to comprise a complex of polyploid hybrids that are distinct from *L. camara sensu strictu* (Howard 1969; Stirton 1977; Sanders 2006). Because the taxonomy of the weed has not been fully resolved, we will use the common name "lantana" rather than a species epithet to minimize causing further confusion. Members of this group have been distributed globally, and are continuing to hybridize in the field (Spies 1984), which presents a genetically highly variable target for a prospective biological control agent. For example, 18 different taxa of lantana were recognized in Natal, S. Africa and five in Australia (Stirton 1999; Sanders 2006; M. Day pers. comm.). The many varieties that have become invasive weeds differ genetically from the original native host plants of *A. lantanae*, and they have a high potential to continue to evolve. Varieties are known to differ in resistance to various natural enemies, and this has been an important obstacle to achieving effective biological control (Neser and Cilliers 1990; Baars and Neser 1999; Day et al. 2003a, b; Day and Urban 2004; Zalucki et al. 2007).

Aceria lantanae comprises two biotypes, or possibly species (Craemer and Neser 1990): one common in South America that forms "crinkle" galls on leaves (Flechtmann 1973; Moura et al. 2008), and one in Central America that forms galls on flower and shoot buds (Cook 1909; Keifer and Denmark 1976; Craemer and Neser 1990; Baars and Neser 1999; Urban et al. 2001a). The latter mite forms a dense witches' broom that may inhibit further flowering and growth (Craemer and Neser 1990; Baars and Neser 1999; S. Neser and A. Urban pers. comm.). The two types of mite are currently morphologically indistinguishable, and both types of galls have been found in Florida, Mexico and Venezuela, occasionally on the same plant. Although eight eriophyid species have been collected on lantana, *A. lantanae* is the only one that causes symptoms sufficiently damaging to warrant consideration as a biological control agent (Craemer 1996).

Host specificity of the inflorescence-galling biotype of *A. lantanae* from Florida was tested in South Africa, and galls formed only on varieties of *L. camara* (Urban et al. 2001a, b, 2004; Mpedi and Urban 2003, 2005). In glasshouse experiments, flower suppression by a Florida strain of the flower gall mite ranged from 10 to 95% among South African lantana varieties and 0–30% among Australian varieties (Urban et al. 2004). Therefore in order to attain widespread seed reduction and weed suppression, additional biotypes of the mite capable of damaging more lantana varieties must be collected and introduced (Craemer and Neser 1990; Urban et al. 2001b, 2004). Possible existence of variety-specific biotypes is suggested by the observation of galls on only one color form of lantana in one part of Cuba and on another color form in another part of the island, despite presence of both forms at both sites (S. Neser pers. comm.).

Heavy infestations of *A. lantanae* have sometimes been observed in the field in Florida (Baars and Neser 1999). However, gall induction depends on the availability of differentiating buds on rapidly growing plants and high humidity, which must occur simultaneously in order to heavily damage plants. Thus, abiotic environmental conditions may also reduce the potential efficacy of the mite. There has been some concern that possible plant stunting caused by flower gall mite infestation may make lantana unsuitable to other potentially more damaging agents; however, others have argued that such interference is unlikely to be important because many natural enemies attack lantana infested with *A. lantanae* in the native range, where the plant is apparently under

natural control (Craemer and Neser 1990; Day et al. 2003b). The potential efficacy of
A. lantanae in Australia has been questioned because there are already many indigenous
and introduced mite species that feed on lantana, without causing noticeable damage
(Walter 1999). It is suspected that these phytophagous mites are limited by the many
predatory mites found on lantana in Australia, and it seems likely that these predators
may hamper establishment and limit the impact of *A. lantanae*. However, this has not
been experimentally tested.

The inflorescence-galling biotype of *A. lantanae* was reportedly first used for biological
control of weedy lantana in the USA (Keifer and Denmark 1976). In South Africa, it was
authorized for release from quarantine in 2007, and the lantana flower gall mite, from a
mixed culture of possible biotypes from Florida and Cuba, is now established on certain
lantana varieties at some trial sites in three provinces (S. Neser and A. Urban pers. comm.).
Application for permission for introduction into quarantine in Australia will be made
pending results of further host-specificity tests being conducted in quarantine in South
Africa on prescribed Australian plant species (M. Day pers. comm.).

Information on other eriophyids that have been considered and/or studied as prospective
biological control agents is listed in Table 1.

Pre-release evaluation of prospective agents

In many countries, scientists must obtain government authorization to release alien spe-
cies for classical biological control (Sheppard et al. 2003). This requires determining the
range of host plants that can be damaged by the prospective agent, as well as an
assessment of the potential benefit of introducing the agent (Sheppard et al. 2005). In
order to help determine the likelihood of establishment of the prospective agent, scientists
also assess suitability of climate, habitat and host plant genotype of the target weed in the
adventive range (e.g., Briese and Cullen 2001; Goolsby et al. 2004, 2005a, b). The
development of computer software, such as CLIMEX, DIVA-GIS and Maxent (Hijmans
et al. 2001; Sutherst et al. 2004; Phillips et al. 2006) have greatly facilitated climate
matching. Increasing availability of molecular genetic techniques and morphometric
analysis have improved our ability to detect cryptic populations (strains and sibling
species) of both host plants and biological control agents (Goolsby et al. 2006; Navajas
and Navia 2008, 2009 in this issue; Vidović et al. 2008; de Lillo et al. (2009) in this
issue). Advances in molecular genetics and phylogenetic analysis help quantify the
relatedness of nontarget plants to the target weed, which is critical for selecting which
nontarget plants to test (Briese 2006). On the other hand, increasing public desire to
protect native species has decreased the tolerance for nontarget damage and increased the
amount of information required to obtain permission to release an agent (Louda et al.
2003; Sheppard et al. 2003). For example, damage to native *Calystegia* species by
A. malherbae observed by Rosenthal and Platts (1990) would very likely have disqualified
the mite for introduction to the USA today, and this mite is still not permitted for release
in California. To date, host specificity assessment of prospective biological control agents
has been extremely reliable (Pemberton 2000). However, it has been difficult to predict
their efficacy from pre-release experiments. Nevertheless, there is an increasing need to
determine the potential efficacy of a prospective agent, not only to make projects more
economical (McClay and Balciunas 2005), but also because significantly reducing the
target weed population is the most likely way to minimize indirect nontarget effects
(Pearson and Callaway 2005; Smith 2006).

Table 1 Eriophyid mites that have been considered for biological control of weeds and that were not discussed in the text

Target plant[a]	Species	Country of the type locality	Notes	Main references[b]
Acacia saligna (Labill.) Wendl. (Fabaceae; orange wattle)	*Aceria acacifloris* Meyer 1990	West Australia (Australia)	Distortion of the inflorescences often entirely preventing flowering; also on *Acacia melanoxylon* R. Br.	Craemer et al. (1996)
Acacia saligna	*Aceria burnleya* Keifer 1965	Victoria (Australia)	Leaf blisters	Craemer et al. (1996)
Acroptilon repens (L.) DC. (Asteraceae; Russian knapweed)	*Aceria sobhiani* Sukhareva 2001	Uzbekistan	Stunting of plants; failed host specificity tests	Littlefield et al. (2001), J. Littlefield pers. comm.
Amaranthus retroflexus L. (Amaranthaceae; redroot amaranth)	*Phyllocoptes amaranthi* (Corti 1917)	Argentina	Galls	
Ambrosia artemisiifolia L. (Asteraceae; common ragweed)	*Aceria boycei* (Keifer 1943)	California (USA)	Leaf blade galls; also on *Ambrosia psilostachya* DC. (western ragweed) shipments from California to USSR failed	Goeden et al. (1974)
Artemisia vulgaris L. (Asteraceae; wormwood)	*Aceria artemisiae* (Canestrini 1891)	Italy	Leaf galls; largely spread in Europe; biological observations	Boczek and Maciejczyk (1995)
Cardaria draba (L.) Desv. (Brassicaceae; hoary cress, whitetop)	*Aceria drabae* (Nalepa 1890)	Austria	Flower deformation and reduction in seed production, preliminary evaluation	Lipa (1976, 1978, 1983), Lipa et al. (1977), Lipa et al. (1998), Craemer et al. (1996) and Rosenthal (1996)
Centaurea diffusa Lam. (Asteraceae; diffuse knapweed)	*Aceria thessalonicae* Castagnoli 1991	Greece	Broom-like deformation and reduction of seed production; biological observations; failed host specificity tests	Castagnoli and Sobhian (1991), Rosenthal (1996), J. Littlefield pers. comm.
Centaurea diffusa, C. stoebe L. (Asteraceae; diffuse knapweed, spotted knapweed)	*Aceria centaureae* (Nalepa 1891)	Austria (presumed)	Leaf blister galls; biological and ecological observations; failed host specificity tests	Sobhian et al. (1989), Castagnoli and Sobhian (1991), Rosenthal (1996) and Littlefield et al. (2000)

Table 1 continued

Target plant[a]	Species	Country of the type locality	Notes	Main references[b]
Centaurea solstitialis L. and C. virgata Lam. ssp. squarrosa (Willd.) Gugler (Asteraceae; yellow starthistle, squarrose knapweed)	Aceria solcentaureae de Lillo et al. 2003	Turkey	Plant stunting	de Lillo et al. (2004)
Centaurea solstitialis and C. virgata ssp. squarrosa	Aceria solstitialis de Lillo et al. 2003	Turkey	Plant stunting; preliminary host specificity	de Lillo et al. (2004), Monfreda et al. (2008); A. Stoeva, pers. comm.
Centaurea virgata ssp. squarrosa	Aceria squarrosae de Lillo et al. 2003	Turkey	Plant stunting	de Lillo et al. (2004)
Chromolaena odorata (L.) King & H. Robinson (Asteraceae; Siam weed)	Acalitus osmia (Cromroy 1958)	Puerto Rico	Erinea	Craemer et al. (1996)
Chromolaena odorata	Aceria striata (Nalepa 1905)	Barbados	Erinea	Craemer et al. (1996)
Chromolaena odorata	Phyllocoptes cruthwellae Keifer 1973	Trinidad	Vagrant	Cruttwell (1977)
Clematis vitalba L. (Ranunculaceae; evergreen clematis)	Aceria vitalbae (Canestrini 1892)	Italy	Bud and leaf deformations	Mihajlović et al. (1998)
Clematis vitalba	Epitrimerus heterogaster (Nalepa 1891)	Austria (presumed)	Many host plants; leaf injuries	Mihajlović et al. (1998)
Convolvulus arvensis L. (Convolvulaceae; field bindweed)	Aceria convolvuli (Nalepa 1898)	Austria	Galls, tubercles; confused with Aculus convolvuli (Nalepa 1891)	[Rosenthal 1983][c]; Craemer et al. (1996)
Cuscuta epithymum (L.) L. (Cuscutaceae; clover dodder)	Eriophyes cuscutae (Molliard 1909)	France	Stunting and plant deformations	Craemer et al. (1996)

Table 1 continued

Target plant[a]	Species	Country of the type locality	Notes	Main references[b]
Cynodon dactylon (L.) Pers. (Poaceae; Bermudagrass)	Aceria cynodoniensis Sayed 1946	Egypt	Economic pest of Bermuda grass in southern USA; plant stunting and decline; relationship in respect to Aceria cynodonis Wilson 1959 needs to be clarified	Reinert et al. (1978, 2008), Cromroy (1983), Rodgers and Baltensperger (2004) and Henry et al. (2005)
Dipsacus fullonum L., D. laciniatus L. (Dipsacaceae; teasel)	Leipothrix knautiae (Liro 1942)	Finland	Vagrant; preliminary host specificity	Rector et al. (2006)
Dipsacus fullonum, D. laciniatus	Leipothrix dipsacivagus Petanović and Rector 2007	Serbia	Leaf, flower, stem injuries; preliminary host specificity	Stoeva et al. (2008)
Eichhornia crassipes (Mart.) Solms (Pontederiaceae; water hyacinth)	Leipothrix eichhorniae (Keifer 1979)	Brazil	Vagrant and rusting	
Elaeagnus angustifolia L. (Elaeagnaceae; Russian olive)	Aceria elaeagnicola Farkas 1963	Hungary	(habitus needs confirmation)	
Elaeagnus angustifolia	Aceria angustifoliae Denizhan et al. 2008	Turkey	Leaf lamina distortion, biological studies	CABI (2008)
Euphorbia cyparissias L. (Euphorbiaceae; cypress spurge)	Phyllocoptes euphorbiae (Farkas 1962)	Hungary	Leaf injuries	Mihajlović et al. (1994) and Petanović and Stevanović (1996)
Euphorbia esula L., E. cyparissias (Euphorbiaceae; leafy & cypress spurge)	Phyllocoptes nevadensis Roivainen 1953	Spain	Leaf rolling causing plant stunting; primarily damages cypress spurge; host specificity tests; develops on 5 nontarget Euphorbia species.	Littlefield and Sobhian (2000)
Euphorbia seguierana Neck. and Euphorbia spp. (Euphorbiaceae; spurges)	Aculops euphorbiae (Petanović 1991)	Serbia	Terminal shoot injuries and drying	Bacic and Petanović (1995), Petanović and Dimitrijević (1995) and Petanović and Stevanović (1996)

Table 1 continued

Target plant[a]	Species	Country of the type locality	Notes	Main references[b]
Galium aparine L. (Rubiaceae; bedstraw)	*Cecidophyes galii* (Karpelles 1984)	Austria (presumed)	Reduced viable seed production by 30–40%; found at more than 50% of sites and in high quantities	Pavlinec (1992)
Galium mollugo L., *G. verum* L. (Rubiaceae)	*Aceria galiobia* (Canestrini 1891)	Italy	Flower and leaf deformations; apparently not host specific	
Geranium carolinianum L. (Geraniaceae; Carolina geranium)	*Aceria mississippiensis* Chandrapatya and Baker 1986	Mississippi (USA)	Plant deformation	Chandrapatya and Baker (1986)
Geranium carolinianum	*Cecidophyes caroliniani* Chandrapatya and Baker 1986	Mississippi (USA)	Leaf edge rolling and erinea; can kill young plants	Baker et al. (1986) and Chandrapatya and Baker (1986)
Geranium dissectum L. (Geraniaceae; cutleaf geranium)	*Aceria dissecti* Petanović 1993	Serbia	Petal and young leaf deformations	
Geranium dissectum	*Aceria geranii* (Canestrini 1891)	Italy	Many host plants; stem and leaf deformations	
Imperata cylindrica (L.) Beauv. (cogon grass)	*Aceria imperata* (Zaher and Abou-Awad 1978)	Egypt	Stunting	van Loan et al. (2002)
Lepidium latifolium L. (perennial pepperweed)	*Metaculus lepidifolii* Monfreda and de Lillo	Turkey	Prevented flowering and/or seed production	CABI (2009) and E. de Lillo and R. Monfreda pers. comm.
Lythrum salicaria L. (Lythraceae; purple loosestrife)	*Aceria jovanovici* Petanović 1993	Serbia	Erinea and leaf edge rolling	
Lythrum salicaria	*Epitrimerus lythri* Petanović 1995	Serbia	Plant stunting	
Melia azedarach L. (Meliaceae; Chinaberry)	*Aceria meliae* (Dong and Xin 1984)	China		Craemer et al. (1996)

Table 1 continued

Target plant[a]	Species	Country of the type locality	Notes	Main references[b]
Mikania micrantha Kunth (Asteraceae; bittervine)	Acalitus mikaniae Keifer 1974	Florida (USA)	On Mikania scandens (L.) Willd. in buds	Cock (1982), Mohanasundaram and Muniappan (1990), Ooi (1992), Waterhouse (1994), Cock et al. (2000), Muniappan and Bamba (2000) and Muniappan et al. (2005)
Plantago spp. (Plantaginaceae; plantain)	Leipothrix coactus (Nalepa 1896)	Germany	Leaf injuries	
Rubus fruticosus L. (Rosaceae; blackberry)	Eriophyes rubicolens (Canestrini)	Italy	Erinea under leaves on several wild species of Rubus in France	Sagliocco and Bruzzese (2004)
Rubus species (Rosaceae; blackberry)	Acalitus essigi (Hassan 1928)	California (USA)	Berry injuries; many host plants	de Lillo and Duso (1996); Scott et al. (2008)
Rubus tomentosus Borkh. (Rosaceae; woolly blackberry)	Phyllocoptes gracilis (Nalepa 1891)	Germany (presumed)	Leaf, bud, berry injuries; many host plants	de Lillo and Duso (1996)
Salsola tragus L. (Chenopodiaceae; Russian thistle)	Aceria salsolae de Lillo and Sobhian 1996	Turkey	Plant stunted, galls; laboratory and field host specificity tests completed; awaiting approval for release	Sobhian et al. (1999) Gerson et al. (2003), Smith (2005), Smith et al. (2009)
Salvia pratensis L., S. verticillata L. (Lamiaceae; introduced sage, lilac sage)	Aceria salviae (Nalepa 1891)	Austria	Leaf deformations, may also affect stems, petals and flowers; also infesting other salvia species as Salvia sclarea L., a potential oil crop (Chumak 1975 and Nachev 1987)	Natchev (1987)
Solanum elaeagnifolium Cav. (Solanaceae; silverleaf nightshade)	Aceria bicornis (Trotter 1900)	Argentina	Leaf galls	Craemer et al. (1996)
Sonchus oleraceus L., S. asper (L.) Hill, S. hydrophilus Boulos (Asteraceae; sowthistles)	Aceria thalgi Knihinicki et al. 2009	West Australia (Australia)	Severe curling and rolling of leaf margins; preliminary host specificity and impact studies	Knihinicki et al. (2009)

Table 1 continued

Target plant[a]	Species	Country of the type locality	Notes	Main references[b]
Spartium junceum L. (Fabaceae; Spanish broom)	*Aceria spartii* (Canestrini 1893)	Italy	Witches' broom growth	Castagnoli (1978) and Craemer et al. (1996)
Tamarix gallica L. and *T. ramosissima* Ledeb. (Tamaricaceae; French tamarisk, saltcedar)	*Aceria tamaricis* (Trotter 1901)	Turkey	Leaf and twig galls; host specificity tests	Castagnoli, (1992) and de Lillo and Sobhian (1994, 1996)
Taraxacum officinale F. H. Wigg. (Asteraceae; dandelion)	*Leipothrix taraxaci* (Liro 1943)	Finland	Leaf injuries (russeting and discoloration); preliminary host specificity tests	Petanović et al. (1984) Petanović (1990a, b) and Rosenthal (1996)
Toxicodendron radicans (L.) Kuntze (Anacardiaceae; poison ivy)	*Aculops toxicophagus* (Ewing 1917) = *Aculops rhois* (Stebbins 1909)	Florida (USA)	Widespread leaf galling and stunted plants in Florida	Cromroy (1977, 1983), Habeck (1990)
Tribulus terrestris L. (Zygophyllaceae; puncturevine)	*Aceria tribuli* (Keifer 1974)	Sudan	Vagrant; preliminary host specificity on population from Bangalore India	Sankaran and Ramaseshiah (1981), Scott (1990), L. Andres pers. comm.

The species in the tables listed by Boczek and Chyczewski (1978), Cromroy (1983), Boczek and Petanović (1996), Petanović (1996) and Briese and Cullen (2001) have not been included

[a] In cases in which plant species names differed among sources, we generally used the name in the USDA PLANTS Database, http://plants.usda.gov

[b] Excluding review papers and strictly taxonomic studies

[c] Rosenthal (1983) mistakenly used the name *A. convolvuli* in early studies on *A. malherbae* (Nuzzaci et al. 1985)

Host specificity testing

Several eriophyid species which were thought to be host specific (i.e., attacking only acceptable target plant species) in the field have been observed to develop on and damage other nontarget plants in laboratory or greenhouse experiments (reviewed by Skoracka et al. (2009) in this issue). We suspect that many of these discrepancies may be caused by the artificial environmental conditions in laboratory tests that are milder than field conditions, such as lower light intensity, moderate temperatures, softer host plant tissues, absence of natural enemies, or absence of wind necessary for aerial dispersal. However, controlled experiments need to be done to test the importance of these factors. The results of field experiments with *A. hyperici*, *A. malherbae* and *Aceria salsolae* de Lillo and Sobhian (Willis et al. 2003; Skoracka et al. (2009) in this issue; Smith et al. 2009; R. Hansen unpublished data) support the general pattern that nontarget plants that can be suitable for development under laboratory conditions are much less populated in the field and sustain little or no damage. However, it is still not known which factors explain this difference, and learning this would improve our ability to assess risk to such nontarget species based on experiments conducted under artificial environmental conditions.

For example, host specificity of *Aceria centaureae* (Nalepa) was evaluated as a prospective biological control agent of *Centaurea diffusa* Lam. (diffuse knapweed, Asteraceae) (Littlefield et al. 2000). In laboratory experiments the mite caused galling on immature safflower (*Carthamus tinctorius* L.) and two native North American plants, *Plectocephalus americanus* (Nuttall) D. Don and *P. rothrockii* (Greenman) D. J. N. Hind, which were previously placed in *Centaurea* (Keil 2006). These results caused the USDA Technical Advisory Group (Cofrancesco and Shearer 2004) to recommend that the mite not be introduced (J. Littlefield pers. comm.). However, in a field experiment in Greece, the mite did not damage safflower (Sobhian et al. 1989), and it has only been collected from at least four species of *Centaurea* in the field (Castagnoli and Sobhian 1991, de Lillo and Amirine, unpublished database). *Plectocephalus americanus* and *P. rothrockii* have not been tested under field conditions, but such testing might show that these plants are not susceptible to significant damage under natural conditions.

Efficacy

Although it is relatively easy to measure impact of mite populations in controlled experiments using infested and uninfested plants, usually conducted under laboratory, greenhouse or shade-house conditions (e.g., Cullen and Moore 1983; Goolsby et al. 2004; Smith 2005), the results may differ greatly from actual impact in the field. Such discrepancies are likely to be caused by critical differences in abiotic (e.g., precipitation, relative humidity, temperature, solar radiation and wind) and biotic (e.g., pathogens, predators, plant genotype, plant phenotypic responses and plant competition) environmental conditions. Conducting field experiments in the region of origin should help provide more realistic results (e.g., Caresche and Wapshere 1974; Jupp and Cullen 1996; Smith et al. 2009). However, because some factors such as plant genotype (mite resistance/susceptibility), climate, or natural enemies, may differ between the native region and the introduced region, it is important to be aware of the effects of such differences on efficacy. The continuing development of computer programs, databases and molecular genetics methods to assess suitability of climate, elevation, latitude and plant genotype are increasing our ability to predict where an agent is likely to become established (discussed above). However, the impact of natural enemies (predators and pathogens) on populations of prospective

eriophyid biological control agents is largely unknown (McCoy 1996; Sabelis 1996), and may often be a critical constraint to the effectiveness of the agent (Goeden and Louda 1976; Smith 2004). It should be noted that there are some well-documented examples of eriophyid crop pests that have been controlled by predatory mites (Sabelis 1996), which suggests that predators may also be able to limit the effectiveness of prospective biological control agents. However, there are also examples in which phytoseiid mites were not able to control eriophyid crop pests (Sabelis 1996), so the potential of predators to interfere with biological control should be evaluated for each prospective agent. Two examples of introduced eriophyid mites attacking invasive alien weeds that appear to be limited by natural enemies are *A. anthocoptes* and *A. chondrillae* (Piper and Andres 1995; Ochoa et al. 2001). Larvae of the acariphagous gall midge *Arthrocnodax* sp. were thought to be the principal factor regulating the abundance of *Aceria acroptiloni* Shevchenko & Kovalev, which is an important natural enemy of *Acroptilon repens* (L.) DC. (Russian knapweed, Asteraceae) in Russia (Kovalev et al. 1975; Volkov and Izhevskii 1996). More studies, especially under field conditions, should be conducted to determine the importance of predation on population dynamics of eriophyid biological control agents.

Inadequate environmental conditions for survival during dormancy and aerial dispersal may also restrict the effectiveness of eriophyid biological control agents. Eriophyids that attack perennial host plants in temperate climates tend to overwinter on their host plant. For example, *A. acroptiloni* overwinters in inflorescences of *Acroptilon repens* (Kovalev et al. 1975), *A. malherbae* moves down to the root buds of *Convolvulus arvensis* when the plant is dormant due to drought or winter conditions (J. Littlefield, pers comm.), *A. genistae* overwinters on *Cytisus scoparius* (Castagnoli 1978), and *Phyllocoptes fructiphilus* overwinters under bud scales of *Rosa multiflora* (Kassar and Amrine 1990). However, relatively little is known about dormancy of eriophyids that attack annual plants. Although wheat is an annual plant, it has early and late varieties, so *Aceria tosichella* Keifer commonly overwinters on new annual growth occurring late in the season or on winter wheat, and then disperses to summer wheat after it appears. However, some eriophyids known to be host specific on annual grasses have never been observed on grasses growing during winter and are hypothesized to overwinter somewhere else (A. Skoracka pers. comm.). *Paraphytoptus pannolus* Keifer overwinters under the seed coat of the annual weed, *Ambrosia trifida* L. (giant ragweed, Asteraceae), by entering through the stigmatal aperture (Amrine and Stasny 1989). Cold winter temperatures appear to have limited the effectiveness of *C. rouhollahi*, which attacks the annual *Galium aparine*, and *A. chondrillae*, which attacks the perennial *Chondrilla juncea* (McClay 2005; Milan et al. 2006). Temperature and condition of host plant tissue can affect induction of dormancy. For example, *A. spartii* consistently produced deutogynes in inland areas of Italy that had a continental climate, whereas in the coastal regions that had a more temperate climate, production of deutogynes depended on the dryness of plant tissue (Castagnoli 1978).

Dispersal

Most eriophyid mites are thought to spread from plant to plant primarily by wind (Sabelis and Bruin 1996). Longevity of mites removed from a host plant is sometimes only a few hours (Bergh 2001), which suggests that most aerial dispersal is over relatively short distances. However, cases where eriophyids appear to survive long periods under extreme cold, desiccating conditions and low oxygen concentration, suggests the potential for long-distance aerial dispersal (Zhao and Amrine 1997). For example, some species held in water at about 4°C survived for up to 5–6 weeks (E. de Lillo and R. Monfreda unpublished data).

The speed, distance and survivorship of eriophyids dispersing among plants are generally poorly known. Information on dispersal rate and the conditions necessary to initiate dispersal behavior would be useful for optimizing release strategies. Phoresy on insects and vertebrates, including humans, is another dispersal method that can be important (Sabelis and Bruin 1996; Duffner et al. 2001). It is logical that phoresy on host-specific herbivorous insects would be advantageous to host-specific eriophyid mite species, but there is little evidence to support this hypothesis. Measurement of eriophyid mite phoresy on polyphagous versus monophagous herbivorous insects could reveal such relationships and indicate the potential for synergistic interactions between eriophyid mites and insect biological control agents to improve control of the target weed. In the absence of phoresy, consideration of the prevailing wind direction may be important during release of eriophyid mite biological control agents. Experimental field releases have shown that eriophyids can disperse among plants at a site within several weeks, although infestation of target plants can be highly variable (McClay 2005; Smith et al. 2009). Other means of enhancing eriophyid spread, such as mowing vegetation at an optimal time may also be beneficial (Lauriault et al. 2004).

Evolutionary stability

The large number of eriophyoid species (de Lillo and Skoracka (2009) in this issue) suggests that members of this taxon speciate relatively quickly. The propensity of monophagy and oligophagy suggests close biochemical and morphological interactions with the host plant species, which scarcely has been investigated (de Lillo and Monfreda 2004; Monfreda and de Lillo 2006; Petanović and Kielkiewicz 2009 in this issue). The fact that phylogeny of close relatives does not always mirror host plant phylogeny (Fenton 2002) suggests that some species have been able to adapt to new host plants that are more distantly related than the nearest relatives of the hosts of their immediate ancestors. In the case of *Cecidophyopsis* species associated with *Ribes* (currants and gooseberries, Grossulariaceae), all observed host plant changes were confined to species within the same genus (Fenton et al. 2000). The short generation time of eriophyids combined with potentially large population sizes expected when used as a classical biological control agent, should theoretically increase their potential to evolve (Hufbauer and Roderick 2005). This raises the question of how safe and stable eriophyids are as classical biological control agents. How rapidly can a mite population adopt a new host plant, and how can we determine what plant species are most likely to be at risk? These questions have not been directly studied, but a phylogenetic study of *Cecidophyopsis* mites associated with *Ribes*, suggests that the minimum time for speciation events associated with changes in host plants was no more than about 0.5 million years and that several changes apparently occurred in much less time (Fenton et al. 2000). Although this time scale appears to be much longer than that usually considered by governments when making decisions, more data would increase our confidence.

There are several examples in which eriophyids have quickly adopted new host plants, although there is no direct evidence of evolutionary change by the eriophyids in any of them. *Cecidophyopsis aurea* Amrine has only been collected in Europe on *Ribes aureum* Pursh, a plant native to North America that was introduced to Europe in the last 100 years (Fenton 2000). The closest relative to *C. aurea* is *C. alpina* Amrine, which has been collected only from *R. alpinum* L. in Europe. So, it is possible that *C. aurea* evolved from *C. alpina* after introduction of *R. aureum*, or that *C. aurea* came from an unknown European host plant and was capable of infesting *R. aureum* without evolutionary change.

Eriophyes insidiosus Keifer and Wilson, which occurs on native plums (*Prunus* spp.) in California and Mexico infests cultivated peach trees (*Prunus persica* [L.] Batsch), which are originally native to Asia (Oldfield et al. 1995). *Aceria guerreronis* Keifer, which appears to be native to the neotropics on an unknown host plant, recently became a major pest of coconut (*Cocos nucifera* L.), which originated from South Asia (Navia et al. 2005, 2006; Manimekalai and Nagarajan 2007). *Aceria thalgi* Knihinicki et al. appears to be indigenous to Australia, but is very damaging to the introduced weed, *Sonchus oleraceus* L. (sowthistle, Asteraceae; Knihinicki et al. 2009). *Rhombacus rheumella* Keifer and *R. asclepiadii* Keifer, which are known only in Australia and belong to an endemic genus whose members are mostly found on *Eucalyptus*, are now found on Rhubarb (*Rheum rhabarbarum* L., Polygonaceae) and *Asclepias fruticosa* L. (African milkweed, Asclepiadaceae), respectively. Both these plants are alien and entered Australia within the last 240 years (J. Amrine unpublished data). These are all examples in which it appears that human activity has suddenly put an eriophyid species in contact with a novel host; however, it is not clearly known whether the mite populations have evolved from their ancestral form and changed host plant specificity or whether the novel host plant simply was already susceptible to attack. In other words, if these eriophyid mites were evaluated in a way similar to that for prospective biological control agents, would these plants have been predicted to be vulnerable?

It would be interesting to study cases of historical biological control introductions such as *A. hyperici* to see if populations have been able to increase their ability to develop on a partially suitable nontarget species (*H. gramineum*), or *A. chondrillae* to see if populations are able to adapt to resistant genotypes of the host plant. Furthermore, adaptation of an eriophyid biological control agent to a different climate may be advantageous to help control an invasive plant that occurs in environmental conditions that differ from those in the native range. Likewise, evolution of resistance to pesticides could improve efficacy of an eriophyid intended to control a weed that occurs in a crop where the pesticides are used to control other pests (e.g., Hoy and Ouyang 1989). In cases where genotypes or forms of the target weed are resistant to a mite population, it would be useful to know how likely or rapidly an introduced population of mites can adapt to the resistant plants.

Future research

Historically, focus of biological control research using eriophyid mites has been on discovery of species and evaluation of host plant specificity and the ability to damage the target plant (e.g., Rosenthal 1996; Briese and Cullen 2001). Successfully achieving biological control depends on attaining high densities of the agent on the target plant, which is necessary to reduce plant fitness and biomass (Smith 2004). Such high populations require the co-occurrence of many ecological factors, including suitable host plants, climate and edaphic environment, and avoidance of predators and mite pathogens. More attention needs to be paid to these factors in order to improve our ability to use eriophyids effectively.

The high degree of host plant specificity of eriophyids previously has been considered advantageous for biological control. However, virulence evolution theory (Ewald 1995) predicts that in such highly coevolved host-parasite systems the plants should have higher levels of resistance and/or tolerance to eriophyid mites and the eriophyids should have lower ability to injure the plant (avirulence). Therefore, eriophyids may provide relatively few species that can effectively control a target plant in an exotic location. For example, of

eight species of eriophyid mites associated with *Lantana camara* L., only one, *A. lantanae*, causes symptoms damaging enough to be considered useful for controlling this plant (Craemer 1996). On the other hand, considering the existence of plant species and "forms" that vary in resistance to an eriophyid biotype, there may be opportunities to employ the little-used "new associates" strategy (Hokkanen and Pimentel 1989), using a biotype or species of mite that has an unusually high virulence for the targeted weed population (e.g., *A. thalgi* for *Sonchus oleraceus*; Knihinicki et al. 2009). Another approach could be to include a virulent plant pathogen that is vectored by the mite, such as in the case of *P. fructiphilus* and rose rosette disease (RRD). However, it is conceivable that efficacy of such a pathogen-vector-host system may decrease over time due to coevolution, similar to what occurred with myxoma virus used to control rabbits in Australia (Kerr 2008). In any case, it is important for us to learn more about the evolutionary stability of host plant specificity and virulence to ensure the future safety and efficacy of eriophyid mites as biological control agents.

The existence of plant genotypes that are resistant to a particular eriophyid population has been an obstacle to achieving widespread successful control in several cases (e.g., *Chondrilla juncea* and *Hypericum perforatum*). However, it is theoretically possible that this level of specificity could be useful in cases where some forms of a plant are invasive whereas others are considered valuable, such as *Cynodon dactylon* (L.) Pers. (Bermuda-grass) (Whitson et al. 2000; Reinert et al. 2008). The ability of *Aceria cynodoniensis* Sayed to damage some varieties of *C. dactylon* has been sufficient to stimulate plant breeders to develop commercial varieties that are resistant to the mite (Reinert et al. 1978, 2008). However, because the plant is invasive in some regions, it would be interesting to find mites that damage the invasive varieties, but not commercial varieties.

In general, arthropod biological control agents should be most effective when they are used in a location that lacks natural enemies that would otherwise limit their populations. So, an eriophyid that is controlled by natural enemies that occur in the adventive region (where the target weed needs to be controlled) is not likely to be an effective agent. However, if an eriophyid is controlled by a specialist natural enemy in its native region (Sabelis et al. 2007), then it is more likely that the eriophyid will control the plant in a region that lacks this natural enemy (Smith 2004). Therefore, it is important to learn more about the identitiy, specificity and efficacy of natural enemies of eriophyids.

Combining studies on molecular genetics, morphology and behavior (e.g., host plant specificity) would help to clarify taxonomic relationships or differences among populations of a nominal eriophyid species. For example, Magud et al. (2007) observed significant morphological differences among populations of *A. anthocoptes* in Serbia that were associated with geography rather than variety of the host plant, *Cirsium arvense*. However, it is unknown if these populations are reproductively isolated or are behaviorally distinct. The studies of *Cecidophyopsis* species associated with *Ribes* included molecular genetics, morphologically identified species and known host plants (Fenton et al. 2000), but the addition of behavioral studies would help clarify whether some species or populations showed different preferences or abilities to attack different plant species. For example, *Abacarus hystrix* (Nalepa), the cereal rust mite, was previously considered to be polyphagous; however, it appears to have races or species associated with specific host plants that differ in morphology and life history and that are reproductively isolated by both pre-zygotic and post-zygotic barriers (Skoracka et al. 2002; Skoracka and Kuczynski 2006; Skoracka 2008).

Few life history studies of eriophyid mites have been published, especially for the mite species associated with weeds, because they are difficult to do, especially under natural

conditions. Information on survivorship both on and off the host plant, and under different environmental conditions is needed. Sudies need to be done on the effects of weather stresses on eriophyid mite physiology, behavior and population dynamics. The factors that influence aerial dispersal, especially in taking off and landing on the target host are unknown.

Below are some other important questions that should be addressed by future research.

- What controls host plant specificity? What is the relative importance of attraction, repellence, resistance, and shelter? What mite-plant physiological interactions are related to host plant recognition and acceptance, feeding, and gall formation?
- What is the evolutionary stability of host plant specificity? How quickly can eriophyid mites evolve to attack novel host plant species or biotypes, and how can we predict which species are most susceptible?
- Are populations of the biological control agent reduced by natural enemies to the level where they do not impact the target weed? How can we predict this with pre-release experiments?
- Mites appear to persist and multiply on some nontarget plants in the laboratory. Does this also occur in the field, and if not, then why? How can we modify laboratory experiments to better predict behavior in the field, which would save time and money and reduce risk?
- How accurate are pre-release studies in predicting post-release efficacy or host specificity in the field? How can we improve the reliability of pre-release studies?
- Do eriophyid mites progress through evolutionary stages of adaptation to a new host plant involving a successive decrease in virulence, ranging from high impact to benign parasitism (virulence evolution theory, Ewald 1995)? If so, then we would expect both the eriophyid and host plant populations to evolve toward a reduction of impact on the target weed. How long would effective biological control last?

The scientific use of eriophyid mites for biological control of weeds is still in the early stages of development. The small size and difficulty of identification previously hindered research, but modern microscopes, morphological and molecular genetic methods have greatly improved our taxonomic ability. The growing impact of invasive alien plants is increasing the demand for environmentally safe, effective methods to control them. Classical biological control is one of the principal methods to control such plants, and eriophyid mites have the potential to be safe effective agents. Answers to the preceding questions will expand our knowledge of eriophyid mites and improve our ability to use them for biological control.

References

Amrine JW Jr (1996) *Phyllocoptes fructiphilus* and biological control of multiflora rose. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier, Amsterdam, pp 741–749

Amrine JW Jr (2002) Multiflora rose. In: Van Driesche R, Lyon S, Blossey B, Hoddle M, Reardon R (eds) Biological control of invasive plants in the eastern United States. USDA Forest Service Publication FHTET-2002-04, pp 265–292

Amrine JW Jr, Stasny T (1989) The eriophyid mite, *Paraphytoptus pannolus* K. on giant ragweed, *Ambrosia trifida* L. Proc West Va Acad Sci 61(1):23

Amrine JW Jr, Stasny TA (1994) Catalog of the Eriophyoidea (Acarina: Prostigmata) of the world. Indira Publishing House, Michigan

Amrine JW Jr, Hindal DF, Williams R, Appel J, Stasny T, Kassar A (1990) Rose rosette as a biocontrol of multiflora rose, 1987–1989. In: Proceedings of the 43rd annual meeting of the Southern Weed Science Society, pp 316–320

Andres LA (1983) Considerations in the use of phytophagous mites for the biological control of weeds. In: Hoy MA, Cunningham GL, Knutson L (eds) Biological control of pests by mites. Univ Calif Agri Exp Stn Special Publ 3304:53–60

Baars JR, Neser S (1999) Past and present initiatives on the biological control of *Lantana camara* (Verbenaceae) in South Africa. Afr Entomol Mem 1:21–33

Bacic J, Petanović R (1995) A study of fluctuations in the spurge eriophyid mite, *Vasates euphorbiae* Pet. populations. In: Kropczynska D, Boczek J, Tomczyk A (eds) The Acari, physiological and ecological aspects of Acari-host relationships. Oficyna Dabor, Warszawa, pp 163–171

Baker GT, Stadelbacher EA, Chandrapatya A (1986) Abnormalities by *Coptophylla caroliniani* Chand. (Eriophyidae) on *Geranium carolinianum*. J Appl Entomol 101:313–316

Bergh JC (2001) Ecology and aerobiology of dispersing citrus rust mites (Acari: Eriophyidae) in central Florida. Environ Entomol 30(2):318–326

Boczek J (1995) Eriophyid mites (Acari: Eriophyoidea) as agents of biological weed control. In: Kropczynska D, Boczek J, Tomczyk A (eds) The Acari, Physiological and ecological aspects of Acari-host relationships. Oficyna Dabor, Warszawa, pp 601–606

Boczek J, Chyczewski J (1978) Eriophyid mites (Acarina: Eriophyoidea) occurring on weed plants in Poland. Rcz nauk Rolnb, ser E 7(1):109–114

Boczek J, Maciejczyk K (1995) [The bionomy of *Aceria artemisiae* (Acari: Eriophyidae) and the possibilities of use of the mite for control of *Artemisia vulgaris*.] Bionomia *Aceria artemisiae* (Acari: Eriophyidae) i mozliwosci wykorzystania tego szpeciela do zwalczania bylicy. Materiay Sesji Instytutu Ochrony Roslin 35(2):138–140

Boczek JH, Petanović R (1996) Eriophyid mites as agents for the biological control of weeds. In: Moran VC, Hoffmann JH (eds) Proceedings of the IX international symposium on biological control of weeds, 19–26 January 1996, Stellenbosch, South Africa, University of Cape Town, pp 127–131

Boldt PE, Sobhian R (1993) Release and establishment of *Aceria malherbae* (Acari: Eriophyidae) for control of field bindweed in Texas. Environ Entomol 22(1):234–237

Boydston RA, Williams MM (2004) Combined effects of *Aceria malherbae* and herbicides on field bindweed (*Convolvulus arvensis*) growth. Weed Sci 52(2):297–301

Briese DT (2006) Host specificity testing of weed biological control agents: initial attempts to modernize the centrifugal phylogenetic method. In: Hoddle MS, Johnson MW (eds) Proceedings of the fifth California conference on biological control, 25–27 July 2006, The Historic Mission Inn, Riverside, California, pp 32–39

Briese DT, Cullen JM (2001) The use and usefulness of mites in biological control of weeds. In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds) Acarology: Proceedings of the 10th international congress. CSIRO Publishing, Melbourne, pp 453–463

Britten DC, Schuster GL, Michels GJ Jr, Owings DA (2003) Using cold-stored or overwintering *Aceria malherbae* Nuzzaci (Acarina: Eriophyiidae [sic]), a gall-forming eriophyid mite, for infestation of field bindweed. Southwest Entomol 28:273–280

Burdon JJ, Groves RH, Cullen JM (1981) The impact of biological control on the distribution and abundance of *Chondrilla juncea* in south-eastern Australia. J Appl Ecol 18(3):957–966

CABI (2008) Weed biological control quarterly report 30 September 2008. CABI Europe–Switzerland, Delémont

CABI (2009) Biological control of perennial pepperweed, *Lepidium latifolium* Annual Report 2008. CABI Europe–Switzerland, Delémont

Caresche LA, Wapshere AJ (1974) Biology and host specificity of the *Chondrilla* gall mite *Aceria chondrillae* (G. Can.) (Acarina, Eriophyidae). Bull Entomol Res 64:183–192

Castagnoli M (1978) [Investigation on the causes of withering and death of *Spartium junceum* in Italy. *Eriophyes genistae* (Nal.) and *E. spartii* (G. Can.) (Acarina, Eriophyoidea): redescription and outlines of biology and damage.] Ricerche sulle cause di deperimento e moria dello *Spartium junceum* L. in Italia. *Eriophyes genistae* (Nal.) e *E. spartii* (G. Can.) (Acarina, Eriophyoidea): ridescrizione, cenni di biologia e danni. Redia 61:539–550

Castagnoli M (1992) Redescription of *Aceria tamaricis* (Trotter, 1901) (Acari, Eriophyidae). Redia 75(2):446–452

Castagnoli M, Sobhian R (1991) Taxonomy and biology of *Acaria centaureae* (Nal.) and *A. thessalonicae* n. sp. (Acari: Eriophyoidea) associated with *Centaurea diffusa* Lam. in Greece. Redia 74(2):509–524

Chan KL, Turner CE (1998) Discovery of the gall mite *Aceria genistae* (Nalepa) (Acarina: Eriophyidae) on gorse and French broom in the United States. Pan-Pac Entomol 74(1):55–57

Chandrapatya A, Baker GT (1986) Biological aspects of the geranium mites, *Coptophylla caroliniani* and *Aceria mississippiensis* (Prostigmata: Eriophyidae). Exp Appl Acarol 2:201–216

Chumak VA (1975) Pests of *Salvia sclarea*. Zashchita Rastenii 12:35–36

Clement SL, Rosenthal SS, Mimmocchi T, Cristofaro M, Nuzzaci G (1984) Concern for U.S. native plants affects biological control of field bindweed. 10th international congress of plant protection 1983. Volume 2. Proceedings of a conference held at Brighton, England, 20–25 November, 1983. Plant protection for human welfare. British Crop Protection Council, Croydon, UK. Publication 5A-R3:775

Cock MJW (1982) Potential biological control agents for *Mikania micrantha* from the neotropical region. Trop Pest Manage 28(3):242–254

Cock MJW (1984) Possibilities for biological control of *Chromolaena odorata*. Trop Pest Manage 30(1):7–13

Cock MJW, Ellison CA, Evans HC, Ooi PAC (2000) Can failure be turned into success for biological control of mile-a-minute weed (*Mikania micrantha*)? In: Spencer NR (ed) Proceedings of the X international symposium on biological control of weeds, 4–14 July 1999, Montana State University, Bozeman, Montana, pp 155–167

Cofrancesco AF Jr, Shearer JF (2004) Technical advisory group for biological control of weeds. In: Coombs EM, Clark JK, Piper GL, Cofrancesco AF Jr (eds) Biological control of invasive plants in the United States. Oregon State University Press, Corvallis, pp 38–41

Cook MT (1909) Some insect galls of Cuba. Secretaria de Agricultura, Comercio y Trabajo de la Republica de Cuba, Estacion Central Agromonica, Second Report, pp 143–146

Cordo HA (1996) [Biological control of weeds in Argentina: progress and actual situation, two decades after its initiation.] Control biologico de malezas en la Argentina: progresos y situacion actual, a dos decadas de su comienzo. In: Zapater MC (ed) El control biologico en America Latina: Actas de la "III mesa redonda de control biologico en el Neotropico". Rio de Janeiro, Brazil, pp 9–15

Craemer C (1995) Host specificity, and release in South Africa, of *Aceria malherbae* Nuzzaci (Acari, Eriophyoidea), a natural enemy of *Convolvulus arvensis* L. (Convolvulaceae). Afr Entomol 3(2):213–215

Craemer C (1996) Eriophyoidea (Acari) associated with *Lantana camara* L., with descriptions of two new species. Afr Plant Prot 2(1):59–66

Craemer C, Neser S (1990) Mites imported against lantana. Plant Prot News 19:3

Craemer C, Neser S, Smith Meyer MKP (1996) [Eriophyid mites (Acari: Eriophyoidea: Eriophyidae) as possible control agents of undesirable introduced plants in South Africa.] Eriophyid-myte (Acari: Eriophyoidea: Eriophyidae) as moontlike beheeragente van ongewense uitheemse plante in Suid-Afrika. AS Tydskrif vir Natuur-wetenskap en Tegnologie 15:99–109

Cromroy HL (1977) The potential use of eriophyoid mites for control of weeds. In: Freeman TE (ed) Proceedings of the IV international symposium on biological control of weeds, University of Florida, Gainesville, Florida, pp 294–296

Cromroy HL (1979) Eriophyoidea in biological control of weeds. In: Rodriguez JG (ed) Recent advances in acarology, vol 1. Academic Press, New York, pp 473–475

Cromroy HL (1983) Potential use of mites in biological control of terrestrial and aquatic weeds. In: Hoy MA, Cunningham GL, Knutson L (eds) Biological control of pests by mites. Univ Calif Agri Exp Stn Special Publ 3304:61–66

Cruttwell RE (1977) Insects and mites attacking *Eupatorium odoratum* L. in the neotropics. 6. Two erio-phyid mites, *Acalitus adoratus* Keifer and *Phyllocoptes cruttwellae* Keifer. Commonwealth Institute of Biological Control Tech Bull 18:59–63

Cruttwell McFadyen RE (1995) The accidental introduction of the Chromolaena mite *Acalitus adoratus* into Southeast Asia. In: Delfosse ES, Scott RR (eds) Proceedings of the VIII international symposium on biological control of weeds, 2–7 February 1992, Lincoln University, Canterbury, New Zealand. DSIR/CSIRO, Melbourne, pp 649–652

Cruttwell McFadyen RE (2002) *Chromolaena* in Asia and the Pacific: spread continues but control prospects improve. In: Zachariades C, Muniappan R, Strathie LW (eds) Proceedings of the fifth international workshop on biological control and management of *Chromolaena odorata*, Durban, South Africa. ARC-PPRI (2002), pp 13–18

Cullen JM, Briese DT (2001) Host plant susceptibility to eriophyid mites used for weed biological control. In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds) Acarology: Proceedings of the 10th international congress. CSIRO Publishing, Melbourne, pp 342–348

Cullen JM, Moore AD (1983) The influence of three populations of *Aceria chondrillae* on three forms of *Chondrilla juncea*. J Appl Ecol 20(1):235–243

Cullen JM, Groves RH, Alex JF (1982) The influence of *Aceria chondrillae* on the growth and reproductive capacity of *Chondrilla juncea*. J Appl Ecol 19:529–537

Day MD, Urban AJ (2004) Ecological basis for selecting biocontrol agents for lantana. In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI international sym-posium on biological control of weeds, 4–8 May, 2003, CSIRO Entomology, Canberra, Australia, pp 79–87

Day MD, Broughton S, Hannan-Jones MA (2003a) Current distribution and status of *Lantana camara* and its biological control agents in Australia, with recommendations for further biocontrol introductions into other countries. Biocontrol News and Inf 24(3):63N–76N

Day M, Wiley CH, Playford J, Zalucki MP (2003b) Lantana: current management status and future pros-pects. ACIAR Monograph 102

de Lillo E, Duso C (1996) Currant and berries. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control, vol 6. Elsevier, Amsterdam, pp 583–592 World Crop Pests

de Lillo E, Monfreda R (2004) Salivary secretions of eriophyoids (Acari: Eriophyoidea): first results of an experimental model. Exp Appl Acarol 34(3–4):291–306

de Lillo E, Skoracka A (2009) What's "cool" on Eriophyoid mites? Exp Appl Acarol. doi: 10.1007/s10493-009-9297-4

de Lillo E, Sobhian R (1994) Taxonomy, distribution and host specificity of a gall-making mite *Aceria tamaricis* (Trotter) (Acari–Eriophyoidea) asociated with *Tamarix gallica* L. (Parietales: Tamaricaceae) in southern France. Entomologica, Bari 28:5–16

de Lillo E, Sobhian R (1996) A new Eriophyid species (Acari Eriophyoidea) on *Salsola* spp. (Centrospermae Chenopodiaceae) and a new report for *Aceria tamaricis* (Trotter). Entomologica, Bari 30:93–100

de Lillo E, Baldari R, Cristofaro M, Kashefi J, Lifflefield J, Sobhian R, Tronci C (2004) Eriophyid mites for the biological control of knapweeds: morphological and biological observations. In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI international symposium on biological control of weeds, 4–8 May, 2003, CSIRO Entomology, Canberra, Australia, pp 88–95

de Lillo E, Craemer C, Amrine JW Jr, Nuzzaci G (2009) Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata). Exp Appl Acarol. doi:10.1007/s10493-009-9311-x

Duffner K, Schruft G, Guggenheim R (2001) Passive dispersal of the grape rust mite *Calepitrimerus vitis* Nalepa 1905 (Acari, Eriophyoidea) in vineyards. Anz Schadl 74(1):1–6

Epstein AH, Hill JH (1999) Status of rose rosette disease as a biological control for multiflora rose. Plant Dis 83(2):92–101

Ewald PW (1995) The evolution of virulence: a unifying link between parasitology and ecology. J Parasitol 81(5):659–669

Fenton B (2002) Speciation and biogeography in eriophyid mites: a review. In: Bernini F, Nannelli R, Nuzzaci G, de Lillo E (eds) Acarid phylogeny and evolution: adaptation in mites and ticks. Pro-ceedings of the IV symposium of the European association of acarologists. Kluwer, Dordrecht, Boston and London, pp 27–34

Fenton B, Birch ANE, Malloch G, Lanham PG, Brennan RM (2000) Gall mite molecular phylogeny and its relationship to the evolution of plant host specificity. Exp Appl Acarol 24(10–11):831–861

Flechtmann CHW (1973) On an Eriophyid mite (Acari) from Lantana from Brazil. An Soc Entomol Brasil 2(1):109–110

Flechtmann CHW, Harley KLS (1974) Preliminary report on mites (Acari) associated with *Lantana camara* in the neotropical region. An Soc Entomol Brasil 3:69–71

Gassmann A, Tosevski I, Petanović R, Rancic D, Magud B, Maia G (2004) Biological control of Canada thistle (*Cirsium arvense*). In: CABI Bioscience Switzerland Centre Annual Report 2003. CABI Bioscience, Delémont, Switzerland, p 13

Gassmann A, Gerber E, Tosevski I, Petanović R, Magud B, Cortat G (2005) Biological control of Canada thistle, *Cirsium arvense*. In: CABI Bioscience Switzerland Centre Annual Report 2004, CABI Bioscience, Delémont, Switzerland, p 27

Gassmann A, Tosevski I, Petanović R, Magud B, Haefliger P, Chevillat V, Rheinhold T (2006) Biological control of Canada thistle, *Cirsium arvense*. In: CABI Bioscience Switzerland Centre annual report 2005. CABI Bioscience, Delémont, Switzerland, p 27

Gerson U, Smiley RL, Ochoa R (2003) Mites (Acari) for pest control. Blackwell Science Ltd., Oxford, UK, pp 117–126

Goeden RD, Andres LA (1999) Biological control of weeds in terrestrial and aquatic environments. In: Bellows TS, Fisher TW (eds) Handbook of biological control. Principles and applications of biological control. Academic Press, San Diego, pp 871–890

Goeden RD, Louda SM (1976) Biotic interference with insects imported for weed control. Annu Rev Entomol 21:325–342

Goeden RD, Kovalev OV, Ricker DW (1974) Arthropods exported from California to the U.S.S.R. for ragweed control. Weed Sci 22:156–158

Goolsby JA, Zonneveld R, Bourne A (2004) Prerelease assessment of impact on biomass production of an invasive weed, *Lygodium microphyllum* (Lygodiaceae: Pteridophyta), by a potential biological control agent, *Floracarus perrepae* (Acariformes: Eriophyidae). Environ Entomol 33(4):997–1002

Goolsby JA, Jesudasan RWA, Jourdan H, Muthuraj B, Bourne AS, Pemberton RW (2005a) Continental comparisons of the interaction between climate and the herbivorous mite, *Floracarus perrepae* (Acari: Eriophyidae). Florida Entomol 88(2):129–134

Goolsby JA, Zonneveld R, Makinson JR, Pemberton RW (2005b) Host-range and cold temperature tolerance of *Floracarus perrepae* Knihinicki & Boczek (Acari: Eriophyidae), a potential biological-control agent of *Lygodium microphyllum* (Pteridophyta: Lygodiaceae). Aust J Entomol 44(3):321–330

Goolsby JA, DeBarro PJ, Makinson JR, Pemberton RW, Hartley DM, Frohlich DR (2006) Matching origin of an invasive weed for selection of a herbivore haplotype for a biological control programme. Mol Ecol 15:287–297

Habeck DH (1990) Insects associated with poison ivy and their potential as biological control agents. In: Delfosse ES (ed) Proceedings of the VII international symposium on biological control of weeds, 6–11 March 1988, Rome, Italy. Istituto Sperimentale per la Patologia Vegetale, Ministero dell'Agricoltura, e delle Foreste, Rome, Italy, pp 329–337

Hansen RW (2008) The accidentally introduced *Canada thistle* mite Aceria anthocoptes in the western USA: utilization of native *Cirsium* thistles? In: Julien MH, Sforza R, Bon MC, Evans HC, Hatcher PE, Hinz HL, Rector BG (eds) Proceedings of the XII international symposium on biological control of weeds. April 22–27, 2007, La Grande Motte, France, CAB International Wallingford, UK, p 635

Henry JM, Wegulo SN, Gibeault VA, Autio R (2005) Turfgrass performance with reduced irrigation and nitrogen fertilization. Int Turfgrass Soc Res J 10:93–101

Hijmans RJ, Guarino L, Cruz M, Rojas E (2001) Computer tools for spatial analysis of plant genetic resources data: 1 DIVA-GIS. Plant Genet Resour Newsl 127:15–19

Hokkanen HMT, Pimentel D (1989) New associates in biological control: theory and practice. Can Ent 121(10):829–840

Hong XY, Dong HQ, Fu YG, Cheng LS, Oldfield GN (2001) Relationships between eriophyoid mites and their host plants, with a case review of Eriophyoidea fauna of China. Syst Appl Acarol 6:119–136

Howard RA (1969) A check list of cultivar names used in the genus *Lantana*. Arnoldia, Jamaica Plain 29:73–109

Hoy MA, Ouyang YL (1989) Selection of the western predatory mite, *Metaseiulus occidentalis* (Acari: Phytoseiidae), for resistance to abamectin. J Econ Entomol 82(1):35–40

Hufbauer RA, Roderick GK (2005) Microevolution in biological control: Mechanisms, patterns, and processes. Biol Control 35(3):227–239

Michels GJ Jr, Carney VA, Lydon J, Ochoa R, Renn RL (2008) New records for *Aceria anthocoptes* (Acari: Eriophyidae) occurring on Canada thistle in Colorado, Nebraska and Wyoming, USA. Entomol News 119(5):483–491

Jupp PW, Cullen JM (1996) Expected and observed effects of the mite, *Aculus hyperici* on St. John's wort, *Hypericum perforatum*, in Australia. In: Moran VC, Hoffmann JH (eds) Proceedings of the IX

international symposium on biological control of weeds, 19–26 January 1996, Stellenbosch, South Africa, University of Cape Town, pp 365–370

Jupp PW, Briese DT, Cullen JM (1997) Evidence for resistance in *Hypericum perforatum* to a biological control agent, the eriophyid mite *Aculus hyperici*. Plant Prot Q 12:67–70

Kassar A, Amrine JW Jr (1990) Rearing and development of *Phyllocoptes fructiphilus* (Acari: Eriophyidae). Entomol News 101(5):276–282

Keifer HH, Denmark HA (1976) *Eriophyes lantanae* Cook (Acarina: Eriophyidae) in Florida. Entomology circular, Division of Plant Industry, Florida Department of Agriculture and Consumer Services 166:1–2

Keil DJ (2006) 21. *Plectocephalus* D. Don. In: Flora of North America Editorial Committee (eds), Flora of North America North of Mexico. Oxford University Press, Inc., New York. 19:175–177

Kelch DG, Baldwin BG (2003) Phylogeny and ecological radiation of New World thistles (*Cirsium*, Cardueae-Compositae) based on ITS and ETS rDNA sequence data. Mol Ecol 12(1):141–151

Kerr P (2008) Biocontrol of rabbits in Australia. Outlooks on Pest Manage 19(4):184–188

Knihinicki DK, McCarren KL, Scott JK (2009) A new species of *Aceria* (Acari: Eriophyidae) damaging sowthistles, *Sonchus* spp. (Asteraceae), in Australia with notes on *Aceria sonchi* (Nalepa, 1902). Zootaxa 2119:23–38

Kovalev OV, Shevchenko VG, Danilov LG (1975) *Aceria acroptiloni*, sp. n. (Acarina, Tetrapodili), a promising phytophage for the biological control of Russian knapweed [*Acroptilon repens* (L.) DC.]. Entomol Rev, Apr/June 1974 (Transl 1975), 53(2):25–34

Lauriault LM, Thompson DC, Pierce JB, Michels GJ, Hamilton WV (2004) Managing *Aceria malherbae* gall mites for control of field bindweed. New Mexico State University, Cooperative Extension Service, Las Cruces, NM. Circular 600

Lindquist EE, Sabelis MW, Bruin J (eds) (1996) Eriophyoid mites–their biology, natural enemies and control, vol. 6. Elsevier, Amsterdam, World Crop Pests

Lindroth JI (1904) Nya och salsynta finska Eriophyider. Acta Soc Fauna Flora Fenn 26(4):3–18

Lipa JJ (1976) A new record of *Aceria drabae* (Nal.) (Acarina: Eriophyidae) on a weed *Cardaria draba* (L.) (Cruciferae) in Poland. Bull Acad Polon Sci Cl 24(8):457–459

Lipa JJ (1978) [Preliminary studies on *Aceria drabae* (Nal.) (Acarina, Eriophyiidae) and its usability in biological control of hoary cress (*Cardaria draba* L.) (Cruciferae).] Wstepne badania nad szpecielem *Aceria drabae* (Nal.) (Acarina, Eriophyiidae) i jego przydatnoscia w biologicznym zwalczaniu chwastu *Cardaria draba* L. (Cruciferae). Pr Nauk Inst Ochr Rosl. Poznan, Panstwowe Wydawn. Rolnicze i Lesne 20(1):139–155

Lipa JJ (1983) Usefulness of *Aceria drabae* in biological control of hoary cress. Proceedings of the tenth international congress of plant protection. Volume 2. Proceedings of a conference held at Brighton, England, 20–25 November, 1983. Plant protection for human welfare, p 773

Lipa JJ, Studzinski A, Malachowska D (1977) Insects and mites associated with cultivated and weedy cruciferous plants (Cruciferae) in Poland and central Europe. Owady i roztocze zwiazane z roslinami uprawnymi i chwastami z rodziny krzyzowych Cruciferae w Polsce i srodkowej Europie. Polish Academy of Sciences, Warsaw, Poland

Lipa JJ, Murillo J, Castro F, Vinuela E, del Estal P, Budia F, Caballero P (1998) [First record of *Aceria drabae* (Nalepa) (Acarina: Eriophyidae) in Spain.] Primera cita de *Aceria drabae* (Nalepa) (Acarina: Eriophyidae) en Espana. Boletin de Sanidad Vegetal, Plagas 24(4):797–802

Littlefield JL (2004) Spatial distribution and seasonal life history of Aceria malherbae (Acari: Eriophyidae) on Convolvulus arvensis in Montana, USA. In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI international symposium on biological control of weeds, 4–8 May, 2003, CSIRO Entomology, Canberra, Australia, p 607

Littlefield JL, Sobhian R (2000) The host specificity of *Phyllocoptes nevadensis* Roivainen (Acari: Eriophyidae), a candidate for the biological control of leafy and cypress spurges. In: Spencer NR (ed) Proceedings of the X international symposium on biological control of weeds, 4–14 July 1999, Montana State University, Bozeman, Montana, pp 621–626

Littlefield JL, Sobhian R, Kashefi J, Sykes R (2000) A petition for the introduction and field release of the gall mite, *Aceria centaureae* (Nalepa) (Acari: Eriophyidae), for the biological control of diffuse and spotted knapweed in Montana. Petition 00-03. Submitted to USDA Technical Advisory Group, March 2000

Littlefield JL, de Meij AE, Sobhian R (2001) Potential host range of two Urophora flies and an eriophyid mite for the biological control of Russian knapweed. In: Smith L (ed) Proceedings, 1st international knapweed symposium of the 21st century; 2001 March 15–16; Coeur d'Alene, ID. U.S. Department of Agriculture, Agricultural Research Service, Albany, California, pp 102–103

Louda SM, Pemberton RW, Johnson MT, Follett PA (2003) Nontarget effects—the Achilles' heel of biological control? Retrospective analyses reduce risk associated with biocontrol introductions. Annu Rev Entomol 48:365–396

Magud BD, Stanisavljević LZ, Petanović RU (2007) Morphological variation in different populations of *Aceria anthocoptes* (Acari: Eriophyoidea) associated with the *Canada thistle*, *Cirsium arvense*, in Serbia. Exp Appl Acarol 42(3):173–183

Mahr FA, Mayo G, Ainsworth N, Jupp P (2000) Monitoring the impact of the biological control agent *Aculus hyperici* on *Hypericum perforatum* across south eastern Australia. In: A.C. Bishop AC, M. Boersma M, Barnes CD (eds) Proceedings of the 12th Australian weeds conference, 12–16 September 1999, Wrest Point Convention Centre, Hobart, Tasmania, pp 335–338

Manimekalai R, Nagarajan P (2007) Use of simple sequence repeat markers for estimation of genetic diversity in coconut (*Cocos nucifera* L.) germplasm accessions. J Plant Biochem Biotechnol 16(1):29–33

Manson DCM (1989) New species and records of eriophyid mites from New Zealand. New Zealand J Zool 16:37–49

Mayo GM, Roush RT (1997) Genetic variability of *Hypericum perforatum* L. (Clusiaceae) and the detection of resistance to the biological control agent *Aculus hyperici* Liro (Eriophyidae). Plant Prot Q 12(2):70–72

McCaffrey JP, Campbell CL, Andres LA (1995) St. Johnswort. In: Nechols JR, Andres LA, Beardsley JW, Goeden RD, Jackson CG (eds) Biological control in the western United States: accomplishments and benefits of regional research project W-84, 1964-1989. Univ Calif Div Agric Nat Res, Oakland. Publication No. 3361, pp 281–285

McClay AS (2005) Field evaluation of a gall mite for biological control of false cleavers. Canola Agronomic Research Program Project #AG-2002-20, Final Report

McClay AS, Balciunas JK (2005) The role of pre-release efficacy assessment in selecting classical biological control agents for weeds–applying the Anna Karenina principle. Biol Control 35(3):197–207

McClay AS, De Clerck-Floate RA (2002) *Convolvulus arvensis* L., field bindweed (Convolvulaceae). In: Mason PG, Huber JT (eds) Biological control programmes in Canada, 1981–2000. CABI Publishing, Wallingford, UK, pp 331–337

McClay AS, Littlefield JL, Kashefi J (1999) Establishment of *Aceria malherbae* (Acari: Eriophyidae) as a biological control agent for field bindweed (Convolvulaceae) in the northern Great Plains. Can Entomol 131(4):541–547

McClay AS, Sobhian R, Zhang W (2002) *Galium spurium* L., false cleavers (Rubiaceae). In: Mason PG, Huber JT (eds) Biological control programmes in Canada, 1981–2000, pp 358–361

McCoy CW (1996) Pathogens of eriophyoid mites. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites–their biology, natural enemies and control, vol 6. Elsevier, Amsterdam, pp 481–490 World Crop Pests

Meyer MKPS (1981) South African Eriophyidae (Acari): The genus *Aceria* Keifer, 1944. Phytophylactica 13:117–126

Mihajlović L, Petanović R, Stevanović V (1994) Entomofauna i akarofauna mlecika (Euphorbia L.) Deliblatske pescare. In: Marinković P (ed) Deliblatski pesak. Zbornik radova VI, pp 229–240

Mihajlović LJ, Spasic R, Petanović R, Mihajlović N (1998) Entomofauna and acarofauna of *Clematis vitalba* L. in Yugoslavia. Acta Entomol Serbica 3(1/2):139–147

Milan JD, Harmon BL, Prather TS, Schwarzlander M (2006) Winter mortality of *Aceria chondrillae*, a biological control agent released to control rush skeletonweed (*Chondrilla juncea*) in the western United States. J Appl Entomol 130(9–10):473–479

Mohanasundaram M, Muniappan R (1990) On the eriophyid fauna of Trinidad and Guyana: description of a new genus and species (Acari: Eriophyidae). Internat J Acarol 16(2):59–62

Monfreda R, de Lillo E (2006) [Current knowledge on the salivary secretions in Eriophyoidea, Acari.] Attuali conoscenze sulle secrezioni salivari negli Acari Eriophyoidea. Atti dell'Accad Naz Itala Entomol Rend 53(2005):379–388

Monfreda R, de Lillo E, Cristofaro M (2008) Eriophyoid mites on *Centaurea solstitialis* L in the Mediterranean area. In: Julien MH, Sforza R, Bon MC, Evans HC, Hatcher PE, Hinz HL, Rector BG (eds) Proceedings of the XII international symposium on biological control of weeds. April 22–27, 2007, La Grande Motte, France, CAB International Wallingford, UK, pp 178–181

Morley TB (2004a) Host-specificity testing of the boneseed (*Chrysanthemoides monilifera* ssp. monilifera) leaf buckle mite (*Aceria neseri*). In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI international symposium on biological control of weeds, 4–8 May, 2003, CSIRO Entomology, Canberra, Australia, pp 297–300

Morley TB (2004b) Application for approval to release the erineum-inducing *Aceria* sp. ex *Chrysanthemoides monilifera* (L.) Norl. spp. *monilifera* (boneseed leaf buckle mite) A potential biological control agent for *Chrysanthemoides monilifera*. Published by the Victorian Government Department of Primary Industries, Fankston, Victoria, Australia

Morley TB, Morin L (2008) Progress on boneseed (*Chrysanthemoides monilifera* subsp. *monilifera* (L.) Norlindh) biological control: the boneseed leaf buckle mite *Aceria* (Keifer) sp., the lacy-winged seed fly *Mesoclanis magnipalpis* Bezzi and the boneseed rust *Endophyllum osteospermi* (Doidge) A. R.Wood. Plant Prot Q 23(1):29–31

Moura MZD, Soares GLG, Isaias RM dos S (2008) Species-specific changes in tissue morphogenesis induced by two arthropod leaf gallers in *Lantana camara* L. (Verbenaceae). Aust J Bot 56(2):153–160

Mpedi PF, Urban AJ (2003) Host specificity report in relation to an application for permission to release the Central American mite, *Aceria lantanae*, from quarantine in Pretoria, for biological control of the noxious weed, *Lantana camara*, in South Africa. Unpublished report to the National Department of Agriculture: Directorate of Plant Health and Quality. ARC-PPRI, Pretoria

Mpedi PF, Urban AJ (2005) Host Specificity Testing of *Aceria lantanae* (Acari: Eriophyidae), a candidate agent for biological control of *Lantana camara* (Verbenaceae). Final report to Department of Natural Resources and Mines, Alan Fletcher Research Station Brisbane, Queensland, Australia PF

Muniappan R, Bamba J (2000) Biological control of *Chromolaena odorata*: successes and failures. In: Spencer NR (ed) Proceedings of the X international symposium on biological control of weeds, 4–14 July 1999, Montana State University, Bozeman, Montana, pp 81–85

Muniappan R, Reddy GVP, Lai PY (2005) Distribution and biological control of *Chromolaena odorata*. In: Inderjit (ed) Invasive plants: ecological and agricultural aspects. Birkhäuser Verlag, Basel, Switzerland, pp 223–233

Muniappan R, Englberger K, Reddy GVP (2006) Biological control of *Chromolaena odorata* in the American Pacific Micronesian Islands. In: Lai P-Y, Reddy GVP, Muniappan R (eds) Proceedings of the seventh international workshop on biological control and management of *Chromolaena odorata* and *Mikania micrantha*, Taiwan, September 12 to 15, 2006, pp 49–52

Nalepa A (1892) Les acarocécides de Lorraine (Suite). In: Kieffer JJ (ed) Feuille jeun naturalistes Rev Mens Hist Nat, sér 3, 22(258):118–129

Natchev PD (1987) [Studies on eriophyid mites in Bulgaria XVI. *Eriophyes salviae* (Nal.) (Acarina: Eriophyoidea), a new species for Bulgaria on salvia (*Salvia sclarea* L.)]. Proucavanije na eofidnite akari v Bulgaria. XVI *Eriophyes salviae* (Nal.) (Acarina, Eriophyoidea). Nov neprijatel po salvijata (*Salvia sclarea* L.). Pochvoznanie, Agrokhimiya i Rastitelna Zashchita [Soil Sci, Agrochem Plant Prot] 22(5):99–102

Nault LR (1997) Arthropod transmission of plant viruses: a new synthesis. Ann Entomol Soc Am 90(5):521–541

Navajas M, Navia D (2008) Critical aspects of DNA-based methods for eriophyoid mite diagnostics and genetic studies: review, prospects and challenges. In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier M-S, Vial L (eds) Integrative acarology. Proceedings of the 6th European congress, European Association of Acarologists, Montpellier, France, 21–25 July 2008, pp 300–305

Navajas M, Navia D (2009) DNA-based methods for eriophyoid mite studies: review, critical aspects, prospects and challenges. Exp Appl Acarol. doi:10.1007/s10493-009-9301-z

Navia D, de Moraes GJ, Roderick G, Navajas M (2005) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyidae): origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. Bull Entomol Res 95(6):505–516

Navia D, de Moraes GJ, Querino RB (2006) Geographic variation in the coconut mite, *Aceria guerreronis* Keifer (Acari: Eriophyidae): a geometric morphometric analysis. Int J Acarol 32(3):301–314

Neser S, Cilliers CJ (1990) Work towards biological control of *Lantana camara*: perspectives. In: Delfosse ES (ed) Proceedings of the VII international symposium on biological control of weeds, 6–11 March 1988, Rome, Italy. Istituto Sperimentale per la Patologia Vegetale, Ministero dell'Agricoltura e delle Foreste, Rome, Italy, pp 363–369

Nuzzaci G, Mimmocchi T, Clement SL (1985) A new species of *Aceria* (Acari: Eriophyidae) from *Convolvulus arvensis* L. (Convolvulaceae) with notes on other eriophyid associates of convolvulaceous plants. Entomologica 20:81–89

Ochoa R, Erbe EF, Wergin WP, Frye C, Lydon J (2001) The presence of *Aceria anthocoptes* (Nalepa) (Acari: Eriophyidae) on *Cirsium* species in the United States. Int J Acarol 27(3):179–187

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vectors of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites–their biology, natural enemies and control, vol 6. Elsevier, Amsterdam, pp 259–275 World Crop Pests

Oldfield GN, Creamer R, Gispert C, Osorio F, Rodriguez R, Perring TM (1995) Incidence and distribution of peach mosaic and its vector, *Eriophyes insidiosus* (Acari: Eriophyidae) in Mexico. Plant Dis 79:186–189

Ooi PAC (1992) Biological control of weeds in Malaysian plantations. Proceedings of the 1st international weed control congress. Weed Science Society of Victoria, Melbourne, Australia 1:248-255

Orapa W, Bofeng I, Donnelly G (2002a) Management of *Chromolaena odorata* in Papua New Guinea: status of a biological control programme. In: Zachariades C, Muniappan R, Strathie LW (eds) Proceedings of the fifth international workshop on biological control and management of *Chromolaena odorata*, Durban, South Africa, 23–25 October 2000. ARC-PPRI (2002), pp 40–45

Orapa W, Donnelly G, Bofeng I (2002b) The distribution of Siam weed, *Chromolaena odorata*, in Papua New Guinea. In: Zachariades C, Muniappan R, Strathie LW (eds) Proceedings of the fifth international workshop on biological control and management of *Chromolaena odorata*, Durban, South Africa, 23–25 October 2000. ARC-PPRI (2002), pp 19–25

Ozman SK, Goolsby JA (2005) Biology and phenology of the eriophyid mite, *Floracarus perrepae*, on its native host in Australia, Old World climbing fern, *Lygodium microphyllum*. Exp Appl Acarol 35(3):197–213

Palmer WA, Pullen KR (1995) The phytophagous arthropods associated with *Lantana camara*, *L. hirsuta*, *L. urticifolia* and *L. urticoides* (Verbenaceae) in North America. Biol Control 5:54–72

Pavlinec M (1992) [The significance of phytophagous insects on *Galium aparine* (Rubiaceae) and other *Galium* species.] Die Bedeutung von Phytophagen an *Galium aparine* (Rubiaceae) und Anderen *Galium*-Arten. Mitt Dtsch Ges Allg Angew Entomol 8(1–3):169–173

Pearson DE, Callaway RM (2005) Indirect nontarget effects of host-specific biological control agents: Implications for biological control. Biol Control 35(3):288–298

Pemberton RW (2000) Predictable risk to native plants in weed biological control. Oecologia 125:489–494

Petanović R (1990a) Host speciality and morphological variation in *Epitrimerus taraxaci* (Acarida Eriophyoidea). In: Delfosse ES (ed) Proceedings of the VII international symposium on biological control of weeds, 6–11 March 1988, Rome, Italy. Istituto Sperimentale per la Patologia Vegetale, Ministero dell'Agricoltura e delle Foreste, Rome, Italy, p 83

Petanović RU (1990b) Host specificity and morphological variation in *Epitrimerus taraxaci* Liro (Acarida: Eriophyoidea) [in Yugoslavia]. Zast Bilja 41(4):387–394

Petanović R (1996) Eriphyoid mites (Acari: Eriophyoidea) agents of biological control of weeds—basis for application and so far experiences. Zast Bilja 47(4):277–300

Petanović R, Dimitrijević J (1995) [Intraspecific variability of *Vasates euphorbiae* Pet. (Acari: Eriophyoidea) on different subspecies of the host plant]. Intraspecijska varijabilnost *Vasates euphorbiae* Pet. (Acari: Eriophyoidea) na razlicitim podvrstama biljke domacina. Zast. Bilja 46(1):17–28

Petanović R, Kielkiewicz M (2009) Plant-eriophyoid mite interactions: cellular biochemistry and metabolic responses induced in mite-injured plant. Part I. Exp Appl Acarol (in press)

Petanović RU, Stevanović V (1996) Eriophyid mites (Acari: Eriophyoidea) on leafy spurges (*Euphorbia* spp.) (Euphorbiaceae) in Yugoslavia–their potential use in biological control. In: Moran VC, Hoffmann JH (eds) Proceedings of the IX international symposium on biological control of weeds, 19–26 January 1996, Stellenbosch, South Africa, University of Cape Town, p 233

Petanović R, Dobrivojević K, Boczek J, Lazic S (1984) [Eriophyid mites (Eriophyoidea, Acarina) occurring on weed plants in the Belgrade Region]. Eriofidne grinje (Eriophyidae, Acarina) no korovskim biljk ama u okolini Beograda. J Sci Agric Res 44(156):455–460

Petanović R, Boczek J, Stojnić B (1997) Taxonomy and bioecology of eriophyids (Acari: Eriophyoidea) associated with Canada thistle, *Cirsium arvense* (L.) Scop. Acarologia 38(2):181–192

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Piper G (1985) Biological control of weeds in Washington: status report. In: Delfosse ES (ed), Proceedings of the sixth international symposium on biological control of weeds, 19–25 August 1984, Vancouver, Canada. Agriculture Canada, Ottawa, Canada, pp 817–826

Piper GL, Andres LA (1995) Rush skeletonweed. In: Nechols JR, Andres LA, Beardsley JW, Goeden RD, Jackson CG (eds) Biological control in the western United States: accomplishments and benefits of regional research project W-84, 1964–1989. Univ Calif Div Agric Nat Res, Oakland. Publication No. 3361, pp 252–255

Piper GL, Coombs EM, Markin GP, Joley DB (2004) *Eriophyes chondrillae* (=*Aceria chondrillae*). In: Coombs EM, Clark JK, Piper GL, Cofrancesco AF Jr (eds) Biological control of invasive plants in the United States. Oregon State University Press, Oregon, pp 298–300

Rancic D, Paltrinieri S, Tosevski I, Petanović R, Stevanović B, Bertaccini A (2005) First Report of multiple inflorescence disease of *Cirsium arvense* and its association with a 16SrIIB subgroup phytoplasmas in Serbia. Plant Pathol 54:561

Rancic D, Stevanović B, Petanović R, Magud B, Tosevski I, Gassmann A (2006) Anatomical injury induced by the eriophyid mite *Aceria anthocoptes* on the leaves of *Cirsium arvense*. Exp Appl Acarol 38(4):243–253

Rector B, Harizanova GV, Sforza R, Widmer T, Wiedenmann RN (2006) Prospects for biological control of teasels. *Dipsacus* spp., a new target in the United States. Biol Control 31(1):1–14

Redfern M, Shirley P, Bloxham M (2002) British plant galls. Identification of galls on plants and fungi. Field Stud 10:207–531

Reinert JA, Dudeck AE, Snyder GH (1978) Resistance in bermudagrass to the bermudagrass mite. Environ Entomol 7(6):885–888

Reinert JA, Taliaferro CM, McAfee JA (2008) Susceptibility of Bermudagrass (*Cynodon*) varieties to bermduagrass mite (*Eriophyes cynodoniensis*). Acta Hort 783:519–528

Rodgers CA, Baltensperger AA (2004) Registration of 'FMC-6' bermudagrass. Crop Sci 44(6):2262–2263

Rodríguez-Navarro S, Flores-Macías A, Torres-Martínez G (2008) Evaluation of infesting field bindweed (*Convolvulus arvensis* L.) with *Aceria malherbae* Nuzzaci (Acari Eriophyidae) under glasshouse conditions. Int J Acarol 34(2):151–154

Roivainen H (1950) Eriophyid news from Sweden. Acta Entomol Fenn 7:1–51

Rosen D, Huffaker CB (1983) An overview of desired attributes of effective biological control agents, with particular emphasis on mites. In: Hoy MA, Cunningham GL, Knutson L (eds) Biological control of pests by mites. Univ Calif Agric Exp Stn Special Publ 3304:2–11

Rosenthal SS (1983) Current status and potential for biological control of field bindweed, *Convolvulus arvensis*, with *Aceria convolvuli*. In: Hoy MA, Cunningham GL, Knutson L (eds) Biological control of pests by mites. Univ Calif Agric Exp Stn Special Publ 3304: 57–60

Rosenthal SS (1996) *Aceria, Epitrimerus* and *Aculus* species and biological control of weeds. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites–their biology, natural enemies and control, vol 6. Elsevier, Amsterdam, pp 729–739 World Crop Pests

Rosenthal SS, Platts BE (1990) Host specificity of *Aceria* (*Eriophyes*) *malherbae*, [Acari: Eriophyidae], a biological control agent for the weed, *Convolvulus arvensis* [Convolvulaceae]. Entomophaga 35(3):459–463

Sabelis MW (1996) Phytoseiidae. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites–their biology, natural enemies and control, vol 6. Amsterdam, Elsevier, pp 427–456 World Crop Pests

Sabelis MW, Bruin J (1996) Evolutionary ecology: life history patterns, food plant choice and dispersal. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites–their biology, natural enemies and control, vol 6. Elsevier, Amsterdam, pp 329–366 World Crop Pests

Sabelis MW, Lesna I, Aratchige NS (2007) A tritrophic perspective to the biological control of eriophyoid mites. IOBC WPRS Bull 30(5):91–94

Sagliocco JL (2008) Biological Control of English broom with the broom gall mite. Landcare Notes. Department of Primary Industries, Frankston, Australia. http://www.dpi.vic.gov.au/dpi/nreninf.nsf/v/550141D14134082ECA257439001413B4/$file/Biological_Control_of_English_Broom_with_the_Broom_Gall_Mite.pdf. Accessed 12 Jan 2009

Sagliocco JL, Bruzzese E (2004) Biological control of *Rubus fruticosus* agg. (blackberry): is the leaf rust the only option for Australia? In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI international symposium on biological control of weeds, 4-8 May, 2003, CSIRO Entomology, Canberra, Australia, pp 141–144

Sanders RW (2006) Taxonomy of *Lantana* sect. *Lantana* (Verbenaceae): I. Correct application of *Lantana camara* and associated names. Sida, Contributions to Botany. Dallas, Texas. 22:381–421

Sankaran T, Ramaseshiah G (1981) Studies on some natural enemies of puncturevine *Tribulus terrestris* occurring in Karnataka State, India. In: Delfosse ES (ed) Proceedings of the v international symposium on biological control of weeds, 22–29 July 1980, Brisbane, Australia. Commonwealth Scientific and Industrial Research Organization, Australia, pp 153–160

Scott JK (1990) *Tribulus terrestris* L. (Zygophyllaceae) in Southern Africa: an outline of biology and potential biological control agents for Australia. Plant Prot Q 5(3):103–106

Scott JK, Yeoh PB, Knihinicki DK (2008) Redberry mite, *Acalitus essigi* (Hassan) (Acari: Eriophyidae), an additional biological control agent for *Rubus* species (blackberry) (Rosaceae) in Australia. Aust J Entomol 47:261–264

Sheppard AW, Hill R, DeClerck-Floate RA, McClay A, Olckers T, Quimby PC Jr, Zimmermann HG (2003) A global review of risk-benefit-cost analysis for the introduction of classical biological control agents against weeds: a crisis in the making? Biocontrol News and Info 24(4):91N–108N

Sheppard AW, van Klinken RD, Heard TA (2005) Scientific advances in the analysis of direct risks of weed biological control agents to nontarget plants. Biol Control 35(3):215–226

Sheppard AW, Hosking JR, Sagliocco JL, Thomann T, Downey PO, Kwong RM (2006) Biological control of brooms in Australia: an update. 15th Australian Weeds Conference, Papers and proceedings, Adelaide, South Australia, 24–28 September 2006: Managing weeds in a changing climate, pp 573–576

Skoracka A (2008) Reproductive barriers between populations of cereal rust mite *Abacarus hystrix* confirm their host specialization. Evol Ecol 22(5):607–616

Skoracka A, Kuczynski L (2006) Host related differences in the development and reproduction of the cereal rust mite, *Abacarus hystrix* (Acari: Eriophyidae) in Poland. Int J Acarol 32(4):397–405

Skoracka A, Kuczynski L, Magowsky W (2002) Morphological variation in different host populations of *Abacarus hystrix* (Acari: Prostigmata: Eriophyoidea). Exp Appl Acarol 26(3–4):187–193

Skoracka A, Oldfield G, Smith L, Cristofaro M, Ochoa R, Amrine JW Jr. (2009) Host plant specificity and specialization in eriophyoid mites. Exp Appl Acarol (in press)

Smith L (2004) Avoiding and exploiting trophic cascading: Its role in the selection of weed biological control agents. In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI international symposium on biological control of weeds, 4–8 May, 2003, CSIRO Entomology, Canberra, Australia, pp 175–179

Smith L (2005) Host plant specificity and potential impact of *Aceria salsolae* (Acari: Eriophyidae), an agent proposed for biological control of Russian thistle (*Salsola tragus*). Biol Control 34(1):83–92

Smith L (2006) Cause and effect, and how to make a better biocontrol agent. Biocontrol News and Info 27(2):28N–30N

Smith L, de Lillo E, Stoeva A, Cristofaro M, Rector B (2008) Challenges to evaluation of eriophyid mites for biological control of invasive plants. In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier M-S, Vial L (eds) Integrative acarology. Proceedings of the 6th European congress, European association of acarologists, Montpellier, France, pp 312–316

Smith L, Cristofaro M, de Lillo E, Monfreda R, Paolini A (2009) Field assessment of host plant specificity and potential effectiveness of a prospective biological control agent, *Aceria salsolae*, of Russian thistle, *Salsola tragus*. Biol Control 48:237–243

Sobhian R, Andres LA (1978) The response of the skeletonweed gall midge, *Cystiphora schmidti* (Diptera: Cecidomyiidae), and gall mite, *Aceria chondrillae* (Eriophyidae) to North American strains of rush skeletonweed *(Chondrilla juncea)*. Environ Entomol 7:506–508

Sobhian R, Katsoyannos BI, Kashefi J (1989) Host specificity of *Aceria centaureae* (Nalepa), a candidate for biological control of *Centaurea diffusa* De Lamarck. Entomol Hell 7:27–30

Sobhian R, Tunç I, Erler F (1999) Preliminary studies on the biology and host specificity of *Aceria salsolae* de Lillo and Sobhian (Acari, Eriophyidae) and *Lixus salsolae* Becker (Col., Curculionidae), two candidates for biological control of *Salsola kali*. J Appl Entomol 123(4):205–209

Sobhian R, McClay A, Hasan S, Peterschmitt M, Hughes RB (2004) Safety assessment and potential of *Cecidophyes rouhollahi* (Acari, Eriophyidae) for biological control of *Galium spurium* (Rubiaceae) in North America. J Appl Entomol 128(4):258–266

Spies JJ (1984) A cytotaxonomic study of *Lantana camara* (Verbenaceae) from South Africa. S Afri J Bot 3:231–250

Stirton CH (1977) Some thoughts on the polyploid complex *Lantana camara* L. (Verbenaceae). In: Balkema AA (ed) Proceedings of the second national weeds conference of South Africa, Cape Town, pp 321–344

Stirton CH (1999) The naturalized *Lantana camara* L. (Lantaneae-Verbenaceae) complex in KwaZulu-Natal, South Africa: A dilemma for the culton concept. In: Andrews S, Leslie AC, Alexander G (eds) Proceedings of the third international symposium on the taxonomy of cultivated plants, Edinburgh, UK, 20–26 July 1998. Royal Botanic Gardens, Richmond, UK, pp 311–324

Stoeva A, Rector BG, Harizanova V (2008) Host-specificity testing on *Leipothrix dipsacivagus* (Acari: Eriophyidae), a candidate for biological control of Dipsacus spp. In: Julien MH, Sforza R, Bon MC, Evans HC, Hatcher PE, Hinz HL, Rector BG (eds) Proceedings of the XII international symposium on biological control of weeds. April 22–27, 2007, La Grande Motte, France, CAB International Wallingford, UK, pp 328–332

Supkoff DM, Joley DB, Marois JJ (1988) Effect of introduced biological control organisms on the density of *Chondrilla juncea* in California. J Appl Ecol 25(3):1089–1095

Sutherst RW, Maywald GF, Bottomley W, Bourne A (2004) CLIMEX v2. Hearne Scientific Software Pty. Ltd, Melbourne, Australia

Tzanetakis IE, Gergerich RC, Martin RR (2006) A new Ilarvirus found in rose. Plant Pathol 55(4):568

Urban A, Day M, Ellison C, den Breeÿen A (2001a) Global lantana biocontrol initiative. Biocontrol News and Info 22:56N–58N

Urban AJ, Mpedi PF, Neser S, Craemer C (2001b) Potential of the flower gall mite, *Aceria lantanae* (Cook) (Acari: Eriophyidae), for biocontrol of the noxious weed, *Lantana camara* L. (Verbenaceae). In: Olckers T, Brothers DJ (eds) Proceedings of the 13th entomological congress organised by the entomological society of Southern Africa, Hatfield, South Africa, pp 67–68

Urban AJ, Simelane DO, Mpedi PF, Day MD, Neser S, Craemer C (2004) Varietal resistance in lantana: fact or fiction? In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings

of the XI international symposium on biological control of weeds, 4–8 May, 2003, CSIRO Entomology, Canberra, Australia, p 232

van Driesche R, Hoddle M, Center T (2008) Control of pests and weeds by natural enemies. Wiley-Blackwell, Malden, Massachusetts

van Loan AN, Meeke JR, Minno MC (2002) Cogon Grass. In: van Driesche R, Lyon S, Blossey B, Hoddle M, Reardon R (eds) Biological control of invasive plants in the eastern United States, USDA Forest Service Publication FHTET-2002-04, pp 353–364

Vidović B, Petanović R, Stanisavljević LJ (2008) Morphological variation of *Aceria* spp. (Acari: Eriophyoidea) inhabiting *Cirsium* species (Asteraceae) in Serbia. In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier M-S, Vial L (eds) Integrative acarology. Proceedings of the 6th European congress, European association of acarologists, Montpellier, France, 21–25 July 2008, pp 331–339

Volkov OG, Izhevskii GG (1996) Tetrapod gall mite as a promising phytophage against repent stagger-bush. Zashchita i Karantin Rastenii 6:32–33

Walter DE (1999) Cryptic inhabitants of a noxious weed: Mites (Arachnida: Acari) on *Lantana camara* L. invading forests in Queensland. Aust J Entomol 38:197–200

Waterhouse DF (1994) 4.4 *Chromolaena odorata* (L.) R. M. King and H. Robinson. In: Biological control of weeds: Southeast Asian prospects. Canberra, ACIAR Monograph No. 26, pp 34–53

Whitson TD, Burrill LC, Dewey SA, Cudney DW, Nelson BE, Lee RD, Parker R (eds) (2000) Weeds of the West. 9th edn. The Western Society of Weed Science, Newark, California

Willis AJ, Berentson PR, Ash JE (2003) Impacts of a weed biocontrol agent on recovery from water stress in a target and a non-target *Hypericum* species. J Appl Ecol 40(2):320–333

Zachariades C, Day M, Muniappan R, Reddy GVP (2009) *Chromolaena odorata* (L.) King and Robinson (Asteraceae). In: Muniappan R, Reddy GVP, Raman A (eds) Biological control of tropical weeds using arthropods. Cambridge University Press, Cambridge, pp 130–160

Zalucki MP, Day MD, Playford J (2007) Will biological control of *Lantana camara* ever succeed? Patterns, processes & prospects. Biol Control 42(3):251–261

Zhao S, Amrine JW Jr (1997) Investigation of snowborne mites (Acari) and relevancy to dispersal. Int J Acarol 23(3):209–213

The impact of eriophyoids on crops: recent issues on *Aculus schlechtendali*, *Calepitrimerus vitis* and *Aculops lycopersici*

C. Duso · M. Castagnoli · S. Simoni · G. Angeli

Abstract The nature of the damage caused by eriophyoid mites and the assessment of yield losses still require detailed studies if appropriate control and risk mitigation strategies are to be planned. The economic importance of eriophyoid mites is increasing worldwide and a lot of species have reached a permanent pest status in certain crops, while others represent a quarantine threat for several countries. Due to their relevant role in Europe and elsewhere, three eriophyoid mites that have been frequently reported in recent research, are here considered as case studies: two of them (the apple rust mite, *Aculus schlechtendali*, and the grape rust mite, *Calepitrimerus vitis*) colonise temperate fruits, while one (the tomato russet mite, *Aculops lycopersici*) affects vegetables. The damage assessment related to the apple rust mite has been evaluated on different apple varieties with implications for pest control. Some factors affecting the spread and economic importance of the grape rust mite have been identified. The complexity and difficulty in controlling the tomato russet mite by chemicals enhances the interest in biological control agents. Considerations on interactions between eriophyoids and host plants (e.g. resistance, varietal susceptibility), on pest management regimes (e.g. impact of fungicides, resistance to acaricides, perspectives on biological control) are presented.

Keywords Apple rust mite · Grape rust mite · Tomato russet mite · Economic importance · Control

C. Duso (✉)
Department of Environmental Agronomy and Crop Science, University of Padua,
Viale dell'Università 16, 32050 Legnaro, Padova, Italy
e-mail: carlo.duso@unipd.it

M. Castagnoli · S. Simoni
CRA-ABP Agricultural Research Council, Research Center for Agrobiology and Pedology,
Via Lanciola 12/a, 50125 Florence, Italy

G. Angeli
FEM, S. Michele all'Adige, Via Mach 1, 38010 Trento, Italy

Introduction

Eriophyoid mites (Acari: Eriophyoidea) have been recognized as important pests in agriculture and forestry all over the world (Lindquist et al. 1996). A number of eriophyoid species are considered to be permanent pests on some crops, while others are known to be a quarantine threat for several countries. Nevertheless, several eriophyoid species seldom attain significant populations and thus their economic importance is a matter of discussion. Knowledge of the economic impact of eriophyoids on crop yields is a fundamental requirement for the improvement of IPM. However, interactions between most eriophyoids and the respective host plants have been poorly investigated. The small size and the behaviour of eriophyoids are frequently implied in misdiagnoses with implications for yield losses.

Two books have given a fundamental contribution to the knowledge of Eriophyoidea, i.e. those by Jeppson et al. (1975) and Lindquist et al. (1996). Since the latter, new findings involving a number of species which are well-known for their economic importance, as well as emerging pests, have been published. We have selected three species that represent a permanent problem for horticultural crops and vineyards, i.e. the apple rust mite (ARM) *Aculus schlechtendali* (Nalepa), the grape rust mite (GRM) *Calepitrimerus vitis* (Nalepa) and the tomato russet mite (TRM) *Aculops lycopersici* (Tryon). Much recent research has studied these species: from 1997 to the present, 75 contributions examine ARM, 55 examine TRM and 44 examine GRM (CAB Abstracts). These numbers increase by about 50% if minor publications are considered (de Lillo, pers. comm.). The most significant findings related to these pests are discussed here. New trends and perspectives in research are suggested.

Apple rust mite, *Aculus schlechtendali*

Plant-mite relationships and damage

Apple rust mite is a vagrant eriophyoid mite which damages apples in Europe and North-America. In recent decades, it has also been recorded in China (Li and Cai 1996). ARMs feed on the flowers, fruits and leaves of apple. Rust mites can only penetrate epidermal cells with their stylets, and thus tissue injury and plant reactions caused by ARM and spider mites are expected to be quite different. Apple leaves damaged by ARM may show rusty under surfaces, roll up longitudinally and sometimes fall prematurely (Jeppson et al. 1975). Early mite feeding on developing fruitlets damages epidermal layer cells, inducing russet on fruits. Russet can be observed typically around the calyx but severe infestations can cause russet and cracking on the cheek. The colour of fruits may be reduced on certain cultivars. The severity of symptoms depends on the mite population size, variety and the age of plants (Ciampolini et al. 1976; Easterbrook and Fuller 1986).

Easterbrook (1996) analysed factors that have changed ARM's pest status from the 1960s onwards (e.g. replacement of fungicides having acaricidal properties, use of non selective insecticides towards predatory mites, ARM resistance to OPs and pyrethroids). He summarised the most significant data on the biology and the behaviour of ARM and stressed that the effects exerted by this pest on tree physiology and growth parameters were poorly known despite the fact that action thresholds must be based on a precise knowledge of these effects. At that time, the effect of ARM on photosynthesis rate was discussed in two papers. Kozlowski (1980) reported that transpiration increased and photosynthesis

decreased when ARM population densities exceed values of ~ 50 mites per cm^2. Solhoy et al. (1991) also mentioned a decrease in photosynthesis when apple leaves were heavily infested in summer. The implications of these effects for apple yields were not clear. Some years after the Easterbrook review (1996), the impact of ARM on net carbon dioxide exchange, transpiration rate, and leaf colour was studied in Switzerland (Spieser et al. 1998, 1999). Young apple plants of two cultivars, i.e. Jonagold and Golden Delicious, were infested with rust mites. Later, some of these plants were treated with bromopropylate to compare the impact of two different mite population levels on gas exchange, leaf colour, and leaf tissue features. The development of mite populations on the two apple varieties was similar and population densities on untreated plants were estimated to be around 4–5,000 mites/leaf in mid-June. These population levels persisted until mid-July when a dramatic decline was observed. Low populations occurred on treated plants. Changes in leaf colour (due to cell damage and oxidation processes within the cell) were detected using a chromameter. Infested leaves became an intense brown, and leaf colour change was associated with mite population increases. Gas exchange alterations were measured by using an infrared gas analyzer system. The increase in leaf brownness affected the net CO_2 exchange (e.g. a reduction of 65% in gas exchange was found for the most infested leaves). Similar effects were seen for transpiration rates. The analysis of leaf tissue damage by cryoscanning electron microscopy and light microscopy showed that rust mites cause multiple puncture wounds on epidermal cells. In severely infested leaves, the stomata were partially open and the guard cells had lost turgor. A desiccation of epidermal cells and of spongy parenchyma cells was reported for these leaves. Similar effects were noticed by Kozowski and Zielinska (1997) on other cultivars. It has been recognized that rust mites cannot feed on photosynthetically active mesophyll. However, ARM may affect photosynthesis indirectly: its damage to the leaf epidermis induces negative effects on leaf mesophyll. The nature of the latter effects requires additional studies. A different susceptibility of cultivars was observed as the effects of ARM were more severe on Jonagold than on Golden Delicious. The results of this study were obtained with high, artificially induced ARM population levels, uncommon in field conditions. In other investigations, where population densities were much lower (<160 mites per leaf), the effects of ARM on photosynthesis proved to be less severe (Easterbrook and Palmer 1996). Additional studies were conducted in insecticide-treated and untreated apple (cv. Red Top) plots in northern Italy. Net photosynthesis and transpiration values were not different between the two treatments despite differences in the population size (Ioriatti et al. 1996). Therefore, the real impact of ARM populations on photosynthesis in field conditions requires additional studies.

Since a number of environmental and cultural factors can influence the impact of ARM on apple crops, there is no agreement on ARM levels which cause economic damage to the apple yield (e.g. Hoyt 1969; Croft 1975; Hohn and Hopli 1990; Easterbrook 1996).

In spring, ARM deutogynes and their progeny can damage developing primary spur leaves of the blossom clusters with potential implications for fruit development. Easterbrook and Palmer (1996) conducted experiments to investigate whether this damage can cause a reduction in fruit set. A number of experiments were carried out on three apple cultivars (e.g. Bramley's Seedling, Crispin and Cox's Orange Pippin). The numbers of fruit set on individual blossom clusters or trees infested with large numbers of ARM, and on those infested with low numbers of mites (due to the use of an acaricide or a glue barrier) were compared. Mite feeding on primary spur leaves of blossom clusters did not affect fruit set in most trials, except in one trial where a reduction in initial fruit set was associated with a population of more than 200 mites per leaf. The time of mite feeding seems to be

crucial for the effects of rust mites on final fruit set. The Bramley cultivar was more susceptible to ARM than the remaining cultivars, but fruit set was not affected in this case either. This study showed that densities of at least 100 rust mites per leaf in spring can be tolerated without consequences for fruit set. A lower threshold could be applied for cultivars susceptible to fruit russeting.

Spieser et al. (1999) reported that rust mite infestation caused a decrease in the fresh weight of fruits of the Jonagold cultivar, but this did not occur for Golden Delicious fruits. The dry weight of fruits of both cultivars was negatively affected by infestation. A lower soluble sugar content was also detected in fruits of both cultivars collected from infested trees. The colour intensity of fruit skins of Jonagold was reduced but this effect was not observed on Golden Delicious fruits. After 2 years of infestation, infested Jonagold trees had 10% fewer flower buds and stem growth was reduced in one growing season.

The latter study stressed cultivar susceptibility as a significant factor affecting plant protection against ARM. Golden Delicious appeared to be less susceptible to the mite infestation than Jonagold. A contribution from northern Italy (Trentino region) has shown that ARM populations can also significantly affect Golden Delicious yield parameters (Angeli et al. 2007). The effects of three mite densities on yield parameters were evaluated. In the first experimental season, rust mite population peaked in July and the three population levels were estimated to reach 2,399, 14,523, and 31,750 mite-days/leaf. The two highest density levels reduced the size, weight and colour of fruits significantly. Fruit russeting was not affected by rust mites. Easterbrook and Fuller (1986) found a significant correlation between the number of ARM on fruitlets and the amount of apple russet at harvest. The formation of calyx-end and cheek russet on fruits occurred when mites fed on the developing fruitlets shortly after blossoming (1–3 weeks). The lack of russeting on fruits observed in the investigation carried out in Trentino may be explained by the time of infestation: in spring, the fruitlets were colonized by relatively low populations and the population size started to increase more than 1 month after petal fall. Soluble solids and malic acid content decreased with higher mite levels but differences among treatments were not significant. One year later, densities of 2,592 and 3,680 mite-days per leaf affected fruit size and weight, while fruit colour and russeting were not influenced.

This study shows that Golden Delicious may be susceptible to ARM, and that consequences on fruit size and weight can be significant when moderate to high populations occur in summer. It should be stressed that the most important problem from the economic point of view was the reduction in fruit size from the optimal values required by the fresh market.

ARM outbreaks are recorded especially in European regions where susceptible cultivars are cultivated. In Northern Ireland, rust mites frequently exceed action thresholds for treatment, especially in orchards made up of the Bramley cultivar which is particularly susceptible to this mite (Cuthbertson and Murchie 2006). In Trentino, Italy, mite damage is lower on Red Delicious orchards than on Golden Delicious. Up to 2 acaricide treatments are applied per year, usually in the post-floral phase, on Golden Delicious and to a lesser extent in Jonagold and Fuji orchards (Ioriatti et al. 1996; Angeli et al. 2008). In North America there are few reports of damage to fruits by ARM. This apparent contradiction may be attributed to a low susceptibility to ARM of apple cultivars commonly grown in the USA. It is not clear if commercial requirements by the US fresh market can influence this situation. Because of the many factors involved, action thresholds to control ARM populations are a matter of discussion. In England, Cross and Berrie suggested an action threshold of 5 mites/leaf but Cuthbertson and Murchie (2006) found that pest densities exceeding these thresholds did not cause economic damage. In Northern Italy, it has been

recognized that damage occurs at mite densities higher than 200 motile forms per leaf but definite threshold levels have not been suggested (Ioriatti et al. 1997).

Control

Chemical control proved to be successful when abamectin, spirodiclofen and lambda-cyhalothrin were used (Raudonis et al. 2007; Angeli et al. 2008). Mineral oil applications can also produce some effects in controlling this pest (Fernandez et al. 2006). Nevertheless, ARM is considered an excellent candidate for biological control in various countries since macropredators and predatory mites can reduce their populations to non-damaging levels. Among the former, predatory bugs (anthocorids and mirids) and lacewings (e.g. *Chrysoperla carnea* Stephens) seem to be the most active (Khan et al. 2004; Chouinard et al. 2006). Macropredators and predatory mites can co-occur in the same orchard but the outcome of these interactions in terms of rust mite control is unclear (Khan et al. 2004).

The impact of predatory mite species belonging to the Phytoseiidae, Stigmaeidae and Anystidae families proved to be significant. The Tydeidae are widely distributed in apple orchards but their role as rust mites predators has not been ascertained (Gerson et al. 2003). In contrast, the impact of phytoseiids has been widely studied. In Europe, *Typhlodromus pyri* Scheuten, *Amblyseius andersoni* (Chant) and *Euseius finlandicus* (Oudemans) play a major role in controlling ARM populations to below economic levels (Easterbrook 1996; Fitzgerald et al. 2003; Duso and Pasini 2003). *Typhlodromus pyri* is also considered an effective predatory mite in Canada (Walde et al. 1997; Hardman et al. 2003). In eastern USA, a number of phytoseiids, e.g. *Galendromus flumenis* (Chant), *G. occidentalis* (Nesbitt), *T. caudiglans* Schuster and *Metaseiulus citri* (Garman and McGregor) can prey upon ARM in untreated orchards (Croft and Luh 2004). However, in commercial orchards this diversity declines and pesticide-resistant predatory mites (e.g. *T. pyri*) tend to dominate (Croft and Slone 1998). Marshall et al. (2001) successfully released pesticide-resistant strains of *T. pyri* in Canadian apple orchards and obtained good results in the control of phytophagous mites, including ARM. Interactions between phytoseiids and ARM populations may be mediated by cultivar features. ARM population sizes can vary greatly on different cultivars and, at the same time, predatory mites can exhibit some preferences for certain cultivars, typically because of their leaf under surface features (Duso et al. 2003; Duso and Pasini 2003).

A number of authors have stressed the role of ARM as an alternative prey for phytoseiids when tetranychids are scarce (Easterbrook 1996; Duso and Pasini 2003; Duso et al. 2003; Hill and Foster 1998). However, this role will depend on the susceptibility of cultivars. The reduction in pesticide use (e.g. by using sex pheromones) can improve predatory mite performance. In experiments conducted in Japanese apple orchards where sex pheromones were applied, phytoseiid numbers increased by feeding on ARM and suppressed tetranychid populations (Funayama 1999).

Zetzellia mali Ewing (Acari: Stigmaeidae) is a well-known predator of rust mites in Europe as well as in North-America but its importance is a matter of debate. *Zetzellia mali* seems to prefer ARM over the European red mite (ERM) *Panonychus ulmi* (Koch) but laboratory choice studies showed that prey preference depends on the relative density of the prey (Walde et al. 1995). In Canada, the impact of *Z. mali* on phytophagous mites was studied in an experimental apple orchard that comprised plots treated with reduced rates of

cypermethrin, or not treated with insecticides or acaricides. *Zetzellia mali* was more abundant in the pyrethroid-sprayed plots than in the control plots. The development of resistance to pyrethroids by *Z. mali* as well as the reduced competition with phytoseiids (affected by pyrethroids) were suggested as factors involved. *Zetzellia mali* proved to be effective in controlling ERM and ARM populations (Villanueva and Harmsen 1998). Phytoseiid and stigmaeids can interact in controlling tetranychid and rust mite populations. Slone and Croft (2001) used Yule's V association index to measure interspecific associations for a number of mite species occurring in an experimental orchard. Predator-predator associations were strong and in particular, negative associations of *T. pyri* with other predators (e.g. *Z. mali*) were found. Walde et al. (1997) analysed direct and indirect interactions affecting the population dynamics of ARM in Canadian apple orchards inhabited by phytoseiids and stigmaeids. In these conditions *T. pyri* played a major role in reducing ARM abundance with respect to *Z. mali*. When both predators co-occurred, *T. pyri* acted earlier in the season. Predation by *Z. mali* was influenced by cultivar and nitrogen levels. Croft and McRae (1993) found that ERM and ARM were effectively controlled where *Z. mali* occurred alone at high levels or with *T. pyri*, despite competition between the two predators. Hardman et al. (1995) also analysed interactions between *T. pyri* and *Z. mali* in an apple orchard treated with different pesticides and suggested implications for IPM.

The prostigmatid mite *Anystis baccarum* (L.) (Acari: Anystidae) is a common predatory mite in Irish as well in Canadian apple orchards. *A. baccarum* is a generalist predator that completes two generations per year; its densities peaking in spring-early summer and in late summer (Cuthbertson and Murchie 2003, 2004). Evidence for the role of *A. baccarum* as a predator of rust mites was suggested in an experimental orchard. The combination of insecticide treatments and sticky traps to exclude *A. baccarum* from apple branches caused a significant increase in ARM in certain seasons (Cuthbertson et al. 2003). This effect was seen only with relatively high ARM densities. Since there were no differences in other trials, relationships between *A. baccarum* and rust mites require additional studies.

The first evidence of interactions between ARM and tarsonemids was reported in Ontario, Canada. In particular the tarsonemid, *Dendroptus* near *suskii*, contributed partially to the summer decrease of ARM (Villanueva and Harmsen 1996).

Knowledge on the effects of insecticides and fungicides frequently used to control major apple pests on predatory mite populations is a fundamental requirement for IPM. Pesticides detrimental to predatory mites can cause phytophagous mite outbreaks (Funayama 1999; Hardman et al. 2003). ARM outbreaks were experimentally induced by using pyrethroids that are detrimental to predatory mites (Croft and Slone 1998). The use of mancozeb was associated with a reduction in *A. baccarum* densities and an increase in ARM numbers compared to other treatments (Cuthbertson and Murchie 2003). Winter-wash treatments and certain insecticides can also affect the balance between predatory mites and ARM with positive effects on pest numbers (Cuthbertson and Murchie 2006b). Extensive studies on the susceptibility of *A. baccarum* to pesticides used in apple orchards have been conducted in Quebec, Canada. Laurin and Bostanian (2007a) confirmed the negative effect of mancozeb compared with other fungicides. At the same time Laurin and Bostanian (2007b) investigated the impact of a number of insecticides on *A. baccarum*. A-cyhalothrin, phosmet and carbaryl were more toxic than other insecticides to the predatory mite.

Some fungicides can strongly reduce rust mite populations and are not detrimental to predatory mites. Their use is encouraged in IPM programmes (De Maeyer et al. 1993).

Grape rust mite, *Calepitrimerus vitis*

Plant-mite relationships and damage

The impact of the GRM in European vineyards has been investigated since the 1960s (Duso and de Lillo 1996). More recently, this pest has been detected in Brazil (Reis et al. 1998) and has proved to be an emerging pest in Australia (Carew et al. 2004; Bernard et al. 2005) and the USA (Prischmann and James 2005; Prischmann et al. 2005).

GRM feeding may prove to be associated with several symptoms: death of the growth point of buds, stunted shoot growth and shortened shoot internodes, development of latent buds and lateral shoots, leaf and cluster deformation, reduced cluster size and flower drop (Duso and de Lillo 1996). Some of these symptoms can be associated with the occurrence of other pests, fungal diseases, viruses and microelement deficiency. Misdiagnoses of rust mite infestations have allowed the mites to cause severe yield losses in various countries.

Recently, the so-called 'Restricted Spring Growth' (RSG) syndrome has been detected in a number of Australian vineyards. Leaf and shoot distortions and retarded shoot growth were observed in early spring. Bernard et al. (2005) showed that these symptoms were associated with high numbers of overwintered GRM females. Severe leaf distortion was associated with more than 400 GRM per spur, while densities higher than 1,000 GRM per spur retarded shoot growth. Shoot length reduction depended on the cultivar (from 27.1 to 47.2%) and was still evident at flowering. The migration of deutogynes from winter shelters to emerging green tissues was monitored using a trapping system. Treatments applied to control GRM populations did not completely prevent the RSG syndrome since a number of unburst buds were associated with populations of the bud strain of *Colomerus vitis* (Pagenstecher). Bernard et al. (2005) also evaluated the effect of GRM on vine fruitfulness, and yield parameters at fruit set but implications of infestation on yields were difficult to assess.

A similar alteration, the so-called Short Shoot Syndrome (SSS), caused severe crop losses especially due to bunch necrosis during early season in the Pacific Northwest of the United States. Additional symptoms were represented by malformed leaves, short and angled shoots in spring, scar tissue and bronzed leaves in summer. SSS was associated with high GRM population densities (Walton et al. 2007). Before bud break, no evidence of damage from rust mites was found inside undeveloped buds while damage became evident at sprouting. Severe crop losses were recorded at harvest (e.g. about 24% in some vineyards).

Factors promoting GRM outbreaks have been investigated in European countries and elsewhere. In Germany, the increase in summer temperatures has been positively related with infestations occurring in the subsequent year (Kast et al. 2004). In these conditions, the pest can develop several generations and probably produce a large stock of overwintering females. Similar effects have been suggested to explain outbreaks recorded in the Trentino region (northern Italy) where the pest was not previously considered as damaging (Varner et al. 2006). The impact of unusual climatic conditions on the balance between predatory mites (e.g. phytoseiids) and rust mites may be an additional factor involved in GRM outbreaks. Sengonca et al. (2003) evaluated the prey consumption, longevity and reproduction of *T. pyri* on leaf discs and in Plexiglas cells at constant temperatures of 25 and 30°C. The European red mite was provided as prey. Prey consumption by *T. pyri* decreased significantly when the temperature increased from 25 to 30°C. Nymphal development, longevity of females and their reproduction decreased significantly with increasing temperatures. It should be stressed that *T. pyri* is the most common predatory mite in vineyards in Germany and in Trentino.

Pesticide use can be a major factor affecting rust mite outbreaks. These mites could have developed some resistance to common fungicides but this event has been poorly investigated. At the same time, a number of fungicides and insecticides commonly used in viticulture can produce lethal and sub-lethal effects to predators of GRM. The role of sulphur in this context seems to be crucial (Bernard et al. 2005; Walton et al. 2007).

Population dynamics and plant colonization

Little is known about the colonization of vineyards by GRM. In Europe, GRM is an important pest in 1–2 year-old vineyards and thus the role of nurseries in mite dispersal is a matter of discussion (Zandigiacomo and Frausin 1998). More recently, Duffner et al. (2001) showed that wind, rain and human activity are major factors in mite dispersal. The role of air currents in long-distance dispersal was suggested by the high number of Eriophyoidea (32.1% being GRM) trapped in a wind chamber during summer. Adults of GRM were washed away from leaves by intense rain but the importance of rain in mite colonization is not clear. Cultural practices were also involved in mite dispersal: a surprising number of GRM were detected on the clothes and hands of people working in vineyards. It should be stressed that these factors also affected the dispersal of the predatory mite *T. pyri*.

New findings on the phenology and the behaviour of GRM in Europe have been published in the last decade. A detailed study on the population dynamics of GRM in Spanish vineyards (Perez-Moreno and Moraza 1998) confirmed some trends which had emerged in previous papers (Duso and de Lillo 1996) and added new information. In vineyards located in the Rioja region, the mite population increased rapidly at the beginning of summer reaching the highest levels in August or early September. The appearance of deutogynes in summer depended on environmental conditions and infestation levels. The sex ratio was relatively high and was most likely affected by population size. High population densities occurred with high temperatures and low relative humidity. Overwintered mites were more abundant on the central buds of the canes. Spur pruning performed in this Spanish area dramatically reduced mite numbers but this species was able to build up large populations anyway.

The migration of deutogynes to their hibernation shelters was investigated in Hungary (Gabi and Meszaros (2000; 2001). Most of these forms moved to the buds in September and this information could be used to control the mite. The authors also described a washing technique to estimate the population of GRM and to make mite sampling easier in summer or winter.

Castagnoli et al. (1997) compared mite diversity and abundance in two vineyards composed of two cultivars having hairy (Canaiolo) or slightly hairy (Sangiovese) leaf under surfaces. They found significant variations among mite groups in the two cultivars and reported GRM as being largely dominant among phytophagous mites occurring on Canaiolo. A higher number of predatory mite species occurred on this cultivar and among phytoseiids, *Typhlodromus exhilaratus* Ragusa being the most frequent. Different colonization patterns by GRM in vineyards constituted by different cultivars were also noticed by Duso and Vettorazzo (1999).

In Australia, Bernard et al. (2005) reported severe symptoms in cultivars (e.g. Cabernet Sauvignon) that require relatively high temperatures for shoot development in early spring. Feeding damage is lower for cultivars characterized by fast growing shoots as GRM numbers per area of green tissue decrease rapidly. Cold conditions in spring are often associated with more damage since the cold retards shoot growth.

Control

An advanced knowledge of the behaviour of GRM will increase the effectiveness of control measures. Long-term experience in South-European vineyards shows that chemical control is required in young vineyards. On the other hand, rust mite antagonists reach low population levels in these vineyards because the natural colonization process takes some time and overwintering sites are not adequate. When rust mite antagonists can build stable populations GRM infestations are not frequent (Duso and Vettorazzo 1999).

Among rust mite antagonists, phytoseiids are considered to be the most important. The impact of *T. pyri* has been recognized in various parts of Europe (Perez-Moreno and Moraza 1997; Duso and Vettorazzo 1999; Wegner-Kib 2003). In central Italy (Tuscany) *T. exhilaratus* was involved in interactions with GRM. The nature of these relationships requires more in-depth studies. *Euseius victoriensis* (Womersley) and *Typhlodromus doreenae* (Schicha) were reported associated with GRM in Australia (Bernard et al. 2005). Phytoseiids and stigmaeids (e.g. *Amblyseius andersoni* and *Z. mali*) may exert a certain role in controlling rust mite populations (e.g. Duso and Vettorazzo, 1999).

Conservation biological control tactics have an important role in preventing rust mite outbreaks. Phytoseiid colonization can take a long time and the role of natural vegetation in this process is controversial (Tixier et al. 2006). Releasing phytoseiids can represent a real option: predatory mites can be released in late winter or during the early growing season. The release of *T. pyri* or of *Kampimodromus aberrans* (Oudemans) has proved to be an effective tool in reducing GRM populations to low levels. In particular, *K. aberrans* releases significantly reduced the densities of phytophagous mites and of native predators (Duso and Vettorazzo 1999).

Chemical control has largely been based on the use of bromopropylate but this acaricide has recently been forbidden in Europe. Other acaricides (e.g. spirodiclofen, fenpyroximate, fenazaquin) seem to be effective (De Lillo et al. 2004, Bernard et al. 2005). The use of certain fungicides (e.g. sulphur and dichlofluanide) can exert some control over GRM (Wegner-Kib 2003, De Lillo et al. 2004) but it should be stressed that their effects on predatory mites must also be taken into account. Moreover, the effects of some fungicides are affected by temperature. The rates of sulphur suggested in Germany and France to control GRM (Goebel et al. 2001; Wegner-Kib 2003) can be phytotoxic in the conditions of southern Europe. Since GRM is a typical pesticide-induced pest, the knowledge of pesticide side-effects towards predators of GRM is a clear prerequisite in developing IPM in vineyards. Present rules in pesticide registration in EC and elsewhere are causing a marked reduction of pesticides available for grape protection in favour of molecules which are relatively safe for human health and the environment. This selection should determine a reduction in pesticides characterised by detrimental effects towards beneficials with positive implications for the control of eriophyoids occurring in vineyards.

Tomato russet mite, *Aculops lycopersici*

Host distribution and biology

Tomato russet mite can be considered an exception to the general statement that eriophyoid mites are highly specialised plant parasites (Lindquist and Oldfield 1996). TRM is cosmopolitan in distribution and widespread in almost all areas where solanaceous crops are grown (Jeppson et al. 1975). The exception is in southern and northern latitudes below and

above 60 degrees, respectively (Perring and Farrar 1986; Perring 1996). This eriophyoid is one of the most common key pests on the commercially grown tomato, *Lycopersicon esculentum* Miller, the most important vegetable in the European Union, and, on a worldwide scale, the key pest on this cultivated plant. However, in addition to tomato, the TRM host range includes, tomatillo, potato, eggplant, poha (cape gooseberry), wild blackcurrant, popolo, wild gooseberry, blackberry, tobacco, bell pepper, cherry pepper, Tolguacha, eggplant, Jerusalem cherry, hairy nightshade, black nightshade, horse nettle, morning glory, Jimson weed, Chinese thorn apple, petunia, nightshade, small flowered nightshade, amethyst, field bindweed, and Brinjal (Perring 1996). Unlike strictly monophagous eriophyoid species, TRM can inhabit a high number of wild hosts and thus competition for food between individuals is reduced.

Due to the typical problems characterizing the biological study of the majority of eriophyoid species (e.g. the difficulty of detection on plants) it is crucial to further the knowledge of: (a) TRM bioecological data useful to improve control strategies; (b) the different specialized intimate interactions that TRM establishes with different plants and/or different areas of the same plant; (c) the strength of the biochemical and physiological mechanisms/steps determining the intensity of closeness/dependence with the host plant.

The acquisition of data on TRM biology has often been ascribable to a wide range of climatic or laboratory conditions. The TRM has several generations per growing season and its population can double in less than 3 days at 25°C. However, it seems able to tolerate considerable variations in temperature and relative humidity (Fischer and Mourrut-Salesse 2005). The majority of the fundamental studies on TRM biology are some tens of years old. Bailey and Keifer (1943) observed that at 21°C, TRM females laid about 15 eggs in their lifetime. Newly emerged females began laying eggs after 2 days. Eggs hatched in 2 days at room temperature, the larval stage was only 1 day, and the nymphal stage lasted 2 days. Rice and Strong (1962) reported that the life cycle was 6.5 days under optimal conditions (21°C and 30% RH) and, with very high temperatures (32°C), low humidity levels are necessary for survival; depending on the environmental conditions, TRM females laid 10–53 eggs and female longevity was 47.5 days at 21°C and 90% RH. On the whole, the best conditions for population increases were temperatures near 26.7°C and 30% RH. Abou-Awad (1979) observed that at experimental conditions of 25°C and 70% RH, males developed in 4.62 days and females in an average of 5.15 days.

TRM-tomato relationships

The biological responses of TRM and the damage levels induced can be significantly affected by the whole set of mechanisms which are generated by the association TRM/plant: the TRM can kill tomato plants by feeding and reproducing very rapidly on plants. Royalty and Perring (1988) suggest that, as TRM population density increases, the feeding activity of each individual mite accelerates too. This "solanum stimulation" (Bailey and Keifer 1943) is also exhibited on tomatillos, potato, eggplant, black nightshade, and horse nettle (Rice and Strong 1962). TRM injury to tomato plants is caused by feeding and the eriophyoid usually begins at the base of the tomato plant, and eventually works its way upwards (Kay 1986). TRM feeds on all green surfaces of the host plant. The greatest concentration of mites is normally the area just ahead of the damaged area.

On the whole, the distribution, intrinsic dispersal and survival abilities of TRM make it seriously noxious to the tomato by causing frequent drawbacks. The sure and timely detection of damage, crucial to address control, is not always possible. The early symptoms are characterized by silvering of the under surface of lower leaves, after which the lower

parts of the stems lose hairs, become dusty brown in colour and sometimes develop small cracks. Mistakes in identifying TRM damage symptoms can happen, since they are similar to those of broad mite and thrips (Royalty and Perring 1988). In addition, TRM usually exhibits a patchy distribution in the tomato field and the level of group aggregation mainly depends on its habits and environmental factors (Hirata et al. 2007). Consequently, the detection and monitoring of TRM is often problematic: critical mite densities may be undetected or underestimated. A theoretical sampling number for different densities of TRMs has been proposed according to the theoretical sampling formula of Iwao-Kuno (Hirata et al. 2007).

Furthermore, the considerably wide interval of climatic conditions allowing the pest's growth in tomato greenhouses generally increases the density of the eriophyoid, while high temperatures and low relative humidity levels are suboptimal for natural enemies (Drukker et al. 2000).

Recently, to further knowledge on TRM biological responses and to better evaluate new control strategies, much research has addressed to what extent the pest–plant association, in particular on tomato, could affect eriophyoid fitness. Research on the tomato/TRM system was developed mainly to determine how host properties could affect the dynamics of the pest and how the different levels of resistance were related to different tomato varieties. These studies on the relationship between the leaf physical and chemical characteristics of tomato varieties and TRMs frequently highlighted notable discrepancies in their survival rates, developmental duration, egg production and other parameters of the experimental populations of the mite on different tomato lines (MeiYu et al. 2008). The different resistance of tomato cultivars to several polyphagous arthropods and to TRM has been related to the presence of high contents of 2-tridecanone and other methyl ketones in the leaves (Gonçalves et al. 1998). The distribution of TRM varies according to the different levels of tridecan-2-one and undecan-2-one, the density and trichome type and the size of leaves on *L. esculentum* and *L. hirsutum* Dunal (Leite et al. 1999). Furthermore, the behaviour of natural enemies is particularly affected and hindered by tomato trichomes, making the hosts more resistant to the antagonists than to the pests (Simmons and Gurr 2005); toxic secondary metabolites (additively in plants and prey) can further intoxicate predators (Roddick 1974). This evidence leads to a further genetic improvement of tomato in terms of increased levels of mite resistance.

Control and perspectives for biological control

The most infested plants are often those subjected to water stress (Gispert et al. 1989); intense attacks in the pre-harvest period are the most injurious in terms of crop losses (Zalom et al. 1986). Prophylactic pesticide applications are usually necessary in areas with recurrent TRM outbreaks (Perring and Farrar 1986).

Given the climate in Northwestern Europe, TRM control is mainly performed by means of biologically-based Integrated Pest Management (Khromova 2001). The adoption of this strategy in Southern Europe is reduced because mild climatic conditions favour a wider spectrum of alternative host plants for the eriophyoid mite and, also, a higher number of pests (Yoldas et al. 1999). Currently, chemical control (e.g. abamectin and sulphur) is mainly used to limit TRM but its dispersal and the wider choice of alternative host plants lower the efficacy of acaricides.

The control of TRM and other tomato pests through petroleum (spray) oils was compared with conventional synthetic pesticide-based programmes used by commercial farmers in Australia (Singh et al. 2000). On fresh tomatoes a significant negative

exponential relationship was found between the level of TRM infestations, and the concentration of petroleum spray oil applied to run-off and leaf area declined as infestations increased (Singh et al. 2000).

In tomato greenhouses in the Mediterranean area, as in many other cases, sulphur applications have proved to be inadequate for limiting mite infestations. In these areas, no biological control strategy has yet been developed on a commercial scale and the use of more specific and effective acaricides has become widespread in protected tomato crops.

At present, the combination of reduced risk pesticides and phytoseiids holds out the most promise of an IPM approach. Some preliminary investigations have recently been conducted under laboratory conditions to evaluate the potential of some insects as biological control agents of TRM. An example in Italy is the mirid *Macrolophus caliginosus* (Wagner) (Nannini and Carboni 2003) that may limit eriophyid mite infestations on tomato and, in Australia, an unidentified predatory midge, *Feltiella* sp., (Steiner and Goodwin 2005) which initially showed promise but its off-plant pupation and mass rearing difficulties could present obstacles for commercial use.

Recent years have seen an increase in research addressing the problem of finding phytoseiids to act as suitable biocontrol agents of TRM. Some species, mainly in the laboratory or semi-field conditions, are able to complete their development on TRM; however, they may not be suitable candidates for exploitation because they cannot cope well with trichomes on the tomato plant. Very frequently, the morphological and chemical traits of the tomato make the biological control of TRM ineffective and/or very expensive. As TRM can live in different natural habitats and on a range of hosts, the search for efficient biocontrol candidates must be screened and tested on a wide scale. Frequently, predator effectiveness can be limited by the presence of tetranychids (i.e. *Tetranychus evansi* (Baker and Pritchard)) in particular by their webbing that hinders the activity of phytoseiids. According to the review of Gerson and Weintraub (2007), currently none (*Neoseiulus californicus* (McGregor), *N. fallacis* (Garman) *N. cucumeris* (Oud.), *Euseius concordis* (Chant), *Amblyseius victoriensis* (Womersley), *Typhlodromalus lailae* (Schicha)) have proved to be successful in controlling TRM.

More recently, studies have been performed to determine the relative nutritional value of TRM as an alternative or natural food source for phytoseiid mites. In particular, under laboratory conditions and generally with motile TRM stages, the survivorship and the reproductive potential of some promising predators were evaluated: TRM active stages provided commensurate nutritional effects on the survivorship, longevity and fecundity of *T. swirsikii* and *T. athiasae* females (Fig. 1) by suggesting that both species show interesting potential as biological control agents of TRM (Momen and Abdel-Khalek 2008). However, Castagnoli et al. (2003) emphasized that the intrinsic rate of natural increase diminished from 0.17 to 0.1 and from 0.20 to 0.07/day in two different strains of *N. californicus* when fed on TRM for three subsequent generations (Fig. 1).

As the tomato is an unsuitable host plant for many species, mainly because of the presence of glandular trichomes, which mechanically entrap or hinder movement and/or secrete toxic exudates, it seems crucial and unavoidable that predators get accustomed to spending several generations on this host for adaptation (Drukker et al. 1997; Castagnoli et al. 1998, 1999). In this context, it is necessary to evaluate if and how the chemical cues co-occurring with TRM vary in time and space, giving the predators the ability to repeatedly associate chemical cues with the presence of prey. It has been suggested that the rate at which the integration of information becomes manifest as a change in behaviour, differs between categories of natural enemies (parasitoids versus insect predators: specialist versus generalist predators). The differences in learning ability or in the time taken
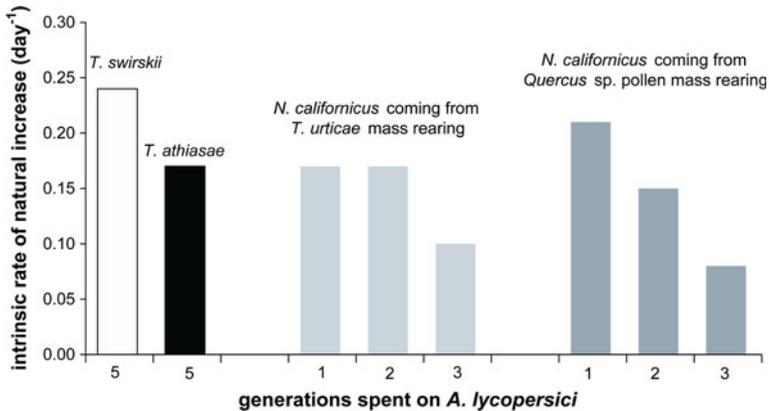
Fig. 1 Intrinsic rate of increase (r_m) calculated on tomato leaves infested by *A. lycopersici* for *T. swirskii* and *T athiasae*, $28 \pm 2°C$ and 70–75% (from Momen and Abdel-Khalek 2008), and for two strains of *N. californicus* in three successive generations (F_1–F_3), $25 \pm 1°C$, $75 \pm 10\%$ RH (from Castagnoli et al. 2003)

to show predatory efficiency on TRM can be ascribed to the ecologically relevant time scale, biotic environment and morpho-chemical traits of tomato varieties (Drukker et al. 2000; van Wijk et al. 2008).

TRM may appear to be an acceptable prey for some species of phytoseiids, which are able to quickly recognize, attack and kill their prey and to utilize the eriophyoid as food to increase the population. However, their feeding ability, population increase and searching performance have to be evaluated after some generations/adaptation in time.

Final remarks

The great variability in the extent of damage caused by ARM has often been related to cultivar susceptibility. However, there is no agreement on the susceptibility level of a certain cultivar. As an example, the susceptibility of Golden Delicious was low to moderate in some trials (Spieser et al. 1998; Kelm et al. 2005) and high in others (Angeli et al. 2008). The role of climatic conditions could explain such variations but this has rarely been explored (Golya and Kozma 2001). In Europe, ARM occurs from Greece to Norway (Markoyiannaki-Printzioui et al. 2000; Hossain and Solhy 2001) but comparative studies on its impact on crop yields in different environmental regions have not been conducted. Studies on morphological, anatomical and biochemical changes induced by ARM on different cultivars could reveal some mechanisms involved in the low susceptibility of some of them (Kozowski 1997). Kozowski and Kozowska (1997) reported that the long-term feeding of ARM negatively affected the content of reducing sugars and this variation depended on the apple cultivar.

Recently, the genetic basis of ARM resistance in apple (*Malus x domestica*) has been explored. This approach will be of help for breeding programmes. Stoeckli et al. (2009) used linkage map data available for F1 progeny plants of the cultivars 'Fiesta' x 'Discovery' to analyze quantitative trait loci (QTLs). Several apple genotypes were monitored for rust mite infestation. Two QTLs for ARM resistance were identified on linkage group 7 of the Fiesta cultivar. Two markers were positioned closest to the QTLs. Putative QTLs

were detected on the Discovery chromosomes. Specific SSR markers may facilitate the breeding of resistant apple cultivars by marker assisted selection. Therefore, promising results in apple resistance breeding programs are expected.

An effective diagnosis of eriophyoid infestations can prevent severe economic losses. This is particularly true for GRM as well as for *Colomerus vitis*. The application of simple and safe methods to extract these mites from plant material (de Lillo et al. 2001) will help people involved in these diagnoses, especially in recent or new viticultural areas. The role of nurseries in spreading eriophyoid mites has probably been underestimated and a stronger effort is required to prevent these problems in new regions.

Concerning TRM, further investigation cannot omit, as a crucial tool, the accurate evaluation of its density on different parts of the tomato plant at different stages. A detailed knowledge of the spatial distribution patterns has to be surveyed in order to define strategies for the management of TRM infestations, to estimate the risk posed by the pest species to a new area, and also to estimate and optimize the release of biocontrol agents.

Literature shows that several aspects of these eriophyoids and, in general, of all other economically important eriophyoids, need to be explored further.

As the demands of the global market call for frequent and substantial changes in commercialized products, the partial knowledge on how environmental and cultural factors affect the impact of eriophyoids on different plant varieties remains a very recurrent problem. Further knowledge on the susceptibility and resistance of host varieties to eriophyoids can allow for a more successful management of their populations in order to minimize damage.

Due to their particular habits and minuscule size, studies on their distribution and behaviour are particularly difficult and time-consuming. This implies that a lot of questions on their intra- and inter-plant distribution and dispersal modality are awaiting precise answers. In particular, the time taken by eriophyoid populations to colonize new plants, the distances covered, and their resistance to limiting factors, have to be investigated in different conditions. Furthermore, a great deal of information on important pests, concerning the survival rate of owerwintering and spring populations, stable age distribution, temperature thresholds and correlation between mite days and damage are lacking.

Another area which has been poorly investigated is that regarding competition with other herbivores (mainly tetranychids) or the different relationships with other organisms colonizing the same microhabits.

In order to enhance biological and ecological studies on these intriguing mites, procedures and techniques should be improved to maintain and rear them in the laboratory. Field investigation will be made easier when monitoring methods to estimate their population are defined.

References

Abou-Awad BA (1979) The tomato russet mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae) in Egypt. Anz Schadlingskd Pfl 52:153–156

Angeli G, Rizzi C, Dorigoni A, Ioriatti C (2007) Population injury levels of the apple rust mite *Aculus schlechtendali* (Nal) on Golden Delicious and Red Delicious apple fruits. Bull OILB/SROP 30(4):255–260

Angeli G, Rizzi C, Giuliani G, Tomasi C, Baldessari M (2008) Valide alternative per il controllo dell'eriofide del melo. Informatore Agrario 64(23):68–71

Bailey SF, Keifer HH (1943) The tomato russet mite, *Phyllocoptes destructor* Keifer: its present status. J Econ Entomol 36:706–712

Bernard MB, Horne PA, Hoffmann AA (2005) Eriophyoid mite damage in *Vitis vinifera* (grapevine) in Australia: *Calepitrimerus vitis* and *Colomerus vitis* (Acari: Eriophyidae) as the common cause of the widespread 'Restricted Spring Growth' syndrome. Exp Appl Acarol 35(1/2):83–109

Carew ME, Goodisman MAD, Hoffmann AA (2004) Species status and population genetic structure of grapevine eriophyoid mites. Entomol Exp Appl 111(2):87–96

Castagnoli M, Liguori M, Nannelli R (1997) Le popolazioni degli Acari nei vigneti inerbiti del Chianti: confronto tra cultivar. Redia 80:15–31

Castagnoli M, Liguori M, Simoni S, Guidi S (1998) Tomato as host plant: effect on some biological parameters of *Phytoseiulus persimilis* Athias-Henriot and *Tetranychus urticae* strains. Redia 81:93–98

Castagnoli M, Liguori M, Simoni S (1999) Effect of two different host plants on biological features of *Neoseiulus californicus* (McGregor). Int J Acarol 25:145–150

Castagnoli M, Simoni S, Liguori M (2003) Evaluation of *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) as a candidate for the control of *Aculops lycopersici* (Tyron) (Acari Eriophyoidea): a preliminary study. Redia 86:97–100

Chouinard G, Bellerose S, Brodeur C, Morin Y (2006) Effectiveness of *Hyaliodes vitripennis* (Say)(Heteroptera: Miridae) predation in apple orchards. Crop Prot 25(7):705–711

Ciampolini M, Rota PA, De Schulthaus S (1976) Rugginosità delle mele causata dall'eriofide *Aculus schlechtendali*. Informatore Agrario 32(40):24243–24245

Croft BA (1975) Integrated control of apple mites. Extension Bulletin Michigan State University E-825, 12 pp

Croft BA, Luh HK (2004) Phytoseiid mites on unsprayed apple trees in Oregon, and other western states (USA): distributions, life-style types and relevance to commercial orchards. Exp Appl Acarol 33(4):281–326

Croft BA, McRae IV (1993) Biological control of apple mites. Impact of Zetzellia mali (Acari, Stigmaeidae) on *Typhlodromus pyri* and *Metaseiulus occidentalis* (Acari, Phytoseiidae). Environ Entomol 22:865–873

Croft BA, Slone DH (1998) Perturbation of regulated apple mites: immigration and pesticide effects on outbreaks of *Panonychus ulmi* and associated mites (Acari: Tetranychidae, Eriophyidae, Phytoseiidae and Stigmaeidae). Environ Entomol 27(6):1548–1556

Cuthbertson AGS, Murchie AK (2003) The impact of fungicides to control apple scab (*Venturia inaequalis*) on the predatory mite *Anystis baccarum* and its prey *Aculus schlechtendali* (apple rust mite) in Northern Ireland Bramley orchards. Crop Prot 22(9):1125–1130

Cuthbertson AGS, Murchie AK (2004) The phenology, oviposition and feeding rate of *Anystis baccarum*, a predatory mite in Bramley apple orchards in Northern Ireland. Exp Appl Acarol 34(3/4):367–373

Cuthbertson AGS, Murchie AK (2006) Environmental monitoring of economically important invertebrate pests in Bramley apple orchards in Northern Ireland. Int J Env Sc Technol 3(1):1–7

Cuthbertson AGS, Bell AC, Murchie AK (2003) Impact of the predatory mite *Anystis baccarum* (Prostigmata: Anystidae) on apple rust mite, *Aculus schlechtendali* (Prostigmata: Eriophyidae) populations in Northern Ireland Bramley orchards. Ann Appl Biol 142(1):107–114

De Lillo E, Guario A, Lasorella V (2001) Un semplice metodo di estrazione per il campionamento degli acari eriofidi (Eriophyoidea). Informatore Fitopatologico 51(10):57–60

De Lillo E, Monfreda R, Baldacchino F (2004) Efficacy of fungicides and acaricides against *Calepitrimerus vitis* (Nalepa). Phytophaga 14:599–603

de Maeyer L, Vinvinaux C, Berge C, van den Merkens W, Peumans H, Verreydt J, Sterk G (1993) Usefulness of tolyfluanid in integrated pest control on apples as a regulator of the mite complex equilibrium and with contribution to intrinsic fruit quality of apple cv Jonagold. Acta Hortic 3:253–264

Drukker B, Janssen A, Ravensberg W, Sabelis MW (1997) Improved capacity of the mite predator *Phytoseiulus persimilis* Athias-Henriot(Acari: Phytoseiidae) on tomato. Exp Appl Acarol 21:507–518

Drukker B, Bruin J, Jacobs G, Kroon A, Sabelis MW (2000) How predatory mites learn to cope with variability in volatile plant signals in the environment of their herbivorous prey. Exp Appl Acarol 24:881–895

Duffner K, Schruft G, Guggenheim R (2001) Passive dispersal of the grape rust mite *Calepitrimerus vitis* Nalepa 1905: (Acari, Eriophyoidea) in vineyards. J Pest Sci 74(1):1–6

Duso C, de Lillo E (1996) Grape. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites-Their Biology, Natural Enemies and Control. Elsevier, Amsterdam, pp 571–582

Duso C, Pasini M (2003) Distribution of the predatory mite *Amblyseius andersoni* Chant (Acari: Phytoseiidae) on different apple cultivars. J Pest Sci 76(2):33–40

Duso C, Vettorazzo E (1999) Mite population dynamics on different grape varieties with or without phytoseiids released (Acari: Phytoseiidae). Exp Appl Acarol 23:741–763

Duso C, Pasini M, Pellegrini M (2003) Distribution of the predatory mite *Typhlodromus pyri* (Acari: Phytoseiidae) on different apple cultivars. Biocontrol Sci Techn 13:671–681

Easterbrook MA (1996) Damage and control of eriophyoid mites in apple and pear. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites-Their Biology, Natural Enemies and Control. Elsevier, Amsterdam, pp 527–541

Easterbrook MA, Fuller MM (1986) Russeting of apples caused by apple rust mite *Aculus schlechtendali* (Acarina: Eriophyidae). Ann Appl Biol 109:1–9

Easterbrook MA, Palmer JW (1996) The relationship between early-season leaf feeding by apple rust mite, *Aculus schlechtendali* (Nal), and fruit set and photosynthesis of apple. J Hortic Sci 71(6):939–944

Fernandez DE, Beers EH, Brunner JF, Doerr MD, Dunley JE (2006) Horticultural mineral oil applications for apple powdery mildew and codling moth, *Cydia pomonella* (L). Crop Prot 25(6):585–591

Fischer S, Mourrut-Salesse J (2005) Tomato Russet Mite in Switzerland (*Aculops lycopersici*: Acari, Eriophyidae). Rev Suisse Viticult Arboric Horticulture 37(4):227–232

Fitzgerald J, Solomon M, Pepper N (2003) Reduction of broad spectrum insecti, cide use in apple: implications for biocontrol of *Panonychus ulmi*. Bull OILB/SROP 26(11):37–41

Funayama K (1999) Studies on control and management of apple rust mite *Aculus schlechtendali* (Nalepa) II Chemical applications to protect against apple rust mites and native predatory mites in apple orchards using synthetic sex pheromones. Bull Akita Fruit Tree Experiment Station 26:1–13

Gabi G, Meszaros Z (2000) A szolo-levelatka (*Calepitrimerus vitis* Nalepa) nepessegmozgalmanak es telelohelyeinek vizsgalata a szekszardi borvideken. Novenyvedelem 36(7):349–355

Gabi G, Meszaros Z (2001) New data to the knowledge of *Calepitrimerus vitis* Nalepa in the vine-growing region of Szekszard, Hungary (Acari: Eriophyidae). Acta Phytopathol Hun 36(1/2):193–200

Gerson U, Weintraub PG (2007) Mites for the control of pests in protected cultivation. Pest Manag Sci 63(7):658–676

Gerson U, Smiley RL, Ochoa R (2003) Mites (Acari) for pest control. Blackwell Science Ltd, Oxford, UK

Gispert MC, Perring TM, de Lara CZ, Cazares CL (1989) Efecto del riego en la fluctuacion poplacional del acaro del tomato (*Aculops lycopersici* (Massee)). Agrociencia 76:153–165

Goebel O, Vergnet C, Heller JJ (2001) Lutte contre l'erinose et l'acariose de la vigne. Phytoma 537:39–41

Golya G, Kozma E (2001) Abiotikus tenyezok szerepe az almatermesuek levelatkajanak (*Aculus schlechtendali* [Nalepa]) populaciodinamikajaban. Novenyvedelem 37(7):345–350

Gonçalves MIF, Maluf W, Gomes LAA, Barbosa LV (1998) Variation of 2-Tridecanone level in tomato plant leaflets and resistance to two mite species (*Tetranychus* sp). Euphytica 104:33–38

Hardman JM, Smith RF, Bent E (1995) Effects of different integrated pest management programs on biological control of mites on apple by predatory mites (Acari) in Nova Scotia. Environ Entomol 24(1):125–142

Hardman JM, Franklin JL, Moreau DL, Bostanian NJ (2003) An index for selective toxicity of miticides to phytophagous mites and their predators based on orchard trials. Pest Manag Sci 59(12):1321–1332

Hill TA, Foster RE (1998) Influence of selective insecticides on population dynamics of European red mite (Acari: Tetranychidae), apple rust mite (Acari: Eriophyidae), and their predator *Amblyseius fallacis* (Acari: Phytoseiidae) in apple. J Econ Entomol 91(1):191–199

Hirata H, Sakamaki Y, Tsuda K (2007) A simple method to monitor the population density of the tomato russet mite, *Aculops lycopersici* on tomato plants. Kyushu Plant Protection Research 53:82–85

Hohn H, Hopli HU (1990) Die Apfelrostmilbe—oft uberschatzt, aber kaum prognostizierbar!. Schweizerische Zeitschrift fur Obst und Weinbau 126(9):259–266

Hossain MS, Solhy T (2001) Densities of *Panonychus ulmi* (Acari: Tetranychidae) and *Aculus schlechtendali* (Acari: Eriophyidae) on three apple cultivars in western Norway. In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds) Acarology: proceedings 10th Int Congress. Collingwood, Australia, pp 300–305

Hoyt SC (1969) Integrated chemical control of insects and biological control of mites on apple in Washington. J Econ Entomol 62:74–86

Ioriatti C, Forti D, Angeli G, Molignoni R (1996) L'eriofide del melo (*Aculus schlechtendali*): morfologia, biologia e danno. Informatore Fitopatologico 46(12):9–13

Ioriatti C, Bertamini M, Catoni M (1997) Influenza di *Aculus schlechtendali* sull'attivita fotosintetica fogliare e sulla colorazione dei frutti di melo. Informatore Fitopatologico 47(9):49–53

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. University of California Press, Berkeley, CA, USA

Kast WK, Rupp D, Schiefer HC, Trankle L (2004) Statistische Beziehungen zwischen Witterungsdaten und dem Auftreten von Krankheiten und Schadlingen im Weinbaugebiet Wurttemberg/Deutschland. Mitteilungen Klosterneuburg, Rebe und Wein, Obstbau und Fruchteverwertung 54(7/8):239–248

Kay IR (1986) Tomato russet mite: a serious pest of tomatoes. Queensland Agr J 112(5):231–232

Kelm M, Lenort M, Licznar-Maanczuk M, Sosna I (2005) Occurrence of apple rust mite *Aculus schlechtendali* Nal (Acari: Eriophyoidea) in different systems of apple orchards. Progress Plant Protection 45(2):776–778

Khan IA, Blaeser P, Sengonca C (2004) Laboratory experiments on prey consumption by *Typhlodromus pyri* Scheuten (Acari, Phytoseiidae) and *Chrysoperla carnea* (Stephens) (Neuroptera, Chrysopidae) on different mite pests of apple and interactions between the two predators. Mitteilungen der Deutschen Gesellschaft fur allgemeine und angewandte Entomologie 14(1–6):377–380

Khromova LM (2001) A dangerous mite on tomatoes in open soil. Zashchita Karantin Rastenii (6), p 34

Kozlowski J (1980) Researches on the occurrence and noxiousness of apple leaf mite *Aculus schlechtendali* (Nal.). Prace Naukowe Instytutu Ochrony Roslin, Tom XXII. zeszyt 2:155–162

Kozowski JJ (1997) Morphological- anatomical symptoms of feeding by the apple rust mite, *Aculus schlechtendali* (Nal) (Acarina: Eriophyidae), in leaves of different apple cultivars. Roczniki Nauk Rolniczych Seria E, Ochrona Roslin 26(1/2):7–11

Kozowski J, Kozowska M (1997) The influence of feeding of the apple rust mite *Aculus schlechtendali* (Nal) (Acarina: Eriophyidae) on biochemical changes in leaves of different apple cultivars. J Plant Prot Res 37(1/2):67–71

Kozowski J, Zielinska L (1997) Cytological changes in apple leaves infested with the apple rust mite - *Aculus schlechtendali* (Nal.) (Acarina: Eriophyidae). J Pl Prot Res 37(1/2):72–84

Laurin MC, Bostanian NJ (2007a) Short-term contact toxicity of seven fungicides on *Anystis baccarum*. Phytoparasitica 35:380–385

Laurin MC, Bostanian NJ (2007b) Laboratory studies to elucidate the residual toxicity of eight insecticides to *Anystis baccarum* (Acari: Anystidae). J Econ Ent 100(4):1210–1214

Leite GLD, Picanço M, Guedes RNC, Zanuncio JC (1999) Influence of canopy height and fertilization levels on the resistance of *Lycopersicon hirsutum* to *Aculops lycopersici* (Acari: Eriophyidae). Exp Appl Acarol 23(8):633–642

Lindquist EE, Oldfield GN (1996) Evolution of Eriophyoid Mites in Relation to their Host Plants. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites - Their Biology, Natural Enemies and Control. Elsevier, Amsterdam, The Netherlands, pp 277–300

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid Mites - Their Biology, Natural Enemies and Control. World Crop Pests. Elsevier, Amsterdam, The Netherlands, pp 1–790

Li QX, Cai RX (1996) Occurrence and damage of the apple rust mite *Aculus schlechtendali*. Plant Prot 22(3):16–17

Markoyiannaki-Printzioui D, Papaioannou-Souliotis P, Zeginis G, Giatropoulos C (2000) Observations on acarofauna in four apple orchards of Central Greece I Incidence of pedoclimatic conditions and agricultural techniques on phytoseiid mites (Acari: Phytoseiidae). Acarologia 41(1/2):109–126

Marshall DB, Thistlewood HMA, Lester PJ (2001) Release, establishment, and movement of the predator *Typhlodromus pyri* (Acari: Phytoseiidae) on apple. Can Entomol 133(2):279–292

MeiYu W, Dong Sheng W, Yong Da Y, XiaoYue H (2008) Development of the tomato russet mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae) on various tomato lines. Acta Entomol Sinica 51(8):839–843

Momen FM, Abdel-Khalek A (2008) Effect of the tomato rust mite *Aculops lycopersici*(Acari: Eriophyidae) on the development and reproduction of three predatory phytoseiid mites. Int J Tropical Insect Sci 28(1):53–57

Nannini M, Carboni MA (2003) A preliminary investigation on the potential of the mirid bug Macrolophus caliginosus Wagner as biological control agent of the tomato russet mite. In: Roche L, Edin M, Mathieu V, Laurens F (eds) Conference: Colloque international tomate sous abri, protection intégrée—agriculture biologique, Avignon, France, 17–18 et 19 septembre 2003 Paris: Centre Technique Interprofessionnel des Fruits et Légumes, 2003, 185–187

Perez-Moreno I, Moraza MML (1997) Etude sur le *Typhlodromus pyri* Scheuten en relation avec le *Calepitrimerus vitis* (Nalepa) dans les vignobles de la Rioja. Bulletin de l'OIV 70(801/802):832–845

Perez-Moreno I, Moraza MML (1998) Population dynamics and hibernation shelters of *Calepitrimerus vitis* in the vineyards of Rioja, Spain, with a description of a new eriophyid extraction technique (Acari: Eriophyidae). Exp Appl Acarol 22(4):215–226

Perring TM (1996) Vegetables. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid Mites - Their Biology, Natural Enemies and Control. Elsevier, Amsterdam, The Netherlands, pp 593–606

Perring TM, Farrar CA (1986) Historical perspective and current world status of the tomato russet mite (Acari: Eriophyidae). Entomol Am Misc Publ 63:1–19

Prischmann DA, James DG (2005) New mite records (Acari: Eriophyidae, Tetranychidae) from grapevines in Oregon and Washington State. Int J Acarol 31(3):289–291

Prischmann DA, James DG, Snyder WE (2005) Impact of management intensity on mites (Acari: Tetranychidae, Phytoseiidae) in Southcentral Washington wine grapes. Int J Acarol 31:277–288

Raudonis L, Valiuskaite A, Surviliene E (2007) Toxicity of Abamectin to rust mite, *Aculus schlechtendali* (Acari: Eriophyidae) in apple tree orchard. Sodininkyste ir Darzininkyste 26(2):10–17

Reis PR, Souza JC, de Goncalves NP (1998) Pragas da videira tropical. Informe Agropecuario Belo Horizonte 19(194):92–95

Rice RE, Strong FE (1962) Bionomics of the tomato russet mite. Vasates lycopersici (Massee). Ann Entomol Soc Am 55:431–435

Roddick JG (1974) The steroidal glycoalkaloid α-tomatine. Phytochemistry 13:9–25

Royalty RN, Perring TM (1988) Morphological analysis of damage to tomato leaflets by tomato russet mite (Acari: Eriophyidae). J Econ Entomol 81(3):816–820

Sengonca C, Khan IA, Blaeser P (2003) Prey consumption during development as well as longevity and reproduction of *Typhlodromus pyri* Scheuten (Acari, Phytoseiidae) at higher temperatures in the laboratori. Anz Schädling 76(3):57–64

Simmons AT, Gurr GM (2005) Trichome of *Lycopersicon* species and their hybrids: effects on pests and natural enemies. Agric For Entomol 7:265–276

Singh P, Beattie GAC, Clift AD, Watson DM, Furness GO, Tesoriero L, Rajakulendran V, Parkes RA, Scanes M (2000) Petroleum spray oils and tomato integrated pest and disease management in southern Australia. General Appl Entomol 29:69–93

Slone DH, Croft BA (2001) Species association among predaceous and phytophagous apple mites (Acari: Eriophyidae, Phytoseiidae, Stigmaeidae, Tetranychidae). Exp Appl Acarol 25(2):109–126

Solhoy T, Dybwad E, Hesjedal K, Hossain M, Hovland B (1991) Observations on *Aculus schlechtendali* (Nal) (Acari: Eriophyidae) in apple orchards in western Norway. In: Dusbabek F, Bukva V (eds) Modern acarology, vol 1. Academia, Prague, SPB Academic Publishing bv, The Hague, pp 533–538

Spieser F, Graf B, Walther P, Noesberger J (1998) Impact of apple rust mite (Acari: Eriophyidae) feeding on apple leaf gas exchange and leaf color associated with changes in leaf tissue. Env Entomol 27(5):1149–1156

Spieser F, Graf B, Hohn H, Hopli HU (1999) Effects of high apple rust mite population densities on gas exchange, yield, fruit quality, tree growth and flower formation. Bull OILB/SROP 22(7):77–85

Steiner M, Goodwin S (2005) Managing tomato russet mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae) in greenhouse tomato crops. Bulletin OILB/SROP 28(1):245–248

Stoeckli S, Mody K, Patocchi A, Kellerhals M, Dorn S (2009) Rust mite resistance in apple assessed by quantitative trait loci analysis. Tree Genetics and Genomes 5(1):257–267

Tixier MS, Kreiter S, Cheval B, Guichou S, Auger P, Bonafos R (2006) Immigration of phytoseiid mites from surrounding uncultivated areas into a newly planted vineyard. Exp App Acarol 39:227–242

van Wijk MP, De Bruijn JA, Sabelis MW (2008) Predatory mite attraction to herbivore-induced plant odors is not a consequence of attraction to individual herbivore-induced plant volatiles. J Chem Ecol 34(6):791–803

Varner M, Mattedi L, Lucin R, Forno F, Feichter M, Mescalchin E, Fellin F (2006) Andamenti climatici anomali favoriscono l'acariosi della vite. Informatore Agrario 62(17):85–89

Villanueva R, Harmsen R (1996) Ecological interactions of tarsonemid mites in apple orchards: predation of apple rust mite and use of *Phyllonorycter blancardella* mines. Proc Entomol Soc Ontario 127:99–106

Villanueva RT, Harmsen R (1998) Studies on the role of the stigmaeid predator *Zetzellia mali* in the acarine system of apple foliage. Proc Entomol Soc Ontario 129:149–155

Walde SJ, Magagula CN, Morton ML (1995) Feeding preference of *Zetzellia mali*: does absolute or relative abundance of prey matter more? Exp Appl Acarol 19(6):307–317

Walde SJ, Hardman JM, Magagula CN (1997) Direct and indirect species interactions influencing within-season dynamics of apple rust mite, *Aculus schlechtendali* (Acari: Eriophyidae). Exp Appl Acarol 21(9):587–614

Walton VM, Dreves AJ, Gent DH, James DG, Martin RR, Chambers U, Skinkis PA (2007) Relationship between rust mites *Calepitrimerus vitis* (Nalepa), bud mites *Colomerus vitis* (Pagenstecher) (Acari: Eriophyidae) and short shoot syndrome in Oregon vineyards. Int J Acarol 33(4):307–318

Wegner-Kib G (2003) Die Krauselmilbe (*Calepitrimerus vitis*), ein ernst zu nehmender Schadling im Weinbau. Obst und Weinbau 139(10):9–12

Yoldas Z, Madanlar N, Gul A, Onogur E (1999) Investigations on integrated control practices in vegetable glasshouses in Izmir. Acta Hort 491:453–460

Zalom FG, Kitzmiller J, Wilson LT, Gutierrez P (1986) Observation of tomato russet mite (Acari: Eriophyidae) damage symptoms in relation to tomato plant development. J Econ Entomol 79(4):940–942

Zandigiacomo P, Frausin C (1998) Problemi entomologici del vivaismo viticolo in Friuli-Venezia Giulia. Informatore Fitopatologico 48:10–14

An insight into some relevant aspects concerning eriophyoid mites inhabiting forests, ornamental trees and shrubs

Marisa Castagnoli · Mariusz Lewandowski · Gabriel S. Łabanowski · Sauro Simoni · Grażyna M. Soika

Abstract Worldwide a great variety of eriophyoid mites inhabit forest canopy trees and ornamental plants that are used in city parks, squares and boulevards. An analysis of the relevant bibliography portrays only a fragmentary knowledge and the majority of our information concerns the temperate zone. Three case studies are presented as examples of different approaches to solve problems connected with eriophyoid mites of forest and ornamental trees. The first example deals with eriophyoids of a temperate zone forest in a natural environment, focusing on conifers which represent the largest component. The second case study documents a possible approach to obtain greater knowledge and control of the bud mite species, *Trisetacus juniperinus* (Nalepa) on Cupressaceae. This is a harmless species in the natural environment which becomes a serious pest in nurseries and young stands of *Cupressus sempervirens* in the Mediterranean region. The final case study reports on long-term studies carried out in Poland on injurious eriophyoid species that are found in nurseries, city greenery and parks. This paper also discusses future perspectives for research on eriophyoid mites living on forest and ornamental plants.

M. Castagnoli (✉) · S. Simoni
CRA, Agriculture Research Council, ABP, Centre for Agrobiology and Pedology, via Lanciola 12/a, 50125 Florence, Italy
e-mail: marisa.castagnoli@entecra.it

M. Lewandowski
Department of Applied Entomology, Faculty of Horticulture and Landscape Architecture, SGGW, Warsaw University of Life Sciences, ul. Nowoursynowska 159, 02-776 Warsaw, Poland

G. S. Łabanowski · G. M. Soika
Research Institute of Pomology and Floriculture, ul. Pomologiczna, 96-100 Skierniewice, Poland

Introduction

In the context of plant-inhabiting animals, eriophyoid mites and vascular plants are known to have one of the most ancient associations, which is usually characterized by high host specificity and involves typical plant reactions (Lindquist 1998). A great diversity of eriophyoid species are present on forest canopy trees and on plants which, in different geographical areas, are considered as ornamentals and used in city parks, squares and boulevards. Probably at least one eryiophyoid mite species inhabits every species of woody or herbaceous dicotyledonous plant, monodicotyledonous and coniferous plant, or fern. More than ten eriophyoid species per plant are known from some species of the following genera, *Acer*, *Carpinus*, *Alnus*, *Fagus*, *Juglans*, *Olea*, *Prunus*, *Salix* and *Mangifera*. On some of them, more than one species can share the same microhabitat. Many eriophyoid species are apparently harmless to the plant host and frequently their presence is not detected because of their minute size. Other eriophyoids can cause a great variety of abnormalities such as erinea, galls on leaves, buds, inflorescences and stems, deformation, discoloration and russeting of leaves, brooming and rosettes of shoots (Castagnoli 1996). All these symptoms can often be confused with plant diseases. Sometimes such deformations are evident and can look peculiar, but under natural conditions they are rarely, highly injurious to plants. They may, however, lower the aesthetic value of plants, which is of crucial importance for ornamentals. On the whole, eriophyoid mites are not important pests of forests, but they may become target pests in nurseries or other non-natural environments where forest plants are grown.

The information on eriophyoid mites of forest and ornamental plants is found scattered in many taxonomic and faunistic papers. There are some rare studies which consider the real impact of these mites and how their relationship with a plant can undergo a significant change from the forest to nursery or urban environment. The last attempt to review all of the known information on eriophyoid mites goes back to the book "Eriophyoid mites, their biology, natural enemies and control (Lindquist et al. 1996), where one of the authors here (M. Castagnoli) took care of a chapter about ornamental conifers and shade trees. Boczek and Shevchenko (1996) described ancient associations between eriophyoid mites and gymnosperms. The list of all world eriophyoid species with plant hosts and type localities was published by Amrine and Stasny (1994); an on-line catalogue is also available (Amrine 2003). The knowledge gap existing at that time in relation to eriophyoids of large tropical regions still has not been filled because the majority of information in consecutive years has dealt with the temperate zone. According to recent literature on eriophyoid mites of forest and ornamental trees knowledge of them is still fragmentary. We can point out only a few examples which have received attention and these are limited to particular regions where eriophyoidologists are present at research institutions.

In this paper, three case studies based on the authors' recent experiences are presented. These exemplify different approaches to problems in relation to eriophyoid mites inhabiting forest and ornamental trees. The first case study concerns eriophyoid mites of temperate zone forests and focuses on conifers which make up the largest component. It may be viewed as an example of the relationship that such mites have with plants in the natural environment. The second case study presents a possible approach to acquire greater knowledge and understanding for controlling a bud mite species, *Trisetacus juniperinus* (Nalepa), that becomes a serious pest in nurseries and young stands of *Cupressus sempervirens* in the Mediterranean region but which is harmless in its natural environment on conifers (Cupressaceae). The final case study

discusses long-term studies carried out in Poland on injurious eriophyoid mite species found in nurseries, green spaces and city parks. It shows species richness that probably could also be recorded in many other countries of the same geographical zone if such research was undertaken. To date, no other country has such a long history of eriophyoid mite studies on ornamentals.

Case study 1: eriophyoid mites inhabiting coniferous trees and shrubs in forests of temperate zones

Habitat and its colonization

Typically for the whole of Europe, Asia and North America, coniferous forests occur mainly in temperate regions which experience warm summers and cool winters. Such habitats can also be found in temperate areas of South America, New Zealand and Tasmania (Australia). The northern parts of North America, Europe and Asia, which form part of the most barren northern areas of the Arctic tree line, are covered by Taiga, a type of coniferous forest dominated by larch (*Larix* spp.), spruce (*Picea* spp.), fir (*Abies* spp.) and pine (*Pinus* spp.). In these regions, broadleaf trees such as birch (*Betula* spp.), aspen (*Populus* spp.), willow (*Salix* spp.) and rowan (*Sorbus* spp.) also can occur. The southern parts of these continents are covered by both coniferous and broadleaf forests where pines, firs and spruces are the most frequent coniferous species, and oaks (*Quercus* spp.), beeches (*Fagus* spp.), maples (*Acer* spp.) and birches (*Betula* spp.) are the most common broadleaf species.

In such environments, tall evergreen trees create stable microhabitats for the development of arthropods and many eriophyoid mite species can also be found. Boczek and Shevchenko (1996) specified factors explaining the occurrence of eriophyoids on coniferous trees. The most important seems to be the long life span of such trees and their occurrence in large monospecific associations. Such conditions facilitate mite dispersal and also deliver a large amount of young plant tissue on which eriophyoids can feed. Their capacity for active movement is, in fact, limited to colonization of the preferred part of the same plant. Long distance dispersal between trees is passive and only possible by wind currents, phoresy or even through human cropping of infested seedlings. Forests with trees growing in large agglomerations can favour active movement and dispersal of eriophyoid mites to other plants if their branches are in contact (Löyttyniemi 1971; Sabelis and Bruin 1996). It is also possible that mites inhabiting large coniferous trees in a forest can colonize a new host by falling from an adult tree onto a seedling or a young tree growing close by Lewandowski. and Kozak (2008) found that *Nalepella shevtchenkoi* Boczek inhabiting Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), occurred on seedlings only on pine. Moreover, density parameters of particular mite species did not significantly differ between adult and young plants of both tree species. Based on these results, one may presume that the development of eriophyoid mites begins on seedlings or young trees and their population increases as a tree grows. This probably helps to explain why there is almost the same eriophyoid species composition in all age groups of plant species studied and similar densities occur on young and adult trees.

Distribution within plant

Limitations on eriophoid mobility can cause their uneven distribution within the plant. This is especially true for large perennials such as coniferous trees where information on the distribution of eriophyoids on such plants and their possible preference for age or plant part is still poor. From the available literature, we can conclude that eriophyoid mites usually prefer the young tissue of plants (Boczek and Shevchenko 1996) and that they infest only the external shoots of a tree crown. However, a little more is now known about the vertical distribution of eriophyoids within tree crowns. Castagnoli and Simoni (2000) compared the distribution of two eriophyoid mite species on *C. sempervirens*, namely, the bud species, *T. juniperinus*, which prefers the top parts of plant crowns, and the free living species, *Epitrimerus cupressi* (Keifer), which was found to be evenly distributed. Similar results were obtained by Lewandowski and Kozak (2008) in a study on Scotch pine and Norway spruce where no differences were detected in the vertical distribution of both eriophyoid species on particular parts of adult trees or between adult and young trees. Such results may indicate that for studies relating to eriophyoid mites on pine and spruce, samples can equally be taken from the bottom part of a tree or from young trees that grow among older trees. This lack of difference in the vertical distribution of eriophyoid mites between particular parts of old trees could be the result of low densities. The infestation rate for vagrant mites found on old and young spruce trees was 4.9 and 5.2 specimens per sample, respectively (based on a 15 cm long shoot). For mites forming large colonies, such as *Trisetacus relocatus* Bagnyuk and Shevchenko, the degree of infestation at bases of the current year's shoots of the same tree species, indicated that this value was much higher for old trees (13.7 specimens per sample) than for young trees (6.1 per sample). The densities of eriophyoid mites living in needle sheaths on pine trees reached 4.5 and 6.2 specimens per 10 needles for old and young trees, respectively (Lewandowski and Kozak 2008).

Injuries

Low eriophyoid mite densities on large coniferous trees can help to explain the lack of evidence of their harmfulness on such hosts. In fact, no serious damage has been attributed to vagrant eriophyoids on trees in ordinary forests, although mass outbreaks have some-times occurred in nurseries and Christmas tree plantations (Boczek 1962; Löyttyniemi 1969, 1975; Siewniak 1971; Marshall and Lindquist 1972; Boczek et al. 2002). Eriophyoid species forming galls, living in buds, fruits, under scales at the basis of shoots or in the needle sheaths seem to have a more significant influence on their hosts (Castagnoli 1996). On coniferous trees, this mite group is represented by *Trisetacus* species. One of the most common species in the temperate zone is *Trisetacus pini* (Nalepa) which forms galls on pine twigs (Nalepa 1887; Shevchenko et al. 1993; Petanovic et al. 1996; Skoracka et al. 2005), spruce and larch shoots (Petanovic et al. 1996). This species can cause serious damage to young pines (Kruel 1963; Shevchenko et al. 1993). Observations by one of the authors (M. Lewandowki, unpublished data) showed that the occurrence of a large number of galls can also cause the death of all branches of a pine tree, although such a situation has only been seen in the case of trees growing at the forest margin. Other *Trisetacus* species, such as *T. laricinae* Smith, *T. abietivagrans* Kadono, *T. bagdasariani* Bagnyuk, *T. piceae* (Roivainen) and *T. grosmanni* Keifer, can cause the death of infested buds that later can inhibit the development of shoots (Roivainen 1951; Keifer 1959; Smith 1979; Kadono 1981; Bagnyuk 1984). However, there are no records of mass outbreaks of the above-mentioned species in forests that could influence the growth of infested trees. A similar

situation has also been observed in the case of *Trisetacus* spp. infesting juniper berries (Smith 1978). The only record of heavy infestation of juniper seeds by mites from this genus comes from Kyrgyzstan and Uzbekistan where *T. kirghisorum* Shevchenko attacked the fruits of *Juniperus semiglobosa* and destroyed its seeds (Shevchenko 1962). Pure juniper forests are dominant in many areas of Central Asia where they provide watershed protection, habitat and food source for indigenous wildlife. Even during years of abundant seed production and the absence of seed pests, dry spells can also hamper natural regeneration. Therefore, periodic failure of seed production in juniper trees as a result of heavy infestation by *T. kirghisorum*, which in some years can infest up to 90% of seeds, may have an adverse effect on natural regeneration and quite possibly, on wildlife (Shevchenko 1995; Orozumbekov and Moore 2007). High numbers of *Nalepella danica* were found in a Christmas tree plantation of *Abies normandiana* where this species occurred together with *N. shevtchenkoi* (Boczek et al. 2002). They severely damaged the needles causing a rusty bronze discoloration due to the chlorosis caused by the feeding of the mites and heavy attacks may even cause defoliation. M. Lewandowski (unpublished data) has also observed *N. danica* on *Abies alba* growing in forests of south and north Poland, but its density was rather low and no injuries were noted.

Species diversity

The diversity of eriophyoid mites inhabiting coniferous trees in temperate forests depends on the plant host. *Pinus* spp. host the most eriophyoid species. To date, 47 eriophyoid species have been described from pine species throughout the world of which 29, belonging to seven genera, have been found in temperate forests. Taking into account the number of eriophyoid species recorded, the most important genus is *Trisetacus* which is represented by ten species, followed by *Setoptus* and *Platyphytoptus*. Twenty out of the 28 mite species known from *Abies* worldwide have been recorded on *Abies* in temperate forests, while on *Picea*, only 15 out of 24 species have been found. *Larix* and *Juniperus* species growing in this region are colonized by seven and eight eriophyoid species, respectively (Table 1).

Species composition of eriophyoid mites on coniferous plants is closely connected with the architecture of such plants. Large perennial plants can create many microhabitats for the feeding and development of eriophyoid mites (Boczek and Shevchenko 1996). The availability of specific microhabitats on host plants can also influence the host specificity of

Table 1 The number of eriophyoid mite genera and species occurring on different host plant genera and microhabitats in coniferous forests of temperate regions of the world

Plant genera	No. of mite species	No. of mite genera	Microhabitat	No. of mite species	No. of mite genera
Abies	20	6	Needles	45	14
Juniperus	8	5	Buds	9	3
Larix	7	3	Scales of shoots	2	2
Picea	15	5	Galls on twigs	1	1
Pinus	29	7	Needle sheaths	8	3
Taxus	4	3	Berries	2	1

eriophyoid mites. The majority of eriophyoids found in forests of temperate regions of the world are specific on a single host plant or a plant species belonging to the same genera. Only 11 eriophyoid species occur on plant hosts belonging to different genera of coniferous trees, but all of them inhabit the same microhabitats. Three eriophyoid species of the genus *Trisetacus*, namely *T. grosmanni*, *T. neopicea* Smith and *T. pini*, have wide range of tree hosts. The first two species were recorded on species of *Abies*, *Picea* and *Pinus* while the third, *T. pini*, was found on species of *Larix*, *Picea* and *Pinus*. *Trisetacus neopicea* occurred only on five host plant species of *Abies*, *Picea* and *Pinus*, whereas *T. grosmanni* and *T. pini* were found on 11 and 15 plant species, respectively. The greatest host plant range is shown by another *Trisetacus* species, namely *T. ehmani*, which inhabits 25 species of plants belonging to only two genera, *Larix* and *Picea* (Amrine 2003). This subject matter was thoroughly described by Smith (1984), who discussed different degrees of host specificity among species of *Trisetacus*.

Furthermore, among seven genera, namely *Boczekella*, *Keiferella*, *Nalepella*, *Phantacrus*, *Platyphytoptus*, *Setoptus* and *Trisetacus*, which comprehend the species living exclusively on coniferous plants, and eight genera, namely, *Acariculus*, *Aculus*, *Calepitrimerus*, *Cecidophyopsis*, *Cupacarus*, *Epitrimerus*, *Tegonotus* and *Phyllocoptes*, with much wider host ranges, 12 eriophyoid species have been found on coniferous plants in temperate forests (Castagnoli 1996). However, members of three other genera, namely *Eriophyes*, *Proiectus* and *Rhyncaphytoptus*, were described later (Amrine 2003; Xue et al. 2006; Xue et al. 2007). Xue et al. (2007) presented an interesting report on the occurrence of *Rhyncaphytoptus* species on coniferous plants: *R. abiesis* Xue, Song & Hong, *R. fabris* Xue, Song & Hong and *R. fargesis* Xue, Song & Hong were found on *Abies fabri* and *A. fargesii* in North China. These were the first records of members of the Diptilomiopidae family to be recorded from Pinaceae trees. Earlier, only three Diptilomiopidae species had been found and these were on the plant genera *Cunninghamia* and *Cryptomeria* belonging to the Taxodiaceae (Kuang 1980; Huang 2001; Xue et al. 2006) (Table 2). Recently, many new eriophyoid species have been described from China. After 2000, 11 new species were recorded on coniferous forest trees located in the temperate region of this country (Kuang et al. 2005; Xue and Hong 2005, 2006; Xue et al. 2006, 2007). At the same time in Europe, only two new species were described, namely, *Nalepella danica* Boczek, Harding & Shi on *Abies nordmanniana* in Denmark (Boczek et al. 2002) and *Calepitrimerus lutocinus* Lewandowski on *P. abies* in Poland (Lewandowski 2006).

Case study 2: *Trisetacus juniperinus,* a mite injurious to cultivated conifers

Importance of the species

Trisetacus juniperinus is a clear example of a bud mite causing quite harmless and localized injuries (described as needles swollen basally and clustered), in natural stands of *Juniperus*, *Chaemacyparis* and *Cupressus*. However, it may often become a key pest species on such plant hosts growing in nurseries and young stands. This usually occurs in the Mediterranean region where evergreen cypress (*C. sempervirens*), one of the most important tree species for landscape and forestry (Panconesi 2007), is widely cultivated for its ornamental value and high quality of wood. *Cupressus sempervirens* also has the additional capacity to colonize even the most arid soil. In the Mediterranean region, *T. juniperinus* and fungal cypress canker, *Seiridium cardinale* (Wag) Sutton & Gibbson,

Table 2 Eriophyoid mite species inhabiting coniferous trees in forests of temperate regions of the world

Host genera	Eriophyoid species	Microhabitat
Abies	*Keiferella abietis* Boczek, 1969	Needles
	Keiferella piceae Boczek, 1969	Needles
	Nalepella danica Boczek, Harding & Shi, 2002	Needles
	Nalepella ednae Keifer, 1951	Needles
	Nalepella longoctonema Hu & Krantz, 1991	Needles
	Nalepella octonema Keifer, 1966	Needles
	Nalepella shevtchenkoi Boczek, 1969	Needles
	Nalepella triceras (Börner, 1906)	Needles
	Nalepella tsugifoliae Keifer, 1953	Needles
	Phyllocoptes fabris Xue & Hong, 2005	Needles
	Rhyncaphytoptus abiesis Xue, Song & Hong, 2006	Needles
	Rhyncaphytoptus fabris Xue, Song & Hong, 2006	Needles
	Rhyncaphytoptus fargesis Xue, Song & Hong, 2006	Needles
	Tegonotus montanus Hu & Krantz, 1991	Needles
	Trisetacus abietis Postner, 1968	Needles
	Trisetacus abietivagrans Kadono, 1981	Buds
	Trisetacus grosmanni Keifer, 1959	Buds
	Trisetacus laricinae Smith, 1979	Male flower buds
	Trisetacus neoabietis Smith, 1984	Needle vagrants
	Trisetacus relocatus Bagnyuk & Shevtchenko, 1982	Under scales of shoots
Juniperus	*Acaricalus juniperi* Szulc, 1967	Needles
	Epitrimerus sabinae Xue & Hong, 2005	Needles
	Eriophyes oxycedri Mitrofanov & Vasilyeva, 1982	Needles
	Keiferella juniperici Boczek, 1964	Needles
	Trisetacus juniperinus	Needles
	Trisetacus neoquadrisetus Smith, 1978	Berries
	Trisetacus quadrisetus (Thomas, 1890)	Berries
	Trisetacus thujivagrans Smith, 1977	Needles
Larix	*Boczekella laricis* Farkas, 1965	Needles
	Boczekella reticulata Bagnyuk, 1987	Under scales of shoots
	Nalepella triceras (Börner, 1906)	Needles
	Trisetacus ehmanni Keifer, 1963	Needle sheaths
	Trisetacus laricinae Smith, 1979	Buds
	Trisetacus laricis (Tubeuf, 1897)	Buds
	Trisetacus pini (Nalepa, 1887)	Galls on twigs
Picea	*Calepitrimerus lutocinus* Lewandowski, 2005	Needles
	Keiferella guanegouensis Xue, Song, Amrine & Hong, 2007	Needles
	Keiferella piceae Boczek, 1969	Needles
	Nalepella haarlovi Boczek, 1962	Needles
	Nalepella haarlovi picea-abietis Löyttyniemi, 1969	Needles
	Nalepella shevtchenkoi Boczek, 1969	Needles
	Phyllocoptes cechi Boczek & Michalska, 1989	Needles
	Phyllocoptes farkasi Boczek, 1969	Needles

Table 2 continued

Host genera	Eriophyoid species	Microhabitat
	Phyllocoptes piceae Soika, 1999	Needles
	Trisetacus grosmanni Keifer, 1959	Buds
	Trisetacus neopiceae Smith, 1984	Needles
	Trisetacus piceae (Roivainen, 1951)	Buds
	Trisetacus pini (Nalepa, 1887)	Galls on twigs
	Trisetacus relocatus Bagnyuk & Shevtchenko, 1982	Under scales of shoots
	Trisetacus uclueletensis Smith, 1984	Needles
Pinus	*Epitrimerus pini* Kuang & Li, 1994	Needles
	Eriophyes armandis Xue & Hong, 2006	Needles
	Phyllocoptes farkasi Boczek, 1969	Needles
	Phyllocoptes paenulatus Oudemans, 1929	Needles
	Phyllocoptes shenyangensis (Kuang & Luo, 2005)	Needles
	Platyphytoptus eldoradensis Keifer, 1954	Needles
	Platyphytoptus monophyllae Keifer, 1953	Needles
	Platyphytoptus multisternatus Keifer, 1939	Not listed
	Platyphytoptus pineae Castagnoli, 1973	Needles
	Platyphytoptus sabinianae Keifer, 1938	Needle sheath
	Platyphytoptus thunbergii Hong & Kuang, 1989	Near bases of needles.
	Proiectus thubergis Xue, Song, Amrine & Hong, 2007	Needles
	Proiectus tabulaeformis Xue, Song, Amrine & Hong, 2007	Needles
	Setoptus jonesi (Keifer, 1938)	Needles
	Setoptus koraiensis Kuang & Hong, 1995	Not listed
	Setoptus pini Boczek, 1964	Needles
	Setoptus strobacus Keifer, 1966	Needle sheaths
	Setoptus thunbergi Hong, 1988	Not listed
	Setoptus multigranulatus Castagnoli, 1973	Needle sheaths
	Trisetacus alborum Keifer, 1963	Needle sheaths
	Trisetacus campnodus Keifer & Saunders, 1972	Needle sheaths
	Trisetacus cembrae (Tubeuf, 1910)	Buds
	Trisetacus ehmanni Keifer, 1963	Needle sheaths
	Trisetacus gemmavitians Styer, Nielsen & Balderstron, 1972	Buds
	Trisetacus grosmanni Keifer, 1959	Buds
	Trisetacus neoabietis Smith, 1984	Needles
	Trisetacus pini (Nalepa, 1887)	Galls on twigs
	Trisetacus strobi Smith, 1979	Needles
	Trisetacus silvestris Castagnoli, 1973	Needle sheaths
Taxus	*Cecidophyopsis psilaspis* (Nalepa, 1893)	Buds
	Epitrimerus gemmicolus (Nalepa, 1895)	Buds
	Nalepella tsugifoliae Keifer, 1953	Needles

are the major problems of young cultivated plants. For the latter, the best control strategy seems to be the selection of resistant varieties (Panconesi and Raddi 1998). This leads us to reconsider the increasing problems with *T. juniperinus* and current control strategies on

account of the susceptibility of newly selected, canker-resistant clones to eriophyoid mite attack.

Biology

The eriophyoid mite, *T. juniperinus*, prefers to live hidden in apical and subapical buds of cypress where populations develop continuously throughout the year (Castagnoli and Simoni 2000). In older plants, this mite species also colonizes the young reproductive organs (Guido et al. 1995). Mites remain in the bud or cone until such time as these become dry, then they migrate towards new buds. As new buds are available throughout the year in cypress trees, massive migration does not appear to take place at any particular time. The association of eriophyoids with fast growing plant tissue, such as active meristems of apical buds, is made clear. It could explain the higher level of injuries observed in nurseries and young stands where plants are constantly maintained in their optimal growing condition in comparison to natural stands. In the latter, eriophyoid populations although generally present, are usually at low levels. This is probably because the availability of active meristems is less and there is more incisive control exerted by natural enemies which help to sustain low eriophyoid populations.

Development of a damage rating system

As for all bud and gall mite monitoring, the real density of *T. juniperinus* populations is very difficult to be ascertained. The best approach for increasing knowledge about this mite species would be to focus on induced symptoms. The symptoms, however, range enormously in severity and more than one type of damage can coexist on the same plant. A rating system which takes into account the type of mite damage observed has proved to be useful for describing the evolution of plant injuries, mite biology and population dynamics. The severity of each damage symptom is graduated as a score from zero (absent) to four

Table 3 Rating system (damage category and intensity scale) for injuries caused by the bud mite *Trisetacus juniperinus* on *Cupressus sempervirens* (modified from Castagnoli et al. 2002)

Symptom category				
A	B	C	D	E
Buds enlarged, deformed, russet and/or branch apex fold	Buds more or less dried	Brachyblasts and/or part of branch dried	Irregular proliferations of axillary buds, blastomania, witches'brooms	Cones deformed producing few seeds

Intensity scale for symptoms					
Score	Number of records/plant	Number of records/plant	Number of records/plant	Percentage of damage in each plant	Number of records/plant
0	Absent	Absent	Absent	Absent	Absent
1	1–4	1–4	1–4	<15	1–4
2	5–15	5–15	5–15	16–30	5–15
3	16–30	16–30	16–30	16–30	16–30
4	>30	>30	>30	>50	>30

(highest intensity) (Table 3). To provide a measure of damage intensity, a global damage index per plant (GDI) can be calculated, by summing the intensity means of all damage categories (A–E) recorded (Castagnoli et al. 2002). By means of this rating system, it was possible to investigate the susceptibility of cypress genotypes. The first damage symptom that appears is 'A' which, after some time, evolves into 'B'. These damages are the most common and can be found at a high level in nurseries and the first stage after transplantation to the field. As the cypress plant grows, damage symptom 'B' can evolve either into 'C' (when a large part of the plant whitens and dies) or into 'D' (when the plant reacts by inducing proliferations of new buds). *Trisetacus juniperinus* is surely responsible for damage symptom 'D' whilst other biotic and abiotic factors probably concur to 'C' damage (Castagnoli and Simoni 1998).

Different susceptibility of *Cupressus sempervirens*

A number of seedlings belonging to 15 different plant families obtained by self-crossing or crossing with a single heterologous pollen, were followed from the nursery (where they had been maintained for 3 years), to 2 years after transplantation into two different field locations. This 5-year experiment evidenced a great variation in susceptibility to mite attack and provided better clarification of the evolution of damage symptoms (Castagnoli et al. 2002). As a result, it was then possible to allocate the cypress family to at least two different levels of susceptibility in the nursery. The control (2 years after transplanting in the field) substantially did not change this initial assessment of the cypress family's susceptibility to the eriophyoid, *T. juniperinus*. However, cypress of the same family showed a significantly higher level of damage symptoms in field stands where higher humidity was registered. So, we can conclude that the environmental conditions experienced in transplanting localities could in some way increase or lower the innate susceptibility of plants to mite attack. Nevertheless, the general trend for the most susceptible plant families remained the considerable increase to damage levels 'C' and 'D' which are predominantly responsible for the loss of aesthetic value of cypress trees. These could then only be restored to partial health with extreme difficulty.

There are two important practical results derived from the study of plant susceptibility based on the rating system above. The first is that the scores for each damage category were strongly positively correlated to each other in all of the plant groups considered. Consequently, the assessment of damage level 'A' (the earliest symptom of mite attack) is sufficient to obtain the same evaluation of cypress susceptibility as if all damage categories are considered. The second result is that there was a negative relationship between damage symptoms scored and increase in tree height. More intensive damages resulted in a smaller-than-average increase in plant height and this contributed considerably to the loss of economic value of young trees.

Impact of mite infestation and control

Another long-term study focused on the evaluation of the impact of mite infestation both on the survival and apical growth of two commercial cypress clones (Agrimed and Bolgheri) and the differently timed pesticide applications to suppress mite populations on newly grafted trees (Simoni et al. 2004). The experiment was conducted in a large specialized nursery in Central Italy where 1 year old seedlings were obtained from seed harvested in selected stands and grown individually in pots in a greenhouse. In January, these were used as rootstocks for grafting scions collected from clonal trees growing in a

nearby orchard. Grafted trees were kept in the same greenhouse until May of the same year, when they were later transferred to the open air. The health of rootstock and grafting material was found to be crucial for limiting the damage caused by *T. juniperinus* because natural infestations rarely occurred. Mites previously infesting rootstock in the nursery can quickly migrate to grafted scions and induce tip deformation. This is connected with growth disturbance and even if the infestation decreased significantly over time, apical growth was significantly still lower in plants from infested rootstock 2 years after grafting. The long lasting effects of this precocious mite infestation can be interpreted as a trade-off between resources that are devoted to growth and also to the defence-reaction of trees in accordance with the GDB (Growth Differentiation Balance) hypothesis of Herms and Mattson (1992). Treatment with bromopropylate reduced the percentage of infested plants in both clones and when this was performed on grafted trees, it resulted in higher growth compared to the control trees. Trials with induced, massive, artificial infestation of trees in the second year of the experiment, confirmed the suppressive effects of bromopropylate treatment on mites which then resulted in a positive effect on tree growth. As the use of bromopropylate and endosulfan has been limited by recent European Union (EU) regulations, further research on effective acaricides for the control of *T. juniperinus* is necessary.

Case study 3: injurious eriophyoid fauna of ornamentals in Poland

Out of 342 eriophyoid mite species which are present in Poland, 157 species were collected from 47 genera of coniferous and deciduous trees and shrubs (G. Łabanowski and G. Soika, unpublished data; Skoracka et al. 2005; Soika and Łabanowski 2006). Among them, 70 species were recorded in nurseries, 104 species in city greenery and 40 species in botanical gardens. In this paper, the authors present 80 eriophyoid species of economic importance that feed either on leaves, needles, buds, shoots or inflorescences. These cause visible damage to ornamental trees and shrubs located in nurseries, botanical gardens and city greenery in different parts of Poland. In Table 4, eriophyoid species found in such locations (unnatural stands) are arranged according to the type of damage induced (mainly rusting and discoloration of leaves or needles; creating different types of galls).

In Poland, 23 species of eriophyoid mites are known to live on coniferous shrubs and trees so far and among them there are seven species that are injurious to plants, namely, *Cecidophyopsis psilaspis* (Nalepa), *Epitrimerus piceae* (Soika), *Eriophyes junipereti* Keifer, *Nalepella schevtchenkoi* Boczek, *Phyllocoptes farkasi* Boczek, *Setoptus pini* Boczek and *T. juniperinus* (Soika and Łabanowski 1999c). The most important pest species is *T. juniperinus* which is common on coniferous plants that are grown in containers in nurseries. This eriophyoid causes the death of terminal buds and considerable shortening of internodes which, in consequence, leads to shoot-rosetting of *Juniperus procumbens*, *J. chinensis* 'Variegata', *J. sargentii* and *J. virginiana* 'Mona'. In city greenery, *N. schevtchenkoi* Boczek which causes severe mosaic discolouration on *Picea jezoensis*, is the most hazardous eriophyoid species by far. In contrast, it causes no visible damage to *Abies alba* and *A. nordmanniana* (Boczek 1969) even though it is present.

Among 150 species of eriophyoid mites living on deciduous trees and shrubs, 73 species cause evident damage to plants. In nurseries, *Shevtchenkella brevisetosa* (Hodgkiss) is the most common species on *Acer negundo* and its cultivars, Aureovariegatum and Flamingo. It feeds on the top-most shoots causing stunted growth of the youngest leaves and shortening of internodes which, in consequence, leads to shoot rosetting. The severe stunting of

Table 4 Eriophyoid mite species found in Poland on ornamental plants in nurseries (nurs.), in city greeneries (city gr.), in botanical gardens (bot. gard.), based on damage symptoms

Mite species	Plant species	Collection site	References
Leaf or needle discolouration/silvering damage			
Aceria loewi (Nalepa, 1890)	*Syringa vulgaris, S. josikaea*	nurs., city gr.	(1)
Acaricalus trinotus (Nalepa, 1892)	*Alnus glutinosa, A. incana*	nurs.	(6)
Aculops allotrichus (Nalepa, 1894)	*Robinia pseudoacacia*	nurs.	(3)
Aculus ligustri (Keifer, 1943)	*Ligustrum vulgare*	nurs.	(3)
Anthocoptes galeatus (Nalepa, 1890)	*Ulmus laevis*	nurs.	(3)
Anthocoptes loricatus (Nalepa, 1889)	*Corylus avellana*	nurs.	(6)
Brevulacus reticulatus Manson, 1984	*Quercus robur*	nurs.	(16)
Diptacus gigantorhynchus (Nalepa, 1892)	*Prunus cistena*	nurs.	(6)
Epitrimerus piceae (Soika, 1999)	*Picea abies*	nurs.	(12)
Nalepella schevtchenkoi Boczek, 1969	*Picea jezoensis*	city gr.	(6)
Pentamerus septemcarinatus (Liro, 1941)	*Rhamnus frangula*	nurs.	(6)
Phyllocoptes farkasi Boczek, 1969	*Pinus nigra, P. jeffreyi*	nurs., bot. gard.	(12)
Setoptus pini Boczek, 1964	*Pinus nigra, P. mugo*	bot. gard., city gr.	(12)
Shevtchenkella serrata (Nalepa, 1892)	*Acer pseudoplatanus, A. monspessulanum*	nurs., city gr.	(6)
Tetraspinus lentus Boczek, 1961	*Syringa vulgaris*	nurs.	(14)
Leaf or shoot rusting/browing			
Aceria taylori (Briones & McDaniel, 1976)	*Syringa vulgaris*	bot. gard.	(18)
Aculus atlantazaleae (Keifer, 1940)	*Rhododendron japonicum, R.* "Knaphill-Exbury", "Mollis"	nurs., city gr., bot. gard.	(1) (3) (15)
Aculus ballei (Nalepa, 1891)	*Tilia × europaea* "Pallida"	nurs.	(1) (5)
Aculus cytisi Łabanowski, 2000	*Cytisus × praecox* "Hollandia"	nurs.	(15)
Aculus epiphyllus (Nalepa, 1890)	*Fraxinus excelsior, F. monophylla, F. pennsylvanica*	nurs.	(1) (14)
Aculus fockeui (Nalepa & Trouessart, 1891)	*Prunus serrulata*	nurs.	(6)
Aculus schlechtendali (Nalepa, 1890)	*Malus domestica*	nurs.	(6)
Aculus tibialis (Liro, 1943)	*Hippaphaë rhamnoides*	city gr.	(18)

Table 4 continued

Mite species	Plant species	Collection site	References
Aculops massalongoi (Nalepa, 1925)	Syringa vulgaris	city gr.	(18)
Aculops oblongus (Nalepa, 1894)	Viburnum lantana, V. carlesi	city gr., bot. gard.	(3) (16)
Calepitrimerus armatus (Canestrini, 1891)	Crataegus monogyna "Compacta"	nurs., city gr.	(18)
Epitrimerus pyri (Nalepa, 1857)	Pyrus calleryana, P. communis	nurs.	(6)
Epitrimerus subacromius Rovainen, 1947	Betula pendula, B. pubescens	nurs.	(3)
Phyllocoptes compressus (Nalepa, 1892)	Carpinus betulus	nurs.	(14)
Rhyncaphytoptus amplus Keifer, 1961	Acer ginnala	nurs.	(6)
Rhyncaphytoptus fagacis Boczek, 1964	Fagus sylvatica	nurs.	(17)
Rhyncaphytoptus platani Boczek & Shi, 1995	Platanus × acerifolia	nurs.	(14)
Rhyncaphytoptus sorbi Liro, 1943	Sorbus aucuparia	nurs.	(3)
Shevtchenkella carinata (Nalepa, 1892)	Aesculus hippocastanum	nurs	(1)
Shevtchenkella ligustri (Farkas, 1965)	Ligustrum vulgare	city gr.	(13)
Tegonotus platynaspis (Nalepa, 1920)	Alnus incana	nurs.	(18)
Tegonotus trouessarti (Nalepa, 1892)	Alnus incana	nurs.	(18)
Tetra concava Keifer, 1939	Ulmus glabra	nurs.	(18)
Leaf or needle with necrotic spots			
Coptophylla gymnaspis (Nalepa, 1892)	Acer platanoides	nurs.	(6)
Platyphytoptus sabinianae Keifer, 1938	Pinus mugo, P. nigra	nurs.	(12)
Leaf deformation: margin rolling or malformation			
Aceria caliberberis Keifer, 1952	Berberis thunbergii	nurs., bot. gard.	(3)
Aceria ligustri (Keifer, 1938)	Ligustrum vulgare	city gr.	(3)
Acalitus stenaspis (Nalepa, 1891)	Fagus sylvatica	city gr.	(17)
Aculus tetanothrix (Nalepa, 1889)	Salix × smithiana	nurs.	(6)
Aculus viburnifoliae Boczek & Shi, 1995	Viburnum lantana	city gr.	(1)
Epitrimerus trilobus (Nalepa, 1891)	Sambucus nigra	nurs., city gr.	(1) (13)
Eriophyes brownei Keifer, 1966	Symphoricarpos albus	nurs., city gr., bot. gard.	(2)

Table 4 continued

Mite species	Plant species	Collection site	References
Eriophyes canestrini (Nalepa, 1891)	*Buxus sempervirens*	nurs.	(1)
Phyllocoptes goniothorax (Nalepa, 1889)	*Crataegus laevigata*	city gr.	(6)
Phyllocoptes spiraeae (Nalepa, 1893)	*Spiraea japonica*	nurs.	(1) (18)
Phytoptus tetratrichus Nalepa, 1890	*Tilia cordata*	bot. gard., city gr.	(7) (9) (13)
Stenacis euonymi (Frauenfeld, 1865)	*Euonymus europaea, E. verrucosa*	city gr.	(6)
Erineum on leaves			
Aceria nervisequa (Canestrini, 1891)	*Fagus sylvatica* "Aspleniifoliae"	bot. gard.	(18)
Aceria pseudoplatanea (Nalepa, 1922)	*Acer pseudoplatanus*	city gr., bot. gard.	(6)
Acalitus brevitarsus (Fockeu, 1890)	*Alnus glutinosa*	city gr.	(6)
Aculops spinitobius (Keifer, 1966)	*Acer pseudoplatanus* "Leopoldii"	nurs.	(6)
Aculus hippocastani (Fockeu, 1890)	*Aesculus hippocastanum*	nurs.	(13)
Eriophyes exilis (Nalepa, 1891)	*Tilia tomentosa, T. americana heterophylla, T. petiolaris, T. japonica, T. cordata,*	bot. gard., city gr.	(7) (8) (13)
Eriophyes nervalis (Nalepa, 1892)	*Tilia cordata, T. americana heterophylla*	city gr.	(8)
Eriophyes viburni (Nalepa, 1889)	*Viburnum carlesii, V. rhytidophyllum, V. burkwoodii, V. × carlcephallum*	nurs., bot. gard.	(3) (14)
Leaf or inflorescence galls/leaf blistering			
Aceria caryae (Keifer, 1939)	*Carya ovata*	nurs.	(18)
Aceria fraxinivora	*Fraxinus excelsior*	city gr.	(6)
Aceria macrorhynchus (Nalepa, 1859)	*Acer pseudoplatanus*	nurs., city gr.	(14)
Aceria tenella (Nalepa, 1892)	*Carpinus betulus* "Quercifolia"	nurs., bot. gard.	(6)
Aculops macrotrichus (Nalepa, 1889)	*Carpinus betulus*	city gr.	(6)
Aculus campestricola (Frauenfeld, 1865)	*Ulmus glabra*	city gr.	(3) (14)
Aculus truncatus (Nalepa, 1892)	*Salix purpurea*	nurs.	(6)
Eriophyes crataegi (Canestrini, 1891)	*Crataegus laevigata*	city gr.	(18)
Eriophyes exilis (Nalepa, 1891)	*Tilia platyphyllos*	nurs., city gr.	(7) (13)

Table 4 continued

Mite species	Plant species	Collection site	References
Eriophyes inangulis (Nalepa, 1892)	*Alnus glutinosa*	city gr.	(6)
Eriophyes laevis (Nalepa, 1889)	*Alnus glutinosa*	city gr.	(6)
Eriophyes pyri (Pagenstecher, 1857)	*Sorbus aucuparia*	city gr.	(13)
Eriophyes tiliae (Pagenstecher, 1857)	*Tilia cordata, T. euchlora, T. americana*	city gr., nurs.	(14)
Stenacis triradiatus (Nalepa, 1892)	*Salix aurita, S. purpurea*	city gr.	(13)
Vasates quadripedes (Shimer, 1869)	*Acer saccharinum*	nurs., city gr.	(13)
Growth stunting of shoots/leaf resetting			
Eriophyes junipereti Keifer, 1960	*Juniperus communis*	city gr.	(4)
Rhinophytoptus platani Boczek & Shi, 1965	*Platanus × acerifolia*	nurs.	(14)
Shevchenkella brevisetosus (Hodgkiss, 1913)	*Acer negundo*	nurs.	(1)
Trisetacus juniperinus	*Juniperus procumbens*	nurs.	(4) (13)
Big buds/drying buds			
Aceria arceosae (Briones & McDaniel, 1976)	*Caragana arborescens*	nurs.	(3) (15)
Cecidophyopsis psilaspis (Nalepa, 1893)	*Taxus baccata*	city gr., bot. gard.	(13) (15)
Phytoptus avellanae Nalepa, 1889	*Corylus avellana* "Purpurea"	nurs.	(6)

References: (1) Łabanowski and Soika 1995, (2) Łabanowski and Soika 1997, (3) Łabanowski and Soika 1998, (4) Łabanowski and Soika 2000, (5) Łabanowski and Soika 2002, (6) G. Łabanowski and G. Soika—personal observations, (7) Soika 2005, (8) Soika 2007, (9) Soika 2008, (10) Soika and Kiełkiewicz 2004, (11) Soika and Łabanowski 1998, (12) Soika and Łabanowski 1999a, (13) Soika and Łabanowski 1999b, (14) Soika and Łabanowski 2000a, (15) Soika and Łabanowski 2000b, (16) Soika and Łabanowski 2002a, (17) Soika and Łabanowski 2002b, (18) Soika and Łabanowski 2006

growth of both leaves and shoots in common box, *Buxus sempervirens*, is caused by *Eriophyes canestrini* (Nalepa). Very detrimental to plants are also eriophyoid species that induce rusting of leaves. The most common eriophyoid species, both in nurseries and botanical gardens, is *Aculus atlantazaleae* (Keifer) which occurs on *Rhododendron japonicum* and other *Rhododendron* hydrids of the Knaphill-Exbury and Mollis group. In nurseries, strong bronzing of leaves is caused by *Aculus ballei* (Nalepa) on *Tilia* × *europaea* 'Pallida' and *T. platyphyllos* 'Rubra'; *Aculus epiphyllus* (Nalepa) on *Fraxinus excelsior* (Globosa, Jaspidea, Simplicifolia and Westhofs Glorie), *F. monophylla* and *F. pennsylvanica* (Aucubaefolia and Crispa); *Aculus fockeui* (Nalepa & Trouessart) on *Prunus serrulata*; *Tetra concava* (Keifer) on *Ulmus glabra* 'Exoniensis', *U.* × *hollandica* and some cultivars of *Ulmus* (Jacqueline Hillier and Camperdownii); *Shevtchenkella carinata* (Nalepa) on *Aesculus hippocastanum*. Silvering of leaves on *Syringa vulgaris* and its cultivars growing in nurseries as well as in botanical gardens and city greenery is induced by *Tetraspinus lentus* Boczek. Discolouration and malformation of leaves on *Robinia pseudoacacia* and its varieties (Bessoniana, Myrtifolia, Rozynskiana, Tortuosa, Umbraculifera) in nurseries and botanical gardens is caused by *Aculops allotrichus* (Nalepa). Similar symptoms are induced by *Phyllocoptes spiraeae* (Nalepa) on *Spiraea japonica* and its cultivars (Anthony Waterer, Crispa, Goldflame, Goldmound). The white erineum produced on both the upper and lower leaf surfaces of *Viburnum carlesii*, *V. rhytidophyllum*, *V.* × *burkwoodii* and *V.* × *carcephalum,* growing in botanical gardens and nurseries, is caused by *Eriophyes viburni* (Nalepa).

In city greenery and botanical gardens, the most commonly observed damage symptoms caused by eriophyoid mites are galls on *Tilia* spp. Among the few known species, the most frequently found are *Eriophyes tiliae* (Pagenstecher) which causes nail-like galls and *Eriophyes exilis* (Nalepa) which induces white erineum on the upper leaf surfaces of *T. tomentosa*, *T. americana heterophylla*, *T. petiolaris* and *T. japonica*. *Eriophyes exilis* can also cause erineum on the lower leaf surface of *T. cordata* and this same species induces galls covered with pubescence within the leaf vein axils on the upper leaf surface of *T. platyphyllos*. The most interesting species is *Phytoptus tetratrichus* Nalepa which causes tight upward leaf-roll galls along the edges of leaves of *T. cordata*. At the same time, this species creates warty galls on the upper leaf surfaces of *Tilia tomentosa* and erineum on the undersides, whereas on *T. americana*, it induces digitate protuberances both on the upper and lower surfaces of leaves.

Concluding remarks

The sparse literature on the eriophyoid mite fauna of forest coniferous trees (see Smith 1984; Castagnoli 1973; Xue et al. 2007) indicates that there is a lack of complex studies on this topic. This may be the result of the low significance of eriophyoid mites as forest pests, even though they may hold great importance from an ecological and evolutionary viewpoint (Lindquist et al. 1996; Sabelis and Bruin 1996). The difficulties in sampling from large sized, old, trees may also help to explain this lack of data. A consequence is that serious problems are then encountered for gathering representative data because of a deficiency in consistent sampling methodology. During such studies, it is important to take into account the diversity of microhabitats in which eriophyoid mites live and the density of their populations. Unfortunately, both the low density of eriophyoids coupled with their diverse living strategies on such tree species, indicates the necessity of taking rather large samples from various plant parts. Therefore, a single sample should be large enough to

contain most microhabitats which eriophyoid mites may inhabit. Satisfying these requirements is a very laborious task. This is also a likely reason for the small number of published papers dealing with eriophyoid mites found on forest coniferous trees.

The same considerations could be extended to the eriophyoid fauna that colonize broad leaf, deciduous plant species. In comparison with conifers, deciduous plants host a more varied eriophyoid species composition, frequently studied only from a faunistic point of view and/or as a consequence of the strange abnormalities that they cause. Few studies have dealt with the real impact of these mites on the natural environment even if they are among the most frequent of plant inhabitants. A study on five woody plants species of a riparian ecosystem (Abras et al. 2005) reported that among all pests and diseases found, eriophyoid mites had a presence ranging from 3.6% on ash and up to 75% on maple trees. The associated injuries always weakened trees and slowed down growth. The leaf size and host plant abundance in a forest in Finland explained that about 66% of eriophyoid species richness was on broad leaf trees (Niemela et al. 2006). It is also likely that in other forest ecosystems, resource availability is one of the most important factors for increasing the probability of random colonization and adaptative radiation of eriophyoid mites.

The strong relationship of eriophyoid mites with their host plants could be more intensively exploited for ecological, evolutionary and functional studies. On this aspect, interesting results were obtained by studying the relationship between *Aceria macrorynchus* (Nalepa) and *Acer opalus*. This tree is characterized by three different sexual morphs and the mite attacks the pollen-bearing morph more often and more harmfully. A possible consequence is that this eriophyoid species could act as a selective force driving the separation of sexes of the plant (Verdù et al. 2004).

Generally, attack by eriophyoid mites seems to be not too debilitating for mature plants. However, it could become particularly injurious to seedlings in nurseries and young plantations. In this case, the higher availability of the plant host to optimal growing conditions which favours eriophyoid mite diffusion and outbreak, as well as the lack of a delicate balance which often controls natural pest populations, contributes to making the avoidance of economic damage very difficult. In some ways, such damage is also difficult to quantify because typically this may have unforeseeable and long lasting effects. For example, unlike other gall-forming arthropods, the gall mite of wild cherry (*Prunus serotina*), namely *Eriophyes cesaricrumena* (Walsh), not only has a negative effect on the photosynthetic rate of galled leaves, but also on gall-free leaves of the same shoot (Larson 1998). In the case of nursery infestation involving *T. juniperinus,* the detrimental effects on tree development were observed even 2 years after transplanting (Castagnoli et al. 2002) and even after mites had died or left the tree (Simoni et al. 2004).

The most effective strategy in reducing damage in ornamental plants was to use healthy rootstock and grafting material. Because of the widespread commercialization of ornamental plants, the risk of introducing exotic eriophyoid species or creating varieties or clones that are more susceptible is extremely high. Appropriate studies dealing with host preferences and different relationships with plants should be expanded.

Scarce attention has also been paid to the effects of air pollution on the eriophyoid mite fauna of trees. In one of the first papers on this topic, Kropczynska et al (1985) did not observe many differences in eriophyoid species diversity between trees in parks and on streets compared with those in the natural environment. Infestations were only occasionally higher in the urban environment. No influence of the urban environment was observed in *Eriophyes tiliae* (Pagenstecher) on lime trees (Buchta et al. 2006). In an ongoing study by two of the authors (M. Castagnoli and S. Simoni), seven eriophyoid species (some of which are probably new to science) were found on *Quercus ilex* at three sites comprising different

levels of urbanization in a restricted area near Florence, Italy. In the city square, only two of the most frequent and numerous species were found, namely *Aceria ilicis* (Canestrini) and *Cecidophyes* sp. In a natural stand, all species were recorded, apart from one species, which was exclusive to the city park. In this location (city park), only four species were collected. Also, for all of the other mite species found, the location of trees did not influence the abundance of mites but affected the number of species found, being higher in the natural environment (M. Castagnoli and S. Simoni, unpublished data). Koricheva et al. (1996) observed that both birch and aspen reacted by producing smaller leaves in the presence of copper-nickel air pollution. The eriophyoid mites of birch and aspen also had a different behaviour with regards to the air gradient created by these heavy metals. On birch, mite densities decreased towards the pollution source and were negatively correlated with the level of heavy metals within the leaf. This same trend does not seem to affect aspen eriophyoid mites.

In the near future, populations of eriophyoid mites living on forest and ornamental plants should constitute an excellent material for studying different and intriguing aspects of relationships among herbivores, host plants and the environment. Since there is usually an ancient and stable relationship between each eriophyoid species and its host plant (Lindquist 1998), any little bias registered on mite behaviour and/or plant reaction could also be an excellent advertisement for change in the environment.

References

Abras S, Chandelier A, Fassotte C, Lissarague J-B, Debruxelles N, Dufays E, Cavalier M (2005) Phytosanitary monitoring of woody species from banks of watercourses in Vallonia. Phytoparasitica 6:69–80

Amrine JW (2003) Catalog of the Eriophyoidea. A working catalog of the Eriophyoidea of the world. Version 1.0 http://insects.tamu.edu/research/collection/hallan/acari/eriophyidae/

Amrine JW, Stasny TA (1994) Catalog of the Eriophyoidea (Acarina: Prostigmata) of the world. Indira Publishing House, West Bloomfield, Michigan 798 pp

Bagnyuk IG (1984) Novii chetirekhnogii kleshch (Acarina, Tetrapodili) iz pochek pikhti sibirskoi. (A new bud mite (Acarina, Tetrapodili) the pest of the Siberian fir (*Abies sibirica*)). Zool Zh 63(3):373–381

Boczek J (1962) *Nalepella haarlovi* n sp. (Acarina, Eriophyidae). Entomol Meddel 31:195–197

Boczek J (1969) Studies on mites (Acarina) living on plants in Poland. XI. Bull Pol Ac Biol 17(6):393–398

Boczek J, Shevchenko VG (1996) Ancient associations: eriophyoid mites and Gymnosperms. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control (World Crop Pests). Elsevier Science B.V., Amsterdam, pp 217–225

Boczek J, Harding S, Shi A, Bresciani J (2002) A new species of *Nalepella* Keifer (Acarina: Eriophyoidea: Phytoptidae) from *Abies* in Denmark. Acarologia 42(1):53–60

Buchta I, Kula E, Krestanpolova M (2006) Occurrence variations and spatial distribution patterns of *Eriophyes tiliae* (Pgst.) (Acari, Eriophyidae) subspecies in the urban environment. J Forest Sci 52(12):547–555

Castagnoli M (1973) Contributo alla conoscenza degli Eriofidi viventi sul genere *Pinus* in Italia. Redia 54:1–22

Castagnoli M (1996) Ornamental coniferous and shade trees. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control (World Crop Pests). Elsevier Science B.V., Amsterdam, pp 661–671

Castagnoli M, Simoni S (1998) Danni da acari eriofidi su cipresso. Ann Acad It Sci For 47:69–78

Castagnoli M, Simoni S (2000) Observations on intraplant distribution and life history of eriophyoid mites (Acari: Eriophyidae, Phytoptidae) inhabiting evergreen cypress (Cupressus sempervirens L.). Int J Acarology 26:93–99

Castagnoli M, Simoni S, Panconesi A, Failla O (2002) Susceptibility of cypress seedlings to the eriophyoid mite *Trisetacus juniperinus*. Exp Appl Acarol 26:195–207

Guido M, Battisti A, Roques A (1995) A contribution to the study of clone and seed pests of the evergreen cypress (*Cupressus sempervirens* L.) in Italy. Redia 78:211–227

Herms DA, Mattson WJ (1992) The dilemma of plant: to grow or to defend. Q Rev Biol 67:283–335

Huang KW (2001) The eriophyid mites of Taiwan: description of eighty-six species from the Tengchih Area. Bull Nat Mus Nat Sci 14:1–84

Kadono F (1981) Two new eriophyid mites from Japan (Acarina, Eriophyidae). Appl Entomol Zool 16(4):419–422

Keifer HH (1959) New Eriophyid mites. Ann Entomol Soc Amer 52(6):649–657

Koricheva J, Lappalainen J, Vuorisalo T, Haukioja E (1996) Density patterns of gall mites (Acarina: Eriophyidae) in a polluted area. Environ Pollut 93(3):345–352

Kropczynska D, van de Vrie M, Tomczyk A (1985) Woody ornamentals. In: Helle W, Sabelis MW (eds) Spider mites-their biology, natural enemies and control, vol 1B. Elsevier, Amsterdam, pp 385–393

Kruel W (1963) Gallmilben an Kiefer (Acarina: Eriophyidae). Beitr Ent 13:566–576

Kuang HY (1980) A new species of the genus *Asetacus* Keifer from China (Eriophyoidea: Rhyncaphytoptidae). Entomotaxonomia 2(3):235–236 (in Chinese, English abstract)

Kuang HY, Luo GH, Wang AW (2005) Fauna of eriophyid mites from China (Acari: Eriophyoidea). China Forestry Publishing House, Beijing, China 176 pp

Łabanowski G, Soika G (1995) Lesser known and unknown mites (Acarina)—pests of ornamental trees and shrubs of nurseries in Poland. In: Boczek J, Ignatowicz S (eds) Proceeding of symposium "Advances of Acarology in Poland". Siedlce, pp 127–132

Łabanowski G, Soika G (1997) Nowe i mniej znane szkodniki występujące na drzewach i krzewach ozdobnych. Progr Plant Protection/Postępy w Ochronie Roślin 37(1):218–223

Łabanowski GS, Soika GM (1998) Zagrożenie drzew i krzewów liściastych w szkółkach roślin ozdobnych przez szkodniki. Progr Plant Protection/Postępy w Ochronie Roślin 38(1):172–179

Łabanowski G, Soika G (2000) Eriophyoid mites (Acari: Eriophyoidea) on ornamental coniferous plants in Poland. Jour Plant Protection Res 40(2):85–93

Łabanowski G, Soika G (2002) Eriophyoid mites (Acari: Eriophyoidea) on ornamental plants in Poland. Fagaceae family: descriptions of three new species. Bull Pol Acad Sc Biol Sc 50(1):49–61

Larson K (1998) The impact of two gall-forming arthropods on photosynthesis rates of their host. Oecologia 115:161–166

Lewandowski M (2006) A new eriophyoid mite species (Acari: Eriophyoidea) on *Picea abies* (Pinaceae). Zootaxa 1304:61–68

Lewandowski M, Kozak M (2008) Distribution of eriophyoid mites (Acari: Eriophyoidea) on coniferous trees. Exp Appl Acarol 44:89–99

Lindquist EE (1998) Evolution of phytophagy in trombidiform mites. Ex Appl Acarol 22:81–100

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites: their biology, natural enemies and control (World Crop Pests). Elsevier Science B.V., Amsterdam

Löyttyniemi K (1969) Akamapunkkilaji (*Nalepella haarlowi* var. *picea-abietis* Loyttyniemi, Acarina, Eriophyidae) kuusen taimien tuholaisena taimitarhoissa. (An Eriophyidae species damaging spruce seedlings in nurseries). Silva Fenn 3(3):191–200

Löyttyniemi K (1971) On the biology of *Nalepella haarlovi* Boczek var. *piceae-abietis* Löyttyniemi (Acarina, Eriophyidae). Comm Int For Fenn 73(3):1–16

Löyttyniemi K (1975) Mass outbreaks of *Epitrimerus pungiscus* Keifer (Acarina, Eriophyidae) on Norway spruce *Picea abies* (L.) Karst. Ann Ent Fenn 41(1):13–15

Marshall VG, Lindquist EE (1972) Notes on the genus *Nalepella* (Acarina: Eriophyioidea) and the occurrence of *N. halourga* on black spruce in Canada. Can Entomol 104:239–244

Nalepa A (1887) Die Anatomie der Phytopten. SB Ak Wiss Wien 96(4):115–165

Niemela P, Roininen H, Vanhanen H, Veteli TO (2006) Species richness of eriophyoid mites on Finnish trees and Shrubs. In: Ozaki K, Yukawa J, Ohgushi T, Price PW (eds) Galling arthropods and their associates ecology and evolution. Springer, New York, pp 21–32

Orozumbekov A, Moore B (2007) Overview of forest pests Kyrgyz Republic. In: Allard G (ed) Forest health and biosecurity working papers. Forest Resources Development Service, Forestry Department, Food and Agriculture Organization of the United Nation, Working Paper FBS/21E, Rome, Italy, pp 1–60. Available via DIALOG: www.fao.org/forestry/media/12294/1/0. Accessed 19 Dec 2008

Panconesi A (2007) Il cipresso: dalla leggenda al futuro. CNR, Istituto per la protezione delle piante, Firenze

Panconesi A, Raddi P (1998) Osservazioni e considerazioni sul cancro del cipresso in Toscana. Ann Acad It Sci For 47:14–34

187 ⓐ Springer

Petanovic RU, Boczek J, Jovanovic S, Stojnic B (1996) Eriophyoidea (Acari: Prostigmata). In: Karaman G (ed) Fauna Dormitora, vol 32, no 18. Crnogorska Akademija Nauka i Umjetnosti, Podgorica, pp 5–42

Roivainen H (1951) Contributions to the knowledge of the eriophyids of Finland. Acta Entomol Fenn 8:1–72

Sabelis MW, Bruin J (1996) Evolutionary ecology: life history patterns, food plant choice and dispersal. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control (World Crop Pests). Elsevier Science B.V., Amsterdam, pp 329–366

Shevchenko VG (1962) Novii chetirekhnogij Kleshch *Trisetacus kirghizorum* sp.n. (Acarina, Eriophyidae) vreditel semjan arci. Tr Kirgh Lesn Opytn Sta 3:299–305

Shevchenko VG (1995) On phototaxis in two species of genus *Trisetacus* (Acari: Eriophyoidea). In: Boczek J, Ignatowicz S (eds) Proceedings of symposium "Advances of Acarology in Poland". Siedlice, pp 77–83

Shevchenko VG, Bagnyuk IG, Rinne V (1993) *Trisetacus pini* (Nalepa, 1889) in some Baltic countries and in Russia (Taxonomy, morphology, biology, distribution). Acarina (Moscow) 1:51–71

Siewniak M (1971) Eine bisher unbekannte Schädigung der Sämlinge von *Picea abies* Karst. durch Gall-milben (Acar. Eriophyoidea). Entomol Nachr (Dresden) 15:66–67

Simoni R, Cantini R, Castagnoli M, Battisti A (2004) Impact and management of the eriophyoid mite *Trisetacus juniperinus* on the evergreen cypress *Cupressus sempervirens*. Agric and Forest Entomology 6:175–180

Skoracka A, Lewandowski M, Boczek J (2005) Catalogue of eriophyoid mites of Poland. Catalogus faunae Poloniae (N.S.), no. 1, Natura optima dux Foundation, Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, 199 pp

Smith IM (1978) Two new species of *Trisetacus* (Prostigmata, Eriophyoidea) from berries of *Juniperus* in North America. Can Entomol 110:1157–1160

Smith IM (1979) Description of new species of *Trisetacus* (Prostigmata, Eriophyoidea) from Pinaceae in Eastern North America. Can Entomol 111:5–429

Smith IM (1984) Review of species of *Trisetacus* (Acari: Eriophyoidea) from North America, with comments on all nominate taxa in the genus. Can Entomol 116:1157–1211

Soika G (2005) Eriophyoid mites (Acari: Eriophyoidea) occurring on lime trees in ornamental nurseries. Biological Letters 43(2):367–373

Soika G (2007) Szpeciele z rodzaju *Eriophyes* występujące na lipach w parkach. Post Plant Protect Ochr Roślin 47(1):374–377

Soika G (2008) Szpeciele galasotwórcze na lipach. Ochrona Roślin 53(1):27–30

Soika G, Kiełkiewicz M (2004) Occurence of *Phytoptus tetratrichus* (Nalepa) (Acari: Eriophyoidea) and differences in the morphology of leaf galls on two linden species. Phytophaga 14:615–622

Soika GM, Łabanowski G (1998) Nowe gatunki szpecieli (Eriophyoidea) w szkółkach roślin ozdobnych. Progr Plant Protection/Postępy w Ochronie Roślin 38(2):416–418

Soika G, Łabanowski G (1999a) Szpeciele—sprawcy wyrośli i zniekształceń na roślinach ozdobnych. Progr Plant Protection/Postępy w Ochronie Roślin 39(2):537–540

Soika G, Łabanowski G (1999b) Types of damages caused by eriophyoid mites (Acari: Eriophyoidea) on ornamental trees and shrubs. In: Mater. XXVI symposium Akarol. "Akarologia Polska u Progu Nowego Tysiąclecia", Kazimierz Dolny, pp 371–380

Soika G, Łabanowski G (1999c) Eriophyoid mites (Acari: Eriophyoidea) on ornamental plants in Poland. Pinaceae family: description of two new species. Bull Pol Acad Sci Biol Sc 47(2):43–52

Soika G, Łabanowski G (2000a) Eriophyoid mites (Acari: Eriophyoidea) on ornamental plants in Poland. Fabaceae family. Descriptions of two new species. Bull Pol Acad Sci Biol Sc 47(2):157–167

Soika GM, Łabanowski G (2000b) Eriophyoid mites (Acari: Eriophyoidea) on ornamental plants in Poland. Fabaceae family. Descriptions of two new species. Bull Pol Acad Sci. Biol Sc 47(2):157–167

Soika G, Łabanowski G (2002a) Eriophyoid mites (Acari: Eriophyoidea) living on *Quercus* spp. (Fagaceae) in Poland. Bull Pol Acad Sci 50(1):63–70

Soika GM, Łabanowski G (2002b) Eriophyoid mites (Acari: Eriophyoidea) living on *Fagus* spp. (Fagaceae) in Poland. Bull Pol Acad Sci 50(1):71–83

Soika G, Łabanowski G (2006) New records of eriophyoid mites (Acari: Eriophyoidea) on ornamental plants in Poland. In: Proceedings of symposium "Advances in Polish Acarology", Warszawa SGGW, pp 385–398

Verdù M, Garcia-Fayos P, Gleiser G (2004) Mites attack males of the sexually polymorphic tree *Acer opalus* more harmfully and more often. Funct Ecol 18:592–597

Xue XF, Hong XY (2005) A new genus and eight new species of Phyllocoptini (Acari: Eriophyidea: Phyllocoptinae) from China. Zootaxa 1039:1–17

Xue XF, Hong XY (2006) Eriophyoid mite fauna from Henan Province, central China (Acari: Eriophyoidea) with descriptions of five new species. Zootaxa 1204:1–30

Xue XF, Song ZW, Hong XY (2006) Six new species of Rhyncaphytoptinae from northwestern China (Acari: Eriophyoidea: Diptilomiopidae). Zootaxa 1225:1–18

Xue XF, Song ZW, Amrine JW, Hong XY (2007) Eriophyoid mites on coniferous plants in China with descriptions of a new genus and five new species (Acari: Eriophyoidea). Int J Acarol 33(4):333–345

Springer

The role of eriophyoids in fungal pathogen epidemiology, mere association or true interaction?

**Efrat Gamliel-Atinsky · Stanley Freeman · Marcel Maymon ·
Eduard Belausov · Ronald Ochoa · Gary Bauchan · Anna Skoracka ·
Jorge Peña · Eric Palevsky**

Abstract   A considerable number of plant feeding mites representing different families such as Acaridae, Siteroptidae, Tydeidae, and Tarsonemidae interact with plant pathogenic fungi. While species within the Eriophyoidea appear to be the most common phytophagous mites vectoring virus diseases, little is known of their role in fungal pathogen epidemiology. In the present article, we present two studies on eriophyoid-fungal relationships.

E. Gamliel-Atinsky
Department of Plant Pathology, University of Georgia, 2311 Plant Sciences, 120 Carlton St., Athens, GA 30602, USA

S. Freeman · M. Maymon
Department of Plant Pathology and Weed Research, The Volcani Center, Agricultural Research Organization (ARO), P. O. Box 6, 50250 Bet Dagan, Israel

E. Belausov
Microscopy Unit, The Volcani Center, ARO, Bet Dagan, Israel

R. Ochoa
Systematic Entomology Laboratory, Agriculture Research Service, US Department of Agriculture, Henry A. Wallace Beltsville Agricultural Research Center, Beltsville, MD 20705, USA

G. Bauchan
Electron and Confocal Microscopy Unit, Agriculture Research Service, US Department of Agriculture, Henry A. Wallace Beltsville Agricultural Research Center, Beltsville, MD 20705, USA

A. Skoracka
Department of Animal Taxonomy and Ecology, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland

J. Peña
Department of Entomology and Nematology, Tropical Research and Education Center, University of Florida, Homestead, FL 33031, USA

E. Palevsky (✉)
Department of Entomology, Newe-Ya'ar Research Center, (ARO), P. O. Box 1021, 30095 Ramat Yishay, Israel
e-mail: palevsky@volcani.agri.gov.il

191   ⸙ Springer

The first focusing on the association between *Aceria mangiferae* and the fungal pathogen *Fusarium mangiferae* in mango is presented as a case study. The second, as the research is still in a preliminary phase, reports on quantitative and descriptive associations between the cereal rust mite *Abacarus hystrix* and rusts caused by *Puccinia* spp. Mango bud tissue colonized with *F. mangiferae*, and wheat and quackgrass leaves colonized with *Puccinia* spp., supported significantly higher populations of eriophyoid mites. Both mite species were observed bearing the spores of the respective pathogens on their body integument. *Aceria mangiferae* vectored the pathogen's spores into the bud, the sole port of entry for the fungal pathogen and the frequency and severity of fungal infection increased in the presence of *A. mangiferae*. While it appears that eriophyoids are playing a role in fungal epidemiology, clearly further research is needed to enhance our understanding of direct and indirect (plant mediated) interactions between plant pathogens and eriophyoid mites in different plant-pathogen systems.

Keywords Eriophyoidea · Fungi · Mite-fungus-plant interactions · *Aceria mangiferae* · *Abacarus hystrix* · *Fusarium mangiferae* · *Puccinia* spp.

Introduction

The evolution of mycophagy in the Acari has been well reviewed by Krantz and Lindquist (1979) based on the premise that the ability to feed on vascular tissues arose through feeding on fungi in some mite groups and also on the adaptive strategies and ecological relationships associated with the mycophagous habits that provide parallels to those related to phytophagy. A considerable number of mites representing many families in different suborders interact with plant pathogenic fungi. Herbivores may facilitate fungal infection by two main mechanisms: either by vectoring pathogen spores or by creating wound sites for fungal penetration (Agrios 1980; Hatcher and Paul 2001).

Abdel-Sater and Eraky (2001) reported that the acarid mites, *Tyrophagus putrescentiae* Shrank and *Rhizoglyphus robini* Claparede, when living on bulbs, transfer the fungal pathogens *Aspergillus niger*, *Nectria haematococca*, *Rhyzopus stolonifer* and *Penicillium chrysogenum* attached to the outside of their bodies. Conversely the transfer of *Aspergillus flavus* and *Aspergillus ochraceus* is performed through their digestive tracts along with their foods. *Rhizoglyphus robini* are attracted to and penetrate *Fusarium* infested bulbs more rapidly than healthy ones (Okabe and Amano 1990, 1991).

Fusarium poae is associated with the siteroptid mite, *Siteroptes avenae* (Muller). Microscopic examination of *S. avenae* feeding on *F. poae* cultures revealed the presence of sporothecae containing microsporidia of the fungus. This close association between the mite and fungus is considered responsible for causing *Fusarium* glume spot on wheat in South Africa (Kemp et al. 1996).

The relationship of tydeid mites and mycophagy was emphasized by Krantz and Lindquist (1979). For instance, the tydeid *Parapronematus acaciae* Baker feeds and breeds on fungi that commonly occur on the leaves of citrus (McCoy et al. 1969). *Lorryia formosa* Cooreman was an effective sanitizing agent in citrus groves because it reduced levels of sooty mould fungi (Mendel and Gerson 1982). *Tydeus caudatus* (Dugés) densities positively correlated with levels of the grapevine downy mildew, *Plasmopara viticola*, in north eastern Italy (Duso et al. 2005). The tydeid, *Orthotydeus lambi* (Baker) plays a role in reducing the severity of powdery mildew on grapes caused by the fungus *Uncinula necator*, suggesting the important role of mycophagous mites as potential biological

control agents of plant pathogenic fungi (English-Loeb et al. 1999). *Vitus viparia* (Vitaceae), with closed off domatia, harbored lowered populations of *O. lambi* and higher levels of *U. necator* (Norton et al. 2001).

The tarsonemid, *Steneotarsonemus spinki* Smiley, appears to open ports of entry for the fungi, *Helmintosporium* and *Sarocladium oryzae* (Cardenas et al. 2003), which are responsible for grain discoloration of rice, *Oryza sativa. Steneotarsonemus ananas* (Tryon), the pineapple leathery pocket mite or pineapple fruit mite, is host specific to pineapples throughout the world (Mourichon 1991; Petty et al. 2002). Trichome cells fed upon by *S. ananas* serve as a favorable substrate for development of the fungus *Penicillium funiculosum*, the causal agent of inter fruitlet corking, leathery pocket, and fruitlet core rot/ black spot (Petty et al. 2002).

While several species within the Eriophyoidea are apparently the most common phytophagous mites vectoring viral diseases (Oldfield and Proeseler 1996), little is known of their role in fungal pathogen epidemiology. In the present article, we present two studies on eriophyoid-fungal relationships. The first focuses on the association between *Aceria mangiferae* Sayed and the fungal pathogen *Fusarium mangiferae* Britz, Wingfield & Marasas in mango and is presented as a case study where we describe some of the underlying mechanisms clarifying the role of the mite in mango malformation epidemiology. In the second study, as the research is still in a preliminary phase, we report on quantitative and descriptive associations between the cereal rust mite *Abacarus hystrix* (Nalepa) and rusts caused by *Puccinia* spp.

The role of the mango bud mite in mango malformation: a case study

Mango malformation is a severe disease, widely distributed in almost all mango-growing regions worldwide (Crookes and Rijkenberg 1985; Kumar et al. 1993; Ploetz 2001; Ploetz et al. 2002; Kvas et al. 2008). Symptoms of disease are associated with hormonal imbalance in the host that results in misshapen growth of both vegetative and reproductive parts of the tree (Majumder and Sinha 1972; Prasad et al. 1972; Kumar et al. 1993; Ploetz 2001, 2003). Vegetative malformation includes hypertrophy of young shoots, shorter internodes, dwarfed malformed leaves and an overall tightly bunched appearance of the shoot. Inflorescence malformation includes short, thick and branched axes of the floral panicles, larger flowers containing increased numbers of male and hermaphroditic flowers that are either sterile or eventually abort. Malformed inflorescences do not bear any fruit, resulting in great economic losses.

The etiology of mango malformation disease was controversial for many years and many factors have been suggested as causal agents of disease such as: nutritional deficiencies, hormonal imbalance, viruses, phytoplasmas, fungi and mites (Narasimhan 1954; Nariani and Seth 1962; Zaher and Osman 1970; Denmark 1983; Ochoa et al. 1994; Ploetz 2001). *Aceria mangiferae*, the mango bud mite, was hypothesized as the causal agent of mango malformation for over 40 years mainly due to high numbers of mites observed in malformed trees, and also because other members of the Eriophyoidea are known to cause proliferation, "witches broom" and gall symptoms of inflorescences in other plants (Westphal and Manson 1996). Despite the fact that the fungal theory was well established following Koch's postulates with several fungi, certain members of the genus *Fusarium* have been shown to cause the disease (Summanwar et al. 1966; Varma et al. 1974; Chakrabarti and Ghosal 1989; Manicom 1989; Ploetz and Gregory 1993; Freeman et al. 1999; Noriega-Cantú et al. 1999; Britz

et al. 2002; Ploetz 2003; Marasas et al. 2006; Kvas et al. 2008; Lima et al. 2009; Rodríguez-Alvarado et al. 2008), It is also clear now that *A. mangiferae* is not the causal agent of mango malformation, however, various studies suggest that the mite interacts with the fungal pathogen resulting in increased severity of disease (Prasad et al. 1972; Sternlicht and Goldenberg 1976; Gamliel-Atinsky et al. 2009a).

Our study was aimed at revealing the possible associations between *A. mangiferae* and the fungal pathogen *Fusarium mangiferae*. The specific objectives of the study were to: (1) assess whether *A. mangiferae* can carry conidia of *F. mangiferae* on or within its body; (2) determine the role of the mite in vectoring fungal conidia into the infection site; (3) determine the role of the bud mite in promoting the fungal infection process, and (4) evaluate the possible role of the bud mite in long-distance aerial dissemination of the fungal conidia. A green fluorescent protein (gfp)-marked strain of *F. mangiferae* was used throughout this study which distinguished it from that used in previous studies (Nariani and Seth 1962; Summanwar and Raychaudhuri 1968; Manicom 1989; Labuschagne et al. 1993) and helped distinguish the pathogen from other contaminants and opportunistic fungi. Below we will briefly describe the major results and implications from this study; a detailed account of this research can be found in Gamliel-Atinsky et al. (2009a).

Bearing conidia on or within the body of *Aceria mangiferae*

In order to test whether *A. mangiferae* can bear *F. mangiferae* conidia, two methods were used: the first one was aimed at determining whether the conidia attach to the outer integument of the mite and if this attachment is specific to a certain part of the body. Mites were exposed to the gfp-marked isolate of *F. mangiferae* and then inspected under a confocal microscope. In the second method, the possibility that the mite carries conidia within its body was assessed using a low-temperature scanning electron microscope (LT-SEM), taking measurements of both conidia and mite stylets (measured directly and indirectly according to the diameter of the feeding holes in the plant). We hypothesized that the diameter of the smallest conidia is larger than the diameter of the mite's stylets. Results from these observations demonstrated that external rather than internal bearing of conidia is feasible since mites were observed with conidia clinging to their body (Fig. 1) and LT-SEM measurements indicated that the width of the mite mouthparts was substantially smaller than the diameter of the smallest conidium (Fig. 2). Moreover, since there is a lack of continuity between the midgut and the hindgut of eriophyoid mites (Nuzzaci and Alberti 1996), fungal spores cannot be transferred and secreted in feces. Internal bearing of pathogens by eriophyoid mites is a known phenomenon with viral pathogens due to their minute size (Oldfield and Proeseler 1996). Associations with fungi is apparently only possible via external-body attachment, such as in the case of acaropathogenic fungi (McCoy 1996).

Vectoring conidia to penetration site

One possible benefit for *F. mangiferae* from this bipartite association is reaching the infection site. Results from our recent study demonstrated that the apical bud is the exclusive penetration site for the fungal pathogen (Gamliel-Atinsky et al. 2009b) which also serves as the exclusive living habitat of *A. mangiferae*. Most conidia of *F. mangiferae* disseminate in the air and randomly fall on the tree canopy which takes up most of the surface area of the orchard. One possible route of reaching the hidden, small apical bud is
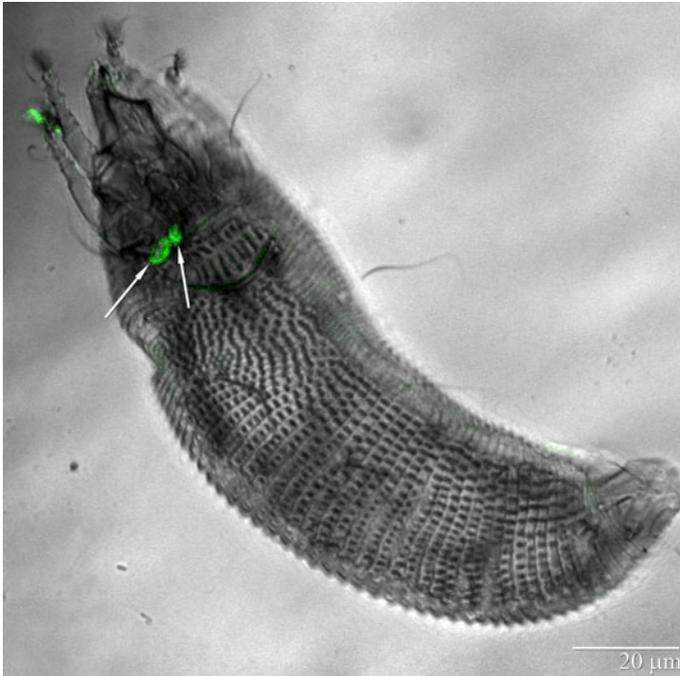
Fig. 1 Mango bud mite, *Aceria mangiferae*, bearing gfp-marked conidia (*arrows*) of *Fusarium mangiferae*, the causal agent of mango malformation disease

via the bud mite which posseses the ability of actively seeking out and reaching the apical bud from any location in the tree. In order to test the role of the mite in vectoring conidia into apical buds, an experiment on potted plants was performed. The experiment consisted of four treatments of different combinations of mites and/or conidia that were placed on leaves 5 cm away from apical buds. Our results showed that conidia reached the apical bud only in the treatment where both mites and conidia were co-inoculated on the leaves, demonstrating the potential of eriophyoid mites as vectors of fungal pathogens (Table 1).

Assisting conidial penetration

Two quantitative evaluations of the possible role of *A. mangiferae* in fungal penetration, a process taking place inside apical buds, were assessed. When apical buds of potted mango plants were inoculated with *F. mangiferae* in the presence and absence of bud mites, the frequency and severity of fungal colonization were significantly higher in buds inoculated with both fungus and mites (Table 2). This result clearly demonstrated that the presence of mites within the buds enhanced fungal colonization.

Association between fungal infestation and mite population levels

Another quantitative evaluation was designed in order to determine whether the presence of the fungus affected mite populations within the bud. Numbers of bud mites were compared within colonized and non-colonized buds by the fungal pathogen during 2006 and 2007. Higher numbers of mites were detected in buds colonized by the fungus rather
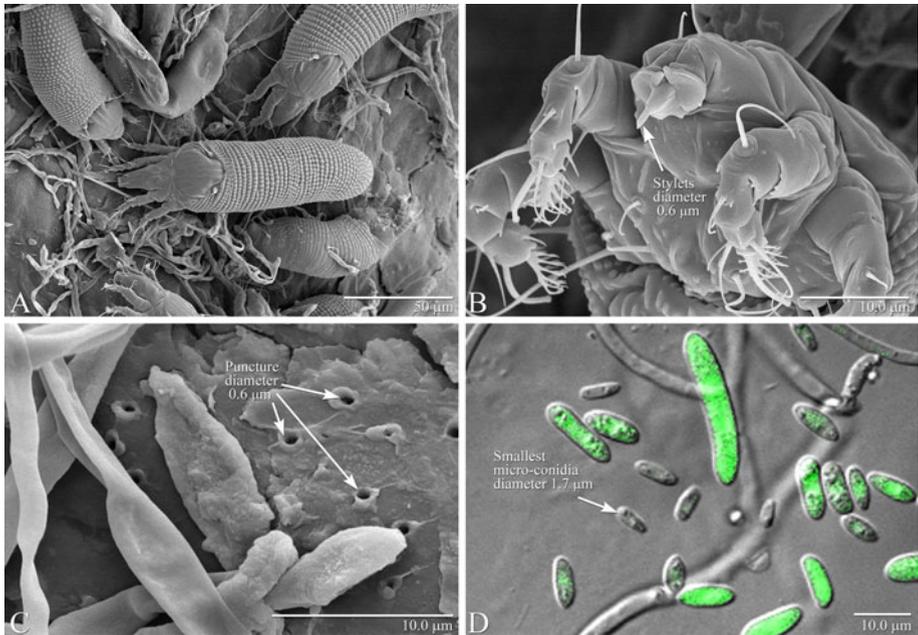
Fig. 2 **a** SEM image of mango bud mites, *Aceria mangiferae*, feeding on bud bracts; **b** SEM image of mango bud mite anterior ventral view of stylet. **c** SEM image of respective feeding puncture holes; **d** confocal image of gfp-marked conidia and micro-conidia of *Fusarium mangiferae*

Table 1 Total number of *Aceria mangiferae* and green fluorescent protein (gfp)-marked conidia of *Fusarium mangiferae* detected within 20 apical mango buds

Inoculation with	Bud mites	Conidia
Mites with gfp conidia	28[a]	9
Mites alone	35	0
Gfp alone	0	0
Untreated control	0	0

[a] All numbers different from zero were found significant ($P < 0.05$), according to a *t*-test analysis of the average number of mites and conidia per apical bud, (modified from Gamliel-Atinsky et al. 2009a)

Table 2 Frequency (%) and severity (%) of green fluorescent protein (gfp)-marked *Fusarium mangiferae* colonization in buds in the presence or absence of *Aceria mangiferae* over a 2 year period

Treatments	Frequency of colonization[a]		Severity of colonization[b]	
	2006	2007	2006	2007
Mites with gfp conidia	81.6	78.4	60.8	44.7
Gfp conidia alone	50.0	57.4	29.5	28.9
P[c]	0.004	0.043	<0.0001	0.009

[a] Statistical analysis was calculated using a chi-square test

[b] Statistical analysis was calculated using a *t* test

[c] Significance refers to each pair of means per year separately
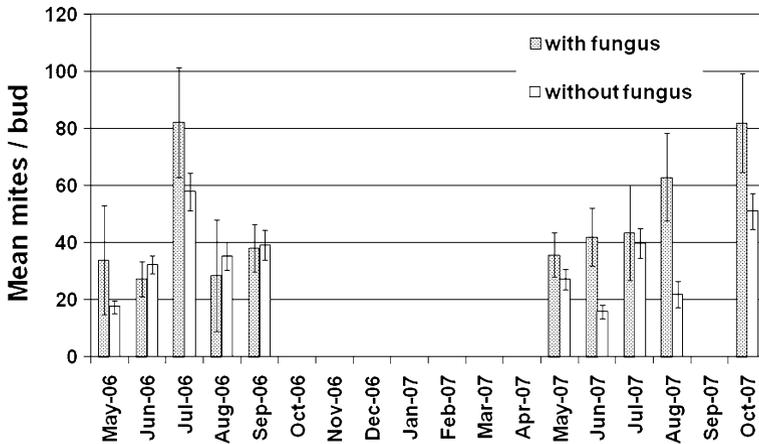
Fig. 3 Mean density of *Aceria mangiferae* within colonized and non-colonized buds by *Fusarium mangiferae* over a 2-year-survey in the Volcani experimental orchard, Bet Dagan, Israel. *Bars* represent standard errors of the mean (±SE). Biannual means were calculated and subjected to *t*-test analysis (results presented in text)

than in non-colonized buds (Fig. 3). When a bi-annual average was calculated for the ten sampling periods and analyzed by *t*-test, a significant difference was detected between 50 mites per bud found in colonized buds vs. 33.6 mites per bud found in non-colonized buds ($P = 0.0002$; $t_{586} = 3.731$).

Qualitative associations were assessed with both confocal and LT-SEM observations of apical buds that were inoculated with both the pathogen and the mites. Microscopic observations supported our finding by demonstrating the physical proximity and the actual contact between the two organisms within infected mango buds. Bud mites were observed in close proximity with gfp-marked hyphae and conidia, using a confocal microscope (Fig. 4a). LT-SEM observations also illustrated bud mites bearing hyphae and conidia on their body (Fig. 4b, c, d).

Assisting aerial conidial dissemination

Since previous attempts to trap conidia in the air failed (Varma et al. 1971) and the role of *A. mangiferae* in aerial dissemination of conidia was proposed (Ploetz 2001) we attempted to monitor both fungal conidia and mango bud mites using several trapping methods in order to shed light on the mode of conidial dissemination in the field. Conidia of *F. mangiferae* were trapped successfully using two trapping methods and an annual peak of dissemination was found in the spring/early summer months (Gamliel-Atinsky et al. 2009a). *Aceria mangiferae* was trapped throughout the season, but no fungal growth was detected after placing these mites on selective media for the fungus *F. mangiferae*. Our findings imply that conidia can reach the mango tree independently of the bud mite and thus the latter does not seem to play a role in the windborne dissemination of the pathogen.
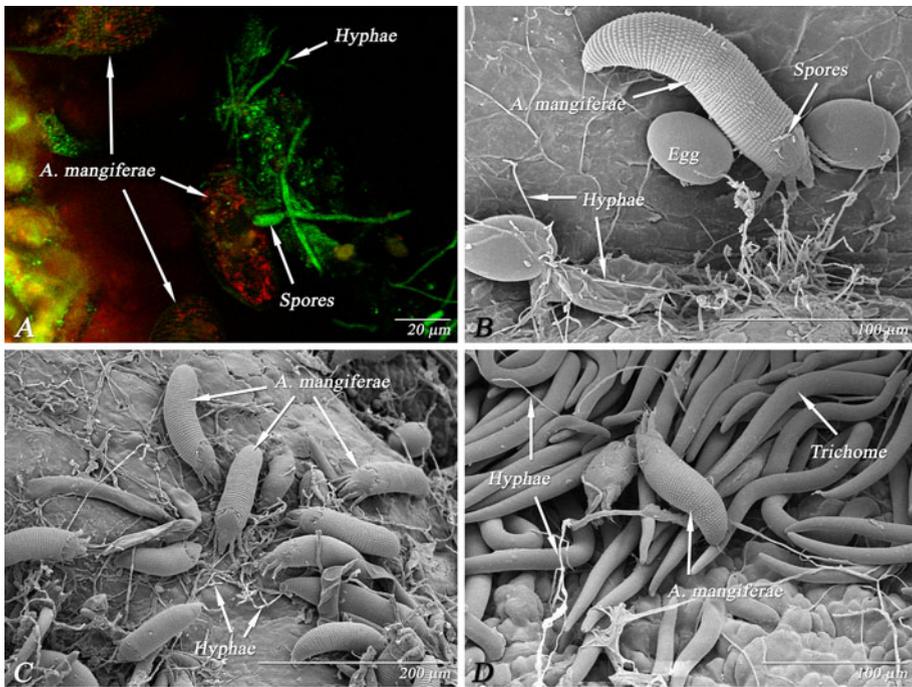
Fig. 4 Microscopic images of the mango bud mite *Aceria mangiferae* and *Fusarium mangiferae* within inoculated apical buds. **a** Confocal microscope image of three *A. mangiferae* mites and gfp-marked *F. mangiferae* hyphae with germinating conidia surrounding them; **b** SEM image of *A. mangiferae* with fungal conidia on their bodies and eggs in close proximity of fungal hyphae; **c** SEM image of a colony of *A. mangiferae* mites and fungal hyphae around and surrounding them; **d** SEM image of *A. mangiferae* near plant trichomes with fungal hyphae proximate to them

Associations between the cereal rust mite *Abacarus hystrix* and rusts caused by *Puccinia* spp.

The cereal rust mite *A. hystrix* is notable among eriophyoid mites in causing losses to cultivated grasslands. It has been found to infest wheat, oats, barley, rye, rice, quackgrass, timothy, orchardgrass and many other (ca. 60–70) cultivated and wild grass species throughout the world (Amrine and De Lillo 2003). *Abacarus hystrix* feeding causes leaf discoloration and inhibition of seed production, and at high densities the mite causes withering of plants and retards their growth (Frost and Ridland 1996). The cereal rust mite is also known to transmit ryegrass mosaic virus (RMV), a serious disease of temperate grasslands, and agropyron mosaic virus (AMV), a minor disease of wheat and quackgrass (Oldfield and Proeseler 1996). The mite lives freely on the upper leaf surfaces and disperses passively on air currents (Nault and Styer 1969).

Rusts caused by *Puccinia* spp. are significant diseases affecting cereal and other grasses worldwide. Infections may occur on stems, leaf sheaths, or leaf blades and glumes. A few days post infection elongated pustules develop, subsequently rupturing the plant epidermis and exposing a mass of reddish brown urediniospores (Fig. 5). Urediniospores are released from the uredinia and may be transported over long distances by wind and infect other plants. In areas with mild climates, infected grass foliage can serve as the overwintering
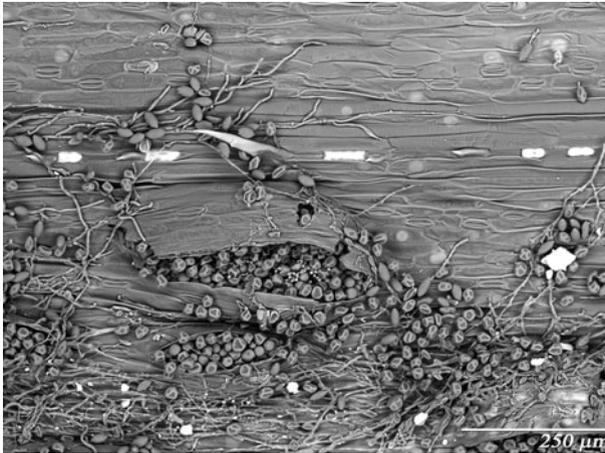
Fig. 5 SEM of a rust pustule caused by *Puccinia* spp. releasing urediniospores on the underside of a quackgrass leaf

site for the mycelium and urediniospores. Another type of rust spore that may overwinter is the teliospore, from which basidiospores are produced. The latter infect non-grass hosts, e.g., barberries *Berberis* spp., and after germination two more spore types (i.e., pycniospores and aeciospores) are formed. Aeciospores can infect only grasses, giving rise to urediniospores and thus completing the life cycle (Cummings 1971; Leonard and Szabo 2005).

During a survey of the eriophyoid fauna on grasses in Poland carried out from 1998 (Skoracka 2004), the concurrent presence of *A. hystrix* and rusts caused by *Puccinia* spp. have been reported on quackgrass and wheat. Moreover, mite specimens bearing rust spores on their bodies have been observed. Up to now, no reports have suggested the existence of relationships between eriophyoid mites and rust fungi. Here we present results of observations regarding the associations between rust fungi and the cereal rust mite.

Association between fungal infestation and mite population levels

Quackgrass *Elymus repens* (L.) Gould and wheat *Triticum aestivum* L. plants were collected in 1998–2001 in west Poland from 23 locations. The material included 143 samples, among them 99 samples contained quackgrass and 44 samples contained wheat. Each sample consisted of 5–10 individual shoots of a given grass species, collected randomly from the sampling location. Shoots were cut just above ground level and put into a plastic bag. The grasses were examined in the laboratory with a stereomicroscope. The presence of rust fungi per leaf was recorded. Mites were counted and mounted on slides, and subsequently identified with a phase-contrast microscope. Mean density of mites on leaves infected with rust [*DR*], and mean density of mites on leaves with no symptoms of rust (clear) [*DC*] were calculated. To test the differences between means two sample *t*-tests was applied. For computations, the S-PLUS software was used (S-PLUS 2005).

The density of the cereal rust mite was significantly higher on leaves infected by rust fungi (*DR*) compared to leaves with no symptoms of rust (*DC*). This result is true for both host species, quackgrass ($P < 0.0001$; $t_{3477} = -14.87$; Fig. 6A), and wheat ($P < 0.0001$; $t_{1212} = -8.86$; Fig. 6B).
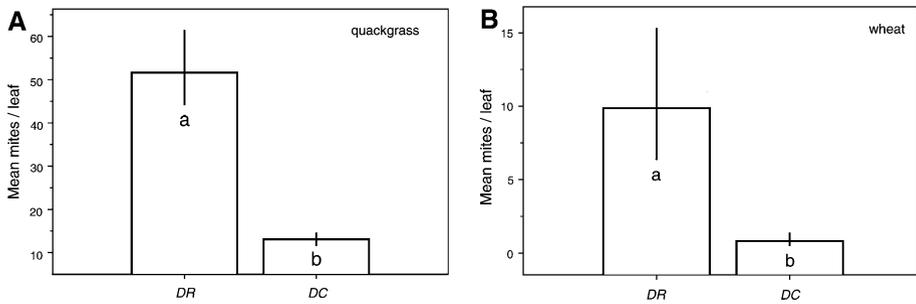
Fig. 6 Mean density of the cereal rust mite *Abacarus hystrix* on leaves infected with *Puccinia* spp. rust (*DR*) and non-infected (*DC*) on **A** quackgrass and **B** wheat. *Bars* represent 95% confidence intervals around means. Different letters represent significant differences ($P < 0.0001$) between combinations based on two sample *t*-test

On the leaves infected by rust, mites aggregated near rust pustules. Some mite specimens bore urediniospores attached to their dorsal opisthosoma. From one to few (about 5–6) urediniospores were observed attaching to the singular mite specimen (Fig. 7a, b).

Discussion

Based on our LT-SEM study of infested mango bud bracts with bud mites and the pathogen (R. Ochoa et al., unpublished), we have no proof that the perforations created by *A. mangiferae* serve as ports of entry for *F. mangiferae*. However, it is clear that the presence of the mite, at least in the case of *A. mangiferae*, increases the frequency and severity of fungal infection. Similarly, *Aceria tulipae* (Keifer) was implicated in the spread of fungus-causing rot of garlic bulbs in the field (Jeppson et al. 1975). Saini and Singh (1989) reported that galls induced by eriophyoid mites harbor overwintering inoculum of the fungus *Microsphaera alphitoides* f. sp. *ziziphi*, the causal agent of powdery mildew of Indian Jujube *Ziziphus mauritania* Lam., thus improving the perpetuation of the disease from one season to the next.

In respect to the effect of the pathogen on mite populations, both mango bud tissue infected with *F. mangiferae* and wheat and quackgrass leaves infected with *Puccinia* spp. supported significantly higher populations of eriophyoid mites. In a bi-seasonal experiment set up to evaluate induced plant responses to herbivores and pathogens in papaya, Fournier et al. (2004) observed higher populations of the papaya rust mite, *Calacarus flagelliseta* Fletchmann, DeMoraes, and Barbosa on plants previously exposed to the powdery mildew, *Oidium caricae*. The authors suggested that exposure to powdery mildew induced plant susceptibility to the papaya rust mite, possibly due to improved plant nutritional value and/ or to lower expression of plant defenses. Peña et al. (2005) found higher densities of *A. mangiferae* mites on the external and middle bracts of mango buds than on the internal bracts next to the dome. The authors proposed that excess relative humidity (RH) between the bracts of the internal region of the bud precludes the bud mites from utilizing this food source. Fungal colonization of the bracts adjacent to the dome by *F. mangiferae* could cause a slight decrease in RH which might allow the mites to enter and occupy the internal region of the bud. In a study designed to evaluate the effects of the tomato spotted wilt virus on its thrips vector, *Frankliniella occidentalis* (Pergande), juvenile survival and
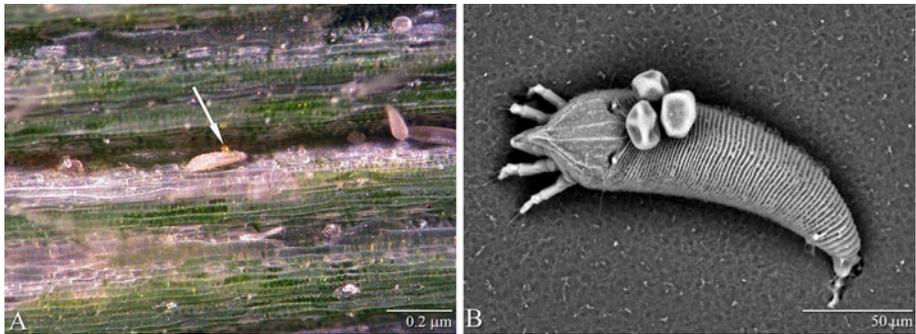
Fig. 7 **a** Stereomicroscope image showing the cereal rust mite, *Abacarus hystrix*, bearing conidia of *Puccinia* spp. on its body on the underside of a quackgrass leaf (spore marked with *black arrow*); **b** SEM image showing the cereal rust mite bearing conidia on its body

developmental rate were consistently higher on virus-infected plants (Belliure et al. 2005). The authors hypothesized that the virus counters the negative effects of the herbivore-induced defense mechanisms thereby improving the performance of its insect vector. One remote possibility that has not been addressed is that eriophyoid mites could be directly feeding on the fungus; however, we did not observe this behavior even though the bud mites were crawling all around the mycelium. While we are aware that eriophyoids are considered obligatory plant feeders; we still think this option should be examined using molecular tools.

As eriophyoid mites and plant pathogens share the same microniche, it can be argued that the clinging of the fungal spores to the mite's body has little impact on the ecology of the system. At least in the case of the mango bud mite, we are convinced that this is not the case because it was demonstrated that the mite can vector the spores to the buds, the fungus's sole port of entry to the plant and enhance disease severity (Gamliel-Atinsky et al. 2009b). Furthermore, the spores could benefit from the ability of the mites to travel long distances by wind (Zhao and Amrine 1997). The significance of this association for the cereal rust mite has yet to be clarified. The large spore size in relation to the mite's body size and the fact that the spores appear to adhere to the mite's body even after the SEM preparation procedure may indicate that this phenomena is not by mere chance. Rust spores are disseminated in the wind and are very resilient to desiccation and ultra violet radiation, thus it is very unlikely that eriophyoid mites are part of the long range dispersal of this fungus. However, mites bearing the rust spores on their body may be playing an important role in short range dispersal by moving the spores about the plant thereby increasing the points of infection. Further investigation is necessary to evaluate the role of the cereal mite as a vector of rust spores and to assess its effect on pathogen penetration of the leaf tissue.

Our mango malformation research suggests that fungal as well as other plant pathogens may play an important role in additional cases where plant disorders have been attributed, till now, solely to eriophyoid mites. For example, on *Lantana camara* L., the lantana gall mite *Aceria lantanae* (Cook), causes vegetative deformations appearing as masses of very small leaves (Smith-Meyer 1996). Similarly vegetative malformations occur on caraway *Carum carvi* L., in association with *Aceria carvi* Nalepa (Zemek et al. 2005). On Protaceae, witches broom has been related to *Aceria proteae* Meyer (Smith-Meyer 1996) but recently a spiroplasma has been isolated from the mite and the diseased plant tissue, possibly indicating a positive interaction between these two organisms (Wieczorek et al.

2003). Even though these examples of plant disorders do not possess the same symptoms as those of mango malformation, there do seem to be marked similarities. We propose that future research on eriophyoid related plant disorders, especially those without typical eriophyoid galls and erinea (Westphal and Manson 1996), should consider and evaluate additional pathogens as causal agents.

In summary, while it appears that eriophyoids are playing a role in fungal epidemiology, clearly further research is needed to broaden our understanding of direct and indirect (plant mediated) interactions between plant pathogens and eriophyoid mites in different plant-pathogen systems.

References

Abdel-Sater MA, Eraky SA (2001) Bulbs micoflora and their relation with three stored product mites. Mycopathologia 153:33–39

Agrios GN (1980) Insect involvement in the transmission of fungal pathogens. In: Harris KF, Maramorosch K (eds) Vectors of plant pathogens. Academic Press, New York, pp 293–324

Amrine JW Jr, De Lillo E (2003) Catalog of the eriophyoidea. A working catalog of the eriophyoidea of the world. Version 1.0 http://insects.tamu.edu/research/collection/hallan/acari/eriophyidae. Accessed 5 Jan 2008

Belliure B, Janssen A, Maris PC, Peters D, Sabelis MW (2005) Herbivore arthropods benefit from vectoring plant viruses. Ecol Lett 8:70–79

Britz H, Steenkamp ET, Coutinho TA, Wingfield BD, Marasas WFO, Wingfield MJ (2002) Two new species of *Fusarium* section liseola associated with mango malformation. Mycologia 94:722–730

Cardenas RM, Gonzalez L, Parra Y, Rivero D, Cruz A (2003) Influence of rice grain discoloration (*Oryza sativa* Lin.) on variety J-104, harmfulness and genera of fungi present. Rev Prot Veg 18:124–128

Chakrabarti DK, Ghosal S (1989) The disease cycle of mango malformation induced by *Fusarium moniliforme* var. subglutinans and the curative effects of mangiferin-metal chelates. J Phytopathol 125:238–246

Crookes CA, Rijkenberg FHJ (1985) A literature review of the distribution, symptomology, cause and control of mango blossom malformation. S Afr Mango Grow Assoc Res Rep 5:15–24

Cummings GB (1971) The rust fungi of cereals, grasses and bamboos. Springer, New York

Denmark HA (1983) *Eriophyes mangiferae* (Sayed) a pest of mango (Acarina: Eriophyidae). Fla Dep Agric Consum Serv Div Plant Ind Entomol Circ 254

Duso C, Pozzebon A, Capuzzo C, Malagnini V, Otto S, Borgo M (2005) Grape downy mildew spread and mite seasonal abundance in vineyards: effects on *Tydeus caudatus* and its predators. Biol Control 32:143–154

English-Loeb G, Norton A, Gadoury D, Seem R, Wilcox W (1999) Control of powdery mildew in wild and cultivated grapes by a Tydeid mite. Biol Control 14:97–103

Fournier V, Rosenheim J, Brodeur J, Johnson M (2004) Inducible responses in papaya: impact on population growth rates of herbivorous mites and powdery mildew under field conditions. Environ Entomol 33:1088–1094

Freeman S, Maimon M, Pinkas Y (1999) Use of GUS transformants of *Fusarium subglutinans* for determining aetiology of mango malformation disease. Phytopathology 89:456–461

Frost WE, Ridland PM (1996) Grasses. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 619–629

Gamliel-Atinsky E, Freeman S, Sztejnberg A, Maymon M, Ochoa R, Belausov E, Palevsky E (2009a) Interaction of the mite *Aceria mangiferae* with *Fusarium mangiferae*, the causal agent of mango malformation disease. Phytopathology 99:152–159

Gamliel-Atinsky E, Sztejnberg A, Maymon M, Vintal H, Shtienberg D, Freeman S (2009b) Infection dynamics of *Fusarium mangiferae*, causal agent of mango malformation disease. Phytopathology 99: 775–781

Hatcher PE, Paul ND (2001) Plant pathogen—herbivore interactions and their effects on weeds. In: Jeger MJ, Spence NJ (eds) Biotic interactions in plant-pathogen associations. CAB International, Wallingford, pp 193–218

Jeppson LR, Keiffer H, Baker EW (1975) Mites injurious to economic plants. University of California Press, Berkeley, 614 pp

Kemp G, Pretorius Z, Wingfield M (1996) Fusarium glume spot of wheat: a newly recorded mite associated disease in South Africa. Plant Dis 80:48–51

Krantz GW, Lindquist E (1979) Evolution of phytophagous mites (Acari). Ann Rev Entomol 24:121–158

Kumar J, Singh US, Beniwal SPS (1993) Mango malformation: one hundred years of research. Annu Rev Phytopathol 31:217–232

Kvas M, Steenkamp ET, Al Adawi AO, Deadman ML, Al Jahwari AA, Marasas WFO, Wingfield BD, Ploetz RC, Wingfield MJ (2008) *Fusarium mangiferae* associated with mango malformation in the Sultanate of Oman. Eur J Plant Pathol 121:195–199

Labuschagne TI, Joubert MH, Steyn A (1993) Role of the mango bud mite, *Aceria mangiferae* (Sayed) in mango malformation. NISSV Inligtingsbull 246:19–24

Leonard KJ, Szabo LJ (2005) Stem rust of small grains and grasses caused by *Puccinia graminis*. Mol Plant Pathol 6:99–111

Lima CS, Pfenning LH, Costa SS, Campos MA, Leslie JF (2009) A new *Fusarium* lineage within the *Gibberella fujikuroi* species complex is the main causal agent of mango malformation disease in Brazil. Plant Pathol 58:33–42

Majumder PK, Sinha GC (1972) Studies on the effect of malformation on growth, sex ratio, fruit set and yield of mango. Acta Hortic 24:230–234

Manicom BQ (1989) Blossom malformation of mango. S Afr Mango Grow Assoc Yearb 10:11–12

Marasas WFO, Ploetz RC, Wingfield MJ, Wingfield BD, Steenkamp ET (2006) Mango malformation disease and the associated *Fusarium* species. Phytopathology 96:667–672

McCoy CW (1996) Pathogens of eriophyoid mites. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 481–490

McCoy CW, Selhime A, Kanavel R (1969) The feeding behavior and biology of *Parapromenatus acacia* (Acarina: Tydeidae). Fla Entomol 52:13–19

Mendel Z, Gerson U (1982) Is the mite *Lorryia formosa* Cooreman (Prostigmata: Tydeidae) a sanitizing agent in citrus groves? Acta Oecol Appl 3:47–51

Mourichon X (1991) Etude sur les maladies du fruit: les taches noires et leathery pocket. Fruits 46:390–394

Narasimhan MJ (1954) Malformation of panicles in mango incited by a species of *Eriophyes*. Curr Sci 23:297–298

Nariani TK, Seth ML (1962) Role of eriophyid mites in causing malformation disease in mango. Indian Phytopathol 15:231–234

Nault LR, Styer WE (1969) The dispersal of *Aceria tulipae* and three other grass-infesting eriophyid mites in Ohio. Ann Entomol Soc Am 62:1446–1455

Noriega-Cantú DH, Téliz D, Mora-Aguilera G, Rodriguez-Alcazar J, Zavaleta Mejía E, Otero-Colinas G, Campbell CL (1999) Epidemiology of mango malformation in Guerrero, Mexico, with traditional and integrated management. Plant Dis 83:223–228

Norton AP, English-Loeb G, Belden E (2001) Host plant manipulation of natural enemies: leaf domatia protect beneficial mites from insect predators. Oecologia 126:535–542

Nuzzaci G, Alberti G (1996) Internal anatomy and physiology. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 101–150

Ochoa R, Aguilar H, Vargas C (1994) Phytophagous mites of central America: an illustrated guide. CATIE, Turrialba, Costa Rica, 234 pp

Okabe K, Amano H (1990) Attractancy of alcohols isolated from culture filtrates of *Fusarium* fungi for the robine bulb mite, *Rhizoglyphus robini* Claparede (Acari: Acaridae), in sand. Appl Entomol Zool 25: 397–404

Okabe K, Amano H (1991) Penetration and population growth of the robine bulb mite, *Rhizoglyphus robini* Claparede (Acari: acaridae), on healthy and *Fusarium*-infected rakkyo bulbs. Appl Entomol Zool 26: 129–136

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vectors of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 259–273

Peña JE, Palevsky E, Otero Colinas G, Ochoa R, Meister CW (2005) Mango bud mite, *Aceria mangiferae* bionomics and control under Florida conditions. P Fl St Hortic Soc 118:228–234

Petty G, Stirling G, Bartholomew D (2002) Pests of pineapple. In: Peña JE, Sharp J, Wysoki M (eds) Tropical fruit pests and pollinators: their economic importance, natural enemies and control. CAB International, Wallingford, pp 157–196

Ploetz RC (2001) Malformation: a unique and important disease of mango, *Mangifera indica* L. In: Summerell BA, Leslie JF, Backhouse D, Bryden WL, Burgess WL (eds) *Fusarium*: Paul E. Nelson memorial symposium. The American Phytopathological Society, St. Paul, MN, pp 233–247

Ploetz RC (2003) Diseases of mango. In: Ploetz RC (ed) Diseases of tropical fruit crops. CABI Publishing, Oxford, pp 327–363

Ploetz RC, Gregory NF (1993) Mango malformation in Florida: distribution of *Fusarium subglutinans* in affected trees, and relationships among strains within and among different orchards. Acta Hortic 341:388–394

Ploetz RC, Zheng QI, Vazquez A, Abdel Sattar MA (2002) Current status and impact of mango malformation in Egypt. Int J Pest Manage 48:279–285

Prasad A, Singh N, Singh S (1972) Mango malformation—a review of work done at the horticultural research institute, Saharanpur, India. Acta Hortic 24:227–229

Rodríguez-Alvarado G, Fernández-Pavía SP, Ploetz RC, Valenzuela-Vázquez M (2008) A *Fusarium* sp. different from *Fusarium oxysporum* and *F. mangiferae* is associated with mango malformation in Michoacán, Mexico. Plant Pathol 57:781

Saini LC, Singh S (1989) Perpetuation of powdery mildew (*Microsphaera alphitoides* f. sp. *ziziphi*) in mite gall tissues on *Ziziphus mauritana* in India. FAO Plant Prot Bull 37:175–177

Skoracka A (2004) Eriophyid mites from grasses in Poland (Acari: Eriophyoidea). Genus 13:1–205

Smith-Meyer MKP (1996) Ornamental flowering plants. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 641–650

S-PLUS 7.0 for Windows (2005) Professional edition. Insightful, Seattle

Sternlicht M, Goldenberg S (1976) Mango eriophyid mites in relation to inflorescence. Phytoparasitica 4:45–50

Summanwar AS, Raychaudhuri SP (1968) The role of eriophyid mite (*Aceria mangiferae*) in the causation of mango malformation. Indian Phytopathol 21:463–464

Summanwar AS, Raychaudhuri SP, Phatak SC (1966) Association of the fungus *Fusarium moniliforme* Sheld. with the malformation in mango (*Mangifera indica* L.). Indian Phytopathol 19:227–228

Varma A, Raychaldhuri SP, Lele VC, Ram A (1971) Preliminary investigations on epidemiology and control of mango malformation. Proc Indian Nat Sci Acad 37:291–300

Varma A, Lele VC, Raychoudhuri SP, Ram A, Sang A (1974) Mango malformation: a fungal disease. Phytopathol Z 79:254–257

Westphal E, Manson DCM (1996) Feeding effects on host plants: gall formation and other distortions. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 231–242

Wieczorek AM, Wright MG, Leonhardt KW (2003) PCR detection of phytoplasma from witches' broom disease on *Protea* spp. (Proteaceae) and associated arthropods. Acta Hortic 602:161–166

Zaher MA, Osman AA (1970) Population studies on mites associated with mango trees in Egypt. Bull Soc Entomol Egypt 54:141–148

Zemek R, Kurowská M, Kameníková L, Zemková Rovenská G, Havel J, Reindl F (2005) Studies on phenology and harmfulness of *Aceria carvi* Nal. (Acari: Eriophyidae) on caraway, *Carum carvi* L., in the Czech Republic. J Pest Sci 78:115–116

Zhao S, Amrine JW Jr (1997) Investigation of snowborne mites (Acari) and relevancy to dispersal. J Intern Acarol 23:209–213

The control of eriophyoid mites: state of the art and future challenges

Thomas Van Leeuwen · Johan Witters · Ralf Nauen · Carlo Duso · Luc Tirry

Abstract The superfamily of the Eriophyoidea is a large and diverse group of mites, including a number of species of economic importance, mainly on perennial plants in agriculture and forestry. This review focuses on the economic importance and pest status of this group of mites, with emphasis on some genera. The available acaricide portfolio is reviewed and the influence of EU legislation policy on the sustainable control of Eriophyoidea is investigated. Possible generic guidelines for sustainable control and resistance management with special reference to the European situation are discussed. Recent advances in biological and integrated control of eriophyid mite pests and the implementation of these techniques in crops are explored. Furthermore, the relevance of studies on behaviour, epidemiology and diagnostics in general terms and as a strategic necessity is pointed out.

T. Van Leeuwen (✉) · L. Tirry
Laboratory of Agrozoology, Department of Crop Protection, Faculty of Bioscience Engineering, Ghent University, Coupure links 653, 9000 Ghent, Belgium
e-mail: Thomas.vanleeuwen@ugent.be

J. Witters
Institute for Agricultural and Fisheries Research (ILVO), Plant Sciences Unit—Crop Protection, Burg. Van Gansberghelaan 96, 9820 Merelbeke, Belgium

R. Nauen
Bayer CropScience AG, Research Insecticides, Alfred Nobel Str. 50, 40789 Monheim, Germany

C. Duso
Department of Environmental Agronomy and Crop Science, University of Padua, Viale dell'Università 16, 32050 Legnaro Padova, Italy

Introduction

Eriophyoid mites are obligate plant parasites that feed on various plant organs causing symptoms that can sometimes be confused with those due to viruses, nutrient deficiency and physiological disorders. Some of these mites can transmit plant pathogens, in particular viruses, with serious implications for crop yield and are considered a quarantine problem in many countries (Oldfield and Proeseler 1996), thus economically rendering eriophyoid mites as the second most important mite species complex after tetranychid mite pests.

Evaluating eriophyoid population densities and related yield losses proved to be difficult in several cases. Their minute size and concealed way of life (several species live and reproduce well hidden in buds or in induced plant structures, like galls, erinea and blisters) represent an obstacle for detailed studies aiming at determining their impact on agricultural crops, ornamental and forest trees. Mathematical models have been employed for a few species to determine relationships between mite densities and yield losses. However, there is also a need for models predicting mite population dynamics in order to obtain information useful for growers (Royalty and Perring 1996). Despite their little size and low mobility, eriophyoid mites can disperse passively through air currents, rain and, especially, human practices. The importance of passive dispersal for this mite group has been understood only recently. They can be spread through commercial trade over long distances.

The economic importance of eriophyoid mites has been estimated in some countries but the variability of environmental conditions, cultural practices, cultivar features and market standards make a generalisation based on these studies difficult. Jeppson et al. (1975) and, more recently, Lindquist et al. (1996) reviewed the most important issues related to eriophyoid mites associated to important crops over the world. It was documented how a number of species emerged as economically important and their pest status has been reconfirmed recently, mainly in crops like citrus, apples, grapes, hazelnuts, coconuts and tomatoes. The current review aims to report on recent developments in the eriophyoids' pest status and their chemical, biological and integrated control.

Eriophyoid mites as crop pests

At least seven eriophyoid mite species are associated with citrus over the world and among them, the citrus rust mite *Phyllocoptruta oleivora* (Ashmead), the citrus bud mite *Aceria sheldoni* (Ewing) and the pink citrus rust mite *Aculus pelekassi* (Keifer) are considered the most injurious (McCoy 1996a). *P. oleivora* activity causes damage to the fruits and its control is often required. The most recent research on *P. oleivora* control provided several new insights, e.g. on sampling. Hall et al. (2005, 2007) investigated the effects of reducing the sample size on the accuracy of estimation of citrus rust mite densities on oranges. They proposed a binomial sampling based on the proportion of eriophyoid infested samples. Binomial sampling can represent an alternative to absolute counts of mites per sample when threshold levels are relatively low. Control of *P. oleivora* on citrus is mainly based on acaricides and resistance has yet to become a problem (Bergh et al. 1999, see section "Chemical control").

The apple rust mite *Aculus schlechtendali* (Nalepa) has achieved a permanent pest status in most fruit growing areas. Among factors affecting outbreaks of this pest, Easterbrook (1996) cited the change in pesticide use, mainly towards that of fungicides lacking

acaricidal activity and of insecticides having a detrimental effect on predatory mites. Croft and Slone (1998) confirmed that *A. schlechtendali* outbreaks can be induced by the use of non-selective pesticides, i.e. pyrethroids. Fresh market requirements are also responsible for the increase in acaricide use against *A. schlechtendali*: in northern Italy up to five acaricide treatments are applied to minimize apple rust mite damage on Golden Delicious (Angeli et al. 2008). The impact of the mites on apple yield strongly depends on cultivar features (Spieser et al. 1998, Curthbertson and Murchie 2006).

Two eriophyoid species are recognized as pests in vineyards: *Colomerus vitis* (Pagenstecher) and *Calepitrimerus vitis* (Nalepa). Duso and de Lillo (1996) discussed the pest status of different strains of *Col. vitis*. More recently, the bud and the erineum strains of *Col. vitis* were considered separate species using molecular markers (Carew et al. 2004) although no morphological differences between the strains have been provided. While in the past *Cal. vitis* outbreaks occurred only in Europe, they have recently been recorded in other continents. An improved knowledge of their behaviour and of factors affecting its population dynamics would help in managing this pest more effectively (Bernard et al. 2005; Walton et al. 2007).

A number of species can feed on filbert trees (*Corylus* sp.) but only the big bud mite *Phytoptus avellanae* (Nalepa) is recognized as a worldwide pest. In southern Europe more than 50% of the buds can be damaged by this pest (Castagnoli and Oldfield 1996). The phenology of both filbert and mites was investigated in New Zealand to obtain valuable data for timing the control of mites. Models based on accumulated heat sums and plant developmental parameters could predict the accumulated mite emergence with some precision (Webber et al. 2008).

Vegetables can be damaged by various eriophyoid mites of which the tomato russet mite *Aculops lycopersici* (Tryon) is the most important on tomato, capsicum, eggplant and several other plant species. Basic studies on the effects of temperature and humidity on the growth rate of *A. lycopersici* can help in understanding its population dynamics, thus supporting plant protection (Haque and Kawai 2003). The effects of NK fertilization levels, canopy height, and trichome densities on plant resistance to mites were evaluated on *Lycopersicon hirsutum* and *Lycopersicon esculentum* (Leite et al. 1999). Resistance increased with high trichome densities and the presence of type VI glandular trichomes (with higher levels of tridecan-2-one in leaves). Russet mite densities can increase on water stressed plants and thus irrigation is a tool to prevent large mite populations. Since sulphur is sometimes ineffective and pesticides can alter the performance of pest antagonists, several predatory mites have been investigated for their potential in the control of *A. lycopersici*. Unfortunately, few species appear to be successful in controlling the tomato russet mite (Brodeur et al. 1997; Gerson and Weintraub 2007, see section "Biological control").

The dry bulb mite *Aceria tulipae* (Keifer) is another worldwide eriophyoid pest of vegetables. It can damage a number of crops (e.g. garlic, onion, tulip) and can transmit viruses causing serious yield losses. The mites feed upon the epidermal cells of bulb scales. Heavily infested bulbs dry up entirely. In garlic bulbs, dry bulb mites cause reductions in emergence (up to 20%) and in yield (up to 23%). *Aceria tulipae* is considered a complex of species (Perring 1996), thus, data on its biology and behaviour should be considered with caution. More recently, detailed studies on the effects of temperature and relative humidity on *A. tulipae* reared on garlic leaves identified optimal conditions for the mite development (Courtin et al. 2000). It seemed that host transpiration influenced humidity conditions, thereby positively affecting mite survival. The infection of garlic plants with allexiviruses by eriophyid mites has been recently investigated. The mites proved to be the vector of

new strains of allexiviruses (Kang et al. 2007). In the past, fumigation as well as orga-
nophosphates or aldicarb were used to control this pest. More recently it was found that
dipping the bulbs first in water and then in acaricide solution proved to be effective. Also,
controlled atmosphere methods showed promising results (Conijn 2006).

Moore and Howard (1996) reported the coconut mite *Aceria guerreronis* Keifer as a
pest of coconut fruits in the Americas and West Africa, although coconut originates from
the Indo-Melanesian region. The absence of *A. guerreronis* from this region suggested that
the mite moved to coconut from another host plant. The analysis of DNA sequence data
from two mitochondrial and one nuclear region from samples of populations from the
Americas, Africa and the Indo-ocean region added new elements to this hypothesis (Navia
et al. 2005). The highest diversity was found in American (Brazilian) strains, while African
or Asiatic strains were very similar suggesting an American origin of the mite. This finding
is significant for quarantine measures and classical biological control strategies. Recent
papers have addressed some important questions regarding this pest. Lawson-Balagbo
et al. (2008) conducted surveys throughout the coconut growing areas of Brazil and found
infestation by *A. guerreronis* in 87% of the visited localities. Some predatory mites
belonging to the family Phytoseiidae appeared to be promising in the control of
A. guerreronis.

The importance of Eriophyoids as pests in forests and ornamental trees is extensively
reviewed by Castagnoli et al. (2009).

Chemical control

The chemical control of eriophyoid mites has been thoroughly reviewed in 1996 by
Childers et al. Although the acaricide portfolio has changed since then, and is expected to
change particularly in Europe even more in the near future, a rather limited amount of
reports has investigated the suitability of modern crop protection compounds for con-
trolling rust, gall, blister and bud mites. Moreover, these reports are mainly restricted to a
number of major crops like citrus and apple orchards and major species as *P. oleivora*. and
A. schlechtendali, respectively. Probably, the main reason for the lack of information on
the toxicity and other aspects of new compounds can be brought back to the lower eco-
nomic importance of these mites, in comparison to other mite pests such as the spider mites
(Acari: Tetranychidae). In addition, much of the ongoing research aiming at controlling
eriophyoid mites in the last decade has focussed on biological control with the use or
conservation of predatory mites.

In general, eriophyoid mites prove to be fairly susceptible to most commonly used
acaricides, as was demonstrated by Childers et al. (1996). When compared to mite species
belonging to the Tetranychidae, eriophyoid mites were at least equally susceptible to well
known acaricides amitraz, dicofol, propargite, bromopropylate, ethion and abamectin.
However, the benzoylphenylurea insecticides diflubenzuron and teflubenzuron, which have
little effect on Tetranychidae, showed very good efficacy on rust mites (Childers et al.
1996; Scarpellini and Clari 1999). Also, fungicides like dithiocarbamates (mancozeb,
maneb, zineb), tolylfluanid (euparen), dinitrophenoles (dinocap) and benzimidazoles
(benomyl) exhibit sometimes strong side-effects on eriophyoid mites and have therefore
long been used to suppress these mites, but they have only limited to moderate activity on
spider mites (Childers et al. 1996; Kalaisekar et al. 2000).

Due to their susceptibility to the available acaricides, one could wonder whether there is
a problem with controlling eriophyoids. Susceptibility is one aspect, but getting the

compounds in contact with the mites is another: the main problem with eriophyoid control is the hidden lifestyle of a number of important species. Mites hiding in galls, blisters and buds are not easily accessible. In these cases, an accurate timing of the applications is important, in order to reach the life stages that (temporarily) leave the hiding places, and can, only at those times, be reached with pesticides. That is why, in most cases, control is directed against the adults which are searching for spots to induce their hiding places for the immature life stages (in case of gall mites) or for existing shelters (for bud mites). Since the appearance of these adults is mostly spread over a number of days or weeks, control is best provided with acaricides providing long residual control. On the other hand, rust mites have a more superficial lifestyle on the underside of leaves, leaving them exposed throughout their life cycle, resulting in easier control.

Understanding the pest and beneficial species complex present in the targeted crop is another challenge for the control of eriophyoid mites. The beneficial species include naturally occurring predatory insects and mites and those released for biological control purposes. It seems that in many cropping systems where eriophyoid mites cause economic damage, such as apple and citrus orchards, Tetranychidae are also main pests, and therefore application timing and product choice should reflect concerns on the economic damage of both species.

Acaricide portfolio

The European pesticide portfolio has recently been impacted seriously by applying Directive 91/414/EEC regulating plant protection product registration, i.e. 589 of the previously listed 952 crop protection products have already been eliminated (Nauen et al. 2008). The Directive 91/414/EEC is currently under revision, and a change from science-based risk assessment to hazard-based regulatory cut-off criteria is under review. In this review process, called the Pesticide Review Program, each substance is to be evaluated as to whether it could be used safely with respect to human health (consumers, farmers, local residents and passers-by) and the environment—in particular, groundwater and non-target organisms, such as birds, mammals, earthworms and bees. This process should also help to achieve a common market (Törnqvist 2007). The current revision will definitely lead to the withdrawal of a substantial number of products (Bielza et al. 2008). Of the 228 listed insecticides listed before 1993, 146 (64%) have already been withdrawn (status August 2009). However, the majority of substances have been eliminated due to economic reasons, e.g. dossiers were either not submitted, incomplete or withdrawn by the industry, and not because of problems with safety (Kidd 2002). The greatest impact for losing unsupported pesticides was on minor uses in horticultural crops (Knott 2007).

When looking specifically at the availability of acaricides in the EU, of the 100 compounds listed as acaricides under review, 72 will most likely be withdrawn, 4 are still pending, and 24 will be included in Annex I, a 'positive' list of compounds that can be used in Europe. For practical reasons, Europe will most likely be split into three distinct pesticide licensing zones: centre, north and south, with compulsory mutual recognition in each zone (Knott 2007). One would expect that the control of Eriophyoidea in some major crops like vine, apple and citrus will be safeguarded, however, many minor crops suffer occasionally for eriophyoid attack, and the question rises if sufficient products will remain on Annex I and, most importantly, if they will be licensed in each zone for use against eriophyoid mites in a certain crop.

Table 1 shows the negative list of compounds which provide good eriophyoid control but will most likely not survive the European Pesticide Review Program carried out under

Table 1 Negative list of compounds with good Eriophyoid control potential (as reviewed by Childers et al. 1996) that will most likely not survive the European Pesticide Review Program carried out under Directive 91/414

Common names	Primary target site	MoA group
Organophosphates: e.g. ethion, dichlorvos, monocrotophos, oxydemeton methyl, diazinon	Acetylcholinesterase inhibitor	1B
Carbamates: e.g. carbaryl, carbosulfan, aldicarb	Acetylcholinesterase inhibitor	1A
Organochlorines: endosulfan	GABA gated chloride channel antagonist	*2A*
Pyrethroids: e.g. fenpropathrin, fenvalerate, fluvalinate	Sodium channel modulators	3A
Hexythiazox	Mite growth inhibitors	*10A*
Diafenthiuron	ATP synthase inhibitors	*12A*
Organotin compounds: fenbutatin oxide, azocyclotin, cyhexatin	ATP synthase inhibitors	*12B*
Propargite	ATP synthase inhibitors	*12C*
Tetradifon	ATP synthase inhibitors	*12D*
Chlorfenapyr, DNOC	Uncoupler	*13*
Benzoylureas: flucycloxuron, flufenoxuron	Inhibitors of chitin biosynthesis type 0	15
Amitraz	Octopamine receptor agonists	*19*
Fenazaquin, pyridaben	METI	21A
Dicofol, chinomethionat	Unknown	Un

Complete mode of action (sub)groups that might disappear are italicized. MoA group refers to the classification provided by the Insecticide Resistance Action Committee (IRAC, www.irac-online.org)

Directive 91/414. It is clear that many acaricides with good action on eriophyoid mites will not be available anymore in the near future. For instance bromopropylate, endosulfan and amitraz have been widely used against eriophyoid mites and proved to be particularly important in the often difficult to control bud mites (Childers et al. 1996; Kalaisekar et al. 2000; Ozman-Sullivan and Akca 2005), but will be banned for use in Europe.

Table 2 summarizes acaricidal active ingredients that are at present included in Annex I, and consequently can be licensed in different European zones, and compounds of which the decision is still pending. Organophosphates such as chlorpyrifos and dimethoate are still available as acaricides, and although they have proven to be efficient in controlling eriophyid mites like the tomato russet mite *A. lycopersici* and the litchi gall mite *Aceria litchii* (Keifer) in the past, their activity was doubtful on economically important species such as citrus rust mite *P. oleivora* and apple rust mite *A. schlechtendali* (Childers et al. 1996). Resistance to organophosphates in spider mites was one of the first characterised cases of arthropod resistance (Smissaert 1964; Voss and Matsumura 1964). Since then, numerous reports have investigated resistance of spider mites to this group of chemicals, and *Tetranychus urticae* Koch has developed resistance to more than 30 organophosphates in more than 40 countries (Georghiou and Lagunes-Tejeda 1991, Arthropod Pesticide Resistance Database). Although organophosphates are usually not used anymore for the control of spider mites in the field, their frequent use on insect pests (35% of global insecticide sale, McCaffery and Nauen 2006) has lead to a continuous selection and many spider mite populations are still resistant. Hence, the use of organophosphates on eriophyoids in crops that are also under attack of spider mites seem not advisable. With the

Table 2 Positive list of compounds with acaricidal activity that will most likely survive the Pesticide Review Program carried out under Directive 91/414

Common names	Primary target	MoA group
Organophosphates: chlorpyrifos, chlorpyrifos-methyl, dimethoate	Acetylcholinesterase inhibitor	1B
Carbamates: oxamyl, formetanate	Acetylcholinesterase inhibitor	1A
Pyrethroids: cyfluthrin, cypermethrin	Sodium channel modulators	3A
Avermectins and milbemycins: abamectin, milbemectin	Chloride channel activators	6
Clofentezine	Mite growth inhibitors	10A
Etoxazole	Mite growth inhibitors	10B
Benzoylureas: diflubenzuron, teflubenzuron, lufenuron	Inhibitors of chitin biosynthesis type 0	15
Acequinocyl	Mitochondrial complex III inhibitor	20B
Fenpyroximate, tebufenpyrad	Mitochondrial complex I inhibitor	21A
Tetronic acid derivatives: spirodiclofen, spiromesifen	Acetyl CoA inhibitor	23
Bifenazate	Uncertain	Un

Compounds with no or limited activity on eriophyoid mites are italicized. MoA group refers to the classification provided by the Insecticide Resistance Action Committee (IRAC, www.irac-online.org)

exception of formetanate and oxamyl, several carbamates with good activity on eriophyoids (carbaryl, aldicarb, carbosulfan) are also no longer available.

Out of the pyrethroids, a number of compounds with excellent miticidal activity (e.g. fenpropathrin, fenvalerate and fluvalinate) (Childers et al. 1996) are most probably no longer included in Annex I (Table 1). One exception might be bifenthrin, which has excellent acaricidal properties on many mite species, including the Eriophyoidea, but still pending. However, resistance to bifenthrin is also well documented in spider mites (e.g. Herron et al. 2001; Ay and Gurkan 2005; Van Leeuwen et al. 2005; Tsagkarakou et al. 2009) and the use of pyrethroids has led in the past to the resurgence of eriophyoid mites (Easterbrook 1996).

The macrocyclic lactone compounds avermectin and milbemectin, which are since long successfully used on many insect and mite pests will fortunately remain available. They have shown good activity on a range of eriophyoid mites, including the pear rust mite *Epitrimerus pyri* Nalepa, *A. schlechtendali, Eriophyes dioscoridis* Soliman & Abou-Awad and *P. oleivora* (Childers et al. 1996; Stansly et al. 2007; Smith et al. 1998; Walston et al. 2005, 2007) However, abamectin and milbemectin are frequently used against other pests, which have developed and are developing resistance, including spider mites (Clark et al. 1995; Campos et al. 1996, Stumpf and Nauen 2002). Variable abamectin susceptibility was also already detected in eriophyoid mites (Bergh et al. 1999), and care should be taken when frequently using these compounds in certain crops.

In the early 1990s, four new compounds were launched for spider mite control: pyridaben, fenpyroximate, tebufenpyrad and fenazaquin (Hirata et al. 1995; Konno et al. 1990; Kyomura et al. 1990; Longhurst et al. 1992). Although these chemicals belong to different chemical families, their mode of action is similar, i.e. inhibiting complex 1 of the respiratory chain, hence their classification in the group of Mitochondrial Electron Transport Inhibitors (METIs) (Hollingworth and Ahammadsahib 1995; Wood et al. 1996). These four compounds became very popular and are used world wide due to their high efficacy, quick knockdown and long residual control. METIs have good activity on eriophyoid mites and

they remain a valuable tool in controlling these species worldwide. Unfortunately pyridaben, which provided excellent control of *P. oleivora* and *A. schlechtendali* is to be discontinued, together with fenazaquin (still available outside Europe), leaving tebufenpyrad and fenpyromixate, of which the latter is most suited to control eriophyoid mites (Sujatha et al. 2004; Walgenbach and Schoof 2006). However, spider mites developed resistance to these compounds in many crops worldwide, and cross-resistance between all four compounds is more the rule than the exception, making a joint control of eriophyoid mites and spider mites difficult (Herron and Rophail 1998; Van Pottelberge et al. 2008; Nauen et al. 2001; Stumpf and Nauen 2001; Auger et al. 2003).

Since the last review on chemical control of eriophyoid mites by Childers et al. (1996), only a few new acaricidal compounds with new unique modes of action have been commercialized in Europe: bifenazate, etoxazole, acequinocyl and the tetronic acids spirodiclofen and spiromesifen (Dekeyser 2005). However, the labels or product use guides of Floramite (bifenazate), Zeal/Baroque (etoxazole) and Kanemite (acequinocyl) explicitly state that these formulated products can not be used to control rust mites, and that their efficacy on gall and bud mites is unknown. The only recently developed chemistry providing control of eriophyoid mites are the tetronic acids spirodiclofen and spiromesifen (Wachendorff et al. 2000, 2002; Nauen et al. 2005; Bretschneider et al. 2007; De Maeyer et al. 2002; Walston et al. 2007), described to inhibit lipid biosynthesis and with no cross-resistance to those compounds mentioned above.

Resistance development

The development of resistance is one of the major threats in crop protection worldwide. According to literature, more than 550 species of insects and mites have developed resistance to one or more classes of insecticides and acaricides (Arthropod Resistance Database). As becomes clear from Table 2, the number of effective chemicals to control crop pests is rapidly decreasing. Apart from the EU-regulations mentioned above, high costs associated with research, development and registration, together with the limited effective lifespan of new molecules (Metcalf 1980) are the most important reasons. To allow sustainable agriculture, it is of utmost importance to safeguard those chemicals which are still providing effective control.

Resistance development in eriophyoid mites was reviewed by Messing and Croft (1996). Reported cases of laboratory confirmed resistance included organophosphate resistance in *Aculus cornutus* (Banks) (Baker 1979) and *A. lycopersici* (Abou-Awad and El-Banhawy 1995) and resistance of *P. oleivora* to dicofol (Omoto et al. 1994), although many more cases of suspected resistance (not confirmed in the laboratory) to chlorobenzilate, endosulfan and oxythioquinox were also listed. Widespread resistance to dicofol in Florida populations of *P. oleivora* is probably best studied (Omoto et al. 1994, 1995). The authors detected a positive relationship between the number of dicofol applications and the frequency of resistance to dicofol, and it was demonstrated how careful resistance monitoring programs and empirical studies can result in recommendations for resistance management. Eriophyoids have also shown to develop resistance to fungicides that are sometimes used to suppress populations. Qu et al. (1997) reported strong resistance to the dithiocarbamate fungicide mancozeb in the pink citrus rust mite, *A. pelekassi*. In the last decade no new serious and well documented cases of resistance development in eriophyoid mites have been reported in literature.

However, the change in acaricide product use can significantly alter the emergence of eriophyoid pests and the necessity to chemically intervene. This is historically best

illustrated by looking at the situation of *A. schlechtendali* in most fruit growing areas. *A. schlechtendali* reached the permanent pest status after a change in pesticide use: the use of non-acaricidal fungicides and treatment with non-selective acaricides such as pyrethroids that have a detrimental effect on predatory mites (Easterbrook 1996). Also, the early removal of endosulfan from the European market has resulted in the resurgence of species, e.g. the big bud mite *P. avellanae* which is now recognized as a worldwide pest (Castagnoli and Oldfield 1996). Considering the possible loss of many compounds with excellent activity on eriophyoids, their control might be less effective in the future. Especially in integrated systems, that further restrict the acaricide portfolio based on selectivity on natural or released biocontrol agents, the number of products become very limited. As previously mentioned, an important factor will be the joint control of spider mites and eriophyoids. Many spider mite populations have developed resistance to acaricides which are still providing good eriophyoid control (listed in Table 2). The use of these chemicals to suppress populations of eriophyoids can lead to spider mite outbreaks, and should be avoided. Evidently, the few products with different mode of action that are still available should be used in alternation as much as possible to avoid resistance development, and a control strategy should be worked out for a certain crops in a certain region to guarantee sustainability. Detailed studies to improve integrated control of spider- and rust mite control in apple orchards, and consequently avoid resistance development, are given by Hardman et al. (2003), De Maeyer et al. (2002) and Croft and Slone (1998).

Biological control

Predators

Biological control of eriophyoid mites is mainly based on the use of predators, and to a lesser extent, on pathogens. Although some eriophyoid species are economically very important pests, which are often difficult to control with pesticides, the biological control of these species clearly has difficulties outgrowing the laboratory. For instance, in Europe, in all existing integrated pest and disease management programmes which are used to prevent and control pest and diseases in tomato, no biological control measure was proposed against *A. lycopersici* or any other eriophyoid mite (van Lenteren 2000).

Many commercialized phytoseiid predators are sold to control Tetranychidae and thrips (Gerson et al. 2003; de Faria and Wraight 2007). However, it is known that the generalist Phytoseiidae (type III and IV) (McMurtry and Croft 1997) not only feed on spider mites, but also prove to be key predators of eriophyoid mites, although none of them have been specifically commercialized for eriophyid control. For instance, *Neoseiulus californicus* McGregor predates on *A. lycopersici* (Castagnoli et al. 2003), *Neoseiulus cucumeris* (Oudemans) on *Aceria tulipae* (Keifer) (Lesna et al. 2004), *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) feed on *A. schlechtendali* (Easterbrook 1996; Duso and Pasini 2003). *Amblyseius andersoni*, although it has been studied for a long time, has only been recently commercialized, thanks to efforts of A. van der Linden in cooperation with a commercial producer (A. van der Linden, Applied Plant Research, Wageningen, The Netherlands, pers. comm.). Since *A. andersoni* is also regularly found in vineyards (Duso and de Lillo 1996; Bonafas et al. 2007), orchards (Duso and Pasini 2003) and tree nurseries (van der Linden and Nouwens 2005; Witters et al. 2006) it may offer new possibilities for implementation in biological control in Europe. Some authors have tried to improve the control of eriophyid mites with commercially available predators. Lesna et al. (2004)

showed that ethylene plays an important role in the control of the bulb mite *A. tulipae* on *Tulipa gesneriana* cv Yokohama using a commercial strain of the phytoseiid mite *N. cucumeris*. In the absence of ethylene no predation by *N. cucumeris* was recorded. However, when tulips were exposed repeatedly to ethylene, they seemed to be well protected from bulb mite damage by *N. cucumeris*. Ethylene increased the distance between the inner bulb scales, thereby facilitating entry of the predator and hence stimulating the control. A similar phenomenon was found in a recent study on the coconut mite *A. guerreronis* by Aratchige et al. (2007). This mite lives well protected against predators under the perianth of coconuts. In this study it was found that the perianth-gap in coconuts infested with *A. guerreronis* was significantly wider than in uninfested fruits. In 68% of the infested fruits the perianth gap was wider than 100 μm, which enables the predatory mite *N. baraki* to enter beneath the perianth and prey on the coconut mite. These new insights in plant defense may become more and more important in implying good control strategies for controlling eriophyid mites.

Next to the commercially available predatory mites, a number of reports exist on predators that have not yet reached the market. In the next paragraphs an overview will be given on the literature of a number of beneficial organisms which may have the potential to control eriophyid mites. A part of the data of these species have been summarized in Table 3.

Amblyseius badryi Yousef and El-Brollosy was found on grasses in Egypt. It was tested as predator for the eriophyid grass mite *Eriophyes dioscoridis* Soliman and Abou-Awad under laboratory conditions. According to Abou-Awad et al. (1998a) *A. badryi* could play an important role in the biological control of the eriophyid grass mite. Moreover, since grasses are often used as banker plants and since *A. badryi* was also found on fallen leaves in orchards, it could be worthwhile to further investigate the effect of *A. badryi* on other economic eriophyoid species inhabiting fruit trees. Abou-Awad et al. (1998b) also studied the potential of another phytoseiid mite, *Cydnoseius negevi* (Swirski and Amita), to control the eriophyid fig mite *Eriophyes ficus* Cotte. Under laboratory conditions, the development and predation of *C. negevi* on *E. ficus* and the tetranychid mite *T. urticae* was studied (Table 3). The results show that *C. negevi* has a stronger preference for *E. ficus* than for *T. urticae*, but could survive on both species. In similar tests, Abou-Awad et al. (1998a) found that the phytoseiid *A. badryi* could not reproduce when fed on *T. urticae*, which led to the suggestion that it could be a specific predator of *E. dioscoridis*. Another phytoseiid mite, *Neoseiulus cydnodactylon* Shehata and Zacher was evaluated as a potential predator of the olive bud mite *Aceria olea* Nalepa and the olive rust mite *Tegolophus hassani* Keifer (Metwally et al. 2005). In this study, life table parameters were determined under different abiotic conditions (temperature and humidity). The authors found that the optimum temperature and relative humidity for reproduction of *N. cydnodactylon* were 25–31°C and 70–80%RH, respectively, which makes them good candidates to become part of biological programs of eriophyoid and tetranychid mites.

Ozman-Sullivan (2006) evaluated the biology of the phytoseiid *Kampimodromus aberrans* (Oudemans), a possible predator of the big bud mite *P. avellanae*, which is a common pest in Turkish hazelnut orchards and concluded that *K. aberrans* can play an important role in IPM programs for control of *P. avellanae* when it released in early spring in order to boost the population prior to *P. avellanae* migration. The phytoseiid mites *Amblyseius largoensis* (Muma), *Neoseiulus baraki* (Athias-Henriot), *Neoseiulus paspalivorus* DeLeon (Phytoseiidae) and the ascid mite *Proctolaelaps bickleyi* (Bramidae) prove to be highly suitable as biological control agents for the coconut mite *A. guerreronis* (Galvão et al. 2007; Lawson-Balagbo et al. 2007; Negloh et al. 2008). Galvão et al. (2007)

Table 3 Life history components and intrinsic rate of population increase (r_m) of phytoseiid and ascid mites when fed on eriophyoid mites

Phytoseiidae species	Eriophyoidea	Temperature, humidity	Egg-to-adult (days)	Oviposition period (days)	Fecundity (eggs)	Oviposition rate (eggs/day)	r_m (1/day)	Reference
Amblyseius badryi	Eriophyes dioscoridis	27°C	7.41	19.25	30.75		0.170	Abou-Awad et al. (1998a)
Amblyseius largoensis	Aceria guerreronis	27°C, 55–65%RH	4.0	5.30	–	1.2	0.180	Galvão et al. (2007)
Amblyseius largoensis	Aceria guerreronis + pollen	27°C, 55–65%RH	4.2	20.00	–	1.7	0.250	Galvão et al. (2007)
Cydnoseius negevi	Eriophyes ficus	27°C	8.39	26.56	35.77	1.35	0.228	Abou-Awad et al. (1998b)
Euseius finlandicus	Aceria sp.	25°C	6.59	29.64	39.73	1.37	0.153	Abdallah et al. (2001)
Kampimodromus aberrans	Phytoptus avellanae	25°C, 76%RH	9.15	6.83	12.67	1.85	0.153	Ozman-Sullivan (2006)
Neoseiulus baraki (Brazilian population)	Aceria guerreronis	25°C, 70–90%RH	6.56	18.4	–	2.22	0.190	Negloh et al. (2008)
Neoseiulus baraki (Beninese pop.)	Aceria guerreronis	25°C, 70–90%RH	5.64	21.3	–	1.20	0.16	Negloh et al. (2008)
Neoseiulus cydnodactylon	Aceria oleae	15°C, 50%RH	10.74	24.6	33.3	1.35	0.122	Metwally et al. (2005)
		25°C, 70%RH	8.41	22.4	50.6	2.26	0.175	
		31°C, 80%RH	5.63	19.8	56.3	2.84	0.225	
Neoseiulus cydnodactylon	Tegolophus hassani	15°C, 50%RH	12.31	24.0	27.7	1.55	0.111	Metwally et al. (2005)
		25°C, 70%RH	8.84	22.0	45.5	2.07	0.167	
		31°C, 80%RH	5.61	20.0	54.2	2.71	0.201	
Neoseiulus paspalivorus	Aceria guerreronis	25°C, 70–90%RH	5.6	12.8	24.7	1.7	0.232	Lawson-Balagbo et al. (2007)
Typhlodromus athiasae	Aculops lycopersici	28°C, 75%RH	8.0	30.7	30.3	0.99	0.167	Momen and Abdel-Khalek (2008)
Amblyseius swirskii	Aculops lycopersici	28°C, 75%RH	7.0	20.6	35.4	1.7	0.265	Momen and Abdel-Khalek (2008)
Ascidae species								
Lasioseius athiasae	Eriophyes dioscoridis	27°C	7.39	19.92	64	3.21	0.212	Abou-Awad et al. (2001)
Proctolaelaps bickleyi	Aceria guerreronis	25°C, 70–90%RH	4.4	7.2	52.4	7.0	0.489	Lawson-Balagbo et al. (2007)

Layout according to Sabelis (1996)

found that oviposition rate, oviposition period and intrinsic rate of population increase of *A. largoensis* were higher when pollen were added to the diet (Table 3) which might suggest that *A. largoensis* can play a role in control *A. guerreronis* under natural conditions. Lawson-Balagbo et al. (2007) concluded that pollen could play an important role as alternative food for *N. paspalivorus* but also that it was inferior to the prey *A. guerreronis*. The same conclusion was made for *P. bickleyi* (Lawson-Balagbo et al. 2007). In another study, a Brazilian and a Beninese population of *N. baraki* were used to test and compare the nutritional value of *A. guerreronis*, pollen and *T. urticae* eggs (Negloh et al. 2008). The results from these laboratory experiments showed that the Brazilian population contained better predators of *A. guerreronis* than the Beninese population.

Momen and Abdel-Khalek (2008) studied the phytoseiid mites *Typhlodromips swirskii* (Athias-Henriot), *Typhlodromus athiasae* Porath and Swirski and *Paraseiulus talbii* (Athias-Henriot) to evaluate their development and reproductive potential when fed on mobile stages of the tomato russet mite *A. lycopersici*. This type of prey proved to be clearly acceptable food for *T. swirskii* and *T. athiasae* but not for *P. talbii*. The latter never reached the adult stage when fed on the tomato russet mite.

Most of the predatory mites listed in Table 3 are closely associated with the studied eriophyoid mites and the crops in which these mites reside. This observation, together with the laboratory results, suggest that these predators might be interesting biological control agents to suppress the endemic eriophyoid pests. The natural occurrence of the predators in the target crops enhances the possibility to use these predators in a conservation strategy. This strategy, i.e. to conserve indigenous natural enemies to control indigenous pests (Smith and Papacek 1991) is gaining more attention in the last decade. However, the search for exotic natural enemies is still going on, since local predators fail or are less successful in controlling the pest. This was the case in Israel where *T. athiasae*, *T. swirskii* and *Iphiseius degenerans* (Berlese) didn't give satisfactory control on the citrus rust mite *P. oleivora*. Argov et al. (2002) evaluated the introduction of the Australian phytoseiids *Amblyseius herbicolus* Chant, *Euseius victoriensis* (Womersley) and *Euseius elinae* (Schicha), the Mediterranean species *Euseius stipulatus* (Athias-Henriot) and the Californian species *Typhlodromus rickeri* Chant for controlling *P. oleivora*. These five phytoseiid mites, known to live on citrus in similar climatic conditions and to prey on citrus rust mite, were reared and released in citrus groves. Although high numbers of phytoseiid mites were released during this 7 year study, only *E. victoriensis* seems to become established on the citrus trees. The other species were completely disappeared in the last observation year. In contradiction with their objectives the authors speculated that competition with the dominant *T. swirskii* could be the reason of this failure.

Besides Phytoseiidae, a range of predators belonging to other taxonomic groups are reported to be suitable as biological control agents of eriophyoid mites. Representatives of the mite family Stigmaeidae are known to play an important role in decreasing eriophyoid mite populations on fruit trees (Thistlewood et al. 1996). Among stigmaeid mites, *Zetzellia mali* Ewing, *Agistemus floridanus* Gonzalez and *Agistemus industani* Gonzalis have been recognized as common predatory mites of *A. schlechtendali* and *P. oleivora*, respectively (Duso et al. 2008; Childers et al. 2001). *Agistemus floridanus* could also survive and reproduce (1.2 egg/female/day) on *Calacarus heveae* Feres, which is a serious pest on rubber trees in Brasil (De Vis et al. 2006). In a study on *A. lycopersici* in Japan, *Homeopronematus anconai* (Baker) (Prostigmata: Tydeidae) occurred spontaneously in the experimental plots where it reproduced very quickly and decreased the population of the tomato rust mite (Kawai and Haque 2004). The impact of the tydeid mite *H. anconai* (Baker) is matter of debate (Kawai and Haque 2004). In Northern Ireland, the whirligig

mite *Anystis baccarum* (Linnaeus) (Prostigmata: Anystidae) is the most abundant predator of *A. schlechtendali* in apple orchards (Curthbertson and Murchie 2006). The impact of predatory mites on *A. schlechtendali* populations has been investigated in depth in several countries (e.g. Croft and McRae 1993; Walde et al. 1997; Curthbertson and Murchie 2004) and their management is essential to minimize rust mite population densities. Therefore, the inclusion of selective pesticides in IPM programs is a fundamental requirement to maintain significant predatory mite populations in apple orchards and to obtain a reduction in acaricide use (e.g. Hardman et al. 2003). Studies on damage assessment are fundamental to establish eriophyoid mite threshold levels but a low number of contributions were reported in Lindquist et al. (1996). Since then, this argument has been investigated regarding *A. schlechtendali* (Spieser et al. 1998)—and *Aculus fockeui* (Nalepa et Trouessart) (Kondo and Hiramatsu 1999). Both papers gave significant insights on interactions between rust mites and the respective host plants.

Also insects were reported to feed on eriophyid mites. Villanueva et al. (2006) demonstrated the feeding capacity of two undescribed Cecidomyiidae species (*Feltiella* n. sp. and one identified as species near the genus *Lestodiplosis*) on *P. oleivora*. The consumption rate of *Feltiella* n.sp. and the second species was respectively 33.8 and 43.0 eggs or 17.2 and 20.6 mobile stages of *P. oleivora* in an observation time of 10 min. Both species seemed to be highly specialized in consuming eggs, larvae and nymphs of *P. oleivora*.

Also, larvae of the orange bagworm *Cryptothelea gloverii* (Packard) (Lepidoptera: Psychidae) decreased the numbers of the citrus rust mite population per cm^2 by 36% in a laboratory trial (Villanueva et al. 2005). Despite its predatory capacity, it has to be taken into account that *C. gloverii* larvae are also herbivores, able to feed on citrus, which makes it less suitable as a biological control agent.

Biocontrol possibilities of mycopathogens

Besides predators, diseases can also cause a significant reduction of the mite populations (Chandler et al. 2000; Van der Geest et al. 2000). Data on the presence and impact entomopathogenic fungi on eriophyoid mites are reviewed in McCoy (1996b), Van der Geest et al. (2000) and Balazy et al. (2008). Recently, studies were conducted in which entomopathogenic fungi were used for the biological control of the coconut mite *A. guerreronis* in India (Sreerema Kumar and Singh 2002, 2008) and Sri Lanka (Fernando et al. 2007; Edgington et al. 2008) and of *P. oleivora* in Brazil (Alves et al. 2005) and Israel (Paz et al. 2007; Gerson et al. 2008). In India, Sreerema Kumar and Singh (2002) checked 15 different Indian strains of *Hirsutella thompsonii* Fisher. They found that all monoconidial isolates were pathogenic for the coconut mite. The strain MF(Ag)5[IMI 3685470] appeared to be the most promising biological control agent and was therefore used for the development of a mycoacaricide 'Mycohit' to control *A. guerreronis* in India. In order to reduce the production cycle of mycelial-conidial formulations of *H. tompsonii*, mycelial applications of *H. tompsonii* were tested both in laboratory and field trials (Sreerema Kumar and Singh 2008). These authors found that by combining the mycelium with the adjuvants glycerol, malt extract broth or yeast extract powder, mycelial application can reduce the mite population significantly. In Brazil the pathogenicity of *Beauveria bassiana* was tested on *P. oleivora* (Alves et al. 2005). The lowest concentration (1×10^6 conidia/ml) of the *B. bassiana* based mycopesticide "Naturalis L" (ATCC74040) caused 24% mortality measured 5 days after inoculation. Intermediate concentrations (5×10^6 and 1×10^7 conidia/ml) and the highest concentration (5×10^7 and 1×10^8 conidia/ml) resulted in 60% and 80–90% mortality, respectively. Alves et al. (2005) conclude that the

lower concentrations (5×10^6 and 1×10^7 conidia/ml) were the most economical, since more applications could be carried out at the same cost of a single application with a higher concentration. Multiple applications also increase the effectiveness of the product, because most entomopathogenic fungi are extremely susceptible to abiotic factors like high temperatures, low humidity and UV radiation. In Israel, Paz et al. (2007) found that grapefruit sprayed with *Meira geulakonigii* was significantly less infected by *P. oleivora*. This pathogen can be included in IPM programs since it is relatively not harmful for predatory mites and tolerates several pesticides (Gerson et al. 2008).

Despite the fact that *H. thompsonii* is the most common fungus found on Eriophyidae (McCoy 1996b), the availability of a commercial strain is restricted to India (de Faria and Wraight 2007). However, commercial strains of *B. bassiana* are marketed worldwide (de Faria and Wraight 2007). Therefore the study of Alves et al. (2005) could be promising for other pest management programs on eriophyoid pests.

Plant resistance

Most plant species contain significant levels of natural genetic and phenotypic variation between individuals within the species to exploit traits like pest and pathogen resistance (Hansen et al. 2007). The utilisation of these native insect and mite resistance genes can be an important factor in their management (Frei et al. 2005). This can be achieved by classical breeding as well as by genetic engineering (Zhu et al. 2006). Recently some progress has been made in exploiting plant resistance genes in the control of eriophyoid mites.

The black currant bud mite *Cecidophyopsis ribis* Westwood) causes typical symptoms (big rounded buds) to blackcurrant and transmit blackcurrant reversion virus (BRV). Research on plant resistance was considered a fundamental way to improve mite control and recently significant progress was achieved. Resistance to BRV and to the gall mite vector was introduced into the host plant with positive implications for plant health (Jones 2000). Kahu et al. (2009) evaluated a number of blackcurrant cultivars in terms of productivity and berry quality, and found that some of them exhibited some resistance to the *C. ribis*. Brennan et al. (2009) developed a PCR-based marker potentially useful for the identification of mite-resistant germplasm. They validated this marker on susceptible and resistant germplasm in the framework of blackcurrant breeding programs.

Recently, Stoeckli et al. (2009) studied the genetic basis of rust mite resistance in apple. An analysis of quantitative trait loci (QTL) was carried out using linkage map data for F1 progeny plants of the cultivars 'Feista' and 'Discovery'. The markers developed in this study may assist in breeding resistant apple cultivars.

Differences between the susceptibility of clones of *Populus* sp. to the cottonwood leafcurl mite *Aculops louliferus* under different silvicultural treatments have also been observed (Coyle 2002).

Conclusions

The Pesticide Review Program within the EU will most-likely seriously affect the way eriophyoid mites can be chemically controlled in Europe. Many of the established compounds used for eriophyoid mite control will no longer be available, and this bears the risk of a resurgence of these pests in certain crops. At the same time, current research has

improved our understanding of eriophyoids as crop pests. Recent developments in the field of the monitoring, collection and identification (Monfreda et al. 2009; Navajas and Navia 2009) of these often hidden species, their potential biological control and several case studies in certain crops (Duso et al. 2009; Castagnoli et al. 2009; Gamliel et al. 2009; Hardman et al. 2003) will most definitely have an impact on the strategies devised for their sustainable control. Taking into account the diversity of the species and crops, a good control strategy should be developed specifically for each cropping system. Special attention should given to studying the complete tritrophic complex (crop, pests and beneficials) to finally reach to an integrated control, safeguarding the efficacy of the few available acaricides by avoiding resistance development.

References

Abdallah AA, Zhang Z-Q, Masters GJ, McNeill S (2001) *Euseius finlandicus* (Acari: Phytoseiidae) as a potential biocontrol agent against *Tetranychus urticae* (Acari: Tetranychidae): life history and feeding habits on three different types of food. Exp Appl Acarol 25:833–847

Abou-Awad BA, El-Banhawy EM (1995) Susceptibility of the tomato russet mite, *Aculops lycopersici* in Egypt to methamidiphos, pyridaphenthion, cypermethrin, dicofol and fenarimol. Exp Appl Acarol 1:11–15

Abou-Awad BA, El-Sherif AA, Hassan MF, Abou-Elela MM (1998a) Life history and life table of *Amblyseius badryi*, as a specific predator of eriophyid grass mite (Acari: phytoseiidae: Eriophyidae). Z Pflanzenk Pflanzensch 105:422–428

Abou-Awad BA, El-Sherif AA, Hassan MF, Abou-Elela MM (1998b) Laboratory studies on development, longevity, fecundity and predation of *Cydnoseius negevi* (Swirski & Amitai) (Acari; Phytoseiidae) with to mite species as prey. Z Pflanzenk Pflanzensch 105:429–433

Abou-Awad BA, Korayem AM, Hassan MF, Abou-Elela MM (2001) Life history of the predatory mite *Lasioseius athiasae* (Acari, Ascidae) on various kinds of food substances: a polypeptide analysis of prey consideration. J Appl Entomol 125:125–130

Alves SB, Tamai MS, Rossi LS, Castigliono E (2005) *Beauveria bassiana* pathogenicity to citris rust mite *Phyllocoptruta oleivora*. Exp Appl Acarol 37:117–122

Angeli G, Rizzi C, Giuliani G, Tomasi C, Baldessari M (2008) Valide alternative per il controllo dell'eriofide del melo. Informatore Agrario 64(23):68–71

Aratchige NS, Sabelis MW, Lesna I (2007) Plant structural changes due to herbivory: do changes in *Aceria*-infested coconut fruits allow predatory mites to move under the perianth? Exp Appl Acarol 43:97–107

Argov Y, Amitai S, Beattie GAC, Gerson U (2002) Rearing, release and establishment of imported predatory mites to control citrus rust mite in Israel. Biocontrol 47:399–409

Arthropod Pesticide Resistance Database: http://www.pesticideresistance.org/DB

Auger P, Bonafos R, Guichou S, Kreiter S (2003) Resistance to fenazaquin and tebufenpyrad in *Panonychus ulmi* Koch (Acari: Tetranychidae) populations from South of France apple orchards. Crop Prot 22:1039–1044

Ay R, Gurkan MO (2005) Resistance to bifenthrin and resistance mechanisms of different strains of the two-spotted spider mite (*Tetranychus urticae*) from Turkey. Phytoparasitica 33:237–244

Baker RT (1979) Insecticide resistance in the peach silver mite *Aculus cornutus* (Banks). N Z J Exp Agric 7:405–406

Balazy S, Mietkiewski R, Thaczuk C, Wegensteiner R, Wrzosek M (2008) Diversity of acaropathogenic fungi in Poland and other European countries. Exp Appl Acarol 46:53–70

Bergh JC, Rugg D, Jansson RK, McCoy CW, Robertson JL (1999) Monitoring the susceptibility of citrus rust mite (Acari: Eriophyidae) populations to abamectin. J Econ Entomol 92:781–787

Bernard MB, Horne PA, Hoffmann AA (2005) Eriophyoid mite damage in *Vitis vinifera* (grapevine) in Australia: *Calepitrimerus vitis* and *Colomerus vitis* (Acari: Eriophyidae) as the common cause of the widespread 'Restricted Spring Growth' syndrome. Exp Appl Acarol 35:83–109

Bielza P, Denholm I, Ioannidis P, Sterk G, Leadbeater A, Leonard P, Nistrup Jorgensen L (2008) Declaration of Ljubljana. Outlooks on Pest Manag 19(6):246–248

Bonafas R, Serrano E, Auger P, Kreiter S (2007) Resistance to deltamethrin, lambda-cyhalothrin and chlorpyriphos-ethyl in some population of *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) (Acari: Phytoseiidae) from vineyards in south-west of France. Crop Prot 26:169–172

Brennan R, Jorgensen L, Gordon S, Loades K, Hackett C, Russell J (2009) The development of a PCR-based marker linked to resistance to the blackcurrant gall mite. Theor Appl Genet 118:205–211

Bretschneider T, Fischer R, Nauen R (2007) Inhibitors of lipid synthesis (acetyl-CoA-carboxylase inhibitors). In: Krämer W, Schirmer U (eds) Modern crop protection compounds. Wiley–VCH Verlag GmbH & Co, Weinheim, pp 909–925

Brodeur J, Bouchard A, Turcotte G (1997) Potential of four species of predatory mites as biological control agents of the tomato russet mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae). Can Entomol 129:1–6

Campos F, Krupa DA, Dubas RA (1996) Susceptibility of populations of two spotted spider mites (Acari: Tetranychidae) from Florida, Holland and the Canary Island to abamectin and characterization of abamectin resistance. J Econ Entomol 89:594–601

Carew ME, Goodisman MAD, Hoffmann AA (2004) Species status and population genetic structure of grapevine eriophyoid mites. Entomol Exp Appl 111:87–96

Castagnoli M, Oldfield GN (1996) Other fruit trees and nut trees. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 543–560

Castagnoli M, Simoni S, Liguori M (2003) Evaluation of *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) as a candidate for the control of *Aculops lycopersici* (Tyron) (Acari Eriophyoidea): a preliminary study. Redia 86:97–100

Castagnoli M, Lewandowski M, Łabanowski GS, Simoni S, Soika GM (2009) An insight into some relevant aspects concerning eriophyoid mites inhabiting forests, ornamental trees and shrubs. Exp Appl Acarol. doi:10.1007/s10493-009-9313-8

Chandler D, Davidson G, Pell JK, Ball BV, Shaw K, Sunderland KD (2000) Fungal biocontrol of Acari. Biocontrol Sci Techn 10:357–384

Childers CC, Eastbrook MA, Solomon MG (1996) Chemical control of eryophyoid mites. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eryophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 695–726

Childers CC, Villanueva R, Aguilar H, Chewning R, Michaud JP (2001) Comparative residual toxicities of pesticides to the predator *Agistemus industani* (Acari: Stigmaeidae) on citrus in Florida. Exp Appl Acarol 25:461–474

Clark JM, Scott JG, Campos F, Bloomquist JR (1995) Resistance to avermectins—extent, mechanisms and management implications. Annu Rev Entomol 40:1–30

Conijn C (2006) Gewijzigde luchtsamenstelling bestrijdt ongedierte in bloembollenbewaarcel. Gewasbescherming 37:1–7

Courtin O, Fauvel G, Leclant F (2000) Temperature and relative humidity effects on egg and nymphal development of *Aceria tulipae* (K.) (Acari: Eriophyidae) on garlic leaves (*Allium sativum* L.). Ann Appl Biol 137:207–211

Coyle DR (2002) Effects of clone, silvicultural, and miticide treatments on cottonwood leafcurl mite (Acari: Eryophidae) damage in plantation *Populus*. Environ Entomol 31:100–1008

Croft BA, McRae IV (1993) Biological control of apple mites. Impact of Zetzellia mali (Acari, Stigmaeidae) on Typhlodromus pyri and Metaseiulus occidentalis (Acari, Phytoseiidae). Environ Entomol 22:865–887

Croft BA, Slone DH (1998) Perturbation of regulated apple mites: immigration and pesticide effects on outbreaks of *Panonychus ulmi* and associated mites (Acari: Tetranychidae, Eriophyidae, Phytoseiidae and Stigmaeidae). Environ Entomol 27(6):1548–1556

Curthbertson AGS, Murchie AK (2004) The phenology, oviposition and feeding rate of *Anystis baccarum*, a predatory mite in Bramley apple orchards in Northern Ireland. Exp Appl Acarol 34:367–373

Curthbertson AGS, Murchie AK (2006) Environmental impact of an orchard winter wash and early season pesticide applications on both a beneficial and a pest mite species in Bramley apple orchards. Int J Environ Sci Tech 3:333–339

de Faria MR, Wraight SP (2007) Mycoinsecticides an mycoacaricides: a comprehensive list with worldwide coverage and international classification of formulation types. Biol Control 43:237–256

De Maeyer L, Schmidt HW, Peters D (2002) Envidor—a new acaricide for IPM in pomefruit orchards. Pflanzenschutz-Nachrichten Bayer 55:211–236

De Vis RJ, de Moraes GJ, Bellini MR (2006) Initial screening of little known predatory mites in Brazil as potential pest control agents. Exp Appl Acarol 39:115–125

Dekeyser M (2005) Acaricide mode of action. Pest Manag Sci 61:103–110

Duso C, de Lillo E (1996) Grape. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 571–582

Duso C, Pasini M (2003) Distribution of the predatory mite *Amblyseius andersoni* (Acari: Phytoseiidae) on different apple cultivars. Anz Schädl—J Pest Sci 76:33–40

Duso C, Castagnoli M, Simoni S, Angeli G (2008) The impact of eriophyoids on crops: new and old case studies. In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier M-S, Vial L (eds) Integrative acarology. Proceedings of the 6th European Congress. Montpellier, 21–25 July

Duso C, Castagnoli M, Simoni S, Angeli G (2009) The impact of eriophyoids on crops: recent issues on *Aculus schlechtendali*, *Calepitrimerus vitis* and *Aculops lycopersici*. Exp Appl Acarol. doi: 10.1007/s10493-009-9300-0

Easterbrook MA (1996) Damage and control of eriophyoid mites in apple and pear. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 527–541

Edgington S, Fernando LCP, Jones K (2008) Natural incidence and environmental profiling of the mite-pathogenic fungus *Hirsutella thompsonii* Fisher for control of the coconut mite in Sri Lanka. Int J Pest Manag 54:123–127

Fernando LCP, Manoj P, Hapuarachchi DCL, Edington S (2007) Evaluation of four isolates of *Hirsutella thompsonii* against coconut mite (*Aceria guerreronis*) in Sri Lanka. Crop Prot 26:1062–1066

Frei A, Blair MW, Cardona C, Beebe SC, Gu H, Dorn S (2005) QTL mapping of resistance to *Thrips palmi* (Karny) in common bean. Crop Sci 45:379–387

Galvão AS, Gondim MGC Jr, de Moreas GJ, de Oliveira JV (2007) Biologia de Amblyseius largoensis (Muma)(Acari: Phytoseiidae), um potencial predator de Aceria guerreronis Keifer (Acari: Eriophyidae) em Coqueiro. Neotrop Entomol 36:465–470

Gamliel-Atinsky E, Freeman S, Maymon M, Belausov E, Ochoa R, Bauchan G, Skoracka A, Peña J, Palevsky E (2009) The role of eriophyoids in fungal pathogen epidemiology, mere association or true interaction? Exp Appl Acarol. doi:10.1007/s10493-009-9302-y

Georghiou GP, Lagunes-Tejeda A (1991) The occurrence of resistance to pesticides in arthropods: an index of cases reported through 1989. Food and Agricultural Organisation of the United Nations, Rome, Italy

Gerson U, Weintraub PG (2007) Mites for the control of pests in protected cultivation. Pest Manag Sci 63(7):658–676

Gerson U, Smiley RL, Ochoa R (2003) Mites (Acari) for pest control. Boston, Blackwell Science 539pp

Gerson U, Gafni A, Paz Z, Sztejnberg A (2008) A tale of three acaropathogenic fungi in Israel: *Hirsutella*, *Meira* and *Acaromyces*. Exp Appl Acarol 46:183–194

Hall DG, Childers CC, Eger JE (2005) Effects of reducing sample size on density estimates of citrus rust mite (Acari: Eriophyidae) on citrus fruit: simulated sampling. J Econ Entomol 98:1048–1057

Hall DG, Childers CC, Eger JE (2007) Binomial sampling to estimate rust mite (Acari: Eriophyidae) densities on orange fruit. J Econ Entomol 100:233–240

Hansen BG, Halkier BA, Kliebenstein DJ (2007) Identifying the molecular basis of QTLs: eQTLs add a new dimension. Trends Plant Sci 13:72–77

Haque MM, Kawai A (2003) Effect of temperature on development and reproduction of the tomato russet mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae). Appl Entomol Zool 38:97–101

Hardman JM, Franklin JL, Moreau DL, Bostanian NJ (2003) An index for selective toxicity of miticides to phytophagous mites and their predators based on orchard trials. Pest Manag Sci 59(12):1321–1332

Herron GA, Rophail J (1998) Tebufenpyrad (Pyranica(R)) resistance detected in two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) from apples in western Australia. Exp Appl Acarol 22:633–641

Herron GA, Rophail J, Wilson LJ (2001) The development of bifenthrin resistance in two-spotted spider mite (Acari: Tetranychidae) from Australian cotton. Exp Appl Acar 25:301–310

Hirata KY, Kawamura Y, Kudo M, Igarasgi H (1995) Development of a new acaricide, pyridaben. J Pest Sci 20:177–179

Hollingworth RM, Ahammadsahib KI (1995) Inhibitors of respiratory complex I: mechanisms, pesticidal actions and toxicology. Rev Pestic Toxicol 3:277–302

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. University of California Press, Berkeley, CA 614pp

Jones AT (2000) Black currant reversion disease—the probable causal agent, eriophyid mite vectors, epidemiology and prospects for control. Virus Res 71:71–84

Kahu K, Janes H, Luik A, Klaas L (2009) Yield and fruit quality of organically cultivated blackcurrant cultivars. Acta Agric Scand B- Soil Plant Sci 59:63–69

Kalaisekar A, Naido VG, Rao NV (2000) Citrus rust mite, *Phyllocoptruta oleivora* (Ashmead) (Eriophyidae: Acarina): effects of its damage on fruit quality and its chemical control. Ind J Plant Prot 28:132–134

Kang SG, Koo BJ, Lee T, Chang MU (2007) Allexivirus transmitted by eriophyid mites in garlic plants. J Microbiol Biotech 17:1833–1840

Kawai A, Haque M (2004) Population dynamics of tomato russet mite *Aculops lycopersici* (Massee) and its natural enemy, *Homeopronematus anconai* (Baker). JARQ 38:161–166

Kidd H (2002) Insect Pests—crumbling defences and new approaches. Pestic Outlook 13:201–203

Knott CM (2007) The impact of European pesticide regulation on product availability for crops. Proc BCPC 1:290–291

Kondo A, Hiramatsu T (1999) Analysis of peach tree damage caused by peach silver mite, *Aculus fockeui* (Nalepa et Trouessart) (Acari: Eriophyidae). Japan J Appl Entomol Zool 43:189–193

Konno T, Kuriyama K, Hamaguchi H, Kujihara O (1990) Fenpyroximate (NNI-850) a new acaricide. Proc BCPC-Pests and Diseases, 71–78

Kyomura N, Fukuchi T, Kohyama Y, Motojima S (1990) Biological characteristics of new acaricides MK-239. Proc BCPC-Pests and Diseases 5:5–62

Lawson-Balagbo LM, Gondim MGC Jr, de Moreas GJ, Hanna R, Schausberger P (2007) Life history of the predatory mites *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi*, candidates for biological control of *Aceria guerreronis*. Exp Appl Acarol 43:49–61

Lawson-Balagbo LM, Gondim MGC, de Moraes GJ, Hanna R, Schausberger P (2008) Exploration of the acarine fauna on coconut palm in Brazil with emphasis on *Aceria guerreronis* (Acari: Eriophyidae) and its natural enemies. Bull Entomol Res 98:83–96

Leite GLD, Picanço M, Guedes RNC, Zanuncio JC (1999) Influence of canopy height and fertilization levels on the resistance of *Lycopersicon hirsutum* to *Aculops lycopersici* (Acari: Eriophyidae). Exp Appl Acarol 23:633–642

Lesna I, Conijn CGM, Sabelis M (2004) From biological control to biological insight: rust-mite induced change in bulb morphology, a new mode of indirect plant defence. Phytophaga 14:285–291

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites—their biology, natural enemies and control world crop pest series vol 6. Elsevier Science Publishers, Amsterdam, The Netherlands 790pp

Longhurst C, Bacci L, Buendia J, Hatton CJ, Petitprez J, Tsakonas P (1992) Fenazaquin, a novel acaricide for the management of spider mites in a variety of crops. Proc BCPC-Pests and Diseases 5:1–58

McCaffery A, Nauen R (2006) The insecticide resistance action committee (IRAC): public responsibility and enlightened industrial self-interest. Outlooks P Manag 17:11–14

McCoy CW (1996a) Stylar feeding injury and control of eriophyoid mites in citrus. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 513–526

McCoy CW (1996b) Pathogens of Eriophyoids. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, pp 481–490

McMurtry JA, Croft BA (1997) Life-style of phytoseiid mites and their roles in biological control. Annu Rev Entomol 42:291–321

Messing RH, Croft BA (1996) Pesticide resistance in eriophyoid mites, their competitors and predators. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eryophyoid mites- Their biology. natural enemies and control. Elsevier, Amsterdam, pp 695–726

Metcalf RL (1980) Changing role of insecticides in crop protection. Annu Rev of Entomol 25:219–256

Metwally AB, Abou-Awad BA, Al-Azzazy MMA (2005) Life table and prey consumption on the predatory mite *Neoseiulus cydnodactylon* Shehata and Zacher (Acari: Phytoseiidae) with three mite species as prey. Z Pflanzenk Pflanz 112:276–286

Momen FM, Abdel-Khalek A (2008) Effect of the tomato rust mite *Aculops lycopersici* (Acari: Eriophyidae) on the development and reproduction of three predatory phytoseiid mites. Int J Trop Insect Sci 28:53–57

Monfreda R, Lekveishvili M, Petanovic R, Amrine JW Jr (2009) Collection and detection of eriophyoid mites. Exp Appl Acarol. doi:10.1007/s10493-009-9315-6

Moore D, Howard FW (1996) Coconuts. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 561–570 790pp

Nauen R, Stumpf N, Elbert A, Zebitz CPW, Kraus W (2001) Acaricide toxicity and resistance in larvae of different strains of *Tetranychus urticae* and *Panonychus ulmi* (Acari: Tetranychidae). Pest Manag Sci 57:253–261

Nauen R, Schnorbach HJ, Elbert A (2005) The biological profile of spiromesifen (Oberon): a new tetronic acid insecticide/acaricide. Pflanzenschutz Nachr Bayer 58:417–440

Nauen R, Leadbeater A, Thompson A (2008) Proposal on the revision of EU Directive 91/414. Outlooks on Pest Management 19(4):150–151

Navajas M, Navia D (2009) DNA-based methods for eriophyoid mite studies: review, critical aspects, prospects and challenges. Exp Appl Acarol. doi:10.1007/s10493-009-9301-z

Navia D, de Moraes GJ, Roderick G, Navajas M (2005) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyidae): origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. Bull Entomol Res 95:505–516

Negloh K, Hanna R, Schausberger P (2008) Comparative demography and diet breadth of Brazilian and African populations of the predatory mite *Neoseiulus baraki*, a candidate for biological control of coconut mite. Biol Control 46:523–531

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vectors of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 259–275 790pp

Omoto C, Dennehy TJ, McCoy CW, Crane SE, Long JW (1994) Detection and characterisation of the interpopulation variation of citrus rust mite resistance to dicofol in Florida citrus. J Econ Entomol 84:566–572

Omoto C, Dennehy TJ, McCoy CW, Crane SE, Long JW (1995) Interface between citrus rust mite (Acari: Eryophyidae) and dicofol- implication for resistance management. J Econ Entomol 88:1129–1137

Ozman-Sullivan SK (2006) Life history of *Kampimodromus aberrans* as a predator of *Phytoptus avellanae* (Acari: Phytoseiidae, Phytoptidae). Exp Appl Acarol 38:15–23

Ozman-Sullivan SK, Akca I (2005) Efficiency of pesticides against big bud mites (*Phytoptus avellanae* Nal, and Cecidophyopsis vermiformis Nal, Acarina: Eryophyoidea) on hazelnut. Acta Hortic 688:393–399

Paz Z, Gerson U, Sztejnberg A (2007) Assaying three new fungi against citrus mites in the laboratory, and a field trial. Biocontrol 52:855–862

Perring T (1996) Vegetables. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 593–606

Qu SC, Tashiro NE, Etoh T, Sadamatsu M (1997) Occurrence of dithiocarbamate-resistant strain and its susceptibilities to several chemicals in the pink citrus rust mite, *Aculops pelekassi* (Keifer) in Saga Prefecture. Kyushu Byogaichu Kenkyukaiho 43:125–129

Royalty and Perring (1996) Nature of damage and its assessment. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 493–508

Sabelis MW (1996) Phytoseiidae. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Amsterdam, Elsevier Science Publishing, pp 427–456

Scarpellini JR, Clari AR (1999) Control of the citrus rust mite *Phyllocoptruta oleivora* Ashmead, 1879 (Acari: Eriophyidae) with diflubenzuron alone or in association with sulphur, in citrus. Redia 74:15–23

Smissaert HR (1964) Cholinesterase inhibition in spider mites susceptible and resistant to organophosphate. Science 143:129–131

Smith D, Papacek DF (1991) Studies of the predatory mite Amblyseius victoriensis (Acarina: Phytoseiidae) in citrus orchards in south-east Queensland: control of Tegolophus australis and Phyllocoptruta oleivora (Acarina: Eriophyidae), effect of pesticides, alternative host plants and augmentative release. Exp Appl Acarol 12:195–217

Smith D, Smith NJ, Smith KM (1998) Effect of abamectin on citrus rust mite *Phyllocoptruta oleivora* and brown citrus rust mite *Tegolohus australis* and the scale natural enemies *Aphytis lingnenensis* and *Chilocorus circumdatus* on oranges. Plant Prot Q 13:136–139

Spieser F, Graf B, Walther P, Noesberger J (1998) Impact of apple rust mite (Acari: Eriophyidae) feeding on apple leaf gas exchange and leaf color associated with changes in leaf tissue. Env Entomol 27(5): 1149–1156

Sreerema Kumar PS, Singh L (2002). Development of 'Mycohit', the first mycoacaricide based exclusively on *Hirsutella thompsonii*, for suppressing the coconut mite in India. In: Reddy SM, Redy SR, Singarachary MA, Girisham S (eds). Proceedings, national symposium on bioinoculants for sustainable agriculture and forestry. India, 16–18 Feb 2001, pp 209–213

Sreerema Kumar PS, Singh L (2008) Enabling mycelia application of *Hirsutella thompsonii* for managing the coconut mite. Exp Appl Acarol 46:169–182

Stansly PA, Riefer RE, Quereshi JA (2007) Acaricidal control of the citrus rust mite, 2006. Arthrop Manag Tests 32:D12

Stoeckli S, Mody K, Patocchi A, Kellerhals M, Dorn S (2009) Rust mite resistance in apple assessed by quantitative trait loci analysis. Tree Genet Genomes 5(1):257–267

Stumpf N, Nauen R (2001) Cross-resistance, inheritance and biochemistry of METI-acaricide resistance in *Tetranychus urticae* (Acari: Tetranychidae). J Econ Entomol 94:1577–1583

Stumpf N, Nauen R (2002) Biochemical markers linked to abamectin resistance in *Tetranychus urticae* (Acari: Tetranychidae). Pest Biochem Physiol 72:111–121

Sujatha A, Kumar DA, Rao NBVC, Rao DVR (2004) Evaluation of certain new chemicals against coconut eriophyid mite, Aceria guerreronis (K.). A.P. Pestology 28:7–11

Thistlewood HMA, Clements DR, Harmsen R (1996) Stigmaeidae. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier Science Publishing, Amsterdam, pp 457–470

Törnqvist L (2007) The commission perspective on the new regulation. Proceedings of the BCPC conference vol 1. pp 284–285

Tsagkarakou A, Van Leeuwen T, Khajehali J, Ilias A, Grispou M, Williamson MS, Tirry L, Vontas J (2009) Identification of pyrethroid resistance mutations in the para sodium channel of the two-spotted spider mite Tetranychus urticae (Acari:Tetranychidae). Insect Mol Biol 18:583–593

Van der Geest LPS, Elliot SL, Breeuwer JAJ, Beerling EAM (2000) Diseases of mites. Exp Appl Acarol 24:497–560

van der Linden A, Nouwens F (2005) Augmentation of predatory mites in Dutch nursery stock. Integrated control in protected crops, temperate climate. IOBC/wprs. Bulletin 28:279–281

Van Leeuwen T, Van Pottelberge S, Tirry L (2005) Comparative acaricide susceptibility and detoxifying enzyme activities in field-collected resistant and susceptible strains of Tetranychus urticae. Pest Manag Sci 61:499–507

van Lenteren JC (2000) A greenhouse without pesticides: fact or fantasy? Crop Prot 19:375–384

Van Pottelberge S, Van Leeuwen T, Nauen R, Tirry L (2008) Resistance mechanisms to mitochondrial electron transport inhibitors in a field-collected strain of Tetranychus urticae Koch (Acari: Tetranychidae). Bull Entomol Res 99:23–31

Villanueva RT, Gagne R, Childers CC (2005) Larval Cryptothelea gloverii (Lepidoptera: Psychidae), an arthropod predator and herbivore on Florida citrus. Exp Apl Acarol 36:83–92

Villanueva RT, Rodrigues JCV, Childers CC (2006) Two species of Cecidomyiidae predacious on citrus rust mite, Phyllocoptruta oleivora, on Florida citrus. Fla Entomol 89:161–167

Voss G, Matsumura F (1964) Resistance to organophosphorus compounds in the two-spotted spider mite: two different mechanisms of resistance. Nature 202:319–320

Wachendorff U, Bruck E, Elbert A, Fisher R, Nauen R, Stumpf N, Tiemann R (2000) BAJ2740, a novel broad spectrum acaricide. Proc BCPC—Pests & Diseases 1:53–58

Wachendorff U, Nauen R, Schnorbach HJ, Rauch N, Elbert A (2002) The biological profile of spirodiclofen (Envidor®)–a new selective tetronic acid acaricide. Pflanzenschutz-Nachrichten Bayer 55:149–176

Walde SJ, Hardman JM, Magagula CN (1997) Direct and indirect species interactions influencing within-season dynamics of apple rust mite, Aculus schlechtendali (Acari: Eriophyidae). Exp Appl Acarol 21(9):587–614

Walgenbach JF, Schoof SC (2006) European red mite control on apples, 2005. Arthrop Manag Tests 31:A24

Walston AT, Farnsworth A, Farnsworth J, Smith L, McCarty G, Riedl H (2005) Pear rust mite control on pears. Arthrop Manag Tests 30:A37

Walston AT, Adams C, Nance L, Richardson M, McCarty G, Riedl H (2007) Pear rust control at pink and petal fall. Arthrop Manag Tests 32:A36

Walton VM, Dreves AJ, Gent DH, James DG, Martin RR, Chambers U, Skinkis PA (2007) Relationship between rust mites Calepitrimerus vitis (Nalepa), bud mites Colomerus vitis (Pagenstecher) (Acari: Eriophyidae) and short shoot syndrome in Oregon vineyards. Int J Acarol 33(4):307–318

Webber J, Chapman RB, Worner SP (2008) Forecasting emergence and movement of overwintering hazelnut big bud mites from big buds. Exp Appl Acarol 45:39–51

Witters J, De Bondt G, Desamblanx, Casteels H (2006) A preliminary survey of predatory mites of Tetranychidae in tree nurseries in Belgium. Abstract XII Internation Congress of Acarology. Amsterdam, The Netherlands, 21–26 August 2006

Wood E, Latli B, Casida JE (1996) Fenazaquin acaricides specific binding sites in NADH: Ubiquinone oxidoreductase and apparently the ATP synthase stalk. Pest Biochem Physiol 54:135–145

Zhu S, Walker DR, Boerma HR, All JN, Parrott WA (2006) Fine mapping of a major insect resistance QTL in soybeen ant its interaction with minor resistance QTLs. Crop Sci 46:1094–1099

Adventive eriophyoid mites: a global review of their impact, pathways, prevention and challenges

Denise Navia · Ronald Ochoa · Cal Welbourn · Francisco Ferragut

Abstract   Eriophyoids have high potential as adventive mite species (AMS) because their small size make them difficult to detect, and can be easily distributed in world trade. Economic, social and environmental impact from adventive eriophyoid mites has been significant. Considerable attention has been given to adventive insect species while adventive mites have received little attention and little information is available for eriophyoids. This paper summarizes information on adventive eriophyoid mites, their impact, and the history of some important invasions. The status of adventive species of eriophyoids introduced as biological control agents of weeds is presented. A list of eriophyoid mites reported as invasive species worldwide is given. Pathways of concern and biosecurity actions to reduce the risk of eriophyoid mites are discussed. The need to raise public awareness of the risk and importance of these tiny organisms as AMS is emphasized. Scientific and technical challenges to deal with adventive eriophyoids are discussed.

Keywords   Acari · Eriophyoidea · Invasive alien species · Pathways · Quarantine · Biosecurity

D. Navia (✉)
Laboratório de Quarentena Vegetal, Embrapa Recursos Genéticos e Biotecnologia,
CP 02372, Brasília, DF 70.770-900, Brasil
e-mail: navia@cenargen.embrapa.br

R. Ochoa
Systematic Entomology Laboratory, Agriculture Research Service,
United States Department of Agriculture, BARC-West, Beltsville, MD 20705, USA
e-mail: Ron.Ochoa@ars.usda.gov

C. Welbourn
Division of Plant Industry, Florida Department Agriculture & Consumer Services,
P.O. Box 147100, Gainesville, FL 32614-7100, USA
e-mail: welbouc@doacs.state.fl.us

F. Ferragut
Instituto Agroforestal Mediterráneo, Universidad Politécnica de Valencia,
Camino de Vera, s/n, 46022 Valencia, Spain
e-mail: fjferrag@eaf.upv.es

Introduction

The term "adventive species" refers to alien or exotic species, subspecies, biotypes, races or strains introduced into an area outside its native range and includes many species that cause ecological or economic problems throughout the world (Wheeler and Hoebeke 2009). Adventive species, also called "Invasive Alien Species" (CBD 2002), are considered to be a direct driver of biodiversity loss across the globe and are causing enormous damage to valuable agricultural systems (McNeely et al. 2001). These species can act as vectors for new diseases, alter ecosystem processes, change biodiversity, disrupt cultural landscapes, reduce land and water value for human activities and cause other socio-economic consequences (DAISIE 2009). Bioinvasion is one of the great economic and ecological issues of our time (McNeely et al. 2001). The cost of adventive species to national economies has been estimated at hundreds of billions of dollars annually (CBD 2002).

The globalization of travel and trade has facilitated introductions of adventive species since the Industrial Revolution in the nineteenth century. Many species introduced decades ago have only recently begun to spread rapidly in ecosystems. There has been an upward trend in the establishment of non-indigenous species and large numbers of invasive species have been documented (Randall and Marinelli 1996; Vitousek et al. 1997; Nico and Fuller 1999; Xie et al. 2000). An adventive species can be transported intentionally or unintentionally by man (di Castri 1990; Wheeler and Hoebeke 2009). Intentional transport is the movement of organisms to a new area for an express purpose, such as the importation of ornamental or crop plants, or as biological control agents. Unintentional transport refers to the movement of non-native species as a secondary result of the intentional transfer of another product. Exotic species can be transported on or within other species, such as on host plants, within cargo holds or in packing materials. The study of adventive species may provide opportunities to understand basic evolutionary processes, predict the risk of their spread in new regions and develop pest control and quarantine strategies.

Phytophagous mites are a group of organisms where adventive species can greatly impact agroecosystems and natural terrestrial ecosystems. Among the phytophagous mites, eriophyoid species have highest potential as adventive mite species (AMS). There are several examples of inadvertent introductions of eriophyoid mites in new areas where they found appropriate conditions to develop in the absence of efficient natural enemies, resulting in accentuated damage to the infested crops and consequent serious social-economic problems.

This paper discusses the importance of eriophyoid mites as AMS, with a brief review of some AMS; their ecological and economic impact, a discussion on the pathways available to eriophyoid mites and the preventive procedures for invasive alien eriophyoid mites. The research related to adventive eriophyoid mites to be addressed in the near future is discussed.

Eriophyoids as adventive species

Phytophagous mites are good candidates to become adventives species, because of the characteristics that make their potential to damage the host plants, vector plant diseases, development of resistance to pesticides, difficulties to detect, capacity to survive adverse conditions, parthenogenetic reproduction, disperse by wind and adaptation to new host plants (Navia et al. 2007a). Most of the mentioned traits can be found among eriophyoid mites making them high potential as adventive species.

Among the plant feeding mites, the Eriophyidae are the second most economically important family of pests after the Tetranychidae (Lindquist and Amrine 1996). Eriophyid species are known to cause considerable damage, assuming pest status in crops of social-economic importance. Eriophyoids can be serious pests of horticultural crops, like *Aculops lycopersici* (Tryon) a key pest of tomato and other Solanaceae worldwide (Perring 1996). In temperate and tropical fruit tree crops, *Aculus schlechtendali* (Nalepa) is a pest of apples in Europe (Easterbrook 1996; Gólya and Kozma 1998; Angeli et al. 2007) and *Aceria guerreronis* Keifer is an important pest of coconut palms, *Cocos nucifera* L., worldwide (Moore and Howard 1996; Fernando et al. 2002; Nair et al. 2005). In cereal crops, *Aceria tosichella* Keifer is a widespread pest of wheat and corn (Oldfield and Proeseler 1996; Harvey et al. 2002) and in forest and ornamental trees, *Trisetacus juniperinus* (Nalepa) is a pest of evergreen cypress in Europe and North America (Castagnoli 1996; Castagnoli et al. 2002; Simoni et al. 2004).

Mites are considered efficient vectors of plant diseases (viruses and virus-like). The transmission of 21 pathogens by 13 species of phytophagous mites to at least 34 plants has been reported in the literature (Oldfield and Proeseler 1996; Seifers et al. 1996, 1998; Chagas et al. 2001; Childers et al. 2001; Stephan et al. 2008). Most mite species that are known to vector plant pathogens are in the Eriophyidae. At least 26 plant diseases are associated with eriophyid mites (Jones 1999). As a result of their tiny size and very short stylets (ca 20 μm) feed only the epidermal cells of their plant hosts where they may acquire and transmit disease agents to these plant cells (Jones 1999). The location of these different viruses in epidermal cells of their plant host suggest that the mode of transmission by their mite vector should be of a non-persistent or semi-persistent type, but the data indicate that some may be of a persistent (circulative) type (Jones 1999). Eriophyoid mites can then disseminate phytovirus to non affected areas if they are transported after the virus acquisition period.

Resistance to pesticides accentuates the economic importance of the pests, due to increased difficulties in their control. Even if a species is already present in an area, new introductions should be avoided because they may include a resistant biotype. Resistance to pesticides has been reported in seven eriophyoid species: *Aculops lycopersici* on tomato and *Aculops pelekassi* (Keifer), *Aculus cornutus* (Banks), *Aculus fockeui* (Nalepa & Trouessart), *Aculus malivagrans* (Keifer), *A. schlechtendali* and *Phyllocoptruta oleivora* (Ashmead; Michigan State University 2004) all on fruit trees.

Mites often are difficult to detect due to their small size and they are often hidden on the host plant. Eriophyoidea are among the smallest arthropods, measuring from 86 to 500 μm in length, and often impossible to detect with the naked-eye or 10× hand lens. Eriophyoidea colonies can commonly develop in buds, sheaths and other protected areas of the plant (Lindquist et al. 1996). Usually symptoms of a mite infestation appear only at high populations. These characteristics make interception of eriophyoid mites associated with plants and plant products at points of entry or departure difficult.

When phytophagous mites are introduced into a new region they may spread in the environment, but if their preferred host is not available they either die or they may adapt to another host. This occurs more frequently in polyphagous species in the Tetranychoidea than in eriophyoids which are usually more host specific. The majority of eriophyoid species described to date are reported from a single host species, others are limited to species within a single genus or on a few species of closely related genera of the same plant family (Oldfield 1996). There are uncertainties regarding the identity of Eriophyidae reported to be host generalists. For example, molecular and host acceptance studies on *Abacarus hystrix* (Nalepa), an eriophyid reported to occur on at least 30 genera of grasses,

supported the hypothesis that this species is a species complex and not a single species (Skoracka 2008).

However, evidence suggests that some invasive species are able to extend their host range. The coconut mite *A. guerreronis* probably originated in tropical America (Navia et al. 2005) and has spread to most of the coconut production areas of the world. *Aceria guerreronis* has been found infesting palmyra palm fruits, *Borassus flabellifer* L., in India (Ramaraju and Rabindra 2002) and Sri Lanka (de Moraes, personal communication). The palmyra palm is native to Southern and Southeast Asia and is widely cultivated in urban and rural areas. The observation of *A. guerreronis* on palmyra palm was made soon after *A. guerronis* was reported in Southeast Asia and the subsequent explosion in its populations, which supports the hypothesis that the mite expanded its host range in a period of adaptation to the new environment. Samples of mites attacking *B. flabellifer* plants in India and Sri Lanka should be tested to confirm that they represent the same taxon reported from coconut and not a cryptic species. The coconut mite has also moved to the queen palm *Syagrus romanzoffiana* (Cham.) Glassman seedlings in nurseries in California and Florida, USA (Ansaloni and Perring 2004; Welbourn unpublished data). This palm is native to South America and is widely cultivated as an ornamental in Florida and California. Nuclear and mitochondrial sequences of coconut mite population from *S. romanzoffiana* from California were identical or similar to that of other populations found on coconut in the Americas (Navia et al. 2005), indicating that it is a single species as opposed to one or more cryptic species. During surveys of eriophyoid mites on native palms (Arecaceae) in Brazil, *S. romanzoffiana* leaves and fruits were extensively sampled in search of new hosts of *A. guerreronis*, in natural areas presenting a high density of this palm. The coconut mite was not found during these surveys which indicate that queen palm is not a host for *A. guerreronis* in its areas of natural occurrence in Brazil (Navia 2004). However, evidences are provided in Navia et al. (2005) that the coconut mite does feed on queen palm seedlings in North America.

Another example of host expansion appears to be *A. lycopersici* that probably originally fed on wild solanaceous plants native to the Americas and its association with tomato is a recent event (Oldfield 1996). Although there is evidence supporting the hypothesis of host range expansion for certain species of eriophyoid mites in new areas, it remains a controversial subject, and there needs to be additional research on host acceptance (see Michalska et al. 2009; Navajas and Navia 2009).

Eriophyoid mites have a considerable capacity to survive adverse conditions. Many species are able to survive the harsh low temperatures of winter in the egg stage or through diapause. Survival of 50–76% of *A. schlechtendali* deutogynes during the winter has been reported in Poland (Kozlowski and Boczek 1987). Eggs of *Aceria tulipae* Keifer can endure temperatures of –31°C for 2.5 min (Jeppson et al. 1975). Generally, mites can survive lower temperatures than their host plants. This characteristic enables mites to survive when associated with plant products transported for extended periods of time at low temperatures, as, for example, fresh fruits, whose are usually transported at temperatures from 2 to 6°C.

Lastly, it is not necessary for a large number of exotic eriophyoid mites to be introduced into a new habitat for its establishment. Arrhenotokous parthenogenesis (i.e. fertilized egg become female and unfertilized eggs become males) is common in most phytophagous mites including the eriophyoids. Arrhenotokous species are able to start a new population from a single female. While arrhenotoky has been reported in the Eriophyoidea, thelytokous parthenogenesis has not been found in this group (Helle and Wysoki 1996).

Adventive eriophyoid mites and their impact

Most agricultural pests are represented by non-native species (Pimentel 2002). Pimentel estimated the annual costs associated with arthropods introduced into the United States to be about 20 billion dollars. Besides the economic losses, the ecological impact by adventive species occurs at different levels including their direct effect on individuals, populations or native communities and indirect effects on ecosystems, through more complex mechanisms and cascading effects (NRC 2002). Literature reviews of the ecological impact of invasive alien species have been published on insects (Kenis et al. 2009), but mites are rarely listed as adventive species because little is known about their ecological effects.

Table 1 summarizes a literature review of eriophyoid species reported as invasive in many geographical areas. The table includes available data on country, host plants and whether the introduction was accidental or deliberate (i.e. as biological control agents of weeds). Eriophyoid mites representing 85 species and 30 genera are mentioned as invasive; genera with the higher number of invasive species include *Aceria* (29), *Eriophyes* (7), *Aculops* (5), *Aculus* (4), *Acalitus* (3), *Phyllocoptes* (3) and *Trisetacus* (3). Most of host plants with invasive eriophyoids were fruit or ornamentals due to the extensive international movement of these plants and/or their products (i.e. fresh fruits, plants for planting, cuttings, and/or budwood).

Adventive eriophyoid mites in Europe

The "Delivering Alien Invasive Species in Europe" (DAISIE) was a 3 years project, funded by the European Union, to provide new knowledge on biological invasions in Europe. This project provided an inventory of more than 11,000 alien species in Europe (including harmful and harmless; DAISIE 2009; www.europe-aliens.org). This list includes thirteen eriophyoid species in the genera *Aculops* (4), *Aceria* (3) and one each in following genera: *Acaphylla*, *Calacarus*, *Eriophyes*, *Phyllocoptes*, *Tegolophus* and *Trisetacus.*

Some pest species of crops in Europe are also found in other regions of the world. Several are vagrant species infesting citrus in the Mediterranean region. The citrus bud mite, *Aceria sheldoni* (Ewing), occurs in all of the citrus-growing regions of the world where it lives under and within the buds of lemons causing structural modifications in leaves and fruits, to develop abnormally (Jeppson et al. 1975). The citrus rust mite, *P. oleivora*, was not included in the DAISIE list but it is already present in Sicily and Cyprus (de Lillo 2004). This eriophyid causes considerable injury to citrus, affecting the quality of fruits in most of the citrus-growing areas of the world, and is a key pest to citrus in Florida and Israel. Symptoms are very characteristic; the affected fruits show russetting and are small in diameter and weight. Similar effects of fruit damage have been observed in the pink citrus rust mite, *A. pelekassi*, another widespread eriophyid mite that also occurs in other European countries or localities, for example in Italy, Greece, Malta, Ukraine and Montenegro (de Lillo 2004).

The pear leaf blister mite, *Eriophyes pyri* (Pagenstecher), is distributed worldwide as an important pest of fruit trees (Easterbrook 1996). The mite causes blisters and galls on the underside of developing pear and apple leaves that turn from red to dark brown and black (Easterbrook 1996). Probably the pear leaf blister mite has been disseminated around the world, including Europe, through transport of pear propagation material (Jeppson et al. 1975).

The tomato russet mite *A. lycopersici* has a cosmopolitan distribution and is a serious pest of tomato plants and other solanaceous crops grown between 60° north and 60° south

Table 1 Literature review of eriophyoid species reported as alien invasive worldwide, with data on the invaded geographical areas, host plants and the purpose of the introduction (accidental or deliberate as biological control agents of weeds)

Species	Invaded area	Host plant	Introduction	Source
Acalitus odoratus Keifer	South and Southeast Asia, Pacific Islands	*Chromolaena odorata*	Accidental	Manson (1972)
Acalitus phloeocoptes (Nalepa)	China	*Prunus* spp.	Accidental	Hong et al. (2006)
Acalitus plucheae (Cook)	USA	*Pluchea* sp., *Rubus* sp.	Accidental	Touhey and White, USDA (personal communication)
Acaphylla theae (Watt & Mann)	China, Italy, Portugal, Spain	*Camellia* spp.	Accidental	DAISIE (2009), de Lillo (2004), Hong et al. (2006)
Acathrix trymatus Keifer	Florida (USA)	*Cocos nucifera*	Accidental	Welbourn (1996, 2007a, b)
Aceria aloinis (Keifer)	USA	No data	Accidental	Touhey and White, USDA (personal communication)
Aceria alpestris (Nalepa)	Czech Republic	*Rhododendron* sp.	Accidental	Šefrová and Laštůvka (2005)
Aceria anthocoptes (Nalepa)	USA	*Cirsium* spp.	Accidental	Ochoa et al. (2001); Michels Jr et al. (2009)
Aceria byersi Keifer	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Aceria caliberberis Keifer	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Aceria chondrillae (Canestrini)	Argentina, Australia, USA	*Chondrilla juncea*	Deliberate	Cullen and Briese (2001)
Aceria diospyri Keifer	USA	*Diospyros kaki*	Accidental	Touhey and White, USDA (personal communication)
Aceria erineus (Nalepa)	Czech Republic	*Juglans regia*	Accidental	Šefrová and Laštůvka (2005)
Aceria eriobotryae (Keifer)	China	*Eriobotrya japonica*	Accidental	Hong et al. (2006)
Aceria ficus (Cotte)	Japan	No data	Accidental	Mito and Uesugi (2004)
Aceria fraxiniflora (Felt)	Canada	*Fraxinus americana*	Accidental	FIAS (2009)
Aceria genistae (Nalepa)	Australia, New Zealand, USA	*Cytisus* spp., *Genista* spp., *Ulex* spp.	Deliberate, Accidental in USA	Smith et al. (2009)
Aceria guerreronis Keifer	USA	*Cocos nucifera* and *Syagrus romanzoffiana*	Accidental	Touhey and White, USDA (personal communication), Howard et al. (1990), Ansaloni and Perring (2004)

Table 1 continued

Species	Invaded area	Host plant	Introduction	Source
Aceria hibisci (Nalepa)	Australia, Caribbean Islands, USA	*Hibiscus rosa-sinensis*	Accidental	Carson (2000), Hara et al. (1996, 2001), Welbourn et al. (2008)
Aceria kenyae (Keifer)	China, Florida (USA)	*Mangifera indica*	Accidental	Hong et al. (2006), Welbourn (2005, 2008b)
Aceria kuko (Kishida)	China	*Lycium chinense*	Accidental	Hong et al. (2006)
Aceria ligustri (Keifer)	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Aceria litchii (Keifer)	China, Japan	*Litchi chinensis*	Accidental	Hong et al. (2006), Mito and Uesugi (2004)
Aceria loewi (Nalepa)	Czech Republic	*Syringa* spp.	Accidental	Šefrová and Laštůvka (2005)
Aceria malherbae Nuzzaci	Canada, South Africa, USA	*Convolvulus arvensis*	Deliberate	Rosenthal (1996)
Aceria mangiferae (Sayed)	USA	No data	Accidental	Touhey and White, USDA (personal communication)
Aceria neseri Meyer	Australia	*Chrysanthemoides monilifera*	Deliberate	Smith et al. (2009)
Aceria pallida Keifer	China	*Lycium chinense*	Accidental	Hong et al. (2006)
Aceria paradianthi Keifer	Japan	No data	Accidental	Mito and Uesugi (2004)
Aceria sheldoni (Ewing)	China	*Citrus* spp.	Accidental	Hong et al. (2006)
Aceria tosichella Keifer	China	*Triticum* spp., *Zea mays*	Accidental	Hong et al. (2006)
	China	*Triticum aestivum*	Accidental	Navia et al. (2006)
	Argentine	*Triticum aestivum*	Accidental	Pereira et al. (submitted)
	Brasil	*Triticum aestivum, Lolium multiflorum, Bromus unioloides*	Accidental	Castiglioni and Navia submitted
	Uruguay		Accidental	
Aceria tristriatus (Nalepa)	Czech Republic	*Juglans regia*	Accidental	Šefrová and Laštůvka (2005)
Aceria tulipae (Keifer)	China, Japan	*Allium sativum, Allium cepa, Tulipa* spp.	Accidental	Hong et al. (2006), Mito and Uesugi (2004)
Aceria zelkoviana Kim	Florida (USA)	*Zelkovia serrata*	Accidental	Welbourn (2000)
Aculops fuchsia Keifer	England, France	*Fuchsia* spp.	Accidental	Streito et al. (2004), DAISIE (2009)
Aculops glediseae (Keifer)	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Aculops lycopersici (Tryon)	China, Japan	*Lycopersicon esculentum*	Accidental	Hong et al. (2006), Mito and Uesugi (2004)

Table 1 continued

Species	Invaded area	Host plant	Introduction	Source
Aculops pelekassi (Keifer)	Greece, Italy, Malta, Montenegro, Ukraine, USA	*Citrus* spp.	Accidental	De Lillo (2004), Denmark (1962)
Aculops tetanothrix Nalepa	USA	No data	Accidental	Touhey and White, USDA (personal communication)
Aculus fockeui (Nalepa &Trouessart)	China, Japan, USA	*Prunus* spp.	Accidental	Hong et al. (2006), Mito and Uesugi (2004), Touhey and White, USDA (personal communication)
Aculus hippocastani (Fockeu)	Czech Republic	*Aesculus hippocastani*	Accidental	Šefrová and Laštůvka (2005)
Aculus hyperici (Liro)	Australia	*Hypericum perforatum*	Deliberate	Briese and Cullen (2001)
Aculus schlechtendali (Nalepa)	Chile, China, Japan, USA	*Malus domestica*	Accidental	Hong et al. (2006), Mito and Uesugi (2004), Altieri and Rojas (1999), Touhey and White, USDA (personal communication)
Amrineus coconuciferae Keifer	USA	*Cocos nucifera*	Accidental	Touhey and White, USDA (personal communication)
Anthocoptes transitionalis Hodgkiss	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Artacris macrorhynchus (Nalepa)	USA	*Acer* sp.	Accidental	Touhey and White, USDA (personal communication)
Calacarus brionesae Keifer	USA (Hawaii)	*Carica papaya*	Accidental	Fournier et al. (2001)
Calacarus carinatus (Green)	China, Hungary, Italy, Poland, Portugal, Spain	*Camellia* spp.	Accidental	Hong et al. (2006)
Cecidophyes rouhollahi Craemer	Canada	*Galium* spp.	Deliberate	McClay et al. (2001)
Cecidophyopsis hendersoni (Keifer)	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Cecidophyopsis ribis (Westwood)	China	*Ribes nigrum*	Accidental	Hong et al. (2006)
Cheiracus sulcatus Keifer	China	*Oryza sativa*	Accidental	Hong et al. (2006)
Colomerus vitis (Pagenstecher)	China, USA	*Vitis vinifera*	Accidental	Hong et al. (2006), Touhey and White, USDA (personal communication)
Coptophylla lamimani (Keifer)	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)

Table 1 continued

Species	Invaded area	Host plant	Introduction	Source
Cosetacus camelliae (Keifer)	Former Yugoslavia, Spain, USA	*Camellia* spp.	Accidental	de Lillo (2004), Touhey and White, USDA (personal communication)
Diptilomiopus assamica Keifer	Florida (USA)	Citrus	Accidental	Welbourn (2008c)
Diptilomiopus panithus (Boczek & Chandrapatya)	Florida (USA)	*Mangifera indica*	Accidental	Welbourn (2005, 2008b)
Epitrimerus cupressi (Keifer)	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Epitrimerus pyri (Nalepa)	China	*Pyrus* sp.	Accidental	Hong et al. (2006)
Eriophyes canestrinii (Nalepa)	Czech Republic, USA	*Buxus* sp., *Vitis* sp.	Accidental	Šefrová and Laštůvka (2005), Touhey and White, USDA (personal communication)
Eriophyes catacardiae Keifer	China	*Prunus* sp.	Accidental	Hong et al. (2006)
Eriophyes emarginatae Keifer	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Eriophyes parabuxi Keifer	USA	*Camellia* spp.	Accidental	Touhey and White, USDA (personal communication)
Eriophyes phyllocoptes (Nalepa)	USA	No data	Accidental	Touhey and White, USDA (personal communication)
Eriophyes pyri (Pagenstecher)	China	*Pyrus* sp.	Accidental	Hong et al. (2006)
Eriophyes wisteriae Keifer	USA	*Cocos nucifera*	Accidental	Touhey and White, USDA (personal communication)
Paraphytoptus chrysanthemumi Keifer	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)
Phyllocoptes azaleae Nalepa	Bulgaria, Czech Republic, Italy	*Rhododendron* spp.	Accidental	DAISIE (2009), de Lillo (2004), Šefrová and Laštůvka (2005)
Phyllocoptes bougainvilleae Keifer	Florida, USA	*Bougainvillea* spp.	Accidental	Welbourn (1995)
Phyllocoptes fructiphilus Keifer	USA	*Rosa multiflora*	Accidental	Amrine (1996)
Phyllocoptruta oleivora (Ashmead)	China, Ciprus, Italy	*Citrus* spp.	Accidental	de Lillo (2004), Hong et al. (2006)
Phyllocoptruta sakimurae Keifer	USA	*Aralia* sp.	Accidental	Touhey and White, USDA (personal communication)
Phytoptus hedericola Keifer	Serbia and Montenegro	No data	Accidental	Glavendekić et al. (2005)

233

Table 1 continued

Species	Invaded area	Host plant	Introduction	Source
Spinacus pagonis Keifer	Florida (USA), Japan	*Mangifera indica*	Accidental	Mito and Uesugi (2004), Welbourn (2005, 2008b)
Stenacis triradiatus (Nalepa)	USA	*Rubus* sp.	Accidental	Touhey and White, USDA (personal communication)
Tegolophus califraxini (Keifer)	Hungary, Italy	*Fraxinus* spp.	Accidental	DAISIE (2009)
Tegolophus zizyphagus (Keifer)	China	*Ziziphus zizyphus*	Accidental	Hong et al. (2006)
Tegonotus mangiferae (Keifer)	China, Florida (USA)	*Mangifera indica*	Accidental	Hong et al. (2006), Welbourn (2005, 2008b)
Tetra lobulifera (Keifer)	China	*Populus* sp.	Accidental	Hong et al. (2006)
Trisetacus juniperinus (Nalepa)	China	Cypress, Chinese juniper, Taiwan juniper	Accidental	Hong et al. (2006)
Trisetacus laricis (Tubeuf)	Central Europe, Great Britain	*Larix decidua*	Accidental	DAISIE (2009)
Trisetacus thujivagrans Smith	Japan	No data	Accidental	Mito and Uesugi (2004)
Vasates acertscrumena (Riley)	Canada	*Acer* spp.	Accidental	Forest invasive alien species Canada
Vasates allotrichus (Nalepa)	Czech Republic	*Robinia pseudoacacia*	Accidental	Šefrová and Laštůvka (2005)
Vasates quadripedes Shimer	Canada, Serbia and Montenegro	*Acer* spp.	Accidental	Glavendekic et al. (2005)

latitudes. Stems with high populations of the mite may affect fruit quality (Perring 1996). Mite feeding produces russetting which turn brown and paperlike but do not wilt down. This mite lives on leaves of many solanaceous plants, but particularly tomato and it usually kills its host (Jeppson et al. 1975). De Oliveria et al. (1982) reported crop reductions of 66.5–1.8% when plants were infested early or late in the season, respectively.

Aceria tristriatus (Nalepa) and *A. erineus* (Nalepa) are widespread in Europe and are the most common and injurious eriophyoids found on cultivated walnuts. The walnut blister mite, *A. tristriatus,* causes the formation of small pustules along midribs and lateral veins. *Aceria erineus* causes the formation of erineum patches covered with yellowish hairs on the underside of leaves among which the mites can be found. Convex swellings occur on the upper surface of the leaf above of these areas. Damage produced by these species causes a reduction in the leaf surface but does not normally affect yield (Castagnoli and Oldfield 1996).

Some invasive eriophyoid mites considered to be pests of ornamentals in Europe are crop pests in other regions of the world. An example of this is the pink tea rust mite, *Acaphylla theae* (Watt & Mann), and the purple tea mite, *Calacarus carinatus* (Green), which are among the most important tea pests in Southern Asia. Both species have been recorded in Italy, Spain and Portugal, and *C. carinatus* has also been reported in Poland and Hungary. In northwest Spain (Galicia) and northern Portugal the mites were found on the leaves of *Camellia* trees in parks and public and private gardens where they were associated with *Cosetacus camelliae* (Keifer), an eriophyid mite commonly found on this host (Mansilla et al. 2003).

Other eriophyoid invasive mites reported in Europe as pests of ornamental crops are *Aculops fuchsia* Keifer, causing galls in fuchsia, and *Phyllocoptes azaleae* Nalepa, causing leaf rolling in *Azalea indica* L. The former is an important pest of fuchsias causing deformation of leaves and flowers. Galls become swollen and blistered and often reddened (Keifer et al. 1982, Koehler et al. 1985). The species was described from southern Brazil and is probably native to South America. It was later recorded in California in 1981, France in 2003 (Streito et al. 2004) and England in 2007. This species was included in the EPPO (European and Mediterranean Plant Protection Organization) Alert Lists because it may threaten fuchsias in the EPPO region.

Šefrová and Laštůvka (2005) published a catalogue of alien animal species in the Czech Republic with data on their origin, pathway of introduction, invasive status and feeding requirements. A total of 595 species were listed, including eight eriophyid mites. Among them *Aculus hippocastani* (Fockeui), a common species which causes erineas under the leaves of the Horse-chestnut, *Aesculus hippocastanum* L., widely cultivated as ornamental tree throughout many temperate countries. The erineas, placed on the angle of the veins of the leaflet, present trichomes that are white at first and turn brown later. *Vasates allotrichus* (Nalepa) produces leaf rolling on the Black locust, *Robinia pseudoacacia* L., a tree native to the United States and widely planted and naturalized elsewhere in temperate North America, Europe and Asia, where it has been considered an invasive species in some areas.

Glavendekić et al. (2005) reviewed the alien insects and mites in Serbia and Montenegro between 1979 and 2004 and twelve Eriophyidae and one Phytoptidae species were included, without host plant information. Some of them, like the privet mite *Aceria ligustri* (Keifer), are potential pests that can cause considerable damage in urban areas. The privet mite lives as vagrant on leaves and buds of *Ligustrum* (Oleaceae) hedges where it can cause curling, bronzing and rusting of infested leaves.

Adventive eriophyoid mites in the United States of America

Several ornamental plants in the United States of America (USA) have been recently invaded by rust mites. One example, the bougainvillea rust mite, *Phyllocoptes bougain-villeae* Keifer (Fig. 1) was discovered in Florida (Welbourn 1995) and in California by Ochoa in 1997. Originally described from Brazil, this rust mite was discovered in Kenya and redescribed as *Vittacus bougainvilleae* by Abou-Awad (1991). This mite causes extensive edgerolling and rusting of the flowers and leaves, with the damage most severe in the white and pink bougainvillea varieties.

The coconut mite, *A. guerreronis*, is a well known pest of coconut, and was discovered in Florida in 1984 (Howard et al. 1990). In 2004 it was reported feeding on the meriste-matic tissue of queen palm (*S. romanzoffiana)* seedlings in California nurseries (Ansaloni and Perring 2004) and causing necrosis, leaf distortion and plant death. *Aceria guerreronis* was also found on queen palm seedlings in some Florida nurseries by Welbourn in 2006 and 2008. This new host represents a serious threat for the ornamental palm business in Florida and California. Another adventive mite associated with monocotyledon plants is *Aculodes duvius* (Nalepa) which feeds on timothy grass, *Phleum pretense* L., and is actively moving from the western USA to the eastern USA (Lamp et al. 2007).

Due to their small size eriophyoids are easily moved around on plant material. For example, mangos are a commercial and dooryard crop in southern Florida and recent surveys of mangos have recently revealed four eriophyids [*Diptilomiopus pamithus* (Boczek & Chandrapatya), *Tegonotus mangiferae* (Keifer), *Spinacus pagonis* Keifer and *Aceria kenyae* (Keifer; = *Cisaberoptus kenyae*)] not previously known from Florida and the USA (Welbourn 2005, 2008b, unpublished data). It is unknown how long these species have been in the USA, but they appear not be significant pests. A similar situation occurred on coconut palms in Florida where *Acathrix trymatus* Keifer (Phytoptidae) and three other genera (*Scolocenus*, *Notostrix* and *Tumescoptes*) were discovered for the first time in the USA (Welbourn 1996, 2007a, b).

Phyllocoptes fructiphilus Keifer is a native USA species that has jumped to multiflora rose, *Rosa multiflora* Thunb., an exotic Asian shrub that had become a serious invasive (Amrine 1996). In addition to feeding on multiflora rose, *P. fructiphilus* transmits Rose rosette disease (RRD; also called witches' broom of rose) to this invasive host, which has been an effective control (Amrine 1996). Efforts to manipulate *P. fructiphilus* for

Fig. 1 The bougainvillea rust mite, *Phyllocoptes bougainvilleae* Keifer, discovered in Florida (1995) and California (1997), USA

weed control are now underway (Epstein and Hill 1999). This system represents a case in which an endemic herbivore has transmitted an apparently native disease to an introduced weed. Under certain circumstances the mite can be a pest of ornamental roses, requiring chemical control (Amrine 1996). *Aceria anthocoptes* (Nalepa) is dispersing within the USA on Canadian thistle (*Cirsium arvense* (L.)) since it was first found in Maryland, in its bordering states, and in two northcentral states (Minnesota and North Dakota; Ochoa et al. 2001; Michels Jr et al. 2009). This mite can be considered an adventive species, in the recent colonized areas where dissemination has been favored by human activity.

The litchi erineum mite, *Aceria litchii* (Keifer), was introduced into Hawaii from Asia on *Litchi chinensis* Sonn. many years ago. Since then there have been two introductions of this mite into Florida from Hawaii on dormant trees. One discovered in 1955 which was declared eradicated in 1960 (Dekle 1957, 1960) and a second infestation in 1993 (Mead 1993). The successful eradication of an exotic eriophyoid is rare, but the use of quarantines and chemical control helped eradicate this mite from Florida. Dekle (1960) noted that the litchi trees were severely damaged by cold in late 1957 and that may have contributed to the eradication of the mite. No litchi erineum mites have been found in Florida since 1993. The litchi erineum mite before considered as a quarantine pest to Brazil (MAPA 2007) was recently reported in the country. Since July 2007 severe damage to newly developed leaves and fruits was observed in litchi orchards in the State of São Paulo and in April 2008 several *A. litchi* specimens were first collected and identified from Brazil (Raga et al. 2008). Control of this mite is expensive and difficult including pesticide application and pruning of trees that can reach 15–20 m tall. Introduction of the litchi erineum mite in Brazil could discourage litchi production that was in expansion.

Aceria zelkoviana Kim was introduced into Florida in 2000 on *Zelkovia serrata* (Thumb.) Mak. bonsai from China (Welbourn 2000), but it appears that this mite has not survived as no new records has been reported. The pink citrus rust mite, *A. pelekassi* was first reported from Florida in 1961 (Denmark 1962) and after the initial discovery an unsuccessful eradication program initiated. Welbourn (2008c) recently discovered *Diptilomiopus assamica* Keifer on citrus in Florida in association with the citrus rust mite, *P. oleivora* (Fig. 2). As with many of the exotic eriophyoids recently discovered in the USA, we have no data on the origin or when they were introduced into the USA. Many of these mites appear not to be pests, but leaf vagrants that entered into the USA on host plants that were poorly inspected or not treated for mites prior to entry into the USA.

The hibiscus erineum mite, *Aceria hibisci* (Nalepa), was described from *Hibiscus rosa-sinensis* L. (Malvaceae) in the Fiji islands and is a good example of an adventive mite in the USA, Australia and the Caribbean region. Feeding by this mite causes deformed young leaves and developing vegetative buds (Welbourn et al. 2008). Hara et al. (1996, 2001) reported *A. hibisci* in Hawaii, USA in 1989. In 1992 the mite was reported from Australia (Carson and Gough 2007). Quilici et al. (1997) reported *A. hibisci* from *Hibiscus* sp. in the Reunion Island. *Aceria hibisci* was first reported in the Caribbean region on the islands of Martinique in 1997 and Guadeloupe in 1998 and 2000 from *Hibiscus rosa-sinensis* and *Hibiscus* sp. (Flechtmann et al. 2000) and Flechtmann and Etienne 2001). De la Torre and Martinez (2004) reported the mite from Cuba on *Talipaariti elatus* (Sw.) Fryxell. (Malvaceae). Specimens from Dominica and Jamaica submitted to the Division of Plant Industry, FDACS, in 2007 and early 2008 were confirmed as *A. hibisci* (Welbourn 2008a).

Fig. 2 The citrus rust mite,
Phyllocoptruta oleivora
(Ashmead), from citrus in
Florida, USA
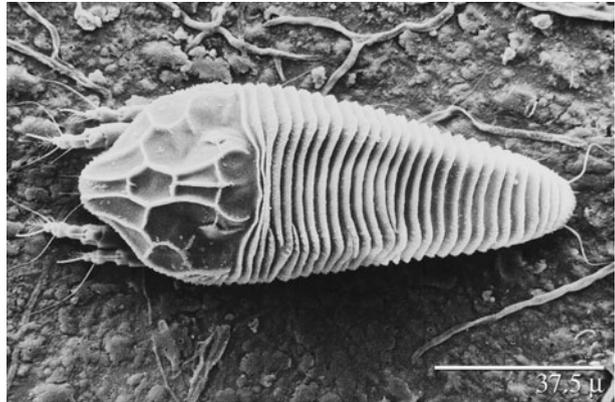
Eriophyoid invasions in mainland China

Hong et al. (2006) listed 25 adventive eriophyoid species in mainland China, 17 on fruit trees, three on forest and tea plants and three from vegetables and other crops (see Table 1). Some have caused considerable agricultural damage, while others are either potentially important economically or produce no damage. A classic and historical example of an invasive alien eriophyoid mite in China is the big bud mite, *Cecidophyopsis ribis* (Westwood) on blackcurrant, *Ribes nigrum* L. This mite is widely distributed in Europe; it was introduced into northeastern Heilongjiang Province, likely from neighboring Russia in the 1930–1940s, but was not reported until the 1980s (Bai 1987; Hong 1998). Other recent invasions into China include the rice rust mite, *Cheiracus sulcatus* Keifer, the tomato russet mite, *A. lycopersici*, and the apple rust mite, *A. schlechtendali* (Nalepa; Hong et al. 2006).

The rice rust mite was first described from rice in northern Thailand and southern India, apparently causing little or no damage (Keifer 1977, Mohanasundaram 1981). However, it caused serious damage to rice in northern Guangdong Provinces (Hong et al. 2005) and has spread to neighboring regions (Hong et al. 2006). Symptoms produced by the feeding of *C. sulcatus* is characterized by long rust stripes on the underside of rice leaves, visible under microscope, and withered and yellowed leaf tips visible to the naked eye. Hong et al. (2006) suggested this mite may have occurred around Shaoguan city for more than 2 years where it damaged many varieties of rice before spreading to other parts of the Province (Hong et al. 2006).

The tomato russet mite was first reported in China in 1983 on tomato, potato and tobacco (Kuang 1983), but no damage was documented until 1999. The first reports of damage were reported in greenhouses in Yunnan and Shangai Provinces (Chen et al. 2000, Kuang et al. 2000). Serious damage was also observed in tomatos in Shanghai greenhouses and shed houses in northeast China (Hebei Province; Jin and Liu 2001).

The apple rust mite was first reported in mainland China in 1995 (Kuang 1995) causing browning or rusting of the undersides of leaves. In heavily infested apple orchards in Sichuan Province, where 80–90% of apple trees were attacked resulting in little growth (Li and Cai 1996). Hong et al. (2006) reported that this mite is not yet widely distributed in China's major apple growing areas.

The adventive wheat curl mite, *Aceria tosichella*, and associated viruses—a new threat to cereal crops in South America

Keifer described the wheat curl mite, *A. tosichella*, from wheat in Yugoslavia in 1969. This eriophyid has been reported from the main wheat production areas in North America, Europe, Asia, the Middle East, Africa and Oceania (Amrine and de Lillo 2006). Although *A. tosichella* occurs mainly in wheat, it can also develop in corn, sorghum, barley, oat, rye, pearl millet and in a large number of grasses of minor economic importance as well as various weeds (Jeppson et al. 1975; Amrine and de Lillo 2006). Yield losses to wheat crops due to *A. tosichella* infestations can reach 30% (Harvey et al. 2002). However, the main damage is the transmission of *Wheat streak mosaic virus* (WSMV) and *High plain virus* (HPV; Oldfield and Proeseler 1996; Malik et al. 2003). WSMV is the etiological agent of one of the most important virus diseases of wheat causing major yield losses in North America, Europe, the Middle East, Oceania and Asia (Oldfield and Proeseler 1996; French and Stenger 2003; Sanchez-Sanchez et al. 2001). The HPV was first observed in 1993 in the High Plains subregion of the Great Plains in the central USA (Jensen et al. 1996). Mixed infections of WSMV and HPV have been observed in the USA making it difficult to estimate the losses associated with each virus. However, losses due to HPV infection in corn in some regions of the USA were estimated to be around 75% (AQIS 2000). Other diseases associated with *A. tosichella* are *Wheat spot mosaic virus* (Jeppson et al. 1975) and Kernel Red Streak Agent (CABI 2002). Recently, two new *A. tosichella* transmitted viruses were reported: *Brome streak mosaic virus* in Europe (Stephan et al. 2008) and *Triticum mosaic virus* in the USA (de Wolf and Seifers 2008); no information is available on losses due to these virus infections.

In South America, the report of *A. tosichella* and its associated viruses is recent. WSMV was discovered in the Province of Buenos Aires, Argentina, in 2002 (Truol et al. 2004). Two years later its vector, *A. tosichella*, was also found in Argentina in association with WSMV infected plants (Navia et al. 2006). These reports drew attention to the possible distribution of the pathosystem *A. tosichella*/WSMV and HPV in the cereal production areas of Argentina's neighbors. A Pest Risk Analysis (PRA) for *A. tosichella* and WSMV/HPV was conducted considering as risk areas the non-affected regions of Argentina and all territories of Brazil, Uruguay and Paraguay. The risk of introduction, establishment and economic importance of the pests in the risk areas was considered as high (Navia et al. 2007a, b).

Considering the high risk of *A. tosichella* and WSMV/HPV to Argentina, Brazil, Paraguay, and Uruguay, a joint project involving a multidisciplinary group of researchers from these countries was initiated in 2006. The main purpose of this project was to follow the status and dissemination of the pathosystem in the region, providing information on the distribution and hosts of *A. tosichella* and associated virus in the main wheat production areas of the forementioned countries.

In Brazil, the presence of *A. tosichella* was confirmed during 2006 surveys in the State of Rio Grande do Sul (Pereira et al. 2009), one of the main wheat production areas of the country on the border with Argentina. The mite was detected in both greenhouses and in the field. However symptoms due to *A. tosichella* infestations were observed only in greenhouse conditions. The wheat curl mite was exclusively found on wheat. The presence of WSMV has not yet been detected in Brazil (Pereira et al. submitted).

The occurrence of *A. tosichella* was also confirmed in Uruguay during surveys that covered most of the traditional agricultural and wheat production areas in November 2007 (Castiglioni and Navia 2009). During these surveys, *A. tosichella* was also found on

ryegrass (*Lolium multiflorum*) and brome (*Bromus unioloides*), being the first report of the mite on other hosts grasses different from wheat in South America.

In Paraguay, a survey was conducted in 2007 which did not detect the presence of *A. tosichella* and associated virus (Espinoza 2008). Subsequent surveys are needed to continue monitoring the presence of *A. tosichella* and associated virus.

In Argentina, WSMV has spread to the main wheat production areas in at least seven Provinces—Santiago del Estero, Salta, Tucumán, La Pampa, Santa Fé, Córdoba and Buenos Aires (Truol et al. 2008). Severe WSMV epiphytes have been observed in wheat in the 2007 and 2008 growing seasons, especially in Balcarce, Buenos Aires Province (Truol and Sagadin 2008a; Truol et al. 2008). The presence of HPV was confirmed also in Argentina in 2007, in the Province of Buenos Aires in mixed infections with WSMV (Truol and Sagadin 2008b). At present, the pathosystem *A. tosichella* and WSMV/HPV is a threat to wheat production in Argentina because all wheat cultivars commonly used in Argentina, of short and intermediate cycles, are susceptible to the pathosystem (Bainotti and Vanzetti 2008).

Although WSMV and HPV have not yet been detected in Brazil, Uruguay and Paraguay, they are likely to soon extend their range into these countries given their proximity to the affected areas and intense movement of vehicles and cereal trade among these countries. The dissemination of *A. tosichella* and associated virus in the main production areas of wheat and winter cereal crops in countries of southern South America seems to be unavoidable. The knowledge of the monitoring and management practices for the *A. tosichella*/WSMV/HPV pathosystem gained by Argentinean technicians and researchers will surely help professionals in neighboring countries. Joint efforts should now be concentrated in search of resistant germplasm as well as continuing to follow the dissemination and status of the pathosystem in areas that are threatened by the mite and virus.

The coconut mite, *Aceria guerreronis*—invasion history, impact and the challenge for classical biological control

The recent spread of the coconut mite to most coconut production areas of the world has made this mite one of the most important coconut pests. Although described by Keifer (1965) there is evidence this mite was present in other areas in the Americas well before 1965 (Ortega et al. 1967; Robbs and Peracchi 1965; Zuluaga and Sánchez 1971). Symptoms characteristic of the mite have been observed in Colombia since 1948 (Zuluaga and Sánchez 1971), in Brazil since 1953 (Arruda personal communication) and in Mexico since 1960 (Ortega et al. 1967). By 1966 the mite was reported from the African Gulf of Guinea Islands and Benin in 1967 (Cabral and Carmona 1969; Mariau 1969). In the 1980s the mite was reported in Tanzania (Seguni 2002). Recent records place the coconut mite in Florida, USA in 1984 (Howard et al. 1990), California, USA in 1997 (Ansaloni and Perring 2004), South Asia (India and Sri Lanka) where the species was unknown until the end of the 1990s (Fernando et al. 2002; Sathiamma et al. 1998), and the Middle East (Oman; de Moraes personal communication).

The coconut mite is considered to be a serious pest of coconut palms throughout its geographical distribution (Moore and Howard 1996), causing significant crop losses. Populations develop in circular whitish areas covered by the perianth in the meristematic zone from which the growing coconut fruit expands. As the damaged surface expands from beneath the perianth and becomes exposed to air, it becomes suberized (i e., develops a brown cork-like surface with deep fissures). If intense mite feeding is concentrated on one side of the fruit meristem, growth of the fruit may be uneven, resulting in a distorted

coconut. Severe damage results in stunted fruit (Mariau 1986, Howard and Moore 2008). High infestations have been reported ranging from 80 to 100% of coconut trees in some regions of Mexico (Ortega et al. 1967), 42–65% in Cuba (Suarez 1991), 90% in Costa Rica, 5–100% in Sri Lanka (Fernando et al. 2000), and 20–70% in India (Nair and Koshy 2000; Muthiah and Bhaskaran 2000). Reductions of near 30% in copra yield have been reported in American and African countries (Hernandez Roque 1977; Julia and Mariau 1979; Moore 1986) and around 40% in India (Nair and Koshy 2000; Muthiah and Bhaskaran 2000). Coconut fruit losses of approximately 70% have been reported in Venezuela due to premature dropping (Doreste 1968) and from 10 to 100% with an average of 21% in Tanzania and coastal islands (Mafia, Zanzibar and Pemba; Seguni 2002).

Coconuts are produced on about 26 million acres in 92 countries worldwide (FAO 2002), and considered to be the most important palm tree from the humid tropical regions and undoubtedly the most economically important plant in the family Arecaceae. In addition to its economic importance, it represents a relevant social crop due to the use of its products as a source of food, fiber, fuel, water, and shelter to communities (UGA 2009). The coconut mite represents a threat to coconut production worldwide. Although the coconut mite is widely distributed in most of the coconut production areas in Asia, Africa and the Americas, this mite has not yet reported from the main coconut production areas in the Philippines and Indonesia represent together more than 50% of world coconut production (FAO 2002).

Chemical measures used to control the coconut mite are expensive and difficult to apply because of colonies develop on the palms (Hernandez Roque 1977; Ramaraju et al. 2002). Acaricides must be applied frequently to control this mite. However, in most production areas, coconut is traditionally grown by small farmers who cannot afford the continuous application of insecticides/acaricides (Moore and Howard 1996; Muthiah and Bhaskaran 2000; Ramaraju et al. 2002). As an alternative, classical biological control has been considered as a promising strategy to mitigate populations of A. guerreronis (Moraes and Zacarias 2002).

Critical to the success of finding effective agents for biological control is the determination of the historical range of the mite. The true origin of the coconut mite remains uncertain since it was first reported almost simultaneously from both the Americas and Africa. To investigate the geographical origin, ancestral host associations, and colonization history of the mite, DNA sequence data from two mitochondrial and one nuclear region were obtained from samples from the Americas, Africa and the Indo-Oceanic region. Mitochondrial DNA 16S ribosomal sequences were most diverse in Brazil, which contained six of a total of seven haplotypes. A single haplotype was shared by the non-American mites. Patterns of the nuclear ribosomal ITS variation were similar to those of the mitochondrial DNA, also with the highest nucleotide diversity found in Brazil. These results suggest an American origin of the mite and suggests the original host of the mite was a non-coconut palm. In contrast to the diversity in the Americas, all samples from Africa and Asia were identical or very similar, consistent with the hypothesis that the mite invaded these regions recently (Navia et al. 2005). These results have encouraged the prospect for finding biological control agents of A. guerreronis in the Americas (Lawson-Balagbo et al. 2007a, b, 2008).

At present, international efforts supported by WOTRO, Netherlands Organization for Scientific Research are directed to the development of a classical biological control program for the invasive coconut mite in Africa and Asia: integrating biological, molecular and socioeconomic studies in the search and introduction of effective natural enemies. The primary objective of this project is to determine prospective natural enemies in the

Americas and introduce them into Africa and Sri Lanka for the biological control of the coconut mite. In addition, the project will conduct studies to determine aspects of the biology and ecology of the coconut mite and the natural enemies selected for introduction, and determine the socioeconomic impact resulting from the intervention. The search for natural enemies will be focused in Brazil, Colombia, Mexico and Venezuela; the target countries for their introduction will be Benin, Tanzania and Sri Lanka. Researchers working on this project include those working at the ESALQ/University of São Paulo-Brazil, the University of Amsterdam in The Netherlands, the IITA in Benin, the Coconut Research Institute in Sri Lanka, and collaborators from Colombia, Mexico and Venezuela.

Eriophyoid mites introduced as biological control agents of weeds: Could they become adventive species?

In a technical sense, every eriophyoid that has been successfully introduced for biological control has become adventive, because it has established and spread in a new geographic region (Smith personal communication). Because most eriophyoid mite species are highly host specific, they have been considered ideal biological control agents for weeds (Rosenthal 1996). However, at present, few exotic species have been released in new regions due to increasing safety levels required for biocontrol agents and the relative lack of knowledge and practical experience using eriophyoids to control weeds (Smith et al. 2008). The potential risks associated with the release of exotic natural enemies have received attention (Howarth 1983, 1991) and an increasing number of countries are now applying risk assessment procedures before a new natural enemy can be imported and released. In the case of weed biological control programs, the effect of the natural enemy is not only determined on the target plant species, but also on native non-target species.

Negative environmental effects due to the release of eriophyoids have rarely been reported. The only case reported of an introduced species developing on non-target plants is *Aculus hyperici* (Liro). This mite is native to Europe and was introduced into Australia in 1991 to control Saint John's wort *Hypericum perforatum* L. Pre-release host specific trials indicated a low risk of impact on the native species *Hypericum gramineum* Forst. Although *A. hyperici* can colonize and develop on the native *H. gramineum*, apparently it has no significant impact on their growth or reproduction, either in the field or under glasshouse conditions (Willis et al. 2003).

Another possibility to be considered is that an eriophyoid introduced as a biological control agent becomes abundant and does not reduce the weed population. In this case it is possible that the mite could cause indirect nontarget effects by becoming an important part of a food web (Pearson and Callaway 2005).

Pathways for eriophyoid mites

There are many pathways for a species to be transported and released into new environments. Following Lockwood et al. (2007), a transport vector is the manner in which the species is carried along a pathway, and a pathway the route between the original region of a species and its release location. Pathways are also defined as any means, natural or "manmade", that allows the entry or spread of a pest (FAO 2006; Kahan 1989). Understanding the vectors and pathways is critical to comprehending the subsequent stages of an invasion process (Lockwood et al. 2007). Natural pathways appear to be a minor component of the

global spread of non-indigenous species in contrast with human-mediated dispersal (NRC 2002).

The most important natural pathways for eriophyoid mites, for short and medium distances include wind, pollinators and water (Lindquist et al. 1996). Although mites actively initiate dispersal, it is a passive process resulting in their random deposition throughout the environment (Bergh 2001).

For long distances, most eriophyoid mites disseminate through human activity. Due to their biological and morphological traits the main pathways for eriophyoid mites are plants including any propagation material, fresh fruits, cut flowers, or bulbs.

There are examples of eriophyoid species that develop inside seeds and undoubtedly could disseminate through their movement. *Trisetacus kirghsorum* Shectchenko colonies develop inside *Juniperus* seed for 2 years, which corresponds with the duration of the ripening period of the seed (Oganezova and Pogosova 1994).

Is unclear whether the seeds of the host plants from which eriophyoid species do not develop inside of could be a pathway. For example, *A. tosichella*, a pest associated with cereal and grasses has been disseminated around the world. Cereal exchange and trade is exclusively done through seeds and processed material. Considering the large number of species of grass that are reported as hosts for the species, one hypothesis on the dissemination of *A. tosichella* is that it is transported on contaminant grasses accompanying potted ornamental plants infested with mites (Navia et al. 2006). Another hypothesis is that *A. tosichella* is disseminated through seeds. It is possible that in high mite populations in the field, or when mites are preparing for aerial dispersal at harvest time, some life stages could survive and accompany seeds during the transport period and colonize new areas where these seeds are planted. The interception of *A. tosichella* and *Aceria zeala* Keifer on wheat and corn germplasm seeds at the Laboratory of Plant Quarantine, Embrapa, Brazil (Navia and Flechtmann 2008) support the possibility of dissemination of these eriophyids on or in seeds. Additional evidence supporting the transport of an eriophyid mite on seeds was the detection of *Aceria zeala* L. (Fig. 3) on corn in a California greenhouse in July 2001. This was the first report of this potentially important pest of corn in North America. Potential hosts (corn and sorghum) surrounding the greenhouse were inspected but no mites were found (Ochoa and Amrine Jr 2007). This suggests the infestation started inside the greenhouse from mites on the seeds. Evidence exists that other phytophagous mites may disseminate through their host seeds, such as the case of the tarsonemid rice mite *Steneotarsonemus spinki* Smiley (Kane 2007).

It would be interesting to determine how long eriophyoid mites associated with seeds and grains are able to survive without feeding on fresh material under different environmental conditions, and if they can colonize new fields when seeds are germinating and growing. This information is important to the development of preventive measures to avoid the introduction of eriophyoid mites into new areas.

Biosecurity and preventive measures to reduce the risk of eriophyoid mites

Biosecurity encompasses all policy and regulatory frameworks to manage risks associated with food and agriculture, including relevant environmental risks (FAO 2001a). Biosecurity actions include protection and mitigation of factors related to bioinvasions.

Pest risk management is an analytical process for identifying risk mitigation options and for evaluating their efficiency, feasibility, and impacts (FAO 2001b). The options to mitigate risks in plant biosecurity include market restrictions, post-entry quarantine,

Fig. 3 *Aceria zeala* Keifer, intercepted in California, USA greenhouse in July 2001
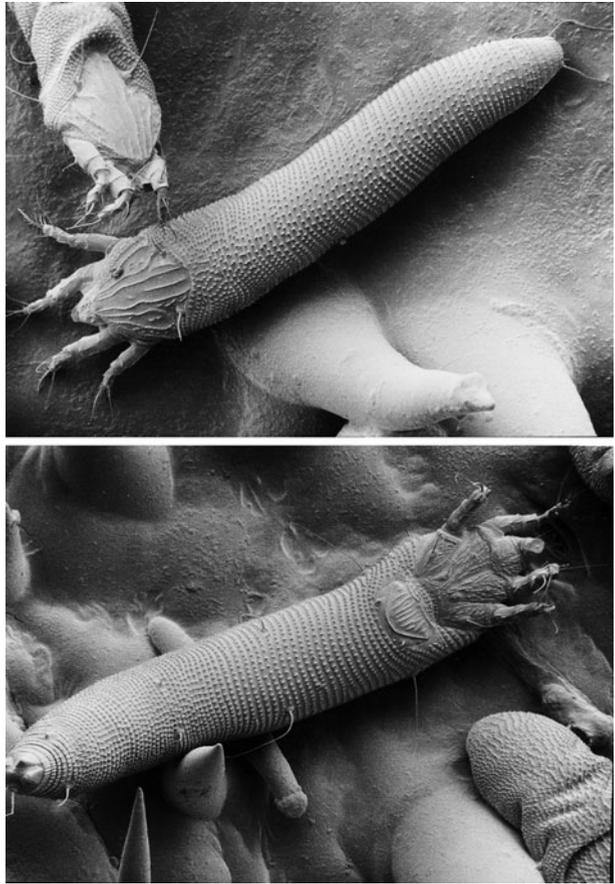
inspection at departure and entry points, quarantine treatments, transport conditions and pre- and postharvest procedures originating from pest-free or low incidence areas. Phytosanitary procedures should be selected according to the risk level represented by the importation of different commodities from different origins.

When eriophyoid mites represent a risk to agricultural and/or natural systems, it is important to concentrate efforts on measures that mitigate the risk of their entry and/or dissemination considering the difficulties and cost of eradication of phytophagous mites. Risk mitigation options for agricultural commodities, when eriophyoid mites are target pests are post-entry quarantine, quarantine treatments and origin from non-infested areas. Limitations of some mitigation measures are discussed below.

Inspection at departure and entry points and post-entry quarantine

The inspection of large cargoes for acarine species at entry or departure points is inefficient and is commonly used as a complementary procedure to other quarantine measures (Navia et al. 2007a). The reduced dimensions and sometimes the hidden location in the plant material decrease the likelihood that mites will be detected at their point of departure or upon their arrival at the point of entry. In the case of eriophyoid mites, both traits—reduced

dimension and hidden location—can be extreme. The smallest phytophagous mites belong to this group and colonies can develop inside cracks, crevices, below bracts, sheath or even inside plant organs (for example buds, bulbs), which accentuates difficulties to their detection.

Inspections specifically aimed at the detection of eriophyoid mites usually focus upon symptoms resulting from their infestation such as plant abnormalities, discolorations, galls and blisters or necrotic spots. In that case, suspect plants are taken to the laboratory to identify the causal agent. This task is especially relevant in the case of eriophyoid mites that do not produce observable symptoms on the host plant or in the cases that the host plants present symptoms only if high infestations occur.

In countries that employ well-trained quarantine inspectors that detect mites, prepare material and take photos of relevant taxonomic characters for identification, the digital or remote identification system can be used as an important tool in plant biosecurity. A distance diagnostic system using digital imaging named Remote Pest Identification Program was implemented by Plant Protection and Quarantine, USDA, USA, in 1996 as a pilot project. The program provides advanced digital imaging technology and microscopy equipment to Plant Protection and Quarantine (PPQ) Identifiers and National Specialists at locations throughout the continental USA, Alaska, Hawaii, Puerto Rico and Guam. These tools facilitate the pest identification process by enhancing communication between port personnel and taxonomic experts allowing for faster processing of imported cargo at US ports of entry.

Imported plant material used for vegetative propagation is considered of high risk for many pests, including phytophagous mites. Post-entry quarantine, that is the official confinement of regulated articles after entry for observation and further inspection (FAO 2006), is the appropriate measure to avoid inadvertent pest introduction through importation of plant material for propagation. The time required to maintain the material under observation depends upon the bioecological characteristics of the target quarantine pest. For eriophyoid mites, which can develop inside plant organs, a lengthy period in post-entry quarantine may be required. Fruit species from arid regions usually are not imported as seeds, but through propagation material (budwoods, cuttings, rooted plants). To these arid fruit trees material Verma and Kapur (1990) have recommended glasshouse confinement for 1–3 seasons to detect latent infestations of eriophyoid mites. Also Dieckmann et al. (1994) have recommended at least 10 months of confinement for *Ribes* fruits. Another possible way to analyze samples is the use of destructive methods during inspection, such as the complete dissection of plant material, to assure the material is not infested with these mites.

Eriophyoid mite interceptions

International trade has long been recognized as a major pathway by which adventive species arrive to and colonize new geographical ranges. Recent reviews have noted the importance of intercepting these species at the border, before they have the opportunity to become established in new countries (NRC 2002). Information on intercepted pests associated with specific commodities is relevant when conducting a pest risk assessment (PRA). Interception of a new pest on an imported commodity is a prerequisite to initiating a PRA. Also, information on the frequency of interception of a specific pest is required during entry risk evaluation (FAO 2006).

Comparing information available in the scientific literature regarding interceptions of eriophyoid mites versus that of adventive insects or other groups of phytophagous mites,

the former is strikingly scarce and difficult to find. Examples of eriophyoids intercepted at the borders include the gardenia bud mite, *Colomerus gardeniella* (Keifer), which lives in the petiole bases on *Gardenia jasminoides* Ellis. The mite is native to Mexico and was first intercepted in 1964 in California (Dekle and Denmark 1970) and later found in other states including Hawaii. *Phyllocoptes acuminatus* Manson was intercepted in New Zealand several times on *Codiaeum* sp. [Euphorbiaceae] from Samoa and Fiji islands, but is not believed to be established there (Manson 1972).

The dry bulb mite *A. tulipae* is able to develop on several plant species in the families Alliaceae and Liliaceae. In the genus *Allium*, its hosts include species such as shallot, onion and garlic and is also known to occur on tulips (*Tulipa*). It is considered one of the most important eriophyoid pests not only because the direct damage on plant but also for its capacity to vector several important viruses such as the *Onion mite-borne latent virus* and the *Shallot mite-borne latent virus* (Perring 1996, Oldfield and Proeseler 1996). This mite is widespread in Europe although it does not occur in the United Kingdom where it was recently detected on infested onion (*Allium cepa*) bulbs used for planting, originating from The Netherlands (Ostoja-Starzewski and Matthews 2006). Due to their economic importance, a pest risk analysis (PRA) was performed in the UK in 2007 to assess the invasive potential of this pest and the economic consequences of establishment. Even though the PRA considered that the mite is capable of establishing both outdoors and in storage facilities, significant damage is not expected in the UK and no phytosanitary measures were recommended (MacLeod 2007). *Aceria tulipae* has also been intercepted in Japan on infested shallots originating from France and the USA (Masaki 1991).

Inspections of seeds, bulbs, seedlings and tubers of cultivated plants conducted at the Laboratory of Plant Quarantine (Embrapa) in Brasilia, Brazil, from 2004 to 2008, revealed the presence of five exotic eriophyid species: *A. hystrix* and *A. tosichella* were intercepted on wheat seeds, *A. zeala* on corn seeds, *A. fockeui* from cherry stakes, and *Oxycenus maxwelli* (Keifer) from olive seedlings. All interceptions included live forms of the mites, even surprisingly those from wheat and corn seeds (Navia and Flechtmann 2008).

Quarantine treatments and eriophyoid disinfestation

For a quarantine treatment to be acceptable all organisms associated with the plant material must receive lethal doses and the material cannot be damaged. In fact, only a few treatments have achieved the high control levels required to be used as a quarantine treatment (MacDonald and Mills 1994). Sometimes postharvest treatments that reduce pest populations are accepted as phytosanitary measures by plant protection organizations if associated with other mitigation options.

A quarantine treatment that has been used on the commercial level for mite disinfestation of fresh plant products is fumigation with methyl bromide (MB). MB fumigation is an extremely toxic treatment that requires special safety facilities, which in some countries is not available for large volumes of commercial material. MB has been evaluated for mite disinfestation of several species/commodities, especially fresh fruits (Katayama et al. 2001). There is little information specific for the disinfestation of eriophyoid mites through MB fumigation. For eriophyoid and other mites infesting bulbs, there are instructions that MB fumigation should be repeated after 10–14 days to kill the eggs (Mackie et al. 1942).

Development of alternative quarantine treatments is important to prevent disruption of international trade and to allow access to new markets. Mite disinfestation studies include controlled atmosphere and irradiation experiments and thermal treatments.

Controlled Atmosphere Treatments (CAT) consists of modifications of carbon dioxide concentration in closed environments which become lethal to the pests. The feasibility of CATs storage to provide quarantine security has been demonstrated for the apple rust mite, *A. schlechtendali* and the European red mite, *Panonychus ulmi* Koch. Eggs are killed in 5.3 months when apples are stored at 2.8°C in an atmosphere of 1% O_2 and 1% CO_2 without detrimental effects to the apples. A possible disadvantage of this treatment may be the length of storage exposure required for sufficient mortality (Lidster et al. 1981). Authors consider that low O_2 storage probably would not replace pre-storage fumigation but may provide a complementary technique for exported apples held for long periods of time.

Irradiation is a viable quarantine treatment which has been studied for over 40 years, although it is of little commercial use. The commercial use and almost all evaluations have been directed toward fruit flies. The two principal obstacles to its commercial application are the fact that the pests are not immediately killed and the need for the development of approved protocols by government regulatory agencies. The measures of efficiency of irradiation to mite disinfestation treatments should rely on the prevention of adult emergence, when only eggs and larvae are present, or sterility, when immatures or adults are present (this is the case of mites), and not on pest absence or mortality. This can be accomplished with relatively low doses that are tolerated by many fruits. In insects, usually females are more susceptible to radiation-induced sterility than males while for Tetranychoidea mites the opposite has been observed. It has been found that the dose of radiation necessary to control Lepidoptera and most mites is about 300 Gy, which is higher than the dose necessary to control several other pest groups. Irradiation has been evaluated for the control of some Tetranychoidea species (Dohino and Tanabe 1994; Majumder et al. 1996 Lester et al. 1997). For eriophyoid mites little or no useful data is available (Molins 2001). Future research should concentrate on evaluating doses for other important groups of organisms including eriophyoid mites (Hallman 1998).

Thermal treatments for eriophyoid mites have been recommended for containment and could be used as a complementary mitigation option. For *A. tulipae* disinfestations, a hot water treatment of bulbs (55°C for 10–20 min, or 60°C for 10–15 min) can reduce mite populations although it may also reduce bulb germination. A post harvest treatment consisting of drying the bulbs can also reduce populations (MacLeod 2007).

Challenges

There are no doubts that eriophyoid mites represent a group of high potential as AMS. Economic, social and environmental impact due to invasion of some species of eriophyoid mites has been notorious. However, these organisms have received little attention from agriculture or environmental agencies. It would be important to raise public awareness of the risk and importance of these tiny organisms as AMS. Perhaps an important step would be quantifying losses caused by adventive eriophyoids. This is not an easy task for any mite pest. Collaboration of economists with a wide perception of environmental impact would be crucial.

Scientific aspects of eriophyoid invasion processes have not been explored. Understanding ecological and genetic aspects of eriophyoid invasions could help to define mitigation measures and management strategies. Knowledge of host specificity and adaptation to new host plants of eriophyoid species could be useful in risk evaluation and in guiding the adoption of control measures (see Michalska et al. 2009). Phylogeography

studies using molecular data could provide information on the origin and colonization routes of invasive eriophyoids, a necessity for guiding adoption of quarantine measures and prospection of biological control agents (Navajas and Navia 2009). Knowledge of the invasion genetic process and biological response to new environmental parameters would help in understanding and previewing population explosions of adventive eriophyoids.

Accurate species identification is a key challenge in the detection and monitoring of adventive species. Scarce information on intercepted eriophyoid mites, crucial in PRA and other biosecurity actions, is primarily a result of the deficiency of Eriophyoidea taxonomists. In decisive instances, lack of information about the correct identity of the mite, to which is associate information on its biology and ecology have caused serious consequences (Ochoa 2005). A deficiency in taxonomic capability is a general problem for most groups of organisms and has been recognized as an impediment (named "taxonomic impediment") to implementing the convention on biological diversity (CBD) in reference to the action of "prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" (CBD 2002). The global taxonomy initiative (GTI) was set up under the Convention to overcome the 'taxonomic impediment'. Its main objectives are to reduce the knowledge gaps in our taxonomic system, the shortage of trained taxonomists and curators and, thereby, to improve decision-making in conservation. This initiative aims to providing relevant taxonomic information for custom and quarantine services on invasive alien species at national and regional levels. Molecular techniques can be extremely helpful in the diagnosis of species and characterization of subspecific taxonomic levels in Eriophyoidea giving support to biosecurity actions (Navajas and Navia 2009).

Research on eriophyoid disinfestation treatments is needed. Presently the options for mite disinfestation of commercial material are scarce. Development of integrated measures for system approaches to minimize risks related to eriophyoid mites is desirable considering the low efficiency of the inspection of commercial material to prevent mite introduction and the frequent inefficacy of single treatments to achieve the security level required. A system approach integrates pest risk management measures to meet the appropriate level of phytosanitary protection and consist in the use of two or more measures that are independent of each other (FAO 2002).

Adventive eriophyoid mites have not been well documented in China (Hong et al. 2006). This observation can be generalized to other countries. Surely a large number of adventive eriophyoids has not been reported as such or if reported have not been listed for official agencies. It would be important to include adventive eriophyoids in official lists aiming to call attention to the need for adoption of preventive or control measures directed to them. Also the development of databases on adventive eriophyoid mites would be desirable, detailing information on known and potential invasive species, taxonomy, native and introduced ranges, biology, physiology, impacts, pathways for introduction and spread and prevention and control methods.

References

Altieri M, Rojas A (1999) Ecological impacts of Chile's neoliberal policies, with special emphasis on agroecosystems. Environ Dev Sustain 1:55–72

Amrine JW Jr (1996) *Phyllocoptes fructiphilus* and biological control of multiflora rose. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology. natural enemies and control. Elsevier, The Netherlands, pp 741–750

Amrine JW Jr, de Lillo E (2006) Database on Eriophyoidea (Acarina: Prostigmata) of the world. Filemaker 4.0. West Virginia University, USA

Angeli G, Rizzi C, Dorigoni A, Ioriatti C (2007) Population injury levels of the apple rust mite *Aculus schlechtendali* (Nal.) on *Golden Delicious* and *Red Delicious* apple fruits. Bull OILB/SROP 30: 255–260

Ansaloni T, Perring TM (2004) Biology of *Aceria guerreronis* (Acari: Eriophyidae) on queen palm. Int J Acarol 28:121–146

AQIS Australian quarantine & inspection service (2000) Import risk analysis for the importation of bulk maize (*Zea mays* L.) from the United States of America. Department of Agriculture, Fisheries and Forestry, Australia. http://www.daff.gov.au/__data/assets/pdf_file/0012/20901/rev_dft_ira_maize.pdf. Accessed on 10 Oct 2008

FIAS (2009). Forest invasive alien species Canada. Galls of hardwoods. www.exoticpests.gc.ca. Accessed on 7 Apr 2009

Bai RX (1987) Blackcurrant mite. North Hort 2:25–26

Bainotti C, Vanzetti L (2008) Perspectivas para el mejoramiento de trigo en la búsqueda de resistencia a *Wheat streak mosaic virus* (WSMV) en américa del Sur. In: Workshop en virosis de cereales transmitidas por el ácaro *Aceria tosichella—Wheat streak mosaic virus* y *High plain virus*—en los países del Cono Sur: situación, detección y manejo, Balcarce, Argentina. Libro de Resúmenes. INTA-IF-FIVE. pp: 9

Bergh JC (2001) Ecology and aerobiology of dispersing citrus rust mites (Acari: Eriophyidae) in Central Florida. Environ Entomol 30:318–326

Carson C, Gough N (2007) Hibiscus erinos mite. Accessed 9/1/2009 from http://www.dpi.qld.gov.au/cps/rde/xchg/dpi/hs.xsl/26_8327_ENA_HTML.htm

CAB International (2002) Crop Protection Compendium. Wallingford. 1 CD-ROM

Cabral RVG, Carmona MM (1969) *Aceria guerreronis* Keifer (Acarina: Eriophyidae), uma espécie nova para S. Tomé e Príncipe. Portugaliae Acta Biológica 10:353–358

Carson C (2000) Hibiscus erinose mite. In: The world of Hibiscus. Hibiscus pests and diseases. http://www.hibiscusworld.com/pests-and-diseases.html. Accessed on 12 Mar 2009

Castagnoli M (1996) Ornamental coniferous and shade trees. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 33–88

Castagnoli M, Oldfield GN (1996) Other fruit trees and nut trees. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 543–559

Castagnoli M, Simoni S, Panconesi A, Failla O (2002) Susceptibility of cypress seedlings to the eriophyoid mite *Trisetacus juniperinus*. Exp Appl Acarol 26:195–207

Castiglioni E, Navia D (2009) Presence of the Wheat Curl Mite, *Aceria tosichella* Keifer (Prostigmata: Eriophyidae) in Uruguay. Agrociencia (in press)

CBD (2002) Alien species that threaten ecosystems, habitats or species. In: sixth conference of the parties (COP 6), Decision VI/23. The Hague, The Netherlands. http://www.cbd.int/decisions/. Accessed on 14 Dec 2008

Chagas CM, Rossetti V, Colariccio A, Lovisolo O, Kitajima EW, Childers CC (2001) *Brevipalpus* mites (Acari: Tenuipalpidae) as vectors of plant viruses. In: Halliday RB, Walter DE, Proctor H, Norton RA, Collof M (eds) Acarology: proceedings of the X international congress. CSIRO Publishing, Melbourne, pp 369–375

Chen B, Luo YZ, Yin SG (2000) New pest of tomato, *Aculops lycopersici*. Yunnan Agri. Sci and Tech. 2:32–33

DAISIE (2009) Handbook of alien species in Europe. Springer, The Netherlands

Childers CC, Kitajima EW, Welbourn WC, Rivera C, Ochoa R (2001) *Brevipalpus* mites on citrus and their status as vectors of citrus leproses. Manejo Integrado de Plagas 60:66–70

De la Torre PE, Martinez H (2004) Lista de los acaros eriofioides (Acari: Prostigmata: Eriophyoidea) de Cuba. Revista Iberica de Aracnologia 9:123–126

de Lillo E (2004) Fauna Europaea: Acari, Eriophyoidea. In: Karsholt O and Nieukerken, EJ van (eds) Fauna Europaea version 1.3. Avalaible at: http://www.faunaeur.org. Accessed on 04 Apr 2009

de Oliveria CAL, Eschiapapti D, Velho D, Sponchiado OJ (1982) Quantitative losses caused by the tomato russet mite, *Aculops lycopersici* (Massee, 1937) in tomato (*Lycopersicon esculentum* Mill.). Ecossistema 7:14–18

de Wolf E, Seifers D (2008) *Triticum* mosaic: a new wheat disease in Kansas. Kansas State University Agricultural Experiment Station and Cooperative Extension Service. EP-145, August 2008, p 2

Dekle GW (1957) Twenty-first biennial Report for the period July1, 2954-June 30, 1956. State Plant Board of Florida 2, Bulletin 11-A: 71–75

Dekle GW (1960) Twenty-third biennial Report for the period July1, 1958-June 30, 1960. State Plant Board of Florida 2, Bulletin 14: 65–70

Dekle GW, Denmark HA (1970) An eriophyid mite, *Eriophyes gardeniella* Keifer, on gardenia (Acarina, Eriophyidae). Entomology circular n 100. Fl Dept Agric & Cons Serv. Division of Plant Industry. p 2

Denmark HA (1962) *Aculus pelekassi* Keifer, Another citrus mite in Florida. Proc Fla State Hort soc 75: 25–27

di Castri F (1990) On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. In: di Castri F, Hansen AJ, Debussche M (eds) Biological invasions in Europe and Mediterranean Basin. Kluwer, The Netherlands, pp 3–16

Dieckmann M, Frison EA, Putter T (1994) FAO/IPGRI technical guidelines for the safe movement of small fruit germplasm. Rome. vol 2

Dohino T, Tanabe K (1994) Electron beam irradiation of immature stages and adult males of two spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae). Res Bull Plant Prot Serv Jpn 30:27–34

Doreste SE (1968) El ácaro de la flor del cocotero (*Aceria guerreronis* Keifer) en Venezuela. Agronomia Tropical 18:370–386

Easterbrook MA (1996) Damage and control of eriophyoid mites in apple and pear. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 527–541

Epstein AH, Hill JH (1999) Status of rose rosette disease as a biological control for multiflora rose. Plant Dis 83:92–101

Espinoza N (2008) Muestreo y diagnóstico de presencia del ácaro *Aceria tosichella* Keifer en gramíneas en Paraguay. In: Workshop en virosis de cereales transmitidas por el ácaro *Aceria tosichella*—Wheat streak mosaic virus y High plain virus en los países del Cono Sur: situación, detección y manejo. Balcarce, Argentina. Libro de Resúmenes. INTA-IFFIVE, pp 19–20

FAO (2001a) Biosecurity in food and agriculture. In: sixteenth session committee on agriculture, Rome, March 26–30 2001. http://www.fao.org/docrep/meeting/003/x9181e.htm. Accessed Apr 2009

FAO (2001b). Pest risk analysis for quarantine pests. International Standard for Phytosanitary Measures (ISPM): Publication No. 11

FAO (2002) The use of integrated measures in a systems approach for pest risk management (ISPM): Publication No. 14

FAO (2006) Glossary of Phytosanitary terms. Secretariat of the International Plant Protection Convention of the Food and Agriculture Organization (FAO) of the United Nations. ISPM No 5

Fernando LCP, Wickramananda IR, Aratchige NS (2002) Status of coconut mite, *Aceria guerreronis* in Sri Lanka. In Fernando LCP, Moraes GJ de, Wickramananda IR (eds) Proceedings of the international workshop on coconut mite *(Aceria guerreronis)*, Lunuwila. Coconut Research Institute, pp 1–8

Flechtmann CHW, Etienne J (2001) Plant mites from Guadeloupe and French Guyana with descriptions of five new species of eriophyid mites (Acari: Eriophyidae, Tenuipalpidae, and Tetranychidae). Int J Acarol 27(4):261–270

Flechtmann CHW, Kreiter S, Etienne J, de Moraes G (2000) Plant mites (Acari) of the French Antilles. 4. Eriophyidae (Prostigmata). Acarologia 40(3):321–342

Fournier V, Rosenheim JA, Johnson M, Brodeur J, (2001) When two invasive pests meet: Rust mite and powdery mildew interactions on papaya. Entomol Soc Am 2001 Annual Meeting

French R, Stenger DC (2003) Evolution of Wheat Streak Mosaic Virus: dynamics of population growth within plants may explain limited variation. Ann Rev Phytopath 41:199–214

Glavendekić M, Mihajlović L, Petanović R (2005) Introduction and spread of invasive mites and insects in Serbia and Montenegro. Proceedings Plant protection and plant health in Europe: introduction and spread of invasive species. Alford DV, Backhaus GF (ed) Berlin, Germany

Gólya G, Kozma E (1998) New data on the apple rust mite (Acari: Eriophyidae). Folia Entomol Hung 59:235–239

Hallman G (1998) Ionizing radiation quarantine treatment. Ann Soc Entomol Brasil 27:313–323

Hara A, Tsuda, D, Tavares J, Yogi J, Hensley D (1996) Hibiscus erineu mite. Univerity of Hawaii at Manoa, Cooperative Extension Service, Insect Pests, Instant Information Series No. 18

Hara A, Tsuda, D, Tavares J, Yogi J, Hensley D (2001) Hibiscus erineum mite. University of Hawaii at Manoa, Cooperative Extension Service, Insect Pests, IP-7

Harvey TL, Martin TJ, Seifers DL (2002) Wheat yield reduction due to Wheat Curl Mite (Acari: Erio-phyidae) infestations. J Agric Urban Entomol 19:9–13

Helle W, Wysoki M (1996) Arrhenotokous parthenogenesis. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 169–172

Hernandez Roque F (1977) Combate químico del eriófido del cocotero *Aceria* (*Eriophyes*) *guerreronis* (K.) en la Costa de Guerrero. Agricultura Técnica en México 4:23–38

Hong XY (1998) Proceedings of blackcurrant mite research. Entomol Knowl 35:185–188

Hong XY, Xue XF, Zhou YJ, Tong GY (2005) *Cheiracus sulcatus*, a newly found invasive eriophyoid mite damaging rice in Guang-dong Province, south china. Acta entomol Sinica 48:279–284

Hong XY, Wang DS, Zhang ZQ (2006) Distribution and damage of recent invasive eriophyoid mites (Acari: Eriophyoidea) in mainland China. Intern J Acarol 32(3):227–240

Howard FW, Moore D (2008) A coconut mite, *Aceria guerreronis* Keifer (Arachnida: Acari: Eriophyidae). University of Florida, IFAS extension. Publication EENY-398, p 7. http://edis.ifas.ufl.edu/IN709. Accessed 11 Apr 2009

Howard FW, Abreu-Rodriguez E, Denmark HA (1990) Geographical and seasonal distribution of the coconut mite, *Aceria guerreronis* (Acari: Eriophyidae), in Puerto Rico and Florida, USA. J Agric, University of Puerto Rico 74: 237–251

Howarth FG (1983) Classical biocontrol: panacea of Pandora's Box? Proc Haw Ent Soc 24:239–244

Howarth FG (1991) Environmental impacts of classical biological control. Annu Rev Entomol 36:485–509

Jensen SG, Lane LC, Seifers DL (1996) A new disease of maize and wheat in the high plains. Plant Dis 80:1387–1390

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. Univ. California Press, Berkeley

Jin HF, Liu YZ (2001) The occurrence of tomato russet mite in shed houses in Yongqing County. Hebei Agri 8:28

Jones AT (1999) Eriophyid mite transmitted viruses and virus-like agents of plants. In: biotic interactions in plant-pathogen associations. BSPP Presidential Meeting, British Society for Plant Pathology. Oxford. http://www.bspp.org.uk/archives/bspp1999/session5.php. Accessed 07 Apr 2009

Julia JF, Mariau D (1979) Nouvelle recherches en Côte-d'Ivoire sur *Eriophyes guerreronis* K., acarien ravageur des noix du cocotier. Oléagineux 34:181–187

Kahan RP (1989) Plant protection and quarantine, v.1: biological concepts. CRC Press, Boca Ratón, p 226

Kane EC (2007) Detection and identification of the rice mite *Steneotarsonemus spinki* Smiley (Acari: Tarsonemidae). USDA-APHIS. Riverdale. 4p. http://www.aphis.usda.gov/plant_health/plant_pest_info/rice_mite/downloads/s_spinki_guide.pdf. Accessed Apr 2009

Katayama M, Mizutani K, Kishino H, Yabuta S, Tomita I, Mizuno T, Yoneda M, Soma Y, Kawakami F (2001) Mortality tests for kanzawa spider mite, six-spotted mite, tropical citrus aphid and citrus psylla on Satsuma mandarins by methyl bromide fumigation. Res Bull Plant Prot Serv Jpn 37:27–33

Keifer HH (1965) Eriophyid studies B-14. Sacramento, California Department of Agriculture, Bureau of Entomology

Keifer HH (1977) Eriophyid studies C-13. Agr Res Svc USDA. 24

Keifer HH, Baker EW, Kono T, Delfinado M, Styer WE (1982) An illustrated guide to plant abnormalities caused by eriophyid mites in North America. USDA. Agric. Handbook n. 573, p 178

Kenis M, Auger-Rozenberg MA, Roques A, Timms L, Péré C, Cock MJW, Settele J, Augustin S, López-Vaamonde C (2009) Ecological effects of invasive alien insects. In: Langor DW, Sweeney J (eds) Ecological impact of non-native invertebrates and fungi on terrestrial ecosystems. Springer, The Netherlands, pp 21–45

Koehler CS, Allen WW, Costello LR (1985) Fuchsia gall mite management. Calif Agric 39(7–8):10–12

Kozlowski J, Boczek J (1987) Overwintering of the apple rust mite *Aculus schlechtendali* (Nal.) (Acarina: Eriophyoidea). Prace Naukowe Instytutu Ochrony Roslin 29:51–62

Kuang HY (1983) Two new species and one new record of eriophyid mites from China. Acta Zootax Sinica 8:389–391

Kuang HY (1995) Acari: Eriophyoidea (1) Economic insect fauna of China. No. 44. Science Press, Beijing

Kuang KY, Wang DS, Yuan YD, Zhang FQ, Wu SC (2000) Major pests and diseases of tomato and their control in modern greenhouses. Acta agric. Shangai: 6–9

Lamp W, Dively G, Ochoa R (2007) Mites. In. Lamp WO, Berberet RC, Higley L, Baird CR (eds) Handbook of forage and rangeland insects. Entomological Society of America, pp. 81–83

Lawson-Balagbo LM, Gondim MGC Jr, de Moraes GJ, Hanna R, Schausberger P (2007a) Life history of the predatory mites *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi*, candidates for biological control of *Aceria guerreronis*. Exp Appl Acarol 43:49–61

Lawson-Balagbo LM, Gondim MGC Jr, deMoraes GJ, Hanna R, Schausberger P (2007b) Refuge use by the coconut mite *Aceria guerreronis*: fine scale distribution and association with other mites under the perianth. Biol Control 43:102–110

Lawson-Balagbo LM, Gondim MGC Jr, deMoraes GJ, Hanna R, Schausberger P (2008) Exploration of the acarine fauna on coconut palm in Brazil with emphasis on *Aceria guerreronis* (Acari, Eriophyidae) and its natural enemies. Bull Entomol Res 98:83–96

Lester PJ, Dentener PR, Bennett KV, Connolly PG (1997) Postharvest disinfestation of diapausing and non-diapausing twospotted spider mite (*Tetranychus urticae*) on persimmons: hot water immersion and cool storage. Entomol Exp et Appl 83:189–193

Li Q, Cai R (1996) Occurrence and damage of the apple rust mite *Aculus schlechtendali*. Plant Prot 22:16–17

Lidster PD, Sanford KH, McRae KB (1981) Effects of modified atmosphere storage on overwintering populations of the apple rust mite and European red mite eggs. HortScience 16:328–329

Lindquist EE, Amrine JWJ (1996) Systematics, diagnoses for major taxa, and keys to families and genera with species on plants of economic importance. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 33–88

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites: their biology, natural enemies and control. World Crop Pests, vol 6. Elsevier, The Netherlands

Lockwood J, Hoopes M, Marchetti M (2007) Invasion ecology. Blackwell Publishing, UK

MacDonald O C, Mills, KA (1994) Plant quarantine treatments: are there alternatives to methyl bromide? P:183–189. In Proceedings Crop Protection Conference—Pests and Diseases. Brighton. Nottingham: Major Print, 1

Mackie DB, Steinweden JB, Carter WB (1942) Methyl bromide fumigation 1942 of narcissus bulbs for the control of bulb flies and bulb mites. Sacramento, California. Dpt Agriculture. www.fao.org/docrep/X5042E/x5042E0z.htm. Accessed 12 Mar 2009

MacLeod L (2007) CSL Pest Risk Analysis for *Aceria tulipae*. www.defra.gov.uk/planth/pra/Aceriatulipae.pdf. Accessed on 15 Mar 2009

Majumder MZR, Bhuiya AD, Chowdhury N (1996) Effects of radiation on mortality, fecundity and sterility of *Oligonychus biharensis* (Hirst) infesting common flower plants in Bangladesh. Bangladesh J Zool 24:25–32

Malik R, Brown-Guedira GL, Smith CM, Harvey TL, Gill BS (2003) Genetic mapping of wheat curl mite resistance genes Cmc3 and Cmc4 in common wheat. Crop Sci 43:644–650

Mansilla JP, Pérez Otero R, Salinero C, López Villarreal MJ, Barrote CR, Meira M (2003) The distribution of eriophyid mites and its presence on Camellias in Galicia and Portugal. Bol San Veg Plagas 29:35–41

Manson DCM (1972) New species and new records of eriophyid mites (Acarina: Eriophyidae) from New Zealand and the Pacific area. Acarologia 14:351–360

MAPA Ministério da Agricultura, Pecuária e Abastecimento (2007) Instrução normativa 52. http://www.extranet.agricultura.gov.br/sislegis-consulta/18316. Accessed 06 Mars 2009

Mariau D (1969) *Aceria guerreronis* Keifer: récent ravageur de la cocoteraie Dahoméenne. Oléagineux 32:101–111

Mariau D (1986) Comportement de *Eriophyes guerreronis* Keifer à l''egard de différentes variétés de cocotiers. Oléagineux, 41: 499–505.Schiliesske J (1988). On the gall mite fauna (Acari: Eriophyoidea) of *Cocos nucifera* L. in Costa Rica. Nachrichtenblatt des deutschen Pflanzenschutzdienstes, 40:124–127

Masaki M (1991) A list of Acarina intercepted in Plant Quarantine. Res Bull Plant Prot Japan 27:87–92

McClay AS, Sobhian R, Zhang W (2001) *Galium spurium* L., false cleavers (Rubiaceae): 358-361. In: Mason PG, Huber JT (eds) Biological Control Programmes in Canada, 1981–2000. Oxon, UK

McNeely JA, Mooney HA, Neville LE, Johan Schei P, Waage JK (2001) Global strategy on invasive alien species. IUCN, Gland and Cambridge, p 50

Mead FA (1993) Entomology section. Tri-ology 32(4):3

Michels Jr GJ, Carney VA, Lydon J, Ochoa R, Renn RL (2009) New records for *Aceria anthocoptes* (Acari: Eriophyidae) occurring on Canada thistle in Colorado, Nebraska and Wyoming. Entomol News 483–491

Michigan State University (2004) Arthropods resistance pesticide database 2004–2009, Whalon ME, Mota-Sanchez D, Hollingworth RM, Duynslager E (eds). http://www.pesticideresistance.com/. Accessed 12 Mar 2009

Michalska K, Skoracka A, Navia D, Amrine Jr JW (2009) Behavioural studies on eriophyoid mites—an overview. Exp Appl Acarology. doi:10.1007/s10493-009-9319-2

Mito T, Uesugi T (2004) Invasive alien species in Japan: the status quo and the new regulation for prevention of their adverse effects. Global Environ Res 8(2):171–191

Mohanasundaram M (1981) Record of rhyncaphytoptid gall mites (Rhyncaphytoptidae: Eriophyoidea) from South India. Oriental Insects 15:45–55

Molins RA (2001) Food irradiation: principles and applications. John wiley, Washington, p 472

Moore D (1986) Bract arrangement in the coconut fruit in relation to attack by the coconut mite *Eriophyes guerreronis* Keifer. Trop Agric 63:285–288

Moore D, Howard FW (1996) Coconuts. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 561–570

Moraes GJ, Zacarias MS (2002) Use of predatory mites for the control of eriophyid mites. In: Fernando LCP, Moraes GJ de, Wickramananda IR (eds) Proceedings of the international workshop on coconut mite *(Aceria guerreronis)*, Lunuwila. Coconut Research Institute, pp 78–88

Muthiah C, Bhaskaran R (2000) Major outbreak of eriophyid mite of coconut in India. The Planter 76:243–246

Nair CPR, Koshy PK (2000) Studies on coconut eriophyid mite, *Aceria guerreronis* Keifer in India. In Programme International Workshop on Coconut Mite *(Aceria guerreronis)*, 1. Coconut Research Institute, Lunuwilla, p 7

Nair CPR, Rajan P, Mohan Chandrika (2005) Coconut eriophyid mite *Aceria guerreronis* Keifer—an overview. Indian J Plant Prot 33:1–10

Navia D (2004) Ácaros Eriophyoidea (Prostigmata) associados a palmeiras (Arecaceae), com ênfase no ácaro do coqueiro, *Aceria guerreronis* Keifer—espectro de hospedeiros e aspectos biogeográficos. Thesis presented at University of São Paulo. http://www.teses.usp.br/teses/disponiveis/11/11146/tde-02072004-142301/. Accessed 11 Apr 2009

Navia D, Flechtmann CHW (2008) Eriophyoid mites intercepted from plant germplasm in Brazil—addressing questions on new introduction pathways. In: Sixth European Congress of Acarology. Abstracts, Montpellier. European Association of Acarologists (EURAAC), pp 58

Navia D, De Moraes GJ, Roderick G, Navajas M (2005) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyidae): Origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. Bull Entomol Res 95(6):505–516

Navia D, Truol G, Mendonça RS, Sagadín M (2006) *Aceria tosichella* Keifer (Acari: Eriophyidae) from Wheat Streak Mosaic Virus-infected wheat plants in Argentina. Int J Acarol 32:189–193

Navia D, Moraes GJ de, Flechtmann CHW (2007a) Phytophagous mites as invasive alien species: quarantine procedures. In: Morales-Malacara JB, Behan-Pelletier V, Ueckermann E, Pérez TM, Estrada E, Gispert C, Badii M (eds) Acarology: Proceedings of the XI international congress. Merida, México, pp 307–316

Navia D, Mendonça RS, Batista MF, Truol G, Pereira PRVS, Guedes JVC, Castiglioni E, Morel NNE (2007b) The Wheat Curl Mite, *Aceria tosichella* Keifer, and associated viruses, Wheat streak mosaic virus and High plain virus—the risks posed to cereal crops in South America In: Proceedings XVI International Plant Protection Congress, Glasgow, 2: 612–613

Navajas M, Navia D (2009) DNA-based methods for eriophyoid mite studies: review, critical aspects, prospects and challenges. Exp Appl Acarology. doi:10.1007/s10493-009-9301-z

Nico L, Fuller P (1999) Spatial and temporal patterns of non-indigenous fish introductions in the United States. Fisheries 24:16–27

NRC (2002) Predicting invasions of non-indigenous plants and plant pests. National Academic Press, Washington

Ochoa R (2005) Invasive plant-feeding mite species (Acari: Prostigmata). http://www.sel.barc.usda.gov/acari/content/invasivespecies.html. Accessed on April 2009

Ochoa R, Amrine Jr JW (2007) *Aceria zeala* (Keifer)—A mite new to North America has been found in a California greenhouse. (http://www.pestalert.org/viewArchPestAlert_print/). Accessed Apr 2009

Ochoa R, Erbe EF, Wergin WP, Frye C, Lydon G (2001) The presence of *Aceria anthocoptes* (Nalepa) (Acari: Eriophyidae) on *Cirsium* species in the United States. Int J Acarol 27(3):179–187

Oganezova GG, Pogosova AR (1994) Ecology and biology of *Trisetacus kirghisorum* (Acariformes, Tetrapodili). Zoologicheskii-Zhurnal 73:58–63

Oldfield GN (1996) Diversity and host plant specificity. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 199–216

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vectors of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 259–275

Ortega CA, Rodriguez VJ, Garibay CV (1967) Investigaciones preliminares sobre el eriófido del fruto del cocotero *Aceria guerreronis* Keifer, en la Costa Grande Guerrero (México). Oleaginéux 6:371–372

Ostoja-Starzewski JC, Matthews L (2006) Onion mite *Aceria tulipae*. Plant Pest Notice No. 41. CSL, New York

Pearson DE, Callaway RM (2005) Indirect nontarget effects of host-specific biological control agents: implications for biological control. Biol Control 35:288–298

Pereira PRVS, Navia D, Salvadori JR, Lau D (2009) Occurrence of *Aceria tosichella* in Brazil. Pesq Agropec Bras 44(5):539–542

Perring TM (1996) Vegetables. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 593–610

Pimentel D (2002) Introduction: non-native species in the world. In: Pimentel D (ed) Biological invasions: economic and environmental costs of alien plant, animal and microbe species. CRC Press, Boca Ratón, pp 3–8

Quilici S, Kreiter S, Ueckermann EA, Vancenot D (1997) Predatory mites (Acari) from various crops on Reunion Island. Int J Acarol 23(4):283–291

Raga A, Mineiro JLC, Sato ME, Moraes GJ, Flechtmann CHW (2008) Primeiro relato de *Eriophyes litchi* Keifer (Prostigmata: Eriophyidae) em plantas de lichia no Brasil. In: Anais do XXII Congresso Brasileiro de Entomologia, 2008, Uberlândia. Sociedade Entomológica do Brasil (CD)

Ramaraju K, Rabindra RJ (2002) Palmyra, *Borassus flabellifer* L. (Palmae): a host of the coconut eriophyid mite Aceria guerreronis Keifer. Pest Manag Hort Ecosyst 7:149–151

Ramaraju K, Natarajan K, Sundara Babu PC, Palanisamy S, Rabindra RJ (2002) Studies on coconut eriophyid mite, *Aceria guerreronis* Keifer in Tamil Nadu, Índia. In Fernando LCP, Moraes GJ de, Wickramananda IR (Eds) Proceedings of the international workshop on coconut mite *(Aceria guerreronis)*, Lunuwila. Coconut Research Institute, pp 13–31

Randall JM, Marinelli J (1996) Invasive plants: weeds of the global garden. Science Press, New York

Robbs CF, Peracchi AL (1965) Sobre a ocorrência de um ácaro prejudicial ao coqueiro (Cocos nucifera L.). Anais da Reunião Fitossanitária, Rio de Janeiro, Ministério da Agricultura, SDSV, pp 65–70

Rosenthal SS (1996) *Aceria*, *Epitrimerus* and *Aculus* species and biological control of weeds. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, The Netherlands, pp 729–739

Sanchez-Sanchez H, Henry M, Cardenas-Soriano E, Alvizo-Villasana HF (2001) Identification of Wheat streak mosaic virus and its vector *Aceria tosichella* in Mexico. Plant Dis 85:13–17

Sathiamma B, Radhakrishnan Nair CPR, Koshi PK (1998) Outbreak of a nut infesting eriophyid mite. Eriophyes guerreronis (K.) in coconut plantations in India. Indian Coconut J 29:1–3

Šefrová H, Laštůvka Z (2005) Catalogue of alien animal species in the Czech Republic. Acta univ agric et silvic Mendel. Brun, LIII, No. 4, pp 151–170

Seguni Z (2002) Incidence, distribution and economic importance of the coconut eriophyid mite, *Aceria guerreronis* Keifer in Tanzanian coconut based cropping systems. In Fernando LCP, Moraes GJ de, Wickramananda IR (eds) Proceedings of the international workshop on coconut mite *(Aceria guerreronis)*, Lunuwila Coconut Research Institute, pp 54–57

Seifers DL, Harvey TL, Kofoid KD, Stegmeier WD (1996) Natural infection of pearl millet and sorghum by wheat streak mosaic virus in Kansas. Plant Dis 80:179–185

Seifers DL, Harvey TL, Martin TJ, Jensen SG (1998) A partial host range of the High Plain Virus of corn and wheat. Plant Dis 82:875–879

Simoni S, Cantini R, Castagnoli M, Battisti A (2004) Impact and management of the eriophyoid mite *Trisetacus juniperinus* on the evergreen cypress *Cupressus sempervirens*. Agr Forest Entomol 6:175–180

Skoracka A (2008) Reproductive barriers between populations of the cereal rust mite *Abacarus hystrix* confirm their host specialization. Evol Ecol 22:607–616

Smith L, de Lillo E, Stoeva A, Cristofaro M, Rector M (2008) Challenges to evaluation of eriophyoid mites for biological control of invasive plants. In: Bertrand M, Kreiter S, McCoy KD, Migeon A, Navajas M, Tixier MS, Vial L (eds) Integrative acarology. Proceedings of the 6th European Congress European Association of Acarologists, pp 312–316

Smith L, de Lillo E, Amrine JW Jr (2009) Effectiveness of eriophyid mites for biological control of weedy plants and challenges for future research. Exp Appl Acarol. doi:10.1007/s10493-009-9299-2

Stephan D, Moeller I, Skoracka A, Ehrig F, Maiss E (2008) Eriophyid mite transmission and host range of a Brome streak mosaic virus isolate derived from a full-length cDNA clone. Arch Virol 153:181–185

Streito J, Coroller M, Kreiter S, Flechtmann CHW (2004) Un nouvel acarien ravageur des fuchsias—découverte en France d'*Aculops fuchsiae* dont c'est le premier signalement en Europe. Phytoma. La Défense des Végétaux, n. 572: 32–34

Suarez A (1991) Distribución y evaluación de daños del acaro *Eriophyes guerreronis* en plantaciones de cocotero de la región de Baracoa. Protección de Plantas 1:75–81

Truol G, Sagadin M (2008a) Presencia de *High plain virus* (HPV) nueva enfermedad del cultivo de trigo en La Província de Buenos Aires. In: VII Congreso Nacional de Trigo, Santa Rosa, Argentina. Resúmenes. INTA/UNIPALM, p 4

Truol G, Sagadin M (2008b) Virosis de los cereales detectadas en Argentina. In: Workshop en virosis de cereales transmitidas por el ácaro *Aceria tosichella—Wheat streak mosaic virus* y *High plain virus*—en los países del Cono Sur: situación, detección y manejo. Balcarce, Argentina. Libro de Resúmenes. INTA-IFFIVE, pp 21–22

Truol G, French R, Sagadin M, Arneodo J (2004) First report of wheat streak mosaic virus infecting wheat in Argentina. Austral Plant Path 33:137–138

Truol G, Sagadin M, Melchiorre G, Izaurralde J (2008) Enfermedades virales asociadas al cultivo de trigo en Argentina: Virus transmitidos por semilla y de importancia en el marco de las exportaciones. Detección en Argentina de sitios geográficos con presencia de *Wheat streak mosaic virus* (WSMV). Informe N. 6, INTA-IFFIVE, Córdoba, Argentina, ISBN 987-521-031-5. 2008, p 3

Verma BR, Kapur M (1990) Eriophyid mites (Acari: Eriophyoidea) of arid zone fruit crops and quarantine. Ind J Ent 52:249–252

Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand J Ecol 21:1–16

Welbourn WC (1995) Entomology section. Tri-ology 34(3): 4. http://www.doacs.state.fl.us/pi/enpp/triology/archive/95-5&6all.htm#ent. Accessed April 2009

Welbourn WC (1996) Entomology section. Tri-ology 35(3): 3 http://www.doacs.state.fl.us/pi/enpp/triology/archive/96-5&6all.htm#ent. Accessed April 2009

Welbourn WC (2000) Entomology section. Tri-ology 39(2): 5 http://www.doacs.state.fl.us/pi/enpp/triology/archive/00-mar-apr.html#ent. Accessed April 2009

Welbourn WC (2005) Entomology section. Tri-ology 44(1): 8 http://www.doacs.state.fl.us/pi/enpp/triology/archive/4401.pdf. Accessed April 2009

Welbourn WC (2007a) Entomology section. Tri-ology 46(2): 5 http://www.doacs.state.fl.us/pi/enpp/triology/archive/4602.pdf. Accessed April 2009

Welbourn WC (2007b) Entomology section. Tri-ology 46(4): 5 http://www.doacs.state.fl.us/pi/enpp/triology/archive/4604.pdf. Accessed April 2009

Welbourn WC (2008a) Entomology section. Tri-ology 47(1): 4 http://www.doacs.state.fl.us/pi/enpp/triology/archive/4701.pdf. Accessed April 2009

Welbourn WC (2008b) Entomology section. Tri-ology 47(1): 5 http://www.doacs.state.fl.us/pi/enpp/triology/archive/4701.pdf. Accessed April 2009

Welbourn WC (2008c) Entomology section. Tri-ology 47(5): 7 http://www.doacs.state.fl.us/pi/enpp/triology/archive/4705.pdf. Accessed April 2009

Welbourn C, Rodriques JC, Peña JE (2008) The hibiscus erineum mite, *Aceria hibisci* (Acari: Eriophyidae) a new introduction in the Caribbean and a potential threa to Florida's Hibiscus. University of Florida IFAS Publicatin ENY http://edis.ifas.ufl.edu/IN777. Accessed April 2009

Wheeler AG Jr, Hoebeke ER (2009) Adventive (Non-Native) insects: importance to science and society. In: Foottit R, Adler P (eds) Insect biodiversity: science and society. Blackwell Publishing, UK, pp 475–521

Willis AJ, Berenson PR, Ash JE (2003) Impacts of a weed biocontrol agent on recovery from water stress in a target and non-target *Hypericum* species. J Appl Ecol 40:320–333

Xie Yan, Zhenyu Li, Gregg WP, Dianmo Li (2000) Invasive species in China—an overview. Biodiv and Conserv 10:1317–1341

Zuluaga CI, Sánchez PA (1971) La roña o escoriación de los frutos del cocotero (*Cocos nucifera* L.) en Colombia. Acta Agronomica: 133–139

DNA-based methods for eriophyoid mite studies: review, critical aspects, prospects and challenges

Maria Navajas · Denise Navia

Abstract Besides their potential for species identification, DNA-based methods are also routinely used for addressing ecological, evolutionary, phylogenetic and genetic questions to study several groups of Acari. However, in contrast to other plant-feeding mites and despite the economical relevance of many species of Eriophyoidea, very few scientists have dared so far to use DNA methods for the study of this group of mites; their very small size certainly has influenced this. In this review we examine the main techniques that have been used to study eriophyoid mites and discuss the results from the literature where DNA methods have provided significant advances to address several essential questions of the eriophyoid biology, e.g., to clarify suspect synonymies, to test hypothesis of cryptic species, to examine the occurrence of biotypes, especially in relation to virus ability or host-plant associations, to understand colonization patterns of invasive species, and for uses as biological control agents against invasive plants. We discuss these questions which might be related to agricultural issues, together with more fundamental aspects as the revision of the phylogeny of the Eriophyoidea. We discuss on the advantages as well as limitations of the most commonly used genetic markers and emphasize prospects and challenges of new molecular approaches. Much is now expected from molecular techniques in many fields of biology and for virtually all taxa. Eriophyoids should not be the exception.

Keywords Eriophyoidea · DNA · Molecular systematics · Phylogeny · Cryptic species · Pest management · Invasive species

M. Navajas
INRA, UMR CBGP (INRA/IRD/CIRAD/Montpellier SupAgro), Campus International de Baillarguet, CS 30016 34988 Montferrier sur Lez, France
e-mail: navajas@supagro.inra.fr

D. Navia (✉)
Laboratory of Plant Quarantine, Embrapa Recursos Genéticos e Biotecnologia, Postal Code 02372, 70.770-900 Brasília, DF, Brazil
e-mail: navia@cenargen.embrapa.br

Introduction

DNA-based methods have revolutionized many fields of biology, and nowadays are currently used in an increasingly number of taxa to address a wide diversity of questions. With the advent of the PCR (1987), the ability to amplify numerous copies of a gene or genomic region of interest opened a world of possibilities not only in terms of identification of organisms, genes and genotypes, but also, data obtained through DNA based analyses can aid to address ecological and evolutionary questions. Genetic markers reflect differences in DNA sequences and are used to provide raw information to make estimates of genetic diversity at all taxonomic levels revealing otherwise unobtainable information of the relationships among taxonomical units (Ben-Ali et al. 2000; Navajas and Fenton 2000; Behura 2006). The utility of molecular data to provide solid taxonomic criteria is now well established, being widely used to accurately differentiate between species (Caterino et al. 2000; Tautz et al. 2003). For population studies, molecular information allows estimating gene flow, identifying haplotypes and lineages or predicting migration and colonization history (Sunnucks 2000; Garant and Kruuk 2005). Molecular methods are also of great interest for testing phylogenetic hypotheses, providing the means to propose solid, statistically supported, phylogenies.

As for other Acari, the Eriophyoidea has also benefit of the rapid development of molecular methods. However the attempts are still scarce compared to other plant mite groups. This is a regrettable observation, because among the plant feeding mites, Eriophyidae represent the second family economically important as crop pests after the Tetranychidae (Lindquist and Amrine 1996). It is also the family with the highest number of taxa (about 3,700 species from 350 genera) (Amrine and De Lillo 2006). DNA-based resources have started to be used in eriophyids about 15 years ago, with the first publications dated from 1995. Although the palette of technical approaches used for this group is still limited, important advances have been done using DNA-based techniques, which had contributed to explore some questions that were difficult to answer some years ago. This paper presents a brief introduction on the use of molecular techniques and their evolution through time, together with a review on the advances they have permitted in the study of eriophyids. Prospects and challenges of the DNA-based methods that have the potential to be used for eriophyoid mite knowledge in the near future are discussed.

Advances in molecular genetics and the use of DNA-based markers

Several key advances in molecular genetics appeared in the last two decades, which have greatly increased the impact of molecular techniques in biology in general. Among the most important are: (1) the development of PCR, which amplifies specified stretches of DNA to useable concentrations; (2) the application of evolutionarily conserved sets of PCR primers (Simon et al. 1994; Ben-Ali et al. 2000; Navajas and Fenton 2000); (3) the advent of hypervariable microsatellite loci (Goldstein and Schlötterer 1999); and (4) the advent of routine DNA sequencing in biology laboratories and technical platforms. These innovations, coupled with the recent explosion of powerful analyses and relatively user-friendly computer programs (Excoffier and Heckel 2006), bring about that much of the power intrinsic to molecular genetic data became accessible for non specialists. A number of informative review papers describing the use of molecular techniques in natural populations have appeared in the recent literature (Sunnucks 2000; DeYoung and Honeycutt 2005; Behura 2006; Gariepy et al. 2007; Cusson 2008). The field continuously progresses

expanding the sequencing capacities at lower costs and miniaturizing the amounts of DNA template. A quantum leap has been done with the advent of the so-called next-generation DNA sequencing (NGS) methods which has the potential to dramatically accelerate biological research (Shendure and Ji 2008). These rapidly progressing technologies increase the speed and capacity of sequencing by 100 to 100,000 fold from current methods and can generate more than a billion bases of data in a single run.

The use of molecular markers is often based on a trade-off between precision and convenience. These techniques are well established and their advantages as well as limitations have been realized, and are summarized in Table 1 for the most commonly used markers. Focusing on important properties of the molecular markers helps to sense making of the methods used (Behura 2006; Cusson 2008). Concerns on their application exist which need to be understood for sense making interpretation of data derived from their use in some situations (Nichols 2001). As an example, Navajas and Boursot (2003) showed that whereas a nuclear marker, the ribosomal ITS2 region, was diagnostic to separate two closely but well defined spider mite species, *Tetranychus urticae* Koch and *T. turkestani* Ugarov & Nikolskii, the same two species were polyphyletic based on DNA sequences obtained with a second marker defined in the mitochondrial genome. Such discrepancies reflect that phylogenetic trees based on genes and true species phylogenies, or species trees might not be the same (Galtier and Daubin 2008). The time back to the branching points, and even the branching order, can be different between the gene tree and the species tree (Nichols 2001; Edwards 2009), which must be taken into account when estimating the speciation events, especially the more recent branches, to avoid inaccurate definition of species. Because separate loci can provide independent test of hypothesis, using several together increases sensitivity. The possibility to use multi-loci approaches follows the advances in molecular techniques (Rodrigo et al. 2008) and is strongly recommended to infer solid phylogenies.

The DNA- Barcoding initiative

One significant application of molecular methods is for species identification. The molecular diagnostics of species has raised much interest in practically all groups of organisms. The excitement around the international Barcode project (Savolainen et al. 2005) is an example. The concept of a DNA barcode has been proposed as a method of diagnosing species, which uses short DNA sequences consisting of unique combinations of bases occurring in conserved regions of genes that are easily amplified with PCR and direct sequencing. For most animals, including the Acari, the cytochrome c oxidase subunit 1 mitochondrial gene (COI) has become the standard barcode region. While popular for molecular diagnostics, several of the limits of barcode uses, which are mainly inherent to mtDNA features, are now well known and should be taken into account when using the barcode approach (Darling and Blum 2007). While there is no doubt that molecular data is useful for species identification, the need in maintenance of the associated morphological information to a barcode not represent a consensus. DNA barcode cannot replace morphology for identification and classification but the two approaches should be synergistically used (Tautz et al. 2003; DeSalle et al. 2005). While DNA barcoding methods were started to be used for species identification in spider mites (Tetranychidae) (Ben-David et al. 2007; Carbonnelle et al. 2007; Hinomoto et al. 2007), the approach has not yet been used for eriophyoid mites. Eriophyid researches will certainly beneficiate from studies on barcoding conducted on other mite groups or even other groups of organisms.

Table 1 Comparison of features of frequently used molecular marker techniques for molecular population biology studies

	Abundance	Reproducibility	Single locus	Degree of polymorphism	Codominant	Technical requirement	Material required	PCR assay	Rapid transfer to new taxa
Mitochondrial									
RFLP	High	Straight	Yes	Low to high	Yes	High	High	Yes	Yes
Sequences	High	Straight	Yes	Medium	Yes	Medium	Low	No[c]	Yes
Multilocus nuclear									
RAPD	High	Limited	No	High	No	Low	Low	Yes	Yes[d]
AFLP	High	Limited	No	High	No	Medium	Medium	Yes	Yes
Single-locus nuclear									
Allozymes	Low	Straight	Yes	Low	Infrequent	Medium	High[b]	No	Yes
Microsatellites	High	Indirect	Yes	High	Yes	High	Low	Yes	Medium
Anonymous scn[e]	High	Indirect	Yes	Medium	Yes	Medium	Low	Yes	Medium[f]
Specific scn	Medium	Straight	Yes	Low	Yes	Medium	Low	Yes	Medium[f]
Ribosomal DNA	Low	Straight	de facto[a]	Medium	Yes	Medium	Low	Yes	Yes

Full name of markers: *RFLP* restriction fragment length polymorphism; *RAPD* random amplified polymorphic DNA; *AFLP* amplified fragment length polymorphism; *scn* single copy nuclear

[a] Ribosomal DNA consists of tandem arrays of a few regions. In some taxa the arrays are effectively identical and regions act as single loci, but in some taxa there can be many different sequences within individuals, in which case rDNA acts more like a multilocus system

[b] Fresh or frozen material is needed for allozymes. By contrast, all other techniques allow using ethanol preserved samples

[c] Sequences it self do not use PCR techniques but they are usually obtained after PCR amplification of the targeted DNA fragment

[d] Transfer of experimental conditions some times difficult because of poor reproducibility among batches of experiences or laboratories

[e] Cloned single-copy nuclear (scn) is non-repetitive nuclear sequences that occur with a frequency of one per haploid genome

[f] Lack of extensive research on this type of markers

When eriophyoid biology and molecular techniques meet

The wealth of resources in molecular genetics are still poorly used to study eriophyids in comparison with other main families of plant mites (Fig. 1). A bibliographic review on studies on plant mites involving molecular tools published during the last 20 years showed a high difference on the number of papers on Tetranychidae (46) and on Eriophyidae (11), which are respectively the first and the second economically important mite families (Fig. 1). A high number of publications on the predator family Phytoseiidae (31) was also found. This family includes the major biological control organisms used against crop mite pests. Likewise, the number of nucleotide sequences deposited in GenBank until March 2009 was significantly lower in Eriophyidae (207) than in Tetranychidae (725). At present, eriophyid nucleotide sequences deposited in GenBank belong to a reduced number of species: 21 species from six genera—*Aceria*, *Calepitrimerus*, *Cecidophyopsis*, *Colomerus*, *Eriophyes* and *Floracarus* (www.ncbi.nlm.nih.gov accessed on 28th March 2009). All these genera are included in the family Eriophyidae. There is no information available on Phytoptidae or Diptilomiopidae mites. Although these two last families are not of economic importance, their phylogenic position among the Eriophyoidea, gained by molecular information, would be of interest for a comprehensive study of the group.

The molecular markers used so far to study eriophyids are the same commonly used in other groups of mites (see Table 2). The nuclear regions include the ribosomal Internal Transcribed Spacers (ITS1 and ITS2) and associated genes (18S, 5.8 and 28S). Using these genomic regions in *Cecidophyopsis* mites (Kumar et al. 1999; Lemmetty et al. 2001) showed that the ITS1 was more informative than the ITS2 to distinguish between closely related species. Among mitochondrial genes, the 16S (the small unit of the mitochondrial ribosomal gene) has been used only to study intraspecific variation of *Aceria guerreronis* Keifer (Navia et al. 2005) and to detect the occurrence of a complex of species in the *Aceria tosichella* Keifer taxon (Carew et al. 2004). In addition, sequences of fragments of the COI of four eriophyid species—*Aceria tulipae* Keifer, *Aceria eximia* Sukhareva, *Eriophyes pyri* (Nalepa) and *Floracarus perrepae* Knihinicki & Boczek—are available (data published on data bases only; source www.ncbi.nlm.nih.gov on 28th March 2009). Among nuclear markers, the D2 region (Divergent region 2) of the large subunit ribosomal DNA, has been reported as having the potential for species identification (Sonnenberg et al. 2007). It was successfully used to investigate intraspecific variation and identify genotypes of the eriophyid *F. perrepae* (Goolsby et al. 2006) and on the occurrence of a complex of species of the *Abacarus hystrix* (Nalepa) taxon (Skoracka and Dabert in press). Also the nuclear Adenine Nucleotide Translocase (*ANT*) gene was evaluated to detect cryptic
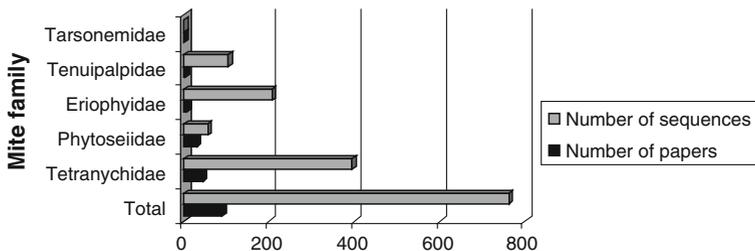
Fig. 1 Contribution of DNA data to the study of several plant mite families, estimated in number of published papers (CAB 1990–2009 database) and number of DNA sequences submitted to GenBank (on March 28th, 2009)

Table 2 PCR-based assays developed for eriophyoid mites

Eriophyoid mite	Region	Primary application	Reference
Cecidophyopsis alpina, *C. aurea*, *C. grossulariae*, *C. ribis*, *C. selachodon*, *C. spicata*, *Phyllocoptes gracilis*	ITS 1	Identification	Fenton et al. 1995
Cecidophyopsis grossulariae, *C. selachodon*	ITS 1,2	Identification, bioecology	Fenton et al. 1996
Cecidophyopsis grossulariae, *C. ribis*, *C. spicata*	ITS 1	Identification	Kumar et al. 1999
Cecidophyopsis alpina, *C. aurea*, *C. grossulariae*, *C. psilaspis*, *C. ribis*, *C. selachodon*, *C. spicata*	ITS 1,2	Phylogeny related to host association	Fenton et al. 2000
Cecidophyopsis alpina, *C. ribis*, *C. selachodon*, *C. spicata*	ITS 1	Identification	Lemmetty et al. 2001
Aceria cajani	ITS 1,2	Assess intraspecific variation	Kumar et al. 2001
Colomerus vitis, *Calepitrimerus vitis*	ITS 1, microsatellite	Identification, cryptic species	Carew et al. 2004
Aceria guerreronis	16S, ITS 1,2	Phylogeography, invasive routes	Navia et al. 2005
Floracarus perrepae	COI; D2	Assess intraspecific variation	Goolsby et al. 2006
Aceria tosichella	16S; ITS1; ANT	Identification, cryptic species	Carew et al. 2009
Acabarus hystrix	COI; D2	Identification, cryptic species	Skoracka and Dabert in press

species associated with *A. tosichella*, however limited sequence variation was observed (Carew et al. 2004). In addition, microsatellite loci have been used by Carew et al. (2004) to evaluate the population structure of a grapevine pest *Colomerus vitis* (Pagenstecher). Using these diverse DNA-based markers (see Table 2), several questions could be addressed on systematics, plant-mite interaction and colonisation patterns in bioinvasions of eriophyoid mites, as summarized below.

Species identification

Eriophyoidea systematic based exclusively on morphological characters may present several limitations. Because of the considerable reduction and simplification in the body plan of eriophyoids, the structures that can be used for eriophyoid morphologically-based systematics are scarce compared to most of the other mites. Another limitation of some species is the absence of ontogenetic diversity as well as the lack of useful characters specific to the adult male (Lindquist and Amrine 1996). An obvious significant cause of mistakes in eriophyoid systematics is the occurrence of deuterogyny (the life cycle usually including two forms of females and one form of male). The two forms of females—protogyne and deutogyne—might have been described as two different taxa often based on their morphological characters letting systematicists to classify them in different genera (Manson and Oldfield 1996). As a consequence, many species are probably junior synonyms of their correspondent deuytogyne/protogyne. It also would be necessary to

establish new combinations for species that were described based on deutogynes when its correspondent protogyne should be classified in a different genus. It is now widely accepted that molecular tools can help to clarify the systematics of taxa presenting such kind of misleading situations. Several examples combining data on nucleotide variation to more traditional morphological features help in establishing reliable criteria to determine species in the Eriophyoidea.

A series of studies on species identification, phylogeny and intraspecific variability in the *Cecidophyopsis* genus, have been conducted since 1995 (Fenton et al. 1995, 1996, 1997, 2000). This group includes mite species known to occur on twelve plant species of the genus *Ribes* and several of them are serious agricultural pests. Some species feed in young buds, causing galls resulting in the sterility of the flower buds and leading to considerable crop losses (De Lillo and Duso 1996). In addition, at least one species, *Cecidophyopsis ribis* (Westwood), transmits the agent of the reversion disease, the most important virus disease of blackcurrants, *Ribes nigrum* L., worldwide (Oldfield and Proeseler 1996). A PCR multiplex technique based on species-specific differences of the ITS-1 sequences, was developed to identify *Cecidophyopsis* mites (Kumar et al. 1999). The PCR multiplex technique presented in Kumar et al. (2001) was used by Lemmetty et al. (2001) to conduct a detailed study on the identification of *Cecidophypsis* mites on *Ribes* in Finland.

Grapevine eriophyoid mites—the bud mite and the blister mite, *C. vitis*, and the rust mite, *Calepitrimerus vitis* Nalepa—are well documented pests. The bud mite and blister mite while morphologically identical are thought to represent two strains of one species based on the type of damage they cause to grapes. The identity of these mites has recently been investigated using molecular markers (Carew et al. 2004). Two types of markers—PCR-RFLP of the ITS-1 and microsatellites—were used to gain insights into the biology and population structure. Results suggested that the bud and blister mite are different entities and should then be treated as separate agricultural problems with distinct control strategies. Importantly, infestations of vineyards with the blister mite will not result in outbreaks of the bud mite.

An important issue that molecular tools can help to address is testing hypotheses of the occurrence of cryptic species. The eriophyid *A. hystrix* has long been considered as a generalist species, having been reported from grasses of at least 30 genera, it was considered as unlikely evolving host specialization. Some studies however aimed to discriminate between three populations of *A. hystrix* from quackgrass, ryegrass and smooth brome. Using sequences of the mitochondrial COI gene and the nuclear D2 region of the 28S rDNA showed that populations from different grasses form distinct clades supporting the hypothesis of *A. hystrix* as being a complex of species and not a single generalist eriophyid taxon (Skoracka and Dabert in press). Likewise, several authors have suggested the occurrence of cryptic species within the wheat curl mite, *A. tosichella*, through morphological variation, although this could never be conclusively demonstrated. Using the mitochondrial 16S rRNA gene and two nuclear—ITS 1 and ANT—regions, it was shown that this taxon from Australia consists of at least two separate lineages that may represent putatively distinct species (Carew et al. 2009).

Plant-mite interaction and pest management

A valuable application of using genetic data to assist pest management is to investigate specialisation of mites to their host plant, which in some cases have uncovered host races. Although poorly used in eriophyoids, the approach has been used to investigate some

economically important issues. The eriophyid mite *Aceria cajani* (Channabasavanna) is the vector of the agent of pigeonpea sterility mosaic disease (PSMD), a very damaging virus-like disease in the Indian subcontinent (Ghanekar et al. 1992). When this disease occurs early in the season, yield losses can reach over 90%. Integrated management of PSMD includes the development of resistant cultivars. However, pigeonpea genotypes resistance was found to be location specific. It is possible that the breakdown in PSMD resistance at various locations is due to the occurrence of different *Aceria* species or biotypes of *A. cajani*. Aiming to test this hypothesis, the variation of *A. cajani* was assessed using nucleotide sequences variation and patterns of restriction enzymes in the ITS region and associated rDNA genes (Kumar et al. 2001). Results strongly suggested that *A. cajani* on pigeonpea across the Indian subcontinent constitutes a single species. It could be concluded that no other *Aceria* species and probably no *A. cajani* biotypes that differ in their vectoring ability are involved in the transmission of the agent of PSMD. It seems most likely therefore that this variation in resistance is due to the occurrence of strains of the PSMD agent and host interaction with these strains.

The phylogenetic relationship of seven species of *Cecidophyopsis* mites—*C. ribis*, *C. selachodon* Eyndhoven, *C. spicata* Jones, *C. grossulariae* (Collinge), *C. alpine* Amrine, *C. aurea* Amrine and *C.* n.sp.—with its *Ribes* hosts—*R. nigrum* L., *R. sativum* (Reichb.), *R. petraeum* Wulfen, *R. rubrum* L., *R. spicatum* Robson, *R. grossularia* L., *R. oxyacanthoides* L., *R. alpinum* L. and *R. aureum* Pursh—was inferred from sequences of the ITS region (Fenton et al. 2000). In addition, a phylogenetic analysis of the associated host plants was conducted. The comparison of the two phylogenetic trees (mites versus hosts) clearly displayed divergent topologies, showing that the mite speciation did not closely follow host plant speciation events. Instead, the three groups of *Ribes*-infesting *Cecidophyopsis* mites derived from a common galling ancestor millions of years ago. Each mite group has recently diversified onto different primary hosts. One group of mites has even lost the galling ability. The results indicated that the speciation process in *Cecidophyopsis* mites has not followed that of their *Ribes* hosts, the later being a much more recent event. The results have implications for the host range and durability of mite-resistance in cultivated *Ribes*.

As part of a biological control program for *Lygodium microphyllum* (Cav.) R. Br., an invasive climbing fern in Florida, USA initiated in 1997, surveys for natural enemies were conducted in the native range of the plant, which includes Australia, Asia and Oceania. Among the herbivores documented the eriophyoid *F. perrepae* causes heavy plant damage and has a high impact on host biomass production. Several genotypes of *F. perrepae* from New Caledonia, China, Thailand, India/Sri Lanka and Cape York and Queensland in Australia, were identified based in mitochondrial (COI) and nuclear (D2 domain two gene region of the 28s rRNA gene) sequences. The different mite genotypes were tested for acceptance of the invasive Florida genotype of the climbing fern. Populations from Cape York performed best and were selected to be introduced in Florida (Goolsby et al. 2006).

Pest-movements, colonisation patterns and bioinvasions: the coconut mite *Aceria guerreronis*, a case study

The tremendous economic impact caused by invasive species has received increasing attention and motivated much research aimed at understanding invasive processes (Grbic et al. 2007; Facon et al. 2008) and help to establish control measures (Fagan et al. 2002). One valuable approach is the study of sources and introduction routes of invasive arthropods facilitated by the use of molecular markers (Darling and Blum 2007).
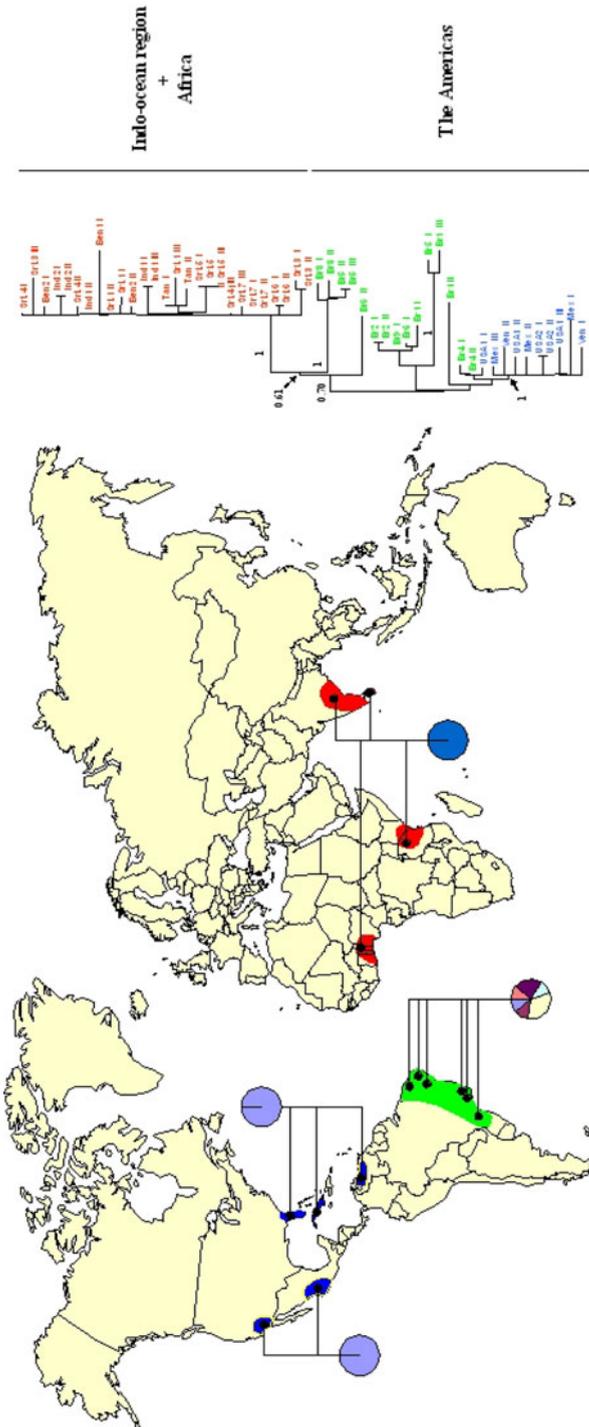
Fig. 2 Phylogeographical history of the coconut mite. The three geographical regions sampled are indicated in *red* (Indo-ocean region), *green* (Brazil) and *blue* (other American countries) **a** different mitochondrial haplotypes detected and their frequency in the different sampled localities (*black dots*) are indicated by the pie charts. The highest nucleotide diversity was found in Brazil where six out of the seven haplotypes were present. By contrasts one haplotype (here in *pink*) was found in Central and North America and a single one (here in *yellow*) was shared by non-American mites from Africa and the Indo-ocean region (India and Sri-Lanka). **b** Congruently, the tree constructed with the nuclear ITS sequences revealed that all non-American samples (in *red*) are very little diversified and cluster together, whereas the Brazilian (in *green*) are represented in several branches of the tree. The rest of the American samples (in *blue*) are gathered in a single cluster (Color figure online)

Molecular information has been used to trace the invasion routes of plant mites, including the eriophyoid coconut mite, *A. guerreronis*. This species has recently spread and rapidly established in important coconut production areas worldwide, being considered as a highly destructive invasive species. The mite has not been recorded in the Indo-Pacific region, the area of origin of the coconut, suggesting that it has infested coconut only recently. In a recent phylogeography study conducted to investigate the geographical origin, ancestral host associations, and colonization history of the mite (Navia et al. 2005), DNA sequences variation from one mitochondrial (16S) and one nuclear region (ITS) were used to investigate mites obtained from samples of 29 populations originating from The Americas, Africa and the Indo-ocean region, the three continents where the mite has been reported (Fig. 2). Mitochondrial sequences were most diverse in Brazil (six out of a total of seven haplotypes recorded). A single haplotype was shared by non-American mites. Accordingly, patterns of nuclear ITS variation was similar, with the highest nucleotide diversity found in Brazil. The results suggested that the mite originates from The Americas and not from the ancestral region of coconut in South East Asia. Thus, colonization of coconut by this mite is a recent event, perhaps facilitated by modern transportation of coconut or propagation material potentially from a palm different from coconut. In addition, the fact that all samples from Africa and Asia were identical or very similar is consistent with the hypothesis that the mite invaded these regions recently and from a common source. The study prompts a reassessment of efforts using quarantine measures by knowing movements of the pest.

Critical technical aspects on the use of molecular methods to study eriophyoid biology

DNA extraction and voucher specimens

One feature that might have discouraged the development of molecular studies on eriophyoid mites is their reduced size. It can be noticed that in most studies on eriophyoid mites, authors have extracted DNA from a pool of specimens (5–20), especially for sequencing uses (e.g. Fenton et al. 2000; Kumar et al. 2001; Navia et al. 2005), except for Carew et al. (2004; 2009) that were successful in extracting DNA of individual eriophyid mites. This contrasts with the common use of single mites which has been reported for other groups of plant mites, e.g. Tetranychidae and Tenuipalpidae (Navajas et al. 2001; Rodrigues et al. 2004). However, the bias to analyze several mites as a single sample seems to be less important in eriophyoids considering that many species reproduce by arrenotokous parthenogenesis (Helle and Wysoki 1996). It is likely that specimens collected from one colony (gall, bud, blister, erineum species) are probably highly inbred and when pooling several specimens in a single sample the genetic diversity would be reduced. Caution however should be taken for species reproducing sexually, through transfer of spermatophore, and being vagrants. In this case, working with a pool of specimens can lead to a loss of information or even give misleading results because the analyzed sample might contain mites coming from distant areas and being genetically divergent. In this regard, it is worthy to notice that recent DNA extraction methods based on whole-genome pre-amplification have proved good results in terms of DNA yield from mites (Konakandla et al. 2006).

Most of the DNA extraction methods that have been used so far in studies with eriophyoid mites are destructive. Whole mites are crushed during the first steps of the extraction protocol, making impossible be used as a voucher specimen. Yet, all study on

DNA-based systematics should be associated to a voucher specimen whose origin and current status should be registered (Ruedas et al. 2000; Marrelli et al. 2006). This requirement is reinforced when observing the growing problem of taxonomic misidentification in public DNA databases which threatens the utility of the deposited sequences database reported by authors working with different groups of organisms (Sperling et al. 1994; Ruedas et al. 2000; Bridge et al. 2003; Vilgalys 2003). It would be interesting to use a nondestructive DNA extraction protocol which allows to preserve vouchers for morphological identification after DNA extraction (Rowley et al. 2007). An interesting DNA extraction protocol have been described and used for feather mites (Analgoidea) which makes possible to prepare slides of specimens after DNA extraction (Dabert et al. 2008). This same protocol was successfully used for *A. hystrix*; exoskeletons of the eriophyoid mites which had been stored in 70% ethyl alcohol until used for preparing microscopic slides (Skoracka and Dabert in press).

Collaboration between molecular and taxonomy experts

As for any taxa, the data on eriophyoid systematics obtained by DNA data would be a more efficient tool if combined with classical systematic information. In some cases, collaboration between both molecular and morphological expertise seems to lack. For example, the work by Carew et al. (2004) based on molecular data supported the occurrence of two taxa which before were considered as "strains" of *C. vitis* in Australia. While useful in defining taxonomical units, these studies would have beneficiated from a detailed morphological study aimed at detecting the characters that could discriminate taxa. Thus, molecular information while helping to detect and define the occurrence of cryptic species has not been concomitantly used by classical taxonomists to guide detailed morphological or morphometric studies in the search for diagnostic characters to be used in the description of new taxa.

Molecular techniques to study eriophyids: new avenues

DNA is progressively invading the field of Acarology. The minute eriophyoids is increasingly benefitting from the fast improvement of techniques to define and use molecular markers by adopting new forms and innovative approaches to detect DNA polymorphism. As a result, much can now be expected from the molecular techniques to gain in knowledge of the eriophyoid. Some of the main issues that we think should take advantage of the molecular approaches in the near future are discussed below.

Although the monophyly of the group is mostly accepted, its relationship to other Prostigmata remains to be investigated. The most recent phylogenetic hypothesis of the Eriophyoidea places the superfamily as a sister group of the Tydeoidea on the basis of a number of characters, none of which are synapomorphies (Lekveishvili et al. 2008). Likewise, the majority of taxonomic groups within the Eriophyoidea are artificial (Lindquist and Amrine 1996). As a result, the current classification has little predictive power. The lack of information on the Eriophyoidea phylogeny has been an important limitation on the progress of the systematics and biology of the group. As an example, the present classification does not reflect patterns of evolution and adaptation of these mites to their host plants (Lindquist and Amrine 1996), limiting the use of this knowledge to solve applied questions, as for instance in detecting host-adapted populations of crop pests. The reconstruction of Eriophyoidea phylogeny using molecular data remains a challenge,

which can nowadays be addressed thanks to methodological advances. For lower taxonomic levels, uncertainties on Eriophyoidea systematics are numerous and molecular techniques could help to answer questions and test hypothesis of different nature, e.g. synonymies and occurrence of cryptic species. For more applied issues, information provided through molecular studies can significantly contribute to define management strategies for eriophyoid pests. A significant pest control concern is the use of eriophyoid mites as biological control agents of weeds or other invasive plants. The knowledge of the genetic intraspecific variability of a biological control agent is the basis to establish efficient biological control strategies. The intraspecific variability is also relevant information on species that are vectors of plant pathogens especially when the pathosystem management should be based on the host genetic resistance. Diverse vector biotypes can present different levels of resistance to host plant genes involved in mite resistance. In addition, among the phytophagous mites, eriophyoids are being increasingly recognized for their potential to become invasive species (Hong et al. 2006). It is necessary to adopt preventive measures to avoid introductions and fast dissemination of eriophyoid pests in new geographical areas. Interception of potential invaders depends on a detailed inspection followed by a reliable and fast identification of the organisms. Information on routes of colonization or pathways of introduction is required to implement quarantine measures.

Looking to the future

Acarolgy is slowly entering the genomics era, with the whole genome sequencing projects of the tick *Ixodes scapularis* Say (Hill and Wikel 2005) and the spider mite *T. urticae* (Grbic et al. 2007) being completed and other sequencing projects that have already been proposed (see http://www.ncbi.nlm.nih.gov/sites/entrez). No doubt that eriophyoids will benefit from the new avenues permitted by these resources and more broadly Acarology will benefit from the technical advances made in other arthropods. With the advent of the genomic tools, that the whole genome projects will provide, the study of biological complex traits to address a diversity of problems caused by arthropod pest (Edwards 2009) in agriculture will be facilitated as reviewed in Heckel (2003) and Grimmelikhuijzen et al. (2007).

References

Amrine JW Jr, De Lillo E (2006) A database on Eriophyoidea of the world. West Virginia University

Behura SK (2006) Molecular marker systems in insects: current trends and future avenues. Mol Ecol 15:3087–3113

Ben-Ali Z, Boursot P, Said K, Lagnel J, Chatti N, Navajas M (2000) Comparaison of ribosomal ITS regions among *Androctonus* spp. scorpions (Scorpionida: Buthidae) from Tunisia. J Med Entomol 37:787–790

Ben-David T, Melamed S, Gerson U, Morin S (2007) ITS2 sequences as barcodes for identifying and analyzing spider mites (Acari: Tetranychidae). Exp Appl Acarol 41:169–181

Bridge PD, Spooner BM, Panchal G (2003) On the unreliability of published DNA sequences. New Phytol 160:43–48

Carbonnelle S, Hance T, Migeon A, Baret PV, Cros-Arteil S, Navajas M (2007) Microsatellite markers reveal spatial genetic structure of *Tetranychus urticae* (Acari: Tetranychidae) populations along a latitudinal gradient in Europe. Exp Appl Acarol 41:225–241

Carew ME, Goodisman MAD, Hoffmann AA (2004) Species status and population genetic structure of grapevine eriophyoid mites. Entomol Exp Appl 111:87–96

Carew M, Schiffer M, Umina P, Weeks A, Hoffmann A (2009) Molecular markers indicate that the wheat curl mite, *Aceria tosichella* Keifer, may represent a species complex in Australia. Bull Entomol Res 99:479–486

Caterino MS, Cho S, Sperling FAH (2000) The current state of insect molecular systematics: a thriving tower of Babel. Ann Rev Entomol 45:1–54

Cusson M (2008) The molecular biology toolbox and its use in basic and applied insect science. Bioscience 58:691–700

Dabert J, Ehrnsberger R, Dabert M (2008) *Glaucalges tytonis* sp.n. (Analgoidea, Xolalgidae) from the barn owl *Tyto alba* (Strigiformes, Tytonidae): compiling morphology with DNA barcode data for taxon descriptions in mites (Acari). Zootaxa 1719:11

Darling JA, Blum MJ (2007) DNA-based methods for monitoring invasive species: a review and prospectus. Biol Invasions 9:751–765

De Lillo E, Duso C (1996) Currants and berries. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 583–591

DeSalle R, Egan MG, Siddall M (2005) The unholy trinity: taxonomy, species delimitation and DNA barcoding. Philos Trans R Soc Lond B Biol Sci 360:1905–1916

DeYoung RW, Honeycutt RL (2005) The molecular toolbox: genetic techniques in wildlife ecology and management. J Wildl Manage 69:1362–1384

Edwards S (2009) Is a new and general theory of molecular systematics emergins? Evolution 63:1–19

Excoffier L, Heckel G (2006) Computer programs for population genetics data analysis: a survival guide. Nat Rev Genet 7:745–758

Facon B, Pointier JP, Jarne P, Sarda V, David P (2008) High genetic variance in life-history strategies within invasive populations by way of multiple introductions. Curr Biol 18:363–367

Fagan W, Lewis M, Neubert M, van den Driessche P (2002) Invasion theory and biological control. Ecol Lett 5:148–157

Fenton B, Malloch G, Jones AT, Amrine JW Jr, Gordon SC, A'Hara S, McGavin WJ, Birch ANE (1995) Species identification of *Cecidophyopsis* mites (Acari: Eriophyidae) from different *Ribes* species and countries using molecular genetics. Mol Ecol 4:383–387

Fenton B, Jones AT, Malloch G, Thomas WP (1996) Molecular ecology of some *Cecidophyopsis* mites (Acari: Eriophyidae) on *Ribes* species and evidence for their natural cross colonisation of blackcurrant (*R. nigrum*). Ann Appl Biol 128:405–414

Fenton B, Malloch G, Moxey E (1997) Analysis of eriophyid rDNA internal transcribed spacer sequences reveals variable simple sequence repeats. Insect Mol Biol 6:23–32

Fenton B, Birch ANE, Malloch G, Lanham PG, Brennan RM (2000) Gall mite molecular phylogeny and its relationship to the evolution of plant host specificity. Exp Appl Acarol 24:831–841

Galtier N, Daubin V (2008) Dealing with incongruence in phylogenomic analyses. Philos Trans R Soc Lond B Biol Sci 363:4023–4029

Garant D, Kruuk L (2005) How to use molecular marker data to measure evolutionary parameters in wild populations. Mol Ecol 14:1843–1859

Gariepy TD, Kuhlmann U, Gillott C, Erlandson M (2007) Parasitoids, predators and PCR: the use of diagnostic molecular markers in biological control of Arthropods. J Appl Entomol 131:225–240

Ghanekar AM, Sheila VK, Benival SPS, Reddy MV, Nene YL (1992) Sterility mosaic of pigeonpea. In: Singh US, Mukhopadhyay AN, Kumar J, Chaube HS (eds) Plant diseases of international importance, vol 1. Prentice Hall, New Jersey, pp 415–428

Goldstein DB, Schlötterer C (1999) Microsatellites, evolution and applications. Oxford University Press, New York, p 352

Goolsby JA, De Barro PJ, Makinson JR, Pemberton RW, Hartley DM, Frohlich DR (2006) Matching the origin of an invasive weed for selection of a herbivore haplotype for biological control programme. Mol Ecol 15:287–297

Grbic M, Khila A, Lee K-Z, Bjelica A, Grbic V, Whistlecraft J, Verdon L, Navajas M, Nagy L (2007) Mite model: *Tetranychus urticae*, a candidate for chelicerate model organism. Bioessays 29:489–496

Grimmelikhuijzen CJP, Cazzamali G, Williamson M, Hauser F (2007) The promise of insect genomics. Pest Manag Sci 63:413–416

Heckel DG (2003) Genomics in pure and applied Entomology. Ann Rev Entomol 48:235–260

Helle W, Wysoki M (1996) Arhenotokous parthenogenesis. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, Amsterdam, pp 169–171

Hill CA, Wikel SK (2005) The *Ixodes scapularis* Genome Project: an opportunity for advancing tick research. Trends Parasitol 21:151–153

Hinomoto N, Tran DP, Pham AT, Le TBN, Tajima R, Ohashi K, Osakabe M, Takafuji A (2007) Identification of spider mites (Acari: Tetranychidae) by DNA sequences: a case study in Northern Vietnam. Int J Acarol 33:53–60

Hong XY, Wang DS, Zhang ZQ (2006) Distribution and damage of recent invasive eriophyoid mites (Acari: Eriophyoidea) in mainland China. Int J Acarol 32:227–240

Konakandla B, Park Y, Margolies D (2006) Whole genome amplification of Chelex-extracted DNA from a single mite: a method for studying genetics of the predatory mite *Phytoseiulus persimilis*. Exp Appl Acarol 40:241–247

Kumar L, Fenton B, Jones AT (1999) Identification of *Cecidophyopsis* mites (Acari: Eriophyidae) based on variable simple sequence repeats of ribosomal DNA internal transcribed spacer-1 sequences via multiplex PCR. Insect Mol Biol 8:347–357

Kumar PL, Fenton B, Duncan GH, Jones AT, Sreenivasulu P, Reddy DVR (2001) Assessment of variation in *Aceria cajani* using analysis of rDNA ITS regions and scanning electron microscopy: implications for the variability observed in host plant resistance to pigeonpea sterility mosaic disease. Ann Appl Biol 139:61–73

Lekveishvili M, Amrine JW Jr, Wells J (2008) Preliminary results of eriophyoid phylogeny (Acari: Prostigmata). In Sixth European Congress of Acarology. European Association of Acarologists, Montpellier, 49

Lemmetty A, Tikkanen M, Tuovinen T, Lehto K (2001) Identification of different *Cecidophyopsis* mites on Ribes in Finland. Acta Hortic 656:115–118

Lindquist EE, Amrine JWJ (1996) Systematics, diagnoses for major taxa, and keys to families and genera with species on plants of economic importance. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, Amsterdam, pp 33–88

Manson DCM, Oldfield GN (1996) Life forms, deuterogyny, diapause and seasonal development. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites: their biology, natural enemies and control. Elsevier, Amsterdam, pp 173–183

Marrelli MT, Sallum MAM, Marinotti O (2006) The second internal transcribed spacer of nuclear ribosomal DNA as a tool for Latin American anopheline taxonomy—a critical review. Mem Inst Oswaldo Cruz 101:817–832

Mullis KB, Faloona FA (1987) Specific synthesis of DNA in vitro via a polymerase-catalyzed chain reaction. Meth Enzymol 155:335–350

Navajas M, Boursot P (2003) Nuclear ribosomal DNA monophyly *versus* mitochondrial DNA polyphyly in two closely related mite species: the influence of life history and molecular drive. Proceedings of the Royal Society of London B (Suppl) 270: S124–S127

Navajas M, Fenton B (2000) The application of molecular markers in the study of diversity in acarology: a review. Exp Appl Acarol 24:751–774

Navajas M, Gutierrez J, Williams M, Gotoh T (2001) Synonymy between two spider mite species, *Tetranychus kanzawai* and *T. hydrangeae* (Acari: Tetranychidae), shown by ribosomal ITS2 sequences and cross-breeding experiments. Bull Entomol Res 91:7

Navia D, GJd Moraes, Roderick G, Navajas M (2005) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyidae): origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. Bull Entomol Res 95:505–516

Nichols R (2001) Gene trees and species trees are not the same. Trends Ecol Evol 16:358–364

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vectors of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, pp 259–275

Rodrigo A, Bertels F, Heled J, Noder R, Shearman H, Tsai P (2008) The perils of plenty: what are we going to do with all these genes? Philos Trans R Soc Lond B Biol Sci 363:3893–3902

Rodrigues JCVR, Childers CC, Gallo-Meagher M, Ochoa R, Adams BJ (2004) Mitochondrial DNA and RAPD polymorphisms in the haploid mite *Brevipalpus phoenicis* (Acari: Tenuipalpidae). Exp Appl Acarol 34:17

Rowley DL, Coddington JA, Gates MW, Norrbom AL, Ochoa RA, Vandenberg NJ, Greenstone MH (2007) Vouchering DNA-barcoded specimens: test of a nondestructive extraction protocol for terrestrial arthropods. Mol Ecol Notes 7:915–924

Ruedas LA, Salazar-Bravo J, Dragoo JW, Yates TL (2000) The importance of being earnest: what, if anything, constitutes a "specimen examined?". Mol Phylogenet Evol 17:129–132

Savolainen V, Cowan RS, Vogler AP, Roderick GK, Lane R (2005) Towards writing the encyclopaedia of life: an introduction to DNA barcoding. Philos Trans R Soc Lond B Biol Sci 360:1805–1811

Shendure J, Ji HL (2008) Next-generation DNA sequencing. Nat Biotechnol 26:1135–1145

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Ann Entomol Soc Am 87:651–701

Skoracka A, Dabert M (in press) The cereal rust mite *Abacarus hystrix* (Acari Eriophyoide) is a complex of species: evidences from mitochondrial and nuclear DNA sequences. Bull Entomol Res. doi: 10.1017/S0007485309990216

Sonnenberg R, Nolte AW, Tautz D (2007) An evaluation of LSU rDNA D1-D2 sequences for their use in species identification. Front Zool 4:12

Sperling F, Anderson G, Hickey D (1994) A DNA-based approach to the identification of insect species used for postmortem interval estimation. J Forensic Sci 39:418–427

Sunnucks P (2000) Efficient genetic markers for population biology. Trends Ecol Evol 15:199–203

Tautz D, Arctander P, Minelli A, Thomas RH, Vogler AP (2003) A plea for DNA taxonomy. Trends Ecol Evol 18:70–74

Vilgalys R (2003) Taxonomic misidentification in public DNA databases. New Phytol 160:3–4

Collection and detection of eriophyoid mites

R. Monfreda · M. Lekveishvili · R. Petanovic · J. W. Amrine Jr.

Abstract   Methods for collecting and detecting eriophyoid mites are crucial components in research, taxonomical and biological studies, and control programs for these organisms. Their small size, their specific host-plant interactions and their hidden life-style make them difficult to find in routine inspections. This review examines successful and unsuccessful approaches for collecting eriophyoid mites, and makes recommendations for their detection, supporting studies in taxonomy, ecology, biology, molecular systematics and population genetics.

Introduction

Among the Acari, eriophyoid mites are second only to the spider mites (Tetranychidae) in their economic importance as plant pests around the world. This pest status is due to the feeding damage and to their role in the transmission of plant pathogens (Lindquist et al. 1996). With the possible exception of one vector species in Tetranychidae (Schulz 1963), and three species in Tenuipalpidae (Chagas et al. 2001), eriophyoids are the only known

R. Monfreda (✉)
Di.B.C.A., Entomological and Zoological Section, Agricultural Faculty, University of Bari,
via Amendola, 165/A, 70126 Bari, Italy
e-mail: monfreda@agr.uniba.it

M. Lekveishvili
Department of Biology, West Virginia University, 53 Campus Dr., PO Box 6057, Morgantown,
WV 26506-6057, USA

R. Petanovic
Department of Entomology and Agricultural Zoology, Faculty of Agriculture, University of Belgrade,
Nemanjina 6, Belgrade-Zemun 11081, Serbia

J. W. Amrine Jr.
Division of Plant & Soil Sciences, West Virginia University, P. O. Box 6108, Morgantown,
WV 26506-6108, USA

mites transmitting plant viruses with at least nine vector species known in Eriophyidae (Oldfield and Proeseler 1996). Furthermore, these mites can be applied as biological control agents against weeds (Rosenthal 1996).

Due to their small size (82–350 μm), their specific host/plant interactions, and often concealed life-style (Monfreda et al. 2008), considerable time and effort must be spent in devising apparatus and techniques to detect them when biological, ecological and control studies are undertaken.

Moreover, considering the importance of eriophyoids as pests of plants and vectors of viruses, and the large scale movement of plants around the world, their detection becomes very useful and necessary for quarantine policies (Flechtmann 2007).

Immunochemical and molecular methods have assumed an increasing importance in pest detection on plant and stored products (Rotundo et al. 2000; Brader et al. 2002; Phillips and Zhao 2003; Krizkova-Kudlikova and Hubert 2007). Being cheap, practicable, highly specific and sensitive, these techniques can also be very useful for determining and quantifying mite infestations. Nowadays, both serological and molecular techniques can be integrated into micro-arrays that allow the simultaneous analysis of many thousands of single tests. However, until now, no applications of serological and molecular techniques on eriophyoid detection have been reported in the literature.

Usually, specimens are collected directly from symptomatic and non-symptomatic plant materials under a dissecting microscope. This method, mainly used in the past, has a wide range of drawbacks: the scarcity of good mite collections, the mobility and tiny size of the eriophyoids, and the shape, size, number and complexity of the host plants. The time required for a collection is often excessive compared to the results; asymptomatic plant organs, often hosting eriophyoid populations, are usually overlooked.

Several methods have been applied in the past, some of which were reviewed by Lindquist et al. (1996). Typical procedures have used trapping or extraction techniques: sticky tape or other adhesive traps, ultrasonic baths, centrifugal flotation, brushing machines or washing methods (Perring et al. 1996). Some of these older methods are seldom used today.

In this review, improvements in the collection and detection methods are analyzed, describing the critical aspects of currently used techniques. All available information on eriophyoid mite collection and storage for further molecular studies are summarized. A synoptic table is provided for extraction procedures (Table 1).

Molecular analysis has proven to be a valuable tool in reconstructing phylogeny and understanding population structures of eriophyoid mites. Although there is no published record on its application on eriophyoid mite phylogeny above species level, several nuclear and mitochondrial markers (18S, EF-1α, COI) have proved to be informative in resolving relationships within and among different genera and families of Eriophyoidea (Lekve-ishvili, unpublished data). Within the relatively little molecular work that has been done on eriophyoids, a number of studies show advances in population genetics (Carew et al. 2004; Navia et al. 2005; Evans et al. 2008) and species identification (Fenton et al. 1993, 1995, 1996, 1997, 2000; Kumar et al. 1999).

Review of techniques

Trapping methods

Two categories of trapping methods are used for sampling and monitoring eriophyoid mites: one to collect mites during their active movements on the plant surface by means of

Table 1 Characteristics of described extraction methods with suggestions for use

Procedure	Chemicals or solutions	Devices	Suggested use
Zacharda et al. (1988)			
Shake and wash technique	80–90% ethanol	Separating funnel	Biological and taxonomical studies when live EMs are not required
Pérez-Moreno and Moraza Zorrilla (1998)			
Wash and sieve technique	70% ethanol, Tap water, 70% ethanol–5% glycerine	25-μm sieve	Biological and taxonomical studies when live EMs are not required
Duffner (1999)			
Shake, wash and sieve technique	Detergent solution in water, Methylene-blue (1%)	90 and 32-μm sieves, Vacuum pump	Biological and taxonomical studies when live EMs are not required
Gabi and Mészáros (2001)			
Shake, wash and sieve technique	Tap water, Azur II eosin	Filtering apparatus (tissue mesh size: 300 and 40 μm)	Biological and taxonomical studies when live EMs are not required
Faraji et al. (2004)			
Shake, wash and sieve technique	Detergent solution in water, 70% ethanol, Methylene blue, Paraffin	45-μm meshed sieve, Centrifuge, U-shaped Plexiglas® mite-counting channel	Mite quantitative determination, when live EMs are not required
Siriwardena et al. (2005)			
Shake and wash technique	Detergent solution in water	Equipment: tube; funnel; and Mohr's clip, Rotor-mixture	Biological and taxonomical studies, EMs quantitative determination, especially when there is high population density
Monfreda et al. (2007)			
Shake and wash technique	Detergent and bleach solution in water, Eggs: kaolin powder and $MgSO_4$	Sieves (mesh size: 850, 180, 53 and 25 μm), Filter holder (mesh size: 20 μm), Eggs: centrifuge	Biological, taxonomical studies, rearing, mass release, host specificity and biological assays, when live specimens are required

EMs eriophyoids

sticky tape or other kinds of adhesive trap; the other for trapping mites during passive aerial dispersal, using sticky glass slides, plates coated with grease, or detergent-water pan traps.

The first category is principally employed to assess eriophyoid population densities in architecturally complex plant structures (e.g. buds or fruits), where it is difficult to visually count them under a dissecting microscope.

David and Varadarajan (2001) developed a technique to study *Aceria guerreronis* Keifer on coconut, based on a glycerine drop trap, where a drop of glycerine was placed within a fixed area using a pin-head. The mites were caught in this drop, and, being unable to move, were easy counted under a dissecting microscope.

Harvey and Martin (1988) developed a sticky-tape method to evaluate the numbers of wheat curl mite *Aceria tosichella* (Keifer) by placing immature wheat spikes on the sticky side of a strip of transparent tape. As the spikes dried, the mites crawled from them and became stuck to the tape. At the end of mite emergence, they were counted with the aid of a microscope at $15\times$ magnification. Davies et al. (2002) applied a synthetic pyrethroid spray to the sticky-tape for estimating the abundance of *Acalitus essigi* (Hassan) from the complex blackberry structure. As in the spike studies, blackberry fruits at the red stage were placed on the centre of the sticky side, and placed in a covered plastic pot to prevent mite aerial dispersal. After the berries dried, the fruit residues were removed and the mites were counted at $20\times$ magnification; insecticide application to the tape significantly increased the detection of the eriophyoids. In addition, the visual fruit receptacle count was much less efficient, in number of collected mites, than sticky-tape (spray and no spray treatments) methods.

Bernard et al. (2005) used a sticky-method, developed by Duffner and Schruft (1998) and Duffner (1999), to trap *Calepitrimerus vitis* (Nalepa) emerging from buds during the spring migration period. Double side sticky-tape was placed above the base of each grape spur and below node-1 buds, and replaced every 3 days. Mite numbers on tapes were counted through transparent plastic sheets, at $50–70\times$ magnification, to assess the population density. Similar techniques were applied by Walton et al. (2007), to monitor eriophyoids in grapevines and to assess mite incidence on dormant plant tissues. Tape was wrapped around each cane, one at the base of a shoot close to the main trunk and another three buds away from the base of each cane. Sticky tape samples were replaced every 15 days and viewed in the laboratory under a dissecting microscope for the presence of mites.

In general, these sticky-tape methods appear to be very useful for eriophyoid spatial and temporal distribution studies, but mite sampling using these traps had some difficulties: moisture could interfere with the tape placement and stickiness, and it could cause discoloration of the adhesive, which may obscure mite viewing and monitoring. Moreover, mites collected from sticky tapes were often deformed and difficult to detach from the glue without destroying them. These methods appear to be unsuitable for taxonomic studies, or when live specimens are required.

The second category of trapping method is principally applied for studying eriophyoid aerial dispersal. These techniques utilize, as a trap, either glass slides or plates coated with grease (silicone grease, petroleum jelly or vaseline; Perring et al. 1996; Duffner et al. 2001), or detergent-water pan traps (Zhao and Amrine 1997). In the latter case, aluminium pans were filled 3/4 full with soapy water (with 2 ml dishwashing detergent) and were placed horizontally on a 15 cm-high support. Twenty-four h after their exposure to the air, the soapy water was collected and vacuum-filtered using filter papers. Mites trapped on the filter papers were examined under a dissecting microscope at $20–80\times$ magnification.

The water-detergent pan method appears to be more efficient than sticky plates in the detection of eriophyoids from the air, by eliminating the considerable time required to screen grease-coated plates under a dissecting microscope and by eliminating the tedious processing of mites contaminated by grease which often deformed or obscured the mites and made them difficult to identify. The detergent-water pan trap technique seems to be suitable for investigation of airborne activity and taxonomic studies on eriophyoids.

Extraction methods

To estimate mite populations it is often necessary to extract eriophyoids from plant material, especially when there are complex plant structures or high trichome density, which can hide small aggregated mite colonies.

Zacharda et al. (1988) developed a shake and wash technique for monitoring both predatory and phytophagous mites in apple orchards, which is useful for monitoring *Aculus schlechtendali* (Nalepa). Infested plant material (leaves, spurs and shoots with undeveloped leaves) were immersed in 80–90% ethanol in a covered beaker and were shaken for 5–10 s. The plant material was then removed and the alcohol containing the preserved mites was poured into a separating funnel. The mites, which settled on the bottom, were transferred to a Petri dish and counted under a dissecting microscope after alcohol evaporation. This technique was 10–20% more efficient than directly counting mites on leaves under a dissecting microscope.

This technique kills mites quickly and preserves them for further study; moreover, it can be applied under both field and laboratory conditions without physical damage to erio-phyoids during their removal from plant material.

Pérez-Moreno and Moraza Zorrilla (1998) developed a standardized method to sample *Calepitrimerus vitis* (Nalepa) using a washing and sieving technique instead of directly observing each leaf under a dissecting microscope or by brushing the mites off the leaves. Grapevine leaf samples were submerged in a 70% ethanol solution for 5 min in order to kill the mites. The leaves were individually washed under tap water and mites collected using a 25-μm sieve, and then transferred to a Petri dish using a solution of 70% ethanol and 5% glycerine. After ethanol evaporation and glycerine embedding, eriophyoids were counted under a dissecting microscope at $70\times$ magnification by placing a sheet of milli-metre graph paper under the dish. A similar procedure was applied to buds and basal cane portions, to study the deutogyne distribution in woody shoots. The bud scales, carefully opened with a pointed forceps, or the basal cane portions after lifting up of the bark, were placed in a jar with 70% ethanol and stirred for 10 min with a magnetic stirrer. The suspension was poured through two sieves: the top one (1 mm opening) retained coarse vegetal material and the lower one (25 μm opening) collected the eriophyoids. The mites were than treated as described above.

This procedure is useful for biological studies for which collected mites can be per-manently mounted on slides. In all the wash methods described above, a toxic chemical (usually ethanol), immediately kills the eriophyoids. However, in some studies such as evaluation of toxic effects of chemical applications on plants, rearing and mass release, etc., researchers need to collect live specimens from infested plant extraction.

Duffner (1999) applied an elaborate procedure to collect *C. vitis* from leaves and buds of grapevine. Vegetal material was placed in a plastic container and covered by a detergent solution in water (0.2% wetting agent). The suspension was vigorously shaken for few minutes and after a 2 h hiatus it was agitated again. The leaves were individually washed under tap water and mites were collected using 90 and 32-μm sieves. The eriophyoids,

retained by the finest sieve, were stained using 1% Methylene-blue to allow differentiation between plant and animal material. Observation and mite counting were made directly on the sieves, after eliminating water by means of vacuum pump and absorbent paper.

Gabi and Mészáros (2001) developed a washing technique to estimate the population of *C. vitis* on grapevine leaves and buds which were cut up in small pieces and shaken in tap water for half an hour. Subsequently, the shaking solution was treated with Azur II eosin dye and the leaf suspension was sieved through a two-phase vacuum sieve. This filtering apparatus was composed of a plastic box with two sieves (tissue mesh size: 300 and 40 μm) fit to a vacuum-tube. Mites were counted at $50\times$ magnification on the sieving dish, which was divided into 35 visual fields.

Faraji et al. (2004) described a method and a device, a U-shaped Plexiglas$^{\circledR}$ mite-counting channel, for extracting and counting mites from leaf samples. This procedure was based on the adherence to liquid paraffin of mite cuticles, which are generally lipophilic (Krantz 1978). Fresh apple leaves were collected in 2-l plastic bottles filled three-quarters with tap water and 3 ml of detergent (cetaline^{TM}). Bottles were shaken three times for a few seconds each during a period of 1–2 h. The suspension was poured onto a 45 μm-meshed sieve. Mites and debris were washed with 70% ethanol and stored in centrifuge tubes. The sediment of the tube was poured into the mite-counting channel and ethanol was added to fill the channel. A few droplets of Methylene-blue (0.5 g powder solved in 50 ml 70% ethanol) were added to stain the ethanol and the solid material, but not the mites. After staining, liquid paraffin was then added to the channel, covering the entire surface of the ethanol. The mites became embedded at the ethanol/paraffin interface, and they were easily counted under a dissecting microscope, appearing whitish or brownish against the blue background. Several experiments were performed to validate this extraction method. The results demonstrated its accuracy, especially when applied to the smallest mites, such as eriophyoids. This procedure allows an easy and quick differentiation between mites and extraneous particles, like debris, often of a size similar to the mites, and it's cheap, rapid and convenient to apply. The only thing that could be problematic is obtaining a mite-counting channel. Moreover, the sieve size is differential in eriophyoid collection: in 45 μm-mesh sieves, most adults of larger species are caught, but the smaller species, mites at juvenile stages, and eggs often are lost. To avoid these undesired losses, Faraji et al. (2004) recommended the use of a finer 20–25 μm-mesh sieve.

Siriwardena et al. (2005) developed an accurate method to estimate the *A. guerreronis* population density on an infested coconut. Simple equipment, composed of a translucent silicone tube, a conical plain funnel and a Mohr's clip, was used to wash plant material and to collect eriophyoids. A solution of 8–10 drops of a detergent (Tween 80) in 250 ml of tap water was used to wash mites from coconuts. The bracts and the meristematic parts beneath the tepals were carefully washed in the funnel in numerous steps. After stirring, plant parts were removed, the clamp between funnel and tube was loosened, and the solution containing eriophyoids washed from plant material, was collected into a test tube. The suspension in the tube was shaken for a few seconds on a rotor-mixture. Counting of eriophyoids was made using a 1 ml aliquot of the washing solution collected from the bottom of the tube, then the total number of mites was proportionally calculated. The main advantages of this method are the simple and cheap equipment required, and the homogeneity of mite distribution in the wash solution immediately after shaking, which thus allows one to count just 1 ml of the wash solution per each extraction.

Monfreda et al. (2007) developed methods for routine detection, collection and extraction of eriophyoid mites and their eggs. Part of the described modified protocols and methods presented by de Lillo (2001) and de Lillo and Monfreda (2004) follow: mites were

washed from fresh or dried vegetal material using a water solution, followed by sieving and/or centrifugation, depending on the needs of the specific research. Infested vegetal material was covered with a washing solution (0.2% household detergent or Tween 80 and 1–2% bleach in tap water) in a large container. The resulting suspension was stirred and mites were collected using four ASTM-stainless-steel sieves (mesh size: 850, 180, 53, and 25 μm) and tap water. The sediments from each sieve were washed into a gridded Petri dish and a few droplets of detergent were added to the suspension to allow mites to sink to the bottom. Mites were counted under a dissecting microscope at 20–25× magnification.

Monfreda et al. (2007) also described procedures to concentrate mites and eggs for rearing and mass release. Eriophyoids were concentrated by pouring the suspension through a filter holder, attached to a water vacuum pump and provided with a nylon filter (mesh size: 20 μm). Eggs were separated from other mite stages by centrifugation, after adding kaolin powder and $MgSO_4$.

This procedure offers some improvements to the older methods and simplifies mite collection and detection. The authors compared the extraction technique with the direct counting of mites on infested grape vine leaves, and they stated the accuracy, efficiency and objectivity of the described method. Mite counting was not affected by plant debris because it was separated in the fraction containing larger mites (180 μm mesh size). Tap water, bleach and domestic detergent are highly effective for washing off mites, readily available and an economic alternative to ethanol or other chemicals. However, sieves and associated equipment such as filter holders and nylon filters are not cheap.

Finally, the main advantage of this extraction and concentration method is that the chemicals and the technique used did not affect either slide-mounting procedures or viability of mites: motile eriophyoids typically remained alive and active after collection. This procedure could be an efficient tool for taxonomical and biological studies, rearing, mass release, host specificity tests and biological assays.

Collection methods for molecular studies

Extracting DNA from eriophyoid mites has been a challenge due to their minute size. High quality DNA is essential for all types of molecular work. Eriophyoid mite researchers often face the problems of obtaining fresh mites for DNA extractions, the typical low quantity of extracted DNA which is often not suitable for amplification (Navia et al. 2005). In most cases, a large number of pooled specimens are used for extraction, ranging from 5 to 25 (Fenton et al. 1996, 2000; Navia et al. 2005) to as many as 50 specimens per extraction (Fenton et al. 1993, 1995). The potential for analyzing multiple species is a serious source of error. However, more recent population genetics studies are based on single mite extracts (Carew et al. 2004; Evans et al. 2008), which undoubtedly produces more accurate analyses. All these studies used either live mites or mites preserved in 95–100% ethanol kept at 4°C that were collected directly from plant material under a dissecting microscope, or by means of wash and sieve techniques, described above. Evans et al. (2008) stored freshly collected mites in dry conditions at −20°C until further use.

Previous studies and recent observations (Lekveishvili, unpublished data) on DNA performance in polymerase chain reactions suggest that several different methods of collecting and storing eriophyoid specimens can be effectively used for DNA extraction: (1) Fresh mites either hand picked under the dissecting microscope or collected by wash and sieve method can be directly used in DNA extraction; (2) Fresh mites killed in dry conditions by freezing and kept at −20°C until further use; (3) Fresh mites killed in 95% ethanol and stored at 4°C or −20°C; (4) Mites removed from stored, dry leaves: after

soaking in warm water, mites can be removed from dried leaves under the dissecting microscope. Specimens as old as 22 years were successfully amplified and sequenced (Lekveishvili, unpublished data). For methods 1–3, a single mite can be used for extraction. As for the mite specimens from dried leaves (method 4), an attempt to extract DNA from a single mite has not been made yet. All dry mite extractions were done on ca. 20–30 pooled mites using DNeasy Tissue Kit (QIAGEN Inc.) with some modification in method. While there were no difficulties with collecting mites from dried (and soaked) galls, picking up vagrant mites from the surface of leaves was more challenging and time consuming. Thus, in the case of vagrant species, using this method is only recommended for mites for which fresh or other types of preserved specimens are not available, and not as a routine method for DNA extraction.

Recent studies have allowed DNA extraction from single mites while preserving each exoskeleton for anatomical analysis and correlation (Dabert et al. 2008; Skoracka and Dabert 2009).

Concluding remarks

In the past two decades, eriophyoid detection has been the object of many studies, some of which are cited here, and which have appreciably improved our knowledge in this matter. Due to the importance of eriophyoids as crop pests, virus vectors and weed control agents, new and more efficient detection methods should be found.

Here are some critical aspects to consider in developing future techniques:

– The necessity to collect live specimens from infested plant material is a relevant aspect of the procedure when collected mites are used for colonizing plants (rearing, host specificity test), or biological assays, or need to be distinguished from dead ones to assess pesticide effects.
– Destructive methods of collection should be avoided, especially for plant organs with high economic value, like fruits or flowers.
– Molecular methods based on DNA sequencing, and serological ones based on recognition of pest's antigens by antibodies, offer great promise for quick eriophyoid identification for quarantine purposes. Developing immune enzyme assays and molecular methods for detection of eriophyoids will be very useful and possibly necessary for quarantine practices and other purposes such as resolving the separation of overlapping symptoms of eriophyoids with phytoplasma diseases.

References

Bernard MB, Horne PA, Hoffman AA (2005) Eriophyoid mite damage in *Vitis vinifera* (grapevine) in Australia: *Calepitrimerus vitis* and *Colomerus vitis* (Acari: Eriophyidae) as the common cause of the widespread 'Restricted Spring Growth' syndrome. Exp Appl Acarol 35:83–109
Brader B, Lee RC, Plarre R, Burkholder W, Kitto GB, Kao CA, Polston L, Dorneanu E, Szabo I, Mead B, Rouse B, Sullins D, Denning R (2002) A comparison of a screening methods for insect contamination in wheat. J Stored Prod Res 38:75–86

Carew M, Goodisman M, Hoffmann A (2004) Species status and population genetic structure of grapevine eriophyoid mites. Entomol Exp Appl 111:87–96

Chagas CM, Rossetti V, Colariccio A, Lovisolo O, Kitajima EW, Childers CC (2001) *Brevipalpus* mites (Acari: Tenuipalpoidae) as vectors of plant viruses. In: Halliday DE, Walter DE, Proctor H, Norton RA, Collof M (eds) Acarology: proceedings of the 10th international congress. CSIRO Publishing, Melbourne, pp 369–375

Dabert J, Ehrnsberger R, Dabert M (2008) *Glaucalges tytonis* sp. n. (Analgoidea, Xolalgidae) from the barn owl *Tyto alba* (Strigiformes, Tytonidae): compiling morphology with DNA barcode data for taxon descriptions in mites (Acari). Zootaxa 1719:41–52

David PMM, Varadarajan MK (2001) A new glycerine drop trap method to sample eriophyoid mites. Entomon 26(1):97–100

Davies JT, Williams MA, Allen GR (2002) A new method for sampling eriophyoid mites from architecturally complex plant structures. J Appl Entomol 126:303–305

de Lillo E (2001) A modified method for eriophyoid mite extraction (Acari, Eriophyoidea). Int J Acarol 27:67–70

de Lillo E, Monfreda R (2004) La saliva degli acari Eriophyoidea: messa a punto di un metodo di indagine e risultati preliminari. Atti del XIX Congresso Nazionale Italiano di Entomologia, Catania, pp 1367–1372

Duffner K (1999) Untersuchungen zur biologie, morphologie und bekämpfung der kräuselmilbe *Calepitrimerus vitis* Nalepa 1905 (Acari, Eriophyoidea). Faculty of Biology, Albert-Ludwigs University, Freiburg im Breigau, Germany, 162 pp

Duffner K, Schruft G (1998) Die klebebandmethode zur erfassung des wanderungsverhaltens von krauselmilben. Deutsches Weinbau-Jahrbuch 49:201–206

Duffner K, Schruft G, Guggenheim R (2001) Passive dispersal of the grape rust mite *Calepitrimerus vitis* Nalepa 1905 (Acari, Eriophyoidea) in vineyards. Anzeiger fr Schdlingskunde J Pest Sci 74:1–6

Evans LM, Allan GJ, Shuster SM, Woolbright SA, Whitham TG (2008) Tree hybridization and genotypic variation drive cryptic speciation of a specialist mite herbivore. Evolution 62–12:3027–3040

Faraji F, Bruin J, Bakker F (2004) A new method for mite extraction from leaf samples. Exp Appl Acarol 32:31–39

Fenton B, Malloch G, Brennan RM, Jones AT, Gordon SC, Amrine JW, McGavin WJ, Birch ANE (1993) Taxonomic evaluation of three reputed species of *Cecidophyopsis* mite on Ribes. Acta Hortic 352: 535–538

Fenton B, Malloch G, Jones AT, Amrine JW, Gordon SC, A'Hara S, McGavin WJ, Birch ANE (1995) Species identification of *Cecidophyopsis* mites (Acari: Eriophyidae) from different *Ribes* species and countries using molecular genetics. Mol Ecol 4:383–387

Fenton B, Jones AT, Malloch G, Thomas WP (1996) Malloch G and Thomas WP (1996) Molecular ecology of some *Cecidophyopsis* mites (Acari: Eriophyidae) on *Ribes* species and evidence for their natural cross colonisation of blackcurrant (*R. nigrum*). Ann Appl Biol 128:405–414

Fenton B, Malloch G, Moxey E (1997) Analysis of eriophyid mite rDNA Internal transcribed spacer sequences reveals multiple simple sequence repeats. Insect Mol Biol 6:23–32

Fenton B, Birch ANE, Lanham PG, Brennan RM (2000) Gall mite molecular phylogeny and its relationship to the evolution of plant host specificity. Exp Appl Acarol 24:831–861

Flechtmann CHV (2007) Eriophyoid mites and quarantine. In: Morales-Malacara JB, Behan-Pelletier V, Ueckermann E, Perez TM, Estrada-Venegas EG, and Badii M (Eds.) Acarology XI: proceedings of the international congress. Mexico, pp 291–292

Gabi G, Mészáros Z (2001) New data to the knowledge of *Calepitrimerus vitis* Nalepa in the vine-growing region of Szekszárd, Hungary (Acari: Eriophyidae). Acta Phytopathol Entomol Hungarica 36(1–2):193–200

Harvey TL, Martin TJ (1988) Sticky tape method to measure cultivar effect on wheat curl mite populations in wheat spikes. J Econ Entomol 81:731–734

Krantz GW (1978) A manual of acarology. Oregon State University Book Stores, Inc., Corvallis, 509 pp

Krizkova-Kudlikova I, Hubert J (2007) The application of immunochemical methods in detection and traceability of arthropod contaminants in stored food. Bulletin-OILB/SROP 30(2):117–126

Kumar L, Fenton B, Jones AT (1999) Identification of *Cecidophyopsis* mites (Acari: Eriophyidae) based on variable simple sequence repeats of ribosomal DNA internal transcribed spacer-1 sequences via multiplex PCR. Insect Mol Biol 8:347–357

Lindquist EE, Sabelis MW, and Bruin J (1996) Eriophyoid mites their biology, natural enemies and control. Elsevier. World Crop Pests 6, 790 pp

Monfreda R, Nuzzaci G, de Lillo E (2007) Detection, extraction, and collection of eriophyoid mites. Zootaza 1662:35–43

281

Monfreda R, Krizkova-Kudlikova I, Petanovic R, and Amrine JW Jr (2008) Consideration on eriophyoid detection. In: M Bertrand S Kreiter KD McCoy A Migeon M Navajas MS Tixier L Vial (Eds.) Integrative Acarology—Proceedings 6th European Congress. European Association of Acarolgists, pp 291–295

Navia D, de Moraes GJ, Roderick G, Navajas M (2005) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyidae): origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. B Entomol Res 95:505–516

Oldfield GN, Proeseler G (1996) Eriophyoid mites as vector of plant pathogens. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites–their biology, natural enemies and control. Elsevier, Amsterdam, pp 259–274

Pérez-Moreno I, Moraza Zorrilla ML (1998) Population dynamics and hibernation shelters of *Calepitrimerus vitis* in the vineyards of Rioja, Spain, with a description of a new eriophyoid extraction technique (Acari, Eriophyidae). Exp Appl Acarol 22:215–226

Perring TM, Farrar CA, Oldfield GN (1996) Techniques. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites–their biology, natural enemies and control. Elsevier, Amsterdam, pp 367–376

Phillips TW and Zhao B (2003) Molecular diagnostic tools for detecting arthropod contamination in stored products. Advanced in stored product protection, Proceeding of the 8th International Working Conference on Stored Product Protection, York, pp 128–130

Rosenthal SS (1996) *Aceria, Epitrimerus* and *Aculus* species and biological control of weeds. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam

Rotundo G, Germinara GS, De Cristofaro A (2000) Immuno-osmophoretic technique for detecting *Sitophilus granarius* (L.) infestations in wheat. J Stored Prod Res 36:153–160

Schulz JT (1963) *Tetranychus telarius* (L.) new vector of virus Y. Plant Dis Rept 47:594–596

Siriwardena PHAP, Fernando LCP, Peiris TSG (2005) A new method to estimate the population size of coconut mite, *Aceria guerreronis*, on a coconut. Exp Appl Acarol 37:123–129

Skoracka A, Dabert M (2009) The cereal rust mite *Abacarus hystrix* (Acari: Eriophyoidea) is a complex of species: evidence from mitochondrial and nuclear DNA sequences. Bull Entomol Res 1–10. doi: 10.1017/S0007485309990216

Walton W, Dreves AJ, Gent DH, James DG, Martin RR, Chambers U, Skinkis PA (2007) Relationship between Rust Mites C*alepitrimerus vitis* (Nalepa), Bud Mites *Colomerus vitis* (Pagenstecher) (Acari: Eriophyidae) and Short Shoot Syndrome in Oregon vineyards. Internat J Acarol 33(4):307–318

Zacharda M, Pulsar O, Muška J (1988) Washing technique for monitoring mites in apple orchards. Exp Appl Acarol 5:181–183

Zhao S, Amrine JW (1997) A new method for studying aerial dispersal behavior of eriophyoids (Acari: Eriophyoidea). Syst Appl Acarol 2:107–210

Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata)

E. de Lillo · C. Craemer · J. W. Amrine Jr. · G. Nuzzaci

Abstract Methods used for sample storage, specimen clearing, slide mounting, species illustration and morphometric description in alpha-taxonomic studies are essential for the Eriophyoidea. Eriophyoid mites are very tiny and delicate, for which truly permanent specimen slides currently cannot be prepared, resulting in eventual loss of material, including type specimens. Often, published descriptions and drawings have not achieved the required level of quality, and thus many relevant taxonomic details have been permanently lost or neglected. These shortcomings can make certain identifications impossible and cause significant confusion. Consequently, there is a considerable need for accurate and uniform descriptive and illustrative data for the Eriophyoidea. Based on their expertise on this topic, the authors provide guidelines and advices, assisted also by illustrations, of the main critical aspects in managing eriophyoid mites in order to supplement and improve techniques for handling and preparation of specimens, and for improving their taxonomic study. The effects of the short- and long-term preservation methods (i.e., fresh, dried and liquid preservative choices) on digesting the internal tissues of the mites are discussed. Clearing and mounting procedures are analyzed, and special tips are suggested for handling mites and designing tools needed during these steps. Methods for recovering specimens from unsuitable slides (i.e., undercleared and overcleared specimens) are proposed and described. Techniques and tricks to produce descriptive line drawings of good

E. de Lillo (✉) · G. Nuzzaci
Dipartimento di Biologia e Chimica Agro-forestale e Ambientale, Facoltà di Agraria,
Università degli Studi di Bari, via Amendola, 165/a, 70126 Bari, Italy
e-mail: delillo@agr.uniba.it

G. Nuzzaci
e-mail: nuzzaci@agr.uniba.it

C. Craemer
ARC-Plant Protection Research Institute, Private Bag X134, Pretoria Queenswood 0121, South Africa
e-mail: CraemerC@arc.agric.za

J. W. Amrine Jr.
Division Plant and Soil Sciences, College of Agriculture and Forestry, West Virginia University,
P.O. Box 6108, Morgantown, WV 26506, USA
e-mail: jamrine@wvu.edu

quality are highlighted, and the content to include in plates is stressed. Finally, detailed instructions for standardization of measurements are given.

Introduction

As for other mites, eriophyoid systematics depends on the quality of studied specimens and morphological description. Conversely, the microscopic size and ultra fine structural details of these tiny and fragile mites make their morphological study more difficult. Furthermore, the accuracy and correctness of descriptions and associated drawings depend on the methods used in processing, mounting and studying the mites.

Several comprehensive accounts (e.g., Nalepa 1906; Hassan 1928; Keifer 1952, 1975; Amrine and Manson 1996) are available on methods for sample preservation and storage, specimen clearing and mounting, drawing, descriptive arrangements and other activities related to taxonomic/systematic investigations/publications. Hassan (1928) extensively described preservation and mounting methods, eventually mounting mites in Canada balsam (miscible with 100% xylene) or euparal (miscible with 95% ethanol). Hassan's material has not been found by the authors, so it is unknown how long such specimens can remain in useable conditions. Amrine mounted mites, including eriophyoids, in both Euparol® and balsam (Permount®) media. In all cases, the mites were slowly dehydrated through a graded series of ethanol solutions (passing at 5% ethanol intervals usually from 60 to 100%) for Euparol®, or they were transferred from 100% ethanol to xylene for Permount®. Despite careful processing, mounted specimens were always badly crumpled and deformed and no useful descriptions could be made.

Keifer experimented with several methods and chemicals for clearing and mounting, and set an excellent standard for making illustrations and taxonomic descriptions of eriophyoids during his career ranging from 1938 to 1991 (see Baker et al. 1996, for a compendium of Keifer's descriptions of species from the USA, including drawings not published before). However, even in 1975, he commented about the general lack of standards for describing eriophyoids. His particular style and high standards for accuracy is conveyed in his reply (Fig. 1) to Nuzzaci who, novice eriophyoidologist, had sent him microscope slides, a draft description and line drawings of a new eriophyoid mite for his assessment and advice. Since Keifer's publications, the major contributions to the interpretation of the external morphology of eriophyoid mites were by Lindquist (1996). Besides, Amrine and Manson (1996) gave a further contribution on the preparation, mounting and descriptive methods of study of these mites; their main intent was to strongly urge "authors to achieve greater uniformity in presenting descriptive, illustrative and biological data" and this seems to have been partially accomplished in the past decade.

However, today many descriptions and drawings still often do not achieve the required standard and quality, even as set by Keifer, and many relevant taxonomic details may be permanently lost or obscured as a result. These shortcomings can lead to incorrect classification, sometimes making certain identifications impossible, or misinterpretation (for example, the prodorsal shield, scapular setae *sc* and coxal setae *1b* and *1a* of *Ashieldophyes* were not clearly described in Mohanasundaram 1984) which can cause considerable confusion. These inadequacies cannot be justified considering the quality of the

```
                                        1112 Swanston Drive
                                        Sacramento, Cal. 95818
                                        July 31, 1973
Giorgio Nuzzaci
Instituto di Enotmologia Agraria
Universita Degli Studi
Via Amendola, 165/A
70126 Bari, Italy

 However, I take most direct exception with the correctness and adequacy of
your drawings. Admittedly all drawings of these mites are but diagrams, but
one must ask - how clearly do the delineations show the precise features of
the species in question? Are the diagrams bare, or do they convey specificity?
 Drawings of these mites are in no sense art. But they must be done with
precise recognition of line direction, of relative size of the parts, and
they must also include angles and points, when they are present. To do a
good job on such depictions takes practice and study.

 You have done the usual thing in regard to drawings - produced rather bare
diagrams. We have too many of such being continually published. If I can
get you to rise above bare delineations or diagrams, and show specific
features of these mites I will have accomplished something worthwhile.
 Dr. Nuzzaci, what I'm trying to do is get you started correctly. All of this
takes practice and study. Actually the study of eriophyids is a full time
job, and if you dilute your time with publications on other mites your efforts
on eriophyids will more or less suffer.
                                    Sincerely           H. H. Keifer
```

Fig. 1 Letter by Keifer commenting on slides, description and descriptive drawings of a new species by Nuzzaci

microscopes and cameras available today. Moreover, a method universally accepted and used for preparing and mounting mites is not available and those methods commonly applied fail to give permanent slides.

Appropriately, Lindquist (2001) emphasized the importance of optimizing the quality of description of mites, including Eriophyoidea. Therefore, standardized descriptions are always imperative and must be continuously promoted, especially in view of the current high rate of description of new eriophyoid genera and species (de Lillo and Skoracka 2009), and also because the best slide mounted specimens rarely last very long and frequently become opaque or precipitated, or too transparent for study (Amrine and Manson 1996). Keifer's slide collection at the US National Museum of Natural History, in Beltsville, Maryland, USA, is a sad example of these shortcomings (Fig. 2). In addition, it should be emphasized that proper interpretation of morphological details certainly support systematic studies, but they are also required for many non-systematic investigations including plant-mite relationships and pest control, identification for quarantine purposes, vectored pathogens, and biological control of weeds.

The present paper provides guidelines and recommendations for techniques that researchers should employ when preparing, studying and describing eriophyoids that supplement techniques previously presented in other articles (e.g., Keifer 1975; Amrine and Manson 1996).

Preservation

Temporary preservation

When working with fresh, mite-infested plant samples, the researcher needs to prevent damage caused by desiccation or fungal degradation.

Fig. 2 Slides in the original eriophyoid collection of Keifer at the US National Museum of Natural History, Beltsville, Maryland, USA. Many slides cannot be used any more because they appear to be completely dark or the mounting medium is dried out

Fresh samples should be brought to the laboratory as soon as possible. They should not be exposed to heat and, therefore, they should be contained in plastic bags and stored in a cooler. Similarly, fresh plant material shipped by courier should be kept cold in a thermally insulated package with a frozen fluid pack or dry ice pack during extended shipment. Mites on plant samples not properly packed and shipped in luggage usually do not survive high altitude aircraft flights or ground transport because of excessive low or high temperatures during transport. Live mites can be extracted from plant samples using a washing solution (Monfreda et al. 2007) and can be stored in water containing a few drops of a commercial surfactant (household detergent or polisorbate as Tween®). Eriophyoids preserved in this manner were able to survive the shipment and stayed alive for 3–4 weeks in a refrigerator at about 4°C. Finally, live mites were successfully collected directly in the field by washing bunches of grapes without cutting them from the plant (de Lillo et al. 2005).

When fresh plant samples with live mites are returned to the laboratory, the mites must be processed within a short time after field collecting. In order to keep the material fresh, the sample can be wrapped in damp (not wet) paper towel, or other paper-like material, then sealed in a plastic bag, preventing it from drying out, and stored in a cold place (e.g., a refrigerator, climate controlled room or cabinet) without freezing the material. Fine holes can be punched in the plastic bag to reduce humidity if necessary (S. Ozman-Sullivan, pers. comm.). Depending on the type of sample and its quality, live mites can still be collected from the plant samples even after a month's, or as in the case of filbert big bud mites (*Phytoptus avellanae* Nalepa), 2 months' storage (S. Ozman-Sullivan, pers. comm.).

Permanent preservation as dried samples

In addition to slide mounted specimens, there is a requirement for additional long term preservation of mite-infested plant material or of mites themselves. Permanent preservation

may be necessary because mite specimens cannot always be processed and slide mounted before being stored or accessed in a collection (also see Keifer 1975), and additional material can be used when slide mounted specimens deteriorate or become totally destroyed, or are lost.

For practical convenience, mainly related to sample transportation, handling and storage, mite samples are often permanently preserved and managed as dried (mummified) specimens on leaves and other plant organs. Particular care must be taken on how the plant sample is dried out. In case of improper desiccation, the mite body may be destroyed or nearly completely invaded by fungi (Fig. 3). As a consequence, morphological details can be obscured, making mite identification frequently difficult or impossible. Therefore, plant samples should be dried out as soon as possible after field collecting and prepared as herbarium specimens for sending to specialists for mite identification or for deposition in a dry specimen collection (i.e., a zoo-cecidotheca). Dehydration of plant material should be carried out applying all possible techniques to prevent fungal infection of the mites (e.g., use of desiccating papers, frequent paper change, sample pressing between absorbent pads, slight warming in sunlight or in an oven). The properly dried samples should afterwards be enclosed in an envelope (letter envelope, transparent paper envelope, transparent plastic specimen bag, etc.) and labeled with all relevant data. A repellent or a deterrent compound (PDB, thymol, etc.) or other protective methods should be applied for preventing museum beetle attacks and deterioration over time. Trotter and Cecconi, authors of the *Cecidotheca Italica* (Fig. 4), were familiar with this method (Trotter 1904) and their dried specimens are still well suited for the identification of species after about one century, as demonstrated by Boczek and Nuzzaci (1988), and Petanović et al. (1993).

Well dried and properly preserved specimens, similarly to freshly collected mites, need usually only a few minutes in a mounting or clearing medium on a hot plate in order to become perfectly cleared and to return to their original shape and size.
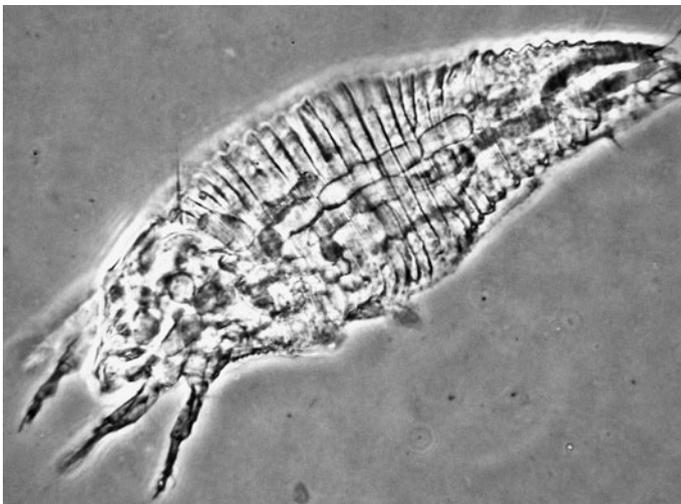
Fig. 3 A *Metaculus* specimen completely invaded by fungi obscuring its morphological details
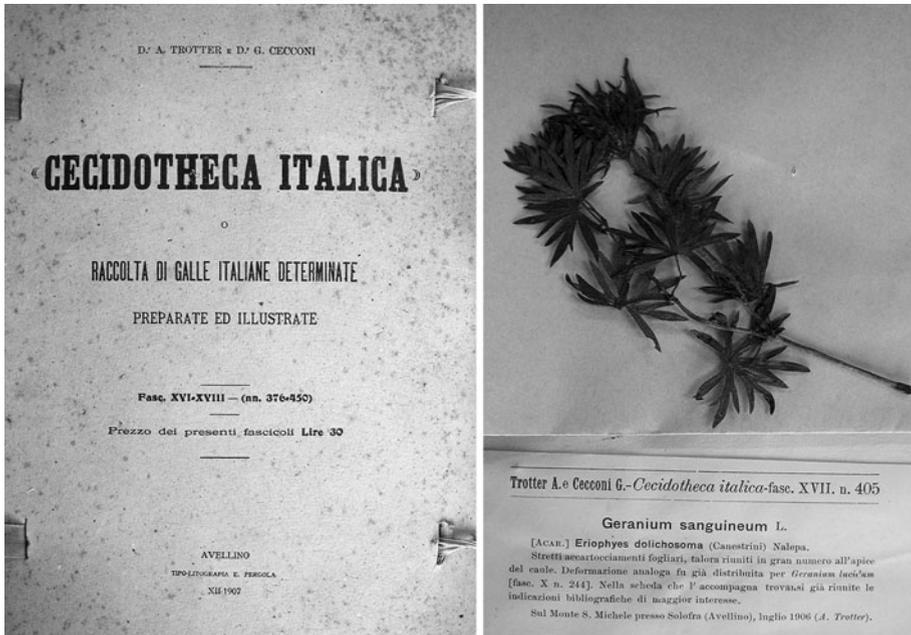
Fig. 4 *Cecidotheca Italica*: front page of a publication by Trotter and Cecconi (1902) (on the *left*); original sample of *Geranium sanguineum* L. from which specimens of *Aceria dolichosoma* (Canestrini) were slide mounted and re-described by Petanović et al. (1993) (on the *right*)

Permanent preservation in liquid preservatives

In contrast with the general good and relatively quick results of clearing fresh and dried specimens, the digestion of non-cuticular structures of specimens preserved and fixed for years in alcoholic solutions (60–70% ethanol in water) requires much more time. This difficulty increases proportionally with length of preservation, and the results are often poor or insufficient for an exhaustive and reliable identification and description (Keifer 1975). Moreover, the alcoholic solutions tend to evaporate, and specimens usually become completely dried out (Fig. 5). Amrine needed to prepare a few specimens of the genus *Phytoptochetus* from a sample preserved in a vial, originally containing ethanol, for about 70 years and belonging to Nalepa's collections (Amrine and Manson 1996; Amrine et al. 2003). A few specimens were found after careful examination of a yellow powder; clearing took a period of 2 months and needed particularly careful and extensive processing. Specimens were heated at about 90°C in a few drops of Keifer's booster (Amrine and Manson 1996) for a few days. Then they were washed in water and transferred to a few drops of lactic acid, heated for a few days, washed in water once more, and hereafter transferred back to Keifer's booster again. This entire procedure was repeated many times. Eventually a collection of suitable mite fragments were found to correctly illustrate the shield, the coxi-genital region, the legs and the opisthosoma to make adequate drawings to define the essential characteristics of *Phytoptochetus*. On the contrary, notwithstanding similar attempts, the re-description of *Aceria sonchi* (Nalepa) from original powder remnants of dried ethanol preserved material was not possible (D. Knihinicki, pers. comm.).

Fig. 5 Original vials from Nalepa's collection containing ethanol preserved *Galium cruciata* (L.) Scop. and associated mites

Usually, the addition of glycerol to the preservatives (as in AGA and Oudeman's solution) makes the tissues softer and less rigidly fixed, allowing them to be more susceptible to the clearing agents. Glycerol also prevents the specimens from completely drying out, as usually happens when other solvents evaporate over time.

In addition, Keifer (1975) found that a mixture of thin sorbitol syrup in a 25% solution of isopropyl alcohol kept the eriophyoids well preserved and suitable for slide preparation. Craemer commonly uses this fluid, composed by 25% solution of propan-2-ol in water to D-sorbitol powder (e.g., add about 4 ml propan-2-ol diluted with 12 ml water to 30 g D-sorbitol powder) until forming a thin syrup with the consistency of heated honey, at most. When the liquid is added to the powder, the mixture is milky white and after a few hours it dissolves properly, becoming clear and slightly thick. At warm and humid environmental conditions, a very small amount of potassium iodide and an iodine crystal should be added to the mixture to prevent mould growth. The mixture should be kept in a sealed and well closed container, because it quickly becomes too thick and crystallizes when exposed to air. Mites are very easily transferred to and from a small amount of this "sorbitol fluid". S. Neser (pers. comm.) uses a novel way to collect and transport mites in this fluid also facilitating easy recovery. A small droplet of this solution is placed inside the lid of a polypropylene micro centrifuge tube (Fig. 6). About 100 specimens can easily be collected in this droplet, and when the vessel is closed, it can be safely transported and mailed. The droplet becomes very sticky, dries out over time and it can be re-hydrated by breathing over it. Otherwise, the entire droplet, even when crystallized, can be added to the clearing medium and processed as normal. The suitability of the mites to be slide mounted over extended periods of preservation in sorbitol has not been tested yet, but the mites are well suited if mounted within a few months.

Alternatively and for populations of a few dozen to a few hundred specimens, eriophyoids can also be kept on work slides (Amrine and Manson 1996). Unfortunately, high

Fig. 6 A small droplet of "sorbitol fluid" into which eriophyoid specimens can be collected (*arrow*), positioned in the side corner of the lid of a 1.5 ml micro centrifuge tube
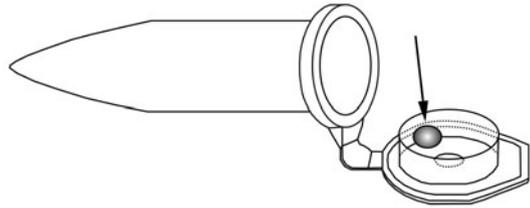
environmental humidity and temperature can reduce the quality of the specimen preservation on these work slides.

Finally, specimens can be preserved in ATL buffer (a buffer containing edetic acid and sodium dodecyl sulphate) stored in a refrigerator some time before DNA isolation according to Dabert et al. (2008). After the DNA extractions, the mite exoskeleton can be mounted and its morphology can be efficiently studied (Skoracka and Dabert 2009).

Handling eriophyoids and tools

Mites are usually found on plant samples with the aid of a stereo dissecting microscope, and can be picked up using pin-like or other tools, even if the plant material is deformed. The moistening of the tip of the tool with water or other media can enhance the ease with which the mites are picked up. When mites are rare on the plant sample or the plant organs are severely modified and architecturally intricate, especially when dried, finding and collecting eriophyoids can become time-consuming and inefficient. Then, collecting can be greatly improved by concentrating the mites (Monfreda et al. 2009). In the case of dried material, mites can be easily recovered as described by Amrine and Manson (1996), or by soaking part of the sample overnight in a water solution with a few drops of a surfactant and bleach at room temperature (Monfreda et al. 2009). Hereafter the suspension is stirred and sieved: the specimens can be more easily detected, because of their restored shape, and picked up from a filter paper or from a filtered sediment (through a 20–25 μm sieve) poured into a Petri dish using water plus a small amount of a surfactant (Monfreda et al. 2007).

Commercially available laboratory needles are usually too thick and robust to be used in picking up, transferring and generally handling eriophyoid mites. Several types of apparatus can be specifically made for this purpose, and each laboratory usually has its own design. Some of these tools are mentioned in the materials and methods of many articles concerning Eriophyoidea. They include an eyelash, or several kinds of fine needles or pins, attached to or stuck into some sort of pen-like rod or wooden dowel in different ways (Fig. 7; Keifer 1975; Amrine and Manson 1996).

Insect mounting pins are suitable for constructing an eriophyoid handling tool. These come in different sizes and materials and stainless steel is recommended. Keifer (1975) proposed a size 00 insect pin for "needling" mites from solution to solution and slide to slide. A pair of size 3 insect pins in wooden dowels is useful for dissecting galls and unrolling leaf margins. These needles can be sharpened as needed on Arkansas soap-stones or other fine grindstones. They are commonly used for mounting delicate insect specimens such as microlepidoptera and small flies. Stainless steel micro-pins, known as Austerlitz® minutens or minuten pins, headless, 0.1 mm in diameter and about 12 mm long, with one sharpened end, can be particularly recommended. They do not chemically react with the preserving, clearing, and mounting media, and they can be manipulated to suit a
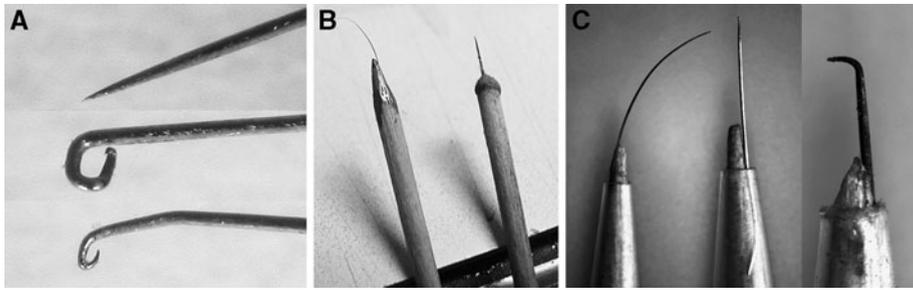
Fig. 7 Handling tools for eriophyoid mites: **A** details of variously shaped micropins; **B** details of an eyelash held in place with nail polish (on the *left*) and short minuten pin held in place with epoxy (on the *right*); **C** eyebrow hair (on the *left*), micropin (on the *center*) and bent pin (on the *right*) inserted into the narrow end of a micropipette and held in place by inserting a toothpick from the other end

researcher's needs, and their physical properties allow them to be dipped into reagents without being altered. These needle probes should be personally prepared by each researcher for making specimen handling comfortable and convenient. They can be mounted on wood or plastic handles. In particular, exhausted fine- or medium-tip markers can be re-cycled, and the blunt end of the micro-pin can be inserted into their felt-tip and fixed to it by a drop of a cyanoacrylic glue which hardens the felt. If preferred or needed, the sharp end of the pin can be curved or bent into a loop for producing a sort of spoon (Fig. 7A), using tweezers or micropliers under a dissecting microscope. Pointed and looped pins are suitable for transferring individuals without injuring or damaging them.

Disposable plastic micropipette tips (1 ml or c. 60 mm long × 8 mm diameter) can also be used for making a variety of handling tools (S. Neser, pers. comm.). A firm, pointed short hair (e.g., from an eyebrow), or micro-pins as above can be inserted into the narrow end and held in place by inserting a toothpick, or other probes of appropriate length from the other end (Fig. 7C). Alternatively root canal files (size 30, c. 0.3 mm in diameter, or thinner) as discarded by dentists, or available from dentist tool suppliers, may be inserted into holders as above.

Comprehensive information on equipment (hot plates, coverslips, plain and cavity slides, tweezers, etc.) and other useful facilities and supplies can be found in Keifer (1975), and Amrine and Manson (1996).

Clearing

An historical review of this aspect is in Keifer (1975), and in Amrine and Manson (1996) in which they underlined the difficulties in preparing adequately cleared specimens on slides.

Currently, many researchers have developed and improved a preferred medium on the basis of the personal experience and convenience, sometimes changing method over time. Eriophyoidologists have been applying the following media with satisfactory results: Heinze's medium (A. Skoracka, S.-G. Wei, pers. comm.), F-medium with Booster medium plus phenol according to Keifer (1975) (C. Craemer, P. Natchev, S. Ozman-Sullivan, pers. comm.), lactic acid (M. Lewandowski, P. Natcheff, R. Petanovic, C.-Q. Wang, pers. comm.), modified Berlese's medium (J.W. Amrine Jr., A. Chandrapatya, pers. comm.),

modified Keifer's Booster solution including water saturated phenol (E. de Lillo, E. Denizhan, R. Monfreda, G. Nuzzaci, pers. comm.), Nesbitt's medium (C.-Q. Wang, pers. comm.), and a stained mixture of Nesbitt's medium with lactophenol (Faraji and Bakker 2008). The applied clearing procedure should always be reported in publications.

A modified Berlese's medium was described by Amrine and Manson (1996). To about 15 ml of freshly made medium, 10–20 drops of glacial acetic acid, ca 100 mg of metallic iodine crystals and 100 mg of potassium iodide powder are added. This medium is placed on a hot plate at 90°C for about 30 min to dissolve the metallic iodine (or left from overnight to 48 h at room temperature). Iodine, included also in Keifer's medium, stains the fine sculptured details of the cuticle, the microtubercles and other cuticular structures, especially the internal apodemes and genitalia (Keifer 1975). Consequently, the brown color often enhances the contrast of fine or delicate features.

A further improvement of the image quality can be offered by digital cameras on microscopes. They can be adjusted to correct the 'white balance' or intensity and contrast adjustments to obtain excellent micrographs, even though the specimen may appear too dark or too pale at first glance.

When the medium used for digesting the mite internal tissue serves also for mounting (e.g., Heinze's medium), most eriophyoids can be placed directly into a small, shallow drop of medium on the slide. Live mites will right themselves and orient in proper position as they attempt to crawl in the thin film to leave the medium; this will not happen if they are immersed or are previously killed. Their orientation can be adjusted by stroking with the sharp tip of a micropin; the opisthosoma can be stroked several times to "right" a lateral mite into dorso-ventral orientation. In some cases, the uncovered slide with adjusted mites can be put on the hot plate margin for a few moments to thicken the medium and hold specimens in proper position. A small drop of the final medium can be added to a clean coverslip. A drop of glacial acetic acid can be added to this drop (e.g., modified Berlese's medium) which is stirred on the coverslip. Then, the coverslip is placed over the uncovered mounted specimen, using the tips of the forceps to guide specimen orientation and position as the coverslip settles. This step allows more rapid spread of the medium (eliminating air bubbles), keeps the orientation of the mites, and aids more rapid and complete clearing of the mites. The fresh slide is then placed on the edge of a hot plate at about 80–90°C to clear within about 30 min. Most live mites can be prepared in this way to make excellent slides in about 1 h. The boiling of the slide must be avoided because it moves the mites from the center to the margin of the coverslip where they cannot be studied.

In case the medium used for clearing is different from that used for mounting, (e.g., mounting in F-medium, after clearing with Keifer's booster medium with added phenol) cavity slides can be used for the clearing process. Mites can be placed directly into a drop of clearing medium and the slide can be heated until the mites are cleared. The mixture must not boil or become too viscous or hard. When the mite body is sufficiently cleared, drops of water or fresh medium can be added to the mixture to make it fluid enough for further passages. Then, mites are transferred to the mounting medium by means of micropins and a coverslip is added.

A few modifications to clearing procedures are used by eriophyoidologists: live mites are cleared, or alternatively are killed in a preserving solution before clearing; mites are cleared at room temperature taking a long time (days or weeks); mites in the clearing medium are heated carefully over an open alcohol flame, or they are kept in an oven or on a hot plate set at 40–60°C.

Overheating and overclearing can easily occur and are the major sources of error. If the covered slide is placed on a spot of the hot plate that is too hot for too long (about 1 h or more), numerous small air bubbles can develop and cannot be removed. These can often obliterate fine details needed for descriptions or photographs. Using new infrared thermometers, the researcher can carefully map the temperatures on a hot plate and know exactly where to place the slide(s) for best results.

For species difficult to clear using this technique, slides can be left in a cooler portion of the hot plate at about 70°C overnight or for 24–48 h. If your hot plate is too hot at the lowest setting, a thick thermal glass can be placed on the plate and will drop the surface temperatures for several degrees. Alternatively, the temperature of the hot plate can also be regulated by means of a rheostat between the receptacle and the hot plate (be sure to match wattage of the rheostat to that of the hot plate).

These methods are tedious, but they allow a researcher to routinely make excellent slides from which type specimens can be selected. This part of specimen preparation represents 90% of quality control for professional preparation of eriophyoid specimens, and a successful method needs to be learnt well. Amrine and de Lillo have prepared slides using the above methods as early as 1987, and these slides are still well suited for microscopic studies.

Mounting

For the final mounting, eriophyoidologists have also been applying different water based mixtures such as Heinze's medium (R. Petanovic, A. Skoracka, C.-Q. Wang, S.-G. Wei, pers. comm.), F-medium according to Keifer (1975) (C. Craemer, E. de Lillo, E. Denizhan, R. Monfreda, P. Natchev, G. Nuzzaci, R. Petanovic, S. Ozman-Sullivan, pers. comm.), modified Berlese's medium (J. W. Amrine Jr., A. Chandrapatya, M. Lewandowski, A. Skoracka, pers. comm.), and a stained Hoyer's medium (Faraji and Bakker 2008). The applied mounting procedure should always be reported in publications.

Most researchers add more or less mounting medium to alter the amount of pressure of the coverslip on the specimens. A few short fibers can be also mounted underneath at the borders of the coverslip to support it above the mite specimens, according to Keifer (1975). The diameter of the fibers can be chosen according to the thickness and width of the specimens to be mounted. Following Keifer's advice, de Lillo and Nuzzaci have selected three different fibers with different thicknesses cut into short lengths: fiberglass (about 10 μm in diameter), kapok (about 20 μm in diameter) and "wool" used for aquariums (about 40 μm in diameter). The main aim in using these fibers is to avoid excessive specimen flattening (Keifer 1975) which can alter feature proportions and the general shape of the mite. For example, ridges and furrows on the dorsal side of the opisthosoma, especially when they are slight, can be often "lost" during examination of flattened specimens. Moreover, the addition of fibers allows the coverslip to be moved more easily on the slide face by pushing one side of the coverslip with a pin or tweezers; of course, the coverslip must not be sealed and the medium must be fluid. In this way the mite can be rolled around its longitudinal axis, allowing observations and descriptions of a species from a single holotype specimen (Amrine and Manson 1996). However, even when fibers have not been added under the coverslip, if the mounting medium is still fluid and the slide has not been sealed yet, the coverslip can be moved changing the mite position, as reported by Nalepa (1906).

It is more difficult, and sometimes impossible, however, to study (draw and photograph) fine details (e.g., prodorsal shield features, female internal genitalia and the ray arrangement of particularly fine empodia presenting intricate details) on specimens that have not been flattened to some extent. It is probably most advisable to mount some specimens without and others with fibers. This will not always be feasible, depending on the specimens and time available. If important, and of consequence, it should also be mentioned in the description which method was used to obtain the particular morphological aspects described, because these can differ considerably, as in the example of the dorsal shield patterns in *Aceria angustifoliae* (Denizhan et al. 2008). It may even be arguable which method will render the best results for identification and comparative purposes. Both methods are difficult to standardize, and likely will vary depending on the mounting medium and amount used, the degree of clearing, and the skill of the worker.

Information on labeling and sealing methods is in Amrine and Manson (1996).

Overcleared slides

In the case of overcleared specimens, slide sealing can be carefully removed by a large pin, scalpel, razor or by other means. Then the coverslip can be loosened using water and heat on a hotplate, and excess water removed. A drop of medium containing iodine stain (preferably using the same medium originally used to prepare the slide) can be placed to one side of the coverslip. An absorbent paper can be held against the other side of the coverslip while the slide is heated to boiling very briefly. In this way, the iodine stained medium is drawn over the mites and fills the coverslip, while the excess medium is removed by blotting. As result, the freshly stained mites can be observed, drawn and photographed. This may not work with very old slides, difficult media such as polyvinyl alcohol, or overly faded specimens; but if the slide is not usable, this technique is worth a try.

Dismounting specimens from slides

Slides can be dismounted when specimens are undercleared or overcleared, or are at the coverslip edges, or when the researcher might need to view a different aspect of a mite, or would apply a different microscopic technique, as Nuzzaci and de Lillo did for the study by scanning electron microscopy of *Aceria caulobia* (Nalepa) and *P. avellanae* (Nuzzaci et al. 1991).

After removing the slide sealant, the water-based media can be made less viscous by addition of water and/or heating, such as in the procedures previously described, or by leaving the slide under a high humidity glass dome for a few hours at room temperature. These media are hygroscopic, absorbing water from the air at the coverslip margin and eventually becoming quite fluid, allowing the coverslip to slide freely, so that it can be propped up by insertion of a small pin from one side so that it can be lifted and removed with a forceps.

Line drawings

Adequately descriptive line drawings of good quality are not easy to produce and appear to be one of the weak points in eriophyoid systematics. The importance of this part of a

description was highlighted by Keifer (1975) and Amrine and Manson (1996), but even stronger emphasis should be made.

Slide mounted eriophyoid specimens, including type material, usually deteriorate over time, and are eventually not adequate for study, and may ultimately be totally destroyed. This deterioration can be caused by several factors, including: the water-based mounting media which may dry out rather quickly, air may penetrate under the coverslip, and, under certain conditions, specimens may continue to be cleared by the chemicals in the mounting medium, and fade away. Other representations of the original type series, including digital images of slide mounted specimens and electron microscope images, should also be archived in addition to slide mounted specimens and they have a support value, as previously mentioned by Amrine and Manson (1996). In the absence of type material, however, the original description and, particularly the drawings, become critically important, usually being the only representation of the described species. In many cases, drawings presented in the original description become the nearest equivalent of a holotype.

Moreover, drawings are rather clearly understood by everyone, and they are useful for a primary comparison whatever language is utilized, and regardless of the interpretation of characters in the text description. Certainly, line drawings in the style of Keifer (Fig. 8) are permanent and universally understandable. They are the core of each description and must be the best basic representation of an eriophyoid species (Keifer 1975; Amrine and Manson 1996).

The adequacy and value of drawing depends largely on the skill and experience of the researcher and on the quality of the slide mounted specimens.

Edward Baker and Richard Newkirk (pers. comm.) observed Keifer working and both related that the researcher made his final drawings directly using a drawing tube (=camera lucida) device with extraordinary care and accuracy. In some cases, Keifer drew freehand from the eyepiece using no drawing aids. But Keifer's talent was certainly unique!

Because of the minute size of these mites and their features, when studying, drawing and describing them, the researcher should always use a good-quality, phase contrast light microscope equipped with an oil immersion $100\times$ objective at a large numerical aperture (one of the best is a fluorite objective with 1.30 numerical aperture or higher), and a drawing tube. A zoom lens on the microscope or drawing tube is very helpful. A $2\times$ objective can additionally be mounted on some drawing tubes to allow the enlargement of very small details to prevent their obstruction by the pencil's point. In addition Amrine employs a chemical apparatus clamp to hold a reversed binocular at the appropriate position and angle to form a small field visible through the drawing tube (Fig. 9). Very detailed structures such as of the empodia (Fig. 9), male genitalia, female genital apodemes, etc. can be drawn using this method.

The illustrator should try to prepare an image eventually on a lower plane than that of the microscope-base level: in this way the illustrator can sketch a larger preliminary draft, and the much larger drawing scale usually helps in reducing the visibility of mistakes and irregular lines when reduced for the final plate. The drawing plane should be illuminated by a table lamp adjustable for light direction and intensity in order to clearly and concurrently see the pencil marks superimposed below the cuticular structures of the mite, both with good contrast. It is advisable for the aspiring illustrator to be taught by an experienced researcher using these techniques if at all possible.

The microscope stage and the slide mounted specimen should be oriented on the horizontal plane in such a way as to make the outlines of the specimen well suited to the illustrator's drawing technique (usually, lines on a paper are more easily drawn when the

Fig. 8 *Diptacus swensoni* Keifer: original inked line drawings by Keifer at the US National Museum of Natural History, Beltsville, Maryland, USA

hand moves from left below to right above for right-handed people). An initial focus plane on the slide is chosen, and the illustrator draws the visible cuticular details in that plane on the paper. The illustrator can then focus on a higher or lower plane and add more details to the original drawing. Progressively, plane by plane, the illustrator can portray all the morphological features critical to the identity of the mite.

During drawing, one can cover the tube opening by one's hand to reduce the external light noise on the slide and to increase the contrast of specimen details. One can additionally cover the field diaphragm by the hand to obscure the mite and see just the sketch through the tube. The repeated, fast alternate movement of the hands facilitates detection of the presence or absence of some details on the line drawing by alternately flashing the two superimposed images.
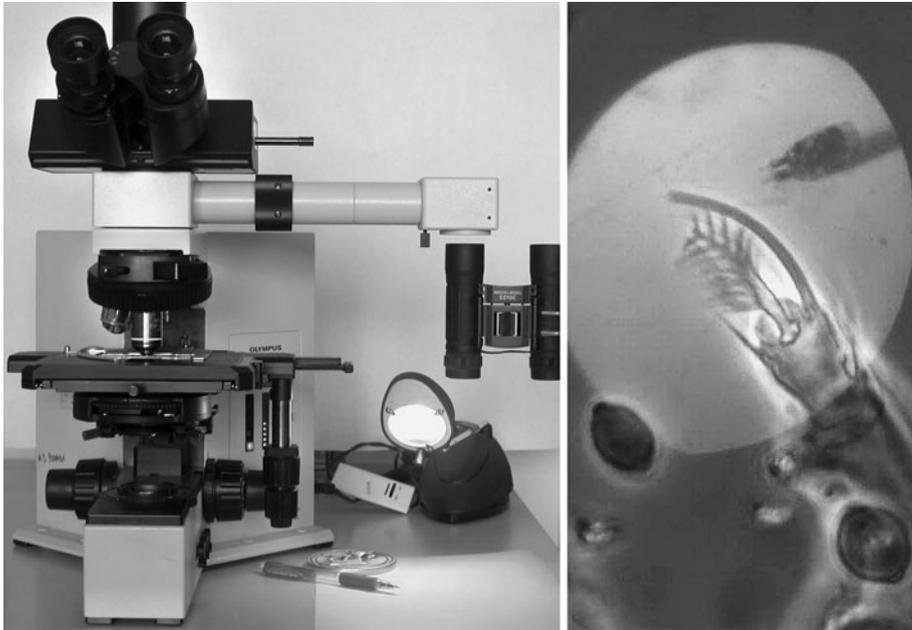
Fig. 9 Apparatus for drawing fine details: inverted binocular placed under the drawing tube opening (on the *left*) to decrease the size of the pencil or pen relative to small structures, such as empodia (on the *right*)

Descriptive drawings are usually semischematic, but they should be sufficiently detailed to portray the real morphology of the holotype specimen as closely as possible, and care should be taken not to "correct", "exaggerate" or interpret the features too much, so that some information is altered (see Keifer's recommendations in Fig. 1). The drawings should show the typical deviation from bilateral symmetry, and drawing one half, then copying the flip side of it to the other side becomes a fabrication, not science. Very often one specimen is not enough to get satisfactory information and additional specimens must be drawn, or even their features can be combined within one plate. This depends on the clearness, orientation and integrity of the specimen, contrast of the cuticle with the mounting media, and, of course, on the ability of the illustrator. This procedure also allows confirmation of some details.

In addition to the holotype specimen, other specimens should be studied to determine intraspecific variation in morphological features, at least in this one sample. Systematically important variations may be depicted in additional drawings if necessary.

Content that should be included in eriophyoid descriptive drawings

Often the content of eriophyoid plates can differ slightly depending on whether the depicted mite belongs to the Phytoptidae, Eriophyinae (Fig. 10), Phyllocoptinae or Diptilomiopidae (Fig. 11).

Amrine and Manson (1996) listed the most important body parts that should be illustrated by line drawings. Attempting to standardize the figure layout will make it
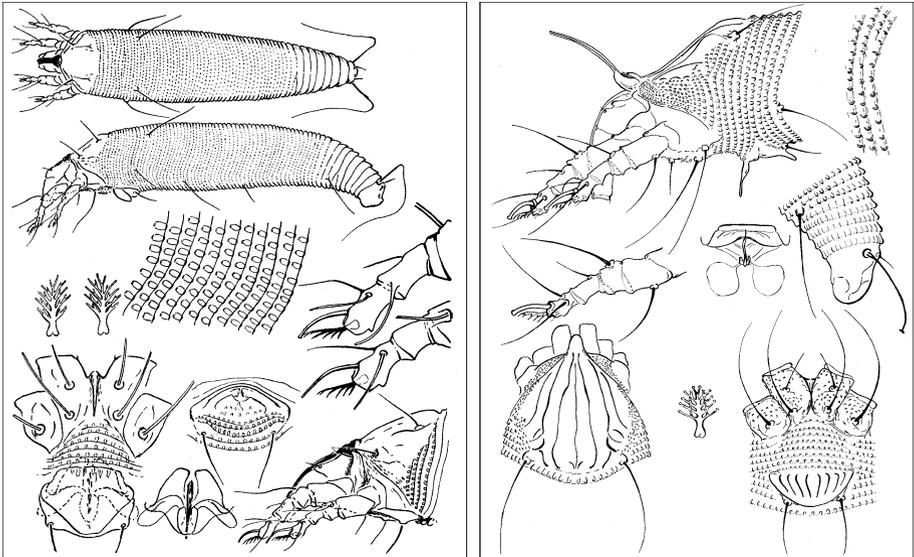
Fig. 10 Line drawings of a phytoptid (*Phytoptus corniseminis* Keifer-redrawn; on the *left*) and an eriophyid mite (*Aceria ficus* [Cotte], drawing by E. de Lillo; on the *right*)
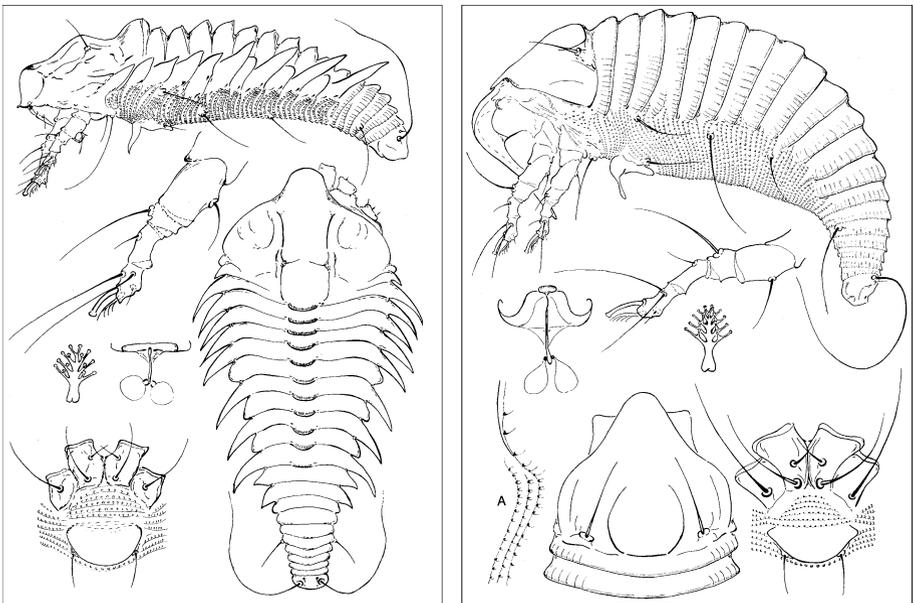
Fig. 11 Line drawings of a phyllocoptid (*Tegonotus heptacanthus* [Nalepa]; on the *left*) and a diptilomiopid mite (*Rhynchaphytoptus ficifoliae* Keifer; on the *right*) (drawings by E. de Lillo)

easier to compare the depiction of different species with each other, and for finding particular details in a drawing. Additional information to enhance their list is provided below.

Scanning electron microscopy pictures can assist in the understanding and perception of all features included in a table, but should never be used to the exclusion of line drawings, light microscopy, or other illustrations.

Prodorsal shield

The prodorsal shield must be depicted dorsally, including all ornamentations such as ridges, lines, granules, dots, cells, frontal lobe, anterior (*vi* and *ve*) and scapular (*sc*) setae and their tubercles, paying attention to the shape and size of these parts. The description of complex prodorsal shield ornamentation is almost always obscure if it is not accompanied by quality line drawings which are a fundamental requirement for a species' description, discrimination and identification although intraspecific variations may occur. Particular care should also be taken in depicting the frontal lobe margin and its shape. This lobe is frequently obscured by underlying gnathosomal and prodorsal elements, and may additionally be very thin and almost translucent, and its presence and margin may be very difficult to detect. It may help to study several specimens in this regard. Additionally, the illustrator must watch out for extremely tiny or obscure features like spines and extensions that may occur on the anterior edge of this lobe.

Coxal area and genitalia

The coxal and genital regions have to be carefully drawn on the ventral view position of the specimen. When illustrating these structures, coxal ornamentation should be studied in detail (e.g., ornamentations on coxae I may differ from that on coxae II) and care should be taken to determine whether lines are internal apodemes (e.g., near the base of coxae II) or surface lines or ridges. The following information should also be depicted: presence, shape and position of coxal tubercles, coxal seta robustness and length, shape and length of the internal coxisternal apodeme (sternal line), number of coxi-genital semiannuli or other structures set between coxae II and female or male external genitalia, and number and shape of microtubercles on these semiannuli. Regarding the genital region, the following features should be depicted: female and male (if found) external genitalia, particularly including details of the female genital coverflap, whether the coverflap seems to be divided in more than one region (e.g., basal and distal region), the ornamentation on these regions, ornamentation just anteriad of the coverflap and whether it is part of the area between coxae II. The length of setae *3a* should also be depicted accurately.

The genital apodemes, and softer parts like the spermathecae, are often difficult to observe and draw because of their size and their internal position and variability. Dissecting a clarified specimen at the level of the coxae or just posterior to the genital region is recommended, in order to have fewer disturbing elements (Keifer 1975). The length of the spermathecal tube and the size of the anterior part of the apodemes should be carefully observed, too.

Legs

For legs in lateral view, the ornamentations (e.g., spines, ridges) along the segments and at the level of the articulations, size of solenidia and shape of its tip, presence, position, and length of all leg setae must be depicted.

Concerning the empodium, particular care is needed in distinguishing the central shaft shape (whether divided or simple), the number of rays, and eventually the shape of branch tips.

Dorso-ventral view of the Diptilomiopidae

The large gnathosoma of the diptilomiopidae usually makes it difficult to have specimens oriented in true dorso-ventral position. In this case, the distal part of their large gnathosoma can be carefully removed or cut by a pin. Even though this is a tedious process, a bit of practice will allow the illustrator to get good results. A sharpened insect pin or fine dissecting scalpel should be used.

Lateral view drawings

With regard to the anterior part of the body, the illustrator needs to represent the lateral view of the gnathosoma, legs, prodorsal shield with its frontal lobe and setae (when present), lateral seta, first annuli after the prodorsal shield, and genital area. When printed, the anterior part of the mite should preferably be oriented to the left of the drawing. Particular care must be paid to the gnathosomal details, including the presence and shape of the palp coxal seta (ep), dorsal palp genual seta (d) and subapical palp tarsal seta (v), shape and size of the prodorsal shield, and any other surface detail (e.g., ornamentation on the pedipalp segments).

The anal lobes and the annuli up to the setae f have to be drawn in lateral view taking care to depict microtubercles, setae and any other detail. The posterior part of the anal lobes should preferably be orientated to the right side of the drawing.

Moreover, a few annuli need to be drawn trying to elucidate the shape and the size of the microtubercles (elliptical, roundish, pointed, etc.), their distribution, orientation, size of dorsal and ventral semiannuli, and details of lateral lobes, if they are present. These should be portrayed in lateral view to show the possible contrast between dorsal and ventral opisthosomal arrangement. Usually, the area chosen to be depicted is between the annuli at the level of opisthosomal setae c_2 and d.

For species with large dorsal semiannuli (e.g., Phyllocoptinae and some Diptilomi-opidae) it might be better to draw the whole specimen in dorsal and/or in lateral view; using particular care to point out ridges, furrows, and lateral lobes on the opisthosoma. If the illustrator draws the specimen in lateral view, the body should be horizontally placed in the plate and the anterior part should preferably be directed to the left. In case of the dorsal view, the body should be orientated in the vertical plane of the table and it should have the anterior part placed near the top of it.

Preparation of the final plate

An initial draft with many notes and details is the result of the work at the drawing tube. The draft might be redrawn by pencil with special attention to the fine details. It should be compared at the microscope with mounted specimens without the light interference of the drawing tube in order to get more contrast and richness in details seen on the slide mounted specimen. Comparison of several specimens will allow you to note details of possible variation of key elements; this information can be presented in the description, or in some cases, a second drawing may be necessary.

After checking the initial draft, a smooth tracing paper can be put over the line drawing and final inking done on it, and not directly on the line drawing itself. For a better result, a large light table can be used for illuminating the draft and the final drawings to increase the line perception. Some researchers draw the final drawing by means of a technical pen (i.e., the well known rapidograph line pens, Rotring[TM] and Steadtler[TM] pens). Nuzzaci and de Lillo prefer metal nibs with pointed tips, of at least two sizes, mounted on a holder without an ink reservoir. The nib needs to be repeatedly refilled with a small amount of ink while drawing. Actually, nibs have the advantages of being easier to clean and to preserve than the tips of technical pens, and for making the size of the line variable by simply changing the pressure applied to the nib tip on the paper. Moreover, the dorsal, ventral and lateral parts of the nibs can be used according to the needed thickness of the line. Opaque black Indian ink is adequate and any mistaken and imperfect line can be removed from the tracing paper using a razor blade. Alternatively, mistakes can be removed from drawings after digitization using appropriate software applications.

The illustrator can initially prepare a large plate, with the drawings arranged on it, generally 42 cm wide and 58 cm high (an A2 sheet size). This large canvas allows the illustrator to reduce or mask defects such as those caused by a trembling hand, line imperfections, dirty marks, wrong lines, corrections, and so on. The large size of the drawing may be a problem for the printer. A scanner can be used to digitize the drawings (also single drawn body parts, if necessary), combine the plate, and to reduce their size keeping the high resolution required for printing. In preparing the final plate, the proportions of the single details should be carefully considered. Usually, the first leg and the microtubercle details are two times larger, and the empodium is four times larger than the other parts. Finally scale bars should be added, too.

Line drawings can be also made on a computer (Li et al. 2006; Wei et al. 2007; Wang et al. 2007) using a digitizer tablet with a digital pen. Drawing digitally can replace the inking process of the initial pencil draft as described above, but first of all it still remains of utmost importance to accurately interpret critical detailed morphology. It should theoretically be possible to take digital images of the slide mounted specimen, and electronically draw directly on the image. However, this procedure is limited by the tiny and intricate morphology of Eriophyoidea and by the need of high magnifications with limited field depth. Images can be stacked, but it has not been tested whether the final image will be sufficiently detailed and contrasted to replace the carefully made initial pencil draft and final inked drawings.

Measurements

Measurement instructions for typical descriptive features of Eriophyoidea were described by Amrine and Manson (1996). Figures demarcating the positions of features that may cause confusion or need better definition or standardization are surely more helpful and will overcome any linguistic misinterpretation (Figs. 12, 13, 14, 15).

Many interpretative doubts on the measurements of some features came out during the present authors' experiences and several of these have relevant importance, especially for phylogenetic studies on the Eriophyoidea. Most of them require a careful consideration about the standardization and correct definition of homologies between taxa.

However, each group, genus or species will present different problems and one precise solution will not fit all. Therefore, the author of a new mite must be flexible and able to
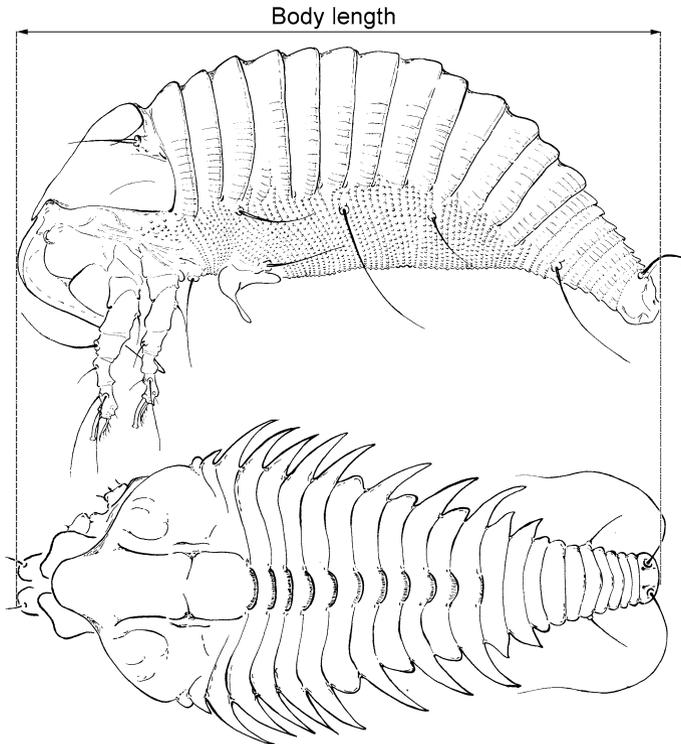
Fig. 12 Body length: from the rear end of the anal lobe to the maximum extent of the gnathosoma (above for *Rhyncaphytoptus ficifoliae* Keifer) or from the rear end of the anal lobe to the tip of the pedipalps (below for *Tegonotus heptacanthus* [Nalepa]; de Lillo's original drawings)

adapt and see the unique characteristics of the specimen at hand. This means, also, that the description paper should give note to the views and ways the measurements were taken.

A stage micrometer slide is used to calibrate the eyepiece reticule. Then, to make measurements of the specimen, the calibrated reticule is simply superimposed over any image viewed through the light path of the microscope and the linear dimensions (length and width) of a specimen feature can be measured. When making many measurements, the researcher often finds tedious, tiring and time consuming all the little movements and rotations needed with the microscope stage and with the eyepiece for matching the reticule scale with the features to be measured, especially when the morphological details are very fine and short.

To alleviate the tedium, the stage micrometer slide is used to draw a scale paper strip through the drawing tube for each objective lens. Then, the operator can measure more details of the same specimen by just re-positioning the scale strip and without changing the position of the slide or of the eyepiece. This technique saves time and makes measurements much more convenient.

Measurements can also be taken with an electronic image analysis set up. A digital camera is mounted on the microscope, and images are captured and transferred to a computer. Then, they are viewed and manipulated on screen to various angles and levels, and details are measured using different techniques, depending on the digital image
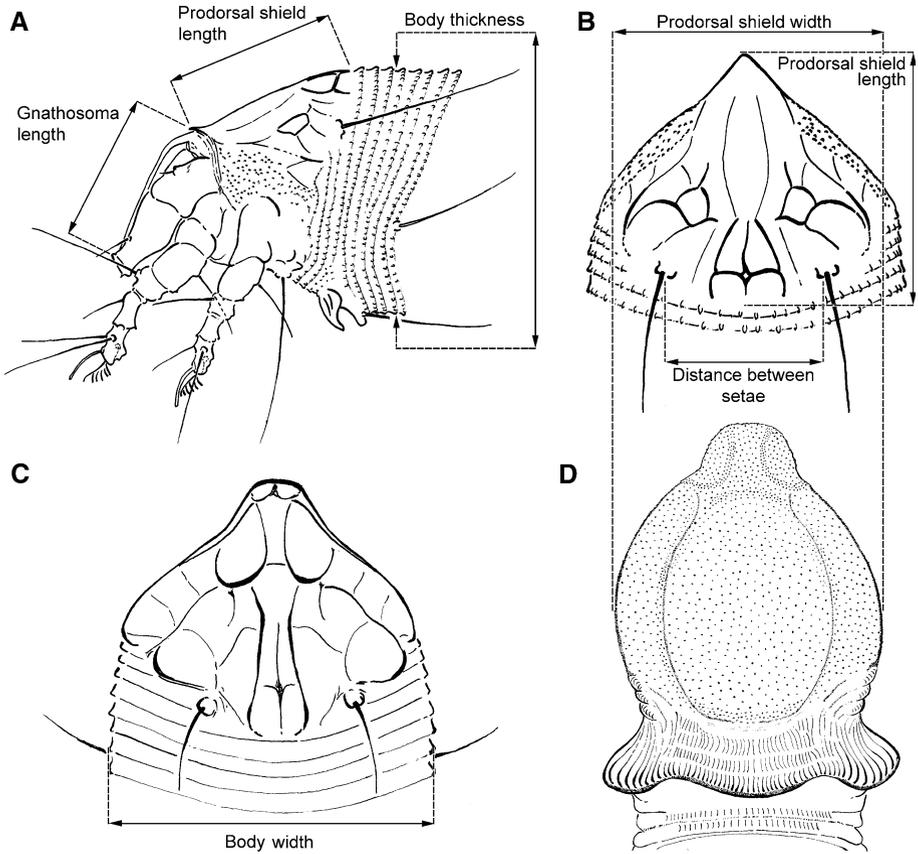
Fig. 13 **A**, **B** *Aceria novellae* Denizhan, Monfreda, Cobanoglu and de Lillo, **C** *Aculops pelekassi* (Keifer), **D** *Bariella farnei* de Lillo. Gnathosoma length: from the proximal margin of the cheliceral bases to the midpoint of the pedipalp tips. Prodorsal shield length: from the most anterior margin (of the prodorsal shield or frontal lobe) to the anterior margin of the first complete annulus posterior to the shield. Prodorsal shield width: from side to side at the level of the first distinct lateral annulus or at the widest level if the shield margins are protruded. Body width: from side to side at the level of setae *c2* or widest dimension if *c2* is absent. Body thickness: from dorsal to ventral aspect of the opisthosoma at the level of setae *c2*, if present. Distance between setae *sc*: from the inside margins of the setal bases. Distance between tubercles of setae *sc*: from the inside margins of the tubercles (de Lillo's original drawings)

software application used. Care should be taken that the system has been correctly calibrated by comparing with a set of *manual* measurements, and that the digital images are clear and have sufficient contrast to show each minor detail to be measured completely (e.g., very fine setae). Craemer conducted more accurate measurements *on live/video* images (where the image can still be focused up and down on the screen), rather than on a captured images, which may not be able to capture the entire structure to be measured at once, even when using different stacking methods.

Concerning measurements of the holotype, de Lillo measures selected specimens of a population and chooses the holotype within this group as the specimen with closest measurements to the average value for the greatest number of details.
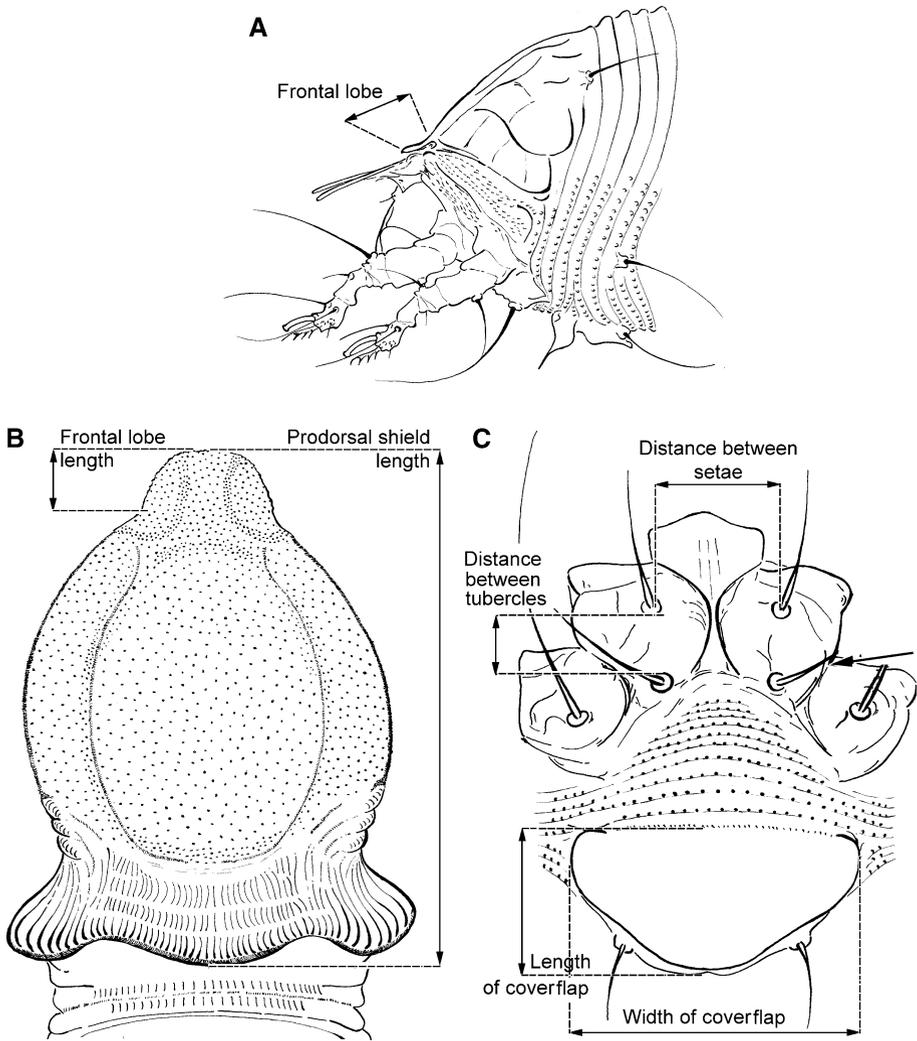
Fig. 14 A *Aculops pelekassi* (Keifer), **B** *Bariella farnei* de Lillo, **C** *Diptacus gigantorhynchus* (Nalepa). Distance between coxal setae: from the inside margins of the setal bases. Distance between tubercles of coxal setae: from the inside margins of the tubercles. *Arrows* indicate the short apodeme exactly where the two legs come together, at their contact, or where they pivot; the apodeme is usually quite distinctive and the anterior edge of this apodeme is used as a reference point for measuring both leg I and leg II length in ventral-dorsal view. Prodorsal shield length: from the most anterior margin (of the prodorsal shield or frontal lobe) to the anterior margin of the first complete annulus posterior to the shield. Frontal lobe length: from the motivator (gnathosomal base) to the anterior edge of the frontal lobe. Genital coverflap width: from its lateral margins. Coverflap length: from the transverse line anteriorly placed to the rear line of the coverflap (de Lillo's original drawings)

Finally, when taking many measurements of many specimens, a spreadsheet such as Microsoft Office's Excel® is very convenient for taking averages and ranges of values for each characteristic; properly designed, the files can be printed as tables to support the description.
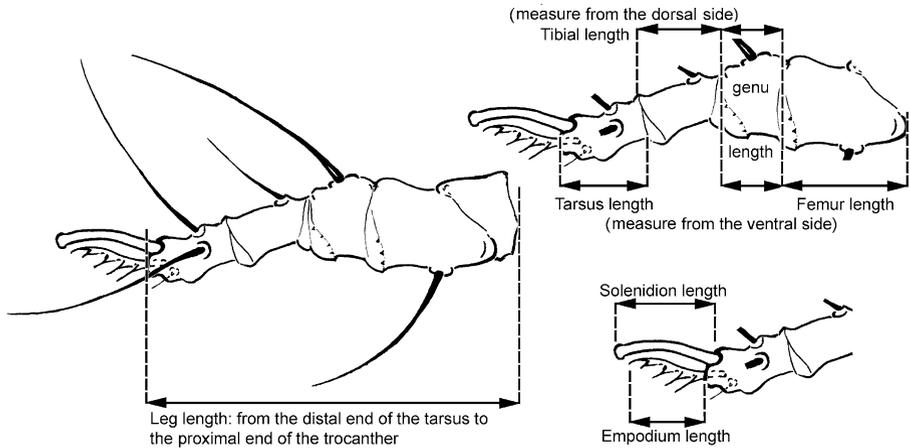
Fig. 15 *Aceria ficus* (Cotte). Length of legs from the trochanter proximal margin to the distal margin of the tarsus excluding the empodium and solenidion. Femur and tarsus length: measured ventrally. Tibial length: measured dorsally. Genu length: measured dorsally or ventrally. Solenidion and empodium lengths: from the pigmented base where inserted to the distal tip (de Lillo's original drawings)

Language

Every researcher is free to choose to publish eriophyoid taxonomic papers in the author's mother tongue. Fortunately, taxonomic articles published in English have been increasing considerably in the past decade, allowing for a wider and more convenient dissemination of information. Nevertheless, many older papers need to be translated because the drawings are often incomplete and cannot show data usually indicated in the morphometric description, and the English abstracts usually lack needed and detailed information. One particular language is not more important than another but, in the scientific environment, English is so widespread and most often understood that it is worth while to have an abstract which contains an English translation, taking care that it should be as complete as possible in order to be useful for identification purposes and morphological comparisons.

Considering the costs of having a paper translated, or of obtaining interlibrary loans, a shared web archive should be arranged and promoted within the copyright rules. The electronic information facilities of public institutions should be preferably used to ensure non-profit designations. This can allow researchers to upload/download translated and other papers in a sort of peer to peer network. Such a network would greatly facilitate sharing important biological and descriptive data, or key publications, and ultimately to promote greater advances in eriophyoid research. Many authorities provide digital copies of their key publications on their web sites, which is enormously helpful.

Completeness of descriptions

Strong recommendations were given by Keifer (1975) and Amrine and Manson (1996) about the need to include knowledge on the host plant identification, mite habit and host plant relationships. Particular care should be taken in finding and collecting males; their morphology often helps to understand the female status as protogyne/deutogyne mites.

Often, in literature, many species are described based on a small population and/or without the male. Such descriptions often have very limited biological data and lack information about the intraspecific morphometric variability. A new species should ideally be described based on widely dispersed samples in order to avoid describing an accidental presence of a mite on an improper host.

Considering the general availability of GPS devices, collection localities should also include latitude and longitude data at least to the level of minutes.

The rules of the International Code of Zoological Nomenclature (ICZN 1999), currently on line at http://www.iczn.org/iczn/index.jsp, must always be followed for nomenclature decisions, name assignment and for gender agreement between genus and species name. Often, patronymic and locality names are assigned after their latinization. Researchers should try to avoid applying genus and species names characterized by a series of contiguous consonants or vowels in order to reduce typing mistakes when these names are listed in tables, indexes and catalogues, as sometimes happens.

Finally, in order to reduce confusion in eriophyoid systematics, species identity should be clearly established when biological observations are specifically carried out, and publications of unnamed or unidentified species should be avoided, such as recently happened for an *Acalitus* sp. of *Carpinus tschonoskii* Maxim (Kawashima and Amano 2004).

Concluding remarks

The information and recommendations given in this article may seem overly demanding and meticulous at first glance. However, these come from our collective and shared experience in studying Eriophyoidea for systematic purposes. It is not meant to be a text book recipe, but hopefully it will spur new ideas and techniques in attaining proper and exact descriptions that will add value and stability in eriophyoid systematics and reduce confusion which is currently prevalent in some groupings.

References

Amrine JW Jr, Manson DCM (1996) Preparation, mounting and descriptive study of eriophyoid mites. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam. World Crop Pest 6:383–396

Amrine JW Jr, Stasny TA, Flechtmann CHW (2003) Revised keys to world genera of Eriophyoidea (Acari: Prostigmata). Indira Publishing House, West Bloomfield

Baker EW, Kono T, Amrine JW Jr, Delfinado-Baker M, Stasny TA (1996) Eriophyoid mites of the United States. Indira Publishing House, West Bloomfield

Boczek J, Nuzzaci G (1988) A new genus and five new species of eriophyid mites (Acari: Eriophyoidea). Entomologica 23:123–138

Dabert J, Ehrnsberger R, Dabert M (2008) *Glaucalges tytonis* sp. n. (Analgoidea, Xolalgidae) from the barn owl *Tyto alba* (Strigiformes, Tytonidae): compiling morphology with DNA barcode data for taxon descriptions in mites (Acari). Zootaxa 1719:41–52

de Lillo E, Skoracka A (2009) What's "cool" on eriophyoid mites? Exp Appl Acarol. doi:10.1007/s10493-009-9297-4

de Lillo E, Bari G, Monfreda R (2005) Preliminary study on the distribution of *Calepitrimerus vitis* (Nalepa) on tendone trained vineyards in Apulia, Southern Italy. Phytophaga XIV(2004):605–610

Denizhan E, Monfreda R, de Lillo E, Cobanoglu S (2008) Two new species of eriophyoid mites (Acari: Eriophyoidea) associated with Elaeagnaceae in Turkey. Zootaxa 1698:41–48

Faraji F, Bakker F (2008) A modified method for clearing, staining and mounting plant-inhabiting mites. Eur J Entomol 105:793–795

Hassan AS (1928) The biology of the Eriophyidae with special reference to *Eriophyes tristriatus* (Nalepa). Univ Calif Publ Entomol 4(11):341–394

International Commission on Zoological Nomenclature (ICZN) (1999) International code of zoological nomenclature. International Trust for Zoological Nomenclature, London

Kawashima M, Amano H (2004) Seasonal occurrence and association of a gall-forming eriophyid mite and predacious phytoseiid mites (Acari: Eriophyidae, Phytoseiidae) in Japan. Int J Acarol 30(1):9–15

Keifer HH (1952) The Eriophyid mites of California (Acarina: Eriophyidae). Bull Calif Insect Surv 2(1):1–123

Keifer HH (1975) Eriophyoidea Nalepa. Injurious eriophyoid mites. In: Jeppson LR, Keifer HH, Baker EW (eds) Mites injurious to economic plants. University of California Press, Berkeley, pp 327–533

Li D-W, Wei S-G, Wang G-Q (2006) A new genus and four new species of Phyllocoptinae (Acari: Eriophyoidea) from China. Zootaxa 1303:35–43

Lindquist EE (1996) External anatomy and notation of structures. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam. World Crop Pest 6:1–30

Lindquist EE (2001) Poising for a new century: diversification in Acarology. In: Halliday RB, Walter DE, Proctor HC, Norton RA, Colloff MJ (eds) Acarology: proceedings of the 10th international congress. CSIRO Publishing, Melbourne, pp 17–34

Mohanasundaram M (1984) New eriophyid mites from India (Acarina: Eriophyoidea). Orient Insects 18:251–283

Monfreda R, Nuzzaci G, de Lillo E (2007) Detection, extraction, and collection of Eriophyoid mites. Zootaxa 1662:35–43

Monfreda R, Lekveishvili M, Petanovic R, Amrine JW Jr (2009) Collection and detection of eriophyoid mites. Exp Appl Acarol. doi:10.1007/s10493-009-9315-6

Nalepa A (1906) Über das präparieren und Konservieren der Gallmilben. Marcellia 5(2):49–61

Nuzzaci G, de Lillo E, Mariani RG (1991) Scanning microscopy in acarology: a new technique for preparation of eriophyids preserved in different ways. Boll Soc Ent Ital 123(1):3–8

Petanović R, Stadelbacher EA, Boczek J (1993) Eriophyid mites (Acari: Eriophyidae) on *Geranium* spp. Geraniaceae: redescription of three known species and description of a new species. Ann Entomol Soc Am 86(4):411–416

Skoracka A, Dabert M (2009) The cereal rust mite *Abacarus hystrix* (Acari: Eriophyoidea) is a complex of species: evidence from mitochondrial and nuclear DNA sequences. Bull Entomol Res: 1–10. doi:10.1017/S0007485309990216

Trotter A (1904) "Cecidotheca Italica" di A. Trotter e Cecconi G. Marcellia 3:76–81 (it is a list of gall makers included in the Cecidotheca Italica up to issue IX–XII, gall number 300)

Trotter A, Cecconi G (1902) "Cecidotheca Italica" o raccolta di galle italiane determinate, preparate ed illustrate. Fasc XVI–XVIII (n. 376–450). Padua

Wang G-Q, Li D-W, Wei S-G (2007) Two new species of *Disella* (Eriophyidae: Nothopodinae: Nothopodini) from South China. Zootaxa 1426:63–67

Wei S-G, Li D-W, Wang G-Q (2007) Description of five new species of eriophyid mites (Acari: Eriophyidae) from Guangxi, China. Int J Acarol 33(2):115–122