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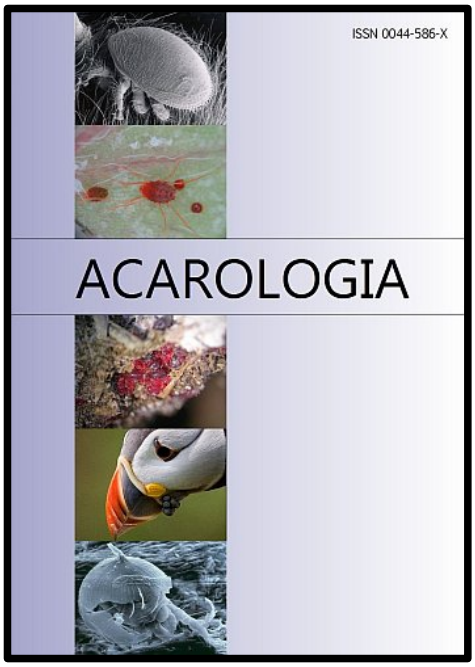

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PEST CONTROL BY MITES (ACARI): PRESENT AND FUTURE

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ABSTRACT — This essay reviews advances in the systematics of mite families containing members that are acarine biocontrol agents (ABAs), including the Phytoseiidae which have several strains or races. Additions to the roster of mites that affect pests (including weeds and pathogens), and of pests that may be, or are, significantly affected by ABAs, were noted. The various pest-debilitating mechanisms used by ABAs, including predation, parasitism, parasitoidism, parasitic castration, competition as well as reductions in weed and phytopathogenic fungal growth are listed. The affected targets include agricultural, veterinary and medical pests, as well as weeds, nematodes and fungi. The effect of intra-guild predation on the ABAs' ability to affect pests is discussed, along with other organisms that increase the controlling impact of ABAs. The influence of host plants, including their architecture, leaf surfaces, domatia, pollen, genetically modified plants (GMOs) and volatiles are then reviewed. Then come mite feeding on soil-inhabiting pests and the newly-discovered effects of arbuscular mycorrhizal (AM) fungi. ABA feeding on weeds and on nematodes is briefly discussed next, along with the few known ABA diseases. The effect of plant-protection chemicals are then considered, followed by new techniques for the better implementation of ABAs. These include mass rearing, modes of distribution, long-term maintenance and the application of molecular methods to determine quantitative and qualitative feeding rates. This review ends with suggestions for further research, including more collecting and assaying of ABAs (especially indigenous species), determining the effects of secondary predators and of light regimes in greenhouses, and increasing studies on the role of volatiles of plant and nematode source, and of ABAs as vectors of pest diseases.

KEYWORDS — Biocontrol; Acari; pests; plants

INTRODUCTION

A major recent shift in the practice and science of biological control (BC) has been the decline in relying on imported, exotic BC agents, with a concomitant increase in the use of indigenous natural enemies, whether arthropods or microbial. As van Lenteren (2012) stated, nowadays there is a trend to look first for indigenous BC agents when new exotic pests establish in new regions (e.g. Furtado *et al.* 2007) as illustrated by the number of natural enemies that were used for the first time in Europe in previous decades. Until 1970, the only two species commercially used in Europe were exotic, and during the following three decades, more new exotics were employed than indigenous species. However, in the last decade this trend has changed and for the first time more indigenous species are being commercialized than exotics.

Whether exotic or indigenous, mites (Acari) figure largely amongst arthropod BC agents, being the second largest taxonomic group (after the Hymenoptera) that were used in commercial augmen-

tative BC in the period 1900 to 2010 (van Lenteren 2012). The dominant family of mites used in BC is the Phytoseiidae, along with a few species assignable to other families. Gerson *et al.* (2003) discussed members of 34 families of acarine biocontrol agents (ABAs) that were shown to reduce the populations of pests (including weeds and pathogens) and /or their injuries. The role of ABAs in greenhouse pest management was discussed by Gerson and Weintraub (2012) and efforts to control phytonematodes with mites were summarized by Gerson (in press).

More information has accumulated since 2003 on several further ABA taxa (Table 1), members of additional mite families that may have potential to affect pest numbers were noted, more pests were affected by ABAs, new relevant technology has been tried and much has been learned about the potential of indigenous predatory or parasitic mites to affect pests. These subjects, illustrated by some examples, are the topics of the present essay.

The importance of identifying and determining the systematic status of the ABAs will be discussed first, followed by notes on their provenance and biology, their interactions with plants (including weeds) and aspects of new methodology. Based on these data, future trends in the use of ABAs will be formulated.

Some key elements on systematics of ABAs

Members of the mesostigmatic family Phytoseiidae, dominant amongst ABAs in pest control (van Lenteren 2012), are the main group being studied. The systematics of their over 2,450 valid members (Demite *et al.* 2014b) has been proposed (Chant and McMurtry 2007), and more species are being added by collecting in hitherto little canvassed countries (Guanilo *et al.* 2008; Tixier *et al.* 2012; Kreiter *et al.* 2013). Demite *et al.* (2014a, b) provided a database (available at the website www.lea.esalq.usp.br/phytoseiidae) for all species named at that date, and Hernandes *et al.* (2012) provided a polytomus key to the world species of the large subgenus *Typhlodromus (Anthoseius)*.(freely available online with other keys at the website (http://www1.montpellier.inra.fr/CBGP/phytoseiidae/index.html)). The application of molecular markers to identify phytoseiids species was used, among others, by Li *et al.* (2012). Two confounding trends are meanwhile impacting on the understanding and use of these species. The first is the recognition that more than a single taxon may be masquerading within the same species. Beard (1999), Noronha *et al.* (2003) and Kanouh *et al.* (2010), among others, argued that the precise status of phytoseiid species may be difficult to determine only with morphological criteria, yet accurate identifications are crucial in BC programs. Molecular methods are thus increasingly being used (Walter and Campbell 2003, and Okassa *et al.* 2009, among others) to resolve issues like misidentifications and synonymies (Tixier *et al.* 2006; Tixier *et al.* 2011, 2012; Bowman and Hoy 2012). The second trend is the realization that some of the common species have strains, or populations, which differ in traits like response to aridity, temperature and (most important) to prey that affect their biocontrol efficacy. Some examples are presented in Table 2.

The relevance of phytoseiid classification to biocontrol was emphazised by McMurtry and Croft (1997), who suggested that different taxa could be placed within four types or categories. Type 1 consists of species that are specialized predators of webbing spider mites essentially of the genus *Tetranychus*. Type 2 also refers to spider mite predators that also feed on other prey. Type 3 includes generalist predators that also consume for instance pollen, honeydew and fungi, and Type 4 includes species that feed and perform better when fed on pollen than on prey. The possibility that further types may exist, possibly more specialized for certain prey, was validated by Adar *et al.* (2012), who proposed that the ability to feed on plants be added as a cross type trait of phytoseiid life-style types. More recently McMurtry *et al.* (2013) formulated a new classification of the lifestyles of phytoseiid mites. The discovery of a phytoseiid whose main food source is the coffee leaf rust fungus (Oliveira *et al.* 2014), suggests that more life styles may be discovered.

TABLE 1: Recent associations of post 2003 non-phytoseiid ABAs.

Family	ABA	Target-Pest	Reference
Acaridae	*Sancassania*	Nematodes	Karagoz *et al.* (2007)
Acarophenacidae	*Acarophenax*	*Rhyzopertha*	Gonçalves *et al.* (2003)
		Tribolium	Oliveira *et al.* (2003)
		Cryptoletes	Oliveira *et al.* (2003)
Anystidae	*Anystis*	*Aculus*	Cuthbertson *et al.* (2003a)
		Rhopalosiphum	Cuthbertson *et al.* (2003b)
Ascidae	*Blattisocius*	*Ephestis*	Nielsen (2003)
Cheyletidae	*Cheyletus*	*Tyrophagus*	Palyvos *et al.* (2006)
Cunaxidae	*Neocunaxoides*	*Meloidogyne*	Shoala and Kady (2009)
Ereynetidae	*Riccardoella*	Arianta	Schuphach and Baur (2008)
Erythraeidae	*Balastium*	Whiteflies	Fuentes *et al* . (2011)
Hemisarcoptidae	*Hemisarcoptes*	*Chionaspis*	Calmaur and Ozbek (2007)
Laelapidae	*Androlaelaps*	*Dermanyssus*	Lesna *et al.* (2012)
	Stratiolaelaps	Fungus gnats	Cabrera *et al* . (2004)
	Hypoaspis	Phoridae	Bingham (2004)
	Hypoaspis	*Frankliniella*	Berndt *et al* . (2004)
Macrochelidae	*Macrocheles*	Thrips	Messelink & van Holstein-Saj (2008)
Otopheidomenidae	*Hemipteroseius*	*Pyrrhocoris*	Lewandowski & Szafranek (2005)
Pterogosomatidae	*Pimelaphilus*	Reduviidae	Martinez-Sanchez *et al.* (2007)
Pyemotidae	*Pyemotes*	*Hyphoborus*	Akşit *et al.* (2007)
Stgmaeidae	*Agistemus*	Diaspididae	El-Sawi & Momen (2006)
	Agistemus	*Schizotetranychus*	Horita *et al.* (2004)
Tarsonemidae	*Tarsonemus*	*Schizotetranychus*	Lin *et al* . (2002)
Trombidiidae	*Trombidium*	*Hypera*	Mohamed and Hogg (2004)
Uropodidae	Macrodinychus	*Paratrechina*	Gonzalez *et al* . (2004)

TABLE 2: Examples of phytoseiid species shown to have several strains.

Species	Differing in	Source
Amblyseius largoensis	Response to *Raoiella*	Carillo *et al.* (2012)
Amblyseius womersleyi	Olfactory responses	Maeda *et al* . (2001)
Euseius scutalis	Longevity, fecundity	Meyerdirk & Coudriet (1986)
Galendromus occidentalis	Mating behavior	Hoy & Cave (1985)
Neoseiulus californicus	Response to humidity	Walzer *et al* . (2007)
Neoseiulus californicus	Reproduction	Toyoshima & Hinomoto (2004)
Phytoseiulus persimilis	Longevity, fecundity	Galazzi & Nicoli (1996)
Phytoseiulus persimilis	Tolerance to aridity	Perring & Lackey (1989)
Phytoseiulus longipes	Feeding preferences	Tixier *et al.* (2010)
Typhlodromus pyri	Temperature responses	Hardman & Rogers (1991)

The systematics of other major ABA families is also being studied. The superfamily Raphignathoidea, containing the families Camerobiidae, Eupalopsellidae and Stigmaeidae, of biocontrol interest, were partially revised by Fan and Zhang (2005). Other recent contributions include van der Schyff *et al*. (2005, Bdellidae); Hartini *et al*. (2009, Macrochelidae); Lindquist and Moraza, (2010, Blattisociidae); Joharchi *et al*. (2011, Laelapidae); Reis *et al*. (2011, Eriophyidae) and Skvarla *et al*. (2014, Cunaxidae). Authors describing new taxa in various families often note that these mites may have potential as BC agents (e.g. de Moraes 2010; Rector and Petanović 2012).

Additions to the roster of ABAs and their prey/hosts

Gerson *et al*. (2003) listed 34 acarine families that include members known, or postulated, to reduce pest (including, as above, weeds and pathogens) numbers and/or their damage. Representatives of one more family (Uroactiniinae) have since been added. Predatory mites that potentially or actually affect pests which have recently invaded new regions (Cox *et al*. 2006; Furtado *et al*. 2007), or pests that have not hitherto been known to be affected by ABAs, are likewise noted.

Adults of the red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae), a pest of palms, were heavily (57-95 %) attacked by *Centrouropoda almerodai* Wisniewski *et al*. (Uroactiniidae), which reduced the lifespan of infested individuals by one-third (Mazza *et al*. 2011). *Macrodinychus sellnicki* (Hirschmann and Zingiebl-Nicol) (Uropodidae) is an ectoparasitoid of the crazy ant, *Paratrechina fulva* (Mayr), a pest of sugar cane in Colombia. The mite feeds on the ant's pupae, which subsequently die. Despite high rates of attack (up to 93 %), the mass production of this ABA was not feasible, and Gonzalez *et al*. (2004) recommended inoculative releases of field-collected, highly parasitized hosts into ant colonies. Three phytoseiids, namely *Neoseiulus cucumeris* (Oudemans), *N. barkeri* (Hughes) and *Amblyseius swirskii* Athias-Henriot, were assayed against the Asian citrus psyllid, *Diaphorina citri* Kuwayama, the vector of the bacterium causing huanglongbing (HLB), the devastating citrus greening disease. All three predators had a significant negative impact on the pest (Juan Belasco *et al*. 2012; Fang *et al*. 2013). Pappas *et al*. (2013) assayed for instance *Phytoseius finitimus* Ribaga against spider mites and whiteflies. Ali *et al.* (2012) indicated that *Dermanyssus gallinae* (De Geer) (Dermanyssidae), a major pest of poultry world-wide, may be partially controlled by *Hypoaspis miles* (Berlese) [probably *Stratiolaelaps scimitus* (Womersley)]. The macrochelid *Macrocheles robustulus* (Berlese) was newly found to be an efficient predator of thrips (Messelink and van Holstein-Saj 2008). *Pimeliaphilus plumifer* (Newell and Ryckman) (Prostigmata: Pterygosomatidae) parasitizes *Meccus pallidipennis* (Stål) (Hemiptera: Reduviidae), a vector of Chagas disease in Mexico. Mite attack increased the mortality and reduced the molting rates in bug nymphs, as well as the longevity and fecundity of the surviving females (Martinez-Sanchez *et al*. 2007). The authors advocated the use of *Pimeliaphilus plumifer* as a control agent of this and other vector species. *Acarophenax lacunatus* (Cross and Krantz) (Acarophenacidae) fed on the eggs of several beetle pests of stored food. Its highest parasitization rates were on the beetles *Rhyzopertha dominica* (Fabricius) (Bostrichidae) and *Tribolium castaneum* (Herbst) (Tenebrionidae), resulting in reduced pest numbers and in increased wheat weight (Oliveira *et al.* 2003). Numbers of the cigarette beetle, *Lasioderma serricorne* (Fabricius) (Anobiidae), a major pest of tobacco, were reduced by about 20 % due to feeding by *Tyrophagus putrescentiae* (Schrank) (Astigmata: Acaridae) (Papadopoulou 2006). According to Canevari *et al.* (2012) this mite killed 54-78 % of the pest's larvae and its use in beetle management programs was advocated. *Riccardoella limacum* (Schrank) (Prostigmata: Ereynetidae) lives in the lung cavity of the land snail *Arianta arbustorum* Linnaeus (Mollusca: Helicidae), of quarantine importance in the United States (Cowie *et al.* 2009). The mite infested 45-70 % of several snail populations, seriously reducing their survival (Schupbach and Baur 2008).

Routine examinations of insect pests often reveal

many associated ABAs (Elkawas 2011), but their effect on the prey/hosts and on the extent of damage remains to be determined.

How ABAs affect pests (including weeds and fungi) and reduce their damages

ABAs reduce pest numbers and/or their damage by various modes; some examples are listed in Table 3. Predation is the commonest, phytoseiids being supreme in this respect. Parasitism (feeding on the host without killing it, but reducing viability and fecundity) is often observed with water mites of the family Arrenuridae (Smith and McIver 1984). Other parasites, feeding on their hosts and killing them, are *Pyemotes* spp. (Pyemotidae) and *Hemisarcoptes* spp. (Hemisarcoprtidae) (Akşit *et al.* 2007; Calmaur and Ozbek 2007, respectively). Parasitic castration of the grasshopper, *Hieroglyphus nigrorepletus* Bolivar (Acrididae) is due to the feeding of *Eutrombidium trigonum* (Hermann) (Badruddin *et al*. 2003) (Trombididae). Members of over 30 mite families (e.g. Acaridae, Alycidae, Galumnidae, Laelapidae and others) feed on nematodes, greatly reducing their numbers (Gerson, in press). The tydeid *Orthotydeus lambi* (Baker) grazed on the mycelia of grape powdery mildew and reduced its spread on the foliage and fruit of nine grape cultivars; extent of disease suppression depended on the specific grape genotypes, their susceptibility to the mildew and on mite numbers (English-Loeb *et al*. 2007).

Indirect damage to a pest can be due to several species of *Tarsonemus* (Tarsonemidae) associ-

Table 3: Examples of the mechanisms by which ABAs affect pest organisms.

Mechanism	Reference	ABA
Predation		
	Carrillo *et al.* (2012)	*Amblyseius*
	Shoala and El Kady (2009)	*Neocunaxoides*
Parasitism		
	Martinez-Sanchez *et al* . (2007)	*Pimeliaphilus*
Parasitoidism		
	Gonzalez *et al* . (2004)	*Macrodinychus*
Fecundity reduction		
	Smith and McIver (1984)	*Arrenurus*
Parasitic castration		
	Badruddin *et al* . (2003)	*Eutrombidium*
Competition		
	Hougen-Eitzman and Karban (1995)	*Eotetranychus*
Disease transmission to pests		
	Seeman (2008)	*Chrysomelobia*
Reduction of fungal growth		
	Enami and Nakamura (1996)	*Scheloribates*
Reduction of weed growth		
	Marlin *et al.* (2013a)	*Orthogalumna*

ated with the southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coleoptera: Curculionidae), a destructive pest of pine trees in North America. The mites carry ascospores of the bluestain fungus *Ophiostoma minus* (Hedgcock), which outcompete fungi carried by *D. frontalis*, critical for its nutrition. The pest larvae seldom survived in the presence of *O. minus* (compared to 83 % survival elsewhere). By disrupting beetle mutualism with *O. minus* the mites indirectly reduced pest numbers (Lombardero *et al.* 2003). The water hyacinth, *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae), is a weed that forms dense mats in waterways in many parts of the world. *Orthogalumna terebrantis* Wallwork (Galumnidae) feeds on the weed, reducing its physiological activity (Marlin *et al.* 2013a).

ABAs can damage pests by transmitting diseases. The Pales weevil, *Hylobius pales* (Herbst) (Curculionidae), a forestry pest, carried a phoretic *Macrocheles* sp. (Macrochelidae). The mites, contaminated with the entomopathogenic fungus *Metarhizium anisopliae* (Metchnikoff) Sorokin (Hypocreales: Clavicipitaceae) transmitted it to the weevils, of which ca 80 % became infected (as compared to 7 % in the mite-free weevil control group) (Schabel 1982).

Intra-ABA interactions

Intraguild predation

Intraguild predation (IGP) can take place when two natural enemies share a host (or prey), and at least one also feeds on the other (Rosenheim *et al.* 1995). IGP is common amongst ABAs but their interactions can also be competitive without predation, or even increase the extent of control. These interactions may promote or hinder pest control. An ABA might win the contest, but if the less efficient predator becomes dominant, the extent of pest control would then be reduced. The outcome of such contests depends on the competing species, on their nutrient requirements (usually pollen for phytoseiids), on the season (Hatherly *et al.* 2005) and whether the competitors are (among phytoseiids) the specific Type 1 predators or more of the generalist Types (e.g. Palevsky *et al*. 2013). Contestants' size, the plant and any applied pesticides are also important, leading to very different outcomes. The phytoseids *N. cucumeris* and *N. barkeri* co-occur in European glasshouses, feeding on *Thrips tabaci* Lindeman. The former is the better predator, but on parthenocarpic cucumbers (which do not produce pollen) it was displaced by *N. barkeri*. This was attributed to the latter's greater mobility, to lesser dependence on pollen and/or to more prey consumed (BrØdsgaard and Stengaard Hansen 1992). On sweet pepper, however, *N. cucumeris* attained higher numbers than *N. barkeri*, even when the latter was released first or in larger numbers (Ramakers 1988). When *A. swirskii* and *N. cucumeris* were applied against the western flower thrips (WFT), *Frankliniella occidentalis* Pergande (Thripidae), they preferred each other's juveniles over the pest (Buitenhuis *et al.* 2010), resulting in less pest control. Seelmann *et al.* (2007) hypothesized that leaf pubescence of apple varieties mediates IGP between the phytoseiids *Kampimodromus aberrans* (Oudemans) (which prefers pubescent leaves) and *Euseius finlandicus* (Oudemans) (which lives mostly on glabrous leaves) and thereby determines their proportional abundance in orchards. The outcome of IGP amongst *N. cucumeris*, the laelapid *S. scimitus* and the beetle *Atheta coriaria* (Kraatz) (Staphylinidae), as it affected thrips control in a greenhouse, was explored by Pochubay and Grieshop (2012). When all three predators co-occurred, numbers of the latter two were reduced whereas prey thrips populations grew five-fold larger than with *N. cucumeris* alone, advocating the use of only the latter for thrips control.

The level and severity of IGP also bears on the establishment, success and survival of exotic natural enemies. Palevsky *et al.* (2013) analysed the history of several exotic phytoseiids introduced into different parts of the world to control mite pests. In most cases the exotic predators, as they became established, enhanced pest control without adversely affecting the local predators. However, the latter (especially species of the pollen-feeding *Euseius*) often reduced the exotic species, either by surviving after numbers of the common prey had been reduced, and /or by feeding on the eggs and juve-

niles of the exotics (Palevsky *et al.* 1999). IGP may be avoided if the contestants inhabit different plant strata (Zannou *et al*. 2007), by placing their eggs in domatia (see below) or by the availability of other nutrients (e.g. pollen, Onzo *et al.* 2005). Plant-protection chemicals also affect the outcome. Sato *et al*. (2001) monitored phytoseiid and stigmaeid populations in Brazilian citrus groves after pesticide applications. The increases in stigmaeid numbers were postulated by the authors to be due to the greater sensitivity of the phytoseiids to the chemicals.

Interactions between ABAs and arthropathogenic fungi form another facet of IGP, which often detracts from ABA efficacy. When the phytoseiid *Phytoseiulus persimilis* Athias-Henriot was offered *Tetranychus urticae* Koch (Prostigmata: Tetranychidae) (the two-spotted spider mite, TSSM) infected with the fungus *Beauveria bassiana* (Balsamo) Vuillemin (Hypocreales: Clavicipitaceae), the predator's fecundity declined (Seiedy *et al.* 2012). When the same predator was assayed, along with the fungus *Neozygites floridana* (Fisher) (Entomophthorales: Neozygitaceae) to control *Tetranychus evansi* Baker and Pritchard (Prostigmata: Tetranychidae), a pest of Solanaceous crops, the predator produced fewer eggs. Wekesa *et al.* (2007) attributed this to increased grooming by *P. persimilis* in order to remove conidia that had become attached to its body. In none of these cases did the fungi infect the predators. These data suggest that applying ABAs with arthropathogenic fungi may not improve pest control.

ABAs that increase the extent of control

At times ABAs alone cannot reduce pest numbers to below their economic injury levels and other natural enemies help to attain that goal. Control of the stored food beetle pest *Oryzaephilus surinamensis* Linnaeus (Silvanidae), by *Cheyletus eruditus* (Schrank) (Cheyletidae) was improved when the hymenopterous parasitoid *Cephalonomia tarsalis* (Ashmead) (Bethylidae) was introduced into the food bin (Ždarkova *et al.* 2003). Another group of natural enemies are nematodes. The release of *Gaeolaelaps aculeifer* (Canestrini) (Laelapidae) (then known as *Hypoaspis aculeifer*) along with nematodes, significantly reduced the numbers of the WFT infesting green beans (Premachandra *et al.* 2003), as well as sciarids and phorids (Diptera), pests of mushrooms in compost and casing substrates (Jess and Bingham 2004). The predatory cecidomyiid *Therodiplosis persicae* (Kieffer) (Diptera) "supported" the control of *T. urticae* by *P. persimilis* on tomatoes in a greenhouse (Fiedler 2005), and the generalist ant *Pristomyrmex punctatus* Mayr "enhanced" the control of the spider mite *Tetranychus kanzawai* Kishida by *Neoseiulus womersleyi* Schicha (Otsuki and Yano 2014). The greatest damage to the leaf surface area of water hyacinth occurred when the Hemipteran *Eccritotarsus catarinens* (Carvalho) (Miridae) was used along with *O. terebrantis* (Marlin *et al.* 2013b).

Such results are generally consistent with the opinions of Stiling and Cornelissen (2005), who calculated that the addition of two or more biocontrol agents, especially if generalists, increased pest mortality by 13 %, decreasing pest abundance by 27.2 %, as compared to single releases or when BC agents were specialists. This may be explained by the ability of generalists to survive on the crop when the numbers of the target-pest are much reduced, and will thus be in place if the pest resurges (e.g. Palevsky *et al.* 2013).

The impact of host plants on ABAs

Plants are the habitat where herbivores live, feed and encounter their natural enemies, and are thus a major, interactive component of BC practices (Cortesero *et al*. 2000). Plants provide suitable or unsuitable arenas for predators (e.g. hairs, domatia), supplementary or entire diets (e.g. the leaf itself, pollen, various exudates) and host/ prey finding cues (e.g. volatiles), thus mediating pest-ABA interactions and their intensity. More predatory mites of the genera *Amblyseius* and *Hypoaspis* were found in soil under *Bromus sterilis* Linnaeus than underneath *Taraxacum officinale* (Linnaeus) (Wissuwa *et al.* 2012). Secondary plants, different plants or a secondary crop, grown along with the primary crop, are known to affect pests and their natural enemies (Parolin *et al.* 2012). An example is the weed

Ageratum conyzoides Linnaeus, intercropped in a citrus orchard, which continuously released volatiles that maintained populations of *Scapulaseius newsami* (Evans) which reduced those of the spider mite pest *Panonychus citri* (McGregor) (Kong *et al.* 2005).

Plant architecture

Pratt *et al*. (2002) compared the efficacy of *Neoseiulus fallacis* (Garman) against spider mites on various ornamentals, and found that plant architecture and foliar density were the major factors in predicting successful BC. This predator was most effective on shrubs and herbaceous perennials, less effective on conifers and shade trees. The foraging of *P. persimilis* on cucumber was affected by variations in plant structures, such as surface area, vestiture and the numbers, kinds and proportions of plant parts (Gontijo *et al*. 2012).

Many ABAs, especially phytoseiids, occur on wild and cultivated plants that grow near or within crops, and may serve as sources for predators (*i.e.* Mailloux *et al.* 2010). This idea was developed by using banker plants, intended to provide and sustain a reproducing and releasing system of natural enemies within a crop, providing long-term pest suppression (Huang *et al.* 2011; Parolin *et al.* 2013). An advantage of this system over augmentative BC is the continuous release of ABAs without their repeated, costly re-colonizations (Frank 2010). An early example was placing potted castor bean plants bearing the phytoseiid *Iphiseius degenerans* (Berlese) among pepper plants. After feeding on the castor bean pollen, the predator moved onto the peppers to control thrips there (Ramakers and Voets 1996).

Phylloplane (hairy leaves and shelters, including domatia)

The leaf surfaces of crops affect foraging ABAs, a topic recently reviewed by Schmidt (2014), will only be briefly discussed. The stigmaeid *Agistemus exsertus* Gonzalez, a predator of pest mites in Egypt, developed best on smooth, glabrous foliage, whereas rough, pubescent leaves were unsuitable for oviposition (Saber and Rasmy 2010). Likewise, more larvae of the onion thrips, *T. tabaci*, were attacked by *N. cucumeris* on the almost glabrous leaves of sweet pepper than on the more pilose foliage of cucumber and eggplant (Madadi *et al.* 2007). As noted, grape leaf pubescence may affect IGP outcomes. Similarly, Duso *et al.* (2003) found that *Typhlodroms pyri* Scheuten (Phytoseiidae) was more abundant on an apple variety with highly pubescent leaves than on foliage with few hairs. Kreiter *et al.* (2002) and Tixier *et al.* (2003) emphasized the importance of complex phylloplanes for *K. aberrans* on various plants, probably because dense trichome "forests" caught more pollen, providing nutrients for this ABA. The glandular trichoms on tomato stems and leaves bear sticky globules that may entrap predators; Drukker *et al.* (1997) have selected strain of *P. persimilis* that has adapted to performing on tomatoes.

Domatia are minute invaginations, pits or pouches that may be hidden by tufts of hairs often located on the undersides of leaves, can house various ABAs and fungivorous mites. These "resident" ABAs (mostly Phytoseiidae and Tydeidae) reduce IGP between ABAs. Leaves of *Cinnamomum camphora* (Linnaeus) J. Presl. bear four types of domatia, which enable the coexistence of antagonistic mites, including Eriophyidae and Phytoseiidae (Nishida *et al.* 2005). The phytoseiids *Amblyseius herbicolus* Chant and *Iphiseiodes zuluagai* Denmark and Muma co-occur on coffee and feed on each-other's larvae. Domatia on detached coffee leaves were either closed with glue or left open, and larvae and adults of both predators were released. Survival of larvae of both species was significantly higher (e.g, less IGP) on leaves with open domatia than on leaves with closed domatia (Ferreira *et al.* 2011). In addition, *I. zuluagai* preferred to place its eggs inside domatia. Matos *et al*. (2004) for instance advocated selecting coffee plants with domatia that would harbor predatory mites, in-built bodyguards, as protection against pest mites.

Pollen

Pollen may be the main diet of some phytoseiids or provide subsistence nutrients, maintaining and allowing predator development when prey is scarce. The availability of pollen can, as noted, affect the outcome of IGP contests between phytoseiids. Not all phytoseiids feed on pollen of the same plant

(Gerson *et al.* 2003); pollen of some plants may be rejected by one species while devoured by another (Kolokytha *et al.* 2011). Pollens of *Carpobrotus edulis* Linnaeus (Aizoaceae) and of *Scrophularia peregrina* Linnaeus enabled 84 % of the larvae of *Neoseiulus californicus* (McGregor) to reach adulthood, whereas only 28 % reached adulthood when fed mint, *Mentha piperita* Linnaeus, pollen (Ragusa *et al.* 2009). The beneficial effects of various pollens, whether from nearby hedgerows or from Rhodes grass, to phytoseiid abundance and pest control, were for instance reported by Duso *et al*. (2004) and by Maoz *et al*. (2011). The availability of pollen may however have unexpected results. Aguilar-Fenollosa *et al*. (2011) studied the effect of pollen of plants that grow in Spanish citrus groves on TSSM BC. Specialist phytoseiids (Type I and II) were consistently found in plots planted with *Festuca arundinacea* Schreber, resulting in better TSSM control. But in citrus plots with wild flower cover more pollen feeding generalists occurred, which competed with and reduced the number of the specialists, resulting in inadequate pest control. The populations of *A. swirskii* in greenhouses were augmented by spraying plants with pollen by electrostatic pollen supplementation (*i.e.* Weintraub *et al.* 2009). Numbers of *A. swirskii*, applied against WFT infesting sweet pepper were higher on the sprayed leaves, even in the absence of prey, thus in place should the pest arrive.

Stigmaeidae can also be reared with pollen. Goldarazena *et al*. (2004) reared three species of *Agistemus* on pollen of the ice plant [*Malephora croceae* (Jacq.) Schwant] and compared their development to individuals maintained on *P. citri*. Only *Agistemus cyprius* Gonzalez and *Agistemus industani* Gonzalez completed their development on this pollen, but produced fewer progeny in comparison with individuals given that prey. Other ABAs, like *Balaustium murorum* (Hermann) (Erythraeidae), feed on various pollens in all active stages, promoting larval survival (Yoder *et al*. 2012).

GMO (genetically modified organisms)

Pest control via transgenic (genetically modified) crops expressing the various *Bacillus thuringiensis* Berliner (Bt) endotoxins has become common (Harwood *et al.* 2005). The potential of genetically modified (GM) plants as components of integrated pest management (IPM) was discussed by Kos *et al*. (2009), who discussed that GM crops which express predator-attracting volatiles could enhance BC, provided their use has no negative non-target effects (Lövei *et al.* 2009); little has been written in regard to ABAs. The effect of pollen from GM maize (expressing the BTCry1Ab toxin) on ABAs was explored by Obrist *et al*. (2006).The development of *N. cucumeris* females offered pollen from transformed (Bt+) maize was slightly prolonged and their fecundity was reduced, in comparison with females offered untransformed (Bt-) pollen. This was attributed to the possible reduction in the nutritional quality of the Bt+ pollen rather than to any direct toxin direct. Zemek (2007) reached similar conclusions in regard to *N. cucumeris, P. persimilis* and *T. pyri* feeding on *T. urticae* infesting GM maize, although large amounts of the toxin accumulate in the preys' bodies (Torres and Ruberson 2008). No detrimental effects of various BTCry toxins, offered at field concentrations, on *Euseius concordis* (Chant) (toxins in drinking water) and on *N. californicus* (preying on *T. urticae* feeding on Bt+ cotton) were found by de Castro *et al*. (2013). A concentration of 0.018 mg/ml however reduced the reproduction of the former. Significantly fewer TSSM were consumed by *P. persimilis* on Bt+ eggplants than on Bt- plants, disrupting pest control (Rovenská *et al.* 2006).

Volatiles

Many pest- and spider mite-damaged plants release volatiles that attract natural enemies (Kessler and Baldwin 2001), including phytoseiids. Although diverse volatiles attract predators (Shimoda *et al.* 2005), methyl salicylate (MeSA) appears to be the commonest attractant especially for *P. persimilis* attracted by plants attacked by *T. urticae*. Several other phytoseiids, including *N. californicus* (Shimoda *et al.* 2005), *N. womersleyi* (Ishiwari *et al.* 2007), *N. cucumeris* (Tatemoto and Shimoda 2008), *N. fallacis* (Gardiner *et al.* 2005); *S. newsami* (Kong *et al.* 2005), *Typhlodromalus manihoti* (de Moraes) and *T.*

aripo De Leon (Gnanvossou *et al.* 2003) showed such attraction. The effect of *A. conyzoides* volatiles on populations of *S. newsami* was noted above.

Finally, in the laboratory the feeding of *Aceria tulipae* Keifer (Eriophyidae) on onion bulbs attracted *N. cucumeris*. However, as the bulbs are belowground, the results show only the potential for odour-mediated interactions in the soil; their significance remains to be demonstrated (Aratchige *et al.* 2004).The potential of attracting predators with plant volatiles in order to promote BC was discussed by Kaplan (2012). The dangers of non-target effects, like attracting enemies of the BC organisms (the "4th level consumers"), which could reduce biological control, and cause changes in BC communities, were among the risks noted.

ABAs in the soil

ABA activities in the soil were reported to limit the numbers of molting thrips, corn root worms (*Diabrotica virgifera* LeConte, Coleoptera: Chrysomelidae) and of nematodes, and in reducing the inoculum of plant-pathogenic fungi (Gerson *et al.* 2003). The great abundance of predatory mites in soils (Lundgren *et al.* 2009), including Phytoseiidae (Mineiro *et al.* 2012), suggests that they are an under-utilized BC resource.

Berndt *et al*. (2004) estimated the predatory capacity of *S. scimitus* and *G. aculeifer* (known in commerce as *Hypoaspis*), which feed on the soil-inhabiting molting stages of WFT. The latter, which was the better predator, had significantly more eggs, reproduced faster and raised larger populations. The authors concluded that *G. aculeifer* could control thrips populations with a release of 520 individuals/ square meter. Their efficacy is due to the fact that they inhabit the same soil strata; the presence of other prey (e.g. nematodes, Collembola) may however detract from their controlling effect (Wiethoff *et al.* 2004). Another soil-borne predator, *Lasioseius fimetorum* Berlese (Ascidae), was compared by Enkegaard and BrØdsgaard (2000) with *S. scimitus*. The former developed faster and had more progeny on thrips prey.

Large populations of *G. aculeifer* were associated with fewer numbers of the pest thrips *Pezothrips kellyanus* (Bagnall), which molts in the soil, and with less damage to citrus fruit. Adding composting manure to the soil was advocated by Navarro-Camposa *et al*. (2012) as a means of increasing mite numbers, thereby promoting the pest's control.

Species of *Gaeolaelaps* and of *Stratiolaelaps* feed on eggs and larvae of corn rootworm in the soil. Prischmann *et al*. (2011a) concluded that although they do not seriously reduce pest numbers, they may regulate immature rootworm populations. Qualitative and quantitative methods for monitoring ABA feeding in the soil are discussed below.

Plants may affect ABAs through their symbiotic associations with arbuscular mycorrhizal (AM) fungi and/or rhizobacteria. The growth rate of *P. persimilis* was enhanced when feeding on TSSM infesting these plants (Hoffmann *et al.* 2011). Further, mycorrhyzal bean plants infested by TSSM attracted more predators than non-mycorrhyzal beans (Schausberger *et al.* 2012). These results were obtained with plants grown in pots; their validity in the field remains to be determined. More *P. persimils* occurred on cucumbers treated with plant growth promoting rhizobacteria than on untreated plants, and more prey (TSSM) were located thereon by the predator (Tomczyk and Burda 2005).

Weeds, nematodes and ABAs

Gorse (*Ulex europaeus* Linnaeus) is an invasive spiny shrub that is an important weed in Australia, Hawaii, New Zealand and North America (Rees and Hill 2001). The early success of *Tetranychus lintearius* Dufour (Tetranychidae) in its control is currently being curtailed by phytoseiid predators (Davies *et al.* 2009).

The great specificity of eriophyids to their host plants has made them ideal agents of weed control (reviewed by Smith *et al.* 2010). The assayed eriophyids were listed and the few that were released and had become established were noted. Although the fitness of the target plants was reduced, it was not clear to what extent did the mites reduce weed populations. Such partial results were attributed to

natural enemies (noted above), resistant plant genotypes, and to adverse abiotic conditions. In addition, some eriophyids have co-evolved with their host weeds and may thus be unsuitable for controlling them (because of low harmufness).

Several eriophyids vector viral plant diseases that could be used for weed control. Weed pathogens can also be spread by other ABAs. The erythraeid *Balaustium* sp. (Prostigmata) carried spores of several plant pathogenic fungi without being infected (Yoder *et al.* 2009).

Members of about 30 families contain nematophagous mites, consisting of members of the Mesostigmata, Astigmatina (Astigmata), Oribatida (Cryptostigmata), Endeostigmata and Prostigmata (Gerson, in press). Such species abound in soils; Beaulieu and Walter (2007) collected almost 70 Mesostigmata from the soil and litter of Australian forests, most of which were generalist predators that fed on nematodes. They differ in their feeding habits: some swallow the entire nematode ("engulfers"), whereas others puncture and mangle their prey, ingesting the body fluids. They may roughly be consigned to three functional groups (Walter *et al.* 1988), namely general feeders, fungivores and detritivores, and specialized predators of nematodes. No member of the latter group is known to reduce populations of pest nematodes.

Soil type strongly affects mite predation on nematodes, being strongest in sandy, light to medium soils (El-Banhawy *et al.* 2006). Evidence for mite control of nematodes in pots was provided, among others, by Shoala and El Kady (2009), who showed that 60 females of the cunaxid *Neocunaxoides andrei* (Baker and Hoffmann) significantly reduced the numbers of *Meloidogyne javanica* (Treub) galls on tomato roots. Other aspects of mite-nematode interactions were discussed by Gerson (in press).

A drawback for using nematophagous mites would be their preying on entomopathogenic nematodes (EPN), applied against other pests. A recent example is *Sancassania polyphyllae* (Zachvatkin) (Acaridae), which attacks the infective nematode juveniles (IJs) of the EPN *Steinernema glaseri* (Steiner) that emerge from cadavers of their beetle host (Cakmak *et al.* 2013).

Diseases of ABAs

The diseases of phytoseids were recently summarized by Bjornson (2008), Hoy and Jeyaprakash (2008) and by Schütte and Dicke (2008); data on other ABAs were unavailable. Microorganisms found on and in various Phytoseiidae were listed by Schütte and Dicke (2008), but only a few caused any damage, mostly when the predators are under stress, as in mass-rearing facilities. The disease factors include the bacterium *Acaricomes phytoseiuli* Schütte *et al.* and several microsporidia. The bacterium, apparently restricted to *P. persimilis*, is transmitted via feces and debris, causing reduced fitness. The phytoseiid *Galendromus occidentalis* (Nesbitt) (formerly in *Metaseiulus*) infected by *Cardinium*, a bacterium from the *Bacteroidetes* group, has a shorter life, fewer progeny and a male-biased sex ratio (Wu and Hoy 2012). The microsporidium *Oligosporidium occidentalis* Becnel *et al.* shortens the life of *G. occidentalis*, reduces its fecundity and causes a male-biased sex ratio (Hoy and Jeyaprakash 2008).

Only few viruses were detected in the Phytoseiidae and their negative effects are unknown (Schütte and Dicke 2008). There are also a few reports of diseases affecting ABAs in the field, e.g. an infection of *Euseius citrifolius* Denmark and Muma by the fungus *Neozygites* sp. in Brazil (Furtado *et al.* 1996). The presence of potential disease factors on and in ABAs in the field may become a problem when they are brought into the laboratory to be mass-reared; requiring screening and sanitation procedures.

The effect of pesticides on ABAs

ABAs are often affected by pesticides applied against co-occurring pests, and information about their effects on ABAs is thus required. The relevant literature is very large and only a sample will be presented. Bernard *et al.* (2004) suggested standards for the ecotoxicological testing of various pesticides and their acute and sublethal effects on phytoseiids. Most data concern *P. persimilis*, which appears to be tolerant to many acaricides and insecticides (Ahn *et al.* 2004; Lash *et al.* 2007; Lee *et al.* 2008). According

to Bostanian *et al*. (2009), thiacloprid, spinosad and methoxyfenoxide were harmless to the adults of *P. persimlis* and had no effect on fecundity, but showed some repellence at 24 h intervals for 72 h. Argolo *et al*. (2014) compared the relative toxicity several pesticides on the phytoseiids *Euseius stipulatus* (Athias-Henriot), *N. californicus* and *P. persimilis.* The most tolerant was *E. stipulatus*, followed by *N. californicus* and by *P. persimilis*, indicating that the latter should be used as an indicator species of pesticide effects on predacious mites occurring in Spanish citrus orchards. *Stratiolaelaps scimitus* was very susceptible to dicofol and chlorpyrifos but the insect growth regulator (IGR) pyriproxyfen and some fungicides were almost harmless (Cabrera *et al*. 2004). The plant-derived rotenone and pyrethrins were very lethal to *P. persimlis* (Duso *et al.* 2008). *Acarophenax lacunatus*, although tolerant to various pyrethroids, still parasitized eggs of *R. dominica* (Gonçalves *et al.* 2004). Diatomaceous earth formulations have been assayed against various food pests. Athanassiou and Palyvos (2006) reported that *Blattisocius keegani* Fox (Mesostigmata, Ascidae) and *Cheyletus malaccensis* (Oudemans) were very susceptible to these compounds. As to fungicides, Auger *et al*. (2004) found that *K. aberrans* and *T. pyri* showed variable resistance to the fungicide mancozeb.

The effects of some modern acaricides with novel modes of action on predatory mites were reviewed by Dekeyser (2005), and Hardman *et al*. (2003) formulated an index for determining the selective toxicities of acaricides to pest and predatory mites, based on data from eastern Canada. Such a useful tool should also be formulated for other crop systems in other areas. The OECD has developed a standardised protocol for testing the effect of plant protection products on soil mites in the European Union, using *G. aculeifer* (possibly actually *S. scimitus*) as a model BC organism (Smit *et al*. 2012). The realization that some phytoseiids (especially those like *Euseius* spp.) feed on plant sap (Adar *et al.* 2012) argues against using systemic pesticides, which could kill these predators.

New techniques in ABA application

Rearing, distributing, long-term maintenance and overwintering of ABAs

Methods for mass-rearing ABAs (those that are not protected by patents) and for quality control were noted by Gerson *et al*. (2003). More recently Nguyen *et al.* (2014) developed an artificial diet for *A. swirskii*, and Freire and de Moraes (2007) described a new method for mass producing *S. scimitus*. BC personnel have used various methods for the distribution of ABAs in greenhouses. A mechanical dispenser to distribute *P. persimilis* in a rose greenhouse was used by Casey and Parrella (2005), reducing TSSM infestations by about 50 %. Opit *et al*. (2005) used mechanical blowers to disperse phytoseiids in a greenhouse, the blowers providing better coverage than the manual method. Shaw and Wallis (2007) applied *P. persimilis* against TSSM infesting hop by a motorized leaf blower, a method four times faster than hand distributing, and Adar *et al*. (2014) provided pollen on-twine for phytoseiids in greenhouses.

Ghazy and Amano (2014) reported that mated females of the Japanese strain of *N. californicus*, maintained at 100 % RH and 5 ºC, survived for several weeks without affecting the quality of their progeny (egg hatchability, survival and sex ratio), data that could promote ABA survival during unexpected changes in temperatures and for storing before releasing.Young females of *P. persimilis* tolerated prolonged (18 days) exposure to either 5 or 10 °C and starvation without compromising their quality (Luczynski *et al.* 2008). Such data promotes the long-term storage of these (and possibly other) phytoseiids. Kawashima and Jung (2010) placed artificial shelters on the ground to monitor the winter survival of several phytoseiids in an apple orchard in Japan. This idea was developed by Szabo and Penzes (2013) who transferred ground litter from orchards containing large numbers of the overwintering phytoseiid *Amblyseius andersoni* (Chant) to young orchards, thereby significantly increasing their numbers in the control plots.

Molecular methods

Cuthbertson *et al*. (2003b) and Prischmann-Voldseth *et al*. (2011b) used PCR (polymerase chain reaction) to determine the extent of feeding by Anystidae and Laelapidae on aphids, and on corn rootworms and nematodes, respectively. Estimates of the consumption of *D. virgifera* immatures by various predators were obtained by Lundgren *et al*. (2009), who analyzed the predators' gut contents by using *D. virgifera*-specific DNA sequences with the quantitative polymerase chain reaction (qPCR). The data were used to generate taxon-specific prey consumption indices for the major predator taxa. The only ABA named in that study was the anystid *Chaussieria*. Read *et al*. (2006) obtained a quantitative estimate of the feeding of *S. scimitus* on nematodes. They sequenced fragments of cytochrome oxidase I (COI) mtDNA and designed species-specific primers that amplified 154-, and 203-bp fragments for each nematode species.

A qualitative molecular method for detecting the nematode remains within the bodies of their predators was developed by Read *et al.* (2006), using specific nematode primers. Heidemann *et al.* (2011), who used this approach, noted that detection time for various prey may differ between nematodes, and determined the extent of nematophagy and detritophagy of several species.

The detection of secondary predators (e.g. predators of predators), by amplified prey DNA, and then that of the first predator, in which the prey DNA was detected, was described by Sheppard *et al.* (2005). DNA was found in the secondary predator up to eight hours after the first had fed on the prey. King *et al.* (2008) reviewed methods for DNA-based approaches to the molecular analysis of predation, including collecting, preservation and preparation of material, designing primers and so on.

The future use and application of ABAs

Phytophagous mites were formerly the main target of predatory Acari, but with the realization that ABAs can also reduce the damage of insect pests, e.g. thrips and whiteflies, as well as nematodes, weeds and even fungi, the spectrum of pernicious targets has expanded, and can be expected to widen further in the future. The above summation attempted to present the current ABA situation in order to try and indicate future possibilities and trends. The oft-repeated cliché that additional ABAs (whether indigenous and/or exotic) should be found and assayed (e.g. Knapp *et al.* 2013) still needs to be emphasized. Surveying (or prospecting) for ABAs (especially phytoseiids) in recent years has resulted in regional faunistic lists of such mites, as well as in the discovery of new species (*i.e.* Halliday 2005; Papadoulis *et al.* 2009; Kreiter *et al.* 2010; Barbar 2013; Döker *et al*. 2014 and others). Such efforts, to include non-phytoseiid ABAs also (like eriophyiids for weed control, Asadi *et al.* 2014), should be encouraged. Practitioners trying any of the newly-found exotics should follow the guidelines of the Convention on Biological Diversity (Cock *et al.* 2009), and the various biosecurity-related legislations for preventing the introduction of alien organisms. With this in mind, the classical method of BC (e.g. introduction) is still practiced (e.g, Smith *et al.* 2010; Maoz *et al.* 2011). Predicting the possible success of exotic BC agents, based on a meta-analysis of historical data, was discussed by Kimberling (2004), an approach that could be useful in predicting the outcome of intentional introductions and their possible ecological outcomes in new environments. Skirvin *et al.* (2002) constructed a model that indicated the importance of plant species and the spatial dynamics of mite pest and phytoseiid predator in determining the outcome of BC in ornamental crops.

Beside introduction, the other two BC modes, augmentation (e.g. Casey and Parrella 2005; Adar *et al.* 2014) and conservation (Kawashima and Jung 2010, and above, effect of pesticides) of ABAs, have become more common. This is due to the increasing use of indigenous ABAs (e.g. Maoz *et al.* 2014), and is expected to become more prevalent. The problem of the decreasing number of traditional mite taxonomists could be offset by applying molecular methods (Gaskin *et al.* 2011) and applying statisti-

cal methods for morphological continuous characters (Tixier 2012, 2013). Next generation sequencing (NGS) was discussed by Pompanon *et al*. (2012), an approach that has the potential to reveal many consumed species simultaneously (DNA metabarcoding) and to identify the species found in pooled samples.

Although most Phytoseiidae of Types II, III and IV are (within broad limits) generalists, some exceptions were noted, e.g, biotypes or more-specialized races (e.g. McMurtry 2013 *et al.* and Table 2). By "conditioning" or learning (Schausberger *et al*. 2010; Peralta-Quesada and Schausberger 2012), such ABAs might become more specialized "biopesticides", being attracted to certain prey (or to their host-plants). Choe *et al*. (2012) recently found that many free-living and parasitic nematodes produce small molecules (ascarosides), used as species-specific signaling for mate finding and aggregation. Conditioning soil predators to becoming attracted to these compounds could enhance their efficacy as nematophages. Subterranean tulip bulbs infested by eriophyid mites produce odours that attract predatory mites (Aratchige *et al.* 2004), a finding that suggests a new approach for exploiting ABAs in the soil.

The efficacy and rearing of ABAs (especially phytoseiids) can be increased by mechanical mite dispensers (Opit *et al.* 2005), by artificial diets (Nguyen *et al.* 2014), by developing methods to predict future phytoseiid numbers on crops (Kawashima and Jung 2010), by providing on-plant shelters, like domatia, and by modeling (e.g. Skirvin *et al.* 2002).

Determining the role of secondary predators, as noted, would help in establishing the actual efficacy of any ABAs whose pest controlling role has been questioned (Roberts *et al.* 2011).

Interactions between ABAs and other BC factors, whether resulting in IGP or other interactions, bear further studies, but the addition of acaropathogenic fungi to ABAs seems to reduce overall control.

The option of introducing ABAs (indigenous and/or exotic) against soil pests may be hindered by the specific conditions pertaining there (e.g. structure and texture, moisture, pH, salinity as well as by resource competition). On the other hand, soil cover (non-crop vegetation or mulch, Navarro-Camposa *et al.* 2012) increases the numbers of natural enemies, including ABAs (Tsitsilas *et al.* 2010). In light of the beneficial effect of AM fungi on ABAs (Schausberger *et al.* 2012), promoting these fungi along with the relevant plant communities may increase predator attraction to pest infested plants (Bennett 2012).

The use of various mites, not necessarily ABAs, as vectors of entomophagous and/or nematophagus fungi and/or viral weed diseases affecting pests is another potential option. In the context of IPM, the effects of various pesticides and their side-effects (including those of plant origin), by standardized toxicological tests (Bernard *et al.* 2004) is to be continued.

The effects of new lighting technologies on plants, and their effects on herbivorous and beneficial arthropods in high-technology greenhouse production (Vänninen *et al.* 2010), may change the impact of ABAs in that environment.

The increasing use of GMO plants requires more studies about their effects on pests and (in the present context) on ABAs. The few cases noted are probably far from the full picture. The option of using GMO plants to produce more ABA-attracting volatiles (Kos *et al.* 2009), suggests yet another approach.

Most efficient ABAs are known to affect mite pests, which beg the question whether ABAs may also reduce the numbers of insect pests, to similar extents. The considerable damage caused by the mites *Varroa* and *Acarapis* to honey bee colonies (Sammataro *et al.* 2000) suggests that other Acari could also seriously reduce insect pest populations.

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