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## Alternative food and biological control by generalist predatory mites: the case of *Amblyseius swirskii*

Arne Janssen · Maurice W. Sabelis

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The use of predatory mites for the control of pests has a long history (Huffaker and Spitzer 1951; Huffaker and Kennett 1956; Fleschner 1959; Bravenboer and Dosse 1962), and started at a time when there was still doubt about the regulation of prey populations by predators (Huffaker and Kennett 1956). One of the first attempts of biological control with predatory mites was carried out in strawberry in California, USA, where the generalist predator *Neoseiulus reticulatus* was released to control cyclamen mites (Huffaker and Kennett 1953, 1956). Generalist predatory mites do not depend on the pest only, but can also use alternative food. Its role in the persistence of predator populations at low pest densities was already acknowledged in these early studies: “A relatively high predator population usually is able to sustain itself for 2 months or more with very low populations of the cyclamen mite. When hungry, these predators have been observed to feed on honeydew, sugar solutions, egg yolk and other liquid foods.” (Huffaker and Kennett 1953). This ability to feed on alternative food was not always considered an advantage for biological control, but was taken as a sign of predators not being well adapted to the pest (Huffaker et al. 1969). Nevertheless, several of the early studies already showed that the presence of alternative prey for the predators did not negatively affect biological control, but rather improved it (Huffaker and Kennett 1956; Collyer 1964).

Nevertheless, the emphasis in biological control of greenhouse pests has been on the use of specialist natural enemies for several decades (*Encarsia formosa* against greenhouse whitefly and *Phytoseiulus persimilis* against spider mites; Gould 1977). Perhaps this was caused by the long-standing conventional wisdom that biological control was most likely successful when using specialist natural enemies (Doutt and DeBach 1964; Murdoch et al.

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In memory of my coauthor, teacher, colleague and dear friend Maurice Sabelis, who sadly did not live to see the appearance of this special issue.

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1985; Parrella et al. 1999; Symondson et al. 2002). Indeed, the majority of successful biological control cases at that time concerned the use of parasitic insects, especially host-specific species (Beirne 1962). The reasons for not using generalist predators were that (1) they could also target non-pest species (van Lenteren et al. 2003), (2) their dynamics would not be synchronized with the pest, and (3) generalists usually do not have a high potential for increase (Murdoch et al. 1985). Whatever the reasons, the early examples of successful biological control with generalist phytoseiids were picked up not earlier than decades later by Ramakers (1980), Ramakers and van Lieburg (1982) and de Klerk and Ramakers (1986). These authors showed that the phytoseiids *Amblyseius barkeri* and *A. cucumeris* can control thrips in greenhouse crops. Moreover, being generalists, these predators could be mass-produced on alternative prey that were cheap and easy to rear (Ramakers and van Lieburg 1982). These predators and other species (e.g., *Iphiseius degenerans*) can feed and reproduce on sweet pepper pollen, and could therefore be introduced into the flowering crop even before the occurrence of thrips (de Klerk and Ramakers 1986, van Rijn et al. 2002).

Since the pioneering work by Ramakers and colleagues, the use of generalist phytoseiids for pest control has gained a strong foothold; however, the original concerns of using generalist predators remain. Especially the first, predators attacking non-pest species, increased with the growing attention for intraguild predation among natural enemies (Rosenheim et al. 1995), obviously occurring more frequently with generalist predators than with specialists. Evidently, this point needs careful attention, but the occurrence of intraguild predation often does not disrupt biological control (Janssen et al. 2006), and biological control with generalist predators (not only phytoseiid mites) has been successful in many cases. The second concern with using generalist predators, i.e. the lack of synchronization with the pest and the relatively low population growth rate, may actually be advantageous for biocontrol. Synchronization of natural enemies with the pest implies that natural enemy densities will decrease when pest densities are low, and this may facilitate new pest invasions. In contrast, pest outbreaks can be prevented by maintaining populations of generalist natural enemies through the presence of alternative food sources (Collyer 1964; Ramakers 1990; Karban et al. 1994; Hanna et al. 1997; Walde et al. 1997; van Rijn et al. 1999; Nomikou et al. 2002; van Rijn et al. 2002; Liu et al. 2006; Nomikou et al. 2010). The presence of such a standing army of natural enemies also remedies the third objection to using generalists, i.e. that of a lower potential of increase.

Until recently, studies on alternative food for phytoseiid natural enemies mainly considered non-pest foods, such as pollen, nectar or relatively harmless herbivorous arthropods (Bakker and Klein 1992; Hanna et al. 1997; Karban et al. 1997; van Rijn et al. 2002). This changed with the introduction of the predatory mite *Amblyseius swirskii*. It was collected from the field (Nomikou et al. 2001) and tested for its capacity to control whiteflies (Nomikou et al. 2001, 2002, 2004), and was subsequently found to be able to control thrips as well (Messelink et al. 2006). Further research showed that this generalist can effectively control both pests at the same time (Messelink et al. 2008; Calvo et al. 2011) and has potential to control other pests as well (Wimmer et al. 2008; Arthurs et al. 2009; van Maanen et al. 2010; Park et al. 2010). This has ignited significant interest in this predatory mite, which is increasingly used for biocontrol (estimated at 30,000 ha worldwide; Knapp and van Houten, Pers Comm, 2015), and is currently subject of much research (over 80 publications during the last 6 years, over 50 during the last 3 years; Web of Science<sup>TM</sup>). This special issue, with contributions of authors from two continents, is an attempt to analyse the causes and consequences of the current success of *A. swirskii*.

## This issue

The first contribution (Calvo et al. 2015) illustrates that the current success of *A. swirskii* in Europe was a matter of being at the right place at the right time, and in the right quantities: the predator became commercially available when German consumers demanded Spanish products with fewer pesticide residues. This forced Spanish growers to change from chemical to biological control with this predatory mite in just a few years. Calvo and colleagues also show that the development of a cheap rearing method contributed significantly to the success. In the second paper of this special issue, Hewitt et al. (2015) show that, together with *A. swirskii*, there is still a role for the predatory mite *N. cucumeris* in controlling thrips in chrysanthemum. This is because *N. cucumeris* is a more cost-effective biological control agent under climate conditions prevalent in this crop during winter. Subsequently, Buitenhuis et al. (2015) review the use of *A. swirskii* in greenhouse crops in North America, with emphasis on greenhouse ornamentals, and conclude that an important reason for the success of this predator is its capacity to control several pests concurrently.

Although persistence of populations of the generalist *A. swirskii* does not depend on the presence of one pest species, it is still desirable to introduce the predators in the crop before pests occur and supply them with alternative food, especially in ornamentals where economic damage levels are much lower than in vegetable crops. In the fourth contribution to this special issue, Kumar et al. (2015) specifically address the establishment of predator populations in a crop before pest invasions. They identify several pepper cultivars that potentially serve as banker plants for *A. swirskii*. Along a similar vein, Delisle et al. (2015a, b) assess the suitability of several types of alternative food for *A. swirskii* and *N. cucumeris*, such as various types of pollen and eggs of the moth *Ephestia kuehniella*. Apple pollen was the most suitable alternative food, and supplementing *A. swirskii* with it resulted in better control of western flower thrips on chrysanthemum (Delisle et al. 2015b). Similarly, Leman and Messelink (2015) test various types of alternative food for *A. swirskii* and *Amblydromalus limonicus*, but they specifically consider the possibility that western flower thrips also benefits from this food (van Rijn et al. 2002). In short-term laboratory experiments, they show that predation of thrips by individual *A. swirskii* was reduced when pollen was present. However, supplying pollen or eggs of *E. kuehniella* in a chrysanthemum crop enhanced control of thrips because of the strong numerical response of the predators to the supplied food.

## Prospects

The paper by Leman and Messelink (2015) addresses a potential problem of switching behaviour of generalist predators: when these natural enemies have a strong preference for one food source, populations of less preferred pest species may temporarily escape from predation and cause significant damage. Indeed, thrips did temporarily escape from control by *A. swirskii* when whiteflies are also present in the crop, but good control of both pests was achieved over a longer period of time (Messelink 2012; van Maanen et al. 2012). A relevant question therefore is how to avoid that predators preferentially feed on the supplied food, resulting in temporary increases of pest populations. In our opinion, supplementing predators such as *A. swirskii* with superior alternative food is a viable biological control practice, as several studies have shown (van Rijn et al. 2002; Nomikou et al. 2010; Delisle et al. 2015b; Leman and Messelink 2015). Especially when predators and alternative food are introduced into the crop before pests occur, the densities of the predators will, after some

time, be limited by the availability of the alternative food. This lack of food will cause the predators to switch to feeding on the pest. Furthermore, predators sometimes perform better on a mixed diet than on single diets (Messelink et al. 2008); hence, they may actually prefer feeding on both alternative food and target prey. A further question is how to supply the alternative food. When alternative food is supplied in pulses with intervals that are relatively long compared to the generation time of the predators, this may result in strong fluctuations in predator densities, and densities of the pests will subsequently also fluctuate (Abrams et al. 1998). Thus, pests may occasionally reach such high densities that damage may exceed economically tolerable levels. Hence, alternative food should probably be added to the crop at intervals that are short relative to the predator's generation time.

In conclusion, the critical attitude towards the use of generalist predators for biological pest control that initially dominated the scientific literature seems to have been countered by examples of excellent control of greenhouse pests by natural enemies such as *A. swirskii*. This does not mean that the original criticism on generalist predators was unfounded. It rather indicates that careful examination of the characteristics of predators and the role of alternative food is needed. The current interest in generalist predators can stimulate such research and help design biological control programs in which the benefits of using generalist predators can be put to practice, while reducing the risks to a minimum. We are convinced that the contributions of this special issue on *A. swirskii* are an important step in this direction.

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