Host plant specificity in several species of generalist mite predators

J . J . B E A R D and G . H . W A L T E R Department of Zoology and Entomology, The University of Queensland, Brisbane, Australia

Abstract. 1. Species in the genus *Neoseiulus* are considered to be generalist predators, with some species used in biological control programmes against phytophagous mites and insects.

2. A general survey of *Neoseiulus* species in inland Australia indicated that different species are associated with particular tree species. This pattern of host plant use was investigated for four *Neoseiulus* species (*N. buxeus*, *N. cappari*, *N. brigarinus*, *N. eremitus*) by means of a sampling programme through time and across space.

3. Each species of *Neoseiulus* was collected entirely or mostly from one species of tree; little or no overlap was detected despite the tree species growing in well-mixed stands. Host plant specificity thus appears to be strong in this genus.

4. Species in two other genera (*Pholaseius* and *Australiseiulus*), also considered to be predatory, showed a similar association with particular tree species.

5. The implications for the use of these predators in biological control are considerable. In particular, phytoseiid species with specific needs in terms of host plants may not be suitable for use as general purpose predators. Meeting the needs of phytoseiids through the modification of host plant attributes may be a step towards enhancing their efficacy as biological control agents.

Key words. *Australiseiulus*, biological control, generalist, mating system, mite, *Neoseiulus*, Phytoseiidae, predator, specialist.

Introduction

Most species in the genus *Neoseiulus* Hughes (Acari: Phytoseiidae) are considered to be generalist predators although some apparently feed selectively on *Tetranychus* spider mites (Acari: Tetranychidae) (McMurtry & Croft, 1997). As generalists, *Neoseiulus* mites are thought to consume a broad range of mite and insect species, including various tetranychids, eriophyids, tarsonemids, acarids, thrips, and whiteflies (Muma, 1971; Hansen & Geyti, 1987; McMurtry & Rodriquez, 1987; Hansen, 1988; Hoy & Glenister, 1991; Teulon, 1991; Gough, 1992; McMurtry & Croft, 1997). They are also thought capable of reproducing on non-prey items including pollen, plant exudates, and honeydew (Dosse, 1961; Ramakers, 1990; van Rijn & Sabelis, 1990; James, 1993; Tanigoshi *et al.*, 1993). Most information about generalist mite predators relates to their feeding habits, and almost invariably

Correspondence: J. J. Beard, Department of Zoology and Entomology, The University of Queensland, Brisbane, Queensland, Australia, 4072.

this information comes from laboratory observation. The primary focus has been on prey selectivity or specificity (Congdon & McMurtry, 1988), and how this and other information relates to the use and importance of phytoseiids in agriculture (Eickwort, 1983; McMurtry, 1991, 1992; McMurtry & Croft, 1997).

The predatory activities of phytoseiids invariably take place on the leaf surface. The mites generally shelter in protected sites, within domatia and leaf axils, for example, and from there they are presumed to attack prey. The local ecology of phytoseiids is, therefore, reputedly influenced strongly by leaf morphology, to the extent that the presence of sheltered habitats on leaves may be more important than food availability in influencing the abundance of some species (Rasmy & El-Banhawy, 1974; Duso, 1992; Karban *et al.*, 1995; McMurtry & Croft, 1997). Although the physical structure of plants is considered to have influenced the evolution of generalist phytoseiids to a greater extent than has their broad diet (McMurtry & Croft, 1997), host plant associations within the Phytoseiidae, and predatory mites in general, have not received much attention in the literature. A

few phytoseiid species are evidently confined to a narrow range of host plants. These include *Typhlodromalus aripo* de Leon (Bakker & Klein, 1993), *T. manihoti* (Moraes) (= *T. limonicus* s.l.) (Garman & McGregor) (de Moraes *et al.*, 1993), the three known species of *Eharius* (de Moraes *et al.*, 1986), *Kampimodromus aberrans* (Hadam *et al.*, 1986), and two species of *Euseius* (*E. hibisci* and *E. tularensis*) (Congdon & McMurtry, 1985; McMurtry & Croft, 1997), however host plant specificity of even these species has not been investigated quantitatively.

It is reported here that several species in the genus *Neoseiulus* are associated differentially with particular plant species, even in mixed stands of woodland. Prior to this study, collection records for this genus in Australia indicated that the group was found most commonly in the drier, inland parts of the country. This pattern was investigated with a preliminary survey for *Neoseiulus* species at six sites across south-east Queensland and northern New South Wales. From these preliminary data, several questions about the plant associations of species in the genus arose and were addressed through a more refined sampling programme. It was demonstrated that plant-specific associations of species within the genus *Neoseiulus* hold through time and across space. These results have implications for biological control, which are discussed together with several possible explanations for such a pattern.

Methods and materials

Preliminary survey

Six sites (described below) were sampled across south-east Queensland and northern New South Wales between Warwick (Queensland, 28°13′S, 152°02′E) and Narrabri (New South Wales, 30°20′S, 149°46′E) for predatory mites in the family Phytoseiidae, on 2–3 November 1996. The most abundant tree species at each site (one to three species) were sampled, and sites were chosen to allow a broad range of tree species and habitat types to be investigated.

Ten samples were taken for each tree species sampled at each site. Each sample consisted of five 20-cm long terminal branchlets (with leaves), and was taken by walking haphazardly through the site and stopping to remove five branchlets from the chosen tree species, within a 3-m radius of the stopping point. Each such sample usually derived from two to five trees. Samples from conspecific plants were a minimum of 30 m apart.

Samples were stored at 4 °C and processed within 10–24 h of collection. The entire surface of all leaves, stems, and bark was examined under a dissecting microscope for the presence of phytoseiids. Particular attention was given to all structures that could shelter mites, including those inherent in the plant's architecture, leaf mines and galls (leaf and stem) with emergence holes, leaves rolled by thrips or other insects, empty pupal cases, disused psyllid (lerp) scales, various insect exuviae, shells of hatched hemipteran and lepidopteran eggs, and any webbing or silk present. Mites were removed using a fine paintbrush, stored in 80% alcohol, cleared in Nesbitt's

solution, and mounted on microscope slides in either Hoyer's medium or Heinze-PVA (Evans, 1992).

All six sites sampled comprised open woodland, mainly *Eucalyptus* (Myrtaceae), with a ground cover of grasses and weeds. Any exceptional conditions, the tree species present, and those tree species sampled are given below.

Site 1: 15 km west of Warwick, 2 November 1996; sampled unidentified species of low-growing *Acacia* (Mimosaceae) and mixed *Eucalyptus* species. Little grass was present and no weeds. Site 2: 80 km west of Warwick, 2 November 1996; sampled unidentified Rutaceae species with needle-like leaves. Site 3: 69 km east of Goondiwindi (28°32′S, 150°18′E) along the bank of the McIntyre River, 2 November 1996; sampled a native cypress pine *Callistris* sp. (Cupressaceae). Site 4: 41 km east of Goondiwindi, 2 November 1996; sampled monoculture of brigalow *Acacia harpophylla* (Mimosaceae). Site 5: 24 km east of Goondiwindi, 2 November 1996; sampled poplar boxwood *Eucalyptus populnea* F. Muell., *Eremophila mitchelli* Benth. (Myoporaceae), and brigalow *A. harpophylla*. Site 6: 60 km south of Moree (29°28′S, 145°50′E), 3 November 1996; sampled *Eu. populnea*, *A. harpophylla*, and a she-oak *Casuarina cristata* Miq. (Casurarinaceae).

Persistence through time

The pattern of host plant specificity within the genus *Neoseiulus* that emerged from the data collected at site 5 during the preliminary survey (see Results) was investigated further. The six most common tree species at site 5 were sampled on four occasions 2 months apart (see below). The processing of samples commenced immediately, using the methods outlined for the preliminary survey, and was completed within 5 days of collection, when all mites were still alive. The tree species sampled and the sampling dates (see below) were: *Eu. populnea* ABCD, *Er. mitchelli* ABCD, *A. harpophylla* ABCD, *Capparis mitchelli* BCD, *Geijera parviflora* Lindl. (Rutaceae) BC, and *Cas. cristata* BC; A = 2 November 1996 (preliminary survey), B = 11 January 1997, C = 8 March 1997, D = 11 May 1997.

Consistency across space

To investigate whether the pattern was also consistent across space, the four species of trees on which mites were present persistently throughout the temporal survey (*Eu. populnea*, *Er. mitchelli*, *A. harpophylla*, *Ca. mitchelli*) were sampled at site 5 and at an additional three sites (7, 8, 9) within 200 km of site 5, on 10 and 11 May 1997. The sites were all extensive stands of open woodland with a thick ground-cover of grasses and weeds. *Capparis mitchelli* and *A. harpophylla* were not present at sites 8 and 9 respectively. Site 7: 37 km east of Moonie (27°43′S, 150°22′E), 10 May 1997. Site 8: 100 km west of Moonie, 10 May 1997. Site 9: 140 km west of Goondiwindi, 11 May 1997. As most individuals of *Eu. populnea* present were taller than 10 m, most of the samples were taken from the lowest foliage. *Eucalyptus populnea*, *Er. mitchelli*, *Ca.*

mitchelli, and *A. harpophylla* were sampled at Site 5 (24 km east of Goondiwindi) on 11 May 1997.

The sampling and processing methods used were the same as those outlined for the preliminary survey, but because *Ca. mitchelli* was uncommon at sites 7 and 9, some samples were taken from individual trees, not from a few trees. Sample processing commenced immediately and was completed within 14 days of collection, by which time virtually all mites located (98.4%, $n = 562$) were still alive; the few that had died were readily identifiable.

Results

Preliminary survey

Adult phytoseiids were collected at only two of the six sites (1 and 5) (Table 1). A few immatures were collected at sites 2 and 4 but species level identification was not possible for these. Overall, 67 phytoseiid adults were collected (Table 1), representing nine species, six of them undescribed previously (Beard, 2001). Site 5 had the greatest diversity of mite species, including three new species of *Neoseiulus* and a new species in each of the genera *Phytoseius* and *Australiseiulus*, namely *P. brigalow* Walter & Beard and *A. goondi* Beard. Each of the three species of *Neoseiulus* was collected from a different species of tree, without any overlap. *Neoseiulus buxeus* Beard ($n = 6$) was collected only from *Eu. populnea*, *N. eremitus* Beard ($n = 1$) from *Er. mitchelli*, and *N. brigarinus* Beard ($n = 5$) from *A. harpophylla*. Although numbers of individuals collected were low, the mites were dispersed among the samples (see ranges in Table 1), indicating that the mites were dispersed throughout the site.

The other phytoseiid species collected, from site 1 (Table 1), included a new species of *Phytoseius*, *P. acaciae* Walter & Beard, from a species of *Acacia*, *Amblyseius waltersi* Schicha from the same species of *Acacia*, and *Olpiseius noncollyerae* Schicha (see Beard, 2001) from mixed *Eucalyptus* spp.

Persistence through time

Adults of each species of *Neoseiulus* at site 5 were collected entirely or predominantly from a single different species of tree, a pattern that held through 6 months (Table 2). All life stages of *N. buxeus*, *N. eremitus*, and *N. edestes* Beard were collected entirely from *Eu. populnea*, *Er. mitchelli*, and *G. parviflora* respectively (Tables 2 and 3). *Neoseiulus cappari* Beard was associated strongly with *Ca. mitchelli*, with 73 of 77 adults collected from this tree species (Table 2). Although *N. brigarinus* adults were collected from two species of tree, *A. harpophylla* (14 adults) and *Casuarina cristata* (11 adults), the mites were present on the latter tree species on only one occasion (8 March 1997). Furthermore, individuals of *N. brigarinus* from *A. harpophylla* differ morphologically from those on *Cas. cristata* in minor ways and they may in fact represent separate species (Beard, 2001).

Consistency across space

The pattern of differential host plant association was also consistent across space (Fig. 1) although numbers of adults collected were low at some sites. *Neoseiulus eremitus* showed the strongest association with a particular plant species (Fig. 1c), being collected at all sites and only ever from *Er. mitchelli*. *Neoseiulus brigarinus* was collected at sites 5 and 7, and only on *A. harpophylla* (Fig. 1d), but its alternative host plant, *Ca. cristata*, was not sampled beyond site 5 during this survey. Although poplar boxwood *Eu. populnea* was sampled at all sites investigated, 97 out of the 98 adult *N. buxeus* collected were found at site 5, and all were taken from this host species. The only other individual, an adult male, was collected at site 7 from *Ca. mitchelli* (Fig. 1b). *Neoseiulus cappari* was collected at all sites and was associated with more tree species than any of the other *Neoseiulus* species; however, at each site where *Ca. mitchelli* was present, *N. cappari* was found on that plant in higher numbers than on any other plant species

Table 1. Total number of adults of each species of Phytoseiidae collected during the preliminary survey, with sample ranges.

Mite species	Site number					
	1	2	3	4	5	6
Phytoseius acaciae	38 (0–7)	0	0	0	0	0
Phytoseius brigalow	0	0	0	0	1	0
Neoseiulus brigarinus	0	0	0	0	5 (0–2)	0
Neoseiulus eremitus	0	0	0	0	1	0
Neoseiulus buxeus	0	0	0	0	6 (0–2)	0
Olpiseius noncollyerae	7 (0–3)	0	0	0	0	0
Amblyseius waltersi	1	0	0	0	0	0
Euseius victoriensis	0	0	0	0	5 (0–2)	0
Australiseiulus goondi	0	0	0	0	3 (0–2)	0

Table 2. Percentage of the total number of individual adults of each species of *Neoseiulus* collected at site 5, for the four sampling dates including the preliminary survey (2 November 1996, 11 January, 8 March, and 11 May 1997), and the host plant from which they were collected. Numbers of individual adults of each species collected on each sampling date are given, in chronological order. Note that *Ca. mitchelli* was not sampled during the preliminary survey and *G. parviflora* and *Cas. cristata* were each sampled only twice (11 January 1997, 8 March 1997).

Mite species	Tree species					
	Eremophila mitchelli	*Acacia harpophylla*	*Eucalyptus populnea*	*Capparis mitchelli*	*Casuarina cristata*	*Geijera parviflora*
N. eremitus	100	0	0	0	0	0
$n = 8, 0, 38, 10$						
N. brigarinus	0	56	0	0	44	0
$n = 5, 0, 17, 3$						
N. buxeus	0	0	100	0	0	0
$n = 6, 7, 39, 97$						
N. cappari	0	5	0	95	0	0
$n = *, 4, 46, 27$						
N. edestes	0	0	0	0	0	100
$n = *, 1, 1, *$						

*Not sampled.

Table 3. Total number of nymphs of *Neoseiulus cappari*, *N. eremitus*, *N. buxeus*, and *N. brigarinus* collected from each tree species at all sites and collection dates.

Mite species	Tree species				
	Capparis mitchelli	*Eremophila mitchelli*	*Eucalyptus populnea*	*Acacia harpophylla*	*Casuarina cristata*
N. cappari	28	1	0	0	0
N. eremitus	0	17	0	0	0
N. buxeus	0	0	51	0	0
N. brigarinus	0	0	0	13	1

sampled. At site 7, *N. cappari* was abundant on *Ca. mitchelli* and in considerably lower numbers on both *A. harpophylla* and *Eu. populnea* (Fig. 1a). *Neoseiulus edestes* was collected from one *Ca. mitchelli* sample at site 7, however its association with, and abundance on, wilga [*G. parviflora*; with which it appears to be associated (Table 2)] was not assessed during this survey.

When the total numbers of individual adults are considered, each of the species of *Neoseiulus* showed strong to very strong host plant specificity (Table 4). From 73% (*N. brigarinus*) to 100% (*N. eremitus*) of individuals of each species were collected from one particular species of tree, over a period of 6 months and across a broad area of mixed habitat.

Nymphs and other species

The host plant associations apparent for the adults of each *Neoseiulus* species also held for their immature stages (Table 3). Identification of nymphs was based on the similarity of certain characters with those of the adults (Beard, 2001).

Additional previously undescribed species of *Neoseiulus* were collected during the spatial survey. Although mostly present in low numbers, they were also associated with particular plant species. The most common of these additional species was *N. paloratus* Beard, collected at sites 7 and 8 from both *A. harpophylla* (48 adults) and *Er. mitchelli* (two adults). Phytoseiids other than *Neoseiulus* were also collected from the spatial samples and they, too, were consistent in their host plant relationships. *Pholaseius colliculatus* Beard and *Australiseiulus goondi* Beard showed a strong association with *Eu. populnea* (Table 5).

Mite shelters

All phytoseiid individuals, regardless of life stage, were found within sheltered microhabitats on the leaves or stems of the tree they inhabited. They were found primarily in deserted leaf and stem galls, in leaf mines, or in the axils of stems and petioles. The locations in which mites were found differed among plant species. On *Eu. populnea*, most of the phytoseiids
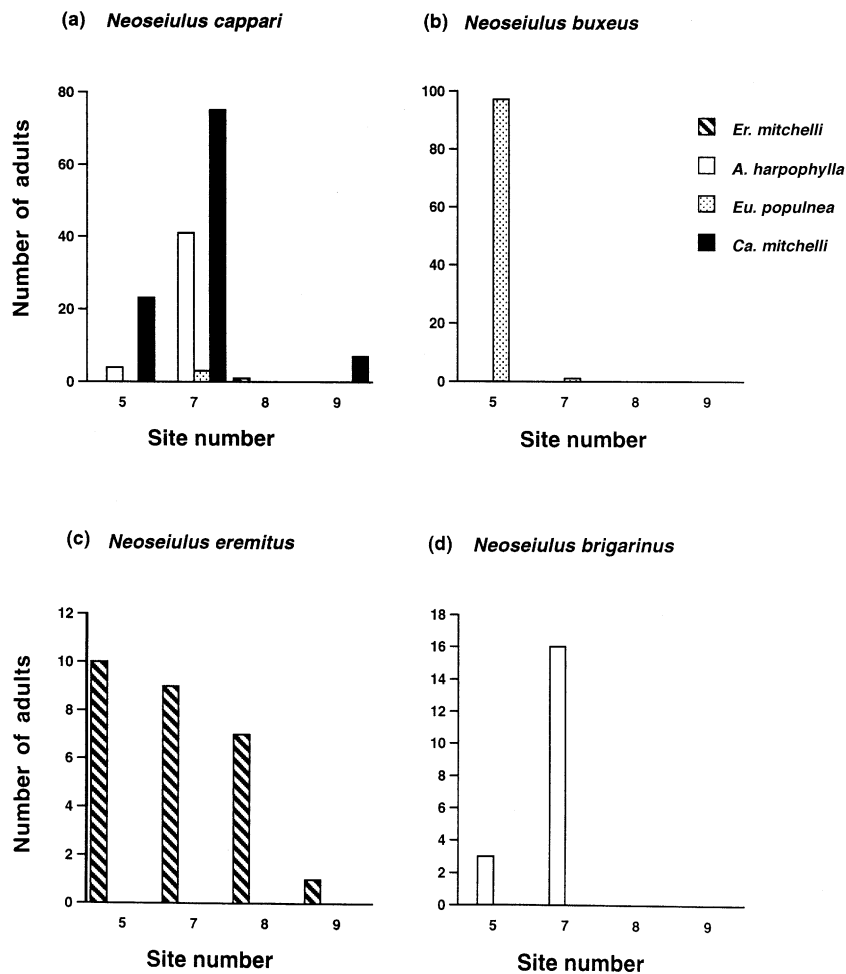
(a) *Neoseiulus cappari*

(b) *Neoseiulus buxeus*

(c) *Neoseiulus eremitus*

(d) *Neoseiulus brigarinus*

Legend:

- ▨ *Er. mitchelli*
- ☐ *A. harpophylla*
- ▦ *Eu. populnea*
- ■ *Ca. mitchelli*

Fig. 1. Number of adults of the different *Neoseiulus* species collected during the survey of consistency across space from each of the host tree species sampled: *Eremophila mitchelli*, *Acacia harpophylla*, *Eucalyptus populnea*, and *Capparis mitchelli*. *Capparis mitchelli* and *A. harpophylla* were not present at sites 8 and 9 respectively.

Table 4. Total number of adults of *Neoseiulus cappari*, *N. eremitus*, *N. buxeus*, and *N. brigarinus* collected at all sites and collection dates, from each of the five most common tree species.

	Tree species				
Mite species	*Capparis mitchelli*	*Eremophila mitchelli*	*Eucalyptus populnea*	*Acacia harpophylla*	*Casuarina cristata*
N. cappari	155	1	3	45	0
N. eremitus	0	73	0	0	0
N. buxeus	1	0	149	0	0
N. brigarinus	0	0	0	30	11

($n = 354$), regardless of species, were collected from within deserted galls in the leaves (84%) and stems (14%). Most phytoseiids collected on *A. harpophylla* ($n = 151$) were collected from leaf galls (54%) or from leaf mines (25%).

On *Er. mitchelli*, phytoseiids ($n = 115$) were associated most commonly with structures on the stems; 57% were collected from within the leaf axil itself or from a cup-like structure under the leaf axil, and 22% were found within empty stem

Table 5. Number of adult *Pholaseius colliculatus* Beard (*P. c.*) and *Australiseiulus goondi* Beard (*A. g.*) collected on each tree species sampled at each site during the survey of consistency across space.

Site number	Tree species							
	Eremophila mitchelli		*Acacia harpophylla*		*Eucalyptus populnea*		*Capparis mitchelli*	
	P. c.	*A. g.*	*P. c.*	*A. g.*	*P. c.*	*A. g.*	*P. c.*	*A. g.*
5	0	0	0	0	0	7	0	0
7	0	0	0	0	33	3	0	0
8	0	0	0	0	27	9	†	†
9	0	1	†	†	27	6	0	0

†Not sampled.

galls. Phytoseiids on *Ca. mitchelli* (*n* = 205) were collected most commonly from stem hollows made by borers or galling insects (65%). The differences in location of predators reflect the availability of sheltered habitats on each plant species, as the type and abundance of each type of shelter differed among plant species.

Discussion

Pattern of Neoseiulus *distribution*

Most Phytoseiidae are considered to be generalist predators and, as they are mobile, they are also assumed to range generally across a diversity of plant species and to take a variety of prey. These premises underpin the evaluation and use of phytoseiids in biological control (e.g. McMurtry, 1992) but they are contradicted by the data presented in Tables 1, 4, and 5 and Fig. 1. Mite species in several genera were associated differentially with, and showed strong fidelity towards, particular species of plants in mixed woodland (Tables 1, 4, and 5, Fig. 1). This pattern indicates that each of the phytoseiid species sampled has differential and specific requirements, and suggests that the notion of *Neoseiulus* species being generalists is somewhat misleading. The data thus extend, to predacious mites, the growing body of evidence that suggests that the concept of generalist has only a limited capacity to explain or predict the behaviour of insects in the field (e.g. Wint, 1983; Velasco & Walter, 1993; Milne & Walter, 2000).

At least three alternative explanations are consistent with the plant-specific distribution documented for the *Neoseiulus* species covered by this paper, but they are not mutually exclusive. The provision of three basic requirements by the host plant may explain the recorded pattern: shelter, food, and the location of sexual partners. Two of these assume that the mite species sampled are indeed primarily predacious, although this proposition needs to be tested in the field because it derives principally from laboratory observations of a limited number of species (e.g. Croft *et al.*, 1998). Each of these explanations of plant species fidelity are distinguished and discussed below, in relation to the requirements of the

mites. Thereafter, the implications of the results for the use of *Neoseiulus* species in biological control are detailed.

Host plant associated microhabitats. Each of the species sampled may have specific requirements, such as shelters or particular oviposition sites, that are met only by the particular host plant species on which they were recorded. For example, every individual phytoseiid, regardless of life stage, was found within a small physical shelter on leaves or stems. The structure of these refuges varied among the plant species sampled, and each refuge type may have characteristics important to the survival of one or more life stages of each particular *Neoseiulus* species. Mites on plants, especially Phytoseiidae, are known to shelter in cracks and crevices and other natural structures such as leaf axils (Chant, 1959; McMurtry *et al.*, 1970; Jeppson *et al.*, 1975), and this strong association with shelters has been demonstrated with work on domatia (O'Dowd & Willson, 1989; Walter, 1992, 1996; Walter & O'Dowd, 1992; Grostal & O'Dowd, 1994). It seems that mites aggregate, and lay eggs, within domatia primarily to avoid the extremes of environment that can be experienced at the leaf surface (Grostal & O'Dowd, 1994), and the presence or absence of domatia on plants has been demonstrated to have a striking effect on the population of predatory mites. The removal of domatia from leaves can lead to a reduction in the abundance, distribution, reproductive activity, and prey consumption of the resident predatory mites (Grostal & O'Dowd, 1994). All types and shapes of domatia are inhabited by predatory mites (O'Dowd & Willson, 1989) but neither the pattern of occupancy at a species level nor the specific requirements of each mite species has been investigated.

Other aspects of leaf and plant morphology, such as hair abundance, have been shown to influence the behaviour and distribution of phytoseiids, and they usually do so independently of prey availability (Overmeer & van Zon, 1984; Duso, 1992; Karban *et al.*, 1995; McMurtry & Croft, 1997). For example, two species of phytoseiid show strong fidelity for the cassava plant *Manihot esculenta* Crantz, and each occupies a specific microhabitat associated with the plant. *Typhlodromalus aripo* is almost invariably found in the apices or growing points of cassava plants, where densities reach well over 100 mites per growing point, despite no prey species ever

being found there (Bakker & Klein, 1993). By contrast, *T. manihoti* is found almost exclusively on the leaves of cassava, and at higher frequencies than any other phytoseiid on cassava (Bakker & Klein, 1993). These observations support the suggestion that the Australian *Neoseiulus* species investigated may well have specific physical and host plant-related requirements; however if the types of shelter available on each of the plant species investigated do not differ (with respect to the requirements of the *Neoseiulus* species), some other aspect of the plant or of the predators' requirements must presumably influence their distribution and plant species associations.

Prey specificity. Prey availability may determine the species of plant with which each predator species is associated. This would most likely occur if the predators were adapted specifically to feeding on a prey species that was itself restricted in host plant range. No evidence from the field is known that would help to assess the validity of this alternative. The patterns of plant associations demonstrated in Tables 1, 4 and 5 and Fig. 1 refute strongly the notion that phytoseiids range generally in nature consuming a variety of prey. The mites may, however, consume the variety of prey that is available on a single plant species. Such behaviour has been demonstrated with the host-plant restricted *T. aripo* and *T. manihoti*. Despite their restricted distribution on cassava (see above), these two predators have a somewhat varied diet as they feed on whatever prey species is present in their specific intra-plant microhabitat (Bakker & Klein, 1993). The species composition of their diet varies with geographic locality, feeding site, and the intra-plant distribution of the prey. If the same is true of the Australian *Neoseiulus* species, the term *generalist* is still not the most appropriate descriptor of their habits and local ecology.

Mating behaviour. The fidelity shown towards particular plant species by each *Neoseiulus* species could be part of the mechanism by which the two sexes are brought together for mating within a spatially heterogeneous environment. That a specific part of the environment provides a focal point for *closure of the life cycle* (Sinclair, 1988) is well known in motile organisms from several taxa. Examples of this are *Muellerianella* bugs associated with particular plant species (Drosopoulos, 1985), aphodiine dung beetles specific to a particular micro-environment within dung pads (Holter, 1982), parasites specific to particular parts within gills of fish (Rohde, 1979), and Atlantic herring that respond to particular currents and physical features within the ocean (Sinclair, 1988). How mites locate mates over a distance in nature seems not to have been considered in the literature, and warrants closer investigation.

Implications for biological control

Most interactions between acarine predators and their prey have been studied for biological control purposes, almost invariably under laboratory conditions or on commercial,

introduced, or cultivated plants (Gerson, 1992). How accurately the derived interpretations reflect what takes place in nature on native plants has yet to be established. Previously, the ecology of phytoseiids has been interpreted strongly in relation to the resources that they are considered to use (see Introduction). In contrast, the data presented here and those published by others (e.g. Bakker & Klein, 1993) suggest that resources represent only one facet of the local ecology of phytoseiid mites. Aspects of the host plant influence the behaviour and distribution of phytoseiids independently of prey availability and distribution. The strong host plant specificity of putative generalist predators, as documented here, must change the way in which such species are investigated and their ecology interpreted. The implications for biological control are considerable.

Phytoseiid species with specific needs in terms of host plants may not be amenable for use as generalist predators in biological control, and the species most appropriate to a particular host plant, pest species, or agricultural situation will have to be sought. Treating such species as generalists, and using them in biological control as generalists, will inevitably result in mismatching of natural enemy species with agricultural situations, and this could well explain the inconsistent levels of control or survivorship commonly recorded for species of phytoseiids across different crop species (e.g. Congdon & McMurtry, 1985; McMurtry, 1992; Scott Brown *et al.*, 1999).

Emphasis in understanding the ecology of predacious mites should be redirected from diet alone and placed on the range of specific requirements of the predatory species, and whether these are satisfied by the plant species on which biological control is desired. Consideration of the effects of different plant species and different plant attributes on natural enemies is becoming more prevalent in biological control research (e.g. Cortesero *et al.*, 2000). It may even be possible that certain attributes of crop plants, in particular those that are favourable to natural enemies (e.g. those with natural shelters or domatia), may be enhanced through breeding or genetic modification to increase the survivorship and reproductive output of natural enemies (Cortesero *et al.*, 2000).

Future opportunities to study native phytoseiid predators should include consideration of the natural host plant associations of the species involved, through appropriate sampling designed to include negative records (see Walter & Benfield, 1994). Further, feeding studies should be conducted on the plant species with which the predator is primarily associated, to yield information about its usual diet. The potential of the species as a biological control agent on other plant species can then be assessed experimentally against these requirements, and testable predictions about biological control performance can be made in relation to the known requirements of the species.

Acknowledgements

Cooperative Research Centre for Tropical Pest Management, The University of Queensland.

References

Bakker, F.M. & Klein, M.E. (1993) Host plant mediated coexistence of predatory mites: the role of extrafloral nectar and extrafloral domatia on cassava. In: *Selecting phytoseiid predators for biological control, with emphasis on the significance of tritrophic interactions* (F. M. Bakker), pp. 33–64. PhD thesis, University of Amsterdam, The Netherlands.

Beard, J.J. (2001) A review of Australian *Neoseiulus* Hughes and *Typhlodromips* de Leon (Acari: Phytoseiidae: Amblyseiinae). *Invertebrate Taxonomy*, **15**, 73–158.

Chant, D.A. (1959) Phytoseiid mites (Acarina: Phytoseiidae). Part I. Bionomics of seven species in southeastern England. Part II. A taxonomic review of the family Phytoseiidae, with descriptions of 38 new species. *Canadian Entomologist*, **91** (Suppl. 12), 5–164.

Congdon, B.D. & McMurtry, J.A. (1985) Biosystematics of *Euseius* on California citrus and avocado with the description of a new species (Acari: Phytoseiidae). *International Journal of Acarology*, **11**, 23–30.

Congdon, B.D. & McMurtry, J.A. (1988) Prey selectivity in *Euseius tularensis* (Acari: Phytoseiidae). *Entomophaga*, **33**, 281–288.

Cortesero, A.M., Stapel, J.O. & Lewis, W.J. (2000) Understanding and manipulating plant attributes to enhance biological control. *Biological Control*, **17**, 35–49.

Croft, B.A., Monetti, L.N. & Pratt, P.D. (1998) Comparative life histories and predation types: are *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) similar Type II selective predators of spider mites? *Environmental Entomology*, **27**, 531–538.

Dosse, G. (1961) Uber die bedeutung der pollennahrung fur *Typhlodromus* (*T.*) *pyri* Scheuten (= *tiliae* Oud.) (Acari, Phytoseiidae). *Entomologia experimentalis et applicata*, **4**, 191–195.

Drosopoulos, S. (1985) Acoustic communication and mating behaviour in the *Muellerianella* complex (Homoptera – Delphacidae). *Behaviour*, **94**, 183–201.

Duso, C. (1992) Role of *Amblyseius aberrans* (Oud.), *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) (Acari, Phytoseiidae) in vineyards. III. Influence of variety characteristics on the success of *A. aberrans* and *T. pyri* releases. *Journal of Applied Entomology*, **114**, 455–462.

Eickwort, G.C. (1983) Recommendations for future basic research on mites as biological control agents. *Biological Control of Pests by Mites* (ed. by M. A. Hoy, G. C. Cunningham and L. Knutson). Proceedings of a Conference held on 5–7 April, 1982 at the University of California, Berkeley, U.S.A., pp. 172–173.

Evans, G.O. (1992) *Principles of Acarology*. CAB International, Wallingford, U.K.

Gerson, U. (1992) Perspectives on non-phytoseiid predators for the biological control of plant pests. *Experimental and Applied Acarology*, **14**, 383–391.

Gough, N. (1992) Prospects for IPM in greenhouse ornamentals in Australia. Report of a study tour on Integrated Pest Management in ornamental crops in Holland, U.K. & U.S.A., July, 1991. Department of Primary Industries, Indooroopilly, Queensland, Australia.

Grostal, P. & O'Dowd, D.J. (1994) Plants, mites and mutualism: leaf domatia and the abundance and reproduction of mites on *Viburnum tinus* (Caprifolicaceae). *Oecologia*, **97**, 308–315.

Hadam, J.J., AliNiazee, M.T. & Croft, B.A. (1986) Phytoseiid mites of major crops in the Willamette Valley, OR, and pesticide resistance in *Typhlodromus pyri* Scheuten. *Environmental Entomology*, **15**, 1255–1262.

Hansen, L.S. (1988) Control of *Thrips tabaci* [Thysanoptera: Thripidae] on glasshouse cucumber using large introductions of predatory mites *Amblyseius barkeri* [Acarina: Phytoseiidae]. *Entomophaga*, **33**, 33–42.

Hansen, L.S. & Geyti, J. (1987) Possibilities and limitations of the use of *Amblyseius mckenziei* Sch. & Pr. for biological control of thrips (*Thrips tabaci* Lind.) on glasshouse crops of cucumber. *Integrated and Biological Control in Protected Crops* (ed. by R. Cavalloro), pp. 145–150. Proceedings of the EC Expert Group, Heraklion, 24–25 April 1985. A. A. Balkema, Rotterdam/Brookfield, The Netherlands.

Holter, P. (1982) Resource utilization and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). *Oikos*, **39**, 213–227.

Hoy, C.W. & Glenister, C.S. (1991) Releasing *Amblyseius* spp. [*Acarina: Phytoseiidae*] to control *Thrips tabaci* [*Thysanoptera: Thripidae*] on cabbage. *Entomophaga*, **36**, 561–573.

James, D.G. (1993) Pollen, mould mites and fungi: improvements to mass rearing of *Typhlodromus doreenae* and *Amblyseius victoriensis*. *Experimental and Applied Acarology*, **17**, 271–276.

Jeppson, L.R., Keifer, H.H. & Baker, E.W. (1975) *Mites Injurious to Economic Plants*. University of California Press, Berkeley, U.S.A.

Karban, R., English-Loeb, G., Walker, M.A. & Thaler, J. (1995) Abundance of phytoseiid mites on *Vitis* species: effects of leaf hairs, domatia, prey abundance and plant phylogeny. *Experimental and Applied Acarology*, **19**, 189–197.

McMurtry, J.A. (1991) Augmentative releases to control mites in agriculture. *Modern Acarology*, Vol. I (ed. by F. Dusbabek and V. Bukva), pp. 151–157. Acadmia, Prague, SPB Academic Publication, The Hague, The Netherlands.

McMurtry, J.A. (1992) Dynamics and potential impact of 'generalist' phytoseiids in agroecosystems and possibilities for establishment of exotic species. *Experimental and Applied Acarology*, **14**, 317–382.

McMurtry, J.A. & Croft, B.A. (1997) Life styles of phytoseiid mites and their roles in biological control. *Annual Review of Entomology*, **42**, 291–321.

McMurtry, J.A., Huffaker, C.B. & van de Vrie, M. (1970) Ecology of tetranychid spider mites and their natural enemies: a review. I. Tetranychid enemies: their biological characters and the impact of spray practices. *Hilgardia*, **40**, 331–458.

McMurtry, J.A. & Rodriquez, J. (1987) Nutritional ecology of phytoseiid mites. *Nutritional Ecology of Insects, Mites and Spiders, and Related Invertebrates* (ed. by F. Slansky and J. Rodriquez), pp. 609–644. John Wiley and Sons, New York.

Milne, M. & Walter, G.H. (2000) Feeding and breeding across host plants within a locality by the widespread thrips *Frankliniella schultzei*, and the invasive potential of polyphagous herbivores. *Diversity and Distributions*, **6**, 243–257.

de Moraes, G.J., de Alencar, J.A., Lima, J.L.S. & Yaninek, J.S. (1993) Alternative plant habitats for common phytoseiid predators of the cassava green mite (Acari: Phytoseiidae, Tetranychidae) in north-east Brazil. *Experimental and Applied Acarology*, **17**, 77–90.

de Moraes, G.J., McMurtry, J.A. & Denmark, H.A. (1986) *A Catalogue of the Mite Family Phytoseiidae*. EMBRAPA-DDT, Brasilia.

Muma, M.H. (1971) Food habits of the Phytoseiidae (Acarina: Mesostigmata) including some common species on Florida citrus. *Florida Entomologist*, **54**, 21–34.

O'Dowd, D.J. & Willson, M.F. (1989) Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. *Biological Journal of the Linnean Society*, **37**, 191–236.

Overmeer, W.P.J. & van Zon, A.Q. (1984) The preference of

Amblyseius potentillae (Garman) (Acarina: Phytoseiidae) for certain plant substrates. *Acarology VI, Vol. 1* (ed. by D. A. Griffiths and E. E. Bowman), pp. 591–596. Ellis Horwood, Chichester, U.K.

Ramakers, P.M.J. (1990) Manipulation of phytoseiid thrips predators in the absence of thrips. *Bulletin of the Section Regionale Ouest Palearctique/West Palaearctic Regional Section*, **8**, 169–172.

Rasmy, A.H. & El-Banhawy, E.M. (1974) Behaviour and bionomics of the predatory mite *Phytoseius plumifer* (Acarina: Phytoseiidae) as affected by physical surface features of host plants. *Entomophaga*, **19**, 255–257.

van Rijn, P.C.J. & Sabelis, M.W. (1990) Pollen availability and its effect on the maintenance of populations of *Amblyseius cucumeris*, a predator of thrips. *International Symposium of Crop Protection, Mededelingen Van de Faculteit der Landbouwwetenschappen Rijksuniversiteit Gent*, **55**, 335–342.

Rohde, K. (1979) A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *American Naturalist*, **114**, 648–671.

Scott Brown, A.S., Simmonds, M.S.J. & Blaney, W.M. (1999) Influence of species of host plants on the predation of thrips by *Neoseiulus cucumeris*, *Iphiseius degenerans* and *Orius laevigatus*. *Entomologia experimentalis et applicata*, **92**, 283–288.

Sinclair, M. (1988) *Marine Populations: an Essay on Population Regulation and Speciation*. Washington Sea Grant Program. University of Washington Press, Seattle and London.

Tanigoshi, L.K., Megevand, B. & Yaninek, J.A. (1993) Non-prey food for subsistence of *Amblyseius idaeus* (Acari: Phytoseiidae) on cassava in Africa. *Experimental and Applied Acarology*, **17**, 91–96.

Teulon, D.A.J. (1991) *Biological Control of Thrips (Thysanoptera) with Reference to New Zealand*. A report submitted to The Lincoln College Foundation and The New Zealand Nurserymen's Association. Pennsylvania State University, University Park, U.S.A.

Velasco, L.R.I. & Walter, G.H. (1993) Potential of host-switching in *Nezara viridula* (Hemiptera: Pentatomidae) to enhance survival and reproduction. *Environmental Entomology*, **22**, 326–333.

Walter, D.E. (1992) Leaf surface structure and the distribution of *Phytoseius* mites (Acarina: Phytoseiidae) in south-eastern Australian rainforests. *Australian Journal of Zoology*, **40**, 593–603.

Walter, D.E. (1996) Living on leaves: mites, tomenta, and leaf domatia. *Annual Review of Entomology*, **41**, 101–114.

Walter, D.E. & O'Dowd, D.J. (1992) Leaves with domatia have more mites. *Ecology*, **73**, 1514–1518.

Walter, G.H. & Benfield, M.D. (1994) Temporal host plant use in three polyphagous Heliothinae, with special reference to *Helicoverpa punctigera* (Wallengren) (Noctuidae: Lepidoptera). *Australian Journal of Ecology*, **19**, 458–465.

Wint, W. (1983) The role of alternative host-plant species in the life of a polyphagous moth, *Operophtera brumata* (Lepidoptera: Geometridae). *Journal of Animal Ecology*, **52**, 439–450.