The contribution of extrafloral nectar to survival and reproduction of the predatory mite *Iphiseius degenerans* on *Ricinus communis*

Paul C.J. van Rijn*‡ and Lynell K. Tanigoshi

Washington State University, Research and Extension Unit, 1919 NE 78th Street, Vancouver, WA 98665, USA

(Received 29 April 1997; accepted 16 April 1998)

ABSTRACT

The phytoseiid mite *Iphiseius degenerans* (Berlese) is an effective predator of western flower thrips, *Frankliniella occidentalis* (Pergande), in Dutch greenhouses. In the Mediterranean area, castor bean, *Ricinus communis* L., is known as a year-round host plant for this predatory mite. On flowering castor bean plants in greenhouses, *I. degenerans* can be found in densities of more than 100 per leaf. For this reason, the plant is being used as a 'banker' plant to augment biological control. It has been shown that pollen produced by the large apical flowers sustains reproduction and development for these mites. The objective of this study was to measure the contribution of the extrafloral nectar of this plant to the reproductive success of this predatory mite. A study conducted at 25°C in presence of free water showed that (1) *I. degenerans* is unable to develop beyond the protonymphal stage when fed only nectar and leaf tissue, (2) its ovipositional rate is higher when pollen is supplemented with nectar, (3) its reproduction ceases within a few days when fed on nectar only, but the predator can survive for several weeks and resume oviposition when fed pollen again and (4) the feeding of young females for one or two weeks with nectar only extends their longevity by approximately the same period and only slightly diminishes their lifetime reproductive potential (R_0), as compared to mites continuously fed pollen. It can be concluded that extrafloral nectar can provide an important contribution to population growth and maintenance of *I. degenerans* on *R. communis*, particularly in pre- and post-blooming periods. Assuming these predators are beneficial to the plant in clearing them of herbivorous mites and thrips, this relationship may be regarded as an example of plant–predator mutualism. The combination of pollen and extrafloral nectar makes castor bean an ideal rearing and banker plant for *I. degenerans*.
Exp Appl Acarol 23: 281–296 © 1999 Kluwer Academic Publishers

Key words: Bodyguards, plant–predator mutualism, tritrophic interactions, castor bean, phytoseiids, life history, pollen, banker plant, biological control.

* To whom correspondence should be addressed at: Tel: +31 20 5257711; Fax: +31 20 5257754; e-mail: rijn@bio.uva.nl

‡ Present address: University of Amsterdam, Section Population Biology, Kruislaan 320, 1098 SM Amsterdam, The Netherlands.

INTRODUCTION

In recent years, extrafloral nectaries (EFNs) have been recognized as an investment in plant–predator mutualism. Predators and parasitoids of a plant's herbivores are known to be attracted by these nectaries (Bentley, 1977; Rogers, 1985; Koptur, 1992; Whitman, 1994) and in turn provide the plant protection against these herbivores. Plant-inhabiting predatory mites, particularly Phytoseiidae, are important predators of herbivorous mites and thrips (Helle and Sabelis, 1985; Sabelis and Van Rijn, 1997), but have generally been overlooked in EFN studies, with a few exceptions. Pemberton (1993) reported on predatory anystid mites (*Anystis* sp.) feeding on extrafloral nectaries of *Prunus* and *Populus* species in South Korea. In addition, Walter and O'Dowd (1995) discussed a laboratory experiment which showed that survival of the predatory phytoseiid mite *Metaseiulus occidentalis* (Nesbitt) on shoots of *Viburnum tinus* L. clearly decreased when the foliar nectaries were excised. Finally, Bakker and Klein (1993) showed that phloem sap exuded at the petioles of cassava, *Manihot esculenta* Crantz, has positive effects on survival of both juveniles and adults of the phytoseiid mite *Typhlodromalus manihoti* Moraes (= *Typhlodromalus limonicus* s.l.). Moreover, Bakker and Klein (1992) experimentally showed that the presence of droplets of a similar sugar source (honey) coincided with higher predator numbers and lower densities of its prey, *Mononychellus tanajoa* Bondar, on the cassava plant.

On castor bean, *Ricinus communis* L. (Euphorbiaceae), several types of EFNs are present: paired disc-shaped nectaries at the leaf base, one or two smaller conical nectaries on the upper side of the petiole and several nipple-like glands on the stem close to the leaf attachments. The nectar consists mainly of sucrose, glucose and fructose in approximately equal amounts and contains at least 14 different amino acids, albeit in considerably lower amounts than in the phloem sap (Baker *et al.*, 1978). Castor bean has been recognized as a good host plant for plant-inhabiting phytoseiid mites and at least 36 different species have been collected from it worldwide (de Moraes *et al.*, 1986), including 16 *Euseius* species and two species found on castor bean only, *Euseius ricinus* Moraes and *Indoseiulus ricini* (Ghai and Menon). The most reported phytoseiid on castor bean in the Mediterranean area is *Iphiseius degenerans* Berlese (Swirski and Amitai, 1961; de Moraes *et al.*, 1986). In the Middle East, *I. degenerans* is commonly present on castor bean year round (Wysoki and Swirski, 1971). As with most phytoseiid species, *I. degenerans* feeds on herbivores such as spider mites (Eveleigh and Chant, 1981; Nwilene and Nachman, 1996) and thrips (Van Houten *et al.*, 1995), two arthropod groups that are commonly present on castor bean (Jeppson *et al.*, 1975; Ananthakrishnan, 1984). In addition to these prey, pollen of castor bean is known to be a good food source for this predator (Ramakers and Voet, 1995). As the pollen-rich male flowers are located at the top of the plant, the pollen becomes readily distributed throughout the plant. Ramakers and Voet (1995, 1996) recognized the possibility of utilizing the castor bean plant as a rearing and 'banker' system for *I. degenerans*, thereby facilitating biological control of western flower thrips on greenhouse-grown

sweet pepper (Van Houten and Van Stratum, 1993). They also observed that these phytoseiid mites could be readily introduced and maintained before the pollen or prey was present. The utilization of extrafloral nectar might account for this survival. Moreover, feeding on leaf tissue is a possibility that should be taken into account as well (Porres *et al*., 1976; Grafton-Cardwell and Ouyang, 1996). The aim of our study, therefore, was to unravel the contribution of pollen, extrafloral nectar and leaf tissue to the reproductive success of *I. degenerans* on castor bean plants.

MATERIAL AND METHODS

Mite cultures
Iphiseius degenerans was originally collected in Morocco by J.A. McMurtry (UC Riverside, CA, USA) and reared on various pollens for many years prior to these experiments. In Vancouver (WA, USA) the mites were kept in a climate room at approximately 25°C and 70% RH. The mites were reared on rectangular PVC arenas (35 × 20 cm) placed on top of a 4 cm high foam pad in a larger water-containing plastic utility tray. To provide a water source for the mite colony, the edges of the arena were covered with wet tissue paper which contacted the water barrier in the tray. As additional water sources three strips of moist filter paper (20 × 1 cm) were placed across the arena at equal distances. Sewing threads served as oviposition substrates. Pollen of hazel (*Corylus avellana* L.) or birch (*Betula pubescens* Ehrh.) was supplied as a food source every other day. New rearing units were started from eggs which resulted in cohorts with a maximum age difference of 2 days.

Experimental conditions
All experiments were performed in a climate room at 24.5 ± 1.0°C, 70 ± 5% RH and L : D 14 : 10 h. Cohorts of *I. degenerans* were transferred to bright green 4 × 5 cm PVC arenas placed on blocks of 2 cm thick polyurethane foam. A pair of these arenas were placed in a PVC tray measuring 22 × 15 × 4.5 cm and their edges were covered by wet tissue paper hanging down into the water. *Iphiseius degenerans* frequently walked on the wet tissue paper without escaping from the tray and such mites were regarded as present. A 1 cm long black cotton thread served as an oviposition substrate and was replaced after every counting.

Survival and oviposition of mites with different combinations of castor bean leaves, nectar and pollen
The contribution of leaf material, extrafloral nectar and pollen of castor bean to the reproductive success of *I. degenerans* was measured using young (13–19 days old) females. Five experimental arenas were used for each treatment containing a cohort

of 12 mites on either PVC substrates or the dorsal side of washed castor bean leaves. The arenas were kept clean (control) or provided with nectar, pollen or both. Fresh nectar, scraped from the EFNs with a small plastic card, was provided in two small droplets per arena and was refreshed every 4 days. Fresh pollen was added every 2 days. Initially, eggs and females were recorded every 24 h. For treatments that allowed continued reproduction, the experiments were terminated after 7 days. The other experiments were continued with a bidaily census until all mites had died. The leaves were refreshed every week. In order to exclude the decline in females due to escapes, survival was calculated as the product of survival ratios over all previous observational intervals. The ratios were calculated as $(N-D)/N$, where N is the number of live mites present at the previous census and D is the number of dead bodies that occurred between two censuses.

Life history on a diet of castor bean pollen with different intervals of nectar feeding

Life table studies were performed with replicates of 30 eggs, each less than 5 h old, per arena. Three different treatments were compared in four replicates each. In one treatment the mites were fed castor bean pollen during the entire study (70 days). New pollen was provided every other day. In the other two treatments the mites were transferred to arenas with only extrafloral nectar 4 days after the onset of reproduction (almost 12 days after the start of the experiment). Three small droplets of freshly collected nectar were provided per arena and refreshed every 3 days. In one treatment the mites were returned to a pollen diet 8 days later and in another treatment 16 days later. Initially, the numbers of mites and eggs were recorded every 12 h. The recording interval was increased to 24 and 48 h, respectively, 7 and 12 days after the start of reproduction, but was temporarily reduced to 24 h around the diet transitions. Eggs and dead mites were removed after every recording. Surviving mites were transferred to clean arenas every 3 weeks. Net reproduction rates (R_0) were calculated for each replicate by multiplying survivorship, ovipositional rate and sex ratio for every recording interval and by summing up these products over time.

Juvenile development on castor bean nectar

To determine juvenile development on a diet of extrafloral nectar only, six cohorts of 12 larvae each (0–5 h after egg hatch) were transferred to six arenas, three with a PVC substrate and three with a leaf substrate and provided with small droplets of freshly collected nectar. Three other cohorts were put on PVC arenas without any food to serve as a control and three cohorts were provided with pollen of castor bean. Their developmental stage and condition was recorded every 24 h until all juveniles matured or died.

RESULTS

Survival and oviposition of mites with different combinations of castor bean leaves, nectar and pollen

When female *I. degenerans* were transferred from a pollen diet to a diet of only water, nectar and/or leaf, their ovipositional rate diminished rapidly, although some eggs were still produced up to 6 days after the transition (Fig. 1a). The total number
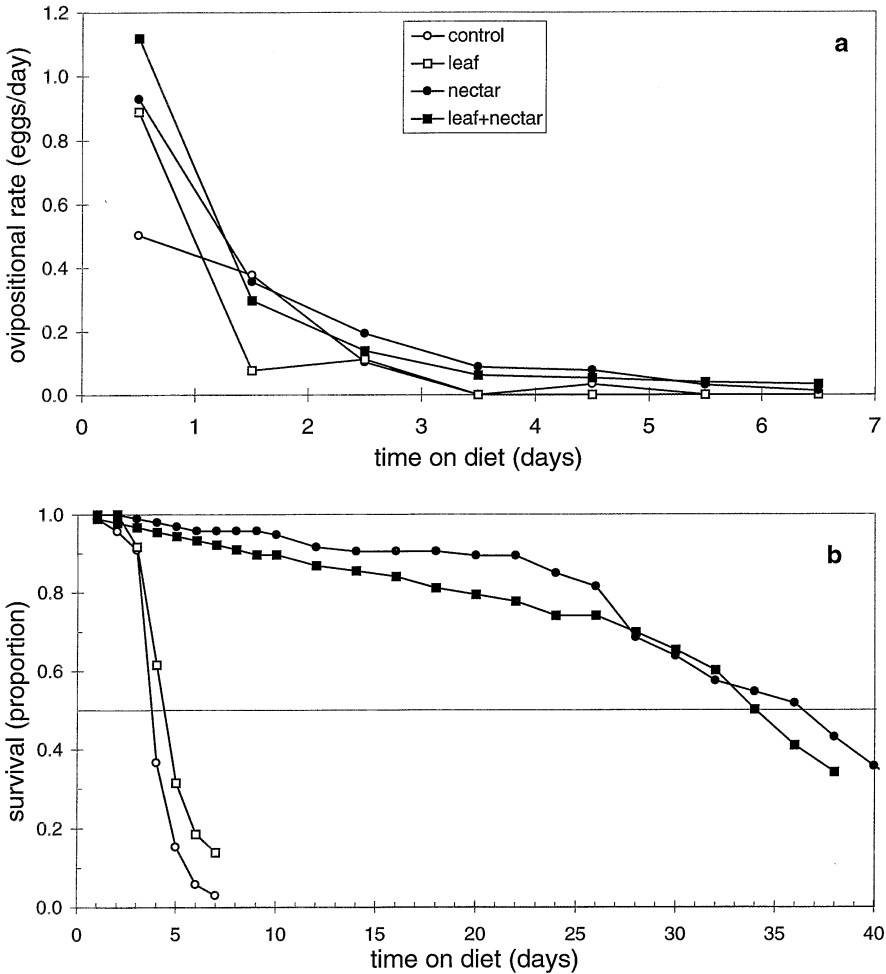

Fig. 1. (a) Oviposition and (b) survival of adult females of *I. degenerans* after transition from a diet of pollen to a diet of only water (open dots), leaf (open squares), extrafloral nectar (closed dots) and leaf and extrafloral nectar (closed squares). Based on five replicate experiments (each consisting of initially approximately 18 young females). Pollen, leaf and extrafloral nectar from *R. communis*.

TABLE 1

Median longevity and egg production of *I. degenerans* after transition to a diet of leaf and/or extrafloral nectar of castor bean (mean ± standard error)[a]

Diet	Median life span (days)	Fecundity (eggs per female)
None (control)	4.0 ± 0.4a	1.02 ± 0.12a
Leaf	4.4 ± 0.4a	1.05 ± 0.04a
Nectar	36.8 ± 2.8b	1.69 ± 0.17b
Leaf plus nectar	34.6 ± 2.7b	1.73 ± 0.16b

[a] Both effects are significant (ANOVA, $p < 0.01$). When two values within one column are followed by the same character the means are not significantly different (Duncan's multiple range test, $p > 0.05$).
Based on five replicate experiments, each consisting of approximately 18 young females.

of eggs produced in this period was only one per female when no nectar was present and almost two with nectar present (Table 1). A much stronger effect of nectar feeding was observed on survival (Fig. 1b). Without nectar 50% of the predators were dead after approximately 4 days, whereas with nectar the median life span of *I. degenerans* was prolonged to approximately 35 days (Table 1). The substrate (plastic or castor leaf) did not have a significant effect on oviposition or survival (Table 1).

On a diet of castor bean pollen no mortality occurred during the first 7 days and oviposition stabilized at a rate of approximately 1.7 eggs per day. When this pollen diet was supplemented with droplets of extrafloral nectar, the ovipositional rate was on average 25% higher (Table 2).

Life history on a diet of castor bean pollen with different intervals of nectar feeding
Iphiseius degenerans fed castor bean pollen began reproducing 8 days after oviposition, reached their maximum ovipositional rate in approximately 20 days

TABLE 2

Ovipositional rate (mean ± standard error) of *I. degenerans* after 4 days on a diet of pollen and/or extrafloral nectar of castor bean (n = number of replicate experiments, each consisting of 12 females of similar age)

Diet	Ovipositional rate (eggs per day per female)[a]	n
Pollen only	1.73 ± 0.03	6
Pollen plus nectar	2.17 ± 0.22	3

[a] Means are significantly different (Student's *t*-test, $P = 0.025$).

and finished reproduction after 50 days (Fig. 2a). When the females were trans-
ferred to a diet of nectar, reproduction dropped to less than 10% within 2 days.
When the mites were fed pollen again after an 8 or 16 days interval, they promptly
resumed reproduction after 1 day and within 3 days their ovipositional rate
surpassed that of the control group. Their reproduction period was extended in
comparison with the control group (Fig. 2a).

During the period of nectar feeding no females died. Their lifespan even
increased with the length of the nectar feeding period; when fed on nectar for 8 or
16 days the median life span of *I. degenerans* increased by 6 or 11 days,
respectively, compared with the control group (Fig. 2b). Although almost no
reproduction occurred during these periods of nectar feeding, lifetime fecundity and
net reproduction (R_o) was not reduced in a linear manner, as it was compensated at
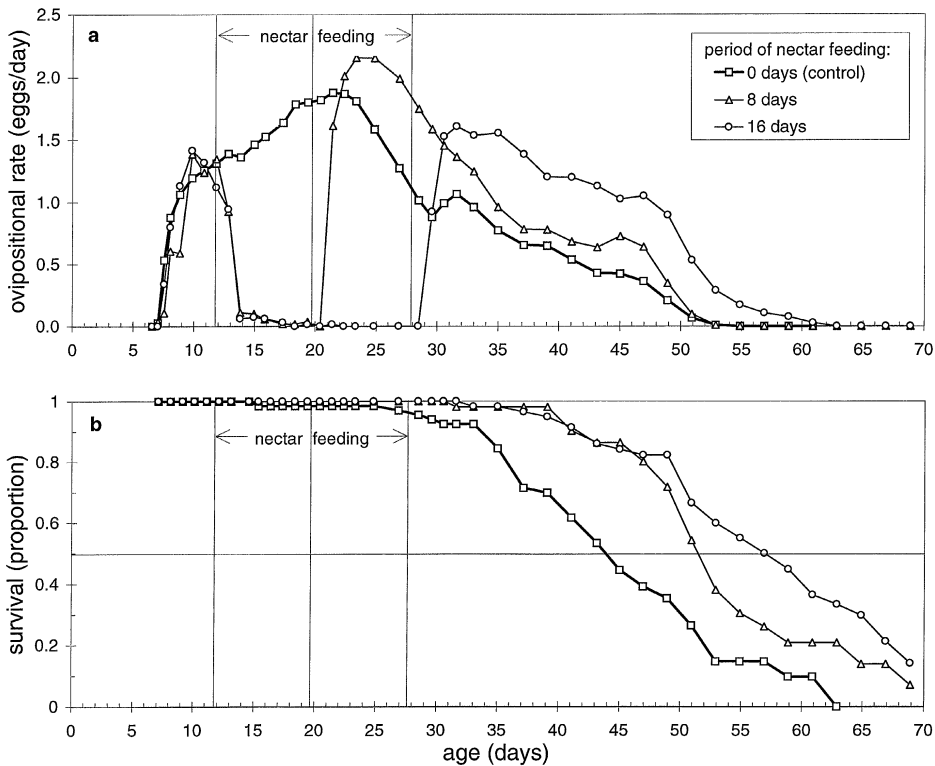

Fig. 2. (a) Age-related oviposition and (b) survival of female *I. degenerans* continuously fed on
a diet of pollen (squares) or interrupted for 8 days (triangles) or 16 days (dots) of feeding on
extrafloral nectar only. Pollen and extrafloral nectar from *R. communis*. Based on four replicate
experiments (each consisting of initially approximately 16 females of similar age). Ovipositional
data are smoothed (three-value moving mean) beyond the point that they surpass 1.5 eggs per
day.

TABLE 3

Effects on survival and reproduction of different intervals of feeding on nectar only for females of *I. degenerans* otherwise fed on pollen of castor bean (mean $\pm$ standard error)[a]

Interval of nectar feeding (days)	Median longevity (days)	Gross fecundity (eggs per female)	Net reproduction (R_0) (females/female)
0	44.3 ± 1.7a	44.6 ± 1.6a	22.5 ± 0.6a
8	50.3 ± 2.6ab	35.8 ± 1.2b	18.4 ± 1.2b
16	55.5 ± 1.3b	35.7 ± 1.2b	17.5 ± 0.7b

[a] All effects are significant (ANOVA, $p = 0.01$). When two values within one column are followed by the same character the means are not significantly different (Duncan's multiple range test, $p > 0.05$).
  Based on four replicate experiments, each consisting of initially approximately 16 females of similar age.

a later age (Table 3). In the control experiment, 95% of R_o was obtained over a period of 32 days. Taking away 8 or 16 days would reduce this period by 25 and 50%, respectively. Net reproduction however, was only reduced by approximately 20% in both cases.

Juvenile development on castor bean nectar
On a diet of pollen, *I. degenerans* larvae developed into adults within 5 days. On water only, larvae moulted to the protonymphal stage, but died within 1 day after moulting. When fed nectar, the mites did not develop beyond the protonymphal stage either, but survived as protonymphs for approximately 4 days. Substrate (PVC versus castor leaf) did not seem to matter.

DISCUSSION

The effects of sugary fluids on development and reproduction of phytoseiid mites
This study showed that extrafloral nectar is a potentially important food source for predatory mites. Extrafloral nectar of castor bean is primarily a solution of different types of sugar (mainly glucose, fructose and sucrose), but it also contains small fractions of amino acids (predominantly glutamic acid, serine and threonine), inorganic compounds (Baker *et al*., 1978) and probably fatty acids (Caldwell and Gerhardt, 1986). For comparison, Table 4 lists life history studies of phytoseiids that contain effects of other sugar-rich solutions such as honeydew produced by homopterans, floral nectar, bee honey and even pure sucrose. These studies show similarities with the present study, as well as some differences.

Reproduction and survival No studies on phytoseiids showed a sustained reproduction on any of the sugar sources listed in Table 4. In some studies, including ours, in the first days after the switch to a sugar diet, the ovipositional rate was

higher than in the control (only water) (Chant and Fleschner, 1960; McMurtry and Scriven, 1965, 1966). In other studies no effects on oviposition could be detected at all (Ferragut *et al.*, 1987; James, 1989).

In all the studies a positive effect on adult survival was observed. For 13 of the 14 species tested no survival was observed after 10 days on water only, whereas in the presence of a sugar source survival ranged from approximately 40% for *Typhlodromus rickeri* (Chant) and *M. occidentalis* (Nesbitt) (McMurtry and Scriven, 1966) to more than 90% for *Euseius stipulatus* (Athias-Henriot), *Euseius victoriensis* (Womersley) and *Typhlodromus phialatus* Athias-Henriot (Ferragut *et al.*, 1987; James, 1989).

TABLE 4

Reported effects of different sugar sources on survival and reproduction of phytoseiid mites (*A.* = *Amblyseius*, *E.* = *Euseius*, *I.* = *Iphiseius*, *N.* = *Neoseiulus*, *P.* = *Phytoseiulus*, *T.* = *Typhlodromus*, *Ta.* = *Typhlodromalus*)

Study	Predator species	Sugar source	Sustained oviposition[a] (%)	Adult survival[b] (%)	Juvenile survival[c] (%)
Chant and Fleschner (1960)	*E. hibisci/Ta. limonicus*	Honeydew (aphids)	0	+	
	E. hibisci/Ta. limonicus	Honey	0	0	
McMurtry and Scriven (1964a)	*T. rickeri*	Honeydew		65	
McMurtry and Scriven (1965)	*Ta. limonicus*	Nectar (orange)	0	++	
McMurtry and Scriven (1966)	*Ta. limonicus*	Sucrose	0	71	
	E. hibisci	Sucrose	0	63	
	M. occidentalis	Sucrose	0	42	
	T. rickeri	Sucrose	0	33	
El-Banhawy (1975)	*E. brazilli*	Honey	0	70	8
Ashihara *et al.* (1978)	*P. persimilis*	Sucrose 10%	0	++	
	P. persimilis	Honey	0	++	
Badii and McMurtry (1983)	*P. longipes*	Sucrose 2%		+	
	P. longipes	Sucrose 10%		+	
	P. longipes	Honey (clover)		++	
Ferragut *et al.* (1987)	*E. stipulatus*	Honeydew (whitefly)	0	95	20
	T. phialatus	Honeydew (whitefly)	0	90	0
James (1989)	*E. victoriensis*	Sugar	0	100	0
	E. victoriensis	Honey	0	100	
Momen and El-Saway (1993)	*A. swirskii*	Honey	0	70	
	A. swirskii	Molasses	0	50	
Tanigoshi *et al.* (1993)	*N. idaeus*	Exudate (cassava)	0	+	0
Bakker and Klein (1993)	*Ta. aripo*	Exudate (cassava)	0	+	48
	Ta. manihoti	Exudate (cassava)	0	+	c.50
Toko *et al.* (1994)	*Ta. manihoti*	Exudate (cassava)	0	40	
Bruce-Oliver *et al.* (1996)	*E. fustis*	Exudate (cassava)	0	0	31
	E. fustis	Honeydew	0	0	27
Present study	*I. degenerans*	EFN (castor bean)	0	100	0

[a] 0: no different from water.

[b] Survival after 10 days of feeding (%, when known; 0, no; +, some; ++, much).

[c] Survival from egg to adult.

TABLE 5

Reported effects of the addition of sugar sources to a diet of spider mites or pollen on survival and reproduction of phytoseiid mites

Study	Predator species	Added sugar source	Basic diet	Oviposition[a]	Juvenile survival[b] (%)
McMurtry and Scriven (1964b)	*E. hibisci*	Honeydew (mealybug)	Spider mites	+	+
			Pollen	+	
Ragusa and Swirski (1977)	*A. swirskii*	Honeydew (scale/mealybug)	Spider mites	+	
Zhimo and McMurtry (1990)	*Euseius tularensis*	Honeydew (aphid/whitefly)	Spider mites	+	0
			Pollen	+	0
	E. stipulatus	Honeydew (aphid/whitefly)	Spider mites	+	0
			Pollen	+	0
	E. hibisci	Honeydew (aphid/whitefly)	Spider mites	+	0
			Pollen	+	0
Bakker and Klein (1993)	*T. manihoti*	Exudate (cassava)	Spider mites	+	
Present study	*I. degenerans*	EFN (castor bean)	Pollen	+	

[a] +: higher oviposition rate when basic diet is supplemented with the sugar source.
[b] +/0: higher/similar survival from egg to adult when basic diet is supplemented with the sugar source.

With respect to the additive effects of a sugar source, Zhimo and McMurtry (1990) conducted an extensive study on the effects of aphid and whitefly honeydew when combined with other effective food sources (i.e. two spider mite species and one type of pollen) for three species of phytoseiid mites (see also Table 5). In 16 out of 18 combinations, honeydew produced a significant increase in the mean oviposition over 11 days, ranging from 38 to 59%. This is larger than the 25% we found when combining extrafloral nectar and pollen. When the supply of the primary food source is limited an even greater effect of the sugar source can be expected (McMurtry and Scriven, 1964b).

Development   Few studies have included the effects of sugar solutions on life stage development of juvenile predators. Similar to our study, James (1989) found that *E. victoriensis* was unable to develop beyond the deutonymphal stage on sugar only. In experiments of El-Banhawy (1975), 8% of *Euseius brazilli* (El-Banhawy) matured on honey only. Ferragut *et al*. (1987) found that 20% of *E. stipulatus* matured on the honeydew of a whitefly, but this was not so for *T. phialatus*. In all of these cases cannibalism was excluded by isolating mites in individual arenas. In combination with spider mites and pollen, honeydew did not affect developmental rate or juvenile survival of the three predatory mite species studied by Zhimo and McMurtry (1990). McMurtry and Scriven (1964b), however, found a higher juvenile survival and a shorter egg to egg period for *Euseius hibisci* when honeydew of *Planococcus citri* (Risso) was added to a diet consisting of citrus red mite, *Panonychus citri* (McGregor).

A different result was obtained in a number of recent studies on the effects of exudate from petioles of cassava (Bakker and Klein, 1993; Tanigoshi *et al*., 1993; Bruce-Oliver *et al*., 1996). When fed this food source, a much higher proportion of juveniles were able to reach maturity than reported in any of the studies mentioned above: approximately 50% for *Typhlodromalus aripo* De Leon (Bakker and Klein, 1993), 48% for *T. manihoti* (Bakker and Klein, 1993) and 31% for *Euseius fustis* (Pritchard and Baker) (Bruce-Oliver *et al*., 1996). Only *Neoseiulus idaeus* Denmark and Muma was unable to mature on cassava exudate (Bakker and Klein, 1993). The four phytoseiid mite species tested so far occur naturally on cassava. It is unknown whether the relatively high maturity ratios can be attributed to an adaptation of these predatory mites to their host plant or to features related to the host plant, such as microorganisms in the phyllosphere. The total amino acid content is no higher in exudate from cassava (on average 0.07% dry weight; Pereira and Splittstoesser, 1987) than in extrafloral nectar from castor bean (0.19% dry weight; Baker *et al*., 1978), but the composition of the two exudates can still be different.

Reproductive potential

Most studies implicitly assumed that mites surviving on a sugar source were still able to reproduce when encountering a better food source, without ever testing this assumption. Ashihara *et al*. (1978), however, showed that *Phytoseiulus persimilis* Athias-Henriot that had been fed on honey for 35 days regained their normal ovipositional rate after 6 days of feeding on two-spotted spider mites. In addition, our study showed that after a period of nectar feeding young females of *I. degenerans* quickly resumed oviposition when offered a better food source such as castor bean pollen and, moreover, were still able to realize a high lifetime reproduction. The period that the mites arrested reproduction and survived on nectar can thus be regarded as a period of quiescence (cf. Danks, 1987). The ability of phytoseiid mites to conserve – almost – full reproductive potential is also observed after periods of total food deprivation (or with access to water only), as shown for *Amblyseius bibens* Blommers (Blommers and Van Arendonk, 1979), *P. persimilis* (Table 24 in Sabelis, 1981) and *N. idaeus* (Megavand and Tanigoshi, 1995). The surplus value of extrafloral nectar or other sugar sources (relative to water) is that the period of quiescence can be much longer without additional mortality.

Predator maintenance

According to Wysoki and Swirski (1971), *I. degenerans* nymphs and adults – but predominantly adults – could be found on castor bean plants in Israel even during autumn and winter, without the occurrence of reproductive diapause (see also Van Houten *et al*., 1995). When the plants are flowering, the phytoseiid population can rapidly build up by feeding on pollen and nectar. On a diet of castor bean pollen the intrinsic rate of increase (r_m) was estimated to be 0.18 per day (Van Rijn and Tanigoshi, 1998). When nectar is available as well, the r_m-value is expected to

increase to 0.22 per day, assuming that total fecundity of *I. degenerans* is not affected. Part of the season, small arthropod herbivores (such as spider mites and thrips) will be available to feed on. During autumn and winter, however, these food resources will usually be scarce. As shown in this study, extrafloral nectar might make an important contribution to survival of phytoseiids during these particularly poor periods and might in some cases be crucial to allow year-round persistence of *I. degenerans* populations on castor bean plants.

Evolutionary consequences

The potential year-round persistence of predatory mites on individual plants may (further) enhance the evolution of plant–predator mutualism. When an individual plant can maintain an independent population of bodyguards on its surface and does not have to compete with other plants for predators in the vicinity, investments in mutualism will likely increase the benefits for the individual plant relative to that of its competitors. Consequently, selection for an increase in mutualism investments is expected, e.g. in quality of nectar and pollen that meets the needs of the predator more closely.

On the predator's part of this relationship, (co)-adaptations in feeding behaviour and dietary and developmental physiology are expected that improve year-round population maintenance. Whereas several phytoseiid species are known to ex-terminate their prey locally and then proceed to disperse in search of new prey patches (Sabelis and Van der Meer, 1986), these oligophagous predators can survive on extrafloral nectar and sustain their wait for new prey to arrive. The lower local reproduction in this case might counterbalance the risk of not finding a suitable food source in time. The relatively high survival on extrafloral nectar and the low tendency to disperse by *I. degenerans* may be symptomatic of such a 'sit and wait' strategy, but comparative experimental work is needed to validate this hypothesis.

Practical implications

Iphiseius degenerans is commercially employed as a natural enemy for the biological control of thrips, such as the western flower thrips, *Frankliniella occidentalis* (Pergande), in greenhouse crops (Van Houten and Van Stratum, 1993). The relatively high population growth rates of this predator on pollen and nectar of castor bean and the long adult survival on nectar makes castor bean an ideal rearing system for this predatory mite, as has been shown by Ramakers and Voet (1995, 1996). Since EFNs are already present on the cotyledons (Zimmerman, 1932) the predator can be introduced onto very young castor bean plants, but without additional food they will not numerically increase until the plant starts flowering. By growing castor bean plants in greenhouses, cultures of *I. degenerans* can easily be maintained year round. With proper timing of planting and trimming, predaceous

mites, up to several hundred *I. degenerans* per leaf, can be obtained when needed without having to rear herbivorous prey (Ramakers and Voet, 1995). Moreover, Ramakers and Voet (1996) have shown how castor bean can be used as banker plants for *I. degenerans* in sweet pepper. In this case, the mites disperse continuously into the crop, but at the same time maintain a population on the flowering castor bean plant for several months.

Other crops (such as cotton, sunflower, bean and *Prunus* species) have EFNs themselves and these might be used to support biological control as well. By selecting genotypes with (higher) nectar production, populations of predatory mites such as *I. degenerans* can be introduced onto the crop at an earlier stage, are expected to be more persistent and will consequently provide better prospects for the biological control of ubiquitous thrips and spider mites.

ACKNOWLEDGEMENTS

REFERENCES

Ananthakrishnan, T.N. 1984. Bioecology of Thrips. Indira Publishing House, Oak Park, MI.

Ashihara, W., Hamamura, T. and Shinkaji, N. 1978. Feeding, reproduction and development of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) on various food substances. Bull. Fruit Tree Res. Stn Japan E2: 91–98.

Badii, M.H. and McMurtry, J.A. 1983. Effect of different foods on development, reproduction and survival of *Phytoseiulus longipes* (Acarina: Phytoseiidae). Entomophaga 28: 161–166.

Baker, D.A., Hall, J.L. and Thorpe, J.R. 1978. A study of the extrafloral nectaries of *Ricinus communis*. New Phytol. 81: 129–137.

Bakker, F.M. and Klein, M.E. 1992. Transtrophic interactions in cassava. Exp. Appl. Acarol. 14: 293–311.

Bakker, F.M and Klein, M.E. 1993. Host plant mediated coexistence of predatory mites: the role of extrafloral nectar and extrafoliar domatia on cassava. In Selecting Phytoseiid predators for biological control, with the emphasis on the significance of tri-trophic interactions, F.M. Bakker (ed), pp. 33–63. PhD thesis University of Amsterdam, Amsterdam.

Bentley, B.L. 1977. Extrafloral nectaries and pugnacious bodyguards. Ann. Rev. Ecol. Syst. 8: 407–427.

Blommers, L. and Van Arendonk, R.C.M. 1979. The profit of senescence in phytoseiid mites. Oecologia 44: 87–90.

Bruce-Oliver, S.J., Hoy, M.A. and Yaninek, J.S. 1996. Effects of some food sources associated with cassava in Africa on development, fecundity and longevity of *Euseius fustis* (Pritchard and Baker) (Acari: Phytoseiidae). Exp. Appl. Acarol. 20: 73–85.

Caldwell, D.L. and Gerhardt, K.O. 1986. Chemical analysis of peach extrafloral nectary exudate. Phytochemistry 25: 411–413.

Chant, D.A. and Fleschner, C.A. 1960. Some observations on the ecology of phytoseiid mites (Acarina: Phytoseiidae) in California. Entomophaga 5: 131–139.

Danks, H.V. 1987. Insect Dormancy. An Ecological Perspective. Biological Survey of Canada, Ottawa.

de Moraes, G.J., McMurtry, J.A. and Denmark, H.A. 1986. A Catalogue of the Mite Family Phytoseiidae. EMBRAPA, Brasilia, Brazil.

El-Banhawy, E.M. 1975. Biology and feeding behaviour of the predatory mite, *Amblyseius brazilli* (Mesostigmata: Phytoseiidae). Entomophaga 20: 353–360.

Eveleigh, E.S. and Chant, D.A. 1981. The feeding and searching behaviour of two species of phytoseiid mites, *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius degenerans* (Berlese), at different prey densities (Acarina: Phytoseiidae). Can. J. Zool. 59: 1419–1430.

Ferragut, F., Garcia-Mari, F., Costa-Commelles, J. and Laborda, R. 1987. Influence of food and temperature on development and oviposition of *Euseius stipulatus* and *Typhlodromus phialatus* (Acari: Phytoseiidae). Exp. Appl. Acarol. 3: 317–329.

Grafton-Cardwell, E.E. and Ouyang, Y. 1996. Influence of citrus leaf nutrition on survivorship, sex ratio, and reproduction of *Euseius tularensis* (Acari: Phytoseiidae). Environ. Entomol. 25(5): 1020–1025.

Helle, W. and Sabelis, M.W. 1985. Spider Mites: Their Biology, Natural Enemies and Control, Vol. 1B. Elsevier, Amsterdam.

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

Jeppson, L.R., Keifer, H.H. and Baker, E.W. 1975. Mites Injurious to Economic Plants. University of California Press, Berkeley, CA.

Koptur, S. 1992. Extrafloral nectary-mediated interactions between insects and plants. In Insect–plant interactions, Vol. IV, E. Bernays (ed.), pp. 108–129. CRC Press, Boca Raton, FL.

McMurtry, J.A. and Scriven, G.T. 1964a. Biology of the predaceous mite *Typhlodromus rickeri* (Acarina: Phytoseiidae). Ann. Entomol. Soc. Am. 57(3): 362–367.

McMurtry, J.A. and Scriven, G.T. 1964b. Studies on the feeding, reproduction, and development of *Amblyseius hibisci* (Acarina: Phytoseiidae) on various food substances. Ann. Entomol. Soc. Am. 57: 649–655.

McMurtry, J.A. and Scriven, G.T. 1965. Life-history studies of *Amblyseius limonicus* with comparative observations on *Amblyseius hibisci* (Acarina: Phytoseiidae). Ann. Entomol. Soc. Am. 58: 106–111.

McMurtry, J.A. and Scriven, G.T. 1966. Effects of artificial foods on reproduction and development of four species of phytoseiid mites. Ann. Entomol. Soc. Am. 59: 267–269.

Megavand, B. and Tanigoshi, L.K. 1995. Effects of prey deprivation on life table attributes of *Neoseiulus idaeus* Denmark & Muma (Acari: Phytoseiidae). Biol. Control 5: 73–82.

Momen, F.M. and El-Saway, S.A. 1993. Biology and feeding behaviour of the predatory mite, *Amblyseius swirskii* (Acarina: Phytoseiidae). Acarologia 34: 199–204.

Nwilene, F.E. and Nachman, G. 1996. Reproductive responses of *Iphiseius degenerans* and *Neoseiulus teke* (Acari: Phytoseiidae) to changes in the density of the cassava green mite, *Mononychellus tanajoa* (Acari: Tetranychidae). Exp. Appl. Acarol. 20: 273–282.

Pemberton, R.W. 1993. Observations of extrafloral nectar feeding by predaceous and fungivorous mites. Proc. Entomol. Soc. Washington 95: 642–643.

Pereira, J.K. and Splittstoesser, W.E. 1987. Exudate from cassava. Agricult. Ecosyst. Environ. 18: 191–194.

Porres, M.A., McMurtry, J.A. and March, R.B. 1976. Investigations of leaf sap feeding by three species of phytoseiid mites by labelling with radioactive phosphoric acid ($H_3^{32}PO_4$). Ann. Entomol. Soc. Am. 68(5): 871–873.

Ragusa, S. and Swirski, E. 1977. Feeding habits, post-embryonic and adult survival, mating, virility and fecundity of the predacious mite *Amblyseius swirskii* (Acarina: Phytoseiidae) on some coccids and mealybugs. Entomophaga 22(4): 381–392.

Ramakers, P.M.J. and Voet, S.J.P. 1995. Use of castor bean, *Ricinus communis*, for the introduction of the thrips predator *Amblyseius degenerans* on glasshouse-grown sweet pepper. Med. Fac. Landbouww. Rijksuniv. Gent 60(3a): 885–891.

Ramakers, P.M.J. and Voet, S.J.P. 1996. Introduction of *Amblyseius degenerans* for thrips control in sweet peppers with potted plants of castor beans as banker plants. IOBC/WPRS Bull. 19(1): 127–130.

Rogers, C.E. 1985. Extrafloral nectar: entomological implications. Bull. Entomol. Soc. Am. 31: 15–20.

Sabelis, M.W. 1981. Biological Control of Two-Spotted Spider Mites using Phytoseiid Predators. Agricultural Research Reports, Wageningen.

Sabelis, M.W. and van der Meer, J. 1986. Local dynamics of the interaction between predatory mites and two-spotted spider mites. In Dynamics of physiological structured populations, J.A.J. Metz and O. Diekmann (eds), pp. 322–344. Springer Verlag, Berlin.

Sabelis, M.W. and Van Rijn, P.C.J. 1997. Predation by insects and mites. In Thrips as crop pests, T. Lewis (ed), pp. 259–354. CAB International, London.

Swirski, E. and Amitai, S. 1961. Some phytoseiid mites (Acarina: Phytoseiidae) of Israel, with a description of two new species. Israel J. Entomol. 3: 95–108.

Tanigoshi, L.K., Megavand, B. and Yaninek, J.S. 1993. Non-prey food for subsistence of *Amblyseius idaeus* (Acari: Phytoseiidae) on cassava in Africa. Exp. Appl. Acarol. 17: 91–96.

Toko, M., O'Neil, R.J. and Yaninek, J.S. 1994. Effect of cassava exudate and prey densities on the survival and reproduction of *Typhlodromus limonicus* (Garman & McGregor) s.l. (Acari: Phytoseiidae), a predator of the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae). Exp. Appl. Acarol. 18: 221–231.

Van Houten, Y.M. and Van Stratum, P. 1993. Biological control of western flower thrips in greenhouse sweet peppers using non-diapausing predatory mites. Proc. Exp. Appl. Entomol. NEV Amsterdam 4: 229–234.

Van Houten, Y.M., Van Rijn, P.C.J., Tanigoshi, L.K., Van Stratum, P. and Bruin, J. 1995. Preselection of predatory mites for year-round control of western flower thrips (*Frankliniella occidentalis*) in greenhouse crops. Entomol. Exp. Appl. 74: 225–234.

Van Rijn, P.C.J. and Sabelis, M.W. 1997. Should plants provide food for predators when it also benefits the herbivores? The effects of pollen on a thrips-predatory mite system. Acarology IX: Volume 2, Mitchell, R., Horn, D.J., Needham, G.R. and Welbourn, W.C. (eds), Proceedings. Ohio Biological Survey, Columbus, OH.

Van Rijn, P.C.J. and Tanigoshi, L.K. 1998. Pollen as a food source for the predatory mites *Iphiseius degenerans* and *Neoseiulus cucumeris* (Acari: Phytoseiidae): dietary range and performance. Exp. Appl. Acarol. in press.

Walter, D.E. and O'Dowd, D.J. 1995. Life on the forest phylloplane: hairs, little houses, and myriad mites. In Forest canopies, M. Lowman and N. Nadkarni (eds), pp. 325–351. Academic Press, New York.

Whitman, D.W. 1994. Plant bodyguards: mutualistic interactions between plants and the third trophic level. In Functional dynamics of phytophagous insects, T.N. Ananthakrishnan (ed), pp. 207–248. Science Publisher Inc., Libanon, NH.

Wysoki, M. and Swirski, E. 1971. Studies on overwintering of predacious mites of the genera *Amblyseius* Berlese, *Typhlodromus* Scheuten and *Iphiseius* Berlese (Acarina: Phytoseiidae) in Israel. In Entomological essays to commemorate the retirement of Professor K. Yasumatsu, pp. 265–292. Hokuryukan Publishing, Tokyo, Japan.

Zhimo, Z. and McMurtry, J.A. 1990. Development and reproduction of three *Euseius* (Acari: Phytoseiidae) species in the presence and absence of supplementary foods. Exp. Appl. Acarol. 8: 233–242.

Zimmerman, M. 1932. Über die extraflorale Nectarien der Angiospermen. Bot. Zentralblatt Beih. 49: 99–196.