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Evaluation of *Tarsonemus bilobatus* and *Podosphaera xanthii* as suitable resources for *Proprioseiopsis mexicanus* in cucurbit systems in the Southeast USA

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Abstract

Tritrophic relationships involving tarsonemids and predatory phytoseiids are common in a variety of agroecosystems, but due to the wide range of diets in both families, it is necessary to understand what food resources they are consuming to determine potential impact on crops. We investigated a frequent association of cucurbit powdery mildew (*Podosphaera xanthii*), *Tarsonemus bilobatus*, and *Proprioseiopsis mexicanus* in watermelon and pumpkin fields to determine whether *P. mexicanus* is consuming either or both of the other organisms. We also examined developmental and reproductive capability of *P. mexicanus* on these diets. If *P. mexicanus* is an effective predator of *T. bilobatus*, it may also be useful in controlling pest tarsonemids, such as broad mites. *Proprioseiopsis mexicanus* either starved or escaped from arenas rather than consume *P. xanthii*. When consuming *T. bilobatus*, *P. mexicanus* females developed from larva to adult in ca. 3 days. On this diet, the preoviposition period was ca. 2 days and *P. mexicanus* laid 1.7 eggs/day. These results are comparable to some of the higher-quality non-prey resources investigated in the literature. Starved female *P. mexicanus* consumed 6.5 *T. bilobatus* of mixed stages in 1 h. This study provides support for further research into the importance of non-pest tarsonemids as a resource to maintain the presence of generalist predatory mites as an early-intervention natural enemy. Further work should examine the efficacy of *P. mexicanus* as a natural enemy of economically important pest tarsonemids.

Keywords Cucurbitaceae · Tritrophic interactions · Plant pathogens · *Tarsonemus bilobatus* · *Proprioseiopsis mexicanus*

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Introduction

In agroecosystems, there are many complex trophic relationships involving crop plants and arthropod associates that require close inspection to understand their significance to the crop and to pest management. In cucurbit crop fields in South Carolina, USA, in 2018–2019, on separate occasions, we encountered *Tarsonemus bilobatus* Suski (Acari: Tarsonemidae) on multiple varieties of *Citrullus lanatus* (Thunb.) Matsum. & Nakai, *Cucurbita maxima* Duchesne ex Poir., and *Cucurbita pepo* L. in association with cucurbit powdery mildew, *Podosphaera xanthii* (Schltdl.) U. Braun & S. Takam., and the generalist predator *Proprioseiopsis mexicanus* Garman (Acari: Phytoseiidae) (Farfan et al. 2021; Schmidt-Jeffris et al. 2021). Because the dietary breadth of generalist phytoseiids can be relatively wide, discerning the nature of tritrophic relationships can tell us much about which are beneficial, harmful, or neutral to crop production. This is particularly important in vegetable systems, where resident phytoseiid biodiversity and their role in pest management is poorly understood (Farfan and Schmidt-Jeffris 2019).

The family Tarsonemidae (Trombidiformes) is a cosmopolitan and ecologically diverse group of mites that includes fungivores, algivores, and herbivores, among others (Walter et al. 2009). Whereas most species are in the genus *Tarsonemus*, the most studied tarsonemids are the pests broad mite, *Polyphagotarsonemus latus* (Banks), and cyclamen mite, *Phytonemus pallidus* (Banks). *Polyphagotarsonemus latus* is known to infest and consume parts of many crop plants including, but not limited to, citrus (Peña et al. 2000; Peña 1990), pepper (de Coss-Romero and Peña 1998; Dhooria and Bindra 1977), and strawberry (Renkema et al. 2017). *Phytonemus pallidus* is a pest of ornamental flowers (Jeppson et al. 1975) and strawberry (Croft et al. 1998). Tarsonemid agricultural pests are challenging to control with chemical applications due to their short life cycles and small size (40–300 µm) that allow them to hide in narrow crevices in bark (Nucifora and Vacante 2004), buds, and blossoms (Gerson et al. 2003). For this reason, it has been suggested that fungal pathogens of tarsonemids and natural enemies, such as phytoseiid mites, which can ‘follow’ pest tarsonemids into hiding spaces, may be an effective part of a viable IPM strategy (Easterbrook et al. 2001; Jovicich et al. 2008; McMurtry et al. 2013).

Though less studied than herbivorous tarsonemids, species in *Tarsonemus* are well known as fungivores and microbivores (Lindquist 1986), and can be collected from soil, detrital systems, and on foliage in agroecosystems (Childers and Ueckermann 2020). *Tarsonemus bilobatus* is a fungivore that has been collected from many crop fields and stored product systems (Na et al. 1998; Nucifora and Vacante 2004; Lotfollahi and Irani-Nejad 2010; Akyazi et al. 2021) including melon (Nakao 1991), as well as litter and soil (Zhang 2003). To our knowledge, this is the first time it has been collected in South Carolina, USA. *Tarsonemus* spp. have been suggested to play a variety of roles in these agroecosystems, from passive vectors of plant pathogens to prey resources for phytoseiids (Croft et al. 1998; McMurtry et al. 2013; Suski 1972; Vangansbeke et al. 2020). They have been observed to successfully consume *Penicillium* (Lindquist 1986), *Alternaria*, *Beauveria*, and *Cladosporium* (Lindquist 1986), *Aspergillus* (Lindquist 1972; Vangansbeke et al. 2020), and *Fusarium* (Beer 1954; Vangansbeke et al. 2020), among other pathogens, however, the importance of plant pathogens to the diets of phytoseiids has been recorded only a few times (Chant 1959; Duso et al. 2003; Momen and Abdelkhader 2010; Zemek 2005; Zemek and Prenerov 1997). Consumption of plant pathogens has implicated some tarsonemids in the passive-vector transmission of apple rot pathogens (Li et al. 2018; Michailides et al. 1994; Van der Walt et al. 2011) and citrus pathogens such as sooty mold (Nucifora and Vacante 2004). Correct determination of the species of *Tarsonemus* and its trophic designation can help in extension education regarding the range of ecologies of foliar arthropods in agricultural fields, thereby assisting growers in making crop management decisions.

Generalist phytoseiids can use a wide range of food resources (McMurtry et al. 2013), with some being more important to survival and reproduction than others. In previous work, we observed *P. mexicanus* consuming small foliar insects, such as western flower thrips and whitefly (MA Farfan unpubl.), in addition to twospotted spider mites (Farfan et al. 2021). Pollen is also often utilized (Abou-Setta et al. 1997; Croft et al. 2004; McMurtry and Croft 1997; McMurtry et al. 2013; McMurtry and Scriven 1964; Nguyen et al. 2019; van Rijn and Tanigoshi 1999; van Rijn and Sabelis 1990; Warburg et al. 2019), and sometimes necessary, for optimal survival and reproduction (Nomikou et al. 2002, 2010; van Rijn et al. 2002). We know they will consume and reproduce on pollen of cucurbits (*C. lanatus*, *C. maxima*, *C. pepo*, *Cucurbita moschata* Duchesne), a succulent [*Delosperma cooperi* (Hook.f.) L. Bolus], a legume (*Trifolium incarnatum* L.), and cattail (*Typha* spp.) (Farfan et al. 2021). Previous evidence has shown that generalist phytoseiids may consume plant pathogens, such as grape downy mildew [*Plasmopara vitivola* (Berk. & Curtis ex de Bary) Berlese & De Toni] (Duso et al. 2003; Pozzebon and Duso 2008), cassava mildew (*Oidium manihotis* Henn.) (Bakker and Klein 1992), coffee rust (*Hemileia vastatrix* Berkeley and Broome) (Vacacela Ajila et al. 2018), *Oidium fragariae* Harz. (Suski 1972), *Podosphaera leucotricha* (Ell. & Everh.) (Suski 1972), and *Erysiphe orontii* Cast. (Zemek and Prenerov 1997), with successful development and survival of the predatory mite. However, these relationships can be complex. James (1993) found that although phytoseiid mite *Typhlodromus doreenae* Schicha would not feed on the fungus *Rhizopus stolonifera* (Ehrenberg ex. Fr.) Lind., it would feed on the fungivorous mite *Tyrophagus putrescentiae* (Schrank), after *T. putrescentiae* fed on *R. stolonifera*. Currently, it is unknown whether *P. mexicanus* is also fungivorous and/or consumes tarsonemid mites. The determination of whether *T. bilobatus* and *P. xanthii* are consumed by *P. mexicanus* would elucidate not only the breadth of food resources consumed but also identify areas of further research into potential pathogen transmission by either mite species.

The frequency and consistency of association of *T. bilobatus*, *P. xanthii*, and *P. mexicanus* together led us to investigate the questions: (1) what is *P. mexicanus* consuming: *T. bilobatus*, *P. xanthii*, or both? (2) If *P. mexicanus* is feeding on *T. bilobatus*, how effective is it as a food resource for survival and reproduction of *P. mexicanus*? And (3) what is the potential for *P. mexicanus* as a natural enemy of tarsonemids? The latter question may indicate whether it should be investigated as a predator of pest tarsonemids (broad mite, cyclamen mite). To answer these questions, we conducted two food resource experiments in which we separately fed *P. xanthii* and *T. bilobatus* to *P. mexicanus* and evaluated developmental time (time from the larval stage to an adult), pre-oviposition time (time from introducing a male *P. mexicanus* to a female and that female laying the first egg), and number of eggs laid over 4 days. We then conducted a timed feeding study in which *P. mexicanus* was provided a known number of *T. bilobatus* and evaluated rate of consumption over an hour at two time points. This study provides evidence justifying more work on the ecological role of the community of tarsonemids inhabiting specialty crops and the potential role of generalist phytoseiid mites in regulating other tarsonemids present on plants in large numbers, such as *P. latus* and *P. pallidus*.

Materials and methods

Mite and *Podosphaera xanthii* cultures

Proprioseiopsis mexicanus individuals were collected from *C. lanatus* and *C. pepo* plants grown at the Clemson University Coastal Research and Education Center research farm (Charleston, SC, USA). These were cultured on lima bean (*Phaseolus lunatus* L.) leaves infested with *Tetranychus urticae* Koch placed on wet cotton sheets in 31.8 × 25.6 × 9.7 cm lidded plastic boxes. The diet of *P. mexicanus* was supplemented with commercially acquired *Typha* spp. pollen (Nutrimite; Biobest USA, Romulus, MI, USA). Boxes were maintained at 26.5 °C, 88% RH and 16:8 L:D photoperiod. *Tarsonemus bilobatus* individuals were collected from *C. pepo* plants and cultured on *C. pepo* leaves inoculated with *P. xanthii* from a long-standing culture at the USDA U.S. Vegetable Laboratory (Charleston, SC). This was also the source of the *P. xanthii* offered to *P. mexicanus* for the consumption experiment. *Tarsonemus bilobatus* cultures were maintained at 26.5 °C, 88% RH and 16:8 L:D photoperiod.

Experimental arenas

Experimental arenas were created by filling 29-mL plastic cups halfway with warm 1% agar solution. When the agar cooled slightly, a disc (22 mm diameter) of black cardstock dipped in paraffin wax was placed in the center and the agar was allowed to cool fully. This arena design was chosen because we wanted to ensure that the only materials available to *P. mexicanus* individuals were the two resources tested, *T. bilobatus* and the fungal material. Arenas for the following experiments were maintained at 26.5 °C, 88% RH and 16:8 L:D photoperiod.

Podosphaera xanthii experiment

To determine the performance potential of *P. mexicanus* regarding developmental time, time to oviposition, and number of eggs produced when consuming only *P. xanthii*, 13 gravid female *P. mexicanus* were haphazardly selected from culture, each placed in its own arena, and starved for 24 h. Eggs laid during this 24-h period were discarded. After 24 h, *P. xanthii* material (mycelia, conidia, ascocarps) was dusted on the arena with a small paintbrush in excess of what could be consumed (>1.5 mg). Oviposition was monitored every 12 h and old *P. xanthii* material was cleaned off and replenished. Eggs laid after the 24-h period were provided their own arena and *P. xanthii* material was provided in excess of what could be consumed (>1.5 mg) and time of oviposition was recorded. In total 12 eggs were evaluated in this experiment. Eggs were monitored for change in developmental stage every 12 h and *P. xanthii* material was replenished. The times of observed change in developmental stage were recorded.

Tarsonemus bilobatus experiment

To determine the developmental and reproductive potential of *P. mexicanus* when consuming *T. bilobatus* only, 13 gravid female *P. mexicanus* were haphazardly selected from culture, each placed in its own arena, and starved for 24 h. Any eggs laid during this period were removed from the arena and discarded. A quantity of *T. bilobatus* mixed stages of individuals in excess of what could be consumed (≥10) was provided to *P. mexicanus* by removing them individually with a brush from culture and placing them on discs in the arenas after 24 h. Oviposition was monitored every 12 h and *T. bilobatus* was replenished. Eggs laid after the 24-h starvation period were given their own arena, provided 10 *T. bilobatus*, and monitored every 12 h for development until reaching the adult stage. This resulted in 52 eggs evaluated during this experiment.

A male *P. mexicanus* was added to the arena of 18 females that reached adulthood and the time of addition was recorded. Females were monitored every 12 h for oviposition and the time of oviposition of first egg and total number of eggs laid over a 4-day period were recorded.

Timed consumption experiment

Fifty-two arenas of the same design as described above were used for the experiment investigating the potential of *P. mexicanus* to consume *T. bilobatus* individuals. Between 9 and 15 *T. bilobatus* of mixed stages and sexes were provided to *P. mexicanus* by removing them individually with a brush from culture and situating them on discs in the arenas and their exact number was recorded. One female *P. mexicanus* was placed on the arena with the *T. bilobatus* and the *T. bilobatus* consumed were counted after 15 min and 1 h. A *T. bilobatus* individual was considered ‘consumed’ when the individual was found not moving and emptied of contents (generally a collapsed exoskeleton).

Data analysis

We performed a one-way ANOVA to compare performance of female *P. mexicanus* when consuming *T. bilobatus* to previous data collected on pollen resources by Farfan et al. (2021): *C. lanatus*, *D. cooperi* (Hardy ice plant), *T. incarnatum* (Crimson clover), and our rearing diet for *P. mexicanus*, *T. urticae* + *Typha* spp. pollen. Means were separated using a Tukey honestly significant difference (HSD) test for Type I sequential sum of squares. To meet assumptions of normality, one observation was removed from the developmental time dataset ($n=110$) and three from the time to oviposition dataset ($n=62$).

Results

Developmental time and reproduction when consuming *Podosphaera xanthii*

Of the 12 eggs (replicates) laid by female *P. mexicanus* from the lab colony, 11 individuals died in the protonymph stage from starvation or from running off into the agar solution. One individual ran off the arena into the agar in the deutonymph stage. We determined that *P. xanthii* is not a suitable food resource for *P. mexicanus* and is not a target organism for consumption. We did not continue this portion of the experiment.

Developmental time and reproduction when consuming *Tarsonemus bilobatus*

Female *P. mexicanus* ($n = 19$) developed from egg to adult in 3.2 days (Table 1). *Proprioseiopsis mexicanus* females reached adulthood in times comparable to the shortest developmental times of pollen resources investigated by Farfan et al. (2021), *C. lanatus*, *D. cooperi*, and *T. incarnatum* (one-way ANOVA: $F_{4,105} = 11.1$, $P < 0.0001$; Table 1), but developed significantly quicker than those on the *T. urticae* + *Typha* spp. pollen diet (4.0 days; Table 1). Males ($n = 15$) developed in 2.7 ± 0.10 (mean ± SE) days when consuming *T. bilobatus*.

The pre-oviposition time for female *P. mexicanus* ($n = 16$) was 2.1 days (Table 1), which was significantly different only from those who consumed *C. lanatus* (1.6 days) (one-way ANOVA: $F_{4,57} = 2.4$, $P = 0.59$; Table 1).

Females produced 1.8 eggs/day ($n = 17$) when consuming *T. bilobatus* which was similar to eggs produced on the *T. urticae* + *Typha* spp. pollen diet (1.4 eggs; Table1), but significantly fewer eggs than those who consumed *C. lanatus* (3.5 eggs), *D. cooperi* (3.0 eggs), and *T. incarnatum* (3.4 eggs) (one-way ANOVA: $F_{4,63} = 20$, $P < 0.0001$; Table 1).

Timed consumption of *Tarsonemus bilobatus*

Proprioseiopsis mexicanus females ($n = 52$) consumed 3.4 ± 0.25 (mean ± SE) *T. bilobatus* after 15 min and 6.5 ± 0.33 after 1 h.

Discussion

Trophic relationships like the one we studied here are very common across multiple agroecosystems, but little is understood about the significance of these to plant health and management. The results of our experiments revealed that a common pathogen of cucurbits, *P. xanthii*, is not a suitable food resource for *P. mexicanus* females. Phytoseiid generalist predators are known to include some plant-based resources in their diet, such as pollen, and sometimes even require it for maximum survival and reproduction, but the importance of plant pathogens to the diet of phytoseiid mites has rarely been recorded. However, although

Table 1 Female *Proprioseiopsis mexicanus* mean (±SE; sample sizes in parentheses) developmental and reproductive performance on pollen and prey food resources: *Citrullus lanatus*, *Delosperma cooperi*, *Trifolium incarnatum*, *Tetranychus urticae* + *Typha* spp. pollen and *Tarsonemus bilobatus*

Food resource	Developmental time (days)	Pre-oviposition time (days)	Oviposition rate (no. eggs/female/day)
*C. lanatus**	2.9 ± 0.15 (16) a	1.6 ± 0.08 (16) a	3.5 ± 0.19 (16) a
*D. cooperi**	3.0 ± 0.19 (10) a	1.8 ± 0.15 (10) ab	3.0 ± 0.40 (11) a
*T. incarnatum**	3.4 ± 0.21 (13) a	1.6 ± 0.11 (13) ab	3.4 ± 0.078 (11) a
T. urticae + *Typha* spp.*	4.0 ± 0.10 (52) b	1.8 ± 0.14 (9) ab	1.4 ± 0.27 (13) b
T. bilobatus	3.2 ± 0.14 (19) a	2.1 ± 0.17 (16) b	1.8 ± 0.10 (17) b

Means within a column with the same letter do not differ significantly (Tukey's HSD test: $P > 0.05$)

*Data from Farfan et al. (2021)

P. mexicanus does not appear to utilize *P. xanthii*, the type of plant pathogens consumed by different species of *Tarsonemus* has been observed to affect the suitability of a *Tarsonemus* species as a food resource for phytoseiid mites. A diet of *Tarsonemus fusarii* Cooreman that consumed *Fusarium venenatum* Nirenberg resulted in a twofold increase in oviposition by *Neoseiulus californicus* (McGregor) compared to a diet of *T. fusarii* that consumed *Aspergillus oryzae* (Ahlburg) E. Cohn. In this respect, we can say that *P. xanthii* is probably a suitable indirect resource for *P. mexicanus*.

Although *P. mexicanus* females were not able to develop on *P. xanthii*, they readily consumed and reproduced on *T. bilobatus*. Whereas *T. bilobatus* proved to be a better resource than *T. urticae* in developmental time, it resulted in longer developmental times than diets of *C. lanatus*, *D. cooperi*, or *T. incarnatum* pollen, and longer pre-oviposition periods than many other pollens tested regarding pre-oviposition time and egg production (Farfan et al. 2021). The oviposition rate we observed by *P. mexicanus* females that consumed *T. bilobatus* is similar to what Vangansbeke et al. (2020) observed when *N. californicus* was provided a diet of *T. fusarii* (1.6 ± 0.4 eggs/female/day). When fed *P. pallidus*, Croft et al. (1998) observed that female *Neoseiulus fallacis* (Garman) and *Neoseiulus cucumeris* (Oudemans) lay 1.63 and 2.19 eggs/female/day, respectively. It was noted that some of this difference may be due to the more specialized lifestyle of *N. fallacis* versus *N. cucumeris*, which is known to perform well on a wider range of resources. Although Vangansbeke et al. (2020) suggest that fungivorous tarsonemids such as *T. fusarii* are a factitious prey for phytoseiids, we suggest in the case of *P. mexicanus* that foliar-provisioning tarsonemids are genuine prey, and may be a useful resource when there are blossoms on crop plants or in the case of cucurbit crops with less suitable pollen that also are prone to *P. xanthii* infection. In general, fungivorous tarsonemids may serve to keep predators of a similar generalist diet breadth present on crop plants as an early-intervention control, as this is not the first observation of a *Proprioseiopsis* species present on a plant with a tarsonemid population (Knisley and Denmark 1978).

We observed that *P. mexicanus* consumed 6.5 *T. bilobatus* mites on average over an hour when starved. Other studies have evaluated the rate of increase of phytoseiid mites by consuming tarsonemids or other reproductive or developmental data, but few have evaluated rate of consumption. Easterbrook et al. (2001) observed two *Neoseiulus* spp. (*cucumeris* and *californicus*) reduced active stages of *P. pallidus* on strawberry plants by 76–87% in approximately 1 month. On our arenas, *P. mexicanus* reduced *T. bilobatus* active stages by 59% over 1 h, but these two studies are not directly comparable as our experiment did not allow for immigration or reproduction of the prey. More research is needed to understand the efficacy of generalist phytoseiids in controlling tarsonemid pests, including prey consumption rates.

Tritrophic relationships that involve crop plants are very common in agroecosystems and some, like one described in this study, may be net beneficial while not directly involving a plant pest. Tarsonemids have been shown to consume and passively transmit plant pathogens. To our knowledge, this is the first time *T. bilobatus* has been observed to consume and be cultured on *P. xanthii*, so passive transmission is a possibility. Further studies are needed to determine whether this is occurring, or whether a pathogen that is already primarily dispersed by wind, like *P. xanthii*, is not likely to be dispersed significantly more by *T. bilobatus*. But, like many other non-pest food resources, species of *Tarsonemus* may play a role in maintaining the presence of generalist phytoseiids on crop plants and assist in the early-intervention pest control. The presence of generalist phytoseiids like *P. mexicanus* in association with fungivorous tarsonemids may be a good indication that they could be capable of early control of a tarsonemid pest, such as *P. latus* or *P. pallidus*, especially if the generalist phytoseiid frequents the locations on a plant where these pests tend to occur. Further work on the effectiveness of control by phytoseiids during the community succession of tarsonemid species from fungivores to herbivore pests would be needed to understand if this is a function of fungivorous tarsonemids. The potential of *P. mexicanus* to control outbreaks of herbivorous pest tarsonemids should also be explored.

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Author contributions All authors contributed to the study concept and design. Material preparation and data collection were performed by MAF and JC. Data analysis was performed by MAF. The first draft of the manuscript was written by MAF and all authors commented on the previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Datasets and supplementary materials are available at figshare.com.

Code availability R Statistical Software base package.

Declarations

Conflict of Interest All authors have no relevant financial or non-financial interests to disclose.

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