

Do leaf domatia mediate intraguild predation and host plant resistance to *Oligonychus aceris* (Shimer) on Red Sunset Maple (*Acer rubrum*)?



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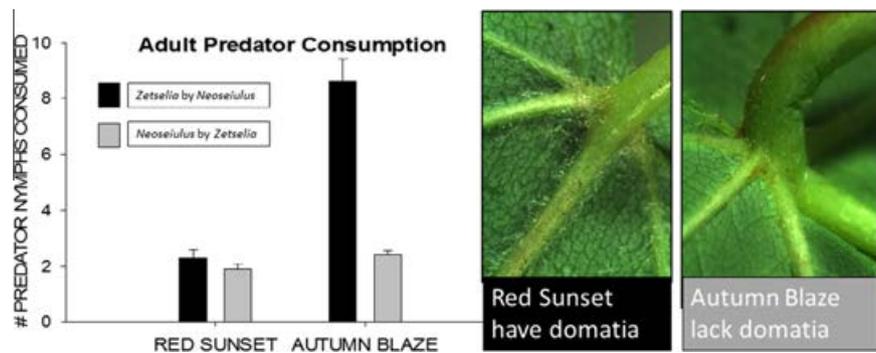
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HIGHLIGHTS

- Red Sunset maples have more leaf domatia than Autumn Blaze maples.
- *N. fallacis* adults consume nymphs of *Z. mali*.
- Leaf domatia provided refugia for *Z. mali* nymphs on Red Sunset maples.
- Predation on *Z. mali* by *N. fallacis* on Autumn Blaze maples reduces predation on *O. aceris*.

GRAPHICAL ABSTRACT



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ABSTRACT

The predatory mites *Neoseiulus fallacis* (Garman) (Acarina: Phytoseiidae) and *Zetzellia mali* (Ewing) (Acarina: Stigmaeidae) have the potential to suppress populations of *Oligonychus aceris* (Shimer) (Acarina: Tetranychidae) on maple cultivars under field conditions. Red Sunset red maples (*Acer rubrum*) are more resistant to *O. aceris* than 'Autumn Blaze' Freeman maple (*Acer × fremanii*). Examination of leaves indicated that the mite resistant Red Sunset trees had more leaf domatia than those from Autumn Blaze. Laboratory assays found that maple cultivars did not affect rates of *O. aceris* consumption by *N. fallacis* or *Z. mali* in a 24 h period. Each predator exhibited distinct preferences for *O. aceris* life stages. *N. fallacis* consumed significantly more protonymphs and adults of *O. aceris*, whereas *Z. mali* consumed more eggs. In contrast, maple cultivars significantly influenced rates of intraguild predation between phytoseiids and stigmaeids. Adult *N. fallacis* consumed more immature stages of *Z. mali* on Autumn Blaze than on Red Sunset maple, but adult *Z. mali* consumed the same numbers of *N. fallacis* nymphs on both cultivars. These findings provide a potential mechanism to explain the resistance of Red Sunset maples to *O. aceris*. On Red Sunset maples, where domatia provide *Z. mali* with refugia from predation by *N. fallacis*, both predators can contribute to the mortality of *O. aceris*. In contrast on Autumn Blaze maples *Z. mali* have no place to hide from *N. fallacis*, so the contribution of this stigmaeid to *O. aceris* mortality is greatly diminished. Thus, differential susceptibility of these cultivars to spider mites may be mediated by the capacity of leaf domatia to influence rates of intraguild predation among phytoseiid and stigmaeid predators.

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1. Introduction

Predatory mites in the family Phytoseiidae and Stigmaeidae have been studied extensively because they regulate populations of their tetranychid prey in certain agro-ecosystems (McMurtry et al., 1970; Jones and Parrella, 1983; Croft et al., 1992; Duso, 1992; Sato et al., 2001). Several studies have documented that *Neoseiulus* and *Typhlodromus* species feed on and regulate *Oligonychus* species (McMurtry and Croft, 1997; Croft et al., 1998; Shrewsbury and Hardin, 2003; Pratt and Croft, 2000). Maple spider mite, *Oligonychus aceris* (Shimer) (Acarina: Tetranychidae), are important pests of nursery grown maples. Studies of susceptibility to *O. aceris* among cultivars showed 'Red Sunset' red maple (*Acer rubrum*) to be less susceptible than 'Autumn Blaze' Freeman maple (*Acer × fremanii*) (Potter and Spicer, 1993; Seagraves et al., 2013; Prado et al., 2014). We propose that this relative resistance to *O. aceris* is due to varietal differences in the relative abundances of leaf domatia that can provide refugia for the two phytoseiids, *Neoseiulus fallacis* (Garman) and *Typhlodromus caudiglans* (Schuster), and one stigmaeid, *Zetzellia mali* (Ewing) mites we have found on these plants.

Leaf domatia, or acarodomatia, are small cavities formed by tissue at the juncture of the vein axils on the underside of leaves. Their most common shapes are pit (invaginations of leaf surface that reach the mesophyll), pocket (cavities beneath expanded veins), dense hair-tufts, or an association between hair-tufts and pits or pockets (Pemberton and Turner, 1989; O'Dowd and Willson, 1991; Nishida et al., 2005). On Red Sunset and Autumn Blaze maples leaf domatia consist of dense hair-tufts at the junction of leaf veins (Prado, 2013). Leaf domatia are commonly inhabited by mites that include predators in the families Phytoseiidae and Stigmaeidae and numerous fungivores (Walde, 1995; Agrawal et al., 2000; Lester et al., 2000; Kreiter et al., 2002). Domatia can increase predatory mite abundance by providing refuge from environmental conditions and intraguild predators (Pemberton and Turner, 1989; O'Dowd and Willson, 1989; Walter, 1996; Walter and O'Dowd, 1992; Norton et al., 2001; Loughner et al., 2008; Ferrerira et al., 2011). As such, leaves with domatia often have more predaceous mites than leaves without domatia (Walter and O'Dowd, 1992; Duso, 1992; English-Loeb et al., 2002; Karban et al., 1995; Loughner et al., 2008).

Although the relationship between leaf domatia and the abundance of predatory mites has been demonstrated in many plant taxa, the abundance of domatia cannot reliably predict reduction in herbivore populations. In a recent meta-analysis Schmidt (2014) attributes the elevated abundance of phytoseiid mites on plants to increased structural complexity that reduces intraguild predation, a hypothesis that has been experimentally validated for phytoseiids (Ferrerira et al., 2011). Yet this same meta-analysis failed to associate the abundance of domatia with reduced herbivory by phytophagous mites in systems where they are found. This confirms the findings of other studies (e.g., Agrawal, 1997; Agrawal et al., 2000; Seelmann, 2007) that suggest effects of domatia on phytophagous herbivores can be weak and variable depending on the structure of the domatia and the predators involved.

In our studies of *O. aceris* on maples, we have found Red Sunset maples to have consistently smaller populations of *O. aceris* than Autumn Blaze despite having equal densities of phytoseiid mites on leaves (Prado et al., 2015). This trend was maintained on trees when applications of soil nitrogen in a randomized complete block design increased foliar N and the abundance of *O. aceris*. We attributed the lower population of *O. aceris* on Red Sunset to the predation by *Z. mali* that were more abundant on this resistant cultivar during that two year study. Both stigmaeid and phytoseiid mites are known to inhabit leaf domatia in a variety of systems

(Clements and Harmsen, 1990; MacRae and Croft, 1996; Slone and Croft, 2001; Nishida et al., 2005). Yet, it is not clear why the structural complexity provided by leaf domatia would favor increased abundance of *Z. mali* over the phytoseiid species without investigating how these domatia affect predation and the outcome of predator-predator interactions. For this reason we quantified the relative abundance of domatia on the two cultivars to determine the extent to which these surface structures affect herbivore and predator abundance, predation of *O. aceris*, and intraguild predation between predatory mite species.

2. Materials and methods

2.1. Natural leaf domatia and mite abundance

Autumn Blaze and Red Sunset maple trees grown at the Purdue Meigs Farm, in Lafayette, IN USA were used for this study. On 29, August 2010, same aged leaves were collected from 24 trees of each variety. A total of 12 leaves from each tree were collected from one branch located in each of four cardinal directions. Entire leaves were inspected under the microscope and scored on a scale of zero to four based on the presence of pubescence along a hierarchical scale of leaf veins. Assessments were started at the primary petiole-leaf blade vein branch and continued to secondary, tertiary and quaternary branching. Leaves lacking domatia were given a score of zero with ranks given in accordance to the level of branching in which at least one domatia was observed. Size of the domatia were not measured. Adult and nymphal stages of spider mites, phytoseiids and stigmaeid predators present on the leaf were also counted when leaf domatia were scored.

Differences in the leaf domatia scores were determined using PROC MIXED for Generalized Linear Models (SAS[®] 9.3 Institute Inc., Cary, NC). The relationship between the total number of predatory mites, *O. aceris* and the average domatia index per tree were determined via Pearson correlation using PROC CORR and linear regression using PROC GLM (SAS[®] 9.3 Institute Inc., Cary, NC) analysis for each cultivar.

2.2. Predator prey interactions

We investigated the capacity of *N. fallacis* (Garman) and *Z. mali* (Ewing) to feed on egg, nymph, or adult stages of *O. aceris* during 24 h while in an experimental arena containing leaves of Red Sunset or Autumn Blaze maples. Leaves used in the study were collected between July and August 2011 from a planting of Autumn Blaze and Red Sunset located at the Purdue Meigs Farm in Lafayette, IN. Each excised leaf was trimmed to a standard size of 47.36 cm² using a leaf shaped template that encompassed primary through quaternary vein branches starting at the junction of the leaf base and petiole. Trimmed leaves were placed on wet cotton with the abaxial surface facing up in a 14.5 cm diameter and 2.5 cm deep Petri dish that was loosely covered with a Petri dish top and maintained in a growth chamber at 25 °C at 16:8 L:D. Prior to each assay leaves were inspected and cleaned of any prey items on the surface.

Each adult female *N. fallacis* and *Z. mali* assayed in this experiment was collected in the Meigs Farm field on Red Sunset maples and starved by isolating them on individual leaves for 24 h prior to each experiment. The number of prey used in each experiment was at least twice the number consumed by a single adult predator in our preliminary experiment. For the *O. aceris* egg consumption assay, five females were allowed to lay eggs on the leaf for 24 h. The number was then reduced so that 20 eggs were present. Twelve *O. aceris* nymphs or adults were transferred to their respective assays. The number of prey items consumed was determined

by subtracting the number of live prey items remaining on the leaves and those caught in cotton beyond the leaf edge after 24 h.

Experiments were conducted using a completely randomized design to determine effects of predator and host plant cultivar on the attack rate of a given type of prey. Each assay was replicated ten times. Only one prey stage was evaluated for each predator in a 24 h period for each cultivar and predator. Thus, 40 assays were conducted each day for each prey stage. Effects of host plant and cultivar were analyzed using PROC GLM for Generalized Linear Models (SAS® 9.3 Institute Inc., Cary, NC) with a two way ANOVA. Both the Levine and Bartlett tests were used to check assumptions of constant variance and a log transformation was applied to the data to correct for non-normality.

2.3. Predator predator interactions

The capacity of individual adult *N. fallacis* to consume adult and nymphal *Z. mali* on Red Sunset or Autumn Blaze maple leaves were conducted using the Petri dish arenas described earlier. Adult and nymphal *N. fallacis* used in this study were collected from Red Sunset and Autumn Blaze maple leaves collected in the field. The number of prey placed before each predator was at least twice the number consumed by a single adult predator in a preliminary experiment. To obtain *Z. mali* adult prey for each assay, leaves were inspected after they were placed on the chamber and all but 12 adults were removed. A total of 12 nymphal stage prey items were obtained using the same inspection and removal method. The capacity of individual adult *Z. mali* to consume adult and nymphal *N. fallacis* were assayed in a manner similar to that described for *N. fallacis* adult predators. Twelve adult or nymphal predators were present in each assay.

Experiments to determine effects of cultivar and prey on predator consumption were conducted using a completely randomized design with ten replicates. Only one prey item was assayed in a single day for each of the two predators. In this way 40 assays were conducted each day. Data were analyzed using the Generalized Linear Models procedure described earlier.

3. Results

3.1. Leaf domatia and mite abundance

Proportions of maximum rank of leaf domatia varied significantly between maple cultivars ($F = 39.11$; $df = 1, 37$; $P < 0.0001$). On Red Sunset, the average domatia ranking on leaves was 0.73 ± 0.02 of the maximum and on Autumn Blaze was 0.08 ± 0.01 (Fig. 1). There were more predatory mites on Red

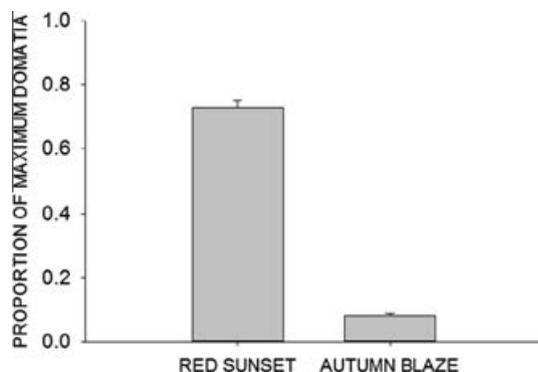


Fig. 1. Proportion of maximum leaf domatia (=Leaf domatia rank/4) on the abaxial surfaces of Red Sunset red maple and Autumn Blaze Freeman maple leaves collected from Miags Farm in Lafayette, Indiana on August 29, 2010. Bars represent means (\pm SE).

Sunset than Autumn Blaze ($F = 39.11$; $df = 1, 37$; $P < 0.0001$). Likewise, there were more *Z. mali* on Red sunset than Autumn Blaze ($F = 46.43$; $df = 1, 37$; $P < 0.0001$). There was no significant difference between the total number of phytoseiid mites (*N. fallacis* and *Typhlodromus caudligans* were combined because *T. caudligans* was rarely encountered) on the two maple varieties ($F = 2.45$; $df = 1, 37$; $P = 0.1323$) (Fig. 2). There were fewer *O. aceris* on Red Sunset ($0.017/\text{cm}^2 \pm 0.001$) than Autumn Blaze ($0.071/\text{cm}^2 \pm 0.006$) maples ($F = 110.34$; $df = 1, 37$; $P = 0.0001$).

Numbers of phytoseiids per cm^2 were not correlated with domatia on maple leaves either for Red Sunset ($r = -0.05$; $df = 1, 37$, $P = 0.8395$) or for Autumn Blaze ($r = -0.05$; $df = 1, 37$; $P = 0.8083$). However, number of *Z. mali* per cm^2 were highly correlated with domatia on leaves of Red Sunset ($r = 0.65$; $df = 1, 37$; $P = 0.0018$) but not for Autumn Blaze maples ($r = 0.09$; $df = 1, 37$; $P = 0.6852$) (Fig. 3). Number of *O. aceris* per cm^2 were not correlated with domatia on maple leaves either for Red Sunset ($r = -0.23$; $df = 1, 37$; $P = 0.3306$) or for Autumn Blaze ($r = 0.05$; $df = 1, 37$; $P = 0.8240$) (Fig. 4).

3.2. Predator prey interactions

Consumption of *O. aceris* eggs, nymphs and adults by single adults differed significantly between *Z. mali* and *N. fallacis* ($F = 80.37$; $df = 1, 36$; $P < 0.001$; $F = 37.13$; $df = 1, 36$; $P < 0.0001$; $F = 35.93$; $df = 1, 36$; $P < 0.0001$, respectively) (Fig. 5). On average, adult *Z. mali* consumed more eggs than mobile stages and adult *N. fallacis* consumed more mobile stages than eggs. During the assay *Z. mali* consumed almost three times the eggs (11.3 ± 0.90) consumed by *N. fallacis* (3.95 ± 0.26). Maple cultivar did not affect consumption of *O. aceris* eggs, nymphs, or adults by each predator ($F = 0.01$; $df = 1, 36$; $P = 0.9630$, $F = 0.55$; $df = 1, 36$; $P = 0.4632$; $F = 0.69$; $df = 1, 36$; $P = 0.4126$; respectively). There was no significant interaction between cultivar and predatory mite on the *O. aceris* eggs, nymphs or adults consumed ($F = 3.82$; $df = 1, 36$; $P = 0.0586$; $F = 2.14$; $df = 1, 36$; $P = 0.1521$; $F = 1.51$; $df = 1, 36$; $P = 0.2269$; respectively).

3.3. Predator-predator interaction

Consumption of nymphs of *Z. mali* by adult *N. fallacis* and consumption of nymphs of *N. fallacis* by adult *Z. mali* was significantly affected by maple cultivar ($F = 67.21$; $df = 1, 36$; $P < 0.0001$) and predator mite species ($F = 58.09$; $df = 1, 36$; $P < 0.0001$) (Fig. 6). *N. fallacis* adults consumed an average of 8.6 ± 0.82 *Z. mali* nymphs on Autumn Blaze cultivar which was nearly four times the

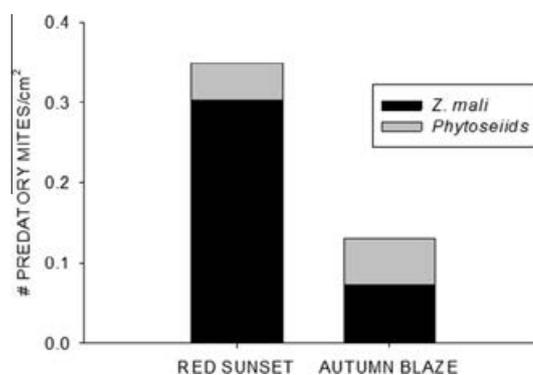


Fig. 2. Density of phytoseiid and stigmatid mite predators on leaves of Red Sunset red maple and Autumn Blaze Freeman maple collected from Miags Farm in Lafayette, Indiana on August 29, 2010. Bars represent means.

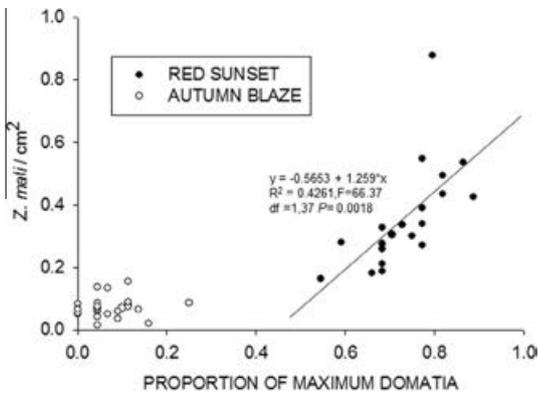


Fig. 3. The relationship between leaf domatia index and the number of *Z. mali* on Red Sunset red maple (solid circles and solid line) and Autumn Blaze Freeman maple (open circles) found on leaves collected from Miegs Farm in Lafayette, Indiana on August 29, 2010.

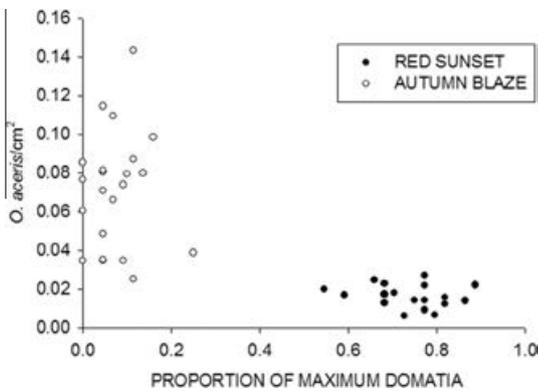


Fig. 4. The relationship between leaf domatia index and the number of *O. aceris* on Red Sunset red maple (solid circle) and Autumn Blaze Freeman maple (open circles) collected from Miegs Farm in Lafayette, Indiana on August 29, 2010.

2.3 ± 0.30 consumed by *N. fallacis* adults on Red Sunset. In contrast, the number of *N. fallacis* nymphs consumed by *Z. mali* adults was almost the same in both cultivars. This resulted in a significant interaction between predator mite species and cultivar ($F = 40.52$; $df = 1, 36$; $P < 0.0001$). Adult *Z. mali* and *N. fallacis* did not consume any adult predators during this assay.

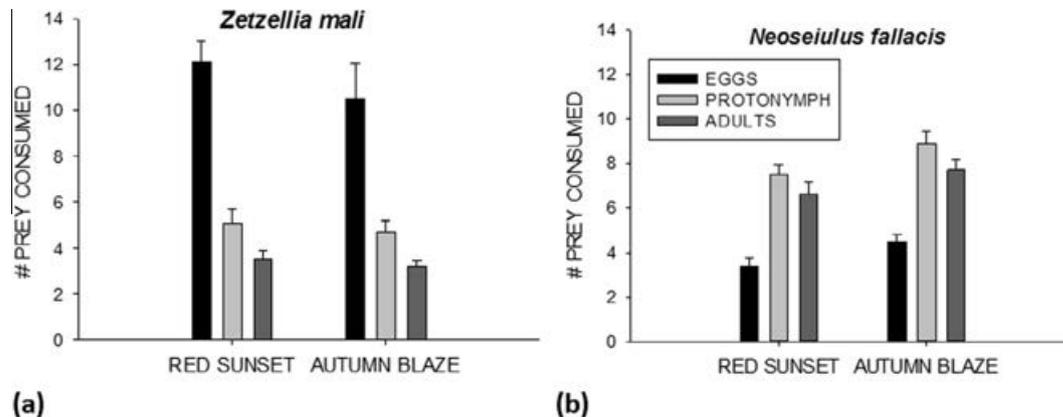


Fig. 5. Predation on eggs, nymphs and adults of *O. aceris* by adult *Z. mali* (a) and *N. fallacis* (b) predatory mites on Red Sunset red maple and Autumn Blaze Freeman maple in 24 h consumption assays conducted with 20 prey. Bars represent means (\pm SE).

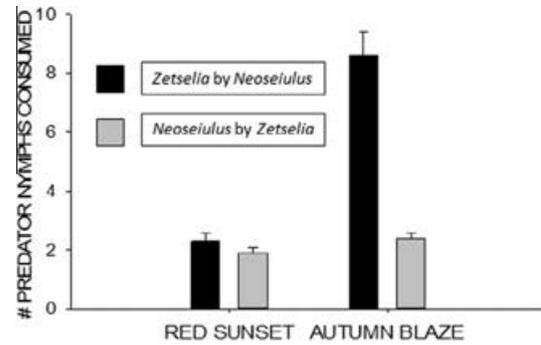


Fig. 6. Intraguild predation on nymphal stages by adult *Z. mali* and *N. fallacis* predators on Red Sunset red maple and Autumn Blaze Freeman maple in 24 h consumption assays conducted with 12 nymphs. Bars represent means (\pm SE).

4. Discussion

Although the structural complexity produced by leaf domatia is strongly linked to the abundance of mite predators, their effects on phytophagous mites can be quite variable due to idiosyncratic differences in the biology of predator and prey species (Schmidt, 2014). The two maples used in our study differed greatly in the abundance of leaf domatia. On Autumn Blaze maples the distribution of leaf domatia was limited to the primary petiole vein juncture, whereas on Red Sunset, domatia were quite common even at the junction of the quaternary veins. As such, the leaf surface of Red Sunset maples is far more structurally complex. Our late season census of these varieties clearly show Red Sunset to have fewer phytophagous *O. aceris* and more predatory mites than Autumn Blaze maples. We took this census late in the season when predators are more abundant (Prado et al., 2014) so that we could find enough predatory mites to determine if there was a relationship to domatia. In other studies, we found cumulative abundance of *O. aceris* to be more than twice that of predatory mites on Red Sunset and more than 10 times the predators on Autumn Blaze (Prado et al., 2015).

Differences we observed in predatory mite abundances were associated with significant increases in the stigmatid but not the phytoseiid predators. This is surprising because of the positive association between domatia and phytoseiids that Schmidt (2014) reports in her survey. As a type II phytoseiid (sensu McMurtry and Croft, 1997; Croft et al., 2004), *N. fallacis* has a wide range of phytophagous hosts, but prefers tetranychids. As such, *N. fallacis* tends to walk and search more when its preferred mite

prey is not present (Pratt et al., 1999). Thus, in our study of maple leaves where *O. aceris* is the predominant prey present, *N. fallacis* may not have responded numerically to domatia because its preferred tetranychid host was absent.

Relationships we found among populations of stigmatids, phytoseiids and *O. aceris* populations may be better understood within the context other studies of mite population dynamics. The capacity of predatory mites to prevent outbreaks of phytophagous species has been attributed to their capacity to survive low densities of prey and respond to rapidly increasing prey populations on host plants (Jansen and Sabellius, 1992). Both phytoseiid and stigmatid mites are important to lowering tetranychid prey populations on apple leaves because of their complementary preference for mobile and sessile stages of prey (Clements and Harmsen, 1990). Models based on life history studies in apples suggest that phytoseiid mites are more effective at controlling at high densities because of their greater reproductive rate and increased capacity to disperse to new patches of mites. Stigmatids are more important at lower densities because of their greater ability to survive on alternate hosts than phytoseiids (Clements and Harmsen, 1992).

Our examination of the biology of *Z. mali* and *N. fallacis* suggest that their prey preferences follow patterns that are consistent with assumptions underlying the apple based model. Both adult *N. fallacis* and *Z. mali* are capable of consuming all stages of *O. aceris* on maple leaves. Each species, however, showed distinct differences in the number and stage of prey consumed. *N. fallacis* attacked more nymphs and adults, whereas *Z. mali* consumed more eggs. We also found a strong potential for antagonistic interactions among phytoseiid and stigmatid predators. In laboratory assays nymphs of *N. fallacis* were consumed by adult *Z. mali* and nymphs of *Z. mali* were consumed by adult *N. fallacis* on both varieties of maple leaves.

Comparisons of the rates at which these predators attack their prey on maple leaves from each cultivar suggest that leaf domatia facilitate reductions in populations of *O. aceris* by mediating interactions among predatory mites. Rates of predation by *Z. mali* and *N. fallacis* on each stage of *O. aceris* are consistent on both maple cultivars. Similarly, adult *Z. mali* consumed equal amounts of *N. fallacis* nymphs on both kinds of maple leaves and this was similar to the rate at which adult *N. fallacis* consumed *Z. mali* nymphs on Red Sunset maples. In contrast, adult *N. fallacis* consumed nearly four times as many *Z. mali* on Autumn Blaze leaves as they did on the domatia rich Red Sunset leaves. This strongly suggests that leaf domatia provide the functional refugia for *Z. mali* nymphs from adult *N. fallacis*. If, as other studies suggest, *Z. mali* adults and nymphs also attack conspecific nymphs and eggs, and eggs of *N. fallacis*, (Croft and MacRae, 1993; Clements and Harmsen, 1990) the protective effect of domatia could extend to other life stages as well.

In conclusion, leaf domatia provide structural refugia on Red Sunset maple leaves that allow them to have more stigmatid predators than the domatia poor Autumn Blaze. As such there are more mite predators on these leaves that are capable of preventing outbreaks of *O. aceris* when populations are low either early in the season or after applications of pesticides (Prado et al., 2014). This finding underscores the importance of accounting for predator-predator as well as predator-prey interactions when determining how cultivars influence the role of beneficial organisms in agroecosystems.

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