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Do leaf domatia mediate a plant–mite mutualism? An experimental test of the effects on predators and herbivores

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Abstract. 1. Leaf domatia are tiny structures in leaf vein axils that are widespread among plant taxa and have been described to be typically inhabited by predatory and fungivorous mites. The mutualism hypothesis for the function of leaf domatia predicts that predatory and/or fungivorous mites benefit from having a favourable place to take refuge and reproduce and that plants benefit indirectly from reduced herbivory and/or pathogen attack.

2. The effect of leaf domatia on populations of predatory and herbivorous mites was examined for avocado, *Persea americana*. In separate experiments, domatia were added to leaves of a variety of avocado plants lacking domatia (Hass) and domatia were blocked on a domatia-bearing variety (Toro Canyon).

3. In two out of the five experiments conducted, domatia-bearing plants had significantly higher numbers of predatory mites compared with controls. Although herbivore numbers were consistently lower on plants with domatia than on plants without domatia, in no case did the presence of leaf domatia result in a statistically significant decrease in herbivorous mite populations.

4. These results suggest that domatia may frequently benefit predatory mites, however, indirect effects on herbivorous mites may not commonly exist or may be too difficult to detect.

Key words. Avocado, domatia, herbivory, leaf structures, mites, mutualism, *Persea americana*, Phytoseiidae, Tetranychidae, trophic interactions.

Introduction

Leaf domatia are tiny structures that can be found on the undersides of leaves in thousands of woody plant species (O'Dowd & Willson, 1989, 1991; Brouwer & Clifford, 1990; Walter, 1996). It has been postulated that potentially beneficial mites (predators and fungivores) benefit from leaf domatia by having a secure structure and humid environment in which to moult, lay eggs, and take refuge from predators; plants are thought to benefit from the association by having the phylloplane cleaned of herbivorous mites, other small damaging arthropods, and fungal pathogens (O'Dowd & Willson, 1989, 1991; Pemberton & Turner, 1989; Whitman, 1994; Walter, 1996; Agrawal & Karban, 1997).

There have been a large number of recent studies detailing different aspects of leaf domatia. The structures can be extremely complex and seem to serve no known physiological function (O'Dowd & Willson, 1989). Most studies, however, have focused on documenting the structures, describing the inhabitants, and comparing the numbers of mites inside and outside the domatia (Pemberton & Turner, 1989; Brouwer & Clifford, 1990; Walter & Denmark, 1991; Willson, 1991; Walter, 1992; Mound, 1993; O'Dowd, 1994; Karban *et al.*, 1995; Rozario, 1995; Walter & O'Dowd, 1995b, in press). Given the number of published observational and comparative studies, it is clear that leaf domatia are exceedingly common and are most often inhabited by mites potentially beneficial to the plants. In almost all cases, plants with leaf domatia had more potentially beneficial mites than plants without leaf domatia. In these same surveys, herbivorous mites have rarely been found in domatia in large numbers.

An accumulating number of studies have identified experimentally the effects of leaf domatia on predatory and fungivorous mites (Putman & Herne, 1964; Walter & O'Dowd, 1992a,b, 1995a,b, in press; Grostal & O'Dowd, 1994; Rozario, 1994; English-Loeb, 1996). These studies demonstrated that

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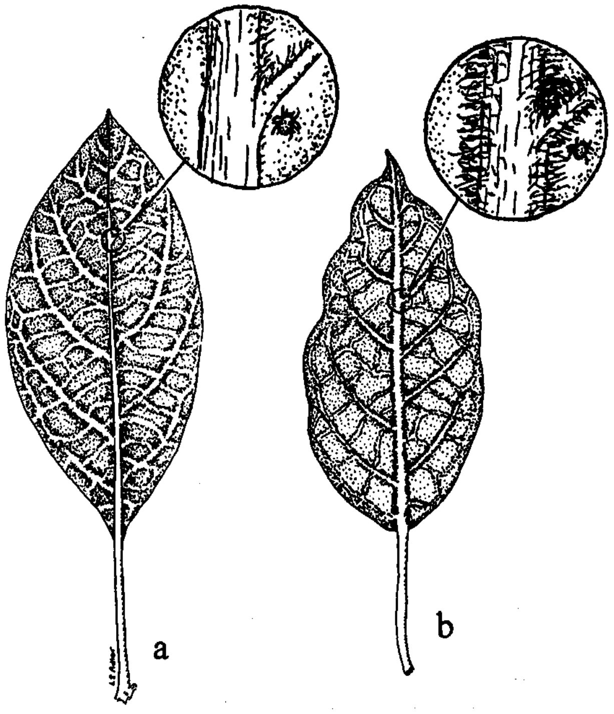

Fig. 1. Illustration of the two avocado varieties used in this study: (a) the glabrous and domatia-less Hass variety, and (b) the pubescent Toro Canyon variety with simple hair tuft domatia.

leaves with domatia removed by shaving the hair tuft or access to domatia blocked with a bitumen paint supported fewer potentially beneficial mites. Yet, a necessary component of the mutualism hypothesis is not only that predatory or fungivorous mites benefit from leaf domatia, but that plants also benefit indirectly via reduced herbivory or pathogen attack (Whitman, 1994; Agrawal & Karban, 1997). Without this link of indirect effects of herbivorous mites or fungal pathogens on the plant, leaf domatia can only be viewed as providing an amensal benefit to predatory and fungivorous mites. Few studies to date have manipulated domatia and measured effects on herbivorous mites (Grostal & O'Dowd, 1994; Walter & O'Dowd, 1995a, in press; Agrawal & Karban, 1997).

The effects of domatia on predatory and herbivorous mites were measured after manipulating domatia on two varieties of avocado, *Persea americana* Miller (Lauraceae), in order to test whether leaf domatia mediate a plant–mite mutualism. Specifically: (i) artificial leaf domatia were added to glabrous leaves of the Hass variety (without domatia), and (ii) access to existing hair tuft domatia on leaves of the Toro Canyon variety was removed (Fig. 1). Two predictions of the mutualism hypothesis for the function of leaf domatia were tested: (i) that predatory mite populations would be higher on leaves with domatia than on leaves without domatia, and (ii) that herbivorous mites would be decreased indirectly, via increased predation, on leaves with domatia compared with leaves without domatia.

Methods

Study system

Avocados, *P. americana*, have been cultivated for less than 100 years, and are native to Mexico and Central America (McMurtry, 1985). The Hass variety is the most popular commercial variety of avocado in the United States; its leaves have a smooth glabrous underside (Fig. 1) and are especially susceptible to mite pests in California (McMurtry, 1985; B. Faber, personal communication). Toro Canyon is an uncultivated variety that is used commercially only as a root stock (W. Brokaw, personal communication) and its leaves have simple hair tuft domatia (Fig. 1) that often contain more hairs in the axil than the sum of the intersecting vein hairs (Brouwer & Clifford, 1990; A. A. Agrawal, personal observation).

Both varieties of avocado are favourable hosts for avocado brown mite, *Oligonychus punicae* Hirst (Tetranychidae), a herbivore native to avocado (McMurtry, 1985). Avocado brown mite can cause reduced photosynthesis, decreased growth, and even complete defoliation (Jeppson *et al.*, 1975; Sances *et al.*, 1982; McMurtry, 1985). The predatory mite used in these experiments, *Galendromus helveolus* Chant (Phytoseiidae) (formerly *Typhlodromus floridanus* Muma), is also thought to be native to avocado and was introduced from collections in Central America (McMurtry, 1985; O. Aponte, personal communication). Previous experiments have detailed the predator–prey relationship between *O. punicae* and *G. helveolus* (Tanigoshi & McMurtry, 1977). Herbivorous avocado brown mites were maintained in a laboratory culture on excised avocado leaves kept in capped test-tubes or on a moist sponge. Predaceous mites were also kept in laboratory growth chambers and were fed spider mite eggs (*Tetranychus* spp.) *ad libitum*, following the methods of McMurtry & Scriven (1965) and Scriven & McMurtry (1971). Unless noted, all saplings used in the experiments were 1.5–2 m tall, and grown in open-bottom plastic containers. All experiments were conducted between October 1995 and April 1996.

Domatia addition experiments

The first experiment took place in a greenhouse in Davis, California where six Hass trees were infected with *O. punicae*. Each tree had five to ten shoots, each of which was considered an experimental unit. Each shoot consisted of four to seven leaves and was assigned randomly to one of the following treatments: (a) domatia were added to each leaf by gluing a small tuft of cotton fibres in each of the vein axils (treatment, $n = 12$ shoots); or (b) leaves were treated with a glue dab in each of the vein axils (control, $n = 13$ shoots). The glue (Elmer's™ School Glue Gel; Borden, Inc., Columbus, Ohio, U.S.A.) had no visible effects on the leaf tissue and when it was dry mites crossed freely over the glued area.

One month after infestation with *O. punicae*, mites were sampled to ensure that they were evenly distributed among the leaves (forty–eighty mites per shoot), and each shoot was isolated by placing a ring of Tanglefoot™ (Tanglefoot, Grand Rapids, Michigan, U.S.A.) at the base of the shoot. Two gravid adult female predatory mites (*G. helveolus*) were released on randomly chosen leaves of each shoot. After 3 weeks all leaves were destructively sampled and all mites were counted under a dissecting microscope. At this time the predatory mites had gone through two or three generations (see Tanigoshi & McMurtry, 1977).

An additional experiment looking at the effects of adding domatia was carried out on Hass seedlings under field conditions. Hass seeds were collected from an orchard maintained by University of California–Riverside and these were germinated in pots in a greenhouse in Davis, California. When the plants had approximately ten leaves they were infested with *O. punicae*. Mites were counted and augmented weekly until twenty-five to forty mites per plant could be counted with the naked eye. Similar to the experiments described above, all leaves of twelve randomly selected treatment plants received artificial domatia and all leaves of eleven control plants received dabs of glue. Two predatory mites were added to each plant. The plants were then moved to a grassy area to expose the plants to field conditions. The plants were destructively sampled after 3 weeks and all mites were counted.

Domatia removal experiments

The first of these experiments was carried out using detached Toro Canyon leaves in the laboratory and looked at effects on *G. helveolus* only. Leaf stems were put in capped test-tubes with water and the leaves were placed on and surrounded by moist paper towels. A total of fifty-four leaves were assigned randomly to treatment (domatia covered with glue) or control (glue next to the domatia) categories. Each leaf was inoculated with three *G. helveolus* and was supplied *ad libitum* with spider mite eggs (*Tetranychus pacificus*). Eggs were added daily to ensure no food limitation. Mites were sampled every other day for 8 days to test the effects of domatia on numbers of predatory mites.

Further experiments to test the effects of domatia removal were conducted in the greenhouse using domatia-bearing Toro Canyon trees, and were performed almost identically to the above described greenhouse experiment on Hass avocados. In the first trial, on each Toro Canyon leaf in the shoot either a bead of glue ($\approx$ 0.5 cm) was placed over the entire midrib and covering the domatia on both sides (treatment, $n = 16$ shoots) or an equal sized bead of glue was placed 1 cm away from the midrib (control, $n = 19$ shoots). Plants were infested with herbivorous and predatory mites as in the Hass greenhouse experiment described above and all mites were counted 3 weeks after predators were introduced.

In the second trial of the experiment to block domatia access, in place of haphazardly infesting the trees, thirty-six *O. punicae* were placed individually over each isolated shoot (treatment, $n = 11$ shoots; control, $n = 12$ shoots, total of three trees). This method was employed to control the numbers of mites per shoot precisely with the intention of reducing variance in the results. Two *G. helveolus* were introduced to each shoot after giving the *O. punicae* 2 weeks to establish and all mites were counted 3 weeks later.

Statistical analysis

Data representing very low mite numbers or with significant heterogeneity of variances were log $(x + 1)$ transformed for analyses to approximate normal distributions with equal variances. Untransformed means and standard errors are presented in the graphs. In all experiments using shoots on trees, analyses were conducted with a one-way ANOVA, blocking by tree. In no case did the effect of tree (block) or the number of leaves on each shoot approach having a significant effect on numbers of predators or herbivores. Whole seedling experiments were analysed using a one-way ANOVA. Laboratory experiments with detached leaves were analysed using a repeated-measures ANOVA. All data were analysed using the MGLH routine in SYSTAT (Wilkinson *et al.*, 1992).

Results

Domatia addition experiments

In the first Hass experiment, plants with leaf domatia added had higher numbers of predatory mites (Fig. 2a). In this experiment, the addition of artificial domatia resulted in a fivefold increase in the mean number of predatory mites found on each Hass shoot after 3 weeks (ANOVA $F_{1,18} = 10.3$, $P = 0.004$). In addition to a few adults, the vast majority of eggs and immatures were found under the cotton fibres that were attached.

The addition of leaf domatia did not have a significant indirect effect on the number of herbivorous mites found after 3 weeks. In this experiment, differences in the predators translated only to a trend of decreased herbivores after an outlier shoot with over 1000 *O. punicae* was removed (ANOVA $F_{1,17} = 0.74$, $P = 0.40$). No other shoot exceeded 150 *O. punicae*. Removing the outlying shoot did not affect the significance level. No *O. punicae* were found in domatia.

In the field trials with Hass seedlings, less than five *O. punicae* were recovered per plant after 3 weeks. There was, however, some colonization of leaves by other species of herbivorous and fungivorous mites. For the analysis of this experiment, all potentially beneficial mites (predators and fungivores) and all herbivores were pooled to examine the effects of domatia on the respective groups of mites. Although there were no measurable effects on predators and fungivores (ANOVA $F_{1,21} = 0.13$, $P = 0.72$), there was a trend of fewer herbivores on the seedlings with added domatia (ANOVA $F_{1,21} = 2.57$, $P = 0.12$) (Fig. 2b).

Domatia removal experiments

When predators were experimentally denied access to domatia in laboratory trials, a 33% reduction in numbers of

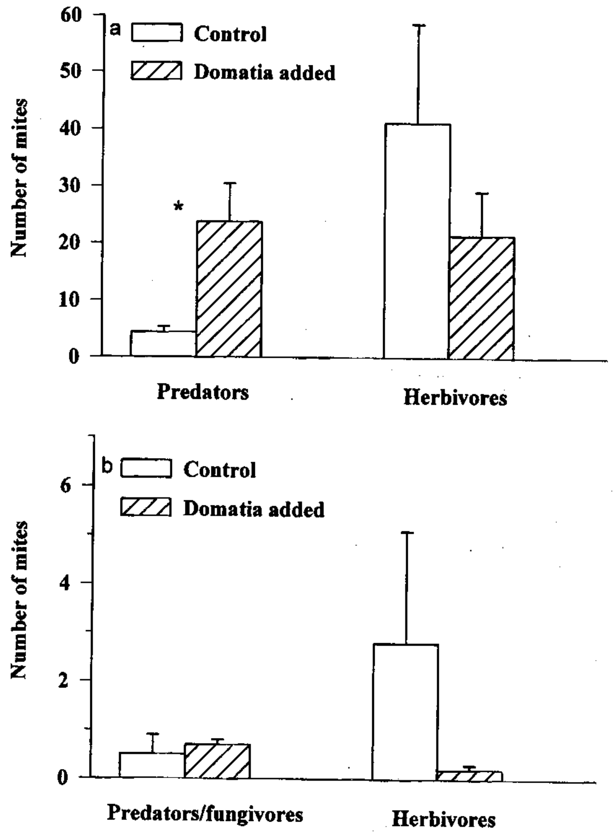

Fig. 2. Effects of leaf domatia on numbers of predatory and herbivorous mites: measuring effects of adding domatia to domatia-less Hass avocado leaves. (a) Greenhouse trial, predators: controls = 4.4 ± 1.0 mites (mean per shoot ± 1 SE); domatia added = 23.7 ± 6.8 mites. Herbivores: controls = 41.2 ± 17.5 mites; domatia added = 21.4 ± 7.8 mites; *indicates significance at $P = 0.01$ using ANOVA. (b) Field trial, predators/fungivores: controls = 0.5 ± 0.4 mites (mean per shoot ± 1 SE); domatia added = 0.7 ± 0.1 mites. Herbivores: controls = 2.8 ± 2.3 mites; domatia added = 0.2 ± 0.1 mites.

predatory mites was detected after 8 days (repeated-measures ANOVA $F_{1,52} = 4.23$, $P = 0.04$) (Fig. 3a). Eggs were often found in the intact domatia.

Surprisingly, in greenhouse experiments in which access to existing domatia was blocked, there was no effect on numbers of predatory mites (Fig. 3b,c). In the first trial very few predators were found on either treatment, and there were no differences between the treatments (ANOVA $F_{1,30} = 0.11$, $P = 0.74$). In the second greenhouse trial, in which the number of *O. punicae* was controlled by precise inoculation, the number of predatory mites was similarly not affected significantly by the treatments (ANOVA $F_{1,19} = 0.03$, $P = 0.86$).

In neither trial of the domatia removal experiments did presence of leaf domatia have a significant indirect effect on the number of herbivorous mites found after 3 weeks (trial 1: ANOVA $F_{1,30} = 2.4$, $P = 0.13$; trial 2: ANOVA $F_{1,19} = 0.68$, $P = 0.42$) (Fig. 3b,c). Avocado brown mites were not observed in the domatia.

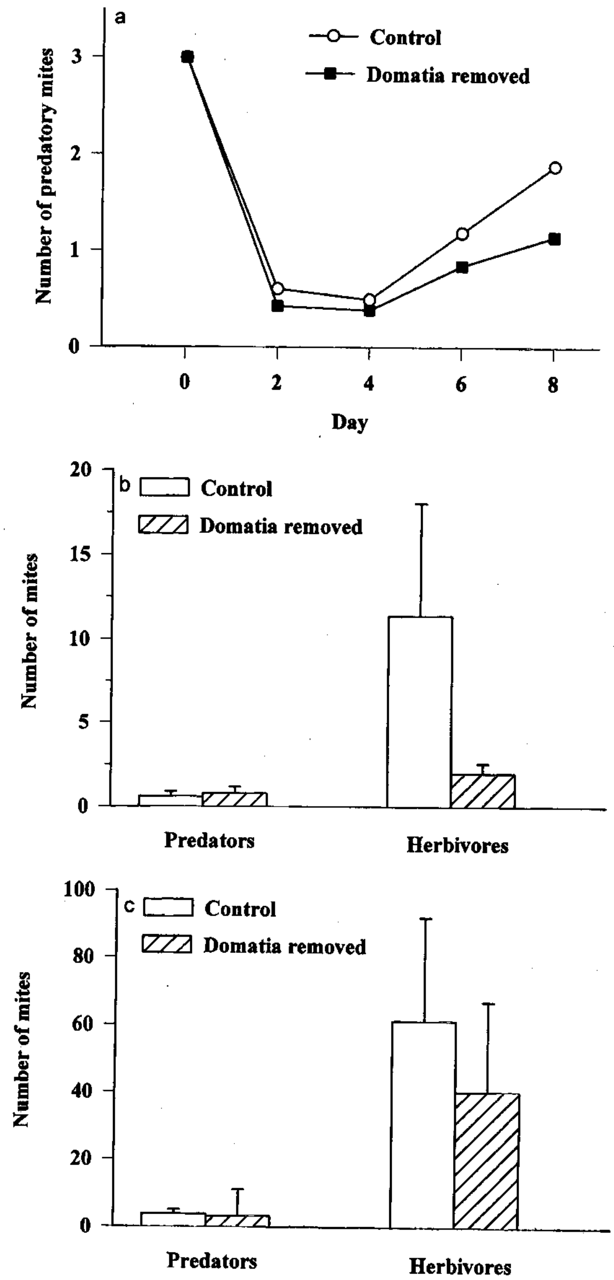

Fig. 3. Effects of leaf domatia on numbers of predatory and herbivorous mites per leaf: measuring effects of blocking access to domatia on Toro Canyon avocado leaves. (a) Laboratory trial, overall means per leaf are given: controls = 2.1 mites; domatia blocked = 1.4 mites. (b) Greenhouse trial 1, predators: controls = 0.6 ± 0.3 mites (mean per shoot ± 1 SE); domatia blocked = 0.8 ± 0.4 mites; herbivores: controls = 11.4 ± 6.7 mites; domatia blocked = 2.0 ± 0.6 mites. (c) Greenhouse trial 2, predators: controls = 3.8 ± 1.3 mites; domatia blocked = 3.2 ± 0.8 mites. Herbivores: controls = 61.4 ± 31.0 mites; domatia blocked = 40.4 ± 26.7 mites.

Discussion

In two out of five trials the presence of leaf domatia significantly benefited populations of predatory mites compared with leaves without domatia. This is consistent with predictions of the mutualism hypothesis that domatia benefit predatory mites. A benefit to predators was seen in one domatia addition experiment and one domatia removal experiment. However, this result did not occur in the greenhouse trials with the Toro Canyon trees. Leaves of Toro Canyon avocados are quite pubescent in addition to having domatia (Fig. 1). The lack of an effect of domatia on predatory mites in the experiments with Toro Canyon trees could have resulted from the fact that *G. helveolus* used other pubescent areas of leaves for activities such as egg laying. Although eggs were often found in the domatia, they were also found under vein hairs. Consistent with this idea, Karban *et al.* (1995) found that, in addition to domatia, vein hairs and axil bristles favoured the presence of predatory mites on grape vines.

Domatia have been hypothesized to benefit predatory or fungivorous mites in several ways. Mite eggs are sensitive to humidity and tend to desiccate under dry conditions (Sabelis, 1985), and domatia are thought to provide a favourable microclimate to support moulting and egg development. Grostal & O'Dowd (1994) demonstrated that the effect of domatia can sometimes only be measured under extreme environmental conditions such as low humidity where predators are susceptible to desiccation outside the domatia. Herbivorous mites are not usually as sensitive to humidity because many species spin protective webbing in which they place eggs and seek refuge. It is possible that the greenhouse environment sheltered the plants and mites from adverse climatic conditions and this partially masked the effect of domatia on mite populations.

In no case was there a significant effect of domatia on populations of herbivorous mites. However, in each of the four experiments where herbivore numbers were recorded, there were consistently fewer herbivorous mites on leaves with domatia than on leaves without domatia. Although it is possible that 3 weeks was not enough time to see indirect effects of domatia on herbivorous mites, a repeated crash of *O. punicae* populations was seen within 3–4 weeks of the introduction of *G. helveolus* in previous experiments by Tanigoshi & McMurtry (1977). The lack of an effect of domatia on herbivorous mites seen in this experiment cannot rule out the possibility that such effects may occur at other times, particularly as these mite populations have been known to cycle (McMurtry & Scriven, 1966, 1968; Tanigoshi & McMurtry, 1977).

Although it is intuitive to think that domatia must benefit plants, this is difficult to demonstrate empirically. Effects on predatory mites have been amply demonstrated by both domatia removal and addition experiments (Putman & Herne, 1964; Walter & O'Dowd, 1992a,b, 1995a,b, in press; Grostal & O'Dowd, 1994; Rozario, 1994; English-Loeb, 1996). However, the few studies that have looked for effects on herbivores have found considerable variation and mixed results at best (Grostal & O'Dowd, 1994; Walter & O'Dowd, 1995a, in press; Walter, 1996; Agrawal & Karban, 1997). Only one study to date (Agrawal & Karban, 1997) has found direct positive effects of leaf domatia on predaceous arthropods, indirect negative effects on herbivorous mites, and an increase in plant reproduction as a result of domatia.

Progress towards understanding the function of leaf domatia will only follow from further manipulative experiments that measure the effects of domatia on predators and fungivores, herbivores and fungal pathogens, and ultimately on plant fitness. Because leaf domatia have only been found on woody perennials where fitness is difficult to assess, research should focus on the effects of domatia on herbivores and pathogens, especially those that are known to be serious pests (see Jeppson *et al.*, 1975; Agrios, 1988; Brouwer & Clifford, 1990). This study provides a link in testing the mutualism hypothesis for the function of leaf domatia by measuring effects of domatia on predators and herbivores. The results presented here provide promising data suggesting that leaf domatia may generally mediate a plant–mite mutualism.

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References

Agrawal, A.A. & Karban, R. (1997) Domatia mediate plant-arthropod mutualism. *Nature*, **387**, 562–563.

Agrios, G.N. (1988) *Plant Pathology*, 3rd edn. Academic Press, Orlando, Florida.

Brouwer, Y.M. & Clifford, H.T. (1990) An annotated list of domatia-bearing species. *Notes from the Jodrell Laboratory*, **12**, 1–33.

English-Loeb, G.M. (1996) Influence of leaf domatia in grapes on beneficial mites and vine susceptibility to herbivores and pathogens. *Bulletin of the Ecological Society of America* (Suppl.), **77**, 130.

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

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

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. (1985) Avocado. *Spider Mites: their Biology, Natural*

Enemies and Control (ed. by W. Helle and M. W. Sabelis), Vol. 1B, pp. 327–332. Elsevier, Amsterdam.

McMurtry, J.A. & Scriven, G.T. (1965) Insectary production of Phytoseiid mites. *Journal of Economic Entomology*, **58**, 282–284.

McMurtry, J.A. & Scriven, G.T. (1966) Studies on predator–prey interactions between *Amblyseius hibisci* and *Oligonychus punicae* (Acarina: Phytoseiidae, Tetranychidae) under green house conditions. *Annals of the Entomological Society of America*, **59**, 793–800.

McMurtry, J.A. & Scriven, G.T. (1968) Studies on predator–prey interactions between *Amblyseius hibisci* and *Oligonychus punicae*: effects of host-plant conditioning and limited quantities of an alternate food. *Annals of the Entomological Society of America*, **61**, 393–397.

Mound, L.A. (1993) The first thrips species (Insecta) inhabiting leaf domatia: *Domatiathrips cunninghamii* gen. et. sp. nov. (Thysanoptera: Phlaeothripidae). *Journal of the New York Entomological Society*, **101**, 424–430.

O'Dowd, D.J. (1994) Mite associations with the leaf domatia of coffee (*Coffea arabica*) in north Queensland, Australia. *Bulletin of Entomological Research*, **84**, 361–366.

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**, 191–238.

O'Dowd, D.J. & Willson, M.F. (1991) Associations between mites and leaf domatia. *Trends in Ecology and Evolution*, **6**, 179–182.

Pemberton, R.W. & Turner, C.E. (1989) Occurrence of predatory and fungivorous mites in leaf domatia. *American Journal of Botany*, **76**, 105–112.

Putman, W.L. & Herne, D.H.C. (1964) Relations between *Typhlodromus caudiglans* Schuster (Acarina: Phytoseiidae) and phytophagous mites in Ontario peach orchards. *Canadian Entomologist*, **96**, 925–943.

Rozario, S.A. (1994) *Domatia and mites: effects of leaf morphology on beneficial mites in semi-natural and managed systems*. PhD thesis, Monash University, Melbourne.

Rozario, S.A. (1995) Association between mites and leaf domatia: evidence from Bangladesh, South Asia. *Journal of Tropical Ecology*, **11**, 99–108.

Sabelis, M.W. (1985) Development. *Spider Mites: their Biology, Natural Enemies and Control* (ed. by W. Helle and M. W. Sabelis), Vol. 1B, pp. 43–52. Elsevier, Amsterdam.

Sances, F.V., Toscano, N.C., Hoffmann, M.P., Lapre, L.F., Johnson, M.W. & Bailey, J.B. (1982) Physiological responses of avocado leaves to avocado brown mite feeding injury. *Environmental Entomology*, **11**, 516–518.

Scriven, G.T. & McMurtry, J.A. (1971) Quantitative production and processing of Tetranychid mites for large-scale testing or predator production. *Journal of Economic Entomology*, **64**, 1255–1257.

Tanigoshi, L.K. & McMurtry, J.A. (1977) The dynamics of predation of *Stethorus picipes* (Coleoptera: Coccinellidae) and *Typhlodromus floridansus* on prey *Oligonychus punicae* (Acarina: Phytoseiidae, Tetranychidae). *Hilgardia*, **45**, 237–288.

Walter, D.E. (1992) Leaf surface structure and the distribution of *Phytoseius* mites (Acarina: Phytoseiidae) in south-eastern Australian forests. *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. & Denmark, H.A. (1991) Use of leaf domatia on wild grape (*Vitis munsoniana*) by arthropods in central Florida. *Florida Entomologist*, **74**, 440–446.

Walter, D.E. & O'Dowd, D.J. (1992a) Leaf morphology and predators: effect of leaf domatia on the abundance of predatory mites (Acari: Phytoseiidae). *Environmental Entomology*, **21**, 478–484.

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

Walter, D.E. & O'Dowd, D.J. (1995a) Beneath biodiversity: factors influencing the diversity and abundance of canopy mites. *Selbyana*, **16**, 12–20.

Walter, D.E. & O'Dowd, D.J. (1995b) Life on the forest phylloplane: hairs, little houses, and myriad mites. *Forest Canopies* (ed. by M. D. Lowman and N. M. Nadkarni). Academic Press, San Diego, California.

Walter, D.E. & O'Dowd, D.J. (in press) The good, the bad, and the ugly: which really inhabit leaf domatia? *Acarology IX: Symposia* (ed. by G. R. Needham, R. D. Mitchell, D. J. Horn and W. C. Welbourn). Ohio Biological Survey, Columbus, Ohio.

Whitman, D. (1994) Plant bodyguards: Mutualistic interactions between plants and the third trophic level. *Functional Dynamics of Phytophagous Insects* (ed. by T. N. Ananthakrishnan), pp. 207–248. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Wilkinson, L., Hill, M., Welna, J.P. & Birkenbeuel, G.K. (1992) SYSTAT for windows: statistics, Version 5 edn. SYSTAT, Inc., Evanston, Illinois.

Willson, M.F. (1991) Foliar shelters for mites in the eastern deciduous forest. *American Midland Naturalist*, **126**, 111–117.

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