Within-Plant Distribution and Diversity of Mites Associated with the Invasive Plant *Schinus terebinthifolius* (Sapindales: Anacardiaceae) in Florida

M. S. WIGGERS, P. D. PRATT,[1] P. W. TIPPING, C. WELBOURN,[2] AND J. P. CUDA[3]

Invasive Plant Research Laboratory, USDA–ARS, 3225 College Ave., Fort Lauderdale, FL 33314

Environ. Entomol. 34(4): 953–962 (2005)

ABSTRACT The exotic Brazilian peppertree, *Schinus terebinthifolius* Raddi, is an invasive plant that readily displaces native vegetation and develops monospecific stands in central and south Florida's native ecosystems. Despite prior arthropod surveys of *S. terebinthifolius* in its adventive range, little is known concerning the acarofauna associated with the weed in Florida. Leaves of *S. terebinthifolius* also vary in the presence and development of domatia, which are small morphological structures that may benefit mites. We assessed the development of new mite associations with *S. terebinthifolius* in Florida and quantified within-plant distribution of these arthropods. Mites inhabited over one-third of the sampled leaves with greatest species diversity in the Prostigmata, followed by Mesostigmata, Astigmata, and Cryptostigmata, respectively. Fungivorous mites (dominated by *Lorryia formosa*) were the most common feeding guild, predatory mites were the most diverse, and herbivorous mites were rarely encountered during the survey. Interior leaves supported greater populations of mites than exterior leaves, whereas height of leaves in the canopy did not affect mite distributions. Foliar domatia varied in development and occurred on nearly two-thirds of the leaves sampled. More than three-quarters of all mites collected were found on domatia-bearing leaves, which supported three times more mites per leaf than leaves without domatia. Mite densities increased concomitantly with the number of domatia, while domatia development only affected tydeids and number of leaves had no effect. The potential influence of domatia-mediated, tritrophic interactions among existing predators and a potential biological control agent of *S. terebinthifolius* are discussed.

KEY WORDS Brazilian peppertree, Acari, *Lorryia formosa*, biological control, exotic weed

BIOLOGICAL INVASIONS THREATEN NATIVE ecosystems by altering hydrological and disturbance regimens, nutrient cycling, energy budgets, and species diversity (Vitousek et al. 1997, Mack et al. 2000). Communities dominated by exotic plants, for instance, are often characterized by a paucity of indigenous faunal assemblages associated with the weed in its adventive range (Goeden 1974, Strong et al. 1984). Similarly, numerous studies have shown that a greater diversity and abundance of natural enemies, specifically herbivores, occur in a plant's native versus adventive range (Goeden 1974, Balciunas and Burrows 1993, Memmott et al. 2000, Costello et al. 2003). This enemy-free space experienced by the invasive plant in its adventive range is a primary explanation for the efficacy of classical weed biological control, which seeks to reestablish top-down regulation of invasive plants by reuniting a weed with coevolved natural enemies from its native range (Williams 1954, Keane and Crawley 2002, Myers and Bazely 2003). However, in most, if not all, systems, a small complex of indigenous fauna exploit the exotic phylloplane, possibly influenced more by structural specialization than by plant species fidelity (McMurtry and Croft 1997). The influence of exotic plant proliferation and concomitant changes in vegetation structure on the development of new associations with opportunistic species remain largely unexplored.

Brazilian peppertree, *Schinus terebinthifolius* Raddi, is a large (to >10 m), evergreen shrub or tree introduced from Brazil as an ornamental into >20 countries (Ewel et al. 1982). In the United States, *S. terebinthifolius* is found in Louisiana, Texas, and California and is an aggressive weed in both Florida and Hawaii (Ferriter 1997, Randall 2000, Hight et al. 2002). This weed successfully colonizes many native plant communities, including those supporting threatened and endangered species, and now occupies >283,000 ha in Florida (Ferriter 1997). A single hectare of suitable habitat can support >2,500 *S. terebinthifolius* individuals (Ewel et al. 1982), with disturbed habitats particularly susceptible to invasion (Ewel 1986). The invasion of this aggressive, woody weed poses a serious

[1] Corresponding author, e-mail: prattp@saa.ars.usda.gov.

[2] Florida Department of Agriculture and Consumer Services, Division of Plant Sciences, PO Box 147100, Gainesville, FL 32614–7100.

[3] University of Florida, Department of Entomology and Nematology, PO Box 110620, Gainesville, FL 32611–0620.

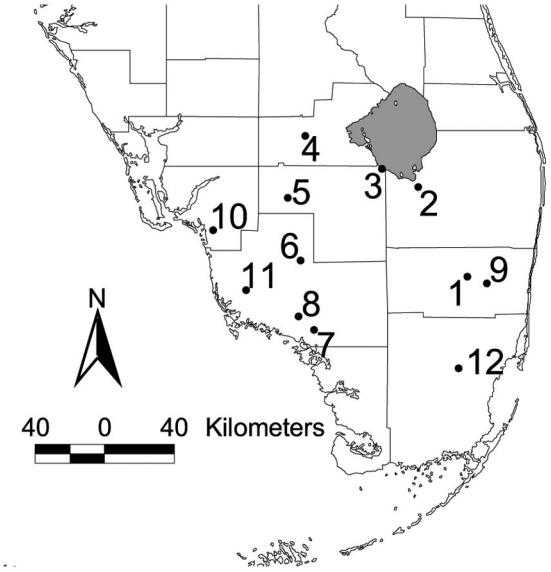

Fig. 1. *Schinus terebinthifolius* study sites in South Florida.

threat to species diversity and was identified in 1969 as having the potential to degrade many of South Florida's natural areas (Morton 1978).

Despite several surveys of *S. terebinthifolius* (Ewel et al. 1982, Cassani 1986, Cassani et al. 1989) in its adventive range, relatively little is known concerning the development of new arthropod associations with this invasive plant in Florida. Of the three previous surveys, only Cassani (1986) reported mites associated with the invasive plant, but these accounted for <4% of the 115 arthropod species encountered. Some leaves of *S. terebinthifolius* possess domatia (Pemberton and Turner 1989), which are known to influence mite populations (Walter 1996). Studies have found that plants with domatia support greater populations of mites than those without domatia (Walter and O'Dowd 1992a, Rozario 1995, O'Dowd and Willson 1997). Given that mites represent one of the largest taxonomic groups of arthropods (Walter and Behan-Pelletier 1999, Walter and Proctor 1999) and their affinity for foliar domatia, it is surprising that so few mites have been reported to be associated with *S. terebinthifolius* in the literature (i.e., Ewel et al. 1982, Cassani 1986, Cassani et al. 1989). In this study, we sought to (1) assess the diversity of acarofauna associated with *S. terebinthifolius* in Florida and (2) quantify within-plant distribution of these mites.

Materials and Methods

Acarological surveys of *S. terebinthifolius* were performed at 12 locations in South Florida (Fig. 1; Table 1) from August 2000 through June 2001. All sites were located in disturbed areas along roadsides and canal rights-of-way. Trees of similar size and vigor were sampled without apparent bias. Sampling consisted of removing 18 compound leaves from a single tree at each site in a randomly stratified method; 3 leaves were removed at each of three heights (low, ≈0.5 m; mid, ≈1 m; high, ≈2 m) from the exterior of the plant canopy, near the branch apex, and from within the interior of the plant canopy, ≈1 m from the branch apex. Each sample was sealed in a polyethylene bag, transported to the laboratory, and observed under a binocular microscope at ×40 magnification within 48 h. Mite diversity, abundance, developmental stage (egg, juvenile, or adult), and domatia development were recorded. To further quantify morphological variation, number of leaflets and domatia per leaf were recorded from December 2000 to June 2001. Adult mites for each species were mounted on glass slides in Hoyer's media for identification. Voucher specimens were deposited in the acarological collection of the Florida Department of Agriculture and Consumer Services, Division of Plant Industry in Gainesville, FL.

Table 1. Location of study sites used to quantify mite diversity associated with the invasive weed *S. terebinthifolius* in South Florida, Aug. 2000 to June 2001

Site	County	Latitude[a]	Longitude[a]	Months sampled[b]
1	Broward	26.17766	80.44888	I–VI, VIII–X, XII
2	Palm Beach	26.65562	80.71247	I–VI, VIII–X, XII
3	Hendry	26.75313	80.90704	I–VI, IX, X, XII
4	Glades	26.9297	81.3142	I–VI, VIII–X, XII
5	Hendry	26.59611	81.40956	I–VI, VIII–X, XII
6	Collier	26.26348	81.3421	I–VI, VIII–X, XII
7	Collier	25.89078	81.26965	I–VI, VIII–X, XII
8	Collier	25.96463	81.35231	I–VI, VIII–X, XII
9	Broward	26.14003	80.34463	I–II, IV–V, VII, X–XII
10	Lee	26.42594	81.80995	II–VI, XI, XII
11	Collier	26.10345	81.63334	III–VI, XI, XII
12	Miami-Dade	25.6885	80.497111	II–VI, IX–XII

[a] Decimal degrees.
[b] Roman numerals correspond to months with I = Jan. through XII = Dec.

The glabrous, compound leaves of *S. terebinthifolius* have slightly rolled margins, and the petioles are often winged. First characterized by Pemberton and Turner (1989), domatia of *S. terebinthifolius* are auriculate folds in the leaf lamina occurring on the abaxial side at the junction of the petiole and leaflet (Fig. 2a). However, we have observed variation in the occurrence and degree of development of domatia on *S. terebinthifolius* and categorized domatia development as undeveloped (flat, Fig. 2b), partially developed (≈50% curled, Fig. 2c), or fully developed (overtopped curl, Fig. 2d). For scanning electron micrographs, domatia were fixed with 3% glutaraldehyde in 0.2 M potassium phosphate buffer and postfixed with 2% osmium tetroxide in 0.2 M potassium phosphate buffer, dehydrated in an alcohol series, critical-point dried, sputter-coated with gold/palladium, and observed with a Hitachi S530 scanning electron microscope (Hitachi High Tech Am. Inc., Pleasanton, CA).

Mite counts were normalized using a $\ln(x + 1)$ transformation before analysis to meet assumptions of normality and homogeneity of variances implicit in the parametric analysis. Mite data were grouped by family and pooled across all sites and dates before determining the effects of leaf morphology and with-

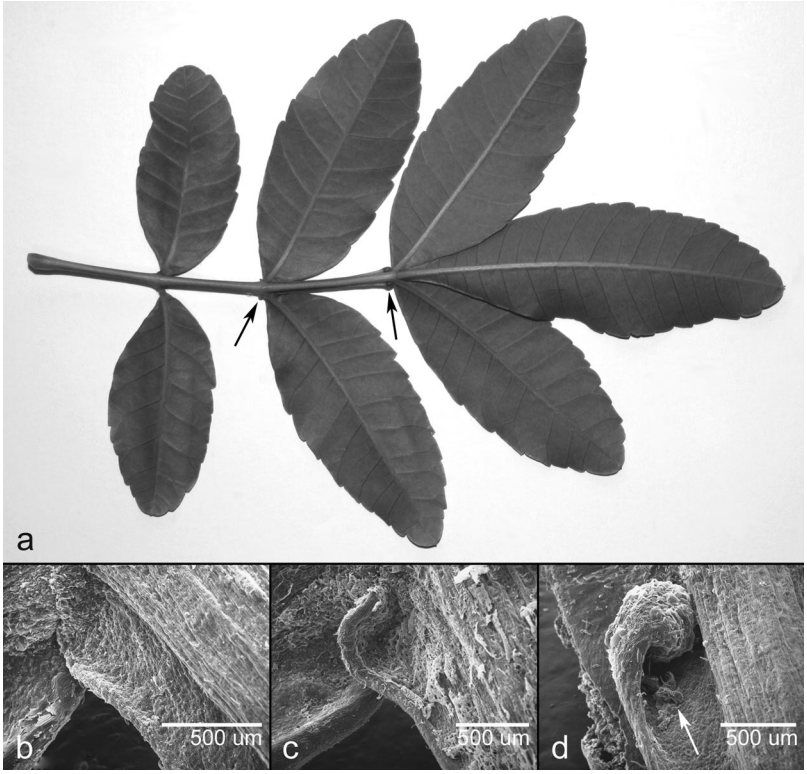

Fig. 2. Abaxial side of *S. terebinthifolius* leaf (a). Black arrows designate domatia locations. Scanning electron micrographs of undeveloped (b), partially developed (c), and fully developed (d) domatia. White arrow indicates mite exuvia.

in-plant leaf distribution on mite populations (PROC GLM; Littell et al. 2002). Post hoc analyses to determine significant differences were performed using Tukey's honest significant difference ($\alpha = 0.05$; Littell et al. 2002). Similar analyses were performed to determine the effect of within-plant leaf distribution on leaf morphology. The influence of within-plant leaf distribution on domatia presence was compared with logistic analysis of variance (ANOVA; PROC GENMOD; Littell et al. 2002).

Results

During the survey, 12,773 mites were observed inhabiting 37.8% of 1,936 *S. terebinthifolius* leaves. Of all mites observed, 23.8% were eggs (1.57 ± 0.19 [SE] per leaf), 42.7% were juvenile (2.82 ± 0.17), and 33.5% were adults (2.21 ± 0.15). At least 19 unique taxa representing 10 families were found (Table 2). Species diversity was greatest for the Prostigmata (nine taxa), followed by Mesostigmata (seven taxa), Astigmata (two taxa), and Cryptostigmata (one taxa). Seven species of fungivorous mites were found and represented the largest proportion of all individuals collected (97.7%), whereas predators were the most diverse (11 species). Tydeids were the most abundant mites encountered and *Lorryia formosa* Cooreman alone represented 95.9% of all mites observed (Table 2). The herbivore guild was limited to a single species, *Polyphagotarsonemus latus* (Banks) (Tarsonemidae). Several undetermined Tarsonemidae (Table 2) were either larvae or damaged specimens.

Leaf morphology was influenced by leaf position (i.e., interior or exterior) within the canopy but not by leaf height. Domatia were found on 62.4% of all leaves and were nearly 1.4 times more abundant on interior leaves than exterior leaves ($\chi^2 = 16.69$; df = 1,1882; $P < 0.0001$). Likewise, domatia tended to be more developed on interior leaves ($F = 30.19$; df = 1,1783; $P < 0.0001$). Number of domatia ranged from zero to seven per leaf (1.14 ± 0.04), whereas the number of leaflets ranged from 2 to 11 per leaf (6.73 ± 0.03). Interior leaves averaged more domatia per leaf (1.31 ± 0.06) than exterior leaves (0.96 ± 0.05; $F = 20.78$; df = 1,1314; $P < 0.0001$) and slightly fewer leaflets per leaf (6.67 ± 0.04 versus 6.79 ± 0.04, respectively; $F = 4.07$; df = 1,1368; $P = 0.0437$).

Abundance of mites in the Tarsonemidae, Tydeidae, and Phytoseiidae families varied among interior and exterior leaves (Table 3). Overall, mites were 2.2 times more abundant on interior than exterior leaves ($F = 50.92$; df = 1,1833; $P < 0.0001$). Interior leaves accounted for 69.2% of all mites collected, including 65.3% of all eggs, 70.5% of all juvenile mites, and 60.1% of all adult mites. Leaf height within the canopy only significantly influenced juvenile phytoseiid popula-

Table 2. Acarofauna associated with *S. terebinthifolius* at 12 sites in South Florida, Aug. 2000 to June 2001

Order	Family	Species	Date(s) collected[a]	Site(s) collected[b]	Total no. collected	Origin[c]	Lifestyle[d]
Astigmata	Acaridae	*Neotropacarus mumai*	I, II, VIII–X, XII	3, 4, 6–9	118	Native	F
	Winterschmidtiidae	*Czenspinskia transversostriata*	VIII–X	3, 9	5	WW	F
Cryptostigmata	Oribatidae	Undetermined spp.	VIII, XI	4, 10	69	?	F
Mesostigmata	Phytoseiidae	*Euseius hibisci*	III–VI, XII	2, 3, 7, 9, 10	6	Native	P
	Phytoseiidae	*Galendromus* sp.	XII	4, 9	3	Native?	P
	Phytoseiidae	*Iphiseoides quadripilis*	I–IV, VI, IX, X, XII	1, 4, 5, 7, 12	12	Native	P
	Phytoseiidae	*Proprioseiopsis* sp.	XII	6	2	Native?	P
	Phytoseiidae	*Typhlodromalus peregrinus*	I–III, VIII, X–XII	1, 2, 4–7, 9–12	29	Native	P
	Phytoseiidae	*Typhlodromina subtropica*	XI, XII	2, 9	5	Native	P
	Phytoseiidae	*Typhlodromips dentilis*	I, VIII, XI, XII	2, 5, 12	7	Native	P
	Phytoseiidae	Undetermined spp.	I–VI, IX–XII	1–7, 9, 10, 12	45	?	P
Prostigmata	Bdellidae	*Bdella* sp.	XII	5	1	Native?	P
	Cunaxidae	*Cunaxa* sp.	X	12	1	Native?	P
	Cheyletidae	*Cheletogenes ornatus*	XII	1	2	WW	P
	Stigmaeidae	*Agistemus* sp.	X	2, 7	3	Native?	P
	Tarsonemidae	*Polyphagotarsonemus latus*	V, X, XII	1, 3	168	WW	H
	Tarsonemidae	Undetermined spp.	IV, V, VIII, X	2, 3, 5, 9	12	?	H?
	Tydeidae	*Lorryia formosa*	I–VI, VIII–XII	1–12	12,237	WW	F/P
	Tydeidae	*Metatriophtydeus* sp.	V, IX	1	5	Native?	F/P?
	Tydeidae	*Tydeus* sp.	VIII–X, XII	4, 6, 8, 12	35	Native?	F/P?
	Tydeidae	*Paraponematus* n. sp.	IX–XII	3, 4, 6, 11	8	Native?	F/P

[a] Roman numerals correspond to months with I = Jan. through XII = Dec.
[b] Sites collected correspond to Fig. 1 and Table 1.
[c] Geographic distribution of species. Native, native to Florida; WW, worldwide distribution; ?, uncertain origin.
[d] Indicates primary feeding guild. P, predacious; F, fungivorous; H, herbivorous; ?, uncertain.

tions (F = 6.97; df = 2,1833; P = 0.0010). Leaves occurring lower in the canopy had more than three times and almost five times more juvenile phytoseiids than mid- or upper leaves, respectively. However, phytoseiid populations remained low throughout the study, with a maximum of 4 per leaf compared with a maximum of 222 tydeids per leaf.

Domatia-bearing leaves harbored 84.2% of all mites found (representing 92.5% of all eggs, 79.7% of all juvenile mites, and 84.4% of all adult mites observed). Individual domatia-bearing leaves supported mite populations more than three times greater than leaves without domatia (F = 104.96; df = 1,1880; $P < 0.0001$). Likewise, eggs were more than seven times (F = 63.14; df = 1,1880; $P < 0.0001$) more abundant on leaves with domatia than on leaves without domatia, whereas juvenile and adult populations were more than two times (F = 52.89; df = 1,1880; $P < 0.0001$) and more than three times (F = 87.47; df = 1,1880; $P < 0.0001$) greater, respectively. The presence of domatia positively influenced abundance of oribatids, phytoseiids, and tydeids (Table 4), whereas other families were not influenced by domatia presence. Overall, phytoseiid and tydeid populations were positively correlated with increases in the number of domatia (Fig. 3). The level of domatia development only influenced adult tydeid population densities, with fully developed domatia supporting over two times and nearly four times more individuals than partially and undeveloped domatia, respectively (F = 2.97; df = 2,1277;

Table 3. Influence of *S. terebinthifolius* leaf location on within-plant distributions of mites

Family	Lifestage	df	F	P	Interior[a]	Exterior[a]
Phytoseiidae	Egg	1	1.18	0.2771	0.01 ± 0.00a	0.00 ± 0.00a
	Juvenile	1	5.54	0.0186	0.02 ± 0.01a	0.01 ± 0.00b
	Adult	1	2.55	0.1108	0.04 ± 0.01a	0.03 ± 0.01a
	Total	1	7.11	0.0077	0.07 ± 0.01a	0.04 ± 0.01b
Tarsonemidae	Egg	1	3.92	0.0478	0.00 ± 0.00b	0.05 ± 0.03a
	Juvenile	1	3.92	0.0478	0.00 ± 0.00b	0.05 ± 0.03a
	Adult	1	8.57	0.0035	0.00 ± 0.00b	0.08 ± 0.03a
	Total	1	7.83	0.0052	0.00 ± 0.00b	0.19 ± 0.09a
Tydeidae	Egg	1	4.45	0.0351	2.00 ± 0.34a	1.03 ± 0.17b
	Juvenile	1	48.14	<0.0001	3.85 ± 0.29a	1.60 ± 0.17b
	Adult	1	58.32	<0.0001	3.00 ± 0.23a	1.18 ± 0.18b
	Total	1	51.20	<0.0001	8.84 ± 0.72a	3.81 ± 0.41b

[a] Mean ± SE. Within rows, means followed by different letters are significantly different at α = 0.05 (Tukey's honest significant difference; Littell et al. 2002); only families significantly influenced by leaf position are listed.

Table 4. Influence of domatia on within-plant spatial patterns of mites on *S. terebinthifolius* leaves

Family	Lifestage	df	*F*	*P*	Domatia present[a]	Domatia absent[a]
Oribatidae	Egg	1	1.73	0.1890	0.02 ± 0.01a	0.00 ± 0.00a
	Juvenile	1	1.73	0.1890	0.02 ± 0.01a	0.00 ± 0.00a
	Adult	1	3.97	0.0465	0.03 ± 0.01a	0.00 ± 0.00b
	Total	1	3.52	0.0608	0.06 ± 0.03a	0.00 ± 0.00a
Phytoseiidae	Egg	1	1.62	0.2028	0.01 ± 0.00a	0.00 ± 0.00a
	Juvenile	1	3.42	0.0646	0.02 ± 0.00a	0.01 ± 0.00a
	Adult	1	14.04	0.0002	0.05 ± 0.01a	0.01 ± 0.00b
	Total	1	16.41	<0.0001	0.08 ± 0.01a	0.02 ± 0.01b
Tydeidae	Egg	1	57.07	<0.0001	2.24 ± 0.31a	0.30 ± 0.09b
	Juvenile	1	46.30	<0.0001	3.53 ± 0.25a	1.52 ± 0.19b
	Adult	1	74.54	<0.0001	2.81 ± 0.23a	0.92 ± 0.12b
	Total	1	90.05	<0.0001	8.58 ± 0.64a	2.75 ± 0.33b

[a] Mean ± SE. Within rows, means followed by different letters are significantly different at $\alpha = 0.05$ (Tukey's honest significant difference; Littell et al. 2002); only families significantly influenced by leaf position are listed.

$P = 0.0514$). Number of leaflets significantly influenced abundance of phytoseiid eggs ($F = 3.13$; df = 8,1277; $P = 0.0016$) and all life stages of tarsonemids (eggs, $F = 3.30$; df = 8,1277; $P = 0.0010$; juvenile, $F = 3.30$; df = 8,1277; $P = 0.0010$; adult, $F = 3.00$; df = 8,1277; $P = 0.0025$); however, results were highly

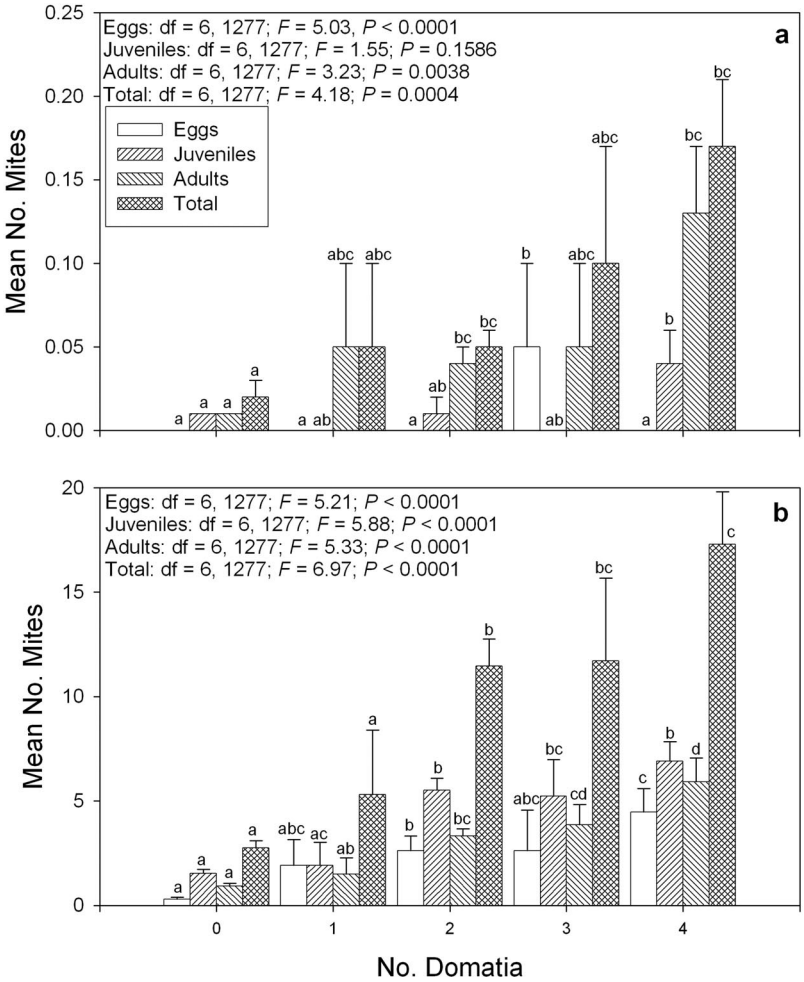

Fig. 3. Influence of domatia quantity on phytoseiid (a) and tydeid (b) population densities inhabiting *S. terebinthifolius* leaves. Different letters above the bars indicate significant differences at $\alpha = 0.05$ (Tukey's honest significant difference; Littell et al. 2002).

variable, with no biologically meaningful trends observed.

Discussion

Habitats dominated by invasive plants are often characterized as degraded systems that harbor few wildlife species. However, a growing body of literature suggests that substantial variation exists in the ability of invasive plants to support native fauna, indicating that habitats dominated by nonindigenous plants are not necessarily biological wastelands (e.g., Mazzotti et al. 1981, O'Hare and Dalrymple 1997, Memmott et al. 2000, Costello et al. 2003, Graves and Shapiro 2003). Data presented herein show that an assemblage of mite species exploits the phylloplane of the invasive tree *S. terebinthifolius* in South Florida. However, as indicated by the paucity of basal trophic levels (i.e., herbivores), this implies that *S. terebinthifolius* is a poor habitat for such fauna. Without comparable data of foliar arthropod diversity in surrounding native habitats and the probability that many species occur at similar (or higher) densities on native vegetation, caution should be exercised when making conclusions concerning the ecological health of *S. terebinthifolius*–invaded systems.

These data also have relevance to top-down regulation and biological control of invasive species. Harris (1975) recommended performing surveys of herbivores associated with an invasive plant in its adventive range as a prelude to the development of a weed biological control project. Historically, scientists have seldom heeded this recommendation, perhaps assuming that native herbivores are already suppressing the weed to the greatest level possible. Native arthropods, however, have been known to significantly damage, and in a few cases, control, nonindigenous weeds (Newman et al. 1998, Newman and Biesoer 2000). In addition to natives, coevolved herbivores and diseases may also be accidentally introduced from the plant's native range. The biological control agents *Megastigmus aculeatus* Hoffmeyer (chalcid wasp) and *Phyllocoptes fructiphilus* Keifer (an eriophyoid mite), for example, were collected in West Virginia during surveys of arthropods associated with the exotic weed *Rosa multiflora* (Thunb.). The eriophyoid mite, and the disease it transmits, is considered the most effective biological control agent of *R. multiflora* (Amrine 1996).

In Florida, however, it seems that *S. terebinthifolius* has not acquired native herbivores at sufficient densities to cause appreciable damage to plants (Cassani et al. 1989). Of the 10 families and 19 species identified in this study, the tarsonemid *P. latus* and possibly some undetermined Tarsonemidae (larvae and damaged specimens) were the only herbivorous mites collected from leaves of the invasive plant (Table 2). *P. latus* is a cosmopolitan and economically important species, attacking agronomic and horticultural plants worldwide (Denmark 1980, Jones and Brown 1983, Gerson 1992, de Coss-Romero and Peña 1998, Dhooria 1998). The occurrence of *P. latus* in this study, however, was limited to two sites (1 and 3) and three sample dates (March, October, and December), yielding 168 individuals and no observable foliar damage or tissue distortion associated with the mite's presence. The paucity of herbivorous species exploiting the seemingly limitless foliar resources of *S. terebinthifolius* is surprising, especially when considering the polyphagous nature of some species (e.g., *Tetranychus urticae* Koch, Bolland et al. 1998; some *Brevipalpus* species, Childers et al. 2003). This trend is also inconsistent with the insect feeding guild composition of *S. terebinthifolius* as reported by Cassani (1986), in which 40% of the species are phytophagous and 51% predatory. In a similar survey, Walter (1999) reported that 31% of mite species associated with the invasive shrub *Lantana camara* L. were phytophagous. Reasons for variation in the development of herbivore assemblages among introduced plants remains unclear, but may be related to time since introduction, relatedness to native species (Wapshere 1974), chemical defenses, or predator acquisition (Yela and Lawton 1997).

In contrast to herbivorous species, predatory mites represented the most diverse feeding type recovered from *S. terebinthifolius* leaves (Table 2). Predatory mites inhabited leaves at all study locations except site 8, with 94% of the individuals in the family Phytoseiidae (Table 2). Among all of the phytoseiid species, the most abundant predators were classified as generalists that feed on a wide range of diets including insects, pollen, spider mites, and other mites (McMurtry and Croft 1997). In addition, the relatively rare occurrence of Bdellidae, Cunaxidae, and Stigmaeidae on leaves (Table 2) may indicate these predators have only an incidental association with *S. terebinthifolius. Euseius hibisci* (Chant) and *Typhlodromalus peregrinus* (Muma) are found on a wide variety of plants in Florida (Muma and Denmark 1970) and are considered important natural enemies of several phytophagous pest mites and insects in agricultural systems (Muma 1971, Tanigoshi et al. 1984, Peña 1992, Fouly et al. 1995, Mehrnejad and Ueckermann 2001). Pemberton and Turner (1989) also found *E. hibisci* on *S. terebinthifolius* leaves in California. The cheyletid, *Cheletogenes ornatus* (Can. and Franz.), is also considered a natural enemy of some phytophagous pests (Gerson et al. 2003), but their low numbers suggest they are not important predators on *S. terebinthifolius.*

Herein, the seven species of fungivorous mites represent the second most diverse feeding guild associated with *S. terebinthifolius.* Consistent with many systems worldwide (Walter and Behan-Pelletier 1999, Walter and Proctor 1999), the most abundant mites associated with *S. terebinthifolius* leaves are fungal and saprophytic feeders, representing 97.7% of all mites collected. The tydeid *Tydeus californicus* (Banks) was reported by Pemberton and Turner (1989) to be similarly abundant on *S. terebinthifolius* leaves in California (occurring on 100% of leaves with domatia). Walter and Denmark (1991) reported that nearly one-half of all mites found on wild grape (*Vitis munsoniana* Michx.) in Central Florida were fungivorous. As with Florida citrus and other plants (Aguilar et al. 2001),

the tydeid, *L. formosa,* was the most common species inhabiting *S. terebinthifolius* leaves (Table 2), representing 95.9% of all observed individuals. While *L. formosa* is well adapted to *S. terebinthifolius* and many other plants, the source of their sustenance remains unclear. *Lorryia formosa* is fungivorous (Mendel and Gerson 1982) and pollenophagous (Aguilar-Piedra 2001), although early reports erroneously suggest that this species may be phytophagous (Smirnoff 1957, Del Rivero 1962, 1963, Flechtmann 1973). Leaves harboring *L. formosa* exhibited no obvious feeding damage, and observations of fungal colonies were rare. Finally, fungivorous mites, especially Tydeidae, have been reported to reduce pathogen impacts in other systems (Mendel and Gerson 1982, English-Loeb et al. 1999, Norton et al. 2000), and the resident populations of fungal feeding mites inhabiting *S. terebinthifolius* leaves may limit the efficacy of potential pathogen-based biological control efforts. Other Tydeidae, *Metatriophtydeus* and *Tydeus* (=*Orthotydeus*), are considered to be primarily fungivores. However, tydeids in the Pronematinae, including *Parapronematus,* may also be predators. Moreover, the Tydeidae serve as alternate food for predatory mites (Flaherty and Hoy 1971, Calis et al. 1988).

Mite densities were not influenced by vertical stratification within the *S. terebinthifolius* canopy, indicating a random distribution within the height range tested herein (≈0.5, 1, and 2 m above the soil line). Architecturally, *S. terebinthifolius* typically forms a dome-shaped canopy in which environmental conditions or resource availability may not vary sufficiently with height to induce vertical aggregation. In contrast, mite densities changed dramatically along the horizontal branch axis, with more mites occurring within the interior of the *S. terebinthifolius* canopy rather than on the branch apices. One explanation for the spatial distribution of mites inhabiting *S. terebinthifolius* may be related to the increased domatia densities on interior (and presumably older) leaves (O'Dowd and Willson 1989, O'Dowd 1994). In addition, interior leaves may provide a refuge from harsh environmental conditions (i.e., shielding mites from direct sunlight, rain, wind, and temperature fluctuations) or predation.

Mite behavior and abundance, especially for predators, is strongly influenced by leaf morphology (Walter 1992, Karban et al. 1995, McMurtry and Croft 1997, Kreiter et al. 2002). Consistent with other systems (Pemberton and Turner 1989, O'Dowd and Willson 1991, Walter and O'Dowd 1992b, O'Dowd and Pemberton 1994), the presence of domatia increased mite population densities on *S. terebinthifolius* leaves, with fungivorous and predatory mites occurring most frequently within domatia. Of the two domatia parameters analyzed herein, domatia development and number of domatia per leaf, only the latter influenced mite densities (Fig. 3), with the exception of adult tydeids. Various studies showed that leaves with larger domatia openings have more mites (O'Dowd 1994, Norton et al. 2000, English-Loeb et al. 2002). For *S. terebinthifolius,* fully developed domatia may be a less suitable refuge as the curl of the leaf lamina commonly occupies space that is otherwise available for mites in partially developed domatia. Studies have also noted that eggs and/or juvenile mites are commonly associated with domatia (Walter and O'Dowd 1992a, Grostal and O'Dowd 1994, English-Loeb et al. 2002, Faraji et al. 2002a) and that females often prefer domatia for oviposition (O'Dowd and Willson 1989, English-Loeb et al. 2002, Faraji et al. 2002b). Herein, the majority of mite eggs and juveniles were found on domatia-bearing leaves, with eggs and juveniles having more than seven times and more than two times greater densities, respectively, over leaves without domatia. These data also support evidence that older (i.e., interior for this system) leaves are more likely to possess domatia (O'Dowd and Willson 1989, O'Dowd 1994). The greater abundance of domatia on interior leaves of *S. terebinthifolius* coupled with the affinity of predatory and fungivorous mites for domatia-bearing leaves may explain, in part, the observed within-plant distribution of these arthropods.

In the absence of appreciable top-down regulation of *S. terebinthifolius* in Florida, a classical weed biological control program was initiated in the 1980s (Habeck et al. 1994, Hight et al. 2002, Cuda et al. 2004). Recent efforts have led to the selection and host specificity testing of several potential biological control agents of the target weed, including the thrips *Pseudophilothrips ichini* Hood (Hight et al. 2002, Cuda et al. 2004). Thrips are among the most notorious pests of agricultural and horticultural systems worldwide (van Rijn and Tanigoshi 1999). However, thrips rarely reach high population densities in natural, unmanaged systems due, in part, to predation by natural enemies. Key components of the predation guild attacking thrips include predatory mites, particularly those in the Phytoseiidae and Ascidae (Grafton-Cardwell et al. 1999, Walter and Proctor 1999, de Courcy Williams 2001). The majority of predatory mites collected from *S. terebinthifolius* leaves are generalist phytoseiids that may feed on small insects (McMurtry and Croft 1997). *Euseius hibisci* (Chant) and *Typhlodromalus peregrinus* (Muma), for instance, are important predators of thrips in agricultural systems and may prey on *P. ichini* once introduced. While typically classified as fungivorous, tydeids have been known to be facultative predators and may also exploit *P. ichini.* However, mites most frequently occurred on older *S. terebinthifolius* leaves located on the interior of the canopy. Therefore, potential interference of biological control from predatory mites may be moderated by *P. ichini* preference for newly developed, expanding foliage at branch apices. Because natural enemies are intentionally employed for the suppression of *S. terebinthifolius* in Florida, it remains unclear if and/or how domatia-mediated tritrophic interactions may interfere with biological control efforts of this weed.

Acknowledgments

We thank R. W. Pemberton and two anonymous reviewers for comments on earlier versions of the manuscript. We also

thank Sheryl Costello for assistance with data collection and Diann Achor of CREC-IFAS-UF for assistance with SEMs.

References Cited

Aguilar, H., C. C. Childers, and W. C. Welbourn. 2001. Relative abundance and seasonal occurrence of mites in the family Tydeidae on citrus in Florida, pp. 376–380. *In* R. B. Halliday, D. E. Walter, H. C. Proctor, R. A. Norton, and M. J. Colloff (eds.), Proceedings of the 10th International Congress of Acarology. CSIRO Publishing, Melbourne, Australia.

Aguilar-Piedra, H. G. 2001. Tydeiidae of Citrus from selected countries: distribution, seasonal occurrence, relative abundance, and feedings habits (Acari: Prostigmata). PhD dissertation, University of Florida, Gainesville, FL.

Amrine, J. W. 1996. *Phyllocoptes fructiphilus* and biological control of multiflora rose, pp. 741–749. *In* E. E. Lindquist, M. W. Sabelis, and J. Bruin (eds.), Eriophyoid mites—their biology, natural enemies and control. Elsevier, Amsterdam, The Netherlands.

Balciunas, J. K., and D. W. Burrows. 1993. The rapid suppression of the growth of *Melaleuca quinquenervia* saplings in Australia by insects. J. Aquat. Plant Manage. 31: 265–270.

Bolland, H. R., J. Gutierrez, and C.H.W. Flechtmann. 1998. World catalogue of the spider mite family (Acari: Tetranychidae). Brill, Leiden, The Netherlands.

Calis, J.N.M., W.P.J. Overmeer, and L.P.S. van der Geest. 1988. Tydeids as alternate prey for phytoseiid mites in apple orchards. Med. Fac. Landbouww. Rijksuniv. Gent. 53: 793–798.

Cassani, J. R. 1986. Arthropods on Brazilian peppertree, Schinus terebinthifolius (Anacardiaceae), in South Florida. Fla. Entomol. 69: 184–196.

Cassani, J. R., D. R. Maloney, D. H. Habeck, and F. D. Bennett. 1989. New insect records on Brazilian peppertree, Schinus terebinthifolius (Anacardiaceae), in South Florida. Fla. Entomol. 72: 714–716.

Childers, C. C., J.C.V. Rodrigues, and W. C. Welbourn. 2003. Host plants of *Brevipalpus californicus,* B. obovatus and *B. phoenicis* (Acari:Tenuipalpidae) and their potential involvement in the spread of viral diseases vectored by these mites. Exp. Appl. Acarol. 30: 29–105.

Costello, S. L., P. D. Pratt, M. B. Rayamajhi, and T. D. Center. 2003. Arthropods associated with above-ground portions of the invasive tree, Melaleuca quinquenervia, in South Florida, USA. Fla. Entomol. 86: 300–322.

Cuda, J. P., D. H. Habeck, S. D. Hight, J. C. Medal, and J. H. Pedrosa-Macedo. 2004. Brazilian Peppertree, *Schinus terebinthfolius:* Sumac Family-Anacardiaceae, pp. 439–441. *In* E. Coombs, J. Clark, G. Piper, and A. Cofrancesco (eds.), Biological control of invasive plants in the United States. Oregon State University Press, Corvallis, OR.

de Coss-Romero, M., and J. E. Peña. 1998. Relationship of broad mite (Acari: Tarsonemidae) to host phenology and injury levels in *Capsicum annuum.* Fla. Entomol. 81: 515–526.

de Courcy Williams, M. E. 2001. Biological control of thrips on ornamental crops: interactions between the predatory mite *Neoseiulus cucumeris (Acari: Phytoseiidae) and western flower thrips, Frankliniella occidentalis* (Thysanoptera: Thripidae), on cyclamen. Biocontrol Sci. Tech. 11: 41–55.

Del Rivero, J. M. 1962–1963. El ácaro amarillo de los agrios. Trabajos (Serie Fitopatalogía). 342: 1–10.

Denmark, H. A. 1980. Broad mite, *Polyphagotarsonemus latus* (Banks) (Acarina: Tarsonemidae) on pittosporum. Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Fla. Dept. Agric. Ent. Cir. 213.

Dhooria, M. S. 1998. Observations on host-range of leaf-curl mite, Polyphagotarsonemus latus (Banks) (Acari: Tarsonemidae) in Punjab. J. Insect Sci. 9: 9–11.

English-Loeb, G., A. P. Norton, D. M. Gadoury, R. C. Seem, and W. F. Wilcox. 1999. Control of powdery mildew in wild and cultivated grapes by a tydeid mite. Biol. Control. 14: 97–103.

English-Loeb, G., A. P. Norton, and M. A. Walker. 2002. Behavioral and population consequences of acarodomatia in grapes on phytoseiid mites (Mesostigmata) and implications for plant breeding. Entomol. Exp. Appl. 104: 307–319.

Ewel, J. 1986. Invasibility: lessons from South Florida, pp. 214–230. *In* H. A. Mooney and J. A. Drake (eds.), Ecology of biological invasions of North America and Hawaii. Springer, New York.

Ewel, J., D. S. Ojima, D. A. Karl, and W. F. DeBusk. 1982. Schinus in successional ecosystems of Everglades National Park. National Park Service, South Florida Research Center, Everglades National Park, Homestead, FL.

Faraji, F., A. Janssen, and M. Sabelis. 2002a. Oviposition patterns in a predatory mite reduce the risk of egg predation caused by prey. Ecol. Entomol. 27: 660–664.

Faraji, F., A. Janssen, and M. Sabelis. 2002b. The benefits of clustering eggs: the role of egg predation and larval cannibalism in a predatory mite. Oecologia (Berl.) 131: 20–26.

Ferriter, A. 1997. Brazilian pepper management plan for Florida. http://www.fleppc.org/schinus.htm.

Flaherty, D. L., and M. A. Hoy. 1971. Biological control of Pacific mites and Willamette mites in San Joaquin Valley vineyards: Part III. Role of tydeid mites. Res. Popul. Ecol. 13: 80–96.

Flechtmann, C.H.W. 1973. *Lorryia formosa* Cooreman, 1958—um ácaro dos citros pouco conhecido no Brasil. Ciencia Cultura. 25: 1179–1181.

Fouly, A. H., M. M. Abou-Setta, and C. C. Childers. 1995. Effects of diet on the biology and life tables of *Typhlodromalus peregrinus* (Acari: Phytoseiidae). Environ. Entomol. 24: 870–874.

Gerson, U. 1992. Biology and control of the broad mite, Polyphagotarsonemus latus (Banks) (Acari: Trasonemidae). Exp. Appl. Acarol. 13: 163–178.

Gerson, U., R. L. Smiley, and R. Ochoa. 2003. Mites (Acari) for pest control. Blackwell Publishing, Blackwell Sci. Ltd., 540 pp.

Goeden, R. D. 1974. Comparative survey of the phytophagous insect faunas of Italian thistle, *Carduus pycnocephalus,* in southern California and southern Europe relative to biological weed control. Environ. Entomol. 3: 464–474.

Grafton-Cardwell, E. E., Y. Ouyang, and R. A. Striggow. 1999. Predaceous mites for control of citrus thrips, Scirtothrips citri (Thysanoptera: Thripidae), in nursery citrus. Biol. Control. 14: 29–36.

Graves, S. D., and A. M. Shapiro. 2003. Exotics as host plants of the California butterfly fauna. Biol. Conserv. 110: 413–433.

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

Habeck, D. H., F. D. Bennett, and J. K. Balciunas. 1994. Biological control of terrestrial and wetland weeds, pp. 523–547. *In* D. Rosen, F. D. Bennett, and J. L. Capinera

(eds.), Pest management in the subtropics: biological control—a Florida perspective. Intercept, Andover, UK.

Harris, P. 1975. General approach to biocontrol of weeds in Canada. Phytoprotection. 56: 135–141.

Hight, S. D., J. P. Cuda, and J. C. Medal. 2002. Brazilian peppertreee, pp. 311–321. *In* R. Van Driesche, S. Lyon, B. Blossey, M. Hoddle, and R. Reardon (eds.), Biological control of invasive plants in the eastern United States. USDA Forest Service, Morgantown, WV.

Jones, V. P., and R. D. Brown. 1983. Reproductive responses of the broad mite, *Polyphagotarsonemus latus* (Acari: Tarsonemidae), to constant temperature-humidity regimes. Ann. Entomol. Soc. Am. 76: 466–469.

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

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17: 164–170.

Kreiter, S., M. S. Tixier, B. A. Croft, P. Auger, and D. Barret. 2002. Plants and leaf characteristics influencing the predaceous mite *Kampimodromus aberrans* (Acari: Phytoseiidae) in habitats surrounding vineyards. Environ. Entomol. 31: 648–660.

Littell, R. C., W. W. Stroup, and R. J. Freund. 2002. SAS for linear models, 4th ed. SAS Institute, Cary, NC.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences and control. Ecol. App. 10: 689–710.

Mazzotti, F. J., W. Ostrenko, and A. T. Smith. 1981. Effects of the exotic plants *Melaleuca quinquenervia* and *Casuarina equisetifolia* on small mammal populations in the eastern Florida Everglades. Fla. Sci. 44: 65–71.

McMurtry, J. A., and B. A. Croft. 1997. Life-styles of phytoseiid mites and their roles in biological control. Annu. Rev. Entomol. 42: 291–321.

Mehrnejad, M. R., and E. A. Ueckermann. 2001. Mites (Arthropoda, Acari) associated with pistachio trees (Anacardiaceae) in Iran (I). Syst. Appl. Acarol. Spec. Publ. 6: 1–12.

Memmott, J., S. V. Fowler, Q. Paynter, A. W. Sheppard, and P. Syrett. 2000. The invertebrate fauna on broom, *Cytisus scoparius,* in two native and two exotic habitats. Acta Oecologia (Berl.). 21: 213–222.

Mendel, Z., and U. Gerson. 1982. Is the mite *Lorryia formosa* Cooreman (Prostigmata: Tydeidae) a sanitizing agent in citrus groves? Acta Oecologia (Berl.). 3: 47–51.

Morton, J. F. 1978. Brazilian pepper—its impact on people, animals and the environment. Econ. Bot. 32: 353–359.

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

Muma, M. H., and H. Denmark. 1970. Phytoseiidae of Florida. Arthropods Fla. Neighboring Areas. 6: 1–150.

Myers, J. H., and D. R. Bazely. 2003. Ecology and control of introduced plants. Cambridge University Press, Cambridge, UK.

Newman, R. M., and D. D. Biesoer. 2000. A decline of Eurasian watermilfoil in Minnesota associated with the milfoil weevil, *Euhrychiopsis lecontei.* J. Aquat. Plant Manage. 38: 105–111.

Newman, R. M., D. C. Thompson, and D. B. Richman. 1998. Conservation strategies for the biological control of weeds, pp. 371–396. *In* P. Barbosa (ed.), Conservation biological control. Academic, San Diego, CA.

Norton, A. P., G. English-Loeb, D. Gadoury, and R. C. Seem. 2000. Mycophagous mites and foliar pathogens: leaf domatia mediate tritrophic interactions in grapes. Ecology. 81: 490–499.

O'Dowd, D. J. 1994. Mite association with the leaf domatia of coffee (*Coffea arabica*) in north Queensland, Australia. Bull. Entomol. Res. 84: 361–366.

O'Dowd, D. J., and M. F. Willson. 1989. Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. Biol. J. Linn. Soc. 37: 191–236.

O'Dowd, D. J., and M. F. Willson. 1991. Associations between mites and leaf domatia. Trends Ecol. Evol. 6: 179–182.

O'Dowd, D. J., and R. W. Pemberton. 1994. Leaf domatia in Korean plants: floristics, frequency, and biogeography. Vegetatio. 114: 137–149.

O'Dowd, D. J., and M. F. Willson. 1997. Leaf domatia and the distribution and abundance of foliar mites in broad-leaf deciduous forest in Wisconsin. Am. Midl. Nat. 137: 337–348.

O'Hare, N. K., and G. H. Dalrymple. 1997. Wildlife in southern Everglades wetlands invaded by melaleuca (*Melaleuca quinquenervia*). Bull. Univ. Fla. Mus. Nat. Hist. 41: 1–68.

Pemberton, R. W., and C. E. Turner. 1989. Occurrence of predatory and fungivorous mites in leaf domatia. Am. J. Bot. 76: 105–112.

Peña, J. E. 1992. Predator-prey interactions between *Typhlodromalus peregrinus* and *Polyphagotarsonemus latus:* effects of alternative prey and other food resources. Fla. Entomol. 75: 241–248.

Randall, J. M. 2000. *Schinus terebinthifolius* Raddi, pp. 282–287. *In* C. C. Bossard, J. M. Randall, and M. C. Hoshovsky (eds.), Invasive plants of California's wildlands. University of California Press, Berkeley, CA.

Rozario, S. A. 1995. Association between mites and leaf domatia: evidence from Bangladesh, South Asia. J. Trop. Ecol. 11: 99–108.

Smirnoff, W. A. 1957. An undescribed species of *Lorryia* (Acarina: Tydeidae) causing injury to citrus trees in Morocco. J. Econ. Entomol. 50: 361–362.

Strong, D. R., J. H. Lawton, and T.R.E. Southwood. 1984. Insects on plants. Community patterns and mechanisms. Blackwell Scientific, Oxford, UK.

Tanigoshi, L. K., J. Y. Nishio-Wang, and J. Fargerlund. 1984. *Euseius hibisci:* its control of citrus thrips in Southern Californian citrus orchards. Acarologia. 4: 717–724.

van Rijn, P.C.J., and L. K. Tanigoshi. 1999. Pollen as food for the predatory mites *Iphiseius degenerans* and *Neoseiulus cucumeris* (Acari: Phytoseiidae): dietary range and life history. Exp. Appl. Acarol. 23: 785–802.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. N.Z.J. Ecol. 21: 1–16.

Walter, D. E. 1992. Leaf surface structure and the distribution of *Phytoseius* mites (Acarina: Phytoseiidae) in Southeastern Australian forests. Aust. J. Zool. 40: 593–603.

Walter, D. E. 1996. Living on leaves: mites, tomenta, and leaf domatia. Annu. Rev. Entomol. 41: 101–114.

Walter, D. E. 1999. Cryptic inhabitants of a noxious weed: mites (Arachnida: Acari) on *Lantana camara* L. invading forests in Queensland. Australia J. Entomol. 38: 197–200.

Walter, D. E., and H. A. Denmark. 1991. Use of leaf domatia on wild grape *Vitis munsoniana* by arthropods in central Florida, USA. Fla. Entomol. 74: 440–446.

Walter, D. E., and D. J. O'Dowd. 1992a. Leaves with domatia have more mites. Ecology. 73: 1514–1518.

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

Walter, D. E., and V. Behan-Pelletier. 1999. Mites in forest canopies: filling the size distribution shortfall? Annu. Rev. Entomol. 44: 1–19.

Walter, D. E., and H. C. Proctor. 1999. Mites: ecology, evolution and behaviour. CABI, New York.

Wapshere, A. J. 1974. A strategy for evaluating the safety of organisms for biological weed control. Ann. Appl. Biol. 77: 201–211.

Williams, J. R. 1954. The biological control of weeds, pp. 95–98. *In* Report of the Sixth Commonwealth Entomological Congress. London, UK, pp. 95–98.

Yela, J. L., and J. H. Lawton. 1997. Insect herbivore loads on native and introduced plants: a preliminary study. Entomol. Exp. Appl. 85: 275–279.

Received for publication 5 April 2005; accepted 13 May 2005.