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Effects of Defoliation on Growth and Reproduction of Brazilian Peppertree (*Schinus terebinthifolius*)

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The exotic Brazilian peppertree is a serious invader of both disturbed and natural areas in central and south Florida, forming fast-growing, impenetrable thickets that dominate entire ecosystems. Brazilian peppertree has been targeted for biocontrol, and two defoliating insect species may eventually be released. This study was done to consider the possible effectiveness of defoliating biocontrol agents. The research investigated the effects of different frequencies of defoliation on height, crown diameter, and berry production of young Brazilian peppertrees. All the foliage was manually clipped from 36 trees in field plots once or twice per year for $\geq$ 1 yr. The effect on berry production of clipping 100% of the leaves from scattered individual branches of one large Brazilian peppertree was also examined. Trees that were completely defoliated five times at 6-mo intervals were significantly smaller and produced significantly fewer fruits than undamaged controls. Plants defoliated one time only, two times in 1 yr, and two times in each of 2 yr were comparable to the undamaged controls. From this simulated herbivory study, we infer that multiple defoliations by insect defoliators have the potential to significantly suppress the growth and fruit production of Brazilian peppertree in Florida.

Nomenclature: Brazilian peppertree, *Schinus terebinthifolius* Raddi, SCITE.
Key words: Biological control, defoliation, invasive, growth response, reproductive response, simulated herbivory, woody plant.

Brazilian peppertree is an evergreen woody shrub or tree that was introduced into the United States from South America in the early 19th century, probably because of the ornamental value of its shiny green foliage and bright red berries (Morton 1978). Also known as Florida holly, pepperberry tree, Christmas-berry, and false pepper, Brazilian peppertree escaped cultivation and has become an invasive weed in California, Hawaii, Florida, Texas, and the Bahamas, and has been reported from Puerto Rico and the U.S. Virgin Islands (Hammerton 2002; USDA, NRCS 2006). In Florida, Brazilian peppertree is listed as a noxious weed (FDACS 1999), and a category I invasive species (FLEPPC 2005). More than 400,000 ha of diverse central and south Florida ecosystems have been invaded by Brazilian peppertree since its introduction into the state in the 1840s (Mack 1991; Ziminski 1999).

This invasive plant outcompetes native species because of its tolerance of extreme moisture (Ewe and Sternberg 2003) and salinity (Mytinger and Williamson 1987), capacity to grow in shady environments (Ewel 1978), and possible allelopathic effects on neighboring plants (Gogue et al. 1974; Morgan and Overholt 2005). In Florida, this weed readily invades disturbed sites (e.g., fallow farmlands) as well as natural communities such as pinelands, hardwood hammocks, and mangrove forests, and is a major invader of the Everglades National Park (Ewel et al. 1982).

Brazilian peppertree is dioecious (Ewel et al. 1982); the fruits, or drupes, are carried in dense axillary panicles, with up to 50 panicles on a single typical mature branch (L. W. Treadwell, pers. obs.). Between 250 and 800 berries are produced per panicle, representing approximately 30 to 70% of flowers that had previously formed (Ewel 1978). Wildlife disperse the seeds widely in their droppings (Morton 1978). The fruits are favored by birds, particularly robins (*Turdus migratorius* L.) (Ewel et al. 1982; Panetta and McKee 1997).

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Brazilian peppertree has been targeted for biological control in Hawaii (Krauss 1963) and Florida (Bennett et al. 1990; Habeck et al. 1994). A suite of promising biological control agents attacking Brazilian peppertree is under development. Particularly promising are two leaf-feeding insects: a larval sawfly (*Heteroperreyia hubrichi* Malaise; Pergidae) and a leaf-rolling caterpillar, (*Episimus utilis* Zimmerman; Tortricidae), both closely associated with the plant in its native range in South America (Cuda et al. 2004, 2006).

Considerable literature exists on the effects of defoliation on woody plant growth and reproduction. Positive, compensatory effects have been noted (e.g., Hjältén et al. 1993; Lovelock et al. 1999), as well as negative effects on seed weight, numbers, or viability (e.g., Janzen 1976; Kaitanieme et al. 1999; Marquis 1984; Ollat and Gaudillere 1998; Stephenson 1980). Outright mortality, particularly of young seedlings, has also occurred as a result of defoliation (e.g., Clark and Clark 1985; Jackson and Bach 1999).

In anticipation of the release of defoliating herbivores in Florida for classical biological control of Brazilian peppertree, this study was undertaken to determine possible effects of defoliation on plant growth and fruit output. We hypothesize that the complete defoliation of small plants immediately following peak flowering, presumably simulating the timing and intensity of herbivory by an aggregation of insect defoliators, would negatively affect tree size and fruit production by female plants. Similarly, defoliation of individual branches within a single female tree at time of flowering would negatively affect fruit production on those branches.

Materials and Methods

In June 2001, 36 young Brazilian peppertree plants, 1- to 2-yr old, were transplanted from pots into three single-row plots of 12 plants each, with plants 6.1 m apart, bordering irrigation canals at the University of Florida's Institute of Food and Agricultural Sciences, Indian River Research and Education Center (IRREC), Fort Pierce, FL. Based on flower morphology, 19 males and 17 females were identified and

Table 1. Treatment groups and schedule of defoliation events.[a]

				Defoliation dates				
				2001	2002		2003	
Treatment[b]	n	M	F	August 27	May 11	September 27	April 26	October 5
Control	12	6	6					
1/1	6	4	2	x				
1/2	6	2	4	x		x		
2/1	6	4	2	x	x			
2/3	6	3	3	x	x	x	x	x

[a] Abbreviations: M, male; F, female.
[b] 1/1, one defoliation yr^{-1} for 1 yr; 1/2, one defoliation yr^{-1} for 2 yr; 2/1, two defoliations yr^{-1} for 1 yr; 2/3, two defoliations yr^{-1} for 3 yr.

distributed among the treatments as detailed in Table 1. Six replications of four defoliation treatments and two controls were randomly assigned within subplots of six plants.

On the dates listed in Table 1, we used scissors to remove all leaflets and terminal meristems from the plants within treatment groups assigned to be defoliated on that date, mimicking feeding damage by insect larvae. The central substem, or rachis, of each compound leaf was left on the plant.

Height and Crown Growth. Starting in June 2001, height of the highest active meristem on each tree was measured every 8 wk. Before the first defoliation event in August 2001, and every 8 wk thereafter, north-to-south and east-to-west crown diameters were measured at their widest points, for a total of 15 sampling dates used in the analysis.

Reproductive Output. *Entire Small Trees.* In November 2002, and again in November 2003, fruits from all branches of bearing plants (n = 17) were separated by tree into large paper bags, dried, counted, and weighed. For trees with fruits filling a volume greater than ~1,000 cm^3, at least three counts were made of berries exactly filling an 80-ml container; that count was averaged and then multiplied by the number of total 80-ml containers from each large-harvest tree.

Because no statistical differences were found in fruit yield from trees defoliated one time in each of 2 yr (treatment [trt] 1/2) or two times in the first year (trt 2/1), data from those two treatments were combined in reporting stem–node data from the first 15 mo as well as flowering and fruiting status of the trees over the course of 27 mo.

Individual Branches. On October 6, 2003, a large, flowering female control tree, 2.7 m tall and with an average crown diameter of 4.3 m, was selected for an experiment to determine effect of defoliating isolated branches of larger plants on fruit output of individual branches within the same tree.

The tree was divided into four quadrants delineated by the four cardinal directions; 33 branches, distributed among the four quadrants, were randomly selected and individually tagged. After the number of nodes bearing flower panicles was counted on each of the 33 branches, nine branches were randomly selected from the 33 and completely defoliated. The other 24 branches served as controls; a ratio of approximately three control : one treatment allowed us to test the degree of variability in fruit production among control branches. The ninth defoliated branch was intended as a reserve in the event of damage or loss. This proved fortuitous because several branches were accidentally destroyed by mowing during the course of the experiment.

Stem–nodes bearing flower or fruit panicles were counted on all intact marked branches at weekly intervals for 6 wk (October 8 to November 19, 2003), until all potential fruits had formed. Fruits were harvested from all intact marked branches (n = 7 defoliated, 15 control) into individually marked paper bags, dried, counted, and weighed.

Data Analysis. Heights and average crown diameters were log-transformed to normalize the data (after testing by the Shapiro–Wilk statistic, QQPlots, and PPPlots) and analyzed using PROC MIXED (SAS 1999), with treatment, date, and the treatment-by-date interaction as fixed factors in the MODEL statement and individual plants, nested within treatments, as random factors in the REPEATED statement. The MIXED procedure, designed specifically to accommodate experimental designs with both random and fixed factors (Littell et al. 1996; Wolfinger and Chang 1998), requires specification of a covariance structure for a particular data set, a determination that is made by trial and error runs (Wolfinger 1993). In this case, a covariance structure of standard variance components was found to give the best fit. Differences between least-square means of log-transformed heights and diameters were compared for significant differences between treatments at $\alpha = 0.05$.

Statistical analyses to determine the effects of defoliation treatments on fruit counts and dry weight were performed by the PROC MIXED procedure (SAS 1999), with five levels of defoliation treatment, two levels of time (2002 and 2003 harvests), treatment by time as fixed factors, plot (n = 3) as a random factor, and time also as a repeated factor. After trial-and-error runs of PROC MIXED, unstructured variance components were found to be the most parsimonious. Differences between least-squares means of log-transformed fruit counts and dry weights were compared for significance among treatments at $\alpha = 0.05$.

The PROC MIXED procedure allowed pooling the yield data from the two field seasons while incorporating "time" as a fixed factor. Treatment differences in fruit numbers and weights on individual branches were compared by ANOVA using the PROC GLM procedure with quadrant and treatment as independent variables and fruit numbers and dry weight as dependent variables (SAS 1999).

Results and Discussion

Height and Crown Diameter. Young Brazilian peppertrees recovered from and even compensated for a single defoliation in the fall, particularly in lateral crown growth, as illustrated by treatment group 1/1 (1 defoliation yr^{-1} for 1 yr; see Table 1) in Figures 1 and 2. In addition, the height and crown diameter of trees that were defoliated twice in the first year (trt 2/1) were not statistically different from the controls 1 yr later. One defoliation in each of 2 yr (trt 1/2) significantly reduced the average height of trees but not the crown diameters. One explanation for this might be that removing apical meristems, simulating feeding by larval *H. hubrichi*, released lateral buds from apical dominance, causing a marked increase in number of activated lateral meristems (L. W. Treadwell, unpublished data). This phenomenon also was

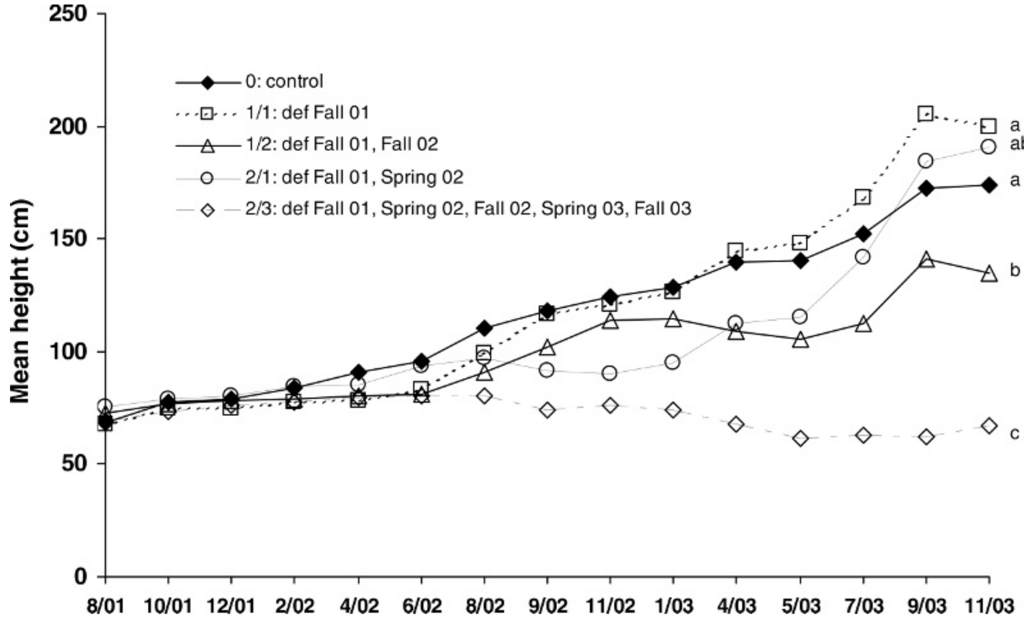

Figure 1. Heights of Brazilian peppertrees subjected to 100% defoliation one or two times per year for 1, 2, or 3 yr. Sequences with the same letter are not statistically different from each other at $\alpha = 0.05$ (SAS PROC MIXED).

reported by Woodall (1979) and suggests diversion of resources from height growth to lateral extension among an increased number of branches.

Contrary to the height decrease in treatment group 1/2, an increase in height of group 2/1, defoliated in August 2001 and May 2002, was observed (Figure 1) and perhaps represents compensatory growth. Some aspects of statistical differences depicted in Figure 1 (i.e., trt 2/1 vs. 1/2) might seem inconsistent with the graphical display, but PROC MIXED analysis is performed over the entire range of sequential data, not just on the final heights. All treatments gained significantly more height and crown diameter than group 2/3, which was defoliated five times in 27 mo. At the end of 2 yr, the average height of this group was actually slightly less than when it had first been planted, a result of dieback at the tops of the trees.

Gain in average crown diameter of the trees defoliated once (trt 1/1) was significantly greater than all other treatments by September 2003, 27 mo after planting (Figure 2). In contrast, the controls were not significantly greater in diameter than trees that had been defoliated twice in 1 yr (trt 2/1) or once a year for 2 yr (trt 1/2). By November 2003, however, treatment group 1/1 had declined in average height (Figure 1). Perhaps, at a certain height, or within some height range, Brazilian peppertree begins diverting more resources to lateral growth. Plants that were defoliated twice (whether twice in the same year or once a year for 2 yr), were essentially identical to each other and to the controls in crown diameter.

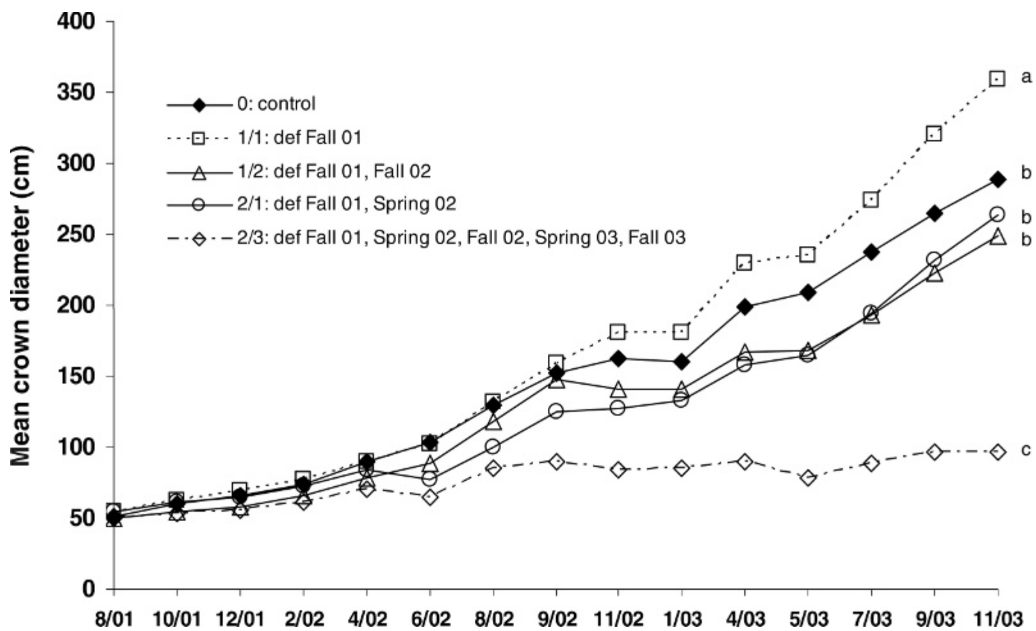

Figure 2. Crown diameters of Brazilian peppertrees subjected to 100% defoliation one or two times per year for 1, 2, or 3 yr. Sequences with the same letter are not statistically different from each other at $\alpha = 0.05$ (SAS PROC MIXED).

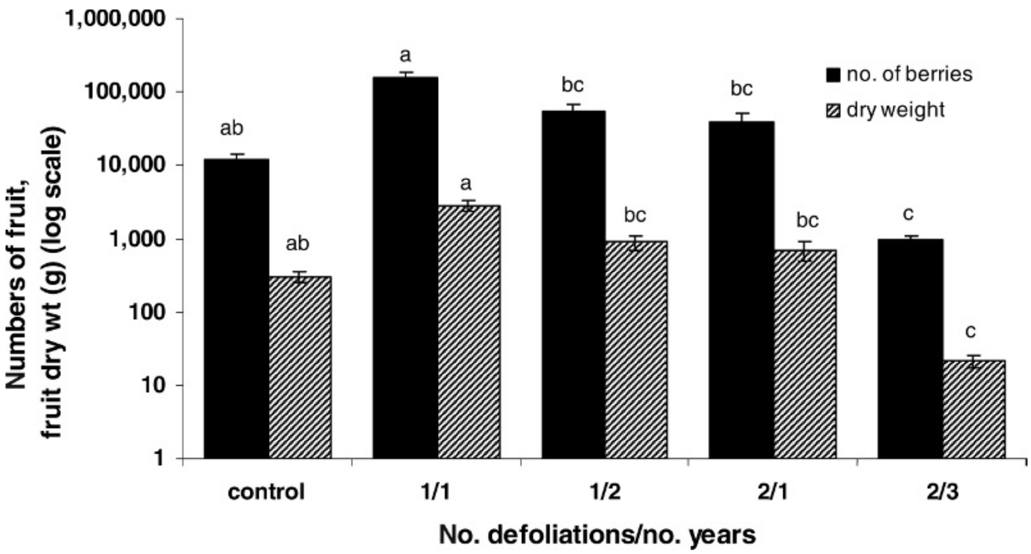

Figure 3. Dry weights and numbers of berries ± SE among 17 female Brazilian peppertrees on various defoliation regimes, total 2002 and 2003 harvests. Refer to Table 1 for sample sizes. Numbers or weights with the same letters are not statistically different at α = 0.05 (SAS PROC MIXED).

All treatments gained significantly more in crown diameter than treatment group 2/3, which remained at < 100 cm in diameter throughout the course of the experiment. Two trees in this treatment group persisted as little more than regrowth of suckers and lateral buds around the bases of bare main stems.

Reproductive Output. *Entire Small Trees.* Female trees defoliated only one time (trt 1/1) appeared to have compensated or, in fact, overcompensated for the damage by producing a large number of fruits (Figure 3). However, the fruit crop was not statistically different from the controls at α = 0.05 (least-squares mean differences, weights: df = 21, P = 0.0979; counts: df = 21, P = 0.1237) (Figure 3).

Trees defoliated one time in each of 2 yr (trt 1/2), or twice in 1 yr (trt 2/1), produced fruit crops that were not statistically different from the other treatments (54,331 drupes per tree ± 13,003 SE in trt 1/2, and 39,996 ± 11,657 in trt 2/1), except for those defoliated one time in 1 yr (Figure 3). Trees defoliated five times (trt 2/3) produced significantly fewer drupes (969 ± 146.5 SE) and with a lower fruit dry weight (21.4 gm ± 3.7 SE) per tree than controls or those defoliated only one time. Thus, defoliation frequency seemed to be mirrored in degrees of reproductive output: plants defoliated once or never produced large fruit crops; those defoliated twice, a moderate amount; and those repeatedly defoliated, few or no fruits (Figure 3).

Individual Branches. Within a single tree, defoliation of individual branches significantly reduced fruit output from those branches. As shown in Figure 4, only 1 wk after treatment, numbers of panicle-bearing stem–nodes on defoliated branches were reduced compared with controls, and this trend continued through the fruiting cycle, when the differences had become significant. Control branches (n = 17) averaged 2,283 drupes per branch ± 194 SE (range, 937

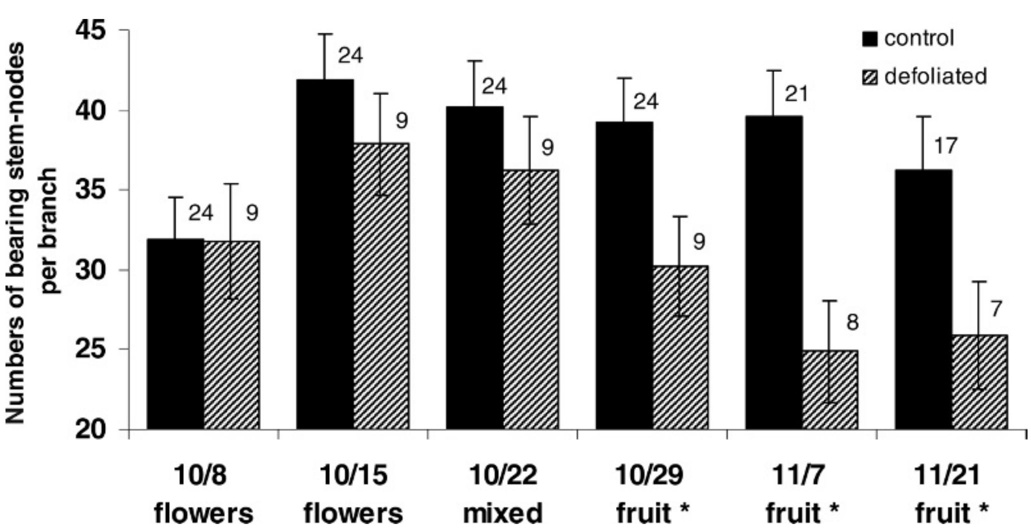

Figure 4. Average number ± SE of stem–nodes per branch bearing panicles of flowers, mixed flowers and fruit, or fruit among individual branches defoliated on October 8, 2003, vs. control branches of a single large Brazilian peppertree, October 8 to November 21, 2003. Numbers at the top of columns indicate number of sampled branches (see text). Asterisk (*) shows control and defoliated results are significantly different (one-tailed t tests, α = 0.05).

to 3,828), whereas defoliated branches ($n = 7$), averaged 373 drupes per branch ± 76 SE (range, 135 to 768) (df = 21, $F = 37.2$, $P < 0.0001$).

In general, the results of this study demonstrate the effect of leaf loss occurring at specific periods in the flowering–fruiting cycle of Brazilian peppertree, and without confounding effects of intra- or interspecific competition. Synchronicity of insect herbivory with the precise period of vulnerability in the transition from flower to fruit (apparently around 6 to 7 wk before the fruit formation) is critical to the effectiveness of defoliators introduced as a biological control agents against this plant.

Small sample size ($n = 2$) for female plants subjected to a single-defoliation event precludes a generalized conclusion that Brazilian peppertree compensates for a single defoliation by increasing its fruit production, height, and crown growth. This possibility warrants further investigation with a larger sample size.

The effect of multiple defoliations, especially when repeated at 6-mo intervals, was more conclusive. Although those trees defoliated only one or two times appeared to overcome any negative effects on growth and reproductive output, those defoliated five times at 6-mo intervals were significantly dwarfed and produced few fruits. Also, fruit production was significantly reduced on defoliated vs. control branches of a single large Brazilian peppertree.

Significant reductions in seed production following defoliation of individual branches have been demonstrated in other tree species, including catalpa [*Catalpa speciosa* (Warder) Warder *ex* Engelm.] (Stephenson 1980), mountain birch [*Betula pubescens* ssp. *czerepanovii* (Orl.) Hämet-Ahti] (Henriksson et al. 1999), and Kentucky coffee tree [*Gymnocladus dioicus* (L.) Koch] (Janzen 1976). In Kentucky coffee tree, an estimated 75% of defoliated branches aborted their pods, and the number of seeds per pod was significantly reduced when defoliation occurred following flower drop.

Still, in light of the ability of Brazilian peppertree to recover from loss of leaves, defoliation of single branches of large individuals is probably far less effective in their control than attacks on seedlings and juveniles, where biomass is proportionately greater in leaves and meristems than in stems and roots, and sufficient resources to overcome repeated defoliations are lacking.

Even in the absence of a precise synchronicity with the vulnerable periods in the cycle of flowering and fruiting of mature trees, however, defoliation of juvenile plants, adventitious sprouts, and regrowth should be particularly effective in reducing growth of, or even killing, individual Brazilian peppertree plants. The present study demonstrates the ability of mature trees to recover from loss of leaves, but the biomass of juveniles and sprouts is proportionately greater in leaves and meristems than in stems and roots and without sufficient stored resources to overcome repeated defoliations.

This strategy, of targeting young plants for biological control, was recommended for suppression of the invasive paperbark tree [*Melaleuca quinquenervia* (Cav.) Blak.] in Florida (Laroche 1999), and of acacia [*Acacia nilotica* ssp. *indica* (Benth.) Brenan] in Australia, where previously introduced biological control agents failed to have any discernible effect on growth and weediness of mature acacia trees (Kriticos et al. 1999).

Another important consideration in evaluating the results of this study is that experimental defoliation that simulates removal of tissue by an herbivore can produce effects that diverge, sometimes considerably, from the effects of natural defoliation by the organism itself. Differential responses by plants can result from lack of precision in imitating the amount, type, age, and timing of tissue removal by herbivores. Capinera and Roltsch (1980), for example, demonstrated differences in responses of wheat (*Triticum aestivum* L.) seedlings to manual defoliation compared with their responses to herbivory by grasshoppers. Baldwin (1990) speculates on the possibility of "selective enrichment" by herbivores on and near their host plants, from inputs of fecal matter or elevated CO_2; in differences between mechanical cutting and insect piercing or biting at a cellular level that elicits subtle damage cues; or, finally, by an unknown process or factor that occurs in the physiological exchange between plant and herbivore, such as salivary constituents, that affect plant growth. Despite these differences, simulated herbivory experiments can still be useful models for inferring the direction of plant response to herbivory (Lehtilä and Boalt 2004), especially when selecting candidate biological control agents because they can provide a "filter of efficacy before the filter of safety" (Raghu and Dhileepan 2005, Wirf 2006).

Overall, the results of this simulated herbivory study suggest that thriving populations of insect defoliators repeatedly attacking young Brazilian peppertree plants in Florida would reduce plant vigor, which would be reflected in decreased fruit output and decreased height and extension. These attacks, especially as one of multiple natural or human-induced stresses on Brazilian peppertree, e.g., disease, allelopathy, plant competition, soil deficiencies, and climatic extremes of drought, freezing, and violent storms, as well as chemical and mechanical control practices (see Cuda et al. 2006), should reduce the competitive advantage that Brazilian peppertree currently holds over native species in Florida.

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