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EFFECTS OF ADULT DIAPREPES ROOT WEEVIL ON LEAF GAS EXCHANGE AND GROWTH OF BUTTONWOOD AND LIVE OAK

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Abstract. **Diaprepes root weevils *Diaprepes abbreviatus* L. (Coleoptera: Curculionidae), feed on a wide variety of ornamental plants grown in southern Florida. Although most damage to plants is caused by larval root feeding, adult leaf feeding has been observed to cause moderate to severe defoliation. Studies were conducted to evaluate the effects of adult Diaprepes root weevil leaf feeding on net CO_2 assimilation, stomatal conductance, transpiration and growth of buttonwood (*Conocarpus erectus* L.) and live oak (*Quercus virginiana* Mill.). Leaf gas exchange of buttonwood in two separate experiments showed variable results. In the first experiment leaf gas exchange of young and mature leaves were not affected by adult weevil leaf feeding. In the second experiment, after 2 months mature leaves of infested plants had higher net CO_2 assimilation, stomatal conductance and transpiration than controls. In both experiments leaf area of buttonwood tended to be less for infested plants than non-infested plants. Leaf, stem and root weight of buttonwood was not affected by weevil infestation in the first experiment. In the second experiment root weight of buttonwood was lower for the infested plants than the non-infested plants. In a third experiment, leaf gas exchange of live oak was not affected by adult leaf feeding. Adult weevils did not cause any significant damage to live oak foliage and leaf gas exchange was not affected by herbivory. Live oaks did not produce any new leaves during the treatment period and all weevils died within a month.**

Diaprepes root weevil *Diaprepes abbreviatus L.* (Coleoptera: Curculionidae), is a polyphagus insect species known to feed on a wide variety of plants throughout Florida. The root weevil has a host range of more than 270 plant species (Simpson et al., 1996). In Florida it is estimated that this weevil causes more than 70 million dollars in damage annually (Weissling et al., 2002). Adult weevils have a voracious appetite and may cause severe defoliation of host plants.

Adult Diaprepes root weevils emerge from the soil year round; however, the peak emergence period is from May through October. As the teneral adults begin to dig their way out of the soil they shed a pair of deciduous mandibles. Adult weevils emerge from the soil and move up the tree canopy to feed and mate. Oviposition generally begins 3 to 7 d after emergence from the soil surface (Wolcott, 1936). The average number of survival days reported for adult weevils reared on an artificial diet is about 147 d for females and 135 d for males (Beavers 1982).

Diaprepes root weevil is known to be associated with a wide variety of ornamental plants grown in nurseries throughout Florida and many nurseries in Miami-Dade County, Florida, are infested with this pest. In a recent field survey of several field nurseries, Mannion et al. (2003) found that characteristic leaf notching and egg masses from adult weevils were widespread on several ornamental tree species that are commonly grown together. Of the plants they inspected, the plant species with the highest percentage of egg masses were live oak, silver buttonwood (*Conocarpus erectus var. sericeus* DC) and black olive (*Bucida buseras* L.).

A basic understanding of plant physiological responses to arthropod herbivory may provide critical information for predicting and preventing crop damage. Leaf gas exchange measurements provide a basis for assessing herbivore effects on different plants and plant parts (Peterson et al., 1998; Schaffer and Mason, 1990; Welter, 1989). Several studies have shown reductions in leaf gas exchange as a result of arthropod feeding on leaves (Lakso et al., 1996; Mobley and Marini, 1990; Schaffer et al., 1986; Schaffer et al., 1997). However, other studies have shown slight or no effects of leaf herbivory on gas exchange (Peterson et al., 1996). Insect herbivory has also been shown to reduce biomass of several plant species (Schaffer and Mason, 1990; Welter, 1991).

Adult Diaprepes root weevils damage plants primarily by leaf notching and generally tend to feed on new leaf flushes and occasionally on fruit. A previous study examined the effect of a root weevil feeding on citrus leaf photosynthesis (Syvertsen and McCoy, 1985). However, there is not much known about the effects of Diaprepes root weevil feeding on leaf physiology of ornamental plants.

As noted above, buttonwood and live oak are known hosts of Diaprepes root weevil, and support all stages of this pest from egg to adult (Mannion et al., 2003). Both tree species are commonly grown together in the same field nurseries in south Florida. Larvae alone cause significant root damage to both species and adult weevils can cause considerable leaf tissue damage in mature trees. However, there are no published data quantifying the effects of leaf feeding damage on these ornamental tree species. The objective of this study was to evaluate the effects of adult Diaprepes root weevil leaf feeding on leaf gas exchange and growth of buttonwood (*Conocarpus erectus* L.) and live oak trees.

Materials and Methods

Three experiments were conducted to assess the effects of adult weevil feeding on live oak and buttonwood trees. All experiments were conducted in spring and summer of 2004 at the University of Florida, Tropical Research and Education Center, Homestead, Fla. (25.5°N latitude and 85.5°W longitude).

In Experiment 1, buttonwood trees in 3.8-L containers were purchased from a commercial nursery (Princeton Nurseries II, Homestead, Fla.) and repotted into 11.4-L containers with well-drained medium consisting of 40% Florida peat, 30% pine bark, 20% cypress sawdust and 10% sand (by volume) amended with 6.80 kg dolomite/0.76 m^3 (Lantana Peat & Soil, Boynton Beach, Fla.). In Experiment 2, buttonwoods in 3.8-L containers were

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purchased from a local nursery (Bill Ingram & Grandsons NSY, Homestead, Fla.) and repotted into 11.4-L containers with the same medium described above. In Experiment 3, live oaks in 3.8-L containers were purchased from a commercial nursery (Action Theory Nursery, Homestead, Fla.) and repotted into 11.4-L containers with the same medium described above. All plants where fertilized once prior to treatment initiation with a 14N-4P-12.4K controlled-release fertilizer (Plantacote®Plus, Helena Chemical Company, Collierville, Tenn.).

Plants were placed in aluminum cages constructed to allow suitable light for normal plant growth while preventing insects from escaping. Aluminum frame cages were 1.21 m _ 61 cm × 61 cm with aluminum screening with a mesh size of 1.6 mm^2. There was one plant per cage.

For all three experiments, adult Diaprepes root weevils were collected from a field nursery (Native Tree Nursery, Homestead, Fla.). Weevils were maintained in acrylic holding cages and fed fresh buttonwood foliage that was replaced every other day along with water supplied in small containers with a dental wick.

Adult weevils were randomly selected from the holding cages and separated by sex. At the start of each experiment 10 males and five females were released into each cage. Each experiment was arranged in a complete block design with two treatments (infested or non-infested) and seven single-plant replications per treatment.

To prevent neonate larvae from entering the soil after eggs hatched, the soil surface of each pot was covered with a 51 cm^2 sheet of Weed Block (Easy Gardener, Inc. P.O. Box 21025, Waco, Texas) and was secured around the plant stems with duct tape. This material was selected because the pore size was small enough to prevent larvae from passing through, but still allowed water to penetrate.

Net CO_2 assimilation (A), stomatal conductance of H_2O (g_s), and transpiration (E) were measured prior to infesting plants and then monthly after insect infestation with a CIRAS-2 portable gas analyzer (PP Systems, Hitchin, Hertfordshire U.K.) between 1000 and 1200 hr. Leaf gas exchange measurements were made at a photosynthetic photon flux (PPF) > 900 $\mu mol \bullet m^{-2} \bullet s^{-1}$ with a halogen lamp fitted on the leaf cuvette as the light source. Leaf gas exchange was determined for two young flushing leaves and two fully expanded leaves from each plant and the averages of each pair of young and mature leaves were used to represent leaf gas exchange of young and mature leaves for each plant. For Experiment 3, there was an insufficient number of new leaf flushes of live oak to measure gas exchange on young leaves; therefore, only two mature leaves were measured per plant.

At the end of each experiment, plants were harvested and the total leaf area per plant was determined with a leaf area meter (Li-3000, Li-Cor, Lincoln, Nebr.). Plants were harvested and roots were washed with tap water to remove media attached to the root hairs. Excess water was allowed to drain from the roots for 24 h. Leaf, stem and root fresh weights were determined. Plant tissues were then oven-dried at 70°C for 2 d and leaf, stem and root dry weights were determined. Data were analyzed by Analysis of Variance and a standard t-test (SAS, SAS Institute, Cary, N.C.).

Results

In both buttonwood experiments the characteristic leaf notching caused by adult Diaprepes root weevil feeding was observed within a day of them being released into cages. Both young and mature leaves had signs of damage; however, during the experimental period it was observed that the weevils preferred the younger foliage and most of the leaf tissues of young leaves, with the exception of the mid-veins, were completely removed by the first month. Mature leaves also had considerable leaf notching primarily on the edges of the lamina. Live oak plants showed very little signs of leaf feeding damage. A few leaves had minor damage on the leaf edges but no significant damage was caused and all weevils died within the first month of the experiment.

In the first buttonwood (expt. 1), there were no significant effects of adult Diaprepes root weevil feeding on A, E or g_s of young or old leaf tissue at one or two months after adult weevil infestation (data not shown). In the second buttonwood experiment (expt. 2), A was significantly lower in young leaves of infested plants compared to those in non-infested treatments (t = -2.73; df = 8.69; P = 0.02) after one month of adult weevil leaf feeding (Table 1). However E and g_s of these young leaves were not significantly different at that time. Gas exchange of mature leaves was not significantly affected by adult weevil leaf feeding. Two months after treatments were initiated, g_s was significantly higher in young leaves of infested than non-infested plants (t = 2.14; df = 10.7; P = 0.05). However A and E of young leaves were not significantly different between treatments. In mature leaves at two months after treatment, A, E and g_s were higher in infested plants than in non-infested plants.

In the live oak experiment, one month after infestation there was almost no visible signs of leaf feeding damage and no significant differences in A, E and g_s between treatments (data not shown). At this time all adult weevils had died and the experiment was terminated and there were no subsequent measurements on leaf area or plant weights.

Buttonwood plants infested with adult weevils had 18.3% and 27.8% less leaf area than the controls in experiments 1 and 2, respectively; however, these differences were not significant (Table 2). Buttonwood leaf, stem and root fresh and dry weights were not significantly different between infested and non-infested treatments in either buttonwood experiment with the single exception of dry root weights in experiment 2 (t = -2.12; df = 11.1; P = 0.05).

Discussion

Live oak was not affected by herbivory presumably because mature, hardened-off leaves were too thick for the mandibles of this insect. Adult weevils were observed trying to feed on oak leaves but were only causing minor scrapes to the leaf margins and all weevils died within a month, most likely because of starvation. During the experiment live oak plants were not in a period of leaf flushing and the reason for the lack of significant difference in leaf gas exchange and growth between treatments was probably related to the phenological stage of the plants at the time of infestation. In subsequent field observations there appeared to be specific periods of time when relatively large populations of adult Diaprepes root weevils were found in live oak canopies. Adult weevils have been observed feeding on live oak during periods of leaf flushing when the young leaves are still succulent and the weevils are able to feed on the foliage.

Leaf feeding by adult Diaprepes root weevil had variable effects on leaf gas exchange of buttonwood. In both button-

Table 1. Mean net CO_2 assimilation (A), transpiration (E) and stomatal conductance (g_s) of buttonwood (expt. 2) infested or non-infested with adult Diaprepes root weevils.

Treatment	Leaf age	Date	Net CO_2 assimilation (µmol CO_2 m^{-2} s^{-1})	Transpiration (mmol H_2O m^{-2} s^{-1})	Stomatal conductance (mol H_2O m^{-2} s^{-1})
		5/18/04			
Pre-Infested	Young		4.96	3.92	180.21
Non-infested	Young		6.13	3.92	192.00
	(P^z)		(0.41)	(0.99)	(0.69)
Pre-Infested	mature		15.17	5.04	295.57
Non-infested	mature		13.63	4.65	260.50
	(P)		(0.22)	(0.29)	(0.31)
		6/18/04			
Infested	Young		3.08	4.78	254.79
Non-infested	Young		7.60	5.01	264.71
	(P)		(0.02)	(0.63)	(0.73)
Infested	mature		13.55	5.25	313.71
Non-infested	mature		14.40	4.78	285.86
	(P)		(0.45)	(0.49)	(0.62)
		7/7/04			
Infested	young		2.47	5.09	200.29
Non-infested	young		0.97	4.13	134.71
	(P)		(0.21)	(0.11)	(0.05)
Infested	mature		14.11	6.76	327.93
Non-infested	mature		9.18	4.83	187.91
	(P)		(0.02)	(0.02)	(0.01)

[z]P = probability that the paired means are different from t-test.

wood experiments, one month after treatments were initiated most young leaves of infested plants had obvious feeding damage and most of the leaf tissue except for the area's around the mid-vein were completely removed. Mature leaves also had signs of feeding damage to the edges of the lamina with no damage observed on the mid-vein. Similarly, Syvertsen and McCoy (1985) reported considerable leaf feeding damage caused by a citrus root weevil, little leaf notcher (*Artipus floridanus* Horn.) to tender citrus leaf margins with no injury to the mid-veins. In our study, adult weevils preferred the young tender foliage over mature leaves; however, the majority of leaves of each plant were mature and the outer areas of almost all leaves had feeding damage. Mature leaves appeared to have more leaf area remaining around the mid-vein compared to the younger leaves.

In the first experiment, A, E and g_s of buttonwood were not significantly different after one or two months of feeding. Some authors have reported that leaf mass consumption by insect herbivores does not negatively impact single-leaf photosynthesis of the remaining leaf tissues (Peterson et al., 1996; Welter, 1989). No reduction in leaf gas exchange was reported for actual or simulated herbivory of tomato (*Esculentum lycopersicon* Mill.). Actual herbivory by tobacco horn worm (*Manduca sexta* L.) larvae or simulated defoliation did not change photosynthetic rates per unit area of tomato leaflets (Welter, 1991). It has previously been reported that leaf feeding in which there is only removal of leaf tissue without injury to the mid-vein only reduces the amount of photosynthetic leaf area but not photosynthetic rates of the remaining leaf tissue (Li and Proctor, 1984; Peterson et al., 1992; 1996; 2004).

However, in the second experiment there were variable leaf gas exchange responses. One month of infestation of buttonwoods resulted in a significant reduction in A, and no reduction of E or g_s of younger leaves or A, E and g_s of mature leaves. After two months of leaf feeding, mature leaves of infested plants had greater leaf gas exchange than controls. Although increases in leaf gas exchange have been previously reported for various plant species, other studies have generat-

Table 2. The effect of adult Diaprepes root weevil leaf feeding on buttonwood leaf area and fresh and dry weights two months after infestation.

			Fresh weight (g)			Dry weight (g)		
Species	Treatment	Leaf area (cm^2)	Leaf	Stem	Root	Leaf	Stem	Root
Exp. 1	Infested	6419	293.53	172.89	230.04	109.17	82.51	104.81
	Non-infested	7861	339.61	183.1	234.8	120.94	88.48	107.90
	(P^z)	(0.10)	(0.19)	(0.67)	(0.90)	(0.34)	(0.61)	(0.84)
Exp. 2	Infested	3401	134.51	36.37	31.94	44.81	11.62	17.32
	Non-infested	4710	155.16	39.31	48.05	50.27	13.14	23.60
	(P)	(0.14)	(0.47)	(0.69)	(0.07)	(0.59)	(0.51)	(0.05)

[z]P = probability that the paired means are different from t-test.

ed contrasting results. While some authors report no difference in leaf gas exchange as a result of arthropod herbivory, others have reported increases or decreases (Detling et al., 1980; Mobley and Marini, 1990; Peterson et al., 1998; Sances et al., 1981; Welter, 1989). Leaf gas exchange response of plants to arthropod herbivory may be dependent on the interaction between the type of damage caused by the herbivore and plant species. In the majority of studies involving selective tissue feeders, mesophyll feeding arthropods, such as leafhoppers and mites, tend to reduce photosynthesis, whereas defoliators which remove partial or entire leaf tissue, tend to increase photosynthesis of remaining leaf tissues (Welter, 1989).

Our second study yielded different results than those of other recent defoliation studies, which found that leaf gas exchange of infested plants was not significantly affected by simulated or actual insect defoliation (Welter, 1991; Peterson et al., 1996; Peterson et al., 2004). These results suggest that plant species may respond differently to defoliation. In our study as with previous others, gas exchange measurements were made on single leaves which may not be a true representation of the whole plants response to herbivory. Further studies on the effects of leaf feeding by Diaprepes root weevils should be conducted at the whole plant canopy level to compare results with single leaf gas exchange.

In both buttonwood experiments, leaf area, leaf, stem and root fresh and dry weights were the same for infested plants as for the controls with the single exception of root dry weights of buttonwoods in the second experiment. Plants were only exposed to adult weevil feeding for a two month period. In longer-duration studies significant differences in gas exchange, leaf area and dry weights might occur between infested and non-infested buttonwood trees. For live oak, future studies should be conducted during periods of leaf flushing when new leaf tissue is tender enough for Diaprepes root weevil to feed on since they apparently starved to death due to lack of food.

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