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LEAF GAS EXCHANGE AND DAMAGE OF MAHOGANY AND POND APPLE TREES FROM ADULT *DIAPREPES ABBREVIATUS* (COLEOPTERA: CURCULIONIDAE) FEEDING AND SOIL FLOODING

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## ABSTRACT

The effects of feeding on leaves by adult *Diaprepes* root weevil, *Diaprepes abbreviatus* L. (Coleoptera: Curculionidae), and flooding on leaf gas exchange [net CO<sub>2</sub> assimilation (*A*), transpiration (*E*), and stomatal conductance (*g<sub>s</sub>*)], plant growth (root, stem, leaf, and total plant dry weights, stem diameter, and plant height) and adult host plant preference (feeding damage and oviposition) were determined on mahogany, *Swietenia mahagoni* Jacq., and pond apple, *Annona glabra* L., trees in outdoor screen cages. Flooding reduced leaf gas exchange, plant growth, and *D. abbreviatus* feeding damage of mahogany trees. Leaf gas exchange of infested and non-infested trees of both mahogany and pond apple were similar except for one measurement date for mahogany. Leaf dry weights were greater for non-infested than infested mahogany trees. There was no effect of infestation on dry weights of pond apple trees. Based on feeding injury to leaves, adults preferred non-flooded to flooded mahogany trees. The lack of response in leaf damage or oviposition to flooding for pond apple was attributable to the avoidance of leaves by adult *D. abbreviatus* of this plant species despite it being a host for root weevil larvae. The results indicate that while flooding of the root zone adversely affects growth and physiology of mahogany trees, it does not predispose trees to greater damage from adult *D. abbreviatus*. In fact, adult insect damage was greater for non-flooded than flooded trees. Pond apple was not greatly affected by root zone flooding and was not a preferred host of adult *D. abbreviatus* under flooded or non-flooded conditions.

Key Words: photosynthesis, transpiration, stomatal conductance, herbivory

## RESUMEN

Se evaluaron los efectos de herbivoría por adultos de *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae) e inundación sobre el intercambio de gases foliar [asimilación de CO<sub>2</sub> (*A*), transpiración (*E*), y conductancia estomática (*g<sub>s</sub>*)], crecimiento (pesos secos de raíces, tallos, hojas, y totales de las plantas, ancho del tallo y altura) y preferencia por huéspedes (daño por herbivoría y oviposición) por los adultos sobre los arboles de caoba, *Swietenia mahagoni* Jacq., y manzana de charca, *Annona glabra* L., en jaulas de tela metálica en campo. La inundación redujo el intercambio de gases foliar, el crecimiento de las plantas, y herbivoría en los arboles de caoba. Además, *A*, *E*, y *g<sub>s</sub>*, de caoba y manzana de charca fueron similares en los arboles infestados y en los no infestados excepto en una de las fechas de registro para caoba. Los pesos secos de las hojas fueron más altos en los arboles no infestados que en los infestados de caoba. No hubo diferencias en pesos secos por infestación en la manzana de charca. De el daño por herbivoría foliar, se observó que los adultos prefirieron los arboles no inundados a los inundados en caoba. En manzana de charca, la falta de respuesta a la inundación en términos del daño de las hojas o en la oviposición fue atribuible a que *D. abbreviatus* evitó a esta especie de planta a pesar de ser un huésped para las larvas. Los resultados indican que aunque la inundación en la zona radical afecta desfavorablemente el crecimiento y fisiología de los arboles de caoba, estos no están predispuestos a más daños por adultos de *D. abbreviatus*; al contrario, el daño causado por adultos fue más alto en los arboles no inundados. La manzana de charca no fue muy afectada por la inundación en la zona radical y no fue un huésped preferido por los adultos de *D. abbreviatus* bajo ninguna de las condiciones de inundación.

*Diaprepes abbreviatus* L. (Coleoptera: Curculionidae: Entiminae), commonly called *Diaprepes* root weevil, was first found in Florida in 1964 in an Apopka citrus nursery and is believed to have entered Florida from its home range of Puerto Rico in a shipment of ornamental plants (Woodruff 1964, 1985). In the United States, it has established in Florida, Texas (Knapp et al. 2001;

Skaria & French 2001), and southern California (Klunk 2005). In Florida, the weevil occurs in 23 counties in the southern and central parts of the state (Anonymous 1996; Peña 1997).

*Diaprepes abbreviatus* has infested about 40,469 ha of citrus in Florida and control costs and losses have been about \$70 million annually (Weissling et al. 2004). The host range of *D. ab-*

*brevis* is very large including at least 317 varieties, 280 species, 180 genera, and 68 families of plants (Simpson et al. 1996, 2000; Knapp et al. 2000; Mannion et al. 2003; Godfrey et al. 2006). The large host range creates management challenges for this pest. Although not all host plants support all life stages, many economically important plants support all stages of the weevil from egg to adult (Simpson et al. 1996). Many common ornamental plant species in south Florida, including mahogany, *Swietenia mahagoni* Jacq., (Simpson et al. 1996) and pond apple, *Annona glabra* L. (Martin et al. 2009), are hosts of *D. abbreviatus*, and if not regulated, may help spread the pest through movement of infested plants.

In addition to damage to the root system caused by Diaprepes root weevil larvae, the adults can cause significant leaf damage and defoliation. The most obvious feeding damage by adult *D. abbreviatus* includes notching along margins of especially young, tender leaves (Wolcott 1936, 1948; McCoy et al. 2002). Adult notching typically begins along the leaf edges and progresses toward the midveins, which can result in moderate to severe defoliation of host plants (Quintela et al. 1998; McCoy et al. 2002; Mannion et al. 2003). In contrast to larval root feeding, prolonged adult feeding does not seem to economically reduce yields of mature citrus trees (McCoy et al. 2002). Citrus trees can sustain up to 50% defoliation without loss of yield (Yuan et al. 2005). However for ornamental plant species, excessive foliar damage makes them less attractive and can reduce sales.

Leaf gas exchange measurements, such as net CO<sub>2</sub> assimilation (*A*), transpiration (*E*), and stomatal conductance (*g<sub>s</sub>*), can reveal insect damage to plants prior to symptoms becoming visible. Insect herbivory, however, has been shown to increase, decrease, or have no effect on leaf gas exchange of host plants (Andersen & Mizell 1987; Welter 1989; Schaffer & Mason 1990; Schaffer et al. 1997). Effects of insect feeding on leaf gas exchange can vary with the type of feeding damage caused by an insect feeding group such as root feeders, stem borers, or leaf consumers or defoliators (Root 1973; Welter 1989). Based on this classification and feeding habits of *D. abbreviatus*, its larvae are in the root-feeder group whereas adults are in the leaf-consumer or defoliator group.

Agriculture in south Florida tends to occur in areas that are prone to periodic flooding (Schaffer 1998). Responses of woody plants to flooding include senescence, shoot dieback, premature leaf abscission, decreased cambial growth, suppression of formation and expansion of leaves and internodes, and reduced photosynthesis and stomatal conductance (Kozlowski 1997). Flooding of the root zone can decrease production of photosynthates allocated for root and leaf growth

thereby decreasing food resources, possibly reducing *D. abbreviatus* larval and adult feeding. Alternatively, flooding may increase insect feeding by stimulating production of chemicals such as ethanol, which are known to attract certain insect species (Schroeder & Weslien 1994).

Mahogany and pond apple trees are native to south Florida, where they are commonly grown in commercial ornamental and native plant nurseries. Mahogany is a widely planted lawn and street tree in south Florida (Watkins & Sheehan 1975; Wunderlin 1998) with variable flood tolerance (Martin 2009; Martin et al. 2010b). Pond apple is native to swamps of central and south Florida (Wunderlin 1998) and is thus very tolerant to flooded soil conditions (Schaffer 1998; Núñez-Elisea et al. 1999; Ojeda et al. 2004). The interaction between infestation by *D. abbreviatus* larvae and flooding of potting media or soil has been studied in citrus (Li et al. 2003, 2004, 2006, 2007; Martin 2009; Martin et al. 2011) and in a few woody ornamental plant species including green buttonwood, *Conocarpus erectus* L. (Diaz 2005; Martin 2009; Martin et al. 2010a, 2011), and live oak, *Quercus virginiana* Mill. (Diaz 2005). However, there have been no reports of combined effects of flooding and adult feeding by *D. abbreviatus* on woody ornamental plants. The main objectives of this study were to test effects of feeding by adult *D. abbreviatus* and flooding on leaf gas exchange and growth of pond apple, a flood-tolerant species, and mahogany, a species with variable flood tolerance, to determine if flooding affects host plant preference by predisposing plants to increased feeding, oviposition, altered physiology, or growth reduction.

## MATERIALS AND METHODS

Two experiments were conducted at the University of Florida, Tropical Research and Education Center, Homestead. One was in the spring and summer of 2008 with mahogany and the other was in the summer and fall of 2008 with pond apple.

### Plant Material

Mahogany trees were obtained by digging seedlings from fields in Homestead, Florida 1.5-2 yrs before beginning the study. Mahogany trees were initially planted in 4-L containers in 2006 and then transplanted into 11-L containers about 1 year later. Pond apple trees in 11-L plastic containers were purchased from a commercial nursery and immediately transplanted into 15-L containers. When the pond apple trees were transplanted, very little disturbance of intact roots was required because of the inverted-cone design of the 11-L containers from the nursery and the slightly larger (15 L) containers used in

the experiment. Hence, roots of both mahogany and pond apple trees were well established in their containers before initiating this study. At the time treatments were initiated, approximate tree ages were 3 yr for both plant species and plant heights (mean  $\pm$  SD) were  $127 \pm 11$  and  $130 \pm 17$  cm for mahogany and pond apple, respectively. Mahogany trees were grown in a standard nursery potting medium (40% Florida peat, 20% pine bark, 20% cypress sawdust, and 20% sand) and pond apple trees were grown in a similar medium (40% Florida peat, 50% pine bark, and 10% sand). Mahogany trees were fertilized 79 d before initiating treatments with a timed release fertilizer (Osmacote Plus® 15-9-12, Scotts, Marysville, Ohio) according to the manufacturer's recommended rate. On the same date, a foliar iron spray (Sequestrene 138 Fe® with 6% chelated iron, Becker Underwood, Ames, Iowa) was applied to each tree at the manufacturer's recommended rate. Pond apple trees were not fertilized after purchase from the nursery and showed no signs of nutrient deficiency prior to initiating treatments.

#### Insect Infestation Treatments

There were 2 infestation treatments, infested and non-infested. Cages (60 cm  $\times$  60 cm  $\times$  1.2 m) covered with aluminum screen mesh (1.5  $\times$  1.5 mm) were used to contain adult *D. abbreviatus* and infested and non-infested plants were placed in separate cages. Screen cages were placed on 1.2-m  $\times$  1.2-m pallets and 2 plants (1 flooded and 1 non-flooded) were placed in each cage. There were a total of 12 cages, 6 infested and 6 non-infested (control). Cages were located in full sun but the aluminum screen blocked approximately 30% of incoming sunlight (Burger et al. 2007).

Adult *D. abbreviatus* used to infest plants were collected from canopies of trees growing in fields at commercial plant nurseries in Homestead, Florida. Adults for each experiment were maintained in 30-cm  $\times$  30-cm  $\times$  30-cm plexiglass cages prior to infestation (approximately 3-22 d) and provided a diet of water and green buttonwood leaves. For each plant species, twenty apparently vigorous adults (10 males and 10 females) were released into each cage of the infested treatments.

#### Flooding Treatments

Plants were divided into 2 flooding treatments, flooded and non-flooded. For the flooded treatment, each plant container was submerged in a 19-L plastic bucket filled with tap water to 10 cm above the surface of the potting medium. Mahogany trees were flooded on 21 May 2008 and pond apples on 18 Sep 2008. Non-flooded plants in each experiment were irrigated for 30 min twice per

day by overhead sprinklers and holes at the bottom of the containers allowed drainage of excess water. For mahogany, the duration of the treatment period was 80 d, which was determined by the first signs of stress to flooded trees, such as reduced *A* and/or wilting. In a previous study (Martin et al. 2010b), flooding did not significantly reduce *A*, *g<sub>s</sub>*, or plant growth of pond apple trees. Therefore in the present study, we did not wait for flooded pond apple trees to exhibit signs of physiological stress, and we removed them from flooded conditions 24 d after initiation of flooding. This date was chosen because the numbers of surviving *D. abbreviatus* adults on pond apple trees were much lower than on mahogany trees when plants were removed from flooding, so they were harvested before there were no surviving adults.

Flooded mahogany trees were infested with adult *D. abbreviatus* 30 d after flooding when plants exhibited early signs of physiological stress as indicated by a slight reduction in *A*. Non-flooded mahogany trees were infested at the same time. Both flooded and non-flooded pond apple trees were infested 1 d after flooding.

#### Temperature and Redox Potential of the Potting Medium

The temperature of the potting medium was recorded at 1-h intervals throughout the experiments with sensors (StowAway Tidbit® temploggers, Onset Co., Pocasset, Massachusetts) buried 6 cm deep and two-thirds the distance from the center to the outer edge of the pot. Redox potential (*E<sub>h</sub>*) of the potting medium solution, an indicator of soil oxygen content (Ponnamperuma 1972, 1984), was measured with a platinum combination electrode attached to a portable volt meter (Accumet AP62, Fisher Scientific, Pittsburgh, Pennsylvania). Measurements were made by inserting the electrode into a polyvinyl chloride (PVC) pipe (20 cm long  $\times$  2.2 cm wide) placed in the potting medium 2 cm from the edge of the pot. Redox potential was recorded at a mean depth of 6 cm below the surface of the potting medium. In each experiment, redox potential was measured daily for 4 flooded plants during the first 6 d of flooding and approximately weekly thereafter.

#### Leaf Gas Exchange

Pond apple has simple leaves, whereas mahogany has pinnately compound leaves with 6-8 leaflets per leaf (Watkins & Sheehan 1975; Wunderlin 1998). Leaf gas exchange measurements included *A*, *E*, and *g<sub>s</sub>*, and were made on 2 randomly selected, recently matured leaves (or leaflets) per plant with a CIRAS-2 portable gas analyzer (PP Systems, Amesbury, Massachusetts). These leaves or leaflets were fully expanded and hardened off within the few weeks preceding measure-

ment and were between the fourth and tenth node below stem tip for mahogany and second to tenth node for pond apple. Leaf gas exchange measurements of 2 leaves (pond apple) or 2 leaflets (mahogany) were averaged to provide a single plant value used as a replication for each treatment combination. All leaf gas exchange measurements for all replications were made within 2 h. During leaf gas exchange measurements, the photosynthetic photon flux in the leaf cuvette was maintained at 1000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  with a halogen lamp attached to the cuvette, and the reference  $\text{CO}_2$  concentration in the cuvette was kept constant at 375  $\mu\text{mol mol}^{-1} \text{CO}_2$ . Leaf gas exchange was measured prior to flooding plants and then periodically during the flooding period. The first leaf gas exchange measurements were made 5 d and 2 d before flooding mahogany and pond apple trees, respectively. Final leaf gas exchange measurements were made after plants were removed from flooding (for the flooded treatment) and adult weevils had been removed from cages (for the infested treatment).

#### Egg Clusters and Leaf Damage

Egg clusters were counted and removed from each plant within cages, and the percentage of leaf damage was visually estimated for all plants and rated on a percentage scale. Plants with less than 10% foliar damage were generally estimated to the nearest 1% and those with at least 10% damage to the nearest 5%. Initial assessment of leaf damage and egg-cluster counts during infestation were made 5 d and 7 d after releasing adult *D. abbreviatus* into cages of mahogany and pond apple, respectively. Insects remained in cages until no egg clusters were found on at least half the plants, and mean numbers of egg clusters per plant did not differ significantly between flooded and non-flooded treatments for 2 consecutive wk. Adults were removed from cages 50 d and 23 d after their introduction to mahogany and pond apple trees, respectively, and for each plant species; this was the same d flooded plants were drained. After removal from each cage, all male and female adult *D. abbreviatus* were counted. Final counts of egg clusters and leaf damage were made 1 d and 2 d after all adults were removed from mahogany and pond apple cages, respectively. Egg clusters on mahogany were removed by detaching the 2 leaflets enclosing them, which resulted in a different number of leaves and leaflets removed among treatments. We compensated for this unequal leaf removal among treatments by removing the same number of leaves from all plants. For pond apple, egg clusters were removed by wiping them off the leaf with a cloth instead of by removing the leaves they were attached to; hence there was no need to compensate for leaves lost by egg cluster

removal. However, pond apple leaves were sensitive to handling and often fell off during evaluation. Thus, same number of leaves was removed from all plants to equalize reduction of leaves.

#### Plant Growth

Stem diameter and plant height were measured on each plant at the beginning and end of each experiment. Stem diameter was measured 10 cm above the surface of the potting medium, and for plants with multiple stems (most pond apple but no mahogany trees), the diameter of the largest stem was recorded. Plant height was measured from the surface of the potting medium to the top of the highest leaf or branch. During harvest, stems were cut off 2-3 cm above the surface of the potting medium and roots were removed from the plant container. The potting medium was shaken off roots and then brushes and water were used to thoroughly remove the remaining potting medium from the roots. At the end of the treatment period, roots, stems, and leaves were oven dried at 75°C to a constant weight and dry weights were determined. For pond apple, dry weights included leaf blades and petioles. For mahogany, leaf dry weights included leaflets, petioles, rachises, and petioles.

#### Experimental Design and Statistical Analyses

Data were analyzed separately for each tree species. For each tree species, there were 2 adult infestation treatments (infested and non-infested) and 2 flooding treatments (flooded and non-flooded) in a 2 × 2 factorial design. There were 6 single-plant replications per treatment combination. A two-way factorial analysis of variance (ANOVA) was used to determine if there were significant interactions between infestation and flooding treatments. For each tree species, the effects of infestation and flooding treatments on leaf gas exchange variables, leaf damage, and egg cluster counts were compared by repeated measures ANOVAs. For growth variables (dry weights, plant height and stem diameter) of each tree species, the main effects and interactions between infestation and flooding treatments were compared by two-way ANOVA. All statistical analyses were done with SAS statistical software (SAS Institute, Cary, NC).

## RESULTS

#### Mahogany Trees

Temperature of the potting medium ranged from 24.5°C to 28.9°C and the redox potential of the potting medium for flooded trees became negative within 2 d after flooding (Fig. 1). There were no significant interactions ( $P > 0.05$ ) between

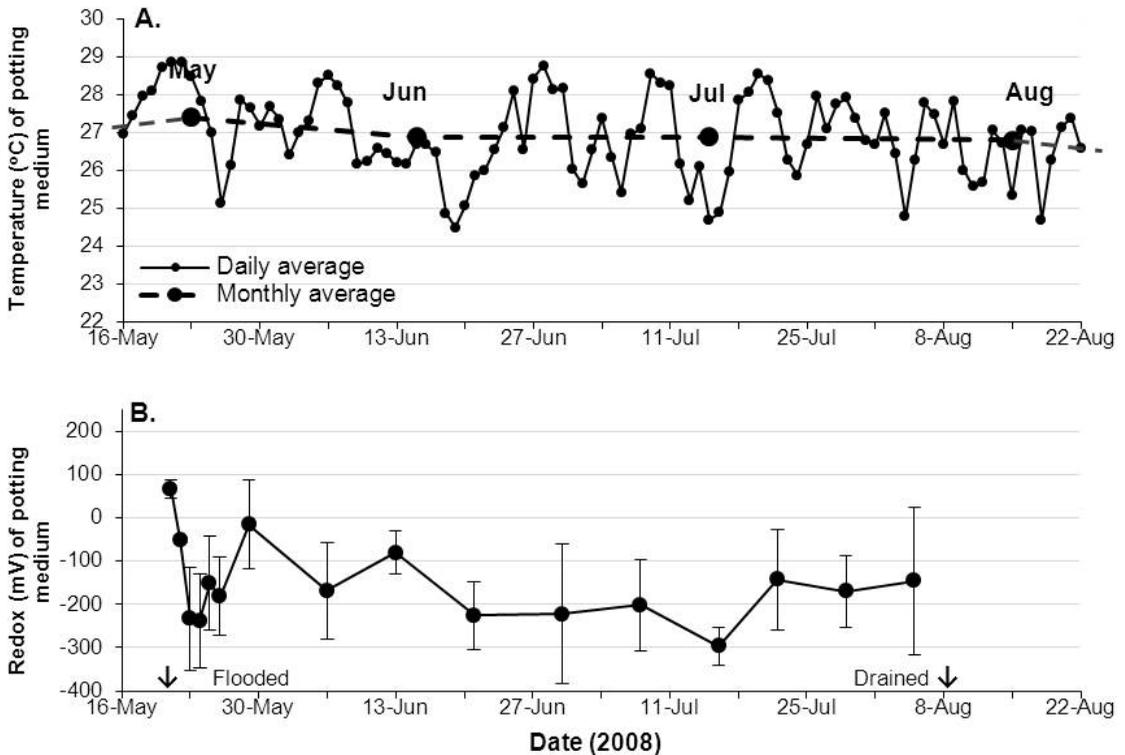


Fig. 1. A) temperature and B) redox potential of flooded potting medium for mahogany trees. For temperature, each point is the value of 1 sensor. For redox potential, each point represents the mean  $\pm$  SD of four sensors. Plants were flooded May 21, infested Jun 20, and unflooded and uninfested Aug 9.

flooding and infestation treatments for  $A$ ,  $E$ ,  $g_s$ , stem diameter, plant height, or for root, stem, leaf, or total plant dry weights on any measurement date. However, there were significant interactions ( $P \leq 0.05$ ) between flooding and infestation treatments for percentage of leaf damage from adult feeding and the number of egg clusters per plant on 2 or more measurement dates. Therefore, flooding treatments were pooled to compare infestation treatments and infestation treatments were pooled to compare flooding treatments for all variables except leaf damage and number of egg clusters per plant.

On the final 4 measurement dates,  $A$  was significantly higher for non-flooded than flooded mahogany trees (Fig. 2a). Stomatal conductance (Fig. 2b) and  $E$  (data not shown) were each significantly higher for non-flooded than flooded trees on the ninth of 11 measurement dates. At the end of the treatment period, non-flooded trees had a significantly greater increase in stem diameter ( $P \leq 0.01$ ) and plant height ( $P \leq 0.05$ ) than flooded trees (data not shown). The mean increase in stem diameter  $\pm$  SD was  $3.7 \pm 1.3$  and  $0.1 \pm 1.3$ , and the increase in tree height was  $27.8 \pm 17.8$  and  $13.8 \pm$

6.8 for non-flooded and flooded trees, respectively. Root and leaf dry weights were significantly higher for non-flooded than flooded trees, but there were no significant differences between flooding treatments in stem or total dry weights (Table 1).

Net  $\text{CO}_2$  assimilation,  $g_s$  (Fig. 3), and  $E$  (data not shown) were similar for infested and non-infested mahogany trees throughout the experiment, except for week 9 of 11 measurement dates (Fig. 3). This was 65 d after flooding and 35 d after infesting trees with adult *D. abbreviatus*. There were no significant differences between infested and non-infested trees in change of stem diameter or plant height (data not shown). Leaf dry weights were significantly higher for non-infested than infested trees, but there were no differences in root, stem, or total dry weights (Table 1). The mean maximum percentage of feeding damage from adult *D. abbreviatus* to mahogany foliage was 42% (non-flooded, infested) and 25% (flooded, infested) in wk 6 and 9, respectively (Fig. 4a). Thus, flooding reduced feeding as there was consistently more leaf damage on non-flooded, infested than on flooded, infested trees throughout the experiment. (Fig. 4a). The mini-

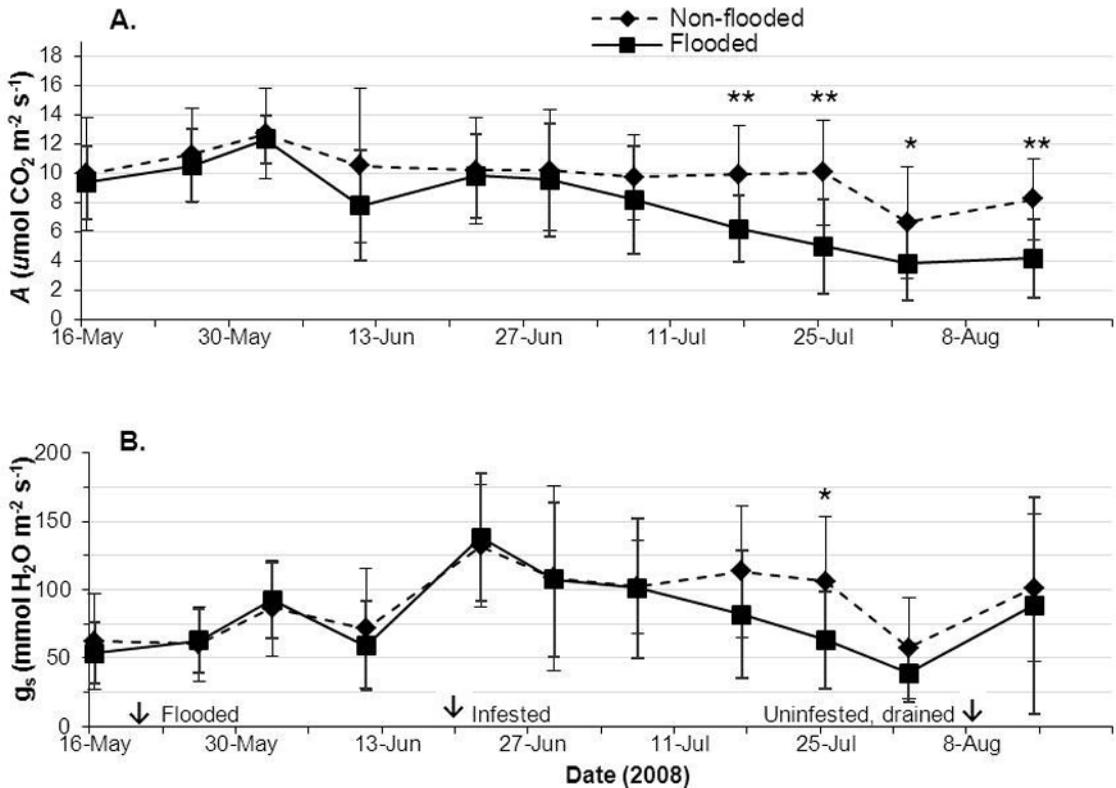


Fig. 2. Effects of flooding on A) net CO<sub>2</sub> assimilation (*A*) and B) stomatal conductance of H<sub>2</sub>O (*g<sub>s</sub>*) of mahogany trees. Symbols represent means ± SD. Asterisks indicate significant differences between treatments at \*  $P \leq 0.05$  and \*\*  $P < 0.01$  according to a repeated measures ANOVA. Plants were flooded May 21, infested Jun 20, and un-flooded and uninfested Aug 9.

mal leaf damage (mean ± SD) to non-infested, flooded ( $4.3 \pm 1.6\%$ ) and non-flooded ( $4.5 \pm 1.0\%$ ) trees was possibly caused by unknown herbivorous insects before trees were placed in cages. The number of egg clusters per tree was significantly higher for non-flooded, infested than flooded, infested trees on wk 1 and 8 with no significant difference between treatments for each of the remaining 7 wk (Fig. 4b). The mean maximum number of egg clusters ± SD per mahogany tree was  $14.5 \pm 7.7$  for non-flooded and  $11.2 \pm 6.6$  for flooded, and both maxima occurred on the second measurement date (Fig. 4b). As expected, no egg clusters were found on non-infested mahogany. The mean ratio (±SD) of female to total adults recovered from mahogany at the end of the experiment was  $0.57 \pm 0.23$  with no significant difference between numbers of males and females (number of males =  $2.0 \pm 2.2$ , number of females =  $2.7 \pm 1.6$ , and total number of adults =  $4.7 \pm 3.3$ ). As there were initially 10 males and 10 females, total populations declined 55 to 95% during the 50-d infestation period.

#### Pond Apple Trees

Temperature of the potting medium ranged from 23.4°C to 27.7°C and the redox potential of the potting medium for flooded trees became negative within 2 d after flooding (Fig. 5). There was a significant interaction ( $P \leq 0.05$ ) between flooding and infestation treatments for *A* on 1 or more measurement dates, but there were no significant interactions ( $P > 0.05$ ) for *E*, *g<sub>s</sub>*, stem diameter, plant height, root, stem, leaf, or total plant dry weights, leaf damage, or egg clusters per plant. Therefore, flooding treatments were pooled to compare infestation treatments and infestation treatments were pooled to compare flooding treatments for all variables except *A*.

Net CO<sub>2</sub> assimilation of pond apple was affected little by infestation or flooding until wk 5, when non-flooded, infested pond apple trees had significantly higher *A* than flooded, infested trees (Fig. 6). Also, there were no significant differences in *g<sub>s</sub>* or *E* (data not shown) between flooded and non-flooded or infested and non-infested trees.

TABLE 1. MEANS ( $\pm$ SD) AND ANOVA PROBABILITY FOR THE EFFECTS OF FLOODING AND ADULT *DIAPREPES ABBREVIATUS* INFESTATION ON DRY WEIGHT OF MAHOGANY TREES ( $N = 6$ ).

Dry weights (g)	Flooding (F)		Infestation (I)		ANOVA		
	Non-flooded	Flooded	Non-infested	Infested	F	I	F $\times$ I
Roots	67.5 $\pm$ 22.5	45.8 $\pm$ 13.8	55.0 $\pm$ 20.5	58.4 $\pm$ 23.1	**	ns	ns
Stem	142.8 $\pm$ 35.4	139.2 $\pm$ 31.8	143.7 $\pm$ 31.6	138.2 $\pm$ 35.5	ns	ns	ns
Leaves	58.5 $\pm$ 27.5	29.6 $\pm$ 17.2	55.6 $\pm$ 28.8	32.4 $\pm$ 19.6	**	*	ns
Total	268.8 $\pm$ 75.2	214.5 $\pm$ 54.3	254.4 $\pm$ 74.6	229.0 $\pm$ 65.5	ns	ns	ns

$P > 0.05$  (ns),  $P \leq 0.05$  (\*),  $P \leq 0.01$  (\*\*).

Flooding reduced root growth but there were no differences between non-flooded and flooded trees in stem, leaf, or total plant dry weights (Table 2). There were no significant differences between infested and non-infested trees in root, stem, leaf, or total plant dry weights (Table 2). There were no significant differences ( $P > 0.05$ ) in change of stem diameter or plant height between flooded and non-flooded trees (data not shown) or between infested and non-infested trees (data not shown). Leaf damage of pond apple trees was not

affected by flooding or infestation from adult *D. abbreviatus* and was  $3.6 \pm 2.0\%$  (mean  $\pm$  SD). Most leaf damage was believed to have resulted from feeding from insects other than *D. abbreviatus* prior to placing plants in the cages. There were no significant differences in the number of egg clusters between flooded and non-flooded trees. The mean  $\pm$ SD number of egg clusters ( $0.1 \pm 0.4$ ) was the same for flooded and non-flooded trees. The maximum number of egg clusters per infested treatment was  $0.9 \pm 0.9$  (mean  $\pm$  SD),

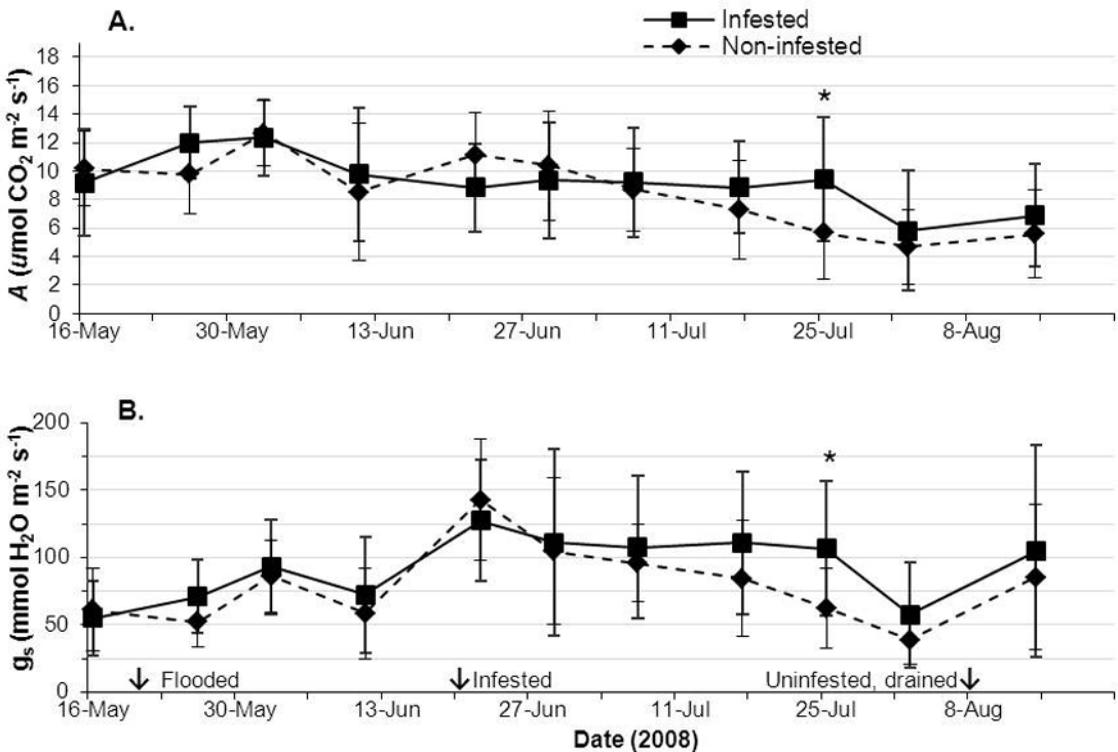


Fig. 3. Effects of adult *D. abbreviatus* infestation on A) net CO<sub>2</sub> assimilation (*A*) and B) stomatal conductance of H<sub>2</sub>O (*g<sub>s</sub>*) of mahogany trees. Symbols represent means  $\pm$  SD. Asterisks indicate significant differences between treatments at  $* P \leq 0.05$  according to a repeated measures ANOVA. Plants were flooded May 21, infested Jun 20, and unflooded and uninfested Aug 9.

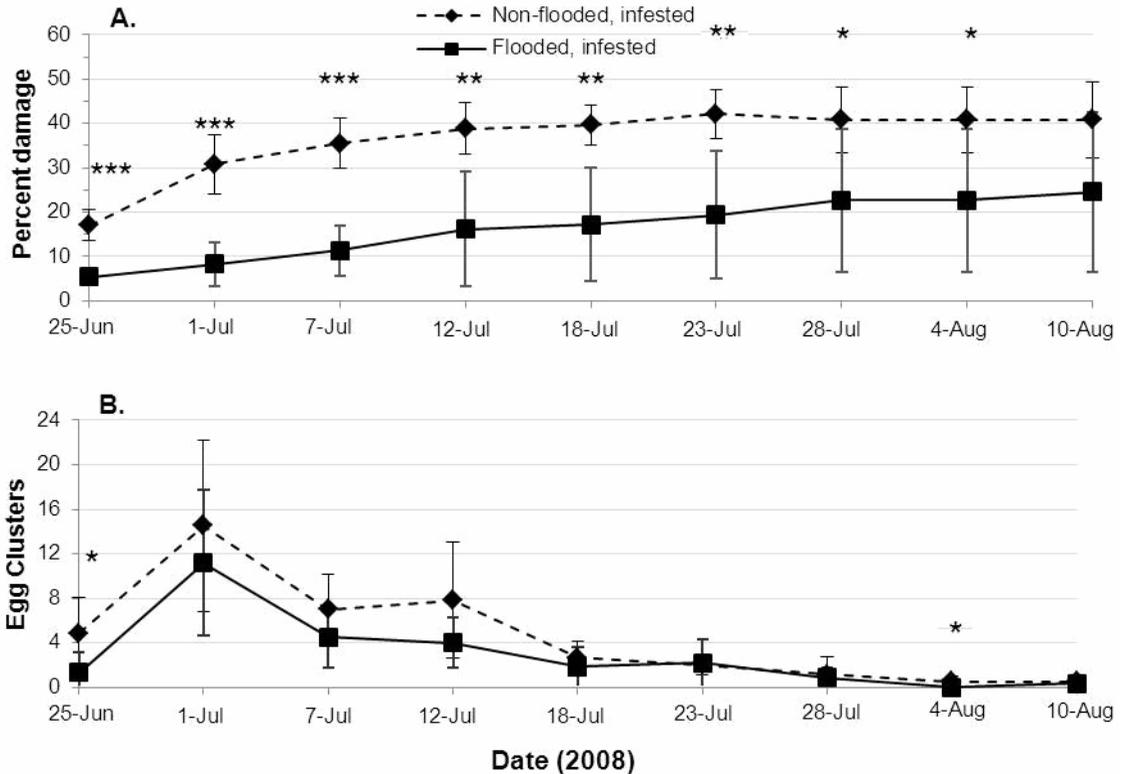


Fig. 4. Effects of flooding on A) adult *D. abbreviatus* feeding damage and B) number of egg clusters per mahogany tree. Symbols represent means  $\pm$  SD. Asterisks indicate significant differences between treatments at \*  $P \leq 0.05$ , \*\*  $P < 0.01$ , and \*\*\*  $P < 0.001$  according to a repeated measures ANOVA. Plants were flooded May 21, infested Jun 20, and unflooded and uninfested Aug 9.

which occurred on the second measurement date. No egg clusters were found on non-infested pond apple trees. The mean ratio  $\pm$  SD of female to total recovered adults per infested cage at the end of the experiment was  $0.40 \pm 0.48$  with no significant difference in numbers of males or females (number of males  $0.50 \pm 0.55$ , females  $0.33 \pm 0.52$ , and total  $0.83 \pm 0.75$ ). Populations declined 90-100% during the 23-d infestation period.

#### DISCUSSION

Effects of soil flooding on the physiology and growth of a woody plant species can vary among soil types and are partly based on the rates of  $O_2$  depletion of the soil or potting medium (Schaffer et al. 1992). Well-oxygenated soils have redox potentials of + 300 mV or more, whereas flooded soils have redox potentials of + 200 mV or less, and anaerobic soils have negative values (Ponnamperuma 1972, 1984). Mean redox potential of potting medium for flooded plants varied from + 67 mV to -297 mV for mahogany and from + 189 mV to - 260 mV for pond apple indicating that hy-

poxic conditions existed in the root zones of flooded plants within 2 d after flooding in both experiments.

For mahogany trees, there were significant interactions between flooding and adult *D. abbreviatus* infestation only for leaf feeding damage and the number of egg clusters per plant. Syvertsen & McCoy (1985) studied the little leaf notcher, *Artipus floridanus* Horn (Coleoptera: Curculionidae), which similar to *D. abbreviatus*, has 2 feeding guilds with larvae in the root-feeder guild and adults in the direct-leaf-consumer guild. They found that increasing adult population densities with their higher consumption of citrus leaf area, decreased *A* and increased water loss, which increased at a faster rate than *A* declined. Hence, interactions between feeding injury and drought stress may be very important (Syvertsen & McCoy 1985).

With the exception of stem and total dry weights, which were not significantly affected by flooding, mahogany trees showed poorer performance in flooded than non-flooded conditions as evidenced by significant reductions in *A*, *E*, *g*, root and leaf dry weights, change in stem diame-

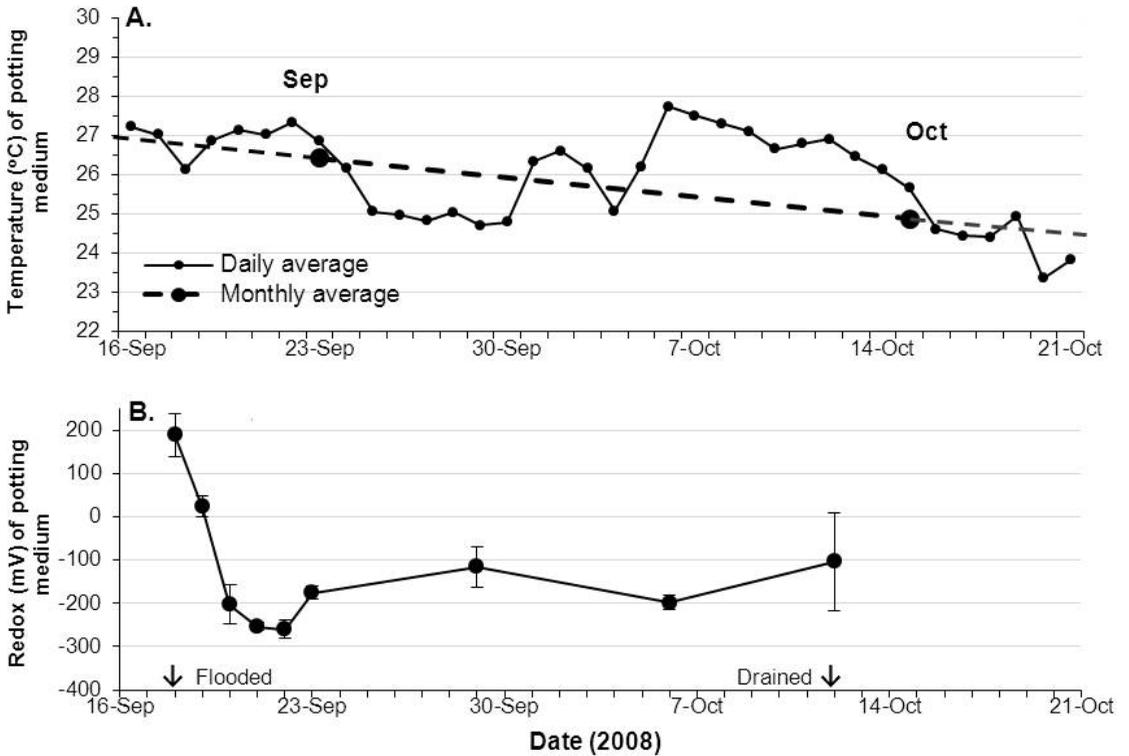


Fig. 5. A) temperature and B) redox potential of flooded potting medium for pond apple trees. For temperature, each point is the average of 3 sensors. For redox potential, each point represents the mean ± SD of four sensors. Plants were flooded Sep 18, infested Sep 19, and unflooded and uninfested Oct 12.

ter, and plant height. Although significant reductions in leaf gas exchange were observed on only 4 measurement dates, it is important to point out that gas exchange in this study was measured on a per-leaf and not a per-plant basis. Thus, on a whole-plant basis, the reduction of leaf area, as expressed by a reduction in leaf dry weight, pre-

sumably resulted in reduced leaf gas exchange on a whole-plant basis.

In the present study,  $A$ ,  $E$ , and  $g_s$  of mahogany were not affected by adult *D. abbreviatus* feeding except for 1 measurement when all 3 leaf gas exchange variables were higher for infested than non-infested trees. However, at the end of the

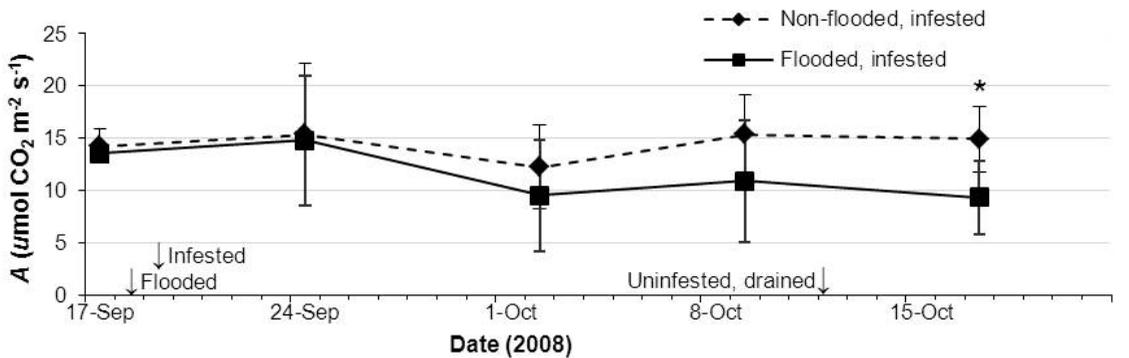


Fig. 6. Effect of flooding on net CO<sub>2</sub> assimilation (A) of infested pond apple trees. Symbols represent means ± SD. Asterisks indicate significant differences between treatments at \*  $P \leq 0.05$  according to a repeated measures ANOVA. Plants were flooded Sep 18, infested Sep 19, and unflooded and uninfested Oct 12.

TABLE 2. MEANS ( $\pm$ SD) AND ANOVA PROBABILITY FOR THE EFFECTS OF FLOODING AND ADULT *DIAPREPES ABBREVIATUS* INFESTATION ON DRY WEIGHT OF POND APPLE TREES ( $N = 6$ ).

Dry weights (g)	Flooding (F)		Infestation (I)		ANOVA		
	Non-flooded	Flooded	Non-infested	Infested	F	I	F $\times$ I
Roots	62.8 $\pm$ 9.6	47.6 $\pm$ 8.6	55.0 $\pm$ 13.7	55.4 $\pm$ 10.3	**	ns	ns
Stem	138.5 $\pm$ 22.4	128.5 $\pm$ 29.7	135.9 $\pm$ 26.2	131.1 $\pm$ 27.2	ns	ns	ns
Leaves	39.3 $\pm$ 9.8	32.0 $\pm$ 10.6	38.5 $\pm$ 8.8	32.8 $\pm$ 11.9	ns	ns	ns
Total	240.6 $\pm$ 34.9	208.0 $\pm$ 44.7	229.4 $\pm$ 43.2	219.3 $\pm$ 43.2	ns	ns	ns

$P > 0.05$  (ns),  $P \leq 0.01$  (\*\*).

study period, dry leaf weights were significantly lower for infested than non-infested mahogany trees, again indicating that leaf gas exchange on a whole-plant basis was presumably lower for infested than non-infested trees. These differences support observations in similar studies that whole-leaf-consuming herbivores can increase leaf gas exchange and decrease plant growth. Ingham & Detling (1986) artificially removed 55% of the foliage of sideoats gramma grass, *Bouteloua curtipendula* (Michx.) Torr. In that study, *A* and *E* increased significantly in the remaining foliage after artificial defoliation, which decreased tiller numbers and root and shoot biomass. Welter (1989) stated that whole leaf consumption by adult insects in the leaf feeding guild often increases *A* on a leaf-area basis; however, this effect is atypical compared to other feeding guilds, such as root-feeders which tend to decrease *A*. With whole-leaf consumption, increased *A* may possibly be explained by the availability of the same quantity of nutrients such as nitrogen delivered to a smaller leaf area after defoliation by the insects. This may render more nitrogen and other nutrients available per remaining leaf area to synthesize chlorophyll and supply other reactions that increase *A*.

Adult *D. abbreviatus* fed significantly more on non-flooded than on flooded mahogany trees in the same cage on 8 of 9 measurement dates and oviposited significantly more on non-flooded than flooded trees on 2 of 9 measurement dates. According to Bernays & Chapman (1994), most phytophagous insect species are confined to certain plant parts which typically determine physical and chemical attributes to which insects respond. Because adult *D. abbreviatus* are foliage feeders, possible reasons for this feeding (and occasional ovipositional) preference for non-flooded over flooded mahogany may include better foliage quality of non-flooded trees and a difference in chemistry, although this was not measured in the present study. In addition, non-flooded mahogany tended to have more leaf material available for feeding as shown by significantly greater dry leaf weight of non-flooded than flooded trees. Wee et al. (2008) tested behavioral and electrophysiological

responses of Fuller's rose weevil, *Pantomorus cervinus* (Boheman) (Coleoptera: Curculionidae), to host plant volatiles from leaves of sweet lemon, *Citrus limonum* Risso., and white clover, *Trifolium repens* L. They showed that healthy, non-flooded plants emitted chemicals that attracted Fuller's rose weevil, which has similar feeding guilds and phenology to *D. abbreviatus*. Eight monoterpene volatiles were detected in lemon leaf oil and 2 green leaf volatiles were identified in white clover leaves; and all these chemicals were detectable by Fuller's rose weevil (Wee et al. 2008). However, none of these compounds seemed to be byproducts of flooding, anaerobic metabolism, or associated microbes (Fulton & Erickson 1964; Wang et al. 1967; Hook et al. 1971; Rowe & Catlin 1971; Culbert & Ford 1972; Ponnamperuma 1984; Kozłowski 1997). There is no indication in the literature that *D. abbreviatus* is attracted to ethanol or other plant metabolites induced by flooding, anaerobic metabolism, or associated microbes, an area of research that merits further investigation.

*Diaprepes abbreviatus* adults may have preferred leaves of non-flooded to flooded mahogany trees because they provided the food quantity, quality, and/or volatiles in the concentration and mixture needed to attract adults, or they may not have produced repellents as readily as flooded plants. Schroeder & Beavers (1985) found that adult male *D. abbreviatus* produced an aggregation pheromone that attracted both male and female adults. Adults may therefore have caused greater leaf damage by aggregating and feeding more on non-flooded than on flooded mahogany trees.

A previous study with *D. abbreviatus* adults involved two other ornamental plant species grown in south Florida, green buttonwood and Surinam cherry, *Eugenia uniflora* L. (Martin 2009). These plant species were grown in similar conditions to those in the present study, but periods of flooding and infestation were generally longer than in the present study (Martin 2009). Morphological and anatomical structures that confer adaptation to prolonged flooding include adventitious roots, increased aerenchyma tissue

in stems, and development of hypertrophic stem lenticels (Schaffer et al. 1992; Kozłowski 1997). Similar to mahogany in the present study, Surinam cherry performed significantly better in non-flooded than flooded conditions for most leaf gas exchange and growth variables and did not show any of these flood adaptations; hence, it was not flood-adapted (Martin 2009). Also similar to mahogany, a feeding preference for non-flooded over flooded Surinam cherry foliage was found on most measurement dates with no differences in oviposition (Martin 2009). Hence, similar mechanisms for attraction or repulsion of adult *D. abbreviatus* discussed previously for mahogany in the present study may have occurred between flooded and non-flooded treatments of Surinam cherry in the previous study.

The effect of *D. abbreviatus* adults on mahogany was different from that on pond apple because adults fed on mahogany stems as well as leaves. They left gouges in the outer stem and bark and chewed up petioles resulting in more leaves and leaflets killed above the wounds than by feeding alone; however, they often avoided older leaves in favor of younger leaves. In a study by Diaz et al. (2005), a lack of young leaves on live oaks may have been why adult *D. abbreviatus* feeding did not significantly affect *A*, *E*, or *g*. Diaz et al. (2005) found that adult *D. abbreviatus* preferred younger over older leaves of live oak suggesting they may have preferred the softer texture of younger leaves because they were easier to consume than the harder, mature leaves. In addition, young leaves often release higher levels of volatile chemicals than older leaves, such as light molecular weight phenols and terpenoids, which are often used by insects to detect host plants (Bernays & Chapman 1994). Hence, although not measured by Diaz et al. (2005), differences in leaf chemistry may have also rendered new live oak leaves more attractive than older leaves for adult feeding. A similar process may have occurred here with mahogany, which rendered new leaves and bark more attractive for feeding than older leaves.

For pond apple, *A* of infested trees was little affected by flooding except after 5 wk. Root dry weight was reduced by flooding, but was the only growth variable that differed significantly between treatments. Despite the good flood tolerance of pond apple trees (Schaffer 1998; Núñez-Elisea et al. 1999; Ojeda et al. 2004), the lack of sufficient time for morphological plant adaptations to flooding (i.e., increased stem aerenchyma tissue and enlarged and adventitious roots; Núñez-Elisea et al. 1999) to develop during the relatively short flooding period in this study may have resulted in reduced root weights of flooded pond apple trees.

For pond apple trees, there was no significant interaction between flooding and insect infesta-

tion except for *A* and no significant differences between infested and non-infested plants for leaf gas exchange or growth variables. There were no significant differences in feeding damage or number of egg clusters between flooded and non-flooded pond apple trees, and mean ( $\pm$ SD) rates of leaf damage were low ( $3.6 \pm 2.0\%$ ). Adults of *D. abbreviatus* tended to congregate on screen tops instead of on pond apple foliage and were rarely seen feeding on leaves. Also, very few of the characteristic semicircular leaf notches were found along pond apple leaf margins, and these notches usually appeared much smaller than on mahogany. Hence, pond apple was not a favorable host for adult *D. abbreviatus* in the present study. However, pond apple was previously found to be a host for *D. abbreviatus*, although it did not appear to significantly affect leaf gas exchange or plant growth (Martin et al. 2009). Pond apple trees can support *D. abbreviatus* larval development, but do not seem to attract adults nor serve as suitable feeding or oviposition sites.

All adult *D. abbreviatus* died within 1 mo on live oaks in the study by Diaz et al. (2005), compared to 96% adult mortality after 23 d infestation on pond apple in the present study, possibly because of starvation in both studies. In the field, however, Diaz et al. (2005) observed adult weevils feeding on live oak leaves during flushing, when leaves were less rigid and more consumable. In the present study, pond apple leaves were regenerated continuously and soft leaves were always available (though sometimes with a few small notches from adult *D. abbreviatus* leaf feeding). Adult *D. abbreviatus* tended to congregate on tops and sides of pond apple screen cages and on stems; and they avoided leaves, unlike with mahogany in the present study or green buttonwood or Surinam cherry in a previous study (Martin 2009).

Mahogany seemed to sustain much higher levels of adult feeding damage, more egg clusters per plant, and greater adult longevity than pond apple. Hence, mahogany appeared to be more susceptible to combined feeding damage from adult *D. abbreviatus* and (occasionally) number of egg clusters per plant than pond apple. Overall, *D. abbreviatus* adults seemed to lay fewer egg clusters and live a shorter lifespan on pond apple than on mahogany in the present study or on green buttonwood or Surinam cherry in the previous study (Martin 2009), although there were no statistical comparisons among plant species. In contrast to pond apple, results for mahogany confirmed the findings of Simpson et al. (1996) that this species is a suitable host plant for adult *D. abbreviatus*.

In conclusion, despite pond apple being a host plant species for *D. abbreviatus* larvae, adult weevils did not feed on the foliage. Hence, flooding did not predispose pond apple trees to, nor protect them from damage by adult *D. abbreviatus*. For

mahogany, however, flooding resulted in less leaf damage from adult *D. abbreviatus* feeding compared to non-flooded trees. Flooding is sometimes used in sugarcane fields of south Florida to control pests like sugarcane grubs *Tomarus subtropicus* (Blatchley) (Coleoptera: Scarabaeidae) (Cherry 1984) and wireworm larvae *Melanotus communis* (Gyllenhal) (Coleoptera: Elateridae) (Hall & Cherry 1993). Larvae of *M. communis* had 80% mortality after 6 wk of submergence at 27°C (Hall & Cherry 1993), and *T. subtropicus* had 100% mortality after only 5-10 d submergence (Cherry 1984). Flooding may be useful for controlling *D. abbreviatus* larvae in sugarcane fields, although only in the summer and fall when floodwater temperatures are close to their maximum (27°C) (Hall & Cherry 1993; Shapiro et al. 1997). In contrast to many sugarcane varieties (Glaz & Morris 2006), mahogany was not flood-adapted in our study as evidenced by significantly less growth of flooded compared to non-flooded trees. Although flooding decreased leaf feeding injury on mahogany trees, it may not be a preferred control measure for *D. abbreviatus* because it also reduced plant growth. Nevertheless, the results of this study may help prioritize decisions for pest management of mahogany and pond apple trees.

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