Effects of Flooding on Physiology and Growth of Four Woody Ornamental Species in Marl Soil of South Florida[1]

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Abstract

In south Florida nurseries, trees are often grown in marl soil, which is heavy, clay-like, calcareous soil that is slow to drain and prone to periodic flooding during the rainy season. Green buttonwood, mahogany, pond apple and Surinam cherry are grown in this soil. We tested effects of flooding on leaf gas exchange and growth of these four species to determine their flood tolerances in marl soil. Green buttonwood, mahogany, and Surinam cherry each had consistently lower leaf gas exchange and plant growth in flooded than in non-flooded marl soil, which suggests low tolerance to flooding. In contrast, flooding had little or no effect on leaf gas exchange and growth of pond apple, indicating that this species was tolerant of flooding in marl soil. Green buttonwood and pond apple had larger stem diameters and more hypertrophic stem lenticels when flooded than when not flooded. Flooded green buttonwood also developed adventitious roots. Pond apple appears to be a good choice for planting in low-lying areas in marl soil typical of outdoor nurseries in south Florida. In contrast, care should be taken to avoid planting green buttonwood, mahogany, and Surinam cherry in marl soil in flood-prone areas.

Index words: waterlogging, green buttonwood, mahogany, Surinam cherry, pond apple.

Species used in this study: *Conocarpus erectus* L. (Combretaceae), green buttonwood; *Swietenia mahagoni* Jacq. (Meliaceae), mahogany; *Annona glabra* L. (Annonaceae), pond apple; and *Eugenia uniflora* L. (Myrtaceae), Surinam cherry.

Significance to the Nursery Industry

Green buttonwood, mahogany, and Surinam cherry are popular landscape plants in southern Florida. In addition to being a native ornamental plant, pond apple is a potential rootstock for improving flood tolerance of other *Annona* species, which are commercially grown as fruit crops such as sugar apple and atemoya. In south Florida nurseries, trees are often grown in marl soil, which is heavy, clay-like, calcareous soil that is poorly drained and prone to periodic flooding during the rainy season (late April to early November). Marl soil was formed in low-lying areas that were historically periodically flooded for several months per year, many acres of which were later developed for agriculture. Hence, plants grown in south Florida nurseries may be periodically flooded when grown in marl soil. We tested effects of flooding on leaf gas exchange (net CO_2 assimilation and stomatal conductance) and growth of green buttonwood, mahogany, pond apple, and Surinam cherry trees to determine their flood tolerances in marl soil. Of the four species tested, only pond apple was tolerant of flooding in this soil. Thus, pond apple may be a good choice for planting in low lying areas in marl soil typical of outdoor nurseries in southern Florida. Nursery operators should avoid planting green buttonwood, mahogany, and Surinam cherry in flood-prone areas with marl soil or possibly adopt practices, such as planting these species on raised beds or hills, to avoid potential flooding stress.

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Introduction

A significant portion of agriculture in southern Florida occurs in low-lying areas prone to soil flooding (17). For agriculture to remain viable in these areas it is important to understand how flooding affects crop physiology, growth, and yield to help identify flood-adapted crops and production systems (17). Flooding or waterlogging of the root zone typically depletes soil oxygen (8). Effects of flooding on the physiology and growth of a woody plant species can vary among soil types and are partly based on depletion rates of soil oxygen and other factors such as soil pH (8, 18). In south Florida plant nurseries, woody ornamental plants are grown in either containers in potting medium or in fields with marl soil, which is classified as loamy, carbonatic, hyperthermic, shallow, typic, fluvaquents (9, 13). Marl soils are derived from limestone in areas that receive several months of heavy rain during the wet season, then little rain for several months enhancing soil aeration during the dry season. During the rainy season (late April to early November), marl soils are prone to periodic flooding. The resulting 'calcite mud' soil is high in calcium, has a pH of 7.4–8.4, and has poor drainage (9).

Responses of woody plants to flooding include senescence, shoot dieback, premature leaf abscission, decreased cambial growth, and the suppression of leaf formation and expansion (8, 18). Early measurable plant responses to flooding include reductions in leaf gas exchange variables such as net CO_2 assimilation and stomatal conductance. Measuring leaf gas exchange has been used to quantify damage from flooding before any visual symptoms appear (14, 15, 17, 18). Some woody plants develop anatomical or morphological adaptations to flooding stress, such as hypertophic (swollen) stem lenticels, which may increase gas exchange to the roots and allow for the excretion of toxic metabolites produced in the roots during anaerobic respiration (1, 6). Other adaptations to flooding include adventitious roots for increased oxygen uptake and development of aerenchyma tissue in the stem and a subsequent increase in stem diameter to improve oxygen movement through plant tissue (8, 18). Soil redox potential is an indirect measure of the amount of oxygen in the soil. A redox potential below 200 mV generally indicates that the soil is anaerobic (18).

Green buttonwood (*Conocarpus erectus* L., Combretaceae), mahogany (*Swietenia mahagoni* Jacq., Meliaceae), pond apple (*Annona glabra* L., Annonaceae), and Surinam cherry (*Eugenia uniflora* L., Myrtaceae) are widely grown in southern Florida. Green buttonwood is a frequently planted ornamental tree or shrub in south Florida and is native to the tidal swamps of central and south Florida (19, 20). In its native area, buttonwood is fairly tolerant of flooding, though it also thrives in non-flooded, moderately moist soil, which is common for landscape plants. Mahogany is native to 'coastal hammocks' in south Florida (20), where it is also a widely planted lawn and street tree (19). Surinam cherry is native to South America, occurs in 'disturbed hammocks' of central and southern Florida (20), and is widely planted in south Florida as a shrub or occasionally as a fruit crop. Pond apple is a native tree to 'swamps' of central and south Florida (20), parts of the Caribbean, and Central and South America (12, 16). It is planted as a native landscape tree and is typically not grown as a commercial fruit crop (12, 16). Although flood tolerance of this species in marl soil has not been reported, in other soils it is very tolerant of flooding (14, 15, 17) and has greatly increased the flood-tolerance of commercial *Annona* species when tested as a rootstock (14). The purpose of this study was to test the tolerance of green buttonwood, mahogany, pond apple, and Surinam cherry trees to flooding in marl soil, using leaf gas exchange and growth measurements as indicators of flood tolerance.

Materials and Methods

The study was conducted at the Tropical Research and Education Center, University of Florida, Homestead from 2006 to 2007. The first test was conducted outside during the spring and summer of 2006 with buttonwood and mahogany. The second test was conducted outside in the late fall, winter, and spring 2006–2007 with pond apple and Surinam cherry.

Plant material. All plants were obtained from local commercial nurseries. When treatments were initiated, trees of buttonwood, mahogany, and Surinam cherry were approximately 2 yrs old and pond apple trees were 1 yr old. At the beginning of the experiment, plant heights (mean ± SD) for non-flooded and flooded plants, respectively, were 34 ± 3.5 and 35 ± 4.6 cm (14 ± 1.4 and 14 ± 1.8 in) for buttonwood; 97 ± 13 and 92 ± 9.1 cm (38 ± 5.0 and 36 ± 3.6 in) for mahogany; 94 ± 7.9 and 93 ± 11 cm (37 ± 3.1 and 37 ± 4.2 in) for pond apple; and 49 ± 7.4 and 45 ± 7.7 cm (19 ± 2.9 and 18 ± 3.0 in) for Surinam cherry. Within each plant species, a non-paired t-test indicated no significant differences between flooded and non-flooded treatments for these initial plant heights. Plants of each species were repotted into marl soil in 11-liter (2.9-gal) plastic containers that had a 22 cm (8.7 in) mean diameter and a 23 cm (9.1 in) mean height and classified as class #2 by the Horticultural Standards Committee (7). Plants were repotted 83 days before initiation of flooding for buttonwood and mahogany and 270 days before initiating flooding for pond apple and Surinam cherry. The soil was collected from a fallow agricultural field in Homestead, FL, and sieved before use through a 2.5 × 2.5 cm (1 × 1 in) mesh screen to remove large objects such as weeds and rocks. All trees were fertilized with liquid fertilizer (Peters 24-8-16 with micronutrients, United Industries, St Louis, MO) at the manufacturer's recommended rate. Trees of buttonwood and mahogany were each fertilized May 9, 2006 (29 days before initiating treatments), while pond apple and Surinam cherry were each fertilized November 22, 2006 (19 days before initiating treatments). No pesticides were used; pests were controlled by hand removal.

Flooding treatments. For each species, six plants in 11 liter (2.9 gal) containers were flooded by placing them into individual 19 liter (5 gal) plastic buckets filled with tap water to 10 cm (4 in) above the soil surface. Another six plants were left unflooded as controls. Flooding durations were 23 days for buttonwood and mahogany and 41 days for pond apple and Surinam cherry. The decision to terminate flooding was made when physiological indicators of plant stress were evident for at least two consecutive weeks on one or more plants tested; these indicators included a statistically significant reduction in net CO_2 assimilation and/or wilting. All trees were irrigated by overhead sprinklers when plants were not flooded. Buttonwood and mahogany were irrigated by overhead sprinklers for 30 min twice a day, whereas pond apple and Surinam cherry were irrigated for 30 min once a day until day 103 when irrigation was changed to 30 min twice a day. During flood periods, however, non-flooded trees were irrigated manually every 2 days with 0.5 liter (0.5 qt) of water per plant; flooded trees were not irrigated, but water levels were maintained at 10 (4 in) cm above the soil surface by adding or removing tap water.

Soil temperature and redox potential. Soil temperature was measured at 1 hr intervals throughout the experiment with temperature sensors (StowAway® Tidbit® temploggers, Onset Co., Pocasset, MA). Sensors were placed 6 cm (2.4 in) below the soil surface, and two-thirds the distance from the center to the outer edge of the pot. Soil temperature for buttonwood and mahogany was determined using four sensors (one in each randomly selected container), whereas three sensors were used for pond apple and Surinam cherry. Soil redox potential was measured with a platinum combination electrode attached to a portable voltage meter (Accumet #AP62, Fisher Scientific, Pittsburgh, PA). Measurements were made by inserting the electrode into a polyvinyl chloride (PVC) pipe (20 cm long × 2.2 cm wide) (7.9 × 0.9 in) that protruded 4 cm (1.6 in) above the soil surface and was placed into the soil 2 cm (0.8 in) from the edge of the pot. Soil redox potential was measured at a mean depth of 6 cm (2.4 in) below the soil surface for the flooded treatment in three pots (replications) and recorded daily for the first 6–7 days of flooding, then at 3–8 days intervals until plants were unflooded.

Leaf gas exchange. Net CO_2 assimilation and stomatal conductance were measured on two fully expanded, recently matured leaves or leaflets (between the fourth and tenth node below the stem apex) per plant with a CIRAS-2 portable gas analyzer (PP Systems, Amesbury, MA). For net CO_2 assimilation and stomatal conductance measurements, the photosynthetic photon flux was maintained at 1000 μmol photons·m^{-2}·s^{-1} with a halogen lamp attached to the leaf cuvette, and the reference CO_2 concentration of air in the cuvette was 375 μmol·mol^{-1} CO_2. Mahogany has pinnately compound leaves with 6–8 similar-sized leaflets per leaf, whereas all the other plant species tested have simple leaves (19, 20). For leaf gas exchange measurements, mahogany leaflets were randomly selected from all positions on the leaf. Leaf gas exchange for each treatment of each plant species was initially measured a few days before flooding commenced and periodically during flooding until a few days after flooding ended.

Plant growth. In each treatment, stem diameter was measured 10 cm (4 in) above the soil surface, and for plants with multiple stems, the diameter of the stem (at 10 cm above the soil surface) that was the largest during each individual measurement was recorded. Plant height was measured from the soil surface to the apex of the highest stem or leaf. Stem diameter and plant height were measured before flooding and again immediately before harvest. At harvest, roots, stems, and leaves of all plants were oven-dried at 75C (167F) to a constant weight and dry weights were determined for each plant organ. Additionally, the number of inflorescences per plant was determined for buttonwood and the numbers and weights of flowers and fruits (including pedicels) per plant were determined for pond apple and Surinam cherry.

Experimental design and statistical analysis. Each plant species was analyzed separately with six single-plant replications per flood treatment arranged in a completely randomized design. Treatment means were compared by a non-paired t-test using SAS statistical software (Version 9.1, SAS Institute, Cary, NC).

Results and Discussion

The range of mean daily soil temperatures was 24.4–30.5C (76–87F) for buttonwood and mahogany and 10.3–25.0C (51–77F) for pond apple and Surinam cherry. Soil redox potential for flooded green buttonwood plants ranged from +310 mV on the first day of flooding to –234 mV on day 14 (Fig. 1). Soil redox potential for flooded mahogany varied from +296 mV on the first day of flooding to –106 mV on day 21 (Fig. 1). For pond apple, soil redox potential in flooded soil ranged from +153 mV on the first day of flooding to –98 mV on day 18 (Fig. 1). Soil redox potential for Surinam cherry ranged from +219 mV on the first day of flooding to –162 mV on day 18 (Fig. 1).

Leaf gas exchange. For green buttonwood, net CO_2 assimilation was lower for plants in flooded than in non-flooded soil on several measurement dates (Fig. 2a). For green buttonwood, stomatal conductance was lower for flooded than for non-flooded plants during weeks 3–7 and 10 (Fig. 2b). Net CO_2 assimilation of mahogany was consistently lower for flooded than for non-flooded plants (Fig. 2c). These differences in net CO_2 assimilation for mahogany were significant between flooded and non-flooded plants on weeks 2–8 and week 10 (Fig. 2c). Stomatal conductance of mahogany was lower for flooded than for non-flooded plants during weeks 2–10 and week 12 (Fig. 2d). Net CO_2 assimilation of pond apple was higher for flooded than non-flooded plants on weeks 10, 12, and 14 (Fig. 2e). There were no significant differences in stomatal conductance between flooded and non-flooded pond apple (Fig. 2f). Net CO_2 assimilation of Surinam cherry was lower for flooded than non-flooded plants during weeks 4–12 (Fig. 2g). Stomatal conductance of Surinam cherry was lower for flooded than non-flooded plants during weeks 4–12 (Fig. 2h).

Plant growth. For green buttonwood, leaf dry weight was lower for flooded than non-flooded plants, but there were no significant differences between flooded and non-flooded plants in root, stem, or total dry weights (Table 1). Hypertrophic (swollen) stem lenticels and small numbers of adventitious roots, fewer than 10 per plant and up to 15 cm (6

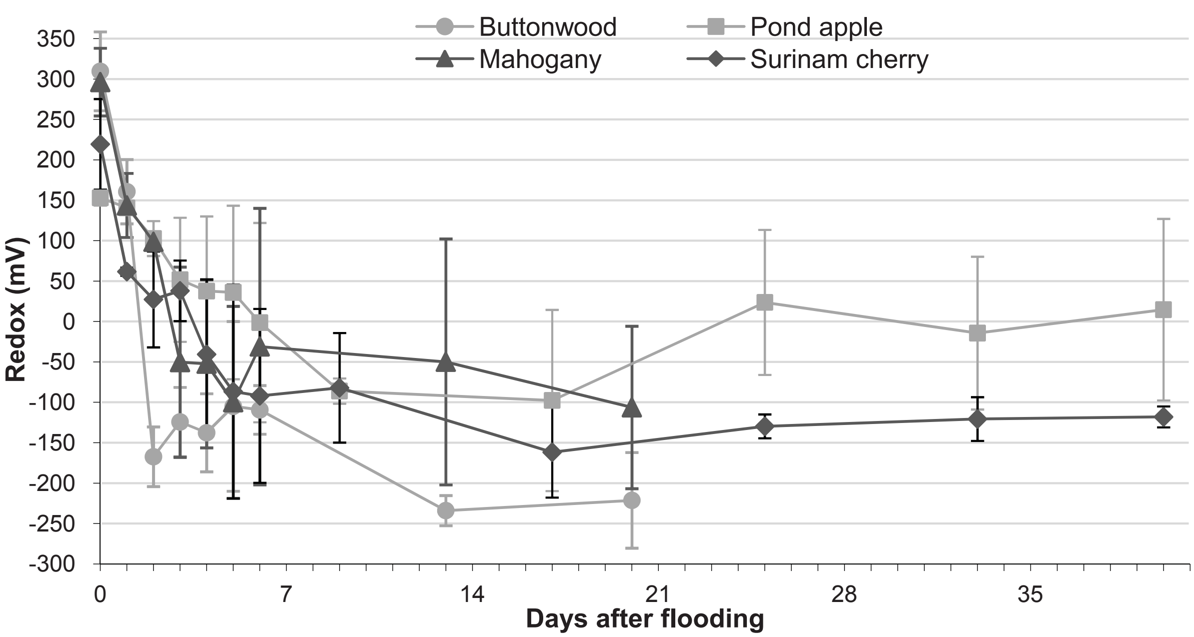

Fig. 1. **Soil redox potential from the time plants were initially flooded to the end of the flooding period. Each point represents the mean ± SD of three measurements per date for each flooded treatment for each plant species.**

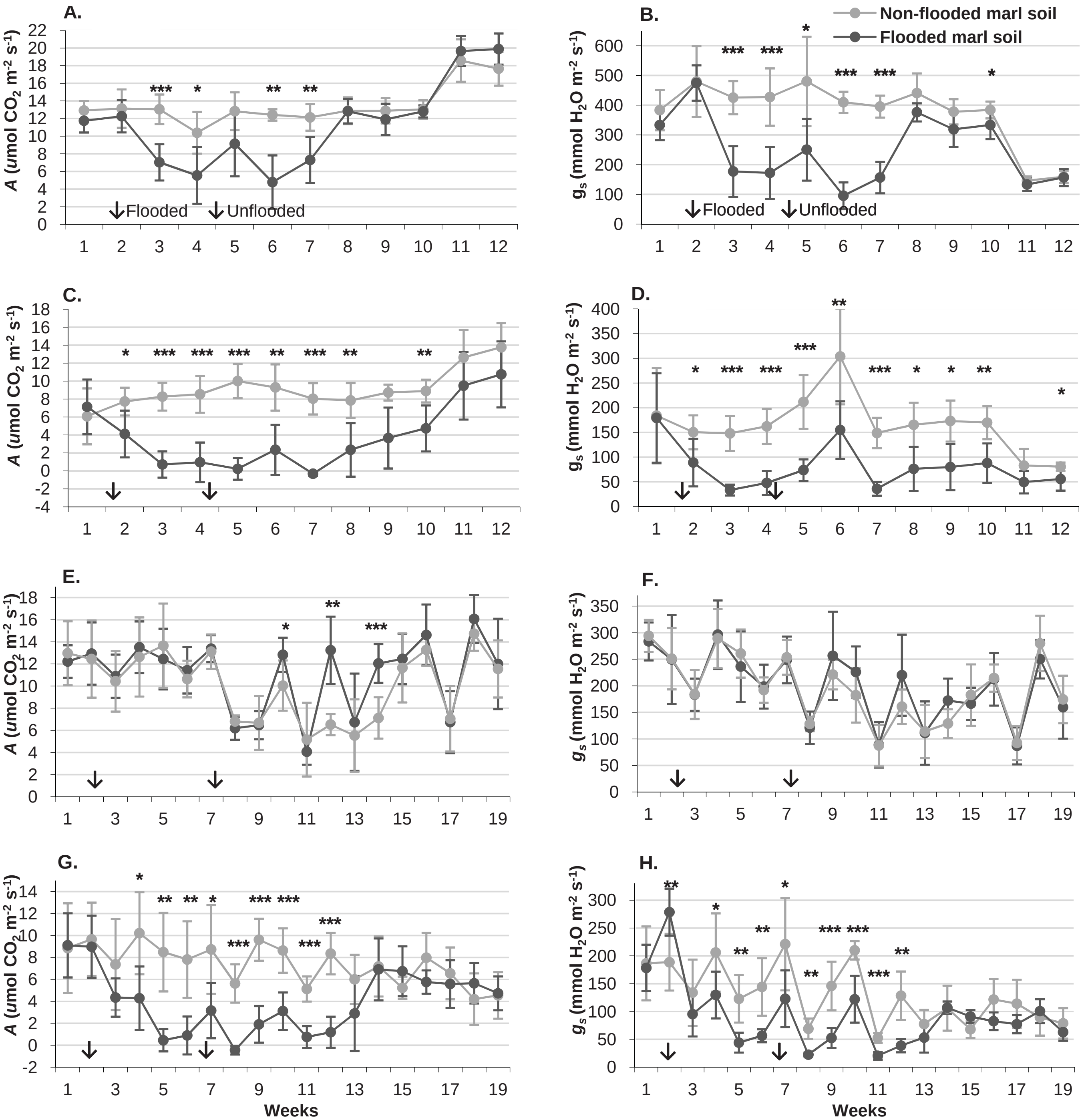

Fig. 2. Effects of flooding on net CO_2 assimilation (A) and stomatal conductance (g_s) of green buttonwood (A, B), mahogany (C, D), pond apple (E, F) and Surinam cherry (G, H) trees in marl soil. Symbols represent means. The first arrow indicates when flooding commenced and the second arrow indicates when flooded plants were removed from flooding (unflooded). Asterisks indicate significant differences between treatments at * $P \le 0.05$, ** $P < 0.01$, and *** $P < 0.001$ according to a non-paired t-test.

in) long, were often observed on flooded green buttonwood plants. For green buttonwood, there were no effects of flooding on change in stem diameter or plant height (Table 1). There were also no statistically significant effects of flooding on the number of inflorescences per buttonwood plant (data not shown, range 0–136).

For mahogany, leaf dry weight was lower for flooded than for non-flooded plants (Table 1). There were no differences in root, stem, or total dry weights between flooded and non-flooded mahogany plants (Table 1). The increase in stem diameter of mahogany was less for flooded than for non-flooded plants (Table 1). There was no significant effect of flooding on the change in plant height of mahogany (Table 1).

Pond apple root, stem, leaf, and total plant dry weights were not significantly affected by flooding (Table 1). The increase in stem diameter of pond apple was greater for flooded than for non-flooded plants (Table 1). In addition, flooded pond apple trees developed hypertrophic stem len-

Table 1. **Effects of flooding on change in plant height[z], change in stem diameter[y], and root[x], stem[x], leaf[x] and total plant dry weights[x] of green buttonwood, mahogany, pond apple and Surinam cherry trees in marl soil.**

Species	Non-flooded		Flooded		Significance[w]
Buttonwood					
Root	50 ± 16	(1.8 ± 0.6)	49 ± 10	(1.7 ± 0.4)	NS
Stem	31 ± 4.3	(1.1 ± 0.2)	30 ± 4.2	(1.1 ± 0.1)	NS
Leaf	36 ± 3.3	(1.3 ± 0.1)	27 ± 3.9	(0.9 ± 0.1)	**
Total	117 ± 18	(4.1 ± 0.6)	106 ± 14	(3.7 ± 0.5)	NS
Change in plant height	20 ± 13	(7.7 ± 5.0)	8.3 ± 3.6	(3.3 ± 1.4)	NS
Change in stem diameter	0.5 ± 1.1	(0.02 ± 0.04)	1.0 ± 0.9	(0.04 ± 0.04)	NS
Mahogany					
Root	46 ± 16	(1.6 ± 0.6)	32 ± 13	(1.1 ± 0.4)	NS
Stem	59 ± 22	(2.1 ± 0.8)	47 ± 24	(1.6 ± 0.8)	NS
Leaf	22 ± 6.7	(0.8 ± 0.2)	10 ± 8.6	(0.4 ± 0.3)	*
Total	127 ± 41	(4.5 ± 1.5)	89 ± 41	(3.1 ± 1.4)	NS
Change in plant height	17 ± 5.1	(6.5 ± 2.0)	10 ± 6.0	(4.1 ± 2.3)	NS
Change in stem diameter	2.8 ± 0.7	(0.11 ± 0.03)	0.4 ± 1.8	(0.02 ± 0.07)	*
Pond apple					
Root	43 ± 7.5	(1.5 ± 0.3)	43 ± 5.4	(1.5 ± 0.2)	NS
Stem	44 ± 3.4	(1.6 ± 0.1)	51 ± 7.1	(1.8 ± 0.3)	NS
Leaf	11 ± 1.0	(0.4 ± 0.0)	11 ± 1.5	(0.4 ± 0.1)	NS
Total	98 ± 10	(3.5 ± 0.4)	105 ± 13	(3.7 ± 0.5)	NS
Change in plant height	0.0 ± 2.4	(0.0 ± 0.9)	1.2 ± 2.7	(0.5 ± 1.1)	NS
Change in stem diameter	1.2 ± 0.9	(0.05 ± 0.04)	3.9 ± 1.7	(0.15 ± 0.07)	**
Surinam cherry					
Root	37 ± 19	(1.3 ± 0.7)	21 ± 10	(0.7 ± 0.4)	NS
Stem	61 ± 21	(2.2 ± 0.7)	34 ± 14	(1.2 ± 0.5)	*
Leaf	39 ± 15	(1.4 ± 0.5)	7.8 ± 11	(0.3 ± 0.4)	**
Total	137 ± 53	(4.8 ± 1.9)	62 ± 34	(2.2 ± 1.2)	*
Change in plant height	21 ± 10	(8.4 ± 4.1)	3.0 ± 4.3	(1.2 ± 1.7)	**
Change in stem diameter	2.5 ± 1.4	(0.10 ± 0.06)	0.0 ± 0.8	(0.0 ± 0.03)	**

[z]Mean ± SD (cm) (inches in parenthesis).

[y]Mean ± SD (mm) (inches in parenthesis).

[x]Mean ± SD (g) (ounces in parenthesis).

[w]Significance. Asterisks indicate significant differences between treatments at * $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$, and NS non-significant according to a non-paired t-test.

ticels. There were no significant effects of flooding on the change in plant height (Table 1) or the number or weight of flowers and fruit (data not shown, ranges 0–1.2 for number and 0–0.83 g or 0–0.03 oz for weight) of pond apple.

Stem, leaf, and total dry weights of Surinam cherry were lower for flooded than non-flooded plants, but there was no significant difference in root dry weight (Table 1). Increases in stem diameter and plant height of Surinam cherry were less for flooded than for non-flooded plants (Table 1). For Surinam cherry, there were no significant differences between flooded and non-flooded plants in the number or weight of flowers and fruit per plant (data not shown, ranges for number 0–19 and for weight 0–8.2 g or 0–0.3 oz).

The most apparent trend in leaf gas exchange for buttonwood, mahogany, and Surinam cherry was lower net CO_2 assimilation and stomatal conductance for flooded than non-flooded plants in marl soil. Similarly, growth of mahogany and Surinam cherry was often less for flooded than non-flooded plants. Mean soil redox potential of flooded plants varied from +310 mV to -234 mV for green buttonwood, +296 mV to -106 mV for mahogany, +153 mV to -98 mV for pond apple, and +219 mV to –162 mV for Surinam cherry indicating flooded soils were hypoxic in each experiment. Reduced photosynthesis (net CO_2 assimilation) in flooded soil may have been a result of stomatal closure (as evidenced by reduced stomatal conductance) which is a common response to soil flooding. However, it has not been determined in flooded plants if reductions in stomatal conductance occur before reductions in photosynthesis or if photosynthesis is reduced first (18). Thus, an alternative explanation for lower net CO_2 assimilation in flooded than non-flooded plants may have been less available energy for photosynthesis as a result of anaerobic respiration in flooded roots. Reduced oxygen availability in flooded soil eventually results in a conversion from aerobic to anaerobic root respiration. Anaerobic respiration in the roots produces considerably less chemical energy than aerobic respiration (4), possibly resulting in less energy for leaf gas exchange.

Green buttonwood exhibited fairly low flood tolerance in marl soil in the present study. This was surprising given the native habitat of green buttonwood, which includes tidal swamps of central and southern Florida (20). In its native range, green buttonwood is fairly tolerant of flooding, although it also thrives in non-flooded, moderately moist soil, which is common for landscape plants. In its native habitat, green buttonwood frequently occurs in soils similar to marl in flood-prone areas; hence, it evolved in and should be well adapted to this environment. Concurrent to the present study, green buttonwood, mahogany, pond apple, and Surinam cherry were also grown in a potting medium (60% Florida peat and 40% hardwood chips) with the same procedures, timing, flooding durations as plants in marl soil (10). Similar to their performance in marl soil, flooded green buttonwood in potting medium developed hypertrophic stem lenticels and adventitious roots (10). However in potting medium, stem diameter of green buttonwood was also significantly increased under flooded conditions, and there were no significant differences between flooded and non-flooded treatments in net CO_2 assimilation, stomatal conductance, change in plant height, or root, stem, leaf or total plant dry weight. Hence, green buttonwood was flood-tolerant in potting medium. However, similar to our observations in marl soil, Diaz (2) found that flooding green buttonwood in a different potting medium (40% Florida peat, 30% pine bark, 20% cypress sawdust and 10% sand) reduced net CO_2 assimilation and stomatal conductance beginning 1 wk after plants were flooded, although flooding did not significantly affect root, stem, or leaf fresh or dry weights. Although green buttonwood is native to tidal swamps of central and southern Florida (20), such as flooded brackish environments, and develops adaptations to flooding when flooded with non-saline ('fresh') water, the variable flood tolerances of this species may be related to soil type.

Flooding green buttonwood initially reduced net CO_2 assimilation and stomatal conductance. However, 2–3 weeks after flooded plants were unflooded, there was an abrupt increase in these variables rendering them nearly equal for flooded and non-flooded plants, whereas for the other species tested, the recovery from flooding was more gradual. Hence, there was evidence of a flood-induced compensatory increase in net CO_2 assimilation and stomatal conductance in green buttonwood plants. Compensatory increases in leaf gas exchange of stressed plants have been noted for green buttonwood plants in response to larval feeding by Diaprepes root weevil (3, 11). In those studies, green buttonwood was the only plant species, of the few tested, with increased leaf gas exchange as a compensatory reaction to stress from insect feeding (3, 11).

Flooded pond apple plants developed swollen stems and hypertrophic stem lenticels in response to flooding. Hypertrophic stem lenticels may allow for increased gas exchange into and out of the stem (5, 6) and may be excretory sites for potentially toxic compounds (i.e., acetaldehyde) produced in the roots of flooded plants during anaerobic respiration (1). Often, swollen stems of flooded plants exhibit increased aerenchyma, which can facilitate movement of O_2 from shoots to submerged roots. Because swollen stem lenticels and aerenchyma tissue increase the stem girth, a greater increase in stem diameter in flooded than in non-flooded soils may indicate adaptation to flooding. Pond apple plants developed significantly larger stem diameters when flooded than when non-flooded, and hypertrophic stem lenticels were conspicuous under flooded conditions for pond apple and green buttonwood. For green buttonwood, more adventitious roots were observed for flooded than non-flooded plants. This suggests that green buttonwood and pond apple are adapted to flooded soil conditions via development of aerenchyma and hypertrophic stem lenticels as well as adventitious roots. Studies by Núñez-Elisea et al. (14), Ojeda et al. (15), and Schaffer (17) in Krome very gravelly loam soils (another calcareous agricultural soil in south Florida) showed that pond apple is well adapted to flooding. In the present study, pond apple was very tolerant to soil flooding in marl soil. When pond apple was grown in potting medium (40% Florida peat, 20% pine bark, 20% cypress sawdust, and 20% sand) and randomized in the same completely randomized design and hence under very similar experimental conditions as plants in marl soil in the present study, they also developed swollen stems, hypertrophic stem lenticels, and tolerated flooding very well (10). Ojeda et al. (15) investigated effects of root-zone temperature and flooding on the physiology and growth of pond apple and soursop (*Annona muricata* L.), another species in the same genus as pond apple. In that study, both species were flooded for 6 weeks (15) which is similar to the flood period for pond apple in our study. Ojeda et al. (15) found that pond apple was more flood-tolerant than soursop and only trees with morphological adaptations such as enlarged trunk bases, hypertrophic stem lenticels, or adventitious roots survived continuous flooding. Núñez-Elisea et al. (14) tested effects of flooding on net CO_2 assimilation and growth of pond apple, seedling of two other *Annona* species, and four scion/rootstock combinations in Krome gravelly loam soil and in potting medium. In one test they flooded plants either continuously for 50 days or in three cycles that alternated 10 day flooding with 10 day non-flooding periods, and in other tests, they flooded plants continuously for 30 days (14). Marl soil used in the present study and Krome gravelly soil loam used in the study by Núñez-Elisea et al. (14) are similar in pH (7.4–8.4), and both have a calcium-rich composition, but marl soil is more poorly drained than Krome gravelly loam soil (9). Núñez-Elisea et al. (14) found that in response to flooding, pond apple plants developed stem aerenchyma and thicker stems caused by enlarged xylem cells, but with reduced xylem density. This concurs with our observation that pond apple developed thicker stems in flooded than in non-flooded marl soil.

Net CO_2 assimilation, stomatal conductance and plant growth of mahogany were similar to those of green buttonwood with lower values for flooded than non-flooded plants. Considering leaf gas exchange and plant growth collectively, mahogany was not flood-tolerant in marl soil. When grown in a potting medium (25% Florida peat, 65% pine bark, and 10% coarse sand) under very similar experimental conditions as plants in marl soil in the present study, mahogany had good flood tolerance with almost no significant differences between flooded and non-flooded plants in leaf gas exchange or growth (10). However, in both studies, mahogany did not exhibit morphological adaptations to flooding, which may reflect its native habitat of coastal hammocks (20) which are typically not flooded and may lack marl soil (9).

Mahogany and Surinam cherry each had significantly lower net CO_2 assimilation and stomatal conductance in flooded than in non-flooded marl soil during similar flooding durations (8–9 measurements each for net CO_2 assimilation and stomatal conductance). Also, Surinam cherry had significantly less increases in plant height and stem diameter, and lower stem, leaf, and total dry weight in flooded than in non-flooded soil. Based on leaf gas exchange and plant growth, Surinam cherry was not flood-tolerant in marl soil. When grown in a potting medium (40% Florida peat, 20% pine bark, 20% cypress sawdust, and 20% sand) under very similar experimental conditions as those in the present study with marl soil, Surinam cherry had fairly poor flood tolerance (10). Although the flower and fruit weights for Surinam cherry in potting medium were significantly increased in flooded compared to non-flooded plants, and the growth data suggested good flood tolerance, it was not flood tolerant based on leaf gas exchange (10). Increased flowering and fruit production has been observed in flood-sensitive trees in response to flooding (18), possibly as a mechanism to naturally propagate new offspring prior to physiological decline of the parent from flooding stress. Similar to mahogany, Surinam cherry did not show morphological adaptations to flooding in marl soil or in potting medium (10). This was indicated by the absence of adventitious roots in Surinam cherry and larger stem diameters in non-flooded than in flooded plants in marl soil. This may reflect the native habitats of Surinam cherry which are 'disturbed hammocks' that are typically non-flooded (9, 20).

Based on leaf gas exchange, growth and development of morphological adaptations to flooding, green buttonwood, mahogany, and Surinam cherry did not appear to be flood-tolerant in marl soil, whereas pond apple was flood-tolerant. Based on these results, pond apple appears to be a good choice for planting in low lying areas in marl soil typical of outdoor nurseries in southern Florida. In contrast, in these nurseries care must be taken to avoid planting green buttonwood, mahogany, and Surinam cherry in flood-prone areas, or possibly practices should be adopted for these species in nurseries with marl soil, such as planting trees on raised beds or hills to reduce the chance of root waterlogging which can occur periodically during the rainy season.

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