WETLANDS, Vol. 26, No. 3, September 2006, pp. 830–844

RESPONSES OF TWELVE TREE SPECIES COMMON IN EVERGLADES TREE ISLANDS TO SIMULATED HYDROLOGIC REGIMES

David T. Jones[1], Jay P. Sah[1], Michael S. Ross[1], Steven F. Oberbauer[2], Bernice Hwang[1], and Krish Jayachandran[1,3]
[1]*Southeast Environmental Research Center*

[2]*Department of Biological Sciences*

[3]*Department of Environmental Studies*
Florida International University
Miami, Florida, USA 33199

Abstract: Twelve tree species common in Everglades tree islands were subjected to three hydrologic regimes under controlled conditions for 25 weeks and assessed for growth and physiological responses. Treatments representing high, low, and no flood were maintained in pools of water to mimic seasonal variation in water depths at different positions in tree islands. Soil inundation under the high flood treatment resulted in reduced tree growth (height, basal diameter, crown volume) that was more pronounced and occurred earlier in mesic forest species than in swamp forest species. Physiological responses differed less among species, although stomatal conductance was a better predictor of the effects of flood stress on growth than either relative water content or chlorophyll fluorescence (F_v/F_m). Some swamp species appeared to be better adapted to rising water levels than others; *Annona glabra, Morella cerifera*, and *Salix caroliniana* responded more positively to flooding, while *Magnolia virginiana, Persea borbonia, Chrysobalanus icaco*, and *Ilex cassine* were less flood-tolerant. The highest mortalities and lowest growth were observed in the five upland species: *Bursera simaruba, Coccoloba diversifolia, Eugenia axillaris, Sideroxylon foetidissimum*, and *Simarouba glauca*. Of these, *Sideroxylon* and *Simarouba* did not survive to the end of the study under the high flood treatment. The moist soil conditions simulated by the low flood treatment resulted in greater growth in all species compared to soil inundation under high flood, except for the most flood-tolerant (*Annona, Morella, Salix*). The arrangement of species according to their responses to experimental flooding roughly paralleled their spatial distribution in the tree islands. The gradient in species responses demonstrated in this experiment may help guide responsible water management and tree island restoration in the Everglades.

Key Words: flood tolerance, tree island, Florida Everglades, hydrologic regime, restoration

INTRODUCTION

Tree islands are among the most distinctive features of the Florida Everglades (USA) and have been described by various workers over the past 90 years (Harshberger 1914, Harper 1927, Davis 1943, Loveless 1959, Craighead 1971, Sklar and van der Valk 2002a). They generally occur on elevated limestone outcrops or above bedrock depressions embedded within a freshwater or brackish marsh or swamp. Because surface elevation at the center of the tree island is typically higher than the surrounding marsh, a vegetation gradient can usually be identified, with tropical and subtropical hardwood species inhabiting the better-drained interior positions and swamp species of mainly temperate origin dominating the frequently flooded edge locations. Tree islands cover less than five percent of the Everglades, yet they perform many vital ecosystem functions, including nutrient cycling and provision of wildlife habitat, and have historical and cultural significance as sites of human habitation (van der Valk and Sklar 2002).

Tree island vegetation is one of the most sensitive components of the Everglades landscape to changes in regional hydrology, where extremes in marsh water levels can have serious consequences (Loveless 1959, Craighead 1971, 1984, McPherson 1973, Alexander and Crook 1984, Brandt et al. 2000, Sklar and van der Valk 2002a). Prolonged periods of high water may adversely affect the condition of tree island vegetation via death or dieback in flood-intolerant species. Similarly, persistent low water may create conditions of extreme fire risk, during which vegetation may be catastrophically damaged. Management-oriented changes in water-flow pattern in the Everglades have resulted in such hydrologic extremes, particularly in some of the Water Conservation Areas (WCA) north of Everglades National Park (ENP), where the number of tree islands has decreased (Schortemeyer 1980) and the vegetation on the existing islands has been altered (Wetzel 2002). Sklar and van der Valk (2002b) reported that tree island number declined 87% in WCA 2A between 1953 and 1995, and 61% in WCA 3 between 1940 and 1995.

The loss of tree islands and their associated historical, cultural, and biological values has raised awareness of the fragility of these habitats and stimulated a resurgence of interest in their study and preservation. Maintaining and/or restoring the health of tree islands (and other Everglades habitats) are components of the Comprehensive Everglades Restoration Plan (CERP), a multi-agency project designed to restore and enhance the freshwater resources and natural environments of southern Florida (USACE 1999). Consequently, there is a need within CERP for tools to assess the health of tree islands and to relate these measures to the hydrologic regime to which they are exposed. Flood tolerance and other ecophysiological characteristics of tree island tree species are a critical element in the formulation of these performance measures.

Flood tolerances of tree island tree species are not well-documented in the literature. Guerra (1997) and Jones et al. (1997) evaluated tree island vegetation in the southern Everglades after a period of prolonged high water in 1994–95 and noted its effects on individual tree and shrub species. Conner et al. (2002) reviewed flood tolerance in ten common tree island species based on flood impact studies conducted largely in bottomland forests in other parts of the southern United States. In the only reported greenhouse study, Gunderson et al. (1988) examined the effects of a range of hydrologic conditions, including flooding, on seedling growth and morphology in five Everglades tree island species. None of these studies attempted to assess physiological responses of plants, and between the latter two, only three subtropical hardwood forest species were examined compared to nine swamp forest species. In order to gain insight into species responses in the field, a controlled study combining morphological and physiological measurements on a broad range of hydric and mesic tree island species growing under different hydrologic regimes is needed.

Studies in other ecosystems have successfully used morphological (e.g., root and stem biomass, height, stem diameter, leaf area, comparative anatomy) and physiological parameters (e.g., chlorophyll fluorescence, leaf water potential, relative water content, gas exchange, stomatal conductance) to elucidate tree responses to water stress induced by flooding and/or drought (Regehr et al. 1975, Pereira and Kozlowski 1977, Ögren and Öquist 1985, Ewing 1996, Schmull and Thomas 2000, Anderson and Pezeshki 2001, Davanso et al. 2002). Previous studies have shown that flooding to or above the soil surface may result in a range of adverse responses, from diminished growth and photosynthesis to death, in seedlings and saplings (Keeley 1979, Pezeshki and Chambers 1986, Ewing 1996, Lopez and Kursar 1999, Schmull and Thomas 2000, Davanso et al. 2002) and trees (Broadfoot and Williston 1973, Harms et al. 1980, Vu and Yelenosky 1991, Ewing 1996, McKevlin et al. 1998).

The objectives of our study were twofold. First, we compared tree height, basal stem diameter, crown volume, plant condition, mortality, stomatal conductance, chlorophyll fluorescence, and leaf relative water content to assess growth, survival, and physiological performance in several common tree island tree species exposed to varying hydrologic conditions under shadehouse conditions. Second, we compared the relative flood tolerances of these species grown in the shadehouse to their observed distribution along the hydrologic gradient in tree islands under natural conditions.

We hypothesized that increased soil flooding would adversely affect the growth and physiological performance of plant species adapted to tree islands. We predicted that the adverse responses would be more pronounced and occur earlier in the tropical hardwood tree species compared to the swamp species, and the greatest effects would be seen under conditions of prolonged soil flooding compared to little or no soil flooding. We also expected that relative flood tolerances of the species tested in the shadehouse would reflect their observed distribution along the hydrologic gradient in tree islands of the southern Everglades.

METHODS

Species Studied

The names and distributions of the 12 tree species used in this study, all native to Florida, are listed in Table 1. Plant species are referred hereafter by their genus name. Seven swamp forest species were selected, all temperate in origin, except *Annona* and *Chrysobalanus*, which are largely tropical. In southern Florida, these species prefer wet habitats and are common elements of the seasonally flooded portions of tree islands. The remaining five upland forest species are broadly distributed in the American tropics, with southern Florida at the northern limit of their ranges. Within the Everglades, they can be found in the most elevated portions of the tree islands, commonly referred to as hardwood hammocks, as well as in other mesic forest sites. All 12 species are evergreen, with the exception of *Salix* (deciduous) and *Annona* and *Bursera* (semi-deciduous) (Tomlinson 1980).

Plant Acquisition and Experimental Design

During May and June of 2001, a minimum of 100 seedlings of each species was collected from tree islands in Shark Slough, ENP. Seedlings were transferred to small peat pots containing commercial organic potting soil and placed in a glasshouse. Eight weeks later, the plants were transferred to 26.5-L plastic pots (one plant per pot) containing garden soil (pH 6.4) and placed in a shadehouse that provided 50% full sun. After eight months of growth, the plants were transferred to inflatable swimming pools placed in the shadehouse in preparation for the flooding experiment. The experimental design was randomized complete block, with 12 species and 3 treatment combinations represented twice in each of four blocks. Plants were stratified among the three treatments according to height and randomly placed within blocks.

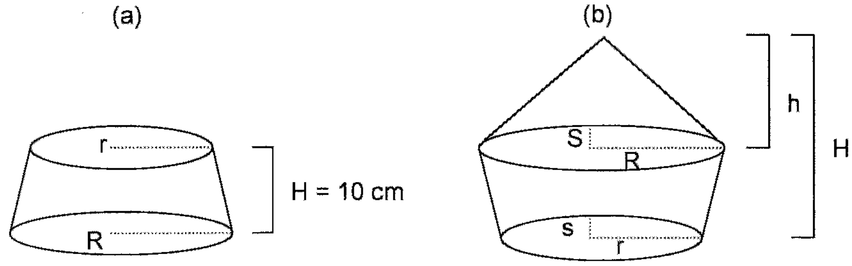
The three treatments – high flood (HF), low flood (LF), no flood (NF) – simulated the range of hydrologic conditions found on tree islands in Shark Slough as determined by topographic surveys. The bottoms of pots under HF and LF were positioned at 0, 27.1, and 57 cm, respectively, above the pool bottom. HF and LF represented realistic hydrologic regimes found at the lower and higher ends, respectively, of the tree island swamp forest environmental gradient, while NF represented hydrologic conditions found in the relatively higher tropical hardwood forest portion of a tree island.

Water levels, equal in all pools, were managed to simulate variation in mean weekly water depths in Shark Slough derived from hydrologic data recorded at U.S. Geological Survey ground-water

Table 1. List of species and their distributions. Species are grouped by their habitat preference in southern Florida.

Species (Common Name)[1]	Family	Distribution[2,3]
	Swamp Forest Species	
Annona glabra L. (Pond Apple)	Annonaceae	southern Florida, West Indies, Mexico to South America, West Africa
Chrysobalanus icaco L. (Coco Plum)	Chrysobalanaceae	southern Florida, West Indies, Mexico to South America, West Africa
Ilex cassine L. (Dahoon)	Aquifoliaceae	Virginia to southern Florida, Cuba, Bahama Islands
Magnolia virginiana L. (Sweetbay)	Magnoliaceae	eastern U.S. from Massachusetts to southern Florida
Morella cerifera (L.) Small (Wax Myrtle)	Myricaceae	Bermuda, Greater Antilles, Central America, eastern U.S. from New Jersey to southern Florida
Persea borbonia L. (Red Bay)	Lauraceae	Gulf and Atlantic States of U.S.
Salix caroliniana Michx. (Carolina Willow)	Salicaceae	southeastern U.S. from Virginia to southern Florida, Cuba
	Upland Forest Species	
Bursera simaruba (L.) Sarg. (Gumbo-Limbo)	Burseraceae	southern Florida, West Indies, Mexico to northern South America
Coccoloba diversifolia Jacq. (Pigeon Plum)	Polygonaceae	southern Florida, West Indies
Eugenia axillaris (Sw.) Willd. (White Stopper)	Myrtaceae	southern Florida, Bermuda, West Indies, Central America
Sideroxylon foetidissimum Jacq. (Mastic)	Sapotaceae	southern Florida, West Indies, Mexico, Belize
Simarouba glauca DC. (Paradise Tree)	Simaroubaceae	southern Florida, West Indies, Central America

[1] Wunderlin (1998),
[2] Little (1978),
[3] Tomlinson (1980).



$$V = \pi h\,(R^2 + Rr + r^2)\,/\,3 \qquad V = \pi RSh/3 + \pi\,(H-h)[RS + (R + S)(r + s)/4 + rs]\,/\,3$$

Figure 1. Tree crown volume diagrams and equations for calculating volumes of (a) conic frustums (used for crown depths greater to or equal to 30 cm) and (b) conic frustums and cones (used for crown depths less than 30 com). V=volume, R=radius at the widest base, S=corresponding perpendicular radius, r=radius at the other base, s=corresponding perpendicular radius, H=height of frustum and cone, h=height of cone.

hydrostation G620 (ENP) for the period 1990–1999. At the start of the experiment (April 2002), coinciding with the beginning of the growing season in southern Florida, pools were filled with piped water (pH 7.7) to a depth of 9.4 cm. Every seven days thereafter, water levels were adjusted by adding or removing water according to the appropriate weekly water depth. Following this schedule, under HF, water levels exceeded the bottoms of pots on day 1 and reached the soil surface at week 10. Under LF, the bottoms of pots first encountered the rising water at week 10 and the soil surface would have been inundated at week 28 had the experiment not been terminated prematurely (see below). Because pots would not be subjected to any flooding under NF, they were randomly placed in a single ring along the outer circumference of their assigned pools. Under NF, plants required regular watering, while all others were watered by hand whenever the soil surface appeared dry, especially in the earlier weeks of the experiment when water levels were still low. For logistical reasons associated with rapid growth in several species × treatment combinations (e.g., competition among individuals for light, outgrowing the shadehouse), the experiment was terminated after 25 weeks of treatment.

Mortality and Overall Plant Condition

Plant condition was determined by subjectively assessing the overall health and vigor of each individual tree and assigning a numerical score from 0 to 5. Visual observations on the conditions of stems and foliage (e.g., coloration, growth) and the occurrence of pests and disease (e.g., gall formation and other insect damage) were used to make each assessment. Individuals that displayed mostly green foliage, leafy stems, active stem growth, and a lack of pests and diseases were perceived as being healthy and vigorous and assigned a value of 5. Individuals that displayed yellowing leaves, premature leaf fall, little or no stem growth, and/or insect or disease damage were assigned a value of 1 to 4, depending on the extent of the observed condition or conditions. Dead individuals were assigned a value of 0. Plant condition was the only measurement used in this study in which all individuals were assessed weekly. Mean condition of surviving individuals was calculated weekly for each species and treatment, and mortality was tracked on the same interval. Plants that appeared dead were kept in their pools and observed for several more weeks; dead trees were removed from blocks.

Growth Measurements

Height, basal diameter, and crown volume of all individuals were measured during the week prior to treatment (week 0), then at 6, 12, 18, and 24 weeks after initiation of the experiment. Height from the top of the soil in each pot to the highest point (leaf, stem, or meristem) of the tree was recorded to the nearest cm. Basal diameter was measured using a plastic dial caliper to the nearest tenth of a millimeter. The diameter of single-stemmed trees was measured at a position along the stem approximately 2 cm above the soil surface; red paint was applied to the stem at this position to ensure consistency when measuring. For individual trees that produced multiple stems arising at or near soil level, as in *Morella* and *Salix*, the most vigorous stem was identified; this stem was measured throughout the study. Crown volume was estimated by modeling the tree crown as a series of conic frustums of 10 cm height and terminal cones of smaller height (Figure 1). Crown volumes of individuals with crown depths of at least 30 cm were measured by taking crown-width measurements at intervals of 10 cm along the stem and totaling the volume of each conic frustum (Figure 1a); volumes of conic frustums were then summed to estimate total crown volume. For individuals with crown depths of less than 30 cm, lengths of the basal and widest portions of the crowns, their perpendicular widths, and their distance to crown tops were measured (Figure 1b). Volumes of the conic frustum and cone were then summed to estimate total crown volume.

Physiological Measurements

Stomatal conductance, chlorophyll fluorescence, and leaf relative water content were measured, at weeks 3, 6, 12, 18, and 24. Four individuals from each species-treatment combination (one from each block) were selected for the measurements. Measurements were conducted in the shadehouse on young, fully expanded, intact, sun leaves. A different leaf on the same tree was selected each sampling week. We attempted to standardize measurements by taking data under sunny, dry conditions between the hours of 0900 and 1500, whenever possible.

A LI-1600 steady state porometer (LI-COR Biosciences, Lincoln, NE, USA) was used to measure conductance to water vapor. Attached leaves were inserted in the porometer and conductance was measured after 60 s.

Fluorescence yield, expressed in terms of the ratio of variable fluorescence to maximal fluorescence (F_v/F_m), was measured using an OS1-FL pulse modulated chlorophyll fluorometer (Opti-Sciences, Inc., Tyngsboro, MA, USA). Leaves were dark-adapted for 10 min before measurement.

To determine relative water content, two 6-mm-diameter discs were punched from a leaf and immediately weighed to obtain fresh weight (fw). Discs were then wrapped in saturated paper toweling and kept in small, sealed petri dishes in the lab at room temperature for 16–20 h and reweighed after blotting dry to obtain saturated weight (sw). Discs were then placed in an oven at 60 °C for 24 h and reweighed to obtain the dry weight (dw). Relative water content was calculated using the formula of J. Čatský (in Slavík 1974):

$$\text{Relative water content } (\%) = (\text{fw} - \text{dw})/(\text{sw} - \text{dw}) \times 100.$$

Statistical Analyses

A split-plot design approach was used to analyze the main effects of species, hydrologic treatment, and time. In standard repeated measures ANOVA, which resembles multivariate analysis of variance (MANOVA), a single missing value causes the entire subject to be omitted from analysis in a listwise deletion procedure. When missing values are common, split-plot ANOVA is an effective alternative approach to analyze repeated measures data (Maceina et al. 1994). In our study, missing values resulted primarily from the mortality of individual plants. In addition, on rare occasions, physiological data could not be collected because of equipment malfunction, or in the aftermath of leaf shedding events or herbivore outbreaks that affected few species.

In preliminary analyses, the effect of Block (the four pools) on all six parameters was found to be non-significant; replicates for each species-treatment combination were therefore pooled together for subsequent analyses. The measurements of stomatal conductance for all species during week 6 were eliminated from the analysis of variance due to a malfunction of the porometer. For all dependent variables, when 'F' tests for main effects in the split-plot ANOVA were found to be significant, multiple comparison tests among treatments were conducted for each species-week combination using the Fisher's least significant difference (LSD).

Trends in plant growth and physiology were examined in more detail in four taxa that represented groups of species with similar response to the three treatments. To define these groupings, we used agglomerative cluster analysis (Goodall 1973), with Euclidean distance used as a dissimilarity measure and Ward's linkage method of calculating relation among species. The analysis was performed on six composite variables obtained by applying Principal Component Analysis (PCA) to response data collected throughout the experiment. Data included periodic mean values for each species for the three morphological variables, stomatal conductance, chlorophyll fluorescence, and overall plant condition, as well as week of occurrence of first mortality in the collection of all seedlings from a given treatment. Responses to the HF and LF treatments were standardized by dividing periodic mean values for each species by their values under the NF treatment.

For each of the four representative species, coefficients of response curves generated by individual plants were analyzed to test whether treatments differed in structural and physiological responses to flooding treatments over time (Meredith and Stehman 1991, Carlton and Bazzaz 1998). For each individual, linear, quadratic, and cubic coefficients of response curves were obtained by calculating weighted sums of the repeated measurements for structural and physiological variables using the relevant contrast coefficients as the weights

(Gurevitch and Chester 1986). Contrast coefficients for morphological variables measured at regular intervals were obtained from Keppel (1973: Table C-2). For physiological variables, which were measured at unequal intervals, linear and quadratic coefficients were calculated using methods described in Keppel (1973). Unequal intervals due to the removal of outliers and missing values (e.g., stomatal conductance measurements at week 6) were handled in the same way. Treatment effects on the response curve coefficients were then assessed by one-way ANOVA. Results were considered statistically different at the $p < 0.05$ level. Prior to using ANOVA, assumptions of normality and homogeneity of variance were tested by the Kolmogrov-Smirnov and Levene's tests, respectively. Except where noted, these assumptions were satisfied.

RESULTS

Flooding treatment had significant ($p < 0.001$) effects on height, basal diameter, and crown volume of the twelve plant species considered over the 25 week study period (Table 2). In eight of 12 species, mean height, basal diameter, and crown volume were greater in LF than in HF and NF treatments. All second- and third-order interactions were significant for the three morphological variables and for chlorophyll fluorescence and stomatal conductance. However, only first order effects were significant for relative water content. Because the preponderance of interaction effects indicated that species were reacting to flooding treatment differently over time, their responses were analyzed separately.

The cluster analysis produced four groups of species at the 50% information remaining level (Figure 2): two groups of swamp forest species, one group of upland forest species, and an intermediate group combining both swamp and upland species. The swamp species group of *Annona* and *Salix* (Swamp Group 1) was linked to a second, larger swamp group comprising *Morella, Chrysobalanus, Magnolia*, and *Ilex* (Swamp Group 2). Four upland species, *Coccoloba, Bursera, Simarouba*, and *Sideroxylon*, formed a single group (Upland Group). The fifth upland species, *Eugenia*, combined with the swamp species *Persea* in a grouping (Intermediate Group) that was most closely aligned with the Upland Group. The results that follow are presented in terms of these groups.

Tree Mortality

Under HF, all four species of the Upland Group and *Eugenia* of the Intermediate Group showed mortalities between 50 and 100%, while *Magnolia* and *Ilex* of Swamp Group 2 and *Persea* of the Intermediate Group showed mortalities between 25 and 40% (Table 3). Seven of these species first showed losses of individuals between weeks 13 and 16 (only *Sideroxylon* showed some mortality at week 13) under this treatment. Mortality was not observed in *Eugenia* until week 19, the latest for any

Table 2. F-statistics from split-plot ANOVA for repeated measures data testing morphological and physiological responses to three hydrologic treatments in twelve species. Number of repeated measures (t) = 5 and number of replicates per species × treatment combination (n) = 8 for height (HT), basal diameter (BD), and crown volume (CV); t = 5 & n = 4 for chlorophyll fluorescence (CF) and relative water content (RWC); and t = 4 and n = 4 for stomatal conductance (SC). * $p<0.05$; ** $p<0.01$, *** $p<0.001$. Degrees of freedom (df) are given in parentheses.

Source	HT	BD	CV	SC	CF	RWC
Species	79.7***	177.9***	50.7***	14.7***	12.0***	10.7***
	(11,256)	(11,256)	(11,260)	(11,135)	(11,119)	(11,120)
Treatment	19.9***	13.1***	30.1***	5.8**	59.7***	3.8*
	(2,258)	(2,257)	(2,265)	(2,149)	(2,126)	(2,122)
Species*Treatment	2.5***	2.9***	3.3***	2.8***	5.2***	0.3
	(22,255)	(22,255)	(22,259)	(22,125)	(22,117)	(22,118)
PlantID (Species*Treatment)	5.8***	5.8***	2.5***	1.4*	0.9	1.0
	(252,948)	(252,948)	(252,948)	(107,261)	(108,395)	(108,364)
Time	966.8***	818.6***	297.1***	20.7***	28.4***	35.3***
	(4,948)	(4,948)	(4,948)	(3,261)	(4,395)	(4,364)
Species*Time	21.3***	50.7***	21.1***	4.7***	2.8***	1.1
	(44,948)	(44,948)	(44,948)	(33,261)	(44,395)	(44,364)
Treatment*Time	35.0***	22.1***	30.8***	9.3***	8.7***	0.7
	(8,948)	(8,948)	(8,948)	(6,261)	(8,395)	(8,364)
Species*Treatment*Time	3.2***	5.6***	3.4***	1.9***	1.9***	1.0
	(85,948)	(85,948)	(85,948)	(63,261)	(85,395)	(85,364)

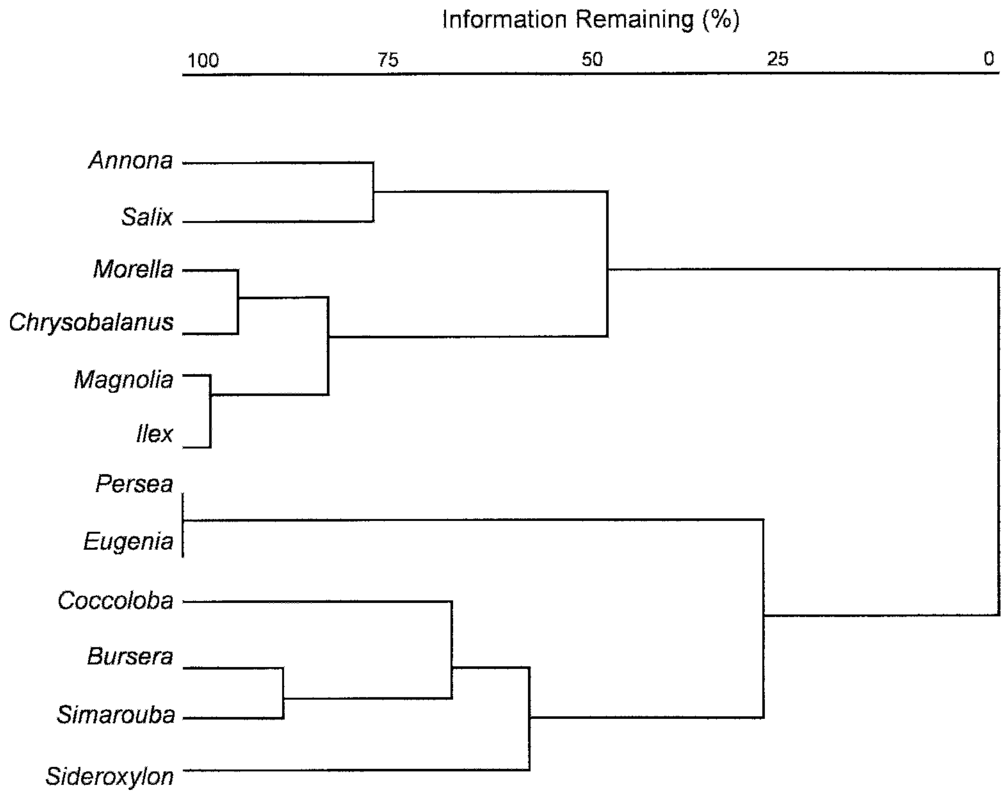


Figure 2. Dendogram produced from agglomerative cluster analysis by applying PCA to plant response data.

species. Only *Simarouba, Sideroxylon*, and *Bursera* of the Upland Group showed some mortality under LF (Table 3); these species had the highest mortality under HF as well. Under LF, *Simarouba* and *Bursera* showed their earliest mortalities at weeks 15 and 17, respectively, values comparable to the first mortalities seen in the majority of species under HF. The single mortality seen in *Sideroxylon* occurred at week 24. Four species, *Annona* and *Salix* (Swamp Group 1) and *Morella* and *Chrysobalanus* (Swamp Group 2), did not experience any mortality under HF and LF. No mortality occurred in any species under NF.

Table 3. Tree mortality after 25 weeks of experimental treatments. Values are percentage of dead individuals. Numbers in parentheses are week of earliest mortality observed. Species are arranged from highest to lowest mortality under HF. *Annona, Chrysobalanus, Morella*, and *Salix* did not experience a single mortality. Treatment: HF, high flood; LF, low flood; NF, no flood.

	Treatment		
Species	HF	LF	NF
Simarouba	100 (15)	25 (15)	
Sideroxylon	100 (13)	13 (24)	
Bursera	75 (15)	50 (17)	
Coccoloba	50 (14)		
Eugenia	50 (19)		
Magnolia	38 (16)		
Ilex	25 (16)		
Persea	25 (16)		

Overall Plant Condition

Under HF, mean overall condition increased in most species within the first eight weeks, followed by a period of no change, then a decline (Figure 3). Compared to the Upland and Intermediate Groups, both Swamp Groups were generally less adversely affected in terms of the onset and rate of this decline. Small declines in overall condition were observed as late as weeks 22 and 18 in *Annona* and *Salix*, respectively. Greater declines were seen in *Morella, Chrysobalanus*, and *Magnolia* of Swamp Group 2 and *Eugenia* and *Persea* of the Intermediate Group, commencing at weeks 19, 14, 12, 13, and 11, respectively. All four species of the Upland Group and *Ilex* of Swamp Group 2 experienced the largest declines. The onset of declining condition in these species occurred at weeks 9–10, when water levels first inundated the soil surface in pots. Yellowing of leaves (widespread in *Magnolia*), premature leaf fall (notable in *Ilex* and *Simarouba*), and insect herbivory (various species, most notably *Coccoloba, Persea*, and *Salix*) were the prevalent health problems affecting overall condition under this treatment.

Under LF, seven species experienced a decline in mean overall condition over time (Figure 3). Compared to HF, the onset of these declines occurred earlier in *Magnolia*, at the same time in *Annona* and *Bursera*, and later in *Coccoloba*, *Eugenia, Sideroxylon*, and *Simarouba*. Among the remaining species, all of which were from the two swamp groups (except *Persea* of the Intermediate Group), mean overall condition under LF either increased or did not change over time. Insect herbivory was the most commonly observed health problem affecting overall condition under this treatment.

Growth Responses

Crown volume, tree height, and basal diameter responses were similar; therefore, only the first is presented here (Figure 4). Crown volumes in *Annona* (Figure 4a) and *Salix* of Swamp Group 1 increased throughout the study under all three treatments. In *Annona*, the treatments elicited significantly different linear ($F_{2,21}$ = 9.77, p = 0.001) and quadratic ($F_{2,21}$ = 4.40, p = 0.025) growth trends (Table 4). In this species, crown volumes did not differ among the three treatments through the first 12 weeks, but there was an acceleration of growth under LF after week 12 (week 18 in *Salix*), resulting in a difference in growth trends under LF and the other two treatments (Table 4). At the end of the study, crown volumes in *Annona* under HF and NF did not differ significantly.

Chrysobalanus, representing Swamp Group 2, was similar to *Annona* in its crown-volume response, although linear growth trends under both LF and NF were significantly ($F_{2,21}$ = 7.33, p = 0.004; LSD pairwise tests, $p < 0.05$) greater than under HF (Figure 4b). Crown volume under LF and NF continued to increase after week 12, when growth under HF started to slow down, resulting as well in a significantly different ($F_{2,21}$ = 8.04, p = 0.003) quadratic trend (Table 4). At the end of the study, crown volume in *Chrysobalanus* under NF did not differ significantly from HF or LF. Among the remaining species in Swamp Group 2 (not shown), *Magnolia* and *Morella* showed similar growth trends to *Chrysobalanus. Ilex* differed, however, experiencing a decline in crown volume under HF after week 12.

Crown volumes in *Persea*, representing the Intermediate Group, increased throughout the study under all three treatments, except for a decline under HF after week 18 (Figure 4c). Differences in linear and quadratic trends among treatments were highly significant in this species (Table 4). The growth trend was similar (roughly linear) under LF and NF, with slight acceleration starting at weeks 12 and 6, respectively. Under HF, the growth trend was quadratic (U-shaped) due to an increase in crown volume through week 18 followed by a decrease. As in Swamp Group 2, crown volumes under LF and NF in *Persea* (and *Eugenia*, also of the Intermediate Group) did not differ throughout the study.

Representing the Upland Group, *Bursera* showed an increase in crown volumes under LF and NF throughout the study but experienced a decrease under HF after week 6 (Figure 4d). In this species, the linear growth trend differed significantly ($F_{2,11}$ = 6.76, p = 0.012) among treatments (Table 4). However, despite an apparent distinction in growth trends among three treatments – an upward trend under LF and NF and an inverted-U shaped trend under HF (Figure 4d) – the quadratic terms did not differ significantly ($F_{2,11}$ = 1.181, p = 0.209) among treatments (Table 4), in part because of low statistical power due to mortality and loss of replication (only three individuals of *Bursera* survived under both HF and LF). The remaining species of this group (not shown) – *Coccoloba, Sideroxylon, Simarouba* – showed similar responses. Like Swamp Group 2 and the Intermediate Group, crown volumes under LF and NF in the Upland Group did not differ throughout the study.

Physiological Responses

Mean leaf relative water content showed little or no change throughout the study. Because stomatal conductance differed significantly among treatments in most species (chlorophyll fluorescence differed in fewer species), we chose to present only stomatal conductance responses here (Figure 5). Most species showed a decreasing trend in stomatal conductance values under HF over time. However, the week when conductance under HF was significantly different from that under LF and NF differed in the four groups of plants.

In *Annona*, representing Swamp Group 1, flooding treatment did not have a significant (Repeated-measures ANOVA: $F_{6,21}$ = 1.554, p = 0.210) impact on physiological performance. In this species, mean stomatal conductance decreased under HF and NF over the study period, while under LF, it peaked at week 12 before declining (Figure 5a). Mean stomatal conductance under LF at week 12 was significantly higher than HF and NF. However, neither the linear nor the quadratic trends differed significantly among treatments (Table 4). Stomatal conductance values under HF for *Salix* (not shown) were the highest of all species after week 3.

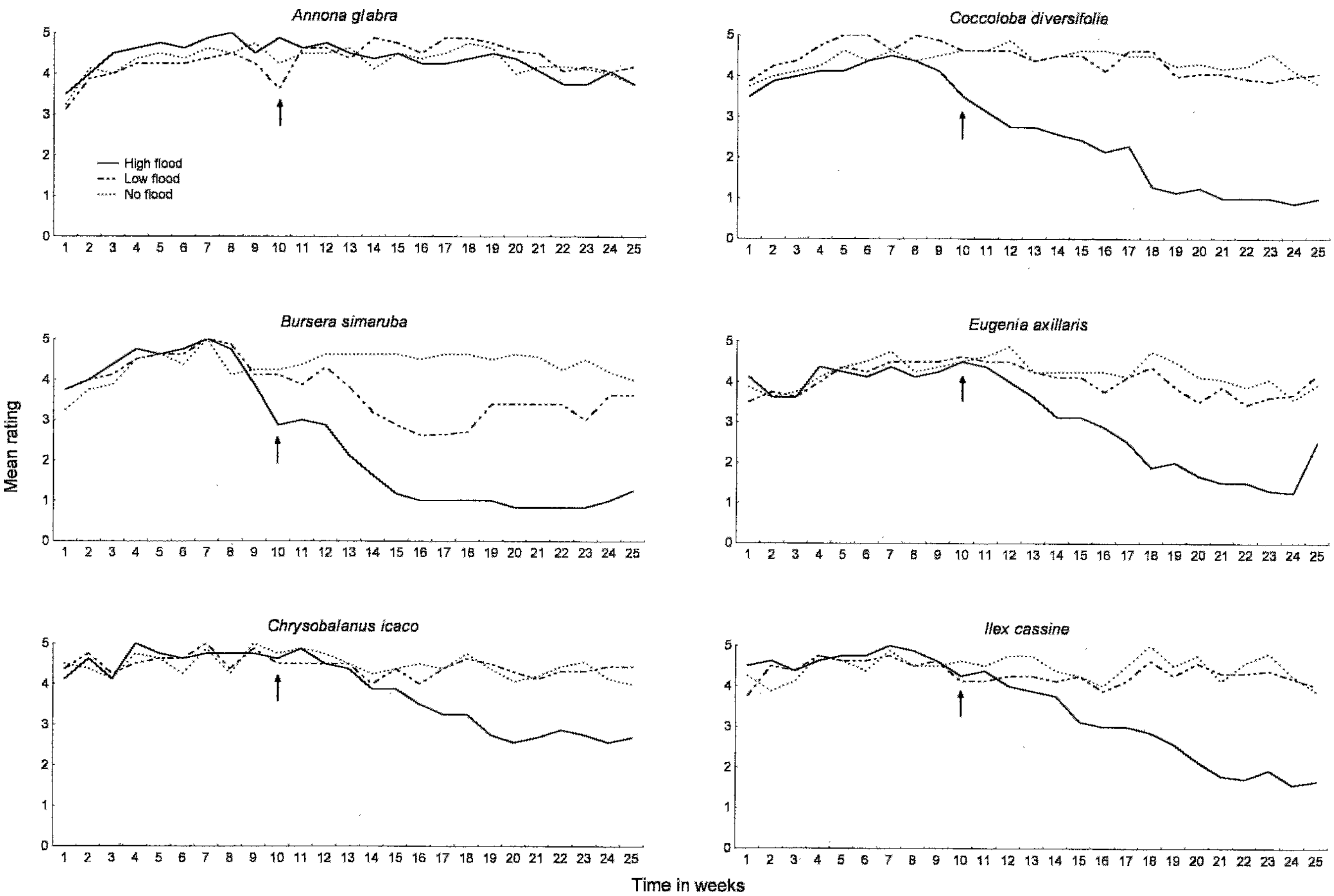


Figure 3. Mean weakly overall condition ratings under the high, low, and no flood treatments, for the 25 week experimental period, arranged by species. Numerical ratings ranged from '0' (representing a dead individual) to '5' (a healthy individual). The arrow indicates when water levels first inundated the soil surface in pots under the high flood treatment at week 10.

In *Chrysobalanus*, representing Swamp Group 2, physiological responses to flooding treatments varied broadly over the study period, with the linear trend in mean stomatal conductance differing significantly among the treatments (Table 4). Mean stomatal conductance was lowest under HF at week 18. In contrast, conductance was highest under LF and NF during week 18 and decreased thereafter (Figure 5b). *Ilex* and *Magnolia* (not shown) showed similar responses, although the decline under HF occurred earlier, at week 12, in the latter species. Stomatal conductance under HF for *Morella* was the highest of all species in Swamp Group 2 after week 12 and was slightly greater than *Salix* of Swamp Group 1 at week 24.

Persea (Figure 5c) and *Eugenia* of the Intermediate Group were most similar to Swamp Group 2, with mean stomatal conductance under HF significantly lower than under LF and NF (Repeated-measures ANOVA: $F_{6,27} = 3.815$, $p = 0.007$; LSD pairwise test: $p < 0.05$). Trend analysis in *Persea* indicated that only the linear term differed significantly ($F_{2,9} = 6.42$, $p = 0.019$) among treatments (Table 4). At week 3, mean stomatal conductance did not differ among treatments; differences first became evident at week 12, and were apparent at weeks 18 and 24.

Bursera (Figure 5d) of the Upland Group showed poor physiological performance, as indicated by the lowest stomatal conductance values under HF of any species during weeks 12 through 24. In this species, stomatal conductance under NF decreased from week 3 through week 24. At week 3, stomatal conductance under LF was significantly lower than under HF or NF (One-way ANOVA: $F_{2,9} = 15.4$, $p = 0.001$; LSD pairwise test: $p < 0.003$ and 0.001, respectively) but peaked under this treatment during week 12 before decreasing. By the end of the experiment, there was no difference in stomatal conductance among treatments. Except in the no-flooding treatment, few *Bursera* individuals survived to the end of the experiment, precluding trend analysis. The responses of *Sideroxylon, Coccoloba*, and *Simarouba* to the HF treatments (not shown)

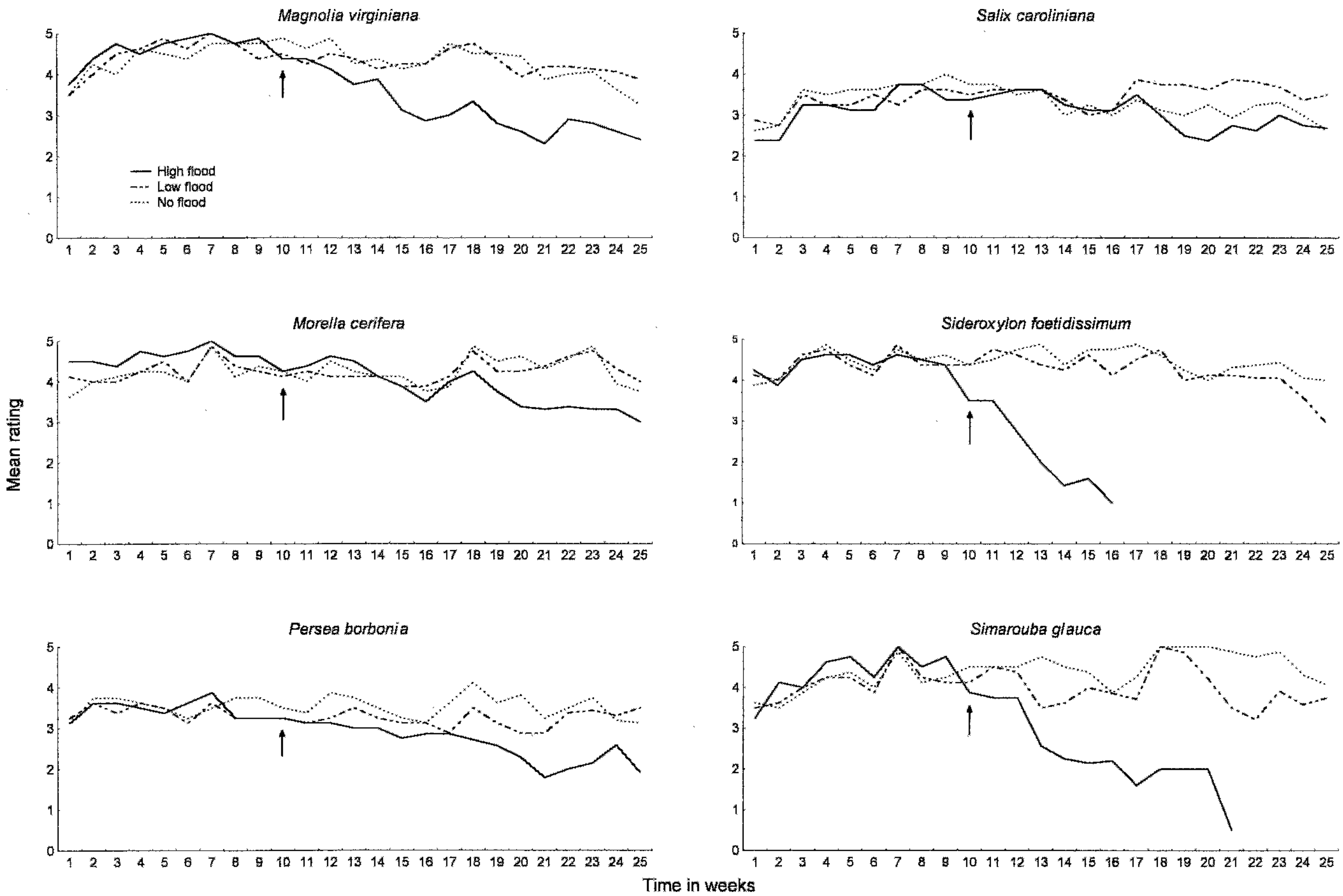


Figure 3. Continued.

were similar to *Bursera* (i.e., an early, precipitous decline in stomatal conductance), but in these species, both LF and NF decreased slowly or remained stable throughout.

DISCUSSION

Of the eight parameters used in this study to compare flooding responses, only relative water content failed to differentiate flood-tolerant and flood-intolerant species. We have found no previous studies in which relative water content was used as a measure of flood stress, although it has been used to study the effects of drought in agricultural species (Teulat et al. 1997, Liu and Stutzel 2002).

Fifteen weeks of soil surface flooding (HF treatment) generally resulted in a reduction of overall health, growth, and stomatal conductance in the species studied, supporting our hypothesis that flooding would diminish performance of upland and swamp forest tree species growing in tree islands. These declines were usually more precipitous in the former group, in which adverse responses in plants were observed as early as two weeks preceding inundation of the soil surface. However, even the swamp forest species showed reductions in most of the study parameters under HF, generally commencing after inundation of the soil surface. In contrast, the greatest tree growth and physiological activity for most species occurred under the saturated soil conditions of the LF treatment, a response similar to the large growth increases observed in bottomland hardwood forest species in the southern United States subjected to rising water levels (Hosner and Boyce 1962, Broadfoot and Williston 1973). Flooding can accelerate tree growth under certain conditions, when timing and duration are not injurious (Kozlowski 1982, Kozlowski and Pallardy 2002).

By averaging the standardized means (i.e., HF/NF ratio) for all growth and physiological variables and overall plant condition at week 24 for each species, we can rank the species tested in order of decreasing flood tolerance as follows: *Annona* > *Morella* > *Salix* > *Chrysobalanus* > *Magnolia* > *Ilex* > *Persea* > *Eugenia* > *Coccoloba* > *Bursera* > *Simarouba* > *Sideroxylon*. The presence of structural and metabolic adaptations to anoxia may account for the

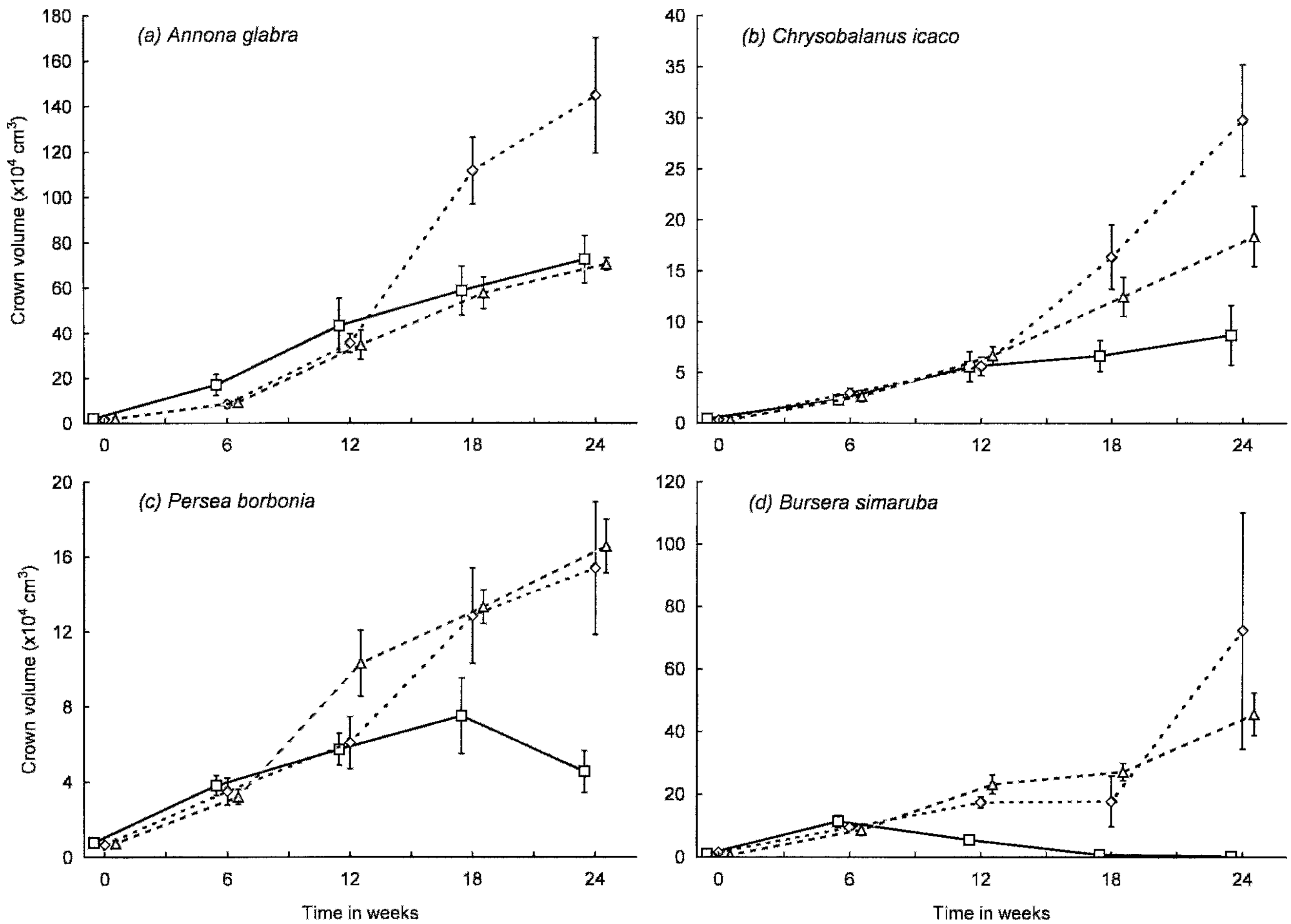


Figure 4. Mean tree crown volumes (± 1 SE) under the high, low, and no flood treatments, at five sampling times, for four representative species. ▭ High flood; ◇ Low flood; △ No flood.

differential flood tolerances observed. Although species were not examined for specific adaptations in this study, adventitious roots, known to occur in a large number of flood-tolerant species (Gill 1970, Kozlowski et al. 1991, Armstrong et al. 1994, Vartapetian and Jackson 1997), were observed only in the seven swamp forest species under HF. Aerenchyma tissue also develops in woody and herbaceous wetland species (Smirnoff and Crawford 1983, Kozlowski et al. 1991, Vartapetian and Jackson 1997), including *Annona* (Zotz et al. 1997) and *Salix* (Jackson and Attwood 1996). *Salix* roots and stems may also develop hypertrophied lenticels (Pereira and Kozlowski 1977, Jackson and Attwood 1996) which further facilitate oxygen uptake and transport in plants.

Structural adaptations can contribute to the maintenance of stomatal conductance during flooding and its recovery afterward (Kozlowski 1984, Pezeshki and Chambers 1986, Sojka 1992, McKevlin

Table 4. Summary of ANOVA results showing linear and quadratic trends in treatment effects (df = 2) on crown volume and stomatal conductance in four species.

	Crown volume					Stomatal conductance				
		Linear		Quadratic			Linear		Quadratic	
Species	df (error)	F	*p*	F	*p*	df (error)	F	*p*	F	*p*
Annona	21	9.77	0.001	4.40	0.025	8	3.59	0.077	0.95	0.427
Bursera	11	6.76	0.012	1.81	0.209	3	2.01	0.280	9.83	0.048
Chrysobalanus	21	7.33	0.004	8.04	0.003	8	7.92	0.013	1.24	0.339
Persea	19	6.27	0.008	7.37	0.004	9	6.42	0.019	0.84	0.463

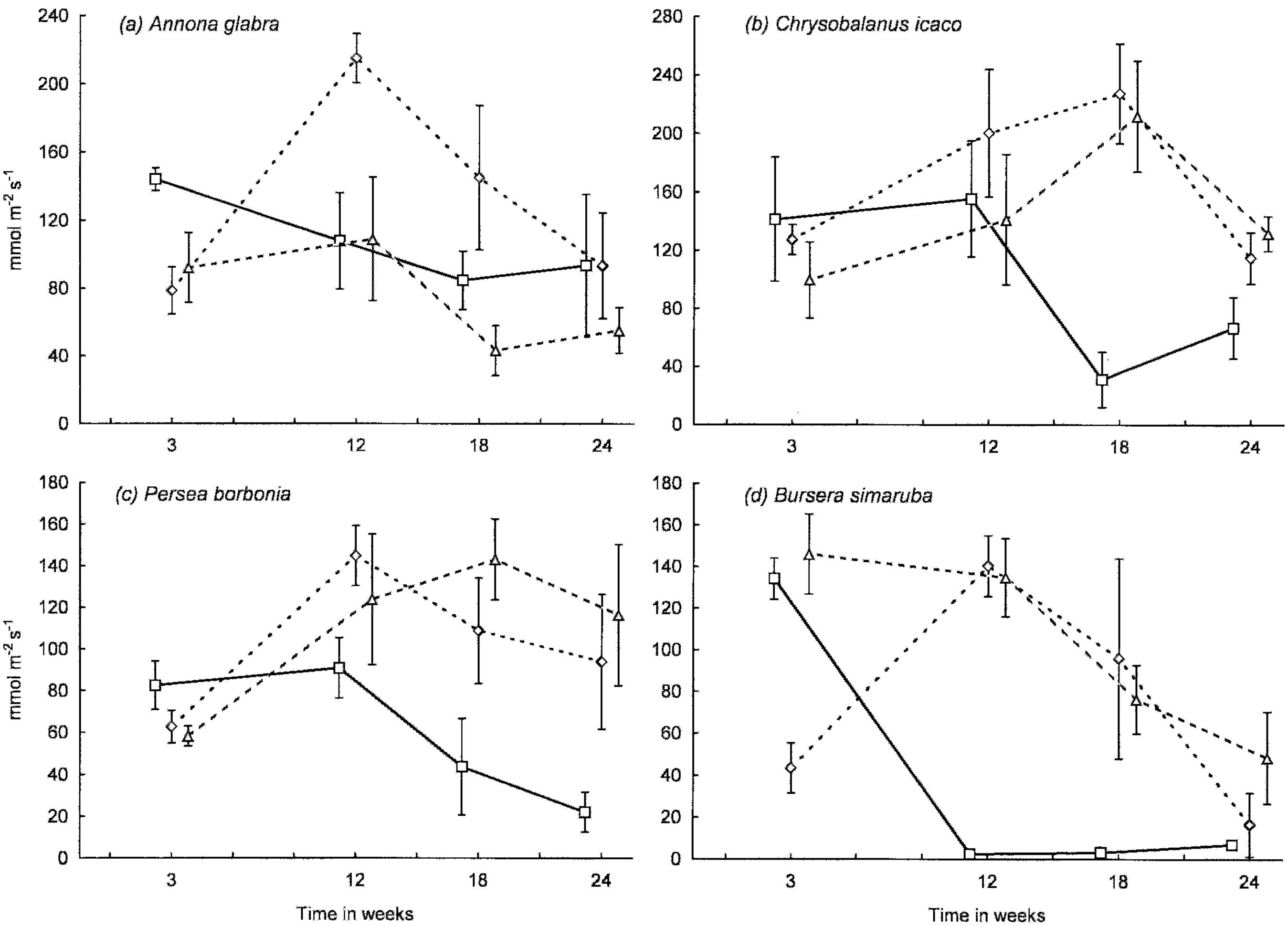


Figure 5. Mean stomatal conductance (± 1 SE) under the high, low, and no flood treatments, at four sampling times, for four representative species. ▭ High flood; ◇ Low flood; △ No flood.

et al. 1998). This may explain the relatively higher stomatal conductance values seen throughout the study in some of the swamp forest species, most notably *Salix*, *Morella*, and to some extent, *Annona*, all of which formed extensive adventitious roots under HF. The less extensive adventitious root systems that developed in the remaining swamp species under HF may have resulted in the relatively lower stomatal conductance values observed in these species. McKevlin et al. (1998) also reported diminished stomatal conductance in flood-tolerant species growing in saturated soil. The early, precipitous declines in stomatal conductance shown by the five upland forest tree species were expected, although this contrasts with a study by Lopez and Kursar (1999), who did not observe sharp reductions in stomatal conductance in three upland tree species in Panama during 90 days of inundation.

The lower survival and relatively poor growth and physiological performance seen under HF in the upland species tested is not surprising, given that they are not found in regularly inundated sites. These and many other important tropical species occurring in upland sites of the region are adapted to seasonally-dry conditions and commonly inhabit thin soils that form directly on limestone (Craighead 1971, Tomlinson 1980, Armentano et al. 2002). Consequently, they are potentially exposed to seasonal drought, although in southern Florida, some may be rooted in ground water. Whether the ability to tolerate or avoid drought among upland tree species is related to the ability to tolerate shoot water stress induced by soil anoxia is not certain. In a study of tropical dry forest trees, Brodribb et al. (2003) found that *Bursera simaruba*, a species that responds to drought in southern Florida by shedding its leaves and avoiding drought, was especially vulnerable to xylem cavitation (hence reduced water conductivity). We found this species to be extremely sensitive to flooding. Specific information on the drought tolerance of the other upland species in our study, however, is lacking. Our findings are in marked contrast to a similar study involving seedlings of three upland tropical tree species subjected to an experimental flooding regime. Lopez and Kursar (1999) reported no mortality or visible leaf damage after 90 days of inundation and concluded that most tropical tree species are relatively tolerant of flooding, yet do not become established in inundated habitats.

The relative flood tolerances of the 12 test species grown under simulated flooding regimes for 25 weeks are roughly related to their observed distribution along the natural hydrologic gradient in tree islands of the southern Everglades. Other studies on flood tolerance in bottomland forest tree species of the United States have suggested a similar relationship between flood tolerance and distribution patterns along flooding gradients (Hosner 1960, Hosner and Boyce 1962, Dickson et al. 1965, Hook and Brown 1973, Larson et al. 1981, McKnight et al.1981, Mitsch and Rust 1984). In this study, flood tolerance rankings of species under natural field conditions were inferred by calculating mean water-level optima for each species from vegetation surveys in plots on three Shark Slough tree islands; using a weighted averaging calibration and regression procedure (Birks et al. 1990), the local hydrologic regime was projected from long-term water-level records. Species rankings under natural field conditions differed little from those in the shadehouse (e.g., *Chrysobalanus* was less flood-tolerant in the tree island, *Simarouba* was more flood-sensitive in the shadehouse). Age and size of plants, as well as water quality, factors known to affect flood tolerance in plants (Gill 1970, Kozlowski et al. 1991), may have accounted for some of the discrepancies in the rankings. The results of the few other studies of flood tolerances in Everglades tree island tree species (Gunderson et al. 1988, Guerra 1997) reveal similar rankings of species as this study.

Extrapolated to the natural setting of a tree island, the results of this study suggest that increasing water depths and durations may have a beneficial yet temporary effect on most hardwood hammock species; prolonged soil surface inundation will hasten reduction in tree growth and lead to death of these species. The more flood-intolerant species of the surrounding swamp forest (*Persea, Magnolia, Ilex*) can be expected to respond similarly, although a delay in the onset of reduced growth and perhaps death would be expected. We terminated our study before it was determined how the most flood-tolerant swamp species (*Annona, Salix, Morella*) would respond to increasingly higher and longer flood waters. This knowledge can allow us to manage species composition on tree islands with water level and may allow early warning of flooding stress in tree islands. With restoration plans under CERP anticipating modifications in hydrologic conditions throughout the Everglades, predicting responses of tree island species to these changes becomes critical.

Knowledge of relative species tolerances, together with ancillary information such as genotypic variation (McKevlin et al. 1998), particularly in species distributed along a soil moisture gradient (Keeley 1979), will become important in selecting suitable species to include in projects aimed at restoring destroyed or degraded tree islands and creating new ones, a CERP objective. For example, Wallace et al. (1996) assessed flood tolerance and seedling growth and survival under varying soil conditions and developed guidelines for the use of nine tree species in wetland restoration and creation in Florida. Several of the species reported in our study have never been evaluated for flood tolerance until now.

ACKNOWLEDGMENTS

This project received funding through the U.S. Department of the Interior's Critical Ecosystem Studies Initiative (CESI). The authors gratefully acknowledge the assistance of the following Florida International University staff for their valuable contributions toward the successful completion of this study: Josh Walters, Darcy Stockman, Debbie Nolan, Pablo Ruiz, Hillary Cooley, and Dave Reed.

This is contribution # 331 of the Southeast Environmental Research Center at Florida International University.

LITERATURE CITED

Alexander, T. R. and A. G. Crook. 1984. Recent vegetational changes in South Florida. p. 199–210. *In* P. J. Gleason (ed.) Environments of South Florida - Present and Past II, second edition. Miami Geological Society, Coral Gables, FL, USA.

Anderson, P. H. and S. R. Pezeshki. 2001. Effects of flood preconditioning on responses of three bottomland tree species to waterlogging. Journal of Plant Physiology 158:227–233.

Armentano, T. V., D. T. Jones, M. S. Ross, and B. W. Gamble. 2002. Vegetation pattern and process in tree islands of the southern Everglades and adjacent areas. p. 225–282. *In* F. H. Sklar and A. van der Valk (eds.) Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Armstrong, W., R. Brändel, and M. B. Jackson. 1994. Mechanisms of flood tolerance in plants. Acta Botanica Neerlandica 43:307–358.

Birks, H. J., J. M. Line, S. Juggins, A. C. Stevenson, and C. J. F. ter Braak. 1990. Diatoms and pH reconstruction. Philosophical Transactions of the Royal Society of London (Series B) 327:263–278.

Brandt, L. A., K. M. Portier, and W. M. Kitchens. 2000. Patterns of change in tree islands in Arthur R. Marshall Loxahatchee National Wildlife Refuge from 1950 to 1991. Wetlands 20:1–14.

Broadfoot, W. M. and H. L. Williston. 1973. Flooding effects on southern forests. Journal of Forestry 71:584–587.

Brodribb, T. J., N. M. Holbrook, E. J. Edwards, and M. V. Gutierrez. 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. Plant, Cell and Environment 26:443–450.

Carlton, G. C. and F. A. Bazzaz. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecological Monographs 68:99–120.

Conner, W. H., T. W. Doyle, and D. Mason. 2002. Water depth tolerances of dominant tree island species: what do we know? p. 207–223. *In* F. H. Sklar and A. van der Valk (eds.) Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Craighead, F. C. 1971. The Trees of South Florida, Volume I - The Natural Environments and Their Succession. University of Miami Press, Coral Gables, FL, USA.

Craighead, F. C. 1984. Hammocks of South Florida. p. 191–198. *In* P. J. Gleason (ed.) Environments of South Florida - Present and Past II, second edition. Miami Geological Society, Coral Gables, FL, USA.

Davanso, V. M., L. A. de Souza, M. E. Medri, J. A. Pimenta, and E. Bianchini. 2002. Photosynthesis, growth and development of *Tabebuia avellanedae* Lor. ex Griseb. (Bignoniaceae) in flooded soil. Brazilian Archives of Biology and Technology 45: 375–384.

Davis, J. H. 1943. The natural features of Southern Florida, especially the vegetation, and the Everglades. Florida Geological Survey, Tallahassee, FL, USA. Geological Bulletin No. 25.

Dickson, R. E., J. F. Hosner, and N. W. Hosley. 1965. The effects of four water regimes upon the growth of four bottomland tree species. Forest Science 11:299–305.

Ewing, K. 1996. Tolerance of four wetland plant species to flooding and sediment deposition. Environmental and Experimental Botany 36:131–146.

Gill, C. J. 1970. The flooding tolerance of woody species – a review. Forestry Abstracts 31:671–688.

Goodall, D. W. 1973. Numerical classification. Handbook of Vegetation Science 5:107–156.

Guerra, R. E. 1997. Impacts of the high water period of 1994–95 on tree islands in Water Conservation Areas. p. 47–58. *In* T. Armentano (ed.) Ecological Assessment of the 1994–1995 High Water Conditions in the Southern Everglades. South Florida Management and Coordination Working Group, Miami, FL, USA.

Gunderson, L. H., J. R. Stenberg, and A. K. Herndon. 1988. Tolerance of five hardwood species to flooding regimes. p. 119–132. *In* D. A. Wilcox (ed.) Interdisciplinary Approaches to Freshwater Wetlands Research. Michigan State University Press, East Lansing, MI, USA.

Gurevitch, J. and S. T. Chester. 1986. Analysis of repeated measures experiments. Ecology 67:251–255.

Harms, W. R., H. T. Schreuder, D. D. Hook, C. L. Brown, and F. W. Shropshire. 1980. The effects of flooding on the swamp forest in lake Ocklawaha, Florida. Ecology 61:1412–1421.

Harper, R. M. 1927. Natural resources of southern Florida. Eighteenth Annual Report. Florida State Geological Survey, Tallahassee, FL, USA.

Harshberger, J. W. 1914. The vegetation of south Florida south of 27° 37′ north, exclusive of the Florida Keys. Transactions of the Wagner Free Institute of Science of Philadelphia 7(3):51–189.

Hook, D. D. and C. L. Brown. 1973. Root adaptations and relative flood tolerance of five hardwood species. Forest Science 19:225–229.

Hosner, J. F. 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. Forest Science 6:246–251.

Hosner, J. F. and S. G. Boyce. 1962. Tolerance to water saturated soil of various bottomland hardwoods. Forest Science 8:180–186.

Jackson, M. B. and P. A. Attwood. 1996. Roots of willow (*Salix viminalis* L.) show marked tolerance to oxygen shortage in flooded soils and in solution culture. Plant and Soil 187:37–45.

Jones, D. T., T. V. Armentano, S. Snow, and S. Bass. 1997. Evidence for flooding effects on vegetation and wildlife in Everglades National Park, 1994–1995. p. 31–45. *In* T. V. Armentano (ed.) Ecological Assessment of the 1994–1995 High Water Conditions in the Southern Everglades. South Florida Management and Coordination Working Group, Miami, FL, USA.

Keeley, J. E. 1979. Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica*. Ecological Monographs 49:89–108.

Keppel, G. 1973. Design and Analysis: A Researcher's Handbook. Prentice Hall Inc., Englewood Cliffs, NJ, USA.

Kozlowski, T. T. 1982. Water supply and tree growth. II. Flooding. Forestry Abstracts 43:145–161.

Kozlowski, T. T. 1984. Plant responses to flooding of soil. Bioscience 34:162–167.

Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The Physiological Ecology of Woody Plants. Academic Press, London, UK.

Kozlowski, T. T. and S. G. Pallardy. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Botanical Review 68:270–334.

Larson, J. S., M. S. Bedinger, C. F. Bryan, S. Brown, R. I. Huffman, E. L. Miller, D. G. Rhodes, and B. A. Touchet. 1981. Transition from wetlands to uplands in southeastern bottomland hardwood forests. p. 225–269. *In* J. R. Clark and J. Benfrado (eds.) Wetlands in Bottomland Hardwood Forests. Elsevier Scientific Publishing, New York, NY, USA.

Little, E. L. 1978. Atlas of United States Trees, Volume 5: Florida. Miscellaneous Publication No. 1361. U.S. Department of Agriculture, Washington, DC, USA.

Liu, F. and H. Stutzel. 2002. Leaf water relations of vegetable amaranth (*Amaranthus* spp.) in response to soil drying. European Journal of Agronomy 16:137–150.

Lopez, O. R. and T. A. Kursar. 1999. Flood tolerance of four tropical tree species. Tree Physiology 19:925–932.

Loveless, C. M. 1959. A study of the vegetation in the Florida Everglades. Ecology 40:1–9.

Maceina, M. J., P. W. Bettoli, and D. R. DeVries. 1994. Use of split-plot analysis of variance design for repeated-measures fishery data. Fisheries 19:14–20.

McKevlin, M. R., D. D. Hook, and A. A. Rozelle. 1998. Adaptations of plants to flooding and soil waterlogging. p. 173–203. *In* M. G. Messina and W. H. Conner (eds.) Southern Forested Wetlands, Ecology and Management. Lewis Publishers, Boca Raton, FL, USA.

McKnight, J. S., D. D. Hook, O. G. Langdon, and R. L. Johnson. 1981. Flood tolerance and related characteristics of trees of the bottomland forests of the southern United States. p. 29–69. *In* J. R. Clark and J. Benfrado (eds.) Wetlands in Bottomland Hardwood Forests. Elsevier Scientific Publishing, New York, NY, USA.

McPherson, B. F. 1973. Vegetation in relation to water depth in Conservation Area 3, Florida. U.S. Geological Survey, Tallahassee, FL, USA. Open File Report 73025.

Meredith, M. P. and S. V. Stehman. 1991. Repeated measures experiments in forestry: focus on analysis of response curves. Canadian Journal of Forest Research 21:957–965.

Mitsch, W. J. and W. G. Rust. 1984. Tree growth responses to flooding in a bottomland forest in northeastern Illinois. Forest Science 30:499–510.

Ögren, E. and G. Öquist. 1985. Effects of drought on photosynthesis, chlorophyll fluorescence and photoinhibition susceptibility in intact willow leaves. Planta 166:380–388.

Pereira, J. S. and T. T. Kozlowski. 1977. Variations among woody angiosperms in response to flooding. Physiologia Plantarum 41:184–192.

Pezeshki, S. R. and J. L. Chambers. 1986. Variation in flood-induced stomatal photosynthetic responses of three bottomland tree species. Forest Science 32:914–923.

Regehr, D. L., F. A. Bazzaz, and W. R. Boggess. 1975. Photosynthesis, transpiration and leaf conductance of *Populus deltoides* in relation to flooding and drought. Photosynthetica 9:52–61.

Schmull, M. and F. M. Thomas. 2000. Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* [Matt.] Lieb., *Fagus sylvatica* L.) to waterlogging. Plant and Soil 225:227–242.

Schortemeyer, J. L. 1980. An evaluation of water management practices for optimum wildlife benefits in Conservation Area 3A. Florida Game and Fresh Water Fish Commission, Tallahassee, FL, USA.

Sklar, F. H. and A. van der Valk (eds.). 2002a. Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Sklar, F. H. and A. van der Valk. 2002b. Tree islands of the Everglades: an overview. p. 1–18. *In* F. H. Sklar and A. van der Valk (eds.) Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Slavík, B. 1974. Methods of Studying Plant Water Relations. Ecological Studies, Volume 9. Springer-Verlag, New York, NY, USA.

Smirnoff, N. and R. M. M. Crawford. 1983. Variation in the structure and response to flooding of root aerenchyma in some wetland plants. Annals of Botany 51:237–249.

Sojka, R. E. 1992. Stomatal closure in oxygen-stressed plants. Soil Science 154:269–280.

Teulat, B., P. Monneveux, J. Wery, C. Borries, I. Souyris, A. Charrier, and D. This. 1997. Relationships between relative water content and growth parameters under water stress in barley: a QTL study. New Phytologist 137:99–107.

Tomlinson, P. B. 1980. The Biology of Trees Native to Tropical Florida. Harvard University Printing Office, Allston, MA, USA.

USACE. 1999. Central and Southern Florida Project, Comprehensive Review Study, Volume 1, Final Integrated Feasibility Report and Programmatic Environmental Impact Statement. U.S. Army Corps of Engineers, Jacksonville District, Jacksonville, FL, USA.

van der Valk, A. and F. H. Sklar. 2002. What we know and should know about tree islands. p. 499–522. *In* F. H. Sklar and A. van der Valk (eds.) Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Vartapetian, B. B. and M. B. Jackson. 1997. Plant adaptations to anaerobic stress. Annals of Botany 79 (Supplement A): 3–20.

Vu, J. C. V. and G. Yelenosky. 1991. Photosynthetic responses of citrus trees to soil flooding. Physiologia Planatarum 81:7–14.

Wallace, P. M., D. M. Kent, and D. R. Rich. 1996. Responses of wetland tree species to hydrology and soils. Restoration Ecology 4:33–41.

Wetzel, P. R. 2002. Analysis of tree island vegetation communities. p. 357–389. *In* F. H. Sklar and A. van der Valk (eds.) Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Wunderlin, R. P. 1998. Guide to the Vascular Plants of Florida. University Press of Florida, Gainesville, FL, USA.

Zotz, G., M. T. Tyree, and S. Patino. 1997. Hydraulic architecture and water relations of a flood-tolerant tropical tree, *Annona glabra*. Tree Physiology 17:359–365.

Manuscript received 13 August 2004; revisions received 25 July 2005 and 17 February 2006; accepted 2 June 2006.