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Photosynthetic light response of flooded cherrybark oak (*Quercus pagoda*) seedlings grown in two light regimes

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Summary Two-year-old cherrybark oak (*Quercus pagoda* Raf.) seedlings raised in full or partial (27%) sunlight were flooded for 30 days to study the effects of light availability and root inundation on photosynthetic light response. Compared with seedlings receiving full sunlight, seedlings receiving partial sunlight developed leaves with 90% greater blade area, 26% less mass per unit volume, and 35% lower nitrogen (N) concentration per unit area, leading to a 15% reduction in leaf photosynthetic capacity when carbon exchange rates were based on blade area. However, when carbon exchange rates were based on leaf mass, leaves acclimated to partial sunlight exhibited a 15% greater photosynthetic capacity realized primarily through an increased initial slope of the photosynthetic light response (*A*/PPFD) curve and increased net photosynthesis at leaf saturation (A_{max}). Short-term flooding increased leaf mass per unit area more than 19%, reduced foliar N concentrations per unit dry mass by 19%, and initiated reductions in A_{max} and apparent quantum yield (ϕ) of seedlings in both light regimes. Greatest impairment of A_{max} (56% area basis, 65% mass basis) and ϕ (40%) were observed in leaves receiving full sunlight, and the declines were concomitant with a 35% decrease in chlorophyll concentration. Flooding also depressed instantaneous photosynthetic N-use efficiency (PPNUE) such that A_{max} decreased 54%, and the initial slope of PPNUE/PPFD curves decreased 33 and 50% for leaves acclimated to partial and full sunlight, respectively. The *A*/PPFD patterns indicated that the magnitude of flood-induced inhibition of the photosynthetic mechanism of cherrybark oak seedlings is determined partly by the light environment.

Keywords: carbon assimilation, nitrogen, photosynthesis, PPNUE, shade, waterlogging.

Introduction

Alluvial floodplain forests are typically underlain by a heterogeneous range of edaphic and hydrologic conditions that govern oxygen availability to plants (Patrick 1981, Stanturf and Schoenholtz 1998). Studies on woody tree species growing on the wettest sites in alluvial floodplains have revealed several mechanisms that allow these plants to function in the anaerobic soil environment (Hook 1984*a*, Kozlowski 1984, McKevlin et al. 1998). Formation of adventitious roots, aerenchyma cells and hypertrophied lenticels is common among hydrophytic trees, and these as well as other anatomical or morphological adaptations generally benefit the plant by improving its oxygen status (Hook et al. 1970, Hook et al. 1972, Hook and Brown 1973, Kawase and Whitmoyer 1980, Kludze et al. 1994). Adjustments to physiological processes are equally critical to the survival of hydrophytic plants in anaerobic soil, and mechanisms utilized by wetland trees include shifts to anaerobic root respiration, reductions in metabolic rates and maintenance of stomatal function (Hook and Scholtens 1978, Crawford 1982, Crawford 1992). Though hydrophytic trees have developed adaptive mechanisms to exist in swampy habitats, most floodplain trees are mesophytic species occurring on sites receiving periodic inundations of unpredictable occurrence (Hook 1984*b*). Although mesophytic species endemic to floodplains can survive anaerobic soil conditions for short periods, they are unable to sustain long-term function in anaerobic soils.

Bottomland oaks (*Quercus* spp.) are mesophytic species that constitute a significant component of hardwood forests associated with river systems of the southern USA. Flooding affects bottomland oaks by significantly altering physiological processes, especially photosynthesis and transpiration, leading to reductions in biomass accumulation and growth (Pezeshki and Chambers 1985, Pezeshki and Chambers 1986, Angelov et al. 1996, Pezeshki et al. 1996, Pezeshki and Anderson 1997, Conner et al. 1998, Gravatt and Kirby 1998). Stomatal control has been implicated as a primary mechanism regulating gas exchange of oak species stressed by anaerobic root conditions (Tang and Kozlowski 1982, Pezeshki and Chambers 1985, Pezeshki and Chambers 1986, Dreyer et al. 1991, Dreyer 1994, Gardiner and Hodges 1996). Species tolerant of low oxygen concentrations in soil can maintain or quickly recover stomatal function during flooding, whereas less tolerant species often exhibit prolonged reductions in gas exchange in response to root hypoxia (Parker 1949, Pezeshki and Chambers 1986, Gardiner and Hodges 1996, Pezeshki et al. 1996, Pezeshki and Anderson 1997, Wagner and Dreyer 1997, Gravatt and Kirby 1998).

Although the relationship between stomatal function and

flooding stress has been well documented, few studies have examined other aspects of carbon assimilation of flood-stressed oaks. Dreyer et al. (1991) studied relationships between assimilation and intercellular CO_2 of three waterlogged oak species and concluded that photosynthesis was probably limited by factors in addition to stomatal closure. Likewise, examination of stable carbon isotope ratios in leaves of hypoxic oaks led Gardiner and Hodges (1996) to surmise that non-stomatal factors also limited carbon assimilation of four bottomland oak species. Recent work by Gravatt and Kirby (1998) indicates that photosynthetic declines in flooded water oak (*Quercus nigra* L.) and white oak (*Q. alba* L.) are linked to starch accumulation in leaves, probably resulting from disrupted translocation of photosynthates. Despite these recent advances, little is known about carbon assimilation of flood-stressed oaks, particularly with respect to interactions with other environmental factors, such as light availability.

Understory light availability can limit the establishment and growth of oak reproduction in bottomland hardwood forests on alluvial floodplains of the southern USA (Jenkins and Chambers 1989, Lockhart et al. 2000). Acclimation of oak seedlings in low-light environments is typically realized through shifts in seedling biomass accumulation patterns (Gardiner and Hodges 1998), and alterations in leaf anatomy such as changes in chlorophyll content, stomatal density, leaf thickness and blade area (Jarvis 1964, Ashton and Berlyn 1994, Hamerlynck and Knapp 1994). These anatomical or morphological changes are typically accompanied by physiological responses that can include a reduction in the irradiance needed to attain leaf compensation or saturation, reduced dark respiration rate, and increased apparent quantum yield (Bazzaz and Carlson 1982, Teskey and Shrestha 1985, Ashton and Berlyn 1994, Hamerlynck and Knapp 1994, Kubiske and Pregitzer 1996). Because light availability substantially alters leaf anatomy and physiology of oak seedlings, carbon assimilation of leaves acclimated to a high-light environment may respond differently to flooding than leaves of seedlings acclimated to a low-light environment. This study was undertaken to quantify effects of light availability and flooding on the photosynthetic light response of cherrybark oak (*Quercus pagoda* Raf.), a shade-intolerant red oak (subgenus *Quercus*, section *Lobatae*) species endemic to moderately well-drained sites in bottomland hardwood forests of the southern USA.

Materials and methods

Seedling material

In December 1995, cherrybark oak acorns were collected from six parent trees in the Noxubee River bottom of Noxubee National Wildlife Refuge, Brookhaven, MS. Acorns were float tested for viability, soaked in water to assure hydration, and then stored at 4 °C until planting. In March 1996, acorns were sown in 0.65-l tubes containing a sintered clay potting substrate (Turface MVP, Applied Industrial Materials Corp., Buffalo Grove, IL). Seeded tubes were placed in a greenhouse at the Southern Hardwoods Laboratory, Stoneville, MS, where a randomly selected half of the seedlings were assigned to a bench beneath 73% neutral density shade cloth (27% sunlight), and the remaining seedlings were maintained in full sunlight in the greenhouse. Because the greenhouse reduced light transmittance by 36%, seedlings receiving full sunlight actually received 64% of ambient light, and seedlings beneath shade cloth received 17% of ambient sunlight. Tubes were misted with deionized water to promote acorn germination, and the subsequent seedlings were watered as needed. In May 1996, seedlings were transplanted to 9.6-l pots containing the sintered clay substrate and a slow-release fertilizer of macro (N:P:K, 17:6:10) and microelements (Osmocote, Scotts-Sierra Horticultural Products Company, Marysville, OH). Seedlings remained in the greenhouse in their respective light environments throughout the first growing season.

Experimental design

In spring 1997, randomly selected seedlings of uniform size were assigned to one of four light and flooding treatment combinations. The four treatment combinations, which included full sunlight + non-flooded, full sunlight + flooded, partial sunlight + non-flooded, and partial sunlight + flooded, were arranged in three replicates (blocks) based on location in the greenhouse. Eight seedlings were assigned to each experimental unit. The flood treatment was initiated in June 1997 by placing the pots in 450-l polypropylene tanks containing deionized water. Dissolved oxygen content in the floodwater averaged 5.7 ± 0.1 mg l^{-1}, floodwater temperature averaged 26.7 ± 0.3 °C and floodwater pH averaged 6.6 ± 0.04 during the study. Water was maintained in the tanks at about 5 cm above the seedling root-collars to ensure complete inundation of all roots. Control seedlings were watered daily to maintain a high water content in the potting medium.

Measurements

Measurement of leaf-level photosynthetic light response was initiated after seedlings were flooded for 30 days, and continued for 15 days. Measurements were conducted on one leaf from three randomly selected seedlings per replicate (nine leaves per treatment combination). Sample leaves were chosen from the terminal flush of seedlings in a quiescent stage of stem and leaf growth (lag stage of ontogeny) to reduce sample variation (Hanson et al. 1986). Thus, sample leaves were fully expanded and acclimated to their specific light environments before initiation of the flooding treatment and subsequent measurements. Net photosynthesis (A) of each leaf was measured at six irradiances with a Ciras-1 Portable Photosynthesis System and an automatic Parkinson leaf cuvette (PP-Systems, Hitchin, Herts, U.K.). Leaves were acclimated to a photosynthetic photon flux density (PPFD) of 1800 μmol m^{-2} s^{-1} for the first measurement, and subsequent measurements were made by decreasing PPFD to 800, 300, 150, 50 and 0 μmol m^{-2} s^{-1}. Measurements were made in a descending sequence because of the lengthy acclimation period needed to achieve a stable CO_2 exchange rate by the sample leaves. Leaves required about 35 min to attain stable A at 1800 μmol m^{-2} s^{-1}, and about

5 min at the subsequent PPFDs. Cuvette air temperature averaged 32 ± 1 °C, and cuvette CO_2 concentration averaged 350 ± 0.1 μmol mol^{-1} during measurements of A. Flooding was maintained during measurements for seedlings receiving that treatment. Sample leaves were harvested after A measurements to determine blade area (cm^2), leaf mass per unit area (mg cm^{-2}), nitrogen concentration per unit dry mass (N_{mass}; %N), and N concentration per unit area (N_{area}; mg cm^{-2}). Nitrogen concentration of dried sample leaves was determined by Dumas combustion techniques (Jones and Case 1990) in the Forest Ecophysiology Laboratory, Department of Forestry, Mississippi State University. An additional leaf was sampled from each seedling to quantify treatment effects on chlorophyll concentration. Total chlorophyll concentration (chlorophyll a + chlorophyll b) of each leaf was determined by a dimethyl sulfoxide extraction technique as described by Hiscox and Israelstam (1979).

Statistical analyses

Nonlinear regression techniques were used to model photosynthetic light response (A/PPFD) of individual sample leaves based on leaf area, leaf mass and N_{area}. Data from each sample leaf were fit to the model $A = A_{max\text{-}g}\text{PPFD}/(K + \text{PPFD}) - R_d$ as presented by Givnish (1988). In this model, A = net photosynthesis rate, $A_{max\text{-}g}$ = gross photosynthesis rate at light saturation, PPFD = photosynthetic photon flux density, K = PPFD required to achieve one half of $A_{max\text{-}g}$ and R_d = dark respiration rate. After each leaf was modeled, apparent quantum yield (ϕ) was calculated from the first derivative of the above equation: $\phi = A_{max\text{-}g}K/(K^2 + 2K\text{PPFD} + \text{PPFD}^2)$. The same equation was used to determine the initial slope of A/PPFD curves based on leaf mass and N_{area}. The initial slopes of A/PPFD curves were determined with PPFD set at the light compensation point (LCP). The LCP for each sample leaf was calculated as: $\text{LCP} = -KR_d/(R_d - A_{max\text{-}g})$. Photosynthetic light response based on N_{area} was used as an index of the instantaneous photosynthetic N-use efficiency (PPNUE) of leaves.

Treatment effects on light response variables (A_{max}, K, ϕ, LCP and R_d), morphological variables (blade area and leaf mass per unit area), and chemical variables (N_{mass}, N_{area} and chlorophyll concentration) were tested with analysis of variance procedures for a randomized block design (factors: block = 2 df, treatment = 3 df). All tests were conducted on means at the 0.05 probability level, and means of significant treatment effects were separated with Duncan's Multiple Range Test.

Results

Low light availability increased leaf blade area by 90% (Table 1). Blade area of flooded seedlings did not differ from blade area of non-flooded seedlings, regardless of light environment. Leaf mass per unit area decreased more than 26% in seedlings raised in partial sunlight. Flooding increased leaf mass per unit area by 26 and 19% in seedlings receiving full and partial sunlight, respectively (Table 1).

Foliar N_{mass} was unaffected by light environment, as N comprised about 1.85% of the dry mass of leaves from both light regimes (Table 1). However, 30–45 days of flooding decreased foliar N_{mass} by 19%. Conversely, light environment had a more pronounced effect on foliar N_{area} than flooding. Leaves of seedlings receiving full sunlight had 47% higher N_{area} than leaves receiving partial sunlight (Table 1). A 30–45-day period of flooding had no affect on N_{area}.

Foliar chlorophyll concentrations remained constant in seedlings in each light regime (Table 1). Flooding reduced foliar chlorophyll concentration by 35% in seedlings receiving full sunlight; however, no reduction in chlorophyll concentration was evident in flooded seedlings receiving partial sunlight (Table 1).

Based on leaf area, A_{max} was 18% higher in seedlings receiving full sunlight than in seedlings receiving partial sunlight (Figure 1, Table 2). However, when expressed on a leaf mass basis (Table 2), A_{max} was 15% higher in seedlings grown in partial sunlight than in seedlings grown in full sunlight (Table 2).

Flooding reduced area-based A_{max} by nearly 50%, with the greatest reductions occurring in seedlings receiving full sunlight (Figure 1, Table 2). A similar trend was observed when A_{max} was expressed per unit mass. Flooding decreased mass-based A_{max} by 65 and 58% for seedlings grown in full sunlight and partial sunlight, respectively (Table 2). These data indicate that the flooding effect on A_{max} was greater for seedlings acclimated to full sunlight than for seedlings acclimated to partial sunlight (Figure 1, Table 2).

Leaves raised in full sunlight required a PPFD of 155 ± 13 μmol m^{-2} s^{-1} to attain half of their saturated rate of A (Table 2). Leaves that developed in partial sunlight exhibited a 22% reduction in K. Flooding reduced K relatively more (36%) for leaves grown in partial sunlight than for leaves grown in full sunlight (18%) (Table 2).

The R_d was not altered by either environmental factor (Figure 1, Table 2). Mean R_d based on leaf area was about 1.05 ± 0.1 μmol CO_2 m^{-2} s^{-1}, whereas R_d based on leaf mass was about 15.5 ± 2 nmol CO_2 g^{-1} s^{-1}. Light environment did not impact ϕ (Table 2). Flooding reduced ϕ and a slightly greater decrease was observed in leaves acclimated to full sunlight than in leaves acclimated to partial sunlight (Table 2, Figure 1). A stronger response was observed when A/PPFD was based on leaf mass compared with leaf area. On a leaf mass basis, leaves acclimated to partial sunlight exhibited a steeper initial slope of the A/PPFD curve, and the depression in the slope resulting from flooding was greater for leaves of seedlings receiving full sunlight (Table 2). Though light environment and flooding altered A_{max} and the initial slope of the A/PPFD curves, LCP was unaffected by either environmental factor and averaged about 23 ± 3 μmol m^{-2} s^{-1} for leaves in all treatment combinations (Figure 1, Table 2).

Leaf-level characteristics of PPNUE tracked mass-based A (Table 2). Seedlings acclimated to partial sunlight exhibited greatest N-use efficiency at relatively low irradiances (as seen in the initial slope of the PPNUE/PPFD curve), but light environment did not alter PPNUE at high irradiances (A_{max}) (Ta-

Table 1. Morphological and chemical characteristics of cherrybark oak leaves harvested from seedlings grown in full or partial (27%) sunlight and subjected to 30–45 days of flooding.

Variable	Full sunlight		Partial sunlight		*P*-value
	Non-flooded[1]	Flooded	Non-flooded	Flooded	
Blade area (cm^2)	84.6 ± 7.5 b	78.9 ± 7.1 b	150.8 ± 9.7 a	159.9 ± 16.4 a	0.0021
Leaf mass per area (mg cm^{-2})	7.6 ± 0.2 b	9.6 ± 0.3 a	5.6 ± 0.2 d	6.7 ± 0.2 c	0.0001
Nitrogen concentration per unit mass (N_{mass}; %)	1.9 ± 0.09 a	1.5 ± 0.07 b	1.8 ± 0.05 a	1.5 ± 0.03 b	0.0118
Nitrogen concentration per unit area (N_{area}; mg cm^{-2})	0.14 ± 0.007 a	0.14 ± 0.005 a	0.09 ± 0.003 b	0.10 ± 0.004 b	0.0026
Total chlorophyll (mg g_{fw}^{-1})	2.39 ± 0.21 a	1.56 ± 0.17 b	2.87 ± 0.12 a	2.45 ± 0.09 a	0.0057

[1] Values are means ± standard error. Means in a row followed by the same letter do not differ at the 0.05 probability level.

ble 2). Flooding reduced PPNUE at high irradiances (54% reduction in A_{max}), regardless of the light environment to which the leaf had acclimated (Table 2). However, seedlings acclimated to full sunlight showed a greater flood-induced decline in the initial slope of the PPNUE/PPFD curve than seedlings acclimated to partial sunlight (Table 2). The R_d relative to N_{area} averaged 0.9 ± 0.1 μmol CO_2 g^{-1} N s^{-1} for seedlings in all treatment combinations (Table 2).

Discussion

Morphological acclimation of leaves to their light environment is widely expressed by oaks, and two commonly observed adjustments are in blade area and leaf mass per unit area (Abrams and Kubiske 1990, Hamerlynck and Knapp 1994). Blade area of oak species typically increases with decreasing light availability, thereby maximizing photosynthetic surface area for light interception. Relative to leaves in full sunlight, leaves acclimated to lower irradiances increased in blade area more than 100% in bur oak (*Q. macrocarpa* Michx.) and chinquapin oak (*Q. muehlenbergii* Englm.), and more than 200% in coast live oak (*Q. agrifolia* Nee) (Callaway 1992, Hamerlynck and Knapp 1994). We observed an increase of 90% in leaves of shade-intolerant cherrybark oak seedlings grown in 27% sunlight. Concurrent with the increase in blade area, leaf mass per unit area decreased under limiting light conditions, as has been observed in other oak species (Abrams and Kubiske 1990, Callaway 1992, Hamerlynck and Knapp 1994). This reduction in leaf mass per unit area may be associated with decreases in cell thickness, palisade cell stacking, or leaf cuticle thickness (Jackson 1967, Ashton and Berlyn 1994).

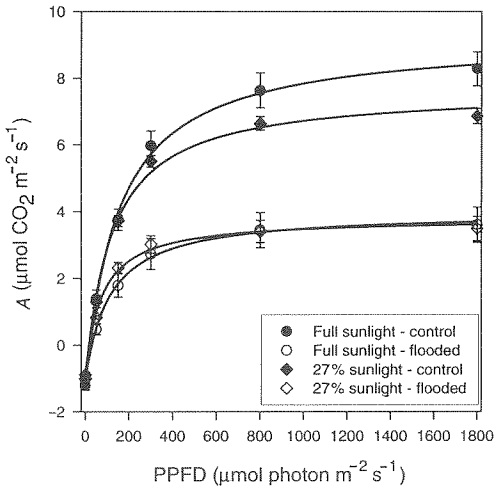

Figure 1. Net photosynthetic light response of cherrybark oak seedlings grown in full or partial (27%) sunlight and subjected to 30–45 days of flooding. Carbon assimilation is reported on a leaf area basis, and each value represents the mean ± standard error for nine leaves.

In addition to the influence of light availability on leaf morphology, anaerobic soil conditions reduce the rate of leaf blade growth and subsequent blade area of broadleaf trees (Smit et al. 1989). Angelov et al. (1996) reported that cherrybark oak exhibited a three- to fourfold decrease in blade area when leaves developed under anaerobic soil conditions. In hybrid poplar (*Populus trichocarpa* Torr. & A. Gray × *deltoides* Bartr. *ex* Marsh.), anaerobiosis reduced blade area by limiting cell enlargement and reducing cell division (Smit et al. 1989, 1990). In contrast, blade area of our cherrybark oak seedlings was unaffected by 30–45 days of flooding. The discrepancy between our results and those of other studies can be attributed to the lack of foliage production during the time our seedlings were flooded (cf. Hanson et al. 1986).

Although blade area was unaffected by flooding, leaf mass per unit area increased during the 30–45-day flood treatment. Harrington (1987) reported that flooded red alder (*Alnus rubra* Bong.) seedlings showed an increase in leaf mass per unit area in response to flooding, whereas black cottonwood (*Populus trichocarpa* Torr. & Gray) did not. It is not known why leaf mass per unit area increases in response to flooding, but one possible explanation centers around the disruption of photosynthate translocation (Vu and Yelenosky 1991, 1992). Gravatt and Kirby (1998) concluded that starch accumulated in leaves of flood-stressed oaks as a result of a decrease in the sink strength of flooded roots. A similar increase in carbohydrate concentrations of flood-stressed oaks was reported by Angelov et al. (1996). It is possible that disruption of photosynthate translocation and subsequent starch accumulation could have contributed to the increase in leaf mass per unit area of our flooded seedlings.

Table 2. Leaf-level photosynthetic characteristics of cherrybark oak seedlings grown in full or partial (27%) sunlight and subjected to 30–45 days of flooding.

Variable[1]	Full sunlight		Partial sunlight		*P*-value
	Non-flooded[2]	Flooded	Non-flooded	Flooded	
A_{max} (μmol CO_2 m^{-2} s^{-1})	8.4 ± 0.5 a	3.7 ± 0.6 c	7.1 ± 0.2 b	3.6 ± 0.4 c	0.0001
A_{max} (nmol CO_2 g^{-1} s^{-1})	111.4 ± 7.4 b	39.4 ± 6.4 c	128.3 ± 7.3 a	54.1 ± 5.3 c	0.0001
PPNUE (A_{max}) (μmol CO_2 g^{-1} N s^{-1})	6.0 ± 0.4 a	2.5 ± 0.3 b	7.3 ± 0.4 a	3.6 ± 0.3 b	0.0004
R_d (μmol CO_2 m^{-2} s^{-1})	1.2 ± 0.2 a	1.0 ± 0.1 a	1.1 ± 0.1 a	0.9 ± 0.1 a	0.5669
R_d (nmol CO_2 g^{-1} s^{-1})	16.5 ± 2.3 a	11.1 ± 1.2 a	20.5 ± 3.4 a	13.9 ± 1.1 a	0.1532
R_d (μmol CO_2 g^{-1} N s^{-1})	0.9 ± 0.1 a	0.7 ± 0.1 a	1.2 ± 0.2 a	0.9 ± 0.1 a	0.3083
ϕ (μmol CO_2 m^{-2} s^{-1}/μmol photon m^{-2} s^{-1})	0.05 ± 0.006 a	0.03 ± 0.005 c	0.06 ± 0.003 a	0.04 ± 0.003 b	0.0026
Initial slope of mass-based *A*/PPFD curves	0.73 ± 0.084 b	0.31 ± 0.058 c	1.04 ± 0.067 a	0.64 ± 0.046 b	0.0004
Initial slope of PPNUE/PPFD curves	0.04 ± 0.004 b	0.02 ± 0.004 c	0.06 ± 0.004 a	0.04 ± 0.004 b	0.0024
LCP (μmol photon m^{-2} s^{-1})	21 ± 2 a	37 ± 9 a	17 ± 2 a	17 ± 1 a	0.0791
K (μmol photon m^{-2} s^{-1})	155 ± 13 a	127 ± 22 b	120 ± 9 b	76 ± 12 c	0.0003

[1] Abbreviations: A_{max} = net photosynthetic rate at light saturation; PPNUE = instantaneous photosynthetic nitrogen-use efficiency; R_d = dark respiration rate; ϕ = apparent quantum yield; LCP = light compensation point; *K* = the value of photosynthetic photon flux density required to achieve one half of A_{max-g}; and *A*/PPFD = photosynthetic light response.

[2] Values are means ± standard error. Means in a row followed by the same letter do not differ at the 0.05 probability level.

The light environment influences foliar N of several broadleaf species from various forest types, including oaks of North American hardwood forests (Field 1983, Walters and Field 1987, Evans 1989*a*, Ellsworth and Reich 1993, Naidu and DeLucia 1997). Leaf N is generally greater in high-light environments than in low-light environments, and under high-light conditions allocation of leaf N shifts from light-harvesting complexes toward carboxylation enzymes and electron transport (Seeman et al. 1987, Chow et al. 1988, Evans 1989*b*, Walters and Bartholomew 1990, Naidu and DeLucia 1997, Mitchell 1998, Rosati et al. 1999). Flooding can also affect foliar N because nitrate uptake by hypoxic roots is inhibited, and denitrification decreases N availability in flooded soil (Kozlowski and Pallardy 1984, Harrington 1987). However, it is not known how flooding influences N allocation among the different compounds in leaves. In agreement with several other reports (Bassow and Bazzaz 1997, Naidu and DeLucia 1997, Mitchell 1998), light availability did not affect N_{mass} of cherrybark oak leaves, but N_{area} was reduced by partial sunlight primarily though alteration of leaf mass per unit area. Conversely, flooding had a stronger effect on N_{mass} than on N_{area} of cherrybark oak leaves. It is possible that the flood-induced effects on the N status of cherrybark oak leaves could also be explained by photosynthate accumulation in leaves of flooded seedlings as described above. If flooding initiated an accumulation of foliar carbohydrates, foliar N_{mass} would subsequently be diluted.

Foliar chlorophyll concentration of broadleaf tree species exhibits a varied response to irradiance. In many species, chlorophyll concentration increases as irradiance decreases (Chow et al. 1988, Walters and Bartholomew 1990, Turnbull 1991, Wiebel et al. 1994); however, some species maintain a constant chlorophyll concentration over a range of irradiances (Wallace and Dunn 1980, Turnbull 1991), and in a few species chlorophyll concentration decreases with decreasing irradiance (Logan 1970, Wallace and Dunn 1980). In contrast, flooding usually causes a reduction in leaf chlorophyll concentration (Vu and Yelenosky 1991, Dreyer 1994, Gravatt and Kirby 1998). Chlorophyll concentration of cherrybark oak leaves was unresponsive to changes in light availability. In contrast, flooding reduced chlorophyll concentration of cherrybark oak leaves acclimated to full sunlight. It is possible that this reduction was caused by an increase in foliar carbohydrate concentration. However, the absence of a parallel response in leaves receiving partial sunlight indicates that flooding hampered chlorophyll synthesis or increased photo-oxidation of chlorophyll in cherrybark oak leaves exposed to full sunlight. An association between root hypoxia and leaf chlorosis has often been reported (Kozlowski and Pallardy 1984).

Light availability determined *A*/PPFD patterns of cherrybark oak in a fashion similar to other shade-intolerant or moderately shade-intolerant tree species (Bazzaz and Carlson 1982, McMillen and McClendon 1983). Leaves acclimated to full sunlight exhibited greater photosynthetic rates per unit leaf area than leaves acclimated to partial sunlight, whereas leaves acclimated to partial sunlight were favored when photosynthesis was expressed per unit leaf mass. These light-response patterns are in agreement with those reported by McMillen and McClendon (1983) for catalpa (*Catalpa speciosa* Warder) and Kentucky coffeetree (*Gymnocladus dioicus* (L.) Koch). Furthermore, these findings are consistent with our observations that leaf mass per unit area and N_{area} were greater in leaves acclimated to full sunlight than in leaves acclimated to partial sunlight. Morphological and physiological acclimation to low irradiance often enables shade-acclimated leaves to function at a similar or higher photosynthetic rate than sun-acclimated leaves when photosynthesis is expressed per unit dry mass (Chabot and Chabot 1977, Chen and Klinka 1997, Pattison et al. 1998). An increase in ϕ and a decrease in R_d are often associated with a decrease in leaf mass per unit area (or vol-

ume per unit area) in leaves grown at low irradiance (Boardman 1977, Dean et al. 1982, Oberbauer and Strain 1986, Man and Lieffers 1997). In cherrybark oak, *A*/PPFD was modified principally through a change in A_{max} when assimilation was expressed per unit leaf area. However, when photosynthesis was based on leaf mass, leaves acclimated to partial sunlight exhibited a 15% greater photosynthetic capacity realized primarily through an increased initial slope of the photosynthetic light response (*A*/PPFD) curve and increased net photosynthesis at leaf saturation (A_{max}).

Although flood-induced declines in photosynthesis are well documented, studies of the effects of root inundation on *A*/PPFD of tree species are limited. Beckman et al. (1992) cited decreased ϕ and A_{max} as primary mechanisms controlling *A*/PPFD of flooded sour cherry (*Prunus cerasus* L. cv. Montmorency/*P. mahaleb* L.) trees. Similarly, we found that flooding altered the *A*/PPFD of cherrybark oak primarily by decreasing ϕ and A_{max}. The flood-induced reductions in ϕ provide additional evidence that non-stomatal mechanisms play a role in limiting photosynthesis of flood-stressed oaks, and corroborate the findings of Beckman et al. (1992) and Davies and Flore (1986) that flooding impairs ϕ of woody plants.

Reductions in the amount or activity of carboxylation enzymes may also contribute to the reduced photosynthetic capacity of flood-stressed oaks (Dreyer et al. 1991, Gardiner and Hodges 1996). This suggestion is supported by observations of an increased intercellular CO_2 concentration accompanying the decline in photosynthetic capacity associated with root hypoxia (Dreyer et al. 1991, Vu and Yelenosky 1991, Dreyer 1994). We observed that flood-induced reductions in A_{max} were accompanied by decreased *K*. This observation provides further evidence that flooding inhibited the photosynthetic mechanism of cherrybark oak leaves. Others have reported similar reductions in the amount of light needed to achieve light saturation in flooded sour cherry (Beckman et al. 1992) and Nuttall oak (*Quercus nuttallii* Palm.) (Pezeshki and Anderson 1997). Reduced photosynthetic capacity at light saturation is indicative of reduced carboxylation enzyme activity (Berry 1975, Zhang et al. 1997). Flooding is known to reduce activity of carboxylation enzymes in citrus trees (Vu and Yelenosky 1991, Vu and Yelenosky 1992), but the specific mechanism by which this reduction is mediated is unknown. There are at least two possible methods by which root hypoxia could disrupt Rubisco activity and thereby reduce photosynthetic capacity. One pathway involves a chemical signal transported from hypoxic roots. Abscisic acid, which has been shown to reduce carboxylation efficiency (Ward and Bunce 1987), is generated in hypoxic roots and may be transported through the xylem to accumulate in leaves (Neuman and Smit 1991). However, the mechanism by which abscisic acid reduces carboxylation efficiency and the consistency with which it does so are unclear (Bradford 1983, Ward and Bunce 1987), and others question whether abscisic acid is transported from hypoxic roots rather than synthesized and accumulated in leaves (Jackson 1990). The second pathway by which root hypoxia could reduce photosynthetic capacity involves carbohydrate signaling in leaves. In this scenario of feedback inhibition, it is thought that an accumulation of foliar carbohydrates inhibits expression of the Rubisco gene (Moore et al. 1999). This explanation is compatible with the observations that flooding reduces the carbohydrate sink in roots, thereby initiating an accumulation of foliar carbohydrates (Vu and Yelenosky 1992, Angelov et al. 1996, Gravatt and Kirby 1998).

Carbon assimilation was disrupted by flooding stress, but the magnitude of the response was determined in part by the light environment in which the leaves developed. Flooding impacted A_{max} and ϕ (or the initial slope of the *A*/PPFD curve) more for leaves acclimated to full sunlight than for leaves acclimated to partial sunlight. Similarly, Wagner and Dreyer (1997) reported greater flood-induced inhibition of *A* for oak seedlings receiving full sunlight compared with those receiving partial sunlight. It is probable that flooding rendered the photosynthetic mechanisms of leaves grown in full sunlight susceptible to the damaging effects of high irradiance, because chlorophyll concentrations were reduced in leaves of flooded seedlings receiving full sunlight. Similar effects of high irradiance on the photosynthetic mechanism have been well documented for plants subjected to water stress and thermal stress (Kozlowski et al. 1991).

Changes in leaf N_{area} resulting from low irradiance may be accompanied by a decreased allocation of N to carboxylation enzymes and electron transport in favor of chlorophyll and associated light-harvesting proteins (Seemann et al. 1987, Evans 1989*a*, 1989*b*). The effect of light availability on the distribution of N among photosynthetic components can be estimated by modeling carbon assimilation per unit leaf N in response to irradiance (PPNUE/PPFD) (Field and Mooney 1986, Field 1988). Examination of PPNUE/PPFD curves for cherrybark oak indicated that leaves acclimated to partial sunlight differed from those acclimated to full sunlight primarily through an adjustment in the initial slope of the response curve. This light-mediated shift in the slope is consistent with a proportional increase in N allocated to the chlorophyll fraction as reported for other broadleaf species in shaded environments (Evans 1989*a*, 1989*b*, Ellsworth and Reich 1993). Additional evidence supporting this speculation is provided by calculating the chlorophyll:N ratio of leaves examined in this study. Leaves of seedlings receiving full sunlight maintained 4.1 mmol chlorophyll mol^{-1} N, whereas leaves receiving partial sunlight maintained 5.2 mmol chlorophyll mol^{-1} N.

We found that flooding altered the potential efficiency of carbon assimilation per unit leaf N for cherrybark oak seedlings acclimated to either light environment. At similar N concentrations, flooding suppressed PPNUE through reductions in A_{max} and the initial slope of the PPNUE/PPFD curve. Additionally, depression of this initial slope relative to N concentration was compounded for leaves receiving full sunlight, indicating that the degree of PPNUE inhibition resulting from root hypoxia is tempered by leaf acclimation to the ambient light environment. We believe that this is the first experimental evidence that flooding decreases the instantaneous photosynthetic N-use efficiency of carbon assimilation. We postu-

late that the flood-induced inhibition of PPNUE is a short-term response to acute stress. This is in contrast to the relatively long-term acclimation effect that the light environment had on N allocation and subsequently PPNUE. Our findings provide evidence that flooding impairs basic functioning of the photosynthetic mechanism of cherrybark oak, and the extent of impairment varies depending on leaf acclimation to the light environment. Debilitation of carbon assimilation appeared to be associated with effects on light-harvesting efficiency, electron transport and carboxylation enzyme activity.

Conclusions

We conclude that the *A*/PPFD curve of flooded cherrybark oak seedlings is partly determined by the seedling's light environment. Cherrybark oak seedlings raised in partial sunlight produced leaves of greater blade area and lower leaf mass per unit area than seedlings raised in full sunlight. Short-term flooding did not affect blade area but initiated an increase in leaf mass per unit area regardless of light availability. Decreased N_{mass} accompanied the increased leaf mass per unit area of flooded seedlings, whereas leaf N_{area} was unaffected by flooding. However, flooding reduced the chlorophyll concentration of leaves acclimated to full sunlight. Modification of *A* accompanied the leaf morphological adjustments, and *A*/PPFD varied relative to leaf area and mass. A relatively high N_{area} and leaf mass per unit area supported the high photosynthetic capacity exhibited by leaves acclimated to full sunlight when *A* was expressed per unit area, but leaves acclimated to partial sunlight exhibited an increased initial slope of the *A*/PPFD curve that contributed to higher *A* per unit mass. Light response patterns revealed that ϕ and A_{max} of cherrybark oak seedlings were greatly reduced by short-term flooding, leading to an overall decline in photosynthetic capacity. Flooding reduced ϕ more in leaves acclimated to full sunlight than in leaves acclimated to partial sunlight, and the decline was paralleled by a decrease in chlorophyll concentration presumably as a result of increased photodegradation. Photosynthetic decline in flooded seedlings was related to a decrease in instantaneous photosynthetic N-use efficiency of leaves, providing further evidence that flooding impairs the photosynthetic mechanism of cherrybark oak. The observed impairments are consistent with dysfunction of light-harvesting functions, electron transport and carboxylation enzyme activity.

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