PHOTOSYNTHETIC LIGHT RESPONSE OF BOTTOMLAND OAK SEEDLINGS RAISED UNDER PARTIAL SUNLIGHT

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Abstract—Seedlings of cherrybark oak (*Quercus pagoda* Rafinesque), Nuttall oak (*Quercus nuttallii* Palmer) and overcup oak (*Quercus lyrata* Walter) were grown under two light levels, partial (20 percent) or full sunlight, to study physiological acclimation of leaves to low light availability. Shifts in leaf morphology were noted for seedlings raised beneath partial sunlight, and photosynthetic light response curves indicated that bottomland oaks varied in their degree of physiological acclimation to low light availability. Greatest shifts in leaf function under partial sunlight were observed for cherrybark oak which exhibited a 48 percent decrease in net photosynthesis at light saturation ($P_{n\text{-}sat}$), and a 55 percent decrease in dark respiration rate (R_d) (based on leaf area). These adjustments to the photosynthetic mechanism were accompanied by a 46 percent decrease in the light compensation point (LCP). In contrast, Nuttall oak leaves showed similar rates of $P_{n\text{-}sat}$, R_d and apparent quantum yield (φ) regardless of the light environment in which they developed. Overcup oak leaves were intermediate in response exhibiting a 53 percent decreased in R_d and a 57 percent increase in φ, but $P_{n\text{-}sat}$ was not decreased for leaves grown under partial sunlight. Silvicultural implications of these results for bottomland oak regeneration are presented.

INTRODUCTION

Bottomland hardwood forests of the southern United States characteristically support a rich diversity of tree species. Of the more than 70 tree species endemic to major and minor river bottoms, bottomland oaks are often primary components of many species-site associations (Putnam and others 1960). Though bottomland oaks are often a primary component of mixed species, bottomland hardwood stands, regeneration of these desired species can be problematic. The problem of obtaining an adequate stocking of vigorous oak (*Quercus* spp.) reproduction following regeneration harvests in southern bottomlands has been addressed by numerous authors for several decades (Chambers and others 1987, Hodges and Janzen 1987, Johnson 1975, Nix and others 1985). Yet, reliable techniques for securing oak regeneration in bottomlands are still unavailable. A stronger understanding of how environmental factors regulate oak seedling establishment and growth is clearly needed to develop silvicultural practices that foster oak regeneration (Hodges and Gardiner 1993).

Previous research in bottomlands has identified several environmental factors that potentially contribute to oak regeneration problems. For example, flooding is a prominent factor in bottomlands that can limit establishment or destroy entire cohorts of oak reproduction (Johnson and Deen 1993, Young and others 1995). Competition from other tree or vine species can be severe in bottomlands, particularly on well drained, productive sites (Gardiner and Yeiser 1999, Johnson 1975). Mast depredation may limit seed tree fecundity, and herbivory often reduces vigor of established seedlings (Johnson 1981, Lockhart and others 2000).

Though many factors potentially contribute to poorly stocked oak regeneration pools in bottomlands, some problems are likely linked to light availability. This may be realized through the observations that oak seedlings are generally intolerant of shade, and light availability in the understory of mature bottomland hardwood forests is generally low (Hodges and Gardiner 1993, Jenkins and Chambers 1989). Recent research has established the importance of sufficient light availability to development of vigorous cherrybark oak (*Quercus pagoda* Rafinesque) reproduction (Gardiner and Hodges 1998). And, silvicultural practices which increase understory light availability can be applied to improve size and vigor of cherrybark oak reproduction (Lockhart and others 2000). Though these findings are promising, much remains to be learned about the basic functioning of oak seedlings relative to their light environment. This experiment was initiated to study the effects of light availability on the photosynthetic light response of seedlings of three bottomland oak species. Additionally, leaf morphology was examined to describe potential changes in functional processes relative to structural acclimation.

METHODS

The experiment was conducted during the 1993 growing season at the Mississippi State University, Blackjack Research Farm located near Starkville, MS (33° 26' N Latitude, 88° 46' W Longitude). Twenty-four, 1-year-old dormant seedlings of cherrybark oak, Nuttall oak (*Quercus nuttallii* Palmer) and overcup oak (*Quercus lyrata* Walter) (72 total seedlings) were transplanted into 18.9-liter pots filled with potting soil and sand (50:50, volume:volume). Pots were fertilized with a 14-14-14 (nitrogen-phosphorous-potassium) time release, granule (Osmocote,

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Grace-Sierra Horticultural Products company, Milpitas, CA), and watered as needed to maintain ample soil moisture. Half of the seedlings were randomly selected and placed in a shade house (20 percent of full sunlight), while the other half were grown under full sunlight in an adjacent field.

Measurements of leaf morphology and physiology began in July after maturation of the second flush of shoot growth. Leaf morphology was characterized through measurements of blade area and leaf mass per area. Measurements were collected on 30 randomly selected leaves for each species and light environment (5 randomly selected leaves from 6 randomly selected seedlings). Blade area (centimeter^2) was measured with a digital image analysis system (Decagon Devices Inc, Pullman, WA, USA). Leaves were oven-dried for 48 hours at 70° Celsius, then leaf mass per area was calculated as blade mass ÷ blade area (milligrams centimeter^{-2}).

Leaf physiology was characterized by measuring the photosynthetic light response of four randomly selected seedlings for each species and light environment. Seedlings were brought into the laboratory where measurements were conducted on a single, fully developed leaf from the terminal flush. Net photosynthesis (P_n) (micromoles centimeter^{-2} second^{-1}) of each sample leaf was recorded at 6 levels of photosynthetic photon flux density (PPFD) (0, 25, 100, 400, 800, 1600 micromoles meter^{-2} second^{-1}) with a LCA-3 gas analyzer and Parkinson leaf cuvette (The Analytical Development Company Ltd, England). P_n measurements on each sample leaf began at the lowest light level and ended with the highest light level. Particular light levels were produced by filtering light from a 300 watt quartz filament bulb with various configurations of neutral density filters. Because of high variation in P_n observed for overcup oak leaves, two additional seedlings from each light environment were sampled for this species.

Curves were fit to photosynthetic light response data according to methods described in Givnish (1988). The model used for this procedure is defined in Equation 1.

$$P_n = [(P_{g\text{-}sat} \times PPFD) \div (K + PPFD)] - R_d \qquad (1)$$

For Equation 1, P_n is net photosynthesis, $P_{g\text{-}sat}$ is gross photosynthesis at leaf saturation, PPFD is photosynthetic photon flux density, K is the PPFD required to achieve half of $P_{g\text{-}sat}$, and R_d is the dark respiration rate. The light compensation point (LCP) for each leaf was calculated with Equation 2.

$$LCP = (-K \times R_d) \div (R_d - P_{g\text{-}sat}) \qquad (2)$$

Apparent quantum yield (φ) of each leaf was calculated with the first derivative of Equation 1 with PPFD set at LCP as presented in Equation 3.

$$\varphi = P_{g\text{-}sat} \times K \div (K^2 + 2K \times PPFD + PPFD^2) \qquad (3)$$

The effect of light availability on photosynthetic light response variables ($P_{n\text{-}sat}$, LCP, R_d, , K) and leaf morphology variables (blade area, leaf mass per area) were analyzed with analysis of variance procedures according to a completely random design for each species. All tests were conducted at an α of 0.05.

RESULTS AND DISCUSSION

Leaf Morphology

Leaves of all three oak species examined in this study exhibited morphological acclimation when seedlings were raised under 20 percent sunlight. Cherrybark oak showed the greatest blade area response with a 129 percent increase on leaves that developed under partial sunlight (table 1). Blade area of Nuttall oak increased 103 percent, while blade area of overcup oak showed a 67 percent increase. Observations on blade area increases from this study illustrate the magnitude of variation in morphological acclimation expressed by different North American oak species. Others have reported blade area increases of 110 percent for bur oak (*Quercus macrocarpa* Michaux), 108 percent for chinkapin oak (*Quercus muehlenbergii* Engelmann), and 208 percent for coast live oak (*Quercus agrifolia* Nee) when these species developed under partial sunlight (Callaway 1992, Hamerlynck and Knapp 1994).

Table 1—Morphological characteristics (mean ± standard error)[a] of leaves from three bottomland oak species raised under full (100 percent) or partial (20 percent) sunlight

Light Level	Cherrybark Oak	Nuttall Oak	Overcup oak
		----------------- Blade Area (cm^2) -----------------	
Full Sunlight (100 pct)	35.7 ± 1.8 b	25.6 ± 1.4 b	25.2 ± 1.2 b
Partial Sunlight (20 pct)	81.9 ± 4.8 a	52.1 ± 2.4 a	42.1 ± 2.5 a
		----------- Leaf Mass per Area (mg cm^{-2}) -----------	
Full Sunlight (100 pct)	11.9 ± 0.2 a	11.0 ± 0.2 a	9.8 ± 0.2 a
Partial Sunlight (20 pct)	7.0 ± 0.2 b	6.8 ± 0.1 b	6.3 ± 0.1 b

[a] Means in a column followed by the same letter are not different at α = 0.05.

Table 2--Photosynthetic light response variables (mean ± standard error)[a] for three bottomland oak species raised under full (100 percent) or partial (20 percent) sunlight

Light Level	Cherrybark Oak	Nuttall Oak	Overcup oak
	-------- Net Photosynthesis Rate (mol m^{-2} s^{-1}) --------		
Full Sunlight (100 pct)	12.9 ± 1.0 a	10.7 ± 0.7 a	10.5 ± 1.5 a
Partial Sunlight (20 pct)	6.8 ± 0.9 b	9.6 ± 1.2 a	7.5 ± 1.4 a
	------- Light Compensation Point (mol m^{-2} s^{-1}) --------		
Full Sunlight (100 pct)	18.3 ± 1.6 a	18.2 ± 3.4 a	22.9 ± 2.1 a
Partial Sunlight (20 pct)	9.8 ± 2.3 b	11.3 ± 0.7 a	7.1 ± 1.1 b
	--------- Dark Respiration Rate (mol m^{-2} s^{-1}) ---------		
Full Sunlight (100 pct)	0.9 ± 0.06 a	0.8 ± 0.14 a	0.9 ± 0.16 a
Partial Sunlight (20 pct)	0.4 ± 0.15 b	0.6 ± 0.16 a	0.4 ± 0.08 b
	--------------- Apparent Quantum Yield ---------------		
Full Sunlight (100 pct)	0.05 ± 0.006 a	0.04 ± 0.003 a	0.04 ± 0.006 b
Partial Sunlight (20 pct)	0.04 ± 0.005 a	0.05 ± 0.011 a	0.06 ± 0.004 a
	---------- Saturation Constant (mol m^{-2} s^{-1}) ----------		
Full Sunlight (100 pct)	319 ± 57 a	279 ± 53 a	319 ± 12 a
Partial Sunlight (20 pct)	226 ± 75 a	235 ± 35 a	142 ± 38b

[a] Means in a column followed by the same letter are not different at $\alpha = 0.05$.

Coupled with the increase in blade area, all species showed a reduced leaf mass per area when raised beneath partial sunlight (table 1). These reductions in mass per area ranged from 41 percent for cherrybark oak to 36 percent for overcup oak. Reductions in leaf mass per area probably result from a decrease in leaf thickness that can be attributed to a decrease in palisade cell stacking, a decrease in leaf cuticle thickness, and/or a decrease in epidermal and palisade cell thicknesses (Ashton and Berlyn 1994, Carpenter and Smith 1981, Jackson 1967). The range of response in mass per area observed between bottomland oaks in this study was comparable to other oak species endemic to the northern United States. Abrams and Kubiske (1990) reported that leaf mass per area decreased under low light availability by 35 percent for northern pin oak (*Quercus ellipsoidalis* E. J. Hill), 36 percent for northern red oak (*Quercus rubra* Linnaeus), 43 percent for bur oak and white oak (*Quercus alba* Linnaeus), and 56 percent for black oak (*Quercus velutina* Lamarck).

For many broadleaved tree species, leaves which developed under low light conditions will usually have enlarged leaf blades and a lower mass per area than those which have developed under ample light availability (Abrams and Kubiske 1990, Jackson 1967, Goulet and Bellefleur 1986). The three bottomland oaks examined in this experiment were no exception. Physiological function of oak seedlings growing in low light environments may benefit from this morphological acclimation. Leaf physiology of oak seedlings may be improved by several mechanisms including increasing the light gathering area of individual leaf blades, increasing the efficiency of harvesting diffuse sunlight because chloroplasts are closer to the leaf surface, and reducing the respiratory demand of leaves per unit area (Chow and others 1988, Hamerlynck and Knapp 1994, Man and Lieffers 1997, Kozlowski and others 1991).

Leaf Physiology

Photosynthetic light response curves revealed that acclimation of the photosynthetic mechanism to low light availability differed between the three bottomland oak species (figure 1, table 2). Cherrybark oak seedlings which developed beneath partial sunlight showed a 50 percent reduction in $P_{n\text{-sat}}$ (table 2). This is in contrast to $P_{n\text{-sat}}$ rates observed for Nuttall oak and overcup oak, which did not show a decrease when seedlings were raised under partial sunlight. The reduced photosynthetic capacity observed for cherrybark oak is consistent with another report on this species, and observations on other shade intolerant broadleaved species (Bazzaz and Carlson 1982, Gardiner and Krauss In Press, Kubiske and Pregitzer 1996). It is not known why Nuttall oak and overcup oak behaved differently, but a light environment effect on overcup oak may have been obscured by the high variance associated with $P_{n\text{-sat}}$ for this species (figure 1, table 2). Photosynthetic capacities of seedlings receiving full sunlight in this study were generally higher than reported observations on field-grown cherrybark oak and Nuttall oak seedlings (Gardiner and others In Press, Sung and others 1999).

In addition to decreased $P_{n\text{-}sat,}$ cherrybark oak seedlings raised under partial sunlight exhibited a 55 percent decrease in R_d (table 2). R_d of overcup oak was similarly reduced, but R_d for Nuttall oak was not altered by light regime (table 2). A decrease in R_d would be expected to accompany reductions in leaf mass per area as noted earlier for these three oak species, because of the reduced cell volume associated with the lower leaf mass per area (Hamerlynck and Knapp 1994, McMillen and McClendon 1983). Results from other studies on cherrybark oak and Nuttall oak are contradictory to the findings in this study. Gardiner and Krauss (In Press) reported a decrease in leaf mass per area for cherrybark oak grown under partial sunlight, but a concomitant decrease in R_d was not measured on those seedlings. And, Nuttall oak grown beneath an eastern cottonwood (*Populus deltoides* Bartram ex Marshall) canopy showed reduced leaf mass per area with a concomitant decrease in R_d (Gardiner and others In Press). These conflicting results indicate that the relative change in leaf mass per area and other uncontrolled environmental factors probably contributed to the disparate results noted between studies. For example, leaf temperature can have a strong effect on R_d, and this variable likely differed between experiments. In the work published by Gardiner and others (In Press) and Gardiner and Krauss (In Press), leaf cuvette temperature was controlled during R_d measurements. Sampling techniques used in this study were not amenable to controlling cuvette temperature.

Associated to the reduced $R_{d,}$ LCP decreased 46 percent and 69 percent, respectively, for cherrybark oak and overcup oak leaves raised under partial sunlight (table 2). Though of overcup oak increased when seedlings developed under partial sunlight (figure 1, table 2), light environment did not alter φ of cherrybark oak, nor did it impact LCP or φ of Nuttall oak. Three other North American oaks exhibited similar reductions in LCPs when leaves were acclimated to low light environments (Kubiske and Pregitzer 1996, Hamerlynck and Knapp 1994). Results from those studies confirm the observation that LCPs were lowered primarily through decreased R_d rather than through an increased φ. However, the higher φ observed for overcup oak seedlings raised under partial sunlight in this study may have lead to a decreased K, which was not observed for cherrybark oak or Nuttall oak (table 2).

MANAGEMENT IMPLICATIONS

Though this study does not consider whole-plant response to light environment, several implications for management of bottomland oak regeneration may be inferred from leaf-level response patterns. First, stand structure of many mixed hardwood forests restricts availability of sufficient light to maximize seedling carbon assimilation. The three bottomland oaks studied appear to require more than 25 to 30 percent of available sunlight for light saturation requirements. Light availability in the understory of mixed bottomland hardwood stands is typically less than 10 percent of available sunlight (Jenkins and Chambers 1989, Lockhart

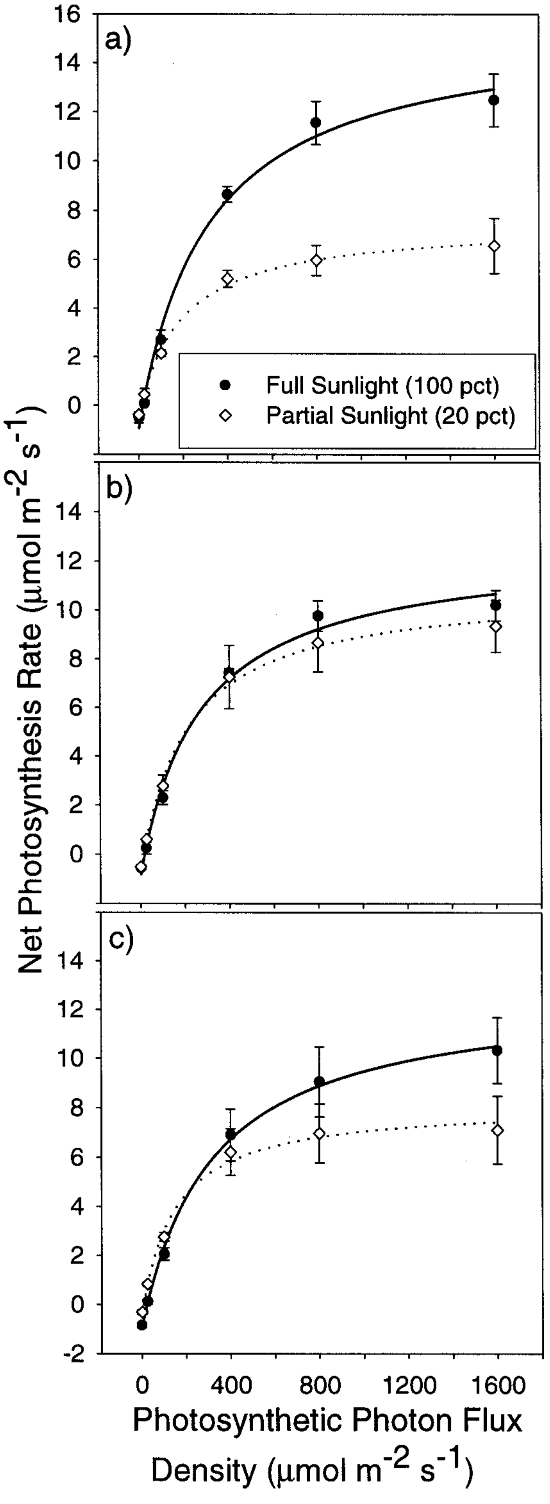

Figure 1—Photosynthetic light response of cherrybark oak (a), Nuttall oak (b) and overcup oak (c) seedlings raised under full (100 percent) or partial sunlight (20 percent).

and others 2000). This study provides physiological evidence supporting the argument that managers will have to implement practices that provide stand structures which improve understory light availability to promote establishment and growth of bottomland oak reproduction (Lockhart and others 2000).

Secondly, bottomland oak seedlings appear to have different light requirements. For example, establishment and growth of cherrybark oak seedlings might require a greater level of understory light availability than other species. The complex aspect of this implication is that bottomland oak species are often found on different sites with different species associations. So, a treatment that provides sufficient light for overcup oak in a slough, may not be adequate for facilitating establishment and growth of cherrybark oak on a ridge.

Related to the second implication is that the different light requirements for each species may also directly effect the length of time seedlings can remain in an understory before being released. Species like Nuttall oak or overcup oak may persist in the reproduction pool of the understory longer than a species like cherrybark oak. Indeed, Johnson (1975) noted that Nuttall oak could persist in the understory for 15 years if seedlings received about 2 hours of direct sunlight a day.

A final management implication gathered from this research revolves around the observation that bottomland oaks differed in their degree of acclimation to light availability. The physiological acclimation observed for cherrybark oak was in association with relatively large shifts in leaf morphology. The implication is that oak seedlings, particularly cherrybark oak, will have to develop a new leaf flush to respond to a richer light environment. It is not known if a species like Nuttall oak, which shows relatively little morphological and physiological acclimation to light availability, can respond quicker to release than a species like cherrybark oak. Nevertheless, oak seedlings will probably require acclimation time before responding to release. A similar finding was noted by Gardiner and Hodges (1998) who considered acclimation of cherrybark oak seedling morphology under various light levels. The slow response to release by cherrybark oak may be seen in the research of Lockhart and others (2000) and Janzen and Hodges (1985). In each of these studies, seedlings required about 3 years before significant response was realized. Regeneration strategies will have to account for this delayed response.

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