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Photosynthesis of Nuttall oak (*Quercus nuttallii* Palm.) seedlings interplanted beneath an eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) nurse crop

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Abstract

An afforestation system which utilizes the pioneer species eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) as a nurse for slower growing, disturbance-dependent species is under evaluation as a forest rehabilitation tool on former agricultural land in the Lower Mississippi River Alluvial Valley, USA. The primary objectives of this study were to quantify understory light availability in the eastern cottonwood plantation, and describe the photosynthetic light response of interplanted Nuttall oak (*Quercus nuttallii* Palm.) seedlings. Photosynthetic photon flux density (PPFD) measured in the understory of a 3-year-old, cottonwood plantation was 43% of full sunlight, and was sufficient to meet leaf saturation requirements over 29% of the diurnal cycle. Oak seedlings established in the cottonwood understory showed no change in blade area, and minimal shifts (<19%) in dry mass per unit area relative to open grown seedlings. A 19% decrease in dark respiration rate (R_d) was measured on a leaf area basis, but gross photosynthesis ($P_{\text{g-sat}}$), net photosynthesis ($P_{\text{n-sat}}$), quantum yield (Q), light compensation point (LCP) and the saturation constant (K) of Nuttall oak leaves were not influenced by the presence of the cottonwood canopy, regardless of leaf area, mass or N content. $P_{\text{n-sat}}$ was strongly determined by foliar N concentration of seedlings in understory and open environments, increasing 1.2 μmol m^{-2} s^{-1} for each 0.1% increase in N concentration. Our data indicate that Nuttall oak seedlings established beneath an eastern cottonwood canopy developed leaves with a capacity for carbon assimilation similar to open-grown plants. However, carbon assimilation by Nuttall oak may be sub-optimal on degraded sites where intensive row cropping has depleted soil N.

Keywords: Afforestation; Rehabilitation; Restoration; Plantations; Nitrogen; Lower Mississippi River Alluvial Valley; Intercropping; Irradiance

1. Introduction

Alluvial floodplains of temperate and tropical regions, such as those associated with the Mississippi River in North America and the Amazon River in South America, are generally characterized as having moist, fertile soils well suited for supporting highly productive riverine forest types (Brinson, 1990; Junk, 1997). These highly productive alluvial soils are also favorable for producing agricultural crops, and therefore, significant deforestation of alluvial floodplains has occurred in many regions (Junk and Piedade, 1997). The 10.1 million ha Lower Mississippi River

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Alluvial Valley, for example, has experienced a loss of over 75% of its original forest cover, a substantial portion of which occurred during the last few decades (MacDonald et al., 1979; Turner et al., 1981). As commodity prices are influenced by the global economy, environmental benefits of wetlands are advocated, and land management philosophies shift towards landscape or regional scales, the value of reestablishing forest cover on alluvial floodplains is being recognized. As a result, afforestation programs have arisen on many parts of the globe, including within the Lower Mississippi River Alluvial Valley. In this region, afforestation programs primarily target reestablishment of bottomland hardwood forest types on alluvial sites which have proven marginally economical for production of agricultural crops (Amacher et al., 1998; Stanturf et al., 1998).

The significant amount of land in the Lower Mississippi River Alluvial Valley being enrolled into afforestation programs, over 180,000 ha projected through the year 2005 in the three states of Louisiana, Mississippi and Arkansas (Stanturf et al., 1998), has precipitated a prevailing need for the development of biologically sound, alternative afforestation systems. Current afforestation practices utilized in the Lower Mississippi River Alluvial Valley typically provide land managers with few options for meeting a relatively narrow range of management objectives. For example, King and Keeland (1999) reported that the majority of afforestation activities in the Lower Mississippi River Alluvial Valley are implemented with the primary objective of enhancing wildlife habitat, and nearly 80% of the planting stock used in these plantations are hard mast, oak (*Quercus* spp.) species. Clearly, additional systems are needed that will afford land managers alternative approaches for meeting a wide array of potentially desirable afforestation objectives.

Innovative examples of afforestation systems designed to facilitate rehabilitation of several ecological processes can be found in other regions of the world, especially tropical regions where fast growing plantation species serve to rehabilitate degraded sites. By rapidly accumulating above and below ground biomass on what are often adverse sites, a number of tree species grown in plantations have proven to be ideally suited for stabilizing soil, increasing soil organic matter, nutrient or water holding capacity, providing understory environments conducive for natural or artificial regeneration of native species, or providing habitat for native fauna (Ashton et al., 1997, 1998; Fisher, 1995; Lugo, 1997; Mapa, 1995; Parrotta, 1999). Furthermore, a properly managed tree plantation may also provide revenue for recouping the initial afforestation investment without significantly disrupting the rehabilitation process (Kosonen et al., 1997; Parrotta, 1992). Thus, these models from other regions illustrate the opportunity for utilizing fast growing plantation species in afforestation programs to rehabilitate ecological processes and establish forest cover on former agricultural land within the Lower Mississippi River Alluvial Valley.

The native, pioneer species eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) is well suited for plantation culture, and could potentially facilitate rapid rehabilitation of forest ecosystems in the Lower Mississippi River Alluvial Valley. Other scientists working in the Lower Mississippi River Alluvial Valley have developed an experimental afforestation system which utilizes eastern cottonwood as a nurse crop for slower growing bottomland hardwood species (Twedt and Portwood, 1997; Schweitzer et al., 1997; Stanturf and Shepard, 1995). In this system, disturbance-dependent hard mast species, such as Nuttall oak (*Quercus nuttallii* Palm.), which exhibit limited seed dispersal under natural conditions, are interplanted within an established eastern cottonwood plantation. The rapid growth of cottonwood plantations are expected to catalyze rehabilitation by providing a favorable understory environment for establishment of the planted oaks and other volunteer woody vegetation, by improving soil quality (Thornton et al., 1998), and by providing stand structure for fauna1 habitat (Twedt and Portwood, 1997). Though this system shows promise as a tool for rapid establishment of mixed species stands, little is known about the understory environment of eastern cottonwood stands, and resource requirements for regeneration of other bottomland hardwood species such as oaks. Establishing base-line values for light availability in the eastern cottonwood understory, and determining how Nuttall oak seedlings acclimate to this environment is vital to development of this nurse crop system. The purpose of this research was to determine if light availability in the understory of an eastern cottonwood plantation was adequate for maintaining photosynthesis of interplanted Nuttall oak seedlings. Our primary objectives were to describe the light environment in the understory of an eastern cottonwood plantation, and quantify the photosynthetic light response of interplanted Nuttall oak seedlings. Additionally, the nitrogen concentration of Nuttall oak leaves was examined to determine its role in the photosynthetic light response of these seedlings established on a former agricultural field.

2. Methods

2.1. Study site and plantation description

The study was established in the Lower Mississippi River Alluvial Valley within the holdings of the Yazoo National Wildlife Refuge, Sharkey County, Mississippi, USA (latitude = 32°58′N, longitude = 90°44′W). Soil on the study site was predominately Sharkey Clay (very fine, smectitic, thermic, chromic EPIAQUERTS). Regional mean air temperatures range from 7.5°C in January to 27.8°C in July (Scott and Carter, 1962). Rainfall in the region averages 1318 mm per year, with about 60% of the yearly precipitation occurring between December and May. Short-term inundations are common on the site during the late winter and early spring of wet years, as a result of backwater flooding of adjacent rivers, and by surface ponding of rainwater due to slow infiltration into the low permeability clay soil. A mixed species bottomland hardwood forest originally occupied the study site which was deforested and cultivated for soybean (*Glycine max* (L.) Merrill) production over 25 years ago. In 1994, agricultural operations ceased and the site was scheduled for afforestation.

The study site was double disked in the fall of 1994 after the soybean crop was harvested. In March of 1995, an eastern cottonwood plantation was established on the site in three, 8.1 ha plots according to methods used by Crown Vantage paper company (Schweitzer et al., 1997). Prior to planting cottonwood, the site was subsoil plowed with furrows spaced 3.7 m apart, and fertilizer was injected into the furrows at a rate of 112 kg N ha^{-1} (50% NH_4NO_3, 50% $CO(NH_2)_2$). Cottonwood cuttings (0.45 m long) were planted on a 3.7 m x 3.7 m spacing in single clone blocks, and a tank mix of oxyfluorofen and glyphosate (0.26 and 1.4 kg ha^{-1}) herbicides was applied over each row while the cuttings were dormant. Additional weed control in the plantation included basal applications of oxyfluorofen in the first growing season, and disking during the first two growing seasons. After the second cottonwood growing season (February 1997), 1-0, bareroot Nuttall oak seedlings were hand planted on a 3.7 m x 7.3 m spacing, i.e. between every other eastern cottonwood row (Schweitzer et al., 1997). At this same time, three Nuttall oak plantings were established at 3.7 m x 3.7 m spacing in open areas adjacent to each cottonwood plot. These Nuttall oak plantings, which are typical of conventional afforestation plantings in the Lower Mississippi River Alluvial Valley, were established to serve as control plots for the measurement of environmental and physiological variables in an open field.

2.2. Environment and physiology measurements

Photosynthetic photon flux density (PPFD) was measured in a randomly selected cottonwood plot and an adjacent open plot throughout the growing season (April–October 1997). A LI-COR® LI-190SA quantum sensor placed in the open and a LI-191SA line quantum sensor placed in the cottonwood understory were used to record PPFD in each environment on a 15 min interval. Environmental and physiology measurements in cottonwood plots were conducted beneath a single, randomly selected cottonwood clone (Stoneville-66) to reduce sample variation.

Fifty Nuttall oak seedlings were randomly selected in each plot to serve as measurement seedlings. Measurement seedlings were protected from small mammal herbivory with 0.6 m tall x 0.6 m diameter wire mesh shelters. The wire mesh shelters afforded effective herbivory protection without influencing ambient light availability.

Photosynthetic response to light availability was measured on Nuttall oak seedlings during their first growing season (September 1997). Six seedlings were randomly selected from the pool of sheltered seedlings in each plot (18 seedlings established beneath cottonwood and 18 seedlings established in the open). Seedlings were watered the evening before sampling, and covered with a cloth canopy that eliminated sunlight. These steps were taken to ensure moisture deficits or early morning photosynthetic activity did not influence measured leaf response. To reduce sample variation, only mature leaves of Lag stage seedlings (those exhibiting a quiescent period of stem and leaf growth) were sampled (Hanson et al., 1986). And, second flush leaves were measured to avoid possible residual effects of nursery culture on leaf development and physiology. Photosynthetic response to light availability was measured at six light levels on one leaf from each sample seedling with a PP-Systems Ciras-1 infrared gas analyzer, automatic leaf cuvette and light attachment. Cuvette CO_2 was maintained at 353 ± 0.2 μmol mol^{-1} and cuvette air temperature was adjusted to 29 ± 0.1°C during sampling. Sample leaves were allowed to acclimate to a maximum PPFD of 1800 μmol m^{-2} s^{-1} before measurements began. After the initial measurement at 1800 μmol m^{-2} s^{-1}, light availability was reduced to produce five subsequent light levels (800, 300, 150, 50, and 0 μmol m^{-2} s^{-1}) at which photosynthesis was recorded. Measurements were taken in this fashion because these Nuttall oak leaves exhibited a relatively slow stomatal response to light. An acclimation period of 20-30 min was typically necessary to reach stable photosynthesis at 1800 μmol m^{-2} s^{-1}, while a 5 min acclimation period was usually adequate at the other light levels. Due to the required sample time, only two or three leaves were measured on a given sample morning.

After photosynthesis measurements, sample leaves were clipped and brought to the laboratory for determination of blade area (cm^2), dry mass per unit area (mg cm^{-2}), nitrogen (N) concentration (%), and N content (mg cm^{-2}). N concentration was quantified on each sample leaf using Dumas combustion techniques described by Jones and Case (1990) at the Forest Ecophysiology Laboratory, Department of Forestry, Mississippi State University, USA.

Mean daily PPFD and total daily PPFD were calculated from PPFD records collected on a cloud-free day during the early (May), mid (July) and late (September) growing season in 1997. The light environment of each treatment was further quantified by computing daily percentages of availability for three critical levels of sunlight on the photosynthetic light response curve.

Photosynthetic light response data were modeled using methods and Eq. (1) as outlined by Givnish (1988).

$$P_{\mathrm{n}} = \frac{P_{\mathrm{g\text{-}sat}} \times \mathrm{PPED}}{(K + \mathrm{PPED})} - R_{\mathrm{d}} \tag{1}$$

In Eq. (1), P_{n} is net photosynthesis rate, $P_{\mathrm{g\text{-}sat}}$ the gross photosynthesis rate at light saturation, K the PPFD required to achieve half of $P_{\mathrm{g\text{-}sat}}$, and R_{d} the dark respiration rate.

Eq. (2) was used to compute the light compensation point (LCP).

$$\mathrm{LCP} = \frac{-K \times R_{\mathrm{d}}}{(R_{\mathrm{d}} - P_{\mathrm{g\text{-}sat}})} \tag{2}$$

Eq. (3) is the first derivative with respect to PPFD of Eq. (1) that was used to determine quantum yield (Q) with PPFD set at the LCP.

$$Q = P_{\mathrm{g\text{-}sat}} \times \frac{K}{(K^2 + 2K \times \mathrm{PPFD} + \mathrm{PPFD}^2)} \tag{3}$$

$P_{\mathrm{g\text{-}sat}}$, $P_{\mathrm{n\text{-}sat}}$, R_{d}, Q, LCP, and K were computed on an area, dry mass, and N content basis for each sample leaf. Analysis of variance according to a randomized block design was used to quantify treatment differences in light response variables, blade area, leaf dry mass per unit area, leaf N concentration, and N content. Simple linear regression was used to model the relationship between leaf N concentration and photosynthesis. All tests of significance were conducted at an a level of 0.05.

3. Results

3.1. Light environment

After initial leaf-out of the eastern cottonwood canopy, PPFD in the understory of the cottonwood plantation was about 75% of that available in the open, with highest availability occurring in the morning (Table 1, Fig. 1). Leaf area of the cottonwood canopy increased over the course of the growing season leading to a further depression of light availability in the cottonwood understory (Fig. 1). By the end of the growing season, the cottonwood canopy appeared to have reached maximum leaf area index, and light availability was reduced to 43% of that available in the

Table 1
Photosynthetic photon flux density (PPFD) in the open and in the **understory** of an eastern cottonwood plantation for 3 clear days in the early, mid and late growing season, Sharkey County, MS, USA

Variable	16 May 1997		18 July 1997		15 September 1997	
	Open	Understory	Open	Understory	Open	Understory
Mean PPFD (μmol m^{-2} s^{-1})	1145	870	1077	526	969	422
Total daily PPFD (mol m^{-2} per day)	58.7	44.6	56.2	26.9	44.5	19.4
PPFD > 500 μm^{-2} s^{-1} (% of day)	75	61	72	49	69	29
PPFD > 80 μmol m^{-2} s^{-1} (% of day)	91	79	90	74	90	76
PPFD > 20ymol m^{-2} s^{-1} (% of day)	96	93	96	93	96	90

open (Table 1). We did not measure leaf area index in the cottonwood plantation, but this point of stand development was evident from the vertical growth of the cottonwood canopy and self-pruning of lower-most branches. Though the fully developed cottonwood canopy limited light availability, the understory received a PPFD greater than 500 μmol m^{-2} s^{-1} nearly 30% of the diurnal period (Table 1, Fig. 1).

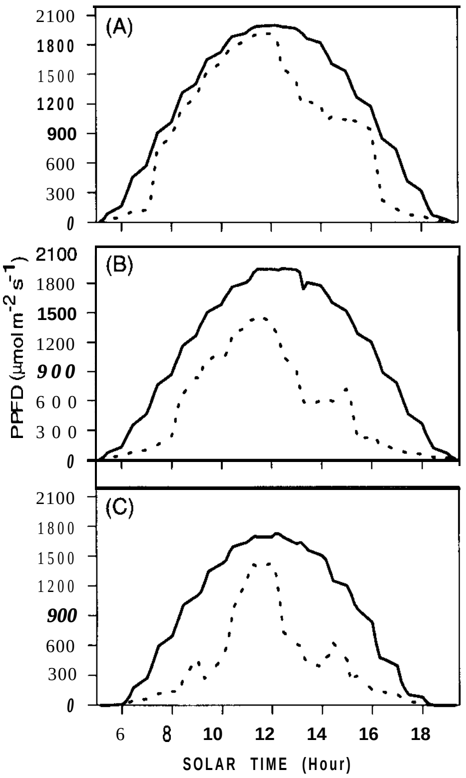

Fig. 1. Diurnal light availability in the open (solid line) and in the understory (dashed line) of an eastern cottonwood plantation on clear days during the early (16 May 1997) (Tile A), mid (18 July 1997) (Tile B), and late (15 September 1997) (Tile C) growing season, Sharkey County, MS, USA (PPFD: photosynthetic photon flux density).

3.2. Leaf morphology and nitrogen content

Nuttall oak seedlings growing in the understory of the eastern cottonwood plantation developed leaf blade areas similar to those of seedlings in the open field (Table 2). However, the leaf mass per unit area was 18% greater for leaves of open-grown seedlings than those of seedlings in the cottonwood understory (Table 2). N concentration of Nuttall oak leaves was similar in both environments and comprised about 1.5% of dry leaf weight (Table 2). N content was greatest in open-grown leaves, because of their greater leaf mass per unit area (Table 2).

3.3. Photosynthetic light response

Photosynthetic light response of Nuttall oak leaves was not substantially altered by the eastern cottonwood canopy (Fig. 2). R_d rates of understory-grown leaves were 19% lower than those of open-grown seedlings, but other light response variables did not differ (Table 2). Nuttall oak leaves exhibited similar values for $P_{g\text{-sat}}$, $P_{n\text{-sat}}$, Q, LCP, and K (Table 2), regardless of the light environment in which they developed (Table 2). Photosynthetic light response results expressed on a dry weight and N content basis were similar to those on an area basis in that the presence of the cottonwood canopy did not incite a change in leaf physiology (Fig. 2, Table 2).

Evaluation of critical points on the Nuttall oak light response curve revealed that light availability in the

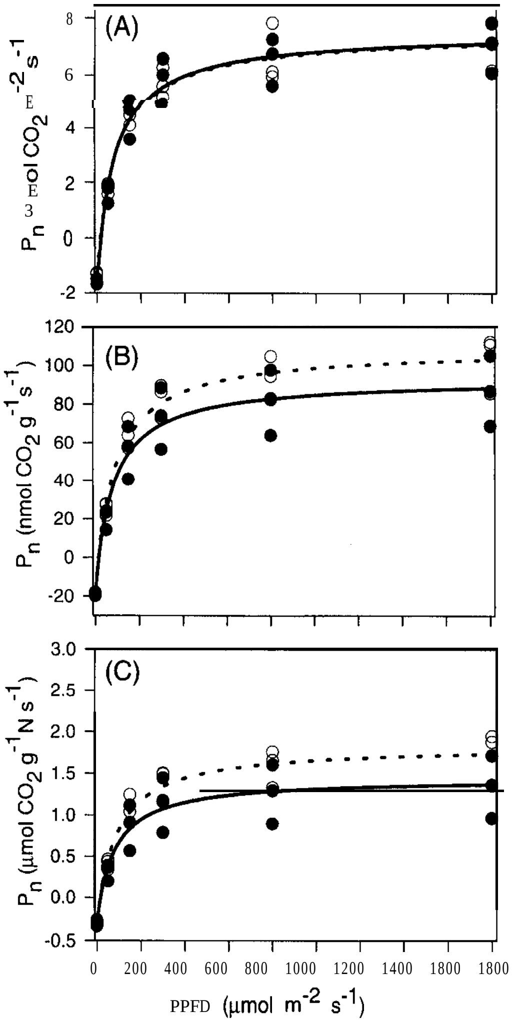

Fig. 2. Light response curves for photosynthesis of Nuttall oak leaves measured on open-grown seedlings (solid line, filled dot) versus seedlings grown in the understory (dashed line, empty dot) of an eastern cottonwood plantation, Sharkey County, MS, USA. Tile (A) is photosynthesis based on leaf area, tile (B) is photosynthesis based on dry leaf mass, tile (C) is photosynthesis based on leaf nitrogen content (PPFD: photosynthetic photon flux density).

cottonwood understory may be adequate for maintaining photosynthetic function of Nuttall oak leaves. Early in the growing season, light availability in the cottonwood understory met leaf-level compensation and saturation requirements for 90 and 60%, respectively, of the diurnal period (Tables 1 and 2). After full development of the cottonwood canopy, light remained sufficiently available to meet requirements for leaf-level compensation over 90% of the diurnal period (Tables 1 and 2). For over 76% of the diurnal period, Nuttall oak leaves in the cottonwood understory received an amount of light sufficient to assimilate carbon at half the saturation level (Tables 1 and 2). And, light availability in the cottonwood understory exceeded leaf-level saturation requirements for about 29% of the diurnal cycle (Tables 1 and 2).

3.4. Nitrogen-photosynthesis relationships

Though light environment did not influence N level of Nuttall oak leaves, leaf N concentrations ranged from 1.06 to 2.02% across the study site. Maximum rates of net photosynthesis showed a strong linear relationship with foliar N, with about 66% of the variation in $P_{\text{n-sat}}$ attributable to leaf N concentration ($P > 0.001$) (Fig. 3). To determine if N concentration influenced other components of photosynthetic light response, light response curves were developed from a sub-sample of six Nuttall oak leaves with relatively low N ($\bar{x} = 1.11\%$) and six leaves with relatively high N ($\bar{x} = 1.85\%$) (Fig. 4). This test revealed that R_d, LCP, and Q were not influenced by leaf N concentration, but that $P_{\text{g-sat}}$ ($P > 0.0001$) was the primary

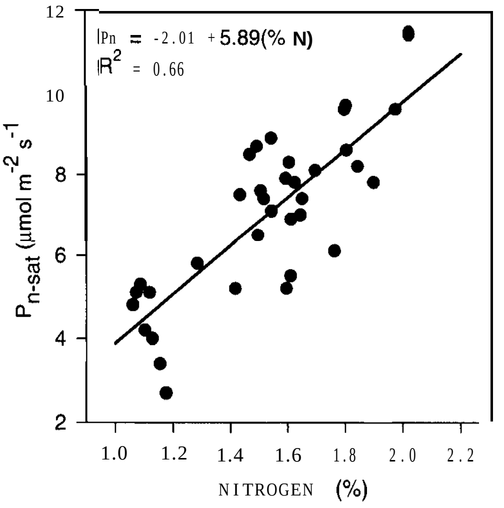

Fig. 3. The relationship between maximum rate of net photosynthesis ($P_{\text{n-sat}}$) and nitrogen concentration in the leaves of Nuttall oak seedlings outplanted on a former agricultural field in Sharkey County, MS, USA.

Table 2
Morphological and photosynthetic characteristics of Nuttall oak leaves measured on open-grown seedlings versus seedlings grown in the understory of an eastern cottonwood plantation, Sharkey County, MS, USA’

Variable[b]	Open	Understory	P-value
	(Mean ± standard error)”	(Mean ± standard error)”	
Blade area (cm*)	23.8 ± 1.4 a	21.2 ± 1.3 a	0.1001
Leaf mass per area (mg cm^{-2})	8.26 ± 0.26 a	6.96 ± 0.14 b	0.0079
Total nitrogen (%)	1.50 ± 0.05 a	1.57 ± 0.08 a	0.1458
Total nitrogen (mg cm^{-2})	0.12 ± 0.01 a	0.10 ± 0.01 b	0.0079
$P_{g\text{-sat}}$ (µmol m^{-2} s^{-1})	9.16 ± 0.44 a	8.81 ± 0.66 a	0.5768
$P_{g\text{-sat}}$ (nmol g^{-1} s^{-1})	113.5 ± 7.2 a	128.6 ± 10.8 a	0.2027
$P_{g\text{-sat}}$ (µmol g^{-1} N s^{-1})	1.76 ± 0.15 a	2.16 ± 0.28 a	0.0837
$P_{n\text{-sat}}$ (µmol m^{-2} s^{-1})	7.10 ± 0.39 a	7.05 ± 0.56 a	0.9318
$P_{n\text{-sat}}$ (nmol g^{-1} s^{-1})	88.3 ± 6.4 a	102.9 ± 9.1 a	0.1755
$P_{n\text{-sat}}$ (µmol g^{-1} N s^{-1})	1.37 ± 0.13 a	1.73 ± 0.23 a	0.0829
R_d (µmol m^{-2} s^{-1})	1.66 ± 0.07 a	1.34 ± 0.07 b	0.0038
R_d (nmol g^{-} s^{-1})	20.3 ± 0.95 a	19.6 ± 1.22 a	0.0554
R_d (µmol g^{-1} N s^{-1})	0.31 ± 0.02 a	0.32 ± 0.03 a	0.1707
Q (µmol CO_2 m^{-2} s^{-1}/µmol photon m^{-2} s^{-1})	0.080 ± 0.004 a	0.078 ± 0.004 a	0.8401
Q (nmol CO_2 g^{-1} s^{-1}/µmol photon m^{-2} s^{-1})	1.00 ± 0.076 a	1.14 ± 0.072 a	0.2650
Q (µmol CO_2 g^{-1} N s^{-1}/µmol photon m^{-2} s^{-1})	0.015 ± 0.001 a	0.018 ± 0.002 a	0.2370
LCP (µmol m^{-2} s^{-1})	17.8 ± 1.37 a	15.0 ± 1.17 a	0.1077
K (µmol m^{-2} s^{-1})	79.3 ± 5.48 a	81.7 ± 7.14 a	0.8164

[a] Photosynthetic variables are expressed on an area basis, dry leaf mass basis and nitrogen content basis.

[b] $P_{g\text{-sat}}$: gross photosynthesis at light saturation, $P_{n\text{-sat}}$: net photosynthesis at light saturation, R_d: dark respiration rate, Q: quantum yield, LCP: light compensation point, K: light needed to attain one-half of $P_{g\text{-sat}}$.

[c] Means in a row followed by the same letter do not differ at the 0.05 probability level.

variable influencing predicted differences in $P_{n\text{-sat}}$. In relation to depressed rates of $P_{g\text{-sat}}$, K was likewise reduced over 50% in leaves with relatively low N ($P = 0.0005$).

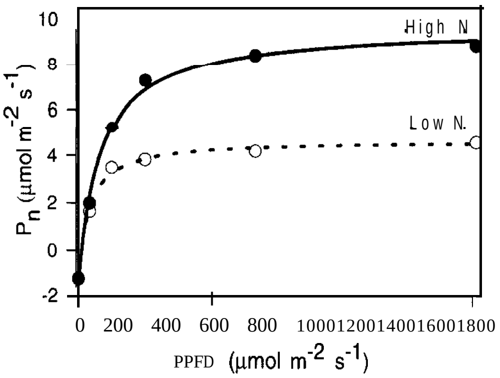

Fig. 4. Light response curves for net photosynthesis (P,) from a sub-sample of Nuttall oak leaves, with relatively high ($\bar{x}$ = 1 .85%) or low ($\bar{x}$ = 1.11%) nitrogen concentrations, collected from seedlings outplanted on a former agricultural field in Sharkey County, MS, USA (PPPD: photosynthetic photon flux density).

4. Discussion

4.1. Light acclimation

Bottomland oak species are typically considered shade intolerant, and low light availability has often been cited as a limitation to establishment and growth of natural oak regeneration (Putnam et al., 1960; Hodges and Gardiner, 1993). Nuttall oak, the species studied in this experiment, is no exception as it is classified as shade intolerant (Filer, 1990; Putnam et al., 1960). Thus, the use of this species in an eastern cottonwood nurse crop system as described above hinges on providing the oak seedling with adequate light to maintain sufficient carbon assimilation for survival and growth. The fully developed eastern cottonwood canopy reduced light availability to 43% of that available in the open. This level of light availability was appreciably higher than those recorded in natural bottomland hardwood stands where understory light availability is often less than 10% of that available in the open (Jenkins and Chambers, 1989). Based on our observations of leaf area and canopy development in the eastern cottonwood plantation, we believe that light availability will remain near 40% through the expected cottonwood rotation (10 years).

Leaves of oak species typically acclimate to low light environments in a morphological fashion similar to leaves of other trees. Environments of low irradiance can incite changes in oak leaf morphology including increased leaf blade area, reduced stomatal density, reduced palisade cell thickness, decreased cuticle thickness, and increased chlorophyll concentration (Abrams and Kubiske, 1990; Ashton and Berlyn, 1994; Hamerlynck and Knapp, 1994; Jarvis, 1964). These morphological responses serve to optimize physiological functioning of leaves in low light environments through several mechanisms. For example, the anatomical or morphological mechanisms listed above may enhance carbon assimilation in low light environments by increasing the light gathering area of leaf blades, facilitating absorption of diffuse light, and increasing photosynthetic yields through decreases in R_d and LCP per unit area (Chow et al., 1988; Hamerlynck and Knapp, 1994; Man and Lieffers, 1997). Nuttall oak leaves that developed in the cottonwood understory in this study did not show an increase in leaf blade area. The mass per unit area for Nuttall oak leaves did decrease in the cottonwood understory, but this decrease was minor relative to other oaks grown in more light limiting environments. Reported values for the decrease in leaf mass per unit area under heavy shade range from 57 to 126% for six other North American oak species (Abrams and Kubiske, 1990; Hamerlynck and Knapp, 1994), while mass per unit area of Nuttall oak in this study decreased less than 19% on leaves that developed in the cottonwood understory.

The principal focus of this research was to examine the physiological acclimation of Nuttall oak leaves growing in an eastern cottonwood understory, specifically the photosynthetic light response. Adjustments to photosynthetic light response made by oak leaves which developed under limiting light in other studies included decreased R_d, decreased LCP, decreased $P_{n\text{-sat}}$, and lowered light levels required for saturation (Bazzaz and Carlson, 1982; Hamerlynck and Knapp, 1994; Kubiske and Pregitzer, 1996; Naidu and DeLucia, 1997; Teskey and Shrestha, 1985). In contrast, Jarvis (1964) reported that shade acclimated *Quercus petraea* leaves had higher $P_{n\text{-sat}}$ rates than sun-grown leaves due to photoinhibition of the open-grown leaves. In this study, the presence of the eastern cottonwood canopy did not induce a significant change in the photosynthetic light response of Nuttall oak leaves. Furthermore, the instantaneous photosynthetic N-use efficiency, which can be governed by light availability (Field, 1988), was not altered by the light environment in the eastern cottonwood understory. R_d rates of leaves were slightly lower on an area basis, but all other components of light response did not differ between the two light environments, regardless of leaf area, leaf mass or N content. Two possible explanations exist for this lack of physiological difference. One explanation is that photosynthesis of open-grown leaves was limited by photoinhibition. A direct measurement of photoinhibition (chlorophyll fluorescence) was not conducted in this study, but this explanation seems unlikely because $P_{n\text{-sat}}$ did not increase under the protection of the cottonwood canopy and Nuttall oak is a shade intolerant species. A more plausible explanation is that the light environment in the cottonwood understory was sufficient enough to allow adequate development of the photosynthetic mechanism. Since eastern cottonwood forms a relatively open crown habit, and branches of plantation grown trees do not usually overlap, much of the radiation in the cottonwood understory was received as full sunlight which penetrated through crowns or between cottonwood rows as large flecks. Thus, it is reasonable to suggest that Nuttall oak leaves in the cottonwood understory experienced appreciable episodes of full sunlight, and developed a photosynthetic mechanism capable of utilizing this radiation. Indeed, these findings are in agreement with Dean et al. (1982) who reported that shade-grown leaves of black walnut (*Juglans nigru* L.) exposed to light flecks develop a photosynthetic capacity similar to open-grown leaves.

4.2. Nitrogen limitations to photosynthesis

Nitrogen has been critically linked to the photosynthetic process of forest trees as a component of the chlorophyll molecule, Rubisco, and other vital proteins (Givnish, 1988; Field and Mooney, 1986; Tan and Hogan, 1995). As found in this study, $P_{\text{n-sat}}$ of oak species typically shows a strong positive relationship with foliar N concentrations (Hollinger, 1992; Reich et al., 1991), presumably resulting in part from the role of N in the carboxylation process by Rubisco (Field, 1988; Givnish, 1988). It has also been demonstrated that N plays a significant role in the acclimation of some woody plant leaves to low light environments and their sensitivity to photoinhibition (Mitchell, 1998; Naidu and DeLucia, 1997; Walters and Field, 1987). In low light environments, a larger fraction of N is typically allocated to chlorophyll synthesis at the expense of Rubisco which is favored in high light environments (Evans, 1989a; Seemann et al., 1987; Björkman, 1981). Though not influenced by the light environment, foliar N concentrations of Nuttall oak seedlings planted on the former agricultural field in this study exhibited nearly two-fold variation. $P_{\text{n-sat}}$ of Nuttall oak was sensitive to foliar N, as it rose almost 1.2 $\mu\text{mol m}^{-2}\,\text{s}^{-1}$ for each 0.1% increase in N concentration. Most of the photosynthetic response to foliar N was observed as a change in $P_{\text{g-sat}}$, indicating that carbon fixation may be impaired under low N and high light due to enzymatic limits on carboxylation (Zhang et al., 1997). This is consistent with observations made by Evans (198913) who noted that as foliar N increases, the proportion of N allocated to Rubisco increases relatively more than the proportion fixed in chlorophyll and other thylakoid proteins. We speculate that the range in foliar N observed on leaves from our study site was reflective of a locally depleted nutrient pool on this former agricultural site. Surface horizon soil samples collected at an adjacent stand of native bottomland hardwoods revealed a N concentration 53% greater than in soil sampled at our study site (Stephen Schoenholtz, Department of Forestry, Mississippi State University, USA, unpublished data, 1995). This evidence of depleted soil N, and the strong dependence of Nuttall oak photosynthesis to foliar N suggests that carbon assimilation will be sub-optimal when Nuttall oak seedlings are established on intensively cropped, N-depleted soils of the Lower Mississippi River Alluvial Valley.

A logical question to follow our findings on leaf physiology is: do the reduced rates of photosynthesis resulting from low foliar N influence seedling survival or growth? Survival of sample seedlings was 100% through the first growing season, indicating that N deficiencies did not lead to first-year mortality. Because the primary objectives of this study were focused on leaf physiology, we did not collect data sufficiently detailed to rigorously test for a relationship between first-year seedling growth and foliar N. However, limited data we collected on seedling biomass did not indicate a significant linear relationship between foliar N and total seedling biomass (P = 0.5204, data not shown). Future studies focused on linkages between oak seedling growth and physiological function in respect to N will be necessary to elucidate the ultimate effect of N on seedling productivity.

5. Management implications

Several implications relevant to afforestation of former agricultural fields in alluvial floodplains may be drawn from this research. Current afforestation practices in the Lower Mississippi River Alluvial Valley do not provide landowners alternatives for optimizing a wide array of potential management objectives. A nurse crop system such as described above for eastern cottonwood and Nuttall oak can provide an early financial return while catalyzing forest rehabilitation. Results of this study indicate that light availability in the cottonwood understory is much greater than those typical of native bottomland hardwood stands. Leaves of Nuttall oak seedlings established in the cottonwood understory showed minimal morphological acclimation and developed the physiological capacity to assimilation carbon at rates similar to open-grown seedlings. These results indicate the potential for successfully intercropping disturbance-dependent species such as Nuttall oak with early successional species like eastern cottonwood. An afforestation system such as this may offer land managers multiple benefits including quick financial return while enhancing other ecological functions on degraded sites.

Afforestation sites are often severely degraded providing harsh conditions for seedling establishment and growth. Nutrient limitations may be encountered on such sites and should be addressed during development of afforestation plans. Our findings warrant concern over current afforestation projects in the Lower Mississippi River Alluvial Valley, because few initiate soil sampling procedures to identify potential deficiencies. Though we recognize that many environmental factors contribute to determining seedling survival and growth, this research has identified that carbon assimilation of Nuttall oak may be less than optimal if seedlings are established on intensively cropped agricultural sites where N pools were depleted. Practices should be implemented to identify soil nutrient deficiencies during planning procedures. Future research is needed to develop cultural practices, such as fertilization, legume crop establishment, or competition control schemes, which improve nutrient availability to seedlings planted on degraded agricultural sites.

Finally, identifying the biological needs of planting stock should be a critical component of forest rehabilitation programs in alluvial floodplains. Loik and Holl (1999) argued that developing cost effective afforestation methods hinges on identifying the ecological factors which govern survival and growth of reproduction. As demonstrated by this research, an understanding of how basic plant functions are affected by environmental factors can be used to develop successful afforestation methods for forest rehabilitation.

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References

Abrams, M.D., Kubiske, M.E., 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. For. Ecol. Manage. 31, 245-253.

Amacher, G.S., Sullivan, J., Shabman, L., Zepp, L., Grebner, D., 1998. Reforestation of flooded farmland. J. For. 96, 10–17.

Ashton, P.M.S., Berlyn, G.P., 1994. A comparison of leaf physiology and anatomy of Quercus (Section *Erythrobalanus*-Fagaceae) species in different light environments. Am. J. Bot. 81, 589-597.

Ashton, P.M.S., Gamage, S., Gunatilleke, I.A.U.N., Guanatilleke, C.V.S., 1997. Restoration of a Sri Lankan rain forest: using Caribbean pine ***Pinus caribaea*** as a nurse for establishing late-successional species. J. Appl. Ecol. 34, 915-925.

Ashton, P.M.S., Gamage, S., Gunatilleke, I.A.U.N., Guanatilleke, C.V.S., 1998. Using Caribbean pine to establish a mixed plantation: testing effects of pine canopy removal on plantings of rain forest tree species. For. Ecol. Manage. 106, 211–222.

Bazzaz, EA., Carlson, R.W., 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54, 313-316.

Björkman, O., 1981. Responses to different quantum flux densities. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Physiological Plant Ecology. I. Responses to the Physical Environment. Encycl. Plant Physiol. New Ser., Springer, New York, Vol. 12A, pp. 57–107.

Brinson, M.M., 1990. Riverine forests. In: Lugo, A.E., Brinson, M.M., Brown, S. (Eds.), Ecosystems of the World, Forested Wetlands. Elsevier, New York, pp. 87-141.

Chow, W.S., Qian, L., Goodchild, D.J., Anderson, J.M., 1988. Photosynthetic acclimation of ***Alocasia macrorrhiza*** (L.) G. Don to growth irradiance: structure, function and composition of chloroplasts. Aust. J. Plant Physiol. 15, 107–122.

Dean, T.J., Pallardy, S.G., Cox, G.S., 1982. Photosynthetic responses of black walnut (*Juglans nigra*) to shading. Can. J. For. Res. 12, 725–730.

Evans, J.R., 1989a. Partitioning of nitrogen between and within leaves grown under different irradiances. Aust. J. Plant Physiol. 16, 533-548.

Evans, J.R., 1989b. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78, 9-19.

Field, C.B., 1988. On the role of photosynthetic responses in contrasting the habitat distribution of rainforest plants. Aust. J. Plant Physiol. 15, 343-358.

Field, C., Mooney, H.A., 1986. The photosynthesis-nitrogen relationship in wild plants. In: Givnish, T.J. (Ed.), On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, pp. 25-55.

Filer, T.H., Jr., 1990. ***Quercus*** *nuttallii* Palmer-Nuttall Oak. In: Bums, R.M., Honkala, B.H., (Tech. Coord.) Silvics of North America, vol. 2, Hardwoods, USDA FS Agriculture Handbook ***654,*** pp. 704–708.

Fisher, R.F., 1995. Amelioration of degraded rain forest soils by plantations of native trees. Soil Sci. Soc. Am. J. 59, 544–549.

Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol. 15, 63-92.

Hamerlynck, E.P., Knapp, A.K., 1994. Leaf-level responses to light and temperature in two co-occurring *Quercus* (Fagaceae) species: implications for tree distribution patterns. For. Ecol. Manage. 68, 149-159.

Hanson, P.J., Dickson, R.E., Isebrands, J.G., Crow, T.R., Dixon, R.K., 1986. A morphological index of Quercus seedling ontogeny for use in studies of physiology and growth. Tree Physiol. 2, 273-281.

Hodges, J.D., Gardiner, E.S., 1993. Ecology and physiology of oak regeneration, In: Loftis, D.L., McGee, C.E. (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations, USDA Forest Service, Asheville, NC, Gen. Tech. Rep. SE-84, pp. 54-65.

Hollinger, D.Y., 1992. Leaf and simulated whole-canopy photosynthesis in two co-occurring tree species. Ecology 73, 1-14.

Jarvis, P.G., 1964. The adaptability to light intensity of seedlings of *Quercus petraea* (Matt.). Liebl. J. Ecol. 52, 545-571.

Jenkins, M.W., Chambers, J.L., 1989. Understory light levels in mature hardwood stands after partial overstory removal. For. Ecol. Manage. 26, 247-256.

Jones, J.B., Case, V.W., 1990. Sampling, handling, analyzing plant tissue samples. In: Westerman, R.L. (Ed.), Soil Testing and Plant Analysis, 3rd ed. Soil Science Society of America, Madison, WI, pp. 3899427.

Junk, W.J., 1997. General aspects of floodplain ecology with special reference to Amazonian floodplains. In: Junk, W.J. (Ed.), The Central Amazon Floodplain, Ecology of a Pulsing System. Ecological Studies, vol. 126. Springer, New York, pp. 3–20.

Junk, W.J., Piedade, M.T.F., 1997. Plant life in the floodplain with special reference to herbaceous plants. In: Junk, W.J. (Ed.), The Central Amazon Floodplain, Ecology of a Pulsing System. Ecological Studies, vol. 126. Springer, New York, pp. 147-185.

King, S.L., Keeland, B.D., 1999. Evaluation of reforestation in the Lower Mississippi River Alluvial Valley. Rest. Ecol. 7, 348-359.

Kosonen, M., Otsamo, A., Kuusipalo, J., 1997. Financial, economic, and environmental profitability of reforestation of *Imperata* grasslands in Indonesia. For. Ecol. Manage. 99, 247-259.

Kubiske, M.E., Pregitzer, K.S., 1996. Effects of elevated CO_2 and light availability on the photosynthetic light response of trees of contrasting shade tolerance. Tree Physiol. 16, 351-358.

Loi, M.E., Holl, K.D., 1999. Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. Rest. Ecol. 7, 382-391.

Lugo, A.E., 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. For, Ecol. Manage. 99, 9-19.

MacDonald, P.O., Frayer, W.E., Clauser, J.K., 1979. Documentation, chronology, and future projections of bottomland hardwood habitat losses in the lower Mississippi Alluvial Plain, vols. 1 and 2. U.S. Fish and Wildlife Service, Washington, DC, 34 PP.

Man, R., Lieffers, V.J., 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. Tree Physiol. 17, 437-444.

Mapa, R.B., 1995. Effect of reforestation using *Tectona grandis* on infiltration and soil water retention. For. Ecol. Manage. 77, 119–125.

Mitchell, A.K., 1998. Acclimation of Pacific yew (*Taxus brevifolia*) foliage to sun and shade. Tree Physiol. 18, 749-757.

Naidu, S.L., DeLucia, E.H., 1997. Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. Tree Physiol. 17, 367-376.

Parrotta, J.A., 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agric. Ecosyst. Environ. 41, 115–133.

Parrotta, J.A., 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. For. Ecol. Manage. 124, 45-77.

Putnam, J.A., Furnival, G.M., McKnight, J.S., 1960. Management and inventory of southern hardwoods. USDA Forest Service, Agricultural Handbook No. 181, 102 pp.

Reich, P.B., Walters, M.B., Ellsworth, D.S., 1991. Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. Plant Cell Environ. 14, 251-259.

Schweitzer, C.J., Stanturf, J.A., Shepard, J.P., Wilkins, T.M., Portwood, C.J., Dorris, L.C., Jr., 1997. Large-scale comparison of reforestation techniques commonly used in the Lower Mississippi Alluvial Valley: first-year results. In: Pallardy, S.G., Cecich, R.A., Garrett, H.G., Johnson, P.S. (Eds.), 11th Central Hardwood Forest Conference, pp. 313–320.

Scott, ET., Carter, R.C., 1962. Soil survey of Sharkey County, Mississippi. United States Department of Agriculture, Soil Conservation Service, 36 pp.

Seemann, J.R., Sharkey, T.D., Wang, J., Osmond, C.B., 1987. Environmental effects on photosynthesis, nitrogen-use efficiency, and metabolite pools in leaves of sun and shade plants. Plant Physiol. 84, 796–802.

Stanturf, J.A., Schweitzer, C.J., Gardiner, E.S., 1998. Afforestation of marginal agricultural land in the Lower Mississippi River Alluvial Valley, USA. Silva Fennica 32, 281-297.

Stanturf, J.A., Shepard, J.P., 1995. Bottomland hardwood restoration in the Lower Mississippi River Alluvial Floodplain, United States. In: Linn, R.M. (Ed.), 8th Conference on Research and Resource Management in Parks and on Public Lands. The George Wright Society, Hancock, Michigan, pp. 250–256.

Tan, W., Hogan, G.D., 1995. Limitations to net photosynthesis as affected by nitrogen status in jack pine (*Pinus banksiana* Lamb.) seedlings. J. Exp. Bot. 46, 407–413.

Teskey, R.O., Shrestha, R.B., 1985. A relationship between carbon dioxide photosynthetic efficiency and shade tolerance. Physiol. Plant. 63, 126–132.

Thornton, F.C., Joslin, J.D., Bock, B.R., Houston, A., Green,T.H., Schoenholtz, S., Pettry, D., Tyler, D.D., 1998. Environmental effects of growing woody crops on agricultural land: first year effects on erosion, and water quality. Biomass Bioenergy 15, 57–69.

Turner, R.E., Forsythe, SW., Craig, N.J., 1981. Bottomland hardwood forestland resources of the southeastern United States. In: Clark, J.R., Benforado, J. (Eds.), Wetlands of Bottomland Hardwood Forests. Elsevier, New York, pp. 13-28.

Twedt, D.J., Portwood, J., 1997. Bottomland hardwood reforestation for Neotropical migratory birds: are we missing the forest for the trees? Wildl. Soc. Bull. 25, 647-652.

Walters, M.B., Field, C.B., 1987. Photosynthetic light acclimation in two rainforest *Piper* species with different ecological amplitudes. Oecologia 72, 449-456.

Zhang, S., Hennessey, T.C., Heinemann, R.A., 1997. Acclimation of loblolly pine (*Pinus taeda*) foliage to light intensity as related to leaf nitrogen availability. Can. J. For. Res. 27, 1032-1040.