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Original article

Effects of light intensity on the growth and energy balance of photosystem II electron transport in *Quercus alba* seedlings

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Abstract – *Quercus alba* (white oak) seedlings were grown at four levels of irradiance (5, 15, 30 and 100% of full sunlight) under a rain out shelter. After one growing season, the greatest diameter and height growth, biomass (root, leaf, and stem) and leaf area were observed on seedlings under 100% of full sunlight. Seedlings under 15, 30 and 100% of full sunlight allocated more biomass to roots (~ 70%) than seedlings under 5% of full sunlight (~ 58%), suggesting a priority in root growth unless light is severely limited. Leaf weight ratio, specific leaf area, and leaf area ratio increased with the degree of shading, indicating acclimation of leaves to different light intensities. Acclimation to light intensity closely correlated with the fluorescence parameter 1–q_P. Non-photochemical quenching was also affected as shade intensity increased. The apparent reduction in electron transport rate (ETR) through photosystem II (PS II) increased with light intensity, and light saturated ETR under 5% of full sunlight was only 46% of that under full sunlight. The shift from photochemical to non-photochemical quenching occurred in response to increasing actinic light and as growth irradiance declined, the 'quenching shift rate' declined as well. Overall, *Quercus alba* seedlings demonstrated strong growth and allometric responses to light intensity.

white oak / shade tolerance / biomass allocation / modulated chlorophyll fluorescence / light acclimation

Résumé – Effets de l'intensité lumineuse sur la croissance et la balance énergétique du transport d'électrons du photosystème II chez des semis de *Quercus alba*. Des semis de *Quercus alba* ont été élevés à quatre niveaux d'éclairement (5, 15, 30, et 100 % du plein éclairement). Après une saison de végétation, le diamètre et la croissance en hauteur, la biomasse (racine, feuille, tige) et la surface foliaire les plus importants ont été observés pour les semis poussant sous 100 % de lumière. Les semis poussant sous 15, 30 et 100 % d'éclairement ont alloué plus de biomasse aux racines (environ 70 %) que les semis poussant sous 5 % de lumière (environ 48 %) suggérant une priorité à la croissance des racines sauf quand l'éclairement est fortement limité. Le poids des feuilles rapporté à la biomasse totale, la surface spécifique des feuilles, la surface des feuilles rapportée à la biomasse totale s'accroissent avec l'importance de l'ombre, indiquant l'acclimatation des feuilles aux différents niveaux d'éclairement. L'acclimatation à la lumière est étroitement corrélée avec le paramètre de flurescence1–qp. Le quenching non-photochimique était aussi influencé par l'accroissement de l'ombre. L'apparente réduction dans le taux de transport d'électrons (ETR) à travers le photosystème II (PS II) s'accroît avec l'importance de l'éclairement et ETR saturé sous 5 % d'éclairement ne représentait que 46 % seulement de celui sous pleine lumière. Le changement entre quenching photochimique et non-photochimique intervient en réponse à l'accroissement de la lumière actinique et comme l'éclairement de croissance diminue, le « taux de changement du quenching » baisse aussi. En général, les semis de *Quercus alba* ont manifesté une forte croissance et des réponses allométriques à l'intensité de l'éclairement.

***Quercus alba* / tolérance à l'ombre / répartition de la biomasse / fluorescence modulée de la chlorophylle / acclimatation à la lumière**

1. INTRODUCTION

Quercus alba (white oak) is one of the most widely distributed tree species in eastern North America [43]. Within its distribution range, *Quercus alba* tends to grow at lower elevation but is found across a broad range of sites except for the wettest and most xeric, rocky, or nutrient poor soils [1]. Before European settlement, oaks, especially *Quercus alba*, dominated in the vast areas of deciduous forest in the eastern United States [1]. Despite its past and current dominance, oaks are facing a widespread regeneration problem, particularly on mesic or good quality sites [30]. For example, very little recruitment of new *Quercus alba* trees occurred during the 20th century [3, 8], and there is evidence of a dramatic decline in *Quercus alba* forest from presettlement to the present day (e.g., [2, 13, 17]). Because this regeneration problem poses a serious threat to the sustainable management of oak forest, numerous ecological and silvicultural studies have been conducted in order to understand and thus solve the problem [1, 27, 30]. These studies have revealed a lack of understanding of ecological and physiological processes involved in oak regeneration.

Light is a critical factor affecting early survival and growth of tree seedlings under a forest canopy [27], but our knowledge on how *Quercus alba* responds to light is rather limited. In fact,

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results generated from studies on a few oak species are commonly generalized and applied to all oak species. *Quercus alba* is generally described as a species of intermediate shade-tolerance [47]. However, it can persist under a forest canopy for more than 90 years and responds well to canopy removal [34, 41, 43]. Because the existence of well-developed seedlings is a prerequisite for regeneration success of oak species [27], it is critical to understand the light condition under which oak seedlings would most benefit.

The shift between photochemical and non-photochemical quenching (chlorophyll fluorescence emission) balances energy input with utilization at the leaf chloroplast level. The transition from photochemical quenching at low light to non-photochemical quenching at high light reduces the quantum yield of PS II ($\phi_{PS\ II}$). Modulated chlorophyll fluorescence can readily measure the adjustment of light harvesting to energy utilization over a short time perspective [46] and has been used to characterize light acclimation of photosynthesis in *Pinus sylvestris* relative to *Quercus robur* [19] and *Fagus sylvatica* relative to *Quercus petraea* [20]. To our knowledge, there are no reports on how *Quercus alba* photochemical and non-photochemical mechanisms balance each other in response to light acclimation. There is a lack of fundamental knowledge of the physiological processes controlling early growth and development of oaks compared to other commercially important tree species in temperate forests.

The objective of the study was to investigate light acclimation in *Quercus alba* seedlings growing under a wide range of light intensities (5, 15, 30, and 100% of full sunlight). Specifically, we examined (1) how growth dynamics and biomass allocation change with light levels and (2) to what extent light intensity influences the rate of electron transport by affecting photochemical and non-photochemical mechanisms.

2. MATERIALS AND METHODS

2.1. Plant material and growth conditions

Before the initiation of aboveground growth, 270 germinated seeds were carefully excavated from under a mature white oak *Quercus alba* tree on the campus of Clemson University. Clemson University (lat. 34° 40' 8"; long. 82° 50' 40") is located within the upper Piedmont physiographic region. These germinated seeds were transplanted into 1.5 L plastic pots containing standard greenhouse potting substrate (Fafard 3B, Fafard Inc., Anderson, S.C.) and irrigated with a 1:100 Hydro Sol 5-11-26 N-P-K (Scotts Co., Marysville, OH). The seeds were allowed to develop in a glasshouse for two weeks. The average Photosynthetic Photon Flux Density (PPFD) from 700–1900 h in the glasshouse was 213 μmol m^{-2} s^{-1} or approximately 10% of full sunlight. Among the 270 transplanted seedlings, 263 survived the transplantation after two weeks in the greenhouse.

From the 263 surviving seedlings, 96 were randomly assigned and transplanted into twenty-four 57 L plastic pots (four seedlings per pot) that contained the same substrate. Initially, all pots were watered to saturation and permitted to drain for 24 h. *Quercus alba* seedlings were grown either in full sunlight (FL) or under one of three shading screen regimes (light shade – LS, medium shade – MS, and high shade – HS) in a rainout shelter. Polyvinyl Chloride (PVC) tubing supported the solar reflecting shade cloth (model XLS Revolux, AB Ludvig Svensson Inc., Kinna, Sweden) in a 1.5 × 1.25 m rectangular box. Six plastic pots (24 seedlings) were randomly assigned into each light level. Under each light level, pots were watered on an as need basis to maintain their water supply at or close to container capacity. The plants were grown for one week in the rain out shelter prior to initiation of the experiment to make sure no mortality resulted from the transplanting process.

On cloud free days, the maximum PPFDs at solar noon averaged 1750, 525, 263, and 88 μmol m^{-2} s^{-1} or 100, 30, 15, and 5% in the FL, LS, MS, and HS treatments, respectively. Under the same conditions, however, the average PPFD from sunrise to sunset was 827, 248, 124, and 41 μmol m^{-2} s^{-1} in the FL, LS, MS, and HS treatments, respectively. The LS, MS, and HS treatments resulted in the gradient of light environments that are characteristic of understory conditions in gap, moderate, and dense vegetation cover in mature oak forests.

2.2. Data collection

Light Measurements: Under each light regime, PPFD was measured every minute using a line quantum sensor and the average logged every 15 min (LiCor Inc., Lincoln, NE, USA). The line sensor was suspended above the canopy via a fixed PVC support rack that did not exceed the width of the sensor. These measurements were used to verify the shading screen light level.

Growth Measurements: Seedling mortality was observed and recorded each week. Only one seedling died in the middle of the experiment under 15% light, and thus was excluded from the study. Height (HT), root collar diameter (RCD), and number of leaves were measured twice a month during the experimental period. Height was measured to the nearest 0.1 cm using a measuring tape, and RCD was measured to the nearest 0.01 mm using a digital caliper. To ensure consistency in diameter measurements, measuring position and direction were marked on each stem using a permanent marker. At the end of the experimental period (September 11, 2003), all seedlings were destructively sampled. Each seedling was carefully excavated, and roots were soaked and washed. Root (RW), stem (SW) and leaf (LW) biomass were determined by drying to a constant mass at 80 °C. Several small circles with known area were cut from each dry leaf to determine specific leaf area for each seedling.

Modulated chlorophyll fluorescence measurements: To prevent photoinhibition prior to measurement, plants scheduled for modulated chlorophyll fluorescence measurement were transferred from the rainout shelter to a humidified growth room in the morning. The growth room light intensity was 375 μmol m^{-2} s^{-1}. Randomly selected plants from each treatment combination were chosen for repeated sampling of modulated chlorophyll fluorescence ($n = 6$). The light response of modulated chlorophyll fluorescence was measured on individual leaves using a portable modulated fluorometer (OS5-FL; Opti-Sciences, Tyngsboro, MA, USA) at room temperature. To prevent photoinhibitory PPFD levels, a preliminary experiment was conducted to determine light saturation using a Gilway Technical Lamp (Woburn, MA, USA) as the actinic light source. When designing the actinic light intensity protocol, it was established that no significant photosynthetic increase occurred above 800 μmol m^{-2} s^{-1}, therefore, a slightly lower but still saturated value of 725 μmol m^{-2} s^{-1} was used as the highest actinic intensity (~ 37% of full sunlight) to prevent photoinhibition. This value is similar to the light saturated maximum rate of net photosynthesis reported by Teskey and Shrestha [47]. Prior to the first measurement, leaves were equilibrated for a minimum of 30 min using dark-adapting leaf clips to determine the dark-adapted initial fluorescence (F_o), and maximum fluorescence (F_m). Leaf ontogeny was consistent, where measurements were taken on the 1–2 youngest fully expanded leaves. The fluorescence measurements with actinic light started at intermediate PPFD, subsided in steps to lower PPFD, back to the initial intermediate PPFD and proceeded to high PPFD to minimize photoinhibition. Steady state fluorescence was achieved at every light level by monitoring the stability of fluorescence (F_s) and the maximal light exposed fluorescence (F'_m). Before the light level was

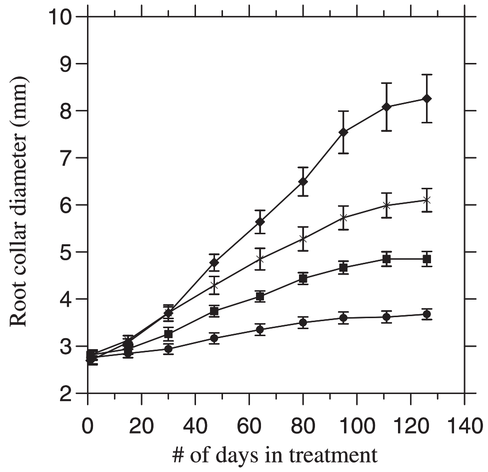

Figure 1. Changes in root collar diameter (mm) over number of days in treatment. The symbols are full sun (◆), light shade (×), medium shade (■), and high shade (●). The data are mean values ($n = 6$) ± SE.

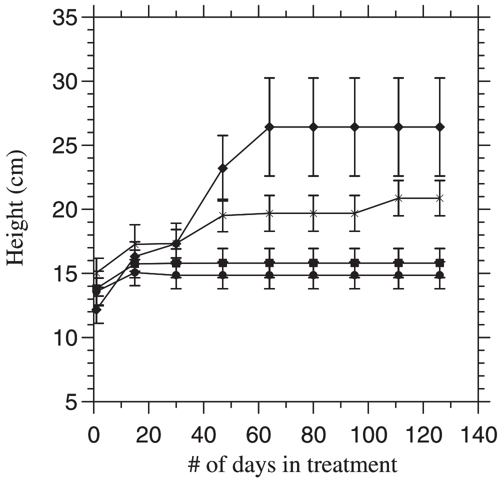

Figure 2. Changes in height (cm) over number of days in treatment. The symbols are full sun (◆), light shade (×), medium shade (■), and high shade (●). The data are mean values ($n = 6$) ± SE.

changed, the minimum fluorescence in the light (F'_o) was determined using a far-red light source (735 nm).

2.3. Data analysis

Based on biomass (oven-dry weight) measurements, total biomass (TB), aboveground biomass (AB), root to shoot ratio (RSR), leaf weight to total biomass ratio (LWR) and leaf weight to root weight ratio (LWRr) were calculated for each seedling. Based on specific leaf area (SLA; $cm^2\ g^{-1}$) and leaf weight measured for each seedling, total leaf area (LA; cm^2) was calculated. Leaf area to total biomass ratio (LAR; $cm^2\ g^{-1}$) and leaf area to root weight ratio (LARr; $cm^2\ g^{-1}$) were also calculated. The potential quantum efficiency of PS II (F_v/F_m) for dark-adapted leaves was calculated, where the maximal and minimal fluorescence yields were subtracted and divided by the maximal fluorescence yield (F_m–F_o/F_m). For leaves exposed to actinic light, the coefficient for non-photochemical quenching (q_N) was calculated as $q_N = 1-(F'_m-F'_o)/F_m-F_o$, whereas the photochemical quenching coefficient (q_P) was calculated as $q_P = (F'_m-F_s)/F'_m-F'_o$ (11, 44, 45). An estimate of the PS II reduction state (PS II closure) was derived as $1-q_P$. Non-radiative dissipation (NPQ) was calculated as $(F_m-F'_m)/F'_m$ [5, 11]. The actual quantum yield of PS II was calculated as $\phi_{PS\ II} = q_P \times \phi_{exc} = \Delta F/F'_m$, where ϕ_{exc} is the efficiency of excitation energy transfer from light harvesting complex II to the PS II reaction center and $\Delta F = F'_m-F_s$ (16). The relative electron transport rate was calculated as ETR = $[(F'_m-F_s)/\ F'_m] \times$ absorbed PPFD or $(\Delta F/F'_m) \times$ absorbed PPFD [11, 16]. The fraction of irradiance absorbed in the leaf was measured indirectly with a Minolta SPAD 502 chlorophyll meter (Minolta Camera Co., Ramsey, NJ, USA) following Bauerle et al. [4]. The light response curve of ETR was fit as described in Ögren and Evans [33]. Except when otherwise noted, third order polynomials were fit to the relationship between light and fluorescence parameters. Chlorophyll fluorescence nomenclature followed that of van Kooten and Snel [49].

The experiment implemented in the study was a complete randomized design, with light level as treatment, pot as replicate, and seedling within each pot as subsample. Repeated measures analysis of variance was used to quantify the effect of light level on RCD and HT and changes in RCD and HT over the experimental period. Due to significant interactions between light treatment and measuring dates, the changes in RCD and HT over the experimental period were analyzed separately for each light level using one-way analysis of variance. Similarly, differences in RCD and HT among light levels were analyzed separately for each measuring date using one-way analysis of variance followed by Bonferroni's multiple comparisons. One-way analysis of variance followed by Bonferroni's multiple comparisons was also used to test the difference in biomass measurement TB, AB, RW, LW, SLA, RSR, LAR, LARr, LWR and LWRr. Previous studies have raised caution about comparing allometric relationships of plants of different size (e.g., [24, 42]), but introducing seedling size (biomass) as a covariate in comparing RSR, LAR, LARr, LWR, and LWRr did not alter our results. All statistical analyses and graphics were conducted using SYSTAT (SYSTAT Software Inc., Richmond, CA, USA).

3. RESULTS

3.1. Growth dynamics and biomass allocation

Mortality due to light limitation was not observed during the study. Although RCD continued to grow (Fig. 1), HT growth stopped at 15 days into the experiment under MS and HS, at 45 days under LS (with exception of two seedlings) and at 60 days under FL (Fig. 2). No seedlings initiated the third flush under HS and MS while 21 and 71% of seedlings initiated the third flush under LS and FL, respectively.

Light level affected ($p < 0.001$) the RCD and HT of oak seedlings. As expected, RCD and HT increased ($p < 0.001$) over the experimental period but their increase depended on light treatment (Figs. 1 and 2). Over the experimental period, height only increased ($p < 0.001$) under FL and LS while RCD increased ($p < 0.001$) under all light levels. At the beginning of the experiment, there was no difference in either RCD ($p = 0.811$) or HT ($p = 0.310$). Difference in RCD was first detected at the 45th day into the experiment, with HS having smaller ($p < 0.002$) RCD than LS and FL at the 45th day into the experiment, and with FL > LS > MS > HS ($p \leq 0.004$) at the end of the experiment. Difference in HT first appeared at the 60th day into the

Table I. Growth and morphological variables (means with standard deviation in brackets) of *Quercus alba* L. seedlings after a full growing season under different light treatments (HS = 5%, MS = 15%; LS = 30%, and FL = 100% full sunlight). Values in the same row with different superscripts are significantly different ($p < 0.05$).

	Light treatment			
Variables	HS	MS	LS	FL
Root collar diameter (RCD; mm)*	3.68^{d} (0.25)	4.83^{c} (0.35)	6.10^{b} (0.55)	8.28^{a} (1.13)
Height (HT; cm)*	14.9^{c} (2.3)	$15.8^{b,c}$ (2.5)	$20.9^{a,b}$ (3.0)	27.4^{a} (8.4)
Total biomass (TB; g)*	3.60^{c} (0.33)	7.03^{b} (0.97)	11.59^{b} (1.72)	30.68^{a} (17.22)
Root biomass (RW; g)*	2.09^{c} (0.13)	4.83^{b} (0.61)	7.78^{b} (1.22)	20.67^{a} (10.96)
Leaf biomass (LW; g)*	1.02^{c} (0.16)	1.30^{bc} (0.24)	2.07^{b} (0.33)	5.06^{a} (3.06)
Stem biomass (SW; g)*	0.49^{c} (0.10)	0.85^{c} (0.22)	1.74^{b} (0.38)	4.93^{a} (3.45)
Root to shoot ratio (RSR)	1.45^{b} (0.23)	2.27^{a} (0.29)	2.32^{a} (0.23)	2.40^{a} (0.40)
Leaf weight ratio (LWR)	0.28^{a} (0.027)	0.20^{b} (0.018)	0.18^{bc} (0.020)	0.16^{c} (0.021)
Leaf weight root ratio (LWRr)	0.49^{a} (0.073)	0.29^{b} (0.038)	0.27^{b} (0.040)	0.24^{b} (0.043)
Leaf area (LA; cm^2)*	185.4^{c} (31.4)	245.5^{bc} (45.5)	340.2^{ba} (57.0)	637.4^{a} (378.1)
Specific leaf area (SLA; $cm^2\ g^{-1}$)*	180.1^{a} (3.0)	180.2^{a} (3.9)	162.7^{b} (1.3)	127.3^{c} (2.2)
Leaf area ratio (LAR; $cm^2\ g^{-1}$)	50.86^{a} (5.63)	35.22^{b} (3.27)	28.72^{c} (3.40)	20.62^{d} (2.74)
Leaf area root ratio (LARr; $cm^2\ g^{-1}$)	88.23^{a} (14.48)	51.54^{b} (6.76)	43.37^{bc} (6.83)	30.45^{c} (5.32)

* Analysis of variance and multiple comparisons were based on log-transformed data. Transformation was made to overcome the problem of unequal variances among groups.

experiment, with FL > HS and MS ($p \leq 0.011$) at the 60th day into the experiment and FL > HS/ MS ($p < 0.005$) and LS > HS ($p < 0.067$) at the end of the experiment.

At the end of the experiment, total biomass and each biomass component differed ($p < 0.001$) among the four light levels, with FL > LS = MS > HS for TB ($p \leq 0.012$) and RW ($p \leq 0.002$), FL > LS > MS = HS for SW ($p \leq 0.047$), and FL > LS/MS/HS ($p \leq 0.012$) and LS > HS ($p = 0.013$) for LW (Tab. I). RSR, LWR and LWRr were lower ($p \leq 0.001$) under HS compared to other light levels.

Leaf area supported by each seedling was affected ($p < 0.001$) by light environment, with FL being larger ($p \leq 0.005$) than MS and HS, and LS being larger than HS ($p = 0.039$) (Tab. I). SLA differed ($p < 0.001$) among the four light levels, with HS = MS > LS > FL ($p < 0.001$) (Tab. I). LAR differed ($p < 0.001$) among the four light levels, with HS > MS > LS > FL ($p \leq 0.047$). LARr differed ($p < 0.001$) among the four light levels, with HS > MS/LS/FL ($p < 0.001$) and MS > FL ($p = 0.003$).

3.2. Photosynthetic light acclimation

Oak seedlings showed light acclimation of photosynthetic performance (Figs. 3A–3D). As growth irradiance declined, q_P decreased from 37–72% in response to shade at higher values of PPFD across all treatments (Fig. 3A). The gradient of percent decline of q_p increased as shade intensity was elevated (Fig. 3A). Non-photochemical quenching (NPQ), a relative estimate of thermal dissipation of excitation energy, was also affected as shade intensity increased. In response to lower growth light levels, NPQ versus actinic light increased by approximately 30% (Fig. 3B). Figure 3B further illustrates that NPQ and PS II reaction centers are affected in response to light acclimation. Figure 3C illustrates a decrease of approximately 58% in $\phi_{PS\ II}$ as actinic PPFD values increase. Oak seedlings also showed a slight decrease of $\phi_{PS\ II}$ as irradiance growth conditions decreased ($\phi_{PS\ II} \sim 0.21 – 0.29$), but the larger affect was due to differences in actinic light. The ETR, illustrated in Figure 3D, followed a more pronounced pattern as opposed to $\phi_{PS\ II}$, where the light saturated ETR was 46% lower in HS as opposed to seedlings grown under FL conditions.

Figure 4 depicts the relationship between ETR and the driving force of electron transport to the reduction of the redox state of the primary electron acceptor of PS II, which is approximated by $1–q_P$. Figure 4 also illustrates an estimate of the flux of electrons through PS II via the ETR. There was a clear separation of irradiance response due to growth irradiance acclimation among the seedlings. As $1–q_P$ approached 1, the decline in ETR curtailed off as shade intensity increased. Specifically, ETR was 56% lower at the extreme difference between HS and FL, where the apparent reduction in yield of ETR through PS II was lowest in HS and highest under FL conditions.

Figure 5 is an indication that the photosynthetic apparatus has a lower conductance as actinic light increases. The conductance estimate is derived by dividing ETR by $1\text{-}q_P$ to obtain an approximate estimate of the conductance of the photosynthetic apparatus [44]. The large drop in the ratio seen at low PPFD in FL plants and slightly evident in HS plants, was a result of a large reduction in the redox state at the lowest PPFD levels. The lower response of HS plants was indicative of an absent or possibly lower PPFD redox state reduction.

Osmond [35] used the ratio $(1–q_P)$/NPQ as a measure of the excess photons that reach PS II. It represents an index of the susceptibility of PS II to light stress [37, 38]. Figure 6A

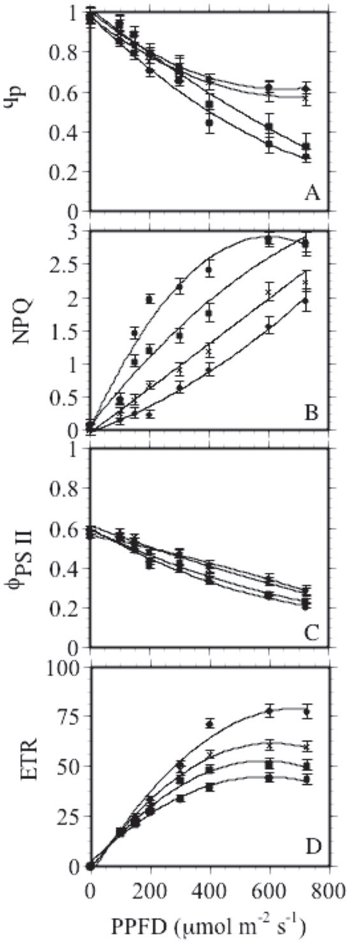

Figure 3. Light acclimation of photosynthesis measured by modulated chlorophyll *a* fluorescence in response to photosynthetic photon flux density (PPFD) of: (A) photochemical quenching (q_P); (B) non-photochemical quenching (NPQ); (C) quantum yield of PS II ($\phi_{PS\ II}$); and (D) electron transport rate (ETR). The symbols are full light (◆), light shade (×), medium shade (■), and high shade (●). The data are mean values (n = 6) ± SE.

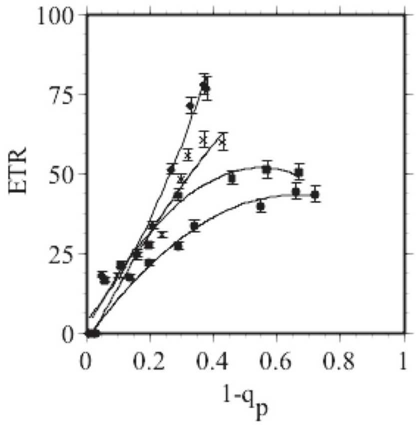

Figure 4. The approximate redox state of the primary electron acceptor ($1–q_P$) and the electron transport rate (ETR). The symbols are full light (◆), light shade (×), medium shade (■), and high shade (●). The data are mean values (n = 6) ± SE.

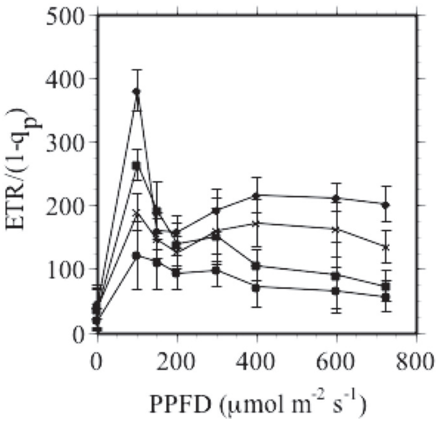

Figure 5. The irradiance dependence of the apparent reduction yield of electron transport ($ETR/1–q_P$). The symbols are full light (◆), light shade (×), medium shade (■), and high shade (●). The data are mean values (n = 6) ± SE.

illustrates that at low irradiance, the ($1–q_P$)/NPQ level peaked in FL and LS conditions, whereas MS and HS presented no clear relationships. A clear separation between treatments is evident in Figure 6B, where the NPQ/q_P ratio versus irradiance level increases with decreasing growth irradiance. Figure 6B further illustrates the shift from photochemical to non-photochemical quenching with increasing actinic light. The slope of this relationship gives a relative value of the 'quenching shift rate' [44]. As growth irradiance declined, the 'quenching shift rate' increased as well, resulting in a decrease of over 3 fold more in the HS versus FL treatment.

4. DISCUSSION

4.1. Growth

Light intensity strongly affected the development of *Quercus alba* seedlings during their first growing season, even though seedlings had been subjected to the same growing conditions for three weeks before the start of the shading experiment. This result agrees with previous studies on several oak species [6, 7, 14, 18, 25, 53]. The strong treatment response indicated that growth and biomass accumulation were determined by the seedling's capacity to harvest energy and produce photosynthates in their respective light environments, despite that light availability may only limit growth after cotyledon reserves are depleted [9, 32].

Although *Quercus alba* may develop up to four growth flushes under optimum conditions, it usually develops only one growth flush under low light beneath a dense canopy [40]. For example, *Quercus alba* seedlings did not initiate the second growth flush when growing naturally under a forest canopy with light intensity between 3 to 18% full sunlight although seedling biomass increased with light level [51]. With a few exceptions, *Quercus alba* seedlings in our study completed two growth flushes even under HS (5% of full sunlight). This apparent contradiction may be attributed to the fact that all seedlings

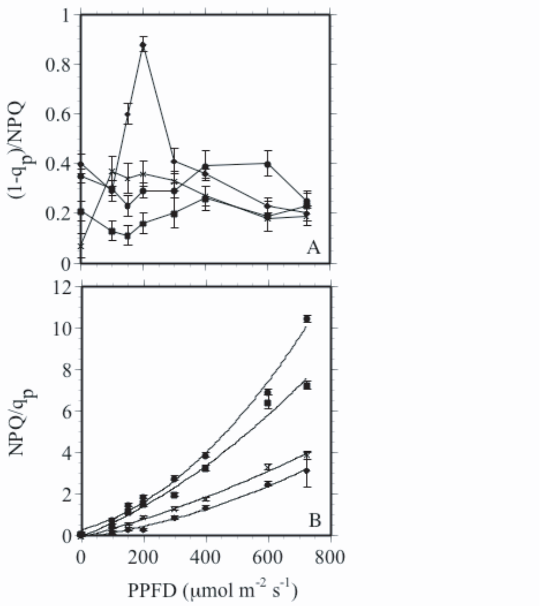

Figure 6. (A) The irradiance dependence of excitation pressure on PS II ($1-q_P$/NPQ). (B) The irradiance dependence of the ratio NPQ/q_P. The symbols are full light (◆), light shade (×), medium shade (■), and high shade (●). The data are mean values ($n = 6$) ± SE.

completed their first growth flush and about 80% initiated their second growth flush during the three-week transplant acclimation time before the start of the experiment. The optimized soil moisture and nutrient condition and the lack of root competition, which are directly in contrast to forest understory environments, may have also helped seedlings to cope with light limitation in the greenhouse [25]. Nevertheless, the proportion of seedlings initiating the third growth flush did reflect light environment, with 0, 0, 20 and 71% seedlings initiating the third growth flush for 5, 15, 30 and 100% of full sunlight, respectively.

Regardless of light level, RCD growth continued during the entire experimental period from May to September, following a typical S-shape curve (Fig. 1). This result, together with the absence of shade-induced mortality, suggested a net gain in carbohydrates for *Quercus alba* seedlings even under HS (5% of full sunlight). However, such a low light intensity may not be sufficient for *Quercus alba* seedlings to survive under a forest canopy. For example, Jarvis [25] reported root competition raised the compensation point of *Quercus petraea* from 6% to 15%. Similarly, Wang et al. [51] suggested a minimum of 15% of full sunlight was needed to facilitate the early establishment of white oak *Quercus alba* seedlings under a forest canopy. Our seedlings achieved the largest diameter under FL, and RCD was significantly reduced by decreasing light intensity (Tab. I). Gardiner and Hodges [14], however, reported that diameter of *Quercus pagoda* was significantly larger at 53% full sunlight during the first growing season. In contrast to RCD, HT growth was both episodic and stopped at a much earlier date (Fig. 2). A very similar height growth pattern was observed in *Quercus rubra* by Phares [39], and height growth stopped in early June, mid-July and early August at 10, 30 and 100% of full sunlight, respectively. Full sunlight seedlings were the tallest, which agreed with McGee's [31] study on northern red oak and Holmes' study [22] on *Quercus lobata* but disagreed with Gardiner and Hodges' study [14] on *Quercus pagoda* and Phares' study [39] on *Quercus rubra*. Compared to height, diameter growth was much more responsive to light intensity, which supports RCD as a more sensitive measure of light competition compared to HT [50, 52].

Because seedlings assigned to each light environment were similar in HT and RCD (Figs. 1 and 2), biomass of these seedlings must have been similar at the start of the experiment. Consequently, the final differences in biomass among light environments suggested a growth difference due to differences in light intensity. Increase in biomass with light intensity together with the highest biomass observed under FL suggest that *Quercus alba* seedlings must have a light saturation point > 30% full sunlight or 525 μmol m^{-2} s^{-1} solar noon (248 μmol m^{-2} s^{-1} daily average) when measured in cloudless day. Teskey and Shrestha [47] reported a light saturation point of 650 μmol m^{-2} s^{-1} for *Quercus alba*, and previous studies on other oak species all reported that ≥ 37% of full sunlight was needed for the maximum biomass accumulation [14, 25, 29, 39, 53]. Compared to the HS, *Quercus alba* seedlings growing under other light levels allocate more to root than shoot as indicated by their higher root to shoot ratio (Tab. I). The ability to maintain a constant RSR from 15% to 100% of FL, with about 70% of total biomass being allocated to roots, suggests root growth takes a clear priority over shoot growth during the first growing season unless light is severely limited. Even under the most limited light condition (5% of full sunlight) about 58% of the total biomass was allocated to roots. This life history strategy should allow *Quercus alba* to survive better under a frequent top-kill due to surface fire as well as on dry sites or during drought periods. The same strategy, however, may have also put *Quercus alba* at a disadvantage under fire suppression as well as on mesic or good quality sites where competition for light outweighs adaptation to fire and/or drought. At the expense of allocating to roots and stems, seedlings allocated more to leaves as light intensity decreased, indicated by their higher LWR and LWRr.

Similar to previous studies on different oak species [18, 25, 29, 48, 53], our study found that SLA increased with shade because of leaf acclimation to low light intensity. The lack of significant difference in SLA between HS and MS is likely attributed to the fact that most leaves had been initiated under FL before the start of the experiment and, unlike seedlings growing under FL and LS, only a small portion of the leaves actually initiated their growth after the start of the experiment. The significant differences in LAR found between light levels indicated that the same amount of total biomass supported more leaf area with decreasing light intensity, which is consistent with several previous studies on oaks (e.g., [6, 18, 25, 29, 48]). With increasing light intensity, photosynthesis rate increased from HS to MS to LS to FL and thus more biomass was produced by the same amount of leaf area. The rapid rise in LAR with decreasing light intensity (Tab. I) together with the ability to maintain a positive carbon balance under 5% of full sunlight suggest that *Quercus alba* may be more shade-tolerant than has previously been reported, which partially explains why *Quercus alba* can persist under forest canopies for more than 90 years [34, 41, 43]. As expected, LARr also decreased with increasing light intensity, likely due to the light induced increase in transpiration rate.

4.2. Chlorophyll fluorescence

To characterize light acclimation of photosynthesis, we used modulated chlorophyll *a* fluorescence. Light acclimation of light-saturated NPQ in *Quercus alba* seedlings is consistent with findings in *Digitalis* [26] and *Hibiscus* [44]. The level of total NPQ at saturating PPFD of 725 μmol m^{-2} s^{-1} in *Quercus alba* is consistent with values found in obligate shade species and sun species [26]. Alternatively, Osmond et al. [36] found that some species acclimate, where plants exposed to high light have a higher NPQ capacity than plants grown in low light. The conflicting results emphasize the light acclimation strategies that occur and the variation in thermal dissipation of excitation energy among species.

Photochemical quenching (q_P) is often used as an indicator of PS II primary electron acceptor oxidation [10, 12, 23, 28, 44, 46], where the $\phi_{PS\ II}$ is the product of q_P and the excitation energy transfer efficiency from the light harvesting complex of PS II to the PS II reaction center [16]. *Quercus alba* showed a larger decline in q_P versus light with decreasing growth irradiance as compared to $\phi_{PS\ II}$. The oxidation of the primary electron acceptor of PS II indicated by q_P was more pronounced than the loss of $\phi_{PS\ II}$, indicated by an increase in non-photochemical quenching. The flux of electrons through PS II can also be estimated as ETR. The relationship between ETR and $1–q_P$ illustrated a clear differentiation of light acclimation within the species, where the apparent reduction yield of electron transport through PS II was lowest in HS and highest in FL.

By dividing ETR by $1–q_P$, we obtained an estimate of conductance of the photosynthetic apparatus. A comparison can then be made to the apparent reduction yield of ETR versus $1–q_P$. Other than low light levels of approximately 100 μmol m^{-2} s^{-1}, the comparison indicates that as actinic light increased, the conductance of the photosynthetic apparatus remained relatively constant with changing irradiance. This is in agreement with the light independent rate constant of reduction of P_{700}+ reported by others [15, 21]. The higher conductance in FL seedlings is not surprising because electron transport chain conductance depends primarily on electron concentration components, which are determined by light acclimation. The difference in electron concentration components in plants exposed to high light has been well established and it is likely the cause of differences in photosynthetic apparatus conductance between light treatments.

To estimate the amount of excess photons reaching PS II, we used an index related to light acclimation, namely the ratio $(1–q_P)$/NPQ [35]. The ratio is also an index of the susceptibility of PS II to light stress. The *Quercus alba* seedlings did not show a constant ratio on $(1–q_P)$/NPQ. Although the highest ratio was found under low light conditions in FL seedlings, other light levels did not follow suit. Other than this one instance, the results do not indicate a clear separation in response to light acclimation. The light response of the NPQ/q_P ratio on the other hand did present a clear light treatment response. The shift from photochemical to non-photochemical quenching occurs as actinic light increases and is a relative indication of the quenching shift rate. The non-linear curves show the demand for electron flux through PS II, where LS, MS, and HS had a lower flux of electrons through a reduced PS II.

In conclusion, *Quercus alba* seedlings demonstrated clear photosynthetic acclimation and strong growth and allometric responses to light intensity. After one growing season, the greatest diameter and height growth were observed on seedlings under 100% of full sunlight, and these seedlings also supported a greater biomass (root, leaf and stem) and leaf area. Seedlings under 15, 30 and 100% of full sunlight allocated more biomass to roots (~ 70%) than seedlings under 5% of full sunlight (~ 58%), suggesting a priority in root growth unless light is severely limited. Leaf weight ratio, specific leaf area, and leaf area ratio increased with the degree of shading, indicating acclimation of leaves to different light intensities. Using a steady-state irradiance during chlorophyll fluorescence measurements of light response, we were able to obtain steady-state results of quenching and provide insight into physiological constraints that manifest themselves in growth and survival responses that may influence oak regeneration. A lack of studies prevents us from directly comparing our greenhouse study with field experiments. Further work is needed to investigate how *Quercus alba* seedlings respond to light intensity under different overstory shading regimes in a dynamic light environment.

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