

PHOTOSYNTHESIS AND THE XANTHOPHYLL CYCLE-MEDIATED PHOTOPROTECTION IN LEAVES OF *QUERCUS RUBRA* AND *Q. ALBA* SEEDLINGS OF DIFFERENT LIGHT ENVIRONMENTS

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Abstract: Two and three years after the outplanting of 1-O northern red oak (*Quercus rubra*, NRO) and white oak (*Q. alba*, WO) nursery stocks, the highest net photosynthetic rates (A_{max}) were observed from seedlings growing on a **clearcut** site followed by those under a pine stand. Both NRO and WO seedlings under a hardwood stand had A_{max} less than 10% of the full sun seedling A_{max} . Oaks grown under hardwoods increased their A_{max} , more in response to **sunflecks** than those under a pine stand. Besides NRO and WO **seedlings**, leaves of several hardwood seedlings and shrubs grown under different light environments were analyzed for pigments and the operation of the xanthophyll cycle. All species investigated shared the following characteristics: higher contents of chlorophyll a+b, a-carotene, **lutein**, and neoxanthin; smaller xanthophyll cycle pool (sum of violaxanthin V, antheraxanthin A, and **zeaxanthin** Z); and lower ratios of Z+A to Z+A+V in leaves of understory plants than leaves of the same species growing in **full** sun. The diurnal xanthophyll cycle (i.e., high **Z+A/Z+A+V** ratio in midday and low **Z+A/Z+A+V** ratio near dawn and dusk) was present in leaves of NRO and WO seedlings on the **clearcut** site. Almost no xanthophyll cycle was operating in understory leaves except that upon sunflecking NRO and WO under hardwoods increased their **Z+A/Z+A+V** ratio. For every unit of the xanthophyll cycle pool, twice as many **chlorophylls** must be protected in shade-grown leaves as in sun-grown leaves. The potential use of leaf a-carotene levels in **silviculture** is discussed.

INTRODUCTION

Competition for light and water between northern red oak (*Quercus rubra*, NRO) and other hardwood and herbaceous species has been attributed to the less than satisfactory results of natural and artificial regeneration of this species (Barton and Gleeson 1996, Crunkilton *et al.* 1992, Gottschalk 1994, Loftis and McGee 1993). It is shown that full-sun grown NRO seedlings have higher net photosynthesis rate and dry weight accumulation than shaded seedlings (Crunkilton *et al.* 1992, Kubiske and Pregitzer 1996, McGraw *et al.* 1990, Sung *et al.* 1997). However, controversial results exist throughout the literature for treatment effects on oak growth between **shelterwood** and **clearcut** site planting (Crunkilton *et al.* 1992, Gottschalk 1987, Teclaw and Isebrands 1993).

In addition to the competition for light, water, and nutrients with other plants, understory oaks that have been growing with less than 5 percent of **full** sun must adapt to full sun when the overstory trees are removed naturally or by harvesting. Leaf chlorophyll bleaching is a well-known phenomenon that has been observed with the released understory plants. Plants have various protective mechanisms to avoid or lessen the effects of photoinhibition resulted **from** excessive sunlight and in combination with other environmental stresses. Enzymes (such as superoxide dismutase, ascorbate peroxidase, and catalase), antioxidants (such as ascorbate, glutathione, and tocopherols), and carotenoids (such as the xanthophyll cycle pigments) are essential for the protection of photosynthesis apparatus against photodamage caused by excessive sunlight and activated oxygen species (Alscher and Hess 1993, Demmig-Adams and Adams 1992a, Gilmore 1997). Under low light and favorable growth conditions, most of the absorbed light is used for photochemistry. With increasing light intensity, the photochemical reactions occur at lower efficiency and leaf chloroplasts engage a xanthophyll cycle-mediated photoprotection mechanism to safely dissipate the excessive absorbed light energy as heat (Demmig-Adams and Adams 1992a, Gilmore 1997). Upon illumination which in **turn** lowers the lumen **pH**, **zeaxanthin** (Z) is formed from the de-epoxidation of violaxanthin (V) via the intermediate antheraxanthin (A). Both Z and A are able to

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dissipate excessive light from the antenna chlorophylls. The reversible conversions of V to A to Z are catalyzed by enzymes, show diurnal cycles, and are influenced by seasons, shading, and drought (Demmig-Adams and Adams 1992b, Gilmore 1997, Logan et al. 1996, 1997, Siefermann-Harms 1994).

In this study, we examine the adaptive responses of photosynthesis, xanthophyll cycle, and pigment contents in leaves of NRO and white oak (*Q. alba*, WO) seedlings outplanted on a clearcut site, under a pine stand, and under a mixed hardwood stand. We show that for both oak species the maximum net photosynthesis (A_{max}) is the greatest with seedlings grown on the clearcut site. We demonstrate that the diurnal xanthophyll cycle is operating in sun leaves but not in shade-grown leaves. The use of u-carotene to indicate true shade-grown leaves in forests is discussed.

MATERIALS AND METHODS

In February 1995, 1-0 nursery-grown NRO, WO, and red maple (*Acer rubrum*) seedlings were outplanted on a clearcut site, under a 15-year-old loblolly pine (*Pinus taeda*) stand, or under a mixed hardwood stand with a 130 ft^2/A density at the Whitehall Experimental Nursery in Athens, Georgia. Each site had 50 seedlings of each species. Herbaceous weeds were controlled among rows on the clearcut site. No addition of fertilizer or irrigation was done on any of the three sites.

All photosynthesis measurements were conducted while the leaves were still attached to the plants. In the 1996 growing season, photosynthesis was measured with a portable, closed system infrared CO_2 analyzer (Li-Cor 6200). Light saturation curves were constructed in summer of 1997 with a portable, open system infrared CO_2 analyzer equipped with a CO_2 mixer and a red-blue light source (Li-Cor 6400).

In the summer of 1997, leaf samples were harvested and immediately frozen in liquid N_2 . Samples were stored at -80°C until analysis for the pigments. Procedures for leaf pigment extraction and analysis were modified from the method by Gilmore and Yamamoto (1991). A Dionex AI-450 high performance liquid chromatograph with a 4.5 mm x 25 cm Zorbax non-encapped C-18 column and a visible light at 445 nm was used (Sung et al. 1997). In addition to the NRO, WO, and red maple samples collected from the three outplanted sites, leaves from several hardwood species in forests of South Carolina, North Carolina, and Georgia were harvested for pigment analysis.

RESULTS

By the third season, the highest mortality rate for all three species occurred on the hardwood site. Survival percentages for NRO, WO, and red maple under hardwoods were 16, 34, and 30%, respectively. More than 90% survival was recorded for all three species on the clearcut site and under pine stand. Most of mortality occurred during summer drought in 1996 and 1997.

Photosynthesis

The average seasonal values of A_{max} , measured between May and September 1996 with the ambient light, were the highest for all three species planted on the clearcut site (Table 1). There were no significant differences in A_{max} among the species. Seedlings grown under pine received higher photosynthetic photo flux density (PPFD) and had greater A_{max} than those under hardwoods. Seedlings planted under hardwoods benefited the most from occasional sunflecks. Under the hardwood stand, even with sunflecks, PPFD at the seedling level was less than 10% of the full sun.

Transient light saturation curves for NRO (Figure 1 a) and WO (Figure 1 b) were made from seedlings grown for the third season after outplanting. Similar to the results obtained in 1996 (Table I), A_{max} , measured at $2000 \mu\text{E m}^{-2} \text{s}^{-1}$, for NRO (Figure 1a) and WO (Figure 1 b) on clear-cut site seedlings was much higher than those for pine and hardwood site

Table 1. Average photosynthetic rate (A_{max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and photosynthetic photon flux density (PPFD, $\mu\text{E m}^{-2} \text{s}^{-1}$) for seedlings grown under different light environments for two years.

| | Northern Red Oak | | White Oak | | Red Maple | |
|---------------|-----------------------|----------|-----------|----------|-----------|----------|
| | A_{max} | PPFD | A_{max} | PPFD | A_{max} | PPFD |
| Full Sun | 11.0±2.4 ^a | 1589±121 | 9.7±3.7 | 1513± 86 | 11.7±4.4 | 1527±153 |
| Under-story: | | | | | | |
| Pine | 3.4±0.3 | 124± 24 | 2.1±0.4 | 135± 88 | 3.1±1.5 | 117± 54 |
| Pine-Sunfleck | 4.9±1.5 | 421±200 | 4.8±1.9 | 550±279 | 3.1±1.5 | 634±247 |
| Hardwood (Hd) | 0.7±0.8 | 27± 20 | 0.6±0.3 | 21± 12 | 0.9±0.3 | 37± 8 |
| Hd-Sunfleck | 3.9±1.4 | 109± 25 | 2.8±0.2 | 102± 54 | 2.9±1.1 | 238±115 |

^a Means and standard deviation of measurements made between May and September 1996.

Table 2. Levels of chlorophylls and carotenoids (nmol $\text{g}^{-1} \text{fw}$) in mature leaves of northern red oak and white oak seedlings grown under different light environments for three years.

| | Chl a+b | Z+A+V | Lutein | Neoxan | a -Caro | β -Caro | T. Carotenoids |
|------------------|-----------|---------|--------|--------|---------|---------------|----------------|
| Northern Red Oak | | | | | | | |
| Full Sun | 2073± 135 | 306±62 | 275±22 | 148±24 | 9± 2 | 239±18 | 977±111 |
| Understory: | | | | | | | |
| Pine | 3952350 | 249±2 1 | 496±33 | 248±17 | 140±35 | 222±11 | 1356±102 |
| Hardwood | 3800±333 | 259±3 1 | 520±45 | 259±30 | 112±18 | 208±14 | 1357±132 |
| White Oak | | | | | | | |
| Full Sun | 1652± 60 | 256±11 | 242± 7 | 106± 6 | 12± 1 | 200± 5 | 816± 15 |
| Understory: | | | | | | | |
| Pine | 4267±138 | 223±13 | 570±38 | 284± 6 | 158±10 | 229± 7 | 1463± 44 |
| Hardwood | 2912±108 | 178± 5 | 410±19 | 189± 6 | 98±10 | 178± 8 | 1053± 34 |

^a Means and standard deviation of five samples taken at 7am, 1pm, 5pm and 8pm.

seedlings. Saturation PPFD for A_{max} of clearcut, pine, and hardwood site NRO seedlings were 660,480, and 120 $\mu\text{E m}^{-2} \text{s}^{-1}$, respectively (Figure 1 a). The PPFD for $1/2 A_{max}$ were 164, 116, and 67 $\mu\text{E m}^{-2} \text{s}^{-1}$ for NRO grown under full sun, pine stand, and hardwood stand, respectively. Saturation PPFD for A_{max} of clearcut, pine, and hardwood site WO seedlings were 900,280, and 260 $\mu\text{E m}^{-2} \text{s}^{-1}$, respectively (Figure 1b). The PPFD for $1/2 A_{max}$ were 186, 70, and 31 $\mu\text{E m}^{-2} \text{s}^{-1}$ for WO grown under full sun, pine stand, and hardwood stand, respectively (Figure 1 b).

Photoprotection

Northern red oak and WO leaves formed under shade showed higher chlorophyll a+b contents than those of leaves on clearcut site (Table 2). There were slightly higher total xanthophyll cycle pigments (Z+A+V) in full sun grow;

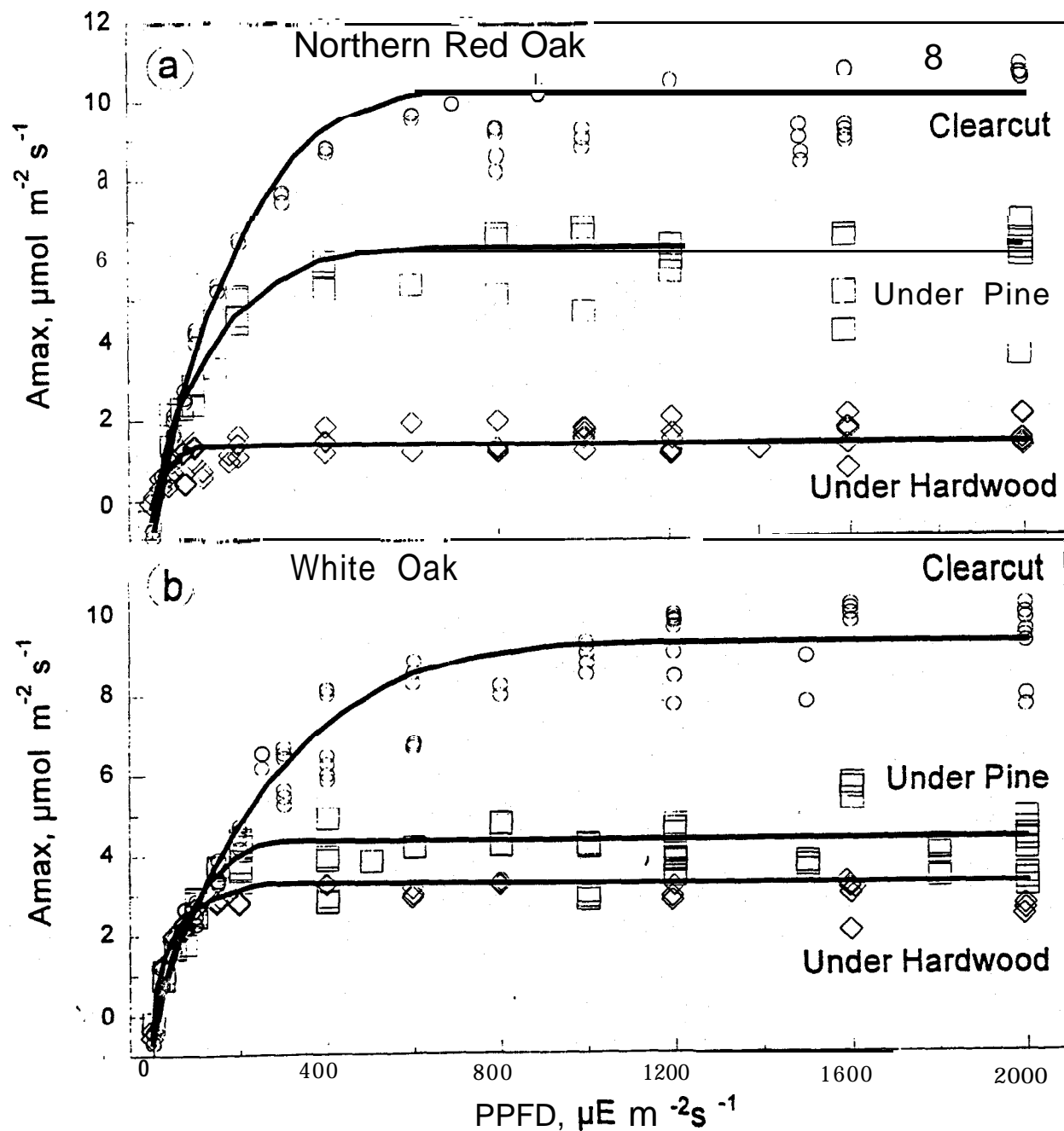


Figure 1. Transient light saturation curves for (a) northern red oak plants and (b) white oak plants grown for the third year on a clearcut site, under a pine stand, and under a mixed hardwood stand. Measurements were made in September 1997.

NRO leaves than shaded leaves whereas the former contained lower levels of lutein, neoxanthin, and total carotenoids than the latter. This was also true with WO leaves. The most obvious differences in pigment compositions between leaves of sun- and shade-grown plants were that a-carotene increased more than g-fold for both oak species when grown understory. Shading did not change β -carotene levels in either species (Table 2).

Both NRO and WO leaves of full sun grown seedlings had greater Chl a to Chl b ratio than the understory **seedling** leaves (Table 3). This was even more so with the ratio of P-carotene to a-carotene. In addition, the xanthophyll cycle pigment pool (Z+A+V) was about 30% **of the** total carotenoids in sun leaves whereas it was less than 20% **of** the total carotenoids in shade leaves for both oaks. The opposite trend was observed with the ratio between chlorophyll contents and xanthophyll cycle pools (Table 3).

Table 3. Ratios of pigments in mature leaves of northern red oak and white oak seedlings grown under different light environments for three years.

| | Chl a/ Chl b | Chl a+b/ Z+A+V | β -Caro/ a -Caro | Z+A+V/ Total Carotenoids |
|------------------|------------------------|-------------------|---------------------------|-----------------------------|
| Northern Red Oak | | | | |
| Full Sun | 3.99±0.20 ^a | 7.05± 1.46 | 28.83±7.73 | 0.314±0.036 |
| Understory: | | | | |
| Pine | 3.12±0.06 | 15.95± 1.60 | 1.65±0.31 | 0.184±0.012 |
| Hardwood | 2.90±0.09 | 14.76±1.11 | 1.89±0.25 | 0.192±0.010 |
| White Oak | | | | |
| Full Sun | 3.57±0.09 | 6.46±0.08 | 16.73±2.32 | 0.314±0.012 |
| Under-story: | | | | |
| Pine | 2.97±0.03 | 19.24±1.61 | 1.46±0.09 | 0.150±0.012 |
| Hardwood | 3.13±0.06 | 16.36±0.25 | 1.84±0.20 | 0.168±0.007 |

^a Means and standard deviation of five samples taken at **7am**, 1 lam, 1pm, 5pm and **8pm**

On the day of sampling for leaf pigment analysis, the PPFD on each site were also measured at the sampling time from 7 am solar time to 8 pm solar time (Figure 2a). Light intensity for pine understory was higher compared to the seasonal average for the previous year (Figure **2a**, Table 1). The same was true for the hardwood understory. The diurnal patterns of the xanthophyll cycle, as expressed as the ratio between Z+A and Z+A+V, were determined for NRO (Figure 2b) and WO (Figure **2c**) seedlings in August 1997. The xanthophyll cycle ratio for leaves of NRO **plants** grown on the **clearcut** site tracked well with the diurnal PPFD. More V was deepoxidized to A and Z with increasing PPFD whereas Z and A were epoxidized to V at the end of the light period (Figure 2b). The xanthophyll cycle did not operate in NRO leaves of seedlings grown under pine or hardwood stands; even though there was a diurnal PPFD cycle under pine stand (Figure **2a,b**). The maximum deepoxidation extents of V were similar for **sun-**grown NRO and WO with WO leaves converting more V to A and Z at 1 lam than NRO leaves (Figure **2b,c**).

Red maple leaves showed similar light responses in terms of chl a+b and a-carotene levels and the xanthophyll cycle ratio as those of NRO and WO (Table 4). **On** rainy days, no xanthophyll cycle was operated in any of the leaves sampled (Table 4). Seedlings grown with full sun all showed the xanthophyll cycle operating near noon whereas the understory seedlings did not. But a southern **red** oak plant grown near the edge of a pine stand did exhibit the conversion of V to A and Z. All understory grown seedlings had high levels of a-carotene as compared to those of the **clearcut** site seedlings. The levels of a-carotene did not change when harvested on rainy days.

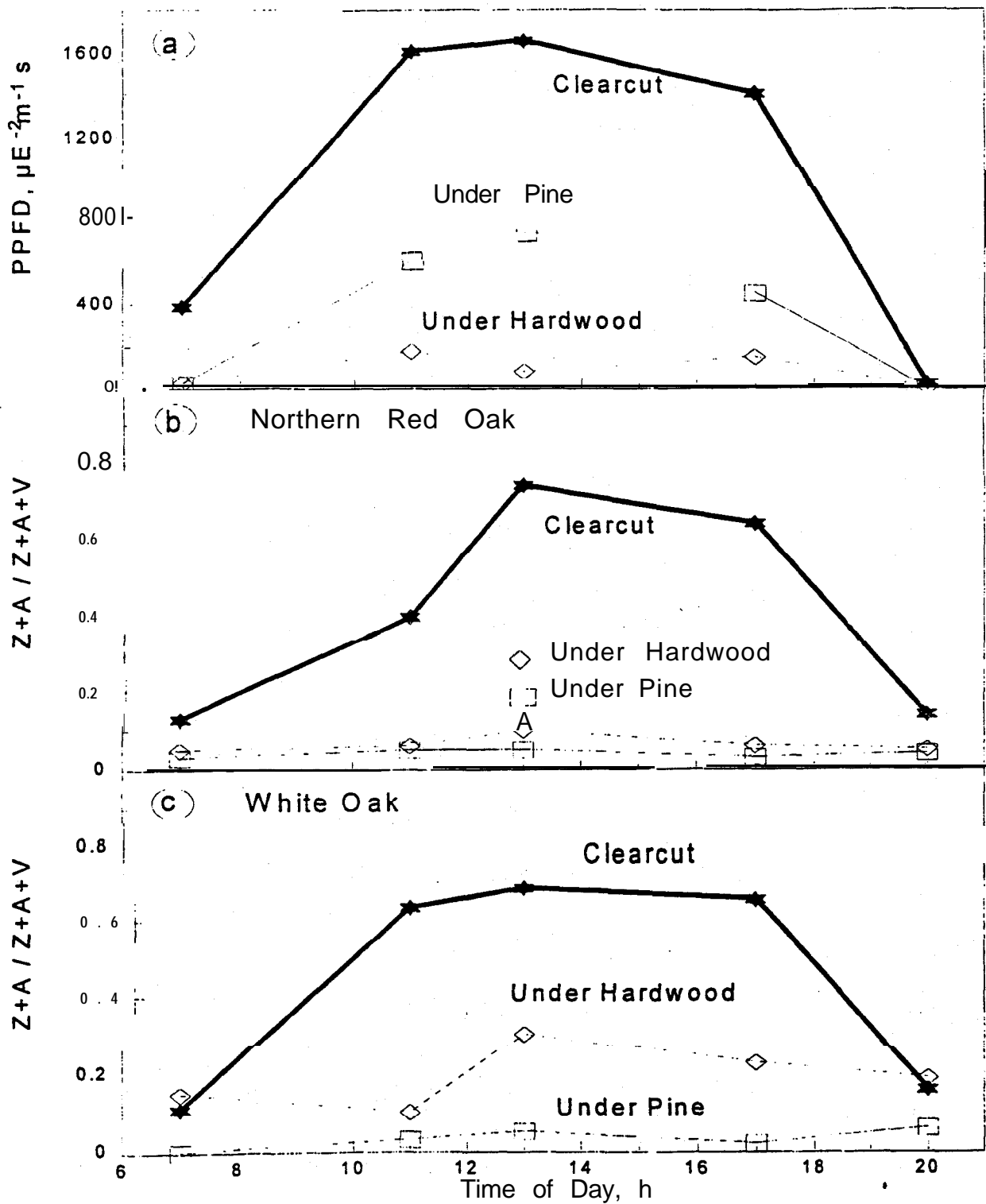


Figure 2. (a) Diurnal photosynthetic photon flux density (PPFD) at the seedling level. These were the **average** values for (b) northern red oak and (c) white oak seedlings whose leaves were sampled to determine the **diurnal** xanthophyll cycle, expressed as $Z+A/Z+A+V$ ratio.

DISCUSSION

Most of the NRO, WO and red maple seedling outplanted under mixed hardwoods died during the summer drought of 1996 and 1997. These seedlings apparently could not compete for water with the surrounding large hardwood trees. When growing under 70% shade cloth for two years, NRO and WO seedlings allocated 8% and **5%**, respectively, of total dry weight to lateral roots as compared to the 22% in NRO and the 12% in WO seedlings grown under full sun (Sung *et al.* 1997). Higher predawn and midday leaf water potentials were measured in NRO seedlings grown on the **clearcut** site than those under shelterwood (Crunkilton *et al.* 1992). They also reported restricted root system development with shelter-wood NRO. Thus, even before considering the negative effects of shading on oak photosynthesis and photoprotection, our results clearly indicated the risks of under-planting the "intermediate" shade tolerant oaks such as NRO and shade tolerant WO.

Photosynthesis

Values of A_{max} for under-planted NRO and WO seedlings in this study (Table 1, Figure 1) were similar to the result of others (Barton and **Gleeson** 1996, Crunkilton *et al.* 1992, Kubiske and Pregitzer 1996). Even measured with saturating light intensity, neither under-planted oak species increased their A_{max} to the same extent of the **full** sun grown seedlings (Figure 1). Results from Barton and **Gleeson (1996)**, Crunkilton *et al. (1992)*, Kubiske and Pregitzer (1996) also showed the negative effects of shading on A_{max} . Naidu and **deLucia (1997)** observed that A_{max} did not increase in shade grown NRO saplings that were exposed to canopy gap for up to three weeks. However, **Ashton** and Beriyn (1994) reported a slightly lower A_{max} in NRO seedlings grown with $1600\mu\text{E m}^{-2} \text{ s}^{-1}$ than those

Table 4. Levels of chlorophyll **and** carotenoids in mature leaves of hardwood seedlings grown under different light environments and sampled during middays in July 1997.

| Species | Site | Chl a+b | Z+A+V | α -Caro | Z+A/ Z+A+V |
|-------------------------|---------------------------------|-------------------------|-------|----------------|---------------|
| | | nmol g ⁻¹ fw | | | |
| Red maple | Clearcut | 1445 | 207 | 11 | 0.71 |
| Red maple | Loblolly pine | 4161 | 315 | 90 | 0.11 |
| Red maple | Mixed hardwood | 2238 | 141 | 28 | 0.10 |
| Northern red oak | Mixed hardwood, sunfleck | 2782 | 144 | 13 | 0.56 |
| Northern red oak | Mixed hardwood, no sunfleck* | 3096 | 148 | 52 | 0.10 |
| Northern red oak | Clearcut, rain | 2187 | 321 | 7 | 0.05 |
| Northern red oak | Loblolly pine, rain | 3118 | 287 | 99 | 0.05 |
| White oak | Clearcut , rain | 1646 | 187 | 14 | 0.05 |
| white oak | Loblolly pine, rain | 3353 | 314 | 95 | 0.04 |
| American chestnut | Nursery | 2686 | 210 | 19 | 0.62 |
| American chestnut | Nursery, rain | 2860 | 267 | 14 | 0.04 |
| Southern red oak | Loblolly pine, stand edge | 1289 | 153 | 4 | 0.56 |
| Southern red oak | Clearcut | 1017 | 129 | 2 | 0.70 |
| Post oak | Mixed hardwood | 2856 | 257 | 63 | 0.07 |
| Beech | Mixed hardwood | 4925 | 319 | 89 | 0.09 |
| Rhododendron | Mixed hardwood | 2167 | 163 | 3 | 0.04 |
| Willow oak | Mixed hardwood | 3481 | 227 | 113 | 0.03 |

*There was no **sunfleck** on this particular understory seedling from 8 am to 5 pm in September, 1997.

under 350 and 800 $\mu\text{E m}^{-2} \text{s}^{-1}$. Factor!, other than PPFD must be considered when explaining this kind of controversy.

Regardless of their light environments, the quick increases in photosynthetic rate upon increasing light intensity occurred in both oaks when PPFD was less than 5% of the full sun ($<100 \mu\text{E m}^{-2} \text{s}^{-1}$) (Figure 1). In other words, under low light intensity, the photon use efficiency was high and most of the absorbed light was used for photochemistry. Nevertheless, the adaptive photosynthetic response to sunflecks was more evident with seedlings grown under hardwood than those under pine (Table 1). Lower PPFD values for A, and $1/2A_{\text{max}}$ in oaks grown under hardwood than under full sun or pine also indicated that planting oaks under hardwoods forced them to adapt to shade and thus compromised their photosynthesis potential (Figure 1, Table 1). Most reports in the literature agreed that when grown with less than 10% of full sunlight, NRO did not grow well (Ashton and Berlyn 1994, Gottschalk 1987). And yet, with $130 \text{ ft}^2/\text{A}$ overstory density, average PPFD at the understory was less than 5% of the full sun. Therefore, lower photosynthesis rate and less dry weight allocation to lateral roots in oaks grown under hardwoods probably are the two major reasons for the less than satisfactory survival and growth results of the shelterwood oak regeneration.

Photoprotection

Higher levels of chlorophyll a+b, a-carotene, lutein and total carotenoids, smaller xanthophyll cycle pool, and lower values for chl a/chl b and $Z+A/Z+A+V$ in understory NRO and WO leaves as compared to full sun grown seedlings (Tables 2, 3, and 4, Figure 2) were in general agreement with the sun vs shade leaf studies by Demmig-Adams and Adams (1992b), Faria et al. (1996), Logan et al. (1996), and Thayer and Bjorkman (1990). Most of these studies dealt with sun and shade leaves within the same plant canopy or species growing under different light environments in the rain forests. The present study was the first one to determine leaf pigments and the operation xanthophyll cycle in outplanted oaks from different light environments. The light-dependent operation of the xanthophyll cycle (i.e., increasing $Z+A/Z+A+V$ ratio upon illumination) is evident in the diurnal pattern of this cycle in full sun grown NRO and WO seedlings and in seedlings receiving sunflecks (Figure 2, Table 4). Low level of de-epoxidation of V to A and Z in samples collected near noon on rainy days (Table 4) was similar to the results of Schindler and Lichtenthaler (1996). They followed the xanthophyll cycle on a mature *Acer platanoides* tree on a cloudy day and observed a constant value of 0.2 for $Z+A/Z+A+V$ throughout the day except when PPFD increasing from <200 to $500 \mu\text{E m}^{-2} \text{s}^{-1}$ for 1 hour. Ratio of $Z+A/Z+A+V$ increased to 0.75 during this period and the decreased afterwards (Schindler and Lichtenthaler 1996).

The conversion of V to A and Z upon sunflecks by shade leaves (Table 4, Logan et al. 1997) indicated that these leaves are capable of dissipating excessive light energy as heat. Increasing chlorophyll contents and decreasing $Z+A+V$ contents, as observed in leaves of shaded seedlings, further increased the ratio between chlorophyll content and the xanthophyll cycle pool. It can be problematic for photoprotecting the photosynthetic apparatus when the understory seedlings are released and the shade leaves are to be exposed with more than 1 O-fold of light intensity for duration. Future study is needed to follow the xanthophyll cycle operation and photosynthesis after releasing the understory seedlings.

The function of u-carotene is yet to be determined. But, the more than 4-fold higher content of this carotenoid pigment in shade leaves (Tables 2,4, Demmig-Adams and Adams 1992b, Logan et al. 1996, Thayer and Bjorkman 1990) might be useful to determine whether a understory plant has ever receives enough light (such as sunfleck) throughout time. For example, the 3-fold difference in a-carotene contents of two adjacent NRO seedlings was due to one received at least a total of 2 h sunflecks and the other did not (Table 4). A southern red oak growing near the edge of the pine stand also did not have high level of a-carotene (Table 4). Furthermore, a-carotene content did not change diurnally as did the xanthophyll cycle pigments (this study, Schindler and Lichtenthaler 1996). Levels of this carotene might provide the long-term light environment history for a given species except for some species that do not have much of the a-carotene (e.g., Rhododendron in Table 4).

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