Physiological responses of three deciduous conifers (*Metasequoia glyptostroboides*, *Taxodium distichum* and *Larix laricina*) to continuous light: adaptive implications for the early Tertiary polar summer

M. ALEJANDRA EQUIZA, 1 MICHAEL E. DAY1,2 and RICHARD JAGELS1

1 Department of Forest Ecosystem Science, University of Maine, 5755 Nutting Hall, Orono, Maine 04469-5755, USA  
2 Corresponding author (day@umenfa.maine.edu)

Received January 26, 2005; accepted June 11, 2005; published online December 15, 2005

**Summary**  
Polar regions were covered with extensive forests during the Cretaceous and early Tertiary, and supported trees comparable in size and productivity to those of present-day temperate forests. With a winter of total or near darkness and a summer of continuous, low-angle illumination, these temperate, high-latitude forests were characterized by a light regime without a contemporary counterpart. Although maximum irradiances were much lower than at mid-latitudes, the 24-h photoperiod provided similar integrated light flux. *Taxodium*, *Larix* and *Metasequoia*, three genera of deciduous conifers that occurred in paleoarctic wet forests, have extant, closely related descendents. However, the contemporary relative abundance of these genera differs greatly from that in the paleoarctic. To provide insight into attributes that favor competitive success in a continuous-light environment, we subjected saplings of these genera to a natural photoperiod or a 24-h photoperiod and measured gas exchange, chlorophyll fluorescence, non-structural carbohydrate concentrations, biomass production and carbon allocation.

Exposure to continuous light significantly decreased photosynthetic capacity and quantum efficiency of photosystem II in *Taxodium* and *Larix*, but had minimal influence in *Metasequoia*. In midsummer, foliar starch concentration substantially increased in both *Taxodium* and *Larix* saplings grown in continuous light, which may have contributed to end-product down-regulation of photosynthetic capacity. In contrast, *Metasequoia* allocated photosynthate to continuous production of new foliar biomass. This difference in carbon allocation may have provided *Metasequoia* with a two fold advantage in the paleoarctic by minimizing depression of photosynthetic capacity and increasing photosynthetic surface.

**Keywords:** allocation, carbon balance, leaf area, light-inhibition, paleoecology, photosynthetic end products.

**Introduction**

During the Cretaceous and early Tertiary (140 to 40 million years BP), polar regions were covered by extensive forests, as documented in Antarctica (Jefferson 1982, Francis 1986), Alaska (Spicer and Parrish 1986), Svalbard (Schweitzer 1980) and the Canadian High-Arctic (LePage and Basinger 1991, Young 1991, McIver and Basinger 1999). The productivity of those paleoforests was comparable with that of living temperate deciduous forests, with trees reaching diameters of 1 m and heights of up to 40 m (Art and Marks 1978, Jefferson 1982, Francis 1986, Falcon-Lang and Cantrill 2000, Williams et al. 2003).

These polar forests developed in an environment that has no extant analogue. Unlike contemporary high-latitude environments, low temperatures would not have restricted plant growth. Physical evidence and climate models show that, during the Cretaceous and early Tertiary, polar regions experienced warm temperate climates (Wolfe 1980, Spicer and Chapman 1990, Greenwood and Wing 1995) and recent modeling suggests that atmospheric and soil water contents were 20–25% higher than at present (Bowen et al. 2004). There is a lack of consensus about atmospheric carbon dioxide (CO₂) concentrations during the Eocene, with estimates ranging from 2,000 ppm (Pearson and Palmer 2000) to near present day values (Royer et al. 2001). Integrated light flux (fluence) would have been similar to that of mid-latitudes (Creber and Chaloner 1984, Jagels and Day 2004); however, the light regime in such a polar environment would differ qualitatively from that to which contemporary temperate tree species are adapted. The light environment would be characterized by a summer of continuous, low-angle, low to moderate irradiance followed by a winter of darkness or extremely low irradiances. Forest trees, growing at latitudes as high as 80° N, would have been subjected to about 4 months of continuous daylight and a similar period of continuous winter darkness (Pielou 1994). In contrast to the predominance of temperature in determining plant distribution in current global climate regimes (Woodward 1987), this polar light regime may have exerted a major control over high-latitude plant distribution during the Cretaceous and early Tertiary.

In contemporary forests, light often determines competitive interactions on a local scale. Shade-tolerant species have an advantage in the diffuse light environment of a closed or partially closed canopy, whereas higher photosynthetic rates and
more rapid growth impart an advantage to less shade-tolerant species growing in a more open canopy (Messier et al. 1999, Bazzaz and Carlson 1982). On a latitudinal scale, crown form may be a critical attribute. For example, Oker-Blom and Kelmokaki (1982) and Creber and Chaloner (1984) suggested that a conical crown form, typical of conifers, is better adapted than a flatter crown for interception of the low-angle illumination that characterizes higher latitudes. In addition, day length establishes the phenological patterns of many species, and the ability of a species to adapt its patterns to the day-length calendar of specific latitudes may determine its range. At high latitudes, a capacity to adapt to extreme seasonal variation in day length may have been critical to the success of tree species in a temperate Arctic environment. Like other resources, light has positive effects on plant growth within a certain range of irradiances and potentially detrimental effects at high irradiances (Johnson et al. 1993). Therefore, the competitive success of a species in a particular environment depends not only on its ability to efficiently carry out photosynthesis under prevailing irradiances, but also its ability to avoid or reduce growth-limiting stresses (Nilsen and Orcutt 2000). In the low to moderate incident irradiances of the Arctic paleoenvironment, shade-adaptive photosynthetic attributes, such as investment in the photosynthetic light harvesting complex, would increase photosynthetic efficiency. However, enhanced ability to harvest light energy in a continuous light (CL) environment presents the risk of hypersaturation of the photosynthetic machinery leading to photoinhibition and long-term reduction in photosynthetic capacity.

Previously, we examined interspecific differences in the characteristics of the photosynthetic response to irradiance and found that Metasequoia possesses a suite of morphological and physiological attributes that optimize its performance at low to moderate irradiances (< 500 µmol m⁻² s⁻¹ photosynthetic photon flux (PPF)) (Jagels and Day 2004). However, there are other aspects of photosynthetic and carbon-balance physiology that may be of critical importance in the distinctive light regime of a temperate Arctic. Studies of tree growth efficiency have shown that foliage density and display may supercede photosynthetic rate as a predictor of tree growth (Boltz et al. 1986, McCrady and Jokela 1998). In addition, variations of net photosynthesis in diurnal and seasonal cycles have powerful implications for carbon balance and growth (Luxmoore 1991). This latter aspect may be especially significant considering the light environment of the high Arctic, which poses both opportunities and difficulties. The long days of a temperate-Arctic growing season provide an integrated fluence of photosynthetically active radiation (PAR, λ = 400–700 nm) similar to mid-latitudes (Jagels and Day 2004). Compared with mid-latitudes, however, the Arctic light regime provides irradiances below the photosynthetic saturation point of many tree species for a greater amount of time (higher proportion of “useful” radiation). In addition, irradiance in the Arctic lies for a greater proportion of time within the more linear portion of the photosynthetic light response curve, where photosynthetic efficiency (mol CO₂ fixed per mol incident quanta) is maximized (Hikosaka and Terashima 1995).

Potentially negative aspects of continuous illumination result from stress associated with damage to photosynthetic and other subcellular systems occurring when absorbed solar energy cannot be adequately dissipated. Damage resulting from the inadequacy of photoprotective mechanisms can result from direct effects on photosynthetic pigment–protein complexes (Demming-Adams and Adams 1996, Park et al. 1996, Streb et al. 1998), instability of cross-membrane pH gradients in the grana of chloroplasts (Briantais et al. 1979, Manuel et al. 1999) and accumulation of excess reducing capacity and free radicals (Kozaki and Takeba 1996, Noctor et al. 1999). Stress caused by excess light can occur when photosynthetic utilization of absorbed irradiance is down-regulated by end-product accumulation or other feedback systems (Paul and Foyer 2001) and non-photosynthetic energy dissipation pathways are inadequate to channel the excess energy (Johnson et al. 1993).

We evaluated the responses to CL of small saplings of three deciduous conifers Metasequoia glyptostroboides H. H. Hu & Cheng, Larix laricina (Du Roi) C. Koch and Taxodium distichum L. Rich. These genera were present in temperate Arctic paleoforests and, because all are adapted to hydric soils, would have been potential competitors in wet forests. However, the distribution of the paleospecies differed greatly from their extant counterparts (Schweitzer 1980, LePage and Basinger 1991, Momohara 1994, Yang and Jin 2000). Fossil remains of Metasequoia, a genus that is now restricted to scattered relict stands, have been found throughout the high Arctic (above 75° N) where it was the dominant tree species at most sites. Larix, now a dominant conifer genus on boreal wet sites, was a frequent co-inhabitant of the Metasequoia-dominated paleoforests, whereas Taxodium, a species of which dominates many contemporary warm-temperate swamp forests in North America, has been reported from a single site only (Svalbard, Norway), where it was a minor component (Schweitzer 1980). Jagels and Day (2004) proposed that competitive success in these high-latitude temperate forests derived from specialized approaches to carbon balance physiology that may be both quantitatively and qualitatively distinct from those that are optimal in present-day temperate forests (Schweitzer 1980). Such a model could explain why the now relict, coniferous genus Metasequoia dominated wet forests in the Eocene Arctic (Schweitzer 1980, Francis 1991, Momohara 1994).

In this replicative study we subjected saplings to one of two light treatments that provided a similar photon fluence but different diel patterns of irradiance: a natural photoperiod for mid-latitudes (DL) and a 24-h photoperiod of moderate irradiance (CL), to test two hypotheses associated with physiological adaptations to CL: (1) in the temperate Arctic paleoenvironment, competitive superiority would have been conferred on species with the highest productivity in continuous moderate irradiance; (2) differences in carbohydrate partitioning provide a mechanistic basis for understanding differences in CL stress-tolerance. Photosynthetic carbon fixation is the primary mechanism for dissipation of excess light energy captured by light-harvesting systems and, in the CL environment, species that partition excess carbohydrates to growth will...
Two-year-old saplings of Metasequoia glyptostroboides, though sensitive to acidic pH, can also grow well on more alkaline soils. Preference for moist to saturated or flooded soils, and tolerance of waterlogged conditions, are common characteristics of NLR species similar to those of their paleo-relatives (Mosbrugger 1999). Jagels and Equiza (2004) have reviewed the evidence supporting use of an NLR approach to explore the ecophysiology of Eocene high-latitude paleoforests.

Fossil Metasequoia was distributed worldwide, including latitudes as high as 80° N, during the early Tertiary (Momohara 1994). Metasequoia glyptostroboides, the single extant species of the genus, was discovered as a relict population in a remote area near the border of Sichuan in south-central China in the 1940s (Hu and Cheng 1948, Chu and Cooper 1950). Because the natural range of Metasequoia is restricted to scattered relict stands in moist, narrow valleys within an area of about 40–50 cm tall. The population of saplings was replaced about 40–50 cm tall. The population of saplings was replaced every three weeks. In 2002, the treatments were maintained for 4 months (May 21–September 26), whereas treatments were maintained for 3 months in 2003 (June 26–September 26).

Mean maximum PPF in the CL treatment was about 34% lower than in the DL treatment (see Figure 1a), and is comparable with the PPFs at high latitudes (Jagels and Day 2004). Fluence did not differ significantly between treatments (see Table 2); however, it varied by day, with CL plants receiving slightly more light during cloudy weather and DL trees receiving more light on sunny days (see Figure 1b). Temperature and humidity did not differ between treatments (see Table 2).

Leaf gas exchange

Gas exchange was measured on fully expanded foliage from the upper-third of the trees with a portable open-flow photosynthesis system (LI-6400, LI-COR) equipped with a LI-COR LI-6400B red/blue LED light source or LI-6400-40 leaf chamber fluorometer. Before all measurement, samples were equilibrated for 15 min to conditions within the cuvette (PPF: 100, 500 or 1000 µmol m⁻² s⁻¹ and CO₂ concentration: 360–400 ml l⁻¹). In 2002, gas exchange was measured in August–September between 1000 and 1400 h on two randomly selected trees from each block-by-treatment group. In 2003, measurements were taken during a 9-day period in early August on three randomly selected trees from each block-by-treatment group, with one tree from each group measured each day. To investigate the diel pattern of photosynthesis, measurements were made every 4 h between 0600 and 1800 h in both treatments and, additionally, at 2200 and 0200 h in CL saplings. We used a standard PPF of 500 µmol m⁻² s⁻¹ for all measurements made in 2003. This PPF was chosen to represent a balance between the mean maximum growth PPFs of the two treatments (see Table 2) and is an approximation of modeled summer PPFs in high-latitude paleoenvironments (Jagels and Day 2004).

Chlorophyll fluorescence

Utilization and dissipation of energy by the photosynthetic apparatus was determined in situ by pulse amplitude modulated fluorometry (Krause and Weiss 1991), using the LI-COR LI-6400-40 leaf chamber fluorometer integrated with the LI-6400-40 leaf chamber fluorometer.
COR LI-6400 portable photosynthesis system. Measurements were made in August 2002, between 1000 and 1400 h, at PPFs of 100, 500 and 1000 µmol m–2 s –1 following a 20-min equilibration at each PPF. The effective quantum yield of photosystem II (Φ) was calculated as \((F_m' - F_s)/F_m'\), where \(F_s\) is the steady-state fluorescence of a light-adapted leaf and \(F_m'\) is the maximal fluorescence of a light-adapted leaf following application of a saturating flash (van Kooten and Snel 1990).

Quenching analysis was initiated by first measuring minimum fluorescence \((F_o)\) and maximum fluorescence \((F_m)\) of a dark-adapted (30 to 45 min) leaf. We measured \(F_s\) and \(F_m'\) following exposure to actinic light (500 µmol m–2 s –1 ) for 20 min and \(F_o'\) (minimum fluorescence of a light-adapted leaf) following a “dark-pulse” of far-red light. We calculated \(q_P\) as \((F_m' - F_s)/(F_m' - F_o')\) and \(q_N\) as \((F_m - F_m')/(F_m' - F_o')\) (van Kooten and Snel 1990).

Chlorophyll concentration
We measured chlorophyll concentration (July 30, September 10) during the 2003 growing season in fully expanded foliage from the upper-third of the saplings. After collecting three composite samples from each block-by-treatment group, chlorophyll was extracted by the dimethyl sulfoxide extraction procedure of Hiscox and Israelstam (1979) followed by spectrophotometric quantification. Chlorophyll concentration was calculated following the equations of Arnon (1949).

Carbohydrate quantification
In 2003, we collected leaves in July and August and measured soluble sugar and starch concentrations in one composite sample for each block-by-treatment-by-time group. Immediately after leaf collection, the samples were dried at 70 °C, ground in liquid nitrogen and the ground powder stored at –20 °C until analyzed. Soluble sugars were quantified by the phenol-sulfuric method (Dubois et al. 1956) after triple extraction of the ground powder in boiling alkaline water (Equiza et al. 1997). Starch was quantified in the remaining pellet by the phenol-sulfuric method, following double extraction with perchloric acid (Rose et al. 1991).

Growth and biomass production
We harvested two randomly selected trees from each block-by-treatment group to quantify total needle and wood (bran-
Table 2. Environmental conditions created by the natural photoperiod (diurnal light) and 24-h photoperiod (continuous light) treatments. Data represent the means of 3 blocks ± 1 standard error. Abbreviation: PPF = photosynthetic photon flux.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Treatment</th>
<th>Diurnal light</th>
<th>Continuous light</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily fluence (mol m^{-2})</td>
<td>15.4 ± 5.5</td>
<td>15.7 ± 3.4</td>
<td></td>
</tr>
<tr>
<td>Maximum PPF (µmol m^{-2} s^{-1})</td>
<td>676 ± 242</td>
<td>447 ± 161</td>
<td></td>
</tr>
<tr>
<td>Day length (h)</td>
<td>14</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Mean temperature (°C)</td>
<td>20.7 ± 2.1</td>
<td>19.5 ± 2.3</td>
<td></td>
</tr>
<tr>
<td>Maximum temperature (°C)</td>
<td>25.2 ± 3.8</td>
<td>22.2 ± 2.8</td>
<td></td>
</tr>
<tr>
<td>Minimum temperature (°C)</td>
<td>16.8 ± 2.3</td>
<td>16.6 ± 2.8</td>
<td></td>
</tr>
<tr>
<td>Relative humidity (%)</td>
<td>84.9 ± 5.9</td>
<td>92.9 ± 4.2</td>
<td></td>
</tr>
</tbody>
</table>

**Statistical analysis**

To test for the effects of light regime, block, species and time, all data were subjected to analysis of variance (ANOVA) for a randomized block design with tree as the experimental unit and, as appropriate, with individual leaves as subsamples (GLM procedure of SYSTAT v. 10.2, Systat, Evanston, IL). We used Tukey’s HSD test for separation of means.

**Results**

**Experimental conditions**

Although mean maximum PPFs were about 50% higher in the DL treatment than in the CL treatment, integrated PAR fluence did not differ significantly between treatments (Table 2). Maximum PPFs were within the range that Jagels and Day (2004) predicted for high-latitude temperate environments (Figure 1). Temperature and relative humidity did not differ significantly between treatments (Table 2); however, distance from evaporative coolers provided a within-treatment temperature gradient, manifested as significant block effects in ANOVA.

**Leaf gas exchange**

The photosynthetic response of *Metasequoia* to irradiance was qualitatively different from that of *Taxodium* and *Larix*. Gas exchange of *Metasequoia* foliage was light-saturated at relatively low irradiances (Figure 2) and showed no significant increase with increasing PPF in either light treatment. The CL treatment caused marked reductions in photosynthetic rates of *Taxodium* and *Larix* (Figure 2) but only a small decrease in the photosynthetic rate of *Metasequoia*. These patterns held throughout the diurnal cycle (Figure 3).

The ratio of total carbon fixation at the leaf level in the CL regime to total carbon fixed in the DL regime was 1.71, 1.54 and 1.43 in *Metasequoia*, *Taxodium* and *Larix*, respectively. Although CL saplings had lower instantaneous CO2 fixation compared with DL saplings, their ability to maintain photosynthetic activity throughout the 24-h photoperiod resulted in higher total carbon fixation. This simplified calculation does not account for foliar nighttime respiration, which should increase the relative fixation in CL foliage. Furthermore, no attempt was made to integrate carbon gain across foliage adapted to various positions in the sun–shade gradient within the tree and the PPF of 500 µmol m^{-2} s^{-1} used to simulate paleoarctic irradiance was below the estimated photosynthetic light-saturation value for *Larix*. Although these aspects of the experimental design limit the usefulness of the data for interspecific comparisons and modeling carbon mass balance, the results shed light on the paradox of suppressed photosynthetic capacity and high growth rates of trees growing in a 24-h photoperiod (Art and Marks 1978, Osborne and Beerling 2003, Williams 2004).

**Chlorophyll fluorescence**

In the first experiment, the effect of the light treatment on the Φ was determined at the PPFs used for the leaf photosynthetic measurements. In all three species, Φ declined with increasing PPF (Figure 4). However, the magnitude of the decrease in Φ was greater in CL saplings than in DL saplings and it also differed among species. For example, at a PPF of 500 µmol m^{-2} s^{-1}, Φ was depressed 25% in *Metasequoia* and *Larix*, but 43% in *Taxodium*. Values of qP were significantly lower in CL sap-
lings than in DL saplings. In *Metasequoia*, the CL treatment caused a 10% reduction in $q_N$ compared with decreases of 23% in *Taxodium* and *Larix* (Figure 5a). Values of $q_N$ did not differ between species or light treatments (Figure 5b).

**Foliar chlorophyll concentration**

In *Metasequoia*, leaf chlorophyll concentration did not differ between light treatments at either sampling time. Compared with DL saplings of *Taxodium*, the chlorophyll concentration of CL saplings was 10 and 38% lower at the first and second sampling time, respectively. In *Larix*, foliar chlorophyll concentration was 16% lower in CL saplings than in DL saplings at both sampling times.

**Foliar carbohydrate concentration**

No differences between light treatments were observed in soluble sugar (SS) concentration in July ($P = 0.561$) (Figure 6a). In August, compared with DL saplings, SS content was significantly higher in CL saplings of *Metasequoia* and *Taxodium* (27 and 35%, respectively), but there were no significant differences in SS concentration between treatments in *Larix* (Figure 6b). Starch concentrations differed between species at both sampling dates (Figures 6c and 6d). Starch concentration in *Metasequoia* did not differ between light treatments at either
Taxodium saplings contained 78% more starch in July and 86% more in August in the CL treatment compared with the DL treatment. In Larix saplings, the CL treatment caused a significant increase in starch concentration in July, but not in August \((P = 0.739)\).

**Growth and biomass production**

The light treatments had no significant effects on height or stem diameter increment in any of the species (data not shown). In all species, aboveground biomass was higher in CL saplings than in DL saplings (Figure 7). This response varied by species with differences in total biomass increment of 32, 23 and 15% in Metasequoia, Taxodium and Larix, respectively. All differences were attributable to foliar biomass, because woody aboveground biomass did not differ between treatments. The ratios of needle biomass to wood biomass in CL saplings were 0.84, 0.50 and 0.63 for Metasequoia, Taxodium and Larix, respectively. The corresponding ratios for DL saplings were 0.53, 0.37 and 0.49. Root biomass increased in response to the CL treatment in Metasequoia and Larix, but not in Taxodium (Figure 7). The CL treatment increased root: shoot biomass ratios in Metasequoia (0.47 to 0.63) and Larix (0.12 to 0.17) and decreased the ratio in Taxodium (0.50 to 0.42).

**Discussion**

Metasequoia was once a dominant component of temperate high-latitude wet forests where it successfully out-competed other genera that dominate contemporary wet forests, such as Taxodium and Larix. If we accept the use of NLR species as useful surrogates for the morphological and physiological attributes of paleospecies, our three deciduous conifers provide...
a system for understanding morphological and physiological attributes that are adaptive to temperate Arctic wet-site forests. In those environments, with temperature and water not limiting (Bowen et al. 2004), light may have played a crucial role in determining species distributions. Adaptations to surviving the long arctic night with irradiances below the photosynthetic light-compensation point have been widely discussed (Spicer and Chapman 1990, Royer et al. 2003). However, the challenges presented by the continuous light of the arctic summer are poorly understood and may have been key factors determining competitive interactions.

Photosynthetic adaptations to continuous light

Adaptation to a temperate polar light regime would favor a combination of attributes that promote efficient photosynthesis at low to moderate irradiances and minimize the adverse effects caused by excess light energy absorption. We found that plants adapted to higher irradiances, such as the sun-adapted genera *Larix* and *Taxodium*, were substantially more stressed in a 24-h photoperiod compared with the more shade-adapted *Metasequoia*. Within a species, different letters indicate a significant difference between DL and CL treatments (P < 0.05). Bars indicate standard errors.
Symptoms of light stress can result when solar energy dissipation through \(q_p\) and \(q_N\) pathways is insufficient to balance the input of energy from the photosynthetic light-harvesting complex (Johnson et al. 1993). Müller et al. (2001) suggested that \(q_N\) is most effective at low irradiances and saturates at moderate irradiances, with the \(q_p\) pathway predominating at moderate and higher irradiances. In support of this suggestion, we found that \(q_N\) rates were unaffected by the light treatments and similar across species (Figure 5b). If \(q_N\) mechanisms are saturated, the plant’s ability to avoid light stress will rely on the \(q_p\) pathway, which ultimately is regulated by the availability of sufficient carbohydrate sink strength to prevent end-product feedback inhibition of \(q_p\).

Sugar sensing is widely held as a pathway inducing end-product feedback inhibition of photosynthesis (Rolland et al. 2002, Gibson 2000) and, therefore, regulating energy movement through the \(q_p\) pathway. Experimentally reducing sink demand in conifers results in increased foliar sugar concentration and a simultaneous decrease in photosynthetic capacity (Myers et al. 1999). In our study, sugar concentrations did not differ between species or light treatments during the peak growing season (July) and showed only a slight relative increase in CL saplings of \(Taxodium\) and \(Metasequoia\) in the CL treatment in August (Figure 6). As Osborne and Beerling (2003) found in a comparative study of the responses of conifers to a combination of CL and elevated CO\(_2\) concentration, soluble sugars could not be explicitly correlated with depression of photosynthetic capacity. The increase in soluble sugar concentration late in the growing season (August) coincided with a decreasing growth rate. Compared with DL saplings, starch concentration was substantially higher in CL saplings of \(Taxodium\) and \(Larix\), but not in CL saplings of \(Metasequoia\) (Figures 6), providing the potential for feedback regulation in \(Taxodium\) and \(Larix\), although the link between starch concentration and regulation of photosynthesis remains poorly understood and controversial (Paul and Foyer 2001). Reduced foliar chlorophyll concentration in CL saplings is consistent with decreased allocation to photosynthetic systems.

Brodribb and Hill (1997) found that \(q_N\) was tightly correlated with sun–shade adaptation in southern hemisphere conifers, with saturation of the light response varying from 500 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) in shade-adapted species to > 2500 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) in sun-adapted species. Our \(q_N\) values, determined at a PPF of 500 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) were similar to the maximum values reported for conifers by Brodribb and Hill (1997). However, unlike that study, we found that the more shade-adapted \(Metasequoia\) had \(q_N\) values similar to those of sun-adapted \(Larix\). This is consistent with the atypical collection of sun- and shade-adaptations that Jagels and Day (2004) propose gave \(Metasequoia\) a competitive advantage in the distinctive light regime of the temperate Arctic.

Carbon balance in continuous light environments and implications for paleoarctic forests

Both assimilation rate and quantum efficiency were reduced by CL in our study species (Figure 8), likely a result of
long-term down-regulation of photosynthetic capacity (Krapp and Stitt 1995, Gibson 2000). However, CL saplings were able to maintain this reduced photosynthetic activity over the 24-h photoperiod. Given the similar quantum fluence (integrated quantum flux) in the DL and CL treatments, the CL saplings received a greater proportion of that fluence at irradiances below the saturating value and may be able to take advantage of this greater proportion of incident PAR. These factors indicate that, in a CL environment resembling the one proposed for the temperate Arctic, both absolute growth and light-resource-use efficiency (based on fluence) could exceed those of the DL environment of lower latitudes. This is consistent with empirical studies of growth rings of fossil wood from high-latitude paleoforests (Creber and Chaloner 1984, Creber and Fancis 1999).

Our comparative study provided insights into the allocation and fate of the carbon fixed by CL saplings. Potential carbon sinks include starch reserves, above- and below-ground biomass and respiration. In comparison with the other species, the strongly indeterminate growth habit of Metasequoia, with substantial CL-treatment-related increases in both above- and below-ground biomass accumulation, potentially reduced sink limitations (Figure 7). The general pattern for all three species indicated that the increase in SS was minimal, whereas both starch and growth (change in biomass) exhibited significant increases in response to the CL treatment.

With respect to the potential competitive success of the study species in a temperate CL environment, Metasequoia showed the greatest increase in total carbon fixed (Figure 8). Metasequoia had the lowest allocation to starch (storage) and Taxodium had the highest allocation to starch, with starch allocation being intermediate in Larix. Relative allocation to biomass production showed the reverse order to starch accumulation. The increase in aboveground biomass in response to the CL treatment in Metasequoia and Larix was principally the result of increased carbon allocation to foliage (foliar density, Figure 8). In an environment where water is not generally the limiting resource, investment in leaf area would be expected to accelerate subsequent relative growth rates up to the point where light becomes a marginal resource from mutual-shading effects (Cornelissen et al. 1996, Poorter and Nagel 2000). Our study indicates that the ability to utilize the continuous light of the temperate Arctic to increase leaf area could competitively favor Metasequoia and Larix over Taxodium, and Metasequoia over Larix. Increased leaf area could provide three advantages: (1) an effective sink mechanism for coping with inhibition from excess solar energy absorption and photosynthetic end-product accumulation; (2) increased photosynthetic surface with multiplicative effects on productivity; and (3) enhanced shading of competitors.

Acknowledgments

The authors thank Damian Cirelli for his invaluable technical support and David Tissue for his comments on an earlier draft of this manuscript. This research was funded by a grant from The Andrew W. Mellon Foundation to R.J. and M.E.D. and USDA McIntire-Stennis support for R.J. This is Publication Number 2814 of The Maine Agriculture and Forest Experiment Station.

References


362 EQUIZA, DAY AND JAGELS

TREE PHYSIOLOGY VOLUME 26, 2006
Hikosaka, K. and I. Terashima. 1995. A model of the acclimation of
Francis, J.E. 1991. The dynamics of polar fossil forests; tertiary fossil
Hiscox, J.D. and G.F. Israelstam. 1979. A method for the extraction of
Hu, S.Y. 1980. The Metasequoia flora and its phytogeographic signif-
Luxmoore, R.J. 1991. A source-sink framework for coupling wa-
Manuel, N., G. Cornic, S. Aubert, P. Choler, R. Bligny and U. Heber.
McCready, R.L. and E.J. Jokela. 1998. Canopy dynamics, light inter-
Messier, C., R. Doucet, J.-C. Ruel, Y. Caveau, C. Kelly and M.J.
Müller, P., X.-P. Li and K.K. Niyogi. 2001. Non-photochemical quen-
Noctor, G., A.-C.M. Arisi, L. Jouanin and C.H. Foyer. 1999. Photo-
Ögren, E. 1990. Evaluation of chlorophyll fluorescence as a probe for


