

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

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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), Svaldbard (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 Kekomaki (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 ($< 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 supersede 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, $\lambda = 400\text{--}700 \text{ nm}$) 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 CO_2 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 (Demmig-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 replicated 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

better avoid downregulation of photosynthetic capacity by end-product accumulation.

Materials and methods

The nearest-living-relative approach

The concept that extant species or “nearest living relatives” (NLRs) are useful surrogates for fossil species is an implicit assumption of paleoecology and associated ecophysiological interpretations. The NLR species are determined on the basis of anatomical and morphological similarities with the fossils and it is assumed that the physiological and ecological characteristics of NLR species are 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 (Momo-hara 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 800 to 1000 km² in Hubei province, at latitude 30°10' N (Chu and Cooper 1950, Bartholomew et al. 1983), knowledge of its ecology is based on limited field and experimental observations (Chu and Cooper 1950, Li 1957, Konoé 1960, Hu 1980, Jagels and Day 2004, Jagels and Equiza 2004, Vann 2004, Williams 2004). Table 1 compares the autecology and physiology of the three genera, *Metasequoia*, *Larix* and *Taxodium*, based on contemporary species. All three genera have a common preference for moist to saturated or flooded soils, and tolerate acidic pH, but can also grow well on more alkaline soils.

Plant material and treatments

Two-year-old saplings of *Metasequoia glyptostroboides*, *Taxodium distichum* and *Larix laricina* were obtained from commercial nurseries and transplanted to large pots (22 dm³) filled with peat:vermiculite:perlite (2:1:1, v/v). The plants were fertilized with a commercial controlled-release fertilizer (N,P,K 19,6,12) and drip-irrigated with an automatic irrigation system. At the beginning of each experiment, the saplings were about 40–50 cm tall. The population of saplings was replaced each year to avoid growth restrictions in the pots.

The saplings were grown in a greenhouse at the University of Maine (45° N) during the spring–summer periods of 2002 and 2003. A light-blocking partition along an N–S orientation (long-axis) divided the greenhouse into two light environments—a photoperiod characteristic of 45° N (DL) and a 24-h photoperiod (CL). An evaporative cooler (south end) and exhaust fans (north end) provided cooling. To provide replication and to compensate for a potential temperature gradient, we divided the greenhouse into three blocks separated by buffer zones. In the CL treatments, six metal-halide lamps (four

lamps of 1000 watts and two of 400 watts) were mounted on the top of each block to provide overnight illumination. Additionally, shade-cloth (about 70% interception) was placed on the outside roof along the CL side to reduce PPF during the day and compensate for the extra light that this treatment received from the lamps during the night. Because these saplings were not growing under a “simulated canopy,” no attempt was made to provide low-angle direct illumination as would have been found in the paleoarctic. Quantum sensors (LI-COR Q190; LI-COR, Lincoln, NE) and humidity sensors/thermistors (Vaisala 50Y, Vaisala, Helsinki, Finland) placed within the treatments at the center of each block and connected to data loggers (CR10X, Campbell Scientific, Ogden, UT), continuously monitored irradiance, humidity and temperature. When we initiated the CL treatments, the photoperiod was gradually increased over 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and CO₂ concentration: 360–400 $\mu\text{l l}^{-1}$). 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ 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-

Table 1. Ecological and physiological attributes of *Metasequoia*, *Larix* and *Taxodium*. Summarized from Chu and Cooper (1950), Li (1957), Konoe (1960), Hu (1980), Johnston (1990), Wilhite and Tolliver (1990), Jagels and Day (2004), Jagels and Equiza (2004) and Vann (2004).

Attribute	<i>Metasequoia</i>	<i>Larix</i> ¹	<i>Taxodium</i>
High latitude paleodistributions (Eocene)	Circumpolar and dominant in lowland swamp forests	Circumpolar, occasionally co-occurring with <i>Metasequoia</i>	Rare, only known from one site (Svalbard Island)
Current natural distribution	One relict species confined to less than 1,000 km ² in south-central China	Ten short-bracted species in North temperate and boreal forests; circumglobal	Two species (& one variety) limited to southeastern USA, Mexico and Guatemala
Site preference	Moist to saturated to flooded	Acidic bogs to dry slopes	Moist to saturated to flooded
Light preference	Probably intermediate shade tolerance	Shade intolerant	Intermediate shade tolerance
Successional status and life span	Pioneer (?) and long-lived	Pioneer; moderately long-lived	Can be a pioneer; long-lived
Maximum height	45 m or greater	Occasionally to 35 m	45 m
Cold tolerance	Moderate	Very high	Moderate
Leaf persistence and growth habit	Deciduous Indeterminate	Deciduous Indeterminate	Deciduous Indeterminate
Photosynthetic properties (μmol m ⁻² s ⁻¹)			
Light saturation point	400–500	900–1000 ²	550
Light compensation point	18	20	22
Foliar dark respiration	0.6	1.1	1.1
Apparent quantum efficiency (%)	3.8	5.7	6.0
Temperature optimum (°C)	15–25	13–24	25–30

¹ Data are for short-bract species.

² Photosynthetic saturation irradiance for *Larix* is for shoot level; values for individual needles are assumed to be lower.

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).

Photochemical (q_p) and non-photochemical (q_n) quenching were determined in August 2003. 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 \pm 1 standard error. Abbreviation: PPF = photosynthetic photon flux.

Attribute	Treatment	
	Diurnal light	Continuous light
Daily fluence (mol m^{-2})	15.4 ± 5.5	15.7 ± 3.4
Maximum PPF ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	676 ± 242	447 ± 161
Day length (h)	14	24
Mean temperature ($^{\circ}\text{C}$)	20.7 ± 2.1	19.5 ± 2.3
Maximum temperature ($^{\circ}\text{C}$)	25.2 ± 3.8	22.2 ± 2.8
Minimum temperature ($^{\circ}\text{C}$)	16.8 ± 2.3	16.6 ± 2.8
Relative humidity (%)	84.9 ± 5.9	92.9 ± 4.2

ches and stem) dry biomass at the end of each experiment. Samples were dried at 60°C for 3 weeks before weighing.

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

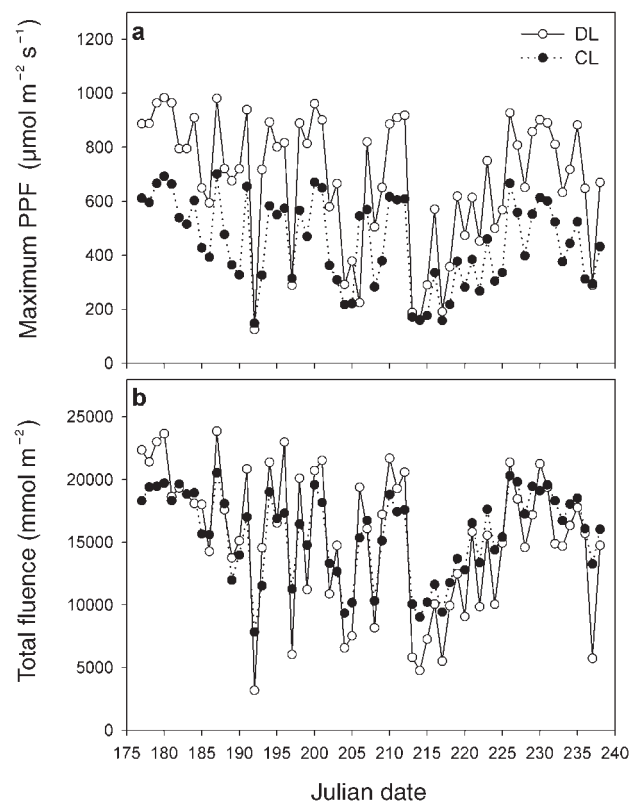


Figure 1. Photosynthetically active radiation ($\lambda = 400\text{--}700\text{ nm}$) characteristics of the diurnal light (DL) and continuous light (CL) treatments. Daily maximum photosynthetic photon flux (PPF) values (a) and total integrated quantum flux or fluence (b) are the means of three sampling blocks for each treatment.

(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 CO_2 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 $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, Φ was depressed 25% in *Metasequoia* and *Larix*, but 43% in *Taxodium*. Values of q_p were significantly lower in CL sap-

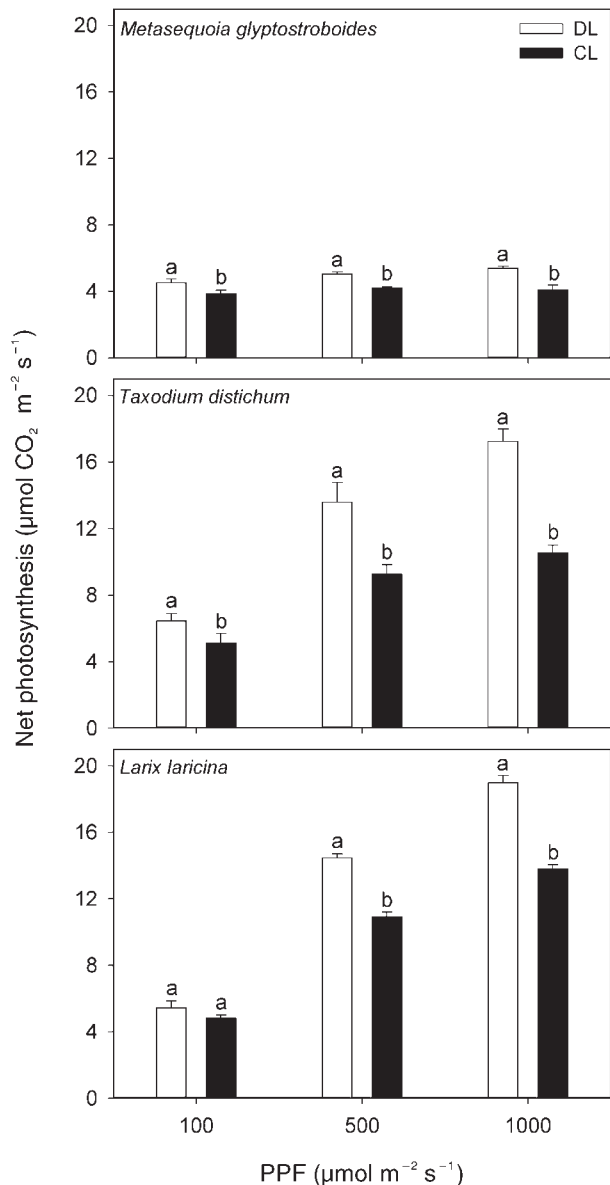


Figure 2. Net photosynthetic rates as a function of photosynthetic photon flux (PPF) in saplings growing in the diurnal (DL) and continuous (CL) light treatments. Within an irradiance treatment, different letters indicate a significant difference between DL and CL treatments ($P < 0.05$). Bars indicate standard errors.

lings than in DL saplings. In *Metasequoia*, the CL treatment caused a 10% reduction in q_P 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 con-

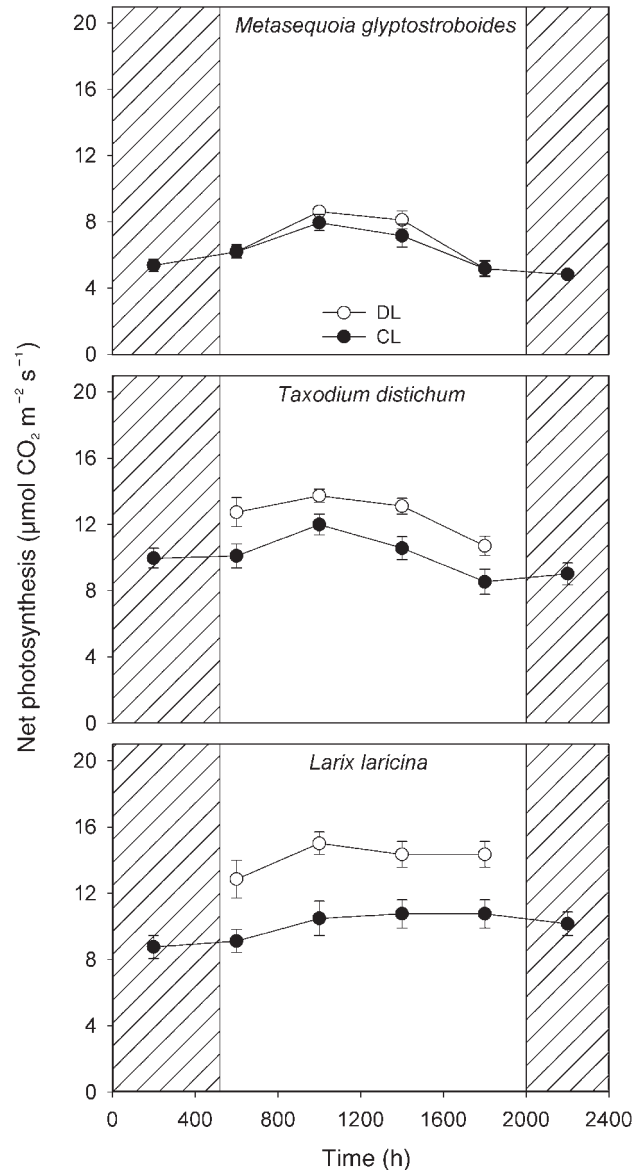


Figure 3. Daily patterns of photosynthetic rates in saplings growing in the diurnal (DL) and continuous (CL) light treatments. Photosynthetic rates of DL saplings were measured during daylight hours only. The shaded portions represent night hours. Bars indicate standard errors.

centration 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

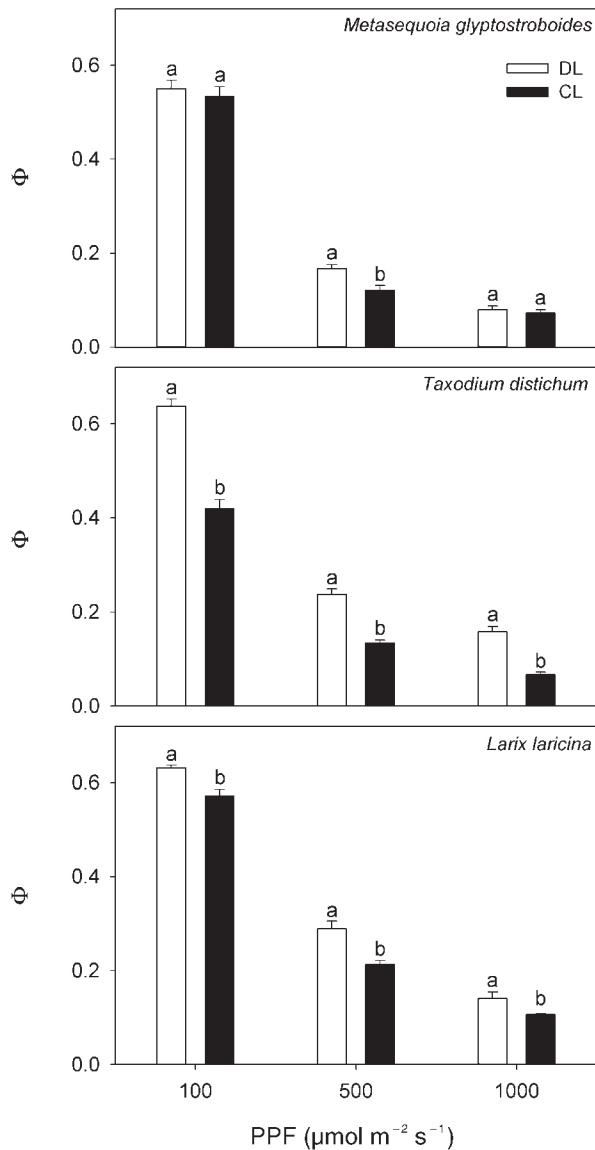


Figure 4. Photosynthetic efficiency of photosystem II (Φ) in saplings growing in the diurnal (DL) and continuous (CL) light treatments, measured at photosynthetic photon fluxes (PPFs) ranging from 100 to 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Within an irradiance treatment, different letters indicate a significant difference between DL and CL treatments ($P < 0.05$). Bars indicate standard errors.

sampling date. *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

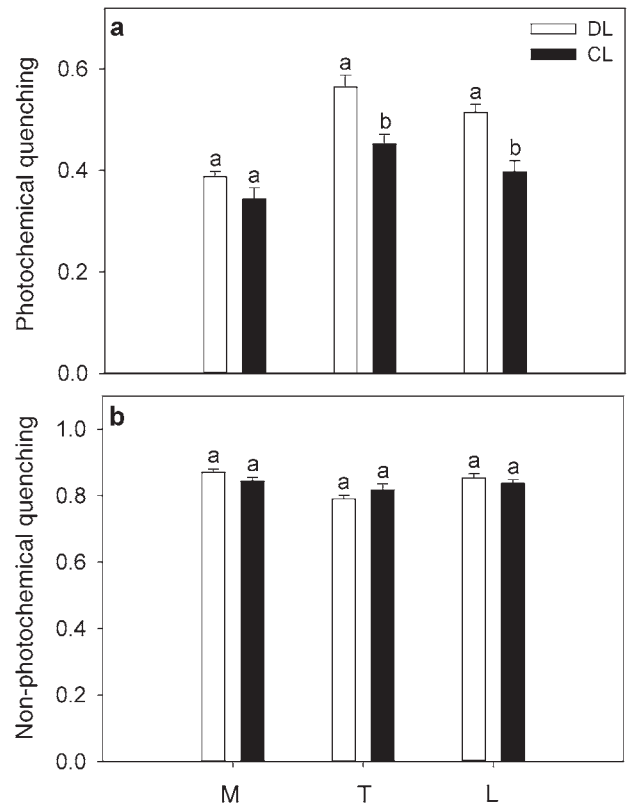


Figure 5. Photochemical (a) and non-photochemical (b) quenching in saplings growing in the diurnal (DL) and continuous (CL) light treatments. Abbreviations: M = *Metasequoia*, T = *Taxodium* and L = *Larix*. Within a species, different letters indicate a significant difference between DL and CL treatments ($P < 0.05$). Bars indicate standard errors.

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

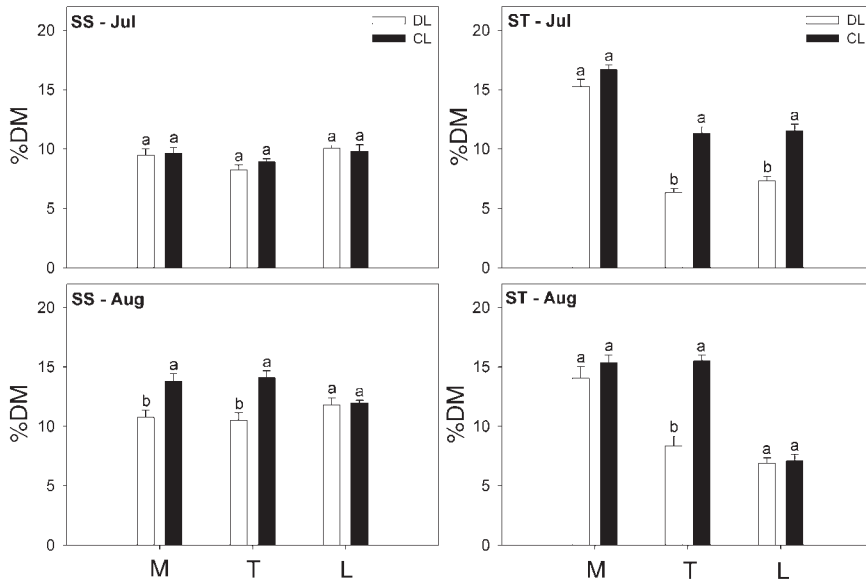


Figure 6. Nonstructural carbohydrate concentration (g g^{-1} dry mass (DM)) in foliage of saplings growing in the diurnal (DL) and continuous (CL) light treatments in July and August. Abbreviations: SS = soluble sugars; ST = starch; M = *Metasequoia*; T = *Taxodium*; and L = *Larix*. Within a species, different letters indicate a significant difference between DL and CL treatments ($P < 0.05$). Bars indicate standard errors.

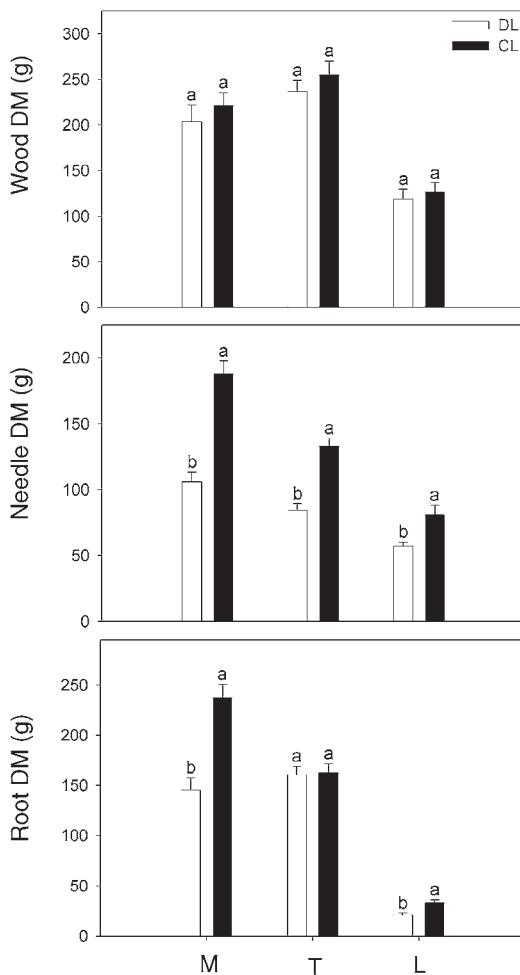


Figure 7. Stem wood, foliar and root dry mass (DM) of saplings growing in the diurnal (DL) and continuous (CL) light treatments. Abbreviations: M = *Metasequoia*; T = *Taxodium*; and L = *Larix*. Within a species, different letters indicate a significant difference between DL and CL treatments ($P < 0.05$). Bars indicate standard errors.

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* (Figure 8). The CL treatment had minimal influence on photosynthetic rates in *Metasequoia*, but substantially decreased photosynthetic rates in *Taxodium* and *Larix*. These interspecies differences were paralleled by the fluorescence data. Because of the sensitivity of photosystem II to stress, relative differences in Φ are widely used as indicators of environmental stress (Ögren 1990, Clark et al. 2000, Rolando and Little 2003). Treatment-by-species effects indicated that CL caused a large and significant decline in Φ in *Taxodium* and *Larix*, but had a nonsignificant effect on Φ in *Metasequoia* (Figure 4). The CL treatment had a greater effect on Φ in *Taxodium* than in *Larix*, even at the lowest irradiances. The greater sensitivity to CL-induced stress may account for the limited occurrence of *Taxodium* in high latitude ($> 60^\circ \text{N}$) forests compared with *Metasequoia* and *Larix* (Aulenback and LePage 1998, Jagels and Equiza 2004).

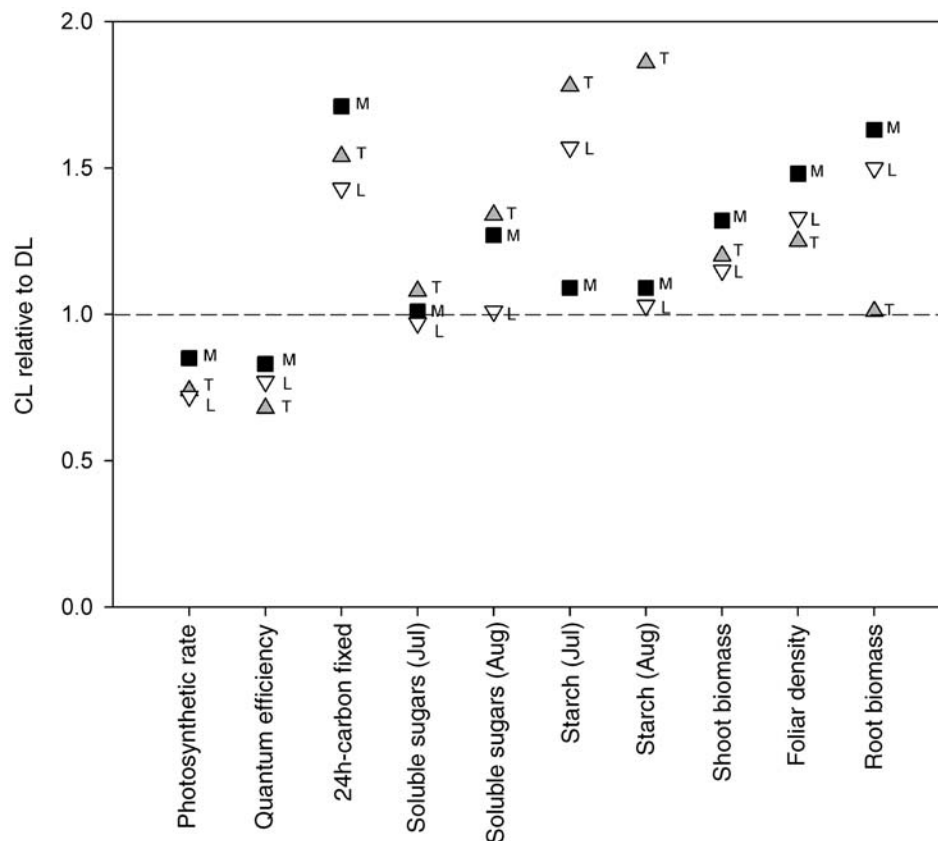


Figure 8. Summary of relative values (continuous light (CL) treatment relative to diurnal light (DL) treatment) for key photosynthetic and carbon allocation attributes of *Metasequoia glyptostroboides* (M), *Taxodium distichum* (T) and *Larix laricina* (L). Values above the 1:1 line show increases in the attributes in CL saplings relative to DL saplings and values below indicate decreases.

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 $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ in shade-adapted species to $> 2500 \mu\text{mol m}^{-2} \text{s}^{-1}$ in sun-adapted species. Our q_N values, determined at a PPF of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 Francis 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.

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