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BIRCH SEEDLING RESPONSES TO DAILY TIME COURSES OF LIGHT IN EXPERIMENTAL FOREST GAPS AND SHADEHOUSES

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Abstract. This study examined the consequences of differing daily time courses of light availability, while controlling for total photon flux density (PFD, measured in moles per square metre), on the physiology, architecture, and growth of seedlings of two birch species (*Betula populifolia* and *B. alleghaniensis*) that differ in shade tolerance. In an experimental garden, seedlings were grown in two sets of contrasting diurnal light regimes, "gaps" and "shadehouses," and at four levels of total integrated PFD (≈12, 27, 50, and 70% of full sun). In gaps, seedlings received relatively more heterogeneous diurnal light regimes, with midday full sun peaks lasting between 40 and 280 min on sunny days, depending on gap size. In shadehouses, seedlings received daily total and average PFDs similar to that in gaps, but received no midday direct sunlight, and an overall more uniform distribution of light.

The daily time course of light availability, independent of total PFD, significantly affected growth of seedlings. For both species, seedlings in shadehouses grew significantly larger than gap seedlings. Differences between diurnal treatments were greatest at lower integrated light levels in *B. populifolia,* but not for the more shade-tolerant *B. alleghaniensis.*

Diurnal light regimes also significantly influenced the degree of plasticity in a seedling's sun–shade responses. However, the magnitude of effect due to diurnal light regime depended on the particular trait investigated, the integrated light level, and the species. At similar total PFDs, most characters (e.g., specific leaf mass, leaf mass ratio) exhibited more of a sun-type response in shadehouses than in gaps, however, maximum net photosynthesis and chlorophyll *a*/*b* ratios reflected more of a sun-type response in gap light regimes.

For most growth, physiological, and morphological characters, seedling responses to increasing total PFD were generally more sensitive in gap than in shadehouse regimes. Our results also show that differences between species were greater when compared along the total PFD gradient in gaps vs. shadehouses. Both these results suggest that experimental studies employing uniform light regimes, which incorporate little of the temporal variability experienced by seedlings in natural gaps, may underestimate plasticity within regenerating tree species, and the potential for species niche differences and coexistence.

Key words: Betula; *gap dynamics; seedling carbon gain; shade tolerance; sun–shade responses; temporal heterogeneity; time course of light availability.*

INTRODUCTION

Forest canopies are not homogenous light filters. Different architectures of canopy trees and the common occurrence of branch and treefall gaps produce a spatial mosaic of light regimes at the forest floor (e.g., Lieberman et al. 1989, Smith et al. 1989, Canham et al. 1990). Seedling responses to this mosaic of light have been considered in many aspects of forest biology, ranging from the biochemistry of leaves to the differential growth, survivorship, and succession of species in forest communities. However, despite this emphasis on light, it remains unclear specifically which aspects of an irradiance regime are responsible for the growth and plastic sun–shade responses of tree seedlings. Seedling performance may be determined by the total amount of incident light per day, or it may be due to other aspects of irradiance regimes such as the magnitudes of daily peaks, the diurnal timing of peaks, or the overall variability in temporal sequences of instantaneous PFD (photon flux density, in micromoles per square metre per second).

Recent advances in radiation measurement have produced a better understanding of the types of light regimes forest seedlings naturally experience (Pearcy 1989). In addition to variation in total integrated PFD, seedlings rooted in different microsites also experience very different daily time courses of light availability. Two sets of characteristics may be distinguished: those independent of the daily PFD sequences, i.e., "atemporal" characteristics vs. sequence-related or "temporal" characteristics.

Considering atemporal characteristics first, forest light regimes often vary in their duration of time above or below critical PFD thresholds, such as photosynthetic

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compensation or saturation points, and this variation has been correlated with various aspects of seedling response (Pearcy 1983, DeJong and Doyle 1985, Chazdon and Field 1987, Oberbauer et al. 1988). Light environments within a forest also differ in characteristics related to the frequency distributions of PFD availability, including aspects such as daily peak and median values, and the overall variability of light distributions. For example, as the size of canopy openings in a Costa Rican rain forest increase, daily peaks, medians, and the overall variability (cv of 10-min means) of daily PFD regimes also increase (Chazdon and Fetcher 1984).

Light environments also vary in temporal characteristics. Due to the solar track of the sun across a patchy canopy, the irregular movements of leaves in the wind, and cloud patterns, a significant proportion of the light available to seedlings growing in understories or gaps arrives in unpredictable sequences of transient sunflecks and sun patches. The ability of plants to utilize transient light can partially depend on the sequential pattern of instantaneous values (Gross 1982, Chazdon 1988, Pearcy 1990). Because species in understory communities vary in their abilities to utilize transient light, temporal heterogeneity of light availability may play a significant role in structuring species composition in understory communities (Chazdon 1988).

While seedlings in the deep understory are generally light limited, seedlings in gaps and larger clearings are more often limited by unfavorable soil and leaf water status (Schulze 1986), low relative humidity (Tenhunen et al. 1987), high leaf temperature (Weis and Berry 1988), photoinhibition (Powles 1984), or some combination of the above (Bjorkman and Powles 1984, Ludlow 1987). These resources and environmental factors also exhibit marked diurnal patterns, often being most limiting at midday when light availability is greatest. This temporal incongruency between light and other diurnally varying factors may be responsible for mid- and late-day depressions in CO_2 assimilation and/or stomatal conductance (Chiariello et al. 1987, Tenhunen et al. 1987, Knapp et al. 1989). Thus, independent of the importance of diurnal patterns of light availability itself, the congruence of diurnal patterns of light availability with other resources or conditions may also influence plant growth.

This study examined the consequences of differing daily time courses of instantaneous PFD availability, independent of total PFD, on the physiology, development, and growth of temperate tree seedlings. Using experimental gaps and shadehouse treatments, we specifically addressed the following questions: (1) Does the diurnal pattern of PFD availability, independent of daily integrated total PFD, influence the growth of birch (*Betula populifolia* and *B. alleghaniensis*) seedlings?; (2) Does the magnitude of effect due to diurnal light regime depend on the level of total integrated PFD?; (3) Are the plastic sun–shade responses of light-related physiological and architectural traits to increasing total PFD modified by diurnal patterns of light availability, and do different traits all respond to the same components of diurnal light regime?; and (4) Do two closely related, sympatric species, which vary in alleged "shade tolerance," respond differently to the contrasting diurnal irradiance regimes?

MATERIALS AND METHODS

Species

Gray birch (*Betula populifolia* Marsh.) and yellow birch (*B. alleghaniensis* Britt.) are deciduous tree species common throughout central New England. Gray birch is considered a very shade-intolerant pioneer of old fields and large forest clearings. It is a relatively short-lived tree or shrub that grows well on nutritionally poor soils and across a broad range of moisture conditions (Burns and Honkala 1990). In contrast, yellow birch is more shade tolerant, longer lived, and much larger at maturity than gray birch. Yellow birch seedlings grow best on rich, moist soils, and can persist for some time in the understory; they require small to medium size gaps, however, for successful reproduction (Marquis 1965, Tubbs 1969).

Seeds of each species were collected from at least eight parent trees distributed across a variety of habitats within the Harvard Forest, Petersham, Massachusetts (latitude 42.5°, longitude 72°), during the fall of 1989. Seeds were first air dried, and then overwintered in a dark cold room at 4°C. On 26 April 1990, seeds of both species were broadcast onto the soil surface of 6.0 cm diameter peat pots filled with a sterilized 2:2:2:1 mixture of sand, soil, turface, and peat. Trays of peat pots were randomly arranged in a glasshouse set at 28°/22°C day/night temperature, with supplemental lighting to attain a 16-h d. As seedlings emerged, they were thinned to one per pot, selecting seedlings of similar size and developmental stage, both within and between species. On 11 June, all seedlings were transplanted into 21.2 cm diameter plastic pots (volume = 1.4 L) filled with the same soil mixture described above. Peat pots were removed and discarded, with care taken to keep soil plus the small root ball intact. Pots were fertilized with 20 mL full strength Peters solution, and then randomly assigned to treatments in an experimental garden. Pots were watered daily and fertilized every 2 wk with 50 mL of full strength Peters solution (NPK = 15:15:15).

Experimental structures and design

To study the consequences of different daily time courses of PFD availability, while controlling for total daily integrated PFD, two sets of structures were designed and constructed in the Harvard University experimental garden in Cambridge, Massachusetts (Fig. 1). Experimental gap environments were created to

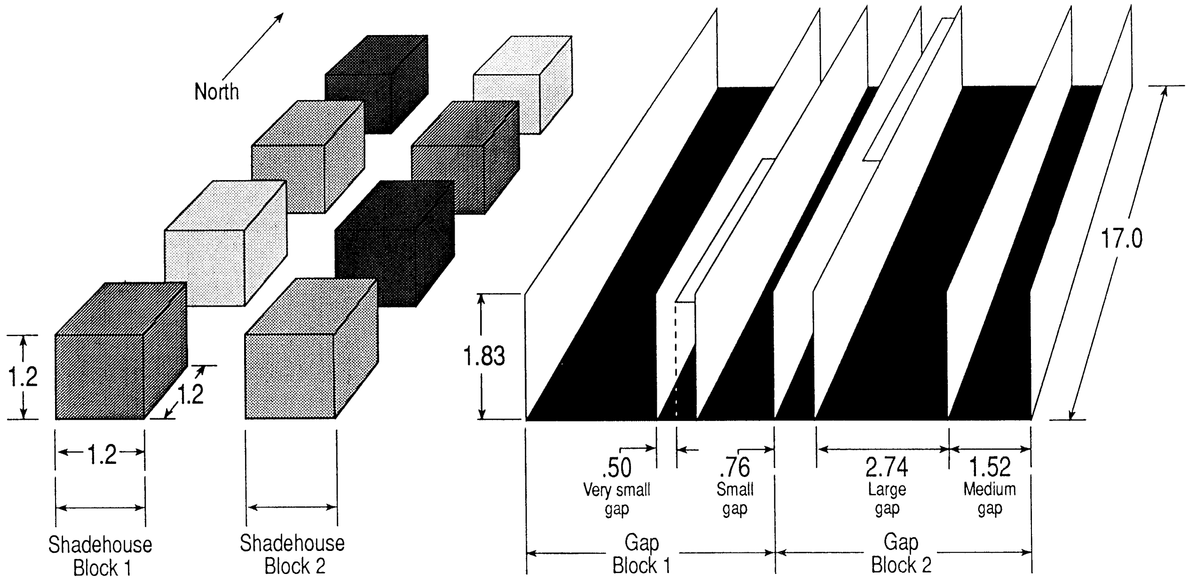


FIG. 1. Schematic and layout of experimental gaps and shadehouses. Figure is not drawn to scale. Distances are in metres.

simulate components of diurnal patterns of PFD availability measured beneath canopy gaps in the Harvard Forest (Sipe 1990), using a design modified from Marquis (1966). The structure consisted of 1.83 m high plywood walls, oriented north-south in 17.0 m long, parallel files. The distances between the files were varied, resulting in small, medium, and large "gaps." As the sun crossed the sky each day, seedlings aligned down the center of these files first experienced low intensity diffuse light, then a period of direct beam radiation, and then low intensity diffuse light again as the sun set. On sunny days, plants in these treatments received ≈1.5, 3.0, and 5.0 h of direct beam radiation in small, medium, and large gaps respectively. A fourth, very small gap was made by erecting bracketed shelves in the small gap, reducing the window of midday direct beam light to ≈1.0 h. These four gap sizes resulted in integrated daily total of ≈12, 27, 50, and 70% of the daily total PFD in adjacent open sites. These integrated light levels are referred to as L1, L2, L3, and L4, respectively. Each gap size/light level was replicated two times forming two adjacent blocks; the placement of gap sizes within a block was randomly arranged (Fig. 1).

For comparison with gap light regimes, neutral density shadehouses were constructed to produce less heterogeneous diurnal regimes with daily and seasonal totals very similar to the four gap light regimes. Eight 1.2 × 1.2 × 1.2 m wooden frames were covered on all sides with neutral density shadecloth. Four shadecloth densities were chosen (based on empirical data) to yield similar daily total PFDs as in the four experimental gap sizes on sunny days: 12, 27, 50, and 70% transmission of ambient light, also referred to as L1 through L4, respectively. A 15.0 cm gap was left between the base of each shadehouse and the ground to allow for air circulation. Each shade cloth treatment was replicated two times, and randomly located within one of two adjacent blocks. All shadehouses were located within 20 m of the experimental gaps.

The experiment was laid out as a modified split-plot design with blocks nested within diurnal regimes. Within each block and diurnal treatment, eight individuals of each species were used. Positions of the resulting 16 plants within each light treatment were randomized repeatedly throughout the season. The overall experimental design was as follows: 2 Diurnal Regimes × 2 Blocks × 4 Total PFD Levels × 2 Species × 8 Replicates = 256 seedlings.

Measurement of light regimes

Light regimes in both gaps and shadehouses were monitored throughout the growth season using two independent systems. To measure total biweekly (i.e., 2-wk intervals) and seasonal PFD received by seedlings in different treatments, photosensitive paper sensors developed by Friend (1961), and further modified by D. A. Ackerly (*personal communication*) were used. Sensors were constructed using 15 layers of Proprint sepia photosensitive paper, surrounded by 2.5 × 2.5 cm cardboard jackets with a 0.6 cm diameter exposure hole in the center. The packets were heat-sealed within small clear plastic packets for weatherproofing. Regressions of the number of layers of exposed papers to the logarithm of integrated PFD measured with PAR sensors resulted in an R^2 of 0.986 ($n = 30$). Two sensors were mounted in each shadehouse, and three in each gap irradiance regime. Paper sensors were exchanged approximately every 2 wk.

LI-COR Quantum (PAR) sensors attached to LI-COR 1000 data loggers, and PAR sensors (Biggs et al. 1971, as modified by R. Chazdon and R. Pearcy, *per-*

sonal communication) attached to Campbell 21X data loggers were used to calibrate paper sensors, and to characterize diurnal patterns of PFD in the different irradiance treatments. Both data loggers were programmed to sample PFD in 10-s intervals, and store 10-min averages. Diurnal PFD patterns were measured on representative sunny days. We also measured the ratio of red : far red light on one representative sunny day in all treatments using a Skye R:Fr light meter.

Biological measurements

Light saturated net photosynthesis (P_{max}) was assessed in a controlled environment (temperature = 28°C relative humidity = 60–70%) between 18 and 20 August. Six replicates from each treatment were brought into the glasshouse, and allowed to equilibrate to supplemented high light ($>1000\ \mu mol \cdot m^{-2} \cdot s^{-1}$) for at least 1.0 h. P_{max} was measured on the youngest, fully developed main stem leaf on each seedling. P_{max} measurements were made between 1000 and 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, light levels shown to be well above saturation for both species (Wayne 1992). Gas exchange was measured using the LI-COR 6200 system.

On leaves of age and position similar to those used for P_{max} measurements, total chlorophyll per unit leaf area and per unit leaf mass, and chlorophyll *a*/*b* ratios were measured using N,N-dimethylformamide (DMF) techniques of Moran and Porath (1980), as modified by Moran (1982) and Inskeep and Bloom (1985). Four 1.57-cm^2 leaf discs were bored from leaves on 28 August. Two samples were immediately placed in 2 mL of DMF and stored in a dark refrigerator; the other two samples were oven dried and weighed. DMF samples were then analyzed at both $\lambda = 664.5$ and 647.0 with a Perkin–Elmer Lambda 3B spectrophotometer. Total Kjeldahl nitrogen concentration was measured using entire leaves of developmental stages equivalent to those used for chlorophyll analyses. Samples were taken from eight seedlings. Nitrogen analysis was conducted using a Tecator Kjeltec Auto 1030 Analyzer system.

Diurnal gas exchange was measured on leaves of seedlings from all diurnal treatments, light levels, and species at 7 times across the day, between 0830 and 1830. Measurements were made on representative clear days using two simultaneously operated LI-COR 6200 gas exchange systems. The L1 and L3 light levels were measured on 19 July; L2 and L4 levels were measured on 20 July. In addition to net photosynthesis and stomatal conductance, the LI-COR 6200 system also recorded PFD, leaf and air temperature, and ambient relative humidity. From the above data, integrated daily carbon gain (IDCG) was estimated per unit leaf area by integrating the area beneath diurnal assimilation curves.

Just prior to final harvest, the proportion of seedlings' leaf area displayed horizontally, when viewed from directly above, was assessed using video imagery analysis. Images of seedlings' canopies were recorded using a Panasonic AG-170 Proline VCR, mounted ≈1.5 m above seedlings. Frozen frame images of canopy displays were hand traced onto tracing paper, and then scanned into a graphics program that calculated area, using a Mirror VS 300 flat bed scanner. The ratio of displayed to total leaf area was calculated for one-half of the seedlings in each treatment. On 1 September 1990, seedlings from all treatments were harvested. Seedling height, leaf, branch, and node number, and total leaf area were recorded. Seedling root, stem plus petiole, and leaf biomass were then partitioned, oven dried, and weighed separately.

Statistical analysis

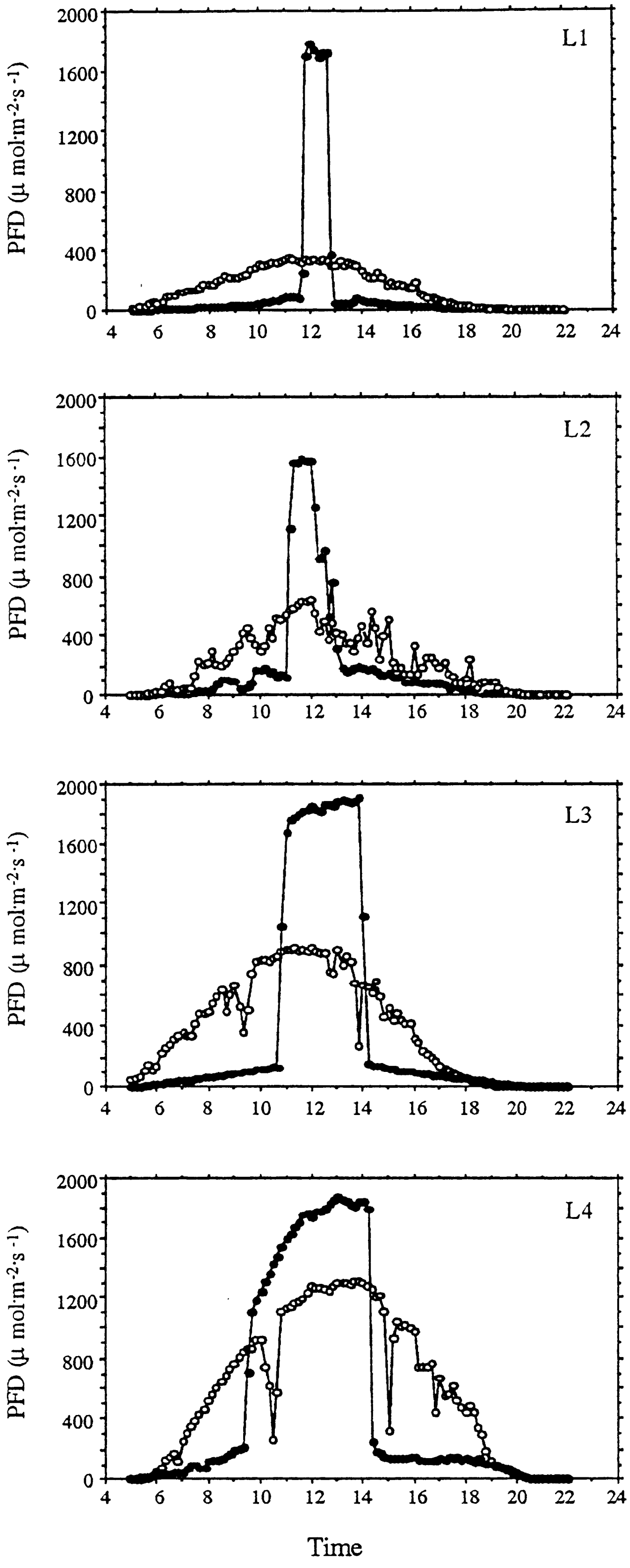
A modified split-plot analysis of variance was conducted on all growth and physiological parameters to test the effects of diurnal treatment, light level, species, and their two- and three-way interactions, using the General Linear Modelling procedure (GLM) in the Statistical Analysis System (Joyner 1985). In the model, diurnal treatment, light level, and species were considered fixed variables, and block was nested as a random variable within diurnal treatments. Diurnal treatment effects were tested against block variance, and light and diurnal treatment × light effects were tested against block × light variances. The variance due to error was used as the F ratio denominator for all other terms. Independent variables were transformed as necessary to meet the assumptions of normality and homoscedasticity of residuals (Sokal and Rohlf 1981). To specifically compare differences between species in their responsiveness to diurnal regimes, contrasts were specified to test for differences in adjusted means between diurnal treatments within both species. Student's *t*-tests with associated Bonferroni probabilities were used to assess differences between diurnal treatments (Joyner 1985).

To more closely evaluate whether diurnal treatments within particular species showed different patterns and magnitudes of plastic responses to total PFD, linear Type I regression analyses comparing both measured and derived variables to total seasonal PFD were performed (Sokal and Rohlf 1981). Because integrated light sensors accounted for the variation in total integrated PFD between replicate blocks of shadehouses and gap treatments, we eliminated the block term from this analysis and compared responses to eight, instead of four light levels, for each diurnal treatment; 97.5% confidence intervals of slopes were calculated and compared between diurnal treatments within both species.

RESULTS

Light regimes

Total integrated seasonal PFD, as measured with photosensitive paper sensors, revealed that shadehouses and gaps received very similar total PFD



L1

Daily Total PFD (mol·m^{-2}·d^{-1})	8.0	8.8
Peak PFD (µmol·m^{-2}·s^{-1})	1776.0	350.6
Daily CV (%)	308.9	84.5
Minutes above 1000 µmol·m^{-2}·s^{-1}	60.0	0

● **Gaps** ○ **Shadehouses**

L2

Daily Total PFD (mol·m^{-2}·d^{-1})	11.8	12.9
Peak PFD (µmol·m^{-2}·s^{-1})	1582.0	633.8
Daily CV (%)	200.5	91.6
Minutes above 1000 µmol·m^{-2}·s^{-1}	70.0	0

L3

Daily Total PFD (mol·m^{-2}·d^{-1})	24.2	23.9
Peak PFD (µmol·m^{-2}·s^{-1})	1911.7	903.9
Daily CV (%)	175.6	84.4
Minutes above 1000 µmol·m^{-2}·s^{-1}	200.0	0

L4

Daily Total PFD (mol·m^{-2}·d^{-1})	32.3	36.9
Peak PFD (µmol·m^{-2}·s^{-1})	1857.7	1312.6
Daily CV (%)	135.9	78.8
Minutes above 1000 µmol·m^{-2}·s^{-1}	280.0	280.0

FIG. 2. Daily time courses of light availability in experimental gaps and shadehouses, and summary statistics, as measured on representative sunny days. Each point represents a 10-min average. Coefficients of variation were calculated using 10-min averages. L1 and L3 were measured on 1 June, L2 on 6 July, and L4 on 17 June, all representative sunny days.

TABLE 1. Summary of results of analyses of variance for all gray and yellow birch characters using a split-plot nested model. Block and error terms are not included. The diurnal treatment term refers to shadehouse vs. gap regimes, and the light term refers to the four total integrated PFD levels.

	Diurnal treatment (Trt)	Light	Trt × Light	Species	Trt × Species	Light × Species	Trt × Light × Species
	Results of ANOVA F tests						
Total biomass (g)	*	*	NS	***	**	*	NS
Leaf mass ratio	NS	*	NS	***	NS	NS	NS
Stem mass ratio	NS	**	NS	NS	NS	**	NS
Root mass ratio	NS	**	*	***	NS	***	NS
Total leaf area (cm^2)	NS	*	NS	***	NS	NS	NS
Leaf area ratio (cm^2/g)	NS	***	*	NS	*	***	**
Specific leaf mass (mg/cm^2)	NS	***	**	***	NS	NS	NS
Total leaf number	NS	NS	NS	***	NS	NS	NS
Total branch number	NS	*	NS	NS	NS	NS	NS
Height (cm)	NS	NS	NS	***	*	NS	NS
Height/total biomass (cm/g)	NS	**	NS	***	NS	NS	NS
Canopy display (%)	NS	**	NS	***	**	NS	NS
Average internode length (cm)	*	NS	NS	***	NS	NS	NS
Maximum net photosynthesis (μmol·m^{-2}·s^{-1})	NS	*	NS	***	NS	NS	NS
Leaf nitrogen content (g/g)	NS	***	**	***	NS	NS	NS
Leaf chlorophyll content (mg/g)	*	***	*	NS	NS	NS	NS
Leaf chlorophyll *a*/*b* ratio	NS	NS	NS	***	***	NS	NS
Integrated daily carbon gain (mol·m^{-2}·d^{-1})	**	**	NS	***	**	NS	NS

*** $P < .001$, ** $P < .01$, * $P < .05$, NS = not significant ($P > .05$).

throughout the growing season. Average daily PFD values for the four integrated light levels in shadehouses vs. gaps were as follows: L1 = 2.3 vs 2.4; L2 = 3.3 vs 3.8; L3 = 4.7 vs. 4.5; and L4 = 5.4 vs. 5.0 mol·m^{-2}·d^{-1}. The relatively low average values reflect the fact that the summer of 1990 in Cambridge was cloudier than average. Of the 92 d of June–August, 47 were cloudy and 27 were partly cloudy (Lautzenheiser 1990).

Diurnal treatments within a light level generally received similar daily totals and averages, but these were generated with very different patterns of availability

TABLE 2. Growth, developmental, and physiological characters of gray and yellow birch seedlings grown in shadehouse and artificial gap light regimes (means ± 1 SE). Means have been adjusted for total integrated light levels, block, and light × block effects in the split-plot model. Significant differences between treatments within each species ($P < .025$) are indicated by different superscript letters.

Character	Gray birch		Yellow birch	
	Shadehouses	Gaps	Shadehouses	Gaps
Total biomass (g)	3.74 ± 0.10^{a}	2.73 ± 0.10^{b}	1.94 ± 0.10^{a}	1.48 ± 0.10^{b}
Leaf mass ratio	0.40 ± 0.005^{a}	0.42 ± 0.005^{a}	0.44 ± 0.005^{a}	0.45 ± 0.005^{a}
Stem mass ratio	0.24 ± 0.003^{a}	0.25 ± 0.003^{a}	0.24 ± 0.003^{a}	0.25 ± 0.003^{b}
Root mass ratio	0.36 ± 0.005^{a}	0.33 ± 0.005^{b}	0.32 ± 0.004^{a}	0.30 ± 0.004^{b}
Total leaf area (cm^2)	380.2 ± 10.0^{a}	329.0 ± 10.4^{b}	205.3 ± 10.0^{a}	182.5 ± 10.0^{a}
Leaf area ratio (cm^2/g)	105.8 ± 1.6^{a}	133.6 ± 1.7^{b}	108.9 ± 1.6^{a}	129.3 ± 1.6^{b}
Specific leaf mass (mg/cm^2)	3.63 ± 0.06^{a}	3.22 ± 0.05^{b}	3.98 ± 0.06^{a}	3.61 ± 0.06^{b}
Total leaf number	1.24 ± 0.01^{a}	1.19 ± 0.01^{b}	1.08 ± 0.01^{a}	1.06 ± 0.01^{a}
Total branch number	0.32 ± 0.03^{a}	0.14 ± 0.03^{b}	0.24 ± 0.03^{a}	0.10 ± 0.03^{b}
Height (cm)	32.79 ± 0.69^{a}	26.7 ± 0.71^{b}	22.1 ± 0.69^{a}	19.2 ± 0.69^{a}
Height/total biomass (cm/g)	9.3 ± 0.37^{a}	10.9 ± 0.39^{b}	12.5 ± 0.37^{a}	14.1 ± 0.37^{b}
Canopy display (%)	0.46 ± 0.019^{a}	0.54 ± 0.019^{b}	0.71 ± 0.020^{a}	0.69 ± 0.019^{a}
Average internode length (cm)	1.87 ± 0.053^{a}	1.57 ± 0.055^{b}	1.58 ± 0.053^{a}	1.46 ± 0.053^{a}
Maximum net photosynthesis (μmol·m^{-2}·s^{-1})	10.26 ± 0.26^{a}	11.34 ± 0.26^{b}	8.13 ± 0.26^{a}	8.70 ± 0.26^{a}
Leaf nitrogen (%)	1.51 ± 0.03^{a}	1.86 ± 0.03^{b}	1.42 ± 0.03^{a}	1.69 ± 0.03^{b}
Chlorophyll (mg/g)	3.96 ± 0.12^{a}	5.33 ± 0.12^{b}	3.84 ± 0.12^{a}	5.31 ± 0.12^{b}
Chlorophyll *a*/*b* ratio	1.96 ± 0.011^{a}	1.90 ± 0.012^{b}	1.76 ± 0.011^{a}	1.91 ± 0.011^{b}
Integrated daily carbon gain (mol·m^{-2}·d^{-1})	54.17 ± 1.87^{a}	57.26 ± 1.87^{a}	54.17 ± 1.87^{a}	38.29 ± 1.87^{b}

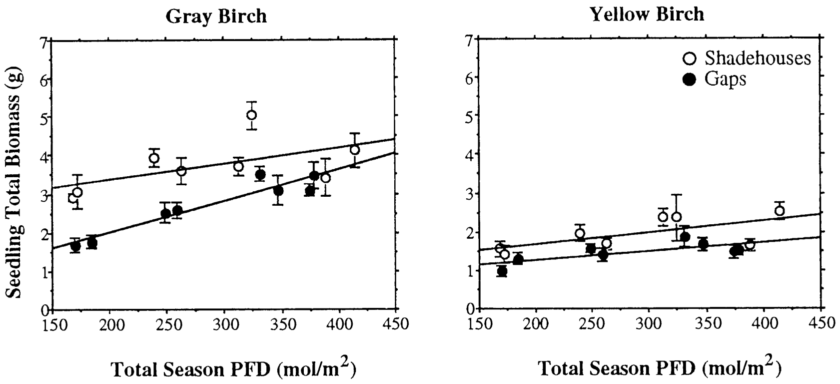


FIG. 3. Relation of gap (●) and shadehouse (○) seedling total biomass to total season integrated PFD, for gray and yellow birch. Linear regressions were fit to all data points, and these regression lines were then superimposed over means for eight light levels. Vertical bars represent ± 1 SE.

(Fig. 2). For example, on representative sunny days, L1 gaps experienced midday peaks >1000 μmol·m^{-2}·s^{-1} for ≈1.0 h, whereas shadecloth regimes never received light above 400 μmol·m^{-2}·s^{-1}. Frequency distributions of PFD classes on representative sunny days, based on 10-min averages, revealed that gap light regimes were much more heterogeneous than shadecloth regimes, particularly at lower integrated light levels (Fig. 2). The coefficient of variation for L1 gaps was 3.6 times greater than for L1 shadehouses. L4 gap regimes were temporally less heterogeneous than L1 gap regimes, but still had a CV 1.7 times greater than L4 shadecloth regimes.

The red : far red ratio of light measured at 1300 on one sunny day was 1.15, and did not substantially differ either between gaps and shadehouses, or across light levels within treatments.

Seedling responses

Analysis of variance revealed that different daily time courses of PFD (i.e., shadehouses vs. gaps) significantly influenced many aspects of birch seedling performance; however, the magnitude of this effect depended on the particular species, the light level, and the character being investigated (Table 1). For 9 of the 17 characters investigated, diurnal treatment, or its interaction with light or species, exhibited significant effects. Light level (total PFD) had a significant effect on nearly all characters, and 5 of the 17 characters showed significant diurnal treatment × light interactions. Species differed significantly in 13 of 17 characters, and 4 characters showed significant species × light interactions (Table 1).

Seedling growth and biomass allocation.—Seedling total biomass increased significantly with increasing total season PFD for both species and diurnal treatments (regression $P < .015$). Across the entire range of total PFD and for both species, total biomass of shadehouse seedlings was significantly greater than that of gap seedlings (Table 2, Fig. 3). For gray birch, differences between diurnal treatments were greatest at lower total PFD, where shadehouse seedlings were nearly twice the size of gap-grown seedlings.

Allocational responses to increasing total PFD also differed between diurnal treatments (Fig. 4). Leaf mass ratio (LMR) of both species decreased with increasing PFD in the gap regimes ($P < .0001$), but showed little response to increasing PFD in shadehouses. Root mass ratio (RMR) showed the opposite trend compared to LMR, increasing significantly with total PFD in all but the yellow birch shadehouse plants ($P < .01$). In most cases, gap seedlings' LMR and RMR showed significantly steeper responses to changes in total PFD than did shadehouse grown seedlings (Table 3). For both species, leaf and stem mass ratios were slightly lower, and root mass ratios higher in shadehouse than in gap-grown seedlings, significantly so for the latter two traits (Table 2).

Shoot development.—Total leaf area did not show any significant (linear) response to total PFD across all treatments and species, and slopes did not differ from one another (Table 3). However, for any given total PFD value, both species showed significantly greater total leaf areas for shadehouse vs. gap-grown seedlings (Fig. 5a, Table 2). Leaf area ratio (LAR) declined significantly with increasing total PFD for both treatments and species ($P < .0001$). In both species, shadehouse seedlings exhibited significantly steeper responses to increasing total PFD than did gap treatment seedlings (Table 3, Fig. 5b). For both species, gap seedlings had overall higher LARs than shadehouse seedlings, with differences being greatest at lower total PFDs (Table 2).

Specific leaf mass (SLM) increased significantly with increasing total PFD for both species and treatments ($P < .001$; Fig. 5c). For gray birch, the slope of SLM on total PFD was significantly steeper for gap seedlings than for shadehouse seedlings (Table 3). Across all light levels, SLM for both species was significantly greater for shadehouse than for gap seedlings (Table 2), but

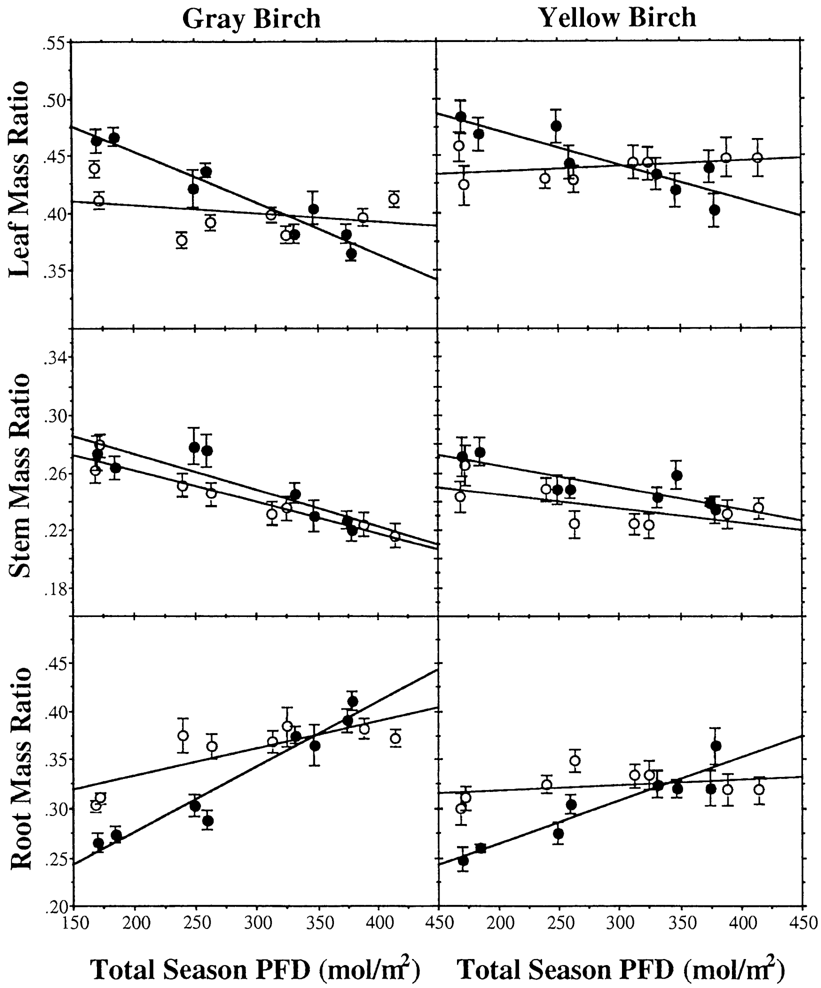


FIG. 4. Responses of gap and shadehouse seedling allocational patterns to total season integrated PFD for gray and yellow birch. Data presentation as in Fig. 3.

these differences were greatest at lower total PFD levels (Fig. 5c). The proportion of seedlings' total leaf area displayed directly above was also influenced by total PFD and diurnal regime (Fig. 5d). Proportional display decreased significantly in response to increases in total PFD for the gray birch shadehouse plants ($P < .001$), but showed little response to changes in total PFD under other treatments. Across all light levels, gray birch gap seedlings displayed a significantly greater proportion of their leaf area than did shadehouse seedlings (Table 2).

At final harvest, both species' total standing leaf number increased in response to higher total PFD under both light regime treatments, significantly so for gray birch ($P < .008$); differences in slopes between treatments within species were not significant (Table 3). Across all light levels, total leaf number was higher for both species in shadehouse than in gap seedlings, again significantly so for gray birch (Table 2). Patterns of final harvest branch numbers showed qualitatively similar patterns (Table 2). Slopes relating shoot height to increasing total PFD in both treatments and species did not significantly differ from zero, or from one another (Table 3). Mean shoot heights at final harvest in both species were significantly greater for shadehouse than for gap seedlings (Table 2). However, the ratio of seedling height to total biomass at final harvest showed a different pattern. Height growth per unit biomass was smaller on average for shadehouse than gap seedlings (Table 2). The response of shoot height-to-biomass ratios to increasing total PFD was significantly negative for both treatments and species ($P < .0001$). For gray birch, this slope was significantly steeper in gap than in shadehouse treatments (Table 3). For all treatments and species, slopes relating shoot internode length to total PFD did not differ significantly from zero, or from one another (Table 3). However, across all light levels, average internode lengths were larger in shadehouse seedlings than in gap seedlings, significantly so for gray birch (Table 2).

TABLE 3. Upper and lower confidence limits (CL) of slopes of regressions relating all growth, development, and physiological characters to increasing total season PFD for both gray and yellow birch. Significantly different slopes ($P < .025$) between shadehouse and gap treatments, within a particular species, are indicated with different lowercase letters.

	Gray birch					
	Shadehouses			Gaps		
Character	Upper CL	Lower CL		Upper CL	Lower CL	
Total biomass (g)	-1.19×10^{-4}	0.008	a	0.005	0.011	a
Leaf mass ratio	-2.16×10^{-4}	7.83×10^{-5}	a	−0.01	-3.25×10^{-5}	a
Stem mass ratio	-3.13×10^{-4}	-1.18×10^{-4}	a	-3.65×10^{-4}	-1.32×10^{-4}	a
Root mass ratio	1.37×10^{-4}	4.28×10^{-4}	a	0.001	0.001	b
Total leaf area (cm^2)	−0.776	−0.044	a	−0.652	0.007	a
Leaf area ratio (g/cm^2)	−0.318	−0.191	a	−0.667	−0.531	b
Specific leaf mass (mg/cm^2)	5.19×10^{-6}	7.97×10^{-6}	a	8.72×10^{-6}	1.13×10^{-5}	b
Log total leaf number	4.26×10^{-4}	0.003	a	4.09×10^{-5}	0.001	a
Height (cm)	−0.045	0.004	a	−0.021	0.021	a
Height/total biomass (cm/g)	−0.022	−0.008	a	−0.048	−0.028	b
Canopy display (%)	-1.3×10^{-4}	-6.0×10^{-4}	a	-9.0×10^{-4}	6.0×10^{-4}	a
Average internode length (cm)	−0.003	0.002	a	−0.001	0.001	a
Maximum net photosynthesis ($\mu mol \cdot m^2 \cdot s^{-1}$)	0.003	0.023	a	−0.002	0.02	a
Leaf nitrogen (%)	−0.002	−0.001	a	−0.004	−0.002	b
Chlorophyll content (mg/g)	−0.014	−0.007	a	−0.021	−0.014	b
Chlorophyll *a*/*b* ratio	-2.39×10^{-4}	3.20×10^{-4}	a	1.62×10^{-4}	0.001	a

Physiological responses.—Light-saturated net photosynthesis (P_{max}) showed a significant positive relationship to increasing total PFD for all treatments and species ($P < .03$), but slopes did not differ significantly from one another (Fig. 6a, Table 3). For gray birch, P_{max} was significantly greater for gap than for shadehouse seedlings (Table 2).

Leaf nitrogen and chlorophyll concentrations decreased significantly with increasing total PFD in both species and treatments ($P < .002$). For both characters, gray birch slopes from gap regimes in response to the gradient of total PFD were significantly more negative than slopes from shadehouse plants (Table 2). Leaf nitrogen (percent) and chlorophyll (in milligrams per gram) concentrations in both species were significantly higher in gap than in shadehouse plants (Fig. 6b, c; Table 2). These differences were greatest at lower total PFD levels.

Chlorophyll *a*/*b* ratios showed complex responses within and between species (Fig. 6d). Only gray birch gap seedlings showed a significant positive relationship between chlorophyll *a*/*b* ratio and total PFD ($P < .0001$); all other slopes did not differ significantly from zero or from one another (Table 3). For gray birch, shadehouse seedlings' chlorophyll *a*/*b* ratios were significantly higher than gap seedlings' *a*/*b* ratios (Table 2), with differences being greatest at lower total PFDs. Yellow birch, however, showed the opposite trend, with gap regime seedlings having significantly higher *a*/*b* ratios than shadehouse seedlings (Table 2), and differences being greatest at higher total PFDs. For both species, patterns of in situ diurnal leaf level gas exchange were quite different in the shadehouse than in gap light regimes, particularly at lower total PFDs (Fig. 7a–h). For example, net photosynthesis of leaves from the L1 (8%) gap regime closely tracked PFD availability. Both species maintained low levels of photosynthesis until midday PFD peaks, at which time net photosynthesis increased to rates near the P_{max} measured under saturating glasshouse conditions. Shadehouse plants, in comparison, maintained slightly higher net assimilation rates than gap plants during nonpeak times, mirroring the slightly higher PFDs. Stomatal conductance followed a similar pattern. At the highest integrated light level (L4, 70%), differences between diurnal regimes were dampened for both species. For gray birch leaves in L4 gaps, photosynthesis was slightly higher across the day than the L4 shadehouse plants. In contrast, yellow birch leaves in L4 shadehouse regimes maintained slightly higher net photosynthetic rates than L4 gap plants across most of the day. For both species and in both L4 diurnal regimes, photosynthetic rates peaked earlier in the day, decreased before the peak in PFD, and did not reach rates as high as P_{max} measured in the glasshouse. Stomatal conductance in L4 showed similar patterns of mid- and late-day depression, despite high light availability. Gas exchange patterns in the L2 and L3 diurnal regimes were intermediate to the extremes presented above.

Integrating the area beneath diurnal assimilation curves for individual seedlings reveals that integrated daily carbon gain (IDCG) per unit leaf area differed between light regimes and total PFD levels. For both treatments and species, IDCG showed a significant positive response to increasing total PFD ($P < .05$). At the lowest light levels (L1), IDCG for both species was greater in shadehouses than in gaps; 10% higher for gray birch and 39% higher for yellow birch. At the

TABLE 3. Continued.

Yellow birch					
Shadehouses			Gaps		
Upper CL	Lower CL		Upper CL	Lower CL	
-3.234×10^{-5}	0.006	a	2.00×10^{-4}	0.004	a
-1.09×10^{-1}	1.93×10^{-4}	a	-4.59×10^{-4}	-1.42×10^{-4}	b
-2.03×10^{-4}	6.70×10^{-6}	a	-2.60×10^{-4}	-4.28×10^{-5}	a
9.10×10^{-5}	2.01×10^{-4}	a	2.88×10^{-4}	0.001	b
−0.361	0.14	a	−0.481	0.002	a
−0.267	−0.173	a	−0.464	−0.354	b
5.60×10^{-6}	8.82×10^{-6}	a	6.92×10^{-6}	1.03×10^{-5}	a
−0.001	0.002	a	−0.001	0.001	a
−0.025	0.016	a	−0.024	0.018	a
−0.036	−0.012	a	−0.046	−0.012	a
-8.0×10^{-4}	5.0×10^{-4}	a	-1.3×10^{-4}	2.0×10^{-4}	a
−0.002	0.002	a	−0.002	0.002	a
1.26×10^{-4}	0.018	a	0.007	0.019	a
−0.002	-2.44×10^{-4}	a	−0.003	−0.001	a
−0.014	−0.006	a	−0.021	−0.011	a
−0.001	2.58×10^{-4}	a	-1.41×10^{-4}	0.001	a

highest level (L4), yellow birch showed a similar pattern with shadehouse leaves gaining 14% more carbon per day than gap leaves; however, gray birch showed the opposite trend, with gap leaves exhibiting a 41% higher IDCG than shadehouse leaves. Combining data across all light levels, gray birch gap IDCG was slightly, but not significantly higher than shadehouse (IDCG (Table 2). Yellow birch had significantly higher IDCG in the shadehouse than in gap regimes.

DISCUSSION

Daily timecourses of light availability, independent of total PFD, significantly affected seedling growth, biomass allocation, shoot architecture, and leaf-level physiology. However, the magnitude and pattern of these effects depend on the level of total integrated PFD, the particular plant trait observed, and the species considered.

Seedling growth

Using total biomass as a measure of 1st-yr performance, shadehouse seedlings outperformed gap seedlings at almost all integrated light levels. For gray birch, but not yellow birch, the magnitude of this difference was dependent on total PFD, with the largest differences at lower total PFDs. A number of alternative, but not mutually exclusive interpretations may explain these observed growth differences.

The saturation hypothesis.—The greater growth of shadehouse vs. gap seedlings may result from their responses to the differing magnitudes and durations of peak PFDs. In gaps, a large proportion of total PFD on sunny days came in quantities well above saturating light levels for leaf photosynthesis. Conceivably, shadehouse seedlings of both species were larger than gap seedlings because they received more utilizable light. Photosynthetic saturation of gray birch leaves grown in the same gaps ranged between 500 and 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$; for yellow birch saturation occurred at lower values, between 350 and 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Wayne 1992). On sunny days, peak PFDs in L1 gaps were near 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$, whereas peaks in L1 shadehouses rarely exceeded 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 2). If all light above saturation (800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as a conservative estimate) is subtracted from daily totals, it becomes clear that plants in shadehouses received much more usable light than plants from gaps (Fig. 2). In the L1 gap regime, 41% of daily total PFD was not utilizable; in the L1 shadehouse regimes, however, no light was supersaturating and the full total was potentially usable. At the other end of the total PFD gradient (L4), gap and shadehouse regimes became more similar with respect to the proportion of supersaturating light, but gap regimes still received a higher proportion of nonusable light (44 vs. 20%). Regression analysis indicated that daily PFD only accounted for 34% of variance in biomass, whereas total daily utilizable light explains near twice as much variance (62%).

Integrated diurnal carbon gain (IDCG) per unit leaf area also supported the "saturation hypothesis." At the lowest light level (L1), IDCG of both species' shadehouse seedlings were greater than IDCG of gap seedlings, 9.5% greater in gray birch and 39.3% greater in yellow birch (Fig. 7). At higher total PFD levels (L4), however, only yellow birch exhibited higher IDCG in shadehouses; for gray birch, IDCG was larger for gap vs. shadehouse seedlings.

Photosynthetic trade-off hypothesis.—Differences in

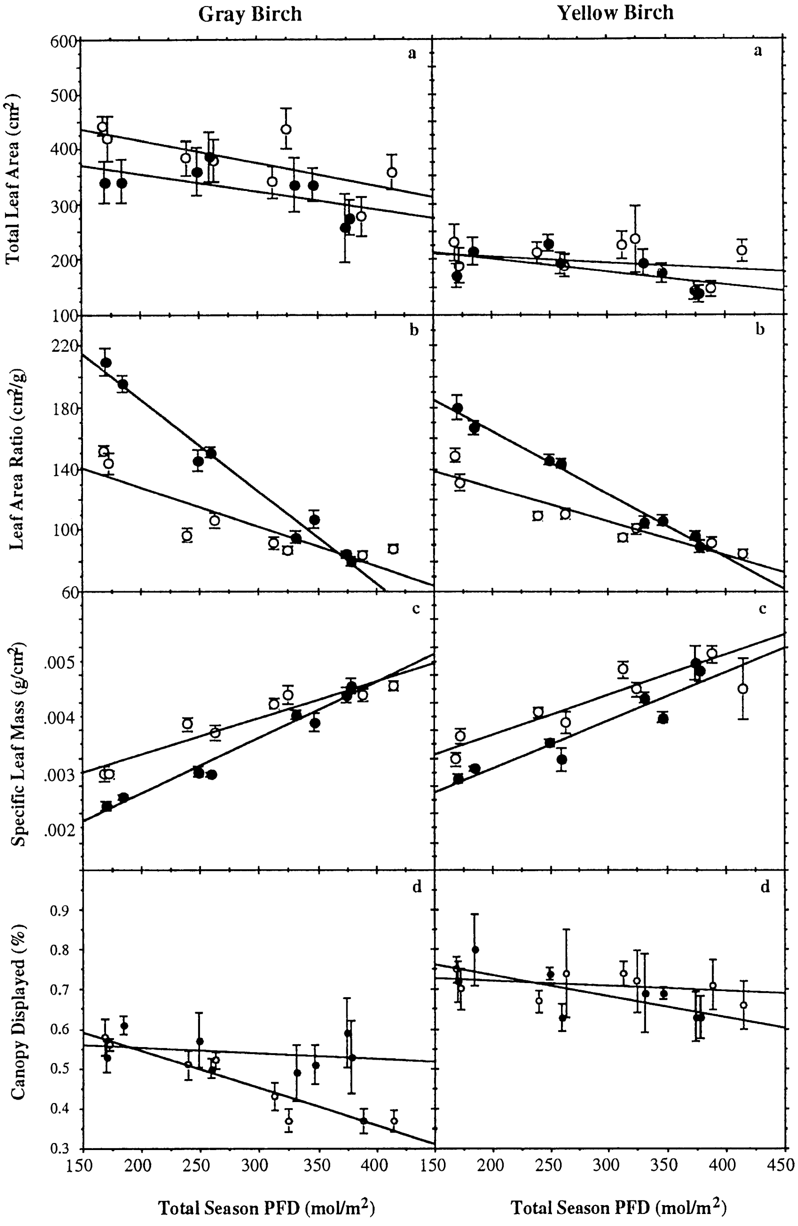


FIG. 5. Architectural and morphological responses of experimental gap and shadehouse seedlings to total PFD for gray and yellow birch. Data presentation as in Fig. 3.

shadehouse and gap seedling growth may also have been caused by differences in seedling photosynthetic acclimation to the contrasting diurnal light regimes. Maximum net photosynthesis ($P_{\max}$) of both species was higher in gap environments across most light levels, suggesting seedlings' photosystems acclimated to the higher midday peaks in gap regimes. Assuming that a trade-off exists between photosynthetic performance at higher vs. low light (e.g., Bjorkman 1981, Pearcy et al. 1987), we would expect gap seedlings to be less efficient at carbon gain during most periods of nonpeak PFD. This "trade-off hypothesis" predicts higher integrated diurnal carbon gain in shadehouse as opposed to gap plants because shadehouse seedlings should have photosystems better adapted to the lower PFD values that they experience during most of the day. The data from diurnal tracks of carbon gain already discussed above partially support this model.

Yellow birch shadehouse seedlings were significantly larger than gap seedlings at all light levels; however, unlike gray birch, differences between diurnal regimes did not decrease with increasing light levels. As a relatively more shade-tolerant species, yellow birch may not be as able as gray birch to acclimate its photosys-

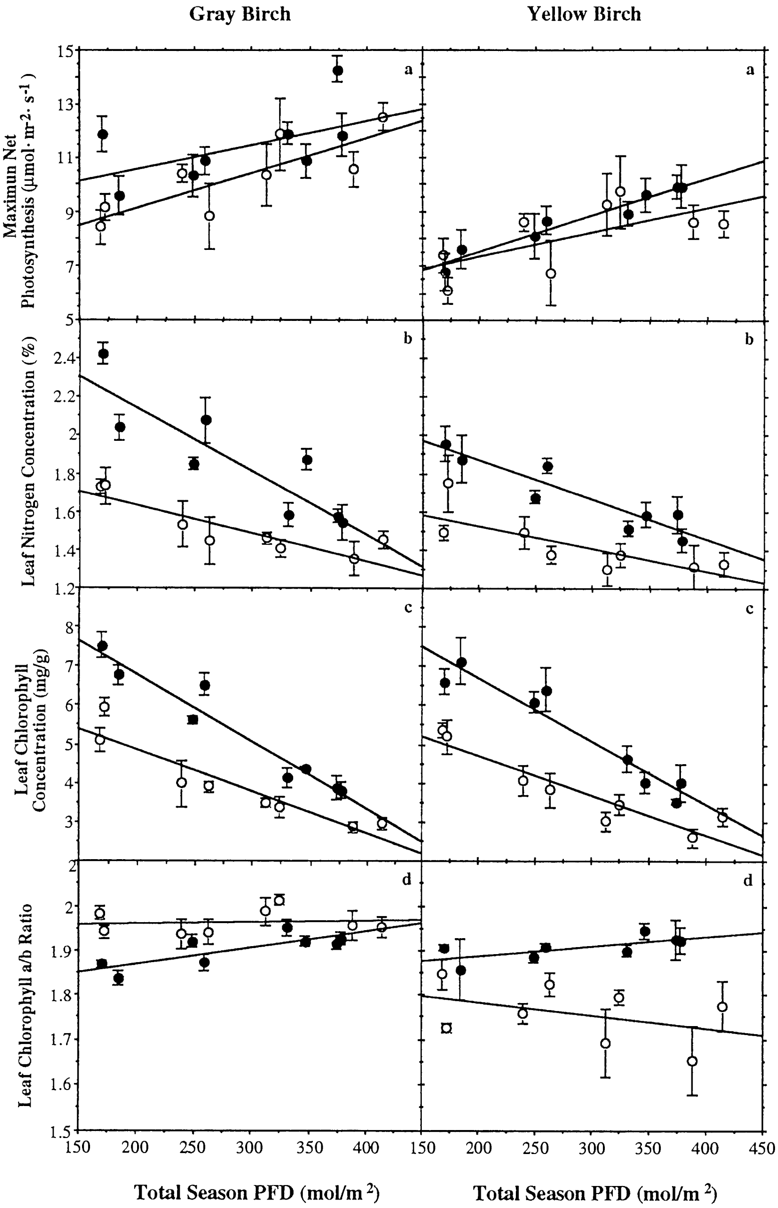


FIG. 6. Leaf physiological and biochemical responses to total PFD in shadehouse and gap light regimes for gray and yellow birch. Data presentation as in Fig. 3.

tems to increased irradiance (Bazzaz and Carlson 1982, Koike 1986, Sims and Pearcy 1989, Strauss-Debenedetti and Bazzaz 1991). Compared to gray birch, P_{max} for yellow birch was on average lower, and did not differ between diurnal treatments as much, especially at lower integrated PFDs (Table 2, Fig. 7b).

Resource congruency hypothesis.—A third potential cause of the differential performance of shadehouse and gap seedlings may be the timing of PFD availability relative to that of other critical resources. In gaps, during midday when seedlings received the majority of their daily light, other resources and environmental conditions were generally least favorable for carbon gain, i.e., the daily patterns of resource availability were "temporally incongruent." Much as they are in natural clearings, middays were generally periods of highest air and leaf temperature, lowest relative humidity, and the least favorable leaf water status for leaf gas exchange (Young and Smith 1980, Kauhanen 1986, Tenhunen et al. 1987, Abrams 1988). In parallel studies with birch seedlings growing in the same experimental gaps, midday leaf water potentials dropped as low as −1.5 and −0.9 MPa (Wayne 1992). In contrast to gap light regimes, shadehouses received PFD more evenly distributed across the day and may not have been as constrained in gaining carbon during midday's less

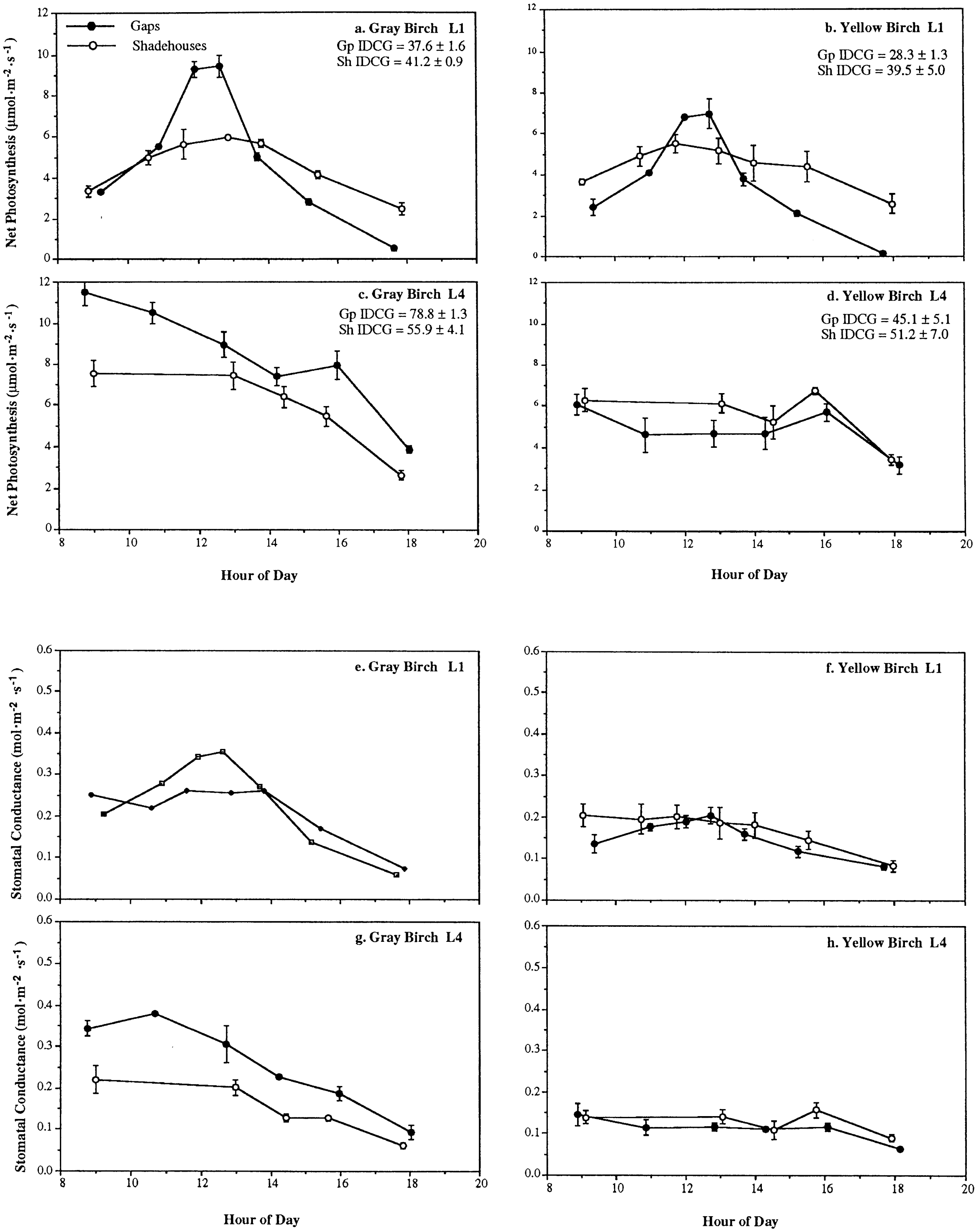


FIG. 7. Diurnal patterns of in situ gas exchange for gray and yellow birch gap and shadehouse seedlings. Net photosynthesis and stomatal conductance area shown for one L1 (12%) and one L4 (70%) light regime for each species. Each point represents means of 3–4 plants; vertical bars show ± 1 SE. L1 measurements were made on 19 July; L4 measurements were made on 20 July, both representative sunny days. Integrated daily carbon gain (IDCG) values are shown in upper right corner of net photosynthesis figures.

favorable conditions. Additionally, shadehouse seedlings received lower peak PFDs than those in gaps, potentially easing leaf energy budget constraints. Thus, this hypothesis would predict greater midday depressions of stomatal conductance and net photosynthesis of seedlings found in gaps compared to shadehouses, especially at higher total light levels. However, there were few regular differences in the overall diurnal patterns of leaf gas exchange between gap and shadehouse seedlings, even at higher total PFDs. Thus, for gap seedlings, temporal resource incongruencies may have resulted in mid- and late-day gas exchange depressions, but no clear gas exchange or growth differences between shadehouse and gap seedlings were directly attributable to these.

In addition to leaf-level gas exchange, other seedling characteristics may also have influenced final biomass differences between plants from the different diurnal light treatments. For both species, but especially for gray birch, shadehouse seedlings had greater total leaf area than did gap seedlings (Fig. 5a, Table 2). However, how seedlings generated these larger leaf areas in shadehouses is not clear. Seedlings allocated relatively more biomass to leaf tissue in gaps than in shadehouses (LMR; Fig. 4a), particularly at lower light levels, the opposite of what would be expected given the biomass results. Similarly, specific leaf mass (Fig. 5c) and leaf area ratio (Fig. 5b) also show that seedlings in gaps were producing more leaf area, both per unit leaf biomass and per unit seedling biomass, the opposite of what would be expected given the greater leaf area in shadehouses. The way leaf area was displayed within canopies in the two diurnal treatments may also have influenced whole seedling growth. Because seedlings in shadehouses were exposed to less intense radiation loads across the whole day, their canopy energy and water balances may have been less constrained. Therefore, they could expose a greater proportion of their canopy surface area to incoming radiation, i.e., less canopy overlap or lower leaf area indices. Canopy projection data does reveal that the proportion of seedlings' leaf area displayed directly above did increase with decreasing total PFD in some treatments (Fig. 5d), however, particularly for gray birch, seedlings in gaps, and not shadehouses, displayed a greater proportion of their leaf area (54 vs. 46%). However, this projection was only recorded from one angle (from directly above), and seedlings, especially in shadehouses, received a great deal of lateral light. Other architectural data suggest that canopies in shadehouses were more open to lateral light. Across all light levels, shoot heights and internode lengths were significantly greater in shadehouse than in gap seedlings. Models have demonstrated that for most phyllotactic arrangements of leaves, increasing internode lengths results in greater light interception for any given leaf area (Niklas 1988).

In summary, while seedling total leaf area and final biomass were highly correlated, shadehouse seedlings' greater leaf area did not apparently result from allocational and morphological adjustments to leaves. Rather, it appears that shadehouse seedlings had greater leaf area simply because they were larger. This suggests that measures of daily carbon gain based on single leaves may have underestimated whole seedling daily carbon gain, either because architectural characteristics increased light interception in the lower parts of shadehouse seedlings' canopies, for which we did not measure gas exchange, and/or because the leaf level differences we did measure were too small a sample size, and did not reflect the real differences in leaf level performances between diurnal treatments.

Plastic responses of sun–shade traits

An important component of plant responses to light environments is morphological and physiological plasticity. Tree seedlings grown under ranges of both natural and experimental light conditions have demonstrated the ability to adjust many traits relevant to effective light utilization, including patterns of biomass allocation, architectural arrangements of canopies, leaf morphology, physiology, and biochemistry (Loach 1967, 1970, Logan 1970, Bjorkman 1981, Bongers and Popma 1988, Strauss-Debenedetti and Bazzaz 1991). For both species, the general responses to total PFD of most light-related traits were similar to those reported in the literature for birch and other tree species. RMR, SLM,and $P_{\max}$ showed positive responses to increasing light, whereas LMR, SMR, LAR, Shoot Height : Biomass ratio, canopy display and leaf nitrogen and chlorophyll concentrations all exhibited negative responses (Table 3). However, chlorophyll *a*/*b* ratios showed a somewhat unusual pattern, with little response to increasing total PFD in gray birch, and a slightly negative response in yellow birch. Lack of changes in chlorophyll *a*/*b* ratios with increasing light have been reported for other species (Chow et al. 1991).

The responses (slopes) of most characters to total PFD were greater for gap than for shadehouse seedlings for nearly all investigated traits. This suggests that seedlings developing in gaps "perceived" a broader gradient of light conditions than did seedlings in the shadehouse diurnal regimes. Both the total amount of utilizable light and the degree of overall variability (percent CV) of light increased more steeply along the gap light gradient than along the shadehouse light gradient.

For nearly all traits, shadehouse seedlings responded with characteristics of plants grown in relatively higher light environments, i.e., seedlings possessed relatively more sun-type traits. For example, specific leaf mass (SLM) of both shadehouse and gap seedlings increased with increases in total PFD (Fig. 5c), thus a higher SLW represents a sun-like response. Continuing with this line of reasoning, since shadehouse plants had higher SLMs at most total PFD levels, shadehouse seedlings responded with more of a sun-type response for this particular trait. A relatively more sun-type response in shadehouse seedlings was also found for most other light-related traits with two important exceptions: P_{max} of both species and chlorophyll *a*/*b* ratio for gray birch.

Conclusions

The study of disturbance-generated microenvironmental heterogeneity has mainly focused on the description of static, spatial variation (Bazzaz and Sipe 1987). Much less is known about the extent and/or significance of changes in temporal light heterogeneity caused by treefall gaps, such as how adjacent microsites in space vary relative to each other through time (Grace 1991). Our results have demonstrated that differing temporal patterns of light availability significantly influence all aspects of seedling performance. First-year seedlings in gaps grew only half as much as those in shadehouses with similar daily totals, and were physiologically and architecturally distinct. Studies in natural forest gaps with three species of maples (*Acer*) also suggest that seedlings receiving similar daily total PFD, but with differing daily time courses of availability, also exhibit different patterns of growth and survivorship (Sipe 1990). Thus, adjacent microsites within forests, which might be considered equivalent when compared with respect to total or average PFD, may still provide different regeneration niches if they differ in certain temporal characteristics. The number and breadth of novel microsites generated by treefall disturbances may be underestimated when characteristics of temporal heterogeneity are not considered.

A significant proportion of our current understanding of tree seedling growth and sun–shade responses has been derived from studies conducted in growth chambers or shadehouses which typically impose constant reduced irradiances ranging from 5 to 90% full sun, eliminating much of the temporal heterogeneity caused by higher intensity sunflecks and sun patches. Our results with experimental gaps suggest that studies that have employed these relatively homogeneous light regimes may have imposed more favorable growth conditions than might be expected in many natural gap light regimes, especially treatments simulating lower total light levels. The greater variation in classical sun–shade traits exhibited by gap (i.e., steeper slopes) as opposed to shadehouse seedlings also suggests that studies using shadehouse or growth chamber light regimes may underestimate the plasticity within species. And finally, growth differences between the pioneer gray birch and the midsuccessional yellow birch were greater when compared along the gap total PFD gradient than when compared along the shadehouse total PFD gradient (Fig. 3); not considering temporal components of light regimes in gaps would have underestimated the potential for these two species to partition light environments in forests, and thus, perhaps, to coexist as seedlings in regenerating forest communities.

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