



Physiological and morphological acclimation of shade-grown tree seedlings to late-season canopy gap formation

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Abstract

Because acclimation to canopy gaps may involve coordination of new leaf production with morphological or physiological changes in existing, shade-developed leaves, we examined both new leaf production and photosynthesis of existing leaves on shade-grown seedlings after exposure to a late-season canopy gap. Midway through the summer, we transferred potted, shade-grown seedlings of four co-occurring temperate deciduous tree species representing a range of shade-tolerance categories and leaf production strategies to gaps. Shade-tolerant *Acer saccharum* was the least responsive to gap conditions. It produced few new, high-light acclimated leaves and increases in photosynthetic rates of shade-developed leaves appeared stomataly limited. Intermediately shade-tolerant *Fraxinus americana* and *Quercus rubra* responded most, by producing new leaves and increasing photosynthetic rates of existing shade-developed leaves to levels not significantly different from gap-grown controls within four weeks of gap exposure. Shade-intolerant *Liriodendron tulipifera* was intermediate in response. In these species, the degree of shoot-level morphological acclimation (new leaf production) and leaf-level physiological acclimation (photosynthetic increases in existing leaves) appear coupled. Mechanisms of acclimation also appear related to intrinsic patterns of nitrogen use and mobilization, the ability to adjust stomatal conductance, and shade tolerance.

Introduction

Canopy gap formation via treefall or branchfall results in sudden increases in light penetration to the forest floor. Light levels in temperate deciduous forest understories are typically less than 2% of incident irradiation; and even in relatively small gaps (e.g., 78 m²), total seasonal light levels can more than double (Canham et al. 1990). In a mixed mesophytic temperate forest, gaps form throughout the year but are most abundant in June, July, and August (Romme & Martin 1982). Such late-season canopy gaps form after leaves have developed under shade conditions and, as such, may be highly stressful for understory seedlings. Furthermore, shade-grown seedlings which survive late-season canopy gap formation may be more important for colonization and closure of canopy gaps than newly-recruited seedlings (Connell 1989, Ehren-

feld 1980, Uhl et al. 1988). Therefore, we assume that the ability of seedlings to acclimate quickly and completely to this abrupt environmental change is advantageous.

Acclimation is the process by which physiological and morphological changes increase carbon gain within the new environment. The ability of plants to acclimate to increasing light may be a function of both the timing (relative to leaf development) and the magnitude of the change (its rate and intensity). Leaves adjust (anatomically, morphologically, and physiologically) to the light environment under which they expand and develop (Abrams & Kubiske 1990; Anderson & Osmond 1987; Björkman 1981; Boardman 1977, Givnish 1988). This allows plants to respond to both slow (e.g., canopy shading) and fast (e.g., gap formation) changes in light environment by generating new leaves within the new environment. Less is

known, however, about the ability of existing leaves to change physiologically or morphologically in response to increased light after leaf development is complete.

The objective of this study was to examine the degree to which understory seedlings can acclimate to late-season canopy gap formation. We focused on the acclimation potential of leaves fully developed in the shade. However, temperate deciduous trees vary in their intrinsic patterns of leaf production from indeterminate species (the number of leaves produced is not pre-determined in the bud) to determinate species (the number of leaves produced is pre-determined). The later vary from single-flushing (one terminal bud produces one set of leaves within a growing season) to multiple-flushing species (several occurrences of terminal bud break within a season). Such intrinsic patterns of leaf production may influence mechanisms of shoot acclimation; therefore, we examined acclimation in co-occurring species with a range of leaf production strategies.

To examine shoot-level acclimation to late-season canopy gap formation, we transferred potted shade-grown seedlings to higher light conditions within the forest after leaves were fully developed. Initially, we examined leaf-level anatomical and physiological responses to canopy gaps in shade-developed leaves of *Acer saccharum* Marsh. (sugar maple, very shade-tolerant) and *Quercus rubra* L. (northern red oak, intermediately tolerant) seedlings. This was extended in a second experiment in which we examined leaf demography in addition to leaf-level acclimation of *Acer*, *Quercus*, *Liriodendron tulipifera* L. (tulip poplar, shade-intolerant), and *Fraxinus americana* L. (white ash, intermediately tolerant; all tolerance rankings are according to Baker, 1949). *Liriodendron* is indeterminate and produces leaves throughout the growing season, whereas the remaining species are typically determinate. However, oaks and ashes are known to produce multiple flushes during a single season under favorable conditions (i.e., high light, well-watered, high nutrients, Zimmerman & Brown 1971).

Methods

Experiment one

The first experiment was designed to determine whether mature shade-developed leaves of *Acer* (shade-tolerant, determinate) and *Quercus* (intermediately tolerant, indeterminate) could acclimate to

canopy gaps via changes in photosynthesis, composition, or anatomy. *Quercus* and *Acer* are co-occurring temperate deciduous trees species that represent two levels of shade-tolerance and two strategies of leaf production. Two-year-old bare-root nursery seedlings (Cold Stream Farm, Free Soil, MI) of each species were obtained in April. Seedlings were approximately 15 to 30-cm tall and had been grown in the shade (light levels 20% of full sun) prior to lifting. Plants were potted in soil:peat:perlite (1:1:1 v/v) in 28×30 cm (18.7 L) pots and moved to Trelease Woods, a University of Illinois ecological research area 8 km northeast of Urbana, IL.

Prior to bud-burst, 65 potted plants of each species were placed in deep shade of the forest understory and under one layer of shade cloth (light levels 30% of full sun) to limit the influence of large sunflecks. Thirteen plants of each species were placed in full sun about 10 m from the south edge of the forest to represent the occurrence of an early-season (relative to leaf-development), large canopy gap. Plants were kept well-watered and fertilized once-per-month with a modified Hoagland's solution. Twice during the growing season, plants were sprayed with insecticide (Orthene, 327 ppm) to reduce insect herbivory.

For plants placed in the shade, leaf length of one arbitrarily-chosen leaf on each of 10 arbitrarily-chosen plants per species was measured periodically to determine the time of full leaf expansion (24 d, *Quercus*; 20 d, *Acer*). To ensure complete leaf development, plants were left in the shade for 35–40 days after complete leaf expansion. At this time (transfer), 30 *Acer* plants and 22 *Quercus* plants were moved from the shade to the full sun area described above; and 10 plants of each species were moved from the shade to a small naturally occurring canopy gap (ca. 35 m²). These moves simulated the occurrence of large and small, respectively, late-season (relative to leaf development) canopy gaps. All plants in full sun and the gap were mulched with peat moss to reduce evaporative losses from the soil, and surrounded by straw to reduce heat load on the sides of the pots. The experiment consisted of four treatments, fully shade-grown plants (Shade), fully sun-grown plants (Sun), shade-grown plants moved to full sun (Shade-Sun), and shade-grown plants moved to a gap (Shade-Gap).

Diurnal measurements of environmental conditions were made periodically during the summer in the shade, sun, and gap areas. Air, leaf, and pot soil temperatures were measured with copper-constantan thermocouples; and photosynthetically active radiation

(PAR, 400–700 nm) with a quantum sensor (Li190SA, Li-Cor Inc., Lincoln, NE). Voltage or current outputs were recorded with a Li1000 (Li-Cor) or Campbell 21X (Campbell Scientific, Logan, UT) data logger.

Five weeks after plants were moved from the shade to the sun or gap, the total number of leaves per plant was recorded. Survival of *Acer* seedlings in the Sun treatment was low (see Results); therefore, no data were collected for this treatment. *Quercus* seedlings in the Sun treatment shed their first flush of leaves, but rapidly produced additional leaf flushes. Most of the leaves on plants of both species in the Shade-Sun treatment died within a few days of being moved from the shade to the sun. Shade-Sun plants were still monitored for the production of new leaves, but no further data were collected on shade-developed leaves. In all other cases, data collection was restricted to healthy plants showing no sign of herbivory or fungal pathogens. Seedlings typically produced four (*Acer*) to six (*Quercus*) leaves per flush; therefore, destructive measurements were restricted to one arbitrarily-chosen leaf per plant. Only leaves from the first flush of foliage (except Sun *Quercus*, see above) were chosen, thus all measurements were made on leaves of similar age (within one to two weeks) that had fully developed prior to transfer.

Gas-exchange was measured on one leaf on each of five arbitrarily-chosen trees. CO₂-saturated (5% CO₂ in hydrated air) net photosynthesis and dark respiration were measured as oxygen evolution with a leaf-disc oxygen electrode (LD2, Hansatech Ltd., Norfolk, England) according to Delieu & Walker (1981). Measurements were made at various times of day (0800–1400 CST) over an eight-day period. Light-response curves were generated by measuring oxygen evolution at different irradiances provided by passing light from a fixed-output metal halogen lamp (LS2, Hansatech) through combinations of neutral-density filters (Melles-Griot, Irvine, CA). Irradiance was measured with a quantum sensor (Li185B, Li-Cor, Inc.). Chamber temperature was maintained at 25 °C by a circulating refrigerated water bath. Before entering the chamber, source light was passed through an infrared filter of 3% aqueous CuSO₄ (5-cm deep) to facilitate temperature control in the chamber. After an initial induction period of repeated dark/light cycles (ca. 750 μmol m⁻² s⁻¹, Sun and Shade-Gap plants; ca. 290, Shade plants), the photosynthetic light response of each leaf disc was measured from low to high irradiance. The light-response curves were fit using a power function as described in DeLucia et al.

(1995). Light- and CO₂-saturated net photosynthesis (A_{\max}) is reported as the treatment mean of the highest measured point on each light-response curve. Apparent quantum yield was calculated as the slope of the initial linear region of the curve (light levels below 100 μmol m⁻² s⁻¹). The same leaf discs ($n = 5$ per species and treatment) were oven-dried (70 °C) to a constant mass, weighed to determine specific leaf area (SLA), and analyzed for nitrogen content using an ammonium analyzer (model 360, Wescan Inst., Santa Clara, CA) following acid digestion (Lowther 1980).

Leaf discs from the same leaves used for photosynthetic and nitrogen determinations were used for chlorophyll analysis ($n = 5$ per species and treatment). Fresh leaf tissue (5.2 cm²) was chopped finely with a razor blade and pigments extracted in 10 ml N,N-dimethylformamide (DMF) as in Porra et al. (1989).

Tissue samples for anatomical measurements were taken from one arbitrarily-chosen leaf on each of five plants per treatment and species. Interveinal leaf tissue sections were cut in the field, fixed for 12 h in 2.5% aqueous glutaraldehyde, and post-fixed in 2% osmium tetroxide for three hours. Both solutions were buffered with 0.2 m Sorensen's phosphate (pH 7.0). After ethanol dehydration, samples were embedded in a 1:1 mixture of Spurr's and Epon 812 resin and sectioned (1–2 mm thick) with an ultramicrotome using glass knives. Four to six sections were placed on a slide and leaf and cell layer thicknesses were measured at five distinct locations on each slide, using a bright-field light microscope with a calibrated ocular micrometer providing a total magnification of 410×. The mean of these five measurements was taken as the value for a given individual seedling.

Experiment two

The second experiment was designed to examine in more detail the potential relationship between new leaf production and acclimation of existing leaves upon exposure of shade-grown plants to canopy gaps. Additional species were added to include a greater range of shade-tolerance and leaf-production strategies. One or two-year-old bare-root nursery seedlings (30 to 46 cm tall) of *Quercus*, *Acer*, *Liriodendron tulipifera* L., and *Fraxinus americana* L. were potted in soil:sand:calcined clay (1:1:1) in 23×38 cm pots (15.5 L), and top-dressed with 30 g slow-release fertilizer (Osmocote, Sierra Chemical Co., Milpi-

tas, CA). Plants were mulched and kept well-watered throughout the experiment.

Because of space limitations within individual gaps, the treatments were evenly divided among three naturally occurring gaps (51, 75, and 280 m²) and three paired understory areas located in deep shade, with some naturally-occurring sunflecks. Diffuse non-intercept radiation (% canopy openness) was recorded with an LAI-2000 plant canopy analyzer (Li-Cor, Inc.). At the beginning of the experiment, there were 60 potted seedlings of each species in the shade and 30 in the gaps. After leaf development was complete (58 days after planting), $\frac{1}{2}$ of the shade-grown plants were arbitrarily chosen and moved to the gap areas (transfer) for the Shade-Gap treatment. The experimental design thus consisted of three treatments: plants grown throughout the season in the forest understory (Shade) or a canopy gap (Gap), and plants grown in the forest understory and moved to a canopy gap (Shade-Gap). Data from each site were pooled within each environment for analysis because of mortality, mainly a result of leaf pathogens and local herbivory, which was similar in all areas. All final data collection was restricted to healthy plants showing no sign of herbivory or pathogens.

Leaf demography was monitored throughout the experiment (until leaf senescence) by marking the petioles of the most recent newly emergent leaf with colored wire once each week on 15 arbitrarily-chosen plants for each treatment and species. Nine times throughout the season, all of the leaves on the plant were counted and the total number of leaves within each cohort (defined as leaves which emerged within the same week) determined by the location of the colored wires. The total number of leaves produced over the entire growing season and the average number of days each leaf lived were calculated for each plant. The percent of plants in each treatment that produced new leaves after the date of transfer was also calculated. Plants that died from herbivore or pathogen damage during the summer (no more than four plants per treatment and species) were dropped from the final demography analysis.

Beginning 30 days after the transfer, light-saturated rates of CO₂ uptake (A_{\max}) and corresponding stomatal conductance (g_s) and internal CO₂ concentration (c_i) were measured in the field on one leaf on each of five to nine plants per treatment and species with a closed infrared gas-analysis system (Li-6200, Li-Cor Inc.). Plants for gas exchange were arbitrarily chosen from those not used for the leaf demogra-

phy measurements. For all measurements, leaves were chosen to be within two to four weeks of the same age, and all had emerged well before the transfer date. Measurements were made under supplemental irradiance (1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, provided with a 50 W projector lamp) in the understory. During the measurements, leaf temperature averaged $27.6 \pm 3.8^\circ\text{C}$ and relative humidity was maintained within 5% of ambient by passing a portion of the air entering the cuvette through a desiccant. Measurements were made between 0800–1500 (CST) over five days.

One week after photosynthetic data were collected, leaves were sampled for nitrogen and SLA as described above. Leaf discs (10 cm²) were collected from leaves of the same age and on the same plants as those used for the photosynthetic measurements.

Data were analyzed with Statistix computer software (version 3.0, Analytical Software, St. Paul, MN). Because of the small sample size, data were analyzed within species using a Kruskal-Wallis (rank sum) non-parametric one-way analysis of variance. If differences ($P < 0.05$) among treatments were found, then pairwise comparisons between treatments were made using a Mann-Whitney U (rank sum) test. Significant differences between treatment pairs are reported at the $P < 0.05$ level.

Results

Gap and understory environment

Integrated daily irradiance was typically 4%, 5%, and 39% of full sun in the understory, small gap (35 m², Experiment One), and medium gap (75 m², Experiment Two), respectively (Table 1). Percent canopy openness was $15.4 \pm 3.4\%$ ($n = 3$) in the gaps and $0.6 \pm 0.1\%$ ($n = 3$) in the understory plots used in Experiment Two. Although maximum air, leaf and soil temperatures in the Small Gap were similar to those in the Shade, temperatures in the Medium Gap were close to those of full sun. Thus, Shade and Gap Treatments differed in light quantity and temperature, and, although not measured in this study, vapor pressure deficit was likely higher in the gap. Although environmental conditions varied among the different-sized gaps used in the two experiments, we assume that the increase in light (total and peak irradiance) was the driving variable in both cases.

Table 1. Daily integrated photosynthetic photon flux density (PPFD), peak irradiance, and maximum and minimum air, leaf and pot soil temperatures in the understory (Shade), two naturally occurring canopy gaps (small gap, 35 m² and medium gap, 75 m²), and full sun (Sun) for a typical summer day. Data for the Small Gap were collected on a separate day from other locations.

	Shade	Small gap	Medium gap	Sun
Total Daily Integrated PPFD (mol m ⁻² d ⁻¹)	1.4	2.0	14.5	37.0
Peak Irradiance (μmol m ⁻² s ⁻¹)	450	900	1650	1900
Maximum/minimum air temperature (°C)	27/22	27/17	30/22	31/21
leaf	26/22	26/17	35/22	37/21
soil	24/23	24/18	28/23	29/23

Experiment one

Leaf production

Mortality, particularly of seedlings growing in the shade, was evident in both species throughout this study. By the end of the experiment, 44% of *Acer* seedlings and 48% of *Quercus* seedlings that stayed in the understory area throughout the experiment appeared dead. Mortality was also high in *Acer* seedlings originally placed in full sun and those moved from the shade to full sun (77% in both cases). *Quercus* seedlings fared better in full sun with 9% and 32% mortality respectively for those originally placed in full sun and those moved to full sun. Although use of previously shade-grown bare-root stock may have increased mortality, especially for plants placed in the full sun, visual evidence of herbivory (deer browse) and fungal pathogens on experimental and naturally occurring seedlings suggest that these were the source of much of the mortality in the understory (personal observation). High levels of mortality in understory seedlings of temperate deciduous forests are not uncommon (e.g., Boerner & Brinkman 1996, Hett & Loucks 1971).

In the Sun and Shade treatment, *Acer* seedlings produced only one flush of leaves (data not shown). In the Sun treatment, the leaves on all of the *Acer* seedlings died shortly after emergence; whereas all of the Shade seedlings still had leaves at the conclusion of the experiment (four weeks after shade plants were moved to the gap and sun). Shade-developed leaves on *Acer* seedlings moved to full sun (Shade-Sun) died shortly after the move, but 23% of the plants pro-

duced a new flush by the end of the experiment (data not shown). Shade-developed leaves on the seedlings moved to the small canopy gap (Shade-Gap) survived, but no new leaves were produced on these plants.

In the full sun treatment, all *Quercus* seedlings produced two flushes of leaves, the first of which died shortly after emergence; 91% of the seedlings produced a third flush; and 45% of the seedlings produced a fourth flush (data not shown). In the Shade treatment, *Quercus* seedlings produced only one flush of leaves during the growing season. Upon being moved to full sun, all the Shade-Sun seedlings lost their shade-developed leaves; 68% produced a new (second) flush of leaves, but the remaining 32% of plants died (data not shown). Upon being moved to a small canopy gap, one *Quercus* plant died and all shade-developed leaves on the remaining seedlings survived, but only one plant produced a second flush of leaves.

Leaf composition

Four weeks after transfer to the canopy gap, Shade-Gap leaves of *Acer* had greater total chlorophyll content per unit leaf area (Chl a+b) than Shade leaves, but not when calculated on a per mass basis (% Chl a+b; Table 2). The ratio of chlorophyll a to b (Chl a/b) was also greater in *Acer* Shade-Gap than Shade leaves. The increase in nitrogen per unit leaf area and the decrease in specific leaf area (SLA) were not significant; however, they combined to cause a significant decrease in nitrogen as a percent of leaf mass (%N) in the Shade-Gap leaves. Because of high mortality, the Sun treatment was omitted for *Acer*.

Sun leaves of *Quercus* had less Chl a+b (by area and by mass), greater Chl a/b, and greater nitrogen per unit area than Shade leaves (Table 2). Specific leaf area of *Quercus* was also greater resulting in lower %N in Sun than in Shade leaves. As in *Acer*, there were changes in leaf composition of mature shade-developed leaves moved to the canopy gap. Chlorophyll content did not differ between Shade and Shade-Gap leaves of *Quercus*, but Shade-Gap leaves had significantly more chlorophyll than Sun leaves. Moreover, Chl a/b of Shade-Gap leaves was significantly greater than Shade leaves but did not differ from Sun leaves. There was a significant increase in nitrogen per unit area and a significant decrease in SLA of Shade-Gap *Quercus* leaves, although changes did not reach levels of Sun leaves, and there was no change in %N in Shade-Gap leaves.

Quercus leaves grown in full sun were significantly thicker than leaves grown in the shade (Table 3).

Table 2. Chlorophyll content per unit leaf area (Chl a+b) and per gram leaf dry mass (% Chl), ratio of chlorophyll a to b (Chl a/b), nitrogen per unit leaf area and per gram leaf dry mass (% nitrogen), and specific leaf area (SLA) of leaves on *Acer saccharum* and *Quercus rubra* seedlings grown in the understory (Shade) or full sun (Sun), or grown in the understory and moved to the gap (Shade-Gap). Means (and SE) are of five plants (one leaf each). Significantly different ($P < 0.05$) treatment means in the same row are followed by different letters.

	Shade	Shade-Gap	Sun
<i>Acer saccharum</i>			
Chl a+b ($\mu\text{g cm}^{-2}$)	21.6 (1.54) ^A	27.0 (0.83) ^B	–
% Chl a+b	1.1 (0.08)	1.0 (0.04)	–
Chl a/b	2.4 (0.03) ^A	2.6 (0.05) ^B	–
Nitrogen ($\mu\text{g cm}^{-2}$)	80.0 (4.48)	87.1 (2.88)	–
% Nitrogen	3.9 (0.24) ^A	3.3 (0.12) ^B	–
SLA ($\text{cm}^2 \text{g}^{-1}$)	487 (6.5)	415 (38.2)	–
<i>Quercus rubra</i>			
Chl a+b ($\mu\text{g cm}^{-2}$)	28.3 (1.94) ^A	29.8 (1.61) ^A	19.4 (1.13) ^B
% Chl a+b	1.0 (0.07) ^A	0.9 (0.04) ^A	0.3 (0.02) ^B
Chl a/b	2.5 (0.06) ^A	2.6 (0.05) ^B	3.2 (0.25) ^B
Nitrogen ($\mu\text{g cm}^{-2}$)	81.4 (0.76) ^A	102.0 (3.64) ^B	169.8 (16.05) ^C
% Nitrogen	2.9 (0.07) ^A	3.0 (0.09) ^A	2.5 (0.09) ^B
SLA ($\text{cm}^2 \text{g}^{-1}$)	357 (7.6) ^A	290 (6.8) ^B	150 (12.6) ^C

Greater total leaf thickness in Sun than in Shade leaves was a result of thicker individual cell layers (upper epidermis, palisade mesophyll, spongy mesophyll), with the exception of the lower epidermis. The thickness of the individual cell layers and the whole leaf of Shade-Gap leaves was not different from Shade leaves in either species.

Photosynthesis

Dark respiration (R_D) and apparent quantum yield (ϕ_a) did not differ significantly among treatments for *Acer* (Table 4). Maximum photosynthetic rate (A_{max}), however, was greater in Shade-Gap leaves than in Shade leaves. The increase in photosynthetic rate was evident even at non-saturating light levels (Figure 1). In *Quercus*, R_D , ϕ_a and A_{max} were greater in Sun than in Shade leaves (Table 4). Dark respiration of Shade-Gap leaves was intermediate between the other two treatments, and ϕ_a and A_{max} of Shade-Gap leaves was greater than Shade leaves but not significantly different from Sun leaves. As in *Acer*, the increase in photosynthetic rate seen in Shade-Gap leaves was evident at non-saturating as well as saturating light levels (Figure 1).

Experiment two

Leaf demography

About one-third of the initial potted seedlings died, and this rate was similar across treatments and species. Mortality in this experiment appeared similar in cause to that of Experiment One. *Acer*, *Fraxinus*, *Liriodendron*, and *Quercus* seedlings all maintained greater numbers of leaves on Gap than on Shade plants throughout most of the growing season (data not shown); and the total number of leaves produced per plant was significantly greater for Gap than for Shade plants of all species except *Quercus* (Table 5). At least some plants of all species within each treatment produced new leaves after transfer of shade-grown plants to the canopy gaps (% Flushing, Table 5); but because this value is a percent of total plants, statistical differences could not be determined. At measurement dates after transfer, Shade-Gap seedlings of all species except *Liriodendron* had more leaves per plant than Shade seedlings (data not shown); however, there was no difference between the total number of leaves produced within the growing season by Shade-Gap versus Shade seedlings with the exception of *Quercus* (Table 5). The average lifespan of leaves differed significantly with treatment only for *Quercus*, where leaves

Table 3. Thickness (μm) of cross-sectional cell layers of leaves on *Acer saccharum* and *Quercus rubra* seedlings grown in the understory (Shade) or open (Sun), or grown in the understory and moved to the gap (Shade-Gap). Means (and SE) are of five plants (one leaf each). Significantly different ($P < 0.05$) treatment means in the same row are followed by different letters.

	Shade	Shade-Gap	Sun
<i>Acer saccharum</i>			
Upper epidermis	10.6 (0.67)	9.0 (0.70)	–
Palisade	19.0 (0.00)	18.6 (0.74)	–
Spongy mesophyll	26.1 (2.12)	22.8 (3.34)	–
Lower epidermis	6.9 (0.50)	7.1 (0.41)	–
Total	62.1 (2.89)	57.5 (3.63)	–
<i>Quercus rubra</i>			
Upper epidermis	15.6 (0.96) ^A	14.8 (0.58) ^A	22.3 (0.91) ^B
Palisade	20.9 (0.98) ^A	20.9 (1.03) ^A	53.5 (4.41) ^B
Spongy mesophyll	32.6 (3.26) ^A	32.6 (1.61) ^A	56.7 (4.07) ^B
Lower epidermis	9.0 (0.60)	8.0 (0.55)	9.0 (0.54)
Total	78.1 (4.05) ^A	76.3 (2.54) ^A	141.6 (7.28) ^B

on Gap plants lived longer than leaves on Shade-Gap plants (Table 5).

The species with indeterminate growth, *Liriodendron*, produced leaves continuously throughout the growing season in all treatments; although production in the Shade slowed in the later half of the season (after transfer) with 53% of the plants producing leaves compared to 100% in the Gap (% Flushing, Table 5). This explains the significantly lower total number of leaves produced within the growing season in the Shade than in the Gap. On average, *Liriodendron* produced fewer leaves than any other species in each treatment (Table 5); and although leaves produced in the gap were large, Shade leaves were small in comparison to other species. For Shade-Gap seedlings of *Liriodendron*, the pattern of leaf demography appears to be set within the early-season growth light environment: shade-grown seedlings did not significantly increase leaf production or leaf lifespan after exposure to higher light (Table 5).

For *Acer*, a second flush (after the moving date) was produced in 23% of shade-grown plants moved to a small canopy gap (Experiment 1, data not shown) and in 36% of shade-grown plants moved to larger canopy gaps (Experiment 2, Table 5). Some of the Shade (18%) and Gap (45%) seedlings also produced a second flush of leaves late in the season. The high degree of flushing observed in the second experiment may have been due partially to the extremely wet summer of that year. Although the increase in the percent

of plants producing leaves after transfer indicates that *Acer* may be capable of producing new leaves when exposed to a gap, there was no significant difference in total leaf production or leaf lifespan between Shade and Shade-Gap *Acer* seedlings (Table 5).

Both *Fraxinus* and *Quercus* produced multiple flushes of leaves under high light conditions (Table 5). For *Quercus*, the actual number of bud break events was highly dependent upon the light level, with from one to four flushes being produced, depending on the experiment and treatment (data not shown). Shade-grown seedlings of both *Fraxinus* and *Quercus* produced new leaves upon transfer to the gap (Table 5). *Quercus* was the only species in which leaf lifespan differed with treatment. The shorter lifespan of Shade-Gap leaves from that of Gap leaves may indicate that these leaves senesced sooner than normal, either because they were damaged by the move to higher light or to make way for new leaf production.

Leaf composition

There was no significant difference in nitrogen per unit leaf area between Shade and Gap leaves of *Fraxinus* and *Liriodendron*; however, both *Acer* and *Quercus* had more nitrogen per unit area in Gap than in Shade leaves (Figure 2). A significantly lower specific leaf area resulted in lower percent nitrogen in Gap than in Shade leaves for all species (Figure 2). Only *Quercus* leaves had significantly greater nitrogen per unit

Table 4. Dark respiration (R_D), apparent quantum yield (ϕ_a), and maximum photosynthetic rate (A_{max} , measured under saturating light and CO_2) of leaves on *Acer saccharum* and *Quercus rubra* seedlings grown in the understory (Shade) or full sun (Sun), or grown in the understory and moved to the gap (Shade-Gap). Means (and SE) are of five plants (one leaf each). Significantly different ($P < 0.05$) treatment means in the same row are followed by different letters. (* $P = 0.057$ for overall treatment effect.).

	Shade	Shade-Gap	Sun
<i>Acer saccharum</i>			
R_D ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	-1.6 (0.12)	-1.8 (0.12)	-
ϕ_a	0.012 (0.0030)	0.023 (0.0033)	-
A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	3.7 (0.24) ^A	8.9 (0.49) ^B	-
<i>Quercus rubra</i>			
* R_D ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	-1.4 (0.24) ^A	-2.0 (0.16) ^{AB}	-2.5 (0.28) ^B
ϕ_a	0.032 (0.0007) ^A	0.043 (0.0033) ^B	0.046 (0.0033) ^B
A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	7.0 (0.31) ^A	14.7 (1.62) ^B	19.4 (2.52) ^B

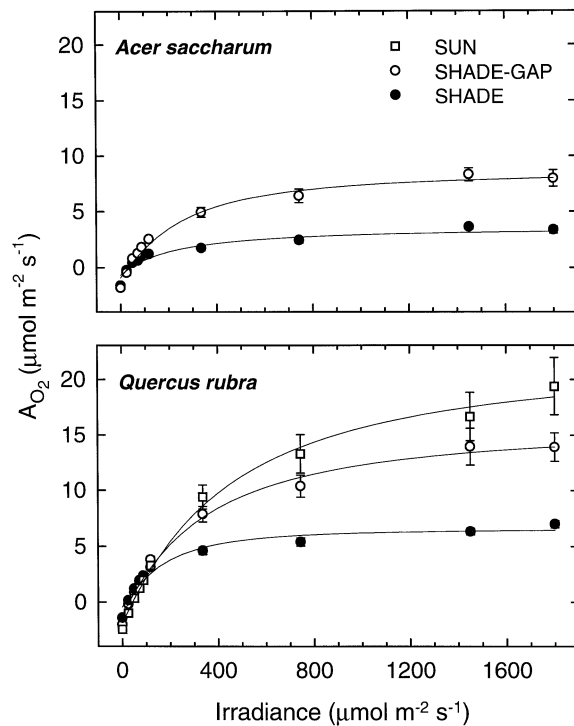


Figure 1. The response of photosynthesis as measured by oxygen evolution (A_{O_2} , measured under saturating light and CO_2), to incident irradiance of *Acer saccharum* and *Quercus rubra* leaves on seedlings grown in the understory (Shade) or full sun (Sun), or grown in the understory and moved to a small (35 m^2) canopy gap (Shade-Gap). Means are of one leaf on each of five plants and error bars of plus and minus one SE are shown except when smaller than the symbol.

area and greater %N in Shade-Gap leaves than in Shade leaves. Percent nitrogen was less in Shade-Gap leaves than in Shade leaves for *Acer* and *Fraxinus*, and was greater than that of Gap leaves in all species except *Acer*. Specific leaf area was significantly less in Shade-Gap than in Shade leaves for all species, and significantly greater than Gap leaves for all but *Liriodendron* (Figure 2)

Photosynthesis

Maximum photosynthetic rate of Gap leaves was significantly greater than that of Shade leaves in all species (Figure 3). Shade-Gap leaves had significantly greater photosynthetic rates than Shade leaves for all species except *Acer* and rates were the same as Gap leaves for *Acer*, *Fraxinus* and *Quercus*. Photosynthetic nitrogen use efficiency (PNUE) was calculated as the mean A_{max} divided by the mean total nitrogen per unit area for each species and treatment (Figure 3). It appears that PNUE was greater in Gap than in Shade leaves for each species, but was greater in Shade-Gap than in Shade leaves only for *Acer* and *Fraxinus*.

Stomatal conductance was significantly greater in Gap than in Shade plants for all species except *Acer*, in which there was no difference in g_s with treatment (Figure 4). Shade-developed leaves of *Fraxinus* and *Quercus* increased g_s after the move to the gap. Leaf internal CO_2 concentrations were lower in Gap than in Shade leaves for all species except *Liriodendron* (Figure 4); and *Acer* and *Quercus* had significantly lower c_i concentrations in Shade-Gap than in Shade leaves.

Table 5. Average total leaves produced per plant over the entire season (Leaves/Plant), percent of plants producing leaves after the transfer date (Flushing), and average lifespan of all leaves produced (Lifespan) on *Acer saccharum*, *Fraxinus americana*, *Liriodendron tulipifera*, and *Quercus rubra* seedlings grown in the understory (Shade) or gap (Gap) or grown in the understory and moved to the gap (Shade-Gap). Means (and SE) and percents are of 11–15 plants per treatment. Significantly different ($P < 0.05$) treatment means in the same row are followed by different letters.

	Shade	Shade-Gap	Gap
<i>Acer saccharum</i>			
Leaves/Plant	12 (2.0) ^{AB}	11 (0.4) ^A	18 (1.9) ^B
Flushing (%)	18%	36%	45%
Lifespan (d)	62 (6)	79 (11)	100 (13)
<i>Fraxinus americana</i>			
Leaves/plant	15 (1.8) ^A	20 (2.5) ^{AB}	28 (3.6) ^B
Flushing (%)	8%	77%	92%
Lifespan (d)	97 (12)	89 (8)	108 (3)
<i>Liriodendron tulipifera</i>			
Leaves/plant	8 (1.0) ^A	9 (1.1) ^A	13 (1.0) ^B
Flushing (%)	53%	61%	100%
Lifespan (d)	82 (12)	75 (8)	104 (5)
<i>Quercus rubra</i>			
Leaves/Plant	16 (1.6) ^A	26 (2.5) ^B	22 (2.9) ^{AB}
Flushing (%)	14%	64%	61%
Lifespan (d)	97 (10) ^{AB}	82 (7) ^A	117 (6) ^B

Discussion

Our results suggest that shade-developed foliage of some species of temperate deciduous hardwoods can acclimate physiologically to abrupt increases in light intensity. When measured under ambient CO₂ concentrations and saturating light, *Quercus*, *Fraxinus*, and *Liriodendron* had greater photosynthetic rates (A_{\max}) in shade-developed leaves moved to higher light than in shade-grown controls after four weeks of exposure to canopy gap conditions. This increase was dramatic for *Quercus* and *Fraxinus* in which photosynthetic rates of Shade-Gap leaves did not differ from those of gap-grown controls. This was true of *Acer* as well, however, A_{\max} of Shade-Gap leaves was also no different from rates of Shade leaves (Figure 3), suggesting that physiological acclimation in shade-grown *Acer* leaves was limited.

The relative magnitude of the increase in irradiance may also influence photosynthetic acclimation. Results for *Quercus* were similar between the two experiments, although the lack of high-light controls for *Acer* in the first experiment prevents complete as-

essment of *Acer* acclimation. Significant increases in A_{\max} of Shade-Gap *Acer* seedlings in Experiment One (Table 4) and not in Experiment Two (Figure 1) may indicate that the larger gap was a greater stress for *Acer*; however, A_{\max} was measured under non-stomatically limited conditions in Experiment One, suggesting that potential limitations may be attributed to stomatal influences.

Photosynthetic acclimation of shade-developed leaves to canopy gaps may be associated with the ability of these leaves to adjust stomatal conductance (g_s) within the higher light conditions. The lack of difference across treatments of g_s and the significant decrease in internal CO₂ concentration (c_i) for Shade-Gap leaves of *Acer* (Figure 4), indicate that photosynthesis of shade-developed leaves moved to the canopy gap was stomatically limited, which may have prevented maximum photosynthetic acclimation in this species (also observed by Ellsworth & Reich 1992a,b). For *Liriodendron* c_i did not differ with treatment, suggesting that A_{\max} is coupled to g_s and that potential stomatal limitations to photosynthesis were similar across treatments. Shade-developed leaves of

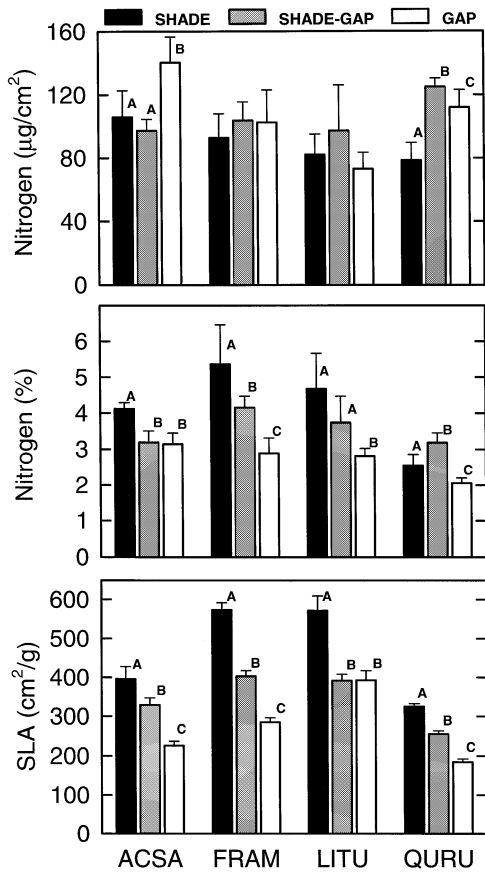


Figure 2. Nitrogen content per unit leaf area and per gram leaf dry mass (% Nitrogen) and specific leaf area (SLA) of *Acer saccharum* (ACSA), *Fraxinus americana* (FRAM), *Liriodendron tulipifera* (LITU), and *Quercus rubra* (QURU) leaves on seedlings grown in the understory (Shade) or canopy gap (Gap), or grown in the understory and moved to the gap (Shade-Gap). Means are of one leaf on each of five to nine plants and error bars indicate one SE above the mean. Significant differences ($P < 0.05$) among treatments within each species are indicated by different letters.

Quercus and *Fraxinus* increased g_s within the gap, which may partially explain their ability to greatly increase photosynthetic rates.

Acclimation of shade-developed leaves to increased light may also depend on their ability to minimize the magnitude or duration of photoinhibition while increasing photosynthetic capacity. In the present study, there was no evidence of photoinhibitory damage in *Quercus* or *Acer* when assessed four weeks after shade-grown plants were moved to a gap (no decrease in quantum yield). However, a separate investigation revealed a transient period of photoinhibition during this acclimation period (Naidu & DeLucia 1997a). In other studies, the magnitude

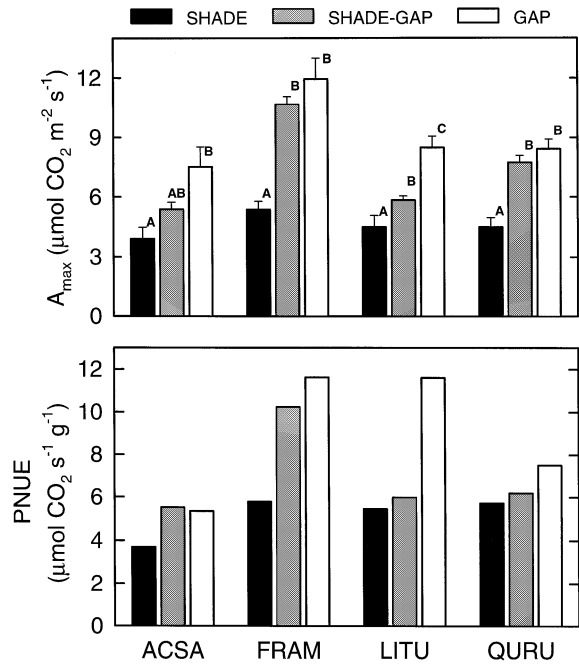


Figure 3. Maximum photosynthesis (A_{max}), as measured by CO_2 uptake on attached leaves, and photosynthetic nitrogen use efficiency (PNUe, photosynthesis per gram nitrogen), of *Acer saccharum* (ACSA), *Fraxinus americana* (FRAM), *Liriodendron tulipifera* (LITU), and *Quercus rubra* (QURU) leaves on seedlings grown in the understory (Shade) or canopy gap (Gap), or grown in the understory and moved to the gap (Shade-Gap). Means are of one leaf on each of five to nine plants and error bars indicate one SE above the mean. Significant differences ($P < 0.05$) among treatments within each species are indicated by different letters.

and duration of photoinhibition in shade-developed leaves abruptly exposed to higher light varied among species and with the conditions of the study (Bauer & Thöni 1988; Besford 1986; Bunce et al. 1977; Chow & Anderson 1987; Ferrar & Osmond 1986; Gauh 1976; Greer & Laing 1992; Kamaluddin & Grace 1992; Lovelock et al. 1994; Mulkey & Percy 1992; Nunes et al. 1993; Rosenqvist et al. 1991; Syvertsen 1984; Turnbull et al. 1993). Photoinhibition can limit increases in whole-plant carbon gain resulting from higher photosynthetic rates within the gap, as can increases in respiration. In Experiment One, there was no significant increase in dark respiration of *Acer* or *Quercus* associated with the move to higher light conditions, although there was a trend towards an increase (Table 4). Increased respiration has often been recorded under similar conditions (Bunce et al. 1977; Gauh 1976; Ruuska et al. 1994; Sims & Percy 1991; Turnbull et al. 1993).

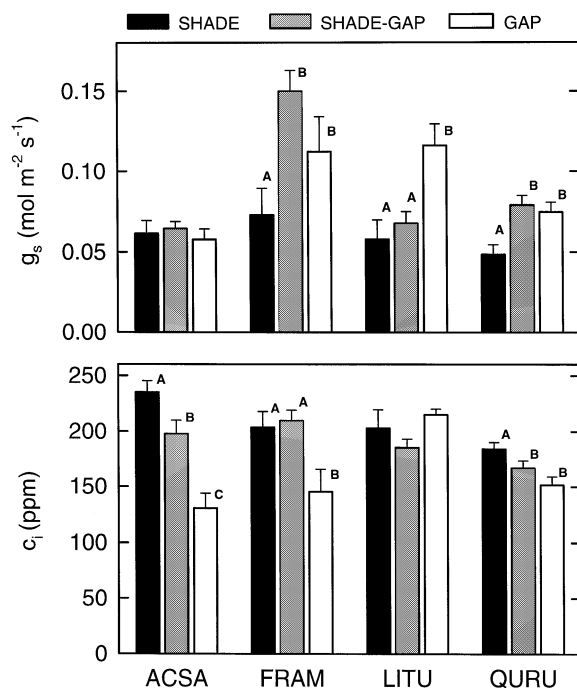


Figure 4. Stomatal conductance (g_s) and internal CO_2 concentration (c_i) of *Acer saccharum* (ACSA), *Fraxinus americana* (FRAM), *Liriodendron tulipifera* (LITU), and *Quercus rubra* (QURU) leaves functioning at maximum photosynthetic rate on seedlings grown in the understory (Shade) or canopy gap (Gap), or grown in the understory and moved to the gap (Shade-Gap). Means are of one leaf on each of five to nine plants and error bars indicate one SE above the mean. Significant differences ($P < 0.05$) among treatments within each species are indicated by different letters.

To begin assessing possible mechanisms of physiological acclimation to changing environments, we measured various aspects of leaf composition under the different light regimes for *Quercus* and *Acer*. Although the ratio of chlorophyll a to b increased for shade-developed leaves upon transfer to the canopy gap, consistent with a decrease in the proportion of light harvesting chl b molecules, chlorophyll content per unit leaf area was the same or greater (Table 2). This contrasts with other studies of tree species in which chlorophyll content of shade leaves decreased upon exposure to higher light (Kamaluddin & Grace 1992; Nunes et al. 1993; Ruuska et al. 1994; Syvertsen & Smith 1984). Perhaps the species in this study were less susceptible to chlorophyll bleaching.

Changes in leaf nitrogen upon transfer to the gap suggest that some species re-allocate this potentially limiting nutrient following an abrupt environmental change, indicating that acclimation of shade-grown seedlings to canopy gaps may be related to whole-

plant nitrogen budgets. Shade-developed leaves of *Acer* and *Fraxinus* had no change in nitrogen per unit area within the gap, but decreased %N because of a decrease in SLA. In contrast, *Quercus* significantly increased leaf nitrogen per unit area and percent nitrogen in Shade-Gap leaves (Table 2, Figure 2), suggesting an ability to either increase uptake of soil nitrogen or re-translocate nitrogen from other internal plant sources. Thus the dramatic increase in photosynthetic rate seen in Shade-Gap leaves of *Quercus* may be partially caused by increased g_s and partially by increased leaf nitrogen content, the latter resulting in little to no change in PNUE. The increased photosynthetic rate in *Fraxinus* was explained more completely by greater g_s as there appears to be an increase in PNUE rather than in leaf nitrogen content. Previous shorter term studies of other tree species saw either no change (Nunes et al. 1993) or a decrease (Syvertsen & Smith 1984) in leaf nitrogen. Potential changes in whole-plant allocation patterns of nitrogen in response to increasing irradiance may also influence future growth (via increased nitrogen storage) as well as photosynthetic acclimation of existing leaves (Naidu & DeLucia 1997b).

The decrease in SLA seen in all species (except for *Acer* in Experiment One) could be a consequence of increased leaf thickness, which has been documented in previous studies in which fully expanded shade leaves were exposed to higher light (Bauer & Thöni 1988; Bunce et al. 1977; Kamaluddin & Grace 1992; Syvertsen & Smith 1984). However, for *Acer* and *Quercus* at least, leaf thickness of Shade-Gap leaves did not increase. Therefore, any decreases in SLA were more likely a result of greater photosynthate or protein accumulation in leaves concomitant with their higher photosynthetic rates. Some of this additional carbon may have enabled the production of new leaves within the gap.

In addition to variation in physiological acclimation of existing shade-developed leaves, patterns of leaf production and leaf lifespan varied in the four species examined. All species except *Liriodendron* had more leaves on Shade-Gap than on Shade plants after the transfer date (data not shown). Previous studies have also reported increased growth (Fetcher et al. 1983; Osunkoya et al. 1991) and leaf production (Lovelock et al. 1994; Rice & Bazzaz 1989; Strauss-Debenedetti & Bazzaz 1991) of some species of shade-grown plants in response to increased light, but not in others (Lovelock et al. 1994; Nunes et al. 1993). A greater number of leaves at any given time

could be a result of increased production or greater longevity; however, there was little plasticity in leaf lifespan in these four species. Thus, any increase in seasonal carbon gain upon exposure of shade-grown seedlings to canopy gaps would be a function of the number of leaves produced and their photosynthetic capacity.

For both *Acer* and *Quercus* the more extreme conditions of the full sun treatment resulted in leaf mortality for shade-developed leaves moved to full sun and for the first set of leaves to emerge on plants initially placed in full sun. Mortality of leaves in full sun was likely a result of both high temperature and irradiance. This was a stress for shade-grown plants moved to full sun and for the initial group of plants placed in full sun, likely because all plants were shade-grown prior to lifting. Subsequent leaves were able to adjust more slowly to this environment as they emerged, with the exception that *Acer* saplings placed in full sun never produced any more leaves. This suggests that interspecific differences in acclimation potential are also determined by the magnitude of the gap event.

Our results indicate that physiological acclimation of existing shade-developed leaves to higher light conditions is coordinated with shoot-level morphological acclimation in *Quercus* and *Fraxinus*, both of which acclimated shade-developed leaves and made new leaves upon exposure to a late-season canopy gap. Presumably, these new leaves were physiologically similar to leaves on Gap plants (Goulet & Bellefleur 1986; Kamaluddin & Grace 1992; Langenheim et al. 1984; Mulkey & Pearcy 1992; Newell et al. 1993; Strauss-Debenedetti & Bazzaz 1991; Strauss-Debenedetti & Berlyn 1994; Turnbull et al. 1993). Shade-developed leaves of both species acclimated to canopy gaps by increasing photosynthetic rates, which was accompanied by an increase in leaf nitrogen per unit area (*Quercus* only) and stomatal conductance (*Quercus* and *Fraxinus*). This linkage between acclimation of existing leaves and rapid production of new leaves in the gap was also seen by Lovelock et al. (1994). These data support previous suggestions that adaptation to different light environments in various hardwood species involves an integration of physiological and morphological traits (Bazzaz & Wayne 1994; Lei & Lechowicz 1990; Walters et al. 1993).

Liriodendron also acclimated existing shade-developed leaves, although not as dramatically as *Quercus* and *Fraxinus*; and although Shade-Gap plants continued to produce leaves after exposure to the canopy gap, patterns of leaf production appeared sim-

ilar to Shade controls. In contrast, both new leaf production and acclimation of existing leaves were limited in *Acer*. This species is known to be highly shade-tolerant and to withstand repeated periods of suppression and release (Canham 1985). These traits may come at the cost of acclimating quickly to canopy gaps when they do occur. Although it is possible that the length of time necessary for physiological acclimation may differ among species and that complete acclimation may occur after four weeks (longer than the duration of this study), species which acclimate more quickly have a competitive advantage due to greater cumulative carbon gain.

In terms of maximizing plant carbon gain, producing new, high-light acclimated leaves may be more advantageous than acclimating existing leaves because total leaf area is maximized. In addition to increased plant carbon gain, an advantage of new leaf production through apical bud-break is that of increased plant height. This may confer a competitive advantage by shading neighbors or escaping herbivory (Küppers 1989). Although all four species produced new leaves upon exposure to the gap, *Fraxinus*, *Quercus* and *Liriodendron* did so to a much greater extent and with greater internode expansion than *Acer*. This suggests that under similar conditions and initial sizes, these species may quickly overtop *Acer*. Similarly, Smith (1983) reported *Liriodendron* > *Quercus* > *Acer* in height and stem diameter 12 years after release within a canopy gap. However, our results also indicate that leaf flushing patterns are highly variable both among and within species. Controls of leaf flushing are not well understood, but likely involve a combination of effects including light, nutrient, and moisture availability. The ability to acclimate existing leaves to changing environmental conditions may allow species to exploit canopy gaps when conditions are unfavorable for new leaf production.

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