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Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps

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Summary We hypothesized that photoinhibition of shade-developed leaves of deciduous hardwood saplings would limit their ability to acclimate photosynthetically to increased irradiance, and we predicted that shade-tolerant sugar maple (*Acer saccharum* Marsh.) would be more susceptible to photoinhibition than intermediately shade-tolerant red oak (*Quercus rubra* L.). After four weeks in a canopy gap, photosynthetic rates of shade-developed leaves of both species had increased in response to the increase in irradiance, although final acclimation was more complete in red oak. However, photoinhibition occurred in both species, as indicated by short-term reductions in maximum rates of net photosynthesis and the quantum yield of oxygen evolution, and longer-term reductions in the efficiency of excitation energy capture by open photosystem II (PSII) reaction centers (dark-adapted F_v/F_m) and the quantum yield of PSII in the light (ϕ_{PSII}). The magnitude and duration of this decrease were greater in sugar maple than in red oak, suggesting greater susceptibility to photoinhibition in sugar maple. Photoinhibition may have resulted from photodamage, but it may also have involved sustained rates of photoprotective energy dissipation (especially in red oak). Photosynthetic acclimation also appeared to be linked to an ability to increase leaf nitrogen content. Limited photosynthetic acclimation in shade-developed sugar maple leaves may reflect a trade-off between shade-tolerance and rapid acclimation to a canopy gap.

Keywords: Acer saccharum, carbon gain, chlorophyll fluorescence, gap, irradiance, leaf absorptance, leaf nitrogen content, photoinhibition, Quercus rubra, red oak, sugar maple.

Introduction

Saplings of many species require one or more canopy gaps, formed by treefall or branchfall, to achieve a position in the canopy and reproduce (Canham 1985, Runkle 1985, 1989). However, gap formation represents a potentially stressful event to understory saplings. Irradiances in the understory of temperate forests, which typically are less than 2% of irradiance incident on the canopy, can dramatically increase when a gap is formed (Canham et al. 1990), and the resulting greater input of radiation can cause substantial increases in leaf temperature (Bazzaz and Pickett 1980). Within the highly competitive environment of a recently formed gap, the ability to acclimate to increased irradiance is advantageous. We define acclimation as the process by which physiological or morphological changes increase the capacity for carbon gain in the new environmental regime. In a mixed mesophytic temperate forest, gap formation is most common in June, July and August (Romme and Martin 1982), thus exposing mature, shade-developed foliage to a dramatic change in environment. For shade-tolerant saplings that primarily rely on one cohort of foliage for their annual carbon gain, the response to this change is important, yet poorly understood.

When plants are transferred from low to high irradiance, expanding leaves (Pearce and Lee 1969, Jurik et al. 1979, Besford 1986, Sims and Pearcy 1992) and leaves produced in the new environment (Langenheim et al. 1984, Kamaluddin and Grace 1992, Mulkey and Pearcy 1992) acclimate to increased irradiance; however, fully shade-developed leaves exposed to high irradiance may undergo a period of photoinhibition (e.g., reviews by Powles 1984, Anderson and Osmond 1987, Long et al. 1994, Osmond 1994, Pearcy 1994). Photoinhibition is a decrease in photosynthetic rate induced by visible light and represents an integration of photodamage, repair processes, and down-regulation of photosynthesis because of various protective mechanisms (Krause 1988, Demmig-Adams 1990, Baker and Ort 1992, Öquist et al. 1992, Krause 1994, Long et al. 1994, Osmond 1994, Adams et al. 1995*a*).

With prolonged exposure to high irradiance (two or more weeks), the duration of photoinhibition varies considerably, and in some cases shade-grown plants remain chronically photoinhibited (Greer and Liang 1992). In many species, photoinhibited leaves recover to initial photosynthetic rates (Syvertsen 1984, Ferrar and Osmond 1986, Sims and Pearcy 1991, Nunes et al. 1993, Turnbull et al. 1993), or even increase their rates beyond the initial values (Ferrar and Osmond 1986, Bauer and Thöni 1988, Kamaluddin and Grace 1992, Turnbull et al. 1993, Lovelock et al. 1994). In other species, photosynthetic rates of shade-developed leaves increase after transfer to high light with no observed period of photoinhibition (Pearce and Lee 1969, Gauhl 1976, Chow and Anderson 1987, Sebaa et al. 1987, Sims and Pearcy 1992). In addition to greater susceptibility to photoinhibition of shade-developed leaves, shade-tolerant plants in general appear more susceptible to

photoinhibition than plants that normally grow in high-light environments (e.g., Björkman 1981, Anderson and Osmond 1987, Johnson et al. 1993, Demmig-Adams and Adams 1994). Thus, depending on the species and the developmental stage of foliage, photoinhibition may restrict the capacity to acclimate to a new growth environment.

We used complementary methods of measuring photosynthesis (O_2 evolution and chlorophyll fluorescence), to determine the influence of photoinhibition on the acclimation response to a sudden increase in irradiance of shade-developed leaves of two temperate tree species representing different acclimation potentials. Previous results (Naidu 1996) suggested that mature shade-developed leaves of red oak (*Quercus rubra* L.) can acclimate to a late-season canopy gap more completely than those of sugar maple (*Acer saccharum* Marsh.). We hypothesized that photoinhibition in shade-developed leaves of deciduous hardwood saplings limits photosynthetic acclimation and predicted that sugar maple, a shade-tolerant species, would exhibit a greater magnitude and duration of photoinhibition in response to late-season canopy gap formation than red oak, which exhibits an intermediate tolerance to shade.

Materials and methods

Experimental design

Eight-cm-tall nursery stock (Cold Stream Farm, Free Soil, MI) of sugar maple and red oak was obtained in late March and stored with moist roots in a darkened cold-room (< 5 °C) until planting (May 27). Saplings were approximately two years old and had previously been grown in 80% shade before lifting in late spring. For each species, 150 saplings were potted in soil/peat/pearlite (1/1/1 v/v) in 23 × 38-cm (15.8 liter) pots and moved to Trelease Woods, a University of Illinois ecological research area 8 km northeast of Urbana, IL. One-hundred saplings of each species were placed in deep shade in the forest understory, and the remaining plants were placed in a nearby, naturally occurring canopy gap (75 m^2). Saplings were fertilized one week after planting with 250 ml per pot of 0.257 g l^{-1} N,P,K (20,20,20) and again three weeks after planting with a top-dressing of 30 g per pot of slow-release fertilizer (Osmocote, Sierra Chemical Co., Milpitas, CA). Pots were mulched with peat moss to reduce evaporation from the soil and were kept well watered throughout the season by natural rainfall. Twice during the growing season, plants were sprayed with insecticide to reduce herbivory (Orthene, 327 ppm). Destruction by mammals was prevented by surrounding the plots with electric fencing.

Leaf expansion for these species in the understory was complete in 20–24 days (Naidu 1996). After an additional five weeks (to ensure complete leaf development within the shaded understory), half of the understory plants were moved to the canopy gap 58 days (Transfer, Day 0) after planting. This move simulated the occurrence of a late-season (relative to leaf development) canopy gap. The experimental design consisted of three treatments, fully shade-grown plants (Shade), fully gap-grown plants (Gap), and shade-grown plants moved to the canopy gap (Shade-Gap).

Diurnal measurements of environmental conditions were made periodically during the summer in the Shade and Gap treatments and in full sun (outside the forest). Air, leaf, and soil temperatures were measured with copper-constantan thermocouples; and irradiance (photosynthetic photon flux density, PPFD, 400–700 nm) was measured with an LI-185B quantum sensor (Li-Cor, Inc., Lincoln, NE). Voltage or current outputs were recorded with a data logger (21X, Campbell Scientific, Logan, UT). Integrated daily irradiance in full sun was typically 37 mol m^{-2}, and was typically 4 and 40% of full sun in the understory and gap, respectively. Maximum air, leaf and soil temperatures in full sun were typically 31, 37, and 29 °C, respectively, and temperatures in the Gap were typically 1–2 °C lower than in full sun. Maximum air and soil temperatures in the shade were typically 4–5 °C lower than in full sun; however, midday leaf temperatures in the shade were as much as 10 °C lower than in the full sun. Therefore, the move from shade to gap conditions represented a 10-fold increase in irradiance and an increase in midday leaf temperatures of as much as 8–9 °C.

Gap-control plants were sampled two days before Transfer (Day −2), and again on Day 31 after Transfer. Shade-control plants were sampled immediately before Transfer (Day 0) and on Day 33 after Transfer. Shade-Gap plants were sampled on Day 2, 4, 7, 14, 21, and 28 (29 for oak) after Transfer. The transfer date was offset by one day for the two species to allow for adequate sampling on each day. In the evening before the day on which plants were to be measured, five plants of the designated treatment and species were arbitrarily selected and placed in a growth chamber with environmental conditions similar to the Shade or Gap area from which they came. The following day, photosynthetic rates were measured on one 10-cm^2 leaf disc from each plant, and fluorescence was measured on an adjacent leaf, excised at the petiole. Samples were taken between 0730 and 1430 h (CST). Only leaves of similar age that had fully developed before Transfer were sampled.

Photosynthetic O_2 evolution

Both CO_2-saturated (5% CO_2 in hydrated air) net photosynthetic rates (A) and dark respiration rates (R_D) were measured with a leaf-disc O_2 electrode (LD2/2, Hansatech Ltd., Norfolk, England) according to Delieu and Walker (1981). Light-response curves were generated by measuring O_2 evolution at different irradiances provided by passing light from a fixed-output metal halogen lamp (LS2, Hansatech Ltd.) through combinations of neutral-density filters (Melles-Griot, Irvine, CA). Irradiance was measured with a Li-Cor LI-185B quantum sensor. Temperature in the O_2 electrode chamber was maintained at 25 °C by a circulating refrigerated water bath.

Leaf discs were placed in the darkened O_2 electrode chamber and R_D measured when the rate became constant (10–15 min); the photosynthetic rate at each irradiance was then measured from low to high irradiance. Immediately following photosynthesis measurements, reflectance (R) and transmittance (T) of the adaxial surface were measured on the same leaf disc with

a Li-Cor LI-185B quantum sensor and a Taylor-type integrating sphere (LI-1800-12, Li-Cor, Inc.). Leaf absorptance was calculated as $1 - R - T$. Oxygen evolution rates are reported on an absorbed-irradiance basis. The quantum yield of O_2 evolution (ϕ_{O_2}) was calculated as the slope of the initial linear region of the light-response curve (irradiances < 100 μmol m^{-2} s^{-1}, excluding zero). Four points on the light-response curves were located in this region.

Leaf composition

The leaf discs used for O_2 electrode measurements were oven-dried (70 °C) to a constant mass and weighed to determine leaf mass per unit area (LMA). Total Kjeldahl nitrogen was then determined with an autoanalyzer (Traacs 800, Bran and Leubbe, Buffalo Grove, IL) following acid digestion (Lowther 1980). Leaf thickness was measured at 10 interveinal positions with a dial-gauge micrometer (Starrett, Athol, MA) on the same leaves used for fluorescence measurements.

Chlorophyll a fluorescence

Chlorophyll a fluorescence was measured with a pulse-amplitude modulated fluorimeter (PAM-101, Walz, Effeltrich, Germany) on leaves adjacent to those used for O_2 evolution measurements. Detached leaves were placed on a moist pad in a light-tight chamber for dark-acclimation (30 min) before measurement. The chamber was maintained at 25 °C and flushed with hydrated 5% CO_2 in air throughout the measurements to overcome potential stomatal limitations caused by stomatal closure. Following dark acclimation, initial fluorescence intensity (F_o) was measured at the leaf surface under a low irradiance (0.06 μmol m^{-2} s^{-1}) modulated measuring beam. A 1-s pulse of saturating irradiance (12000 μmol m^{-2} s^{-1}), sufficient to close all open (oxidized) photosystem II (PSII) reaction centers, was delivered from an FL 103 saturation pulse lamp by means of a PAM-103 control unit and repeated every minute thereafter. Maximal fluorescence (F_m) was recorded after the first pulse, and dark-adapted variable fluorescence ($F_v = F_m - F_o$) over maximal fluorescence (F_v/F_m) was calculated. Dark-adapted F_v/F_m quantifies the efficiency of photon capture by open PSII reaction centers (Butler and Kitajima 1975). Fluorescence nomenclature follows van Kooten and Snel (1990).

Immediately following the F_m flash, the actinic lamp (1000 μmol m^{-2} s^{-1} incident irradiance) was switched on (PAM 102). This light intensity was 95% saturating (or greater) but not photoinhibiting for these species in the Gap and Shade treatments (Naidu 1996). Maximal fluorescence (induced by the saturating pulses, F_m') and steady-state fluorescence (fluorescence intensity between saturating pulses, F_s) during actinic illumination were recorded after 1–20 min, by which time both were constant. After this time, the actinic and pulse lamps were switched off and minimal fluorescence (F_o') recorded. These data were used to calculate photochemical (q_P) and nonphotochemical (q_N) quenching as described by Schreiber et al. (1986) and the quantum yield of photosystem II during illumination (ϕ_{PSII}) was calculated as described by Genty et al. (1989). Photochemical quenching provides an approximate measure of the number of open PSII centers and q_N includes all other potential forms of fluorescence quenching, resulting in nonradiative energy dissipation; i.e., down-regulation of photosynthesis (e.g., Baker and Ort 1992). Such processes include the ΔpH- and xanthophyll-dependent dissipation of excess energy as heat within the antenna complex (e.g., Gilmore and Yamamoto 1993, Gilmore and Björkman 1995, Demmig-Adams and Adams 1996), and are generally assumed to protect against damage (e.g., reviews by Krause 1988, Baker and Ort 1992, Dau 1994, Osmond 1994, Demmig-Adams and Adams 1996). The quantum yield of PSII was determined by the number of open PSII centers and the excitation energy capture efficiency of those PSII reaction centers (Genty et al. 1989).

Statistical analysis

To determine the magnitude of physiological acclimation in Shade-Gap leaves, pairwise comparisons were made between Shade-Gap and Shade leaves and between Shade-Gap and Gap leaves for values measured at the end of the experiment only. For simplicity, comparisons between Shade and Gap controls are not discussed. Data were analyzed with SAS statistical software (ver. 6.10, SAS Institute Inc., Cary, NC). Because of the small sample size, pairwise comparisons were made with a Mann-Whitney U (rank sum) test, and significant differences are reported at the $P < 0.05$ level.

Results

Photosynthetic O_2 evolution

By the end of the four-week acclimation period, Shade-Gap leaves of sugar maple and red oak had greater photosynthetic rates than Shade leaves, and this increase in net photosynthesis (measured as O_2 evolution) was evident over a range of irradiances (Figure 1). For both species, the light-saturated photosynthetic rate (A_{max}; measured at 1200–1600 μmol m^{-2} s^{-1}, PPFD) and the rate measured under sub-saturating irradiance (A_{200}; 200 μmol m^{-2} s^{-1}, PPFD) for Shade-Gap leaves exceeded values for Shade controls ($P < 0.05$, except $P < 0.08$ for A_{max} of red oak) by the end of the experiment (Figure 2). For red oak, these values were not significantly different from Gap controls ($P > 0.05$). Leaf absorptance of Shade-Gap leaves decreased over the acclimation period but recovered to control values (Shade-Gap = Shade, $P > 0.05$) by the end of the experiment (Figure 3). The confounding effects of this change in leaf absorptance on photosynthesis were eliminated by calculating photosynthetic rates on an absorbed irradiance basis.

To examine the kinetics of photosynthetic acclimation, light-response curves were generated throughout the experiment for Shade-Gap leaves and compared to Shade and Gap controls measured before and after the four-week acclimation period. Three representative points on the light-response curve (R_D, A_{200}, and A_{max}) are plotted over the course of the experiment in Figure 2. Shade-Gap leaves increased rates of R_D after exposure to the gap conditions. By the end of the experiment,

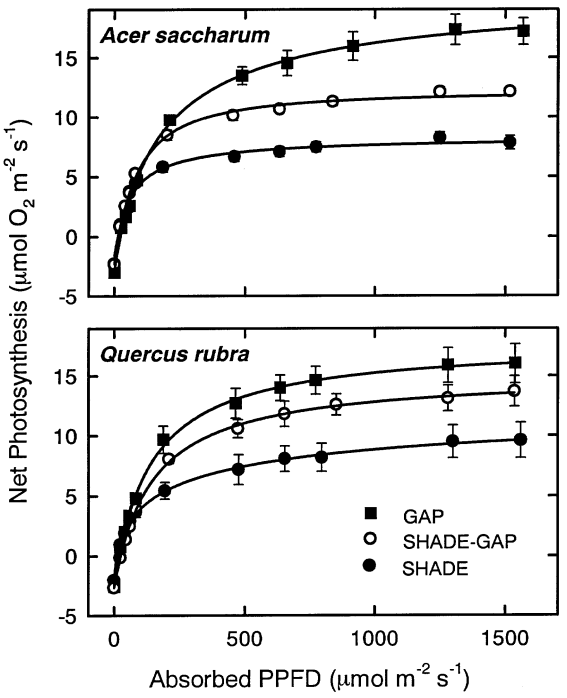

Figure 1. Response of net photosynthesis, measured as O_2 evolution, to absorbed photosynthetic photon flux density (PPFD) of *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Light-response curves shown were measured four weeks after the date of Transfer. Means are of four or five leaves, each from a different plant, per treatment and error bars of plus and minus one standard error are shown except when smaller than symbol size. A line was fit to the data using a power function as described in DeLucia et al. (1995).

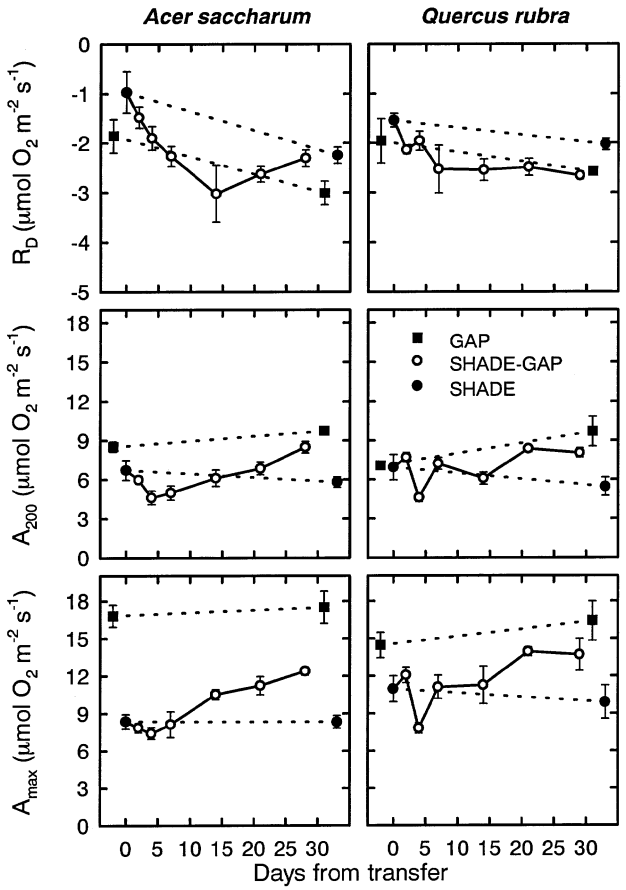

Figure 2. Dark respiration (R_D), net photosynthesis at 200 μmol m^{-2} s^{-1} absorbed irradiance (A_{200}), and maximum net photosynthesis (A_{max}, highest measured point on the light response curve) of *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Measurements of Shade and Gap controls were made before and four weeks after transfer of shade-grown plants to the canopy gap, and Shade-Gap leaves were measured throughout the four-week acclimation period. Means are of four or five leaves, each from a different plant, per treatment and error bars of plus and minus one standard error are shown except when smaller than the symbol size.

Shade-Gap leaves of red-oak had R_D rates equal to Gap leaves ($P > 0.05$); however, Shade-Gap leaves of sugar maple had rates equal to Shade leaves ($P > 0.05$; Figure 2). In shade-developed leaves, A_{200} and A_{max} decreased on exposure to the canopy gap (Figure 2) but exceeded the Shade controls by the end of the experiment (see above). The lowest rates of net photosynthesis occurred on Day 4 with recovery to initial values by Day 7 (except A_{200}, sugar maple). It is unclear why the quantum yield of O_2 evolution (ϕ_{O_2}) for control plants was lower than values reported for a variety of other species (Björkman and Demmig 1987); however, ϕ_{O_2} was similar between species and treatments at the beginning of the experiment and remained relatively constant across the season in control plants of sugar maple, although final values for Shade and Gap controls of red oak diverged. On exposure to the canopy gap, quantum yield was reduced in shade-developed leaves of sugar maple (Figure 4), with the maximum reduction occurring on Day 7 followed by an increase thereafter. The initial pattern is less clear in red oak, but by Day 7 ϕ_{O_2} had begun to increase. By the end of the experiment, ϕ_{O_2} of Shade-Gap leaves was greater ($P < 0.05$) than that of Shade leaves and did not differ significantly from that of Gap leaves ($P > 0.05$) for both species.

Leaf composition

The LMA of Shade-Gap leaves increased slightly over the duration of the experiment and final values were greater than those of Shade leaves ($P < 0.05$) but less than those of Gap leaves ($P < 0.05$; Figure 5). The increase in LMA was not the result of an increase in leaf thickness, because leaf thickness decreased over the duration of the experiment in all treatments (Figure 5). In shade-developed leaves, leaf nitrogen concentration calculated on a dry mass basis (%N) decreased on exposure to the canopy gap, but recovered to initial values by Day 21 in sugar maple and Day 14 in red oak (Figure 6). For both species, final values were not significantly different from those of Shade or Gap controls ($P > 0.05$). However, when calculated on an area basis, leaf nitrogen content of Shade-Gap

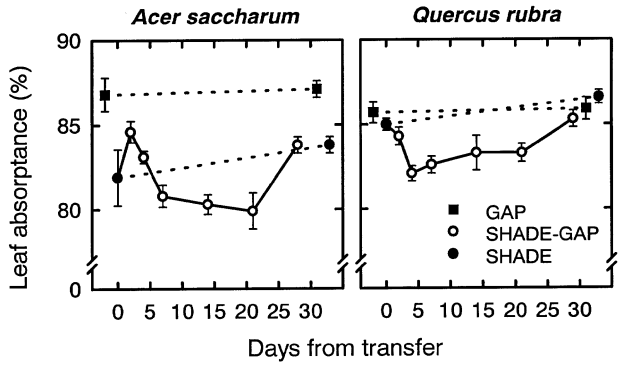

Figure 3. Absorptance of *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Measurements, sample size, and symbols are as in Figure 2.

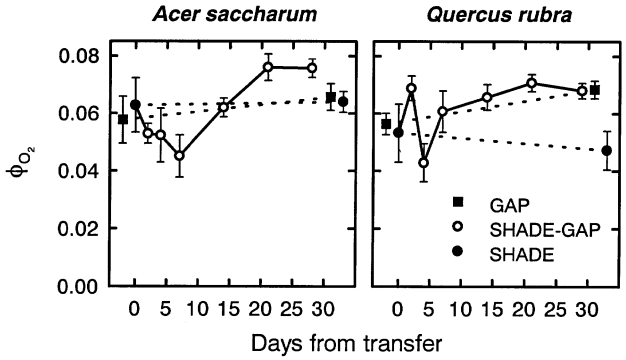

Figure 4. Quantum yield of O_2 evolution (moles O_2 evolved per mole absorbed photons; ϕ_{O_2}) of *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Measurements, sample size, and symbols are as in Figure 2.

leaves remained steady initially, increasing after about a week; final values were greater than in Shade but less than in Gap leaves ($P < 0.05$; Figure 6).

Chlorophyll a fluorescence

To assess the magnitude and duration of photoinhibition within shade-developed leaves on exposure to a canopy gap, fluorescence parameters of dark-adapted leaves and quenching of fluorescence in the light were monitored throughout the experiment. Shade-developed leaves exhibited an immediate decrease in F_v/F_m on exposure to the canopy gap, with the maximal decrease occurring by Day 7 in sugar maple and Day 4 in red oak, followed by a subsequent slow recovery (Figure 7). By the end of the experiment, F_v/F_m of Shade-Gap leaves was still lower than that of Shade ($P < 0.05$) and Gap ($P < 0.05$, sugar maple; $P < 0.08$, red oak) controls. For sugar maple, the decrease in F_v/F_m was mostly a result of an increase

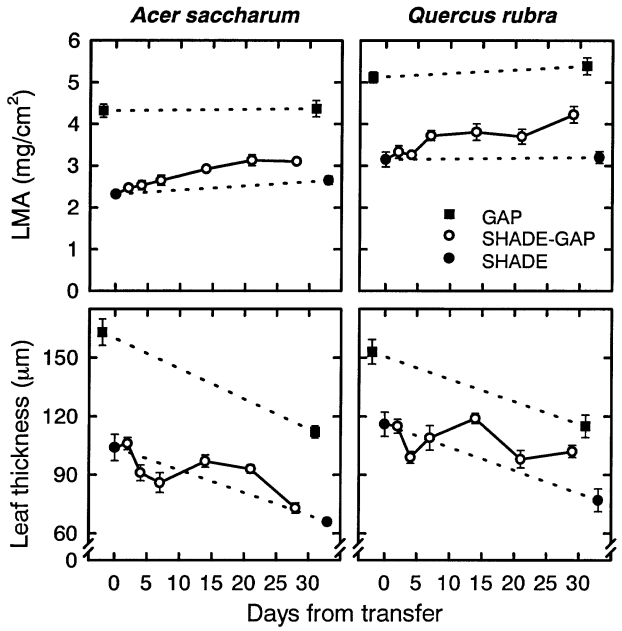

Figure 5. Leaf mass per unit area (LMA) and interveinal leaf thickness of *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Measurements, sample size, and symbols are as in Figure 2.

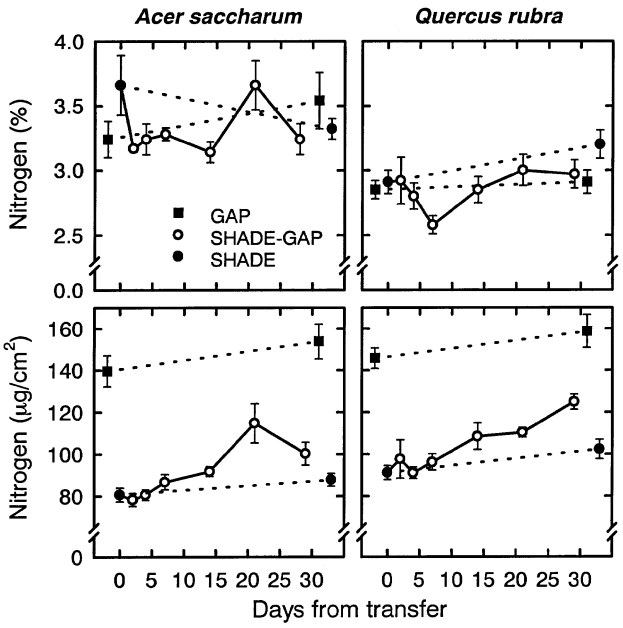

Figure 6. Leaf nitrogen on a dry-mass basis (%) and an area basis of *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Measurements, sample size, and symbols are as in Figure 2.

in F_o (reported as a percentage of the highest F_m obtained for each species; Figure 7) because there was little change in F_m, except on Day 14, when F_m was 5% higher than the initial

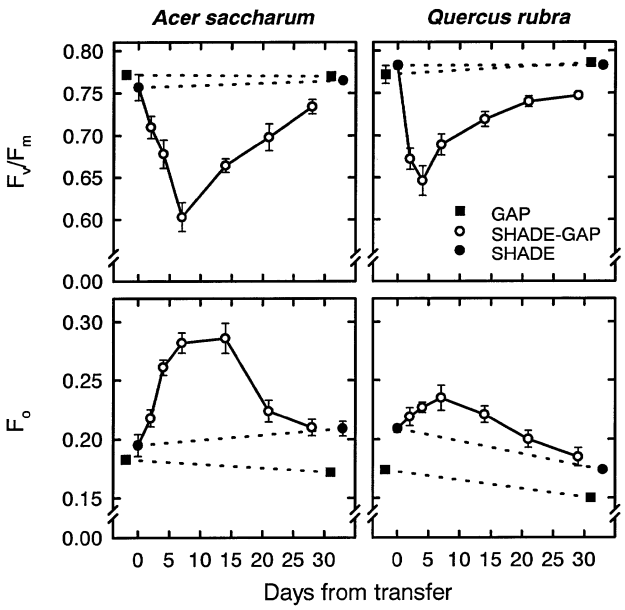

Figure 7. The ratio of variable (F_v) to maximal (F_m) fluorescence (F_v/F_m) and initial fluorescence (F_o) of dark adapted *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Measurements, sample size, and symbols are as in Figure 2. Each point represents an average of four or five leaves measured between 0730 and 1430 h (CST) on the same day (see Methods for details).

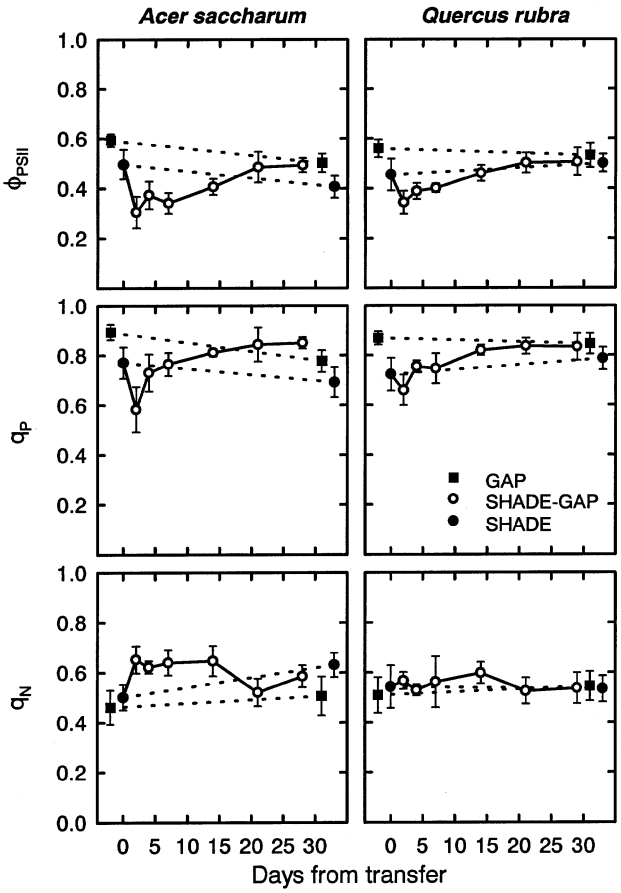

Figure 8. The quantum yield of photosystem II during illumination (ϕ_{PSII}), photochemical quenching (q_P), and nonphotochemical quenching (q_N) in the light (1000 μmol m^{-2} s^{-1}) of *Acer saccharum* and *Quercus rubra* leaves on plants grown in a canopy gap (Gap) or the forest understory (Shade) or grown in the forest understory and transferred to a canopy gap (Shade-Gap). Measurements, sample size, and symbols are as in Figure 2.

value in Shade controls (data not shown). Conversely, the decrease in F_v/F_m in red oak was mainly the result of a decrease in F_m, which was 33% lower than the initial value in Shade controls by Day 4, but rose to values similar to those of the Gap controls by Day 7. The rise in F_o for Shade-Gap red oak leaves may also have contributed to the decrease in F_v/F_m. The maximum increase in F_o occurred by Day 14 for sugar maple and Day 7 for red oak. In both species, F_o for Shade-Gap leaves recovered by the end of the experiment (Shade-Gap = Shade, $P > 0.05$).

Shade-developed leaves showed a reduction in the quantum yield of photosystem II reaction centers in the light (ϕ_{PSII}) on exposure to the canopy gap, with maximal reduction by Day 4 and recovery by Day 14, so that final values were not significantly different from Gap controls ($P > 0.05$). Shade-Gap leaves showed a small initial reduction of short duration in q_P with final values greater than those of Shade and Gap leaves ($P < 0.05$) in sugar maple, but equal to values in control leaves in red oak ($P > 0.05$; Figure 8). A sustained increase in q_N from Day 4 to Day 14 was evident for Shade-Gap leaves of sugar maple, but final values were not significantly different from Shade or Gap leaves (Figure 8). There was no difference in q_N with treatment in red oak ($P > 0.05$). Similar trends were seen when nonphotochemical quenching was calculated as Stern-Volmer type fluorescence quenching ($F_m/F_m' - 1$; Bilger and Björkman 1990, data not shown).

Discussion

On exposure to higher irradiance and temperature within a canopy gap, shade-developed leaves of red oak and sugar maple underwent a period of photoinhibition (Figure 2). The reduction of net photosynthesis at sub-saturating (A_{200}) as well as saturating (A_{max}) irradiance indicates that carbon gain was limited in these species over a range of irradiances (i.e., throughout the day, under field conditions). The actual reduction in photosynthetic capacity was of short duration, and shade-developed leaves of sugar maple and red oak began to acclimate to increased irradiance by increasing photosynthetic rates compared to shade-grown controls within two weeks of exposure to a canopy gap (Figure 2). After four weeks, acclimation was more complete in red oak (Shade-Gap leaves had photosynthetic rates not significantly different from gap-grown controls) than in sugar maple (Figures 1 and 2), which suggests that photosynthetic rates were intrinsically limited in sugar maple, perhaps by long-term photoinhibition. Further-

more, acclimation of photosynthetic CO_2 uptake appears to be correlated with an ability to increase stomatal conductance, and photosynthesis in sugar maple may be stomatally limited under natural CO_2 concentrations within a canopy gap (Naidu 1996).

In contrast to red oak, Shade-Gap leaves of sugar maple, exhibited an immediate decrease in the photosynthetic efficiency of O_2 evolution (ϕ_{O_2}, Figure 4) in addition to the decrease in photosynthetic capacity (A_{max}, Figure 2), suggesting that a portion of photoinhibition may be the result of actual damage to some component of the photosynthetic apparatus (e.g., Osmond 1994). The rise in ϕ_{O_2} that occurred after Day 7 in Shade-Gap leaves of sugar maple suggests that, if present, damage is repaired or ameliorated in some way. The rise in q_N of Shade-Gap sugar maple leaves (Figure 8) over time also indicates that mechanisms for excess energy dissipation associated with photoprotection are in place for this species. The extent of potential photodamage in Shade-Gap leaves of red oak is unclear from the ϕ_{O_2} data alone, but if present, recovered quickly (ϕ_{O_2} was consistently similar to Gap controls by Day 7).

Recent studies have indicated that sustained decreases in F_m, resulting from operation of photoprotective energy dissipation by the xanthophyll cycle, may result in artificially low calculations of q_N (Adams et al. 1995*a*, 1995*b*). Such a situation can arise if q_N is not fully relaxed during the dark acclimation period preceding measurement of F_m (Gilmore and Björkman 1995). Thus, protective mechanisms may be operating in red oak as well, although they were not revealed as an increase in q_N. The initial lag (Day 2, Figure 2) in the reduction of net photosynthesis for red oak suggests that avoidance or protective mechanisms are either constitutive or rapidly induced (Raven 1989), which may explain the lack of a consistent decrease in ϕ_{O_2}. Increases in dark respiration have been reported in shade-developed leaves exposed to higher irradiance (Gauhl 1976, Bunce et al. 1977, Sebaa et al. 1987, Sims and Pearcy 1991, Turnbull et al. 1993, Lovelock et al. 1994), and were also seen in the present study (Figure 2). Such increases are consistent with the energetic costs of damage repair (Raven 1989) or increased production of photosynthetic machinery during the acclimation process.

The reduction in dark-adapted F_v/F_m of Shade-Gap leaves of both species following transfer to the canopy gap reveals a decrease in the efficiency of excitation energy capture by open PSII reaction centers (Butler and Kitajima 1975). A decrease in F_v/F_m accompanied by a decrease in F_m (as in red oak), could result from damage to PSII or from sustained, high rates of energy dissipation. Thus, although the decrease in F_v/F_m in Shade-Gap red oak leaves may indicate photodamage, it is also consistent with the presence of sustained rates of photo-protective nonphotochemical quenching.

In sugar maple (and somewhat in red oak), the decrease in F_v/F_m was coupled with an increase in F_o, the initial fluorescence at low irradiance arising from the bulk chlorophyll (Figure 7). A sustained increase in F_o could result from either a reduction in the overall rate of photochemistry or a reduction in the rate of energy transfer from the pigment bed to PSII (Butler 1978, Krause 1988). Although this may be the result of photodamage (Krause 1988, Franklin et al. 1992), true F_o is difficult to measure and may be complicated by other processes, such as fluorescence originating from photosystem I (Genty et al. 1990), reverse electron flow generated by ATP hydrolysis (Schreiber 1980, Gilmore and Yamamoto 1992*a*, 1992*b*), or nonradiative energy dissipation (Gilmore and Björkman 1995). Furthermore, it has recently been suggested that rearrangement of the antenna system (which can cause a rise in F_o) is a mechanism of photoprotection and should not be considered damage (Ottander et al. 1995). The sustained decrease in leaf absorptance over three weeks of the acclimation period (Figure 3) may indicate some damage to chlorophyll pigments causing partial bleaching. Alternatively, the reduction in absorptance may have resulted from avoidance mechanisms such as restructuring within chloroplasts or movements of chloroplasts within the mesophyll cells (see review by Raven 1989).

The quantum yield of PSII during illumination is determined by both the efficiency of excitation energy capture by PSII reaction centers (i.e., F_v'/F_m') and the number of open (oxidized) centers (indicated by q_P). The initial decrease of ϕ_{PSII} in Shade-Gap leaves was caused in part by a reduction in the number of open PSII reaction centers (initial decrease in q_P, Figure 8). However the reduction in q_P was minimal in red oak, and recovered quickly in both species, with values similar to those of Gap controls by Day 14. Therefore, the slower recovery in ϕ_{PSII} must have been a result of the long-term reduction in F_v'/F_m' which was evident in both species (data not shown). Sustained decreases were also present in dark-adapted F_v/F_m, which was the only fluorescence parameter that did not completely recover by the end of the experiment (Figure 7). This prolonged decrease in F_v/F_m indicates long-term photoinhibition, but by the end of the experiment, lowered efficiency of open PSII reaction centers was no longer limiting the quantum yield of O_2 evolution (Figure 4) or the quantum yield of PSII at its actual reduction state in the light (Figure 8). There are two possible explanations for this discrepancy. First, the reduced efficiency may be ameliorated by increased photosynthetic capacity, indicated by an increase in the number of open PSII centers (q_P). This may explain why the recovery of ϕ_{O_2} (Figure 4) preceded the recovery of F_v/F_m (Figure 7) by a week or more. Also, if absorbed photons can be shunted from damaged to functional PSII centers (Raven and Samuelsson 1986), ϕ_{O_2} could remain high although F_v/F_m was low. Second, because a majority of emitted fluorescence comes from the first layer of palisade cells within the leaf (Bornman et al. 1991), fluorescent measurements assess photosynthesis of the upper leaf surface only, whereas measurements of O_2 evolution integrate whole-leaf photosynthetic function. Also, photoinhibitory damage to leaves appears to be concentrated in the upper leaf surface (Powles and Björkman 1982, Krause and Somersalo 1989, Nishio et al. 1994). Greater efficiency in lower layers of the leaf may compensate for photoinhibition at the leaf surface.

The magnitude and duration of photoinhibition, as measured by the quantum yield of O_2 evolution (Figure 4), dark adapted

fluorescence parameters (Figure 7), and quenching of fluorescence in the light (Figure 8), were greater in sugar maple than in red oak. Although the differences between species were small, the more prolonged decrease in photosynthetic parameters for sugar maple suggests that longer-term photoinhibition may be limiting more complete or faster acclimation relative to red oak. By the end of the experiment, Shade-Gap leaves of red oak had completely acclimated (photosynthetic rates were not significantly different from Gap controls), whereas sugar maple had not. It is possible that the length of time necessary for physiological acclimation differs among species and that complete acclimation in sugar maple might occur after four weeks (longer than the duration of this study). However, because photosynthetic rates of both sun and shade leaves of temperate deciduous trees (including sugar maple and red oak) maintain a relatively constant maximum from June through September (Jurik 1986), it is unlikely that losses in carbon gain resulting from slower acclimation can be offset by increasing rates of photosynthesis beyond the rates of the gap controls. Therefore, red oak, which acclimates more quickly than sugar maple, may have a competitive advantage over sugar maple saplings of the same initial size because of greater cumulative carbon gain within the season of gap formation. The more limited acclimation response of sugar maple may reflect a trade-off between shade-tolerance and rapid exploitation of canopy gaps.

The ability of shade-developed leaves to increase nitrogen content on exposure to higher irradiance, either through internal reallocation or increased nitrogen uptake from the soil, may also influence the magnitude of photoinhibition and capacity for acclimation (Castro et al. 1995, Hikosaka and Terashima 1995, Naidu 1996). Increased leaf nitrogen can result from greater protein content associated with higher photosynthetic rates (Ferrar and Osmond 1986, Field and Mooney 1986, Evans 1989) or repair of photoinhibitory damage (Nunes et al. 1993), and the latter may explain why nitrogen fertilization decreases plant susceptibility to photoinhibition (Ferrar and Osmond 1986, Nunes et al. 1993). In the current study, nitrogen content per unit area of shade-developed leaves increased after exposure to the canopy gap, although this increase began to reverse in sugar maple by the end of the experiment (Figure 6). The lack of a faster or more dramatic final increase (especially in sugar maple) of nitrogen content of Shade-Gap leaves may have limited the acclimation process. Despite the increase in leaf nitrogen per unit leaf area, %N content decreased for two weeks before recovering (Figure 6). This decrease in %N probably resulted from dilution by carbohydrate accumulation associated with higher net photosynthetic rates. This is supported by the slow increase in LMA, which was not a result of increased leaf thickness (Figure 5).

In addition to acclimation of pre-existing leaves, some species produce more than one flush of leaves within a growing season. Because newly emergent leaves tend to be acclimated to the light regime in which they develop (Boardman 1977, Björkman 1981, Anderson and Osmond 1987, Givnish 1988, Abrams and Kubiske 1990), such species have the capacity to produce new, high-light acclimated leaves on exposure to a canopy gap. New leaves would contribute substantially to whole-plant carbon gain, yet seasonal carbon gain could be even greater if old leaves also acclimate. Shade-developed red oak saplings can produce more leaves on exposure to a gap, as can sugar maple, although to a much lesser extent (Naidu 1996). However, the production of these new, "sun-type" leaves (they would presumably be very similar to Gap controls) does not come at the expense of acclimation of pre-existing leaves, which suggests that acclimation includes a variety of integrated responses from physiological to allocational changes (Naidu 1996). Other whole-plant acclimation responses have been observed in red oak saplings and include increased root growth to offset higher water-demand in gaps, and carbohydrate storage in preparation for increased growth in the growing season following gap formation (Naidu 1996).

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