Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments

Marilou Beaudet, Christian Messier, David W. Hilbert, Ernest Lo, Zhang M. Wang, and Martin J. Lechowicz

Abstract: Leaf-level photosynthetic-light response and plant-level daily carbon gain were estimated for seedlings of moderately shade-tolerant yellow birch (*Betula alleghaniensis* Britton) and shade-tolerant sugar maple (*Acer saccharum* Marsh.) and beech (*Fagus grandifolia* Ehrh.) growing in gaps and under a closed canopy in a sugar maple stand at Duchesnay, Que. All three species had a higher photosynthetic capacity (A_{max}) in the gaps than in shade, but yellow birch and beech responded more markedly than sugar maple to the increase in light availability. The high degree of plasticity observed in beech suggests that the prediction that photosynthetic plasticity should decrease with increasing shade tolerance may not hold when comparisons are made among a few late-successional species. Unit-area daily carbon gain (C_A) was significantly higher in the gaps than in shade for all three species, but no significant difference was observed between light environments for plant-level carbon gain (C_W). In shade, we found no difference of C_A and C_W among species. In gaps, beech had a significantly higher C_A than sugar maple but similar to that of birch, and birch had a significantly higher C_W than maple but similar to that of beech. Sugar maple consistently had lower carbon gains than yellow birch and beech but is nevertheless the dominant species at our study site. These results indicate that although plant-level carbon gain is presumably more closely related to growth and survival of a species than leaf-level photosynthesis, it is still many steps removed from the ecological success of a species.

Résumé : La réponse photosynthétique à la lumière, au niveau de la feuille, et le gain journalier en carbone au niveau de la plante ont été estimés chez les semis hémisciaphiles du bouleau jaune (*Betula alleghaniensis* Britton) et sciaphiles de l'érable à sucre (*Acer saccharum* Marsh.) et du hêtre d'Amérique (*Fagus grandifolia* Ehrh.) dans des trouées et sous couvert fermé dans un peuplement d'érable à sucre à Duchesnay, au Québec. Les trois espèces avaient une plus grande capacité photosynthétique (A_{max}) dans les trouées qu'à l'ombre. Toutefois, le bouleau jaune et le hêtre répondaient de façon plus marquée que l'érable à sucre à l'augmentation de la luminosité. Le haut degré de plasticité observé chez le hêtre suggère que la prédiction concernant la décroissance de la plasticité photosynthétique avec l'accroissement de la tolérance à l'ombre pourrait ne pas tenir lorsqu'on compare entre elles quelques espèces de fin de succession. Le gain journalier en carbone par unité de surface (C_A) était, chez les trois espèces, significativement plus élevé dans les trouées qu'à l'ombre. Cependant, aucune différence significative de gain en carbone au niveau de la plante (C_W) n'a été observée entre les trouées et les conditions ombragées. À l'ombre, il n'y avait pas de différence quant au C_A et au C_W entre les espèces. Dans les trouées, le hêtre avait un C_A significativement plus élevé que celui de l'érable à sucre, mais similaire à celui du bouleau. Ce dernier avait un C_W significativement plus élevé que celui de l'érable, mais similaire à celui du hêtre. L'érable à sucre présentait des gains en carbone plus faibles que le bouleau jaune et le hêtre tant à l'ombre que sous les trouées; néanmoins, il est l'espèce dominante sur le site étudié. Ces résultats indiquent que bien que le gain en carbone au niveau de la plante entière soit présumément lié plus étroitement à la croissance et à la survie d'une espèce que la photosynthèse foliaire, il est encore assez éloigné du succès écologique d'une espèce.

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M. Beaudet, C. Messier,[1] D.W. Hilbert,[2] and E. Lo. Groupe de recherche en écologie forestière interuniversitaire (GREFi), Département des sciences biologiques, Université du Québec à Montréal, P.O. Box 8888, Centre-ville Branch, Montréal, QC H3C 3P8, Canada.
Z.M. Wang and M.J. Lechowicz. GREFi, Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montréal, QC H3A 1B1, Canada.

[1]Corresponding author. e-mail: messier.christian@uqam.ca
[2]Current address: Tropical Forest Research Centre, Commonwealth Scientific and Industrial Research Organisation, Division of Wildlife and Ecology, P.O. Box 780, Atherton QLD 4883, Australia.

Introduction

In the temperate deciduous forests of eastern North America, canopy gap formation is a major factor affecting forest dynamics (Runkle 1985). Canopy openings can result from a variety of natural causes (e.g., ice storm damage, branch- and tree-falls, etc.) as well as from silvicultural practices (e.g., selection cutting). Canopy gaps affect several environmental conditions in the understory, one of the most obvious consequences being to locally and temporarily increase light availability (Canham et al. 1990).

Tree seedlings can respond to this variability of light conditions by modifying several traits important for effective light capture and utilization, including leaf biochemistry, morphology, and physiology (Boardman 1977; Bazzaz 1979; Björkman 1981), as well as plant-level features such as the pattern of biomass allocation and crown architecture (Canham 1988; Küppers 1989, 1994; Givnish 1995). Tree species differ in their pattern of response to this light gradient. Such interspecific differences in patterns of light utilization can have significant implications for forest dynamics and have been suggested to be a factor that could explain the coexistence of species in forest ecosystems (Denslow 1985; Canham 1989; Sipe and Bazzaz 1995; Zipperlen and Press 1996; Barker et al. 1997).

Several studies on species adaptation to sun and shade have focused on the photosynthetic response of leaves (e.g., Björkman 1981; Bazzaz and Carlson 1982; Pearcy 1987; Walters and Field 1987; Chazdon 1992; Ellsworth and Reich 1992a; Kamaluddin and Grace 1993; Barker et al. 1997; Gill et al. 1998). It has been shown that photosynthetic capacity (A_{max}) and light saturation and compensation points generally increase in response to increased light availability (Bazzaz and Carlson 1982; Pearcy 1987; Di Benedetto and Cogliatti 1990; Ellsworth and Reich 1992a; Kamaluddin and Grace 1993). Comparisons among species indicated that early successional species generally have higher photosynthetic rates than late-successional ones (Boardman 1977; Bazzaz 1979; Björkman 1981; Amthor et al. 1990; Reich et al. 1995). A number of studies also reported a higher degree of photosynthetic plasticity in early compared with late-successional species (Bazzaz and Carlson 1982; Strauss-Debenedetti and Bazzaz 1991; Chazdon 1992; Chazdon and Kaufmann 1993; Bazzaz and Wayne 1994; Ducrey 1994; Huante and Rincón 1998). This higher degree of photosynthetic plasticity in early successional species has been suggested to be an adaptive response to a higher degree of environmental variability in early successional habitats (Bazzaz 1979; Bazzaz and Wayne 1994). Other studies, however, found no relationship between the degree of physiological plasticity of the species and their successional status (Turnbull 1991; Abrams and Mostoller 1995).

Although photosynthesis is a physiological process of primary importance for plants, it is many steps removed from the ecological success of a species. Therefore, shade tolerance and distribution patterns of species often cannot be accurately predicted from leaf-level photosynthesis alone (Field 1988; Matthes-Sears and Larson 1990; Küppers 1994; Sipe and Bazzaz 1994). Plant-level carbon gain is presumably more closely related to plant growth and survival than leaf-level carbon gain, since it also includes the effects of plant-level characteristics such as patterns of biomass allocation and crown architecture (Givnish 1988; Walters et al. 1993a, 1993b; Kitajima 1994; Küppers 1994; Pearcy and Sims 1994; Sipe and Bazzaz 1994).

Several plant-level characteristics should be taken into account to scale up from leaf- to plant-level carbon gain, including the leaf area ratio (LAR) and a number of crown structural features (Ellsworth and Reich 1993; Pearcy and Yang 1996). The LAR is known to be a major determinant of growth that varies both among species and in response to variations in light availability (Lambers and Poorter 1992; Walters et al. 1993a, 1993b; Pearcy and Sims 1994). The LAR is generally higher in intolerant compared with tolerant species and under shade compared with high-light conditions (Popma and Bongers 1988; Kamaluddin and Grace 1993; Walters et al. 1993a; Kitajima 1994; Pearcy and Sims 1994). Crown architecture also plays an important role in plant-level carbon gain, primarily through its effect on light interception by leaves (Chazdon 1985; Canham 1988; Kohyama 1991; Pearcy and Yang 1996). Many studies have shown the importance of taking into account the spatial distribution of leaves and gradients of light availability within the crown for estimating plant-level carbon gain (e.g., Caldwell et al. 1986; Ellsworth and Reich 1993). Presumably, interspecific variations in such plant-level structural features, through their effects on plant-level carbon gain, will influence the differential performance of species along the gap–understory gradient (Canham 1988; Sipe and Bazzaz 1994; Givnish 1995; Pearcy and Yang 1996).

In this study, we compared the leaf- and plant-level carbon gain of yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), and beech (*Fagus grandifolia* Ehrh.) seedlings growing under two contrasting forest light regimes: under a closed canopy and canopy gaps. The three species differ in shade tolerance with yellow birch being a moderately tolerant species (Baker 1949; Erdmann 1990) and sugar maple and beech being both very shade tolerant (Godman et al. 1990; Tubbs and Houston 1990). A more detailed description of the study species is provided in the Methods section. Our first objective was to characterize the photosynthetic-light response of the three species in the two forest light regimes. Although the photosynthetic-light response of these three species has been studied by Amthor et al. (1990) in a clearcut site, to our knowledge there has been no study to date that compared the photosynthetic response of these species under contrasting forest light regimes. The hypothesis for our first objective was that the less tolerant species (yellow birch) would have a higher photosynthetic capacity and would be more plastic across forest light environments than the more shade-tolerant species (sugar maple and beech). Our second objective was to estimate plant-level daily carbon gain in seedlings of the three study species in the two light environments based on their leaf-level photosynthetic-light response and on plant-level characteristics such as the LAR, the pattern of distribution of leaf area in the crown (i.e., the fraction of total leaf area in different crown layers), and the pattern of light transmission within the crown. We also determined the confidence intervals around our carbon gain estimates to test for significant differences in carbon gain among species and between light environments. The hypotheses for the carbon

gain estimates were that (*i*) the less tolerant species (yellow birch) would be more responsive to the increase in light availability from the shade to the gap environment, (*ii*) yellow birch would have a higher plant-level daily carbon gain than the other two species under canopy gaps, and (*iii*) the two shade-tolerant species (sugar maple and beech) would have a higher plant-level carbon gain than yellow birch under a closed canopy.

Methods

Study species

The three study species co-occur in the sugar maple – yellow birch – beech forest type. Yellow birch is thought to be too intolerant to rely on advanced regeneration (Forcier 1975; White et al. 1985). Yellow birch seedlings require small- to medium-size gaps to reach the canopy (Payette et al. 1990; Seymour 1994). Under canopy gaps, yellow birch seedlings have greater height growth rates than sugar maple and beech (Beaudet and Messier 1998). Sugar maple and beech can persist in the understory for long periods of time and still maintain their ability to respond to canopy openings with relatively rapid growth (Canham 1985, 1989, 1990). Under low-light conditions, beech generally has a greater height growth rate (Canham 1988; Beaudet and Messier 1998) and greater survival (Forcier 1975; Kobe et al. 1995) than sugar maple.

Study area, seedlings, and forest light environment

This study was conducted in a sugar maple – yellow birch – beech stand at the Duchesnay Experimental Forest, near Québec (46°55′N, 71°40′W), Canada. The study area is located at an elevation of 200–300 m, on a moderate south-facing slope (5–10°), and has a moder humus form, a humo-ferric podzol soil, and is underlain with well-drained glacial till. Mean annual precipitation is 1200 mm, and mean daily temperatures range from –12.8°C in January to 18.3°C in July (Environment Canada 1982).

Part of the stand was subjected to a selection cut of hardwood species in the fall of 1989. Approximately 30% of the basal area was harvested through a mix of single- and multiple-tree selection that created several canopy gaps ranging in size from approximately 50 to 300 m^2. In 1993, five study plots were established in this stand under two contrasting forest light environments: three plots (approximately 10 m × 10 m) were established under canopy gaps and two plots (approximately 15 m × 15 m) were established under a closed canopy (hereafter referred to as the gap and shade environment, respectively).

Yellow birch, sugar maple, and beech seedlings 0.5–2 m in height were selected in each study plot. Selected individuals were not of stump-sprout origin and were dominant compared with the surrounding understory vegetation. For beech, we did not distinguish between individuals of seed and root sprout origin. A total of 10 and 15 seedlings per species were tagged in the gap and shade environment, respectively.

Light availability above these seedlings was evaluated using the method described in Parent and Messier (1996). These authors have shown that an instantaneous measurement of the percentage of above-canopy PPFD (photosynthetic photon flux density, 400–700 nm) taken under overcast sky conditions is an accurate estimate of the mean daily %PPFD reaching a location in the understory under both clear and overcast conditions. Light measurements were taken in July 1993. Above-canopy PPFD (PPFD$_0$) was measured using a point quantum sensor (LI-190SA, LI-COR, Lincoln, Neb.) installed in an open area near the study site. This sensor was linked to a datalogger (LI-1000, LI-COR, Lincoln, Neb.) which recorded 1-min averages of readings taken every 5 s.

A second quantum sensor was used to measure PPFD above each seedling (PPFD$_s$). The time of each measurement was recorded and %PPFD above each seedling was calculated as (PPFD$_s$/PPFD$_0$) × 100, where PPFD$_0$ and PPFD$_s$ were PPFD values recorded at the same time (±1 min). Percent PPFD above the seedlings ranged from 1 to 8% in the shade plots (mean 3%, hereafter referred to as percent of above-canopy light in the shade: PACL$_{SHADE}$) and from 12 to 40% in the gap plots (mean 25%, hereafter referred to as percent of above-canopy light in the gap: PACL$_{GAP}$).

Field gas-exchange measurements

Field gas-exchange measurements were made on previously tagged yellow birch, sugar maple, and beech seedlings located in the study plots. Our goal was to collect gas-exchange data under a wide range of light intensities to obtain photosynthesis light response curves for each species, in each of the two forest light environments. Since an artificial light source was not available in the field, measurements were made under natural light conditions.

Measurements were made on 5 days in 1993 (August 8, 10, 16, 18, and 19) and 5 days in 1994 (July 11, 12, 14, 15, and 29) between 09:00 and 17:30 eastern standard time (EST), under mostly clear sky conditions. We used a LI-6200 portable gas-exchange measurement system (LI-COR, Lincoln, Neb.) equipped with a 1-L leaf chamber. The LI-6200 infrared gas analyser (IRGA) was calibrated on each measurement day with a span gas of known CO$_2$ concentration. The IRGA and the flow meter were zeroed several times during the day. Measurements were made under ambient CO$_2$ concentration, temperature, and humidity. During measurements, vapor pressure in the leaf chamber was maintained approximately constant at ambient level by adjusting the rate of air flowing through a desiccant tube of magnesium perchlorate. During measurements, the mean CO$_2$ concentration in the leaf chamber was 349.0 ± 0.6 ppm (mean ± SE) and 339.8 ± 1.2 ppm, leaf temperature was 23.2 ± 0.2°C and 24.2 ± 0.3°C, and relative humidity was 52.7 ± 1.1% and 63.1 ± 0.6% for measurements taken in the shade and gap environments, respectively.

Gas-exchange measurements were made on leaves that had been exposed to a given light intensity for at least 10 min prior to measurement. The typical sampling scheme was to take two measurements per seedling (each on a different leaf) and to sample seedlings of all three species alternately. A given seedling was generally selected for measurements at two or three occasions during the day, depending on variations in the light conditions. Measurements were made on healthy and fully developed leaves. During measurements, leaves were kept as close to their natural position as possible. Incident PPFD was measured using a point quantum sensor (LI-190SA, LI-COR, Lincoln, Neb.) attached to the leaf chamber in the same plane as the leaf. A total of 339 gas exchange measurements were made in 1993 and 1994.
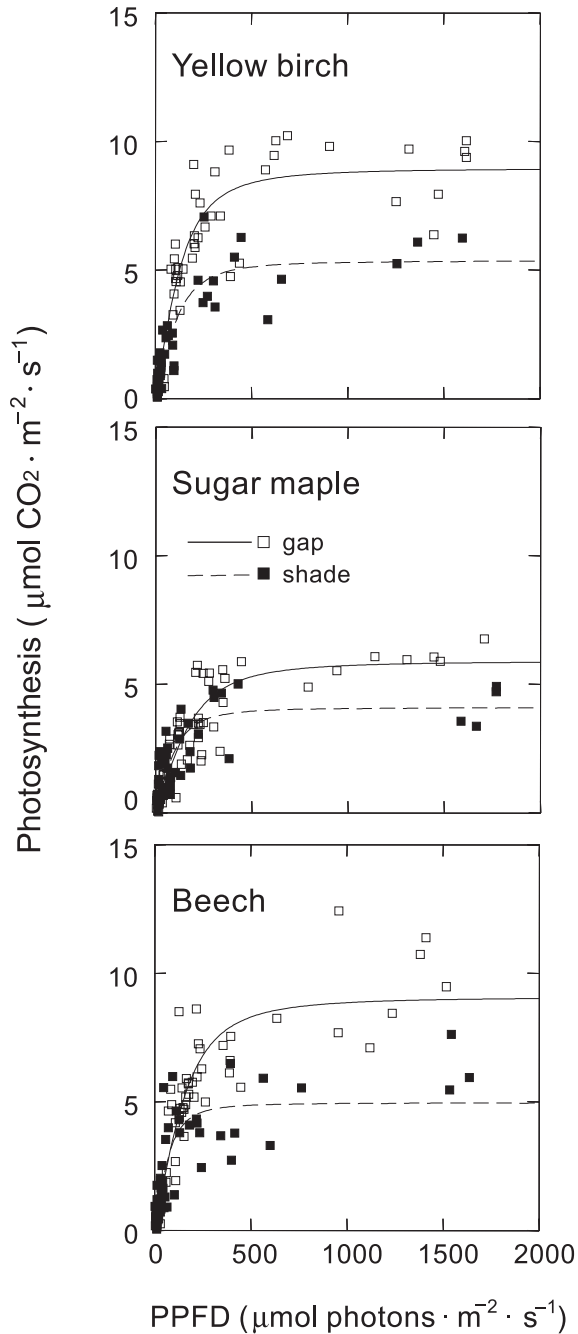
Analysis of photosynthesis data

Gas-exchange data were sorted by species and forest light environment, yielding six data sets. To describe the photosynthetic light response of each species in each light environment, a nonrectangular hyperbolic function was fitted to the data to estimate the value of parameters A_{max} and α (Weber et al. 1985):

$$[1] \qquad A = \frac{\alpha L A_{max}}{\sqrt{A_{max}^2 + (\alpha^2 L^2)}}$$

where A (μmol CO$_2$·m^{-2}·s^{-1}) is the photosynthetic rate, α (mol CO$_2$/mol photons) is the initial slope of A in response to light availability (apparent quantum yield efficiency), L (μmol photons·m^{-2}·s^{-1}) is the incident light intensity during measurement, and A_{max} is the light-saturated photosynthetic rate. For each of the

Fig. 1. Photosynthesis light response curves for yellow birch, sugar maple, and beech seedlings growing under a closed canopy (shade: solid symbols and broken line) and under canopy gaps (gap: open symbols and solid line). Fitted regression lines are of the form described in eq. 1. Values of parameters A_{max} and α are presented in Table 1. For yellow birch in shade $R^2 = 0.844$, in gaps $R^2 = 0.722$; for sugar maple in shade $R^2 = 0.690$, in gaps $R^2 = 0.731$; for beech in shade $R^2 = 0.734$, in gaps $R^2 = 0.746$.

Estimation of plant-level daily carbon gain

We estimated the daily carbon gain for a theoretical seedling of each species in each forest light environment. The modeled seedlings had a 50-g aboveground dry mass. The daily carbon gain estimation was based on the following assumptions: (*i*) light availability was considered to be the single most important environmental factor driving photosynthesis, and possible limitations by other environmental factors such as temperature, atmospheric water vapor deficit, and soil water conditions were not considered; (*ii*) the crown of the modeled seedlings was described as being composed of three horizontal layers of equal thickness; (*iii*) the leaves in each crown layer all shared the same photosynthetic characteristics; (*iv*) light availability was homogeneous within each crown layer; and (*v*) photosynthetic induction caused by rapid fluctuations of light (i.e., sunflecks) was not considered.

The data required for estimation of daily carbon gain included (*i*) the photosynthetic-light response of leaves; (*ii*) several diurnal courses of PPFD in the shade and gap environments; (*iii*) the total leaf area in the crown of a 50-g seedling; (*iv*) the vertical pattern of leaf area distribution within the crown; and (*v*) the pattern of light attenuation within the crown.

The photosynthetic-light response of leaves was determined for each species and forest light environment as described previously (results in Fig. 1 and Table 1). Six different diurnal courses of PPFD were obtained in each of the shade and gap environment. These six different diurnal courses per light environment came from PPFD measurements made at three different locations and two different dates in each of the shade and gap environments. PPFD measurements were made under mostly clear sky conditions using a quantum sensor (LI-190SA, LI-COR, Lincoln, Neb.) installed 1.5 m aboveground and linked to a datalogger (LI-1000, LI-COR, Lincoln, Neb.), which recorded 2-min averages of measurements taken every 5 s (examples of results in Fig. 2). Hereafter, the 2-min PPFD averages will be referred to as above-seedling light during time interval INT (ASL_{INT}).

The total leaf area (LA_T) in the crown of a 50-g seedling was calculated for each species and light environment from allometric equations of LA_T as a function of aboveground dry mass, based on data in Beaudet (1994) (see Appendix 1).

The vertical patterns of leaf area distribution and light attenuation in the crown were obtained from Messier and Nikinmaa (2000). They measured seedlings of similar size as ours and growing in the same light environments as described above ($n = 5–10$ per species and light regime). For each seedling, light availability (PPFD) was simultaneously measured above the seedling and at the center of the upper, middle, and lower third of the crown to determine the fraction of above-seedling light transmitted to the center of each crown layer ($FASL_{CL}$) (results in Table 2). Light measurements were made under overcast sky conditions with a point quantum sensor (LI-190SA, LI-COR, Lincoln, Neb.). The seedlings were brought back to the laboratory where leaves from each crown layer were removed, dried, and weighed. The total leaf area in each crown layer was obtained by multiplying the leaf dry mass by the specific leaf area (leaf area per unit dry mass), which had previously been determined for a subsample of leaves. The fraction of leaf area in each crown layer (FLA_{CL}) was calculated from these measurements (results in Table 2).
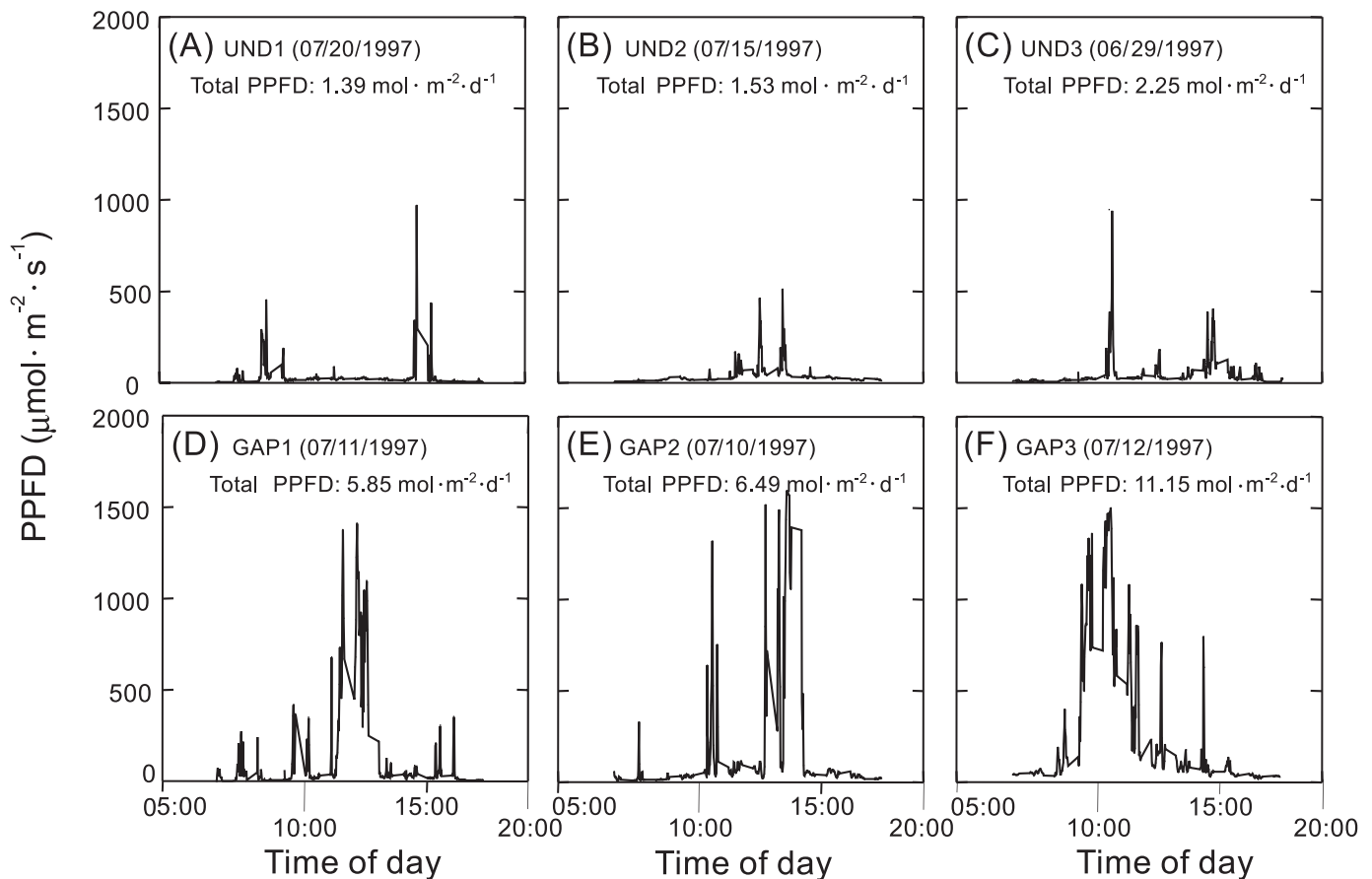
The detailed calculations used to estimate the daily carbon gain are presented in Appendix 2 and the variables name, units, and description are listed in Table 3. In summary, carbon gain was calculated for each crown layer over 2-min intervals for an entire day. We assumed that light availability was constant within a crown layer for each 2-min interval. Carbon gain for each crown layer in a 2-min interval was simply the product of the instantaneous unit-area photosynthetic rate, the leaf area in that crown layer, and time (120 s). Plant-level daily carbon gain was calculated by summing the results from all three crown layers and every 2-min interval

six data sets, we estimated the parameters A_{max} and α and their 95% confidence interval by parametric (least squares fit of the nonlinear equation) and bootstrap (resampling with replacement 850 times for each data set) methods. Since both methods yielded very similar results, we only present the values obtained from the parametric estimation.

Table 1. Light saturated photosynthetic rate (A_{max}, $\mu mol \cdot m^{-2} \cdot s^{-1}$) and quantum yield efficiency (α, $mol \cdot mol^{-1}$) values obtained from field gas-exchange measurements on yellow birch, sugar maple, and beech seedlings growing under a closed canopy (shade) and canopy gaps (gap).

	Yellow birch		Sugar maple		Beech	
	Shade	Gap	Shade	Gap	Shade	Gap
n	63	42	64	50	72	48
A_{max}	5.36±0.28*b*	8.95±0.37*c*	4.09±0.30*a*	5.89±0.35*b*	4.96±0.30*ab*	9.07±0.48*c*
α	0.034±0.004*abc*	0.048±0.004*c*	0.030±0.004*ab*	0.024±0.002*a*	0.049±0.006*c*	0.041±0.003*bc*

Note: Values of A_{max} and α are estimates ± 1SE from eq. 1. Within rows, values with the same letter have overlapping 95% confidence intervals and are, therefore, not significantly different ($P > 0.05$). n, number of gas-exchange measurements.

Fig. 2. Examples of daily course of PPFD obtained at three different microsites under a closed canopy (UND1–UND3) and three different microsites located under small canopy gaps (GAP1–GAP3). Light measurements were taken at a height of 1.5 m, from 07:30 to 18:30, under mostly clear sky conditions. Values of 2-min average PPFD were used in the calculation of daily carbon gain and are referred to as above-seedling light during time interval INT (ASL_{INT}).

over an entire day. Daily carbon gain was then either expressed as whole-plant carbon gain (C_W), or per unit of leaf area (C_A).

We calculated the 95% confidence intervals for each of the carbon gain values. These confidence intervals result from the propagation of measurement and statistical uncertainties in the field data and were calculated using a first-order uncertainty analysis technique described in Appendix 3.

Statistical analysis

Differences in A_{max}, α, LA_T, C_A, and C_W among species and light environments were tested for significance based on the 95% confidence interval around the estimated values. Two values with nonoverlapping 95% confidence intervals were considered to be significantly different at $P < 0.05$. For A_{max} and α, the confidence intervals were obtained, as described previously, from least-squares nonlinear parametric estimation in SYSTAT (version 7.0). For LA_T, the standard error around the LA_T value corresponding to a dry mass of 50 g was obtained from SAS, using the procedure REG with the option /CLI. The upper and lower limits of the 95% confidence interval were calculated as the mean ± 1.96SE (Sokal and Rohlf 1981). For C_A and C_W, the error around the estimated values was calculated using the procedure described in Appendix 3. The upper and lower limits of the 95% confidence intervals around the carbon gain estimates were calculated as the carbon gain estimate ± 1.96SE (Sokal and Rohlf 1981). For FLA_{CL} and $FASL_{CL}$, a three-way analysis of variance (ANOVA) was used on rank-transformed data to test for the effect of species, light

Table 2. Total leaf area (LA_T) in the crown of a 50-g (aboveground dry mass) seedling, leaf area ratio (LAR), fraction of total leaf area in each crown layer (FLA_{CL}), and fraction of above-seedling light in each crown layer ($FASL_{CL}$) for yellow birch, sugar maple, and beech seedlings growing under two contrasting forest light regimes.

	Yellow birch		Sugar maple		Beech	
	Shade	Gap	Shade	Gap	Shade	Gap
LA_T (m²)*	0.450±0.029*d*	0.381±0.011*cd*	0.384±0.011*cd*	0.320±0.009*b*	0.365±0.008*c*	0.271±0.013*a*
LAR (m²·g⁻¹)†	0.0090	0.0076	0.0077	0.0064	0.0073	0.0054
FLA_{CL}‡						
Upper CL	0.19±0.04	0.27±0.10	0.21±0.04	0.28±0.05	0.23±0.05	0.22±0.06
Middle CL	0.35±0.07	0.36±0.07	0.49±0.07	0.32±0.04	0.42±0.04	0.39±0.05
Lower CL	0.46±0.05	0.36±0.05	0.31±0.05	0.41±0.06	0.36±0.05	0.39±0.06
$FASL_{CL}$‡						
Upper CL	0.95±0.15	0.90±0.07	0.86±0.07	0.86±0.05	0.78±0.05	0.70±0.08
Middle CL	0.79±0.08	0.37±0.07	0.79±0.07	0.44±0.07	0.65±0.03	0.51±0.12
Lower CL	0.66±0.14	0.19±0.08	0.53±0.05	0.15±0.04	0.62±0.09	0.20±0.06

Note: Values are means ± SE. CL, crown layer.

*Values of LA_T were calculated from allometric equations between LA_T and aboveground dry mass from data in Beaudet (1994) (Appendix 1). Values with the same letter are not significantly different ($P > 0.05$).

†LAR is LA_T/aboveground dry mass (i.e., 50 g).

‡From Messier and Nikinmaa (2000).

environment, and crown layer (and their interactions). Rank transformation was used because untransformed and arcsine-transformed data did not meet the normality assumption (Potvin and Roff 1993).

Results and discussion

Leaf-level photosynthetic-light response

Differences of leaf-level photosynthetic response among species and light environments have been the focus of several studies (e.g., Wallace and Dunn 1980; Björkman 1981; Bazzaz and Carlson 1982; Pearcy 1987; Walters and Field 1987; Chazdon 1992; Ellsworth and Reich 1992a; Kamaluddin and Grace 1993; Barker et al. 1997; Gill et al. 1998). These studies addressed a number of questions, including the following:

(1) How is the photosynthetic-light response affected by changes in light availability in the growth environment for a given species?

(2) How do species of different shade tolerance differ in terms of photosynthetic response in a given light environment?

(3) How do species of different shade tolerance differ in terms of photosynthetic plasticity when grown under different light environments?

In relation to the first question, our results showed that, for each of the three species, the photosynthetic-light response differed between forest light environments (Fig. 1). The light saturation point increased from approximately 400 μmol photons·m⁻²·s⁻¹ in the shade to 600–700 μmol photons·m⁻²·s⁻¹ in the gap environment (Fig. 1), and all three species had significantly higher A_{max} values in the gap than in the shade environment (Table 1). The A_{max} of yellow birch increased from 5.36 μmol CO_2·m⁻²·s⁻¹ in shade (Table 1), a value close to that observed by Walters et al. (1993a) in a similar light environment, to 8.95 μmol CO_2·m⁻²·s⁻¹ in gaps (Table 1), a value which is in the same range as values reported elsewhere (Amthor et al. 1990; Walters et al. 1993a; Wayne and Bazzaz 1993a, 1993b). The A_{max} of sugar maple increased from 4.09 μmol CO_2·m⁻²·s⁻¹ in shade to 5.89 μmol CO_2·m⁻²·s⁻¹ in gaps (Table 1); both values were slightly higher than generally reported in the literature (Weber et al. 1985; Jurik et al. 1988; Amthor et al. 1990; Matthes-Sears and Larson 1990; Ellsworth and Reich 1992a, 1992b; Walters et al. 1993a; Sipe and Bazzaz 1994; Lei and Lechowicz 1997a, 1997b; Gill et al. 1998) but lower than values obtained by Ellsworth and Reich (1993). The A_{max} of beech increased from 4.96 μmol CO_2·m⁻²·s⁻¹ in shade, a value which is within the range of values observed by Teskey and Shrestha (1985) and Jurik et al. (1988), to 9.07 μmol CO_2·m⁻²·s⁻¹ in gaps, a value higher than previously reported (Teskey and Shrestha 1985; Jurik et al. 1988; Amthor et al. 1990). Although we did not observe any significant difference of apparent quantum yield efficiency (α) between the two light environments for any species (Table 1), the increases in light saturation point and A_{max} are in agreement with the typical sun–shade response of photosynthesis (Bazzaz and Carlson 1982; Pearcy 1987; Kitajima 1994; Ellsworth and Reich 1992a).

In relation to the second and third questions, a number of studies indicated that early successional species generally have a higher photosynthetic capacity and a greater photosynthetic plasticity than late-successional species (e.g., Boardman 1977; Bazzaz 1979; Bazzaz and Carlson 1982; Björkman 1981; Amthor et al. 1990; Strauss-Debenedetti and Bazzaz 1991; Chazdon 1992; Chazdon and Kaufmann 1993; Ducrey 1994; Reich et al. 1995; Huante and Rincón 1998). Other studies, however, found no relationship between the degree of photosynthetic plasticity and the successional status of the species (Turnbull 1991; Abrams and Mostoller 1995). Our results do not agree with the prediction that the photosynthetic capacity and photosynthetic plasticity should be lower in shade-tolerant species (Bazzaz 1979; Bazzaz and Carlson 1982). In terms of photosynthetic capacity, yellow birch and beech had similar A_{max} values (Table 1), although these two species are generally considered to be the least and the most shade tolerant of our three study species (Baker 1949). In terms of photosynthetic plasticity, beech was

Table 3. List of symbols, units, and definitions for the variables used in the calculation of daily carbon gain.

Symbol	Units	Definition	From
C_A	mmol CO_2·m^{-2} per day	Daily carbon gain per unit leaf area	Equation A1
C_W	mmol CO_2 per day	Whole-plant daily carbon gain	Equation A2
LA_T	m^2	Total leaf area in the crown of a 50-g seedling	Table 2 and Appendix 1
$C_{CL,INT}$	µmol CO_2/30 min	Carbon gain of crown layer CL during time interval INT	Equation A3
$A_{CL,INT}$	µmol CO_2·m^{-2}·s^{-1}	Unit area photosynthetic rate of leaves in crown layer CL during time interval INT	Equation A4
FLA_{CL}		Fraction of LA_T in crown layer CL	Table 2
$L_{CL,INT}$	µmol photons·m^{-2}·s^{-1}	Light availability in crown layer CL during time interval INT	Equation A5
ASL_{INT}	µmol photons·m^{-2}·s^{-1}	Above-seedling light during time interval INT	Fig. 2
$FASL_{CL}$		Fraction of above-seedling light in crown layer CL	Table 2
$A_{max,ADJ,CL}$	µmol CO_2·m^{-2}·s^{-1}	A_{max} adjusted for light conditions in crown layer CL	Equation A6
$\alpha_{ADJ,CL}$	mol CO_2/mol photons	α adjusted for light conditions in crown layer CL	Equation A7
$A_{max,GAP}$	µmol CO_2·m^{-2}·s^{-1}	Parameter A_{max} of the photosynthesis light response curve in the gap environment	Table 1
$A_{max,SHADE}$	µmol CO_2·m^{-2}·s^{-1}	Parameter A_{max} of the photosynthesis light response curve in the shade environment	Table 1
α_{GAP}	mol CO_2/mol photons	Parameter α of the photosynthesis light response curve in the gap environment	Table 1
α_{SHADE}	mol CO_2/mol photons	Parameter α of the photosynthesis light response curve in the shade environment	Table 1
$PACL_{GAP}$	%	Percent of above-canopy light in the gap environment	In text
$PACL_{SHADE}$	%	Percent of above-canopy light in the shade environment	In text
$PACL_{CL}$	%	Percent of above-canopy light in crown layer CL	Equation A8
$PACL_{ENV}$	%	Percent of above-canopy light in the light environment of the seedling, where ENV is either gap or shade	In text

Note: Variables without units are dimensionless. CL, crown layer; INT, half hour time interval; ADJ, adjusted value.

the most responsive species to increased light availability from the shade to the gaps. The A_{max} of beech in gaps was 83% higher than in shade, while the A_{max} of yellow birch and sugar maple in gaps were, respectively, 67 and 44% higher than in shade (Table 1). Our results suggest that the trend of decreasing photosynthetic plasticity with increasing shade tolerance hypothesized for successional gradients from open field to forest understory conditions (Bazzaz 1979) and observed across species ranging from early successional annuals to late-successional tree species (Bazzaz and Carlson 1982), may not appear as clearly, or may not hold, when comparisons are made among a few late-successional species. Our results also suggest that leaf-level photosynthetic characteristics alone may be of limited use in elucidating the determinants of shade tolerance (Field 1988; Küppers 1994; Henry and Aarssen 1997). Photosynthetic characteristics are several steps removed from whole-plant carbon gain, since the effect of leaf-level characteristics on plant-level carbon gain is mediated by several plant-level characteristics, including the pattern of biomass allocation and the crown architecture (Canham and Marks 1985; Körner 1991; Küppers 1994).

Unit-area and plant-level daily carbon gain

The diurnal courses of PPFD used for carbon gain simulations (examples in Fig. 2) ranged in cumulative PPFD from 1.22 to 2.55 mol photons·m^{-2} per day in the shade environment and from 3.27 to 14.98 mol photons·m^{-2} per day in the gap environment (Table 4). On average for the sampled microsites and days, the total daily PPFD was nearly five times higher in the gap than in the shade environment (8.38 vs. 1.79 mol photons·m^{-2} per day; Table 4). However, the variation in carbon gain between forest light environments was less extensive than the variation in total daily PPFD, as observed by Chazdon et al. (1996) and Barker et al. (1997). The values of C_A were only 1.6 to 1.8 times greater in gaps than in shade, and C_W did not differ significantly between the two light environments (Table 4). Several factors could explain this discrepancy between the magnitude of the variation in total PPFD and carbon gain. First, light availability in gaps (Figs. 2D, 2E, and 2F) often exceeded light saturation, which occured between 600 and 700 µmol photons·m^{-2}·s^{-1} (Fig. 1) in these relatively shade-tolerant species. It is well known that the relationship between total PPFD and carbon gain is not necessarily linear because of the saturation response of photosynthesis (Pearcy and Yang 1996). Second, seedlings in gaps generally had a lower LAR than those in shade (Table 2). Such a decrease in LAR, often observed in response to high light intensity (Logan 1970; Kamaluddin and Grace 1993; Walters et al. 1993a; Kitajima 1994; Pearcy and Sims 1994), partly offsets the increased rate of carbon assimilation per unit leaf area observed under higher light regimes. Third, light attenuation

Table 4. Daily carbon gain per unit leaf area (C_A) and whole-plant daily carbon gain (C_W) estimated for yellow birch, sugar maple, and beech seedlings on two different dates for each of three different locations in the understory of a closed canopy stand (UND1 to UND3) and three different locations under canopy gaps (GAP1 to GAP3).

Shade						Gap					
Site	Date	Total PPFD	Yellow birch	Sugar maple	Beech	Site	Date	Total PPFD	Yellow birch	Sugar maple	Beech
C_A (mmol CO$_2$/m^2 per day)											
UND1	07/15/1997	1.22	25.9±3.5	21.8±2.6	31.7±3.5	GAP1	07/10/1997	3.27	36.7±5.9	27.7±3.3	43.7±5.8
UND1	07/20/1997	1.39	27.3±3.3	22.4±2.3	32.0±3.1	GAP1	07/11/1997	5.85	50.4±6.6	36.8±3.5	56.0±5.7
UND2	06/29/1997	2.43	44.7±4.8	35.8±3.2	50.4±4.2	GAP2	07/10/1997	6.49	50.9±6.7	36.5±3.4	55.9±5.9
UND2	07/15/1997	1.53	33.4±4.4	27.8±3.2	40.2±4.2	GAP2	07/11/1997	8.49	58.9±6.8	42.7±3.6	63.6±5.7
UND3	06/29/1997	2.25	45.3±5.4	36.9±3.8	52.8±5.0	GAP3	07/11/1997	14.98	106.6±12.1	72.5±5.5	110.1±9.3
UND3	07/15/1997	1.89	39.7±4.9	32.4±3.5	46.8±4.7	GAP3	07/12/1997	11.15	92.4±11.8	62.9±5.3	97.2±9.3
Mean			36.1±4.4*ab*	29.5±3.1*a*	42.3±4.1*abc*				66.0±8.2*cd*	46.5±4.1*bc*	71.1±6.9*d*
C_W (mmol CO$_2$ per day)											
UND1	07/15/1997	1.22	11.7±1.7	8.4±1.0	11.6±1.3	GAP1	07/10/1997	3.27	13.9±2.2	8.8±1.1	11.8±1.7
UND1	07/20/1997	1.39	12.3±1.7	8.6±0.9	11.7±1.2	GAP1	07/11/1997	5.85	19.2±2.6	11.7±1.2	15.2±1.7
UND2	06/29/1997	2.43	20.1±2.5	13.8±1.3	18.4±1.6	GAP2	07/10/1997	6.49	19.4±2.6	11.7±1.1	15.1±1.8
UND2	07/15/1997	1.53	15.0±2.2	10.7±1.2	14.7±1.6	GAP2	07/11/1997	8.49	22.4±2.7	13.6±1.2	17.2±1.8
UND3	06/29/1997	2.25	20.4±2.8	14.2±1.5	19.3±1.9	GAP3	07/11/1997	14.98	40.6±4.8	23.2±1.9	29.8±2.9
UND3	07/15/1997	1.89	17.9±2.5	12.5±1.4	17.1±1.7	GAP3	07/12/1997	11.15	35.2±4.6	20.1±1.8	26.3±2.8
Mean			16.2±2.2*abc*	11.3±1.2*a*	15.5±1.5*abc*				25.1±3.2*c*	14.9±1.4*ab*	19.2±2.1*bc*

Note: Carbon gain ± 1SE. The total cumulative PPFD (mol·m^{-2} per day) of the daily course of PPFD is presented for each combination of site and date. Within rows mean values C_A and C_W with the same letter are not significantly different ($P > 0.05$).

within the crown was more pronounced in seedlings from the gap than from the shade environment ($P < 0.001$ for the interaction between crown layer and light environment). Only 15–20% of above-seedling light reached the lower third of the crown in gap seedlings compared with 53–66% in shade seedlings (Table 2).

Our unit-area daily carbon gain estimates (C_A; Table 4) were in the same range as previously reported values for yellow birch and sugar maple (Weber et al. 1985; Ellsworth and Reich 1992*a*, 1993; Wayne and Bazzaz 1993*a*). The C_A values were significantly higher in the gap than in the shade environment for all three species (Table 4). For yellow birch, C_A was 1.8 times higher in the gap than in shade, while it was 1.7 and 1.6 times higher for beech and sugar maple, respectively (Table 4). In the shade environment, C_A did not differ significantly among species (Table 4). In the gap environment, beech had the highest C_A, followed by yellow birch and sugar maple, but only beech and maple were significantly different (Table 4).

C_W is presumably more closely related to seedling growth and survival than C_A, since differences of LAR (i.e., LA_T for an aboveground dry mass of 50 g) between species and light environments are also taken into account to estimate C_W. However, C_W did not differ significantly between the shade and the gap environment for any of the three species (Table 4). In the shade, C_W did not differ significantly among species (Table 4). In the gaps, birch had the highest C_W, followed by beech and sugar maple, but only birch and maple were significantly different (Table 4).

According to the prevailing model of shade tolerance, which is mainly based on carbon economy (Matthes-Sears and Larson 1990; DeLucia et al. 1998), we would expect (*i*) the more shade-tolerant species (sugar maple and beech) to have higher whole-plant net carbon gain than the less tolerant species (yellow birch) in shade, and (*ii*) the less tolerant species to have a higher whole-plant net carbon gain than more tolerant species in gaps. In shade, we did not observe any significant difference of C_W among the three species. Note that the C_W values do not take into account the respiration of nonphotosynthetic tissue and are therefore estimates of gross carbon gain. Interspecific differences in respiration rates could contribute to differentiate the species in terms of net carbon gain. Reid and Strain (1994), for instance, observed that beech had a lower ratio of carbon uptake over carbon losses to respiration than sugar maple. Also, possible differences among species in terms of biomass allocation to roots could affect plant-level net carbon gain and differentiate species in shade. A higher biomass allocation to roots in more shade-tolerant species was observed in shade in sugar maple compared with yellow birch (Logan 1965).

In gaps, the rank order of the species for C_W was the same as observed for height growth rates among these three species growing in gaps (Beaudet and Messier 1998). The higher C_W of yellow birch compared with sugar maple, in gaps, is in agreement with the prediction that less tolerant species should have a higher carbon gain than more tolerant species in gaps. However, beech also had a relatively high C_W in gaps, a C_W value that was not significantly different from that of birch. Therefore, when the C_W values for all three species are considered simultaneously, our results do not agree with the predictions that shade-tolerant species should have a higher plant-level carbon gain in shade (compared with less tolerant species) and that less tolerant species should have a higher carbon gain in gaps (compared with more tolerant species).

Although whole-plant carbon gain is presumably more closely related to growth and survival of a species than leaf-level photosynthesis alone, it is still many steps removed from the ecological success of a species. Sugar maple, for instance, is the dominant species in the study area, comprising more than 60% of the stand basal area. However, this species had consistently lower C_A and C_W values than yellow birch and beech. Clearly, many other factors than the carbon gain are also determinant of the ecological success of a species, including variations in seed production, germination, early establishment requirements, as well as drought, pathogen, and herbivore resistance (Walters and Reich 1996, Barker et al. 1997).

Estimation of daily carbon gain: possible limitations of the method and needs for further studies

Daily carbon gain of individual plants and whole forest canopies has been estimated in several studies (e.g., Caldwell et al. 1986; Ellsworth and Reich 1992*a*; Ellsworth and Reich 1993; Pearcy and Yang 1996; Barker et al. 1997; Oberbauer and Noudali 1998). Daily carbon gain can be measured in situ by integrating over time the instantaneous carbon gain recorded continuously or at several different times throughout the day (e.g., Barker et al. 1997). Models for estimating plant- or stand-level carbon gain are an alternative approach to direct measurement of carbon gain. Such models range in complexity from very simple calculations based solely on diurnal course of light availability and photosynthetic-light response curves (e.g., Oberbauer and Noudali 1998) to much more sophisticated models that take into account factors such as the photosynthetic response of leaves to other environmental factors than light (e.g., temperature and vapor pressure deficit), the dynamic response of photosynthesis to sunflecks, the three-dimentional representation of crown structure, the spatial arrangement and optical properties of leaves, etc. (e.g., Caldwell et al. 1986; Ellsworth and Reich 1993; Pearcy and Yang 1996).

In this study, daily carbon gain was estimated for tree seedlings using a relatively simple model in which whole-plant carbon gain was calculated from the photosynthetic-light response of leaves and the vertical patterns of leaf area distribution and light transmission among crown layers. The confidence intervals around the estimates of daily carbon gain were calculated and presented in this study. Such confidence intervals are rarely provided in the literature. Yet, they are an important component of the calculations, as they allow a quantitative comparison of carbon gain values between species and habitats. As observed in this study, it can be difficult to detect possible differences of carbon gain between species and light environments given the uncertainty (i.e., SE) associated with the carbon gain estimates. Such levels of uncertainty come from the propagation of the errors (i.e., SE) associated with the measured variables from which the carbon gain is determined. Further studies should aim at reducing the error associated with the parameters from which the carbon gain is estimated. Also, studies should

try to provide an assessment of the confidence around their carbon estimates. It is likely that at least some of the published conclusions about differences of carbon gain between species and light environments would not hold if confidence intervals around the carbon gain estimates had been determined.

One of the limitations of the simple model we used to estimate carbon gain is that it does not take into account the effects of rapid fluctuations of light on photosynthetic dynamics. Steady-state models that ignore the dynamic response of photosynthesis to rapid fluctuations in light availability can lead to an overestimation of actual carbon gain by 5–25% (Gross 1982; Pfitsch and Pearcy 1989; Berninger 1994; Pearcy and Yang 1996).

Our estimates of daily carbon gain are based on the assumption that light is the single most important factor driving photosynthesis, and possible limitations by other environmental factors such as temperature, atmospheric water vapor deficit, and soil water conditions are not explicitly considered. Carbon gain estimates that do not consider limitations by other environmental factors than light can overestimate actual carbon gain by 20–40% (Ellsworth and Reich 1992*a*). However, overestimations of this magnitude occur when photosynthetic-light response curves are obtained in the laboratory (i.e., under near-optimal environmental conditions) and then used to estimate carbon gain in the field. In this study, our photosynthetic-light response curves were obtained from field measurements. Thus, the measured photosynthetic response curves already incorporate some of the effects of other potentially limiting environmental conditions than light. Therefore, we would expect the possible overestimation of carbon gain to be lower than that reported by Ellsworth and Reich (1992*a*).

Taking into account the vertical pattern of light attenuation in the crown ($FASL_{CL}$) in the calculations of plant-level daily carbon gain presumably improved the accuracy of our daily carbon gain estimates. Pearcy and Yang (1996), for instance, showed that self-shading reduced whole-plant daily carbon assimilation by 57% in a tropical shrub species. The pattern of light attenuation in the crown was especially important to consider, since it differed between light environments; light attenuation was much more pronounced in the crown of seedlings from the gap than from the shade environment. Therefore, ignoring patterns of light attenuation in the crown would not only have led to an overestimation of the carbon gain but also to a bias in the evaluation of the difference of carbon gain between the two light environments.

Although taking into account the light attenuation in the crown presumably improved the accuracy of our carbon gain estimates, it did not contribute to differentiate the species contrary to what was expected. This is due to the fact that the results of Messier and Nikinmaa (2000) that we used to estimate the carbon gain showed no difference of $FASL_{CL}$ among species. This is surprising, since yellow birch, sugar maple, and beech are known to differ in terms of leaf shape, leaf display, and crown architecture (Beaudet and Messier 1998).

Clearly, further studies are needed to better assess the relationships between species-specific crown architecture and patterns of within-crown light availability and to determine how these factors influence plant-level carbon gain. Presumably, variations between species in such plant-level features could influence the differential performance of the species along the gap–understory gradient (Canham 1988; Sipe and Bazzaz 1994; Givnish 1995; Pearcy and Yang 1996). Experimental studies, such as that by Hilbert and Messier (1996), as well as tree-level carbon gain simulation models that take into account crown architecture (e.g., YPLANT: Pearcy and Yang 1996; LIGNUM: Perttunen et al. 1996) are potentially useful tools to improve our understanding of relationships between crown architecture, patterns of within-crown light availability, and plant-level carbon gain.

Acknowledgements

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Appendix 1

Calculation of LA_T

Table A1. Regression equations of total leaf area (LA_T, cm^2) as a function of aboveground dry mass (DM, g) for yellow birch, sugar maple and beech seedlings growing under two contrasting forest light environments.

Light environment	Species	Regression equation	P	R^2	n
Shade	Yellow birch	$LA_T = 64.2DM + 1292.4$	<0.001	0.779	12
Shade	Sugar maple	$LA_T = 71.2DM + 280.4$	<0.001	0.929	13
Shade	Beech	$LA_T = 62.7DM + 517.1$	<0.001	0.963	13
Gap	Yellow birch	$LA_T = 57.4DM + 934.0$	<0.001	0.871	30
Gap	Sugar maple	$LA_T = 51.7DM + 610.8$	<0.001	0.904	28
Gap	Beech	$LA_T = 37.0DM + 857.4$	<0.001	0.913	30

Note: The equations were obtained from data in Beaudet (1994) and were used to estimate the LA_T in the crown of a 50-g seedling of each species in each light environment.

Appendix 2

Estimation of daily carbon gain

The daily carbon gain per unit leaf area (C_A, mmol $CO_2 \cdot m^{-2}$ per day) was calculated as

[A1] $$C_A = \frac{C_W}{LA_T}$$

where C_W (mmol CO_2 per day) is the whole-plant daily carbon gain and LA_T (m^2) is the total leaf area in the crown of a 50-g seedling.

Values of C_W were calculated from the sum of the carbon gains in each crown layer and over each 2-min interval ($C_{CL,INT}$):

[A2] $$C_W = \frac{\sum\limits_{CL=1}^{3} \sum\limits_{INT=1}^{330} C_{CL,INT}}{1000}$$

Note that the division by 1000 is for units conversion (from micromoles to millimoles).

The variable $C_{CL,INT}$ (μmol CO_2/2 min) is equal to the instantaneous unit area photosynthetic rate of leaves in crown layer CL during time interval INT ($A_{CL,INT}$), multiplied by the time interval (120 s) and the leaf area in crown layer CL. The leaf area in crown layer CL is equal to the product of total leaf area (LA_T) and the fraction of total leaf area in crown layer CL (FLA_{CL}). The equation for $C_{CL,INT}$ is:

[A3] $$C_{CL,INT} = A_{CL,INT}(LA_T \times FLA_{CL}) \times 120$$

The instantaneous unit area photosynthetic rate of leaves in crown layer CL during time interval INT ($A_{CL,INT}$, μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is modeled using eq. 1, as follows:

[A4] $$A_{CL,INT} = \frac{\alpha_{ADJ,CL} \times L_{CL,INT} \times A_{max,ADJ,CL}}{\sqrt{A_{max,ADJ,CL}^2 + (\alpha_{ADJ,CL}^2 \times L_{CL,INT}^2)}}$$

The $L_{CL,INT}$ (μmol photons$\cdot m^{-2} \cdot s^{-1}$) is equal to the product of ASL_{INT}, and the fraction of above-seedling light in crown layer CL ($FASL_{CL}$):

[A5] $$L_{CL,INT} = ASL_{INT} \times FASL_{CL}$$

In eq. A4, we used A_{max} and α values that were adjusted to light conditions prevailing in each crown layer (i.e., $A_{max,ADJ,CL}$ and $\alpha_{ADJ,CL}$). We adjusted α and A_{max} values because of the variation in light conditions between crown layers, and because of previously reported adjustments of leaf photosynthetic characteristics to such variation in light conditions (Hollinger 1989; Ellsworth and Reich 1993). Values of A_{max} and α were adjusted to the light conditions prevailing in each crown layer using a linear interpolation between the measured A_{max} and α in each light environment and the average light conditions prevailing in each of these two forest light environments (i.e., percent of above-canopy light (PACL) of 3 and 25% in the shade and gap environments, respectively). The equation for the adjusted A_{max} (that represents the linear interpolation) is shown below:

$$[A6] \quad A_{\text{max,ADJ,CL}} = \left[\left(\frac{A_{\text{max,GAP}} - A_{\text{max,SHADE}}}{\text{PACL}_{\text{GAP}} - \text{PACL}_{\text{SHADE}}} \right) \times \text{PACL}_{\text{CL}} \right] - \left[\text{PACL}_{\text{SHADE}} \times \left(\frac{A_{\text{max,GAP}} - A_{\text{max,SHADE}}}{\text{PACL}_{\text{GAP}} - \text{PACL}_{\text{SHADE}}} \right) \right] + A_{\text{max,SHADE}}$$

The α value was adjusted for light conditions prevailing in each crown layer in the same manner as $A_{\text{max,ADJ,CL}}$, i.e., using eq. A6 with α values instead of A_{max} values.

The percent of above-canopy light in crown layer CL (PACL_{CL} in eq. A6) was calculated as:

$$[A7] \quad \text{PACL}_{\text{CL}} = \text{PACL}_{\text{ENV}} \times \text{FASL}_{\text{CL}}$$

where PACL_{ENV} is the percent of above-canopy light in the forest light environment ENV (either gap or shade), and FASL_{CL} is the fraction of above-seedling light in crown layer CL.

Equations A1–A7 describe the stages used to calculate the carbon gain from the measured field data. Equations A1–A5 can be combined into a single algebraic expression:

$$[A8] \quad C_{\text{W}} = \frac{\displaystyle\sum_{\text{CL}=1}^{3} \sum_{\text{INT}=1}^{330} \left(\left\{ \frac{[\alpha_{\text{ADJ,CL}} \times (\text{FASL}_{\text{CL}} \times \text{ASL}_{\text{INT}}) \times A_{\text{max,ADJ,CL}}]}{\sqrt{A_{\text{max,ADJ,CL}}^2 + [\alpha_{\text{ADJ,CL}}^2 \times (\text{FASL}_{\text{CL}} \times \text{ASL}_{\text{INT}})^2]}} \right\} \times (\text{LA}_{\text{T}} \times \text{FLA}_{\text{CL}}) \times 120 \right)}{1000}$$

Appendix 3

Calculation of error in the carbon gain

The uncertainty or error in the carbon gain is assumed to be produced by the uncertainties in the measured observables from which it is determined. In this discussion, the term observable will denote the measured variables from which the carbon gain was calculated. The uncertainties in these observables are the standard errors in their mean values. Hence the calculation of error amounts to the propagation of the statistical uncertainties from the observables to the carbon gain.

The expression of the carbon gain in a single algebraic equation (eq. A8) permits the calculation of the error using a standard first-order uncertainty analysis extended to correlated variables (Clifford 1973; Taylor 1997). The analysis technique and its application to the carbon gain will be described.

Uncertainty in a function of independent and correlated variables

Suppose that x_1, x_2, ..., x_n are measured with uncertainties σ_{x_1}, σ_{x_2}, ..., σ_{x_n} and covariances $\sigma_{x_1 x_2}$, $\sigma_{x_1 x_3}$, ..., and that these measured values are used to compute the function $q(x_1, x_2, ..., x_n)$. If the uncertainties in x_1, x_2, ..., x_n are random in nature, then the uncertainty in q is determined by the equation:

$$[A9] \quad \sigma_q^2 = \left(\frac{\partial q}{\partial x_1} \right)^2 \sigma_{x_1}^2 + \left(\frac{\partial q}{\partial x_2} \right)^2 \sigma_{x_2}^2 + ... + \left(\frac{\partial q}{\partial x_n} \right)^2 \sigma_{x_n}^2 + ... + 2 \frac{\partial q}{\partial x_1} \frac{\partial q}{\partial x_2} \sigma_{x_1 x_2} + 2 \frac{\partial q}{\partial x_1} \frac{\partial q}{\partial x_3} \sigma_{x_1 x_3} + 2 \frac{\partial q}{\partial x_2} \frac{\partial q}{\partial x_3} \sigma_{x_2 x_3} + ...$$

The uncertainty in the function q is hence equal to the sum of squares of the uncertainties in the observables each multiplied by a coefficient equal to the square of the partial derivative of the function q with respect to that observable, added to "cross terms" that include all of the possible pairwise combinations between the observables. Note that these cross terms reflect either the augmentation (due to positive reinforcement) or reduction (due to cancellation) of uncertainties caused by the correlation between observables. Calculation of the propagated error hence amounts to the calculation of the partial derivatives of the function (De Sapio 1978; Taylor 1997).

Implementation of the error equations

Equation A9 is implemented to determine the error in the carbon gain arising from the propagation of error from the measured parameters. The equation for the carbon gain described in eq. A8 is used in place of the function q. There are 11 observables, which represent the measurements from which the greatest amounts of uncertainty are thought to occur. These are as follows: α_{GAP}, α_{SHADE}, $A_{\text{max,GAP}}$, $A_{\text{max,SHADE}}$, FASL_{CL} (CL = 1, 2, 3), FLA_{CL} (CL = 1, 2, 3), and LA_{T}. The substitution of the carbon gain and its observables into the error equation (eq. A9) yields:

$$[A10] \quad \begin{aligned} \sigma_C^2 &= \left(\frac{\partial C}{\partial \alpha_{\text{GAP}}} \right)^2 \sigma_{\alpha_{\text{GAP}}}^2 + \left(\frac{\partial C}{\partial \alpha_{\text{SHADE}}} \right)^2 \sigma_{\alpha_{\text{SHADE}}}^2 + ... + \left(\frac{\partial C}{\partial \text{LA}_{\text{T}}} \right)^2 \sigma_{\text{LA}_{\text{T}}}^2 + 2 \frac{\partial C}{\partial \alpha_{\text{GAP}}} \frac{\partial C}{\partial A_{\text{max,GAP}}} \sigma_{\alpha_{\text{GAP}} A_{\text{max,GAP}}} \\ &\quad + 2 \frac{\partial C}{\partial \alpha_{\text{SHADE}}} \frac{\partial C}{\partial A_{\text{max,SHADE}}} \sigma_{\alpha_{\text{SHADE}} A_{\text{max,SHADE}}} + 2 \frac{\partial C}{\partial \text{FLA}_1} \frac{\partial C}{\partial \text{FLA}_2} \sigma_{\text{FLA}_1 \text{FLA}_2} + 2 \frac{\partial C}{\partial \text{FLA}_1} \frac{\partial C}{\partial \text{FLA}_3} \sigma_{\text{FLA}_1 \text{FLA}_3} \\ &\quad + 2 \frac{\partial C}{\partial \text{FLA}_2} \frac{\partial C}{\partial \text{FLA}_3} \sigma_{\text{FLA}_2 \text{FLA}_3} \end{aligned}$$

Note that eq. A10 above shows all of five of the variable pairs that were found to be correlated in the carbon gain calculation. σ_C represents the standard error in the calculated carbon gain and is the desired result.

The standard errors and covariances are readily determined from the measured data sets. Equations for the partial derivatives were determined analytically from eq. A8. These equations as well as eq. A10 were then entered into an Excel Spreadsheet. Values of the observables and their standard errors and covariances were read into the spreadsheet to calculate the error in the carbon gain. The method was applied to determine the error in carbon gain for each species and light environment.

It can be shown that, to calculate the error in the average carbon gain determined from different test sites (over which the daily light curves vary but all other variables remain the same), each of the partial derivatives in eq. A10 must be replaced by the average partial derivative of the carbon gains.