

Leaf-level acclimation to gap creation in mature *Acer saccharum* trees

T. A. JONES^{1,2} and S. C. THOMAS¹

¹ Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto ON, M5S 3B3, Canada

² Corresponding author (trevor.jones@utoronto.ca)

Received November 30, 2005; accepted April 9, 2006; published online November 1, 2006

Summary Leaf-level morphological and physiological responses of mature, winter-deciduous, shade-tolerant *Acer saccharum* Marsh. trees to gap formation caused by selection harvest were studied experimentally over a 2-year period. We found no evidence for either physiological stress or positive acclimation following gap creation during the 1–2-week post-harvest period. Rather, lower-canopy leaves showed gradual increases in area-based maximum photosynthetic rates ($A_{\text{max-area}}$), stomatal conductance (g_s), and leaf nitrogen concentration (N_{area}) over the entire 2-year study. These acclimation responses were directly related to changes in leaf mass per unit area (LMA) in the subsequent two leaf flushes. No change in $A_{\text{max-area}}$, g_s , N_{area} , or photosynthetic nitrogen-use efficiency was observed that could not be accounted for by changes in LMA. The gradual acclimation responses in the lower canopy may account, in whole or in part, for the ~2-year lag in post-harvest growth response observed in *Acer saccharum*.

Keywords: canopy trees, gap creation, gas exchange, leaf morphology, light acclimation, nitrogen content, photosynthetic nitrogen use efficiency, selection management, shade leaves, sun leaves.

Introduction

In both natural and managed forests, resource availability is spatially and temporally heterogeneous and is highly dependent on disturbance events that alter forest structure. In natural forests, the process of disturbance and recovery is often referred to as gap phase dynamics (Smith et al. 1997). In selection management, which is thought to emulate aspects of natural gap phase dynamics, single or small groups of trees are removed across the harvested area. Although typically two-thirds or more of canopy trees are retained post-harvest, irradiances within gaps and within the remaining forest are dramatically increased (Canham et al. 1990, Beaudet and Messier 2002, Beaudet et al. 2004, Ritter et al. 2005), and post-harvest increases in soil water availability and N mineralization have also been documented (Gray et al. 2002, Clinton 2003, Ritter et al. 2005).

Tree regeneration under selection management is achieved through manipulation of the understory light environment. The responses of tree seedlings and saplings to changing

understory light availability have been well studied, particularly responses to photosynthetic traits (Kubiske and Pregitzer 1997, Naidu and DeLucia 1997a, Tognetti et al. 1997, Parker and Mohammed 2000, Krause et al. 2001), water relations (Naidu and Delucia 1997b), and leaf morphology (Naidu and Delucia 1997b, Grassi and Minotta 2000, Oguchi et al. 2003). These physiological responses have in turn been linked to responses in growth and biomass allocation of the seedlings and saplings (Claussen 1996, Naidu and Delucia 1997b, Huante and Rincon 1998, Bloor and Grubb 2004).

Although increases in growth of mature trees following selection harvests have been documented (Jones and Thomas 2004), we are unaware of previous studies examining the physiological responses of mature canopy trees to gap formation. Only a few studies have examined how canopy trees acclimate to changes in resource availability (Brooks et al. 1996, Cavender-Bares and Bazzaz 2000, Graham et al. 2003). The lack of physiological acclimation studies in canopy trees is largely due to the logistical challenges of working in the canopy where access is either dangerous (tree climbing) or expensive (use of canopy cranes, mobile elevating work platforms or towers). Mature canopy trees commonly show substantial differences in gas exchange and other physiological parameters from seedlings and saplings (Thomas and Winner 2002); they must move water and other resources and hormonal signals over larger distances (Maggs 1964, Hubbard et al. 1999), and show increased allocation to structural support (Givnish 1988) and reproductive structures (Thomas 1996). Higher in the canopy, the gap microenvironment is likely to be substantially different from that near the ground (Beaudet et al. 2004). As a result, large trees are likely to differ substantially from seedlings and saplings in their acclimation responses following gap formation.

Previous studies on seedlings and saplings, and correlative measurements in forest canopies, suggest several alternative hypotheses to account for the photosynthetic responses of large trees to gap creation. Hypothesis 1 states that there will be an immediate reduction in maximum photosynthetic rate as a result of increased photodamage and oxidative phosphorylation following gap creation. Previous studies on short-term responses to increases in light availability have demonstrated varying degrees of photoinhibition or photodamage in response to increased radiation (Ellsworth and Reich 1992a,

Mulkey and Pearcy 1992, Turnbull et al. 1993, Lovelock et al. 1994, Naidu and DeLucia 1997a). However, the magnitude and duration of the decline in photosynthesis may depend on the successional status or shade tolerance of the species (Kitao et al. 2000). Hypothesis 2 states that, following gap creation, there will be a rapid increase in photosynthetic capacity (Oguchi et al. 2003) as a result of increased rubisco and nitrogen turnover rates (Clearwater et al. 1999, Frak et al. 2001, Valladares et al. 2002). The magnitude of this increase will be dependent on the successional status (Yamashita et al. 2000, Oguchi et al. 2003), leaf age (Sims and Pearcy 1992, Yamashita et al. 2002) and the magnitude of change in the availability of light and other resources (Popma and Bongers 1988). A third hypothesis is that acclimation to gap creation will be gradual, either as a result of counteracting effects of photosynthetic up-regulation and photoinhibition, or because of a lengthier period of morphological acclimation and altered allocation. In particular, physiological and morphological acclimation may not occur until the year following gap creation owing to leaf developmental constraints (Newell et al. 1993, Turnbull et al. 1993, Uemura et al. 2000).

The present study was designed to investigate acclimation responses to gap formation in leaf morphology, photosynthetic parameters, and leaf nitrogen in the crowns of large winter-deciduous, shade-tolerant *Acer saccharum* Marsh. trees over a 2-year period. Given that upper-canopy leaves of mature trees are already acclimated to high-light environments, our a-priori hypothesis was that upper-canopy leaves would not experience an acclimation response, but that the lower-canopy leaves would experience pronounced changes in physiological and morphological characteristics over both the short and long term.

Materials and methods

Site description

The study was conducted at Haliburton Forest and Wildlife Reserve, a 25,000 ha privately owned forest in Ontario, Canada (45°13' N 78°35' W) that has been selection managed for the past 30 years. The study area was a 0.25 km² uneven-aged closed-canopy stand in the north-east portion of the forest reserve. Canopy species composition in the stand is 93% *Acer saccharum* Marsh., 4% *Fagus grandifolia* Ehrh. with the remaining 3% comprising *Betula alleghaniensis* Britt. and *Prunus serotina* Ehrh. (Jones unpub. data). Basal area of the stand was 22 m² ha⁻¹ before harvest.

To evaluate how within-canopy leaf-level physiological and morphological traits respond to gap creation, 12 (six control and six gap) trees were sampled. Gap and control treatment trees were selected in the stand so that two gaps were created and so that the control trees were located at least two large tree crowns away from the created gaps. Trees to be removed to create the gaps were chosen by a certified tree marker and were felled by a professional logger to minimize residual damage and to mimic the process of logging as closely as possible.

During harvest, the crown of one of the selected gap trees was severely damaged and had to be removed for safety reasons. Subsequently, a neighboring tree, of similar DBH, crown depth and height, was measured for the remainder of the experiment. Tree canopies were accessed from a mobile elevating work platform (Scanlift 240) so that samples could be obtained from both the top (16–25 m) and bottom thirds of the canopy (6–12 m). Irradiances in the canopies of the study trees were measured by hemispherical photography for total, diffuse and direct incident radiation before and after the gap treatments were applied. Irradiance was calculated with the gap light analyzer (GLA) imaging software (Frazer et al. 1999). Trees were sampled four times over a 2-year period: pre-harvest (July 18–25, 2002), 1–2 weeks post-harvest (August 1–8, 2002), 1 year post-harvest (August 1–8, 2003) and 2 years post-harvest (July 23–30, 2004).

Photosynthesis

Maximum photosynthetic rate (A_{\max}), stomatal conductance (g_s) and transpiration rate (E) for the calculation of instantaneous water-use efficiency ($WUE_{\text{inst}} = A_{\max}/E$) were measured with an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE) with a 6-cm² cuvette and a red/blue (6400-02B Red-Blue, SI-0951) light source providing a photosynthetic photon flux of 1000 $\mu\text{mol m}^{-2} \text{s}^{-2}$ at the leaf surface. Leaf temperature was maintained near ambient temperature of ~22 °C and CO₂ concentration was set at 350 ppm, relative humidity was maintained between 70 and 80% and leaf to air vapor pressure deficit was maintained between 0.9 and 1.2 kPa. Measurements were made from 0800 to 1300 h to avoid potential diurnal changes in photosynthetic rates. Leaves from all canopy locations were placed in the fully lit chamber for 10 min or until photosynthetic rates were stable for 2 min. Three leaves per canopy location and per tree were measured during each of the four sampling periods. When variation in photosynthetic rates of leaves within a canopy position was high, 1–3 additional leaves were measured. Immediately following completion of photosynthetic measurements, leaves were harvested and leaf morphological traits measured. For the gap trees, leaves were sampled only from the gap-facing side of the tree. All samples were taken from the same branches on each tree in each of the measurement periods.

Leaf morphology and nutrient analysis

Fresh leaves were scanned with a flat bed scanner (Epson perfection 640U) immediately after harvest. The area of each image was analyzed with Idrisi32 (Clark Labs, Worcester, MA), a pixel-based image analysis software package. Calibration of leaf area was made against standards of known area. Leaves were subsequently dried and weighed to calculate mass-based photosynthetic rates and tissue density. Leaf thickness was measured with a low-force micrometer (No. 227-101; Mitutoyo Corporation, Japan) for all leaves from the fourth sampling period. Leaf carbon and nitrogen were measured with an ECS 4010 analyzer (Costech Analytical Technologies,

Valencia, CA.) on pooled leaf samples from each sample date and within-canopy location per sample tree. Photosynthetic nitrogen-use efficiency (PNUE) was calculated as $A_{\max\text{-area}}/N_{\text{area}}$.

Statistical analyses

A separate repeated measures analysis of variance (ANOVA; GLM procedure, version 8.2; SAS Institute, Cary, NC) was conducted for both upper- and lower-canopy positions to test for differences between control and gap trees and for differences among measurement intervals. To avoid pseudo-replication, the mean value from each canopy position within a sample tree and sample date was calculated. Data for the damaged tree and the substitute tree were combined to maintain sample size in the multivariate repeated measures procedure. Differences between upper- and lower-canopy leaves across treatments were evaluated by *t* tests. Differences between gap and control treatments for leaf thickness and leaf density in 2004 were evaluated by two-way ANOVA with an interaction term that evaluated differences between gap and control treatments across canopy positions.

The responses of physiological and morphological traits to changes in leaf nitrogen and LMA were analyzed based on the assumption that each leaf was independent. Control values for this analysis consisted of the upper (sun) and lower (shade) canopy leaves from the control trees for each harvest interval as well as the upper- (sun) and lower- (shade) canopy leaves from the pre-harvest gap trees. We treated leaves as independent values to increase the sample size, so that curves could be fit by nonlinear least squares regression. A Michaelis-Menten function was fit to the control values of the $A_{\max\text{-area}}/N_{\text{area}}$, $A_{\max\text{-mass}}/N_{\text{mass}}$, $A_{\max\text{-area}}/LMA$ and N_{area}/LMA relationships, and a nonlinear decreasing function was fit to the control values of the $A_{\max\text{-mass}}/LMA$ and N_{mass}/LMA relationships. Residual values (the difference between the observed measured values and the value that would be expected as determined by the functions fit to the control values) were calculated for both the control and gap leaves. Residual values were subjected to one-way analysis of variance to test for differences between control and gap leaves.

Results

Irradiances

Irradiances were significantly higher in the upper canopy than in the lower canopy both before and after harvest regardless of gap treatment (Figure 1). As expected, there was a large treatment effect on light availability in the lower canopy, with incident radiation increasing by ~100% for gap trees (Figure 1b). Irradiances in the upper canopy were somewhat higher in control trees than in gap trees even before gap creation, but the difference was not significant (Figure 1a). The upper canopy showed a significant post-harvest increase in irradiance of ~40% relative to pretreatment values as a result of gap creation (Figure 1a).

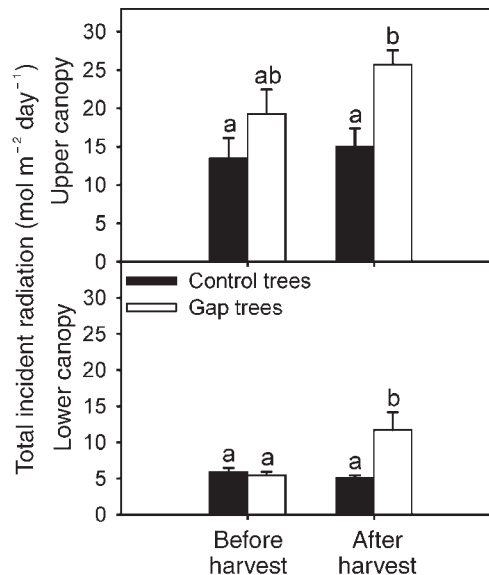


Figure 1. Mean total incident radiation, obtained by hemispherical photography, for leaves in upper- (top panel) and lower-canopy (lower panel) positions of gap (open bars) and control (filled bars) treatment trees from before and after application of gap treatment. Error bars are standard errors of the mean. Different letters above bars within canopy positions represent significant differences ($P < 0.05$) as determined by a Tukey-Kramer test.

Leaf morphology

Leaves in the upper canopy were significantly ($P = 0.004$) smaller ($60.6 \pm 6.05 \text{ cm}^2$) than in the lower canopy ($69.6 \pm 5.55 \text{ cm}^2$). Leaf area did not change significantly in response to the gap treatment for either canopy position or sampling interval; however, leaf mass in the lower canopy of gap trees increased significantly from an average of $0.27 \pm 0.03 \text{ g}$ to $0.57 \pm 0.04 \text{ g}$ and $0.48 \pm 0.03 \text{ g}$ in the two years post-harvest (Table 1, Figure 2c). Leaf mass in the lower canopies of control trees did not change significantly during the sampling period and averaged $0.29 \pm 0.03 \text{ g}$. Leaf mass in the upper canopy increased significantly over the four sampling periods although no difference was observed between gap ($0.56 \pm 0.06 \text{ g}$) and control trees ($0.52 \pm 0.06 \text{ g}$) in any of the four sampling intervals. Leaf mass per unit area (LMA) increased significantly in the lower canopy in the two years following gap creation (Table 1, Figure 2e). There were no significant differences in LMA in upper-canopy leaves between treatments, although significant differences among sampling periods were observed (Table 1, Figure 2f).

Leaf thickness and leaf tissue density in the upper canopy did not change significantly in either the gap or control trees (Table 2). Lower-canopy leaves had significantly lower leaf tissue densities than upper-canopy leaves, and lower-canopy leaves of gap trees had significantly greater leaf thickness and tissue density than lower-canopy leaves of control trees (Table 2). Gap treatment effects on LMA were attributable to similar increases in both leaf thickness and leaf tissue density (Table 2).

Table 1. The F values and significance levels from a repeated measures analysis of variance for leaf physiological and morphological parameters for within-measurement-date differences, between-measurement-date differences and interaction terms for harvest and gap treatment. Significance levels are indicated by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Variable	Gap	Before 2002	After 2002	After 2003	After 2004	Date	Date \times Gap
Leaf area (cm ²)	Lower	0.04	1.07	1.34	0.29	1.79	1.36
	Upper	1.00	0.78	1.28	0.01	2.76	0.96
Leaf mass (g)	Lower	0.12	0.12	5.88*	43.05***	7.04**	4.38*
	Upper	1.81	2.60	1.01	0.25	8.82***	1.80
LMA (g cm ⁻²)	Lower	0.49	0.28	2.01	31.99***	16.03***	7.74***
	Upper	1.28	1.60	0.35	0.34	31.52***	1.38
$A_{\max\text{-area}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Lower	0.05	0.90	2.72	17.33*	7.37***	3.03*
	Upper	1.29	6.57*	0.09	2.35	2.25	1.97
$A_{\max\text{-mass}}$ ($\text{nmol g}^{-1} \text{s}^{-1}$)	Lower	0.45	0.21	0.03	0.48	4.93**	0.37
	Upper	0.12	0.13	0.03	1.86	5.41**	0.19
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	Lower	0.32	0.76	6.22*	6.47*	1.78	2.06
	Upper	0.46	1.32	0.36	0.19	0.34	0.5
N_{area} (g m^{-2})	Lower	0.20	0.02	1.27	37.92***	8.82***	7.64**
	Upper	0.52	0.12	0.00	0.19	8.11***	0.25
N_{mass} (mg g^{-1})	Lower	0.35	2.66	0.36	0.04	16.38***	1.93
	Upper	0.37	4.26	0.37	0.12	27.05***	2.85
C_{area} (g m^{-2})	Lower	0.50	0.30	2.22	33.36***	16.06***	7.73***
	Upper	1.51	1.47	0.42	0.29	31.96***	1.37
C_{mass} (mg g^{-1})	Lower	0.03	0.20	4.77	0.00	0.50	1.84
	Upper	1.64	0.19	0.27	0.01	4.76**	0.26
C:N ratio	Lower	0.38	1.81	0.96	0.04	12.28***	1.54
	Upper	0.51	3.19	0.56	0.26	30.97***	2.04
PNUE ($\mu\text{mol CO}_2 \text{g N}^{-1} \text{s}^{-1}$)	Lower	0.90	1.18	0.00	0.07	7.19**	0.87
	Upper	0.37	1.22	0.06	0.84	3.62*	0.67
WUE _{inst} (mmol mol^{-1})	Lower	0.00	0.98	0.15	51.91***	9.38***	1.61
	Upper	0.07	1.90	0.07	6.43*	13.34***	2.26

Foliar nutrients

Upper-canopy leaves had significantly higher leaf carbon ($P = 0.013$, C_{area}) and nitrogen ($P = 0.005$, N_{area}) per unit area than lower-canopy leaves; however, there were no significant differences between upper- and lower-canopy for either C_{mass} or N_{mass} . Lower-canopy leaves from gap trees had higher N_{area} and C_{area} than from control trees two years post-harvest (Figures 3a and 3e). Neither carbon nor nitrogen concentration in the upper canopy varied between gap and control trees. With the exception of C_{mass} in lower-canopy leaves, there was significant year-to-year variation in the remaining measures of leaf carbon and nitrogen concentration at both canopy heights (Table 1, Figures 3c and 3g). There were no significant differences in C:N between gap and control trees in either the upper or lower canopies at any sampling period (Table 1, Figures 3i and 3j); however, C:N in both the upper- and lower-canopy leaves showed significant year-to-year variability (Table 1, Figures 3i and 3j).

Photosynthesis

Upper-canopy leaves of both gap and control trees showed relatively little change in physiological characteristics during the experiment (Table 1, Figures 4b, 4d, 4f and 4h). This was predicted because of the relatively small increase in irradiance to

leaves in the upper portions of trees as a result of gap creation (Figure 1). The only exception was a significant difference in $A_{\max\text{-area}}$ in the upper canopy immediately post-harvest as a result of a slight increase in $A_{\max\text{-area}}$ of gap trees together with a slight decrease in $A_{\max\text{-area}}$ of control trees. This apparent increase in $A_{\max\text{-area}}$ post-harvest could have been caused by the replacement of the one damaged gap tree with a tree that had slightly higher photosynthetic rates. In the years following harvest, $A_{\max\text{-area}}$ of upper-canopy leaves did not differ between control and gap trees. We found no changes in g_s (Figure 4), N_{area} (Figure 3), PNUE, WUE_{inst} (Figure 5) or in any morphological traits (Figure 2) immediately post-harvest (Table 1). Likewise, there was no significant difference in $A_{\max\text{-mass}}$ immediately post-harvest in upper-canopy foliage (Table 1). There were also no treatment effects on upper-canopy foliage for other physiological or morphological traits in the years following gap creation, with the exception of instantaneous water-use efficiency in 2004 (two years post-harvest), with gap trees showing lower water-use efficiency than control trees (Figure 5d).

Treatment effects on gas exchange were most pronounced in the lower canopy and at the second year post-harvest; inter-annual variation in photosynthetic rates was also more pronounced in the lower canopy (Table 1). Lower-canopy leaves of gap trees showed a pattern of gradually increasing $A_{\max\text{-area}}$ relative to control trees, which was significant by year 2

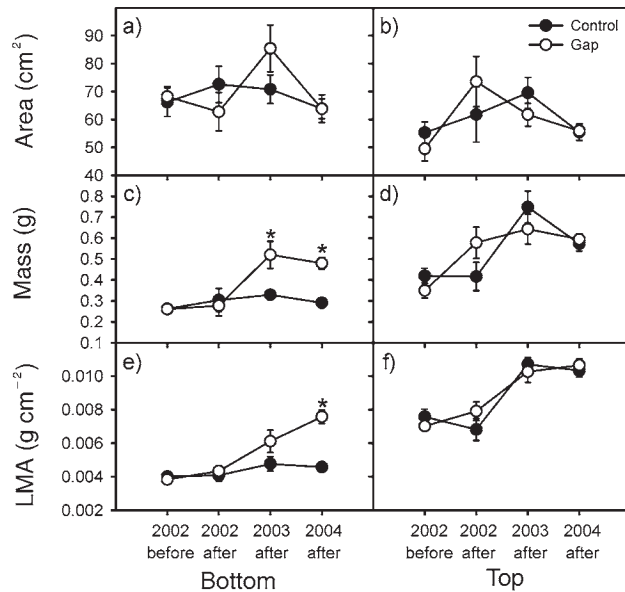


Figure 2. Mean \pm SE of six gap (○) and six control (●) treatment *Acer saccharum* trees for four measurement periods of: (a) canopy-bottom leaf area; (b) canopy-top leaf area; (c) canopy-bottom leaf mass; (d) canopy-top leaf mass; (e) canopy-bottom LMA; and (f) canopy-top LMA. Asterisks above values represent a significant ($P < 0.05$) treatment effect within the measurement date.

(Table 1, Figure 4a). Maximum photosynthetic rate expressed on a mass basis ($A_{\max\text{-mass}}$) revealed a slightly different pattern. There were significant differences in $A_{\max\text{-mass}}$ between upper ($111.8 \pm 9.7 \text{ nmol g}^{-1} \text{ s}^{-1}$) and lower ($90.7 \pm 8.1 \text{ nmol g}^{-1} \text{ s}^{-1}$) canopy positions ($P < 0.001$) and also significant inter-annual variation in photosynthetic rates (Table 1), but no significant differences between gap and control trees for either upper- or lower-canopy leaves at any sampling interval (Figure 4, Table 1). Similar to the $A_{\max\text{-area}}$ results, stomatal conductance showed a gradual increase in gap trees relative to control trees during the study (Table 1, Figure 4e). There was no significant year-to-year variation in g_s in the lower-canopy leaves. Upper-canopy leaves ($0.092 \pm 0.011 \text{ mol m}^{-2} \text{ s}^{-1}$) had significantly higher area-based g_s than lower-canopy leaves ($0.074 \pm 0.009 \text{ mol m}^{-2} \text{ s}^{-1}$); however g_s of upper-canopy leaves showed no gap treatment effect or variation among sampling periods (Table 1).

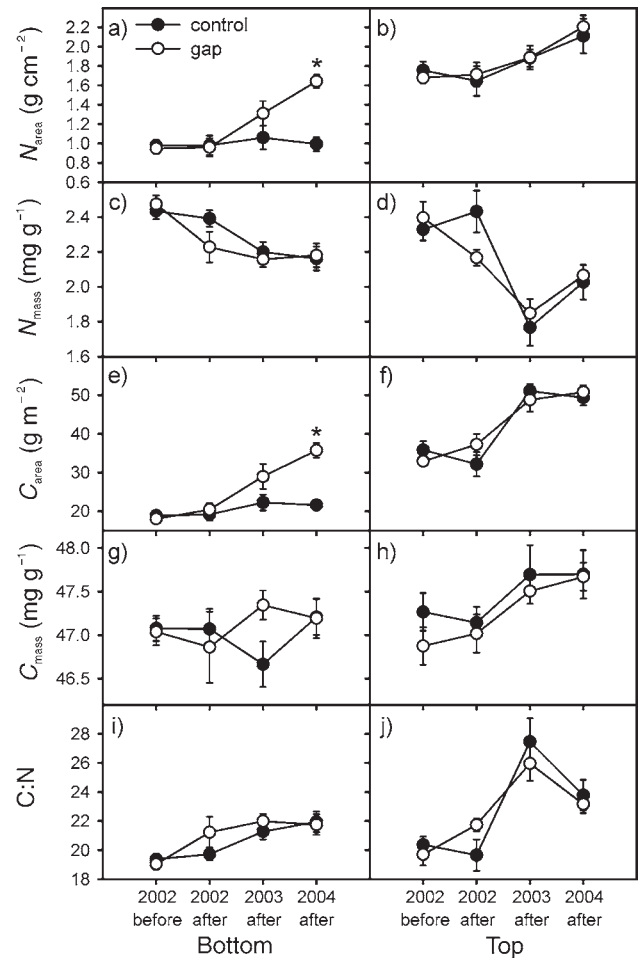


Figure 3. Mean \pm SE of six gap (○) and six control (●) treatment *Acer saccharum* trees for four measurement periods of: (a) canopy-bottom nitrogen (N); (b) canopy-top N; (c) canopy-bottom N; (d) canopy-top N; (e) canopy-bottom carbon (C); (f) canopy-top C; (g) canopy-bottom C; (h) canopy-top C; (i) canopy-bottom C:N; and (j) canopy-top C:N. Asterisks above values represent a significant ($P < 0.05$) treatment effect within the measurement date.

Nitrogen- and water-use efficiency

Photosynthetic nitrogen-use efficiency (PNUE) was proportionally similar whether expressed on a mass or an area basis, with no difference between gap and control trees in either the

Table 2. Mean \pm SE of leaf thickness and density for lower-canopy and upper-canopy positions of gap and control trees. Repeated measures analysis of variance for main effects plus interactions for canopy position and gap treatment effects. Letters following means represent significant ($P < 0.05$) differences between gap and control treatments (Tukey–Kramer post-hoc test). Abbreviations: P = position; and T = treatment.

Parameter	Position	Gap	Control	Source	F value (P value)
Leaf thickness (mm)	Lower	0.19 \pm 0.005 ^a	0.14 \pm 0.006 ^b	P	74.63 (0.0001)
	Upper	0.23 \pm 0.006 ^c	0.22 \pm 0.009 ^c	T	15.43 (0.0008)
				P \times T	8.86 (0.0075)
Leaf density (g cm ⁻³)	Lower	0.39 \pm 0.015 ^a	0.31 \pm 0.008 ^b	P	100.58 (0.0001)
	Upper	0.47 \pm 0.010 ^c	0.47 \pm 0.010 ^c	T	13.43 (0.0015)
				P \times T	13.39 (0.0016)

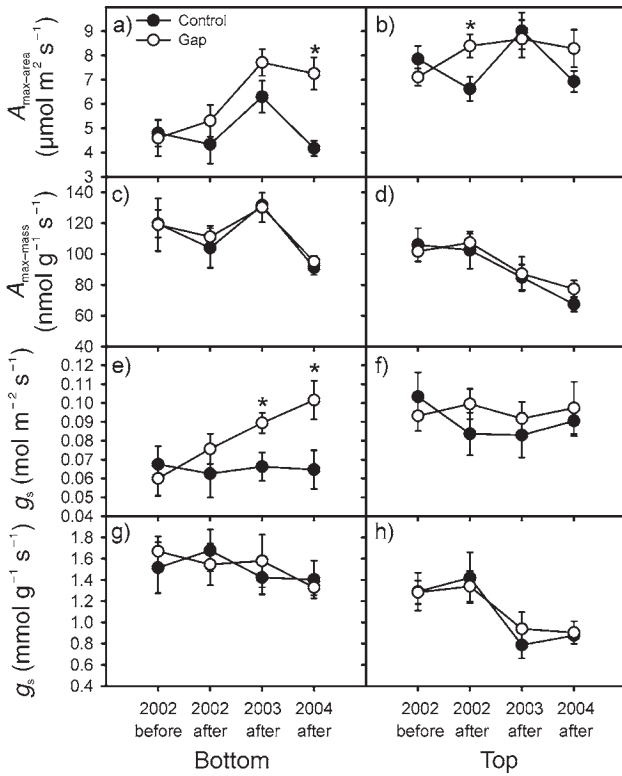


Figure 4. Mean \pm SE of six gap (\circ) and six control (\bullet) treatment *Acer saccharum* trees for four measurement periods of: (a) canopy-bottom $A_{\max\text{-area}}$; (b) canopy-top $A_{\max\text{-area}}$; (c) canopy-bottom $A_{\max\text{-mass}}$; (d) canopy-top $A_{\max\text{-mass}}$; (e) canopy-bottom $g_{s\text{-area}}$; (f) canopy-top $g_{s\text{-area}}$; (g) canopy-bottom $g_{s\text{-mass}}$; and (h) canopy top $g_{s\text{-mass}}$. Asterisks above values represent a significant ($P < 0.05$) treatment effect within the measurement date.

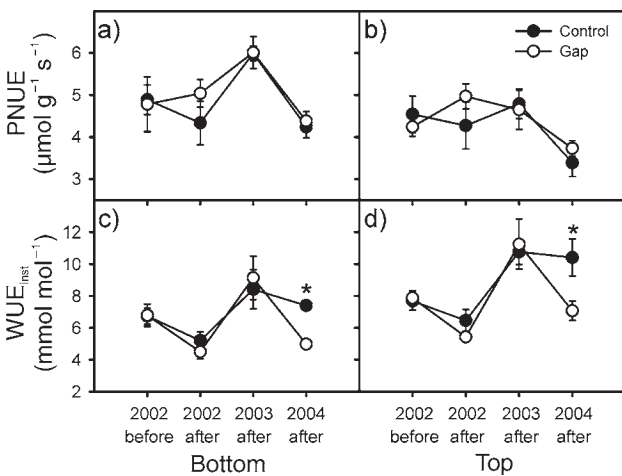


Figure 5. Mean \pm SE of six gap (\circ) and six control (\bullet) treatment *Acer saccharum* trees for four measurement periods of: (a) canopy-bottom PNUe; (b) canopy-top PNUe; (c) canopy-bottom instantaneous WUE (WUE_{inst}); and (d) canopy-top WUE_{inst} . Asterisks above values represent a significant ($P < 0.05$) treatment effect within the measurement date.

upper or lower portions of the canopy (Figure 5, Table 1); however, PNUe varied significantly from year-to-year (Figure 5, Table 1). Water-use efficiency in both the upper and lower canopies varied significantly from year-to-year, with higher WUE_{inst} in 2003 and 2004 than in 2002. There was also a significant difference between gap and control trees in both the upper and lower canopy positions in 2004 such that gap trees had significantly lower WUE_{inst} than control trees (Figure 5, Table 1).

The relationship between $A_{\max\text{-area}}$ and N_{area} was asymptotic with lower-canopy leaves having lower N_{area} and $A_{\max\text{-area}}$, whereas upper-canopy leaves approached an asymptote at higher N_{area} (Figure 6a). Lower-canopy leaves exposed to high irradiances had intermediate N_{area} and $A_{\max\text{-area}}$ relative to shaded lower-canopy leaves and upper-canopy sun leaves. On a mass basis, there was a positive linear relationship between N_{mass} and $A_{\max\text{-area}}$, but no significant difference between upper- and lower-canopy leaves or between lower-canopy sun-exposed and lower-canopy shade leaves (Figure 6b).

Photosynthesis and nitrogen versus LMA

The relationship between $A_{\max\text{-area}}$ and LMA was markedly nonlinear, with A_{\max} approaching an asymptote at high values of LMA (Figure 7a). Similar to the $A_{\max\text{-area}}$ versus N_{area} rela-

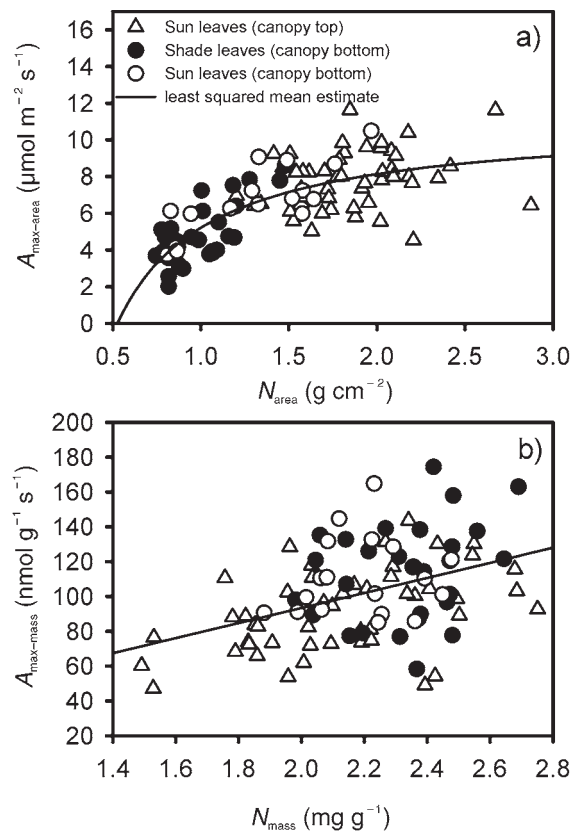


Figure 6. Relationships between (a) N_{area} and $A_{\max\text{-area}}$ and (b) N_{mass} and $A_{\max\text{-mass}}$. Symbols: \triangle = sun-exposed leaves from the upper-canopy; \bullet = shaded lower-canopy leaves from the control treatment; and \circ = sun-exposed leaves from the lower-canopy of the gap treatment.

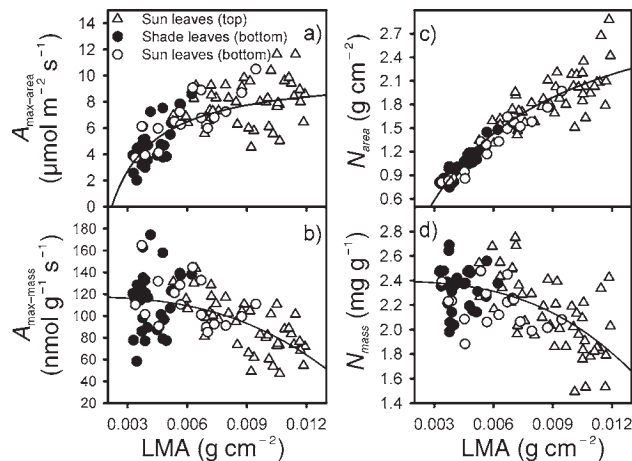


Figure 7. Relationship between (a) $A_{\max\text{-area}}$, (b) $A_{\max\text{-mass}}$, (c) N_{area} , (d) N_{mass} and LMA. Δ = sun-exposed leaves from the upper-canopy; \bullet = shaded lower-canopy leaves from the control treatment; and \circ = sun-exposed leaves from the lower-canopy of the gap treatment.

relationship, lower-canopy shade-adapted leaves had lower values of A_{\max} and LMA than either lower-canopy sun-adapted leaves or upper-canopy sun-adapted leaves, which had intermediate and high values of A_{\max} and LMA, respectively (Figure 7a). The relationship between N_{area} and LMA was similar to that of $A_{\max\text{-area}}$ and LMA in relative order along a fitted Michaelis-Menten function (Figure 7c). On a mass basis, the relationship between A_{\max} or N_{mass} and LMA was nonlinear and decreased with increasing LMA such that leaves with the highest $A_{\max\text{-mass}}$ or N_{mass} had the lowest LMA (Figures 7b and 7d).

Discussion

Based on experimental studies of tree seedlings and saplings and analyses of within-canopy physiological and morphological traits, several hypotheses were formulated as to how large trees would respond to gap creation. The first hypothesis was that lower-canopy shade-adapted leaves experience physiological stress as a result of a sudden increase in irradiance, temperature and water stress following gap creation. Because *Acer saccharum* is considered to be one of the most shade-tolerant species in northern hardwood forests (OMNR 1998), and leaves were fully developed before gap creation, we predicted large negative responses to increased irradiance following gap creation (e.g., Naidu and DeLucia 1997a, Valladares et al. 2002, Shimizu et al. 2006). However, no immediate reduction in photosynthetic rates or stomatal conductance was observed in lower-canopy leaves of the gap trees within the two weeks immediately following gap creation. Previous studies on temperate forest seedlings and sapling have generally found at least modest short-term reductions in A_{\max} or g_s following gap formation (Naidu and DeLucia 1997a). The only short-term effect of gap creation on gas exchange parameters of the mature trees we studied was an apparent increase in $A_{\max\text{-area}}$ in the upper canopy (Figure 4a, Table 1).

Hypothesis 2 predicted rapid up-regulation in A_{\max} in response to increased irradiance in the lower canopy following gap creation. However, despite a doubling in irradiance, we found no evidence of an immediate increase in lower-canopy A_{\max} , on either a mass or an area basis, before new foliage was produced. Furthermore, we found no evidence of an increase in A_{\max} in the year following gap creation, although significant increases in $A_{\max\text{-area}}$ were observed in the second year post-harvest (Figure 4a). Photosynthetic acclimation has often been observed to depend on morphological and anatomical changes in leaf structure (Sims and Pearcy 1992, Oguchi et al. 2003). *Acer saccharum* is a highly shade-tolerant species, and at the sapling stage it often does not respond positively to gap creation, because of stomatal limitation and slow leaf turnover rates (Naidu and DeLucia 1998).

Our overall results support the third hypothesis of a slow physiological acclimation response to gap creation driven by changes in leaf morphology. In the two years following gap creation, lower-canopy leaves of the gap trees began to take on morphological characteristics similar to those of upper-canopy leaves (Figure 2c–f). Morphological acclimation was gradual, and no significant differences in LMA were found until the second year post-harvest. A pattern of increasing LMA with increasing irradiance has been widely observed in other studies of acclimation to light gradients and is one of the best known patterns of photoacclimation both within canopies (Ellsworth and Reich 1993, Leal and Thomas 2003) and along natural light gradients in the understory (Ellsworth and Reich 1992a, Beaudet and Messier 1998). In addition, the lag in increasing LMA may be partially explained by the timing of the selection harvest, which occurred late in the growing season of 2002. Uemura et al. (2000) observed that the number of palisade layer cells is determined by the previous-year light environment, but that palisade cell length and all photosynthetic parameters (area based) are determined by the current-year light environment. In the first year of our study, the light environment in the lower canopy positions was low through the first half of the season before harvest. This suggests that during the first year post-harvest palisade tissue maintains the cell type and cell layer numbers of shade-acclimated leaves, but that the cells themselves acclimate to higher light, resulting in a leaf anatomy intermediate between that of sun- and shade-adapted leaves.

The observed increases in LMA (Figure 2e) without increased leaf area (Figure 2a) suggest nonstructural carbohydrate (NSC) accumulation (Frak et al. 2001). Because N_{mass} did not change during the study (Figure 3c, 3d), if NSC concentrations in leaves were increasing post-harvest, then C:N ratio would also be expected to increase. Although we did not determine NSC concentrations directly, increases in leaf thickness (31.8%) and density (25.3%) in the lower canopy two years post-harvest did not correspond to changes in C:N ratios (Figure 3i, Table 1). Short-term responses of LMA and other variables were negligible, suggesting that NSC accumulation was not involved in observed changes in LMA over either the short or long term. Similarly, Niinemets (1997b) observed no significant increase in NSC-free LMA in *Acer platanoides*

across a light gradient. Acclimation of leaf anatomical characteristics to increasing irradiance (Björkman 1981, Baltzer and Thomas 2005), specifically increased palisade layer thickness, are more likely the primary mechanism underlying the observed changes in LMA, leaf thickness, leaf tissue density, and area-based photosynthetic parameters. We suggest that the adaptive advantages of such anatomical changes, including increased convective heat dissipation (Schuepp 1993) and increased allocation to photosynthetic dark cycle reactions (Niinemets and Tenhunen 1997), may be of particular importance in the case of canopy trees subject to both enhanced limitations on water transport as well as enhanced demands on fixed carbon.

Several lines of evidence suggest that, although gap creation resulted in increased $A_{\max\text{-area}}$, g_s and N_{area} in lower-canopy leaves, such changes were essentially driven by morphological acclimation responses. First, we observed no changes in $A_{\max\text{-mass}}$ or related parameters (including N_{mass}) on any time scale. This result contrasts with prior studies of seedling and sapling physiological traits in which slight increases in $A_{\max\text{-mass}}$ in response to high irradiances have often (Ellsworth and Reich 1992b, Walters and Reich 1996, Kubiske and Pregitzer 1997, Clearwater et al. 1999), though not always (Grassi and Minotta 2000), been observed. Second, analysis of relationships between leaf nitrogen and photosynthetic capacity indicate a shift along preexisting patterns rather than a change in the pattern itself (i.e., no differences between gap and control trees along the N_{area} axis of variation) (Figures 6a and 6b). In addition, the relationship between N_{mass} and $A_{\max\text{-mass}}$ was not as strong as the $N_{\text{area}}-A_{\max\text{-area}}$ relationship and there was no apparent gradient between upper- and lower-canopy leaves or between sun and shade leaves as there was in the area-based relationship (Figure 6a). Niinemets and Tenhunen (1997) found a similar pattern and surmised that vertical gradients in $A_{\max\text{-area}}$ are due primarily to the increase in LMA and are unrelated to changes in leaf nitrogen itself. Third, a shift in N allocation from light-harvesting functions to rubisco and electron transport proteins might be expected to result in increased PNUE in gap trees compared with control trees (Niinemets and Tenhunen 1997, Frak et al. 2001). Although we found slight differences in PNUE between lower- and upper-canopy leaves as well as inter-annual variation, there was no difference in PNUE between gap and control trees in either the upper or lower portions of the canopy (Figures 5a and 5b, Table 1). These results are similar to those of Naidu and DeLucia (1998) and Kubiske and Pregitzer (1997) who observed no difference in PNUE in saplings exposed to increased irradiances. Likewise, we found no shifts in relationships between $A_{\max\text{-area}}$ or N_{area} and LMA between treatments, indicating that $A_{\max\text{-area}}$ and N_{area} are scaling directly to changes in LMA (Figures 7a and 7c). This pattern of responsiveness, which occurs along an axis of trait variation, has been documented among species (Reich et al. 1995) and seems to occur along a similar axis of variation within canopies of mature *Acer saccharum*.

Although not the primary focus of the study, our results bear on the mechanisms that account for vertical gradients in pho-

tosynthetic parameters in tree canopies. Many studies have assumed that such gradients are determined by direct acclimation responses to light (Niinemets and Valladares 2004); however, vertical gradients in hydraulic limitation have also been invoked recently (McDowell et al. 2002, Marshall and Monserud 2003, Woodruff et al. 2004). In addition, there is some evidence for effects of other micro-environmental parameters, such as light quality (Frak et al. 2002), and for effects of within-canopy variation in reproductive allocation and crown damage (Leal and Thomas 2003). Our results provide experimental evidence that light acclimation responses are of primary importance in *Acer saccharum*, though we cannot exclude influences of micro-environmental parameters that closely track irradiances. This result is consistent with studies that have simultaneously considered leaf height and ambient irradiance as statistical predictors of ecophysiological traits (Niinemets and Kull 1995, Poorter et al. 1995, Niinemets 1997a, Rijkers et al. 2000, Frak et al. 2002).

The ability of leaf morphology and physiology to track changes in light gradients in the canopy following disturbance is expected given the well documented strong static relationships between leaf traits and ambient light. However, we did not predict the long temporal scale over which leaf-level acclimation occurs or the degree to which leaf-level physiological parameters are driven by morphological acclimation responses. Our results indicate a multi-year lag in responses of area-based measures of photosynthesis that coincides with slow leaf morphological adjustments, potentially due to predetermined palisade layer and cell numbers (Uemura et al. 2000). Such slow acclimation responses may be a major cause for deviations between theoretically optimal and observed distributions of N and photosynthetic capacity in forest canopies (Niinemets and Valladares 2004). Growth responses of mature *Acer saccharum* trees show a suggestively similar lagged response, with little or no growth increase found during the first two years post-harvest (Jones and Thomas 2004); similar time-lags appear to be widespread among conifers (Youngblood 1991, Latham and Tappeiner 2002, Bebbler et al. 2004, Bevilacqua et al. 2005) and other temperate deciduous trees (Jones 2006). The match of temporal patterns is consistent with the hypothesis that slow acclimation is a primary cause for the time-lag in post-harvest growth responses, although additional mechanisms (such as slow release and uptake of nutrients released during harvests) may contribute to lagged growth responses. More generally, we speculate that slow physiological acclimation responses in mature tree canopies may represent an important but overlooked mechanism influencing forest growth dynamics in both managed and natural systems.

Acknowledgments

We thank Haliburton Forest and Wildlife Reserve for supporting our research as well as Jennifer Baltzer, Elise Benczkowski, Tomasz Gradowski, Rachel Mayberry, Tyler Peet, Megan Saprunoff, Hilary Thorpe and Liora Zimmerman for their contributions both in the field and in the laboratory. This research was supported the National Sciences and Engineering Research Council of Canada, the Ontario Pre-

mier's research excellence award program, and a University of Toronto Faculty of Forestry grant-in-aid.

References

- Baltzer, J.L. and S.C. Thomas. 2005. Leaf optical responses to light and soil nutrient availability in temperate deciduous trees. *Am. J. Bot.* 92:214–223.
- Beaudet, M. and C. Messier. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* 28:1007–1015.
- Beaudet, M. and C. Messier. 2002. Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. *Agric. For. Meteorol.* 110:217–228.
- Beaudet, M., C. Messier and A. Leduc. 2004. Understorey light profiles in temperate deciduous forests: recovery process following selection cutting. *J. Ecol.* 92:328–338.
- Bebber, D.P., S.C. Thomas, W.G. Cole and D. Balsillie. 2004. Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. *Trees* 18:29–34.
- Bevilacqua, E., D. Puttock, T. Blake and D. Burgess. 2005. Long-term differential stem growth responses in mature eastern white pine following release from competition. *Can. J. For. Res.* 35:511–520.
- Björkman, O. 1981. Responses to different quantum flux densities. *In* Encyclopedia of Plant Physiology, New Series, vol. 12a. Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H. Springer-Verlag, Berlin, pp 57–107.
- Bloor, J.M.G. and P.J. Grubb. 2004. Morphological plasticity of shade-tolerant tropical rain forest tree seedlings exposed to light changes. *Funct. Ecol.* 18:337–348.
- Brooks, J.R., D.G. Sprugel and T.M. Hinckley. 1996. The effects of light acclimation during and after foliage expansion on photosynthesis of *Abies amabilis* foliage within the canopy. *Oecologia* 107:21–32.
- Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20:620–631.
- Cavender-Bares, J. and F.A. Bazzaz. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 124:8–18.
- Claussen, J.W. 1996. Acclimation abilities of three tropical rain forest seedlings to an increase in light intensity. *For. Ecol. Manage.* 80:245–255.
- Clearwater, M.J., R. Susilawaty, R. Effendi and P.R. van Gardingen. 1999. Rapid photosynthetic acclimation of *Shorea johorensis* seedlings after logging disturbance in central Kalimantan. *Oecologia* 121:478–488.
- Clinton, B.D. 2003. Light, temperature, and soil moisture responses to elevation, evergreen understory, and small, canopy gaps in the southern Appalachians. *For. Ecol. Manage.* 186:243–255.
- Ellsworth, D.S. and P.B. Reich. 1992a. Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. *Funct. Ecol.* 6:423–435.
- Ellsworth, D.S. and P.B. Reich. 1992b. Water relations and gas exchange of *Acer saccharum* seedlings in contrasting natural light and water regimes. *Tree Physiol.* 10:1–20.
- Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96:169–178.
- Frak, E., X. Le Roux, P. Millard, B. Adam, E. Dreyer, C. Escuit, H. Sinoquet, M. Vandame and C. Varlet-Grancher. 2002. Spatial distribution of leaf nitrogen and photosynthetic capacity within the foliage of individual trees: disentangling the effects of local light quality, leaf irradiance, and transpiration. *J. Exp. Bot.* 53:2207–2216.
- Frak, E., X. Le Roux, P. Millard, E. Dreyer, G. Jaouen, B. Saint-Joanis and R. Wendler. 2001. Changes in total leaf nitrogen and partitioning of leaf nitrogen drive photosynthetic acclimation to light in fully developed walnut leaves. *Plant Cell Environ.* 24:1279–1288.
- Frazer, G.W., C.D. Canham and K.P. Lertzman. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Givnish, T.J. 1988. Adaptation to sun and shade—a whole-plant perspective. *Australian J. Plant Physiol.* 15:63–92.
- Graham, E.A., S.S. Mulkey, K. Kitajima, N.G. Phillips and S.J. Wright. 2003. Cloud cover limits net CO₂ uptake and growth of a rain forest tree during tropical rainy seasons. *Proc. Natl. Acad. Sci. USA* 100:572–576.
- Grassi, G. and G. Minotta. 2000. Influence of nutrient supply on shade-sun acclimation of *Picea abies* seedlings: effects on foliar morphology, photosynthetic performance and growth. *Tree Physiol.* 20:645–652.
- Gray, A.N., T.A. Spies and M.J. Easter. 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can. J. For. Res.* 32:332–343.
- Huante, P. and E. Rincon. 1998. Responses to light changes in tropical deciduous woody seedlings with contrasting growth rates. *Oecologia* 113:53–66.
- Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus Ponderosa* trees. *Tree Physiol.* 19:165–172.
- Jones, T.A. 2006. Growth and physiological responses of canopy tree species to selection harvests in a northern hardwood forest. Ph.D. thesis, Faculty of Forestry, University of Toronto, Toronto, ON, Canada, 149 p.
- Jones, T.A. and S.C. Thomas. 2004. The time course of diameter increment responses to selection harvests in *Acer saccharum*. *Can. J. For. Res.* 34:1525–1533.
- Kitao, M., T.T. Lei, T. Koike, H. Tobita and Y. Maruyama. 2000. Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. *Plant Cell Environ.* 23:81–89.
- Krause, G.H., O.Y. Koroleva, J.W. Dalling and K. Winter. 2001. Acclimation of tropical tree seedlings to excessive light in simulated tree-fall gaps. *Plant Cell Environ.* 24:1345–1352.
- Kubiske, M.E. and K.S. Pregitzer. 1997. Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO₂. *Funct. Ecol.* 11:24–32.
- Latham, P. and J. Tappeiner. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiol.* 22:137–146.
- Leal, D.B. and S.C. Thomas. 2003. Vertical gradients and tree-to-tree variation in shoot morphology and foliar nitrogen in an old-growth *Pinus strobus* stand. *Can. J. For. Res.* 33:1304–1314.
- Lovelock, C.E., M. Jebb and C.B. Osmond. 1994. Photoinhibition and recovery in tropical plant-species—response to disturbance. *Oecologia* 97:297–307.
- Maggs, D.H. 1964. The distance from tree base to shoot origin as a factor in shoot and tree growth. *J. Hort. Sci.* 39:298–307.

- Marshall, J.D. and R.A. Monserud. 2003. Foliage height influences specific leaf area of three conifer species. *Can. J. For. Res.* 33:164–170.
- McDowell, N.G., N. Phillips, C. Lurch, B.J. Bond and M.G. Ryan. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiol.* 22:763–774.
- Mulkey, S.S. and R.W. Pearcy. 1992. Interactions between acclimation and photoinhibition of photosynthesis of a tropical forest understorey herb, *Alocasia macrorrhiza*, during simulated canopy gap formation. *Funct. Ecol.* 6:719–729.
- Naidu, S.L. and E.H. DeLucia. 1997a. Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. *Tree Physiol.* 17:367–376.
- Naidu, S.L. and E.H. DeLucia. 1997b. Growth, allocation and water relations of shade-grown *Quercus rubra* L. saplings exposed to a late-season canopy gap. *Ann. Bot.* 80:335–344.
- Naidu, S.L. and E.H. DeLucia. 1998. Physiological and morphological acclimation of shade-grown tree seedlings to late-season canopy gap formation. *Plant Ecol.* 138:27–40.
- Newell, E.A., E.P. McDonald, B.R. Strain and J.S. Denslow. 1993. Photosynthetic responses of *Miconia* species to canopy openings in a lowland tropical rain-forest. *Oecologia* 94:49–56.
- Niinemets, U. 1997a. Distribution patterns of foliar carbon and nitrogen as affected by tree dimensions and relative light conditions in the canopy of *Picea abies*. *Trees* 11:144–154.
- Niinemets, U. 1997b. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Funct. Ecol.* 11:518–531.
- Niinemets, U. and O. Kull. 1995. Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*—variation in shoot structure. *Tree Physiol.* 15:791–798.
- Niinemets, U. and J.D. Tenhunen. 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant Cell Environ.* 20:845–866.
- Niinemets, U. and F. Valladares. 2004. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. *Plant Biol.* 6:254–268.
- Oguchi, R., K. Hikosaka and T. Hirose. 2003. Does the photosynthetic light-acclimation need change in leaf anatomy? *Plant Cell Environ.* 26:505–512.
- OMNR. 1998. A silvicultural guide for the tolerant hardwood forest in Ontario. Ontario Min. of Nat. Resour. Queen's Printer for Ontario, Toronto, 500 p.
- Parker, W.C. and G.H. Mohammed. 2000. Photosynthetic acclimation of shade-grown red pine (*Pinus resinosa* Ait.) seedlings to a high light environment. *New For.* 19:1–11.
- Poorter, L., S.F. Oberbauer and D.B. Clark. 1995. Leaf optical properties along a vertical gradient in a tropical rain forest canopy in Costa Rica. *Am. J. Bot.* 82:1257–1263.
- Popma, J. and F. Bongers. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain-forest species. *Oecologia* 75:625–632.
- Reich, P.B., B.D. Kloeppel, D.S. Ellsworth and M.B. Walters. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104:24–30.
- Rijkers, T., T.L. Pons and F. Bongers. 2000. The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Funct. Ecol.* 14:77–86.
- Ritter, E., L. Dalsgaard and K.S. Eirhorn. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *For. Ecol. Manage.* 206:15–33.
- Schuepp, P.H. 1993. Leaf boundary-layers. *Tansley Review No. 59. New Phytol.* 125:477–507.
- Shimizu, M., A. Ishida, T. Tange and H. Yagi. 2006. Leaf turnover and growth responses of shade-grown saplings of four *Shorea* rain forest species to a sudden increase in light. *Tree Physiol.* 26:449–457.
- Sims, D.A. and R.W. Pearcy. 1992. Response of leaf anatomy and photosynthetic capacity in *Alocasia macrorrhiza* (Araceae) to a transfer from low to high light. *Am. J. Bot.* 79:449–455.
- Smith, D.M., B.C. Larson, M.J. Kelty and P.M.S. Ashton. 1997. The practice of silviculture: Applied forest ecology. John Wiley and Sons, Inc., New York, 560 p.
- Thomas, S.C. 1996. Reproductive allometry in Malaysian rain forest trees: biomechanics versus optimal allocation. *Evol. Ecol.* 10: 517–530.
- Thomas, S.C. and W.E. Winner. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiol.* 22:117–127.
- Tognetti, R., J.D. Johnson and M. Michelozzi. 1997. Ecophysiological responses of *Fagus sylvatica* seedlings to changing light conditions. 1. Interactions between photosynthetic acclimation and photoinhibition during simulated canopy gap formation. *Physiol. Plant.* 101:115–123.
- Turnbull, M.H., D. Doley and D.J. Yates. 1993. The dynamics of photosynthetic acclimation to changes in light quantity and quality in 3 Australian rain-forest tree species. *Oecologia* 94:218–228.
- Uemura, A., A. Ishida, T. Nakano, I. Terashima, H. Tanabe and Y. Matsumoto. 2000. Acclimation of leaf characteristics of *Fagus* species to previous-year and current-year solar irradiances. *Tree Physiol* 20:945–951.
- Valladares, F., J.M. Chico, I. Aranda, L. Balaguer, P. Dizengremel, E. Manrique and E. Dreyer. 2002. The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees* 16:395–403.
- Walters, M. and P. Reich. 1996. Are shade tolerance, survival, and growth linked? Low light and, nitrogen effects on hardwood seedlings. *Ecology* 77:841–853.
- Woodruff, D.R., B.J. Bond and F.C. Meinzer. 2004. Does turgor limit growth in tall trees? *Plant Cell Environ.* 27:229–236.
- Yamashita, N., A. Ishida, H. Kushima and N. Tanaka. 2000. Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. *Oecologia* 125:412–419.
- Yamashita, N., N. Koike and A. Ishida. 2002. Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status. *Plant Cell Environ.* 25: 1341–1356.
- Youngblood, A.P. 1991. Radial growth after a shelterwood seed cut in a mature stand of white spruce in interior Alaska. *Can. J. For. Res.* 21:410–413.