

Ecophysiology and growth of advance red spruce and balsam fir regeneration after partial cutting in yellow birch–conifer stands

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Summary We investigated ecophysiological and growth responses of short (0.4 to 1.3 m in height) advance regeneration of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* L.) six years after removal of 0, 40, 50, 60 and 100% of the overstory basal area (BA) in two yellow birch–conifer stands. Partial cuts significantly increased stomatal conductance of red spruce only. Light-saturated photosynthesis (leaf-area basis) of both species increased with BA removal, but unlike red spruce, specific leaf area (SLA) of balsam fir decreased with increased cutting intensity. Partial cuts appreciably increased the concentration of N and Ca in red spruce and balsam fir foliage, respectively, and resulted in decreased foliar concentrations of K in red spruce and Mg in balsam fir. The height and lateral growth of both species increased with BA removal, although partial cuts were more beneficial to balsam fir. The data suggest that short advance regeneration of red spruce and balsam fir can coexist under partial overstory conditions, but balsam fir has physiological characteristics and a capacity for morphological adjustment (SLA) that places it at an advantage when in competition with red spruce.

Keywords: crown morphology, gas exchange, natural regeneration, nutrient status, partial overstory, photosynthetic acclimation, specific leaf area, temperate mixed-wood forest, water stress.

Introduction

Red spruce (*Picea rubens* Sarg.) is a conifer found exclusively in northeastern North America. It can live for 400 years and its wood is prized by both the forest industry and specialized industries such as manufacturers of musical instruments. A forest management strategy unsuited to the ecophysiological characteristics of red spruce has caused a scarcity of the species in its natural range (Dumais and Prévost 2007). Red spruce seedlings and saplings are well adapted to partial shade (Alexander et al. 1995, Major et al. 2003) and to cool conditions (Vann et al. 1994, Day 2000) found under a partial overstory or in gaps smaller than 800 m² (Kneeshaw and Prévost 2007). Natural canopy openings created by windthrow

and insect epidemics are therefore the ecological basis of red spruce regeneration (Foster and Reiners 1983, White et al. 1985), and long-term conservation of this shade-tolerant species depends, largely, on advance regeneration.

Studies, cited in Dumais and Prévost (2007), indicate that partial overstory removal favors physiological acclimation and subsequent growth of red spruce advance regeneration. However, several authors have shown that balsam fir (*Abies balsamea* L.) advance regeneration generally has better juvenile growth, and can adapt more rapidly than red spruce to increased irradiances after canopy opening (Davis 1989, Moores et al. 2007, Pothier and Prévost 2008). Although juvenile growth of these species has often been compared, there is a need to study the specific ecophysiological characteristics of red spruce and balsam fir to explain the difference in their growth under partial overstory conditions.

It is well known that canopy opening causes some stress to advance regeneration, especially to that of species adapted to low-light (Tucker et al. 1987, Mohammed and Parker 1999). The capacity for, and rate of, physiological and morphological acclimation to increased solar irradiance differ among species (Renninger et al. 2007). Acclimation may require years and cause a delay in the onset of significant shoot growth, because the majority of carbohydrates are being allocated to root growth (Kneeshaw et al. 2002). Once advance regeneration has fully acclimated, shoot growth should be favored by the new conditions. However, the moderate light conditions that are essential for survival and physiological acclimation of red spruce after canopy opening may not be optimal for subsequent growth, especially when there is competition from balsam fir (see Blum 1990, Seymour 1995).

We investigated physiological and growth responses of short advance regeneration of red spruce and balsam fir following removal of varying proportions of the overstory. We predicted that the shoot growth response in both species would be more perceptible a few years after overstory removal when full acclimation has occurred than immediately after cutting. We hypothesized that physiological and morphological responses differ between red spruce and balsam fir and that relative growth performance can be explained by differences in ecophysiological characteristics.

Materials and methods

Study sites and experimental design

The study was carried out in two yellow birch (*Betula alleghaniensis* Britt.)–conifer stands in eastern Quebec, Canada. The Armagh site (46°50' N, 70°32' W) is located in the sugar maple (*Acer saccharum* Marsh.)–yellow birch bioclimatic domain, and the Duchesnay site (46°54' N, 71°41' W) is in the balsam fir–yellow birch bioclimatic domain. The stands at both sites are composed mainly of yellow birch, red spruce, balsam fir and red maple (*A. rubrum* L.). Sugar maple, paper birch (*B. papyrifera* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) are present as companion species. The stands have an uneven-aged structure and the coniferous advance regeneration is dominated by red spruce and balsam fir seedlings and saplings.

At each location, the study comprised three completely randomized blocks, each containing five treatments: removal of 0, 40, 50, 60 and 100% of merchantable basal area (BA). The study sites and the complete experimental design are described in detail in Prévost (2008).

Plant material

Six years after cutting, the study was carried out on advance red spruce and balsam regeneration, varying from 0.4 to 1.3 m in height, which had been randomly selected in a 50 × 50 m central plot of each experimental unit (EU). The selected trees were free of insect pests, pathogens and morphological defects. Information about microtopography, neighboring vegetation and canopy opening were noted. When necessary, tree selection was adjusted to cover a variety of microenvironmental conditions.

Ecophysiological parameters

Field measurements were made on three red spruce trees per EU at Armagh (2003) and on three red spruce and two balsam fir trees per EU at Duchesnay (2004). Sampling was conducted on three dates (mid-July, mid-August and mid-September). Gas exchange measurements were carried out at ambient CO₂ concentration (about 390 ppm) on a 1-year-old shoot (4 cm in length) on a randomly selected lateral branch in the upper half of each tree. Measurements were confined to 1-year-old foliage because bud break in red spruce is late and new foliage is too fragile to be handled easily without damage in midsummer. The use of 1-year-old foliage may also be justified by the major contribution it makes to the photosynthetic production of the crown (Zimmermann et al. 1988) and because the influence of developing needles can be avoided (Radoglou and Teskey 1997), which is desirable because net photosynthesis generally increases during needle development, but in an unpredictable way depending on light conditions. Light-saturated photosynthetic rate ($A_{\max}$), stomatal conductance (G) and the ratio of intercellular to ambient CO₂ concentration (C_i/C_a) were measured between 1000 and 1530 h, solar time, with a photosynthesis system (LCA4, Analytical Development, Hoddesdon, U.K.) equipped with a 0.2-l

chamber. Preliminary tests indicated that $A_{\max}$ occurred at a photosynthetic photon flux (PPF) of about 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Ambient light was supplemented with light from a 20-W dichroic halogen lamp unit adapted to fit the chamber lid to ensure that PPF remained slightly above the target value for light saturation. Air temperature and relative humidity inside the chamber were recorded. After the gas exchange measurements, the shoot was severed and shoot water potential (Ψ_d) measured with a pressure chamber (Model 600, PMS Instruments, Corvallis, OR). The shoot was then enclosed in a plastic bag, and placed in a cooler for transport to the laboratory. Shoots were frozen later the same day in a cold room ($-5 \pm 1^\circ\text{C}$) in preparation for subsequent analyses. The ecophysiological measurements in the clearcut were conducted once (mid-August) in one block at each site.

The needles of each shoot used for gas exchange measurements were scanned and their total projected area determined with imaging software (WinSEEDLE, Régent Instruments, Québec, QC). Current-year, 1-year-old, and the remaining foliage of each shoot was then separated, dried at 65 °C for 48 h, and weighed.

Analyses of the main foliar elements were performed on 100 mg of ground dry needles. Foliage was digested with concentrated sulfuric acid in the presence of selenium and hydrogen peroxide at 370 °C for 1 h (Walinga et al. 1995). Concentrations of phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) were measured by plasma atomic emission spectrometry (ICAP 61E, Thermo Jarrel Ash Instruments, Franklin, MA). Nitrogen (N) Kjeldahl was measured by calorimetry (Quickchem 8000, Lachat Instruments, Milwaukee, WI).

Morphological parameters

The 1-year-old foliage used for gas exchange measurements was also used to determine specific leaf area (SLA). The other morphological measurements were taken on at least eight red spruce and five balsam fir trees per EU, including those used for physiological measurements. Initial height (H_0), final height (H_6), final diameter (D_6), height growth (HG) and lateral growth (LG) were measured. For HG, post-cutting internode increments (T_1 to T_6) were measured. Only one branch per whorl was randomly chosen for LG measurements, and each branch increment adjacent to T_1 to T_6 was measured. The degree of apical control was assessed based on the annual HG/LG ratio (Greis and Kellomäki 1981).

Data analysis

Statistics were performed by analyses of variance (and covariance), and contrasts were used to separate treatment effects into simple degrees of freedom ($P \leq 0.05$). For both locations, site was considered a random effect. The ecophysiology of each species was analyzed separately (balsam fir was investigated only at Duchesnay). The relationships between morphological parameters and H_0 were subjected to regression analysis to determine the pertinence of using H_0 as a covariate in the model (covariance analysis). Homogeneity of variances and normality of data were verified graphically. To satisfy the

Table 1. Analyses of variance and associated probabilities ($P > F$) for effects of treatment and sampling date on daytime shoot water potential (Ψ_d), stomatal conductance (G), light-saturated photosynthesis on a surface-area basis ($A_{\max}$), ratio of intercellular to ambient CO_2 concentration (C_i/C_a), specific leaf area (SLA), and concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) measured in 1-year-old foliage of advance regeneration of *Picea rubens*.

Source of variation	df ¹	Ψ_d	G	$A_{\max}$	C_i/C_a	SLA	N	P	K	Ca	Mg
Cutting (C)	3	0.7272	0.0198	0.0048	0.5484	0.1864	0.0005	0.7374	0.1257	0.1759	0.6471
C linear (lin)	(1)	0.3069	0.0104	0.0008	0.4962	0.4132	< 0.0001	0.8482	0.0250	0.0498	0.3452
Time (T)	2	0.0016	0.0968	0.0040	0.0159	0.0011	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0001
T lin	(1)	0.0005	0.5131	0.0028	0.0357	0.0987	< 0.0001	< 0.0001	0.6001	< 0.0001	0.0004
T quadratic (qua)	(1)	0.4082	0.0402	0.1293	0.2435	0.0008	0.2359	0.0020	< 0.0001	0.0958	0.0111
$C \times T$	6	0.1793	0.0085	0.4760	0.2160	0.5393	0.9075	0.5560	0.0423	0.4322	0.1118
C lin $\times T$ qua	(1)	0.2124	0.0330	0.9645	0.1367	0.0800	0.6264	0.9476	0.0213	0.1327	0.2176
C qua $\times T$ qua	(1)	0.3110	0.0395	0.2770	0.4658	0.7497	0.5123	0.9127	0.5615	0.6797	0.9123

¹ Degrees of freedom of numerator; values in parentheses refer to contrasts. To simplify table presentation, degrees of freedom of denominator, some nonsignificant or less important fixed effects and contrasts, as well as all random effects are not shown.

assumptions of variance (and covariance) analysis, a square root transformation was used for HG and LG analyses, and data were retransformed into their original form for presentation. Statistical analyses were not conducted on the physiological parameters measured in the clearcut, because only a few red spruce survivors were available.

Results

Daytime shoot water potential

Partial overstory removal did not significantly affect Ψ_d in either species (Tables 1 and 2). However, Ψ_d in red spruce was 34% lower in the clearcut than in the partial cuts, whereas clearcutting only slightly reduced Ψ_d in balsam fir (Figure 1). In both species, Ψ_d increased linearly with time ($P \leq 0.0542$, data not shown).

Stomatal conductance and photosynthesis

In red spruce, G increased quadratically with partial BA removal, but the effect was less pronounced in August

($P = 0.0395$, Table 1, Figure 1). In balsam fir, G did not increase significantly following partial cutting (Table 2). In the clearcut, G in red spruce was 19% higher than in the partial cuts, whereas G in balsam fir did not differ appreciably.

In both species, area-based $A_{\max}$ increased linearly with partial BA removal ($P \leq 0.0348$, Tables 1 and 2, Figure 1), and values were higher in the clearcut (+39% for red spruce and +59% for balsam fir) than in the partial cuts. The $A_{\max}$ in both species also increased with time, exhibiting a linear relationship for red spruce ($P = 0.0028$), and a quadratic relationship for balsam fir ($P = 0.0056$, data not shown). Mass-based $A_{\max}$ increased linearly with partial BA removal in red spruce ($P = 0.0020$). Although $A_{\max}$ did not change significantly with BA removal in balsam fir, it was 18% lower in the clearcut than in the partial cuts. Cutting did not significantly affect the C_i/C_a ratio in either species, but values decreased linearly with time ($P \leq 0.0357$, Tables 1 and 2, data not shown).

Specific leaf area

Partial cuts did not significantly affect SLA in red spruce (Table 1), but it was 26% lower in the clearcut than in other treat-

Table 2. Analyses of variance and associated probabilities ($P > F$) for effects of treatment and sampling date on daytime shoot water potential (Ψ_d), stomatal conductance (G), light-saturated photosynthesis ($A_{\max}$) on surface-area basis, ratio of intercellular to ambient CO_2 concentration (C_i/C_a), specific leaf area (SLA), and concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) measured in 1-year-old foliage of advance regeneration of *Abies balsamea*.

Source of variation	df ¹	Ψ_d	G	$A_{\max}$	C_i/C_a	SLA	N	P	K	Ca	Mg
Cutting (C)	3	0.7800	0.3234	0.0997	0.7480	< 0.0001	0.3332	0.4611	0.2458	0.1136	0.0914
C linear (lin)	(1)	0.6053	0.0978	0.0348	0.4003	< 0.0001	0.7691	0.5268	0.1099	0.0369	0.0380
Time (T)	2	0.0055	0.6395	0.0038	0.0066	0.3218	< 0.0001	< 0.0001	0.0324	0.4533	0.3454
T lin	(1)	0.0542	0.3738	0.0486	0.0042	0.1762	< 0.0001	< 0.0001	0.0117	0.4523	0.1796
T quadratic	(1)	0.0820	0.9027	0.0056	0.1530	0.2901	0.6882	0.2236	0.5330	0.3350	0.5927
$C \times T$	6	0.2180	0.5339	0.2416	0.2679	0.6323	0.7027	0.8494	0.9598	0.4519	0.6891

¹ Degrees of freedom of numerator; values in parentheses refer to contrasts. In order to simplify table presentation, degrees of freedom of denominator, some nonsignificant or less important fixed effects and contrasts, as well as all random effects, are not shown.

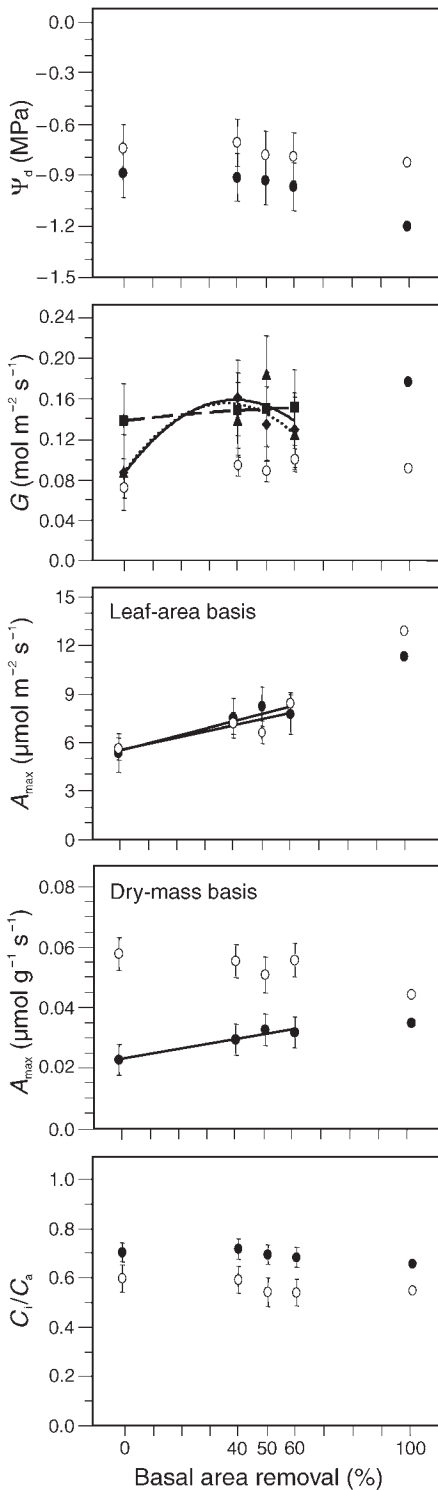


Figure 1. Relationship between basal area removal and daytime shoot water potential (Ψ_d), stomatal conductance (G), light-saturated photosynthesis ($A_{\max}$), ratio of intercellular to ambient CO_2 concentration (C_i/C_a), measured in 1-year-old foliage of *Picea rubens* (●) and *Abies balsamea* (○). For date interaction: July = ▲ with solid line; August = ■ with dashed line; September = ◆ with dotted line). Values are the mean of 18 spruces (six in the clearcut, no statistic) and six firs (two in the clearcut, no statistic). Otherwise, values are the mean of all dates (54 spruces, six in the clearcut, and 18 firs, two in the clearcut). Vertical bars represent standard errors.

ments (Figure 2). Unlike balsam fir, SLA in red spruce varied with time, increasing from July to August and decreasing in September ($P = 0.0008$, data not shown). In balsam fir, SLA decreased linearly with increasing removal of BA ($P < 0.0001$, Table 2) and was 42% lower in the clearcut than in the partial cuts. In general, SLA was higher in balsam fir than in red spruce.

Nutrient concentrations in 1-year-old foliage

Foliar concentrations of N, P and K in both species, and Ca and Mg in red spruce, increased with time ($P \leq 0.0324$, Tables 1 and 2, data not shown). In red spruce, N concentration increased linearly with partial BA removal ($P < 0.0001$, Figure 3), but in balsam fir, N concentration was not significantly affected. Partial cuts did not significantly affect P concentrations in either species. In red spruce, the difference in foliar K concentrations among cutting intensities increased significantly over time ($P = 0.0213$). Partial cuts did not significantly affect K concentration in balsam fir. Potassium concentration was lower in the clearcut than in the partial cuts. In both species, Ca concentration increased linearly with partial BA removal ($P \leq 0.0498$), but the effect was less pronounced in red spruce (Figure 3). In the clearcut, Ca concentration in balsam fir was higher than in the partial cuts. Partial cutting did not significantly affect Mg concentration in red spruce, whereas in balsam fir it decreased linearly with increasing partial BA removal ($P = 0.0380$), and was 26% lower in the clearcut than in the partial cuts. Similar responses were observed in current-year foliage, but with concentrations being higher than in 1-year-old foliage (data not shown).

Height and diameter

The H_0 decreased linearly with increasing BA removal ($P < 0.0001$, Table 3, data not shown), but it differed little among the partial cutting treatments (Figure 4). Red spruce was initially taller than balsam fir (54 versus 45 cm; $P < 0.0001$). Both H_6 and D_6 increased linearly with BA removal ($P < 0.0001$, data not shown). Balsam fir surpassed red spruce ($P = 0.0004$), because of a superior H_6 in the partial cuts ($P = 0.0186$). Compared with the control (12 mm) and the clearcut (26 mm), D_6 was similar in all the partial cuts (16 to 17 mm).

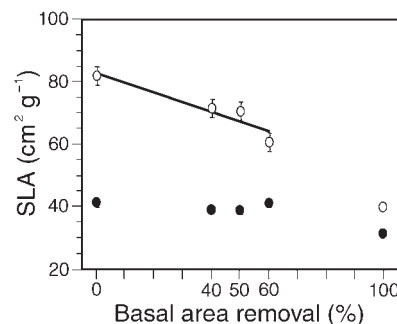


Figure 2. Relationship between basal area removal and specific leaf area (SLA) measured in 1-year-old foliage of *Picea rubens* (●) and *Abies balsamea* (○). Values are the mean of 54 spruces (six in the clearcut, no statistic) and 18 firs (two in the clearcut, no statistic). Vertical bars represent standard errors.

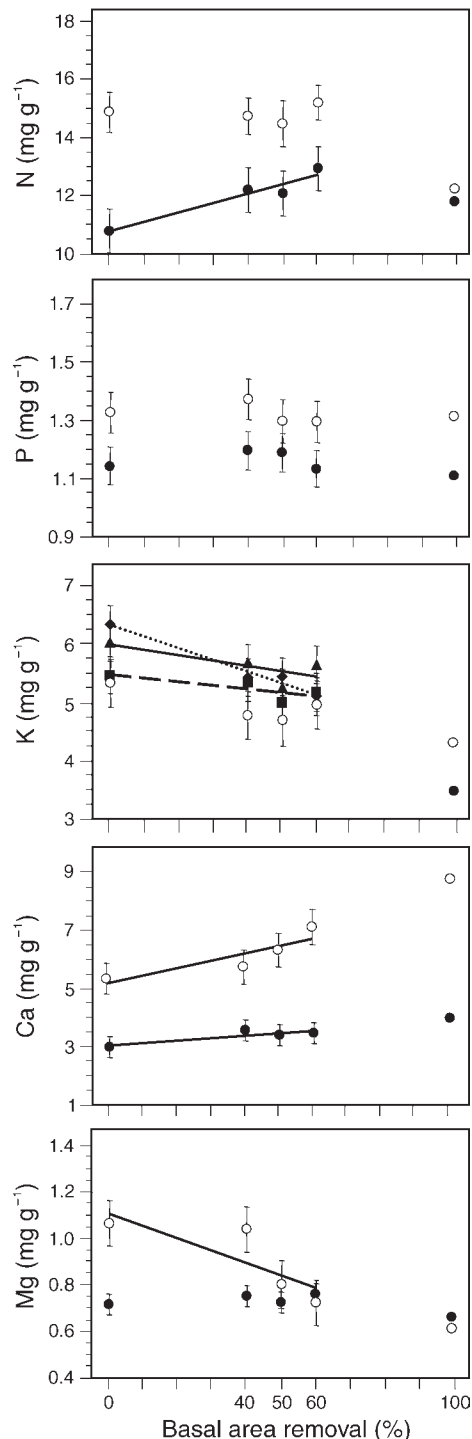


Figure 3. Relationship between basal area removal and concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg), in 1-year-old foliage of *Picea rubens* (●) and *Abies balsamea* (○). For date interaction: July = ▲ with solid line; August = ■ with dashed line; September = ◆ with dotted line. Values are the mean of 18 spruces (six in the clearcut, no statistic) and six firs (two in the clearcut, no statistic). Otherwise, values are the mean of 54 spruces (six in the clearcut, no statistic) and 18 firs (two in the clearcut, no statistic). Vertical bars represent standard errors.

Height growth, lateral growth and apical control

In both species, HG increased linearly with BA removal ($P < 0.0001$, Table 3, data not shown). Balsam fir grew more rapidly than red spruce ($P = 0.0002$, Figure 4), and showed higher gains in partial cuts (6 cm year^{-1}) than red spruce (4 cm year^{-1}). Response over time was cubic ($P = 0.0427$), and the differences among the cutting intensities and the species changed significantly over time ($P = 0.0002$).

Lateral growth increased quadratically with BA removal ($P = 0.0196$, Table 3, data not shown). Balsam fir grew more rapidly than red spruce ($P < 0.0001$, Figure 4), and showed greater gains in partial cuts than red spruce. Differences in LG among the cutting intensities changed significantly between species ($P = 0.0311$, data not shown). Response of LG over time was cubic ($P = 0.0303$), and the differences among the cutting intensities and the differences among species both changed significantly over time ($P < 0.0001$).

The HG/LG ratio increased linearly with BA removal ($P < 0.0001$, Table 3, data not shown) and the effect was more pronounced in red spruce than in balsam fir ($P = 0.0048$). Response of HG/LG over time was cubic ($P = 0.0230$, Figure 4), and the differences among the cutting intensities and species changed significantly over time ($P = 0.0214$).

Discussion

Physiological responses

Our measurements on the water relations of red spruce and balsam fir 6 years after treatment showed that both species acclimated to the conditions created by partial cutting. Even in the clearcut, where mean Ψ_d of red spruce fell to -1.2 MPa , we observed no decline in gas exchange (Figure 1). Under partial overstory conditions, the C_i/C_a ratio in both species did not differ with cutting intensity, indicating that G did not limit $A_{\max}$ (Stewart and Bernier 1995). Compared with balsam fir, high G in red spruce corresponded to lower Ψ_d , suggesting that the higher water stress observed in red spruce was caused by higher transpirational losses. Results of other studies suggest that red spruce trees generally have higher transpiration rates than balsam fir trees (Alexander et al. 1995, Reinhardt and Smith 2008). Partial overstory removal improved $A_{\max}$ similarly in both red spruce and balsam fir, indicating comparable photosynthetic acclimation in these species. Increases in $A_{\max}$ with increasing light exposure are reported for spruce and fir species, although such adjustments are not a general rule. For example, Norway spruce (*Picea abies* (L.) Karst.) can acclimate to high PPF by increasing $A_{\max}$ (Grassi and Bagnaresi 2001, Stancioiu and O'Hara 2006). In contrast, Black et al. (2005) observed no $A_{\max}$ difference between fully exposed and 50% shaded-shoots of Sitka spruce (*P. sitchensis* (Bong.) Carr.). Johnson and Smith (2005) found that $A_{\max}$ in Fraser fir (*Abies fraseri* (Pursh) Poiret) was higher at open-canopy sites than at closed-canopy sites. However, Landhäusser and Lieffers (2001) observed little plasticity of $A_{\max}$ in balsam fir compared with white spruce. Pothier and Prévost (2002) also reported no effects of 0, 35, 50, 65 and 100% BA removals on

Table 3. Analyses of variance (covariance) and associated probabilities ($P > F$) for effects of treatment and sampling date on initial height (H_0), final height (H_6), final diameter (D_6), height growth (HG), lateral shoot growth (LG) and HG/LG ratio, measured on advance regeneration of *Picea rubens* and *Abies balsamea*.

Source of variation	df ¹	H_0	H_6	D_6	HG	LG	HG/LG
H_0	1	–	< 0.0001	< 0.0001	< 0.0001	–	–
Cutting (C)	4	0.0008	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
C linear (lin)	(1)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
C quadratic (qua)	(1)	0.1586	0.4729	0.0531	0.2701	0.0196	0.8422
Species (S)	1	< 0.0001	0.0004	0.0537	0.0002	< 0.0001	< 0.0001
$S \times C$	4	0.2054	0.1340	0.8457	0.1801	0.2363	0.0159
$S \times C$ lin	(1)	0.1893	0.7996	0.4851	0.1668	0.0311	0.0048
$S \times C$ qua	(1)	0.9558	0.0186	0.6654	0.1100	0.2545	0.0806
Time (T)	5	–	–	–	< 0.0001	< 0.0001	< 0.0001
T cubic	(1)	–	–	–	0.0427	0.0303	0.0230
$C \times T$	20	–	–	–	< 0.0001	< 0.0001	< 0.0001
$S \times T$	5	–	–	–	< 0.0001	< 0.0001	< 0.0001
$S \times C \times T$	20	–	–	–	0.0002	0.1744	0.0214

¹ Degrees of freedom of numerator; values in parentheses refer to contrasts. To simplify table presentation, some nonsignificant or less important fixed effects and contrasts, as well as all random effects, are not shown.

balsam fir $A_{\max}$ in a trembling aspen–conifer stand, 3 and 4 years after cutting.

Specific leaf area response

Generally, an increase in solar irradiance results in the modifications in leaf anatomy and morphology (Tucker et al. 1987, Grassi and Bagnaresi 2001). We observed a significant decrease in SLA in balsam fir with increasing light (Figure 2), which accords with several studies on fir species (Tucker et al. 1987, Pothier and Prévost 2002, Mori and Takeda 2004, Stancioiu and O'Hara 2006). However, partial overstory removal did not change SLA in red spruce. Day et al. (2001) also reported similar SLA values for sun and shade foliage of young red spruce trees. Other studies reported that SLA values in white spruce and Norway spruce were greater in shade than in exposed areas (Man and Lieffers 1997, Grassi and Bagnaresi 2001, Grassi and Giannini 2005). Our data indicate a decrease in SLA in red spruce in the clearcut only (Figure 2), suggesting that a larger increase in PPF is required for SLA acclimation in red spruce compared with balsam fir.

Foliage nutrient concentrations

Effects of partial overstory removal on nutrient availability and uptake are not well known (Kranabetter and Coates 2004), and our results provide new information for red spruce and balsam fir. Concentrations of N in 1-year-old needles of red spruce increased with increasing partial BA removal (Figure 3), which may be explained by higher allocation to the upper part of the shoots or to sun needles in response to an increase in PPF (Hollinger 1996, Stenberg et al. 1998). Furthermore, a reduction in the living root system at the stand level can contribute to increased N availability for the residual trees (Vitousek and Matson 1985). In the clearcut, lower foliar N

concentration suggests increased leaching or an important post-cut uptake by competitive species. Likewise, the decrease in K concentration in red spruce foliage and a similar trend for balsam fir may reflect post-cut leaching of this mobile element (Rosén and Lundmark-Thelin 1987, Duchesne and Houle 2006) or assimilation by neighboring vegetation. Lower K concentrations were also observed by Richardson (2004) in sun needles compared with shade needles for both red spruce and balsam fir, suggesting a lower K allocation under conditions of higher PPF. Our results indicate that the impact of overstory removal on divalent cations Ca and Mg was clearly detectable in balsam fir only. The observed increase in foliar Ca concentration with increasing partial BA removal is in line with results of Richardson (2004) who observed higher Ca concentrations in sun needles of balsam fir compared with shade needles. Furthermore, the decrease in foliar Mg concentration with increasing partial BA removal in our study is similar to results reported by from Kranabetter and Coates (2004) for hybrid spruce (*P. glauca* (Moench) Voss $\times$ *P. sitchensis*). In our study, foliar concentrations of N, P, Ca and Mg were consistently higher for balsam fir than for red spruce, whereas K concentrations were similar for both species, which accords with the findings of Richardson (2004).

Growth responses

Water relations, gas exchange and growth patterns suggest that, after a few years, the advance regeneration was acclimated to the moderate increases in irradiance created by partial overstory removal. Beyond this crucial acclimation period, our growth results are in line with the accepted knowledge that well-established red spruce requires at least 50% of full sunlight for optimal growth (Blum 1990, Seymour 1995). Five years after the treatments, the best growth of red spruce was

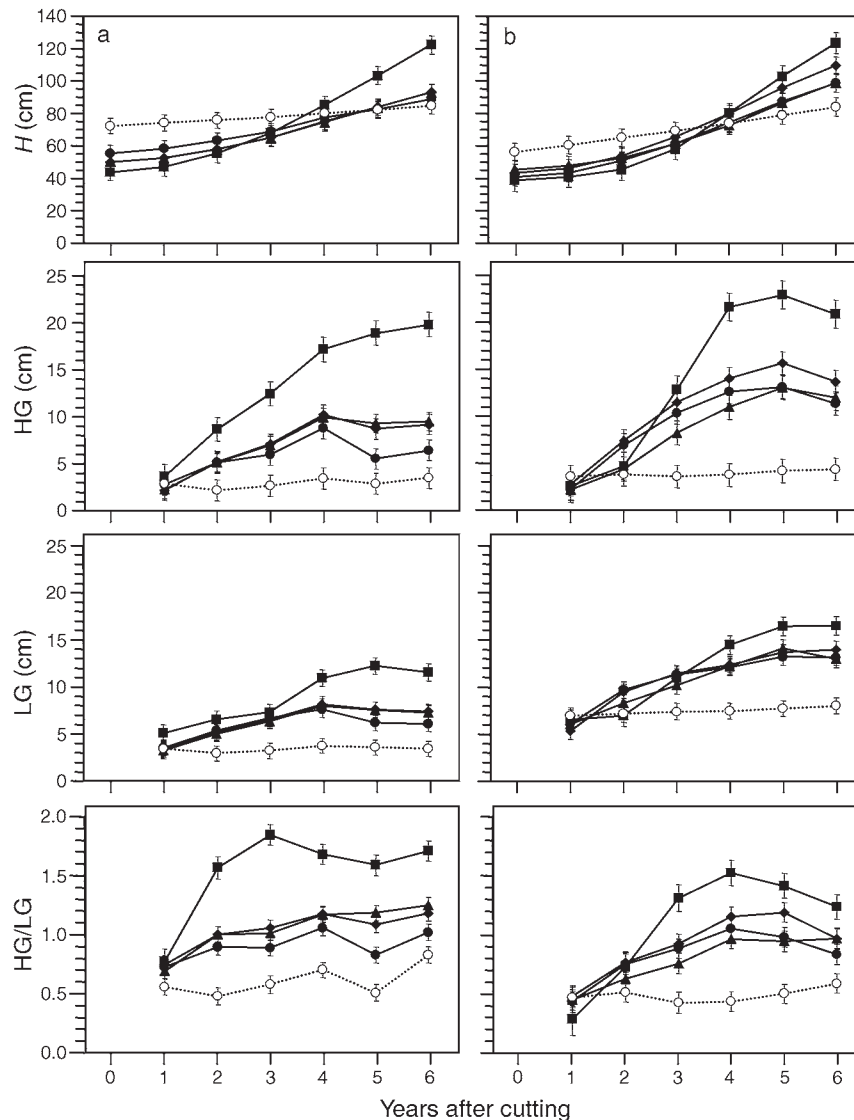


Figure 4. Time courses of height (H), height growth (HG), lateral growth (LG) and HG/LG ratio of (a) red spruce (*Picea rubens*) and (b) balsam fir (*Abies balsamea*) in five overstory removal treatments: 0% ($\circ$); 40% ($\bullet$); 50% ($\blacktriangle$); 60% ($\blacklozenge$); and 100% ($\blacksquare$). Each value is the mean of at least 48 observations on spruces (27 available in the clearcut) and at least 30 observations on firs (18 in the clearcut). Vertical bars represent standard errors.

observed in the clearcut (Figure 4), where PPF varied from 45 to 65% of full light (Prévost 2008), compared to partial cuts receiving between 15 and 21% of full light. Despite a lower H_0 , balsam fir surpassed red spruce in height six years after cutting, mainly because of its superior growth potential in partial cuts. It is known that balsam fir exhibits better juvenile growth after partial overstory removal than red spruce (Moores et al. 2007, Pothier and Prévost 2008). It is also known that firs have a higher capacity than spruces for horizontal crown expansion in partial shade (Messier et al. 1999, Claveau et al. 2002, Mori and Takeda 2004). In our study, HG/LG differences between red spruce and balsam fir were minimal compared with the results of other studies (Takahashi 1996, Mori and Takeda 2003). Growth differences between red spruce and balsam fir will decrease with stand development, because growth of balsam fir tends to peak earlier (Davis 1989). Moreover, HG of balsam fir showed a slight drop at Year 6 in our study. Even if balsam fir initially had a slight competitive advantage over red spruce, it will be necessary to

monitor future growth to confirm the long-term response. Recently, Fortin (2005) suggested that competition by balsam fir would not be a major cause of red spruce depletion.

Growth of advance regeneration of red spruce under partial overstory conditions seems to depend mainly on additional carbon gain brought about by enhanced photosynthesis in response to increased PPF. Acclimation of balsam fir in partial cuts was partly physiological, but mainly morphological (cf. Stancioiu and O'Hara 2006). Adjustment of SLA appears to underlie the growth enhancement of this species in moderate light. According to Evans and Poorter (2001), changes in morphological traits, such as SLA, are more effective at increasing carbon gain than cellular-level acclimation. A reduction in SLA with increasing light availability may permit a higher photosynthetic capacity (Jordan and Smith 1993). However, other hypotheses could explain the higher growth rate of balsam fir compared with red spruce under partial overstory conditions. For example, balsam fir could have a higher light-use efficiency, with high foliar N (Figure 3) enabling more effi-

cient light-capture and higher $A_{\max}$ in partial shade. It is also possible that a higher respiration rate in red spruce than in balsam fir (not measured) enables the latter species to maintain a more positive carbon balance at low or moderate PPF (Messier et al. 1999, Grassi and Bagnaresi 2001, Pothier and Prévost 2002). Finally, balsam fir has a longer seasonal period of active photosynthesis than red spruce (Gage and DeHayes 1992), which likely contributes to its superior growth in light-limited conditions.

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References

- Alexander, J.D., J.R. Donnelly and J.B. Shane. 1995. Photosynthetic and transpirational responses of red spruce understory trees to light and temperature. *Tree Physiol.* 15:393–398.
- Black, K., P. Davis, J. McGrath, P. Doherty and B. Osborne. 2005. Interactive effects of irradiance and water availability on the photosynthetic performance of *Picea sitchensis* seedlings: implications for seedling establishment under different management practices. *Ann. For. Sci.* 62:413–422.
- Blum, B.M. 1990. Red spruce. In *Silvics of North America*, Vol. 1. R.M. Burns and B.H. Honkala (technical coordinators). Agric. Handbook No. 654, USDA For. Serv., Washington, DC, pp 250–259.
- Claveau, Y., C. Messier, P.G. Comeau and K.D. Coates. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Can. J. For. Res.* 32:458–468.
- Davis, W.C. 1989. The role of released advance growth in the development of spruce–fir stands in eastern Maine. Ph.D. Diss., Yale Univ., New Haven, CT, 104 p.
- Day, M.E. 2000. Influence of temperature and leaf-to-air vapor pressure deficit on net photosynthesis and stomatal conductance in red spruce (*Picea rubens*). *Tree Physiol.* 20:57–63.
- Day, M.E., M.S. Greenwood and A.S. White. 2001. Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiol.* 21:1195–1204.
- Duchesne, L. and D. Houle. 2006. Base cation cycling in a pristine watershed of the Canadian boreal forest. *Biogeochemistry* 78: 195–216.
- Dumais, D. and M. Prévost. 2007. Management for red spruce conservation in Québec: the importance of some physiological and ecological characteristics—a review. *For. Chron.* 83:378–392.
- Evans, J.R. and H. Poorter. 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant Cell Environ.* 24:755–767.
- Fortin, M. 2005. Étude rétrospective de la croissance en diamètre du sapin baumier (*Abies balsamea* (L.) Mill.) et de l'épinette rouge (*Picea rubens* Sarg.) en peuplements mixtes après une coupe à diamètre limite. *For. Chron.* 81:791–800.
- Foster, J.R. and W. Reiners. 1983. Vegetation patterns in a virgin sub-alpine forest at Crawford Notch, White Mountains, New Hampshire. *Bull. Torrey Bot. Club* 110:141–153.
- Gage, S.F. and D.H. DeHayes. 1992. Variation in seasonal patterns of photosynthesis among red spruce and balsam fir provenances. In *Proc. First Northern Forest Genetics Association Conference*, Burlington, VT. Eds. D.H. DeHayes and G.J. Hawley. Aiken Cent. Nat. Res., School Nat. Res., Vermont University, pp 109–120.
- Grassi, G. and U. Bagnaresi. 2001. Foliar morphological and physiological plasticity in *Picea abies* and *Abies alba* saplings a natural light gradient. *Tree Physiol.* 21:959–967.
- Grassi, G. and R. Giannini. 2005. Influence of light and competition on crown and shoot morphological parameters of Norway spruce and silver fir saplings. *Ann. For. Sci.* 62:269–274.
- Greis, I. and S. Kellomäki. 1981. Crown structure and stem growth of Norway spruce undergrowth under varying shading. *Silva Fenn.* 15:306–322.
- Hollinger, D.Y. 1996. Optimality and nitrogen allocation in a tree canopy. *Tree Physiol.* 16:627–634.
- Johnson, D.M. and W.K. Smith. 2005. Refugial forests of the southern Appalachians: photosynthesis and survival in current-year *Abies fraseri* seedlings. *Tree Physiol.* 25:1379–1387.
- Jordan, D.N. and W.K. Smith. 1993. Simulated influence of leaf geometry on sunlight interception and photosynthesis in conifer needles. *Tree Physiol.* 13:29–39.
- Kneeshaw, D.D. and M. Prévost. 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. *Can. J. For. Res.* 37:1534–1544.
- Kneeshaw, D.D., H. Williams, E. Nikinmaa and C. Messier. 2002. Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. *Can. J. For. Res.* 32: 255–265.
- Kranabetter, J.M. and K.D. Coates. 2004. Ten-year postharvest effects of silviculture systems on soil-resource availability and conifer nutrition in a northern temperate forest. *Can. J. For. Res.* 34:800–809.
- Landhäusser, S.M. and V.J. Lieffers. 2001. Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. *Tree Physiol.* 21:243–250.
- Major, J.E., D.C. Barsi, A. Mosseler, M. Campbell and O.P. Rajora. 2003. Light-energy processing and freezing-tolerance traits in red spruce and black spruce: species and seed-source variation. *Tree Physiol.* 23:685–694.
- Man, R. and V.J. Lieffers. 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. *Tree Physiol.* 17:437–444.
- Messier, C., R. Doucet, J.-C. Ruel, Y. Claveau, C. Kelly and M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.* 29: 812–823.
- Mohammed, G.H. and W.C. Parker. 1999. Photosynthetic acclimation in eastern hemlock (*Tsuga canadensis* (L.) Carr.) seedlings following transfer of shade-grown seedlings to high light. *Trees* 13: 117–124.
- Moores, A.R., R.S. Seymour and L.S. Kenefic. 2007. Height development of shade-tolerant conifer saplings in multiaged Acadian forest stands. *Can. J. For. Res.* 37:2715–2723.

- Mori, A. and H. Takeda. 2003. Architecture and neighbourhood competition of understorey saplings in a subalpine forest in central Japan. *Écoscience* 10:217–224.
- Mori, A. and H. Takeda. 2004. Functional relationships between crown morphology and within-crown characteristics of understorey saplings of three codominant conifers in a subalpine forest in central Japan. *Tree Physiol.* 24:661–670.
- Pothier, D. and M. Prévost. 2002. Photosynthetic light response and growth analysis of competitive regeneration after partial cutting in a boreal mixed stand. *Trees* 16:365–373.
- Pothier, D. and M. Prévost. 2008. Regeneration development under shelterwoods in a lowland red spruce–balsam fir stand. *Can. J. For. Res.* 38:31–39.
- Prévost, M. 2008. Effect of cutting intensity on microenvironmental conditions and regeneration dynamics in yellow birch–conifer stands. *Can. J. For. Res.* 38:317–330.
- Radoglou, K. and R.O. Teskey. 1997. Changes in rates of photosynthesis and respiration during needle development of loblolly pine. *Tree Physiol.* 17:485–488.
- Reinhardt, K. and W.K. Smith. 2008. Leaf gas exchange of understorey spruce–fir saplings in relict cloud forests, southern Appalachian Mountains, USA. *Tree Physiol.* 28:113–122.
- Renninger, H.J., F.C. Meinzer and B.L. Gartner. 2007. Hydraulic architecture and photosynthetic capacity as constraints on release from suppression in Douglas-fir and western hemlock. *Tree Physiol.* 27:33–42.
- Richardson, A.D. 2004. Foliar chemistry of balsam fir and red spruce in relation to elevation and the canopy light gradient in the mountains of the northeastern United States. *Plant Soil* 260:291–299.
- Rosén, K. and A. Lundmark-Thelin. 1987. Increased nitrogen leaching under piles of slash. A consequence of modern forest harvesting techniques. *Scand. J. For. Res.* 2:21–29.
- Seymour, R.S. 1995. The Northeastern region. *In* Regional Silviculture of the United States, 3rd Edn. Ed. J.W. Barrett. John Wiley and Sons, New York, pp 31–79.
- Stancioiu, P.T. and K.L. O'Hara. 2006. Morphological plasticity of regeneration subject to different levels of canopy cover in mixed-species, multiaged forests of the Romanian Carpathians. *Trees* 20:196–209.
- Stenberg, P., H. Smolander, D. Sprugel and S. Smolander. 1998. Shoot structure, light interception, and distribution of nitrogen in an *Abies amabilis* canopy. *Tree Physiol.* 18:759–767.
- Stewart, J.D. and P.Y. Bernier. 1995. Gas exchange and water relations of 3 sizes of containerized *Picea mariana* seedlings subjected to atmospheric and edaphic water stress under controlled conditions. *Ann. Sci. For.* 52:1–9.
- Takahashi, K. 1996. Plastic response of crown architecture to crowding in understorey trees of two co-dominating conifers. *Ann. Bot.* 77:159–164.
- Tucker, G.F., T.M. Hinckley, J.W. Leverenz and S.-M. Jiang. 1987. Adjustments of foliar morphology in the acclimation of understorey Pacific silver fir following clearcutting. *For. Ecol. Manage.* 21:249–268.
- Vann, D.R., A.H. Johnson and B.B. Casper. 1994. Effect of elevated temperatures on carbon dioxide exchange in *Picea rubens*. *Tree Physiol.* 14:1339–1349.
- Vitousek, P.M. and P.A. Matson. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology* 66:1360–1376.
- Walinga, I., J.J. van der Lee, V.J.G. Houba, W. van Vark and I. Novozamsky. 1995. Plant analysis manual. Kluwer Academic Publishers, Dordrecht, 40 p.
- White, P.S., M.D. MacKenzie and R.T. Busing. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce–fir forests. *Can. J. For. Res.* 15:233–240.
- Zimmermann, R., R. Oren, E.-D. Schulze and K.S. Werk. 1988. Performance of two *Picea abies* (L.) Karst. stands at different stages of decline. II. Photosynthesis and leaf conductance. *Oecologia* 76:513–518.