

Nutrient and Light Availability to White Spruce Seedlings in Partial and Clearcut Harvested Aspen Stands

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White spruce is a commercially important tree species in Canada's boreal forest, and studies are underway to determine the best conditions for planting nursery grown seedlings in the field. Here, we studied effects of low thinning (1/3 harvested), shelterwood (2/3 harvested), and clear-cut harvesting on soil chemical properties, on the growth and nutrition of white spruce seedlings, and on diffuse non-intercepted (DIFN) light levels at 75 cm above the soil surface. The study was conducted on a nutrient-rich clayey soil in the Abitibi region of Québec. DIFN light was lowest in non-harvested control plots and increased curvilinearly with basal area removal. Thus, DIFN light in clear-cut plots was more than twice the amount in shelterwood plots. At three years post-planting, significant linear relationships were found between DIFN light and seedling growth parameters, which were significantly higher in clear-cut than in other treatment plots. Harvesting treatments had no significant effects on soil chemical properties or on four indices of mineral N availability. Needle mass increased with harvesting intensity. Mg and K concentrations in current-year needles were lower in clear-cut than in other treatment plots. In previous-year needles, Ca concentration was higher and Mg concentrations lower in clear-cut plots, whereas as K concentration was higher in non-harvested control plots. Nutrient concentrations were nearly all sufficient in all harvesting treatments according to diagnostic norms established for white spruce. Relative nutrient content (mg nutrient needle⁻¹) of current-year late-summer needles increased, whereas relative nutrient concentration (mg nutrient mg⁻¹ needle) varied slightly, with increasing harvesting intensity, indicating that all nutrients were sufficient in all treatments. There were significant linear relationships between seedling growth and needle Ca, Mg and K concentrations. We conclude that light availability, rather than nutrient limitations, is the main determinant of white spruce seedling growth on these fertile soils.

Keywords DIFN light, foliar nutrients, *Picea glauca*, soil mineral nitrogen, vector analysis

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1 Introduction

White spruce (*Picea glauca* (Moench) Voss) is a widely distributed tree species in Canada's boreal forest, and highly valued by the forest products industry as a source of pulpwood and construction-grade lumber. Natural regeneration of white spruce sometimes fails, because of limited availability of viable seed and seedbed conditions following fire or clear-cutting (Wurtz and Zasada 2001, Purdy et al. 2002). Consequently, efforts have been made to increase the merchantable volume of white spruce by establishing plantations in clear-cuts, or by under-planting existing vegetation in uncut or partially harvested forest stands (Stewart et al. 2000, Delong 2004, Maundrell and Hawkins 2004). It is still uncertain, however, which of these silvicultural options will favor white spruce seedling growth. The degree of canopy removal can influence the performance of seedlings, as these must compete with other vegetation for available soil nutrients, water and light.

Youngblood and Zasada (1991) found higher white spruce seedling growth in clear-cuts than in shelterwood plots, but did not propose an explanation. It is possible that white spruce seedlings in their study responded to higher mineral N supply in clear-cuts, given that i) greater soil mineral N pools are sometimes found in clear-cuts compared to shelterwood or uncut stands (Kim et al. 1995, Grenon et al. 2004), ii) site indices of white spruce have been correlated to soil mineralizable-N (Wang 1995, 1997), and iii) seedling growth for a variety of late-seral conifers, including white spruce, responds positively to mineral N fertilizer (Weetman et al. 1993, Paquin et al. 1998). Others have argued to the contrary (e.g., Kronzucker et al. 1997), suggesting that clear-cutting can decrease N nutrition for white spruce by favoring soil NO_3^- production and subsequent growth of competing herbaceous vegetation. Similarly, white spruce seedlings growing in partially harvested stands, especially deciduous stands, could potentially benefit from favorable nutritional conditions created by sustained litter inputs to the forest floor (Thomas and Prescott 2000). As each of these proposed mechanisms is plausible and may apply differently across different sites, studies should be conducted to evaluate the nutrition

and growth response of white spruce seedlings to various levels of canopy retention, within specific sets of environmental conditions.

There is disagreement over the importance of available light on white spruce seedling growth. For example, some studies have concluded that shading in partially harvested hardwood forests, or under competing early seral vegetation, can lead to a prevalence of light competition over nutrient competition in planted white spruce seedlings (Groot 1999, Jobidon 2000). Others have argued that white spruce seedlings growing under an aspen canopy can acclimate to low light conditions during summer, with steeper light response curves and lower photosynthetic compensation and saturation points (Man and Lieffers 1997, Awada and Redmann 2000). Given these divergent findings, we propose that the importance of available light is positively related to site nutritional quality. In other words, white spruce seedling growth should respond to an increase in the most limiting resource, whether it be soil nutrients or light. We predict, therefore, that white spruce seedling growth will respond to light availability at different levels of canopy removal, where soils are fertile.

The Canadian Council of Forest Ministers (1997) proposed that sustainable forest management be monitored using indicators of future forest productivity. Monitoring the performance of seedlings may prove to be a useful method of assessing forest productivity over the longer term. For example, Mitchell et al. (2003) found that above-ground seedling biomass three years post-planting predicted future growth rates of both amabilis fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*), and concluded that this variable could be used as an indicator of future growth performance, or as an early warning of incipient growth stagnation. Foliar analysis is a possible alternative to repeated growth measurements and can be used to infer which nutrients are at adequate levels and which are likely to limit growth (Kranabetter et al. 2003). Given that seedlings are more sensitive than mature trees to nutrient supplies, foliar nutrient analysis can potentially be used to relate white spruce seedling growth performance to site quality (Wang and Klinka 1997, Kranabetter et al. 2003).

We report on a study in which we monitored

the growth of white spruce seedlings planted in uncut, as well as in partial- and clear-cut harvested aspen stands. Our objective was to identify correlates of seedling growth in variable retention plots by studying soil chemical properties, soil N supply, light intensity and foliar nutrient concentrations.

2 Methods

2.1 Study Site and Treatments

Our study was conducted at the Lake Duparquet Research and Teaching Forest, an area of about 8000 ha located in the southern boreal mixed-wood forest, 45 km northwest of Rouyn-Noranda, Canada ($48^{\circ}29'N$, $79^{\circ}25'W$). The experimental forest lies within the “Northern Clay Belt,” a physiographic region characterised by lacustrine clay deposits left by pro-glacial Lakes Barlow and Ojibway (Vincent and Hardy 1977). Soils are mainly Orthic Grey Luvisols (Soil Classification Working Group 1998) with mor humus layers. The age structure and species composition of the various forest stands are described in detail by Bergeron and Dubuc (1989).

The experiment was conducted in three separate 75-year-old aspen stands, which included a very minor component of white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Miller). Mean basal area of these stands was estimated at $43\text{ m}^2\text{ ha}^{-1}$ (Brais et al. 2004). The main shrub species were mountain maple (*Acer spicatum* Lam.) and speckled alder (*Alnus incana* ssp. *rugosa* (L.) Moench (Du Roi) Clausen), whereas the most abundant herbaceous species were large leaf aster (*Aster macrophyllus* L.), wild sarsaparilla (*Aralia nudicaulis* L.) and blue bead lily (*Clintonia borealis* (Ait) Raf.).

During the winter of 1999, four 1–2 ha plots were established within each aspen stand, and then four treatments were randomly allocated among these plots. Treatments consisted of a non-harvested control, two partial harvesting systems corresponding to one-third and two-thirds removal of merchantable basal area (“low-thinning” and “shelterwood harvesting” treatments,

respectively), and a clear-cut harvested treatment. The partial-harvested plots were logged using chainsaws whereas the clearcut plots were mechanically (stem-only) harvested with minimum soil disturbance (CPRS), as mandated by the Quebec provincial government (MRNFP 2003). Two years following treatments, total density of aspen suckers was roughly 5, 29, 63 and $103 (\times 10^3)$ stems in the control, 1/3, 2/3 and clearcut harvested plots, respectively (Brais et al. 2004). Compared to the non-harvested control plots, the annual biomass increment of the herbaceous vegetation was two times greater in both partial harvesting treatments, and five time greater in clearcut harvested plots (Brais et al. 2004).

In spring 1999, 25 white spruce seedlings (2-years old, greenhouse grown, containerized, non-nutrient loaded) were randomly planted within a 100 m^2 area near the centre of each plot.

2.2 Soil Sampling and Analyses

Surface mineral soil and forest floor (F-horizon) material were collected from each experimental plot in early-June, mid-July and late-August, 2001. On each date, 15 cores of forest floor ($2\text{--}5\text{ cm} \times 5\text{ cm}$ diameter) and mineral soil ($10\text{ cm} \times 5\text{ cm}$ diameter) were taken along two transects which passed through the planted section of each plot. Cores were sieved (5-mm mesh) and bulked in the field to yield one sample (ca. 1 kg fresh mass) of forest floor and one sample of mineral soil per plot. The composite samples were transported under ice packs to the Soil Ecology Laboratory – University of Sherbrooke, where they were kept at 4°C . Chemical analyses were conducted within one week of sampling.

Chemical characterization of the samples included measurement of pH in distilled water. Percent organic-C was determined by loss-on-ignition using conversion factors of 0.45 and 0.55, respectively, for forest floor and mineral soil. Fresh subsamples (5 g dry mass equiv.) were extracted in Bray-1 reagent (Kuo 1996), and extracts were analysed immediately for available-P by automated colorimetry (Ammonium molybdate - antimony potassium tartrate assay). Aliquots of both forest floor (200 mg) and mineral soil (500 mg) were digested in a hot (340 °C)

mixture of H_2SO_4 , Li_2SO_4 , H_2O_2 and Se (Parkinson and Allen 1975), and the digests were analyzed for total N and major base cations (as described below).

The potential for the forest floor and surface mineral soil to supply mineral N to plants was assessed using four standard assay methods (Binckley and Hart 1989): i) Mineral N concentrations were estimated by mixing 15 g of newly collected soil in 100 mL 2.0 M KCl solution, shaking the mixture for 1 h, passing the supernatant through Whatman No. 42 cellulose filter disks, and analysing the filtrate for NH_4^+ (salicylate, NaOCl, nitroprusside) and NO_3^- (Cd-reduction, sulphamamide) by continuous-flow colorimetry. ii) Net in situ ammonification and nitrification rates were measured in both forest floor and mineral soil horizons, using the buried bag incubation method (Eno 1960). Fresh subsamples were weighed in the field (ca. 60 g forest floor and 100 g mineral soil), sealed in polyethylene bags (200 cm^3), returned to a hole in the ground and left to incubate 30 days. Bags were then collected and transported in coolers to the laboratory to be analyzed for NH_4^+ and NO_3^- concentrations (as previously described). iii) Potentially mineralizable N also was assessed using aerobic laboratory incubations (Fyles et al. 1990) of fresh forest floor (10 g dry mass equiv.) and mineral soil (30 g dry mass equiv.) subsamples. Incubations were conducted for two and four month periods (22°C in the dark), after which 2 M KCl-extractable NH_4^+ and NO_3^- were determined (as previously described). iv) The fourth index of available-N consisted of anaerobic incubations (22°C in the dark) of fresh material (5–10 g), which was submerged in deionized water (added to 45 mL snap-cap vials) for 14 days (Waring and Bremner 1964). The saturated soils were extracted with an equal volume of 2 M KCl (yielding a 1 N solution), filtered, and analyzed for NH_4^+ as previously described.

2.3 Seedling Growth and Foliar Analyses

All seedlings were measured in September 1999, 2000 and 2001. Stem basal diameter was averaged from two perpendicular measurements ($\pm 0.1 \text{ mm}$) for each seedling. Total height and annual height increment were measured to the nearest $\pm 1 \text{ mm}$.

Relative growth rate (RGR) between successive years (1999–2000 and 2000–2001) was calculated as $\text{RGR} = (\ln \text{H}_2 - \ln \text{H}_1) / (\text{y}_2 - \text{y}_1)$, where H1 and H2 are seedling height at two consecutive years (i.e., y_1 and y_2).

One branch was collected from 12 randomly chosen seedlings in each plot in early-June, mid-July and late-August 2001. Current- and previous-year needles from each plot were sorted, bulked and oven-dried (35°C for 48 h). Average mass of 250 current- and previous-year needles was calculated for each plot. Needles were finely ground and digested in hot (340°C) mixture of H_2SO_4 , Li_2SO_4 , H_2O_2 and Se. Concentrations of total N and P in the digests were determined by automated colorimetry (Technicon II auto-analyser, Pulse Instrumentation, Saskatoon, Canada), while base cations (K, Ca, Mg) were analysed by atomic absorption spectrometry (Analyst-100, Perkin-Elmer Corporation, Norwalk, U.S.A.). Logistical constraints prevented us from measuring foliar P in early-July and late-August.

2.4 Light Measurements

Relative light intensity was estimated in each plot 75 cm above the ground (i.e., above the crown of the seedlings), at 1 m intervals along two 50 m transects. Light measurements were made in each study plot using a LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, U.S.A.), while a second sensor recorded light intensity in nearby open terrain. Readings were made in early September 1999, before litter fall, on a uniformly overcast day. The LAI-2000 sensor uses a wide-angle lens and sensor to measure the fraction of open sky reaching a point from different angles in the sky (Comeau 2000) and thus provides an estimate of Diffuse Non-Interceptance (DIFN). DIFN has been correlated with seasonal light transmittance under various canopy densities in northern hardwood forests (Comeau et al. 1998, Gendron et al. 1998).

2.5 Data Analyses

The effects of harvest treatment on seedling growth and DIFN light were tested by one-way

ANOVA, adjusting for the block effect. Since harvest treatment is a quantitative factor, significant effects also were decomposed into linear and quadratic trends using orthogonal polynomial trend analysis to determine whether growth responses and light changed gradually or abruptly with progressive basal area removal. The effects of harvest treatment and sampling date on soil and foliar nutrient variables were tested by two-way ANOVA. Post hoc comparisons of means were performed using Student-Neuman-Keuls tests. The effects of treatments on foliar elemental concentrations (N, Ca, Mg, and K) for both current and previous year needles also were analyzed by two-way MANOVA, in order to assess the “whole needle” response of seedlings to the harvest treatment and sampling date (Tabachnick and Fidell 1996). The significance of multivariate main effects and interactions was determined from Wilks’ Λ statistics. Least-squares regression and correlation analysis were used to explore possible relationships between seedling growth and indices of soil N supply, DIFN light, and needle nutrient concentrations. The level of significance for all tests was set at $\alpha=0.05$.

Elemental concentrations of current-year (2001) needles sampled in late-August were compared to the diagnostic norms established by Ballard and Carter (1986) for white spruce. Interpretations of directional changes in dry mass and nutrient status of white spruce needles in response to the four harvest treatments were based on vector analysis (Timmer 1991, Haase and Rose 1995), using current-year needles sampled in late-August. For species with determinate needle growth, such as white spruce, vector analysis may be applied to compare the growth, foliar nutrient concentration, and foliar nutrient content in an integrated graphic format that allows interpretation of plant responses to various treatments, independent of predetermined critical levels (Haase and Rose 1995, Macdonald et al. 1998). This vector analysis used the nutrient content and nutrient concentrations of seedlings growing in the control plots as reference values normalized to “100.”

3 Results

3.1 Diffuse Non-Intercepted Light and Seedling Growth

DIFN at 75 cm above the ground surface was lowest in the non-harvested control plots and increased with basal area removal according to a significant ($P<0.001$) quadratic trend: 7.7% in non-harvested control plots, 13.7% in 1/3 harvested plots, 25.0% in 2/3 harvested plots, and 58.3% in clear-cut plots. The average standard deviation in DIFN light was 8.8% within plots, and 3.2% within treatments. In 2001, harvest treatment had a significant effect on RGR for 2000–2001 ($P<0.001$), stem height ($P=0.01$) and stem diameter ($P=0.01$) of planted white spruce seedlings. These three growth parameters were significantly higher ($P<0.001$) in clear-cut plots than in the other three treatment plots. Average DIFN values of each plot were significantly related to the 2000–2001 RGR ($P<0.001$), and to the 2001 stem height ($P<0.001$) and stem diameter ($P<0.001$) (Fig. 1).

3.2 Soil Chemical Properties and Mineralizable N

Harvesting treatment had no significant effects on soil chemical properties, therefore each variable is presented in Table 1 as the mean for the 12 treatment plots. Harvesting treatment also had no significant effect on any of the four mineral N availability indices (data not shown). Likewise, seedling growth parameters were not significantly related to any of the N availability indices. The few significant seasonal differences (i.e., Sampling Date effects) in mineral-N availability included assays of 30-day buried-bag ammonification (mineral soil, $P=0.012$; forest floor, $P=0.036$) and nitrification (mineral soil, $P=0.004$). There were no statistically significant interactions (Treatment by Sampling Date) controlling any of the soil variables.

3.3 Foliar Nutrients: Effects of Harvesting

At each sampling date, harvesting treatments dif-

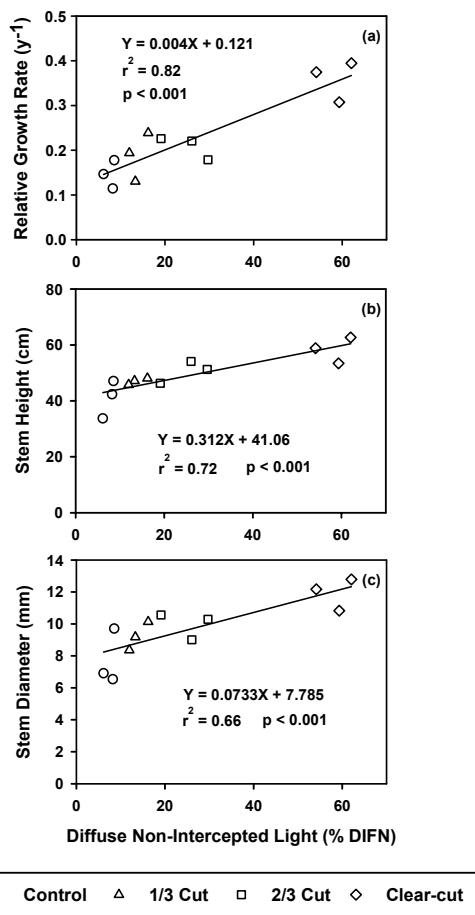


Fig. 1. Seedling growth responses to harvest treatment as functions of % DIFN (diffuse non-intercepted light; (a) relative growth rate (2000–2001), (b) stem height (2001), and (c) stem diameter (2001).

fered significantly ($P < 0.001$) based on a multi-variate comparison (MANOVA) of foliar nutrient concentrations, for both current and previous-year needles. Two-way ANOVA tests revealed a significant treatment effect on current-year Mg ($P = 0.01$) and K ($P < 0.01$) concentrations, as well as on previous-year Ca ($P < 0.01$), Mg ($P < 0.01$) and K ($P < 0.01$) concentrations. More specifically, Mg and K concentrations (both current and previous year needles) were lower, whereas Ca concentrations (previous year needles) were higher, in clear-cut compared to non-

Table 1. Chemical properties of forest floor and surface mineral soil, which did not significantly differ among the four harvest treatments. Means ($\pm 1 \text{ SE}$) of the pooled treatment plots ($n=12$) are shown for each horizon. Concentrations are reported as $\text{mg nutrient} \cdot \text{g}^{-1}$ oven-dry mass.

| Property | Forest floor | Mineral soil |
|---------------|--------------------|------------------|
| pH | 5.45 ± 0.06 | 5.58 ± 0.06 |
| Total C | 306.69 ± 17.94 | 20.49 ± 1.00 |
| Total N | 17.31 ± 1.52 | 1.39 ± 0.21 |
| Extractable P | 0.11 ± 0.01 | 0.02 ± 0.01 |
| Total Na | 23.97 ± 1.13 | 2.68 ± 0.26 |
| Total K | 7.91 ± 0.85 | 13.44 ± 0.58 |
| Total Ca | 14.27 ± 0.95 | 1.16 ± 0.14 |
| Total Mg | 3.15 ± 0.41 | 9.46 ± 0.21 |

harvested plots (Table 2). In the two partially harvested treatments, needle concentrations of these three nutrients were either similar to values in clear-cuts, or to those in non-harvested plots (Table 2). Sampling date had a significant effect on current-year N, K, Ca and Mg, as well as on previous-year N, Ca and Mg concentrations (all effects at $P < 0.01$; data not shown). There were no significant interactions (i.e., Treatment by Sampling Date) controlling needle nutrient concentrations.

3.4 Foliar Nutrients: Indices of Seedling Growth

Simple linear regression analysis was used to relate RGR for 2000–2001 to foliar nutrient concentrations that were significantly affected by harvesting treatments. Significant positive relationships were found at each sampling date between RGR and Ca concentrations in previous-year needles (Fig. 2a, 2b, 2c). There were significant negative relationships between RGR and Mg concentrations in current-year (early-June and late-August) and previous-year (mid-July and late-August) needles (Fig. 2d, 2e, 2f). Significant negative relationships were also found between RGR and K concentrations in current-year (early-June and late-August) and previous-year (early-June) needles (Fig. 2g, 2h).

Table 2. Seasonal mean (\pm SD) nutrient concentrations (mg g^{-1}) of current and previous year white spruce needles sampled in 2001. Means (n=9) on the same line followed by the same lowercase letter do not significantly differ at $p=0.05$, using Student-Neuman-Keuls tests.

| Needle nutrient | Harvest treatment | | | |
|----------------------|-------------------|---------------|---------------|----------------|
| | Non-harvested | 1/3-Harvest | 2/3-Harvest | Clear-cut |
| Current year | | | | |
| N | 15.74a (4.32) | 12.93a (3.03) | 14.15a (1.68) | 14.96a (3.18) |
| Ca | 3.19a (1.47) | 2.92a (1.30) | 3.27a (1.52) | 2.90a (1.52) |
| Mg | 1.07a (0.17) | 1.06a (0.13) | 1.05ab (0.16) | 0.91b (0.13) |
| K | 9.15a (3.35) | 9.39a (2.61) | 9.12a (2.95) | 7.72b (2.69) |
| P | 1.61a (0.48) | 1.99a (0.19) | 2.06a (0.06) | 1.81a (0.02) |
| Previous year | | | | |
| N | 10.49a (1.89) | 8.75b (1.97) | 9.89ab (1.98) | 10.26ab (0.68) |
| Ca | 4.32b (1.28) | 4.30b (0.99) | 4.94b (0.84) | 7.01a (0.84) |
| Mg | 0.87a (0.17) | 0.84a (0.17) | 0.83ab (0.12) | 0.70b (0.10) |
| K | 5.74a (1.77) | 4.62ab (0.74) | 5.06ab (0.52) | 3.94b (0.80) |
| P | 1.48a (0.51) | 1.33a (0.14) | 1.47a (0.19) | 1.16a (0.12) |

3.5 Diagnostic Norms and Vector Analysis

Based on diagnostic norms established by Ballard and Carter (1986) for white spruce (i.e., 2.0 mg Ca, 5.0 mg K, 14.5 mg N and 1.2 mg Mg g^{-1} tissue), there was only “slight” N deficiency in 1/3 harvested and clear-cut stands, and “slight” Mg deficiency in clear-cut stands. All other nutrient concentrations in all other treatments were sufficient in the current-year needles sampled in late-August 2001. The slope of the diagonals in the vector diagram decreased with decreasing canopy cover, indicating that needle biomass increased with progressive canopy removal (Fig. 3). Two-way ANOVA tests confirmed that treatment effects on current-year needle mass were indeed significant ($P<0.01$). With the exception of needle N in the 1/3 harvested plots, relative nutrient content of needles increased with harvesting intensity, whereas relative nutrient concentration of needles remained relatively unchanged. The resulting shifts to the right for most nutrients along the horizontal in the vector diagram (Fig. 3) is interpreted as meaning that seedlings were sufficient in most nutrients (Haase and Rose 1995) and that a factor other than soil fertility was responsible for increased seedling growth with progressive canopy removal. In the case of N in the 1/3 harvested plots, a shift down and to the

left in the vector diagram normally indicates that this nutrient is in excess and could potentially be detrimental to seedling growth (Haase and Rose 1995).

4 Discussion

Positive relationships were found between seedling growth parameters and DIFN light, whereas most needle nutrient concentrations were above diagnostic norms or “sufficient” according to our vector diagram. This is consistent with the reported high fertility of lacustrine clay soils in the Abitibi region (Béland et al. 2003). Taken collectively, our results suggest that light was the main determinant of white spruce seedling growth in this particular ecosystem, not nutrient limitation.

The relationship between harvesting intensity and DIFN light followed a quadratic trend, such that the largest difference in available light occurred between 2/3 harvested and clear-cut plots. The regenerating aspen suckers in the clear-cut plots filtered 42% of DIFN light, but the remaining 58% was more than twice the amount of light available to seedlings in the 2/3 harvested plots. Accordingly, the largest growth

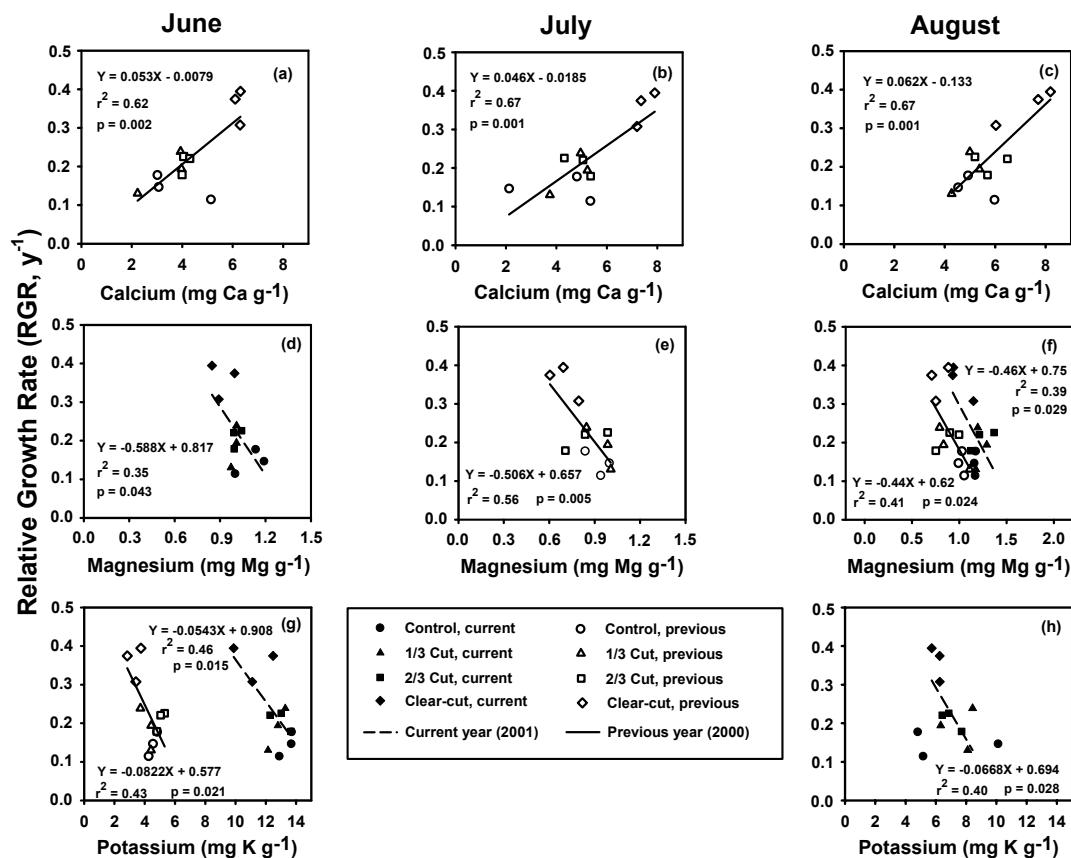


Fig. 2. Relative growth rate (2000–2001) as a function of foliar nutrient concentrations in current and previous year needles sampled in late-August 2001. Closed symbols are means of current-year concentrations, while open symbols are means of previous-year concentrations. The three rows are, respectively, Ca (Fig. 2a,b,c), Mg (Fig. 2d,e,f) and K (Fig. 2g,h). The three columns summarize the regression results for early-June, mid-July and late-August sampling dates.

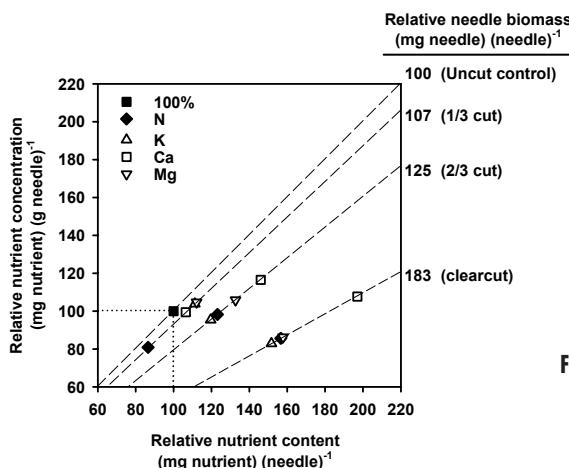


Fig. 3. Vector diagram showing the average shifts in nutrient content, nutrient concentration and needle mass for each treatment relative to values measured in the uncut control plots.

increment occurred between these two treatments. Unlike our study, which only describes a relationship between percent DIFN light and seedling growth, Mitchell (2001) compared needle nutrient concentrations, physiological parameters related to photosynthesis, and the growth of western hemlock and amabilis fir seedlings planted in shelterwood and clear-cut plots. He concluded that 25% retention of canopy trees can limit the early growth of regenerating conifer seedlings as a result of a reduction in available light, and not as a result of reduced nutrient availability. Although we worked with a different species than Mitchell (2001), there are reasons to believe that white spruce seedlings also can respond positively to DIFN light. Morphological characteristics are said to be more plastic in shade-tolerant than shade-intolerant species (Chen 1997), but we reason that responsiveness to light may be greater in species capable of growing under a wider range of light conditions. White spruce, a semi-tolerant species (Lieffers and Stadt 1994), should tolerate low light conditions and at the same time maintain physiological attributes that predispose it to respond to higher light availability. This hypothesis is consistent with the findings by Middleton et al. (1997), who showed that chlorophyll content and gas exchange in white spruce is significantly higher, and stomatal limitation lower, than in black spruce (a tolerant species).

Nitrogen often has been considered a growth-limiting nutrient, as reflected in studies reporting positive relationships between needle N and spruce growth (e.g., Wang and Klinka 1997, Paquin et al. 1998). We initially expected greater mineral N availability in clear-cut plots, as several studies have shown a flush of mineral N occurring 2–3 years following clear-cutting (e.g., Nohrstedt et al. 1994, Stevens et al. 1995, Simard et al. 2001, Bradley et al. 2002) and lasting several years thereafter (e.g., Frazer et al. 1990, Simard et al. 2001). Our results showed, however, that different harvesting intensities in aspen stands had no significant effects on indices of soil mineral N availability. Grenon et al. (2004) compared soil mineral N dynamics across different ecosystems and concluded that increases in mineral N availability following clear-cutting are not universal and are best explained by site-specific factors. In this particular ecosystem, clear-cut aspen plots

are rapidly recolonized by rapidly growing aspen root suckers, and this, we believe, will sustain the “forest influence” (e.g., maintain a flow of soil available-C, restore plant N uptake, etc.) on soil N dynamics following disturbance. Although we did not find differences in soil mineral N availability across the different canopy retention treatments, results from foliar analyses did not indicate a serious growth limiting soil N status for seedlings of all treatments. Foliar N concentrations that brought about a diagnosis of “slight” N deficiency in the 1/3 harvested (13.0 mg N g^{-1}) and clearcut stands (13.7 mg N g^{-1}), are actually quite near the critical norm developed by Ballard and Carter (1986) for white spruce. The apparent contradiction with diagnostic vector analysis, which found “excess” N in the 1/3 harvested stands, is due to foliar characteristics in one particular plot. When we remove this outlier, we find that the average shift in the vector diagram of the remaining 1/3 harvested plots is to right along the horizontal, as for the other treatments, and suggests non-limiting soil N status.

We did not measure availability indices for soil nutrients other than N, therefore we cannot test whether treatment-induced changes in needle Ca, Mg or K concentrations were related to changes in the capacity of soils to supply these nutrients. Because vector analysis did not detect nutrient deficiencies or nutrient excesses in non-harvested plots, we propose that these shifts in needle nutrient concentrations were related to physiological adaptations brought on by increased seedling growth. For example, Burgess and Wetzel (2000) provided evidence that Ca concentrations in white pine (*Pinus strobus* L.) respond positively to new light conditions created by harvesting, rather than to a greater availability of Ca in the soil. There is evidence that this relationship may be generalized, given similar results obtained by Munson et al. (1995), who found that removal of competing vegetation markedly increased needle Ca of white spruce seedlings as well as growth rates. On the other hand, K and Mg are known to be taken up by spruce in luxury amounts (Landis 1985, Wells and Warren 1997), such that lower K concentrations in clear-cut plots may actually result from a dilution effect brought on by larger seedling and needle mass. Contrary to Ca, foliar Mg and K are more mobile within foliar tissues. Alternatively,

lower needle Mg and K concentrations in clearcut plots may be due to a reduced input of these two nutrients in litter following the elimination of the overstory. Regardless of which explanation is correct, our results agree with those of Granhus and Braekke (2001) who found that increasing harvest intensity resulted in lower concentrations of foliar K and Mg and a concomitant increase in the growth of Norway spruce (*Picea abies* L.) saplings.

One of our objectives was to determine whether foliar nutrient concentrations could be linked to seedling growth performance, because seedling growth is considered a good predictor of future growth rates in some conifer species (Mitchell et al. 2003). Based on the relationships shown in Fig. 2, we suggest that Ca concentration in previous year needles is the more robust foliar indicator of future growth rates, for two reasons: first, the relationship between previous year needle Ca concentration and RGR explains the highest percentage of the variance (i.e., highest r^2 value) among all the nutrients that were tested; second, this relationship persists throughout the growing season (i.e., all three sampling dates). We note, however, that this relationship is strongly influenced by the increase in the value of these two variables in clearcut plots. Although forest harvesting will often cause a loss of biologically available Ca that is tied up in vegetation (Federer et al. 1989, Reiners 1992), it is unlikely that post-harvest Ca deficiency occurred on these clay rich soils of Abitibi, where high soil Ca status has been reported (Lamarche et al. 2004). The relationships shown in Fig. 2 (a,b,c) bring up two separate questions:

1) *Why are previous year foliar Ca concentrations higher in clearcut plots?*

Given the important role of Ca in cell wall synthesis, it is logical that increased Ca uptake would be more evident in second year needles, where Ca crosslinking within the cell wall structure is more complete than in current year needles. McLaughlin and Wimmer (1999) explained that higher Ca uptake may be the result of lower soil acidity, higher root exploration, or higher soil moisture. Each of these three factors potentially explain higher Ca uptake on clearcut plots in the present study. For example, clearcutting may increase soil pH (Smolander

et al. 1998), which can in turn significantly increase the Ca:Al ratio in soil solution and promote root uptake of Ca (McLaughlin and Wimmer 1999). Alternatively, higher soil volume exploration by spruce seedlings may occur in clearcut plots as a result of reduced root competition from overstory trees. Thirdly, clearcut plots typically have higher soil moisture than non-harvested stands for several years following disturbance (Adams et al. 1991), and Ca uptake is correlated with periods of soil water availability (Osonubi et al. 1988).

2) *Is the association between foliar Ca concentrations and RGR causal or spurious and, assuming it is causal, what mechanism(s) are responsible?*

Previous studies have shown that Ca concentrations in tree tissues can be directly related to tree vigor and growth (Cronan and Grigal 1995). Fertilization experiments in Sweden (Nohrstedt et al. 1993) showed a positive growth response of Norway spruce to added Ca. It was proposed that Ca increases the effectiveness of N in stimulating growth. The importance of Ca supply for promoting N uptake has also been demonstrated in several liming studies (Huettl 1989). Improved Ca nutrition may also be linked to increased fine-root production and function (McLaughlin and Wimmer 1999). Hence, in spite of the strong evidence suggesting that light availability, rather than nutrient limitations, is the main determinant of white spruce seedling growth in the present study, more work is required to test whether Ca uptake is also related to seedling growth performance on these plots.

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