

Thinning Effects on Jack Pine and Black Spruce Photosynthesis in Eastern Boreal Forests of Canada

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Goudiaby, V., Brais, S., Grenier, Y. & Berninger, F. 2011. Thinning effects on jack pine and black spruce photosynthesis in eastern boreal forests of Canada. *Silva Fennica* 45(4): 595–609.

A decrease in the average diameter of commercially harvested tree species in the Eastern boreal forest of Canada has led to a decrease in availability of quality wood for the forest industry. Commercial thinning has been proposed as a means to increase stem diameter growth. However, little is known about physiological responses underlying species responses to thinning. We assessed the effect of canopy opening on the photosynthetic response of mature jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) trees. Two years after thinning and for each species, light response curves and the diurnal course of photosynthesis were characterized from measurements taken in a completely randomized block experiment on current-year and one-year-old needles of 12 trees from stands subjected to different levels of canopy opening. Soil water content, air and soil temperatures, and needle N concentration were not affected by thinning for either species. However, light availability increased with basal area removed and could explain the significantly positive relationship between thinning intensity and diurnal course of photosynthesis for one-year-old needles of jack pine. Black spruce photosynthesis did not respond to increases in light. Light-saturated rate of net photosynthesis (A_{\max}), photosynthetic efficiency (α), light compensation point (LCP), and diurnal respiration (R_d) did not vary with thinning for either of the species. Jack pine and black spruce responses to thinning should be interpreted in light of species autecology.

Keywords light, nitrogen, *Picea mariana*, *Pinus banksiana*, photosynthesis, thinning

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Received 1 June 2011 **Revised** 15 August 2011 **Accepted** 31 August 2011

Available at <http://www.metla.fi/silvafennica/full/sf45/sf454595.pdf>

1 Introduction

Jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) are two tree species common in the eastern Canadian boreal forests that are of great commercial value. The thinning of mature stands of these species has proven to be an effective means to increase individual stem biomass and diameter growth (Weetman 1971, Barbour et al. 1994, Newton and Jolliffe 2003). The objective of thinning in forestry is usually to accelerate individual tree growth by reducing competition for light (Hale 2003), soil nutrients, and water (Latham and Tappeiner 2002). However, the physiological process underlying these responses remains unclear for mature jack pine and black spruce, as photosynthesis measurements from mature thinned stands have yet to be reported for these two species. While competition and photosynthesis responses to light (Ter-Mikaelian et al. 1999), nitrogen, and water (Robinson et al. 2001) were tested on jack pine seedlings, these results can hardly be transferred to mature trees because, as demonstrated in a review, gas exchange parameters significantly change with ontogeny (Thomas and Winner 2002).

Greater light availability as a result of thinning has been shown to induce changes in foliage physiology (Tang et al. 1999) and to increase light-saturated rate of net photosynthesis (A_{\max}), and dark respiration rate (R_d), as well as the photosynthetic light compensation point (LCP) (Loach 1967, Pothier and Prévost 2002). However, the capability to respond to increased light availability depends on the shade tolerance of the tree species (Wright et al. 1998). Rates of photosynthesis, light-saturated rate of net photosynthesis, apparent quantum yield (α), and dark respiration, as well as the photosynthetic light compensation point tend to be greater for shade-intolerant species than for shade-tolerant ones (Bazzaz 1979). In response to increased light availability, shade-intolerant species have demonstrated greater photosynthetic plasticity and were likely to reach A_{\max} at higher light intensities (Bazzaz 1979, Loach 1967, Pothier and Prévost 2002).

Regardless of their shade tolerance, increasing

light availability may lead to a very irregular response in leaf respiration because it increases in some species and decreases in others (Loach 1967). Increased light interception at the tree scale (Tang et al. 1999) following thinning can lead to higher stomatal conductance and transpiration. Therefore, response to thinning is a combination of water loss by evapotranspiration and carbon (C) uptake by photosynthesis, owing to the stomata being the dual pathway for water loss and C uptake. However, stand transpiration in boreal forest stands does not strongly change in response to thinning because understory vegetation (Vesala et al. 2005) compensates for reduced foliage area. Increases in tree growth after thinning in such conditions would likely be a consequence of photosynthesis increase at the expense of water loss.

The aims of this study were to assess changes in tree photosynthesis induced by thinning of pure, even-aged black spruce and mature jack pine stands and to relate those changes to measurements of light and water availability. Our hypotheses were that 1) for jack pine, an early successional and shade-intolerant species, the photosynthetic response to thinning corresponds to a decrease in the competition for light, water, and nutrients; and that 2) black spruce, although likewise sensitive to light, water, and nutrients, has less photosynthetic responsiveness because of its greater shade tolerance (Hom and Oechel 1983). Moreover, it has been shown that black spruce has little ability to take advantage of favourable conditions (Groot and Hökkä 2000).

2 Materials and Methods

2.1 Study Site

The study was carried out in Abitibi-Témiscamingue, a region situated in the boreal shield of northwestern Quebec (Rowe 1972). Black spruce, white spruce (*Picea glauca* Moench. Voss.), jack pine, and balsam fir (*Abies balsamea* (L.) Mill.) are all common species of this ecological zone (Rowe 1972). The jack pine experiment (block 1 (48°32'45"N and 77°49'04"W); block 2 (48°32'21"N and 77°49'21"W)) was located in the

Table 1. Site information and stand characteristics two years after thinning of jack pine and black spruce stands.

Block	Age (year)	Basal area (m ² ha ⁻¹)								
		Before thinning	Control After thinning	Percent removed	Before thinning	Moderate After thinning	Percent removed	Before thinning	Intensive After thinning	Percent removed
JACK PINE										
Block 1	82	22.30	22.30	0	19.70	17.90	9.14	18.50	14.10	23.78
Block 2	81	26.80	26.80	0	23.60	20.60	12.71	23.00	14.10	38.70
BLACK SPRUCE										
Block 1	72	43.84	43.84	0	32.07	22.56	29.66	42.51	29.07	31.62
Block 2	77	50.05	50.05	0	34.56	26.70	22.75	39.72	20.45	48.51

Township of Landrienne in an 82-year-old natural jack pine stand. The topography is relatively flat and the elevation approximately 352 m. The average daily temperature is 1.1°C with an average minimum of -22.9°C in February and an average maximum of 23.1°C in July. Total annual average precipitation is 920 mm with a maximum monthly average of 107.5 mm falling in July (Environment Canada 2009). Soils, classified as orthic podzol, evolved from a well-drained, glaciolacustrine sandy loam surface deposit (AAFC 1998). The black spruce study was set in two different locations (Township of Bacon or block 1: 49°24'31"N and 78°39'42"W; Township of Rainboth or block 2: 49°22'16"N and 78°31'37"W). The topography is also relatively flat and the elevation approximately 300 m. The average daily temperature is 0.8 °C with an average minimum of -24.3°C in January and an average maximum of 23.3°C in July (Environment Canada 2009). Total annual average precipitation is 857 mm with a maximum monthly average of 113.2 mm falling in September. The soils are developed on poorly drained clay to sandy clayey loam glaciolacustrine deposits and are classified as gleyed luvisols (AAFC 1998).

2.2 Experimental Design

Jack pine and black spruce experiments were separately conducted as completely randomized block designs with two blocks and three treatments each. Thinning was done from below in 0.5 ha experimental units in the summer of 2002 for jack pine and in 4 ha experimental units for black spruce in the winter of 2003. Relative densities of 0.5 (moderate thinning) and 0.4 (intensive

thinning) were targeted for black spruce and 0.4 (moderate thinning) and 0.3 (intensive thinning) for jack pine using density management diagrams (Grenier et al. 2001, Grenier and Harvey 2004). Two to four 200 m² permanent plots were sampled in each experimental unit before and after treatment for basal area estimation (Table 1).

2.3 Gas Exchange Measurements

For each species, photosynthesis measurements were conducted in one 200 m² permanent plot per block-treatment combination for a total of 6 plots per species. In each plot, the two dominant trees closest to the experimental plot centre were retained. Because tree photosynthesis response to thinning has been shown to occur in the lower crown (Tang et al. 1999), measurements were conducted in the lower third of the crown, i.e., 1.5 m above the crown base, which is accessible with ladders and platforms. Three shoots per tree were sampled for measurements at opposing directions around the outer crown, closer to the tips of the branches, where light exposure is maximized. Measurements were conducted on current-year and one-year-old needles on each shoot for a total number of 24 measured shoots (irrespective of the needle age or the thinning intensity applied) per species. Measurements for diurnal course of photosynthesis and for light response curves were conducted on different occasions and on different shoots. Measurements were respectively conducted with a conifer LI-6400-05 and a broad-leaf LI-6400 3×6 chamber units. The number of needles enclosed in the chamber was on average 19 and 65, corresponding to surface areas of 6.0 cm² and 4.1 cm² for jack pine and

black spruce, respectively. At the end of the measurements, the needles were carefully detached from the collected shoots and sent to the laboratory for nitrogen concentration, surface area, and weight characterization.

2.3.1 Photosynthetic Light Response Curve

Measurements were conducted in July 2005, between 09:00 and 12:00 hours, when photosynthetic rates were at their highest. A LI-6400 was equipped with a red-blue 6400-02B light source. Prior to measurements, the CO₂ mixer and light source were calibrated. Temperature and relative humidity in the chamber were set close to ambient air values. Photosynthesis was measured after needles were first equilibrated with light saturation (2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$); then, photon irradiances were gradually decreased to 1500, 500, 200, 100, 50, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The lower window of the chamber unit was covered so that the light in the 3×6 chamber unit exclusively came from the light source, without any interference from ambient light. This allowed us to determine the exact amount of light that reached the needles enclosed in the chamber – a quantity that happened to correspond with the range of irradiances targeted during the photosynthetic light response survey. The Mitscherlich nonlinear function (Potvin et al. 1990) was used to fit photosynthetic light response curves:

$$A = A_{\max} [1 - e^{-a(\text{PPFD} - \text{LCP})}]$$

where A represents net photosynthetic CO₂ assimilation, A_{\max} is the light-saturated rate of net photosynthesis, a corresponds to the initial slope of the curve (photosynthetic efficiency or apparent quantum yield), PPFD refers to the incident photosynthetic photon flux density, and LCP is the x-intercept of the curves and refers to the photosynthetic light compensation point. The Mitscherlich nonlinear function was fitted to the data because, as all the parameters of the function refer to physiological processes, the function fits the data better than quadratic models. As such, fitting a function to data has become the standard means of light curve fitting in physiological ecology (Peek et al. 2002, Heschel et al. 2004). Dark

respiration (R_d) does not appear in the equation but was directly measured on trees as the rate of CO₂ evolution at zero incident photosynthetic photon flux density.

2.3.2 Diurnal Course of Photosynthesis

Diurnal course of photosynthesis measurements were conducted in 2004 for jack pine and in 2005 for black spruce under natural light conditions with an automatic 6400-05 conifer chamber mounted on the LI-6400. Transpiration and assimilation rates provided by the LI-6400 were based on the computation of the concentration differences between reference and sample infrared gas analyzers (IRGA). Sample and reference IRGAs were matched at the beginning of the measurements and every 30 minutes afterwards. Chamber temperature and relative humidity were set close to ambient values, and the chamber was clamped onto the shoot. Data were logged when, over a time period of 20 seconds, fluctuation in photosynthesis were lower than 0.1 mmol CO₂ m⁻² s⁻¹ and when variations of conductance were lower than 0.05 mol H₂O m⁻² s⁻¹.

For jack pine, instantaneous photosynthesis was measured with the LI-6400 approximately every two hours. The first and last measurements of the day were done before sunrise and after sunset, respectively. The PPFD was concurrently measured with a LI-190SA external quantum sensor (LI-COR Biosciences, Lincoln, Nebraska) mounted on the LI-6400. For black spruce, time limitation and distance between blocks did not allow us to conduct a full diurnal survey and measurements were taken approximately every three hours. In all, 8 measurements were conducted throughout the day for jack pine and 6 for black spruce. In addition, as it was impossible to measure all trees in a single day, measurements were taken for each species over a period of 6 days.

2.4 Specific Leaf Area and Nutrient Status of the Needles

At the end of the survey, measured needles were removed, placed in plastic bags, refrigerated in a

cooler, and transferred to the laboratory. Needles were scanned and surface areas were measured using the software Winseedle 5.0 (Regent Instruments Inc., Quebec City, QC, Canada). Needles were then weighted (Sartorius, BP 210) to the nearest 0.1 mg after drying in a ventilated oven at 65°C for 48 hours. Specific leaf area (SLA) was determined from the ratio of projected needle surface area to needle dry mass. Gas exchange values initially measured on an area basis were then expressed on a mass basis by dividing them by their corresponding SLA.

Sampled needles were oven dried (65°C for 48 h) and ground to 2 mm with a Wiley Mill equipped with stainless steel cutters and a sieve. After subjecting the samples to another drying process, 0.5 g of the sample was digested for 90 min with 10 ml of H₂SO₄-H₂O₂-Se at 380°C (Parkinson and Allen 1975). Total N was determined using an FIA (Tecator Flow Injection Analyzer).

2.5 Environmental Parameter Measurements

2.5.1 Soil Water Status

Environmental parameters were measured two growing seasons after thinning, i.e., in 2004 for jack pine and in 2005 for black spruce. Soil was sampled with an auger in each experimental plot from surface soil to 70 cm depth at every 10 cm, for a total of seven soil samples per experimental plot. Gravimetric soil water content (SWC) was calculated for each of the 7 soil samples after weighting and drying (105°C). Field capacity (FC_{mass}; g) was measured on undisturbed soil samples at a tension value of -10 kPa according to Cassel and Nielsen (1986). Permanent wilting point (PWP_{mass}; g) was estimated on sieved (2 mm) samples at a tension value of -1500 kPa using the same procedure. Available water holding capacity (AWHC_{mass/mass}; g g⁻¹) was computed as the difference between water retained at field capacity and permanent wilting point. Finally, AWHC_{mass/mass} was expressed on a volume basis (AWHC_{vol/vol}; cm³ cm⁻³) by multiplying it by the sample's bulk density.

Available soil water content on the day of the measurements (Cassel and Nielsen 1986) was

reported as depth (SWC_{depth}; cm) of the water as if it was accumulated in a layer and was computed as follows:

$$\text{SWC}_{\text{depth}} = [(\text{AWHC}_{\text{vol/vol}}) \times (\text{unit area} \times \text{length})] / (\text{unit area})$$

where the unit area represents the cross-sectional area of the auger and where length refers to the 70 cm soil depth.

2.5.2 Air and Soil Temperatures

Air temperature and relative humidity were continuously measured in each experimental plot using an automated weather station consisting of a data logger (CR10, Campbell Scientific Ltd., Leicestershire, United Kingdom) and a temperature and a relative air humidity probe (MP300, Campbell) mounted 2 m above ground level and close to the middle of the experimental plot. The measurement intervals for the air temperature and the relative air humidity sensors were set according to manufacturer's recommendations and the data average recording interval to 5 min; the data were then averaged for each hour of the months of July and August.

Soil temperature was measured close to the middle of each experimental plot, in the vicinity of the measured trees, using two soil temperature probes (Hobo 4-Channel External Data Logger), one located in the forest floor and the other one in the mineral layer, at around 5 cm depth within each layer. The temperature probes continuously measured at a time step of one minute and the data were averaged for each hour of the months of July and August.

2.6 Statistical Analyses

Statistical analyses were performed using SAS software package (SAS Institute version 9.1, Cary, North Carolina, 2002). Photosynthetic light response curves were obtained by plotting photosynthesis against PPFD for each needle age at the tree level. The Mitscherlich nonlinear function was fitted to light response and A_{max}, α, LCP, and R_d were derived from the NLIN procedure.

Because of differences in the initial basal area between experimental units and blocks, and because of variations in the basal area that was removed during treatment, a regression approach was preferred over a means comparison between treatments. Dependant variables were explained in terms of relative basal area removed [(basal area removed / initial basal area) × 100]. A mixed linear model analysis, allowing for random and nested effects, was used in order to benefit from each observation (tree level) while taking into account the non-independence of nested effects (trees nested within experimental plot, and plot nested within block). Statistical analyses were separately conducted on current-year and one-year-old needles. Shoot values (N = 3) were averaged for each tree, removing in this way the shoot effect from the models. The following general model was used to test the effect of the relative basal area removed on diurnal photosynthesis.

$$Y_{bpti} = \beta_0 + b_1 G_{rbp} + \beta_2 T_{bpti} + \beta_3 G_{rbp} T_{bpti} + \beta_4 T_{bpti}^2 + \mu_b + \varepsilon_{bpti}$$

where Y_{bpti} represents the dependent variable (b = block, p = plot, and t = tree) for the *i*th measurement, β_0 the intercept, β_1 the regression coefficient of the relative basal area removed (G_{rbp}), β_2 the regression coefficient for time of day (T_{bpti}), β_3 the regression coefficient of the interaction between relative basal area removed and time of day ($G_{rbp} T_{bpti}$), β_4 the regression coefficient of the quadratic effect of time (T_{bpti}^2), μ_b the random effect for block, and ε_{bpti} the error term. As photosynthesis measurements were repeated over time, and owing to the variation that had occurred, in some case, in the time elapse between two consecutive measurements, we used a REPEATED statement applied to time (T_{bpti}) with a SP(POW) covariance structure for unequally spaced data. We used Kenward-Roger (KR) approximation method of degree of freedom (Kenward and Roger 1997) because it is the most appropriate for models with random effect and repeated statement (Saavedra and Douglass 2002).

For A_{max} , α , LCP, R_d , N, soil water content, and soil and air temperatures, basal area removed was the only explanatory variable included in the model. A visual analysis of residuals was con-

ducted and variables were transformed (square root), when necessary, in order to improve residuals normality and to eliminate any trend between residuals and predicted values. Fixed effects were considered significant at $p < 0.05$ based on type III test of fixed effects.

3 Results

3.1 Evaluation of the Thinning Treatment

Thinning removed 11% and 26% of initial basal area in the moderate treatment and 31% and 40% in the intensive treatment for jack pine and black spruce, respectively (Table 1). For both species, no significant differences in initial basal area and relative basal area removed were found between experimental plots of the same thinning treatment.

3.2 Environmental Factors

Average soil water contents of jack pine (17.7 mm) and black spruce (41.3 mm) stands were not affected by relative basal area removed during the course of measurements. On a diurnal time scale, minimum air temperature occurred early in the morning and maximum air temperature between 14:00 and 16:00 hours (Fig. 1). Mean minimum and maximum air temperatures during the measurement period were respectively, 9.7°C and 28.3°C for jack pine and 11.7°C and 31.1°C for black spruce plots. Relative air humidity displayed higher values in the morning for both jack pine and black spruce and remained lower for the rest of the day. Average soil temperatures in the forest floor and in the mineral layer were respectively, 15.7°C and 14.3°C for jack pine and 14.1°C and 12.7°C for black spruce. Relative basal area removed had no significant effect, for either species, on mean minimum and maximum air temperatures, relative air humidity, and soil temperature. Soil temperatures in the forest floor and mineral layer were generally around 10–15°C in the morning and reached a maximum of approximately 15°C between 14:00 and 16:00 hours.

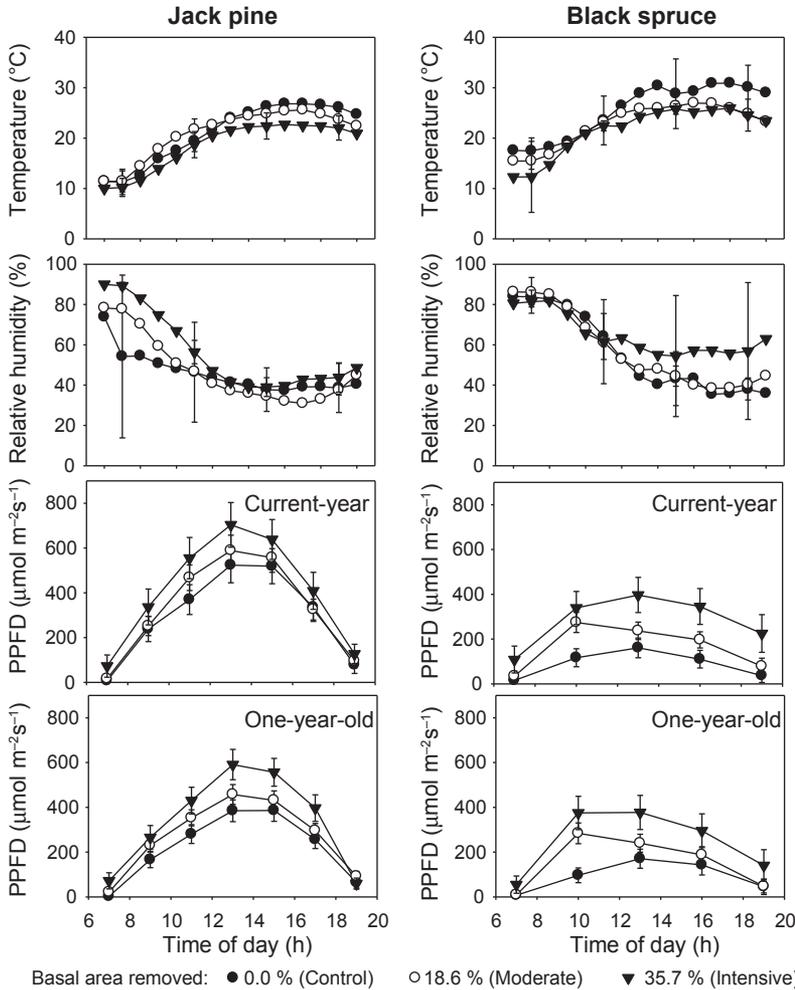


Fig. 1. Diurnal course of needle photosynthesis based on predicted values of models for jack pine current-year (N = 96) and one-year-old needles (N = 96) and black spruce current-year (N = 72) and one-year-old needles (N = 72) on a needle surface area and a mass basis two years after thinning treatment. The number of measured trees per thinning treatment and per species is 4. Error bars represent standard errors.

Significant linear and quadratic effects of time were observed on PPFD for both species (Fig. 1), with the highest values observed between noon and 14:00 hours. For jack pine, PPFD did not significantly vary with relative basal area removed in the vicinity of current-year needles (Table 2), while it significantly increased in the vicinity of one-year-old needles (Table 2). In addition, the interaction between relative basal area removed

and time had a significant effect on PPFD at the vicinity of one-year-old needles. For black spruce, relative basal area removed had a significant effect on PPFD in the vicinity of one-year-old needles while the effect was not significant in the vicinity of current-year needles (Table 2). No significant interactions were found between basal area removed and time.

Table 2. Effects of relative basal area removed (G_r) on diurnal course of photosynthetic photon flux density (PPFD) in the vicinity of current-year and one-year-old needles of jack pine and black spruce two years following thinning. Type III test of fixed effects.

	Current-year needles			One-year-old needles		
	Den DF	F value	p > F	Den DF	F value	p > F
JACK PINE						
G_r	3.2	1.19	0.438	3.2	0.41	0.040
T	88.8	38.92	< 0.001	81.2	30.11	< 0.001
$G_r \times T$	80.1	0.01	0.273	79.8	0.02	0.05
T ²	83.4	80.35	< 0.001	82.2	71.24	< 0.001
BLACK SPRUCE						
G_r	4.7	0.38	0.057	3.6	2.40	0.050
T	141.2	14.44	< 0.001	82.5	23.86	< 0.001
$G_r \times T$	80.3	0.27	0.542	81.6	0.00	0.948
T ²	85.4	17.75	< 0.001	86.1	21.16	< 0.001

Note: T: time of day, T²: quadratic effect of time of day, F: Fisher value, p: probability at 0.05, and Den DF: denominator degree of freedom. For jack pine and black spruce, numerator degree of freedom is 1. For jack pine: N = 96, measurements were taken 8 times a day. For black spruce: N = 78, measurements were taken 6 times a day (one missing shoot). For one-year-old needles in both species: homoscedasticity of residuals was obtained using square root transformation of PPFD.

Table 3. Effects of relative basal area removed (G_r) on current-year and one-year-old needles photosynthetic parameters (surface area and mass basis) of jack pine and black spruce two years following thinning. Type III test of fixed effects.

	Surface area basis			Mass basis		
	Den DF	F	p > F	Den DF	F	p > F
JACK PINE						
<i>Current-year needles</i>						
A_{max}	6	0.20	0.674	6	4.14	0.088
LCP	6	0.12	0.738	6	0.07	0.802
α	6	0.97	0.362	6	0.97	0.362
R_d	6	1.13	0.328	6	0.05	0.823
<i>One-year-old needles</i>						
A_{max}	6	0.59	0.470	6	1.02	0.353
LCP	6	0.06	0.344	6	1.87	0.220
α	6	1.05	0.344	6	5.46	0.058
R_d	6	1.51	0.265	6	2.11	0.197
BLACK SPRUCE						
<i>Current-year needles</i>						
A_{max}	5	0.00	0.970	5	0.36	0.575
LCP	5	0.26	0.630	5	0.39	0.560
α	5	0.22	0.662	5	0.22	0.662
R_d	5	0.04	0.857	5	0.06	0.821
<i>One-year-old needles</i>						
A_{max}	5	0.13	0.734	5	0.00	0.985
LCP	5	0.46	0.526	5	0.69	0.443
α	5	0.05	0.833	5	0.05	0.833
R_d	5	0.66	0.454	5	0.95	0.375

Note: A_{max} : light-saturated rate of net photosynthesis, LCP: light compensation point, α : apparent quantum yield, R_d : diurnal respiration, Den DF: denominator degree of freedom, F: Fisher value, and p: probability at 0.05. For jack pine and black spruce, numerator degree of freedom is 1. For jack pine N = 12 and for black spruce N = 11 (one missing value).

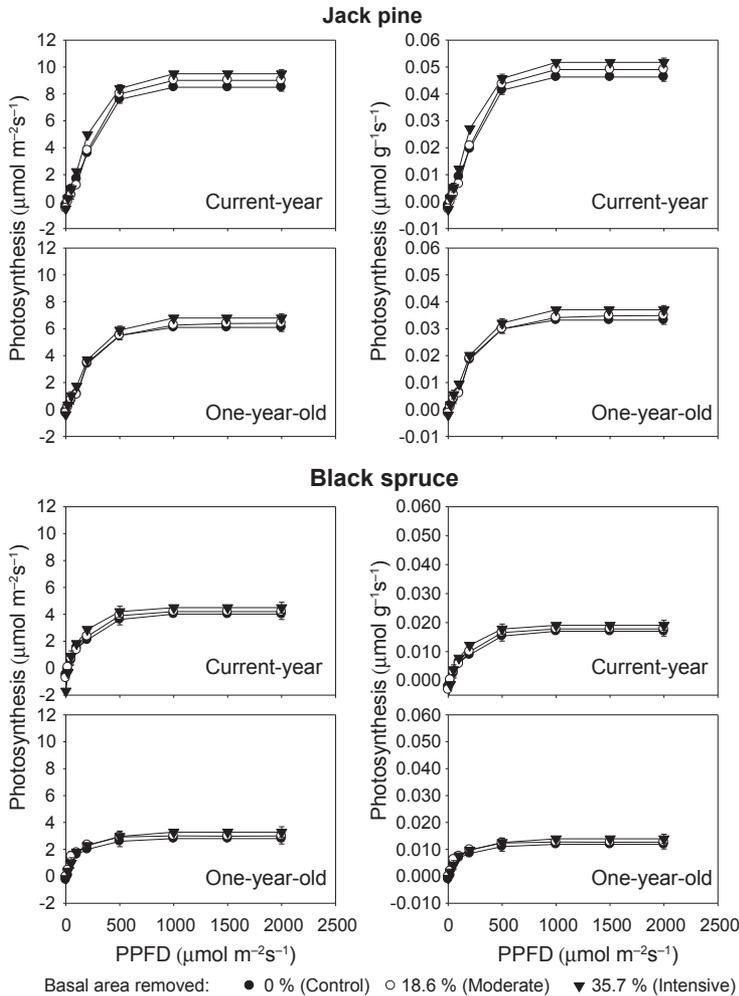


Fig. 3. Diurnal course of air temperature and relative humidity per plot with the same thinning treatment (N = 2) and photosynthetic photon flux density (PPFD) for current-year and one-year-old needles for jack pine (N = 96) and black spruce (N = 72) two years after thinning treatment. Each value represents the average of two experimental plots with the same thinning treatment. Error bars represent standard errors.

3.3 Gas Exchange

3.3.1 Photosynthetic Light Response and Derived Parameters

The Mitscherlich nonlinear function used to fit jack pine and black spruce photosynthetic light response data explained over 90% of the variance of the data (individual tree curves not shown) on a mass as well as on an area basis (Fig. 2). Observed

values of A_{max} , α , LCP, and R_d in control stands (on a needle surface area basis) were respectively, 8.07, 0.028, 17.70, and $-0.20 \mu\text{mol m}^{-2} \text{s}^{-1}$ for jack pine and 3.65, 0.027, 13.47, and $-0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$ for black spruce. Relative basal area removed had no significant effect on jack pine or black spruce current-year or one-year-old needle A_{max} , α , LCP, and R_d , whether expressed on a needle surface area or on a mass basis (Table 3).

Table 4. Effects of relative basal area removed (G_r) on diurnal course of photosynthesis for current-year and one-year-old needles (surface area and mass basis) of jack pine and black spruce two years following thinning. Type III test of fixed effects.

	Den DF	Surface area basis F	p > F	Den DF	Mass basis F	p > F
JACK PINE						
<i>Current-year needles</i>						
G_r	2.7	0.38	0.590	2.8	0.34	0.689
T	69.1	156.90	< 0.001	70.6	192.32	< 0.001
$G_r \times T$	61.4	1.37	0.093	62.0	0.85	0.059
T ²	66.9	96.3	< 0.001	67.3	116.51	< 0.001
<i>One-year-old needles</i>						
G_r	4.9	21.57	< 0.001	5.1	35.61	< 0.001
T	83.5	233.56	< 0.001	83.5	309.99	< 0.001
$G_r \times T$	84.2	0.13	0.007	85.3	0.51	0.005
T ²	80.8	97.50	< 0.001	81.7	99.33	< 0.001
BLACK SPRUCE						
<i>Current-year needles</i>						
G_r	5.3	0.02	0.377	4.3	0.09	0.463
T	99.0	8.58	0.047	98.3	8.79	0.004
$G_r \times T$	80.3	0.72	0.388	80.7	0.77	0.402
T ²	85.4	10.61	0.002	86.2	11.62	0.002
<i>One-year-old needles</i>						
G_r	6.1	0.05	1.188	6.3	0.05	1.384
T	96.3	33.44	< 0.001	97.1	35.54	< 0.001
$G_r \times T$	85.1	0.08	0.718	86.2	0.16	0.683
T ²	85.4	24.87	< 0.001	85.8	28.25	< 0.001

Note: T: time of day, T²: quadratic effect of time of day, F: Fisher value, p: probability at 0.05, and Den DF: denominator degree of freedom.

For jack pine and black spruce, numerator degree of freedom is 1.

For jack pine: N = 96, measurements were taken 8 times a day.

For black spruce: N = 78, measurements were taken 6 times a day (one missing shoot).

Homoscedasticity of residuals was obtained using square root transformation of photosynthesis.

All significant variables have positive relationships, except for T², which has a negative relationship.

3.3.2 Pattern of Diurnal Course of Photosynthesis

Irrespective of the thinning treatment and species, values of diurnal course of photosynthesis were low in the morning, reached a maximum in the middle of the day, and declined thereafter to their lowest values observed at the end of the day, when light availability became very low (Fig. 3).

Photosynthesis of current-year needles of jack pine in control plots increased from 6:00 until 11:00 hours and then decreased until sunset. The linear and quadratic effects of time on photosynthesis were highly significant for current-year and one-year-old needles (Table 4, Fig. 3). Photosynthesis of one-year-old needles expressed on a surface area or on a mass basis significantly increased with basal area removed (Table

4, Fig. 3) while no significant effect of basal area removed was observed on photosynthesis for current-year needles. Also, for one-year-old needles, the interaction between time and relative basal area removed generally had a significant effect on photosynthesis. Jack pine models for diurnal course of photosynthesis expressed on a needle surface area or on a mass basis, respectively explained 88% and 97% of diurnal course of photosynthesis for one-year-old needles.

For black spruce current-year and one-year-old needles, time had significant linear and quadratic effects on photosynthesis, with highest values observed between 12:00 and 14:00 hours. Basal area removed had no effect on photosynthesis for black spruce current-year and one-year-old needles.

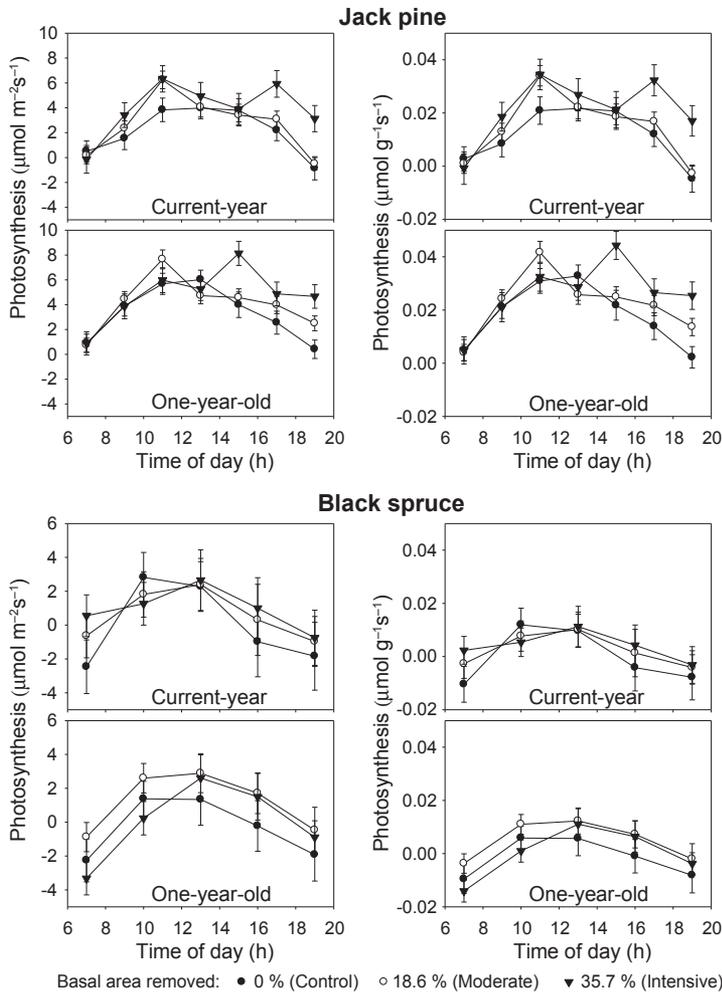


Fig. 2. Photosynthetic light response curves based on predicted values of models expressed on a needle surface area and a mass basis for jack pine (N = 12) and black spruce (N = 11) in the vicinity of current-year and one-year-old needles. The number of measured trees per thinning treatment and per species is 4. Error bars represent standard errors.

3.4 Specific Leaf Area and Nutrient Status of the Needles

For the jack pine control treatment, SLA was 6.41 and 5.71 m² kg⁻¹ for current-year and one-year-old needles, respectively. For black spruce, SLA was 4.79 and 4.08 m² kg⁻¹ for current-year and one-year-old needles, respectively. No significant relationship was found between SLA and relative basal area removed for either species.

Needle nitrogen concentrations were 9.7 g kg⁻¹ and 7.6 g kg⁻¹ for jack pine current-year and one-year-old needles, respectively. For black spruce, needle nitrogen concentrations were 7.6 g kg⁻¹ and 7.3 g kg⁻¹ for current-year and one-year-old needles, respectively. For both species, relative basal area removed did not have any effect on needle N concentrations and no significant interaction between relative basal area removed and needle age was found.

4 Discussion

Thinning is a common silvicultural practice, which aims to enhance tree growth by decreasing between-tree competition for light, nutrients, and water (Aussenac 2000). We hypothesized that jack pine response to thinning would be related to a decrease in competition for light, water, and nutrients, while black spruce would be less responsive in terms of photosynthetic activity. During the course of measurements, we found no relationships between relative basal area removed and soil water availability, soil temperature, or N availability expressed by N foliar concentration for both species. In these experiments, slash as well as non-merchantable stems were left on the ground and presumably contributed to reduce soil water evaporation and to creating a possible buffer against changes in soil temperature.

However, the observed increase in light availability after thinning may have played a role in the increase in diurnal course of photosynthesis of one-year-old jack pine needles despite the fact that measured trees were dominant and not as likely to be light-limited as the trees removed by thinning operations. Comparing thinned and unthinned loblolly pine (*Pinus taeda* L.) stands, Tang et al. (2003) found that light availability was the only significant variable predicting needle level photosynthesis rates after thinning, while Wang et al. (1995) also identified nitrogen concentration of leaves as contributing factors allowing white birch (*Betula papyrifera* Marsh.) to increase its photosynthesis following thinning. Both studies were conducted on very young stands (less than 16-year-old).

Observed photosynthetic parameters were within the range of those previously reported for jack pine (Sullivan et al. 1997) and black spruce (Rayment and Jarvis 1999, Johnsen et al. 2003). The increase in light availability observed for both species did not lead to any increase in photosynthetic efficiency, as shown by the lack of changes in photosynthetic parameters. No comparable studies relating gas exchange, mainly photosynthesis and respiration, to thinning for mature trees were found in the literature. However, an increase in a in response to light increase was reported for herbaceous species (Peri et al. 2005). The lack of

changes in needle α , A_{\max} , LCP, and R_d following an increase of PPFD indicates that jack pine and black spruce do not actively adjust their physiology after thinning to enhance their efficiency in light utilization.

Generally α and A_{\max} are positively correlated with nitrogen and negatively with SLA (Wang et al. 1995). Considering the lack of response to thinning of foliar N concentrations and SLA, the positive response in diurnal course of photosynthesis observed for jack pine one-year-old needles can only be explained by longer periods of higher irradiation. This was not the case for black spruce, characterized by a low-light photosynthesis saturation capability, with the effect that following stand opening, observed values of photosynthesis were in the same range as those observed in the control stands.

Midday decreases in photosynthesis, such as the one observed for jack pine on current-year needles, result from a combination of high temperature and dry air (mostly occurring in the middle of the day) leading to an increasing vapour pressure difference (VPD) that partially closes stomata. Such a decrease in photosynthesis is referred to as midday stomatal closure and has been described for Norway spruce (Zweifel et al. 2002) and jack pine (Baldocchi et al. 1997). Sullivan et al. (1997) have shown that for mature jack pine and black spruce, CO_2 assimilation is stomatally limited and that environmental factors altering conductance (e.g., VPD) have a strong influence on CO_2 fluxes. Contrary to jack pine, black spruce did not show any midday stomatal closure, which is consistent with the fact that jack pine usually has greater stomatal sensitivity to VPD than black spruce (Dang et al. 1997).

Although we cannot statistically compare jack pine with black spruce, differences in photosynthetic parameters and responses to an increase in light availability merit an interpretation in the context of differing autecologies. Higher values of A_{\max} , α , LCP, and R_d observed for jack pine compared to black spruce are consistent with their respective successional and shade tolerance status (Bazzaz 1979). Jack pine is a fast growing, shade-intolerant, early successional species, while black spruce is mid to late successional and moderately shade tolerant (Sims et al. 1990). It has also been shown that shade-intolerant species can respond

to increases in light at higher ranges of light availability, while shade-tolerant species cannot adapt easily (Wright et al. 1998).

Measurements were taken two years following treatments and, as trees have a capacity for acclimation to changing environments, long-term photosynthetic response to thinning may be different from what we reported. Photosynthesis is known to be significantly affected by time of day or season of measurement (Yang et al. 2002) as well as temperature. Therefore, observed photosynthetic parameters provided in our experiment can hardly be taken to apply to other periods.

Our objective was to provide insight into photosynthetic parameters, diurnal course of photosynthesis, nitrogen concentration, and light availability shifts after thinning at the needle scale of individual trees as well as soil water availability at the plot scale. However, differences among needles may have been skewed due to low-tree replications, and the vertical nitrogen and photosynthesis gradient within the crown – factors that had not been accounted for in our experiment. Therefore, the possibility to generalize our results to whole trees is somewhat limited. As is well known, photosynthetic parameters are distributed along a bottom-up and lateral gradient, a phenomenon that is closely linked to light availability at the relative location of the corresponding needles (Schoettle and Smith 1999). Consequently, any attempt to scale up from needle to individual, without taking these previous considerations into account would be biased.

5 Conclusion

This study provides new insight into jack pine and black spruce photosynthesis and their responses to changes in resource availability induced by stand opening following thinning. Little information of this kind is currently available in the literature owing to the difficulties inherent in measuring mature trees. Linking ecophysiology to silviculture is a challenge, as short-term and small-scale measurements need to be related to longer-term and larger-scale processes. Our study is potentially useful for forest practitioners, as our investigation of photosynthesis, which is a

proxy of tree growth, may help explain how thinning affects tree growth. Results from our study are already being successfully used in a carbon balance algorithm for process-based C model parameterization.

Acknowledgements

This research was funded by the Canadian Natural Sciences and Engineering Research Council (CFSPJ 256356-01), NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Scierie Landrienne Inc., Domtar Inc., Tembec Inc. and Abitibi-Consolidated Inc. We are grateful to Toma Guillemette, Marie-Hélène Longpré and Mario Major for logistical and technical support and to two anonymous reviewers and to the editor for their helpful comments.

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