Changes in specific leaf area and photosynthetic nitrogen-use efficiency associated with physiological acclimation of two hybrid poplar clones to intraclonal competition

Lahcen Benomar, Annie DesRochers, and Guy R. Larocque

Abstract: Photosynthesis is the most important process driving productivity, and its acclimation to intraclonal competition is not well understood in hybrid poplars. The aim of this study was to examine the physiological response of the crown of two hybrid poplar clones, BT747215 (*Populus balsamifera* L. × *Populus trichocarpa* Torr. & A. Gray) and MB915319 (*Populus maximowiczii* A. Henry × *P. balsamifera*), to intraclonal competition. We measured light-saturated photosynthesis ($A_{\max}$), leaf N content on an area basis (N_{area}), specific leaf area (SLA), and photosynthetic N-use efficiency (PNUE) for three successive growing seasons on trees planted at three spacings (1 m × 1 m, 3 m × 3 m, and 5 m × 5 m). Crowns were sampled at 10 locations corresponding to vertical and horizontal subdivisions. Significant changes took place at the crown level in the closest spacing (1 m × 1 m) compared with the wider spacings (3 m × 3 m and 5 m × 5 m): (*i*) 30% decrease in N_{area}, (*ii*) 20% increase in SLA, and (*iii*) 40% increase in PNUE. The slope of the $A_{\max}$–N_{area} curve was greatest in the closest spacing, indicating a greater change in $A_{\max}$ per unit change in N_{area}. The two hybrid poplar clones had a similar morphophysiological response to changes of spacing. Both clones showed physiological acclimation of their foliage in response to intraclonal competition through modulation of SLA and PNUE.

Résumé : La photosynthèse est le processus qui a le plus d'impact sur la productivité et son acclimatation face à la compétition intraclonale n'est pas bien comprise chez les peupliers hybrides. Le but de cette étude consistait à examiner la réponse physiologique de la cime de deux clones de peuplier hybride, BT747215 (*Populus balsamifera* L. × *Populus trichocarpa* Torr. & A. Gray) and MB915319 (*Populus maximowiczii* A. Henry × *P. balsamifera*), face à la compétition intraclonale. Nous avons mesuré la photosynthèse à saturation lumineuse ($A_{\max}$), la teneur en N par unité de surface foliaire (N_{area}), la surface foliaire spécifique (SLA) et l'efficacité de l'utilisation photosynthétique du N (PNUE) pendant trois saisons de croissance successives sur des arbres plantés selon trois espacements (1 m × 1 m, 3 m × 3 m et 5 m × 5 m). La cime a été échantillonnée à 10 endroits correspondant à des subdivisions verticales et horizontales. Des changements importants sont survenus dans la cime lorsque l'espacement était le plus faible (1 m × 1 m) comparativement aux espacements plus grands (3 m × 3 m et 5 m × 5 m) : (*i*) une diminution de 30 % de N_{area}, (*ii*) une augmentation de 20 % de SLA et (*iii*) une augmentation de 40 % de PNUE. La pente de la courbe $A_{\max}$–N_{area} était la plus forte lorsque l'espacement était le plus faible, ce qui correspond à une plus grande variation de $A_{\max}$ par unité de variation de N_{area}. Les deux clones de peuplier hybride avaient une réponse morpho-physiologique semblable aux changements d'espacement. Il y avait donc une acclimatation physiologique du feuillage des deux clones en réponse à une compétition intraclonale via une modulation de SLA et PNUE.

[Traduit par la Rédaction]

Introduction

In light of predicted shortages of wood from natural forests, there is a renewed interest in short-rotation forestry in many parts of the world (Dickmann et al. 2001). Hybrid poplars (*Populus* spp.) are particularly well suited to short-rotation forestry, since they can reach very high productivity within relatively short periods of time for efficient fiber or energy production, CO_2 sequestration, or phytoremediation of polluted lands (Dickmann et al. 2001).

Biomass production in short-rotation forestry is a result of various factors and their interactions, including spacing, site quality, weed management, fertilization, and genetic background (Makeschin 1999). Spacing determines the intensity of competition between trees, which is known to affect resource availability, stand dynamics, and productivity (DeBell et al. 1996). In hybrid poplar improvement programs, most selected traits, such as sylleptic branchiness, productivity, net photosynthesis, and stomatal characteristics, have been examined under conditions of low competition (large spacings)

Received 5 April 2011. Accepted 5 May 2011. Published at www.nrcresearchpress.com/cjfr on 11 July 2011.

L. Benomar and A. DesRochers. Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue, 341, rue Principale Nord, Amos, QC J9T 2L8, Canada.
G.R. Larocque. Ressources naturelles Canada, Centre de foresterie des Laurentides, 1055 rue du P.E.P.S, C.P. 10380, succ. Sainte-Foy, Québec, QC G1V 4C7, Canada.

Corresponding author: Lahcen Benomar (e-mail: Lahcen.benomar@uqat.ca).

Can. J. For. Res. 41: 1465–1476 (2011) doi:10.1139/X11-073 Published by NRC Research Press

(Green et al. 2001). Previous studies have shown great variability in growth responses to inter- or intraclonal competition (DeBell et al. 1996; Fang et al. 1999). Hence, a better understanding of hybrid poplar trait plasticity under different competitive regimes is essential for selecting appropriate planting densities and genetic materials (Green et al. 2001). For instance, hybrid poplar clones that perform well under high levels of intra- and interclonal competition have been characterized by high light-use efficiency (Green et al. 2001) and high water- and nutrient-use efficiency (Bungart and Hüttl 2004; Yin et al. 2005). However, knowledge is lacking regarding the physiological response and foliage acclimation of hybrid poplars to different levels of intraclonal competition.

Nitrogen and light are common resources driving photosynthesis and plant C gain (Chapin et al. 1987). Accordingly, photosynthesis at light saturation ($A_{\max}$) is strongly positively related with light and leaf N content on an area basis (N_{area}). In forest plantations, competition for light and N is strongly governed by spacing between trees (Szendrödi 1996). As a consequence, competition for these resources increases in parallel to the reduction of their growing space. Plants respond to competition for site resources partially through physiological acclimation of their foliage (Grams and Andersen 2007). The acclimation process allows plants to compensate for reduced resources by improving uptake and utilization efficiency of site resources. Yet, acclimation capacity can vary considerably among species (Grams and Andersen 2007), and a better understanding of this phenomenon is essential for determining the competitive potential of different hybrid poplars in specific environments.

Photosynthetic acclimation to conditions of reduced photosynthetically active radiation (PAR) occurs through changes in specific leaf area (SLA) (leaf area to dry mass ratio) and N allocation to carboxylation, electron transfer, and light-harvesting processes (Evans and Poorter 2001). The modulation of SLA in response to changes in PAR allows plants to optimize N investment in foliage (Hirose et al. 1988). Thus, patterns of leaf N distribution are intimately linked to PAR gradients in the canopy (Hirose and Werger 1987; Anten et al. 1998). Plants may also respond to multiple environmental factors (N, light, or water availability) by modulating SLA (Chapin et al. 1987; Grams and Andersen 2007). SLA has been reported to be correlated positively with rainfall (Gouveia and Freitas 2009) and negatively with N availability (Chapin et al. 1987; Rosati et al. 1999). These observations suggest that a plant's capacity to modulate SLA can play a key role in photosynthetic acclimation to intraspecific competition.

SLA increases as leaf thickness decreases (Aranda et al. 2004; Onoda et al. 2004) or leaf area/mass increases, which may contribute to (*i*) increasing canopy light interception and transmittance (Vile et al. 2005) and (*ii*) a lower light compensation point in leaves (Niinemets and Sack 2006). The fraction of leaf N allocated to light harvesting may decrease, leaving more N for carboxylation and electron-transfer processes (Evans and Poorter 2001). Increases in SLA are also associated with a decreases in leaf construction costs (Feng et al. 2008) and decreases in the fraction of leaf N allocated to cell walls, leaving more N for the photosynthetic machinery (Onoda et al. 2004). Improvement of N partitioning between and within leaves through the modulation of SLA under competition may increase photosynthetic N-use efficiency (PNUE) at all levels of the crown, thereby altering the steepness of the photosynthesis–N curve. Indeed, a strong relationship has been found between SLA and PNUE (Poorter and Evans 1998). Hence, the increase in SLA is very important in maximizing PNUE and C gains within the canopy at high intensities of competition (Schieving and Poorter 1999). However, there is a lack of knowledge with respect to the physiological acclimation of hybrid poplars to competition, in particular regarding the role of SLA and PNUE in photosynthetic acclimation to changing PAR and N under different levels of competition.

In this study, we examined the physiological responses of the crown in two hybrid poplar clones, BT747215 (*Populus balsamifera* L. × *Populus trichocarpa* Torr. & A. Gray) and MB915319 (*Populus maximowiczii* A. Henry × *P. balsamifera*), to increasing intensities of intraclonal competition and the effect of competition on leaf traits such as SLA, gas exchanges, leaf N, and PNUE. There is little knowledge on hybrid poplar ecophysiology in boreal conditions under various intensities of intraclonal competition. We hypothesized that increasing intraclonal competition would be associated with increases in SLA and PNUE. This study would contribute not only to the evaluation of the critical role of changing SLA and PNUE in the physiological acclimation to intraclonal competition and clonal selection in hybrid poplar but also to the examination of the influence that these two leaf traits exert on the $A_{\max}$–N_{area} relationship, which is fundamental to ecophysiological modelling of leaf photosynthesis.

Materials and methods

Study area

The study was located in the boreal region of Abitibi-Témiscamingue, western Quebec, Canada. Three sites were randomly selected for this study: Amos (48°36′N, 78°04′W), Rivière Héva (48°11′N, 78°16′W), and Nédelec (47°45′N, 79°22′W). The Amos site was an abandoned farmland with heavy clay soils, which were dominated by grasses and a few patches of speckled alder (*Alnus incana* subsp. *rugosa* (Du Roi) Clausen), willow (*Salix* spp.), and trembling aspen (*Populus tremuloides* Mich.). Rivière Héva was also on abandoned farmland with heavy clay soils, which had been colonized by shrubs including patches of alder, willow, and trembling aspen. Nédelec had been previously forested but was now dominated by scattered trembling aspen, white or paper birch (*Betula papyrifera* Marsh.), and pin cherry (*Prunus pensylvanica* L. f.). This last site was characterized by soils with a sandy–loam soil texture and had been commercially harvested in 2000. The mean numbers of growing degree-days (above 5 °C, 30-year average) were 1387 for Amos and Rivière Héva and 1480 for Nédelec (Environment Canada 2008). Precipitation over the three growing seasons of our study averaged 420, 352, and 620 mm for 2006, 2007, and 2008, respectively (Ministère du Développement Durable de l'Environnement et des Parcs 2009).

Site preparation before planting was conducted in 2002. A bulldozer was used to remove tree stumps at Nédelec, while shrubby vegetation at Rivière Héva was removed using a brush shredder mounted on a farm tractor. At Amos, scattered tree stumps and shrub clumps were removed using chains and a farm tractor. Sites were then ploughed to a depth of about 30 cm followed by disking in spring 2003 to level the soil surface and remove most woody debris. Large, dormant bareroot hybrid poplar stock, which averaged 1.36 and 1.15 m in height for clones MB915319 and BT747215, respectively, was planted during the last week of May 2003 at Amos, the last week of June at Nédelec, and the second week of July at Rivière Héva. During the first five growing seasons, competing weedy vegetation was removed mechanically to a depth of about 5–10 cm using a farm tractor equipped with disks. Mechanical weed control was conducted twice each year from 2003 to 2007, after which disking was conducted only once in 2008 due to heavy precipitation that limited access to the sites.

Experimental design

The experiment was designed as a split-plot array with initial square spacing as the whole-plot factor (three levels) and each site as a replicate. Each level of spacing was then subdivided into two clones (the subplot factor). Three square spacings were tested: 1 m × 1 m, 3 m × 3 m, and 5 m × 5 m; these were equivalent to about 10 000, 1111, and 400 stems·ha^{-1}, respectively. The size of the experimental units was related to spacing and contained 36 trees (6 × 6 rows of trees) in which the 16 interior trees were sampled, leaving 2 × 2 rows of border trees as a buffer zone. The clones that were selected, viz. BT747215 (BT747) (*P. balsamifera* × *P. trichocarpa*) and MB915319 (MB915) (*P. maximowiczii* × *P. balsamifera*), are among those clones that have been recommended by the MRNFQ (Quebec Ministry of Natural Resources and Wildlife) for the region.

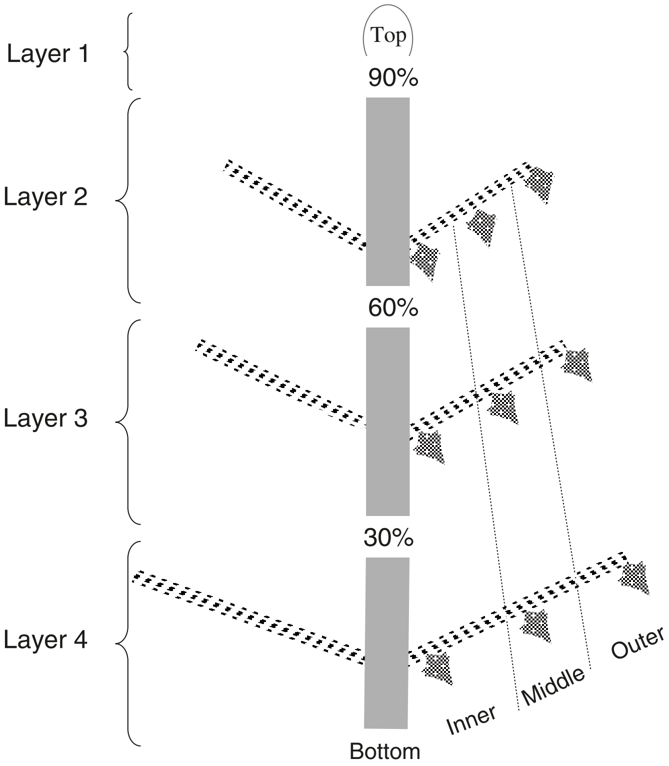
Sampling

Physiological measurements began in 2006 when canopies began to overlap in the closest spacing (1 m × 1 m). Two trees were randomly selected within each treatment for physiological measurements ($N = 36 = 3$ spacings × 2 clones × 3 sites × 2 trees). The crown of each sampled tree was divided vertically into four layers from the bottom to the top of the crown (Fig. 1). The first layer consisted of the top 10% of the crown, the second layer corresponded to the middle 30% of the crown, the third layer was located between 30% and 60% of crown depth, and the fourth layer consisted of the lowest 30% of crown depth. One leaf from three points corresponding to horizontal subdivisions (inner, middle, and outer leaves) was sampled in the second, third, and fourth layers, while one leaf from the terminal shoot was sampled from the top layer. During the third (2006), fourth (2007), and fifth (2008) growing seasons, leaf gas exchange and SLA were measured at the different crown levels, while leaf N was measured only in 2007 and 2008. All measurements were conducted between 15 July and 15 August. This period corresponds to the seasonal peak in leaf area index based on our LAI measurements (plant canopy analyzer LAI-2000; LI-COR Biosciences, Lincoln, Nebraska) during the growing season of 2008 (unpublished data). Size and leaf area index of the two clones after six growing seasons are given in Table 1.

Gas exchange measurements

Measurements of $A_{\max}$ and stomatal conductance (Gs) were performed using a portable infrared gas analyzer operating in an open mode (CIRAS-2; PP Systems, Amesbury, Massachusetts). The infrared gas analyzer was equipped with a broadleaf cuvette that was illuminated using an LED light unit (PLC6-broad; PP Systems). PAR, flow rate, and CO$_2$ concentration in the leaf cuvette were maintained, respectively, at 1600 μmol·m^{-2}·s^{-1}, 300 mL·min^{-1}, and 360 μmol·mol^{-1}. Measurements were made at 50%–75% relative humidity and under a vapour pressure deficit between 0.8 and 1.8 kPa. All measurements were taken between 0900 and 1200. Hourly variation in relative humidity, vapour pressure deficit, and temperature was minimized between treatments by randomizing the order of measurement of selected trees. Ambient temperature recorded inside the cuvette ranged between 16 and 28 °C during measurements.

Fig. 1. Scheme of sample positions within crowns for physiological measurements. Layer 1, top of the crown; layer 2, between 60% and 90% of crown height; layer 3, between 30% and 60% of crown height; layer 4, lowest 30% section of crown height.



Photosynthetic light response curves (A–Q curves) were constructed in August 2007 using leaves from the upper layer of the crown. Measurements were taken following a 10 min steady-state period of illumination at 1600 μmol PAR·m^{-2}·s^{-1}. Thereafter, PAR was raised to 2000 μmol·m^{-2}·s^{-1} and subsequently stepped down to the following levels: 1600, 1000, 900, 800, 700, 600, 500, 400, 300, 100, 50, and 0 μmol·m^{-2}·s^{-1} based on Peek et al. (2002). Within the leaf cuvette, air temperature was maintained at 25 ± 0.5 °C, while vapour pressure deficit and CO$_2$ concentration were fixed at 1 kPa and 360 μmol·mol^{-1}, respectively. Dark respiration (Rd) corresponds to net CO$_2$ exchange at the end of each A–Q curve (i.e., 10 min after reducing PAR to 0 μmol·m^{-2}·s^{-1}).

Table 1. Size and leaf area index (LAI) of the two hybrid poplar clones (BT747 and MB915) for each spacing (1 m × 1 m, 3 m × 3 m, and 5 m × 5 m) after six growing seasons.

Clone	Spacing	Diameter at breast height (cm)	Height (m)	LAI
BT747	1 m × 1 m	3.32a	4.11b	2.93e
	3 m × 3 m	3.28a	3.28a	0.79c
	5 m × 5 m	3.84a	3.27a	0.21a
MB915	1 m × 1 m	3.61a	5.03c	2.84e
	3 m × 3 m	5.27b	5.63c	1.17d
	5 m × 5 m	7.94c	6.64d	0.59b

Note:. Within a column, means followed by the same letter do not significantly differ at $\alpha = 0.05$.

SLA and leaf N content

Leaf samples were immediately harvested and packed in dry ice following gas exchange measurements in the field. The area of each sampled leaf (including petioles) was measured with a leaf area meter (LI-3100C; LI-COR Biosciences) before oven-drying (72 °C for 72 h) and weighing. SLA was calculated as the ratio of leaf area (square centimetres) to leaf dry mass (grams). Samples from 2007 and 2008 were then ground using a Wiley mill (model 3383-L10; Thomas Scientific, Swedesboro, New Jersey) equipped with a 0.4 mm mesh sieve. Leaf N concentrations (milligrams per gram) were determined by high-temperature combustion using a LECO elemental analyzer (CNS2000; Leco Corp., St. Joseph, Michigan) at the Forest Resources and Soil Testing Laboratory, Lakehead University (Thunder Bay, Ontario) and N content per unit dry mass (N_{mass}) was then converted to an area basis using the SLA measurements for each sample. PNUE was defined as A_{max} divided by N_{area}.

Light measurement

Available PAR at each sampled position in the crown was measured following gas exchange measurements in 2008. Measurements were conducted between 1200 and 1400 (zenith) using a CIRAS-2 PAR sensor (PP Systems). Above-canopy light was measured using permanent micrometeorological stations. These measurements indicated the maximum light that was intercepted at each sampled position within the crowns.

Statistical analyses

Data were analyzed in SAS version 9.1 (SAS Institute Inc., Cary, North Carolina). The A_{max}, SLA, N_{area}, and PNUE were subjected to repeated-measures analysis of variance with year as the repeated measure in the following model:

$$[1] \quad Y_{tsclh} = \mu + \beta_t + \beta_s + \beta_c + \beta_l + \beta_h + \beta_{int} + E_{site} + E_{tree} + E_{site \times spacing} + \varepsilon$$

where Y is the dependent variable, μ is the grand mean, β_t is the fixed effect of time (years), β_s is the fixed effect of spacing, β_c is the fixed effect of clone, β_l is the fixed effect of layer, β_h is the fixed effect of horizontal position, β_{int} is the fixed effect of all interactions, E_{site} is the random effect of site, E_{tree} is the random effect of tree, $E_{site \times spacing}$ is the random effect of the site × spacing interaction, and ε is the residual error. The mixed-model procedure PROC MIXED was used with maximum likelihood estimates of the variance components, except in the case of A_{max} where MIVQUE0 (i.e., minimum variance quadratic unbiased estimates) was used because maximum likelihood estimates failed to converge on a solution (infinite likelihood). The Satterthwaite method was used to test the fixed effects, i.e., generate approximate F tests, and to compute their associated denominator degrees of freedom (Littell et al. 2006). An autoregressive covariance matrix was selected to represent the structure of the repeated measures model rather than the usual assumption of compound symmetry, as the former had the lowest Akaike information criterion among the candidate matrix structures (Littell et al. 2006). Nitrogen and SLA data were log-transformed to achieve homoscedascity, likelihood distance, and normality of residuals. Orthogonal contrasts were used to compare spacings, years, clones, and their interactions. To test the effect of spacing on response variables at each crown position (layer × horizontal position) using orthogonal contrasts, two adjustments were made to the model in eq. 1: (*i*) layer and horizontal position variables were gathered to form a new variable called position in the crown and (*ii*) analysis was made by clone.

Individual light response curves were analyzed using the nonlinear Mitscherlich function (Peek et al. 2002):

$$[2] \quad A = A_{max}\left[1 - e^{-\mathrm{Aqe}(Q - \mathrm{Lcp})}\right]$$

where Q is PAR, A_{max} the light-saturated photosynthetic rate, Aqe is the apparent quantum yield (the slope of the linear phase of the response curve), and Lcp is the light compensation point. The model was fitted using nonlinear least-squares regression (NLIN procedure SAS version 9.1, SAS Institute Inc.). For the iterative procedure, the Gauss–Newton algorithm was used. Parameter estimates from the photosynthetic light response curve (A_{max}, Aqe, Lcp, and Rd) were subjected to analysis of variance as dependent (response) variables using the following model:

$$[3] \quad Y_{sc} = \mu + \beta_s + \beta_c + \beta_{spacing \times clone} + E_{site} + E_{site \times spacing} + \varepsilon$$

where Y is the dependent variable (A_{max}, Aqe, Lcp, and Rd), $\beta_{spacing \times clone}$ is the fixed effect of the spacing × clone interaction, and the other terms are as in eq. 1. Treatment means were compared using orthogonal contrasts.

Different functional relationships between leaf traits were analyzed using linear regression (GLM procedure in SAS): SLA versus N_{area}, PNUE, and Lcp, N_{area} versus A_{max}, PNUE,

Table 2. Average photosynthetically active radiation fractions intercepted at each horizontal and vertical position within the crowns of the two hybrid poplar clones, which were been planted at three spacings (1 m × 1 m, 3 m × 3 m, and 5 m × 5 m).

		BT747			MB915		
Spacing	Vertical	Inner	Middle	Outer	Inner	Middle	Outer
1 m × 1 m	Layer 1			1.0h			1.0j
	Layer 2	0.40c	0.63e	0.95gh	0.64f	0.50e	0.90i
	Layer 3	0.14a	0.27b	0.37c	0.08a	0.25b	0.27b
	Layer 4	0.09a	0.10a	0.14a	0.10a	0.14a	0.12a
3 m × 3 m	Layer 1			1.0h			1.0j
	Layer 2	0.45c	0.75f	0.90g	0.37c	0.82h	0.98i
	Layer 3	0.22b	0.40c	0.45c	0.20ab	0.60f	0.62f
	Layer 4	0.11a	0.26b	0.30b	0.12a	0.33c	0.34c
5 m × 5 m	Layer 1			1.0h			1.0j
	Layer 2	0.40c	0.75f	0.90g	0.30c	0.68fg	0.98i
	Layer 3	0.15a	0.54d	0.55d	0.40d	0.40d	0.96i
	Layer 4	0.12a	0.27b	0.50cd	0.10a	0.33c	0.97i

Note: For each clone, means followed by the same letter do not significantly differ at $\alpha = 0.05$.

and Rd, and N$_{\mathrm{area}}$ versus relative irradiance. The slopes of the curves were compared among spacing treatments and clones (analysis of covariance).

Results

Variation in crown light environments

Generally, the proportion of PAR that was intercepted by the foliage decreased with crown depth in each spacing treatment, with the pattern of PAR reduction being more pronounced as spacing decreased (Table 2). The fraction of available PAR declined rapidly from the top to the bottom of the crown for all horizontal positions in the closest spacing. The bottom of the crown in the 1 m × 1 m spacing received only 12% of incident radiation, while in the 3 m × 3 m spacing, light attenuation was comparatively moderate relative to the closest spacing so that the bottom of the crown received about 32% of incident PAR for the outer and middle leaves (Table 2). In the 5 m × 5 m spacing, the decrease in PAR as a function of crown depth occurred at all crown positions for clone BT747 but only in the inner and middle leaf positions for clone MB915 (Table 2).

$A_{\max}$ and Gs

Mean $A_{\max}$ of trees growing in the closest spacing (1 m × 1 m) was 12.13 ± 0.2 µmol CO$_2$·m^{-2}·s^{-1}, which was significantly lower than $A_{\max}$ for trees growing in the 3 m × 3 m and 5 m × 5 m spacings (14.41 ± 0.19 and 14.96 ± 0.2 µmol CO$_2$·m^{-2}·s^{-1}, respectively) (Table 3). Moreover, the pattern of change in $A_{\max}$ with spacing was similar for both clones (spacing × clone interaction, $P = 0.13$) (Table 3). Clone MB915 had a greater $A_{\max}$ (14.48 ± 0.17 µmol CO$_2$·m^{-2}·s^{-1}) than BT747 (13.18 ± 0.16 µmol CO$_2$·m^{-2}·s^{-1}). The $A_{\max}$ values in 2006 (13.31 ± 0.16 µmol CO$_2$·m^{-2}·s^{-1}) were similar to those of 2007 (13.49 ± 0.17 µmol CO$_2$·m^{-2}·s^{-1}) for both clones and significantly greater in 2008 (14.17 ± 0.18 µmol CO$_2$·m^{-2}·s^{-1}) compared with the two previous years. The effect of spacing on $A_{\max}$ was independent of time (spacing × time interaction, $P = 0.42$) (Table 3). The Gs was similar for the three spacings and the two clones (305 ±17 mmol·m^{-2}·s^{-1}) (Table 3) but significantly greater in 2008 (436 ±30 mmol·m^{-2}·s^{-1}) compared with 2006 (226 ±29 mmol·m^{-2}·s^{-1}) and 2007 (252 ±29 mmol·m^{-2}·s^{-1}).

In general, $A_{\max}$ decreased vertically from the top to the bottom of the crown (Table 4). Mean $A_{\max}$ at the top of the crowns (layer 1) was 19 µmol CO$_2$·m^{-2}·s^{-1}, which was similar among all spacings and between clones. The $A_{\max}$ of layer 2 did not differ between spacings for the outer leaves of clone MB915 but was significantly lower for BT747 at the 1 m×× 1 m compared with the 3 m × 3 m and 5 m × 5 m spacings (Table 4). In the third and fourth layers, $A_{\max}$ in the closest spacing was significantly reduced compared with the wider spacings for all horizontal positions for MB915 and mostly for the outer leaves of BT747 (Table 4). Mean $A_{\max}$ in the 3 m × 3 m spacing was significantly lower than in the 5 m × 5 m spacing, but only for the fourth layer (Table 3). For each layer, $A_{\max}$ significantly increased from inner to outer leaf positions, except for the fourth layer in the 1 m × 1 m spacing of clone BT747 where there were no differences among leaf positions (Table 4).

SLA

Reduced spacing significantly increased SLA for the two hybrid poplar clones (Table 3). Clone MB915 had greater SLA than BT747 at all spacings (Table 5), but both clones responded in a similar fashion to changes in spacing (Table 3). For both clones, mean SLA was significantly greater in the 1 m × 1 m spacing than in the 3 m × 3 m and 5 m × 5 m spacings; however, SLA was similar in the 3 m × 3 m and 5 m × 5 m spacings (Table 3). Mean values for MB915 were 119, 104, and 99 cm^2·g^{-1} for the 1 m × 1 m, 3 m × 3 m, and 5 m × 5 m spacings, respectively, and for for BT747 were 109, 90, and 91 cm^2·g^{-1} for the 1 m × 1 m, 3 m × 3 m, and 5 m × 5 m spacings, respectively. The spacing effect was also time dependent with respect to SLA, which significantly increased from 2006 to 2008 (Table 3). SLA significantly increased vertically from the top to the bottom of the crown and horizontally from the crown edge to the inside of the crown near the stem (Table 5) at all spacings. Unlike $A_{\max}$, SLA significantly increased at all levels of the crown, including the top layer, as spacing decreased (Table 5).

Table 3. Repeated-measures analysis of variance giving sources of variation, *F* values, and associated probabilities for light-saturated photosynthesis (A_{max}), stomatal conductance (Gs), specific leaf area (SLA), leaf N content per leaf area unit (N_{area}), and photosynthetic N-use efficiency (PNUE).

	A_{max}		Gs		SLA		N_{area}		PNUE	
Source	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Spacing (S)	15.10	<0.001	0.55	0.57	23.85	<0.001	17.42	<0.001	3.15	0.04
Contrast										
1 m × 1 m vs. 3 m × 3 m + 5 m × 5 m	5.46	<0.001			6.85	<0.001	5.75	<0.001	2.11	0.03
3 m × 3 m vs. 5 m × 5 m	0.69	0.49			0.99	0.32	1.37	0.17	1.37	0.17
Clone (C)	8.66	<0.001	2.60	0.10	17.86	<0.001	5.41	0.02	26.72	<0.001
S × C	2.05	0.13	0.05	0.94	0.49	0.61	0.22	0.80	0.76	0.46
Year (Y)	10.83	<0.001	57.78	<0.001	10.09	<0.001	6.87	0.009	11.55	0.001
Contrast										
2006 vs. 2007 + 2008	4.18	<0.001	1.33	0.16	4.88	<0.001				
2007 vs. 2008	2.14	0.03	4.22	<0.001	5.07	<0.001	2.62	0.009	3.40	0.001
S × Y	0.96	0.42	0.55	0.69	2.29	0.05	0.08	0.92	0.38	0.68
C × Y	0.14	0.86	2.01	0.13	1.10	0.33	0.13	0.71	1.43	0.23
S × C × Y	1.32	0.26	0.13	0.97	0.39	0.81	0.49	0.61	0.25	0.77

Table 4. Mean light-saturated photosynthesis ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) for each horizontal and vertical position within the crown by spacing treatment (1 m × 1 m, 3 m × 3 m, and 5 m × 5 m) and clone (BT747 and MB915).

		BT747			MB915		
Spacing	Vertical	Inner	Middle	Outer	Inner	Middle	Outer
1 m × 1 m	Layer 1			19.8g			18.7g
	Layer 2	10.1ab	13.3c	16.7e	9.9b	14.8d	18.6g
	Layer 3	9.8a	12.2b	13.7c	8.2a	12.2c	14.4d
	Layer 4	8.2a	8.9a	8.4a	6.6a	9.1b	10.8b
3 m × 3 m	Layer 1			19.1g			19.9g
	Layer 2	9.8a	13.3c	19.1g	10.8c	16.9de	18.8g
	Layer 3	8.1a	13.4bc	16.7e	11.1c	14.8d	18.0f
	Layer 4	9.1a	12.1b	14.7d	9.4b	13.2d	17.1e
5 m × 5 m	Layer 1			19.6g			18.4 g
	Layer 2	11.1b	14.3d	19.2g	14.6d	17.6e	18.6g
	Layer 3	7.1a	11.2b	18.6f	11.0c	17.5e	19.4g
	Layer 4	8.1a	12.7b	17.0e	11.2c	13.5d	17.6e

Note: For each clone, means followed by the same letter do not significantly differ at $\alpha = 0.05$.

Table 5. Mean specific leaf area ($cm^2 \cdot g^{-1}$) for each horizontal and vertical position within the crown by spacing treatment (1 m × 1 m, 3 m × 3 m, and 5 m × 5 m) and clone (BT747 and MB915).

		BT747			MB915		
Spacing	Vertical	Inner	Middle	Outer	Inner	Middle	Outer
1 m × 1 m	Layer 1			80g			99ed
	Layer 2	93d	91e	95de	104c	100d	104cd
	Layer 3	105c	96d	94d	115b	121b	103cd
	Layer 4	133a	108c	96d	122b	142a	95e
3 m × 3 m	Layer 1			73h			87f
	Layer 2	91e	85e	77h	115bc	94cd	78g
	Layer 3	101c	89f	78g	122b	118b	88e
	Layer 4	103c	93d	102d	129b	110b	95e
5 m × 5 m	Layer 1			69i			70h
	Layer 2	100d	89e	76h	111c	92e	77g
	Layer 3	116bc	109c	85f	115b	102c	71h
	Layer 4	111c	108c	84f	131b	110b	86f

Note: For each clone, means followed by the same letter do not significantly differ at $\alpha = 0.05$.

Table 6. Mean leaf N concentration (g·m^{-2}) for each horizontal and vertical position within the crown by spacing treatment (1 m × 1 m, 3 m × 3 m, and 5 m × 5 m) and clone (BT747 and MB915).

		BT747			MB915		
Spacing	Vertical	Inner	Middle	Outer	Inner	Middle	Outer
1 m × 1 m	Layer 1			2.65f			1.87d
	Layer 2	1.50c	1.84d	1.99d	1.32ab	1.68c	1.76d
	Layer 3	1.23a	1.66c	1.69c	1.24a	1.38ab	1.60bc
	Layer 4	1.14a	1.28b	1.53c	1.15a	1.08a	1.53c
3 m × 3 m	Layer 1			3.25g			2.72f
	Layer 2	1.77d	2.24e	2.87f	1.52c	2.01d	2.50e
	Layer 3	1.57c	1.86cd	2.63f	1.41a	1.67ac	2.30e
	Layer 4	1.51c	1.63c	2.06e	1.24a	1.51c	2.01d
5 m × 5 m	Layer 1			3.41g			2.99f
	Layer 2	1.81d	2.24e	3.09fg	1.75d	2.04d	2.69e
	Layer 3	1.62c	1.71cd	2.67f	1.59c	1.96cd	2.73e
	Layer 4	1.32b	1.70d	2.53f	1.29a	1.68c	2.28de

Note: For each clone, means followed by the same letter do not significantly differ at $\alpha = 0.05$.

Fig. 2. Relationships between (*a* and *b*) leaf N content on an area basis (N_{area}), (*c* and *d*) photosynthetic N-use efficiency (PNUE), and (*e* and *f*) light compensation point (Lcp) versus specific leaf area (SLA) for the two hybrid poplar clones (BT747 and MB915).

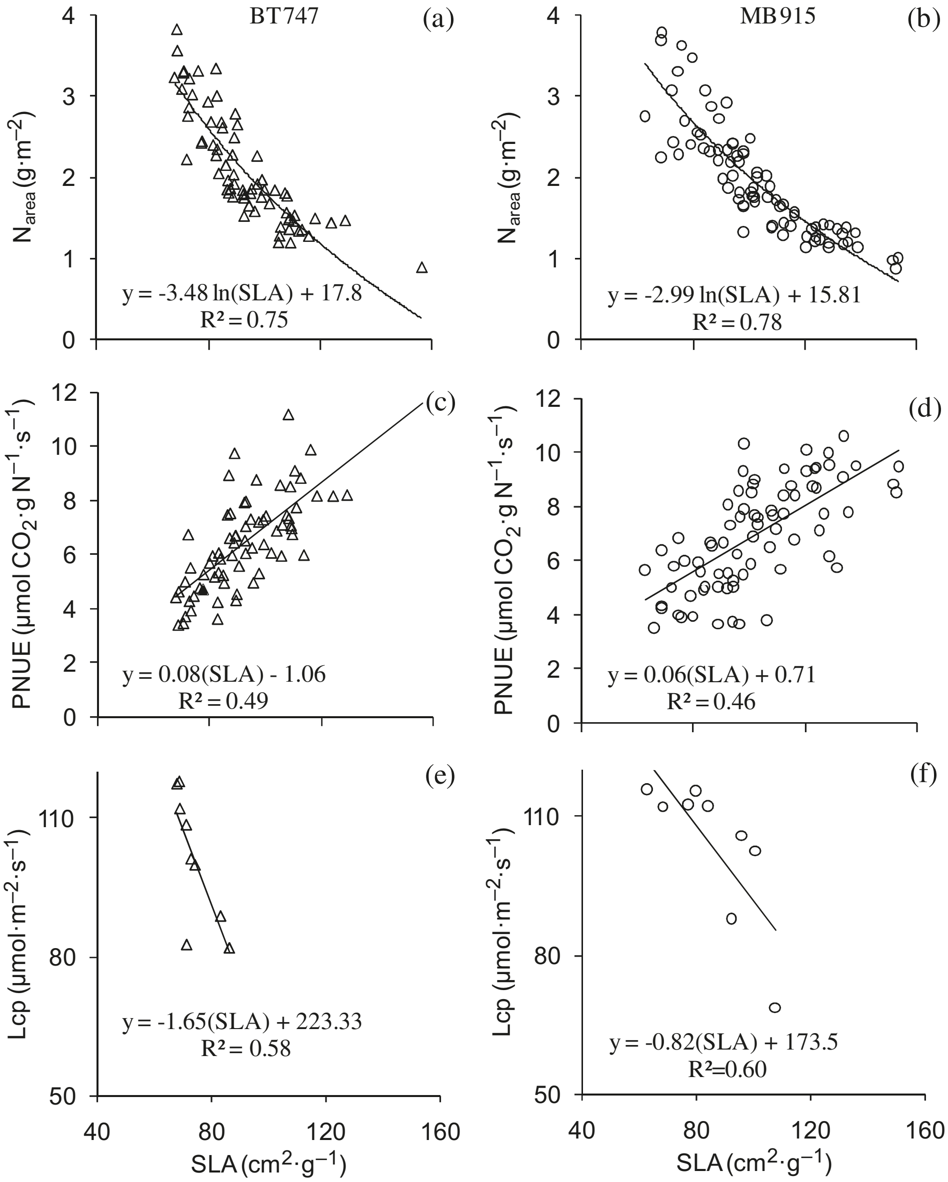
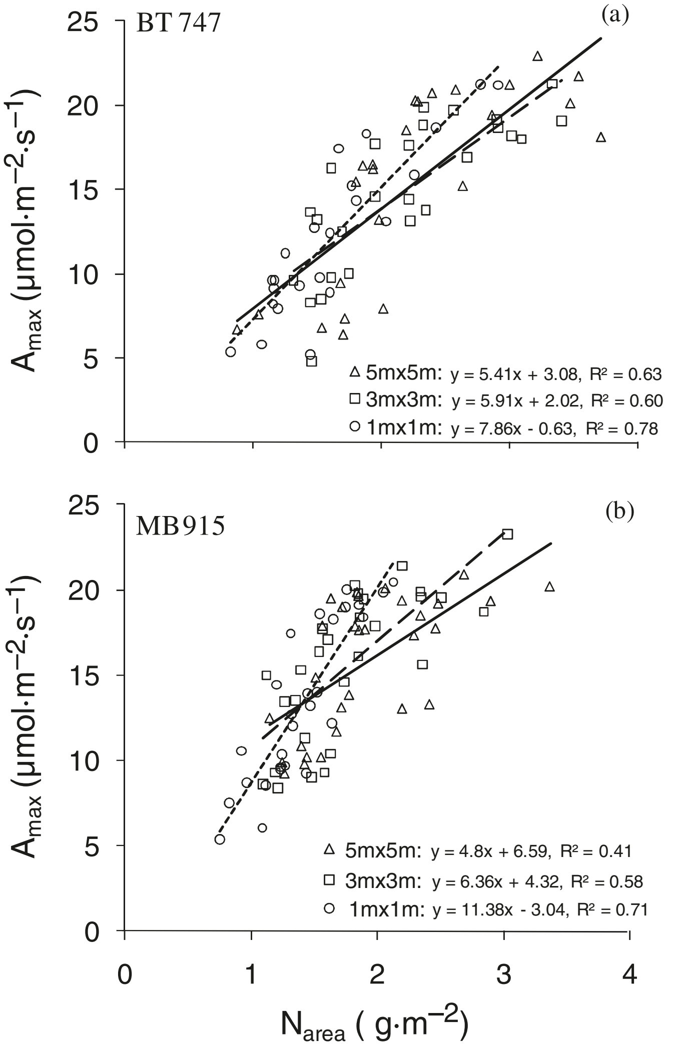


Fig. 3. Relationships between light-saturated photosynthesis (A_{max}) and leaf N on an area basis (N_{area}) for clones (*a*) BT747 and (*b*) MB915.



Leaf N content (N_{area}) and PNUE

The increase in spacing between trees significantly increased N_{area} (Table 3). Indeed, N_{area} of trees growing in the closest spacing (1.55 g·m^{-2}) was about 27%–30% lower than that of trees growing in the 3 m × 3 m (2.01 g·m^{-2}) and 5 m × 5 m spacings (2.14 g·m^{-2}), while there was no difference in N_{area} between the 3 m × 3 m and 5 m × 5 m spacings. Clone BT747 had greater mean N_{area} (1.99 g·m^{-2}) than clone MB915 (1.81 g·m^{-2}). Mean N_{area} was lower in 2008 (1.81 g·m^{-2}) compared with 2007 (1.98 g·m^{-2}). Like A_{max}, the effect of spacing on leaf N_{area} was also independent of time, as there was no interaction between spacing and year (P = 0.92) (Table 3). Leaf N_{area} distribution within crowns showed patterns similar to A_{max}, increasing from the bottom to the top of the crown and from the inner to outer leaves (Table 6). Leaf N_{area} was significantly lower in the 1 m × 1 m spacing compared with the wider spacings at all crown positions (Table 6). Except for the fourth layer of clone BT747, there was no difference in N_{area} between the 3 m × 3 m and 5 m × 5 m spacings (Table 6).

PNUE was significantly higher in the closest spacing (7.96 µmol CO_2·g·N^{-1}·s^{-1}) compared with the 3 m × 3 m (7.45 µmol CO_2·g N^{-1}·s^{-1}) and 5 m × 5 m spacings (7.06 µmol CO_2·g N^{-1}·s^{-1}) (Table 3). Clone MB915 had greater PNUE mean values (8.3 µmol CO_2·g N^{-1}·s^{-1}) than clone BT747 (6.7 µmol CO_2·g N^{-1}·s^{-1}) (Table 3). PNUE increased by 13% from 2007 (7.06 µmol CO_2·g N^{-1}·s^{-1}) to 2008 (7.93 µmol CO_2·g N^{-1}·s^{-1}) in all spacing treatments (Table 3).

Light response curves

In the upper crown, spacing affected neither A_{max} nor Aqe (P = 0.3) and their values were statistically similar between the two clones (P = 0.23). Across all treatments (spacing and clone), A_{max} and Aqe averaged 18.5 µmol CO_2·m^{-2}·s^{-1} and 0.0017 g·µmol^{-1}, respectively. The Rd was significantly lower (P = 0.02)in the 1 m × 1 m spacing (2.3 µmol CO_2·m^{-2}·s^{-1}) than in the 3 m × 3 m and 5 m × 5 m spacings (3.5 µmol CO_2·m^{-2}·s^{-1}). Also, Lcp was significantly lower (P = 0.03) in the 1 m × 1 m spacing (83 µmol PAR·m^{-2}·s^{-1}) than in the 3 m × 3 m and 5 m × 5 m spacings (110 µmol PAR·m^{-2}·s^{-1}). The Rd and Lcp were similar between the two hybrid poplar clones.

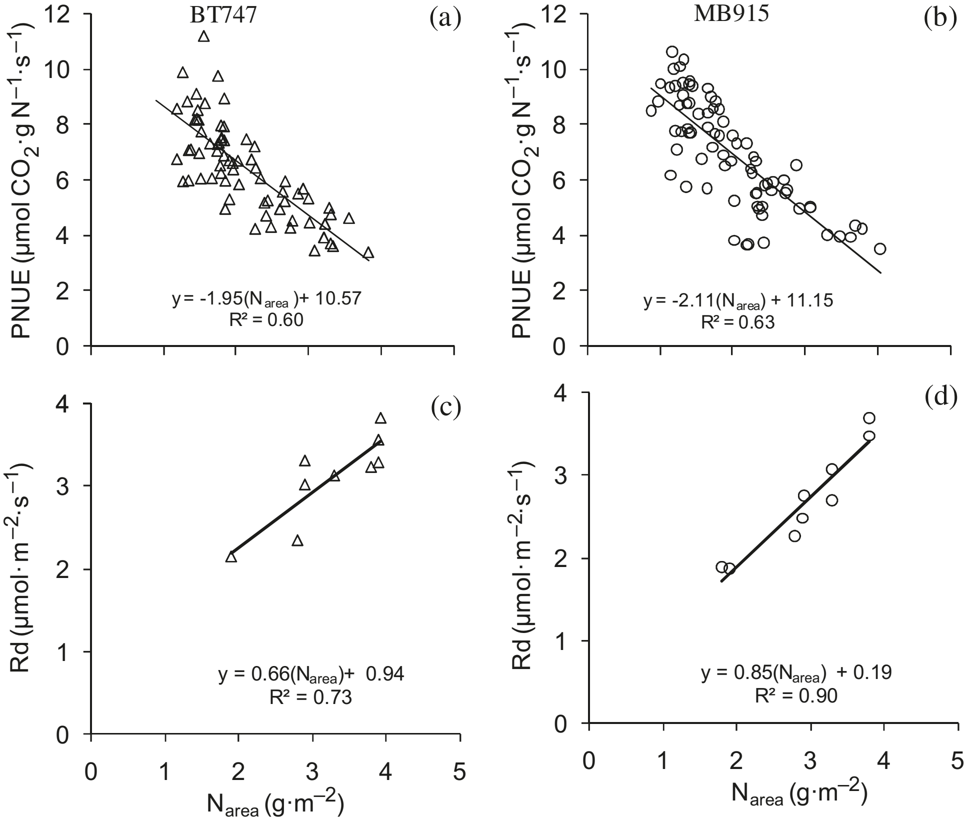
Leaf trait relationships

SLA and N_{area} were significantly and negatively associated with a log-linear relationship (P = 0.001) (Figs. 2*a* and 2*b*). PNUE and SLA were positively and linearly associated (Figs. 2*c* and 2*d*). The slope of this relationship was similar for the two clones. The Lcp decreased with SLA (Figs. 2*e* and 2*f*). The A_{max} increased with foliar N when the latter was expressed on an area basis (N_{area}) (Fig. 3). For each value of A_{max}, MB915 had lower values of N_{area} compared with BT747, as determined by a greater slope for the A_{max}–N_{area} relationship for MB915 (P = 0.001). In other words, for a given investment in leaf N, clone MB915 had greater values of A_{max} than did clone BT747. Also, the slope of the A_{max}–N_{area} relationship was greatest in the closest spacing compared with the two wider spacings (Fig. 3). Slopes of A_{max}–N_{area} did not significantly differ between the 3 m × 3 m and 5 m × 5 m spacings. The A_{max}–SLA relationship was negative and significant (P = 0.001), although SLA explained only 30% of the variation in A_{max}. A linear relationship was found between PNUE and N_{area} (Figs. 4*a* and 4*b*), and the slope of this relationship was similar for the two clones (P > 0.05). A strong negative and linear relationship was found between Rd and N_{area} (Figs. 4*c* and 4*d*), with similar slopes for the two clones (P > 0.05). A linear relationship was found between N_{area} and relative irradiance, and slope of this relationship did not significantly differ among the three spacings for both clones (Fig. 5).

Discussion

Changes in SLA reflect leaf structure modulation, which can be described as the main mechanism for light acclimation within a canopy (Anten et al. 1998; Hikosaka et al. 1999), although SLA adjustments may also be related to nutrient availability (Meziane and Shipley 2001), water stress (Marron et al. 2002), and competitive ability (Burns and Winn 2006). This study showed how an increase in intraspecific

Fig. 4. Relationships between (*a* and *b*) photosynthetic N-use efficiency (PNUE) and (*c* and *d*) dark respiration (Rd) and leaf N on an area basis (N_{area}) for the two hybrid poplar clones (BT747 and MB915).

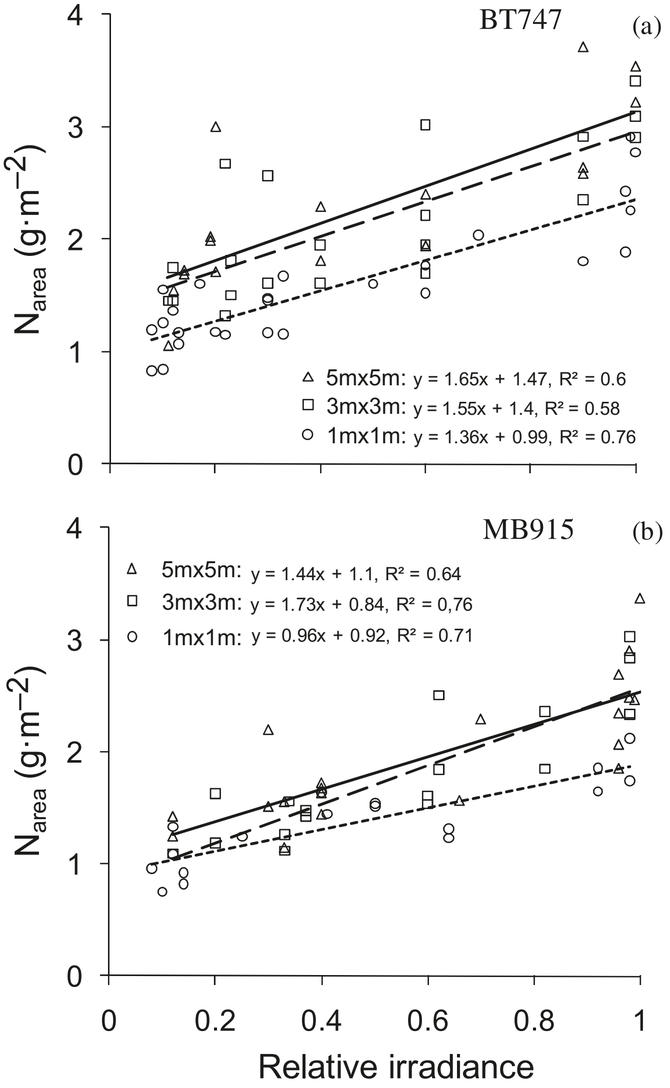


competition increased the SLA of trees in all vertical crown layers, except for inner leaves. Similar results were reported by Larocque (1999) for other hybrid poplar clones. Results of the present study suggest that, in addition to changes in PAR, nutrient availability affected SLA. As shown in Table 5, significant differences in SLA were also observed in the first section at the top of the crown where leaves were growing under full sunlight. The increase in SLA with decreased spacing at the top of the crown was also correlated with decreases in Lcp and Rd. The consequence of increasing SLA under high intraclonal competition was an increase in light capture per unit of leaf area and therefore optimization of C and N investment in the leaf (Niinemets and Sack 2006). SLA also decreased from the inner to the outer crown and from the bottom to the top of the crown in all spacing treatments. This indicates foliage acclimation to irradiance, as indicated by previous studies (Iio et al. 2005; Medhurst and Beadle 2005). However, in our study, part of the horizontal variation in SLA was not explained by changes in the light environment. This is maybe due to the time scale (minutes) of our light measurements, but leaf aging could also explain this variation (Field 1983). The effect of competition on SLA increased from 2006 to 2008, which suggested progressive acclimation of the leaf structure to competition. This progressive reaction of foliage to competition is probably a consequence of parallel changes in site resources and in other tree variables such as biomass allocation and tree morphology (Grams and Andersen 2007). Photosynthetic acclimation through progressive changes in leaf structure reflects the dynamic nature of photosynthetic acclimation (Walters 2005).

The increase in mean A_{max} that we observed in the two widest spacings was the result of changes in A_{max} of the foliage in the lower and middle zones of the crown due to decreased light availability, while the top half of the crowns was more or less unchanged by competition (Table 4). Similar results have been obtained for *Eucalyptus globulus* Labill. (Henskens et al. 2001) and *Eucalyptus nitens* (Deane & Maiden) Maiden (Medhurst and Beadle 2005) under increasing competition. In contrast, Kolb et al. (1998) found a decrease in A_{max} at the top of the crowns under increasing competition. In our study, trees in the 1 m × 1 m spacing treatment had grown under a closed-canopy environment since 2006, while crown closure in the 3 m × 3 m and 5 m × 5 m spacings did not occur until 2008. Light attenuation in the wider spacings was more pronounced in clone BT747 than in clone MB915. This response was due to different crown structures between the two hybrid poplar clones: clone BT747 was characterized by acute branching angles and greater leaf area density compared with clone MB915 (unpublished data).

Leaf N_{area} values for trees growing in the two widest spacings were comparable with published values for other hybrid poplar clones (Casella and Ceulemans 2002; Ripullone et al. 2003) but were greater than those reported by Curtis et al. (2000) and Coll et al. (2007). However, values of N_{area} in the closest spacing (1 m × 1m), and particularly for clone MB915, were somewhat lower than these published values. The decrease in spacing from 5 m × 5 m to 1 m × 1 m was associated with a 30% decrease in N_{area}. These results are consistent with previous studies, which have argued that N_{area}

Fig. 5. Relationships between leaf N on an area basis (N_{area}) and relative irradiance for clones (*a*) BT747 and (*b*) MB915.



is sensitive to tree growing space (Szendrödi 1996; Medhurst and Beadle 2005). A gradient in N_{area} was apparent in both vertical and horizontal planes. Variation in N_{area} within the crown was proportional to the light microenvironments experienced by the leaves (Fig. 5). As such, our results support the N allocation theory in that N_{area} was distributed within the crown in a pattern paralleling the light environment (Field 1983). This optimal distribution of N_{area} may lead to an optimization of PNUE at the canopy level (canopy PNUE). The theory of optimal N_{area} distribution within the crown has demonstrated that canopy PNUE can be optimal through the allocation of more N_{area} for more strongly illuminated leaves and less N_{area} for more shaded leaves within the crown (Field 1983). Clone BT747 had greater N_{area} than clone MB915, which may have been due to differences in N uptake capacity in relation to root morphology (Al Afas et al. 2008) or to biomass investment in roots (Johnson and Biondini 2001).

Correlations between A_{max} and N_{area} were found in all treatments (Fig. 3). Our results are in agreement with other data showing a linear A_{max}–N_{area} relationship in hybrid poplars (Curtis et al. 2000; Casella and Ceulemans 2002; Ripullone et al. 2003). The variation in steepness of the A_{max}–N_{area} curve is largely recognized as being species dependent due to species-related variation in PNUE (Reich et al. 1995). In our study, the slope of the A_{max}–N_{area} relationship was steeper in the 1 m × 1 m spacing compared with the 3 m × 3 m and 5 m × 5 m spacings due to greater PNUE values in the 1 m × 1 m spacing, which were associated with lower N_{area}. This suggests that the decrease in N_{area} might have been associated with an increase in the proportion of N allocated to the photosynthetic apparatus and (or) changes in the efficiency of N partitioning among photosynthetically derived compounds (Hikosaka and Terashima 1995). In the light of these results, a change in PNUE was induced by both light and N availability. PNUE was positively correlated with SLA in a manner consistent with other studies (Poorter and Evans 1998; Schieving and Poorter 1999) and that showed that SLA and PNUE modulation can be induced by the same processes; changes in leaf structure through SLA also could be the cause of variation in PNUE. The latter case could be explained by reduction in SLA through reduction in cell wall thickness (Onoda et al. 2004; Vile et al. 2005) and consequently reduction in N allocation to processes other than photosynthesis. The decrease in Lcp that paralleled the increase in SLA allows leaves to increase C assimilation at low PAR (Niinemets et al. 1998).

Conclusions

Intraclonal competition affected N_{area} and light availability within the crown. Trees in the closest spacing were characterized by a pronounced gradient of light attenuation within the crown and by low leaf N content. Foliage response to intraclonal competition was manifested by increases in SLA and PNUE. Leaves used N more efficiently when N and and (or) light were limiting resources. The slope of the A_{max}–N_{area} curve was increased under competitive conditions because of increases in PNUE. Hence, the A_{max}–N_{area} relationship not only characterized the species but also reflected photosynthetic acclimation of the species to growth conditions. As our study suggests, SLA and PNUE may be important traits in photosynthetic acclimation to intraclonal competition in hybrid poplar. Comparative studies with other hybrid poplar clones under a wide range of intraclonal competitive conditions would be necessary for determining the growth advantages provided by SLA and PNUE acclimation to competition. Finally, the influence of SLA and PNUE increases on other ecophysiological traits, such as leaf photosynthetic capacity (i.e., maximal carboxylation rate V_{cmax} and maximal photosynthetic electron transport rate J_{max}), should be essential in future study.

Acknowledgements

We thank W. Parsons for his comments on the manuscript and numerous field technicians for their help. This research was funded by Canada Economic Development, Quebec's Ministry of Natural Resources and Fauna (MRNF), the Natural Sciences and Engineering Research Council of Canada through a Collaborative and Research Development grant to A.D., and the Program on Energy Research and Development of Natural Resources Canada. We also thank Réseau Ligniculture Québec, Norbord Inc., Alberta-Pacific Forest Industries Inc., CRSNG-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Center for Forest Management (CEF), and Natural Resources Canada, Laurentian Forestry Centre, for their support.

References

Al Afas, N., Marron, N., Zavalloni, C., and Ceulemans, R. 2008. Growth and production of a short-rotation coppice culture of poplar – IV: Fine root characteristics of five poplar clones. Biomass Bioenergy, **32**(6): 494–502. doi:10.1016/j.biombioe.2007.11.007.

Anten, N.P.R., Miyazawa, K., Hikosaka, K., Nagashima, H., and Hirose, T. 1998. Leaf nitrogen distribution in relation to leaf age and photon flux density in dominant and subordinate plants in dense stands of a dicotyledonous herb. Oecologia (Berl.), **113**(3): 314–324. doi:10.1007/s004420050382.

Aranda, I., Pardo, F., Gil, L., and Pardos, J.A. 2004. Anatomical basis of the change in leaf mass per area and nitrogen investment with relative irradiance within the canopy of eight temperate tree species. Acta Oecol. **25**(3): 187–195. doi:10.1016/j.actao.2004.01.003.

Bungart, R., and Hüttl, R.F. 2004. Growth dynamics and biomass accumulation of 8-year-old hybrid poplar clones in a short-rotation plantation on a clayey–sandy mining substrate with respect to plant nutrition and water budget. Eur. J. For. Res. **123**(2): 105–115.

Burns, J., and Winn, A. 2006. A comparison of plastic responses to competition by invasive and non-invasive congeners in the commelinaceae. Biol. Invasions, **8**(4): 797–807. doi:10.1007/s10530-005-3838-5.

Casella, E., and Ceulemans, R. 2002. Spatial distribution of leaf morphological and physiological characteristics in relation to local radiation regime within the canopies of 3-year-old *Populus* clones in coppice culture. Tree Physiol. **22**(18): 1277–1288. PMID: 12490425.

Chapin, S.F., III, Bloom, A.J., Field, C.B., and Waring, R.H. 1987. Plant responses to multiple environmental factors. Bioscience, **37**(1): 49–57. doi:10.2307/1310177.

Coll, L., Messier, C., Delagrange, S., and Berninger, F. 2007. Growth, allocation and leaf gas exchanges of hybrid poplar plants in their establishment phase on previously forested sites: effect of different vegetation management techniques. Ann. For. Sci. **64**(3): 275–285. doi:10.1051/forest:2007005.

Curtis, P.S., Vogel, C.S., Wang, X., Pregitzer, K.S., Zak, D.R., Lussenhop, J., Kubiske, M., and Teeri, J.A. 2000. Gas exchange, leaf nitrogen, and growth efficiency of *Populus tremuloides* in a CO_2 enriched atmosphere. Ecol. Appl. **10**(1): 3–17.

DeBell, D.S., Clendenen, G.W., Harrington, C.A., and Zasada, J.C. 1996. Tree growth and stand development in short-rotation *Populus* plantings: 7-year results for two clones at three spacings. Biomass Bioenergy, **11**(4): 253–269. doi:10.1016/0961-9534(96)00020-7.

Dickmann, D.I., Isebrands, J.G., Eckenwalder, J.E., and Richardson, J. 2001. Poplar culture in North America, NRC Research Press, Ottawa, Ont.

Environment Canada. 2008. Normales climatiques au Canada 1971–2000. National Climate Archive. Available from http://climate.weatheroffice.gc.ca/climate_normals/index_e.html.

Evans, J.R., and Poorter, H. 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**(8): 755–767. doi:10.1046/j.1365-3040.2001.00724.x.

Fang, S., Xu, X., Lu, S., and Tang, L. 1999. Growth dynamics and biomass production in short-rotation poplar plantations: 6-year results for three clones at four spacings. Biomass Bioenergy, **17**(5): 415–425. doi:10.1016/S0961-9534(99)00060-4.

Feng, Y.L., Fu, G.L., and Zheng, Y.L. 2008. Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive alien congeners. Planta, **228**(3): 383–390. doi:10.1007/s00425-008-0732-2. PMID:18392694.

Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. Oecologia (Berl.), **56**(2–3): 341–347. doi:10.1007/BF00379710.

Gouveia, A., and Freitas, H. 2009. Modulation of leaf attributes and water use efficiency in *Quercus suber* along a rainfall gradient. Trees: Struct. Funct. **23**(2): 267–275.

Grams, T.E.E., and Andersen, C.P. 2007. Competition for resources in trees: physiological versus morphological plasticity. Prog. Bot. **68**(4): 356–381. doi:10.1007/978-3-540-36832-8_16.

Green, D.S., Kruger, E.L., Stanosz, G.R., and Isebrands, J.G. 2001. Light-use efficiency of native and hybrid poplar genotypes at high levels of intracanopy competition. Can. J. For. Res. **31**(6): 1030–1037. doi:10.1139/x01-041.

Henskens, F., Battaglia, M., Cherry, M., and Beadle, C. 2001. Physiological basis of spacing effects on tree growth and form in *Eucalyptus globulus*. Trees:Struct. Funct. **15**(6): 365–377.

Hikosaka, K., and Terashima, I. 1995. A model of the acclimation of photosynthesis in the leaves of C3 plants to sun and shade with respect to nitrogen use. Plant Cell Environ. **18**(6): 605–618. doi:10.1111/j.1365-3040.1995.tb00562.x.

Hikosaka, K., Sudoh, S., and Hirose, T. 1999. Light acquisition and use by individuals competing in a dense stand of an annual herb, *Xanthium canadense*. Oecologia (Berl.), **118**(3): 388–396. doi:10.1007/s004420050740.

Hirose, T., and Werger, M.J.A. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia (Berl.), **72**(4): 520–526. doi:10.1007/BF00378977.

Hirose, T., Werger, M.J.A., Pons, T.L., and Rheenen, J.W.A. 1988. Canopy structure and leaf nitrogen distribution in a stand of *Lysimachia vulgaris* L. as influenced by stand density. Oecologia (Berl.), **77**(2): 145–150. doi:10.1007/BF00379180.

Iio, A., Fukasawa, H., Nose, Y., Kato, S., and Kakubari, Y. 2005. Vertical, horizontal and azimuthal variations in leaf photosynthetic characteristics within a *Fagus crenata* crown in relation to light acclimation. Tree Physiol. **25**(5): 533–544. PMID:15741146.

Johnson, H.A., and Biondini, M.E. 2001. Root morphological plasticity and nitrogen uptake of 59 plant species from the Great Plains grasslands, U.S.A. Basic Appl. Ecol. **2**(2): 127–143. doi:10.1078/1439-1791-00044.

Kolb, T.E., Holmberg, K.M., Wagner, M.R., and Stone, J.E. 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. Tree Physiol. **18**(6): 375–381. PMID:12651362.

Larocque, G.R. 1999. Performance and morphological response of the hybrid poplar DN-74 (*Populus deltoides* × *nigra*) under different spacings on a 4-year rotation. Ann. For. Sci. **56**(4): 275–287. doi:10.1051/forest:19990402.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., and Schabenberber, O. 2006. SAS for mixed models. 2nd ed. SAS Institute Inc., Cary, N.C.

Makeschin, F. 1999. Short rotation forestry in central and northern Europe — introduction and conclusions. For. Ecol. Manag. **121**(1–2): 1–7.

Marron, N., Delay, D., Petit, J.-M., Dreyer, E., Kahlem, G., Delmotte, F.M., and Brignolas, F. 2002. Physiological traits of two *Populus*

× *euramericana* clones, Luisa Avanzo and Dorskamp, during a water stress and re-watering cycle. Tree Physiol. **22**(12): 849–858. PMID:12184974.

Medhurst, J.L., and Beadle, C.L. 2005. Photosynthetic capacity and foliar nitrogen distribution in *Eucalyptus nitens* is altered by high-intensity thinning. Tree Physiol. **25**(8): 981–991. PMID: 15929929.

Meziane, D., and Shipley, B. 2001. Direct and indirect relationships between specific leaf area, leaf nitrogen and leaf gas exchange. effects of irradiance and nutrient supply. Ann. Bot. (Lond.), **88**(5): 915–927. doi:10.1006/anbo.2001.1536.

Ministère du Développement Durable de l'Environnement et des Parcs. 2009. Climatologie, direction du suivi de l'état de l'environnement, Ministère du Développement Durable de l'Environnement et des Parcs, Québec, Qué.

Niinemets, Ü., and Sack, L. 2006. Structural determinants of leaf light-harvesting capacity and photosynthetic potential. Prog. Bot. **67**: 386–419.

Niinemets, Ü., Kull, O., and Tenhunen, J.D. 1998. An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. Tree Physiol. **18**(10): 681–696. PMID:12651418.

Onoda, Y., Hikosaka, K., and Hirose, T. 2004. Allocation of nitrogen to cell walls decreases photosynthetic nitrogen-use efficiency. Funct. Ecol. **18**(3): 419–425. doi:10.1111/j.0269-8463.2004.00847.x.

Peek, M., Russek-Cohen, E., Wait, A., and Forseth, I. 2002. Physiological response curve analysis using nonlinear mixed models. Oecologia (Berl.), **132**(2): 175–180. doi:10.1007/s00442-002-0954-0.

Poorter, H., and Evans, J.R. 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia (Berl.), **116**(1–2): 26–37. doi:10.1007/s004420050560.

Reich, P.B., Walters, M.B., Kloeppel, B.D., and Ellsworth, D.S. 1995. Different photosynthesis–nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia (Berl.), **104**(1): 24–30. doi:10.1007/BF00365558.

Ripullone, F., Grassi, G., Lauteri, M., and Borghetti, M. 2003. Photosynthesis-nitrogen relationships: interpretation of different patterns between *Pseudotsuga menziesii* and *Populus* × *euro-americana* in a mini-stand experiment. Tree Physiol. **23**(2): 137–144. PMID:12533308.

Rosati, A., Esparza, G., DeJong, T.M., and Pearcy, R.W. 1999. Influence of canopy light environment and nitrogen availability on leaf photosynthetic characteristics and photosynthetic nitrogen-use efficiency of field-grown nectarine trees. Tree Physiol. **19**(3): 173–180. PMID:12651580.

Schieving, F., and Poorter, H. 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. New Phytol. **143**(1): 201–211. doi:10.1046/j.1469-8137.1999.00431.x.

Szendrödi, L.B. 1996. Growing space–age related three-dimensional modeling of biomass production of hybrid poplar. Biomass Bioenergy, **10**(5–6): 251–259. doi:10.1016/0961-9534(95)00119-0.

Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M.L., Roumet, C., Lavorel, S., Díaz, S., Hodgson, J.G., Lloret, F., Midgley, G.F., Poorter, H., Rutherford, M.C., Wilson, P.J., and Wright, I.J. 2005. Specific leaf area and dry matter content estimate thickness in laminar leaves. Ann. Bot. **96**(6): 1129–1136. doi:10.1093/aob/mci264. PMID:16159941.

Walters, R.G. 2005. Towards an understanding of photosynthetic acclimation. J. Exp. Bot. **56**(411): 435–447. doi:10.1093/jxb/eri060. PMID:15642715.

Yin, C., Wang, X., Duan, B., Luo, J., and Li, C. 2005. Early growth, dry matter allocation and water use efficiency of two sympatric *Populus* species as affected by water stress. Environ. Exp. Bot. **53**(3): 315–322. doi:10.1016/j.envexpbot.2004.04.007.