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The effects of spacing on growth, morphology and biomass production and allocation in two hybrid poplar clones growing in the boreal region of Canada

Lahcen Benomar · Annie DesRochers · Guy R. Larocque

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Abstract Intra-clonal competition was studied in young hybrid poplar plantations to assess the effects of spacing on growth, biomass production and allocation, and morphological characteristics of above- and below-ground tree parts. Three spacings were used as whole-plots (1 × 1 m, 3 × 3 m and 5 × 5 m), with two hybrid poplar clones as subplots (BT747, *Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray; MB915, *P. maximowiczii* A. Henry × *P. balsamifera* L.) in a split-plot design. After six growing seasons, diameter at breast height (dbh) increased by about 120% from the 1 × 1 m to the 5 × 5 m spacing for clone MB915, while there was no significant change in dbh for the other clone. The effect of spacing on height growth was opposite for the clones; it increased by about 175% from the narrowest to the widest spacing for clone MB915, while it decreased by about 27% for clone BT747. Estimates of above-ground biomass production after six growing seasons were significantly reduced with increasing spacing, with 29.6, 4.9 and 3.2 MgDM ha^{-1} on average from the narrowest to the widest spacing. Branch traits and the vertical distribution of leaf area were the most affected by spacing for both clones, while live crown ratio and percentage of syllepsis did not change. Spacing also affected proportions of biomass allocated to stem, leaves, and branches, but allocation to roots did not change.

Keywords *Populus* spp. · Intra-clonal competition · Coarse roots · Spatial distribution of leaf area · Crown and branch traits · Syllepsis

Introduction

In boreal forest regions across Canada, short-rotation forestry (SRF) using hybrid poplar (*Populus* spp.) plantations has a great potential for (1) restoring abandoned agricultural lands and degraded forests, (2) reducing harvesting pressure on natural forests, and (3) becoming sustainable sources of wood supplies. However, a better understanding of the factors that influence biomass production is required to maximize the productivity of plantations. Among the site factors that govern productivity, stand density is critical, as it affects establishment costs, site occupancy, average piece size, and wood quality. Studies of tree response to initial spacing have previously focused on growth traits such as height, diameter at breast height (dbh), stem volume, and above-ground biomass (Cannell 1980; DeBell et al. 1996; Fang et al. 1999; Ferm et al. 1989; Larocque 1999; Strong and Hansen 1993; Willebrand et al. 1993). Even though estimates of productivity exist, little is known on the effects of spacing on biomass allocation, crown architecture, and root distribution in hybrid poplar plantations.

Crown architecture plays an important role in SRF productivity (Ceulemans et al. 1990; Wu and Stettler 1994). For example, a strong relationship was found between crown diameter and dbh for several species (Foli et al. 2003; Hemery et al. 2005). This relationship may offer substantial information that is required to optimize spacing between

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L. Benomar (✉) · A. DesRochers
Centre d'étude de la foret (CEF) and Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue, 341, rue Principale Nord, Amos, QC J9T 2L8, Canada
e-mail: Lahcen.benomar@uqat.ca

G. R. Larocque
Ressources naturelles Canada, Service canadien des forêts, Centre de foresterie des Laurentides 1055, rue du P.E.P.S., C.P. 10380, succ. Sainte-Foy, Québec, QC G1V 4C7, Canada

trees (Hall 1994; Hemery et al. 2005). Crown architecture varies widely among poplar species and their hybrids (Burk et al. 1983; Ceulemans et al. 1990; Dunlap et al. 1995; Gielen et al. 2002), and since it determines the spatial distribution of foliage and, consequently, solar radiation interception efficiency (Mitchell et al. 1992), such differences may explain the variation in growth responses to intra-clonal competition (Cannell 1980; Hall 1994; Harper 2008; Nelson et al. 1981). Branch characteristics (number, size, and orientation) have a decisive role in controlling crown architecture (Ceulemans et al. 1990). Hybrid poplar trees produce two types of branches: (1) sylleptic branches, in which bud formation and branch elongation occur in the same year and (2) proleptic branches, which are formed when the bud undergoes dormancy and the branch develops only a year later (Mitchell et al. 1992). Sylleptic branches, in contrast to proleptic branches, are known to translocate (export) a larger proportion of their photosynthates to the main stem (Scarascia-Mugnozza et al. 1999). Increasing syllepsis (percentage of sylleptic branches) can also increase leaf area of the tree, resulting in a higher growth rate (Ceulemans et al. 1990; Wu et al. 2000). Hence, syllepsis has become an important criterion in selective breeding of hybrid poplar clones with respect to productivity (Ceulemans et al. 1990; Wu and Stettler 1994, 1998), and geographic variation, and phenotypic plasticity (Dillen et al. 2007). The involvement of syllepsis in tree responses to intra-clonal competition remains unknown. The increase in syllepsis in response to decreased spacing between trees could be a plastic response that optimizes crown architecture in narrow spacings through (1) efficient filling of available space within the crown, (2) increased allocation of biomass to the stem, or (3) an increase in crown leaf area.

The pattern of biomass allocation also varies greatly among hybrid poplar clones (Wu and Stettler 1998; Wullschleger et al. 2005; Zsuffa 1995) and constitutes an important information because of its influence on harvestable biomass (Alcorn et al. 2007; Fang et al. 1999; Pinkard and Neilsen 2003). When spacing between trees is reduced, biomass that is allocated to branches and foliage usually decreases to the benefit of the stem (Fang et al. 1999; Pinkard and Neilsen 2003). However, the influence of initial spacing on below-ground biomass remains unknown. Plasticity of rooting patterns in response to competition likely plays a role in nutrient uptake when resources are limited. For example, maximum rooting depth is expected to increase under high competitive stress, to enhance access to soil nitrogen (Casper and Jackson 1997).

The main objective of this study was to determine the effects of intra-specific competition on growth, crown architecture, biomass allocation, and coarse root system distribution in two young hybrid poplar clones (MB915; *P. maximowiczii* × *P. balsamifera* and BT747; *P. balsamifera* × *P. trichocarpa*) growing at three spacings in the boreal region of Quebec, Canada. We hypothesized that a decrease in spacing between trees would (1) increase allocated biomass to below-ground parts of trees; (2) increase rooting depth; (3) decrease the length, diameter and angle of origin and termination of branches; and (4) increase branch syllepsis.

Materials and methods

Study area and experimental design

The study area was located in the boreal region of Abitibi-Témiscamingue, Quebec, Canada. Three sites were 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 soil, which was dominated by grasses and sparse patches of speckled alder [*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen], willow (*Salix* spp.), and trembling aspen (*Populus tremuloides* Michaux). Rivière Héva was also an abandoned farmland site with heavy clay soil, which was dominated by shrubs, again including alder, willow, and trembling aspen. Nédelec was previously dominated by a trembling aspen forest type which was commercially harvested in 2000. The main species that were present included, in addition to trembling aspen, white or paper birch (*Betula papyrifera* Marsh.) and pin cherry (*Prunus pensylvanica* L.) growing on a sandy-loam soil. Based on the 30-year running average, Amos and Rivière Héva experience 1,387 degree-days above 5°C annually, while the annual total for Nédelec is 1,480 degree-days (Environment Canada 2008). Additional details on site preparation prior to planting and weed management can be found in Benomar et al. (2011).

The experiment was designed as a split-plot layout with initial square spacing as the whole plot factor and each site as a replicate. Each spacing was sub-divided into two clones (sub-plot factor). Three square spacings were tested: 1 × 1 m, 3 × 3 m, and 5 × 5 m, which are equivalent to about 10,000, 1,111, and 400 stems ha^{-1}, respectively. The size of the experimental unit was related to initial spacing, and consisted of 36 trees (6 × 6 rows of trees), of which the 16 interior trees were considered for the study, leaving a 1-row buffer on each plot edge. The two hybrid poplar clones were BT747 (*Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray) and MB915 (*P. maximowiczii* A. Henry × *P. balsamifera* L.). Selection of these clones was based on their availability at the local tree nursery. They constitute two of the eight clones that are recommended for the region by the Quebec Ministry of Natural Resources and Wildlife (Périnet et al. 2006).

Growth

Immediately following planting and after the first six growing seasons, total height, stem basal diameter (D, m: 10 cm above the soil surface), and survival at the end of each growing season (mid-October) were measured. Diameter at breast height (dbh, m) was only measured for the last five growing seasons because stem dieback damage was observed for most trees during the first season (most trees were under 1.3 m height). Measurements were made on the 16 central trees in each plot. Trees that died in 2003 and 2004 were replaced in 2005 to maintain competition levels representative of the spacing; the replacement trees were not included in our calculations. A slenderness index (SI), which is a good indicator of competitive status, was calculated as follows: SI = height (m)/dbh (m).

Crown traits

During the fourth growing season (2006), morphological characteristics were examined on four randomly selected trees in the center of each spacing × clone × site combination, for a total of 72 trees. Crown morphology was assessed by measuring crown diameter (CD, m), live crown length (L, m), total number of branches, and number of current year sylleptic and proleptic branches. Because of their continuous development from a terminal meristem, sylleptic branches can be identified by their lack of basal bud scales and the first pair of leaves having similar size and shape as adult leaves, while proleptic branches have one or more basal bud scales due to their discontinuous growth (Mitchell et al. 1992). These measures allowed us to derive the following variables: (1) crown volume = 0.3927 CD^2L (assuming a parabolic form of the crown); (2) live crown ratio (LCR) = live crown length/stem height; and (3) syllepsis = number of current year sylleptic branches/number of current year total branches.

Branch characteristics

Only first-order branches from each of the 72 trees were measured and divided into three groups according to their ages: (1) bottom crown section branches (branches of the first and second growing seasons), (2) middle crown section branches (branches of the third growing season), and (3) upper crown section branches (branches of the current growing season). The upper group was subdivided into two subgroups according to their origin, i.e., proleptic versus sylleptic. The following variables were measured for each branch: length, diameter, and angles of origin and termination.

Spatial distribution of leaf area

Following the measurement of crown and branch characteristics for each tree (end of July), its crown was subdivided into three equal vertical sections (33% of crown length for each section: bottom, middle, and upper). The total amount of foliage in each section was manually harvested. Total leaf area for each section was measured using a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE). Dry mass was measured after drying to constant mass at 72°C.

Biomass allocation and coarse root morphology

On 15 July 2007, one tree per treatment (3 sites × 2 clones × 3 spacings = 18 total trees) was selected for biomass allocation sampling. The tree that was sampled in each plot was selected based on its dbh that best represented a treatment mean. Total height (H), dbh, and basal diameter were measured in the field. Following the removal of foliage from each tree, the branches were separated from the stem. Coarse roots >5 mm in diameter were excavated manually using picks and shovels and root number and depth was recorded. Root depth was measured at the end of the root, where it had reached less than 5 mm in diameter. Total leaf area was measured using a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE). All tree parts were oven-dried (at 72°C for 8 days), after which dry mass was recorded. Percentages of biomass for leaves, stem, branches, and roots were obtained by dividing the biomass of each component by the total tree biomass (i.e., leaves + stem + branches + roots).

The above-ground biomass of an additional 17 trees was harvested by the end of summer of 2008 to relate growth traits (D, dbh, and height) to leafless above-ground biomass per tree. These additional trees were taken from the plot buffer strips to cover a maximum range of dbh. Based on our data, the relationship between dbh and above-ground biomass (AGB) was nonlinear. Data were fitted iteratively, using procedure NLIN (SAS Inc., 2000), to the following power function model:

$$W = a\ \mathrm{dbh}^b \qquad (1)$$

where W is above-ground biomass (AGB, kg dry mass), dbh is the diameter at breast height (cm), and a and b are estimated parameters of the model. Above-ground biomass production per hectare was calculated in absolute terms from the derived equations.

Statistical analyses

All data were analyzed using the Mixed Procedure in SAS (version 9.2, SAS Institute, Cary, NC, USA). Response variables such as survival, proportion (%) of biomass allocated to roots, stem, branches, and leaves and crown characteristics were analyzed separately using the following general linear mixed model with spacing and clone as a fixed effects, and site as a random effect:

$$\begin{aligned} Y_{\mathrm{SSC}} = \mu + E_{\mathrm{Site}} + \beta_{\mathrm{S}} + E_{\mathrm{Site*S}} + \beta_{\mathrm{C}} \\ + \beta_{\mathrm{S*C}} + E_{\mathrm{Site*S*C}} + E_{\mathrm{r}} \end{aligned} \qquad (2)$$

where Y is the dependent variable, μ is the grand mean, β_{S} is the fixed effect of spacing, β_{C} is the fixed effect of clone, $\beta_{\mathrm{S*C}}$ is the spacing by clone interaction, and E_{Site}, $E_{\mathrm{Site*S}}$, $E_{\mathrm{Site*S*C}}$ are the random effect for site, whole plot and subplot, respectively. E_{R} is the residual error. Biomass allocation data were arcsine transformed to satisfy model assumptions (homoscedasticity and normality of residuals).

Aboveground biomass and growth in terms of D, dbh, and height were subjected to repeated-measures analysis using the following mixed model:

$$\begin{aligned} Y_{\mathrm{SSCT}} = \mu + E_{\mathrm{Site}} + \beta_{\mathrm{S}} + E_{\mathrm{Site*S}} + \beta_{\mathrm{C}} + \beta_{\mathrm{S*C}} + E_{\mathrm{Site*S*C}} \\ + \beta_{\mathrm{T}} + E_{\mathrm{Site*T}} + \beta_{\mathrm{S*T}} + E_{\mathrm{Site*S*T}} + \beta_{\mathrm{C*T}} \\ + \beta_{\mathrm{S*C*T}} + E_{\mathrm{Site*S*C*T}} + E_{\mathrm{r}} \end{aligned} \qquad (2)$$

where Y_{SSCT} is the dependent variable, μ is the grand mean, β_{T} is the fixed effect of time, $\beta_{\mathrm{S*T}}$ is the spacing by time interaction, $\beta_{\mathrm{C*T}}$ is the clone by time interaction, $\beta_{\mathrm{S*C*T}}$ the spacing by clone by time interaction, and $\mathrm{E}_{\mathrm{Site*T}}$, $\mathrm{E}_{\mathrm{Site*T*S}}$, $\mathrm{E}_{\mathrm{Site*T*S*C}}$, are the random time specific for site, whole plot and subplot, respectively, and the remaining parameters are defined as in (Eq. 2). The variance component was estimated by restricted maximum likelihood (REML). An autoregressive covariance structure was chosen because of between-subject correlation (Richard et al. 1987). The growth data were log-transformed to satisfy model assumptions (homoscedasticity and normality of residuals). Proportion of leaf area by crown section, and frequency of roots by depth, were analysed after arcsine transformation using the model in Eq. 3 and substituting the time factor by section or depth as a fixed effect factor. Means comparisons were performed using Tukey tests. All differences were considered significant at $P \leq 0.05$.

Results

Growth

Tree basal diameter increased by about 44 and 131% for clones BT747 and MB915, respectively, as spacing increased from 1 × 1 m to 5 × 5 m. Trees had reached a mean dbh of 3.48 and 5.61 cm and a mean height of 3.55 and 5.77 m, respectively, for clones BT747 and MB915, after six growing seasons (Table 1). There was a significant interaction between spacing and clone for height and basal diameter growth (Table 2), with the two clones showing opposite reactions to changes in spacing; Height decreased by about 20% for clone BT747, while it increased by 32% for clone MB915, when spacing rose from 1 × 1 m to 5 × 5 m (Table 1). Growth in term of dbh depended on spacing × clone × time interaction, and increased by 120% with spacing from 1 × 1 m to 5 × 5 m for clone MB915, while dbh of clone BT747 was unaffected by the change in spacing. For the latter, basal diameter did increase with an increase in spacing but the gains were modest compared with those of clone MB915 (Table 1).

Spacing effect on growth was time dependent (Table 2) as indicated by two different growth phases; The first phase was characterized by the absence of a spacing effect, which lasted 2 years for clone MB915 and 4 years for clone BT747 (Fig. 1). The second phase was characterized by an increase in dbh at the greatest spacing, particularly for clone MB915 (Fig. 1). After six growing seasons, mean tree survival ranged from 60 to 94%. Survival was greater in the 1 × 1 m and 3 × 3 m spacings compared with that of the 5 × 5 m spacing, and greater for clone BT747 than for MB915 (Table 1).

Biomass predictions

There was a very significant relationship between aboveground biomass (AGB; leafless) as a function of stem dbh (Table 3). The models for the two clones were highly significant ($P = 0.001$), with 96–99% of the variation in above-ground biomass explained by the model for clones BT747 and MB915, respectively.

Table 1 Characteristics of two hybrid poplar clones (BT747and MB915) at three spacings (1 × 1 m, 3 × 3 m and 5 × 5 m), after six growing seasons

Clone	Spacing (m)	Survival (%)	dbh (cm)	Basal diameter (cm)	Height (m)
BT747	1 × 1	94	3.32^{a}	5.20^{a}	4.11^{b}
	3 × 3	95	3.28^{a}	6.21^{b}	3.28^{a}
	5 × 5	75	3.84^{a}	7.47^{c}	3.27^{a}
Mean		88	3.48	6.29	3.55
MB915	1 × 1	78	3.61^{a}	5.45^{a}	5.03^{c}
	3 × 3	81	5.27^{b}	8.00^{d}	5.63^{c}
	5 × 5	60	7.94^{c}	12.57^{e}	6.64^{d}
Mean		73	5.61	8.67	5.77

Dbh diameter at breast height

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

Table 2 Repeated-measures ANOVA giving sources of variation, degrees of freedom (*DF*), *F* values, and associated probabilities for height, basal diameter, and dbh

Source	*DF*	Height		Basal diameter		dbh	
		F	*P* value	*F*	*P* value	*F*	*P* value
Spacing	2	3.91	0.049	14.38	0.0001	3.39	0.068
Clone	1	186.26	<0.0001	69.96	0.0004	11.42	0.006
S*C	2	11.43	0.0005	7.1	0.0047	2.14	0.161
Time	5 (4)	2,912.01	<0.0001	5,190.35	<0.0001	450.35	<0.0001
S*T	10 (8)	1.65	0.103	40.39	<0.0001	10.32	<0.0001
C*T	5 (4)	129.02	<0.0001	38.68	<0.0001	42.12	<0.0001
S*C*T	10 (8)	4.47	<0.0001	2.75	0.005	3.74	0.0054

Numerator *DF* in parentheses is for dbh (diameter at breast height). Dbh measurements began at the second growing season

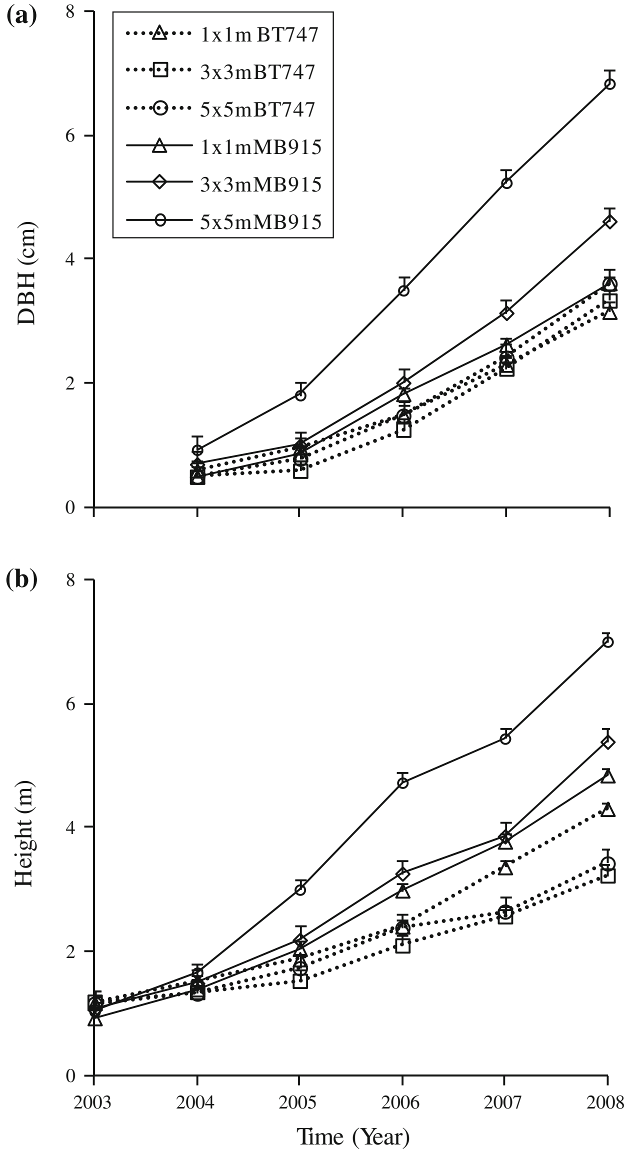

Fig. 1 Diameter at breast height (dbh) (**a**) and height (**b**) growth during six growing seasons for two hybrid poplar clones, BT747 and MB915, growing at three initial square spacings (1 × 1 m, 3 × 3 m and 5 × 5 m)

Biomass production and allocation

Increased spacing between trees significantly increased above-ground biomass (AGB) at the individual tree level (kg tree^{-1}), but decreased it at the plot level (Mg DM ha^{-1}) after the first six growing seasons (Table 4). Estimated biomass production after 6 years on a per-hectare basis was 8–20 times greater in the 1 × 1 m spacing compared with the 3 × 3 m and 5 × 5 m spacings, respectively, for clone BT747, while clone MB915 produced 3.5–5.5 more AGB in the 1 × 1 m spacing compared with the 3 × 3 m and 5 × 5 m spacings, respectively. Similarly, mean annual production of above-ground biomass on a per hectare basis was also greater in the 1 × 1 m spacing (Table 4). In all spacing treatments, clone MB915 produced greater biomass than clone BT747. However, clonal differences were less pronounced in the 1 × 1 m spacing compared with the two other spacings.

Biomass allocation to branches and leaves was significantly influenced by both spacing and clone, while biomass allocated to the stem depended only on spacing (Table 5). Biomass allocated to roots, however, was not significantly affected by spacing (Table 5), although BT747 allocated 3% more biomass to roots than did MB915. When spacing increased from 1 × 1 m to 3 × 3 m, biomass that was allocated to the stem decreased significantly, to the benefit of branches, a trend not observed when spacing increased from 3 × 3 m to 5 × 5 m (Table 6). The effect of spacing on biomass that was allocated to leaves was clone-dependent; leaf biomass for BT747 was unaffected by spacing but greater for MB915 in the 3 × 3 m and 5 × 5 m spacings, compared with trees growing in the 1 × 1 m spacing (Table 6).

Crown structure and foliage distribution

Crown volume dramatically increased with spacing from 1 × 1 m to 5 × 5 m (812% for clone MB915 and 276% for clone BT747; Table 7). The interaction between spacing and clone was significant (Table 5) and reflected the

Table 3 Parameters of the power function model ($Y = a\,X^{b}$) relating dbh of individual trees to above-ground (leafless) biomass (kg)

Clone	Model parameters		N	R^2
	a	b		
BT747	0.32 (0.07)	1.92 (0.16)	17	0.96
MB915	0.28 (0.05)	1.79 (0.08)	18	0.99

N number of observations, Y biomass (kg dry mass tree^{-1}), X diameter at breast height (cm)

Table 4 Above-ground biomass (leafless) and mean biomass productivity following six growing seasons of two hybrid poplar clones (BT747 and MB915) at three initial spacings (1 × 1 m, 3 × 3 m, and 5 × 5 m)

Clone	Spacing (m)	AGB (Mg ha^{-1})	AGB (kg Tree^{-1})	Yield (Mg ha^{-1} year^{-1})
BT747	1 × 1	27.00^{b}	1.10^{e}	5.15^{b}
	3 × 3	2.89^{e}	1.66^{d}	0.55^{e}
	5 × 5	1.32^{f}	2.98^{c}	0.26^{f}
MB915	1 × 1	32.19^{a}	1.68^{d}	6.15^{a}
	3 × 3	6.98^{c}	6.79^{b}	1.37^{c}
	5 × 5	5.00^{d}	10.63^{a}	1.25^{d}

AGB above-ground biomass

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

Table 5 Analysis of variance giving sources of variation, F values, and associated probabilities for biomass allocation and crown characteristics

Response variable	Spacing		Clone		Spacing*clone	
	F	$Pr > F$	F	$Pr > F$	F	$Pr > F$
% of biomass in branches	46.27	0.001	23.48	0.002	3.24	0.111
% of biomass in stem	20.86	0.007	1.74	0.235	1.55	0.286
% of biomass in foliage	4.47	0.040	4.06	0.071	3.3	0.324
% of biomass in roots	2.08	0.240	11.1	0.0158	0.64	0.5598
Crown volume	40.91	<0.0001	83.86	<0.0001	24.54	<0.0001
LCR	0.25	0.781	9.52	0.007	5.02	0.019
Syllepsis	2.04	0.32	72.71	<0.0001	1.10	0.345
SI	56.28	0.001	0	0.961	0.96	0.434

LCR live crown ratio, *SI* slenderness index (H/dbh)*100

Table 6 Proportion (%) of biomass allocated to roots, stem, branches, and leaves of individual trees for two hybrid poplar clones (BT747 and MB915) growing under three spacings (1 × 1 m, 3 × 3 m and 5 × 5 m)

Clone	Spacing (m)	Roots	Branches	Stem	Leaves
BT747	1 × 1	27.2^{b}	19.9^{a}	35.9^{a}	16.8^{b}
	3 × 3	28.1^{b}	25.1^{b}	27.2^{b}	19.7^{b}
	5 × 5	30.4^{b}	30.1^{c}	23.4^{b}	16.1^{b}
MB915	1 × 1	25.6^{a}	22.6^{a}	41.5^{a}	10.1^{a}
	3 × 3	24.6^{a}	31.3^{c}	25.9^{b}	18.1^{b}
	5 × 5	26.3^{a}	32.6^{c}	25.4^{b}	15.5^{b}

Data were collected after five growing seasons (2007). Values are the averages of three harvested trees for each treatment

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

Table 7 Crown characteristics after four growing seasons of two hybrid poplar clones (BT747 and MB915) growing at three initial spacings (1 × 1 m, 3 × 3 m and 5 × 5 m)

Clone	Spacing (m)	Crown volume (m^3)	LCR	SI (m m^{-1})	Syllepsis (%)
BT747	1 × 1	1.46^{a}	0.92^{a}	140.4^{a}	43.6^{a}
	3 × 3	2.12^{a}	0.89^{a}	111.6^{b}	43.5^{a}
	5 × 5	5.50^{b}	0.92^{a}	94.5^{c}	40.7^{a}
MB915	1 × 1	2.42^{a}	0.92^{a}	140.5^{a}	62.4^{b}
	3 × 3	10.5^{c}	0.95^{b}	117.7^{b}	56.2^{b}
	5 × 5	22.1^{d}	0.94^{b}	87.7^{c}	57.7^{b}

LCR live crown ratio, *SI* slenderness index (H/dbh)*100

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

Table 8 Analysis of variance giving sources of variation, F values, and associated probabilities for proportion of leaf area

Source	DF	F	$Pr > F$
Spacing	2	8.79	0.055
Clone	1	1.9	0.172
Spacing*Clone	2	0.03	0.970
Section	2	107.05	<0.0001
Spacing*Section	4	109.4	<0.0001
Clone*Section	2	46.7	<0.0001
Spacing*Clone*Section	4	89.32	<0.0001

much greater increase for clone MB915. LCRs increased only slightly with spacing for clone MB915 (Tables 5, 7). The slenderness index (SI) decreased markedly with spacing (Table 7) for both clones (Table 5). Spacing had no significant effect on the level of syllepsis for both clone, however, it was greater for clone MB915 (58%) compared with BT747 (42%) (Tables 5, 7).

Spacing effect on leaf area distribution in the crown depended significantly on both clone and crown section (three-way interaction, Table 8); There was a sharp decrease in foliage allocated to the bottom section in the 1 × 1 m spacing for clone MB915 while it slightly increased in the two larger spacings. In contrast, clone BT747 had similar leaf area distribution in the upper and middle crown sections among the spacings and less foliage in the bottom crown section for all spacings (Fig. 2).

Branch characteristics

Spacing and crown section had strong effects on branch dimension and orientation (Table 9). First, an increase in spacing increased branch diameter and length (Table 10), similarly between all crown sections and clones (Table 9). Mean branch diameter and length increased from the upper to bottom crown sections (Table 10). The interaction between clone and crown section for branch size revealed that mean branch length of clone MB915 was greater than that of BT747 only for the bottom and middle crown sections (Table 10).

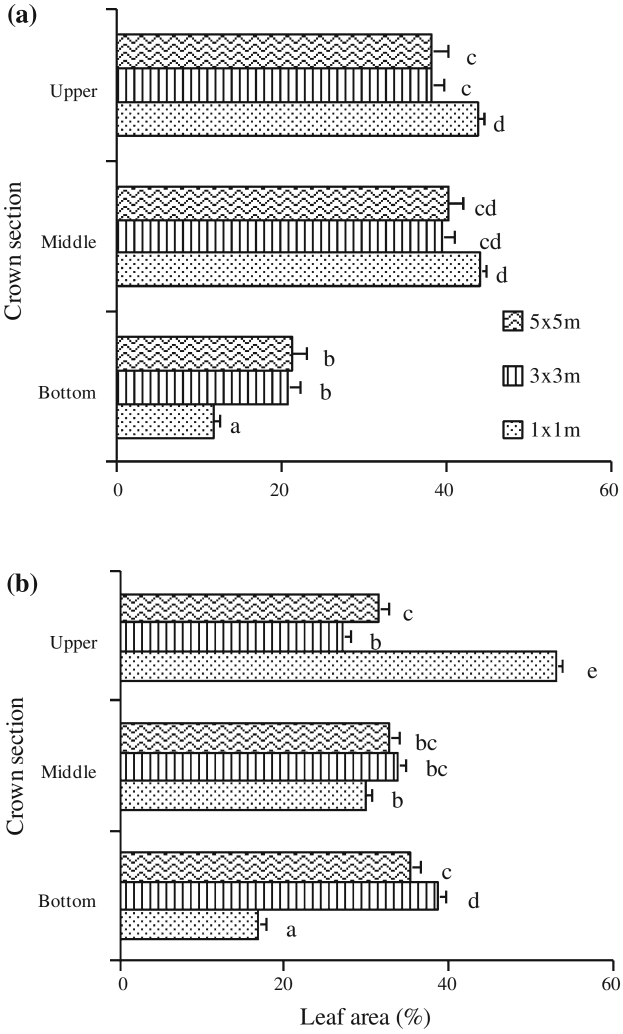

Fig. 2 Leaf area distribution within the crown of two hybrid poplar clones **a** BT747 and **b** MB915, growing at three initial spacings (1 × 1 m, 3 × 3 m and 5 × 5 m). For each crown section, columns followed by the same letters are not significantly different at $\alpha \leq 0.05$

Mean angle of origin was unaffected by spacing in the bottom and middle sections of the crown, whereas it increased significantly with an increase in spacing in the upper crown section (Tables 9, 10). Except for the upper crown section, clone MB915 had a greater mean angle of origin than clone BT747 (Table 10). Branches of clone MB915 generally had a greater mean angle of termination than clone BT747, and it increased with an increased in spacing only in the bottom and upper crown sections for clone MB915, and only in the upper crown section for clone BT747 (Tables 9, 10).

Root characteristics

Root numbers per tree were similar among spacings for clone MB915, while they were significantly greater in the 3 × 3 m and 5 × 5 m than in the 1 × 1 m spacing for clone BT747 (data not shown). Maximum rooting depth observed in this study was about one meter with mean rooting depth at 25 cm. The pattern of root distribution was unaffected by both spacing and clone (Table 11). Over 80% of roots were located between 0 and 40 cm.

Discussion

Spacing effects on stem size

Basal diameter increased predictably as spacing between trees increased (Table 3), as has been observed elsewhere (Alcorn et al. 2007; DeBell et al. 1996). An increase in dbh with spacing was only observed for clone MB915, which is likely the result of smaller changes in crown dimensions with increasing available space for BT747 (Table 7), showing the greater grown plasticity of clone MB915 to rapidly take advantage of the available space.

Interestingly, the height growth response to increases in spacing was opposite for the two clones (Table 1). While height growth is commonly assumed to be insensitive to changes in spacing between trees (Lanner 1985; Woodruff et al. 2002), this may be only true in softwood species. In fast-growing hardwoods, tree height may increase, decrease, or remain unchanged with increasing spacing between trees (Alcorn et al. 2007; DeBell et al. 1996; Fang et al. 1999; Kerr 2003; Pinkard and Neilsen 2003). Variations in height growth with changes in available growing space could be attributed to ontogeny, to the range of tested spacing treatments, or to species. Height growth plays an important role in morphological acclimation to light competition (Lanner 1985), with plants tending to allocate more photosynthate to height than diameter growth, which results in increasing stem slenderness (Table 7). This response could explain why height growth was greater in the 1 × 1 m spacing for clone BT747, while faster growth

Table 9 Analysis of variance giving sources of variation, *F* values, and associated probabilities for mean angle of origin, angle of termination, diameter and length of branch

Source	*DF*	Diameter		Length		Θ_1		Θ_2	
		F	Pr > *F*	*F*	Pr > *F*	*F*	Pr > *F*	*F*	Pr > *F*
Spacing	2	226.08	<0.0001	105.69	<0.0001	7.78	0.001	6.25	0.002
Clone	1	0.08	0.7711	62.92	<0.0001	43.35	<0.0001	4.21	0.040
S*C	2	0.22	0.8056	0.75	0.471	7.06	0.001	7.93	0.001
Section	2	336.12	<0.0001	370.51	<0.0001	11.16	<0.0001	14.25	<0.0001
S*Section	4	1.92	0.094	2.07	0.082	12.56	<0.0001	3.31	0.011
C*Section	2	3.53	0.0294	4.07	0.017	6.32	0.002	0.52	0.594
S*C*Section	4	0.28	0.890	0.08	0.989	0.94	0.440	1.20	0.310

$\Theta 1$ angle of origin of branches, $\Theta 2$ angle of termination of branches

Table 10 Mean angle of origin, angle of termination, diameter and length of branch of two hybrid poplar clones (BT747 and MB915) growing at three initial spacings (1 × 1 m, 3 × 3 m and 5 × 5 m) after four growing seasons

Crown section	Clone	Spacing (m)	Θ_1 (°)	Θ_2 (°)	Diameter (mm)	Length (cm)
Upper	BT747	1 × 1	54^{ab}	46^{ab}	6.14^{a}	44.35^{a}
		3 × 3	57^{b}	50^{b}	7.67^{b}	55.64^{b}
		5 × 5	65^{c}	50^{b}	8.58^{c}	58.64^{b}
	MB915	1 × 1	50^{a}	43^{a}	5.64^{a}	48.48^{a}
		3 × 3	58^{bc}	57^{c}	7.64^{b}	65.52^{bc}
		5 × 5	62^{bc}	58^{c}	8.91^{c}	80.10^{d}
Middle	BT747	1 × 1	60^{b}	42^{a}	7.91^{a}	67.39^{a}
		3 × 3	58^{b}	41^{a}	11.39^{b}	86.51^{c}
		5 × 5	59^{b}	42^{a}	14.29^{c}	111.82^{d}
	MB915	1 × 1	50^{a}	44^{a}	7.64^{a}	78.50^{b}
		3 × 3	51^{a}	39^{a}	11.34^{b}	106.31^{d}
		5 × 5	53^{a}	49^{a}	14.13^{c}	144.85^{e}
Bottom	BT747	1 × 1	64^{b}	43^{ab}	9.39^{a}	83.55^{a}
		3 × 3	60^{b}	45^{ab}	13.28^{b}	102.24^{b}
		5 × 5	66^{b}	42^{ab}	16.11^{c}	124.65^{c}
	MB915	1 × 1	54^{a}	35^{a}	10.13^{a}	109.74^{b}
		3 × 3	53^{a}	47^{b}	14.50^{b}	141.41^{d}
		5 × 5	55^{a}	52^{c}	17.65^{c}	171.19^{e}

$\Theta 1$ angle of origin of branches, $\Theta 2$ angle of termination of branches

For each crown section, means within column followed by the same letter do not differ significantly at $\alpha = 0.05$

and the associated trade-off between mechanical stability of the stem and height growth may explain why the trend was reversed for clone MB915.

Spacing effects on biomass production

Cumulative above-ground biomass (leafless) per ha after six growing seasons increased as spacing between trees decreased, probably due to an increase in LAI (Fang et al. 1999; Gower 2003). By the end of the sixth growing season, the estimated yield at the greatest spacing was very low (<1.5 Mg ha^{-1} year^{-1}) compared with published data under the same spacing conditions (Fang et al. 1999). Average yield attained under the 1 × 1 m spacing was about 6.15 Mg ha^{-1} year^{-1} and 5.15 Mg ha^{-1} year^{-1} for clones MB915 and BT747, respectively (Table 4). Reported above-ground yields in dense plantations of different hybrid poplar clones in central Europe, the USA, and Canada are greater, and range between 10 and 30 MgDM ha^{-1} year^{-1} (Cannell and Jeffery 2004; DeBell et al. 1996; Dowell et al. 2009; Labrecque and Teodorescu 2003). Our results mirror yields under boreal (cold temperate) conditions; In Sweden, Christersson (2010) reported that average yields ranging 3–10 MgDM ha^{-1} year^{-1} in 5-year-old plantations, while Willebrand et al. (1993) reported average yields that varied between 8 and 14 MgDM ha^{-1} year^{-1} in 6-year-old plantations. In spite of the short duration of the growing season and low soil nitrogen in boreal Canada, a 10-MgDM ha^{-1} year^{-1} yield should easily be achieved by adding fertilizer and selecting appropriate clones and spacings (Weih 2004). However, several elements suggest that above-ground yields will change with respect to spacing in the future, as canopy closure occurs in the greater spacings: (1) the absence of significant differences in LCR between spacings (Table 7) indicates that competition was not yet severe enough to cause density-dependent mortality in the close spacing, (2) full occupancy of space in the large spacings had not yet occurred at the end of the six growing seasons to successfully counterbalance yields for the low stand densities. We thus anticipate an increase in above-ground yield in the 3 × 3 m and 5 × 5 m spacings after canopy closure and a decrease in biomass production in the 1 × 1 m spacing due to intensification of intra-clonal competition.

Spacing effects on biomass allocation

Biomass allocation is involved in growth efficiency and plastic responses of trees to their environment (Casper

Table 11 ANOVA analysis of variance giving sources of variation, *F* values, and associated probabilities for the frequency distribution of roots

Effet	*DF*	*F*	Pr > *F*
Spacing	2	0.02	0.9773
Clone	1	0.07	0.799
Spacing*Clone	2	0.32	0.7457
Depth	3	12.05	0.0002
Spacing*Depth	6	0.54	0.7733
Clone*Depth	3	1.78	0.1911
Spacing*Clone*Depth	6	0.43	0.8482

et al. 1998; McCarthy and Enquist 2007; Reich et al. 1998). In this study, biomass allocation was substantially affected by changes in spacing between trees. In large spacings, biomass that was allocated to branches exceeded biomass that was allocated to the stem (Table 6), which is not desirable for lumber production. Light availability likely stimulated growth and production of branches (Benomar et al. 2011). However, spacing seemed to have little effect on biomass allocation to leaves, while biomass allocation to leaves may decrease under low-nitrogen conditions (Hegazy et al. 2008; Poorter and Nagel 2000; Proe et al. 2002). Under low-nitrogen conditions, the increase in specific leaf area (SLA, the ratio of leaf area to leaf dry mass) may compensate for a decrease in biomass allocation to leaves. According to our previous results (Benomar et al. 2011), SLA was significantly and negatively associated with spacing between trees. Biomass allocated to leaves did not change with spacing for clone BT747, probably due to low levels of below-ground competition and slower growth rate of this clone. According to advanced theoretical concepts in biomass partitioning (optimal partitioning theory; McCarthy and Enquist 2007), biomass is allocated in order of priority for the acquisition of limiting resources. Thus, the fraction of biomass that is allocated to roots is predicted to increase under conditions of nitrogen limitation and to decrease under competition for light. Under intraspecific competition (dense plantation), both nitrogen and light presumably decrease. Our results showed similar investments of biomass in roots among spacings (Table 6), and similar results were reported by Bernardo et al. (1998) and Casper et al. (1998). However, our sampling was limited to the structural roots (taproot and lateral roots) and did not include functional parts (fine roots). It is possible that trees responded to the increase in competition by increasing fine root density, fine root longevity or by increasing the rate of N uptake rather than increasing coarse root depth (Casper and Jackson 1997; Espeleta and Donovan 2002; Litton et al. 2003).

Spacing effects on branch size and orientation

Our results showed that reduced spacing between trees reduced the frequency and development of branches (Alcorn et al. 2007; DeBell et al. 1996; Henskens et al. 2001). Crown volume (space occupied by foliage) and spatial distribution of the foliage are important in carbon gain at the crown level. This is because of their direct effect on the availability and efficient use of light within the crown (Roeh and Maguire 1997; Wang and Jarvis 1990). Crown volume increased with an increase in spacing between trees, more so for clone MB915 than clone BT747 (Table 7). This occurred by increasing branch length and angles of origin and termination (Table 10). Indeed, in contrast to clone MB915, branches of clone BT747 had similar angles of termination in low and middle crown sections at the various spacings, explaining why leaf area distribution remained unchanged. In contrast, taller and less acute branches at the bottom of the crown in large spacings resulted in both a greater crown volume and proportion of leaf area in the bottom crown section for clone MB915. Longer branches for clone MB915 (Table 10) allowed this clone to display more leaf area per branch (Ceulemans et al. 1990) and, thus, experience faster growth rates. Plasticity in angles of origin and termination allows trees to display their foliage efficiently, thereby maximizing light capture (Burk et al. 1983; Ceulemans et al. 1990). In this study, the angle of origin was unaffected by spacing in the bottom and middle parts of crown, probably because these branches were developed before crown closure occurred in this part of the crown, during the first years following establishment. LCR was also insensitive to changes in spacing due to the absence of branch mortality at the time of measurement, since canopy closure had only started to occur in the plots.

Our results show that branch traits are important in clonal selection for spacing trials. Clone BT747 had acute short branches even at the greatest spacing, which decreased its utility for efficient biomass production under various conditions. In contrast, clone MB915 had less acute and longer branches, making its selection more appropriate for growth at large spacings. In addition, this clone showed plasticity in branch traits and other crown traits in response to spacing. Retention of this plasticity is very useful if dense plantations are followed by thinning. Our results do not support the involvement of syllepsis in morphological plasticity in response to competition. Increased syllepsis has been found to be positively related to radial growth (Wu and Stettler 1998), and this response could explain the superior growth of clone MB915. Further, it suggests that syllepsis is an attribute of fast growth but not necessarily an attribute of morphological plasticity.

Conclusion

The results of our study showed that as spacing increased, basal diameter growth increased, and dbh increased or remained unchanged, depending on the clone. At the same time, height growth increased or decreased, again depending on the clone. Above-ground biomass per ha was maximized at the 1 × 1 m spacing, mostly likely due to the young age of the plantation, since canopy closure had not yet been attained at greater spacings. Crown structure of the two hybrid poplar clones was under considerable control by the level of competition between trees (spacing), through changes in branch development and orientation, which led to changes in the spatial distribution of leaf area. Syllepsis apparently had no effect on morphological acclimation to intra-clonal competition. Trees responded to the increase in competition by decreasing their investment in branches. Decreases in biomass allocation to leaves in response to the increase of competition depended on clone. Both rooting depth and biomass allocation to roots were insensitive to changes in spacing between trees.

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