



## Research paper

## Short-term growth and morphological responses to nitrogen availability and plant density in hybrid poplars and willows

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## ABSTRACT

Morphological characteristics of poplar and willow clones were determined in order to identify main characteristics leading to superior growth under increased plant competition with low or high nitrogen (N) availability. Seven hybrid poplar (*Populus* spp. including one hybrid aspen) and five willow (*Salix* spp.) clones were grown under greenhouse conditions for 13 weeks at three spacings (20 × 20, 35 × 35, and 60 × 60 cm) and two N levels (20 and 200 mg kg<sup>-1</sup>). The decrease in spacing from 60 to 20 cm reduced leaf area by 50% but clones had similar aboveground biomass per tree under all spacings, with increasing their height per unit leaf area. More productive clones had greater leaf area (+102%), leaf area per unit plant biomass (+12%) and lower root-to-shoot ratios (−27%) compared to less productive clones. There were positive relationships between leaf area and above-ground biomass per tree for both more and less productive clones. Compared to low N level and 60 cm spacing, trees growing in high N level and 20 cm spacing reached similar root collar diameter, crown width, and leaf area values and even greater height, suggesting that an addition of N could help mitigate negative effects of tree competition.

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## 1. Introduction

There is growing interest in short rotation forestry (SRF) plantations of hybrid poplars, aspens, and willows on degraded agricultural and forest lands across Canada. These species are generally fast-growing under dense stands in local conditions and harvested between 2 and 8 years after plantation establishment, for the purpose of biomass production [1]. Woody crop biomass for bio-energy may potentially 1) enhance energy security as a fossil fuel substitute, 2) offset greenhouse gases produced by the use of fossil fuels, and 3) revitalize rural economies by increasing employment opportunities in the forest industry while providing a locally available and renewable energy source [2,3]. However, for

economically feasible SRF plantations, silviculture costs (e.g., site preparations and maintenance costs) must be minimized and biomass production must be maximized by using the best available clones and practices [4].

Among the factors that affect growth and associated biomass production, stand density and site nutritional status are critical for maximizing the productivity of plantations. If spacing decreases from 3 to 0.5 m between stems, hybrid poplars (including aspens) (*Populus* spp.) and willows (*Salix* spp.) can show greater biomass production per unit area on short rotation time intervals [5–9]. When tree competition occurs in dense plantations where available resources per tree are limited, more resources are allocated to height growth at the expense of diameter growth in *Populus* spp., resulting in an increase in slenderness ratio (SR) (= stem height/diameter at breast height or root collar diameter) [9,10]. *Populus* trees can also increase their photosynthetic capacity by optimizing spatial distribution of foliage for irradiance interception within the

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crown [11–14] and efficiently increase whole-plant leaf area (LA) per unit plant biomass (LAR) under high competition [7]. However, intense plant competition can also cause nutritional deficiencies, particularly nitrogen (N), resulting in decreasing amounts of harvestable biomass per tree [15]. Since N can increase leaf area and overall plant growth and decrease the root-to-shoot mass ratios under close spacing (<3 m) of SRF management [16–20], N fertilization may contribute to reducing negative effects of tight spacing on tree growth.

Currently, there is incomplete understanding on growth and morphological responses of *Populus* and *Salix* clones when growing under different densities and N availability. To better understand growth strategies of superior growth-performant clones, we selected 12 clones from the database of Poplar and Willow Council of Canada [21], commonly used in either research or industry field research of Canada, that were also expected to have great productivity under SRF conditions [7,9,22–29]. Previous studies reported that various clones demonstrated differences in growth patterns under changes in tree density or N availability, partly resulting from genotypic differences in carbohydrate partitioning [6,9,18,30]. For example, clone MB915 (*Populus maximowiczii* × *P. balsamifera*) showed faster growth than clone BT747 (*P. balsamifera* × *P. trichocarpa*) under relatively close spacing (1 × 1 m), because MB915 allocated a greater proportion of biomass to longer stems and branches supporting more leaf area, resulting in greater total above-ground biomass (leafless) [9]. Plants that can display this form of plastic responses of biomass allocation to their environment can enhance growth efficiency and maximize productivity [18].

Growth information using desirable morphological and physiological traits may be useful for early clone selection and thereby save time and expenses [31]. Conventional selection processes to identify the most productive *Populus* and *Salix* clones are based on field comparisons for biomass productivity over several years. However, this traditional approach is time consuming and requires considerable investments. This is particularly true in the boreal forest [32]. Therefore, the development of methodologies and procedures that can accelerate the selection process of the productive clones could have considerable benefits. Using greenhouse facilities, it is possible to perform experimentation all year. Although field studies remain necessary to examine adaptability to local field conditions and susceptibility to diseases, the primary advantage of controlled environments is to be able to provide a consistent repeatable environment compared to field studies. Greenhouse conditions can reduce the amplitude of natural variability (environmental variance) compared to field conditions [33], which may facilitate the characterization of the relationships between growth and morphological attributes and estimation of genetic control on these traits.

The objectives of this study were to determine how a reduction in spacing, under high or low N availability, affected morphological characteristics of poplar and willow clones and how particular growth strategies could result in superior growth performance. We hypothesized that superior clones would be able to maintain similar above-ground biomass per tree with a decrease in spacing by producing greater leaf area per unit plant biomass (LAR), increasing slenderness ratio (SR), and lowering root-to-shoot mass ratios (RSR). We also hypothesized that negative effects of increased plant density such as crown recession or decreased root collar diameter (RCD) could be mitigated by an increase in N availability. Lastly we hypothesized that growth strategies between *Populus* and *Salix* clones under increasing tree density would differ because *Populus* clones generally have greater RCD and larger size of leaves, while *Salix* clones tend to have multiple stems of smaller diameter with a greater number of narrow leaves.

## 2. Materials and methods

### 2.1. Experimental design and measurements

The research trial took place in a greenhouse at the Laurentian Forestry Centre of the Canadian Forest Service in Quebec (46°46'N, 71°16'W). The experimental design was set up as an incomplete block design with six hybrid poplar clones (*Populus maximowiczii* × *P. balsamifera*, 915319; *P. balsamifera* × *P. trichocarpa*, 747210; *P. deltoides* × *P. balsamifera*, 1081; *P. deltoides* × *P. nigra*, DN-74; *P. maximowiczii* × *P. nigra*, NM6; and *P. deltoides* × *P. petrowskyana*, Walker), one hybrid aspen clone (*P. tremuloides* × *P. tremula*, 2782), and five willow clones (*Salix amygdaloides*, HAN-A5; *S. discolor*, LEV-D5; *S. eriocephala*, SHE-E9; *S. interior*, LAF-I4; and *S. nigra*, TCH-N4). Since there was not enough space to complete all experimental work in a greenhouse, the experiment had 6 blocks over a two-year period. Within each block (growing period of 13 weeks), each combination of six clones, two fertilization levels [20 and 200 mg kg<sup>-1</sup> of nitrogen (N)] and three spacings [20 (20 × 20), 35 (35 × 35), 60 (60 × 60) cm] was assigned to 36 planting boxes, which were randomly positioned in the greenhouse. The plant pot sizes were 1 × 1 × 0.4 m for the 20 cm spacing, 1.4 × 1.4 × 0.4 m for the 35 cm spacing, and 1.2 × 1.2 × 0.4 m for the 60 cm spacing. Each combination of clones, spacings and fertilizer levels was replicated three times, once in each of three different blocks. In the 20 and 35 cm spacings, 16 cuttings of 10 cm in length were planted per planting box and four central cuttings were measured and used for statistical analyses. In the 60 cm spacing, five cuttings were planted per planting box for the 60 cm spacing and one central cutting was measured and used for statistical analyses. Hybrid aspen clone 2782 were established as 20 cm long rooted plants from in-vitro culture as aspens are difficult to root from cuttings [34].

A 100 cm<sup>3</sup> aliquot of tap water per tree including all macro and micro nutrients were supplied twice a week using an irrigation system (O'Jet Olson Bleu 300, Harnois Inc., St-Thomas, QC, Canada). Thus, nutrients (1600 cm<sup>3</sup>: 16 cuttings) per planting box were provided in the 20 and 35 cm spacings and (500 cm<sup>3</sup>: 5 cuttings) in the 60 cm spacing. Two levels of N (20 and 200 mg kg<sup>-1</sup>) were applied as ammonium-nitrate (NH<sub>4</sub>NO<sub>3</sub>). Phosphorus (1.5 g P) was provided as monobasic calcium orthophosphate [Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub> · H<sub>2</sub>O] for each tree. Calcium (1.55 g Ca per tree) was supplied as above for calcium orthophosphate as well as CaCO<sub>3</sub> for pH control. Potassium (50 mg K), magnesium (11.9 mg Mg), and sulfur (15.7 mg S) of macronutrient solutions were also supplied to each tree with K<sub>2</sub>SO<sub>4</sub> and MgSO<sub>4</sub> · 7H<sub>2</sub>O. Micro nutrients were also provided per tree, including 1.35 mg of iron (chelated Fe), 0.5 mg of manganese (Mn), 0.013 mg of molybdenum (Mo), 0.04 mg of copper (Cu) and 0.39 mg of boron (B).

Daily photoperiod was set at 16 h of daylight (06h00–22h00) using natural light supplemented with artificial light (400 W high pressure sodium bulbs, Litmore Distributors Ltd., Edmonton, Alta.) in periods of shorter photoperiods. Temperature was set at 24 °C during daylight and 18 °C during the dark period. Soil mixture in the planting boxes consisted of peat, vermiculite and sand (1:1:1 by volume), a commercial potting substrate PRO-MIX (Premier Horticulture Ltd, Dorval, Québec, Canada). The pH in the boxes averaged 6.0 (range 5.5–7).

Root collar diameter (RCD) (±1 mm), height (±1 cm), and crown width (CW: the average length of two perpendicular lines across the crown area) (±1 cm) were measured every two weeks. Cuttings that had failed to root in the first few weeks after planting were replaced to maintain competition levels but the replaced trees were not included in the analyses. After three months, the plants in the centre of the box were harvested and stems (including branches), roots and leaves were separated. Leaf area (LA) was measured with

a leaf area meter (LI-3100, LI-COR, Inc., Lincoln, NE, USA). Then, stems, roots and leaves were oven-dried at 55 °C until no change in mass was detected.

2.2. Data analyses

Relative growth rate (RGR) is a growth-efficiency measure that calculates the amount of growth per unit of time adjusted by the accumulated size [35]. RGR was calculated as:

$$(\ln RCDH_2 - \ln RCDH_1) / (T_2 - T_1) \tag{1}$$

where RCDH<sub>2</sub> and RCDH<sub>1</sub> represent RCD and height at the time of growing period T<sub>2</sub> and T<sub>1</sub>, respectively. The slenderness ratio (SR), calculated as height (cm)/RCD (mm), is a competitive status indicator of individual plants [9]. Leaf area ratio (LAR) estimates the proportion of photosynthesizing biomass relative to respiring biomass [36]. It was calculated as the ratio of leaf area to total plant biomass, including leaves, stems, and roots (excluding the original cuttings). The root-shoot mass ratio (RSR), which represents the proportion of the absorbing surface to the transpiring surface [35], was calculated as the ratio of root biomass to stem and leaf biomass. For the proportion of biomass allocation, percentages of biomass for leaves, stems, and roots were calculated by dividing the biomass of each component by total plant biomass. All the analyses were performed at the genus and clonal levels. Genus level represented the respective means of *Populus* and *Salix* clones.

All data were analyzed using the Mixed Model Procedure in SAS (version 9.2, SAS Institute, Cary, NC, USA). The model includes fixed effects for genus or clone, nitrogen, spacing, and their interactions in a factorial treatment structure. RCD, height, CW, RCD RGR, and height RGR were measured every two weeks and also subjected to repeated-measures analysis using the following mixed model:

$$Y_{bgcnpt} = \mu + E_b + \beta_{gc} + \beta_n + \beta_s + \beta_{gc*n} + \beta_{n*s} + \beta_{gc*s} + \beta_{gc*n*s} + E_p + E_{gc*n*s*p} + \beta_t + \beta_{gc*t} + \beta_{n*t} + \beta_{gc*n*t} + \beta_{s*t} + \beta_{n*s*t} + \beta_{gc*s*t} + \beta_{gc*n*s*t} + E_{p*t} + E_r \tag{2}$$

where Y<sub>bgcnsp</sub> is the dependent variable, μ the overall mean, β<sub>gc</sub> the fixed effect of genus or clone, β<sub>n</sub> the fixed effect of nitrogen, β<sub>s</sub> the fixed effect of spacing, β<sub>gc\*n</sub> the genus or clone by nitrogen interaction, β<sub>n\*s</sub> the nitrogen by spacing interaction, β<sub>gc\*s</sub> the genus or clone by spacing interaction, and β<sub>gc\*n\*s</sub> the genus or clone by nitrogen by spacing interaction. E<sub>b</sub>, E<sub>p</sub>, and E<sub>gc\*n\*s\*p</sub>, are the random effects for block, planting box, and tree, respectively. β<sub>t</sub> is the fixed effect of time, β<sub>gc\*t</sub> the genus or clone by time interaction, β<sub>n\*t</sub> the nitrogen by time interaction, β<sub>gc\*n\*t</sub> the genus or clone by nitrogen by time interaction, β<sub>s\*t</sub> the spacing by time interaction, β<sub>n\*s\*t</sub> the nitrogen by spacing by time interaction, β<sub>gc\*s\*t</sub> the genus or clone by spacing by time interaction, β<sub>gc\*n\*s\*t</sub> the genus or clone by nitrogen by spacing by time interaction, and E<sub>p\*t</sub> the random time specific for planting box. Er is the residual error.

In the following model, the dependent variables were RCD, height, CW, morphological measures including LA, LAR, SR, and RSR, above-ground biomass, and proportion of biomass allocated to stems, roots, and leaves measured at the end of growing period:

$$Y_{bgcnsp} = \mu + E_b + \beta_{gc} + \beta_n + \beta_s + \beta_{gc*n} + \beta_{n*s} + \beta_{gc*s} + \beta_{gc*n*s} + E_p + E_{gc*n*s*p} + E_r \tag{3}$$

where Y<sub>bgcnsp</sub> is the dependent variable, μ the overall mean, the all parameters are defined in Eq (2).

Linear regression analysis was undertaken to verify relationships between LA and RCD or height and CW of all treatments. Slopes among treatments were compared using analysis of covariance (ANCOVA). Based on morphological characteristics such as leafless aboveground biomass per tree (AGBT), leafless above-ground biomass per square metre (AGBM), LA, LAR, SR, and RSR, more productive (superior) and less productive (inferior) clones were grouped. Linear regression analysis was also used to verify relationships between AGBT and LA for superior clones and inferior clones as a group. ANCOVA was also used to compare the slopes between superior and inferior clones.

**Table 1**  
F values, and associated probabilities for root collar diameter (RCD), height, crown width (CW), RCD relative growth rate (RGR), and height RGR at the genus and clonal levels.

Source of variation	DF	RCD		Height		CW		RCD RGR		Height RGR	
		F	P value	F	P value	F	P value	F	P value	F	P value
G	1	26.9	<b>0.001</b>	1.5	0.250	6.9	<b>0.010</b>	23.5	<b>&lt;0.001</b>	4.5	<b>0.030</b>
N	1	36.5	<b>&lt;0.001</b>	37.2	<b>&lt;0.001</b>	24.3	<b>0.001</b>	32.3	<b>&lt;0.001</b>	58.0	<b>&lt;0.001</b>
S	2	3.3	0.074	0.8	0.471	7.9	<b>0.008</b>	13.4	<b>&lt;0.001</b>	17.5	<b>&lt;0.001</b>
N × S	2	0.3	0.748	0.1	0.878	1.0	0.405	0.3	0.780	0.7	0.498
G × N	1	0.6	0.448	0.3	0.628	2.2	0.170	0.0	0.923	0.0	0.866
G × S	2	1.1	0.354	0.2	0.823	0.5	0.624	1.3	0.286	0.7	0.519
G × N × S	2	1.3	0.301	0.7	0.532	2.6	0.118	0.7	0.494	0.5	0.629
T	5	553.3	<b>&lt;0.001</b>	169.7	<b>&lt;0.001</b>	152.2	<b>&lt;0.001</b>	52.0	<b>&lt;0.001</b>	555.9	<b>&lt;0.001</b>
G × T	5	10.6	<b>&lt;0.001</b>	0.8	0.519	5.1	<b>&lt;0.001</b>	54.9	<b>&lt;0.001</b>	4.8	<b>0.000</b>
N × T	5	6.1	<b>&lt;0.001</b>	10.9	<b>&lt;0.001</b>	5.0	<b>&lt;0.001</b>	0.9	0.487	2.4	<b>0.030</b>
S × T	10	3.5	<b>0.001</b>	2.9	<b>0.001</b>	3.8	<b>&lt;0.001</b>	0.9	0.543	3.0	<b>0.001</b>
N × S × T	10	0.2	0.993	0.2	0.998	0.7	0.757	1.0	0.490	0.6	0.788
G × N × T	5	0.3	0.891	0.3	0.941	1.5	0.190	0.4	0.876	1.6	0.163
G × S × T	10	0.1	1.000	0.4	0.949	0.3	0.985	0.5	0.883	1.9	<b>0.036</b>
G × N × S × T	10	0.5	0.911	0.4	0.931	0.7	0.758	0.8	0.647	0.2	0.996
C	11	14.4	<b>&lt;0.001</b>	13.0	<b>&lt;0.001</b>	13.6	<b>&lt;0.001</b>	17.8	<b>&lt;0.001</b>	10.2	<b>&lt;0.001</b>
C × N	11	4.7	<b>&lt;0.001</b>	2.5	<b>0.006</b>	0.8	0.597	0.8	0.673	0.5	0.899
C × S	22	2.8	<b>&lt;0.001</b>	1.7	<b>0.020</b>	1.1	0.328	0.5	0.977	0.4	0.994
C × N × S	22	2.7	<b>&lt;0.001</b>	2.4	<b>&lt;0.001</b>	2.7	<b>&lt;0.001</b>	0.5	0.953	0.2	1.000
C × T	55	9.0	<b>&lt;0.001</b>	6.2	<b>&lt;0.001</b>	22.4	<b>&lt;0.001</b>	23.7	<b>&lt;0.001</b>	13.0	<b>&lt;0.001</b>
C × N × T	55	1.3	0.102	0.5	1.000	1.6	0.081	0.3	0.984	0.3	0.984
C × S × T	110	0.6	0.999	0.4	1.000	2.0	<b>0.003</b>	0.8	0.750	0.4	0.997

In source of variation, G: genus (*Populus* vs *Salix*), N: nitrogen, S: spacing, T: time, and C: clone. Significant P values are indicated in bold.

### 3. Results

#### 3.1. Growth development

At the end of the 13-week growing period, the *Populus* clones had significantly greater RCD and smaller CW than the *Salix* clones, while there was no significant difference in height between the two genera (Table 1, A.1).

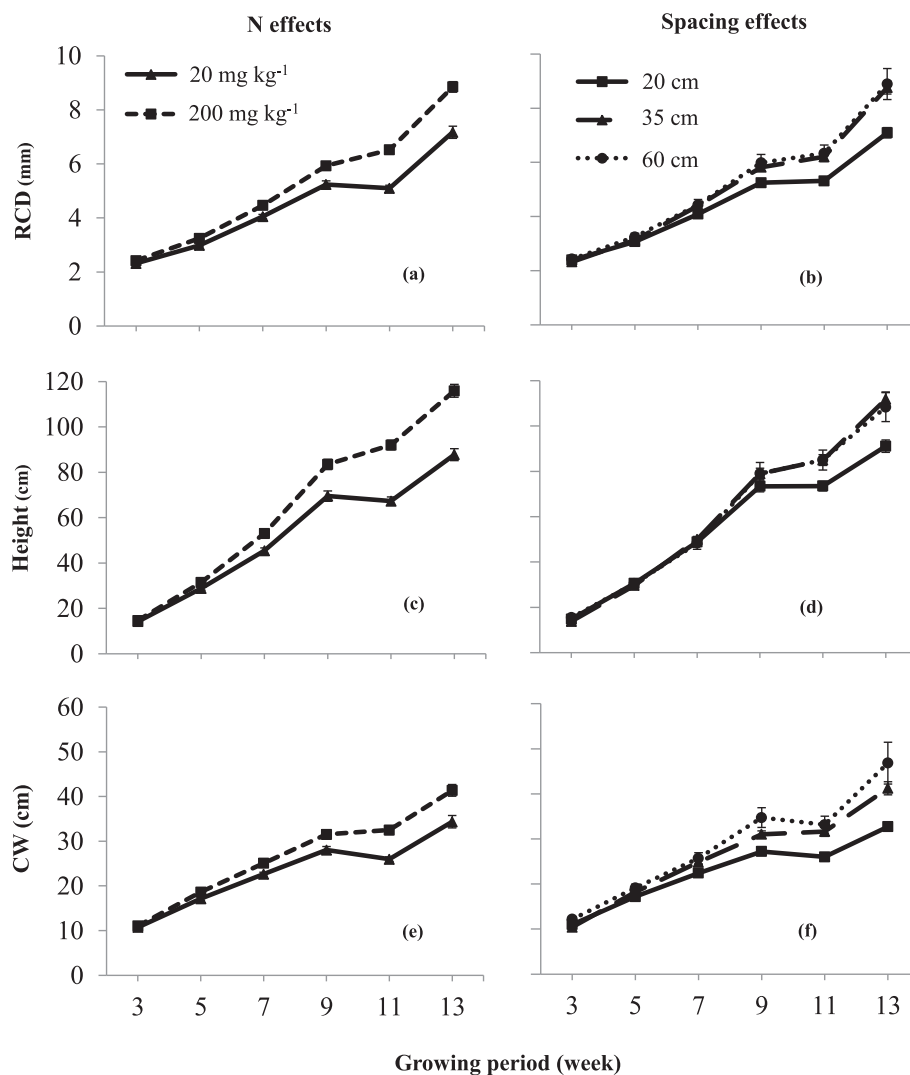
The increase in N significantly increased RCD, height and CW after five weeks, followed by greater differences between high and low N level by the end of the growing period (significant N  $\times$  T interaction, Fig. 1a,c,e, and Table 1). The increase in spacing also increased RCD after 7 weeks, height after 11 weeks, and CW after 5 weeks (significant S  $\times$  T interaction, Fig. 1b,d,f, and Table 1). Both *Populus* and *Salix* groups responded similarly in RCD, height, and CW to changes in N and spacing levels (non-significant G  $\times$  N; G  $\times$  S interactions, Table 1), although there were variations among individual clones in RCD and height with N level and spacing (significant C  $\times$  N; C  $\times$  S interactions, Table 1). There were also significant three way interactions (C  $\times$  N  $\times$  S) for RCD, height, and CW at the clonal level (Table 1, A.1).

During the growing period, the pattern of change in RCD RGR

differed significantly between *Populus* and *Salix* and among clones (G  $\times$  T; C  $\times$  T interactions, Fig. 2a,b, and Table 1). RGR for *Populus* clones peaked in the first three weeks, followed by a rapid decrease and subsequently, relatively similar values for the remainder of the growing period (Fig. 2a). Clone 2782 initially showed the most rapid development of RCD RGR (Fig. 2b). On the other hand, *Salix* clones as a group initially had a slower development in RCD RGR than *Populus* clones, followed by a rapid increase (Fig. 2a). This trend was noticeably evident for *Salix* clone SHE-E9 (Fig. 2b). Height RGR for both *Populus* and *Salix* clones initially peaked and then, gradually declined over time (Fig. 2c). At the clonal level, height RGR for individual clones significantly differed over time (C  $\times$  T interaction, Fig. 2d and Table 1).

#### 3.2. Morphological characteristics

Nitrogen (N) addition at the high level resulted in an increase in leaf area (LA) differently under the different spacings such that it had a greater effect under the large spacing (N  $\times$  S interaction; Fig. 3 and Table 2). LA significantly decreased by 50% with the decrease in spacing from 60 to 20 cm, but increased with N level by 30, 47, and 88% at 20, 35, and 60 cm spacings, respectively (Fig. 3).



**Fig. 1.** Changes in mean root collar diameter (RCD), height, crown width (CW), and height relative growth rate (RGR) under two N levels (20 and 200 mg kg<sup>-1</sup>) (a) (c) (e) and three spacings (20, 35, and 60 cm) (b) (d) (f) during 13 growing weeks.

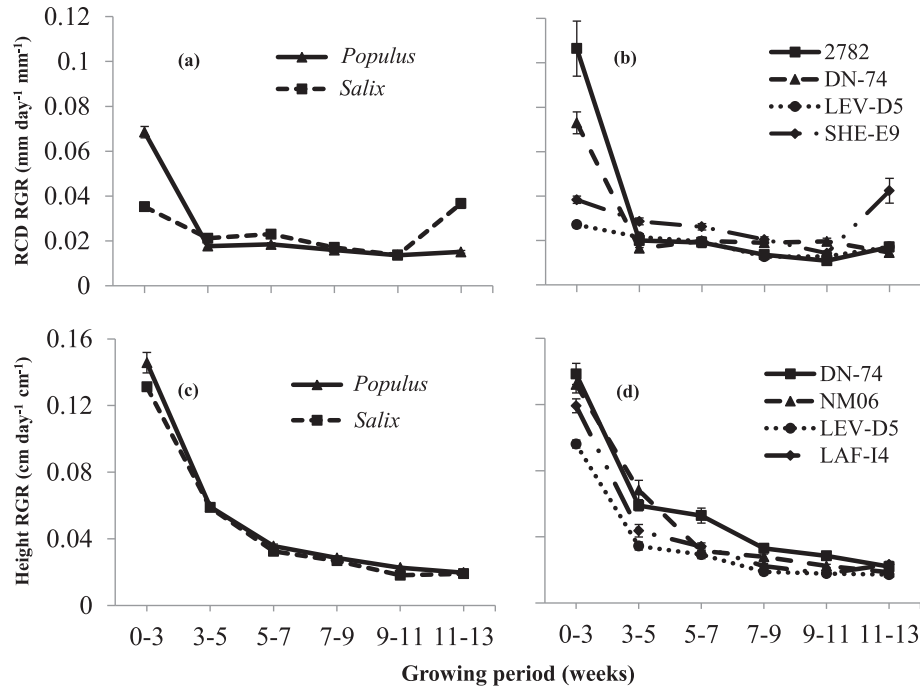


Fig. 2. Changes in mean root collar diameter (RCD) relative growth rate (RGR) and height RGR for *Populus* and *Salix* (a) (c) and for two *Populus* and two *Salix* clones (b) (d) during 13 growing weeks.

At the genus level, there was no significant difference in LA between *Populus* and *Salix* (Table 2). At the clonal level, there were significant differences in LA among clones from 1230 cm<sup>2</sup> for LEV-D5 to 4147 cm<sup>2</sup> for NM06 (Table A.2). Although LA significantly increased with higher N level, the amount of increasing LA varied among clones (Table 3). The amount of leaf area (LA) in this study was a good indicator to predict growth performance of clones as LA was positively related to root collar diameter (RCD), height, and crown width (CW) for all clones in all treatments (Table 4). RCD per unit increase in LA was only significantly different between 60 cm and 200 mg kg<sup>-1</sup> and the other treatments (Table 4). Height per unit increase in LA generally increased from 60 to 20 cm spacing, while CW per unit increase in LA did not show any changes within

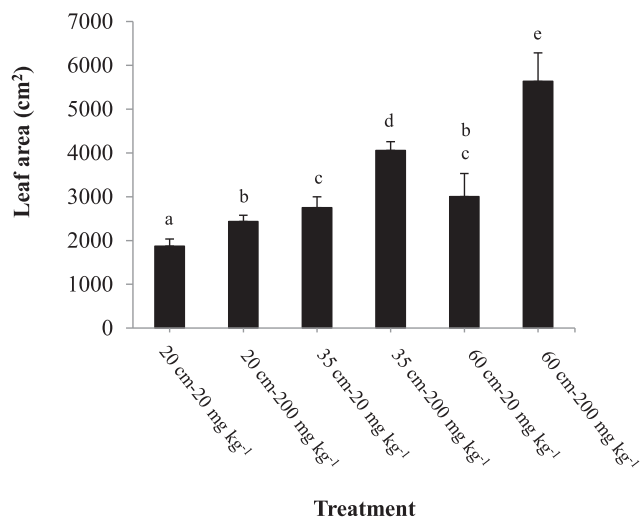


Fig. 3. Mean leaf area for all clones combined under three spacings (20, 35, and 60 cm) and two N levels (20 and 200 mg kg<sup>-1</sup>) after 13 growing weeks. Means followed by the same letter on the bar do not significantly differ at  $\alpha = 0.05$ .

all treatments (Table 4).

Spacing had no effect on leaf area ratio (LAR), while the increase in N level significantly increased LAR by 4% (Tables 2 and 5). *Populus* clones had higher LAR than *Salix* clones (Table 2, A.2), and LAR also varied among clones from 81.0 cm<sup>2</sup> g<sup>-1</sup> for LAF-14 to 143.2 cm<sup>2</sup> g<sup>-1</sup> for DN-74 (Table 2, A.2). Slenderness ratio (SR) significantly increased with an increase in N by 10% (Tables 2 and 5). At the genus level, SR for the *Populus* clones significantly increased from the 60 to 20 cm spacing while there were no changes for the *Salix* clones (G  $\times$  S interaction, Fig. 4 and Table 2). At the clonal level, there were significant changes in SR among clones from 11 for LEV-D5 to 16.6 cm mm<sup>-1</sup> for HAN-A5 (Table 2, A.2). Root-to-shoot mass ratios (RSR) significantly decreased by 44% with an increase in N level (Table 5). At the clonal level, there were significant changes in RSR among clones from 0.07 g g<sup>-1</sup> for NM06 to 0.21 g g<sup>-1</sup> for LEV-D5 (Table 2, A.2).

### 3.3. Biomass productivity and allocation

The increase in N level significantly increased leafless above-ground biomass per tree (AGBT) by 53% and leafless above-ground biomass per m<sup>2</sup> (AGBM) by 50% after the growing period (Tables 5 and 6). Spacing had no significant effect on AGBT, but a significant increase in AGBM for both *Populus* and *Salix* was observed with the decrease in spacing (Table 6, Fig. 5). At the clonal level, there were significant differences in AGBT among clones from 7 g for LEV-D5 to 21.9 g for SHE-E9 (Table 6, A.2).

*Populus* had a greater proportion (%) of leaf biomass (PLB) than *Salix* (Table 6, A.2). However, PLB significantly varied among clones depending on changes in spacing (C  $\times$  S interaction, Table 6, A.3). Generally, PLB for most clones increased with an increase in spacing (Table A.3). The proportion (%) of stem biomass (PSB) significantly increased with an increase in N by 14% (Tables 5 and 6). At the genus level, PSB was greater for *Salix* compared to *Populus* (Table 6, A.2). At the clonal level, PSB significantly varied among clones from 33.2% for 747210 to 50.9% for HAN-A5 (Table 6, A.2). Although there

**Table 2**

Analysis of variance giving sources of variation, degrees of freedom (DF), *F* values, and associated probabilities for morphological characteristics of leaf area (LA), leaf area ratio (LAR), slenderness ratio (SR), and root-to-shoot mass ratios (RSR).

Source of variation	DF	LA		LAR		SR		RSR	
		<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value
G	1	3.2	0.073	58.7	<b>&lt;0.001</b>	20.6	<b>&lt;0.001</b>	0.0	0.884
N	1	65.8	<b>&lt;0.001</b>	6.9	<b>0.009</b>	10.8	<b>0.001</b>	33.3	<b>&lt;0.001</b>
S	2	33.8	<b>&lt;0.001</b>	0.5	0.589	3.7	0.020	0.5	0.626
G × N	1	0.0	0.877	0.9	0.337	0.0	0.968	0.2	0.632
G × S	2	2.1	0.128	1.3	0.278	3.1	<b>0.040</b>	1.6	0.203
N × S	2	4.3	0.010	0.1	0.869	0.6	0.560	0.0	0.959
G × N × S	2	1.7	0.186	0.4	0.666	0.7	0.523	0.4	0.645
C	11	5.0	<b>&lt;0.001</b>	6.7	<b>&lt;0.001</b>	4.7	<b>&lt;0.001</b>	6.1	<b>&lt;0.001</b>
C × N	11	2.2	<b>0.016</b>	0.9	0.584	0.7	0.755	1.8	0.056
C × S	22	1.0	0.426	1.3	0.165	0.6	0.922	0.9	0.649
C × N × S	22	1.4	0.140	1.2	0.234	0.7	0.844	0.6	0.941

In source of variation, G: genus (*Populus* vs *Salix*), N: nitrogen, S: spacing, and C: clone. Significant *P* values are indicated in bold.

**Table 3**

Mean leaf area (cm<sup>2</sup>) for seven hybrid poplar and five willow clones under two nitrogen levels (20 and 200 mg kg<sup>-1</sup>) and all three spacings (20, 35, and 60 cm) after a growing period of 13 weeks.

Clone	Leaf area (cm <sup>2</sup> )	
	20 mg kg <sup>-1</sup>	200 mg kg <sup>-1</sup>
<i>Populus</i>		
1081	3834 ± 785 <sup>a</sup>	3830 ± 507 <sup>a</sup>
2782	3152 ± 443 <sup>a</sup>	4082 ± 538 <sup>a</sup>
747210	1760 ± 296 <sup>a</sup>	3132 ± 401 <sup>b</sup>
915319	1464 ± 257 <sup>a</sup>	3271 ± 382 <sup>b</sup>
DN-74	2758 ± 532 <sup>a</sup>	4900 ± 556 <sup>b</sup>
NM06	3842 ± 608 <sup>a</sup>	4451 ± 357 <sup>a</sup>
Walker	1319 ± 233 <sup>a</sup>	3709 ± 469 <sup>b</sup>
<i>Salix</i>		
HAN-A5	3215 ± 631 <sup>a</sup>	4056 ± 709 <sup>b</sup>
LEV-D5	664 ± 57 <sup>a</sup>	1795 ± 213 <sup>b</sup>
SHE-E9	3429 ± 400 <sup>a</sup>	3744 ± 423 <sup>a</sup>
LAF-I4	596 ± 71 <sup>a</sup>	1901 ± 223 <sup>b</sup>
TCH-N4	2242 ± 396 <sup>a</sup>	3335 ± 442 <sup>a</sup>

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

All values are presented with  $\pm$  standard errors.

were no significant changes in the proportion of root biomass (%) (PRB) between *Populus* and *Salix*, PRB for individual clones varied under an increase in N level (C × N interaction, Table 6, A.3). The increase in N level generally decreased PRB for all clones (A.3).

### 3.4. Morphological characteristics of superior clones

This study showed great genotypic differences in morphology and growth among clones. Characteristics of more productive or superior clones 2782, NM06, HAN-A5, SHE-E9, and TCH-N4 showed 153%, 263%, 136%, 102%, and 12% greater AGBT, AGBT under low N, AGBM, LA, and LAR, respectively and 27% lower RSR compared to less productive or inferior clones 747210, 915319, LEV-D5, and LAF-I4 (Table 7). Superior and inferior clones showed significant relationships between AGBT and LA ( $P < 0.05$ ) and superior clones showed significantly greater AGBT per unit increase in LA compared to inferior clones (Fig. 6).

## 4. Discussion

For the selection process, it is desirable to identify clones that can grow well under intensive plant competition and low N level so that these clones can maximize biomass production per unit area with reduced fertilization cost. In this study, spacing did not

**Table 4**

Linear regression analysis between leaf area and RCD (root collar diameter), height, and CW (crown width) for all clones under three spacings (20, 35, and 60 cm) and two nitrogen levels (20 and 200 mg kg<sup>-1</sup>).

Treatment	Intercept	Slope	R <sup>2</sup>	<i>F</i>	<i>P</i>
<b>RCD</b>					
20 cm-20 mg kg <sup>-1</sup>	4.9	0.001 <sup>b</sup>	0.42	100.3	<b>&lt;0.001</b>
20 cm-200 mg kg <sup>-1</sup>	5.9	0.001 <sup>b</sup>	0.34	68.6	<b>&lt;0.001</b>
35 cm-20 mg kg <sup>-1</sup>	5.4	<0.001 <sup>b</sup>	0.44	103.1	<b>&lt;0.001</b>
35 cm-200 mg kg <sup>-1</sup>	6.7	<0.001 <sup>b</sup>	0.29	53.8	<b>&lt;0.001</b>
60 cm-20 mg kg <sup>-1</sup>	5.1	<0.001 <sup>b</sup>	0.45	29.0	<b>&lt;0.001</b>
60 cm-200 mg kg <sup>-1</sup>	7.6	<0.001 <sup>a</sup>	0.20	9.2	<b>0.005</b>
<b>Height</b>					
20 cm-20 mg kg <sup>-1</sup>	59.6	0.015 <sup>c</sup>	0.56	180.0	<b>&lt;0.001</b>
20 cm-200 mg kg <sup>-1</sup>	78.0	0.015 <sup>c</sup>	0.38	79.3	<b>&lt;0.001</b>
35 cm-20 mg kg <sup>-1</sup>	63.4	0.011 <sup>b</sup>	0.60	192.8	<b>&lt;0.001</b>
35 cm-200 mg kg <sup>-1</sup>	84.4	0.011 <sup>b</sup>	0.36	73.4	<b>&lt;0.001</b>
60 cm-20 mg kg <sup>-1</sup>	61.0	0.012 <sup>bc</sup>	0.59	49.0	<b>&lt;0.001</b>
60 cm-200 mg kg <sup>-1</sup>	90.2	0.007 <sup>a</sup>	0.45	26.6	<b>&lt;0.001</b>
<b>CW</b>					
20 cm-20 mg kg <sup>-1</sup>	23.2	0.002 <sup>a</sup>	0.33	68.7	<b>&lt;0.001</b>
20 cm-200 mg kg <sup>-1</sup>	30.0	0.002 <sup>a</sup>	0.11	17.1	<b>&lt;0.001</b>
35 cm-20 mg kg <sup>-1</sup>	28.7	0.003 <sup>a</sup>	0.21	36.2	<b>&lt;0.001</b>
35 cm-200 mg kg <sup>-1</sup>	30.8	0.003 <sup>a</sup>	0.11	15.8	<b>&lt;0.001</b>
60 cm-20 mg kg <sup>-1</sup>	25.1	0.005 <sup>a</sup>	0.29	14.8	<b>0.001</b>
60 cm-200 mg kg <sup>-1</sup>	32.2	0.004 <sup>a</sup>	0.24	11.1	<b>0.002</b>

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

Significant *P* values are indicated in bold.

significantly affect above-ground biomass per tree (AGBT) for any clones (Table 6), indicating that all clones acclimated well to the closer spacing for the time period of the study. Therefore, above-ground biomass accumulated per m<sup>2</sup> was maximized with the

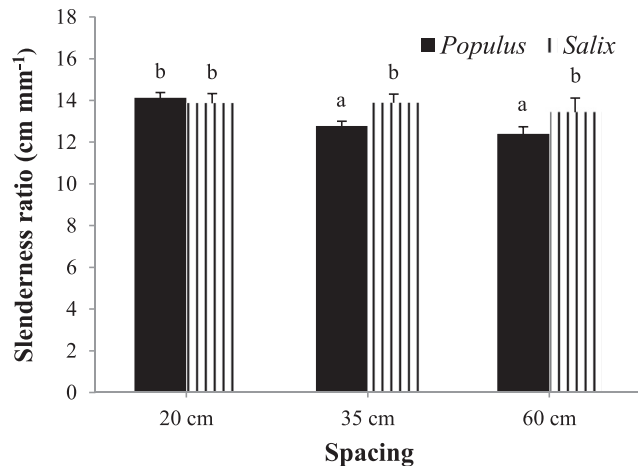
**Table 5**

The effects of N level on mean leaf area ratio (LAR), slenderness ratio (SR), root-to-shoot mass ratios (RSR), leafless above-ground biomass per tree (AGBT), leafless above-ground biomass per m<sup>2</sup> (AGBM), proportion (%) of stem biomass (PSB), and proportion (%) of root biomass (PRB) after a growing period of 13 weeks.

Growth trait	Nitrogen level	
	20 mg kg <sup>-1</sup>	200 mg kg <sup>-1</sup>
LAR (cm <sup>2</sup> g <sup>-1</sup> )	112.2 ± 5.6 <sup>a</sup>	116.6 ± 2.5 <sup>b</sup>
SR (cm mm <sup>-1</sup> )	12.9 ± 0.2 <sup>a</sup>	14.2 ± 0.2 <sup>b</sup>
RSR (g g <sup>-1</sup> )	0.16 ± 0.00 <sup>b</sup>	0.09 ± 0.00 <sup>a</sup>
AGBT (g)	10.8 ± 0.8 <sup>a</sup>	16.5 ± 0.8 <sup>b</sup>
AGBM (g m <sup>-2</sup> )	143.3 ± 12.1 <sup>a</sup>	215.5 ± 14.0 <sup>b</sup>
PSB (%)	41.2 ± 0.7 <sup>a</sup>	47.0 ± 0.6 <sup>b</sup>
PRB (%)	12.9 ± 0.5 <sup>b</sup>	8.4 ± 0.3 <sup>a</sup>

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

All values are presented with  $\pm$  standard errors.



**Fig. 4.** The effects of spacing on mean slenderness ratio for *Populus* and *Salix* after 13 growing weeks. Means followed by the same letter on the bar do not significantly differ at  $\alpha = 0.05$ .

decrease in spacing. This capacity of clones to maintain biomass production per tree under higher density was not explained by leaf area ratio (LAR) and root-to-shoot mass ratios (RSR) as we had hypothesized, but by height growth per unit increase in leaf area (LA) (Table 4), even though LA decreased by 50% from 60 to 20 cm spacing (Fig. 3). This indicates an efficient photosynthate allocation to shoot growth in the leader stem relative to diameter growth of the main stem. Under intensive competition, more resources are allocated to height of the leading shoot than to diameter growth [37], resulting in a significant increase in the slenderness ratio (SR) with the decrease in spacing (Table 2). This efficient increase in height in the highest density may have achieved great light interception in the upper crown [9,38], thereby leading to the increase in shoot growth and subsequently to the absence of significant changes in AGBT with decreased spacing (Table 6). Lack of response of height growth to changes in spacing has been reported [6]; however, variations in height under changes in spacing are not uncommon and depend on genotype, the range of tested spacing treatments, or the length of the growing period [7–9]. This study also showed clonal differences in height response under changes in spacing and N level, which may have been caused by differences in nitrogen-uptake capacity related to root morphology [39] or production capacity of leaf area [40,41].

Compared to 60 cm spacing and low N, trees growing in 20 cm spacing and high N level showed similar root collar diameter (RCD),

**Table 7**

Differences in mean leafless aboveground biomass per tree (AGBT), AGBT under low N (Low N AGBT), on leafless above-ground biomass per m<sup>2</sup> (AGBM), leaf area (LA), leaf area ratio (LAR), slenderness ratio (SR), and root-to-shoot mass ratios (RSR) between superior clones 2782, NM06, HAN-A5, SHE-E9, and TCH-N4 as a group and inferior clones 747210, 915319, LEV-D5, and LAF-I4 as a group after a growing period of 13 weeks.

Variable	Superior clones	Inferior clones
AGBT (g)	19.7 ± 1.1 <sup>b</sup>	7.8 ± 0.5 <sup>a</sup>
Low N AGBT (g)	17.4 ± 1.5 <sup>b</sup>	4.8 ± 0.5 <sup>a</sup>
AGBM (g m <sup>-2</sup> )	259.0 ± 18.2 <sup>b</sup>	110.0 ± 9.0 <sup>a</sup>
LA (cm <sup>2</sup> )	3643 ± 174 <sup>b</sup>	1800 ± 111 <sup>a</sup>
LAR (cm <sup>2</sup> g <sup>-1</sup> )	110.8 ± 6.4 <sup>b</sup>	98.9 ± 2.6 <sup>a</sup>
SR (cm mm <sup>-1</sup> )	14.8 ± 0.3 <sup>a</sup>	12.9 ± 0.3 <sup>a</sup>
RSR (g g <sup>-1</sup> )	0.11 ± 0.00 <sup>a</sup>	0.15 ± 0.01 <sup>b</sup>

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

All values are presented with ± standard errors.

crown width (CW), and LA values and even greater height for all clones (Fig. 3 and Table A.1), indicating that the negative impact of competition was reduced by increased N fertilization. Since leafloss rarely occurred during the short growing period of this study, the smaller increase in LA with the increase in N level in the closer spacing may have been due to limited length of sylleptic branch development corresponding to reduced available growing space [9]. Sylleptic branch development may have played an important role in explaining clonal differences in LA development with an increase in N as longer sylleptic branches directly allow clones to have more leaf area per branch [11,41–43]. For example, long branches of clone MB915 (*P. maximowiczii* × *P. balsamifera*) had greater LA and biomass production compared to short branches of clone BT747 (*P. balsamifera* × *P. trichocarpa*) [9]. On the other hand, the increase in N level caused similar increases in AGBT under all spacings (non significant N × S interaction; Table 6). Since the increase in height per unit increase in LA was greater in the 20 cm spacing and high N level compared to the 60 cm spacing and high N (Table 4), greater stem-growth efficiency in the 20 cm spacing and high N may have resulted in an efficient increase in AGBT despite greater limited resource availability between trees.

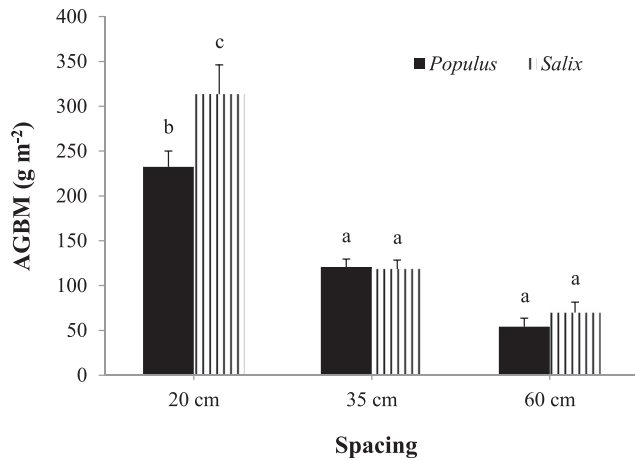
Nitrogen fertilization also increased LAR (Table 5), showing that resource allocation to leaf area production was prioritized with an increase in N level [41]. The increase in N level also increased the proportion of stem biomass and reduced the proportion of root biomass, resulting in lower RSR (Table 5). Previous studies also reported lower RSR as availability of N increases [16,18,44]. The lower RSR with an increase in N level may be explained by several

**Table 6**

Analysis of variance giving sources of variation, degrees of freedom (DF), *F* values, and associated probabilities for leafless above-ground biomass per tree (AGBT), leafless above-ground biomass per m<sup>2</sup> (AGBM), proportion (%) of leaf biomass (PLB), proportion (%) of stem biomass (PSB), and proportion (%) of root biomass (PRB).

Source of variation	DF	AGBT		AGBM		PLB		PSB		PRB	
		<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value
G	1	2.4	0.122	2.9	0.091	27.3	<b>&lt;0.001</b>	39.4	<b>&lt;0.001</b>	1.5	0.217
N	1	38.2	<b>&lt;0.001</b>	8.6	<b>0.040</b>	0.4	0.524	24.1	<b>&lt;0.001</b>	37.9	<b>&lt;0.001</b>
S	2	2.7	0.069	41.8	<b>&lt;0.001</b>	3.3	<b>0.030</b>	2.2	0.108	0.5	0.622
G × N	1	0.7	0.418	0.0	0.948	0.2	0.623	0.1	0.730	0.1	0.816
G × S	2	0.6	0.557	3.1	0.050	0.1	0.895	1.2	0.312	1.2	0.293
N × S	2	1.5	0.234	1.3	0.285	0.3	0.713	1.0	0.383	0.3	0.726
G × N × S	2	0.1	0.907	0.2	0.850	0.3	0.782	0.1	0.895	0.6	0.545
C	11	3.5	<b>&lt;0.001</b>	2.0	0.092	9.5	<b>&lt;0.001</b>	10.6	<b>&lt;0.001</b>	7.2	<b>&lt;0.001</b>
C × N	11	1.0	0.440	0.3	0.871	1.5	0.113	1.4	0.163	2.0	<b>0.030</b>
C × S	22	0.4	0.994	0.7	0.672	1.7	<b>0.030</b>	1.2	0.229	1.1	0.374
C × N × S	22	0.6	0.943	0.1	0.997	1.2	0.206	1.2	0.211	0.5	0.956

In source of variation, G: genus (*Populus* vs *Salix*), N: nitrogen, S: spacing, and C: clone. Significant *P* values are indicated in bold.

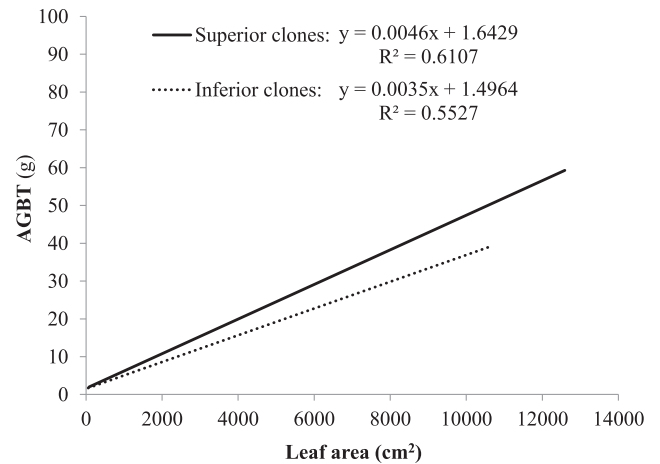


**Fig. 5.** The effect of spacing on mean leafless above-ground biomass per m<sup>2</sup> (AGBM, g) for *Populus* and *Salix* after 13 growing weeks. Means followed by the same letter on the bar do not significantly differ at  $\alpha = 0.05$ .

factors: First, as biomass allocation is prioritized based on the acquisition of limiting resources [45], greater RSR under low N level may be due to increased requirement for further soil N uptake [46]. Second, as this study used very close spacings of 20–60 cm, the increase in N possibly intensified root competition, which limited root development between trees as *Populus* and *Salix* species are known to be very sensitive to root competition [47–49]. Third, a weekly N application probably did not require trees to produce further root development for N uptake as contact area for N fertilization was limited around trees by the irrigation system.

Genotypic differences resulted in large variation in biomass productivity. Growth of the one clone (the hybrid aspen, clone 2782) which originated from rooted plants rather than unrooted cuttings may have confounding effects of material origin, but in any case, they are restricted to this particular clone. Compared to the inferior clones 747210, 915319, LEV-D5, and LAF-I4, superior clones 2782, NM06, SHE-E9, HAN-A5, and TCH-N4 showed 153%, 263%, and 136% greater AGBT, AGBT with low N level, and leafless above-ground biomass per m<sup>2</sup> (AGBM), respectively (Table 7). These superior clones also had greater productivity under all treatments compared to inferior clones. The greater productivity of superior clones in this study can be primarily explained by 102% greater LA, which was significantly related to biomass productivity (Fig. 6 and Table 7). Indeed, LA is an important determinant for plant growth under competition as the relationship between LA and plant growth is widely recognized because the production of forest stands has been strongly associated with total amount of intercepted irradiance [50]. Despite no significant difference in SR between superior and inferior clones, 27% lower RSR, 12% greater LAR, and greater AGBT per unit increase in LA of superior clones led to greater shoot production capacity of superior clones (Fig. 6 and Table 7).

The differences in crown morphology between *Populus* and *Salix* may explain their different growth patterns; the *Populus* clones such as DN-74, NM06, and Walker showed a long, narrow crown, greater RCD and height per unit increase in LA compared to other clones (Table A.4). *Populus* clones allocated resources to a few dominant stems that enabled trees to achieve rapid shoot growth and also to distribute to the weaker sink of diameter growth [51], resulting in greater RCD relative growth rate (RGR) and height RGR compared to *Salix* clones (Fig. 2). The advantage of using these clones under SRF management is an efficient vertical shoot growth with a small CW under limited space that can delay crown



**Fig. 6.** Relationship between leafless aboveground biomass per tree (AGBT) and leaf area for superior clones 2782, NM06, HAN-A5, SHE-E9, and TCH-N4 as a group and inferior clones 747210, 915319, LEV-D5, and LAF-I4 as a group after 13 growing weeks.

occupancy and consequently leaf senescence [13]. *Salix* clones such as HAN-A5 and TCH-N4 had greater number of stems per plant (>3) (data not shown) compared to *Populus* clones with mostly a single stem, resulting in the relatively greater CW per unit increase in LA (Table A.4). The slower initial RCD RGR for *Salix* compared to *Populus* was thus probably influenced by a greater number of stems per tree for *Salix* (Fig. 2a,b). Multiple-stem growth for the *Salix* reduced biomass allocation to each stem per tree, which increased a demand for the growth of leading shoots at the expense of diameter growth [51]. Thus, *Salix* clones had significantly greater SR and PSB than *Populus* clones (Table A.2). After 11 weeks of growth, *Salix* rapidly increased RCD RGR (Fig. 2a,b), as *Salix* leaves mature more slowly and show longer leaf retention [51].

*Salix* clones LEV-D5 and LAF-I4 demonstrated the greatest height per unit increase in LA (Table A.4), but also showed the lowest height and LA of all clones (Tables A.1, A.2). This may be explained by physiological changes in foliage after aphid attack that frequently occurred during the growing period; Aphids generally cause leaf senescence and abscission, but they have also been found to enrich leaf nitrogen on the remaining leaves because of introduced metabolic compounds into host plants [52,53]. We also noticed that mean leaf N concentration of LEV-D5 and LAF-I4 was the highest (1.2 g m<sup>-2</sup> and 1.3 g m<sup>-2</sup>, respectively) of all clones (data not shown). As a result, since leaf N content is mostly allocated to photosynthetic apparatus [54], they had higher net photosynthesis per unit leaf area at a given irradiance (data not shown). This compensatory photosynthesis after aphid feeding has been also reported by previous studies [53,55]. Therefore, the greatest height per unit increase in LA for clones LEV-D5 and LAF-I4 may not be owing to inherent growth capacity under competitive stress but likely higher photosynthetic capacity influenced by aphid attack.

## 5. Conclusion

All clones produced greater AGBM with the decrease in spacing. Trees growing in the high N level and 20 cm spacing showed similar RCD, CW, and LA values and even greater height than trees growing in low N and 60 cm spacing, indicating that an addition of N could play an important role in increasing plant growth under intensive competition. The greater biomass productivity of superior clones was mainly explained by 102% greater LA, 27% lower RSR, 12% greater LAR, and greater AGBT per unit increase in LA. Finally, even though a three month study period is relatively short, this study



showed significant clonal differences in morphological characteristics of trees under intensive competition (LA, LAR, RSR, AGBT per unit increase in LA), illustrating the possibility for early clonal selection.

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### Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.biombioe.2015.06.003>.

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