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Effects of mixing clones on hybrid poplar productivity, photosynthesis and root development in northeastern Canadian plantations

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ABSTRACT

Mixing tree cultivars or species in forest plantations can be efficient to reduce the risk of pest damages and could have a positive effect on yields if complementarity or facilitation between trees occurs. Four hybrid poplar clones (747215, *Populus trichocarpa* Torrey & A.Gray × *P. balsamifera* L.; 915004 and 915005, *P. balsamifera* × *P. maximowiczii* Henry; and 915319 *P. maximowiczii* × *P. balsamifera*) were planted in monoclonal and polyclonal plantations in three sites located in Quebec, Canada, to assess effects of clonal diversity on (i) aboveground biomass productivity, (ii) net photosynthesis and nutrient status of trees, and (iii) root spatial distribution. Stem growth was measured over five growing seasons, while root development, foliar nutrient concentrations and photosynthesis were measured during the fifth growing season. Results showed frequent but not general overyielding of trees in the polyclonal plots compared to monoclonal plots, five years after plantation establishment. Overall, stem volumes were 21% higher in the polyclonal (7.4 m^3 ha^{-1}) *vs.* monoclonal (6.1 m^3 ha^{-1}) plots. Effects of clone mixing on growth were greater in sites where soil nutrients were more limiting. However, foliar macronutrient concentrations (N, P, K, Ca and Mg) in trees growing in polyclonal plots were similar to those in monoclonal plots. Root development differed between the two plot layouts, with mean root:shoot ratio being greater in monoclonal (0.41:1) *vs.* the polyclonal (0.35:1) plots. Mixing clones increased biomass allocation aboveground, which we attributed to reduced competition between individuals of different clones and could explain overyielding in the polyclonal plots. The root fraction most distant from the stem ($\geqslant$60 cm) was greater in monoclonal (67% of total root biomass) compared to polyclonal (47% of total root biomass) plots, suggesting greater belowground competition in the former, which forced roots to extend further from the stems. Effects of plot layout on net assimilation rate (P_n) depended on site, with trees in polyclonal plots having greater P_n in two of the three sites. Root total non-structural carbohydrates were greater in the polyclonal (216 mg g^{-1}) compared to the monoclonal (159 mg g^{-1}) plots. Mixing hybrid poplar clones often resulted in greater aboveground growth, lower root:shoot ratios, and different spatial root distributions, when compared to clones planted in monocultures.

1. Introduction

Much research has been conducted over the past twenty years to evaluate effects of diversity on ecosystem functioning, and has demonstrated that biomass production increases with increasing diversity (Loreau et al., 2001). The mechanisms underlying the positive effects of diversity on productivity have been classified into (i) complementarity and facilitation interactions between species, based on niche partitioning theory or the benefit that one species can receive from another, and (ii) sampling effects, which stipulate that within a group of species, one or more would dominate and increase overall ecosystem yield (Loreau et al., 2001). Most earlier trials tested this relationship on grass and shrub species, but many studies have now attempted to demonstrate the universality of this principle and are trying to elucidate the mechanisms that might explain diversity-productivity relationships (Menalled et al., 1998; Petit and Montagnini, 2006; Horner-Devine et al., 2003). Results from forest ecosystems would appear to confirm previous findings and overall, a positive effect of tree diversity on biomass production in both natural stands and plantations has been found (Tilman, 1999; Balvanera and Aguirre, 2006; Potvin and Gotelli, 2008; Lei et al., 2009; Paquette and Messier, 2011).

Intensively managed forest plantations are used to produce large quantities of wood on limited land areas. In 2010, the total area of planted forests was only 7% of natural forest areas worldwide, while their contribution was about 40% of global fiber needs (FAO, 2010).

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Plantations, however, are often managed as monocultures and have been described by some as "biodiversity deserts" (Evans and Turnbull, 2004; Brockerhoff et al., 2008). Forest plantation monocultures are more common than mixtures of species or clones because they are easier to manage, nutrient requirements are easier to assess, harvesting operations can be uniform, and the timber that is logged has similar characteristics (Kelty, 2006). In contrast, exhaustion of soil nutrients, the deterioration of soil physical and chemical properties, and increased vulnerability of crops to pest and pathogen attacks are often associated with monocultures (Bonduelle, 1983; McCracken and Dawson, 1997). When compared to natural forest stands, tree monocultures decrease biodiversity across the landscape and affect a wide spectrum of other plant and animal species, ranging from soil microorganisms to macrofauna (Stephan et al., 2000; Harvey et al., 2006; Eisenhauer et al., 2010). Mixtures of cultivars were originally used in afforestation and intensively managed plantations as biocontrol strategies against the attacks of pests and pathogens that frequently target certain genotypes (Miot et al., 1999; Jactel and Brockerhoff, 2007). Reducing pest damages was based on "Widespread Intimately Mixed Plantations" (WIMPs) approach where genotypes are randomly intermixed and in a lesser extent on "Mosaics of monoclonal stands (MOMS)" where stands of different genotypes are mixed (Libby, 1987; Lindgren, 1993). Current studies have shown that mixing cultivars may also positively affect biotic and abiotic environments through optimal use of nutrients according to niche differentiation theory (Diaz and Cabido, 2001; Schmid, 2002; Erskine et al., 2006) and, in this way, they can enhance specific and functional biodiversity relative to monospecific plantations. Other experiments that have been carried out in plantations have shown an effect on productivity that is sometimes positive (i.e., overyielding) and sometimes neutral (Benbrahim et al., 2000; Berthelot, 2001; Joshi et al., 2001; Potvin and Gotelli, 2008).

In 2006, plantations with more than one genotype represented less than 0.1% of the total area of industrial plantations worldwide (Nichols et al., 2006). It is expected that this area will increase in the future if benefits of mixing cultivars on productivity can be clearly demonstrated (Paquette and Messier, 2011). Overyielding in mixtures of cultivars could be related to a facilitative interaction, for example, the facilitation of N uptake by interplanting N_2-fixing species (genera such as *Alnus* or *Acacia*). Complementarity, on the other hand, is related to the stratification of aboveground (for light) or belowground (for water and nutrients) niches (Hooper and Dukes, 2004; Potvin and Dutilleul, 2009). Complementarity can also occur if the timing of nutrient uptake or the phenology of two companion species is different (Garber and Maguire, 2004; Oelmann et al., 2010) or if distinct nutrient species are used by trees (e.g., nitrate *vs*. ammonium nitrogen; Persson et al., 2006). Consequently, competition for resources is minimized between species or cultivars, overall photosynthetic activity is greater and more biomass can be allocated to aboveground structures (Montagnini, 2000; Zeugin et al., 2010). When individuals share the same niche, resources become less available and root systems become denser and more extensive (Forrester et al., 2006). However, tree root systems are much less studied compared to aboveground structures, although they should provide important insights into belowground interactions between individuals in mixed stands (Fargione et al., 2007). Root development has a fundamental influence on tree productivity and is closely linked to nutrient assimilation and photosynthetic activity (Kalliokoski et al., 2008; Ouimet et al., 2008). This study examined the diversity–productivity relationship of intensively managed tree plantations, to determine whether a mixture of hybrid poplar (*Populus* spp.) clones would increase the overall productivity of plantations relative to monocultures. The effects of clonal diversity on (i) aboveground biomass production in hybrid poplar plantations, (ii) net photosynthesis and nutrient status of trees, and (iii) spatial separation of niches at the root level were evaluated. We hypothesized that mixing clones would reduce biomass allocation to roots and change root distribution, increase nutrient uptake and net assimilation, and improve the overall growth of trees.

2. Materials and methods

2.1. Site description and plant material

The study sites were located in the Abitibi-Témiscamingue region of northwestern Québec, Canada, under a humid continental climate. Replicate plantations were established on three different sites. The first site was abandoned farmland located in the municipality of Duhamel (47°19′N, 79°25′W) in the sugar maple (*Acer saccharum* Marshall)-yellow birch (*Betula alleghaniensis* Britton) western bioclimatic sub-domain (Grondin, 1996). The site had been previously cultivated for hay. The soil at Duhamel was a clayey Luvisol (45% clay; Agriculture and Agri-food Canada, 2012) with mean annual precipitations and temperature of 820 mm and 2.8 °C, respectively (Environment Canada, 2013). The second site was previously forested before being harvested in 2004 (48°29′N, 97°26′W). It was located near the municipality of Duparquet in the balsam fir (*Abies balsamea* L.)-paper birch (*Betula papyrifera* Marshall) bioclimatic western sub-domain (Grondin, 1996) with mean annual precipitations and temperature of 918 mm and 1.2 °C, respectively. The soil at this site was classified as heavy clay Brunisol (70% clay; Agriculture and Agri-food Canada 2012). The third site was located in the municipality of Villebois and had been previously farmed organically for cereals and hay. This site (49°09′N, 79°10′W) was in the black spruce (*Picea mariana* (Mill.) BSP)-feather moss (*Pleurozium* spp.) domain (Grondin, 1996) and the soil type was clay Grey Luvisol (50% clay). Mean annual precipitations and temperature at this site are 890 mm and 1.2 °C, respectively (Environment Canada, 2013).

Four hybrid poplar clones that had been recommended for the region by the Ministère des Ressources Naturelles et de la Faune du Québec (MRNFQ) were selected for planting: clone 747215 (*Populus trichocarpa* Torrey & A. Gray × *balsamifera* L.), clones 915004 and 915005 (*P. balsamifera* × *maximowiczii* Henry), and clone 915319 (*P. maximowiczii* × *balsamifera*). Prior to plantation establishment, stumps and woody debris at the Duparquet site were removed with a bulldozer. This site was then ploughed to a depth of 30 cm in autumn 2004 with a forestry plough pulled by a skidder and disked in spring 2005 to level the soil before planting. Duhamel and Villebois sites were ploughed using an agricultural cultivator in autumn 2004. Trees were planted in June 2005 at 4×3 m spacing, corresponding to a density of about 833 trees/ha. Stock type was bare-root dormant trees and the average tree height at planting was 96.3 cm. Following planting, weeds were mechanically removed twice a year by cultivating between rows with a farm tractor and by tilling between trees with a Weed Badger (model 4020-SST, Marion, ND, USA).

The experimental design was comprised of three monoclonal and three polyclonal replicates (blocks) of the four hybrid poplar clones at each site. A monoclonal plot consisted of five rows of five trees of one clone, while a polyclonal plot consisted of a mixture of eight rows of eight trees where the position of the four clones was randomly assigned ($N = 1476$).

2.2. Growth

Height and basal diameter of all trees were measured at planting (spring 2005) and at the end of each growing season until autumn 2009. Stem volume was estimated with the equation:

$$V = A_b \cdot H/3$$

where V is stem volume (m^3), A_b is basal area (mm) and H is height (cm) (Brown and van den Driessche, 2002).

2.3. Specific leaf area (SLA) and chemical analyses

In May 2007, five soil samples were collected at Duhamel, and 10 at Duparquet and Villebois (more heterogeneous) for chemical and physical characterization (Table 1). Soil samples were collected diagonally along plots (periphery and centre of the two diagonals). Two sub-samples from the 0–20 cm and 20–40 cm horizons were collected separately for each sample. Soils were subsequently dried in an oven at 50 °C, ground, sieved to pass a 60 μm mesh, and then pooled for analysis. Total carbon concentrations in the soil were determined by high temperature combustion with a LECO N-analyzer (Leco Corp., St. Joseph, MI, USA). Soil concentrations of available cations (Ca^{2+}, K^+, Mg^{2+} and Na^+) and cation exchange capacity (CEC, $cmol_c\ kg^{-1}$) were determined after ammonium acetate extraction. Soil samples pH were obtained from a water-saturated paste. Leaf and soil nitrogen concentrations were quantified with the LECO N-analyzer. KCl (2 M) extraction was first performed on the soil, according to application bulletin CHNP2-84 (Leco Corp, 1986).

In mid-July 2009, leaf samples were collected at the three sites for measurement of specific leaf area (SLA) and for analyses of N, P, K, Ca and Mg concentrations. Nine recently matured leaves from three randomly selected trees of each clone were collected from the monoclonal and polyclonal plots; three leaves were selected from the upper-third, middle-third and lower-third of the crown. Leaf samples were immediately packed in dry ice and their area was measured with a leaf area meter (Li-3100C, Li-COR Biosciences, Lincoln, NE, USA) before oven-drying at 70 °C for 72 h and weighing. Specific leaf area (SLA) was calculated as the ratio of leaf area (cm^2) to leaf dry mass (g). Leaves were then ground in a Wiley mill to pass a 60 μm-mesh sieve and pooled to obtain a composite sample for the determination of nutrient concentrations. Soil and leaf concentrations of P, K, Ca and Mg were quantified by inductively-coupled plasma (ICP) spectroscopy following HNO_3–HCl digestion (Masson and Esvan, 1995).

2.4. Photosynthesis

Net photosynthesis (P_n) was measured on two trees within each replicate, for each clone and for each layout type (monoclonal and polyclonal) at the three sites with a CIRAS-2 portable photosynthesis system using an infra-red analyzer (PP Systems, Amesbury, MA, USA) for the period 13–17 July 2009 ($N = 144$). Measurements were made on recently matured and well exposed leaves that did not show any apparent sign of senescence. The CIRAS-2 system was coupled with a broadleaf cuvette (PLC6-U, 25 mm diameter), which was equipped with a LED unit for automatic light control. Air flow and CO_2 concentrations in the cuvette were maintained at 300 mL min^{-1} and 360 μmol mol^{-1}, respectively. Photosynthetically active radiation (PAR) was set at 1600 μmol m^{-2} s^{-1} and measurements were taken between 8h30 and 12h00. During measurements, air temperature ranged between 18 °C and 25 °C, while relative humidity was between 50% and 70%. The order of tree measurements was randomized to reduce the time effect on photosynthesis parameters between 8h30 and 12h00. To avoid edge effect, trees of a buffer row around each plot were not sampled for photosynthesis, SLA and nutrients measurements.

2.5. Destructive sampling

The root and shoot systems of two randomly chosen trees per replicate for each clone and layout type ($N = 24$) were selected for destructive sampling at the Duparquet site. Roots were excavated, either using an AIR-SPADE (Arbortools, Hong Kong) or hydraulically with a high pressure water pump (Mark III, Wajax, Lachine, QC, Canada). Small roots were dug out manually using pickaxes, shovels and trowels. Roots were grouped into three classes according to their distance (d) from the stem: (i) $d \leqslant 30$ cm; (ii) 30 cm $< d \leqslant 60$ cm; (iii) $d > 60$ cm. Maximum depth (D_{max}, cm) and maximum radial elongation (L_{max}, cm) of roots were also measured for each excavated tree. After roots were dried, the total length of coarse roots (diameter > 2 mm) and the mass of each root group were measured. Stems, branches and leaves of excavated trees were separated, dried (at 75 °C) and weighed to calculate biomass allocation to roots and shoots. At the beginning of each tree excavation, a root sample of about 1 cm in diameter and 10 cm in length was collected for total non-structural carbohydrates (TNC) determination. Samples were located 50–70 cm from the stem to homogenize sampling.

Root samples were transported on ice from the field before being frozen (−20 °C) prior to TNC analyses. Root samples were then oven-dried at 75 °C, ground and sieved in a Wiley mill through a 40 μm mesh. Starch and sugar concentrations were measured colorimetrically according to Chow and Landhäusser (2004).

Table 1
Soil chemical properties of the three sites measured in 2007.

Soil depth	Site					
	Duhamel		Duparquet		Villebois	
	0–20 (cm)	20–40 (cm)	0–20 (cm)	20–40 (cm)	0–20 (cm)	20–40 (cm)
pH	5.6	5.5	4.9	5.8	6.8	5.7
Extractable cations ($mg\ kg^{-1}$)						
Ca	1853	2212	4392	4968	4528	2056
K	116	130	266	265	159	131
Mg	372	482	668	797	342	347
Na	16	27	43	51	24	28
CEC ($cmol_c\ kg^{-1}$)	12.7	15.5	28.3	32.3	51	13.6
Moisture content	0.016	0.021	0.035	0.035	0.015	0.017
Total C ($g\ kg^{-1}$)	15.60	10.64	7.98	7.17	15.25	16.65
Total N ($g\ kg^{-1}$)	1.32	0.87	0.82	0.62	0.90	1.05
Total Ca ($g\ kg^{-1}$)	6.18	6.48	7.05	9.23	11.28	6.28
Total K ($g\ kg^{-1}$)	2.91	3.80	7.50	7.30	4.35	3.84
Total Mg ($g\ kg^{-1}$)	10.41	12.26	17.59	17.59	12.60	11.28
Total P ($g\ kg^{-1}$)	0.54	0.46	0.37	0.55	0.61	0.54

Note: CEC, cation exchange capacity.

Table 2
ANOVA summaries for tree volume (V, repeated measures factor = year), net photosynthesis (P_n), specific leaf area (SLA), nutrients concentrations (N, P, K, Ca and Mg) of four hybrid poplar clones in the three sites showing sources of variation F and P values. Statistically significant values are indicated in bold.

	V		Pn		SLA		N		P		K		Ca		Mg	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Source of variation																
Site (S)	146.1	**<0.01**	55.3	**<0.01**	5.9	0.05	10.8	**<0.01**	33.7	**<0.01**	15.3	**<0.01**	14.2	**<0.01**	2.6	0.08
Layout (L)	6.3	**0.01**	0.6	0.43	1.3	0.32	0.8	0.38	0.3	0.59	2.1	0.15	1.1	**<0.01**	0.1	0.76
Clone (C)	64.6	**<0.01**	3.2	**0.02**	5.9	**<0.01**	10.8	**<0.01**	19	**<0.01**	1.4	0.26	17.5	**<0.01**	36.9	**<0.01**
Year (Y)	1895.8	**<0.01**														
L ∗ C	8.8	**<0.01**	1.1	0.38	0.9	0.42	0.3	0.84	0.7	0.56	1.3	0.27	4.1	0.01	3.4	**0.02**
L ∗ S	16.6	**<0.01**	4.9	**0.01**	0.2	0.82	12.9	**<0.01**	20.2	**<0.01**	1.1	0.33	3.9	**0.02**	8.2	**<0.01**
L ∗ Y	8.8	**<0.01**														
L ∗ C ∗ Y	0.17	**0.99**														
L ∗ C ∗ S	3.19	**<0.01**	1.2	0.34	0.8	0.54	0.06	0.99	1.8	0.12	2.4	**0.03**	1.2	0.32	1.2	0.31
S ∗ L ∗ Y	1.54	0.15														
C ∗ S	3.5	**<0.01**	0.4	0.87	0.8	0.58	2.3	**0.04**	1.6	0.17	2.5	**0.03**	1.4	0.25	1.6	0.17
C ∗ Y	1.05	0.37														
S ∗ Y	18.05	**<0.01**														
S ∗ C ∗ Y	0.32	0.99														
S ∗ L ∗ C ∗ Y	0.26	0.99														

Soluble sugars were extracted from 50 mg of root tissue with hot ethanol (5 mL). Sugar extracts were reacted with phenol–sulphuric acid (Dubois method), and their absorbances were measured by UV spectrophotometry (at 490 nm). Starch residue left after soluble sugar extraction was hydrolyzed to glucose with a mixture of α-amylase and amyloglucosidase. Glucose in the hydrolysate was measured colorimetrically (at 525 nm) using peroxidase-glucose oxidase-o-dianisidine colour reagent.

2.6. Statistical analyses

Linear mixed-effect models (nmle) analyzed the relationships between response variables and explanatory variables (Version 2.11.1, R Development Core Team, Vienna, Austria). Tree volume was subjected to repeated measures analysis of variance with year as the repeated measure. Clone, layout (monoclonal *vs.* polyclonal), year and site were considered as fixed effects, while block (replicate) was considered as a random effect in all models. Net photosynthesis, specific leaf area and nutrient concentrations were analyzed using a model similar to that used for stem volume, without the repeated measures. To test the effects of clone, layout and site (fixed effects) on the root distribution variables and TNC concentrations, the data were subjected to three-way analysis of variance (ANOVA) after a tangent transformation (tan) to respect homoscedasticity assumption. Means were compared using Tukey's honest significant differences (HSD) for all possible comparisons and the significance level for all tests was set at $\alpha = 0.05$. Pearson product-moment correlations (r) were used to test relationships between root distribution traits and total non-structural carbohydrate concentrations, and stem volume.

3. Results

3.1. Stem volume

In 2009, differences in tree volume between the monoclonal and the polyclonal plots were significant but depended on clones and sites (Table 2). Five years after plantation establishment, stem volume of the four clones across the three sites ranged from 2.2 to 12.4 $m^3\ ha^{-1}$ in the monoclonal plots and from 3.6 to 14.5 $m^3\ ha^{-1}$ in the polyclonal plots (Fig. 1). Overyielding of stem volume in polyclonal plots compared to monoclonal plots ranged between 17% and 84% and was not significant for two of the four clones at Duhamel. At Duparquet and Villebois, stem volume in the polyclonal plots were greater than that in the monoclonal plots (especially for clone 747215), but not at Villebois for clone 915319, which was the best performing clone (Fig. 1). Difference in stem volume between monoclonal and polyclonal plots showed the same trends in 2008 as in 2009, while no significant difference in tree volumes was recorded between plot layouts during the first three growing seasons (2005–2007; Appendix).

3.2. Nutrient concentrations

Nitrogen and P concentrations were significantly greater in the polyclonal plots at Duparquet compared to monoclonal plots, but were similar at Duhamel and Villebois (Table 2 and 3). For the other macronutrients (Ca, K and Mg), leaf concentrations between monoclonal and polyclonal plots varied, depending upon site (Layout × Site, $P < 0.01$), but were often greater in the polyclonal

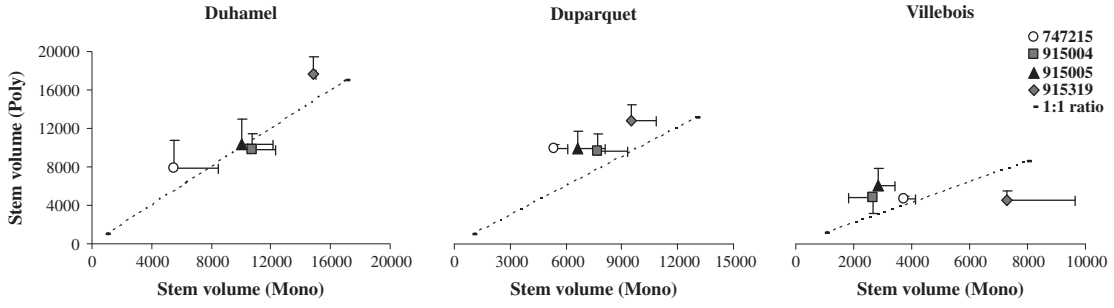

Fig. 1. Mean stem volume ($10^{-3}\ m^3\ tree^{-1}$) in the fifth growing season of four hybrid poplar clones in monoclonal (Mono) *vs.* polyclonal (Poly) plots at Duhamel, Duparquet and Villebois. Dotted line indicates equal stem volumes in polyclonal *vs.* monoclonal plots (1:1 ratio). Horizontal and vertical bars are standard errors (SE) for monoclonal and polyclonal plots, respectively.

plots (Table 2). Leaf Ca concentration was on average 11.2 mg g^{-1} *vs.* 9.2 mg g^{-1} in polyclonal plots compared to monoclonal plots ($P < 0.01$) (Table 3).

3.3. Specific leaf area and net photosynthesis

Specific leaf area (SLA) was similar between monoclonal and polyclonal plots, although it was different between clones and marginally different between sites ($P = 0.05$, Table 2). At Duhamel, average SLA of the monoclonal and polyclonal plots ranged between 79.4 cm^2 g^{-1} (clone 747215) and 89.4 cm^2 g^{-1} (clone 915004). At Duparquet and Villebois, average SLA ranged between 67.5 and 89.1 cm^2 g^{-1}, and between 74.7 and 90.8 cm^2 g^{-1}, respectively (Table 4A).

The effect of plot layout on net photosynthetic assimilation (P_n) depended upon site (Layout × Site, $P = 0.01$, Table 2). P_n was greater in the polyclonal plots for two clones (747215 and 915005) at Duhamel and was usually similar between monoclonal and polyclonal plots at Duparquet and Villebois (Table 4B). P_n ranged from 17.9 to 22.1 μmol CO_2 m^{-2} s^{-1} at Duhamel and from 15.1 to 17.1 μmol CO_2 m^{-2} s^{-1} at Duparquet (clone 915319 excluded, Table 4B).

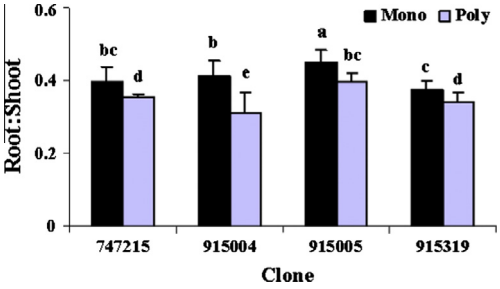

Fig. 2. Mean root:shoot ratios of four hybrid poplar clones in monoclonal (Mono) *vs.* polyclonal plots (Poly) at Duparquet in the fifth growing season. For the same trait, values followed by the same letters do not differ at $P < 0.05$.

3.4. Biomass allocation

Biomass measurements that were made at Duparquet in 2009 showed that root:shoot ratios of trees in the monoclonal plots were significantly greater than those of the polyclonal plots ($P = 0.03$, Fig. 2). Average shoot biomass of the four clones in the polyclonal plots was 4.55 kg DM $tree^{-1}$ while root biomass was 1.61 kg DM $tree^{-1}$, giving an average root:shoot ratio of 0.35 (Fig. 2). In the monoclonal plots, this ratio was 0.41, as mean root and shoot biomasses were respectively 1.57 and 3.85 kg DM $tree^{-1}$. Depending upon clone, total aboveground biomass represented 69–72% of the total tree biomass in the monoclonal plots and 72–76% in the polyclonal plots, respectively. The same pattern was observed for stem biomass, with mean values of 2.39 kg DM $tree^{-1}$ in polyclonal plots and 1.88 kg DM $tree^{-1}$ in monoclonal plots, which each represented 39% and 35% of total biomass (Fig. 2). Plot layout did not affect the proportion of leaves and branches, and average percentages of total tree biomass were 17% for leaves and 18% for branches (data not shown). The proportion of leaves and branches was different between clones and ranged from 14% (clone 915319) to 20% (clone 915004) for leaves while branches represented 17–21% of the total tree biomass.

3.5. Radial distribution of roots

Mean total coarse root length within the first 30 cm from the stem was similar in the monoclonal *vs.* polyclonal plots for all

Table 3
Leaf concentration ranges (mg g^{-1}) of macronutrients (N, P, K, Ca and Mg) of the four hybrid poplar clones in the monoclonal and polyclonal plots at the three sites, measured in the fifth growing season.

	Monoclonal	Polyclonal
Layout		
Duhamel		
N	21.2–25.4	20.6–25.2
P	1.9–2.5	1.7–2.4
Ca	7.9–11	8.2–12
K	9.3–11.1	9.7–11.1
Mg	2.0–2.8	2.0–2.8
Site		
Duparquet		
N	15.7–18.2	18.7–21.0
P	1.6–2.1	2.1–2.5
Ca	8.7–12.5	10.6–14.9
K	9.6–12.9	11.2–11.5
Mg	1.6–2.7	2.2–2.7
Villebois		
N	18.8–23.5	20.7–25.6
P	1.9–2.6	2.1–3.0
Ca	7.8–11.7	8.5–13.5
K	11.8–13.3	11.6–12.6
Mg	2.1–2.5	2.1–3.0

Table 4
(A) Mean specific leaf area (SLA, cm^2 g^{-1}) and (B) mean net photosynthesis (μmol CO_2 m^{-2} s^{-1}) of the four hybrid poplar clones in the monoclonal and polyclonal plots at the three sites measured in the fifth growing season.

	Site					
	Duhamel		Duparquet		Villebois	
Clone	Monoclonal	Polyclonal	Monoclonal	Polyclonal	Monoclonal	Polyclonal
(A)						
747215	61.98 ± 0.4^a	67.43 ± 10.94^a	81.52 ± 5.41^a	74.58 ± 2.55^b	89.23 ± 5.63^a	84.76 ± 5.2^b
915004	79.01 ± 7.85^b	65.78 ± 7.9^a	82.05 ± 2.56^a	56.34 ± 21.42^c	83.28 ± 4.29^b	78.28 ± 5^c
915005	77.67 ± 5.64^c	72.17 ± 5.32^c	79.3 ± 1.25^c	71.29 ± 4.08^b	83.4 ± 5.1^b	80.96 ± 2.29^c
915319	85.49 ± 1.78^d	99.06 ± 19.37^d	89.22 ± 3.02^d	98.54 ± 22.45^d	93.6 ± 4.74^d	87.05 ± 9.67^b
Mean	76.04 ± 9.57^c	76.11 ± 8.02^c	83.02 ± 5.60^a	75.19 ± 6.14^b	87.38 ± 7.28^b	82.76 ± 8.12^c
(B)						
747215	19.43 ± 1.16^a	22.07 ± 1.06^b	16.2 ± 0.42^a	17.15 ± 1.2^a	15.7 ± 0.6^a	16.67 ± 1.77^a
915004	20.2 ± 1.47^a	20.53 ± 1.37^a	15.15 ± 0.91^b	17.1 ± 0.98^c	17.8 ± 2.1^a	15.97 ± 1.03^a
915005	17.9 ± 2.49^c	21.67 ± 0.96^b	15.7 ± 0.56^b	16.6 ± 0.98^b	16.67 ± 1.04^a	15.73 ± 1.1^a
915319	21.03 ± 2.5^b	21.6 ± 1.87^b	18.4 ± 0.84^d	16.35 ± 0.21b^c	18 ± 1.25^b	17.43 ± 1.19^b
Mean	19.64 ± 1.58^a	21.47 ± 1.25^b	16.36 ± 1.1^c	16.8 ± 0.74^b	17.04 ± 1.08^a	16.45 ± 0.8^a

Note. Within the same site, values followed by same letters do not differ at $P < 0.05$.

Table 5
ANOVA summary showing sources of variation and *P*-values for fine and coarse root distribution of four hybrid poplar clones at Duparquet in the fifth growing season: proportion of total roots at 0–30 cm, 30–60 cm and > 60 cm from the stem, maximum horizontal extension of roots from the stem (L_{max}), maximum vertical depth of roots from the soil surface (D_{max}), total non-structural carbohydrates (TNC), starch and soluble sugars concentrations of roots (mg g^{-1} DM).

Source of variation	*P*-value										
	Coarse roots (%)			Fine roots (%)			L_{max}	D_{max}	TNC	Starch	Soluble sugars
	0–30	30–60	>60	0–30	30–60	>60					
Layout	0.49	**<0.01**	**0.02**	**<0.01**	0.33	**<0.01**	0.19	0.95	**0.02**	**<0.01**	0.80
Clone	0.40	0.56	0.35	**0.01**	0.06	**0.02**	0.16	0.86	0.19	**0.02**	0.40
Layout × clone	0.76	0.68	0.62	**<0.01**	0.27	**<0.01**	**0.02**	0.89	0.29	0.92	0.66

P-values inferior to 0.05 have been embolded showing that the effect of a factor was statistically significane on the corresponding variable. e.g. the effect of Layout on TNC: $P = 0.02$.

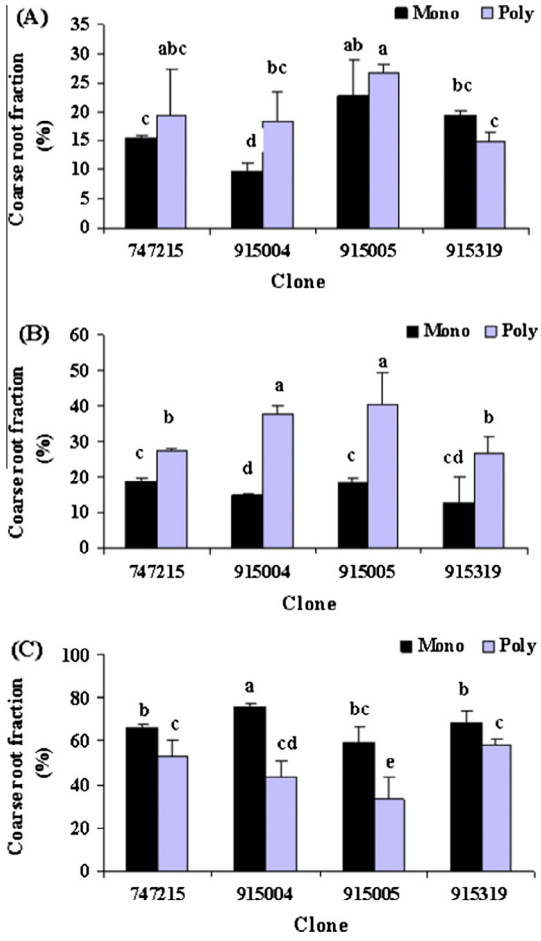

Fig. 3. Coarse root fraction relative to total root length (%) of four hybrid poplar clones in the monoclonal (Mono) *vs.* polyclonal (Poly) plots at 0–30 cm (A), 30–60 cm (B) and >60 cm (C) distances from the stem at Duparquet in the fifth growing season. For the same trait, values followed by the same letters do not differ at $P < 0.05$.

clones at Duparquet (Table 5). The root fraction relative to the total length of coarse roots contained in the 0–30 cm distanced class averaged 18% (range: 10–27%; Fig. 3A). The relative coarse root fraction within 30–60 cm from the stem was greater in the polyclonal compared to monoclonal plots (Fig. 3B, Table 5). In contrast, the fraction of roots that was located >60 cm from the stem was significantly greater ($P = 0.02$) in the monoclonal plots compared to the polyclonal plots (67% *vs.* 47%, respectively) (Fig. 3C). Mean fine root fraction within 30 cm from the stem, relative to total fine root dry matter, was greater in the polyclonal plots compared to monoclonal plots ($P < 0.01$); this proportion ranged between 10% and 60% respectively (Fig. 4A). Fine root fractions within 30–60 cm from the stem were similar in the two types of plot layout (Table 5), averaging 20% of the total.

The >60 cm fraction of fine roots for clones 915004, 915005 and 915319 was significantly greater in monoclonal plots and, for clone 747215, was not affected by layout (Table 5). Relative fine root fraction at this distance ranged between 61% and 763% in the monoclonal plots, and between 55% and 64% in the polyclonal plots, respectively (Fig. 4C). Maximum radial root elongation (L_{max}) was greater in the monoclonal plots compared to the polyclonal plots, except for clone 915005 (clone × layout interaction,

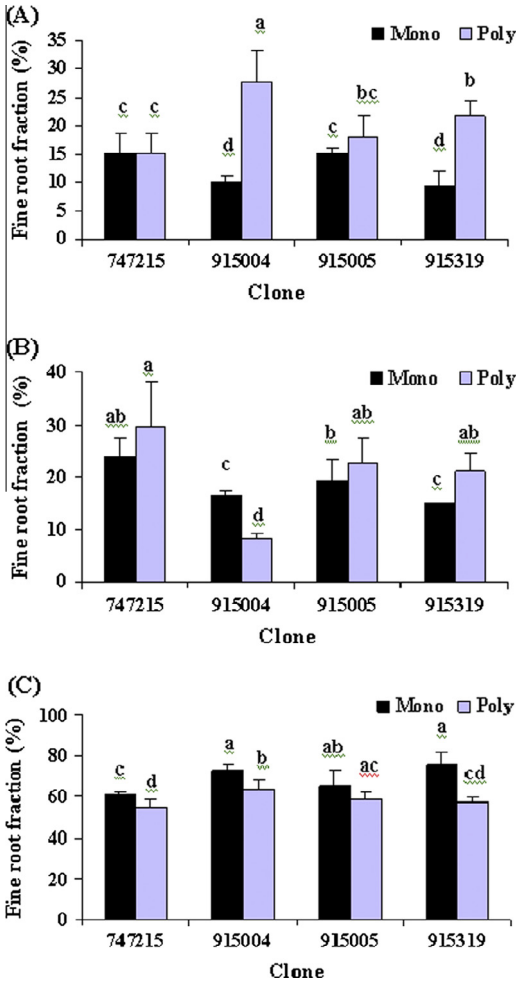

Fig. 4. Fine root fraction relative to total fine root dry matter (%) of four hybrid poplar clones in the monoclonal (Mono) *vs.* polyclonal (Poly) plots at 0–30 cm (A), 30–60 cm (B) and >60 cm (C) distances from the stem at Duparquet in the fifth growing season. For the same trait, values followed by the same letters do not differ at $P < 0.05$.

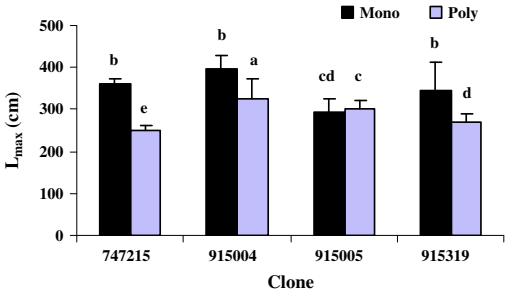

Fig. 5. Maximum root length (L_{max}) of four hybrid poplar clones in the monoclonal (Mono) *vs.* polyclonal (Poly) plots at Duparquet in the fifth growing season. For the same trait, values followed by the same letters do not differ at $P < 0.05$.

$P = 0.02$; Table 5). L_{max} values ranged respectively between 294 and 394 cm in the monoclonal plots *vs.* 251–324 cm in the polyclonal plots (Fig. 5). Maximum root depth (D_{max}) was not affected by clone or plot layout (Table 5), averaging 76 cm (data not shown). Tree volume and the coarse root fraction within the 30–60 cm distance class were positively correlated ($r = 0.52$, $P = 0.02$; Fig. 6A), while the proportion of roots at distances >60 cm was negatively correlated with tree volume ($r = -0.47$, $P = 0.05$; Fig. 6B).

3.6. TNC content of roots

Coarse root analysis showed that TNC concentrations were greater in polyclonal plots than in monoclonal plots ($P = 0.02$) and averaged 216.2 and159.2 mg g^{-1} DM, respectively (Fig. 7A, Table 5). Soluble sugar concentrations did not differ between the different layouts or clones (Table 5). Mean soluble sugar concentrations of the monoclonal and polyclonal plots, when averaged for the four clones, was 103 mg g^{-1} (data not shown). Root

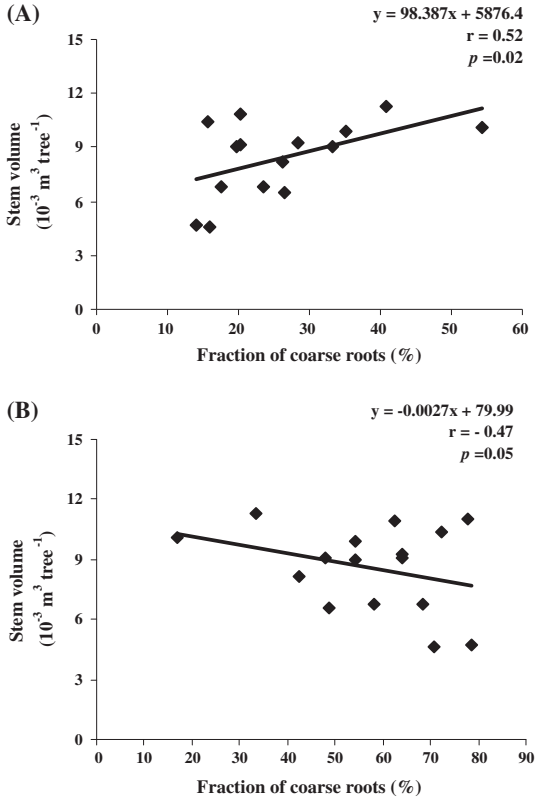

Fig. 6. Relationship between coarse root fraction (%) and stem volume of four hybrid poplar clones at 30–60 cm (A) and >60 cm (B) distances from the stem at Duparquet in the fifth growing season.

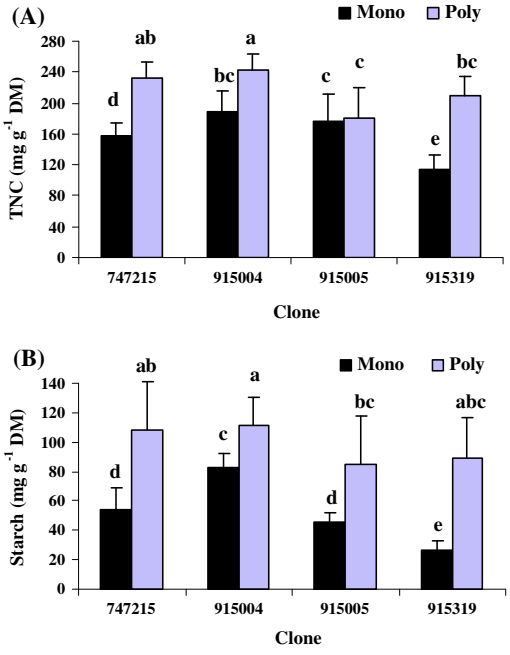

Fig. 7. Mean total non-structural carbohydrates (TNC) (A) and starch (B) concentrations (mg g^{-1} DM) of coarse roots of four hybrid poplar clones in the monoclonal (Mono) *vs.* polyclonal (Poly) plots at Duparquet in the fifth growing season. For the same trait, values followed by the same letters do not differ at $P < 0.05$.

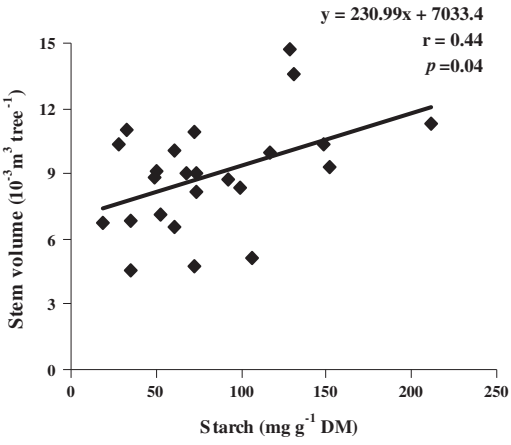

Fig. 8. Relationship between coarse root concentrations (mg g^{-1} DM) starch and tree volume (V) of all four hybrid poplar clones at Duparquet in the fifth growing season.

starch concentrations, however, were significantly ($P < 0.01$, Fig. 7B) greater for trees in the polyclonal plots (84–111 mg g^{-1}) compared to monoclonal plots (26–82 mg g^{-1}). Starch concentrations of roots also differed between clones ($P = 0.02$) and ranged from 58 mg g^{-1} (mean of polyclonal and monoclonal plots of clone 915319) to 108 mg g^{-1} (clone 915004, Fig. 7B). There was a positive correlation between root starch concentrations and stem volume ($P = 0.04$, Fig. 8), and between starch concentrations and N and P concentrations ($P = 0.01$ and $P = 0.05$, respectively; data not shown).

4. Discussion

Yield differences between pure and mixed forest stands depend on environmental conditions, and overyielding is often more noticeable in nutrient-poor sites compared to fertile sites

(Pretzsch et al., 2010). In our study, growth was not always greater in the polyclonal plots, as the effects of mixing clones depended upon both clones and sites. Our sites were located in the boreal region of Quebec and are known to be poor in nutrients, especially N. This has been confirmed by nutrient deficiencies in hybrid poplar that was planted in the same areas (Guillemette and DesRochers, 2008; Elferjani et al., 2013). Soil N concentrations in our soils were below 1.1 g kg^{-1}, while they can typically reach 2–5 g kg^{-1} in other forest ecosystems, and up to 25 g kg^{-1} in cultivated lands (Martinelli et al., 1999). In fertile soils, high nutrient availability reduces competition between species or genotypes and could reduce segregation of niches by root stratification (Oelmann et al., 2010). P deficiencies and low Ca availability that is due to high acidity (low pH) have also been reported in boreal conditions and could contribute to the presence of overyielding in the polyclonal plots (Ericsson, 1995; Lindahl et al., 2002). Soil pH of our sites ranged between 4 and 6, which favours immobilization of P by aluminium, reducing availability to plants (Marschner, 1996). In a fertilizer experiment that was conducted on the same sites (Duparquet and Duhamel), hybrid poplar clones showed substantial differences in macronutrient requirements (Elferjani et al., 2013). In our current study, differences in leaf macronutrient concentrations were often noticeable between monoclonal and polyclonal plots at the clone level suggesting an effect of clone mixing on nutrient uptake.

Differences between the two types of planting layouts were greater at Duparquet and Villebois than at Duhamel. In these first two sites, soil N was less available and overyielding was more frequently observed relative to Duhamel. These results are consistent with previous work, which has shown that mixing species in poor sites result in increased macronutrient concentrations in aboveground tissues of some species compared to monocultures; in turn, this response suggests a greater complementarity in nutrient uptake compared to richer sites (Rothe and Binkley, 2001; Oelmann et al., 2010; Richards et al., 2010). Clones that were used in our study also showed differences in phenological traits such as bud -break and bud-set dates (unpublished data), which might differentiate growth cycle niches between clones and, consequently, reduce competition for nutrients (Kelty, 2006). We also noted that clone mixtures enhanced growth more strongly for lower yielding clones (747215 and 915004) than they did for higher yielding clones (915319 and 915005). Further, clone mixing favoured growth of less productive clones, suggesting that these were subjected to greater intra-clonal competition in monoclonal plots, when compared to the most productive clones.

Nitrogen leaf concentration strongly affect net photosynthetic rate (P_n) of woody species (Marenco et al., 2001). At Duparquet, net photosynthesis and leaf N concentrations were correlated, and both were greater in the polyclonal compared to the monoclonal plots. Nitrogen is a major component of Rubisco and other enzymes that are involved in photosynthetic processes. Many studies have reported a strong relationship between leaf N concentration and net photosynthesis (Evans, 1989; Ripullone et al., 2003), but we were unable to demonstrate a relationship between these two variables at the Duhamel and Villebois sites. This discrepancy might be explained by greater N soil concentrations at Duhamel compared to Duparquet, but not at Villebois.

For the other macronutrients, plot layout did not affect leaf concentrations at Duhamel, even though yields were different. Greater nutrient uptake in polyclonal plots was probably masked by a dilution effect due to greater growth rates at Duhamel compared to the other sites, which resulted in similar nutrient concentrations in polyclonal *vs.* monoclonal plots. Numerous studies have reported a nutrient dilution effect for fast-growing species when tree growth is more rapid than nutrient accumulation (Lteif et al., 2008; Rivest et al., 2009).

When light is reduced by shade, leaves of trees acclimate by adjusting their specific leaf area (SLA) to increase light interception (Benomar et al., 2012). Our study showed that SLA was unaffected by the layout, which suggested that aboveground competition for light was not important with our 4 × 3 m spacing, five years after plantation establishment.

Root development was noticeably different between monoclonal and polyclonal plots for coarse and fine roots. Overall, the density of fine roots that were located next to the stem (0–30 cm class) was greater in the polyclonal plots for clones 915004 and 915319, and similar for the other clones, while the density of roots (coarse and fine) that were located beyond the 60 cm distance was greater in the monoclonal plots. Maximum horizontal rooting (L_{max}) was also greater in the monoclonal plots (except for clone 915005). Belowground competition could force trees to extend their roots further in monoclonal plots to acquire nutrients because trees of the same clone had similar rooting patterns and, thus, exploited the same soil volumes, making resources less available. As a consequence, trees acclimated by expanding their root systems further from the stem to overcome competition. Previous work has shown that roots can explore a greater soil volume and forage to a greater distance when nutrients, especially N, are limiting (Bhatti et al., 1998). Hodge et al. (1999) reported that grass species competition induced root proliferation and elongation, and that this elongation depended upon soil nutrient richness and heterogeneity. Kobe et al. (2010) found similar results with roots of black oak (*Quercus velutina* Lambert), sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrhart) and black cherry (*Prunus serotina* Ehrhart) growing at high *vs.* low N soil concentrations. Different clones often have different rooting patterns and occupy different soil layers, which could lower competition for nutrients (Kelty, 2006). It was similarly shown that when trees were subject to lower competition in mixed stands, fine roots were more concentrated next to the tree boles (Wang, 2002). Other factors such as nutrient distribution within a volume of soil can modulate root elongation to increase uptake (Hutchings and John, 2004).

Competition for nutrients between plants is often greater in monocultures and can lead to greater allocation of resources to establishing, maintaining and developing the belowground system (Ericsson, 1995; Gersani et al., 2001). Consequently, root:shoot ratio increases and fewer resources are allocated to aboveground structures. This acclimation to nutrient limitation might explain the lower stem volumes that were recorded in our monoclonal plots. The horizontal distribution of roots in the polyclonal *vs.* monoclonal plots was an indirect indicator of resource allocation to shoots since growth was – moderately – correlated with the horizontal distribution of roots. Growth was positively correlated ($r = 0.52$) with the root fraction near the stem (30–60 cm) and negatively correlated with the root fraction farthest from the stem ($r = 0.47$). This finding indicated that when the trees invested in longer roots (further from the stem), less biomass was allocated to shoots and aboveground volumes decreased. This result agrees with previous studies, which have shown that root elongation was triggered or inhibited by nutrient availability via signal transduction pathways that measure nutrient concentrations external and internal to the roots (Takei et al., 2002; Malamy, 2005).

The root system not only supplies nutrients but also acts as a major storage organ during the growing season for starch, which is mobilized as soluble sugars during the dormancy period for maintenance respiration and tree survival (Kobe et al., 2010). Non-structural carbohydrates are also essential for bud flush and early growth until foliar production of photosynthates meets tree needs. A lack of starch reserves might decelerate startup growth of trees and reduce plantation yields (Canham et al., 1999). Starch and soluble sugar concentrations in roots are subject to seasonal changes and are also affected by environmental factors such as soil

nutrient availability (Von Fircks and Sennerby-Forsse, 1998). Soluble sugars also tend to accumulate in roots in response to disturbance and might be an indicator of stress in forest ecosystems (McLaughlin et al., 1996; Landhäusser and Lieffers, 2002; Kasuga et al., 2007). Greater amounts of non-structural carbohydrates (TNC) are frequently stored in the roots of hybrid poplars and other pioneer species compared to later serial species (Bollmark et al., 1999). We found greater concentrations of starch in coarse roots of trees within the polyclonal plots, which could have indicated lower competition for nutrients between trees of different clones. The negative correlation between root elongation and biomass production supports the hypothesis that genotype mixtures reduced competition for nutrients, resulting in better growth and greater carbohydrate reserves. We argue that greater competition for nutrients between trees in monoclonal plots reduced the availability of N (and other nutrients) and its uptake, which then decreased photosynthesis rate and accumulation of carbohydrate reserves in the roots. Wargo et al. (2002) demonstrated that correcting nutrient imbalance of a maple plantation with fertilizer inputs decreased stress-indicating poly-amines and increased root starch concentrations. Application of a water stress to two black poplar (*Populus nigra* L.) clones substantially mobilized stored starch and decreased allocation of carbohydrates to roots (Régier et al., 2010). Therefore, TNC concentrations could be a good indicator of tree vigour or of stressful growing conditions.

In conclusion, mixing clones did not always increase yield and its effect differed among clones and sites. On the whole, the effect of clone mixing was positive, but it occasionally yielded null or negative responses. When growth was greater in the polyclonal plots, overyielding was more frequent and greater at Duparquet and Villebois compared to Duhamel. This response could be explained by a greater complementarity effect among clones in poor sites where soil nutrients limited growth. Horizontal root distribution was noticeably different between the two types of layouts and also differed among clones, suggesting a belowground niche partitioning among clones. We also noted greater investment in root systems in the monoclonal plots compared to polyclonal plots, which resulted in greater root:shoot ratios in the former compared to the latter. This response suggests that competition for soil nutrients was lower among trees in the polyclonal plots, which might explain their frequently greater aboveground growth. Greater TNC concentrations in roots of polyclonal plots was consistent with the positive effects of mixing on the status of most of the nutrients (e.g., N and P) and supported the hypothesis that mixing clones might decrease competition among trees and enhance carbon assimilation and growth. Net photosynthesis was generally greater in the polyclonal plots at Duhamel and Duparquet, while specific leaf area was unaffected by the type of layout, which suggested limited aboveground competition in the monoclonal plots. Assessing clonal interactions within the polyclonal plots in the future would be interesting since aboveground competition should increase in the next years, together with belowground interactions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.05.013.

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