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

Raed Elferjani *, Annie DesRochers, Francine Tremblay

Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue, 341, rue Principale Nord, Amos, QC J9T 2L8, Canada

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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 (⩾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).

* Corresponding author. Tel.: +1 819 732 8809; fax: +1 819 732 8805.
E-mail address: relferjani@yahoo.fr (R. Elferjani).

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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:

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