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Plasticity of bud phenology and photosynthetic capacity in hybrid poplar plantations along a latitudinal gradient in northeastern Canada

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ABSTRACT

Intensively managed plantations are being established in a wide range of environmental conditions to satisfy the high demand for wood products and reduce the exploitation pressure on natural forests. In this study, we investigated the plasticity of four hybrid poplar (*Populus* spp.) clones established in 2005 along a latitudinal gradient in northwestern Quebec, Canada. The effect of latitudinal gradient on maximum rates of electron transfer (J_{max}) and carboxylation (Vc_{max}), dark respiration (R_d), spring and fall bud phenology, net photosynthesis (P_n), specific leaf area (SLA), per mass nitrogen leaf concentration (N_m) were assessed in order to evaluate if clonal plasticity would result in increased overall productivity.

Growth season duration between the southernmost to the northernmost sites ranged 21–32 days, and was positively correlated to stem volume and negatively correlated to bud burst and bud set duration. Growth increment (stem volume) along the latitudinal gradient ranged 100–184% between the least and most productive clone. Clone 747215 had the most stable but the slowest growth. Leaf net photosynthesis decreased or did not change northwards except for the most productive clone for which it increased slightly likely due to a significant decrease in SLA. Maximum rates of carboxylation and photosynthesis electron transfer (Vc_{max} and J_{max}) decreased northwards for three of the four clones, suggesting that photosynthesis of trees did not acclimate to lower temperatures from south to north. Plasticity of photosynthetic variables, measured with trait plasticity index was usually greater than that of SLA and N_m.

1. Introduction

Forests of north eastern Canada represent a major source of wood for the timber industry, especially *Populus* spp. which account for about half of the total timber volume in Canada (Zasada et al., 2001). The decrease of harvestable natural forests near wood mills and increasing conservation pressures have prompted managers to develop intensively managed plantations scenarios to maintain or even increase wood allocations (Messier et al., 2009). Fast-growing plantations can produce greater volumes of timber on a limited land area through intensive silvicultural management such as heavy site preparation, weeding and fertilization. Plasticity of structural and functional traits of woody species can also be important to increase tree productivity in a silvicultural context (Gornall and Guy, 2007; Soolanayakanahally et al., 2009). The actual and predicted impacts of climate changes and especially global warming, might compromise the establishment and growth of forest trees (Rehfeldt and Jaquish, 2010). Expected temperature increase in the next decades should be considered in the choice of cultivars suitable for a geographical region and plasticity might contribute in counterbalancing the effects of fast climate shifts in the future (Richter et al., 2012).

Phenotypic plasticity expresses the capacity of a genotype to exhibit different phenotypes in response to distinct environmental conditions (Bradshaw, 1965). Recent studies on plants acclimation demonstrated the importance of phenotypic plasticity in overcoming effects of short-term environmental conditions changes and maintaining physiological integrity and productivity (Schlichting, 1986; Van Kleunen and Fischer, 2005; Visser, 2008). Studying phenotypic variation is thus important to anticipate the increasing occurrence of extreme climatic events such as episodic drought or flooding with climate change (IPCC, 2007). Species with a large geographical distribution such as *Populus* constitute good models for studying plasticity (Hansen et al., 2012). The link between

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phenotypic plasticity to stressful or heterogeneous environments and growth has yet to be established, but some previous works on horticultural and forest trees found that plasticity in some physiological traits such as stem water potential and photosynthetic capacity were correlated with productivity (Sadras and Trentacoste, 2011; Paquette et al., 2012). However, phenotypic plasticity can sometimes cause structural and developmental shifts that could affect normal plant development and slow growth (DeWitt et al., 1998).

Bud burst and bud set are prominent events in the annual cycle of tree species and are related to growth rate since they determine the length of the growing season (Rathcke and Lacey 1985; Chuine and Beaubien, 2001). In temperate and boreal climates, bud burst timing is crucial since spring frost could irreversibly damage tissues, very vulnerable at this stage. On the other hand, early onset of dormancy decreases aboveground growth since growth ceases while nutrients and photosynthates are redirected to storage (Keskitalo et al., 2005). Bud phenology was reported to be a plastic attribute for many forest tree species (Vitasse et al., 2009; Hall et al., 2007; Fabbrini et al., 2012).

The shorter growing season at northern latitudes might be compensated by more efficient photosynthetic activity. Plasticity of photosynthesis was reported for many species in response to variation in temperature, photoperiod and leaf nitrogen (Benowicz et al., 2000; Reich and Oleksyn, 2004). Recent works on forest tree species showed that populations from northern latitudes exhibited greater photosynthetic efficiency than populations from lower latitudes (Gornall and Guy, 2007; Soolanayakanahally et al., 2009), while leaf nitrogen was inversely proportional to mean annual temperature (Reich and Oleksyn, 2004); This suggest compensatory photosynthetic response to cooler temperatures and shorter growing seasons. Numerous studies have also shown that slower growth rates of trees at higher latitudes were not due to lower photosynthetic efficiency but to the shorter length of the growing season (Benowicz et al., 2000; Ellis et al., 2000). Under boreal conditions, maximum growth rates of conifers were also related to longer days rather than warmer temperatures (Rossi et al., 2006).

In this study, bud phenology of four hybrid poplar clones was monitored at the beginning and at the end of the growing season along a latitudinal gradient in the boreal region of eastern Canada. This region (Abitibi-Témiscamingue) is widespread and has lots of abandoned farmlands available for the establishment of fast growing plantations. With a climatic gradient encompassing five plant hardiness zones (Agriculture and Agri-Food Canada, 2013), highly productive but plastic cultivars are more desirable than specific cultivars that do very well only under specific conditions (Marron et al., 2006); Plasticity may enhance economical profitability in heterogeneous environments and cultivation conditions (Marron et al., 2006). The main objective of the study was to evaluate the relationship between plasticity of photosynthetic capacity and bud phenology vs. yield stability along a latitudinal gradient. Bud phenology and stem volume were assessed to evaluate the response of clones to the latitudinal gradient and the relationship between phenology and growth performance. Photosynthetic capacity, specific leaf area and nitrogen concentration were measured to characterize the response of hybrid poplar clones to shorter growth season and colder temperature northwards. We tested the following hypotheses: (i) variation in length of the growing season (timing of bud set and bud burst) between clones will be linked to growth performance (stem volume) along the latitudinal gradient, (ii) photosynthetic capacity will increase northwards to compensate for the shorter growing season, (iii) clones showing greater plasticity in photosynthesis and specific leaf area will have more stable volume growth along the latitudinal gradient.

2. Materials and methods

2.1. Study sites and plant material

The three study sites were located in the Abitibi-Témiscamingue region, in north-western Québec, Canada which the climate is humid continental. The northernmost site was located next to Villebois village, in the James Bay municipality (49°09′N, 79°10′W), and had been previously farmed organically for cereals and hay. This site was in the black spruce *Picea mariana* (Mill.) BSP-feather moss (*Pleurozium* spp.) domain (Grondin, 1996) and the soil was a clay-grey luvisol (50% clay). Mean annual precipitations and temperature in this location were 890 mm and 1.2 °C, respectively (Environment Canada, 2013). The second site was located in the Research and Teaching Forest of Lake Duparquet (48°29′N, 97°9′W, Alt. 295 m). This site was in the balsam fir (*Abies balsamea* L.)-paper birch (*Betula papyrifera* Marshall) bioclimatic western sub-domain (Grondin, 1996) and had been previously forested until harvested in 2004. Mean annual precipitations and temperature were 918 mm and 1.2 °C respectively, and the soil of this site was classified as a heavy clay brunisol (70% clay; Agriculture and Agri-food Canada, 2013). The southernmost site was an abandoned farmland next to the town of Duhamel (47°32′ N, 79°59′ W, Alt. 209 m). The site is located in the sugar maple (*Acer saccharum* Marshall)-yellow birch (*Betula alleghaniensis* Britton) western bioclimatic sub-domain (Grondin, 1996), and had been cultivated for hay in previous years. The soil was a clayey luvisol (45% clay; Agriculture and Agri-food Canada, 2013) and mean annual precipitations and temperature were respectively 820 mm and 2.8 °C (Environment Canada, 2013). Extensive site preparation and maintenance were performed both prior to planting and following plantation establishment. Duhamel and Villebois sites were ploughed using an agricultural cultivator in autumn 2004. Prior to plantation establishment at Duparquet, stumps and woody debris were removed with a bulldozer. The site was then ploughed to a depth of 30 cm in autumn of 2004 with a forestry plough pulled by a skidder and disked in spring 2005 to level the soil before planting. Trees were planted at the three sites in June 2005 at 1 × 4 m spacing. Following planting, weeds were mechanically removed twice a year by cultivating between rows with a farm tractor and discs and by tilling between trees with a Weed Badger™ (4020-SST, Marion, ND, USA).

The clones selected for planting had been recommended for the region by the Ministère des Ressources Naturelles et de la Faune du Québec (MRNFQ): clone 747215 (*Populus trichocarpa* Torrey & A. Gray × *balsamifera* L.), clones 915004 and 915005 (*Populus* balsamifera × *maximowiczii* Henry) and clone 915319 (*Populus* maximowiczii × *balsamifera*). Stock type was bare-root dormant trees and average tree height at planting was 96.3 cm. The experimental design consisted of three replicates (blocks) of the four hybrid poplar clones at each site. Each block contained a plot for each genotype (*N* = 840). Positions of clones in the blocks were randomly assigned.

2.2. Phenology

Bud burst was assessed in April-May 2009 and divided into six phenophases based on a visual observation of terminal bud development as followed; stage 0: all buds are completely closed, stage 1: bud is split and tiny leaves are appearing and are barely coming out of bud scales, stage 2: fusiform and wrapped leaves double bud length; Stage 3: leaves are still wrapped and fusiform but become bifurcated, stage 4: leaves are half unfolded but remain in bunch; stage 5: leaves unfurl and are completely separated. Bud set was assessed in September-November and divided into five phenophases based on the visual observation of bud and foliage