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

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

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

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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^{TM} (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 presence: stage 5: the foliage is completely present and the bud is active (green), stage 4: 33% of foliage has fallen, stage 3: 66% of foliage has fallen; stage 2: 100% of foliage has fallen and buds are barely active (green), stage 1: all buds are closed and brown in color (dormant). The growing season length was defined as the number of days between the last stage of bud burst (BBLS) date (stage 5) and the stage 4 of bud set, marking the beginning of growth cessation. All the trees of each Site × Block × Clone combination were visually inspected ($N = 540$) and phenology stage (S_x) was assigned for each block when 60% of trees reached S_x.

2.3. Meteorological data

Meteorological data of the three sites were obtained from nearby station of the National Climate Data and Information database (Environment Canada, 2013). Frost free days of bud burst month (April, FFA), mean annual temperature (MAT), degree days (5 °C base, Cannell and Smith, 1986) of the bud burst month (April, DDA), degree days of the growth months (May–October, GDD) and annual rainfall (AR) were used to calculate their correlation with photosynthesis traits: dark respiration (R_d) and maximum rates of carboxylation and electron transfer ($Vc_{max}J_{max}$), bud burst last stage (BBLS), bud burst duration (BBD), growing season duration (GD) and leaf nutrient concentration (%) of N, P, K, Ca and Mg (Table 1).

2.4. Growth

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

$$V = A_b \times \frac{H}{3}$$

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

To better describe growth rate in relation to the growing season duration (in days), mean daily increment (MDI) for tree volume of each clone was calculated using the following formula:

$$\text{MDI} = V_{2009} - \frac{V_{2008}}{\Delta t}$$

where V_{2009} and V_{2008} are, respectively, tree volume per hectare (cm^3 tree^{-1}) at the end of 2009 and 2008 growing seasons; Δt is the 2009 growing season duration in days as defined on the basis of phenological observations. MDI was expressed in cm^3 tree^{-1} day^{-1}.

2.5. Leaf nitrogen concentration and specific leaf area (SLA)

Leaf samples were collected at each of the three sites in mid-July 2009 for analyses of nitrogen concentration per mass (N_m) analyses and measurement of specific leaf area (SLA). Nine recently matured leaves were collected from three randomly selected trees of each clone in each plot ($N = 108$ trees); 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 surface 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 with a Wiley mill grinder to pass a 60 μm sieve (Thomas Scientific, Swedesboro, NJ, USA) and pooled to obtain a sample for determination of nutrients concentrations. Nitrogen concentration per mass (N_m) was obtained after dry combustion using a LECO N-analyzer (Leco Corp., MI, USA) (Leco Corp., 1986).

2.6. Photosynthesis

Net photosynthesis (P_n), maximum rate of photosynthesis electron transport (J_{max}), dark respiration (R_d) and maximum rate of carboxylation limited by Rubisco (Vc_{max}) of the four clones were estimated using CO$_2$ assimilation rate *vs* internal leaf CO$_2$ concentration (A–C$_i$) curves at the three sites. A–Ci curves were built for three randomly selected trees of each clone, at the three sites (one tree per plot $N = 36$). Net photosynthesis (P_n), a productivity-related trait, was measured for each clone × plot × site combination ($N = 36$), in mid-July 2009 to evaluate the effect of competition on yields. Measurements were made on recently matured leaves that did not show any apparent sign of senescence, between 9 am and 12 am. The order of tree clone was randomized to reduce the time effect on photosynthesis parameters. Photosynthesis was measured with a CIRAS-2 portable photosynthesis system using an infra-red analyzer (PP systems, MA, USA) and coupled with a broadleaf cuvette, which was equipped with a LED unit for automatic control of light (PLC6-U, 25 mm, PP Systems). Leaf chamber temperature, vapour pressure deficit and photosynthetically active radiation were set to 25 °C, 10 mbar and 1500 μmol m^{-2}, respectively. During measurements, air temperature ranged 18–25 °C and humidity 50–70%. To obtain A–Ci curves, CO$_2$ partial pressure was set to 360 μmol mol^{-1} and kept at a steady state during 10 min before measurement was recorded, and then changed in the following sequence: 360, 250, 100, 60, 40, 360, 500, 600, 700, 800, 1000, 1200 and 1400 μmol mol^{-1} during measurement. J_{max}, R_d and Vc_{max} were obtained using *Photosyn Assistant* software based on models proposed by Farquhar et al. (1980) and modified by Von Caemmerer and Farquhar (1981), Sharkey (1985) and Harley et al. (1992). Net photosynthesis was obtained with the same parameters except for CO$_2$ partial pressure which was set to 360 μmol mol^{-1} and not changed. To avoid edge effect, trees of a buffer row around each plot were not sampled for photosynthesis, SLA and nutrients measurements.

Table 1
Climatic normals (1971–2000)[1] of the three sites.

	Duhamel	Duparquet	Villebois
FFA (frost free days in bud burst month, April)	7.9	6.8	5.1
FFO (frost free days of the bud set month, October)	16.6	14	10.1
MAT (mean annual temperature, C)	2.8	1.2	0.7
SPG (sunshine period of growth months, hours)	1209.4	1128.3	N/A
GDD (growth degree days, 5C)	1600.6	1400.2	1340
DDA (Degree days of the bud burst month)	36.8	25.3	31.5
AR (annual rainfall, mm)	624	671	583
Total day length of growth months (hours)	2211	2225	2235

[1] Source: Environment Canada, 2013.

2.7. Plasticity

Phenotypic plasticity of traits related to leaf phenology and photosynthesis was measured using the trait plasticity index (TP_i) elaborated by Valladares et al. (2000) to quantify the variability and possible acclimation of traits across environments. TP_i formula included the mean of the trait value and the difference of the trait values between each couple of sites:

$$TPi = \frac{\sum_i^n |x_i - x_j|}{\bar{x}}$$

where x_i and x_j are the trait value of a clone in sites i and j (sites = i, j, ...,n), and x is the trait mean of a clone in “i,j, ...,n” environments.

Growth stability of clone “i” along the latitudinal gradient was measured with the coefficient of variability (CV_i) of Francis and Kannenberg (1978) in order to evaluate the effect of changing environments on productivity variation of each of the four clones, using the formula: $CV_i = \frac{\sqrt{S_i^2} \times 100}{m_i}$where $S_i{}^2$ and m_i are, respectively, the stem volume or mean day increment variance (environmental variance) and mean of clone “i” across sites. CV_i is a widely used index for crops and preferred to the environmental variance because variance is often related to the mean (Stelluti et al., 2007; Barić et al., 2004). The lower the value of CV, the greater is the clone stability among environments. $S_i{}^2$ is calculated using the following formula.

$$S_i^2 = \frac{\sum_{j=1}^{q} (X_{ij} - m_i)^2}{(q-1)}$$

where X_{ij} is the mean stem volume or mean day increment of clone i, at the j^{th} site and q is the number of sites.

2.8. Statistical analysis

Linear mixed-effect models (nlme) were used to analyze the relationships between response variables and explanatory variables (Version 2.11.1, R Development Core Team, Vienna, Austria). Data was checked to respect normality of residuals and homoscedasticity and transformed when required. Clone and site were considered as fixed effects, while block (replicate) was considered as a random effect in all models. To evaluate the clone plasticity (with plasticity index) along the latitudinal gradient, one way ANOVA within linear mixed model package (nlme) was used to test the difference between clones. Pearson's product-moment correlations (r) were used to test relationships between photosynthesis and phenology traits, and climatic normals. Means were compared using Tukey's honest significant differences (HSD) and significance level for all tests was set at $\alpha = 0.05$.

3. Results

3.1. Clonal growth patterns

Stem volume (V, m^3 $tree^{-1}$) was the greatest at the southernmost site ranging between 3.44 and 16.68 10^{-3} m^3 $tree^{-1}$ from north to south after five growing seasons (Tables 2 and 4). Average V was 12.78 10^{-3} m^3 $tree^{-1}$ in 2009 for the most productive clone (915319) and 4.88 10^{-3} m^3 $tree^{-1}$ for the least productive clone (747215). Average V decreased respectively by 39% and 36% for these two clones from the southernmost to the northernmost sites (Table 4). Growth of the other two clones was similar and V ranged between 3.44 and 10.36 10^{-3} m^3 $tree^{-1}$ decreasing by 54% on average from south to north. Mean daily increment (MDI) followed the same pattern than V for all clones and decreased northwards (Table 4). The best performing clone (915319) had the greatest MDI at the southernmost site (59.7 cm^3 $tree^{-1}$ day^{-1}) and it decreased by 50% northwards. The least performing clone (747215) had a MDI of 25.7 cm^3 $tree^{-1}$ day^{-1} at the southernmost site and it decreased by 41% northwards.

3.2. Growth stability

The stability index (CV_{FK}, Francis and Kannenberg, 1978) of tree volume (V) was the most stable across sites for clone 747215 ($CV_{FK} = 28.1$), while it was the most variable for 915005 ($CV_{FK} = 62.4$) and intermediate for clones 915004 and 915319 (Table 6). Variance of MDI of clones across sites followed the same trends as V, and CV_{FK} ranged between 31.1 (747215) and 60.8 (915319) (Table 6).

3.3. Bud phenology

Growing season duration (GD) was 132 to 153 days at the southernmost site (Dhl), 115 to 135 at Dpq and 111 to 126 at the northernmost site (Vlb) (Table 5). The difference in GD between Dhl and Vlb ranged from 20 (915004) to 31 days (915005). The difference in growth duration between Dhl and Dpq vs Dpq and Vlb was 17 *vs* 4 days (747215), 20 vs 0 days (915004), 16 vs 15 days (915005) and 18 vs 11 days (915319).

3.4. Kinetics of bud burst (BB) and bud set (BS)

At the southernmost site (Dhl), the last stage of BB was synchronous for clones 747215, 915004 and 915005 (134 DOY) while it occurred later for clone 915319 (140 DOY) (Fig. 1). At Dpq, the last stage of BB occurred 10–12 days later than at Dhl depending on clones (DOY 146 to 150) and again clone 915319 was the latest to reach the last stage of BB (DOY 150). The last stage of BB was synchronized at the 150th DOY at Vlb and Dpq for all clones (Table 5). Time required for BB completion was the shortest for clone 915319 at the three sites, and ranged from 25–30 days (Fig. 1).

Bud set started after 261 DOY (Dpq and Vlb) and 266 DOY (Dhl) (Table 5). Difference in BS between the northernmost and southernmost site ranged from five (747215 and 915004) to 17 days (915319) (Table 5). Bud set was completed at Vlb and Dpq first, then at Dhl where the last stage of fall phenophases occurred after 300–315 DOY depending on clone (Fig. 2). Clone 747215 was the first to complete BS at the three sites (293 at Vlb and 300 DOY at Duh) while 915319 was the latest (15 days later). Bud set duration was significantly different ($P < 0.001$) between clones at the southernmost site and ranged between 22 and 37 days (Tables 3 and 5).

3.5. Specific leaf area and nitrogen concentration

Specific leaf area (SLA) was different between clones and ranged between 77.9 and 112.3 cm^2 g^{-1} (Tables 3 and 4). SLA variation

Table 2
Analysis of variance of stem growth traits of hybrid poplar clones. Degree of freedom (d.f), F and P value are reported.

Source of variation	d.f.	*V*		MDI	
		F	*P*	*F*	*P*
Site	2	79.4	**	39.6	**
Clone	3	56.6	**	12.4	**
Site × Clone	6	8.6	**	2.5	ns

V: stem volume (10^{-3} m^3 $tree^{-1}$), MDI: mean daily increment (cm^3 $tree^{-1}$ day^{-1}).
** $P < 0.01$; ns: non significant.

Table 3
Analysis of variance of physiological and phenological traits in hybrid poplar clones showing degree of freedom (d.f), F and *P* value.

Source of variation		SLA		P_n		N_m		BBLS		BBD		BSS		BSD		GD		J_{max}		Vc_{max}		R_d		J_{max}/Vc_{max}	
	d.f	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	FF	*P*	*F*	*P*	*F*	*P*	FF	*P*	FF	*P*
Site	2	5.7	*	120.5	**	4.3	**	341.7	**	995.3	**	1437.8	**	110.5	**	2244.2	**	12.5	**	109.6	**	7.6	**	10.1	**
Clone	3	5.1	*	16.2	**	5.6	**	51.2	**	130.4	**	19.9	**	629.6	**	905.8	**	6.7	**	30.3	**	*0.7*	ns	0.8	ns
Site × Clone	6	1.8	ns	1.7	ns	1.25	**	34.1	**	24.4	**	22.5	**	189.6	**	634.6	**	0.8	ns	10.9	**	3.9	**	4.6	**

SLA: Specific leaf area ($cm^2\,g^{-1}$), N_m: per mass nitrogen concentration ($mg\,g^{-1}$), P_n: net assimilation rate ($\mu mol\,s^{-1}\,m^{-2}$), BBLS: bud burst last stage, BBD: bud burst duration, BSS: bud set start, BSD: bud set duration, GD: growth season duration, J_{max}: maximum rate of photosynthesis electron transport ($\mu mol\,s^{-1}\,m^{-2}$), Vc_{max}: maximum rate of carboxylation limited by Rubisco ($\mu mol\,s^{-1}\,m^{-2}$), R_d: dark respiration ($\mu mol\,s^{-1}\,m^{-2}$).

** $P < 0.01$.

* $0.05 < P < 0.01$; ns: non significant ($P > 0.05$).

Table 4
Means of growth and growth-related traits of hybrid poplar clones at the three sites measured in 2009. Values of the same variable within the same clone labeled with different letters are statistically different at $P < 0.05$.

Clone	Site	*V*	MDI	SLA	N_m	P_n
747215	Dhl	5.87 ^{a}	25.7 ^{a}	77.9 ^{c}	23.6 ^{a}	21.4 ^{a}
	Dpq	3.77 ^{c}	15.1 ^{b}	89.8 ^{b}	21.2 ^{b}	20.9 ^{a}
	Vlb	5.00 ^{b}	23.8 ^{a}	95.2 ^{a}	20.6 ^{b}	17.8 ^{b}
915004	Dhl	10.36 ^{a}	44.6 ^{a}	89.6 ^{a}	25.2 ^{a}	18.7 ^{a}
	Dpq	6.99 ^{b}	26.9 ^{b}	83.4 ^{b}	21 ^{b}	17.7 ^{ab}
	Vlb	5.76 ^{c}	21.2 ^{c}	87.5 ^{a}	15.7 ^{c}	16.7 ^{b}
915005	Dhl	9.72^{a}	36.6 ^{a}	83.2 ^{c}	20.1 ^{b}	16.1 ^{b}
	Dpq	3.44^{c}	11.5 ^{c}	94.3 ^{a}	16 ^{c}	20.1 ^{a}
	Vlb	6.12 ^{b}	23.3 ^{b}	88.7 ^{b}	23.5 ^{a}	16.2 ^{b}
915319	Dhl	16.68 ^{a}	59.7 ^{a}	112.3 ^{a}	18.8 ^{a}	16.6 ^{b}
	Dpq	11.66 ^{a}	29.9 ^{c}	88.8 ^{b}	19.2 ^{a}	15.1 ^{c}
	Vlb	10.01^{c}	36.4 ^{b}	91.5 ^{b}	18.8 ^{a}	17.2 ^{a}

V: stem volume ($10^{-3}\,m^3\,tree^{-1}$), MDI: mean daily increment ($cm^3\,tree^{-1}\,day^{-1}$), SLA: Specific leaf area ($cm^2\,g^{-1}$), N_m: per mass nitrogen concentration ($mg\,g^{-1}$), P_n: net assimilation rate ($\mu mol\,s^{-1}\,m^{-2}$), Dhl: Duhamel, Dpq: Duparquet, Vlb: Villebois.

along the latitudinal gradient (max-min/max) ranged between 6.9% and 20.9% depending on clone. However, SLA varied differently among clones, as it substantially decreased northwards for clone 915319 while it increased for clone 747215. Similarly to SLA, nitrogen concentration (N_m) differed between clones and among sites ranging between 15.7 and 25.2 $mg\,g^{-1}$ (Tables 3 and 4). From south to north, N_m decreased by 37.7% and 12.7% for clones 747215 and 915004 respectively while it increased by 14.5% for clone 915005.

3.6. Physiological response pattern

Net photosynthesis (P_n) decreased from south to north by 17% and 10% for two clones (747215 and 915004) and did not change for clone 915005 being 16.1 $\mu mol\,s^{-1}\,m^{-2}$ on average. P_n of the best performing clone (915319) increased a little (4%) from the southernmost (Dhl) to the northernmost site (Tables 3 and 4).

Maximum photosynthetic rate of electron transport (J_{max}) was the highest in the southernmost site (Dhl) where it ranged between 165 to 209 $\mu mol\,s^{-1}\,m^{-2}$. Then J_{max} decreased to 127 $\mu mol\,s^{-1}\,m^{-2}$ at Dpq (clone 915004) and did not significantly

Table 5
Phenological traits of the four hybrid poplar clones across the three sites. Values of the same variable labeled with different letters are statistically different ($P > 0.05$).

Clone	747215			915004			915005			915319		
Site	Dhl	Dpq	Vlb	Dhl	Dpq	Vlb	Dhl	Dpq	Vlb	Dhl	Dpq	Vlb
BBLS (DOY)	134 ^{a}	146 ^{b}	150 ^{c}	134 ^{a}	150 ^{c}	150 ^{c}	134 ^{a}	150 ^{c}	150 ^{c}	140 ^{d}	150 ^{c}	150 ^{c}
BBD (phase 0–5, days)	19 ^{a}	28 ^{b}	32 ^{c}	21 ^{d}	29 ^{b}	32 ^{c}	21 ^{d}	34 ^{e}	36 ^{f}	21 ^{d}	25 ^{g}	29 ^{b}
BSS (DOY)	266 ^{a}	261 ^{b}	261 ^{b}	270 ^{c}	266 ^{d}	266 ^{d}	286 ^{e}	286 ^{e}	271 ^{c}	293 ^{f}	285 ^{e}	276 ^{g}
BSD (phase 4–1, days)	34 ^{a}	32 ^{b}	32 ^{b}	37 ^{c}	41 ^{d}	34 ^{a}	29 ^{e}	41 ^{d}	20 ^{f}	22 ^{g}	31 ^{b}	21 ^{f}
GD (days)	132 ^{a}	115 ^{b}	111 ^{c}	136 ^{d}	116 ^{e}	116 ^{e}	152 ^{f}	136 ^{d}	121 ^{g}	153 ^{f}	135 ^{d}	126 ^{h}

BBLS: bud burst last stage, BBD: duration of bud burst, BSD: duration of bud set, GD: length of the growing season duration. Dhl: Duhamel (47°N). Dpq: Duparquet (48°N). Vlb: Villebois (49°N). DOY: day of the year.

Table 6
Plasticity index (TP_i) and stability index (CV_{FK}) of traits measured in hybrid poplar clones in three sites along a latitudinal gradient. Values are means of three replicates for each site and those labeled with different letters within the same variable are statistically different at $P < 0.05$.

Clone	Trait plasticity index (TP_i)											Mean TP_i	Stability index (CV_{FK})	
	SLA	N_m	Photosynthesis				Phenology						*V*	MDI
			R_d	J_{max}	Vc_{max}	J_{max}/Vc_{max}	BBLS	BSS	BBD	BSD	GD			
747215	4.9 ^{b}	22.4 ^{b}	77.4 ^{a}	53.4 ^{c}	18.1 ^{d}	52.1 ^{b}	22.3 ^{a}	3.8 ^{c}	98.7 ^{a}	12.2 ^{d}	35.2 ^{c}	36.4 ^{c}	28.1 ^{d}	31.1 ^{d}
915004	6.8 ^{a}	21.2 ^{b}	68.1 ^{b}	74.7 ^{a}	56.4 ^{c}	73.9 ^{a}	22.1 ^{a}	3 ^{d}	80.5 ^{b}	37.5 ^{c}	32.6 ^{d}	43.3 ^{b}	36.4 ^{c}	48.4 ^{c}
915005	1.3 ^{c}	9.4 ^{c}	71.6 ^{b}	69.7 ^{b}	100.9 ^{a}	32.5 ^{c}	22.1 ^{a}	10.7 ^{b}	98.9 ^{a}	101.2 ^{a}	45.5 ^{a}	51.2 ^{a}	62.4 ^{a}	60.8 ^{a}
915319	1.1 ^{c}	42.4 ^{a}	21.8 ^{c}	59.8 ^{c}	83.4 ^{b}	31.1 ^{c}	13.6 ^{b}	11.9 ^{a}	64 ^{c}	81.1 ^{b}	39.1 ^{b}	40.8 ^{b}	52.7 ^{b}	57 ^{b}

SLA: Specific leaf area ($cm^2\,g^{-1}$), N_m: per mass nitrogen concentration ($mg\,g^{-1}$), J_{max}: maximum rate of photosynthesis electron transport ($\mu mol\,s^{-1}\,m^{-2}$), Vc_{max}: maximum rate of carboxylation limited by Rubisco ($\mu mol\,s^{-1}\,m^{-2}$), R_d: dark respiration ($\mu mol\,s^{-1}\,m^{-2}$), BBLS: bud burst last stage (DOY), BSS: bud set start (DOY), BBD: duration of bud burst (days), BSD: duration of bud set (days), GD: duration of the growing season (days), *V*: stem volume ($10^{-3}\,m^3\,tree^{-1}$), MDI: mean daily increment ($cm^3\,tree^{-1}\,day^{-1}$).

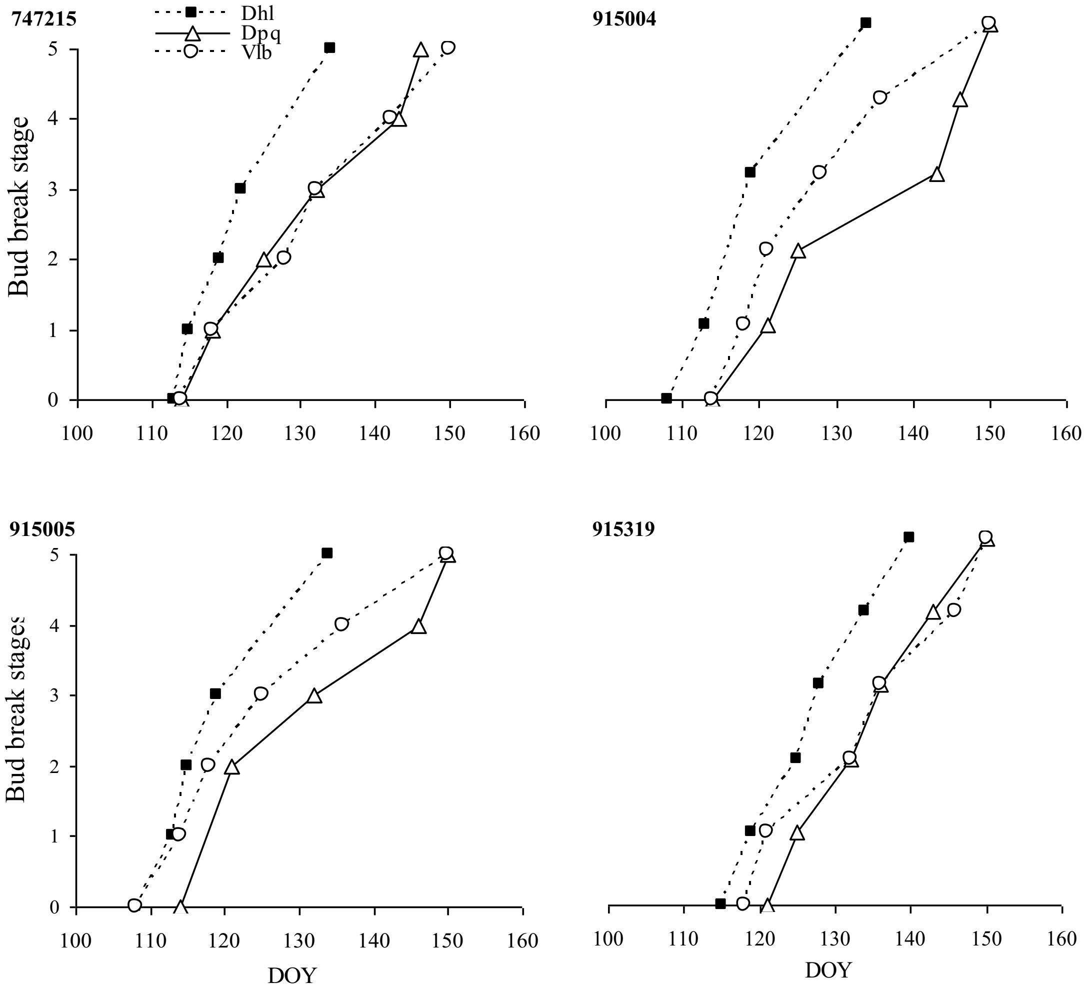

Fig. 1. Bud burst stages in 2009 for four hybrid poplar clones at the three sites (*) located along a latitudinal gradient in the boreal region of eastern Canada. Error bars were removed for clarity (*) Sites. Dhl: Duhamel; Dpq: Duparquet; Vlb: Villebois. DOY: Day of the year.

change between Dpq and Vlb except for clone 747215, where it was greater (Fig. 3A).

Maximum carboxylation rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (Vc_{max}) was the highest for all clones at the southern site (Dhl) where it ranged between 88 and 113 μmol s^{-1} m^{-2}. Mean Vc_{max} decreased northwards (Vlb) by 8% to 40% except for clone 747215 (Fig. 3B). Dark respiration (R_d) was the lowest at Dhl for clones 747215 and 915004 (4 and 5.2 μmol s^{-1} m^{-2} respectively) and increased northwards except for the clone 915005 (Fig. 3C). Mean R_d of clone 915319 did not change across the three sites and was 4.8 μmol s^{-1} m^{-2} (Fig. 3C).

The ratio J_{max}/Vc_{max} was similar between the four clones at the southernmost site (mean = 1.75). It decreased significantly at Dpq and then increased at Vlb for clones 747215 and 915005 (Fig. 3D). Meanwhile J_{max}/Vc_{max} did not vary between Dhl and Dpq (1.74 on average) for the other clones and it increased northwards (Fig. 3D).

3.7. Plasticity

Leaf N_m plasticity along the latitudinal gradient (plasticity index TP_i) was greater than the plasticity of SLA (Table 6). The variance of SLA was particularly high for clones 747215 and 915004 (TP_i = 4.9 and 6.8 respectively), compared to clones 915005 and 915319 (TP_i = 1.2, on average). Leaf nitrogen concentration (N_m) variation along the latitudinal gradient was different between clones as TP_i ranged between 9 and 42 (Table 6). Plasticity of the photosynthesis variables (J_{max}, Vc_{max} and R_d) was greater than plasticity of the other leaf traits (SLA and N_m) with TP_i values often higher than 50 (Table 6). Clones had similar TP_i for R_d and J_{max} (72 and 64 on average, respectively) except for clone 915319 which had smaller values (TP_i = 22). The plasticity index for Vc_{max} was more variable between clones than J_{max} and R_d (TP_i for Vc_{max} ranged between 18 and 101; Table 6).

Bud burst last stage (BBLS) and BSS (Bud set starting) were less influenced by the latitude compared to their duration as TP_i for BBLS and BSS ranged 14–22 and 3–12, respectively, while TP_i of bud BBD and BSD ranged 64–99 and 12–101, respectively (Table 6). Plasticity of BB variables was more similar between clones than plasticity of BS variables. Bud set stages and BSD plasticity for clones 747215 and 915004 were much lower (TP_i = 12.2 and 37.5) than those of the other two clones (TP_i = 81 and 101). Plasticity of GD along the latitudinal gradient differed slightly between clones as TP_i ranged between 33 to 45 (Table 6).

3.8. Relationships between variables

Stem volume (V) was positively correlated with temperature (FFA, MAT, DDA and GDD) but not with mean annual rainfall (Table 7). It was also positively correlated with GD, N_m, J_{max} and Vc_{max} (data not shown) but negatively correlated with the DBB (Table 7). Leaf nitrogen concentration (N_m) was also negatively correlated with the DBB (Table 7). On the other hand, BS was not

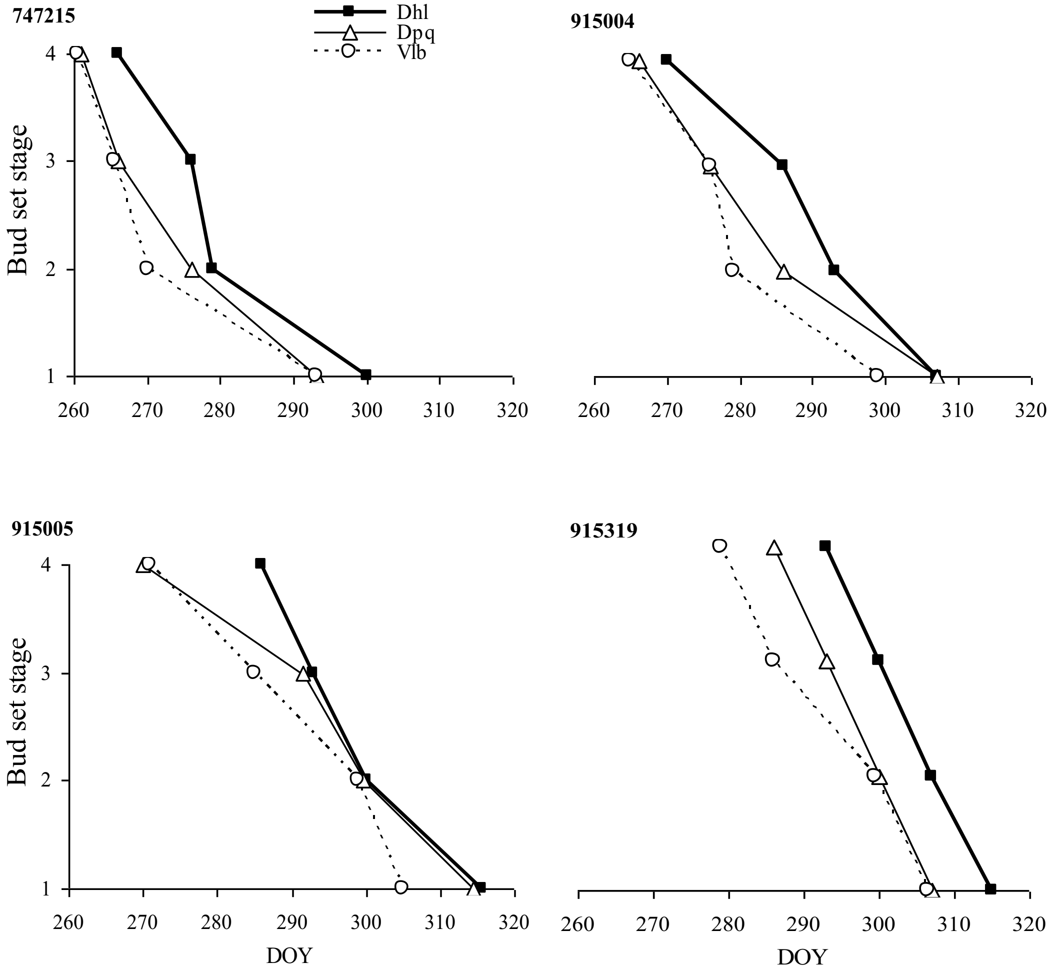

Fig. 2. Bud set stages in 2009 for four hybrid poplar clones at the three sites (*) located along a latitudinal gradient in the boreal region of eastern Canada. Error bars were removed for clarity (*) Sites. Dhl: Duhamel; Dpq: Duparquet; Vlb: Villebois. DOY: Day of the year.

correlated with any of the variable mentioned above (data not shown). Leaf nitrogen concentration (N_m) was correlated with J_max and Vc_max (Table 7). Maximum rate of electron transfer (J_max) was positively correlated to DDA and negatively correlated to precipitations (AR, Table 7).

4. Discussion

As expected, tree growth was greater at the southernmost site and decreased towards the north. Stem volume was positively correlated with the number of frost free days in April (FFA) and the mean annual temperature (MAT, Table 7). The number of FFA was determinant for the growing season length since bud burst is triggered by warm temperatures while MAT influences growth rate (Sakai and Larcher, 1987; Hanninen, 1990). Huang et al. (2010) reported that growing season temperature had a significant effect on growth of *Populus tremuloides* Michx. and *B. papyrifera* Marshall, along a latitudinal gradient in the boreal region of Canada. In the boreal zone, bud burst and leaf unfolding start earlier at lower latitudes where temperatures are warmer in early spring, marking the beginning of photosynthetic activity and biomass accumulation (Saxe et al., 2001 and references therein). In contrast, day length and thus the photoperiod is longer further north (from March 21 to September 21), which may partially compensate for the shorter growing season (Edmond et al., 1979). In this study, the difference in day length between the southernmost and the northernmost site was approximately 24 h over a growing season (2235 vs 2211 h, respectively). This may not have been long enough to compensate for the colder climate.

In addition to the latitudinal gradient, other environmental factors such as soil characteristics, topography, etc., could affect tree development. In our study, edaphic conditions (elevation and soil characteristics) were similar between sites (Elferjani et al., 2014) and temperature was the main difference between sites (Table 1). Site temperature did affect the timing of bud burst and also its duration. The period required between the start of bud burst and complete unfolding of leaves (phases 0 to 5) was 19, 28 and 32 days from the south to the north for the slowest growing clone (747215) which represents a difference of 13 days. This difference was only eight days for clone 915319, and it might reflect clonal differences in plasticity in response to changing temperature at the beginning of the growing season. The speed of bud flushing can be analogous of an increase in photosynthetic activity in the spring, measuring how fast trees can respond to the changes in temperature (Gu et al., 2003). Our results showed that clones with high speed of bud burst also had greater growth (e.g. clone 915319), showing a high level of plasticity to temperature variations which is consistent with previous works on poplar bud phenology (Kramer 1995; Rohde et al., 2011). The timing of bud set was more similar between sites compared to bud burst, probably because fall phenophases are mainly triggered by photoperiod (<10 h) and secondarily affected by temperature

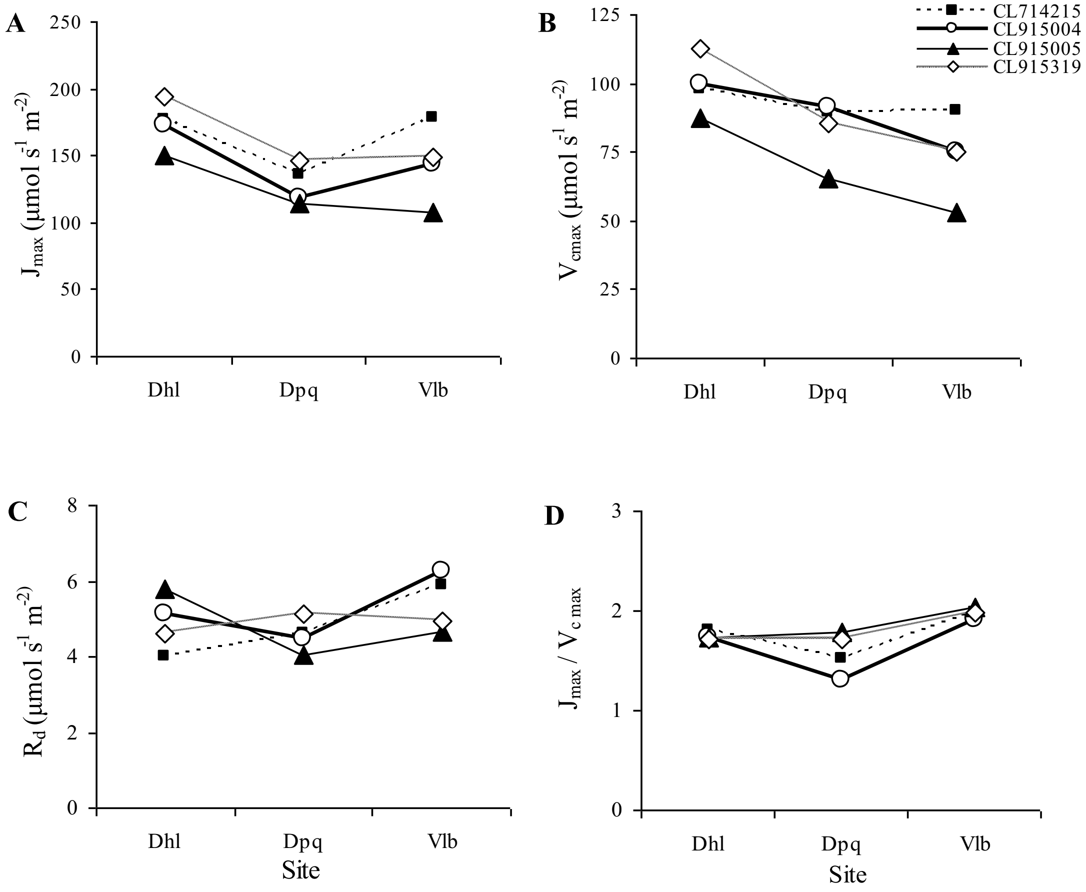

Fig. 3. Photosynthetic activity measurements in 2009: maximum photosynthetic rate of electron transport (J_{max}), maximum carboxylation rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (Vc_{max}), dark respiration (R_d) and J_{max}/Vc_{max} for four hybrid poplar clones at three sites $^{(*)}$ located along a latitudinal gradient in the boreal region of eastern Canada. Error bars were removed for clarity Sites. Dhl: Duhamel; Dpq: Duparquet; Vlb: Villebois.

Table 7
Pearsons' correlation coefficients (r) and corresponding *p*-values between meteorological and photosynthesis variables, bud phenology traits and leaf nitrogen concentration of the four hybrid poplar clones across the three sites. Significant correlations ($P < 0.05$) are in bold.

	V (2009)		Photosynthesis			Bud phenology			N_m
		R_d	Vc_{max}	J_{max}	Vc_{max}/J_{max}	BBLS	BBD	GD	
FFA (days)	**r = 0.59** **P = 0.04**	r = −0.30 P = 0.32	**r = 0.60** **P = 0.04**	r = 0.03 P = 0.91	**r = 0.62** **P = 0.03**	**r = -0.80** **P = < 0.01**	**r = -0.85** **P < 0.01**	**r = 0.72** **P < 0.01**	r = 0.27 P = 0.39
MAT (°C)	**r = 0.70** **P = 0.01**	r = −0.13 P = 0.68	**r = 0.62** **P = 0.03**	r = 0.11 P = 0.30	r = 0.40 P = 0.20	**r = -0.87** **P < 0.01**	**r = -0.85** **P < 0.01**	**r = 0.72** **P < 0.01**	r = 0.30 P = 0.35
DDA (°C)	**r = 0.65** **P = 0.02**	r = 0.35 P = 0.26	r = 0.49 P = 0.10	**r = −0.68** **P = 0.01**	r = −0.18 P = 0.56	**r = −0.78** **P < 0.01**	**r = -0.6** **P = 0.04**	r = 0.52 P = 0.08	**r = 0.54** **P = 0.05**
GDD (°C)	**r = 0.61** **P = 0.03**	r = −0.24 P = 0.44	**r = 0.68** **P = 0.01**	r = 0.31 P = 0.32	r = 0.40 P = 0.18	**r = −0.87** **P < 0.01**	**r = −0.85** **P < 0.01**	**r = 0.72** **P < 0.01**	r = 0.40 P = 0.19
AR (mm)	r = −0.06 P = 0.85	r = −0.53 P = 0.07	r = −0.10 P = 0.76	**r = −0.57** **P = 0.05**	**r = 0.71** **P = 0.01**	r = −0.13 P = 0.68	r = −0.26 P = 0.4	r = 0.22 P = 0.48	r = −0.2 P = 0.51

V: stem volume (10^{-3} m^3 tree^{-1}), N_m: per mass nitrogen concentration (mg g^{-1}), BBLS: bud burst last stage, BBD: bud burst duration, GD: growth season duration, J_{max}: maximum rate of photosynthesis electron transport, Vc_{max}: maximum rate of carboxylation limited by Rubisco, R_d: dark respiration, (mm), FFA: frost free days in bud burst month (April, days), MAT: mean annual temperature (°C), DDA: degree days of the bud burst month (°C), GDD: growing season degree days (°C), AR: annual rainfall.

(Vegis 1964; Howe et al., 1996; Rohde et al., 2011). Soolanayakanahally et al. (2009) reported that difference in bud set timing of balsam poplar (*Populus balsamifera* L.), grown at two sites with close latitudes but different mean temperatures (9.7 and 2 °C) was 28 days, while the difference in bud burst date was 44 days. In the present work, bud set duration was shorter northwards but bud set speed was greater for the most productive clones (Table 5). Heide (2003) demonstrated that bud burst and bud set are not completely independent processes as he found that warmer temperature during fall phenophases in boreal regions delayed the bud burst dates the following year for *Betula pendula* Roth, *Betula* pubescens Ehrh. and *Alnus glutinosa* (L.) Moench.

Warmer temperatures at the southern site might affect the magnitude of photosynthetic activity and tree growth. Generally, photosynthetic rate of cold adapted species increases with increasing temperature to reach an optimum around half of its thermal range (i.e. 15 °C; Larcher, 2003). When photosynthesis is not limited by light availability, the optimal temperature corresponds to the maximum thermodynamic activity of the enzymes (Sage and Kubien, 2007). In our study, P_n and Vc_{max} often decreased significantly northwards (Table 3 and Fig. 3), which is consistent with the pattern of photosynthetic response to temperature between 0 and 15 °C, described above. Ambient temperature might affect photosynthesis and tree growth of deciduous trees through soil temperature, which controls root system activity.

The shifts in photosynthetic capacity of higher plants in response to lower temperatures help maintaining carbon assimilation homeostasis (Schlichting, 1986; Sultan, 2000). Numerous studies have shown that photosynthetic rates of northern populations were greater than those of southern populations in temperate and boreal regions (Benowicz et al., 2000; Gornall and Guy, 2007; Soolanayakanahally et al., 2009). Other studies also demonstrated a decrease in the optimal temperature of photosynthesis when trees were moved from warmer to colder environments (Jonas and Geber, 1999). In our study, plasticity of J_{max} and Vc_{max} were greater than plasticity of the other leaf traits (SLA and N_m) and were also significantly different between clones across the three sites (Table 3). Mean J_{max} and Vc_{max} decreased northwards for all clones, except 747215, for which these parameters changed little across the latitudinal gradient. This suggests the presence of photosynthetic acclimation to lower temperatures (Jonas and Geber, 1999; Way and Yamori, 2013), but at the price of a slower growth rate. Indeed, the increasing R_d of clone 747215 (and 915004) northwards showed greater plasticity but implied greater carbon losses by respiration for biosynthesis and maintenance processes at the expense of growth (Atkin and Tjoelker, 2003; Yamori et al., 2009). This finding is consistent with the lower productivity of these clones northwards, compared to the best performing clones (915319 and 915005) for which R_d was steady or decreased. Remote sensing analysis showed that the duration of the growing season in the northern hemisphere has increased on average by 5 days per °C of temperature rise between 1981 and 1991 (Zhang et al., 2004). If we consider the effect of global warming, clone 747215, in contrast with the other clones, was too conservative and may not benefit from rising temperatures at northern latitudes.

Our results showed that mean SLA increased by 24% and 6% northwards for two of our clones (747215 and 915005), suggesting an acclimation to lower temperatures. Greater specific leaf area might contribute in increasing photosynthetic assimilation rate as it increases light interception area and reduces leaf thickness (Gunn et al., 1999; Niinemets, 2001, 2004). This result is consistent with the findings of Groom and Lamont (1997) and Prior et al. (2005), who showed that leaf mass per area (inverse of SLA) was lower and leaves were thicker when temperatures were higher or precipitations lower. Lower SLA reflects a greater investment in leaf structure (e.g. cell wall) and then leaf thickness for longer lifespan but also represents a limit for CO_2 diffusion from stomata to chloroplasts (Wright et al., 2002). This acclimation did not lead to similar yields between the northern and southern sites in our study, most probably because the growing season length overcame SLA changes. However, SLA of the most productive clone (915319) decreased northwards without decreasing net photosynthesis, which shows again contrasting responses of clones to changes of the environment along the gradient.

Previous studies on tree acclimation to unfavourable environments showed that modulation of developmental traits can be at the expense of biomass production (Nolet et al., 2008). In our study, the least productive clone had the lowest mean plasticity index (of all the traits) to latitudinal gradient (although greater TP_i for some leaf traits, Table 6), while the other clones (more productive) had greater mean TP_is. Taulavuori et al. (2010) found no growth reduction for southern provenances of *Pinus sylvestris* L. transplanted to northern latitudes in Finland. Our results showed that greater growth was often linked to greater clonal plasticity along the latitudinal gradient, particularly for phenological traits and SLA, suggesting a positive effect of plasticity on growth. However, we could not find a relationship between plasticity of photosynthetic capacity and growth performance of the clones across the three sites.

In conclusion, growth performance was not related to growth stability along the latitudinal gradient in our study, suggesting that low growth clones might adapt better to harsher environments without a noticeable decrease of productivity. Specific leaf area decreased northwards for the most productive clone and increased for the least productive one. This demonstrates that the effect of plasticity of leaf traits in reducing the impact of a less favourable environment on growth depends on clones and is not a general rule as suggested by some studies.

The plasticity of bud phenology was noticeable and correlated to stem volume growth along the latitudinal gradient. The most productive clone had a longer growing season, due to a faster development of bud burst (but not earlier) and a later bud set. Most clones did not show acclimation of their photosynthetic capacity to colder temperatures along the latitudinal gradient as Vc_{max} and J_{max} were low in the northern site and increased southwards. Consequently, establishing these clones at northern sites could be advantageous in the future since their photosynthetic capacity should increase in response to global rising temperatures. Clone 747215, however, had a steady photosynthesis capacity and a more stable growth across sites which suggest a greater adaptative photosynthesis for this clone, but at the cost of growth rate.

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References

Agriculture and Agri-food Canada. 2013. Plant hardiness zones of Canada. http://atlas.agr.gc.ca/agmaf/ (acessed May 2013.).

Atkin, O.K., Tjoelker, M.G., 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci. 8, 343–351.

Barić, M., Pećina, M., Šarčević, H., Kereša, S., 2004. Stability of four Croatian bread winter wheat (*Triticum aestivum* L.) cultivars for quality traits. Plant Soil Environ. 50 (9), 402–408.

Benowicz, A., Guy, R.D., El-Kassaby, Y.A., 2000. Geographic pattern of genetic variation in photosynthetic capacity and growth in two hardwood species from British Columbia. Oecologia 123, 168–174.

Bradshaw, A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13, 115–155.

Brown, K., van den Driessche, R., 2002. Growth and nutrition of hybrid poplars over 3 years after fertilization at planting. Can. J. For. Res. 32, 226–232.

Cannell, M., Smith, R., 1986. Climatic warming spring budburst and forest damage on trees. J. Appl. Ecol. 177–191.

Chuine, I., Beaubien, E.G., 2001. Phenology is a major determinant of tree species range. Ecol. Lett. 4, 500–510.

DeWitt, T.J., Sih, A., Wilson, D.S., 1998. Costs and limits of phenotypic plasticity. Trends Ecol. Evol. 13, 77–81.

Edmond, J.B., Senn, T., Andrews, F., Halfacre, R., 1979. Fundamentals of horticulture. Tata McGraw-Hill Publishing Co..

Elferjani, R., DesRochers, A., Tremblay, M.F., 2014. Effects of mixing clones on hybrid poplar productivity, photosynthesis and root development in northeastern Canadian plantations. For. Ecol. Manage. 327, 157–166.

Ellis, A.R., Hubbell, S.P., Potvin, C., 2000. In situ field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. Can. J. Bot. 78, 1336–1347.

Environment Canada. 2013. http://climate.weatheroffice.gc.ca. (accessed on May 2013.).

Fabbrini, F., Gaudet, M., Bastien, C., Zaina, G., Harfouche, A., Beritognolo, I., Beritognolo, I., Marron, N., Morgante, M., Scarascia-Mugnozza, G., Sabatti, M., 2012. Phenotypic plasticity, QTL mapping and genomic characterization of bud set in black poplar. BMC Plant Biol. 12, 47.

Farquhar, G.D., von Caemmerer, S., Berry, J.A., 1980. A biochemical model of photosynthetic C02 assimilation in leaves of C3 species. Planta 149, 78–90.

Francis, T., Kannenberg, L., 1978. Yield stability studies in short-season maize: I. A descriptive method for grouping genotypes. Can. J. Plant Sci. 58, 1029–1034.

Gornall, J.L., Guy, R.D., 2007. Geographic variation in ecophysiological traits of black cottonwood (*Populus trichocarpa*). Botany 85, 1202–1213 This article is one of a selection of papers published in the Special Issue on Poplar Research in Canada.

Grondin, P., 1996. Ecologie forestière. In: Bérard, J., Côté M, M. (Eds.), Manuel de foresterie. Presses de l'Université Laval, Québec, pp. 135–279.

Groom, P., Lamont, B.B., 1997. Xerophytic implications of increased sclerophylly: interactions with water and light in Hakea psilorrhyncha seedlings. New Phytol. 136, 231–237.

Gu, L., Post, W.M., Baldocchi, D., Black, T.A., Verma, S.B., Vesala, T., Wofsy, S.C., 2003. Phenology of vegetation photosynthesis. In: Schwartz, M.D. (Ed.), Phenology: An Integrative Environmental Science. Kluwer Dordrecht, pp. 467–486.

Gunn, S., Farrar, J.F., Collis, B.E., Nason, M., 1999. Specific leaf area in barley: individual leaves versus whole plants. New Phytol. 143, 45–51.

Hall, D., Luquez, V., Garcia, V.M., St Onge, K.R., Jansson, S., Ingvarsson, P.K., 2007. Adaptive population differentiation in phenology across a latitudinal gradient in European aspen (*Populus tremula* L.): a comparison of neutral markers, candidate genes and phenotypic traits. Evolution 61, 2849–2860.

Hanninen, H., 1990. Modelling Bud Dormancy Release in Trees from Cool and Temperate Regions (No. 213). Finnish Forest Research Institute.

Hansen, J., Sato, M., Ruedy, R., 2012. Perception of climate change. Proc. Natl. Acad. Sci. 109, 2415–2423.

Harley, P.C., Thomas, R.B., Reynolds, J.F., Strain, B.R., 1992. Modelling photosynthesis of cotton grown in elevated CO_2. Plant Cell Environ. 15, 271–282.

Heide, O., 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. Tree Physiol. 23, 931–936.

Howe, G.T., Gardne r, G., Hackett, W.P., Furnier, G.R., 1996. Phytochrome control of short-day induced bud set in black cottonwood. Physiol. Plant. 97, 95–103.

Huang, J., Tardif, J.C., Bergeron, Y., Denneler, B., Berninger, F., Girardin, M.P., 2010. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. Global Change Biol. 16, 711–731.

IPCC (Intergovernmental Panel on Climate Change), 2007. Climate Change 2007: The Physical Science Basis. Cambridge University Press, Cambridge, UK.

Jonas, C.S., Geber, M.A., 1999. Variation among populations of *Clarkia unguiculata* (*Onagraceae*) along altitudinal and latitudinal gradients. Am. J. Bot. 86, 333–343.

Keskitalo, J., Bergquist, G., Gardeström, P., Jansson, S., 2005. A cellular timetable of autumn senescence. Plant Physiol. 139, 1635–1648.

Kramer, K., 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warmin. Plant Cell Environ. 18, 93–104.

Larcher, W., 2003. Physiological plant ecology: Ecophysiology and stress physiology of functional groups, 4th ed. Springer, Berlin, Germany.

Leco Corp, 1986. CHN-600 elemental analyzer for macrosamples system. Application Bull. CHNP 2-84. LECO Corp., St. Joseph, MI 785-500.

Marron, N., Bastien, C., Sabatti, M., Taylor, G., Ceulemans, R., 2006. Plasticity of growth and sylleptic branchiness in two poplar families grown at three sites across Europe. Tree physiol. 26, 935–946.

Messier, C., Tittler, R., Kneeshaw, D.D., Gélinas, N., Paquette, A., Berninger, K., Rheault, H., Meek, P., Beaulieu, N., 2009. TRIAD zoning in Quebec: experiences and results after 5 years. For. Chron. 85, 885–896.

Niinemets, Ü., 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82, 453–469.

Niinemets, Ü., 2004. Adaptive adjustments to light in foliage and whole-plant characteristics depend on relative age in the perennial herb *Leontodon hispidus*. New Phytol. 162, 683–696.

Nolet, P., Delagrange, S., Bouffard, D., Doyon, F., Forget, E., 2008. The successional status of sugar maple (*Acer saccharum*), revisited. Ann. For. Sci. 65 208–208.

Paquette, A., Fontaine, Bastien, Berninger, F., Karine Dubois, K., Lechowicz, M.J., Christian Messier, C., Posada, J., Valladares, F., Brisson, J., 2012. Norway maple displays greater seasonal growth and phenotypic plasticity to light than native sugar maple. Tree Physiol. 32, 1339–1347.

Prior, L., Bowman, D., Eamus, D., 2005. Intra-specific variation in leaf attributes of four savanna tree species across a rainfall gradient in tropical Australia. Aust. J. Bot. 53, 323–335.

Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. Ann. Rev. Ecol. Syst. 16, 179–214.

Rehfeldt, G.E., Jaquish, B.C., 2010. Ecological impacts and management strategies for western larch in the face of climate change. Mitig. Adaptation Strategies Global Changes 15 (3), 283–306.

Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. PNAS 101, 11001–11006.

Richter, S., Kipfer, T., Wohlgemuth, T., Guerrero, C.C., Ghazoul, J., Moser, B., 2012. Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. Oecologia 169 (1), 269–279.

Rohde, A., Bastien, C., Boerjan, W., 2011. Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. Tree physiol. 31, 472–482.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2006. Conifers in cold environments synchronize maximum growth rate of tree ring formation with day length. New Phytol. 170, 301–310.

Sadras, V.O., Trentacoste, E.R., 2011. Phenotypic plasticity of stem water potential correlates with crop load in horticultural trees. Tree Physiol. 31, 494–499.

Sage, R.F., Kubien, D.S., 2007. The temperature response of C3 and C4 photosynthesi. Plant Cell Environ. 30, 1086–1106.

Sakai, A., Larcher, W., 1987. Frost survival of plants. Responses and Adaptation to Freezing Stress. Springer-Verlag, Berlin, Germany.

Saxe, H., Cannell, M.G., Johnsen, Ø., Ryan, M.G., Vourlitis, G., 2001. Tree and forest functioning in response to global warming. New Phytol. 149, 369–399.

Schlichting, C.D., 1986. The evolution of phenotypic plasticity in plants. Ann. Rev. Ecol. Syst. 17, 667–693.

Sharkey, T.D., 1985. O_2-insensitive photosynthesis in C_3 plants: Its occurrence and a possible explanation. Plant Physiol. 78, 71–75.

Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Drewes, E.C., Schroeder, W.R., 2009. Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsamifera* L.). Plant Cell Environ. 32, 1821–1832.

Stelluti, M., Caliandro, A., Stellacci, A.M., 2007. Influence of previous crop on durum wheat yield and yield stability in a long-term experiment. Ital. J. Agron. 2 (3), 333–340.

Sultan, S.E., 2000. Phenotypic plasticity for plant development, function and life history. Trends Plant Sci. 5, 537–542.

Taulavuori, E., Taulavuori, K., Niinimaa, A., Laine, K., 2010. Effect of ecotype and latitude on growth, frost hardiness, and oxidative stress of south to north transplanted Scots pine seedlings. Int. J. For. Res. 162084.

Valladares, F., Wright, S.J., Lasso, E., Kitajima, K., Pearcy, R.W., 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a panamian rainforest. Ecology 81, 1925–1936.

Van Kleunen, M., Fischer, M., 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. New Phytol. 166, 49–60.

Vegis, A., 1964. Dormancy in higher plants. Ann. Rev. Plant Physiol. 15, 185–224.

Visser, M.E., 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proc. R. Soc. B: Biol. Scie. 275, 649–659.

Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R., Kremer, A., 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Can. J. For. Res. 39, 1259–1269.

Von Caemmerer, S.V., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376–387.

Way, D.A., Yamori, W., 2013. Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. Photosynth. Res. 1–12.

Wright, I.J., Westoby, M., Reich, P.B., 2002. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. J. Ecol. 90, 534–543.

Yamori, W., Noguchi, K., Hikosaka, K., Terashima, I., 2009. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species. Plant Cell Physiol. 50, 203–215.

Zasada, J., David, A., Gilmore, D., Landhausser, S., 2001. Ecology and silviculture of natural stands of *Populus* species. In: Dickmann, D.I., Isebrands, J.G., Eckenwalder, J.E., Richardson, R. (Eds.), Poplar culture in North America. NRC Research Press, Ottawa, pp. 119–151.

Zhang, X., Friedl, M.A., Schaaf, C.B., Strahler, A.H., 2004. Climate controls on vegetation phenological patterns in northern mid and high latitudes inferred from MODIS data. Global Change Biol. 10, 1133–1145.