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Yield in 8 year-old hybrid poplar plantations on abandoned farmland along climatic and soil fertility gradients

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ABSTRACT

We evaluate, after 8 growing seasons, the effect of climate and soil characteristics on the biomass and volume yields of eight hybrid poplar plantations established on abandoned farmland sites, all planted during the same week, with the same five unrelated clones (D × N, T × D, N × M, DN × M, and M × B hybrids), and with the same silvicultural treatments. These plantations are located along an elevation (from 80 to 450 m), or climatic gradient, but also along an edaphic gradient (from rich bottomlands to poorer hillside slopes). The largest effect that affected poplar volume yield was the Site effect (*F* ratio = 134), followed by the Clone effect (*F* ratio = 17), both effects being highly significant ($p < 0.001$). However, a highly significant Site × Clone interaction suggests that the unrelated hybrid poplar clones used in this study respond differently to the environmental gradients. The large Site effect was expressed by hybrid poplar yield (5 clones mean) being as high as 22.4 m^3 ha^{-1} $year^{-1}$ in the bottomlands of the Bedford site, where all clones reached their highest yield, and as low as 1.1 m^3 ha^{-1} $year^{-1}$ on the poorer soils of hill slopes at Stornoway. Only one clone was the highest yielding at all sites, the N × M hybrid.

The yield extremes observed highlight the strong control of elevation (proxy for climate), but also site fertility in terms of P availability on hybrid poplar productivity after 8 years. Results from the stepwise regressions showed that *Populus maximowiczii* hybrids (N × M, DN × M, and M × B) productivity was first influenced by P availability followed by elevation, while D × N and T × D hybrids productivity was primarily influenced by elevation followed by P availability. Hybrid poplars related to the *Tacamahaca* section, and especially *P. maximowiczii* hybrids, were therefore able to produce relatively high yields (above 10 m^3 ha^{-1} $year^{-1}$) on fertile sites located at higher elevation. In addition, simple regression models between elevation and productivity showed that the M × B hybrid, which has both of its parents from the *Tacamahaca* (balsam poplar) section, was the least influenced by elevation, an indication of its greater adaptation to colder climate.

Because all clones strongly responded to soil P availability, clone selection cannot compensate for inadequate site selection in terms of soil fertility. Choosing high fertility abandoned farmland sites is therefore of paramount importance for hybrid poplar production.

1. Introduction

It is forecasted that by 2050, 75% of the industrial timber supply will come from planted forests, and about 50% from fast-growing plantations, in order to meet the increasing demand for wood, fibre and biomass (Sedjo, 2001). These fast-growing plantations are expected to be established on small portions of the land, while natural forests will be increasingly protected and managed for multiple ecosystem services (non-timber forest products, wildlife refuges, carbon sequestration, recreation and tourism, culture and knowledge, etc.), and not exclusively for wood production (Hunter, 1990; Sedjo, 2001).

The conversion of natural forests to higher yielding plantations is very common throughout the world (FAO, 2001), with noticeable impacts on biodiversity and ecosystem services, such as carbon sequestration (Guo and Gifford, 2002; Schroth et al., 2002; Kanowski et al., 2005; Sohngen and Brown, 2006; Danielsen et al., 2009). On the other hand, afforestation of degraded lands or abandoned farmland appears to be a sustainable alternative to forest conversion because it has the potential to provide wood and many other ecosystem services outside of natural forests (Licht and Isebrands, 2005; Chazdon, 2008; Metzger and Hüttermann, 2009).

In temperate ecosystems, fast-growing species such as hybrid poplars are frequently used to afforest marginal agricultural lands (Christersson, 2008; Mao et al., 2010). High productivity,

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versatility, and ease of cloning by vegetative means has made hybrid poplars one of the most planted and studied trees in temperate ecosystems (Dickmann, 2001; Ball et al., 2005; Cooke and Rood, 2007). Besides their high yields, afforested stands of hybrid poplars in agricultural landscapes also have the potential to improve flood control (Perry et al., 2001), carbon sequestration (Niu and Duiker, 2006), water quality, sediment and erosion control (Updegraff et al., 2004), native plant habitat (Weih et al., 2003; Fortier et al., 2011) and nutrient storage (Fortier et al., 2010b).

In south-eastern Canada, hybrid poplar cultivation is mainly done on clearcut sites and abandoned farmlands (Lteif et al., 2007). The most productive poplar plantations are usually in agricultural areas where volume and biomass yields can reach 29 m^3 ha^{-1} $year^{-1}$ and 18 tDM ha^{-1} $year^{-1}$ (Zsuffa et al., 1977; Labrecque and Teodorescu, 2005). Hybrid poplar yields as high as 39.6 m^3 ha^{-1} $year^{-1}$ after 6 years have also been reported in riparian buffer strips growing along a stream in a fertile pasture of southern Québec (Fortier et al., 2010a). However, in the same study, yields as low as 4 m^3 ha^{-1} $year^{-1}$ were also reported on the least fertile study site, clearly illustrating the high sensitivity of hybrid poplars to site quality.

In terms of land area, more than 85,000 ha of abandoned farmlands exists in southern Québec and some of these may be suitable for hybrid poplar cultivation (Vouligny and Gariepy, 2008). The gradual concentration and intensification of agricultural practices in the St-Lawrence valley over the last 50 years has been identified as the main cause of the abandonment of vast areas of less productive or stonier agricultural lands, often pastures (Pan et al., 1999; Bélanger and Grenier, 2002).

In terms of site characteristics (soil, vegetation, previous land use, etc.), these abandoned farmlands are dissimilar (Benjamin et al., 2005) and may offer unequal potential for hybrid poplar cultivation, as observed in France (Soulères, 1995). In fact, some abandoned farmland of southern Québec have an excellent potential for poplar cultivation (Labrecque and Teodorescu, 2005), while others may need high inputs of fertiliser to become marginally productive (Lteif et al., 2007).

This is not surprising given the high sensitivity of hybrid poplars to site quality. Strong correlations between growth and nitrogen availability have been measured in southern Québec (Fortier et al., 2010a) and elsewhere (Stanturf et al., 2001; Brown and Driessche, 2002; Coleman et al., 2006). Other soil characteristics such as soil texture, pH, drainage, and water availability are also known to strongly affect hybrid poplar growth (Boysen and Strobl, 1991; Tabbush and Beaton, 1998; Stanturf et al., 2001; Bergante et al., 2010; Pinno et al., 2010). Elevation, or growing season length, is another major factor identified by Tabbush and Beaton (1998). These authors also pointed out that different poplar hybrids and clones respond differently over elevation and site fertility gradients.

Consequently, clone selection is a key aspect of poplar cultivation (Lo and Abrahamson, 1996; Stanturf et al., 2001). In Québec, a list of about 40 recommended clones exits (Périnet et al., 2008). However, not much is known about their real productivity across different soil and climatic conditions, and potential genotype × environment (Site × Clone) interactions (Zalesny et al., 2009b) are unknown. In fact, studies that have taken all of these factors into consideration are generally rare worldwide (Tabbush and Beaton, 1998; Bergante et al., 2010). In a previous study, we observed large growth differences between clones of differing parentage, with hybrids *Populus nigra* × *Populus maximowiczii* (N × M) and *P. maximowiczii* × *Populus balsamifera* (M × B) being very productive in riparian buffers of southern Québec (Fortier et al., 2010a). Is this high productivity possible as well in older upland hybrid poplar plantations?

In this study we evaluate, after 8 growing seasons, the effect of elevation (climate) and soil characteristics on the biomass and volume yields of eight poplar plantations on abandoned farmland sites, all planted during the same week, with the same five unrelated clones, and with the same site preparation and silvicultural treatments. These plantations are located along an elevation gradient (from 80 to 450 m), but also along an edaphic gradient (from rich bottomlands to poorer hillside slopes).

The main objectives of this study are (1) to determine the yields (volume and biomass) of 8-year old hybrid poplar plantations across eight representative abandoned farmland sites of southern Québec, Canada, (2) to determine which clones are the most productive along these environmental gradients, and (3) to evaluate which environmental factors have the most influence on site productivity, as well as individual clone productivity.

2. Materials and methods

2.1. Study sites

The study sites are all located on privately owned abandoned farmland in the Eastern Townships region of southern Québec, Canada (Fig. 1). Eight different plantation sites, belonging to three forest vegetation zones, from milder to colder climate (and generally better to poorer soils) were selected for this study. The plantation sites were chosen along a regional gradient of elevation (climate) and soil characteristics, with abandoned farmland vegetation varying from herbaceous weed cover only, to important shrub cover, possibly reflecting different times since abandonment of agriculture (Tables 1 and 2). The geology of the study area is complex, but the bedrock is almost completely covered with thick surface deposits (Robitaille and Saucier, 1998). The region is characterised by a continental subhumid moderate climate for the sugar maple-hickory and the sugar maple-basswood forest vegetation zones, and a continental subpolar–subhumid climate for the sugar maple-yellow birch forest vegetation zone (Robitaille and Saucier, 1998). Climate data from Environment Canada (2010) show variations in growing season precipitation, annual mean temperature and growing degree days (above 5 °C) for meteorological stations nearest to the different plantations sites (Table 1). Although some sites are located in hilly landscapes, all plantation sites were nearly flat, with slopes always under 5%. All plantations were established on thick glacio-fluvial or glacial surface deposits (>2 m of available rooting depth), which is typical of agricultural sites of the studied region (Cann and Lajoie, 1943; Cann et al., 1948; Robitaille and Saucier, 1998).

2.2. Experimental design

A randomised block plantation design was used at each of the 8 sites, with 3 blocks (replicates) and 9 poplar clones. Only the 5 clones with the most different parentages were used in this study. Therefore, the present study was done with a total of 120 experimental plots (8 sites × 5 clones × 3 blocks) analysed in a factorial experiment (Petersen, 1985). In this study, blocking was used to control for environmental heterogeneity at the site level (Gotelli and Ellison, 2004). Blocks were nested within sites. Each block contained 5 experimental plots (one per clone). Each experimental plot was 12 m × 12 m in size (144 m^2) and contained 12 trees of a single clone, for a total of 180 trees per site and 1440 trees across the whole experimental design. At each site, one guard row of poplar trees was planted around the entire perimeter of the plantation to reduce edge effects on poplar growth.

This design allowed us to test 5 poplar clones in 8 different sites simultaneously, as a series of similar experiments, a procedure quite common in crop cultivar evaluation (Steel and Torrie,

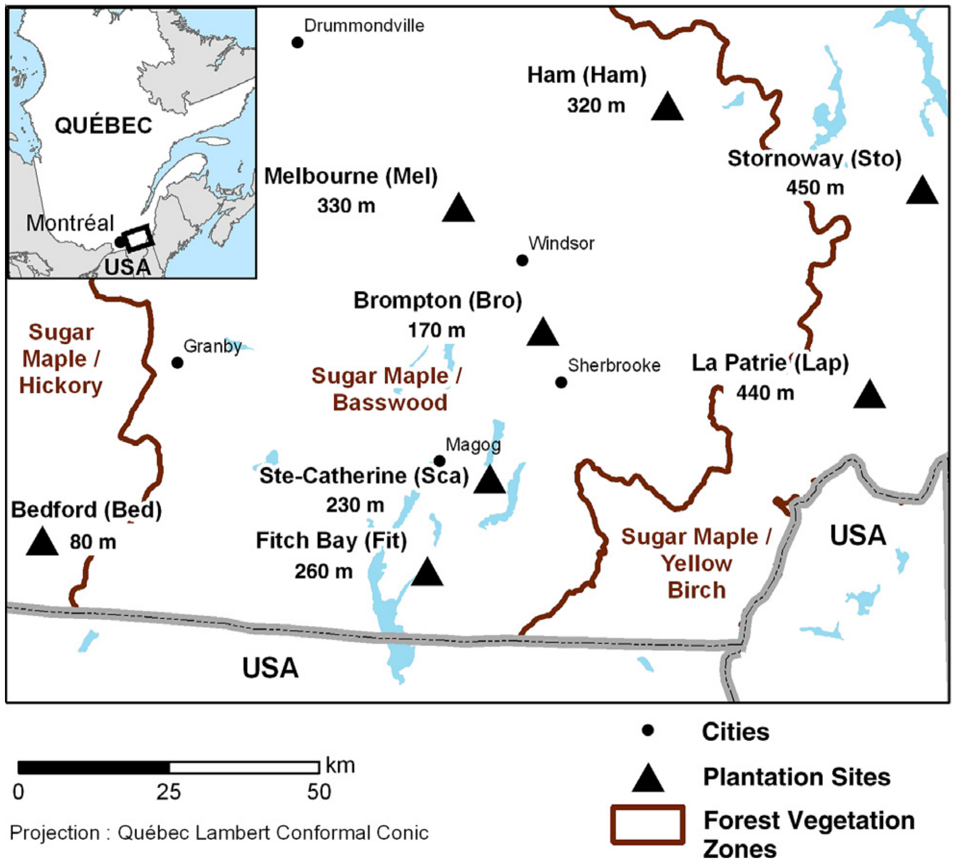

Fig. 1. Plantation location sites in southern Québec, Eastern Canada (Sherbrooke 45.40°N; 71.88°W).

Table 1
Elevation, forest vegetation zones, pre-plantation vegetation and climatic data of the hybrid poplar plantation sites.

Sites	Elev. (m)	Forest vegetation zones[a]	Pre-plantation vegetation	Mean annual temp. (°C)[b]	Degree days (>5 °C)[b]	May–Sept. precip. (mm)[b,c]
Bedford	80	Sugar maple-hickory (1a-T)	Herbs	6.0	2061.3	106.5
Brompton	170	Sugar maple-basswood (2c-T)	Herbs	5.3	1884.1	113.7
Ste-Catherine	230	Sugar maple-basswood (2c-T)	Herbs	5.3	1859.9	109.7
Fitch Bay	260	Sugar maple-basswood (2c-T)	Herbs and shrubs	5.1	1805.6	110.7
Ham	320	Sugar maple-basswood (2c-T)	Herbs	4.0	1648.5	114.5
Melbourne	330	Sugar maple-basswood (2c-T)	Herbs and shrubs	5.3	1860.7	108.9
La Patrie	440	S. maple-yellow birch (3d-M)	Herbs	3.7	1582.8	116.6
Stornoway	450	S. maple-yellow birch (3d-M)	Shrubs	3.3	1489.9	122.5

[a] Forest vegetation zones are described in the materials and methods section.
[b] Mean annual temperature, growing degree-days and precipitation data are approximate. They were obtained from the nearest meteorological station; these are often as much as 50 km distant from plantations and at different elevations.
[c] May–September precipitation data (growing season) are the 30 years climatic normal.

Table 2
Soil characteristics (0–15 cm) of the hybrid poplar plantation sites.

Sites	Textural class	pH (water)	C/N ratio	Organic matter (%)	N total (g kg^{-1})	P avail. (kg ha^{-1})	Ca (kg ha^{-1})	K (kg ha^{-1})	Mg (kg ha^{-1})
Bedford	Sandy loam	5.36	8.2	4.87	3.20	76.6	2781	156	183
Brompton	Clay loam	5.51	8.9	5.81	2.91	60.0	2745	217	271
Ste-Catherine	Loam	5.00	11.3	6.69	3.13	50.4	594	117	171
Fitch Bay	Loam	5.30	10.1	6.14	3.03	11.9	1297	109	226
Ham	Loam	4.77	10.5	8.46	3.97	25.5	616	93	51
Melbourne	Loam	5.37	10.4	6.67	3.36	17.4	1403	107	104
La Patrie	Silty loam	5.09	9.4	6.34	3.51	58.3	2079	125	103
Stornoway	Silty loam	5.45	11.8	9.85	4.34	9.0	3100	136	209
SE		0.04	0.1	0.25	0.14	7.8	129	8	13
$p <$		0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001

1980). All poplars were planted with a spacing of 4 m × 3 m, for an initial density of 833 stems per hectare.

Site preparation included ploughing and disking each abandoned farmland site in fall 1999, to physically enhance soil conditions and facilitate plantation the following spring. Neither lime nor fertiliser applications (organic or chemical) were made before or during the course of the study. In the spring of 2000, rooted cuttings with 2 m-long stems were planted manually with shovels at 30–40 cm depth, in 3 rows of 4 trees per experimental plot, 4 m between rows and 3 m between trees within a row. Rooted cuttings were preferred to standard cuttings, as recommended by Zsuffa et al. (1977), in order to improve initial survival in more widely spaced plantations, where each tree is important. Planting stock (1–0) was provided by the Berthierville nursery of the Ministère des Ressources naturelles et de la Faune (MRNF) of Québec.

Five unrelated hybrid poplar clones were used in this study: *Populus trichocarpa* × *deltoides* (T × D-3230), *Populus deltoides* × *nigra* (D × N-3570), *Populus canadensis* × *maximowiczii* (DN × M-915508), *P. nigra* × *maximowiczii* (N × M-3729) and *P. maximowiczii* × *balsamifera* (M × B-915311) (Table 3). The 5 poplar clones were chosen because they had different growth patterns, physiological characteristics, and because they had been selected for superior disease resistance/tolerance and growth characteristics in MRNF genetic selection trials in southern Québec (Périnet et al., 2008).

None of the planted poplar clones were protected against deer browsing with fences or chemical deterrents. Competing vegetation was eliminated with glyphosate herbicide application over the entire plantation area in June 2000, and between plantation rows only in June 2001. No herbicide application was made in the third year of the study (2002) or thereafter. Herbicide spray applications were done with a modified Argo-type small recreational vehicle, with a boom sprayer equipped with a rubber skirt to avoid damaging the trees with spray drift.

2.3. Soil characteristics

One composite soil sample was taken at 0–15 cm depth (mainly the Ap horizon) in each experimental plot in 2007, in order to determine soil pH and concentrations of Ca, Mg, K, available P, total N, total C and C/N ratio (Table 2). A composite sample at the block level was used to determine soil textural class (Table 2). All soil samples were air dried and shipped to Agridirect Inc. soil analysis lab in Longueuil (Québec); methods used are those recommended by the Conseil des productions végétales du Québec (1988). For particle size analyses, the Bouyoucos (1962) method was used and textural class was determined in accordance with the Canadian Soil Classification Committee (Comité d'experts sur la prospection pédologique d'Agriculture Canada, 1987). The determination of soil pH was made using a 2:1 ratio of water to soil. Calcium, Mg, K and P were extracted with the Mehlich III method (Tran and Simard, 1993) and determined using ICP spectrophotometry (US Environmental Protection Agency, 1983). Soil total N and C content were determined by the combustion method at high temperature (960 °C) followed by thermal conductivity detection. Carbon and N analyses were conducted by the Centre for Forest Research Soil Laboratory at the University of Sherbrooke (Qc, Canada).

2.4. Survival and deer browsing

In each plot, survival of poplar trees was determined in October 2007. The presence or absence of deer browsing, on the dominant stem of each poplar tree, was recorded in 2000 at the end of the first growing season. In this study, deer browsing is expressed as the number of trees browsed in a plot divided by the total number of trees in the plot (expressed as a percentage).

2.5. Hybrid poplar sampling, regression procedures and yield measurements

Near the end of the 8th growing season (from September to October 2007), we selected one representative hybrid poplar in each experimental plot, for a total 120 trees (each tree represents 12 m^2 of plot area). In each plot, this representative tree was selected because it was the closest to the average diameter at breast height of all hybrid poplars in the plot. The diameter at breast height (DBH) range for these 120 trees was 3.0–25.2 cm (Table 4). Trees were cut and aboveground compartments (branches and stem) were separated and weighed fresh using a tripod scale. Branches were only weighted in 40 trees (8 trees per clone). Subsamples from stem and branches were immediately weighed in the field and taken back to the lab for determining dry weight.

In order to calculate stem volume (outside of the bark) for the 120 sampled trees the following measurements were taken: tree base diameter, DBH, length from the tree base to 10 cm diameter, and length from the tree base to 3 cm diameter. For larger trees (DBH > 10 cm), stem volume was calculated for three sections of the stem: (1) tree base diameter to DBH, (2) DBH to 10 cm diameter, and (3) 10 cm diameter to 3 cm diameter. For smaller trees (DBH < 10 cm) volume was calculated for two sections of the stem: (1) tree base diameter to DBH and (2) DBH to 3 cm diameter. Volumes of different stem sections were then summed to obtain total stem volume for each of the sampled hybrid poplars (Fortier et al., 2010a). Volume calculations were made using the following equation (Perron, 1996):

$$V = \pi/12(D_1^2 + D_2^2 + D_1D_2)L$$

where, V is the volume of a stem section, D_1 is the base diameter of the stem section, D_2 is the diameter at the top of the stem section, and L is the length of the stem section.

With data from the stems of 24 trees per clone and branches from 8 trees per clone, regression models for volume and biomass versus DBH were developed, with DBH being the predictor variable (x) and biomass (stem or branches) and stem volume being the response variable (Y) (Table 4). Residuals were plotted and compared to a normal distribution in order to determine the goodness-of-fit according to the Shapiro–Wilk W test. Regression model selection was based on both the fit (R^2) of the regression and the goodness of fit (W). Therefore, when the fit of two different models was comparable for a given clone, the model with the highest normality in the distribution of residuals was always chosen. Final regression models, developed using only power and

Table 3
Name and parentage of the five hybrid poplar clones.

Clone number	Scientific name (common name)	Parentage	Section	Origin
3230	*P.* × *generosa* A. Henry (Boelare)	T × D	*Tacamahaca* × *Aigeiros*	Belgium
3570	*P.* × *canadensis* Moench	D × N	*Aigeiros* × *Aigeiros*	Belgium
3729	*P. nigra* × *P. maximowiczii* (NM6)	N × M	*Aigeiros* × *Tacamahaca*	Germany
915311	*P. maximowiczii* × *P. balsamifera*	M × B	*Tacamahaca* × *Tacamahaca*	Québec
915508	*P.* × *canadensis* × *P. maximowiczii*	DN × M	(*Aigeiros* × *Aigeiros*) × *Tacamahaca*	Québec

Table 4
Regressions between diameter at breast height (cm), as predictor variable (x), and stem volume (dm^3), stem dry biomass (kg), and branch dry biomass (kg), as response variables (Y). For each model, goodness of fit, expressed by the Shapiro–Wilk statistic (W), is presented with its associated p-value. All models are significant at $p < 0.001$ and all coefficients are significant at $p < 0.05$.

Tree components and clone number	Trees harvested (n)	DBH range (cm)	Model	R^2	F-value	W	$p < W$
Stem volume							
T × D-3230	24	4.4–24.1	$Y = 0.1095x^{2.4796}$	0.99	2882	0.99	0.999
D × N-3570	24	3–25.2	$Y = 0.1135x^{2.4817}$	0.99	2676	0.97	0.60
N × M-3729	24	6.5–21.6	$Y = 0.0727x^{2.6667}$	0.99	2225	0.95	0.28
M × B-915311	24	5.7–19.8	$Y = 0.9592x^2–10.311x + 39.614$	0.98	515	0.95	0.28
DN × M-915508	24	5.5–20.4	$Y = 1.0122x^2–10.924 + 39.894$	0.98	648	0.98	0.79
5 Clones	120	3–25.2	$Y = 0.102x^{2.5334}$	0.99	12,487	0.99	0.88
Stem biomass							
T × D-3230	24	4.4–24.1	$Y = 0.0967x^{2.1448}$	0.97	726	0.94	0.21
D × N-3570	24	3–25.2	$Y = 0.0717x^{2.233}$	0.98	1033	0.97	0.78
N × M-3729	24	6.5–21.6	$Y = 0.388x^2–5.0416x + 25.595$	0.96	233	0.96	0.39
M × B-915311	24	5.7–19.8	$Y = 0.3178x^2–3.6051x + 16.71$	0.96	246	0.96	0.53
DN × M-915508	24	5.5–20.4	$Y = 0.4032x^2–5.058x + 21.657$	0.98	286	0.98	0.82
5 Clones	120	3–25.2	$Y = 0.0741x^{2.27}$	0.97	3740	0.97	0.02*
Branch biomass							
T × D-3230	8	7.9–22.5	$Y = 0.0127x^2 + 0.7656x - 3.1258$	0.94	41	0.98	0.96
D × N-3570	8	5.0–21.4	$Y = 0.0344x^2 + 0.0023x + 0.7317$	0.98	144	0.96	0.83
N × M-3729	8	6.5–21.6	$Y = 0.0055x^2 + 1.5728–7.7484$	0.98	96	0.95	0.69
M × B-915311	8	5.9–18.8	$Y = 0.1029x^{1.8669}$	0.98	267	0.96	0.83
DN × M-915508	8	5.5–20.4	$Y = 0.0848x^{1.9031}$	0.98	309	0.95	0.68
5 Clones	40	5.5–22.5	$Y = 0.0947x^{1.8164}$	0.90	338	0.93	0.02*

* A small p-value rejects the null hypothesis (H_0 = residuals follow a normal distribution).

polynomial functions, had a R^2 ranging from 0.98–0.99 for stem volume, 0.96–0.98 for stem biomass, 0.94–0.98 for branch biomass; all were highly statistically significant at $p < 0.001$ (Table 4). Because tree architecture and parentages vary from one poplar clone to another, different regression models were used for each clone. This is a common procedure to evaluate hybrid poplar yields (Heilman et al., 1994; Laureysens et al., 2004; Fortier et al., 2010a). We also produced general regression models, which were done with the 120 harvested trees. These models may be used to calculate volume and biomass of clones that were not included in the design. However, the 5 clones stem and branch biomass regressions should be used with caution because the distributions of residuals lack normality according to the Shapiro–Wilk test (Table 4). This is not surprising given the different tree architecture and wood density of the hybrid poplar clones studied (Pliura et al., 2007; Fortier et al., 2010a).

Regressions developed for each clone were then used to estimate aboveground biomass and volume yield for each living tree in the entire experimental design. The DBH measurements were taken from late October to early November 2007, at the end of the 8th growing season. All biomass and volume data per plot were then scaled up to one hectare area and divided by poplar age (8 years) in order to produce yield data for purposes of comparison with other studies. In each plot, mean volume per tree data were also obtained by dividing total volume accumulated in a plot divided by the number of living trees.

In this study the term "woody biomass" represents the sum of stems and branches on a per hectare basis, which is the total harvestable dry aboveground woody biomass. The term "volume" refers to the stem wood volume outside the bark.

2.6. Statistical analyses

ANOVA tables were constructed in accordance with Petersen (1985), where degrees of freedom, sum of squares, mean squares and F values were computed. When a factor is declared statistically significant (Site, Clone and Site × Clone interactions), the standard error of the mean (SE) was used to evaluate differences between means for three levels of significance ($^*p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$). For total volume yield, mean volume per tree and survival data, we did not include standard errors (SE) in graphs showing Site × Clone interactions for the sake of clarity. However, levels of significance and standard errors (SE) are always mentioned on the figures. All of the ANOVAs were run with the complete set of data (8 sites, 5 clones, 3 blocks = 120 experimental plots). For the presentation of results in figures, abbreviations of the names of plantation sites are used (Bedford = Bed, Brompton = Bro, Fitch Bay = Fit, Ham = Ham, La Patrie = Lap, Melbourne = Mel, Ste-Catherine = Sca, Stornoway = Sto).

A stepwise multiple regression procedure was used to determine which environmental factors explain the most variation in hybrid poplar volume yield. Volume yield ($m^3\ ha^{-1}\ year^{-1}$) was used as the response variable, while environmental factors (elevation, soil characteristics and deer browsing) were used as predictor variables. Regressions were run separately for the 5 clones included in the study (n = 24 plots per clone) (Tabbush and Beaton, 1998; Bergante et al., 2010), but a regression with the complete data set (all 5 clones) was also done (n = 120 plots).

Prior to regression analyses, a correlation matrix was used to eliminate variables showing high colinearity (Gotelli and Ellison, 2004). The correlation threshold for making a decision concerning variable elimination was set at $r > 0.5$. When two correlated predictor variables were identified, the one that was the most correlated with the response variable (volume yield) was chosen. The following predictor variables were retained to model hybrid poplar productivity: elevation, deer browsing, soil P availability, soil Ca, soil K and soil Mg. The plantation site elevation variable was chosen over growing degree days and mean annual temperature because these two climatic variables are approximate. They were obtained from the nearest meteorological stations, which are often as much as 50 km distant from plantation sites and at different elevations. Based on simple regression models developed between key environmental variables and volume yield, natural logarithmic (ln) transformation of some environmental variables was done when considered appropriate.

For each stepwise regression, the choice of predictor variable entering the model (forward selection) was based on the change in F-statistic of the fitted model (Gotelli and Ellison, 2004). All statistical analyses were done with JMP 6 from the SAS Institute (Cary, NC).

3. Results and discussion

In this study, the largest effect that affected hybrid poplar volume yield on abandoned farmland after 8 years was the Site effect (F ratio = 134), followed by the Clone effect (F ratio = 17), both being highly significant ($p < 0.001$) (Fig. 2). However, a highly significant Site × Clone interaction (F ratio = 2.6, $p < 0.001$) suggests that the unrelated hybrid poplar clones used in this study respond differently to the environmental gradients along which plantations were established (Fig. 2). The Site effect was also the largest effect, followed by the Clone effect, for mean deer browsing (Table 5), total aboveground woody biomass (Table 6), mean volume per tree (Fig. 3) and survival (Fig. 4). Significant or nearly significant interactions were also observed (interaction results not shown for deer browsing and total aboveground biomass). First, we discuss why the Site effect was so large in this study, and secondly, why important Site × Clone interactions were observed for volume yield, mean volume per tree and survival.

3.1. Elevation and site fertility: the main factors controlling hybrid poplar volume yield on abandoned farmland

The large Site effect was expressed by hybrid poplar yield (5 clones mean) being as high as 22.4 m^3 ha^{-1} $year^{-1}$ at Bedford and as low as 1.1 m^3 ha^{-1} $year^{-1}$ at Stornoway (Fig. 2). These extremes in yields highlight the strong control of elevation, a proxy for mean annual temperature or growing degree days, but also of site soil fertility, particularly in terms of P availability, on hybrid poplar growth after 8 years (Figs. 5 and 6, Tables 7 and 8). When considering the five clones in the model (n = 120), the stepwise regression shows that elevation was the most important factor affecting hybrid poplar yield, followed by soil P availability and soil Ca content (Table 8). Elevation had a negative effect on volume yield, while soil P availability and Ca content had a positive effect (Table 8). This corroborates the findings of Tabbush and Beaton (1998) who showed that hybrid poplar growth in England was negatively affected by elevation and positively affected by soil fertility (higher soil P content and soil pH).

Table 5
Mean percent deer browsing at the end of the planting year (2000) at each site and for each clone.

Sites	Deer browsing (%)	Clone	Deer browsing (%)
Fitch Bay	89.1	T × D-3230	80.9
Melbourne	72.2	D × N-3570	77.1
Ham	67.0	N × M-3729	57.6
Ste-Catherine	60.0	DN × M-915508	44.8
Stornoway	56.9	M × B-915311	20.0
La Patrie	54.4		
Bedford	42.8		
Brompton	6.1		
SE	4.2	SE	3.3
p <	0.001	p <	0.001

Elevation appears to be a very important factor affecting hybrid poplar growth in abandoned farmland of southern Québec, not only because hybrid poplars are sensitive to growing season length (Tabbush and Beaton, 1998), but also because favourable soil characteristics (low C/N ratio, high P and K) for poplar growth are likely to be found on sites at lower elevations (Table 7). Soil nitrate (NO_3) availability was the main factor related to volume growth in hybrid poplar riparian buffers located in the same study area (Fortier et al., 2010a), but only total N was measured in this study and it was not positively associated to hybrid poplar growth (Table 7).

It is not surprising that the highest yield (5 clones mean = 22.4 $m^3 ha^{-1}$ $year^{-1}$) was obtained on the Bedford site, in the St-Lawrence valley lowlands. This site is located were intensive annual crop agriculture (corn and soy) is the most highly developed in the study area (Robitaille and Saucier, 1998). It has the lowest elevation (80 m), the best climate (mean annual temperature, annual growing degree days) and the highest soil P availability, but also relatively high Ca and K soil content compared to the other sites (Tables 1 and 2). A high volume yield was also obtained at the Brompton site (5 clone mean = 15.7 m^3 ha^{-1} $year^{-1}$), which is also located at low elevation (170 m) and has a relatively high soil fertility (highest soil pH, second highest soil P availability and soil Ca, highest soil K) (Tables 1 and 2). The Stornoway site is at the low end of the yield gradient (Fig. 2); the very low yield (5 clones

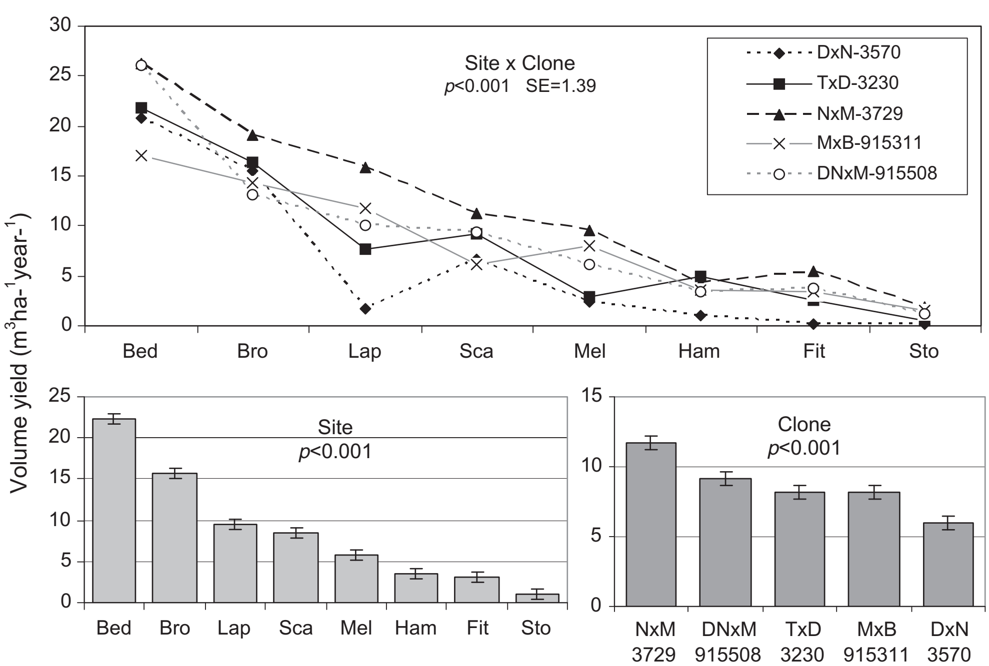

Fig. 2. Site × Clone interaction and main effects for mean annual volume yield (m^3 ha^{-1} $year^{-1}$) in 8 year-old hybrid poplar plantations. Vertical bars represent SE.

Table 6
Total aboveground dry biomass production (tha^{-1}) and yield (tha^{-1} year^{-1}) at the 8 sites and for the 5 clones at the end of the 8th growing season. Percentage of each tree compartment versus total biomass is also indicated.

Sites and Clones	Stem biomass (tha^{-1})	%	Branch biomass (tha^{-1})	%	Woody biomass (tha^{-1})	Woody biomass yield (tha^{-1} year^{-1})
Sites						
Bedford	60.5	77	18.2	23	78.7	9.8
Brompton	42.7	75	14.4	25	57.1	7.1
La Patrie	26.6	72	10.3	28	36.9	4.6
Ste-Catherine	24.2	72	9.6	28	33.7	4.2
Melbourne	16.5	69	7.3	31	23.9	3.0
Ham	10.5	67	5.2	33	15.7	2.0
Fitch Bay	9.1	68	4.3	32	13.4	1.7
Stornoway	4.4	69	2.0	31	6.4	0.8
$p <$	0.001		0.001		0.001	0.001
SE	1.6		0.5		2.1	0.3
Clones						
N × M-3729	35.6	73	13.5	27	49.1	6.1
DN × M-915508	26.4	73	9.8	27	36.1	4.5
M × B-915311	22.7	69	10.4	31	33.1	4.1
T × D-3230	22.0	76	6.8	24	28.9	3.6
D × N-3570	14.8	79	4.0	21	18.9	2.4
$p <$	0.001		0.001		0.001	0.001
SE	1.3		0.4		1.7	0.2

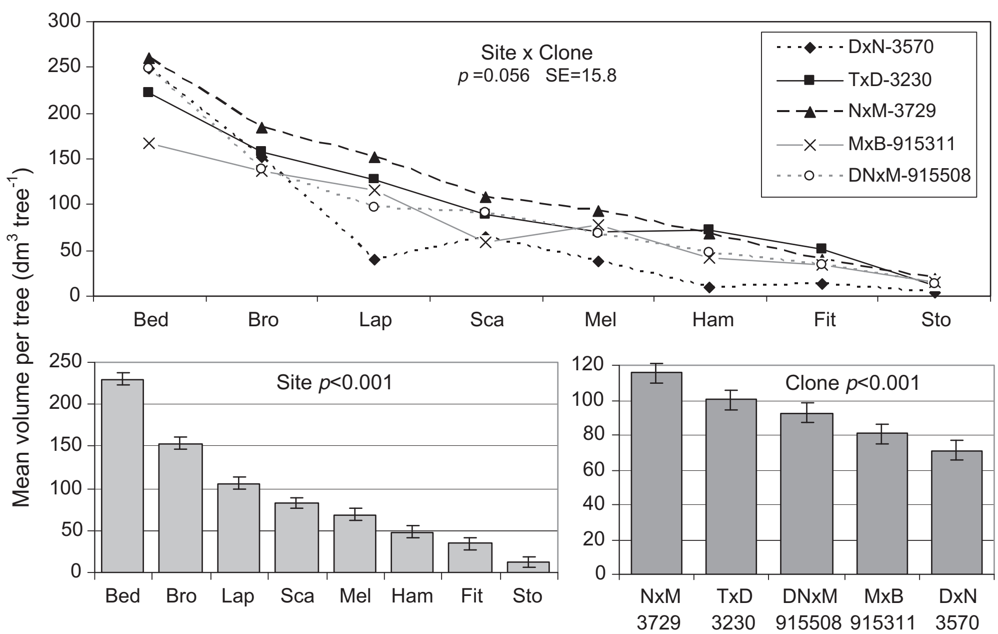

Fig. 3. Site × Clone interaction and main effects for mean volume per tree (dm^3 tree^{-1}) in 8 year-old hybrid poplar plantations. Vertical bars represent SE.

mean = 1.1 m^3 ha^{-1} year^{-1}) at this site was probably related to its high elevation (450 m), or short growing-season, as well as its low soil fertility, particularly in terms of soil P availability (Table 2).

Besides elevation (or climate) and soil fertility, other secondary environmental factors such as deer browsing during the planting year can have a significant negative effect on poplar yield (Table 7). This was the case at the Fitch Bay site (5 clones mean = 3.1 m^3 ha^{-1} year^{-1}) where 89% of the trees were browsed and only 53% of poplars survived. However, deer browsing alone cannot explain the low growth at this low fertility site, which has the second lowest soil P availability. As discussed later, deer browsing was also uneven among the five unrelated clones.

Although elevation was an important factor affecting hybrid poplar yield in abandoned farmland of southern Québec, relatively high yields can still be obtained on high fertility sites located at high elevation. The La Patrie site (440 m of elevation and mean volume yield of 9.4 m^3 ha^{-1} year^{-1}) is a good example, with its low soil C/N ratio and high soil P availability and Ca content. Volume yield (5 clones mean) would surely have been higher at La Patrie, by planting only clones best adapted to the cooler climate.

3.2. Site × Clone interaction: selecting the best clone for each site

The Site × Clone interactions and results of the stepwise regressions for individual clones clearly show that the unrelated hybrid poplar clones used it this study responded differently to the environmental gradients of elevation and site fertility (Figs. 2–6), which corroborates the findings of Tabbush and Beaton (1998). Only one clone was the highest yielding at all sites, the N × M-3729 clone. All four other clones in this study had different yield

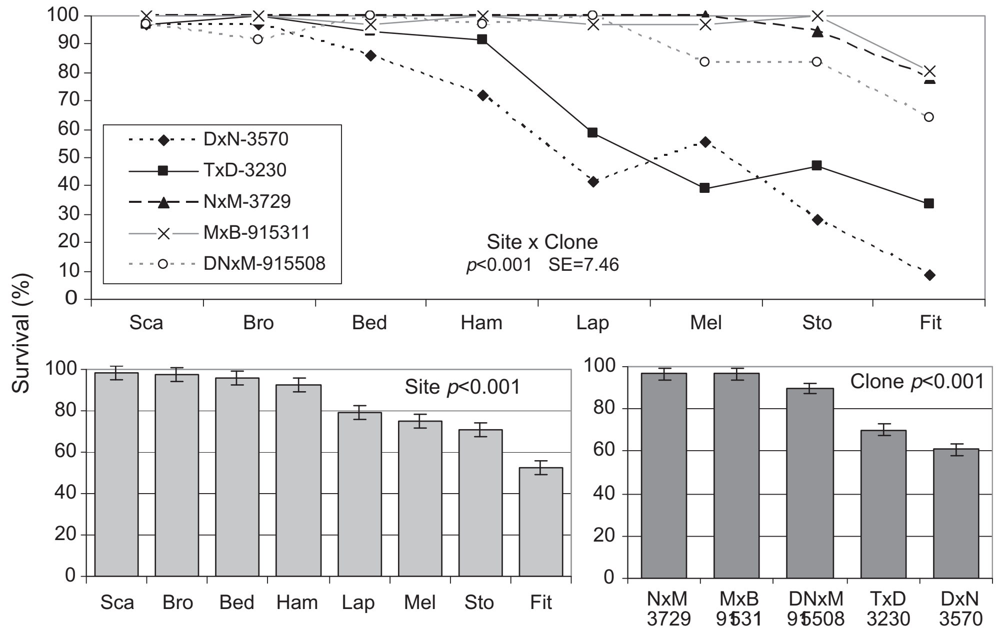

Fig. 4. Site × Clone interaction and main effects for mean survival (%) in 8 year-old hybrid poplar plantations. Vertical bars represent SE.

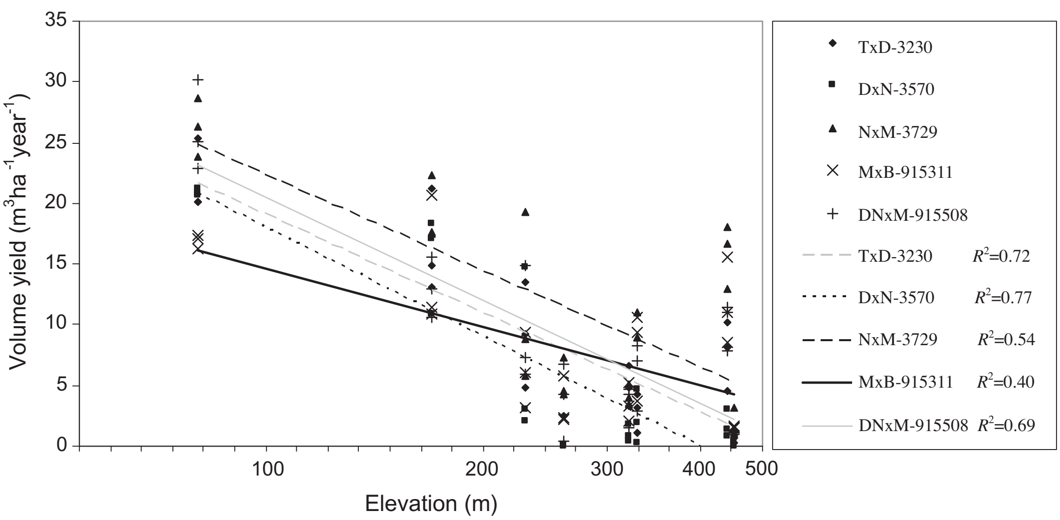

Fig. 5. Relationship between plantation site elevation and volume yield (m^3 ha^{-1} $year^{-1}$) for each hybrid poplar clone. For all relationships: $n = 24$ and $p \leqslant 0.001$.

rankings across the 8 abandoned farmland sites (Fig. 2). On the more fertile sites, N × M-3729 yield reached 26.3 m^3 ha^{-1} $year^{-1}$ at Bedford, 19.1 m^3 ha^{-1} $year^{-1}$ at Brompton, and 15.9 m^3 ha^{-1} $year^{-1}$ at La Patrie, although this later site is located at 440 m of elevation (Fig. 2). The high yield of clone N × M-3729 after 8 years of growth may be related to its very high early-growth and exceptional early-rooting (Brown et al., 1996; Green et al., 2003; Zalesny et al., 2009a), but also its very high survival rate at each site (Fig. 4).

In addition, most results obtained in this study tend to confirm previous observations that poplar hybrids with one or both parents from the *Tacamahaca* section (T × D-3230, N × M-3729, M × B-915311, and DN × M-915508) are generally better adapted to cooler climates, than hybrid poplars with both parents from the *Aigeiros* section (D × N-3570) (Zsuffa et al., 1977; Cooke and Rood, 2007; Périnet, 2007; Dickmann and Kuzovkina, 2008). This was particularly the case for *P. maximowiczii* hybrids (N × M-3729, M × B-915311, and DN × M-915508), with yields best predicted first by P availability, followed by elevation. The opposite pattern, elevation first and P second, was observed for D × N and T × D hybrids in multiple regression models (Table 8).

P. maximowiczii hybrids also had the highest survival rate and were less browsed by deer (Fig. 4, Table 5). Low deer browsing on these hybrids may be related to their high phenolics content and lower N concentration in leaves, as compared to D × N and T × D hybrids (Telfer, 1974; Mattson, 1980; Bryant et al., 1991; Hanson, 1994; Schimel et al., 1998; Gruppe et al., 1999; Broberg and Borden, 2005). Very low survival rates were observed for clone D × N-3570 and clone T × D-3230 at Fitch Bay, where deer browsing pressure was highest (Fig. 4, Table 5). At this site, deer browsing reached 100% for clone D × N-3570, resulting in a catastrophic survival rate of only 8% and a very low volume yield (Figs. 2 and 4).

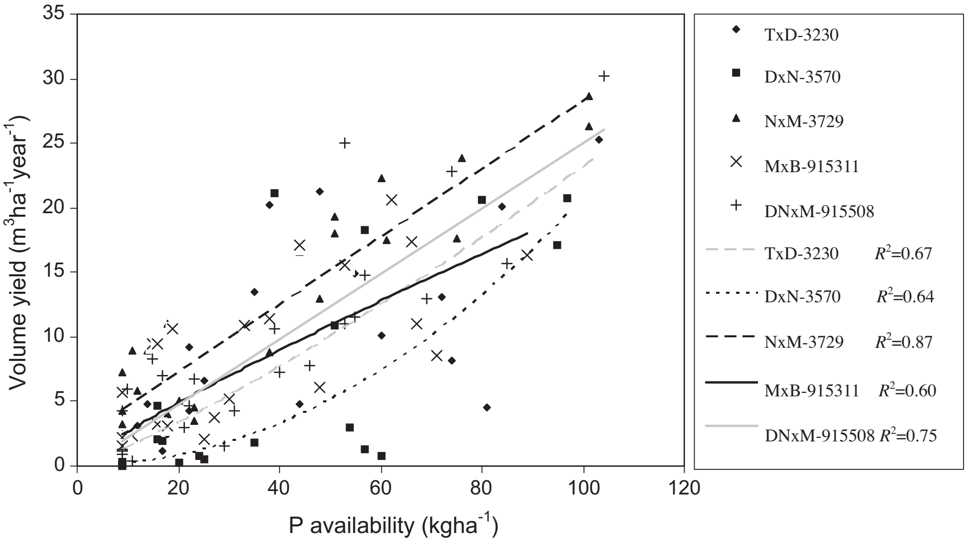

Fig. 6. Relationship between P availability in soil (kg ha^{-1}) and volume yield (m^3 ha^{-1} $year^{-1}$) for each hybrid poplar clone. For all relationships: $n = 24$ and $p < 0.001$. Best fitting models are the following for each clone: linear functions for clone N × M-3729 and DN × M-915508, power functions for clones D × N-3570, T × D-3729 and M × B-915508.

Table 7
Pairwise correlations between environmental variables and volume yield, survival, and site elevation of hybrid poplar plantations ($n = 120$).

	Volume yield (m^3 ha^{-1} $year^{-1}$)	Survival (%)	Elevation (m)
Volume yield	–	0.50***	−0.68***
Elevation	−0.68***	−0.27**	–
C/N ratio	−0.67***	−0.13	0.57***
P availability	0.58***	0.25**	−0.35***
Organic matter	−0.56***	−0.07	0.61***
Survival	0.50***	–	−0.27**
C total	−0.49***	−0.06	0.58***
K	0.48***	0.19*	−0.34***
Precipitation (30 years)	−0.47***	−0.13	0.77***
Deer browsing	−0.44***	−0.52***	0.24**
Ca	0.34***	−0.02	−0.03
N total	−0.29**	−0.02	0.47***
Mg	0.25**	−0.01	−0.31***
pH (water)	0.24**	−0.14	−0.16

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

A simple regression model between elevation and productivity also showed that the M × B hybrid, which has both of its parents from the *Tacamahaca* (balsam poplar) section, was the least influenced by elevation, a sign of its greater adaptation to cooler climate. This may explain why this clone was the one that showed the smallest yield variation across the 8 sites (1.5–17 × m^3 × ha^{-1} × $year^{-1}$). Although clone M × B-915311 was one of the best performing clones on sites that were located at higher elevation (La Patrie, Melbourne), this clone was generally outperformed by the other clones on rich sites located at low elevation (Bedford, Brompton) (Fig. 2). This is quite surprising because this clone was the second highest yielding clone at all four sites after 6 years in riparian buffers strips located along a smaller elevation gradient (140–360 m) (Fortier et al., 2010a). Perhaps its high biomass allocation to branches (Table 6) was possibly more profitable in the narrow buffer strips, where light availability was higher.

Overall, although some clones may be better adapted to cooler climates, the yield of all studied unrelated clones generally sharply declined as both elevation increased and soil fertility decreased (Figs. 5 and 6, Table 8). This is in agreement with the autecology of all five parental species in this study (*P. deltoides*, *P. nigra*, *P. balsamifera*, *P. trichocarpa* and *P. maximowiczii*), with all five attaining their largest size on rich soils, in humid and warm alluvial or coastal bottomland habitats, although poplars from the *Tacamahaca* section are more northerly in their distribution (Dickmann, 2001; Farrar, 2006; Cooke and Rood, 2007; Dickmann and Kuzovkina, 2008). Therefore, clone selection alone cannot compensate for inadequate site selection in terms of soil fertility.

3.3. Management implications for hybrid poplar cultivation in Québec

3.3.1. Abandoned farmland site selection: elevation and soil fertility

Elevation and soil fertility (P availability and Ca) were by far the main factors affecting hybrid poplar yield on abandoned farmland sites of southern Québec (Figs. 5 and 6), although the right choice of clone is necessary to optimise wood production under particular site conditions. Consequently, hybrid poplar plantations should be established, in priority, on low elevation and fertile soil sites since yield can be as high 17–26.3 m^3 ha^{-1} $year^{-1}$ depending on the clone planted (Fig. 2). With the most productive clone (N × M-3729), upland fertile sites can also yield as much as 19.1 m^3 ha^{-1} $year^{-1}$, at low elevation (170 m), and as much as 15.9 m^3 ha^{-1} $year^{-1}$, at higher elevation (440 m).

Based on this study, the following are indicators of site quality for hybrid poplar production on loam soils of agricultural landscapes of southern Québec: low elevation, (below 200 m); C/N < 10; high soil P availability (>50 kg ha^{-1}); high Ca and K soil content; pH > 5; organic matter <7%; low deer herbivory (Table 2). High soil NO_3 availability is also important (Fortier et al., 2010a). It is interesting to observe that all high yielding sites (Bedford, Brompton and La Patrie) were probably recently abandoned since they were dominated by herbaceous vegetation prior to planting (Table 1). This is an indication that these sites still had good agricultural potential. At the higher end of the elevation gradient, Stornoway was the only site dominated by shrubs, which may indicate that it was abandoned a longer time ago, reflecting its low agricultural potential (Table 1).

Given the marginal volume yield observed at Ham, Fitch Bay and Stornoway, it is obvious that not all abandoned farmland sites

Table 8
Results of stepwise regressions between different environmental variables (predictor variables) and volume yield (m^3 ha^{-1} $year^{-1}$) (response variable) for the five hybrid poplar clones. All models and predictor variable parameters are significant at $p < 0.05$.

Hybrid poplar clones	Environmental factors	Parameter estimate	R^2	ΔR^2
5 Clones (n = 120)	1. ln elevation (m)	−7.24	0.58	
	2. ln P availability (kgha^{-1})	4.04	0.75	0.17
	3. ln Ca (kg ha^{-1})	1.70	0.78	0.03
	Intercept	23.0		
T × D-3230 (n = 24)	1. ln elevation (m)	−7.21	0.71	
	2. ln P availability (kg ha^{-1})	2.94	0.88	0.17
	3. Deer browsing (%)	−0.072	0.92	0.04
	Intercept	44.2		
D × N-3570 (n = 24)	1. ln elevation (m)	-9.96	0.77	
	2. ln P availability (kg ha^{-1})	2.75	0.89	0.12
	3. ln Ca (kg ha^{-1})	1.79	0.92	0.03
	Intercept	39.0		
N × M-3729 (n = 24)	1. P availability (kg ha^{-1})	0.264	0.87	
	Intercept	1.94		
M × B-915311 (n = 24)	1. ln P availability (kg ha^{-1})	4.10	0.58	
	2. ln elevation (m)	−3.71	0.68	0.10
	3. ln Ca (kg ha^{-1})	2.10	0.75	0.07
	Intercept	0.28		
DN × M-915508 (n = 24)	1. P availability (kg ha^{-1})	0.165	0.75	
	2. ln elevation (m)	−6.78	0.87	0.12
	Intercept	40.6		

are suitable for poplar cultivation in southern Québec, particularly when considering the high costs of plantation establishment and maintenance (Dancause, 2008; Yemshanov and McKenney, 2008). Therefore, low fertility sites, particularly those located at high elevation, should not be afforested with hybrid poplars. It could be argued that lower quality sites could be fertilised. But this would increase plantation costs and potentially affect the environment (Lteif et al., 2007), without the certainty that it would result in a yield increase (DesRochers et al., 2006).

In a context where the Government of Québec is implementing a zoning approach to its forest management (Hunter, 1990; Gouvernement du Québec, 2008) (i.e. conservation zones, ecosystemic management zones and small intensive production zones), there is a need to select high quality sites, such as low elevation fertile abandoned farmland sites, in order to transfer productivity gains obtained in plantations into an increase in areas of protected forests and of forests under ecosystemic management. If poplar plantations are not established on high prime agricultural or abandoned farmland sites, but on forest sites instead, as is the dominant trend in Québec, the very low yields obtained on such sites (Bilodeau-Gauthier et al., 2011) will require much larger areas of lower yielding plantations to produce an equivalent wood volume.

Gelhaye et al. (1997) concluded that hybrid poplar plantations on clearcut sites outside of agricultural valleys had a marginal yield, even in the most intensive fertilisation treatments, suggesting that poplar cultivation on these low quality forest sites had no real future in France. The same conclusion was reached in Maine, USA (Czapowskyj and Safford, 1993). It is no coincidence that poplar plantations are located worldwide in fertile valleys dominated by agricultural land-use (Berthelot et al., 2000; Stanturf et al., 2001; Weih et al., 2003; Swamy et al., 2006; Bergante et al., 2010).

It should be recognised that afforestation with fast-growing poplars can create multiple ecosystem services in intensively managed agricultural landscapes, including habitat creation for local plant and animal populations (Schultz et al., 2004; Updegraff et al., 2004; Archaux and Martin, 2009; Fortier et al., 2011). It is in intensively managed and oversimplified landscapes that agro-environmental schemes are likely to bring the most biodiversity and ecosystem system services (Tscharntke et al., 2005). It is in those landscapes that small-scale afforestation of abandoned farmland, combined with productive agroforestry practices may be used to increase complexity, while increasing economic and ecological diversity (Weih et al., 2003; Rockwood et al., 2004; Licht and Isebrands, 2005). It is also in those landscapes that hybrid poplar yields are likely to be the highest (i.e. Bedford site). An important reform of subsidies is therefore needed within the forestry and agricultural sectors in order to include some form of payment for ecosystem services provided by private owners of afforested plantations (Bull et al., 2006).

Finally, from a restoration perspective, the lower yielding plantations (Ham, Fitch Bay, and Stornoway) could remain un-harvested, or only be partially harvested, in order to promote the re-establishment of shade-tolerant hardwood species (Lust et al., 2001; Boothroyd-Roberts, 2011) and, eventually the decay of large trees, producing snags and fallen deadwood, which is paramount for biodiversity conservation in plantation systems (Hartley, 2002; Boesch et al., 2007). Poplar plantations may also provide understory attributes needed for the reintroduction of valuable hardwoods such as oaks (Truax et al., 2000; Gardiner et al., 2004), but also valuable ornamental, medicinal and edible plants (Boothroyd-Roberts, 2011).

3.3.2. Clone selection

There were two factors that had a major effect on the yields of different clones across the environmental gradients of the present study: (1) elevation and (2) site fertility (P availability). At a few sites and for some clones, deer browsing was also a noticeable factor. Although all clones responded to the elevation gradient (Fig. 5), it seems that clone D × N-3570 was the most strongly influenced (Table 8). Therefore, this clone should only be planted on low elevation fertile sites of the sugar maple-hickory and sugar maple-basswood forest vegetation zones, as recommended by Périnet et al. (2008).

Although large planting stock (2 m-high bare-root) was used in our study, it was not an insurance against heavy browsing damage to clones preferred by deer (D × N-3570 and T × D-3230) (Table 5). In areas where deer browsing pressure is high, the full potential of these clones may only be fully attained with the use of 3 m-high whips (Heilman, 1999). Their low proportion of branch biomass (Table 6) and a relatively high stem wood density make T × D and D × N hybrids optimal for sawlog and veneer production, compared to M × B hybrids (Pliura et al., 2007).

On the other hand, hybrid poplars with a *P. balsamifera* or *P. maximowiczii* parentage are less browsed (Table 5) and better adapted to colder sites of southern Québec (sugar maple-yellow birch zone; Fig. 1). However, on low elevation fertile sites, clones such as M × B-9153111 may not be the ideal choice because they may be outperformed by clones having one or both of their parents from the *Aigeiros* section, as observed at the Bedford site (Fig. 2).

Finally, although it was obvious that clone N × M-3729 was the highest yielding clone on almost all sites, this clone appeared more susceptible to stem canker (Truax and Fortier, pers. obs.). Production of more disease tolerant N × M hybrids should therefore be encouraged given their very high productivity in southern Québec and elsewhere (Lo and Abrahamson, 1996; Fortier et al., 2010a). This highlights the importance of using a diversity of clones to enhance the resilience of plantations, since poplars are generally vulnerable to insect pests and diseases (Mattson et al., 2001).

4. Conclusion

This study has shown that elevation and soil fertility (P availability) are the prime factors to consider for obtaining high yield hybrid poplar plantations in southern Québec. The strong response of poplars to these factors resulted in a very large Site effect for volume and biomass yields across the environmental gradients along which plantations were established. A secondary and weaker factor is clone selection. Although significant Site × Clone interactions for volume yield suggests that some clones are better adapted to cooler climate, all unrelated clones used in this study reached their highest yield on fertile sites located at low elevation. Still, clones with parent species from the *Tacamahaca* section, especially *P. maximowiczii* hybrids, also had the potential to produce high yields on fertile sites located at higher elevation. Finally, based on the results of this study, inadequate site selection in terms of soil fertility cannot be compensated by clone selection, even when hybrids with parents from the *Tacahamaca* section are selected.

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