



The impact of climate change on growth of local white spruce populations in Québec, Canada

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Abstract

In the near future, forest tree species growing in eastern Canada are expected to be affected by climate change due to an increase of human-induced greenhouse gas emissions. In this study, models were developed to estimate the impact of climate change on growth in white spruce (*Picea glauca* (Moench) Voss). Data were collected in a genecological test, replicated in three locations, and involving 45 distinct geographical seed sources, most of them represented by five open-pollinated families. Transfer models predicting the performance of seed sources were developed, based on temperature and precipitation differentials between the geographical origin of seed sources and the experimental site locations. These models were validated using data collected in a second genecological test series. We found that white spruce populations located within the sampled area were optimally adapted to their local environment for thermal conditions but not for moisture conditions; populations that originated from sites receiving more precipitation generally showed higher tree growth than the local sources. We predict that the adaptive lag currently related to precipitation will increase under global warming conditions. Simulations of growth under various scenarios of climate change indicated that it would be diminished tangibly under more intense warming. However, for a given temperature increase, the relative loss in growth will be less if precipitation is reduced than if it increases. Consequently, predictions based solely on temperature change appear inaccurate, and more effort should be directed toward better anticipating the magnitude and the direction of changes in precipitation patterns at the regional scale. The necessity of human intervention to assist tree migration under climate change is examined.

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1. Introduction

General circulation models (GCM) developed over the last 20 years to estimate the impact of greenhouse gas emissions (e.g., Hansen et al., 1983; Flato et al., 2000) predict a rapid climate change. Following the models' estimates, the mean annual temperature in the northern hemisphere will rise, and patterns of precipitation will be modified. Over the last two decades, many studies have attempted to evaluate the potential impact of these global phenomena on forest ecosystems and more precisely on their composition, functioning and productivity (e.g., in Ontario for North American boreal forest, Papadopol, 2000; Lasch et al., 2002). However, the response of complex biological systems such as forest ecosystems, species or populations is difficult to assess, especially because the magnitude and the direction of the predicted climate changes at the regional scale remain poorly known (Chen et al., 2003).

Davis and Shaw (2001) underlined the importance of microevolution and migration associated with range shifts in plant response to climate change. The current rate of global warming, together with potential modification of migration through human land use, can threaten adaptation. The prediction of a lag in tree response to change is exacerbated by the long life span of tree species and potential genetic constraints (Etterson and Shaw, 2001), which limit their capacity to respond to selection pressure triggered by rapid environmental change. The study of differentiation in adaptive traits in relation to environmental heterogeneity within a species' natural range should help understand the potential evolutionary response to climate change. Most forest tree species show genetic variation at the regional scale, in response to variation in environmental conditions (Morgenstern, 1996). In this respect, replicated test plantations of seed sources should be helpful to obtain indirect estimates of the potential response of individual species to climate change (Mátyás, 1996). These tests should also be very helpful to quickly identify potential seed sources for assisting populations to maintain their evolutionary potential in the face of environmental change or to colonize new empty favorable sites (Hufford and Mazer, 2003). In these trials, many seed sources from various locations are tested. The performance of any seed source can be expressed in differential terms with

regard to that of the local seed source in each test plantation site. One can then develop general transfer models, relating relative seed source performance to geographical or ecological distances existing between the origins of the seed sources and the location of the planting sites. The adaptation of a given seed source to its local environment is assessed by comparing its actual performance with the optimum predicted by the transfer model. The response of local seed sources to climate change can also be simulated by estimating the impact of moving seed sources along environmental gradients within the range of environments covered by the sites available for study. Climate shift associated with the transfer of the seed sources is supposed to mimic scenarios of future climate change. Such studies have been recently carried out for various tree species (Schmidtling, 1994; Carter, 1996; Mátyás, 1996; Persson, 1998; Rehfeldt et al., 1999a,b).

One potential weakness of the recently developed transfer models is that they only use one climatic or one geographic independent variable to predict the responses of seed sources, generally the mean annual temperature or the latitude. Moreover, they are not always validated with independent data sets. In the present study, we developed general transfer functions using multiple regression analysis with both temperature and precipitation predictors, and we employed an extensive validation procedure. General circulation models provide fairly inaccurate estimates of precipitation patterns (Loehle and LeBlanc, 1996; Bergeron et al., 1999). However, since precipitation is one of the main factors affecting forest tree growth and survival, estimates of the response of seed sources to variation in precipitation and in temperature should be useful to obtain more precise estimates of the potential impacts of climate change.

White spruce (*P. glauca* (Moench) Voss) occurs naturally across almost all Canadian territory (Farrar, 1995) and is found as a major forest component in all forested regions except the Pacific coast. This species has a central ecological position in the North American boreal forest and is intensively harvested for lumber production. Actual growth and adaptive traits of local populations could be affected by a change in environmental conditions (Corriveau et al., 1990; Li et al., 1993). Despite its importance for the Canadian economy, very few studies have been carried out to estimate the potential impact of climate change

on this major resource, and no mitigation actions have been proposed so far.

In the present study, we developed regression models for two indicators of growth: tree diameter (dbh) and height. While our sample of seed sources was restricted to only a portion of the entire white spruce natural range, our main objectives were: (1) to explore local adaptive patterns of white spruce to macroclimate conditions; (2) to examine the evolution of tree growth performance of local populations in response to climate change and (3) to examine the practical implications of our results for forest managers decision making.

2. Material and methods

2.1. Plant materials

General transfer models were developed using data collected in a provenance-progeny test replicated on three sites (Fig. 1, Table 1) and including seed sources sampled in Québec. Seeds were sown in January 1976 at the Laurentian Forestry Centre, Québec, Canada in Japanese paper pots, and raised in a plastic greenhouse until the end of June of the same year. Then, seedlings were transferred to the Valcartier Forest Station in Québec (latitude, 46.95°N; longitude, 71.48°W; elevation, 152 m), where they were planted in a nursery and grown outside under natural photoperiod for 3 years. They were irrigated and fertilized according to a commonly used schedule for spruce seedling production in Québec nurseries (Langlois and Gagnon, 1993). The 4-year-old seedlings were lifted in May 1979 and transplanted into the three field sites (Fig. 1), following a randomized six complete blocks design with five-tree row plots.

Forty-five seed sources were retained for development of the models. However, only 42 were available in one of the sites due to damage by wild animals. The seed sources were represented each by two to five open-pollinated families in each block. Of an overall total of 792 site-by-block-by-seed source combinations, 90% were represented by five open-pollinated families. A total of 15 436 trees were measured to estimate the seed sources growth traits, i.e., 22-year height and 22-year diameter at breast height (dbh).

The general transfer models developed were validated using data collected in a range-wide provenance-progeny test established in Québec (Fig. 1). Fifty-eight seed sources were sampled, among which, 32 were the same as those used for the development of the transfer models. The remaining 26 other seed sources were from west of the Québec border, in eastern Ontario. Details on the experimental design of this genecological test are provided by Li et al. (1993). The following traits were measured according to the method described above: 19-year height and 19-year dbh.

2.2. Meteorological data

Climatic conditions prevailing at the plantation test sites (Table 1) and at the locations of seed sources (Table 2) were represented by five temperature variables, which are the mean annual temperature, the mean minimum daily temperature, the mean maximum daily temperature, the number of days without frost, the frost-free period (the maximum number of consecutive days without frost per year), and by two precipitation variables, i.e., the total annual precipitation, and the total summer precipitation (June, July and August). These seven climatic variables were chosen because: (1) they can be easily obtained using existing climatic data, (2) they can be used for delineating the different climate change scenarios (see below) and (3) they well summarize a priori the local weather conditions. Data were obtained using BioSIM (Régnière, 1996). This simulation software uses weather records of the nearest meteorological stations to each seed source or planting site location to estimate the normal climatic conditions prevailing there. Weather records consisted of 30-year monthly averages as well as minimum and maximum daily air temperatures and total monthly precipitations. Because of the stochastic nature of weather regimes generated by the software, simulations for each geographical point were replicated 10 times, and the results were averaged prior to further analyses.

2.3. Statistical analysis

Analyses of variance were performed using the GLM procedure (SAS Institute, 2000) in order to test

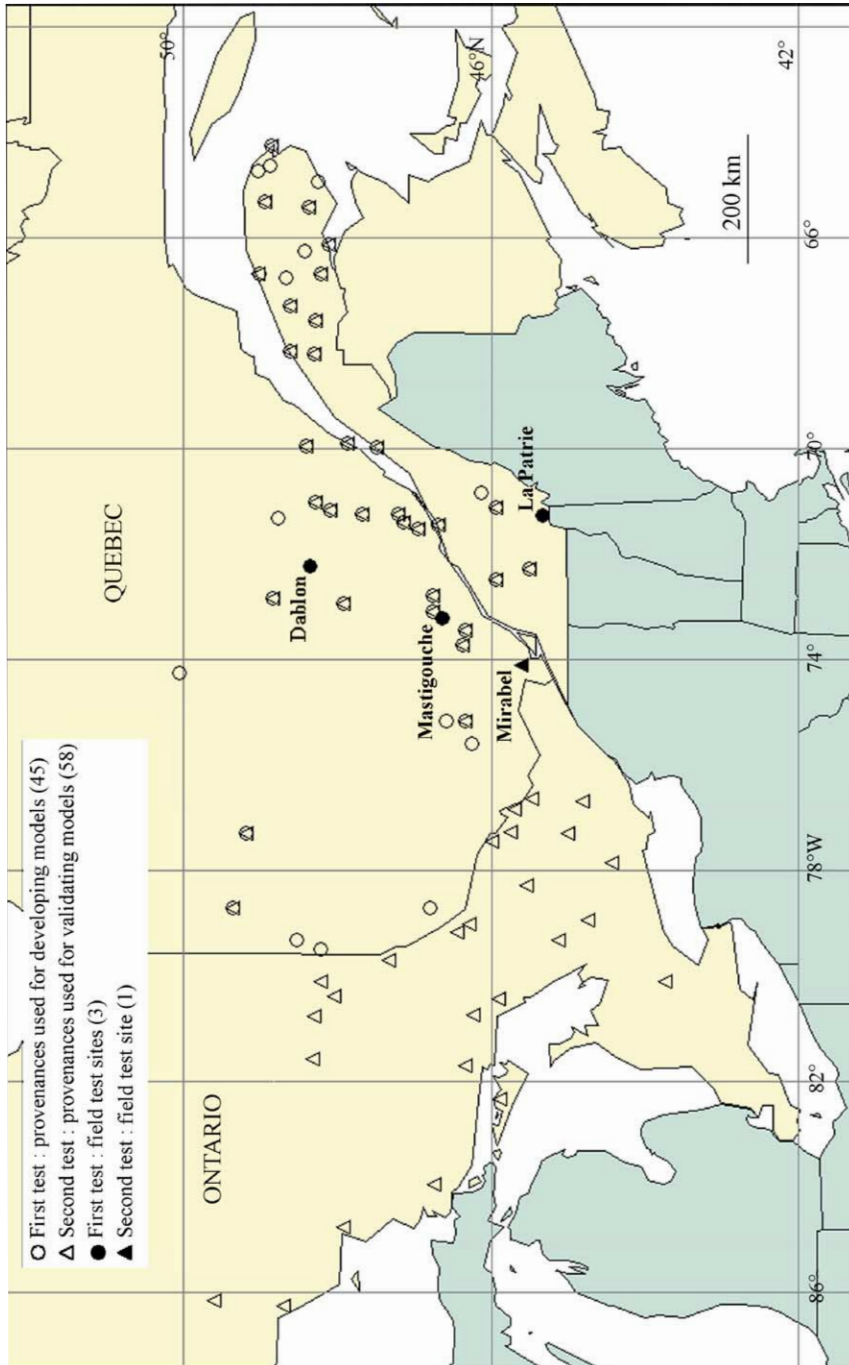


Fig. 1. Geographical locations of eastern white spruce seed sources and plantation test sites used in this study (in parentheses, the number of seed sources or sites within each provenance-progeny test).

Table 1

Location and general climatic parameters of the four planting sites of two provenance-progeny tests used for developing and validating general transfer models

Sites	Latitude (°N)	Longitude (°W)	MAT (°C)	MINT (°C)	MAXT (°C)	FFP (days)	DWF (days)	AP (mm)	SP (mm)
Used to develop models									
La Patrie	45.33	71.25	3.9	−11.0	17.2	112	185	824	555
Dablon	48.35	72.22	1.2	−16.3	16.3	101	164	652	477
Mastigouche	46.63	73.21	2.9	−13.8	17.5	103	169	772	466
Used to validate models									
Mirabel	45.62	74.08	5.5	−10.8	19.6	139	202	770	435

Abbreviations: MAT, mean annual temperature; MINT, mean maximum daily temperature; MAXT, mean minimum daily temperature; FFP, length of the frost-free period per year; DWF, number of days without frost; AP, total annual precipitation; SP, total summer precipitation.

for the significance of differences among the provenances and sites. All effects were considered as random except for the sites, which were considered as fixed. Normality and homogeneity of the variance of the residuals were verified (Sokal and Rohlf, 1995).

Two types of climate transfer models were constructed in this study. The first ones, called temperature-transfer models, are based on temperature variables only. This type of model is used extensively in climate change studies. Assuming that trees respond not only to temperature but also to moisture, the second class of models involves both temperature and precipitation. To obtain statistical models easy to interpret, only those with one or two climatic variables were selected as candidate models. However, these models potentially included quadratic terms that were systematically tested as the relationship between growth and climate is generally non-linear (see Rehfeldt et al. (1999b) and equations below). All regression analyses were conducted on seed source means estimated for each plantation test

site. To avoid biased arithmetic estimation of seed source means, least-squares means were estimated using best linear unbiased predictions [BLUP] (Littell et al., 1996) for each combination of seed source and plantation test site. These estimations were done with the MIXED procedure and the ESTIMATE statement (SAS Institute, 2000) applied to our mixed model. As site effect was not significant for both, height and diameter (see Table 3), data from the three plantation test sites were pooled to develop transfer models.

2.3.1. Temperature-transfer models

Regression models, referred to as temperature-transfer models, were developed to predict height or dbh of each seed source at each plantation site by using each of the five temperature variables at a time in the following two functions:

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} \quad (1)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 (D_{-Tij})^2 \quad (2)$$

where Y_{ij} is the mean height or dbh of the seed source i at planting test site j , and D_{-Tij} is the difference between the temperature conditions prevailing at the location of the seed source i and that observed at the plantation test site j , and this for each of the five temperature variables. Thus, 10 regression models were tested for each of height and dbh. Positive values of D_{-Tij} reflect the transfer of a seed source to a colder site. The estimate of the local seed source phenotype is obtained by solving the regression model for $D_{-Tij} = 0$. For each of height and dbh, the best model was selected among the 10 tested, using the second-order Akaike information criterion (AIC_c) (Burnham

Table 2

Distribution parameters of the seven climatic variables for each of the 45 seed sources of the provenance-progeny test used for developing general transfer models

Climatic variables ^a	Mean	Median	Minimum	Maximum
MAT (°C)	2.30	2.56	−1.52	5.76
MINT (°C)	−13.53	−13.13	−19.90	−10.3
MAXT (°C)	16.38	16.39	13.45	19.97
FFP (days)	98	100	50	139
DWF (days)	167	169	138	205
AP (mm)	712	686	518	964
SP (mm)	478	464	356	674

^a See Table 1 for definitions.

Table 3

Analysis of variance of growth traits measured in the 22-year-old provenance-progeny test of white spruce replicated on three sites

Source of variation	Effect ^a	Height			Dbh				
		d.f. ^b		F-values ^d	d.f. ^b		F-values ^d		
		d.f. _n	d.f. _d ^c		d.f. _n	d.f. _d ^c			
Sites	F	2	16.271	2.93	ns	2	15.752	0.37	ns
Block (site)	R	15	737.75	19.43	***	15	744.67	24.2	***
Seed source	R	49	119.8	4.54	***	49	94.403	4.45	***
Site × seed source	R	91	309.72	1.35	*	91	319.14	1.25	ns
Seed source × block (site)	R	700	2874.6	1.11	*	700	2920.1	1.16	**
Family (seed source)	R	200	377.85	1.76	***	200	379.02	1.37	**
Site × family (seed source)	R	372	2929.4	1.35	***	372	2995.8	1.29	***
Block (site) × family (seed source)	R	2715	12431	1.87	***	2710	12266	1.48	***
Residuals	R	12431				12266			

^a F: fixed effect; R: random effect.^b d.f., degrees of freedom; d.f._n, degrees of freedom of the numerator; d.f._d, degrees of freedom of the denominator.^c Estimated using the Satterthwaite's (1946) approximation method.^d ****P* < 0.001; ***P* < 0.01; **P* < 0.05; ns, not significant.

and Anderson, 1998; Johnson and Omland, 2004). This method based on the information theory uses likelihood criteria penalized by the number of parameters and allows to efficiently compare models that are not necessarily nested (Burnham and Anderson, 1998). Selected models are then the most parsimonious ones, since they are the most informative with regard to the number of parameters included.

2.3.2. Temperature/precipitation-transfer models

For each of height and dbh, a set of eight bivariate functions (functions 3–10) including one temperature (D_{-Tij}) and one precipitation (D_{-Pij}) variable was developed similarly as above:

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} \quad (3)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} + \beta_3 (D_{-Tij})^2 \quad (4)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} + \beta_3 (D_{-Pij})^2 \quad (5)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} + \beta_3 (D_{-Tij})^2 + \beta_4 (D_{-Pij})^2 \quad (6)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} + \beta_3 D_{-Tij} \times D_{-Pij} \quad (7)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} + \beta_3 D_{-Tij} \times D_{-Pij} + \beta_4 (D_{-Tij})^2 \quad (8)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} + \beta_3 D_{-Tij} \times D_{-Pij} + \beta_4 (D_{-Pij})^2 \quad (9)$$

$$Y_{ij} = \beta_0 + \beta_1 D_{-Tij} + \beta_2 D_{-Pij} + \beta_3 (D_{-Tij})^2 + \beta_4 (D_{-Pij})^2 + \beta_5 D_{-Tij} \times D_{-Pij} \quad (10)$$

Because there were five temperature and two precipitation variables, 10 combinations of temperature–precipitation variables were tested for each of eight above functions, for a total of 80 models for each of height and dbh. For each, we selected the best among the 80 models tested using the AIC_c.

Validation of the transfer models was conducted using an independent range-wide provenance-progeny test located in southern Québec (Fig. 1). Observed average height and dbh for each provenance were calculated. Then, correlations were estimated between observed and predicted values by the models (Y_{ij}) using all the seed sources sampled in the range-wide provenance-progeny test ($n = 58$).

2.3.3. Simulation of climate change

To simulate the potential impacts of climate change on white spruce, four scenarios were tested. The temperature/precipitation-transfer models developed with the mean maximum daily temperature and the total summer precipitation were considered in the delineation of the scenarios. These two variables were

retained as the most informative ones in the various models tested (see Section 3). Values to be tested were determined from the span of climate distances observed in our data set between the locations of origin of seed sources and the plantation test sites and from the changes predicted by general circulation model (Bergeron et al., 1999). Hence, scenarios A and B forecasted an increase of 4 °C in mean maximum daily temperature. For scenarios C and D, the temperature shift was 1 °C. These temperature shifts are within the limits of those predicted for Québec (Bergeron et al., 1999). Scenarios A and B as well as scenarios C and D differed with regard to precipitation, scenarios A and C forecasting a 50 mm increase in total summer precipitation, while scenarios B and D forecasting a decrease of 50 mm in total summer precipitation. For the various scenarios, absolute changes in total summer precipitation corresponded to a decrease or increase of approximately 10%. These values are realistic as, in Québec, predicted precipitation changes range from –10 to +30% (Bergeron et al., 1999). An increase of temperature or precipitation in these scenarios corresponded to positive climatic differences between the locations of plantation test sites and that of origin of seed sources.

3. Results

3.1. Genetic control of growth

For all traits studied, there were significant differences among the seed sources close to $\alpha = 0.001$ (Table 3). The family-within-seed-source effect was also significant. As seed source-by-plantation-test-site interaction was significant for height (Table 3) and nearly significant for diameter ($P = 0.0832$), the relative seed source performances (ranks) appeared to be variable from site to site.

3.2. Temperature-transfer models and the utility of adding precipitation to these models

Among the 10 temperature-transfer models tested for each of height and dbh, the second-order one involving the mean maximum daily temperature had the minimum AIC_c information criterion for both height and dbh, with values of 1259.6 and 167.9,

respectively (Table 4). According to the criteria of Burnham and Anderson (1998), these were the best temperature-transfer models. Maximum daily temperature accounted for about 14% of the total variation in the two growth traits (Table 4).

Considering both temperature and precipitation at the same time helped to develop models with smaller values of the AIC_c criterion and higher proportion of variance explained, for each of height and dbh. These models showed in Table 5 and involving mean maximum daily temperature and total summer precipitation, were the most parsimonious models among the overall 90 (10 univariate + 80 bivariate) tested in this study for each of height and dbh. However, for dbh, the difference between the AIC_c of the temperature/precipitation-transfer model and that of the temperature-transfer model was only 0.4 unit. The addition of total summer precipitation helped explain a much larger portion of the variation observed in dbh, as seen by comparing the adjusted R^2 between univariate and bivariate models (Tables 4 and 5).

Validation of the models was good as correlations between observed and predicted values were always positive and reached statistical significance (Tables 4 and 5). Overall, validation success was better for dbh than for height.

3.3. Local adaptation and optimal growth performance

Temperature-transfer models peaked near the origin, which corresponds to a null temperature distance (Fig. 2). For both height and dbh, the maximum value occurred inside the 95% confidence interval of the predicted phenotype at a null transfer distance ($D_{\text{CLIMATE}ij} = 0$) and therefore, did not differ significantly from it. Hence, provenances appeared optimally adapted for growth at locations where temperature matches that of the original seed source location. This trend for thermal transfer was maintained when considering simultaneously temperature and precipitation. However, the response surfaces did not peak near the origin for precipitation (Fig. 3). Rather, maximum growth values were observed for maximum precipitation differences between seed sources and planting sites. Thus, optimal growth should occur by transferring populations from their native climate to locations with drier climate during summer.

Table 4
Best temperature-transfer models developed for height and dbh of white spruce provenances

Phenotypic trait	Temperature-transfer model ^a	AIC _c ^b	Adjusted R ^{2c}	Validation correlation coefficient ^d (n = 58)
22-year height	476.127 + 2.754 MAXT – 2.902 MAXT ² (3.217) (2.016) (0.875)	1259.6	0.137	0.304 (0.020)
22-year dbh	6.572 + 0.009 MAXT – 0.049 MAXT ² (0.047) (0.029) (0.013)	167.9	0.128	0.343 (0.008)

The provenance-progeny test used for developing the models was replicated on three sites. Validations were obtained from a correlation analysis between seed sources values predicted by the regression models and the observed values in an independent range-wide provenance-progeny test used for validation. The set of seed sources used for validation contained 58 seed sources. Among them, 32 were in common with the 45 seed sources from the provenance-progeny test used for developing models.

^a MAXT, the difference in mean maximum daily temperature between the location of a given seed source and that observed at the plantation test site. The S.E. associated with estimates is given in parentheses below each coefficient.

^b AIC_c, second-order AIC to account for small sample size with respect to the number of parameters (Burnham and Anderson, 1998).

^c R² adjusted for the number of parameters in the model (See Neter et al., 1983).

^d P-values are given in parentheses.

3.4. Potential impacts of climate change

Lowest AIC_c, largest R² and largest correlation coefficients between observed and predicted values were obtained with the regression models considering both temperature and precipitation. Hence, these models were used to predict the potential impacts of climate change on growth performance of local populations. For both traits, all scenarios but scenario D (1 °C increase and 10% precipitation decrease) predicted a significant reduction relative to the performance obtained under the no climate change

scenario (Table 6). Growth reductions were always magnified under 4 °C increase, with a maximum negative deviation of 18% for height under scenario A. For height and dbh, the deviation from the predicted growth under the no climate change scenario was always smaller under a 10% decrease than for a 10% increase in precipitation for the same temperature conditions (scenario B compared to A and scenario D compared to C, Table 6). However, a statistically significant difference in growth between the two precipitation regimes was only observed for height between scenarios C and D.

Table 5
Best temperature/precipitation-response models developed for height and dbh of white spruce provenances

Phenotypic trait	Temperature/precipitation-response model ^a	AIC _c ^b	Adjusted R ^{2c}	Validation correlation coefficient ^d (n = 58)
22-year height	484.149 + 0.199 SP + 1.459 MAXT – 4.525 MAXT ² (3.092) (0.031) (1.779) (0.809)	1229.6	0.337	0.275 (0.037)
22-year dbh	6.6479 + 0.0019 SP – 0.0030 MAXT – 0.0644 MAXT ² (0.0488) (0.0005) (0.0281) (0.0128)	167.5	0.210	0.392 (0.002)

The provenance-progeny test used for developing the models was replicated on three sites. Validations were obtained from a correlation analysis between seed sources values predicted by the regression models and the observed values in an independent range-wide provenance-progeny test used for validation. The set of seed sources used for validation contained 58 seed sources. Among them, 32 were in common with the 45 seed sources from the provenance-progeny test used for developing models.

^a SP, the differences in total summer precipitation (June, July and August) between the location of a given seed source and that observed at the plantation test site; MAXT, the difference in mean maximum daily temperature between the location of a given seed source and that observed at the plantation test site. The S.E. associated with estimates is given in parentheses below each coefficient.

^b AIC_c, second-order AIC to account for small sample size with respect to the number of parameters (Burnham and Anderson, 1998).

^c R² adjusted for the number of parameters in the model (see Neter et al., 1983).

^d P-values are given in parentheses.

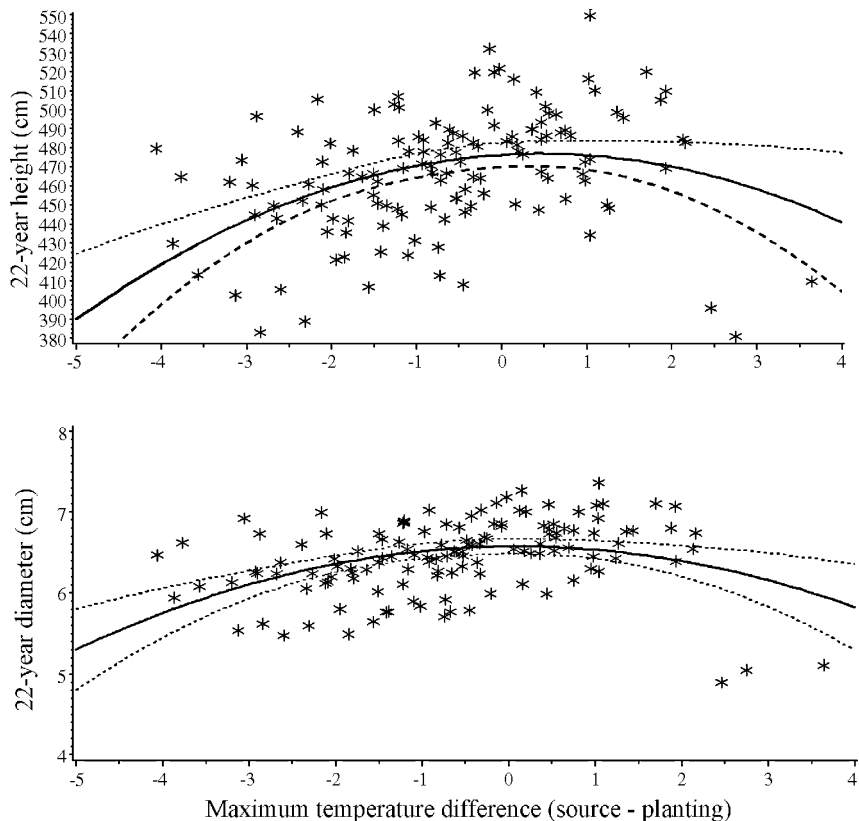


Fig. 2. Plot of the two phenotypic traits on the best selected temperature variable. Data collected on the three field sites of the provenance-progeny test used to develop models are pooled. On the y-axis, traits values are expressed as seed source means estimated for each plantation test site. On the x-axis, the temperature variable is expressed as the differential between the seed sources and the plantation test sites.

4. Discussion

The goal of this study was to evaluate the magnitude of the potential impacts of climate change on the growth performance of local white spruce populations. Such evaluation can only be obtained, if there is sufficient genetic variation among populations, which would be shaped by natural selection incurred by differential climatic conditions. Thus, the first objective was aimed at exploring local adaptive patterns of white spruce to macroclimate conditions. We showed that a significant proportion of the total phenotypic variation in growth could be explained by the geographical origin of seed, either for height or dbh (Table 3). These findings confirm previous results published for growth in the same species (e.g., Beaulieu and Corriveau, 1985; Li et al., 1993, 1997; Jaramillo-Correa et al., 2001). A substantial

proportion of this differentiation (21 and 34% of the variance in temperature/precipitation-transfer models for dbh and height, respectively, Table 5) could be explained by macroclimate variation among the origins of seed sources, in agreement with previous reports based on other areas of the species natural range (Carter, 1996).

This evidence suggests that selection processes triggered and/or partially controlled by climate are involved in shaping the genetic structure of growth traits. Temperature seems to be the most important factor promoting differentiation of populations. For instance, in the best bivariate regression model presented in Table 5 for height, the quadratic term involving the maximum daily temperature had a partial R^2 value of 0.20, as compared to a value of 0.11 for the linear term involving total summer precipitation. This finding is in agreement with the latitudinal

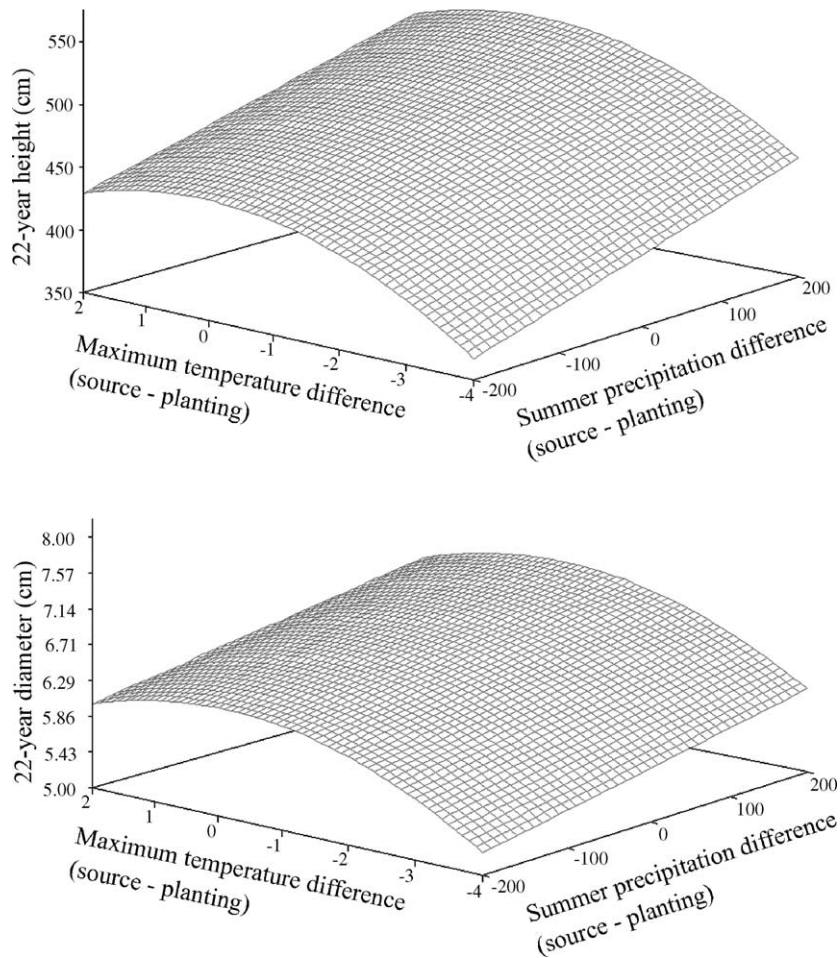


Fig. 3. Plot of the two phenotypic traits on the selected climatic variables related to temperature and precipitation. Data collected on the three field sites of the provenance progeny test used to develop models are pooled. On the y-axis, traits values are expressed as seed source means estimated for each plantation test site. On the x-axis, temperature and precipitation variables are expressed as the differential between the seed sources and the plantation test sites.

pattern of genetic variation commonly found in this species (e.g., Li et al., 1997). Local moisture conditions also seem to play a significant role. Indeed, for both traits investigated, the proportion of among-population variation explained by climatic models increased by adding precipitation as an independent variable. For dbh, the predictive power of transfer-model taking into account precipitation also increased. Thus, in white spruce, the patterns of population differentiation in growth seem to be partially shaped not only by temperature but also by precipitation variation, which does not follow strictly latitudinal or longitudinal gradients in Québec (see Environment

Canada, 1986). This observation is also consistent with trends reported for other species such as Norway spruce (*Picea abies* (L.) Karst.) (Mäkinen et al., 2000) and black spruce (*Picea mariana* (Mill.) BSP) (Beaulieu et al., 2004).

While the regression models developed herein appear appropriate to model patterns of variation among white spruce populations as a function of climate variables, the nature of the data available imposes some limitations, if one wants to use them to estimate the potential impacts of climate change. Indeed, provenance tests were not designed to develop models to be used in the context of climate change.

Table 6

Growth values for seed sources growing in the present climate (local seed sources) and submitted to the four scenarios of climate change delineated (see Section 2.3.3)

Phenotypic trait	No change ($T +0\text{ }^{\circ}\text{C}$, $P +0\%$) ^a	Scenario A ($T +4\text{ }^{\circ}\text{C}$, $P +10\%$)	Scenario B ($T +4\text{ }^{\circ}\text{C}$, $P -10\%$)	Scenario C ($T +1\text{ }^{\circ}\text{C}$, $P +10\%$)	Scenario D ($T +1\text{ }^{\circ}\text{C}$, $P -10\%$)
22-year height (cm) ^b	484.1 (478.0, 490.3)	396.0 (376.2, 415.8)	415.8 (397.3, 434.3)	468.2 (462.7, 473.8)	488.1 (480.3, 495.9)
Deviation from growth under no climate change (%) ^c	–	–18.2 (–22.4, –14.1)	–14.1 (–18.0, –10.2)	–3.3 (–4.9, –1.6)	0.8 (–1.2, 2.9)
22-year dbh (cm) ^b	6.648 (6.551, 6.744)	5.535 (5.222, 5.847)	5.723 (5.431, 6.015)	6.492 (6.405, 6.580)	6.681 (6.558, 6.803)
Deviation from growth under no climate change (%) ^c	–	–16.7 (–21.4, –11.9)	–13.9 (–18.4, –9.3)	–2.3 (–4.2, –0.4)	0.5 (–1.8, 2.8)

See Table 4 for the temperature/precipitation- transfer model used for each phenotypic trait.

^a T , temperature, P , precipitation.

^b 95% confidence intervals given in parentheses (from regression models).

^c 95% confidence intervals were calculated by using a resampling procedure (10 000 iterations). Values for height or dbh were sampled from a normal distribution defined by the mean and variance corresponding to the different scenarios, including the “no change” scenario. For each set of sampled values, the deviation from the scenario with “no change” was calculated. This allowed us to construct the distribution of deviations and hence, the 95% confidence intervals.

Accordingly, the lack of northern and eastern planting sites limits the validity of the transfer models to south-western and south-central regions. However, as the validation of our models was successful within the limits of the conditions tested, the predictions derived from the models should be valid.

Our results suggest that white spruce populations are locally adapted to the temperature but not to the moisture conditions of their native climate. Optimal growth was obtained when the temperature transfer distance was zero, while transfer to drier climate always produced an increase in tree growth, in the range of precipitation values tested here. Rehfeldt et al. (1999b) also showed for *Pinus contorta* that natural populations tended to occupy suboptimal environments. Evolutionary theory indicates that adaptation to local environment depends on a balance between selection and gene flow. White spruce is a wind-pollinated and outcrossing species with little population differentiation, which is indicative of extensive gene flow and large population sizes (Jaramillo-Correa et al., 2001). These factors likely reduce the efficiency of selection promoting adaptation to local conditions. Under such circumstances, only relatively strong directional selection could shape adaptation to local temperature conditions, as observed here. Other studies, assessing the patterns of genetic variation in white spruce, showed the occurrence of a latitudinal cline (Khalil, 1986; Furnier et al., 1991; Li et al., 1997).

As temperature is negatively correlated with latitude, these results appear to be in good agreement with ours, indicating a good selective response to temperature. The fact that we were not able to show optimality of local populations to moisture conditions might be due to the limited range of moisture conditions in the limited area studied, thus making it difficult to detect selection response to this factor. It should also be noted that the improved growth of seed sources from moister locations did not show maximum limits in the range of summer precipitation differences tested in this study (see Fig. 3).

It should be recalled that only traits partially involved in fitness could be assessed in this study. Hardiness and survival, two other important fitness components, often show patterns of genetic variation that are different from that of growth in conifers (Eriksson et al., 1980; Persson, 1994; Schmidting, 1994). Loehle (1998) showed the presence of a strong genetic trade-off between frost tolerance and annual growth at the interspecific and the intraspecific levels for several tree species. In white spruce, genetic correlations were positive between annual growth and the date of budset, indicating that an increased growth was generally associated with a delayed preparation to winter dormancy (Li et al., 1997). In addition, these distinct responses are likely to vary when the energy allocation strategies are changed in response to unconstrained or constrained climatic conditions

(e.g., late or early frosts, drought stress). In addition, provenance-progeny tests such as those used in this study are established in a limited set of environmental conditions where tree competition is reduced and does not operate during the entire life cycle. Thus, observing a non-optimality of local seed sources for some climate dimension and some fitness components such as growth is more expected under these partially controlled environmental conditions. In addition, our study system is located in a part of the world where precipitation are abundant (Fig. 1, Tables 1 and 2) and do not constitute a limiting growth factor. Hence, selection that would be associated with precipitation is not expected to be as strong as that associated with temperature. Selection might also simply not operate at the temporal scale examined.

The second objective of this study was to predict the evolution of growth performance of white spruce local populations in response to climate change. To address this objective, we used the climate distances between the locations of the seed sources and the plantation test sites to simulate the climatic shift expected in the future and develop mathematical models to predict its impacts. Based on these models, it seems reasonable to expect, from a temperature increase of 4 °C, a significant decrease in growth of local trees. Keeping in mind the particular regional climatic context of our study, the reduction in growth was even more severe when a precipitation increase of 10% was considered. However, for a less pessimistic temperature change scenario of only 1 °C increase, the changes in growth seemed marginal (Table 6, scenarios C and D).

It has been suggested that with climate change, some species could be favored and others adversely affected by a modification of competitive interactions between species (Kirschbaum, 2000). Rapid shifts in environmental constraints could increase competition from fast-growing and rapidly dispersing plant species (Tilman and Lehman, 2001). Hence, a reduced height growth for local white spruce populations facing the new combination of environmental constraints brought about by climate change might mean a lower capacity to intercept light and to compete with early successional species. Moreover, with the simultaneous increase in carbon dioxide concentration, species with rapid growth rates are expected to be more responsive than slower growing species (Hunt et al., 1991). Based on climate change simulations, Talkkari (1998)

suggested that broadleaf species such as birch could out-compete conifer species in southern Finland, while in the north of the country, conifers would maintain their actual growing stocks. A similar situation could happen for white spruce in Québec after a temperature increase, based on simulations presented by Shafer et al. (2001). However, the response of nutrient cycling processes to climate change was not taken into account by Shafer et al. (2001) in their simulations, and this response could have a large influence on the species' fate (Johnson et al., 2000).

The third objective of this study was to examine the practical implications of our results for forest managers. These implications should be considered at two levels: possible implications in terms of economic losses and implications for the establishment and the maintenance of well-adapted white spruce stands. If only economic losses in character value are considered, cost/benefit studies would have to be conducted before implementing any large-scale transfer program aimed at replacing or moving local populations. As for most conifers, because most of the genetic variation in quantitative characters resides within stands in white spruce (Li et al., 1993), there exist large amounts of adaptive variation at the local level, and changes in gene frequencies might operate given that the pace of climate change is moderate. Otherwise, assuming that local populations would be displaced, some authors have proposed that the migration speed in conifers would not be high enough to follow the rate of climate change, particularly in the context of actual fragmented landscapes (Honnay et al., 2002). Under such circumstances, assisting the migration of adapted genotypes through human intervention might be relevant (Rehfeldt et al., 1999a). However, it is not clear how new interspecific interactions driven by climate change could affect white spruce survival, reproduction and abundance (see above), and how severe these impacts would be. As well, plant migration speed and patterns are still poorly understood (Higgins and Richardson, 1999). In weighting the need for human-assisted migration, one must also consider the role of marginal allopatric populations in the colonization process (e.g., Laberge et al., 2000) and the role of long-distance dispersion events (e.g., Gamache et al., 2003), the frequency of which is poorly documented in conifers. Hence, case-by-case studies appear to be warranted.

More importantly, climate change is likely to result in more severe weather extremes and temporal variability, particularly for rainfall (Raisanen, 2002), with possible negative impacts on long-term tree survival or commercial value. For instance, frost damages can become more frequent (Hänninen, 1991), and some native tree species can be more sensitive than others. Thus, more research efforts should be directed toward a better understanding of the long-term response of tree species to these climatic extremes. The follow-up of long-term genealogical tests such as those used in this study should facilitate this task. Together with the findings reported herein, these studies should help to improve our prediction of the potential impacts of climate change on important conifer species such as white spruce.

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