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Assessing effects of seed source and transfer potential of white birch populations using transfer functions

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ABSTRACT

Trees have adapted to their local climates, but with changes in the climate, they may currently or in the near future occupy climates that are sub-optimal for growth and survival. The goal of current reforestation is therefore to establish a new generation of trees with growth adapted to the future climate(s). Here, we present preliminary data of a study assessing the effects of seed source and transfer potential of white birch populations. Seeds from twenty-five white birch (*Betula papyrifera* Marsh.) populations collected across Canada were grown in the greenhouse and observed for emergence time, germination and growth. The seedlings were later planted in a common garden. After one year, the seedlings were measured for height, root-collar diameter (RCD) and survival rate and average volume per seedling calculated. Transfer functions were used to estimate the climatic distance from which populations may be transferred to the test site. There was a significant effect of population on all growth variables. Initial height was positively correlated with 1-year height and survival. Germination rate negatively correlated with emergence time. Principal component analysis showed effects of seed origin on performances of the populations in the common garden. Summer temperature was the best predictor of the transfer distance.

Keywords: Climate Change; Populations; Common Garden; Transfer Function

1. INTRODUCTION

The global climate system is continually evolving and significant ecological changes occur at all timescales. This is because climate is multivariate and ecological transitions and transformations are all related to climate [1]. However, the rapid change in the global climate may cause unprecedented disruption of the biological processes [2]. One of the implications of a novel shift in the climate system is that species may currently or in the future be relegated to climates that are sub-optimal for growth and survival [3]. Also, shrinkage in the coverage of the boreal forest and extinction of some important members of the forest is anticipated [4]. Boreal forest is an important component of the global carbon sink system that is sensitive to temperature [5].

There are predictions concerning the migratory pattern of trees in response to climate change [6-8]. However, some of the predictions were made from coarse scale observations which may not take into consideration the intraspecific genetic responses [9]. Some tree species comprises of populations that are physiologically attuned to different climates [10]. In addition, there are factors (e.g. lakes and mountains) other than climate that may influence the migratory pattern of a species. It is therefore important to assess trees' responses at individual species level [11].

One proposed strategy to offsetting potentially negative impacts of climate change on forest systems is to match genotypes with the future climates [12-14]. This idea is based on the provenance trials traditionally used to introduce seed sources to a new climate [15]. The provenance trials have been combined with a statistical model (response function) to predict species response to climate change [16,17]. The underlying hypothesis for the model is that geographic variables are surrogate for elusive climate that governs micro-evolution and adaptation at local scale [18]. However, the resulting predictions are often complex. In addition, implementing this approach requires a long-term provenance study and populations are necessarily planted in multiple sites [17]. With the bourgeoning availability of climate data, climate-transfer function was developed to estimate the climatic distance to which populations may be transferred. It is based on the view that organismal distributions are primarily controlled by climate with other factors being secondary. Its advantage is that populations may not necessarily be planted in more than one site to generate a reliable result [19]. This approach has been popularly used to assess species level response to climate change [2,20-22].

In this paper, we present preliminary data of a study where we used transfer functions to assess the transferability of 25 populations of white birch to a test site in Northern Ontario. White birch (*Betula papyrifera* Marsh.) is a widely distributed species in North America and the most prevalent of all the birches [23]. It is an ecologically important hardwood species in the Canadian boreal forest. There is a rising commercial interest in its products and its inclusion in hardwood-conifer stand management. Although there is an increased silvicultural knowledge base for the species [23-30], information about local populations, transfer potentials and climatic guidelines for its transfer in order to take advantage of its genetic diversity is still limited. Previous studies have reported variations in climatic response between seed sources from its southern and northern limits. The northern seed sources appear to germinate at low temperatures compared with the southern sources [31-32]. Such variation has been reported for some other temperate species [33] but caution is sounded against any generalization without first testing the seed sources in a uniform environment [34,35]. So far, no such testing exists for white birch. Although one seed source testing of white birch was done, the sources used in the study and the test sites were only restricted to the interior of British Columbia [36]. The objective of this study was to investigate how variations in seed source determine the success of white birch in the field and to understand the underlying climatic factors that may influence the transfer potential of the species. In this study we were able to directly relate the influence of the seed sources to the outcomes of the transfer functions.

2. MATERIALS AND METHODS

2.1. Greenhouse Operations

White birch seeds from different (twenty-five) forest regions covering seven provinces (Ontario, British Columbia, New Brunswick, Newfoundland, Nova Scotia, Quebec and Prince Edward Island) were grown under ambient condition at the Lakehead University's greenhouse. The selected populations ranged from latitude 45˚16'N - 54˚43'N and elevation 70 - 800 m. The seeds were sown in styroblocks (5 seeds per cavity) on 18th of April 2008. Each styroblock consisted of 45 cavities. The potting medium was a pre-mixed peat moss. The seedlings were fertilized with a regular fertilizer (N-P-K 20:20:20). During the germination phase, the seedlings were observed for emergence time, germination percentage and height in the greenhouse. The seedling emergence time was recorded as the number of days after sowing when the seedlings were visible. Germination was expressed as a percentage, based on the numbers of cavities with seedlings and the total number of cavities in the styroblock. Height (initial) was measured with a ruler on 28th of July 2008 (10 weeks after sowing of seeds). The seedlings were grown for 12 weeks in the greenhouse.

2.2. Field Operations

The common garden site is located in northwest Ontario (Thunder Bay) on a forested land that was recently disturbed by a wild fire. It is located on 48'22'N, 89'19'W with elevation of 183.3 m. The site has mean January temperature of −15˚C, mean July temperature of 18˚C and an average annual precipitation of 704 mm. The field preparation and fencing were carried out between 25th and 31st of July 2008. Field preparation involved removal of weeds, dead woods and stumps on the site. The fencing was necessary to prevent damages to the seedlings by deer. The seedlings were planted in a completely randomized design between 5th and 7th of August 2008. Thirty three seedlings were planted for each population using a spacing of 1.5 m × 1.5 m. The site was kept weed free. On July 25th 2009 (after 1 year), the seedlings were measured for height and root-collar diameter and were also scored for survival. The volume per seedling was also calculated using the formula:

$$h\times\left(\Pi d^2\right)/4$$

where h = tree height, d = root-collar diameter and Π = 22/7.

2.3. Climate Data and Analysis

All the climate data were normalized climate data (1971- 2000) collected from weather stations closest to the population's origins or use of multiple weather stations where the former was not applicable. Fifty climate variables; minimum, maximum and mean monthly temperatures, mean monthly precipitation, mean annual temperature, and mean annual precipitation were used as independent variables. Six derived climate variables; mean temperature of the coldest month (MTCM), mean temperature of the warmest month (MTWM), annual moisture index (AMI), summer-winter temperature difference (SWTD), degree days (DD) < 0˚C, degree days >5˚C and 3 geographic variables (latitude, longitude and elevation) were also used in the analyses. The data were collected from Environment Canada. The growth variables were tested for normality. Where there was a departure from normality, the data were transformed using a polynomial or logarithm transformation. One way analysis of variance (ANOVA) was used to determine if there were significant effects of populations on the growth variables.

The climate variables were screened with simple linear regression model. Regressions that were significant at $\alpha = 0.05$ were retained for use in further analysis. The linear model was:

$$Y_i = b_0 + b_1 X_1 + e \quad (1)$$

where Y_i is the predicted height, root collar diameter (RCD), survival or average volume, b_0 is the intercept, b is the regression coefficient, X is climatic or geographic variables of the populations and e is the residual. The successfully screened climatic or geographic variables from the simple linear models were used in the development of transfer functions. A transfer function is a regression used to describe performance of multiple seed sources at a single test site. The model is given as:

$$Y_i = b_0 + b_1 X_1 + b_2 X_1^2 + e \quad (2)$$

where Y_i is the predicted height or productivity, b_0 is the intercept, b_1 and b_2 are the regression coefficients, X_1 is climatic or geographic variable (common garden climate minus population climate) and e is the residual.

Principal component analysis (PCA) was used to summarize the growth variables. The component that explained most of the variations was used to build a transfer regression. The principal component regression model was:

$$PC1 = b_0 + b_1 X_1 + b_2 X_1^2 + e \quad (3)$$

where $PC1$ is the first principal component which explained most of the variation in the data, b_0 is the intercept, b_1 and b_2 are the regression coefficients, X_1 is climatic variable (common garden climate minus population climate) and e is the residual. All the analyses were performed using SAS 9.1 (SAS institute Cary, NC) and sigma plot 11 (Systat Software, San Jose, CA).

3. RESULTS

3.1. Greenhouse

There were significant differences in emergence time, germination percentage, and initial height among the populations ($p < 0.0001$). Seedlings emergence time ranged from 7 to 15 days (**Figure 1**) while germination percentage ranged from 29% to 100% (**Figure 2**). Initial height ranged from 22.5 cm in Porcupine population to 38.6 cm in Millvale population (**Figure 3**). Some of the populations germinated within 7 days especially the populations

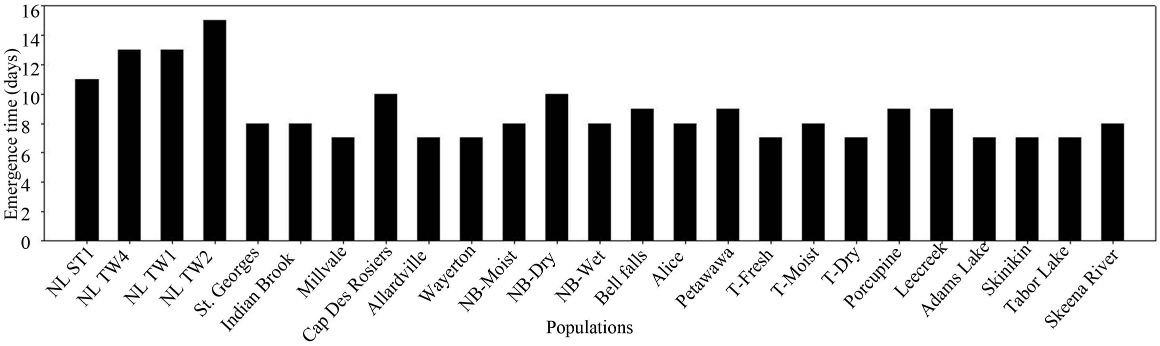


Figure 1. Emergence time (east-west) in days of the 25 white birch populations after sowing.

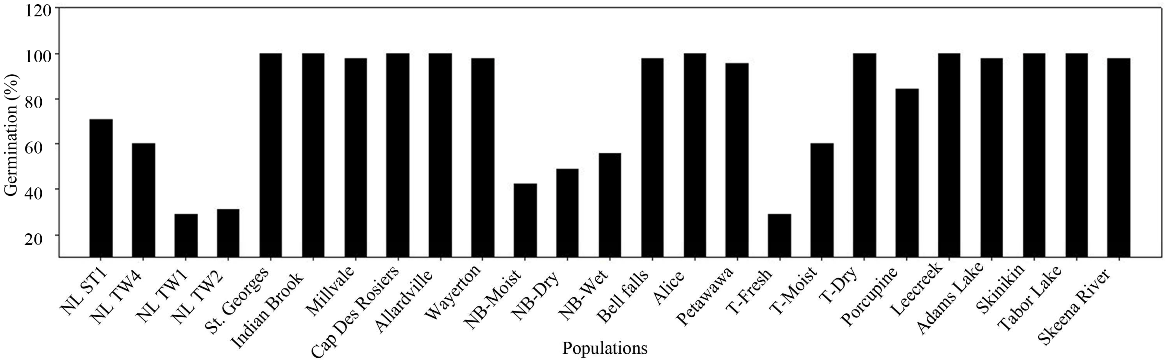


Figure 2. Percentage germination of the 25 populations of white birch.

from the west coast. Most of the populations germinated within 10 days. With the exception of the population from St. Georges which germinated within 10 days, populations from Newfoundland generally took much longer to germinate. Most of the populations that germinated early had higher germination percentages and higher initial height compared with those that germinated late. The latitude, longitude and elevation of the populations had no bearing on either of germination or seedlings emergence time.

3.2. Common Garden

There were significant differences in 1-year height and root-collar diameter ($p < 0.0001$) among the 25 populations. The 1-year height ranged from 30.1 cm in St. Georges population to 57.9 cm in Skimikin (**Figure 4**). The root-collar diameter (RCD) ranged from 4.35 mm in St. Georges population to 6.67 mm in Wayerton (**Figure 5**). Survival among the populations ranged from 21% in NL-TW1 population to 88% in Skimikin (**Figure 6**). The average survival was 65%. The average volume per tree was also significant ($p < 0.0001$). Volume ranged from approximately 4.4 cm^3 in population from Timmins (Moist) to 20.99 cm^3 in Skimikin (**Figure 7**).

There were correlations between the greenhouse and

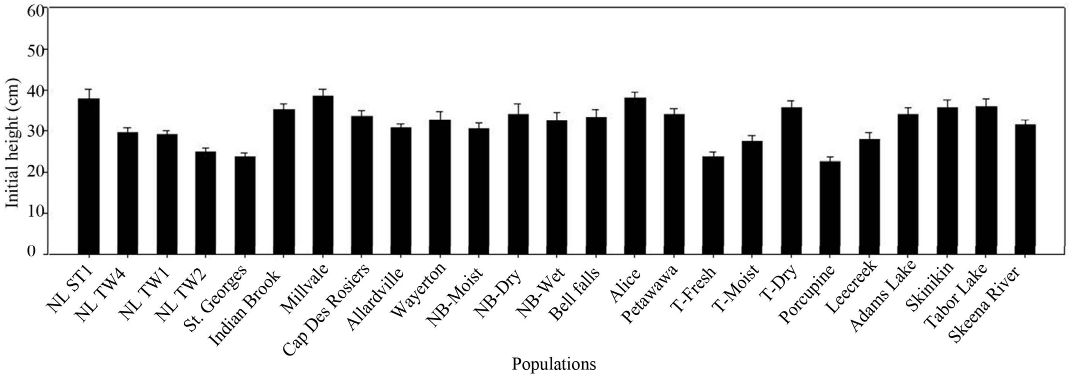


Figure 3. Initial heights of the 25 white birch populations.

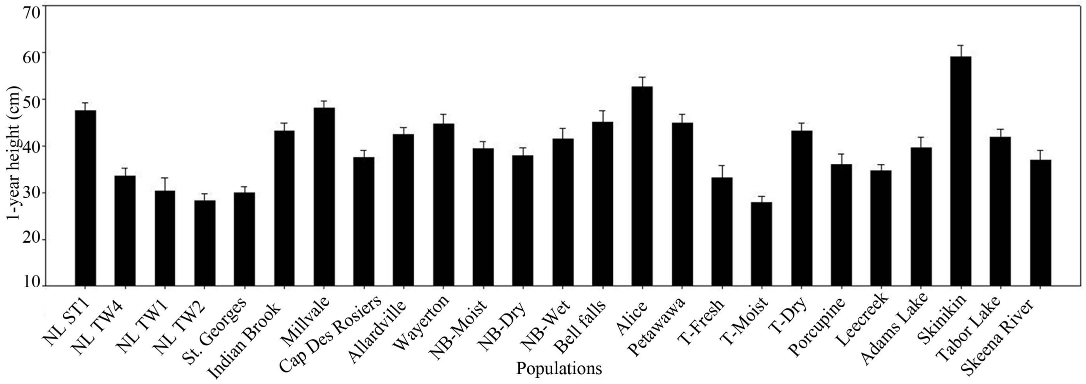


Figure 4. Height (in cm) after 1 year in the common garden.

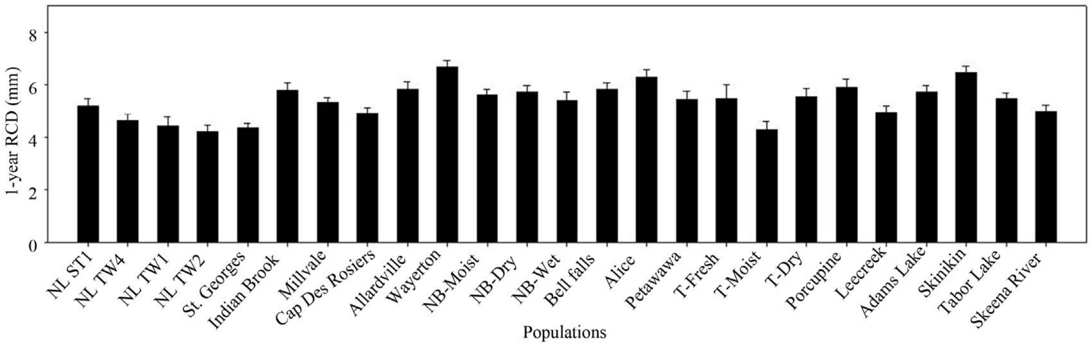


Figure 5. Root-collar diameter (in cm) after 1 year in the common garden.

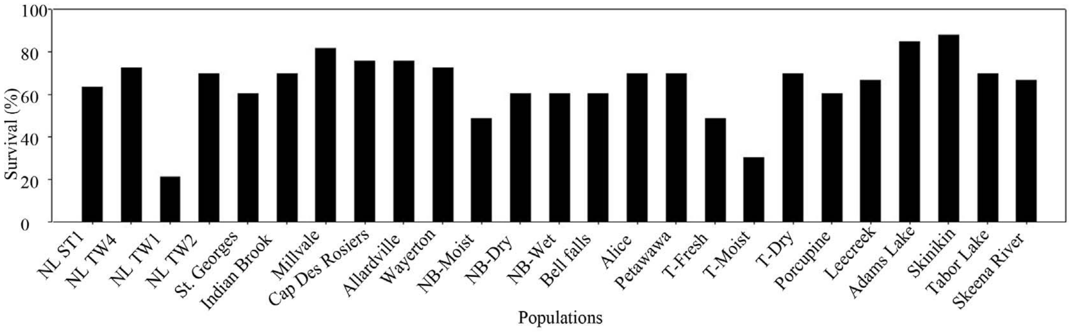


Figure 6. Percentage survival after 1 year in the common garden.

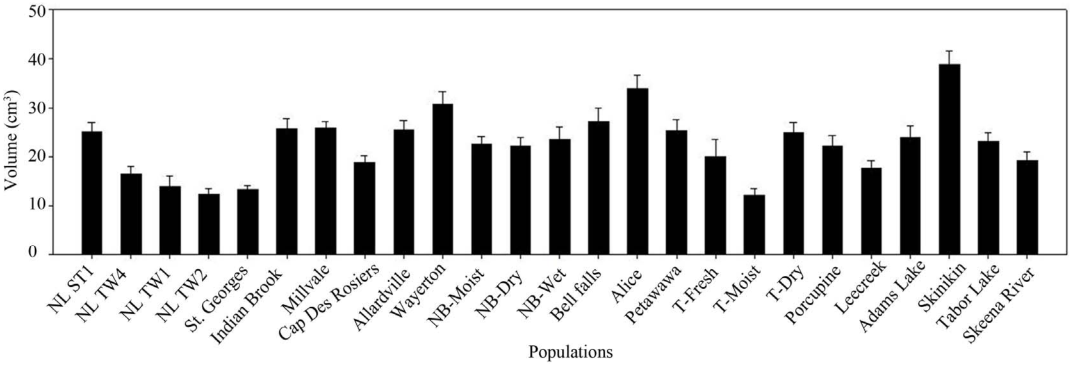


Figure 7. Volume per populations after 1 year in the common garden.

the field observations. The initial height positively correlated with 1-year height and survival ($r = 0.74$ and 0.51 respectively). Populations with higher initial heights maintained best height growth after one year. Also, survival was higher in the populations with higher initial height. Germination was negatively correlated with emergence time ($r = -0.71$) meaning that the longer it takes a population to germinate, the lower the germination percentage. Negative correlation ($r = -0.47$) between emergence time and 1-year RCD indicated that most populations that took longer time to germinate had lower RCD.

3.3. Transfer Functions

Screening of the 56 climate and 3 geographic variables using simple linear regressions were generally significant for regression of mean summer temperatures (mostly June and July) against height, RCD and volume (**Table 1**). No significant regression was observed for survival. Mean summer temperature was also a significant predictor of volume. In addition to mean summer temperatures, regressions of growth variables against some derived climate variables (DD > 5˚C, MTWM and AMI) were also significant.

All significant regressions and previously established key variables (MTWM, DD > 5˚C, MTWM, SWTD, DD < 0˚C, AMI, MAT and MAP) (Rehfeldt 1995) were used to build the transfer functions. Transfer functions with $p > 0.1$ were discarded. Seven populations were excluded from further analyses because their locations were too close to one or more populations which would have required the use of a single weather station for more than one population.

In the transfer functions, all the variables that were successfully screened produced statistically significant regressions with the exception of May minimum temperature which had a p-value greater than 0.1. The transfer functions showed that the mean summer temperature (June, July and August) is a stronger predictor of white birch performance compared with the derived climate variables (**Figures 8-10**); r^2 ranged from 0.27 - 0.39 for height and 0.35 - 0.58 for RCD and 0.30 - 0.57 for volume (**Table 2**). AMI was the only predictor of survival ($r^2 = 0.34$). Also, performance was generally better in populations from warmer climates. Since transfer distance was calculated as common garden climate minus population climate, positive values denote transfers from climate that are cooler than the climate of the test site while negative values represent transfers from climates warmer than that of the test site. Zero denotes the climate of the test site and the best match.

Two principal components (PC) were retained by the PCA. Both components explained a cumulative variation of 73% with PC1 explaining 51% of the variation and PC2 explaining 22%. Initial height, 1-year height, RCD

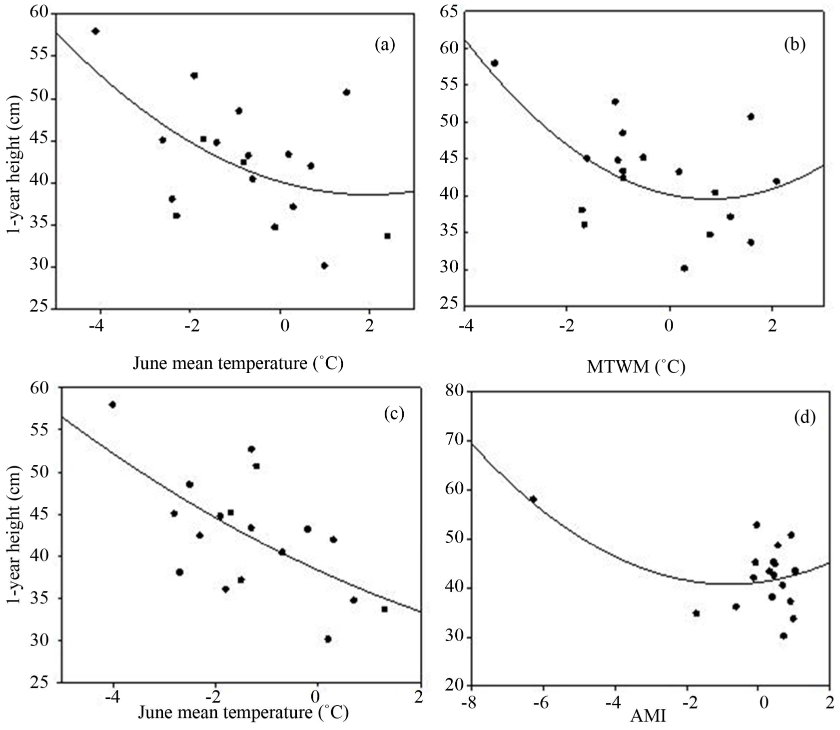


Figure 8. 1-year height transfer distances (common garden climate minus population climate) of the white birch populations in the units of (a) June mean temperature, (b) Mean temperature of the coldest month, (c) June minimum temperature and (d) Annual moisture index.

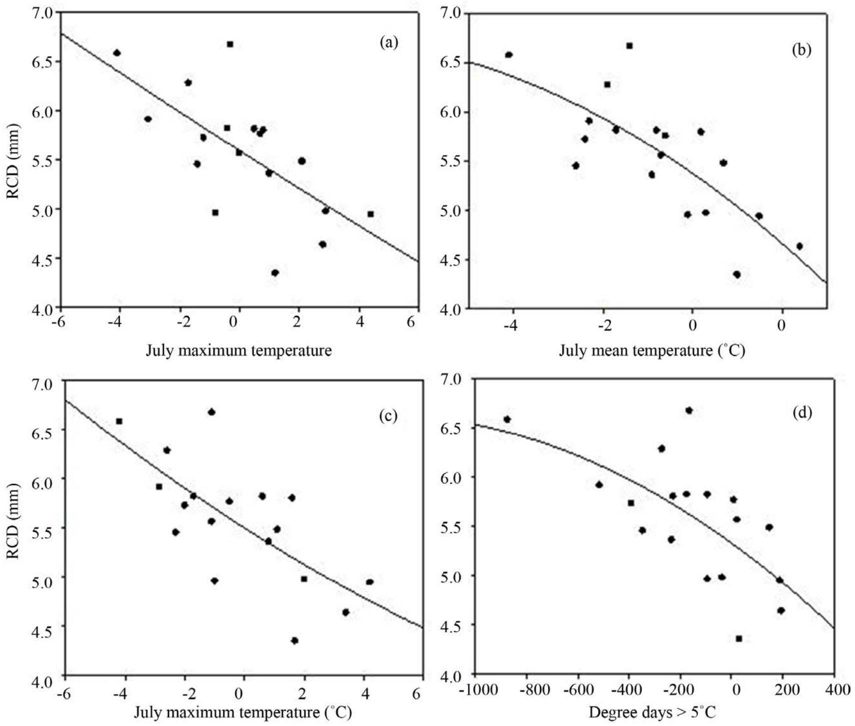
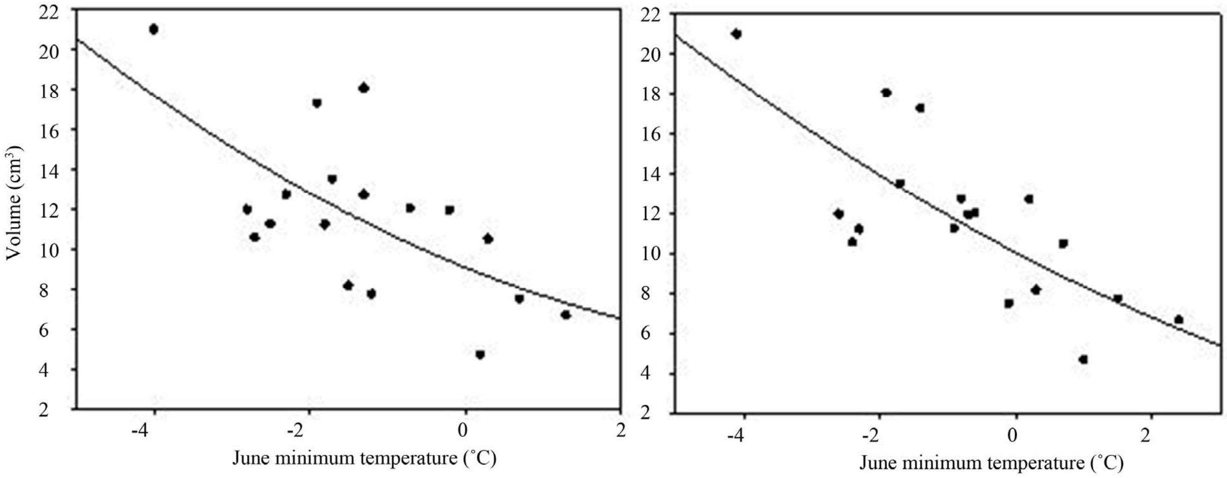


Figure 9. Root-collar diameter transfer distances (common garden climate minus population climate) of the white birch populations in the units of (a) July maximum temperature, (b) June mean temperature, (c) June maximum temperature and (d) Degree days > 5˚C.



(a) (b)

Figure 10. Volume transfer distances (common garden climate minus population climate) of the white birch populations in the units of (a) June minimum temperature and (b) Degree days > 5˚C.

Table 1. Simple linear regression of height, RCD and volume against each of 54 climate and 3 geographic variables.

Variables	R^2	Sig.	Predictors
1yr-Height	0.38	0.0059	JunMinT
	0.24	0.0355	JunMeanT
RCD	0.35	0.0097	MayMeanT
	0.57	0.0003	JunMeanT
	0.44	0.0026	JulMeanT
	0.30	0.0166	AugMeanT
	0.44	0.0026	MTWM
	0.49	0.0011	JunMaxT
	0.42	0.0035	JulMaxT
	0.36	0.0088	AugMaxT
	0.40	0.0048	JunMinT
	0.25	0.0339	MayMinT
Volume	0.41	0.0041	JunMinT
	0.57	0.0164	JunMeanT
	0.48	0.0014	JunMaxT
	0.32	0.0148	AugMeanT
	0.32	0.0140	AugMaxT
	0.49	0.0013	JulMeanT
	0.55	0.0058	DD > 5˚C
	0.48	0.0040	MTWM

Significant at $p < 0.05$.

Table 2. Statistical significance and r^2 of the quadratic transfer functions of 1-year height, RCD, volume and survival against climate predictors (summer mean temperatures).

Variables	R^2	Sig.	Predictors
1yr-Height	0.39	0.0255	JunMinT
	0.28	0.0826	JunMeanT
	0.31	0.0628	MTWM
	0.27	0.0914	AMI
RCD	0.35	0.0413	MayMeanT
	0.58	0.0014	JunMeanT
	0.46	0.0095	JulMeanT
	0.33	0.0503	AugMeanT
	0.46	0.0095	MTWM
	0.50	0.0057	JunMaxT
	0.43	0.0141	JulMaxT
	0.39	0.0245	AugMaxT
	0.40	0.0211	JunMinT
	0.42	0.0161	DD > 5˚C
Volume	0.42	0.0174	JunMinT
	0.57	0.0017	JunMeanT
	0.52	0.0040	JulMeanT
	0.51	0.0050	JunMaxT
	0.33	0.0477	AugMaxT
	0.35	0.0418	AugMeanT
	0.45	0.0117	DD > 5˚C
	0.52	0.0042	MTWM
	0.30	0.0703	AMI
Survival	0.34	0.0437	AMI

Significant at $p < 0.1$.

positively loaded on PC1. Emergence also loaded (negatively) on PC1. Germination loaded negatively on PC2. Regression of PC1 against volume resulted in r^2 of 0.88. Simple linear regression of PC1 against each of the 56 climate variables produced only two significant regressions (June minimum temperature and June mean temperature). R^2 equals 0.32 and 0.29 respectively. Because germination was the only variable loading on PC2, climate variables were not regressed against PC2.

4. DISCUSSION

What is striking in this study is the direct relationships between the greenhouse growth performances and the first year field data, especially the correlation between the initial height and survival. Indeed, seedling growth investment guarantees survival and it may also be a requisite for resource acquisition and resource balance of seedlings [37]. Moreover, collectively, emergence time, height and RCD are considered factors of growth and fitness [38,39]. This result suggests that relative performances of white birch populations in the field, to some extent, could be estimated from germination and pre-planting performances.

We expected that survival among the populations would be influenced by cold winter temperature at the common garden site because most of the populations in the experiment were from climates that are warmer than the common garden climate: That was not the case. Surprisingly, most of the populations with good performances in common garden were from locations with warmer climates. However, a study has shown that it is possible for species to perform differently at different climatic extremes. For instance, in a 6 year provenance study of white ash, the provenances with tallest height in the coldest climate were the shortest in a relatively warmer environment and vice versa [40]. The authors pointed out that such result underpins the genetic basis for trade-off between growth and cold tolerance. However, white birch appears to be a generalist with regards to frost tolerance [36]. Mortality was only observed later in the spring and could not be attributed to frost damage. More importantly, mortality was lowest among the populations from Western Canada where the climate is much warmer than in Northern Ontario. Nonetheless, we exercise caution here because short-term growth investment may lead to future mortality when populations from warm climates are transferred to cold climates [41,42].

Growth potential of some species is directly linked to summer temperature [3]. Also in this study, summer temperature proved to be a strong predictor of climatic distance to which white birch populations may be transferred. This was consistent with the parallel factorial experiment that we conducted in the greenhouse. We used two temperatures (30°C day/20°C night and 22°C day/14°C night) and two water regimes (regular watering and drought stressed). Seedlings in the high temperature environment outperformed those in the low temperature environment (unpublished data). In theory, it implies that white birch populations will benefit from transfers to warmer climates. However, successful transfer is most probable if the climate of the test site matches that of the populations [18]. This is because there is a potential risk of maladaptation when transferring species along climate or geographic range [43,44]. Also, populations might express adaptation to their original environments even when planted in common gardens [17]. For these reasons, a conservative climatic distance will be more appropriate. Out of the populations tested, the closest matches for the common garden site were populations from Timmins (T-Dry) in Northern Ontario and St George's in Newfoundland. Although St George's is a climatic match for the common garden site, the population's performance was not very impressive.

Apart from being a match, in the absence of a population from Thunder Bay (due to lack of viable seeds) in this experiment, populations from Timmins invariably serve as surrogate for the test site. Timmins is located in Northern Ontario with similar cold northern climate as the test site. However, this is not a conclusive outcome because the performances of the remaining two populations from Timmins are less than average even though they were from locations which are a few kilometers apart. This poses a question of how much influence do seed sources have on the post-planting performance of white birch. Also, it should be pointed out that white birch has different ploidy levels with polyploids being generally more tolerant than the diploids [45]. It is difficult to know if there is a confounding effect of ploidy level in addition to population effects. Growth and survival is controlled by many factors other than climates and it is important to understand genotype performance from both genetic, developmental and growth viewpoints to adequately capture the dimension of variations among the populations. However, the prediction of the transfer functions is not trivial. The models summarized the important climate variables relevant to the species transfer and aided the matching of populations with the test site. This will provide a useful guide in the decision making process. At this stage of this experiment, we use the term "match" with caution and we are itching to know what the populations' performances might be in a few years from now.

5. ACKNOWLEDGEMENTS

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