

ADAPTIVE AND PHENOTYPIC RESPONSES OF WHITE
BIRCH PROVENANCES TO CLIMATE VARIATIONS

Oluwatobi Adeyemi Oke

A Graduate Thesis
Submitted in partial fulfilment of the requirements
For the degree of
Masters of Science in Forestry

Faculty of Forestry and the Forest Environment
Lakehead University

November 02, 2009

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for the Master of Science in Forestry degree at Lakehead University in Thunder Bay, I agree that the University will make it freely available for inspection.

This thesis is made available by my authority solely for the purpose of private study and research and may not be copied or reproduced in whole in part (except as permitted by copyright law) without my written authority.

Signature: _____

Date: _____

A CAUTION TO THE READER

This MScF thesis has been through a semi-formal process of review and comment by at least two faculty members. It is made available for loan by the Faculty of Forestry and the Forest Environment for the purpose of advancing the practice of professional and scientific forestry.

The reader should be aware that the opinions and conclusions expressed in this document are those of the student and do not necessarily reflect the opinions of the thesis supervisor, the faculty or Lakehead University.

ABSTRACT

Oke, O.A. 2009. Adaptive and phenotypic response of white birch to climate. Master of Science in Forestry. Advisor, Dr. Jian Wang.

Keywords : climate change, provenance, common garden, transfer distance, photosynthesis, water-use efficiency, growth, biomass allocation.

Trees have adapted to their local climate, but with changes in the climate 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 future climate(s). Seed from twenty-five white birch (*Betula papyrifera* Marsh.) provenances collected across Canada were grown in the greenhouse and observed for emergence time, germination and elongation. 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. There was a significant effect of provenance on all growth variables. Initial height was positively correlated with 1-year height and survival ($r = 0.74$ and 0.51 respectively). Germination rate negatively correlated with emergence time ($r = -0.71$). Principal component analysis was used to summarise the growth variables. The first component which explained 51% of the variations represented growth and fitness. Transfer functions were used to estimate the climatic distance across which local provenances may be transferred. Summer temperature was the best predictor of transfer distance.

The common garden experiment was followed up by a greenhouse experiment to investigate the morphological and physiological responses of white birch provenances to high temperature and drought. Four provenances of white birch (Leecreek, Petawawa, Skeena, and Timmins) were selected along a moisture gradient (high, low and moderate) and grown in the greenhouse for 8 weeks. The experiment was split plot design with, two temperatures (30°C day / 20°C night and 22°C day / 14°C night) and two water regimes (regular watering and drought stressed). The seedlings were assigned equally to the treatments combinations and measured for height, RCD, relative growth rate, biomass partitioning, photosynthesis, water-use efficiency and pre-dawn leaf water potential. The seedlings in the high temperature treatments had best height and RCD growth even in the low water treatments. Carbon partitioning between root and shoot was not different between provenances in the low water treatments. Proportionally, more carbon allocation to leaves was observed in the low water treatments. Evidence of provenance adaptation to local environments was noticed in the rate of photosynthesis. Differences in water-use efficiency was observed between provenances in the low water

CONTENTS

ABSTRACT	v
CONTENTS	vi
TABLES	viii
FIGURES	viii
ACKNOWLEDGEMENTS.....	xi
Chapter I	12
GENERAL INTRODUCTION	12
Chapter II.....	14
ASSESSING TRANSFER RESPONSES OF WHITE BIRCH POPULATIONS TO CLIMATE... 14	
2.0 INTRODUCTION	14
2.1 Study Objectives.....	17
2.2 METHOD	18
2.2.1 Climate Data	21
2.2. 2 Data Analysis.....	22
2.3 RESULTS.....	24
2.4 DISCUSSION.....	36
Chapter III	39
PHYSIOLOGICAL RESPONSES OF WHITE BIRCH POPULATIONS TO SIMULTANEOUS EFFECTS OF DROUGHT AND TEMPERATURE	39
3.0 INTRODUCTION	39
3.1 Study Objectives.....	43
3.2 MATERIALS AND METHODS	44
3.2.1 Experimental Design	46
3.2.2 Data Collection	46
3.2.3 Data Analysis.....	48
3.3 RESULTS.....	50
3.4 DISCUSSION.....	68
Chapter IV	74
CONCLUSION	74
REFERENCES	76

TABLES

Table 2.1. Location, geographic coordinates and climates of the 25 white birch provenances.	19
Table 2.2. Simple linear regression of height, RCD and volume against each of 54 climate and 3 geographic variables	30
Table 2.3. Significance and r^2 of the quadratic transfer functions of 1-year height, RCD, volume and survival against climate predictors	31
Table 2.4. Variable loadings for the two principal components	35
Table 3.1. Details of provenance location of the 4 provenances used in this study	44
Table 3.2. Summary of ANOVA results for the progressive measurements of height, root-collar diameter at 4, 6 and 8 weeks and relative height growth rate	52
Table 3.3. Summary of ANOVA results for leaf, shoot, root, total biomass, leaf mass ratio, root mass ratio and root shoot ratio	56
Table 3.4. Regression parameters for the relationships between leaf, shoot, root and total mass of the four white birch provenance under low temperature and high water and high temperature and low water	60
Table 3.5. Summary of ANOVA results for photosynthesis, stomata conductance, Water-use efficiency and Pre-dawn leaf water potential	63
Table 3.6. Regression parameters for the relationships between water-use efficiency, photosynthesis and stomatal conductance of the four white birch provenances under low temperature and high water and high temperature and low water	65

FIGURES

Fig. 2.1. Locations of the 25 provenances in Canada	20
Figure 2.2. Emergence time of the 25 white birch provenances after sowing of the seeds	24
Figure 2.3. Percentage germination of the 25 provenances of white birch	25
Figure 2.4 Initial height of the 25 white birch provenances	25
Figure 2.5. One year height of the common garden trial of 25 white birch provenances	27
Figure 2.6. One year root-collar diameter of the common garden trial of 25 white birch provenances.	27
Figure 2.7. Percentage survival of the common garden trial of 25 white birch provenances after 1 year.	28
Figure 2.8. One-year total volume per provenance (productivity) of the common garden trial of 25 white birch provenances.	28
Figure 2.9. One-year height transfer distances of the white birch provenances in the units of June mean temperature (A), mean temperature of the coldest month (B), June minimum temperature (C) and annual moisture index (D).	32
Figure 2.10. RCD transfer distances of the white birch provenances in the units of July maximum temperature (A), June mean temperature (B), June maximum temperature (C) and degree days > 5°C (D).	33
Figure 2.11. Volume transfer distances of the white birch provenances in the units of June minimum temperature (A) and degree days > 5°C (B).	34
Figure 2.12. Survival functions of the white birch provenances in the units of annual moisture index (AMI).	34
Figure 3.1. Mean annual monthly temperature and precipitation of the four white birch provenances.	45
Figure 3.2. Means and one standard errors of height growths of four white birch provenances at 4 weeks.	52

Figure 3.3. Means and one standard errors of height growths of four white birch provenances at 6 weeks.	53
Figure 3.4. Means and one standard errors of height growths of four white birch provenances at 8 weeks.	53
Figure 3.5. Means and one standard errors of height relative growth rate of four white birch provenances between 4 and 8 weeks	54
Figure 3.6. Total biomass of four white birch provenances at different growth conditions.	56
Fig. 3.7. Pattern of biomass allocation of four white birch provenances at different growth conditions.	57
Figure 3.8. Means and standard errors of leaf mass ratio, root-shoot ratio, and root mass ratio of four white birch provenances.	58
Figure 3.9. Correlations between total biomass and leaf mass of four white birch provenances under low temperature and high water and high temperature and low water.	61
Figure 3.10. Means and standard errors of photosynthesis, stomata conductance, water-use efficiency and pre-dawn leaf water potential of the four white birch provenances.	64
Figure 3.11. Correlation between water-use efficiency and stomata conductance of four white birch provenances under low temperature and high water and high temperature and low water.	66
Figure 3.12. Correlation between photosynthesis and stomata conductance of four white birch provenances under low temperature and high water and high temperature and low water.	67

The earth's failing strength

The cry of the babies

The paternal and maternal love

The symbols of charity

The valour of the heroes

The hopes of the Halcyon days

ACKNOWLEDGEMENTS

This study was funded by National Sciences and Engineering Research (NSERC). I would like to thank the Lakehead greenhouse manager Joan Lee who was of great assistance during the greenhouse operations. I would also like to thank Patrick Howe, Patrick Cybulski and Martin Kuwaiton for helping out during the field preparations.

Special thanks to Gabriel Yangadery who was of great help during the planting and data collection in the field. I am also grateful to Junlin Li for sharing his knowledge with me. I also like to thank Lois-Ann Bender and Eva Scollie for always willing to help.

I appreciate my committee member Dr. Parker and Dr. Dang for their constructive comments toward my proposal for this study and their valuable comments on my thesis. I also like to thank Dr. Chander Shahi for assisting with my statistical models. Special thanks to the external examiner for his critical comments.

I am mostly grateful to my advisor Dr. Jian Wang, with whom I have grown in potentials. I really appreciate him for encouraging me and holding me in higher standards.

Lastly, I would like to thank my family and friends especially my brother Yemi Oke who has been an inspiration to me.

Chapter I

GENERAL INTRODUCTION

The global climate system is continually evolving and significant ecological change occurs at all time scales (Jackson 2005). However, the rapid global climate change is causing an unprecedented disruption of biological processes (Wang et al. 2006). The implication of this on forest systems is enormous. Specifically, shrinkage in the coverage of the boreal forest and extinction of some important members of the forest is anticipated (Peters and Lovejoy 1990). A goal of current reforestation is to establish a new generation of trees with optimal growth and adaptation (Rehfeldt et al. 1999a). This requires the understanding that the distribution of species is controlled by elements of climate, and that species are composed of provenances that are physiologically attuned to different climates (Rehfeldt 1999b; Rehfeldt et al. 2003). In addition, frequent heat and drought stress has been predicted for some parts of the boreal forest (Cherry 1998). Therefore, understanding the morphological and physiological responses of provenances to climate extremes will be important in the selection of seed sources to meet specific site conditions.

Birches are common trees of boreal forests across North America from the Alaskan and Canadian Arctic to the northern tier of the American states (Perala and Alm 1990). They are from a genetically plastic genus with continuous morphological variations. They have high genetic variability and varying chromosome numbers which could be 70 or 84 (rarely 42 or 56) (Perala and Alm 1990). Macroclimatic temperature fluctuation has changed the distribution pattern of birch in the northern limit of birch across Alaska and Canada (Perala and Alm 1989).

White birch (*Betula papyrifera* Marsh.) is the most prevalent of all the birches (Safford et al. 1990). It tolerates both low winter temperature and high summer temperature where water is not limiting (Benowicz et al. 2000). However, it rarely grows where average July temperature exceeds 21°C; it is mostly found in places with short, cool summers and long cold winters (Safford et al. 1990). White birch tolerates wide variations of precipitation and drought patterns (Safford et al. 1990; Simard et al. 1996). Consistent with its wide range, white birch grows on almost any soil type but performs better on deeper well-drained to moderately drained Spodosols, Inceptisols and Entisols of glacial origin (Safford et al. 1990).

White birch is one of the most ecologically important hardwood species and there is a rising commercial interests for its products and hardwood-conifer management. However, lack of information on the deployable properties of white birch may constrain these interests. Although, there is increased ecological and silvicultural knowledge base for white birch, information about local populations, transferability and potential range of sites where it may be planted is limited. The main objective of this project is to understand the underlying climatic factors influencing white birch distribution and also to investigate its adaptive strategies to climate extreme.

The thesis consists of two main parts. The first part involves the application of climate regression models (transfer functions) to a common garden experiment which provides insight to climatic factors influencing the distribution of white birch. The second part is a greenhouse experiment which addresses the physiological and morphological responses of white birch provenances to high temperature and drought.

Chapter II

ASSESSING TRANSFER RESPONSES OF WHITE BIRCH PROVENANCES

2.0 INTRODUCTION

Due to climate change, forest climate zone boundaries could shift at a pace that is out of proportion for trees' migration potential (Roberts 1989). This shift implies that populations could be relegated to climates that are sub-optimal for growth and survival (Rehfeldt et al. 2003) and in the worst case scenario, extinctions. One proposed strategy for offsetting the full implications of climate change on forest systems is to match genotypes with the future climates (Parker et al. 2000; Rehfeldt et al. 2002). However, predictability of forest response to climate change is often constrained by lack of adequate information on the extent and distribution of genetic variability of many species (Cherry 1998).

There are models predicting species migration in response to climate change (Joyce et al. 1990; Matyas 1994; Carter 1996). However, these models often fail to recognize the intrinsic nature of tree species as modular organisms that are capable of plastic response to both favourable and extreme climates. These models also tend to ignore the importance of intraspecific genetic variations which may extend the range of a species beyond the predicted climate boundaries (Marchin et al. 2008). Species with similar ecological preference may respond differently to changing climate conditions and a community may reflect a disparate biogeography and evolutionary history (Rehfeldt et al. 1999b; Ackerly et al. 2004).

Widespread tree species are composed of populations that are physiologically attuned to different climates (Morgenstern 1996). In addition, some tree species exhibit

sub-specific genetic differentiation and enormous ecophysiological and functional diversity that underlies growth rates and adaptation to a broad range of climates (Ackerly et al 2000; Rehfeldt et al. 2002). This broad congruence with climate can be viewed as “(i) short-term plastic responses that accrue in endemic populations as physiological systems adjust to change and (ii) as a long-term evolutionary process that realigns genetic variability with environmental diversity” (Rehfeldt et al. 2001). All these ecological transitions and transformations are related to climate. Climate is multivariate and species respond differently and independently to climatic variables such that they migrate in different directions and at different rates (Jackson 2005).

Trees occupy shifting geography (Savolainen et al. 2007) and given the constraint to migration and adaptation, local populations are not always the fittest (Matyas 1994). There is evidence that populations do occupy sub-optimal climate for growth and survival (Rehfeldt et al. 1999b; 2001, 2002; Arthur 1987; Matyas and Yeatman 1992) and growth and survival may improve away from local habitats. For instance, at the northernmost range of *Pinus sylvestris* L. and *Larix* spp., growth and survival can increase by more than 30% when transferred to a location 5° of latitude to the south (see Savolainen et al, 2007). Also, Carter (1996) showed that eight of ten tree species studied would grow better in a cooler climate with the optimum located north of their current sites. Selective factors such as climate, edaphic factors and parasites could trigger local adaptation, which on a spatial scale may lead to genetic differentiation among populations (Savolainen et al. 2007).

Climate regression models (e.g. response and transfer functions) are important statistical concepts used in plant distribution and adaptation studies (Rehfeldt et al. 1999b). The underlying hypothesis of climate regression models is that variation in the climate

occurs geographically, and that elements of the climate can be predicted from geographic descriptors (Rehfeldt et al. 1999b). Transfer functions have been used to determine the underlying climatic factors influencing performance and distribution of many of the boreal species (Rehfeldt et al. 2003; Wang et al. 2006; Thomson and Parker 2008). The relative advantage of using transfer functions is that populations may not necessarily be planted in more than one site for a reliable result (Rehfeldt et al. 2003). Also, individual species, provenances and test sites alike are unique in establishing transfer distances.

There are no universal predictors of performance, however, Rehfeldt et al. 2004 established that climatic variables such as summer temperatures (degree-days $>5^{\circ}\text{C}$ and mean maximum temperature of July), winter temperatures (degree-days $<0^{\circ}\text{C}$ and mean minimum temperatures of January) and an annual moisture index (ratio of degree-days $>5^{\circ}\text{C}$ to mean annual precipitation) are consistently and closely linked to genetic differentiation of populations. The author further demonstrated that converting clines with geographic drivers to those with climatic drivers is not only feasible but also may lead to alternative interpretations.

Historically, white birch is one of the species which occurred as localized and dispersed populations during the last glacial maximum (Jackson 2005). It appears that its current geographic range could be attributed to the favourable effects of the previous climate change on its populations. Many of the widely distributed and dominant species of the last glacial period are now localized and highly fragmented (Jackson 2005). Species considered most sensitive to past climate change shows evidence of latitudinal and elevational shifts in response to changing conditions (Nowak et al. 1994). This response has not been established for white birch. In addition, there are few studies on the pattern of

genetic variation of white birch across climate gradients. Relative magnitudes of genetic differences among trees within stands, between stands within geographic areas and between broad geographic areas have not been studied (Carlson et al. 2000).

2.1 Study Objectives

The objectives of this study are (i) to understand the underlying climatic factors affecting the distribution of white birch (ii) to investigate how variations in the seed conditions/origins determine the success of white birch in the field and (iii) to explore the suitability of the transferred provenances to the northern climates. The factors influencing the performance of white birch across climate gradients have not been established and this chapter is intended to provide information on the factors that are important for transferability of white birch.

2.2 METHOD

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 Islands) were grown under ambient conditions at the Lakehead University's greenhouse. The selected provenances ranged from latitude 45° 16'N – 54° 43'N and elevation 70 - 800m (Table 1). The seeds were sown on the 18th of April 2008. The seeds were sown in styroblocs with 5 seedlings per cavity. Each styrobloc consisted of 45 cavities. Different styrobloc was used for each provenance. The potting medium was a pre-mixed peat moss. The seedlings were fertilized weekly with a regular fertilizer (N-P-K 20:20:20).

The seedlings were observed for emergence time, germination percentage and height in the greenhouse. The seedling emergence time was recorded for 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 styrobloc. 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.

Table 2.1. Location, geographic coordinates and climates variables for the 25 white birch provenances.

Provenance	Latitude	Longitude	Elevation	MAT	MAP	MTCM	MTWM	AMI
NL ST1	48.32	54.34	304	3.83	1201.9	-7.9	16	1.03
NL TW4	47.37	57.57	140	3.83	1201.9	-7.9	16	1.03
NL TW1	47.37	57.57	140	3.83	1201.9	-7.9	16	1.03
NL TW2	47.37	57.57	140	3.83	1201.9	-7.9	16	1.03
St. Georges	48.5	58.16	70	4.42	2062.6	-8.2	17.3	0.68
Indian Brook	46.35	60.55	10	6.16	1700.5	-5.1	18.5	0.98
Millvale	46.4	63.4	70	5.23	1140.7	-8.6	18.5	1.46
Cap Des Rosiers	48.11	65.41	200	3.33	1147.2	-10.1	16	1.08
Allardville	47.6	65.42	100	3.91	969.9	-11.3	18.5	1.58
Wayerton	47.22	65.93	300	3.99	1032.6	-11.9	18.6	1.55
NBM	45.54	66.38	20	5.62	1124.1	-9.5	19.3	1.62
NBW	45.54	66.39	20	5.62	1124.1	-9.5	19.3	1.62
NBD	45.54	66.39	20	5.62	1124.1	-9.5	19.3	1.62
Bell falls	46.45	75.1	330	3.28	1014.7	-14.3	18.1	1.58
Alice	45.75	77.13	300	4.07	829.65	-12.6	18.65	2.05
Petawawa	45.97	77.47	130	4.28	853.3	-13	19.2	1.99
Timins Fresh	48.14	80.37	295	1.36	831.4	-17.5	17.4	1.7
Timins Moist	48.34	81.22	295	1.36	831.4	-17.5	17.4	1.7
Timins Dry	48.34	81.22	295	1.36	831.4	-17.5	17.4	1.7
Porcupine	49.15	117.1	840	8.05	742.08	-3.2	19.25	2.63
Leecreek	50.56	119.32	600	5.41	409	-7.1	16.8	3.73
Adams lake	51.43	119.83	400	5.01	1076.5	-6.9	16.7	1.32
Skimikin	50.43	120.25	547	8.88	279	-4.2	21	13.11
Tabor Lk	53.55	122.22	800	3.95	600.8	-9.6	15.5	2.14
Skeena river	54.3	128.34	70	6.32	1322.3	-4.3	16.4	1.11

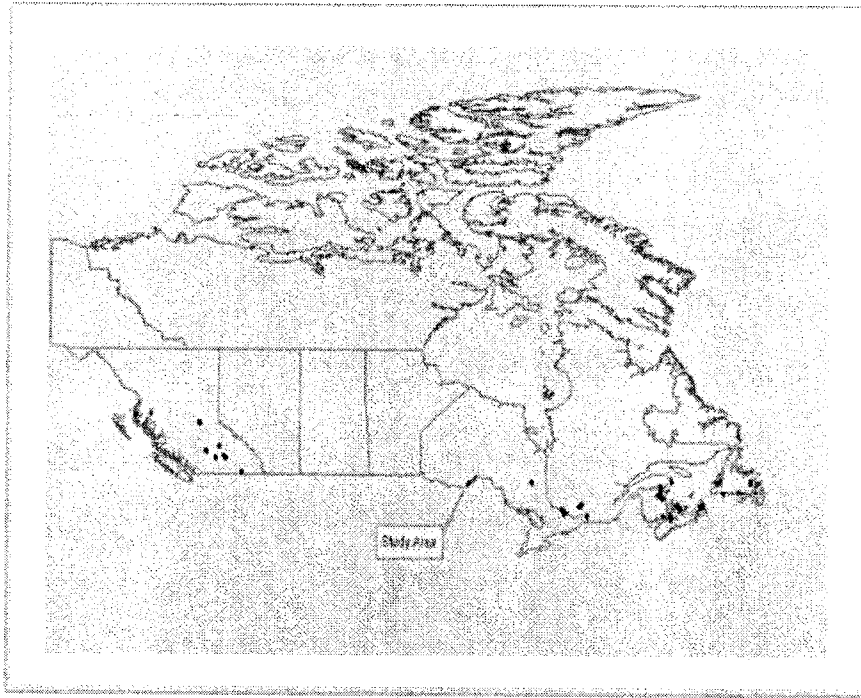


Fig. 2.1. Locations of the 25 provenances in Canada.

Field Operations

The common garden site is located in Northwest Ontario (Thunder Bay) on plot of a forested land that was recently disturbed by a wild fire. The location is $48^{\circ} 22' N$, $89^{\circ} 19' W$ with elevation of 183.3m. The mean January temperature is $-15^{\circ}C$ while the mean July temperature is $18^{\circ}C$ and an average annual precipitation of 704 mm. The field preparation and fencing was carried out between 25th and 31st of July 2008. The field preparation involved removal of weeds, dead woods and stumps on the site. The fencing was necessary to prevent deer damages. The seedlings were planted in a completely randomized design between 5th and 7th of August 2008. Thirty three seedlings were planted for each provenance using a spacing of 1.5m x 1.5m. The site was kept weed free. On July 25th 2009

(after 1 year), the seedlings were measured for height and root-collar diameter and also scored for survival. The volume per seedling was also calculated using the formula $h \times (\pi d^2)/4$; where h = tree height, d = root-collar diameter and $\pi = 22/7$.

2.2.1 Climate Data

All climate data were normalized climate data (1971-2000) using the weather stations closest to the provenances 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 $< 0^\circ\text{C}$, degree days $> 5^\circ\text{C}$ and 3 geographic variables (latitude, longitude and elevation) were also used in the analyses. All climate data were normalized climate data (1971-2000) using the weather stations closest to the provenances or use of multiple weather stations where the former was not applicable. The data were collected from Environment Canada.

2.2. 2 Data Analysis

All the data were analysed for normality using Shapiro- Wilk test and where there was a departure from normality, the data were transformed using polynomials or logarithm transformations. One way analysis of variance (ANOVA) was used to determine if there were significant effects of provenance on the growth variables. The ANOVA model used was;

$$Y_{ij} = \mu + P_i + \varepsilon_{ij}$$

Where Y_{ij} is the growth observation of replication j of provenance i , μ is the provenance mean, P_i random effect of provenance i , and ε_{ij} is the random error effect of replication j of provenance i .

Fifty-four climate and 3 geographic variables were screened with simple linear models. Regressions that were significant at $\alpha = 0.05$ were retained for further analysis. The linear model was;

$$Y_i = b_0 + b_1X_1 + e$$

Where Y_i is the predicted height, RCD, survival or average volume, b_0 is the intercept, b is the regression coefficients, X is climatic or geographic variables of the provenances and e is the residual.

The resultant significant climatic or geographic variables from the simple linear model 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, and it is could also be

used to predict the optimum performance of seed sources at a given test site. The quadratic transfer function model was;

$$Y_i = b_0 + b_1X_1 + b_2X_1^2 + e$$

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 provenance climate) and e is the residual.

Each provenance's performance was expressed as a function of the growth variables (emergence time, germination, initial height, 1-year height and RCD) using principal component analysis (PCA). The resultant components that explained most of the variations in the data were used in the transfer function regression. The principal component regression model was;

$$PC1 = b_0 + b_1X_1 + b_2X_1^2 + e$$

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 provenance climate) and e is the residual.

The data were analysed using SAS and sigma plot.

2.3 RESULTS

Greenhouse results

There was a significant difference in the emergence time, germination, and initial height ($p < 0.0001$). Seedlings emergence time ranged from 7 to 15 days (Fig. 2.2) while germination percentage ranged from 29% to 100% (Fig. 2.3). Initial height ranged from 22.5cm in Porcupine provenance to 38.6cm in Millvale provenance (Fig. 2.4). Some of the provenances germinated within 7 days especially the provenances from the west coast. Most provenances germinated within 10 days. Provenances from Newfoundland took much longer to germinate except the provenance from St. Georges which germinated within 10 days. Most of the provenances that germinated early had higher germination percentages and higher initial height compared with those that germinated late. The latitude, longitude and elevation of the provenances had no bearing on either of germination or seedlings emergence time.

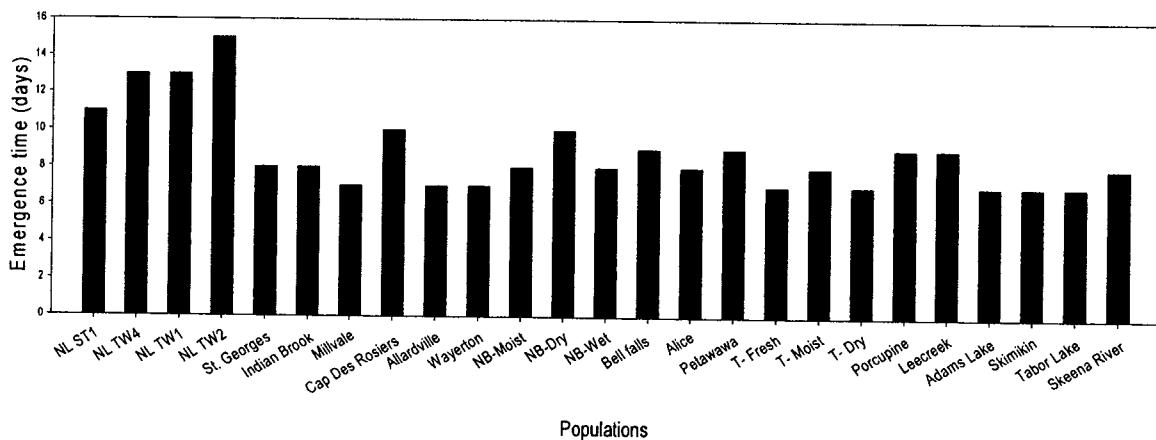


Fig. 2.2. Emergence time of the 25 white birch provenances after sowing of the seeds.

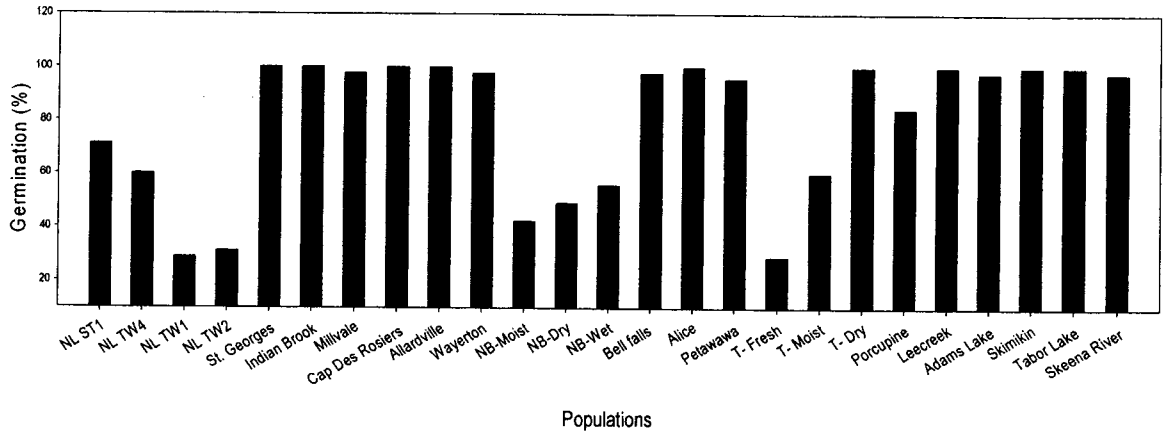


Fig. 2.3. Percentage germination of the 25 provenances of white birch

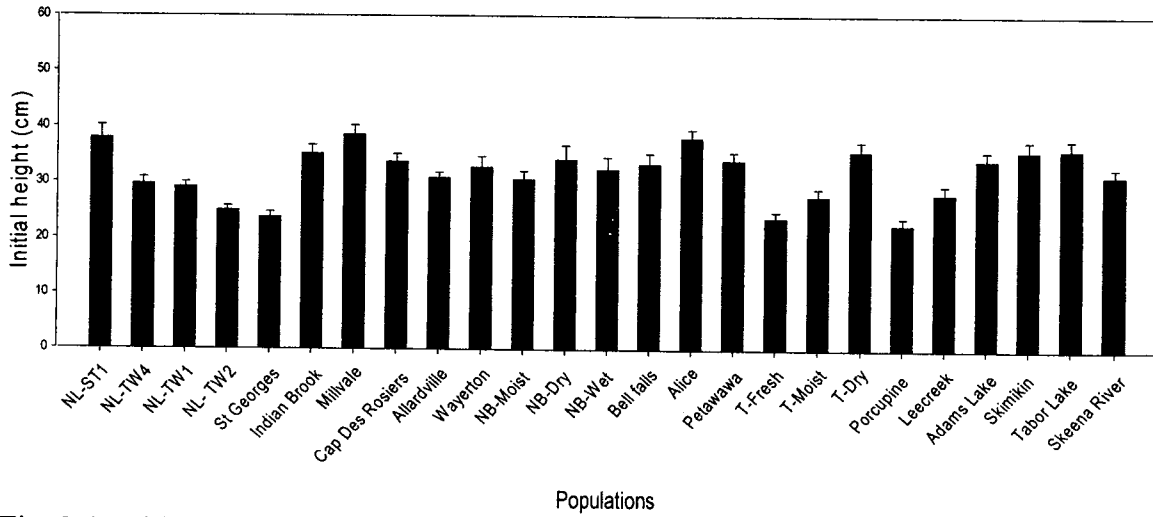


Fig. 2.4. Initial heights of the 25 white birch provenances

Common Garden Results

There were significant differences in 1- year height and root-collar diameter ($p < 0.0001$) among the 25 provenances. The average volume per tree was also significant ($p < 0.0001$). The 1-year height ranged from 30.1cm in St. Georges provenance to 57.9cm in Skimikin (Fig. 2.5). The root-collar diameter (RCD) ranged from 4.35mm in St. Georges provenance to 6.67mm in Wayerton (Fig. 2.6). Survival among the provenances ranged from 21% in NL-TW1 provenance to 88% in Skimikin (Fig. 2.7). The average survival was 65%. Volume ranged from approximately 4.4cm^3 in provenance from Timmins (Moist) to 20.99cm^3 in Skimikin (Fig. 2.8).

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

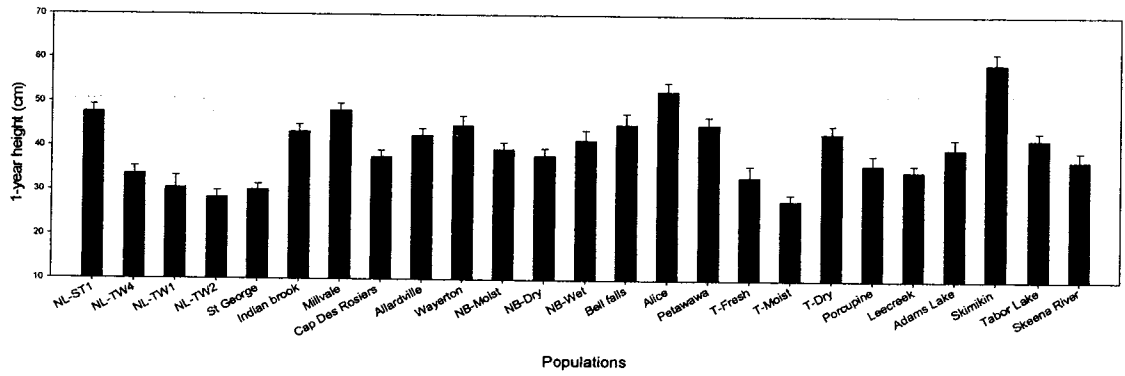


Fig. 2.5. One year height and standard errors of the common garden trial of 25 white birch provenances.

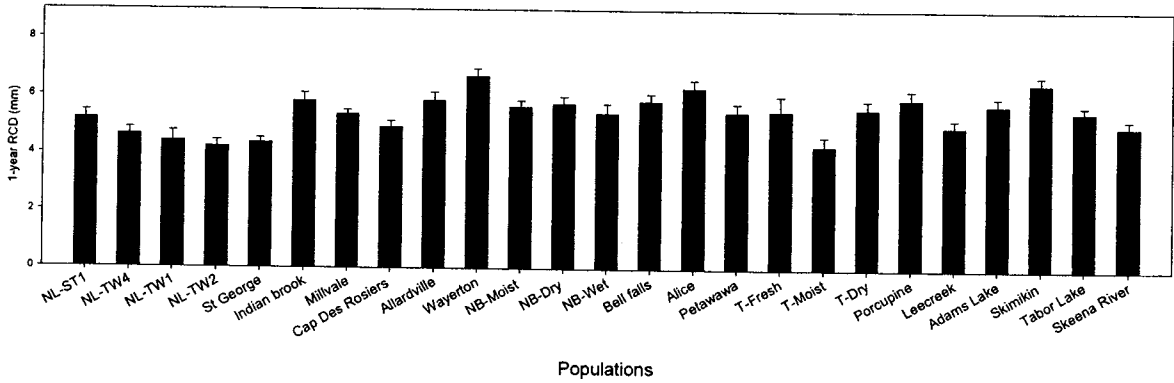


Fig. 2.6. One year root-collar diameter of the common garden trial of 25 white birch provenances.

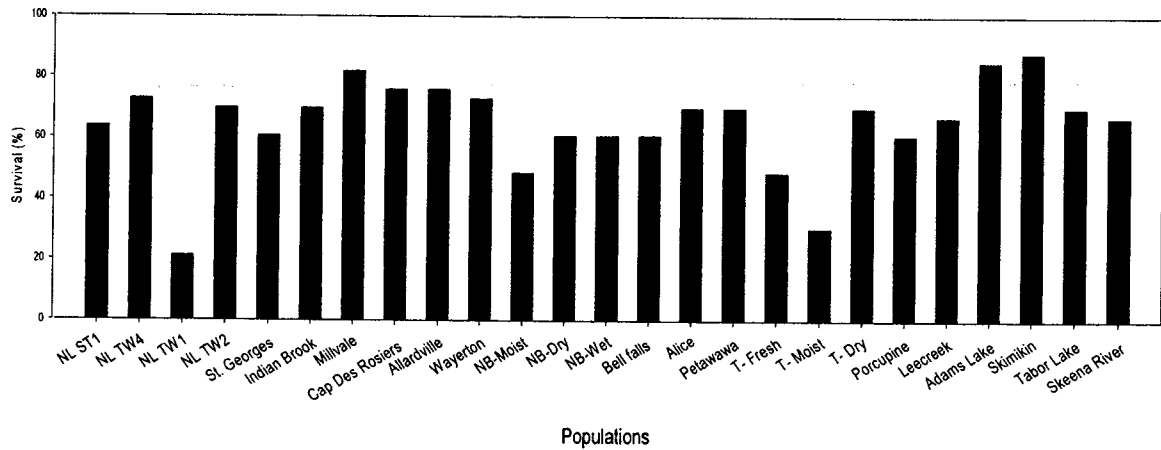


Fig. 2.7. Percentage survival of the common garden trial of 25 white birch provenances after 1 year.

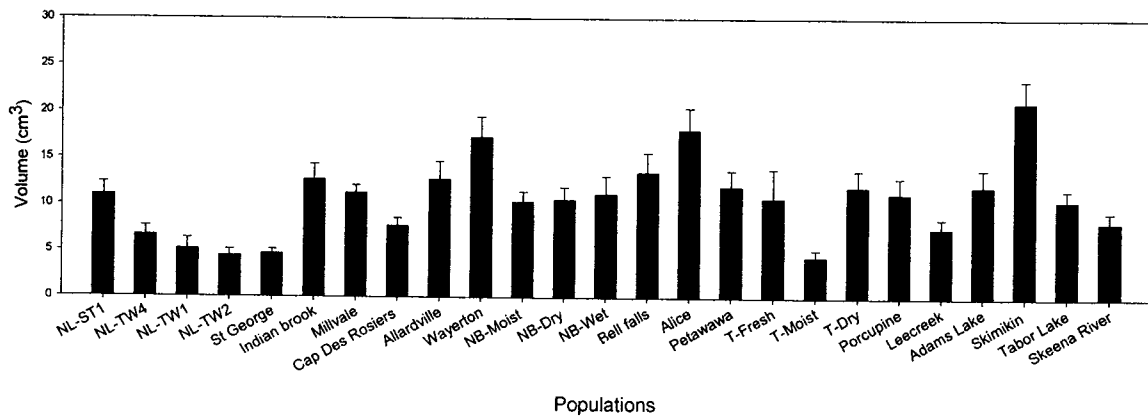


Fig. 2.8. One year volume of the common garden trial of white birch provenances.

Simple linear regressions of the growth variables against each of 56 climate and 3 geographic variables were significant for some predictor variables. Summer mean temperatures (June and July) produced consistent and significant regressions against height, RCD and volume (Table 2.2). 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 derived climate variables (DD>5°C, MTWM and AMI) were also significant. These results are an indication that temperature variables are strong predictors of white birch performance.

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

All the significant simple linear regressions used in the transfer function were retained except for 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 strong predictor of white birch performance compared with the derived climate variables (Fig. 2.9 - 2.11). 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 2.3). AMI was the only predictor of survival ($R^2 = 0.34$) (Fig. 2.12). Since transfer distance was calculated as common garden climate minus provenance climate, positive values denote transfers from climate warmer than the provenance origin while negative values represent transfer to climate cooler than the provenance origin. Zero denotes the climate of the common garden and best match.

Table 2.2. 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
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 2.3. 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
RCD	0.27	0.0914	AMI
	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
Volume	0.42	0.0161	DD>5°C
	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 $p < 0.1$

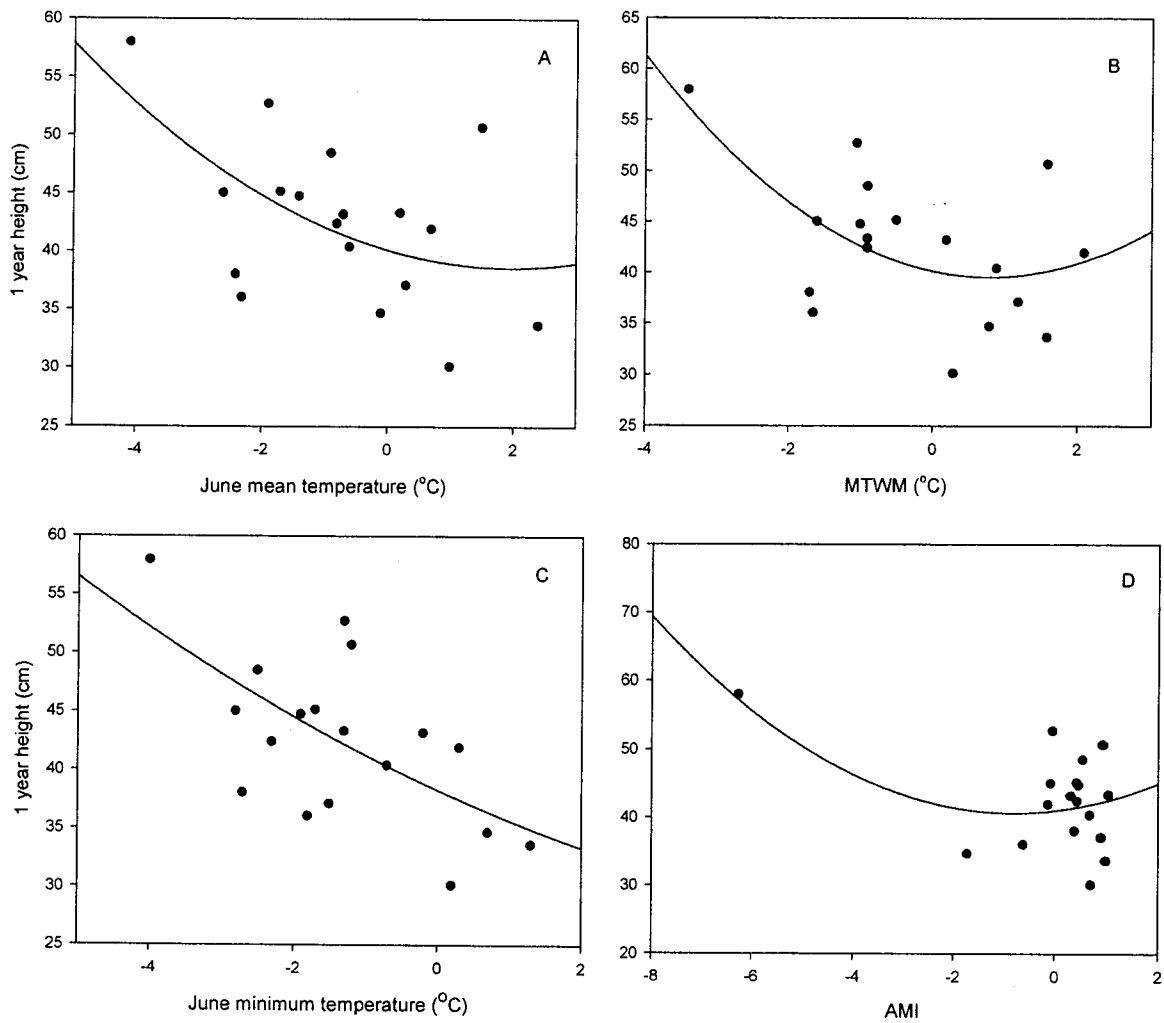


Fig. 2.9. One-year height transfer distances (common garden climate minus provenance climate) of the white birch provenances in the units of June mean temperature (A), mean temperature of the coldest month (B), June minimum temperature (C) and annual moisture index (D).

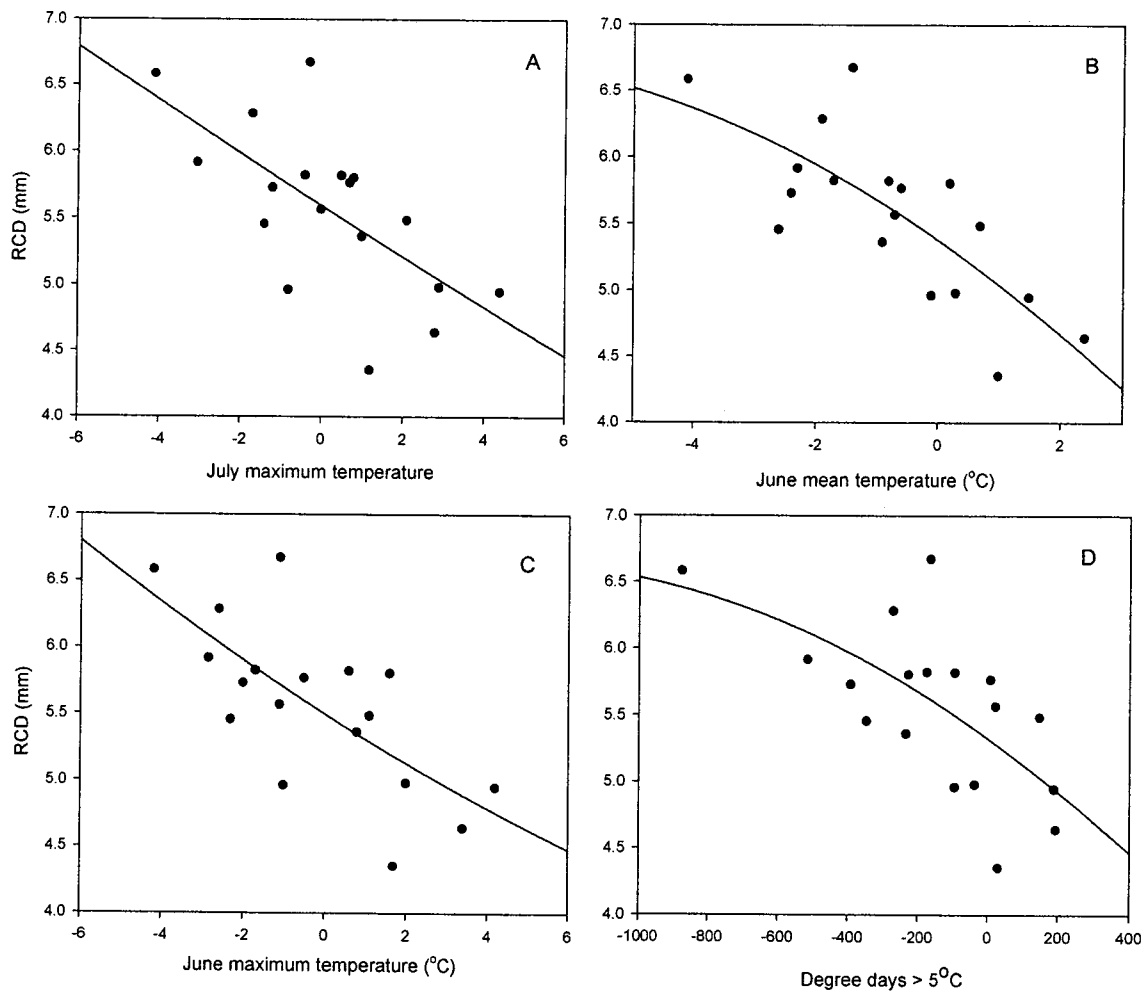


Fig. 2.10. Root-collar diameter transfer distances (common garden climate minus provenance climate) of the white birch provenances in the units of July maximum temperature (A), June mean temperature (B), June maximum temperature (C) and degree days > 5°C (D).

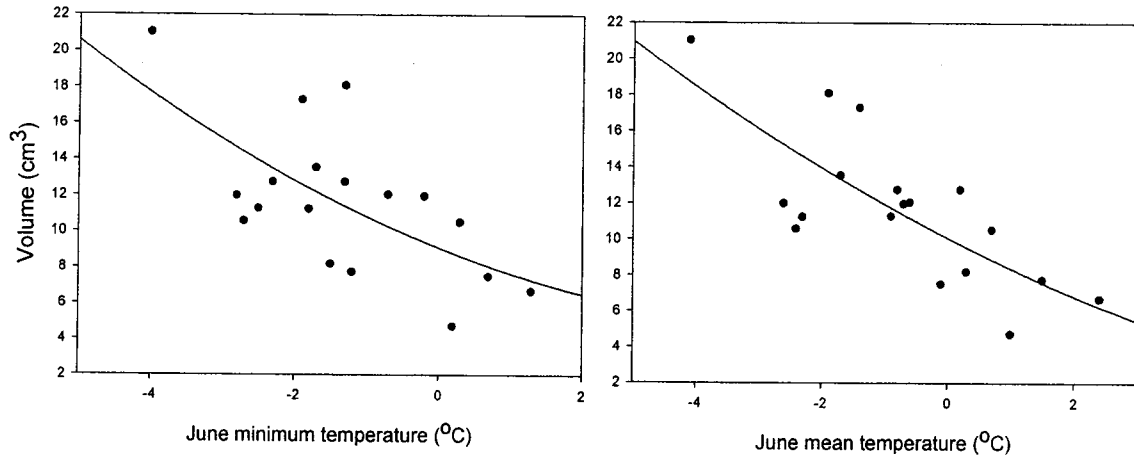


Fig. 2.11. Volume transfer distances (common garden climate minus provenance climate) of the white birch provenances in the units of June minimum temperature (A) and degree days > 5°C (B).

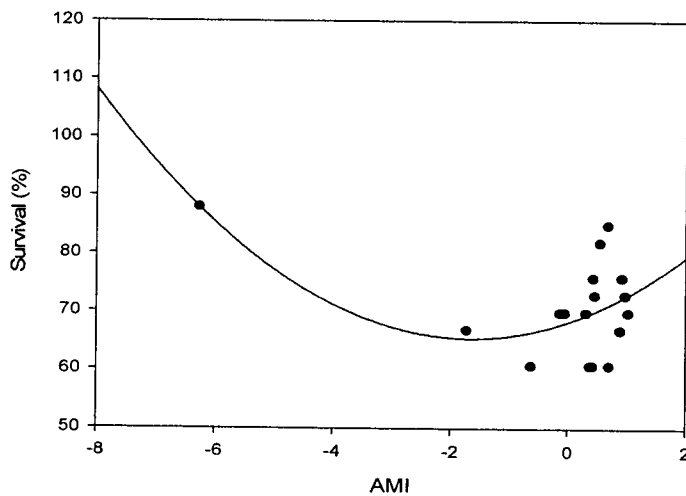


Fig. 2.12. Survival transfer distance (common garden climate minus provenance climate) of the white birch provenances in the units of annual moisture index (AMI).

Two principal components were retained by the PCA of the growth variables (emergence time, germination, initial height, 1 year height, RCD). Both components explained a cumulative variation of 73% with PC1 explaining 51% of the variation while

PC2 explained 22%. Initial height, 1 year height, RCD loaded fairly strongly and positively on PC1 while emergence time loaded negatively on PC1 (Table 2.4). Germination loaded strongly and negatively on PC2. PC1 incorporates height, RCD and emergence time which represents factors of growth and fitness (Dey and Parker 1997; Ackerly et al. 2000).

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 is the only variable loading on PC2, climate variables were not regressed against PC2.

Table 2.4. Variable loadings for the two principal components

Variable	PC1	PC2
1yr height	0.5593	0.1202
Initial height	0.4939	0.1955
RCD	0.4853	0.3023
Emergence time	-0.4148	0.3606
Germination	0.1888	-0.8519

2.4 DISCUSSION

Significant differences were found among the provenances for both the greenhouse and the field observations. The correlations between the growth variables observed in the greenhouse and in field are indications that success of trees in the field also depends on the origins of the seed.

It was expected that survival among the provenances would be influenced by winter temperature because most of the provenances are from climates that are warmer than the common garden climate. This was not the case. White birch appears to be a generalist with regards to frost tolerance (Carlson et al. 2000). Mortality among the provenances was not due to frost damage in spite of the fact that many of the provenances original habitats are warmer than the planting site. Mortality was observed later in the spring was not attributed to frost damage.

Growth potential has been directly related to summer temperature (Rehfeldt et al. 2003). Most of the provenances with best height and RDC growth in the common garden experiment came from locations with warmer climates. Summer temperature proved to be consistent predictor of climatic distance to which the white birch provenances may be transferred. The climate variables that were significant predictor of height also predicted RCD and average volume per tree. The derived climatic variables such as degree days $> 5^{\circ}\text{C}$ and mean temperature of the warmest month were also important predictors. However, these variables are related to summer temperature. The narrower gradients observed in functions of annual moisture index against survival and height indicates that moisture index of about three units is optimal for most of the provenances. Most of the provenances

examined should benefit from a transfer to a warmer climate. Provenances from Timmins Dry and St. George are matches the common garden climate.

Growth and survival is controlled by many factors other than climates and it is important to understand genotype performance from both developmental and growth viewpoints to adequately capture the dimension of variations among the provenances. The principal component loadings showed the relative importance of various factors that influence growth. The Principal Component 1 (PC1) which explained 51% of the variations could be interpreted as a fitness component because of strong positive loadings for all factors of growth. Regressions of PC1 against June minimum temperature and June mean temperature corroborates the notions functions that summer temperature is an important climate variable driving the performance of white birch provenances. It was not surprising that summer temperature was a consistent predictor of white birch performance given the fact that white birch is a deciduous tree with short growing season.

The findings of this study and the expansion of white birch range since the last glacial period are strong indications that increased temperature has contributed to its wide distribution. Nevertheless, white birch is still largely distributed within in regions characterised by cold climates. The large distribution of white birch within the northern limits could be as result of the limitation posed on migration by the Great Lakes and other barriers like mountains. Genecologic principles state that provenances will express adaptation to their original environments even when planted in common garden (Rehfeldt et al. 1999b). The boreal forest of the northern Ontario is one of the coldest ranges of white birch and if provenances truly express adaptation to their original climate, transfer of provenances from warmer climates to this region may not be advisable. Therefore, for the

purpose of regenerating white birch in the North-western Ontario, more provenances from colder climates should be included in the test, and replications of the studied provenances at different test sites is required to further validate this testing procedure.

Chapter III

PHYSIOLOGICAL RESPONSES OF WHITE BIRCH PROVENANCES TO SIMULTANEOUS EFFECTS OF DROUGHT AND TEMPERATURE

3.0 INTRODUCTION

Atmospheric greenhouse gas build-up can result in simultaneous exposure of plants to both high temperature and drought (Zheng et al. 2008) and limits of tolerance for survival may be exceeded (Vitousek 1994). Changes in species composition are anticipated as the climate change exceeds the tolerance limit of some members of the species assemblage (Gunderson et al. 1998). The greatest warming is expected in the boreal and subarctic regions (IPCC 1995) which necessitates a profound understanding of the response of the boreal species to impending climate change.

Adaptation in the event of global change would depend on inherent adaptation of genotypes to different habitats and/or genotypes' ability to exhibit phenotypic plasticity (Ward and Strain 1997; Ward and Kelly 2004). Therefore, understanding both short-term physiological and population-level adaptations to climate change is important for predicting forest responses (Gunderson et al. 1998). In addition, knowledge of ecophysiological variation among species is essential to understand the intricacies of adaptive evolution and genetic mechanisms underlying ecophysiological diversity among species (Ackerly et al. 2000).

There are numerous studies on the effects of drought on physiology and morphology of tree. For instance, Lechowicz and Ives (1989) examined the drought

resistance of *Acer saccharum* Marsh. and *Fraxinus Americana* Lam. in nursery plots by comparing their gas exchange properties. The species were not only different in some of the gas exchange characteristics across treatments but they also showed different means of avoiding desiccation and maintaining productivity which were consistent with their genetic structures and atmospheric cycles of their habitats. Zhang et al. (2004) studied the physiological and morphological response of *Populus davidiana* Dode. populations to progressive drought stress. The authors reported that growth and gas exchange properties were impacted more by water stress in populations from dry climates than in provenances from wet climates. However, higher water-use efficiency and root-shoot ratio were observed in the populations from dry climates which were considered as indications of arid adaptation. Populations from the wet climate were believed to have evolved a prodigal water-use strategy, in which they tend to rapidly consume water and hence rapid tissue turnover until all water from the soil is exhausted. The authors established that the disparities among the populations are indications of the inherent adaptive strategies conferred on them by the environments in which they had evolved. Similar pattern was reported by Li and Wang (2003) in their study of the response of three provenances of *Eucalyptus microthea* F. Muell. to three water regimes.

Aspelmeier and Leuschner (2006) studied genotypic variation in drought response of silver birch (*Betula pendula* Roth.) clones. Variations in the leaf and root morphologies as well as in carbon partitioning were observed among clones. Reduction in leaf sizes and shift in allocation to the below ground organs at the expense of shoot growth was observed in the drought treated clones. The differences between the irrigated and non-irrigated clones were attributed to their genetic compositions and inherent adaptive strategies.

The implication of climate change on growth and productivity largely depends on the balance between biomass allocated to photosynthetic versus structural tissues (Zheng et al. 2008). Growth rates and water-use are both a functions of biomass allocated to different organs and by the physiological and morphological properties of these organs (Boogaard et al. 1997). Under dry conditions, the relative allocation of biomass to roots usually increases (Bongarsten et al. 1987) and this is an indication of increased capacity for water uptake (Lambers et al. 2008). Plants may also adapt to temperature changes via change in biomass allocation (Zheng et al. 2008), and pattern of biomass allocation in response to temperature varies among species (Peng and Dang 2002).

A Plant's capacity to resist drought results from integration of a variety of adaptive characteristics and mechanisms (Raney et al. 1991). Plants subject to water stress not only show a general reduction in size but also exhibit characteristic modification in structures such as leaves (Kramer 1969; Wang et al. 1998a; Aspelmeier & Leuschner 2006). Thus, such modifications are viewed as adaptive strategies to drought rather than inability to cope (Aspelmeier & Leuschner 2006). Physiologically, stomatal closure can serve to limit water loss and postpone development of damaging water deficits (Raney et al. 1991). Net photosynthesis decreases with increase in leaf temperature during a drought event. The tendency of plants to maintain photosynthesis during drought event is directly related to survival and recovery after drought (Kruger and van Rensburg 1995). Also, the capacity of plants to maintain turgor is related to maintenance of stomatal conductance and photosynthesis under water stress (Raney et al. 1991).

Temperature affects all plant processes (Lambers et al. 2008). Respiration increases at high temperatures, thus, higher carbon fixation is required to sustain growth and survival

(Griffin et al. 2004). Photosynthesis is one of the cellular functions most sensitive to high temperatures (Daas et al. 2008). Thermal acclimation of photosynthesis is an important means of compensating for harmful effects of rising temperature (Way and Sage 2008). A plant's capacity to acclimate and maintain photosynthesis at high temperatures is related to thermal tolerance (Wise et al. 2004).

Although resource driven plasticity has been reported for trees (Lambers et al. 2008), knowledge of plant's response to changing environments is limited by what resources are being varied and what traits are being measured (Navas and Garnier 2002). Effects of drought and high temperature on plant growth have been investigated separately but there is a direct relationship between temperature and drought (Machado and Paulsen 2001). Even though a direct effect of water stress is often noticeable, the severity of any drought is highly dependent on temperature (Machado and Paulsen 2001). Most often, plants are simultaneously exposed to a variety of environmental stresses such as drought and high temperatures (Griffin et al. 2004). Therefore, it is not enough to induce drought effect without accounting for the cause.

To increase the predictive power, a model approach that clearly defines both operating environments and populations at optimal level to ensure adequate representation of species performance is required (Grossnickle et al. 2005). In addition, there is evidence that growth traits (e.g. survivorship, growth rate, morphology) (Arntz and Delph, 2001) and other ecophysiological traits (e.g. water-use efficiency, total biomass) are correlated to fitness and are under selection (Farris and Lechowicz 1990). Examination of these traits in heterogeneous environments that adequately reflect the plants' experiences may give a more reliable insight into the process of adaptation in the event of global warming.

White birch possesses physiological characteristics that apply to the species wherever it occurs. General management experience may not be applicable across its natural range given the bio-geo-climatic variation over its wide geographic range (Peterson et al. 1997). There are numerous studies on separate response of white birch to air or soil temperature or drought stress (e.g. Ranney et al. 1991; Li et al. 1996; Wang et al. 1998a; Wang et al. 1998b; Catovsky and Bazzaz, 1999; Zhang and Dang 2005). However, its response to simultaneous effects of high temperature and drought has not been studied.

3.1 Study Objectives

The objective of this study was to investigate the adaptive responses of white birch provenances to high temperature and drought through quantitative assessment of their physiological and morphological characteristics. Four white birch provenances were selected along precipitation gradients and subjected to different temperatures and water regimes. The seedlings were observed for morphological and physiological traits. The hypothesis was that provenances from habitats with moderate precipitation will have greatest height growth, biomass accumulation, photosynthesis and water use-efficiency in drought stress conditions due to the climate fluctuation experienced in those habitats. It is hoped that this study will provide an insight to how best to choose provenances for afforestation with regard to the potential of a warming climate.

3.2 MATERIALS AND METHODS

The experiment was conducted at Lakehead University's greenhouse. Seeds of four white birch provenances were selected along a moisture (low, medium and high) gradient (Table 3.1). These provenances were also used in the field study described in Chapter 2. Provenances from Petawawa and Timmins have similar precipitation but Timmins provenance is from a colder (more northerly) region (Fig. 3.1). The seeds were grown separately in germination trays under ambient conditions. After 8 weeks, 160 seedlings were transplanted into 152mm radius pots. The potting medium was comprised of a mixture of peat moss and vermiculite (2:1). Forty seedlings were selected from each provenance and 10 seedlings were assigned to each treatment combination. The seedlings were allowed 1 week of conditioning in the pots before the initiation of the treatments.

Table 3.1. Details of provenance location of the 4 Provenances used in this study

Provenances	Location	Latitude	Longitude	Elevation	Precipitation
Leecreek	BC	50° 56'	119° 32'	600	409
Petawawa	ON	45° 97'	77° 47'	183	853
Skeena River	BC	54° 30'	128° 34'	70	1160
Timmins Dry	ON	48° 34'	81° 22'	285	871

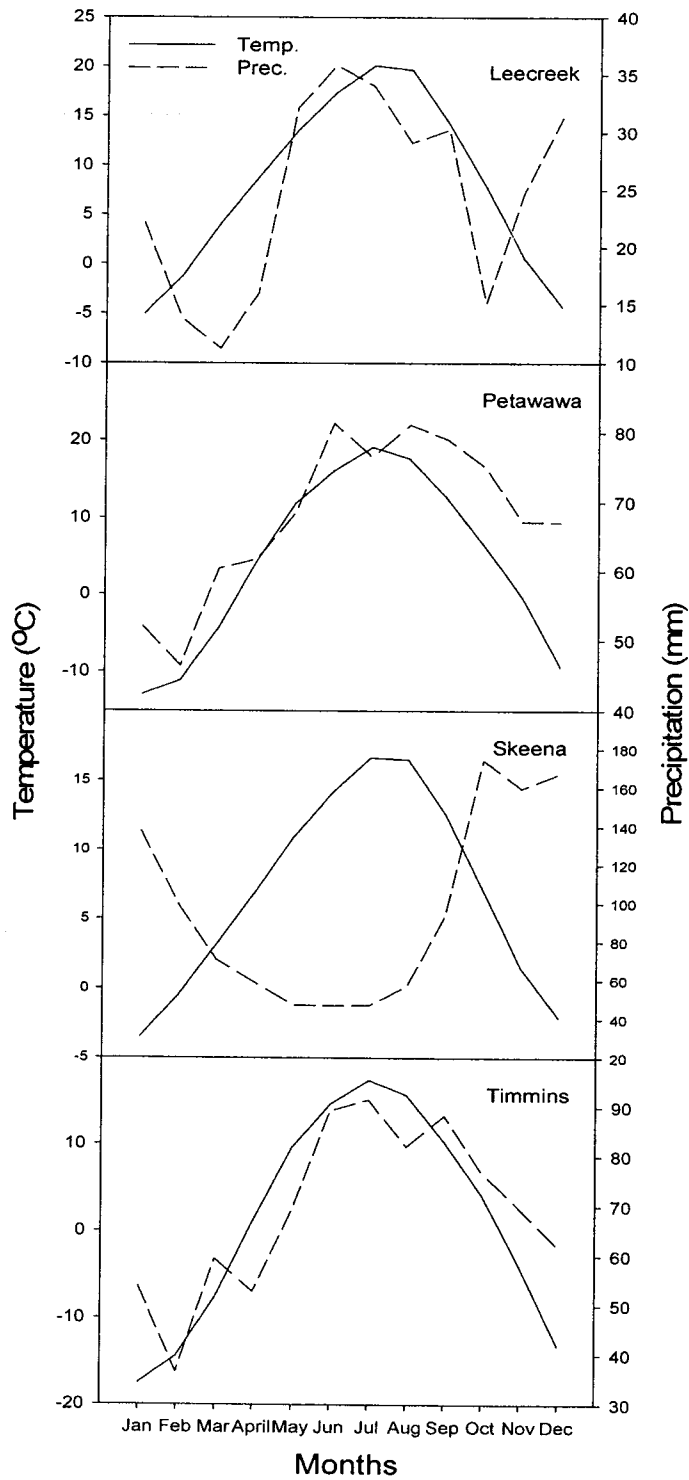


Fig. 3.1. Mean annual monthly temperature and precipitation of the four white birch provenances.

3.2.1 Experimental Design

The experiment was a factorial design (split-plot) with temperature being the main plot while provenance and water regime were subplots. Two temperatures (30°C day / 20°C night and 22°C day / 14°C night) and two water regimes (regular watering and drought stressed) were used. The water content in the drought stressed pots was kept between 25 and 30%. The water contents were monitored by weighing of the pots. Ten pots devoid of seedlings were used as gauges. There were 4 treatment combinations; low temperature/low water (LTLW), low temperature/high water (LTHW), high temperature/low water (HTLW) and high temperature/ high water (HTHW). Seedlings were blocked and randomly positioned and were moved around every week within the blocks throughout the experiment. The seedlings were fertilized with regular fertilizer (20N-20P-20K) once a week. Fertilizer applications were made to coincide with the timing of the irrigation. Environmental conditions were monitored and controlled with an Argus control system (Argus Vancouver). The relative humidity was kept at 40% and photoperiod at 16-hr (artificial light was supplied on cloudy days and in the evenings). The experiment lasted for 8 weeks.

3.2.2 Data Collection

All the seedlings were measured for height at 4 weeks after the implementation of the treatments. At 6 and 8 weeks, the seedlings were also measured for height, root-collar diameter (*RCD*). Height relative growth rate (RGR_{ht}) was calculated using Fisher's equation;

$$\text{RGR} = (\ln H_2 - \ln H_1)/(T_2 - T_1),$$

where H_1 = height at 4 weeks, H_2 = height 8 weeks and T_1 and T_2 are respectively the time between the first measurement and the time of final (8 weeks) measurement. At 6 and 8 weeks, three seedlings per treatment per provenance were randomly selected and measured for photosynthesis (A) ($\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (g_s) ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and transpiration (E) with a portable gas exchange system (LI-6400, Lincoln, NE, U.S.A) on fully developed leaves (4th leaf from the top). All gas exchange measurements were carried out at ambient CO_2 ($360 \mu\text{mol mol}^{-1}$) and photosynthetically active radiation of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ between 11:00 and 15:00pm. Instantaneous water-use efficiency (WUE) ($\mu\text{mol mmol}^{-1}$), was calculated as the ratio of A and E (A/E). Also at 8 weeks, three seedlings per treatment per provenance were randomly selected and measured for pre-dawn leaf water potential (ψ_{pd}) on upper twigs between 4:30am and 5:30am using pressure chamber technique (Scholander 1965). The drought stressed seedlings were not watered 24hours before the measurement of photosynthesis and ψ_{pd} at 8 weeks.

At the end of the experiment, all seedlings were harvested and separated into leaf, root, and shoot. The harvested biomasses were oven dried at 70°C for 48hrs and measured for dry mass. The dry biomass was further analyzed by leaf mass ratio (LMR), root-shoot ratio (RSR), and root mass ratio (RMR).

3.2.3 Data Analysis

Data were analysed for normality and where there was a departure from normality, they were transformed using natural logarithm or polynomial methods. Three-way analysis of variance (ANOVA) was used to determine if there were significant effects of the treatments on the morphological and physiological properties. Where there was a significant provenance effect, Duncan multiple range test was used to determine the difference among the provenances. Regression analysis was used to determine the relationship between the morphological and physiological traits using only the data in the HTLW and LTHW treatments because these conditions are most likely in nature. All the analyses were performed using SAS and SigmaPlot.

The split-plot linear model used was:

$$Y_{ijkl} = \mu + T_i + \delta_{(i)} + W_j + WT_{ij} + P_k + TP_{ik} + WP_{jk} + TWP_{ijk} + \varepsilon_{(ijk)l}$$

Where $i = 1, 2$

$j = 1, 2$

$k = 1, 2, 3, 4$

Y_{ijkl} = growth observation from the treatment combination

μ = grand mean or provenance mean

T_i = fixed effect of temperature

$\delta_{(i)}$ = restriction error on randomization of irrigation

W_j = fixed effect of water

TW_{ij} = interaction effect of irrigation and temperature

P_k = fixed effect of provenance

TP_{il} = interaction effect of temperature and provenance

WP_{jk} = interaction effect of water and provenance

TWP_{ijk} = interaction effect of irrigation, temperature and provenance

$\varepsilon_{(ijk)l}$ = random error.

3.3 RESULTS

Morphological Responses

There was a significant T x W interaction for height growth ($p = 0.0173$) (Table 3.2) at 4 weeks. All other main and interaction effects were not significant. At this stage, there was clear difference in height across the treatments (Fig 3.2). Overall, provenance from Timmins had highest growth across the treatments while Petawawa provenance had the lowest.

At all three measurement periods, (4, 6 and 8 weeks), there was a significant provenance effect on height growth ($p < 0.0001$). There were no significant interaction effects at 6 weeks, including T x W that was initially significant at 4 weeks. At the opposite ends of the treatments (LTLW and HTHW), there were large differences in height which highlights the effects of the treatments. Effect of temperature was noticeable considering the higher height growth in the high temperature treatments compared with the low temperature treatments (Fig. 3.3). At this stage, provenance from Timmins maintained the best height growth.

For root-collar diameter (RCD) at 6 weeks, the effect of provenance was significant ($p < 0.0001$) as was the T x W interaction ($p = 0.0076$). All other interactions effects were not significant. All the provenances had smaller RCD in the low water treatments compared with high water treatments. Highest RCD was observed at HTHW treatment for all the provenances, which further indicates the influence of temperature on growth (Fig 3.3). Overall, the Timmins provenance had the highest RCD.

There was a significant T x W interaction effect on height and RCD ($p = 0.0018$ and 0.0438 , respectively) in the final measurement. Overall, the provenance from Timmins had the best height growth. All four provenances showed similar response to the treatments with consistent increase in height and RCD with increasing water and temperature (Fig. 3.4). The greatest height growth and RCD was observed in the HTHW treatment. Also in drought stressed seedlings, height growth at high temperature was higher than at low temperature. The final mean height growth was 56-60% greater at HTHW than at LTLW. The difference between HTHW and LTHW was 23-38% while the difference between HTLW and LTHW was 19 – 32%. No clear difference was observed in RCD between LTLW and HTLW. There was a slightly higher RCD at HTHW compared with LTHW (Fig. 3.4). Mean comparison showed that there was a significant effect of provenance ($p < 0.001$), however, provenance from Timmins appeared to be the only one that was consistently different from other provenances.

There were no significant interaction effects for RGR_{ht} . The provenance effect was not significant ($p = 0.0753$) but the main effects of water and temperature were significant ($p < 0.0001$). RGR_{ht} increased with increasing temperature and water, with the highest being in the high temperature and high water treatment. Although the provenance effect was not significant, Petawawa provenance appeared to have highest RGR_{ht} while Timmins provenance had the lowest RGR_{ht} in all the treatments (Fig. 3.5).

Table 3.2. Summary of ANOVA results for the progressive measurements of height, root-collar diameter (RCD) at 4, 6 and 8 weeks and height relative growth rate (RGR_{ht}). P = provenance, T = temperature, W = water, P x T = interaction of provenance and temperature, P x W = interaction of provenance and water, T x W = interaction of temperature and water, P x T x W = interaction of provenance, temperature and water.

Source	Df	Height (4wks)	Height (6wks)	Height (8wks)	RCD (6wks)	RCD (8wks)	RGR_{ht}
P	3	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	0.0753 ^{ns}
T	1	0.0376*	<0.0001*	<0.0001*	0.0002*	0.0002*	<0.0001*
W	1	0.0564 ^{ns}	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
P x T	3	0.2150 ^{ns}	0.2032 ^{ns}	0.1666 ^{ns}	0.0753 ^{ns}	0.8079 ^{ns}	0.4934 ^{ns}
P x W	3	0.7981 ^{ns}	0.5864 ^{ns}	0.5567 ^{ns}	0.1072 ^{ns}	0.0555 ^{ns}	0.9852 ^{ns}
T x W	1	0.0173*	0.1706 ^{ns}	0.0018*	0.0076*	0.0438*	0.1829 ^{ns}
P x T x W	3	0.3597 ^{ns}	0.3430 ^{ns}	0.1452 ^{ns}	0.0975 ^{ns}	0.4793 ^{ns}	0.0753 ^{ns}

*Significant difference ($p < 0.05$), ns = no significant difference ($p > 0.05$)

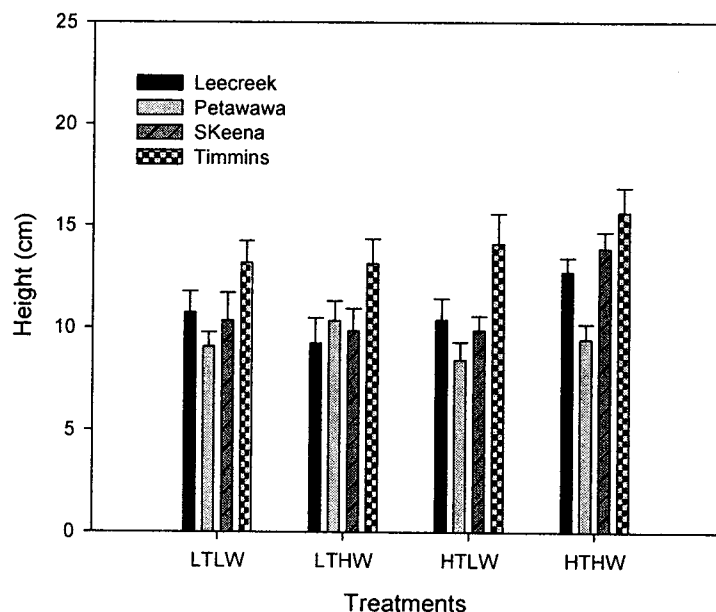


Fig. 3.2. Means and one standard errors of height growths of four white birch provenances at 4 weeks. LTLW = low temperature and low water, LTHW = low temperature and high water, HTLW = high temperature and low water, HTHW = high temperature and high water.

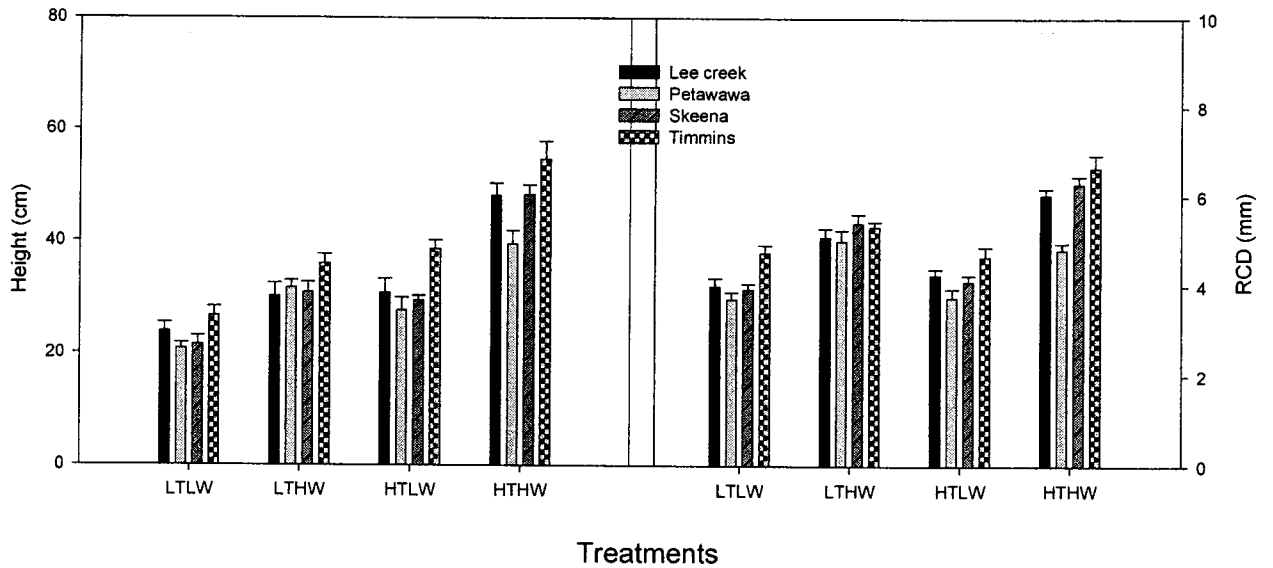


Fig. 3.3. Means and one standard errors of height growths of four white birch provenances at 6 weeks.

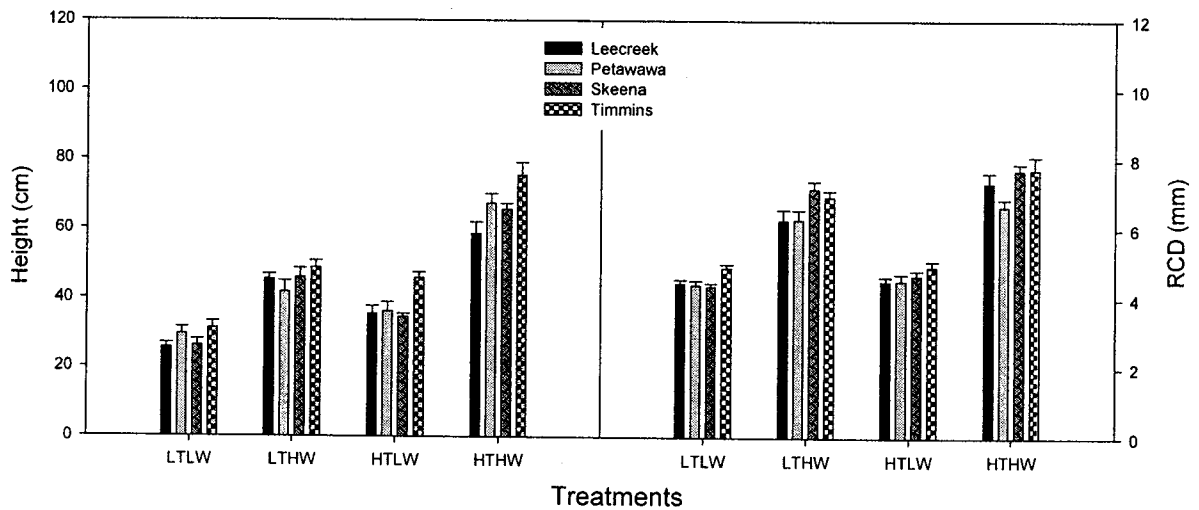


Fig. 3.4. Means and one standard errors of height growths of four white birch provenances at 8 weeks.

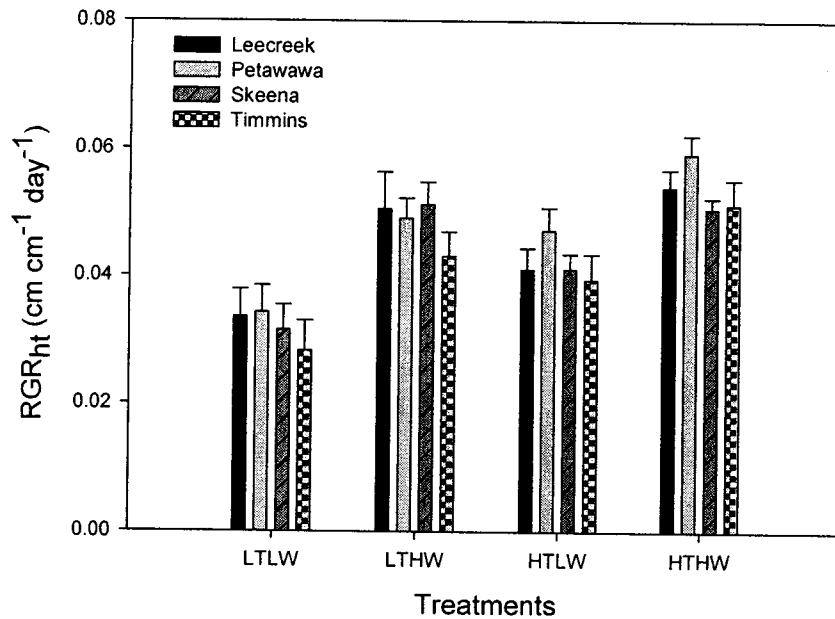


Fig. 3.5. Means and one standard errors of height relative growth rate (RGR_{ht}) of four white birch provenances between 4 and 8 weeks.

There were significant provenance effects of $P \times W$ and $T \times W$ ($p = 0.0016$ and $p < 0.0001$ respectively) for total biomass (Table 3.3). Comparatively at low temperature, total biomass increased from approximately 3.2, 2.9, 2.6, and 4g per plant in low water regime to about 7.3, 8.6, 12 and 10.3g per plant in high water regime for Leecreek, Petawawa, Skeena and Timmins provenances respectively. Similarly at high temperature, total biomass increased from 2.6, 2.7, 2.7, and 3.4g per plant in low water regime to approximately 12.3, 9.7, 14.8, and 13.2g per plant in high water regime for Leecreek, Petawawa, Skeena and Timmins provenances respectively (Fig. 3.6). Differences in total biomass among the provenances were apparent in the high water treatments with the highest being at high temperature. Contrast to height growth where provenance from Timmins consistently had

the best height growth, provenance from Skeena had the highest total biomass in high water regimes. Mean comparisons show that there were differences in mean total biomass among the provenances in both low and high water treatments ($p < 0.0001$).

There was a significant effect $P \times T \times W$ for leaf and root mass ($p = 0.0107$ and 0.0018 respectively) but not for shoot mass (0.9896). $T \times W$ was significant for shoot mass ($p < 0.0001$). All the provenances allocated more biomass to leaves across treatments (Fig. 3.7). However, proportionally, more biomass was allocated to the leaves in the low water treatments. In the low water treatments, 60 – 65 % biomass was allocated to the leaves (lower for Timmins) compared with 54 – 60% allocated to leaves in the high water treatments. All four provenances allocated less biomass to roots in the high water treatment. There was no clear difference in biomass allocation between roots and shoots for all the provenances in the low water treatments.

There was a significant effect of $P \times T \times W$ for RSR and RMR ($p = 0.0296$ and 0.0184 respectively). There was a significant $T \times W$ for LMR ($p = 0.0006$). Provenance from Petawawa had a poor growth and yet comparatively, it had highest LMR in all the treatments while Timmins provenance had the lowest LMR (Fig 3.8). The difference in RSR across treatments was only obvious in the high temperature and low water treatment, with provenance from Petawawa having the highest and Leecreek provenance had the lowest. No clear pattern of increase or decrease among the provenances was observed for RMR.

Table 3.3. Summary of ANOVA results for leaf, shoot, root, total biomass, leaf mass ratio (LMR), root mass ratio (RMR) and root shoot ratio (RSR).

Source	Df	Leaf	Shoot	Root	Total	LMR	RMR	RSR
P	3	0.0053*	0.0002*	<0.0001*	<0.0001*	<0.0001*	0.0084*	0.6995 ^{ns}
T	1	0.1848 ^{ns}	0.8176 ^{ns}	0.0001*	0.0452*	0.0118*	<0.0001*	0.0025*
W	1	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
P x T	3	0.5897 ^{ns}	0.2159 ^{ns}	0.0757 ^{ns}	0.3836 ^{ns}	0.3045 ^{ns}	0.0415*	0.1078 ^{ns}
P x W	3	0.0015*	0.0765 ^{ns}	<0.0001*	0.0016*	0.2541 ^{ns}	0.0039*	0.0668 ^{ns}
T x W	1	0.0002*	<0.0001	0.0006*	<0.0001*	0.0006*	0.8879 ^{ns}	0.0138*
P x T x W	3	0.0107*	0.9896 ^{ns}	0.0018*	0.0690 ^{ns}	0.6607 ^{ns}	0.0184*	0.0296*

*Significant difference ($p < 0.05$), ns = no significant difference ($p > 0.05$).

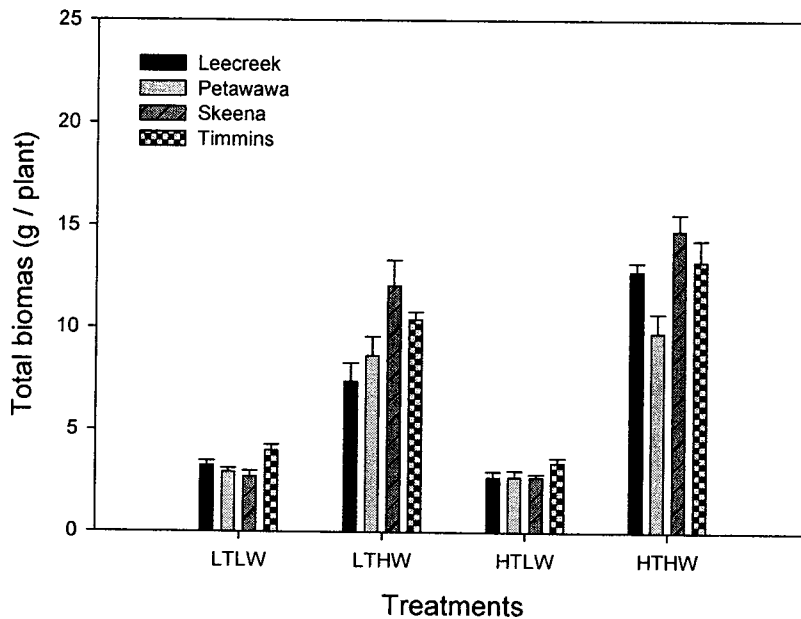


Fig. 3.6. Total biomass of four white birch provenances at different growth conditions. LTLW = low temperature and low water, LTHW = low temperature and high water, HTLW = high temperature and low water, HTHW = high temperature and high water.

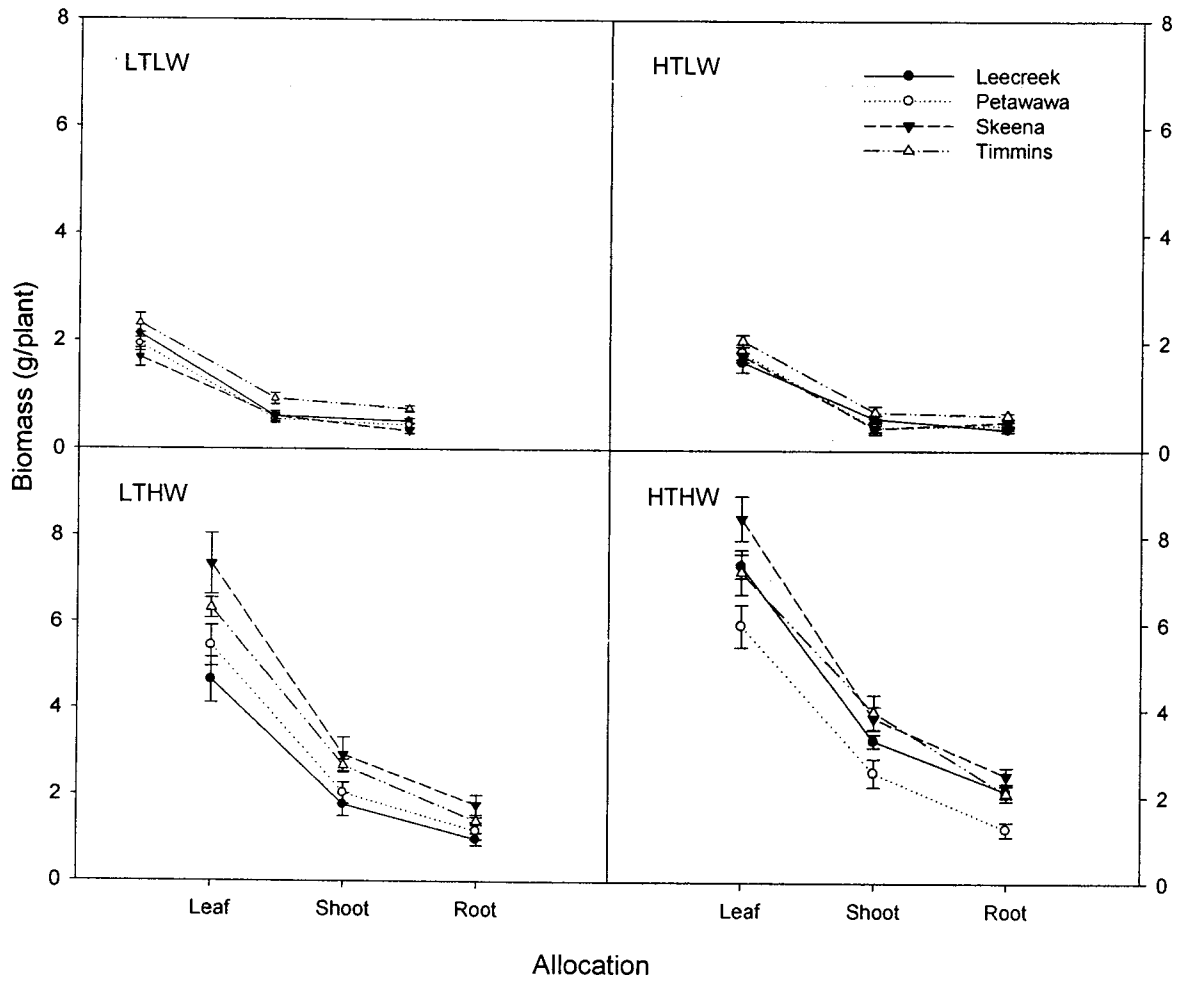


Fig. 3.7. Pattern of biomass allocation of four white birch provenances at different growth conditions. LTLW = low temperature and low water, LTHW = low temperature and high water, HTLW = high temperature and low water, HTHW = high temperature and high water.

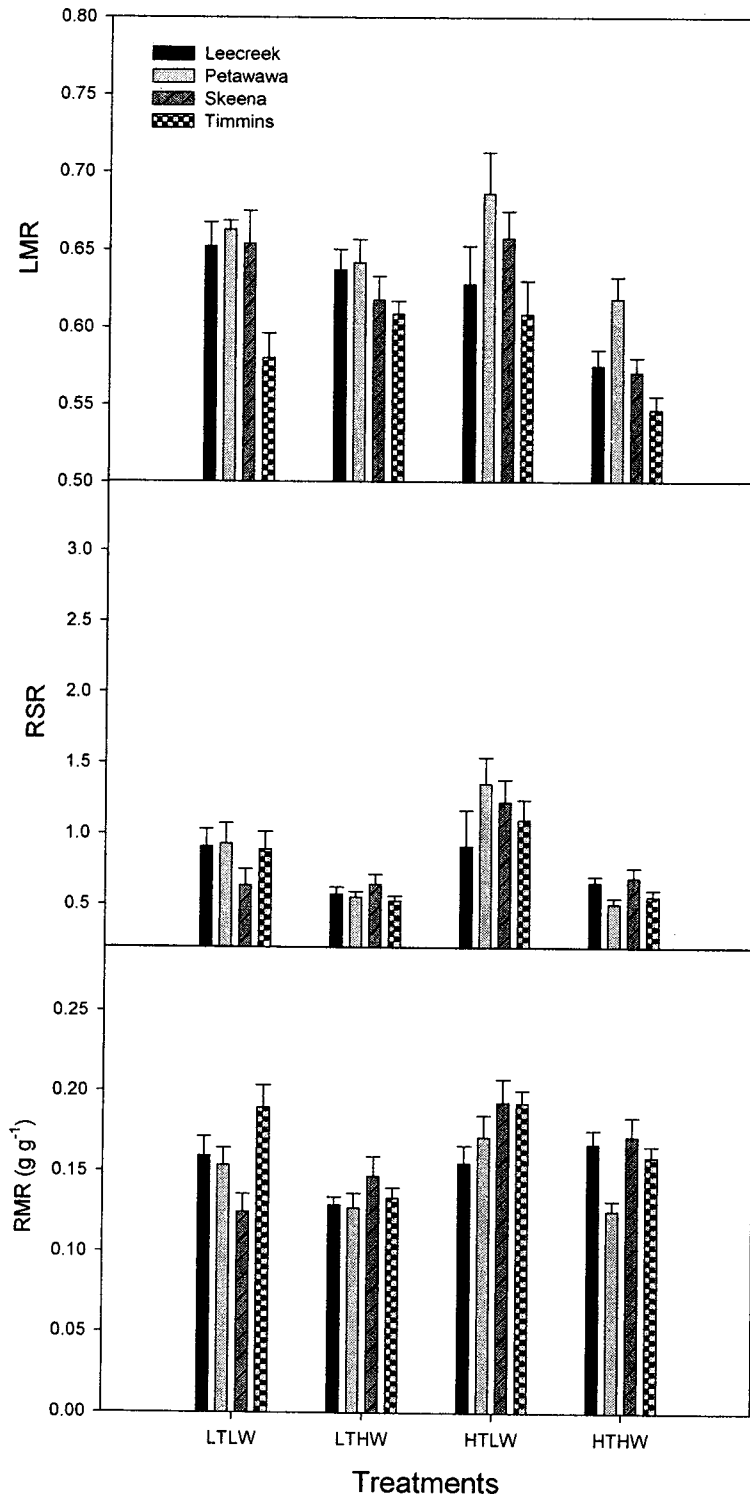


Fig. 3.8. Means and standard errors of leaf mass ratio (*LMR*), root-shoot ratio (*RSR*), and root mass ratio (*RMR*) of four white birch provenances.

Relationship between biomass allocations

Leaf mass was positively related to root mass (Table 3.4). There was also a relationship between leaf mass and shoot mass in most cases, but not L-HTLW, S-HTLW, and T-LTHW. However, there were no significant relationship between leaf mass and shoot mass for Leecreek and Skeena provenances in the high temperature and low water treatment and also for Timmins in the low temperature and high water treatment ($p > 0.05$). Strikingly, there was no significant relationship between root mass and shoot mass for Timmins provenance in high water treatment. In the low water treatment, there was a significant relationship between root mass and shoot mass for Timmins but not for other provenances. There was a positive relationship between total mass was leaf mass for all the provenance across the treatments (Fig. 3.9).

Table 3.4. Regression parameters for the relationships between leaf mass (LM), shoot mass (SM), root (RM) and total mass (TM) of the four white birch provenance under low temperature and high water (LTHW) and high temperature and low water (HTLW). L = Leecreek, P = Petawawa, S = Skeena and T = Timmins. b_0 = intercept, b_i = slope.

Regression	Provenance/ treatment	b_0	b_i	r^2	p
LM v SM	L-LTHW	-0.1898	0.4221	0.65	0.0031*
	L-HTLW	0.1973	0.2296	0.26	0.0931 ^{ns}
	P-LTHW	-0.6864	0.5009	0.93	<0.0001*
	P-HTLW	-0.4876	0.5081	0.45	0.0204*
	S-LTHW	-0.9313	0.5242	0.82	0.0002*
	S-HTLW	-0.3952	0.4627	0.13	0.1622 ^{ns}
	T-LTHW	0.7364	0.3070	0.19	0.1128 ^{ns}
	T-HTLW	-0.8444	0.7658	0.47	0.0166*
RM v SM	L-LTHW	0.1302	1.6944	0.75	0.0007*
	L-HTLW	0.2469	0.8331	0.17	0.1513 ^{ns}
	P-LTHW	0.7260	1.287	0.82	0.0002*
	P-HTLW	0.1098	0.6705	0.04	0.2624 ^{ns}
	S-LTHW	0.7282	1.1235	0.43	0.0244*
	S-HTLW	0.2540	0.3036	0.00	0.4405 ^{ns}
	T-LTHW	1.9337	0.5339	0.02	0.3050 ^{ns}
	T-HTLW	-0.4808	1.8335	0.60	0.0055*
LM v RM	L-LTHW	-0.2176	0.2553	0.91	<0.0001*
	L-HTLW	0.1055	0.1761	0.48	0.0160*
	P-LTHW	-1.0241	0.4021	0.91	<0.0001*
	P-HTLW	-0.1206	0.3298	0.58	0.0063*
	S-LTHW	0.0636	0.2329	0.45	0.0191*
	S-HTLW	-0.6152	0.6531	0.49	0.0139*
	T-LTHW	-0.2367	0.2579	0.37	0.0373*
	T-HTLW	0.0380	0.3014	0.36	0.0386*
LM v TM	T-HTLW	-0.8064	2.0672	0.80	0.0003*
	L-LTHW	-0.4073	1.6775	0.96	<0.0001*
	L-HTLW	0.3214	1.3969	0.92	<0.0001*
	P-LTHW	-1.7106	1.9030	0.99	<0.0001*
	P-HTLW	-0.6081	1.8379	0.93	<0.0001*
	S-LTHW	-0.8677	1.7571	0.96	<0.0001*
	S-HTLW	-1.0105	2.1158	0.87	0.0003*
	T-LTHW	0.4996	1.5649	0.86	<0.0001*
T-HTLW	-0.8064	2.0672	0.79	0.0003*	

*Significant ($p < 0.05$), ns = no significant difference ($p > 0.05$)

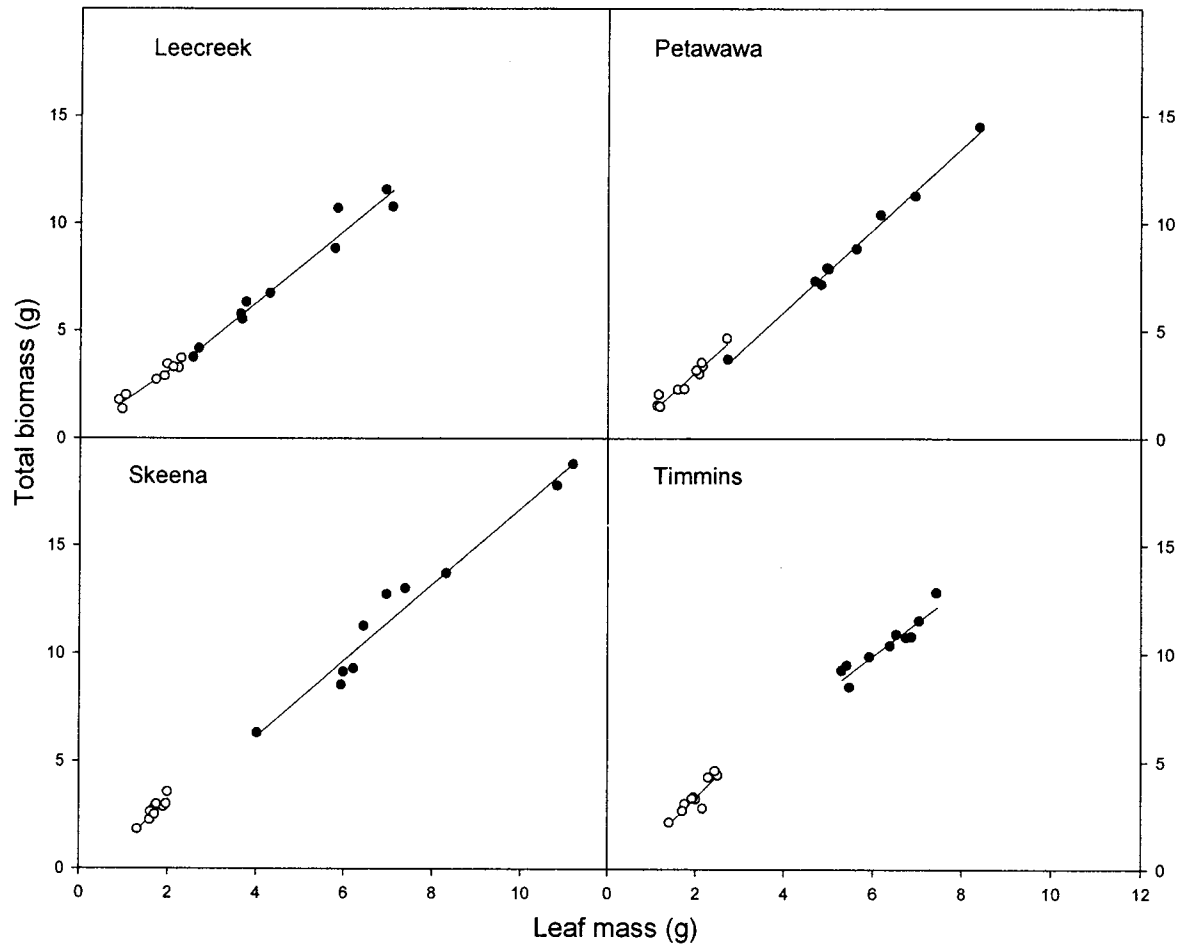


Fig. 3.9. Regressions between total biomass and leaf mass of four white birch provenances under low temperature and high water (closed circle) and high temperature and low water (open circle).

Physiological Responses

There were significant interaction effects of P x T and P x W for photosynthetic assimilation A ($p < 0.0001$) (Table 3.5). Also, there was a notable response patterns with respect to A across temperature and water treatments. Provenance from Petawawa showed almost a flat response across the treatments, indicating that it is less sensitive to changing conditions (Fig. 3.10). Provenance from Leecreek showed a clear and consistent difference at both ends of the water regime (high and low) which suggests that it is more sensitive to water stress. Provenances from Timmins clearly showed a preference for low temperature; it had relatively higher A only at low temperature. Skeena provenance responded to high water and also showed a preference for low temperature. Generally, photosynthetic rate was higher in the low temperature and high water treatment for all the provenances.

There was a significant effect of P x T x W ($p = 0.0124$) for g_s but there was no evidence of significant provenance differences ($p = 0.5671$). Stomatal conductance (g_s) increased with water availability but decreased at high temperature (Fig. 3.10). However, referencing the implication of g_s on the rate of A , a unit increase in g_s did not result in a unit increase in A . Like A , highest g_s was observed in the low temperature and high water treatment.

There was a significant P x T x W for WUE ($p = 0.0002$). Differences in WUE among the provenances were only obvious in the low water treatments (Fig. 3.10). Provenance from Skeena had higher WUE in the low water treatments. In the low temperature and low water treatment, provenances from Petawawa and Timmins showed a similar response while provenance from Leecreek had the least WUE . However, in the high temperature and low water treatment, provenance from Petawawa had the least WUE .

The provenances were not significantly different in ψ_{pd} ($p = 0.3987$). There was a significant effect of T x W for ψ_{pd} ($p = 0.0013$) (Fig. 3.10). Highest ψ_{pd} was observed at high temperature. ψ_{pd} ranged from -1.0 to -1.4 MPa at LTLW and -0.9 to -1.2 MPa at HTLW. The range was very narrow in the high water treatments.

Table 3.5. Summary of ANOVA results for photosynthesis (A), stomata conductance, (g_s), water-use efficiency (WUE) and pre-dawn leaf water potential (ψ_{pd}).

Source	DF	A	g_s	WUE	ψ_{pd}
P	3	0.1462 ^{ns}	0.5671 ^{ns}	0.0334*	0.3987 ^{ns}
T	1	<.0001*	<.0001*	0.4615 ^{ns}	<.0001*
W	1	<.0001*	<.0001*	<.0001*	<.0001*
P x T	3	<.0001*	0.0605 ^{ns}	0.4060 ^{ns}	0.2242
P x W	3	<.0001*	0.0001*	<.0001*	0.2876 ^{ns}
T x W	1	0.7372 ^{ns}	0.0085*	0.5508 ^{ns}	0.0013*
P x T x W	3	0.922 ^{ns}	0.0124*	0.0002*	0.1970 ^{ns}

*Significant ($p < 0.05$), ns = no significant difference ($p > 0.05$)

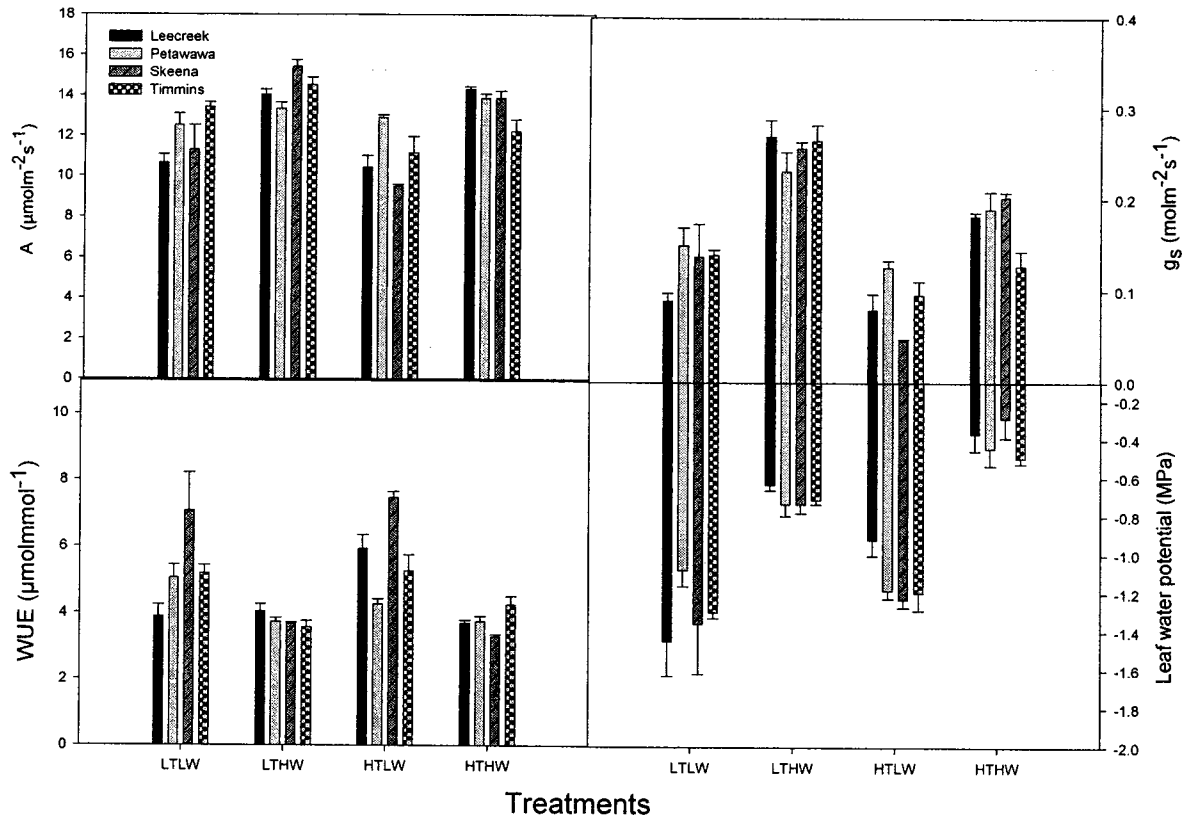


Fig. 3.10. Means and standard errors of photosynthesis (A), stomata conductance (g_s), water-use efficiency, (WUE) and pre-dawn leaf water potential (ψ_{pd}) of the four white birch provenances.

Relationship between A , g_s and WUE

There was a positive relationship between stomatal conductance and WUE for Timmins and Skeena provenance in the high water treatment but the relationship was negative for Petawawa provenance (Fig. 3.11). There were negative relationships between g_s and WUE in the high water treatments for all the provenances. There were positive relationship between stomatal conductance and photosynthesis in both low and high water treatments (Fig. 3.12). There was no significant relationship between WUE and g_s for Leecreek in the low water treatment ($p < 0.05$) (Table 3.6).

Table 3.6. Regression parameters for the relationships between water-use efficiency, photosynthesis and stomatal conductance of the four white birch provenances under low temperature and high water (LTHW) and high temperature and low water (HTLW). L = Leecreek, P = Petawawa, S = Skeena and T = Timmins. b_0 = intercept, b_i = slope.

Regression	Provenance/ treatment	b_0	b_i	r^2	P
WUE x g_s	L-LTHW	4.5581	-1.9257	0.00	0.5696 ^{ns}
	L-HTLW	7.8011	-23.4882	0.98	<0.0001*
	P-LTHW	4.9561	-5.3005	0.93	<0.0001*
	P-HTLW	6.8449	-20.4274	0.91	<0.0001*
	S-LTHW	2.8788	3.1326	0.67	0.0001*
	S-HTLW	13.4088	-127.2102	0.96	<0.0001*
	T-LTHW	1.0081	9.6696	0.79	<0.0001*
	T-HTLW	8.0785	-29.2605	0.76	0.0001*
A x g_s	L-LTHW	11.3469	9.9472	0.43	0.0048*
	L-HTLW	7.7165	33.7658	0.99	<0.0001*
	P-LTHW	9.8717	14.9855	0.99	<0.0001*
	P-HTLW	11.2306	13.0382	0.41	0.0059*
	S-LTHW	3.5745	46.1871	0.93	<0.0001*
	S-HTLW	6.5969	61.7204	0.83	<0.0001*
	T-LTHW	9.4271	19.2029	0.83	<0.0001*
	T-HTLW	6.0142	53.2056	0.93	<0.0001*

*Significant ($p < 0.05$), ns = no significant difference ($p > 0.05$)

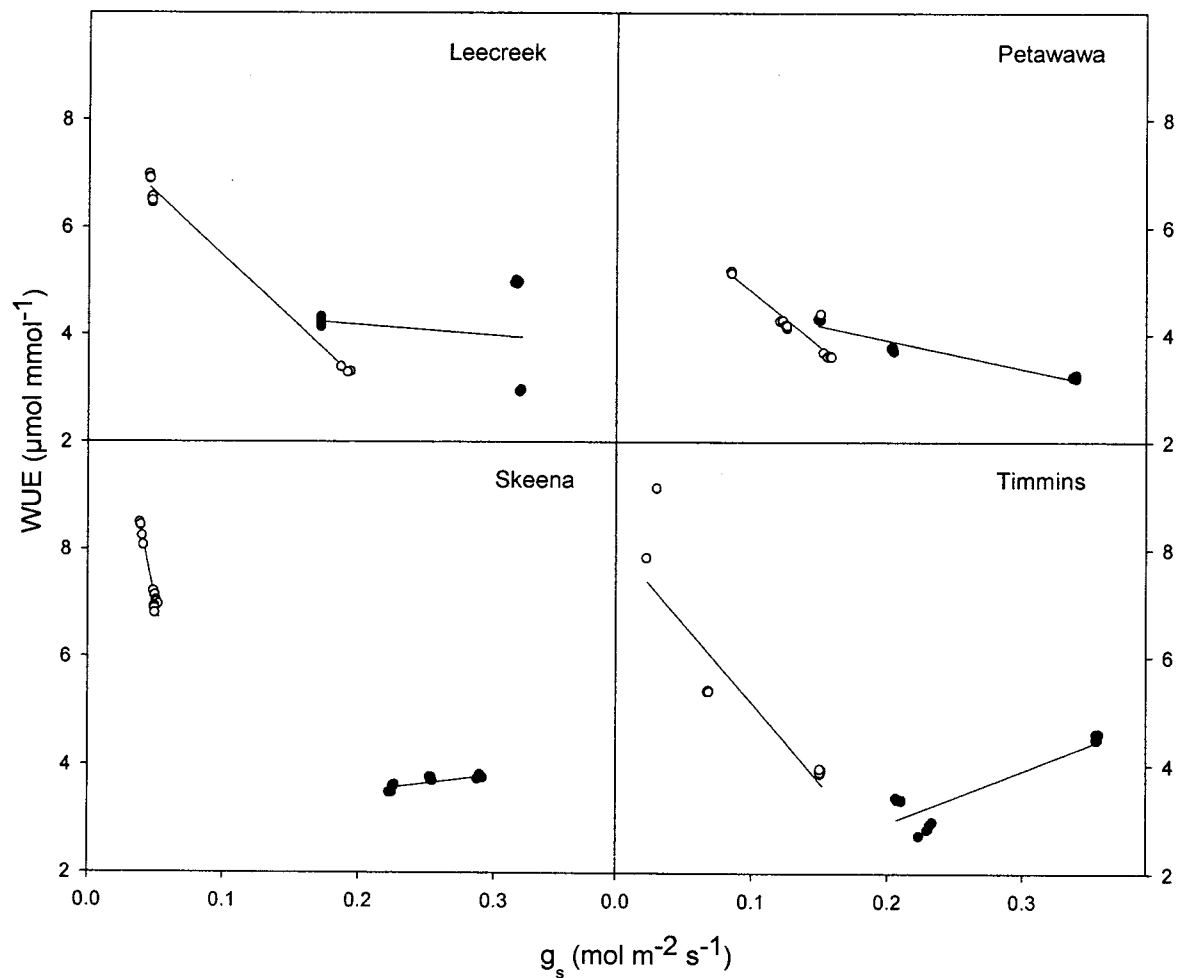


Fig. 3.11. Regressions between water-use efficiency (WUE) and stomata conductance (g_s) of four white birch provenances under low temperature and high water (open circle) and high temperature and low water (closed circle).

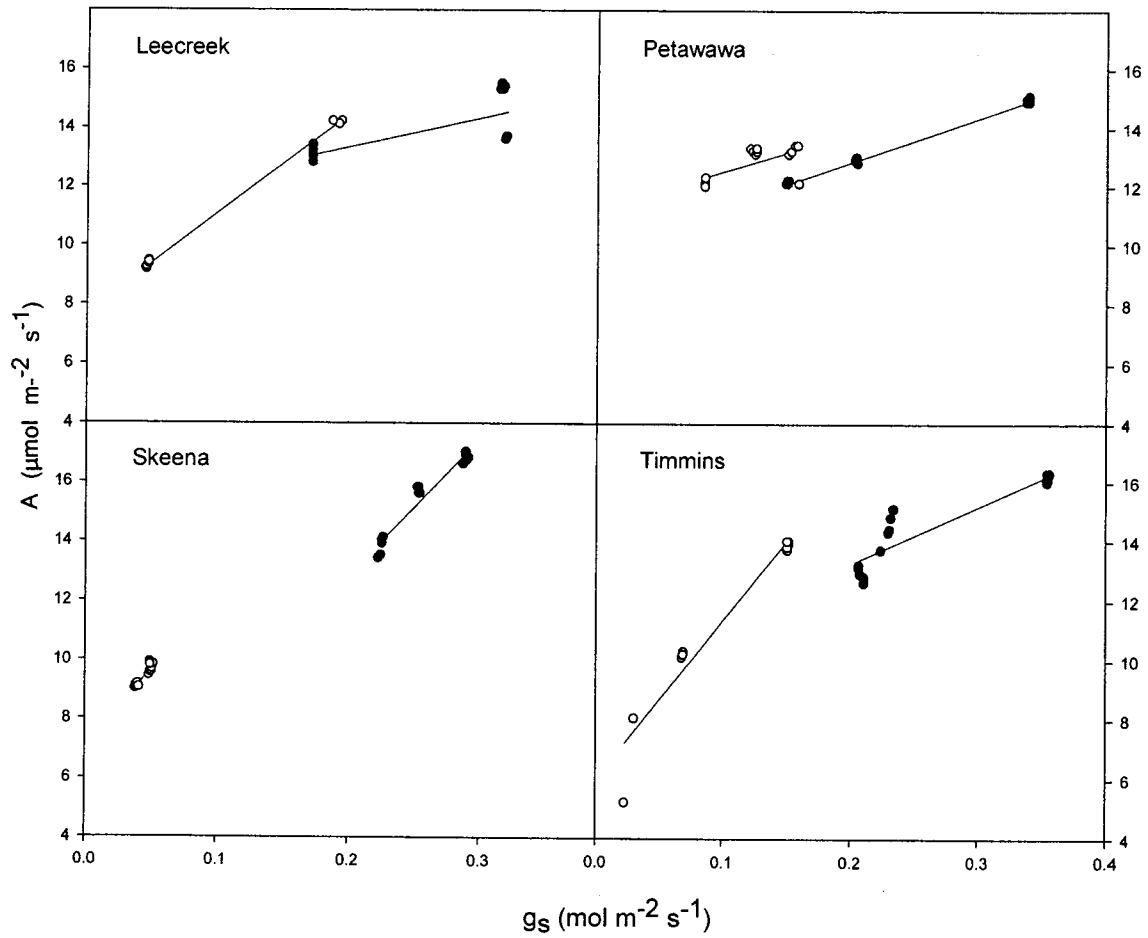


Fig. 3.12. Regressions between photosynthesis (A) and stomata conductance (g_s) of four white birch provenances under low temperature and high water (closed circle) and high temperature and low water (open circle).

3.4 DISCUSSION

Height is a good fitness surrogate (Wu and Ying 2004) and RCD gives an indication of future growth in many species (Dey and Parker 1997). Provenances from Timmins showed a superior height and RCD from other provenances in all treatments. Considering biomass accumulation of each provenance in the high water treatments, Timmins and Skeena provenances appeared to be more productive compared with provenances from Leecreek and Petawawa.

Although the provenance effect was not significant with respect to RGR_{ht} , provenance from Petawawa consistently had higher RGR_{ht} while Timmins provenances which had the best height growth consistently had the lowest RGR_{ht} in all the treatments. Leecreek provenance was expected to have lowest RGR_{ht} in this case because it is from a drier environment where there is high evaporative demand. Plants from low resource and stressful environment are thought to have lower RGR compared with plants from more favourable environments (Lambers et al. 2008). This was not observed in this study. This result raises a question about the ecological significance of RGR. It has been suggested that RGR is not a selectively neutral trait; rather than RGR, one or more of its associated components are the target of natural selection (Lambers et al. 2008). Therefore, RGR is not a stable trait and just like any plastic trait, it could be influenced by the environment. The changes observed in RGR_{ht} at different treatment combinations shows that RGR could be influenced by the environment.

Productive genotypes are more sensitive to drought compared with the less productive genotypes (Monclus et al. 2006). This observation was true for Skeena provenance in the low water treatments. However, the provenance from Timmins had a

slightly higher total biomass compared with Leecreek and Petawawa provenances in the low water treatments. This observation means that Timmins provenance is less sensitive to drought. This response by the Timmins provenance partly supports the hypothesis that provenances from mild precipitation range will perform better in less favourable conditions. However, this hypothesis was not true for Petawawa.

Factors influencing biomass accumulation remain unclear in the absence of verifiable evidence across resource limitation trials. For instance, Wang et al. (1998a) reported that nitrogen influenced total biomass of four white birch provenances even where water was limited. Adams et al. (1997) and Teskey and Will (1999) reported that dry matter accumulation was a function of temperature. Fraser et al. 2009 reported that total biomass was influenced by water. It is true that water plays a major role in biomass accumulation. This study shows that the roles of water and temperature in biomass accumulation are inextricably linked and genotype dependent. Although white birch is adapted to cold climates, biomass accumulation of white birch is sensitive to temperature increase and moisture. All the provenances produced more biomass at a higher temperature (30°C) and moisture. This result is consistent with the report of Teskey and Will (1999). However, the authors noted a decline in biomass as the temperature increased beyond 30°C. Also, the authors did not account for the possible effects of soil moisture.

Proportionally, all four provenances allocated slightly more biomass to leaves ($p = 0.032$) in low water treatments compared with the high water treatments. Drought tolerance may be related to foliage biomass (Li and Wang, 2003). Lambers et al. (2008) suggested that a positive carbon balance could be maintained at adverse temperature by changing resource allocation to leaves. Also, Bongarten and Teskey (1987) found that repeated

exposure of loblolly pine seedlings to drought did not affect leaf biomass. These findings may also be true for white birch.

In the low water treatments, there were no clear differences in allocation between roots and shoots for all the provenances. An increase in allocation to roots with decreasing water availability has been reported for many species (Bongarsten and Teskey 1987; Navas and Garnier 2002; Zheng et al. 2008; Lambers et al. 2008). This was not exactly expressed by white birch in this study. Such deviation from optimal partitioning theory has been reported by Lopez et al. (2009) for a plant grown in an extreme drought condition. It is noteworthy that drought induced in this experiment was extreme and continuous rather than cyclical. Results of this study agree with Aspelmeier and Leuschner (2006) that carbon partitioning between root and shoot is influenced by both the duration and intensity of the drought and genotypic character.

Lambers et al. (2008) suggests that LMR is largely under genetic influence and accounts for some of the variation in dicotyledonous plants. This may be true for white birch. Petawawa and Timmins provenances are from locations with similar annual precipitation, yet they greatly differ in LMR. Whereas Leecreek and Skeena originated from locations with different precipitation patterns, they were not significantly different in LMR.

Provenance from Petawawa had the highest RSR but this was expected of Leecreek provenance because it is from a drier environment where there is high evaporative demand. Skeena also had a relatively higher RSR. These results are surprising but consistent with the findings of Wang et al. (1998a) for Leecreek. Skeena has a very low growing season

rainfall and this may account for the high RSR observed in this provenance. Relatively lower LMR and RSR are indications that provenance from Timmins allocated more biomass to structural tissues than photosynthetic tissue compared with Petawawa provenance which had higher LMR and RSR.

Optimum temperature for *A* may differ for provenances from contrasting thermal environment, and inherited provenance-level adaptations to climate have been reported for some species (Gunderson et al. 1998; Ishikawa et al. 2007). There was an evidence of population adaptation in photosynthesis. Provenance from Petawawa showed a conservative response to the changing environmental conditions. Acclimation of photosynthesis at high temperature is an indication of shift from optimum temperature to the growth temperature (Teskey & Will 1999). Both Leecreek and Petawawa provenances have similar average summer temperature and Leecreek has lower summer precipitation than Petawawa but the provenance from Leecreek was more sensitive to water availability. Timmins is relatively colder than Leecreek and Petawawa and it appears that the provenance from Timmins is acclimated to maximizing *A* at a temperature lower than 30°C. Skeena provenance was also sensitive to moisture which was consistent with the fact that this provenance has evolved under high moisture environment.

Photosynthesis rarely correlates with productivity (Ackerly et al. 2000). All the provenances maximized photosynthesis at low temperature and high water, but more biomass was produced at high temperature. If biomass is an indication of productivity, what is the trade-off between photosynthesis and biomass allocation at high temperatures? Lambers et al. (2008) observed that there is a correlation between plants capacities to perform at extreme temperatures and their capacities to photosynthesize at these

temperatures. This observation may be true for the provenance from Petawawa given the fact that its net photosynthesis was not affected by temperature changes. Teskey and Will (1999) suggested that lower photosynthetic rate at high temperature may have been compensated for by the higher carbon allocation to the leaf and lower allocation to the root. This may be true for white birch because of the higher proportion of biomass allocated to the leaf compared with allocation to the root at high temperature.

The provenance effect was not statistically significant with respect to stomatal conductance, but the variation in photosynthetic pattern showed that a provenance could be more effective in its photosynthetic capacity in spite of the stomata openings. Generally, there was an indication that optimum temperature for photosynthesis for these provenances is below 30°C. However, the optimum temperature could not be suggested in this study because photosynthesis was measured at growth temperatures.

Theoretically, when water is limiting, a plant that has a conservative water-use is expected to grow rapidly, and a high *WUE* is an adaptation to drought (Wang et al. 1998b; Li 2000; Monclus et al. 2006). The provenance from Timmins fits this description given its superior growth, but had a relatively lower *WUE* at low water regimes compared with Skeena provenance. Strikingly, the Skeena provenance had the highest *WUE* which is unexpected of a coastal provenance that has evolved under high moisture condition. Similar response was reported by Wang et al. (1998b) for the Skeena provenance.

Different water-use strategies may be employed in drought conditions (Zhang et al. 2004), and a provenance may evolve more than one water-use strategy (Li and Wang 2003). Another way to increase *WUE* is by partial closure of the stomata, thus, restricting

photosynthesis (Li 2000; Lambers et al 2008). This may be true for provenances from Leecreek because it consistently had low g_s in the low water treatments. This may also be true for Skeena provenance at HTLW. In addition, g_s strongly correlated with both A and WUE , but the variations in the directions of the relationships between g_s and WUE may be a reflection of the stomata dynamics. This may be an indication that WUE is a function of g_s (Wang et al. 1998b; Monclus et al. 2005).

Higher ψ_{pd} was observed at high temperature even in the low water treatments. This may not be interpreted as sensitivity of ψ_{pd} to temperature but an indication of relatively higher biomass accumulation in the high temperature treatments. A and g_s measured simultaneously with ψ_{pd} showed that gas exchange was zero at this point (data not shown). Although the seedlings were not watered in 24 hours before the measurement of ψ_{pd} but the provenances did not show any sign of wilting at ψ_{pd} of about -1.4.

It is evident that no single climatic (drought or temperature) factor tested under controlled conditions could adequately predict the likely response of species in the event of global warming. In this study, interaction of temperature and water was consistently significant for most of the traits measured except for photosynthesis and WUE. However, interaction of temperature and water was significant for stomatal conductance, which appears to be strongly and positively related to the rate of photosynthesis at any condition of moisture and temperature.

Chapter IV

CONCLUSION

Understanding the climatic factor influencing the distribution of white birch is a crucial step in establishing its transfer guidelines. While summer temperature appears to be a consistent predictor of performance in white birch, the implications of other environmental factors on growth is unpredictable at this stage of the study. Past studies on plant adaptation to climate change involved much older common garden experiments and in such cases, the potential impacts of other environmental factors other than climate (e.g. pests and diseases) are often negligible. In addition, such trials are usually carried out in more than one location indicating a weakness at this stage of this study. However, numerous reports of significant juvenile-mature correlations in forest trees support the effectiveness of short term testing program for studying ecological genetics. This study serves as a preliminary effort to understanding the adaptation of white birch to different climates and its transferability along climatic gradients.

Phenotypes are the result of growth, morphology, life history and physiology (Gratani et al. 2003). While functional traits are believed to have evolved with the plants' environments, the abilities of provenances to respond according to the environmental circumstances cannot be ruled out. The differences in the measured traits among the provenances studied in the greenhouse explain both the limitations imposed on these traits by the changing conditions and the inherent phenotypic variations. For instance, Provenances from Timmins and Skeena were from different climatic gradient, but their responses were comparable in favourable conditions. Also, there were similarities between provenances from Leecreek and Petawawa. Provenance from Petawawa displayed more

characteristics of an arid provenance which was expected of Leecreek provenance. Petawawa and Timmins provenances have similar annual precipitation and yet they were different in most of the measured traits. Conversely, in the field study, the growth and survival of Timmins and Petawawa provenances were comparable. Similarly, the growth and survival of Skeen and Leecreek provenances were comparable.

Both studies show that performance of white birch is dependent on temperature. However, because of the difficulties inherent in estimating the climate of the remote locations where forests typically grow, physiological studies under relatively controlled conditions are important to screen potential seed sources. The seasonal climatic fluctuations across white birch range appear to have shaped the genetic structure of its provenances and these variations would be important in predicting the response of white birch at a given site.

REFERENCES

- Ackerly, D.D., Sultan, S.E., Schmitt, J.S., Linder, C.R., Sandquist, D.R., Geber, M.A., Evans, A.W., Dawson, T.E., Lechowicz, M.J. 2000. The evolution of plant ecophysiological traits: Recent advances and future directions. *Bioscience* Vol.50, 979-994.
- Adams, S.R., Pearson, S., and Hadley, P, 1997. An analysis of the effects of temperature and light integral on the vegetative growth of Pansy cv. universal violet (*Viola x wittrockiana* Gams.). *Annals of Botany* 79, 219-225.
- Arntz, A.M., and Delph L.F 2001. Pattern and Process: Evidence for the evolution of photosynthetic traits in natural populations. *Oecologia* 127, 455-467.
- Arthur, W., 1987. The niche in competition and evolution. Wiley and Sons, New York.
- Aspelmeier, S., and Leuschner, C., 2006. Genotypic variation in drought response of silver birch (*Betula pendula* Roth): leaf and root morphology and carbon partitioning. *Trees* 20, 42-52.
- Benowicz, A., Guy, R., Carlson, M.R., and El-Kassaby, Y.A., 2000. Genetic variation among paper birch (*Betula papyrifera* Marsh.) populations in germination, frost hardiness, gas exchange and growth. *Silvae Genetica* 50, 7-13.
- Bongarten, B.C., Teskey, R.O., Cregg, B.M., Dougherty, P.M., Hennessey, T.C., 1987. Dry weight partitioning and its relationship to productivity in loblolly pine seedlings from seven seed sources. *Tree physiol.* 3, 41-61.
- Boogaard, R.V., Alewijnse, D., Veneklaas, E.J & Lambers, H 1997. Growth and water-use efficiency of 10 *Triticum aestivum* cultivars at different water availability in relation to allocation of biomass. *Plant, Cell & Env.* 20, 200-210.
- Carlson, M.R., Berger, V.G. and Hawkins, C.D.B., 2000 Seed source testing of paper birch (*Betula papyrifera*) in the Interior of British Columbia. *J. Sust. For.* 10.25-34.
- Carter, K.K., 1996. Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. *Can. J. For. Res* 26, 1089-1095.
- Catovsky, S., and Bazzaz, F. A., 1999. Elevated CO₂ influences the responses of two birch species to soil moisture: implications for forest community structure. *Glob. Change Biol.* 5, 507 - 518.
- Cherry, M.L., 1998. Genetic implications of climate change; in *The Impacts of Climate Change on Ontario's Forests*, (ed.) S.J. Colombo and L.J. Buse, Ontario Ministry of Natural Resources, Forest Research Information Paper.
- Daas, C., Montpied, P., Belgacem, H., and Dreyer, E., 2008. Responses of photosynthesis to high temperatures in oak saplings assessed by chlorophyll-a fluorescence: inter-specific diversity and temperature-induced plasticity. *Ann. For. Sci.* 65, 305.
- Dey, D.C., and Parker, W.C., 1997. Morphological indicators of stock quality and field performance of red oak (*Quercus rubra* L.) seedlings underplanted in a central Ontario shelterwood. *New Forests* 14, 145-156.
- Farris, M.A., and Lechowicz M.J., 1990. Functional interactions among traits that determine reproductive success in a native annual plant. *Ecology* 71, 548-557.
- Fraser, L.H., Greenall, A., Cameron, C., Turkington, R., and Friedman, C.R., 2009. Adaptive phenotypic plasticity of *Pseudoroegneria spicata*: response of stomatal density, leaf area and biomass to changes in water supply and increased temperature. *Annals of Botany* 103, 769-775.
- Gratani, L., Meneghini, M., Pesoli, P., Crescente, M.F., 2003. Structural and functional plasticity of *Quercus ilex* seedlings of different provenances in Italy. *Trees* 17, 515-521.

- Griffin, J.J., Ranney, T.G. and Pharr, M.D., 2004. Heat and drought influence photosynthesis, water relations and soluble carbohydrates of two ecotypes of redbud (*Cercis canadensis*). J. Amer. Soc. Hort. Sci. 129, 497-502.
- Grossnickle, S.C., Fan, S., and Russel, H., 2005. Variation in gas exchange and water use efficiency patterns among populations of western redcedar. *Trees* 19, 32-42.
- Gunderson, A.C., Norby, J.R., and Wullschleger, S.D. , 1998. Acclimation of photosynthesis and respiration to stimulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. *Tree physiology* 20, 87-96.
- IPCC, 1995. Intergovernmental panel on climate change: synthesis report. World Meteorological Organization, Geneva, Switzerland.
- Ishikawa, k., Onoda, Y., & Hikosaka, K., 2007. Intraspecific variation in temperature dependence of gas exchange characteristics among *Plantago asiatica* ecotypes from different temperature regimes. *New Phytol.* 176, 356-364.
- Jackson, S.T., 2005. Impacts of past climate change on species distribution of woody plants in North America. Proceedings of the Twenty-Ninth Meeting of the Canadian Tree Improvement Association Part 2, 7-11.
- Joyce, L.M., Fosberg, M.A., and Comanor, J.M. 1990. Climate change and America's forest. USDA For. Ser., Rocky Mount. For. Range Exp. Sta., Gen. Tech. Rep. RM-187. 12p.
- Kramer, P.J., 1969. Plant and soil water relationships: A modern synthesis. McGraw-Hill series in organismic biology.
- Kruger, G.H.J., and van Rensburg, L., 1995. Carbon dioxide fixation: Stomatal and non-stomatal limitation in drought-stressed *Nicotiana tobacum* L. cultivars. In: P. Maths (ed.). Photosynthesis: From light to biosphere. Kluwer Academic Publishers, Dordrecht, The Netherlands. 4, 505-510.
- Lambers, H., Chapin, F.S., and Pons, T.L., 2008. Plant Physiological Ecology. 2nd ed. Springer-Verlag, New York. ISBN: 978-0-387-78340-6.
- Lechowicz, M.J., and Ives, N.E., 1989. Comparative ecology of drought response in hardwood trees: *Acer saccharum* versus *Fraxinus Americana*. SPB Academic publishing bv, The Hague, The Netherlands., 283-292.
- Li, C., 2000. Differences in water-use efficiency of *Eucalyptus microtheca* seedlings under different watering regimes. *physiologia plantarum* 108, 134-139.
- Li, C., and Wang, K., 2003. Differences in drought responses of three contrasting *Eucalyptus microtheca* F. Muell. populations. *For. Eco. & Mgt* 179, 377 - 385.
- Li, W., Berlyn, G.P., and Ashton, P.M.S., 1996. Polyploids and their structural and physiological characteristics relative to water deficit in *Betula papyrifera* (Betulaceae). *Bot. Soc. Ame.* 83, 15-20.
- Lopez, R., Rodriguez-Calcerrada, J., and Gil, L., 2009. Physiological and morphological response to water deficit in seedlings of five proveniences of *Pinus canariensis*: potential to detect variation in drought-tolerance. *Trees* 23, 509-519.
- Machado, S., and Paulsen, G.M, 2001. Combined effects of drought and high temperature on water relations of wheat and sorghum. *Plant Soil* 233, 179-854.
- Marchin, R.M., Sage, E.L., and Ward, J.K., 2008. Population-level variation of *Fraxinus americana* (white ash) is influenced by precipitation differences across the native range. *Tree Physiol.* 28, 151-159.
- Matyas, C. 1994. Modeling climate change effects with provenance test data. *Tree phyiol.* 14:797-804.

- Matyas, C., and Yeatman, C.W, 1992. Effect of geographical transfer on growth and survival of jack pine (*Pinus banksiana* Lamb.) populations. *Silvae Genet* 41, 370-376.
- Monclus, R., Dreyer, R.E., Villae et al., 2005. Impact of drought on productivity and water-use efficiency in 29 genotypes of *Populus deltoids* x *Populus nigra*. *New Phytol* 169, 765-777.
- Morgenstern, E.K., 1996. Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. UBC Press, Vancouver, BC.
- Navas, M.-L., and Garnier, E., 2002. Plasticity of whole plant and leaf traits in *Rubia peregrina* in response to light, nutrient and water availability. *Acta oecologica* 23, 375-383.
- Neilson, R.P., Pitelka, L.F., Solomon, A.M., Nathan, R., Midgley, G.F., Fragoso, J.M.V., Lischke, H., and Thompson, K., 2005. Forecasting regional to global plant migration in response to climate change. *Bioscience* 55, 749-759.
- Nowak, C.L., Nowak R.S., Tausch, R.J. and Wigand, P.E. , 1994. Tree and shrub dynamics in northwestern Great Basin woodland and steppe during the late-Pleistocene and Holocene. . *Am. J. Bot* 81, 265-277.
- Parker, W.C., Colombo, S.J., Cherry, M.L., Flannigan, M.D., Greifenhagen, S., McAlpine, R.S., Papadopol, C., and Scarr, T., 2000. Third millenium forestry: what climate change might mean to forests and forest management in Ontario. *For. Chron.* 76, 445-463.
- Peng, Y.Y., and Dang, Q.-L 2002. Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. *For. Eco. & Mgt* 180, 1-9.
- Perala, D.A., and Alm, A.A, 1990. Reproductive ecology of birch: a review. *For. Eco. & Mgt* 32, 1-38.
- Peters, R.L., and Lovejoy, T.L, 1990. Global warming and biological diversity. Yale University Press, New Haven, CT, 298-308.
- Peterson, E.B., Peterson, N. M., Simard, S. W., and Wang, J. R. , 1997. Paper Birch Managers' handbook for British Columbia. FRDA II, Victoria, B.C.
- Raney, T.G., Bir, R.E and Skroch, W.A 1991. Comparative drought resistance among six species of birch (*Betula*): influence of mild water stress on water relations and leaf gas exchange. . *Tree Physisology* 8, 351-360.
- Rehfeldt, G.E., 1994. Adaptation of *Picea engelmannii* populations to the heterogeneous environment of the Intermountain West. *Can. J. Bot* 72, 1197-1208.
- Rehfeldt, G.E., Tchebakova N.M., and Parfenova, E.I., 2004. Genetic responses to climate and climate change in conifers of the temperate and boreal forests. *Adv. Gen. Breed.* 1, 113-130
- Rehfeldt, G.E., Tchebakova, N.M. and Barnhardt, L.K. , 1999a. Efficacy of climate transfer functions: introduction of Eurasian populations of *Larix* into Alberta. *Can. J. For. Res.* 29, 1660-1668.
- Rehfeldt, G.E., Tchebakova, N.M., Milyutin, L.I., Parfenova, Y.I, Wykoff, W.R. and Kouzima, N.A., 2003. Assessing population response to climate in *Pinus sylvestris* and *Larix* spp. of Eurasia with climate-transfer models. *Eurasian J. For. Res.* 6-2, 83-98.
- Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I, Wykoff, W.R., Kuzmina, N.A and Milyutin, L.I. , 2002. Intraspecific response to climate in *Pinus sylvestris*. *Glob. Change Biol.* 8, 912-929
- Rehfeldt, G.E., Wykoff, R.A., Ying, C.C., 2001. Physiologic plasticity, evolution, and impacts of a changing climate in *Pinus contorta*. *Clim.Change* 50, 355.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A. , 1999b. Genetic responses to climate change in *pinus contorta*: niche breadth, climate change, and reforestation. *Ecol.Mng.* 69, 379-407.

- Roberts, L., 1989. How fast can trees migrate? *Science* 243, 735-737.
- Safford, L., Bjorkbom, J.C., and Zasada, J.C, 1990. *Betula papyrifera* Marsh. paper birch. In: Burns RM, Honkala BH (eds) *Silvics of North America*, vol 2. Hardwoods, Agricultural Handbook 654. USDA Forest Service, Washington, DC, 604–611.
- Savolainen, O., Pyhajarvi, T., and Knurr T. , 2007. Gene flow and local adaptation in trees. *Annual Rev. Ecol. Syst.* 38, 595-619.
- Scholander, P.F., Hammel, H.T., Bradstreet, E.D., Hemmingsen, E.A., 1965. Sap pressure in vascular plants. *Science*, 148:339-346.
- Simard, S.W., 1996. *Ecological and silvicultural characteristics of paper birch in the southern interior of British Columbia*. . In: Comeau, P.G., Harper, G.J., Blache, M.P., Boateng, J.L., Thomas, K.D. (eds.), *Ecology and Management of British Columbia Hardwoods: Workshop Proceedings, Dec. 1-2, 1993, Richmond, B.C.* Ministry of Forests, Victoria, B.C. FRDA Report No. 255, 157-165.
- Teskey, O.R., and Will, E.R 1999. Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. *Tree physiology* 19, 519-525.
- Thomson, A.M., and Parker, W.H. , 2008. Boreal forest provenance tests used to predict optimal growth and response to climate change. *Can. J. For.Res.* 38, 157-170.
- Vitousek, P.M., 1994. Beyond global warming: Ecology and global change. *Ecology* 75, 1861-1876.
- Wang, J.R., Hawkins, C.D.B., and Letchford, T. , 1998a. Relative growth rate and biomass allocation of paper birch (*Betula papyrifera*) populations under different soil moisture and nutrient regimes. *Can. J. For. Res.* 28, 44-55. .
- Wang, J.W., Hawkins, C.D.B., and Letchford, T., 1998b. Photosynthesis, water and nitrogen use efficiencies of four paper birch (*Betula papyrifera*) populations grown under different soil moisture and nutrient regimes. *For. Eco. & Mgt* 112, 233-244.
- Wang, T., Hamann, A., Yanchuk, A., O'Neill, G.A., and Aitken, S.N. , 2006. Use of response functions in selecting lodgepole pine populations for future climates. *Global Change Biology* 12, 2404-2416.
- Ward, J.K., and Kelly, J. , 2004. Scaling up evolutionary response to elevated CO₂: lessons from *Arabidopsis*. . *Ecol. Lett.* 7, 427-440.
- Ward, J.K., and Strain, B.R. , 1997. Effects of low and elevated CO₂ partial pressure on the growth and reproduction of *Arabidopsis thaliana* from different elevations. *Plant Cell & Envt.* 20, 254-260.
- Way, D.A., and Sage, F.R., 2008. Thermal acclimation of photosynthesis in black spruce [*Picea mariana* (Mill) B.S.P] *Plant Cell and Environment* 31, 1250-1262.
- Wise, R.R., Olson, A.J., Schrader, S.M., and Sharkey, T.D, 2004. Electron transport is the functional limitation of photosynthesis in field-grown Pina cotton plants at high temperature. *Plant, Cell and Envt.* 27, 717-724.
- Wu, H.X and Ying, C.C., 2004. Geographic pattern of local optimality in natural populations of lodgepole pine. *For. Ecol. Manage.* 194, 177-198.
- Zhang, S., and Dang, Q, 2005. Effects of soil temperature and elevated atmospheric CO₂ concentration on gas exchange, *in vivo* carboxylation and chlorophyll fluorescence in jack pine and white birch seedlings. *Tree Physiol.* 25, 609-617.
- Zhang, X., Zang, R., and Li, C., 2004. Populations differences in physiological and morphological adaptations of *Populus davidana* seedlings in response to drought stress. *Plant Science.* 166, 791-797.

Zheng, Y., Rummington, G.M., Xie, Z., Zhang, L., An, P., Zhou, G., Li, X., Yu, Y., Chen, L., and Shimizu, H. , 2008. Responses of air temperature and soil moisture of growth of four dominant species on sand dunes of central Inner Mongolia. *J. Plant Res.* 121., 473-482.