GENETIC VARIATION AND ADAPTATION OF WHITE BIRCH POPULATIONS ACROSS CANADA

By

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ABSTRACT

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Keywords: white birch, climate change, population, common garden, growth, phenology

Trees adapt to local climates, however growing concern surrounding climate change has generated predictions suggesting mass extinction or redistribution of taxa across the landscape. A lack of redistribution will result in species inhabiting sub-optimal conditions for growth and survival. Current reforestation efforts are to understand how species will respond to different climates. Seed representing twenty-one white birch (*Betula papyrifera* Marsh.) populations were collected, grown and planted in a common garden study. Populations were observed for height, root collar diameter (RCD) and survival percentage. There was a significant effect of population on each growth variable. Survival had a positive correlation with height and RCD growth (May to September) (Pearson's r = 0.828 and 0.660 respectively). Summer temperature had a strong relationship to each measured trait (r^2 = 0.326 to 0.682 respectively).

The second set of observations was bud flush, bud cessation and leaf yellowing. Bud flush observations began in early May and categorized bud development into six stages from dormant to fully flush. Bud cessation commenced in the first week of September every four days until bud set requirements were met. Leaf yellowing was observed simultaneously with bud cessation until 50% leaf yellowing was achieved. These traits represent phenological responses to temperature and photoperiod. There was a significant effect of population on each variable. Bud flush had a strong negative relationship with height growth, RCD growth and survival (r = -0.735, -0.693 and -0.539 respectively). Bud set influenced season length (Julian days), which had a positive correlation to height growth, RCD growth and survival (r = 0.568, 0.407 and 0.537 respectively). Leaf yellowing also showed a positive correlation to height growth and survival (r = 0.443 and .590 respectively).

Principal component analysis was utilized to summarize the 21 white birch populations in regards to their growth and phenological responses to the common garden study. Principal component analysis produced two components, which represented 24.2% and 16.61% of the variation respectively. No definitive titles were given to each principal component. Temperature was a main predictor of growth and phonological responses during the study. Summer and winter temperatures, along with growing degree days (a function of temperature), were influential in predicting both growth and phenological responses.

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Chapter I

1.0 GENERAL INTRODUCTION

The global climate system constantly changes, becoming a primary focus because climate has been identified as one of the primary controls on the geographic distribution of plants (Woodward 1987). Climate change is occurring at an alarming rate, raising concern for species extinction (Ricciardi and Simberloff 2009). Climate experts believe that on average temperature will increase between 2 to 5°C in North America, with northern latitudes expected to experience greater increases by the year 2100 (IPCC 2007).

Although it has been documented that some species have accommodated rapid climate change in the past (Pitelka et al. 1997; Kullman 1998), it is likely that without human intervention (assisted migration) many species will not survive as a result of not being able to migrate toward higher latitudes and altitudes quick enough (Malcom et al. 2002, Aitken et al. 2008 and Hoegh-Guldberg et al. 2008). There are indications that climate change has already had an impact on species geographical distributions (Walther et al. 2002; Parmesan 2007). Thomas et al. (2004) suggests that by the year 2050 approximately 18 to 35% of species may become extinct (plants, animals, insects and so forth). Projections made by Thuiller (2007) suggest that for each degree Celsius of temperature increase, ecological zones shift northward by approximately 160 km.

Many would conclude that in order to maintain forest productivity during global warming, forests would require a “wholesale” redistribution across the landscape (Rehfeldt et al 1999). A precursor to any action is to first understand and accept that the distribution of species is controlled in part by climatic elements, and that each population of a species may be adapted to perform best under specific conditions (Rehfeldt et al. 1999; Rehfeldt et al. 2003). Therefore, understanding growth and phenological responses of different populations of a specific species to climate variables is important in understanding how to manage forest species amidst climate change.

White birch (*Betula papyrifera* Marsh) is a prevalent species in the boreal forest, making up a large component of mixed-hardwood stands (Safford et al., 1990). This is due to the wide range of environmental conditions to which white birch may persist as a result of exhibiting considerable genetic variation in growth, morphology and drought tolerance (Simard et al. 1997). White birch has emerged as one of the more commercially valuable hardwood species in Canada's boreal forest, being used within the value-added industry to create high quality veneer and furniture products. On a management level, white birch can be used on riparian buffers to help reduce erosion of stream banks. White birch aids in the enhancement of wildlife by providing browse for moose, snowshoe hare and white-tailed deer, along with small mammals and birds by providing buds, catkins and seeds as a food source.

Although there are studies that have focused on white birch (Benowicz et al. 2000, 2001), there is a lack of information surrounding white birch populations from across North America and their ability to grow in new locations. These previous studies focused on populations from only British Columbia, reporting on growth, frost hardiness, gas exchange and germination. This study, unlike others, utilizes white birch populations from across the country to explore nationwide genetic variation using a common garden study. The main objective of this project is to study the effects of climatic factors influencing white birch and test for genetic variation among populations in growth and phenological traits.

The thesis contains three main sections. The first section will focus on the variations of growth characteristics, utilizing simple regression models (transfer function) for insight into which climatic factors are influencing the distribution patterns of white birch populations from the common garden experiment. The second will focus on the variations of phenological characteristics. The third section will utilize principal component analysis to attempt to discern groupings among populations.

1.1 GENERAL MATERIALS AND METHODS

Seed Source & Study Area

The experimental trial site was established in 2008 at the 25th Side Road in Thunder Bay, Ontario. White birch seeds were collected from various locations in several provinces, representing different site conditions (Table 1.1). Seed collection took place in British Columbia, New Brunswick, Quebec, Newfoundland and Labrador, Nova Scotia, Prince Edward Island and several locations in Ontario. The trial site was established to form a common garden experiment, allowing for the study of genetic variation. Below, Figure 1.1 shows the location of each population and common garden trial site, while Table 1.1 contains the locations and climatic variables (see Chapter 2.2) for each population utilized in the study.

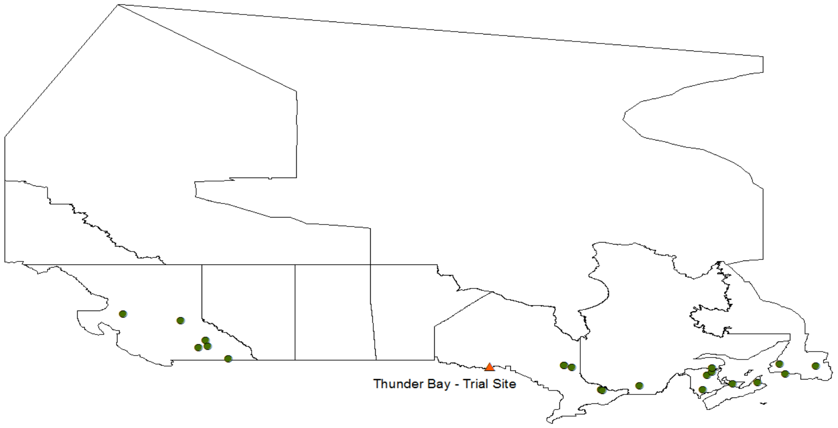

Figure 1.1. Map showing population locations and trial site location in Thunder Bay, ON.

Table 1.1. Location name, geographic co-ordinates and several climatic variables of all white birch seed collections.

Population	Latitude	Longitude	Elevation	MAT (°C)	MTCM (°C)	MTWM (°C)	AP	AMI	Degree Days > 5°C
BC 414	54.30	128.34	70.00	6.90	-3.50	16.60	1160.00	1.29	1499.80
BC 427	53.55	122.22	800.00	4.00	-9.60	15.50	600.80	2.14	1283.80
BC SKIM	50.43	120.25	547.00	8.90	-4.20	21.00	279.00	8.28	2309.00
BC 553	51.26	119.50	400.00	6.30	-6.70	18.00	474.90	3.59	1705.90
BC 403	50.56	119.32	600.00	7.30	-4.20	18.90	548.70	3.35	1837.00
BC 420	49.12	117.10	840.00	8.40	-2.70	19.90	755.20	2.71	2048.90
ON 264	48.34	81.22	295.00	1.36	-17.50	17.40	831.40	1.70	1410.00
ON 550	48.34	81.22	295.00	1.36	-17.50	17.40	831.40	1.70	1410.00
ON 400	48.14	80.37	295.00	1.36	-17.50	17.40	831.40	1.70	1410.00
ON 423	45.58	77.28	130.00	4.28	-13.00	19.20	853.40	2.08	1779.00
ON 355	45.45	77.08	300.00	4.10	-12.90	19.10	816.20	2.15	1754.00
QB 112	46.00	73.20	30.00	5.60	-11.90	20.70	1006.00	2.00	2016.00
NB DMW	45.54	66.39	20.00	5.62	-9.50	19.30	1124.10	1.62	1824.00
NB 092	47.22	65.93	300.00	3.10	-12.50	18.20	1115.30	1.31	1461.70
NB 1071	47.60	65.42	100.00	3.90	-11.30	18.50	969.90	1.57	1526.00
QB 411	48.06	65.41	200.00	3.90	-11.20	17.80	984.00	1.52	1491.00
PE 403	46.24	63.24	70.00	5.60	-7.60	18.80	1240.80	1.37	1704.00
NS 1109	46.35	60.55	10.00	6.20	-4.90	18.30	1391.00	1.22	1703.30
NL 106	48.50	58.16	70.00	3.50	-8.30	15.70	1519.90	0.78	1191.60
NL TW	47.37	57.57	140.00	3.83	-7.40	16.00	1201.90	1.03	1238.00
NL STL	48.32	54.34	304.00	3.83	-7.40	16.00	1201.90	1.03	1238.00

Note: MAT: mean annual temperature; MTCM: mean temperature in the coldest month; MTWM: mean temperature in the warmest month; AP: annual precipitation; AMI: annual moisture index.

Experimental Design

The seeds were germinated in the greenhouse at Lakehead University for 12 weeks, before field planting. The planting site is located at 48°21’ N, 89°23’ W, with an elevation of 183 meters. The site has a mean temperature of -14.8°C in January, while the mean July temperature is 17.6°C, with an annual precipitation of 711.16 mm and 1433.6 growing degree days above 5°C. The site was fenced and received site preparation in the form of partial weed, stump and course woody debris removal. The experiment was established using a complete random design (CRD), with 11 trees per row with spacing of 1.5 m x 1.5 m. There were three replicate rows for each of the 26 populations. The layout of the trial site may be found in APPDENDIX.

After further analyzing the origin data for each population, the list was condensed into 21 appropriate populations. Amalgamating populations was based on key factors such as geographic co-ordinates, elevations and moisture regimes. In total five populations were selected to be combined. The first three populations condensed were New Brunswick dry, moist and wet. They were combined because they were collected from the same site on a small slope, providing little true variation in environmental settings. Each seed source represented a microsite change at that location, rather than three separate sites each representing a moist, wet or dry site. The following combinations were made because they were collected from the same geographic area and represented by the same geographic and climatic data. BC 214 was combined with BC 414, while ON 355 was combined with ON 353, and ON 420 combined with ON 264. The layout of the trial site will reflect these changes.

REFERENCES

Aitken, S.N., S. Yeahman, J.A. Holliday, T. Wang and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutional Applications. 1(1): 95-111.

Benowicz, A., R. Guy, M.R. Carlson and Y.A. El-Kassaby. 2001. Genetic variation among paper birch (Betula papyrifera Marsh.) populations in germination, frost hardiness, gas exchange and growth. Silvae Genetica 50(1): 7-13.

Benowicz, A., R. Guy and Y.A. El-Kassaby. 2000. Geographic pattern of genetic variation in photosynthetic capacity and growth in two hardwood species from British Columbia. Oecologia 123(2): 168-174.

Coomes, D.A., and Allen, R.B. 2007. Effects of size, competition and altitude on tree growth. Journal of Ecology 95(5): 1084–1097.

Hoegh-Guldberg, O., L. Hughes., S. McIntyre., D.B. Lindenmayer., C. Parmesan., H.P. Possingham., and C.D. Thomas. 2008. Ecology: Assisted colonization and rapid climate change. Science 321(5887): 345-346.

IPCC. 2007. Climate change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Kullman, L. 1998. Non-analogous tree flora in the Scandes Mountains, Sweden, during the early Holocene-macrofossil evidence of rapid geographic spread and response to paleoclimate. Boreas 27(3): 153-161.

Malcom, J.R., A. Markham, R.P. Neilson and M. Garacil. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography. 29(): 835-849.

McKenney, D.W., J.H. Pedlar., K. Lawrence., K. Campell and M.F. Hutchinson. 2007. Potential Impacts of Climate Change on the Distribution of North American Trees. BioScience 57(11): 939-948.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenoligcal response to global warming. Global Change Biology 13(9): 1860-1872.

Pitelka, L.F. 1997. Plant migration and climate change. American Scientist. 85(5): 464-473.

Rehfeldt, G.E., Tchebakova, N.M ., M ilyutin, L .I., Parfenova, Y.I, Wykoff, W.R. and N.A. Kouzima.N.A ., 2003. Assessing population response to climate in Pinus sylvestris and Larix spp. Of Eurasia with climate-transfer models. Eurasian Journal of Forest Research 6-(2): 83-98

Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse and D.A. Hamilton Jr. 1999. Genetic responses to climate in Pinus contorta: nice breadth, climate change and reforestation. Ecological Monographs 69(3): 375-407.

Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology & Evolution 24(5): 248-253.

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.

Simard, S.W., D.A. Perry., M.D. Jones., D.D. Myrold.,D.M. Durall and R. Molina. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388(6642): 579-582.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips and S.E. Williams. 2004. Extinction risk from climate change. Nature 427 (6970): 145-148.

Thuiller, W. 2007. Climate change and the ecologist. Nature Publishing Group 448(7153):550-552.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg and F. Bairlein 2002. Ecological responses to recent climate change. Nature 416 (6879): 389-395.

Woodward, F.I. 1987. Climate and plant distribution. Cambridge University Press, Cambridge. 188 pp.

Chapter II

EXPLORING PHYSIOLOGICAL RESPONSES OF WHITE BIRCH POPULATIONS IN COMMON GARDEN STUDY

2.0 INTRODUCTION

Tree growth is a result of the complex interaction between genes and environment, with the contributions of individual genes forming the genetically fixed range of tolerance of a given tree species. Individual trees within a species grow in an array of environments, and therefore are expected to become adapted to the variation within its environment, reaching a balance with its environment (Callaham 1962).

Common garden studies (genecology study) are one way to make it possible to reveal genetic variation expressed by individual trees. An early and widely accepted definition of provenance is the original natural geographic source of a seedlot. Testing the adaptability of trees, to climatic conditions different from their origins, will reveal patterns in genetic variation among geographic populations, which have evolved under different climatic conditions. This method provides the best way to explore intraspecific differences among populations (Rehfeldt et al., 2002).

Growth rate influences on survival, biotic interactions and long-term establishment (Coomes and Allen 2007). Traditionally, it is assumed that there is an optimum temperature to facilitate maximum growth, with deviation from this optimum temperature influencing tree growth. Thus for, tree growth can be viewed as an indicator to adaptation, since trees fully express their potential under optimal growing conditions. Many forest growth models have been based on unimodel growth responses to temperature, whether it be heat sum, growing degree days or a function of photosynthesis (Schenk 1996; Loehle and LeBlanc 1996).

Temperature affects all plant processes (Lambers et al., 2008). Following a latitudinal gradient it is expected to encounter growth tradeoffs in the form of adaptation to cooler temperatures. At higher altitudes and latitudes physiological traits that increase frost hardiness will be favored, at the expense of growth (Korner 2003). In warmer or more favorable conditions, growth rate increases. This provides species with the ability to be more competitive, improving survival and long-term success (Loehle 1998; Coomes and Allen 2007). Therefore, it is likely to expect populations originating from moderate to warmer temperatures would exhibit greater growth rates than those from cooler environments.

Increased temperatures causes increased respiration cost, therefore, a higher carbon fixation is required to maintain growth and survival (Griffen et al., 2004). Photosynthesis has been widely regarded as one of the most sensitive processes affected by temperatures (Berry and Bjorkman 1980). Species from cooler climates often have lower capacities for photosynthetic acclimation to increased temperatures (Atkin et al. 2006; Ow et al. 2008).

Like temperature, water availability is one of the most important factors that influence both growth and spatial distribution of plant species (Tyree 2003). There are several physiological responses to soil or atmospheric moisture deficits. When species allocate more carbon to transportation tissues, a decrease in allocation to leaf area and reduction of productivity is possible (Magnani et al. 2000). Domec and Gartner (2003) found hydraulic characteristics within ponderosa pine to be correlated with height growth rate, but not diameter. Many studies have been conducted regarding effects of drought stress, which will not be discussed (see Chaves et al. 2002; Farooq et al. 2009).

Growth rates and water use are functions of biomass allocated to various organs, dictated by both the morphological and physiological needs of the organs (Boogaard et al., 1997). Plants respond to water deficit by either avoidance or tolerance. Avoidance is usually achieved with morphological changes such as reduced stomatal conductance, decreased leaf area, development of extensive root systems and an increase in the root/shoot ratio (Levitt, 1980). Tolerance is achieved by very specific tissue physiological changes, biochemical, and molecular mechanisms. Some of these changes come at the detriment of growth aspects such as height. Given that optimal white birch growing conditions are on well drained, sandy loams on moist site (Safford et al. 1990) it would be expected populations from moist to moderately moist environments would exhibit better growth than those from very wet to dry locations.

Phenological indicators have a direct influence on the growth of trees because they regulate the timing of growth (Kuparinen et al., 2010) and have a direct impact on fitness (Vitassee et al., 2009). Phenological indicators refer to phonological events such as bud flush and bud cessation. This topic of discussion will be covered in Chapter 3 of this thesis. Fitness may be defined as an individual's relative presence or abundance and success of its genes over multiple generations (Nicotra et al. 2010). This is often measured as survival, however other attributes such as biomass, seed species and growth rates may be used as surrogate attributes in the absence of adequate survival data (Nicotra et al. 2010).

2.1 Study Objectives

The objective of this study was to investigate the physiological differences in regards to height, root collar diameter and survival in response to being planted in a common garden study. The populations were selected to represent varying environmental conditions. This allows the study to reflect the effects of different geographic origin, temperatures and moisture regimes on height growth, RCD growth and survival. The hypothesis was that populations from origin habitats with moderate to warm temperatures and moderate annual precipitation would exhibit the greatest amount of growth. Habitats that experience fluctuations around their mean would in theory have provided populations the opportunity to adapt to a range of conditions. This study will provide further insight into the variation between populations of white birch and how a changing climate may affect them.

2.2 MATERIALS AND METHODS

Data Collection

Physical measurements were attained at the end of each month between May and September. Due to the young age of the trial site, the trees ranged in heights above and below one meter, without exceeding 3 meters, making the meter stick the most reasonable method of measurement. The second physical measurement measured was root collar diameter (RCD) measured in millimeters, with digital root calipers.

Survival will be a visual observation, where a tree is considered to be dead if there is “no green” on the tree. In other words if a branch still has some living leaves on it the tree will be considered living, otherwise the tree will be marked as deceased.

Climate Data

The geographic and climatic data was collected from Environment Canada's 'Climate Normals & Averages' dataset (1971-2000), utilizing weather stations closest to the seed collection site of each population in question. At times particular weather stations were used for more than one population, which contributed to grouping of populations, creating a reduced total number of populations. Climate variables were mean temperature cold month (MTCM) (°C), mean monthly temperatures (°C), monthly minimum and maximum temperatures (°C), along with total annual precipitation (mm) and growing degree days at 0, 5 and 10°C. Annual moisture index (AMI), was derived as a function of GDD divided by annual precipitation. Growing degree days was calculated by subtracting the selected threshold value (0, 5 or 10°C) from the daily mean temperature if the daily mean temperature was greater than the threshold. The sum of the values up until a specific date reflects GDD.

Climatic data for Thunder Bay (representing the common garden experiment site) was used against the origin climate data to create the transfer climate data, which was then utilized to create the individual response curves, representing transfer functions (Table 2.1). The transfer functions were conducted utilizing SPSS to create both linear and quadratic regressions.

Table 2.1. Population name, geographic location and climatic factors used with quadratic curves.

Population						May Temp (°C)			June Temp (°C)			July Temp (°C)			August Temp (°C)					
	Lat	Long	Elev	A.P	MTCM (°C)	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	MAT (°C)	AMI	DD > 5°C
BC 414	6.09	39.11	-144	448.84	11.3	1.4	2.6	0.3	0.1	1.2	-1	-1	-0.1	-1.9	-0.1	0.8	-1	4.4	-0.723	66.2
BC 427	5.34	32.99	586	-110.36	5.2	0.4	0.7	0.1	-0.7	-0.3	-1.1	-2.1	-2.2	-2.1	-1.8	-2.2	-1.4	1.5	0.121	-149.8
BC SKIM	2.22	31.02	333	-432.16	10.6	4.9	5	4.9	4.1	4	4.2	3.4	2.7	4.1	3.9	3.1	4.7	6.4	6.260	875.4
BC 553	3.05	30.27	186	-236.26	8.1	2.6	2.2	3.2	1.5	1	2.1	0.4	-0.9	1.6	0.9	-0.6	2.2	3.8	1.576	272.3
BC 403	2.35	30.09	386	-162.46	10.6	2.8	3.8	1.9	2.1	2.9	1.4	1.3	1.5	1.1	2.1	2.4	1.7	4.8	1.332	403.4
BC 420	0.905	27.87	626	44.04	12.1	3.6	3.8	3.4	2.7	2.5	3	2.3	1	3.5	3.1	1.5	4.6	5.9	0.697	615.3
ON 264	0.13	-8.01	81	120.24	-2.7	0.1	0	0.2	0.7	0.2	1.1	-0.2	-0.5	0	-0.9	-1	-0.8	-1.14	-0.320	-23.6
ON 550	0.13	-8.01	81	120.24	-2.7	0.1	0	0.2	0.7	0.2	1.1	-0.2	-0.5	0	-0.9	-1	-0.8	-1.14	-0.320	-23.6
ON 400	-0.07	-8.86	81	120.24	-2.7	0.1	0	0.2	0.7	0.2	1.1	-0.2	-0.5	0	-0.9	-1	-0.8	-1.14	-0.320	-23.6
ON 423	-2.63	-11.95	-84	142.24	1.8	2.6	2.8	2.3	2.6	2.8	2.3	1.6	1.7	1.4	1.3	1.7	0.7	1.78	0.069	345.4
ON 355	-2.76	-12.15	86	105.04	1.9	2.4	2	2.9	2.1	1.6	2.7	1.5	0.8	2.1	1	0.7	1.4	1.6	0.133	320.4
QB 112	-2.21	-16.03	-184	294.84	2.9	3.6	4.5	2.7	4.2	5	3.5	3.1	3.9	2.3	2.6	3.4	1.8	3.1	-0.012	582.4
NB DMW	-2.67	-22.84	-194	412.94	5.3	1.7	2.5	1	2.4	2.7	2	1.7	2.2	1.2	2	2.5	1.5	3.12	-0.393	390.4
NB 092	-0.99	-23.3	86	404.14	2.3	-0.8	0.4	-1.9	0.7	1.6	-0.2	0.6	1.6	-0.5	0.2	1.2	-0.9	0.6	-0.705	28.1
NB 1071	-0.61	-23.81	-114	258.74	3.5	-0.8	1.2	-2.7	0.8	2.3	-0.6	0.9	2.2	-0.5	0.7	2.3	-0.9	1.4	-0.443	92.4
QB 411	-0.15	-23.82	-14	272.84	3.6	-0.4	1.5	-2.3	0.6	2.2	-0.9	0.2	2	-1.6	0.4	2.1	-1.3	1.4	-0.501	57.4
PE 403	-1.97	-25.99	-144	529.64	7.2	-0.4	1.8	-2.5	0.8	2.7	-0.9	1.2	3.1	-0.7	1.7	3.5	-0.1	3.1	-0.643	270.4
NS 1109	-1.86	-28.68	-204	679.84	9.9	-0.5	1.9	-2.7	0.3	2.3	-1.7	0.7	3	-1.5	1.4	3.6	-0.9	3.7	-0.791	269.7
NL 106	0.29	-31.07	-144	808.74	6.5	-2.5	-1.7	-3.3	-2.3	-2	-2.5	-1.9	-1.1	-2.8	-1.3	-0.5	-2.1	1	-1.232	-242
NL TW	-0.84	-31.66	-74	490.74	9.3	-3.9	-0.3	-7.5	-4.5	-1	-7.9	-4.1	-0.6	-7.7	-1.9	1.2	-5	1.5	-0.102	-410.9
NL STL	0.11	-34.89	90	490.74	7.4	-2.8	-0.8	-4.7	-2.4	-1.3	-3.4	-1.6	-0.3	-2.8	4	0.6	-2.5	1.33	-0.986	-195.6
*TBAY	48.21	89.23	214	711.16	-14.8	9.5	2.5	16.4	14	7.3	20.6	17.6	11	24.2	16.6	10.1	23.1	2.5	2.02	1433.6

*Represents the geographic and climatic factors for the common garden study site in Thunder Bay, Ontario Canada.

*Variables in order are latitude (Lat), longitude (Long), elevation (ELev), annual precipitation (A.P.), mean temperature cold month (MTCM), mean, minimum (Min) and maximum (Max) monthly temperatures, mean annual temperature (MAT), annual moisture index (AMI) and degree days greater than 5°C

*Values were derived as origin value subtracted by Thunder Bay value.

Statistical Analysis

Statistical Package for the Social Sciences 20 (SPSS 2011) was utilized for all statistical procedures. Height and RCD measurements were examined to ensure that each dataset conforms to the assumptions of homogeneity of variance, as well as a normal distribution (Shapiro-Wilk test). The next step was to examine the relationship between each response (growth and survival) and the populations, to determine significant differences among the populations studied. One-way analysis of variance (ONE-WAY ANOVA) was applied to each response factor to determine significant differences between populations. The ANOVA model used was:

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

Where:

Y_{ij} = is j^{th} growth observation of population i
μ = is the overall mean
P_i = fixed effect of population i
ε_{ij} = is the random error effect of replication j within population i.

Since data was repeatedly collected at the end of each month, the data set is considered a repeated measures dataset. Repeated measures ANVOA was used to test the total growth response to population:

$$Y_{ijk} = \mu + P_i + M_j + PM_{ij} + \varepsilon_{(ij)k}$$

Where:

Y_{ijk} = is the growth observation of the j^{th} replicate of the i^{th} population on month k
μ = is the population mean
P_i = random effect of population i
M_j = fixed effect of the monthly measurement
PM_{ij} = fixed effect of the population by month interaction
$\varepsilon_{(ij)k}$ = is the random error effect of replication j of population i in month k.

Transfer Functions

Quadratic functions were utilized because they provide a better estimation of the significant relationships between the population's performances and climatic or geographic variables. Linear functions were explored and found similar results (based on r^2 and significance values) and will not be presented. Significance was tested at the 95% confidence interval or significant at $\alpha = 0.05$.

Quadratic functions allowed all of the populations to be graphed at once against the selected geographic or climatic variable. The resulting curve is helpful in determining and predicting seed source performance (relative to height and RCD growth) across many environmental gradients. Note that the X variable represents the origin climate minus the population trial climate. This provides the basis of a transfer function, since the X variable now represents the difference of the variable by each location. The basic quadratic equation is as follows below;

$$Y_i = \beta_0 + \beta_1 X_1 + \beta_2 X_1^2 + \epsilon$$

Where:

Y_i = the predicted accumulative height or root collar diameter growth through May to September
β_0 = is the intercept
$\beta_1 X_1$ = is the regression estimate β for variable X
$\beta_2 X_1^2$ = is the regression estimate β variable X creating the quadratic function
ε = is the residual error

2.3 RESULTS

Height data was examined to ensure normality before proceeding with analysis. The skewness value was 0.124, indicating the data was normally distributed. The value for kurtosis was 0.495, which means the data set is slightly leptokurtic. Both the kolmogorov-Smirnov (0.072) and Shapiro-Wilk test (0.069) (Table 2.2) produced significance values that were greater than 0.05, which implies that we fail to reject the null hypothesis. This means that there is normality within the residual data set.

Table 2.2. Tests of normality for height growth (cm), RCD growth (mm) & survival (%)

	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.	Statistic	Df	Sig.
Standardized Residual for HeightGrowthcm	0.04	464	0.072	0.994	464	0.069
Standardized Residual for RCDgrowthmm	0.036	458	0.193	0.994	458	0.063
Standardized Residual for Survival (%)	.094	92	.045	.970	92	.034

Graphical methodology was also utilized to ensure normality within the dataset (Figure 2.1). A histogram of the data was fit with a normal distribution curve to illustrate the fit of normality, because the means are distribution fairly evenly. The boxplot depicts even quartiles since the median value is located in the middle of the box (between the 75th and 25th percentiles). The error bars are evenly spaced, with no significant outliers present.

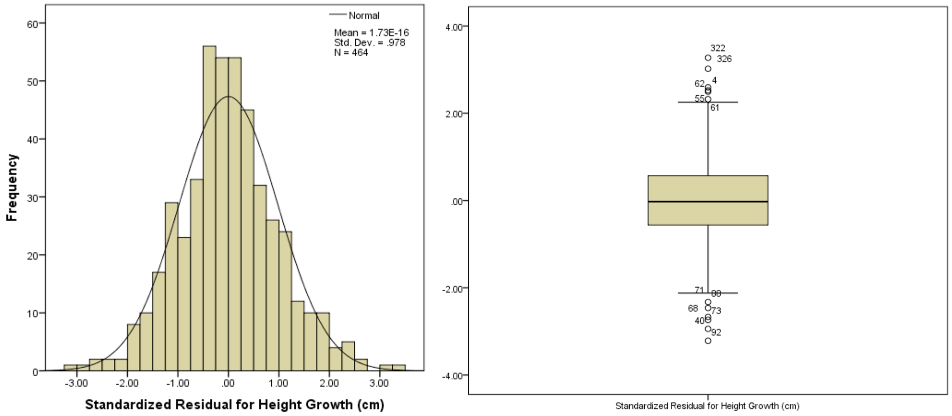

Figure 2.1. Histogram and boxplot for Height growth (cm) for 21 populations.

Height (cm) was tested on the basis of monthly heights and total height growth from May through September. The first trait tested was height growth to determine if there was any significance among the variations in total mean height growth among populations. The result shows that there is a significant difference in the total mean height growth (cm) among populations with a p value of 0.000 (Table 2.3).

Table 2.3. One-way ANOVA result for growth of height (cm), RCD (mm) and survival (%) among the 21 populations.

Factor		Sum of Squares	df	Mean Square	F	Sig.
Height Growth	Between Groups	60576	20	3028	14.2	<0.001
	Within Groups	94770	443	214		
	Total	155347	463			
RCD Growth	Between Groups	1146.066	20	57.303	10.336	<0.000
	Within Groups	2422.726	437	5.544		
	Total	3568.792	457			
Survival (%)	Between Groups	20935.826	20	1046.791	2.076	0.013
	Within Groups	35797.914	71	504.196		
	Total	56733.741	91			

The populations are sorted based upon longitude (west to east) (Figures 2.2a & b). The top performing population was BC SKIM amassing a total mean growth increase of 52.02 cm, while the poorest performer was NL TW with a mean growth increase of 9.15 cm. The mean growth across all 21 populations was 28.29 cm.

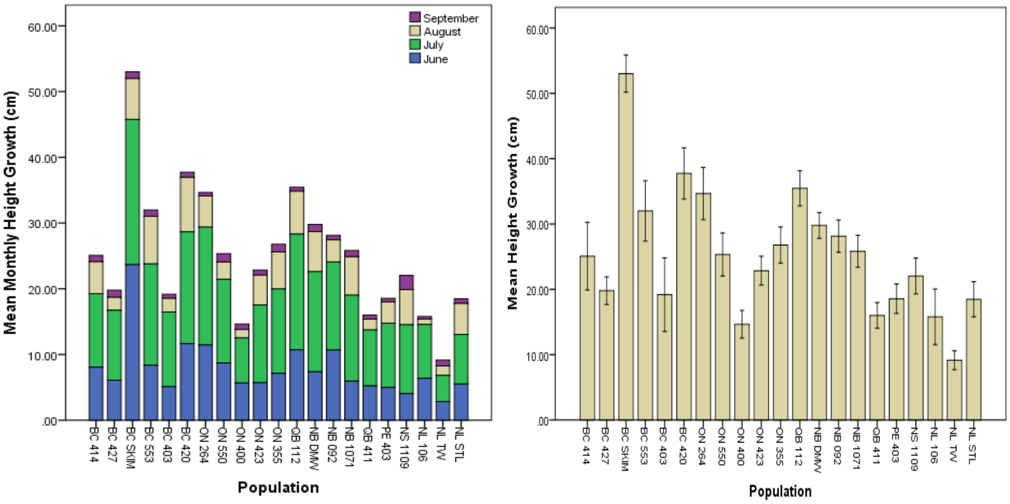

Figure 2.2. (a). Mean accumulated height growth (cm) per tree each month grouped by population and sorted by longitude.(b) Mean accumulated height growth (cm) with standard error (+/- 1 SE).

Since height measurements were conducted at the end of each month, a one-way ANOVA utilizing repeated measures was conducted to test for significance among the populations over the span of five months (May through September) (Table 2.4). The Mauchly's test had a significant p-value of < 0.000, indicating that the data does not satisfy the hypothesis of sphericity. Based upon the Epsilon values, SSPS produces corrections affecting the degrees of freedom, mean square values and p-values.

Table 2.4. Significance test for repeated measures of height growth (cm) & RCD growth (mm).

Factor	Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon^b		
						Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Height Growth	Month	0.002	2849.126	9	<.000	0.296	0.31	0.25
RCD Growth	Month	0.062	1213.417	9	<0.000	0.44	0.462	0.25

Root collar diameter data was explored to ensure normality before proceeding with analysis. The skewness was 0.196, indicating fairly strong symmetry, while the kurtosis value of 0.308 indicates a slightly leptokurtic distribution. The Kolmogorov-Smirnov (0.193) and Shapiro-Wilk (0.063) tests, indicate that the null hypothesis is not rejected, implying normality within the data (Table 2.2).

Both the histogram and boxplot indicate normality. The data distribution follows a normal distribution closely, with departures from normality occurring equally on either side of zero. The boxplot depicts even quartiles since the median value is located between the 75th and 25th percentiles. The error bars are fairly even without any significant outliers present (Figure 2.3).

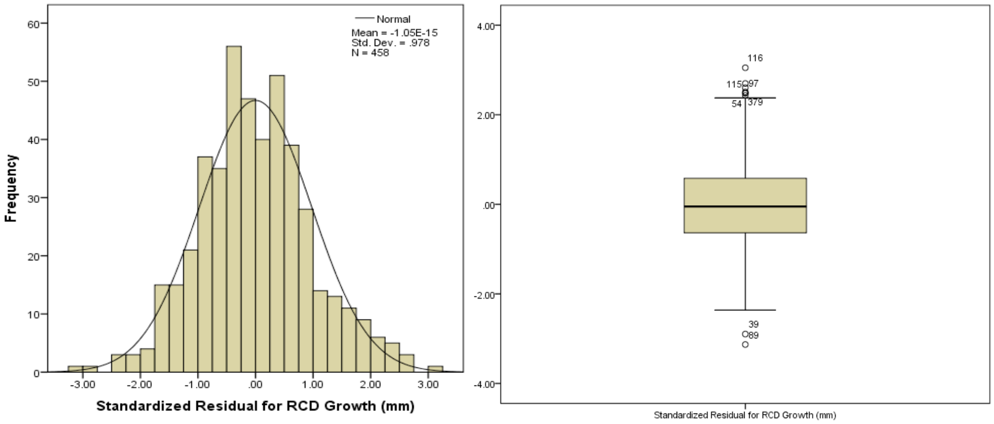

Figure 2.3. Histogram and boxplot for RCD (mm) growth of the 21 populations

Root collar diameter (RCD mm) was tested on the basis of monthly RCD and total RCD growth from May through September. The first trait tested was root collar diameter growth to determine if there was any significance among the variations in total mean root collar diameter growth among populations. The result shows that there is a significant difference in the total mean height growth (cm) among populations with a p value of <0.000 (Table 2.3).

Graphical representation was used to show the total mean growth by month. The populations are sorted based upon longitude (west to east) (Figure 2.4a & b). The top performing population was BC SKIM amassing a total mean RCD growth per tree of 9.37 (mm), while the poorest performer was NL TW with a mean RCD per tree of 3.27 (mm) per tree. The mean growth per tree among all 21 populations was 5.63 (mm).

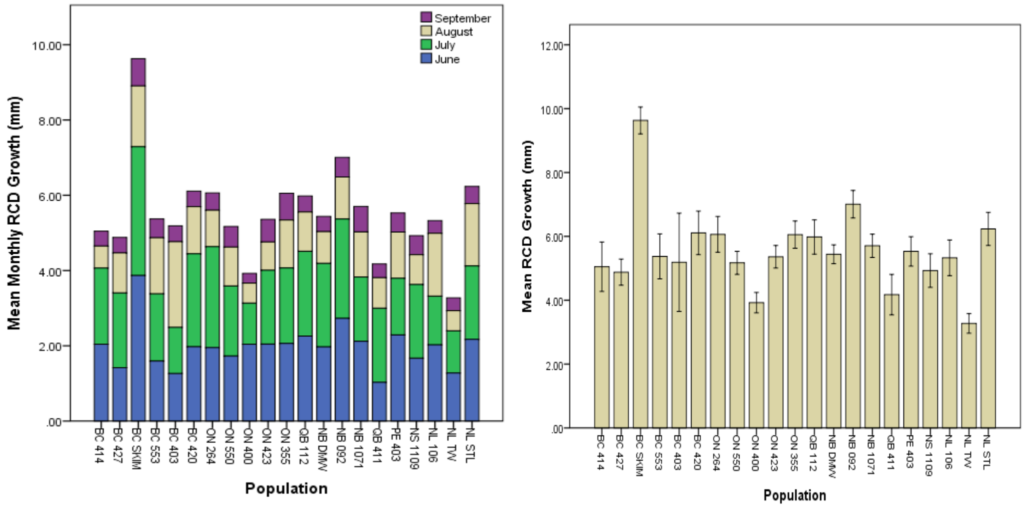

Figure 2.4 (a). Mean accumulated RCD growth (mm) per tree each month grouped by population and sorted by longitude.(b) Mean accumulated RCD growth (mm) with standard error (+/- 1 SE).

Root collar diameter measurements were conducted at the end of each month, while height measurements were also being taken. A one-way ANOVA utilizing repeated measures was conducted to test for significance among and within the populations over the span of five months (May through September) (Table 2.4). The Mauchly's sphericity has been violated with a significant p-value of 0.00. Based upon the Epsilon values, SPSS produced corrections affecting the degrees of freedom, mean square values and p-values.

Survival was found to have a slightly non-normal distribution (Table 2.2), however the levene's test suggests that the error of variance of the response is fairly equal across all groups (0.683). This is a result of some rows having no survivorship since being planted. These rows were left during analysis because they are a result of the stochasticity found in this type of study. There were significant differences among populations for survival percentage with a p-value of 0.013 (Table 2.3). The bar chart error bars allude to populations with completely dead rows with the extension above and below the bar.

The population with the greatest survivorship was BC SKIM, with approximately 74% of the seedlings surviving, while ON 400 had the lowest survivorship with approximately 21 % of the seedlings surviving (Figure 2.5). The overall mean from the study was approximately 47% survival.

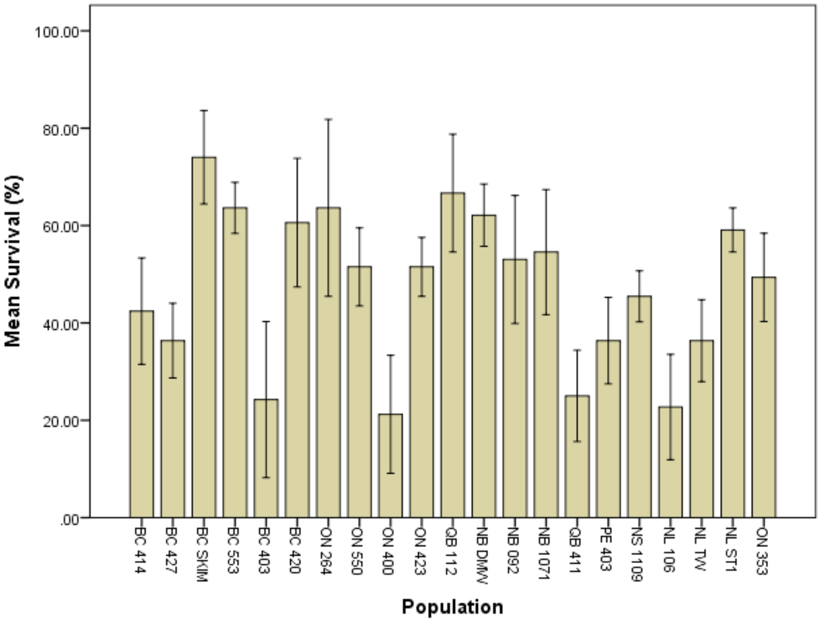

Figure 2.5. Mean survival (%) for each of the 21 white birch populations with standard error (+/- 1 SE).

Transfer Functions

Many of the climatic variables were found to be significant at α=0.05 as seen below in Table 2.11. Included among the figures (Figure 2.6, 2.7 & 2.8) are both latitude and longitude for height, RCD growth and survival, which although greater than 0.05, displayed a visible trend despite the r^2 and significance values.

Table 2.5. Significance and R^2 of the quadratic transfer functions of height and RCD against climatic and geographical variables.

Variables	R^2	Significance	Predictors
Total Height Growth	.334	.026	Annual Precipitation
	.595	.000	May mean temperature (°C)
	.477	.003	May minimum temperature (°C)
	.584	.000	May maximum temperature (°C)
	.585	.000	June mean temperature (°C)
	.326	.029	June minimum temperature (°C)
	.626	.000	June maximum temperature (°C)
	.563	.001	July mean temperature (°C)
	.682	.000	July maximum temperature (°C)
	.284	.050	August mean temperature (°C)
	.657	.000	August maximum temperature (°C)
	.472	.003	Mean Annual Temperature (°C)
	.481	.003	Annual Moisture Index
	.627	.000	Degree Days > 5°C
	.617	.000	Degree Days > 10°C
Total RCD Growth	.298	.041	Annual Precipitation
	.347	.021	May mean temperature (°C)
	.369	.016	May minimum temperature (°C)
	.288	.047	May maximum temperature (°C)
	.324	.030	June mean temperature (°C)
	.319	.031	June maximum temperature (°C)
	.403	.010	July mean temperature (°C)
	.418	.008	July maximum temperature (°C)
	.406	.009	August mean temperature (°C)
	.402	.010	August maximum temperature (°C)
	.302	.039	Mean Annual Temperature (°C)
	.565	.001	Annual Moisture Index
	.469	.003	Degree Days > 5°C
	.456	.004	Degree Days > 10°C
Survival	.287	.048	May mean temperature (°C)
	.295	.043	May maximum temperature (°C)
	.366	.017	June mean temperature (°C)
	.382	.013	June maximum temperature (°C)
	.353	.020	July mean temperature (°C)
	.382	.013	July maximum temperature (°C)
	.315	.033	August maximum temperature (°C)
	.325	.029	Degree Days > 5°C
	.350	.021	Degree Days > 10°C

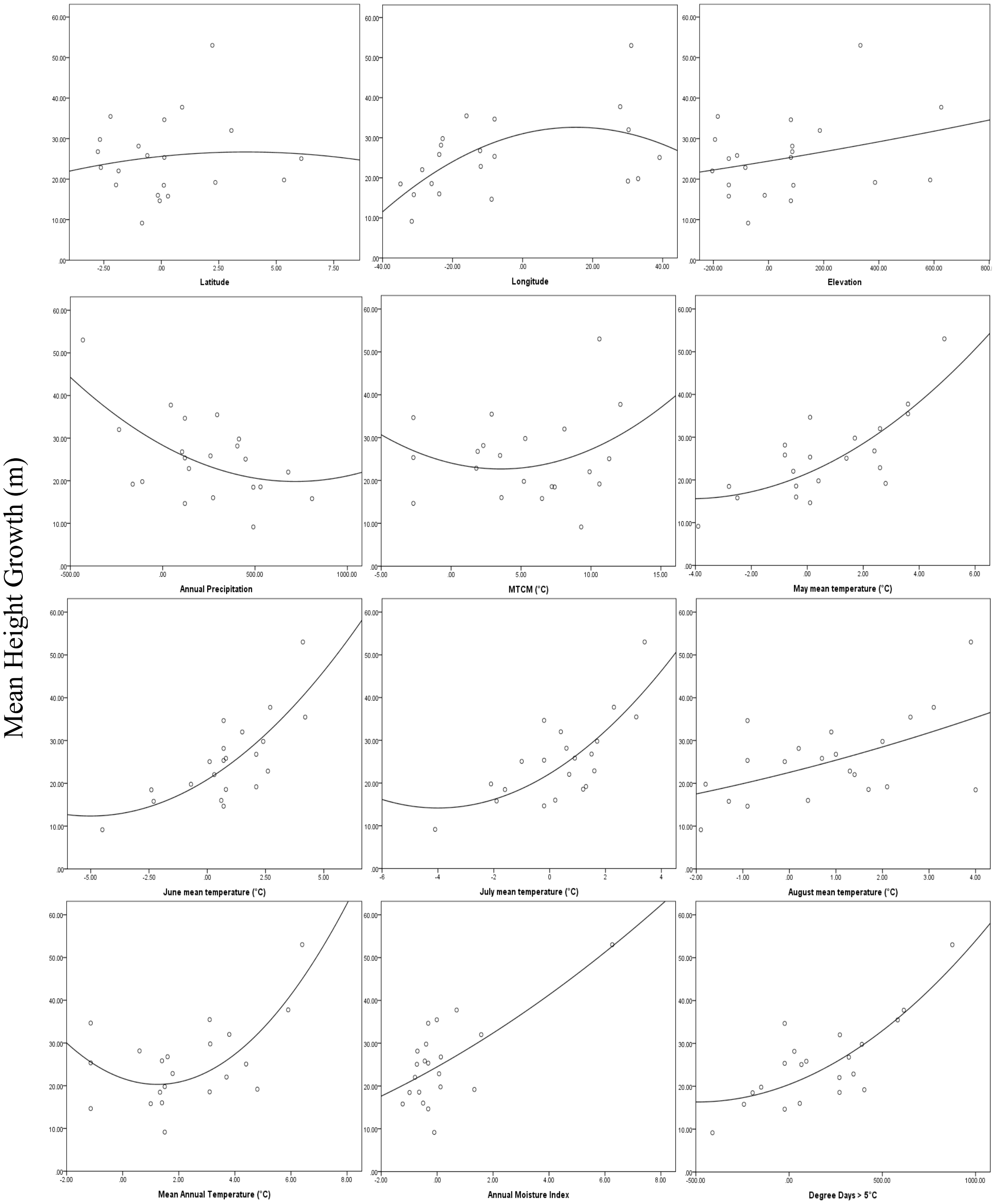

Figure 2.6. Quadratic transfer function curves for mean height growth (cm) to geographic and climatic factors.
*Thunder Bay is represented by the zero on the x-axis.

The quadratic transfer functions produced an array of statistically significant relationships between climate and geographical characteristics in relation to both height and root collar diameter growth. Generally, a positive value in Table 2.1, represents a population which originates from an area that is 'greater' or 'larger' for the given characteristic (e.g. + value for temperature means a warmer origin temperature), and vice versa.

The greatest significance for height growth was in relation to July temperatures with r-square values of 0.563 for mean temperature and 0.682 for maximum temperature. RCD growth had the strongest statistical relationship with the annual moisture index (AMI) with an r-squared value of 0.565.

Populations from lower latitudes exhibited better average growth, while longitude was relatively neutral, with the exception of one western population exhibiting superior height growth. Populations from slightly moisture and lower elevations exhibited greater height growth than those from higher elevations with less moisture. As the temperatures increased (mean and maximum) there was a strong positive trend with growth increasing. Mean annual temperature and degree days greater than 5 degrees Celsius also had a positive trend.

Root collar diameter indicated that populations from more southern and eastern regions performed best. Populations from areas of greater precipitation performed best, while AMI was tightly grouped together. Lower elevations coincided with warmer monthly temperatures and increased performance. The months of June, July and August depict the wide range performance and temperature the best. Areas with greater amounts of growing degree days above 5 degrees Celsius exhibited more consistent growth patterns.

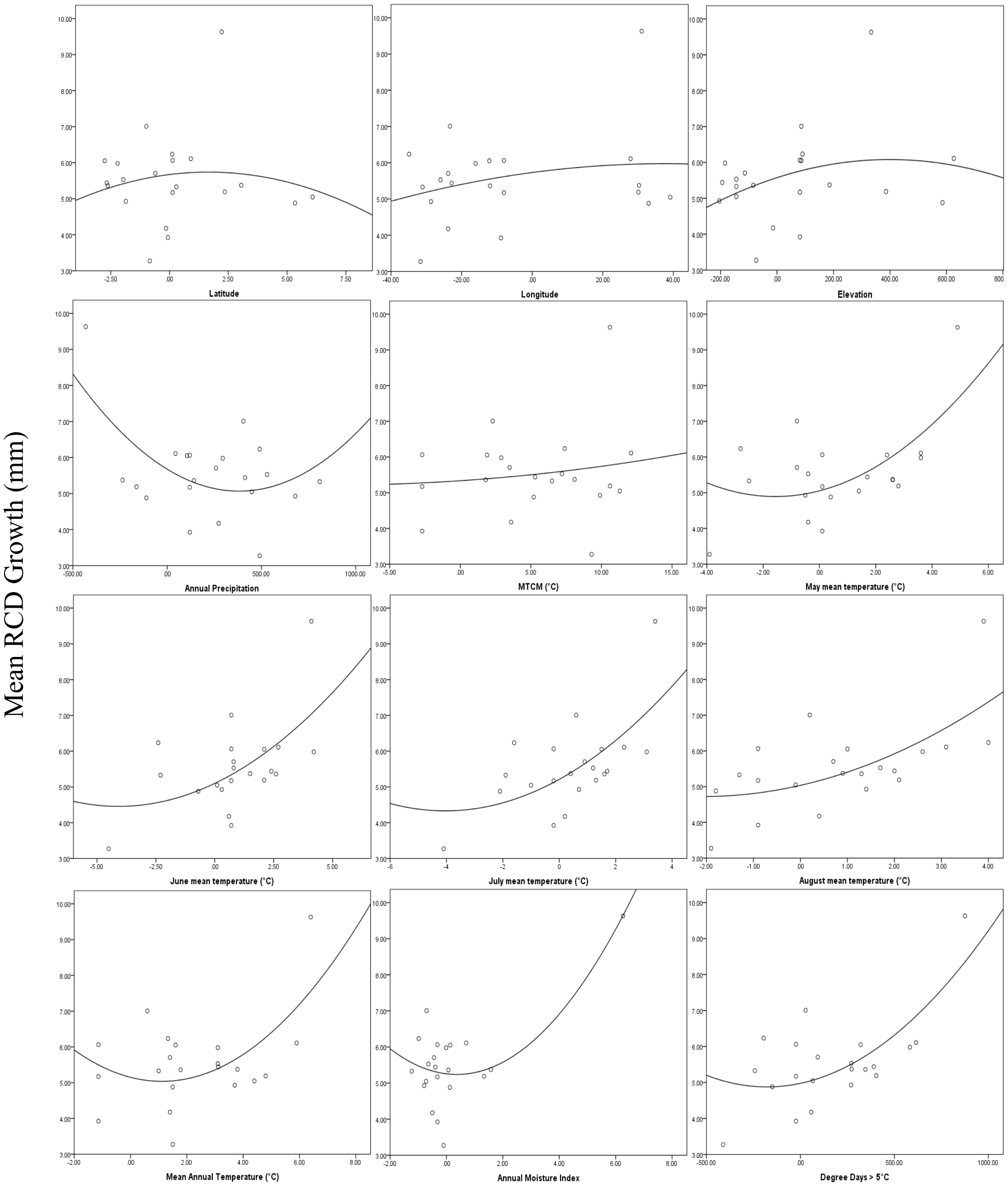

Figure 2.7. Quadratic transfer function curves for mean RCD growth (mm) to geographic and climatic factors.

The quadratic transfer functions for survival produced nine significant relationships (Table 2.11). The strongest relationship was found to be June and July maximum temperatures in degrees Celsius (r^2=.382), with June and July mean temperatures being the next most significant relationships (r^2=.366 and r^2=.353). This continues the trend of temperature being a strong predictor for fitness, which can be represented by surrogate traits such as growth, although survival is most common when applicable.

Geographical factors did not produce significant relationships. Latitude indicated no significant trend other than many of the poorer performers being around the same latitude as the study site. Otherwise populations originating from higher and lower latitudes exhibited success. Longitude indicated that both eastern and western populations had success and failures, with elevation indicating the same pattern. Annual precipitation suggests locations with moderate to higher increases in moisture had greater success, with annual moisture index dispersing around zero (Thunder Bay). Growing degree days >°5 indicated that a greater number of GDD resulted in a higher survival percentage.

Overall, temperature was the greater predictor of survival, generally indicating populations originating from warmer climates than that of Thunder Bay had greater overall survival.

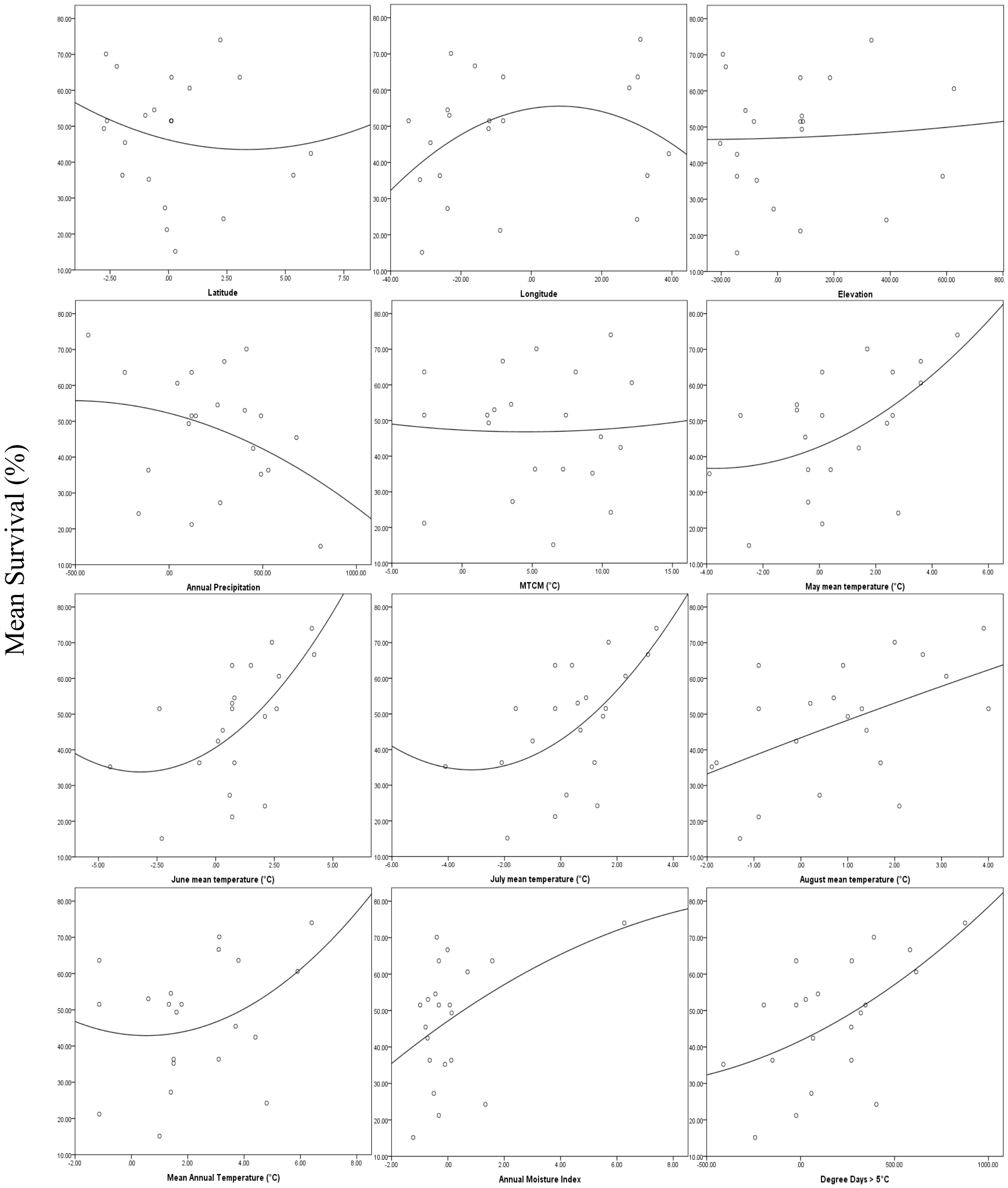

Figure 2.8. Quadratic transfer function curves for mean survival (%) to geographic and climatic factors.

2.4 DISCUSSION

Changes in current climate will impact the fitness of tree populations on an individual basis as a result of local adaptation and differences in genetic variation and plasticity. Given the extensive range of white birch across the country (Safford et al. 1990) since post-glacial expansion, some populations have evolved independently (Petit et al. 2002), leading to local adaptation among populations which are likely adapted to factors beyond climate.

Height, root collar diameter and survival are three ways to monitor impacts of climatic changes regarding fitness of tree populations in a common garden study. Temperature was the most influential factor impacting tree growth and survival, while annual moisture had some impact. Survival indicated a relationship to temperature, however due to the ambiguity surrounding causes of mortality, the overall influence of temperature may vary in significance. Overall, it was found populations originating from warmer climates with lower to moderate annual precipitation exhibited greater fitness.

Significant differences were detected between populations. It was assumed that the populations originating from moderate to warmer climates would express superior growth and survival. It is also common for populations from more northern locations to be superior in common garden studies as opposed to lower latitude populations. There was a clear pattern within the dataset that indicated the hypothesis to be true (populations originating from moderate to warm temperatures and moderate precipitation would perform best), which will be discussed referencing the quadratic functions.

High latitude and elevation are generally associated with lower temperatures, which suggest a tradeoff between growth potential and cold hardiness (Vitasse et al. 2009A). However, in this study latitude, longitude and elevation did not produce significant relationships with any of the three measured traits. Despite a lack of significance, there was some evidence indicating the influence of latitude and elevation. The lack of a significant relationship is a result of populations originating from higher elevation and latitude areas, having warmer temperatures, which goes against the common assumption stated above. Referencing the quadratic curves and climate data table it indicates that populations from higher latitudes and elevation produced some of the more superior growth and survival rates.

Several of the higher latitude populations also had warmer summer and annual temperatures (BC 420, BC SKIM, BC 403, BC 553), which may explain the weak correlation with latitude and elevation in regards to the quadratic curves. Interestingly, BC 427 had the second greatest latitude and elevation, which had the lowest mean temperature warm month, fitting the common assumption of latitude and temperature. This particular population performed poorly compared to the other northern populations despite experiencing similar climatic changes.

Many populations from areas with greater MAT (°C) and higher temperatures during summer months displayed better overall growth rates and total growth for the studied growing season. Many of the variables that were found to be good predictors for height were also good for RCD, which is expected as a result of correlation between both measurements as utilizing Pearson's correlation in Chapter 3 (Table 3.2). Mean summer temperatures proved to be the best predictor of tree performances following white birch population seed transfer. Other variables such as growing degree days greater than 5°C and 10°C (related to summer temperatures) and annual moisture index displayed fairly strong relationships. Annual moisture index had a very narrow gradient, only spanning two units, indicating that many of the populations may persist is similar moisture regimes.

Growing degree days is a function of temperature and reflected significant relationships with each of the observed traits. Generally, populations originating from locations with a greater number of growing degree days exhibited higher levels of fitness, with the exception of BC 403. Populations with similar GDD to the common garden study exhibited mixed results, with populations from fewer GDD origins exhibiting poorer results.

Moisture showed significant effects on growth traits. The trend indicated populations from similar or slightly wetter moisture regimes exhibited greater growth potential. Annual precipitation for the trial site in Thunder Bay was 711 mm, with an annual moisture index of 2.02. Moisture conditions were likely not a constraint on growth, with populations originating from dryer and moister conditions, exhibiting success in height and RCD growth. Therefore, it is appropriate to conclude that the populations with the highest growth potential performed better, as opposed to those which performed poorer were under stress.

The observed range for survival rate was approximately 15 to 74% for the 21 white birch populations. These values also reflect the effects of pooling populations together due to similarities in geographic and climatic traits. It is expected that populations from areas with warmer MAT (°C) and MTCM (°C), would suffer from frost damage due to inadequate adaptation to the colder winters. No significant relationship was found among the quadratic functions. Among the higher survival rate there was a mix of populations from climates that were significantly warmer than Thunder Bay and or comparable, which survived the best (BC SKIM, NB DMW, QB 112, and ON 264). Many of the top surviving populations also exhibited greater growth as compared to populations exhibiting poor growth, this being a reflection to their overall fitness. Populations from moister sites also had greater survival in the common garden study.

The results indicate that the strongest performing populations were those originating warmer temperatures with comparable moisture regimes. Populations exhibiting these traits often outperformed the most local population for height, RCD and survival percentage. Populations from cooler climates did not perform as strongly. This suggests that they were unable to respond to the more favourable conditions as a result of becoming adapted to their origin climates. This may suggest a lack of genetic adaptation within some populations.

Poor performances by populations originating from cooler climates, suggests that the cooler ranges of white birch may suffer in overall fitness as climates continue to increase over the next century. Populations in the warmer ranges appear to be able to adapt more easily suggesting they may have higher amounts of adaptability and may be more suitable for future climates. These populations should be considered for further studies and would likely be useful for consideration of assisted migration. The other possibility is that since post-glacial redistribution that white birch has yet to reach equilibrium due to dispersal constraints (Svenning & Skov 2004).

The findings of this chapter indicate temperature has a strong influence on white birch performance, therefore it is likely that temperature has had a strong influence on the range and distribution of white birch since glaciation. White birch occupies many cooler areas, with northern Ontario being one of the coldest ranges of white birch, and as a result many of the populations studied originated from warmer climates. However, several populations from higher elevations and latitudes and or warmer climates exhibited excellent growth and survival, suggesting northern Ontario to possibly be a less preferable seed source for white birch. Further studies should include several more populations from colder regions since this study had few and should also include populations from regions similar to or slightly warmer than Thunder Bay's climate.

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REFERENCES

Atkin, O.K., I. Scheurwater, and T.L. Pons. 2006. High thermal acclimation potential of both photosynthesis and respiration in two lowland Plantago species in contrast to an alpine congeneric. Global Change Biology 12(3): 500-515.

Boogaard, R., D. Alewijnse., Veneklaas, E.J. and H. Lambers. 1997. Growth and water-use efficiency of 10 Triticum aestivum cultivars at different water availability in relation to allocation of biomass. Plant, Cell and Envrionment 20(2): 200-210.

Berry, J, and O. Bjorkman. 1980. Photosynthetic reponse and adaption to temperature in higher plants. Annual Reviews Plant Physiology 31(1): 491-543.

Callaham, R.Z. 1962. Geographic variability in growth of forest trees. In Tree growth (ed. T.T. Kozlowski). The Ronald Press Company, New York. pp 311-325.

Chaves, M.M., J.S. Pereira., J. Maroco., M.L. Rodrigues., C.P.P. Ricardo., M.L. Osorio., I. Carvalho., T. Faria, and C. Pinheiro. 2002. How plants cope with water stress in the field? Photosynthesis and Growth. Annals of Botany 89(7): 907-916.

Dang, Q. 2008. Lecture in Forestry 2330. Lakehead University, 2008.

Domec, J.C. and B.L. Gartner. 2003. Relationship between growth rates and xylem hydraulic characteristics in young, mature and old-growth ponderosa pine trees. Plant, Cell and Environment 26(3): 471-483.

Farooq, M., A. Wahid., N. Kobayashi., D. Fujita, and S.M.A. Basra. 2009. Plant drought stress: effects, mechanisms and management. Sustainable Agriculture 29(1): 185-212.

Gould, P.J., C.A. Harrington and J.B. St. Clair. 2011. Incorporating genetic variation into a model of budburst phenology of coast Douglas-fir (Pseudotsuga menziesii var. menziesii). Canadian Journal of Forest Research. 41(1): 139-150.

Griffin, J.J., T.G. Ranney, and M.D. Pharr. 2004. Heat and drought influence photosynthesis, water relations and soluble carbohydrates of two ecotypes of redbud (Cercis Canadensis). Journal of American Society for Horticultural Science 129(4): 497-502.

Harrington, C.A., P.J. Gould, and J.B. St. Clair. 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. Forest Ecology and Management. 259(4): 798-808.

Howe, G.T., P. Saruul, J. Davis and T.H. Chen. 2000. Quantitative genetics of bud phenology, frost damage, and winter survival in an F_2 family of hybrid poplars. Theoretical and Applied Genetics. 101(4): 632-642.

Junttila, O. 1989. Physiological responses to low temperature. Annals of Forest Science 46:604-613.

Körner, C. 2003. Alpine plant life: functional plant ecology of high mountain ecosystems. Springer-Verlag, Berlin, Heidelberg, and New York. 344 pp.

Kuparinen, A., O. Savolainen and F.M. Schurr. 2010. Increased mortality can promote evolutionary adaptation of forest trees to climate change. Forest Ecology and Management 259(5): 1003-1008.

Lambers, H., Chapin, F.S., and T.L. Pons. 2008. Plant Physiological Ecology. 2nd ed. Springer-Verlag, New York . pp 321-374.

Li, C., A. Vihera-Aarnio, T. Puhakainen, A. Junttila, P. Heino and E.T. Palva. 2003. Ecotype-dependent control of growth, dormancy and freezing tolerance under seasonal changes in Betula pendula Roth. Trees 17(2):127-132.

Lo, Y.H., J.A. Blanco and J.P. Kimmins. 2010. A word of caution when planning forest management using projections of tree species range shifts. The Forestry Chronicle 86(3): 312-316.

Loehle, C. and D. Leblanc. 1996. Model-based assesments of climate change effects on forests: a critical review. Ecological Modelling. 90(1): 1-31.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. Journal of Biogeography 25(4): 735-742.

Magnani, F., M. Mencuccini, and J. Grace. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant, Cell and Environment 23(3): 251-263.

Matyas, C. 1996. Climatic adaption of trees: rediscovering provenance tests. Euphytica 92(1-2): 45-54.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R et al. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12(10): 1969-1976.

Morin, X., Lechowicz, M.J., Augspurger, C., O'Keefes, J., Viner, D and I. Chuine. 2009. Leaf phenology in 22 North American tree species during the 21st century. Global Change Biology. 15(4): 961-975.

McKenney, D.W., J.H. Pedlar., K. Lawrence., K. Campell and M.F. Hutchinson. 2007. Potential Impacts of Climate Change on the Distribution of North American Trees. 57(11): 939-948.

Murray, M.B., M.G.R. Cannell, and R.I. Smith. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. Journal of Applied Ecology. 26(2): 693-700.

Nicotra, A.B., O.K. Atkin., S.P. Bonser., A.M. Davidson., E.J. Finnegan., U. Mathesius., P. Poot., M.D. Purugganan., C.L. Richards., F. Valladares and M. van Kleunen. 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15(12): 684-692.

Ow, L.F., K.L. Griffen., D. Whitehead., S.A. Walcroft, and M.H. Turnbull. 2008. Thermal acclimation of leaf respiration but not photosynthesis in Populus deltoids x nigra. New Phytologist 179(1): 123-134.

Petit, R.J., U.M. Csaikl and S. Bordacs. 2002. Chloroplast DNA variation in European white oaks phylogeography and patterns of diversity based on data from over 2600 populations. Forest Ecology and Management 156(1-3): 5-26.

Rehfeldt, G.E., N.M. Tchebakova., L.I. Milyutin., Y.I. Parfenova., Wykoff, W.R. and N.A. Kouzima. 2003. Assessing population response to climate in Pinus sylvestris and Larix spp. Of Eurasia with climate-transfer models. Eurasian Journal of Forest Research 6(2): 83-98.

Rehfeldt, G. E., N. M. Tchebakova., Y. I. Parfenova., W. R. Wykoff., N.A. Kouzmina, and L. I. Milyutin. 2002. Intraspecific responses to climate in Pinus sylvestris. Global Change Biology 8(9):912–929.

Rehfeldt, G. E., W. R. Wykoff, and C. C. Ying. 2001. Physiologic plasticity, evolution, and impacts of a changing climate on Pinus contorta. Climatic Change 50(3):355–376.

Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse and D.A. Hamilton Jr. 1999. Genetic responses to climate in Pinus contorta: nice breadth, climate change and reforestation. Ecological Monographs 69(3): 375-407.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C and J.A. Pounds. 2003. Fingerprits of global warming on wild animals and plants. Nature 421(6918): 57-60.

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., F. Bokma., R. Garcia-Gil., P. Komulainen and T. Repo. 2004. Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of Pinus sylvestris to climatic changes. 197(1-3): 79-89.

Schenk, J.H. 1996. Modeling the effects of temperature on growth and persistence of tree species: A critical review of tree population models. Ecological Modeling. 92(1): 1-32.

Schwartz, M.D. and J.M. Hanes. 2009. Short Communication Continental-scale phenology: warming and chilling. International Journal of Climatology. 30(11): 1595-1598.

Svenning., J.C. and F. Skov. 2004. Limited filling of the potential range in European tree species. Ecolgoy Letters 7(7): 565-573.

Tyree, M.T. 2003. The ascent of water. Nature. 423:923.

Vitasse, Y., S. Delzon, C. Bresson, R. Michalet and A. Kremer. 2009A. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Canadian Journal of Forest Research 39(7): 1259-1269.

Chapter III

PHENOLOGICAL RESPONSES OF WHITE BIRCH POPULATIONS IN COMMON GARDEN STUDY

3.0 INTRODUCTION

Phenology can be defined as the study of seasonal plant and animal life cycles, which are driven by environmental changes. For this reason phenology is largely considered the simplest process in which we track changes in the ecology of plant and animal species in response to ongoing changes in seasonal weather. Changes in phenological events are responsive to temperature and have been documented among the first responses to climate change (Root et al. 2003; Menzel et al. 2006). Phenological events include bud flush, bud cessation, flowering, leaf colouring and leaf fall.

Several phenological studies have concluded that there are important effects as a result of warming, such as the onset of spring becoming more advanced, with autumn senescence becoming delayed across mid-latitude temperate climates (Schwartz and Hanes 2009). Warming temperatures result in a “dual phase” influence on the timing of growth. This refers to the effects of warmer temperatures and the required temperature accumulations that trigger bud set and bud flush. Past studies indicate the possibility of a delay in budburst (Blum 1987; Murray 1989), as opposed to the comment notion of advancement in phenology. Recently, Morin et al. (2009) found that abnormal leaf unfolding occurred predominately within the southern range of species, with less advancement or delay. It is for these reasons that the following phenological events will be explored: i) bud break (flush) timing; ii) bud set timing (cessation of growth) and iii) leaf yellowing.

Growth cessation is defined as the time to which the tree stops growing. The timing is simply an adaptation to the length of the growing season and is temporally related with bud set in the fall. Growing season length can be measured as the temperature sum of days that are above 5°C (Savolainen et al. 2004). Interestingly, Kuparinen et al. (2010), states that the number of growing degree-days has the potential to increase by approximately 50 GDDs by the end of the century. Photoperiod has also been found to have a large influence, if not control both the initiation and cessation of growth (Clausen 1968). This is based on the knowledge that plants are known to measure day length, and adjust accordingly with photoperiodic reactions (Savolainen et al. 2004).

More specifically Li et al. (2003) explored the significance of short day photoperiod and found that it initiated growth cessation, dormancy development and induced cold acclimation. They found that the northern ecotypes of silver birch were more responsive to seasonal changes, which resulted in earlier growth cessation, cold acclimation and dormancy development in autumn. It is expected that populations from further north (higher latitude) will cease growing first, with populations from continental climates and shorter growing seasons achieving bud cessation before those originating from maritime climates (Matyas, 1996).

Before shoot growth can resume in the spring, plants must undergo endodormancy, which develops in the fall and is defined as sustained exposure to low, near-freezing temperatures (Howe et al. 2000). It is the combination of chilling units (CU) and forcing units (FU) that allow budburst to occur, with the requirement of chilling units ensuring budburst does not occur during periods of favorable weather before risk of frost damage has passed (Gould et al. 2011). There are several models that use this concept to determine budburst, with the unified model comprising of three components: (i) response functions for the effects of temperature on bud dormancy, (ii) the period when temperature is significant and (iii) the threshold to which budburst occurs. The threshold is the combination of CU and FU resulting in budburst, which has been termed the possibility line by Harrington et al. (2010). Although it is known that different species have different requirements, little research has focused on the differences among populations within a species (Morin et al. 2008). Gould et al. (2011) tested for genetic variation among populations and only found a small difference for the required FU based on an 80% range shift. They found that the average difference for budburst was 8 and 16 days in each trial. Previous studies indicate that this is normal when studying coniferous species (Douglass-fir), nevertheless this study is concerned with white birch in particular.

Bud set is temporally associated with the cessation of shoot elongation in the fall, while bud flush signals the start of shoot elongation in the spring, which indicates endodormancy release. Genotypes from northern areas and high elevations are adapted to shorter growing seasons, and tend to stop growing and set bud earlier in the fall. This has been proven by a number of population trials (Howe et al. 2000). Bud flush has been found to be more complex, but typically populations from more northern, higher elevation and more continental regions will break bud earlier in a common garden study

(Morgenstern 1996; Howe et al. 2006). The likely explanation for this is that populations are molded by natural selection from their origin. As previously mentioned the number of growing degree days are likely to increase under climate change scenario, which would have the ability to change the timing of budburst, which is a key factor in forecasting climate-change impacts on an ecosystem (Gould et al. 2011). Locally adapted populations may become outcompeted by southern populations. Low temperatures and short day photoperiod influence bud set, while bud flush is primarily influenced by temperature (Junttila 1989).

3.1 Study Objectives

The objective of this study was to investigate the phenological responses of white birch populations in a new environment, through quantitative and visual assessment of physiological and morphological traits. Populations were selected from a wide range of environmental gradients were studied across the North American boreal forest. The hypothesis was that populations from more northern areas would exhibit initiation of the various phenological stages earlier than those from southern origins.

3.2 MATERIALS AND METHODS

Seed Source & Study Area

The experimental trial site was established in 2008 at the 25th Side Road in Thunder Bay, Ontario. White birch seeds were collected from various locations in several provinces, representing different site conditions (Table 1.1). Seed collection took place in British Columbia, Saskatchewan, New Brunswick, Quebec, Newfoundland and Labrador, Nova Scotia, Prince Edward Island and several locations in Ontario. The trial site was established to form a common garden experiment, allowing for the study of genetic variation. Refer to Chapter I for Table 1.1 showing each population and Figure 1.1 displaying the locations of each population and common garden study location.

Experimental Design

The seeds were germinated in the greenhouse at Lakehead University for 12 weeks, before field planting. The planting site is located at 48°21’ N, 89°23’ W, with an elevation of 183 meters. The site has a mean temperature of -14.8°C in January, while the mean July temperature is 17.6°C, with an annual precipitation of 711.16 mm and 1433.6 growing degree day above 5°C. The site was fenced and received site preparation in the form of some weed, stump and course woody debris removal. The experiment was established as a completely randomized design (CRD), with a spacing of 1.5 m x 1.5 m. Each row consisted of eleven seedlings, with a total of three replicate rows for each of the 26 populations. Extra rows were planted for particular populations when the trial site was established. The layout of the trial site may be found in APPDENDIX.

Bud Flush

Timing of bud flush was recorded when the first fully unfolded leaf was observed. The number of growing degree days (at daily mean temperature greater than 5°C) to bud flush was determined from the 31st of December. This is a common practice and has been cited by many authors such as Howe et al (2000) and Li et al (2003). Observations were broken down into several stages from winter bud dormancy until a leaf has fully unfolded. The intermediate stages were bud swell and bud-burst. This design is similar to that used by Vitasse et al. (2009b). The observations were conducted on individual trees at a two to four days interval by the same observer depending on weather conditions influencing the progression of bud flush in the spring. Leaf unfolding date was documented on the basis of 50% of the buds having reached the threshold of bud flush.

Bud Cessation & Leaf Yellowing

Bud set measurements began in the first week of September and were measured every 3 to 5 days. Measurements ceased when at least 50% bud cessation had been reached on an individual tree basis. This required the stipules of the foliage leaves to cover the shoot apex and the youngest foliage leaf to be offset from the central axis of the shoot apex. In the rare case that a bud resumed growth, the first date of bud set was to be used for analysis. It is plausible to assume that some trees were likely to be damaged or killed as a result of failing to set bud quickly enough at the end of a growing season. Howe et al (2000) used the day to which the frost killed the tree as the bud set date. This likely causes a slight bias downward. Recorded alongside cessation of growth was leaf yellowing in the autumn. Leaf senescence was monitored approximately every four days. Observations included leaf yellowing, with percentages yellow leaves being recorded. Leaf senescence date was considered to be reached when approximately 50% of the leaves were missing or have changed colour (Vitasse et al. 2009B).

Statistical Analysis

One-way analysis of variance was utilized to test for significant differences among the three measured responses (bud flush date, bud set date and leaf yellowing) among the 21 white birch populations. Julian days were used when computing analysis of variance. Refer to Chapter II section 2.2 for details on one-way analysis of variance.

Pearson's Correlation Coefficient

The Pearson correlation coefficient was utilized to explore relationships between the six measured responses of the 21 white birch populations. The 'simple correlation coefficient' may be calculated as:

$$r = \frac{\Sigma xy}{\sqrt{(\Sigma x^2 \Sigma y^2)}}$$

The letter 'r' represents the correlation coefficient between variables x and y, which is used to determine if there is a positive, negative or no relation between the two variables at a given confidence interval. The variables included height growth, RCD growth, survival (%), bud flush date, bud set date and leaf yellowing (%).

RESULTS

Bud flash date differed significantly among populations (Table 3.1). Graphical representation was used to overlay the average bud flush date (y-axis) for each population (x-axis) against the number of growing degree days (GDD) (>= 5°C) (z-axis; red line) (Figure 3.1). Growing degree days (GDD) was computed utilizing a threshold value of 5°C, to determine the number of GDD up to the date of bud flush. The average number of Julian days to reach bud flush was 117 days, which is the equivalent of 143 GDD. The population to reach bud flush the earliest was BC SKIM at an average of 138 Julian days (78 GDD). The population that flushed the slowest was ON550, with an average Julian date of 148 (134 GDD), while the average was 117 Julian days and 143 GDD.

Table 3.1. One-way ANOVA results for bud flush, bud set and leaf yellowing among the 21 white birch populations.

Factor		Sum of Squares	df	Mean Square	F	Sig.
Bud Flush	Between Groups	2945.427	20	147.271	34.253	<.0001
	Within Groups	2132.542	496	4.299		
	Total	5077.969	516			
Bud Set	Between Groups	2066.390	20	103.319	6.961	<.0001
	Within Groups	6916.937	466	14.843		
	Total	8983.326	486			
Leaf Yellowing	Between Groups	1323.165	20	66.158	5.782	<.0001
	Within Groups	1086.952	95	11.442		
	Total	2410.117	115			

Populations originating from locations with a greater MTWM (°C) and a milder MTCM (°C), reached bud flush earlier than those from locations which had either cooler summers or colder winters. Latitude and elevation did not show a clear trend. Populations in this study at times came from higher latitudes and or elevations, yet had warmer and milder winters than populations from lower latitudes and elevations.

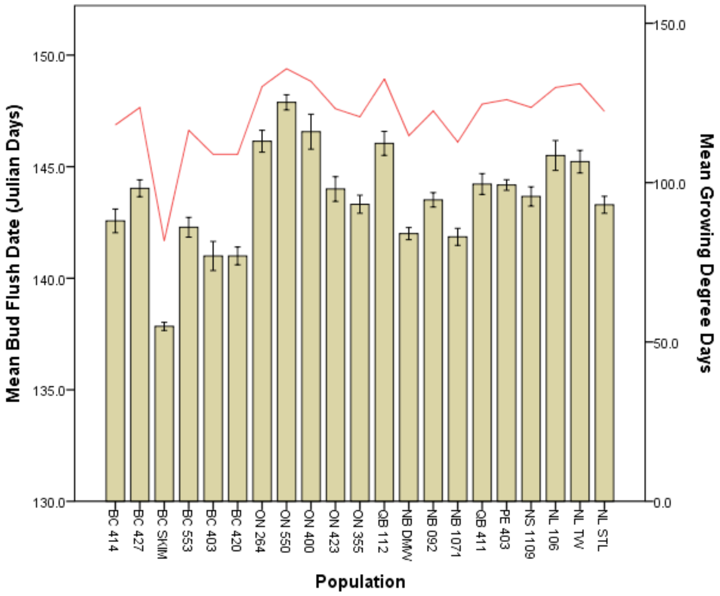


Figure 3.1. Mean bud flush date & growing degree days (red line) for the 21 populations with standard error (+/- 1 SE).

One-way ANOVA results indicate a significant difference in the number of Julian days required to achieve bud cessation (Table 3.1). Graphical representation (Figure 3.2) displays the mean number of Julian day to reach bud set on the y-axis, while the z-axis (represented by the red line) shows the number of Julian days between the date of bud flush until bud set, representing the length of individual growing season for the population in question.

The mean number of Julian days required to reach cessation was 268 Julian days and 125 GDD (Figure 3.2). BC SKIM setting the earliest at an average Julian date of approximately 265 days (127 GDD). The population to set the latest was QB 112 at approximately 273 days (127 GDD). As expected, populations from higher latitudes reached bud set earlier, with mid to lower latitudes varying. This is likely a result of photoperiod, with populations adjusting to photoperiod length. However, lower latitude and maritime populations did not show the pattern suggested by Matyas (1996, 2002). In fact NB 092 was the fourth population to reach growth cessation.

There was a slight trend between growth cessation and both MTWM (°C) and MTCM (°C). Populations originating from warmer climates tended to reach cessation earlier than those from colder climates. Interestingly, QB 112 has a warm summer temperature and a colder MWCM (°C), and reach cessation last among the 21 populations. BC 414 and BC 427 each originate from higher latitudes and reached cessation quickly, conforming to the notion that higher latitudes will reach cessation earlier in a common garden study.

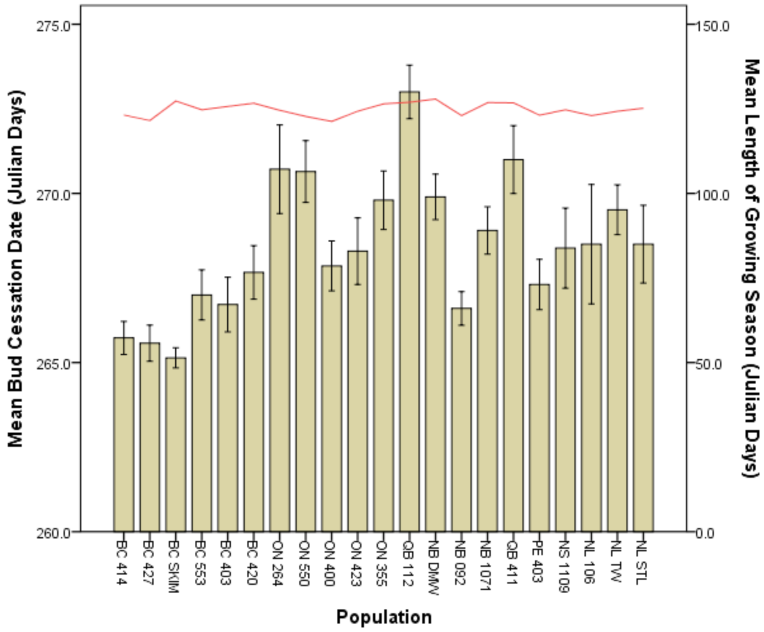


Figure 3.2. Mean bud cessation date & length of growing season for the 21 populations with standard error (+/- 1 SE).

One-way analysis of variance indicates that there is a significant difference in the number of Julian days required to reach completion of leaf yellowing. This is indicated by the p-value, which is less than 0.05, with a value of 0.00 (Table 3.1). The graphical representation is a bar chart of the data, including error term bars as seen below in Figure 3.3.

Leaf yellowing showed a large amount of variation among each population. NL 106 achieved complete leaf yellowing on an average Julian date of approximately 269. Populations BC SKIM and NB 1071 took until approximately Julian day 280, while BC 553 and NL STL took until Julian day 278 respectively. Leaf yellowing did not show a definite pattern regarding geographic location, elevation or temperature.

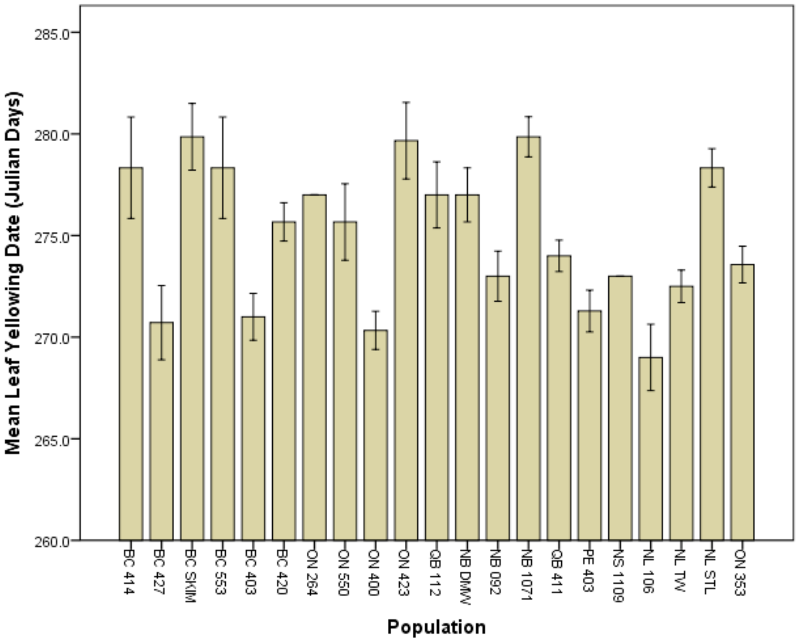


Figure 3.3. Mean Julian date for 100% leaf yellowing among the 21 populations with standard error (+/- 1 SE).

<u>Correlation between observed traits of the white birch populations</u>

Pearson's correlation was utilized to identify potential relationships between the growth traits measured in Chapter 2 and the phenological traits measured in Chapter 3. Identifying these relationships, aids in explaining general trends within the populations, while bringing the two chapters together. Pearson's correlation indicated one significant relationship at the 95% confidence interval and three at the 90% confidence interval (Table 3.2).

Table 3.2. Pearson's Correlation results for phenological and growth traits representing the 21 white birch populations.

Pearson Correlation (PC)		Height Growth	RCD Growth	Survival (%)	Bud Flush Date	Bud Set Date	Season Length	Leaf Yellowing Date
Height Growth	PC							
	Sig.							
RCD Growth	PC	.865**						
	Sig.	.000						
Survival (%)	PC	.828**	.660**					
	Sig.	.000	.001					
Bud Flush Date	PC	-.735**	-.693**	-.539*				
	Sig.	.000	.001	.012				
Bud Set Date	PC	-.171	-.309	.013	.415			
	Sig.	.459	.172	.956	.061			
Season Length	PC	.568**	.407	.537*	-.614**	.463*		
	Sig.	.007	.067	.012	.003	.034		
Leaf Yellowing Date	PC	.443*	.322	.590**	-.257	.152	.382	
	Sig.	.044	.155	.005	.260	.512	.087	

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

The first relationship between height growth and leaf yellowing date suggests greater height growth results in later leaf yellowing. Height growth is also positively correlated with season length, suggesting that greater height growth is in part a result of a longer growing season, which is in line with later leaf yellowing. Both height and RCD growth had a negative significant relationship with bud flush. This suggests that an earlier bud flush date results in larger amounts of growth (Figure 3.4). An earlier bud flushing date has the potential to lengthen a trees growing season, allowing for more time to accumulate height and RCD growth. Neither growth parameter was found to be significantly related to bud set date. However, since growth traits had significant relationships to season length and leaf yellowing date, it is reasonable to assume there is some significance since season length and leaf yellowing is directly related to bud set.

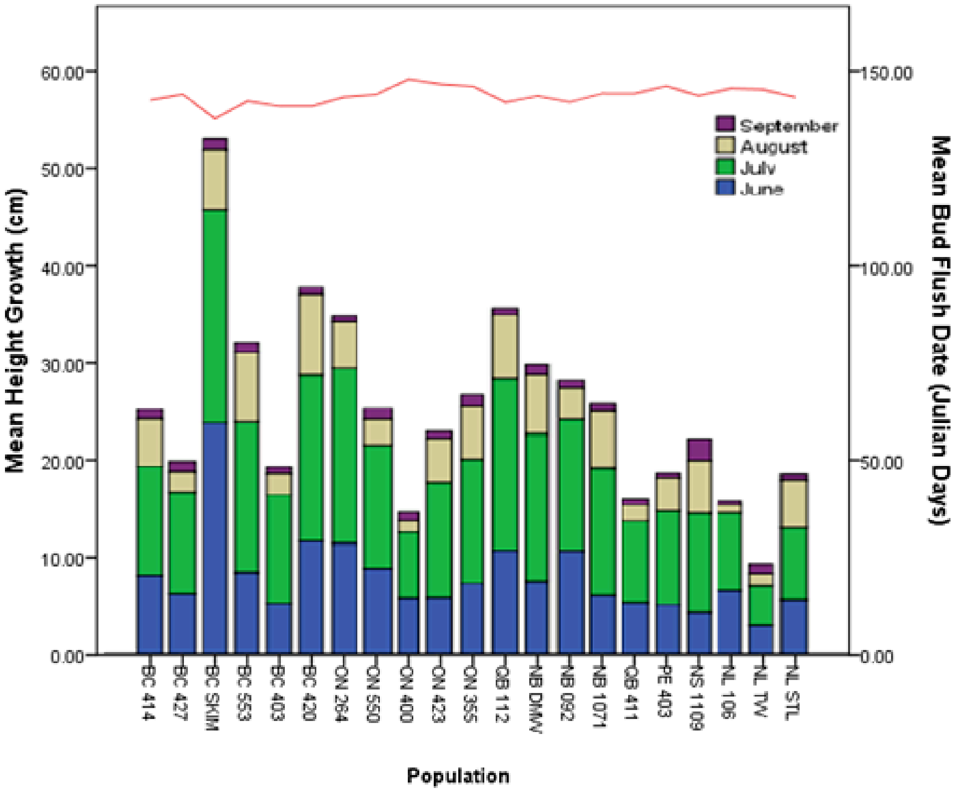


Figure 3.4. Association between mean height growth (cm) and mean bud flush date (Julian date; red line) for each of the white birch populations.

3.4 DISCUSSION

Significant differences were found among the 21 populations, which are directly attributed to the origin of the seed. The shifts each population experienced in regards to climate (primarily temperature) reflect previous studies which suggest phenological events are highly influenced by temperature, because they regulate the timing of growth, directly influencing fitness.

The maximum difference in date of bud flush between populations in the trial was ten Julian days or 56 growing degree days, using 5°C as the threshold value. The maximum difference within a population was 13 Julian days with the shortest being four

Julian days. Interannual studies have reported variation in date of budburst by up to ten days for given populations, over a study period of six years (Rousi and Pusenius 2005). Repeated measures of this study would be ideal to make comparisons to other studies.

It appears that the main controlling factor for bud flush was growing degree days accumulated leading up to bud break, which is a function of temperature. Populations requiring fewer growing degree days in Thunder Bay to achieve bud flush originated from areas with warmer annual temperatures and often greater number of growing degree days. Utilizing growing degree days is equivalent to using heat sum accumulation. Heat sum also requires a threshold value to be utilized and relies on spring temperatures being more influential than the possible effects of autumn temperatures. Juntilla et al. (2003) shows that warm spring conditions were a primary driver for bud flush.

The findings indicate that there was a significant difference in bud flush date among different white birch populations, indicating differences in the temperature requirement to reach bud flush (Table 3.1, Figure 3.1). The variation is the expression of each population’s genetic footprint as a result of local adaptation. The maximum difference of 13 days is rather large; however Rousi and Pusenius (2005) had a maximum difference of 15 days, utilizing European white birch from southern Finland in two studies. Caution is required when interpreting a study presenting observations on a short time-scale, however the results did indicate a strong phenotypic relationship determining bud burst, which allows for variable responses among white birch population to changes in environmental temperature.

The relationship between height growth and bud flush date, was found to be fairly strong, indicating an earlier date of bud break would result in greater height growth (Table 3.2). The pattern is clear (Figure 3.4) indicating populations with larger monthly and total height growth gains tended to flush with fewer total growing degree days. The second best predictor of growth was found to be growing season length at population origin (Table 3.2). This pattern applied to RCD as well.

Populations with earlier flushing were often those from higher elevations, latitudes and warmer climates (BC SKIM, BC 403, BC 420, QB 112 and BC 553). These results coincide in part to Li et al. (2003), who found that northern Betula ecotypes had earlier bud flush and growth initiation in the spring. This is because northern ecotypes often require a shorter amount of chilling in order to obtain complete bud burst, however extended periods may lead to a reduction in time to achieve bud burst (Heide 1993, Junttila et al. 2003). The three fastest flushing populations in this study originated from locations with milder winters compared to Thunder Bay. This suggests cooler autumn and winter temperatures allowed them to satisfy their required chilling units earlier than other populations and their origin location. It is likely the combination of genetic variation as a result of adaptation to origin climate and an earlier accumulation of chilling units (CU) that allowed these particular populations to respond to warming spring temperatures and accumulate the necessary amount of forcing units.

Chilling and forcing units are a unique combination for each population, to ensure optimal flushing to avoid environmental damage (Gould et al. 2011). The accumulation of these units has been altered as a result of an altered climate. Populations achieving flushing earlier than they normally would, become more susceptible to early spring frost damage. Any damage sustained will hinder the growth of the tree, potentially causing mortality depending on the severity of the damage. If accumulation of each unit causes bud flush to occur later into the spring, the population risks a shorter growing season, or extending late into the season risking frost damage as a result of lowering autumn temperatures.

Maximum variation within bud set in this study was approximately seven Julian days, with populations taking between five and seventeen days once cessation commenced. Generally, it is believed that this variation is caused by the phenotypic response of each population to lower temperatures in late summer to early fall and changes in short day photoperiod. The variation in the trial is misleading since QB 112 took nearly two days longer than any other population, causing the range to appear much larger. Despite variation observed within bud set date, it was not statistically significant regarding tree height and RCD growth. There was a slightly negative relationship with height and RCD growth; indicating earlier cessation would cause less growth. It is thus concluded that bud flush was the best predictor of growth (Table 3.2), while the main influence on season length was bud set, since it was significant at 95% confidence, while bud flush was only significant at 90%. These results were in agreement with the conclusions by Rousi and Pusenius (2005).

Since growth cessation is assumed to be a result of photoperiodic responses to changes in day length (Junttila 1989; Thomas and Vince-Prue 1997) and or a result of accumulated heat (Sarvas 1974), Savolainen et al. (2004) questioned whether it mattered if light or temperature had the greater influence. The argument is that current day lengths in more northern locations are longer than that of southern and lower latitude locations, while temperatures in southern locations are thought to be what northern locations will become. Li et al. (2003) found that for Betula pendula Roth, that short day photoperiod initiated growth cessation and dormancy development in all the ecotypes present. Studies utilizing Betula seedlings have found that the rate of dormancy and depth of the dormancy period influenced by higher temperatures during shortening photoperiods as opposed to lower temperatures (Junttila et al. 2003; Heide 2003).

Leaf yellowing was found to vary significantly among the populations, displaying a significant relation with only height growth (Table 3.2) with an r value of .443 significant at 95%. Jensen and Hansen (2008) found no statistically significant relationship between yellowing and growth; however they noted that populations that yellowed later in the season tended to have higher amounts of growth. Populations to show leaf yellowing first tended to be from lower to mid-latitudes, with higher latitude populations showing more of a delay. The strong relationship with growth is logical, since well-timed senescence contributes to optimal offspring production and overall survival within a species niche (Lim et al. 2007).

The other findings of this study indicated that populations from higher latitudes and elevations began growth cessation earlier in the season. Drought and extreme temperature (Lim et al. 2007) are two abiotic factors that have an effect of leaf senescence other than then integrated response of leaf cells in relation to age and various other internal and environmental signals. However, there was no clear pattern between annual precipitation and temperature among the populations. Therefore, it is likely local adaptation that has resulted in each population expressing leaf senescence at varying points in time.

This study produced similar results as the physical growth study, regarding which populations performed best. It appears that the most influential predictor for height and RCD is bud flush (-0.735 and -0.693), which has an influence to growing season length. Given that some reviews suggest spring phenological events are to increase by upwards of 2.3 days per decade and 2.5 days for each unit increase in degrees Celcius (Menzel et al. 2006), further studies utilizing study sites with a warmer climate would be useful. Also, the inclusion of several more populations from colder climates would be helpful, in determining if climates as cold as northern Ontario are perhaps not optimum for white birch.

REFERENCES

Blum, B. 1988. Variation in the phenology of bud flushing in white and red spruce. Canadian Journal of Forest Research. 18(3): 313-319.

Gould, P.J., C.A. Harrington and J.B. St. Clair. 2011. Incorporating genetic variation into a model of budburst phenology of coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Canadian Journal of Forest Research. 41(1): 139-150.

Harrington, C.A., P.J. Gould, and J.B. St. Clair. 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. Forest Ecology and Management. 259(4): 798-808.

Heide., O.M. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. Physiologia Plantarum 88(4): 531-540.

Howe, G.T., P. Saruul, J. Davis and T.H. Chen. 2000. Quantitative genetics of bud phenology, frost damage, and winter survival in an F_2 family of hybrid poplars. Theoretical and Applied Genetics. 101(4): 632-642.

IPCC. 2007a. Climate change 2007: impacts, adaptation, and vulnerability, Chapter 1. Assesment of Observed Changes and Responses in Natural and Managed Systems. IPCC Secretariate. Geneva, Switzerland. http://www.ipcc.ch/pdf/assessment-report/ar4/wg2/ar4-wg2-chapter1.pdf

Jensen, J.S., and J.K. Hansen. 2008. Geographical variation in phenology of Quercus petrae (Matt.) Liebl and Quercus robur L. oak grown in a greenhouse. Scandinavian Journal of Forest Research 23(2): 179-188.

Junttila, O. 1989. Physiological responses to low temperature. Annals of Forest Science 46(Supplement):604-613.

Junttila., O. J. Nilsen and B. Igeland. 2003. Effect of temperature on the induction of bud dormancy in ecotypes of betula pubescens and Betula pendula. Scandinavian Journal of Forest Research 18(3): 208-217.

Kuparinen, A., O. Savolainen and F.M. Schurr. 2010. Increased mortality can promote evolutionary adaptation of forest trees to climate change. Forest Ecology and Management. 259(5): 1003-1008.

Li, C., A. Vihera-Aarnio, T. Puhakainen, A. Junttila, P. Heino and E.T. Palva. 2003. Ecotype-dependent control of growth, dormancy and freezing tolerance under seasonal changes in Betula pendula Roth. Trees 17(2):127-132.

Lim, P.O., H.J. Kim and H.G. Nam. 2007. Leaf Senescence. The Annual Review of Plant Biology 58(1): 115-136.

Menzel, A., T. Sparks., N. Estrella., E. Kock., A. Aasa et al. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12(10): 1969–1976.

Morgenstern, E.K. 1996. Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. UBC Press, University of British Columbia, Vancouver, B.C.

Morin, X., Lechowicz, M.J., Augspurger, C., O'Keefes, J., Viner, D and I. Chuine. 2009. Leaf phenology in 22 North American tree species during the 21st century. Global Change Biology. 15(4): 961-975.

Morin, X., Viner, D., and I. Chuine. 2008. Tree species range shifts at a continental scale: new predictive insights from a process based model. Journal of Ecology. 96(4): 784-794.

Murray, M.B., M.G.R. Cannell, and R.I. Smith. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. Journal of Applied Ecology. 26(2): 693-700.

Rousi., M and J. Pusenius. 2005. Variations in phenology and growth of European white birch (*Betula pendula*) clones. Tree Physiology 25(2): 201-210.

Sarvas, R. 1974. Investigations on the annual cycle of development of forest trees. II. Autumn and winter dormancy. Communicationes Instituti Forestalis Fenniae. 84(1): 1-101.

Savolainen, O., F. Bokma., R. Garcia-Gil., P. Komulainen and T. Repo. 2004. Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of Pinus sylvestris to climatic changes. 197(1-3): 79-89.

Schwartz, M.D. and J.M. Hanes. 2009. Short Communication Continental-scale phenology: warming and chilling. International Journal of Climatology. 30(11): 1595-1598.

Thomas, B. and D. Vince-Prue. 1997. Photoperiodism in Plants. Second Edition. Academic Press, New York.

Vitasse, Y., S. Delzon, C. Bresson, R. Michalet and A. Kremer. 2009A. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Canadian Journal of Forest Research. 39(7): 1259-1269.

Vitasse, Y., S. Delzon, E. Dufrene, J-Y. Pontailler, J-M. Louvet, A. Kremer and R. Michalet. 2009b. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? Agricultural and Forest Meteorology 149(5): 735-744.

CHAPTER IV

DETERMINING COMMUNALITIES BETWEEN WHITE BIRCH POPULATIONS

4.0 INTRODUCTION

There are indications that climate change has already had an impact on species geographical distributions (Parmesan, 1996; Walther et al. 2002). Possible shifts in distribution suggest that some populations may become hindered by occupying areas not ideal for optimal growth and survival (maladapted) (Hampe, 2004; Rehfeldt et al., 2003). Assisted migration of tree species and or populations has been proposed and discussed as a potential forest management option to combat climate change (i.e. maintain productivity and biodiversity) (Rehfeldt et al., 1999; O'Neil et al., 2008). Although it has been documented that some species have accommodated rapid climate change in the past (Pitelka et al., 1997; Kullman,1998), it is likely that without human intervention (assisted migration) many species will not survive as a result of not being able to migrate toward higher latitudes and altitudes at an adequate pace (Malcom et al., 2002; Aitken et al., 2008; Hoegh-Guldberg et al., 2008).

There are many predictive modeling options to aid in forecasting future distributions of species in response to changes in climate. Some of the options available in the field of modeling range from dynamic ecosystem and biogeochemistry models (Woodward and Beerling, 1997), spatially explicit mechanistic models (Hill et al., 2001), physiologically based (Walther et al., 2005) and correlative bioclimatic envelope models (Box et al., 1993; Huntley, 1995; Thuiller, 2003). Genearlized linear models

(GLMs) and generalized additive models (GAMs) are two other options, which provide a good tool for handling non-linear datasets, and were considered for use within this synthesis.

A common criticism thrust upon predictive models is that there are many other factors other than climate that can have a significant effect on species distributions and the rate of spatial changes predicted across the given landscape (Hampe, 2004). Heikkinen et al. (2006), states that models must account for genetic variation in populations from different areas with its naturally occurring range, species dispersal and changes in biotic interactions. These limitations, among others suggest that tree species may react differently (due to plasticity and genetic adaptation) to the same climatic changes due to geographic location (Lo et al., 2010; Rehfeldt et al. 1999, 2001, 2002).

Populations of tree species become locally adapted to their environmental conditions over time. This can lead to a population having a lower plasticity, which may be defined as a genotype's capacity to render varying phenotypes under a range of environmental conditions (Garzon et al., 2011). Over time as there are changes to environmental conditions, evolutionary processes such as selection, migration, mutation and drift, will dictate the distribution of genotypes by placing them in areas to which they are best suited to optimize fitness (Rehfeldt et al., 2001). A lack of plasticity may introduce a scenario of mal-adaptation or extinction.

Principal component analysis and simple linear regressions were utilized to explore the relation between the growth and phenological observations and the differences between each population as a whole. This will allow insight into how they are grouped together despite originating from different locations. This will create a scale to which it may be suggested which populations are best to trans-locate to northwestern Ontario. This approach was utilized because more complex options such as GLMs and GAMs require data sets much larger than this study in order to construct the model and to verify the model. For this reason any conclusions are to be taken on a smaller scale in context to this study.

The white birch populations collected for the study are from a range of environments, thus bringing varying phenotypic responses with them. This chapter is not to study each factor effecting growth specifically; however it is to denote the differences in growth and to discern the possibilities of these differences. However, there are studies that have explored some of the aforementioned characteristics individually.

4.1 STUDY OBJECTIVES

The main objective focuses on the underlying factors influencing the 'success' of the white birch populations within the trial. The two main components of this study were (i) the influence of climatic factors (origin and study climate) affecting the growth and success of each population and (ii) the suitability of transferring populations to new climates. This study provides insight into a wide gradient of conditions to which white birch persist, providing insight into the variability and adaptability of white birch populations.

4.2 MATERIALS AND METHODS

Principal component analysis is a multiple step process requiring the data to be adjusted by subtracting the mean from each dimension. Then the covariance is calculated, followed by eigenvectors and eigenvalues, which are utilized to determine the number of components to be attained. Principal component analysis was completed utilizing SSPS (2011). Each population represents an independent variable, with their responses from the previous chapter representing the dependent variable.

Three basic principal component analyses were conducted. The first utilizes the six responses from Chapter 2 and 3, while the second PCA utilizes a combination of the six responses and the origin geographic and climatic data to reflect each population.

4.3 RESULTS

Six inputs were utilized with principal component analysis, retaining two principal components, reflecting the growth parameters (Table 4.1 and Figure 4.1). Combined, the two components explain 80.1% of the total variation within the data, with PC1 accounting for 52.7% and PC2 accounting for 27.4% of the variation. Survival, height and RCD growth had a strong and positive loading on PC1, while bud flush had a strong negative loading. Bud set and bud flush had a strong positive loading on PC2, while the other factors had minimal loading.

Table 4.1. Principal component variable loadings for the six measured traits for each white birch population with the varimax rotation.

Variable	PC1	PC2
Height Growth	.899	-.314
RCD Growth	.738	-.513
Survival	.919	-.010
Bud Flush	-.636	.604
Bud Set	.054	.892
Leaf Yellow	.747	.351

Principal component 1 is best interpreted as a representative of fitness. As previously stated survival is a common expression of fitness, with growth factors being an appropriate alternative. Principal component 2 is best interpreted as season length or growing season. An earlier bud flushing date or bud cessation date directly relates to the length of growing season, which will impact variables such as growth.

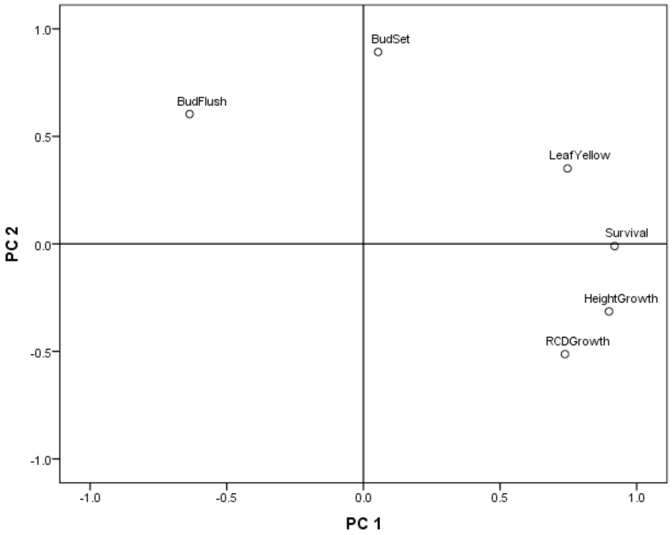


Figure 4.1. Principal component loading plot for PC1 (fitness) and PC2 (growing season) for the 21 white birch populations.

Two principal components were extracted when testing the relationship between the 21 populations of white birch. The first principal component (PC 1) accounted for 24.2% of the variation among the populations, while principal component two (PC 2) accounted for 16.61% of the variation, with the loadings of each variable below (Table

4.2). These are the loadings utilizing the varimax rotation in SPSS. PC 1 displayed strong positive and negative loadings for populations' origination from Ontario and British Columbia. PC 2 displayed strong positive and negative correlations to populations from British Columbia and Quebec. Several populations comprised of a cluster showing weak to moderate positive and negative correlations to PC 1 and weak to moderate negative correlations to PC2 (Figure 4.2).

Table 4.2. Principal component variable loadings for the 21 white birch populations reflecting the response data utilizing the varimax rotation.

Rotated Component Matrix	Principal Component	
	PC 1	PC 2
BC 414	0.13	0.795
BC 427	-0.039	-0.271
BC SKIM	0.044	-0.403
BC 553	0.555	-0.211
BC 403	-0.826	-0.23
BC 420	0.746	0.052
ON 264	0.602	0.571
ON 550	0.77	0.087
ON 400	-0.891	-0.13
ON 423	0.816	0.143
ON 355	-0.205	-0.113
QB 112	-0.023	-0.525
NB DMW	-0.194	-0.261
NB 092	-0.041	-0.293
NB 1071	-0.073	-0.306
QB 411	0.455	0.725
PE 403	0.178	-0.304
NS 1109	0.449	0.727
NL 106	-0.53	0.299
NL TW	0.116	-0.249
NL STL	0.525	0.561

PC 1 shows influences from survival; however it is not possible to discern any particular pattern. PC 2 appears to be influenced marginally by various factors and therefore it is difficult to indicate on particular factor (Figure 4.2). However, it is clear that there are several driving factors influencing the responses of each population.

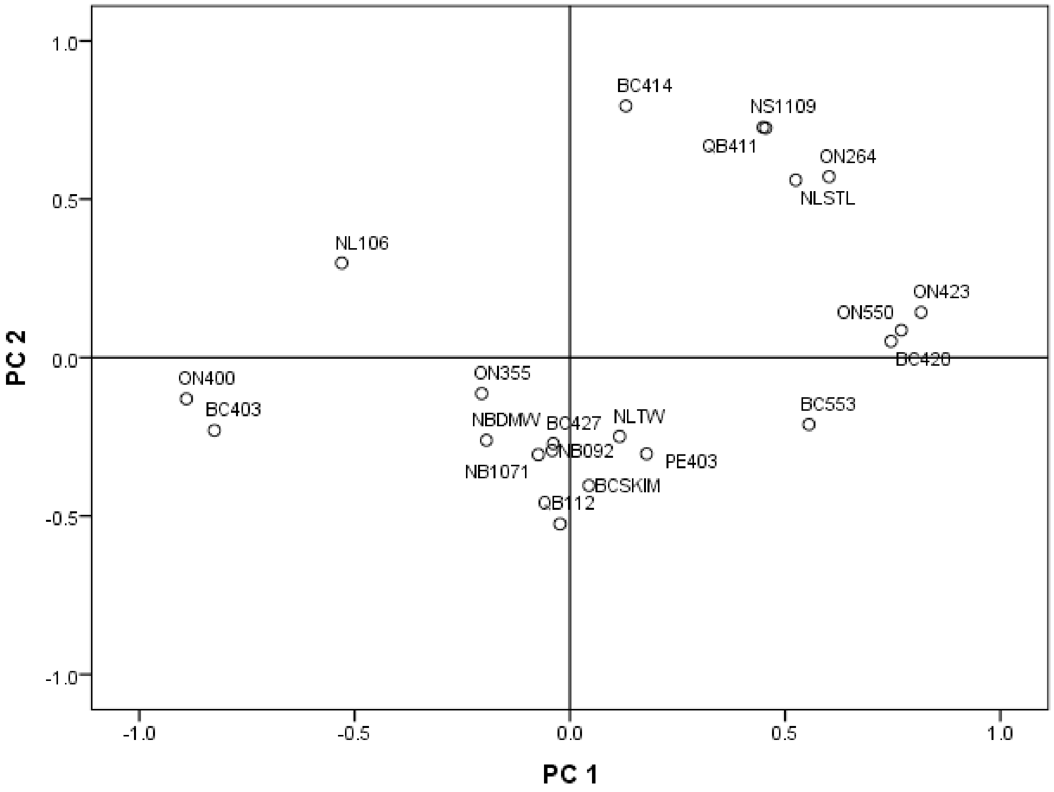


Figure 4.2. Principal component load plots derived from the 21 white birch populations utilizing the varimax rotation.

4.4 DISCUSSION

Predictive models are useful tools for exploring possible impacts of climatic changes on the distribution and success of tree species. Models require large amounts of data to carry out and therefore, are not always feasible. Principal component analysis allows for cursory analysis and prediction by identifying the variance within the data.

The 21 white birch populations represent a wide range of habitat characteristics and displayed variation among tested responses.

Principal component analysis grouped populations into clusters that are intended to be similar, however not all groupings were easily explained, indicating variation within populations not explained in this simple ordination. Although each analysis grouped responses and or populations differently, neither definitively indicates superior growth or survival. Each principal component only explained partial amounts of the variation with the data set. Originally, based on eigenvalues upwards to seven components were to be extracted. Therefore, reducing the number of components down to two makes it difficult to identify clear trends since nearly sixty percent of the variation is not being displayed. It also may be possible that mixed results such as this are a result of white birch being a generalist species, capable of adapting to different situations.

It is believed that temperature continues to be one of the main predictors with the balance between moisture and growing degree days playing an underlying role. However, the mixed results using PCA make it unclear whether the results are due to high amounts of variation between each population or if other factors not utilized in this study are having a significant impact. The final possibility is that each population falls under different ecosite classification zones across Canada. It is possible that analyzing the data on a broader scale such as that, that a clearer pattern would emerge.

REFERENCES

Aitken, S.N., S. Yeahman, J.A. Holliday, T. Wang and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutional Applications. 1(): 95-111.

Box, E.O. 1981. Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography. Dr. W. Junk Publishers, The Hague, Netherlands, 272 pp.

Garzon, M.B., R. Alia, T.M. Robson and M.A. Zavala. 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. Global Ecology and Biogeography. 20(5): 766-778.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeography.

Heikkinen, R.K., M. Luoto, M.B. Araujo, R. Virkkala, W. Thiller and M.T. Sykes. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30(6): 1-27.

Hoegh-Guldberg, O., L. Hughes., S. McIntyre., D.B. Lindenmayer., C. Parmesan., H.P. Possingham., and C.D. Thomas. 2008. Ecology: Assisted Colonization and Rapid Climate Change. Science 321(5887): 345-346.

Huntley, B.1995. Plant species response to climate change: implications for the conservation of European birds. Ibis, 137(1), 127–138.

Kullman, L. 1998. Non-analogous tree flora in the Scandes Mountains, Sweden, during the early Holocene-macrofossil evidence of rapid geographic spread and response to paleoclimate. Boreas 27(3): 153-161.

Lo, Y.H., J.A. Blanco and J.P. Kimmins. 2010. A word of caution when planning forest management using projections of tree species range shifts. The Forestry Chronicle 86(3): 312-316.

Malcom, J.R., A. Markham, R.P. Neilson and M. Garacil. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography. 29(): 835-849.

O'Neil, G., A. Hamann and T. Wang. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. Journal of Applied Ecology 45(): 1040-1049.

Parmesan, C. 1996. Climate and species range. Nature 382: 765-766.

Pitelka, L.F. 1997. Plant migration and climate change. American Scientist. 85(5): 464-473.

Rehfeldt, G.E., N.M. Tchebakova., L.I. Milyutin., Y.I. Parfenova., Wykoff, W.R. and N.A. Kouzima. 2003. Assessing population response to climate in Pinus sylvestris and Larix spp. Of Eurasia with climate-transfer models. Eurasian Journal of Forest Research 6(2): 83-98.

Rehfeldt, G. E., N. M. Tchebakova, Y. I. Parfenova, W. R. Wykoff, N. A. Kuzmina, and L. I. Milyutin. 2002. Intraspecific responses to climate in Pinus sylvestris. Global Change Biology 8(9):912–929.

Rehfeldt, G. E., W. R. Wykoff, and C. C. Ying. 2001. Physiologic plasticity, evolution, and impacts of a changing climate on Pinus contorta. Climatic Change 50(3):355–376.

Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse and D.A. Hamilton Jr. 1999. Genetic responses to climate in Pinus contorta: nice breadth, climate change and reforestation. Ecological Monographs 69(3): 375-407.

Thuiller, W. 2003. BIOMOD- optimizing predictions of species distributions and projecting potential future shifts under global change.Global Change Biology 9(): 1353-1362.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg and F. Bairlein 2002. Ecological responses to recent climate change. Nature 416 (6879): 389-395.

Woodward, F.I. and D.J. Beerling. 1997. The dynamics of vegetation change: health warnings for equilibrium 'dobo' models. Global Ecology and Biogeography Letters 6: 413-418.

CHAPTER V

5.1 CONCLUSION

Gaining perspective and understanding on the climatic factors influencing the growth patterns, and ultimately the distribution of white birch is a necessary step forward in an attempt to establish transfer guidelines under future climates. Summer temperatures (June and July) at population's origin appear to consistently be the strongest predictor of fitness among white birch populations, with other environmental and geographical factors having varying amounts of influence. In order to make more assertive conclusions studies like this are best suited as long-term studies, carried out at multiple locations to allow for adequate and thorough analysis. However, studying seedlings and younger trees have provided compelling results in the past and therefore tend to provide an excellent first step in understanding a phenomenon.

Phenotypic plasticity represents the range of phenotypes that a single genotype can express as a direct function of its environment (Nicotra et al. 2010). A genotype often becomes adapted to its 'local environment' and therefore any phenotypic expression is thought to be a result of that environment. However, upon being transferred to a new environment, the ability to maintain fitness is a result of genetic variation and plasticity. The variation in response variables in this study indicate that white birch has the ability to adapt to a variety of environmental situations as a result of genetic variation and plasticity.

Populations such as BC SKIM, BC 403 and BC 420 originate from areas with similar environmental conditions, which differ greatly from that in the common garden experiment site in Thunder Bay. Populations such as NB 092 and QB 112 are from lower latitudes, with higher amounts of moisture and cooler winter temperatures. Despite these differences they often performed similarly to the British Columbia populations. This suggests a great deal of genetic variation throughout the natural range of white birch in Canada. Origin summer temperatures however tended to be the strongest indicator of fitness, with winter temperature acting as a secondary control.

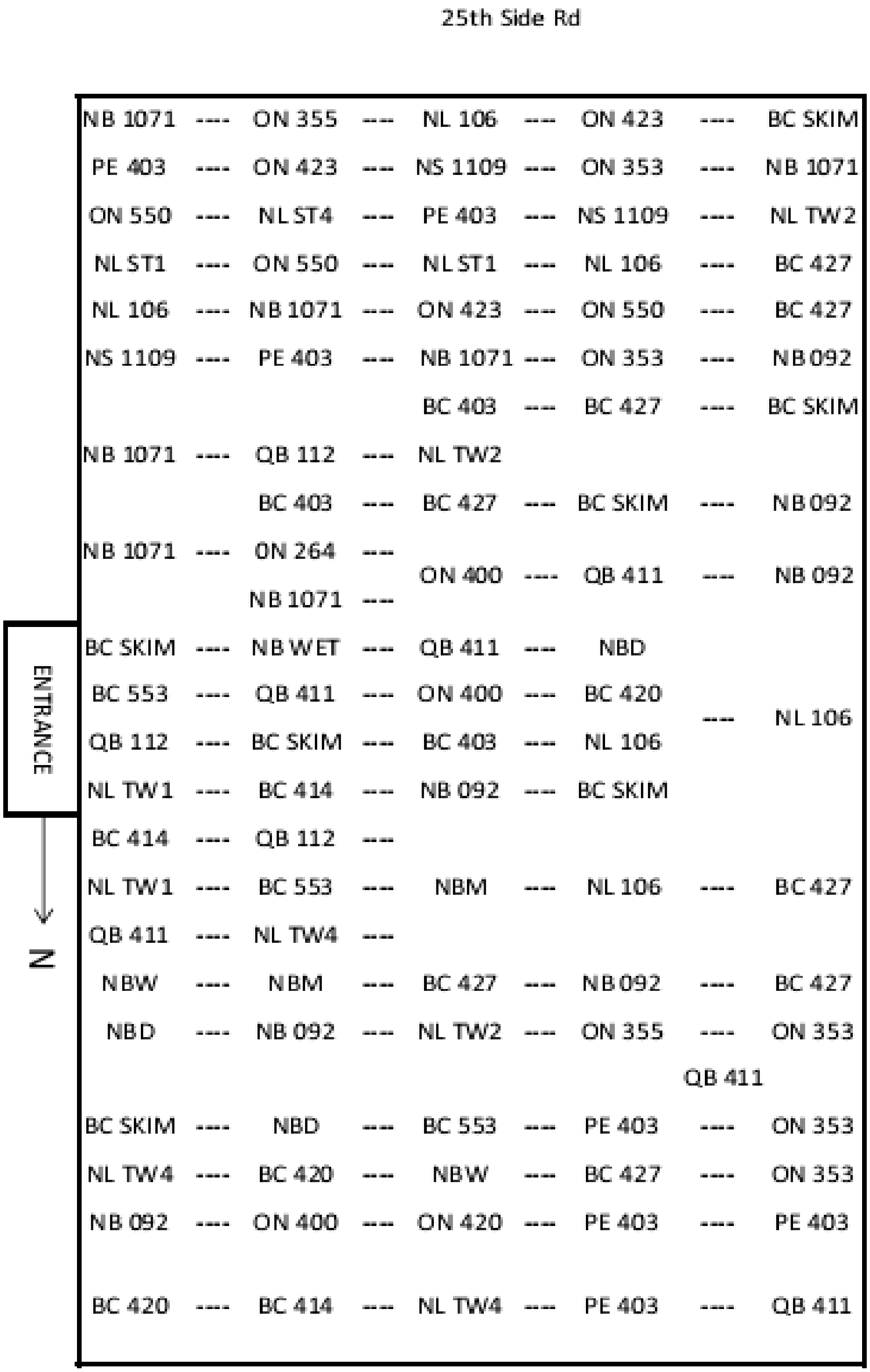
Results of this study displayed reliance on temperature as a control for performance. Studies aiming to predict future climates can play an integral role in these types of studies. By estimating conditions in rural and remote locations, studies may be placed in appropriate locations to best study phenotypic traits of white birch. The variation within climates across the range of white birch has led to appreciable genetic variation, which is important when predicting varying responses of white birch to environmental changes, in particular the increasing climate to which we live in.

REFERENCES

Nicotra, A.B., O.K. Atkin., S.P. Bonser., A.M. Davidson., E.J. Finnegan., U. Mathesius., P. Poot., M.D. Purugganan., C.L. Richards., F. Valladares and M. van Kleunen. 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15(12): 684-692.

APPENDICIES

Appendix 1: Common Garden Study



NB 1071 ---- ON 355 --- NL 106 --- ON 423 ---- BC SKIM
PE 403 ---- ON 423 --- NS 1109 --- ON 353 ---- NB 1071
ON 550 ---- NL ST4 --- PE 403 --- NS 1109 ---- NL TW2
NL ST1 ---- ON 550 --- NL ST1 --- NL 106 ---- BC 427
NL 106 ---- NB 1071 --- ON 423 --- ON 550 ---- BC 427
NS 1109 ---- PE 403 --- NB 1071 --- ON 353 ---- NB 092
BC 403 --- BC 427 ---- BC SKIM
NB 1071 ---- QB 112 --- NL TW2
BC 403 --- BC 427 --- BC SKIM ---- NB 092
NB 1071 ---- ON 264 ---
ON 400 ---- QB 411 --- NB 092
NB 1071 ---
BC SKIM ---- NB WET --- QB 411 --- NBD
BC 553 ---- QB 411 --- ON 400 --- BC 420
--- NL 106
QB 112 ---- BC SKIM --- BC 403 --- NL 106
NL TW1 ---- BC 414 --- NB 092 --- BC SKIM
BC 414 ---- QB 112 ---
NL TW1 ---- BC 553 --- NBM --- NL 106 ---- BC 427
QB 411 ---- NL TW4 ---
NBW ---- NBM --- BC 427 --- NB 092 ---- BC 427
NBD ---- NB 092 --- NL TW2 --- ON 355 ---- ON 353
QB 411
BC SKIM ---- NBD --- BC 553 --- PE 403 ---- ON 353
NL TW4 ---- BC 420 --- NBW --- BC 427 ---- ON 353
NB 092 ---- ON 400 --- ON 420 --- PE 403 ---- PE 403
BC 420 ---- BC 414 --- NL TW4 --- PE 403 ---- QB 411