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Population Differentiation and Climatic Adaptation for Growth Potential of White Spruce (*Picea glauca*) in Alberta, Canada

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Abstract

Genetic differentiation among white spruce populations in Alberta, Canada, was studied using time series data of height and diameter and a climatic index developed by principal component analysis. The objectives were to discern patterns of variation for growth poten-

tial and predicted optimum climate; compare optimum climate between populations, between height and diameter at the same age and between height or diameter at different ages; and to see if optimum climate differed from the climate inhabited by populations. Using cluster analysis we found that: (1) populations from mid-latitudes (54° – 57°N) and mid-elevations (600 – 800 m) were grouped together and exhibited high growth potential; populations from north of 57°N were grouped with those from elevations higher than 900m in the Rocky

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Mountains and exhibited low growth potential; and (2) With minor exceptions, populations from similar climates or geography were grouped together in terms of predicted optimum climate. (3) Analysis of variance showed that optimum climate differed significantly ($P < 0.05$) among populations; among heights at different ages; among diameters at different ages and between height and diameter at the same ages. However, there was no consistent trend in the direction of change in optimum climate with tree age. (4) The range of climate inhabited by the populations ($P_{I_1} = -5.792$ to 4.483) was much wider than the range of their predicted optimum climate ($\hat{P}_{O_1} = -1.001$ to 0.842), which suggests that in terms of growth potential some populations inhabit sub-optimal climates. Implications of the results on management of white spruce in Alberta are discussed.

Key words: Multivariate Climatic Index, Cluster Analysis, Genetic Variation, Optimum Climate, Principal Component, Response Functions.

Introduction

Uncovering the pattern of genetic variation among populations is a primary step in the domestication of forest trees. Although genotypes arise through mutation and recombination, their survival and frequency depends on natural selection (FUTUYAMA, 1979). If we ignore biotic interactions among species, elements of the physical environment such as climate, soils and photoperiod are the main agents of natural selection in plants. Studies have shown that the pattern of genetic variation among populations for growth potential follows closely the pattern of variation in the environment (e.g., LANGLET, 1971; LINHART and GRANT, 1996; RWEYONGEZA et al., 2007).

Although there are many abiotic factors affecting survival, growth and phenology of forest trees, climate has been a major focus of genecological studies in conifers. For example, variation for height growth in Jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill] BSP) populations corresponds to variation in thermo environment (MATYAS and YEATMAN, 1992; THOMSON and PARKER, 2008; THOMSON et al., 2009). In lodgepole pine (*Pinus contorta* Dougl.), variation in height growth potential among populations correlates with measures of climatic severity (e.g., REHFELDT et al., 1999). More recently, the relationship between climate and population differentiation has been used to simulate climate change in an effort to predict survival, growth and productivity of future forests in a changed climate (e.g., REHFELDT et al., 2001; WANG et al., 2006; RWEYONGEZA et al., 2007).

Most studies have used climate to describe or predict height and occasionally diameter growth usually at the current tree age (e.g., REHFELDT et al., 2002; ANDALO et al., 2005; SCHMIDLING, 1994). Because trees are perennial species, the relationship between growth and climate may vary with age as shoot and root biomass, and structure changes. Thus, there is a need to study the relationship between climate and tree growth at different ages. Height growth studied by foresters arises from meristematic activity of the terminal shoot. In northern

conifers, terminal annual height growth is restricted to complete elongation of preformed shoot components (LANNER, 1976) and last only for a few weeks. In contrast, growth in diameter depends on the activity of the cambium, growth hormones and photosynthates translocated from the needles (KRAMER and KOZLOWSKI, 1979). In addition, growth in diameter occurs over a longer period than height growth. While the number of preformed terminal shoot components depends on moisture and temperature of the previous growing season, diameter growth depends on moisture and temperature of the current season (KRAMER and KOZLOWSKI, 1979). Thus, height and diameter may respond differently to climatic displacement.

Many studies (e.g., REHFELDT et al., 1999; RWEYONGEZA et al., 2007; THOMSON et al., 2009) have used individual climatic variables to model the response of height or diameter to the climate of the test sites. However, climate is a complex variable of moisture and precipitation and their seasonal variation. Climatic variables are normally highly inter-correlated, because they are either derived from each other or are integral components of a single compound variable. Characterizing tree populations based on single variable response or transfer functions fails to recognize this complexity of climate, and does not account for the effect of unknown but important interactions among variables. Thus, there is a need to model population response to climate using multivariate climatic indices that integrate all climatic variables based on their relative weights in describing population and test site locations.

In the present study, we examined genetic variation among white spruce (*Picea glauca* [Moench] Voss) populations in Alberta, Canada, using time series data of height and diameter measurements, and multivariate climatic indices as predictor variables. Time series data are used to discern possible age trends in the response of populations to climate, whereas multivariate climatic indices are used to synthesize many climatic variables into single meaningful descriptors of population and test site climates. Our objectives were to determine if (1) population differentiation for growth potential exhibits a pattern that can be environmentally described, (2) populations differ with respect to predicted optimum climate, (3) predicted optimum climate change with tree age, (4) predicted optimum climate differ between height and diameter, (5) predicted optimum climate differ from the climate inhabited by the populations, and (6) populations from similar climates or locations exhibit similar predicted optimum climate.

Materials and Methods

Biological Data

The data were measurements of height and diameter of 19 populations planted at 8 locations in Alberta, Canada (Table 1; Figure 1), which are a subset of the 46 populations described by RWEYONGEZA et al. (2007). Because some of the analyses in this study used data derived from population response functions, the 27 populations planted on fewer sites were omitted because their response functions could not be reliably developed.

However, the 19 populations are sufficient for describing the pattern of variation of white spruce, because they span the range of the 46 populations tested in this series of provenance trials and most of the climatic range of white spruce in Alberta (*Figure 1*).

Prior to sowing, seeds were cold stratified at 2°C for 21 days. Seedlings were raised in a greenhouse for one growing season, transplanted to nursery beds and grown for three more years. The 4-year old seedlings were used to establish field trials between 1980 and 1983. All sites have a randomized complete block design with 5 replications, 9-tree row plots and 2.5 x 2.5-metre spacing between trees. Traits covered in this study are total height in metres at ages 12, 15, 21, 24 and 27, and diameter at breast height in centimetres at 21, 24 and 27 years from seeds. These traits are coded as H12, H15, H21, H24, H27, D21, D24 and D27, respectively.

Climatic Data

Because weather data were not available for remote forest areas in Alberta, we used data generated by the

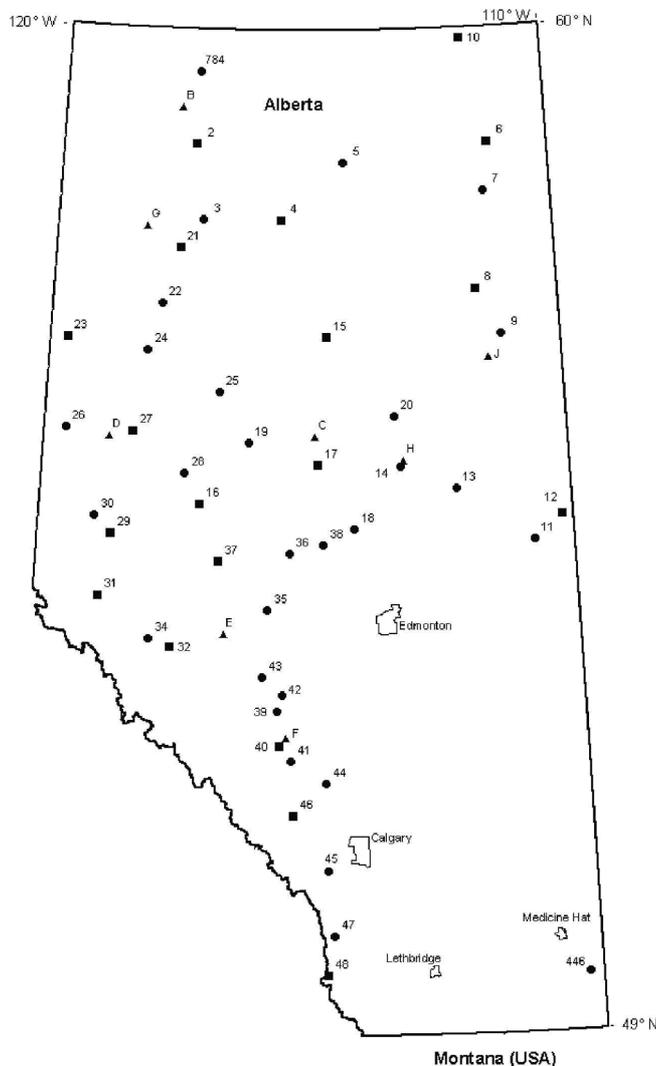


Figure 1. – Distribution of populations (numeric ID; dot markers) and test sites (character ID; triangle markers) in a white spruce series of provenance trial in Alberta, Canada. Populations covered in this article are identified by numeric ID and square markers.

Alberta Climate Model (ACM) as described by ALBERTA ENVIRONMENT (2005). The model predicts values of individual climatic variables for the 1961–1990 period based on a location's latitude, longitude and elevation. The 1961–1990 period was chosen for developing ACM to conform to IPCC guidelines (CARTER et al., 1999). Monthly weather data for Alberta and adjacent areas in Saskatchewan, British Columbia and the USA were obtained from ENVIRONMENT CANADA (1993), US DEPARTMENT OF COMMERCE (1994) and EARTHINFO (1994). Primary variables were monthly averages of daily temperature, daily maximum temperature, daily minimum temperature and monthly mean precipitation. An additional 14 biologically relevant variables were derived from these 48 base climatic variables. These are mean annual temperature (MAT); mean temperature for the coldest month (TCM); mean temperature for the warmest month (TWM); mean minimum daily temperature for the coldest month (MMN); mean maximum daily temperature for the warmest month (MMX); degree days below 0°C, also called negative degree days (NDD); degree days above 5°C, normally called growing degree days (GDD); summer-winter temperature differential (TWM minus TCM), used here as an index of continentality (CI); mean annual precipitation (MAP); mean summer precipitation (MSP), expressed as total precipitation during a potential growing season (April to September); winter precipitation (WP), derived as MAP minus MSP; annual moisture index (AMI), expressed as GDD ÷ MAP; summer moisture index (SMI), expressed as GDD ÷ MSP; and mean Julian day on which the GDD sum reaches 100 (GDD100).

We used 11 of the 14 derived climatic variables to obtain climatic indices by principal component analysis (PCA) using PROC PRINCOMP (SAS INST., 2004). Climatic variables were selected by fitting population response functions of individual variables to identify variables that fit the data well and also based on knowledge from published work (e.g., REHFELDT et al., 1999, 2002, RWEYONGEZA et al., 2007). To simplify the interpretation of PCA axes, we avoided using the ratio variables AMI and SMI in conjunction with GDD, MAP and MSP from which they were derived. The use of MSP and WP in conjunction with MAP was considered appropriate because MSP and WP describe the seasonal distribution of annual precipitation. Thus, the 11 variables explain population and test site locations in terms of average temperature, seasonal temperatures and their extremes, annual precipitation and its seasonal distribution, and continentality. In performing PCA, data for the 46 populations and all test sites were combined into a single dataset to provide climatic index scores for the whole white spruce range in Alberta covered by this series of provenance trials.

The Eigenvalues for the first (P_{11}) and second (P_{12}) climatic principal components were, respectively, 8.22 and 1.85 or 74.8% and 16.9% of the variance in climate. All other components accounted for less than 1% of the variance in climate. Thus, only P_{11} and P_{12} were retained for describing tree growth. Population and test site scores for P_{11} and P_{12} are in *Table 1*. Correlations between individual climatic variables and Eigenvectors are summarized in *Table 2*.

Table 1. – Location and climatic description of populations and test sites for white spruce provenance trials in Alberta, Canada. Numeric and character ID identify populations and test sites, respectively.

ID	LOCATION	LAT ⁺	LON ⁺	ELE	MAT	TCM	MMN	NDD	TWM	MMX	GDD	CI	MAP	GSP	WP	P_{I_1}	P_{I_2}
2	Footner Lake	58.73	117.25	335	-1.6	-21.9	-27.7	-2654.1	16.0	22.6	1196.5	37.9	417.5	272.3	145.2	-3.998	-1.382
4	Footner Lake	57.92	115.50	360	-0.4	-20.9	-25.9	-2343.6	16.4	22.5	1281.9	37.3	434.8	301.4	133.4	-3.361	-0.179
6	Athabasca Forest	58.73	111.25	235	-1.8	-23.9	-29.1	-2738.2	16.9	22.8	1244.4	40.8	396.8	255.1	141.7	-5.017	-1.335
8	Athabasca Forest	57.13	111.63	274	-0.2	-21.1	-27.1	-2329.3	16.9	23.7	1348.8	38.0	465.4	309.1	156.3	-3.725	-0.237
10	Athabasca Forest	59.88	111.72	183	-2.6	-25.2	-29.1	-2968.0	16.7	22.9	1181.2	41.9	338.4	212.0	126.4	-5.792	2.067
12	Lac La Biche	54.63	110.22	610	0.6	-18.0	-23.2	-2009.3	16.2	22.1	1308.6	34.2	489.9	341.8	148.1	-1.817	-0.622
15	Slave Lake	56.63	114.58	731	-0.1	-17.5	-23.6	-2028.6	14.8	20.3	1091.7	32.3	557.9	378.3	179.6	-0.346	-1.067
16	Slave Lake	54.80	116.98	731	2.5	-12.7	-18.2	-1418.5	15.6	21.9	1297.9	28.3	577.0	391.2	185.8	0.947	1.912
17	Slave Lake	55.23	114.77	610	1.6	-15.0	-20.5	-1685.5	15.7	21.4	1263.1	30.7	541.6	380.7	160.9	-0.034	1.097
21	Peace River	57.60	117.52	460	-0.5	-20.6	-26.5	-2320.2	15.8	22.1	1228.1	36.4	449.4	291.3	158.1	-2.948	-0.745
23	Peace River	56.57	119.67	762	-0.2	-18.0	-23.9	-2077.3	14.7	20.7	1097.2	32.7	465.7	295.3	170.4	-1.231	-1.238
27	Grande Prairie	55.58	118.30	640	1.6	-15.7	-21.0	-1726.9	15.9	22.1	1328.1	31.6	507.6	324.5	183.1	-0.773	1.141
29	Grande Prairie	54.45	118.63	940	1.8	-12.9	-19.0	-1459.1	14.5	20.6	1118.2	27.4	645.6	427.2	218.4	2.029	0.440
31	Edson	53.77	118.80	1402	0.7	-11.7	-17.3	-1440.1	12.1	18.6	788.4	23.8	652.9	388.8	264.1	3.763	-2.097
32	Edson	53.23	117.47	1340	1.5	-11.4	-17.2	-1344.8	13.3	19.9	943.0	24.7	635.5	436.1	199.4	3.109	-0.225
37	Whitecourt	54.18	116.62	945	2.4	-11.1	-16.9	-1324.9	14.8	20.9	1167.2	25.9	624.4	438.4	186.0	2.312	1.414
40	Rocky/Clearwater	52.17	115.47	1341	1.4	-11.5	-18.8	-1353.3	13.2	20.3	922.6	24.7	657.2	472.1	185.1	3.088	-0.131
46	Bow/Crow	51.40	115.22	1600	0.8	-11.5	-18.1	-1430.5	12.5	18.8	811.3	24.0	613.8	415.1	198.7	3.326	-1.440
48	Bow/Crow	49.65	114.62	1585	2.1	-9.3	-13.9	-1132.3	13.6	20.5	950.0	22.9	763.1	356.0	407.1	4.485	-0.764
B	Hay River	59.13	117.57	370	-2.3	-23.1	-28.8	-2843.9	15.7	22.2	1147.3	38.8	418.7	267.4	151.3	-4.272	-2.221
C	Zeidler Mills	55.55	114.83	670	1.2	-15.5	-21.2	-1745.2	15.5	20.8	1218.7	31.0	571.9	394.8	177.1	0.180	0.481
D	Soxsmith	55.52	118.75	805	1.2	-14.9	-20.4	-1710.4	15.1	20.9	1208.6	30.0	531.9	338.6	193.3	0.155	0.246
E	Swartz Creek	53.38	116.50	990	2.1	-11.6	-18.3	-1355.1	14.5	21.3	1132.5	26.1	614.1	434.6	179.5	2.034	1.175
F	Prairie Creek	52.25	115.35	1220	1.7	-11.7	-19.1	-1348.2	13.5	20.8	974.8	25.2	666.5	479.1	187.4	2.893	0.303
G	Chinchaga	57.83	118.20	470	-0.8	-20.8	-26.8	-2384.5	15.7	21.9	1200.5	36.5	454.0	298.2	155.8	-2.953	-1.038
H	Calling Lake	55.28	113.15	625	0.9	-17.6	-23.2	-1879.4	15.9	22.0	1253.7	33.5	512.2	359.2	153.0	-1.267	0.623
J	Hangington	56.38	111.43	550	0.2	-18.7	-23.9	-2087.7	16.1	22.0	1258.0	34.8	539.3	370.8	188.5	-1.497	0.019

+ – latitude and longitudes minutes expressed in decimals; LAT – latitude (°N); LON – longitude (°W); ELE – elevation (m); MAT – mean annual temperature (°C); TCM – mean temperature for the coldest month (°C); MMN – mean minimum daily temperature for the coldest month (°C); NDD – degree days below 0°C; TWM – mean temperature for the warmest month (°C); MMX – mean maximum daily temperature for the warmest month (°C); GDD – degree days above 5°C; MAP – mean annual precipitation (mm); MSP – mean summer precipitation; WP – winter precipitation or snowfall (mm); CI – continentality index (TWM-TCM); P_{I_1} and P_{I_2} – population and test site scores for the first and second principal components derived from PCA of the 11 climatic variables.

Table 2. – Correlation coefficients between climatic variables at population and test site locations and Eigenvectors for the first and second climatic principal components from PCA of 11 climatic variables.

	Pearson's Correlation Coefficients											Eigenvectors	
	MAT	TCM	MMN	NDD	TWM	MMX	GDD	CI	MAP	MSP	WP	P_{I_1}	P_{I_2}
MAT	1.00											0.243	0.518
TCM	0.85	1.00										0.336	0.182
MMN	0.83	0.99	1.00									0.335	0.149
NDD	0.91	0.99	0.97	1.00								0.320	0.283
TWM	-0.32	-0.76	-0.75	-0.66	1.00							-0.306	0.297
MMX	-0.22	-0.65	-0.67	-0.55	0.92	1.00						-0.283	0.359
GDD	-0.06	-0.57	-0.57	-0.45	0.96	0.89	1.00					-0.258	0.456
CI	-0.75	-0.99	-0.97	-0.95	0.85	0.75	0.69	1.00				-0.344	-0.069
MAP	0.59	0.86	0.87	0.81	-0.81	-0.79	-0.72	-0.89	1.00			0.330	-0.074
MSP	0.76	0.86	0.80	0.86	-0.65	-0.57	-0.47	-0.85	0.81	1.00		0.296	0.218
WP	0.20	0.55	0.62	0.46	-0.67	-0.70	-0.68	-0.61	0.82	0.32	1.00	0.241	-0.336

MAT – mean annual temperature (°C); TCM – mean temperature for the coldest month (°C); MMN – mean minimum daily temperature for the coldest month (°C); NDD – degree days below 0°C; TWM – mean temperature for the warmest month (°C); MMX – mean maximum daily temperature for the warmest month (°C); GDD – degree days above 5°C; MAP – mean annual precipitation (mm); MSP – mean summer precipitation; WP – winter precipitation or snowfall (mm); CI – continentality index (TWM-TCM); P_{I_1} and P_{I_2} – population and test site scores for the first and second principal components derived from PCA of the 11 climatic variables.

Biological Data Analysis

Data for mean height and diameter used to describe growth potential of populations were predictions from the following single-site mixed model, which was fitted in PROC MIXED (SAS INST., 2004):

$$Y_{ijn} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijn} \quad [1]$$

where Y_{ijn} = height or diameter for the n th tree in the j th population planted in the i th replication (block), μ = test

site mean, α_i = effect of the i th replication, β_j = effect of the j th population, $\alpha\beta_{ij}$ = population x replication interaction (experimental error) and ε_{ijn} = residual (sampling error). Except μ , all terms on the right side of the model were considered random effects with zero expectations and respective variances (variance components are of no of further interest in this study).

To obtain a measure of population response to climate, population response functions were developed by

regressing predicted population means (Eq. 1) on test site P_{I_1} and P_{I_2} (Table 1) on an individual population basis using PROC REG in SAS follows:

$$Y_i = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \varepsilon_i \quad [2]$$

where Y_i = population mean height or diameter at the i th test site; β_0 , β_1 and β_2 = regression coefficients; ε_i = residual; and $X_i = P_{I_1}$ or P_{I_2} score for i th test site. A quadratic model (Eq. 2) was selected based on preliminary analyses and our previous study on these populations (RWEYONGEZA et al., 2007). Regression coefficients were then used to obtain predicted optimum climate (elsewhere simply called “optimum climate”), which is a P_{I_1} or P_{I_2} score corresponding to the maximum predicted height or diameter ($\hat{P}_O = -\beta_1 / 2\beta_2$, where \hat{P}_O = optimum climate) on the response function. The response functions for P_{I_2} had low coefficients of determination (r^2) and were largely simple linear, which made them unsuitable for estimation of \hat{P}_O needed for further analyses. Thus, characterization of populations based on their growth response to test site climate was done only for P_{I_1} . As previously discussed (RWEYONGEZA et al., 2007), site C is located on an abandoned sawmill with significant soil compaction. Consequently, trees on this site were much smaller than trees on sites with comparable climate and soil fertility. Because tree growth on this site is affected by soils not climate, site C was omitted when fitting response functions. However, site C was included in all other non-climatic analyses.

The pattern of population differentiation was examined using two criteria, namely, variation in growth potential and variation in optimum climate. The objective of the growth potential analysis was to answer the following question: does variation in growth potential among white spruce populations in Alberta exhibit a pattern that can be environmentally described? To achieve this objective, predicted population means (Eq. 1) for H12, H15, H21, H24 H27, D21, D24 and D27 from all 8 sites were combined into one dataset, that is, 152 data points (19 populations from 8 sites) for 8 traits. This 152 x 8 table was subjected to a canonical discriminant analysis (CDA) using PROC CANDISC in SAS with population as a classification variable. The resulting matrix of Mahalanobis distances between populations was used to perform a cluster analysis in PROC CLUSTER in SAS with the unweighted pair-group method with arithmetic mean (UPGMA). The dendrogram of population clusters was developed using PROC TREE in SAS.

The objective of the predicted optimum climate analysis was to answer the following questions: (1) Does the optimum climate differ among populations? (2) Does a population's optimum climate change with tree age? (3) Does the optimum climate differ between height and diameter at the same age? (4) Does the overall optimum climate for growth differ from the climate currently inhabited by the populations? (5) Do populations of similar geographic or climatic origins exhibit similar optimum climates? These questions were addressed using optimum climate (\hat{P}_{O_1}) for the first PCA climatic index (P_{I_1}).

To answer questions (1) through (3), \hat{P}_{O_1} score for all 8 traits (H12, H15, H21, H24, H27, D21, D24 and D27) were combined into one dataset (N = 19 populations x 8 traits) to perform the following analysis of variance:

$$Y_{ij} = \mu + \gamma_i + \tau_j + \varepsilon_{ij} \quad [3]$$

where $Y_{ij} = \hat{P}_{O_1}$ for the j th population and i th trait; μ = general mean; γ_i = effect of the i th trait, i.e., height and DBH at different ages ($i = 1, 2, \dots, 8$); τ_j = effect of the j th population ($j = 1, 2, \dots, 19$); and ε_{ij} = residual. We used PROC MIXED with the DIFF option to perform multiple comparisons for the trait and population as fixed effects. In this model, the significance test for τ addresses question (1), multiple comparisons between serial height or diameter measurements (γ) address (2) and multiple comparisons of height and diameter at the same age address (3).

To answer question (4), we first computed Pearson's correlation coefficients (r_p) for population \hat{P}_{O_1} between 8 traits. The resulting 28 correlations ranged from 0.89 to 0.98 ($P < 0.0001$). We also observed that r_p for population mean heights and diameters at the same age ranged from 0.88 to 0.94. Age-to-age r_p of population means ranged from 0.72 to 0.97 for height and 0.92 to 0.97 for diameter. These high correlations show that populations with high mean heights also had high mean diameters and vice versa; populations with better growth at a young age had better growth at all subsequent ages and vice versa; and populations with high \hat{P}_{O_1} for one trait had high \hat{P}_{O_1} for other traits and vice versa. Consequently, we averaged the eight \hat{P}_{O_1} values to obtain a single mean optimum climate (\hat{P}_{O_1}) for each population. The resulting \hat{P}_{O_1} was compared with P_{I_1} of population origin (column 17 in Table 1) in a paired T-test.

Question (5) was analyzed by developing the pattern of population grouping with respect to \hat{P}_{O_1} of both height and diameter. To do this, growth in height and diameter were treated as two traits each with \hat{P}_{O_1} at age 21, 24 and 27 years. Thus, predicted \hat{P}_{O_1} for H21, H24, H27, D21, D24 and D27 were combined in a single dataset. The resulting 57 x 2 table was then subjected to CDA to generate a matrix of Mahalanobis distances between populations, followed by a cluster analysis and dendrogram developed similar to that previously described for absolute heights and diameter growths.

Results and Discussions

Interpretations of Climatic Indices

The interpretation of the P_{I_1} climatic index is essential for better understanding of the pattern of population differentiation described in subsequent sections. Table 1 shows that P_{I_1} describes a continuum of climatic gradient ranging from the highest latitudes and lowest elevations in the north (most negative P_{I_1} scores) to the lowest latitudes and highest elevations in the southwest (most positive P_{I_1} scores). The northernmost part of Alberta has the coldest winters, warm summers due to long summer days, lowest precipitation and highest continentality (the difference between winter and summer temperature extremes). The Rocky Mountains in the southwest have the warmest winters due to the Pacific

Ocean influence, shortest growing seasons due to low GDD at high elevations, highest precipitation and lowest continentality. At mid-latitudes and mid-elevations is a relatively mild climate (low negative and low positive P_{T_1} scores), which is transitional between the north and southwest.

Differences among Sites

Table 3 summarizes site means and range of population means for height and diameter. The northernmost lowest elevation (B) and southernmost highest elevation (F) sites had the lowest height and diameter. In contrast, the highest growth occurred on sites such as E and J located at mid-latitudes and mid-elevations. This shows that realization of full growth potential requires a balance between moisture and heat (e.g., STEPHENSON, 1990; THORTHWAITE, 1948). Sites B and F lack either adequate moisture or heat leading to low annual growth.

Variation for Growth Potential

Graphically, the dendrogram developed from heights and diameters (Figure 4) suggests the existence of four main groups. Population 48 (Group I) is separated from all others. Although it grew better at site F and D, it had the lowest growth potential across sites. In terms of the Mahalanobis distance, population 48 differs significantly ($P < 0.05$) from all populations, except 31, 32 and 46. Together with population 40, populations 31, 32, 46 and 48 are from the highest elevations (> 1300 m) and based on GDD (< 1000), the shortest growing season. In addition, the four populations are very similar in terms of overall climate with the highest positive P_{T_1} scores (Table 1).

In other species, high elevation populations exhibit low growth potential (e.g., WU and YING, 2004;

REHFELDT, 1978), which is also demonstrated in the present study. Moreover, populations 31, 32, 46 and 48 are from a region where white and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) coexist and hybridize (LA ROI and DUGGLE, 1968; RAJORA and DANCİK, 2000). Thus, due to their geographic proximity to Engelmann spruce, these populations are potentially putative hybrids, which could also account for their distinctively low growth potential.

Populations 2, 4, 32, 37, and 40 (Group II) and 6, 10, 31 and 46 (Group III) are mixtures of populations from north of latitude 57°N or from elevations higher than 900 m in the Rocky Mountains (Table 1). Populations in both groups had low growth potential across sites, but grew better than average on sites closest to their origins. In terms of the Mahalanobis distance, populations in Groups II and III do not differ both within and between the two groups. A common characteristic of these populations is that they originated from regions characterized by either very cold winters (Table 1) or warm winters but short growing seasons with potential for mid-season frosts (see AARD, 2005). Thus, although these populations are geographically separated, they all belong to climatically marginal environments, which may explain their overall low growth potential (NAMKOONG, 1969; GIERTYCH, 1979; KRUTZSCH, 1992; LOEHLE, 1998).

Populations 8, 12, 15, 16, 17, 21, 23, 27 and 29 (Group IV) exhibited high growth potential across sites, although their superior growth tended to decline compared to local populations when planted at a high latitude (B) and high elevation (F) site. In terms of the Mahalanobis distance, populations in this group do not significantly ($P > 0.05$) differ from each other. With minor exceptions (8, 21 and 29), populations in this group are from between latitude 54°N and 57°N and

Table 3. – Overall mean (\pm – standard error) and range of population means for height (m) and diameter at breast height (cm) for 19 populations planted across eight white spruce provenance trials in Alberta, Canada.

Site	Statistic	H12	H15	H21	H24	H27	D21	D24	D27
B	Mean	1.30 \pm 0.05	2.13 \pm 0.09	3.52 \pm 0.13	4.58 \pm 0.18	6.05 \pm 0.20	4.90 \pm 0.19	6.61 \pm 0.22	8.63 \pm 0.28
	Range	0.91 – 1.47	1.30 – 2.43	2.32 – 4.03	2.95 – 5.20	4.15 – 6.76	3.67 – 5.57	5.25 – 7.50	6.11 – 9.78
C	Mean	0.84 \pm 0.07	1.39 \pm 0.14	2.81 \pm 0.28	3.75 \pm 0.30	5.14 \pm 0.35	3.28 \pm 0.57	5.83 \pm 0.65	7.70 \pm 0.76
	Range	0.64 – 1.04	0.93 – 1.92	2.02 – 3.76	2.85 – 4.70	3.78 – 6.25	1.80 – 5.73	4.10 – 8.58	5.05 – 10.96
D	Mean	1.77 \pm 0.06	2.93 \pm 0.11	5.19 \pm 0.13	6.39 \pm 0.14	7.64 \pm 0.15	8.48 \pm 0.26	10.72 \pm 0.24	12.88 \pm 0.32
	Range	1.66 – 1.95	2.72 – 3.28	4.43 – 5.72	5.46 – 7.09	6.73 – 8.37	2.22 – 9.39	9.39 – 11.74	11.68 – 15.49
E	Mean	1.84 \pm 0.04	2.75 \pm 0.07	5.17 \pm 0.13	6.49 \pm 0.15	7.86 \pm 0.17	7.78 \pm 0.22	10.31 \pm 0.26	12.11 \pm 0.26
	Range	1.61 – 2.05	2.27 – 3.07	4.10 – 5.78	5.22 – 7.27	6.48 – 8.78	6.33 – 8.81	8.64 – 11.52	10.39 – 13.35
F	Mean	1.38 \pm 0.07	2.23 \pm 0.11	3.99 \pm 0.17	4.91 \pm 0.20	5.95 \pm 0.24	5.83 \pm 0.32	7.97 \pm 0.37	9.65 \pm 0.39
	Range	1.18 – 1.70	1.85 – 2.70	3.36 – 4.68	4.00 – 5.77	4.76 – 6.86	4.42 – 7.50	6.35 – 10.04	8.02 – 11.91
G	Mean	1.88 \pm 0.05	2.94 \pm 0.10	5.05 \pm 0.17	6.28 \pm 0.25	7.21 \pm 0.29	7.30 \pm 0.29	8.75 \pm 0.37	9.83 \pm 0.42
	Range	1.41 – 2.13	2.24 – 3.33	3.86 – 5.55	5.00 – 6.85	5.78 – 7.89	6.18 – 7.82	7.00 – 9.26	7.83 – 10.39
H	Mean	1.69 \pm 0.05	2.27 \pm 0.08	4.24 \pm 0.15	5.43 \pm 0.18	6.91 \pm 0.24	7.01 \pm 0.26	8.70 \pm 0.28	11.13 \pm 0.32
	Range	1.36 – 1.93	1.76 – 2.63	3.25 – 5.04	4.26 – 6.19	5.35 – 7.89	5.30 – 8.23	6.73 – 10.12	8.90 – 12.51
J	Mean	2.04 \pm 0.09	2.84 \pm 0.13	5.17 \pm 0.21	6.49 \pm 0.21	7.82 \pm 0.23	7.74 \pm 0.37	9.66 \pm 0.39	12.16 \pm 0.44
	Range	1.39 – 2.30	1.86 – 3.27	3.29 – 5.84	4.22 – 7.18	5.37 – 8.67	5.01 – 8.64	6.27 – 10.62	8.82 – 13.48

H12, H15, H21, H24 and H27 – total height at ages 12, 15, 21, 24 and 27 years from seeds, respectively; D21, D24 and D27 – total diameter at breast height at age 21, 24 and 27 years from seeds, respectively.

elevation of 600 to 800 m (*Table 1*). Based on P_{I_1} , populations in Group IV have evolved in a region where the climate is transitional between high latitude climates (highly negative P_{I_1} scores) and high elevation climates in the Rocky Mountains (highly positive P_{I_1} scores). Studies of other species have shown that populations from warm and moist climates normally found at low latitudes and elevations tend to have high growth potential when planted across a range of environments (e.g., LANGLET, 1959; NAMKOONG, 1969; REHFELDT, 1978). Thus, growth potential of populations in Group IV conforms to our expectations.

Generally, this study shows that population differences in growth potential are determined by their geographic and climatic proximity. For example, in terms of the Mahalanobis distance, the most northern population 10 in Group III differs significantly ($P < 0.05$) from all populations in Group IV, except 21 ($P = 0.0628$) and 23 ($P = 0.2022$). In contrast, population 6 located about 1° of latitude south of population 10 differ with populations in Group IV at the 5% (12 and 15 and 16) and 10% (17, 21 and 27) levels of probability. It differs only slightly ($P = 0.1122$) from population 8 located less than 1° of latitude north at approximately the same longitude and elevation (*Table 1*). Likewise, the highest elevation population 46 (Group II) differ significantly with all populations in Group IV ($P < 0.05$), and only slightly with 23 ($P = 0.0830$). While population 2 does not differ significantly from any population in Group IV, population 31 and 32 differ from some members of Group IV depending on elevation proximity. Thus, the four generalized groups serve only to illustrate a discernable gradual decline in growth potential from the centre of white spruce's natural range in Alberta to climatically marginal environments at high latitudes and high elevations.

In this case, the most distinct populations are found at the extreme ends of the climatic continuum (*Table 1*).

Height vs. Diameter Response Functions

Table 4 is a summary of the coefficients of determination (r^2) and \hat{P}_{O_1} for the 19 population response functions, and averages of r^2 across populations (\hat{P}_{O_1}). Examples of response functions are illustrated by *Figures 2* and *3* using H27 and D27, respectively. The pattern of r^2 shows that: (1) the relationship between height and site climate was lower for populations from high latitudes (2, 4, 6, 8, 10) than populations from other areas, (2) the relationship between diameter and site climate was similar for all populations, (3) site climate explained diameter better than it explained height growth.

For northern conifers, current year height growth is only an extension of stem components preformed in the bud in a previous year (DOAK, 1935; CANNELL, 1974; LANNER, 1976). Thus, height growth ceases in mid-summer once available stem components have fully elongated, even though temperature and moisture are still suitable for shoot growth. In contrast, growth in diameter is due to cambial activity, photosynthesis and action of growth hormones translocated from needles (KRAMER and KOZLOWSKI, 1979), which extend into autumn depending on temperature and moisture availability. This suggests that, physiologically, terminal height growth is only partially dependent on site climate. In contrast, annual diameter growth is wholly dependent on site climate. Thus, the fact that site climate explained diameter better than height growth is not surprising.

Low r^2 for high latitude populations is due to choice of test sites. The fitted response functions depended great-

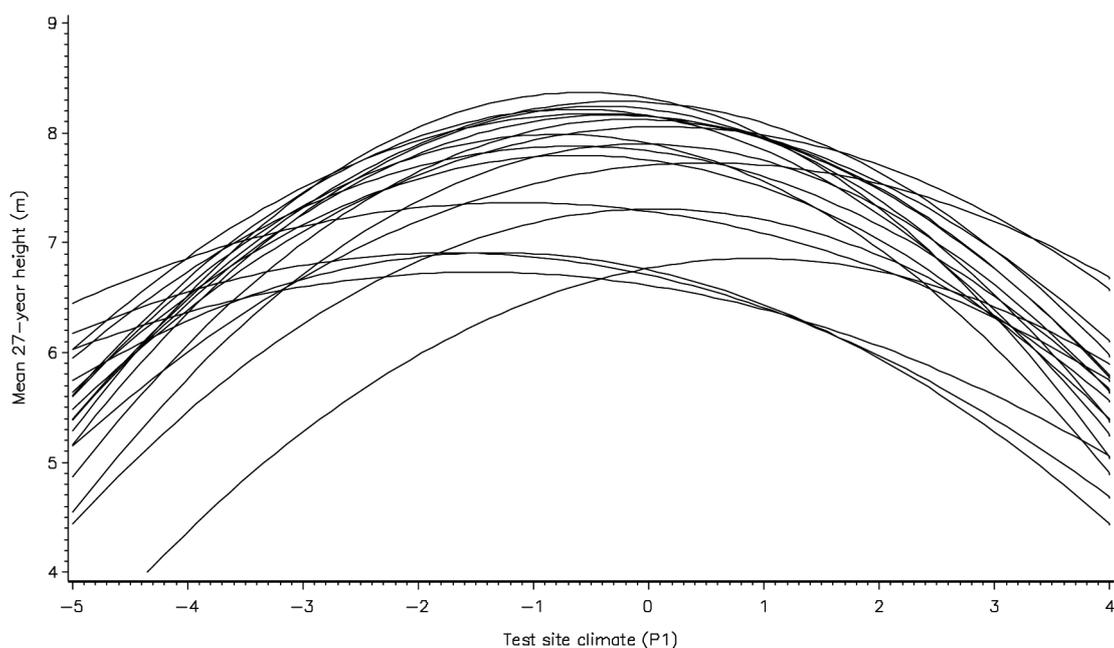


Figure 2. – Graphic presentation of 27-year height response functions for 19 white spruce populations planted at seven sites in Alberta, Canada. Similar response functions were observed for height growth at previous ages (see *Table 4* for r^2).

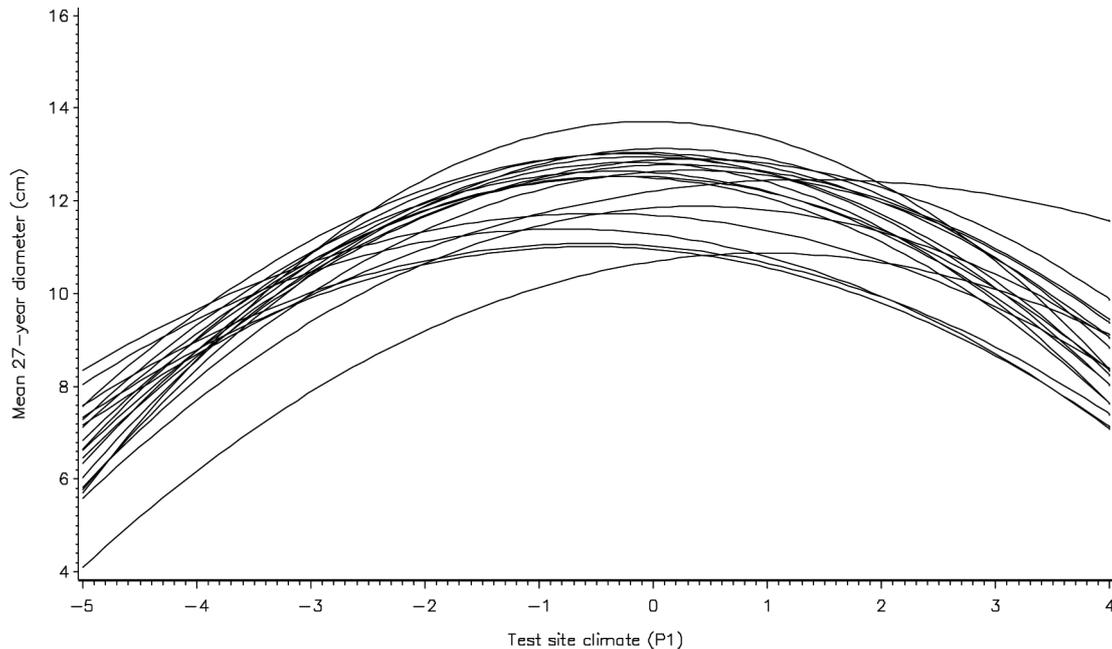


Figure 3. – Graphic presentation of 27-year diameter at breast height response functions for 19 white spruce populations planted at seven sites in Alberta, Canada. Similar response functions were observed for diameter growth at previous ages (see Table 4 for r^2).

ly on growth at sites B and F, which are at the opposite ends of the P_{I_1} continuum. The strength of the response functions depended on how climatically distant P_{I_1} of the populations were from P_{I_1} of site B and F. High latitude populations are climatically the closest to site B where they grew better than other populations. Growth of these high latitude populations was considerably reduced only when they were planted at site F leading to relatively weak response functions. Implicitly, this would equally apply for high elevation populations when planted at site F.

The reason why the location of populations with respect to site B and F affected height more than diameter (Table 4) is generally unclear. However, probable physiological differences regarding control of height and diameter by climate may be partly responsible as previously described. Population variation in height growth could also be strongly controlled by non-climatic factors. The most plausible non-climatic factor that would affect height and diameter differently is photoperiod. Although we had no data to test the contribution of photoperiodic adaptation to population variability in growth potential and response to climate, population adaptation to photoperiod is well established. Photoperiod is considered the main reason for high latitude populations showing superior height when locally planted and inferior height when transferred to low latitudes (e.g., VAARTAJA, 1954; 1959). Day length recognition affect the onset of shoot dormancy (TAIZ and ZEIGER, 2006), which may affect height more than diameter growth (WAREING and ROBERTS, 1956; MELLEROWICZ et al., 1992). Diameter is only partly dependent on the activity of terminal shoot elongation (WAREING and ROBERTS, 1956; LARSON, 1962). Thus, there is theoretical evidence to suggest that photoperiod may influence the way climatic indices fit height and diameter growth data. Because variation in

day length and its recognition by plants is dependent on latitudes (TAIZ and ZEIGER, 2006; MORGENSTERN, 1996), adaptation to climate is likely to be confounded with adaptation to photoperiod in studies such as ours where population origins span almost 10° of latitudes.

Variation for Optimum Climate

Generally, \hat{P}_{O_1} differed significantly among populations ($F = 81.66$; $P < 0.0001$). However, multiple comparisons showed no significant ($P > 0.05$) difference among populations in groups A1 (4, 8, 15, 21 and 23), A2 (6, 10 and 46), A3 (12, 16, 27 and 29), A4 (17 and 31), A5 (32 and 37) and A6 (40 and 48). These groups can be visualized in Figure 5, even though the dendrogram of \hat{P}_{O_1} is more complicated than that of growth potential. There are similarities and differences among populations grouped together. In A1, all populations are from north of latitude 56°N and south of 58°N, whereas in A3 all populations are from north of latitude 54°N and south of 56°N. Populations 40 and 48 in A6 are among the southernmost and highest elevation (> 1300 m) sources. Thus, groups A1, A3 and A6 suggest that populations of similar geographic or climatic origins can be expected to have similar optimum climate.

In A2, populations 6 and 10 are grouped with 46, although they differ from it by at least 8° of latitudes and 1365 m in elevation. Large elevation differences also exist between populations in A4 and A5 (Table 1). There is no simple explanation for populations of different climatic or geographic origins having similar optimum climates. However, it is conceivable that because temperature decreases with an increase in latitude and elevation, similar thermo climates may exist at low elevations in high latitudes as well as at high elevations in the low latitudes allowing populations with similar adaptation to thermo climate to evolve in geographically

disparate regions. The Alberta side of the Rocky Mountains is an exception, in that winters are warmer at higher than at lower elevations, and summers are warmer at lower than at higher elevations.

ACM prediction of the frost-free period (FFP) at site B and F is 88 and 45 days, respectively. Sites located in mid-latitudes and mid-elevations have FFP of 81 to 110 days, which overlap considerably with FFP of populations at high latitudes (data not presented). Thus, FFP is an unlikely distinguishing feature between populations in groups such as A2. AARD (2005) shows that the number of days with temperature below 5°C is similar

between much of northern Alberta and lower to medium slopes of the Rocky Mountains. Thus, there may be some climatic similarities between distantly separated regions that are not captured by P_{I_1} , which is based on average temperatures and precipitations. Identifying and characterizing regions in terms of climatic indicators that capture critical growth limiting factors would better explain the association of populations in A2.

An example of geographically separated populations with similar climate only for some of growth limiting variables can be seen in A5. Populations 32 and 37 are separated by 395 m in elevation and about 1° of latitude.

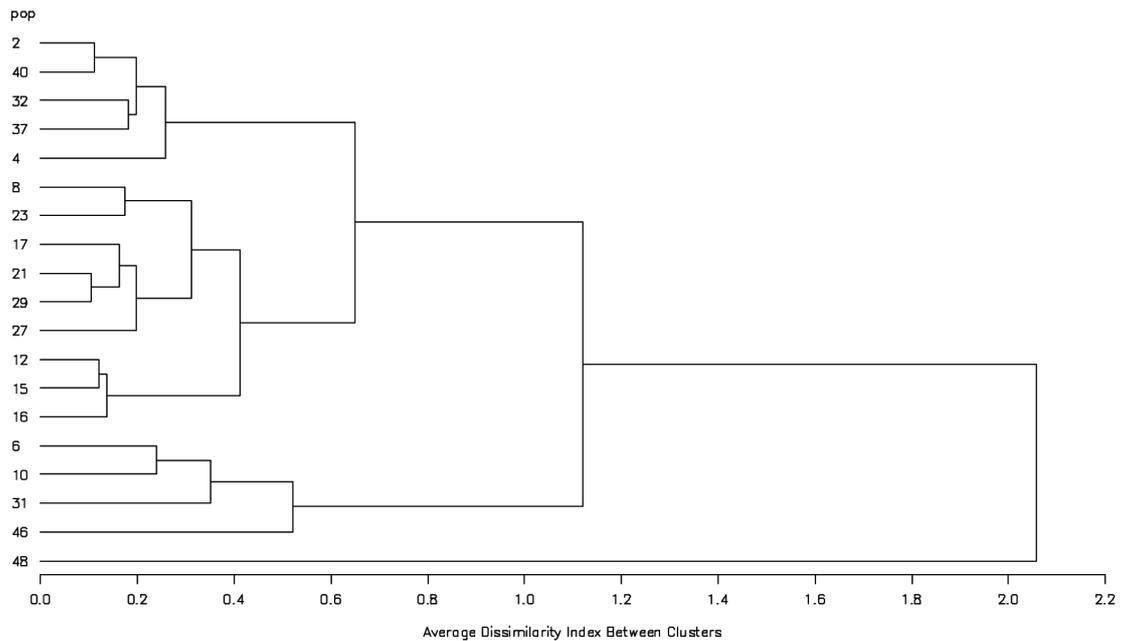


Figure 4. – Dendrogram illustrating the clustering of white spruce populations based height and diameter growth measured at different ages on eight sites in Alberta, Canada.

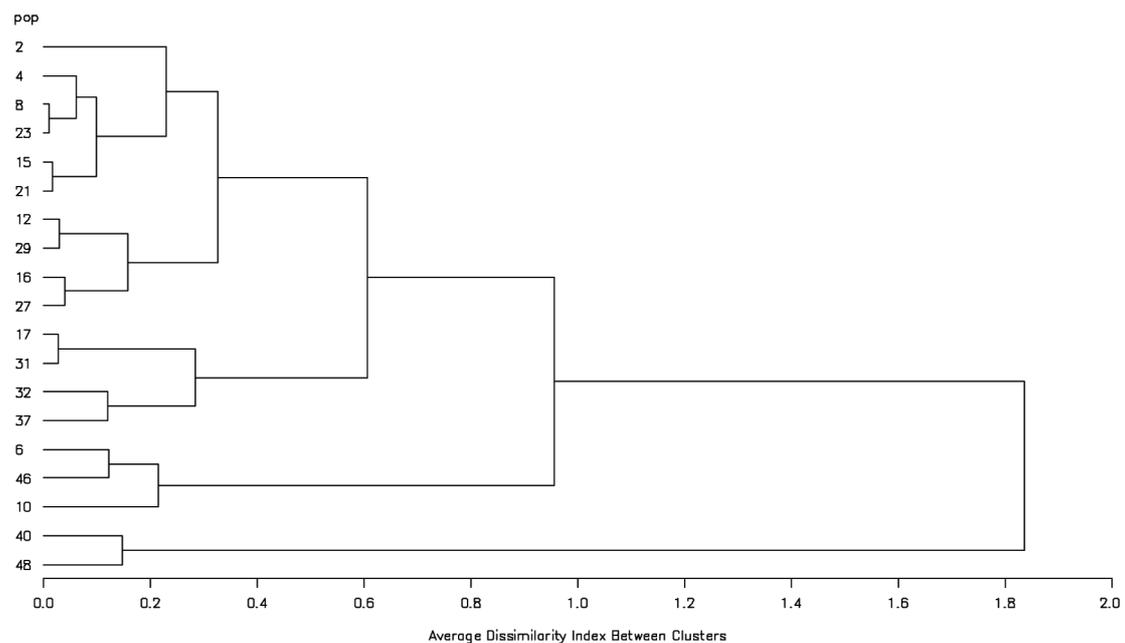


Figure 5. – Dendrogram illustrating the clustering of white spruce populations based on predicted optimum climates (P_{O_1}) for height and diameter growth in Alberta, Canada.

With a slightly northerly origin, population 37 has about the same NDD as population 32 at a higher elevation south (Table 1). Thus, climatic similarity for populations in A5 is reflected in overall winter temperature defined by NDD. In addition to chilling, the correlation between winter temperatures and tree growth is related to the timing of initiation and cessation of growth, which determines the length of the growing season and the amount of annual shoot growth. Similarity in \hat{P}_{O_1} for populations in A4 is probably a statistical anomaly, because there is no conceivable climatic similarity between the two populations.

Figure 5 shows population 2 slightly separated from other high latitude populations. From multiple comparisons, this population differ significantly ($P > 0.05$) from all others, except 4, 8 and 23. Population 2 is geographically and climatically the closest to site B. As previously discussed, site B does not anchor the response functions for population 2 at the same extent as it does for other populations. Consequently, population 2 has the lowest r^2 for 7 of the 8 traits (Table 4). Poorly fitting response functions are generally less likely to produce reliable predictions of optimum climates, which may explain the separation of populations 2 from all others.

Generally, incidences in which populations of distinct geographic or climatic origins were grouped together in terms of \hat{P}_{O_1} constitute a minor component of results in this study. This suggests that populations from similar climates may generally be expected to have similar optimum climates.

Optimum Climate: Height vs. Diameter

Multiple comparisons of height and diameter showed that predicted \hat{P}_{O_1} differed significantly ($P < 0.0001$) between D24 and H24, D27 and H27 but not H21 and D21. The \hat{P}_{O_1} for diameter growth was warmer, moister and less continental than that of height growth (Table

4). This may be explained partly by differences in the strength and trajectory of the response functions whereby r^2 was higher for diameter than height (Table 4). In addition, if non-climatic factors were to affect height more than diameter as previously explained, improvement in heat and moisture would be reflected in an increase in diameter more than height growth.

Optimum Climate: Age Trend

The change of \hat{P}_{O_1} with tree age was analyzed by comparing \hat{P}_{O_1} of the earliest measurements of height and diameter with \hat{P}_{O_1} of the same trait at subsequent ages. Multiple comparisons showed that \hat{P}_{O_1} of H12 was significantly ($P < 0.01$) different from that of H21 and H24 but not H15 and H27. For diameter, \hat{P}_{O_1} for D21 differed with that of D24 and D27 ($P < 0.01$). Similarity of \hat{P}_{O_1} between H12 and H27, and inconsistencies in the direction of change in the value of optimum climate for both height and diameter renders a few observed significant cases inconsequential. Because ages at which measurements were made do not correspond to any ontogenetic stage in the development of white spruce, observed significant cases probably represent random events.

Inhabited vs. Optimum Climate

Inhabited population climate (P_{I_1}) scores ranged from -5.792 to 4.485, indicating a high variability in the climate of seed origin (Table 1). In contrast, the mean optimum climate for populations (\hat{P}_{O_1}) ranged from -1.001 to 0.842 with 14 of the 19 populations having \hat{P}_{O_1} between 0.0 and -1.001 (Table 4). In absolute value, P_{I_1} and \hat{P}_{O_1} differed by 0.133 to 4.947 (average 2.459), with the largest differences (2.339 to 4.947) involving populations from high latitudes and high elevations (Table 4). In contrast, P_{I_1} and \hat{P}_{O_1} differed only by 0.133 to 1.481 for populations at mid-latitudes and mid-elevations. The paired T-test showed that the differences between P_{I_1}

Table 4. – Coefficient of determination, optimum climate and differences between optimum climate and climate currently inhabited by the populations.

Population	Coefficient of Determination (r^2)								\hat{P}_{O_1}								\hat{P}_{O_1}	$P_{I_1} - \hat{P}_{O_1}$
	H12	H15	H21	H24	H27	D21	D24	D27	H12	H15	H21	H24	H27	D21	D24	D27		
2	0.35	0.09	0.23	0.23	0.27	0.49	0.43	0.53	-0.901	-1.046	-0.510	-0.755	-1.134	-0.470	-0.206	-0.481	-0.688	3.310
4	0.47	0.32	0.35	0.44	0.50	0.62	0.57	0.66	-0.815	-0.914	-0.546	-0.691	-0.791	-0.465	-0.196	-0.213	-0.579	2.782
6	0.62	0.35	0.40	0.46	0.53	0.76	0.54	0.72	-0.729	-0.839	-0.922	-1.284	-1.333	-0.703	-0.566	-0.557	-0.867	4.150
8	0.48	0.24	0.45	0.41	0.51	0.80	0.71	0.76	-0.773	-1.002	-0.535	-0.644	-0.655	-0.346	-0.094	-0.328	-0.547	3.178
10	0.48	0.20	0.17	0.25	0.29	0.47	0.38	0.46	-0.855	-1.118	-0.744	-1.300	-1.461	-0.505	-0.227	-0.555	-0.846	4.947
12	0.65	0.52	0.72	0.65	0.67	0.86	0.84	0.83	-0.582	-0.455	-0.344	-0.405	-0.418	-0.306	-0.064	-0.115	-0.336	1.481
15	0.65	0.52	0.67	0.71	0.75	0.91	0.89	0.84	-0.748	-0.836	-0.441	-0.438	-0.585	-0.411	-0.175	-0.199	-0.479	-0.133
16	0.53	0.34	0.56	0.53	0.57	0.77	0.81	0.90	-0.618	-0.565	-0.261	-0.318	-0.323	-0.107	0.272	0.186	-0.217	-1.164
17	0.61	0.27	0.60	0.52	0.62	0.75	0.77	0.81	-0.178	0.157	0.206	0.114	0.117	0.189	0.511	0.343	0.182	0.216
21	0.47	0.30	0.48	0.51	0.52	0.80	0.79	0.80	-0.853	-0.834	-0.445	-0.511	-0.646	-0.396	-0.089	-0.225	-0.500	2.448
23	0.54	0.31	0.43	0.46	0.53	0.81	0.72	0.79	-0.702	-0.879	-0.522	-0.564	-0.623	-0.447	-0.199	-0.329	-0.533	0.698
27	0.66	0.46	0.54	0.55	0.58	0.79	0.76	0.75	-0.609	-0.606	-0.167	-0.242	-0.250	-0.201	0.043	-0.044	-0.259	0.514
29	0.67	0.31	0.53	0.47	0.51	0.80	0.74	0.76	-0.571	-0.564	-0.280	-0.331	-0.456	-0.291	0.004	-0.145	-0.329	-2.359
31	0.70	0.41	0.52	0.49	0.58	0.67	0.71	0.78	-0.027	0.151	0.375	0.139	0.055	0.163	0.439	0.391	0.211	-3.552
32	0.88	0.65	0.73	0.80	0.87	0.85	0.87	0.92	-0.364	-0.111	0.002	-0.027	-0.055	0.008	0.354	0.315	0.015	-3.093
37	0.68	0.44	0.71	0.76	0.76	0.88	0.89	0.93	-0.391	-0.205	-0.108	-0.089	-0.136	-0.033	0.261	0.103	-0.075	-2.386
40	0.52	0.39	0.64	0.70	0.78	0.86	0.88	0.92	-0.009	0.638	0.726	0.560	0.498	0.620	1.571	1.387	0.749	-2.339
46	0.40	0.20	0.23	0.26	0.28	0.41	0.33	0.42	-1.061	-1.146	-0.829	-1.015	-1.712	-0.837	-0.625	-0.782	-1.001	-4.327
48	0.74	0.59	0.58	0.58	0.67	0.54	0.58	0.76	0.402	0.761	0.956	0.650	0.929	0.602	1.476	0.964	0.842	-3.643
Mean	0.58	0.36	0.50	0.52	0.57	0.73	0.70	0.75	-0.547	-0.496	-0.231	-0.376	-0.473	-0.207	0.131	-0.015	-0.277	

P_{I_1} -inhabited population climate; \hat{P}_{O_1} – predicted optimum climate for individual traits; \bar{P}_{O_1} – mean predicted optimum climate averaged over response function on individual traits ($1/2 \sum \hat{P}_{O_1}$); H12, H15, H21, H24 and H27 – total height at ages 12, 15, 21, 24 and 27 years from seeds, respectively; D21, D24 and D27 – total diameter at breast height at age 21, 24 and 27 years from seeds, respectively. All response functions with $r^2 \geq 0.78$ and $r^2 \geq 0.70$ are significant at 5% and 10% level of probability, respectively.

and $\hat{P}_{\bar{O}_1}$ were significant ($t = 7.49$, $P < 0.0001$). These results show that populations at high latitudes and those at high elevations in Alberta inhabit suboptimal climates.

Studies in lodgepole pine (REHFELDT et al., 1999) and Scotch pine (*Pinus sylvestris* L.) (REHFELDT et al., 2002) showed that populations, especially those at high latitudes and high elevations often inhabit suboptimal climates. This was also evident in the Ontario studies by THOMSON and PARKER (2008) and THOMSON et al. (2009) where the differences between inhabited and optimum climates of jack pine and black spruce were greater for populations from north of the sampled area than those from the central and southern latitudes. In lodgepole pine (REHFELDT et al., 1999; WANG et al., 2006) and white ash (*Fraxinus americana* L.) (ROBERDS, 1990), a population's optimum location existed at the centre of the species' natural range where climate is the mildest and populations of highest growth potential have also evolved. In the present study, P_{I_1} was developed using data from most of the white spruce range in Alberta (Figure 1). Generally, the $\hat{P}_{\bar{O}_1}$ for 14 of the 19 populations (Table 4) correspond to the P_{I_1} of populations from a region between latitude 54°N and 56°N and elevation of 550 m and 823 m (mostly 600 to 700 m). This region is also a source of populations with the highest growth potential over wide range environments in Alberta. Thus, results of this study are consistent with expectations from studies of other conifers.

Conclusions

In this study, we used time series height and diameter data to characterize populations according to their growth potential and optimum climate for growth. Within the limits of the sampled populations, test environments and the analyses performed, we conclude that (1) white spruce in Alberta is genetically differentiated for growth potential along a climatic pattern determined by latitude and a complicated topography; (2) populations differ significantly in terms of predicted optimum climate, even though the range of their optimum climate may be narrower than the range of their inhabited climate; (3) the predicted optimum climate for diameter was warmer, moister and less continental than optimum climate for height growth suggesting that a better climate may support higher diameter than height growth; (4) in light of inconsistent age trends of predicted optimum climate for both height and diameter, there was no evidence to suggest that the optimum climate for growth potential is age-dependent; (5) although exceptions may be found, geographically or climatically similar populations can be expected to exhibit similar optimum climate; and (6) populations at high latitudes and high elevations inhabit climate that is highly suboptimal than populations at mid-latitudes and mid-elevations.

Management Implications

Findings of this study may be used to (1) modify seed transfer guidelines across existing seed zone boundaries in the interim, and in the long term, amalgamate some

of the seed zones to align them with the observed pattern of genetic variation; (2) realizing the pattern of genetic variation provides a mechanism for designing an effective gene conservation programme for white spruce in Alberta; and (3) although climate change is out of the scope of this study, the observed pattern of genetic variation may be used to plan for assisted population migration in the event of climate change.

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