Multivariate Analyses of Causal Correlation between Growth and Climate in Sitka Spruce

By P. Xu[1])[3]), C. C. Ying[2]) and Y. A. El-Kassaby[1])[4])

(Received 18th July 2000)

Abstract

Growth traits of 43 IUFRO Sitka spruce (*Picea sitchensis* (Bong.) Carr.) provenances (populations) at 10 test sites in British Columbia were analyzed in relation to 10 climatic variables of the test sites and the population origins for the first 20 years after planting. Multivariate analyses, canonical correlation and redundancy analyses, were used to examine the climatic effect of the test sites on tree growth and the forcing effect of climate at population origin on population differentiation. The analyses present a tractable multivariate framework on the inter-relationship between growth and climate. The results suggested an age trend in which control of tree growth shifted from genetic to environmental components and from temperature- to moisture-related climatic factors of the test sites as the tree aged. Despite the fact that Sitka spruce is a highly moisture sensitive species, temperature (winter coldness) and photoperiod (likely as a cue signal) at population origin might have played the major forcing role in natural selection for population differentiation. Based on the experiment-wise analysis, it is estimated that up to 63% of the genetic variability in growth of the species was attributable to the climatic variability of the population origins.

Key words: Sitka spruce, provenance trial, growth traits, climatic condition; multivariate analysis.

Introduction

Sitka spruce (*Picea sitchensis* (Bong.) Carr.), a fast growing conifer species native to North America, occurs in a long and narrow land strip along the Pacific west coast, the 'fog belt', covering over 22 degrees of latitude (Daubenmire, 1968). Mild year-long temperature and high annual rainfall characterize the prevailing climate within the species natural range (Harris, 1990; Peterson *et al.*, 1997). Farr and Harris (1979) reported up to one-meter increase in site index per degree of latitudinal change from north to south, reflecting the determinant effect of heat sum. Within this climate gradient, Sitka spruce attains its best growth at well-aerated, moist and nutrient-rich sites (Kayahara and Pearson, 1995). In British Columbia (B. C.), many productive sites have the capacity to generate a site index of 40 m (predicted height at age 50), comparable to that of coastal Oregon and Washington. Though a coastal species, its range extends well inland along river valleys in British Columbia where maritime climate is still prevailing (Peterson *et al.*, 1997). Along these river valleys, e.g. the Nass-Skeena river basin in northwest B. C., Sitka spruce comes into contact with white spruce (*Picea glauca* (Moench) Voss) and natural hybridization occurs (Roche, 1969).

White pine weevil (*Pissodes strobii* (Peck)) is the most damaging natural enemy for Sitka spruce. Frequent attacks of the weevil on Silka spruce's young stands can so severely deform a plantation as to render it unharvestable (Alfaro, 1982). This problem has limited any significant planting of Sitka spruce to the weevil-free northern Vancouver Island and Queen Charlotte Islands despite its high timber value (Ying, 1991; Peterson *et al.*, 1997). Contrarily, Sitka spruce is abundant as a plantation tree over large areas of western Europe (British Isles in particular), a successful endeavor that is attributable to its exceptional growth vigor, straight form and quality wood, in addition to its versatility with soil conditions and tolerance of tidal climate (Holmes, 1987; Hermann, 1987). Much of the knowledge and experience of its plantation ecology and genetic properties have been learned in Europe (cf. Henderson and Faulkner, 1987; cf. Ying and McKnight, 1993).

Sitka spruce is highly variable in economical (Peterson *et al.*, 1997) and adaptive traits (Falkenhagen, 1977 and 1978; Roche and Haddock, 1987; Ying, 1997) as well as biochemical genetic markers (Yeh and El-Kassaby, 1980). Variability in growth and adaptive traits (e.g. cold tolerance) are largely habitat-correlated and genetically based (Burley, 1966; Roche, 1969; Falkenhagen, 1977 and 1978; Farr and Harris, 1979; Morgenstern, 1996).

Attempting to explore the species' genetic potential for selection of productive and weevil-tolerant seed sources for reforestation, the B.C. Ministry of Forests, in conjunction with the International Union of Forest Research Organizations (IUFRO), established three series of Sitka spruce long-term provenance trials in the early 1970s. These trials encompassed a total of 43 provenances (populations) tested at 12 locations. Growth of trees, i.e., total height and diameter at breast height (DBH) of individual trees were measured periodically over 20 years from planting. The effective use of productive and weevil-tolerant populations in reforestation programs, which are ecologically based and have taken into consideration the uncertainties facing environmental changes such as global warming, requires a good understanding of the dynamic correlation of genetic variability in the context of ecological and climatic setting.

Illingworth (1978) and Ying (1997) examined growth variation of these populations in relation to geographic coordinators of latitude, longitude and elevation (surrogate for environment) for the purpose of identifying suitable sources for reforestation. This approach, assuming temporal environmental variability remains constant in relation to geographical coordinates, is static (Rehfeldt *et al.*, 1999). Both genetic and climatic factors play determinant roles on growth of Sitka spruce, but the magnitude of their role may change from early to late years. We thus focused on the temporal pattern of climate effect on growth and the relative magnitude of effect of climatic variables at both test site and population origin. The main objec-

---

[1]) Department of Forest Sciences, Faculty of Forestry, The University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada

[2]) British Columbia Ministry of Forests, Research Branch, P. O. Box 9519, Stn. Prov. Govt. Victoria, British Columbia V8W 9C2, Canada

[3]) Current address: Department of Biology, 208 Mueller Lab., Pennsylvania State University, State College, Pennsylvania 16802, USA.

[4]) Corresponding author: Y. A. El-Kassaby
e-mail: yelkassaby@cellfor.com
phone: (250) 381-1404 extension 230
fax: (250) 381-0250

tive of this study is to establish firstly the correlation between site climate and growth of Sitka spruce in general, and secondly the magnitude of the forcing effect of climate at population origin on genetic differentiation of populations. Provenance, geographic origin of seedling progenies, represents a sample of origin-specific population. The term provenance and population are used in synonym in this report and tree age refers to the number of years after planting.

Experimental Design and Data Profile

The Sitka spruce provenance trials were established in 1973 and 1975 in three series, with a total of 43 populations initially tested at 12 sites (*Fig. 1*). Complete lists of the population origins and test sites, including the geographic locations and average growth performances during the measured years, are posted on the web site http://www.personal.psu.edu/users/p/x/pxx 102/public.htm.

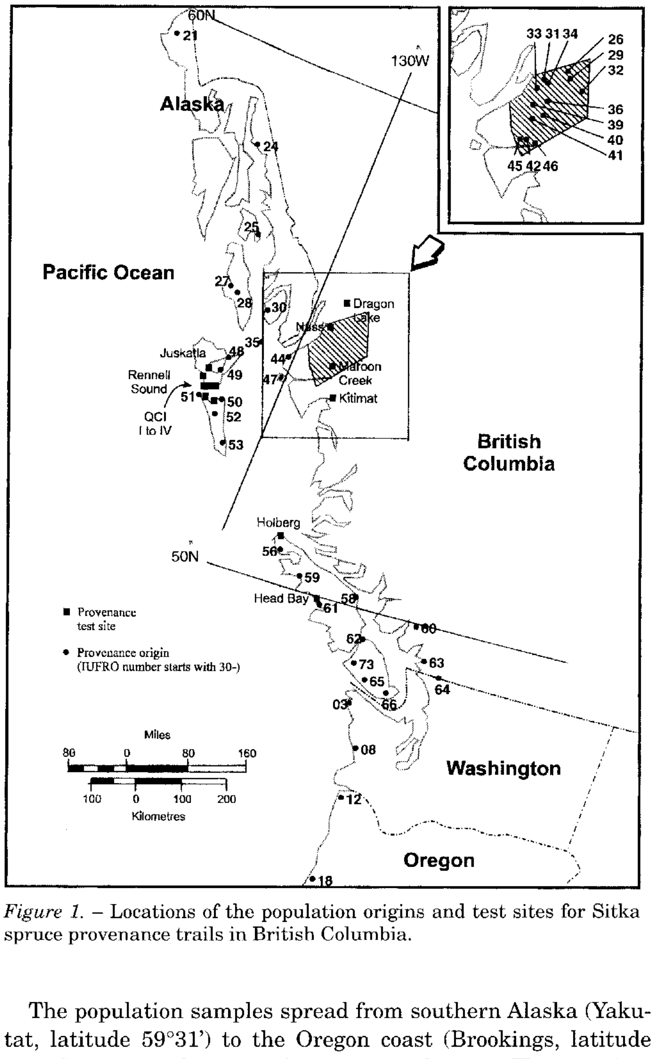

Figure 1. – Locations of the population origins and test sites for Sitka spruce provenance trails in British Columbia.

The population samples spread from southern Alaska (Yakutat, latitude 59°31') to the Oregon coast (Brookings, latitude 42°15') covering the species' main natural range. The test sites extends from 49°48' N to 55°19' N, 126°28' W to 132°30' W, and sea level to 600 m. Among these sites, Dragon Lake (DL) is sub-continental and outside the natural distribution of pure Sitka spruce. Maroon Creek (MN) at elevation 600 m is at the periphery climatically, and Juskatla (JU) is central climatically, but edaphically marginal (poor drainage). The remaining nine test sites cover the range of natural habitats considered ecologically central where Sitka spruce is the choice species for reforestation (POJAR *et al.*, 1987; PETERSON *et al.*, 1997), unless the threat of the white pine weevil is of major concern. The climate gradient where Sitka spruce occurs naturally in coastal B.C. is weil represented by the 12 test sites, except a portion of the mid-coast where access is extremely difficult even today (*Fig. 1*). However, diverse multiple population samples tested in diverse environments seem to be particularly attractive for the evaluation of the ecological behavior of the species in relation to the environmental factors.

The provenance trials were implemented with completely randomized block design (KUEHL, 1994) at all test sites, with varied numbers of blocke across different series. In Series I, the four test sites on Graham Island (QC I to IV) have four to six blocke each, randomly accommodating the same set of 38 populations. Series II and III have nine blocke at each site and each block has 10 populations, six of which overlapp so that a total of 14 populations were tested in Series I and II. In all the three series, every population is represented with either a nine-tree row or square plot within each block. Trees were planted at 3 m x 3 m spacing. The total number of trees planted in Series I was 6840 (9 trees x 38 populations x 20 blocks), and that in Series II and III was 3240 each (9 trees x 10 populations x 9 blocke x 4 sites). As of age 20, mortality rates were low (0.04 ~ 14.69%) except at Nass River (NS) and Dragon Lake (DL) where 31.98% and 51.73% of the trees died, respectively. High mortality at NS was caused mainly by road expansion, whereas winter killing was the major cause at DL, where only the local population grew normally (YING, 1991 and 1997). The two sites were therefore excluded from this study, leaving 10 test sites with a total of approximately 220 population-by-site means for each growth measurement (see below).

Growth of the trees was measured individually. Height of the tree was measured to the nearest decimeter in the 3rd, 6th, 10th, 15th and 20th year after planting (referred to as HT3, HT6, and so on). Diameter at breast height (DBH) was measured to the nearest millimeter in the 6th (but not at all sites), 10th, 15th and 20th year (referred to as DBH6, DBH10, etc.). Where a tree was less than 4 meters in height, its diameter was measured at 1/3 of the total height. When both height and diameter of a tree were available, tree volume was calculated in cubic decimeters (referred to as VOL6, VOL10, and so on for the measured years), using KOVATS' (1977) volume function for juvenile conifer trees. Diameter and volume data of living trees were not complete at all test sites until the 15th year after planting.

Ten macro climatic variables for both test sites and population origins were used for the analyses of growth-climate correlation in this study (*Table 1*). The ranges of these climatic indices are provided in *table 1* for both test sites and population origins. These variables generally define temperature, moisture and photoperiod conditions. The climatic data for the population origins were obtained from the IUFRO information system (LINES, 1973), and that for the test sites in Series II and III were from the weather stations climatically close to the individual test sites with complete weather records over the past five decades. For the test sites in Series I, we estimated the values for these variables using REHFELDT *et al.*'s climate models (1999) because no close weather station was available for the four sites (QC I to IV). The climate variables for test sites are prefixed with 'S' (SMAT, SMAP, and so on), and those for population origins with 'P' (PMAT, PMAP and so on). The climatic data are available from the author upon request.

Methods of Statistical Analysis

Effect of test site climate on tree growth

Repeated growth measurements of the same individual trees are innately correlated. Similarly, correlation can be expected

Table 1. – The ten macro-climate variables used in this study, along with the range of these climate indices for the test sites and population origins.

Symbol	Definition of the climate variable	Range for test sites	Range for population origins
MAP	Mean Annual Precipitation (mm),	1100 ~ 3850	3132 ~ 5250
MSP	Mean Summer Precipitation (mm) (May-September),	300 ~ 760	650 ~ 1550
MAT	Mean Annual Temperature (°C),	3.0 ~ 8.8	2.4 ~ 12.0
MTCM	Mean Temperature of the Coldest Month (i.e., January) (°C),	–13.0 ~ 2.7	–12.0 ~ 8.4
MTWM	Mean Temperature of the Warmest Month (i.e., July) (°C),	11.2 ~ 17.4	11.6 ~ 17.5
NFFD	Annual Number of Frost Free Days (day),	135 ~ 327	170 ~ 345
FFP	Annual continuously Frost Free Period (day),	50 ~ 240	95 ~ 270
DD5	Annual accumulated Degree Days above 5°C (degree day),	990 ~ 1845	1020 ~ 2080
DD0	Annual accumulated Degree Days below 0°C (degree day), and	32 ~ 1050	10 ~ 900
DAYL	Accumulated DAY-Length (hour) during growth season (April-October), derived from latitude.	3017 ~ 3128	2907 ~ 3246

between climatic variables derived from temperature and precipitation records at the same weather stations. It seems to be biologically apt to employ multivariate correlation, which takes into account the innate relationships among these highly correlated variables. We thus used canonical correlation analysis to delineate the multivariate relationships between the two groups of variables, the eight growth variables (HT3, HT10, HT15, HT20, DBH15, DBH20, VOL15 and VOL20) and the ten macro-climatic variables for the test sites listed above, in an attempt to unveil the temporal pattern of response in growth of Sitka spruce (represented by 43 populations) to test site climate.

Canonical correlation analysis is a multivariate statistical method suitable for studying simultaneous relationships between two groups of self-correlated variables (GITTINS, 1985; JOHNSON and WICHERN, 1998). The analysis starts with deriving two sets of canonical variables that are linear combinations of the original variables of the two groups, respectively. The correlation between each pair of the canonical variables are maximized in derivation such that the first pair of canonical variables has the maximum correlation with each other, and the second pair has the second highest correlation, and so on. The relationships of the two groups of variables are evaluated by the canonical correlation between pairs of canonical variables. With as large a sample size as in this study, the significance of the kth and all its following canonical correlations can be tested by a likelihood ratio test under the assumption that at least one of the two sets of the variables is multivariate normal (JOHNSON and WICHERN, 1998). The loading and cross-loading of each original variable onto the two sets of canonical variables are defined by the correlation coefficients between the original variables and the canonical variables within and between groups, which is termed canonical structure. The relative importance of each original variable to the relationships between the two sets of canonical variables is quantified by the canonical structure. The extent to which the original variables are represented by the canonical variables can be evaluated by the proportions of raw variations in original variables explained by both sets of canonical variables, which is referred to as the redundancy of the canonical variables. The above analysis was conducted using SAS CANCORR procedure (SAS, 1990). To avoid the scale problem of the original variables, canonical variables in this analysis were derived based on the correlation matrices within and between the two groups of original variables at the population-by-site mean level (XU, 1998).

Forcing effect of climate at population origin on population differentiation

That population variability is habitat-correlated in adaptive mode (ROCHE, 1969; FALKENHAGEN, 1977 and 1978; MORGENSTERN, 1996) implies natural selection instigated through environmental variability at population origin forcing genetic differentiation. Having multiple populations tested at multiple sites in this experiment also allows examination of the relationships between growth variations and climate variations at population origins. We are interested in the forcing effect of climate on population differentiation. That is, we want to estimate the proportion of population variation in growth traits that can be explained by the climatic variability at their origin, and to uncover climatic factor(s) that may have played causative roles. We employed redundancy analysis for this purpose.

Redundancy analysis is an alternative to canonical correlation analysis (WOLLENBERG, 1977). The two methods differ from each other only in that, in redundancy analysis the eigenvectors for determining canonical variables are generated to maximize the variations in one group's original variables cross-explained by the opposite group's canonical variables, rather than to maximize the correlation between pairs of canonical variables which is the case in canonical correlation analysis. To be more specific, redundancy analysis generates two sets of canonical variables (called 'redundancy variables' to differ from canonical analysis) based on the two groups of original variables such that, the first redundancy variable of one group maximally accounts for variations of the opposite group, and the second accounts for the second maximal variations of the opposite group, and so on. In this study, by using redundancy analysis on growth variables in relation to climate variables at population origins, growth variations cross-explained by climate variability of population origins were quantified to the maximum. Conceptually, redundancy analysis treats one set of variables as response variables and another as explanatory variables, whereas no such differentiation exists in canonical correlation analysis. The former is equivalent to simple regression and the latter to simple correlation in the case of a single pair of variables. See WOLLENBERG (1977), and JOHNSON and WICHERN (1998) for mathematical details and GITTINS (1985) for application in ecology of these two multivariate analyses.

Similarly as with canonical correlation analysis, the loading (represented by the correlation coefficient) of an original variable to the first redundant variable of its own group indicates the relative importance of this original variable in explaining variations of the opposite group. That is, the major climatic factor(s) driving genetic differentiation among the populations in growth can be unveiled by comparing the redundancy loadings of the original climatic variables to the first redundant variable of its own group. We conducted the redundancy analysis on ten growth variables (i.e., HT3, HT6, etc.) and ten climatic variables for population origins (i.e., PMAT, PMTCM, etc.), through matrix operations using SAS IML procedure. (The SAS code for this analysis is available from the above mentioned web site). Again, the redundancy analysis is based on the correlation matrices within and between the two groups of original variables to avoid the scale problem. The growth related correlation matrices were derived from plot means for the purpose of comparing our previous analysis of variance of the growth variation components due to population variation (XU, 1998).

It may be worthwhile to point out that a redundancy variable maximizes the redundancy of the opposite group but does not necessarily maximize the redundancy of its own group. Consequently, the first redundancy variable of either group may be a good representative of the opposite group, but not necessarily of its own group. On the other hand, canonical correlation analysis only maximizes the canonical correlation between two groups of variables, not the redundancy of one group upon another, so that the biological meaning of a canonical variable can become blurred if its redundancy is low with respect to the original variables. Effective use of either analytical approach depends on the focal biological questions that we are seeking to answer.

Results and Discussion

Effect of test site climate

The canonical correlation analysis of the eight growth variables and the ten climatic variables for test sites yielded eight pairs of canonical variables. The canonical variables derived for growth variables were named as Grow1, Grow2, and so on, and those for test site climatic variables were named as Sclim1, Sclim2 etc. All pairs of canonical variables were significantly correlated ($p<0.0001$ for the first six pairs), as shown by the likelihood ratio tests (*Table 2*). The first pair of canonical variables accounted for nearly 60% of the total canonical variation and had the maximal canonical correlation at $R^2=0.954$; and the second pair had canonical correlation at $R^2=0.872$ and accounted for an additional 19% of the total canonical variation (*Table 2*). High correlations imply strong influence of test site climate on tree growth. The first two pairs of canonical variables, accounting for more than two thirds (79%) of the total canonical variation, may be adequate to reveal the intrinsic structure of multivariate correlation. We thus focus the examination of the temporal mode of growth and site climate multivariate relationship on the first two pairs of canonical variables (i.e., Grow1 with Sclim1 and Grow2 with Sclim2, *Tables 3* and *4*).

In *table 3,* all growth variables had moderate to strong positive correlation with Grow1, and the correlation coefficient increased with age (with a sharp increase from ages 3 to 10). This age-related pattern of correlation suggests that Grow1 contained a strong temporal component, representing the vector of cumulative growth over the years. The pattern of correlation was most apparent with height growth, a significant adaptive trait that confers the advantage in competing for light and space for vegetative and reproductive vigor. This age-related pattern held also with the correlation between growth variables and Sclim1 (*Table 3*) which suggests the causative role of site climate on growth as well as its temporal pattern.

Table 2. – Canonical correlations and explained canonical variance percentage of each pair of canonical variables between growth variables and test site climatic variables.

Pair of Canonical variables	Canonical Correlation (R^2)	Explained Variance (%)	P value*
1st	0.954	59.2	<0.0001
2nd	0.872	19.3	<0.0001
3rd	0.806	11.8	<0.0001
4th	0.693	6.4	<0.0001
5th	0.398	1.9	<0.0001
6th	0.266	1.0	<0.0001
7th	0.088	0.3	0.0002
8th	0.040	0.1	0.0167

*) Likelihood Ratio test with F approximation.

Table 3. – Canonical structure of the original growth variable with the first two pairs of canonical variables, represented by the correlation coefficients.

Original growth variables	Growth canonical variables		Test Site climatic canonical variables	
	Grow1	Grow2	Sclim1	Sclim2
HT3	0.483	-0.570	0.471	-0.532
HT10	0.794	-0.260	0.776	-0.243
HT15	0.916	-0.174	0.895	-0.163
HT20	0.960	-0.064	0.937	-0.060
DBH15	0.801	0.120	0.782	0.112
DBH20	0.813	0.229	0.794	0.214
VOL15	0.855	0.013	0.835	0.012
VOL20	0.877	0.045	0.856	0.042
Total Redundancy	73.9%	1.7%	70.5%	1.5%

Table 4. – Canonical structure of the test site climatic variables with the first two pairs of canonical variables, represented by the correlation coefficients (in descending order for the first pair of canonical variables).

Original climatic variables	Test site climatic canonical variables		Growth canonical variables	
	Sclim1	Sclim2	Grow1	Grow2
SMSP	0.864	-0.318	0.844	-0.297
SMAP	0.609	-0.463	0.595	-0.432
SNFFD	0.596	-0.453	0.583	-0.423
SMTCM	0.555	-0.471	0.542	-0.440
SMAT	0.441	-0.673	0.430	-0.628
SFFP	0.289	-0.250	0.282	-0.233
SDAYL	0.167	0.787	0.163	0.735
SDD5	-0.350	-0.584	-0.348	-0.546
SMTWM	-0.337	-0.653	-0.329	-0.609
SDD0	-0.300	0.202	-0.293	0.188
Total Redundancy	34.0%	19.9%	32.5%	17.3%

Canonical structure for test site climate variables revealed that growing season precipitation (SMSP) had the strongest correlation with Sclim1, and several other climatic variables such as SMAP, SMAT, SMTCM and SNFFD also had high correlation with Sclim1 (*Table 4*). In essence, Sclim1 represents firstly the amount of precipitation (SMSP and SMAP), and secondly, winter coldness (SMTCM) and length of growing season (SNFFD) of site climate. Importantly, the same mode of correlation of climate variables with Grow1 also held (*Table 4*). Comparing the temporal pattern of canonical structure in *table 3* with the mode of correlation in *table 4*, a structured correlation framework becomes clear. First, the role of site climate becomes increasingly deterministic as trees grow older (age association of increasing correlation of growth with Sclim1, *Table 3*), which implies declining effect of the species' biological (genetic) factor on growth in the context of interactive influence of species and site climate where the trees grow. Second, winter coldness and length of growing season played an important role during the establishment phase of tree growth, and after that precipitation becomes increasingly critical to sustain the growth rate. In short, canonical structure of the first pair of canonical variables has provided a diagnostic framework revealing a temporal structure of correlation within the set of growth variables and also between the sets of variables, that is, both the influence of genetics (innate growth determinant) and climate (environment where it grows) on the growth of Sitka spruce change with the age of the trees.

Canonical structure of the second pair of canonical variables was quite different from that of the first one. Within the set of growth variables, HT3 showed the strongest correlation with Grow2 and Sclim2 in the same direction (negative) (*Table 3*). Excluding HT3, correlation of both within and between sets was rather weak, judging from the magnitude of their correlation coefficients. Thus the second pair of canonical correlation appeared to reflect essentially the relationship of HT3 or early growth with site climate (*Table 3*). Canonical structure of Sclim2 revealed a contrast between winter harshness (SDAYL as indicator), and degree of mildness in temperature (SMAT and SMTWM) and amount of precipitation (*Table 4*). The opposite direction of correlation between SDD5 (cumulative degree days above 5 °C, an index of heat sum during the growing season) and SDDO (cumulative degree days below 0 °C, an index of winter coldness) rendered support to the above interpretation that canonical Sclim2 represents a contrast between mild versus harsh site climate. SDAYL is latitude-dependent and its strong correlation with Sclim2 ($r = 0.79$, *Table 4*) suggests a latitudinal connection, that is, the mild-harsh contrast is associated with a north-south gradient. Indeed, regression models (XU, 1998) indicated high sensitivity of southern populations to winter temperatures (suppressed expression of innate growth potential), and latitudinal division between southern and northern populations with respect to climatic sensitivity at 46°N to 48°N, approximately. Close parallel of the vectors of correlation coefficients of climate variables with both Sclim2 and Grow2 (*Table 4*) suggests high explanatory redundancy that seedling height growth (before year 10) was very sensitive to latitudinal location associated with temperature of test site. In short, the second pair of canonical variables reinforced the conclusion drawn from the first pair of canonical variables that indicated a temporal pattern of causal growth-site climate correlation, i.e., winter coldness played a deterministic role in seedling development of Sitka spruce at early ages.

The results are much in line with the conclusion by YING (1997) who analyzed the geographic trends in growth at different ages, and found appreciable declines in expression of latitudinal trend (i.e., genetic control) in height growth with increasing ages, except for a few extremely mild sites with strong maritime climate. Both studies support the notion that heritability of growth traits decline with age and are conditioned by environmental factors (NAMKOONG and KANG, 1990). The results also support the analysis of FARR and HARRIS (1978) that site productivity is closely associated with latitude ($R^2=0.99$) as a surrogate of total heat sum. However, they did not consider precipitation as another critical factor, somewhat different from what our analyses have indicated. This is most likely due to the distribution of their sites along the maritime coast, whereas ours are extended inland (*Fig. 1*). In practical terms, selection for genetic capacity for climatic adaptability can be more efficiently done at early ages, and selection of suitable planting sites (without severe moisture deficiency) is most critical in order to sustain growth vigor in reforestation.

We also examined the redundancy of the canonical variables, that is, the proportion of the variance in the original variables explained by the canonical variables. The results show that Sclim1, carrying 34.0% (*Table 4*) of original variation of its own group, explained 70.5% of original growth variation at the population-by-site mean level (*Table 3*). This indicates that growth variation is well accounted for by test site climatic conditions, which agrees with previous results (YING, 1997; XU, 1998) that test site influences were dominant on the overall growth variation. On the other hand, Grow1, which carries about 73.9% (*Table 3*) of original variation of its own group, accounted for 32.5% (*Table 4*) of the raw variation in test site climatic conditions. The wide geographic range of the population sample and significant population-by-site interactions (XU, 1998) contributed to the relatively low redundancy of canonical variables on test site climatic variation. The high redundancy of growth variations suggested high predictability of average growth performance in Sitka spruce from planting site climatic conditions, precipitation in particular. Our results support the study by WORRELL and MALCOLM (1990) in which they predicted Sitka spruce's productivity in Britain based on site elevation and climatic conditions of which moisture was heavily weighted.

It is worthy of notice that the temporal pattern of climatic sensitivities of tree growth in Silka spruce delineated in the above canonical correlation analysis is general to all the populations tested. Different populations, however, are expected to respond differently to the climate. This will be addressed in the next section.

Forcing effect of climate on population

Ten growth variables and ten macro-climatic variables at population origin were used in the redundancy analysis of climatic effect on population differentiation. Including DBH10 and VOL10 in the group of growth variables forced the removal of a certain number of observations at a few harsh test sites in order to generate a balanced rectangular matrix, but was

Table 5. – Original variations in growth and population origin climatic conditions cross-explained by the first three pairs of redundancy variables of the opposite group.

Original variables	**Growth redundancy variables**			**Population origin climatic redundancy variables**		
	GrowR1	GrowR2	GrowR3	Pclim1	Pclim2	Pclim3
Growth variables				5.23%	0.26%	0.16%
Population origin climatic variables	18.98%	0.68%	0.20%			

helpful in examining the age trend of genetic control in diameter and volume growth. The resulting ten pairs of redundant variables were named GrowR1, GrowR2, and so on for growth variables, and Pclim1, Pclim2, and so on for the climatic variables at population origin. The redundancies of these ten redundancy variables were all very low so that we only present the first three pairs of them (*Table 5*). The first growth redundancy variable (GrowR1) accounted for 18.98% of climatic variation, and the first climate redundancy variable (Pclim1) accounted for only 5.23% of the growth variation at plot mean level (*Table 5*). This seemingly low forcing effect of climate at population origin on the expression of growth traits was due largely to the high provenance-by-site interaction which accounted for about 40% of the total variation (Xu, 1998). Micro site variation of plot means, the input growth unit in redundancv analysis no doubt masked also the full expression of population growth.

The growth redundancy was somewhat greater if the input correlation matrix for growth variables was at the population-by-site mean level (in which case it was 8.7%, details not shown). We chose to use plot means instead of population-by-site means for growth variation in order to compare the present results with that of Xu (1998). Based on the experiment-wise analysis of variance (ANOVA), Xu (1998) estimated that about 8.33% of the growth variation (of all growth measurements) were due to genetic variability among the 43 populations. We could then deduce that the forcing effect of climate at population origin might account for a maximum of about 63% (i.e., 5.23% over 8.33%) of the population variability in growth. In other words, genetic variability among populations in Sitka spruce is highly habitat-correlated. Climate at population origin, acting as an agent of natural selection, played a major forcing role in population differentiation in growth.

The redundancy structure reveals relationships between the original variables and the redundancy variables of the opposite group. Since only the first redundant variables accounted for a meaningful amount of variation of the opposite group, we focused on the structure of the first pair of redundancy variables to examine the forcing effect of climate on population differentiation (i.e., Pclim1, *Table 6*).

Table 6. – Redundancy structure (canonical correlation coefficients) of the original variables with the first redundancy variable for population origin climatic variables (Pclim1).

Growth variable	Corr. Coeff. with Pclim1	Pop. climatic variable	Corr. Coeff. with Pclim1
HT3	0.359	PMAP	0.368
HT10	0.229	PMSP	0.080
HT15	0.153	PMAT	0.845
HT20	0.120	PMTCM	0.863
DBH10	0.241	PMTWM	0.199
DBH15	0.231	PNFFD	0.858
DBH20	0.232	PFFP	0.825
VOL10	0.232	PDD5	0.668
VOL15	0.204	PDD0	-0.873
VOL20	0.209	PDAYL	-0.835

The low rate of redundancy naturally resulted in low correlation between growth variables and Pcliml, none of which was greater than $|R| = 0.4$. However, the correlation pattern showed an association of decreasing coefficient with increasing age in height growth (*Table 6*). This suggests that the forcing effect of climate at population origin was more influential during the establishment phase than at late stages. The correlation structure of climatic variables at population origin with Pclim1 ought to shed some lights on the relative importance of different climatic variables in their forcing effect. Indeed, *table 6* reveals a low association of both precipitation-dependent variables (PMAP and PMSP) with Pcliml, which seems to rule out any primary role of precipitation affecting population differentiation. PDD0 and PDAYL showed the strongest correlation with Pclim1, but were in the opposite direction from other temperature-driven variables, PMAT, PMTCM, PNFFD, PFFP and PDD5 (*Table 6*). Both PDD0 (cumulative degree days below 0 °C) and PDAYL (cumulative day-length in growing season, a latitude-dependent variable) are indices of winter coldness and highly positively correlated ($R^2 = 0.74$). Their strong associations with Pclim1 indicated the significance of winter temperature as a forcing force in natural selection resulting in the north-south gradient mode of Sitka spruce population differentiation (Illingworth, 1978; Henderson and Faulkner, 1987; Ying, 1997). PDAYL is likely to function as a cue signal associated with photoperiod triggering the onset of growth cessation in the fall and beginning of growth in the spring. Sitka spruce is sensitive to photoperiod: the northern population from Alaska ceased growth in under a 13-hour photoperiod, while the southern population from the Oregon coast continued stem elongation even after the photoperiod declined to 8 hours. Similarly, northern populations exhibited a much more rapid development of primordial shoot than southern ones in response to the same rate of photoperiod decline (Pollard *et al.*, 1975). This species is susceptible to both spring and fall frost (Cannell, 1984 and 1985), and the population sensitivity to photoperiod change may reflect an adaptive mechanism to minimize frost risk (Pollard *et al.*, 1975). The high correlation of PMTCM (mean temperature of coldest month), in contrast to weak correlation of PMTWM (mean temperature of warmest month), with Pcliml seems to render further evidence in favor of winter rather than summer temperature as the major forcing factor.

In summary, the above redundancy structure reveals that 1) temperature, not precipitation, and winter, rather than growing season temperature seems to have played the major forcing role in population differentiation, 2) the forcing role of temperature at population origin is closely associated with photoperiod as an ecological cue resulting in a dominantly north-south mode of population differentiation, and 3) the forcing effect is likely instigated through natural selection at early ages of the tree (during the establishment phase). This redundancy structure fits the ecological framework within the species' primary natural habitats that is dominantly maritime climate with mild growing season temperature and rare occurrence of moisture deficiency (Peterson *et al.* 1997). In other words, only variation in winter temperature seems to be steep enough in instigating selection on population differentiation.

Conclusions

Both canonical and redundancy analyses succeeded in generating a structured and tractable framework of multivariate correlation from the three sets of very different but correlated variables that facilitates the examination of growth-climate inter-relationship. The first two pairs of canonical variables roughly accounted for over two thirds of the variation between growth and test site climate (*Table 2*), which implied high predictability of growth and yield of Sitka spruce plantations from planting site climate. Canonical structure (*Tables 3* to *4*) further suggested an age trend of growth-site climate inter-relationship, in which the control of tree growth, especially of height growth, shifted from genetic to environmental (climatic) components. Influence of site temperature on tree growth was strong before age 6, but availability of site moisture, particularly summer precipitation, was likely to become a determinant factor for sustained growth vigor.

The two-way multivariate inter-relationships using redundancy analysis revealed that thermal climate variables that define winter coldness played a major forcing role in population differentiation in growth performance (*Table 6*). This forcing effect seems to be instigated through association with photoperiod as the ecological cue signal, resulting in a predominantly north-south mode of population differentiation. A significant portion (up to 63%) of genetic variability in growth of the species might be accounted for by climatic variability of the source environments, acting as natural selection agents during population differentiation.

The results also indicate the effectiveness of canonical correlation approach in dimension reduction and data disentangling (Gittins, 1985).

Acknowledgments

This paper is based on a portion of a dissertation by P.X. submitted in partial fulfillment of the requirements for a M.Sc. degree at the Faculty of Forestry, the University of British Columbia. We are grateful to the British Columbia Ministry of Forests for supplying the invaluable data for this study. We also thank Drs. G. Namkoong and S. Aitken from the University of British Columbia for their critiques and suggestions on the initial manuscript of this paper. The study is supported by research grants made to Y.A.E., and by the U.B.C. Edward Bassette Memorial Award in Reforestation made to P.X.

References

Alfaro, R. I.: Fifty-year-old Sitka spruce plantations with a history of intensive weevil attack. J. Entomol. Soc. British Columbia **79**: 62–65 (1982). — Burley, J.: Genetic variation in seedling development of Sitka spruce, *Picea sitchensis* (Bong.) Carr. Planta. **99**: 283–289 (1966). — Cannell, M. G. R.: Spring frost damage on young *Picea sitchensis*. 1. Occurrence of damaging frosts in Scotland compared with Western North America. Forestry **57**: 159–169 (1984). — Cannell, M. G. R.: Autumn frost damage on young *Picea sitchensis*. 1. Occurrence of autumn frosts in Scotland compared with Western North America. Forestry 58: 131–143 (1985). — Daubenmire, R.: Some geographic variations in *Picea sitchensis* and their ecological interpretation. Can. J. Bot. **46**: 787–798 (1968). — Falkenhagen, E. R.: Genetic variation in 38 populations of Sitka spruce. Silvae Genet. **26**: 67–75 (1977). — Falkenhagen, E. R.: Parent tree variation in Sitka spruce populations, an example of geographic variation. Silvae Genet. **27**: 24–29 (1978). — Farr, W. A. and Harris, A. S.: Site index of Sitka spruce along the Pacific coast related to latitude and temperatures. Forest Science **25**: 145–153 (1979). — Gittins, R.: Canonical Analysis: A review with applications in ecology. In: Biomathematics, Vol. 12, Springer-Verlag, Berlin (1985). — Harris, A. S.: *Picea sitchensis* (Bong.) Carr. Sitka spruce. In Silvics of North America. Volume 1, Conifers. R. M. Burns and B. H. Honkala (technical coordinators). U.S. Dep. Agric. For. Serv., Washington, D. C. Agric. Handb. 654. pp. 260–267 (1990). — Henderson, D. M. and Faulkner, R. (eds.): Sitka spruce. In: Proc. Royal Soc. Edinburgh. (Section B, Biolocical Sciences). Edinburgh, Scotland. 234p. (1987). — Hermann, R. K.: North American tree species in Europe; transplanted species offer good growth potential on suitable sites. J. Forestry **85**: 27–32 (1987). — Holmes, G. D.: Foreword. In: Proc. Royal Soc. Edinburgh. 93B: v. (1987). — Illingworth, K.: Sitka spruce population trials three years after planting in British Columbia. In: Proc. IUFRO Joint meeting of Working Parties, Douglas-fir, lodgepole pine, Sitka spruce and true firs. Vol. 2: 311–326. Vancouver, Canada (1978). — Johnson, R. A. and Wichern, D. W.: Applied Multivariate Statistical Analysis. (4th ed.). Prentice-Hall Inc. and Simon and Schuster/A Viacom Company, Upper Saddle River, NJ, USA. p. 587–627 (1998). — Kayahara, G. J. and Pearson, A. F.: Relationships between site index, and soll moisture and nutrient regimes for western hemlock and Sitka spruce. Research Branch, B. C. Ministry of Forests. 15 pp. (1995). — Kovats, M.: Estimating juvenile tree volumes for population and progeny testing. Can. J. For. Res. **7**: 335–342 (1977). — Kuehl, R. O.: Statistical Principles of Research Design and Analysis. Duxbury Press. p. 256–304 (1994). — Lines, R.: Sitka spruce IUFRO collection. Rep. For. Res., p. 42–45 (1973). — Morgenstern, K. K.: Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. UBC Press. Vancouver, B.C., Canada (1996). — Namkoong, G. and Kang, H.: Quantitative Genetics of Forest Trees. Plant Breeding Review **8** (Chpt. 5): 139–188 (1990). — Peterson, E. B., Peterson, N. M., Weetman, G. F. and Martin, P. J.: Ecology and management of Sitka spruce, emphasizing its natural range in British Columbia. UBC Press, Vancouver, B. C., Canada (1997). — Pojar, J., Klinka, K. and Meidinger, D. V.: Biogeoclimatic ecosystem classification in British Columbia. For. Eco. Manage. **22**: 119–154 (1987). — Pollard, D. F. W., Teich, A. H. and Logan, K. T.: Seedling shoot and bud development in provenances of Sitka spruce, *Picea sitchensis* (Bong.) Carr.. Can. J. For. Res. **5**: 18–25 (1975). — Rehfeldt, G. E., Ying, C. C., Spittlehouse, D. L. and Hamilton Jr. D. A.: Genetic responses to climate for *Pinus contorta* in British Columbia: niche breadth, climate change, and reforestation. Ecological Monographs **69**: 375–407 (1999). — Roche, L.: A genecological study of the genus *Picea* in British Columbia. New Phytologist. **68**: 505–554 (1969). — Roche, L. and Haddock, P. G.: Sitka spruce (*Picea sitchensis*) in North America with special reference to its role in British forestry. In Proc. Royal Soc. Edinburgh, 93B: 1–12 (1987). — SAS Institute Inc.: SAS/STAT User's Guide. Version 6, 4th edition. Vol. 1 (pp. 943) and Vol. 2 (846 p.). Cary, NC, USA (1990). — Wollenberg, A. L.: Redundancy analysis – an alternative for canonical correlation analysis. Psychometrika **42**(2): 207–219 (1977). — Worrell, R. and Malcolm, D. C.: Productivity of Sitka spruce in northern Britain 1. The effects of elevation and climate. 2. Prediction from site factors. J. Forestry **63**: 105–118 (1990). — Xu, P.: Long-term Growth Responses in Sitka Spruce Populations to Geoclimatic Changes from IUFRO Provenance Trials in British Columbia. M. Sc. thesis, Faculty of Forestry, the University of British Columbia. Vancouver, B. C., Canada. 171p. (1998). — Yeh, F. C. and El-Kassaby, Y. A.: Enzyme variation in natural populations of Sitka spruce (*Picea sitchensis*) 1. Genetic variation patterns among trees from 10 IUFRO populations. Can. J. For. Res. **10**: 415–422 (1980). — Yeh, F. C. and Rasmussen, S.: Heritability of growth in 10-year old Sitka spruce. Can. J. Genet. Cyt. **27**: 729–734 (1985). — Ying, C. C.: Genetic resistance to the white pine weevil in Sitha spruce. Research Notes No. 106, Research Branch, Ministry of Forests, British Columbia, Victoria, B. C., Canada (1991). — Ying, C. C.: Effects of site, population, and population and site interaction in Sitka spruce in coastal British Columbia. For. Genet. **4**: 99–112 (1997). — Ying, C. C. and McKnight, L. A. (eds.): Proceedings of the IUFRO Sitka Spruce Provenance Experiment. Sitka Spruce Working Group (S2.02.12) Meeting, 1984, Edinburgh, Scotland. A Joint Publication by the B. C. Ministry of Forests, Research Branch, Victoria, B. C. Canada, and the Irish Forestry Board, County Wicklow, Ireland (1993).