

LONG-TERM GROWTH RESPONSES IN SITKA SPRUCE POPULATIONS
TO
GEOCLIMATIC CHANGES
FROM
IUFRO PROVENANCE TRIALS IN BRITISH COLUMBIA

by

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PREFACE

In the history of tree domestication and improvement, provenance trials served as the first step of systematic and scientific research. They have been conducted for more than 200 years in many commercially important tree species, in studies where seeds from different locations (populations) within the natural range of a species were collected, and the seedlings were planted together in a test site, namely, a ‘common garden’, to observe the growth potentials or other interested traits of these populations in the planted area. As theories in forest genetics and experimental design developed over the latest forty years, the range and scale of provenance trials also expanded, involving more seed sources and tested at more sites, some even being internationally cooperative. The original practical target of simply identifying suitable seed source for planting also developed into many theoretical purposes such as, the assessment of the species’ inter- and intra-population genetic variations and characterization, phenotypic flexibility and sensitivity, and genotype-by-environment (G x E) interaction. The most recently proposed approach of using provenance trial data to simulate long-term growth response to rapid climate change (Langlet 1971; Koski 1989) has expanded the use of provenance trials beyond forest genetics.

Sitka spruce, *Picea sitchensis* (Bong.) Carrière, a fast growing softwood species, occurs naturally along a narrow strip of the western Pacific coast of North America from Alaska to California over 22 degrees of latitudes (Daubenmire 1968). Primarily a coastal species, it extends well inland along river valleys in British Columbia (BC) in areas of high humidity. It has become abundant as a plantation tree over large areas of western Europe, a successful

endeavor that is accounted for by the tree's qualities, including its exceptionally great vigor, straight form, versatility to soil conditions and high timber quality (Holmes 1987). It is also expected to be the most prominent reforestation species in its native habitat, once the white pine weevil (*Pissodes strobi*) is under control (Ying 1991).

In order to guide seed transfer and screen for weevil resistant populations, the British Columbia Ministry of Forests (MoF) launched three series of Sitka spruce provenance trials in 1973 and 1975, two series of which are part of the international provenance trials of Sitka spruce, coordinated by the International Union of Forest Research Organizations (IUFRO). These trials are located at 13 sites of southern coastal BC and together test 43 Sitka spruce IUFRO provenances, the range of which covers the species main natural distribution from southern Alaska to Oregon coast spanning over 17 degrees of latitude. Growth and health conditions of all trees have been recorded periodically for 20 years since planting. Preliminary reports on height growth from these trials were made by Illingworth (1978) and Ying (1997). However, the valuable 20-year data on every single tree had not be fully analyzed.

The objective of this study is to use the above mentioned data to address the multiple purposes of provenance trial, either practical or theoretical as stated before, within the limitations set by the experimental design and data availability. Thus the thesis is written in four separate chapters each addresses one major aspect of the study. Chapter One mainly addresses genetic variations and phenotypic sensitivity of the species in growth traits. Emphases were given to the underlying ecological factors that drive geographical trends and climatic sensitivities of trees. Since extensive attacks of white pine weevil occurred at four of the test sites under study, Chapter Two is devoted to weevil resistance, assessing the damage of weevil attack to height growth over the 20-year period, and exploring sources accounting for the variability of weevil

attack frequencies. Chapter Three is targeted at the primary goal of provenance trials, i.e., evaluating the growth responses from latitudinal seed transfer, and defining suitable seed source range for planting under given site conditions in BC. Finally, Chapter Four follows the new approach of using provenance trial data to predict the impact of global warming on this species in term of volume growth. This approach is feasible because of the wide span of latitudinal distribution in this species, but relatively small variations in elevational distribution and minimal soil diversity of the seed sources and test site locations used in this study. Although these four chapters are dealing with different aspects of biological and ecological characters as well as forestry practice guidelines in the species, they are intrinsically related to each other. Therefore, I compiled them as one volume for the thesis.

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Ping Xu

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1. Geoclimatic trends and the underlying major ecological factors in growth of 43 Sitka spruce provenances tested in British Columbia

Abstract: Sitka spruce, (*Picea sitchensis* (Bong.) Carr.), a highly moisture sensitive conifer, has populations (provenances) differentiated in growth by temperature (especially winter harshness) and photoperiod regimes of source environments. The 20-year growth data of 43 Sitka spruce IUFRO provenances tested at 11 sites in British Columbia were analyzed along with the geoclimatic conditions of the test sites and of provenance origins. Multivariate analyses, including multiple regression, canonical correlation analysis and redundancy analysis, were applied to reveal the inherent geographic trends among provenances, and the climatic sensitivities of the tree in growth traits, as well as the underlying major climatic factors accounting for growth variation among provenances. Results indicated that about 63% of the genetic variability in growth of the species was explained by variation of climatic conditions of the provenance origins.

Keywords: climatic sensitivity; geographic trend; growth trait; provenance trial; Sitka spruce (*Picea sitchensis* (Bong.) Carr).

1.1. Introduction

Sitka spruce, *Picea sitchensis* (Bong.) Carr., a fast growing softwood species native to the Pacific west coast of North America, occupies a long, narrow strip from Alaska to California spanning over 22 degrees of latitude (Daubenmire 1968). Primarily a coastal species, it also extends well inland along river valleys in British Columbia (BC) where high humidity is available. It has also become abundant as a plantation tree over large areas of western Europe (British Isles in particular (Hermann 1987)), a successful endeavor that is attributable to the species' qualities, i.e., its exceptionally great vigor, straight form, versatility to soil conditions and high timber quality (Holmes 1987). It is also expected to be the most prominent reforestation species in its native habitat, once the threat from the white pine weevil (*Pissodes strobi*) is under control (Ying 1991).

With a wide latitudinal distribution, Sitka spruce, in common with most other North American conifers that are widely distributed, is remarkably variable (Roche and Haddock 1987). This variability is habitat-correlated and genetically based (Burley 1965; Roche 1969; Falkenhagen 1977). Although studies have been conducted on the biological and ecological aspects of the species (see Henderson and Faulkner 1987), the genetic potential of the tree has not yet been fully exploited in forestry practice (Roche and Haddock 1987). With high genetic variability, Sitka spruce is not only expected to be able to overcome the weevil problem, eventually, but also to be able to cope adaptively with the potential of negative impacts from rapid climate changes (e.g., global warming). However, we were not very clear before this study how much genetic variability the species possesses in growth performance, what the underlying

ecological force(s) are that have resulted in differentiation of these provenances, and how the species will respond in face of rapid climate changes.

In order to guide seed transfer and screen for weevil resistant populations, the British Columbia Ministry of Forests (MoF) established three series of Sitka spruce provenance trials in early 1970s in southern coastal area of British Columbia (BC), two series of which are part of the international provenance trials of Sitka spruce, coordinated by the International Union of Forest Research Organizations (IUFRO). Preliminary reports on height growth from these trials were made by Illingworth (1978) and Ying (1997). However, the data collected on individual trees over the 20 years since planting have not be fully analyzed. The objectives of this chapter are: 1) to assess the magnitude of genetic variability in growth traits among Sitka spruce populations; 2) to examine geographic trends among the provenances in growth performance; and 3) to unveil the underlying ecological forces that driving the genetic variability as well as the phenotypic sensitivity in growth of the species.

1.2. Data Profile and Abbreviation

Three series of Sitka spruce provenance trials in BC (Illingworth 1978; Ying 1991 and 1997) were used in this study. Growth and geoclimatic data were supplied by the Research Branch of MoF. The plantations were established in 1973 and 1975, using 43 Sitka spruce IUFRO provenances, at 13 sites along coastal BC area including a few peripheral inner coastal sites. Locations of the test sites and provenance origins are illustrated in Fig. 1-1, with details in

Tables 1-1 and -2. Originally, Series I was designed for guiding seed transfer on the Queen Charlotte Islands, north of the natural range of the white pine weevil to allow for successful planting of this species. There are five test sites in this series, four of which are on the Graham Island at approximate 53° N and 132° W. The remaining site is on Moresby Island, which is excluded from this study due to poor survival (C.C. Ying, BC MoF, personal communication). Geographic distances among the four test sites on the Graham Island are very short, with elevation varying from 33 m to 460 m (Table 1-1). Series II and III, each has four test sites, are part of the IUFRO international cooperative Sitka spruce provenance trials. These eight test sites are located from 49°48" to 55°19" N and from 126°28" to 132°30" W, with elevation variations from sea level to 600 m. Unlike those in Series I, the test sites in Series II and III are deliberately located in some contrasting environments (Ying 1997) such that some peripheral inland habitats of Sitka spruce (e.g., Dragon Lake, Maroon Creek, and Nass River) are included. Consequently, the climatic conditions at these sites vary substantially, for instance, mean temperature of the coldest month varies between 2.7 to -13 C, whereas mean annual precipitation from 1100 to 3850 mm. All the test sites are located in the Coastal Western Hemlock (CWH) biogeoclimatic zone (BC's ecological classification of the land, see Pojar *et al* 1987), except Dragon Lake which is in the Interior Cedar-Hemlock (ICH) biogeoclimatic zone (Table 1-1) and was excluded from this study due to high mortality (see below).

When pooling the three series together, 43 provenances were tested in this study, the range of which covers the species' main range from southern Alaska to Oregon coast, extending inland into the Sitka x white spruce hybridization zone, with elevation varying from sea level to

660 m. The range of the 12 test sites covers coastal BC, extending from 49°48" to 55°19" N and from 126°28" to 132°30" W with elevations from sea level to 600m (Fig. 1-1, Tables 1-1 and -2).

Table 1-1. Geographic locations of the 12 test sites in the 3 series of Sitka spruce provenance trials.

Site Name	Site Code	BGC zone ^a	Latitude	Longitude	Elevation (m)	Series
Graham Is. A1	QC I	CWHwh1	53°33"	132°20"	460	I
Graham Is. A2	QC II	CWHwh1	53°31"	132°11"	33	I
Graham Is. A3	QC III	CWHwh1	53°24"	132°16"	85	I
Graham Is. A4	QC IV	CWHwh1	53°22"	132°16"	100	I
Dragon Lake^b	DL	ICHmc2	55°19"	128°58"	210	II
Holberg Site	HG	CWHvh1	50°44"	128°07"	60	II
Maroon Creek	MN	CWHws2	54°46"	128°39"	600	II
Nass River	NS	CWHws1	55°04"	129°26"	15	II
Head Bay	HB	CWHvm1	49°48"	126°28"	15	III
Juskatla	JU	CWHwh1	53°34"	132°30"	20	III
Kitimat Valley	KT	CWHws1	54°12"	128°33"	100	III
Rennell Sound	RS	CWHvh2	53°23"	132°28"	50	III

^aBGC zone = Biogeoclimatic zone (ecological classification of the land in BC, see Pojar *et al* 1987).

^bThis test site was excluded from the study due to high mortality.

Table 1-2. Name, IUFRO number, and the geographic locations of the 43 IUFRO Sitka spruce provenances along with their planting series designation.

Prov. Name	IUFRO No.	BGC zone ^a	Latitude	Longitude	Elevation(m)	Tested in Series
Forks WA	3003	USA	48°04"	124°18"	137	II, III
Hoquiam WA	3008	CWHvm1	47°05"	124°03"	5	III
Necanicum WA	3012	USA	45°49"	123°46"	45	II, III
Brookings OR	3018	USA	42°15"	124°23"	90	II
Yakutat AK	3021	USA	59°31"	139°42"	12	II
Duck Creek	3024	USA	58°22"	134°35"	30	I, III
Ohmer Creek	3025	USA	56°35"	132°44"	15	I
Derrick Lake	3026	ICHmc1	55°41"	128°41"	240	I
Craig	3027	USA	55°30"	133°08"	0	I
Old Hollis	3028	USA	55°28"	132°40"	0	I
Cranberry R.	3029	ICHmc2	55°28"	128°14"	510	I
Ward Lake AK	3030	USA	55°25"	131°42"	15	I, III
Dragon L.Prov	3031	ICHmc2	55°21"	128°57"	255	I
Kitwanga	3032	ICHmc2	55°10"	127°52"	660	I, II
Zolap Creek	3033	ICHmc2	55°09"	129°13"	15	I
Fulmar Creek	3034	ICHmc2	55°09"	128°58"	390	I
Moss Point AK	3035	USA	55°02"	131°33"	0	I
Cedarvale	3036	ICHmc2	55°01"	128°19"	240	I
Kitsumkalum Lk	3039	CWHws1	54°43"	128°46"	135	I
Usk Ferry	3040	CWHws1	54°38"	128°24"	135	I, III
Shames	3041	CWHws1	54°24"	128°57"	30	I
Kasiks River	3042	CWHvm1	54°17"	129°25"	30	I
Inverness	3044	CWHvh2	54°12"	130°15"	30	I, II, III
Aberdeen Cr.	3045	CWHvh2	54°12"	129°55"	0	I
Wedene R.	3046	CWHvm1	54°08"	128°37"	165	I
Humpback Cr.	3047	MHwh1	54°02"	130°22"	300	I
Masset Sound	3048	CWHwh1	53°55"	132°05"	0	I
Link Road	3049	CWHwh1	53°30"	132°10"	90	I, II, III
Copper Creek	3050	CWHwh1	53°08"	131°48"	75	I
Moresby Camp	3051	CWHwh1	53°03"	132°04"	60	I
Tasu Creek	3052	CWHvh2	52°52"	132°05"	15	I
Jedway	3053	CWHwh1	52°17"	131°13"	15	I
Holberg Prov.	3056	CWHvm1	50°37"	128°07"	30	I, II, III
Salmon Bay	3058	CWHxm2	50°02"	125°57"	0	I
Fair Harbour	3059	CWHvm1	50°03"	127°02"	30	I
Squamish R.	3060	CWHdm	49°53"	123°15"	30	I
Tahsis Inlet	3061	CWHvm1	49°50"	126°40"	0	I, II
Big Qualicum R	3062	CDFmm	49°23"	124°37"	0	I, II, III
Haney	3063	CWHdm	49°14"	122°36"	300	I
Vedder	3064	CWHxm1	49°07"	121°56"	30	I
Port Renfrew	3065	CWHvh1	48°35"	124°24"	15	I
Muir Creek	3066	CWHxm2	48°23"	123°53"	0	I
Blenheim Mt.	3073	CWHvm1	48°54"	124°57"	240	I

^aBGC zone = Biogeoclimatic zone (ecological classification of the land in BC, see Pojar *et al* 1987).

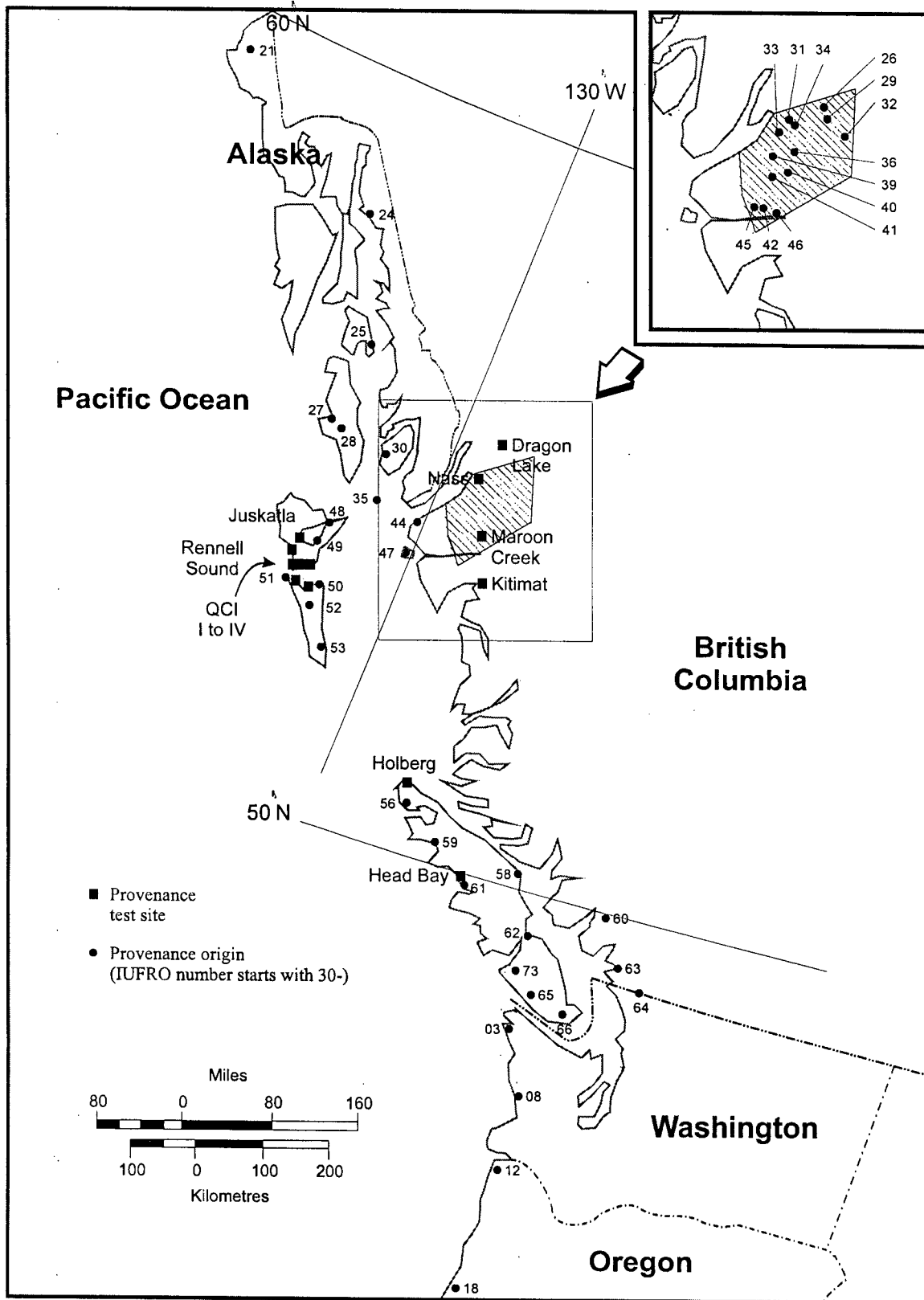


Fig. 1-1. Locations of the provenance origins and test sites for Sitka spruce provenance trials in British Columbia.

1.2.1. *Experimental designs*

Completely randomized block designs were used at all test sites. However, the number of blocks used varied over test sites (Ying 1991 and 1997). The four test sites on Graham Island (i.e., QC I to IV) of Series I has four to six blocks each, randomly accommodating 38 provenances. Series II and III have identical experimental design, that is, nine blocks at each site and each block accommodating ten provenances with six common to both series, which makes a total of 14 provenances tested in these two series. In all the series, provenances were represented by a 9-tree-row plot within each block. Trees were planted at a spacing of 3×3 m. The number of trees planted in Series I is 6840 (9 trees \times 38 provenances \times 20 blocks for 4 sites together), while the number of trees planted in Series II and III is 3240 each (9 trees \times 10 provenances \times 9 blocks \times 4 sites). As of year 20, mortality rates were low (0.04 ~ 14.69%) at all the test sites except Nass River (NS) and Dragon Lake (DL) where 31.98% and 51.73% of the trees died, respectively (see Appendix I). Mortality at NS was caused mainly by road expansion, whereas winter killing was the major cause at DL which was therefore excluded from this study. Thus, the remaining 11 test sites under this study have a total of 1390 plot-means and 220 provenance-by-site means for each growth measurement (see below).

1.2.2. *Growth measurements*

At the 11 test sites studied, growth and health condition of the trees were recorded on individual tree base. Height (HT) of each 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) of each tree was measured to the nearest millimeter at the 6th (occasionally),

10th, 15th and 20th year (referred to as DBH6, DBH10, etc.). In cases where a tree was less than 4 meters in height, diameter was measured at 1/3 of the total height. When both height and diameter of an individual tree were available, the tree volume (referred to as VOL6, VOL10, etc.) was calculated in cubic decimeters, using Kovats' (1977) volume function for juvenile conifer trees. Diameter and volume data were not complete for all test sites until the 20th year after planting.

1.2.3. Geoclimatic data for test site and provenance origin

Geoclimatic data are available for the 11 test sites as well as for the 43 provenance origins. The three geographic variables, i.e., latitude (LAT), longitude (LONG), and elevation (ELEV), were used in this study and were identified by adding the prefix 'S-' for test site, 'P-' for provenance origin. That is, the site geographic variables were abbreviated as SLAT, SLONG, and SELEV for test site while PLAT, PLONG, and PELEV specify provenance origin. Details of the geographic locations of the test sites and provenance origins are listed in Tables 1-1 and -2, respectively.

Two sets of climatic data with ten macro-climatic variables (see below) were used in this study, one set for test sites and one for provenance origins. Since long-term growth response over the macro-geographic range is the primary goal, macro-climatic data are suitable for use. These ten macro-climatic variables generally define temperature, moisture and photoperiod conditions of the test sites as well as of provenance origins. The acronyms and units of these climatic variables are as follows, adding prefix 'S-' where they are for test site while 'P-' for provenance origin:

MAP	= Mean Annual Precipitation (mm)
MSP	= Mean Summer Precipitation (mm) (May ~ September)
MAT	= Mean Annual Temperature (°C)
MTCM	= Mean Temperature of the Coldest Month (i.e., January) (°C)
MTWM	= Mean Temperature of the Warmest Month (i.e., July) (°C)
NFFD	= annual Number of Frost Free Days (day)
FFP	= annual continuously Frost Free Period (day)
DD5	= annual accumulated Degree Days <u>above</u> 5°C (degree day)
DD0	= annual accumulated Degree Days <u>below</u> 0°C (degree day)
DAY*	= accumulated available day-length (hour) of the growth season (April ~ October)

In Series II and III the macro-climatic data for test sites were obtained from the weather station closest to each test site. However, since no close weather station is applicable to the four sites on Graham island, the macro-climatic data in Series I were derived from climate models developed by Rehfeldt *et al* (1998). These models are applicable to BC, the United States above 48°30" N, the Alaska panhandle, and the narrow strips of Alberta and the Yukon along the BC border (C.C. Ying, BC MoF, personal communication). Macro-climatic data for the provenance origins were obtained from IUFRO information system (C.C. Ying, BC MoF, personal communication).

1.3. Methods of Data Analyses

1.3.1. *Partitioning growth variations*

Repeated growth measurements are highly correlated variables. To avoid redundancy of analysis of variance (ANOVA) when partitioning the variations of growth measurement variables, these variables were synthesized by principal component analysis (PCA) using the

* Using computer program downloaded from the web site: <http://www.netti.fi/~jjlammi/sum/html>

SAS PRINCOMP procedure to generate uncorrelated (orthogonal) principal components (Jolliffe 1986). The variance-covariance matrix of the growth variables based on logarithmically transformed plot-means was the input matrix for this PCA procedure. The first principal component of growth measurements (GPC1) was used as an index of growth performance in general as it accounts for most (95%) of the original variations in growth measurements (see below, Table 1-3). The partition of variation in GPC1 was performed by the SAS MIXED procedure to obtain the Random Effect Maximum Likelihood (REML) estimates of the variances of all variation sources assuming they are random effects. The percentage contributions of the variation sources to total variation in growth were calculated based on these REML estimates. The significance of the variation among sources was tested by the SAS GLM procedure. Although the assumption of randomness of all experimental effects is statistically arguable under real situation of provenance trial, it is a prerequisite to obtain the REML estimates and to interpret the variation sources, representing the species' span by these provenances and environmental gradient by the test sites.

1.3.2. Examining geographic trends in growth

Based on plot-means of the growth variables, multiple regression was applied site specifically on each growth variable using the SAS REG procedure, by relating the growth performance to geographic location of provenance origin (including quadratics and cross-products of geographic variables). Diameter and volume growth before year 20 was not examined due to high rate of missing observation in several hash test sites. Forward selection ($\alpha = 0.01$) was used to screen the significant geographic factor(s) and thus examine the inherent

geographic trend(s) in growth traits. The extent to which the geographic trends was expressed, evaluated by partial and model R^2 (coefficient of determination), was related to age, growth trait and site mildness. In this study, site mildness is represented by the first principal component for site climatic conditions derived by PCA on the ten macro-climatic variables (see below).

1.3.3. *Revealing phenotypic sensitivity to test site climatic conditions*

To reveal the general climatic sensitivity of all the provenances to site conditions, canonical correlation analysis was performed by the SAS CANCORR procedure on two groups of variables. One group is of the eight growth variables (i.e., HT3, HT10, HT15, HT20, DBH15, DBH20 VOL15 and VOL20) and the other of the ten macro-climatic variables for test sites (see above). Diameter and volume growth measurements in year 6 and 10 were excluded due to the high rates of missing observations at several harsh sites in these years. Canonical correlation analysis is a multivariate statistical approach suitable for the study of relationships between two groups of self-correlated variables (Gittins 1985). As stated before, repeated growth measurements on same individuals are highly correlated, and so are many climatic variables. Therefore, the relationships between these growth variables and climatic variables should be addressed based on multivariate correlations rather than pair-wise simple correlations, because simple correlations do not take into account the inter-relationship among these highly correlated variables.

Canonical correlation analysis produces two sets of canonical variables that are linear combinations of the original variables of the two groups, respectively, while maximizing the correlations between each pair of the canonical variables such that, the first pair of canonical

variables has the maximum correlation with each other, and the second has the second highest correlation, and so on. The relationships of the two groups of variables are evaluated by the canonical correlations between pairs of canonical variables, and the significance of each canonical correlation is tested by likelihood ratio F -test under the assumption of multivariate normality. The loading and cross-loading of each original variables onto the two sets of canonical variables were defined by the correlation coefficients between original variables and the canonical variables within and between groups, namely, canonical structures. Thus, the relative importance of each original variable to the relationships between the two sets of canonical variables can be quantified. The extent to which the original variables were represented by the canonical variables can also be evaluated by the proportions of raw variations in original variables explained by both sets of canonical variables within and between groups. 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 *provenance-by-site means* level. Consequently, the ratio of raw variation explained is based on the analysis with standardized original variables.

1.3.4. *Unveiling the underlying major climatic factor for the geographic trends*

In order to unveil the major ecological factors underlying the observed geographic trends, redundancy analysis was applied on the two groups of variables, i.e., growth variables and climatic variables for provenance origins, through matrix algebra manipulated by the SAS IML procedure (Dr. Val Lemay, Faculty of Forestry of UBC, personal communication). In multivariate analyses, redundancy analysis is 'an alternative to canonical correlation analysis'

(Wollenberg 1977) which, instead of maximizing the correlation between two groups of self-correlated variables, maximizes the variations in one group cross-explained by, or say, 'redundant' on variations of the opposite group variables. Consequently, the linear combination of original variables in one group maximally accounts for variations of the opposite group but not necessarily accounts for variations of its own group to the maximum. In other words, redundancy analysis generates two sets of eigenvalues for determining the redundant variables of the two groups, respectively, such that the first redundant variable of one group maximally accounts for the variations of the opposite group (but not necessarily accounts for variations of its own group to the maximum), and the second redundant variable accounts for second maximal variations of the opposite group (but not necessarily accounts for the second maximal variations of its own group), and so on (see Wollenberg 1977 for details). Therefore, redundancy analysis is suitable for determining the variations in some multiple correlated traits purely due to some other suspected environmental sources that are also closely correlated. The notion that genetic variability is habitat-correlated in adaptive mode (Burley 1965; Roche 1969; Falkenhagen 1977) implies that, to some extent, growth variations among different provenances are conferred by seed origin's climatic conditions. Using redundancy analysis, growth variations among the provenances that are accounted for by provenance origin's climatic conditions can be quantified to the maximum. Similarly, 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. Thus, the major climatic factor(s) driving the genetic differentiation among the provenances in growth can be unveiled by comparing the redundancy loadings of the original climatic variables to the first redundant

variable of its own group. Again, the redundancy analysis performed here is based on the correlation matrices within and between groups to avoid the scale problem.

Although redundancy analysis is more suitable than canonical correlation analysis for the interpretation of the variation in one group of variables explained by another group of variables, it also has a drawback that, as indicated before, when a redundant variable of one group maximizes the redundancy of the other group it does not maximize the redundancy of its own group. Consequently, the first redundant variable of either group could be a good representative of the other group, but not necessary of its own group. Therefore, it is not as advantageous using redundancy analysis to interpret simultaneously the mutual relationships of two groups of variables, as using canonical correlation analysis. On the other hand, canonical correlation analysis only maximizes the canonical correlations between two groups of variables, not the redundancy of one group upon another group. Therefore, it is more advantageous using redundancy analysis to determine the variation in one group (which is the interested group) explained by another group of variables (which are causal factors). In the previous section's analysis on the relationships between growth variables and site climatic variable, attentions were given to the multiple correlations between these two groups, not the redundancy of growth variation upon site climatic variability which could change substantially over different experimental settings. Therefore, canonical correlation analysis was used in that section's analysis. However, in this section, interests are on the determination of the magnitude of explained growth variation by provenance climatic variations and in conjunction with this redundancy, the major climatic factors underlying the differentiation among provenances in growth traits. Therefore, redundancy analysis is more suitable for the purposes of this study.

1.3.5. Statistical criteria

All the growth measurements were transformed into natural logarithmic values before analyses to achieve approximate normal distributions of the response variables. To avoid scale problem of growth and geoclimatic variables, data standardization (i.e., subtracting the mean and then dividing by the standard deviation of that mean) was performed whenever needed (e.g., multiple regression). All the significance related tests were performed under the assumptions of single variable and multivariate normalities and homogeneous variances of the response variables across different levels of experimental effects and geoclimatic regimes. The significance criterion was set at $\alpha = 0.01$ level unless otherwise specified. All data analyses were performed with SAS procedures (SAS Inc. 1990).

1.4. Results and Discussions

1.4.1. Partitioning of Variations in growth traits

Based on plot-means, the eight growth variables (i.e., HT3, HT10, HT15, HT20, DBH15, DBH20, VOL15, and VOL20) were used to generate principal components of all the growth measurements. The PCA results indicated that the first principal component (GPC1) accounted for the majority (94.7%) of the original growth variations (Table 1-3). The contributions of the original growth variables to GPC1, represented by the correlation coefficients, varied greatly among the eight growth measurements (Table 1-3). However, the volume growth (VOL15 and VOL20), also the most important growth trait, contributed the most to GPC1. Therefore, GPC1 is considered a good representative of all the growth measurements to be used as the response variable in the

following analysis of variance (ANOVA) to partition the growth variations into different sources of variation.

Table 1-3.* Coefficients of the original growth variables with the first two growth principal component (GPC1 and GPC2) and the percentage of original variations in growth accounted for by GPC1 and GPC2, respectively.

Original growth variables	Coefficient of the original variable with	
	GPC1	GPC2
HT3	0.1076	0.6545
HT10	0.1782	0.4447
HT15	0.2152	0.1697
HT20	0.2408	-0.081
DBH15	0.2174	0.0221
DBH20	0.2151	-0.3000
VOL15	0.6147	0.2555
VOL20	0.6173	-0.428
Variance explained	94.7%	2.6%

*From the SAS PRINCOMP procedure on the eight growth variables based on covariance matrix, using logarithmically transformed plot means.

Pooling the 11 test sites, assuming the response variable (GPC1) is normally distributed, and homogeneous variance exists across different sites, blocks and provenances, and all levels of these experimental effects were randomly chosen (though it is difficult to achieve these assumptions in a real situation of provenance trial), the SAS GLM model has high coefficient of determination ($R^2 = 0.87$). The variance component of each variation source was estimated by the SAS MIXED procedure which computed the REML estimates for the variances of all the experimental effects under the random assumption, and from which the relative contributions of these effects to the total variations were calculated and listed in Table 1-4.

Table 1-4. ANOVA for the first growth principal component (GPC1) of eight growth measures.

Variation Source	DF	Type III			REML Estimate	Relative Variance Contribution
		Mean Square	F Value	Pr > F		
Site	10	190.30	26.76*	<0.0001	2.1165	65.42%
Provenance	42	7.82	8.14*	<0.0001	0.2559	7.91%
Site x Prov.	159	0.96	2.22	<0.0001	0.0871	2.69%
Block(Site)	64	6.57	15.23	<0.0001	0.3504	10.83%
Exp. Error	1014	0.43			0.4256	13.15%

* pseudo *F* -test

Clearly, site effects were dominant, accounting for 65.4% of the total variation in growth (Table 1-4). This is not surprising as test sites are located in very contrasting environments (Ying 1997). In addition to the prevailing site influence, growth variation due to provenance variability was also highly significant. The ratio of inter- over intra-provenance variation can be approximated from the REML estimate of variance for Provenance and for Experimental Error which is the variation due to sources within block, provenance and site sources. Thus, the ratio was $0.2559 : 0.4256 \approx 1 : 1.66$. Note this approximation likely overestimated the ratio because the inter-provenance variance contained both genetic and non-genetic components, and by using plot-means the within-plot variation which is also part of intra-population variation was excluded. The ratio estimate is thus much higher than that from Yeh and El-Kassaby's (1980) allozyme study with ten IUFRO provenances of the species, in which they estimated 92% of the genetic (allozyme) diversity reside within the populations. The difference, however, is a very common phenomenon in forest tree species in genetic partition based on morphological and growth traits versus biochemical markers (Morgenstern 1996).

Block effects and provenance-by-site (G x E) interaction were also significant. Comparing to the sources of Site and Provenance, the G x E interaction had a low rate of

contribution (2.69%) to growth variation on average, although its magnitude was about 1/3 of that of Provenance. The large amount of degree of freedom for the Error term, on which the G x E interaction was tested, seems also to suggest that the significance of the G x E interaction was statistically marginal on average. However, the real situation of G x E interaction in growth of this species could be far from the results hitherto because of the following reasons:

First, full expression of G x E interaction needs adequately wide geoclimatic span of test sites, as well as sampling range of provenances. In the above ANOVA, three series of the provenance trials were pooled together in order to include maximum numbers of provenance and test site for the scale of this study, while ignoring the differences of experimental setting among these series (see 1.2.1. of this chapter). Secondly, low expression of the G x E interaction on average could also be resulted from the pooled ANOVA which gives an equal weight to the provenances tested in different environments. So that in the above unweighted ANOVA, the 38 provenances tested in Series I had greater influences than the 14 provenances in Series II and III due to their large amount of observation, while the environments in Series I were too similar to allow for expression of G x E interactions (see below).

More detailed ANOVA on GPC1 were also performed for the three series specifically, with results presented in Table 1-5. These smaller-scaled ANOVA clearly indicate the differences among the series. As mentioned above, the four sites in Series I are closely located with few environmental differences except for elevational variation. Consequently, the G x E interaction was not significant in Series I. In contrast, the three sites in Series II are located in very contrasting environments, therefore, the G x E interaction constituted a great portion of growth variation (35.5%) for Series II, while the effects of provenance variation were not

significant on average at all. The case in Series III was somehow intermediate between Series I and II since it has moderate environmental variations for the four sites. The contradictory of the above ANOVA results suggests that G x E interaction is subject to different experimental settings (the amplitude of environmental gradient and provenance sampling), and to different levels of analyses as well as different methods of analyses (e.g., weighted or unweighted ANOVA). It is imprudent and could be misleading if drawing conclusions based on a single approach of ANOVA analyses.

In forestry practice, the G x E interaction is a major concern of provenance trial, because a provenance can retain high growth vigor only within certain geoclimatic ranges, and these ranges are critical in selecting seed sources for a planting area. As the expression of this interaction is conditional on different experimental settings, it can be of practical importance involving harsh inland environment in provenance trials (Ying 1997).

The causes of the G x E interactions also deserve attention and will be discussed in later analyses (e.g., Chapter 3). Comparisons of the growth ranks of the 14 provenances tested in Series II and III (Table 1-6), where the G x E interactions were statistically significant, imply the causes of the interactions were mainly due to some reversal responses of a few provenances to weevil attack and harsh winter conditions, which certainly are very important to seed transfer. For instance, provenance Necanicum (No. 3012) was a high-yield provenance at most test sites, but dropped to the lowest rank at Maroon Creek (MN) which is the harshest site among these sites; while provenance Kitwanga (No. 3032) had low yield at mild sites, but relatively thrived at MN due to its noticeable resistance to white pine weevil attack (see Chapt.2).

Table 1-5. Partitioning of the general growth variation in GPC1 for each series of the Sitka spruce provenance trials in BC.

Var. Source	Series I				Series II				Series III			
	DF	MS	F	Var%	DF	MS	F	Var%	DF	MS	F	Var%
Site	3	130.5	15.7	54.2	2	38.2	16.6	50.1	3	129.1	43.1	61.8
Provenance	37	2.2	11.0	8.6	9	3.0	1.4 ^{NS*}	0.1	9	12.2	14.6	14.0
Site x Prov.	111	0.2	0.9^{NS}	--	17	2.4	16.7	35.5	27	0.8	3.1	2.8
Block (Site)	16	8.3	36.4	18.2	21	0.5	3.7	3.5	32	2.4	9.0	9.5
Exp. Error	590	0.2		19.0	161	0.1		10.8	288	0.3		11.9
model R ²		0.8231				0.8764				0.8850		
# of plots		758 (760)				211 (270)				360 (360)		
% of data		57%				16%				27%		

* NS = not significant ($\alpha = 0.05$).

Table 1-6. Ranks of the general growth performance of the provenances tested in Series II & III, where significant G x E interactions were detected.

Growth Rank	Series II			Series III			
	HG ^a	NS	MN	HB	RS	JU	KT
1	18 ^b	62	49	12	12	12	62
2	12	32	62	62	03	49	03
3	03	49	32	08	08	08	08
4	62	03	44	03	62	62	40
5	49	12	03	49	56	03	56
6	61	56	56	56	49	40	12
7	56	61	61	44	44	44	49
8	44	44	21	40	40	56	44
9	21	21	12	30	30	30	30
10	32	18	18	24	24	24	24

a. Test site code (see Table 1-1); Test sites were listed in descending order (left to right) of site climate mildness within each series.

b. Provenance represented by Sitka spruce IUFRO number starting with "30-".

1.4.2. Geographic trends inherited by the provenances

Based on plot-means, geographic trends among the 43 Sitka spruce provenances were examined site specifically by relating growth performances (HT, DBH and VOL) at different ages of each provenance to its origin's geographical variables, including quadratics and cross-products, using multiple regression analysis. Forward selection ($\alpha = 0.01$) was applied in these regressions. The regression models were highly significant ($p < 0.0001$) for all the sites and growth traits with a few exceptions where geographic trends in growth were suppressed by winter harshness and/or weevil attack at sites JU and MN (see below). The significant predictor(s) and the partial R^2 's of them as well as the model R^2 of each regression model were presented in Table 1-7. The results proved that there were strong geographic trends, mainly latitudinal, underlying the 43 Sitka spruce provenances in growth traits at different ages. However, there was also great variability of the geographic trends over sites, growth traits and ages, even when considering the latitudinal trend only. This variability implies that the expression of genetic control in growth traits was highly conditional upon environmental condition (which is one of the expression of the G x E interaction) and can change with age. The following implications can be drawn by comparing the significant predictors (i.e., 'Factor') and the R^2 values over sites, ages and growth traits in Table 1-7:

First, the geographic trends were highly site-dependent. At extremely mild sites (e.g., HG and HB) the latitudinal trend tended to be linear and explained a high level of variation in growth. This means that the more southern a provenance is the better the growth performance it has at these sites. At less favorable sites (e.g., QC III and KT) the latitudinal trend was quadratic (concave down), which means that provenances from either extreme north or south were less

favorable than those from the central part of the latitudes (i.e., the species range). This was because at these sites southern provenances were more susceptible to winter injuries than the central ones which could still grow better than further northern ones. At the very harsh sites (with low winter temperatures, e.g., MN and NS) the latitudinal trend was suppressed, or substituted by longitudinal or elevational trends with very low levels of variation in growth explained by provenance origin's locations.

Secondly, the latitudinal trend (LAT and/or LAT^2) varied with age and growth traits. Considering height growth only, the latitudinal trend was almost linear at early ages but later switched to be quadratic, most apparent at northern and inland sites (e.g., KT and MN). This could be explained by the fact that the southern provenances suffered winter injuries at northern harsh environments from year 3 to 10 and slowed down their height growth. The 20-year data did not show any evidence suggesting that the quadratic latitudinal trend will switch back to be linear when trees grown older. Instead, there were perceivable declines in the expression of the latitudinal trend in height growth on average with increasing age, except for a few test sites that are extremely mild and wet (e.g., HG, RS and QC II). This agrees with previous knowledge that heritability of some traits in trees, especially growth traits, declines with age (Namkoong and Kang 1990).

Table 1-7. Partial R^2 's for the significant predictive geographic variables ('factor') of provenance origins and the average model R^2 's of all the regression models on the 5 growth measures at each test site specifically (from SAS REG procedure with forward selection at $\alpha = 0.01$ level).

Site	Site Information			HT3		HT10		HT20		DBH20		VOL20		Ave. model R^2
	#	prov	sitePC1	Factor	R^2	Factor	R^2	Factor	R^2	Factor	R^2	Factor	R^2	
HG	10		2.98	Lat	0.77	Lat	0.65	Lat	0.61	Lat*Elev	0.48	Lat	0.50	0.746
				Lat*Elev	0.07	Lat*Elev	0.10	Lat*Elev	0.09	Lat ²	0.24	Lat*Elev	0.22	
HB	10		1.71	Lat	0.59	Lat	0.58	Lat	0.56	Lat ²	0.54	Lat	0.54	0.562
RS	10		1.68	Lat	0.74	Lat ²	0.82	Lat ²	0.71	Lat ²	0.80	Lat ²	0.81	0.776
QC II	38		1.07	Lat ²	0.13	Lat	0.28	Lat	0.31	Lat*Elev	0.29	Lat*Elev	0.31	0.378
				Long	0.04	Long	0.06	Lat*Long	0.17	Lat ²	0.14	Lat ²	0.16	
QC IV	38		0.78	Lat	0.25	Lat ²	0.15	Lat*Elev	0.06	Lat*Elev	0.10	Lat*Elev	0.08	0.144
				Elev	0.04	Lat*Long	0.04							
QC III	38		0.36	Lat ²	0.17	Lat ²	0.16	Lat ²	0.13	Lat*Elev	0.08	Lat ²	0.08	0.178
				Long	0.03	Long	0.04	Lat*Long	0.08	Lat ²	0.04	Lat*Long	0.08	
JU	10		-0.08	Lat ²	0.52	Lat ²	0.21	Lat ²	0.05	No trend	---	Lat ²	0.08	0.172
KT	10		-0.98	Lat ²	0.60	Lat ²	0.23	Long ²	0.23	Lat*Long	0.17	Lat*Long	0.17	0.280
QC I	38		-1.35	Lat ²	0.19	Lat*Elev	0.09	Lat*Elev	0.03	Lat*Elev	0.10	Lat*Elev	0.08	0.122
				Lat*Long	0.08	Lat	0.04							
NS	10		-2.34	Lat ²	0.47	Long ²	0.23	Long ²	0.22	Long ²	0.23	Long ²	0.32	0.488
						Lat	0.13	Lat ²	0.09	Lat	0.20	Lat	0.20	
						Lat*Long	0.08	Lat*Long		Lat*Long	0.12	Lat*Long	0.13	
MN	10		-5.92	Lat ²	0.20	Long	0.07	Long*Elev	0.07	No trend	---	No trend	---	0.140
				Lat	0.16	Lat	0.10							
				Long ²	0.10									

Further analyses with the site-dependency of the geographic trends confirmed that the extent to which the geographic trends expressed (i.e., the genetic characters expressed in growth traits) was closely associated with site mildness.

PCA was used to reduce the ten macro-climatic variables to a few, informative and orthogonal variables for both test sites and provenance origins. The first principal component (climPC1) accounted for 62.8% of the total variation in the original ten macro-climatic variables after data standardization (Table 1-8). Except for MTWM, the macro-climatic variables contributed almost evenly to climPC1, indicating that climPC1 is an effective index representing most macro-climatic variables. The negative coefficients of DD0 and DAY with climPC1 and the positive coefficients of the remaining climatic variables with climPC1 imply that a higher value for climPC1 means milder climate or more southerly located. Accordingly, the higher the climPC1 value for a test site (referred to as sitePC1), the higher the average growth performance at that test site. The associations of site productivity (represented by the site means for HT20 in percentages relative to the highest site mean for HT20), site mildness index (sitePC1) and the average model R^2 (transformed into percentage, i.e., R^2 %) are illustrated in Fig.1-2 and Fig. 1-3. With a few exceptions (see below), the levels for these three different statistics varied concomitantly over the 11 test sites. This provided evidence that the milder the site, the higher performance achieved in height growth and the more pronounced the geographic trends exhibited at that site (since a higher model R^2 means a greater proportion of growth variations are accounted for by the provenance's geographic origin).

Table 1-8. Results of PCA on the 10 macro-climatic variables for the 11 test sites and 43 provenance origins altogether, showing correlation coefficients and percentages of explained variance (based on standardized data, from the SAS PRINCOMP procedure).

Climatic variables	climPC1	climPC2	climPC3	climPC4
DAY	-0.330	0.261	-0.066	0.553
MAP	0.295	0.297	0.555	-0.128
MSP	0.216	0.490	0.487	0.243
MAT	0.380	-0.133	-0.026	0.007
MTCM	0.379	0.107	-0.204	-0.025
MTWM	0.097	-0.593	0.354	0.563
NFFD	0.366	0.094	-0.309	0.128
FFP	0.348	0.026	-0.309	0.477
DD5	0.259	-0.452	0.225	-0.215
DD0	-0.371	-0.094	0.202	0.099
Variance explained	62.8%	20.0%	8.1%	3.9%

(Note: climPC1 = the 1st principal component of the 10 climatic variables, climPC2 = the 2nd principal component of the 10 climatic variables, and so on.)

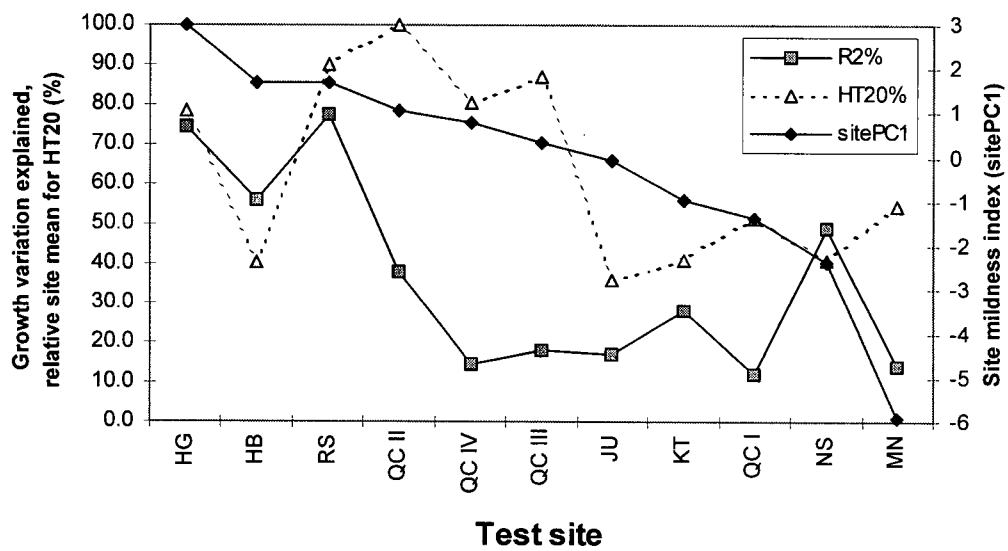


Fig. 1-2. Growth variation explained by provenance geographic location (average model R^2 's in previous regressions) along with site mildness index and relative site mean for HT20 (%).

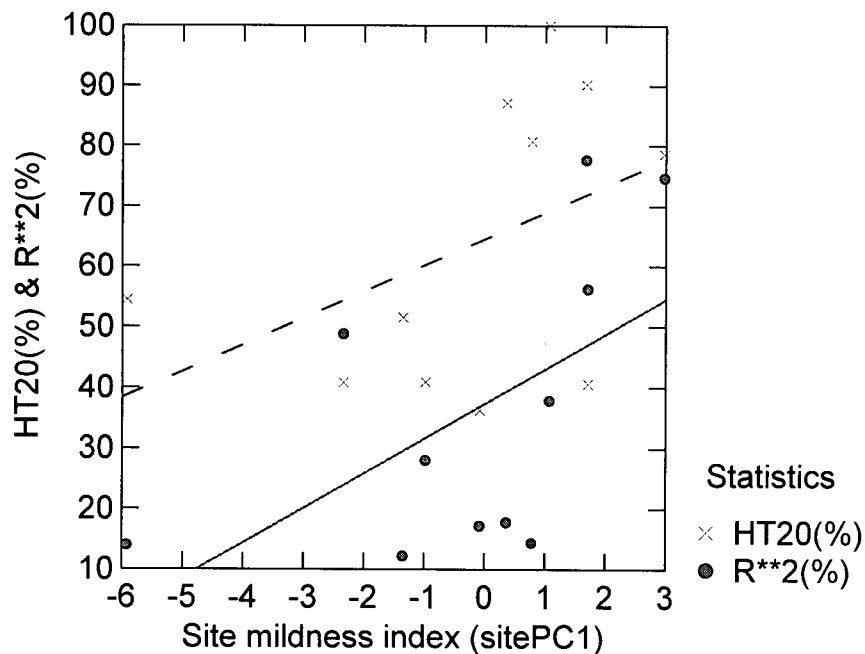


Fig. 1-3. Associations of site productivity (HT20(%)) and the amount of explained growth variation by provenance origin's locations ($R^{**2}(\%) = R^2 \cdot 100$) with test site mildness (sitePC1).

Note that the number of provenances used in these regression analyses varied from 10 to 38 among different sites; that is, the sites in Series I test 38 provenances while those in Series II and III test only 10 provenances (Table 1-7, also see section 1.2.1.). Model R^2 declines with the number of levels for the predictive variables, especially quickly within the range of $n = 30$ (Draper and Smith 1966). Therefore, the average model R^2 's for the four sites in Series I (i.e., QC I ~ IV) were relatively low for their site mildness compared to the remaining sites. The extra low level of model R^2 for site HB was due to the occurrences of extensive white pine weevil attack during the measured years. That is, weevil attack might also suppress expression of geographic variation in tree growth.

1.4.3. *Climatic sensitivities to site conditions*

The previous results indicate that site influences were dominant on the overall growth variation (Table 1-4). With ten macro-climatic variables defining site climatic conditions, the climatic sensitivities of Sitka spruce in different growth traits to different climatic variables can be revealed by canonical correlation analysis. As mentioned before, canonical correlation analysis is effective for presenting an overall view of the relationships between two groups of self-correlated variables in the multivariate sense. Two groups of variables were used in this analysis, one consisting of the eight growth variables (i.e., HT3, HT10, HT15, HT20, DBH15, DBH20, VOL15 and VOL20), and the other of the ten macro-climatic variables for test sites (i.e., SDAY, SMAP, etc.).

Eight canonical variables were derived based on the correlation matrices within and between the two groups of variables, namely, Grow1, Grow2, and so on for the growth canonical

variables, and Sclim1, Sclim2 and so on for the site climatic canonical variables. The results presented in Table 1-9 show that there were strong positive correlations between growth and site climatic variables, indicating that high growth performance is associated with milder site climatic conditions. The first pair of canonical variables, accounting for 59.2% of the total canonical variation, has the maximum canonical correlation as $R^2 = 0.954$, and the second pair has the second highest canonical correlation as $R^2 = 0.872$. Under the assumption of multivariate normality of the two groups of variables, canonical correlations between each pair of canonical variables were tested by *F*-tests on the likelihood ratios for the hypotheses that the canonical correlations between the current pair and the following pairs do not differ from zero. The probabilities that the hypotheses are true were presented in Table 1-9 under the column, “Pr > F (likelihood)”, which indicate that all pairs of canonical variables were significantly correlated with each other, except the last one. However, for the ease of interpretation, only the first two pairs of canonical variables (i.e., Grow1 with Sclim1 and Grow2 with Sclim2) will be used in further analyses. These two canonical variables were selected due to their high eigenvalues (> 1) and the fact that together they accounted for 78.5% of the total canonical variation (Jackson 1993) (Table 1-9).

Canonical structures (Tables 1-10 and -11) of the first two pairs of canonical variables reveal the relationships between the original variables and the canonical variables. For the growth measurements, all the growth variables had moderately strong correlation with Grow1, but relatively low correlation with Grow2 (Tables 1-10). This was also true with the correlations between growth variables and Sclim1 and Sclim2, since the first pair of canonical variables had the maximum canonical correlation. Focusing on the canonical structure of the first pair, Grow1

was most strongly correlated with HT20 and HT15, followed by diameter and volume growth, and then HT10, but least strongly correlated with HT3. The same pattern of correlation ranks was found between growth variables and Sclim1. This indicates that the environmental component of height growth due to test site increased while genetic variation among provenances decreased with age, that is, accumulative effects of site climatic conditions tended to become a determinant in height growth as age increased. Diameter and volume growth were also strongly influenced by site effects though not as strongly as height growth. On the other side of the canonical structures with site climatic variables (Table 1-11), SMSP had the strongest correlation with Sclim1, while SMAP, SMAT, SMTCM and SNFFD ranked second in their correlations with Sclim1. Therefore, the first canonical correlation implies that site climatic conditions, mostly defined by moisture regimes (SMSP and SMAP) and next determined by site winter harshness (SMTCM and SNFFD), had the strongest influences on later height growth, less strong but considerable influences on volume and diameter growth, and least strong influences on early height growth.

The case with the second pair of canonical variables was quite different from that of the first one. On the growth variable side (Table 1-10), all the heights had negative correlations with Grow2 and Sclim2, while diameter and volume variables had positive but weak correlation with grow2 and Sclim2. Negative correlations between heights and Sclim2 declined sharply with increasing age, indicating height growth became more and more unaffected by those site climatic conditions defined by Sclim2. On the other hand, Sclim2 was strongly and negatively correlated with temperature conditions (SMAT, SMTWM, SDD5 and SMTCM), and had the strongest and positive correlation with SDAY. This implies that a higher value for Sclim2 means colder and/or

further north site conditions. Therefore, the canonical correlation between Grow2 and Sclim2 could be interpreted as that seedling height growth (before Year 10) was very sensitive to site temperature conditions, and diameter and volume growth were also influenced by site conditions (mainly in photoperiod, summer temperature SMTWM and heat sum SDD5) to certain degree. However, later height growth was almost unaffected by site temperatures and latitudinal location, and became to be more strongly influenced by site moisture conditions (i.e., Sclim1), known from the first pair of canonical variables.

Table 1-9. Canonical correlations and explained variance percentage of each pair of canonical variables (Cans) between growth measures and site climate variables.

Cans	Can R²	Eigenvalue	Variance (%)	Pr > F (likelihood)
1st	0.954	20.89	59.2	<0.0001
2nd	0.872	6.81	19.3	<0.0001
3rd	0.806	4.16	11.8	<0.0001
4th	0.693	2.26	6.4	<0.0001
5th	0.398	0.66	1.9	<0.0001
6th	0.266	0.36	1.0	<0.0001
7th	0.088	0.10	0.3	0.0002
8th	0.040	0.04	0.1	0.0167

Table 1-10. Canonical structure of the growth variables with the first two pairs of canonical variables.

Growth variables	Growth canonical variables		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
VOL20	0.855	0.013	0.835	0.012
VOL20	0.877	0.045	0.856	0.042

Table 1-11. Canonical structure of the site climate variables with the first two pairs of canonical variables, represented by the correlation coefficients (listed in the descending order).

Climate variable	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
SDAY	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

It is worthy of notice that the climatic sensitivities of different growth traits in Sitka spruce delineated in the above canonical correlation analysis are general to all the provenances tested. Different provenances, however, could have different climatic sensitivities even when tested at same environments. Preliminary regression analyses on the plot-means of the growth measurements of 11 frequently tested provenances (tested at least at eight sites) to site climatic variables (screening by forward selection at $\alpha = 0.01$) had indicated that when these provenances were tested in British Columbia, the growth of southern provenances was more sensitive to winter temperatures than northern provenances did in general, and that the latitudinal line between southern and northern provenances for this purpose could be drawn at 46 - 48° N, approximately (see Appendix II).

The redundancy, i.e., explained raw variance, appended to the above canonical correlation analysis (Table 1-12) shows that the first canonical variable for site climatic variables, which carries 34.0% original variation of its own group, explained 70.5% original variation in growth

variables at provenance-by-site mean level. This means that growth variation was well accounted for by site climatic conditions, which agrees with the previous ANOVA result that site influences were dominant on overall growth variation. On the other hand, the first growth canonical variable, which carries about 73.9% of original variation of its own group, accounted for 32.5% of the raw variation in site climatic conditions. Growth variations were well explained by the opposite group, suggesting high predictability of growth performance in Sitka spruce from planting site climatic conditions.

Table 1-12. Redundancies of the canonical variables for both growth and site climate variables.

Original Variation	Growth canonical variables		Site climatic canonical variables	
	Grow1	Grow2	Sclim1	Sclim2
Growth variation	73.9%	1.7%	70.5%	1.5%
Site climate variation	32.5%	17.3%	34.0%	19.9%

1.4.4. Underlying major ecological factors that differentiate the provenances

Significant geographic trends, mainly latitudinal, were observed which underlie the growth performance of the 43 Sitka spruce provenances. Since genetic variability is habitat-correlated and genetically based (Burley 1965; Roche 1969; Falkenhagen 1977), it is desirable to examine the major ecological force(s) driving the geographic trends of growth among the provenances. In order to do this, growth measurements were related to climatic conditions of the provenance origins by redundancy analysis. As mentioned in section 1.3.4., redundancy analysis

is especially useful in genetics data analysis for determining possible causal relationship with environmental factors.

Ten growth variables (i.e., HT3, HT10, HT15, HT20, DBH10, DBH15, DBH20, VOL10, VOL15 and VOL20) and the ten macro-climatic variables for provenance origin (i.e., PMAP, PMSP, and etc.) were used in this redundancy analysis. The involving of DBH10 and VOL10 sacrificed some observations at a few harsh test sites, but would be helpful to examine the age trend of genetic control in these growth traits, which was not analyzed in the previous multiple regression analyses (see 1.4.2.). The analysis was performed on the within and between group correlation matrices that were obtained by the SAS CANCORR procedure based on original data at plot-mean level to avoid scale problem.

The redundancy analysis results indicate that the amount of growth variation was poorly explained by the provenance origin's climatic conditions when all the test sites were pooled together (Table 1-13). Only 5.23% of the growth variation at plot-mean level was explained by the first redundant variable of climatic variables for provenance origin (Pclim1). Low expression of genetic effects in growth traits is not surprising, because heritability of trees in growth is usually low compared to other traits such as morphological traits (Falkenhagen 1977). This rate (5.23%), however, should not be considered as a surrogate for heritability. It could be greater if the input matrix for growth variables is at provenance-by-site level (in this case, the rate was 8.7%, details not shown here). The plot-mean level for growth variation was chosen to comply with the level of former ANOVA to make the following approximation, under the knowledge that different levels of growth variation could only affect the magnitude of explained variance, not the ranks the original climatic variables in contributing to the redundant variables. Recalling

the previous ANOVA result that 7.91% of the overall general growth variation (represented in GPC1, which carries 95% of the totally growth variations) was due to provenance variability (Table 1-4), a conclusion could be drawn that nearly 63% ($= 5.23\% \div (7.91\% \div 95\%)$) of the genetic variability of the provenances in growth was accounted for by the climatic variation of provenance origin environments, acting as an agent of natural selection. This conclusion supports the assumption that genetic variability is habitat-correlated.

On the other side, variations in provenance origin's climatic conditions were better explained (maximally 18.98%, Table 1-13) by the growth variables than vice versa. This is because there were less variations in the climatic variables than in growth variables as the former are actually on provenance level while the latter on plot-mean level.

Table 1-13. Raw variations in growth and provenance origin place's climate conditions cross-explained by their opposite redundant variables from the redundancy analysis based on the within and between correlation matrices of growth measures and provenance origin climate variables.

Raw variation (%)	Growth redundant variables				Prov. climate redundant variables			
	Grow1	Grow2	Grow3	Grow4	Pclim1	Pclim2	Pclim3	Pclim4
Growth Var.					5.23	0.26	0.16	0.01
Prov. Climate Var.	18.98	0.68	0.20	0.08				

In this analysis, the redundancy structure (Table 1-14), assessed by the correlation coefficients between redundant variables and original variables, are probably more interesting than the redundancy itself as it presents an overall view of the contributions of the original variables onto the redundant variables and thus, reveals relationships between the original

variables of the redundant variables with the opposite group. Since none of the redundant variables, but the first one, accounted for the variations of the opposite group noticeably, only the structure for the first pair of redundant variables deserves concern. Again, as we are interested in the climatic factors that underlie growth variation among provenances, attentions were only given to the first redundant variable of the ten provenance climatic variables (i.e., Pclim1).

Low rate of redundancy of growth on provenance climatic conditions resulted in low correlations between growth variables and Pclim1, none of which was greater than $|R| = 0.4$ (Table 1-14). Relatively, HT3 was most closely correlated with Pclim1, followed by the diameters and volumes. There were rapid declines in the correlations of heights with Pclim1 as age increased, which agrees with the previous multiple regression analyses of geographic trends in growth (Table 1-7). However, the correlation between diameter and volume with Pclim1 remained as tree grew older, indicating more persistent genetic control in diameter and volume growth than in height growth, though not so strong as in early height growth.

On the other side, the correlations of the provenance climatic variables with Pclim1 are more meaningful as they indicate the relative importance of different climatic variables for provenance origins when their linear combination (Pclim1) maximally accounted for variation of the growth variables. Results in Table 1-14 indicate that all the climatic variables were closely associated with Pclim1, except PMAP, PMSP and PMTWM which define provenance origin's moisture conditions as well as warmth in summer. Among the closely correlated variables, PDD0 and PMTCM (which define winter harshness of the provenance origin places) had the strongest correlations with Pclim1. The length of frost-free period (PNFFD and PFFP) as well as the mean annual temperature (PMAT) had second-highest correlations with Pclim1. PDAY, a

function of provenance latitude, also had strong negative correlation with Pclim1, indicating that provenances from northern areas were less favored than southern ones in general. PDD5 had less strong correlation with Pclim1 than PDD0 did, indicating that the amount of warmth of provenance origin environments was less important to growth performance than winter coldness. Therefore conclusions were made that temperature related climatic conditions, especially those defining winter harshness of the provenance origins, along with photoperiod_condition, contributed the most in differentiating growth performance of the provenances; while moisture related conditions and the amount of warmth of provenance origins did not affect much in characterizing growth performance of these provenances.

The results can be well explained by the natural distribution of Sitka spruce. That is, with different temperature and light-climatic regimes while relatively even moisture conditions along the long, narrow strip of the Pacific west coast where Sitka spruce occurs naturally, the species could differentiate its populations in growth only by temperature and photoperiod regimes.

Table 1-14. Redundancy structure (correlation coefficients) of the original variables with the first provenance climate redundant variables (Pclim1).

Correlation coefficients of the Pclim1 with			
Original growth variable		Original provenance climatic variable	
HT3	0.359	PDAY	-0.835
HT10	0.229	PMAP	0.368
HT15	0.153	PMSP	0.080
HT20	0.120	PMAT	0.845
DIA10	0.241	PMTCM	0.863
DIA15	0.231	PMTWM	0.199
DIA20	0.232	PNFFD	0.858
VOL10	0.232	PFFP	0.825
VOL15	0.204	PDD5	0.668
VOL20	0.209	PDD0	-0.873

1.5. Conclusions

1. Great genetic variability in growth performance among the 43 Sitka spruce provenances were observed despite the dominant influences of site conditions. Nearly 63% of the growth associated genetic variability among the provenances was directly explained by the climatic conditions of the provenance origins.
2. Strong geographic trends, mainly latitudinal, underlie the growth performance of the provenances: southern provenances outgrew northern provenances, but the southernmost provenances did not fare well. The expression of the geographic trends was highly site, age and trait dependent. The milder the planting site, the stronger the geographic variation expressed, and the greater the likelihood that the latitudinal trend being linear. The strength of geographic patterns of variation was greatest in early height growth and declined rapidly with increasing age, but remained significant for diameter and volume growth at year 20.
3. The major ecological forces driving the geographical trend in growth performance of the provenances were predominantly temperature related, particularly for climatic elements related to winter harshness. That is, Sitka spruce populations were differentiated by temperature and photoperiod regimes of their origins.
4. The phenotypic expression of a provenance at different test sites was mostly correlated with the moisture conditions of the site, especially to summer precipitation. Moisture related site influences enhanced on later height growth while temperature related site climatic influences were influential on early height growth and diameter growth.

5. Growth variation was well accounted for by site climatic conditions, which implies high possibility of predicting growth from planting sites using climatic models.

1.6. References

- Box, G.E.P., Draper, N.R.** 1987. *Empirical Model-Building and Response Surfaces*. John Wiley and Sons, Inc. New York.
- Burley, J.** 1965. Karyotype analysis of Sitka spruce. *Silvae Genetica*. 14: 127~132.
- _____. 1966. Genetic variation in seedling development of Sitka spruce, *Picea sitchensis* (Bong.) Carr. *Planta*. 99: 283~289.
- Campbell, R.K., Pawuk, W.A., and Harris, A. S.** 1989. Microgeographic genetic variation of Sitka spruce in southeastern Alaska. *Can. J. For. Res.* 19: 1004~1013.
- Cooley, W.W., and Lohnes, P.R.**, 1971. *Multivariate Data Analysis*. Wiley, New York.
- Daubenmire, R.** 1968. Some geographic variations in *Picea sitchensis* and their ecological interpretation. *Can. J. Bot.* 46: 787~798.
- Draper, N.R. and Smith, H.** 1966. *Applied regression analysis*. John Wiley and Sons Inc., New York.
- Falkenhagen, E.R.** 1977. Genetic variation in 38 provenances of Sitka spruce. *Silvae Genet.* 26: 67~75.
- _____. 1978. Parent tree variation in Sitka spruce provenances, an example of geographic variation. *Silvae Genet.* 27: 24~29
- _____. and **Nash, S.W.** 1978 Multivariate classification in provenance research. *Silvae Genet.* 27: 14~23.
- Farr, W.A. and Harris, A.S.** 1979. Site index of Sitka spruce along the pacific coast related to latitude and temperatures. *For. Sci.* 25:145~153.
- Gittins, R.** 1985. *Canonical Analysis: A review with applications in ecology*. In: *Biomathematics* Vol. 12, Springer-Verlag, Berlin.
- Gregorius, H.R. and G. Namkoong** 1986. Joint analysis of genotypic and environmental effects. *Theor. Appl. Genet.* 72: 413~422.
- Hall, P.M.** 1994. Ministry of Forests' perspectives on spruce reforestation in British Columbia. In: Alfaro, R.I., Kiss G. and Fraser R.G. (eds) *The white pine weevil: biology, damage and management*. Symp. Proc. pp1~6. Jan. 19-21, 1994, Richmond, B.C. Canada.
- Henderson, D.M. and R. Faulkner** (eds) 1987. *Sitka spruce*. In: *Proceedings of the Royal Society of Edinburgh*. (Section B, Biological Sciences). Edinburgh: 22 George St. 234pp.
- Holmes, G.D.** 1987. Foreword. *Proceedings of the Royal Society of Edinburgh*, 93B, v.
- Hormann, R.K.** 1987. North American tree species in Europe. *J. Forestry*. 85: 27~32.

- Ilingworth, K.** 1978. Sitka spruce provenance 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 Pp 311~326. Vancouver, B.C. Canada.
- Jackson, D.A.** 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology*. 74(8): 2204 ~ 2214.
- Jolliffe, I.T.** 1986. *Principal Component Analysis*. Springer-Verlag, New York, USA.
- Kendall, M.G. and Stuart, A.** 1967. *The Advanced Theory of Statistics: Vol2. Inference and Relationship*. (2nd ed). Hafner Publishing Company, New York.
- Khalil, M.A.K.** 1993. Performance of genotypic stability of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Newfoundland, Canada. In: Ying, C.C. and Mcknight, L.A. (eds) *Proc. IUFRO International Sitka spruce provenance Experiment*. Pp 59~80. Edinburgh, Scotland. Ministry of Forests of B.C., Victoria, BC Canada and The Irish Forestry Board, Co. Wicklow, Ireland.
- Kovats, M.** 1977. Estimating juvenile tree volumes for provenance and progeny testing. *Can. J. For. Res.* 7: 335~342.
- Lines, R.** 1973. Sitka spruce IUFRO collection. *Rep. For. Res.* 42~45.
- MacSiurtain, M.P.** 1981. *Distribution, management, variability and economics of Sitka spruce in coastal British Columbia*. M.Sc. thesis. Fac. For., UBC., Vancouver, B.C., Canada. 256p.
- Malcol, D.C.** 1987. Some ecological aspects of Sitka spruce. In: Henderson, D.M. and Faulkner, R. (eds) *Proc. Royal Soc. Edinburgh*, 93B. Pp 85~92. Edinburgh, Scotland.
- Morgenstern, E.K.** 1996. *Geographic variation in forest trees: genetic basis and application of knowledge in silviculture*. UBC Press, Vancouver, British Columbia, Canada.
- Namkoong, G. and Kang H.** 1990. Quantitative Genetics of Forest Trees. *Plant Breeding Review*. 8 (Chpt.5): 139~188.
- Pojar, J., K. Klinka and D.V. Meidinger.** 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Eco. Manag.* 22: 119~154.
- Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse and D.A. Hamilton.** 1998. Genetic responses to climate for *Pinus contora* in Brititsh Columbia: niche breadth, climate change, and reforestation. (in press)
- Roche, L.** 1969. A genecological study of the genus *Picea* in British Columbia. *New Phytologist*. 68: 505~554.
- _____ and **P.G. Haddock,** 1987. Sitka spruce (*Picea sitchensis*) in North America with special reference to its role in British forestry. *Proceedings of the Royal Society of Edinburgh*, 93B: 1~12.
- SAS Institute Inc.** 1990. SAS/STAT User's Guide, Version 6, 4th edition. Vol .1 (pp 943) and Vol. 2 (pp 846). Cary, NC, USA.
- Wetherill, G.B.** 1986. *Regression Analysis with Applications*. Chapman and Hall Ltd., New York.
- Wollenberg, A.L.** 1977. Redundancy analysis --- An alternative for canonical correlation analysis. *Psychometrika* 42(2): 207 ~219.
- Worrell, R. and Malcolm, D.C.** 1990. Productivity of Sitka spruce in northern Britain; 1. The effects of elevation and climate. 2. Prediction from site factors. *Forestry* 63: 105~118.
- Yeh, F.C. and El-kassaby, Y.A.** 1980. Enzyme variation in natural populations of Sitka spruce (*Picea sitchensis*); 1. Genetic variation patterns among trees from 10 IUFRO provenances. *Can. J. For. Res.* 10: 415~422.

- Yeh, F.C. and Rasmussen, S.** 1985. Heritability of growth in 10-year old Sitka spruce. *Can. J. Genet. Cyt.* 27 (6): 729~734.
- Ying, C.C.** 1991. *Genetic resistance to the white pine weevil in Sitka spruce*. Research Notes No. 106, Research Branch, Ministry of Forests B.C., Victoria, B.C., Canada.
- Ying, C.C.** 1997. Effects of site, provenance, and provenance and site interaction in Sitka spruce in coastal British Columbia. *Forest Genetics*. 4(2): 99~112.

2. Effect and probability of white pine weevil attacks on height growth of 14 Sitka spruce provenances

Abstract: White pine weevil (*Pissodes strobi* (Peck)) attacks were recorded along with height growth of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) periodically for 20 years since planting at four test sites of IUFRO provenances trials in British Columbia. Data were analyzed in two directions: examining the effects and persistence of weevil attacks on height and height increment rate and exploring the possible sources of variation accounting for the probability of weevil attack occurrence at different measurement intervals. Results indicated that both early and later attacks (before and after year 10) significantly slowed down height growth, though later attacks were about three times more frequent than early attacks. Weevils caused loss in height increment rate of around 30% over the measurement intervals. Height loss in absolute value was barely perceivable before year 10 as early weevil attacks tended to occur on taller than shorter trees within plantations. Height loss from weevil attack was 12 and 23% at year 15 and 20, respectively. Tree could resume normal height growth in about three years from early weevil attacks, but would not recover in terms of height growth rate until five to 10 years after attacks. The occurrences of later weevil attacks highly depended on previous attack history. Probabilities of weevil attacks on previously attacked trees were about three times greater than on unweeviled trees. Previous tree heights influenced the probabilities of weevil attacks at early years (before year 10) such that taller trees were more at risk to weevil attacks. The frequency of weevil attacks also varied among blocks within plantation, which implies non-random spatial pattern of

weevil activity. At young ages, weevil attack rates increased with site mildness and provenance latitudinal gradient (north to south), but these trends were not evident after year 15. This suggests that possibly height at the time of attack, not site mildness and provenance latitudinal location, caused variations of weevil attack rates among sites and provenances in early years. Different provenances did not exhibit different levels of weevil resistance until after year 10, suggesting weevil resistance observed in several provenances of Sitka spruce could be a stimulated biological response by weevil attack which has genetic background that varies among the provenances. Of the 14 provenances studied, three are recommended for further study as weevil resistant and/or tolerant provenances.

Keywords: height growth; probability; provenance trial; Sitka spruce (*Picea sitchensis* (Bong.) Carr.), white pine weevil (*Pissodes strobi* (Peck)).

2.1. Introduction

Sitka spruce (*Picea sitchensis* (Bong.) Carr.), a fast growing conifer native to the Pacific west coast of North America and a thriving plantation species in Great Britain (Herman 1987), could have been the most productive reforestation species in coastal British Columbia (BC) if not for the impact of the white pine weevil (*Pissodes strobi* (Peck)) on height growth at juvenile ages (Ying 1991; Hall 1994). Weevil damage results from larva and adults (occasionally) feeding on the tree leader and consequently, disabling the main stem growth and/or causing defects of the

stem or even deformity of the whole tree (Alfaro 1989a; Alfaro and Omule 1990; Alfaro 1994). Control of the weevil damage has been long concerns to forestry practices and the Ministry of Forests (MoF) of BC (Ying 1991; Hall 1994). However, none of the control techniques tested thus far, including shading, clipping, insecticides, or biological control, have proved to be sufficiently effective and practical (Cozens 1983; Hall 1994). There is increased interest in genetic control, alone and in combination with other control methods, since the discovery of apparent provenance differences in tolerance of weevil attack (Wood 1987; Alfaro and Ying 1990; Ying 1991). However, long-term benefits from genetic resistance is questionable until the mechanism of genetic resistance, the mode of inheritance, and the integration of resistant trees with silvicultural systems have been well understood (Ying 1991). Although weevil damage on Sitka spruce is frequently reported, the details of weevil attack pattern over years (i.e., temporal pattern) have seldom been studied, which is particularly valuable and interesting in understanding weevil behavior in relation to host selection.

In early 1970s, the BC MoF launched a Sitka spruce provenance testing program, in cooperation with the international Sitka spruce provenance trials coordinated by the International Union of Forest Research Organizations (IUFRO). Extensive weevil attacks occurred at four out of eight IUFRO test sites located at coastal BC (Ying 1991). Weevil attacks were recorded at these four sites along with the height growth on individual trees periodically over 20 years since planting. The data provided a good opportunity to systematically investigate the temporal pattern of weevil attacks at different locations and ages and on different Sitka spruce provenances. In this chapter, the 20-year height growth along with weevil attack are analyzed to quantify weevil damage and height growth temporal patterns, and to examine the explanatory sources of variation

accounting for the probabilities of weevil attack occurrences across different levels of experimental factors and at different ages.

2.2. Materials

Data from four test sites of Sitka spruce provenance trials in BC were applied in this study (for more detailed information regarding the trials, see Illingworth (1978) and Ying (1991 and 1997), or Chapter One). The four sites are Head Bay (HB), Kitimat Valley (KT), Maroon Creek (MN), and Nass River (NS). Except HB, the remaining three sites are located at peripheral inner coastal areas that are less favorable (harsh in winter) for Sitka spruce to grow (Table 2-1). The unfavorable growing conditions of these sites were assessed by summarizing the climatic data for 10 macro-climatic variables that were collected from the British Columbia Sitka spruce provenance trials, which totally involve the test of 43 Sitka spruce IUFRO provenances at 12 sites (see Chapt.1 for details). Principal component analysis (PCA) was used for reducing these climatic variables into a few, informative variables for defining climatic conditions of test site and of provenance origin (see Chapt.1 for explanation). The first principal component (climPC1) accounted for 62% of the original climate variations and was used as an index of test site mildness (sitePC1): a higher value for sitePC1 is an indication of milder site.

The experiment followed a completely randomized block design with nine blocks per site. Ten provenances were tested at each site with six common to all the four sites (Table 2-2). A total of 14 provenances were involved, which cover the species' main coastal range from southern Alaska to Oregon coast, extending inland into the hybridization zone of Sitka x white

spruce (Ying 1991; Table 2-2). Within block each provenance tested is represented by a 9-tree-row plot. Trees were planted at even space of 3 x 3 m. The number of trees planted per site is 810, that is, totally 3240 trees are planted.

Extensive weevil attacks occurred during the first 20-year period after planting. Upon year 20, only 8.3, 34.8, 36.3 and 4.4% of the trees escaped from weevil attack at site HB, MN, KT and NS, respectively. Accordingly, the mortality rate at year 20 was 11.9, 14.7, 2.7 and 32.0% for these sites, respectively. The high mortality at site NS is partly (about 4%) due to road construction in those years.

Tree height was measured to the nearest decimeter at the 3rd, 6th, 10th, 15th and 20th year after planting (referred to as HT3, HT6, and so on) on individual trees. At year 3, the length of tree leader was also recorded (referred to as Lead3). Since year 6, weevil attacks were observed and recorded during each measurement interval that is between two successive measurement years of height. For instance, weevil attacks during year 3 to 6 were recorded at year 6 and referred to as WV6, and same rule with WV10, WV15 and WV20. Ordinal codes were used to classify the intensity of weevil attacks. A value of 0, 1, 2, and up to 5 were given for no, one, two attacks and so on, respectively. A value of 6 was given to dead trees (i.e., the tree died either from 1, 2, or more attacks) which no longer had height measures. It should be mentioned that any weevil code value equal to or greater than 2 implies the attacks could have occurred at either successive years or non-successive years during the measurement interval. In this chapter, the five height measurements along with the four weevil attack codes at individual tree level were employed in the analyses.

Table 2-1. Locations and the first principal component values (sitePC1) describes site mildness of the four weeviled test sites.

Site	Code	BGC ¹ Zone	Latitude	Longitude	Elevation (m)	sitePC1 ²
Head Bay	HB	CWHvm1	49°48"	126°28"	15	1.71
Kitimat Valley	KT	CWHws1	54°12"	128°33"	100	-0.98
Maroon Creek	MN	CWHws2	54°46"	128°39"	600	-5.92
Nass River	NS	CWHws1	55°04"	129°26"	15	-2.34

¹BGC Zone = Biogeoclimatic Zone (BC's ecological classification of the land, see Pojar *et al* 1987).

²See Chapter One for explanation.

Table 2-2. Names, IUFRO number, and place of origin for the 14 provenances tested at the four weeviled sites.

Provenance Name	IUFRO No.	BGC ^a Zone	Latitude	Longitude	Elevation (m)	Tested at ^b			
						HB	KT	MN	NS
Forks WA	3	(USA)	48° 04"	124° 18"	137	x	x	x	x
Hoquiam WA	8	CWHvm1	47° 05"	124° 03"	5	x	x		
Necanicum WA	12	(USA)	45° 49"	123° 46"	45	x	x	x	x
Brookings OR	18	(USA)	42° 15"	124° 23"	90			x	x
Yakutat AK	21	(USA)	59° 31"	139° 42"	12			x	x
Duck Creek	24	(USA)	58° 22"	134° 35"	30	x	x		
Ward Lake AK	30	(USA)	55° 25"	131° 42"	15	x	x		
Kitwanga	32	<i>ICHmc2</i>	55° 10"	127° 52"	660			x	x
Usk Ferry	40	CWHws1	54° 38"	128° 24"	135	x	x		
Inverness	44	CWHvh2	54° 12"	130° 15"	30	x	x	x	x
Link Road	49	CWHwh1	53° 30"	132° 10"	90	x	x	x	x
Holberg	56	CWHvm1	50° 37"	128° 07"	30	x	x	x	x
Tahsis Inlet	61	CWHvm1	49° 50"	126° 40"	0			x	x
Big Qualicum	62	CDFmm	49° 23"	124° 37"	0	x	x	x	x

^a BGC Zone = Biogeoclimatic zone (Ecological zone in British Columbia); CWH= Coastal Western Hemlock Zone; ICH= Interior Cedar-Hemlock Zone (*ICHmc2* is a hybridization zone of Sitka x white spruce).

^b see Table 2-1 for test site code.

2.3. Methods of Data Analyses

2.3.1. Examining the effects of weevil attack on height growth over measured years

In order to examine the effects of weevil attacks on height growth over the assessed years along with experimental effects, height variation sources were tested by analysis of variance

(ANOVA), using the SAS GLM procedure based on repeated measures of height. As heights and weevil attacks were recorded on individual trees at five different ages, the use of repeated measurement analysis (Kuehl 1994) not only examines the sources of weevil attacks and experimental effects (i.e., Site, Provenance, Site-by-Provenance interaction, and Block within Site,), but also reveals age (time) trend and age interactions (i.e., Age x Site, Age x Provenance, and Age x Weevil attacks). Age trend of height growth reflects the tree's responses to experimental effects and to weevil attacks over years, which is very important for understanding the temporal host-pest interaction. In this analysis, heights were treated as different observations (not different variables) for the single dependent variable, HT, which is contingent with the measurement years (i.e., ages) under the variable, Age. Weevil attacks were tested as a discrete covariate along with other experimental effects. Leader length at year 3 (i.e., Lead3) was also included in the GLM model as a continuous covariate due to its significant effect on later height growth (see below). The interactions between weevil attack and the experimental effects were also included in the GLM model, which can be illustrated as follow:

$$HT = f \{(\text{Site, Provenance, Site x Provenance, Block within Site}), (\text{Weevil, Weevil x Age, Weevil x Site, Weevil x Provenance, Weevil x Site x Provenance, Weevil x Block within Site}), (\text{Age, Age x Site, Age x Provenance, Age x Block within Site}) \text{ and Lead3}\}.$$

Height growth-loss from weevil attack is more likely to be reflected by height increment rates (HIR) at different measurement intervals than by current height (HT) itself. Therefore, the significance of weevil effect on current height and its lasting effect on later height growth were tested by Multivariate Analysis of Variance (MANOVA) using HIR's at different measurement intervals as multiple response variables, while weevil attacks (when applicable) as well as other experimental effects as explanatory variables, using MANOVA within the SAS GLM procedure.

MANOVA is an extension of ANOVA which is to include more than one dependent variable in the analysis (Bernstein 1988). When several responses to experimental effects are measured, one possibility is to perform an analysis of each dependent variable separately using ANOVA. However, this will result in very high Type I error rate (i.e., α) for all analyses combined and the analysis ignores the dependence among the response variables. Specifically, the error rate for the k independent tests results in a Type I error rate of $(1-(1-\alpha)^k)$. However, by using MANOVA this kind of problem can be avoided as MANOVA treats all dependent variables simultaneously, while controlling for a specific α level. The methodology of MANOVA is analogous to that of ANOVA as it tests the equality of vectors of means, instead of one single mean as in ANOVA, over different treatments. In ANOVA, the total sum of squares is divided into that for treatment and for error. For MANOVA, the total sums of squares and cross products matrix (SSCP) is divided into the SSCP for treatment and for error. Similar to the test of Mean Square treatment to Mean Square error for ANOVA, MANOVA uses the ratio of SSCP for error to SSCP for treatment to test for significantly different vectors of means.

In this analysis, however, we only have five repeated measurements (i.e., $k = 5$), by using $\alpha = 0.01$ for separate ANOVA we still can achieve the overall level of $\alpha = 0.05$ without severe inflation of the Type II error rate (i.e., $\beta = 1-\alpha$) for the ANOVA. Therefore, both ANOVA and MANOVA were performed in analyzing the height growth rates for better understanding of the weevil attack impacts. The analyses were performed site specifically, as the four test site differed noticeably in site mildness, early weevil attack frequency and height growth rate. The extent of weevil caused height growth loss was evaluated by multiple comparisons of the height means and

means of height increment rate that correspond to different levels of weevil attacks by Student-Newman-Keuls (SNK) range test within the GLM procedure.

There are a few limitations for analyses of this section. First, the four test sites are virtually from two series of the Sitka spruce IUFRO provenance trials (i.e., Series II and III, see Chapt.1). When pooling the four sites with different experimental settings in the repeated measurement ANOVA, it is virtually intangible to isolate the effects of weevil attack from the effects of test site and provenance as they are already confounded with each another. Secondly, repeated measurement ANOVA has the advantage of being able to reveal the temporal patterns, but has the disadvantage of inflating the degree of freedom for the error term when sampling size is already large (in this case, five times the original measurement size), and thus cause inflation of the F test values for the variation sources tested directly against the error term. Third, significance related tests in the separate ANOVA for height increment rates were made under the assumptions of univariate response variable across experimental levels and weevil attack intensities, while those in MANOVA were made under the assumption of homogeneous variance-covariance matrix (SSCP) across different experimental levels and weevil attack intensities. These assumptions are not always valid in real world. Therefore, the AVOVA and MANOVA of this section should be considered referential rather than inferential.

2.3.2. Exploring the sources of variation accounting for weevil attack frequencies over measured years

In order to explore the possible sources accounting for the temporal pattern of weevil attacks, logistic regressions were performed on weevil cases (i.e., weeviled tree and unweeviled

tree), using site mildness index (sitePC1), provenance latitude, block, previous weevil attack(s) and previous tree height before current weevil attacks as explanatory variables. The analysis was performed for each measurement interval specifically, using the SAS LOGISTIC procedure with backward selection ($\alpha = 0.05$) for the predictive models. The general predictive model for the probability (p) of a tree being attacked at current measurement interval is

$$\text{Ln}(p) = f(\text{sitePC1, provenance origin's latitude, block, previous height, previous weevil attack}).$$

The use of backward regression is for the purpose of retaining as many as possible the explanatory variables in the model within the limitation of significance level (i.e., $\alpha = 0.05$). There could be some minor differences in the results of multiple regression between backward and forward selection, as backward selection starts with the elimination of the independent variable which has the smallest contribution to model R^2 among all the independent variables, while forward selection starts with the entering of the independent variable that has the biggest contribution to model R^2 . Both backward and forward selection continue the same process as per their first steps for the remaining independent variables till that the remaining ones are all significant in backward selection model, while those are all not significant for entering into forward selection model. Therefore, backward regression is considered suitable for retaining as many as possible (set by α level) independent variables, while forward selection more suitable for retaining as few as possible independent variables in the regression model. In this analysis, the suspected sources accounting for variation of weevil attack probability deserves full consideration, therefore, backward selection was used in the logistic regression modeling.

In all the analyses of this chapter, values for growth variables (HT's and HIR's) were transformed into natural logarithmic values in order to approach normal distributions. All the

significance related tests were under the assumptions of multivariate normality and homogenous variance and/or covariance of the response variable(s) across different levels of experimental factors and weevil attacks. Significance criterion for all the tests was set at $\alpha = 0.05$ level if not specified otherwise. All data analyses were performed with SAS procedures (SAS Inc. 1990).

2.4. Results and Discussions

2.4.1. *Experimental effects, Weevil effects, age trends and interactions*

With a high coefficient of determination ($R^2 = 0.899$), linear model was constructed by using five repeated height measures (HT3, HT6, HT10, HT15 AND HT20) over years as the response variable, while the experimental factors (site, provenance, site x provenance, and block within site) as independent variables, in addition with three types of covariates that are 1) weevil attack effects and its interactions with age and experimental effects, 2) age and its interactions and 3) Lead3. Assuming levels of all the experimental factors were randomly chosen while those for the other effects are fixed, using the SAS GLM procedure, F tests and pseudo- F tests proved that the effects of all these sources were significant with respect to height variation (Table 2-3). However, it should be noted that those variation sources tested directly against the experimental error term could be inflated due to large amount of degree of freedom for this term (see section 2.3.1). These variation sources are the three-factor-interactions (e.g., WV*Site*Provenance) and Lead3 (referred to the EMS column in Table 2-3).

The variance component for weevil effects ranked the highest level (45.02%), indicating that weevil attack became the predominant effects (instead of site effects as indicated by the

ANOVA in Chapt.1) accounting for height variations. That is, height variations at the four weeviled test sites were largely due to this biological effect, aside of experimental effects. The experimental effects still contributed considerably to height variations, except that Site effects were suppressed by weevil effects to certain degree. The provenance-by-site interaction endured the weevil effects, suggesting that when attacked by the weevil, different provenances could change height growth rates differently, sometime inversely, over environmental gradients.

The exceptionally great F values for the age-by-site interactions suggest that mild site could have higher early heights but lower later heights due to more severe weevil attacks compared to harsh sites. The age-by-weevil interaction also had a large F value, though not a large variance contribution (0.27%), indicating there could be a temporal switch of the sign in host-pest correlation pertaining to tree height. The plot of the height means for this interaction (Fig. 2-1) shows that height at early ages (before year 8) was greater for weeviled trees than unweeviled trees on average. Height means for unweeviled trees began to surpass weeviled trees at year 8, approximately. This age-by-weevil interaction suggests that height was not merely the influenced term by weevil, but also could be a causal factor to weevil attack occurrences at early years.

The significant interactions of weevil-by-site and weevil-by-provenance means that weevil effects were also conditional on site and provenance effects and that the latter are genetically controlled. The age-by-site and age-by-provenance being significant implies that the ranks of average heights for site as well as for provenance could change substantially over measured years in the presence of weevil attacks, which means that early height growth at weeviled sites is not reliable for determining rank of later growth.

However, one must notice the limitations in the present study. As stated before (section 2.3.1.), the experimental effects are confounded to each other to certain extent due to unbalanced setting, which caused virtual intangibility of the isolation of weevil effects from experimental effects as well as the partitioning of all the variation sources, under rigorous statistical criteria. In addition, the repeated measurement analysis introduced large amount of degrees of freedom for the experimental error term (five times greater than the size of using individual measurements independently), which resulted in very small (hence, sensitive) Mean Squares for the error term (MSE) and thus caused inflation of the F tests in which the MSE was used as the denominator for testing. Therefore, the interpretation for this ANOVA of repeated height measures should be considered as descriptive rather than inferential, which are based on the information from the GLM that has valid assumptions as stated before.

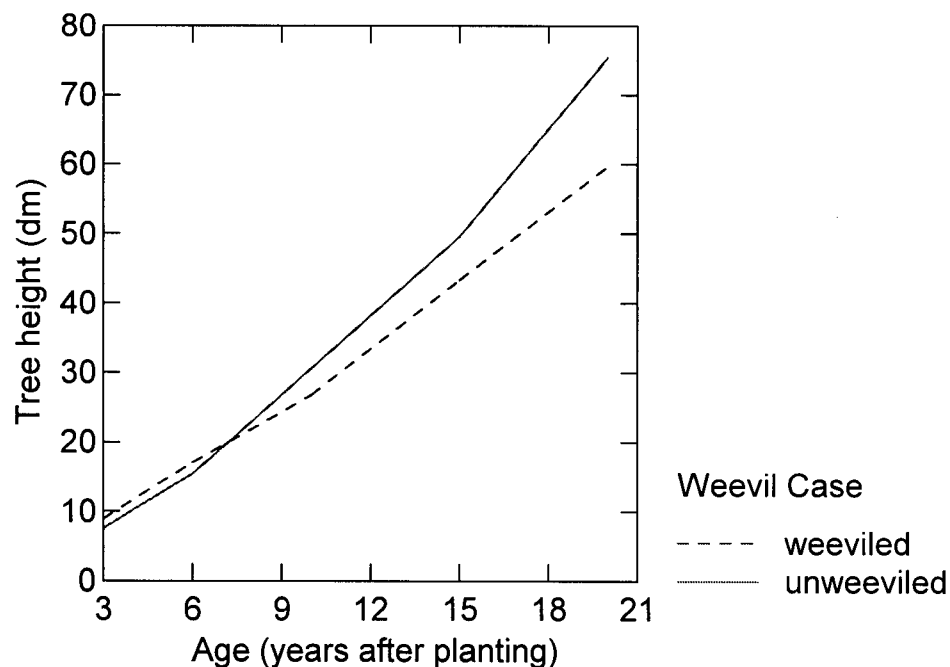


Fig. 2-1 Mean height trends of weeviled and unweeviled trees over measured years.

Table 2-3. ANOVA of the repeatedly measured heights at the four test sites for the experimental effects, weevil attacks, and age trend and the interactions of weevil, age with experimental effects.

Source	DF	Type III MS	F	Pr > F	Var.% ¹	EMS (expected Mean Squares)
<i>experimental effects (assuming random effects):</i>						
SITE	3	2.08	8.04 ^{*2}	0.0001	5.21	Var(Error) + 7.0097 Var(BLOCK(SITE)) + 3.8741 Var(SITE*PROV) + 42.676 Var(SITE)
PROV	13	1.34	4.50 [*]	0.0001	8.49	Var(Error) + 6.9195 Var(SITE*PROV) + 24.156 Var(PROV) + Q ⁴ (PROV*WV, SITE*PROV*WV)
SITE*PROV	31	0.69	8.66	0.0001	5.28	Var(Error) + 19.155 Var(SITE*PROV) + Q(SITE*PROV*WV)
BLOCK(SITE)	24	0.28	3.52	0.0001	0.70	Var(Error) + 24.515 Var(BLOCK(SITE)) + Q(BLOCK*WV(SITE))
<i>weevil and weevil interactions as covariates:</i>						
WV	9	10.26	129.61 [*]	0.0001 ^{**3}	45.02	Var(Error) + Q(WV, SITE*WV, PROV*WV, SITE*PROV*WV, BLOCK*WV(SITE))
WV*AGE	7	24.06	304.10	0.0001	0.27	Var(Error) + Q(AGE*WV)
WV*SITE	19	0.33	4.13 [*]	0.0001 ^{**}	0.11	Var(Error) + Q(SITE*WV, SITE*PROV*WV, BLOCK*WV(SITE))
WV*PROV	72	0.37	4.71 [*]	0.0001 ^{**}	0.87	Var(Error) + Q(PROV*WV, SITE*PROV*WV)
WV*SITE*PROV	80	0.35	4.38	0.0001	2.24	Var(Error) + Q(SITE*PROV*WV)
WV*BLOCK(SITE)	93	0.18	2.33	0.0001	0.52	Var(Error) + Q(BLOCK*WV(SITE))
<i>age and age interactions as covariates:</i>						
AGE	1	2.79	35.29 [*]	0.0001 ^{**}	2.38	Var(Error) + Q(AGE, AGE*WV, AGE*SITE, AGE*PROV, AGE*SITE*PROV, AGE*BLOCK(SITE))
AGE*SITE	3	8.79	110.97 [*]	0.0001 ^{**}	0.05	Var(Error) + Q(AGE*SITE, AGE*SITE*PROV, AGE*BLOCK(SITE))
AGE*PROV	13	1.35	17.09 [*]	0.0001 ^{**}	0.02	Var(Error) + Q(AGE*PROV, AGE*SITE*PROV)
AGE*SITE*PROV	31	0.91	11.47	0.0001	0.04	Var(Error) + Q(AGE*SITE*PROV)
AGE*BLOCK(SITE)	24	0.29	3.64	0.0001	0.00	Var(Error) + Q(AGE*BLOCK(SITE))
<i>covariate:</i>						
LEAD3	1	336.99	4257.77	0.0001	0.08	Var(Error) + Q(LEAD3)
Model	440	22.65	286.2	0.0001	71.29	
Exp. Error	14188	0.08			28.71	

1. Variance component rate (%), estimated by REML estimates using the SAS MIXED procedure, under the randomness assumption all sources of variation.

2. F values with * marks are Pseudo-F values computed by SAS GLM procedure under the RANDOM statement.

3. F tests with ** marks are tested assuming the other fixed effects are null.

4. "Q" symbol under the Expected Mean Square column means the multiplier for the variance term(s) inside the brackets is inestimable due to unbalanced data set.

2.4.2. Impacts of weevil attacks on height growth at different ages

Using height increment rates (HIR's) at different measurement intervals as multiple response variables, the significance of weevil attacks were tested by ANOVA (on each HIR) and by MANOVA (testing all the HIR's simultaneously), aside of the experimental effects (omitted from Table 2-4). The tests were performed site specifically because of substantial differences in site mildness and early weevil attack frequencies as well as the provenances tested among these four test sites. The MANOVA results in Table 2-4 indicate that, at each measurement interval, weevil attacks significantly reduced height growth rates of the current measurement interval and subsequently (with only one exception at NS site where WV15 did not influence the growth increment rate of the same period and subsequently). However, the ANOVA results indicate the persistence of the weevil effects varied from age to age and site to site. Generally, early weevil attacks (WV6) did not influence height growth rate of later measurement intervals (i.e., HIR10, HIR15, and HIR20), but later attacks (i.e., WV10, WV15, and WV20) did (see Table 2-4). This possibly is due to stronger recovery ability of younger trees, and could also be due to the fact that early weevil attack is much less extensive than later attacks. It could be proposed that the impacts of weevil attacks lasted for no more than three years before year 6, but for about four years during year 7 to10, and five to ten years during year 11 to15. This agrees with Cozens (1983) that 'a major weevil attack may destroy three years of growth, as the destruction of the previous year's stem will kill the current year's growth as well'. Though not adequately precise, it appears that the earlier the attack, the less the number of years required for the resumption of normal height growth rate due to higher vigor of younger trees. However, recovery of stem form

is not clear in this study. Stem defects after weevil attack were once reported by Alfaro *et al* (1989a).

From Table 2-4 one could also see that the lack of early attack (WV6) at sites KT and MN seems making it more difficult for the tree to recover from later attacks as compared to those at site HB and NS. This suggests that weevil tolerance could be possibly a stimulated response to weevil attacks of young trees. However, as for the limitations stated before (see section 2.3.1.), these test results should not be considered robust (i.e., indifferent of validations of the assumptions).

Since weevil attacks were scored as ordinal variables, one might also wonder if height growth-loss corresponded to different levels of weevil attack intensity. This was resolved by using Student-Newman-Keuls (SNK) range tests on the means for height increment rate (HIR) and height (HT) that correspond to different levels of weevil attacks at different measurement intervals (Table 2-5). Results indicate that the rank of weevil attack reflected the rank of height increment rate but did not well reflect the rank of height itself. That is, once weeviled, height means for the trees did not vary much among different levels of weevil attacks. The reason for this phenomenon could be that weevils attacked more intensively on taller and robust trees at early ages than on shorter and less robust trees to ensure better food resources (Silver 1968, Gary *et al* 1971; Alfaro 1989b and 1994), so that the growth increment rates were affected but the absolute height values did not vary accordingly to different levels of weevil attacks. Hence, pooling different levels of weevil attacks in the analyses of the remainder of this chapter is justified. By pooling the levels of weevil attacks, weevil caused height-loss was manifested at a rate of 12 to 23% between year 10 and 20, and the loss in growth increment rate compared to

unweeviled trees was 20 to 32% at all measurement intervals after pooling the four sites studied (Table 2-5).

The following implications, drawn from Table 2-5, deserve further consideration. First, weevil seems to be inclined to attack taller trees at early ages (before year 6) but later switched to shorter trees after year 10 (also see Fig. 2-1) because of repeated attacks (see below). Second, although weevil attack before year 6 caused loss in height increment rate during year 4 and 6, the ranking of total height at year 6 remains the same as year 3 between weeviled and unweeviled trees, indicating weevil attack occurred more often on taller trees but not severe enough to upset their rankings. Third, the influence of early attack lasted for no more than three years or so and tree could resume normal height growth rate from early weevil attack; but the effects of later attacks (year 10 and after) will last for about five to 10 years, in terms of height growth rate.

Table 2-4. Probabilities of the computed F statistics greater than the critical F values in testing the null hypothesis that there were no weevil influences on height increment rates (HIR's) at each measurement intervals since weevil attack recorded, based on SAS ANOVA of effects on each single RHT and MANOVA of overall effects on all the HIR's. (Testing of the experimental effects were also performed along with the tests for weevil effects but not shown in this table).

Weevil Attacks		WV6				WV10				WV15				WV20			
Sites	n	HB	KT	MN	NS	HB	KT	MN	NS	HB	KT	MN	NS	HB	KT	MN	NS
HIR6		0.0001	noWV	noWV	0.0001												
HIR 10		0.1190	noWV	noWV	0.2958	0.0001	0.0061	0.0039	0.0001								
HIR 15		0.0288	noWV	noWV	0.4666	0.0222	0.0002	0.0001	0.0600	0.0014	0.0001	0.0001	0.2101				
HIR 20		0.9147	noWV	noWV	0.3047	0.4588	0.0041	0.0036	0.9936	0.4766	0.0001	0.0001	0.8987	0.0001	0.0001	0.0001	0.0005
HIR overall		0.0001	noWV	noWV	0.0001	0.0001	0.0001	0.0001	0.0001	0.0065	0.0001	0.0001	0.5511	~	~	~	~

(Note: values in bold face are lower than the $\alpha = 0.05$ criterion, which means the rejections of the null hypotheses)

Table 2-5. Means for Height Increment Rates (HIRs, in percentage) and Heights (HT, in decimeter) and Student-Newman-Keuls (SNK) test results for these means corresponding to weevil attack codes at different measured years at the 4 test sites.

Weevil Code ¹	n	HIR6		HIR10		HIR15		HIR20		HT3		HT6		HT10		HT15		HT20	
		mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK
Year6:																			
1	69	72.9	b ²	78.2	b	55.1	a	34.5	a	9.2	a	16.0	a	28.7	a				
0	1876	103.4	a	91.4	a	47.4	b	35.7	a	7.3	b	14.8	b	28.4	a				
		(loss 29.5%)																	
Year10:																			
3	22	123.8	a	54.3	d	59.5	a	45.6	a			15.0	ab	23.3	c	37.2	b	54.3	a
2	156	111.0	ab	65.6	c	53.5	a	41.4	ab			16.1	a	26.8	b	41.4	a	58.7	a
1	494	102.9	b	81.0	b	55.8	a	40.2	b			14.0	b	25.4	bc	39.9	ab	56.3	a
0	1273	100.5	b	99.2	a	43.8	b	33.2	c			15.1	ab	30.1	a	43.5	a	58.3	a
		(loss 16.4%)																	
Year15:																			
5	37	105.2	a	107.4	a	35.7	c	34.9	a					30.8	a	42.1	b	56.9	b
4	127	107.1	a	115.4	a	35.1	c	36.0	a					30.0	ab	40.8	b	55.5	b
3	348	110.0	a	110.6	a	43.7	b	37.4	a					27.8	b	40.2	b	55.5	b
2	485	99.1	a	87.6	b	47.7	b	35.4	a					28.1	b	41.8	b	57.0	b
1	686	98.9	a	80.6	b	48.2	b	34.0	a					28.4	ab	42.4	b	57.1	b
0	262	103.7	a	86.8	b	60.5	a	38.2	a					29.1	ab	47.2	a	65.8	a
		(loss 12.2%)																	
Year20:																			
4	13	96.1	a	103.6	a	37.3	c	39.4	b							36.0	c	50.4	c
3	78	101.0	a	97.9	ab	40.3	bc	35.2	b							39.2	bc	53.2	bc
2	360	100.8	a	108.7	a	46.0	b	35.4	b							39.2	bc	53.2	bc
1	1303	102.3	a	86.3	b	47.1	b	34.5	b							42.7	b	57.8	b
0	191	105.1	a	87.4	b	59.4	a	45.2	a							47.8	a	69.8	a
		(loss 23.1%)																	

¹ Weevil Codes: 0 = unweeviled, 1 = once weeviled, 2 = twice weeviled, and so on

² Means with same letter not significantly differ from each other at $\alpha = 0.05$ level.

2.4.3. Explanatory sources accounting for weevil attack occurrence

By pooling the levels of weevil attacks, trees at each measured year were categorized into weeviled or unweeviled trees. The frequency of weeviled trees varied among different sites, provenances, and ages (Figs. 2-2 and -3). When pooling the four sites together, the frequency of weevil attacks at each measurement intervals was 4.4, 27.5, 69.2 and 75.9% during year 3 to 6, year 7 to 10, year 11 to 15, and year 16 to 20, respectively. This shows that later attacks (after year 10) were about three times more extensive than early attacks. The probability of weevil attack occurrence is therefore examined by logistic regression for each measurement interval separately.

Weevil case is used as the binary response variable which is encoded by transforming the original weevil codes into a binary variable, such that, 1 = unweeviled tree, 2 = weeviled tree (pooling all levels of weevil attacks). Previous weevil attacks might induce more attacks in later years. The age x weevil interaction illustrated in Fig. 2-1 suggests that, to certain degree, previous height itself accounted for the occurrence of weevil attack at early ages (i.e., weevil seems to attack taller trees at early ages). Therefore, to examine possible sources of variation accounting for the probability of weevil attack, logistic regressions were performed on experimental effects as well as on previous weevil attacks, and previous height *immediately before* the current measurement interval. The experimental effects used are Site, Provenance and Block within Site (excluding Provenance-by-Site interaction for ease of interpretation), where, the sites were represented by the values for site mildness index (i.e., sitePC1) while the provenances by provenance origins' latitudes (PLAT). This was chosen because Sitka spruce has provenances differentiated primarily by temperature and photoperiod regimes along the north-

south Pacific coastal line (see Chapt.1 for explanation). Backward selection ($\alpha = 0.05$) was applied to the logistic regression models to eliminate as few as possible insignificant variation source(s). The results are summarized in Table 2-6.

As indicated in Table 2-6, the prediction models were all highly significant ($p < 0.0001$), which means the probabilities of weevil attack occurrence were well accounted for by the models. However, the goodness-of-fit tests (Hosmer and Lemeshow 1989) indicate that the associations of predicted probabilities and observed responses were significantly departed, except for the earliest model (i.e., the one predicts Prob(WV6)). Nevertheless, the concordant rates (i.e., the percentages of correctly predicted weevil cases) were around 80%, suggesting the predictions are still reliable, especially when taking into account the undetermined targeting of weevil attacks.

The maximum likelihood estimates and their associated chi-square significance tests showed that the suspected sources significantly accounted for the variations of weevil attack probability (Table 2-6). Previous weevil attacks was the number one source accounting for later attacks, especially after year 10. The estimated coefficient for previous weevil attack(s) accounting for the probability of attacks during year 7 to 10 (i.e., Prob(WV10)) was 2.84, and those for year 11 to 15 and year 16 to 20 were 2.88 and 3.81, respectively (Table 2-6). The mean predicted probabilities of weevil attack occurrence for previously weeviled and unweeviled trees at different measurement intervals were computed and presented in Table 2-7, from which one could see that the probabilities of weevil attack(s) occurrences on previously weeviled trees (immediately before the current measurement interval) were about two to three times greater than on previously unweeviled trees. This is in accordance with Alfaro and Ying (1990) and Alfaro *et*

al (1993) who studied the association of weevil attack probability on a tree and the distance of that tree from the nearest previously attacked tree, and reported 're-attack' tendency of the weevil.

Table 2-7. Mean Predicted probabilities of weevil attack(s) occurrence for previously weeviled and unweeviled trees at different measurement intervals.

Previous weevil attack case	Probability of weevil attack(s)		
	Prob(WV10)	Prob(WV15)	Prob(WV20)
Year6:			
Unweeviled	0.2713	0.6588	0.7146
Weeviled	0.8353	0.9643	0.9446
Year10:			
Unweeviled		0.5592	0.6499
Weeviled		0.9433	0.9257
Year15:			
Unweeviled			0.2889
Weeviled			0.9550

Table 2-6. Maximum Likelihood estimates and logistic regression model information in predicting the probabilities of weevil attack occurrences at different measurement intervals (Prob(WV6), Prob(WV10) and so on) by previous height (HT3, HT6 and so on), site mildness (sitePC1), block and provenance origins' latitudinal (PLAT), based on individual trees observations and the use of backward selection at $\alpha = 0.05$ level.

Factors	Prob(WV6)			Prob(WV10)			Prob(WV15)			Prob(WV20)		
	Parameter estimates	Wald X ²	Pr > X ²	Parameter estimates	Wald X ²	Pr > X ²	Parameter estimates	Wald X ²	Pr > X ²	Parameter estimates	Wald X ²	Pr > X ²
Previous weevil attack(s):												
WV6				2.84±0.35	67.60	0.0001	1.24±0.62	3.95	0.0470	N/A ^a	2.86	0.0907
WV10							2.88±0.17	300.65	0.0001	0.71±0.20	12.38	0.0004
WV15										3.81±0.14	697.14	0.0001
Previous height(s):												
HT3	1.39±0.35	15.82	0.0001									
HT6				1.64±0.15	121.40	0.0001						
HT10							N/A	0.86	0.3544	N/A	2.57	0.1089
HT15												
Experimental effects:												
sitePC1	0.65±0.13	25.48	0.0001	0.56±0.03	285.56	0.0001	N/A	1.00	0.3185	N/A	0.37	0.5448
PLAT	-0.07±0.03	7.49	0.0062	-0.03±0.01	6.53	0.0106	-0.02±0.01	4.28	0.0386	N/A	1.60	0.2054
block	0.16±0.02	57.56	0.0001	0.22±0.01	616.47	0.0001	-0.04±0.01	65.14	0.0001	-0.05±0.01	37.15	0.0001
Model fitting:												
	-2LogL ^b = 875.377, x ² = 131.74 (p < 0.0001, DF = 4)			-2LogL = 2618.820, x ² = 1013.14 (p < 0.0001, DF = 5)			-2LogL = 3175.074, x ² = 562.65 (p < 0.0001, DF = 4)			-2LogL = 1791.980, x ² = 1495.127 (p < 0.0001, DF = 3)		
Goodness-of-fitting:												
Concordant Rate = 77.7% G ^c = 9.21 (p = 0.3245, DF = 8)			Concordant Rate = 82.6% G = 124.65 (p < 0.0001, DF = 8)			Concordant Rate = 73.0% G = 56.74 (p < 0.0001, DF = 8)			Concordant Rate = 88.6% G = 82.74 (p < 0.0001, DF = 8)			
a. N/A = Not Applicable (i.e., parameter not estimated as the effect is not significant at α = 0.05 level);												
b. -2LogL = -2Log Likelihood value (SAS Inc. 1990);												
c. G = Goodness-of-fit statistics (Hosmer and Lemeshow 1989).												

a. N/A = Not Applicable (i.e., parameter not estimated as the effect is not significant at $\alpha = 0.05$ level);

b. -2LogL = -2Log Likelihood value (SAS Inc. 1990);

c. G = Goodness-of-fit statistics (Hosmer and Lemeshow 1989).

Previous tree height also contributed significantly to the encounters of weevil attacks at early ages, especially before year 10. Positive estimates of the coefficients for the previous heights in the models (Table 2-6) indicated that taller trees at early ages were more susceptible to weevil attacks than shorter trees. This supports previous report that the weevil intends to feed on the highest trees with the longest, thickest leader (Alfaro 1989a). However, there were no significant associations between previous height and weevil attack occurrence after year 10. As weevils inclined to re-attack (i.e., attack those previously attacked), there was a switch in the sign of the correlation between previous height and probability of weevil attack before and after year 10. Taller trees had higher susceptibility to early weevil attacks which caused growth-loss to the trees and enhanced probability for those tree to encounter later attacks due to re-attack tendency of the weevil.

The density plots of weeviled and unweeviled (i.e., healthy) trees corresponding to the *immediately* previous height at different measurement intervals (Fig. 2-2) also revealed the height 'preferences' of weevil attacks at different ages. Another hypothetical reason explaining this phenomenon can be proposed here as that, weevils can attack successfully only within certain range of tree height, namely 'height-window'. Before year 6, trees seldom suffered from attack as tree height had not reached the height-window for weevil attack. Younger taller trees who reached the lower height limit early in their life became the ones that encountered weevil attacks first. After year 15, trees that had grown above the upper height limit for weevil attack were more likely to escape the attack. According to the data under this study, the tree height range within which extensive weevil attack occurred was between 0.89 and 4.4 m (Table 2-8). However, the observed large standard deviations of these height means suggest that the actual

height range prone to weevil attacks was much wider and undetermined. The age of the tree reaching the lower height limit for weevil attack was around year 6 to 8, and this was also the critical period for weevil controlling (e.g., clipping or eliminating weeviled trees). It could be very difficult to control the pest after year 10 since weevil populations exploded at this stage (deduced from the difference between the numbers of trees weeviled and unweeviled, Table 2-8) and repeated attacks became very common. However, the number of years for Sitka spruce seedlings to reach the proposed 'height-window' largely depends on planting site conditions and seed source used, therefore, the tree age should not be considered as the only criteria for timing of weevil control.

Block effects on the probability of weevil attack occurrence were significant over all the measurement intervals (Table 2-6), indicating group activity tendency of the insect, or micro-environmental variation affecting weevil activities. This agrees with the observed pattern of weevil population aggregation in the dispersal studies using mark and release techniques (Harman 1975).

Table 2-8. Mean and standard deviation of the mean of previous height (in decimeter) for weeviled ('yes') and unweeviled ('no') trees immediately before weevil attack occurrence at each measurement intervals.

Previous height	WV6		WV10		WV15		WV20	
	no	yes	no	yes	no	yes	no	yes
HT3:								
mean	7.6±3.1	8.9±4.1						
SNK	b	a						
n	3098	142						
HT6:								
mean			15.3±6.7	15.2±6.1				
SNK			a	a				
n			2349	891				
HT10:								
mean					28.8±9.8	29.4±12.1		
SNK					a	a		
n					997	2243		
HT15:								
mean							49.3±15.2	43.9±15.2
SNK							a	b
n							780	2460

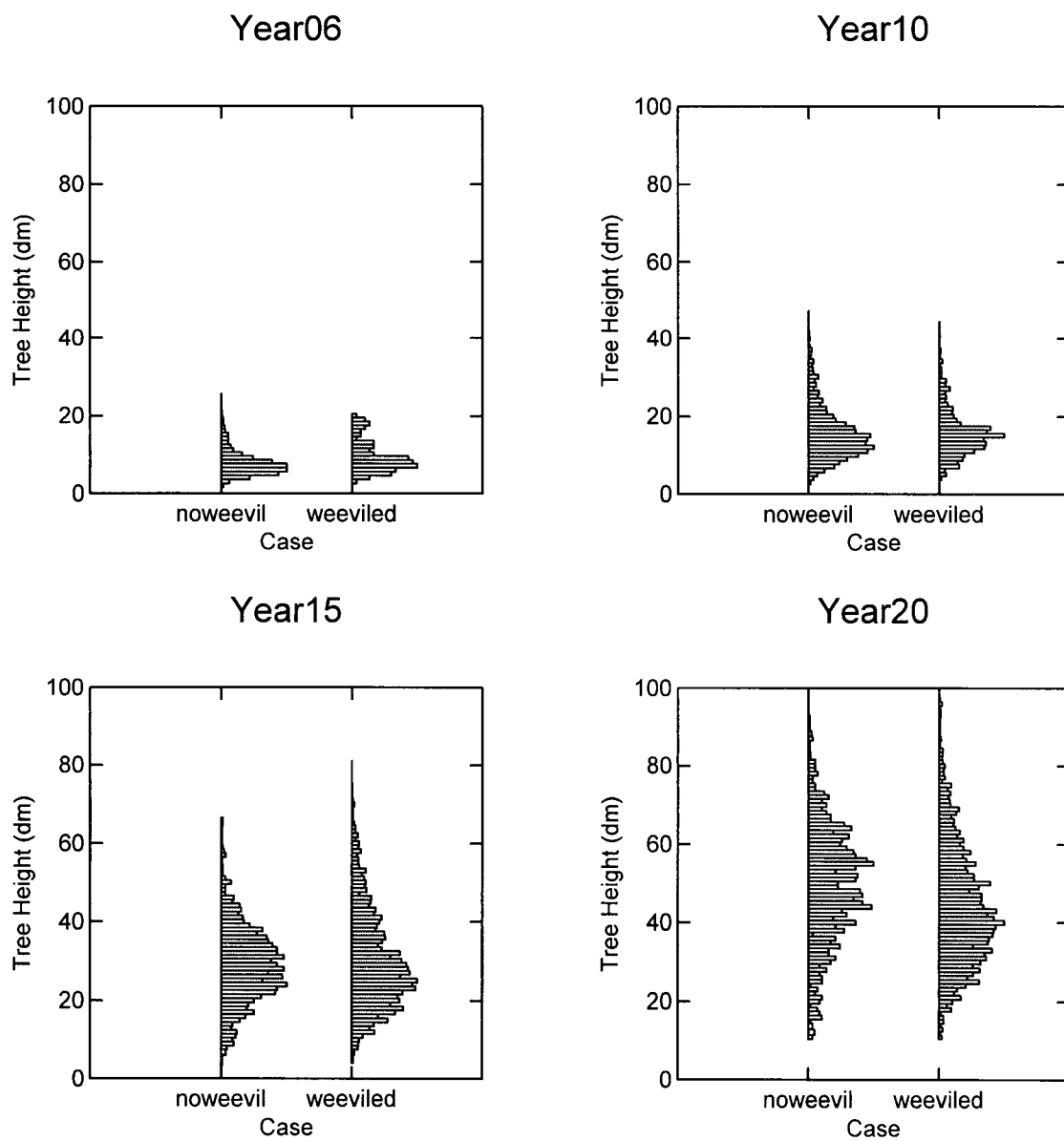


Fig. 2-2. Density plots of weeviled and unweeviled trees at current measurement interval corresponding to the immediately previous height at the four measured years (illustrated on top of each plot), respectively.

Site mildness also accounted for the occurrence of weevil attacks at early ages before year 10. Positive estimates of the regression coefficient with sitePC1 (i.e., site mildness index) suggests that weevils were more active at milder sites in early years (Table 2-6). This could possibly due to the fact that trees at milder site grew faster so that reached the lower height limit of weevil attack earlier than at harsher site. However, when the tree grew above the lower height limit of weevil attack, site differences diminished so that after year 10 there were no more significant differentials in weevil attack frequency among different sites (Table 2-6 and Fig. 2-3). The outbreak of weevil attack reached 'equilibrium' (Alfaro 1994) during year 15 to 20 after its 'exponential increase' of attack frequency since year 4 (Fig. 2-3). There has not yet a perceivable decline of attack frequency at these sites that is supposed to occur around 30 to 40 years after planting (Alfaro 1994).

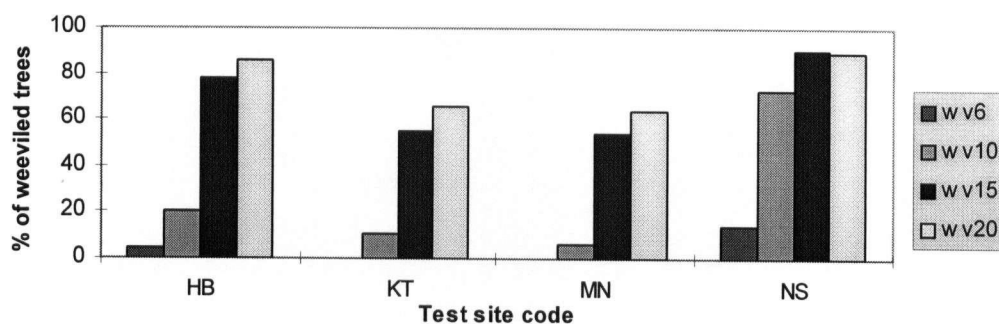


Fig. 2-3. Frequencies of weevil attack occurrences in measured years and at different test sites.

Provenance latitude (PLAT) seems also related to early weevil attacks. The negative estimated regression coefficients with PLAT up to year 15 suggest that southern provenances

were more subject to weevil attacks than northern ones before year 15 (Table 2-6). However, after year 15 this latitudinal trend also diminished, that is, the effect of PLAT no longer significantly affected the probability of weevil attack occurrence and hence are removed from the predictive model (Table 2-6). Previous analyses (Chapt.1) have indicated that the latitudinal trend of height growth among different provenances declined as trees grew older. Therefore, it might be the inherited height growth rate of the provenances, not inherited weevil resistance, which induced the latitudinal trend of weevil attack frequency at early ages.

Aside from the effects of provenance latitude, different provenances *did* show different levels of weevil resistance after year 10 (Fig. 2-4). The observed mean frequencies of weevil attacks on different provenances indicated that provenances Nos. 3032, 3021, 3062 and 3061 were relatively resistant to later weevil attacks which, based on previous analyses (see above), were more extensive and influential on height growth than early attacks. Age trend of the weevil attack frequencies also indicated that these provenances did not exhibit perceivable weevil resistance until after year 10. Within each provenance, the resistance level during year 11 and 15 was very consistent with that during year 16 and 20 (Fig. 2-4). The above results suggest that weevil resistance and/or tolerance, if any, in some of the Sitka spruce provenances, are stimulated responses by weevil attack (during year 6 and 10) and are genetically controlled, so that the abilities of developing the stimulation varies among different populations. The mechanisms of weevil resistance and/or tolerance, however, are not clearly understood yet. Similar induced resistance to the weevil attack was also found in white spruce and discussed by Alfaro (1995), which gave us the hope that Sitka x white spruce hybrids might be more resistant to weevil attack than non-hybrids.

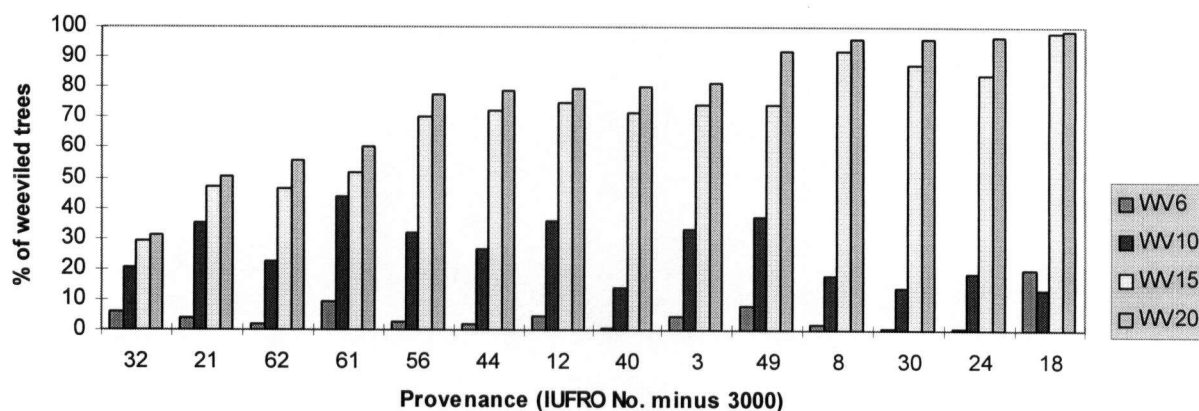


Fig.2-4. Frequencies of weevil attack occurrences at measurement intervals and on different provenances.

By examining the height means (HTs) and mean height increment rates (HIRs) of the 13 provenances (excluding No. 3018 which almost jeopardized at these sites) at different ages, the ranks of height and height increment rate of the provenances were presented in Table 2-9. It is noticeable by this table that provenance Nos. 3008, 3032 and 3062 suffered from weevil attacks but still remained as the tallest or taller provenances, which means that they were more tolerant or resistant to weevil attacks. Provenance Kitwanga (No. 3032), a poor grower at other test sites where the weevil did not attacked (data not shown), exhibited exceptionally strong *resistance and tolerance* to weevil attack among the studied provenances. It kept the lowest level of weevil attack frequency during outbreak of the weevil (Fig. 2-4), while its height growth rate topped the other provenances over the measured years and consequently, it joined the ‘tallest group of provenance’ at year 15 and almost surpassed the tallest provenance (No. 3062) at year 20 (Table 2-9). Provenance Hoquiam (No. 3008) showed possible weevil *tolerance* in that it kept both highest frequency of weevil attack and top class of its height. In contrast, provenance Big

Qualicum (No. 3062) showed its possible weevil *resistance* in that it maintained lower level of attack frequency during the outbreak of weevil attack while its height kept at top class among the provenances. The mechanisms of possible weevil tolerance and/or resistance in provenance Kitwanga and Big Qualicum are most interested to forest geneticists, since Kitwanga is a suspected hybrid of Sitka x white spruce (El-Kassaby et al 1988), while Big Qualicum is a high yield 'generalist' among the provenances tested (Ying 1997). Further studies are highly recommended on the three provenances, i.e., Kitwanga, Hoquiam and Big Qualicum, to exploit the genetic potential of weevil tolerance and/or resistance in Sitka spruce populations.

Table 2-9. Height (HT, in decimeter) means and mean height increment rates (HIR, in percentage) along with the Student-Newman-Keuls (SNK) multiple range test results of these means for the 13 provenances tested at the four test sites.

Prov	n	HIR 6		HIR 10		HIR 15		HIR 20		HT 3		HT 6		HT 10		HT 15		HT 20	
		mean	SNK ¹	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK	mean	SNK
32	56	133.8	a	119.2	a	90.9	a	53.3	a	5.0	f	11.5	d	24.3	bc	46.9	ab	72.9	ab
21	50	121.0	b	77.5	de	67.3	b	47.8	b	4.0	g	8.8	e	15.9	d	26.6	d	39.6	fg
24	144	108.0	c	95.4	bc	44.2	d	34.6	e	5.5	ef	11.4	d	22.2	c	32.2	c	43.5	fg
56	205	103.9	c	88.8	bcd	43.3	de	35.1	e	7.3	bcd	14.8	abcd	28.0	abc	40.5	abc	54.8	cdef
30	132	103.8	c	95.0	bc	41.9	de	31.5	ef	6.1	def	12.5	cd	24.6	bc	35.2	bc	46.8	efg
40	135	102.6	c	111.1	b	54.1	c	39.8	d	6.4	cdef	12.9	cd	27.2	abc	42.2	abc	59.5	bcde
44	203	102.2	c	84.9	cd	45.3	d	35.1	e	6.7	cde	13.5	bcd	25.0	bc	36.8	bc	50.0	def
49	195	100.2	c	83.7	cd	40.8	de	30.2	f	7.8	abcd	15.7	abcd	29.0	abc	41.0	abc	53.4	cdef
61	55	97.9	c	71.9	e	61.4	b	44.9	bc	6.5	cdef	13.0	cd	22.5	c	36.7	bc	53.2	cdef
3	219	106.2	c	85.3	cd	44.9	d	35.1	e	8.4	abc	17.1	abc	32.0	ab	46.5	ab	63.2	abcd
8	146	96.3	c	100.8	b	37.4	e	31.1	ef	9.4	ab	18.6	ab	37.2	a	51.4	a	67.5	abc
12	207	94.2	c	80.7	de	39.6	b	32.0	cd	9.9	a	19.2	a	35.0	a	49.1	a	65.2	abc
62	223	94.7	c	97.5	b	63.6	de	41.4	ef	8.5	abc	16.5	abc	32.7	ab	53.9	a	76.5	a

¹ Means with same letter do not significantly differ from each other at $\alpha = 0.05$ level.

2.5. Conclusions

1. Weevil attacks significantly slowed down height growth of young Sitka spruce at each current measurement interval. The average loss in height growth rate from weevil damage was around 30%. Weevil caused height loss was barely perceivable before year 10 because early weevil attacks tended to occur on taller than shorter trees within a plantation. Height loss was 12 to 23% between year 10 and 20. However, once a tree was attacked, the loss in height did not vary greatly among different levels of weevil attack intensity. It took about three years for the tree to resume its normal height growth rate from early attacks (before year 10), but five to ten years to recover from later attacks.
2. The probabilities of weevil attack highly depended on age, previous weevil attack history, and previous tree height at early ages. The average frequency of weevil attacks at each measurement intervals was 4.4, 27.5, 69.2 and 75.9% during year 3 to 6, year 7 to 10, year 11 to 15, and year 16 to 20, respectively. Weevil attacks in later years (after year 10) were approximately three times as extensive as in early years (before year 10). Early weevil attack occurrences were highly correlated with tree height such that, the taller the tree the higher the risk it had to encounter weevil attack. The occurrences of later weevil attacks highly depended on previous attack history. The risk of repeated attack on previously weeviled tree was about two to three times greater than on previously unweeviled tree. The frequency of weevil attacks also varied among blocks within plantation, which implies group activity tendency of the weevils, or spatial sensitivity to micro-environmental differences.

3. Dependencies of weevil attacks on both a multivariate measure of site mildness and provenance latitudinal origins were perceivable only at early ages, but not after year 15. Weevil attacks were more severe at milder than harsher site, and on southern provenances than on northern ones during early years. This suggests that tree height at attack, not site mildness and provenance latitudinal origin, might be the cause accounting for different attack rates among sites and provenances at early ages. Different provenances did not exhibit different levels of weevil resistance until after year 10, suggesting that weevil resistance, observed in several provenances, could be a biological response that is stimulated by weevil attack and has genetic background varying among the provenances. Three of the 14 provenances tested, i.e., Kitwanga, Hoquiam and Big Qualicum, were recommended for further study as weevil resistant and/or tolerant provenances.

2.6. References

- Agresti, A.** 1984. *Analysis of Ordinal Categorical Data*. New York: John Wiley & Sons, Inc.
- Alfaro, R.I.** 1982. Fifty-year-old Sitka spruce plantations with a history of intensive weevil attack. *J. Entomol. Soc. British Columbia* 79: 62~65.
- _____. 1989a. Stem defects in Sitka spruce induced by Sitka spruce weevil, *Pissodes strobi* (Peck). In: R.I. Alfaro and S.G. Glover (eds). *Proc. IUFRO Working Group on insects affecting Reforestation*. Vancouver, B.C., pp. 177~185.
- _____. 1989b. Probability of damage to Sitka spruce by the Sitka spruce weevil, *Pissodes strobi*. *J. Entomol. Soc. B.C.* 86: 48~54.
- _____. and **C.C. Ying.** 1990. Levels of Sitka spruce weevil, *Pissodes strobi* (Peck), damage among Sitka spruce provenances and families near Sayward, British Columbia. *Can. Ent.* 122: 607-615.
- _____. and **S.A.Y. Omule.** 1990. The effects of spacing on Sitka spruce weevil damage to Sitka spruce. *Can. J. For. Res.* 20: 179~184.
- _____. 1992. Forecasting spruce weevil damage. In: Ebata, T. (ed.) *Proceedings of a Spruce weevil Symposium*. Terrace, BC, March 12, 1992. BC MoF, Price Rupert Region. Pp 10~16.

- _____. **Hulme, M. and Ying, C.C.** 1993. Variation in attack by Sitka spruce weevil, *Pissodes strobi* (Peck), within a resistant provenance of Sitka spruce. *J. Entomol. Soc. B.C.* 90: 24~30.
- _____. 1994. The white pine weevil in British Columbia: biology and damage. In: Alfaro, R.I., Kiss G. and Fraser R.G. (eds) *The white pine weevil: biology, damage and management*. Symp. Proc. Pp7~22. Jan. 19-21, 1994, Richmond, B.C. Canada.
- _____. 1995. An induced defense reaction in white spruce to attack by the white pine weevil, *Pissodes strobi*. *Can. J. For. Res.* 25: 1725~1730.
- Bernstein, I.H.** 1988. *Applied multivariate analysis*. Springer-Verlag. Pp 315~344.
- Cozens, R.D.** 1983. The spruce weevil *Pissodes strobi* Peck (Coleoptera: Curculionidae): a review of its biology, damage and control techniques with reference to the Prince George Timber Supply Area. B.C.Min. For., Victoria, B.C. Internal Rep. PM-PG-3.
- _____. 1987. Second broods of *Pissodes strobi* (Coleoptera: Curculionidae) in previously attacked leaders of interior spruce. *J. Entomol. BC.* 84: 46~49.
- El-Kassaby, Y.A., A. Sigurgeirsson, and A.E. Szmidt.** 1988. The use of restriction analysis of chloroplast DNA in classifying hybrid spruce seedlots. In: Proc. Frans. Kempa Symp., Molecular Genetics of Forest Trees. June, 1988. Umea, Sweden (J.E. Hallgeren, ed.). Institute of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences. Umea, Sweden. Report No. 8:67-88.
- Gary, R.I., R.L. Carlson and B.F. Hrutfiord.** 1971. Influence of some physical and host factors on the behaviour of the Sitka spruce weevil, *Pissodes sitchensis*, in southern Washington. *Ann. Ent. Soc. Am.* 64: 467~471.
- Kuehl, R.O.** 1994. *Statistical principals of research design and analysis*. (Chapt. 15: Repeated Measures Designs). Duxbury Press, Behust, Canada. Pp 499~528.
- Hall, P.M.** 1994. Ministry of Forests' perspectives on spruce reforestation in British Columbia. In: Alfaro, R.I., Kiss G. and Fraser R.G. (eds) *The white pine weevil: biology, damage and management*. Symp. Proc. pp1~6. Jan. 19-21, 1994, Richmond, B.C. Canada.
- Harman, D.M.** 1975. Movement of individually marked white pine weevil, *Pissodes strobi*. *Environ. Entomol.* 4: 120~124.
- Hormann, R.K.** 1987. North American tree species in Europe. *J. Forestry.* 85: 27~32.
- Hosmer, D.W. and Lemeshow, S.** 1989. *Applied Logistical Regression*. New York: John Wiley & Sons, Inc.
- Ilingworth, K.** 1978. Sitka spruce provenance 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 Pp 311~326. Vancouver, B.C. Canada.
- Kiss, G.K. and A.D. Yanchuk.** 1991. Preliminary evaluation of genetic variation of weevil-resistance in interior spruce in British Columbia. *Can. J. For. Res.* 21: 230-234.
- Mitchell, R.G., K.H. Wright, and N.E. Johnson.** 1990. Damage by Sitka spruce weevil (*Pissodes strobi*) and growth patterns for 10 spruce and hybrids over 26 years in the Pacific Northwest. U.S. Dep. Agric. For. Serv. Res. Pap. PNW-RP-434.
- Pojar, J., K. Klinka, and D.V. Meidinger.** 1987. Biogeoclimatic ecosystem classification in British Columbia. *Forest Ecology and Management.* 22: 119~154.
- SAS Institute Inc.** 1990. *SAS/STAT User's Guide*, Version 6, 4th edition. Vol .1 (pp 943) & Vol. 2 (pp 846). Cary, NC, USA.
- Silver, G.T.** 1968. Studies on the Sitka spruce weevil, *Pissodes sitchensis*, in British Columbia. *Can. Ent.* 100: 93~110.

- Wood, P.M.** 1987. Development of Sitka spruce phenotypes resistant to the spruce weevil: a summary of recent and planned research projects in B.C.. BC MoF, Vancouver Forest Region. Internal Rep. PM-V-10.
- Ying, C.C.** 1991. Genetic resistance to the white pine weevil in Sitka spruce. Research Notes No.106, BC MoF, Victoria, British Columbia.
- _____. 1997. Effects of site, provenance, and provenance and site interaction in Sitka spruce in coastal British Columbia. *Forest Genetics*. 4(2): 99~112.

3. Long-term growth responses in Sitka spruce populations to seed transfer from IUFRO provenance trials in British Columbia

Abstract: The 20-year growth of Sitka spruce provenances tested in British Columbia were analyzed towards the goal of defining latitudinal seed transfer limits for higher-than-local growth performance of the provenances planted at coastal BC areas. Growth responses were quantified by modeling volume deviation of endemic (i.e., non-local) provenances from local sources at year 20 to geoclimatic changes resulted from seed transfer of 41 Sitka spruce IUFRO provenances at 11 test sites. The predictions were again related to test site's geoclimatic conditions by response surface analyses to predict the volume response from seed transfer pertaining to site geoclimatic conditions. Volume contours were also developed responding to each effective predictor for planting site as well as for provenance origin to attempt to define suitable ranges of seed source and planting area. Results indicated that northward seed transfer along the Pacific coast is favored in this species, an average ultimate volume-gain was predicted from using seed source 5.5 ° of latitude south of a planting site. The volume response is contingent with site geoclimatic conditions such that, the milder and/or the more southern the planting site is, the wider the limits of northward seed transfer that allows for pursuing higher-than-local growth, and also the greater the amount of volume-gain can be achieved through the transfer. High dependency of growth response on site summer precipitation was also found such that, a minimum of 500 mm summer rainfall was required to achieve higher-than-local growth performance. With high site precipitation (e.g., SMSP > 700 mm), about 40% of volume-gain

could be achieved by northward seed transfer up to 12 ° of latitude. The selection of planting site is more important than selection of provenance origin. A minimum of 670 mm summer precipitation at planting site is required for high volume production with this species.

Keywords: growth response; seed transfer; provenance trial; Sitka spruce (*Picea sitchensis* (Bong.) Carr.).

3.1. Introduction

Sitka spruce, *Picea sitchensis* (Bong.) Carr., a fast growing conifer native to North America, occurs naturally in the Pacific coast 'fogbelt', a long, narrow strip adjacent to the Pacific Ocean spanning over 22 degrees of latitude (Daubenmire 1968; Pojar, *et al* 1987). Its growth vigor, high wood quality and versatility to soil conditions made it a recommended species for reforestation in coastal areas where the white pine weevil (*Pissodes strobi* (Peck)) threat is low (Ying 1997). In order to exploit the potential of genetic superiority of ecademic (i.e., non-local) provenance over local provenance in growth, the Research Branch of Ministry of Forestry of British Columbia (BC MoF) established three series of Sitka spruce provenance trials in early 1970s (Illingworth 1978a; Ying 1991 and 1997; Chapt.1). These trials under this study involve a total of 43 provenances that are tested at 11 sites in coastal BC (see Fig. 1-1 in Chapt.1). The provenances were collected along the Pacific coast from Oregon coast to southern Alaska and formed the core sample of the Sitka spruce IUFRO (International Union of Forest Research

Organizations) provenance trials. Height and diameter of the trees were measured on individual trees over 20 years since planting.

The primary objective for provenance trial is to identify suitable seed source(s) by comparing the performance of local to ecdemic (non-local) populations. Many provenance trials have shown that local seed sources are often not the optimum in growth, and that provenances from mild and/or southern areas usually outgrow those from harsh and/or northern areas, but are more vulnerable to winter injuries (e.g., Mergen *et al.* 1974; Campbell and Sorenson 1978; Illingworth 1978a and b; Rehfeldt 1983 and 1995). Previous analyses with the 20-year growth data of these Sitka spruce provenance trials found considerable genetic variability among the 43 provenances, despite the dominance of site effects over contrasting environments (Ying 1997; Chapt.1). Linear and quadratic trends that are inverse to latitude were found in growth measures where the test site is favorable for Sitka spruce and free of weevil attack. With increasing age, the latitudinal trends tended to be stable in both height and diameter growth, with different levels of expression, by the 20th year after planting (see Section 1.4.4. in Chapt.1 for details). The geographic trends stabilizing by year 20 justifies the notion that this is an appropriate age to address the species' seed transfer limits, a question that silviculturists are most interested in, though it is still too early to make a final assessment if considering the species' rotation length (Ying 1997).

This chapter is a summary of the predictions with the 20-year growth data towards the primary goal of provenance trials. The objectives are 1) to quantify the volume-gain and -loss, i.e., growth response, resulting from seed transfer in these trials; 2) to define the limits of seed transfer that allow for higher-than-local growth performance under a given plantation's

geoclimatic conditions, assuming volume production is the primary goal of reforestation with this species; 3) to provide graphical views of suitable geoclimatic ranges for planting area and seed source selection within the experimental span.

3.2. Data profile and Abbreviation

Data from three series of Sitka spruce provenance trials in British Columbia (supplied by Research Branch of BC MoF) were applied in this study. These trials together have 43 provenances and 11 test sites (see Tables 1-1 and -2 in Chapt.1 for the names and geographic locations of the provenances and test sites). The provenance trials were established using a completely randomized block design, with 4, 5, 6 or 9 blocks at different test sites. Within blocks, each provenance is represented by a 9-tree-row plot. Not all provenances were tested at all sites so that a total of 220 provenance-by-site means were available for each growth measurement. Growth measurements available are height at year 3, 6, 10, 15 and 20 after planting (termed as HT3, HT6 and so on), and diameter at breast height at year 10, 15 and 20 (termed as DBH10, DBH15 and so on). Individual tree volume was calculated after Kovats (1977) when both height and diameter are available for a tree. For long-term simulation and silvicultural concerns, volume at year 20 (termed as VOL20) was selected as the growth trait of interest.

Macro-climatic data were obtained from the nearest weather stations to each test site (i.e., site climatic variables) as well as to each provenance origin place (i.e., provenance climatic

variables). Adding "S-" as a prefix for site climatic variables while "P-" for provenance climatic variables, the acronyms of the 10 macro-climatic variables that define temperature, moisture and photoperiod conditions are as follows:

MAP	= Mean Annual Precipitation (mm)
MSP	= Mean Summer Precipitation (mm) (May ~ September)
MAT	= Mean Annual Temperature (°C)
MTCM	= Mean Temperature of the Coldest Month (i.e., January) (°C)
MTWM	= Mean Temperature of the Warmest Month (i.e., July) (°C)
NFFD	= annual Number of Frost Free Days (day)
FFP	= annual Frost Free Period (day)
DD5	= annual accumulated Degree Days <u>above</u> 5°C (°C)
DD0	= annual accumulated Degree Days <u>below</u> 0°C (°C)
DAY	= accumulated daylength (hour) of the growth season (April ~ October) (calculated as a function of latitude)

Following the same convention, the acronyms for latitude, longitude and elevation are LAT, LONG and ELEV, respectively, with the prefix "S-" for test site and "P-" for provenance origin. Geoclimatic differences between provenance origin and test site were obtained by subtracting the values for provenance origins from those for test sites where the provenances were tested. These geoclimatic distance variables are named as "Diff-" variables, i.e., DiffLAT, DiffMAT, etc. For instance, $\text{DiffLAT} = \text{PLAT} - \text{SLAT}$. These Diff- variables are mostly correlated with each other (see Table III-13 in Appendix III). The variation ranges of these Diff-variables are presented in Table III-14 in Appendix III, which should be used as the range limits for interpreting the prediction results, namely, within the experimental span.

Growth responses are expressed in the ratio of an ecademic provenance's growth performance over the local growth performance where the ecademic provenance is tested (after Schmidting 1993). These growth responses are termed as "Devi-" variables, i.e., DeviHT3, DeviVOL20, etc. For instance, $\text{DeviVOL20} = (\text{Ecdemic provenance's VOL20}) \div (\text{Local$

provenance's VOL20). Again, for the long-term simulation and silvicultural concerns, DeviVOL20 was selected as the growth response of interest among all the Devi- variables.

The ecademic provenance's growths were evaluated as the Least-Squares means for the growth measurements at provenance-by-site level, computed from the SAS GLM procedure (adjusting for missing observations that are plot-mean based). Local performances were obtained either from the local or "close-to-local" provenances. Close-to-local provenance performances were derived from regression models that are site specific in relation to provenance geographic locations.

3.3. Methods of analyses and limitations of the predictions

3.3.1. Identifying effective geoclimatic predictors

Predicting growth response (i.e., DeviVOL20) using all the geoclimatic distance variables is difficult to interpret and unnecessarily complicated. In order to screen for effective geoclimatic predictors among the Diff- variables for predicting the growth response, redundancy analysis was applied on the multivariate relationships of the two groups of variables, i.e., Diff- variables and Devi- variables. The analysis was performed through matrix algebra with the SAS IML procedure, based on the correlation matrices within and between these two groups to avoid scale problem of the original Diff- and Devi- variables.

Redundancy analysis is effective for determining the variation in one group of self-correlated variables accounted for by the variability of another group of self-correlated variables. It derives two sets of redundant variables that are linear combination of the original variables of

the two groups, respectively, such that the variations in one group were maximally accounted for by the opposite group's redundant variables (Wollenberg 1977). From the loadings of the original variables onto the redundant variables, the relative importance of the original variables of one group in explaining the variations of the other group is determined. In this study, growth response variables (i.e., Devi- variables) are closely correlated, and so are the Diff- variables (see Table III-13). Therefore, the redundant loadings of the Diff- variables to their own redundant variables can reveal the relative importance of the Diff- variables in explaining variations of the Devi- variables.

3.3.2. *Quantifying general volume response from geoclimatic changes*

The growth-gain or -loss resulted from each predictive Diff- variables, as determined by the redundancy analysis before, were quantified by modeling the volume response (i.e., DeviVOL20) with each effective Diff- predictor, using the SAS GLM procedure.

Predictions based on the five geoclimatic variables simultaneously would be largely redundant because of the close inter-correlations among the independent variables (see Table III-13 in Appendix III). Predictions with each variables separately, on the other hand, could also be deemed as over simplification, but in fact it is the way to quantify the volume response without turning into linear transformations of the original predictive variables (e.g., through Principal Component Analysis (PCA)) and thus making the results difficult to interpret and apply. If predicting the volume response using the principal components of these five geoclimatic distance variables, which Matyas (1994) called 'ecodistance' between seed source and planting site, it is not only unable to interpret the prediction in the original geoclimatic sense, but also difficult to

apply the predictive results to seed transfer practices. Every time when one needs to foresee a growth performance for a new provenance or a new planting site, he would have to go back to the PCA to derive a new ecodistance of the seed transfer in order to determine the growth response from that transfer. In other words, predictions with ecodistance are data specific. Provisionally, all the geoclimatic data needed are available for provenance origin as well as for planting site which is uneasy, if not impossible, to obtain at a real situation. Hence, the predictions and subsequent response surface analyses in this chapter would be using one geoclimatic predictor at one time to present simple predictions and to avoid the above mentioned problems.

The models were set up to the second power of the independent variables to comply with the quadratic trends found in scatter plots, and under the constraint that the intercept of the model equal zero. By making null intercept, the predicted value for *DeviVOL20* at the point of testing a provenance without geoclimatic distance from the origin is zero, which means the ratio of the tested provenance's growth over the local source's is 1:1 (i.e., the performance of the tested provenance is identical to local one's). The geoclimatic distance ranges that allow for pursuing higher-than-local growth performance in seed transfer were then delineated from the mean predicted values for *DeviVOL20*.

3.3.3. Predictions pertaining to site geoclimatic conditions

As volume response is highly conditional on site geoclimatic conditions (see below), the general prediction could only present the average level of the response. In order to provide more operable transfer limits, the volume response to each effective Diff- predictor was related to the

corresponding geoclimatic variable for test site by response surface analysis, using the SAS RSREG procedure. Site summer precipitation (SMSP) was also used in the response surface analysis with DiffLAT to DEviVOL20, because of high sensitivity of this species to SMSP (see Section 1.4.3. in Chapt.1). Illustrated by a series of contour graphs, the results presented a more sophisticated view of the previous general predictions pertaining to site geoclimatic conditions. However, there are also a few limitations for the application of these contour graphs, from the bias sources as stated in the following section (3.3.5.).

3.3.4. *Graphical approach for seed transfer guidelines*

In conjunction with the above predictions and response surface analyses, the ranges of suitable planting area and seed source under given geoclimatic conditions within the experimental span were also discussed by another series of contour graphs. The graphs were constructed after the method proposed by Kung & Clausen (1983), using pairs of the predictive geoclimatic variables for test site as well as for provenance origin as the two-dimensional independent variables and the growth vigor (represented by VOL20, based on provenance-by-site means) as the response variable. The six predictive geoclimatic factors (i.e., LAT, MAT, MTCM, DD0, NFFD and MSP) were determined by previous analyses as stated before (Section 3.3.3.).

This kind of contour graph can present a direct view of volume productivity of different provenances (represented by the geoclimatic conditions of their origins) at different areas. The graphic approach can reveal the relative importance of site and provenance selection in seed transfer practice. The graphs are also capable of showing the presence or absence of provenance-

by-site interactions for a particular geoclimate factor. However, the use of VOL20 as the response variable brings back the experimental effects (see Section 1.4.1. in Chapt.1) into the modeling. Consequently, there could be significant 'lack-of-fit' error due to these experimental effects, and to lack of fine geoclimatic gradients in site location selection and lack of randomness in provenance sampling, coupled with the drastic weevil damages observed at four test sites (Chapt.2). However, by substituting the relative growth vigor (i.e., DeviVOL20) with the observed VOL20, the models can also avoid the impact of possible inaccuracy from some of the local source performance that are derived from regressions in this study (see Section 3.3.5.). Therefore, the graphic approach of this section and the last section both have merits and demerits compared to each other, and the results of both approaches should be considered descriptive rather than inferential.

3.3.5. Limitations of the predictions and modeling

Several bias sources of the predictions should be mentioned here, some of which are applicable to all the predictions, some are to a specific analytical approach, as per the following:

First, the latitudinal seed transfer in this species is virtually northwest-southeast oriented, because the Pacific coast of British Columbia is oblique, not paralleled with longitudes. The prediction using latitudinal distance as predictor can not distinguish a northwest-southeast trend from a north-south trend. Therefore, the predictions with DiffLAT could be biased somehow due to this reason. IN THIS STUDY WHEN "NORTHWARD SEED TRANSFER" IS REFERRED, IT ACTUALLY MEANS "SOUTHEAST TOWARD NORTHWEST SEED TRANSFER". Again, response surface analysis only works well when the data structure is symmetric. The test

sites are not symmetrically distributed, so are sampling of the provenances as well as is the Pacific coast which is northwest-southeast oriented. Therefore, the response surfaces that are associated with latitudinal factors can not avoid biases from this structural problem, and hence are less reliable than those associated with climatic factors.

Second, climatic gradients along the coast line of BC are generally gradual, but very steep from coast (maritime) to inland (submaritime). Therefore, the response curves for coastal region can be very different from those of inland. However, there are only three submarine test sites (see below in Section 3.4.2), and the sampling of provenances at these test sites were not ample enough to allow for separate prediction from those maritime test sites. The pooling of maritime and submarine sites caused the general predictions being general to the whole region of coastal BC, but not specifically good for either outer coastal area or peripheral inland area.

Third, the three test sites, i.e., Head Bay, Nass River and Rennel Sound, had no local source tested. The local growth performance at these sites were derived from site-specific regression models (details not presented). These regression models are set up by relating the performances of those provenances at the test site to their origin locations, at provenance-by-site mean level. These "close-to-local" performances could bring in certain degree of bias to the predictions relative to local performance.

Fourth, the four test sites that weevil attacked (i.e., HB, KT, MN and NS) are included in the predictions under the assumptions that, there were no overall substantial differences in weevil resistance among the provenances tested at the attacked sites, and that provenances (local and ecdemic) suffered similar weevil damages at a specific site. These 'equal-weevil-effects' assumptions were made for not sacrificing the four weeviled sites which have contrasting

environments. The including of these test sites can help better expression of the $G \times E$ interactions in growth performance (see Chapt.1), which is important to assess the seed transfer limits, although it could bring in certain degree of inaccuracy to the predictions in the fact that, previous analyses show that a few (i.e., three or four) provenances exhibited considerable weevil resistance and/or tolerance at these attacked sites (Chapt.2).

The last but not least limitation of the predictions is the tree age. Although the 20-year data has show the stabilizing of the geographic trends in growth traits by year 20 (Chapt.1), these trees have not been exposed to extreme climate events that might happen once every five to ten decades. Comparing to the species' rotation length (100 years long, see Ying 1997), the 20-year period is still short for prudent assessment.

3.3.6. *Statistical criteria*

All data analyses were performed by SAS procedures (SAS Inc. 1990). The predictions were made on the response variables that are transformed into natural logarithmic values to approach normal distribution, but results are interpreted in the original units of the response variables.

Statistical tests and inferential analyses were based on the assumptions that, multivariate normality and simple normality exist in the growth response variables, variations of the response variables are homogeneous across different levels of experimental effects, and the residuals from the predictive models are normally and independently distributed, with a zero mean and a common variance. The significance criterion was set at $\alpha = 0.05$ level if not stated otherwise.

3.4. Results and Discussions

3.4.1. *Effective geoclimatic predictors*

Redundancy analysis was used to determine the effective geoclimatic predictors by the 'loadings' of the original variables onto the first pair of redundant variables which maximally cross-explains the variations of the opposite group. The two groups of variables are the five Devi- variables (i.e., DeviHT3, DeviHT10, DeviHT20, DeviDBH20 and DeviVOL20) and the 12 Diff- variables (i.e., all the geoclimatic distance variables but DiffDAY). The results show that 46.4% of total variations in 'Devi-' variables were explained by the first redundant variable of the 'Diff-' group (Table 3-1). That is, to the maximum, 46.4% of the total variations of the growth responses were accounted for by the geoclimatic distances between seed source and test site. This implies the growth responses are predictable by the geoclimatic distances in seed transfers of this experiment.

Since the first redundant variable of the 'Diff-' group accounted for the maximum variations of the growth response variables (i.e., opposite group), attentions were directed to the correlations (loadings) between the original 12 geoclimatic distance variables onto its first redundant variable, and between the original five growth response variables onto this redundant variable (Table 3-2). These redundancy loadings indicate that only the 'Diff-' variables describing thermal difference (especially winter temperature) and latitudinal distance between seed source and test site were essential to reflect the growth response variations. The top five Diff- variables with highest correlation coefficients to the first redundant variables of their own group were thus selected as the effective geoclimatic predictors to be used in the subsequent modeling. They are DiffDD0, DiffMTCM, DiffMAT, DiffNFFD (i.e., thermal differences) and

DiffLAT (i.e., latitudinal distance). It should be pointed out that, DiffDAY is also an effective predictor for DeviVOL20, just as DiffLAT is, but was excluded from the analysis because it is a function of latitude.

Redundancy loadings in the other group (i.e., 'Devi-' variables) indicate that upon year 20, DeviDBH20 was most predictable among the five growth response variables (Table 3-2). However, for silvicultural concerns, the remainder of this chapter is focused on the predictions of the volume response in year 20 (i.e., DeviVOL20), which is also highly redundant on the variation of the Diff-group.

Table 3-1. The amount of original variations of the 'Devi-' variables and 'Diff-' variables explained by the redundant variables of their opposite group.

Original	Redundant variable of the 'Devi-' group				Redundant variable of the 'Diff-' group			
Variations	1st	2nd	3rd	4th	1st	2nd	3rd	4th
'Devi-' group					46.37%	2.02%	1.55%	0.47%
'Diff-' group	23.4%	4.90%	1.90%	0.38%				

Table 3-2. Correlation coefficients (i.e., redundancy loadings) between the original variables with the first redundant variable of the 'Diff-' group.

Correlation coefficients for the original geoclimatic Diff- variables		Correlation coefficients for the original growth response Devi- Variables	
DiffLAT	-0.803	DeviHT3	0.821
DiffLONG	-0.147	DeviHT10	0.637
DiffELEV	-0.348	DeviHT20	0.605
DiffMAP	0.413	DeviDBH20	0.747
DiffMSP	0.057	DeviVOL20	0.560
DiffMAT	0.775		
DiffMTCM	0.742		
DiffMTWM	0.103		
DiffNFFD	0.646		
DiffFFP	0.416		
DiffDD5	0.614		
DiffDD0	-0.816		

(Note: Characters and values in bold represent the selected effective geoclimatic predictors)

3.4.2. Trends from the scatter plots

The scatter plots of DeviVOL20 versus the five effective geoclimatic predictors (Figs. 3-1 to -5) indicated that the growth response depending on these predictors were quite similar, with quadratic trends that are concave down, except that the directions for DiffLAT and DiffDD0 were opposite to the remaining predictors. This is because of the negative correlations of these two variables (DiffLAT and DiffDD0) with other three variables (Table III-13 in Appendix III).

Substantial volume growth variation at year 20 was found among the 11 test sites in that, the site means for VOL20 varied with good sites producing volumes that were ten more times higher than that for poor sites (see Chapt.1). The volume growth response related to local source performance (i.e., DeviVOL20), on the other hand, turned out to be consistent from site to site and based on one predictor or another. This is because Devi- variables integrated the variation from both test site and provenance origin, and thus removed the effects of Site and Provenance, as well as the G x E interactions. The effects from block within test site were also removed when determining local and ecademic growth performances, based on provenance-by-site means. The consistency of the trends allows for making general predictions that can be applied to most of the coastal regions of British Columbia.

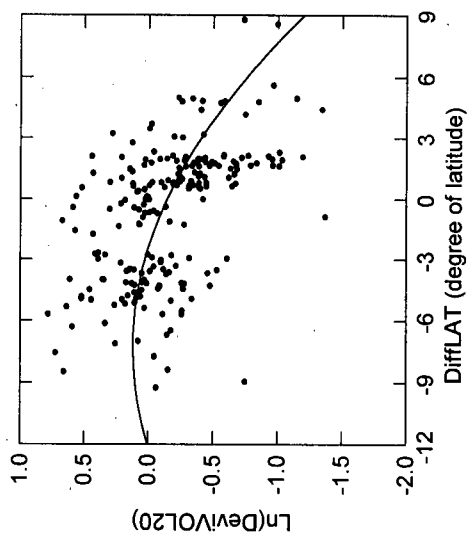


Fig.3-1 Scatter plot of DeviVOL20 versus DiffLAT and the quadratically smoothed trend.

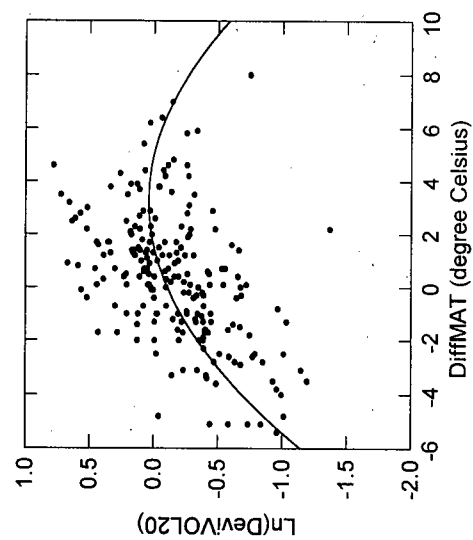


Fig.3-2. Scatter plot of DeviVOL20 versus DiffMAT and the quadratically smoothed trend.

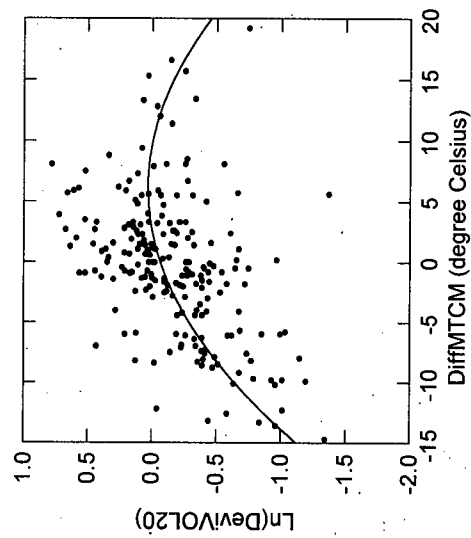


Fig.3-3. Scatter plot of DeviVOL20 versus DiffMTCM and the quadratically smoothed trend.

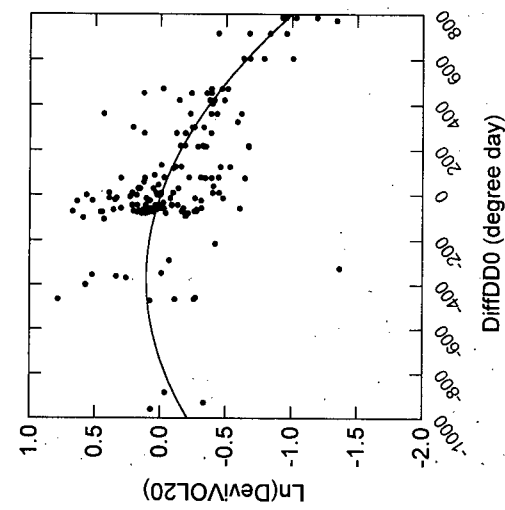


Fig.3-4. Scatter plot of DeviVOL20 versus DiffDD0 and the quadratically smoothed trend.

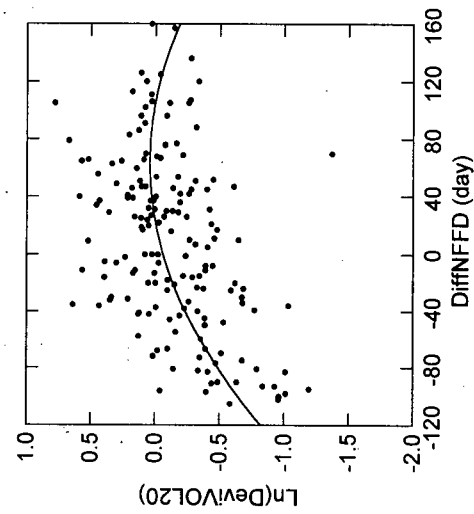


Fig.3-5. Scatter plot of DeviVOL20 versus DiffNFFD and the quadratically smoothed trend.

3.4.3. General predictions on each effective geoclimatic predictor

Slight difference in volume response were observed between maritime (i.e., wet) sites (mean annual precipitation $> 2000\text{mm}$, eight sites together) and sub-maritime (i.e., less-wet) sites (mean annual precipitation $\leq 2000\text{mm}$, three sites together). The divergence was pronounced particularly when involving maximal transfer of southern provenances to northern areas (see Figs.IV-1 to -5 in Appendix IV). In less-wet sites, the range of northward transfer was wide enough to cause loss of growth superiority of southern provenances over local sources. However, this trend was not observed in wet sites. Without the less-wet sites, the prediction models that are based on DiffLAT, DiffMAT and DiffMTCM tended to be linear rather than quadratic. Sufficient precipitation somehow compensated unfavorable thermal-climatic conditions during winter for the southern provenances at northern outer coastal areas.

However, if comparing the common range of geoclimatic distance of the seed transfers occurred between wet and less-wet sites, there were no substantial differences between these two site types. Growth response would be expected to be sub-optimal when the northward seed transfer exceeds certain range of geoclimatic distances no matter how wet a test site is. Besides, the experimental range and data availability did not allow for making separate predictions for these two site types. Therefore, I decided to pool the test sites together to make general predictions, while leaving the problem of the moisture differences among sites to the next section (3.4.4.) of this chapter, in which the volume response was related to both geoclimatic distances and site geoclimatic conditions. The general predictions in this section reflect the average volume-gain and -loss in seed transfer, and the results are applicable to the whole coastal BC area

(including maritime and sub-maritime regions) where the environment allows for successful planting with this species.

Predictions were made on the five effective geoclimatic predictors (i.e., DiffLAT, DiffMAT, DiffMTCM, DiffDD0 and DiffNFFD), respectively. Values for the response variable (i.e., DeviVOL20) are at provenance-by-site mean level. Three outlier provenances were detected from the scatter plots. They are: Brookings (No. 3018, the southernmost provenance from Oregon) and Yakutat (No. 3021, the northernmost one from Alaska) tested at Nass River site, and Necanicum (No. 3012, from Washington) tested at Maroon Creek site (the harshest one of the 11 test sites). The outliers were eliminated from the model to exclude the extreme cases of seed transfer in the provenance trials.

The results indicated that all the prediction models fit well to quadratic curves that are concave down (Table 3-3). This could be proved either by the significance levels of the parameter estimates and the model R^2 's, or from the residual plots (not presented here). In all the prediction models, both linear and quadratic parameter estimates were significantly different from zero ($\alpha = 0.05$), which means that there were significant effects of these geoclimatic distance variables (linear and quadratic) on the variation of DeviVOL20. The gross model R^2 ranged from 0.308 to 0.476 (Table 3-3), indicating that about 31 to 48% raw variation in DeviVOL20 were accounted for by these models (not purely by the predictors as the R^2 was not adjusted by the intercept that is set to zero). The residual means from these models ranged from -0.0037 to 0.0027, and none of which was significantly different from zero (t -test, Table 3-3), suggesting that the models represent unbiased predictions.

The predicted values for DeviVOL20 (in logarithmic values) were transformed into percent deviations of the growth response from local source performance, namely, DeviVOL20(%). The values for DeviVOL20(%) along with the transformed standard errors of the predicted means are listed in Table 3-4, in and comply with the ascending order of DiffLAT. The same prediction results were also visualized by plotting the predicted curves along with the standard errors of the mean predicted values plotted as vertical bars across the curves (Figs. 3-6 to -10).

Table 3-3. Estimated parameters for the prediction models along with the quality information of the models.

(1) $\text{DeviVOL20} = f(\text{DiffLAT}, \text{DiffLAT}^2)$				
Factor	Parameter Estimate	Standard Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffLAT	-0.0800827549	0.00825244	-9.70	<0.0001
DiffLAT ²	-0.0073923605	0.00147519	-5.01	<0.0001
$n = 217$, Model $R^2 = 0.3075$, Root MSE = 0.3275, Mean Residual = -0.0036690 (t-test for H_0 : Mean Residual = 0 is $ t = 0.1646 < t_{0.05} = 1.97$)				
(2) $\text{DeviVOL20} = f(\text{DiffMAT}, \text{DiffMAT}^2)$				
Factor	Parameter Estimate	Standard Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffMAT	0.0931227597	0.00909669	10.24	<0.0001
DiffMAT ²	-0.0149617111	0.00198997	-7.52	<0.0001
$n = 217$, Model $R^2 = 0.3739$, Root MSE = 0.3128, Mean Residual = -0.0026960 (t-test for H_0 : Mean Residual = 0 is $ t = 0.1060 < t_{0.05} = 1.97$)				
(3) $\text{DeviVOL20} = f(\text{DiffMTCM}, \text{DiffMTCM}^2)$				
Factor	Parameter Estimate	Standard Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffMTCM	0.0327584368	0.00377511	8.68	<0.0001
DiffMTCM ²	-0.0025321835	0.00033773	-7.50	<0.0001
$n = 217$, Model $R^2 = 0.3757$, Root MSE = 0.3175, Mean Residual = 0.000485961 (t-test for H_0 : Mean Residual = 0 is $ t = 0.0019 < t_{0.05} = 1.97$)				
(4) $\text{DeviVOL20} = f(\text{DiffDD0}, \text{DiffDD0}^2)$				
Factor	Parameter Estimate	Standard Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffDD0	-0.0005775073	0.00005998	-9.63	<0.0001
DiffDD0 ²	-0.0000006145	0.00000008	-7.81	<0.0001
$n = 176$, Model $R^2 = 0.4762$, Root MSE = 0.2833, Mean Residual = 0.0027209 (t-test for H_0 : Mean Residual = 0 is $ t = 0.0758 < t_{0.05} = 1.98$)				
(5) $\text{DeviVOL20} = f(\text{DiffNFFD}, \text{DiffNFFD}^2)$				
Factor	Parameter Estimate	Standard Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffNFFD	0.0035561698	0.00039717	8.95	<0.0001
DiffNFFD ²	-0.0000279873	0.00000393	-7.12	<0.0001
$n = 176$, Model $R^2 = 0.3660$, Root MSE = 0.3055, Mean Residual = -0.0010111 (t-test for H_0 : Mean Residual = 0 is $ t = 0.0366 < t_{0.05} = 1.98$)				

(Note: As the intercept of the model was set to zero, the model R^2 was not adjusted for the mean.)

Table 3-4. Mean predicted values for the percent deviations of volume growth from local performance (DeviVOL20 (%)) and the approximate standard errors of the means predicted from DiffLAT, DiffMAT, DiffMTCM, DiffDD0 and DiffNFFD, respectively (arranged in the ascending order of DiffLAT).

DiffLAT (°N)	DeviVOL20 (%)	DiffMAT (°C)	DeviVOL20 (%)	DiffMTCM (°C)	DeviVOL20 (%)	DiffDD0 (dd)	DeviVOL20 (%)	DiffNFFD (day)	DeviVOL20 (%)
-12.5	14.3±16.3	9.0	-31.2±10.8	21	-27.2±13.5	-1000	-3.6±9.6	160	-7.4±13.4
-12.0	-9.8±15.7	8.5	-25.1±10.5	20	-22.5±13.2	-950	-0.6±9.1	150	-6.7±10.7
-11.5	-5.5±15.0	8.0	-19.1±10.2	19	-18.0±12.8	-900	2.2±8.6	140	-5.9±8.5
-11.0	-1.3±14.3	7.5	-13.3±9.7	18	-13.5±12.2	-850	4.8±8.1	130	-4.7±6.9
-10.5	2.6±13.5	7.0	-7.8±9.1	17	-9.3±11.6	-800	7.1±7.5	120	-3.4±5.9
-10.0	6.4±12.7	6.5	-2.6±8.4	16	-5.3±10.9	-750	9.1±6.9	110	-2.0±5.2
-9.5	9.8±11.8	6.0	2.0±7.7	15	-1.6±10.2	-700	10.9±6.4	100	-0.5±4.9
-9.0	13.0±10.9	5.5	6.1±6.9	14	1.8±9.4	-650	12.3±5.8	90	0.9±4.7
-8.5	15.8±10.0	5.0	9.6±6.1	13	4.8±8.6	-600	13.4±5.2	80	2.3±4.5
-8.0	18.2±9.1	4.5	12.3±5.3	12	7.4±7.8	-550	14.1±4.7	70	3.5±4.2
-7.5	20.3±8.2	4.0	14.2±4.6	11	9.5±6.9	-500	14.5±4.1	60	4.4±3.9
-7.0	21.9±7.3	3.5	15.3±3.9	10	11.2±6.1	-450	14.5±3.6	50	4.9±3.4
-6.5	23.1±6.5	3.0	15.6±3.2	9	12.4±5.3	-400	14.2±3.1	40	5.1±2.8
-6.0	23.9±5.8	2.5	14.9±2.6	8	13.0±4.5	-350	13.5±2.6	30	4.7±2.2
-5.5	24.2±5.0	2.0	13.5±2.0	7	13.1±3.8	-300	12.5±2.2	20	3.8±1.4
-5.0	24.1±4.4	1.5	11.2±1.4	6	12.7±3.1	-250	11.2±1.8	10	2.2±0.7
-4.5	23.5±3.8	1.0	8.1±0.9	5	11.8±2.4	-200	9.5±1.4	0	0.0±0.0
-4.0	22.4±3.3	0.5	4.4±0.5	4	10.4±1.9	-150	7.6±1.0	-10	-2.9±0.7
-3.5	20.9±2.8	0.0	0.0±0.0	3	8.4±1.3	-100	5.3±0.6	-20	-6.5±1.2
-3.0	19.0±2.4	-0.5	-4.9±0.4	2	6.0±0.8	-50	2.8±0.3	-30	-10.8±1.7
-2.5	16.7±2.0	-1.0	-10.2±0.9	1	3.2±0.4	0	0.0±0.0	-40	-15.8±2.0
-2.0	14.0±1.6	-1.5	-15.9±1.3	0	0.0±0.0	50	-3.0±0.3	-50	-21.3±2.2
-1.5	10.9±1.2	-2.0	-21.8±1.7	-1	-3.6±0.4	100	-6.2±0.6	-60	-27.2±2.4
-1.0	7.5±0.8	-2.5	-27.8±2.1	-2	-7.4±0.7	150	-9.6±0.8	-70	-33.5±2.6
-0.5	3.9±0.4	-3.0	-33.9±2.4	-3	-11.6±1.1	200	-13.1±1.1	-80	-40.0±2.8
0.0	0.0±0.0	-3.5	-39.9±2.8	-4	-15.9±1.4	250	-16.7±1.3	-90	-46.6±3.1

Table 3-4 (continued).

DiffLAT (°N)	DeviVOL20 (%)	DiffMAT (°C)	DeviVOL20 (%)	DiffMTCM (°C)	DeviVOL20 (%)	DiffDD0 (dd)	DeviVOL20 (%)	DiffNFFD (day)	DeviVOL20 (%)
0.5	-4.1±0.4	-4.0	-45.8±3.0	-5	-20.4±1.7	300	-20.4±1.5	-100	-53.2±3.4
1.0	-8.4±0.8	-4.5	-51.4±3.2	-6	-25.0±2.0	350	-24.2±1.7	-110	-59.5±3.8
1.5	-12.8±1.3	-5.0	-56.8±3.3	-7	-29.7±2.2	400	-28.1±1.9	-120	-65.5±4.1
2.0	-17.3±1.7	-5.5	-61.9±3.4	-8	-34.4±2.5	450	-31.9±2.1		
2.5	-21.8±2.1	-6.0	-66.6±3.4	-9	-39.0±2.7	500	-35.8±2.3		
3.0	-26.4±2.5	-6.5	-71.0±3.4	-10	-43.6±2.9	550	-39.6±2.5		
3.5	-30.0±2.9			-11	-48.1±3.1	600	-43.3±2.6		
4.0	-35.5±3.3			-12	-52.5±3.3	650	-47.0±2.7		
4.5	-40.0±3.6			-13	-56.7±3.4	700	-50.6±2.8		
5.0	-44.3±3.9			-14	-60.7±3.5	750	-54.1±2.9		
5.5	-48.5±4.1			-15	-64.5±3.5	800	-57.5±2.9		

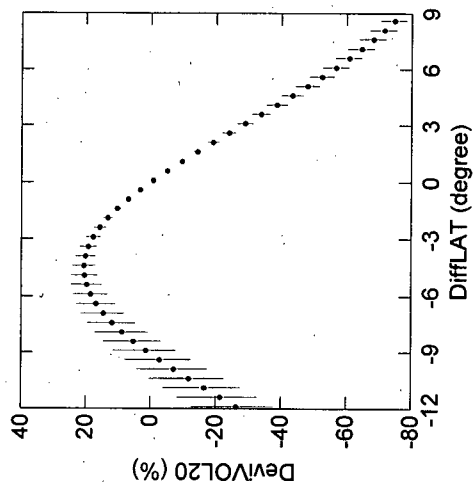


Fig. 3-6. Standard Error of the mean prediction on DiffLAT

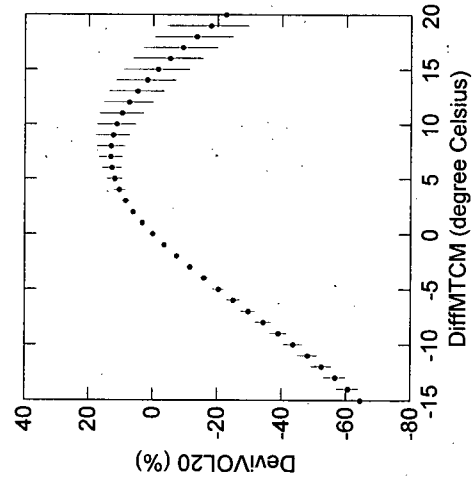


Fig. 3-8. Standard Error of the prediction on DiffTCM

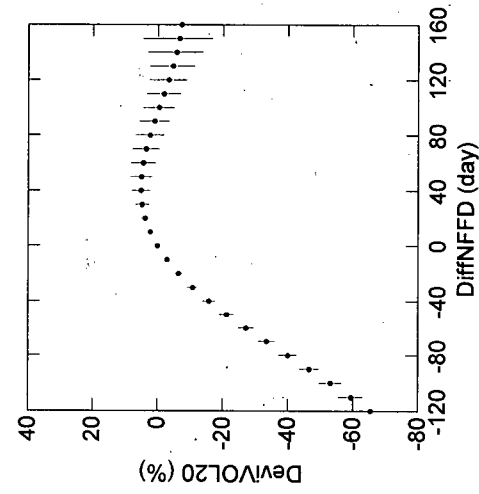


Fig. 3-10. Standard Error of the prediction on DiffNFFD

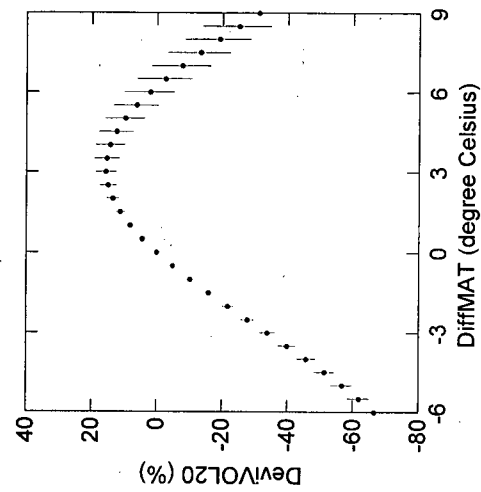


Fig. 3-7. Standard Error of the mean prediction on DiffMAT.

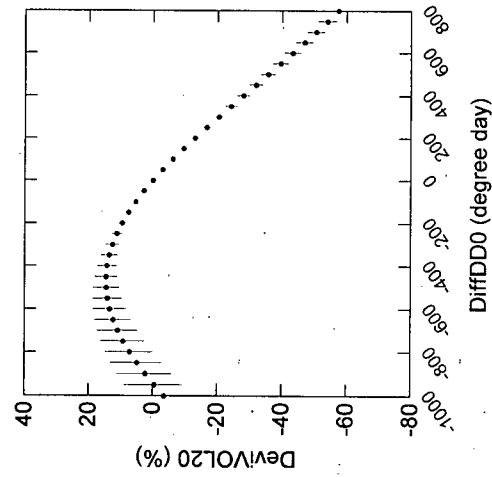


Fig. 3-9. Standard Error of the prediction on DiffDD0.

Positive values for DevVOL20(%) in Table 3-4 implies higher-than-local volume growth. Results show that the predicted higher-than-local performances were only associated with seed transfer from southern or mild sites to northern or harsh sites within certain ranges. This allows for drawing such a conclusion that in Sitka spruce, northward seed transfer is favored while southward transfer is unfavorable in volume growth as compared with using local seed source. From Table 3-4, the predicted ranges of northward seed transfer for a provenance remaining superior or at least equal to local source in term of VOL20 are as follows:

DiffLAT	= 0 ~ -10 ° N
DiffMAT	= 0 ~ 6°C
DiffMTCM	= 0 ~ 14°C
DiffDD0	= 0 ~ -900 degree days
DiffNFFD	= 0 ~ 90 days

These northward seed transfer ranges should be considered as limits rather than best ranges in coastal BC, as the predictive models only accounted for about 40% variation in the volume growth response variable. In applying the predictions, one should check the ultimate growth-gain in a given situation and chose the best possible seed source for planting.

Ultimately, one could expect a mean volume-gain over local source of about 24.2% that is associated with a northward seed transfer of 5.5° of latitude (i.e., DiffLAT = -5.5°, see Table 3-4). That is, an average ultimate volume-gain of 24% at year 20 is expected by transferring seed 5.5 degrees of latitude north as compared with using local seed source (Table 3-4). Note, this is only applicable to seed transfer in the oblique southeast-to-northwest direction along the coastal line of BC.

Common to all the predictive models is that, the predictions within the range of DevVOL20(%) of -20 to 10% had smaller standard error than those outside this range (Figs. 3-6

to -10), which means the predictions are reliable within this range of volume response comparing to local performance. Predictions are least reliable when the transfer towards the upper limits of geoclimatic changes in northward seed transfer (i.e., $\text{DeviVOL20}(\%) > 20\%$). This was due to the divergent patterns of volume response at wet sites and less-wet sites for the upper limits (see Figs. IV-1 to -5 in Appendix IV). Therefore, applications of the results in Table 3-4 when approaching to the upper limits of northward seed transfer should be cautious. If standard error is considered an additional constraint in achieving growth-gain through seed transfer, northward seed sources should not exceed 3° of latitude (Fig. 3-6), 2.5°C mean annual temperature (Fig. 3-7), 2.5°C mean temperature of the coldest month (Fig. 3-8), 200 degree days below 0°C (Fig. 3-9), and 20 frost-free days (Fig. 3-10). These limits may be considered as average distance of transfer for the species in the whole region of coastal of BC. The above limits are generally in line with the current seed transfer guidelines for Sitka spruce in BC (BC MoF 1995).

The predicted rate of volume-gain from northward seed transfer, and the distance of the transfer that allows for higher-than-local performance, differed from one predictor to another. For instance, the ultimate growth-gain was 24.2, 15.6, 13.1, 14.5% and 5.1%, that is associated with geoclimatic change of $\text{DiffLAT} = -5.5^\circ\text{N}$, $\text{DiffMAT} = 3^\circ\text{C}$, $\text{DiffMTCM} = 7^\circ\text{C}$, $\text{DiffDD0} = -500 \sim -450$ degree days, and $\text{DiffNFFD} = 40$ days, respectively (Table 3-4). In other words, predicted volume-gain from northward seed transfer for DiffLAT was most pronounced, and those for DiffMAT , DiffMTCM and DiffDD0 (i.e., thermal-climatic changes) were similar and moderately high, but that for DiffNFFD (i.e., changes in growing season length) was least pronounced.

The reason for the observed differences of volume response to different geoclimatic distance variables can be explained by the biological bases of southern provenance outgrowing local source of northern planting area. When a southern provenance transferred to a northern area, the major geoclimatic change that is beneficial to seed transfer practice is the latitudinal change (i.e., DiffLAT), which introduces noticeable lengthened photoperiod of growing season (DiffDAY) and lengthened growing season (DiffNFFD) as well. The thermal-climatic changes from northward seed transfer are generally unfavorable for southern provenances. However, being a coastal species, Sitka spruce is highly sensitive to moisture conditions rather than to thermal-climatic conditions (Chapt.1). Therefore, as long as the thermal-climatic changes in northward seed transfer do not exceed the winter tolerance of a southern provenance (e.g., frost hardness), it can outgrow the local source of northern areas with higher photosynthesis capacity to make better use of lengthened photoperiod of the growing season and lengthened growing season, to offset the effects of lowered thermal-climates. Therefore, latitudinal change (i.e., DiffLAT, actually northwest-southeast oriented) is the primary factor accounting for the reason of southern provenance out-growing northern ones, and this could explain why the growth response to DiffLAT was most pronounced. The predicted DevVOL20 on DiffMAT, DiffMTCM and DiffDD0 were similar and moderately high, indicating the variations in these three Diff- variables were highly redundant on that of DiffLAT. This was also known from the strong correlations of these thermal-climatic change variables with DiffLAT (Table III-13). However the changes in NFFD was not so contingent with changes in latitude, so that the volume response due to DiffNFFD was much lower than those due to DiffLAT and thermal-climatic changes. The predicted volume-gain rate for DiffLAT is about five times high as that for

DiffNFFD, suggests that higher-than-local growth performance in northward seed transfer is largely due to geographic changes rather than to climatic changes (since they are mostly unfavorable changes). The question will be addressed in detail in Chapter Four where the effects of photoperiod change is distinguished from thermal-climatic changes in latitudinal seed transfer.

3.4.4. *Predictions pertaining to site conditions*

Although the prediction models are developed by now, it should be noticed that these predictions are still not operable for seed transfer practice. The extent to which the volume-gains can be achieved by northward seed transfer, compared with using local source, highly depends on the planting area's geoclimatic conditions (see below). The actual volume-gain or -loss could be greatly different from the predictions if the planting site is noticeably divergent from the average maritime condition of coastal BC areas. Therefore, to apply these models properly, one needs to look into the contour graphs relating the growth response (DeviVOL20) to both Diff- variables and the corresponding site geoclimatic variables (Figs. 3-11 to -16).

Response surface analyses were performed by relating DeviVOL20 to Diff- predictors and the corresponding site geoclimatic variables, in addition with the number one site climatic factor, SMSP (Site Mean Summer Precipitation) as determined by the previous analyses (Section 1.4.3. in Chapt.1). The quality of these response surfaces on the five Diff- predictors and six site climatic variables are listed in Tables III-1 to -6 (see Appendix III), respectively. The lack-of-fit tests for the six models were all not significant, which means all these response surfaces fit well to the second polynomial (see the 'lack-of-fit' F -tests in Tables III-1 to -6 in Appendix III). Variations of the response variable were noticeably accounted for by the surfaces ($R^2 = 0.33 \sim$

0.50). Partial F -test for the cross products of Diff- predictors with site geoclimatic variables were all not significant at $\alpha = 0.05$ level, indicating that the predicted general trends in last section are good within the experimental span. This is because the using of DeviVOL20 as response variable moved all the experimental effects, as indicated before (Section 3.4.2.). Canonical analyses of these quadratic response surfaces show that the growth response varied mainly along the axes of site geoclimatic variables, while geoclimatic distance variables 'modify' the rate of growth response to site geoclimatic gradients. This again emphasizes the dependency of growth response upon planting area's geoclimatic conditions.

It is clear from these contour graphs that, the milder (or the more southern) the planting site is; the greater the range of northward seed transfer that allows for pursuing higher-than-local performance, and also the greater the amount of volume-gain can be achieved through northward seed transfer. For instance if by looking into Fig. 3-11, suppose at a planting site with latitude of 52° N, by using a seed source from 6° of latitude south of the site, one could expect an average volume-gain of 50% over local source, and a maximum of 60% volume-gain could be achieved by using a seed source approximately 8° of latitude south of the site. Note that this kind of high volume-gain is only theoretically achievable if northward seed transfer is strictly along the outer coast 'fog-belt' (Pojar, *et al* 1987). However, according to the same contour graph, suppose the planting site is located at 55° N, it is very unlikely to achieve any volume-gain because southern provenances could jeopardize from winter injuries at so high a latitude.

Another example can be made by looking into Fig. 3-12, suppose the planting site has an average MAT (Mean Annual Temperature) of 8°C , by using seed source from a place that is warmer than the planting site by 2.2 or 4.0°C in MAT, one would expect an average volume-gain

of 20 or 40%, respectively. However, if the planting site has MAT at 6°C, then, to the maximum of 10% volume-gain could be achieved by using seed source from a place warmer than the planting site by approximate 5°C. Once more, if the planting site is even more colder, say, with MAT of 5°C, it is very unlikely that any volume-gain could be achieved comparing to local seed source performance.

The same kind of projections can be applied to the remaining contours (i.e., Figs. 3-13 to -16). However, when applying these contours, one should not exceed the experimental span (Table III-14 in Appendix III) to make unrealistic extrapolation. At this point, one should also be aware of the fact that, the predictions for thermal-climatic variables were more reliable, though possibly less operable, than for the latitudes, because temperatures are less related to geographic orientation while latitudinal transfer in this species in BC is virtually southeast-to-northwest oriented (see Section 3.3.5). Again, the high volume-gains are only theoretically achievable if northward seed transfer is strictly along the outer coast 'fog-belt' (Pojar, *et al* 1987).

Summer precipitation of test site is the most important factor affecting growth of Sitka spruce (Chapt.1), the volume response to DiffLAT and SMSP (Fig. 3-16) hence should be given particular attention in reforestation with this species. Based on this contour, high-than-local growth could be achieved only when the planting site has a minimum summer rainfall of 500 mm, approximately. Local source remained optimal when planting area has less than 500 mm summer rainfall. This emphasizes that the northward seed transfer of this species should be restricted in the fogbelt along coastal BC. From 500 to 700 mm SMSP for test site, there was a steady increase in volume-gain over local source by northward seed transfer, which is also summarized in Table 3-5. Results show that at a site with 500 to 600 mm summer rainfall,

northward seed transfer should be limited between 3 to 8° of latitude, while at a site with 600 to 700 mm summer rainfall, this limit could be expanded up to 12° of latitude. This shows high dependency of volume response on site moisture conditions.

The present results somehow contradict with the current seed transfer guidelines of 2 to 4° of latitude in Sitka spruce set by BC MoF (BC MoF 1995; Ying 1997). Though the analytical results here support my projections, one should be aware of the limitations of this analytical approach as stated before (section 3.3.5.). Again, the projections made in the present study are focused on higher-than-local performances only. That is, the range of northward seed transfer allows for higher-than-local performance does not mean the range that allows southern provenance transferred north without suffering from winter injuries of northern planting areas. Another limitation for applying the contour graphs is that the planting areas climatic condition (say, summer precipitation) has to be known in advance before the seed transfer limit can be determined, which is not always realistic. It should also be noticed that volume growth was only evaluated in the present study. In real situations of forestry practice, matters could be more complicated in which the selection of provenances should also take wood quality, disease and pest resistance and many other aspects into account.

Table3-5. Volume-gains in northward seed transfer that are conditional upon site summer precipitation.

Site major climatic factor SMSP (mm)	Northward seed transfer range and volume-gain	
	DiffLAT (°C)	DeviVOL20 (%)
500 ~ 600	-3 ~ -8	0 ~ 4
600 ~ 700	-2 ~ -12	4 ~ 20
700 ~ 750	-3 ~ -12	20 ~ 40
> 750	-6 ~ -12	≥ 40

Contour of GainVOL20 (%) with DiffLAT & SLAT

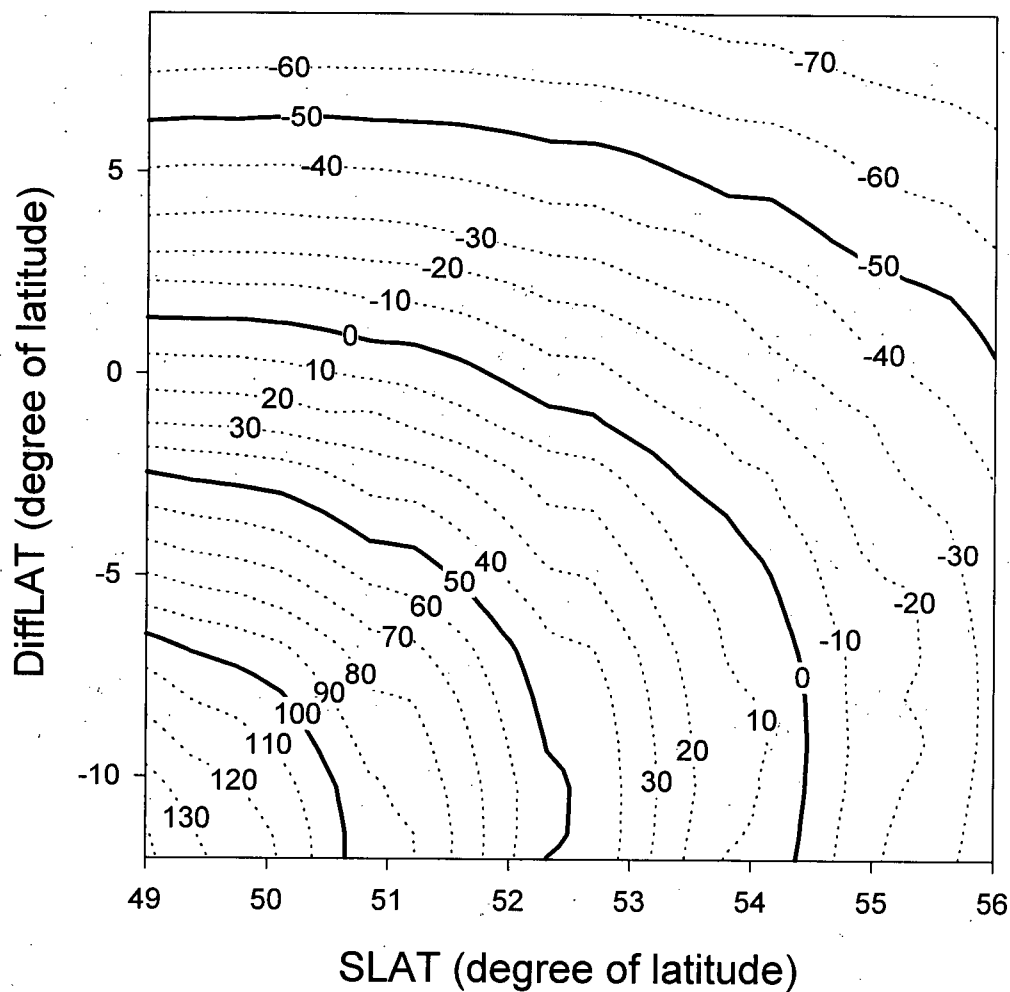


Fig. 3-11. Contour graph reflecting the predictions of DeviVOL20 (%) on DiffLAT (= PLAT - SLAT) pertaining to site latitude conditions (SLAT).

Contour of DeviVOL20 (%) with DiffMAT & SMAT

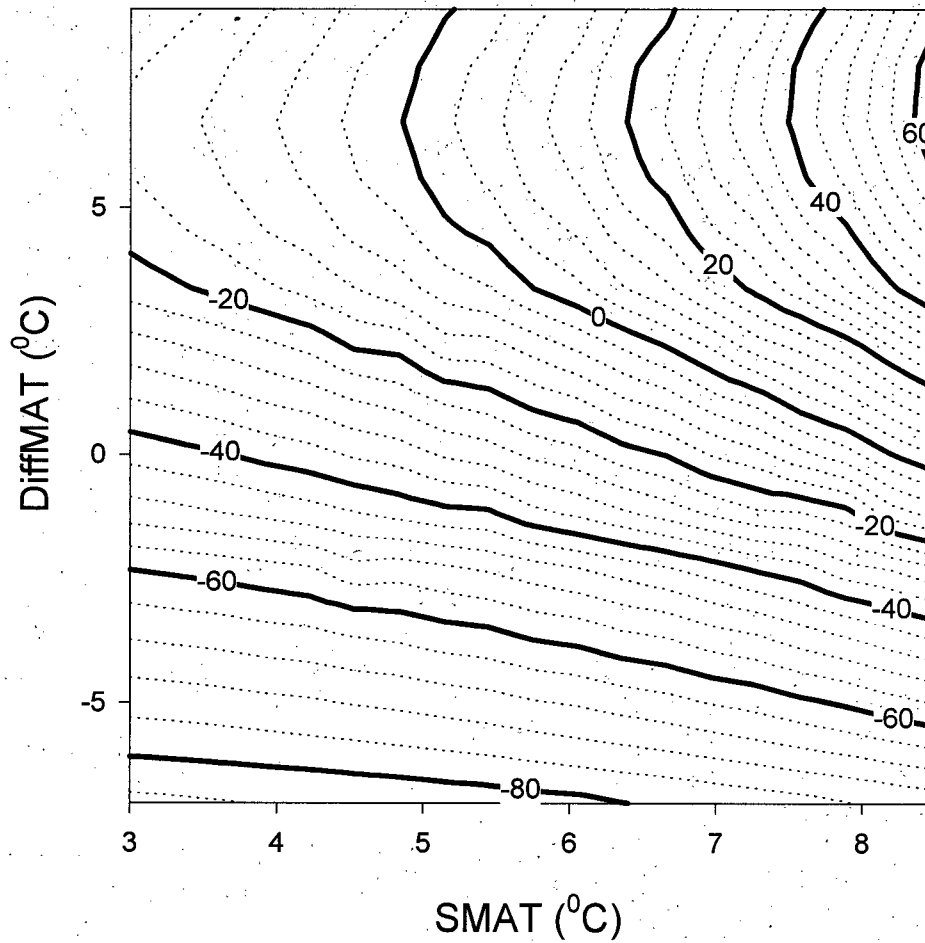


Fig. 3-12. Contour graph reflecting the predictions of DeviVOL20 (%) on DiffMAT (= PMAT - SMAT) pertaining to site mean annual temperature conditions (SMAT).

Contour of DeviVOL20 (%) with DiffMTCM & SMTCM

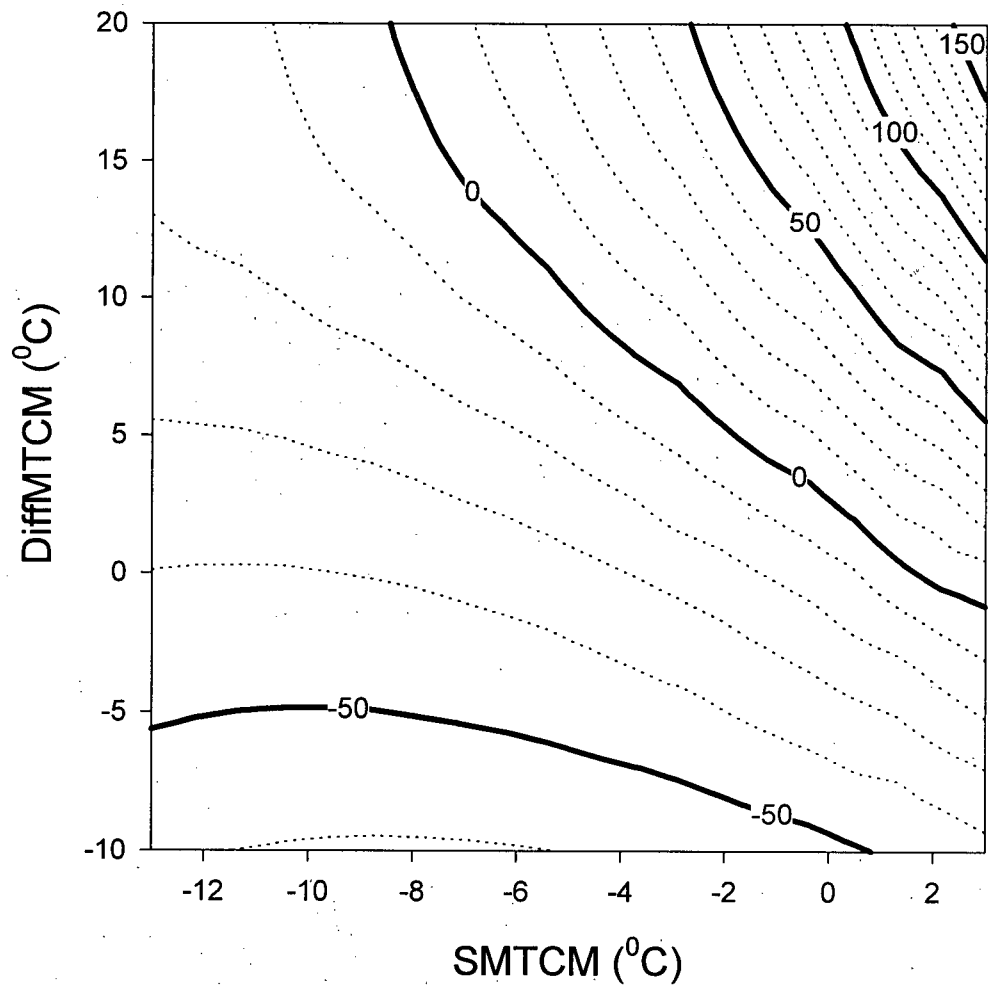


Fig. 3-13. Contour graph reflecting the predictions of DeviVOL20 (%) on DiffMTCM (= PMTCM - SMTCM) pertaining to site mean coldest month temperature conditions (SMTCM).

Contour of DeviVOL20 (%) with DiffDD0 & SDD0

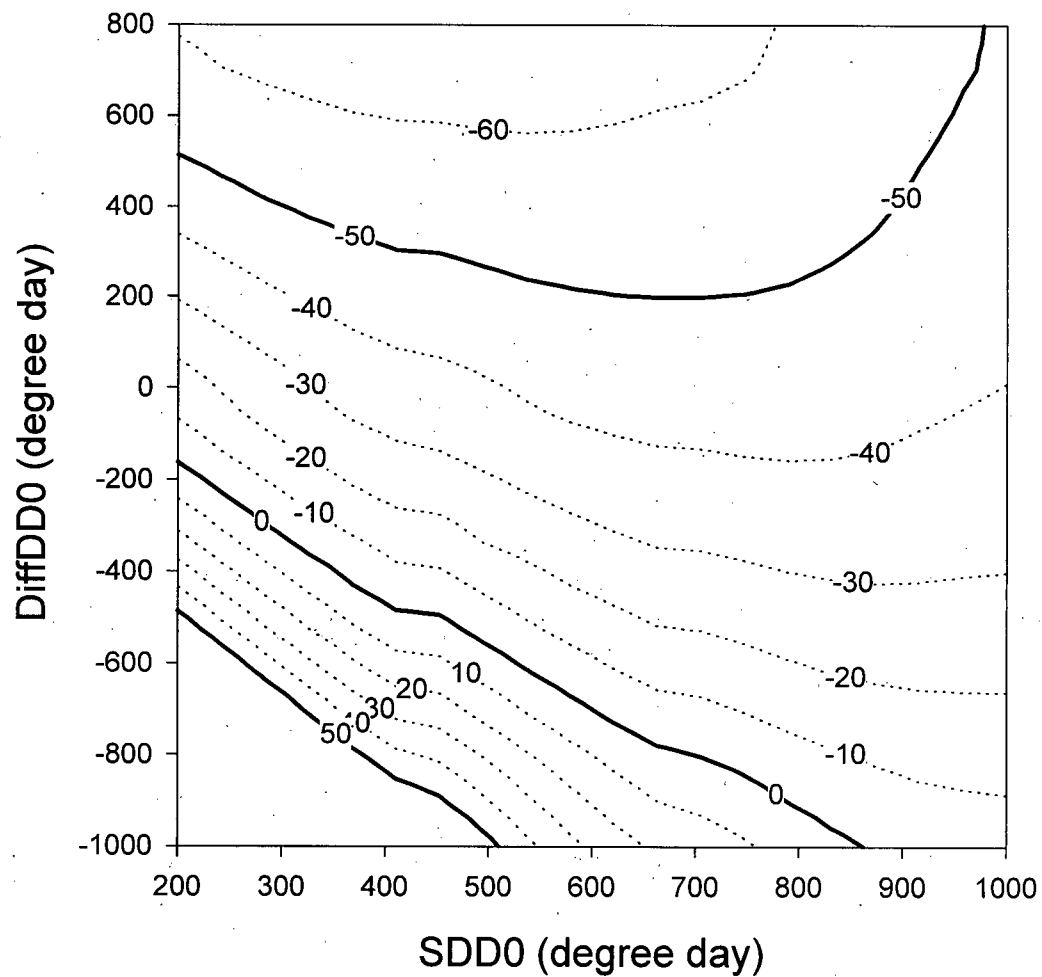


Fig. 3-14. Contour graph reflecting the predictions of DeviVOL20 (%) on DiffDD0 (= PDD0 - SDD0) pertaining to the amount of winter coldness of the planting sites (SDD0).

Contour of DeviVOL20 (%) with DiffNFFD & SNFFD

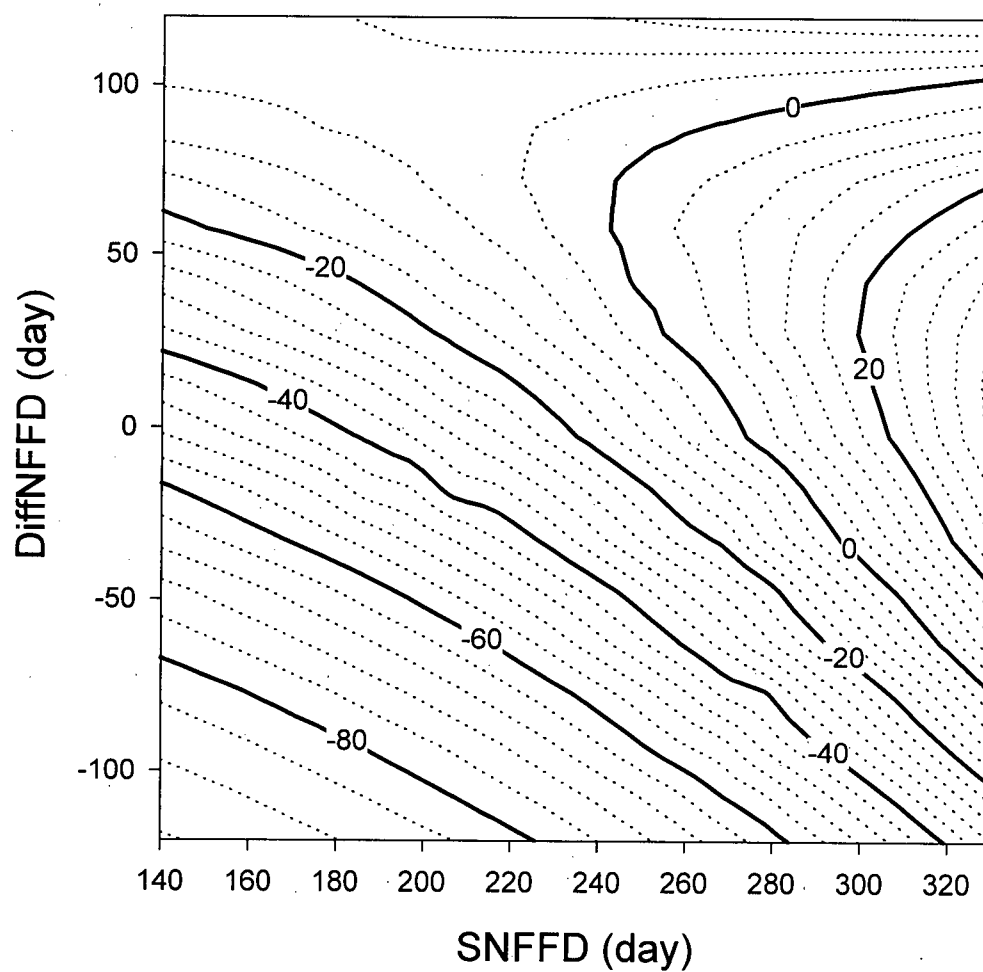


Fig. 3-15. Contour graph reflecting the predictions of DeviVOL20 (%) on DiffNFFD (= PNFFD - SNFFD) pertaining to lengths of annual frost free period of the planting sites (SNFFD).

Contour of DeviVOL20 (%) with DiffLAT & SMSP

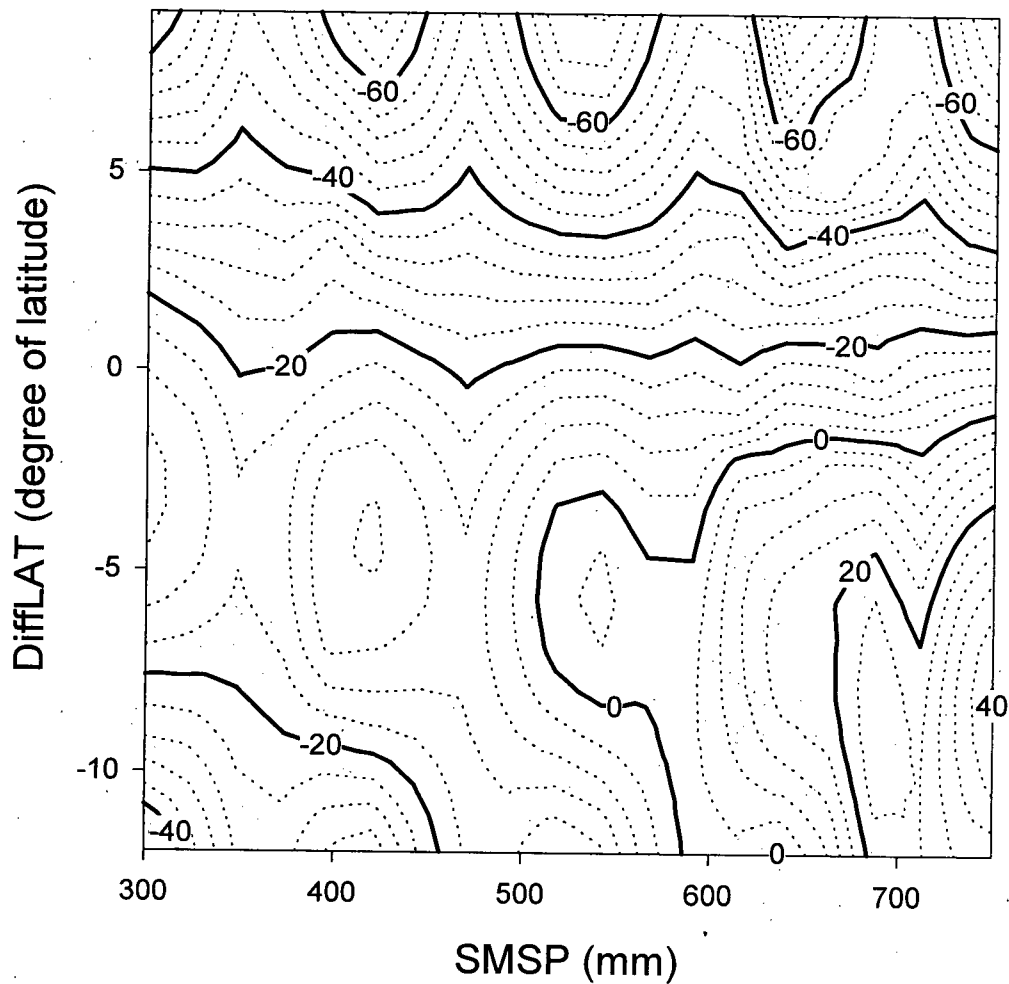


Fig. 3-16. Contour graph reflecting the predictions of DeviVOL20 (%) on DiffLAT (= PLAT - SLAT) pertaining to lengths of mean summer precipitation of the planting sites (SMSP).

3.4.5. Contours assisting the guide of seed transfer in BC

An alternative way of defining the range of suitable seed source under given site geoclimatic conditions is by plotting contour graphs relating growth vigor with pairs of site and provenance geoclimatic variables that are influential on the growth vigor. The method was

proposed by Kung and Clausen (1983). In this study, the growth vigor was represented by volume growth (VOL20), and the two dimensional independent variables were the effective geoclimatic factor for provenance origin and for test site.

Response surface were constructed by using VOL20 (at provenance-by-site mean level) as the dependent variable, site and the corresponding provenance geoclimatic factors as the two independent variables (i.e., SLAT with PLAT, SMAT with PMAT, and etc.), using the SAS RSREG procedure. The five effective geoclimatic variables (i.e., LAT, MAT, MTCM, DD0, NFFD) were determined by the previous redundancy analysis (see section 3.4.1.), while MSP is adopted because SMSP is the predominant climate factor for test site, as determined by previous analyses on the climatic sensitivity in Sitka spruce (see section 1.4.3. for detail). The models were all set to the second polynomial to comply with the previous predictions and response surface analyses. The contour graphs from these models are presented as Figs. 3-17 to -22, and the quality information of these models are listed in Tables III-7 to -12 (see Appendix III).

The results indicate that the effects for the six pairs of geoclimate factors on the volume productivity were all highly significant ($p < 0.0001$) based on partial F -tests. This agrees with the previous analysis of variance result that the effects of Site and Provenance were both highly significant on the growth measurements (Chapt.1). Variations of the response variable are well accounted for by the models for MTCM, NFFD and MSP (R^2 ranging from 0.40 to 0.43), but not so well accounted for by those for LAT, MAT and DD0 (R^2 ranging from 0.18 to 0.29). Linear effects of these geoclimatic factors were all significant. The quadratic effects and the provenance-by-site interactions were not always significant among these factors, implying that milder site is generally more favorable for volume growth. Significant provenance-by-site

interactions (i.e., G x E interactions) were detected as PMTCM x SMTCM and PNFFD x SNFFD, which proved that winter coldness and length of growing season were the two major causes of the G x E interactions in growth of the provenances. However, as expected from the previously mentioned bias sources (i.e., location of test sites and weevil damage), the quadratic smoothing procedure of the response surfaces generated significant portion of 'lack-of-fit' error in total errors for all these models (see 'Lack-of-fit' tests in Tables III-7 to -12 in Appendix III). This emphasizes the descriptive rather than inferential nature of the contours from these models, which could only be used in assistance with the previous general predictions and response surface analyses.

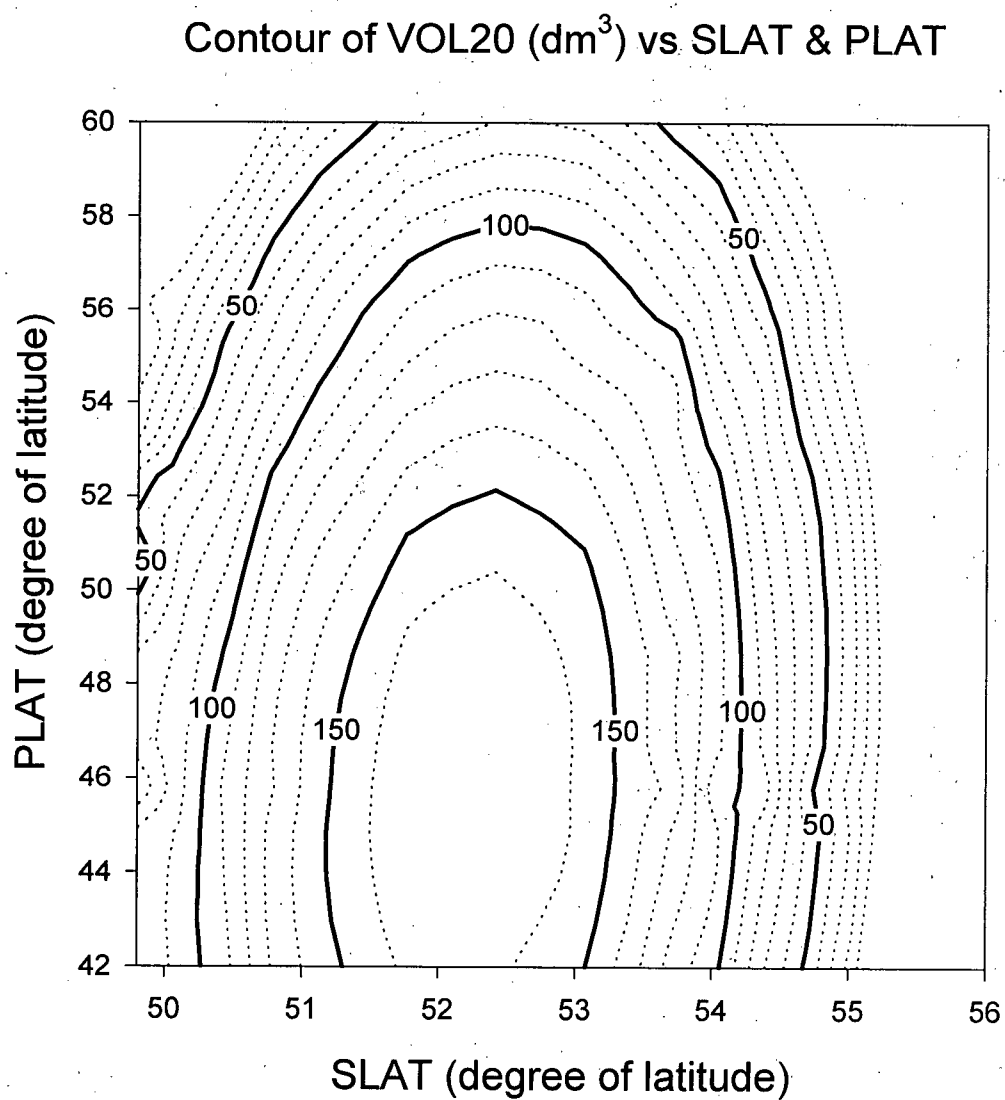


Fig. 3-17. Contour graph of VOL20 (dm³) on SLAT (site latitude) and PLAT (provenance origin's latitude).

Contour of VOL20 (dm³) vs SMAT & PMAT

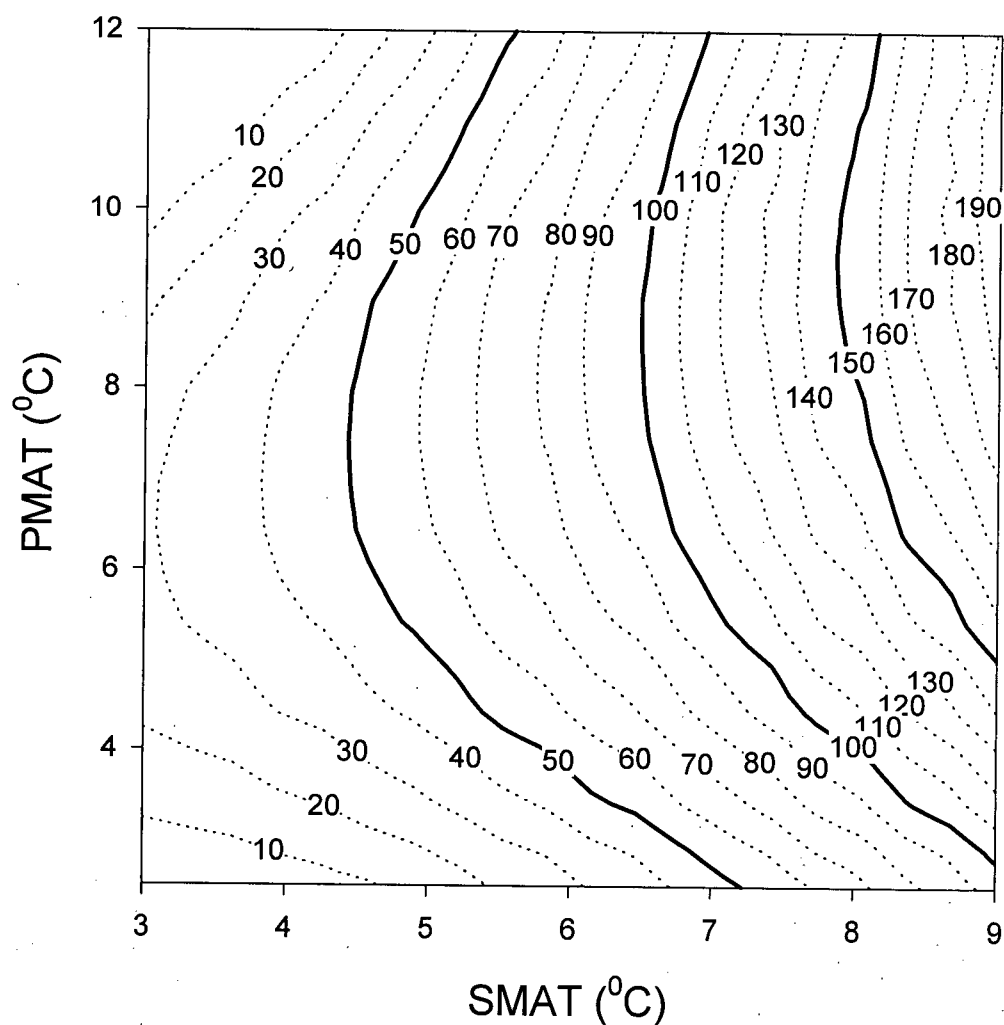


Fig. 3-18. Contour graph of VOL20 (dm³) on SMAT (Site Mean Annual Temperature) and PMAT (Provenance origin's Mean Annual Temperature).

Contour of VOL20 (dm³) vs SMTCM & PMTCM

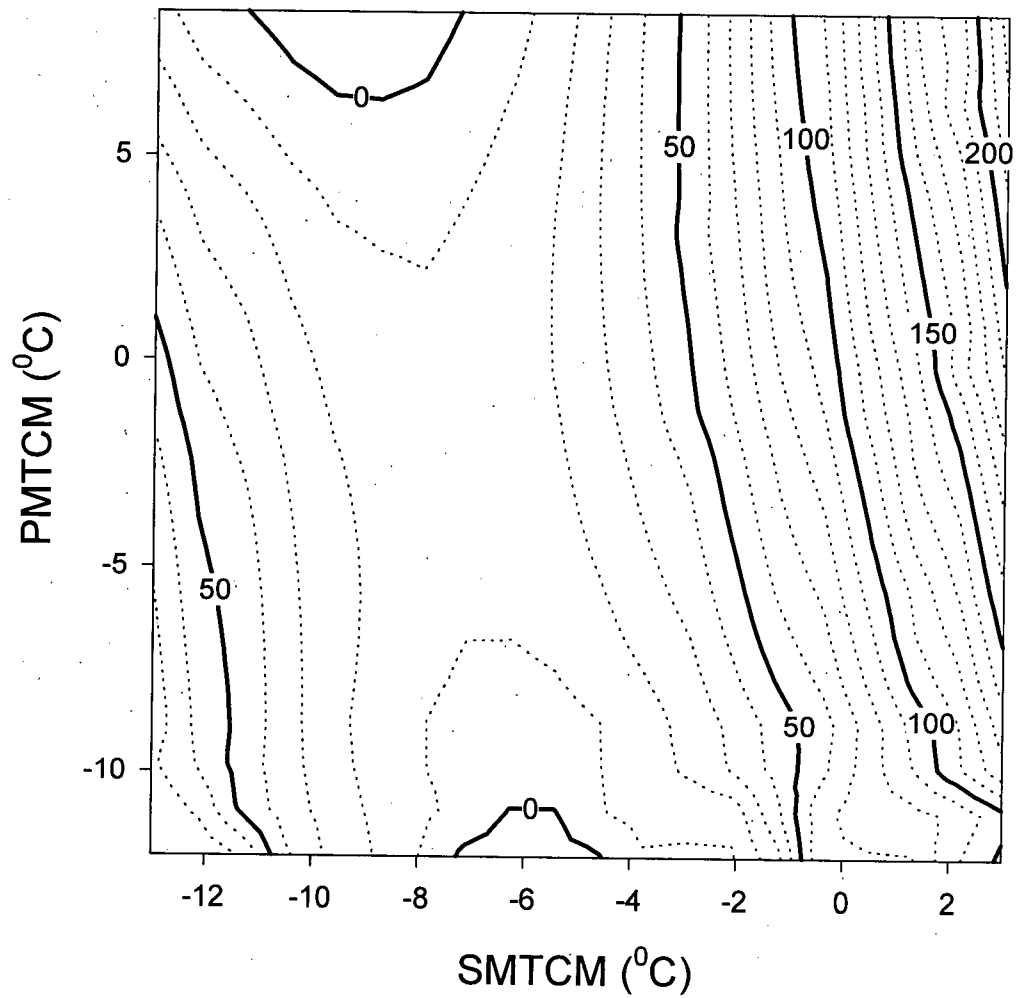


Fig. 3-19. Contour graph of VOL20 (dm³) on SMTCM (Site Mean Temperature of the Coldest Month) and PMTCM (Provenance origin's Mean Temperature of the Coldest Month).

Contour of VOL20 (dm³) vs SDD0 & PDD0

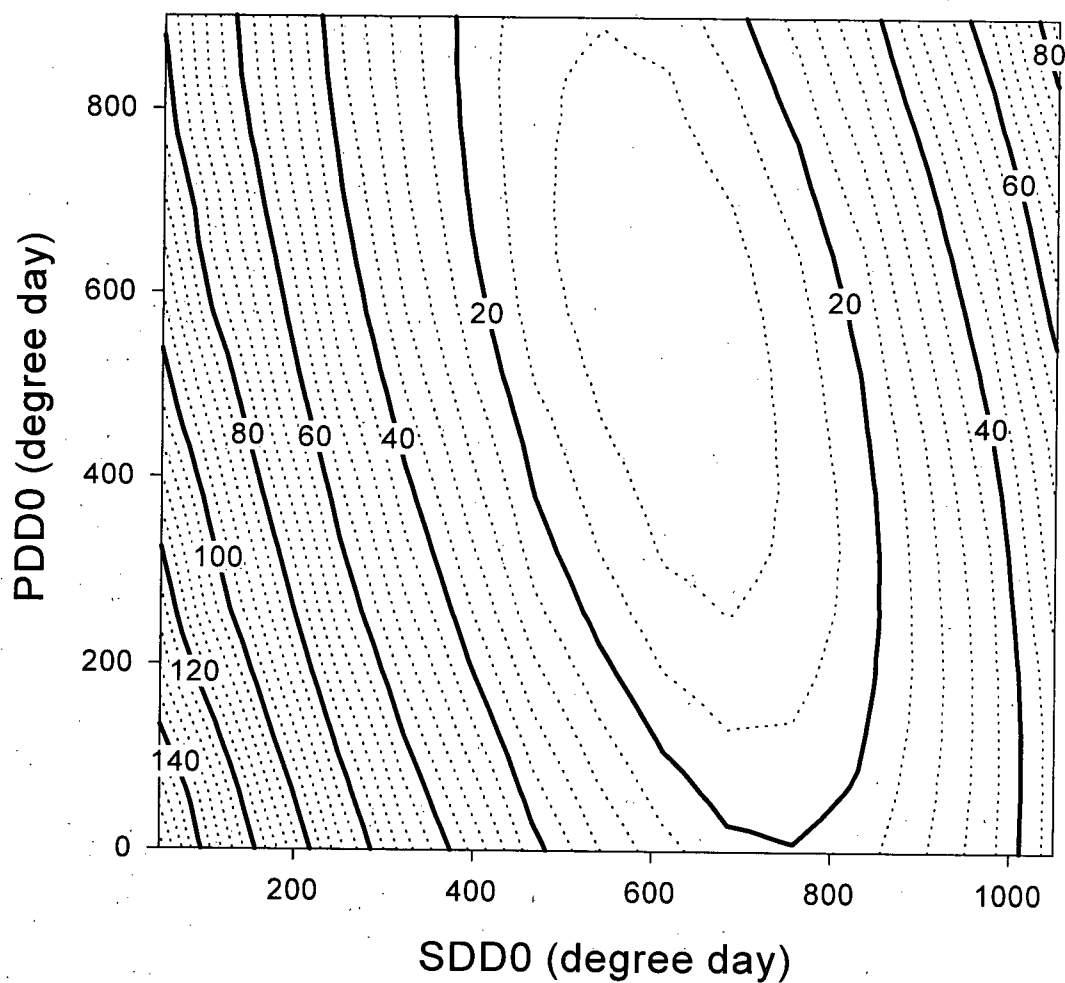


Fig. 3-20. Contour graph of VOL20 (dm³) on SDD0 (Site annual accumulated Degree Days below 0°C) and PDD0 (Provenance origin's annual accumulated Degree Days below 0°C).

Contour of VOL20 (dm³) vs SNFFD & PNFFD

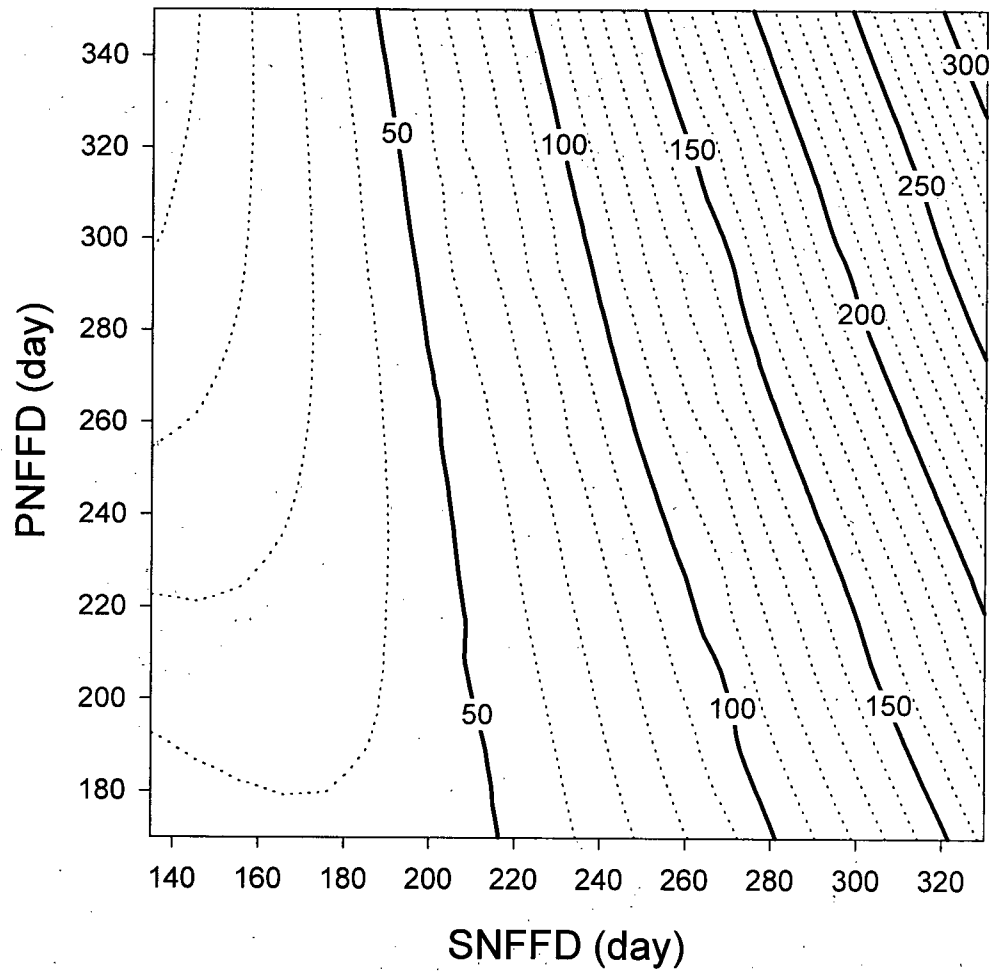


Fig. 3-21. Contour graph of VOL20 (dm³) on SNFFD (Site annual Number of Frost Free Days) and PDD0 (Provenance origin's annual Number of Frost Free Days).

Contour of VOL20 (dm³) vs SMSP & PMSP

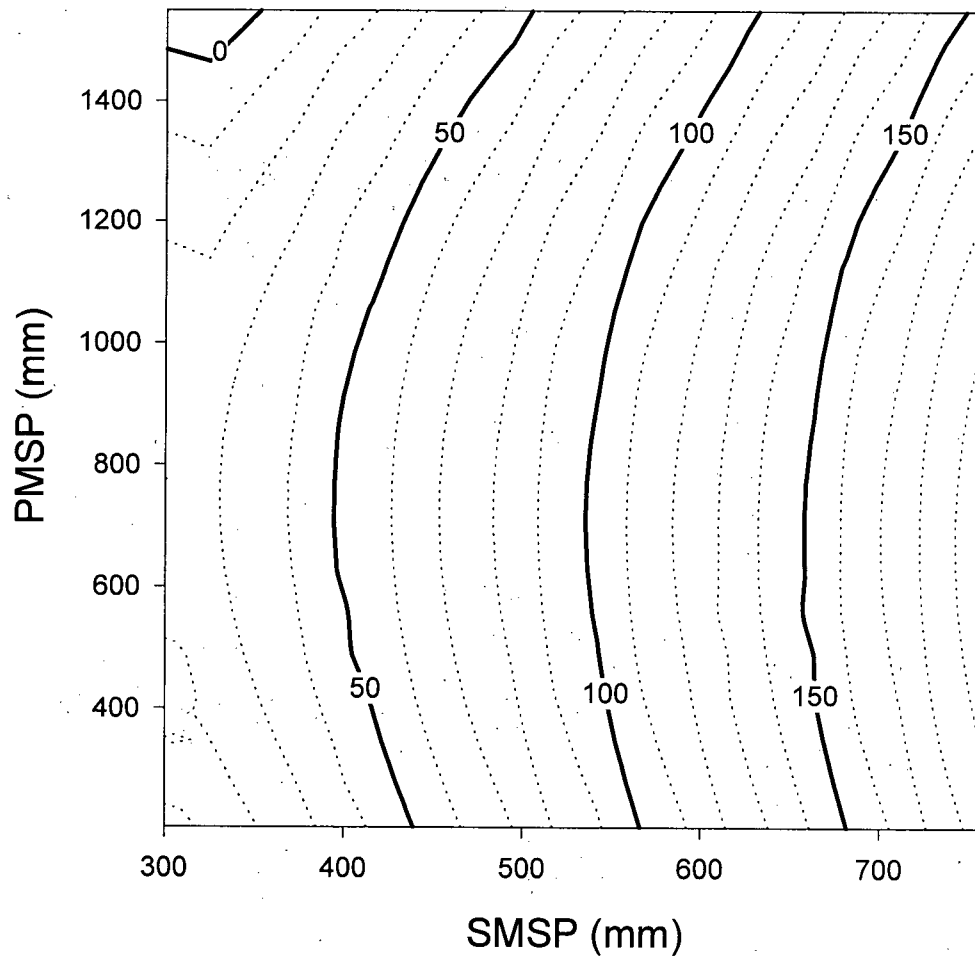


Fig. 3-22. Contour graph of VOL20 (dm³) on SMSP (Site mean Summer Precipitation) and PMSP (Provenance origin's mean Summer Precipitation).

Observing Figs. 3-17 to 3-22 gives the impression that the directions of the contours line almost paralleled (or obliquely paralleled) along with site geoclimatic gradients, which implies that the selection of planting site is more important than the selection of provenance in Sitka spruce. One maximum and one minimum of the volume production were found corresponding to

LAT and DD0, respectively. They were located at SLAT = 52°15" N and PLAT = 45°45" N for LAT (peak), and SDD0 = 613 degree days and PDD0 = 573 degree days for DD0 (valley), respectively (see Table III-7 and -10 in Appendix III). However, the peak found in LAT (Fig. 3-17) should not be considered a real maximum. It occurred due to excellent growth at the test sites on Queen Charlotte Islands (i.e., Holberg, Rennel Sound, and those on Graham Island), but exceptionally poor growth at the more southern test site (i.e., Head Bay) due to drastic weevil impacts (see Chapt.2).

The other remaining contours had no maxima or minima, but exhibited saddle shapes, which means southern provenances grew well in milder and/or southern areas but did not fare well in northern and/or harsh areas. This is caused by the G x E interactions in growth performance of the provenances. From these remaining contours (i.e., Figs.3-18, -19, -21 and -22), one could still perceive that the possible maxima of volume production lie beyond the test range at a direction pointing to milder and/or moister areas of planting site and of provenance origins.

If taking $VOL20 = 150 \text{ dm}^3$ as a high level of volume growth, the suitable ranges of planting site and provenance origin for this volume productivity could be defined based on the contour graphs of this section. These ranges are summarized in Table 3-6. It is clear from this table that the ranges for planting site selection are much narrower than those for provenance selection. Especially in MSP, high volume productivity is exclusively associated with high site moisture condition, with a minimum summer precipitation requirement of 670 mm, approximately. For the relative importance of planting site selection over provenance selection, this moisture criterion should be considered the number one site factor for reforestation with

Sitka spruce. In application, one should be aware of the limitations of this graphic approach as stated before (Sections 3.3.4. and 3.3.5.), keeping in mind that the limits presented here are by-and-large due to lack-of-fit error in the contour constructions. In seed transfer practice, one needs to think about the given site geoclimatic conditions comprehensively while taking the best possible advantage of northward seed transfer.

Table 3-6. Suitable geoclimatic ranges at BC for planting areas along with provenance origins if VOL20 = 150 dm³ is the level of individual tree volume growth at year 20 to be achieved.

	Influential geoclimatic factor					
	LAT ¹	MAT	MTCM	DD0	NFFD	MSP
Planting site condition	51° ~ 53° N	≥ 8 °C	≥ 1 °C	≤ 80 dd ²	≥ 260 days	> 670 mm
Prov. origin condition	≤ 51°30" N	≥ 5 °C	≥ -7 °C	≤ 100 dd	≥ 170 days	indifferent

1. The range for SLAT is least reliable due to the biases from test site locations and weevil damage as stated before.
2. dd = degree days (below 0°C, in this table).

3.5. Conclusions

1. General predictive models have been developed by relating volume growth response to geoclimatic distances between provenance origin and planting site (i.e., DiffLAT, DiffMAT, DiffMTCM, DiffDD0 and DiffNFFD) to predict the average volume growth of ecademic provenances relative to local seed source of the planting site. Volume response predicted was most pronounced for DiffLAT, less pronounced for DiffMAT, DiffMTCM and DiffDD0, but least pronounced for DiffNFFD. Predictive results proved that northward seed transfer is favored for this species, and latitudinal change is the major beneficial change to northward

seed transfer practice. Predictions are reliable within the range of -20 to 10% in volume-gain over local source after 20 years from planting. An average ultimate volume-gain was predicted in association with a 5.5 ° of latitude transfer from southeast to northwest along the coast line of BC. Results largely support the current seed transfer guidelines in this species in BC, but also indicate possible wider limits for planting at maritime areas.

2. The range and extent of northward seed transfer which allows for higher-than-local performance are subject to planting area's geoclimatic conditions: the milder (or the more southern) the planting site is, the greater the range of northward seed transfer that allows for pursuing higher-than-local performance, and also the greater the amount of volume-gain can be achieved through the transfer. High dependency of volume response on site moisture condition was found that, a minimum of 500 mm summer rainfall (SMSP) was required to achieve higher-than-local growth performance. In outer coastal areas with high precipitation (e.g., SMSP > 700 mm), about 40% of volume-gain could be achieved by northward seed transfer up to 12 ° of latitude.
3. The geoclimatic ranges of suitable planting site and provenance origin were defined for high volume production of this species by a series of contours, constructed by relating the volume growth to both site and provenance geoclimatic conditions on each predictive factors, respectively. Results indicated that the selection of planting area is much more important than selection of provenance origin. A minimum of 670 mm summer precipitation at planting site is required for high volume productivity of the species.

3.6. References

- BC Ministry of Forests. 1995. *British Columbia Forest Practice Code: Seed and Vegetative Material Guidebook*. Government of British Columbia, Ministry of Forests, Victoria, Canada.
- Beuker, E. 1994. Long-term effects of temperature on the wood production of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. in old provenance experiments. *Scand. J. For. Res.* 9: 34~45.
- Box, G.E.P., Draper, N.R. 1987. *Empirical Model-Building and Response Surfaces*. John Wiley and Sons, Inc. New York.
- Burley, J. 1966. Genetic variation in seedling development of Sitka spruce, *Picea sitchensis* (Bong.) Carr.. *Planta*, 99: 283~289.
- Campbell, R.K., and F.C. Sorenson. 1978. Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. *Theor. Appl. Genet.* 51: 233~246.
- Daniel, C. and F. S. Wood. 1980. *Fitting Equations to Data*. (2nd edition). John Willy and Sons. pp.458.
- Daubenmire, R. 1968. Some geographic variations in *Picea sitchensis* and their ecological interpretation. *Can. J. Bot.* 46: 787~798.
- Draper, N.R. and Smith, H. 1966. *Applied regression analysis*. John Wiley and Sons Inc., New York.
- Falkenhagen, E.R. 1978. Parent tree variation in Sitka spruce provenances, an example of geographic variation. *Silvae Genet.* 27: 24~29.
- Hormann, R.K. 1987. North American tree species in Europe. *J. Forestry*. 85: 27~32.
- Jarvis, N.J. and Mullins, C.E. 1987. Modelling the effects of drought on the growth of Sitka spruce in Ilingworth, K. 1978a. Sitka spruce provenance 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 Pp 311~326. Vancouver, B.C. Canada.
- _____. 1978b. Study of lodgepole pine genotype-environment interaction in British Columbia. *Proc. IUFRO joint meeting*. Vancouver, Canada. Vol. 2. B.C. MoF, Victoria, B.C. Pp.151~158.
- Kovats, M. 1977. Estimating juvenile tree volumes for provenance and progeny testing. *Can. J. For. Res.* 7: 335~342.
- Kung, F.H. and Clausen, K.E. 1983. Graphic solution in relating seed sources and planting sites for white ash plantations. *Silvae Genet.* 33: 46~53.
- Lines, R. 1973. Sitka spruce IUFRO collection. *Rep. For. Res.* 42~45.
- MacSiurtain, M.P. 1981. *Distribution, management, variability and economics of Sitka spruce in coastal British Columbia*. M.Sc. thesis. Fac. For., UBC., Vancouver, B.C., Canada. 256p.
- Malcol, D.C. 1987. Some ecological aspects of Sitka spruce. In: Henderson, D.M. and Faulkner, R. (eds) *Proc. Royal Soc. Edinburgh*, 93B. Pp. 85~92. Edinburgh, Scotland.
- Matyas, C. and Yeatman, C.W. 1994. Effect of geographic transfer on growth and survival of jack pine (*Pinus banksiana* Lamb.) populations. *Silvae Genet.* 41: 370~376.
- Mergen, F., J. Burley, and G.M. Furnival. 1974. Provenance-temperature interaction in four conifer species. *Silv. Genet.* 23: 200~210.
- Pojar, J., K. Klinka and D.V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Eco. Manag.* 22: 119~154.

- Raymond, C.A. and Lindgren, D.** 1990. Genetic flexibility ---- A model for determining the range of suitable environments for a seed source. *Silvae Genet.* 39: 112~120.
- Rehfeldt, G.E.** 1983. Adaptations of *Pinus contorta* populations to heterogeneous environments in northern Idaho. *Can. J. For. Res.* 13: 405~411.
- _____. 1995. Genetic variation, climate models and the ecological genetics of *Larix occidentalis*. *Forest Ecology and Management.* 78: 21~37.
- SAS Institute Inc.** 1990. SAS/STAT User's Guide, Version 6, 4th edition. Vol .1 (pp 943) and Vol. 2 (pp 846). Cary, NC, USA.
- Schmidtling, R.C.** 1993. Use of provenance tests to predict response to climate change: loblolly pine and Norway spruce. *Tree Physiology.* 14: 805~817.
- Skroppa, T. and Johnson, O.** 1994. The genetic response of plant populations to a changing environment: the case for non-Mendelian processes. In: Boyle, T.J.B. and Boyle, C.E.B. (eds) *Biodiversity, temperate ecosystems and global change*. Springer-Verlag, Berlin. Pp 183~199.
- Wareing, P.F.** 1956. Photoperiodism in woody plants. *Annu. Rev. Plant. Physiol.* 7: 191~214.
- Wetherill, G.B.** 1986. *Regression Analysis with Applications*. Chapman and Hall Ltd., New York.
- Wollenberg, A.L.** 1977. Redundancy analysis --- An alternative for canonical correlation analysis. *Psychometrika* 42(2): 207 ~219.
- Worrell, R. and Malcolm, D.C.** 1990. Productivity of Sitka spruce in northern Britain; 1. The effects of elevation and climate. 2. Prediction from site factors. *Forestry* 63: 105~118.
- Ying, C.C.** 1991. *Genetic resistance to the white pine weevil in Sitka spruce*. Research Notes No. 106, Research Branch, Ministry of Forests B.C., Victoria, B.C., Canada.
- Ying, C.C.** 1997. Effects of site, provenance, and provenance and site interaction in Sitka spruce in coastal British Columbia. *Forest Genetics.* 4(2): 99~112.

4. Sitka spruce IUFRO provenance trials in British Columbia: old experiment new approach

Abstract: The 20-year growth data from Sitka spruce provenance trials in British Columbia were used to simulate volume growth response to rapid thermal-climatic changes after adjusting out the effects of photoperiod change in latitudinal seed transfer. The predictive models are biased and with low precision due to many limitations of this approach. Results predicted that the advantage this species can take from global warming is not substantial if there is not a precipitation increase accompanying global warming trend. The predicted ultimate volume-gain from thermal-climatic changes is 2.3%(±1.3%) on average that is associated with a 1.5°C increase in mean annual temperature, or 4.3%(±2.2%) with a 300-degree-day's decrease in annual accumulated degree days below 0°C which is the amount of winter coldness. If global warming brings about 50-day's increase of frost free days per annum, a 4.4%(±1.9%) volume-gain from the lengthened growing season would be expected. The volume response to elevated winter temperature is predicted to be less pronounced, with just a 1.6%(±1.1%) volume-gain that could be expected from a 3°C increase in monthly mean temperature of January. The study also suggests that volume growth of Sitka spruce could respond more quickly and linearly to an increase in precipitation compared to rapid thermal-climatic changes. Dependency of the volume response to thermal-climatic change upon site summer moisture condition was analyzed. Results show that changes in mean annual temperature could result in positive effect on volume growth only when there is enough summer rainfall at the planting site (i.e., SMSP > 500mm). The

higher summer precipitation a planting site has, the greater volume-gain could be expected at that site from elevated thermal-climatic conditions, and the wider range for this species growing at that site to benefit from global warming scenario. At maritime areas with more than 700 mm summer precipitation, up to 20% volume-gain was projected from an increase in mean annual temperature by 5°C.

Keywords: global warming; growth response; provenance trial; Sitka spruce (*Picea sitchensis* (Bong.) Carr.).

4.1. Introduction

It is becoming widely acknowledged that we are entering a period of climate change at an unprecedented rate. The global mean annual temperature has been projected to increase by 2.5°C from 1989 to 2050 as a result of the greenhouse effect (Schneider 1989). If this global warming scenario is true, its impact would be more pronounced at higher than lower latitudes areas. For instance, a winter temperature increase of 7°C and a summer temperature increase of 4°C were projected for British Columbia region by Canadian Climate Program Board (CCPB 1991). Although a great deal of uncertainty still surrounds these projections, most meteorological data forewarn about the global warming trend. The real uncertainty seems to be related to the level of warming and how it will affect the amount and distribution of precipitation (Ledig and Kitzmiller 1992).

Assuming that rapid climate change is taking place, there is concern about how climate change will affect tree growth and survival. Trees, with their long life spans, are less able to respond by migration and genetic selection in a relatively short period of time. To date, tree responses to the expected rapid climate change are largely unknown. The responses in growth rate and its directions (i.e., negative or positive) were addressed by physiologists with growth chamber experiments. These models are based on extrapolation from short term trials conducted on seedlings under artificial settings. There is a lack of experiments with mature trees under natural conditions with temperature fluctuations and biological effects retained intact. This is vital, long-term growth responses of trees are different from those in seedlings, and trees grown under natural conditions may be different from those seedlings grown in growth chambers.

An effective way to measure the response of a tree species to climate change is to establish a long-term experiment where trees of known origins and genetic background are planted in many climatically different environments. The growth of the trees in the experiment is measured periodically, preferably well past reproductive maturity. Coincidentally, this kind of experiment has been conducted by foresters for more than 200 years, under the name of provenance trial (Langlet, 1971). This idea was recently advocated by the Finnish scholar, Koski (1989). With widening recognition of the global warming trend, the issue aroused much interests and several studies have been reported (Matyas 1994; Schmidting 1994; Beuker 1994 and 1996). The main advantage of this new approach is that many old provenance trials with most of the commercial tree species are already in place with data available, so that one can easily make the best possible use of them within the limitations set by the experimental designs.

Sitka spruce, *Picea sitchensis* (Bong.) Carr., a fast growing coastal conifer native to North America, occupies a long, narrow strip along the Pacific coast spanning over 22 degrees of latitude (Daubenmire 1968). Its high growth rate, great stumpage and wood quality made it a recommended species for reforestation in coastal areas of British Columbia (BC) where the white pine weevil (*Pissodes strobi* (Peck)) threat is low (Ying 1997). In order to exploit the potential of genetic superiority of ecdemic (non-local) provenances over local seed source in growth and screen for weevil resistant provenance, the Research Branch of British Columbia Ministry of Forests (MoF) launched a long-term project of Sitka spruce provenance trials in early 1970s which included 43 IUFRO Sitka spruce provenances, collected along the coast from Oregon coast to south Alaska, tested at 11 test sites of coastal BC areas (Illingworth 1978; Ying 1991 and 1997; Chapt.1). The main factor considered in these trials is latitudinal seed transfer, with changes in elevation and edaphic conditions as secondary (For details of the locations of provenance origin and test site, see Tables 1-1 and -2 in Chapt.1). Growth of individual trees in these trials were measured periodically over the first 20 years since planting. These growth data, along with the geoclimatic data for provenance origins and test sites, provided a good opportunity to simulate growth response to rapid climate changes, if the effects of photoperiod change from latitudinal transfer are eliminated. The objective of this chapter is to simulate growth responses of Sitka spruce to the potential of rapid climate changes (focusing on global warming trend) in term of volume growth at the 20th year after planting. As latitudinal trend in growth of the provenances by year 20 has been proved to be relatively stable compared to early height growth (Chapt.1), the projections made in this study can be considered as long-term growth response.

There are quite a few limitations, however, for using provenance trial data to predict tree growth response to rapid climatic changes. First, provenance trials were not designed for this simulation purpose. That is, symmetric latitudinal and longitudinal strictures and random sampling for test site location and provenance origin are rare, and consequently, fine gradients of climatic change are rare in old provenance trials. Second, it is possible that changes in growth rate could be over-estimated since climate change is a gradual process in any given location, while in provenance trials the climate change associated with long-distance transfer is immediate. Third, latitudinal seed transfer results in both temperature and photoperiod changes, which means the simulation may over-estimate the growth response due to temperature change only. In this study, although the latitudinal effects were accounted for by adjusting out the effects of photoperiod changes in growing season, this procedure also removed certain effects of thermal-climatic changes as well, because the thermal-climatic change variables are closely correlated with latitudinal change and thus with photoperiod change (see Table III-13 in Appendix III). Therefore, it is almost impossible to remove the effects of photoperiod change from latitudinal seed transfer while retaining the effects of thermal-climatic changes intact. Thus, the predictions in this study could under-estimate the effects of thermal-climatic changes only. Forth, the predictions only focus on climatic changes between test site and seed origin, but in fact, other environmental changes, e.g., soil differences between test site and origin and among test sites, could also affect the tree's growth response noticeably. Another big limitation of this study is due to the fact that the range of provenance origins exceeds the range of test sites considerably (see Fig.1-1 in Chapt.1), which means, it is impractical to derive the autochthonous growth performances of the provenances at their origin places. Therefore, the growth response presented

in this study is relative to local performance rather than to autochthonous performance of a provenance itself. This is vital, because high-than-local growth is generally associated with northward seed transfer (see Chapt.3), that is, positive growth response is associated with lowered thermal-climatic conditions for the provenances transferred north, which certainly can not be true for the growth response relative to autochthonous performance. Therefore, in this study, the thermal-climatic changes were given reversed signs between test site and provenance origin, i.e., the climatic differences were defined by subtracting the values for provenance origin by the values for test site, instead of vice versa. How much bias having resulted from this manipulation is largely unknown, but this is the best I can do to approach the research purpose. The use of growth response relative to local than to autochthonous performance could also result in under-estimations when seed is transferred south while over-estimations when seed is transferred north, if considering that the local performance is usually higher than sources north of the site but lower than sources south of the site in this species. At this point, contradictorily, one might also want to argue that the predictions would be over-estimated when seed is transferred south but under-estimated when seed is transferred north, if accounting for the fact that the autochthonous performance of a southern provenance is generally greater than local ones but that of a northern provenance is generally poorer than local ones. Finally, the predictions made are under the assumption that trees are genetically well adapted to new climatic conditions, which could also bring about over-estimation of the actual growth response. In conclusion of the above limitations, the predictions made in this chapter should be considered descriptive rather than inferential. I expect effects resulting in under-estimation are to some extent offset by those over-estimating response. Thus, the predictions made here are probably as accurate as extrapolations

based on growth chamber data, while taking the advantages of available data and the fact that the trees are grown in natural environments.

4.2. Materials and Methods

Data from three series of Sitka spruce provenance trials in coastal BC (supplied by the Research Branch of MoF), which include the test of 43 Sitka spruce IUFRO provenances at 11 sites, were used in this study (Ying 1991 & 1997; also see Chapt.1 for details). The experiments have completely randomized block design, with 4, 5, 6 or 9 blocks at different test sites. Within a block each provenance tested is represented by a 9-tree-row plot. Not all provenances tested at all sites, thus there are 220 provenance-by-site means for the simulation process (see Chapt.3). For long-term simulation, the growth measurement selected for analysis is volume in the most recently measured year, i.e., the 20th year after planting. Individual tree volume was calculated by Kovas' volume function (1977) and termed as VOL20. Volume growth response is expressed in logarithmic values for the ratio of an ecademic provenance's growth performance over the local performance where the ecademic one was tested, and symbolized as DeviVOL20. The estimation of the ecademic provenance's growth performances and the local performances were described in Chapter Three.

Macro-climatic data were obtained from the nearest weather station to a test site as well as to a provenance origin place. With prefix "S-" added for all site climatic variables, and "P-"

for all provenance climatic variables, the acronyms of the six climatic variables that describe thermal-climatic, photoperiod and summer moisture condition are as follows:

MAT	= Mean Annual Temperature (°C)
MTCM	= Mean Temperature of the Coldest Month (i.e., January) (°C)
DD0	= annual accumulated Degree Days below 0°C (°C)
NFFD	= annual Number of Frost Free Days (day)
DAY	= accumulated daylength of a growing season (April ~ October) (in hours, calculated as a function of latitude)
MSP	= Mean Summer Precipitation (mm) (May ~ September)

The climatic differences between provenance origin and test site were obtained by subtracting the values for provenance origins by those for test sites where the provenances tested, correspondingly. These climatic difference variables were named with a “Diff-” prefix, i.e., “DiffMAT”, “DiffMTCM”, and etc. For instance, $\text{DiffMAT} = \text{PMAT} - \text{SMAT}$.

In order to eliminate the effect of photoperiod changes from the gross effect of latitudinal seed transfer, curvilinear regression (quadratic) was performed on *DeviVOL20* with *DiffDAY*, a variable that defines the photoperiod difference between provenance origin and test site in growing season. The residual (the observed value subtracting the predicted value) from this regression model is the net growth response in *VOL20* mainly to thermal-climatic changes. It was therefore termed as “*NDeviVOL20*” (Net growth Deviation in *VOL20*), and was used as the growth response variable in the subsequent simulations for rapid climate changes. Thus, the only difference between the simulation models in this chapter and those in Chapter Three is that the observed volume response (*DeviVOL20*) is substituted by *NDeviVOL20* to distinguish the effects of thermal-climatic changes from photoperiod change in latitudinal seed transfer.

The response in NDeviVOL20 to thermal-climatic changes were quantified by curvilinear regressions relating NDeviVOL20 to the thermal Diff- variables, respectively. The prediction models were set up as quadratic functions of the Diff- variables, respectively. The predicted values were transformed back from logarithmic values into percent deviation of volume growth relative to the growth under current temperature conditions (i.e., local performance) for reporting results. The ranges of thermal-climatic changes that did not cause growth-loss on average were also defined by the mean predicted values for NDeviVOL20.

Growth response to different moisture conditions of planting site was also explored by examining the volume productivity (VOL20, transformed into logarithmic value) of the 11 frequently tested provenances (see Appendix II) to test site summer precipitation (SMSP). Dependency of the predicted growth response to thermal-climatic changes on test site summer moisture condition was analyzed by two-dimensional response surface analysis using second degree polynomials. DiffMAT was selected as the major thermal-climatic factor while SMSP as the most influential site moisture index in this response analysis. Results were presented in a contour graph corresponding to the smoothed surface.

All data analyses were performed with SAS procedures (SAS Inc. 1990). Growth response variables were transformed into natural logarithmic values in all the analyses to approach normal distribution, but interpreted in the original units in reporting. To avoid scale problems with growth and climatic variables, response surface analysis was based on standardized data (i.e., subtracting the mean and then dividing by the standard deviation of that mean). All tests of significance are valid under the assumptions of normality and homogeneous

variance of the response variables across different levels of experimental effects and climatic gradients. The significance criterion was set at $\alpha = 0.05$ level unless otherwise specified.

4.3. Results and Discussions

4.3.1. Growth response to thermal-climatic changes only

Net volume growth response to thermal-climatic changes were obtained from the curvilinear (quadratic) regression of DeviVOL20 with DiffDAY. The regression model is highly significant ($p < 0.0001$), with relatively high model R^2 (coefficient of determination) as 0.296. The residuals from this regression model were used as the net volume response variable, i.e., NDeviVOL20, for the subsequent simulations. The effect of photoperiod change was eliminated from the original volume response to both thermal-climatic changes and photoperiod change from latitudinal seed transfer. This is evident from the residual plot of NDeviVOL20 with DiffDAY (Fig. 4-1), ---- no discernible trend left for the growth response to DiffDAY.

However, as mention before, the removal of photoperiod effects, i.e. latitudinal effects, also eliminated the effects from thermal-climatic changes to some extents, because the latter ones are contingent with, or say redundant on the changes in latitudes. This could be seen from the pair-wise correlations between DiffDAY (or DiffLAT) and Diff- thermal variables (Table III-13 in Appendix III), and was also discussed in Chapter Three (Section 3.4.3). The correlation coefficients between these variables ranged from 0.65 to 0.79, and were statistically significant ($p < 0.0001$). Therefore, the use of NDeviVOL20 as the response variable for the subsequent simulation will under-estimate the growth response due to thermal-climatic changes only.

Scatter plots were used to observe the growth response trend by plotting NDeviVOL20 (in natural logarithmic values) versus the thermal-climatic change variables, respectively (Figs. 4-2 to -5). One can see from these plots the quadratic response trends of the net growth response to all these thermal-climatic changes. However, the trends are quite flat, which means that the growth did not respond highly to thermal-climatic changes between seed source and test site. This agrees with the previous results that Sitka spruce is highly sensitive to moisture conditions, not to thermal conditions in later growth (Chapt.1). However, as stated before, the response to thermal-climatic change effects were depleted by the removal of photoperiod changes, so that the flat response curves are rather expected. There were large amount of variations of NDeviVOL20 surround these quadratic trends, suggesting that growth response of individual provenance could be greatly different from the mean predicted growth response, that is, the predictions could not be precise, though statistically unbiased prediction can be achieved.

Regression analyses proved that the volume responses fit well to the quadratic curves for the four thermal-climatic change variables separately (Table 4-1). The prediction models are all highly significant ($p < 0.0001$), but the values of model R^2 's are relatively low (ranging from 0.11 to 0.24, and in the fact that these R^2 's are not adjusted for the null intercept). Low coefficients of determination imply that a great portion of variation in the volume response was not accounted for by the prediction models. This is partly attributable to the adjustment for DiffDAY which removed the effects of thermal-climatic changes to certain extent. As a result, the precision of the predictions are low, especially below the peak region of the response curves. However, the residual means for the prediction models are not significantly from zero at $\alpha = 0.01$ level (t -test on the residual means in Table 4-1), which means the predictions are statistically unbiased.

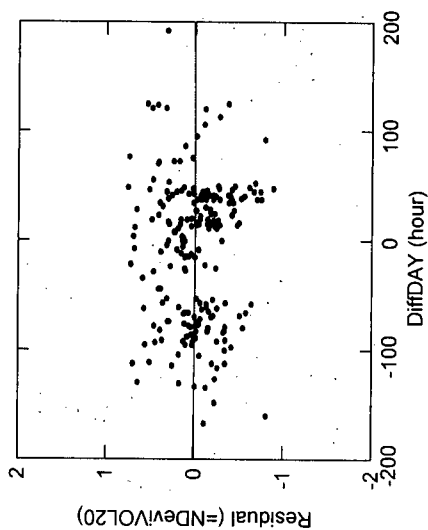


Fig.4-1. Residual plot for the curvilinear regression model of $\text{DeviVOL20} = f(\text{DiffDAY}, \text{DiffDAY}^2)$.

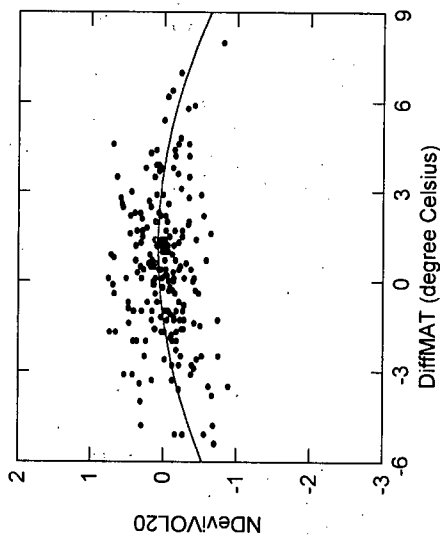


Fig.4-2. Scatter plot of NDeviVOL20 (in logarithmic value) versus DiffMAT and the quadratically smoothed trend.

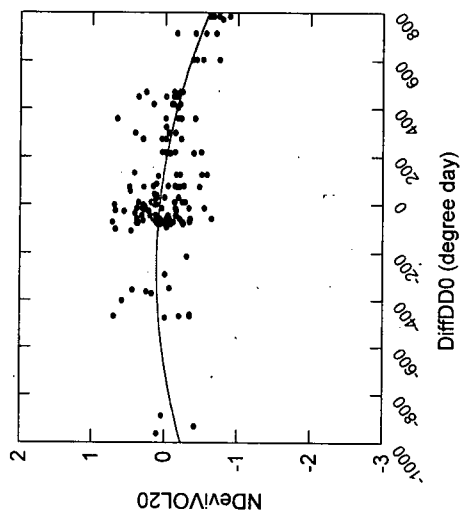


Fig.4-4. Scatter plot of NDeviVOL20 (in logarithmic value) versus DiffDD0 and the quadratically smoothed trend.

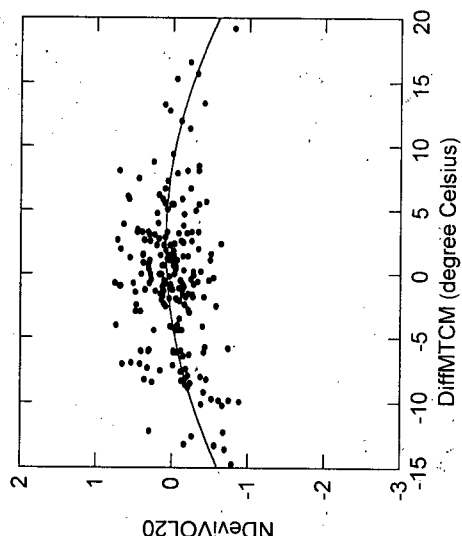


Fig.4-3. Scatter plot of NDeviVOL20 (in logarithmic value) versus DiffMTCM and the quadratically smoothed trend.

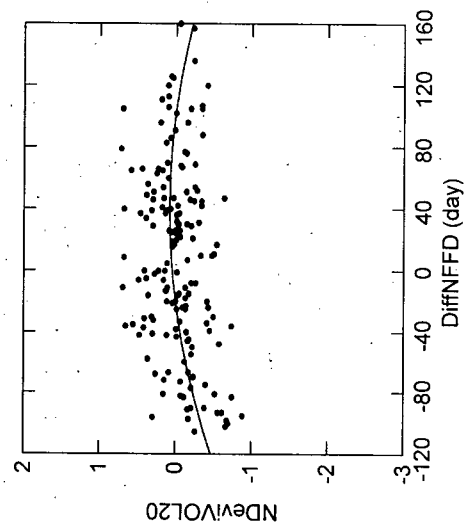


Fig.4-5. Scatter plot of NDeviVOL20 (in logarithmic value) versus DiffNFFD and the quadratically smoothed trend.

Table 4-1. Estimated parameters for the prediction models relating NDeviVOL20 to the four thermal-climatic change variables, respectively, along with the quality information for these models.

(1) $\text{Ln}(\text{NDeviVOL20}) = f(\text{DiffMAT}, \text{DiffMAT}^2)$

Factor	Parameter Estimate	St. Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffMAT	0.0293827710	0.00908803	3.23	0.0014
DiffMAT ²	-0.0093562460	0.00198807	-4.71	<0.0001
<i>Model $R^2 = 0.1086$, Root MSE = 0.3125, $n = 212$, Residual Mean = 0.0408</i>				
<i>(t-test for H_0: Residual Mean = 0 is $T = 1.90 < T_{0.025} = 1.97$)</i>				

(2) $\text{Ln}(\text{NDeviVOL20}) = f(\text{DiffMTCM}, \text{DiffMTCM}^2)$

Factor	Parameter Estimate	St. Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffMTCM	0.0103435873	0.00365795	2.83	0.0051
DiffMTCM ²	-0.0016755210	0.00032725	-5.12	<0.0001
<i>Model $R^2 = 0.1361$, Root MSE = 0.3077, $n = 212$, Residual Mean = 0.0529</i>				
<i>(t-test for H_0: Residual Mean = 0 is $T_{0.005} = 2.60 > T = 2.50 > T_{0.025} = 1.97$)</i>				

(3) $\text{Ln}(\text{NDeviVOL20}) = f(\text{DiffDD0}, \text{DiffDD0}^2)$

Factor	Parameter Estimate	St. Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffDD0	-0.0002696064	0.00006080	-4.43	<0.0001
DiffDD0 ²	-0.0000004297	0.00000008	-5.21	<0.0001
<i>Model $R^2 = 0.2403$, Root MSE = 0.2796, $n = 173$, Residual Mean = 0.0455</i>				
<i>(t-test for H_0: Residual Mean = 0 is $T_{0.005} = 2.60 > T = 2.14 > T_{0.025} = 1.97$)</i>				

(4) $\text{Ln}(\text{NDeviVOL20}) = f(\text{DiffNFFD}, \text{DiffNFFD}^2)$

Factor	Parameter Estimate	St. Error of the Estimate	T for H_0 : Parameter = 0	Pr > T
DiffNFFD	0.0017662612	0.00038191	4.62	<0.0001
DiffNFFD ²	-0.0000181254	0.00000378	-4.79	<0.0001
<i>Model $R^2 = 0.1620$, Root MSE = 0.2937, $n = 173$, Residual Mean = 0.02779</i>				
<i>(t-test for H_0: Residual Mean = 0 is $T = 1.24 < T_{0.025} = 1.97$)</i>				

Of the four prediction models, the model based on DiffDD0 has the highest R^2 value (Table 4-1). This is in accordance with the previous results that, it is the difference in winter coldness ('harshness') between provenance origin and test site that contributed the most to the growth deviations of ecademic provenances from local source among all the thermal-climate differences (Table 3-2 in Chapt.3).

Using these prediction models, the volume responses to rapid climatic changes are quantified within the experimental span (see Table III-14 in Appendix III) and presented in Table 4-2, along with the standard errors of the mean predicted values. These predicted response show that the volume-gain from thermal-climatic changes alone was rather small when compared to that with both thermal-climatic changes and photoperiod changes considered (see Section 3.4.2., Chpat.3). For instance, in the previous prediction for DiffMAT, a 1.5°C difference of mean annual temperature between provenance origin and planting site was predicted to result in an average volume-gain of 11.2% over local source (Table 3-5 in Chapt.3), but now will only result in an average volume-gain of 2.3% when the effects of photoperiod change were eliminated (Table 4-2). However, the predictions made here are very likely to underestimate the growth response to thermal-climatic changes. As stated before, the effects of thermal-climatic changes are largely redundant on the effects of photoperiod change. The removal of photoperiod change effects also removed the effects of thermal-climatic changes to certain extent. Therefore, these predictions are considered biased. Nevertheless, unlike the predictions for the other Diff-variables, the predictions for DiffNFFD were almost unaffected by the adjustment of photoperiod change. For instance, in the previous prediction for DiffNFFD, a 50-day increase of annual number of frost free days (NFFD) was predicted to bring in an average of 4.9% volume-gain

(Table 3-5, Chapt. 3). Similar prediction was found that upon a 50-day increase of NFFD, a 4.4% volume-gain was predicted when the effects of photoperiod change were eliminated (Table 4-2). This indicates that the effects of changes in growing season length were almost not redundant on that of photoperiod changes (also see Section 3.4.3.), and thus, the prediction for DiffNFFD could be considered more reliable than for those temperature change variables.

The predicted ultimate volume-gain from thermal-climatic changes is 2.3%(±1.3%) on average that is associated with a 1.5°C increase in MAT, or 4.3%(±2.2%) with a 300-degree-day's decrease in DD0 which is the amount of winter coldness, or 4.4%(±1.9%) that is associated with a 50-day's increase in NFFD (table 4-2). The volume response to elevated winter temperature is predicted to be less pronounced, with just a 1.6%(±1.1%) volume-gain that could be expected from a 3°C increase in MTCM. These results seem suggesting that the advantage Sitka spruce could take from global warming (thermal effect only) is very limited. Instead, either rapid warming or 'cooling' trend is predicted to be more likely to bring in volume-loss rather than -gain in this species. Evidently this is because an increase in temperature affects growth positively only within the physiological and ecological tolerance limits of the species (Matyas 1994).

The ranges for Sitka spruce to buffer rapid thermal-climatic changes without suffering volume-loss are defined according to the mean predicted values (Table 4-2) as follows:

$$\begin{aligned}\text{DiffMAT} &= 0 \sim 3.0 \text{ }^{\circ}\text{C}, \\ \text{DiffMTCM} &= 0 \sim 6.0 \text{ }^{\circ}\text{C}, \\ \text{DiffDD0} &= -600 \sim 0 \text{ degree days},\end{aligned}$$

which is not far from the projections of global warming trend (Harrington 1987; CCPB 1991) for British Columbia region. That is, probably we do not have to worry about the impact of global

warming scenario on Sitka spruce at least in BC, neither can we expect big 'bonus' of stumpage increase of this species from elevated thermal-climate conditions *only*, if global warming does advent in the next century.

The present projections are similar to those of Beuker (1994), Matyas (1994), and Schmidting (1993) who all demonstrated that tree growth responses to thermal-climatic changes are quadratic, though the rates of growth-gain from elevated thermal-climatic conditions are different from case to case. The major difference between the current projections with Sitka spruce and other projections with other species is that, while the above mentioned authors predicted high growth response of other tree species to changes of annual temperature sum above 5 °C (i.e., the amount of warmth), I found that Sitka spruce did not respond significantly to changes in the amount of *warmth* ($p = 0.6367$, $R^2 = 0.0053$), but respond to changes in the amount of *coldness* significantly (e.g., with DD0, $p < 0.0001$ and $R^2 = 0.2403$, Table 4-1). The difference is mainly attributable to this species' unique coastal nature. Being a coastal species, Sitka spruce is highly sensitive to moisture, not temperature, conditions (Chapt.1). As long as a provenance of this species grows in an area without severe winter injury, its growth responds to moisture abundance rather than to the warmth of the area, and thus we can not detect the growth response to changes in warmth but to changes in coldness (e.g. DD0 and MTCM). This draws concerns on another bias source of the current projections that, the predictions did not take the changes in moisture conditions into account which should have more pronounced influence on the species, and which, according to the CCPB predictions, is likely to occur with a decrease of up to 10% summer precipitation in coastal BC areas by the middle of the next century (CCPB 1991).

Table 4-2. Predicted volume responses (NDevVOL20 (%)) from thermal-climatic changes between provenance origin and planting site in seed transfer of the provenance trials in the 20th year after planting.

DiffMAT (°C)	NDevVOL20 (%)	DiffMTCM (°C)	NDevVOL20 (%)	DiffDD0 (dd)	NDevVOL20 (%)	DiffNFFD (day)	NDevVOL20 (%)
-6.5	-44.4±6.52	-15	-41.3±5.51	800	-38.8±4.09	-120	-37.7±5.14
-6.0	-40.1±6.16	-14	-37.7±5.22	750	-35.8±3.88	-110	-33.9±4.76
-5.5	-35.9±5.74	-13	-34.1±4.91	700	-32.9±3.66	-100	-30.1±4.36
-5.0	-31.7±5.28	-12	-30.6±4.56	650	-30.0±3.43	-90	-26.3±3.93
-4.5	-27.5±4.77	-11	-27.1±4.20	600	-27.1±3.19	-80	-22.7±3.48
-4.0	-23.5±4.24	-10	-23.7±3.82	550	-24.3±2.95	-70	-19.1±3.02
-3.5	-19.5±3.68	-9	-20.5±3.43	500	-21.5±2.70	-60	-15.7±2.56
-3.0	-15.8±3.12	-8	-17.3±3.03	450	-18.8±2.44	-50	-12.5±2.10
-2.5	-12.4±2.55	-7	-14.3±2.64	400	-16.2±2.18	-40	-9.5±1.65
-2.0	-9.2±2.00	-6	-11.5±2.24	350	-13.7±1.92	-30	-6.7±1.22
-1.5	-6.3±1.46	-5	-8.9±1.85	300	-11.3±1.66	-20	-4.2±0.79
-1.0	-3.8±0.95	-4	-6.6±1.47	250	-9.0±1.40	-10	-1.9±0.39
-0.5	-1.7±0.46	-3	-4.5±1.10	200	-6.9±1.13	0	0.0±0.00
0.0	0.0±0.00	-2	-2.7±0.73	150	-4.9±0.86	10	1.6±0.38
0.5	1.2±0.45	-1	-1.2±0.36	100	-3.1±0.58	20	2.8±0.75
1.0	2.0±0.88	0	0.0±0.00	50	-1.4±0.30	30	3.7±1.12
1.5	2.3±1.32	1	0.9±0.37	0	0.0±0.00	40	4.3±1.50
2.0	2.2±1.78	2	1.4±0.75	-50	1.2±0.31	50	4.4±1.90
2.5	1.5±2.26	3	1.6±1.14	-100	2.3±0.64	60	4.2±2.32
3.0	0.4±2.76	4	1.5±1.56	-150	3.1±0.98	70	3.5±2.77
3.5	-1.2±3.31	5	1.0±1.99	-200	3.7±1.35	80	2.6±3.26
4.0	-3.2±3.88	6	0.2±2.45	-250	4.1±1.74	90	1.2±3.78
4.5	-5.6±4.49	7	-1.0±2.94	-300	4.3±2.15	100	-0.5±4.34
5.0	-8.3±5.12	8	-2.4±3.44	-350	4.3±2.58	110	-2.5±4.92
5.5	-11.4±5.76	9	-4.2±3.97	-400	4.0±3.04	120	-4.8±5.52
6.0	-14.8±6.41	10	-6.2±4.51	-450	3.5±3.51	130	-7.4±6.13
6.5	-18.5±7.04	11	-8.5±5.06	-500	2.8±4.01	140	-10.2±6.74
7.0	-22.3±7.64	12	-11.1±5.61	-550	1.8±4.52	150	-13.3±7.35
7.5	-26.4±8.21	13	-13.8±6.16	-600	0.7±5.04	160	-16.6±7.94
8.0	-30.5±8.72	14	-16.8±6.70	-650	-0.6±5.58	170	-20.0±8.51
8.5	-34.7±9.18	15	-19.9±7.22	-700	-2.2±6.12		
9.0	-38.9±9.57	16	-23.2±7.71	-750	-3.9±6.67		
		17	-26.5±8.17	-800	-5.8±7.21		
		18	-30.0±8.60	-850	-7.8±7.75		
		19	-33.5±8.97	-900	-10.0±8.28		
		20	-37.1±9.30	-950	-12.3±8.80		
		21	-40.6±9.58	-1000	-14.8±9.30		

4.3.2. Growth response to thermal-climatic change pertaining to site moisture condition

High volume growth response to moisture gradient was observed by plotting the provenance-by-site means for VOL20 of the 11 frequently tested provenances (see Appendix II for Chapt.1) to the amount of summer precipitation (i.e. SMSP) of the 11 test sites (Fig. 4-6). This plot indicate that VOL20 was much higher at SMSP > 600 mm level than at SMSP = 400 mm level. The mean for Ln(VOL20) at SMSP > 600 mm is around 4.7 (i.e., VOL20 = $\exp(4.7) \approx 110 \text{ dm}^3$) and that at SMSP \approx 400 mm is around 3.3 (i.e., VOL20 = $\exp(3.3) \approx 27 \text{ dm}^3$). That is, the increase of SMSP from 400 mm to 600 mm brought in about four times higher volume growth at year 20. The moisture response is so astonishing that it suggests reforestation with Sitka spruce should be applied to areas where at least 600 mm summer rainfall is available (also see Table 3-6, Chapt.3). However, at the four weevil attacked sites, there were no perceivable moisture trends in VOL20 (Fig. 4-6). This could possibly due to the fact that there were not enough weeviled sites to observe the moisture response trend at weeviled sites. The distribution pattern of weeviled sites versus unweeviled sites in relation to the amount of SMSP also suggests that, drier sites are more risky to weevil attack as compared to moister sites.

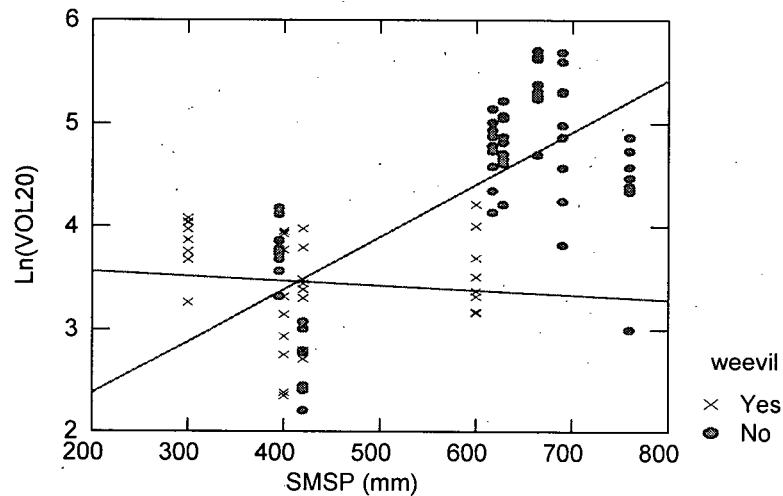


Fig. 4-6. Scatter plot of the provenance-by-site means for VOL20 (in logarithmic values) of 11 frequently tested provenances at the 11 test sites to the amount of site summer precipitation (SMSP).

Due to experimental constraints, namely, lack of sufficient and even number of provenances tested at a variety of moisture conditions, lack of fine moisture gradient for test sites within the experimental span, and significant weevil (*Pissodes strobi* (Peck)) damage occurred at four out of the 11 test sites (see Chapt. 2), I was unable to predict the growth response solely to moisture fluctuations in this study. However, the dependency of the volume response (to thermal-climatic changes) upon site moisture conditions can still be analyzed without high precision.

Followed the idea in Chapter Three, the net growth response (NDevVOL20) to thermal-climatic change (represented by DiffMAT only) was related to the number one site climatic factor (i.e., SMSP), using response surface analysis. The response surface model is set to the second polynomial and is highly significant ($p < 0.0001$) with a model R^2 of 0.147 (see Table V-1 in Appendix V). However, the partial F -test for SMSP shows that generally the effects of

SMSP were not significant ($p = 0.2552$). This seems ironical, but is largely due to the drastic weevil influence at four out of the 11 test sites that might suppressed the tree's moisture sensitivity. Nevertheless, the contour graph of this response surface (Fig. 4-7) can still serve the general discussion purpose of this section. This contour graph clearly shows the dependency of the volume response to the thermal-climatic change upon site moisture conditions. Changes in MAT could result in *positive* effect only when there was enough summer precipitation at the test site (i.e., SMSP > 500 mm). As SMSP increasing from 500 to 750 mm, there was an increase in volume-gain to temperature rise, in general. The predicted net volume-gains to DiffMAT that are conditional on SMSP gradient are listed in Table 4-3, derived from this contour graph. These predictive results show that the higher the summer precipitation a planting site has, the greater the volume-gain could be expected at that site from elevated thermal-climatic conditions, and the wider the range of global warming trend that is beneficial to the tree growth at that site. Surprisingly when comparing with the projections in previous section of this chapter, at maritime areas with a minimum SMSP of 700 mm, up to 20% volume-gain was projected from the rise of the mean annual temperature by 5 °C, approximately (Table 4-3).

However, one should be advised the descriptive rather than inferential nature of the above predictions, due to the limitations as stated before (Section 4.1. and 4.2.) and to the biases from the significant lack-of-fit error in this contour construction. Particularly, one should be aware of the limitation that the predictions made here did not take soil conditions into account. The amount of SMSP is not equal to the amount of available soil moisture, which is the actual affecting agent of moisture on volume production, and which is determined not only by precipitation, but also by soil properties, e.g., depth, texture, slope angle and position as well as

soil nutrition contents. Unfortunately, the available information for this study prevents more precise prediction to many environmental variations.

Table 4-3. Net expectable volume-gains to changes in mean annual temperature (DiffMAT) that are conditional upon site summer precipitation (SMSP).

Site major climatic factor	Net volume-gain to DiffMAT	
	DiffMAT (°C)	NDeviVOL20 (%)
500 ~ 650	0 ~ 4	0 ~ 4
650 ~ 700	-2 ~ 7	0 ~ 10
700 ~ 750	-1 ~ 0.5 or 5 ~ 6	10 ~ 20
700 ~ 750	0.5 ~ 5	≥ 20

Contour of NDeviVOL20 (%) with DiffMAT & SMSP

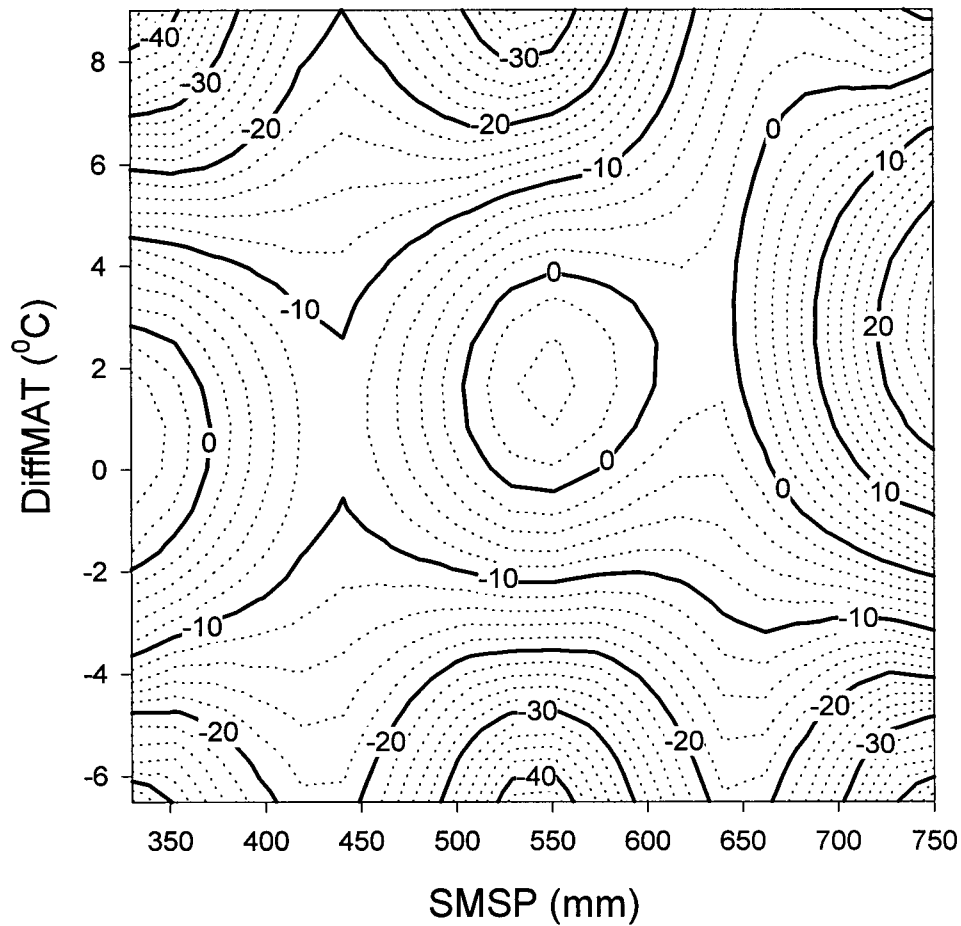


Fig. 4-7 Contour of the quadratically smoothed response surface of NDeviVOL20 (%) to changes in mean annual temperature (DiffMAT) over site summer precipitation (SMSP) gradient.

4.4. Conclusions

1. Quadratic volume growth responses were detected to rapid thermal-climatic changes when the effects of photoperiod changes were accounted for. Predictive models were set up separately

for the thermal-climatic change variables; namely, DiffMAT, DiffMTCM, DiffDD0 and DiffNFFD. The predictions were unbiased and with low precision because of the removal of photoperiod change which also removed the effects of thermal-climatic changes to certain extent due to the fact that, the former is highly correlated with the latter ones. Based on the predictive results, the advantage that Sitka spruce could take from global warming alone was not substantial. The ultimate volume-gain from thermal-climatic change was 2.3% on average that is associated with a 1.5°C increase in MAT, or 4.3% with a 300-degree-day's decrease in DD0 which is the amount of winter coldness. If global warming brings about 50-day's increase of frost free days per annum, a volume-gain of 4.4% would be expected. The volume response to elevated winter temperature is predicted to be less pronounced, to the maximum of only 1.6% volume-gain that could be expected from a 3°C increase of MTCM.

2. The study also suggests that volume growth of this species could respond more rapidly and linearly to changes in precipitation than to rapid thermal-climatic changes. High dependency of the volume response to thermal-climatic change upon site summer precipitation was found and analyzed. Results show that changes in MAT could result in positive effect only when there was enough summer precipitation at the planting site (i.e., SMSP > 500 mm). The higher the summer precipitation a planting site has, the greater the volume-gain could be expected at that site from elevated thermal-climatic conditions, and the wider the range for this species growing at that site to benefit from global warming scenario. At maritime areas with a minimum SMSP of 700 mm, up to 20% volume-gain was predicted from an increase of MAT by 5°C, approximately.

3. Despite of the many limitations of the predictions, provenance trials remained at present the only available mean of generating long-term growth data of a species grown in rapidly changed climate conditions under natural environments, and thus are a unique resource for simulating mature tree growth responses to rapid climate changes and evaluating the genetic and physiological flexibility of the species in buffering rapid climate changes.

4.5. References

- Beuker, E.** 1994. Long-term effects of temperature on the wood production of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. in old provenance experiments. *Scand. J. For. Res.* 9: 34~45.
- Beuker, E.** 1996. Implications of climate adaptability in provenance trials with Scots pine and Norway spruce in Finland for possible effects of climate warming. D.Sc.(Agr. And For.) thesis, Faculty of Forestry, University of Joensuu, Finland.
- Box, G.E.P., Draper, N.R.** 1987. *Empirical Model-Building and Response Surfaces*. John Wiley & Sons, Inc. New York.
- Cannell, M.G.R., Grace, J. and Booth, A.** 1989. Possible impacts of climatic warming on trees and forests in the United Kingdom: a review. *Forestry* 62: 337~364.
- Harrington, J.B.** 1987. Climatic changes: a review of causes. *Can. J. For. Res.*, 17: 1313~1339.
- Harding, L.E.** 1992. Atmospheric Changes in British Columbia. In: *Biodiversity in British Columbia*. (Chapt.24). BC Ministry of Environment, Lands, and Parks; BC Ministry of Forests. Pp 323~341.
- Illingworth, K.** 1978. Sitka spruce provenance trials three years after planting in British Columbia. In: Proceedings of IUFRO Joint Meeting of Working Parties, Douglas-fir, lodgepole pine, Sitka spruce and true firs. Vol.2. Pp. 311~326. 1978. Vancouver, Canada. B.C. Ministry of Forests.
- Kellomaki, S. and Kolstrom, M.** 1995. The influence of climate change on the productivity of Scots pine, Norway spruce, Pendula birch and Pubescent birch in southern and northern Finland. *For. Eco. And Manag.* 65: 201~217.
- Kendall, M.G. and Stuart, A.** 1967. *The Advanced Theory of Statistics: Vol2. Inference and Relationship*. (2nd ed). Hafner Publishing Company, New York.
- Koski, V.** 1989. Siemenssiirrot ja ilmaston sopeutuminen. *Metsantutkimuslaitoksen tiedonantaja*. 328: 20~37. (in Finnish)
- Kovats (1977).** Estimating juvenile tree volumes for provenance and progeny testing. *Can. J. For. Res.* 7: 335~342.
- Langlet, O.** 1971. Two hundred years of genecology. *Taxon*. 20: 653~722.

- Larsen, J.B.** 1991. Breeding for physiological adaptability in order to counteract an expected increase in environmental heterogeneity. *For. Tree Imp.* 23: 5~9.
- Ledig, F.T. and Kitzmiller, J.H.** 1992. Genetic strategies for reforestation in the face of global climate change. *For. Eco. And Man.* 50: 153~169.
- Matyas, C.** 1994. Modeling climate change effects with provenance test data. *Tree Physiol.* 14: 797~804.
- SAS Institute Inc.** 1990. SAS/STAT User's Guide, Version 6 (4th edition). Vol .1 (pp 943) & Vol. 2 (pp 846). Cary, NC, USA.
- Schmidtling, R.C.** 1994. Use of provenance tests to predict response to climate change: loblolly pine and Norway spruce. *Tree Physiol.* 14: 805~817.
- Schneider, S.H.**,1989. The greenhouse effect: science and policy. *Science.* 243:771~781.
- Skroppa, T. and Johnson, O.** 1994. The genetic response of plant populations to a changing environment: the case for non-Mendelian processes. In: Boyle, T.J.B. and Boyle, C.E.B. (eds) *Biodiversity, temperate ecosystems and global change.* Springer-Verlag, Berlin. pp 183~199.
- Ying, C.C.** 1991. *Genetic resistance to the white pine weevil in Sitka spruce.* Research Notes No. 106, Research Branch, Ministry of Forests B.C., Victoria, B.C., Canada.
- Ying, C.C.** 1997. Effects of site, provenance, and provenance and site interaction in Sitka spruce in coastal British Columbia. *Forest Genetics.* 4(2): 99~112.

RECOMMENDATIONS

1. Sitka spruce populations are differentiated by photoperiod and winter temperature regimes. Physiological studies are recommended to evaluate the photosynthesis capacity and cold hardiness of southern Sitka spruce provenances, and to screen for relatively cold resistant southern provenance(s) with high photosynthesis capacity for planting at coastal British Columbia.
2. Three provenances, i.e., Kitwanga, Hoquiam and Big Qualicum, deserve further studies on the mechanisms of induced weevil resistance and/or tolerance, and the genetic bases accounting for these properties.
3. To ensure high volume productivity, the planting of Sitka spruce should be restricted to low weevil-hazard areas with a minimum of 600mm summer precipitation.
4. Northward seed transfer is favored when planting this species in coastal BC. The warmer and moister the planting site is, the farther seed can be transferred. A transfer of 6 to 8° of latitude could be applied to most of the maritime favorable areas.

APPENDICES

Appendix I. Site mortality rates.

Table I-1. Mortality rate (%) of the trees over 20 years after planting at 12 sites of the three series of Sitka spruce provenance trials in BC,

Age	Series I					Series II				Series III			
	QCI	QCII	QCIII	QCIV	DL	HG	MN	NS	HB	JU	KT	RS	
Year3	1.57	3.74	2.36	4.55	---	0.12	6.54	3.95	0.00	1.48	0.00	0.00	
Year6	2.99	6.28	4.37	4.91	11.85	0.61	9.87	8.27	1.85	2.46	0.74	---	
Year10	3.09	7.32	4.72	5.25	---	0.74	11.85	11.97	8.02	3.70	0.86	0.01	
Year15	3.86	7.77	4.96	5.91	44.81	1.11	13.33	31.11	10.74	6.42	1.85	0.04	
Year20	3.88	7.99	5.14	6.26	51.73	1.24	14.69	31.98	11.85	10.00	2.71	0.04	

Appendix II. Examining site climatic sensitivity by the 11 frequently tested provenances.

Table II-1. R^2 of the forward regression ($\alpha=0.01$) of plot means of the 11 frequently tested provenances (from S to N) with site climate variables.

Prov. IUFR O	No.	PLAT	# sites	n	model R^2	HT6		HT10		HT15		HT20		VOL20	
						Ave.	Factors	R^2	Factors	R^2	Factors	R^2	Factors	R^2	Factors
	3012	45°49"	7	59	0.82		MAT MTWM	0.72 0.08	NFFD FFP	0.75 0.06	NFFD DD0	0.67 0.13	NFFD DD0	0.54 0.28	NFFD DD0
	3003	48°04"	7	58	0.77		MAP MTWM	0.65 0.12	NFFD FFP	0.64 0.08	NFFD DD0	0.54 0.27	MSP DD5 DD0	0.48 0.15 0.12	MSP MAT MAP
	3062	49°23"	11	78	0.57		NFFD FFP	0.61 0.09	MTCM DD0 MAT	0.45 0.11 0.10	MSP WV15	0.43 0.07	MSP DD0	0.47 0.08	MSP MTWM
	3061	49°50"	7	43	0.83		MAT MAP	0.81 0.07	MAT MAP	0.70 0.17	MAT MAP	0.59 0.26	MAT MAP	0.53 0.30	MTCM MAP DD0
	3056	50°37"	11	79	0.62		NFFD MTWM	0.55 0.13	NFFD FFP	0.48 0.14	MSP WV15	0.48 0.12	MSP WV20	0.46 0.17	MSP MTWM
	3049	53°30"	11	79	0.61		MAP MAT	0.53 0.14	MAP WV10	0.38 0.16	MSP WV15	0.39 0.21	MSP MTWM DD0	0.42 0.20 0.14	MSP MTWM
	3044	54°12"	11	78	0.58		MTCM MAT	0.48 0.12	MTCM MAT	0.35 0.21	MSP WV15	0.42 0.18	MSP MTWM	0.43 0.21	MSP MTWM
	3040	54°38"	8	56	0.79		MSP DD0	0.69 0.10	MSP FFP	0.46 0.20	MSP NFFD	0.72 0.11	MSP NFFD	0.79 0.10	MSP NFFD
	3032	55°10"	7	42			MAT MAP	0.51 0.25	MAT MAP	0.52 0.28	MAP NFFD	0.37 0.21	no trend		no trend

Prov. IUFR O	No.	PLAT	# sites	n	model R ²	HT6		HT10		HT15		HT20		VOL20	
						Ave.	Factors	R ²	Factors	R ²	Factors	R ²	Factors	R ²	Factors
3030	55°25"		8	56	0.76	MSP DD0	MSP	0.57	MAP	0.37	MSP	0.68	MSP	0.79	MSP
							DD0	0.17	MTWM	0.21	NFFD	0.10	NFFD	0.11	NFFD
3024	58°22"		8	56	0.70	MSP DD0	MSP	0.57	MAP	0.32	MSP	0.56	MSP	0.70	MSP
							DD0	0.18	MTWM	0.20	FFP	0.19	NFFD	0.15	NFFD

Appendix III. Supporting information for the response surface analyses in Chapter Three.

Table III-1. Technical report of the response surface analysis for variable DeviVOL20 with DiffLAT and SLAT (from SAS RSREG procedure).

Quadratic Response Surface for Variable DeviVOL20 with DiffLAT and SLAT

Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	9.248407	0.2797	45.460	0.0000
Quadratic	2	2.176159	0.0658	10.697	0.0000
Crossproduct	1	0.279667	0.0085	2.749	0.0988
Total Regress	5	11.704233	0.3540	23.013	0.0000
Residual	DF	SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	195	18.315903	0.093928	0.463	0.9911
Pure Error	15	3.045338	0.203023		
Total Error	210	21.361241	0.101720		
Factor	DF	SS	Mean Square	F-Ratio	Prob > F
DiffLAT	3	11.403337	3.801112	37.368	0.0000
SLAT	3	1.830416	0.610139	5.998	0.0006

Canonical Analysis of Response Surface (based on standardized data)

Eigenvalues	Eigenvectors	
	DiffLAT	SLAT
0.187604	0.208164	0.978094
-0.527740	0.978094	-0.208164

Table III-2. Technical report of the response surface analysis for variable DeviVOL20 with DiffMAT and SMAT (from SAS RSREG procedure).

Quadratic Response Surface for Variable DeviVOL20 with DiffMAT and SMAT

Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	11.009293	0.3437	60.016	0.0000
Quadratic	2	1.875821	0.0586	10.226	0.0001
Crossproduct	1	0.252602	0.0079	2.754	0.0985
Total Regress	5	13.137716	0.4101	28.647	0.0000
Residual	DF	SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	200	18.184086	0.090920	0.768	0.7422
Pure Error	6	0.710241	0.118374		
Total Error	206	18.894327	0.091720		
Factor	DF	SS	Mean Square	F-Ratio	Prob > F
DiffMAT	3	13.079519	4.359840	47.534	0.0000
SMAT	3	1.656048	0.552016	6.018	0.0006

Canonical Analysis of Response Surface (based on standardized data)

Eigenvalues	Eigenvectors	
	DiffMAT	SMAT
0.274555	0.311957	0.950096
-0.407817	0.950096	-0.311957

Table III-3. Technical report of the response surface analysis for variable DeviVOL20 with DiffMTCM and SMTCM (from SAS RSREG procedure).

Quadratic Response Surface for Variable DeviVOL20 with DiffMTCM and SMTCM

Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	10.695283	0.3339	55.657	0.0000
Quadratic	2	1.240033	0.0387	6.453	0.0019
Crossproduct	1	0.303758	0.0095	3.161	0.0769
Total Regress	5	12.239073	0.3821	25.476	0.0000
Residual	DF	SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	200	19.099996	0.095500	0.827	0.6971
Pure Error	6	0.692975	0.115496		
Total Error	206	19.792970	0.096082		
Factor	DF	SS	Mean Square	F-Ratio	Prob > F
SMTCM	3	1.381291	0.460430	4.792	0.0030
DiffMTCM	3	12.196499	4.065500	42.313	0.0000

Canonical Analysis of Response Surface(based on standardized data)

Eigenvalues	Eigenvectors	
	SMTCM	DiffMTCM
0.418391	0.894314	0.447440
-0.281142	-0.447440	0.894314

Table III-4. Technical report of the response surface analysis for variable DeviVOL20 with DiffDD0 and SDD0 (from SAS RSREG procedure).

Quadratic Response Surface for Variable DeviVOL20 with DiffDD0 and SDD0

Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	10.890052	0.4521	75.621	0.0000
Quadratic	2	0.931075	0.0387	6.465	0.0020
Crossproduct	1	0.243221	0.0101	3.378	0.0679
Total Regress	5	12.064348	0.5008	33.510	0.0000
Residual	DF	SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	161	11.359404	0.070555	0.636	0.8414
Pure Error	6	0.665326	0.110888		
Total Error	167	12.024730	0.072004		
Factor	DF	SS	Mean Square	F-Ratio	Prob > F
SDD0	3	0.304234	0.101411	1.408	0.2422
DiffDD0	3	11.462213	3.820738	53.063	0.0000

Canonical Analysis of Response Surface (based on standardized data)

Eigenvalues	Eigenvectors	
	SDD0	DiffDD0
0.371984	0.816891	0.576792
-0.222090	-0.576792	0.816891

Table III-5. Technical report of the response surface analysis for variable DeviVOL20 with DiffNFFD and SNFFD (from SAS RSREG procedure).

Quadratic Response Surface for Variable DeviVOL20 with DiffNFFD and SNFFD

Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	8.314372	0.3452	52.345	0.0000
Quadratic	2	2.248079	0.0933	14.153	0.0000
Crossproduct	1	0.263548	0.0109	3.318	0.0703
Total Regress	5	10.825999	0.4494	27.263	0.0000
Residual	DF	SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	161	12.473063	0.077472	0.588	0.8757
Pure Error	6	0.790016	0.131669		
Total Error	167	13.263078	0.079420		
Factor	DF	SS	Mean Square	F-Ratio	Prob > F
SNFFD	3	2.691800	0.897267	11.298	0.0000
DiffNFFD	3	10.587899	3.529300	44.439	0.0000

Canonical Analysis of Response Surface (based on standardized data)

Eigenvalues	Eigenvectors	
	SNFFD	DiffNFFD
0.193687	0.972673	-0.232180
-0.893776	0.232180	0.972673

Table III-6. Technical report of the response surface analysis for variable DeviVOL20 with DiffLAT and SMSP (from SAS RSREG procedure).

Quadratic Response Surface for Variable DeviVOL20 with DiffLAT and SMSP					
Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	8.394406	0.2539	39.842	0.0000
Quadratic	2	1.616696	0.0489	7.673	0.0006
Crossproduct	1	0.931924	0.0282	8.846	0.0033
Total Regress	5	10.943026	0.3310	20.776	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	195	19.077110	0.097831	0.482	0.9874
Pure Error	15	3.045338	0.203023		
Total Error	210	22.122448	0.105345		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
DiffLAT	3	10.845739	3.615246	34.318	0.0000
SMSP	3	1.069209	0.356403	3.383	0.0191

Canonical Analysis of Response Surface(based on standardized data)

Eigenvalues	Eigenvectors	
	DiffLAT	SMSP
0.092387	-0.242795	0.970078
-0.596366	0.970078	0.242795
Stationary point is a saddle point.		

Table III-7. Technical report of the response surface analysis for variable VOL20 with SLAT and PLAT (from SAS RSREG procedure).

<u>Quadratic Response Surface for Variable VOL20 with SLAT and PLAT</u>					
Regression	DF	Type I SS	R ²	F-Ratio	Prob > F
Linear	2	29438	0.0214	2.965	0.0537
Quadratic	2	276531	0.2009	27.854	0.0000
Crossproduct	1	3271	0.0024	0.659	0.4178
Total Regress	5	309240	0.2247	12.459	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	203	1052091	5182.715227	4.104	0.0043
Pure Error	12	15156	1262.994935		
Total Error	215	1067247	4963.940141		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
SLAT	3	234344	78115	15.736	0.0000
PLAT	3	76860	25620	5.161	0.0018

Canonical Analysis of the Response Surface(based on standardized data)

Factor	Critical Value	
	Coded	Uncoded
SLAT	-0.073844	52.238876
PLAT	-0.597312	45.726544
Predicted value at stationary point	170.610482 (maximum)	

Eigenvalues	Eigenvectors	
	SLAT	PLAT
-36.106074	0.107107	0.994248
-127.291792	0.994248	-0.107107

Table III-8. Technical report of the response surface analysis for variable VOL20 with SMAT and PMAT (from SAS RSREG procedure).

<u>Quadratic Response Surface for Variable VOL20 with SMAT and PMAT</u>					
Regression	DF	Type I SS	R ²	F-Ratio	Prob > F
Linear	2	348927	0.2609	38.505	0.0000
Quadratic	2	20467	0.0153	2.259	0.1070
Crossproduct	1	11817	0.0088	2.608	0.1078
Total Regress	5	381212	0.2851	16.827	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	207	954834	4612.722944	15.339	0.0079
Pure Error	4	1202.836194	300.709049		
Total Error	211	956036	4530.978605		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
SMAT	3	305654	101885	22.486	0.0000
PMAT	3	77126	25709	5.674	0.0009

Canonical Analysis of Response Surface(based on standardized data)

Factor	Critical Value	
	Coded	Uncoded
SMAT	-1.652955	1.106431
PMAT	-0.392365	5.316650
Predicted value at stationary point		18.648332 (saddle)

Eigenvalues	Eigenvectors	
	SMAT	PMAT
22.144357	0.972302	0.233728
-45.560396	-0.233728	0.972302

Table III-9. Technical report of the response surface analysis for variable VOL20 with SMTCM and PMTCM (from SAS RSREG procedure).

<u>Quadratic Response Surface for Variable VOL20 with SMTCM and PMTCM</u>					
Regression	DF	Type I SS	R ²	F-Ratio	Prob > F
Linear	2	393339	0.2941	54.010	0.0000
Quadratic	2	156064	0.1167	21.429	0.0000
Crossproduct	1	19514	0.0146	5.359	0.0216
Total Regress	5	568917	0.4254	31.247	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	207	767103	3705.810573	12.071	0.0124
Pure Error	4	1227.993637	306.998409		
Total Error	211	768331	3641.378115		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
SMTCM	3	512315	170772	46.898	0.0000
PMTCM	3	83185	27728	7.615	0.0001

Canonical Analysis of Response Surface (based on coded data)

Factor	Critical Value	
	Coded	Uncoded
SMTCM	-0.286072	-7.395667
PMTCM	-0.038074	-2.188353
Predicted value at stationary point		13.346541 (saddle)

Eigenvalues	Eigenvectors	
	SMTCM	PMTCM
.98.591957	0.981028	0.193866
-17.772827	-0.193866	0.981028

Table III-10. Technical report of the response surface analysis for variable VOL20 with SDD0 and PDD0 (from SAS RSREG procedure).

<u>Quadratic Response Surface for Variable VOL20 with SDD0 and PDD0</u>					
Regression	DF	Type I SS	R ²	F-Ratio	Prob > F
Linear	2	148938	0.1369	14.000	0.0000
Quadratic	2	41840	0.0385	3.933	0.0214
Crossproduct	1	8594.574916	0.0079	1.616	0.2055
Total Regress	5	199372	0.1833	7.496	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	163	887749	5446.314094	37.817	0.0014
Pure Error	4	576	144.017680		
Total Error	167	888325	5319.312982		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
SDD0	3	136295	45432	8.541	0.0000
PDD0	3	86791	28930	5.439	0.0014

Canonical Analysis of the Response Surface(based on standardized data)

Factor	Critical Value	
	Coded	Uncoded
SDD0	0.142067	613.312284
PDD0	0.265448	573.124331
Predicted value at stationary point	8.041711 (minimum)	

Eigenvalues	Eigenvectors	
	SDD0	PDD0
76.538187	0.975194	0.221352
7.025716	-0.221352	0.975194

Table III-11. Technical report of the response surface analysis for variable VOL20 with SNFFD and PNFFD (from SAS RSREG procedure).

Response Surface for Variable VOL20 with SNFFD and PNFFD					
Regression	DF	Type I SS	R ²	F-Ratio	Prob > F
Linear	2	392525	0.3609	50.099	0.0000
Quadratic	2	23871	0.0219	3.047	0.0502
Crossproduct	1	17081	0.0157	4.360	0.0383
Total Regress	5	433478	0.3985	22.130	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	163	652938	4005.754334	12.505	0.0116
Pure Error	4	1281.365267	320.341317		
Total Error	167	654219	3917.480968		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
SNFFD	3	362169	120723	30.817	0.0000
PNFFD	3	85274	28425	7.256	0.0001

Canonical Analysis of Response Surface (based on standardized data)

Factor	Critical Value	
	Coded	Uncoded
SNFFD	0.100569	240.654649
PNFFD	-2.252780	60.381715
Predicted value at stationary point		52.447748 (saddle)

Eigenvalues	Eigenvectors	
	SNFFD	PNFFD
58.229444	0.897021	0.441987
-5.303387	-0.441987	0.897021

Table III-12. Technical report of the response surface analysis for variable VOL20 with SMSP and PMSP (from SAS RSREG procedure).

<u>Quadratic Response Surface for Variable VOL20 with SMSP and PMSP</u>					
Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	526416	0.3937	69.446	0.0000
Quadratic	2	10980	0.0082	1.448	0.2373
Crossproduct	1	136.998974	0.0001	0.0361	0.8494
Total Regress	5	537532	0.4020	28.365	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	211	799716	3790.123683	inestimable	inestimable
Pure Error	0	0	inestimable	inestimable	
Total Error	211	799716	3790.123683		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
SMSP	3	529296	176432	46.550	0.0000
PMSP	3	10357	3452	0.911	0.4366

Canonical Analysis of Response Surface (based on standardized data)

Factor	Critical Value	
	Coded	Uncoded
SMSP	-4.426165	-488.017966
PMSP	0.022806	892.836840
Predicted value at stationary point		-98.885203

Eigenvalues	Eigenvectors	
	SMSP	PMSP
10.038501	0.999061	-0.043318
-24.905545	0.043318	0.999061
Stationary point is a saddle point.		

Table. III-13. Pearson Correlation coefficients between pairs of geoclimatic distance variables (i.e., Diff- variables).

	DiffLAT	DiffLONG	DiffLEV	DiffMAP	DiffMSP	DiffMAT	DiffMTCM	DiffMTWM	DiffNFFD	DiffFFP	DiffDDS	DiffDD0
DiffLONG	0.713											
	(0.000)											
DiffLEV	0.189	-0.054										
	(0.005)	(0.429)										
DiffMAP	-0.241	0.127	-0.451									
	(0.000)	(0.065)	(0.000)									
DiffMSP	0.204	0.431	-0.444	0.856								
	(0.003)	(0.000)	(0.000)	(0.000)								
DiffMAT	-0.795	-0.325	-0.629	0.505	0.198							
	(0.000)	(0.000)	(0.000)	(0.000)	(0.004)							
DiffMTCM	-0.672	-0.075	-0.619	0.585	0.334	0.926						
	(0.000)	(0.277)	(0.000)	(0.000)	(0.000)	(0.000)						
DiffMTWM	-0.450	-0.669	-0.360	-0.061	-0.235	0.426	0.129					
	(0.000)	(0.000)	(0.000)	(0.380)	(0.001)	(0.000)	(0.061)					
DiffNFFD	-0.634	-0.016	-0.643	0.600	0.523	0.866	0.922	0.127				
	(0.000)	(0.837)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.095)				
DiffFFP	-0.547	-0.097	-0.610	0.479	0.408	0.742	0.758	0.257	0.847			
	(0.000)	(0.204)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.001)	(0.000)			
DiffDDS	-0.813	-0.585	-0.241	0.315	-0.020	0.674	0.487	0.621	0.499	0.442		
	(0.000)	(0.000)	(0.001)	(0.000)	(0.790)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)		
DiffDD0	0.669	-0.080	0.529	-0.641	-0.438	-0.854	-0.936	-0.001	-0.827	-0.670	-0.510	
	(0.000)	(0.297)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.987)	(0.000)	(0.000)	(0.000)	
DiffDAY	0.996	0.705	0.191	-0.250	0.197	-0.796	-0.677	-0.451	-0.655	-0.561	-0.814	0.693
	(0.000)	(0.000)	(0.005)	(0.000)	(0.004)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)	(0.000)

1. The value inside the brackets is the probability of the above correlation coefficient being not significantly different from zero.

Table III-14. Geoclimatic distance ranges of the seed transfer used in the three series of Stika spruce provenance trials in BC, i.e., the experimental span.

Geoclimatic distance	Range used
DiffLAT	-12.5 ~ 9.0 °N
DiffLONG	-10.5 ~ 11.5 °N
DiffELEV	-557 ~ 627 m
DiffMAT	-6.5 ~ 9.0 °C
DiffMTCM	-15 ~ 21.5 °C
DiffMTWM	-4.4 ~ 6.3 °C
DiffMAP	-3200 ~ 3020 mm
DiffMSP	-555 ~ 1155 mm
DiffNFFD	-122 ~ 162 day
DiffFFP	-104 ~ 153 day
DiffDD5	-695 ~ 860 degree day
DiffDD0	-1032 ~ 810 degree day
DiffDAY	-208 ~ 213 hour

Appendix IV. Scatter plots for the differences in growth response to geoclimatic distances of seed transfer between wet and less-wet sites.

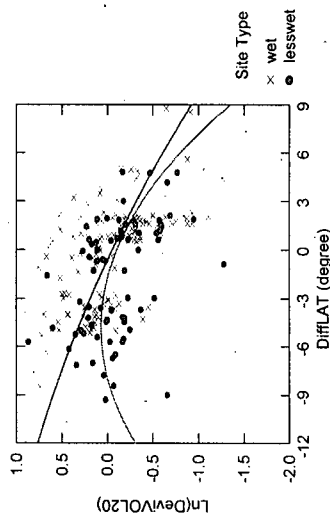


Fig. IV-1. Scatter plot of DeviVOL20 (in logarithmic value) versus DiffLAT ($^{\circ}$ N) and the quadratic smoothers for wet site and less-wet sites.

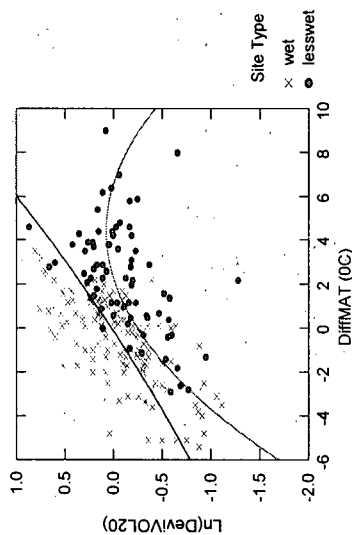


Fig. IV-2. Scatter plot of DeviVOL20 (in logarithmic value) versus DiffMAT ($^{\circ}$ C) and the quadratic smoothers for wet site and less-wet sites.

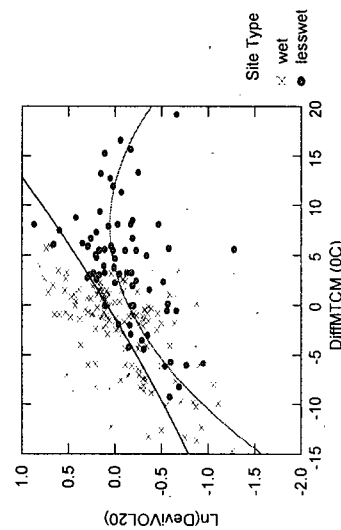


Fig. IV-3. Scatter plot of DeviVOL20 (in logarithmic value) versus DiffMTCM ($^{\circ}$ C) and the quadratic smoothers for wet site and less-wet sites.

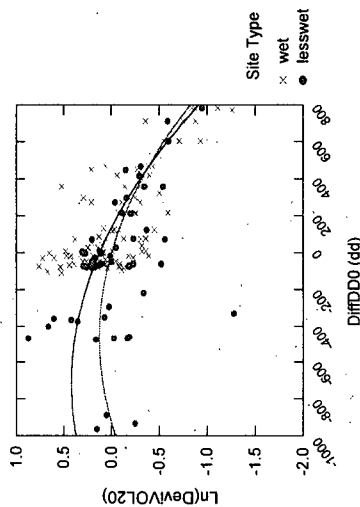


Fig. IV-4. Scatter plot of DeviVOL20 (in logarithmic value) versus DiffDD0 (degree days) and the quadratic smoothers for wet site and less-wet sites.

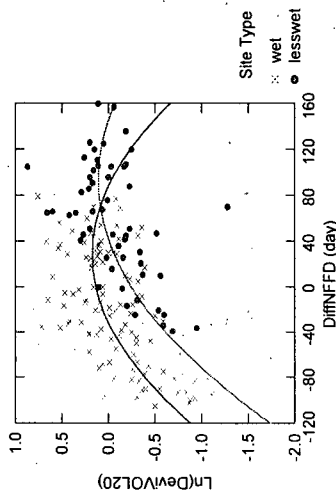


Fig. IV-5. Scatter plot of DeviVOL20 (in logarithmic value) versus DiffNFFD (day) and the quadratic smoothers for wet site and less-wet sites.

Appendix V. Technical report on the response surface analyses in Chapter Four.

Table V-1. Technical report of the response surface analysis for variable NDeviVOL20 (in logarithmic value) with DiffMAT and SMSP (from SAS RSREG procedure).

Response Surface for Variable DAYRESID with DiffMAT and SMSP					
Regression	DF	Type I SS	R-Square	F-Ratio	Prob > F
Linear	2	0.857834	0.0373	4.503	0.0122
Quadratic	2	2.382519	0.1036	12.506	0.0000
Crossproduct	1	0.140493	0.0061	1.475	0.2260
Total Regress	5	3.380846	0.1470	7.099	0.0000
Residual	DF	Type I SS	Mean Square	F-Ratio	Prob > F
Lack of Fit	200	18.915283	0.094576	0.803	0.7156
Pure Error	6	0.707023	0.117837		
Total Error	206	19.622306	0.095254		
Factor	DF	Type I SS	Mean Square	F-Ratio	Prob > F
SMSP	3	0.389467	0.129822	1.363	0.2552
DiffMAT	3	3.219888	1.073296	11.268	0.0000

Canonical Analysis of Response Surface(based on standardized data)

Factor	Critical Value	
	Coded	Uncoded
SMSP	-0.352715	448.875629
DiffMAT	0.049586	1.157019
Predicted value at stationary point		0.025981

Eigenvalues	Eigenvectors	
	SMSP	DiffMAT
0.122577	0.989862	0.142034
-0.522631	-0.142034	0.989862

Stationary point is a saddle point.