

THE GROWTH OF *ABIES AMABILIS* (DOUGL. EX FORBES) IN  
RELATION TO CLIMATE AND SOILS IN SOUTHWESTERN  
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by

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## Abstract

The coastal high-elevation forest has been increasingly used as a timber resource, despite uncertainties about the growth performance of second-growth stands. To provide comprehensive and coherent information on productivity and on the factors that constrain growth of mature trees, I studied the growth of amabilis fir (*Abies amabilis*) across the native range of the species in southern coastal British Columbia in five relatively independent studies.

I developed conventional polymorphic and climate-specific height growth and site index models for amabilis fir from stem analysis data obtained from 67 study plots, which were deliberately chosen to represent the largest variation in climate and soil conditions across the study area. When tested against an independent data set consisting of 31 plots, the climate-specific models improved height and site index predictions compared to the conventional polymorphic models. The previously available model for amabilis fir was biased. Thus, the models developed in this study are recommended for height and site index estimation of amabilis fir stands within a range of breast-height age from 15 to 160 years in southern coastal British Columbia.

To quantify the gradient of plant available nutrients on high-elevation sites, samples were collected of forest floor and mineral soil (0 to 30 cm) from montane and subalpine sites across a continentality gradient. Using discriminant analysis 70% agreement was found between field-identified SNRs and the classification based on measured (chemical) soil properties. Nitrogen-related variables (total N, mineralizable-N, and C:N ratio) and the sum of extractable Ca, Mg, and K were the properties most strongly related to the field-identified SNRs. These findings agree with the results of previous studies suggesting that mineralizable-N of the mineral soil is the best property for a quantitative characterization of a soil nutrient gradient.

A dendroecological approach was used to identify climatic factors that limit radial growth of amabilis fir at high-elevation sites in the study area. I developed 11 residual ring-width chronologies and 3 residual maximum density chronologies from stands on intermediate sites located along a continentality gradient. According to principal components, correlation, and pointer-year analyses, three types of growth responses to year-to-year variations in climate were associated with a strong regional ring-width pattern: i) a negative response to April 1<sup>st</sup>

snow depth, ii) a positive response to July temperature of the current year, and iii) a negative response to summer temperature of the previous year. A strong positive radial growth response to winter temperature was observed only in subarctic and subcontinental strata but not in the maritime strata, indicating that harsh winter conditions in a subcontinental climate appear to limit radial growth of *amabilis* fir near the easternmost limits of its distribution.

To determine the influence of elevation, continentality of climate, soil, and seasonal weather patterns on 9 tree-ring properties, I utilized dbh-discs from three dominant trees sampled at 62 stem analysis plots (Studies 1 and 5). I correlated (i) 30-year plot-averages of tree-ring properties with site factors and (ii) chronologies for 9 tree-ring properties for each of 8 site groups (combination of two continentality strata, two orographic strata, and two soil strata) with series of monthly climate data. The widths of earlywood and latewood as well as total ring width decreased significantly with increasing elevation. Width of earlywood and total ring width showed a significant decrease on nutrient-deficient sites, while percent latewood and ring density increased. Ring width, latewood width, and maximum density were reduced by a delayed start of the growing season and by low summer temperature in montane and subalpine. Moreover, the response to these two climatic factors was stronger on subalpine sites. Due to the differential responses, width of earlywood and latewood, and maximum density are recommended for studying tree growth responses to weather patterns.

To provide quantitative information about the influence of the environment on *amabilis* fir growth, I examined relationships between continentality strata, orographic strata, elevation, soil moisture regime, and soil nutrient regime with site index and the diameter at breast height (1.3 m) at 30 years (D30). Stem analysis data provided site index and D30 from 98 stands across the study area (see Study 1). The study area was delineated into 3 continentality strata – maritime windward, maritime leeward, subarctic/subcontinental. On zonal sites, site index decreased by 1.9 m every 100m increase in elevation in the maritime windward stratum, by 2.7 m in the maritime leeward stratum, and by 0.8 m in the subarctic/subcontinental stratum. The influence of soil moisture regime and soil nutrient regime was significant for site index and D30. Two predictive models for site index were presented, one climate model ( $R^2 = 0.75$ ) and one model using elevation, continentality, and the variable SOIL ( $R^2 = 0.83$ ). Both models were unbiased when tested against independent data. Precision was relatively low for both models restricting their application to the forest level rather than to the stand level.



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## Preface

This thesis was designed as a series of 5 studies. Two chapters (Studies 1 and 2) have already been published. Study 1 (chapter 2) was published as an article in BC Journal of Ecosystems Management: Splechtna, B.E. 2001. Height growth and site index models for Pacific silver fir in southwestern British Columbia. British Columbia Journal of Ecosystems and Management, 1: 1-14. <http://www.siferp.org/jem/2000/vol1/no1/art5.pdf>. Study 2 (chapter 3) was published jointly with my supervisor, Dr. Karel Klinka, in Geoderma: Splechtna, B.E. and Klinka, K., 2001. Quantitative characterization of nutrient regimes of high-elevation forest soils in the southern coastal region of British Columbia, Canada. Geoderma, 102: 141-162. For this article, data analysis and writing were done by myself with Dr. Klinka reviewing earlier versions of the manuscript.

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# 1. General Introduction

## 1.1 Background, Rationale, and Questions

In southern coastal British Columbia most easily accessible low-elevation old growth stands have been harvested during the last century. Most existing second-growth stands have not yet reached rotation age. As a result, there is a shortage of easily accessible low-elevation timber. To bridge this gap in timber supply, the high-elevation coastal forest has been used as a timber resource since the 1960's. While some of the high-elevation old-growth stands have accumulated large volumes over the centuries, little is known about the productivity and wood quality that can be expected from second-growth stands. This information is essential to rational decision-making in forest management, e.g., to adjust annual allowable cuts (AAC) for the decrease in productivity with increasing elevation. Otherwise, as it is the practice now, inclusion of high-elevation stands in AAC scenarios together with low-elevation stands will lead to liquidation of these stands (Klinka and Chourmouzis 2001).

In recent years logging using the clear-cut method continues in yet higher elevations despite concerns and uncertainties on (i) the effects of disturbance, (ii) potential productivity of crop tree species, (iii) the feasibility of managing the forest for timber production, and (iv) the most appropriate methods for cutting and regenerating the forest (Klinka *et al.* 1992, Brett 1997). Much of these concerns and uncertainties can be attributed to poor understanding of how vegetation patterns and tree growth varies with site quality, and factors related to local and regional climate (continentality, elevation, aspect, snow depth) in particular. This study is part of a recent effort to provide information on these vegetation – environment relationships (Brett 1997, Klinka and Chourmouzis 2001). While Brett (1997) concentrated on regeneration ecology and patterns or effects of disturbance, this study focussed on the growth of mature trees. My goal was (i) to advance the understanding of the factors controlling high-elevation tree growth in the Pacific Northwest and to provide (ii) tools for estimating forest productivity, and (iii) basic information for resolving the question of the feasibility of timber production on high-elevation coastal sites. On one hand this study complements site quality – site productivity studies, on the other hand a detailed dendroecological analysis helps to identify growth-limiting climatic factors for mature trees.

Climate is a major determinant of vegetation patterns and growth of plants at a regional and local scale. In many temperate regions of the world tree growth at low elevations is limited by moisture supply (and thus precipitation), while at high elevations tree growth is generally limited by temperature (Fritts 1976, Schweingruber *et al.* 1979). In the high-elevation forest of southwestern BC, tree growth has been shown to be limited mainly by cool summer temperatures and a short growing season (e.g., Brooke *et al.* 1970). At low elevations climate is very favourable for tree growth and assumed to be non-limiting. Although precipitation is plentiful, dry spells do occur in July and August in southwestern BC and may also limit tree growth.

This study consists of five interrelated studies answering several specific questions about site quality and the growth of amabilis fir (*Abies amabilis* (Dougl. ex Loud. Forbes)). This species was chosen, because it is a major timber species in the coastal high-elevation forest but occurs also at low elevations and therefore has a large elevation range. I was interested in answering the following main questions:

- 1) How do climate changes associated with the elevation and continentality gradients influence growth of amabilis fir? Which climate factors constrain amabilis fir growth?
- 2) How do soil moisture and soil nutrient regimes influence growth of amabilis fir?
- 3) What wood quality and productivity can be expected from second growth stands in the coastal high-elevation forest? Can productivity of amabilis fir stands be predicted from synoptic variables?

To address above questions, I took two different approaches: (i) an examination of the relationships between averaged growth of dominant trees (growth indices) and measures of soil moisture regime, soil nutrient regime, and climate and (ii) a dendroecological approach. The use of direct climatic information was hindered by a nearly complete absence of climatic stations in high elevations. Similarly, direct measures of plant-available soil nutrients and soil moisture regime are difficult to obtain. Thus, I used indirect measures of climate and indirect, synoptic measures of soil moisture regime and soil nutrient regime to explain variation in height and diameter growth (Study 5). Indirect measures of climate included elevation, slope, aspect, orographic strata, continentality strata, biogeoclimatic subzone or variant (Krajina 1965, Pojar *et*

*al.* 1987). I used field-identified soil moisture and soil nutrient regimes, which are based on soil morphological properties augmented by identification of indicator species (Green and Klinka 1994).

The study of the productivity – site relationship was complemented by the calibration of polymorphic height growth and site index functions (Study 1), an evaluation of the field-identified soil nutrient regimes using directly measured soil nutrient contents (Study 2), a dendroecological identification of limiting climate factors by relating time series of climate data to time series of indexed ring width and other tree-ring properties (Studies 3 and 4), and an investigation of the variation in tree ring properties with elevation and soil conditions (Study 4).

An exploration of height growth patterns using stem analysis data and the calibration and testing of polymorphic height growth and site index functions provide new productivity information for amabilis fir stands growing in maritime and subarctic/subcontinental continentality strata (Study 1). The use of height and age data is commonly viewed as the most accurate approach for site index (potential productivity) estimation (e.g., Assmann 1970) and thus provides (in the context of question 3) a baseline model against which I compared results from site index estimation using synoptic variables (Study 5).

Study 2 deals with soil fertility assessment and provides a quantification of field-identified soil nutrient regimes. Soil nutrient regimes (SNRs) are commonly estimated in the field from easily observable soil morphological properties and indicator plants (Ellenberg 1974, 1978, Pojar *et al.* 1987, Klinka *et al.* 1989, Green and Klinka 1994). However, the indirect and subjective nature of identifying SNRs in the field calls for quantification of SNRs using directly measured soil nutrient properties. This study was designed to investigate reliability of field-estimated SNRs in relation to measured soil nutrient properties as well as site index of amabilis fir.

Previous productivity studies using indirect measures of climate (i.e. subzone or elevation) did not attempt to identify climate factors that were associated with these indirect measures. In Studies 3 and 4, I used a dendroecological approach to answer the question of which climatic factors are limiting amabilis fir growth along elevation and continentality gradients. This study represents the first in-depth analysis of tree-ring patterns of amabilis fir and the first study in coastal British Columbia that attempted to include samples from low elevations (submontane and montane). The dendroecological approach I used is based on relating the yearly variations of ring width and other properties to yearly variations in monthly

and seasonalized climate data from existing climate stations. If data are sampled from trees growing along ecological gradients (e.g. elevation and continentality), limiting factors that are associated with these gradients can be identified.

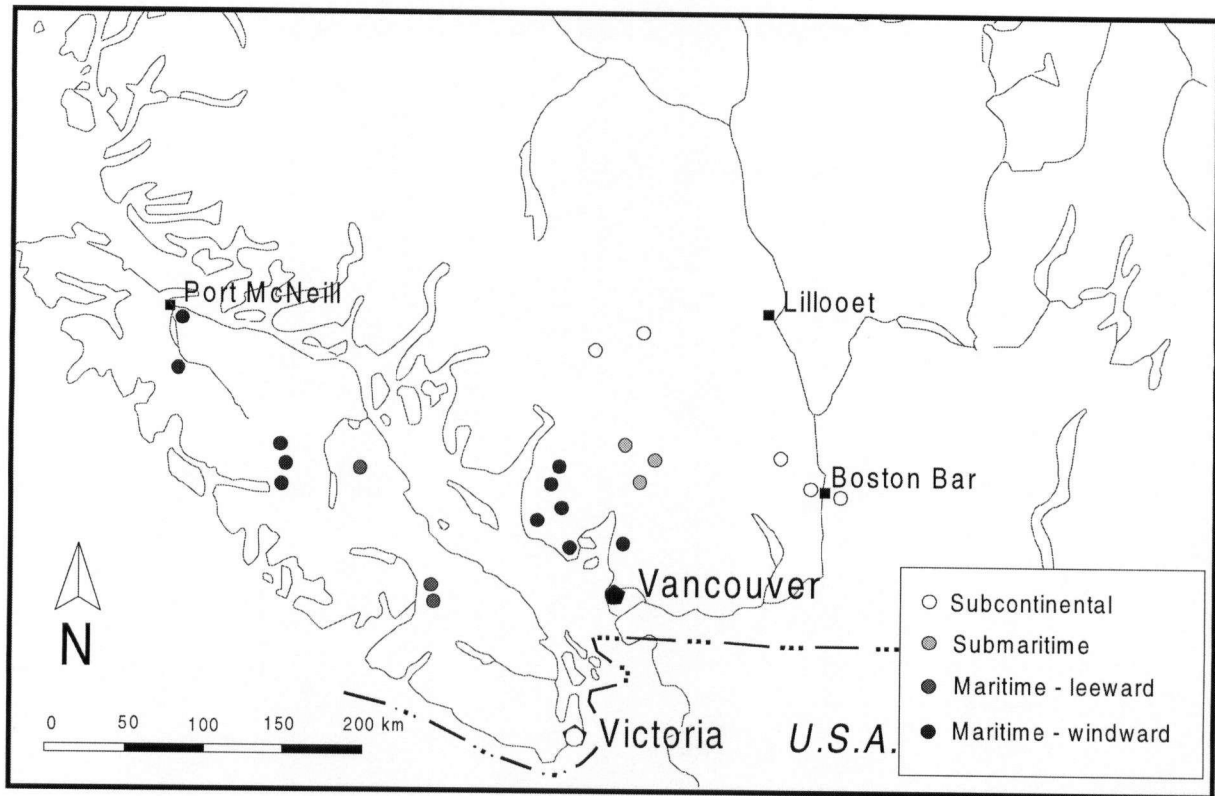


Figure 1.1 Continentality strata in the study area and general locations of study plots (dots represent locations of more than one plot). Native range of amabilis fir given in Klinka *et al.* 2001.

## 1.2 Study Area and Species

The study area was restricted to the southern portion of the coastal forest south of the Port McNeill–Lillooett line ( $50^{\circ}30'N$ ) and west of Boston Bar ( $121^{\circ}20'W$ ), and included the entire native range of amabilis fir in southwestern British Columbia (Figure 1.1). In this area, the native range of amabilis fir is confined to the Insular Mountains on Vancouver Island and the Coast Mountains on the mainland (Klinka *et al.* 2001), both of which extend in north-south direction. Together with patterns in atmospheric pressure that create mainly onshore (westerly) winds, these mountain ranges contribute to a relatively steep continental gradient (i.e., temperature differences between July and January increases from west to east) (Klinka *et al.* 1989, 2000). From May to September the weather is usually influenced by a high-pressure

system near the coast that creates relatively dry and cool, yet typically sunny summers. The Aleutian Low weather system dominates the remainder of the year and a series of storms provide heavy cloud cover and increased precipitation. Annual precipitation at high elevations can reach up to 5000 mm. Between October and March precipitation is typically as snow above elevations of 600 to 900 m. Thus heavy snow packs tend to accumulate in high-elevation coastal forests. While there is the possibility of snowfall in any month of the year, warm fronts in winter regularly bring rain to the mountaintops. Snow in the Insular and Coast Mountains is usually wet and does not melt completely until after end of June on high elevation sites, which results in a short growing season (Brooke *et al.* 1970). Because of the rain-shadow and orographic effects in the mountains, precipitation varies over short distances across the region, but is generally lower on the leeward side of the mountains, thus following the thermic continentality gradient.

Owing to the generally high precipitation and the cool to cold climate throughout the study area, the main soil processes include accumulation of acidic organic matter, leaching, eluviation, illuviation, and gleying; in consequence, the dominant soils are Podzols and Folisols. In lower elevations many Podzols lack an eluvial horizon, probably because the heavy leaching is offset by the rapid addition of organic colloids (Pojar *et al.* 1991). Folisols – defined by an organic layer thicker than 40 cm – occur, when decomposition of organic material is extremely slow due to cold and wet conditions in higher-elevations or wetter subzones (Brooke *et al.* 1970, Pojar *et al.* 1991).

Amabilis fir is a major component of the wetter subzones of the Coastal Western Hemlock (CWH) and Mountain Hemlock (MH) biogeoclimatic (BEC) zones (Krajina 1969, Klinka *et al.* 1991, Nuzsdorfer and Boettger 1994). The differences in climate associated with the elevation and continentality gradient are reflected in the composition of vegetation. In the CWH zone, amabilis fir is typically associated with western hemlock (*Tsuga heterophylla* (Raf.) Sarg), western redcedar (*Tuja plicata* (Donn. ex D. Don) Spach), and less frequently Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The transition from the CWH zone to the MH (along the elevation gradient) is indicated by the successive replacement of western hemlock by mountain hemlock (*Tsuga mertensiana* (Bong.) Carr), and Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) replaces western redcedar. In the MH zone, amabilis fir often forms stands with mountain hemlock or Alaska yellow-cedar or both. Pure old-growth stands of amabilis fir are not very common, but do occur. Of the lesser vegetation, *Hylocomium splendens* and *Rhytiadelphus loreus* are diagnostic species for the CWH zone, whereas

abundance of *Vaccinium ovalifolium*, *Rubus pedatus*, and *Coptis aspleniifolia* differentiates the MH zone from the CWH (Klinka *et al.* 1991). Towards more continental climates, occurrence and abundance of *Clintonia ubiflora*, *Orhtilia secunda*, and *Pleurozium schreberi* increase. In the subcontinental areas amabilis fir and Alaska yellow-cedar reach their distribution limits and occur in the moist and warm subzone of the Engelmann spruce – subalpine fir (ESSF) zone together with mountain hemlock and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt). The latter species replaces amabilis fir at the upper timberline in these areas.

Amabilis fir is one of the few species with a wide elevation range, as it occurs from sea-level to the upper timberline. In terms of continentality, the range of this species extends from (hyper)maritime sites to subcontinental sites (Klinka *et al.* 2001). Its elevation range narrows with increasing continentality, as the eastern distribution limit on subcontinental sites occurs only above 800 m and does not reach the timberline. Amabilis fir is probably the most water-demanding evergreen tree species in British Columbia (Krajina 1969, Klinka *et al.* 2001). It does not grow in continental climates because it is susceptible to frost (Klinka *et al.* 2001) and it does not tolerate frozen soil (coastal soils are commonly protected from freezing by a high snowpack) (Brooke *et al.* 1970). Amabilis fir is one of the most shade tolerant tree species and thus advanced regeneration of amabilis fir is a major component of the shrub-layer of old-growth stands. After disturbances, amabilis fir appears to be recruited mainly from the pool of advanced regeneration (Lertzman 1991, Brett 1997).

### **1.3 Sample Plots**

Study stands were located in four continentality strata following the BEC system (Krajina 1965, Pojar *et al.* 1987) given in Klinka *et al.* (1989). However, in addition to subcontinental (SC), submaritime (SM), and maritime (M) strata, a fourth stratum (maritime leeward: ML) was defined. Located on the leeward side of the Insular Mountains, the ML stratum is characterized by warmer and drier summers than the other maritime areas (Figure 1.1). Consequently, the maritime (M) stratum was designated as the maritime-windward (MW) stratum.

All study stands were naturally regenerated, unmanaged, fully stocked, relatively even-aged, and did not have a history of damage. They were distributed over a wide range of climatic conditions (measured by continentality stratum, elevation, and aspect) and soil moisture and nutrient conditions. The selected stands had an unknown, but obvious, history of stand-initiating

disturbance by fire, wind, avalanche, or less frequently by timber harvesting. I assumed that the selected stands had grown under full light conditions except in the earliest stages, when competing vegetation or deep snow cover might have influenced tree growth. Many candidate stands were rejected from the sample base because increment cores taken at breast height from dominant trees suggested suppression beyond breast height age. Despite these difficulties, 124 sample plots were established within the stands (see Appendix I for site descriptions).

After randomly locating a sample plot of 0.04 ha in each selected stand, soil moisture regime (SMR) and soil nutrient regime (SNR) were estimated using a combination of topographic and soil morphological properties, as well as understory vegetation (Green and Klinka 1994). Elevation was measured using a Thommen pocket altimeter, slope using a clinometer, and aspect using a compass. In each sample plot, the three largest diameter amabilis fir trees without observable damage were felled. Total height and length of the live crown were measured for each sample tree. Stem discs were cut at 30, 80, 130 cm above the ground, and then equally spaced discs at 100-cm intervals were taken to the top of each tree. Discs were transported to the laboratory for further analysis.

## 2. Height Growth and Site Index Models (Study 1)

### 2.1 Introduction

Accurate estimates of forest productivity are needed for sustainable forest management in order to determine annual allowable cut and rotation periods, and to make tree species selection decisions. As harvesting progresses increasingly into high-elevation forests, growth and yield information for these forests is urgently needed to accommodate forestry decision making.

Despite climatically unfavorable conditions, high timber volumes have accumulated in the high-elevation old-growth coastal forest of British Columbia over several centuries. However, the time needed to produce economically feasible and ecologically sustainable second-growth timber crops is unknown. Existing growth and yield information for these forests is limited to investigations of early growth performance (Arnott *et al.* 1995) or to different geographic areas (Hoyer and Herman 1989, Murray *et al.* 1991).

Notwithstanding recognized limitations (e.g., Monserud 1984a), site index (top height at reference age 50 years at breast height) is the most commonly used index of forest productivity in North America. Together with height growth models, it is widely used in models designed to estimate forest- and stand-levels yields in even-aged stands (e.g., Mitchell 1975, Wykoff and Monserud 1987, Pretzsch 1994, Sterba 1995). Accurate estimates for site index and height depend on how well the models estimate the height growth pattern (i.e., the trajectory of height over age) of the top-height trees of a stand. However, height growth patterns vary with site (e.g., Carmean 1956, 1972, Assmann 1970, Beck 1971, Marschall 1976).

To account for differences in height growth pattern with site, height growth is commonly modelled by polymorphic functions. These functions allow different shapes of height growth curves for each site index (e.g., Curtis 1964, Heger 1968, Beck 1971, Carmean 1972, Curtis *et al.* 1974a, Alemdag 1991, Thrower and Goudie 1992, Chen *et al.* 1998a). This approach assumes that the same height growth pattern will be followed regardless of which factors lead to a certain level of height growth (site index class). However, some studies found different height growth patterns for the same site-index class of the same tree species (e.g., Monserud 1984b, Klinka *et al.* 1996). Hence, site factors were incorporated into polymorphic models to make them site-specific (e.g., Monserud 1984b, Milner 1988). Such site-specific models showed



increased precision compared to conventional polymorphic models (Monserud 1984b, Van der Ploeg and Moore 1989), and indicated that height growth patterns varied with climate, soils, or genetics (Monserud 1984b, Monserud and Rehfeldt 1990, Wang *et al.* 1994a). In contrast, some authors concluded that conventional polymorphic curves described height growth patterns sufficiently well (e.g., Beck 1971, Carmean 1972, Alemdag 1991). Therefore, a decision on whether or not to develop and use site-specific curves must be based on:

- the observed differences in height growth pattern,
- the improved performance of site-specific models compared to conventional polymorphic models, and
- the desired level of precision.

Amabilis fir is a major component of the high-elevation coastal forests together with mountain hemlock and yellow-cedar. In contrast to the latter two species, amabilis fir also occurs on low-elevation sites. The height growth curves that have been used in British Columbia for both height and site index estimation of Amabilis fir were developed from low-elevation data (191 sectioned trees) on Vancouver Island (Kurucz 1982). Since the height growth pattern may be significantly different between low- and high-elevation sites, the validity of these curves for low site-index classes (15 and below) is uncertain. The only existing curves developed for high-elevation sites are from a different (warmer) climatic region in the Washington and Oregon Cascades, and are based on data from only 40 sectioned trees (Hoyer and Herman 1989). Considering the small sample size, it is uncertain whether the data reflected the “true” variability of amabilis fir height growth pattern. Moreover, the validity of these curves for British Columbia is questionable as many studies have shown that the transferability of curves of the same species from one region to another is limited (e.g., Marschall 1976, Monserud 1985, Thrower and Goudie 1992, Chen *et al.* 1998a).

The objectives of this study were to develop accurate height growth and site index models for amabilis fir in coastal southern British Columbia and to evaluate the improvement of height and site index estimates over the currently used model. To achieve these objectives, I:

- examined the changes in height growth pattern with soil and climate,
- developed conventional polymorphic models and site-specific models according to exploratory height growth pattern analysis, and
- compared performance of site-specific models to conventional polymorphic models and the currently used model using a set of independent data.

## 2.2 Material and Methods

Stem discs from 2 or 3 trees from each of the 124 plots (Appendix 1) were brought to the laboratory and rings were counted. Carmean's (1972) formula (see Dyer and Bailey 1987) was used to estimate the "true" tree height corresponding to the ring counts at the crosscuts. Height-over-age plots of every sampled tree were visually examined for patterns of suppression and release and growth anomalies beyond breast-height age. Suppressed trees were deleted from the analysis, and only the sample plots with two or three site trees were kept in the database. Consequently, 26 sample plots were deleted from the data set leaving data from 98 plots for model construction and testing (Table 2.1). The relatively high number of rejected plots emphasize that shade-tolerant amabilis fir is a very difficult species for site index estimation (Curtis *et al.* 1974a). Slight suppression, especially when subsequent release was gradual, was not always recognized when trees were cored before felling, but became apparent on height-over-age plots. The effect of a deep snowpack on the early growth of amabilis fir located on high-elevation sites added to the difficulties in distinguishing true suppression. I considered snow as a site factor, and retained a few plots where site trees showed release above breast height in the database. This was done only when:

- a deep and long-lasting snowpack was evident in the area (inferred from topography, height of epiphytic lichens, and observations of the snowpack in late spring),
- a similar height growth pattern was observed in all site trees within the same plot, and
- similar stands in the same area showed a similar height growth pattern.

For every site tree, I obtained a record of heights at 5-year breast-height-age intervals by linearly interpolating between the height and age pairs that resulted from Carmean's formula. Average plot curves were computed as the arithmetic mean of these values. This provided height versus age data at 5-year intervals starting from age 5 years for each plot, and site index values for each plot as the corresponding height at breast-height-age 50. A single, quantitative measure of height growth pattern for each plot was calculated as the ratio (*z*-ratio) between heights at breast height age 60 and 30 (Hoyer and Chawes 1980). This ratio was proposed by Zeide (1978) and has been used in numerous studies to characterize curve shape (Hoyer and Chawes 1980, Milner 1988, Wang *et al.* 1994a). I used the *z*-ratio in an exploratory analysis to identify site factors that were related to height growth patterns. As not all trees had reached 60 years breast height age, the data set used contained data from 43 plots. Linear models were used to test the effect of climate (measured by elevation and continentality stratum) and edatope (any

given combination of soil moisture regime and soil nutrient regime) on height growth pattern.

The height growth data beyond 100 years at breast height age were mainly from medium- and low-productivity, high-elevation plots. To achieve a more balanced sample distribution, I included only data up to 100 years of breast height age in the data set used to calibrate the height and site index models. This was a compromise between a completely balanced distribution and the desired range of data. Since validation of height and site index models is preferably done by using an independent data set (Marshall and Northway 1993, Nigh and Sit 1996), 31 plots were set aside as a test data set and 67 plots were used for model calibration using a random number generator (table 2.1). Although this is not necessarily the case, the simple randomization procedure, resulted in two data sets that represented all continentality strata well.

Table 2.1. General statistics for study plots according to the calibration, test, and all plots

		Breast height age (years)	Top height (m)	Site index at 50 years (m)
Calibration data	<i>N</i>	67	67	67
	Minimum	37	7.7	4.8
	Mean	92	23.7	17.6
	Maximum	312	55.0	36.7
	Std. Deviation	51	8.6	7.9
Test data	<i>N</i>	31	31	31
	Minimum	36	8.9	4.6
	Mean	82	22.0	18.2
	Maximum	173	32.3	36.4
	Std. Deviation	38	5.1	8.4
All data	<i>N</i>	98	98	98
	Minimum	36	7.7	4.6
	Mean	89	23.1	17.8
	Maximum	312	55.0	36.7
	Std. Deviation	48	7.7	8.0

To find the most suitable function for estimating height growth, the three main types of functions commonly used to describe height growth of trees were fitted to the calibration data:

- a conditioned logistic function (Thrower and Goudie 1992, Wang and Klinka 1995, Chen *et al.* 1998a),
- a Chapman-Richards' function (Payandeh 1974, Carmean and Lenthall 1989, Thrower and Goudie 1992, Chen *et al.* 1998a), and
- a conditioned Weibull function (Payandeh and Wang 1995).

Since two different least square problems are solved for height growth and site index models (Curtis *et al.* 1974b), two separate polymorphic models were fitted for estimating height growth and site index of amabilis fir. When fitting the site index models, the data points associated with ages 5 and 10 were excluded because a strong relationship between top height and site index before breast height age 15 was not expected (Carmean and Lenthall 1989, Thrower and Goudie 1992). All non-linear models were fitted using the least square Marquart-Levenberg procedure of the SPSS™ program (SPSS Inc. 1993). The best polymorphic model was chosen based on fitting statistics ( $R^2$  and MSE) and bias. Results from the height growth pattern analysis and the best height growth and site index model, were used to develop climate-specific height growth curves.

Three criteria were used to compare performance of polymorphic models to climate-specific models and currently used models: precision, bias, and potential for extrapolation beyond the calibration range. Precision was evaluated by the predicted mean squared error (PMSE); bias and extrapolation potential were assessed by examining residual plots by age and site index. The common procedure for testing site index models is to use every known pair of height and age to estimate site index; this is analogous to the procedure used for height models (e.g., Thrower and Goudie 1992, Chen *et al.* 1998a). However, I decided to use only the originally measured top height of the trees at the time of sampling. This approach yields only one estimate per plot and eliminates the known problems caused by autocorrelation (Monserud 1984b, Nigh and Sit 1996). As this approach is closest to their application, I considered this to be the ultimate test for site index models, providing that a wide range in top height and age test data exist. In addition to the graphical examination of residuals, paired *t*-tests were used to detect significant differences between predicted and measured site indices.

## **2.3 Results**

### ***Examination of the Variation in Height Growth Patterns***

Height growth patterns, as measured by z-ratios, were poorly correlated with site index ( $r =$

0.09,  $p = 0.57$ ,  $n = 43$ ). Analysis of variance showed no significant difference in mean  $z$ -ratio between edatopes ( $F = 2.2$ ,  $p = 0.07$ ,  $n = 43$ ). A significant relationship existed between height growth patterns and climate, although of the two tested variables in the model only continentality stratum was significant ( $F = 3.49$ ,  $p = 0.025$ ,  $n = 43$ ) but elevation was not ( $F = 0.06$ ,  $p = 0.81$ ,  $n = 43$ ). While no conclusion can be drawn about the true relationship between height growth patterns and site factors, this exploratory analysis clearly indicates that among the measured variables continentality stratum was most strongly correlated with height growth patterns.

Consequently, continentality strata were used in further analysis. Based on the results of the exploratory analysis, the maritime windward and maritime leeward strata were combined to form the maritime (M) stratum, and the submaritime and subcontinental strata were combined to form the submaritime/subcontinental (SS) stratum. Stands within these two strata showed significantly different height growth patterns (Figure 2.1). These two continentality strata were then used as dummy variables in height growth and site index models (equations [2] and [4]).

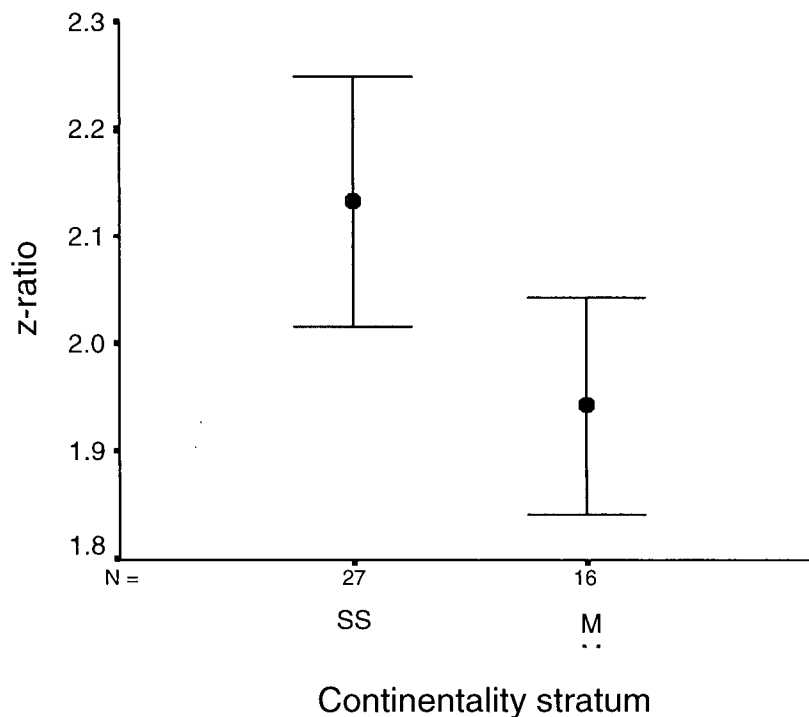


Figure 2.1. Mean  $z$ -ratios and confidence intervals ( $\alpha = 0.05$ ) for plots in the submaritime/subcontinental (SS) and maritime (M) continentality strata. N is the number of plots in each stratum used for the analysis.

### Height Growth Models

Based on examinations of residuals and fitting statistics ( $R^2 = 0.98$ ,  $MSE = 1.13$ ,  $df = 994$ ), the conditioned logistic function was chosen as the baseline model:

$$[1] \quad H = 1.3 + (S - 1.3) \frac{1 + e^{[9.486 - 1.362 \ln(50) - 1.181 \ln(S - 1.3)]}}{1 + e^{[9.486 - 1.362 \ln A - 1.181 \ln(S - 1.3)]}}$$

where:  $H$  = top height (m);  $S$  = site index (top height at 50 years breast height age);  $A$  = breast height age (years);  $e$  = the base of  $\ln$ ; and  $\ln$  = natural logarithm.

Equation [1] was extended to accommodate variation in height growth pattern with continentality by using the two continentality strata as dummy variables, which resulted in:

$$[2] \quad H = 1.3 + M \left\{ (S - 1.3) \frac{1 + e^{[8.704 - 1.306 \ln(50) - 0.980 \ln(S - 1.3)]}}{1 + e^{[8.704 - 1.306 \ln A - 0.980 \ln(S - 1.3)]}} \right\} + SS \left\{ (S - 1.3) \frac{1 + e^{[9.761 - 1.549 \ln(50) - 1.109 \ln(S - 1.3)]}}{1 + e^{[9.761 - 1.549 \ln A - 1.109 \ln(S - 1.3)]}} \right\}$$

where:  $H$  = top height (m);  $S$  = site index (top height at 50 years breast height age);  $A$  = breast height age (years);  $e$  = the base of  $\ln$ ; and  $\ln$  = natural logarithm; and  $M$  and  $SS$  are either 0 or 1 depending on the pl Site index

This climate-specific model had a similar  $R^2$  (0.98) as equation [1] and a slightly lower MSE (1.07,  $df = 991$ ), indicating only a slight increase in precision. It yielded two sets of curves, one for each continentality stratum that displayed the greatest differences past the calibration range ( $> 100$  years breast height age) (Figure 2.2). For all site-index classes, curves of the SS stratum were more sigmoidal than the curves of the M stratum. This implies that culmination of height growth occurs earlier and (potential) maximum heights reached for a given site-index class are lower in the SS stratum than in the M stratum. Prior to the index age, height estimates in the SS stratum were always lower compared to the M stratum. Beyond the index age, however, differences in estimated heights varied with site-index class. For low site-index classes of 5 and 10 m, height estimates for the SS stratum were higher than for the M stratum; for site index classes of 15 and 20 m, little difference was evident between the curves of the two strata; for site-index classes of greater than 25 m the predicted heights were increasingly higher for the M than for the SS stratum. Within the tested range, the largest difference in top height between the two strata given by the model was about 4 m for site-index class 35 and breast height age of 160 years (Figure 2.2).

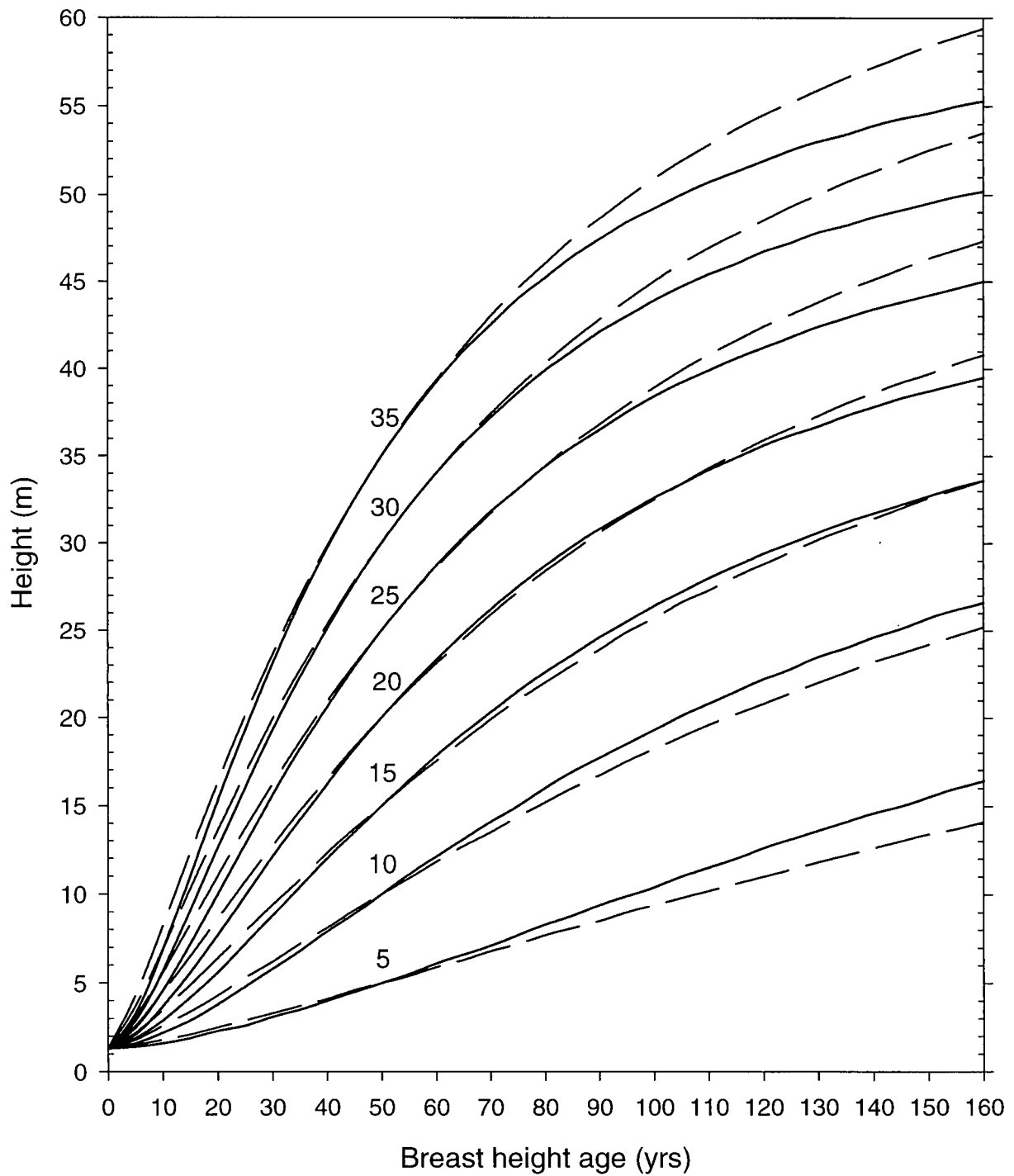


Figure 2.2. The plot of the climate-specific height growth curves from the selected model (eq. [2]) for given site indices. Solid lines refer to the subarctic/subcontinental (SS) continentality stratum and dashed lines refer to the maritime (M) continentality stratum.

When tested against independent data within the calibration range, little difference in bias was evident between the models. The patterns of residuals versus age were similar for both models up to 100 years (Figure 2.3). Both models underestimated height for most age classes; however, this underestimation was only greater than two standard errors of the mean at age class 5 years.

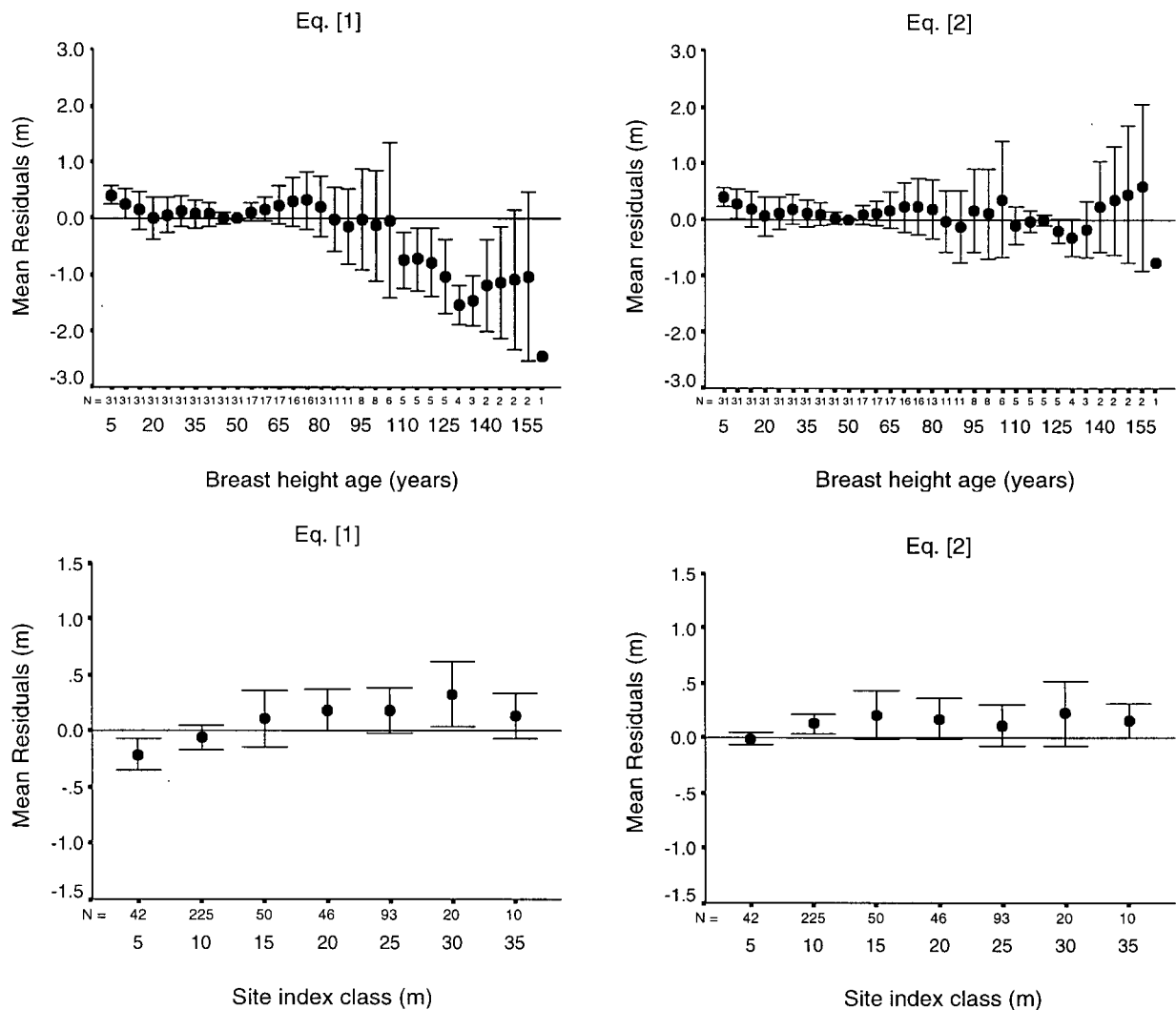


Figure 2.3. Validation of height models using the test data set. The upper figures: mean and two standard errors by breast height age; lower figures: site index for residuals of height models fitted by conditioned logistic (eq. [1]) and the climate-specific function (eq. [2]). N is the number of observations used to calculate error bars.



When residuals were plotted over site index classes, the climate specific model [2] was only slightly biased for site index class 10 (mean bias = 0.1 m) (Figure 2.3). Equation [1] was significantly negatively biased for site index classes 5 and positively biased for site index class 30 (Figure 2.3). Model [2] (PMSE = 0.50, N = 486) was also slightly more precise than model [1] (PMSE = 0.69, N = 486).

Past the calibration range, the climate-specific model (equation [2]) performed better than the conventional polymorphic model (equation [1]). The mean residuals never deviated from zero by more than 0.6 m and lay within two standard errors of the mean for all age classes. The conventional polymorphic model (equation [1]) yielded a large negative bias past 110 years (Figure 2.3). Thus, the use of the climate-specific model is recommended within a breast-height-age range of 5–160 years.

### *Site Index Models*

After fitting the initially selected functions to the calibration data, the residuals for all the models showed a cubic pattern with breast height age. Therefore, several other functions were tried and finally an equation, previously used by Carmean and Lenthall (1989) and Thrower and Goudie (1992), was selected:

$$[3] \quad S = 1.3 + 0.694(50 - A)A^{-0.558} + 0.368(H - 1.3) + 31.771(H - 1.3)A^{-1}$$

where:  $H$  = top height (m);  $S$  = site index (top height at 50 years breast height age); and  $A$  = breast height age (years).

Although equation [3] also showed a slight cubic pattern with age, the mean residuals never deviated more than two standard errors from zero for any age class. Therefore, equation [3] was selected as the “best” conventional polymorphic model ( $R^2 = 0.96$ ,  $MSE = 2.43$ ,  $df = 859$ ).

Using continentality strata, a climate-specific model was developed:

$$[4] \quad S = 1.3 + M \left\{ 0.694(50 - A)A^{-0.558} + 0.368(H - 1.3) + 31.771(H - 1.3)A^{-1} \right\} + \\ SS \left\{ 0.592(50 - A)A^{-0.578} + 0.183(H - 1.3) + 41.659(H - 1.3)A^{-1} \right\}$$

where:  $H$  = top height (m);  $S$  = site index (top height at 50 years breast height age);  $A$  = breast height age (years); and  $M$  and  $SS$  are either 0 or 1 depending on the plot location.

The climate-specific model did not improve prediction when tested against the calibration data. A gain in accuracy was neither apparent from the fitting statistics ( $R^2 = 0.92$ ,  $MSE = 2.33$ ) nor from examination of residuals. However, when the independent test data were used for evaluation of potential differences between equations [3] and [4] in operational use, differences between the models were significant. Paired  $t$ -tests showed that estimates from equation [3] were significantly biased for the M stratum and that the climate-specific model [4] removed this bias (Table 2.2). Moreover, residual plots of the climate-specific model showed a better distribution of residuals (Figure 2.4). Equation [3] exhibited a decreasing variance of the residuals with site index as well as a tendency to underestimate site index for ages over 100 years. The climate-specific model [4] was also more precise as measured by a lower PMSE of 0.59 ( $N = 31$ ) compared to the conventional polymorphic model [3] (PMSE = 0.73,  $N = 31$ ). This gain in precision was mainly achieved by reducing the extreme values of the residuals by adjusting for continentality (Figure 2.4).

Table 2.2. Test of bias of different site index models. Results of the paired  $t$ -tests using measured site index and predicted site index from polymorphic (SI [3]) and climate-specific models (SI [4] of this study and from Kurucz's models (SI [KU]) and Hoyer and Herman's models (SI [HO]). M and SS refer to continentality strata maritime and sub-maritime/subcontinental, respectively.

	Continental- ity stratum	Mean difference (m)	Standard error (m)	$t$	$df$	$p$
SI – SI [3]	M	0.338	0.148	2.277	17	.036
	SS	-0.330	0.280	-1.175	12	.263
SI – SI [4]	M	0.047	0.134	0.355	17	.727
	SS	0.193	0.278	-0.694	12	.501
SI – SI [HO]	M	0.451	0.130	3.473	17	.003
	SS	-0.616	0.293	-2.100	12	.057
SI – SI [KU]	M	-0.167	-0.231	-0.723	17	.480
	SS	-1.469	0.336	-4.368	12	.001

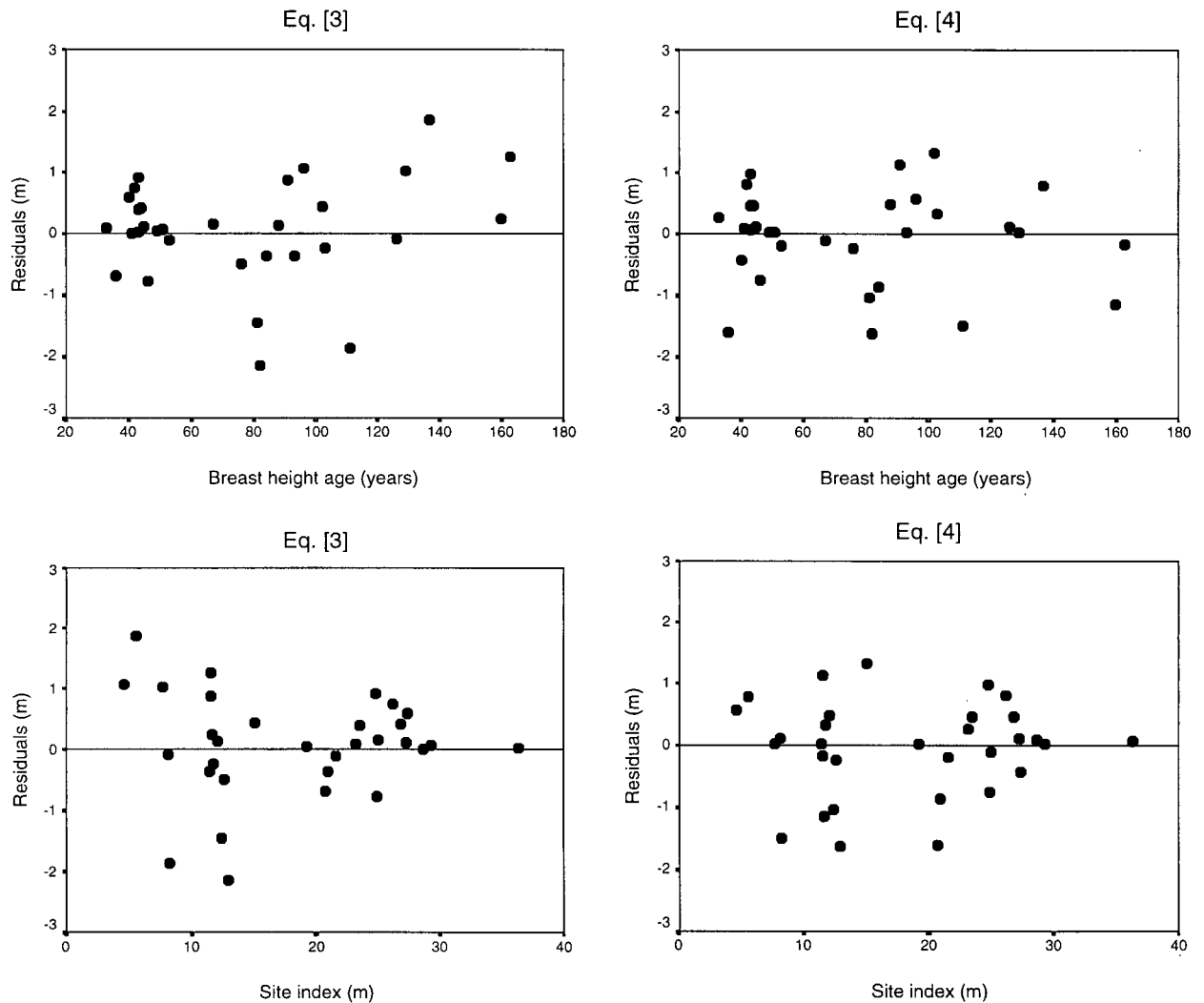


Figure 2.4. Residual plotted by breast height age (upper figures) and site index (lower figures) for the polymorphic function (eq. [3]) and the climate-specific function (eq. [4]).

### ***Applicability of the Existing Height Growth and Site Index Models for Amabilis Fir***

When Kurucz's height growth model was used for prediction, height estimates were significantly biased. The residuals showed trends with age and site index class. This resulted in:

- overestimation of height before the index age and underestimation of height beyond the index age, and

- underestimation of height on low-productivity sites and overestimation of height on high productivity sites (Figure 2.5).

When Kurucz's model was used to predict site index from top height and breast height age, a paired  $t$ -test showed a significant mean bias of  $-0.71$  m ( $\alpha = 0.01$ ,  $N = 31$ ). This overall bias was attributed to a significant mean bias for the SS stratum, whereas, on average, the estimates of the M stratum were unbiased (Table 2.2). Residuals showed trends with both age and site index (Figure 2.6). Site index was underestimated when top height was measured on the trees younger than the index age, but overestimated when top height was measured on the trees older than the index age. Similarly, site index was overestimated for low site-index classes and slightly underestimated for high site-index classes (Figure 2.6).

Application of the model developed by Hoyer and Herman (1989) resulted in predictions that were significantly biased for the M stratum as shown by paired  $t$ -tests (Table 2.2). Residual plots showed trends with both age and site index. The model underestimated site index using the trees younger than the index age and overestimated site index when using the trees older than 100 years, and overestimated site index on low-productivity sites and underestimated on high-productivity sites (Figure 2.6).

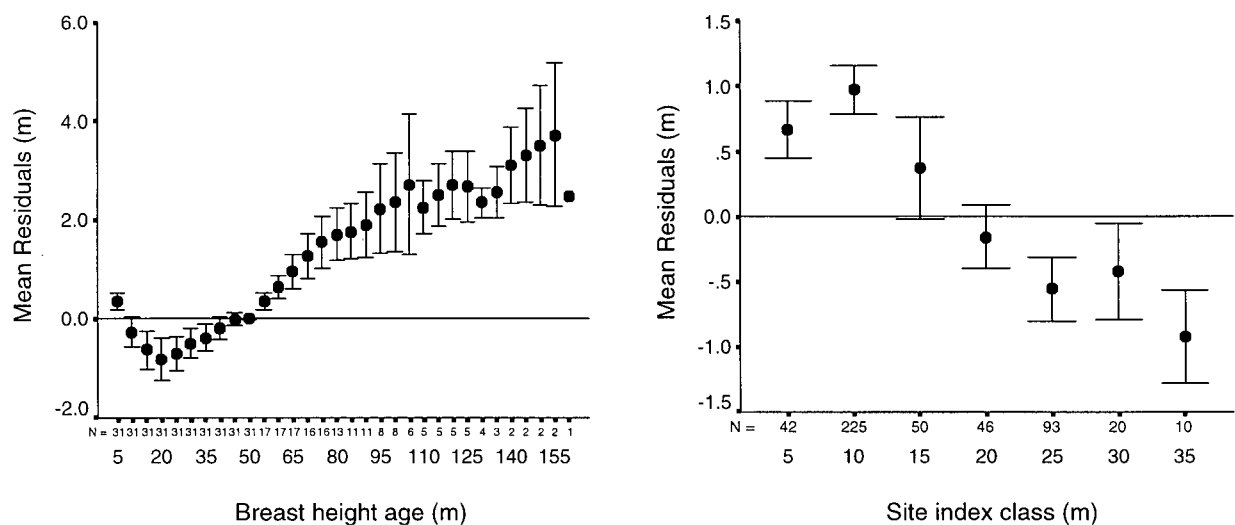


Figure 2.5. Mean and two standard errors of residuals by breast height age and site index class as calculated from Kurucz's curve using the test data set. N is the number of observations used to calculate error bars.

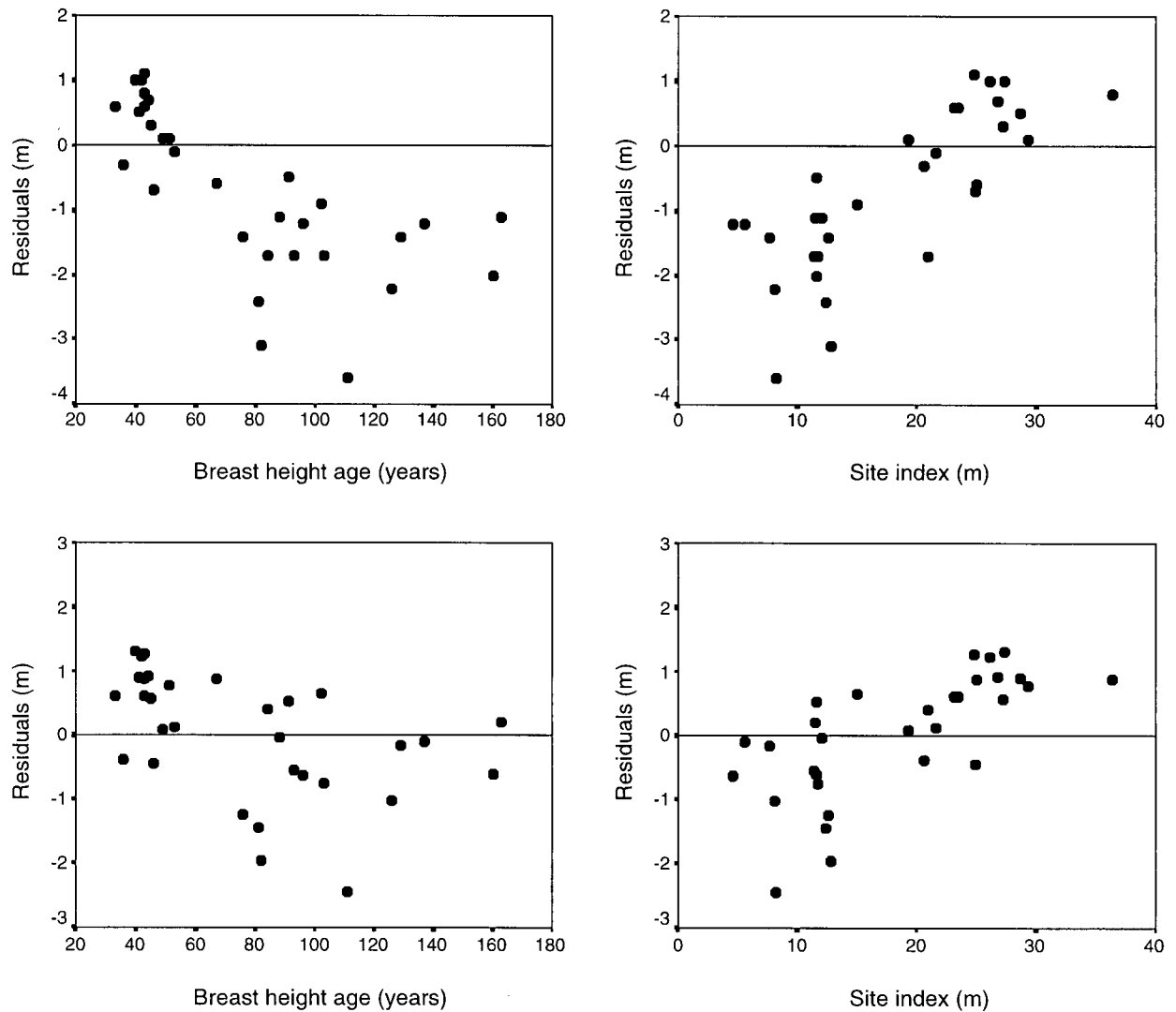


Figure 2.6. Residuals plotted by breast height age and site index calculated from Kurucz's function (upper figure) and the function from the Cascades in Oregon and Washington (lower figure).

## 2.4 Discussion

### *Differences in Height Growth Pattern between Continentality Strata*

Differences in the height growth pattern between maritime and submaritime/subcontinental continentality strata were observed when height growth pattern was measured as a single-valued ratio ( $z$ -ratio). When the two continentality strata were used as dummy variables in climate-specific height growth and site index models, the resulting curves showed obvious differences in height growth pattern (Figure 2.2) and improved the accuracy of height and site index estimates

(Figures 2.3 and 2.4, Table 2.2). A relationship between regional climate and height growth pattern was suggested for several tree species as height growth patterns have been found to vary from region to region (e.g., Marschall 1976, Monserud 1985, Thrower and Goudie 1992, Chen *et al.* 1998a). The results also agree with several studies that reported relationships between climatic variables and height growth patterns (Hoyer and Chawes 1980, Milner 1988, Wang *et al.* 1994a, Klinka *et al.* 1996).

However, numerous climatic and non-climatic factors may act and interact to produce height growth patterns. The association of continentality strata with variation in height growth pattern of amabilis fir may be indirect. Non-climatic factors that are associated with continentality strata may cause differences in height growth pattern; for example, differences in continentality may be associated with different populations of amabilis fir, which may have adapted different height growth patterns (Monserud and Rehfeldt 1990).

#### ***Application of Height and Site Index Models***

The previously existing models to estimate height and site index for amabilis fir were significantly biased when applied to the entire study area (Figures 2.5 and 2.6). Consequently, estimates of yield for the coastal high-elevation forest based on these curves are likely to be incorrect. When the performance of the conventional polymorphic and climate-specific height growth and site index models was compared using an independent set of data, residual plots and the PMSE statistics showed that the climate-specific models were more accurate. The improvement over the conventional polymorphic models was mainly attributed to a reduced bias past the calibration range (Figures 2.3 and 2.4). This is consistent with the finding that differences between the height growth curves for the two continentality strata were largest between 100 and 160 years of age (Figure 2.2).

For amabilis fir stands growing in southwestern British Columbia, I recommend the application of the models developed in this study for height and site index estimation. The models should only be used within the age range of 15 to 160 years. Since the results of this study indicate that height growth patterns of amabilis fir vary with climate, caution must be used when the models are applied to stands growing in central or northern coastal British Columbia.

### 3. Quantitative Characterization of Nutrient Regimes for High-elevation, Coastal Forest Soils (Study 2)

#### 3.1 Introduction

Soil fertility is the capacity of the soil with respect to its ability to supply nutrients essential for plant growth (SSSA 1973). Together with climate, soil moisture, and soil aeration, soil fertility is considered to affect plant growth and spatial distribution of plant communities (e.g., Major 1963, Krajina 1969). Therefore, knowledge of soil fertility is needed for ecological studies and vegetation management. The assessment of soil fertility is a complex task because nutrient availability is a result of the entire physical, chemical, and biological characteristics of the soil (e.g., Kimmins 1997, pp. 252). To simplify this complexity, one can divide a regional soil fertility (nutrient) gradient into a number of classes or soil nutrient regimes (SNRs), such as very poor, poor, medium, rich, and very rich (e.g., Krajina 1969, Pojar *et al.* 1987, Wang 1997).

Soil nutrient regimes are commonly estimated in the field from easily observable soil morphological properties and indicator plants (Ellenberg 1974, 1978, Pojar *et al.* 1987, Klinka *et al.* 1989, Green and Klinka 1994). However, the indirect and subjective nature of identifying SNRs in the field calls for quantification of SNRs using directly measured soil nutrient properties. Two main questions arise: (1) Are the one-dimensional field-identified SNRs representing the complex soil nutrient gradients well? (2) Is the gradient depicted by the SNRs relevant for tree growth?

An explicitly formulated forest site classification system has been developed in British Columbia (BC): the biogeoclimatic ecosystem classification (BEC) system (Krajina 1965, Pojar *et al.* 1987). In the BEC system, SNRs are identified in the field with a key that uses several selected soil morphological properties of forest floor and mineral soil; in addition, the identification may be augmented by indicator plant analysis (Pojar *et al.* 1987, Klinka *et al.* 1994, Green and Klinka 1994). Because the BEC system was designed for the entire province, diverse BC forests are particularly suited to answer the above questions and to study the portability of results across different climatic regions.

Several studies demonstrated that field-identified SNRs are efficient means of providing estimates of soil nutrient conditions of a forest site and direct soil nutrient measures (Kabzems and Klinka 1987a, Courtin *et al.* 1988, Klinka and Carter 1990, Klinka *et al.* 1994, Chen *et al.*

1998b). These studies concluded that mineralizable-N concentrations within 0-30 cm of the mineral soil provide the best single measure for characterizing a regional soil nutrient gradient and discriminating between field-identified SNRs. In addition, these studies demonstrated that SNR is a good and portable predictor explaining a significant amount of the variation in site index (top height at reference age 50 years at breast height) of various tree species (Kabzems and Klinka 1987b, Courtin *et al.* 1988, Klinka and Carter 1990, Wang 1992, Wang 1993, Wang *et al.* 1994b, Klinka *et al.* 1994, Chen *et al.* 1998b).

Quantitative characterizations of field-identified SNRs were carried out for low- and high-elevation forest soils in the interior regions of British Columbia, which are influenced by a continental climate (Klinka *et al.* 1994, Chen *et al.* 1998b). Such a characterization exists also for low-elevation forest soils in the coastal region of British Columbia (Klinka and Carter 1990, Kayahara 1992). However, no such study has been done for high-elevation forest soils in the coastal region, which includes the Insular and Coast Mountain ranges. Influenced by montane cold mesothermal and maritime subalpine boreal climates, high-elevation coastal soils differ significantly from low-elevation coastal soils. The cool and moist conditions together with the short growing season lead to slow decomposition of organic materials and, hence, a large accumulation of organic matter (Brooke *et al.* 1970). Thus, uncertainties exist whether the heuristic procedure used for field-identification of SNRs provides meaningful estimates of soil nutrient conditions for high-elevation coastal soils.

Similarities between levels of mineralizable-N for the same SNRs in different climatic regions suggest a general applicability of existing field keys (Klinka *et al.* 1994, Chen *et al.* 1998b). However, where different levels were found between different climate regions, the significance of these differences could not be readily assessed because of differences in sampling. In this study, montane and subalpine soils across a high-elevation continentality gradient were sampled and analyzed using the same sampling and analytical procedures. Therefore, the variation in soil nutrient concentrations with climate (expressed as orographic and continentality strata, respectively) could be tested within every SNR.

The objectives of this study were (1) to qualitatively and quantitatively characterize the soil nutrient gradient in high-elevation coastal soils using field-identified SNRs and direct measures of selected plant nutrients, (2) to examine the relationships between measured nutrients and field-identified SNRs and forest productivity measured by site index of amabilis fir, and (3) to examine the agreement of field-identified SNRs with quantitatively derived



classes based on selected nutrient properties, and (4) to test if the soil nutrient gradient varies between climate (continentality and orography) strata of southern coastal BC.

### **3.2 Materials and Methods**

Of the 124 plots, available in total (Appendix I), 79 were selected for this study (Table 3.1, Figure 2.1). Because the objective was to quantify the soil nutrient regime of high-elevation forest soils, only montane and subalpine sites were selected. Following the estimation of soil moisture regime (SMR) and SNR for each plot using a combination of topographic and soil morphological properties as well as understory vegetation (Green and Klinka 1994), it became apparent that sites with extreme soil nutrient conditions (with very poor and very rich SNRs) could not be sampled because they occurred very rarely and did not support suitable stands of the study species. As a result, I sampled a narrower range of a regional soil nutrient gradient that included poor, medium, and rich SNRs. Elevation was measured using a Thommen pocket altimeter, slope using a clinometer, and aspect using a compass.

In each sample plot, forest floor and mineral soils were sampled at 12 randomly allocated points. The samples were taken in soil pits from the entire forest floor as well as from the first 30 cm of mineral soil. The subsamples from each plot were composited into two samples (forest floor and mineral soil) for chemical analysis. Samples were then immediately air-dried to constant mass. Using air-dry samples for soil chemical analysis is a standard procedure and has been used for all previous studies of quantification of field-identified SNRs (e.g., Kabzems and Klinka 1987a, Courtin *et al.* 1988, Kajahara 1992, Klinka *et al.* 1994, Chen *et al.* 1998b) as well as studies dealing with nitrogen mineralization (e.g., Zak *et al.* 1989). Forest floor samples were ground in a Wiley mill to pass 2-mm sieve size and mineral soil samples were passed through a 2-mm sieve to separate coarse fragments. Each sample was analyzed for acidity (pH), total carbon (tC), total N (tN), mineralizable-N (min-N), extractable P (eP), extractable SO<sub>4</sub>-S (eSO<sub>4</sub>-S), and extractable Ca, Mg, and K (eCa, eMg, and eK) using the analytical procedures described by Klinka *et al.* (1994). Mineralizable-N was determined by the anaerobic incubation procedure of Powers (1980) with released NH<sup>4+</sup> determined colorometrically. This method was selected for its simplicity and robustness against potential storage effects (Powers 1980) and was also used by Kabzems and Klinka (1987a,b), Klinka *et al.* (1994), Kayahara *et al.* (1995), and Chen *et al.* (1998b). All nutrient measures were

expressed as concentrations on a dry mass basis. To describe the quality of soil organic matter the C/N ratio was calculated.

Table 3.1. Number of plots within continentality strata (bold print), orography strata (italics), and soil nutrient regimes (normal print).

		Poor	Medium	Rich	Total	
<b>Maritime</b>	<i>montane</i>	1	6	4	11	
<b>windward</b>	<i>subalpine</i>	1	7	3	11	<b>22</b>
<b>Maritime –</b>	<i>montane</i>	1	5	-	6	
<b>leeward</b>	<i>subalpine</i>	8	5	2	15	<b>21</b>
<b>Submaritime</b>	<i>montane</i>	1	2	3	6	
	<i>subalpine</i>	2	-	2	4	<b>10</b>
<b>Subcontinental</b>	<i>montane</i>	5	2	3	10	
	<i>subalpine</i>	4	8	4	16	<b>26</b>
		23	35	21		<b>79</b>

Site index was taken from study 1 (Splechtna 2001). However, because of suppression that occurred on several plots site index could be determined for only 55 plots.

I screened each soil variable for normality, univariate outliers, and linearity using box-whisker and one-by-one scatter plots (Tabachnik and Fidell 1996), and for homogeneity of variance between field-identified SNRs using Levene's test (SPSS<sup>TM</sup> Inc. 1993). Variables that did not meet the assumptions were transformed using the natural logarithm or square root. Multivariate outliers were detected by a single linkage cluster technique (SPSS<sup>TM</sup> Inc. 1993). This led to deletion of three plots because of extremely high values for single nutrients that could not be explained and may have been the result of an error in sampling or chemical analysis.

To examine the relationship among the soil samples in a multidimensional space and to identify variables that explain a high amount of variation between soil samples without *a priori* classification, I applied principal components analysis (PCA) followed by a varimax rotation procedure (Webster and Oliver 1990). Prior to PCA, variables had been transformed to z-scores (mean = 0, standard deviation = 1). To test the relationship between field-identified SNRs and single soil nutrient properties, sample plots were stratified according to field-identified SNRs and analysis of variance and multiple comparisons of means for each property were carried out.

To keep  $\alpha$ -levels constant for multiple comparisons, Bonferroni's correction was applied (SPSS<sup>TM</sup> Inc.1993).

To examine the agreement between field-identified SNRs and groups obtained using chemical soil variables, I used discriminant analysis (DA) with all variables entered at once. Agreement between quantitative classification (based on nutrient concentrations) and field-identified SNRs was assessed by percentage of cases that were classified into the same classes by both classification schemes. To examine the ability of nitrogen-related variables to discriminate between field-identified SNRs, I also applied DA using only nitrogen-related variables (in a stepwise procedure). McNemar's repeated-measures chi-square provided a test determining whether the full model (using all chemical variables) was superior in classifying cases into SNRs compared to the function using only nitrogen-related variables (Tabachnik and Fidell 1996, p. 545). The test is based on a comparison of the number of cases that were correctly classified using all data but incorrectly classified using only nitrogen related variables (B), with the number of cases correctly classified by the latter but incorrectly classified by the former (C). The chi-square was calculated as  $\chi^2 = (B-C)^2/(B+C)$  and compared to the critical  $\chi^2 = 3.84$  (1 degree of freedom,  $\alpha = 0.05$ ).

To test whether soil nutrient levels within a given field-identified SNR varied with climate, the following general linear model was applied:

$$[1] \quad n = m + \text{SNR} + \text{ORO} + \text{CONT} + \text{SNR} * \text{ORO} + \text{SNR} * \text{CONT} + \text{ORO} * \text{CONT} + \varepsilon,$$

where  $n$  is a soil nutrient variable,  $m$  is the overall mean, SNR is the field-identified soil nutrient regime, ORO is the orographic stratum, CONT is the continentality stratum, SNR\*ORO, SNR\*CONT, and ORO\*CONT are the interaction terms, and  $\varepsilon$  is the error term.

When significant differences were found between marginal means of the continentality strata, post-hoc multiple range tests with Bonferroni's correction were applied using the observed means.

Regression analysis was applied to examine relationships between soil nutrient variables (continuous variables and SNRs) and site index of *amabilis* fir. Since climate has a large influence on site index of the species (chapters 3, 4, and 5), elevation (an indirect measure of climate) was used as a covariate in all regression models. To minimize the influence of soil moisture, this analysis included only fresh and moist sites ( $n = 42$ ). I applied PCA separately for forest floor and mineral soil properties and used the first four factor scores as independent variables in regressions on site index. This was done to obtain an estimate of (i) the maximum of

variation in site index that could be explained by direct soil nutrient measures, and (ii) the relative importance of forest floor and mineral soil for tree growth. Using factor scores reduced the number of predictors but contained much of the variation in the soil nutrient gradient.

### **3.3 Results**

#### ***Characterization of Soil Nutrient Gradients without a priori Classification***

The first 3 principal components of all measured soil properties explained 60% of the total variance between the 79 plots. Plots of the first three components showed no clear grouping of plots in the soil variable space (Figure 3.1). The sum of extractable bases and pH of mineral soil and forest floor loaded highly on the first component (29% of total variance explained). Mineral soil tC, eK, and min-N loaded positively, but eSO<sub>4</sub>-S of the forest floor loaded highly negatively on the second component (18% of total variance explained). The third component explained 13% of the total variation and was associated with high concentrations of forest floor tN and low C/N ratios of forest floor and mineral soil (negative loading). The first component represents a gradient of acidity and extractable bases, the second component mainly a gradient of mineral soil nutrients and the third component describes organic matter quality of the forest floor and mineral soil.

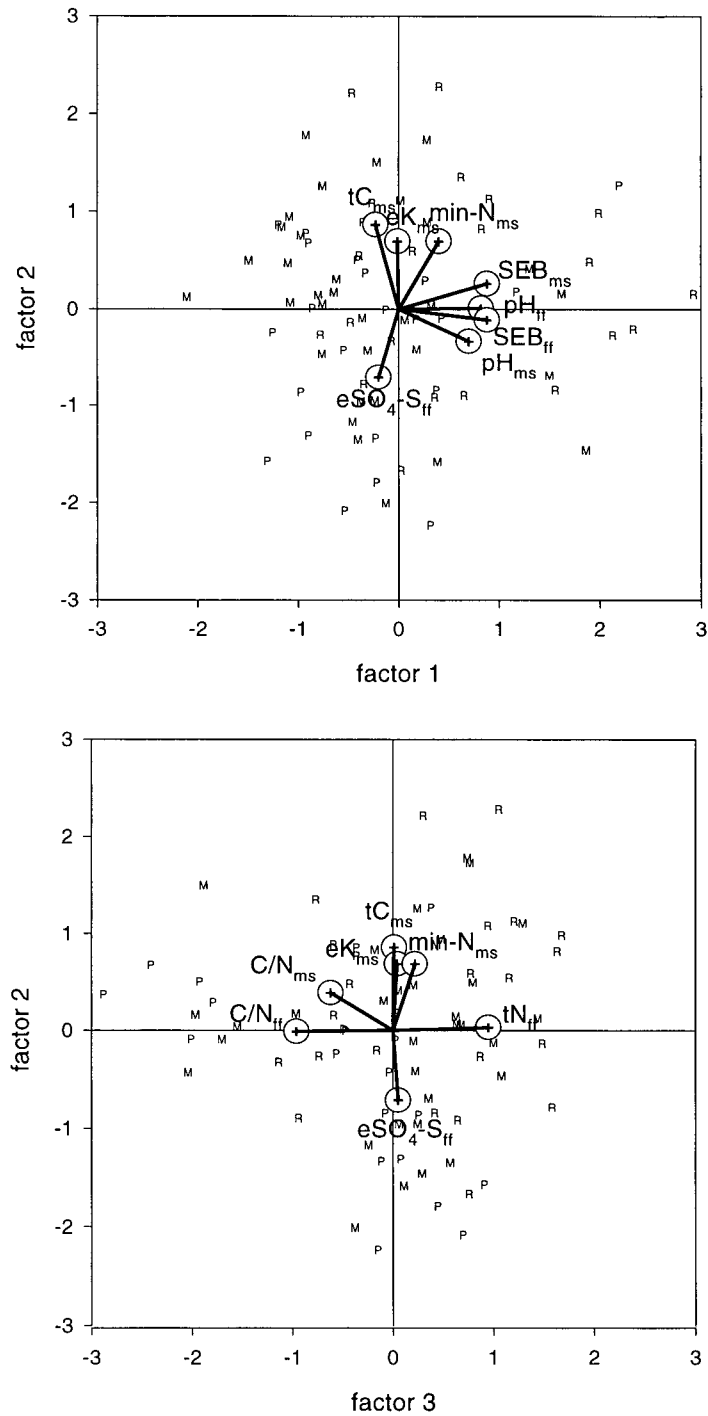


Figure 3.1 Ordination plots according to the first and second component (top) and third and second component (bottom) of principal components analysis using all soil nutrient properties. Arrows indicate directions of highly loading soil properties. Sites are labeled as P (poor), M (medium) and R (rich) according to field-identified SNRs.

Table 3.2. Means and standard errors of mean for measured forest floor nutrient properties. Values in the same row with same superscript are not significantly different ( $\alpha = 0.05$ ); variables without superscripts do not show significant differences between soil nutrient regimes.

Property	Poor	Medium	Rich
N	23	35	21
pH	3.9±0.1 <sup>a</sup>	4.0±0.1 <sup>a</sup>	4.3±0.1 <sup>b</sup>
Total C (g kg <sup>-1</sup> )	446.9±4.3 <sup>b</sup>	439.3±5.1 <sup>b</sup>	412.7±9.5 <sup>a</sup>
Total N (g kg <sup>-1</sup> )	7.7±0.4 <sup>a</sup>	9.3±0.4 <sup>ab</sup>	10.1±0.6 <sup>b</sup>
C:N ratio <sup>~</sup>	64.7±5.8 <sup>b</sup>	51.6±3.2 <sup>ba</sup>	44.7±3.5 <sup>a</sup>
Mineralizable-N (mg kg <sup>-1</sup> ) <sup>~</sup>	124±6 <sup>a</sup>	158±13 <sup>ab</sup>	172±17 <sup>b</sup>
Extractable SO <sub>4</sub> <sup>-</sup> (mg kg <sup>-1</sup> )	59±4	57±3	55±4
Extractable P (mg kg <sup>-1</sup> )	90±8	84±7	87±10
Extractable Ca (mg kg <sup>-1</sup> ) <sup>~</sup>	2581±281 <sup>a</sup>	2848±279 <sup>a</sup>	4385±589 <sup>b</sup>
Extractable Mg (mg kg <sup>-1</sup> ) <sup>~</sup>	389±22	449±37	463±28
Extractable K (mg kg <sup>-1</sup> )	651±42	620±27	531±42
Sum of extractable Ca, Mg, and K (mg kg <sup>-1</sup> ) <sup>~</sup>	3621±294 <sup>a</sup>	3917±295 <sup>a</sup>	5379±595 <sup>b</sup>

<sup>~</sup> Variables have been transformed using natural logarithm or square root for the analysis.

***Agreement between Field-identified SNRs (a priori Classification) and Quantitative Classification based on Directly Measured Soil Nutrients.***

In general, the selected nutrient properties showed the same increases or decreases along the presumed soil nutrient gradient that were reported in several previous studies (Tables 3.2 and 3.3, Figure 3.2). In order from poor to rich SNRs, the forest floor pH, tN, min-N and the sum of eCa, eMg, and eK (SEB) increased and tC and C/N ratio decreased. Acidity, tC, and SEB separated rich sites from poor and medium sites, and min-N separated poor sites from rich sites. Similarly, the mineral soil pH, tC, tN, min-N, and SEB increased and C/N ratio decreased from poor to rich sites. Min-N and SEB separated rich sites from poor and medium sites, and tN and C/N ratio separated rich from poor sites. The sum of eCa, eMg, and eK was largely determined by eCa. Forest floor and mineral soil eCa and mineral soil eMg showed similar patterns with SNRs as SEB, while forest floor and mineral soil eK and forest floor eMg did not

show significant trends. Forest floor eP and eSO<sub>4</sub>-S also did not show significant variation between SNRs. Mineral soil eSO<sub>4</sub>-S peaked on medium sites. (Tables 3.2 and 3.3).

Table 3.3. Means and standard errors of mean for measured 0 – 30 cm mineral soil nutrient properties according to field-identified soil nutrient regimes. Values in the same row with same superscript are not significantly different ( $\alpha = 0.05$ ); variables without superscripts do not show significant differences between soil nutrient regimes.

Property	Poor	Medium	Rich
N	23	35	21
pH	4.6±0.1 <sup>ba</sup>	4.5±0.1 <sup>a</sup>	4.8±0.1 <sup>b</sup>
Total C (g kg <sup>-1</sup> )	45.7±5.6	55.3±5.2	63.9±7.4
Total N (g kg <sup>-1</sup> ) <sup>~</sup>	1.7±0.3 <sup>a</sup>	2.8±0.5 <sup>ab</sup>	4.5±1.1 <sup>b</sup>
C:N ratio	34.2±3.5 <sup>b</sup>	28.4±1.9 <sup>ba</sup>	22.4±2.3 <sup>a</sup>
Mineralizable-N (mg kg <sup>-1</sup> ) <sup>~</sup>	9.1±1.8 <sup>a</sup>	15.3±2.2 <sup>a</sup>	33.3±4.9 <sup>b</sup>
Extractable SO <sub>4</sub> <sup>-</sup> (mg kg <sup>-1</sup> )	8.0±0.7 <sup>a</sup>	10.3±0.6 <sup>b</sup>	8.8±0.5 <sup>ab</sup>
Extractable P (mg kg <sup>-1</sup> ) <sup>~</sup>	17±4	10±2	15±4
Extractable Ca (mg kg <sup>-1</sup> ) <sup>~</sup>	78±40 <sup>a</sup>	81±25 <sup>a</sup>	492±145 <sup>b</sup>
Extractable Mg (mg kg <sup>-1</sup> ) <sup>~</sup>	24±4 <sup>a</sup>	42±9 <sup>ab</sup>	59±13 <sup>b</sup>
Extractable K (mg kg <sup>-1</sup> )	38±4	38±3	39±5
Sum of extractable Ca, Mg, and K (mg kg <sup>-1</sup> ) <sup>~</sup>	140±44 <sup>a</sup>	161±31 <sup>a</sup>	590±155 <sup>b</sup>

<sup>~</sup> Variables have been transformed using natural logarithm or square root for the analysis.

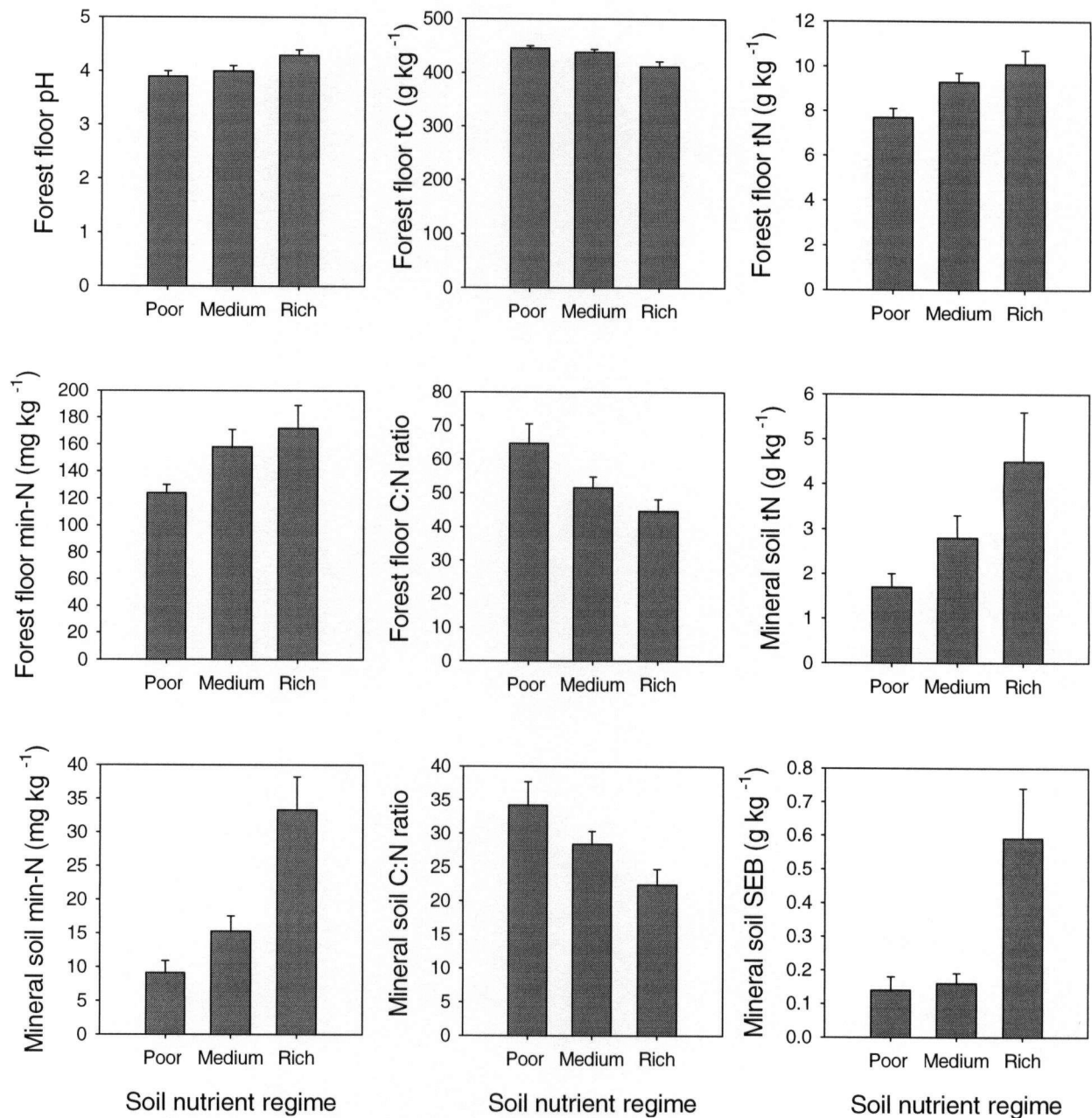


Figure 3.2. Direct measures of selected soil properties stratified according to field-identified SNRs. Error bar is one standard error of the mean.

Discriminant analysis of all measured soil properties after *a priori* classification (field-estimated SNRs) resulted in one significant function, which explained 74.7 % of the variance



(canonical correlation = 0.72). Mineral soil min-N, SEB, tN loaded highly positively and forest floor acidity, tC, and C:N ratio loaded highly negatively on the first component. When the quantitative classification based on measured soil nutrient properties was compared to field-estimated SNRs, 55 study sites (70 %) fell into the corresponding classes (Table 3.4). The two classifications agreed well on the poor and rich sites, with 78% and 76% of the study sites being allocated into the corresponding classes, respectively. However, one poor site was allocated into class C (corresponding to rich) and one rich site was allocated into class A (corresponding to poor), indicating disagreement between the two classifications. Medium sites showed the lowest agreement (60%) as 40 % of the study sites were allocated into either the A or C classes. This also indicated disagreement between the two classifications. However, 70 % agreement between the two classification methods indicates that both methods, in general, provide consistent estimates of plant available nutrients in coastal high-elevation soils.

Table 3.4. Comparison of the classification based on field-identified soil nutrient regimes (rows) with the quantitative classification based on direct soil nutrient measures and discriminant function analysis (columns)\*.

Class	A (Poor)	B (Medium)	C (Rich)	Total	Agreement (%)
Poor	<b>18</b>	4	1	23	78
Medium	9	<b>21</b>	5	35	60
Rich	1	4	<b>16</b>	21	76
Total	28	29	22	79	70

\*Values in bold print indicate number of cases that have been allocated into corresponding classes (agreement).

When only nitrogen-related variables were used in DA in a stepwise procedure, only one function was significant and explained 98.1 % of the variance (canonical correlation = 0.59). Only the mineral soil min-N (loading 0.86) and forest floor C/N ratio (loading -0.56) were selected in the model. However, forest floor and mineral soil tN loaded also highly on the first component. When the results of quantitative classification were compared between predictor set one (all measured variables) and predictor set two (only nitrogen-related variables), there was no significant difference in allocating sites correctly to field-identified SNRs. Calculated chi-square ( $\chi^2 = (10-6)^2 / (10+6) = 1$ ) was smaller than the critical  $\chi^2$  of 3.87 with one degree of freedom (Table 3.5). This indicated that direct measures of the nitrogen gradient were sufficient to quantify field-identified SNRs.

Table 3.5. Table for calculation of  $\chi^2$  for testing quality of classification between two predictor sets used in discriminant analysis. Numbers in bold print (used to calculate  $\chi^2$ ) represent the number of sites allocated correctly by one set of predictors but incorrectly allocated by the other. Numbers in normal print represent sites that were allocated the same way (either correctly or incorrectly) by both sets of predictors.

		Classification using only nitrogen-related variables	
		Correct	Incorrect
Classification using all variables	Correct	48	<b>10</b>
	Incorrect	<b>6</b>	15

***Characterization of the Soil Fertility Gradient in Relation to Climate (Measured by Continentality and Orography)***

Examination of the variations in soil nutrient properties with orographic strata using a general linear model (eq. [1]) showed a higher soil organic matter content in the subalpine mineral soils than montane mineral soils. The forest floor and mineral soil eK concentrations were significantly higher in the subalpine soils than montane soils, whereas the forest floor eSO<sub>4</sub>-S concentrations were significantly higher in the montane soils than subalpine soils (Table 3.6). No other properties showed significant differences with orographic strata.

The same model revealed that the forest floor tC, tN, C/N ratio, min-N, and eP as well as the mineral soil pH, tC, tN, C/N ratio, eSO<sub>4</sub>-S, and eP varied significantly across the continentality strata. Forest floor and mineral soil eP consistently increased with increasing continentality, whereas mineral soil tC and eSO<sub>4</sub>-S showed the opposite trend (Figure 3.3). For all of these soil properties, interactions between SNRs and continentality strata were not significant. Post-hoc tests of observed means suggested that the forest floor tN and C/N ratio were similar for maritime-windward (MW), submaritime (SM), and subcontinental (SC) strata, but were significantly lower and higher, respectively, for the maritime-leeward (ML) stratum.

The mean value for the forest floor C/N ratio of 78.5 for the ML stratum was extremely high in absolute terms (Table 3.7). Mean values for the mineral soil tN and C/N ratio were similar except for the subcontinental stratum, which featured the highest tN concentration and the lowest C/N ratio. However, the higher mineral soil tN concentration was mainly due to a

very high tN concentration on rich sites (Figure 3.3). The forest floor min-N was lower in the ML and subarctic strata compared to the MW and subcontinental strata. The mineral soil min-N was not significantly different across either continentality strata or orographic strata.

Table 3.6. Observed means and standard errors of means for measured forest floor and 0 – 30 cm mineral soil nutrient properties according to orographic strata. Listed are only variables that showed significant differences between marginal means of the tested general linear (eq. [1]) model ( $\alpha = 0.05$ ).

N	Montane 33	Subalpine 46
<b>Forest floor</b>		
Extractable $\text{SO}_4^-$ (mg kg <sup>-1</sup> )	62.5±3.0	53.1±2.4
Extractable K (mg kg <sup>-1</sup> )	520.4±28.0	673.1±25.6
<b>Mineral soil</b>		
Total C (g kg <sup>-1</sup> )	43.4±4.6	63.9±4.7
Extractable K (mg kg <sup>-1</sup> )	29.0±1.9	46.0±2.8

Table 3.7. Observed means and standard errors of means for selected forest floor and 0 – 30 cm mineral soil nutrient properties according to continentality strata. Values in the same row with same superscript are not significantly different tested using a post hoc multiple range test with Bonferroni's adjustment ( $\alpha = 0.05$ ). Variables without superscript are not significantly different between continentality strata.

N	Maritime - windward 22	Maritime - leeward 21	Sub- maritime 10	Sub- continental 26
<b>Forest floor</b>				
Total C (g kg <sup>-1</sup> )	434.2±6.7 <sup>ab</sup>	452.8±3.8 <sup>b</sup>	431.4±11.7 <sup>ab</sup>	420.9±6.7 <sup>a</sup>
Total N (g kg <sup>-1</sup> )	10.2±0.5 <sup>b</sup>	6.5±0.5 <sup>a</sup>	9.9±0.6 <sup>b</sup>	9.7±0.3 <sup>b</sup>
C:N ratio <sup>~</sup>	44.5±2.3 <sup>a</sup>	78.5±6.2 <sup>b</sup>	44.6±2.5 <sup>a</sup>	44.6±1.9 <sup>a</sup>
Mineralizable-N (mg kg <sup>-1</sup> ) <sup>~</sup>	165±20 <sup>ab</sup>	116±9 <sup>a</sup>	122±5 <sup>a</sup>	182±12 <sup>b</sup>
Extractable P (mg kg <sup>-1</sup> )	58±8 <sup>a</sup>	75±6 <sup>ab</sup>	96±7 <sup>bc</sup>	117±7 <sup>c</sup>
<b>Mineral soil</b>				
pH	4.5±0.08 <sup>a</sup>	4.5±0.07 <sup>a</sup>	4.9±0.09 <sup>b</sup>	4.8±0.06 <sup>b</sup>
Total C (g kg <sup>-1</sup> )	76.8±6.2 <sup>a</sup>	65.1±6.2 <sup>ab</sup>	44.3±9.1 <sup>bc</sup>	32.0±3.3 <sup>c</sup>
Total N (g kg <sup>-1</sup> ) <sup>~</sup>	2.6±0.2 <sup>a</sup>	1.8±0.2 <sup>a</sup>	1.6±0.4 <sup>a</sup>	4.7±1.1 <sup>b</sup>
C:N ratio <sup>~</sup>	30.4±1.7 <sup>b</sup>	38.9±2.6 <sup>b</sup>	30.0±2.0 <sup>b</sup>	17.9±2.5 <sup>a</sup>
Mineralizable-N (mg kg <sup>-1</sup> )	24.5±4.0	15.2±2.8	17.3±5.0	15.9±3.9
Extractable $\text{SO}_4^-$ (mg kg <sup>-1</sup> )	11.3±0.5 <sup>b</sup>	11.0±0.7 <sup>b</sup>	7.8±0.8 <sup>a</sup>	6.6±0.5 <sup>a</sup>
Extractable P (mg kg <sup>-1</sup> ) <sup>~</sup>	6.1±0.9 <sup>a</sup>	8.4±1.3 <sup>a</sup>	15.8±3.7 <sup>ab</sup>	22.2±4.2 <sup>b</sup>

<sup>~</sup> Variables have been transformed in the analysis to meet assumption of equal variances between groups.

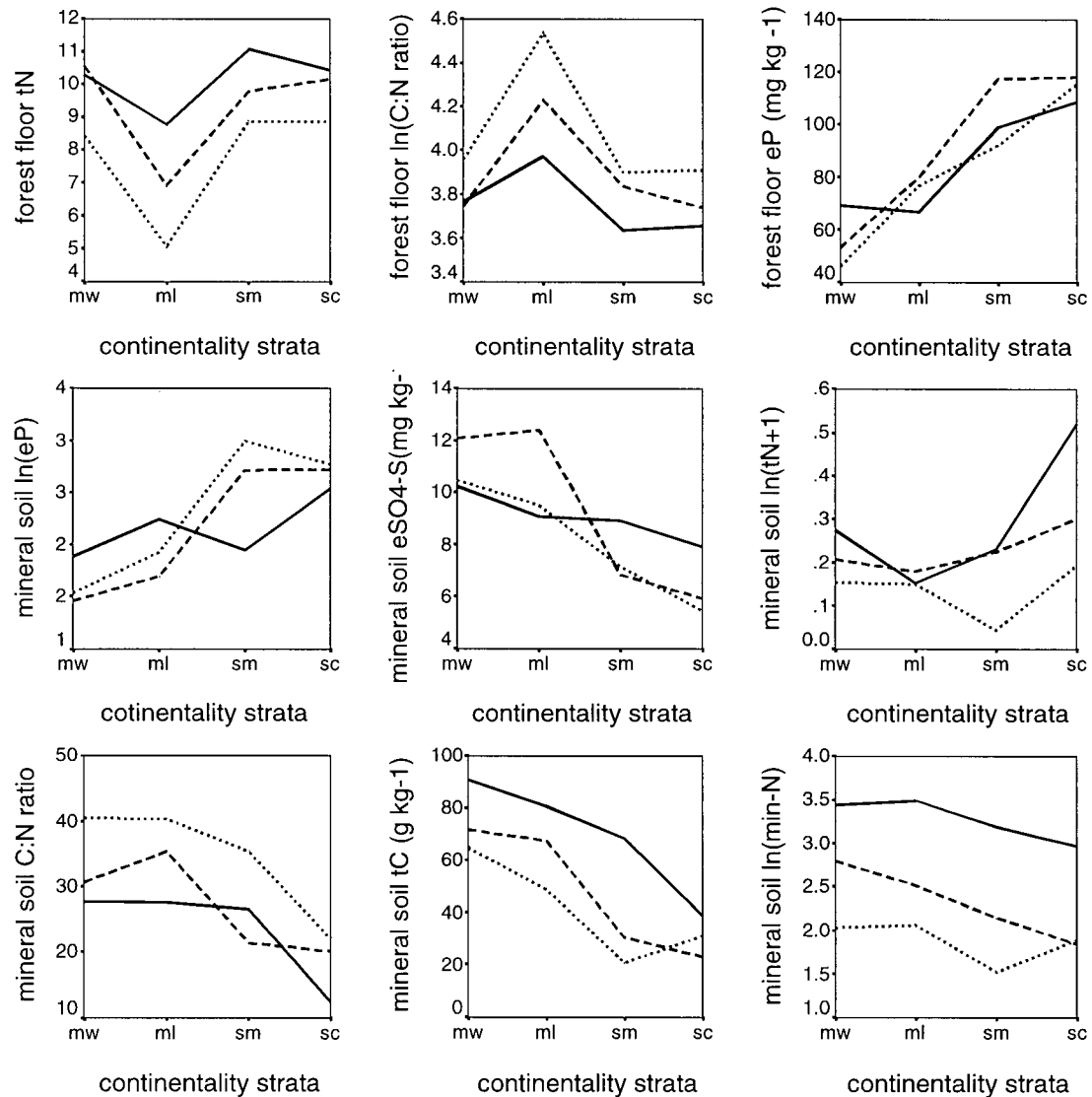


Figure 3.3. Variation of soil nutrients across the study area. Marginal means of selected soil nutrient properties stratified according to maritime-windward (MW), maritime-leeward (ML), sub-maritime (SM, and subcontinental (SC) strata separately for poor (dotted line), medium (broken line), and rich (solid line) sites distinguished according to the general linear model (eq.[1]).

### ***Relationship of Soil Fertility Measures to Site Index***

Compared to elevation, the relationship of soil nutrient measures to amabilis fir site index was relatively weak; the elevation model alone (eq. [2]) explained 57 % of the variation in site index (Table 3.8). The model using elevation and the forest floor and mineral soil factor

scores derived from PCA explained 69 % of the variation in site index (eq. [5]). The forest floor and mineral soil nutrient measures explained a similar amount of the variation in site index (eq. [3] and [4]). The only measured soil nutrient concentrations that were significantly related to site index (using elevation as covariate) were the forest floor and mineral soil tN and C/N ratio; min-N was not found to be significantly related to site index. The best model (based on adjusted  $R^2$  and SEE) that included actual measurements of soil nutrient concentrations [eq. 6] used elevation and the forest floor and mineral soil tN as predictors and explained 67% of the variation. The field-identified SNRs were significantly related to site index, although the explained variation (63%) of the SNR-model [eq. 7] was somewhat lower compared to the model using continuous variables [eq. 6].

Table 3.8. Models for the regression of amabilis fir site index (SI) on direct and indirect measures of soil fertility. Elevation (ELE) was used as covariate. FF<sub>2</sub> and MS<sub>3</sub> are factor scores of the second and third component, respectively, resulting from principal component analysis of chemical soil nutrient properties for forest floor and mineral soil, respectively. tN<sub>ff</sub> and tN<sub>ms</sub> are concentrations of total forest floor and mineral soil nitrogen, and Poor and Medium represent dummy coded variables of field-estimated soil nutrient regimes.

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[2]	SI = 33.215 – 0.015(ELE)			
	Adj $R^2$ = 0.57	RMSE = 4.5 m	p < 0.001	n = 42
[3]	SI = 43.378 – 0.017(ELE) + 2.073(FF <sub>2</sub> )			
	Adj $R^2$ = 0.65	RMSE = 4.1 m	p < 0.001	n = 42
[4]	SI = 36.672 – 0.019(ELE) + 2.212(MS <sub>3</sub> )			
	Adj $R^2$ = 0.64	RMSE = 4.1 m	p < 0.001	n = 42
[5]	SI = 36.805 – 0.019(ELE) + 1.630(FF <sub>2</sub> ) + 1.712(MS <sub>3</sub> )			
	Adj $R^2$ = 0.69	RMSE = 3.8 m	p < 0.001	n = 42
[6]	SI = 29.029 – 0.019(ELE) + 7.109(tN <sub>ff</sub> ) + 5.038(tN <sub>ms</sub> )			
	Adj $R^2$ = 0.67	RMSE = 3.9 m	p < 0.001	n = 42
[7]	SI = 35.246 – 0.0154(ELE) – 5.970(Poor) – 2.041(Medium)			
	Adj $R^2$ = 0.63	RMSE = 4.2	p < 0.001	n = 42

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### 3.4 Discussion

This study compared assessment of soil nutrient conditions of forest sites using two different approaches: (1) direct measures of soil nutrient properties and (2) estimation of soil nutrient properties via field-identified SNRs using soil morphological properties. While the first approach has the advantage of providing direct measurements, it is uncertain whether these measurements reflect the level of plant-available nutrients for several reasons, including (i) uncertainties regarding the best analytical methods, (ii) the spatial and temporal variation in soil nutrient concentrations, (iii) influence of soil temperature on plant nutrient availability, (iv) influence of the temporal nutrient input through seepage, and (v) uncertainties regarding the portion of a soil profile to be sampled (e.g., Powers 1980, Wang 1997, Kimmins 1997, pp. 252).

The shortcoming of the second approach is the lack of a quantitative basis as SNRs are inferred from morphological soil characteristics and indicator plant species. However, morphological soil characteristics do reflect the integrated long-term effect of soil processes and hence, to some degree soil nutrient conditions. Similarly, indicator plant species do reflect to some degree the level of plant-available soil nutrients including those that are difficult to detect through standard soil chemical analysis, such as nutrient inputs by seepage. Thus, while the direct measurements may provide quantities of potentially available nutrient to plants, the use of SNRs may be better suited for efficient estimation of plant-available soil nutrients over time and space (e.g. Mueller-Dombois and Ellenberg 1974, Daubenmire 1976, Klinka *et al.* 1989). The credibility of using SNRs requires validation by quantitative characterized classes. Agreement between the 'subjective' and 'objective' classes will lend credibility to both approaches, while disagreement would not resolve uncertainty whether soil nutrient conditions were assessed correctly with either approach.

I used several methods to evaluate agreement between measured soil nutrients and field-estimated SNRs. Without *a priori*-classification, there was only a weak relationship between soil chemical measures and SNRs, as indicated by a large scatter and overlap of SNRs when plotted on principal components of soil properties (Figure 3.1). In general, soil data rarely show distinct clustering in space, as they tend to be weakly structured (Webster and Oliver 1990). However, the relative low percentage of explained variation by the first and second components and the differential loading of soil properties on the first three components suggest complexity of the studied soil nutrient gradient. This may also explain the weak relationship with SNRs, which represent a one-dimensional soil nutrient gradient. On low-elevation sites on Vancouver

Island, the essential mineral soil nutrients were all positively associated with the first PCA component, indicating a much more homogeneous soil nutrient gradient (Kabzems and Klinka 1987a). The indicated heterogeneous nutrient gradient in this study may be partly caused by differences in soil nutrient gradients in different climatic regions within the study area.

Seventy percent agreement was obtained between field-identified SNRs and a quantitative classification based on all measured soil properties. However, the *a posteriori* quantitative classification cannot be viewed as being completely independent of the *a priori* SNR classification. The reason is that discriminant function analysis (applied to a data set grouped according to SNRs) assigns unequal weights to soil nutrient properties to maximize discrimination between SNRs. Nevertheless, this method provides a good assessment of the relationship between SNRs and measured soil properties. Chen *et al.* (1998b) found a similar agreement for continental high-elevation soils. However, this study compared only three SNRs; thus percent of correct allocation by chance was increased to 33 % compared to 20%, when using five classes. This suggests that the relationship between direct soil nutrient measures and SNRs was somewhat weaker for coastal high-elevation soils than for their continental counterparts.

High variable loadings of min-N, tN, C/N ratio, and SEB on the first discriminant function show that a soil nitrogen gradient and to some extent a soil extractable base gradient was captured by field-identified SNRs. This was also corroborated by the univariate approach. Min-N of the mineral soil, other nitrogen-related properties (tN and C/N ratio) of the forest floor and mineral soil, as well as extractable bases of the mineral soil showed a consistent increase in order from poor to rich sites. This is in agreement with several studies in the area that all found that SNRs might be viewed as nitrogen-driven indices of plant-available soil nutrients (Klinka and Carter 1990, Klinka *et al.* 1994, Chen *et al.* 1998b). Since it is commonly agreed that nitrogen is the most common growth-limiting nutrient in forest soils (e.g. Keeney 1980, Lea and Ballard 1982, Vitousek *et al.* 1982, Carter *et al.* 1998), a strong relationship between nitrogen-related properties and SNRs is desired. This study showed that in coastal high-elevation soils mineral soil min-N and forest floor C/N ratio predicted SNRs equally well as all measured soil properties together. This indicated that the nitrogen gradient was well captured by the heuristic field-procedure, despite a relatively heterogeneous nature of the soil nutrient gradient in the study area.

To further explore the heterogeneity of the soil nutrient gradient in the study area, I examined the variation in nutrient concentrations with climate according to orographic and continentality strata. There was little variation in most soil nutrient properties between montane and subalpine sites but most soil nutrient properties varied with continentality. Consistent trends with increased continentality suggest an influence of higher summer temperature and lower precipitation on soil processes. However, in this study, I focused the interpretation of above results on the potential of the different soil nutrient properties to quantify SNRs at a regional scale.

A few soil properties (e.g., forest floor eP and eK, and mineral soil eSO<sub>4</sub>-S, tN, eK, and eP) displayed different trends with climate (represented by continentality strata), but showed none or only a weak relationship with SNRs, indicating a low potential for quantification of field-identified SNRs. Other properties (forest floor tN and C/N ratio and mineral soil tC and C/N ratio) showed more or less consistent trends for poor, medium, and rich sites, indicating a potential for relative characterization of SNRs across the continentality gradient. Min-N showed a strong relationship to SNRs but was not significantly related to continentality strata, indicating a strong potential for quantitative characterization of SNRs. These findings support the practice of (i) interpreting SNRs as nitrogen-driven index of soil nutrient availability and (ii) using min-N as the sole property for quantification of field-identified SNRs (e.g. Klinka *et al.* 1994, Chen *et al.* 1998b).

The mean values of mineral soil min-N for poor (9.1 mg kg<sup>-1</sup>), medium (15.3 mg kg<sup>-1</sup>), and rich (33.3 mg kg<sup>-1</sup>) sites agreed with results from previous studies from other climatic regions. The agreement was particularly high with a study carried out in low-elevation coastal Douglas-fir (*Pseudotsuga mezesii*) forests on Vancouver Island, which defined poor, medium, and rich sites by the mean values of min-N of 9.5 mg kg<sup>-1</sup>, 17.5 mg kg<sup>-1</sup>, and 31.1 mg kg<sup>-1</sup>, respectively (Klinka and Carter 1990). Studies carried out in continental boreal forests found similar values for poor and medium sites but slightly higher values for rich sites (51.9 mg kg<sup>-1</sup> on subalpine sites (Chen *et al.* 1998b) and 47.0 mg kg<sup>-1</sup> on montane sites (Klinka *et al.* 1994)). The general agreement across different climatic regions is surprising considering differences in parent material and soil types. It indicates that the heuristic field procedure (field-identified SNRs) is capable of providing reliable estimates of min-N across different climatic regions. Comparison of mean values of min-N with other studies corroborates the assertion that the soil



nutrient gradient within the range of sampled amabilis fir stands is relatively narrow and encompasses only three SNRs.

A similar accountability of direct soil nutrient measures and SNRs in the variation in amabilis fir site index justifies the use of field-identified SNRs as estimates of soil nutrient availability. A generally weak relationship between site index and soil nutrient measures has been found in several other studies (e.g., Wang 1992, Klinka *et al.* 1994, Chen *et al.* 1998b). These results reflect the large number of factors that directly or indirectly affect site index. The strength of the relationship depends on the nutrient requirements of the studied species, including potential mediation of nutrient uptake on nutrient-poor sites by mycorrhizal fungi. It is known that amabilis fir is an intensely mycorrhizal (*Cenococcium graniforme*) species (Minore 1979). The association with mycorrhizae fungi circumvents the direct nutrient uptake and may also explain why min-N was not selected as a predictor of site index.

Forest floor and mineral soil properties explain a similar proportion of the variation in site index; this indicates the relatively high importance of the forest floor on tree growth on coastal high-elevation sites. While this may be partly due to a higher percentage of fine roots of amabilis fir being located in the forest floor (Brooke *et al.* 1970, Crawford and Oliver 1990), I always found roots in the mineral soil on the studied second growth sites. The only soil properties significantly related to site index were mineral soil and forest floor tN and C/N ratio, whereas concentration of mineral soil min-N was not related to site index. While similar results were found in some previous studies (e.g. Wang 1992, Klinka *et al.* 1994), other studies found a strong relationship of min-N and site index (Kabzems and Klinka 1987b, Kayahara 1992). The discrepancy in results may be explained by differences in tree species including the effect of association with mycorrhiza and differential climate and soils between regions (Powers 1980, Klinka *et al.* 1994). However, the lack of a relationship of site index with the leading soil property to describe the nutrient gradient and SNRs poses questions either on the general usage of the mineral soil min-N for quantification of SNRs, or on the usage of site index as productivity measure in soil fertility studies.

It has already been stated that results may depend on the choice of sampling and on the analytical procedure used. In this study, as in many others, min-N was measured after anaerobic incubation as  $\text{NH}_4^+$ -N. Recent work in Britain suggests that min-N measured as  $\text{NO}_3^-$ -N after aerobic incubation is the best index of soil nitrogen in relation to Ellenberg's (1974) indicator species values (Wilson *et al.* 1998). However, Wilson *et al.* (1998) also report significant

correlation between chemical soil nutrient measures and the General Yield Class for Scots pine and Japanese larch but no such relationship for oak. These findings also suggest that the relationship between indices of soil nitrogen and forest productivity varies with species and a universal index or analytical procedure to determine plant available nitrogen (nutrients) has yet to be found. To shed light on the relationships of nitrogen mineralization across regions with forest productivity, more detailed studies should consider the use of aerobic and *in situ* incubation methods for determining N-mineralization and usage of total biomass or aboveground net primary production as productivity measures (e.g. Nadelhoffer *et al.* 1983, Zak *et al.* 1986, Zak *et al.* 1989, Reich *et al.* 1997).

## 4. Radial Growth of Subalpine Amabilis Fir in Relation to Weather and Continentality (Study 3)

### 4.1 Introduction

The dendroclimatological investigations of weather – tree growth relationships have contributed to the identification of spatial weather patterns and reconstructions thereof (e.g., La Marche and Fritts 1971, Villalba *et al.* 1992, Chbouki *et al.* 1995, Wiles *et al.* 1996, Villalba and Veblen 1997, Luckman *et al.* 1997). These investigations focused on extracting the information on the short-term or long-term variation in climate contained in tree-ring chronologies. Best results in reconstruction of climate were obtained using tree-ring networks; i.e., a large number of tree-ring chronologies covering a large area (e.g., Meko *et al.* 1993). Sampling on different sites over a large area accounted for the spatial variability in tree growth response. This is especially important in mountainous areas, where climatic gradients may be steep and differences in tree-growth response may occur over relative short distances (Tessier *et al.* 1997).

Ecological studies on the influence of climate on tree growth demonstrated that growth response to climate variations might vary with species, aspect, altitude, and longitude (e.g., Brubaker 1980, Graumlich 1992, Rolland 1993, Peterson and Peterson 1994, Kienast *et al.* 1987, Smith and Laroque 1998, Dittmar and Elling 1999, Laroque and Smith 1999, Rolland *et al.* 1999, 2000). These studies inferred information on the climate – tree growth relationship by studying the growth response of trees to weather patterns along climatic gradients. For example, in southern Germany Dittmar and Elling (1999) found that growth of Norway spruce (*Picea abies* [L.] Karst) was limited by water supply below 600 m in elevation but by cool summer temperatures and solar radiation above 800 m.

Several studies showed that growth of northern or high-elevation tree species is limited by cool summer temperatures (e.g., Conkey 1979, Briffa *et al.* 1988, Colenutt and Luckman 1991, 1995, D'Arrigo *et al.* 1992, Earle *et al.* 1994, Schweingruber *et al.* 1993, Smith and Laroque 1998, Laroque and Smith 1999). However, for some areas, particularly the Pacific Northwest, winter precipitation and spring snowpack appear to be important determinants of tree growth on high-elevation sites (Heikkinen 1985, Graumlich and Brubaker 1986, Peterson and Peterson 1994, Smith and Laroque 1998, Laroque and Smith 1999).

Initial work by Dobry *et al.* (1996) and Dobry and Klinka (1998) demonstrated the climate sensitivity of ring width and maximum latewood density of high-elevation amabilis fir. Ring width (RW) was negatively related to the previous year's summer temperatures and current year's July precipitation, whereas maximum density (MXD) was strongly positively related to spring and summer temperatures. However, these results were based on RW and MXD chronologies from one site and therefore may not describe the regional response well. The present study represents the first in-depth investigation of the relationship between amabilis fir radial growth and climate.

Throughout the native range of amabilis fir, the Coast and Insular Mountains in southern British Columbia are influenced by the same large-scale weather systems. In general, similar variations in climate parameters within an area influenced by the same large-scale weather patterns may create (i) similar growth responses throughout the area, and (ii) differential responses in different parts of the area (e.g., differential growth response in trees growing under warmer and drier conditions compared to trees growing under cooler and wetter conditions) (Brubaker 1980). Because the climatic amplitude of amabilis fir is relatively narrow (Klinka *et al.* 2001), a similar growth response of amabilis fir to year-to-year climate variations may be expected on high-elevation sites across southern BC.

However, along the longitudinal gradient from west to east, summers get warmer and winters get colder (i.e. thermic continentality increases). In general, there is a gradient of decreasing precipitation associated with increasing thermic continentality. Amabilis fir is a moisture-demanding species and is very susceptible to winter frost and does not tolerate frozen soil (Krajina 1969, Brooke *et al.* 1970, Klinka *et al.* 2001). It may be that summer drought or winter frost may become important growth determinants with increasing continentality.

Establishment of the weather pattern– radial growth relationship along a continentality gradient will improve understanding of the effect of climate on growth of amabilis fir. The recent warming trend and the questions of how climate change will affect tree-growth and vegetation patterns have increased interest in the climate – tree growth relationships of high-elevation tree species. Thus, this study will not only contribute to a better understanding of the autecology of the species, but may also allow for better predictions of the species-specific growth response to global warming scenarios.

The objectives of this study were (i) to examine the spatial variation of ring width pattern in high-elevation amabilis fir, (ii) to identify climate factors that influence its radial growth, and

(iii) to determine whether the climate factors limiting radial growth vary with continentality. These objectives were achieved by comparing continuous data series (tree-ring chronologies and monthly climate data) as well as discontinuous data series (pointer years in tree ring series) (Schweingruber *et al.* 1990, Dittmar and Elling 1999).



Figure 4.1. Location of 11 study sites in four different continentality strata (circles), 4 low-elevation climate stations (solid squares), and 3 high-elevation snow course stations (stars).

## 4.2 Materials and Methods

### *Sampling and Sample Preparation*

Study stands were closed canopy stands dominated or co-dominated by amabilis fir on high-elevation sites with intermediate soil moisture and soil nutrient conditions. Intermediate sites were selected in order to obtain information about the general influence of climate fluctuations on radial growth, exclusive of site influences. As three RW chronologies and one MXD chronology from the MW stratum were already available (Dobry *et al.* 1996; and Dobry, unpublished data), I selected three sites in the ML stratum, one site in the SM stratum, and four sites in the SC stratum (Figure 4.1, Table 4.1). Sampling in the SC stratum was emphasized over

sampling in the SM stratum because differences in growth response to climate variations were expected to be strongly expressed close to the distribution limits of the study species.

Table 4.1. Characteristics of the study sites ordered from west to east. ML is maritime-leeward, MW is maritime-windward, SM is subarctic, and SC is subcontinental continentality stratum.

Location	Code	Latitude (°N)	Longitude (°W)	Elevation (m)	Continentality stratum	Aspect
Mt. Cain	MCA	50°14'	126°20'	1300	ML	W
Mt. Washington	MWA	49°46'	125°18'	1150	ML	S
Mt. Arrowsmith	MAR	49°15'	124°34'	1250	ML	E
Capilano 1*	CA1	49°31'	123°04'	1000	MW	W
Capilano 3*	CA3	49°31'	123°05'	1000	MW	N
Edwards Lake*	EDL	49°31'	123°38'	1130	MW	N
Hurley Pass	HUP	50°33'	123°00'	1350	SC	W
Mt. Whistler	MWH	50°03'	122°50'	1430	SM	N
Nahatlatch	NAH	50°01'	121°39'	1400	SC	N
Boston Bar West	BBW	49°52'	121°29'	1150	SC	E
Boston Bar East	BBE	49°50'	121°20'	1330	SC	N

\* Data from Dobry *et al.* 1996 and Dobry, unpublished data

At each selected stand, 20 to 30 dominant, undamaged trees were selected for sampling. From every tree, two cores were extracted from opposite directions perpendicular to the slope to avoid reaction wood. The cores were placed on core holders in the field with masking tape. After air drying, they were glued onto the same holders and sanded to a high polish (up to 400 grit). Cores were crossdated using marker rings (conspicuously narrow rings occurring in most cores on a site) (Stokes and Smiley 1968) and ring width was measured using a scanner and the WinDENDRO<sup>TM</sup> system (Guay *et al.* 1992). Crossdating is a procedure to synchronize series of tree-ring properties so that the exact year of ring formation is known and comparison can be made with other time series (e.g. climate records). After measuring, dates were checked using the program COFECHA (Holmes 1983, Grissino-Mayer *et al.* 1997). Measurement and dating errors were identified and corrected. When dating problems could not be resolved by careful inspection of the cores, these cores were truncated or deleted from the analysis.

To obtain series of maximum density, a sub-sample of the well-correlated cores that did not show reaction wood or damage was selected from every sampled site for densitometric analysis. X-ray densitometry was conducted on the cores by Forintek Canada Inc. according to the procedure described in Parker *et al.* (1980). The RW measurements resulting from x-ray densitometry matched results obtained using the WinDENDRO system only for 40% of the cores. Unfortunately samples submitted to Forintek fell apart during sample preparation and could not be placed together correctly. Thus, only MXD data from cores that had matching ring width measurements from scanning and x-ray were used for the analysis. To ensure sufficient sampling depth, data from the three ML sites were merged and, likewise, the data from all sites in the SC stratum. Since only two cores from the SM site were correctly measured by the x-ray technique, a data set for building a MXD chronology could not be obtained for this stratum. The dating of the MXD series was verified using COFECHA (Holmes 1983).

The raw RW and MXD data were detrended by fitting a cubic smoothing spline to every series (Cook and Peters 1981, Blasing *et al.* 1983) as provided by the ARSTAN program (Cook 1985) that retained 50 % of the variance at 50-year intervals. This procedure was chosen, because a visual inspection of the series indicated that abrupt growth changes occurred in the majority of them that were unlikely responses to climate but were attributed to stand effects, e.g., death of a neighboring tree. The 50-year spline was chosen because visual inspection of the fitted spline to the data indicated that a more flexible spline was not needed, while applying a less flexible spline did not remove the abrupt growth changes. After fitting the spline, every series was indexed by dividing the raw measurement by the curve value (RW series) or by subtracting the raw measurement by the curve value (MXD series). The series' for each site were averaged in order to obtain standard chronologies using the bi-weight robust mean. Considering that statistical analysis of time series assumes non-correlated (white-noise) chronologies (Monserud 1986), residual chronologies were developed by applying autoregressive models to each series. All these operations were carried out using the ARSTAN program (Cook 1985).

### ***Statistical Analysis***

The variation in ring width patterns in the study area was examined using 11 residual RW chronologies, 3 previously developed chronologies (Dobry 1994, Dobry *et al.* 1996, and Dobry unpublished data) and 8 chronologies developed in this study. Three methods were used

to assess similarity or dissimilarity between RW chronologies: i) comparison of occurrence of marker rings, ii) correlation analysis, and iii) principal components analysis (PCA) applied to the residual RW chronologies for the common 251 year period of 1740 to 1991. The period was chosen so that at least 5 ring-width series per site spanned the entire period. In the PCA sites are usually entered as variables and years as cases (Peters *et al.* 1981), so that the PCA components indicate common patterns of variation in tree ring chronologies (e.g., Brubaker 1980, Graumlich 1992, Villalba and Veblen 1997).

The climate data were taken from four low-elevation stations within the study area, i.e., Nanaimo, Powell River, Agassiz, and Hope (Environment Canada) (Figure 4.1, Table 4.2) as no climate station at higher elevations has a sufficiently long climatic record. The climate stations were selected based on the length and quality (continuity and homogeneity) of the climate records. Monthly mean temperatures and monthly total precipitation were transformed into standard deviations and missing values for individual stations were calculated according to the mean deviation from the other stations for that particular month and year. Then the standard deviations were regionalized by calculating the arithmetic mean of the normalized standard deviations using a routine contained in the ITRDB program library (Grissino-Mayer *et al.* 1997). It has been shown that regionalized data are more closely related to tree-ring chronologies because of peculiarities associated with single station data that are not shared with the sample site (Blasing *et al.* 1981). Therefore the regionalized data were used for all correlation analysis with tree-ring data across the study area.

In addition to the monthly climate data, information on snowpack on April 1<sup>st</sup> was acquired for the three high-elevation snow survey stations with the longest records, i.e., Grouse Mountain (49°23' N, 123°05' W, 1100 m), Forbidden Plateau (49°39' N, 125°13' W, 1130 m), and Tenquille Lake (50°32' N, 122°56' W, 1680 m) (BC Ministry of Environments and Parks, Victoria) (Figure 4.1). Snow data were also regionalized by averaging the standardized deviations from the average snow depths of the three stations.



Table 4.2. Normals of mean monthly temperatures (T, °C) and monthly precipitation (P, mm) of the 4 stations used to calculate regional monthly climate variables indicating similar seasonality across the study area, and two high-elevation stations (last two columns).

Station	Powell River		Nanaimo		Agassiz		Hope		Hollyburn Ridge		Hope Slide	
Month	T	P	T	P	T	P	T	P	T	P	T	P
Jan	3.4	127	2.2	166	1.8	217	0.3	259	-1.7	336	-2.6	156
Feb	4.7	95	4.0	127	4.4	171	3.4	189	0.0	292	-0.2	121
Mar	6.3	80	5.5	106	6.7	147	6.1	153	0.6	246	2.7	88
Apr	9.2	58	8.3	63	9.8	119	9.6	123	2.8	186	5.8	75
May	12.8	52	12.0	43	13.2	89	13.2	81	6.1	151	8.8	74
Jun	15.9	54	15.0	40	15.7	80	15.9	69	9.5	133	12.2	57
Jul	18.3	37	17.5	25	18.0	55	18.4	49	12.9	108	14.7	49
Aug	18.1	47	17.3	30	18.0	59	18.5	48	13.0	120	15.0	49
Sep	15.2	56	14.4	40	15.6	96	15.7	100	10.5	176	11.2	65
Oct	10.8	117	9.5	102	10.9	180	10.5	186	5.8	343	6.6	108
Nov	6.7	141	5.1	148	6.0	224	4.8	249	0.9	397	0.9	192
Dec	4.4	143	2.9	192	3.1	236	1.6	268	-1.6	391	-2.2	163
<b>Ann.</b>	<b>10.5</b>	<b>1006</b>	<b>9.5</b>	<b>1109</b>	<b>10.3</b>	<b>1672</b>	<b>9.8</b>	<b>1773</b>	<b>4.9</b>	<b>2878</b>	<b>6.1</b>	<b>1197</b>

The relationship between weather and tree-ring data was obtained by comparing continuous data series; i.e monthly or seasonalised temperature and precipitation data with the tree ring chronologies using correlation analysis. As a second approach, single-year analysis was applied. On intermediate sites in high-precipitation climates, climate may be limiting tree-growth only in climatically extreme years (Graumlich 1992). Single-year analysis concentrates on these extreme years and may be able to derive a clearer picture of the limiting climate factors in complementing the correlation analysis (Kienast *et al.* 1987, Dittmar and Elling 1999).

To provide an objective means for selecting years of low and high growth, single years were selected according to the principal components scores. Five years were selected with the highest positive and negative scores on the first PCA component, corresponding to years with wide and narrow ring width throughout the study area (Villalba and Veblen 1997). Five years

with highest positive and negative scores on the second component, and indifferent scores on the first component ( $-1 < \text{PCA1} < 1$ ) were selected to depict between-site differences in growth pattern. For these selected years, deviations from the long-term mean of seasonalized temperature and precipitation were plotted to identify common climate fluctuations associated with different tree-ring patterns.

### **4.3 Results**

#### ***Variation in Ring-Width Pattern Across the Study Area***

Chronology statistics for the 11 RW chronologies described the variation of residual chronologies as well as the variance held in common between all the series used to build the chronologies. Mean sensitivity (MS), standard deviation (SD), and the common variance explained by the first principal component of the series (CV) were similar for all RW chronologies (Table 4.3). Measures of the high-frequency variation (MS, SD) were relatively low compared to chronologies from semiarid sites, but were comparable to the statistics describing the chronologies in eastern North America, the Pacific Northwest, Europe, and South America (Graumlich 1992, Villalba and Veblen 1997, Dittmar and Elling 1999, Laroque and Smith 1999). Differences observed in signal-to-noise ratio (SNR) merely reflect differences in sample size, as the SNR varies non-linearly with the number of trees (Wigley *et al.* 1984). The variance held in common (CV varied between 44.3% and 52%) between all of the series from any one stand indicated a strong climate signal in all chronologies (Table 4.3).

The rings for 1775, 1779, 1810, 1876, 1899, 1956, 1974, and 1991 were distinctly narrow in virtually all ring width series throughout the study area and thus these years represent negative pointer years (Schweingruber *et al.* 1990). In addition to these common pointer years, the rings for 1752, 1815, 1945, 1952, and 1953 were negative pointer years for MW and ML sites, while the rings for 1764, 1893, 1894, 1925, 1950, 1951, and 1980 were negative pointer years for SM and SC study sites.

Correlation at high significance levels ( $p < 0.01$ ) between all chronologies (Table 4.4) indicated a strong common ring width pattern across the entire study area. However, chronologies from SM and SC sites were more strongly correlated with each other than with chronologies from MW and ML sites and vice versa. This suggested differences in ring-width patterns, which are associated with the continentality gradient.

Table 4.3. Chronology statistics. Codes for ring width (RW) chronologies are as given in Table 4.1, codes for maximum density chronologies refer to continentality strata (MMW is maritime-windward, MML is maritime-leeward, and MSC is subcontinental maximum density chronology). The autocorrelation is given for the standard chronologies, the autoregressive model (AR) model refers to the order used to develop residual chronologies. All other statistics are given for the residual chronologies.

Chronology	Site	Auto-correlation	AR mode l	Signal-to-Noise ratio	Common variance	Standard deviation	Mean sensitivity	No. of series
RW	CA1	0.24	2	11.9	49.0	0.20	0.23	30
	CA3	0.26	2	11.3	48.5	0.19	0.19	32
	EDL	0.22	2	11.4	44.8	0.15	0.17	28
	MAR	0.11	0	18.5	48.9	0.18	0.21	36
	MWA	0.20	1	16.6	46.2	0.15	0.17	36
	MCA	0.20	1	26.2	52.0	0.17	0.19	42
	MWH	0.25	2	24.8	48.6	0.16	0.15	49
	HUP	0.29	2	29.0	49.9	0.15	0.15	50
	NAH	0.32	1	22.3	44.3	0.15	0.14	53
	BBW	0.13	1	14.8	46.2	0.14	0.16	33
	BBE	0.26	2	20.7	44.3	0.14	0.16	52
MXD	MMW	0.14	1	2.8	41.8	0.04	0.04	5
	MML	0.16	3	2.6	42.4	0.35	0.43	7
	MSC	0.32	2	3.8	41.0	0.42	0.53	10

Two components were extracted using PCA for the common interval from 1740 to 1991. The first and second components explained 61% and 15% of the variance, respectively. All sites loaded highly positively on the first component, indicating that the first PCA component was capturing the ring-width pattern common across the study area (Figure 4.2). On the second PCA component, chronologies from MW sites loaded highly positively, chronologies from ML sites loaded weakly positively, but chronologies from SM sites loaded weakly negatively and chronologies from SC sites loaded highly negatively; thus, the chronologies were ordered according to the continentality gradient (Figure 4.2).

Table 4.4. Correlation between 11 residual ring width chronologies for the period 1740 to 1991. All correlations are significant at  $\alpha = 0.01$ .

	BBE	BBW	NAH	HUP	MWH	CA1	CA2	EDL	MAR	MWA	MCA
BBE	1										
BBW	.76	1									
NAH	.86	0.73	1								
HUP	.78	.65	.84	1							
MWH	.72	.65	.71	.77	1						
CA1	.42	.46	.40	.45	.54	1					
CA3	.36	.39	.38	.37	.46	.83	1				
EDL	.41	.49	.39	.43	.60	.73	.63	1			
MAR	.49	.54	.50	.52	.67	.63	.55	.71	1		
MWA	.43	.46	.42	.49	.59	.63	.51	.68	.76	1	
MCA	.45	.45	.45	.53	.65	.55	.44	.64	.73	.66	1

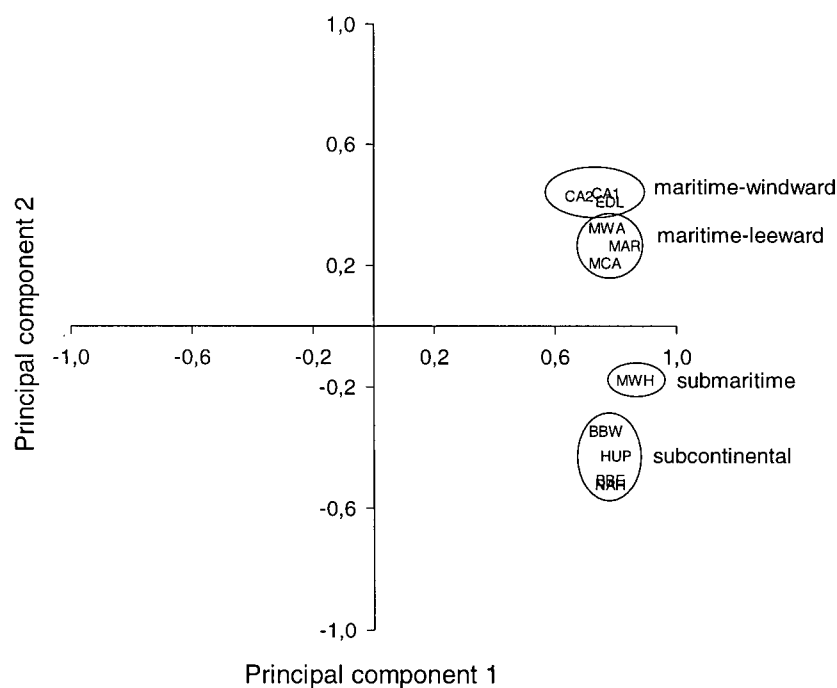


Figure 4.2. Loadings of the 11 RW residual chronologies on the two extracted principal components for the common period of 1740 to 1991. Circles encompass sites within the same continentality stratum.

Considering the similarity in ring-width patterns (as shown by the PCA) between (i) MW and ML sites and (ii) SM and SC sites, I built two regional chronologies. I pooled all detrended series from sites in the MW and ML strata to obtain the regional chronology for the maritime-windward – maritime-leeward stratum (M chronology). Similarly, I used the pooled series data from all sites within the subarctic and subcontinental strata to obtain the regional chronology for these two strata (SS chronology) (Figure 4.3). The same dendrochronological techniques for constructing these regional chronologies were used as described earlier for the individual stand RW chronologies.

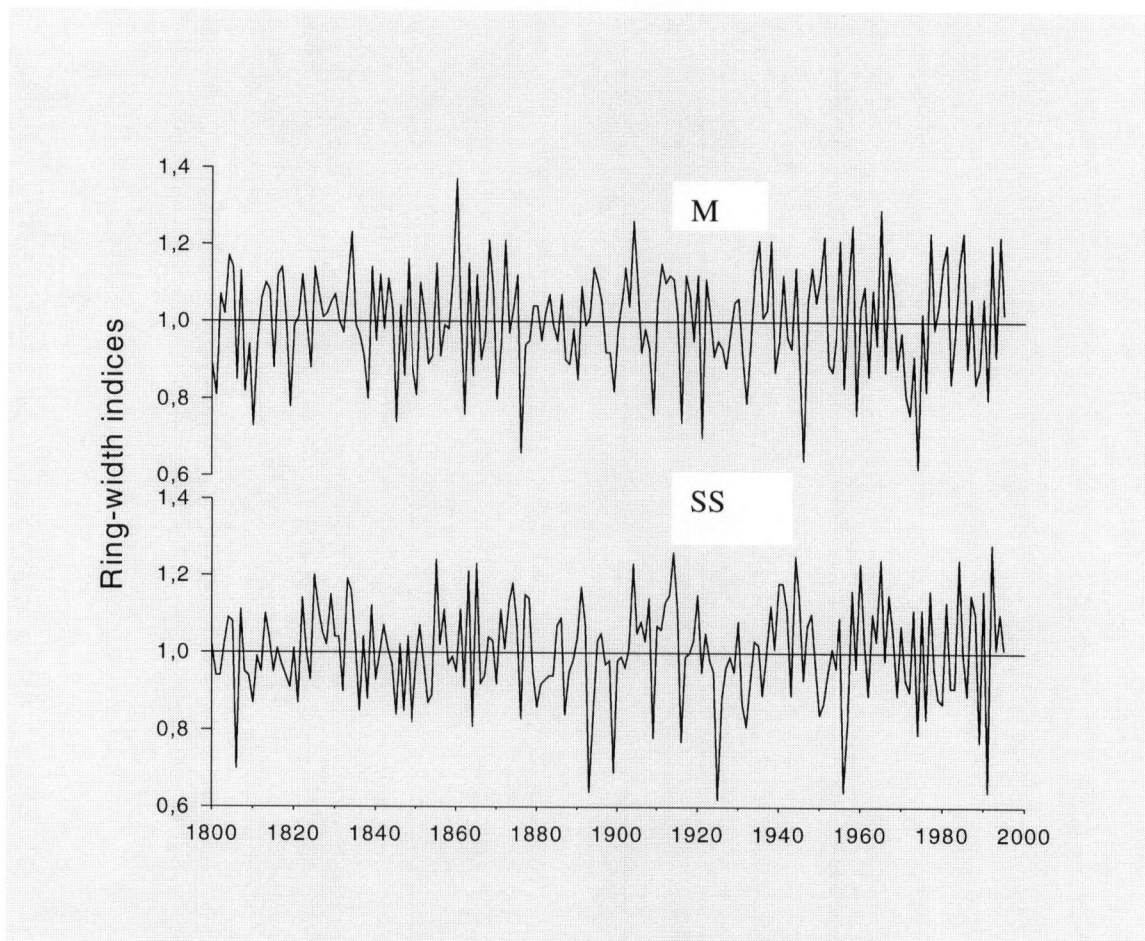


Figure 4.3. Regional ring-width chronologies for the maritime (M) and subarctic/subcontinental (SS) strata, respectively.

#### ***Tree-ring Chronologies in Relation to Continuous Series of Climate Variables***

Correlations of the regional RW chronologies with climate variables (34 variables, mean monthly temperature and total monthly precipitation for a sequence starting in May of the year prior to ring formation and ending in September of the year of ring formation, respectively) for the period 1924 to 1992 followed similar seasonal patterns. A negative correlation with previous

May to August mean temperatures was followed by a positive relationship to monthly temperature means for October to April, a weak negative relationship to May temperature, and a positive relationship to the monthly temperature means from June to August. The correlation with precipitation mirrored the correlation pattern for temperature (Figure 4.4).

Differences between the regional RW chronologies for the two continentality strata occurred in strength rather than in sign. The M chronology, which featured a significant negative relationship to previous July temperature and a significant positive relationship to previous August precipitation ( $\alpha=0.01$ ), showed a stronger relationship to previous summer conditions than the SS chronology. The SS chronology, which featured a significant positive correlation with mean monthly temperature from October to March, showed a stronger relationship to winter temperature than the M chronology. Both chronologies displayed a strong negative relationship to October (significant only for the SS chronology) and March monthly precipitation sums and a positive relationship to July temperature. The M chronology was also significantly positively related to June temperature and significantly negatively related to June precipitation (Figure 4.4). Similar responses to year-to-year climatic variation were obtained when the 11 RW chronologies of individual stands were used in correlation analysis (Figure 4.5). While this analysis shows the variability in response between individual stands, the same similarities and differences between chronologies in the M and SS strata remained, indicating that the M and SS chronologies represent the regional growth response of the two continentality strata well.

Correlations of seasonalised climate data (mean temperature and precipitation sums for the previous summer, defined as June to August of the previous year, winter, defined as October to March, spring, defined as April and May, and current summer, defined as June to August) with the original site RW-chronologies showed the same general trends but also differences between M and SS continentality strata (Table 4.5). Amabilis fir growth on all but one site showed a significant negative relationship to height of snowpack on April 1<sup>st</sup>. Growth was strongly positively related to winter temperatures on all SS sites and strongly negatively related to winter precipitation on all but one SS site. Amabilis fir growth on M sites appeared strongly linked to previous summer conditions with a significant negative relationship to temperature and a significant positive relationship to precipitation on all sites. Responses to current summer conditions were generally negative to precipitation and positive to temperatures, but were significant only for a few chronologies (Table 4.5).

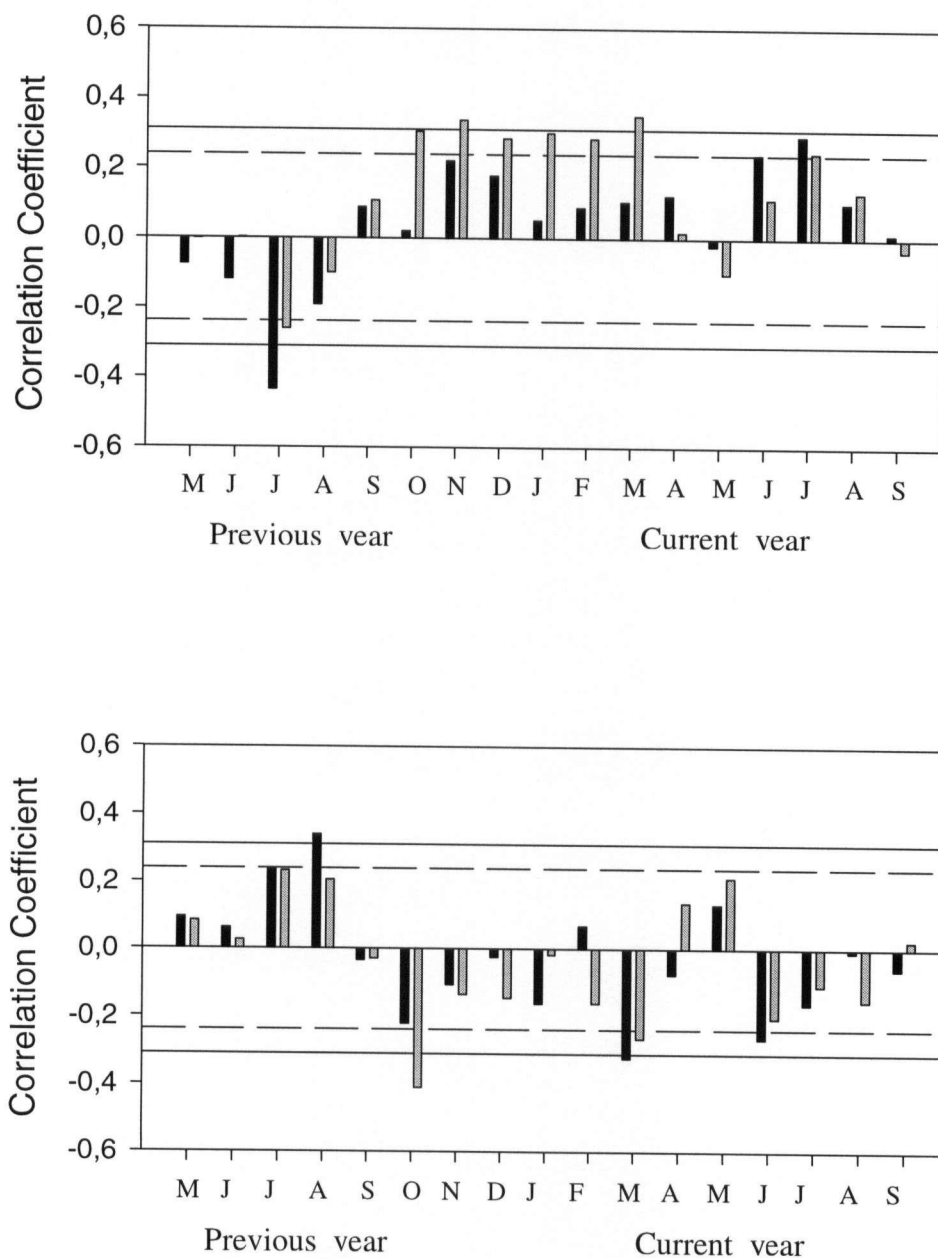


Figure 4.4. Correlation between the regional residual ring-width chronologies (M – black bars, SS – shaded bars) and mean monthly temperature (upper figure) and monthly precipitation sums (lower figure) from May of the year previous to ring formation to September of the year of ring formation for the period 1924 to 1992. Broken and solid horizontal lines indicate significant correlation at  $\alpha=0.05$  and  $\alpha=0.01$ , respectively.

MXD was positively related to temperatures from January through September and strongly positively related to late winter, spring and summer temperatures of the current year (Figure 4.5). The response to the previous year temperatures was negative, as were relationships with winter and current year precipitation, particularly for August and September.

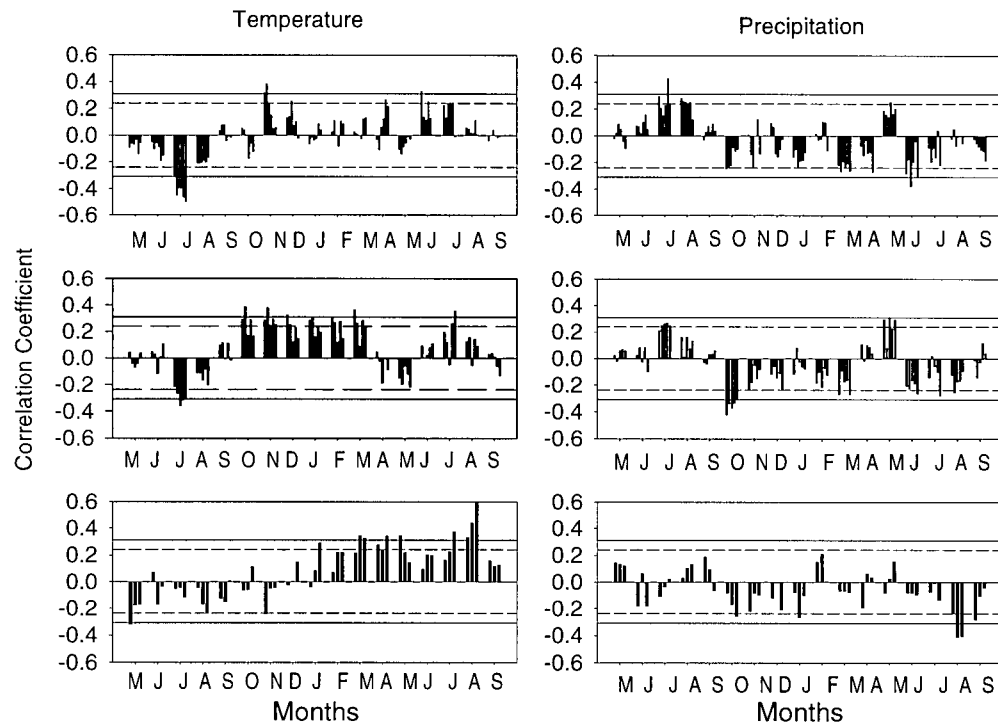


Figure 4.5. Correlation between residual chronologies and mean monthly temperature (left figures) and monthly precipitation (right figures) from previous to current September for the period 1924 to 1992. The upper figures show the correlations with 6 maritime-windward and maritime-leeward chronologies, figures in the middle show correlations with 5 submaritime and subcontinental chronologies, and figures at the bottom show correlations with the maximum density chronologies. Horizontal lines indicate significant levels as defined in figure 4.4.



Table 4.5 Correlation between RW residual chronologies and seasonalised climate data: Mean temperature (T) and total precipitation (P) for the previous summer (previous June to August), winter (previous October to current March), current summer (June to August) as well as snowpack at April 1<sup>st</sup> (snow ht.). The chronologies are ordered by continentality strata; codes for the chronologies are as given in Table 4.1. N is the number of years used for correlation analysis. (\*) and (\*\*) represent significant correlation at the 95% and 99% levels, respectively.

Code	Cont.	prev. Summer		Winter		curr. Summer		April 1 <sup>st</sup>
	Stratum	N = 68		N = 68		N = 68		N = 56
		T	P	T	P	T	P	Snow ht.
CA1	MW	-.41**	.33**	.13	-.18	.24*	-.21	-.44**
CA3	MW	-.39**	.49**	.05	-.12	-.00	.01	-.37**
EDL	MW	-.32**	.24*	-.02	-.25*	.25*	-.33**	-.37**
MAR	ML	-.37**	.38**	.20	-.17	.15	-.22	-.47**
MWA	ML	-.32**	.31**	.14	-.23	.18	-.19	-.41**
MCA	ML	-.27*	.24*	.15	-.35**	.30*	-.30*	-.46**
MWH	SM	-.19	.17	.34**	-.36**	.27*	-.37**	-.36**
HUP	SC	-.19	.25*	.48**	-.30*	.23	-.26*	-.40**
NAH	SC	-.17	.24*	.56**	-.32**	.13	-.23	-.39**
BBW	SC	-.31**	.21	.27*	-.23	-.04	-.26*	-.11
BBE	SC	-.13	.24*	.56**	-.45**	.20	.27*	-.46**

### *Radial Growth in Relation to Weather Patterns Using Discontinuous Data Series*

As spring snowpack may confound the relationship between monthly climate data and ring width (Peterson and Peterson 1994), I applied correlation analysis to subsets of low- and high spring snowpack. I divided the data into two subsets below and above the median of April 1<sup>st</sup> snowpack. Both sets consisted of 30 years of data. For low- and high-snowpack years there was a strong positive correlation between winter temperature and ring width in the SS stratum (Figure 4.6). For low-snowpack years, the negative relationship to previous summer temperatures was enhanced and equally strong for both continentality strata. This relationship

was not the result of a few extreme years, but was linear across the range of observed temperature variation (Figure 4.7).

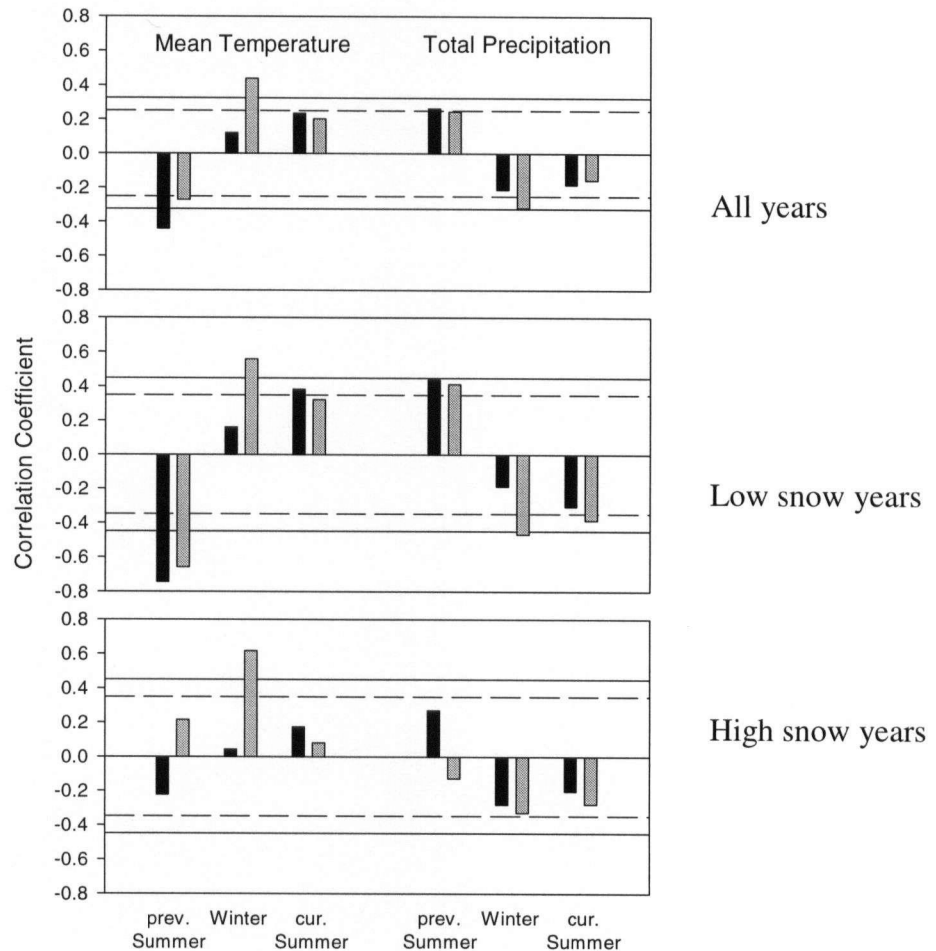


Figure 4.6. Correlation between seasonal climate variables (as defined in Table 4.5) and ring width for all years, years with April 1<sup>st</sup> snowpack below the median ( $n=30$ ), and years with April 1<sup>st</sup> snowpack above the median ( $n=30$ ). Black bars represent correlations with the M chronology and shaded bars represent correlations with the SS Chronology. Horizontal lines indicate significance levels of  $\alpha=0.01$  (solid lines) and  $\alpha=0.05$  (broken lines), respectively.

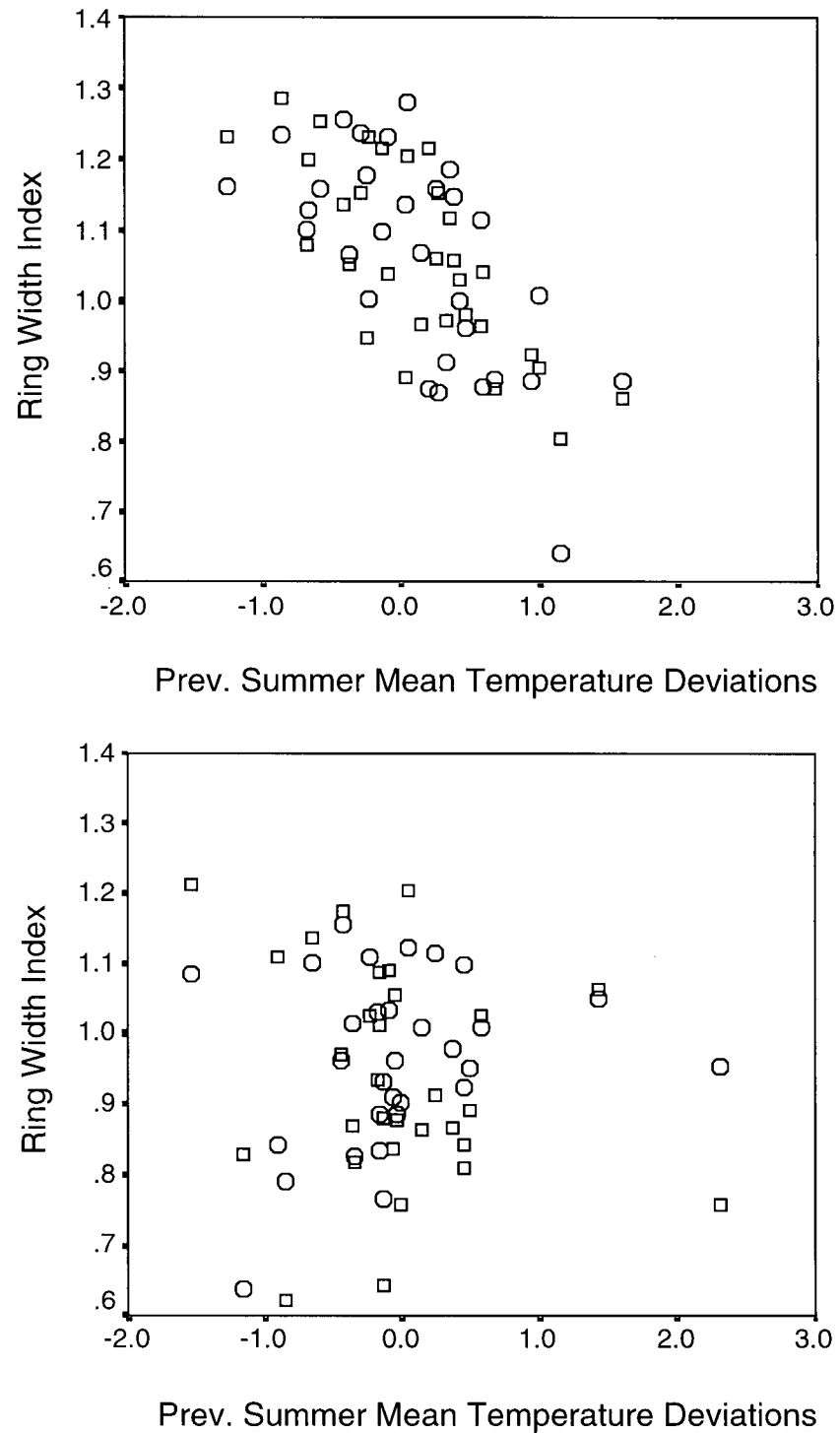


Figure 4.7. Relationship between ring width and previous summer temperature of the M chronology (circles) and the SS chronology (squares) for years with low (upper figure) and high (lower figure) snowpack on April 1<sup>st</sup>.

The five years with the highest negative scores on the first PCA component were all valuable marker rings for crossdating and were considered negative pointer years across the study area (Table 4.6). Narrow rings were either associated with hot summers in the previous year as in 1899 and 1991, or with cool and wet (snowy) winters as for years 1916, 1956, and 1974 (Figure 4.8). All five years with the highest positive scores on the first PCA component were wide, positive pointer years throughout the study area (Table 4.6). Wide rings were associated with cool, wet previous summers and warm, dry winters (Figure 4.8). The snow survey record showed lower than normal snowpacks for 1944, 1965, 1977, and 1984.

Table 4.6. Pointer year analysis: (i) Years with the five highest and lowest scores on the first principal component (PCA1) and (ii) years with the five highest and lowest scores on the second principal component (PCA2) but scores between  $-1$  and  $+1$  on PCA1 in relation to negative (x) and positive (o) pointer years observed in the 11 RW chronologies. Blanks indicate that the particular year was no pointer year in the given chronology. Chronologies are ordered by continentality strata, labelled as in Table 4.1.

Year	BBE	BBW	NAH	HUP	MWH	MAR	MWA	MCA	CA1	CA3	EDL
			SC		SM		ML			MW	
(i) Years with highest positive or negative PCA1 scores											
1899	x	x	x	x	x	x	x	x	x	x	x
1904		o	o	o	o	o	o	o	o	o	
1916		x	x	x	x	x	x	x	x	x	x
1944	o	o	o	o	o	o	o	o	o	o	o
1956	x	x	x	x	x	x	x	x	x	x	x
1965	o	o	o	o	o	o	o	o	o	o	o
1974	x	x	x	x	x	x	x	x	x	x	x
1977	o	o	o	o	o	o	o	o	o	o	o
1984	o	o	o	o	o	o	o	o	o	o	o
1991	x	x	x	x	x	x	x	x	x	x	x
(ii) Years with highest positive or negative PCA2 scores											
1894	x	x	x	x		o	o	o	o	o	o
1908	o	o	o	o	o						
1940	o	o	o	o			x				
1945	o	o	o	o	o		x	o	x	x	x
1950	x	x	x	x				o			
1951	x		x	x		o	o	o		o	o
1957	x	x	x	x	x		o		x		
1973	o	o	o	o	o						
1980	x	x	x	x		o	o	o			
1988	o		o	o				x	x	x	x

The five years with the lowest scores on the second PCA component but without high positive or negative scores on the first component (1908, 1940, 1945, 1973, 1988) were wide positive pointer rings in SS chronologies; however, they were either average or narrow rings in

the M chronologies (Table 4.6). These years were associated with warm dry winters except for the ring of 1973. The five years with the highest scores on the second component, without high positive or negative scores on the first component (1894, 1950, 1951, 1957, and 1980), were narrow negative pointer rings in SS chronologies, but average or wide rings in M chronologies (Table 4.6). These years were associated with cold winters for all years but 1980 (Figure 4.9).

#### **4.4 Discussion**

##### ***Common Growth Response to Weather Patterns Throughout the Study Area***

This study confirmed the preliminary conclusion that the year-to-year variation in ring width of high-elevation amabilis fir is consistent within stands and thus facilitates crossdating (Dobry *et al.* 1996). The number of pointer years that were shared by all study sites showed the presence of a consistent regional ring-width pattern for this species at high-elevations. This finding was corroborated by significant correlations between all site-chronologies and the high portion (61%) of variance that was explained by the first PCA component. Such a regional ring width pattern is the result of a similar growth response to seasonal weather patterns (e.g., Fritts 1976; Brubaker 1980).

Three patterns of radial growth response to weather patterns have been previously established for high-elevation and northern tree-line conifers that may apply to the high-elevation coastal forest in BC: (1) a positive response of ring width and maximum density to summer temperatures (e.g., Conkey 1979, Briffa *et al.* 1988, Colenutt and Luckman 1991, 1995, D'Arrigo *et al.* 1992, Schweingruber *et al.* 1993, Earle *et al.* 1994, Smith and Laroque 1998, Laroque and Smith 1999); (2) a negative response of ring width to winter precipitation and to spring snowpack, particularly in the Pacific Northwest (Heikkinen 1985, Graumlich and Brubaker 1986, Peterson and Peterson 1994, Smith and Laroque 1998); and (3) a negative response to previous summer temperatures (Conkey 1979, Peterson and Peterson 1994, Villalba and Veblen 1997, Dobry and Klinka 1998, Laroque and Smith 1999, Parish *et al.* 1999, Rolland *et al.* 2000). All three response patterns were found in RW and the MXD chronologies developed for amabilis fir in this study.

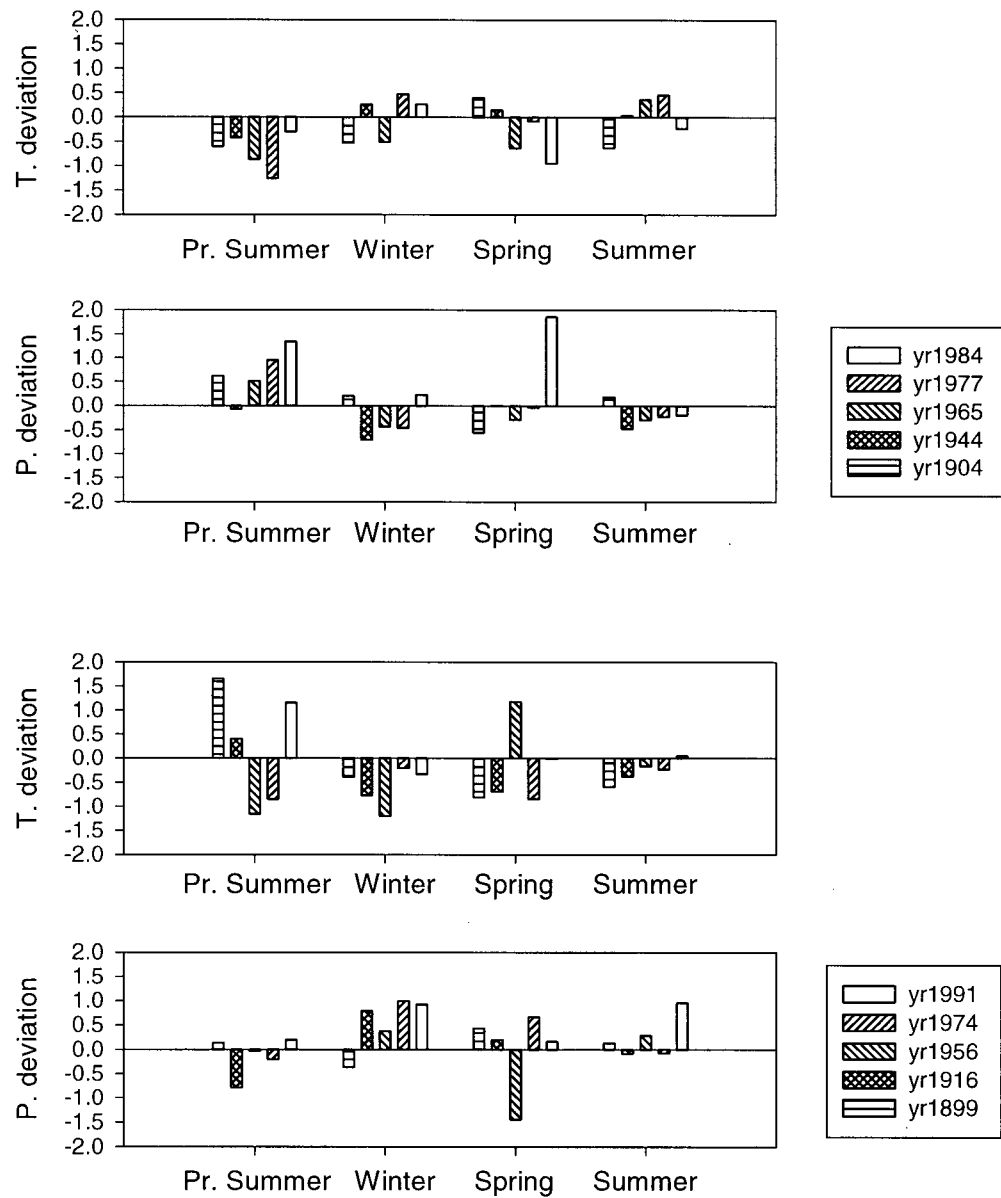


Figure 4.8. Weather pattern for 5 positive (upper two figures) and 5 negative (lower two figures) pointer years throughout the study area. T. deviation is standardized deviation from the average mean temperature, P. deviation is standardized deviation from the average precipitation sums for four seasons: previous June to August (Pr. Summer), previous October to current March (Winter), current April and May (Spring), and current June to August (Summer).

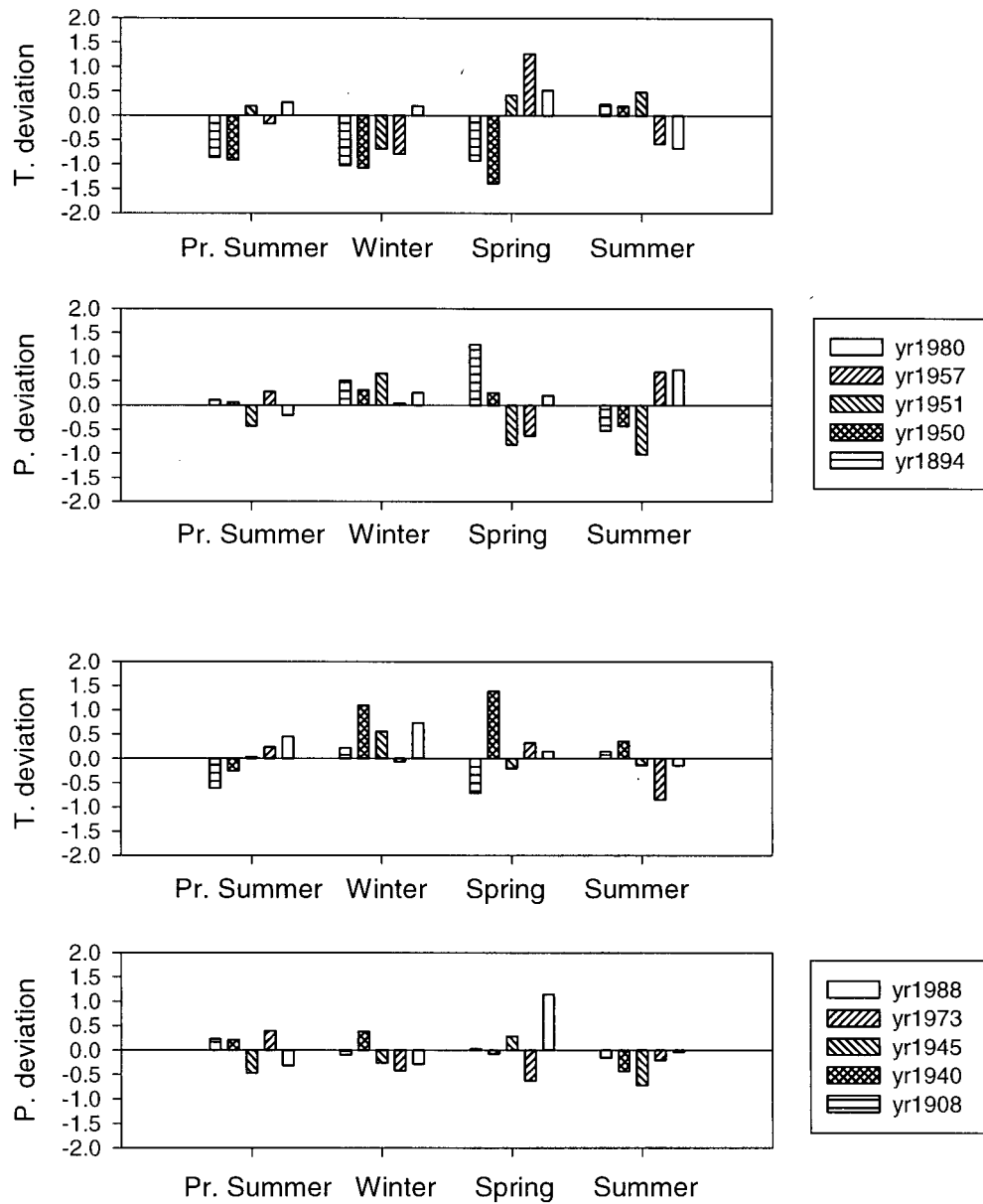


Figure 4.9. Weather pattern for 5 years with the highest positive loading on PCA2 (upper two figures) and 5 years with the highest negative loading on PCA2 (lower two figures) displaying differential growth between continentality strata. T. deviation and P. deviation for four seasons are as defined in Figure 8.

The most consistent growth response on intermediate sites across the study area was a negative influence of spring snowpack on the ring width, regardless of continentality and location. These findings corroborate the earlier results that tree growth in the coastal high-elevation forest is limited by the length of the growing season, which largely coincides with the snow-free period (Brooke *et al.* 1970).

Ring width was only significantly related to current growing season temperature in a few individual chronologies. However, maximum density was clearly favoured by warm summers. This is in agreement with previous findings stating that ring width is not as strongly related to regional summer temperature as maximum density (Schweingruber *et al.* 1979, Conkey 1986, D'Arrigo *et al.* 1992). The positive effect of warmer temperatures on wood formation may be due to earlier onset of the growing season (Fritts 1976) or increased radiation because of its association with lower cloud cover. In general, it is probably best understood as an effect of increased physiological processes and enzyme activity, as the rates of most physiological processes attain a maximum in the range of 20° C to 35° (Kozłowsky and Pallardy 1997). The stronger relationship of summer temperatures to maximum density is due to the close link between the process of cell-wall thickening and the available amount of photosynthates (Larson 1969, Conkey 1986, Antonova and Stasova 1993, 1997).

Considering the positive effect of warmer temperatures in summer on the physiological processes in high-elevation trees, a strong negative effect of warm temperatures during the summer of the previous growing season appears to be counterintuitive. Two explanations have been suggested: (1) high temperatures associated with low precipitation may lead to water stress and thus will negatively influence the physiological processes so that next year's radial growth is reduced (Laroque and Smith 1999), or (2) under the favourable conditions of warm temperatures trees allocate the available resources to height growth and reproductive growth of the next year (Parish *et al.* 1999). For coastal high-elevation amabilis fir, the first interpretation seems unlikely for the following reasons: (i) Teskey *et al.* (1984a) found that amabilis fir in the Washington Cascades did not experience water stress at any point during the growing season of the year 1981, (ii) the observed positive temperature influence during summers on the same year's ring width and maximum density, (iii) the lack of an increase of the negative influence of warm summers with increasing continentality in this study.

The reduced growth in the year following warm summers appears to be due to intrinsic factors and therefore may be considered a consistent feature of evergreen conifers with



preformed height growth (Rolland *et al.* 1999). In trees with fully preformed shoots in the winter bud, height growth is more closely related to the year of bud formation than to the year of shoot elongation (Kozlowsky and Pallardy 1997). Under favourable conditions the onset of buds with a large amount of preformed tissue for the following year (and possibly cones) may direct carbon allocation in the next year to height and reproductive growth rather than radial growth. Less favourable conditions in the year of bud formation will reduce the carbon demand for height and reproductive growth. Ring width in mast years is known to be reduced in several tree species (Eis *et al.* 1965, Jazewitsch von 1953, Dittmar and Elling 1999). There is also evidence that below average precipitation and above average summer temperature may trigger a mast year in the next season (Wachter 1964). Other potential reasons for the observed response include that insect infestations may be triggered by warm previous summers.

### ***Evidence for Differential Response to Weather Patterns Associated with the Continentality Gradient***

Analysis of ring width patterns across the study area suggested that the 11 RW chronologies could be segregated into two groups, which coincided with the combined maritime-windward and maritime-leeward (M) continentality strata and the combined submaritime and subcontinental (SS) continentality strata. Since the study stands within each stratum were isolated from each other but RW chronologies showed very similar ring width patterns and shared nearly all pointer years, the differences between the two strata are very likely caused by differential response to similar weather patterns.

Climate conditions on SS sites differ from those on M sites mainly in having warmer and drier summers and colder and drier winters. If the difference in ring width patterns between the two continentality strata was directly related to continentality, one would expect detectable differences in the response of ring width to summer or winter temperatures. However, there was no evidence of large differences in the growth response to summer conditions between the continentality strata as both featured a similar cycle of negative response to previous summer temperatures and positive response to current year's growth. There was a strong positive relationship to winter temperature that was observed only in the SS stratum and appeared to have occurred independently of spring snow depth, since it remained strong for years with high and low April 1<sup>st</sup> snowpack. A direct link of this response to photosynthetic activity during the winter months is very unlikely, because there is evidence that low water conductance by roots

below root temperatures of 2° C prevents assimilation in amabilis fir (Teskey *et al.* 1984b). The winter temperature response may be attributed in part to winter frost damage. It is well known that amabilis fir is susceptible to winter frost. Temperatures below -35°C may cause crown damage (Klinka *et al.* 2001). The temperature records indicate an extreme frost event for February 1950, which showed a narrow ring only in the SS chronologies. After this event reduced growth continued for another year in most trees growing in the SS stratum, which may indicate severe frost damage in 1950. Although at the same time temperature was also low in the M stratum, critical values might not have been reached because of the generally milder conditions.

A similar response to winter temperatures is well established in Europe for *Abies alba* and was believed to be a typical response of a maritime species (Rolland *et al.* 2000). A positive relationship of winter temperatures and ring width was also reported for *Abies balsamea* ((L.) Mill) growing at high-elevations in the Appalachian Mountains (Marchand 1980). While extreme frost may cause severe damage to buds, needles and branches, generally low winter temperatures may cause stress to trees, because storage products and water cannot be mobilized under these conditions. Furthermore, harsh winter conditions may increase needle loss (Marchand 1980). Amabilis fir relies strongly on the combined photosynthetic capacity of many years of foliage, particularly the previous year's needles (Teskey *et al.* 1984a). High needle retention favoured by relatively mild winters may contribute to the observed response.

## **5 Variations in Tree-Ring Properties of Amabilis Fir with Weather Patterns, Elevation, and Soils (Study 4).**

### **5.1 Introduction**

In southern coastal British Columbia a shortage in timber supply has led to increased harvesting of upper montane and subalpine stands. However, little is known about the productivity and wood quality that can be expected from second-growth crops in high-elevation coastal forests. Amabilis fir is a major timber species in these forests, where it occurs over a wide elevation range. As its timber is used for pulp and construction wood, high wood density is desired. However, the effects of changes in climate associated with the elevation gradient on wood density and other wood properties are not known.

Results from Study 3 suggest that amabilis fir growth on subalpine sites is limited by the length of the growing season and summer temperature. Whether these relationships hold for montane and submontane sites featuring a reduced snow pack, a longer growing season, and higher temperature is not clear. Since summer dry spells occur in the study area, relatively higher summer temperatures could trigger water stress in submontane and montane amabilis fir. Furthermore, if there is a significant water stress in years with dry summers, radial growth is expected to be lower and the relationship of summer temperature to ring width, and possibly other tree ring properties, is expected to be negative.

As a result of the interplay of external (environmental) and intrinsic (e.g., levels of growth hormones) factors (Savidge 1988, Ludlow 1997), a single layer of wood is produced during the growing season, i.e., an annual growth ring. These annual growth rings are readily visible in most temperate tree species, because of the distinct boundary between latewood and earlywood. Earlywood cells with large lumina and thin cell-walls are produced in the early growing season, while latewood cells having small lumina, but thick cell walls, are produced towards the end of the growing season. The highest density within a ring (maximum density) is reached close to the ring boundary (Larson 1969). Wood formation is believed to be primarily linked to shoot and needle growth and thus crown development (Lindström 1996). However, environmental factors may act to enhance or reduce the length of the period or the rate of earlywood and/or latewood formation (Larson 1969, Tranquillini 1979). Because variations in

earlywood and latewood densities are relatively small, the relationship between earlywood and latewood within the annual ring widely determines the average ring density.

In general, a negative influence of growth rate on wood density is assumed for conifers (Lindström 1996). However, the generality of this assumption has been questioned (Dutilleul 1998). Despite reduced ring widths in high-elevation, percent latewood and wood density are believed to be lower in high-elevation conifers, because a short growing season more strongly affects width of latewood (Cieslar 1897 cited in Tranquillini 1989, Vorreiter 1937 cited in Tranquillini 1979, Schweingruber *et al.* 1993). However, in an earlier study conducted on subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in the interior of BC, percent latewood and ring density were found to be unrelated to elevation when adjusted for latitude (Splechtna *et al.* 2000). While adverse high-elevation climates, moisture stress, and soil nutrient deficiencies have all been shown to reduce growth, it remains unclear how these factors will affect the relationship between ring width and density.

A wealth of dendroclimatological studies has established that variations in ring widths of trees growing in various climatic environments are related to variations in climate (Fritts 1976, Schweingruber 1988). However, it has been acknowledged that tree ring-climate fluctuation relationships may be different for other tree-ring properties than ring width and use of additional tree-ring properties could enhance our understanding of climate – growth relationships (Conkey 1979, Schweingruber *et al.* 1979, Cleaveland 1986). In particular, maximum density was used in addition to ring width for climate reconstruction of temperature (Conkey 1986, Briffa *et al.* 1988, D'Arrigo *et al.* 1992, Wiles *et al.* 1996). In the last two decades a few dendroecological studies dealt with the differences in climate – radial growth relationships of the same species on sites along various environmental gradients (Kienast *et al.* 1987, Peterson and Peterson 1994, Dittmar and Elling 1999, Rolland *et al.* 1999, 2000). However, very few studies used multiple tree ring properties to describe the relationship for a given species (Splechtna *et al.* 2000, Lebourgeois *et al.*, 2000, Pant *et al.* 2000).

Because different ring properties can be linked to different periods during the growing season, inclusion of multiple tree-ring properties in dendroecological studies may aid the interpretation of the statistical relationships obtained. Furthermore, the prospect of global warming requires a detailed description of climate – growth relationships for two reasons: (i) to aid in prediction of the effects of global warming; and (ii) to monitor changes in these

relationships that may be caused by global warming. Since the response to weather and long-term climate variations appears to be species-specific, establishing relationships for many different species seems particularly warranted.

I am interested in the factors that limit tree growth in second-growth amabilis fir stands on different sites along altitudinal and edaphic gradients in this study. The objectives of the study are: (i) to examine the relationship between wood properties of amabilis fir and edaphic conditions and weather; (ii) to study the relationship between tree-ring properties and weather by comparing their year-to-year variation on different sites; (iii) to examine presumed differences in response of radial growth of amabilis fir to differences in weather between montane and subalpine sites; and (iv) to assess the climatic information that can be obtained from chronologies of different tree-ring properties. These objectives were achieved by: (i) correlation analysis between mean values of tree ring properties obtained for the last 30 years and elevation, continentality, and soil; and (ii) dendroecological analysis of tree-ring series.

## **5.2 Material and Methods**

Of the 124 plots (Figure 1.1, Appendix 1), 62 were selected for this study and the discs cut at breast height (dbh-discs) were utilized. In the laboratory, these discs were sanded and two radial samples were cut (ca. 5 mm wide) from each disc from opposite directions, perpendicular to the slope, so as to avoid reaction wood. The samples were glued to holders and sanded to a fine polish (grit size 400  $\mu\text{m}$ ). Then the samples were crossdated using the list method (Yamaguchi 1991) and by relying on marker rings from the regional chronologies from old-growth stands developed earlier (Study 3).

Ring width was measured using the WinDendro software (Guay *et al.* 1992) in conjunction with a scanner. As the variation in ring width due to asymmetric growth was found to be low, only one of the two samples was submitted to Forintek Canada Corp. for X-ray densitometry, which was done according to the methodology described in Parker *et al.* (1980). The following measurements were taken for each ring: earlywood width, latewood width, ring width, earlywood density, latewood density, ring density, minimum density within a ring, and maximum density within a ring. The boundary between earlywood and latewood was defined as a fixed value set to  $0.44 \text{ g}\cdot\text{cm}^{-3}$ , which is the typical value used for second growth amabilis fir by Forintek Canada Corp. (pers. comm. John Gordon). This corresponded well with the point of

maximum density increase in the intra-ring density profiles of most samples. Percent latewood was calculated from latewood width and ring width.

I calculated the arithmetic mean of all nine tree-ring properties for every tree for a 30-year period from 1965 to 1994. The values for each tree-ring property were averaged from all site trees in order to obtain one mean for every site to build the raw data set. Because ring width measured at a fixed height on the stem changes with tree age, depending on diameter and crown development of the tree (Larson 1969; Lindström 1996), polynomial regressions were fitted to the bulk of the data for each tree-ring property (Paulsen *et al.* 2000). The raw data were detrended by dividing the raw measurement by the corresponding curve value, which yields an age-corrected data set for every tree-ring property. Raw and detrended data sets were examined for normality using K-means test, and for heterogeneity of variance when grouped into continentality and soil strata using Levene's test (SPSS Inc. 1993).

For the analysis of changes in tree-ring properties along climatic and edaphic gradients, I used the four continentality strata and elevation as surrogate variables for climate, and three soil strata to describe differences in soil moisture and soil nutrient regimes. Based on previous results on the relationship of amabilis fir site index and soil (Splechtna and Klinka 2001), the three soil strata were defined as: (i) dry and poor (combination of slightly dry and poor sites); (ii) moist and poor (combination of the fresh and poor sites); and (iii) moist and rich (remaining SMRs and SNRs combinations) (Table 5.1). I used the average growth of the last 30-years of trees from 44 sites with stands of ages 60 years and older at breast height in further analysis in order to avoid problems that might have influenced results due to differences between juvenile wood and mature wood (Jozsa and Middleton 1994).

Table 5.1. Number of sample sites stratified according to field-identified soil moisture regime and soil nutrient regime.

Soil Moisture Regime	Soil Nutrient Regime			Total
	Poor	Medium	Rich	
Slightly dry	8	n.a.	n.a.	8
Fresh	11	18	2	31
Moist	n.a.	6	17	23
Total	19	24	19	62

It has been shown that stand density strongly affects radial growth because of its effect on crown development (Larson 1969, Lindström 1996). Therefore, I used crown-ratios measured at the time of felling as a covariate to adjust for differences related to stand development. To detect for differences in ring properties between the soil strata, an analysis of variance was used with the raw data and analysis of covariance was used with the detrended data and crown ratio as covariate. In the analysis of changes in tree-ring properties along climatic gradients, nutrient- and water-deficient sites were excluded from the analysis, leaving a subset of 30 sites (of the 44 sites). The raw data without adjustment for crown ratio and the detrended data were used in partial correlation analysis while controlling for crown ratio. The sites were stratified according to continentality and an analysis of covariance was carried out to detect significant differences in the ring properties between continentality strata with crown-ratio as the covariate.

The dendrochronological analysis was based on a 58-year time series (1937 to 1994) for mean chronologies obtained from sites grouped according to orographic, continentality, and edaphic strata (Table 5.2). Because of the limited sample size, and based on previous results, only two strata were used for each category. The orographic strata were not based on absolute elevation, but on vegetation patterns (i.e., biogeoclimatic zones). Sites within the Coastal Western Hemlock (CWH) zone were considered as montane and sites within the Mountain Hemlock (MH) and the Engelmann Spruce – Subalpine Fir (ESSF) zones were considered as subalpine. The two maritime strata were combined and the submontane and subcontinental strata were combined to form the submontane/subcontinental (SS) stratum. Likewise the dry and poor and the moist and poor strata were combined to form the poor stratum. Thus, an attempt was made to develop 72 tree ring chronologies, one for every combination of the 9 tree-ring properties with the 8 site groups; i.e., maritime montane rich (MMR), maritime montane poor (MMP), maritime subalpine rich (MSR), maritime subalpine poor (MSP), submontane/subcontinental montane rich (SSMR), submontane/subcontinental montane poor (SSMP), submontane/subcontinental subalpine rich (SSSR), and submontane/subcontinental subalpine poor (SSSP) (Table 5.2).

Crossdating was checked for each site group, based on the ring width and maximum density series using the program COFECHA (Holmes 1983). However, many maritime montane series had to be excluded because of uncertainties regarding the dating due to low year-to-year variation. This resulted in low sample sizes for some of the site groups (Table 5.2). However,

crossdating was achieved for all selected groups based on ring width and maximum density measurements from the regional old-growth chronologies (Study 3). For a few tree-ring properties and site groups, inter-series correlations were very low or negative and, as such, averaging these series to obtain chronologies appeared unwarranted. In these cases, it was concluded that the given tree-ring property was not controlled by climate and therefore, these cases were excluded from the chronology for the analysis of the given property and site group. This situation occurred for montane site groups only. As a result of this procedure, there was no chronology for latewood (for site groups MMP, SSMR, and SSMP), and for earlywood density and minimum density (for site groups MMP and SSMR). This reduced the total number of developed chronologies from the maximum of 72 by 7 to 65.

Table 5.2. Site groups according to continentality (maritime and submaritime/subcontinental – sm/sc), orographic, and soil nutrient strata. The biogeoclimatic zone (Zone) mean elevation and number of series used for development of chronologies– maritime montane rich (MMR), maritime montane poor (MMP), maritime subalpine rich (MSR), maritime subalpine poor (MSP), submaritime/subcontinental montane rich (SSMR), submaritime/subcontinental montane poor (SSMP), submaritime/subcontinental subalpine rich (SSSR), and submaritime/subcontinental subalpine poor (SSSP); Coastal Western Hemlock (CWH) zone were considered as montane and sites within the Mountain Hemlock (MH) and the Engelmann Spruce – Subalpine Fir (ESSF) zones were considered as subalpine.

Site group	Continentality	Orography	soil stratum	Zone	Elevation (m)	No. series
MMR	Maritime	montane	rich	CWH	636	23
MMP	Maritime	montane	poor	CWH	839	7
MSR	Maritime	subalpine	rich	MH	1235	20
MSP	Maritime	subalpine	poor	MH	1250	7
SSMR	sm/sc	montane	rich	CWH	1027	6
SSMP	sm/sc	montane	poor	CWH	1095	8
SSSR	sm/sc	subalpine	rich	MH/ESSF	1443	24
SSSP	sm/sc	subalpine	poor	MH/ESSF	1191	11

Residual chronologies were obtained using the ARSTAN program (Cook 1985) for the remaining 65 combinations of tree ring properties and site groups (Table 5.3). As significant variation in ring width due to non-climatic effects (age and stand development) was found, a 50-year cubic smoothing spline was applied to the series to remove non-climate variation (Cook and Peters 1981). The decision on the flexibility of the spline was made based on visual inspection of the fit to the tree ring series as described in Study 3. The standardized tree-ring index was obtained by division for width measurements and by subtraction for density



measurement. The index series were averaged using the bi-weight robust mean. Although the autoregressive modelling used to build the residual chronologies likely removed all low-frequency variation, the common high frequency variation was emphasized (Monserud 1986).

Table 5.3. Descriptive statistics for the ring width series used to build the chronologies for site groups— maritime montane rich (MMR), maritime montane poor (MMP), maritime subalpine rich (MSR), maritime subalpine poor (MSP), submaritime/subcontinental montane rich (SSMR), submaritime/subcontinental montane poor (SSMP), submaritime/subcontinental subalpine rich (SSSR), and submaritime/subcontinental subalpine poor (SSSP); N is number of series, time span is given for the longest series, SD is Standard deviation, MS is mean sensitivity, AR1, AR2, and AR3 are partial correlation coefficients of order 1, 2, and 3, respectively.

Site group	N	Time span (years)	Mean (mm)	SD (mm)	MS	AR1	AR2	AR3
MMR	23	1909-1995	3.20	1.07	0.17	0.68	0.15	0.01
MMP	7	1935-1995	2.50	0.98	0.19	0.75	0.13	-0.08
MSR	20	1834-1995	1.60	0.70	0.27	0.63	0.29	0.08
MSP	7	1851-1995	0.71	0.24	0.26	0.43	0.20	0.06
SSMR	6	1892-1994	2.17	0.57	0.22	0.54	0.14	0.13
SSMP	8	1880-1994	0.90	0.32	0.27	0.51	0.11	0.05
SSSR	24	1880-1994	1.69	0.57	0.23	0.55	0.28	0.14
SSSP	11	1860-1994	0.97	0.32	0.24	0.49	0.15	0.05

Principal components analysis (PCA) (Peters *et al.* 1981) was used to explore the relationships between the chronologies. For the correlation matrix used in the eigenvector analysis, chronologies were entered as variables and years were entered as cases. Thus, the PCA components indicate common patterns of variation in tree-ring chronologies. Similarly, all chronologies produced for a given tree-ring property were subjected separately to PCA. The first component scores of tree-ring chronologies represent the joint pattern of variation for a given tree-ring property (Peters *et al.* 1981, Graumlich 1992). Therefore, the first PCA scores were used to quantify the relationship between tree-ring properties.

I used the same set of regionalized monthly climate data and snow data as in study 3 (Table 4.2, Figure 4.1). The correlations between the chronologies of first PCA components of every tree ring property and a 16-months sequence of mean monthly temperature and monthly precipitation sums from June of the year prior to ring formation (previous year) to September of the year of ring formation (current year) were examined in order to explore the relationships between variations in tree ring properties and weather. To detect differences in responses to climate between the montane and subalpine sites, I correlated the original residual chronologies

of selected tree-ring properties to the same sequence of monthly climate variables and the snow depth record for April 1<sup>st</sup>.

### 5.3 Results

#### *Correlation of Plot Means of Wood Properties with Elevation, Continentality and Soil Strata*

The relationships between site means of the tree-ring properties and climate surrogate variables (elevation and continentality stratum) were relatively weak. Using the raw data, all ring properties decreased with increasing elevation except for minimum density, however, only latewood width showed a significant trend (Table 5.4). In addition to latewood width, ring width and earlywood width also decreased significantly with increased elevation when tree-ring properties were adjusted for age and crown ratio. For all other variables, the partial correlation coefficients were similar to those obtained using the raw data (Table 5.4). No significant differences between continentality strata were observed for any of the tree-ring properties adjusted for age and crown ratio.

Table 5.4. Correlation coefficients (r), and partial correlation coefficients (partial r) for tree ring properties with elevation. The partial r was calculated from age-corrected data adjusted for crown-ratios.

Tree-ring property	r	p	partial r	p
Ring width	-0.33	0.074	-0.50	0.011
Earlywood width	-0.24	0.197	-0.42	0.038
Latewood width	-0.51	0.004	-0.54	0.005
Latewood percentage	-0.25	0.186	-0.30	0.152
Ring density	-0.33	0.078	-0.27	0.194
Earlywood density	-0.09	0.621	0.05	0.821
Latewood density	-0.24	0.200	-0.32	0.116
Minimum density	0.10	0.585	0.29	0.156
Maximum density	-0.28	0.130	-0.35	0.083

Using the raw data, except for latewood density and maximum density, all tree-ring properties varied significantly with soil conditions ( $p < 0.05$ ). Little difference was observed for tree-ring properties between dry and poor or moist and poor sites. However, trees growing on poor sites had much narrower rings and earlywood width than trees growing on rich sites. Latewood width showed the same trend, however, it was only slightly (non significantly) reduced on poor sites (Figure 5.1). Consequently, trees on poor sites featured a higher percent latewood and thus higher ring density. Similarly, earlywood density and minimum density (within the earlywood) increased for poor sites, while latewood density and maximum density

(within the latewood) did not show a significant change with soil strata. I obtained similar results using age-detrended data adjusted for crown ratio. However, the relationship between the dry and poor and the moist and poor sites changed slightly, so that the dry group had the lowest earlywood and latewood widths, and the highest percent latewood (Figure 5.2). Only the differences between dry and poor and rich sites were significant.

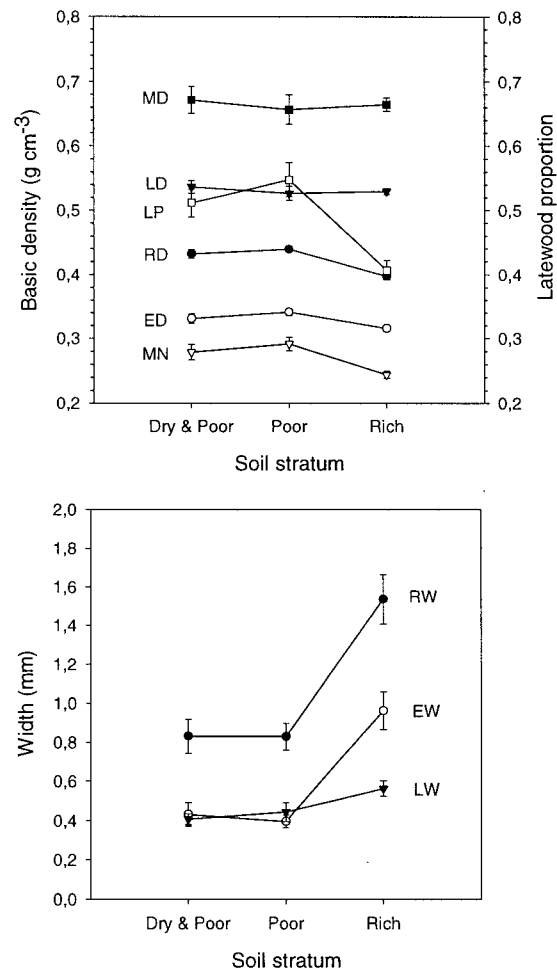


Figure 5.1. Variation in wood properties with soil strata. Mean and standard error of the mean derived from the raw data for earlywood width (EW), latewood width (LW), total ring width (RW), minimum density (MN), earlywood density (ED), average ring density (RD), percent latewood (LP), latewood density (LD), and maximum density (MD) for dry and poor, moist and poor (poor), and rich sites.

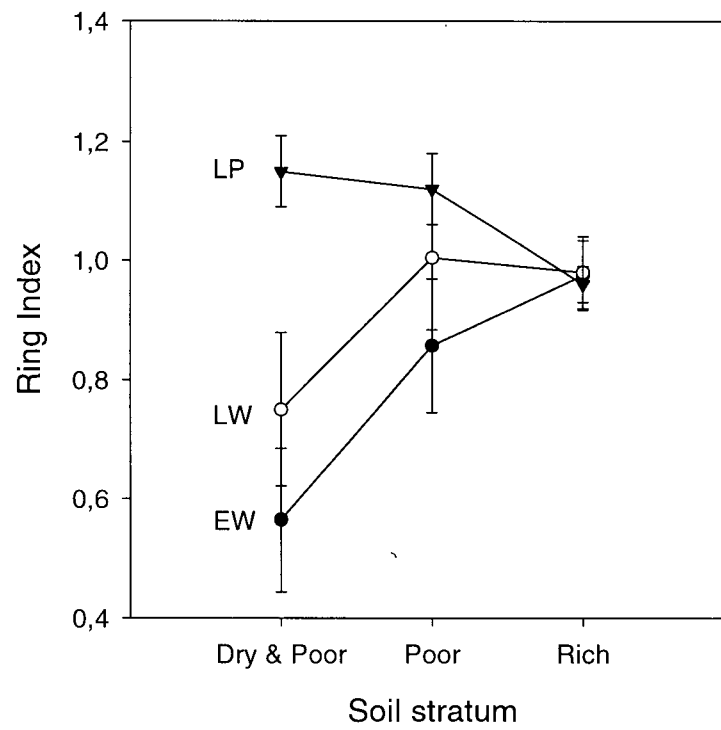


Figure 5.2. Marginal means and standard errors of the means of earlywood width, latewood width, and percent latewood obtained using age-detrended data in analysis of covariance with crown-ratio as covariate.

### ***Relationship Between Chronologies of Tree-ring Properties***

The first two PCA components of the rich site chronologies jointly explained 58 % of the total variation, while the first two PCA components of the poor site chronologies jointly explained 55 % of the total variation. For both the rich and poor data sets, the chronologies were divided into 3 groups according to tree-ring variables (Figure 5.3). Ring width and earlywood width chronologies loaded strongly negatively on the first PCA component, while percent latewood, ring density, earlywood density, and minimum density chronologies loaded strongly positively on the first PCA component. Latewood width and density, and maximum density chronologies loaded either weakly negative or weakly positive on the first PCA component. There was no apparent grouping of chronologies according to site groups associated with the extracted components.

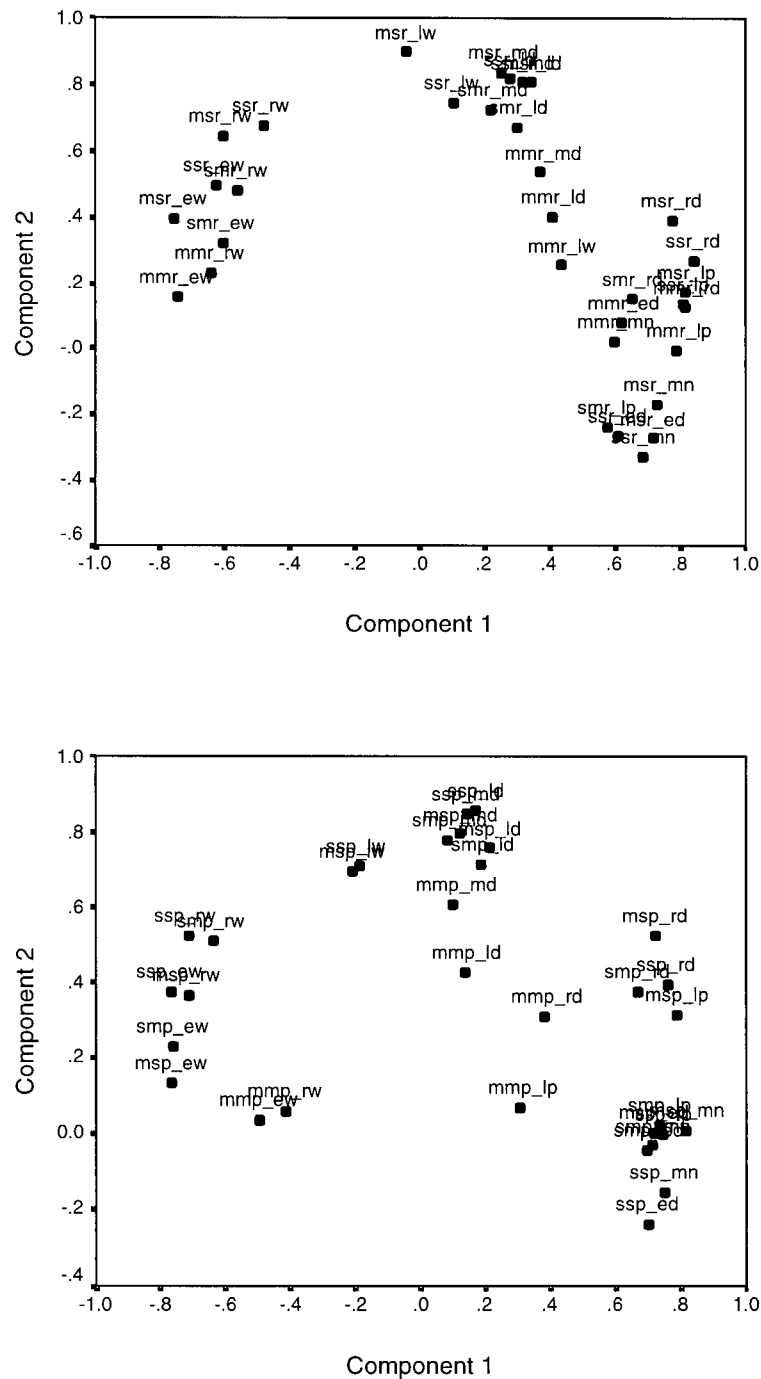


Figure 5.3. Component plots of the first and second PCA component using all chronologies from rich sites (upper figure) and poor sites (lower figure). The codes of the sites are as given in table 5.2.

The chronologies for every tree-ring property were separately subjected to PCA in order to investigate the variation in tree ring patterns between site-group chronologies. For all tree-

ring properties, chronologies showed similar year-to-year variation as indicated by a high loading of all site-group chronologies on the first PCA component. A second PCA component was extracted for only ring width and percent latewood as the chosen cutoff procedure prevented extraction of further components (almost the entire variation was captured by the first component). For ring width, the second PCA component appeared to be associated with the continentality gradient. As little difference between tree-ring patterns between site groups was found, the first PCA component scores were used to summarize the year-to-year variation for each tree-ring property, in view of the strong pattern in all chronologies of the same tree-ring property regardless of site group.

The correlation between the first PCA component scores for each tree-ring property showed: (i) a high positive association of ring and earlywood widths; and (ii) a negative relationship of earlywood and total ring widths to percent latewood, ring density, earlywood density, and minimum density (Table 5.5). Latewood width was only moderately positively related to total ring and earlywood widths. It was slightly, but significantly, positively related to density and strongly positively to latewood and maximum densities. Percent latewood was strongly positively related to ring, earlywood, and minimum densities.

Table 5.5. Correlation matrix between principal component factor scores of 9 tree-ring properties; ring width – RW, earlywood width – EW, latewood width – LW, latewood percentage – LP, average ring density – RD, average earlywood density – ED, minimum ring density – MN, average latewood density – LD, and maximum ring density – MD. Correlation coefficients in bold print are significant at  $p < 0.01$  ( $N = 58$ ).

	RW	EW	LW	LP	RD	ED	MN	LD	MD
RW	1.00								
EW	<b>0.93</b>	1.00							
LW	<b>0.64</b>	<b>0.37</b>	1.00						
LP	<b>-0.66</b>	<b>-0.85</b>	0.12	1.00					
RD	<b>-0.45</b>	<b>-0.69</b>	<b>0.34</b>	<b>0.92</b>	1.00				
ED	<b>-0.72</b>	<b>-0.79</b>	-0.21	<b>0.75</b>	<b>0.71</b>	1.00			
MN	<b>-0.78</b>	<b>-0.86</b>	-0.22	<b>0.82</b>	<b>0.76</b>	<b>0.93</b>	1.00		
LD	0.22	0.00	<b>0.70</b>	<b>0.37</b>	<b>0.65</b>	0.08	0.13	1.00	
MD	0.32	0.09	<b>0.74</b>	0.28	<b>0.59</b>	0.02	0.06	<b>0.97</b>	1.00

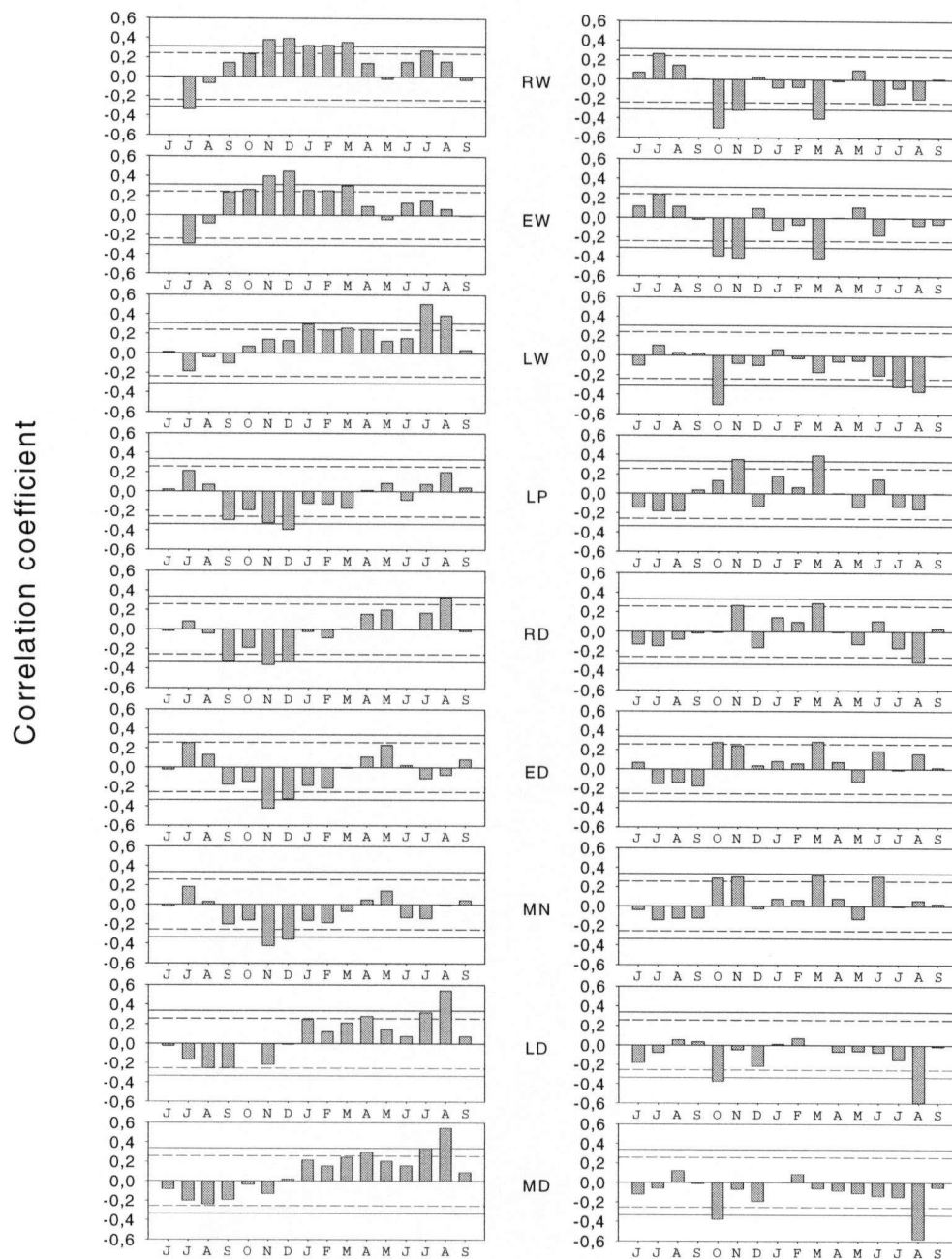


Figure 5.4. Climate Response for 9 different ring properties as defined in Figure 5.1. The pattern for every tree-ring property was summarized using the scores of the first PCA components. Correlation coefficients of these scores to a sequence of monthly climate data (mean temperatures on the left, and precipitation sums on the right) 16 months from previous June to current September are represented by the bars. Significance levels at  $\alpha = 0.05$  and at  $\alpha = 0.01$  are represented by broken lines and solid lines, respectively.

***Relationship Between Tree-ring Chronologies and Year-to-Year Variation of Monthly***

### *Climate Variables*

Ring and earlywood widths were both strongly related to July temperature of the previous year, and positively to winter temperature (October – March) (Figure 5.4). In addition, ring width was positively related to current July temperature. Both properties were negatively related to October, November, and March precipitation. The three tree-ring properties associated with the latewood (width, density, and maximum density) responded similarly to climate variation. The chronologies for these properties showed: (i) a strong positive relationship to July and August temperature in the year of ring formation and to winter temperature from January to April; and (ii) a strong negative relationship to precipitation in the previous October and current August. The response of earlywood density, minimum density, percent latewood, and ring density to climate fluctuations was negative to fall and early winter temperatures, but positive to precipitation in November and March. No strong relationships were observed with the current growing season, except for ring density, which was positively associated with August temperature and negatively with August precipitation (Figure 5.4). The first PCA component scores of ring and earlywood widths were strongly negatively related to snow depth on April 1<sup>st</sup>, but percent latewood, earlywood and minimum densities were related positively (Table 5.6).

Table 5.6. Relationship between tree-ring property chronologies and a yearly record of snow depth on April 1<sup>st</sup>. Correlation coefficients in bold print are significant at  $p < 0.01$ .

	Correlation Coefficient
Ring width	<b>-0.53</b>
Earlywood width	<b>-0.49</b>
Latewood width	-0.32
Latewood percentage	<b>0.40</b>
Ring density	0.24
Earlywood density	<b>0.37</b>
Minimum density	<b>0.42</b>
Latewood density	-0.15
Maximum density	-0.24



In agreement with the results from PCA, there were only slight differences between the response of montane and subalpine chronologies. In general, a similar response pattern was found; however, it was stronger for subalpine chronologies (Figures 5.5, 5.6, and 5.7). Ring width showed a stronger positive relationship to current July temperature and a stronger negative relationship to precipitation in October and March on subalpine sites, but the positive relationship to winter temperature, especially on subarctic/subcontinental sites, did not change (Figure 5.5). The positive response to August temperature was enhanced in subalpine maximum-density chronologies (Figure 5.6). Compared to montane sites, percent latewood on subalpine sites was more strongly positively related to March precipitation and August temperature. The only existing MMR chronology for latewood width showed a response to climate that was quite different from the one displayed by the subalpine chronologies. The only significant relationship found between latewood width on MMR sites and climate variables was a positive association with May temperature. Latewood width on subalpine sites was strongly positively related to current July and August temperature (Figure 5.7) and winter temperature, as well as negatively to October and current July and August precipitation, similar to the response pattern obtained by the first PCA component scores.

The relationship to snow depth was also enhanced on subalpine sites compared to montane sites (Figure 5.8). For earlywood and ring widths all site groups were significantly ( $p < 0.05$ ) negatively related to April 1st snow depth except for the MMP site group. The relationship with earlywood and total ring widths was always higher on subalpine sites for a given combination of continentality and soil strata. For latewood width, only the MSR site group was significantly negatively related to snow depth (Figure 5.8).

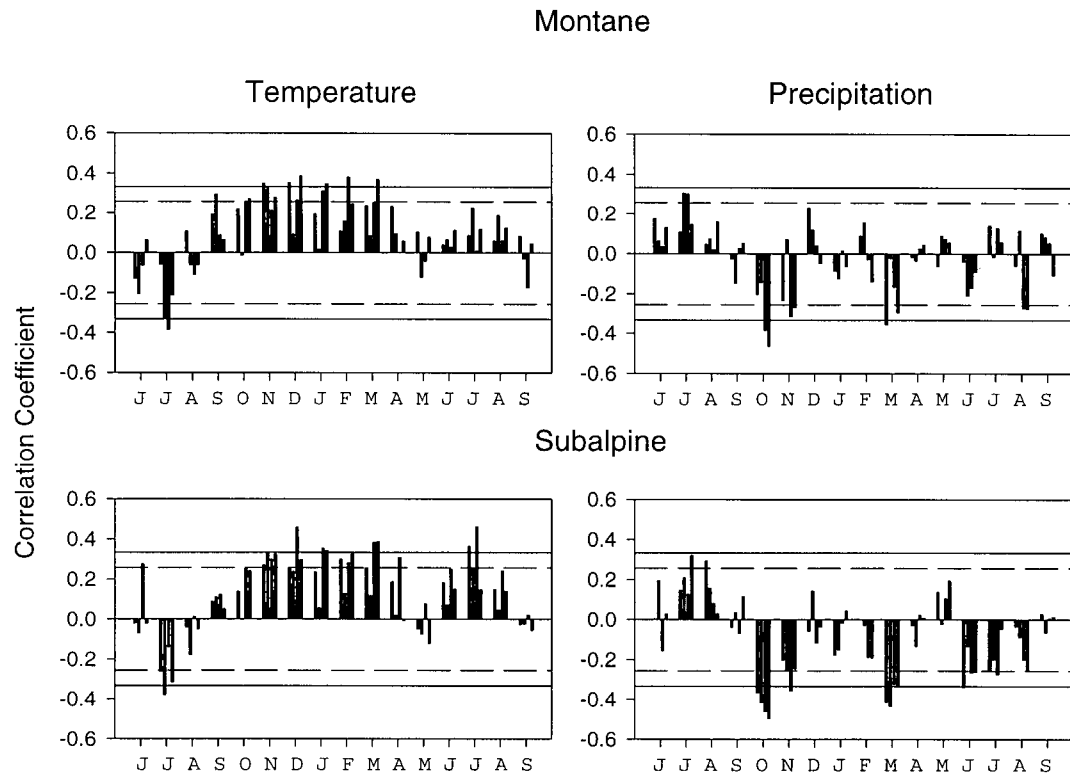


Figure 5.5. Correlation between the residual ring width chronologies for montane (upper figures) and subalpine (lower figures) stands and mean monthly temperature and monthly precipitation sums from June of the year prior to ring formation to September of the year of ring formation for the period 1937 to 1994. Horizontal lines indicate significance levels at  $\alpha=0.05$  (broken lines) and  $\alpha=0.01$ , respectively.

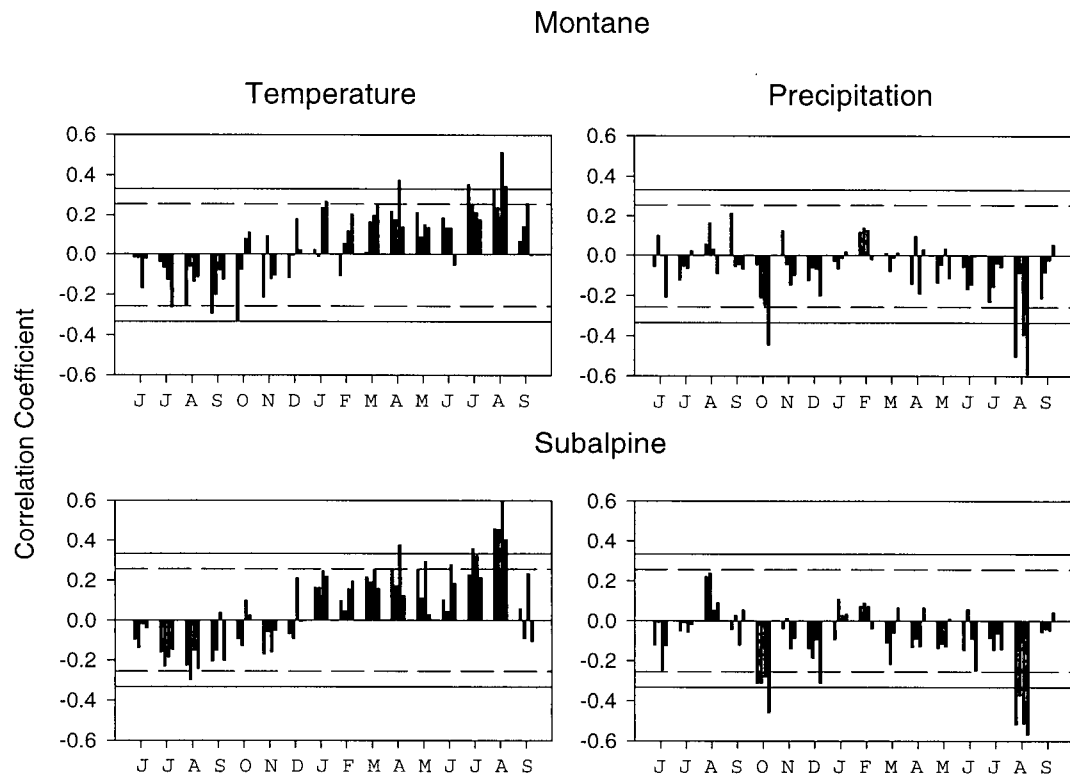


Figure 5.6. Correlation between the residual maximum density chronologies for montane (upper figures) and subalpine (lower figures) stands and mean monthly temperature and monthly precipitation sums from June of the year prior to ring formation to September of the year of ring formation for the period 1937 to 1994. Horizontal lines indicate significance levels as defined in figure 5.5.

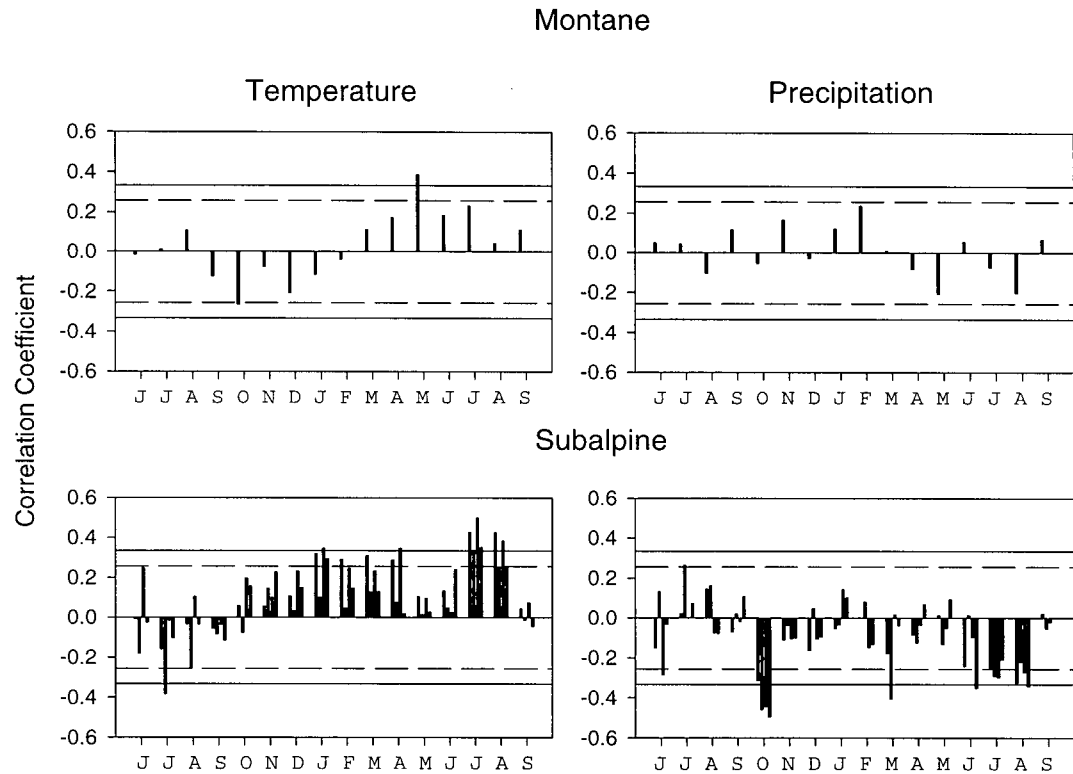


Figure 5.7. Correlation between the residual latewood width chronologies for montane (upper figures) and subalpine (lower figures) stands and mean monthly temperature and monthly precipitation sums from June of the year prior to ring formation to September of the year of ring formation for the period 1937 to 1994. Horizontal lines indicate significant levels as defined in figure 5.5.

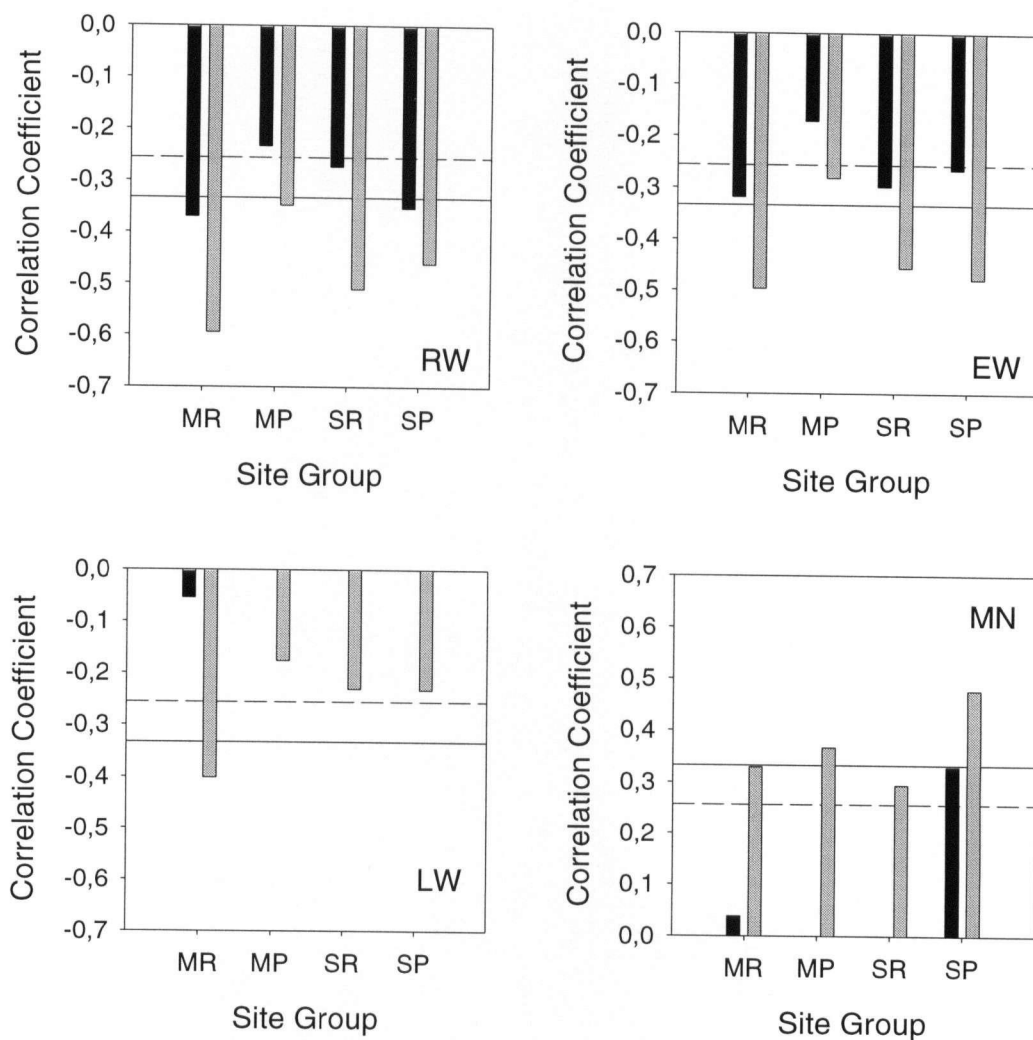


Figure 5.8. Correlation between April 1<sup>st</sup> snow depth record for montane (black bars) and subalpine (shaded bars) residual chronologies of selected tree –ring properties (ring width (RW), earlywood width (EW), latewood width (LW), and minimum density (MN)), separately for the different site groups, MR (maritime – rich), MP (maritime – poor), SR (submaritime/subcontinental – rich), and SP (submaritime/subcontinental – poor). Horizontal lines indicate significant levels as defined in figure 5.5.

## 5.4 Discussion

### *Ring Density Changes With Elevation and Soils*

Both earlywood and latewood widths and, therefore, total ring width showed the expected significant decrease with increasing elevation. Percent latewood decreased slightly (not significantly) with elevation indicating that latewood width was reduced more strongly than earlywood width with increasing elevation. This is in agreement with earlier reports that percent latewood is reduced in high-elevation conifers (Tranquillini 1979, Schweingruber *et al.* 1993). Percent latewood is the principal determinant of ring density, since variations in earlywood and latewood densities are relatively low compared to the variation in percent latewood (Barbour *et al.* 1994). The expected decrease for the study stands in ring density with increasing elevation was only slight and was not significant. This is in agreement with results obtained for subalpine fir growing in the interior of British Columbia under the influence of continental climate (Splechtna *et al.* 2000). The slight decline in percent latewood, latewood density, and ring density will have only minor impact on the wood quality of amabilis fir growing in high-elevation closed-canopy stands.

Amabilis fir does not show strongly reduced maximum density with increased elevation. Because of the known dependence of maximum density on summer temperatures (Schweingruber *et al.* 1979, Conkey 1979, Splechtna *et al.* 2000), a stronger response was expected. A weaker response may be partly due to a stronger temperature gradient related to elevation in continental climates (Adam 1995). Adaptations to the high-elevation climate may reduce the observable effects of elevation. It is known that amabilis fir has a much higher needle retention on high-elevation sites (up to 20 years) than in low-elevation sites (about 8 years) and the temperature thresholds for bud burst of high-elevation provenances are significantly lower than for low-elevation provenances (Worrall 1983). Compared to low-elevation sites, black pine (*Pinus uncinata* (Mill. *ex* Mirb.) Forbes) growing in high elevations started growth later, but had a higher maximum tracheid formation rate (Camarero *et al.* 1998).

The effect of nutrient availability on average tree ring properties was stronger than the one exerted by climate. A reduced ring width on poor sites was due to the reduced earlywood width and increasing percent latewood and ring density. A similar reduction was found on dry and poor sites. Since earlywood density was increased on poor sites, nutrient deficiency probably suppresses cell enlargement and may also shorten the period of earlywood formation as it was suggested by Brix (1972) when interpreting the results of a fertilizer trial on Douglas-

fir. No significant differences were found between dry and moist poor sites indicating that nutrient deficiency might be more strongly limiting than water stress. However, because these two factors are somewhat confounding in the natural distribution of the sites (slightly dry sites were always poor), these differences could not be tested.

These findings suggest that growth-wood density relationships among trees from different sites vary with the environmental factors that are limiting. Dutilleul *et al.* (1998) found a negative relationship between ring width and ring density in a thinning trial for only slow growing trees, which suggests that genetic differences associated with the growth rate of trees may alter the growth-wood density relationship.

In agreement with the findings of Dutilleul *et al.* (1998) for Norway spruce, I found the yearly ring-width variation to be related to earlywood-width variation, in view of a moderately strong negative relationship between tree growth and ring density. Therefore, on any given site, there was a negative relationship between ring width and ring density. This may well be a feature common to all conifers with a gradual transition from earlywood to latewood, such as Douglas-fir, true firs, and spruces (Dutilleul *et al.* 1998). A portion of the variation in earlywood width could be related to weather, possibly to the length of seasons. It has been noted that cambial age has to be taken into account when growth and density are compared among trees (Jozsa and Middleton 1994). I surmise that in mature wood the year-to-year variation in climate maybe equally or more important than cambial age, and that both calendar year and cambial age should be taken into account (Lebourgeois *et al.* 2000).

### ***Limiting Factors for Radial Growth on Montane and Subalpine Sites***

There were only minor differences in response patterns for any of the nine tree-ring properties to yearly weather variation between site groups. This indicated that radial growth on montane and subalpine sites across the study area was limited by similar climatic factors, i.e. growing-season length, current summer temperature, winter temperatures and precipitation (snowpack), and previous years summer temperature. My results agree with the previous findings for high-elevation old-growth stands of amabilis fir (Study 3) and other species in the Pacific Northwest, which all concluded that growing-season length and current growing-season temperature are the most limiting factors to tree growth on subalpine sites (Heikkinen 1985, Peterson and Peterson 1994, Smith and Laroque 1998, Laroque and Smith 1999). The influence of both these factors was enhanced on subalpine sites compared to montane sites further

indicating that reduced length of growing-season and summer temperatures are the principal factors explaining the observed reduction in ring width with increasing elevation.

The findings of this study [(i) similar factors affect the tree-ring properties on montane and subalpine sites; (ii) the responses were stronger on subalpine sites; and (iii) the response to precipitation during the growing season was negligible or negative] all suggest that moisture stress is not the growth limiting factor on montane and subalpine sites. Similar conclusions were drawn for Norway spruce sampled along a transect from central Finland to the arctic spruce timberline (Mäkinen *et al.* 2000). Expected difficulties in crossdating tree-ring series from low-elevation sites further confirm that the climate control over radial growth is weak on these sites. The failure of detecting a relationship between temperature and precipitation may well be related to the fact that amabilis fir does not tolerate sites with significant water deficit and is in low elevations restricted to cooler and relatively wetter sites (Klinka *et al.* 2001).

The negative influence of previous year July temperatures to ring and earlywood widths found in this study for old-growth stands of amabilis fir has also been found for many other conifers in cool and moist environments (Peterson and Peterson 1994, Laroque and Smith 1999, Rolland *et al.* 1999, Mäkinen *et al.* 2000). Laroque and Smith (1999) attributed a similar response in yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach.) to water stress, while Parish *et al.* (1999) working on subalpine fir attributed it to changes in carbon allocation to reproductive growth. This response may be typical for conifers with preformed growth (Rolland *et al.* 1999). Favourable conditions for photosynthesis may trigger larger terminal buds and cone onset, creating strong carbon sinks for the next growing-season, leading to a reduced radial growth (Ettl and Peterson 1995). However, this relatively consistent pattern should be examined further and the causality tested by short-term field experiments.

### ***Different Climate Response of Different Tree-ring Properties***

The largest differences in tree-ring patterns among all chronologies were due to differences in tree-ring property, as were the non-significant differences between site groups. Since earlywood and latewood widths showed different responses to climate fluctuations, it could be beneficial to use them separately as proxy-climate data (Conkey 1986). A stronger negative relationship between earlywood width and April 1<sup>st</sup> snow depth suggests that a delayed start in the growing-season will affect mainly earlywood growth. A reduced summer



temperature affected latewood formation most strongly, since all properties associated with the latewood showed a strong positive relationship to July and August temperature.

Variation in ring width is mainly driven by variations in earlywood width as shown by their similar patterns and similar response to climate. The tree-ring properties negatively related to earlywood width (i.e., earlywood density and minimum density) mirror the responses in the width of earlywood, suggesting that a wider earlywood band is the result of cells having larger lumina, and as such, density is decreased (Lebourgeois *et al.* 2000). Percent latewood and ring density are negatively correlated to earlywood width and positively to latewood width. The weak response of percent latewood and ring density to climate, detected by correlation analysis, is likely due to their dependence on many processes throughout the growing-season. Latewood density and maximum density are closely related and respond similarly to climate fluctuations. Their responses to current summer temperature are similar to that of latewood width, but are stronger to August temperature. A very strong negative response to August precipitation probably reflects the negative effect of cyclones on temperature and solar radiation. The common practice to use ring width and maximum density for summer temperature reconstruction in humid climates is supported by the results of this study. In the absence of densitometric data, the separate use of earlywood width and latewood width appears to be a valid alternative.

## 6. Site Index and Diameter at 30 years of *Amabilis* fir in Relation to Site Quality (Study 5).

### 6.1 Introduction

Linking measures of forest productivity to site quality or ecological site classification is a recurring theme in forest research (e.g., Carmean 1975, Kayahara 1989, Neumann 1993, Pretzsch 1994, J.S. Thrower and Associates 1996). Two main questions addressed in these studies are: 1) How strongly is tree growth influenced by climate and soils? and 2) How well can forest productivity be predicted from ecological variables? In general, site quality may be defined as the sum of site factors that directly affect plant growth: climate (light and heat), soil moisture regime (SMR), soil nutrient regime (SNR), and soil aeration regime (SAR) (Major 1963, Krajina 1969). Quantification of the relationship between these site factors and tree growth helps clarify the relative importance of these factors for a given ecosystem and to support management decisions.

The most commonly used measure of forest productivity is site index (top height at reference age 50 years at breast height) (Monserud 1984a). In the absence of suitable trees on a given site, site factors provide an alternative for site index estimation. Numerous studies have developed predictive equations for site index using site variables (Moosmayer and Schöpfer 1972, Carmean 1975, Kayahara 1989, Green et al. 1989, Wang 1992, Wang 1993). The precision and applicability of such models depend widely on the proper identification of factors limiting tree growth. A number of studies have demonstrated that the use of synoptic site factors in a conceptual model for site index prediction may be superior (e.g., Klinka and Carter 1990, Kahn 1994, Wang and Klinka 1996) to the use of large numbers of environmental variables in complex regression models. Therefore, a synoptic approach was adopted for this study using the framework of the biogeoclimatic ecosystem classification (BEC) system in British Columbia (Krajina 1965, Pojar *et al.* 1987).

*Amabilis* fir is a major timber species in the montane and subalpine forest in southwestern British Columbia. It grows on a wide range of sites extending from sea level to the upper timberline. In terms of continentality, its range extends from hypermaritime to maritime sites to subcontinental sites. Previous studies suggest that on high-elevation sites *amabilis* fir

growth is mainly limited by growing season duration and summer temperature (Study 3) and that height growth patterns of top-height trees varies between maritime and submaritime/subcontinental sites (Splechtna 2001). However, there is no quantitative information on the extent of height and radial growth reduction expected with increasing elevation, or on how height and radial growth are affected by continentality or soil conditions.

The objectives of this study were: (i) to examine the relationships of height and radial growth to indirect measures of climate, soil moisture regime, and soil nutrient regime, (ii) to develop predictive equations for site index from these site factors, and (iii) to test these models against an independent data set.

## **6.2 Material and Methods**

### ***Sampling Procedure and Sample Preparation***

As described earlier, I stratified the study area into four continentality strata (Figure 1.1). As (i) very few study stands could be found within the submaritime stratum, (ii) similar height growth patterns have been found for SM and SC strata (Splechtna 2001), and (iii) ring width patterns were similar between the SC and SM strata, the submaritime stratum was combined with the subcontinental stratum (submaritime/subcontinental (SS)).

Site index for every plot was calculated as the arithmetic mean of the height reached at 50 years breast height age of the three site trees (see Splechtna 2001 for details, Chapter 2). Radial growth was measured as the mean diameter of the first 30 years at breast height (inside bark) of the three plot trees (D30). I assumed that differences in stand development for the first 30 years after reaching breast height were not large between stands or did not largely affect diameter growth of dominant trees.

### ***Statistical Analysis***

Regression analysis was used to examine the relationship between site index, D30 and climate (continentality and elevation) using a climosequence (42 plots) (i.e., a data set comprised of sites with fresh or moist soil moisture regime and medium soil nutrient regime (Table 6.1)). To examine relationships of the growth indices with SMR and SNR, I used plots across a hygrosequence (plots with medium SNR (Table 6.1)) and a trophosequence (plots with fresh and moist SMR (Table 6.1)), respectively. In analysis of covariance, elevation was the covariate, because elevation was expected to exert a strong influence on growth.

To develop and test predictive models for amabilis fir site index, the data were randomly split into a calibration data set (67 plots) and a test data set (31 plots) (Table 2.1). Multiple regression analysis was used to fit predictive models for site index from climate and/or soil variables. Fitted models were tested against independent data in evaluating precision by the root-mean square prediction error (the square root of the mean squared differences between predicted and measured site index – root-MSPR) and bias was assessed using paired t-tests. The best model was compared to a polymorphic site index model that accounted for differences in height growth patterns associated with continentality (Splechtna 2001).

Table 6.1. Number of plots sampled according to edatopes (combinations of soil moisture regime and soil nutrient regime). Plots used for a hygrosequence are in bold print, plots across a trophosequence are underlined, and zonal plots across a climosequence are shaded. Boxes refer to WD (water-deficient sites), ND (nutrient-deficient sites), and WNS (sites with sufficient water and nutrient supply) used in predictive model [2].

	Poor	Medium	Rich	Total
Slightly dry	14 <span style="border: 1px solid black; padding: 2px;">WD</span>	<b>3</b>	-	17
<u>Fresh</u>	<u>11</u> <span style="border: 1px solid black; padding: 2px;">ND</span>	<u><b>32</b></u>	<u>2</u>	<u>45</u>
<u>Moist</u>	-	<u><b>10</b></u> <span style="border: 1px solid black; padding: 2px;">WNS</span>	<u>21</u>	<u>31</u>
Very Moist	-	-	5	5
Total	25	<b>45</b>	28	98

### 6.3 Results

#### *Examination of Relationships Between Site Factors and Site Index and D30*

Site index and D30 were strongly correlated ( $r = 0.9$ ) and showed similarly strong relationships to indirect measures of climate (continentality strata, orographic strata, and elevation), SMR, and SNR (Figures 6.1, 6.2, 6.3, and 6.4). Along a climosequence, growth indices showed the expected decrease from submontane to montane and subalpine sites and from maritime windward to maritime leeward and submaritime/sucontinental sites. Compared to

montane sites, site index was significantly lower at subalpine sites, although the differences were less pronounced in the subarctic/subcontinental stratum. Within the subalpine stratum, differences in growth indices between the continentality strata were not significant (Figure 6.1). Site index decreased 1.6 m with every 100 m increase in elevation, regardless of continentality. The slopes of the regression lines differed between the continentality strata, particularly in the SS stratum, where growth decreased relatively little with increasing elevation (0.8 m for every 100 m) compared to decreases of 2.7 m and 1.9 m for every 100 m increase in elevation in the ML and MW strata, respectively (Figure 6.2). For similar elevations, MW sites had the highest growth and ML sites the lowest. At very high elevations (over 1,350 m) site index was highest in the SS stratum. Relationships between D30 and elevation and continentality were similar to those described for site index, albeit not as strong (Figure 6.2).

Relationships between the growth indices and the soil variables were also statistically significant. Analysis of covariance, using elevation as covariate, followed by a comparison of marginal means, showed that the growth indices were significantly lower on slightly dry sites along a hygrosequence compared to fresh and moist sites. Growth indices were not significantly different between fresh and moist sites. (Figure 6.3). Similarly, along a trophosequence, growth was significantly reduced on poor sites compared to medium and rich sites, but no significant differences in either site index or D30 were detected between medium and rich sites (Figure 6.4).

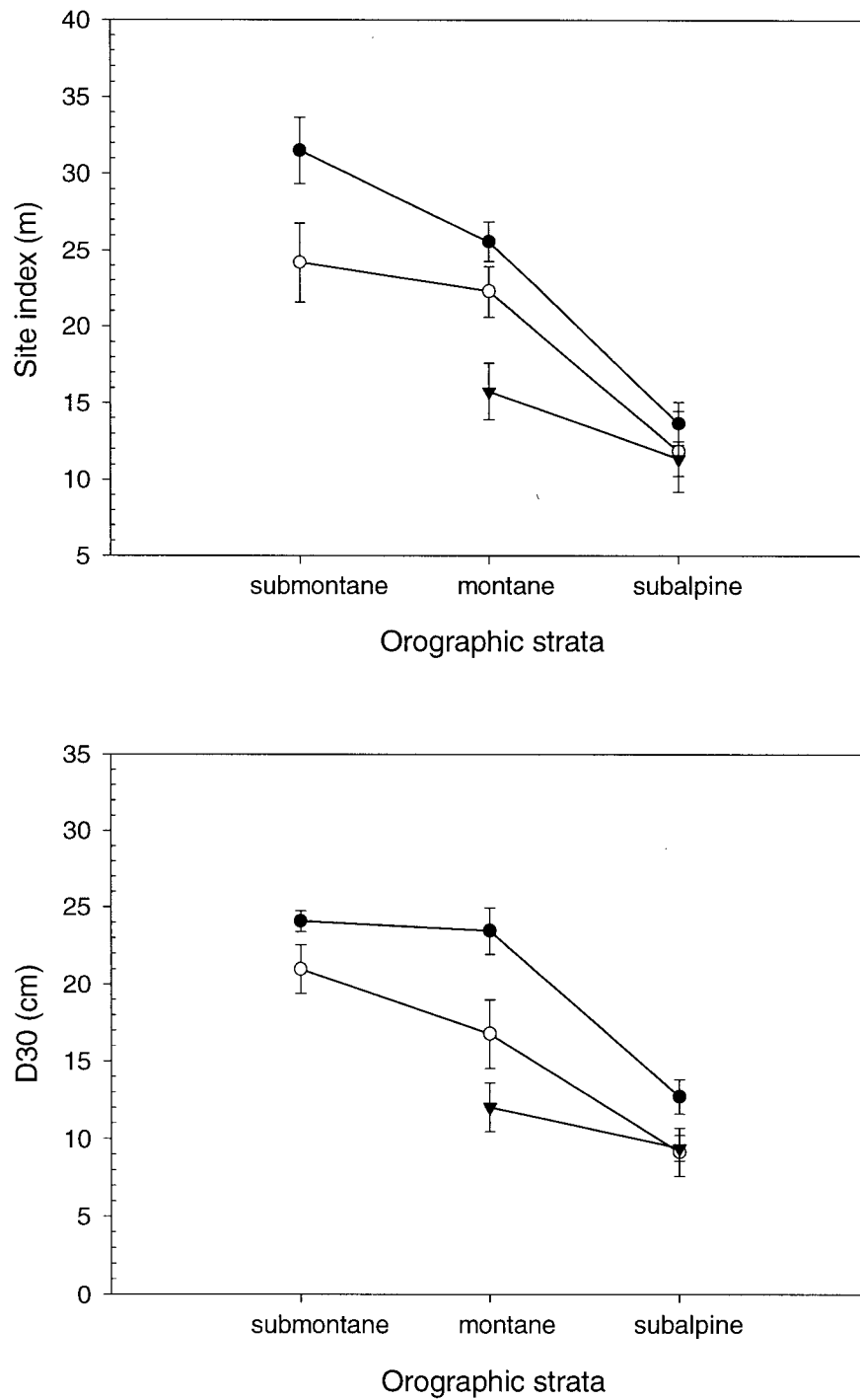


Figure 6.1. Variation in site index and D30 with orographic strata. Mean site index (top figure) and mean D30 (bottom figure) according to orographic strata within maritime windward (black dots), maritime leeward (white dots), and submaritime/subcontinental (triangles) continentality strata based in a climosequence as defined in table 6.1.

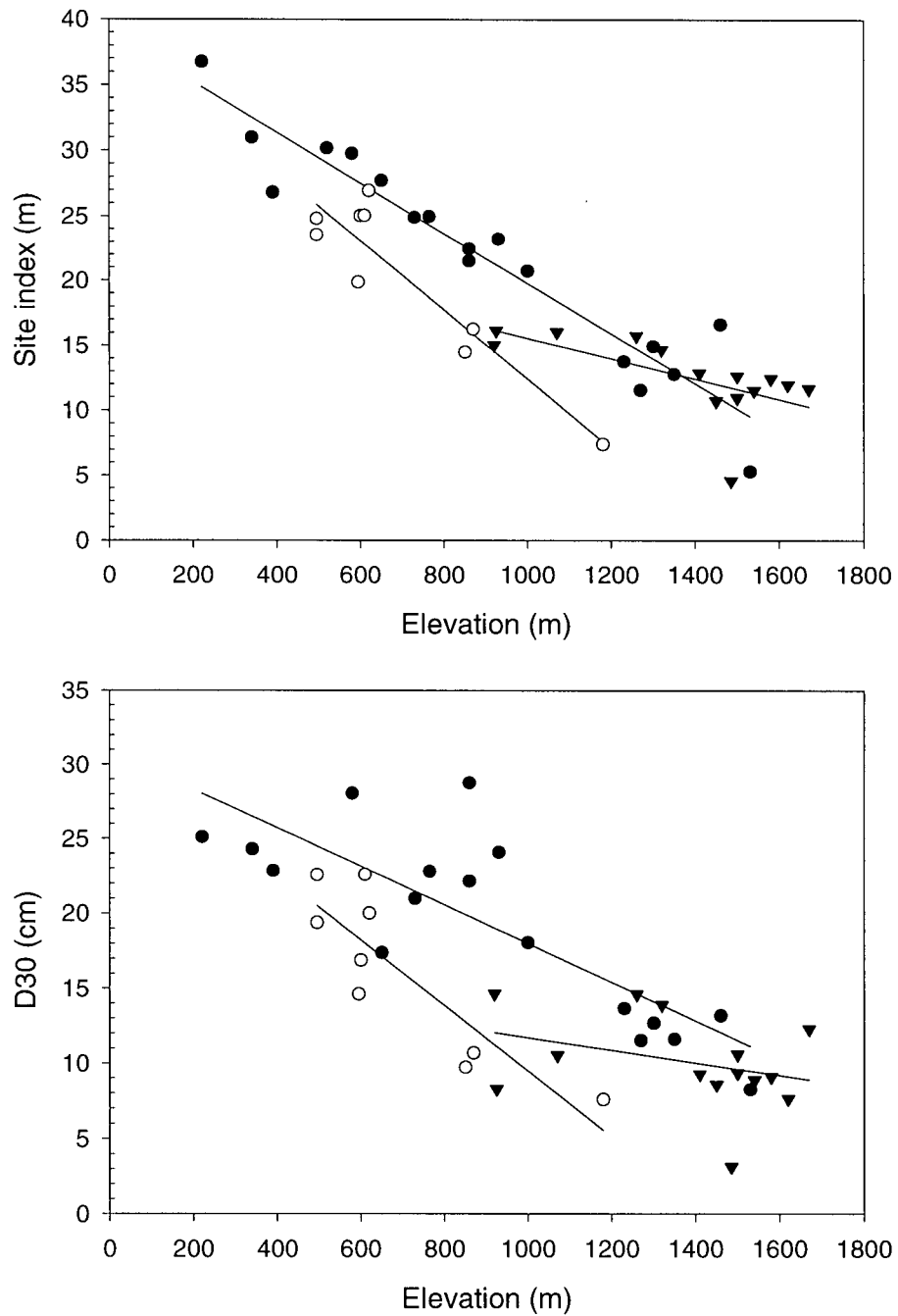


Figure 6.2. Relationship and linear regression lines between elevation and site index (top figure) and D30 (bottom figure) separately for maritime windward (black dots), maritime leeward (white dots), and submaritime/subcontinental (triangles) continental strata.

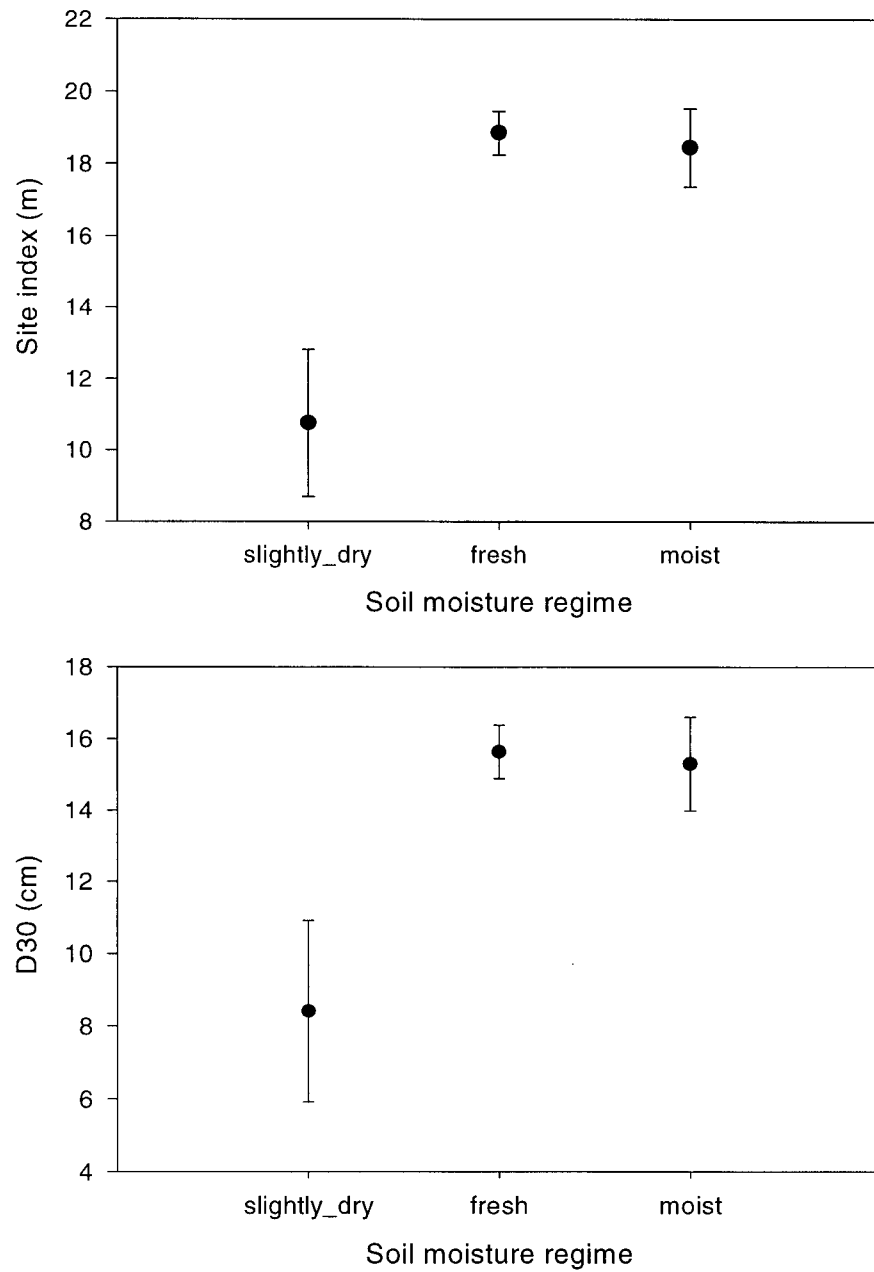


Figure 6.3. Marginal means of site index (top figure) (N = 45) and D30 (bottom figure) (N= 44) stratified according to soil moisture regimes along a hygrosequence as defined in table 6.1. Marginal means for site index and D30 were calculated for the mean elevation of 992 m and 1003 m, respectively.



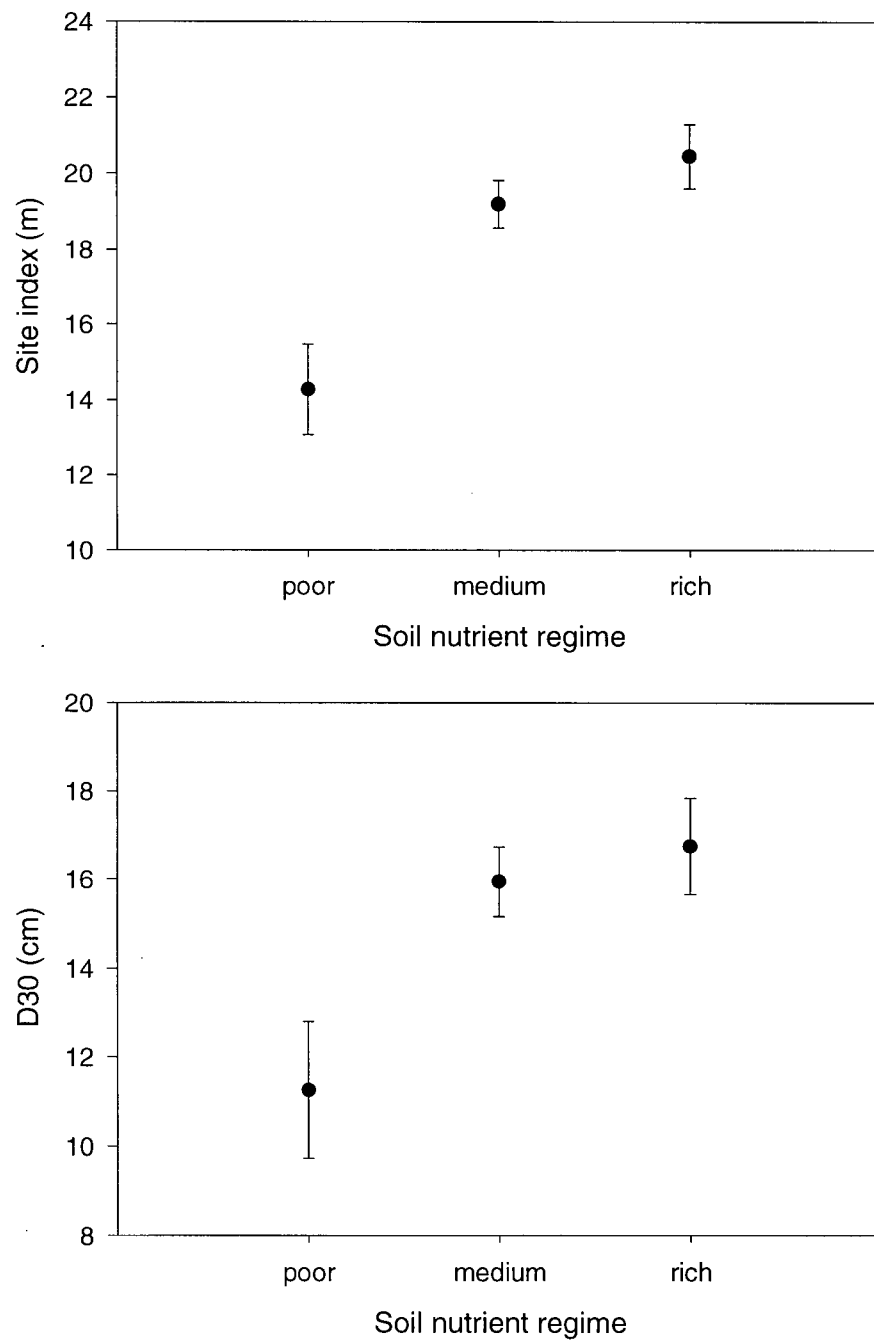


Figure 6.4. Marginal means of site index (top figure) ( $N = 76$ ) and D30 (bottom figure) ( $N = 74$ ) stratified according to soil nutrient regimes along a trophosequence as defined in table 6.1. Marginal means for site index and D30 were calculated for an elevation of 969 m and 982, respectively.

### *Predictive Models for Site Index*

The following variables were considered as independent variables for site index estimation: elevation, orographic stratum, continentality stratum, SMR, SNR, and SOIL. The variable SOIL consisted of 3 strata: water-deficient sites (slightly dry sites, WD), nutrient-deficient sites (fresh but poor sites, ND), and water- and nutrient-sufficient sites (remaining edatopes, WNS) (Table 6.1). The best climate model accounted for 75%, whereas the best model using both climate and soil variables explained 83% of the variation in site index (Table 6.2). The climate model predicted a steep decline in site index for the MW and ML strata and a moderate decline in site index for the SS stratum with increasing elevation, similar to the results obtained along the climosequence. The combined model predicted a 6 m lower site index at water-deficient sites and a 3 m lower site index at nutrient-deficient sites compared to sites with sufficient water and nutrients.

When tested against independent data, both models were unbiased, as the paired t-test of residuals showed no significant deviation from 0 (Table 6.3, Figure 6.5). The combined model proved to be slightly more precise as the root mean square prediction error was 3.32 compared to 3.83 for the climate model (Table 6.3).

Table 6.2. Models for predicting site index (SI, 50 yr @ bh) from only climate variables (Eq. [1]) and climate (elevation in meters asl. and continentality strata as dummy variables) and soil variables (as dummy variables) (Eq. [2]). All models are significant ( $P < 0.001$ ,  $n = 67$ ).  $R^2_{adj}$  is adjusted for the number of independent variables. SEE is standard error of estimate. Root-MSPR is the square root of the mean squared differences between predicted and measured site index using the test data ( $n=31$ ). ELE is elevation (m), MW is maritime windward, ML is maritime leeward, ELE\*MW and ELE\*ML are interaction terms, and ND and WD are as defined in Table 6.1.

	Regression function	$R^2_{adj}$	SEE	root-MSPR
Eq. [1]	SI = 21.437 – 0.0069(ELE) – 0.0144(ELE*MW) – 0.0141(ELE*ML) + 19.007(MW) + 12.635(ML)	0.75	3.94	3.83
Eq. [2]	SI = 23.162 – 0.0070(ELE) – 0.0131(ELE*MW) – 0.0164(ELE*ML) + 17.034(MW) + 14.536(ML) – 3.092(ND) – 6.048(WD)	0.83	3.23	3.32

Table 6.3. Paired t-tests for differences between measured and predicted site index resulting from the climate model (eq. 1) and combined model (eq. 2) as described in table 6.2 using the test data (table 2.1).

Model	Mean difference	Standard error	t	df	p
Climate Model	-0.448	0.695	-0.645	30	0.524
Combined Model	-0.270	0.605	-0.446	30	0.659

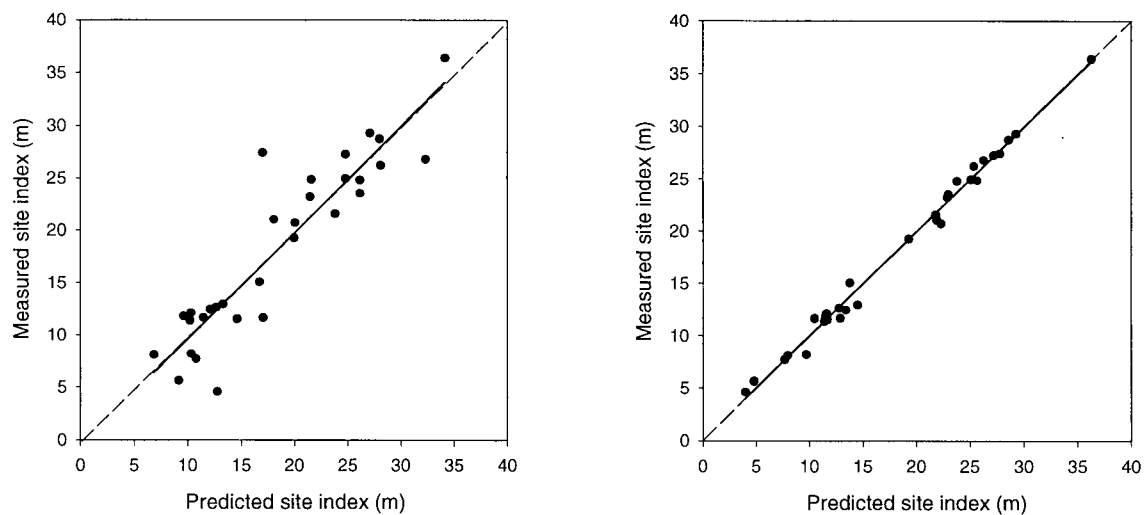


Figure 6.5. Predicted site index versus measured site index from the combined model of this study (left figure) and from polymorphic site index curves (right figure, study 1). Broken lines represent a perfect relationship ( $x = y$ ); solid lines are linear regression lines.

## 6.4 Discussion

### *Influence of Site Factors on Height and Diameter Growth*

The approach taken in this study was based on a simple conceptual model. Forest growth was assumed to be a function of five factors: light, heat (temperature), SNR, SMR, and SAR (Klinka and Carter 1990, Kayahara 1992, Wang 1992, Wang 1993, Wang *et al.* 1994b). For dominant trees, light levels were assumed to be similar and not growth limiting. Similarly, soil

aeration was also assumed to be not growth limiting, as the soils in the study stands were well drained. The relationships between SMR, SNR, and temperature and tree growth were individually examined, while keeping the other factors constant at intermediate levels using a climosequence, hygrosequence, and trophosequence, respectively. None of the remaining three factors was measured directly. Heat was measured by three surrogate (proxy) measures: orography, continentality, and elevation. SMR and SNR were estimated using soil morphological properties. It has been shown that the field estimates of SMRs and SNRs are good estimates of soil moisture and available nitrogen, respectively (Kabzems and Klinka 1987a,b, Green *et al.* 1989, Kayahara 1992, Wang and Klinka 1996, Chen *et al.* 1998, Splechtna and Klinka 2001).

Growth of amabilis fir was most strongly limited by climate, as site and diameter indices notably decreased with increasing elevation or from montane to subalpine sites. The main environmental changes along an elevation gradient are decreased temperature and length of growing season due to later snowmelt (Brooke *et al.* 1970). As amabilis fir occurs along such a wide elevation range and as a previous study suggested that the factors most limiting to amabilis fir growth were growing season length and cool summer temperatures (Chapters 4 and 5), a strong relationship between amabilis fir growth and elevation was expected. However, growth decreased less with elevation in the SS stratum compared to the MW and ML strata. Climate conditions in subcontinental climates differ from maritime climates by having higher summer temperatures, lower winter temperatures, less precipitation and rapid transitions between cold winters and warm summers. Because of warmer summer temperatures and, in general, less cloud cover in more continental climates, the upper timberline in the SS stratum is usually found at higher elevations. For similar reasons, the transition from the montane to subalpine stratum is found at higher elevations in the SS stratum than in the maritime strata. On the other hand, high temperatures may lead to water stress at lower elevations in the SS stratum, while at low elevations in the maritime strata, cool summers, warm winters, and abundant precipitation favor tree growth. Compared to maritime sites, growing conditions at more continental sites are less favourable at low elevations but more favourable at high elevations. Therefore the reduction in growth with increasing elevation should be less pronounced in more continental climates than in maritime climates. In the interior of BC under the influence of continental climate, a decrease of 1.0 m and 1.1 m for every 100 m elevation increase was found for site index of subalpine fir and

Engelmann spruce (*Picea engelmannii*), respectively (Klinka *et al.* 1996), which is slightly higher than the rate found for the subarctic/subcontinental stratum in this study.

Amabilis fir does not occur below 800 m in elevation in the subcontinental stratum. It is also limited by cold winters and, therefore, rarely occurs at timberline in this stratum, being replaced by subalpine fir. These two factors reduce the elevation range for amabilis fir at subcontinental sites and may contribute to a relatively weak relationship between elevation and amabilis fir growth in this stratum.

For the same elevation, site index on zonal sites was lower on maritime leeward sites compared to maritime windward or subarctic continental sites. This may be due to the drier and warmer summers compared to maritime windward sites and the longer snow duration (thus shorter growing season) compared to subarctic/subcontinental sites. However, other (non-climatic) factors that could not be accounted for may have influenced the result.

The growth response to different soil-moisture levels showed a similar reduction in height and radial growth on sites with moisture deficits, while no growth increase was detected on moist sites. With increasing soil fertility from poor to medium sites, growth increased significantly, but differences between medium and rich sites were not significant, indicating that amabilis fir is not very nutrient demanding and grows well on nutrient-medium sites. Amabilis fir is known to be a highly mycorrhizal species and may be able to obtain a significant portion of its nutrient demand via associations with mycorrhiza (Minore 1979).

Thus, at a regional scale, soil conditions appear to be less limiting to amabilis fir growth than climate. However, poor sites are very common at high elevations, – even more so than medium sites, so that the influence of soil fertility is an important consideration for managing the coastal high-elevation forest. On the other hand, water-deficient sites are fairly uncommon and are typically associated with rock outcrops, sites that should be excluded from industrial timber production because of regeneration difficulties (Klinka and Chourmouzis 2001).

Genetic variability may alter or even have a larger influence than the observed environmental effects, as has been demonstrated for Douglas-fir (Rehfeldt and Monserud 1990). Thus, the observed elevation effect may be partly due to differences between high and low-elevation provenances rather than climate. Other studies show that genetic variability in amabilis fir, unlike in Douglas-fir, is relatively low (Crawford and Oliver 1990), although

adaptations to high-elevation climates have been found (Worrall 1983, Worrall unpublished data, cited in Klinka *et al.* 2001).

### ***Site Index Models***

Two models are presented in this study: a climate model and a combined model using climate and soil variables. The climate model was mainly used to test the improvement in predictive power due to the inclusion of soil variables. Because not all combinations of SMR and SNR existed on sites supporting growth of amabilis fir, the interactions between the two soil factors could not be tested. Therefore, I used combinations of SMRs and SNRs in the model by creating a soil variable based on the exploratory analysis described above. Inclusion of the soil variable slightly improved precision of the model. However, climate appeared to be the most important variable for site index prediction.

Although the models explained a large portion of the variation in site index and both models were unbiased when tested against independent data, their precision was relatively low. Not surprisingly, the polymorphic models using height and age measurements for site index estimation (Splechtna 2001) were much more precise, and are thus recommended whenever suitable site trees are found. The models presented here are an alternative, when such site trees are lacking or site characteristics have changed over time. However, application at the stand level is limited due to the relatively low precision. At the forest level, the models provide a good estimate of how growth declines with increasing elevation in three different continentality strata in southwestern BC, as well as insight into the influence of nutrient and water deficiency on site index. This information could be useful for adjusting AACs for the coastal high-elevation forest, and helpful in determining sites at which timber production ceases to be economically and ecologically feasible.

## 7 Conclusions

### ***7.1 Influence of Climate on Amabilis Fir Growth***

Study 4 demonstrated the expected decline of ring width with increasing elevation for second growth amabilis fir; however, latewood width was reduced more strongly than earlywood width. No significant trend was found for any of the ring density measurements with elevation or for any of the tree-ring properties with continentality. Study 5 showed that site index and diameter growth index (D30) on zonal sites were both significantly and similarly related to indirect measures of climate (elevation and continentality strata). On zonal sites, elevation explained a large portion of the variation in site index and D30. Regardless of continentality site index decreased 1.6 m every 100 meters increase in elevation. However, on subcontinental and submaritime sites, growth decline with elevation was less than on maritime sites, indicating the effect of continentality on the climate associated with a given elevation.

Study 3 demonstrated that there is a regional ring-width pattern in high-elevation amabilis fir in southwestern British Columbia. The pattern was explained by (i) a negative effect of late snowmelt on the growing season duration and (ii) a negative influence of high summer temperatures on the growth in the next year. I interpret the latter as a result of a change in carbon allocation towards height growth and reproductive growth rather than as adverse growing conditions due to drought. Warm summers represent rather favorable growing conditions as suggested by (i) the positive effect of the current July temperature on ring width and (ii) spring and summer temperature on maximum density across the study area. Differences in ring width patterns between trees growing in the maritime and submaritime-subcontinental strata appeared to be mainly related to a negative influence of cold winters characteristic of the submaritime-subcontinental stratum.

Using multiple ring properties aided crossdating and enhanced interpretation of results of the dendroecological analysis of second growth amabilis fir (Study 4). Maximum density and ring width jointly carried the main climate information. A separate analysis of earlywood and latewood width may be beneficial, especially when no densitometric data are available. Across the study area, tree-ring patterns found in second growth stands were similar to the ones found in old growth. In old-growth as well as in second-growth stands differences in tree-ring patterns between maritime and submaritime/subcontinental regions appeared to be mainly due to cold

winter temperatures rather than warmer summer temperatures. On some lower elevation sites – particularly in the maritime strata – no common ring pattern between trees was evident (crossdating was not possible even when using multiple ring properties) indicating that climate was not limiting growth on these sites. The strength of the relationship between delayed snowmelt and ring width and between cool summer temperature and maximum density increased from montane to subalpine sites. This suggests that these are the main growth-limiting factors associated with the elevation gradient. There was no negative influence of high summer temperatures or low precipitation on low-elevation sites. Thus, even though dry spells do occur in the study area, especially in the maritime leeward and subcontinental region, their growth-limiting effect on amabilis fir appears to be weak.

### ***7.2 Influence of Soil Moisture Regime and Soil Nutrient Regime on Amabilis Fir Growth***

Before I investigated the influence of soil factors on amabilis fir growth, I evaluated the reliability of field-estimates of soil nutrient regimes by comparing field-estimated SNRs to direct soil nutrient measures (Study 2). The two methods of assessing fertility of high-elevation coastal forest soils gave similar results, indicating that reliable estimates of the levels of plant-available soil nutrients for a given site can be obtained using either method. Mineral soil min-N, which did not vary with continentality, was the best single variable to discriminate between SNRs in this as well as the previous studies. The assertion that nitrogen is the most growth-limiting nutrient in the Pacific Northwest was corroborated by a strong relationship of nitrogen-related variables (tN, C/N ratio) to amabilis fir site index. The lack of relationship of min-N with site index and a relatively low relationship between soil nutrient measures and site index (compared to the influence of climate), in this and some, but not all, previous studies suggest species- and region-specific differences. However, Study 2 demonstrated that soil fertility assessment based on field-identified soil nutrient regimes does reflect the soil nutrient gradient – particularly the gradient of mineralizable nitrogen across the native range of amabilis fir in southwestern BC.

The influence of soil moisture and soil nutrient regimes on site index and average diameter growth was significant, but not as strong as the influence of climate (Study 5). On nutrient poor sites, growth was reduced compared to medium and rich sites. Even though there was a slight increase in growth from medium to rich sites, the analysis corroborates previous findings that amabilis fir is not very nutrient demanding, probably because of association with



mycorrhiza. Site index and D30 were significantly reduced on slightly dry sites manifesting the high-water demand of the species.

Study 4 showed that radial growth reduction due to water or soil nutrient deficiency occurred more strongly in the earlywood and thus increases the latewood percentage and, in turn, ring density. However, as mentioned above, the dendrochronological analysis did not reveal any significant positive relationship to variations in precipitation during the growing season. Very likely the soil moisture regime depends mainly on soil conditions (soil depth, soil texture) rather than on the variation in precipitation on sites supporting amabilis fir in the study area. Water deficit occurs on such sites in all years leading to the observed average growth reduction.

### ***7.3 Wood Quality and Productivity of Amabilis Fir in the Coastal High-elevation Forest***

Wood density measured within trees was negatively related to ring width (Study 4). This is the expected relationship for a species with gradual transition from earlywood to latewood. However, between trees on different sites the relationship between growth rate and ring density depended on the growth-limiting factor. While soil factors, (soil moisture and/or soil nutrient deficiency) reduced earlywood width more strongly than latewood width, climate factors associated with elevation reduced latewood width more strongly. Thus wood density was positively correlated with ring width along the elevation gradient and negatively along soil nutrient and soil moisture gradients. Thus, strength and sign of the growth rate – density relationship depends also on the ecological factors that are limiting growth. The influence of soil factors on wood density was much stronger than the one of the temperature gradient associated with elevation.

The best productivity prediction for amabilis fir can be obtained using site index and height growth functions developed in this study (Study 1). The observed height growth patterns differ between maritime and subarctic/subcontinental strata; in consequence, two separate functions should be used for the two strata. The calibrated models were unbiased when tested against independent data, while previously available models were biased. Whenever height and age data from non-suppressed (top height trees) are available these should be used for site index estimation within an age range between 15 and 160 years.

The models predicting site index from ecological variables were unbiased though not very precise (Study 5). However, they provide valuable tools that can be used to adjust annual

allowable cuts at the forest level and quantify the relative importance of climate and soil for amabilis fir productivity. The influence of climate on productivity was stronger than that of soil factors. Elevation and continentality alone explained 75 % of the variation in site index. The combined model predicted with every 100 m increase in elevation a reduction in site index of 2.0 m for the maritime windward stratum, 2.3 m for the maritime leeward stratum, and 0.7m for the submaritime, subcontinental stratum. Compared to zonal sites, site index was reduced by 6.0 m and 3.1 m on water- and nutrient- deficient sites, respectively.

In light of the finding of the dendroecological analysis, it becomes apparent that productivity will be lower than predicted from the model on high snow-pack sites. Future models should include snow data, if only indirectly inferred from micro topography, slope, aspect, and height of epiphytic lichens. Water-deficient sites supporting amabilis fir are relatively rare and mainly restricted to rock outcrops. These sites should be excluded from commercial logging because of low economic value, potential erosion, and following regeneration difficulties on the shallow soils. Since nutrient-deficient sites are common (more so than zonal sites) in the high-elevation forest, overall the productivity in the high-elevation coastal forest must be considered low.

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## Appendix I: Listing of All Sample Plots

Boston Bar (Subcontinental Stratum)									
Plot	Subzone	SMR	SNR	Aspect	Elevation (m)	Tree sp.	Age bh	Height (m)	DBH (cm)
9501	ESSFmw	F	M	W	1450	Ba 3	84 - 91	20.2	23.4
9502	ESSFmw	SD	P	F	1465	Ba 3	103 - 139	16.5	19.5
9503	ESSFmw	F	M	W	1500	Ba 3	89 - 93	19.0	23.9
9505	ESSFmw	F	M	W	1540	Ba 3	82 - 89	19.9	23.0
9507	ESSFmw	M	M	E	1580	Ba 3	75 - 86	20.7	22.2
9510	CWHms2	SD	P	W	1300	Ba 3	61 - 101	18.9	20.9
9511	CWHms2	SD	P	S	1070	Ba 3	93 - 103	20.9	20.4
9512	CWHms2	F	M	S	1070	Ba 2	98 - 103	25.1	30.8
9513	CWHms2	M	VR	W	1050	Ba 3	102 - 106	32.0	31.8
9514	ESSFmw	SD	P	W	1470	Ba 3	124 - 130	19.7	22.0
9515	ESSFmw	F	M	W	1320	Ba 2	105 - 106	23.8	30.9
9516	ESSFmw	M	R	S	1545	Ba 2	100 - 103	25.1	32.3
9519	ESSFmw	M	M	E	1620	Ba 2	84 - 92	22.4	25.8
9520	ESSFmw	F	M	S	1670	Ba 2	90 - 90	19.2	34.9
9524	ESSFmw	M	M	E	1500	Ba 2	71 - 77	18.5	27.0
9525	ESSFmw	F	M	E	1500	Ba 3	73 - 79	18.7	24.5
9528	CWHms2	SD	P	N	975	Ba 3	84 - 90	19.6	21.2
9529	CWHms2	SD	P	E	985	Ba 3	90 - 96	20.2	21.0
9530	CWHms2	SD	P	S	970	Ba 2	101 - 113	20.5	24.7
9531	CWHms2	F	P	E	1180	Ba 3	111 - 116	22.7	25.5
9532	CWHms2	F	M	S	1260	Ba 2	70 - 76	20.6	27.4
9533	CWHms2	SD	P	E	1260	Ba 2	78 - 78	15.4	19.7
9534	CWHms2	SD	P	E	1280	Ba 3	73 - 78	15.7	17.8
Squamish (Submaritime Stratum)									
9535	CWHms2	F	M	E	925	Ba 2	120 - 129	30.2	34.2
9538	ESSFmw	F	M	W	1410	Ba 3	92 - 94	20.3	28.4
9539	ESSFmw	SD	P	W	1420	Ba 3	106 - 133	16.9	23.8
9540	ESSFmw	M	R	W	1405	Ba 3	86 - 97	24.6	30.5
9543	ESSFmw	M	R	W	1410	Ba 2	78 - 86	22.6	33.6
9547	CWHms2	M	M	N	905	Ba 3	71 - 90	18.0	29.7
9549	MHmm2	F	P	N	945	Ba 2	137 - 138	26.8	30.5
9550	MHmm2	F	P	W	935	Ba 2	123 - 139	25.1	31.3
9552	CWHms2	M	R	W	825	Ba 2	127 - 133	35.7	43.5
9553	CWHms2	MD	P	N	850	Ba 3	124 - 138	19.2	21.7
9555	CWHms2	M	R	S	880	Ba 3	40 - 68	22.4	22.7
9558	MHmm2p	F	M	S	1485	Ba 2	78 - 114	8.9	17.3
9560	CWHms2	F	P	S	930	Ba 3	92 - 102	21.2	21.5
9561	CWHms2	F	M	S	920	Ba 2	101 - 103	26.0	33.6
9562	CWHms2	F	M	S	895	Ba 2	139 - 139	28.9	32.1
9563	CWHms2	M	R	E	960	Ba 2	60 - 62	27.8	37.6
9564	MHmm2	M	VR	N	1150	Ba 2	91 - 104	29.2	39.0
9565	MHmm2	M	R	N	1150	Ba 2	92 - 99	30.6	44.2
9566	MHmm2	VM	VR	N	1160	Ba 3	79 - 113	10.4	17.0
9604	MHmm1	F	M	S	1000	Ba 3	34 - 37	16.1	23.0
9605	MHmm1	F	P	S	1005	Ba 3	35 - 37	11.6	20.2
9606	MHmm1	F	P	S	1005	Ba 3	36 - 38	12.0	18.2



9609	CWHvm2	F	M	S	580	Ba 3	56 - 61	32.4	38.8
9610	CWHvm2	M	R	S	580	Ba 3	58 - 64	36.1	51.5
9611	CWHvm2	F	M	S	730	Ba 3	66 - 66	30.8	33.8
9612	CWHvm2	F	M	S	765	Ba 3	65 - 68	24.7	38.0

## Nimpkish (Maritime Windward Stratum)

9613	CWHvm1	M	R	F	100	Ba 3	55 - 56	33.9	34.9
9614	CWHvm1	F	M	E	140	Ba 3	53 - 57	31.0	34.4
9615	CWHvm1	M	M	N	140	Ba 3	61 - 65	33.1	32.4
9616	CWHvm1	F	P	F	135	Ba 3	64 - 68	29.4	33.9
9617	CWHvm1	M	R	W	75	Ba 3	46 - 50	33.7	46.5
9618	CWHvm1	F	M	E	220	Ba 3	43 - 45	32.7	33.3
9621	CWHvm1	F	M	N	340	Ba 3	38 - 40	25.7	31.3
9622	CWHvm1	M	R	W	300	Ba 3	41 - 45	32.3	40.7
9623	CWHvm2	F	R	F	600	Ba 3	41 - 43	22.1	30.3
9624	CWHvm2	M	R	N	580	Ba 3	40 - 42	26.6	37.0
9625	CWHvm2	F	M	N	605	Ba 3	41 - 42	24.5	36.0

## Gold River (Maritime Windward Stratum)

9629	CWHvm1	M	VR	E	500	Ba 3	186 - 191	55.0	73.7
9630	CWHvm1	F	M	E	520	Ba 3	184 - 201	53.0	85.2
9631	MHmm1	M	R	W	980	Ba 3	61 - 79	22.4	37.5
9632	CWHvm2	M	M	W	660	Ba 2	78 - 81	38.7	50.3
9634	CWHvm2	F	M	W	560	Ba 3	80 - 84	33.9	44.6
9635	CWHvm2	VM	R	W	550	Ba 3	79 - 83	35.9	48.8
9636	CWHvm2	F	M	W	555	Ba 3	77 - 81	35.8	36.9
9601	CWHvm2	M	R	F	550	Ba 3	83 - 94	38.6	43.3

## Mt. Washington (Maritime Leeward Stratum)

9640	CWHmm1	F	M	N	515	Ba 3	48 - 72	20.3	22.7
9641	CWHmm1	F	M	W	500	Ba 3	48 - 65	19.0	23.0
9642	CWHmm1	M	M	W	495	Ba 3	41 - 45	20.4	29.2
9643	CWHmm1	SD	M	E	500	Ba 3	42 - 44	14.7	20.8
9644	CWHmm1	F	M	E	495	Ba 3	42 - 45	21.1	28.7
9646	CWHmm1	F	M	E	600	Ba 3	43 - 47	21.8	22.7
9647	CWHmm1	MD	P	E	610	Ba 3	39 - 41	10.3	13.2
9648	CWHmm1	SD	P	E	610	Ba 3	37 - 42	15.4	18.2
9649	CWHmm1	SD	M	E	610	Ba 2	44 - 48	17.1	21.8
9650	CWHmm1	F	M	E	595	Ba 3	46 - 54	19.5	22.3
9682	MHmm1	F	M	E	1190	Ba 3	306 - 312	19.2	31.2
9683	MHmm1	F	P	S	1220	Ba 3	144 - 190	15.6	28.2
9684	MHmm1	F	P	E	1290	Ba 3	247 - 325	12.2	22.0
9685	MHmm1	M	P	F	1320	Ba 3	165 - 250	13.7	29.0
9686	MHmm1	F	M	E	1180	Ba 3	294 - 312	22.6	35.2
9687	MHmm1	M	P	N	1070	Ba 3	314 - 321	27.1	43.0
9688	MHmm1	M	R	N	960	Ba 3	75 - 77	31.9	40.7
9689	CWHmm2	M	M	N	850	Ba 3	79 - 85	25.8	25.3
9690	CWHmm2	M	R	N	840	Ba 3	83 - 85	31.5	34.7

## Port Alberni (Maritime Leeward Stratum)

9667	MHmm1	M	M	S	870	Ba 3	128 - 164	28.8	38.0
9668	MHmm1	M	R	S	885	Ba 3	157 - 173	30.2	37.5
9669	MHmm1	F	P	F	1080	Ba 2	266 - 276	23.6	39.8
9670	MHmm1	F	P	S	1090	Ba 3	128 - 144	13.6	20.2
9671	MHmm1	SD	P	E	1180	Ba 3	284 - 290	10.0	16.8
9672	MHmm1	F	P	S	1050	Ba 3	182 - 204	27.3	45.6
9673	CWHmm2	F	M	W	620	Ba 3	58 - 59	30.2	33.5

9674	CWHmm2	F	M	F	610	Ba 3	53 - 55	26.2	33.0
9675	CWHmm2	M	R	W	610	Ba 3	56 - 60	30.7	33.8
9676	CWHmm2	M	VR	F	600	Ba 3	55 - 60	28.8	39.0
9677	MHmm1	F	P	N	1220	Ba 3	150 - 161	18.4	28.3
9678	MHmm1	F	P	N	1220	Ba 3	123 - 150	12.1	19.2
9679	MHmm1	F	P	N	1220	Ba 3	150 - 180	20.4	29.3

## Sunshine Coast (Martime Windward Stratum)

9651	CWHvm2	M	M	W	840	Ba 3	38 - 41	23.2	41.0
9652	CWHvm2	M	M	W	860	Ba 3	41 - 42	19.5	34.0
9653	CWHvm2	F	M	W	860	Ba 3	37 - 39	16.4	28.5
9654	CWHvm2	F	M	W	930	Ba 3	28 - 36	16.3	25.7
9656	CWHvm2	M	M	S	650	Ba 3	51 - 54	28.3	29.5
9657	CWHvm2	VM	R	S	650	Ba 3	51 - 52	29.6	29.3
9661	CWHvm2	F	P	S	770	Ba 3	45 - 64	24.4	35.2
9662	CWHvm2	F	P	S	875	Ba 3	40 - 47	27.3	36.3
9663	CWHvm2	F	P	E	660	Ba 3	50 - 56	22.7	25.8
9664	CWHvm2	VM	VR	S	765	Ba 3	39 - 46	23.5	41.5
9691	MHmm1	VM	R	W	1290	Ba 2	55 - 63	16.8	27.3
9692	MHmm1	M	M	W	1300	Ba 3	105 - 110	27.7	35.2
9693	MHmm1	M	M	W	1250	Ba 2	138 - 145	25.3	36.0
9694	MHmm1	F	M	W	1230	Ba 3	160 - 171	33.0	52.5
9695	MHmm1	F	M	W	1270	Ba 3	159 - 167	27.8	36.7
9696	CWHvm1	M	R	F	380	Ba 3	42 - 44	24.8	29.5
9697	CWHvm1	VM	R	F	380	Ba 3	39 - 49	25.0	38.8
9698	CWHvm1	F	M	N	390	Ba 3	42 - 47	23.7	29.0
9699	MHmm1	F	M	W	1240	Ba 3	110 - 125	27.3	38.5
96100	MHmm1	SD	P	N	1270	Ba 3	140 - 151	10.6	18.5
96101	MHmm1	F	M	W	1530	Ba 3	55 - 92	7.7	18.8
96102	MHmm1	F	M	W	1460	Ba 3	40 - 56	13.5	23.2
96103	MHmm1	M	M	W	1460	Ba 3	124 - 133	17.6	28.8
96104	MHmm1	F	M	W	1350	Ba 3	113 - 120	23.5	33.7

## Explanation of Abbreviations:

Plot = Plotnumber

Subzone: Biogeoclimatic subzone:

ESSFmw	= Moist, Warm - Engelmann Spruce-Subalpine Fir zone
CWHms1	= Southern, Moist, Submaritime - Coastal Western Hemlock variant
CWHmm1	= Submontane, Moist, Maritime - Coastal Western Hemlock variant
CWHmm2	= Montane, Moist, Maritime - Coastal Western Hemlock variant
CWHvm1	= Submontane, Very Wet, Maritime - Coastal Western Hemlock variant
CWHvm2	= Montane, Very Wet, Maritime - Coastal Western Hemlock variant
MHmm1	= Windward, Moist, Maritime - Mountain Hemlock zone variant
MHmm2	= Leeward, Moist, Maritime - Mountain Hemlock variant

SMR = actual soil moisture regime

MD	moderately dry
SD	slightly dry
F	fresh
M	moist
VM	very moist

SNR = soil nutrient regime

VP	very poor
P	poor
M	medium
R	rich
VR	very rich

Aspect

N	north
E	east
S	south
W	west
F	flat

Elevation in meters

Tree sp. Tree species, and number of trees sampled

Age bh range of age @ breastheight within the plot

Height (m) average total height

DBH (cm) average diameter at breastheight in centimeters

LC (m) average total length of living crown