ECOLOGICAL AND HEIGHT GROWTH ANALYSIS OF SOME SUB-BOREAL IMMATURE LODGEPOLE PINE STANDS IN CENTRAL BRITISH COLUMBIA

by

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ABSTRACT

This study investigated relationships between lodgepole pine (*Pinus contorta* Dougl. *ex* Loud.) height growth and ecological site quality. Vegetation, environmental, and stand data, obtained from seventy-two sample plots established in immature stands over wide range of soil moisture and soil nutrient conditions in the montane boreal climate in central British Columbia, were analyzed using the methods of biogeoclimatic ecosystem classification and numerical analysis. The analysis produced categorical and continuous measures of ecological site quality which were then related to measures of height growth obtained from stem analysis of one hundred and sixty-two site trees.

The seventy-one diagnostic species and ten vegetation units identified by tabular analysis were strongly correlated with, and occupied relatively narrow segments of climatic, soil moisture, and soil nutrient gradients. Heat index was used to characterize the climatic gradient represented by three biogeoclimatic subzones. Actual/potential evapotranspiration ratio and the depth of the growing-season water table or gleyed soil horizons were used to characterize the soil moisture gradient and to classify the study plots into eleven soil moisture regimes. Soil mineralizable-N and the sum of exchangeable bases were used to characterize the soil nutrient gradient and to classify the study plots into five soil nutrient regimes. Correlations between vegetation and categorical or continuous measures of ecological site quality implied that these measures had a meaning relative to moisture and nutrient conditions experienced by plants. Eleven site associations circumscribed by vegetation units and characterized by a range of climatic, soil moisture, and soil nutrient regimes, stratified the study plots into qualitatively and

quantitatively distinct, field recognizable, segments of regional gradients of ecological site quality.

Regression analysis showed that the most strongly related ecological variables to lodgepole pine site index were: (1) ecotopes, defined either by a combination of categorical variables (biogeoclimatic subzone, soil moisture regime, and soil nutrient regime) (adj. $R^2 = 0.85$) or by a combination of continuous variables (potential evapotranspiration, and the depth of water table or gleyed soil horizons, and soil mineralizable-N) (adj. $R^2 = 0.82$), (2) site associations (adj. $R^2 = 0.81$), (3) site series (adj. $R^2 = 0.84$), and (4) vegetation units (adj. $R^2 = 0.83$). Lodgepole pine appears to have a potential to grow on nitrogen-rich sites with pH < 7.

The three-parameter Chapman-Richards growth function precisely described height growth of site trees over a wide range of sites. The pattern of height growth changed with ecological site quality. Site series and ecotope (defined either by a combination of categorical or continuous variables) had a stronger relationship with the function parameters than site index. The two site-specific height growth models developed—the site unit model and the ecotope model—were more effective than an existing site-index driven growth models.

The above results support the use of either categorical or continuous synoptic ecological variables in describing the variation of lodgepole site index in relation to ecological site quality, which can be inferred from the understory vegetation developed in mid-seral stands. The derived site index and site-specific height growth models showed strong relationships between height growth and several measures of ecological site quality produced by biogeoclimatic ecosystem classification. In consequence, categorical or continuous ecological variables could be used in polymorphic growth modelling to predict lodgepole pine height growth so that the effects of site, and environmental changes, including management practices, on forest productivity can be better understood.

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1. GENERAL INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl. *ex* Loud.) is the most widely distributed coniferous tree species in western North America (Wheeler and Critchfield 1985). Its distribution extends approximately from 64^0 N latitude and 144^0 W longitude in the Yukon Territory to 31^0 N latitude in Baja California and 105^0 W longitude in South Dakota (Burns and Honkala 1991). Lodgepole pine is a major timber species—ranking second in volume among tree species harvested in British Columbia and Alberta, exceeded only by spruce (Kennedy 1985). In this wide geographical range, lodgepole pine grows under a wide variety of ecological conditions both in extensive, pure stands and in association with many other conifers (Burns and Honkala 1991). It is one of a few tree species with a remarkably wide climatic and edaphic amplitude (Krajina 1969).

In view of lodgepole pine's importance for timber production, it is important to know the relationships between its growth performance and site conditions. Grier *et al.* (1989) recommended systematic quantitative research into relationships between forest productivity and both extrinsic and intrinsic site factors. This dissertation focusses on the relationships between height growth and ecological site quality in order to establish a stronger link between the provincial system of biogeoclimatic ecosystem classification (BEC) and growth and yield studies. The limited quantitative information on how site conditions affect forest growth constitutes an unfortunate void in the ecology of trees species and forest management of British Columbia.

Two major theses were adopted:

(1) Sound forest management requires an ecological basis and ecosystem-specific approach. This is necessary because each tree species is adapted to a certain range of ecological conditions; therefore each species will grow and behave in ways that depend on the ecosystems or sites in which it grows (Klinka and Feller 1984). Understanding ecosystems means understanding the ecological basis of productivity (Van Dyne 1969).

(2) The application of an ecosystem-specific approach requires that a forest, which consists of many different ecosystems, be stratified into ecologically uniform segments. When it is stratified, management of that forest can be simplified and, at the same time, given a sound ecological foundation (Klinka *et al.* 1990b). A consistent and ecologically meaningful stratification requires, in turn, an appropriate ecological classification system.

If the BEC system is an appropriate ecological classification system, then it should yield a useful means for explaining the variation in growth performance of different tree species on different forest sites. If this assumption can be convincingly confirmed, then this study will provide principal evidence of the usefulness of the BEC system to forest research and management.

Ecosystem studies carried out in British Columbia by Krajina and his students resulted in the development of the biogeoclimatic ecosystem classification (BEC) system. The B.C. Forest Service adopted this system, and in the past decade, the BEC system has become entrenched in forest research and management as a means of recognizing different types of forest sites and of characterizing their ecological quality (e.g., Krajina 1972, Kimmins 1977, Pojar *et al.* 1987, Klinka *et al.* 1990b, Meidinger and Pojar 1991).

In all forest site-productivity studies, the question at once arises as to what is the concept and definition of site, and on what basis are site data to be evaluated in order to clarify site-productivity relationships. The BEC system considers site (habitat or ecotope) to be the physical environment (climate, topography, and soil) of a geographically circumscribed ecosystem, and organizes ecosystems into environmentally characterized classes (Pojar *et al.* 1987). This implies the recognition of environmentally different kinds (types) of sites, each with different ecological conditions or quality for plant growth. Thus, from the ecological perspective, the extrinsic and intrinsic environmental factors affecting the biotic community of an ecosystem define quality of a site (e.g., Daubenmire 1968, Daniel *et al.* 1979, Spurr and Barnes 1980, Grier *et al.* 1989).

While it is fairly easy to work with individual environmental factors, it is very difficult to determine their integrated effect on plants due to compensating effects (Bakuzis 1969, Damman 1979, Assmann 1970, Oliver and Larson 1990). As a result, sites with different combinations of environmental factors can have similar ecological qualities. To clarify plant-site relationships and to define ecological site quality, the BEC system uses the primary factors that have a direct and major influence on plant establishment, survival, and growth: climate (light and temperature), soil moisture, soil nutrients, and soil aeration (e.g., Cajander 1926, Pogrebnyak 1930, Hills 1952, Major 1963, Krajina 1969, Grier *et al.* 1989).

To determine ecological quality of a site means to determine the expression or value of these primary factors on that site. As forest productivity is the consequence not the cause of ecological site quality, it can not be a true measure of ecological quality of the site (although it can be considered an associated characteristic), and ecological site quality can not be a true measure of forest productivity.

Forest productivity has always been an essential consideration in stand management, and site index has always been the most widely used measure of site quality, *i.e.*, the inherent capacity of a site to support forest growth. It is recognized that site index is an indirect and incomplete measure of forest productivity (*i.e.*, the growth performance of a tree species on a given site) or site productivity (*i.e.*, the capacity of the site to support the growth of the species), as it only indicates the height growth performance at a given point in time (e.g., Jones 1969; Burger 1972, Carmean 1975, 1982; Hägglund 1981; Spurr and Barnes 1981; Clutter *et al.* 1983; Monserud 1984, 1988). As this study investigates only how height growth changes with ecological site quality, site index was adopted as the measure of lodgepole pine growth performance on ecologically different sites.

The most prevalent restriction in using site index to estimate height growth is that it must be estimated from trees whose height growth has not been affected by anything other than the factors constituting ecological quality of the site. The top height concept (*i.e.*, using only dominant trees of the stand that have been likely dominant throughout the life of the stand) has been widely accepted as a reasonable measure of height for site index (*op. cit.*) and a better measure of site quality than diameter or total volume growth (Oliver and Larson 1990).

The goal of the research carried out in this study was to answer two questions for immature lodgepole pine stands growing in the Sub-boreal Pine--Spruce (SBPS) and Sub-boreal Spruce (SBS) zones of central British Columbia:

(1) How does height growth change with ecological site quality? and

(2) What is the strength of the relationships between the measures of ecological site quality and height growth?

Specific objectives of this ecological investigation were:

(a) to locate study stands along climatic and edaphic gradients within the montane boreal region of central British Columbia;

(b) to obtain qualitative and quantitative climatic, soil, understory vegetation, and stand data for characterizing plant communities, soil moisture and nutrient regimes, ecological site quality, foliar nutrients, and height growth of the study stands;

(c) to stratify and classify the study stands according to their vegetation and ecological site quality;

(d) to develop regression models that use categorical or continuous measures of ecological site quality, for the prediction of site index;

(e) to specify a height growth model, which uses categorical or continuous measures of ecological site quality, for the prediction of site index and for the prediction of height growth.

The dissertation is comprised of six chapters. Chapter 1 gives the general introduction and Chapter 2 describes the study area. Chapter 3 through 5 each include introduction, materials and methods, results and discussion, and conclusions sections. These three chapters are related, but also independent of each other. Ecological analysis of the study sites is reported in Chapter 3 which lays a foundation for the central part of this dissertation—Chapter 4 investigating the relationships between lodgepole pine site index and measures of ecological site quality, and Chapter 5 in which stem analysis data are combined with the most useful measures of ecological site quality in the three-parameter Chapman-

Richards growth function to derive and evaluate site-specific height growth models. Conclusions are given in Chapter 6.

2. THE STUDY AREA

The study area is situated in the central interior of British Columbia between 52-55^0 N latitude and 123-125^0 W longitude. Physiographically, the area occurs within the Interior Plateau (Holland 1976), and climatically, within the Sub-boreal Spruce (SBS) and Sub-boreal Pine—Spruce (SBPS) zones (B.C. Min. For. 1988, Meidinger and Pojar 1991). The study plots were distributed in three distinct segments of a regional climatic gradient (biogeoclimatic subzones) based on precipitation and temperature (Table 2.1) and in three widely separated sampling areas: south of Anahim Lake, north of Burns Lake, and east and southeast of Prince George (along Bowron River and Willow Roads) (Figure 2.1). The Anahim Lake area lies within the Very Dry and Cold SBPS subzone (SBPSxc), the Burns Lake area within the Moist and Cold SBS subzone (SBSmc), and the Prince George area within the Wet and Cool SBS subzone (SBSwk) (Meidinger and Pojar 1991).

The Interior Plateau ranges from 600 m to 1200 m above sea level and is covered with glacial till which usually bears a close association mineralogically with the underlying bedrock (Valentine and Dawson 1978). The predominant basic basalt lavas contribute to the high base saturation of many soils. The Anahim Lake area occurs on the gently rolling Fraser Plateau formed primarily by basaltic lava flows. The Burns Lake area is within the low relief Nechako Plateau which was also formed from lava flows covering older volcanic and sedimentary rocks, with a few granitic intrusions (Pojar *et al.* 1984, Meidinger and Pojar 1991). The Bowron River and the Willow Road sampling areas are located on a large and deep glaciofluvial deposit in the eastern corner of the Fraser Basin.

Table 2.1. Selected climatic characteristics for the study area[a].

Subzone Sampling area	SBPSxc[b] Anahim Lake	SBSmc Burns Lake	SBSwk Prince George
Climatic station	Anahim Lake Kleena Kleene	Burns Lake Topley Landing	Aleza Lake
Elevation (m)	1097 (899)	704 (722)	625
Mean annual precipitation (mm)	305	492	897
Mean annual snowfall (%MAP)	49	48	38
Mean precipitation May-Sept. (mm)	118	221	353
Mean precipitation of the driest summer month (mm)	15.5	32.8	54.7
Mean precipitation of the wettest winter month (mm)	36.4	54.8	97.8
Mean annual temperature (°C)	0.4	2.4	3.0
Mean temperature of the warmest month (°C)	11.4	14.0	15.3
Mean temperature of the coldest month (°C)	-13.7	-12.9	-12.9
Potential evapotranspiration (mm/year)[c]	411	439	460
Heat index[c]	13.4	18.5	21.5
Index of continentality[c]	36.9	34.4	38.8

[a]Climatic data are from Canadian Climate Normals 1951-1980 (Environm. Canada).
[b]SBPSxc - Very Dry and Cold SBPS subzone, SBSmc - Moist and Cold SBS subzone, and SBSwk - Wet and Cool SBS subzone.
[c]Calculated from Canadian Climate Normals using methods described in Chapter 3.

The SBS and SBPS zones are parts of the Canadian Boreal Forest region which is a part of Microthermal Coniferous formation (Krajina 1969, 1972). The climate of both zones is montane boreal (Dfc, Köppen in Trewartha 1968). It can be best described as drier (in the SBPS zone) to wetter (in the SBS zone), continental (warm summer and cold winter), with a short growing season, less precipitation in spring than in summer, autumn, and winter, frequent cloudiness, and light (in the SBPS zone) to heavy (in the SBS zone) snow cover. In comparison to a typical boreal climate, sub-boreal climate is slightly less continental or polar/arctic, thus slightly warmer in January and cooler in July. Consequently, sub-boreal winters are shorter and the growing season slightly longer with a smaller loss of water due to the lower evapotranspiration than in the typical boreal climate (Krajina 1969). As a result of favorable climatic characteristics, forest productivity in the SBS zone is higher than in the SBPS zone, which is located in the rain shelter of the coastal mountains, Boreal White and Black Spruce (BWBS) zone, which is located at higher latitudes, and subalpine boreal Engelman Spruce-Subalpine Fir (ESSF) zone, which is located at higher altitudes.

Major tree species in the prevailing upland coniferous forest in the SBS and SBPS zones include: lodgepole pine, white spruce (*Picea glauca* Moench), subalpine fir (*Abies lasiocarpa* Hook.), and black cottonwood (*Populus trichocarpa* Torr. *et* Gray *ex* Hook.); minor tree species are: black spruce [*Picea mariana* (Mill.) B.S.P.], trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), and Engelmann spruce (*Picea engelmannii* Parry *ex* Engelm.) (Hosie 1979).

Due to the frequent occurrence of forest fires, a large area of the SBS and SBPS zones is occupied by pure, even-aged lodgepole pine and trembling aspen stands in various stages of secondary succession. There is a general tendency for lodgepole pine to dominate early seral forests on coarse-textured and acidic soils. In the SBS zone, the old-growth forests are dominated by white spruce, but may contain significant amounts of lodgepole pine on drier sites and subalpine fir on wetter sites (Pojar *et al.* 1984). In the SBPS zone, due to a drier climate, lodgepole pine appears to be more shade-tolerant than in the SBS zone, and constitutes a significant component in a few scattered old-growth forests.

Old-growth forests on zonal sites are dominated by white spruce and/or its hybrids, with a significant proportion of lodgepole pine in the SBPS zone. Poorly to moderately developed shrub and herb layers typically contain *Arctostaphylos uva-ursi, Rosa acicularis, Shepherdia canadensis,* and *Spiraea betulifolia* etc. (in the SBPS zone), *Vaccinium caespitosum, V. membranaceum, V. myrtiloides, Amelancher alnifolia, Sorbus scopulina, Cornus canadensis,* and *Arnica cordifolia* etc. (in the SBS zone). *Hylocomium splendens, Pleurozium schreberi, Ptilium crista-castrensis, Dicranum polysetum* (in the SBS zone), and *Cladonia spp.* (in the SBPS zone) are the major species in the moderately to well developed moss and lichen layers.

Till, lacustrine, and fluvial materials derived from volcanic (less often granitic) rocks are the most common soil parent materials. The soils formed from the till and lacustrine materials on zonal sites are typically moderately deep, loamy-skeletal, weakly acidic Gray Luvisols, less frequently Brunisols and Podzols (Agric. Can. Expert Committee on Soil Survey 1987) with thin and poorly decomposed forest floors (Valentine 1978), or poorly developed Mors (Klinka *et al.* 1981). The presence of a fine-textured and angular blocky Bt horizon at the 30 to 50 cm depth, in which clay has been accumulated, tends to restrict drainage, permeability, and aeration characteristics of the soils (Pojar *et al.* 1984). As a result, these soils become extremely wet in the spring causing root mortality and inducing a shallow rooting pattern. The soil formed from the fluvioglacial materials on zonal sites are basically deep, sandy-skeletal, more acidic Dystric Brunisols or Podzols due to more effective precipitation and intensive leaching of bases with a bleached sandy Ae horizon and better developed Mor or Moder humus forms (*op. cit.*). The occurrence of the coarse-textured sandy soils leads to good permeability, drainage, and aeration of the soils, therefore, causing a deeper rooting system. Nevertheless, leaching of bases is intense in these soils. Organic materials have also been found in depressions and water-receiving sites.

3. ECOLOGICAL ANALYSIS OF THE STUDY ECOSYSTEMS

3.1 INTRODUCTION

Applying the ecosystem concept to forest management and research requires that a forest be ecologically stratified in order to determine the kind and pattern of component ecosystems. Ecological stratification implies identification, description, and mapping of ecosystems which must be based on taxonomic classification and carried out effectively and consistently. The ecological stratification also implies that recognized strata or units reflect and clarify to the greatest extent vegetation-environment relationships (Krajina 1965a).

The most pervasive ecological classification in western Canada is a biogeoclimatic ecosystem classification, adapted by the British Columbia Forest Service from the pioneering work by V.J. Krajina and his students (e.g., Krajina 1965b, 1969; Pojar 1983, 1985; Pojar *et al.* 1986, 1987; Klinka and Krajina 1986; Green *et al.* 1989; Meidinger and Pojar 1991). This classification (also referred to as the BEC system) results from an analysis and synthesis of vegetation, climate, and soil data. The approach to classification is hierarchical, with three interrelated levels of integration: local, regional, and chronological. The multiple-category vegetation and site classifications organize local ecosystems, the multiple-cateory zonal classification organizes regional ecosystems, and, using the framework of the site classification, the vegetation classification deals with vegetation dynamics.

The product of any multiple-category taxonomic classification are classes, units, or taxa which were distinguished by using a chosen set of differentiating characteristics and arranging them into a hierarchy. If the vegetation, zonal, and site classifications of the BEC system are truly ecological, then differentiating characteristics or classes produced by each of the component classifications should express and signify certain kinds of vegetation-environment relationships. In consequence, the major theme of the study described in this chapter was to carry out ecosystem classification using the methods and system of biogeoclimatic ecosystem classification, and to demonstrate the ecological relationships discovered or integrated by the resulting classifications. In further chapters, the differentiating characteristics applied, and the classes produced, will be used to establish the link to forest productivity.

The classes produced by the vegetation classification represent floristically uniform classes of plant communities in the sense of the Braun-Blanquet approach (1932), which is based on the floristic composition of the entire plant community. This approach has been widely used in Europe (e.g. Becking 1957; Dahl 1956; Poore 1955; Moore 1962), Soviet Union (Sukachev 1964), China (Wu 1980), the United States (Daumenmire 1952; 1968), and Canada (Krajina 1969). The approach identifies and uses species with relatively narrow ecological amplitudes as the basis for grouping (differentiation); such species are termed 'diagnostic', and a group of them constitute a 'diagnostic combination of species' (Pojar *et al.* 1987). The underlying assumption is that diagnostic species provide, at the same time, floristically as well as ecologically uniform classes of ecosystems. Apart from classification, some diagnostic species have been used for the direct indication of synoptic, and to a lesser degree, individual factors of ecological site quality (Klinka *et al.* 1989a, 1989b).

The actual vegetation that develops on a particular site depends on and reflects the site, disturbance, chance, and time, whereas climax vegetation reflects principally the influence of the site. As this study analyzed mid-seral successional stages, their vegetation classification might have been confounded by the effects of disturbance and site factors. To deal with temporary variations in vegetation, the BEC system uses the vegetation of late-seral, near-climax, and climax successional stages to develop site classification for organization of ecosystems into site units on the basis of more or less stable environmental attributes and the concept of ecological equivalence. This principle implies that sites with the same or equivalent properties have the same vegetation and productivity potential (Cajander 1926, 1949, Bakuzis 1969, Odum 1971).

Considering physiological and ecological perspectives implicit in literature, and addressing the problem of environmental compensation (Assmann 1970), the site classification in the BEC system employs three synoptic environmental factors with a direct and major influence on plant establishment, survival, and growth: climate (radiation, temperature, and precipitation), soil moisture, and soil nutrients (Pojar *et al.* 1987). Where appropriate, other environmental factors directly affecting vegetation development are included as differentiating characteristics. Independently from classification, these factors have been used for direct indication of ecological site quality in coastal British Columbia (Klinka *et al.* 1984, 1989a; Klinka and Carter 1990). Therefore, to facilitate the use of indicator plants and the direct assessment of the ecological quality of forest sites in the study area, special attention was given to quantitative characterization and classification of soil moisture and nutrient regimes.

The main objective of the research reported in this chapter was to lay a foundation for investigating relations of lodgepole pine height growth to measures of ecological site quality (Chapters 4 and 5). Secondary objectives were to investigate (1) the usefulness of the understory vegetation in immature lodgepole pine stands in site classification, (2) the applicability of the understory species as indicators of ecological site quality, (3) the usefulness of mineralizable-N as an index of soil nutrient availability, and (4) vegetation-environmental relationships between the study plots. The objectives were accomplished by analyzing, synthesizing, and interpreting the vegetation and environmental data obtained from 72 sample plots using phytosociological and numerical techniques.

3.2 Materials and Methods

3.2.1 Sample Plots and Sampling

The study plots were located in three geographically disjunct biogeoclimatic subzones: (1) Very Dry and Cold Sub-boreal Pine—Spruce (SBPSxc), (2) Moist and Cold Sub-boreal Spruce (SBSmc), and (3) Wet and Cool Sub-boreal Spruce (SBSwk), each representing a distinct segment of a regional, montane boreal, climatic gradient (B.C. Min. For. 1988; Meidinger and Pojar 1991) (Figure 2.1; Table 2.1).

All sample plots used in the study were located in even-aged (30 to 80 years), unmanaged, naturally established, lodgepole pine-dominated stands, which were uniformly and fully stocked, but not overstocked (60% to 95% tree canopy cover, exceptionally < 50% on wet sites), and which were free of disturbance and damage. These conditions provide the best estimation of site index at a given index age of 50 years (Fries 1978, Clutter *et al.* 1983). In each sampling area, sample plots were selected across the widest possible range of soil moisture and nutrient gradients (Harrington 1986, Verbyla and Fisher 1989). Soil moisture regimes were estimated in the field using selected topographic and soil properties and indicator plant species following the methods described by Klinka *et al.* (1984, 1989b). In each study stand, a 400 m^2 (0.04 ha) sample plot was subjectively selected (Orlóci 1988) to represent an ecosystem relatively uniform in topography, soil, understory vegetation, and stand characteristics. Of the 72 plots was used in the study — 18 SBPSxc plots were located south of Anahim Lake, 18 SBSmc plots north of Burns Lake, and 36 SBSwk plots east and southeast of Prince George.

Site descriptions for each plot included measurements or identification of elevation, slope position, slope aspect, slope gradient, bedrock geology, and soil parent material. The vegetation description followed the procedure outlined by Walsmley *et al.* (1980) and Luttmerding *et al.* (1990), including identification of all vascular plants, mosses, liverworts, and lichens and estimation of species cover by percentage or significance values according to the A (tree), B (shrub), C (fern, herb, and graminoid), and D (moss and lichen) layers. The Domin-Krajina scale (Krajina 1933 cited by Mueller-Dombois and Ellenberg 1974) was used to estimate species significance. Species nomenclature followed Hitchcock and Cronquist (1973) for vascular plants, Ireland *et al.* (1980) for mosses, Stotler and Crandall-Stotler (1977) for liverworts, and Hale and Curberson (1970) and Vitt *et al.* (1988) for lichens. A complete checklist of plant species on the study ecosystems is given in Appendix I.

Four dominant trees with no obvious evidence of abnormal growth performance in each plot were measured for breast height age, using an increment bore, and top height, using a Suunto clinometer. Site index of each sample plot was then determined using appropriate tables for lodgepole pine (Goudie 1984).

In each sample plot, four sample points were systematically located in each quadrant and soil pits were dug down to the root-restricting layer (highly compacted Bt horizon or water table), or to a depth of 1 m from ground surface if the restricting layer was absent. The forest floor and mineral soil were described and identified according to Klinka *et al.* (1981) and Agriculture Canada Expert Committee on Soil Survey (1987), respectively. The major rooting depth, the depth of water table, gleyed horizon, or other restricting layers were recorded. Four forest floor samples were taken as close as possible on each side of the soil pit and composited for chemical analysis; similarly, mineral soil for chemical analysis was sampled on each side of the soil pit to a depth of 30 cm, or less if a root restricting layer was present, and composited.

Projected leaf area index (LAI) was estimated for 58 plots by converting canopy transmittance (Q_i/Q_0) using the Beer-Lambert law:

[3.2.1] $$LAI = -\ln(Q_i/Q_0)/k,$$

where Q_i = photosynthetically active radiation below canopy; Q_0 = photosynthetically active radiation above canopy. An average of 50 sample points of Q_i was taken on a systematic basis in each plot using the Sunfleck Ceptometer (Model SF-80, Decagon Devices, Inc., 1987). Q_0 was measured using the same Ceptometer immediately before, during, and after the Q_i measurements for 40 plots, and measured continuously using the LI-1000 Datalogger (Li-Cor Inc. 1986) for the additional 18 plots. Measures were taken either under clear sky or continuous cloud cover in order to minimize variation in both Q_i and Q_0. All data were measured from 10:00 am to 2:00 pm during the month of September. Calibration for Q_i from the Ceptometer and Q_0 from the Datalogger was recently carried out (H. Qian, Department of Forest Sciences, University of British Columbia, pers. comm.). The Ceptometer measures (Q_i) were consistently 5-10% lower than the Datalogger measures (Q_0), therefore, adjustment to the Q_i was made; k = the light extinction coefficient and was calculated using the ellipsoidal leaf angle distribution function (Campbell 1986, Carter *et al.* 1991):

$$[3.2.2] \qquad k = \frac{(X^2 + 1/\tan^2\theta)^{(1/2)}}{1.47 + 0.45X + 0.1223X^2 - 0.013X^3 + 0.000509X^4},$$

where θ = the sun elevation angle and X = the ratio of horizontal to vertical semi-axes of the ellipsoid. The Beer-Lambert law assumes that the foliage is randomly distributed in space and leaf inclination angles are spherically distributed (Jarvis and Leverenz 1983); therefore, X was assumed to have a value of 1. The sun elevation angles ranged from 56.3 to 68.4 degrees from vertical. The average corresponding value for k was calculated as 0.55, which falls just above the mid-point of the range of extinction coefficient reported for conifer canopies by Jarvis and Leverenz (1983).

3.2.2. Foliar Nutrient Analysis

Foliar sampling and chemical analysis followed the guidelines and procedure given by Ballard and Carter (1986). In brief, the current year's foliage from the upper crown of fifteen dominant or codominant healthy trees on each of 54 plots was sampled in early October using a shot gun. The analyses for total N, P, K, S, Ca, Mg, Fe, Al, Mn, Cu, Zn, B, available SO_4-S, and active Fe, were conducted by Pacific Soil Analysis Inc., Vancouver, B.C. Both the concentration (dry-mass basis) and the total weight (mg) per 100 needles were used in evaluating the nutrient status of each stand.

3.2.3. Soil Physical and Chemical Analyses

From each soil pit, coarse fragments larger than 2.5 cm in diameter were weighed and the pit dimensions were measured to determine total soil volume. Seventy-two forest floor samples for bulk density were collected by cutting out a small piece of forest floor, measuring its dimensions, and weighing its mass after oven-drying at 105^0 C for 24 hours. Seventy-two mineral soil samples for bulk density were determined by cutting out a core, measuring its volume using a water replacement method after filling the resulting hole with a thin plastic bag and recording its mass after oven-drying at 105^0C for 24 hours. Subsequently, these bulk density samples were sieved and the total weight, and the weight of coarse fragments larger than 2 mm in diameter, were recorded. The coarse fragment-free bulk density was then calculated using the following equation (Nuszdorfer 1981):

$$[3.2.3] \qquad D_b = \frac{M_{<2\ mm}}{V_{<2\ mm}} \quad ,$$

where D_b = bulk density (kg/m^3);

($M_{<2\ mm}$) = (mass of soil < 2 mm in diameter) = (total dry mass of sampled soil) - (mass of the soil ≥ 2 mm in diameter);

($V_{<2\ mm}$) = (volume of the soil < 2 mm in diameter) = (total volume of the sampled soil) - (volume of the soil ≥ 2 mm in diameter) which equals to the mass of soil ≥ 2 mm in diameter divided by 2.65 (kg/m^3) (average solid particle density).

Soil particle size in the < 2 mm fraction was determined by the hydrometer method (Day 1965, Gee and Bauder 1986) using a < 2 mm soil suspension (50 g/L) in distilled water and sodium-hexametaphosphate (HMP) solution in a 1 L sedimentation cylinder. The analysis was done by Pacific Soil Analysis Inc., Vancouver.

After being air-dried to a constant mass, forest floor samples were ground using a Wiley mill, and mineral soil samples were sieved through a 2-mm sieve to remove the coarse fragments larger than 2 mm in diameter. Subsequent chemical analysis was carried out on the basis of the fine fraction. All chemical analysis was carried out by Pacific Soil Analysis Inc. Vancouver.

The pH of the forest floor was determined using a 1:5 suspension in distilled water and measured with a pH meter (Peech 1965). Mineral soil pH was measured with a pH meter using a 1:1 suspension in distilled water. Total carbon (C_t) was determined using a Leco Induction Furnace (Bremner and Tabatabai 1971). Total nitrogen (N_t) of the mineral soil was determined by the semimicro-Kjeldahl digestion method (Bremner and Mulvaney 1982) followed by colorimetric analysis for NH_4, using a Technicon Autoanalyzer (Anonymous 1976). Mineralizable nitrogen (mN) was measured using the anaerobic incubation procedure of Waring and Bremner (1964), modified by Powers (1980). Exchangeable potassium (K), magnesium (Mg), and calcium (Ca) were extracted using 1 M NH_4OAc adjusted to pH 7 (Page 1982) and measured by atomic absorption spectrophotometry (Price 1978). Mineral soil extractable phosphorus (P_{ex}) was determined using the extraction procedure of Mehlich (1978). The extractable sulphate-sulphur $(SO_4\text{-}S)_{ex}$ of the mineral soil was determined by ammonium acetate extraction (Bardsley and Lancaster 1965) and turbidimetry. Total nitrogen (N_t) and total phosphorus (P_t) of the forest floor were determined using a modified Parkinson and Allen (1975) procedure. Total sulfur of the forest floor (S_t) was determined using a Fisher Sulfur Analyzer Model 475 (Lowe and Guthrie 1984).

Soil nutrient variables were expressed as concentrations on a dry mass basis and on a mass per unit area basis. The mass per unit area conversion used bulk density (D_b) corrected for coarse fragments content for both forest floor and mineral soil, and represented kilograms of nutrients per hectare (kg/ha) in the forest floor and the surface 0-30 cm on average of mineral soil with some exceptions (shallow soils). The formula that was used for both forest floor and mineral soils (see Nuszdorfer 1981) was:

$$[3.2.4] \qquad X(\text{kg ha}^{-1}) = (1 - CF)\left(\frac{X_{\text{con<2mm}}}{10^2 \text{ or } 10^6}\right)\left(\frac{\text{kg}}{10^3\text{g}}\right)D_b\left(\frac{\text{g}}{\text{cm}^3}\right)V_s(\text{cm}^3\ \text{ha}^{-1}),$$

where X (kg ha^{-1}) = a nutrient mass in kg per hectare;

CF = fraction of coarse fragments on a volume basis;

$X_{\text{con<2mm}}$ = nutrient concentration in the fine soil fraction (% or ppm);

kg/10^3g = a conversion factor;

V_s = volume of soil in one hectare = (soil depth in cm)(10^8cm^2 ha^{-1}).

The soil nutrient values obtained from chemical analysis were used as potential variables for characterizing soil nutrient gradient and for discriminating between soil nutrient regimes following the approach described by Kabzems and Klinka (1987), and Klinka *et al.* (1989b).

3.2.4. Soil Moisture Analysis

The mean monthly growing-season precipitation (mm), temperature (^{0}C), and solar radiation flux density (MJ/m^2/day) for each subzone were obtained from the nearest climatic station (Anonymous 1982) for calculation of the actual evapotranspiration and the annual water balance using the Energy/Soil-Limited model of Spittlehouse and Black (1981). The model was expressed as:

$$[3.2.5] \qquad \theta_i = \theta_{i-1} + (P_i - E_i - D_i - R_i)\Delta_t/\zeta,$$

where θ = the average volumetric water content of the rooting zone [(mm)^3 water/(mm)^3 soil);

P = precipitation (mm/day);

E = evapotranspiration (mm/day);

D = drainage from the rooting zone (mm/day);

R = run off (mm/day) which is usually neglected for forested area on a flatter landscape;

Δ_t = time intervals of one day;

ζ = soil rooting depth (mm);

i = 1, 2, ..., n (1 = the first day of the growing season, n = the last day of the growing season).

The model, driven by solar radiation, temperature, and precipitation, uses soil rooting depth (mm), soil texture, and fraction of soil coarse fragments (*CF*) to estimate available water storage capacity[1]. The soil rooting depth in mm was adjusted by using the equation as follows[1]:

[3.2.6] the "adjusted" ζ = measured $\zeta(1 - CF)$

Soil texture was used to estimate 5 parameters required by the model[1]: the water content at field capacity (θ_{max}), water content at wilting point (θ_{min}), water potential at air entry (ψ_e), an empirical coefficient (m), and aeration porosity (θ_s). Potential or energy limited evapotranspiration (E_{max}) and actual or soil limited evapotranspiration (E_t) were calculated as monthly totals during the growing-season (May to September). Total growing-season water deficit (Δ_w) was calculated as the sum of E_{max} minus E_t for each month during the growing-season, *i.e.*,

[3.2.7] $$\Delta_w = \sum_{j=1}^{m} (E_{max} - E_t) \ ,$$

where m is the number of months in the growing season.

The E_{max}, E_t, and Δ_w and the depth of the soil water table and gleyed horizon were used to characterize actual soil moisture regimes for the study plots as suggested by Klinka *et al.* (1989b).

[1]Instructions to the computer program to calculate simple water balances by D. L. Spittlehouse, 1987.

In addition to the Spittlehouse and Black method, the Thornthwaite (1948) procedure was also used for calculating potential evapotranspiration (PET) and heat index (HI). The Rose and Grant method (1976) was used for calculating the index of continentality (see Table 1.1).

3.2.5. Indicator Plant Species Analysis

A computer-assisted spectral analysis (Emanuel 1987, Mueller-Dombois and Ellenberg 1974; Klinka *et al.* 1989b) was carried out to characterize vegetation and site units and to determine the usefulness of indicator plants for inferring ecological site quality. The relative frequencies of indicator species for a given indicator species group (ISG) (e.g., very poor to poor, medium, and rich to very rich) and a given site attribute (climate, soil moisture, or soil nitrogen) for each plot, or group of plots (unit) was calculated according to Klinka *et al.* (1989b) with a correction:

[3.2.8] $$F_{jk} = \frac{\sum_{i=1}^{m} C_{ijk}}{\sum_{i=1}^{n} C_{ik}} 100 ,$$

where F_{jk} = relative frequencies for a given ISG j and a given site attribute k; $\sum C_{ijk}$ = sum of midpoint percent cover value of species i (i = 1, 2, ..., m) for a given ISG j and a site attribute k; $\sum C_{ik}$ = sum of midpoint percent cover value of species i (i = 1, 2, ..., n) for a given site attribute k. Frequency values were used to produce spectral histograms for each study plot, to aid the interpretation of soil moisture and nutrient analysis, and to serve for further regression analysis.

3.2.6. Vegetation and Site Classification

Study plots were classified according to the methods of biogeoclimatic ecosystem classification as described by Pojar *et al.* (1987). Vegetation classification was based on a tabular method (Mueller-Dombois and Ellenberg 1974), diagnostic criteria proposed by Pojar *et al.* (1987), and a computerized tabling program (VTAB) (Emanuel 1987). The diagnostic species identified for the distinguished vegetation units were then used in a principal components analysis (PCA) (Dillon and Goldstein 1984), for the purpose of (1) aiding in the formation of floristically uniform groups of study plots, (2) obtaining ordination scores for diagnostic species, and (3) examining floristic affinities among the distinguished vegetation units. The PCA was performed using the SYSTAT statistical package (Wilkinson 1990). Analysis of concentration (AOC) (Feoli and Orlóci 1979; Lausi and Nimis 1985) was used to examine the relationships between the vegetation units and indicator plant species groups (ISGs).

Site classification was based on climate (biogeoclimatic subzones), soil moisture regime, and soil nutrient regime determined for each study plot. A site association was only recognized when it could be characterized by an exclusive combination of climate, soil moisture, and soil nutrients (*i.e.*, when it could be distinguished by an exclusive range of climate, soil moisture, and soil nutrient regimes). To delineate site associations, it was further necessary to determine whether the distinguished basic vegetation units reflected differences in ecological site quality. This examination was carried out in a process of successive approximation (*cf.* Poore 1962).

3.2.7. Statistical Analysis between Vegetation, Soil , and Foliage Variables

All data were summarized and analyzed using the SYSTAT, SYGRAPH (Wilkinson 1990), and SAS (SAS Institute Inc. 1985) statistical packages with the aid of the Quattro Pro (Borland International, Inc. 1989) spreadsheet package on a IBM compatible personal computer. The MIDAS statistical package (Fox and Guire 1976) on the UBC mainframe computing system was also used for the analyses.

Prior to statistical analysis, soil chemical variables and foliar nutrient variables used in the analyses were examined for normality using a probability plot (Chambers *et al.* 1983). Those variables that exhibited non-normality were logarithmically transformed and tested again. Variables that appeared to have non-homogeneity of variance between groups in discriminant analysis were handled using Smith's (1947) quadratic function (Dillon and Goldstern 1984).

Principal components analysis (PCA) (Dillon and Goldstern 1984) was used for vegetation ordination based on a reduced data base (diagnostic species) (Klinka *et al.* 1990a). Cluster analysis (CA) (Sneath and Sokal 1973) was used for pre-identifying underlying soil nutrient groups. Stepwise discriminant analysis (SDA) was used for variable selection. Canonical discriminant analysis (CDA) (Dillon and Goldstern 1984) was applied for finalizing soil moisture and soil nutrient groups. Relationships between vegetation, soil factors, and foliar nutrients were explored using canonical correlation analysis (CCA) (Gittins 1985; Dillon and Goldstern 1984) combined with PCA, which summarized the original variables into a small number of components. Regression analysis (Chatterjee and Price 1977) was used to examine the relationships between nitrophytic indicator species, soil nitrogen, and foliar nitrogen.

3.3. Results and Discussion

3.3.1. Vegetation Classification and Indicator Plants

All 72 sample plots were classified into a hierarchy of vegetation units (plant alliances, associations, and subassociations) consisting of ten basic vegetation units (six associations and four subassociations) (Table 3.1). These ten units, each representing a mid-successional stage of lodgepole pine-dominated forest communities, were delineated according to the floristic differences (diagnostic combinations of species) between the groups of plots, and named by the generic names of the dominant plant species (Tables 3.1 and 3.2). For the sake of brevity, '*Pinus*' was omitted from the name and only the generic names of diagnostic and/or dominant understory species were used; specific names were used only to prevent ambiguities. The classification produced implies that there are ten different ecological strata represented among the study plots using floristic criteria.

The 71 diagnostic species summarized in Table 3.2 were submitted to principal components analysis (PCA) to explore floristic affinities among the distinguished vegetation units and their relation to environmental gradients. The first two components extracted accounted for 38% of the total variance in vegetation data, with the first component accounting for 23% of the total variance and the first ten components accounting for 75% of the total variance (Table 3.3). A scree plot (Dillon and Goldstern 1984) (Figure 3.1) also showed that the first ten components were good enough to explain the variation in the data.

The PCA results suggested the presence of structure in the vegetation data and, in conjunction with environmental characteristics and indicator values (Tables 3.4, 3.5, and 3.6), the potential for evaluating environmental affinities between vegetation units. Ordination of plots on the first two PCA axes,

Table 3.1. Synopsis of the vegetation units distinguished in the study plots.

Plant alliance
    Plant association
        Plant subassociation

Stereocaulon
    Arctostaphylos
        Arctostaphylos-typic (A)[1]
        Arctostaphylos-Shepherdia (B)
    Arnica (C)

Empetrum
    Empetrum (D)

Vaccinium
    Vaccinium myrtiloides (E)
    Vaccinium membranaceum (F)

Ribes
    Ribes (G)
    Gymnocarpium
        Gymnocarpium-typic (H)
        Gymnocarpium-Equisetum (I)

Sphagnum
    Sphagnum (J)

[1]An alphabetical symbol for a basic vegetation unit.

Table 3.2. Diagnostic combinations for the plant alliances (all.), associations (a.), and subassociations (sa.) distinguished in the study plots.

Vegetation unit and species	[1]Diagnostic value	A	B	C	D	E	F	G	H	I	J
Number of plots		5	7	9	5	9	8	8	6	8	7
		[2]Presence class and [3]mean species significance									
Stereocaulon all.											
Arctostaphylos uva-ursi	(d,c)	5 5	V 4	III 1	3 2						I +
Cladonia cornuta	(d)	4 2	V 1	IV 1	2 +	II +		I +			II +
Cladonia gracilis	(d,c)	3 1	V 2	V 1	2 +	IV 2	I +	II +	I +		I +
Stereocaulon tomentosum	(d,c)	5 3	V 1	V 2	1 +	II +		I +			
Arctostaphylos a.											
Arctostaphylos uva-ursi	(d,c)	5 5	V 4	III 1	3 2						I +
Juniperus sibirica	(d)	2 +	III 1		1 +	I +	I +				I +
Solidago spathulata	(d)	4 1	IV 1		2 1						
Arctostaphylos-typic sa.											
Cetraria islandica	(d)	3 1									
Arctostaphylos-Shepherdia sa.											
Anemone multifida	(d)		III 1								
Aster ciliolatus	(d)	1 +	III +		2 1			II 1	III 1	II 1	
Carex concinnoides	(d)	1 +	III 1		1 +			I +			
Ceratodon purpureus	(d)		III +	I +	1 +	I +					
Cladonia gracilis	(d,c)	3 1	V 2	V 1	2 +	IV 2	I +	II +	I +		I +
Equisetum scirpoides	(d)		III +		4 2			II +	II +		II +
Fragaria virginiana	(d)		IV 2	III 2	4 2			III 2			II 3
Shepherdia canadensis	(d,cd)	2 3	V 5	IV 2	4 1	I +		II 1	I +		I +
Arnica a.											
Arnica cordifolia	(d,c)		II +	V 2	3 1			IV 3	II 1		II +
Calamagrostis canadensis	(d,c)		III 1	V 1	5 3	I +	I 1	V 2	V 3	V 3	V 4
Festuca occidentalis	(d)			IV 1				II +		I +	II 1
Orthilia secunda	(d)		I +	IV +	4 1	II +	III 1	IV 1	IV 1	II 1	
Spiraea betulifolia	(d)	1 2	III 2	IV 3	1 1	V 4	V 4	III 1	IV 3	I +	I 1
Vaccinium membranaceum	(d)			III 3		II 3	V 6	III 2	III 2	II 1	
Empetrum all. & a.											
Empetrum nigrum	(d,c)		III 1	II +	5 3						I +
Equisetum arvense	(d)		I +	I +	3 +			I +			I +
Salix drummondiana	(d)				3 3						I 3
Sanguisorba canadensis	(d)				4 4			I +			II 1
Vaccinium all.											
Abies lasiocarpa	(d,c)			II +		IV 4	V 3	IV 3	V 4	II 2	I +
Dicranum polysetum	(d,c)			I +		V 2	V 4	IV 2	IV 1	II +	
Pleurozium schreberi	(dd)		III 1	V 4	4 2	V 8	V 8	V 6	V 5	IV 4	III 2
Spiraea betulifolia	(d,c)	1 2	III 2	IV 3	1 1	V 4	V 4	III 1	IV 3	I +	I 1
Vaccinium myrtilloides	(d,cd)					V 6	V 5	I +	III 1	I +	I 1
Vaccinium myrtilloides a.											
Cladonia gracilis	(d)	3 1	V 2	V 1	2 +	IV 2	I +	II +	I +		I +
Maianthemum canadense	(d,c)					V 2	II 2	I 1	IV 3	II +	
Rubus parviflorus	(d)			I +		IV 1		II 1	V 4	III 4	
Tsuga heterophylla	(d)					III 1		I +	II 1	I 1	
Vaccinium membranaceum a.											
Amelanchier alnifolia	(d,c)					II 1	V 2		III 1	II +	I +
Clintonia uniflora	(d)			II +			III 1	I 1	III 3	II 1	I +
Geocaulon lividum	(d)		I +			II 1	IV 3				
Oryzopsis asperifolius	(d)					II 1	IV 1				
Rubus pedatus	(d,c)						V 4	II 3	III 3	IV 4	III 1
Sorbus scopulina	(d,c)			II +		II 1	V 2	I +	II +	II +	
Vaccinium caespitosum	(d,c)	4 2	III 1	V 4	2 1	III 2	V 3	IV 2	II 1	I +	III 1
Vaccinium membranaceum	(d,cd)			III 3		II 3	V 6	III 2	III 2	II 1	
Viola orbiculata	(d,c)						V 2		I 1	II 1	
Ribes all.											
Lycopodium annotinum	(d)		I +	II +	1 +		I +	III 2	V 2	II +	I +
Ribes lacustre	(d,c)						I +	V 2	V 2	V 3	
Ribes triste	(d)					I +		III 1	IV 2	IV 2	I +
Ribes a.											
Arnica cordifolia	(d)		II +	V 2	3 1			IV 3	II 1		II +
Aster foliaceus	(d)			II +	1 2			III 1	I +	I +	II +
Dicranum fuscescens	(d)		III +	II +				IV 1	I +	II 1	
Osmorhiza chilensis	(d)							IV +	I +	I 1	
Vaccinium caespitosum	(d)	4 2	III 1	V 4	2 1	III 2	V 3	IV 2	II 1	I +	III 1
Gymnocarpium a.											
Gymnocarpium dryopteris	(d,cd)							I +	V 5	V 6	I +
Rubus parviflorus	(d)			I +		IV 1		II 1	V 4	III 4	
Smilacina racemosa	(d)			I +			II +	II +	IV 1	IV 1	
Tiarella trifoliata	(d)							I +	IV 1	IV 3	
Viburnum edule	(d,c)			III 1			II +	II 1	V 4	IV 3	I +
Gymnocarpium-typic sa.											
Aralia nudicaulis	(d,c)					I +		I +	V 3	II 3	
Goodyera oblongifolia	(d)			II +		II +			III +		
Lycopodium annotinum	(d,c)		I +	II +	1 +		I +	III 2	V 2	II +	I +
Maianthemum canadense	(d)					V 2	II 2	I 1	IV 3	II +	
Petasites palmatus	(d,c)		I +	III 1	3 1			V 2	V 2	III 2	III 1
Polytrichum commune	(d)		I +		1 1	III 3	II +	II 2	IV 3	II 3	III 3
Populus tremuloides	(d,c)		I +	I +	2 2	II 1		II 1	V 4	II 3	
Rhytidiadelphus triquetrus	(d)		I +			I +		I 1	IV 2	II +	
Rubus parviflorus	(d,c)			I +		IV 1		II 1	V 4	III 4	
Gymnocarpium-Equisetum sa.											
Alnus sinuata	(d)			III 4				III 2	I 1	IV 4	II 2
Aster subspicatus	(d)							I +		III 3	
Athyrium filix-femina	(d)									IV 2	I +
Betula papyrifera	(d)					I +		II 1	I +	III 2	I +
Dryopteris expansa	(d)									III 2	
Equisetum palustre	(dd,cd)				1 1		I 1	IV 3	IV 1	V 5	III 3
Galium triflorum	(d)							I +	II 1	IV 2	
Heracleum lanatum	(d)							II +		III 2	I +
Sphagnum all. & a.											
Betula glandulosa	(d)		I 3	I +	2 1		I +	I +			IV 5
Carex disperma	(d)				1 1					I +	III 2
Ledum groenlandicum	(d,cd)		I +		2 4		I +	II +		II +	V 6
Potentilla palustris	(d)										III 1
Salix sitchensis	(d)					I +		I +	I +	II 1	III 4
Sphagnum nemoreum	(d,cd)			I +		I +		II +		II 1	V 7
Spiraea douglasii	(d)				1 3		I +		I 2	II 3	III 3
Trientalis arctica	(d)									II +	III 1

[1]Species diagnostic values: d - differential, dd - dominant differential, cd - constant dominant, c - constant, ic - important companion (Pojar et al. 1987).
[2]Presence classes as percent of frequency: I = 1-20, II = 21-40, III = 41-60, IV = 61-80, V = 81-100. If 5 plots or less, presence class is Arabic value (1-5).
[3]Species significance class midpoint percent cover and range: + = 0.2 (0.1 - 0.3), 1 = 0.7 (0.4 - 1.0), 2 = 1.6 (1.1 - 2.1), 3 = 3.6 (2.2 - 5.0), 4 = 7.5 (5.1 - 10.0), 5 = 15.0 (10.1 - 20.0), 6 = 26.5 (20.1 - 33.0), 7 = 41.5 (33.1 - 50.0), 8 = 60.0 (50.1 - 70.0), 9 = 85.0 (70.1 - 100).

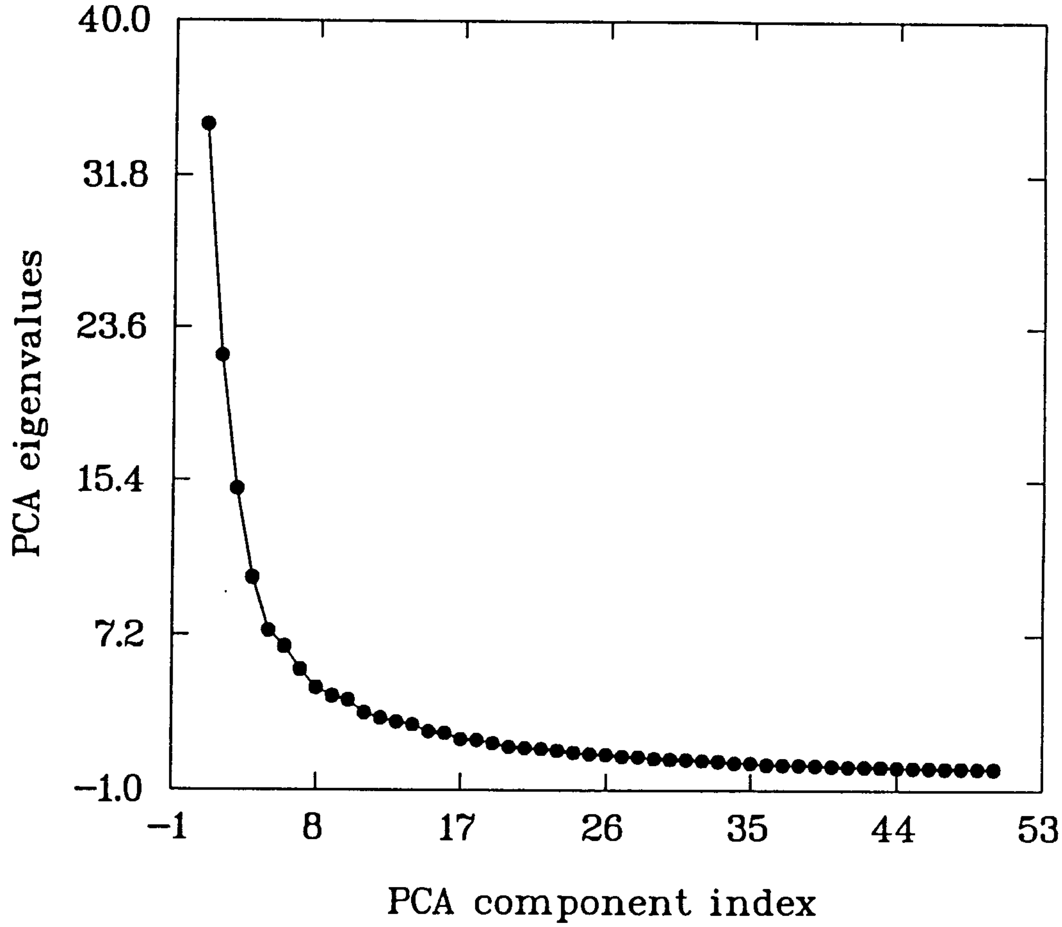

Figure 3.1. Scree plot of PCA eigenvalues on diagnostic species.

Table 3.3. The eigenvalues (λ) and cumulative accounted-for variance of PCA applied to a covariance matrix with the diagnostic species significance values.

Component	λ	Cumulative % of total variance
1	34.49	22.9
2	22.08	37.5
3	14.96	47.4
4	10.24	54.2
5	7.46	59.2
6	6.61	63.6
7	5.41	67.2
8	4.46	70.1
9	4.02	72.8
10	3.81	75.3

with 70% confidence ellipses superimposed for the ten vegetation units, portrays the main similarity relationships among the units (Figure 3.2).

The study plots of all SBPS vegetation units (A, B, and D and distinctly azonal C and J) were scattered in the left region of the ordination, while the majority of the SBS units occurred toward the right (Figure 3.2). Thus, the first PCA axis coincided with a climatic gradient from relatively dry and cold (the SBPS subzone) to relatively wet and warm (the SBSwk subzone) montane boreal climate. With the notable exception of *Pleurozium schreberi*, all positively correlated diagnostic species with the first PCA component were either absent or occurred with a low frequency in the SBPSxc subzone; the negatively correlated species (*Arctostaphylos uva-ursi*—group) occurred in the SBPSxc subzone and, in the SBSmc and SBSwk subzones, on azonal (driest or wettest) sites (Tables 3.2, 3.4, and 3.5, Figure 3.2).

The second PCA axis represented a combined moisture and nutrient gradient: water-deficient and nitrogen-poor study plots [vegetation units A, B, C, D (in part), E, and F] occurred in the lower region of the ordination, whereas the remaining plots [vegetation units D (in part), G, H, I, J, and K] were scattered in the upper region (Figure 3.2). The negatively correlated diagnostic species (*Arctostaphylos uva-ursi*—group) were typically indicators of very dry and nitrogen-poor sites, and the positively correlated diagnostic species (*Ribes lacustre*—group) were predominantly indicators of fresh to very moist and nitrogen-rich sites (Klinka *et al.* 1989b) (Tables 3.2, 3.3, and 3.6, Figures 3.2 and 3.3.). The PCA pointed out a few inconsistencies in indicator values for some plants; for example, *Vaccinium caespitosum*, reportedly an indicator species of fresh to very moist on a poor site (Klinka et al. 1989b), exhibited a wide amplitude along a soil moisture gradient in this study (Tables 3.2 and 3.5).

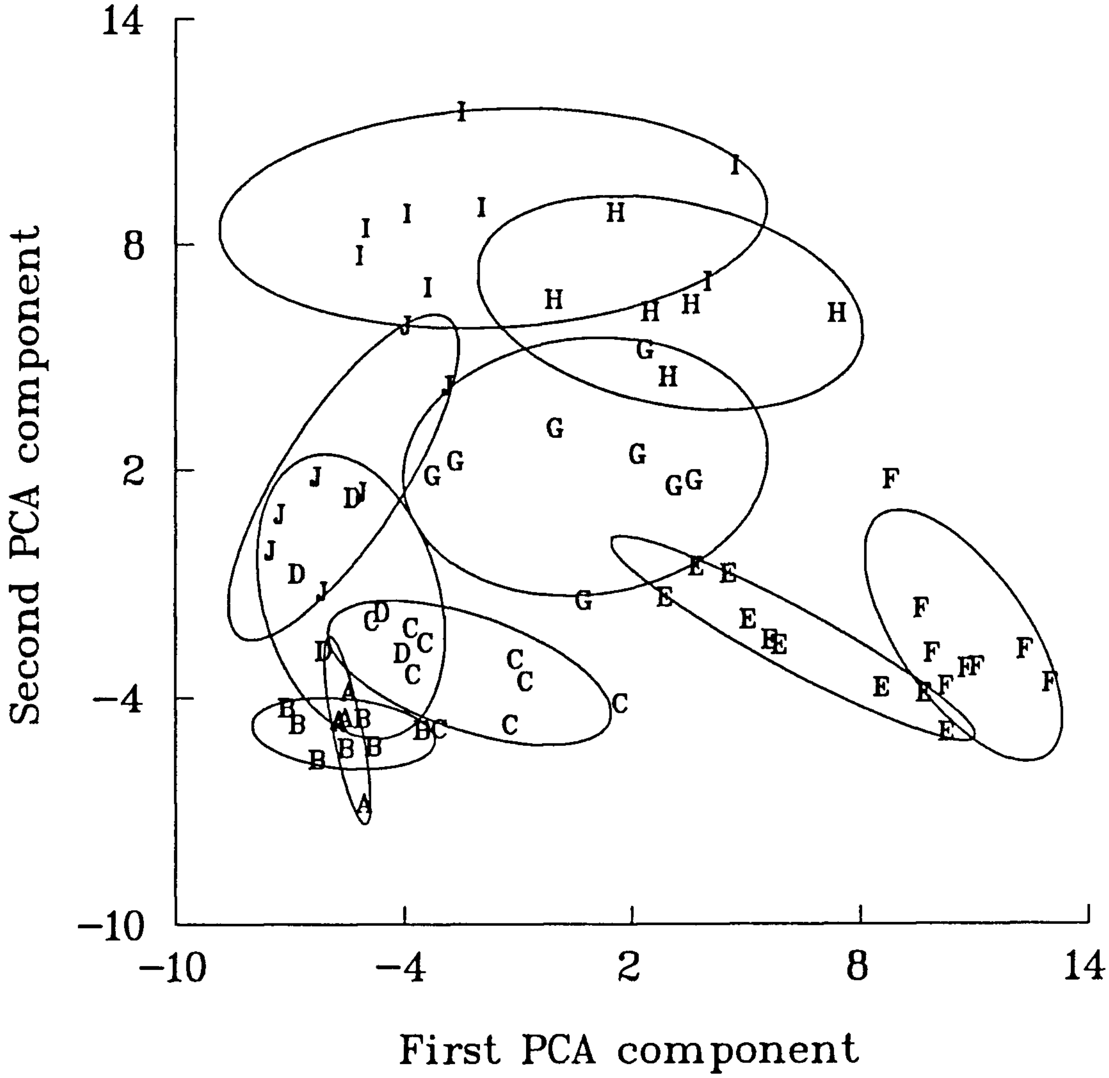

Figure 3.2. Ordination of sample plots along the first two PCA axes on diagnostic species showing 70% confidence ellipsoids for each basic vegetation unit. Each sample plot is represented by an alphabetical symbol that designates a vegetation unit (Table 3.1).

Table 3.4 Means of selected climatic, soil, and stand characteristics of the ten distinguished vegetation units. Symbols for vegetation units are given in Table 3.1.

Vegetation unit	A	B	C	D	E	F	G	H	I	J
Number of plots	5	7	9	5	9	8	8	6	8	7
Biogeoclimatic subzone	SBPSxc	SBPSxc	SBSmc	SBPSxc	SBSwk	SBSwk	SBSmc SBSwk	SBSmc SBSwk	SBSmc SBSwk	SBPSxc SBSmc SBSwk
E_t (mm/yr)[1]	101	119	194	205	217	231	245	235	234	246
E_t/E_{max}[2]	0.42	0.50	0.79	0.86	0.93	0.99	1.0	1.0	1.0	1.0
Growing-season water deficit (mm/yr)	140	120	52	33	16	1.6	0	0	0	0
Depth of soil water table(w) or gleyed horizon (g) (cm)[3]	na	40^{g1}	38^{g2}	$43^{g2,w3}$	na	na	$48^{g2,w1}$	$53^{g2,w1}$	$44^{g4,w3}$	25^{w7}
Forest floor C/N	68	53	50	37	41	36	41	39	29	32
Mineral soil C/N	105	70	56	38	50	25	43	31	26	41
Forest floor & mineral soil mN (kg ha^{-1})	3.7	9.9	12.2	45.6	15.6	37.8	33.8	36.4	133	61.8
Forest floor & mineral soil exchangeable Ca, Mg, and K (kg ha^{-1})	1330	4177	1510	6030	535	637	4149	2175	6608	3580
Measured site index (m @ 50 years B.H.age)	10.6	12.3	17.4	13.7	17.3	18.9	20.1	21.87	22.5	13.5

[1]actual growing season evapotranspiration;
[2]actual growing seasson evapotranspiration/potential evapotranspiration ratio;
[3]number of plots used to calculate the mean value is given by a numerical superscript after g or w.

Table 3.5. Diagnostic species correlated positively or negatively with the first PCA component and their edaphic indicator values (after Klinka *et al.* 1989b).

Indicator species	Pearson correlation coefficient(r)	Indicator value soil moisture	Indicator value soil nitrogen
Pleurozium schreberi	0.88		P
Dicranum polysetum	0.87	MD-F	P
Vaccinium myrtiloides	0.84	MD-F	P
Vaccinium membranaceum	0.77	MD-F	P
Amelancher alnifolia	0.73	MD-F	M
Abies lasiocarpa	0.72		
Sorbus scopulina	0.72	MD-F	P
Geocaulon lividum	0.62		P
Viola orbiculata	0.60	MD-F	M
Spiraea betulifolia	0.57	VD-MD	M
Oryzopsis asperifolia	0.54		P
Maianthemum canadense	0.52		P
Rubus pedatus	0.49	F-VM	P
Clintonia uniflora	0.32	MD-F	P
Vaccinium caespitosum	0.31	F-VM	P
Arctostaphylos uva-ursi	-0.53	VD-MD	P
Fragaria virginiana	-0.39		M
Calamagrostis canadensis	-0.38	M-W	M
Solidago apathulata	-0.38	VD-MD	P
Cladonia cornuta	-0.38	ED-VD	P
Shepherdia canadensis	-0.35	VD-MD	M
Sphagnum nemoreum	-0.31	W-VW	P
Betula glandulosa	-0.31		P
Stereocaulon tomentosum	-0.30	ED-VD	P
Empetrum nigrum	-0.30		P
Equisetum scirpoides	-0.29		R
Ledum groenlandicum	-0.28	W-VW	P
Carex concinnoides	-0.28	MD-F	M
Carex disperma	-0.26	W-VW	P
Sanguisorba canadensis	-0.25	VM-W	
Salix drummondiana	-0.25	VM-W	R

Table 3.6. Diagnostic species correlated positively or negatively with the second PCA component and their edaphic indicator values (after Klinka *et al.* 1989b).

Indicator species	Pearson correlation coefficient(r)	Indicator value soil moisture	Indicator value soil nitrogen
Ribes lacustre	*0.75*		*R*
Equisetum palustre	*0.73*	*VM-W*	*P*
Gymnocarpium dryopteris	*0.71*	*F-VM*	*R*
Tiarella trifoliata	*0.67*	*F-VM*	*R*
Ribes triste	*0.65*	*VM-W*	*P*
Galium triflorum	*0.63*	*F-VM*	*R*
Calamagrostis canadensis	*0.56*	*VM-W*	*M*
Viburnum edule	*0.56*	*F-VM*	*R*
Athylium filix-femina	*0.53*	*VM-W*	*R*
Aralia nudicaulis	*0.53*	*F-M*	*R*
Petasites palmatus	*0.52*	*VM-W*	*R*
Smilacina racemosa	*0.52*		*R*
Rubus parviflora	*0.51*		*R*
Betula papyrifera	*0.50*		
Lycopodium annotinum	*0.43*	*MD-F*	*M*
Aster subspicatus	*0.42*	*VM-W*	*R*
Alnus sinuata	*0.40*	*F-VM*	*R*
Heracleum lanatum	*0.40*	*F-VM*	*R*
Rubus pedatus	*0.39*	*F-VM*	*P*
Polytrichum commune	*0.38*	*F-VM*	*P*
Spiraea douglasii	*0.37*	*VM-W*	*M*
Populus tremloides	*0.37*	*F-VM*	*R*
Dryopteris expansa	*0.34*	*F-VM*	*R*
Clintonia uniflora	*0.33*	*MD-F*	*M*
Rhytidiadelphus triquetrus	*0.33*	*F-VM*	*M*
Trientalis arctica	*0.29*	*W-VW*	*P*
Arctostaphylos uva-ursi	*-0.53*	*VD-MD*	*P*
Stereocaulon tomentosum	*-0.52*	*ED-VD*	*P*
Shepherdia canadensis	*-0.46*	*VD-MD*	*M*
Vaccinium caespitosum	*-0.46*	*F-VM*	*P*
Cladonia cornuta	*-0.43*	*ED-VD*	*P*
Cladonia gracilis	*-0.39*	*ED-VD*	*P*
Solidago spathulata	*-0.38*	*VD-MD*	*P*
Spiraea betulifolia	*-0.37*	*VD-MD*	*M*
Juniperus sibirica	*-0.28*	*VD-MD*	*M*

The results of the tabular comparison and PCA implied that diagnostic species and, in consequence, vegetation units have relatively narrow ecological amplitudes. To further explore the affinities of the vegetation units to their diagnostic combinations of species, an analysis of concentration (AOC) was carried out. The purpose of this analysis was to quantify relationships between the vegetation units and the diagnostic species grouped according to their climatic and edaphic indicator values (Klinka *et al.* 1989b) (Table 3.7, Figure 3.3).

The first and second canonical correlations (r) between the vegetation units and the climatic indicators were 0.35 and 0.31, respectively. Seventy-three percent of the total variance was explained by the first two canonical variates. The majority of vegetation units were clearly associated with the indicators of boreal and cool temperate climates. The *Arctostaphylos*-typic unit (A) showed a strong affinity to alpine tundra & boreal and cool temperate & semiarid climates, the *Gymnocarpium-Equisetum* unit (I) showed a weak affinity to cool temperate & mesothermal and subalpine boreal & cool mesothermal climates, and the *Sphagnum* unit (J) showed a weak affinity to a cool mesothermal climate (Tables 3.3 and 3.7, Figure 3.3).

The vegetation units showed a stronger relationship to soil moisture ISGs with first and second canonical correlations of 0.75 and 0.47, respectively. Eighty-seven percent of the total variance was explained by the first and second variates. The *Arctostaphylos*-typic unit (A) was strongly related to the indicators of excessively dry to very dry sites (suggestive of uniformity in available soil moisture in the study plots), whereas the *Ribes* unit (G) was intermediate between the indicators of fresh to very moist and very moist to wet sites (suggestive of heterogeneity in available soil moisture in the study plots).

Table 3.7. The eigenvalue (λ), variance, and canonical correlation for the canonical variates obtained from analysis of concentration on the diagnostic species stratified according to their indicator values of climate, soil moisture and soil nitrogen into indicator species groups (ISGs).

Canonical variates	Eigenvalue (λ)	Percent variance	Cumulative variance	Canonical correlation(r)
		Climatic ISGs		
1	0.123	41.0	41.0	0.349
2	0.095	32.0	73.0	0.308
3	0.063	21.2	94.2	0.251
Σ	0.297			
		Soil moisture ISGs		
1	0.563	62.4	62.4	0.750
2	0.223	24.7	87.1	0.472
3	0.098	10.9	98.0	0.313
Σ	0.902			
		Soil nitrogen ISGs		
1	0.217	68.7	68.7	0.466
2	0.099	31.3	100.0	0.314
Σ	0.315			

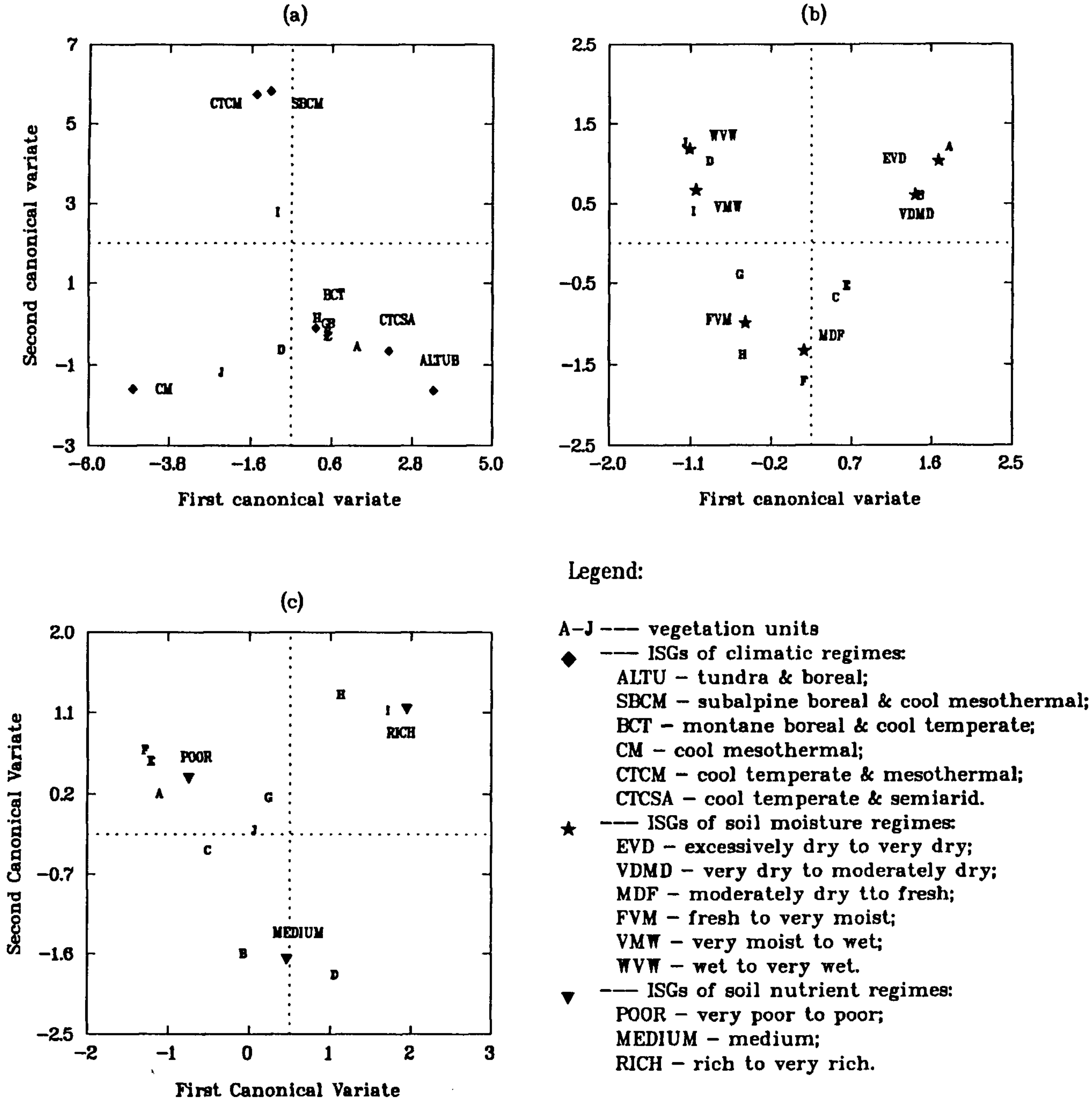

Figure 3.3. Ordinations of vegetation units and climatic (a), soil moisture (b), and soil nitrogen indicator species groups (ISGs) as a function of the first two canonical variates determined by analysis of concentration. Symbols for vegetation units (A - J) are defined in Table 3.1.; symbols for ISGs are explained in the legend.

In relation to soil nitrogen ISGs, the first and second canonical correlations were 0.47 and 0.31, respectively. Almost 100% of the total variance was explained by the first and second variates. The *Gymnocarpium-Equisetum* unit (I) was very strongly related to the indicators of nitrogen-rich sites (suggestive of uniformity in available soil nitrogen in the study plots), whereas the *Ribes* unit, plotted close to the center of ordination, was intermediate between the indicators of nitrogen-poor and -rich sites (suggestive of heterogeneity in available soil nitrogen in the study plots) (Tables 3.3 and 3.7, Figure 3.3).

3.3.2. Soil Moisture Analysis

In the BEC system, the soil moisture regime (SMR) is one of the basic components of ecological site quality and one of the differentiating characteristics used in site classification (Pojar *et al.* 1987). Unambiguous characterization of soil moisture conditions for plant growth requires quantitative criteria which can then be used to divide a soil moisture gradient into ecologically meaningful regimes (classes). This study adopted the criteria proposed by Klinka *et al.* (1989b) for coastal British Columbia (Table 3.9), and used the Energy/Soil-Limited model {equations [3.2.5], [3.2.6], and [3.2.7]} to calculate the annual water balances for each study plot. Each study plot was then assigned an appropriate actual SMR either according to the depth of growing season water table or depth of the gleyed soil horizon, or according to the value of the actual/potential evapotranspiration ratio ($Et/E\max$). The absence of either of the above criteria resulted in the study plot being assigned to the fresh SMR (Table 3.10).

Klinka and Carter (1990) pointed out several shortcomings using the soil water balance model of Spittlehouse and Black (1981) in their study for coastal Douglas fir. One of the limitations was that the monthly time-step of 30 year normals used in the calculations likely resulted in an underestimation of soil water deficit. In the present study, 30 year climate normals were also used since daily or annual data were not accessible at the time when the model was applied. This might also have resulted in some underestimation of soil water deficit for lodgepole pine stands. In order to compare the differences between using annual data in a monthly time-step, annual data in a daily time-step, and 30 year climate normals in a monthly time-step, a test, based on 3 plots representing slightly dry, fresh, and moist SMRs, was carried out later when the annual and daily data were available. As was suggested by A.T. Black (Department of Soil Science, University of British Columbia, pers. comm.), the daily measurements in 1977 were combined into 5 day time-steps since the amount of water could be held in the soil for at least 2-3 days after saturation by a rainfall. The results showed that there was no difference for moist SMR, but a slight underestimation of the water deficit using normals was found for fresh and slightly dry SMRs (Table 3.8). As SMRs are quite broadly defined classes, this underestimation for fresh, slightly dry, and other 'drier' SMRs would not strongly affect the original allocation of the study sites, and 30 year normals could still be used for soil water balance modelling if annual or daily data are not available. Another shortcoming in the model was that no adjustments were made for aspect and slope. In this study, this was recovered by comparing similarities and consistency in topographic and soil properties (Klinka *et al.* 1984) and soil moisture spectra (Klinka *et al.* 1989b). As a result, some plots were reassigned, and three special SMRs were recognized to characterize soil moisture conditions on sites with a strongly fluctuating water table (Table 3.10, Figure 3.4).

These special SMRs parallel those defined for coastal British Columbia by Bernardy (1989) (*cf.* Banner *et al.* 1990). They occurred in situations where the

Table 3.8. Comparisons of soil water deficit calculated on the basis of 30 year normals in a monthly time-step, annual data in a monthly time-step, or annual data in a daily time-step using the Energy/Soil-Limitted water balance model.

		Soil water deficit (mm/year)		
Plot number	SMR	5 day-step annual	monthly-step annual	monthly-step normals
70	SD	26.5	0	7.4
68	F	14.1	0	0
60	M	0	0	0

Table 3.9. The criteria used for the characterization and classification of actual soil moisture regime of the study plots (sites with fluctuating water table are not included) (after Klinka *et al.* 1989b).

1a. Water deficit occurs

  2a. E_t/E_{max}[1] ≤ 0.40 -- **excessively dry** (ED)

  2b. $E_t/E_{max} > 0.40$ but ≤ 0.60 -- **very dry** (VD)

  2c. $E_t/E_{max} > 0.60$ but < 0.90 ------------------------------- **moderately dry** (MD)

  2d. $E_t/E_{max} \geq 0.90$ --- **slightly dry** (SD)

1b. Water deficit does not occur

  3a. Utilization of soil-stored water occurs and
  growing-season soil water table or
  gleyed horizons absent -- **fresh** (F)

  3b. No utilization occurs or growing-season water
  table or gleyed horizons present

    4a. Growing-season soil water table or
    gleyed horizon $\geq$ 60 cm deep ------------------------------------ **moist** (M)

    4b. Growing-season soil water table or
    gleyed horizon > 30 cm but < 60 cm ----------------- **very moist** (VM)

    4c. Growing-season soil water table or
    gleyed horizon $\leq$ 30 cm deep -- **wet** (W)

[1] E_t/E_{max} - actual/potential evapotranspiration ratio during the growing season.

Table 3.10. Mean values of selected components of the annual water balance for the study plots stratified according to soil moisture regimes (SMRs).

Actual SMR	Number of plots	[1]E_t (mm/yr)	[2]Δ_w (mm/yr)	[3]E_t/E_{max}	[4]W_d (cm)	[5]G_d (cm)
Excessively dry	2	92	152	0.38	na	na
Very dry	8	110	128	0.46	na	na
Moderately dry	5	191	46	0.80	na	na
Slightly dry	16	212	25	0.90	na	na
Fresh	7	242	0	1.00	na	na
Moist[6]	11	235	0	1.00	53[(3)]	60[(2)]
Very moist[6]	9	239	0	1.00	35[(5)]	53[(3)]
Wet[6]	6	246	0	1.00	24[(5)]	na
Moderately dry to moist[6]	2	136	104	0.57	na	40[(1)]
Slightly dry to very moist[6]	5	202	33	0.86	40[(2)]	48[(3)]
Fresh to wet[6]	1	244	0	1.00	30[(1)]	na

[1] E_t - soil actual evapotranspiration.
[2] Δ_w - growing-season soil water deficit.
[3] E_t/E_{max} - actual evapotranspiration/potential evapotranspiration ratio.
[4] W_d - depth of soil water table.
[5] G_d - depth of soil gleyed horizon.
[6] Number of plots used to calculate the mean value is given by a numerical superscript in parenthesis.

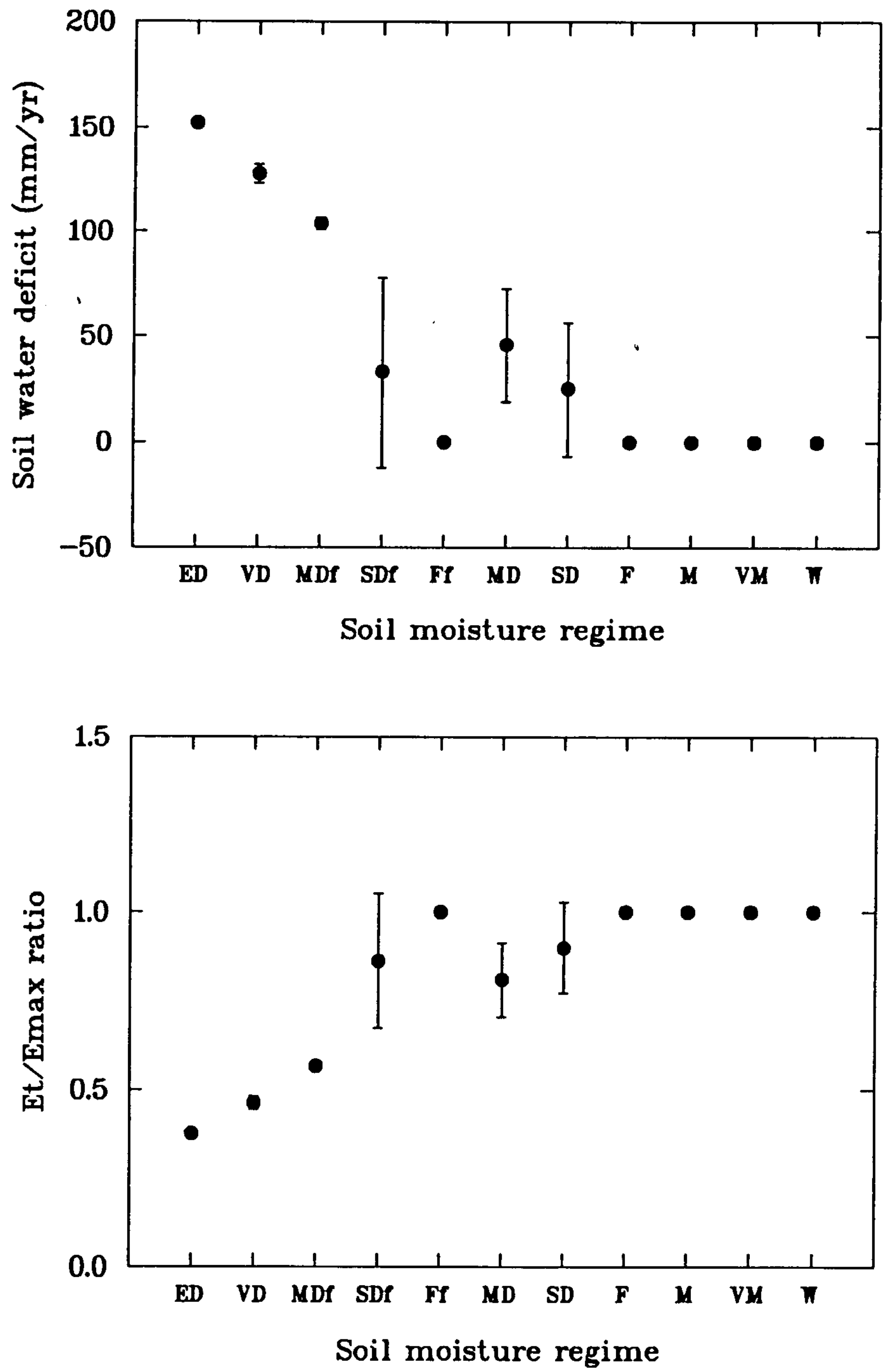

Figure 3.4. Categorical plots showing means and standard deviations of soil water deficit (upper) and actual/potential evapotranspiration (E_t/E_{max}) ratio (lower) in relation to soil moisture regimes (SMRs). Symbols for SMRs are explained in Table 3.8.

soils were moderately to slowly pervious and imperfectly or poorly drained (typically located on flats or in depressions), but surplus water was not evident in the soils for a large part of the growing season. Precipitation normals and soil characteristics suggested that the soils are at, or above, field capacity in late fall and during and after snowmelt. This was quite evident from the presence of gleyed soil horizons within 20 to 60 cm of the ground surface, and a frequently observed above-ground or near-surface water table following major growing-season precipitation events. During relatively dry and warm periods, the water table gradually receded to a greater depth to a point where excess water was no longer evident in the soil, and soils were below field capacity and with a water deficit in the upper soil layer. A combination of two adjectives was used to describe the upper and lower limits in variation of soil moisture conditions. For example, slightly dry-very moist SMR described soil moisture conditions of the sites which show both slight growing-season water deficit and periodic waterlogging (Tables 3.9 and 3.10, Figure 3.5). Such SMRs were denoted by the superscript **f** (fluctuating) attached to the adjective describing the 'drier' limit of soil moisture conditions (e.g., SD^f).

To confirm the recognized SMRs from soil characteristics, and to determine their relations with the understory vegetation, canonical discriminant analysis based on logarithmic transformed frequencies of soil moisture ISGs and recognized SMRs was carried out. The analysis assigned 78% of the study plots into the source SMRs. 'Misclassifications' of individual samples suggested by the analysis were mostly confined to adjacent SMRs. An ordination of the study plots as a function of the first two canonical variates showed that all SMRs were significantly different from each other (Table 3.11) and were separated with no overlap of their 75% confidence regions (Figure 3.5). Confidence regions could not be shown for excessively dry (ED), moderately dry-moist (MD^f), and fresh-wet (F^f) SMRs as they

Table 3.11. Multivariate statistics and F approximations for testing group means in the canonical discriminant analysis of 11 soil moisture regimes (SMRs) under H0: all group means in the population are equal.

Statistic	Value	F	df	P > F
Wilks' lambda (Λ)	0.008	7.521	60,298	0.000
Pillai's trace (V)	2.748	5.155	60,366	0.000
Hotelling-Lawley trace (U)	12.170	11.021	60,326	0.000

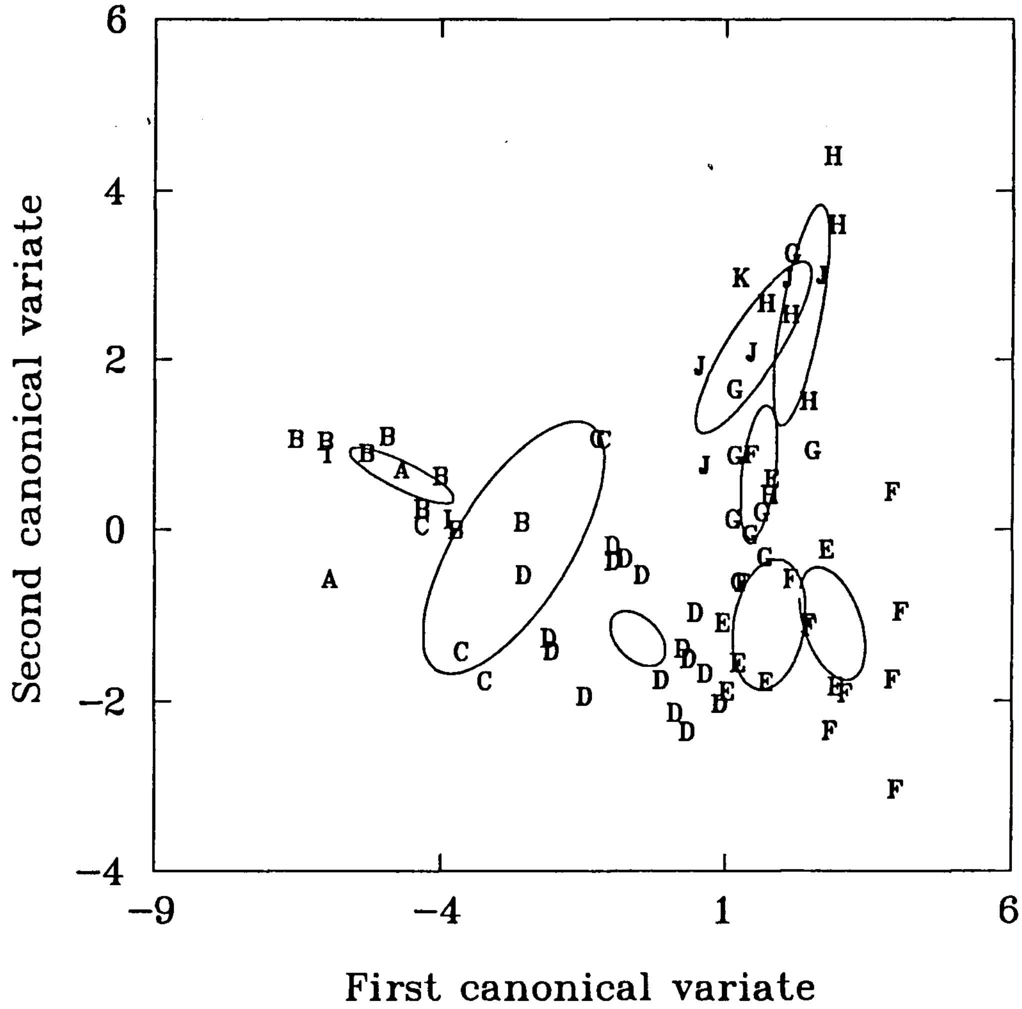

Figure 3.5. Ordination of the study plots as a function of the first two canonical variates determined by canonical discriminant analysis showing 75% confidence regions for soil moisture regime (SMR) means. Each plot is represented by an alphabetical symbol that designates SMR: excessively dry (A), very dry (B), moderately dry (C), slightly dry (D), fresh (E), moist (F), very moist (G), wet (H), moderately dry-moist (I), slightly dry-very moist (J), and fresh-wet (K).

included too few study plots. The ordination arranged SMRs along the first canonical variate in order of decreasing water deficit from left to right, and along the second canonical variate in order of decreasing depth of water table or gleying.

3.3.3. Soil Nutrient Analysis

As was the case for the soil moisture regime, the soil nutrient regime (SNR) is one of the basic components of ecological site quality and one of the differentiating characteristics used in site classification (Pojar *et al.* 1987). Unambiguous characterization of soil nutrient conditions for plant growth requires quantitative criteria which can then be used to divide a soil nutrient gradient into ecologically meaningful regimes (classes). This study adopted the approach used by Courtin *et al.* (1988) and Kabzems and Klinka (1987). Since nitrogen appeared to be the only limiting factor to lodgepole pine growth in this study according to foliar nutrient analysis (reported later in this section), the use of soil nitrogen as a one dimensional representation of the soil nutrient gradient was justified (T.M. Ballard, Department of Soil Science, University of British Columbia, pers. comm.).

The variables selected for the analysis included: pH and C/N ratio for forest floor and mineral soil, and for both forest floor and mineral soil, mineralizable-N (mN) (kg ha^{-1}) and sum of exchangeable Ca, Mg, and K (kg ha^{-1}) (SEC). Due to the curvilinearity of the variables, transformations were made. In the first step, cluster analysis, based on the selected six variables and Euclidean distance and Ward's minimum variance algorithm (Sneath and Sokal 1973), was used to recognize the presence of five natural groups of study plots to be consistent with the existing SNR classification.

In the second step, the five groups produced by cluster analysis were subjected to stepwise discriminant analysis for the selection of variables which would explain the largest amount of variation in the data set. This analysis identified two variables—mN and SEC—determining the structure in the data set at a 95% confidence level with partial R^2 of 0.84 and 0.41, respectively.

In the last step, canonical discriminant analysis was used to determine to what extent mN and SEC would assign the study plots into the five groups created by the cluster analysis. Incorrectly assigned plots were reassigned into the groups indicated by the analysis, and the analysis was repeated until the results stabilized, *i.e.*, further reassignments did not improve the success of discrimination (Tables 3.12 and 3.13). The final analysis resulted in 96% of the study plots being assigned into their source groups. The first canonical variate was mainly correlated to mN (loading = 0.97) and was accounted for 94% of the total variance. The SEC was mainly correlated to the second canonical variate (loading = 0.69) (Tables 3.12 and 3.13).

Figure 3.6 showed an ordination of the study plots on the first two canonical variates, with the five SNRs indicated by 95% confidence ellipses centered on the group means. All means were significantly different from each other (Table 3.14), and all groups were separated with no overlap of their 95% confidence regions. The ordination arranged the study plots along the first canonical variate, which represents a soil mN gradient, ranking from nitrogen-poorest (group 1 on left) to nitrogen-richest (group 5 on right). At this point, the five delineated soil nutrient groups were considered to represent five SNRs, perhaps more appropriately, soil nitrogen regimes: 1 - very poor, 2 - poor, 3 - medium, 4 - rich and 5 - very rich.

A summary of all the soil nutrient variables of the study plots stratified according to the five delineated soil nutrient regimes, indicated that the two selected differentiating characteristics—mN and SEC—provided a a good basis for

Table 3.12. Results of the canonical discriminant analysis for five soil nutrient regimes using on mineralizable-N (kg ha^{-1}) and sum of exchangeable bases (kg ha^{-1}) as variables

Variable	Canonical loadings on the first two canonical variates	
	1st	2nd
mN	0.956	-0.292
SEC	0.722	0.692
Canonical variate	1st	2nd
Canonical correlation (R)	0.95	0.60
Squared R (R^2)	0.90	0.36
Eigenvalue	8.91	0.57
Proportion of variance	0.94	0.06
Cumulative variance	0.94	1.00

Table 3.13. Percentage of study plots identified by canonical discriminant analysis into the source soil nutrient groups on the basis of mineralizable-N (kg ha^{-1}) and sum of exchangeable bases (kg ha^{-1}).

	Percent	Number of plots assigned by discriminant analysis					
Source	correct	1	2	3	4	5	Σ
1	100	**6**	0	0	0	0	6
2	100	0	**16**	0	0	0	16
3	90	0	0	**18**	2	0	20
4	95	0	0	1	**19**	0	20
5	100	0	0	0	0	**10**	10
Σ	96						72

Table 3.14. Multivariate statistics and F approximations for testing group means in the canonical discriminant analysis of five soil nutrient groups under H0: all group means in the population are equal.

Statistic	Value	F	df	P > F
Wilks' lambda (Λ)	0.057	52.722	8, 132	0.000
Pillai's trace (V)	1.265	28.818	8, 134	0.000
Hotelling-Lawley trace (U)	10.939	88.880	8, 130	0.000

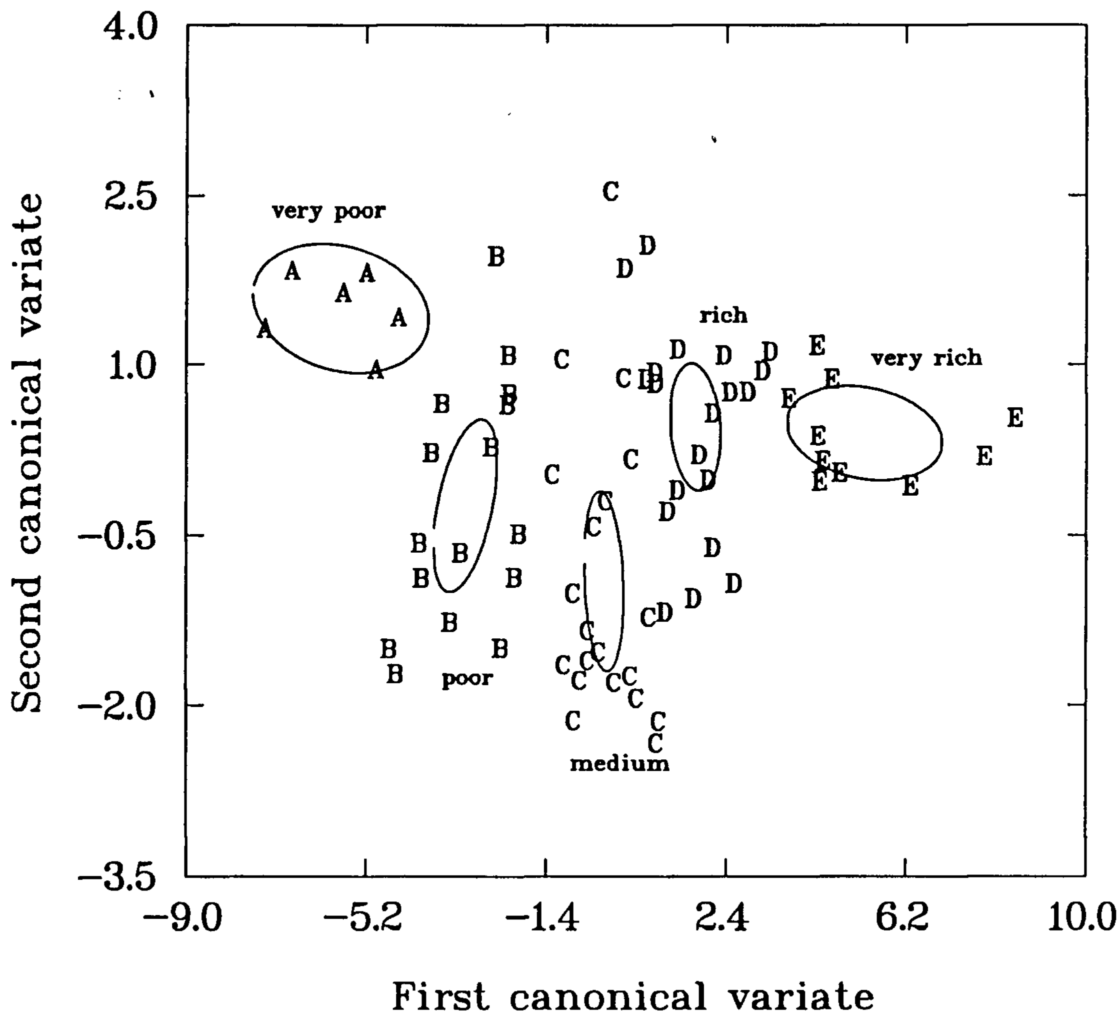

Figure 3.6. Ordination of the study plots as a function of the first two canonical variates determined by canonical discriminant analysis showing 95% confidence regions for soil nutrient regime (SNR) means. Each study plot is represented by an alphabetical symbol that designates soil nutrient group: A - very poor, B - poor, C - medium, D - rich, and E - very rich.

Table 3.15. Means of all available soil nutrient variables and frequency of nitrophytic plants for five soil nutrient regimes.

	Soil nutrient regime[1]				
Variable	VP (n=6)	P (n=15)	M (n=21)	R (n-20)	VR (n=10)
Forest floor					
pH	4.3	4.4	4.4	5.3	5.9
C/N	63	50	39	39	33
total P (kg/ha)	15	33	67	94	302
total S (kg/ha)	21	39	58	118	474
Mineral soil					
pH	5.9	5.5	5.1	6.1	6.1
C/N	95	65	35	39	29
available P (kg/ha)	142	81	54	40	17
available SO_4-S (kg/ha)	5.3	4.3	3.3	3.2	3.5
Forest floor & mineral soil					
mN (kg/ha)	2.7	9.7	29.7	38.3	130.1
Ca (kg/ha)	539	535	1002	3188	7206
Mg (kg/ha)	599	398	214	372	497
K (kg/ha)	65	107	160	400	576
SEC (kg/ha)	1203	1040	1376	3960	8278
Others					
Frequency of nitrophytic ISG	1.5	3.7	9.3	25.2	38.2

[1] VP - very poor, P - poor, M - medium, R - rich, and VR - very rich.

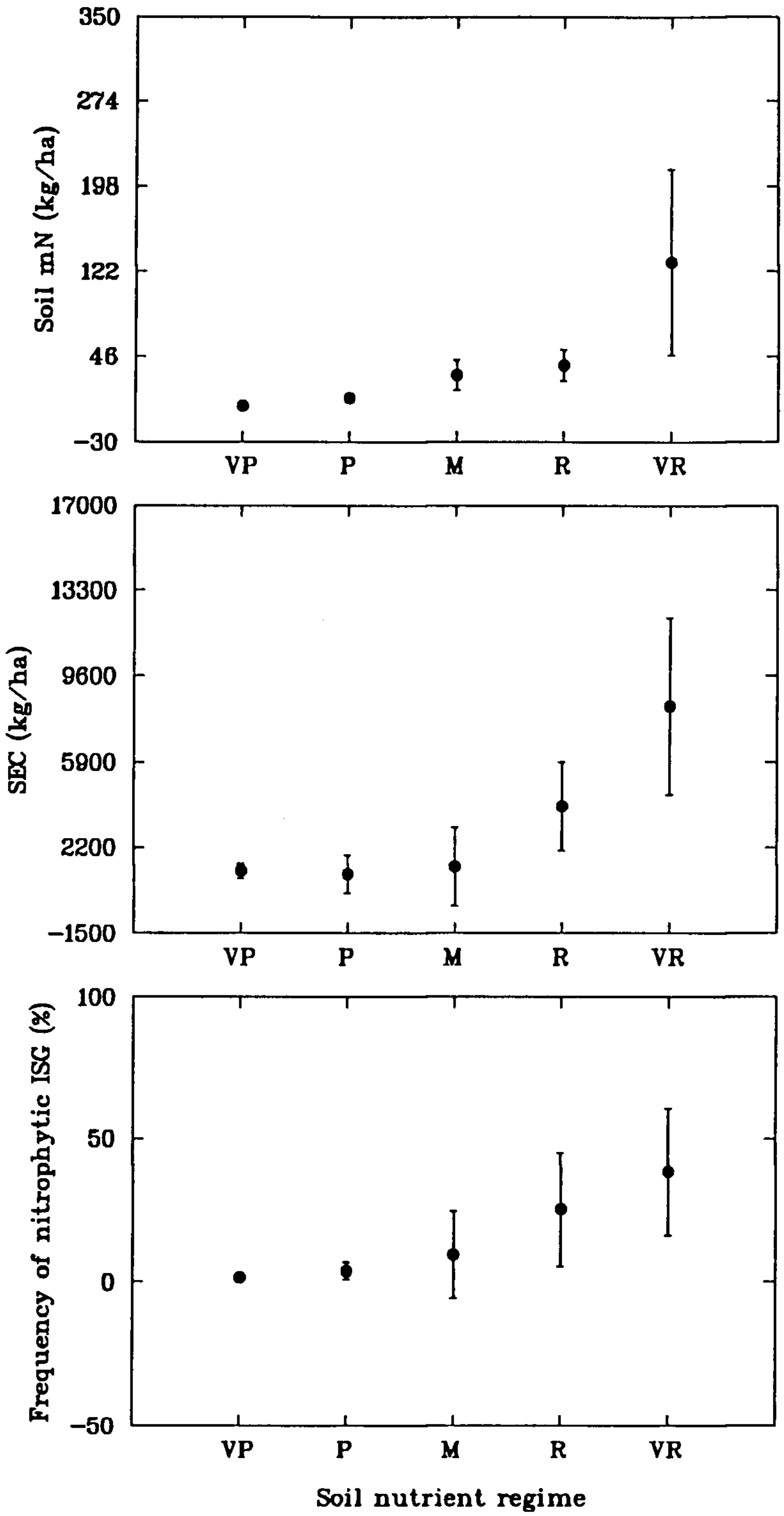

Figure 3.7. Categorical plots showing means and standard deviations for soil mineralizable-N (mN) (kg ha^{-1}) (upper), sum of exchangeable Ca, K, and Mg (kg ha^{-1}) (middle), and frequency of nitrophytic species ($F_{NITR3\%}$) (lower) in relation to soil nutrient regimes (SNRs). Symbols for SNRs are: very poor (VP), poor (P), medium (M), rich (R), and very rich (VR).

classification (Figure 3.7), as they are strongly correlated with a number of the other variables (Table 3.15). Nearly all the accessory variables showed either an increase or decrease along the soil mN gradient, *i.e.*, from very poor through to very rich SNRs. Positive correlations were apparent for the forest floor pH, total P and S, and the total soil Ca and K, while negative correlations were noted for both forest floor and mineral soil C/N and the mineral soil available-P and SO_4-S. No obvious trend was detected for the mineral soil pH and Mg.

The soil nutrient properties identified in this study for characterization of soil nutrient gradients, and the SNR themselves, are consistent with the results of previous studies carried out by Courtin *et al.* (1988), Kabzems (1985), and Carter and Klinka (1991). For example, mineralizable-N and exchangeable Ca, K, Mg were identified by Courtin *et al.* (1988) as differentiating variables for the soil nutrient gradient in southwestern British Columbia and by Kabzems (1985) as the best properties for characterization of the soil nutrient gradient on southern Vancouver Island. The mean values of mN for the five SNRs reported by Carter and Klinka (1991) for the SNRs of 149 Douglas-fir stands in the Very Dry and Dry Maritime subzones of the Coastal Western Hemlock zone of southern B.C. are comparable to those determined in this study for a population of ecologically entirely different stands (Table 3.16).

If the delineation of SNRs is ecologically sound and not merely an arbitrary artifact of the data and the procedure used, then relationships should exist between the mN or SNRs and understory vegetation and lodgepole pine foliar N, and between soil nutrient and foliar nutrients.

To quantify the relationship between the frequency of nitrophytic plants ($F_{NITR3\%}$) (Klinka *et al.* 1989b) and forest floor mineralizable-N, a nonlinear

Table 3.16. Comparisons of the means of mineralizable-N (mN) and sum of exchangeable Ca, Mg, and K (SEC) for soil nutrient regimes (SNRs) stratified from this study and the studies on the coastal B.C.

SNRs	VP	P	M	R	VR
This study					
mN (kg/ha)	2.7	9.7	29.7	38.3	130.1
SEC (kg/ha)	1202	1040	1376	3960	8278
Other studies					
[1]mN (kg/ha)	7.3	13.1	25.2	46.6	176.5
[2]SEC (kg/ha)	1386	873	1225	1743	5066

[1] From Carter and Klinka 1991.
[2] From Courtin *et al.* 1988.

regression model using the natural logarithm of $F_{NITR3\%}$ and untransformed forest floor mN was developed (equation [3.3.1], Figures 3.8):

[3.3.1] $F_{NITR3\%} = \exp[0.597(mN)^{(0.451)}]$

$r^2 = 0.73$ SEE = 3.5 % n = 68.

The model indicates that $F_{NITR3\%}$ increases exponentially as soil nitrogen availability increases. The use of $F_{NITR3\%}$ as an index of soil nitrogen availability is strongly supported by variation in forest floor mN. This result is similar to that obtained by Klinka *et al.* (1990) in their study among humus forms, forest floor nutrients, and understory vegetation.

Fifty-three foliar samples were evaluated for stand macronutrient status. Comparing measured concentrations to the limits proposed by Ballard and Carter (1986) suggested that there were no deficiencies for P, Ca, Mg and SO_4-S in any of the study stands, possible slight-moderate K deficiency in all study stands, and severe N deficiency in 80% of the study stands.

Stratification of foliar macronutrient concentrations according to the SNRs showed the presence of a nitrogen gradient (Table 3.16). Although almost all stands were diagnosed to have severe N deficiencies, there was a slight increase in N concentrations from very poor through very rich SNRs. Regressions of soil mineralizable-N against foliar N were developed (Table 3.18).

These nonlinear models (Table 3.18) using foliar N dry mass (mg/100 needles) as the dependent variables and various measures of soil mN as independent variables, had similar good fits. Equation [3.3.4] was chosen to illustrate the relations between fNw and soil mN (Figure 3.9). As was the case for

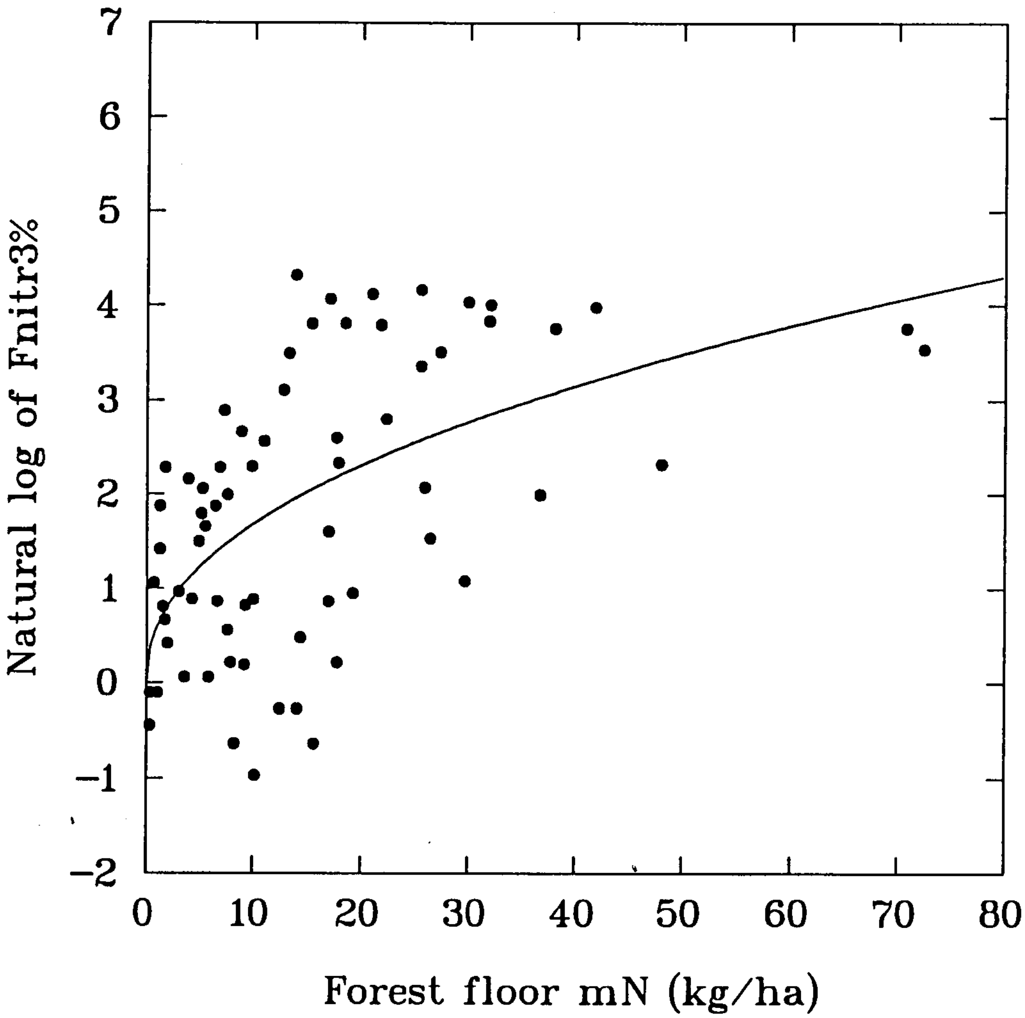

Figure 3.8. Scattergram and regression of forest floor mineralizable-N (kg ha^{-1}) against frequency of nitrophytic plants ($F_{NITR3\%}$).

Table 3.17. Means of foliar macronutrient concentrations in the study stands stratified according to soil nutrient regimes (SNRs). Symbols in columns are: a - adequate, nd - no deficiency; psd - possible deficiency, smd - slight-moderate deficiency, sd - severe deficiency.

	Number	Foliar macronutrients (%)						
SNR	of stands	N	P	K	Ca	Mg	S	SO4-S
Very poor	6	1.08sd*	0.15a	0.46smd	0.21nd	0.103nd	0.083pd	0.0096nd
Poor	13	1.08sd	0.15a	0.44smd	0.19nd	0.107nd	0.081pd	0.0098nd
Medium	9	1.13sd	0.15a	0.45smd	0.19nd	0.108nd	0.085pd	0.0099nd
Rich	17	1.15smd	0.16a	0.46smd	0.19nd	0.116nd	0.089pd	0.0109nd
Very rich	8	1.19smd	0.16a	0.44smd	0.19nd	0.116nd	0.090pd	0.0099nd

* Interpretations are based on Ballard and Carter (1986).

Table 3.18. Regression models based on foliar nitrogen dry mass (fNw) and soil mineralizable nitrogen (mN).

[3.3.2] $fNw = 0.955(fmN_{con})^{0.287}$ N =50

$I^2 = 0.962$ (corrected $I^2 = 0.553$) SEE = 0.870 (mg)

where fmN_{con} = forest floor mN concentration (ppm).

[3.3.3] $fNw = 0.905(fmmN_{con})^{0.295}$ N =50

$I^2 = 0.964$ (corrected $I^2 = 0.567$) SEE = 0.855 (mg)

where $fmmN_{con}$ = combined mN concentration of forest floor and mineral soil

[3.3.4] $fNw = 2.178(fmmN_{kg})^{0.224}$ N = 50

$I^2 = 0.962$ (corrected $I^2 = 0.549$) SEE = 0.872 (mg)

where fmmNkg = combined dry mass of forest floor and mineral soil mN (kg ha^{-1}).

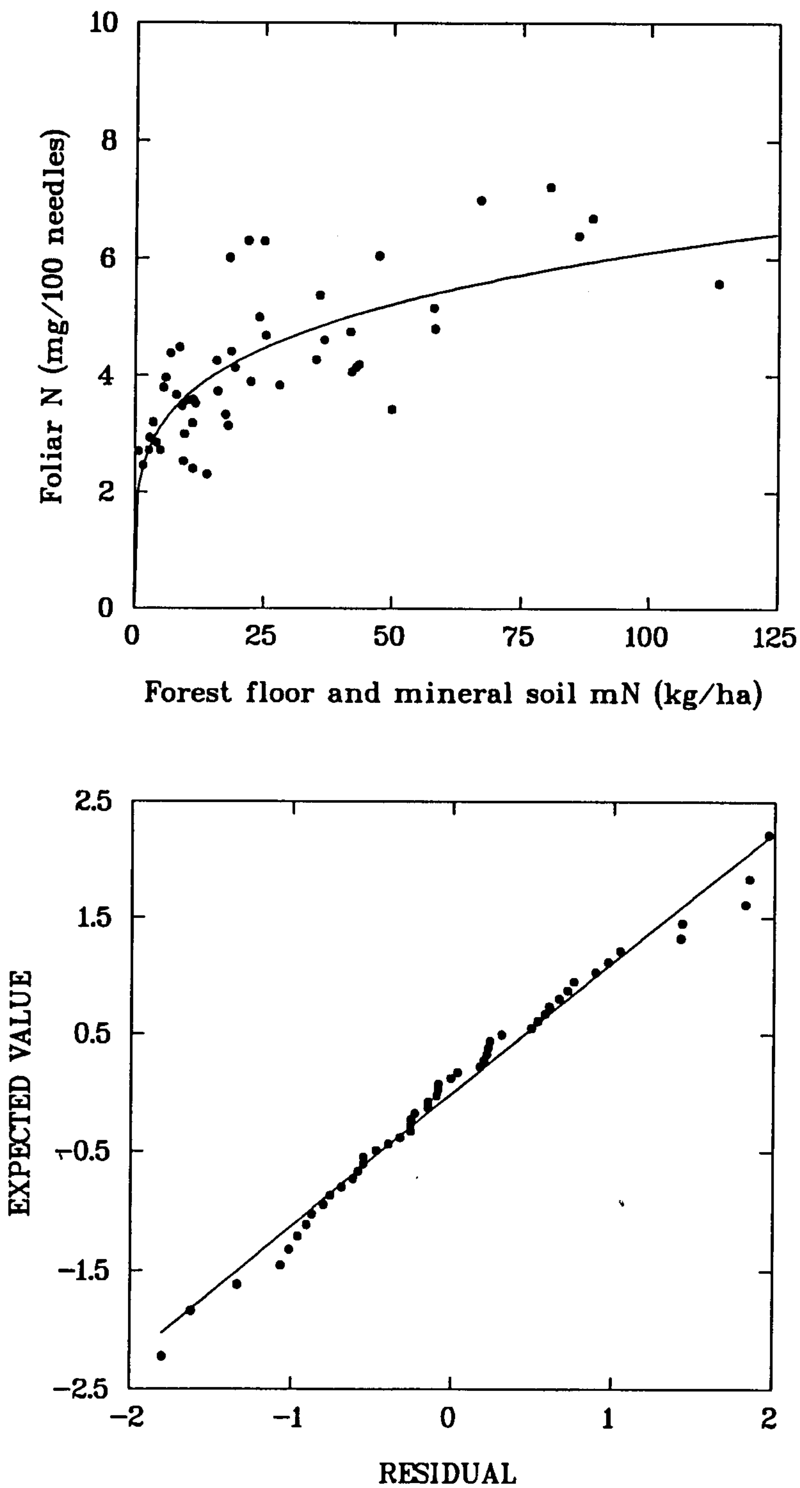

Figure 3.9. Scattergram and regression of forest floor mineralizable-N (kg ha^{-1}) against foliar N (mg/100 needles) using equation [3.3.4].

the $F_{nitr3\%}$ and forest floor mN, equation selected, the content of foliar N increases as a power function of combined dry mass of forest floor and mineral soil mN (kg ha^{-1}). The performance of the models was comparable to that of foliar N concentrations and mineral soil mN reported by Powers (1980) for *Pinus jeffreyi* and *P. ponderosa* (quadratic function), and by Klinka and Carter (1990) for *Pseudotsuga menziesii* using either concentrations or contents (mg/100 needles) of foliar N.

A canonical correlation analysis (CCA) was used to summarize the general relationships between foliar macronutrients (mg/100 needles) (N, P, K, Ca, Mg, S, and SO_4-S) and soil macronutrients (kg/ha) (forest floor C/N, total P, and total S, mineral soil C/N, and combined forest floor and mineral soil mN, K, Ca, and Mg). All these variables were transformed using a common logarithm since non-normality existed in the data. The first and second canonical correlations, 0.85 and 0.79, suggested strong linear relationships between the logarithms of foliar and soil macronutrients. Graphical ordination of the 53 study plots on the first foliar canonical variate and the first soil canonical variate associated with the classified SNRs (Figure 3.10) showed general linear relationships between these two sets of measurements. Although overlaps between SNRs occurred, the plots classified to a particular SNR tended to be associated together.

3.3.4. Site Classification

Classifying study plots into vegetation units, and knowing the regional climate (biogeoclimatic subzone), SMR, and SNR for each study plot, made it possible to stratify the study plots into classes that have similar ecological site quality and, hence, similar potential vegetation and productivity. This quality and potential are best indicated by near-climax or climax plant communities, but can be

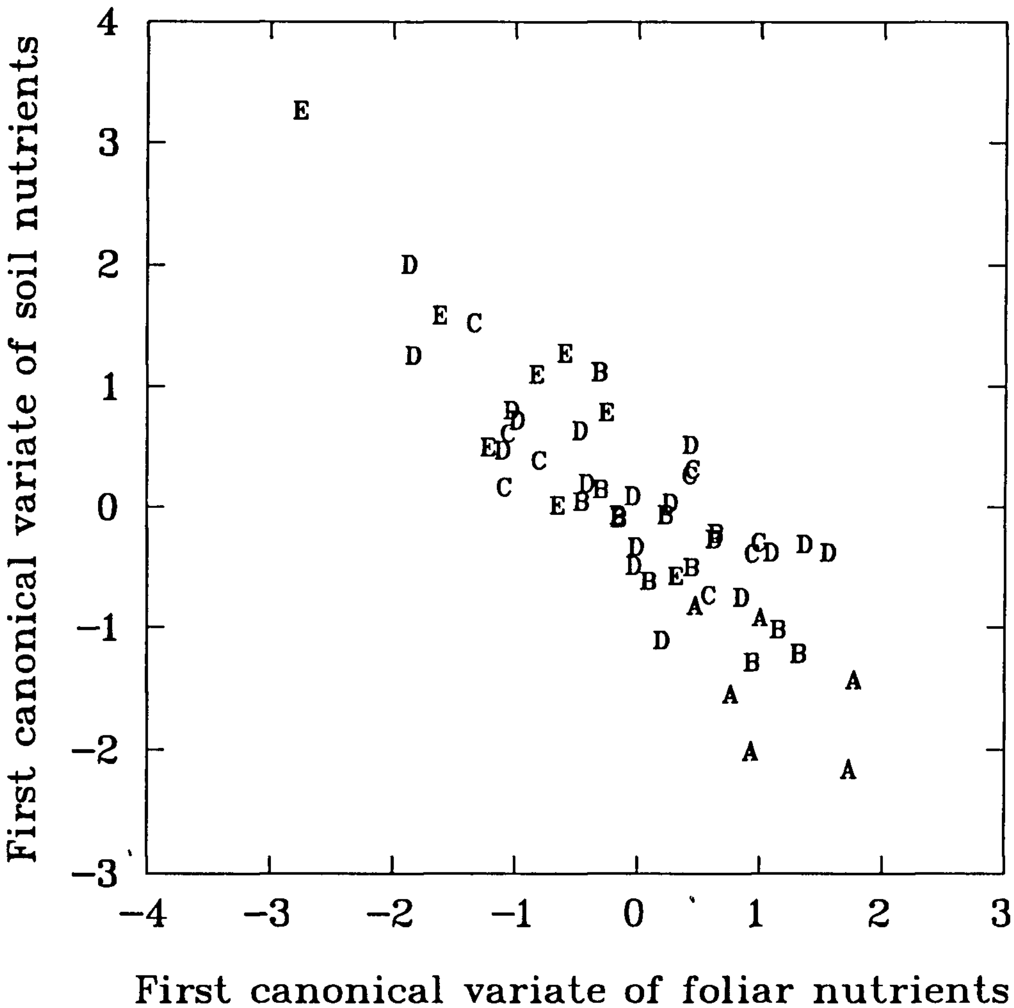

Figure 3.10. Ordination of the study stands as a function of the first pair of soil and foliar nutrients canonical variates determined by canonical correlation analysis. Each study plot is represented by an alphabetical symbol that designates SNR: A - very poor, B - poor, C - medium, D - rich, and E - very rich.

also inferred from understory vegetation in late-seral communities. Dealing with mid-seral lodgepole pine-dominate communities, any inferences of vegetation potential were avoided in this study, as they would be merely speculation.

The basic unit of site classification is the site association, each site association representing a group of ecologically-equivalent sites. Site associations are circumscribed by late-seral, near-climax, or climax vegetation units and characterized by a range of climatic, soil moisture, and soil nutrient regimes. Site series simply represent a climatically uniform segments of a site association, *i.e.*, that portion of a site association that occurs within a biogeoclimatic subzone forms a site series (Pojar *et al.* 1987).

When developing site classification, one to one correspondence between vegetation units and site associations can not be expected. Different combinations of diagnostic species do not always reflect differences in ecological site quality; thus, vegetation units do not always have equal importance or value for site classification (Pfister and Arno 1980). For example, the difference in late-seral to climax vegetation on ecologically-equivalent sites can often be attributed to variation in the composition and cover of a tree layer or ground surface materials.

In order to delineate site associations, it was necessary to examine whether the floristic differences among the recognized vegetation units (Table 3.2) manifested, in fact, differences in ecological site quality. The objective was to eliminate variation in vegetation due to non-site influences, *i.e.*, disturbance, chance, and time. A site association was only recognized when it could be distinguished from all other site associations by an exclusive range of climatic, soil moisture, soil nutrient regimes, and, eventually, by an additional environmental factor.

The examination was carried out in several steps resembling the process of successive approximation (Poore 1962) and was assisted by computerized tabling programs and ordination techniques. In the first step, the tabulated environmental plot data were examined to determine whether each vegetation unit had an exclusive range in climatic, soil moisture, soil nutrient regimes, with appropriate considerations for additional controlling environmental factors (e.g., fluctuating water table). Those units that met this condition were set aside, the others were submitted to a further analysis.

In the second step, the vegetation units that overlapped in ecological site quality were inspected. The sample plots identified as outliers and the borderline plots were assigned to the environmentally most closely related unit. The relocation of these plots brought about another set of differentiable site associations.

In the third step, the remaining, usually nearly completely overlapping, vegetation units were grouped, considering both floristic and environmental affinities. The newly tabulated environmental data were inspected and differentiable groups were identified. Grouping was continued until all groups could be differentiated.

In the last step, new vegetation and environment tables were produced (Tables 3.19 and 3.20). Applying the principles of environmental pattern analyses (Whittaker 1957, 1967, 1978), the recognized site associations were plotted on a mosaic chart (Shimwell 1971) composed of climatic, soil moisture, and soil nutrient gradients (Figure 3.11). The tables and the chart were used to compare site associations for floristic and environmental affinities and conformity to a general pattern of relationships.

Table 3.19. Synopsis and differentiating characteristics of the site associations distinguished in the study plots.

Name (symbol)	Climate[1]	SMR[2]	SNR[3]
Stereocaulon (A)	SBPSxc	ED	VP-P
Arctostaphylos (B)	SBPSxc	VD	VP-M
Sherpherdia (C)	SBPSxc	MD^f	M-VR
Aulacomnium (D)	SBPSxc	SD^f	M-VR
Salix (E)	SBPSxc	F^f	M-VR
Pleurozium (F)	SBSmc	MD	VP-M
Vaccinium myrtiloides (G)	SBSwk	MD	VP-M
Vaccinium membranaceum (H)	SBSmc, SBSwk	SD	VP-M
Gymnocarpium (I)	SBSmc, SBSwk	F-M	M-VR
Equisetum (J)	SBSmc, SBSwk	VM	R-VR
Carex (K)	SBSmc, SBSwk	W	M-VR

[1] represented by biogeoclimatic subzones: SBPSxc - Very Dry and Cold Sub-boreal Pine Spruce Subzone, SBSmc - Moist and Cold Sub-boreal Spruce Subzone, SBSwk - Wet and Cool Sub-boreal Spruce Subzone.

[2] soil moisture regimes: ED - excessively dry, VD - very dry, MD^f - moderately dry to moist, SD^f - slightly dry to very moist, F^f - fresh to wet, MD - moderately dry, SD - slightly dry, F - fresh, M - moist, VM - very moist, W - wet.

[3] soil nutrient regimes: VP - very poor, P - poor, M - medium, R - rich, VR - very rich.

Table 3.20. Means of selected climatic, soil, and stand characteristics of the distinguished site associations (SAs). Symbols for SAs, biogeoclimatic subzones, soil moisture regimes (SMRs), and soil nutrient regimes (SNRs) are explained in Table 3.19.

Site association	A	B	C	D	E	F	G	H	I	J	K
Number of plots	2	8	2	5	1	1	4	16	18	9	6
Subzone	----------SBPBxc----------					SBSmc	SBSwk	----SBSmc & SBSwk----			
Actual SMR	ED	VD	MD[f]	SD[f]	F[f]	MD	MD	SD	F-M	VM	W
Actual SNR	VP	VP-M	R	R-VR	VR	P	P-M	P-M	M-R	R-VR	M-VR
E_t (mm/year)[1]	92	110	136	202	244	158	202	212	227	239	246
E_t/E_{max}	0.38	0.46	0.57	0.86	1.00	0.63	0.85	0.90	1.00	1.00	1.00
Growing-season water deficit (mm/year)	152	128	104	32	0	93	32	25	0	0	0
Depth of gleyed horizon[2] or water table[3] (cm)	na	na	40[2] (1)[4]	48[2,3] (5)	30[3] (1)	na	na	na	53[2,3] (7)	44[2,3] (8)	24[3] (5)
Forest floor C/N	71	60	46	37	25	62	42	42	39	32	34
Mineral soil C/N	138	80	51	38	31	70	47	47	33	32	43
Forest floor & mineral soil min-N (kg ha^{-1})	2.1	6.4	16.1	45.6	104	7.5	15.8	19.4	34.8	121.6	54.8
Forest floor & mineral soil exchangeable Ca, Mg, and K (kg ha^{-1})	1006	2628	6425	6029	5523	499	488	839	2059	7740	3257
Foliar N (mg/100 needles)	2.71	2.94	3.28	3.91	6.39	3.79	3.47	3.84	4.88	5.25	4.66
Measured site index (m/50 yr of b.h.age)	8.2	12.1	12.9	13.7	11.4	15.6	15.9	18.2	20.6	21.3	13.9
FNITR3%	0.8	3.1	11.1	21.1	42.8	4.1	2.3	3.0	27.3	36.4	11.6

[1] E_t - actual evapotranspiration.
[2] Denotes the depth of gleyed horizon.
[3] Denotes the depth of water table.
[4] Numerical numbers in parenthesis indicate the number of plots used to calculate the soil water table and depth of gleyed horizon.

The sample plots were classified into 11 site associations and 15 site series (Table 3.19), named for brevity by the generic or specific names of a dominant indicator plant. These were selected from a diagnostic species summary table for site associations, as potential climax tree species could not be determined. The classification implied that there are eleven different ecological strata within the population of the study plots, each representing a segment of an ecological site quality gradient.

To support the significance of, and to quantify the environmental affinities between the recognized site associations, canonical discriminant analysis using selected environmental variables was carried out. The environmental variables were: heat index (Table 2.1), E_t/E_{max} ratio, growing-season water deficit or the depth of water table or gleyed soil horizon, and soil mineralizable-N (Table 3.20). Multivariate statistics showed that all site associations were significantly different based on the means of those selected environmental variables (Table 3.21).

The analysis assigned 74% of the study plots into their source site associations. 'Misclassifications' of study plots by the analysis were confined to *Gymnocarpium* (I) and *Equisetum* (J) plots. Overlap between I- and J-plots is likely a reflection of difficulties or inaccuracies in precisely characterizing or measuring growing-season soil water surplus conditions using a single point in time, *i.e.*, the depth of water table or gleyed soil horizons (Table 3.20).

Ordination of the study plots as a function of the first two canonical variates showed a remarkable pattern (Figure 3.12). Firstly, the study plots were clearly separated along the first canonical variate according to climate in order from the SBPSxc subzone (left) to the SBSmc subzone to the SBSwk subzone (right), with the SBPSxc plots appearing more climatically dissimilar than SBSmc and SBSwk

Subzone	SBPSxc	SBSmc	SBSwk

Very poor (VP), poor (P), and medium (M) soil nutrient regimes

Actual soil moisture regime	SBPSxc	SBSmc	SBSwk
excessively dry	*Stereocaulon* 0–2/VP–P		
very dry	*Arctostaphylos* 3–4/VP–M		
moderately dry		*Pleurozium* 1–2/VP–M	*V. myrtilloides* 1/VP–M
slightly dry		*V. membranaceum* 3–4/VP–M	2–3/VP–M
fresh			
moist			
very moist			
wet			

Medium (M), rich (R), and very rich (VR) soil nutrient regimes

Actual soil moisture regime	SBPSxc	SBSmc	SBSwk
excessively dry			
very dry			
moderately dry			
slightly dry			
fresh		*Gymnocarpium* 4–5/M–VR	4–5/M–VR
moist	*Shepherdia* 5f/M–VR		
very moist	*Aulacomnium* 6f/M–VR	*Equisetum* 6/M–VR	6/M–VR
wet	*Salix* 7f/M–VR	*Carex* 7/M–VR	7/M–VR

Figure 3.11. An environmental chart showing the site associations distinguished in the study plots in relation to biogeoclimatic subzones, relative (Arabic numbers) and actual soil moisture regimes, and soil nutrient regimes.

Table 3.21. Multivariate statistics and F approximations for testing group means in the canonical discriminant analysis of 11 site associations (SA) under H0: all group means in the population are equal.

Statistics	Value	F	df	P > F
Wilks' lambda (Λ)	0.003	14.117	50,263	0.000
Pillai's trace (V)	2.883	8.308	50,305	0.000
Hotelling-Lawley trace (U)	17.400	19.279	50,277	0.000

plots. This justified classification of the SBPSxc plots into a different site association, whereas climatic affinities between the SBSmc and SBSwk subzones justified classification of ecologically-equivalent sites into the same site associations but different site series.

Secondly, the study plots were arranged in order of increasing soil moisture and nitrogen along the second canonical variate, with most water- and nitrogen deficient plots shown on bottom and most waterlogged and nitrogen-rich plots shown on towards the top. The pattern of the study plots along the second canonical variate indicated that they represent points on a combined soil moisture and nitrogen gradient. In consequence, the distinguished site associations were floristically inferred segments of climatic, soil moisture, and soil nitrogen gradients (*i.e.*, an ecological site quality gradient). It was recognized that climate, soil moisture, and soil nitrogen, are continuous properties, and so site associations are not discrete groups, they change along each gradient into other associations. The limits of a particular site association should be based on statistics derived from observed and measured properties of samples of that association.

3.4. Conclusions

Using numerical techniques and the methods of biogeoclimatic ecosystem classification, ecological analysis of the study plots produced indirect and direct categorical and continuous measures of ecological site quality for investigating their relations to lodgepole pine height growth. Floristic analysis showed that the understory vegetation in mid-seral lodgepole pine stands was sufficiently developed to indicate differences in ecological site quality between the study plots. Diagnostic species of the distinguished vegetation units were found to be strongly correlated with regional climatic, soil moisture, and soil nutrient gradients.

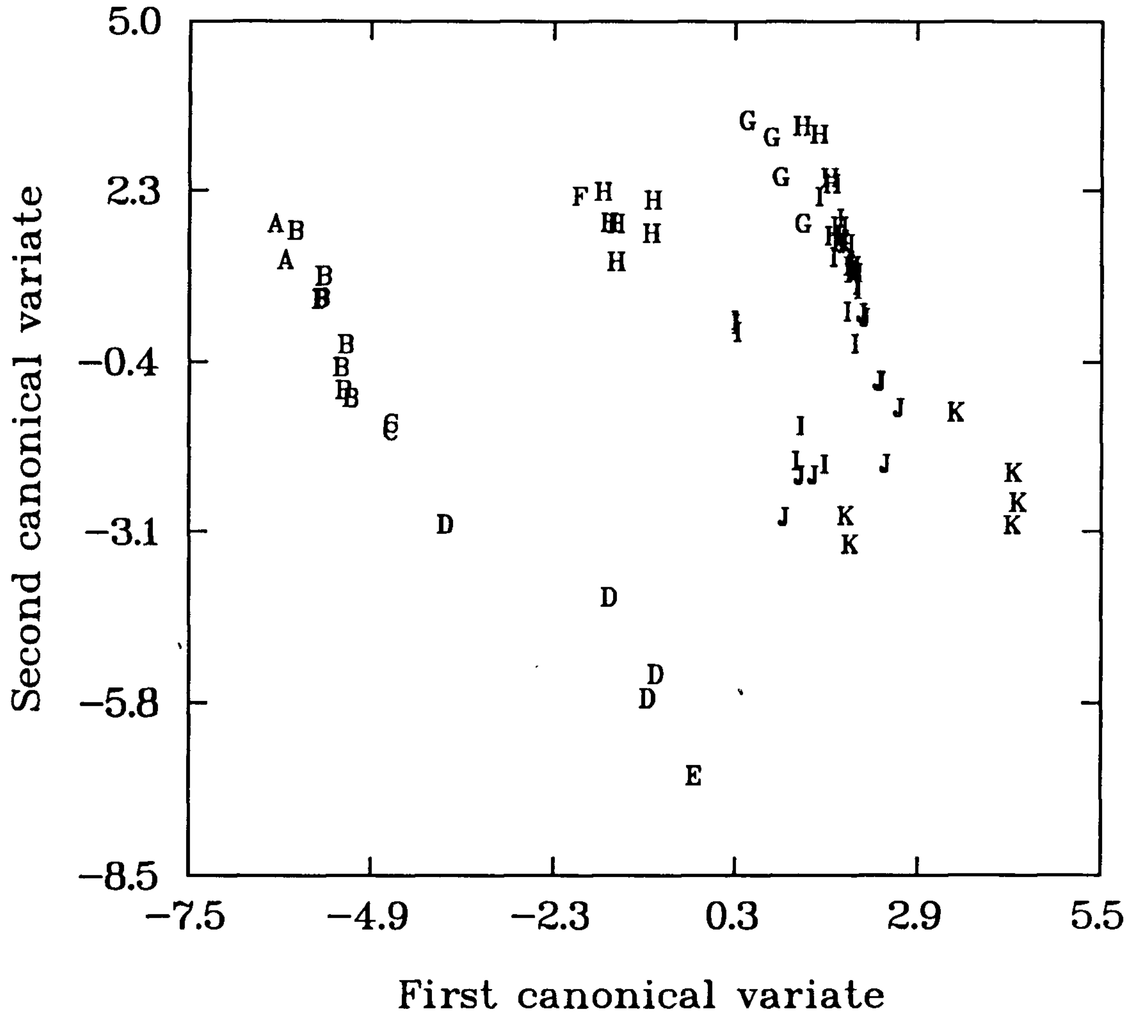

Figure 3.12. Ordination of the study plots as a function of the first two canonical variates determined by canonical discriminant analysis on selected environmental variables. Each study plot is represented by an alphabetical symbol that designates site association (SA). Symbols for SA are given in Table 3.18.

The application of the criteria proposed by Klinka *et al.* (1989b), and those of the Energy/Soil-Limited model (Spittlehouse and Black 1981), resulted in successful stratification of the study plots into actual soil moisture regimes. Soil mineralizable-N and the sum of exchangeable Ca, Mg, and K were the properties used to characterize a soil nutrient gradient and five traditionally used soil nutrient regimes. Correlations between understory vegetation and categorical or continuous measures of soil moisture suggested that these measures were not arbitrary, but had a meaning relative to soil moisture conditions experienced by plants. Similarly, correlations between soil mN and the frequency of nitrophytic plants, between foliar N and soil mN, and between foliar and soil macronutrients suggested that (1) a complex soil nutrient gradient can be exemplified, but not replaced by a soil nitrogen gradient, and (2) the criteria and limits used to stratify the study plots into classes of the soil nitrogen gradient were not arbitrary, but might have a meaning relative to general nutrient supply for plants.

The criteria used to classify the study plots into site associations resulted in recognition of qualitatively and quantitatively distinct, field recognizable, segments of regional gradients of ecological site quality.

4. RELATIONSHIPS BETWEEN LODGEPOLE PINE SITE INDEX AND MEASURES OF ECOLOGICAL SITE QUALITY

4.1. INTRODUCTION

Classification of forest ecosystems is recognized as being an essential prerequisite for the implementation of site-specific silvicultural management. To make silvicultural decisions that have a desirable effect on both forest and site productivity, a forester should know (1) the ecological quality of different sites, (2) the ecological characteristics of different trees, and (3) the relationship between growth performance of tree species and ecological site quality. This knowledge can then be used to select specific species and silvicultural regimes that will sustain or enhance forest and site productivity.

Although there are some limitations to site index, it has been widely used for its practicality as a measure of (1) growth performance or productivity of a particular tree species on particular site and (2) site quality, *i.e.*, a site's capacity to support forest growth (e.g., Spurr and Barnes 1981, Hägglund 1981, Monserud 1984). Evidently, site index can be neither a complete nor a precise measure of forest productivity as it only indicates the height growth performance of a tree species, at a given point in time.

However, there are some conceptual problems in relating site index to site quality. Firstly, the site index of two different tree species growing on the same site may be different; thus site index is the measure of forest productivity or site quality relative to a given species, not a measure of a site's quality to support forest growth, in general. Secondly, the same tree species may have the same site index on two ecologically different sites; hence, these two sites are said to have the same site quality in supporting growth of the species. However, this contradicts the ecological perspective that defines site quality as the sum of all the many environmental factors affecting the biotic community of an ecosystem (Daniel *et al.* 1979, Spurr and Barnes 1980). Therefore, it is more appropriate to use the term ecological site quality than site quality in describing ecological characteristics of forest sites.

In British Columbia, biogeoclimatic ecosystem classification is widely used to recognize different types of forest ecosystems according to the ecological quality of their sites (Pojar *et al.* 1987). Although the classification has improved silvicultural decision-making, the link between the classification (or ecological site quality) and forest productivity has not yet been established. In consequence, one cannot determine potential forest productivity of different tree species on different forest sites as the relationship between forest productivity and measures of ecological site quality has not yet been examined for all major crop tree species.

Relationships between environmental factors and site index have been the subject of many studies and reviews. Most of these studies had limited success in accounting for a major portion of the variation in site index over a large area, and in advancing the understanding of relationships between ecological site quality and tree growth. Kabzems and Klinka (1987), Courtin *et al.* (1988), Green *et al.* (1989), Carter and Klinka (1990, 1991), and Klinka and Carter (1990) applied various measures of ecological site quality for estimating and describing the influence of these measures on Douglas-fir site index. Using the approach and principles of biogeoclimatic classification, they identified several ecological variables that were strongly related to Douglas fir site index. However, there is a need to expand and test the results of their studies for other tree species and in different environments.

The usefulness of the measures of ecological site quality determined by biogeoclimatic ecosystem classification in site-productivity studies was examined in this Chapter by asking one pivotal question: how does lodgepole pine productivity vary with measures of ecological site quality? In consequence, the specific objective was to evaluate relationships between several selected ecological variables determined in Chapter 3 and the site index of immature sub-boreal lodgepole pine stands. This objective was accomplished by relating environment, vegetation, and site index data from these stands through simple and multiple regression analysis.

4.2. Materials and Methods

The 72 plots described previously were used for this analysis. The ecological analysis reported in Chapter 3 produced a number of variables that were used as independent variables in regression analysis. These variables, representing various measures of ecological site quality, were categorized according to origin (environment and vegetation variables), mode of measuring ecological site quality (indirect and direct variables), and expression [categorical and continuous (analytical) variables] (Table 4.1). The same categorization was adopted for regression analysis in order to avoid redundant combinations and collinearity of variables, and complexity of models. For example, vegetation variables were not used together with environmental variables, indirect variables were not used together with direct variables, and categorical variables were not used together with continuous variables.

Simple and multiple least squares regression analyses (Rawlings 1988, Wilkinson 1990) were used to regress site index on selected combinations of ecological variables. The analysis considered several categorical models (Table 4.2) and analytical models (Table 4.3).

Table 4.1 Synopsis of the ecological variables stratified according to origin, mode, and expression (categorical variables are in normal face, continuous variables are in italic face).

ORIGIN	Mode	
	Indirect	Direct
VEGETATION		
	Vegetation unit (VU)	
	Frequency of indicator species groups (ISGs) (F_{jk})	
	Q-type PCA scores on diagnostic species (PCA_v)	
	Leaf area index (LAI)	
	Q-type PCA scores on foliar nutrients (PCA_f)	
ENVIRONMENT		
	Biogeoclimatic subzone (BGC)	Soil nutrient regime (SNR)
	Site association (SA)	Soil moisture regime (SMR)
	Site series (SS)	*Potential evapotranspiration (PET)*
	Forest floor carbon-nitrogen ratio (C/N)	*Water deficit (Δ_w)*
	Mineral soil carbon-nitrogen ratio (C/N)	*Depth of water table (W_d)*
	Q-type PCA scores on soil nutrients (PCA_s)	*Depth of soil gleying (G_d)*
		Mineralizable nitrogen (mN)
		Sum of exchangeable Ca, Mg, K (SEC)

Site index (m/50 yr) was investigated for normality using graphical analysis (probability plot) (Chambers *et al.* 1983; Wilkinson 1990). All soil nutrient variables and foliar nutrient variables were transformed using a common logarithm to reduce their heterogeneity of variance. In order to specify appropriate linear models, the relationships between the dependent variable and the independent variables were checked for nonlinearity using a graphical display (Chambers *et al.* 1983; Wilkinson 1990). Min-N and SEC were transformed due to their curvilinear relationship with site index. Dummy variables (qualitative variables or indicator variables) (Chatterjee and Price 1977) were used in categorical models. Multicollinearity (Rawlings 1988), a common problem of ecological data, was examined using Pearson correlation analysis (Wilkinson 1990). Principal component regression (Rawlings 1988) was introduced due to multicollinearity among the variables studied.

Means and standard deviations of site index in relation to vegetation units, site associations, SMRs, and SNRs, were shown in categorical plots (Wilkinson 1990). A distance weighted least square (DWLS) smoothing method (McLain 1974, Wilkinson 1990) was used to superimpose the isolines of site index onto a two-dimensional edatopic grid. The relationship among site index, SMRs, and SNRs was displayed in a three-dimensional space with a projected contour plot.

Table 4.2 Synopsis of the general forms of categorical models used to test the relationships between lodgepole pine site index and selected ecological variables. SI is site index (m @ 50 years of breast height age).

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[1] $SI = f(VU_i)$

where VU_i are dummy variables representing vegetation units from 1 through 10; VU_1 = *Arctostaphylos*-typic, VU_2 = *Arctostaphylos-Shepherdia*, VU_3 = *Arnica*, VU_4 = *Empetrum*, VU_5 = *Vaccinium myrtiloides*, VU_6 = *V. membranaceum*, VU_7 = *Ribes*, VU_8 = *Gymnocarpium*-typic, VU_9 = *Gymnocarpium-Equisetum*, or VU_{10} = *Sphagnum*.

[2] $SI = f(BGC_i)$

where BGC_i are dummy variables representing biogeoclimatic subzones: SBPBxc, SBSmc, or SBSwk.

[3] $SI = f(SMRs)$

where SMRs are dummy variables representing soil moisture regimes from ED through W; ED = excessively dry, VD = very dry, MD = moderately dry, SD = slightly dry, F = fresh, M = moist, VM = very moist, W = wet, MD^f = moderately dry to moist, SD^f = slightly dry to very moist, and F^f = fresh to wet.

[4] $SI = f(SNRs)$

where SNRs are dummy variables representing soil nutrient regimes from VP through VR; VP = very poor, P = poor, M = medium, R = rich, and VR = very rich.

[5] $SI = f(SA_i)$

where SA_i are dummy variables representing site associations from 1 through 11; SA_1 = *Stereocaulon*, SA_2 = *Arctostaphylos*, SA_3 = *Shepherdia*, SA_4 = *Pleurozium*, SA_5 = *Vaccinium myrtiloides*, SA_6 = *V. membranaceum*, SA_7 = *Gymnocarpium*, SA_8 = *Aulacomnium*, SA_9 = *Equisetum*, SA_{10} = *Salix*, and SA_{11} = *Carex*.

[6] $SI = f(SS_i)$

where SS_i are dummy variables representing site series from 1 through 15; SS_1 = SBPSxc/*Stereocaulon*, SS_2 = SBPSxc/*Arctostaphylos*, SS_3 = SBPSxc/*Shepherdia*, SS_4 = SBSmc/*Pleurozium*, SS_5 = SBSwk/*Vaccinium myrtilloides*, SS_6 = SBSmc/*V. membranaceum*, SS_7 =SBSwk/*V.membranaceum*, SS_8 = SBSmc/*Gymnocarpium*, SS_9 = SBSwk/*Gymnocarpium*, SS_{10} = SBPSxc/*Aulacomnium*, SS_{11} = SBSmc/*Equisetum*, SS_{12} = SBSwk/*Equisetum*, SS_{13} = SBPSxc/*Salix*, SS_{14} = SBSmc/*Carex*, SS_{15} = SBSwk/*Carex*.

[7-10] $SI = f(BGC_i, SNRs, SMRs)$

where BGCi, SNRs, and SMRs are explained above.

Table 4.3 Synopsis of the general forms of analytical models used to test the relationships between lodgepole pine site index and selected ecological variables. SI is site index (m @ 50 years of breast height age).

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[11] SI = f (F_{jk})

where F_{jk} is relative frequency of selected ISG j (EVD = excessively dry to very dry, VDMD = very dry to moderately dry, MDF = moderately dry to fresh, FVM = fresh to very moist, VMW = very most to wet, WVW = wet to very wet, P = very poor to medium, M = poor to rich, and R = medium to very rich) of site attribute k (SMR and SNR).

[12-13]SI = f (PCA_v)

where PCA_v are Q-type PCA scores on diagnostic species.

[14] SI = f (PCA_f)

where PCA_f are Q-type PCA scores on foliar nutrient variables.

[15] SI = f (LAI)

where LAI is projected leaf area index.

[16] SI = f (PET)

where PET is potential evapotranspiration.

[17] SI = f (DGW, Dummy)

where DGW is the combination of the depth of soil water table (W_d) or the depth of soil gleying horizon (G_d) and soil water deficiency (Δ_w); Dummy is a dummy variable representing G_d, W_d, and Δ_w.

[18-20]SI = f (mN, SEC)

where mN is soil mineralizable nitrogen and SEC is sum of exchangeable CA, Mg, and K.

[21-22]SI = f (fC/N, mC/N)

where fC/N and mC/N are representing forest floor and mineral soil carbon-nitrogen ratios, respectively.

[23-29]SI = f (PET, DGW, Dummy, mN, SEC)

where PET, DGW, Dummy, mN, SEC are explained above.

[30] SI = f (PCA_s)

where PCA_s are Q-type PCA scores on soil nutrient variables.

4.3. Results

Stratification of all sample plots (n = 72) according to site associations (SA_i), soil moisture regimes (SMRs), and soil nutrient regimes (SNRs), manifested three important trends in the variation of lodgepole pine site index (Figures 4.1, 4.2, and 4.3). Site index was lowest on very poor sites and clearly different from all other sites, but the differences among the poor, medium, rich, and very rich sites were not obvious (Figure 4.1). This indicated that the lodgepole pine productivity gradient is poorly related to the soil nutrient gradient, *i.e.*, increase in available soil nitrogen over the level defined for the poor SNR has a negligible influence on site index.

Stratification of the sample plots according to SMRs produced different results than the stratification based on SNRs (Figure 4.2). The categorical plot showed the presence of two distinct populations of sample plots and a strong productivity gradient coinciding with the soil moisture gradient. All low-site index (SI < 15 m, except for the wet SMR) SMRs occurred in the SBPSxc subzone, while all high-site index (SI ≥ 15 m) SMRs occurred in the SBSmc and SBSwk subzones. This suggests (1) a strong climatic influence on the soil moisture gradient and (2) affinity between SBSmc and SBSwk climates. Lodgepole site index increased with an increasing available soil moisture to a maximum, and then it decreased with an increasing temporary (fresh SMR) or permanent (wet SMR) water table.

Stratification of the sample plots according to site associations (SA_i) produced nearly identical results (Figure 4.3), *i.e.*, the presence of two populations of sample plots and a strong productivity gradient coinciding with an ecological site quality gradient. All low-site index [SI < 15 m, except for the SA_{11} (*Carex* site association)] SA_i were confined to the SBPSxc subzone, whereas all high-site index

($SI \geq 15$ m) SA_i were confined to the SBSmc and SBSwk subzones. This indicates that (1) the ecological site quality gradient coincides with climatic and soil moisture gradients and (2) SA_i represent vegetation-inferred segments of the combined climatic and soil moisture gradient.

When the results of these three trends are taken into account, it appears that the climatic and soil moisture regimes of the study stands are strongly related to a lodgepole pine productivity gradient (measured by site index).

To quantify relationships between lodgepole pine site index and selected measures of ecological site quality (Table 4.1), various categorical and analytical regression models were examined (Tables 4.2 and 4.3). A total of 30 models were developed, and all models were significant at $p \leq 0.01$, except for model [19] (Table 4.6).

The models using vegetation variables (Table 4.4) had moderate to strong relationships with site index ($0.41 < R^2 < 0.83$), but the VU model (equation [1]) accounted for the largest proportion of the variation in site index of all vegetation models examined ($R^2 = 0.83$) (Figure 4.4). Taking into account the strength of the models using various expression of understory vegetation (equations [11], [12], and [13]), it appears that the understory vegetation in early-seral lodgepole pine stands is well enough developed as to serve as a good indicator of ecological site quality.

The LAI model (equation [15]) showed a quadratic relationship between site index and LAI, and indicated that site index did not increase with increasing LAI across the complete LAI gradient, but appears to reach a maximum when LAIs are approximately at 3.0 m^2 m^{-2}, with higher LAIs not necessarily resulting in higher lodgepole pine site indices or productivity (Figure 4.5).

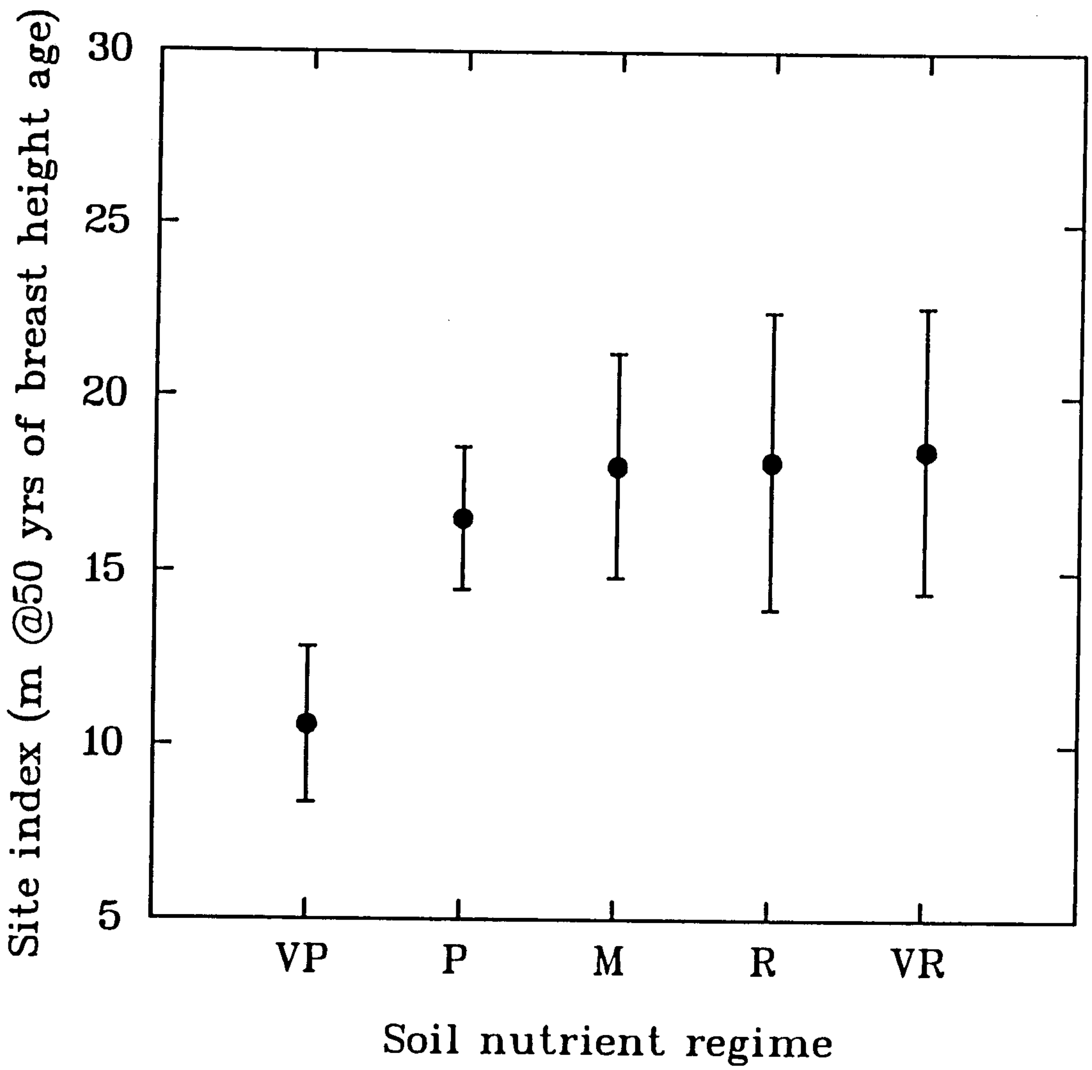

Figure 4.1. Categorical plot of lodgepole pine site index in relation to soil nutrient regimes (SNRs). Symbols for SNRs are defined in Table 4.2.

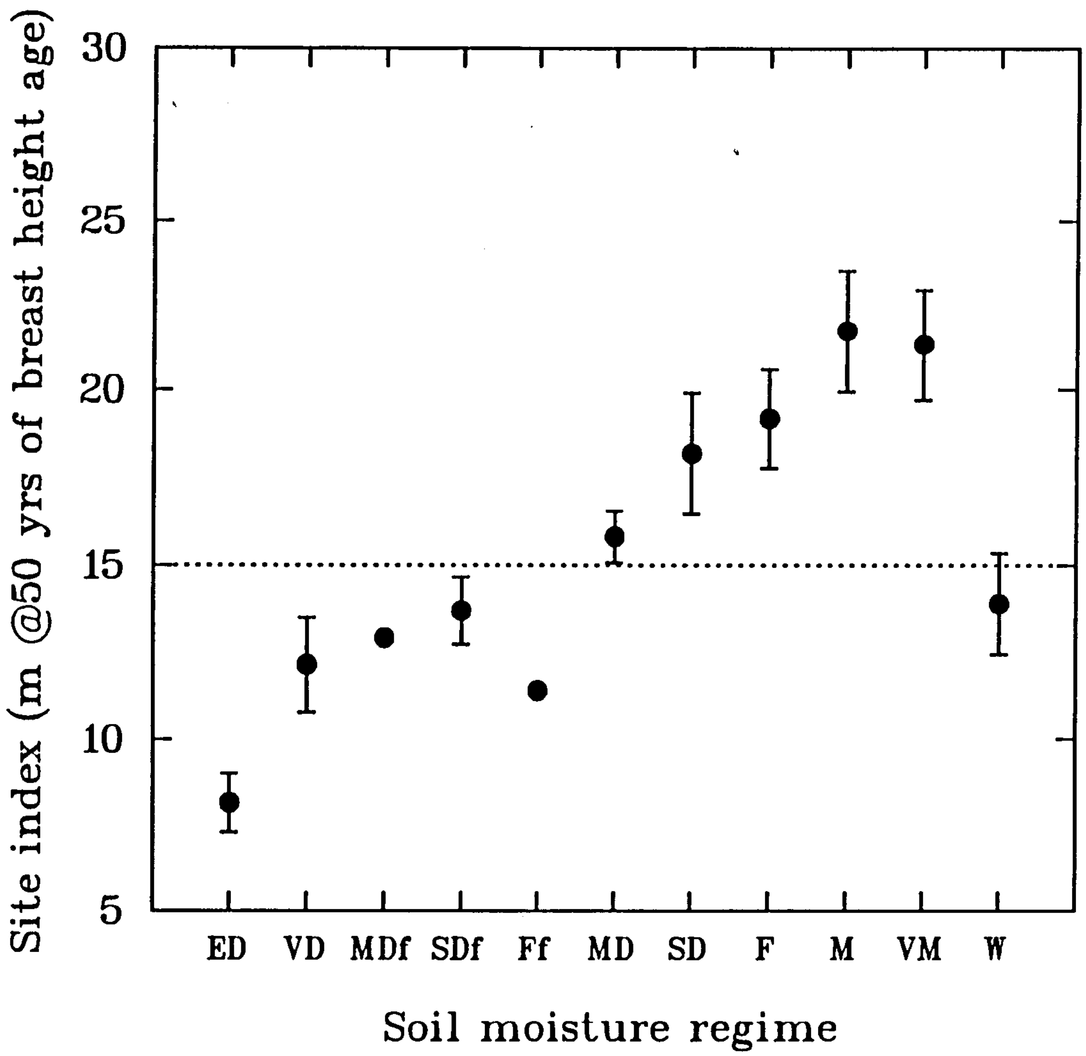

Figure 4.2. Categorical plot of lodgepole pine site index in relation to soil moisture regimes (SMRs). Symbols for SMRs are defined in Table 4.2.

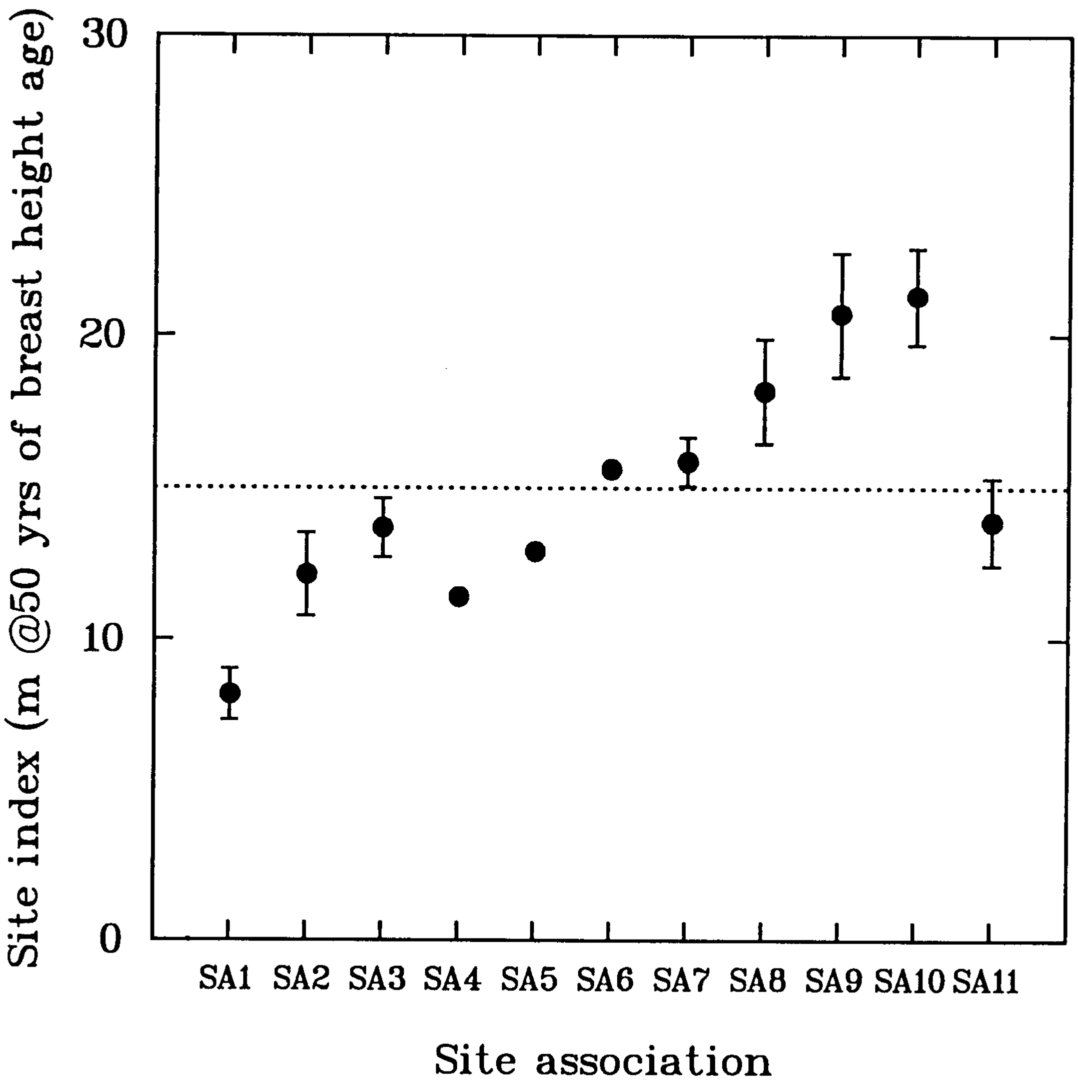

Figure 4.3. Categorical plot of lodgepole pine site index in relation to site associations (SA_i). Symbols for SAs are defined in Table 4.2.

Table 4.4. Models for the regression of lodgepole pine site index on selected vegetation variables. Symbols for all variables are defined in Table 4.2 and 4.3.

---

[1] $SI = 13.529 - 2.909(VU_1) - 1.229(VU_2) + 3.871(VU_3) + 0.151(VU_4) + 3.783(VU_5) + 5.421(VU_6) + 6.534(VU_7) + 8.238(VU_8) + 8.959(VU_9) + 0.0(VU_{10})$

adjusted $R^2 = 0.83$ SEE = 1.68 m n = 72

[11] $SI = 17.263 - 10.165(EVD) - 5.636(VDMD) + 3.965(MDF) + 4.522(FVM) - 7.018(WVW) + 3.558(R)$

adjusted $R^2 = 0.64$ SEE = 2.41 m n = 72

[12] $SI = 17.185 + 0.340(PCA_1) + 0.534(PCA_2) - 0.320(PCA_3) + 0.040(PCA_4) + 0.322(PCA_5) + 0.067(PCA_6) - 0.045(PCA_7) - 0.189(PCA_8) - 0.004(PCA_9) + 0.055(PCA_{10})$

adjusted $R^2 = 0.75$ SEE = 2.00 m n = 72

[13] $SI = 17.185 + 0.340(PCA_1) + 0.534(PCA_2) - 0.320(PCA_3) + 0.322(PCA_5)$

adjusted $R^2 = 0.76$ SEE = 1.97 m n = 72

[14] $SI = 15.709(PCA_1) + 0.651(PCA_2) + 0.996(PCA_4) + 1.228(PCA_5) - 0.983(PCA_8) + 1.096(PCA_9) + 0.919(PCA_{10})$

adjusted $R^2 = 0.45$ SEE = 3.00 m n = 53

[15] $SI = 6.235 + 8.655(LAI) - 1.285(LAI)^2$

adjusted $R^2 = 0.41$ SEE = 3.08 m n = 58

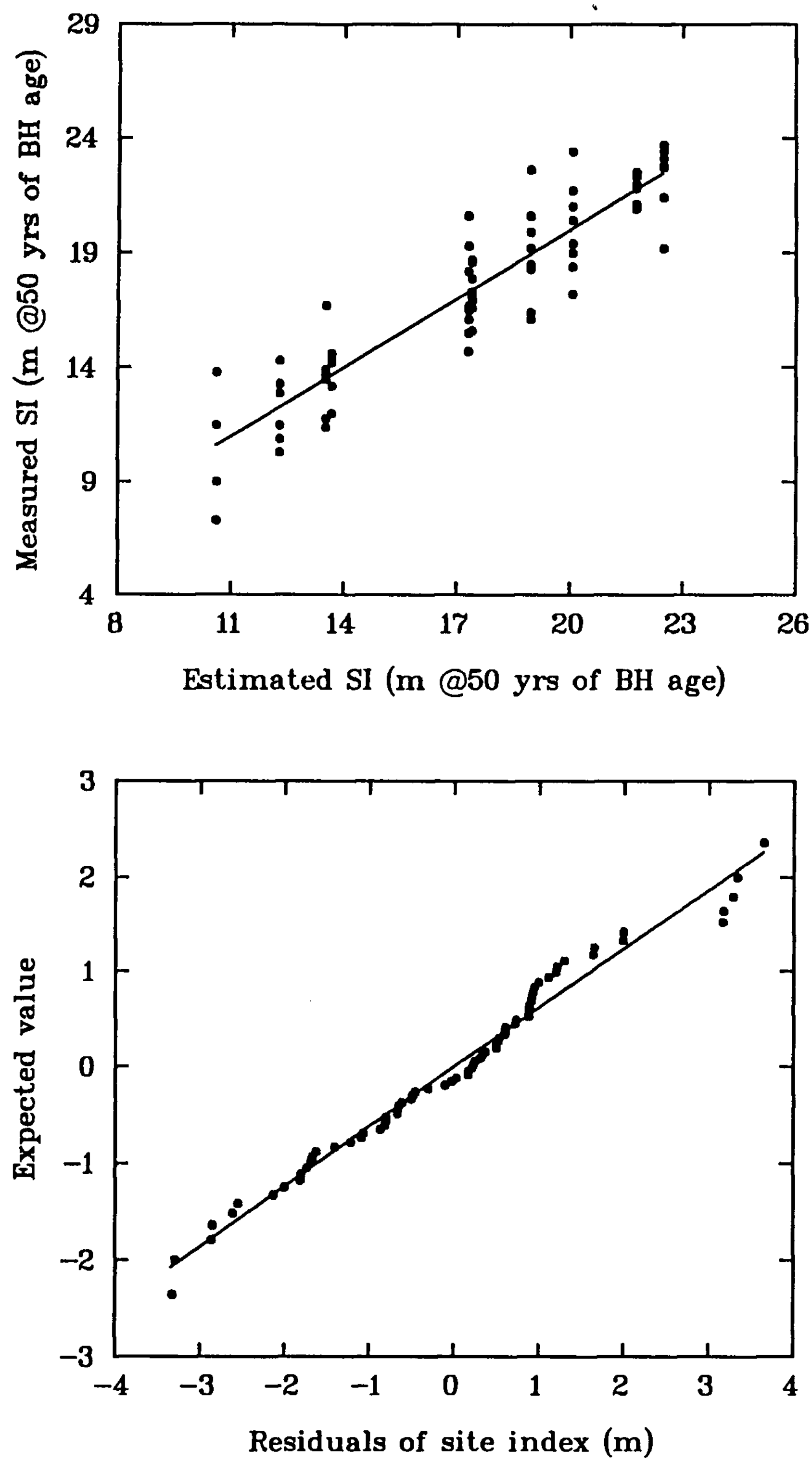

Figure 4.4. Relationship between estimated (VU model, equation [1]) and measured lodgepole pine site index values and probability plot of residuals from regression analysis.

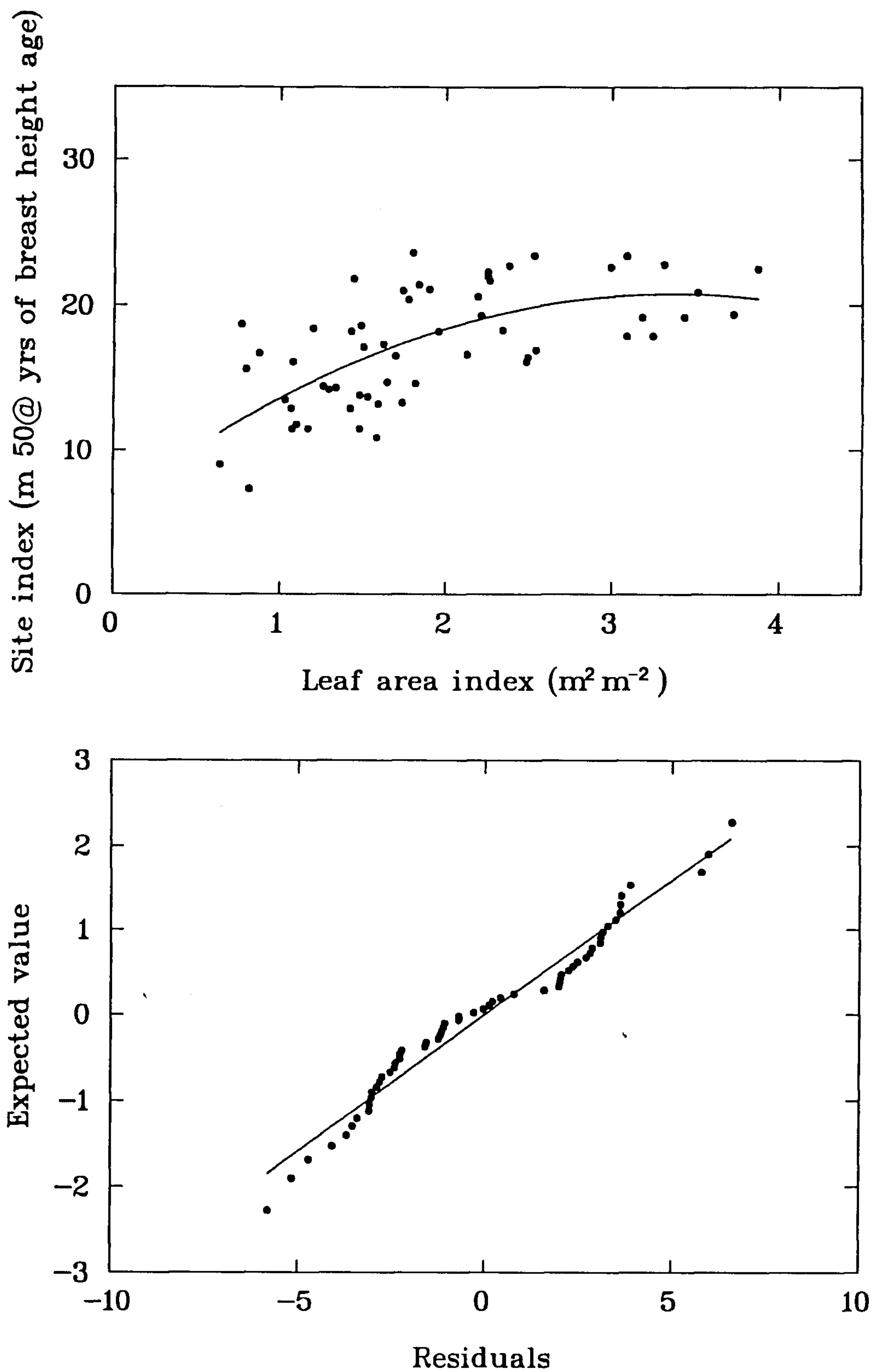

Figure 4.5. Relationship between estimated (LAI model, equation [15]) and measured lodgepole pine site index values and probability plot of residuals from regression analysis.

The PCA_f model (equation [14]), using stepwise selected PCA components (PCA_1, PCA_2, PCA_4, PCA_5, and PCA_6) that accounted for 88% of the total variation in foliar nutrients, explained 45% of the variation in site index.

The categorical models using selected environmental variables (Table 4.5) showed poor to very strong relationships with site index ($0.23 < R^2 < 0.85$). Ranking according to adjusted R^2 and SEE for the three single factor models (equation [2], [3], and [4]), their performance improved in order from the SNR model (equation [4]) to the BGC model (equation [2]) to the SMR model (equation [3], Figure 4.6). The SMR model accounted for the largest proportion of the variation in site index of all nine categorical models examined ($R^2 = 0.84$, SEE = 1.60 m) (Figure 4.7). The performance of the SA model (equation [5]) , SS model (equation [6], Figure 4.8), combined BGC and SMR model (equation [8]), combined SMR and SNR model (equation [9]), and combined BGC, SMR, and SNR model (equation [10], Figure 4.7) were very comparable to that of the SMR model. The combined BGC, SMR, and SNR model (equation [10]) was the best model for explaining lodgepole pine site index in terms of adjusted coefficient of determination ($R^2 = 0.85$) and standard error of estimate (SEE = 1.54 m). Comparison of model performance implies that (1) SNR, as a categorical variable, was found to be significant but did not improve the performance of the models using SMRs, BGCs, or their combination, (2) SMR and BGC exhibit a high collinearity, (3) SMR is the major determinant of lodgepole site index, and (4) more complex SA, SS and combined BGC, SMR, and SNR models do not necessarily produce better results than a simple SMR model.

Table 4.5. Categorical models for the regression of lodgepole pine site index on selected environmental variables (n = 72). Symbols for categorical variables are defined in Table 4.2 and Table 4.3.

---

[2] SI = 19.18 - 7.01(SBPSxc) - 0.95(SBSmc) - 0.00(SBSwk)

adjusted R^2 = 0.52 SEE = 2.80 m

[3] SI = 13.88 - 5.73(ED) - 1.75(VD) - 0.98(MD^f) - 0.20(SD^f) - 2.48(F^f) + 1.92(MD) + 4.30(SD) + 5.29(F) + 7.84(M) + 7.44(VM) + 0.00(W)

adjusted R^2 = 0.84 SEE = 1.60 m

[4] SI = 18.48 - 7.91(VP) - 1.97(P) - 0.46(M) - 0.33(R) - 0.0(VR)

adjusted R^2 = 0.23 SEE = 3.53 m

[5] SI = 11.40 - 3.25(SA_1) + 0.74(SA_2) + 1.50(SA_3) + 4.20(SA_4) + 4.45(SA_5) + 6.78(SA_6) + 9.33(SA_7) + 2.28(SA_8) + 9.92(SA_9) + 0.00(SA_{10}) + 2.48(SA_{11})

adjusted R^2 = 0.81 SEE = 1.74 m

[6] SI = 11.40 - 3.25(SS_1) + 0.74(SS_2) + 1.50(SS_3) + 4.20(SS_4) + 4.45(SS_5) + 6.13(SS_6) + 7.17(SS_7) + 8.02(SS_8) + 9.99(SS_9) + 2.28(SS_{10}) + 8.70(SS_{11}) + 10.53(SS_{12}) + 0.00(SS_{13}) + 3.80(SS_{14}) + 1.83(SS_{15})

adjusted R^2 = 0.84 SEE = 1.64 m

[7] SI = 20.05 - 2.72(VP) - 2.20(P) - 1.23(M) + 0.15(R) + 0.0(VR) - 6.77(SBPSxc) - 1.09(SBSmc) - 0.0(SBSwk)

adjusted R^2 = 0.58 SEE = 2.62 m

[8] SI = 12.12 - 4.75(ED) - 0.762(VD) + 0.00(M^f) + 0.78(VM^f) - 1.5(W^f) + 1.149(MD) + 4.014(SD) + 5.157(F) + 7.409(M) + 7.122(VM) - 0.316(W) + 0.78(BGC_i)

where BGC = 1 for SBPSxc, 2 for SBSmc, and 3 for SBSwk.
adjusted R^2 = 0.85 SEE = 1.58 m

[9] SI = 14.69 -3.89(ED) -0.27(VD) -0.93(MD^f) - 0.33(SD^f) - 3.29(F^f) + 3.25(MD) + 5.46(SD) + 5.84(F) + 8.15(M) + 6.92(VM) + 0.0(W) - 2.65(VP) - 2.29(P) - 1.57(M) - 0.86(R) - 0.0(VR)

adjusted R^2 = 0.84 SEE = 1.60 m

[10] SI = 9.379 - 2.682(ED) + 0.788(VD) + 0.00(M^f) + 0.642(VM^f) - 2.189(W^f) + 2.7663(MD) + 5.114(SD) + 5.67(F) + 7.687(M) + 6.688(VM) - 0.292(W) + 0.689(SNRs) + 0.765(BGC_i)

where SNR = 1 for VP, 2 for P, 3 for M, 4 for R, and 5 for VR; BGC = 1 for SBPSxc, 2 for SBSmc, and 3 for SBSwk.
adjusted R^2 = 0.85 SEE = 1.54 m

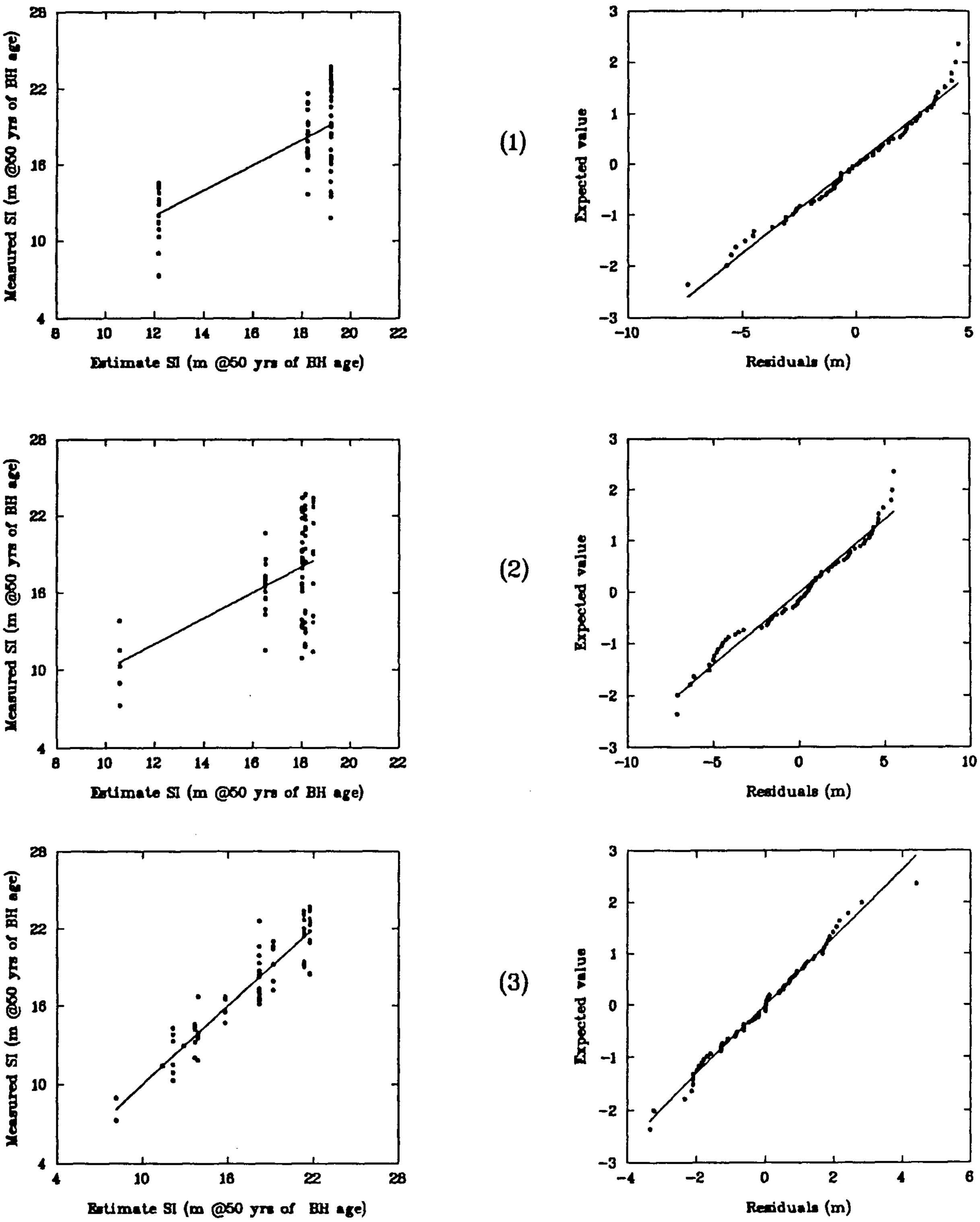

Figure 4.6. Relationship between estimated ((1) BGC model [2], (2) SNR model [4], and (3) SMR model [3]) and measured lodgepole pine site index values and probability plot of residuals from regression analysis.

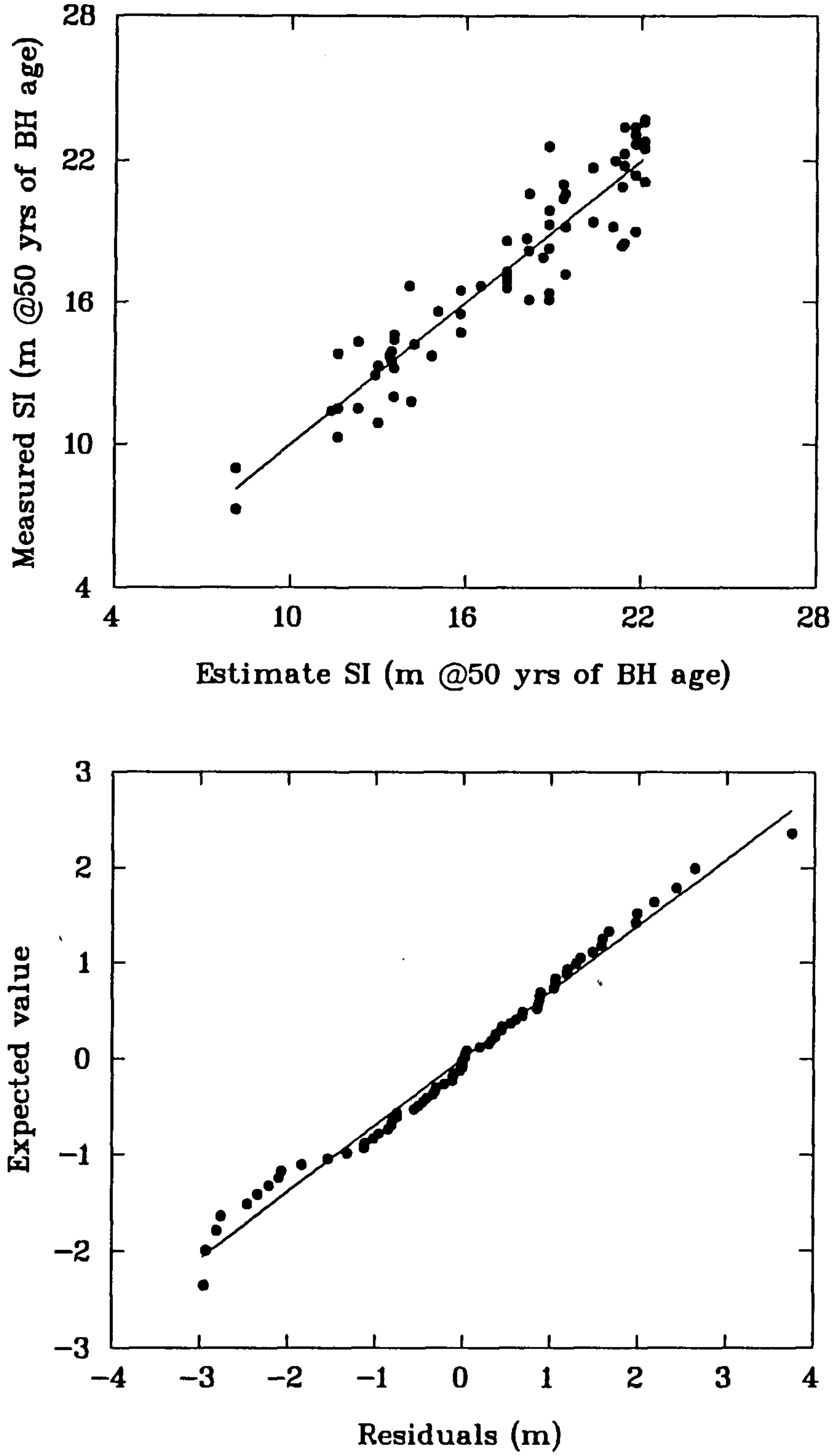

Figure 4.7. Relationship between estimated (combined BGC, SMR, and SNR model [10]) and measured lodgepole pine site index values and probability plot of residuals from regression analysis.

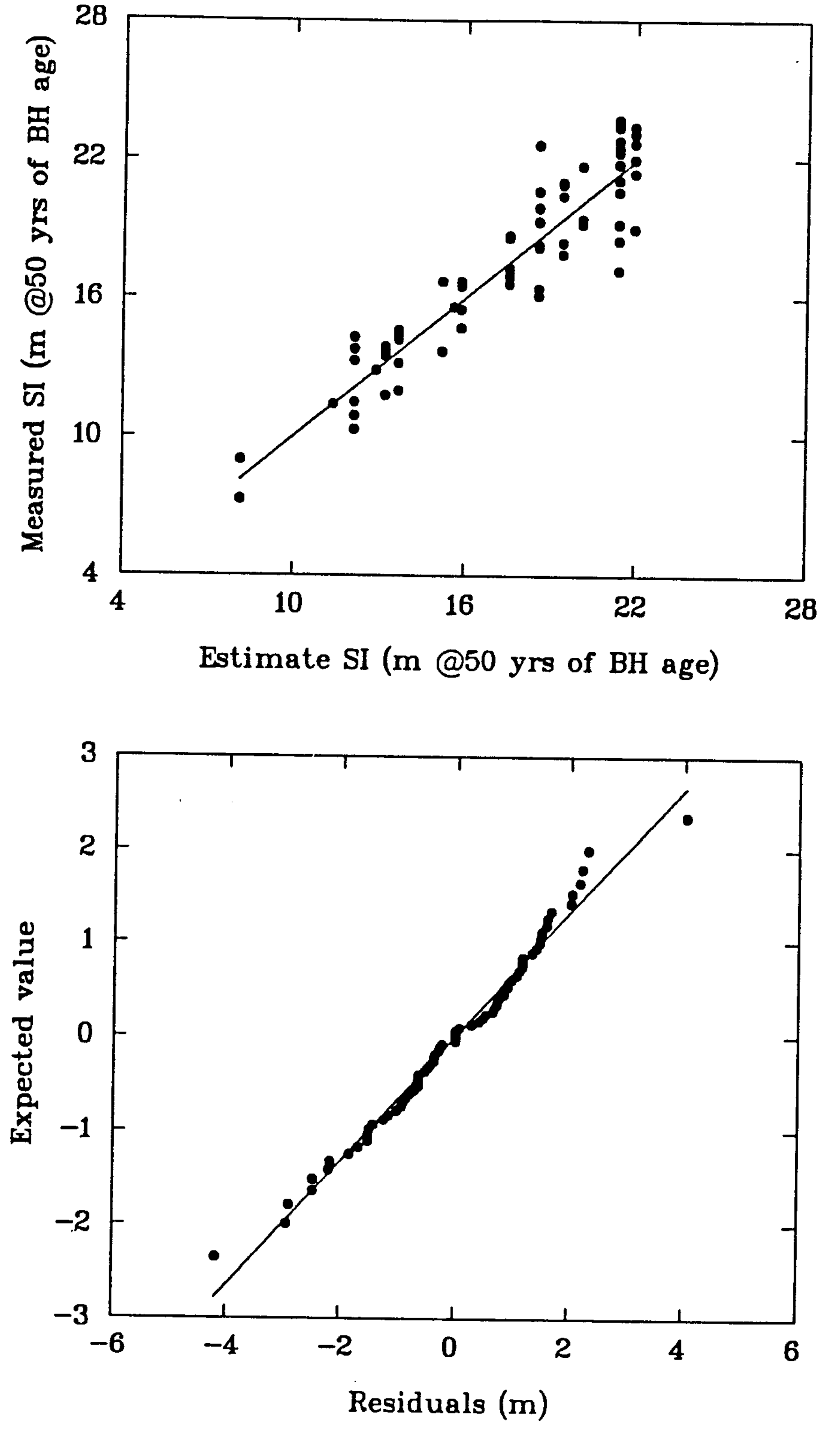

Figure 4.8. Relationship between estimated (SS model [6]) and measured lodgepole pine site index values and probability plot of residuals from regression analysis.

The analytical models using selected environmental variables produced comparable results and trends to the categorical models (Table 4.6). When ranked according to adjusted R^2 and SEE for four single factor models, their performance improved in order from the soil nutrient models (equations [18], [19], and [21]) to the climatic model (equation [16]) to the soil water model (equation [17]). The combined model (equation [27]) had the best fit and accounted for the largest proportion of the variation in site index of all analytical models examined (R^2 = 0.82, SEE = 1.72 m) (Figure 4.9).

As with the comparable categorical variables, analytical soil nutrients showed significant but poor relationships with lodgepole pine site index (Figure 4.9). The models using any of the selected direct soil nutrient measures (mN, SEC and C/N) accounted for less than 35% of the variation in site index. When used with other analytical variables, performance of the resulting models was only marginally improved. In addition, SEC showed a strong collinearity to mN and had no significant relationships with site index in the study (equation [19]) (R^2 = 0.00, SEE = 4.06 m). This indicated that there were no differences in terms of the sum of exchangeable Ca, Mg, and K in the study sites. Lodgepole pine site indices increased without correspondence with SEC because the SEC was rich enough for lodgepole pine growth throughout all the study sites.

The relationship between lodgepole pine site index and mN {equation [18], Figure 4.9(3)} revealed that site index did not increase with increasing mN across the complete mN gradient, but reached a maximum as mN approached approximately 63 kilograms per hectare. Continuously increasing soil nitrogen does not necessarily promote lodgepole pine height growth or productivity [Figure 4.9 (3)].

Table 4.6. Analytical models for the regression of lodgepole pine site index on selected environmental variables (n = 72). Symbols for analytical variables are defined in Table 4.2 and 4.3.

[16] $SI = -706.01 + 3.181(PET) - 0.003(PET^2)$

adjusted $R^2 = 0.52$ SEE = 2.80 m

[17] $SI = 3.64 + 0.034(DGW) + 14.78(Dummy)$

adjusted $R^2 = 0.62$ SEE = 2.50 m

[18] $SI = 7.509 + 10.908log(mN) - 2.511[log(mN)]^2$

$R^2 = 0.28$ SEE = 3.43 m

[19] $SI = 16.845 + 0.105log(SEC)$

$R^2 = 0.00$ SEE = 4.06 m

[20] $SI = 18.462 + 5.687log(mN) - 2.785log(SEC)$

adjusted $R^2 = 0.32$ SEE = 3.34 m

[21] $SI = 35.30 - 11.19log(mC/N)$

$R^2 = 0.35$ SEE = 3.28

[22] $SI = 36.47 - 1.25log(fC/N) - 10.67log(mC/N)$

adjusted $R^2 = 0.33$ SEE = 3.30

[23] $SI = -692.199 + 3.126(PET) - 0.003(PET)^2 + 2.23log(mN)$

adjusted $R^2 = 0.57$ SEE = 2.65 m

[24] $SI = -687.554 + 3.108(PET) - 0.003(PET)^2 + 0.026(DGW) + 11.35(Dummy)$

adjusted $R^2 = 0.79$ SEE = 1.85 m

[25] $SI = 0.64 + 0.03(DGW) + 14.20(Dummy) + 2.77log(mN)$

adjusted $R^2 = 0.69$ SEE = 2.25 m

[26] $SI = 5.02 + 3.42log(mN) - 1.43log(SEC) + 0.03(DGW) + 13.46(Dummy)$

adjusted $R^2 = 0.70$ SEE = 2.19 m

[27] $SI = -702.504 - 3.179(PET) - 0.004(PET)^2 + 0.025(DGW) + 11.615(Dummy) + 1.826log(mN)$

adjusted $R^2 = 0.82$ SEE = 1.72 m

[28] $SI = -610.288 + 2.703(PET) - 0.003(PET)^2 + 0.024(DGW) + 11.073(Dummy) + 1.869log(SEC)$

adjusted $R^2 = 0.82$ SEE = 1.72 m

[29] $SI = -656.058 + 2.939(PET) - 0.003(PET)^2 + 0.024(DGW) + 11.365(Dummy) + 1.104log(mN) + 0.98log(SEC)$

adjusted $R^2 = 0.82$ SEE = 1.71 m

[30] $SI = 17.185 + 0.667(PCA_1) - 0.764(PCA_2) - 0.695(PCA_4) + 0.650(PCA_5) + 2.412(PCA_6)$

adjusted $R^2 = 0.44$ SEE = 3.03 m

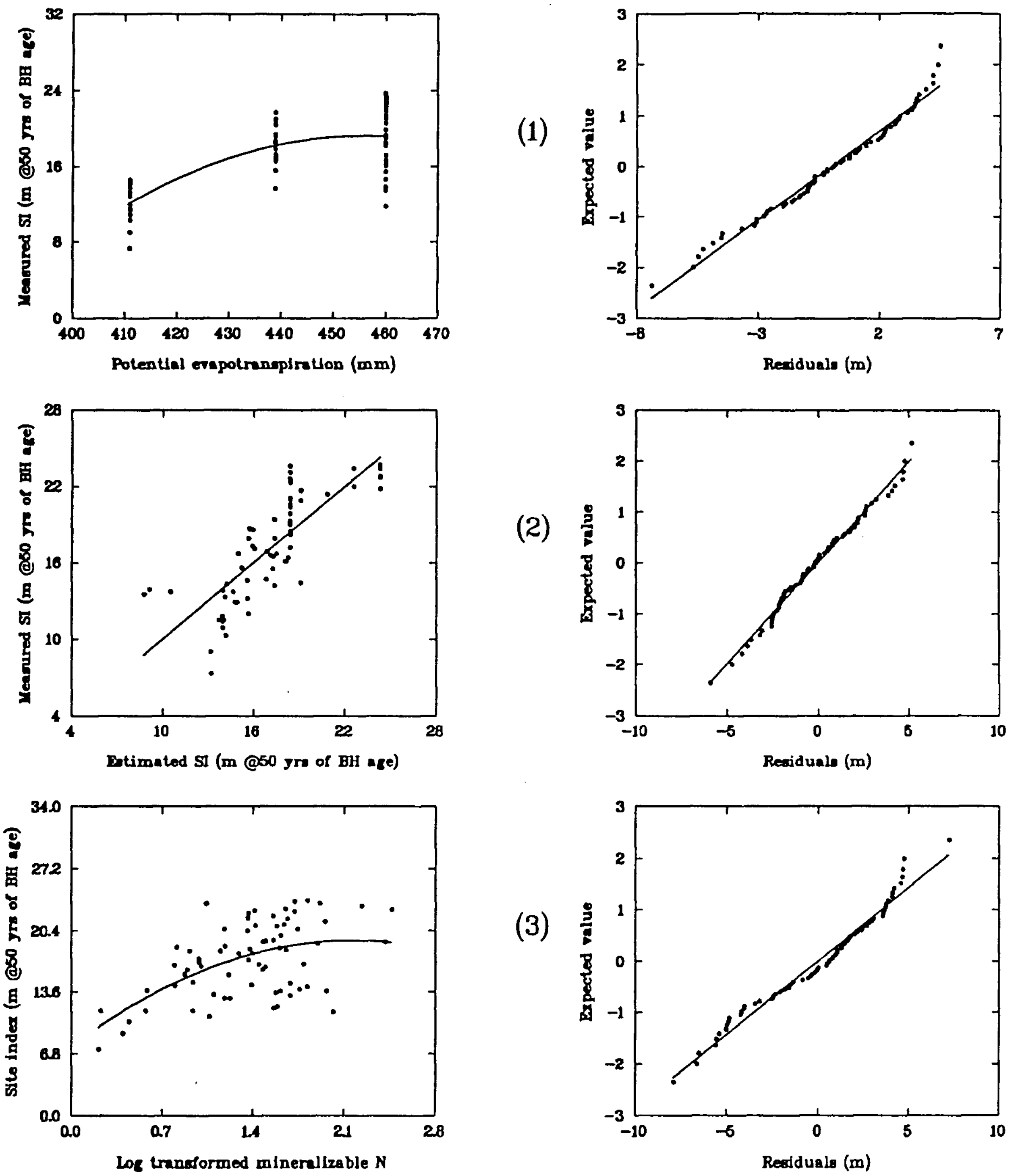

Figure 4.9. Relationship between estimated (PET model [16], DGW model [17], and mN model [18]) and measured lodgepole pine site index values and probability plot of residuals from regression analyses.

Comparing the analytical to the categorical models, the PET model (Figure 4.9, equation [16]) and the BGC model (equation [2]) showed identical performance (R^2 = 0.52, SEE = 2.80 m), the DGW model (equation [17], Figure 4.9) was inferior (R^2 = 0.62) to the SMR model (equation [3]), and the combined PET, DGW, and mN model (equation [27], Figure 4.9) was similar (R^2 = 0.82, SEE =1.72 m) to the SMR model (equation [3]) (R^2 = 0.84, SEE = 1.60 m) or the combined BGC, SMR, and SNR model (equation [10]) (R^2 = 0.85, SEE = 1.54 m). Thus, two relatively simple direct measures of climate and soil water appear to be sufficient to explain a large amount of the variation in site index in the study plots.

The PCA_s model (equation [30]), using stepwise selected PCA components (PCA_1, PCA_2, PCA_4, PCA_5, and PCA_6) which accounted for 91% of the total variation in soil nutrients, explained 44% of the variation in site index. The first PCA component (PCA_1), which was highly correlated to mN, N_t, C_t, S_t, and P_t, explained 60% of the total variation. Relating the soil nutrient PCA model (equation [30], Table 4.6) to the foliar nutrient PCA model (equation [15], Table 4.5), the former showed almost identical fit (R^2 = 0.44, SEE = 3.03 m) as did the later (R^2 = 0.45, SEE = 3.00 m). This implies that soil and foliar nutrients appear to play the same role and contribute the same value in evaluating lodgepole pine site index or productivity.

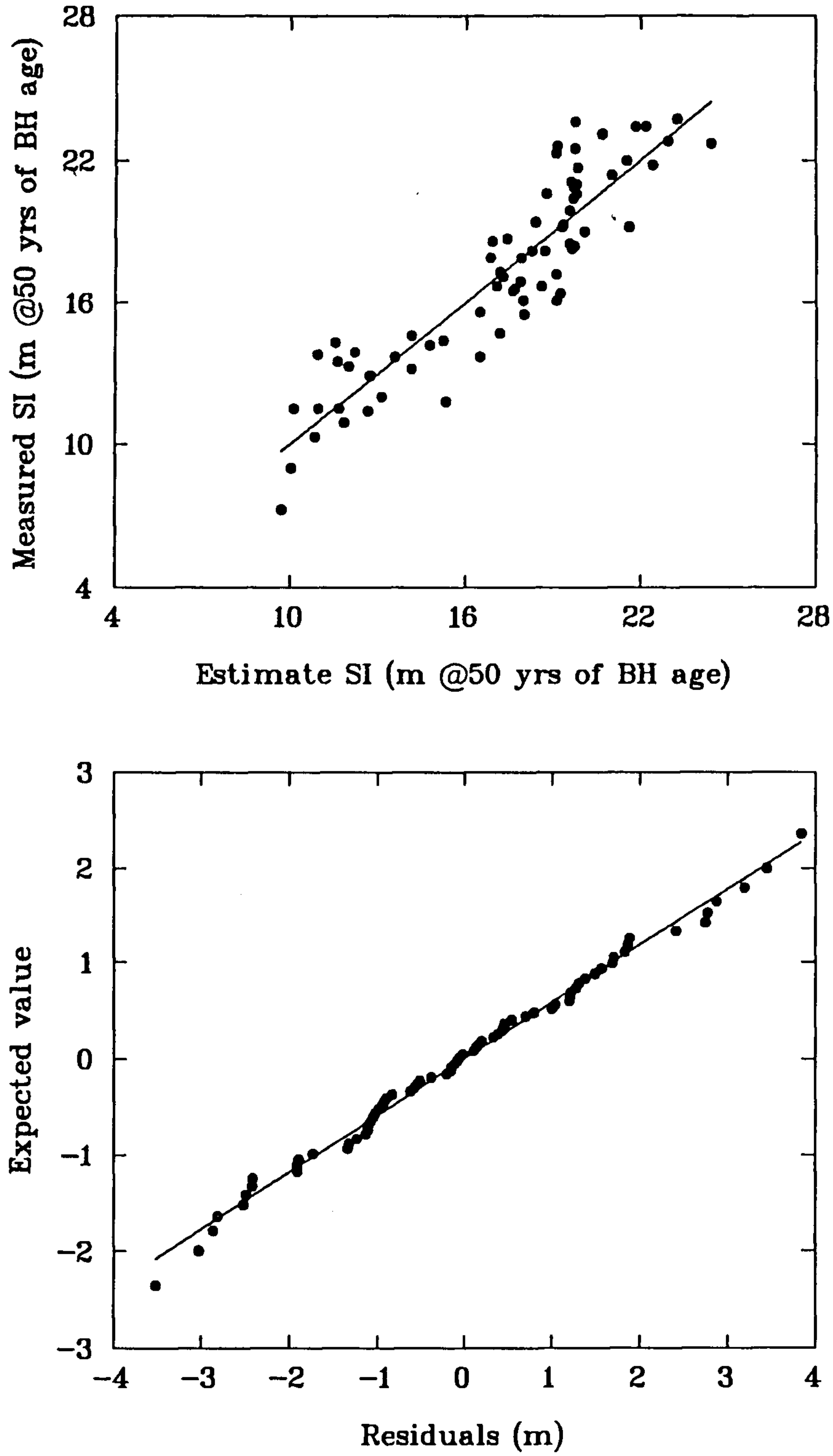

Figure 4.10. Relationship between estimated (combined PET, DGW, and mN mode [27]) and measured lodgepole pine site index values and probability plot of residuals from regression analysis.

4.4. Discussion

Klinka and Carter (1990) suggested that it is possible to use a simple conceptual model—*site index = f (heat, soil moisture, soil nutrients, soil aeration)*—for investigating growth-site relationships under certain assumptions. Despite a limited representation of climates and some combinations of SMRs and SNRs, the large amount of variation in site index explained by this model revealed the presence of strong relationships between lodgepole pine site index and selected measures of ecological site quality, using either categorical or analytical and indirect or direct measures. Indirect measures of heat, soil moisture and soil nutrients had good relationships with their direct measures. However, it was necessary to recognize and characterize soil moisture conditions featuring fluctuating water table. The results obtained for lodgepole pine conformed well with those reported for Douglas-fir in the Very Dry and Dry Maritime Coastal Western Hemlock subzones by Green *et al.* (1989), Carter and Klinka (1990), and Klinka and Carter (1990), and a few studies involving lodgepole pine (Illingworth and Arlidge 1960, Duffy 1964, Youngberg and Dahms 1970, Mason and Tigner 1972, Mogren and Dolph 1972, Corns and Pluth 1984).

How does lodgepole pine productivity measured by site index vary with ecological site quality? It is clear that lodgepole pine' productivity increases with increasing potential evapotranspiration in British Columbia, *i.e.*, from cool to warm climates. Krajina (1969) concluded that the potential for the most productive lodgepole pine growth is in the Coastal Western Hemlock and Interior Western Hemlock zones. Within montane boreal climates, the productivity will be lower than in cool mesothermal and temperate climates, and the productivity gradient will coincide with a growing-season temperature gradient, presumably reflected by zonal classification. Biogeoclimatic subzones, eventually variants, provide a first order of site stratification, while soil moisture and nutrient regimes provide a second and third order, respectively.

The ecological amplitude of lodgepole pine in relation to a soil moisture gradient is very wide; it extends from excessively dry through wet sites (e.g., Krajina 1969, Lotan and Perry 1983, Cochran 1985, Burns and Honkala 1990). This study showed that the rate of increase in site index from excessively dry to moist and the rate of decrease from moist to wet sites was evidently higher than the rate of change along a soil nutrient gradient (Figures 4.11, 4.12, and 4.13).

Surprisingly, little is known about lodgepole pine nutrient relations (e.g., Krajina 1969, Lotan and Perry 1983, Cochran 1985). Some studies have shown no or weak relationships between soil nutrient levels and growth (e.g., Holmes and Tackle 1962, Duffy 1964), whereas others claimed significant responses to nitrogen fertilization (Sander 1966, Etter, 1969, Cochran 1975, Weetman *et al.* 1985). On the basis of this study, it is suggested that lodgepole pine is a relatively low demanding species for nitrogen to maintain its growth level within given climatic and soil moisture conditions.

In all three subzones, the most productive growth occurred on moist and nutrient-very rich sites (Figures 4.14, 4.15, and 4.16). This finding differs from the proposition of Krajina (1969) who suggested that the most productive sites are nutrient-rich, and that nutrient-very rich sites do not support lodgepole pine growth. It is suggested that this discrepancy is due to the difference in characterizing the soil nutrient gradient and differentiating soil nutrient regimes between this study (*cf.* Chapter 3) and Krajina (1969). Krajina considered nutrient-very rich sites to have not only high available-N levels but also to be Ca-rich, with pH > 6 in the surface mineral soil horizon. It appears that lodgepole pine is absent

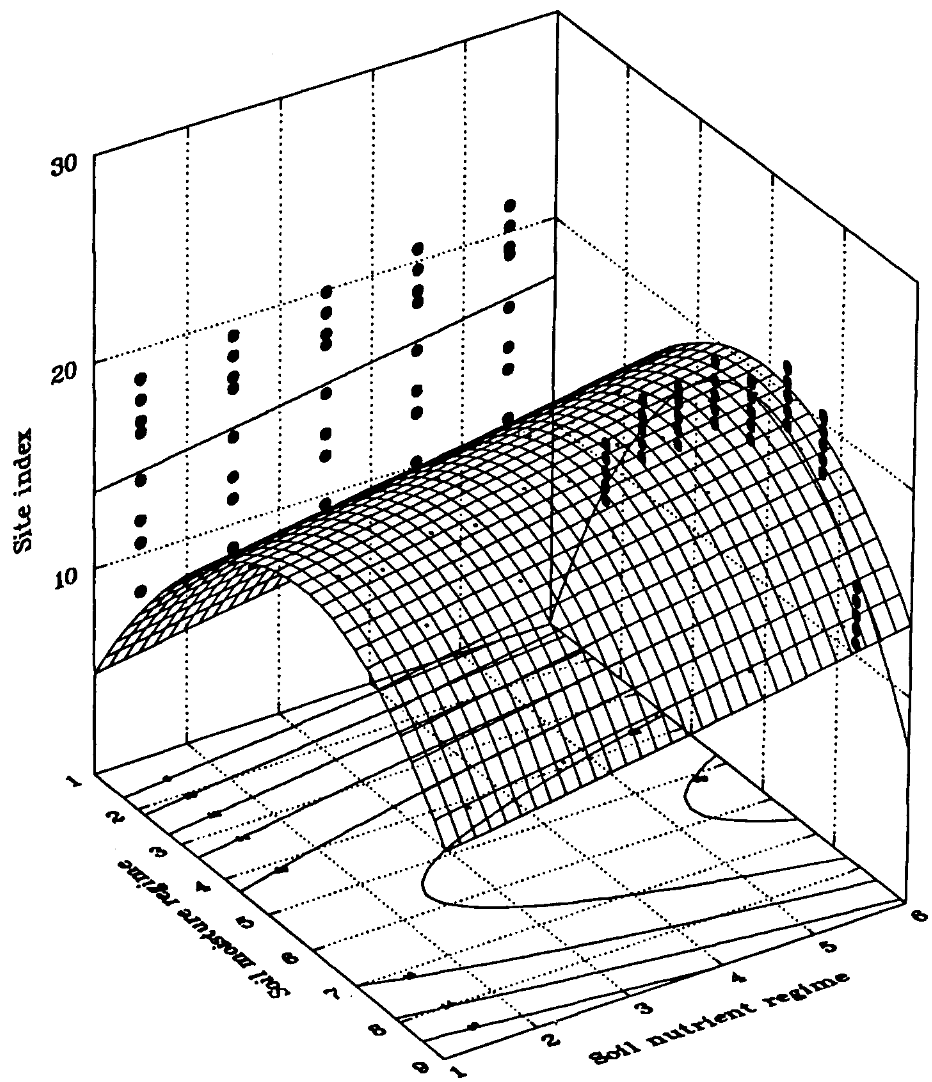

Figure 4.11. Response surface showing the relation between estimated lodgepole pine site index, soil moisture regime, and soil nutrient regime in the SBPSxc subzone using equation [10]. Symbols for soil moisture regimes and soil nutrient regimes are defined in Table 4.2.

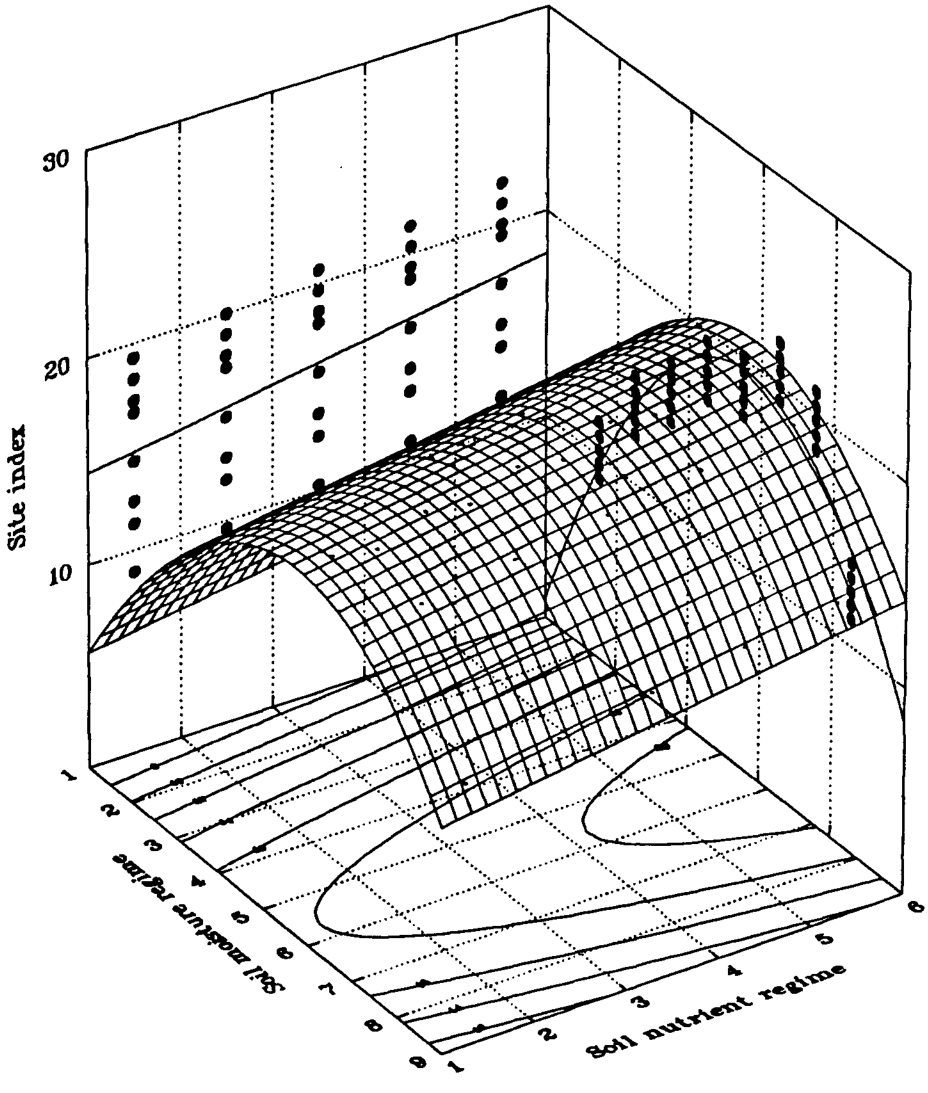

Figure 4.12. Response surface showing the relation between estimated lodgepole pine site index, soil moisture regime, and soil nutrient regime in the SBSmc subzone using equation [10]. Symbols for soil moisture regimes and soil nutrient regimes are defined in Table 4.2.

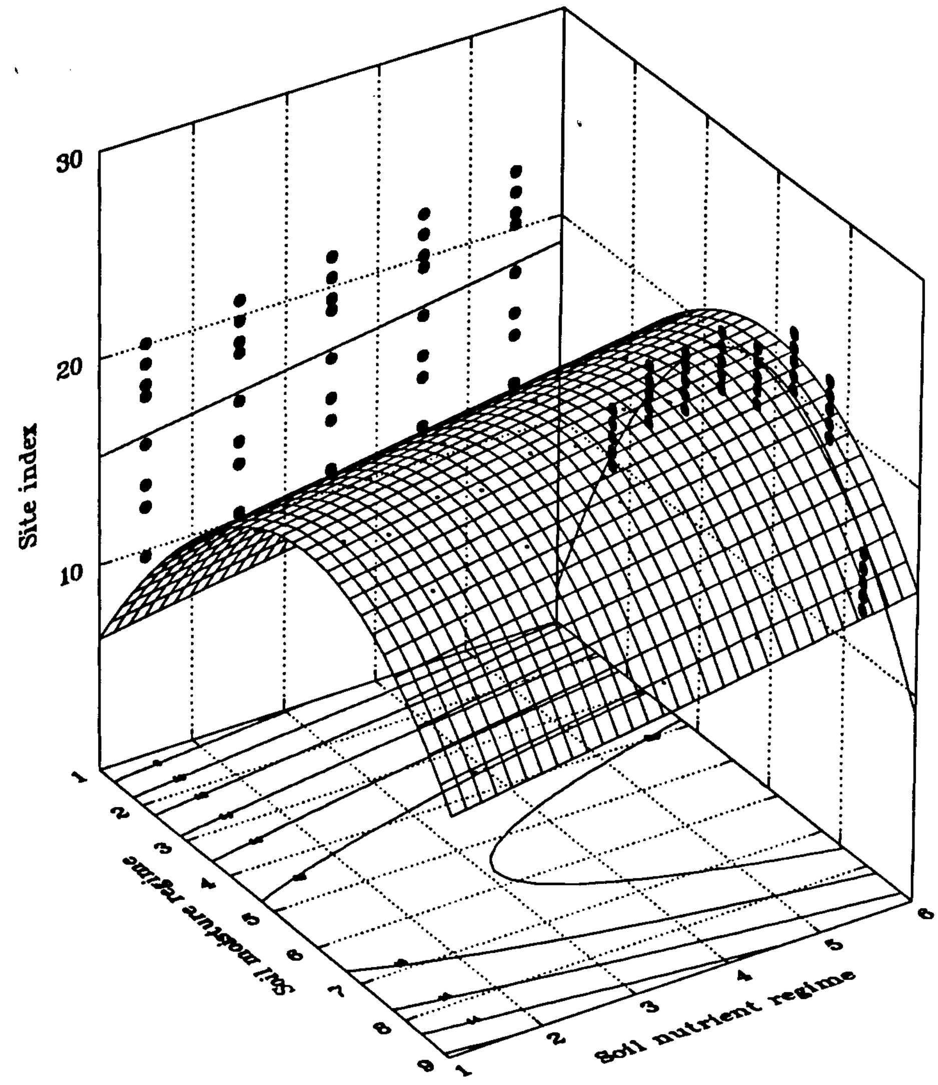

Figure 4.13. Response surface showing the relation between estimated lodgepole pine site index, soil moisture regime, and soil nutrient regime in the SBSwk subzone using equation [10]. Symbols for soil moisture regimes and soil nutrient regimes are defined in Table 4.2.

on alkaline soil with pH approaching 8 (Cochran 1985).

Implementation of site-specific management requires good information on forest productivity. With biogeoclimatic ecosystem classification in place, and relationships between site index and ecological site quality analyzed, it is possible to use the models developed to estimate lodgepole site index. The analytical models should be most useful in determining the effects of environmental change on forest growth, whereas categorical models should be appropriate for operational applications. Considering the wide usage of edatopic grids and SMRs and SNRs in site identification, it is proposed that site index estimated by the combined BGC, SMR, and SNR model (equation [10]), and plotted for each subzone onto an edatopic grid (Figures 4.14, 4.15, and 4.16), represents both an effective means and format for predicting site index for any given site by forestry personnel. Although the site series model (equation [6]) is also suitable, it simply assigns the estimated mean site index for a given site series to a stand that falls within that site series, regardless of the SMR and SNR present.

The application of the combined model requires site diagnosis, *i.e.*, stratification of a given area into component ecosystems, examination of each component, and site identification according to basic ecological site qualities (biogeoclimatic unit, SMR, and SNR). In British Columbia, this is being done routinely prior to making any silviculture decision.

This model should be tested and validated using an independent data set to evaluate its performance and portability. If justified, it should be further developed using an expanded data base, including a climatically wider range of lodgepole pine ecosystems.

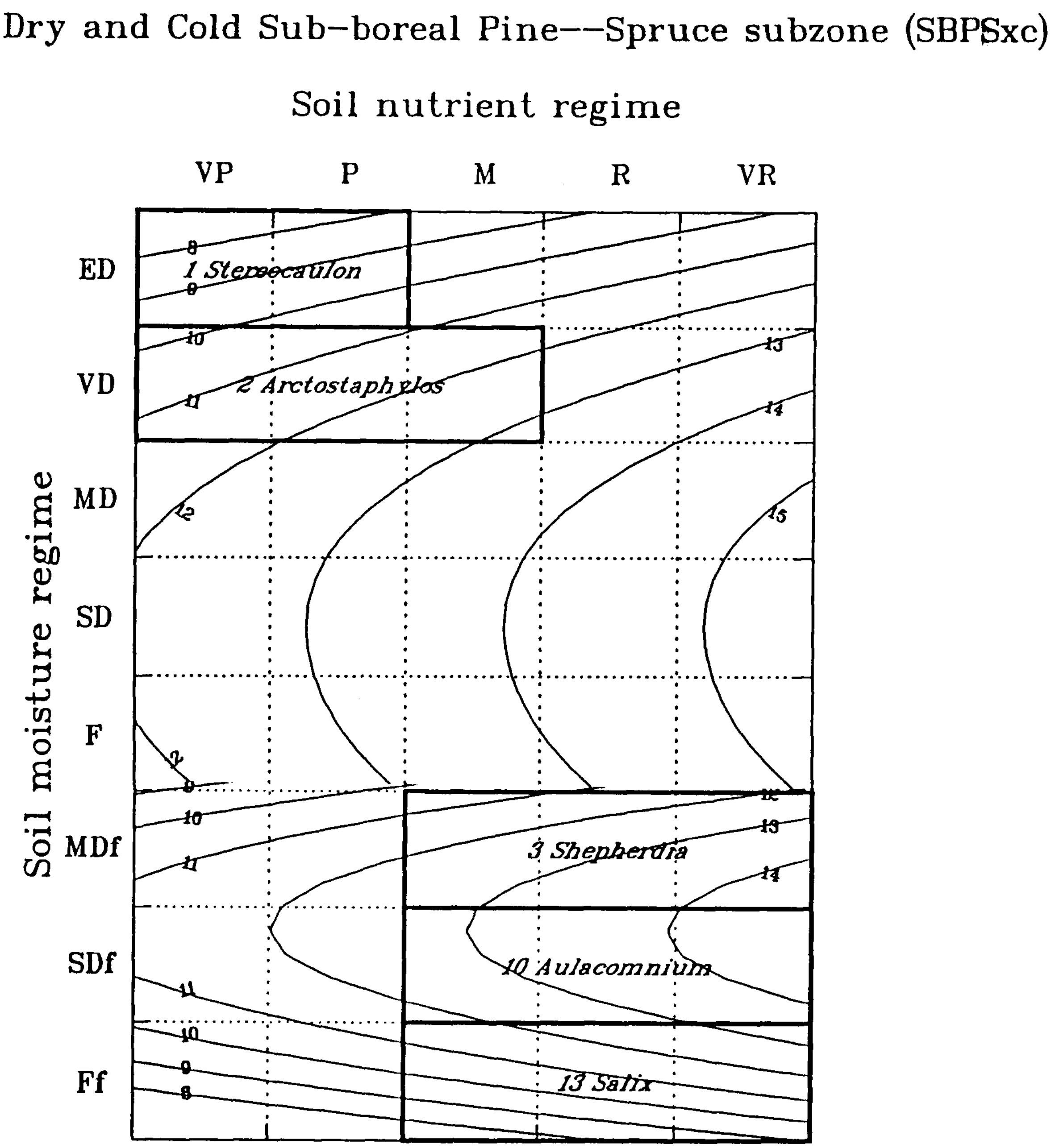

Figure 4.14. An edatopic grid showing SBPSxc site series (1, 2, 3, 10, and 13) and lodgepole pine site index isolines calculated from equation [10] and fitted using a distance weighted least squares smoothing algorithm. Symbols for site series, soil moisture regimes, and soil nutrient regimes are defined in Table 4.2.

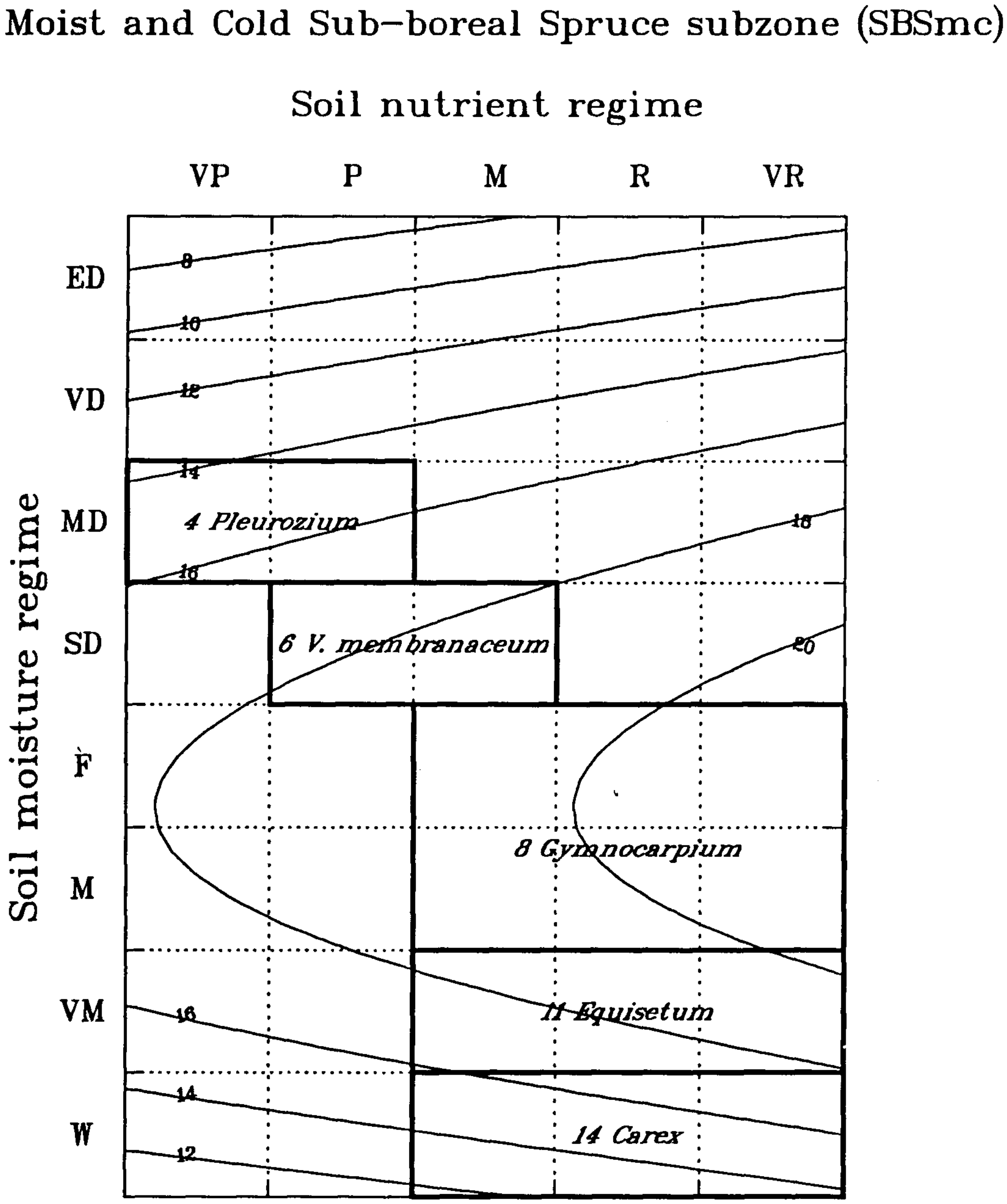

Figure 4.15. An edatopic grid showing SBSmc site series (4, 6, 8, 11, and 14) and lodgepole pine site index isolines calculated from equation [10] and fitted using a distance weighted least squares smoothing algorithm. Symbols for site series, soil moisture regimes, and soil nutrient regimes are defined in Table 4.2.

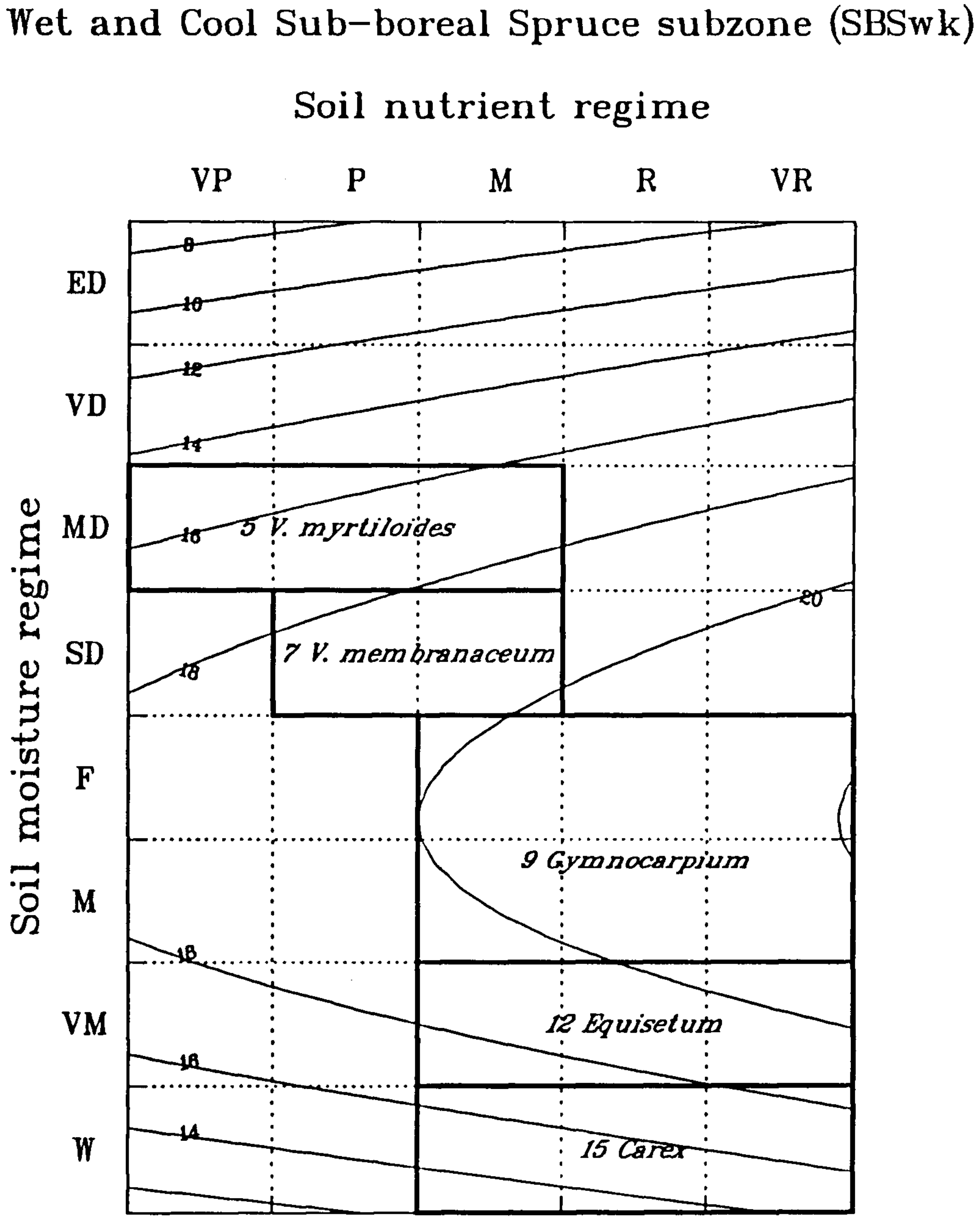

Figure 4.16. An edatopic grid showing SBSwk site series (5, 7, 9, 12, and 15) and lodgepole pine site index isolines calculated from equation [10] and fitted using a distance weighted least squares smoothing algorithm. Symbols for site series, soil moisture regimes, and soil nutrient regimes are defined in Table 4.2.

4.5. Conclusions

Regression analysis demonstrated that several selected measures of ecological site quality were strongly related to lodgepole pine site index in the study area. The most useful categorical variables were vegetation unit, soil moisture regime, site association, and site series. The most useful analytical variables were potential evapotranspiration, water deficit, and the depth of water table or the gleyed soil horizon. Soil nutrient variables, although significant, were poorly related to site index. Understory vegetation in early-seral lodgepole pine stands was found to be a good indicator of ecological site quality, and soil moisture regime was considered to be most strongly related to the variation in lodgepole pine site index. In order to estimate lodgepole pine productivity on sub-boreal sites, the use of the soil moisture regime, site association, or site series model is recommended when age and height measurements are not appropriate; however, testing of these models over a wider range of sites is needed.

5. SITE SPECIFIC HEIGHT GROWTH MODELS BASED ON STEM ANALYSIS AND MEASURES OF ECOLOGICAL SITE QUALITY

5.1 INTRODUCTION

The prediction of forest growth and future yields is central to forest science and forest management. This study is centered on the relationship between height growth and ecological site quality in order to establish a strong link between biogeoclimatic ecosystem classification and growth and yield studies. In British Columbia, the biogeoclimatic ecosystem classification system is used to recognize and characterize ecologically different sites for the application of different silvicultural treatments. Site index is used as a measure of productivity and to predict height growth of tree species on different sites. As the ecological quality of a site determines the growth performance or productivity of a particular tree species on that site, it would therefore seem profitable to relate site index to ecological site quality. The presence of strong relationships would mean that (a) there is an ecological basis for estimating site index and height growth, (b) ecological variables could be used to estimate site index and growth more precisely than can be done at present, and (c) the effects of environmental changes, including management practices, on site productivity could be better understood, evaluated, and predicted.

In Chapter 4, it was shown that several selected measures of ecological site quality were strongly related to site index, with soil moisture being the major determinant. This chapter focuses on height growth and addresses the central question: does the pattern of lodgepole pine height growth change with ecological site quality?

Height growth of plants can be described by a growth function. As most factors affect height growth randomly, the growth process is also random. The growth of a given species changes as random factors and time change. Random factors in this case can be defined as site attributes, such as climate, soil moisture, and soil nutrients, which are the primary factors that directly affect growth. As a result, the height growth rate will change with changes in ecological site quality and time. Thus, early growth will be faster and later growth will be slower on some sites than on others (Hall 1987, 1989). This suggests that the height at an arbitrary age (such as site index) might not give the best measure of site productivity for a given tree species. Therefore, it is necessary to develop tree species-specific and site-specific height growth models in order to precisely describe the patterns of height growth over time on different sites. Despite some previous attempts documented in the literature (e.g. Carmean 1970, Monserud 1984), site-specific height growth modelling has not yet been fully developed. This may be due to a lack of useful and easily obtainable measures of ecological site quality and a lack of cooperation between biometricians and ecologists.

The specific objectives of the research reported in this chapter are (1) to quantitatively describe height growth of the study stands and (2) to develop site-specific height growth curves for the different sites recognized by biogeoclimatic ecosystem classification. These objectives were accomplished by: (1) selecting a model for describing the height growth of each stand, (2) examining the effect of site index and ecological variables on the performance of the selected model, (3) choosing the most effective concomitant variable(s) for the growth model, (4) computing site-specific curves for describing the height growth of immature sub-boreal lodgepole pine stands, and (5) comparing the site-specific approach to the existing site index approach for height growth modelling. The data and results of the previous chapters were used and extended to address the above objectives.

5.2. Literature Review

General reviews of the methodology of site quality evaluation and height growth modelling were given by Jones (1969), Carmean (1975), Hägglund (1981), and Clutter *et al.* (1983). The idea that height growth varies with site and time resulted in the concept of polymorphic growth curves. A number of attempts have been made to describe the patterns of height growth of different tree species, using variables such as stand density, height at a given age (*i.e.*, site index), and/or early growth rate.

Site index is commonly used to construct polymorphic height growth curves. One of the assumptions underlying the use of site index is that if tree heights for a given species are the same at index age then they should have the same growth rate at different ages regardless of the ecological quality of the site on which they grow. This has led to site index controlling the shape of height growth curves (Beck 1971, Graney and Burkhart 1973, Trousdell *et al.* 1974, Monserud 1984). However, this assumption may or may not be true because trees may grow faster or slower in earlier or later ages on different sites, but they may reach the same height at a certain age. Site index as a single indicator of height growth (one point system; Zeide, 1978) may not truly describe the pattern of height growth, and the site index driven height growth model may overestimate or underestimate height growth before or after the index age for different sites. To deal with this problem, vegetation or site variables have been used to modify the height growth curves—a site-specific growth modelling approach. For example, Cajander and Ilvessalo (1921) related major site types to Scots pine growth and stated that the difference in tree growth rates resulted from the difference in productivity potential of site-types. In North America, Carmean (1956) used soil physical properties to modify Douglas-fir site index curves, and constructed site-specific height growth curves for different soil groups. After working on the relationships between height growth and site properties (soil and topography) for several species, Carmean (1970) concluded that soil and topography were the specific features that usually related to polymorphic height growth patterns. By using habitat types as concomitant variables in his height growth model for Douglas-fir, Monserud (1984) concluded that the habitat types could determine the shape of both height growth and site index curves. However, he still used site index as a variable to control curve shape within each habitat type in his model. As habitat types represent a relatively wide range in ecological site quality (Pfister and Arno, 1980), the habitat type height growth model might not be able to precisely describe height growth. Goudie (1984) adopted a similar approach for lodgepole pine by stratifying forest sites into two categories: dry (upland) and wet (wetland). This study used his model for comparison.

The height growth modelling efforts described above were unable to accurately determine the growth patterns anywhere besides index age due to a lack of appropriate ecological variables and of the knowledge how these variables affect site index. Site index does account for part of the variation in height growth curves, but a serious bias could occur when they are used for estimating the growth before or after index age. The one point system does not really explain polymorphic growth patterns.

In 1978, Zeide proposed a two-point system for approximating height growth curves. This system is a method of estimating growth patterns from sequential observations of height and age. The assumption of the two-point system is that site index as one-point in approximating growth curves is not sufficient to determine the curve suitable for a given stand; however, two points are sufficient. The two-point system assumes that if different stands have the same growth values at any two ages (two points), the values for these stands will be the same at any other age (other points). In other words, growth curves may intersect only once.

Milner (1987a, b) concluded that Zeide's two-point system is an accurate method of approximating height growth curves. He found that the index of curve shape, Z, was a useful attribute in assessing the applicability of the published site curves to a local population and the shape of the height growth curve was not correlated with site index. Although the two-point system addresses the major weakness of the site index system, it still remains unreliable as the growth rate is assumed to be consistent over entire life period of the tree. This may not be the case due to changes in environmental factors.

Strub and Sprinz (1987) developed a piece-wise linear growth equation that defined the shape and trend of height growth curves to support their claim that both anamorphic and polymorphic models are not flexible enough to describe the shape of the height-age relationship. Although it addressed the major weaknesses of anamorphic and polymorphic models, the piece-wise linear approach brought in new theoretical difficulties. It is known that as age increases, plants consistently reduce their growth rate or growth performance before maximum growth is reached. Therefore, there is no real linear relationship existing within any time interval before the maximum, no matter how many segments are approximated.

Eis *et al.* (1982) used third degree polynomials to fit lodgepole pine and white spruce height growth curves using mean growth values for each of three vegetation-inferred sites. Their model illustrated a linear relationship in terms of the parameters estimated. As pointed out above, a linear model may approximate model parameters very well statistically, but does not meet the biological assumption that plant growth will reach its maximum at infinity.

5.3. Materials and Methods

Examination of lodgepole pine height growth was based on 95 trees from 40 sample plots. Eighteen stands of the total of 36 in the Bowron River sampling area (SBSwk subzone) were less than 40 years breast height age (b.h.a.), and 14 stands in the Anahim Lake (SBPSxc subzone) and the Burns Lake (SBSmc subzone) sampling areas were less than 40 years b.h.a. These stands were too young to estimate accurately the height at the site index age of 50 years b.h.a. (Goudie 1984) and were excluded from the following stem analysis.

The sample plots were located in even-aged, immature, lodgepole stands with a relatively narrow range in age (between 40 and 70 years b.h.a.) and stocking, with a similar history of establishment and development, and without a history of damage. The study plots were chosen to represent the widest possible range of lodgepole pine stands in relation to soil moisture and nutrient gradients within three regional climates in central British Columbia.

Three well-formed dominant trees, without any evidence of physical damage and disease symptoms, were selected in each of the 40 sample plots for stem analysis. The trees were felled and measured for the total height, and discs were cut at 0.3, 0.6, and 1.3 m and at 1 m intervals thereafter. The age of each disc was determined by counting rings in the laboratory.

The study area, and methods of sample plot location, site description, vegetation and soil sampling, site index determination, soil physical and chemical analysis, foliar analysis, soil moisture analysis, vegetation and site classification, and indicator plant analysis were described in Chapter 3.

Ecological analysis (Chapter 3) identified and computed values for a number of variables which were used as independent variables in regressions against lodgepole pine site index in Chapter 4. The categorical and continuous variables that showed a strong relationship to site index were adopted as concomitant variables in models describing lodgepole pine height growth (Table 5.1).

Carmean's (1972) method of estimating the true height corresponding to a particular year was used to correct heights at each section, as it was considered to be the most accurate of the techniques available (Dyer and Bailey 1987). This procedure is based on the assumption that sectioned points will fall in the middle of the annual leaders. Thus, by adding one-half the estimated length of the annual leader to the sectioned height, the bias can be removed. The formula is expressed as follows:

[5.3.1] $$H_{ij} = \frac{h_i + (h_{i+1} - h_i)}{2(r_i - r_{i+1})} + \frac{(j - 1)(h_{i+1} - h_i)}{r_i - r_{i+1}}$$

where H_{ij} = corrected height at the *i*th section and the *j*th ring, h_i = uncorrected total height at the *i*th section, r_i = the number of growth rings at the *i*th section, i = 1,2, ... ,n, j = 1,2, ... ,r, and n = the number of sections. Since my only interest was the true height at each sectioning point, (*i.e.*, the first ring at each section), the term **j** was always equal one and the last term of the formula was zero. Consequently, the formula actually used in this study was:

[5.3.2] $$H_{i1} = \frac{h_i + (h_{i+1} - h_i)}{2(r_i - r_{i+1})}$$

Table 5.1. Synopsis of the ecological variables used in the height growth models and stratified according to expression (categorical or continuous).

CATEGORICAL VARIABLES

BGC_i - biogeoclimatic subzones from 1 through 3; 1 = SBPSxc, 2 = SBSmc, and 3 = SBSwk

SMRs - soil moisture regimes from ED through W; ED = excessively dry, VD = very dry, MD = moderately dry, SD = slightly dry, F = fresh, M = moist, VM = very moist, W = wet, MD^f = moderately dry to moist, SD^f = slightly dry to very moist, and F^f = fresh to wet

SNRs - soil nutrient regimes from VP through VR; VP = very poor, P = poor, M = medium, R = rich, and VR = very rich

Combination of BGC_i, SMRs, and SNRs

SA_i - site associations from 1 through 11; 1 = *Stereocaulon*, 2 = *Arctostaphylos*, 3 = *Shepherdia*, 4 = *Pleurozium*, 5 = *Vaccinium myrtiloides*, 6 = *V. membranaceum*, 7 = *Gymnocarpium*, 8 = *Aulacomnium*, 9 = *Equisetum*, 10 = *Salix*, and 11 = *Carex*

SS_i - site series from 1 through 15; 1 = SBPSxc/*Stereocaulon*, 2 = SBPSxc/*Arctostaphylos*, 3 = SBPSxc/*Shepherdia*, 4 = SBSmc/*Pleurozium*, 5 = SBSwk/*V. myrtilloides*, 6 = SBSmc/*V. membranaceum*, 7 =SBSwk/*V.membranaceum*, 8 = SBSmc/*Gymnocarpium*, 9 = SBSwk/*Gymnocarpium*, 10 = SBPSxc/*Aulacomnium*, 11 = SBSmc/*Equisetum*, 12 = SBSwk/*Equisetum*, 13 = SBPSxc/*Salix*, 14 = SBSmc/*Carex*, 15 = SBSwk/*Carex*

CONTINUOUS VARIABLES

PET - potential evapotranspiration (mm)

DGW - the depth of soil water table (W_d) (mm), the depth of soil gleying horizon (G_d) (mm), or soil water deficiency (Δ_w) (mm)

mN - soil mineralizable nitrogen (kg/ha)

Combination of PET, DGW, and mN

Individual tree height-age curves were plotted and checked for evidence of early suppression or top damage in order to avoid the use of abnormal trees in modelling. Twenty-five trees out of the total of 120 trees initially analyzed were not used in any further analysis because of evidence of early suppression or damage. In order to reduce the potential noise caused by suppression in very early growth stages, the modelling was based on breast height age.

Site index was defined as the average height of three dominant trees on a plot at 50 years b.h.a., calculated for each stand using the heights obtained from stem analysis. A linear extrapolation technique was employed for determining height at 50 years b.h.a. when the age was less than 50.

Paired height and age were used to compute the average height growth for each stand. The Chapman-Richards growth function (Richards, 1959; Chapman, 1961; Pienaar and Turnbull, 1973) was chosen to fit the height growth data:

[5.3.3] $$H = \beta_1(1 - e^{-\beta_2 A})^{\beta_3} + \varepsilon,$$

where H = total height (m), A = age at breast height (years), e = base of natural logarithm, ε = error of the model, and β_1, β_2, and β_3 = parameters of the model to be estimated. This function was initially derived from Von Bertalanffy's (1951) anabolic-catabolic growth function. Most of the other growth functions appear to be different forms of the Chapman-Richards equation (Pienaar and Turnbull, 1973). The logistic (Verhulst), monomolecular (Mitscherlich), and Gompertz growth functions (Richards, 1969) can all be considered as special cases of the Chapman-Richards function. Obviously, the Chapman-Richards growth function has a great flexibility in describing growth of organisms, and parameter changes in the Chapman-Richards equation are not expected to produce greatly different results.

The parameter prediction method described by Clutter *et al.* (1983) was used to develop the parameter prediction equations using selected ecological variables (Table 5.1) and/or site index.

To support the use of ecological variables in the modelling system, a dummy variable approach (Cunia 1973, Habgood 1985) was used to test whether the ecological variables could significantly improve the performance of the parameter prediction equations. Consequently, to derive ecologically based polymorphic height growth models that would precisely describe the shape of the height growth curves, selected measures of ecological site quality (Table 5.1) were examined for each stand in relation to parameters estimated for the model (equation [5.3.3]). For comparison, the relationship between site index and the function parameters were also examined. The generalized prediction equations were as follows:

[5.3.4] $\beta_1, \beta_2, \beta_3 = f(\text{ecological factors, site index}),$

where ecological factors were either categorical variables or continuous variables (Table 5.1).

The variables that showed the highest correlations with the parameters were then substituted into equation [5.3.3] to produce a site-specific height growth model. By examining the curve shapes, similar curves from adjacent sites were combined in order to simplify the modeling system.

Current and mean annual height increments were computed for each site unit using equation [5.3.3]. Graphical determination and residual analysis were used to verify and validate the model performance. The effect of density on height growth was examined by checking for correlation between site index and the number of stems per hectare using a graphical method.

As Goudie's (1984) height growth model for lodgepole pine is driven by site index and the model developed in this study is driven by ecological variables, the performance of the two models was compared. To compare the growth rate in relation to ecological site quality, physiological growth parameters derived from Von Bertalanffy's anabolic-catabolic function (1951) were calculated for different site units.

All data analyses were done by using the Quattro Pro (Borland International Inc. 1989) spreadsheet package and the NLIN (nonlinear) and MGLH (multiple general linear hypothesis) modules of the SYSTAT (Wilkinson 1990) statistical package. All graphs were drawn using SYGRAPH module of SYSTAT.

5.4 Results and Discussion

5.4.1. Averaging Height Growth Data

Average growth curves were constructed for each of the 40 sample plots using equation [5.3.3]. The results are summarized in Table 5.2. The mean value of the index of determination (I^2) was 0.998 and the standard error of estimate was 0.522 m. Thus, the function appeared to provide an appropriate means to summarize the lodgepole pine height growth data.

For ecologically different sites, the asymptotic value (b_1) and the growth rate (b_2), and the shape (b_3) will likely not be the same. Therefore, there appears to be an opportunity to relate the model parameters to variables representing the ecological quality of forest sites.

Table 5.2. A summary of average growth curves for each of the 40 sample plots.

Plot#	b.h.a.	Parameter estimated b_1	b_2	b_3	I^2	Corrected I^2	SEE (m)
4	46	22.7	0.04	1.48	1	0.999	0.234
5	46	37.3	0.01	1.02	0.999	0.996	0.379
7	48	40.7	0.01	1.12	1	0.999	0.131
10	48	29.5	0.02	1.07	1	0.999	0.192
11	50	26.8	0.02	1.27	1	0.998	0.254
12	51	26.1	0.02	0.98	0.998	0.990	0.456
13	52	20.9	0.02	1.04	0.998	0.984	0.599
14	53	40.7	0.01	0.98	0.999	0.997	0.337
15	48	40.4	0.01	1.33	1	0.999	0.119
16	52	29.6	0.02	1.19	0.999	0.996	0.403
17	50	28.9	0.02	1.16	0.997	0.997	0.649
19	49	22.0	0.02	1.18	0.999	0.996	0.262
20	48	20.2	0.02	1.15	1	0.997	0.213
21	46	9.52	0.04	1.48	0.999	0.995	0.188
22	49	19.1	0.01	0.91	1	0.998	0.119
23	49	30.5	0.01	1.11	1	0.998	0.178
24	48	30.7	0.01	1.02	1	1	0.109
26	45	32.0	0.01	1.46	1	0.999	0.710
27	48	25.6	0.01	0.95	0.999	0.996	0.217
29	41	21.3	0.02	1.38	0.999	0.997	0.164
31	46	22.3	0.02	1.57	0.999	0.997	0.172
36	40	19.3	0.02	1.10	0.999	0.994	0.238
55	67	25.6	0.03	1.57	0.999	0.996	0.441
56	64	27.3	0.03	1.52	0.997	0.985	0.936
57	70	22.0	0.04	1.45	0.998	0.991	0.652
58	73	22.4	0.04	1.57	0.998	0.987	0.805
59	68	16.7	0.04	1.64	0.998	0.989	0.546
60	68	43.7	0.02	1.23	0.999	0.995	0.609
61	71	19.5	0.03	1.29	0.996	0.978	0.770
62	72	27.7	0.04	1.56	0.998	0.991	0.778
63	73	35.8	0.02	1.08	0.999	0.993	0.694
64	73	23.8	0.03	1.09	0.997	0.984	0.790
65	72	27.3	0.03	1.34	0.997	0.986	0.889
66	73	19.9	0.04	1.57	0.992	0.960	1.235
67	72	31.7	0.03	1.47	0.998	0.992	0.755
68	73	27.2	0.03	1.48	0.997	0.985	0.941
69	46	11.2	0.05	1.83	0.994	0.870	1.387
70	70	19.8	0.04	1.42	0.991	0.949	1.362
71	75	22.0	0.03	1.53	0.997	0.986	0.619
72	71	37.8	0.02	1.34	0.997	0.986	1.003

5.4.2. Height Growth and Stand Density

Relationships between site index and the number of stems per hectare were examined to determine the possible effect of stand density on height growth (Figure 5.1). The number of stems per hectare was the only measure of stand density collected in the study.

According to the concept of ecological equivalence, even-aged stands that belong to the same site unit have the same or similar growing conditions and, hence, they are expected to have the same or similar site index, assuming similar history of establishment and growth. Thus, by comparing the variation in site index between stands of the same site series and similar age, the effect of density on site index can be evaluated. Visual analysis of Figure 5.1 gives no evidence of any consistent relationships between site index and number of stems per hectare for any site unit. Therefore, density as a factor was not included in further analysis.

Height growth of most tree species is generally considered to be relatively independent of stand density over a wide range of density and amount of foliage, except at extremely narrow spacings (Oliver and Larson 1990). The height growth of some pines, including lodgepole pine, was found to be affected by stand density at extremes, particularly by overcrowding (e.g., Alexander *et al.* 1967, Oliver 1967, Carmean 1975, Clutter *et al.* 1983). By stratifying 20 year-old lodgepole pine stands near Williams Lake in B.C. into four density classes, Roydhouse *et al.* (1985) found that stagnation may begin at stand densities between 20,000 and 50,000 stems per hectare. In contrast, the present maximum density in the study plots ranged from 3,300 to 8,200 stems per hectare—far below the values reported by Roydhouse *et al.* (1985).

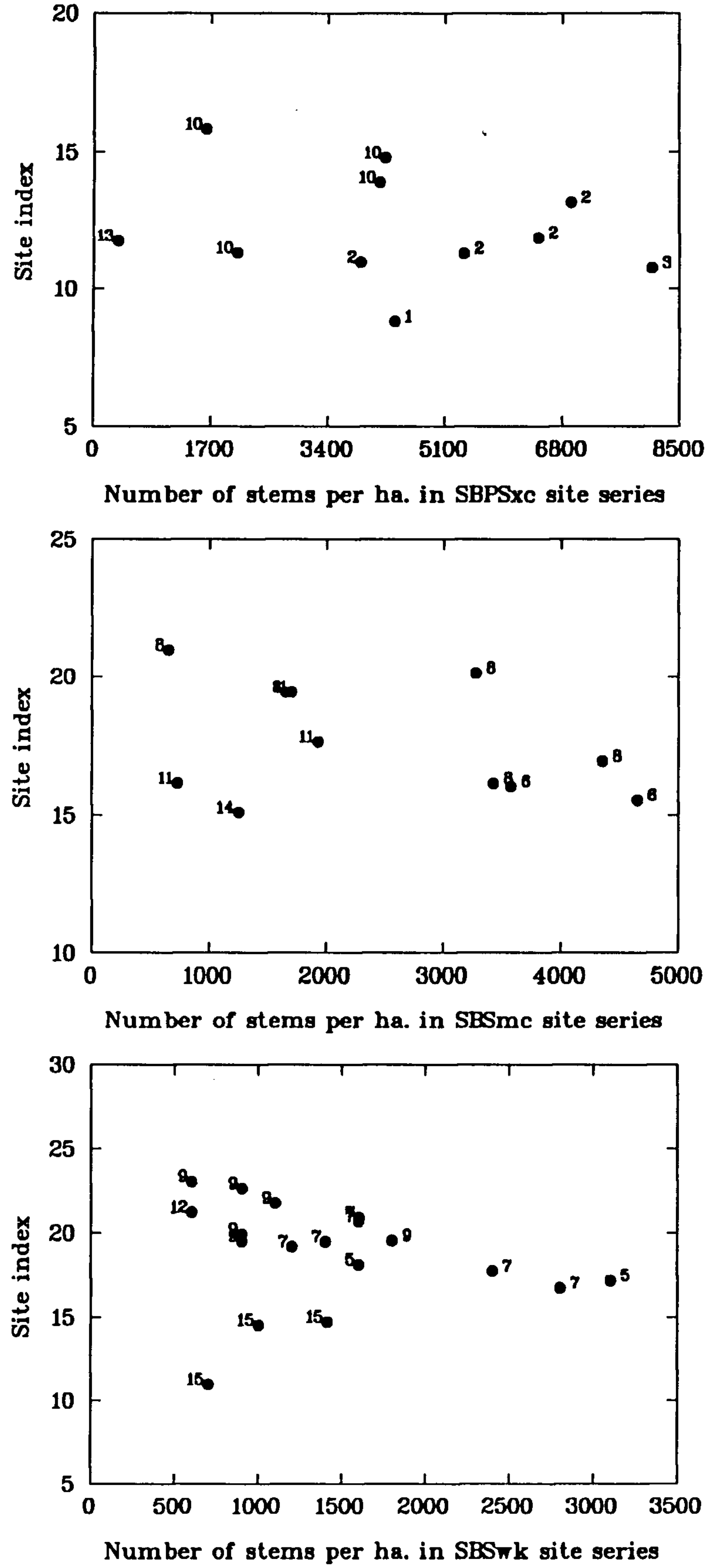

Figure 5.1. Relationships between site index and number of stems per hectare for each stand and site series, according to biogeoclimatic subzones. Symbols for site series are defined in Table 5.1.

5.4.3. Height Growth in Relation to Ecological Variables and Site index

Using Cunia's (1973) method, four linear regression models were fitted for each of the three parameters using the site units and site index as independent variables (Appendix II). Three hypotheses were tested: (1) both intercepts and slopes together are not significantly different, (2) intercepts are not significantly different, and (3) slopes are not significantly different. The results (Table 5.3) showed that, at the 0.05 level, (1) both intercepts and slopes together were not significantly different in relation to b_1, but significantly different in relation to b_2 and b_3; (2) intercepts alone were not significantly different in relation to any parameters; (3) slopes were not significantly different in relation to b_1, but significantly different in relation to b_2 and b_3. It was expected that ecological variables would not improve the model performance in terms of the intercepts because the curves started with a similar point in all cases. Ecological variables were highly related to the slopes that control the curve shapes. This relationship indicated that the use of ecological variables in height growth modelling is necessary and important in order to precisely describe the curve shapes.

Plots of the height growth curves for each site series showed affinities and differences in curve shapes. Affinities were observed between climatically and edaphically closely related site series, the differences were obvious among climatically or edaphically contrasting site series, even when the heights at 50 years of b.h.a., were the same (Figure 5.2).

The shapes of the height growth curves on very dry sites [*Arctostaphylos* site series (SS2)] and wet sites [*Salix* site series (SS13)]) in the SBSxc subzone were different, yet the value of measured actual site index (11.3 m) was the same for both site series [Figure 5.2(A)]. Consequently, using site index in a one-point

Table 5.3. Testing for site index in relation to the parameters estimated for the Chapman-Richards growth function using regressions with site units as dummy variables. Site units were defined in Table 5.6.

Hypothesis	Parameter	DF	Calculated F	Critical F ($\alpha = 0.05$)
1. Both Intercepts and slopes are the same	b1	15,21	1.26	2.18
	b2	15,21	3.11	2.18
	b3	15,21	2.27	2.18
2. Intercepts are the same	b1	7,21	0.45	2.49
	b2	7,21	1.27	2.49
	b3	7,21	1.10	2.49
3. Slopes are the same	b1	8,21	0.36	2.42
	b2	8,21	2.92	2.42
	b3	8,21	6.35	2.42

height growth model will introduce bias for either site. It would be reasonable to suggest that using site index alone in the parameter prediction approach is inappropriate in situations where height growth curves have the same site index but different shapes.

The shapes of the height growth curves on very moist and nutrient rich sites in the SBPSxc, SBSmc, and SBSwk subzones were different for each site series involved [*i.e.*, SBPSxc/*Aulacomnium* (SS10), SBSmc/*Equisetum* (SS11), and SBSwk/*Equisetum* (SS12)] [Figure 5.2(B)]. This was particularly true for the SS10 site series, whereas the curves for the SS11 and SS12 site series were quite similar. The extent of these differences parallels the pattern in climatic differences between the subzones (Table 2.1).

To determine ecological factors that are highly related to the parameters estimated for the Chapman-Richards growth function, parameter prediction equations were developed using both site index alone and selected measures of ecological site quality (Table 5.1). The coefficients of determination and standard errors of estimation from the parameter prediction models were used to determine which of the ecological variables had the strongest relationships with the parameters (Table 5.4).

Similar to the results obtained in Chapter 4, the combination of BGC_i, SMRs, and SNRs (ecotope), site series, and the combination of PET, mN, and DGW, were found to have the strongest relationships to all three curve parameters. It was decided to proceed with testing site series and ecotopes as concomitant variables in a site-specific height growth model since the continuous variables (PET, mN, and DGW) are appropriate for models studying the effect of environmental changes on forest productivity, but may not useful in practice. This decision recognized the

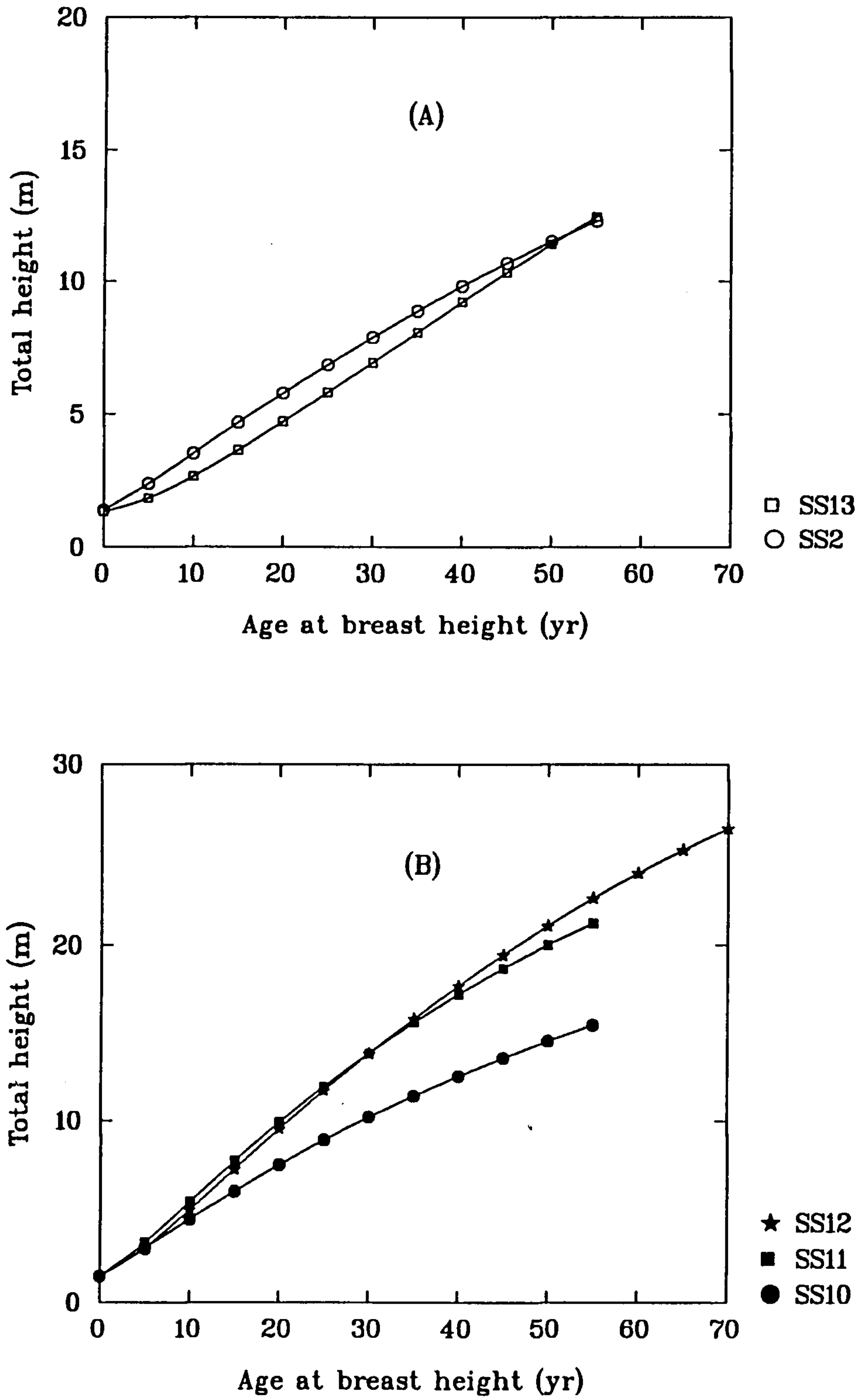

Figure 5.2 Height growth curves for (A) climatically similar and edaphically different site series and (B) climatically different and edaphically similar sites series. Symbols for site series are defined in Table 5.1.

need for ecological strata in the application of the model. Although useful, the continuous variables can not accommodate this need. By definition, site series represent relatively uniform, climatically and edaphically consistent segments of a regional ecological gradient (Pojar *et al.* 1987).

Comparing the parameter predictions based on site series, ecotopes, and site index showed that only b_1 had a significant relationship with site index (Table 5.5.). This means that site index is weakly correlated to two of the curve parameters and it can not be considered as a reliable variable by itself in fitting and describing lodgepole pine height growth patterns. With all three parameters significantly correlated to site series and ecotopes, these variables should be more useful concomitant variables than site index.

5.4.4 Site-specific and Site Index Driven Height Growth Models

Substituting equations [5.4.4], [5.4.5], and [5.4.6] into model [5.3.3], a site series-specific model was constructed:

[5.4.10]
$$H = \mathrm{h} + [15.792 - 6.272(SS1) + 6.456(SS2) + 5.514(SS3) + 6.05(SS5) + 7.710(SS6) + 8.952(SS7) + 16.997(SS8) + 14.897(SS9) + 9.374(SS10) + 14.989(SS11) + 21.972(SS12) + 16.247(SS13) + 24.630(SS14) + 0.000(SS15)]\{1 - e^{-[0.039 - 0.002(SS1) - 0.025(SS2) - 0.023(SS3) - 0.007(SS5) - 0.020(SS6) - 0.007(SS7) - 0.022(SS8) - 0.011(SS9) - 0.023(SS10) - 0.017(SS11) - 0.020(SS12) - 0.027(S13) - 0.027(SS14) - 0.00(SS15)]A}\}^{[1.585 - 0.108(SS1) - 0.433(SS2) - 0.210(SS3) - 0.259(SS5) - 0.577(SS6) - 0.123(SS7) - 0.479(SS8) - 0.180(SS9) - 0.490(SS10) - 0.334(SS11) - 0.244(SS12) - 0.127(SS13) - 0.258(SS14) - 0.00(SS15)]},$$

where '*H*' is the total height estimated; 'h' equals corrected average height for the 1.3 meter section for each corresponding site series; 'e', and 'A' are as previously defined; variable names were defined in Table 5.1.

Similarly, by substituting equations [5.4.7], [5.4.8], and [5.4.9] into model [5.3.3], an ecotope-specific model was constructed:

Table 5.4. Coefficients of determination (R^2) and standard errors of estimation (SEE) from parameter prediction models for ecological variables (N = 40). Symbols for ecological variables are defined in Table 5.1.

Variable	parameters	R^2	adjusted R^2	SEE
Categorical variables				
(1) Biogeoclimatic units	b_1	0.17	0.12	7.396
	b_2	0.41	0.38	0.009
	b_3	0.34	0.30	0.193
(2) Soil moisture regimes	b_1	0.42	0.22	6.95
	b_2	0.39	0.18	0.01
	b_3	0.28	0.03	0.229
(3) Soil nutrient regimes	b_1	0.30	0.22	6.945
	b_2	0.19	0.10	0.01
	b_3	0.22	0.13	0.216
(4) Combination of	b_1	0.66	0.51	5.386
(1), (2), and (3)	b_2	0.57	0.39	0.008
(N = 38)	b_3	0.52	0.32	0.195
(5) Site associations	b_1	0.42	0.25	6.834
	b_2	0.36	0.17	0.01
	b_3	0.26	0.04	0.227
(6) Site series	b_1	0.63	0.45	5.868
	b_2	0.62	0.43	0.008
	b_3	0.55	0.33	0.189
Continuous variables				
(7) PET (mm)	b_1	0.17	0.12	7.396
	b_2	0.41	0.38	0.009
	b_3	0.34	0.30	0.193
(8) DGW (mm)	b_1	0.40	0.37	6.259
	b_2	0.04	0.0	0.011
	b_3	0.05	0.0	0.232
(9) mN (kg/ha)	b_1	0.19	0.17	7.181
	b_2	0.01	0.0	0.011
	b_3	0.07	0.05	0.226
(10) Combination of	b_1	0.58	0.52	5.489
(7), (8), and (9)	b_2	0.50	0.43	0.008
	b_3	0.45	0.37	0.183

Table 5.5. Comparisons of parameter predictions for b_1, b_2, and b_3 based on site index, site series, and ecotopes (N = 40). Symbols for ecological variables are defined in Table 5.1.

Site index (SI)

[5.4.1] $b_1 = 6.894 + 1.175(SI)$ $R^2 = 0.31$ SEE = 6.612

[5.4.2] $b_2 = 0.0196 - 0.00002(SI)^2$ $R^2 = 0.03$ SEE = 0.011

[5.4.3] $b_3 = 1.942 - 0.087(SI) + 0.0028(SI)^2$ $R^2 = 0.03$ SEE = 0.234

Site series (SS_i)

[5.4.4] $b_1 = 15.792 - 6.272(SS_1) + 6.456(SS_2) + 5.514(SS_3) + 6.05(SS_5) + 7.710(SS_6) + 8.952(SS_7) + 16.997(SS_8) + 14.897(SS_9) + 9.374(SS_{10}) + 14.989(SS_{11}) + 21.972(SS_{12}) + 16.247(SS_{13}) + 24.630(SS_{14}) + 0.000(SS_{15})$

$R^2 = 0.63$ (adj. $R^2 = 0.45$) SEE = 5.870

[5.4.5] $b_2 = 0.039 - 0.002(SS_1) - 0.025(SS_2) - 0.023(SS_3) - 0.007(SS_5) - 0.020(SS_6) - 0.007(SS_7) - 0.022(SS_8) - 0.011(SS_9) - 0.023(SS_{10}) - 0.017(SS_{11}) - 0.020(SS_{12}) - 0.027(S13) - 0.027(SS_{14}) - 0.00(SS_{15})$

$R^2 = 0.62$ (adj. $R^2 = 0.43$) SEE = 0.008

[5.4.6] $b_3 = 1.585 - 0.108(SS_1) - 0.433(SS_2) - 0.210(SS_3) - 0.259(SS_5) - 0.577(SS_6) - 0.123(SS_7) - 0.479(SS_8) - 0.180(SS_9) - 0.490(SS_{10}) - 0.334(SS_{11}) - 0.244(SS_{12}) - 0.127(SS_{13}) - 0.258(SS_{14}) - 0.00(SS_{15})$

$R^2 = 0.55$ (adj. $R^2 = 0.33$) SEE = 0.189

Ecotope (combination of BGC_i, SNRs, and SMRs) (N = 38)

[5.4.7] $b_1 = 3.742 + 2.640(ED) + 11.415(VD) + 2.568(MD^f) + 5.568(SD^f) + 10.662(MD) + 12.061(SD) + 16.461(F) + 15.360(M) + 12.830(VM) + 0.00(W) + 3.953(SNRs) - 0.814(BGC_i)$

$R^2 = 0.66$ (adj. $R^2 = 0.51$) SEE = 5.386

[5.4.8] $b_2 = 0.018 + 0.011(ED) - 0.009(VD) - 0.004(MD^f) - 0.003(SD^f) - 0.009(MD) - 0.008(SD) - 0.014(F) - 0.010(M) - 0.009(VM) - 0.00(W) - 0.002(SNRs) + 0.009(BGC_i)$

$R^2 = 0.57$ (adj. $R^2 = 0.39$) SEE = 0.008

[5.4.9] $b_3 = 0.550 + 0.586(ED) + 0.244(VD) + 0.430(MD^f) + 0.145(SD^f) - 0.238(MD) - 0.139(SD) - 0.141(F) - 0.198(M) - 0.085(VM) - 0.00(W) + 0.018(SNRs) + 0.323(BGC_i)$

$R^2 = 0.52$ (adj. $R^2 = 0.32$) SEE = 0.195

$$[5.4.11] \qquad H = h + [3.742 + 2.640(ED) + 11.415(VD) + 2.568(MD^{f}) + 5.568(SD^{f}) + 10.662(MD) + 12.061(SD) + 16.461(F) + 15.360(M) + 12.830(VM) + 0.00(W) + 3.953(SNRs) - 0.814(BGC_{i})]\{1 - e^{-[0.018 + 0.011(ED) - 0.009(VD) - 0.004(MDf) - 0.003(SDf) - 0.009(MD) - 0.008(SD) - 0.014(F) - 0.010(M) - 0.009(VM) - 0.00(W) - 0.002(SNRs) + 0.009(BGCi)A]}\}^{[0.550 + 0.586(ED) + 0.244(VD) + 0.430(MDf) + 0.145(SDf) - 0.238(MD) - 0.139(SD) - 0.141(F) - 0.198(M) - 0.085(VM) - 0.00(W) + 0.018(SNRs) + 0.323(BGCi)]},$$

where 'h' equals corrected average height for the 1.3 meter section for each corresponding ecotope; '*H*', 'e', and 'A' are as previously defined; variable names were defined in Table 5.1.

Equations [5.4.10] and [5.4.11] were used to compute lodgepole pine height growth for all site series and all ecotopes represented in the study, respectively.

Using tabular and graphical data (Appendix III), the height growth curves were compared for similarities, differences, consistency, and conformity to a general pattern of relationships by stand, site series, and ecotopes. Consequently, a framework of site units (site series or their groupings), and parameter prediction equations for b_1, b_2, and b_3 based on these site units, were constructed (Table 5.6). For example, SS2 and SS3 were combined as site unit 2, SS8 and SS11 as site unit 5, and SS9 and SS12 as site unit 8. Comparing the parameter prediction equations for the site series, ecotope, and site unit models (Table 5.7) showed that the relations between height growth curve parameters and ecological variables were slightly improved based on adjusted R^2 and SEE by using site units as expressive variables to explain the variation of the height growth parameters. By substituting equations [5.4.12], [5.4.13], and [5.4.14] into model [5.3.3], the site unit model was developed:

$$[5.4.15] \qquad H = h + [15.792 - 6.272(SU1) + 6.268(SU2) + 9.374(SU3) + 7.710(SU4) + 16.244(SU5) + 6.050(SU6) + 8.952(SU7) + 15.908(SU8) + 0.00(SU9)]\{1 - e^{-[0.039 - 0.002(SU1) - 0.024(SU2) - 0.023(SU3) - 0.020(SU4) - 0.020(SU5) - 0.007(SU6) - 0.007(SU7) - 0.012(SU8) - 0.00(SU9)]A}\}^{[1.585 - 0.108(SU1) - 0.388(SU2) - 0.490(SU3) - 0.577(SU4) - 0.425(SU5) - 0.259(SU6) - 0.123(SU7) - 0.189(SU8) - 0.00(SU9)]},$$

Table 5.6. Parameter prediction equations for b_1, b_2, and b_3 based on site units (SU_i) (N = 38).

[5.4.12] $$b_1 = 15.792 - 6.272(SU_1) + 6.268(SU_2) + 9.374(SU_3) + 7.710(SU_4) + 16.244(SU_5) + 6.050(SU_6) + 8.952(SU_7) + 15.908(SU_8) + 0.00(SU_9)$$

$R^2 = 0.57$ (adj. $R^2 = 0.45$) SEE = 5.713

[5.4.13] $$b_2 = 0.039 - 0.002(SU_1) - 0.024(SU_2) - 0.023(SU_3) - 0.020(SU_4) - 0.020(SU_5) - 0.007(SU_6) - 0.007(SU_7) - 0.012(SU_8) - 0.00(SU_9)$$

$R^2 = 0.56$ (adj. $R^2 = 0.44$) SEE = 0.008

[5.4.14] $$b_3 = 1.585 - 0.108(SU_1) - 0.388(SU_2) - 0.490(SU_3) - 0.577(SU_4) - 0.425(SU_5) - 0.259(SU_6) - 0.123(SU_7) - 0.189(SU_8) - 0.00(SU_9)$$

$R^2 = 0.51$ (adj. $R^2 = 0.37$) SEE = 0.187

where SU_1 to SU_9 representing site units from 1 through 9; 1 = SBPSxc/*Stereocaulon*, 2 = SBPSxc/*Arctostaphylos*, 3 = SBPSxc/*Aulacomnium*, 4 = SBSmc/*V. membranaceum*, 5 = SBSmc/*Gymnocarpium*, 6 = SBSwk/*V. myrtilloides*, 7 = SBSwk/*V.membranaceum*, 8 = SBSwk/*Gymnocarpium*, 9 = SBSwk/*Carex*

Table 5.7. Comparisons of parameter prediction equations for site series, ecotope, and site unit height growth models.

Model		R^2	adj. R^2	SEE
Site series (SS_i)				
[5.4.4]		0.63	0.45	5.870
[5.4.5]	(N = 40)	0.62	0.43	0.008
[5.4.6]		0.55	0.33	0.189
Ecotope (combination of BGC_i, SNRs, and SMRs)				
[5.4.7]		0.66	0.51	5.386
[5.4.8]	(N =38)	0.57	0.39	0.008
[5.4.9]		0.52	0.32	0.195
Site unit (SU_i)				
[5.4.12]		0.57	0.45	5.713
[5.4.13]	(N =38)	0.56	0.44	0.008
[5.4.14]		0.51	0.37	0.187

where 'h' equals corrected average height for the 1.3 meter section for each corresponding site unit; '*H*', 'e', and 'A' are as previously defined; site units were defined in Table 5.6. Equation [5.4.15] was then used for producing site unit height growth tables and curves (Tables 5.8 and 5.9, Figure 5.3).

The SBPSxc/*Arctostaphylos*, SBSmc/*V. membranaceum*, and SBSwk/*Gymnocarpium* site units were selected for comparing performance between the site unit curves and their related ecotope curves (Table 5.10, Figure 5.4). It is quite clear that curves developed by these two different approaches are very similar. The implication is that the complicated ecotope curves can be satisfactorily represented by the simplified site unit curves.

Each height growth curve has different parameter values (Tables 5.8, 5.11 and 5.12) which are based on site unit, site series or ecotope; thus the curves are site-specific and polymorphic. Once an ecotope and, hence, site series or site unit are identified, then a particular ecotope, site series, or site unit equation is defined and the site index for that ecotope, site series, or site unit can be determined at any index age. The reader is reminded that some site series, site units, and, particularly some ecotopes, were not represented by an adequate number of stands. This is a result of limited sampling, the pattern of sites in the selected sampling areas, and deleting young stands, or those exhibiting atypical growth. Due to non-homogeneous variance in certain cases, weighted regression should be considered in future studies. All curves generated were extrapolated to 100 years; however, prediction beyond 70 years is not recommended.

Table 5.8. Height growth parameters computed for site unit height growth model [5.4.15] using equations [5.4.12], [5.4.13], and [5.4.14]. Site units are defined in Table 5.6.

Site unit	b_1	b_2	b_3
SU_1	9.520	0.037	1.477
SU_2	22.060	0.015	1.197
SU_3	25.166	0.016	1.095
SU_4	23.502	0.019	1.008
SU_5	32.036	0.019	1.160
SU_6	21.842	0.032	1.326
SU_7	24.744	0.032	1.462
SU_8	31.700	0.027	1.396
SU_9	15.792	0.039	1.585

Table 5.9. Lodgepole pine height growth by site units based on equation [5.4.15] and parameters given in Table 5.8. Symbols for sites units are given in Table 5.6.

B.H. Age	SU1	SU2	SU3	SU4	SU5	SU6	SU7	SU8	SU9
0	1.40	1.43	1.46	1.54	1.50	1.56	1.56	1.49	1.42
1	1.47	1.57	1.73	1.97	1.79	1.78	1.72	1.69	1.51
2	1.59	1.76	2.03	2.39	2.18	2.11	1.99	2.01	1.68
3	1.74	1.96	2.34	2.81	2.59	2.48	2.31	2.39	1.90
4	1.91	2.16	2.66	3.22	3.01	2.88	2.68	2.81	2.16
5	2.09	2.38	2.98	3.63	3.45	3.29	3.07	3.25	2.44
6	2.28	2.60	3.30	4.03	3.89	3.72	3.49	3.72	2.74
7	2.47	2.83	3.61	4.42	4.33	4.16	3.93	4.21	3.05
8	2.67	3.05	3.93	4.80	4.77	4.60	4.37	4.71	3.38
9	2.88	3.28	4.25	5.18	5.22	5.04	4.83	5.22	3.71
10	3.08	3.51	4.56	5.55	5.66	5.48	5.29	5.73	4.05
11	3.29	3.75	4.88	5.91	6.10	5.92	5.75	6.25	4.36
12	3.49	3.98	5.19	6.27	6.53	6.36	6.21	6.77	4.74
13	3.70	4.21	5.49	6.62	6.97	6.79	6.68	7.28	5.08
14	3.90	4.44	5.80	6.97	7.40	7.22	7.14	7.80	5.42
15	4.10	4.67	6.10	7.30	7.83	7.64	7.60	8.32	5.76
16	4.30	4.90	6.40	7.64	8.25	8.06	8.06	8.83	6.10
17	4.49	5.13	6.69	7.96	8.67	8.47	8.51	9.35	6.43
18	4.68	5.36	6.98	8.28	9.08	8.87	8.96	9.85	6.76
19	4.87	5.59	7.27	8.59	9.49	9.26	9.40	10.35	7.08
20	5.05	5.81	7.55	8.90	9.89	9.65	9.83	10.85	7.40
21	5.23	6.04	7.84	9.20	10.29	10.03	10.26	11.34	7.70
22	5.41	6.26	8.11	9.50	10.69	10.40	10.68	11.82	8.01
23	5.58	6.48	8.39	9.79	11.08	10.76	11.10	12.30	8.30
24	5.75	6.70	8.66	10.08	11.46	11.12	11.50	12.77	8.59
25	5.92	6.92	8.93	10.36	11.84	11.46	11.90	13.23	8.88
26	6.08	7.13	9.19	10.63	12.21	11.80	12.29	13.68	9.15
27	6.23	7.35	9.45	10.90	12.57	12.13	12.68	14.13	9.42
28	6.38	7.56	9.71	11.17	12.94	12.45	13.05	14.57	9.68
29	6.53	7.77	9.96	11.43	13.30	12.77	13.42	15.01	9.94
30	6.67	7.98	10.21	11.68	13.65	13.08	13.78	15.43	10.18
31	6.81	8.18	10.46	11.93	13.99	13.38	14.13	15.85	10.42
32	6.95	8.39	10.71	12.18	14.34	13.67	14.47	16.26	10.66
33	7.08	8.59	10.95	12.42	14.68	13.95	14.81	16.66	10.88
34	7.21	8.79	11.18	12.66	15.01	14.23	15.13	17.05	11.10
35	7.33	8.98	11.42	12.89	15.33	14.50	15.45	17.44	11.32
36	7.45	9.18	11.65	13.12	15.65	14.76	15.76	17.82	11.52
37	7.57	9.37	11.88	13.34	15.97	15.02	16.06	18.19	11.72
38	7.68	9.56	12.10	13.56	16.28	15.26	16.36	18.55	11.92
39	7.79	9.75	12.32	13.78	16.59	15.51	16.65	18.91	12.10
40	7.90	9.94	12.54	13.99	16.89	15.74	16.93	19.25	12.29
41	8.00	10.12	12.75	14.20	17.18	15.97	17.20	19.59	12.46
42	8.10	10.31	12.97	14.40	17.48	16.19	17.47	19.93	12.63
43	8.20	10.49	13.18	14.60	17.76	16.41	17.73	20.25	12.80
44	8.29	10.67	13.38	14.80	18.04	16.62	17.98	20.57	12.96
45	8.38	10.84	13.58	14.99	18.32	16.82	18.22	20.88	13.11
46	8.47	11.02	13.78	15.18	18.59	17.02	18.46	21.19	13.26
47	8.56	11.19	13.98	15.36	18.86	17.21	18.70	21.49	13.40
48	8.64	11.36	14.18	15.54	19.12	17.40	18.92	21.78	13.54
49	8.72	11.53	14.37	15.72	19.38	17.58	19.14	22.06	13.67
50	8.79	11.69	14.56	15.90	19.64	17.76	19.35	22.34	13.80

Table 5.9. (continued)

51	8.87	11.86	14.74	16.07	19.89	17.93	19.56	22.61	13.93
52	8.94	12.02	14.92	16.24	20.13	18.09	19.76	22.88	14.05
53	9.01	12.18	15.10	16.40	20.38	18.26	19.96	23.14	14.16
54	9.08	12.34	15.28	16.57	20.61	18.41	20.15	23.39	14.28
55	9.14	12.49	15.46	16.72	20.85	18.57	20.34	23.64	14.38
56	9.20	12.65	15.63	16.88	21.08	18.71	20.52	23.88	14.49
57	9.26	12.80	15.80	17.03	21.30	18.86	20.69	24.12	14.59
58	9.32	12.95	15.97	17.18	21.53	18.99	20.86	24.35	14.69
59	9.38	13.10	16.13	17.33	21.74	19.13	21.03	24.57	14.78
60	9.43	13.24	16.29	17.48	21.96	19.26	21.19	24.79	14.87
61	9.49	13.39	16.45	17.62	22.17	19.39	21.34	25.00	14.96
62	9.54	13.53	16.61	17.76	22.37	19.51	21.49	25.21	15.04
63	9.59	13.67	16.77	17.90	22.58	19.63	21.64	25.42	15.12
64	9.63	13.81	16.92	18.03	22.78	19.75	21.78	25.62	15.20
65	9.68	13.95	17.07	18.16	22.97	19.86	21.92	25.81	15.28
66	9.72	14.08	17.22	18.29	23.17	19.97	22.05	25.99	15.35
67	9.77	14.21	17.37	18.42	23.36	20.08	22.18	26.18	15.42
68	9.81	14.35	17.51	18.54	23.54	20.18	22.31	26.36	15.48
69	9.85	14.48	17.65	18.66	23.72	20.28	22.43	26.54	15.55
70	9.88	14.60	17.79	18.78	23.90	20.37	22.55	26.71	15.61
71	9.92	14.73	17.93	18.90	24.08	20.47	22.67	26.88	15.67
72	9.96	14.86	18.06	19.02	24.25	20.56	22.78	27.04	15.73
73	9.99	14.98	18.20	19.13	24.42	20.65	22.89	27.20	15.79
74	10.02	15.10	18.33	19.24	24.59	20.73	22.99	27.36	15.84
75	10.06	15.22	18.46	19.35	24.75	20.81	23.09	27.51	15.89
76	10.09	15.34	18.59	19.46	24.91	20.90	23.19	27.65	15.94
77	10.12	15.45	18.71	19.56	25.07	20.97	23.29	27.80	15.99
78	10.15	15.57	18.83	19.67	25.23	21.05	23.38	27.94	16.03
79	10.17	15.68	18.96	19.77	25.38	21.12	23.47	28.07	16.08
80	10.20	15.80	19.08	19.87	25.53	21.19	23.56	28.21	16.12
81	10.23	15.91	19.19	19.96	25.68	21.26	23.64	28.34	16.16
82	10.25	16.01	19.31	20.06	25.82	21.33	23.73	28.46	16.20
83	10.28	16.12	19.42	20.15	25.96	21.39	23.81	28.59	16.24
84	10.30	16.23	19.54	20.24	26.10	21.45	23.88	28.71	16.28
85	10.32	16.33	19.65	20.33	26.24	21.52	23.96	28.82	16.31
86	10.34	16.44	19.76	20.42	26.37	21.57	24.03	28.94	16.35
87	10.36	16.54	19.86	20.51	26.51	21.63	24.10	29.05	16.38
88	10.38	16.64	19.97	20.60	26.64	21.69	24.17	29.16	16.41
89	10.40	16.74	20.07	20.68	26.76	21.74	24.24	29.26	16.44
90	10.42	16.83	20.18	20.76	26.89	21.79	24.30	29.36	16.47
91	10.44	16.93	20.28	20.84	27.01	21.84	24.36	29.46	16.50
92	10.46	17.02	20.38	20.92	27.13	21.89	24.42	29.56	16.53
93	10.47	17.12	20.48	20.99	27.25	21.94	24.48	29.66	16.55
94	10.48	17.21	20.57	21.07	27.36	21.98	24.54	29.75	16.58
95	10.51	17.30	20.67	21.15	27.48	22.03	24.59	29.84	16.60
96	10.52	17.39	20.76	21.22	27.59	22.07	24.65	29.93	16.62
97	10.53	17.48	20.85	21.29	27.70	22.11	24.70	30.01	16.65
98	10.55	17.57	20.94	21.36	27.81	22.15	24.75	30.10	16.67
99	10.56	17.65	21.03	21.43	27.91	22.19	24.80	30.18	16.69
100	10.57	17.74	21.12	21.50	28.02	22.23	24.84	30.26	16.71

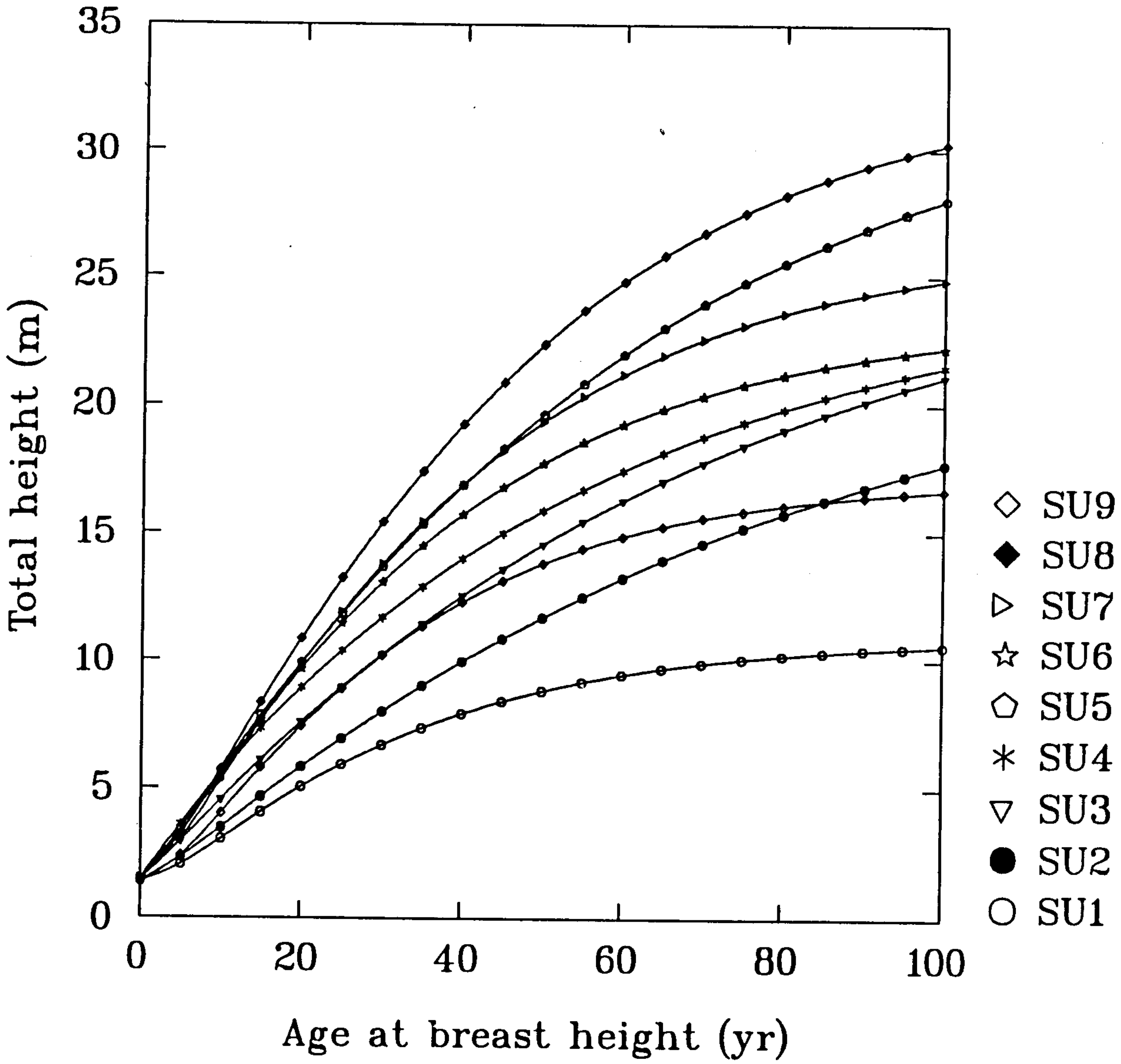

Figure 5.3. Lodgepole pine height growth curves by site units based on equation [5.4.15] and parameters given in Table 5.8. Symbols for sites units are given in Table 5.6.

Table 5.10. Comparisons of lodgepole pine height growth predicted by site unit and ecotope models based on equations [5.4.11] and [5.4.15] and parameters given in Tables 5.8 and 5.12. Symbols for site units are given in Table 5.6, and for SMRs and SNRs in Table 5.1.

	Estimated height									
	SBPSxc			SBSmc		SBSwk				
Age	SU_2	VD*VP	VD*M	SU_4	SD*P	SU_8	F*M	M*M	M*R	VM*R
5	2.38	2.42	2.37	3.63	3.90	3.25	2.88	3.32	3.32	2.90
10	3.51	3.52	3.47	5.55	6.05	5.73	4.91	5.78	5.86	5.08
15	4.67	4.60	4.60	7.30	7.96	8.32	7.11	8.31	8.52	7.48
20	5.81	5.64	5.72	8.90	9.66	10.85	9.29	10.73	11.11	9.86
25	6.92	6.62	6.82	10.36	11.18	13.24	11.39	12.97	13.55	12.15
30	7.98	7.55	7.89	11.68	12.52	15.43	13.36	15.02	15.80	14.28
35	8.98	8.43	8.91	12.89	13.73	17.44	15.18	16.86	17.86	16.24
40	9.94	9.25	9.90	13.99	14.79	19.25	16.86	18.50	19.72	18.02
45	10.84	10.01	10.85	14.99	15.75	20.88	18.38	19.96	21.39	19.62
50	11.69	10.73	11.75	15.90	16.60	22.34	19.77	21.25	22.88	21.05
55	12.49	11.39	12.61	16.72	17.35	23.64	21.01	22.38	24.21	22.32
60	13.24	12.01	13.43	17.48	18.03	24.79	22.13	23.37	25.38	23.45

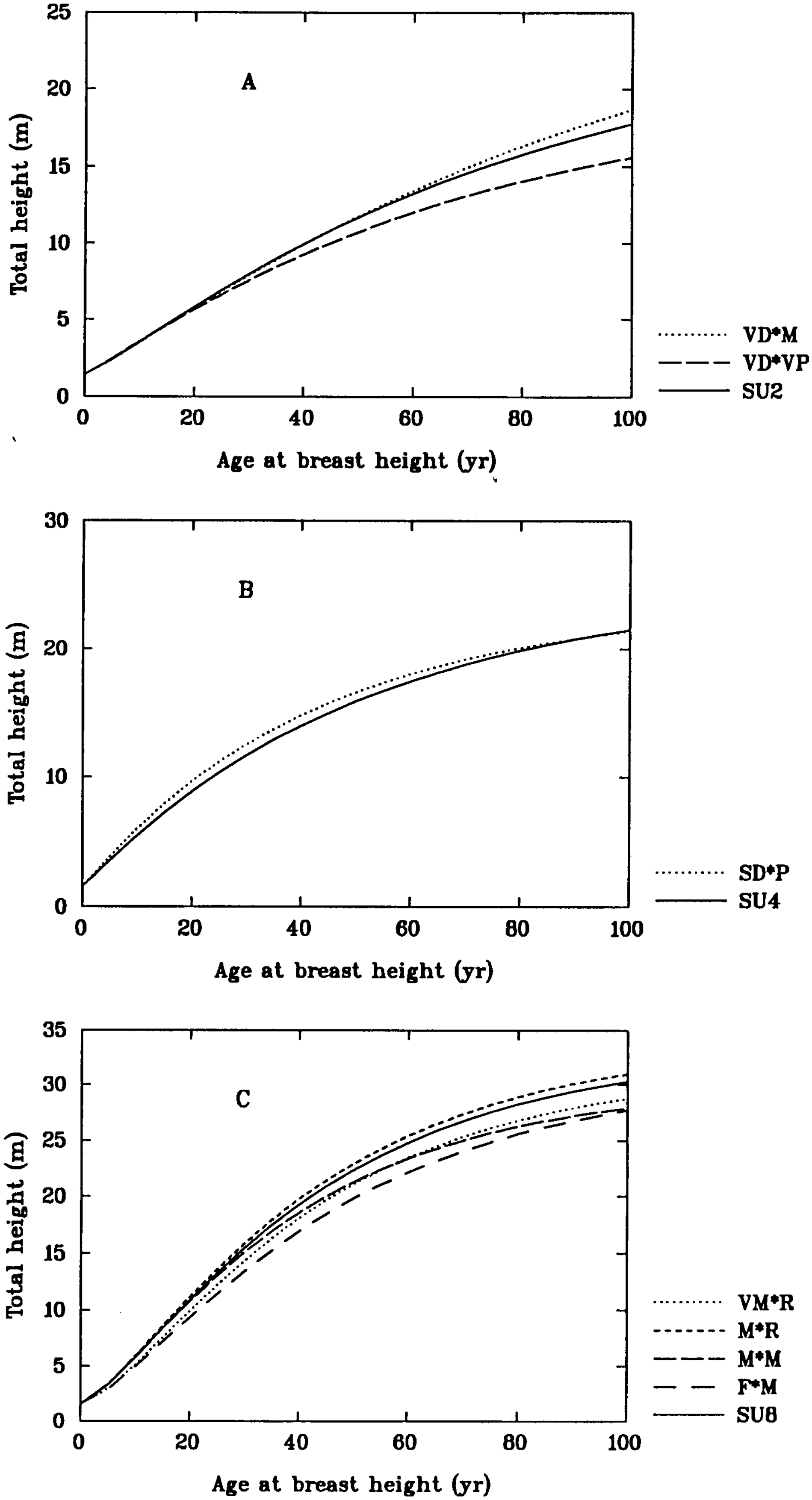

Figure 5.4. Comparison of site unit and ecotope lodgepole pine height growth curves based on equations [5.4.15] and [5.4.11]. Symbols for sites units are given in Table 5.6, for BGC, SMRs, and SNRs are explained in Table 5.1.

Table 5.11. Height growth parameters computed for the site series height growth model using equations [5.4.4], [5.4.5], and [5.4.66]. Symbols for site series are given in Table 5.1.

Site series	b_1	b_2	b_3
SS_1	9.52	0.037	1.477
SS_2	22.25	0.015	1.153
SS_3	21.31	0.016	1.375
SS_5	21.84	0.032	1.326
SS_6	23.50	0.020	1.008
SS_7	24.74	0.033	1.462
SS_8	32.79	0.017	1.106
SS_9	30.69	0.028	1.405
SS_{10}	25.17	0.016	1.095
SS_{11}	30.78	0.022	1.251
SS_{12}	37.76	0.019	1.341
SS_{13}	40.42	0.012	1.327
SS_{14}	32.04	0.012	1.458
SS_{15}	15.79	0.039	1.585

Table 5.12. Height growth parameters computed for the ecotope height growth model using equations [5.4.7], [5.4.8], and [5.4.9]. Symbols for BGC, SMR, and SNR are given in Table 5.1.

BGC	SMR	SNR	b_1	b_2	b_3
SBPSxc	ED	VP	9.522	0.036	1.477
	VD	VP	18.296	0.016	1.135
	VD	M	26.202	0.012	1.171
	MD[f]	R	21.318	0.015	1.375
	SD[f]	R	24.318	0.016	1.090
	SD[f]	VR	28.260	0.014	1.108
SBSmc	SD	P	22.080	0.024	1.093
	F	M	30.434	0.016	1.109
	F	R	34.387	0.014	1.127
	M	R	33.286	0.018	1.090
	VM	R	30.756	0.019	1.183
	VM	VR	34.709	0.017	1.210
SBSwk	MD	P	19.868	0.032	1.317
	MD	M	23.821	0.030	1.335
	SD	M	25.220	0.031	1.434
	F	M	29.620	0.025	1.432
	M	M	28.519	0.029	1.375
	M	R	32.472	0.027	1.393
	VM	R	29.942	0.028	1.506
	W	M	13.159	0.039	1.573
	W	VR	21.065	0.035	1.609

Using parameter values calculated from site index equations [5.4.1], [5.4.2], and [5.4.3] (Table 5.1) in a site index driven height growth model, some serious biases were observed (Figure 5.5). One of the biases was that the site index driven curves consistently overestimated height by about 2 m at any site index (Table 5.13). According to Clutter *et al.* (1983), one of the major problems with using site index in growth modelling is that the curve does not pass through that height at index age (Table 5.13, Figure 5.5). The cause of this problem is simply that the relations between site index and the curve parameters are too weak to precisely describe height growth patterns. It is still a common practice to constrain the curves through the height at index age by proportionally adjusting the curves. These adjusting procedures could assign too much weight to the curve shape and cause additional noise resulting in erratic and non-tenable curves. For site-specific height growth curves constructed without site index in the model, the site index will always be the height at index age without any need for adjustment.

Another problem with the site index-driven approach is that site index can not be computed explicitly for a given age and height unless graphical determination or tedious iterative computation are employed following the formulation of a model. This may result in somewhat erratic estimation of site index and more complex modelling. Finally, with site index in the parameter prediction equations, choice of index age affects the shape of height growth curves and results in different curves for different index ages. However, without site index in the parameter prediction equations for site-specific height growth models, the choice of index age has no effect on curve shapes and results in the same curves for any index ages.

Table 5.13. Comparisons between lodgepole pine site index estimated using equation [5.3.3] with parameters calculated from site index equations [5.4.1], [5.4.2], and [5.4.3], and the height corresponding to the index age of 50 years.

Site index (m)	Height at index age (m)	Difference (m)
5	7.70	-2.70
10	12.12	-2.12
15	17.09	-2.09
20	22.20	-2.20
25	27.29	-2.29
30	32.49	-2.49

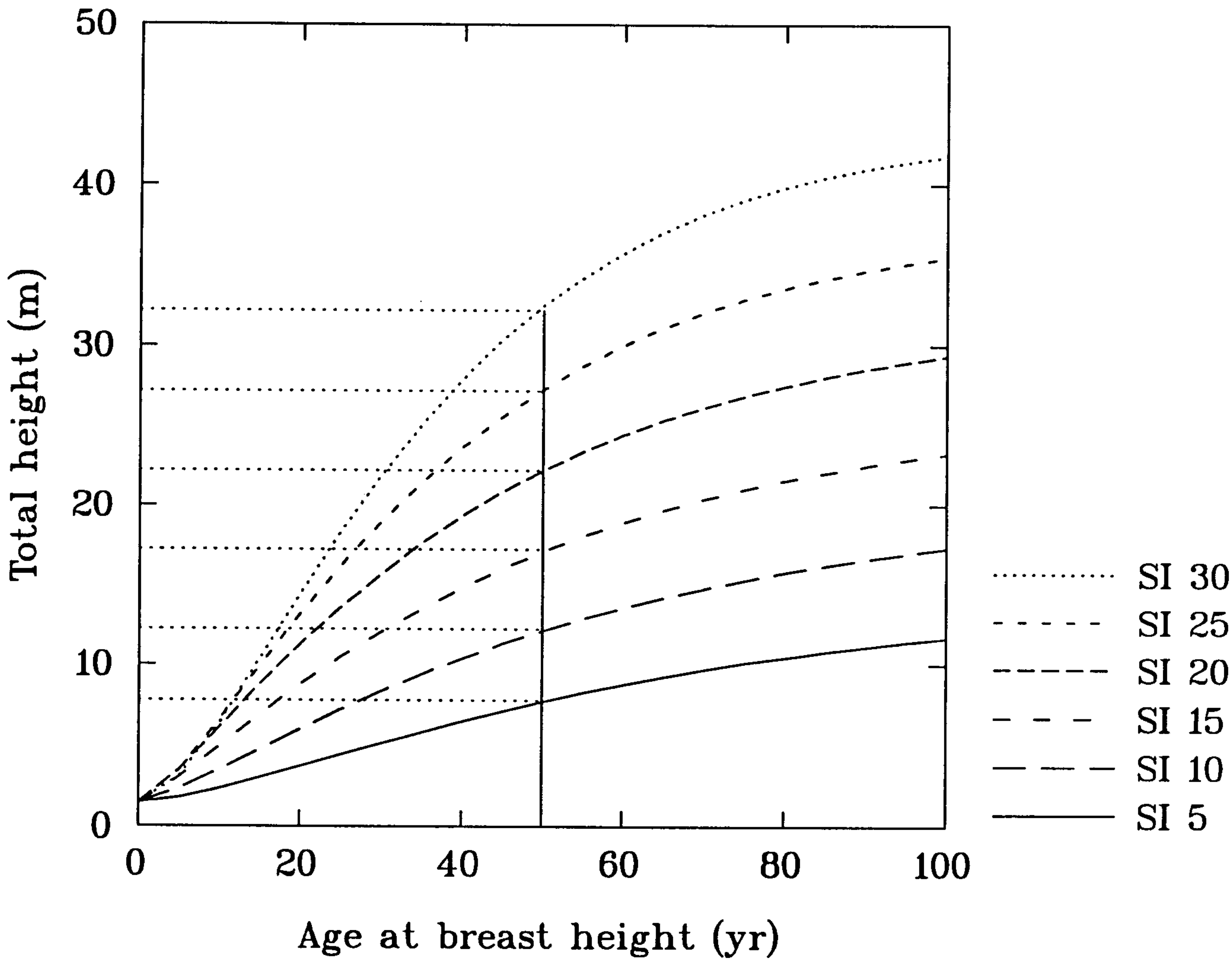

Figure 5.5 Lodgepole pine height growth curves derived by using site index in parameter prediction equations ([5.4.1], [5.4.2], and [5.4.3]).

5.4.5. Increment Characteristics of Height Growth

Cumulative or total height growth for each site unit was described using equation [5.4.15]. Current annual height increment (CAI) was computed as (Pienaar and Turnbull 1973):

[5.4.16] $$CAI = b_2 b_3 H[(\frac{b_1}{H})^{(1/b_3)} - 1] \quad ,$$

where H, b_1, b_2, and b_3 are defined in section 5.4.4, and mean annual height increment (MAI) was computed as (Pienaar and Turnbull 1973):

[5.4.17] $$MAI = \frac{b_1(1 - e^{-b_2 A})^{b_3}}{A_t} \quad ,$$

where b_1, b_2, b_3, and e are as defined in section 5.4.4, and 'A_t' equals total age in years, which is breast height age plus age to breast height calculated using Goudie's (1984) equation:

[5.4.18] $$\text{Age to breast height} = 8.60 + \frac{42.64}{SI} \quad ,$$

Function [5.4.17] can be simply expressed as MAI = H/A_t where H = total height in meters. Obviously, [5.4.16] and [5.4.17] are derivative functions of [5.4.15].

The estimated values of CAI and MAI for each site unit are presented in Figure 5.6; Figures 5.7 and Figure 5.8 show the patterns of CAI and MAI for site units stratified by biogeoclimatic subzones; and Table 5.14 gives tabulated data of estimated H, CAI, and MAI for the site units studied.

Since CAI and MAI curves were derived from a site-specific model, it was not surprising that both CAI and MAI curves are site-specific, *i.e.*, the curve shape and, to lesser degree culmination and intersection points vary with ecological site

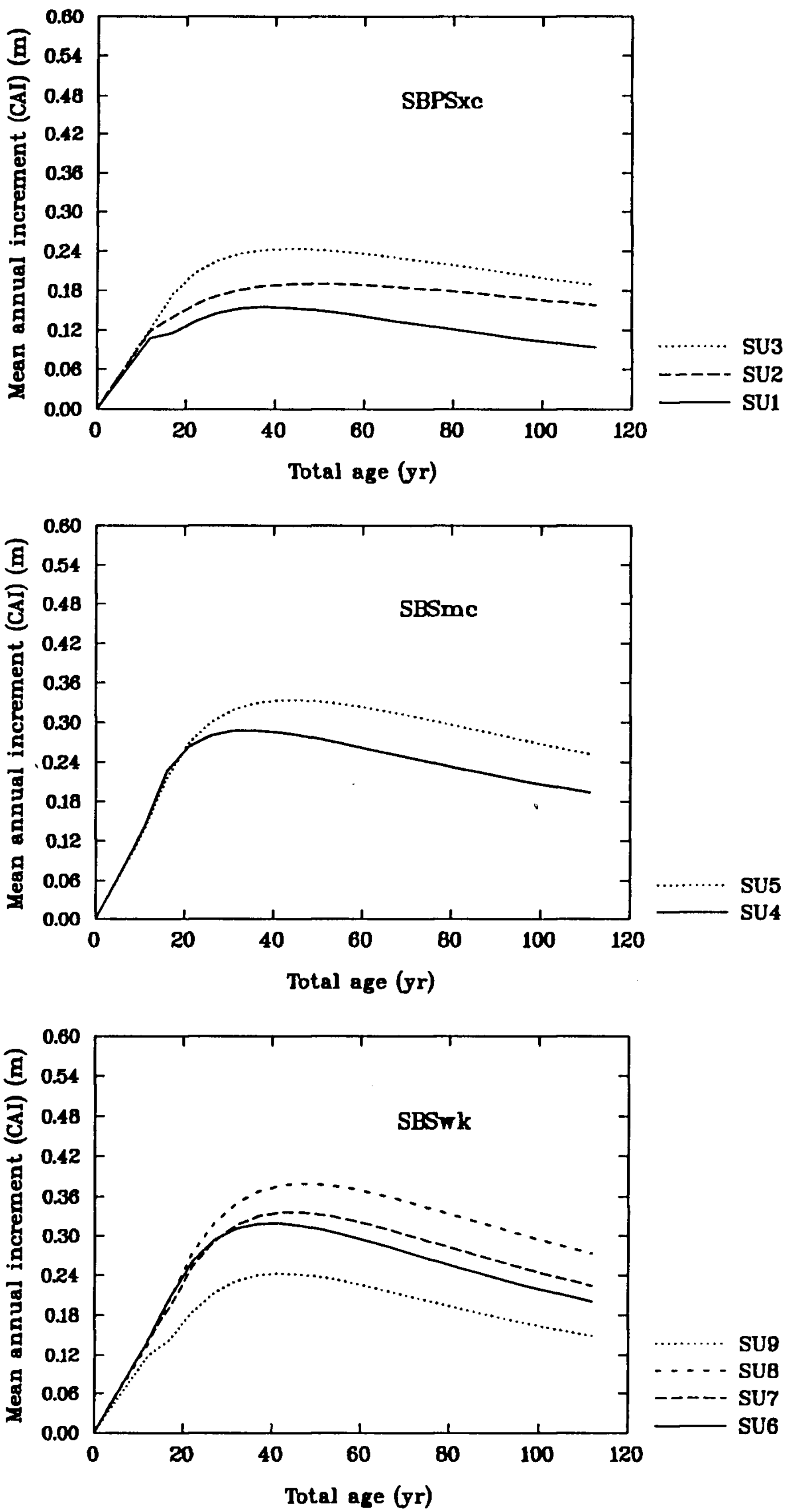

Figure 5.6. The plot of estimated mean annual increments (MAI) for site units stratified according to biogeoclimatic subzone. Symbols for biogeoclimatic subzones and site units are explained in Table 5.1 and 5.6.

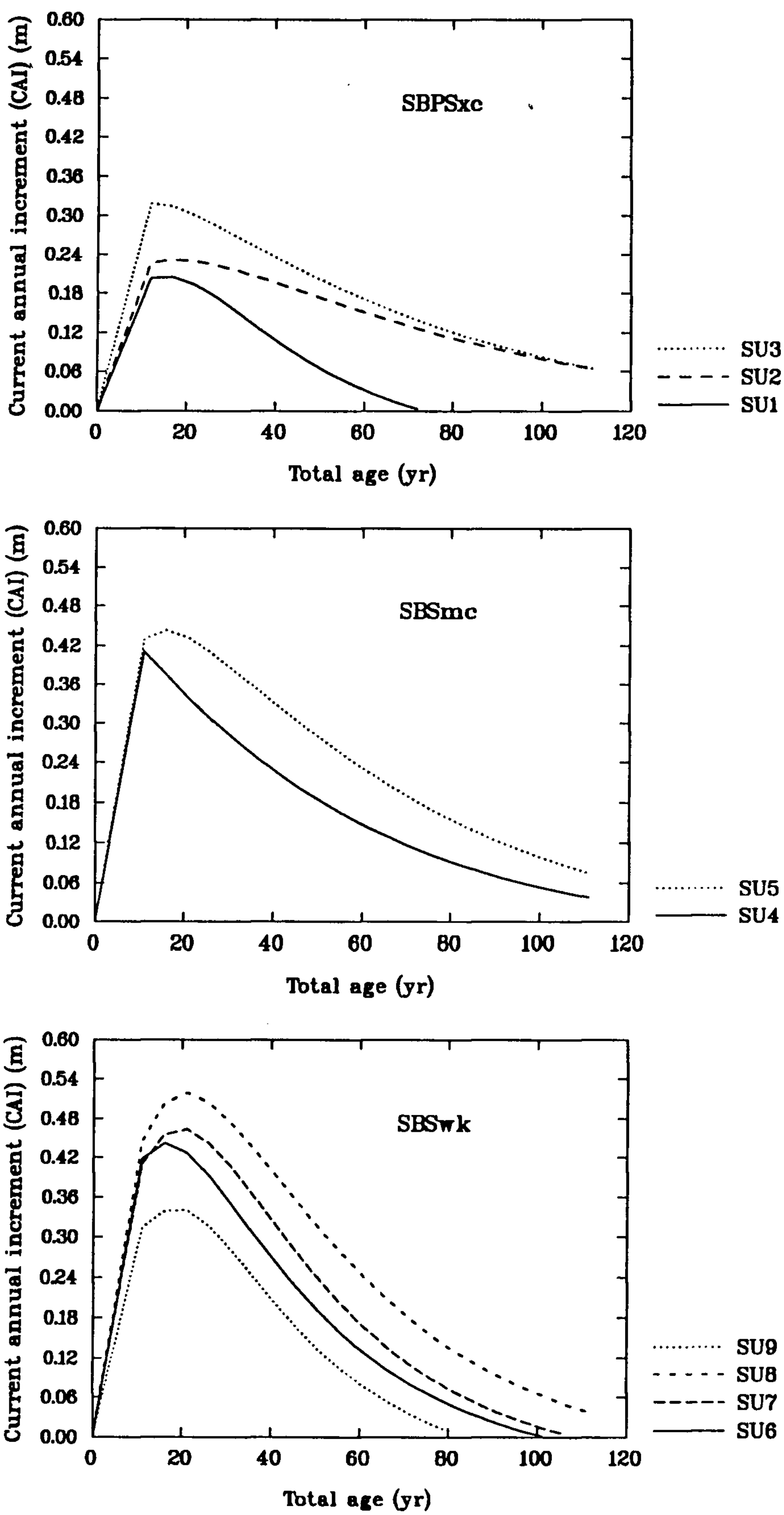

Figure 5.7. The plot of estimated current annual increments (CAI) for site units stratified according to biogeoclimatic subzones. Symbols for biogeoclimatic subzones and site units are explained in Table 5.1 and 5.6.

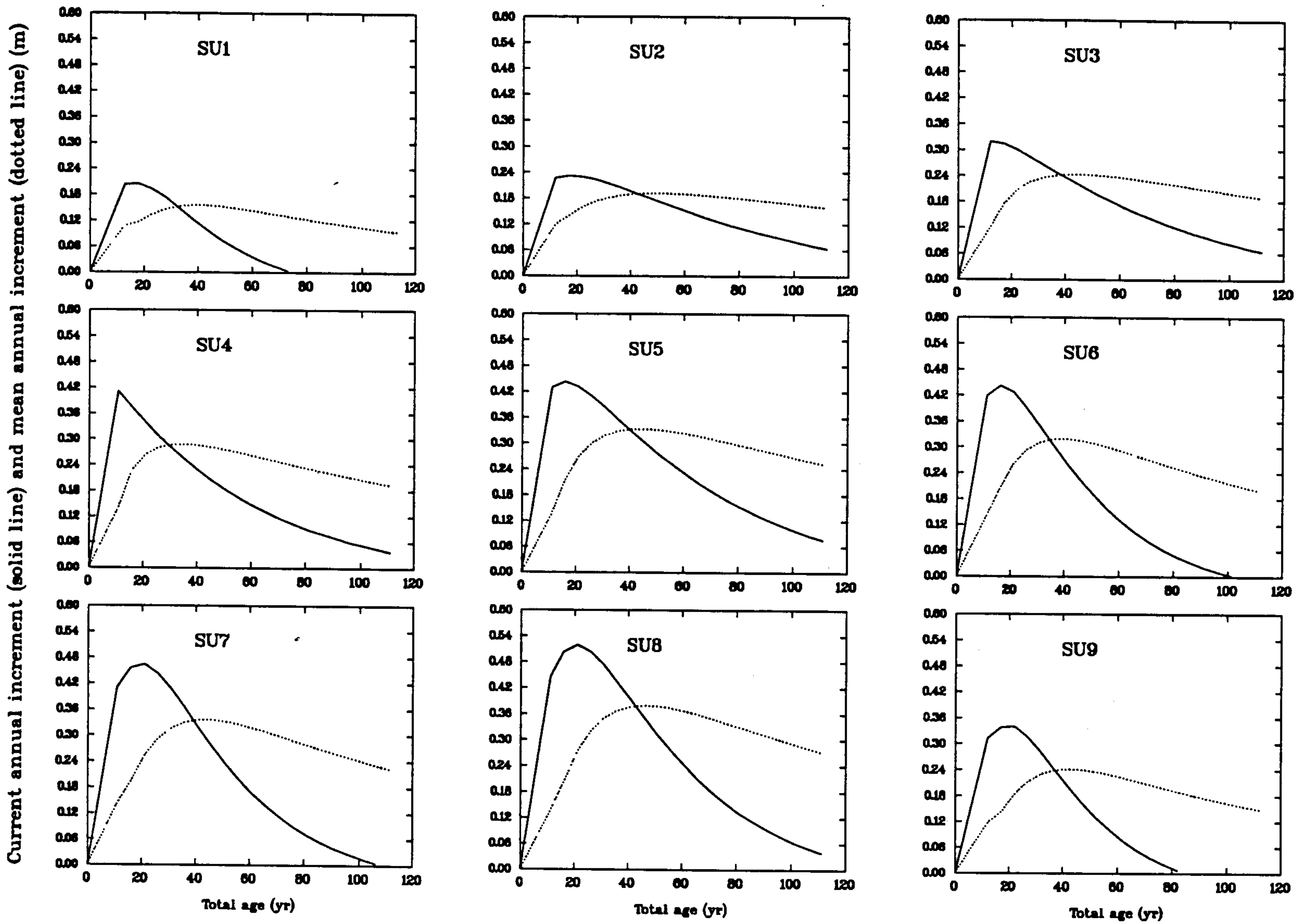

Figure 5.8.The plot of estimated current annual increments (CAI) and mean annual increments (MAI). Symbols for site units are explained in Table 5.6.

Table 5.14. Cumulative growth (H), current annual increment (CAI), and mean annual increment (MAI) for each site unit. Bold fonts indicate the total age of maximum mean annual increment and its corresponding growth. Symbols for site units are explained in Table 5.6. Breast height age is in parentheses.

Total age	H	CAI	MAI	H	CAI	MAI	H	CAI	MAI
	Site unit 1			Site unit 2			Site unit 3		
12(00)	1.40	0.20	0.11	1.43	0.23	0.12	1.46	0.32	0.12
22(10)	3.08	0.19	0.13	3.51	0.23	0.16	4.56	0.30	0.21
32(20)	5.05	**0.15**	**0.15**	5.81	0.21	0.18	7.55	0.26	0.24
42(30)	6.67	0.10	0.16	7.98	**0.19**	**0.19**	10.21	**0.23**	**0.24**
52(40)	7.90	0.06	0.15	9.94	0.17	0.19	12.54	0.20	0.24
62(50)	8.79	0.03	0.14	11.69	0.15	0.19	14.56	0.17	0.23
72(60)	9.43	0.003	0.13	13.24	0.13	0.18	16.29	0.14	0.23
82(70)	9.88	0.00	0.12	14.60	0.11	0.18	17.79	0.12	0.22
92(80)	10.20		0.11	15.80	0.09	0.17	19.08	0.10	0.21
102(90)	10.42		0.10	16.83	0.08	0.17	20.18	0.08	0.20
112(100)	10.57		0.09	17.74	0.06	0.16	21.12	0.06	0.19
	Site unit 4			Site unit 5			Site unit 6		
11(00)	1.54	0.41	0.14	1.50	0.43	0.14	1.56	0.41	0.14
21(10)	5.55	0.34	0.26	5.66	0.43	0.27	5.29	0.46	0.25
31(20)	8.90	**0.28**	**0.29**	9.89	0.38	0.32	9.83	0.40	0.32
41(30)	11.68	0.22	0.28	13.65	**0.33**	**0.33**	13.78	**0.32**	**0.34**
51(40)	13.99	0.18	0.27	16.89	0.27	0.33	16.93	0.23	0.33
61(50)	15.90	0.14	0.26	19.64	0.23	0.32	19.35	0.17	0.32
71(60)	17.48	0.11	0.25	21.96	0.19	0.31	21.19	0.11	0.30
81(70)	18.78	0.09	0.23	23.90	0.15	0.30	22.55	0.07	0.28
91(80)	19.87	0.07	0.22	25.53	0.12	0.28	23.56	0.04	0.26
101(90)	20.76	0.05	0.21	26.89	0.10	0.27	24.30	0.01	0.24
111(100)	21.50	0.04	0.19	28.02	0.08	0.25	24.84	0.00	0.22
	Site unit 7			Site unit 8			Site unit 9		
11(00)	1.56	0.41	0.14	1.49	0.45	0.14	1.42	0.31	0.12
21(10)	5.29	0.46	0.25	5.73	0.52	0.27	4.05	0.34	0.18
31(20)	9.83	0.40	0.32	10.85	0.47	0.35	7.40	0.28	0.23
41(30)	13.78	**0.32**	**0.34**	15.43	**0.39**	**0.38**	10.18	**0.20**	**0.24**
51(40)	16.93	0.23	0.33	19.25	0.31	0.38	12.29	0.13	0.24
61(50)	19.35	0.17	0.32	22.34	0.24	0.37	13.80	0.08	0.22
71(60)	21.19	0.11	0.30	24.79	0.18	0.35	14.87	0.04	0.21
81(70)	22.55	0.07	0.28	26.71	0.13	0.33	15.61	0.007	0.19
91(80)	23.56	0.04	0.26	28.21	0.09	0.31	16.12	0.00	0.18
101(90)	24.30	0.01	0.24	29.36	0.06	0.29	16.47		0.16
111(100)	24.84	0.00	0.22	30.26	0.04	0.27	16.71		0.15

quality (Table 5.14, Figure 5.6). Changes in growth rates can be related to climatic, soil moisture, and soil nutrient conditions. Height growth rates were slightly higher in the SBSwk subzone than in the SBSmc subzone, and very low in the SBPSxc subzone. Within a biogeoclimatic subzone, growth rates increased from water deficient sites to very moist sites and decreased from very moist to wet sites. These trends reflect the climatic and edaphic effects on height growth which were discussed in detail in Chapter 4.

The height CAI culminated at or before 11 to 21 years of total age for the study stands, based on the site unit height growth model (Table 5.14). According to the site unit height growth model, MAI culminated for the study stands within a relatively narrow range—between 30 and 40 years of total age (Table 5.14). The earlier maximum occurred on drier and nutrient-poorer sites while the later maximum was for wetter and nutrient-richer sites (Table 5.14).

5.4.6. Test of the Site-specific Height Growth Model

The plot of measured and estimated heights against breast height age showed that the model fitted the data well, and there was not any obvious serious bias for any SU, with the exception that the height growth for ages greater than 40 years in the SBSwk/*Gymnocarpium* SU was slightly over-estimated (Figure 5.9).

The results of residual analysis between measured and estimated heights at 5 year intervals at breast height age for each of the 38 stands are summarized in Table 5.15. Heights in 87% of stands were correctly estimated with less than $|1.0|$ m error. 12% of the stands were one class off, *i.e.*, within $|1.0\text{-}1.5|$ m of measured heights. If 1.5 m estimation error is considered acceptable for estimating lodgepole pine height, then the heights in 99% of stands were acceptably estimated.

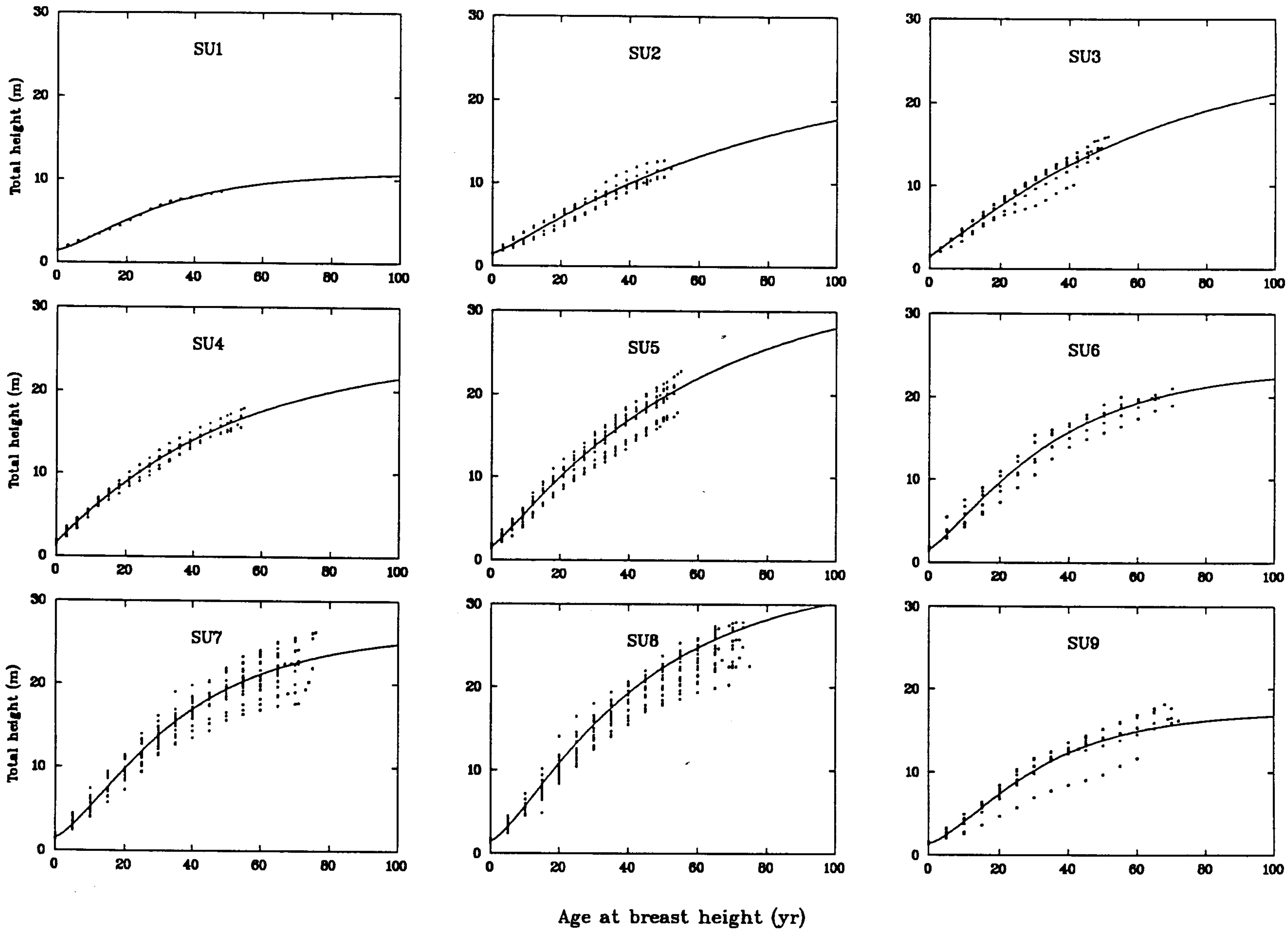

Figure 5.9. Relationships between measured and estimated heights for site units. Symbols for site units are explained in Table 5.6.

Table 5.15. Residual analysis based on equation [5.4.15] at 5-year intervals at breast height age for each stand.

Age (yr)	Number of stands for each class (proportion in parentheses)			
	Correct[1]	1 class off	2 classes off	Total
5	38 (100)			38
10	35 (92.1)	3 (7.9)		38
15	35 (92.1)	2 (5.3)	1 (2.6)	38
20	32 (84.2)	5 (13.2)	1 (2.6)	38
25	34 (89.5)	3 (7.9)	1 (2.6)	38
30	34 (89.5)	3 (7.9)	1 (2.6)	38
35	33 (86.8)	4 (10.5)	1 (2.6)	38
40	33 (86.8)	4 (10.5)	1 (2.6)	38
45	32 (84.2)	6 (15.8)		38
50	24 (77)	7 (23)		31
55	16 (73)	6 (27)		22
60	18 (86)	3 (14)		21
Average	30.3 (86.8)	3.8(11.9)	0.5(1.3)	34.6

[1] Correct: within 1 m of measured heights; 1 class off: within 1 - 1.5 m; 2 classes off: within 1.6 - 2 m.

5.4.7. Comparison of the Site Unit Model and Goudie's Models

Goudie's site index (SI) driven height growth curves for lodgepole pine are widely used in British Columbia (Goudie 1984). Goudie constructed his curves using the Logistic model, stratifying sites into two site classes (dry and wet), and applying a modified Dahms (1975) parameter prediction approach, as did Monserud (1984). Goudie's curves and the SU curves for this study appeared similar for some SUs such as SBSmc/*Gymnocarpium* (SU5) and SBSwk/*Gymnocarpium* (SU8) (Figure 5.10, Table 5.16). However, there were some discrepancies that should be noted.

Firstly, although Goudie's curves paralleled the SU curves quite well in some cases, their fit was inferior to that achieved by the SU curves. The mean difference between the SI calculated from the Goudie's model and that measured in stem analysis was 0.73 m; the mean difference between the SI calculated from the SU model and that measured in stem analysis was 0.43 m, *i.e.*, about 37% improvement in precision (Table 5.16).

Secondly, the SU model estimated SI with > 1 m error for two SUs [SBSmc/*Gymnocarpium* and SBSwk/*Gymnocarpium*]; Goudie's model estimated SI with > 1 m error for 4 SUs [SBPSxc/*Stereocaulon* (SU1), SBSmc/*V. membranaceum* (SU4), SBSmc/*Gymnocarpium*, and SBSwk/*V. myrtiloides* (SU6)] (Table 5.16). Goudie's model consistently overestimated heights for 5 water-deficient SUs [SBPSxc/*Stereocaulon*, SBPSxc/*Arctostaphylos* (SU2), SBSxc/*Aulacomnium* (SU3), SBSmc/*V. membranaceum*, SBS/*V. myrtiloides*, and SBSwk/*V. membranaceum* (VU7)] and one waterlogged SUs [SBSwk/*Carex* (SU9)] (Table 5.16, Figure 5.10). Over estimation was especially severe for extremely dry and wet sites (SBPSxc/*Stereocaulon*, SBSwk/*Carex*). It is evident that biases from

Table 5.16. Comparison of site index estimated from the site unit model, Goudie's site index driven model, and measured site index.

Site unit (38 stands)	Goudie SI	Site unit SI	Actual SI	Errors G-A[1]	SU-A[2]
SBPSxc/*Stereocaulon*	7.3	8.79	8.70	-1.40	0.09
SBPSxc/*Arctostaphylos*	12.02	11.69	11.40	0.62	0.29
SBPSxc/*Aulacomnium*	13.80	14.56	14.00	-0.20	0.56
SBSmc/*Vacc. membranaceum*	16.75	15.90	15.75	1.20	0.15
SBSmc/*Gymnocarpium*	19.80	19.64	18.55	1.25	1.09
SBSwk/*Vacc. myrtiloides*	16,15	17.76	17.60	-1.45	0.16
SBSwk/*Vacc. membranaceum*	18.77	19.35	19.15	-0.38	0.20
SBSwk/*Gymnocarpium*	21.49	22.34	20.97	0.52	1.37
SBSwk/*Carex*	13.70	13.80	13.57	0.13	0.23
Average (n = 9)				0.73	0.43

[1] Errors between Goudie's site index and actual site index;
[2] Errors between site unit-specific site index and actual site index.

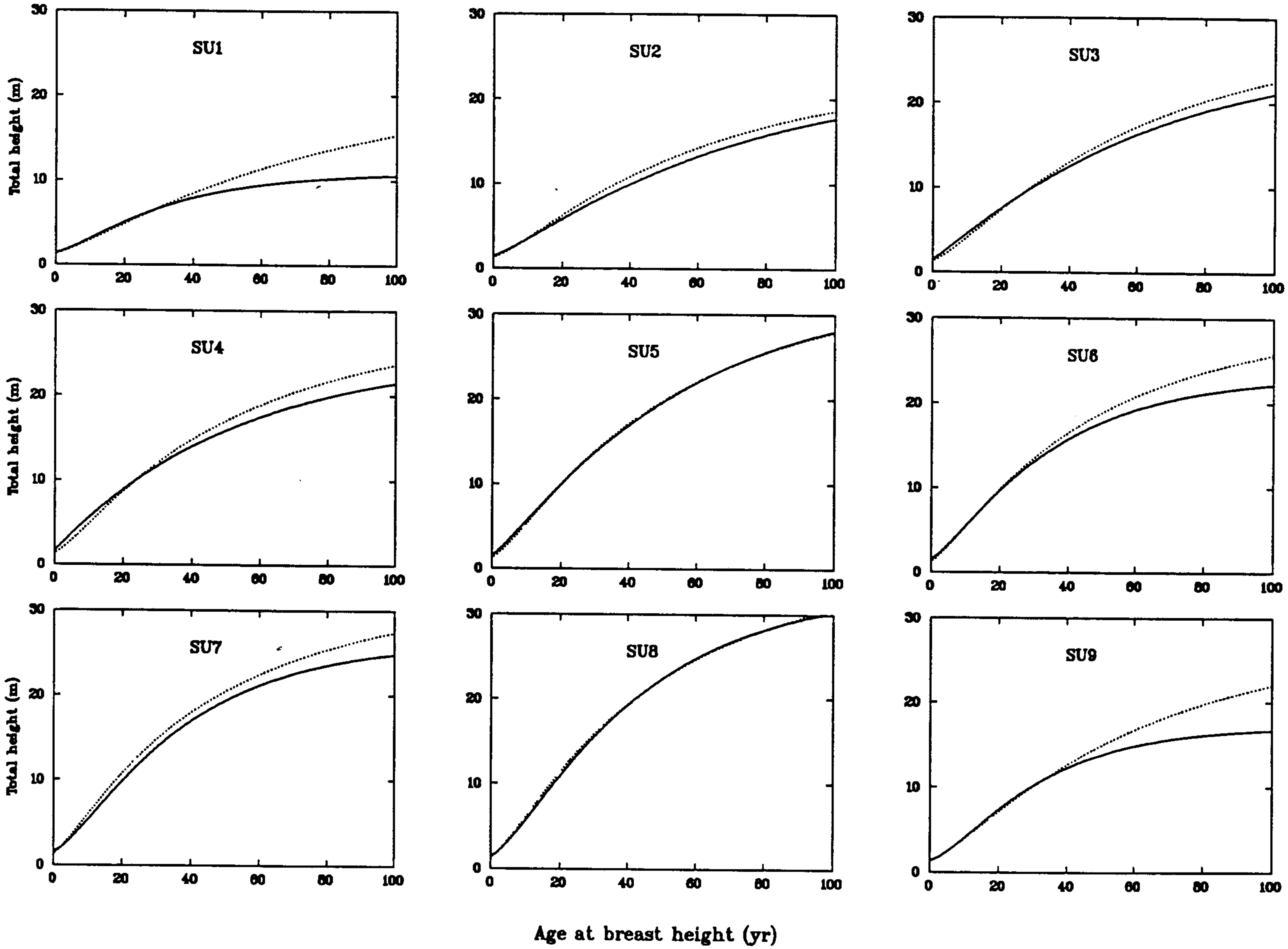

Figure 5.10. Comparison between site unit (solid lines) and Goudie's (dotted lines) height growth curves. Symbols for site units are explained in Table 5.6.

Goudie's model increase as soil moisture increases from very moist to very wet and decreases from fresh to slightly dry, moderately dry, very dry, and excessively dry. Thus, Goudie's curves appeared to be consistently biased for water-deficient sites and waterlogged sites, but for mesic (fresh, moist, and very moist) sites they described lodgepole pine height growth as well as the site unit height growth model.

Thirdly, Goudie's model does not solve the three problems inherent in site index driven modelling system described by Clutter *et al.* (1983). These problems are: (1) height growth curves do not pass through the height at index age, (2) height growth curves change when index age changes, and (3) site index can not be solved explicitly for a given age and height. The site-specific models developed in this study solve these three problems by not using site index in the model. Site index as a one point system can not possibly accurately explain polymorphic height growth patterns.

5.4.8. Physiological Characteristics of Height Growth

The Chapman-Richards growth function has a physiological premise. The function assumes the growth rate to be the result of two processes: anabolic rate (constructive metabolism such as photosynthesis) and catabolic rate (destructive metabolism such as respiration), *i.e.*, growth rate = anabolic rate - catabolic rate. In the case of height growth, the anabolic rate is assumed to be proportionally related to the height of trees and raised to a power (allometric constant), while the catabolic rate is assumed to be proportionally related to the height of trees only. These relationships can be expressed in the following form:

[5.4.19] $dH/dA = \alpha H^{m} - \beta H$, where dH/dA is the height growth rate, 'H' is the height, and 'A' is age of trees; 'α' is the anabolic constant; 'β' is the catabolic constant; 'm' is the allometric constant.

Equation [5.4.19] is known as the Chapman-Richards modified Von Bertalanffy growth function. When this function is solved by using *Bernoulli*'s equation for integration of differential equations with the special initial condition that H = 0 when A = 0, the resulting function is (Pienaar and Turnbull 1973):

[5.4.20] $$H = [(\frac{\alpha}{\beta})(1 - e^{-\beta(1 - m)A})]^{[1/(1 - m)]}$$

If $(\alpha/\beta)^{[1/(1 - m)]} = \beta_1$, $\beta(1 - m) = \beta_2$, and $1/(1 - m) = \beta_3$, then the outcome is the three parameter Chapman-Richards function (equation [5.3.3]). When β_1, β_2, and β_3 are estimated, it then becomes possible to compute the physiological parameters as follows (Pienaar and Turnbull 1973):

[5.4.21] the allometric constant $$m = 1 - \frac{1}{\beta_3}$$

[5.4.22] the catabolic constant $$\beta = \frac{\beta_2}{1 - m}$$

[5.4.23] the anabolic constant $$\alpha = [\frac{\beta_2}{1 - m}]\beta_1^{(1 - m)} \text{ or } \beta\beta_1^{(1 - m)}$$

Since all three physiological parameters were derived from a site-specific model, it was not surprising that the variation in the values of the computed physiological parameters (metabolic rate) for each site unit is related to the variation in climate, soil moisture, and soil nutrients (Table 5.17). This was also observed from the analysis of MAI and CAI. Lodgepole pine height growth in the SBSmc and SBSwk subzones has a higher metabolic rate than in the SBPSxc subzone. Within each subzone, the metabolic rate appears to increase with increasing soil moisture from excessively dry to very moist, and decrease with increasing soil moisture from very moist to wet.

Table 5.17. The physiological parameters derived from the Chapman-Richards function for site units stratified according to climate, soil moisture, and soil nutrient. Symbols for soil moisture and soil nutrient regimes are explained in Table 5.1.

Site unit	α	*β*	m	SMR	SNR
SBPSxc/*Stereocaulon*	0.251	0.055	0.323	ED	VP-P
SBPSxc/*Arctostaphylos*	0.238	0.018	0.165	VD-MD	VP-M
SBPSxc/*Aulacomnium*	0.333	0.018	0.087	MD-F	M-R
SBSmc/*Vacc. membranaceum*	0.439	0.019	0.008	SD	P-M
SBSmc/*Gymnocarpium*	0.438	0.022	0.138	F-VM	M-VR
SBSwk/*Vacc. myrtiloides*	0.434	0.042	0.246	MD	VP-M
SBSwk/*Vacc. membranaceum*	0.420	0.047	0.316	SD	P-M
SBSwk/*Gymnocarpium*	0.448	0.038	0.284	F-VM	M-VR
SBSwk/*Carex*	0.352	0.062	0.369	W	M-VR

5.4.9. Potential Application of the Site-specific Height Growth Models

The same ecological variables used in the model recommended to estimate site index (*i.e.*, biogeoclimatic subzone, soil moisture regime, and soil nutrient regime) are required for (1) identification of site series and (2) the application of the site unit or ecotope height growth model. With biogeoclimatic ecosystem classification in place and a site-specific height growth model constructed, it is logical to continue its development as it offers a very simple and effective tool to assess forest productivity. Knowledge of ecological quality for a site, regardless of whether it supports the growth of a particular tree species, is itself sufficient to estimate height growth at any point in time. Grouping site series within a zone or group of climatically related subzones into site units, on the basis of similarity and coherence in their height growth curves, should provide an acceptable number of site units for height growth prediction modelling.

Evidently, the model will perform correspondingly to the capability of a user to recognize different sites and to determine basic elements of ecological site quality. As this is being done routinely by practitioners in the course of preparing preharvest silvicultural prescriptions, the skills necessary for using the model would justify its further development, strengthening linkage between biogeoclimatic ecosystem classification and forest growth.

5.5. CONCLUSIONS

The pattern of height growth in the immature lodgepole pine stands studied was found to change with ecological site quality. The three-parameter Chapman-Richards growth function was successful in describing height growth of stands over a wide range of sites. In contrast to site index, several selected measures of ecological site quality had strong relationships to the function parameters. These were site series, ecotope (combination of biogeoclimatic subzone, soil moisture regime, and soil nutrient regime), and the combination of potential evapotranspiration, water deficit, the depth of water table or gleyed soil horizon, and mineralizable soil nitrogen. Two site-specific height growth models were developed using categorical ecological variables in parameter prediction—the site unit model and the ecotope model, each describing more precisely the shape of height growth curves and site index than Goudie's site index driven model based on the data that the site-specific model derived. However, no independent data were available for testing the site-specific models in comparison to Goudie's model. As the required ecological variables are routinely available from pre-harvest silvicultural prescriptions, it is logical to recommend that the site-specific models be further developed and tested, and then implemented.

6. SUMMARY AND CONCLUSIONS

(1) The diagnostic species and tabular analysis distinguished ten vegetation units. Both diagnostic species and vegetation units are strongly correlated with, and useful indicators of, relatively narrow segments of regional climatic, soil moisture, and soil nutrient gradients. The understory vegetation in unmanaged, mid-seral (30 to 80 year-old) immature lodgepole pine stands was sufficiently developed to indicate the ecological site quality of the study plots.

(2) On the basis of actual/potential evapotranspiration ratio and the depth of growing-season water table or gleyed soil horizon, eleven actual soil moisture regimes, with three regimes being recognized for sites with a strongly fluctuating water table, were successfully stratified. The criteria proposed by Klinka *et al.* (1989b) and the energy/soil-limited model (Spittlehouse and Black 1981) can be used to stratify the study sites into actual soil moisture regimes.

(3) Five soil nutrient regimes were delineated according to soil mineralizable-N and the sum of exchangeable Ca, K, and Mg. Similar to several previous studies, soil mineralizable-N and the sum of exchangeable Ca, K, and Mg are the most useful measures for the characterization of a soil nutrient gradient, and for the delineation of five traditionally used soil nutrient regimes. A complex soil nutrient gradient can be represented, but not replaced by a soil nitrogen gradient, *i.e.*, a one dimensional representation of soil nutrient gradient.

(4) Strong relationships exist between understory vegetation and categorical or continuous measures of soil moisture. These ecological measures have a meaning relative to soil moisture conditions experienced by plants. Similarly, there are strong relationships between soil mineralizable-N with frequency of nitrophytic plants, and with foliar N. Soil nitrogen is the primary determinant of the soil nutrient gradient in the study area, and the criteria and limits used to stratify the study plots into soil nutrient regimes have meaning relative to the general nutrient supply for plants.

(5) Eleven site associations were distinguished based on climate, soil moisture, and soil nutrient regimes in this study. Site associations can stratify the forest sites into qualitatively and quantitatively distinct, field recognizable, segments of regional gradients of ecological site quality.

(6) Thirty regression models were developed to examine the relationships between site index and ecological site quality. The most strongly related ecological variables to lodgepole pine site index are: ecotopes defined either by a combination of categorical variables (biogeoclimatic subzone, soil moisture regime, and soil nutrient regime) (adj. $R^2 = 0.85$) or by a combination of continuous variables (potential evapotranspiration, the depth of water table or gleyed soil horizon, and mineralizable soil nitrogen) (adj. $R^2 = 0.82$), site associations (adj. $R^2 = 0.81$), site series (adj. $R^2 = 0.84$), and vegetation units (adj. $R^2 = 0.83$). Either categorical or continuous synoptic ecological variables can be used in describing the variation of lodgepole pine site index with a change in ecological site quality. Lodgepole pine appears to have a potential to grow on nitrogen-rich sites with pH < 7. The plotting of site index isolines onto edatopic grids represents both effective format and

useful means for field personnel to estimate lodgepole pine height growth on any given site.

(7) The three-parameter Chapman-Richards growth function, fit from stem analysis data, precisely described height growth of immature lodgepole stands over a wide range of sites. Site series and ecotope, defined either by a combination of biogeoclimatic subzone, soil moisture regime, and soil nutrient regime or potential evapotranspiration, the depth of water table or gleyed soil horizon, and mineralizable soil nitrogen, had a stronger relationship with the function parameters than site index. The pattern of lodgepole pine height growth in the study area changes with ecological site quality. There is a strong link between lodgepole pine height growth and measures of ecological site quality derived from the biogeoclimatic ecosystem classification of the study plots. Categorical or continuous ecological variables can be used in polymorphic height growth modelling to precisely predict lodgepole pine height growth so that the effects of site, environmental changes, including management practices, on forest productivity can be better understood. The site-specific height growth models are more effective and precise in describing lodgepole pine height growth than site index driven height growth models.

REFERENCES

Agriculture Canada Expert Committee on Soil Survey. 1987. The Canadian system of soil classification. Agric. Canada Publ. 1646. Ottawa, Ontario. 164 pp.

Alexander, R.R., D. Tackle, and W.G. Dahms. 1967. Site index for lodgepole pine, with corrections for stand density: methodology. USDA For. Ser. Res. Pap. RM-29, Fort Collins, Colorado. 18 pp.

Anonymous. 1976. Technicon Analyzer II methodology: individual/simultaneous determination of nitrogen and/or phosphorus in BD acid digests. Industrial Method No. 328/74W/A. Technon Corp., Tarrytown, New York.

Anonymous. 1982. Canadian climate normals. 1951-1980. Temperature and precipitation. Vol. 6. Environment Canada. Atmospheric Environment Service. Ottawa, Ontario. 276 pp.

Assmann, E. 1970. The principles of forest yield study. Pergamon Press, New York. 506 pp.

Bakuzis, E.V. 1969. Forestry viewed in an ecosystem perspective. pp. 189-258. *In* G.M. Van Dyne (ed.), The ecosystem concept in natural resource management. Academic Press, New York.

Ballard, T.M. and R.E. Carter. 1986. Evaluating forest stand nutrient status. Land Manage. Rep. No. 20., B.C. Min. For., Victoria, B.C. 60 pp.

Banner, A., R.N. Green, K. Klinka, D.S. McLennan, D.V. Meidinger, F.C. Nuszdorfer, and J. Pojar. 1990. Site classification for coastal British Columbia: a first approximation. B.C. Min. For., Victoria B. C. 2 pp. (a coloured pamphlet).

Barksley, C.E. and J.D. Lancaster. 1965. Sulfur. *In* C.A. Black et al. (eds.) Methods of soil analysis. Agron. No. 9. Am. Soc. Agron., Inc., Madison, Wisconsin.

B.C. Ministry of Forests, Research Branch. 1988. Biogeoclimatic zones of British Columbia (a colorized map). Min. For. Res. Branch, Victoria, British Columbia.

Beck, D.E. 1971. Polymorphic site index curves for white pine in the southern Appalachians. USDA For. Ser., Res. Pap. SE-80. Asheville, North Carolina. 8 pp.

Becking, R.W. 1957. The Zurich-Montpellier school of phytosociology. Bot. Rev. 23: 411-488.

Borland International, Inc. 1989. Quattro Pro. Scotts Valley, California.

Braun-Blanquet, J. 1932. Plant sociology. (Transl. by Fuller, G.D. and H.S. Conard). New York. 439 pp.

Bremner, J.M. and C.S. Mulvaney. 1982. Nitrogen--Total. pp. 595-624. *In* A.L. Page (ed.) Methods of soil analysis. Agron. No. 9. part 2. Am. Soc. Agron.,Inc. and Soil Sci. Soc. Am., Inc. Wisconsin.

Bremner, J.M. and M.A. Tabatabai. 1971. Use of automated combustion techniques for total carbon, total nitrogen, and total sulfur analysis. pp. 1-15. *In* Walsh, L.M. (ed.) Instrumental methods for analysis of soil and plant tissue. Soil Sci. Soc. Am., Inc. Wisconsin.

Burger, D. 1972. Forest site classification in Canada. Mitteilungen des Vereins für Forsliche Standortskunde und Forstpflanzenzüchtung 12: 20-36.

Burns, R.M. and B.H. Honkala 1990. Silvics of North America. Agriculture Handbook 654 vol 1. USDA For. Ser., Washington D.C. 675 pp.

Cajander, A.K. 1926. The theory of forest types. Acta For. Finn. 29: 1-208.

Cajander, A.K. and Y. Ilvessalo. 1921. Über waldtypen II. Acta For. Finn. 20: 1-77.

Cajander, A.K. 1949. Forest types and their significance. Acta For. Finn. 56: 1-69, 1-71.

Campbell, G.S. 1986. Extinction coefficients for radiation in plant canopies calculated using ellipsoidal inclination angle distribution. Agrc. and For. Meter. 36: 317-321.

Carmean, W.H. 1956. Suggested modifications of the standard Douglas-fir site curves for certain soils in Southwestern Washington. For. Sci. 2: 242-250.

Carmean, W.H. 1970. Tree height growth patterns in relation to soil and site. pp. 499-512. *In* C.T. Youngberg and C.B. Davey (eds.) Tree growth and forest soils. Proceedings of Third North American Forest Soils.

Carmean, W.H. 1972. Site index curves for upland oaks in the Central States. For. Sci. 18: 102-120.

Carmean, W.H. 1975. Forest site quality evaluation in the United States. Advances in Agronomy 27: 209-269.

Carmean, W.H. 1982. Soil-site evaluation for conifers in the upper great lakes region. *In* Artificial regeneration of conifers. Michigan Technological University, Michigan.

Carter, R.E. and K. Klinka. 1990. Relationships between growing-season soil water-deficit, mineralizable soil nitrogen and site index of coastal Douglas fir. For. Ecol. Manage. 30: 301-311.

Carter, R. and K. Klinka. 1991. Use of ecological site classification in the prediction of forest productivity and response to fertilization. pp. 382-392 *In* A.P.G. Schönau (ed.) Intensive forestry: the role of eucalypts. IUFRO symposium proceedings. Durban, South Africa.

Carter, R.E., Q. Wang, J.A.P. Neumann, and K. Klinka. 1991. Relationships between leaf area and ecological site quality in immature lodgepole pine stands of British Columbia. Unpublished manuscript.

Chambers, J.M., W.S. Cleveland, B. Kleiner, and P.A. Tukey. 1983. Graphical methods for data analysis. Wadsworth & Brooks/Cole Pub. Com. California. 395 pp.

Chapman, D.G. 1961. Statistical problems in population dynamics. pp. 147-162 *In* Proc. Fourth Berkerley Symp. Math. Stat. and Prob. Univ. California Press, Berkerley and Los Angeles.

Chatterjee, S. and B. Price. 1977. Regression analysis by example. John Wiley & Sons, New York. 228 pp.

Clutter, J.L., J.C. Fortson, L.V. Pienaar, G.H. Brister, and R. Bailey. 1983. Timber management: a quantitative approach. John Willey & Sons, New York. 331 pp.

Cohran, P.H. 1975. Natural regeneration of lodgepole pine in south-central Oregon. USDA For. Ser. Res. Notes. PNW-204. Portland, Oregon. pp 18.

Cochran, P.H. 1985. Soils and productivity of lodgepole pine. pp. 89-93. *In* D.A. Baumgartner *et al.*(eds.) Lodgepole pine, the species and its management. Symposium proc. Pullman, Washington.

Corns, I.G.W. and D.J. Pluth. 1984. Vegetational indicators as independent variables in forest growth prediction in west-central Alberta, Canada. For. Ecol. Manage. 9: 13-25.

Courtin, P.J., K. Klinka, M.C. Feller, and J.P. Demaerchalk. 1988. An approach to quantitative classification of nutrient regimes of forest soils. Can. J. Bot. 66: 2640-2653.

Cunia, T. 1973. Dummy variables and some of their uses in regression analysis. Proc. IUFRO Subject Group S4.02. Vol. 1: 1-146.

Curtis, J.T. 1959. The vegetation of Wisconsin; An ordination of plant communities. Univ. Wisconsin, Madison, Wisconsin. 657 pp.

Dahms, W.G. 1975. Gross yield of central Oregon lodgepole pine. pp. 208-232. *In* D.M. Baumgartner (ed.) Management of lodgepole pine ecosystems. Symposium Proc. Wash. State Univ., Coop. Ext. Serv., Pullman, Washington.

Dahl, E. 1956. Rondane: Mountain vegetation in south Norway and its relation to the environment. Skr. norske Vidensk-Akad. Mat. Naturv. Kl. No. 3. 374 pp.

Damman, A.W.H. 1979. The role of vegetation in land classification. For. Chron. 55: 175-182.

Daniel, T.W., J.A. Helms, and F.S. Baker. 1979. Principles of silviculture. 2nd. ed. McGraw-Hill Book Company, New York. 500 pp.

Daubenmire, R.F. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22: 301-330.

Daubenmire, R.F. 1968. Plant communities. Harper & Row, Inc., New York. 300 pp.

Day, P.R. 1965. Particle fractionation and particle-size analysis. pp. 545-567. *In* Black, C.A. *et al.* (eds) Methods of soil analysis, Part I. Agron. no 9. Am. Soc. Agron. and Soil Sci. Soc. Am. Madison, Wisconsin.

Decagon Devices. 1987. Sunfleck ceptometer users manual. Decagon Devices, Pullman, Washington. 27 pp.

Dillon, W.R. and M. Goldstein. 1984. Multivariate analysis. Methods and applications. John Wiley & Sons, Inc., New York. 587 pp.

Duffy, P.J.B. 1964. Relationships between site factors and growth of lodgepole pine (*Pinus contorta* Dougl. *var. latifolia* Engelm.) in the foothill section of Alberta. Can. Depart. For., Publ. 1065. Ottawa, Ontario. 60 pp.

Dyer, M.E. and R.L. Bailey. 1987. A test of six methods for estimating true heights from stem analysis data. For. Sci. 33: 3-13.

Eis, S., D. Craigdallie, and C. Simmons. 1982. Growth of lodgepole pine and white spruce in the central interior of British Columbia. Can. J. For. Res. 12: 567-575.

Emanuel, J. 1987. A vegetation classification program (VTAB). Fac. For., Univ. British Columbia, Vancouver, B.C. 26 pp.

Etter, H.M. 1969. Growth metabolic components and drought survival of lodgepole pine seedlings at three nitrate levels. Can. J. Plant Sci. 49: 393-402.

Feoli, E. and L. Orlóci. 1979. Analysis of concentration and detection of underlying factors in structure tables. Vegetatio 40: 49-54.

Fox, D.J. and K.E. Guire. 1976. Documentation of MIDAS. Statistical Research Laboratory, Univ. Michigan, Illinois, Michigan. 203 pp.

Fries, J. 1978. The assessment of growth and yield and the factors influencing it. Special paper presented at the VIII IUFRO World Forestry Congress, Jakarta, Indonesia.

Gee, G.W. and J.W. Bauder. 1986. Particle-size analysis. *In* Page, A.L. *et al.* (eds.) Methods of soil analysis, Part I, Physical and Mineralogical Methods. Agron. Monog. no. 9. Am. Soc. Agron and Soil Sci. Soc. Am. Madison, Wisconsin.

Gittins, R. 1985. Canonical analysis. Springer-Verlag, New York. 351 pp.

Goodall, D.W. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. Aust. J. Bot. 2: 304-324.

Goudie, J.W. 1984. Managed stand yield tables for interior lodgepole pine: initial and post-spacing density. B.C. Min. For., Victoria, B. C. 14 pp.

Graney, D.L. and H.E. Burkhart. 1973. Polymorphic site index curves for shortleaf pine in the Ouachita Mountains. USDA For. Ser., Res. Pap. SO-85. New Orleans, Louisiana. 14 pp.

Green, R.N., P.L. Marshall, and K. Klinka. 1989. Estimating site index of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) from ecological variables in southwestern British Columbia. For. Sci. 35: 50-63.

Grier, C.C., K.M. Lee, N.M. Nadkarni, G.O. Klock, and P.J. Edgerton. 1989. Productivity of forests of the United States and its relation to soil and site factors and management practice: a review. USDA, For. Ser. Gen. Techn. Rep. PNW-222. Portland, Oregon. pp. 51.

Habgood, H.L. 1985. Estimation of browse biomass production of *Salix spp.* and *Betula glandulosa* using multiple linear regression. M. Sc. thesis. The University of British Columbia, Vancouver, B.C. 107 pp.

Hägglund, B. 1981. Evaluation of forest site productivity. For. Abs. 42: 515-527.

Hale, M.E.Jr. and W.L. Curberson. 1970. A fourth checklist of the lichens of the continental United States. The Bryologist 73: 499-543.

Hall, F.C. 1987. Growth basal area handbook. USDA For. Ser. R6-Ecol. 181b-1984. Portland, Oregon. 84 pp.

Hall, F.C. 1989. The concept and application of growth basal area: a forestland stockability index. USDA For. Ser., R6-Ecol. Tech. Pap. 007-89. Portland, Oregon. 86 pp.

Harrington, C.A. 1986. A method of site quality evaluation for red alder. USDA For. Ser. Gen. Tech. Rep. PNW-192. Portland, Oregon.

Hills, G.A. 1952. The classification and evaluation of site for forestry. Dept. of Lands and For., Res. Rep. 24. Toronto, Ontario. 41 pp.

Hitchcock, C.L. and A. Cronquist. 1973. Flora of the pacific northwest. An illustrated manual. Univ. of Wash. Press, Seattle, Washington. 730 pp.

Holland, S.S. 1976. Landforms of British Columbia. A physiographic outline. Bull. No. 8. 2nd ed. B.C. Dept. of Mines and Mineral Resources, Victoria, British Columbia. 138 pp.

Holmes, J.R.B. and D. Tackle. 1962. Height growth of lodgepole pine in Montana related to soil and stand factors. Bull. 21. Montana State Univ. Missoula, Montana. pp. 12.

Hosie, R.C. 1979. Native trees of Canada. 8th ed. Fitzhenry & Whiteside Ltd. Toronto, Ontario. 380 pp.

Illingworth, K. and J.W.C. Arlidge. 1960. Interim report on some forest site types in lodgepole pine and spruce-alpine fir stands. Res. Notes 35. Min. For. Ser., B.C., Victoria, British Columbia. 44 pp.

Ireland, R.R., C.D. Bird, G.R. Brassard, W.B. Schofield, and D.H. Vitt. 1980. Checklist of the mosses of Canada. National Museum of Natural Science publication in Botany, No. 8. National Museums of Canada, Ottawa, Ontario. 75 pp.

Jarvis, P.G. and J.W. Leverenz. 1983. Productivity of temperate, deciduous and evergreen forests. pp. 233-280 *In* O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler (eds.). Ecosystem processes: mineral cycling, productivity and man's influence. Physiological Plant Ecology: new series. Vol. 12D. Springer-Verlag, New York.

Jones, J.R. 1969. Review and comparison of site evaluation methods. USDA For. Ser., Res. Pap. RM-51. Fort Collins, Colorado. 27 pp.

Kabzems, R.D. 1985. Characterization of soil nutrient regimes in Douglas-fir ecosystems in the Drier Maritime Coastal Western Hemlock subzone. M. Sc. thesis, Faculty of Forestry, Univ. B.C., Vancouver, British Columbia.

Kabzems, R.D. and K. Klinka. 1987. Initial quantitative characterization of soil nutrient regimes. Can. J. For. Res. 17: 1557-1571.

Kennedy, R.W. 1985. Lodgepole pine as a commercial resource in Canada. pp. 21-23. *In* D.M. Baumgartner *et al.* (eds.) Lodgepole pine - the species and its management. Symposium proceedings. Wash. State Univ. Pullman, Washington.

Kimmins, J.P. 1977. The need for ecological classification in B.C. B.C. Forestry 2(1). 2 pp. Assoc. of B.C. Prof. Foresters. Vancouver, British Columbia.

Klinka, K. and M.C. Feller. 1984. Principles of tree species selection used in regenerating forest sites in southwestern British Columbia. For. Chron. 60: 77-85.

Klinka, K. and V.J. Krajina. 1986. Ecosystems of the University of British Columbia Research Forest. Fac. of For., Univ. B.C., Vancouver, British Columbia. 123 pp.

Klinka, K., Q. Wang, and R.E. Carter. 1990a. Relationships among humus forms, forest floor nutrient properties, and understory vegetation. For. Sci. 36: 564-581.

Klinka, K., R.N. Green, R.L. Trowbridge, and L.E. Lowe. 1981. Taxonomic classification of humus forms in ecosystems of British Columbia. B.C. Min. of For., Land. Manag. Rep. No. 8., Victoria, British Columbia. 54 pp.

Klinka, K., R.E. Carter, M.C. Feller, and Q. Wang. 1989a. Relations between site index, salal, plant communities, and sites in coastal Douglas-fir ecosystems. Northwest Sci. 63: 19-28.

Klinka, K. and R.E. Carter. 1990. Relationships between site index and synoptic environmental variables in immature coastal Douglas-fir stands. For. Sci. 36: 815-830.

Klinka, K., V.J. Krajina, A. Ceska, and A.M. Scagel. 1989b. Indicator plants of coastal British Columbia. Univ. B.C. Press, Vancouver, British Columbia. 288 pp.

Klinka, K., M.C. Feller, R.N. Green, D.V. Meidinger, J. Pojar, and J. Worrall. 1990b. Ecological principles: applications. pp. 55-72 *In* D.P. Lavander *et al* (eds.). Regenerating British Columbia's forests. Univ. B.C. Press, Vancouver, British Columbia.

Krajina, V.J. 1933. Die Pflanzengesellschaften des Mlynica-Tales in den Vysoke Tatry (Hohe Tatra) mit besonderer berücksichtingung ökologischen Verhältnisse. Bot. Centralbl. Abt. 2, 50: 744-956, 51: 1-244.

Krajina, V.J. 1965a. Philosophy of ecology. Ecol. West. N. Amer. 1: 102-111.

Krajina, V.J. 1965b. Biogeoclimatic zones of British Columbia. Ecol. West. N. Amer. 1: 1-17.

Krajina, V.J. 1969. Ecology of forest trees in British Columbia. Ecol. West. N. Amer. 2: 1-146.

Krajina, V.J. 1972. Ecosystem perspectives in forestry. H.R. MacMillan Forestry Lecture Series, Faculty of Forestry, Univ. B.C., Vancouver, British Columbia. 31 pp.

Lausi, D. and P.L. Nimis. 1985. Roadside vegetation in boreal South Yukon and adjacent Alaska. Phytocoenologia 13: 103-138.

Li-Cor Inc. 1986. Li-cor radiation sensors instruction manual. Li-Cor Inc. Lincoln, Nebraska. 24 pp.

Lotan, J.E. and D.A. Perry. 1983. Ecology and regeneration of lodgepole pine. USDA For. Ser. Agric. Handbook No. 606. Washington, D.C. 51 pp.

Lowe, L.E. and T.F. Guthrie. 1984. A comparison of methods for total sulfur analysis of tree foliage. Can. J. For. Res. 14: 470-473.

Luttmerding, H.A., D.A. Demarchi, E.C. Lea, D.V. Meidinger, and T. Vold (eds.). 1990. Describing ecosystems in the field. 2nd ed., B.C. Min. For., Victoria, British Columbia. 213 pp.

MacLean, C.D. and C.L. Bolsinger. 1973. Estimating Dunning's site index from plant indicators. USDA For. Serv. Res. Note PNW-152. Portland, Oregon. 18 pp.

Major, J. 1963. A climatic index to vascular plant activity. Ecol. 44: 485-498.

Mason, R.R. and T.C. Tigner. 1972. Forest-site relationships within an outbreak of lodgepole pine needle miner in central Oregon. USDA For. Ser. Res. Pap. PNW-146. Portland, Oregon. 18 pp.

McLain, D.H. 1974. Drawing contours from arbitrary data points. The Computer Journ. 17: 318-324.

Meidinger, D. and J. Pojar (eds.). 1991. Ecosystems of British Columbia. Special Report Series, no. 6. B.C. Min. For., Victoria, British Columbia. 330 pp.

Mehlich, A. 1978. New extractant for soil test evaluation of phosphorus, magnesium, calcium, sodium, manganese, and zinc. Comm. Soil. Sci. Plant Anal. 9: 477-492.

Milner, K.S. 1987a. The development of site specific height growth curves for four conifers in western Montana. Ph.D. Dissertation. Univ. of Montana, Missoula, Montana. 169 pp.

Milner, K.S. 1987b. Constructing site specific height growth curves. *In* Ek et al. (eds) Forest growth modelling and prediction 1:411-418. Proceedings of the IUFRO Conference. USDA For. Ser., General Tech. Rep. NC-120. St. Paul, Minnesota.

Mogren, E.W. and K.P. Dolph. 1972. Prediction of site index of lodgepole pine from selected environmental factors. For. Sci. 18: 314-316.

Monserud, R.A. 1984. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. For. Sci. 30: 943-965.

Monserud, R.A. 1988. Variation on the theme of site index. In Forest growth modeling and prediction. USDA For. Ser. Gen. Tech. Rep. NC-120. St. Paul, Minnesota.

Moore, J.J. 1962. The Braun-Blanquet system: a reassessment. J. Ecol. 50: 761-769.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Willey & Sons, New York. 547 pp.

Nuszdorfer, F.C. 1981. Methods of sampling and analysis. 48-53. In Klinka et al. Taxonomic classification of humus forms in ecosystems of British Columbia. Land Manage. Rep. no. 8. B.C. Min. For., Victoria, British Columbia. 54 pp.

Odum, E.P. 1971. Fundamentals of ecology. 3rd ed. W.B. Saunders Co., Toronto, Ontario. 574 pp.

Oliver, C.D. and B.C. Larson. 1990. Forest stand dynamics. McGraw-Hill, New York. 467 pp.

Oliver, W.W. 1967. Ponderosa pine can stagnate on a good site. J. For. 65: 814-816.

Orlóci, L. 1988. Community organization: recent advances in numerical methods. Can. J. Bot. 66: 2626-2633.

Page, A.L. (ed.). 1982. Methods of soil analysis. Agron. No. 9. part 2. Am. Soc. Agron., Inc. and Soil Sci. Soc. Am., Inc. Madison, Wisconsin.

Parkinson, J.A. and S.E. Allen. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineralizable nitrogen in biological material. Comm. Soil. Sci. Plant Anal. 6: 1-11.

Peech, M. 1965. Hydrogen-ion activity. 914-926. *In* C.A. Black *et al.* (eds.). Methods of soil analysis. Agron. no. 9. Am. Soc. Agron. Madison, Wisconsin.

Pfister, R.D. and S.F. Arno. 1980. Classifying forest habitat types based on potential climax vegetation. For. Sci. 26: 52-69.

Pienaar, L.V. and K.J. Turnbull. 1973. The Chapman-Richards generalization of Von Bertalanffy's growth model for basal area growth and yield in even-aged stands. For. Sci. 19: 2-22.

Pogrebnyak, P.S. 1930. Über die methodik der standortsuntersuchungen in verbindung mit den waldtypen. pp. 455-471 *In* Verhandlungen des II. Internationalen Kongresses Forstlichen Versuchsanstalten. Stockholm.

Pojar, J. 1983. Forest ecology. pp. 221-318 *In* S.B. Watts (ed.), Forestry handbook for British Columbia. The For. Undergraduate Soc., Faculty of For., Univ. B.C. Vancouver, British Columbia.

Pojar, J. 1985. Ecological classification of lodgepole pine in Canada. pp. 77-88 *In* D.M. Baumgartner *et al.* (eds.), Lodgepole pine: The species and its management. Symp. Proc., Wash. State Univ., Pullman, Washington.

Pojar, J., R. Trowbridge, and D. Coates. 1984. Ecosystem classification and interpretation of the Sub-Boreal Spruce zone, Price Rupert Forest Region, British Columbia. Land Manage. Rep. 17. B.C. Min. For., Victoria, British Columbia. 319 pp.

Pojar, J., K. Klinka, and D. Meidinger. 1986. Ecosystem classification by the British Columbia Forest Service. pp. 68-88 *In* H. van Groenewoud (compiler), Forest site classification method. Proceedings of the workshop of the IUFRO working party on site classification and evaluation. Canadian For. Ser.-Maritimes. Fredericton, New Brunswick. pp. 182.

Pojar, J., K. Klinka, and D.V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. 22: 119-154.

Poore, M.E.D. 1955. The use of phytosociological methods in ecological investigations. Part I, II, III. J. Ecol. 43: 226-244, 245-269, 606-651.

Poore, M.E.D. 1962. The method of successive approximation in descriptive ecology. Adv. Ecol. 11: 57-77.

Powers, R.F. 1980. Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. Soil Sci. Soc. Am. J. 44: 1314-1320.

Price, W.J. 1978. Analytic atomic absorption spectrophotometry. Heyton and Son Ltd., London. 239 pp.

Rawlings, J.O. 1988. Applied regression analysis: a research tool. Wadsworth, Inc., California. 553 pp.

Richards, F.J. 1959. A flexible growth function for empirical use. J. Exptl. Bot. 10: 290-300.

Richards, F.J. 1969. The quantitative analysis of growth. pp. 3-76. *In* F.C. Steward (ed.) Plant physiology, a treatise. vol. 5A. Academic Press, New York.

Roydhouse, F.M., J.L. Crane, and J.H. Bassman. 1985. Biomass distribution in young stands of stagnant and non-stagnant lodgepole pine. pp. 379. *In* Lodgepole pine, the species and its management. Symposium proceedings. Wash. State Univ., Pullman, Washington.

Rose, M.F. and C. Grant. 1976. Remote station climate prediction model. Environment and Land Use Committee, Data Service Division, Victoria, B.C. (mimeo.).

Sander, D.H. 1966. Effect of urea and urea-formaldehyde on the growth of lodgepole pine seedlings in a nursery. Tree Plant. Notes 79: 18-23.

SAS Institute Inc. 1985. SAS user's guide: statistics. Ver. 5. SAS Institute Inc. Cary, North Carolina. 956 pp.

Shimwell, D.W. 1971. The description and classification of vegetation. Univ. Washington Press, Seattle, Washington. 322 pp.

Smith, C.A.B. 1947. Some examples of discrimination. Annals of Eugenics. 13: 272-282.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy. Freeman, San Francisco, California.

Spittlehouse, D.L. and T.A. Black. 1981. A growing-season water balance model applied to two Douglas-fir stands. Water Resour. Res. 17: 1651-1656.

Spurr, S.H. and B.V. Barnes. 1980. Forest ecology. 3rd ed. John Wiley & Sons, New York. 687 pp.

Stottler, R. and B. Grandall-Stottler. 1977. A checklist of the liverworts and hornworts of North America. Bryologist 80: 405-428.

Strub, M.R. and P.T. Sprinz. 1987. Comparisons of southern pine height growth. *In* Elk et al. (eds) Forest growth modelling and prediction 1: 428-434. Proceedings of the IUFRO Conference. USDA For. Ser., General Tech. Rep. NC-120. St. Paul, Minnesota.

Sukachev, V.N. 1964. Main concepts of forest biogeocoenology (In Russian). In Osnovy lesn. biogeotsenologii. 5-59. Moscow.

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. The geographical review. 38: 55-94.

Trewartha, K.W.G. 1968. An introduction to climate. 4th ed. McGraw-Hill Book Co., New York. 408 pp.

Trousdell, K.B., D.E. Beck, and F.T. Lloyd. 1974. Site index for loblolly pine in the Atlantic Coastal Plain of the Carolinas and Virginia. USDA For. Ser., Res. Pap. SE-115. Asheville, North Carolina. 11 pp.

Valentine, K.W.G. and A.B. Dawson. 1978. The interior plateau. pp. 121-134 *In* K.W.G. Valentine *et al.* (eds.) The soil landscape of British Columbia. Min. Environm., Resource Anal. Branch, Victoria, British Columbia. 197 pp.

Van Dyne, G.M. (ed.) 1969. The ecosystem concept in natural resource management. Academic Press, New York. 383 pp.

Verbyla and Fisher 1989. An alternative approach to conventional soil-site regression modeling. Can. J. For. Res. 19: 179-184.

Vitt, D.H., J.E. Marsh, and B.B. Bovey. 1988. Mosses, lichens, and ferns of northwest North America. A photographic field guide. Lone Pine Publ., Edmonton, Alberta. 296 pp.

Von Bertalanffy, L. 1951. Theoretiche biologie. Franke, Bern. 403 pp.

Walsmley, M., G. Utzig, T. Vold, D. Moon, and J. van Barnveld (eds.). 1980. Describing ecosystems in the field. B.C. Min. Env., RAB Tech. Pap. 2, B.C. Min. For., Land Manage. Rep. No. 7. Victoria, British Columbia. 225 pp.

Waring, S.A. and J.M. Breminer 1964. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. Nature 201: 951-952.

Wheeler, N.C. and W.B. Critchfield. 1985. The distribution and botanical characteristics of lodgepole pine: biogeographical and management implications. pp. 1-12. *In* D.M. Baumgartner *et al.* (eds.) Lodgepole pine, the species and its management. Symposium proceedings. Wash. State Univ., Pullman, Washington.

Weetman, G.F., R.C. Yang, and I.E. Bella. 1985. Nutrition and fertilization of lodgepole pine. pp. 225-232. *In* D.M. Baumgartner *et al.* (eds.) Lodgepole pine, the species and its management. Symposium proc. Wash. State Univ., Pullman, Washington.

Whittaker, R.H. 1956. Vegetation of the Great Smoky mountains. Ecol. Monogr. 26: 1-80.

Whittaker, R.H. 1967. Gradient analysis of vegetation. Biol. Rev. 42: 207-264.

Whittaker, R.H. (ed.) 1978. Ordination of plant communities. Junk, The Hague, Boston. 388 pp.

Wilkinson, L. 1990. SYSTAT: The system for statistics. Evanston, Illinois. SYSTAT Inc. 822 pp.

Wu, Zh. Y. (ed. in chief). 1980. Vegetation of China. Science Press. Beijing, China. 1375 pp. (in Chinese).

Youngberg, C.T. and W.G. Dahms. 1970. Productivity indices of lodgepole pine on pumice soils. J. For. 68: 90-94.

Zeide, B. 1978. Standardization of growth curves. J. For. 76: 289-292.

APPENDIX I

LIST OF PLANT SPECIES FOUND IN THE STUDY PLOTS

Coniferous trees

1 *Abies lasiocarpa* (Hook.) Nutt.
2 *Picea glauca* (Moench) Voss
3 *P. mariana* (Mill.) BSP.
4 *Pinus contorta* Dougl. *ex* Loud.
5 *Thuja plicata* Donn *ex* D. Don
6 *Tsuga heterophylla* (Raf.) Sarg.

Broad-leaved trees

7 *Betula papyrifera* Marsh.
8 *Populus tremuloides* Michx.
9 *P. trichocarpa* Torr. *et* Gray *ex* Hook.
10 *Prunus pensylvanica* L.f.

Evergreen shrubs

11 *Andromeda polifolia* L.
12 *Arctostaphylos uva-ursi* (L.) Spreng.
13 *Chimaphila umbellata* (L.) Barton
14 *Empetrum nigrum* L.
15 *Gaultheria hispidula* (L.) Muhlenb. *ex* Bigel.
16 *Kalmia microphylla* (Hook.) Heller
17 *Ledum groenlandicum* Oeder
18 *Juniperus sibirica* L.

Deciduous shrubs

19 *Alnus sinuata* (Regel) Rydb.
20 *Amelanchier alnifolia* (Nutt.) Nutt.
21 *Betula glandulosa* Michx.
22 *Cornus sericea* L.
23 *Lonicera involucrata* (Richards.) Banks *ex* Spr.
24 *Menziesia ferruginea* Sm.
25 *Ribes glandulosum* Grauer.
26 *R. hudsonianum* Richards.
27 *R. lacustre* (Pers.) Poir.
28 *R. oxyacanthoides* L.
29 *R. triste* Pall.
30 *Rosa acicularis* Lindl.
31 *Rubus idaeus* L.
32 *R. parviflorus* Nutt.
33 *Salix barclayi* Anderss.
34 *S. bebbiana* Sarg.
35 *S. drummondiana* Barratt
36 *S. maccalina* Rowlee
37 *S. monticola* Bebb. *ex* Coult.

38 *S. planifolia* Pursh
39 *S. pyrifolia* Anderss.
40 *S. rigida* Muhlenb.
41 *S. scouleriana* Barratt
42 *S. sitchensis* Sanson
43 *Sambucus racemosa* L.
44 *Shepherdia canadensis* (L.) Nutt.
45 *Sorbus scopulina* Greene
46 *Spiraea betulifolia* Pall.
47 *S. douglasii* Hook.
48 *Symphoricarpos albus* (L.) Blake
49 *V. caespitosum* Michx.
50 *V. membranaceum* Dougl. *ex* Hook.
51 *V. myrtilloides* Michx.
52 *V. ovalifolia* Sm.
53 *Viburnum edule* (Michx.) Raf.

Ferns

54 *Athyrium filix-femina* (L.) Roth
55 *Botrychium virginianum* (L.) Sw.
56 *Dryopteris expansa* (Presl) Fraser-Jenkins
57 *Equisetum arvense* L.
58 *E. hyemale* L.
59 *E. palustre* L.
60 *E. scirpoides* Michx.
61 *E. sylvaticum* L.
62 *Gymnocarpium dryopteris* (L.) Newm.
63 *Lycopodium annotinum* L.
64 *L. complanatum* L.
65 *L. obscurum* L.

Graminoids

66 *Agrostis oregonensis* Vasey
67 *Agropyron smithii* Rydb.
68 *Aira praecox* L.
69 *Calamagrostis canadensis* (Michx.) Beauv.
70 *Carex concinnoides* Mack
71 *C. disperma* Dew.
72 *C. pauciflora* Lightf.
73 *C. rossii* Boott
74 *C. sitchensis* Prescott
75 *Cinna latifolia* (Trev. *ex* Goepp.) Griseb
76 *Danthonia intermedia* Vasey
77 *Elymus glaucus* Buckl.
78 *E. hirsutus* Presl
79 *Eriophorum scheuchzeri* Hoppe
80 *Festuca idahoensis* Elmer
81 *F. occidentalis* Hook.
82 *F. subulata* Trin.
83 *F. subulifolia* Scribn.
84 *Hordeum jubatum* L.
85 *Juncus ensifolius* Wikstr.

86 *Luzula parviflora* (Ehrh.) Desv.
87 *Oryzopsis asperifolia* Michx.
88 *Stipia richardsonii* Link.

Herbs

89 *Achillea millefolium* L.
90 *Actaea rubra* (Ait.) Willd.
91 *Anaphalis margaritacea* (L.) Benth.
92 *Anemone multifida* Poir.
93 *Angelica genuflexa* Nutt.
94 *Antennaria microphylla* Rydb.
95 *A. neglecta* Greene
96 *Aquilegia flavescens* Wats.
97 *A. formosa* Fisch.
98 *Aralia nudicaulis* L.
99 *Arnica cordifolia* Hook.
100 *A. latifolia* Bong.
101 *Aster ciliolatus* Lindl.
102 *A. conspicuus* Lindl.
103 *A. foliaceus* Lindl.
104 *A. subspicatus* Nees
105 *Calypso bulbosa* (L.) Oakes
106 *Castilleja miniata* Dougl. *ex* Hook.
107 *Circaea alpina* L.
108 *Clintonia uniflora* (Schult.) Kunth
109 *Cornus canadensis* L.
110 *Delphinium glaucum* Wats.
111 *Disporum trachycarpum* (Wats.) Benth. *et* Hook.
112 *Drosera anglica* Huds.
113 *D. rotundifolia* L.
114 *Epilobium angustifolium* L.
115 *E. latifolium* L.
116 *Erigeron sp.*
117 *Fragaria vesca* L.
118 *F. virginiana* Duchesne
119 *Galium boreale* L.
120 *G. triflorum* Michx.
121 *Gentianella amarella* (L.) Boerner
122 *Geocaulon lividum* (Richards.) Fern.
123 *Geum macrophyllum* Willd.
124 *Goodyera oblongifolia* Raf.
125 *Heracleum lanatum* Michx.
126 *Hieracium albiflorum* Hook.
127 *Impatiens noli-tangere* L.
128 *Lathyrus nevadensis* Wats.
129 *L. ochroleucus* Hook.
130 *Leptarrhena pyrolifolia* (D. Don) R. Br. *ex* Ser.
131 *Linnaea borealis* L.
132 *Listera borealis* Morong
133 *L. cordata* (L.) R. Br.
134 *Lupinus arcticus* Wats.
135 *Maianthemum canadense* Desf.
136 *Melampyrum lineare* Desr.

137 *Menyanthes trifoliata* L.
138 *Mertensia paniculata* (Ait.) G. Don
139 *Mitella nuda* L.
140 *Nothocalais troximoides* (Gray) Greene
141 *Orthilia secunda* (L.) House
142 *Osmorhiza chilensis* Hook. *et* Arn.
143 *Parnassia fimbriata* Koenig
144 *Pedicularis sp.*
145 *Penstemon procerus* Dougl. *ex* Graham
146 *Petasites palmatus* (Ait.) Gray
147 *Phleum alpinum* L.
148 *Platanthera dilatata* (Pursh) Lindl. *ex* Beck
149 *P. obtusata* (Banks *ex* Pursh) Lindl.
150 *P. orbiculata* (Pursh) Lindl.
151 *Polemonium pulcherrium* Hook.
152 *Potentilla arguta* Pursh
153 *P. gracilis* Dougl. *ex* Hook.
154 *P. palustris* (L.) Scop.
155 *Pyrola asarifolia* Michx.
156 *P. chlorantha* Sw.
157 *P. minor* L.
158 *Ranunculus eschscholtzii* Schlecht.
150 *R. occidentalis* Nutt.
159 *Rubus pedatus* Sm.
160 *R. pubescens* Raf.
161 *Sanguisorba canadensis* L.
162 *Senecio pauperculus* Michx.
163 *S. pseudaureus* Rydb.
164 *S. triangularis* Hook.
165 *Smilacina racemosa* (l.) Desf.
166 *S. stellata* (l.) Desf.
167 *Solidago canadensis* L.
168 *S. spathulata* DC.
169 *Stellaria crispa* Cham. *et* Schlecht.
170 *Streptopus amplexifolius* (L.) DC.
171 *S. roseus* Michx.
172 *Taraxacum ceratophorum* (Ledeb.) DC.
173 *T. officinale* Weber
174 *Thalictrum occidentale* Gray
175 *Tiarella trifoliata* L.
176 *T. unifoliata* Hook.
177 *T. arctica* Fisch. *ex* Hook.
178 *Urtica dioica* L.
179 *Vaccinium oxycoccus* L.
180 *Valeriana sitchensis* Bong.
181 *Veratrum viride* Ait.
182 *Vicia americana* Muhlenb. *ex* Willd.
183 *Viola adunca* Sm.
184 *V. blanda* Willd.
185 *V. canadensis* L.
186 *V. glabella* Nutt.
187 *V. nephrophylla* Greene
188 *V. orbiculata* Geyer ex Hook.
189 *V. palustris* L.

190 *V. renifolia* Gray

Parasites & saprophytes

191 *Corallorhiza trifida* Chat.

Mosses

192 *Aulacomnium palustre* (Hedw.) Schwaegr.
193 *Brachythecium albicans* (Hedw.) B.S.G.
194 *B. curtum* (Lindb.) Brid.
195 *B. hylotapetum* B. Hig. *et* N. Hig.
196 *B. salebrosum* (Web. *et* Mohr) B.S.G.
197 *Bryum caespiticium* Hedw.
198 *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer *et* Scherb.
199 *Ceratodon purpureus* (Hedw.) Brid.
200 *Claopodium crispifolium* (Hook.) Ren. *et* Card.
201 *Climacium dendroides* (Hedw.) Web. *et* Mohr.
202 *Dicranum acutifolium* (Lind. *et* H.Arnell) C. Jens.
203 *D. fuscescens* Turn.
204 *D. polysetum* Sw.
205 *D. scoparium* Hedw.
206 *D. undulatum* Brid.
207 *Drepanocladus fluitans* (Hedw.) Warnst.
208 *D. uncinatus* (Hedw.) Warnst.
209 *Eurhynchium pulchellum* (Hedw.) Jenn.
210 *Funaria hygrometrica* Hedw.
211 *Helodium blandowii* (Web. *et* Mohr.) Warnst
212 *Hylocomium splendens* (Hedw.) B.S.G.
213 *Hypnum cupressiforme* Hedw.
214 *Mnium sp.*
215 *Plagiomnium ellipticum* (Brid.) Kop.
216 *P. insigne* (Mitt.) Kop.
217 *P. medium* (B. S. G.) Kop.
218 *Pleurozium schreberi* (Brid.) Mitt.
219 *Pohlia cruda* (Hedw.) Lindb.
220 *P. nutans* (Hedw.) Lindb.
221 *Polytrichum commune* Hedw.
222 *P. juniperinum* Hedw.
223 *P. piliferum* Hedw.
224 *Ptilium crista-castrensis* (Hedw.) De Not.
225 *Rhizomnium glabrescens* (Kindb.) Kop.
226 *Rh. nudum* (Britt. *et* Williams) Kop.
227 *Rh. punctatum* (Hedw.) Kop.
228 *Rhytidiadelphus loreus* (Hedw.) Warnst.
229 *Rh. squarrosus* (Hedw.) Warnst.
230 *Rh. triquetrus* (Hedw.) Warnst.
231 *Sphagnum centrale* C. Jens. *ex* H. Arnell *et* C. Jens.
232 *S. fuscum* (Schimp.) Klinggr.
233 *S. girgensohnii* Russ.
234 *S. magellanicum* Brid.
235 *S. nemoreum* Scop.
236 *S. squarrosum* Crome
237 *Tetraplodon mnioides* (Hedw.) B.S.G.

238 *Tetraphis pellucida* Hedw.
239 *Thuidium recognitum* (Hedw.) Lindb.
240 *Timmia austriaca* Hedw.
241 *Tomenthypnum nitens* (Hedw.) Loeske

Liverworts

242 *Barbilophozia barbata* (Schmid) Loeske
243 *Barbilophozia hatcheri* (Evans) Loeske
244 *B. lycopodioides* (Wallr.) Loeske
245 *Barbula vinealis* Brid.
246 *Blepharostoma trichophyllum* (L.) Dum.
247 *Cephalozia sp.*
248 *C. connivens* (Dicks.) Lindb.
249 *Lepidozia reptans* (L.) Dum.
250 *Lophozia ascendens* (Warnst.) Schust.
251 *L. guttulata* (Lindb. *et* H. Arnell) Eva
252 *L. sp.*
253 *L. ventricosa* (Dicks.) Dum.
254 *Marchantia polymorpha* L.
255 *Metzgeria sp.*
256 *Ptilidium pulcherrimum* (G. Web.) Hampe

Lichens

257 *Cetraria islandica* (L.) Ach.
258 *Cladina arbuscula* (Wallr.) Hale *et* W. Culb.
259 *C. mitis* (Sandst.) Hale *et* W. Culb
260 *C. rangiferina* (L.) Harm.
261 *Cladonia carneola* (Fr.) Fr.
262 *C. cenotea* (Ach.) Schaerer
263 *C. chlorophaea* (Florke ex Somm.) Spreng
264 *C. cornuta* (L.) Hoffm.
265 *C. deformis* (L.) Hoffm.
266 *C. fimbriata* (L.) Fr.
267 *C. furcata* (Huds.) Schrad.
268 *C. gracilis* (L.) Willd.
269 *C. multiformis* Merr.
270 *C. ochrochlora* Florke
271 *C. phyllophora* Ehrh. *ex* Hoffm.
272 *C. verticillata* (Hoffm.) Schaer
273 *Peltigera aphthosa* (L.) Willd.
274 *P. canina* (L.) Willd.
275 *P. malacea* (Ach.) Funk
276 *Stereocaulon tomentosum* Fr.

APPENDIX II

Cunia's (1973) method of testing significance of intercepts and slopes was used to test site index and ecological variables in relation to the parameters estimated for the Chapman-Richards growth function. The procedure was as follows:

1. Regressions without intercepts were fitted for b_1, b_2, and b_3, respectively, using the site units as dummy variables and site index multiplied by each of the 9 dummy variables as new independent variables. The general model was as follows:

[1] $b_1, b_2, b_3 = SU1 + SU2 + \ldots + SU9 + (SU1)(SI) + (SU2)(SI) + \ldots + (SU9)(SI),$

2. To test if both intercepts and slopes together were not significantly different, equations with single intercept and single slope were fitted for b_1, b_2, and b_3, respectively, using site index alone as independent variable:

[2] $b_1, b_2, b_3 = c_0 + c_1(SI),$

where c_0 and c_1 are parameters to be estimated.

3. To test if intercepts were not significantly different, regressions were fitted for b_1, b_2, and b_3, respectively, using site index multiplied by each of the 9 dummy variables, but only one intercept:

[3] $b_1, b_2, b_3 = c_0 + (SU1)(SI) + (SU2)(SI) + \ldots \ldots + (SU9)(SI),$

4. To test if slopes were not significantly different, regressions were fitted for b_1, b_2, and b_3, respectively, using 9 dummy variables, but only one slope coefficient for site index:

[4] $b_1, b_2, b_3 = SU1 + SU2 + \ldots \ldots + SU9 + c_1(SI),$

For each of the 3 parameters (b_1, b_2, b_3), the difference between the residual sum of squares from the step 1 and the residual sum of squares from steps 2, 3, and 4 (SS_{dif}) were calculated and divided by the difference in the residual degrees of freedom (DF_{dif}) to obtain the difference mean squares (MS_{dif}). Consequently, an F test was carried out for (1) both intercepts and slopes together, (2) intercepts, and (3) slopes as follows:

[5] $$F = \frac{MS_{dif}}{MS_{res}} ,$$

where MS_{res} is the mean square of the residual from equation [1].

APPENDIX III

Table A1. Site series lodgepole pine height growth based on equation [5.4.10] and parameters given in Table 5.11. Symbols for sites series are given in Table 5.1.

B.H.Age	SS1	SS2	SS3	SS5	SS6	SS7	SS8	SS9	SS10	SS11	SS12	SS13	SS14	SS15
0	1.40	1.42	1.38	1.57	1.60	1.55	1.51	1.50	1.45	1.46	1.48	1.36	1.40	1.49
1	1.47	1.58	1.45	1.79	2.02	1.70	1.86	1.69	1.71	1.71	1.66	1.41	1.51	1.58
2	1.59	1.77	1.56	2.11	2.45	1.97	2.27	2.01	2.02	2.06	1.93	1.49	1.68	1.75
3	1.74	1.98	1.69	2.48	2.87	2.30	2.69	2.39	2.33	2.44	2.26	1.60	1.87	1.97
4	1.90	2.19	1.84	2.88	3.28	2.66	3.12	2.81	2.64	2.85	2.61	1.73	2.09	2.22
5	2.08	2.41	2.00	3.30	3.68	3.06	3.55	3.25	2.96	3.27	2.98	1.86	2.32	2.50
6	2.27	2.64	2.17	3.73	4.08	3.48	3.99	3.72	3.28	3.71	3.38	2.01	2.57	2.80
7	2.47	2.86	2.35	4.16	4.47	3.91	4.42	4.21	3.60	4.15	3.79	2.17	2.82	3.12
8	2.67	3.09	2.53	4.60	4.86	4.36	4.86	4.71	3.92	4.60	4.21	2.34	3.09	3.44
9	2.87	3.32	2.72	5.04	5.24	4.81	5.29	5.22	4.23	5.05	4.63	2.51	3.36	3.78
10	3.08	3.55	2.91	5.49	5.61	5.27	5.72	5.73	4.55	5.50	5.07	2.69	3.64	4.12
11	3.28	3.78	3.11	5.93	5.97	5.73	6.14	6.25	4.86	5.95	5.51	2.88	3.92	4.46
12	3.49	4.01	3.31	6.36	6.33	6.20	6.56	6.77	5.17	6.41	5.95	3.07	4.21	4.80
13	3.69	4.23	3.51	6.80	6.68	6.66	6.98	7.29	5.48	6.86	6.40	3.26	4.50	5.15
14	3.89	4.46	3.72	7.22	7.02	7.13	7.40	7.80	5.78	7.30	6.85	3.46	4.79	5.49
15	4.09	4.69	3.92	7.65	7.36	7.59	7.81	8.32	6.08	7.75	7.30	3.67	5.09	5.83
16	4.29	4.91	4.13	8.06	7.69	8.04	8.21	8.83	6.38	8.19	7.75	3.87	5.39	6.16
17	4.49	5.14	4.34	8.47	8.02	8.50	8.61	9.34	6.67	8.63	8.20	4.08	5.69	6.50
18	4.68	5.36	4.55	8.87	8.34	8.94	9.01	9.84	6.97	9.06	8.64	4.29	5.99	6.82
19	4.87	5.58	4.76	9.27	8.65	9.38	9.40	10.34	7.25	9.49	9.09	4.51	6.29	7.14
20	5.05	5.80	4.97	9.65	8.96	9.82	9.79	10.83	7.54	9.91	9.54	4.72	6.60	7.46
21	5.23	6.02	5.17	10.03	9.26	10.25	10.17	11.32	7.82	10.33	9.98	4.94	6.91	7.77
22	5.41	6.24	5.38	10.40	9.56	10.67	10.55	11.80	8.10	10.74	10.42	5.16	7.21	8.07
23	5.58	6.45	5.59	10.77	9.85	11.08	10.92	12.27	8.37	11.15	10.86	5.38	7.52	8.37
24	5.75	6.66	5.80	11.12	10.13	11.49	11.29	12.74	8.64	11.55	11.29	5.61	7.83	8.66
25	5.91	6.87	6.01	11.47	10.41	11.89	11.65	13.20	8.91	11.95	11.72	5.83	8.13	8.94
26	6.07	7.08	6.22	11.81	10.69	12.28	12.01	13.65	9.18	12.34	12.15	6.05	8.44	9.22
27	6.23	7.29	6.42	12.14	10.96	12.66	12.36	14.09	9.44	12.72	12.58	6.28	8.75	9.49
28	6.38	7.50	6.63	12.46	11.22	13.04	12.71	14.52	9.69	13.10	13.00	6.50	9.05	9.75
29	6.53	7.70	6.83	12.77	11.48	13.40	13.05	14.95	9.95	13.48	13.41	6.73	9.36	10.00
30	6.67	7.90	7.03	13.08	11.74	13.76	13.39	15.37	10.20	13.85	13.82	6.96	9.66	10.25

Table A1. (continued)

31	6.81	8.10	7.23	13.38	11.99	14.11	13.72	15.78	10.45	14.21	14.23	7.18	9.96	10.49
32	6.95	8.30	7.43	13.67	12.23	14.46	14.05	16.18	10.69	14.56	14.63	7.41	10.27	10.72
33	7.08	8.49	7.63	13.96	12.48	14.79	14.38	16.58	10.93	14.91	15.03	7.63	10.57	10.95
34	7.21	8.69	7.83	14.23	12.71	15.12	14.70	16.96	11.17	15.26	15.43	7.86	10.87	11.17
35	7.33	8.88	8.03	14.50	12.95	15.44	15.01	17.34	11.40	15.60	15.81	8.09	11.17	11.38
36	7.45	9.07	8.22	14.77	13.17	15.75	15.32	17.71	11.63	15.93	16.20	8.31	11.46	11.59
37	7.57	9.25	8.41	15.02	13.40	16.05	15.63	18.07	11.86	16.26	16.58	8.54	11.76	11.79
38	7.68	9.44	8.60	15.27	13.62	16.35	15.93	18.43	12.09	16.58	16.95	8.76	12.05	11.98
39	7.79	9.62	8.79	15.51	13.83	16.63	16.22	18.78	12.31	16.89	17.32	8.99	12.35	12.17
40	7.90	9.80	8.98	15.75	14.04	16.91	16.52	19.12	12.52	17.20	17.69	9.21	12.64	12.35
41	8.00	9.98	9.17	15.97	14.25	17.19	16.80	19.45	12.74	17.51	18.05	9.43	12.93	12.53
42	8.10	10.16	9.35	16.20	14.45	17.45	17.09	19.77	12.95	17.81	18.41	9.65	13.22	12.70
43	8.20	10.33	9.53	16.41	14.65	17.71	17.37	20.09	13.16	18.10	18.76	9.87	13.50	12.86
44	8.29	10.51	9.71	16.62	14.85	17.96	17.64	20.40	13.37	18.39	19.10	10.09	13.79	13.02
45	8.38	10.68	9.89	16.83	15.04	18.21	17.91	20.70	13.57	18.67	19.44	10.31	14.07	13.17
46	8.47	10.85	10.07	17.02	15.23	18.45	18.18	21.00	13.77	18.95	19.78	10.53	14.35	13.32
47	8.55	11.02	10.24	17.22	15.42	18.68	18.44	21.29	13.97	19.22	20.11	10.75	14.63	13.47
48	8.63	11.18	10.42	17.40	15.60	18.91	18.70	21.57	14.16	19.49	20.44	10.97	14.91	13.60
49	8.71	11.34	10.59	17.59	15.78	19.13	18.95	21.84	14.35	19.75	20.76	11.18	15.18	13.74
50	8.79	11.51	10.76	17.76	15.95	19.34	19.20	22.11	14.54	20.01	21.08	11.40	15.45	13.87
51	8.86	11.67	10.92	17.93	16.12	19.55	19.45	22.37	14.73	20.26	21.39	11.61	15.73	13.99
52	8.94	11.82	11.09	18.10	16.29	19.75	19.69	22.63	14.91	20.51	21.70	11.82	16.00	14.11
53	9.00	11.98	11.25	18.26	16.46	19.95	19.93	22.88	15.09	20.75	22.00	12.03	16.26	14.23
54	9.07	12.13	11.41	18.42	16.62	20.14	20.17	23.12	15.27	20.99	22.30	12.24	16.53	14.34
55	9.14	12.28	11.57	18.57	16.78	20.32	20.40	23.36	15.44	21.22	22.59	12.45	16.79	14.45
56	9.20	12.43	11.73	18.72	16.94	20.50	20.62	23.59	15.61	21.45	22.88	12.66	17.05	14.55
57	9.26	12.58	11.89	18.86	17.09	20.68	20.85	23.82	15.78	21.67	23.17	12.86	17.31	14.65
58	9.32	12.73	12.04	19.00	17.24	20.85	21.07	24.04	15.95	21.89	23.45	13.07	17.57	14.75
59	9.37	12.87	12.20	19.14	17.39	21.01	21.29	24.25	16.12	22.11	23.73	13.27	17.82	14.84
60	9.43	13.02	12.35	19.27	17.53	21.17	21.50	24.46	16.28	22.32	24.00	13.47	18.08	14.94
61	9.48	13.16	12.50	19.39	17.67	21.33	21.71	24.67	16.44	22.53	24.27	13.67	18.33	15.02
62	9.53	13.30	12.64	19.52	17.81	21.48	21.92	24.87	16.60	22.73	24.53	13.87	18.58	15.11
63	9.58	13.44	12.79	19.64	17.95	21.62	22.12	25.06	16.75	22.93	24.79	14.07	18.82	15.19
64	9.63	13.57	12.93	19.75	18.08	21.77	22.32	25.25	16.91	23.13	25.04	14.26	19.07	15.26
65	9.67	13.71	13.07	19.87	18.22	21.90	22.52	25.44	17.06	23.32	25.29	14.46	19.31	15.34
66	9.72	13.84	13.21	19.97	18.35	22.04	22.71	25.62	17.20	23.50	25.54	14.65	19.55	15.41
67	9.76	13.97	13.35	20.08	18.47	22.17	22.90	25.79	17.35	23.69	25.78	14.84	19.79	15.48
68	9.80	14.10	13.49	20.18	18.60	22.29	23.09	25.96	17.49	23.87	26.02	15.03	20.02	15.55
69	9.84	14.23	13.62	20.28	18.72	22.42	23.28	26.13	17.64	24.04	26.26	15.22	20.26	15.61
70	9.88	14.35	13.75	20.38	18.84	22.53	23.46	26.29	17.78	24.22	26.49	15.41	20.49	15.68

Table A1. (continued)

71	9.92	14.48	13.88	20.47	18.96	22.65	23.64	26.45	17.91	24.39	26.72	15.60	20.72	15.74
72	9.95	14.60	14.01	20.56	19.07	22.76	23.81	26.60	18.05	24.55	26.94	15.78	20.95	15.79
73	9.99	14.72	14.14	20.65	19.19	22.87	23.99	26.75	18.18	24.71	27.16	15.96	21.17	15.85
74	10.02	14.84	14.27	20.74	19.30	22.98	24.16	26.90	18.31	24.87	27.38	16.15	21.40	15.90
75	10.05	14.96	14.39	20.82	19.41	23.08	24.33	27.04	18.44	25.03	27.59	16.33	21.62	15.96
76	10.08	15.08	14.51	20.90	19.51	23.18	24.49	27.18	18.57	25.18	27.80	16.51	21.84	16.01
77	10.11	15.19	14.64	20.98	19.62	23.27	24.65	27.31	18.70	25.33	28.00	16.68	22.06	16.05
78	10.14	15.31	14.75	21.05	19.72	23.37	24.81	27.44	18.82	25.48	28.20	16.86	22.27	16.10
79	10.17	15.42	14.87	21.13	19.82	23.46	24.97	27.57	18.94	25.62	28.40	17.03	22.49	16.14
80	10.20	15.53	14.99	21.20	19.92	23.54	25.12	27.70	19.06	25.76	28.60	17.21	22.70	16.19
81	10.22	15.64	15.10	21.27	20.02	23.63	25.28	27.82	19.18	25.90	28.79	17.38	22.91	16.23
82	10.25	15.75	15.22	21.33	20.11	23.71	25.43	27.93	19.29	26.03	28.98	17.55	23.11	16.27
83	10.27	15.85	15.33	21.40	20.21	23.79	25.57	28.05	19.41	26.17	29.16	17.71	23.32	16.31
84	10.29	15.96	15.44	21.46	20.30	23.87	25.72	28.16	19.52	26.29	29.35	17.88	23.52	16.34
85	10.32	16.06	15.55	21.52	20.39	23.94	25.86	28.27	19.63	26.42	29.53	18.05	23.73	16.38
86	10.34	16.17	15.65	21.58	20.48	24.02	26.00	28.38	19.74	26.55	29.70	18.21	23.92	16.41
87	10.36	16.27	15.76	21.64	20.57	24.09	26.14	28.48	19.85	26.67	29.87	18.37	24.12	16.44
88	10.38	16.37	15.86	21.69	20.65	24.15	26.27	28.58	19.96	26.79	30.04	18.53	24.32	16.48
89	10.40	16.47	15.96	21.74	20.73	24.22	26.41	28.68	20.06	26.90	30.21	18.69	24.51	16.51
90	10.42	16.56	16.07	21.80	20.82	24.29	26.54	28.77	20.16	27.02	30.37	18.85	24.70	16.54
91	10.43	16.66	16.17	21.85	20.90	24.35	26.67	28.87	20.26	27.13	30.54	19.01	24.89	16.56
92	10.45	16.76	16.26	21.90	20.98	24.41	26.79	28.96	20.36	27.24	30.69	19.16	25.08	16.59
93	10.47	16.85	16.36	21.94	21.05	24.47	26.92	29.04	20.46	27.34	30.85	19.32	25.27	16.62
94	10.48	16.94	16.46	21.99	21.13	24.52	27.04	29.13	20.56	27.45	31.00	19.47	25.45	16.64
95	10.50	17.03	16.55	22.03	21.20	24.58	27.16	29.21	20.65	27.55	31.15	19.62	25.63	16.67
96	10.52	17.12	16.64	22.08	21.28	24.63	27.28	29.29	20.75	27.65	31.30	19.77	25.81	16.69
97	10.53	17.21	16.73	22.12	21.35	24.68	27.40	29.37	20.84	27.75	31.45	19.92	25.99	16.71
98	10.54	17.30	16.82	22.16	21.42	24.73	27.51	29.45	20.93	27.84	31.59	20.07	26.17	16.73
99	10.56	17.39	16.91	22.20	21.49	24.78	27.63	29.52	21.02	27.94	31.73	20.21	26.35	16.75
100	10.57	17.47	17.00	22.23	21.56	24.83	27.74	29.60	21.10	28.03	31.87	20.36	26.52	16.77

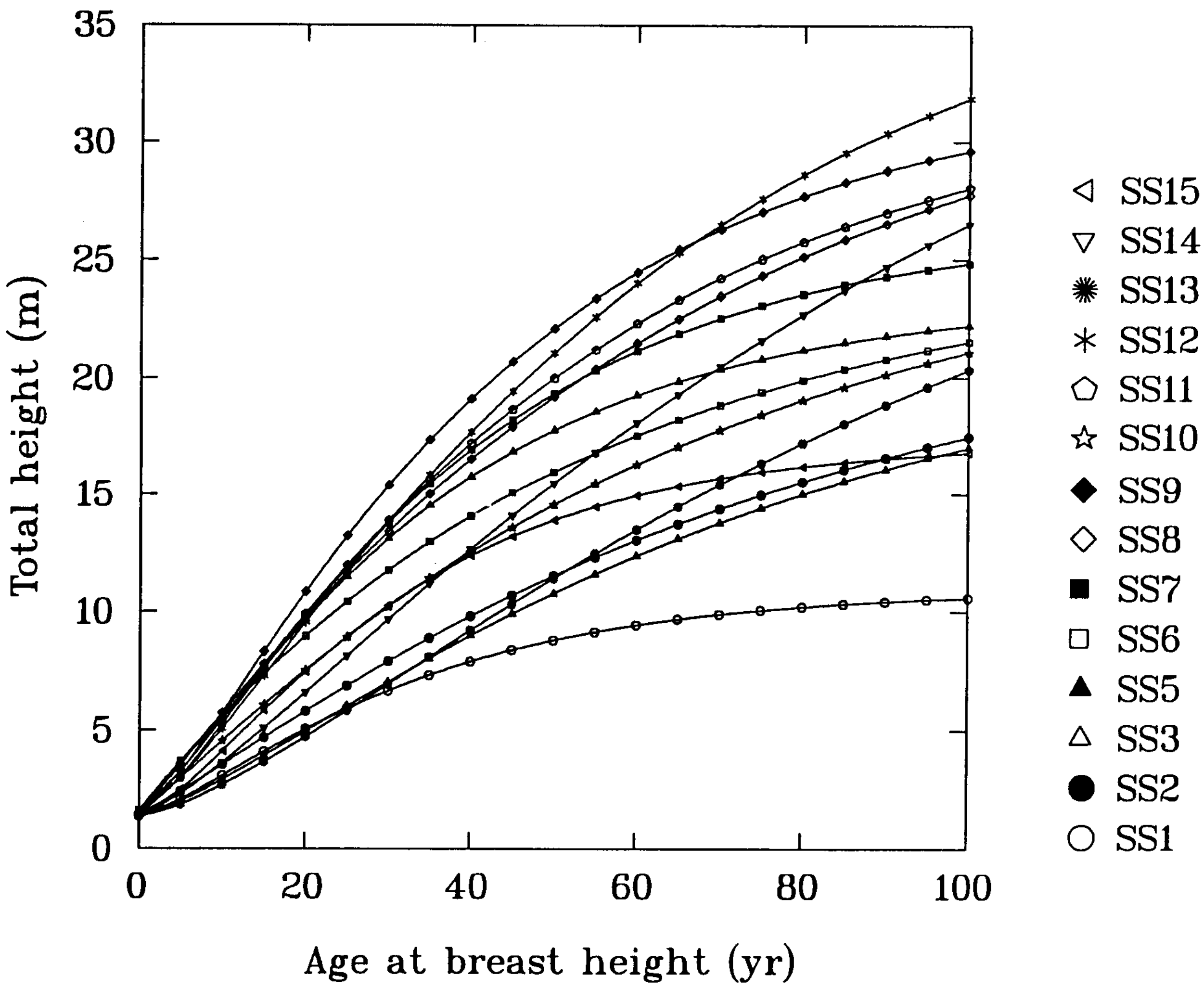

Figure A1. Site series lodgepole pine height growth curves based on equation [5.4.10] and parameters given in Table 5.11. Symbols for sites series are given in Table 5.1.

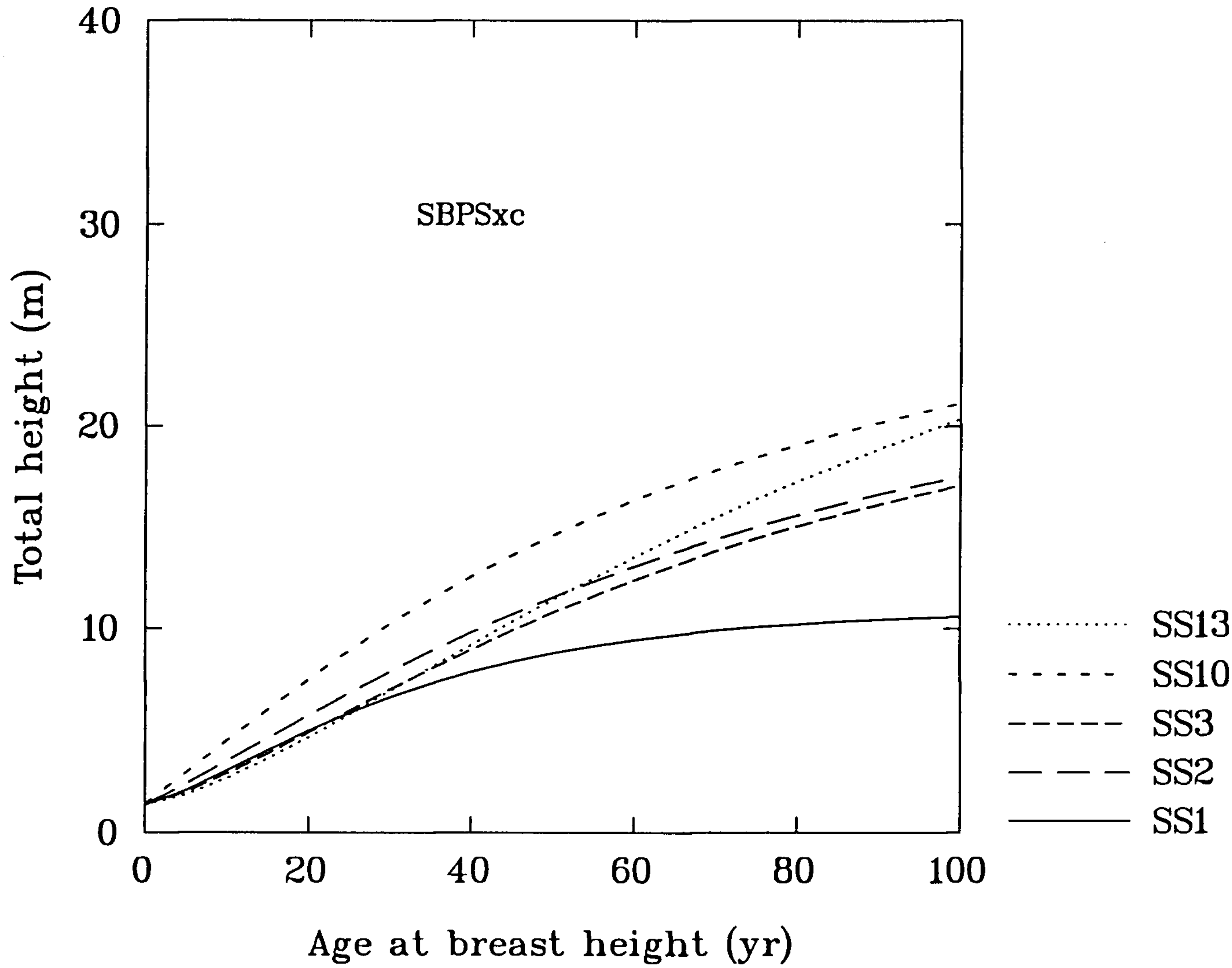

Figure A2. Site series lodgepole pine height growth curves for SBPSxc subzone based on equation [5.4.10] and parameters given in Table 5.11. Symbols for site series are explained in Table 5.1.

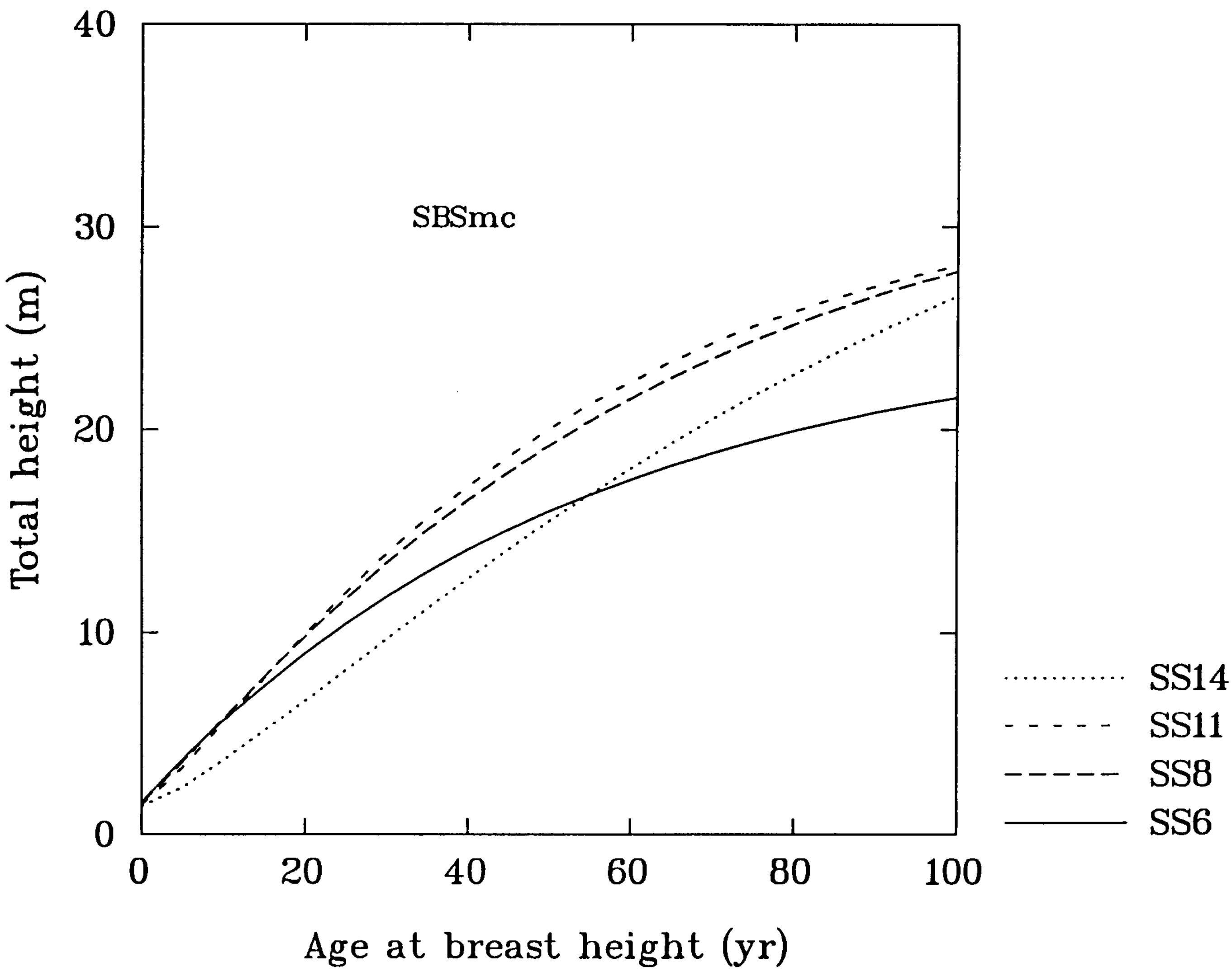

Figure A3. Site series lodgepole pine height growth curves for SBSmc subzone based on equation [5.4.10] and parameters given in Table 5.11. Symbols for site series are explained in Table 5.1.

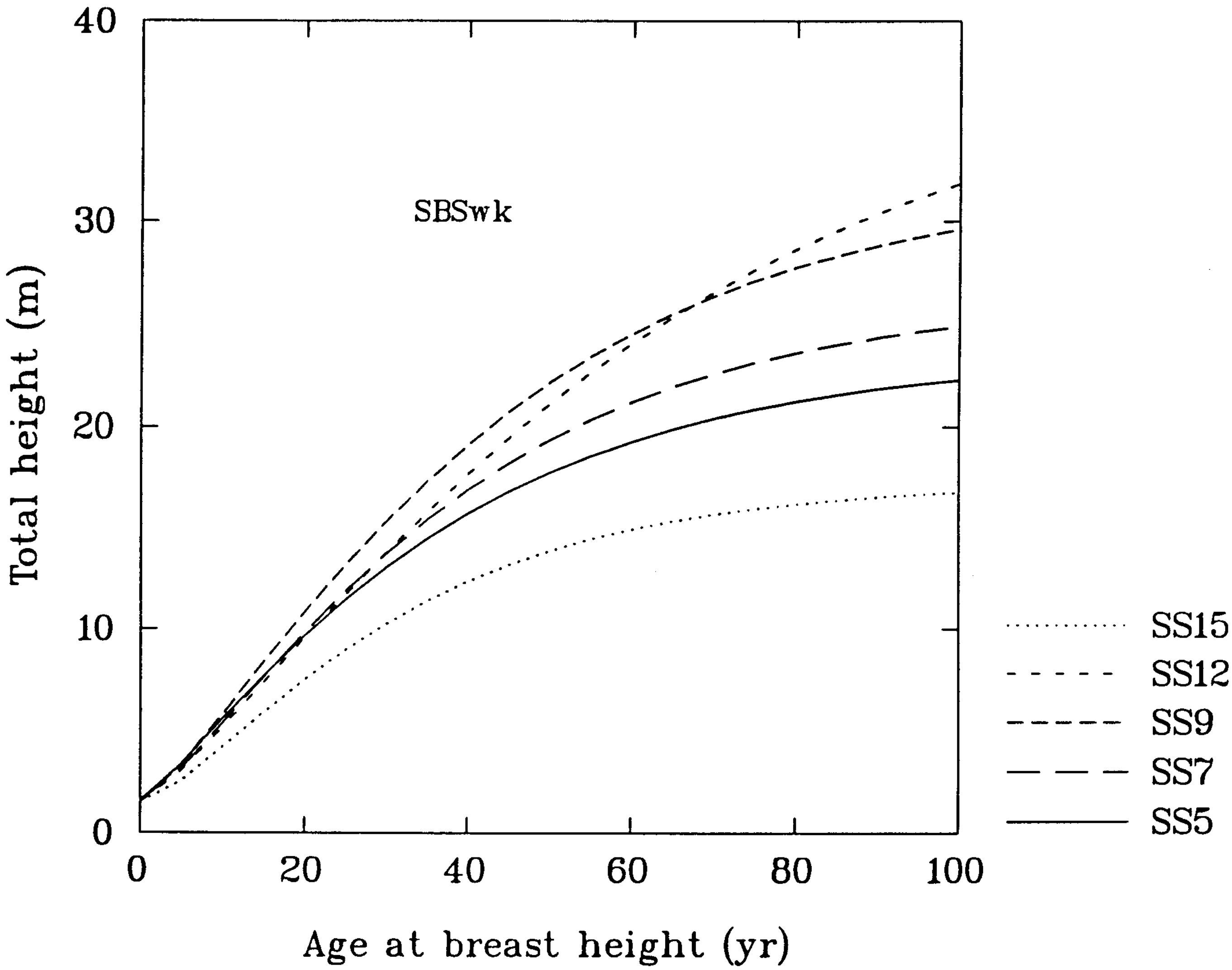

Figure A4. Site series lodgepole pine height growth curves for SBSwk subzone based on equation [5.4.10] and parameters given in Table 5.11. Symbols for site series are explained in Table 5.1.

Table A2. Ecotope lodgepole pine height growth based on equation [5.4.11] and parameters given in Table 5.12. Symbols for BGC, SMRs, and SNRs are given in Table 5.1.

B.H.Age	Total height																				
BGC	SBPSxo						SBSmc						SBSwk								
SMR	ED	VD	VD	MDf	SDf	SDf	SD	F	F	M	VM	VM	MD	MD	SD	F	M	M	VM	W	W
SNR	VP	VP	M	R	R	VR	P	M	R	R	R	VR	P	M	M	M	M	R	R	R	VR
0	1.43	1.43	1.43	1.43	1.43	1.43	1.47	1.47	1.47	1.47	1.47	1.47	1.50	1.50	1.50	1.50	1.50	1.50	1.50	1.50	1.50
1	1.50	1.60	1.58	1.50	1.70	1.68	1.98	1.78	1.75	1.92	1.75	1.73	1.71	1.72	1.66	1.65	1.71	1.71	1.63	1.58	1.59
2	1.62	1.79	1.76	1.60	1.99	1.96	2.48	2.13	2.07	2.40	2.10	2.06	2.01	2.04	1.93	1.89	2.05	2.04	1.87	1.72	1.78
3	1.76	2.00	1.95	1.72	2.30	2.25	2.97	2.49	2.41	2.89	2.47	2.41	2.35	2.40	2.25	2.19	2.44	2.43	2.17	1.91	2.02
4	1.92	2.21	2.16	1.86	2.60	2.55	3.44	2.86	2.76	3.39	2.86	2.79	2.72	2.80	2.61	2.52	2.86	2.86	2.52	2.13	2.30
5	2.09	2.42	2.37	2.00	2.91	2.86	3.90	3.24	3.12	3.88	3.27	3.18	3.10	3.21	2.99	2.88	3.32	3.32	2.90	2.36	2.61
6	2.28	2.64	2.58	2.16	3.23	3.17	4.35	3.62	3.48	4.38	3.67	3.58	3.50	3.64	3.40	3.26	3.79	3.80	3.30	2.62	2.95
7	2.47	2.86	2.80	2.32	3.54	3.47	4.79	3.99	3.85	4.86	4.09	3.98	3.90	4.08	3.82	3.66	4.28	4.30	3.73	2.88	3.31
8	2.66	3.08	3.02	2.49	3.85	3.78	5.22	4.37	4.21	5.35	4.50	4.39	4.30	4.53	4.25	4.07	4.77	4.81	4.17	3.16	3.68
9	2.86	3.30	3.25	2.67	4.15	4.09	5.64	4.75	4.57	5.83	4.92	4.80	4.70	4.98	4.69	4.49	5.27	5.33	4.62	3.44	4.07
10	3.06	3.52	3.47	2.85	4.46	4.40	6.05	5.12	4.94	6.30	5.33	5.21	5.11	5.43	5.14	4.91	5.78	5.86	5.08	3.72	4.46
11	3.26	3.74	3.70	3.03	4.76	4.70	6.45	5.50	5.30	6.77	5.74	5.62	5.51	5.88	5.59	5.35	6.29	6.39	5.55	4.01	4.86
12	3.46	3.96	3.92	3.21	5.06	5.00	6.84	5.87	5.67	7.24	6.16	6.03	5.91	6.32	6.04	5.78	6.80	6.92	6.03	4.30	5.26
13	3.66	4.17	4.15	3.40	5.36	5.31	7.22	6.23	6.03	7.69	6.57	6.44	6.30	6.77	6.49	6.22	7.30	7.46	6.51	4.59	5.67
14	3.85	4.39	4.37	3.59	5.65	5.61	7.60	6.60	6.39	8.14	6.97	6.85	6.69	7.21	6.94	6.66	7.81	7.99	6.99	4.87	6.08
15	4.05	4.60	4.60	3.78	5.95	5.91	7.96	6.96	6.74	8.59	7.38	7.26	7.08	7.64	7.38	7.11	8.31	8.52	7.48	5.15	6.49
16	4.24	4.81	4.83	3.98	6.24	6.20	8.32	7.31	7.10	9.03	7.78	7.66	7.46	8.07	7.83	7.55	8.80	9.05	7.96	5.44	6.89
17	4.43	5.02	5.05	4.17	6.52	6.50	8.67	7.67	7.45	9.46	8.18	8.07	7.83	8.50	8.27	7.99	9.29	9.57	8.44	5.71	7.30
18	4.62	5.23	5.28	4.37	6.80	6.79	9.01	8.02	7.80	9.89	8.57	8.47	8.20	8.92	8.70	8.42	9.78	10.09	8.92	5.98	7.70
19	4.80	5.43	5.50	4.56	7.08	7.07	9.34	8.36	8.15	10.31	8.96	8.87	8.55	9.33	9.13	8.86	10.25	10.60	9.39	6.25	8.09
20	4.98	5.64	5.72	4.76	7.36	7.36	9.66	8.71	8.49	10.72	9.35	9.26	8.91	9.73	9.56	9.29	10.73	11.11	9.86	6.52	8.48
21	5.16	5.84	5.94	4.95	7.63	7.64	9.98	9.05	8.83	11.13	9.73	9.65	9.25	10.13	9.97	9.72	11.19	11.61	10.33	6.77	8.87
22	5.34	6.04	6.17	5.15	7.90	7.92	10.29	9.38	9.17	11.54	10.10	10.04	9.59	10.52	10.39	10.14	11.65	12.11	10.80	7.03	9.25
23	5.51	6.23	6.39	5.35	8.17	8.20	10.59	9.71	9.51	11.93	10.47	10.42	9.92	10.90	10.79	10.56	12.10	12.60	11.25	7.27	9.62
24	5.67	6.43	6.60	5.54	8.43	8.48	10.89	10.04	9.84	12.32	10.84	10.80	10.24	11.28	11.19	10.98	12.54	13.08	11.70	7.51	9.99
25	5.84	6.62	6.82	5.74	8.69	8.75	11.18	10.36	10.17	12.70	11.20	11.18	10.56	11.65	11.58	11.39	12.97	13.55	12.15	7.75	10.34
26	5.99	6.81	7.04	5.93	8.94	9.02	11.46	10.68	10.49	13.08	11.56	11.55	10.86	12.01	11.97	11.79	13.40	14.02	12.59	7.98	10.70
27	6.15	7.00	7.25	6.13	9.20	9.29	11.73	10.99	10.82	13.45	11.91	11.92	11.16	12.36	12.34	12.19	13.82	14.48	13.02	8.20	11.04

Table A2. (continued)

28	6.30	7.19	7.46	6.32	9.44	9.55	12.00	11.30	11.14	13.82	12.26	12.28	11.46	12.70	12.71	12.59	14.22	14.93	13.45	8.42	11.38
29	6.45	7.37	7.68	6.51	9.69	9.81	12.27	11.61	11.45	14.18	12.60	12.65	11.74	13.04	13.08	12.97	14.63	15.37	13.87	8.63	11.71
30	6.59	7.55	7.89	6.71	9.93	10.07	12.52	11.91	11.76	14.53	12.94	13.00	12.02	13.37	13.43	13.36	15.02	15.80	14.28	8.83	12.03
31	6.73	7.73	8.09	6.90	10.17	10.33	12.78	12.21	12.07	14.88	13.28	13.35	12.29	13.69	13.78	13.73	15.40	16.23	14.69	9.03	12.35
32	6.86	7.91	8.30	7.09	10.41	10.58	13.02	12.51	12.38	15.23	13.60	13.70	12.56	14.01	14.12	14.10	15.78	16.65	15.09	9.23	12.66
33	6.99	8.08	8.51	7.28	10.64	10.83	13.26	12.80	12.68	15.56	13.93	14.04	12.82	14.31	14.46	14.47	16.15	17.06	15.48	9.42	12.96
34	7.12	8.26	8.71	7.46	10.87	11.07	13.50	13.09	12.98	15.90	14.25	14.38	13.07	14.61	14.78	14.83	16.51	17.46	15.86	9.60	13.25
35	7.25	8.43	8.91	7.65	11.10	11.32	13.73	13.37	13.28	16.22	14.56	14.72	13.31	14.90	15.10	15.18	16.86	17.86	16.24	9.78	13.54
36	7.37	8.60	9.11	7.84	11.32	11.56	13.95	13.65	13.57	16.54	14.87	15.05	13.55	15.19	15.41	15.53	17.20	18.25	16.61	9.95	13.82
37	7.48	8.76	9.31	8.02	11.54	11.80	14.17	13.92	13.86	16.86	15.17	15.37	13.78	15.47	15.71	15.87	17.54	18.63	16.97	10.11	14.09
38	7.60	8.93	9.51	8.20	11.75	12.03	14.38	14.20	14.15	17.17	15.47	15.70	14.00	15.74	16.01	16.21	17.87	19.00	17.33	10.27	14.35
39	7.71	9.09	9.71	8.38	11.97	12.27	14.59	14.46	14.43	17.47	15.77	16.01	14.22	16.00	16.30	16.53	18.19	19.36	17.68	10.43	14.61
40	7.82	9.25	9.90	8.56	12.18	12.50	14.79	14.73	14.71	17.77	16.06	16.33	14.44	16.26	16.59	16.86	18.50	19.72	18.02	10.58	14.86
41	7.92	9.40	10.09	8.74	12.39	12.72	14.99	14.99	14.99	18.07	16.34	16.64	14.64	16.51	16.86	17.17	18.81	20.07	18.35	10.73	15.10
42	8.02	9.56	10.28	8.92	12.59	12.95	15.19	15.25	15.26	18.36	16.63	16.94	14.84	16.76	17.13	17.49	19.11	20.41	18.68	10.87	15.34
43	8.12	9.71	10.47	9.09	12.79	13.17	15.38	15.50	15.53	18.65	16.90	17.24	15.04	17.00	17.39	17.79	19.40	20.74	19.00	11.00	15.56
44	8.21	9.86	10.66	9.27	12.99	13.39	15.57	15.75	15.80	18.93	17.17	17.54	15.23	17.23	17.65	18.09	19.68	21.07	19.31	11.13	15.79
45	8.30	10.01	10.85	9.44	13.19	13.61	15.75	15.99	16.06	19.20	17.44	17.83	15.42	17.46	17.90	18.38	19.96	21.39	19.62	11.26	16.00
46	8.39	10.16	11.03	9.61	13.38	13.82	15.93	16.24	16.32	19.47	17.71	18.12	15.59	17.68	18.14	18.67	20.23	21.70	19.92	11.38	16.21
47	8.48	10.30	11.21	9.78	13.57	14.03	16.10	16.48	16.58	19.74	17.96	18.41	15.77	17.89	18.38	18.95	20.49	22.00	20.21	11.50	16.42
48	8.56	10.45	11.39	9.95	13.76	14.24	16.27	16.71	16.84	20.00	18.22	18.69	15.94	18.10	18.61	19.23	20.75	22.30	20.49	11.62	16.62
49	8.64	10.59	11.57	10.11	13.94	14.45	16.44	16.94	17.09	20.26	18.47	18.96	16.10	18.31	18.84	19.50	21.00	22.59	20.77	11.73	16.81
50	8.72	10.73	11.75	10.28	14.13	14.65	16.60	17.17	17.34	20.51	18.72	19.24	16.26	18.50	19.06	19.77	21.25	22.88	21.05	11.84	16.99
51	8.80	10.86	11.92	10.44	14.30	14.85	16.76	17.40	17.58	20.76	18.96	19.51	16.42	18.70	19.27	20.03	21.49	23.16	21.31	11.94	17.18
52	8.87	11.00	12.10	10.60	14.48	15.05	16.91	17.62	17.82	21.01	19.20	19.77	16.57	18.89	19.48	20.28	21.72	23.43	21.57	12.04	17.35
53	8.94	11.13	12.27	10.76	14.66	15.24	17.06	17.84	18.06	21.25	19.43	20.03	16.71	19.07	19.68	20.53	21.94	23.69	21.83	12.14	17.52
54	9.01	11.26	12.44	10.92	14.83	15.44	17.21	18.06	18.30	21.49	19.66	20.29	16.86	19.25	19.88	20.77	22.16	23.95	22.08	12.23	17.69
55	9.07	11.39	12.61	11.07	15.00	15.63	17.35	18.27	18.53	21.72	19.89	20.54	16.99	19.42	20.08	21.01	22.38	24.21	22.32	12.32	17.84
56	9.14	11.52	12.78	11.23	15.16	15.82	17.50	18.48	18.76	21.95	20.11	20.79	17.13	19.59	20.26	21.25	22.59	24.45	22.56	12.40	18.00
57	9.20	11.64	12.94	11.38	15.33	16.00	17.63	18.69	18.99	22.17	20.33	21.04	17.26	19.75	20.45	21.48	22.79	24.69	22.79	12.49	18.15
58	9.26	11.77	13.11	11.53	15.49	16.19	17.77	18.89	19.22	22.39	20.55	21.28	17.38	19.91	20.62	21.70	22.99	24.93	23.01	12.57	18.29
59	9.32	11.89	13.27	11.68	15.65	16.37	17.90	19.09	19.44	22.61	20.76	21.52	17.51	20.07	20.80	21.92	23.18	25.16	23.23	12.65	18.44
60	9.37	12.01	13.43	11.83	15.80	16.55	18.03	19.29	19.66	22.82	20.97	21.76	17.62	20.22	20.96	22.13	23.37	25.38	23.45	12.72	18.57
61	9.43	12.13	13.59	11.97	15.96	16.73	18.15	19.48	19.88	23.03	21.17	21.99	17.74	20.36	21.13	22.34	23.55	25.60	23.66	12.79	18.70
62	9.48	12.24	13.75	12.12	16.11	16.90	18.28	19.67	20.09	23.24	21.37	22.22	17.85	20.50	21.29	22.55	23.73	25.82	23.86	12.86	18.83
63	9.53	12.36	13.90	12.26	16.26	17.07	18.40	19.86	20.30	23.44	21.57	22.44	17.96	20.64	21.44	22.75	23.91	26.02	24.06	12.93	18.96
64	9.58	12.47	14.06	12.40	16.41	17.24	18.51	20.05	20.51	23.64	21.76	22.66	18.06	20.78	21.59	22.95	24.08	26.23	24.25	12.99	19.08

Table A2. (continued)

65	9.63	12.58	14.21	12.54	16.55	17.41	18.63	20.23	20.71	23.84	21.95	22.88	18.17	20.91	21.74	23.14	24.24	26.43	24.44	13.06	19.19
66	9.67	12.69	14.36	12.68	16.70	17.58	18.74	20.41	20.92	24.03	22.14	23.09	18.26	21.04	21.88	23.33	24.40	26.62	24.63	13.12	19.30
67	9.72	12.80	14.51	12.82	16.84	17.74	18.85	20.59	21.12	24.22	22.32	23.31	18.36	21.16	22.02	23.51	24.56	26.81	24.81	13.17	19.41
68	9.76	12.91	14.66	12.95	16.98	17.90	18.96	20.77	21.32	24.40	22.50	23.51	18.45	21.28	22.15	23.69	24.71	26.99	24.98	13.23	19.52
69	9.80	13.01	14.80	13.08	17.11	18.06	19.06	20.94	21.51	24.58	22.68	23.72	18.54	21.40	22.28	23.86	24.86	27.17	25.16	13.28	19.62
70	9.84	13.12	14.95	13.22	17.25	18.22	19.16	21.11	21.71	24.76	22.86	23.92	18.63	21.51	22.41	24.04	25.00	27.35	25.32	13.33	19.72
71	9.88	13.22	15.09	13.35	17.38	18.38	19.26	21.28	21.90	24.94	23.03	24.12	18.72	21.62	22.54	24.20	25.14	27.52	25.48	13.38	19.81
72	9.92	13.32	15.23	13.47	17.51	18.53	19.36	21.44	22.08	25.11	23.19	24.32	18.80	21.73	22.66	24.37	25.28	27.69	25.64	13.43	19.91
73	9.95	13.42	15.37	13.60	17.64	18.68	19.46	21.61	22.27	25.28	23.36	24.51	18.88	21.83	22.77	24.53	25.41	27.85	25.80	13.48	19.99
74	9.99	13.52	15.51	13.73	17.76	18.83	19.55	21.77	22.45	25.45	23.52	24.70	18.95	21.93	22.89	24.68	25.54	28.01	25.95	13.52	20.08
75	10.02	13.61	15.65	13.85	17.89	18.98	19.64	21.92	22.63	25.61	23.68	24.89	19.03	22.03	23.00	24.84	25.66	28.16	26.09	13.57	20.16
76	10.05	13.71	15.79	13.97	18.01	19.12	19.73	22.08	22.81	25.78	23.84	25.07	19.10	22.13	23.10	24.99	25.78	28.31	26.24	13.61	20.25
77	10.08	13.80	15.92	14.09	18.13	19.27	19.82	22.23	22.99	25.93	23.99	25.25	19.17	22.22	23.21	25.13	25.90	28.46	26.38	13.65	20.32
78	10.12	13.89	16.06	14.21	18.25	19.41	19.90	22.38	23.16	26.09	24.14	25.43	19.24	22.31	23.31	25.28	26.02	28.60	26.51	13.68	20.40
79	10.14	13.98	16.19	14.33	18.37	19.55	19.99	22.53	23.33	26.24	24.29	25.60	19.31	22.40	23.41	25.42	26.13	28.74	26.64	13.72	20.47
80	10.17	14.07	16.32	14.45	18.49	19.69	20.07	22.68	23.50	26.39	24.44	25.78	19.37	22.48	23.50	25.55	26.24	28.88	26.77	13.76	20.54
81	10.20	14.16	16.45	14.56	18.60	19.82	20.15	22.82	23.67	26.54	24.58	25.95	19.43	22.56	23.60	25.69	26.34	29.01	26.90	13.79	20.61
82	10.23	14.24	16.58	14.68	18.71	19.96	20.22	22.96	23.84	26.69	24.72	26.11	19.49	22.64	23.69	25.82	26.45	29.14	27.02	13.82	20.68
83	10.25	14.33	16.70	14.79	18.82	20.09	20.30	23.10	24.00	26.83	24.86	26.28	19.55	22.72	23.78	25.94	26.55	29.26	27.14	13.86	20.74
84	10.28	14.41	16.83	14.90	18.93	20.22	20.37	23.24	24.16	26.97	25.00	26.44	19.61	22.80	23.86	26.07	26.64	29.39	27.26	13.89	20.80
85	10.30	14.50	16.95	15.01	19.04	20.35	20.45	23.37	24.32	27.11	25.13	26.60	19.66	22.87	23.94	26.19	26.74	29.51	27.37	13.91	20.86
86	10.32	14.58	17.07	15.12	19.14	20.48	20.52	23.51	24.48	27.24	25.26	26.76	19.72	22.94	24.03	26.31	26.83	29.62	27.48	13.94	20.92
87	10.34	14.66	17.19	15.22	19.24	20.60	20.59	23.64	24.63	27.37	25.39	26.91	19.77	23.01	24.10	26.42	26.92	29.74	27.58	13.97	20.98
88	10.37	14.74	17.31	15.33	19.35	20.73	20.65	23.77	24.78	27.51	25.51	27.06	19.82	23.08	24.18	26.54	27.01	29.85	27.69	14.00	21.03
89	10.39	14.81	17.43	15.43	19.45	20.85	20.72	23.89	24.93	27.63	25.64	27.21	19.87	23.14	24.25	26.65	27.09	29.95	27.79	14.02	21.08
90	10.41	14.89	17.55	15.53	19.55	20.97	20.78	24.02	25.08	27.76	25.76	27.36	19.91	23.21	24.33	26.75	27.18	30.06	27.89	14.05	21.13
91	10.42	14.97	17.66	15.64	19.64	21.09	20.85	24.14	25.23	27.88	25.88	27.51	19.96	23.27	24.40	26.86	27.26	30.16	27.98	14.07	21.18
92	10.44	15.04	17.78	15.74	19.74	21.21	20.91	24.26	25.37	28.01	26.00	27.65	20.00	23.33	24.46	26.96	27.33	30.26	28.08	14.09	21.23
93	10.46	15.11	17.89	15.83	19.83	21.32	20.97	24.38	25.52	28.12	26.11	27.79	20.04	23.39	24.53	27.06	27.41	30.36	28.17	14.11	21.27
94	10.48	15.19	18.00	15.93	19.93	21.44	21.03	24.50	25.66	28.24	26.23	27.93	20.09	23.44	24.59	27.16	27.48	30.45	28.26	14.13	21.32
95	10.49	15.26	18.12	16.03	20.02	21.55	21.09	24.62	25.79	28.36	26.34	28.06	20.13	23.50	24.65	27.26	27.55	30.55	28.34	14.15	21.36
96	10.51	15.33	18.23	16.12	20.11	21.66	21.14	24.73	25.93	28.47	26.45	28.20	20.16	23.55	24.71	27.35	27.62	30.64	28.43	14.17	21.40
97	10.53	15.39	18.33	16.22	20.20	21.77	21.20	24.84	26.07	28.58	26.55	28.33	20.20	23.60	24.77	27.44	27.69	30.72	28.51	14.19	21.44
98	10.54	15.46	18.44	16.31	20.28	21.88	21.25	24.95	26.20	28.69	26.66	28.46	20.24	23.65	24.83	27.53	27.76	30.81	28.59	14.21	21.48
99	10.56	15.53	18.55	16.40	20.37	21.99	21.30	25.06	26.33	28.80	26.76	28.59	20.27	23.70	24.89	27.62	27.82	30.89	28.67	14.23	21.52
100	10.57	15.59	18.65	16.49	20.45	22.09	21.35	25.17	26.46	28.90	26.86	28.71	20.31	23.75	24.94	27.70	27.88	30.97	28.74	14.24	21.55

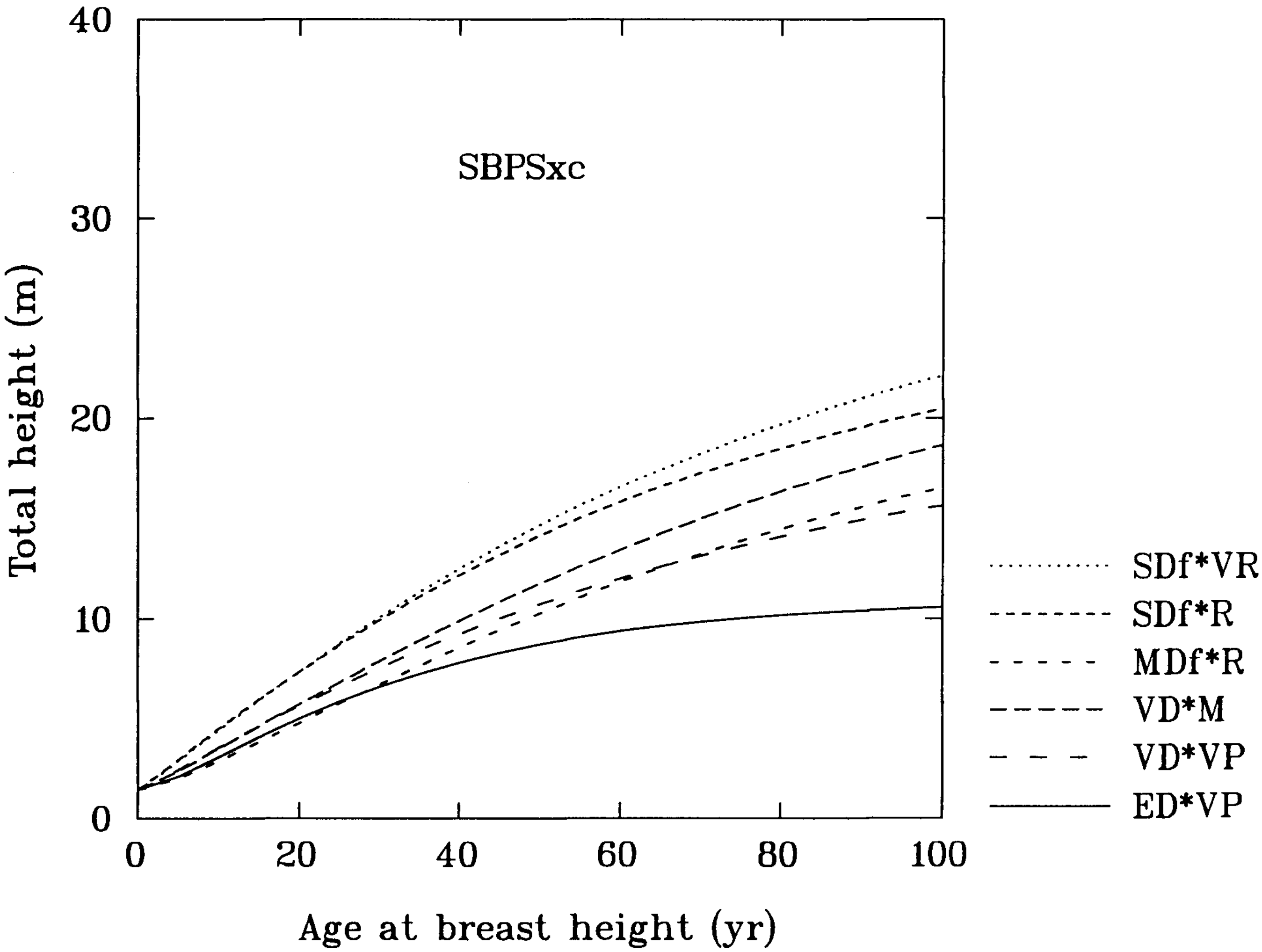

Figure A5. Ecotope lodgepole pine height growth curves for SBPSxc subzone based on equation [5.4.11] and parameters given in Table 5.12. Symbols for BGC, SMRs, and SNRs are given in Table 5.1.

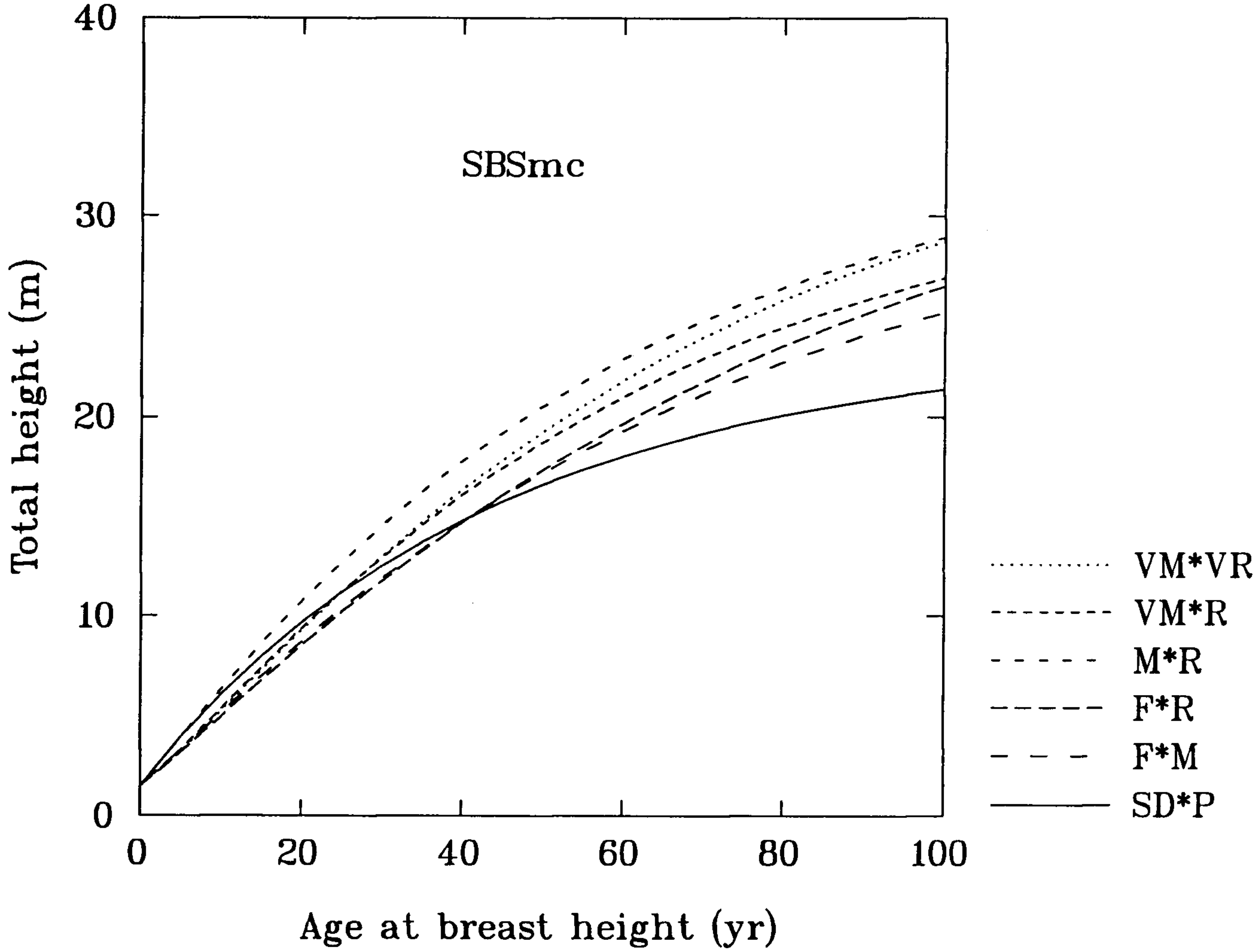

Figure A6. Ecotope lodgepole pine height growth curves for SBSmc subzone based on equation [5.4.11] and parameters given in Table 5.12. Symbols for BGC, SMRs, and SNRs are given in Table 5.1.

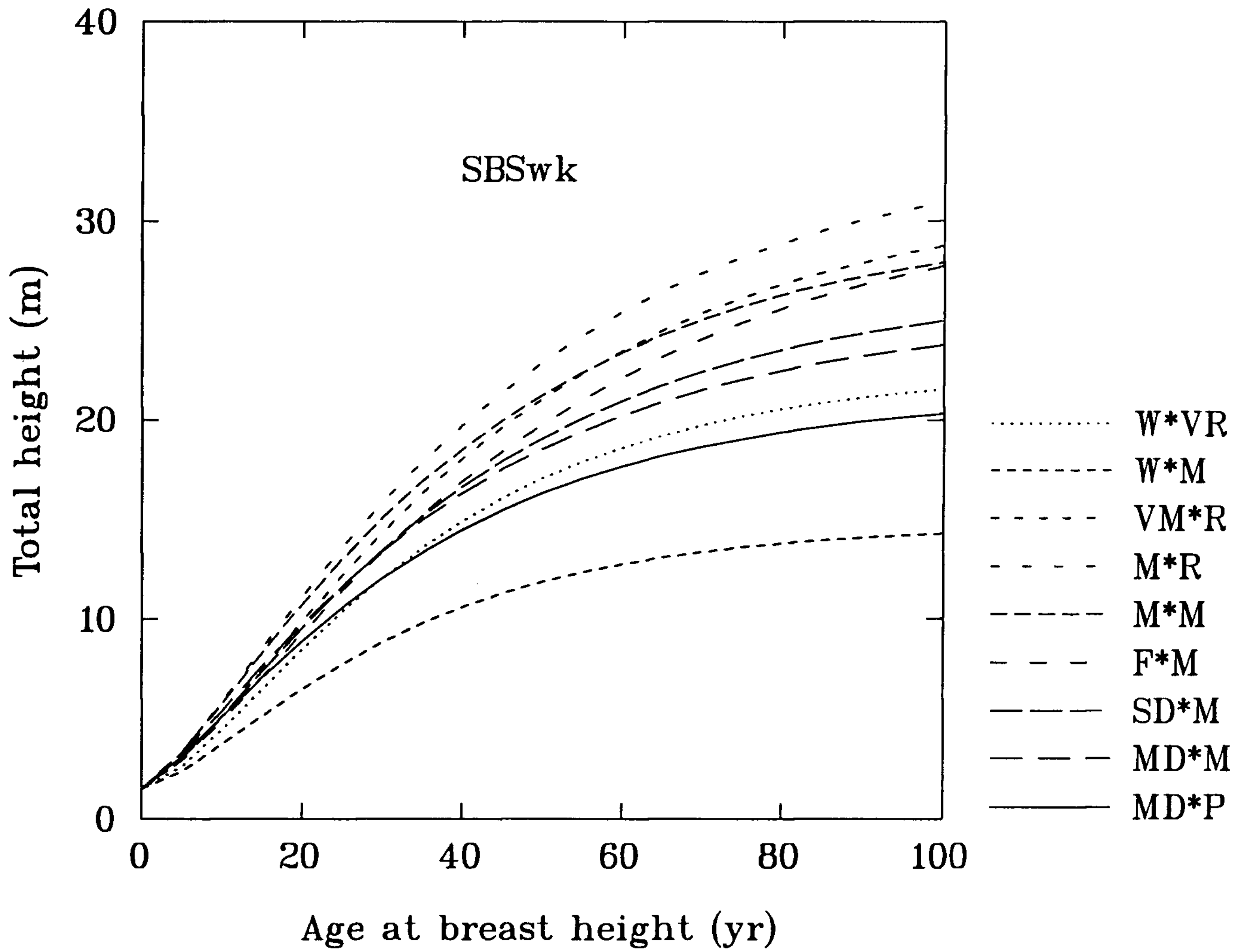

Figure A7. Ecotope lodgepole pine height growth curves for SBSwk subzone based on equation [5.4.11] and parameters given in Table 5.12. Symbols for BGC, SMRs, and SNRs are given in Table 5.1.