

**ECOLOGICAL SITE QUALITY AND PRODUCTIVITY OF WESTERN
HEMLOCK ECOSYSTEMS IN THE COASTAL WESTERN HEMLOCK ZONE
OF BRITISH COLUMBIA**

by

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Abstract

To assess relationships within the biogeoclimatic ecosystem classification(BEC) system, 102 sample plots were established in immature western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] stands distributed within the submontane very wet maritime variant of the Coastal Western Hemlock Zone in coastal British Columbia. Using the methods described in the BEC system, plant associations, and field derived soil nutrient regimes (SNR) and soil moisture regimes (SMR) were identified. Direct measures of SNRs, i.e., soil chemical measures of the forest floor and mineral soil expressed on a concentration basis, and site index (height at a reference age) were determined for each stand.

Despite a lack of understory species, both plant associations and 6 diagnostic species were linked to an underlying nutrient gradient. For the former, the use of canonical discriminant analysis on the principal components analysis (PCA) scores of the soil chemical measures showed a definite but overlapping trend. This trend was correlated most positively with nitrogen, and negatively with the C:N ratio and potassium. For the latter, canonical correlation analysis of 6 diagnostic species with 4 forest floor chemical measures resulted in the 4 chemical canonical variates explaining 37% of the variance in the species domain. Generally, oxylophytic species varied negatively with total and mineralizable nitrogen, and positively with available potassium and magnesium. The relationships with nitrophytic species were reversed.

A PCA ordination showed the soil nitrogen measures to be the most important factors in accounting for the variation in the soil chemical data. Discriminant analysis, used to see how well the nitrogen properties could

distinguish SNRs, correctly classified 91% of the plots into their source group. However, this high success rate was not repeatable; on a validation set, the discriminant function correctly classified only 54% of the plots.

All regression models reported, relating site index (m/50 yr) to indirect and direct variables, showed significant ($p < 0.05$) results, and had adjusted R^2 values ranging from 0.35 to 0.81. The standard errors of estimate (SEE) were relatively high, ranging from 4.5 m to 8.8 m. The best fit regression equation, having the highest adjusted R^2 value and lowest SEE, was the categorical model which related site index as a function of SMRs and SNRs. The best fit analytical model related site index as a function of nitrogen positively and potassium negatively (adjusted $R^2 = 0.67$, SEE = 5.61m). However, this model failed to adequately predict, within 3 meters, the site index of the data set from which it was derived. Applied to a test data set, the prediction results improved but the equation tended to underestimate site index. Multicollinearities among the soil nutrient properties were noted and therefore, PCA regression used to supplement the interpretation. Examination of the loadings of the axes of the final regression equation (adjusted $R^2 = 0.63$, SEE = 5.89) indicated that the strongest relationships with site index were positively related with sulphur and logarithmic transformations of nitrogen, and negatively with the C:N ratio and potassium. Supplementary relationships were also noted.

It was concluded that there exists a relationship between nitrogen measures and field derived SNRs. Further, the SNRs can be combined with SMRs to predict western hemlock site index. As well, soil chemical measures can also predict site index. However, there was a relatively large variation associated with predictions made using the regression equations.

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PROLOGUE

...without classification there would be no science of ecosystems, and no ecology. And indeed, no science.

V.J. Krajina ¹

Human interest in the relationship between plants and the land which supports them is undoubtedly as old as human existence. The recognition of land capable of supporting food plants and the subsequent mental categorizing of this information must have been a natural reaction for survival. Thus, the seeds of the need for classification start; it is a natural and inherent process to create some semblance of order from an apparent disorderly assembly, and an endeavour which, as far as we know, is a uniquely human attribute.

During the spring of 1985, while I was employed as a forester on Vancouver Island, British Columbia, a treeplanting crew was working on a site which we foresters would designate as "moist/very rich". One of the treeplanters, having many years of planting experience and having grown up in the rural areas of the Maritimes, decided that this area was "rich" enough to plant some potatoes among the rows of Sitka spruce. Watching this small attempt at agroforestry, the question arose: how could this treeplanter with entirely different experiences than myself come to the same conclusion that this site was "very rich"?

The treeplanter's assessment was based on planting in several
different areas in Canada and on a Maritime experience of recognizing

¹ Krajina, V.J. 1960. Ecosystem classification of forests. *Silva Fennica* 105: 107-110.

"farmland". As a forester, my assessment was based on a university education supplemented by several years of field application. Therefore, was our similar but separately derived decisions, based on two very different learning experiences, merely subjective? And if it was subjective, why then did this treeplanter not plant potatoes on a dry, poor site and why would I not choose to plant Sitka spruce on that same site? Subjective? I think not.

Rather, both of us based our decisions on combined, although different, experiences and a knowledge base using what is referred to as an *heuristic* procedure. This allowed both of us to identify this small, seemingly inconsequential, tract of land as having similar vegetation potential. For confirmation of my heuristically derived decision, I had the benefit of being able to analyze the soil with various chemical tests and also measuring the performance of the planted trees years later. Both confirmed that, indeed, this site was "very rich", and by recognizing other similar areas I am able to infer that they are also "very rich". Accompanying this recognition are a variety of accessory characteristics associated with this "class", such as soil chemical properties and productivity. Using these basic principles and processes it is also possible to extend this recognition of land areas to different ones and eventually formalize them into a generalized classification. Thus the basic, albeit simplistic, principle of ecosystem recognition, classification, confirmation, and inference of associated relationships is demonstrated.

As far as the treeplanter's decision, the confirmation lay in the harvest that fall of a modest but substantial potato crop. I received some of that crop and now I am able to confirm that this treeplanter's heuristically arrived conclusion was also correct -- the potatoes were delicious!

1. INTRODUCTION

1.1 Background

Productivity, recognition, and classification of land are three interests which are as old as agriculture and whose recorded intellectual interest in the Western World dates to the centuries B.C. (Kimmins 1988). Productivity of sites was a driving force behind recognition and classification. For trees, the first recorded observations of growth on sites of various moisture status was made by Theophrastus (370-285 B.C.), a student of Aristotle (Makkonen 1968; Tesch 1981). Recorded attempts at recognition and classification of sites soon followed. The Roman Cato (234-139 B.C.) associated certain plants with soil conditions indicating good wheat land (Kelly 1922), and then developed a subjectively based land classification which included land best suited for wine production, pasture-forest land, and commercial forest land (Makkonen 1969; Tesch 1981).

The subjective nature of site classification, being based on broad quality classes or loosely based on physical characteristics such as soil exposure, remained as the primary method until the eighteen hundreds (Cajander 1926). Then, throughout Europe, plant geographers developed formalized vegetation classifications, and throughout the 1800's divergent approaches developed into regional traditions adapting to different kinds of landscapes and research interests (Shimwell 1971; Whittaker 1962, 1980).

It was also during this period that there was the realization of the importance of soil physical and chemical properties in controlling growth, which ultimately resulted in such familiar ecological rules such as Liebeg's "Law of the Minimum" (reported in Tesch 1981). The application of this

knowledge of soil chemistry resulted in some success in forestry applications where, during the 1870's in northern Germany, Schütze followed by v. Falckenstein (reported in Cajander 1926) demonstrated the correlation between forest yield capacity and some soil chemical measures that were available at that time. However, it was not until the late 1920's and early 1930's that significant contributions to soil testing in evaluation of soil nutrients were obtained (Melsted and Peck 1973).

The earliest comprehensive study that synthesized the relationship between a vegetation classification system, soil chemical properties and productivity was that of Cajander (1926) in Finland. Using the Northern Tradition of vegetation classification (Frey 1980), the boreal forest of Finland was recognized to be of five types. Ilvessalo (1927) related productivity to each of these types. Valmari (reported in Cajander 1926) found differences in amounts of loss of weight on ignition, of electrolytes (e.g sodium chloride), and nitrogen in the upper eight inches of soil, and Aaltonen (reported in Cajander 1926) found differences in nitrogen and pH of the humus between the types.

At present, interest in the relationship between productivity, recognition, and classification of land is becoming more important as pressure for resources in a growing population continues (Kimmins 1988). Additionally, there is the realization of the need to develop an understanding of the underlying processes of what is holding a community intact and functioning as an organic entity (Orlóci 1988). To this end there has been recognition of the value of a multifactor, integrative, hierarchical forest classification system (Krajina 1972; Kimmins 1977; Spurr and Barnes 1980; Barnes *et al.* 1982; Barnes 1984, 1986; Monserud *et al.* 1990).

This concept and approach are inherent to the biogeoclimatic

ecosystem classification (BEC) system (Pojar *et al.* 1987), now widely used in British Columbia, which provides a framework for organization of knowledge of forest ecosystems. The classification is based, with some modifications, on the work of Dr. V.J. Krajina and his students in the 1960's and 1970's at the University of British Columbia (see Krajina 1959, 1965, 1969, 1972; Wali 1988). Sites are classified according to their potential to produce similar vegetation. Plant communities at a relatively stable stage of development (mature, climax or near-climax) are considered a reflection of this potential and form the basis for classification. Classes derived through this process, termed "site units", are subsequently characterized by their climate, soil moisture and soil nutrients. A result of this classification is presented as a series of edatopic grids of soil moisture regimes (SMR) and soil nutrient regimes (SNR) (Pogrebniak 1930 cited in Krajina 1972). Thus each grid is developed within a regional climate, and distinguishes site units with environmental properties inferred to be similar or equivalent and, hence, having similar vegetation potential.

Having classified, the next step is that of testing, validating and demonstrating the importance of the derived units. A relationship between forest productivity and site units derived from the BEC system was proposed by Krajina (1969). Subsequently, the relationship of productivity, using site index¹, to vegetation units, site associations, site series, and their formative elements [biogeoclimatic unit (subzone or variant), actual soil moisture regime, soil nutrient regime] have been demonstrated (Kojima 1983; Courtin *et al.* 1988; Green *et al.* 1989; Klinka *et al.* 1989; Carter and Klinka 1990; Klinka and Carter 1990).

¹ Site index is taken to be the height of a specified character and number of trees at a specified age. This is used as an empirical gauge of a site's capacity to support forest growth for the specific species measured.

As well, characterization of soil nutrient regimes, to relate the site units to objective and meaningful criteria, has been investigated (Kabzems and Klinka 1987a) and an approach for an objective means of defining SNRs proposed (Courtin *et al.* 1988). To objectively define soil moisture regimes, Klinka *et al.* (1984) used the occurrence and duration of phases of water use, complemented by the ratio between actual and potential evapotranspiration, and the occurrence and depth of the water table.

1.2 Purpose and Objectives

In an effort to further assess the classification, and in order to describe western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] ecosystems through the use of statistical patterns, this thesis is an investigation into the relationships between western hemlock ecosystems, as derived from the biogeoclimatic ecosystem classification system (Pojar *et al.* 1987), associated soil chemical and physical properties, and productivity as measured by site index (height at 50 years breast height age). It seeks to provide a practical tool for silviculturists, to describe relationships as related to western hemlock and site units, to increase understanding of western hemlock nutrition, to increase understanding of the many interacting factors that make up an ecosystem, and to provide direction for further research.

The specific objectives are:

- (i) to explore the relationship of individual understory species, and the collective expression of individual species through plant associations derived using the Braun-Blanquet method, to soil nutrient measures.

- (ii) to explore whether the inferred soil nutrient regimes and soil moisture regimes, as derived from the field procedures prescribed by the BEC system, are related to direct measures of soil nutrients for the former, and to the ratio between actual and potential evapotranspiration for the latter.
- (iii) to assess relationships of western hemlock site index with indirect and direct measures of ecological site quality. This includes vegetation units and site units, as derived from the BEC system, individual species, and individual soil nutrient measures.

2. LITERATURE REVIEW

2.1 Introduction

Productivity, recognition, and classification of sites all developed in a parallel and concurrent manner, resulting in many different approaches with much overlap. Productivity, however, is the common link and, in North America, was the focus in the development of classification systems. Since the measure of productivity used in this thesis will be site index, the following literature review will start with the concept of site index to establish the validity of this method in assessing productivity. A review of the many studies involving correlation between a measure of potential productivity with individual factors of the site, the so called soil-site studies, is unnecessary since many excellent reviews have been done in the past. Similarly, a review of the many varied classification systems throughout the world is beyond the scope of this study. However, commentary on certain soil-site studies will be made with emphasis on the principles used as a framework for this thesis, and reference will be made to some of the more popular and familiar (without a connotation of "better") classification systems. The three concepts of site recognition, productivity, and classification will then be brought together in a review of some needed concepts of the BEC system. Finally, a review of studies related directly to western hemlock productivity and nutrition will be made.

2.2 Site Index

Modern methods and principles for evaluating forest productivity developed in Europe starting at the end of the 18th century. From the

1790's to the 1870's individual tree volume curves were developed from early anamorphic and stem analysis procedures, and from permanent sample plots (Cajander 1926; Tesch 1981). In 1824, Huber introduced stem analysis on dominant trees to determine the normal development of stand height, named the index method (reported in Cajander 1926). This was the first method founded on the assumption that the dominant trees of a stand had always been dominant. The claim that height is a sensitive measure of differences in site was based on comparisons of volume and height of 100 year-old stands reported by Professor Schwappach in Germany in 1908 (cited in Roth 1916). Schwappach regarded "... height, leaving out some abnormal cases, as the best criterion of the site in the stands of middle age and older, while the volume of the main stand is suited for this purpose if the stand has been properly cared for and is in normal condition for a long period". Roth (1916) supplemented this claim with comparisons of volume and height on different sites from five studies carried out in the United States.

The use of height of the dominant tree as an indicator of volume production was imported into the United States during the early 1900's (Mader 1963; Tesch 1981). The reasons for adopting height as a method of site classification were: (1) height is a sensitive measure of differences in site; (2) height is independent of stocking and species mixture within broad limits; and (3) the height/age relationship is easy to determine and thus, is convenient, simple, and practical (Roth 1916, 1918; Watson 1917; Society of American Foresters 1923).

For several decades beginning in the 1920's, the site index concept was used in reporting most yield tables in the United States (Tesch 1981). Bruce (1923, 1926) established the anamorphic approach for height curve

construction, where a central guide curve or average curve was fit through the data and curves for each site index class were then derived proportionately, as the primary method of determining site index.

Since then, site index has become the most widely accepted measure of productivity, based on the observation that the height of dominant trees (that have always been dominant) of a given species and age is more related to the capacity of a given site to produce wood than any other single measure, besides volume itself (Spurr and Barnes 1980). However, problems with using site index as a measure of productivity have been reported (Monserud 1984a). Mader (1963) felt that height and volume growth may not react in exactly the same way to site differences, thus height differences alone may not fully reflect site differences. Monserud (1984a) pointed out that sites having the same height growth potential need not necessarily have the same basal area growth potential. Others (Sammi 1965; Hall 1983; Monserud 1988) have stated that since volume is the measure of interest, volume itself should be used directly.

Also, specific problems with the anamorphic approach have been reported (Carmean 1970; Beck and Trousdell 1973; Monserud 1984a). These include (i) the possibility of sampling bias due to a disproportional sample of site and age during curve construction, and (ii) the assumption that the shape of the height growth curve is the same for all sites. This was recognized by Bruce (1926) and was soon after demonstrated for red pine with the construction of polymorphic height curves on sites grouped according to height at 15 years (Bull 1931). Since then, a polymorphic trend between different sites has been demonstrated for mixed hardwood plant associations using the Braun-Blanquet approach (Lemieux 1964), jack pine (*Pinus banksiana* Lamb.) using soil pore pattern, soil moisture and

vegetation as distinguishing factors of different sites (Jameson 1963), black spruce [*Picea mariana* (Mill.) B.S.P.] using the regolith system (VanGroenwoud and Ruitenberg 1982), interior Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco] using Daubenmire's habitat types (Monserud 1984b) and others (see Jones 1969; Monserud 1984a).

The height growth of chosen site index trees is assumed to be independent of stand density over a wide range of stocking (Hägglund 1981). Empirical evidence from thinning experiments indicates that within wide limits of stand density, height growth of dominants and codominants seems to be unaffected by thinning (Lynch 1958; Clutter *et al.* 1983). Some exceptions occur where height increment is severely reduced in very dense stands, and is most apparent on poor sites (Lynch 1958). Studies involving natural stands, planting trials or spacing trials found that this was the case for lodgepole pine (*Pinus contorta* Dougl.) (Parker 1942; Smithers 1956; Alexander *et al.* 1967), ponderosa pine (*Pinus ponderosa* Dougl.) (Lynch 1958; Barrett 1965, 1970, 1973), and slash pine (*Pinus elliotii* Engelm.) (Collins 1967; Bennett 1975). Reukema (1979) found that the height at age 51 years increased with increasing spacing for Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] on a poor site. For western hemlock specifically, evidence suggests that there is no difference in top height in stands of densities from 300-1000 stems/hectare when growing on medium sites (Reukema and Smith 1987). Wiley (1978) found that densities at age 50 from less than 200 to 600 trees per acre did not have an effect on site index.

In breeding programs, trees superior in production (so-called "plus trees"), can be identified on the basis of superior height growth (Wright 1976). Yet, in site index, this factor influencing height growth is ignored.

Presumably, the idea is that with a measure such as "top height", where 100 of the largest diameter trees are chosen as site index trees, this genetic factor will somehow "even out". However, a study by Monserud and Rehfeldt (1990) gives evidence that a "genetic index" of standardized 3-year seedling heights (Rehfeldt 1989) explains more of the variation in height growth for Douglas-fir than site factors, although King (1966) showed that this effect falls off as trees get older.

Physiological ecological theory suggests that characteristics such as height are controlled by many genes of small effect. Thus plant growth is extremely plastic, allowing it to respond to an unpredictable environment, and a plant's size directly reflects the conditions under which it is growing (Waller 1986). It is generally accepted that these variations are related to the acquisition of limiting resources, at least in part. Changes in environmental conditions are met by allocation of growth resources to the organ that is capable of alleviating the limitation (Fitter 1986). Keyes and Grier (1981) found differences in partitioning of resources between Douglas fir on a low and high productivity site. They proposed that on harsh sites which may impose water or nutrient deficiencies, this shift in production allocation from above to belowground may be an essential mechanism to avoid or alleviate stress. This subsequently has been supported for lodgepole pine (Comeau 1986) and for Douglas-fir (Vogt *et al.* 1983; Kurz 1989).

2.3 Soil-Site studies

In the United States during the early 1900's, there was considerable debate over what method should be adopted to unify the approaches to site evaluation. The standards suggested and debated were height growth,

volume growth, and site types. Although in the end height growth became the accepted standard for the classification of sites (Society of American Foresters 1923), a general recognition seemed to exist that the use of site type and either volume or height measures were not in conflict but rather served complementary purposes. Even proponents of using height growth as a measure of site quality stated that a classification plan based on physical factors was fundamental. However, since the knowledge at that time was inadequate for such a classification, an indicatory measure such as height growth was suggested for use in the interim (Mader 1963).

Emphasis, from that time, was placed on the classification of sites based on productivity, and the development of site index curves using an anamorphic approach. Subsequently, many investigations of the relationship between a productivity measure, usually site index, and chemical and physical components of the site have been carried out. These have come to be known as "soil-site" studies and have had an objective of finding an alternative method to predict productivity for areas where site index could not be determined (for reasons such as lack of the species of interest, age, top damage, excessive stand density, *etc.*).

It was not until the 1960's that other systems involving climate, physiography (geomorphology, landform, terrain), soil, and vegetation received a major focus (Barnes 1986). The components of an ecosystem (the climate, landform, soils, and vegetation) can be used together in various combinations to form a multi-component ecosystem classification system. The varieties of classification involving forests in North America are briefly reviewed by Barnes (1986), by Burger and Pierpoint (1990) for Canada, and by Pojar and Meidinger (1991) specifically for British Columbia.

Soil-site studies have been reviewed thoroughly (e.g. Colle 1952;

Rennie 1963; Ralston 1964; Jones 1969; Tamm 1971; Carmean 1970, 1975, 1986; Shrivastava and Ulrich 1976; Daniel *et al.* 1979; Spurr and Barnes 1980; Tesch 1981; Hägglund 1981; Gessel and Oliver 1981; Pluth and Corns 1983; Clutter *et al.* 1983; Grigal 1984; and Packee 1988); therefore, only general description and comments will be given.

The methods reported can generally be organized into two major groupings: (1) methods combining individual components of the site to directly estimate a measure of productivity, what has been termed a *factorial* approach; and (2) methods utilizing classes or taxa of ecological or land classification systems to directly estimate a measure of productivity, an *integrative ecological* approach.

Relationships between a productivity measure and various soil, environmental and chemical factors, have been studied extensively, with algorithms developed for a wide range of species, using a wide range of factors, over most of the world. The environmental variables thought to have the greatest influence on tree growth are selected, combined and then related to a measure of productivity. This approach has been referred to as a "factorial approach" to measuring productivity, for it tries to approximate forest productivity by relating it to one or more limiting factors of the physical environment (Coile, 1952; Jones, 1969).

The purpose of the derived equations has been either (1) to predict forest productivity from site factors when the species of interest is absent, or (2) to try to establish factors that are correlated with the productivity of a particular species. The most common method is the use of multiple linear regression where a measure of productivity, usually site index, is used as the dependent variable and environmental components of the site thought to have an influence on productivity are used as the independent variables.

Both field and laboratory physical and chemical measures have been used as independent variables. However, equations using chemical properties measured in the laboratory usually have a different purpose than those derived from field measurable properties. The practical usefulness of regression analysis for predicting site index from soil chemical variables is severely restricted by the cost and the difficulty of assessing nutrient supply. As noted by Hägglund (1981), properties measured through laboratory analysis usually will not be included in functions intended for practical field work. However, these techniques may have value when trying to evaluate some of the nutrient properties correlated with tree growth.

Considering the multitude of varying results and successes, it is debatable whether the factorial method, as currently used, is really leading anywhere. The number of different techniques and results caused Hägglund (1981) to pose the question of whether we are on our way towards development of aids for practical productivity estimation or whether site evaluation research is trapped in a "maze". At best it seems that successful equations can be obtained on small, relatively homogeneous areas with uniform climates and distinctive soil conditions (Hodgkins, 1956; Monserud *et al.* 1990). The one generalization from the many factorial studies was that the growth potential of trees is chiefly affected by the amount of soil occupied by tree roots and by the availability of soil moisture and nutrients in this limited space (Spurr and Barnes 1980).

There are inherent problems in studies that choose arbitrarily to sample across a diversity of sites. Multicollinearity of both physical and chemical factors can cause instability of multiple regression equations and conflicting or even misleading results if not specifically addressed. If the equations are used for interpretation, interactions with soil moisture,

nutrients, aeration and temperature can make this difficult. Only by holding moisture, aeration and temperature constant and varying nutrients only, may a nutrient effect become clear. However, for example, if soil texture varies from sand to clay, then with decreasing soil particle size there may be an increase in nitrogen, but a concomitant decrease in aeration. Productivity may then seem to vary inversely with nitrogen content. This was the case in a soil-site study of western catalpa (*Catalpa speciosa*, Ward), where Walker and Reed (1960) found significant negative correlations between height and total nitrogen (%). However, total nitrogen was highly correlated with the silt-plus-clay content of the soil, which in turn was negatively correlated with height. They concluded that the negative correlation between height and nitrogen was a "trailer effect" of the negative correlation between height and the silt-plus-clay content.

Broadfoot (1969) felt that there were insurmountable problems with using a factorial method to objectively select measurable soil properties to predict site index for southern hardwoods over wide geographic areas. A combined subjective and objective approach was developed to predict site index, based on an understanding of the site requirements of the species. Using this experience, site factors were "subjectively" chosen and combined to derive a site index value. For southern hardwoods this technique was satisfactory (Baker and Broadfoot 1977, 1979). Harrington (1986) used stepwise discriminant analysis to derive the factors in an objective manner for red alder (*Alnus rubra* Bong.).

The second group of soil-site studies involves adding forest productivity measures to a taxonomic system which then can allow derived taxa or their groupings to be used directly to estimate a productivity measure. Taxonomic classifications are not restricted to productivity since

the units can be used for other management or scientific purposes. Since the taxonomic units usually are thought of as an expression of many different environmental factors, multicollinearities are thought simply to express themselves into a few emergent properties. This identification of units also has potential for polymorphic site index curve development.

Soil classification systems (Soil Survey Staff 1975; Agriculture Canada Expert Committee on Soil Survey 1987) are the obvious systems with which to relate productivity measures, soil being the rooting medium of vegetation. However, in many studies based on earlier versions of soil classification systems, the variation in productivity measures, usually site index, within and between soil series or soil mapping units has been too high for soil taxa alone to be related to productivity (Jones 1969; Carmean 1970, 1975; and others). The range of physical and chemical properties of the soil taxa of the past seemed to be too wide to accurately reflect the major edaphic and topographic factors that influence tree growth (Coile 1952; Ralston 1964; Jones 1969; Carmean 1975). Generally, the position was that high correlations between a site productivity estimate and soil classification unit occurs only in restricted areas of limited variation (Doolittle 1957; Trimble and Weitzman 1956). However, further study is required to assess the correlation with productivity using present-day versions of soil classification (for example Agriculture Canada Expert Committee on Soil Survey 1987), especially at the soil series and phase level.

Another classification system, which has popularity in the United States, is Daubenmire's habitat system (Daubenmire 1968). Briefly, all land areas potentially capable of producing similar plant communities at climax may be represented by one habitat type in this system. The climax plant community, because it is the end result of plant succession, is thought to

reflect the most meaningful integration of the environmental factors affecting vegetation. Thus, each habitat type represents a relatively narrow segment of environmental variation and delineates a certain potential for vegetative development. Habitat types can be identified during most intermediate stages of succession by comparing the relative reproductive success of the tree species present with known successional trends and by observing the existing undergrowth vegetation.

Studies relating habitat type to productivity have had promising but inconclusive results. Pfister *et al.* (1977) reported the estimated yield capabilities of habitat types in Montana showing a large variation within habitat types, but a gradient between habitat types. In other studies, habitat types were grouped into productivity classes with significant differences in productivity (Roe 1967; Johnson *et al.* 1987). Using stem analysis Monserud (1984b) not only found different site indices between habitat types but also found different shaped height curves for each type.

Derived units from soil, vegetation and ecosystem classification systems have potential for use in estimating site index. Correlation of productivity to interpretive units would in fact be an integral part of the testing of classification systems to discover relationships. The derived taxa also allow for the construction of site-specific polymorphic height curves, but perhaps more importantly, the classification system itself provides a needed framework of which productivity is one integral, but not the only, function.

2.4 The System of Biogeoclimatic Ecosystem Classification

The biogeoclimatic ecosystem classification system organizes ecosystems according to the principal of ecological equivalence, which

results in groups that have similar ecological site quality and potential vegetation (Pojar *et al.* 1987). This basic unit of site classification is the site association. Site association represents a group of ecologically equivalent sites that have a similar vegetation potential. They are subsequently characterized by a certain range of climates, soil moisture and soil nutrient regimes, plus additional features if required. On these sites, similar plant communities will develop at late successional stages. The concept of ecological equivalence and the use of indicator species acknowledges interaction as an inherent property of ecosystems.

A site association can contain ecosystems from several different climates thus varying in actual site conditions. Dividing the site associations into site series using subzones and variants produces site units that are climatically, and therefore usually edaphically, more uniform. Site units are presented through edatopic grids, a form of an environmental matrix, composed of two major gradients, hygrotape (soil moisture regimes) and trophotape (soil nutrient regimes) (Pogrebniak 1930 cited in Krajina 1972).

Soil moisture regime (SMR) represents the long-term balance between the amount of available water and the demand for that water by vascular plants. Krajina (1969) adopted nine classes (0 to 8) of relative SMRs and applied them consistently in each climate (variant). These, in effect, reflect moisture holding capacity, and the actual water available for plants is dependent on the circumscribing climate. Actual SMRs for coastal British Columbia, based on the ratio between actual and potential evapotranspiration, the annual water balance, and the depth of the growing season groundwater table, were proposed by Klinka *et al.* (1984).

Soil nutrient regime (SNR) is the average amount of essential soil

nutrients that are available to vascular plants over several years. Krajina (1969) adopted six classes (A to F) of SNRs and applied them in different climates and for soils with different SMRs.

The identification of site series is based on a combination of climate, soil moisture regime and soil nutrient regime. Climate is identified through the variant, while SMR and SNR are assessed according to a heuristic synthesis of individual physiographic and soil properties, expressed in a node and link key (Klinka *et al.* 1984; Banner *et al.* 1990), and modified by vegetation. The soil properties chosen use identifiers which are themselves emergent properties integrating causal factors into a physically identifiable characteristic. Thus humus order (Klinka *et al.* 1981), which has been shown to reflect decomposition rate (Klinka *et al.* 1990), soil colour, which is related to soil organic matter content (Soil Survey Staff 1975), and the character of the A horizon, which indicates pedogenic processes, for example, are used to help identify a SNR. The presence of mottling which indicates reduction-oxidation reactions caused by a fluctuating water table is a property to help identify a SMR. Heuristic procedures, although not completely objective, take advantage of the current knowledge of "experts" and are especially useful when no algorithm exists. (Pearl 1984; see also Groner *et al.* 1983).

The concept of nutrient availability can be viewed from two perspectives, (i) as a nutrient availability, the rate at which nutrients can be supplied for plant uptake, which is site dependent, and (ii) as nutrient limitation, which is the extent to which productivity is reduced by an inadequate rate of nutrient supply, and is not only site dependent, but species dependent as well (Chapin *et al.* 1986). Nutrient characterization of SNRs derived from the BEC system is a measure of the former and the

relationship to productivity a measure of the latter.

On an initial quantification of the field-estimated SNRs recognized in the BEC system (poor, medium, rich and very rich), Kabzems and Klinka (1987a) found that the sums of mineral soil plus forest floor mineralizable nitrogen, total nitrogen, and exchangeable calcium and magnesium, expressed in kg/ha, were the properties that best differentiated the SNRs. Individually, $\ln(x+1)$ transformations of mineral soil, and the sum of mineral soil and forest floor mineralizable nitrogen and total nitrogen showed significant differences (Student-Neumann-Keulls test, $p < 0.05$). Using cluster and discriminant analysis, Courtin *et al.* (1988) were successful in differentiating soil nutrient regimes in coastal British Columbia on the basis of pH and carbon-nitrogen ratio of the forest humus form, and total soil nitrogen and the sum of available calcium, magnesium, and potassium (kg/ha) within the soil rooting zone.

The relationship of site units, derived from the BEC system, with productivity has been reported for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) located within the very-dry-maritime and the dry-maritime subzones of the Coastal Western Hemlock biogeoclimatic zone of British Columbia. Kabzems and Klinka (1987b) found significant ($p < 0.05$) differences in site index (height at 50 years breast height age) for Douglas-fir between each SMR (very dry, dry, and fresh) and each SNR (poor, medium, rich, and very rich) with the ordering of increasing site index corresponding to the ordering of SMR and SNR. Mineral soil (alone) and forest floor plus mineral soil mineralizable nitrogen, total nitrogen, exchangeable calcium, exchangeable magnesium, and mineral soil extractable phosphorus were the soil chemical properties most highly correlated with site index. Other results (Green *et al.* 1989; Klinka *et al.* 1989; Klinka and Carter 1990; and

Carter and Klinka 1990) show that Douglas-fir site index can be reliably predicted using site associations, certain indicator species groups, SMRs and SNRs, and mineralizable nitrogen combined with growing-season water-deficit (Table 2.1).

Table 2.1 Reported Douglas-fir site index relationships with variables derived from the BEC system within the very-dry-maritime and the dry-maritime subzones of the CWH zone.

Variables	R ²	S.E. (m)	n	Author
site associations	0.86	3.18	88	Green <i>et al.</i> 1989
plant indicator species groups	0.77	3.95	88	Green <i>et al.</i> 1989
field estimated SMRs and SNRs	0.86	1.99	56	Klinka <i>et al.</i> 1989
	0.85	2.00	99	Klinka and Carter 1990
growing-season water deficit and natural log of mineral soil mineralizable nitrogen (anaerobic incubation)	0.67	3.10	53	Carter and Klinka 1990
actual evapotranspiration during May and June, natural log of forest floor and mineral soil mineralizable nitrogen (anaerobic incubation)	0.71	2.90	53	Klinka and Carter 1990

2.5 Western Hemlock Soil-Site Studies

There have been several soil site studies on the relationship of western hemlock to its environment and productivity. The first reported study was by Taylor (1929) on what was referred to as a hemlock-spruce type in southeastern Alaska. One hundred and sixty-six tenth-acre plots were sampled and a simple compilation of per cent occurrence of dominant

vegetation and the associated site index was made. As Table 2.2 shows, there was a correlation between the occurrence of these five species and site index (total height at 100 years for combined hemlock and spruce). By applying current knowledge as to the indicator values of these species, the relationship between site index and soil nutrients can be inferred. *O. horridus* and *R. spectabilis* are considered nitrophytic species (species that inhabit substrates that contain easily available nitrogen as a result of strong nitrification) while *V. ovalifolium*, *C. canadensis*, and *R. pedatus* are

Table 2.2: Relation between site index of a hemlock-spruce type and indicator plants in southeastern Alaska (Taylor 1929). Site index is based on both hemlock and spruce combined.

Species	Site index [height(m) @ 100yrs breast height age]							
	12.1	15.1	18.2	21.2	24.2	27.3	30.3	33.3
	% of species in total vegetation							
Salmonberry (<i>Rubus spectabilis</i>)			0.2	3.2	8.0	14.6	23.6	32.2
Devil's club (<i>Oplopanax horridus</i>)		0.4	3.0	6.5	10.5	16.0	23.0	32.0
Blueberry (<i>Vaccinium ovalifolium</i>)		32.0	28.6	25.4	22.0	18.8	15.4	
Bunchberry (<i>Cornus canadensis</i>)	24.5	20.6	16.5	1.4	8.3	4.2		
Trailing raspberry (<i>Rubus pedatus</i>)	20.8	15.6	11.5	8.0	5.2			

considered oxylophytic species (species that inhabit acid (approximately pH < 4.5) substrates with low nitrification) (Klinka *et al.* 1989). Hence, site index of western hemlock also seemed to be correlated indirectly with the nitrogen status of the soils. However, the number of spruce and hemlock on which site index is based is not known.

Eis (1962) sampled 139 plots on specific plant communities around Vancouver and Haney, B.C. The results (Table 2.3) indicated that site index for western hemlock varies according to plant community, although

statistical tests were not carried out.

Stephens *et al.* (1969, reported in Heilman 1976) found a correlation between site index and total nitrogen in the surface organic matter ($r = 0.83$) based on twenty-five samples in Alaska. In Oregon, several studies of western hemlock site relationships with site index have been carried out. Wooldridge (1961) investigated the relationship between site index and chosen physical and chemical properties. Relationships worth noting were total soil depth ($r = 0.80$), elevation (50-1500ft.) ($r = -0.70$), pH (1:1 soil-water ratio with pH meter) ($r = 0.55$), clay% ($r = -0.77$), cation exchange capacity (ammonium acetate method) ($r = -0.69$), and extractable potassium (ammonium acetate method) ($r = -0.76$). The association of low site indexes with high per cent clay was interpreted as being an effect of poor aeration. Although Wooldridge interpreted that the per acre available levels of sodium, potassium and phosphate were related positively to growth, one has to be careful since these may simply be a reflection of soil depth (which was correlated to site index with $r = 0.80$) from which they were calculated.

Table 2.3: Western hemlock site index in different plant communities at Vancouver and Haney B.C. (Eis 1962).

Plant community	No. of plots	site index ¹ (m@100 yrs)	SD (m)	SE (m)
<i>Vaccinium-Gaultheria</i>	9	17.5	3.5	1.2
<i>Gaultheria</i>	16	27.7	5.9	1.5
<i>Vaccinium-Lysichitum</i>	9	29.0	6.4	2.1
<i>Mahonia</i>	7	31.2	6.6	2.4
<i>Vaccinium-Moss</i>	26	32.2	6.5	1.6
<i>Ribes-Oplopanax</i>	9	33.7	7.1	2.4
Moss	26	36.7	5.3	1.1
<i>Blechnum</i>	24	36.7	7.1	1.5
<i>Polystichum</i>	24	39.3	5.3	1.2

¹ Site index was calculated from the average height of dominant and codominant tree using curves from Barnes (1949).

In 38 second growth and 18 old growth hemlock in the Washington Cascades, Heilman (1976) found no relationship between site index (height at reference age of 100 years breast height age) and the soil depth or depth of the humus layer, although it was noted that site index appears to be reduced when rooting depth is less than about 24 inches. Again elevation (0-2000ft) showed a negative correlation with site index ($r = -0.55$). Very little correlation with site index was found between forest floor total nitrogen(%) ($r = 0.03$), pounds of nitrogen per acre in the top 10 inches of the soil ($r = 0.03$) and pounds of nitrogen per acre in the rooting depth ($r = 0.09$). A better correlation was obtained with the carbon-nitrogen ratio in the A1 horizon ($r = -0.39$), with a reduction in site index when the ratio was above 15. The high available phosphorus (Bray method no. 1) of 84 ppm in the forest floor suggested that the variation in site index was not related to phosphorus. There was no evidence that pH or concentration of exchangeable potassium, calcium, or magnesium was related to site index.

In the Oregon Coast Range, Meurisse (1972, 1976) investigated the relationship between site index (height at 100 years breast height age) and selected soil properties from fourteen sites. Once again, elevation (90-200 feet) and effective soil depth showed a significant ($p < 0.05$) relationship with site index with $r = -0.91$ and $r = 0.71$ respectively. There was little relationship between pH, as measured in water and in 1M KCl, and site index, with all soils having a low pH value (3.9-5.0). Site index had significant but weak correlations ($r = 0.50$) with total nitrogen (kg/ha)¹, and the sum of extractable calcium, magnesium, and potassium (kg/ha) ($r =$

¹ Except for pH, all other chemical analysis in Meurisse (1972, 1975) was referred to the Oregon State University Soil Testing Laboratory (Roberts, S.R., R.V. Vodraska, M.D. Kauffman and E.H. Gardner. 1971. Methods of soil analysis used in the soil testing laboratory at Oregon State University. Corvallis, Oregon State University, Department of Soils. Agricultural Experiment Station Special Report 321).

0.30). Increasingly higher correlations with site index were found with cation exchange capacity (meq/100g) having an $r = -0.66$, organic matter(kg/ha) ($r = 0.67$), and available phosphorus (kg/ha) ($r=0.78$). Using multiple regression, the best fit equation was:

$$SI = 176.6 - 0.101(\text{elevation in m}) + 0.742(P \text{ in kg/ha}) - 0.026(Na \text{ in kg/ha}) + 0.008(K \text{ in kg/ha})$$

$$SEE = 9.5 \text{ ft}$$

$$R^2 = 0.93$$

Variables representing: P = available phosphorus; Na = extractable sodium; K = extractable potassium.

The model not including elevation was:

$$SI = 101.0 + 2.8(P \text{ in kg/ha}) - 0.038(\text{total N} \times 10^{-3} \text{ in kg/ha})^2 + 0.95 \times 10^{-6}(\text{Sum of bases in kg/ha})^2$$

$$SEE = 15.6 \text{ ft.}$$

$$R^2 = 0.78$$

Variables representing: P = available phosphorus; total N = total nitrogen; sum of bases = sum of extractable calcium, magnesium, and potassium.

However, caution must be used in interpreting these equations since multicollinearities exhibited by the factors were not thoroughly investigated and high bivariate correlations were reported.

Using physical field measurable or estimable properties, Els (1962) developed the following regression equation, among several others, for work in the field if site index can not be measured directly. The model, based on soil and moisture factors and including a variable for plant community, was:

$$SI = 100.2 + 2.102(\text{depth of soil}) + 4.197(\text{soil moisture}) - 4.633(\text{soil permeability}) - 2.494(\text{thickness of organic horizons}) + 4.668(\text{plant community})$$

$$R^2 = 0.63$$

Variables such as depth of soil were expressed in actual measurement and variables such as soil permeability and plant community were coded.

Steinbrenner (1976) developed a regression equation for western hemlock site index for predictive and comparative studies, based on a total of 103 sample plots. The area was stratified into glaciated and non-glaciated soils and the following two equations were reported:

Non-glaciated soils:

$$SI = 99.5 + 2.29(\text{depth of "A"}) - 0.028(\text{depth of "A"})^2 - 8.48 (\text{Log} [\text{depth of "A"}]) + 340/(\text{silt+clay in "A"}) - 0.035(\text{Elevation})$$

$$R^2=0.82$$

$$SE=5.4 \text{ feet}$$

Glaciated soils:

$$SI = -184.9 + 2.75^*(\text{total depth}) + 11314/(\text{total depth}) - 12296/(\text{total depth})^2 + 39.2/(\text{clay in "A"}) + 5.77^*(\text{elevation})^2 + 151.6/(\text{elevation})^2 - 0.025^*(\text{elevation X precipitation}) - 1526513/(\text{elevation X precipitation})^3 - 5.6\text{Log}(\text{elevation X slope position})$$

$$R^2 = 0.77$$

$$SE = 5.8 \text{ feet}$$

Although these equations are unwieldy with virtually no capacity for interpretation, they were intended for prediction only in this restricted area.

2.6 Western Hemlock Nutrition

The nutritional requirements of western hemlock are low with the best growth occurring where there is a well balanced supply of nutrients in small quantities (Krajina 1969). It has been found that western hemlock survives any deficiency treatment better than other conifers growing in British Columbia (with the exception of mountain hemlock which reacts similarly), and will grow even in such nutrient-poor soils where nutrients are available in the smallest possible quantities (Krajina *et al.* 1982). However, a complicated system of feedback, symbiosis and specialization seems to be involved with western hemlock nutrition.

Western hemlock seedlings seem to have a preference for ammonium sources of nitrogen as compared to nitrate (Taylor 1935; Swan 1960; Van den Driessche 1971; Krajina *et al.* 1973), although there is a significant interaction between nitrogen source and pH (Van den Driessche 1976). Turner and Franz (1985) suggested that the absence of nitrification is one of the characteristics of the hemlock nutrient cycling regime. This was believed to involve the inhibition of nitrifying bacteria caused by the low pH of the soil and forest floor, higher phenolic contents of the foliage and consequently the litter, and the higher forest floor fungal biomass which would exude organic acids.

In a trial using a hydroponic solution, western hemlock seedlings were distinctly more tolerant than Douglas-fir or western redcedar to pH 3.0 (Ryan *et al.* 1986). Rygielwicz *et al.* (1984) reported that the ratio of H^+ ions extruded to ammonium ions taken up is higher than Douglas-fir, although mycorrhizae appear to act as a rhizosphere buffer where mycorrhizal plants take up ammonium at faster rates than nonmycorrhizal plants, but do not release H^+ at a faster rate. This pH relationship suggests that hemlock may have exploited a niche on acid soils, the higher acidity possibly reducing competition for available nutrients from bacteria, other fungi and other plant roots (Rygielwicz *et al.* 1984).

This may be a reason why western hemlock is so closely associated with rotting wood. Regeneration of western hemlock has been reported to occur frequently on stumps and prostrate logs (Fowells 1965; Minore 1972), with nurse-logs and stilt-rooted trees being conspicuous in the hemlock forests of the Pacific Northwest (Franklin and Dyrness 1973; Christy and Mack 1984) (Figure 2.1). Christy and Mack (1984) and Harmon and Franklin (1989) concluded that the role of decaying logs is to provide



Figure 2.1. Western hemlock growing on the side of a blown-over Sitka spruce, exhibiting the stilt-root characteristic. The location is the Carmanah Valley on Vancouver Island, British Columbia. (Photo by A. Inselberg)

elevated safe sites in a forest understory where seedling establishment on the forest floor is thwarted by litter burial and competition with herbs and mosses. Organic matter also seems to stimulate root branching, resulting in dense mats of fine roots near the soil surface. Eis (1974, 1987) found that the greatest concentration of fine roots was in the organic horizon and the top 10 cm of mineral soil, and roots also tended to follow decaying roots of the previous forest or buried rotten wood.

Although rotting wood is nutritionally a substantially poorer substrate when compared to mineral soil (Harmon *et al.* 1986), there is evidence that wood with a high moisture content and in an advanced stage of decay is a potential environment for nitrogen fixation by bacterial symbiotes (Larsen *et al.* 1978; Spano *et al.* 1982; Jurgensen *et al.* 1984, 1987; Harvey *et al.* 1989). Larsen *et al.* (1978) suggested a strong nutritional relationship between mycorrhizae and nitrogen fixation. Only a small amount fixed seems likely (a few kilograms per hectare per year), although this amount represents a net input to the ecosystem. However, the accuracy for measuring such low-level nitrogen fixation, as expressed by the technique of acetylene reduction to ethylene, has been questioned (Silvester *et al.* 1982; Harmon *et al.* 1986).

Ectomycorrhizal association is a widespread phenomenon, infection being a normal and regular event in nature (Richards 1987). The benefits to the plant are through enhanced water, nutrient (particularly phosphorus) uptake, the production of enzymes, and possibly with pathogen resistance (Marks and Kozlowski 1973; Laursen 1985). It has been observed that phosphorus and nitrogen levels are enhanced in mycorrhizal plants, and since mor humus forms have large reserves of organic phosphorus and nitrogen, mycorrhizal infection could be of importance if it provides access

to these reserves (Read 1983).

Specifically for western hemlock, fifty fungi have been demonstrated to form ectomycorrhizae in pure culture synthesis (Molina 1980; Kropp 1982a; Kropp and Trappe 1982; Molina and Trappe 1982). An additional 102 were considered to be probable mycorrhizal formers based on field observation (Molina 1980b; Kropp 1982b, 1982c; Kropp and Trappe 1982). This probably does not represent the total potential mycorrhizal fungi associated with western hemlock as most were found as the opportunity for field work arose (Kropp and Trappe 1982).

Most of the mycorrhizal fungi were non-host-specific, unlike those associated with earlier successional species such as alder or Douglas-fir, which seem to be host specific. Kropp and Trappe (1982) hypothesized that late successional species, such as western hemlock, enter and adapt to the mycorrhizal system already established with the overstory hosts. Hence, the selection pressure would be against hemlock specificity. However, rotten wood seemed the most likely substrate for evolution of hemlock-specific fungi, if they do exist, since this is a rather specialized microhabitat in which fungi might encounter relatively little competition from previously established mycorrhizal fungi. Harvey *et al.* (1986) reported a trend of reduced active ectomycorrhizal short root types in the deep mineral fraction and high numbers in the organic fractions, particularly humus and decayed wood. They suggested that the apparent ability of mycorrhizal fungi to detoxify soil phenolics may contribute to the ability of conifer roots to thrive in decayed wood on and in forest soils.

Krajina (1969) suggested that western hemlock is also adapted to nitrogen supply in the form of amino acids. This may be mycorrhiza mediated since some mycorrhizal fungi have been reported capable of

utilizing simple organic nitrogen in laboratory culture trials (Lundberg 1970). Stribley and Read (1980) have demonstrated, in sand culture, that young mycorrhizal plants of *Vaccinium macrocarpon*, an oxylophytic species characteristic of mor-humus soils of low nitrogen availability, could utilize amino acids as a nitrogen source. This capacity was a specific feature of mycorrhizal infection. Evidence also confirms this uptake mechanism for the simplest of the organic phosphorus sources (Mitchell and Read 1981). However, the significance of these for total nitrogen and phosphorus uptake under field conditions is yet unknown (Raisin *et al.* 1987), and not investigated specifically for western hemlock.

Western hemlock has been noted to exert an influence on soil development, especially as it pertains to podzolization. Crampton (1982, 1984) reported differences in the thickness of the Ae horizon in various locations under the canopy of individual western hemlock trees. Lowe and Klinka (1981) found that productive growth of western hemlock was associated with chemical indicators of podzol development and of low biological activity. However, they cautioned that the correlation did not establish either a cause or an effect. On three study sites, Alban (1969), compared soil properties between western hemlock and western redcedar growing on the same site, and reported larger values of pH, calcium and cation exchange capacity under western redcedar. Turner and Franz (1985) found there were significantly lower ($p < 0.05$) total microbial counts, number of ammonium oxidizing bacteria, and significantly higher fungal spore counts in the litter and A1 horizon associated with western hemlock compared to western redcedar.

The most common criterion for defining nutritional status is growth response to fertilization (Binkley 1986). For western hemlock, the response

(generally basal area or radial increment increase) to nitrogen fertilization with urea has been inconsistent, typically with wide ranges of responses and frequent negative responses being recorded (Webster *et al.* 1976; Olsen *et al.* 1979). Growth responses range from increases of 50 per cent or more to apparent reductions of about 20 percent. Webster *et al.* (1976) concluded that Inland Washington responses are generally more positive than Coastal Washington, although the range of responses is still large. However, Olsen *et al.* (1979) noted that strong geographical trends were not apparent. Again there are conflicting reports on the effect of stand condition on the response to nitrogen fertilization. Webster *et al.* (1976) stated that generally, spaced stands respond positively to fertilization while Olsen *et al.* (1979) noted comparable responses between unspaced and spaced stands. In a greenhouse study, Radwan and DeBell (1980b) suggested that the source of nitrogen in the fertilizer does not appear to be responsible for the reported variability in response of natural stands. Radwan and DeBell (1989) found significant basal area and volume growth with the use of sulphur-coated urea, but attributed the effect to the slow release of nitrogen from the fertilizer. Greenhouse fertilization studies (Heilman and Ekuan 1973; Anderson *et al.* 1982) and plantation fertilization trials (Gill and Lavender 1983b; Radwan and Shumway 1983) suggest that low supplies of other important nutrient elements, such as phosphorus, may be important in explaining the lack of success with nitrogen fertilization of western hemlock. However, no clear trend has emerged in the relationship between response to fertilizers and soils, site class, or site index. Gill and Lavender (1983a) found that urea fertilization of hemlock stands initially increased mortality of mycorrhizae and then changed relative populations of mycorrhizal types. They concluded that significant changes in total mycorrhizae and in relative

populations of mycorrhizal types after fertilization could substantially affect the nutrient status and growth of western hemlock.

2.7 Literature Review Summary

Site index is the most widely accepted measure of productivity, and is more related to the capacity of a given site to produce wood than any other single measure, besides volume itself. Studies relating site index to individual physical and chemical properties factorially has demonstrated the problem of multicollinearity. However, the BEC system provides a framework within which interacting site factors are integrated heuristically into site units, or integrated through plants acting as "phytometers".

Soil-site studies with western hemlock, have demonstrated some success, but there are no consistent nutrient variables between studies. Research into western hemlock nutrition indicate that western hemlock productivity will likely be positively correlated with ammonium production. Productivity should not show a relationship, or may even show a negative relationship, to areas with high nitrification. Western hemlock relationships with decaying wood, mycorrhizae, amino acid uptake, and nonsymbiotic nitrogen fixers are yet to be clearly understood. All of this adds to the inconsistent results of fertilization studies and the elusive nature of western hemlock nutrition.

3. METHODS

3.1 Study Area

The study sites were located in three areas of southwestern British Columbia in the Vancouver Forest Region. Two areas were on Vancouver Island, the first near the municipalities of Gold River, Tahsis and Zeballos, the second near the municipality of Port MacNeil, and the third area was located in the Seymour Valley, near Vancouver (49° North latitude and 123°-126° West longitude).

Most plots were within the Submontane Very Wet Maritime Coastal Western Hemlock (CWHvm1) variant but some plots were in the Outer Very Wet Hypermaritime (CWHvh1) and Western Very Dry Maritime (CWHxm2) variants (Klinka *et al* 1984; Klinka *et al* 1991). The use of mainly one variant, with extreme azonal sites only being sampled from adjacent variants, concentrated analysis on the within-variant effects.

The climate is marine, with a relative lack of sunshine, cool summers and mild winters, with heavy precipitation concentrated in the winter. Mean annual precipitation ranges from 1500 to 4400 mm with less than 15% as snowfall (Valentine *et al.* 1981; Pojar and Klinka 1983). The CWH zone has been characterized by Krajina (1969) as part of the Pacific Coastal Mesothermal Forest region, within the Mesothermal formation. Using Köppen's classification of climates (Trewartha and Horn 1980) this would be classified as *Cfb*, mild temperate rainy climates, with mild winters, no distinct dry season, and cool summers.

The area is located within the Vancouver Island Ranges and Estevan Coastal Plain of the Vancouver Island Mountains and the Nahwitti Lowland

in the Western System of the physiographic subdivision, the Canadian Cordilleran Region (Holland 1976). This area is characterized mainly by volcanic rock with numerous granitic batholiths, and some sedimentary rock. Surficial materials that form the parent material of the soils in this area were formed during and since the time British Columbia was covered by the Cordilleran Glacier Complex which disappeared at the end of the Pleistocene some 10,000 years ago (Armstrong *et al.* 1965; Fulton 1971). The most extensive of the surficial material encountered in this study was Pleistocene till. This till is a non-sorted and non-stratified sediment which contains a heterogeneous mixture of particle sizes which includes large boulders. Fluvioglacial materials, deposited by glacial meltwater, fluvial materials transported and deposited by rivers, and colluvial materials, products of mass wasting, were other surficial materials encountered.

The main features distinguishing the soils of the coastal area are the prevalence of deep reddish to yellowish brown B horizons enriched with sesquioxides and organic matter, the absence of a continuous Ae horizon, and thick mor forest floors (Lewis 1976; Valentine *et al.* 1981). Root channels (Martin and Lowe 1989) were common in the Bf horizons. The soils in the study plots were mainly Ferro-Humic Podzols, and Humo-Ferrie Podzols, with some Dystric Brunisols and Humic Folisols (Agriculture Canada Expert Committee on Soil Survey 1987). The forest floors of the study plots were classified mainly as Hemihumimors and Humimors, with some Mormoders, Leptomoders and Mullmoders (Klinka *et al.* 1981). The majority of forest floors were thick (up to 60 cm) and included woody material in various stages of decomposition.

3.2 Study Sites

Sites were selected to represent a wide range of environments supporting the growth of western hemlock. The majority of the ecosystems selected for study supported naturally established, even-aged, immature (the range of ages of the stands was approximately 30-100 years old), uniformly stocked, western hemlock stands. Fourteen plots were located on extremely low productive sites in non-forested ecosystems to establish very low productivity sites for comparison. Twenty plots from a fertilizer trial data set were located in stands that had been juvenile-spaced. All trees were free of damaging agents, and the plots represented the nearly complete inferred soil moisture and soil nutrient gradients for the growth of western hemlock within the CWHvm1 variant. The sites sampled outside this variant were sites needed for poorly represented soil moisture and nutrient gradients. These sites were azonal, thus are mainly controlled by local conditions (Mueller-Dombois and Ellenberg 1974). Consequently, the plots will be combined and used as if sampled from the CWHvm1 variant. Not found, and therefore not included, in this study were rich sites which were slightly dry through extremely dry and very rich, fresh to moist sites.

Within each ecosystem, a representative sample plot of size 0.04 ha. was used based on the recommendations for relevé sizes by Mueller-Dombois and Ellenberg (1974) for temperate forests. Plots were located subjectively without preconceived bias (Mueller-Dombois and Ellenberg 1974) for typification and pattern analysis of a segment of the landscape judged to be relatively uniform in climate, soil, and plants (Knapp 1984; Orlóci 1988; Kenkel *et al* 1989). For the non-forested extreme ecosystems, selected open-grown hemlock were chosen for study with sampling and

description based on a subjective assessment of an area thought to be occupied by the root system.

3.3 Sampling and Site Description

Description of vegetation followed the methods outlined in Pojar *et al.* (1987). Vegetation description included identification of all vascular plants, bryophytes, and lichens and estimates of cover for each species using the Domin-Krajina cover abundance scale (Krajina 1933 cited in Mueller-Dombois and Ellenberg 1974) modified for local conditions. The use of significance class values allows both quantitative (density) and qualitative (presence-absence) information to be expressed without either dominating the other (Gauch 1986) (i.e., not complete equality of presence as in the former measure nor complete equality of species as in the latter measure). Species growing as epiphytes and on decaying coarse woody debris or coarse fragments and rock were not included in the analysis.

Complete site description (elevation, aspect, slope position, shape, gradient, etc.), followed the procedure of Walmsley *et al.* (1980) [revised by Luttmerding *et al.* 1990]. Relative soil moisture regimes (SMRs) and soil nutrient regimes (SNRs) of each plot were identified according to keys which consider selected topographic and soil morphological attributes (Klinka *et al.* 1984; Banner *et al.* 1990). The relative SMRs were adjusted to actual SMRs using the respective biogeoclimatic subzone to circumscribe the relative SMR according to Banner *et al.* (1990).

Site index was used as an indicator of productivity and tree selection was based on top height (100 largest trees per hectare). Thus it was determined from the heights of the four largest trees per 0.04 hectare plot using the height growth curves of Wiley (1978). It is recognized that the

Wiley curves were derived based on a sample consisting of the 10 trees of largest dbh from a group of 50 adjacent individual hemlocks, and that the best estimate of site index would thus be obtained by following the procedure used in developing the curves. However, it was the opinion of Mitchell and Polsson (1987) that the difference in basing site index on top height instead is small.

The actual heights and ages measured on several sites in this study were beyond the limit used in developing the Wiley curves, making extrapolation beyond the intended range necessary. However, as figure 3.1 indicates, the general form of the Wiley curves is maintained for the lower site index values; therefore, such extrapolation was judged as acceptable. On the non-forested sites, where four individual trees were chosen as a basis for site index, the trees in many cases were very short. For trees of such short height, age was taken at 0.3 meters above point of germination and adjusted linearly for a breast height age to be used in the Wiley equation. Although this was using the equation well beyond the range of the data from which it was derived, the margin of error in estimating site index was very small because the height growth was so slow. For all other forested sites, age was taken at breast height of 1.3 meters above the point of germination.

The soil description in the survey phase was qualitative, and included thickness of forest floor, humus form, soil particle size, coarse fragment content, root distribution, and both potential and an estimate of actual rooting depth. A soil pit was excavated approximately 1 m² in plane area and, where possible, to the depth of the control section of each site. Soils were identified using the Canadian System of Soil Classification (Agriculture Canada Expert Committee on Soil Survey 1987) and humus forms were

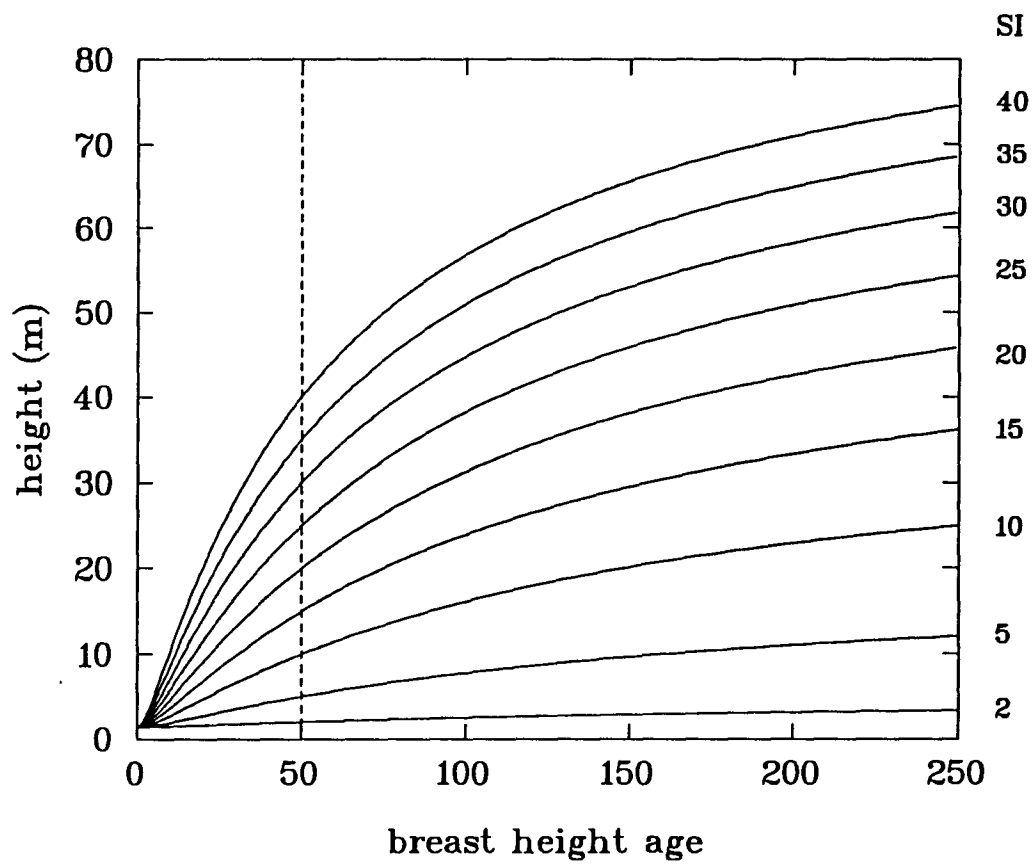


Figure 3.1. Western hemlock height growth curves of Wiley (1978) showing extrapolated curves (SI 2,5,10 and 15) beyond the range used in developing the curve.

identified according to Klinka *et al.* (1981).

To assess the available nutrient status of the soil, chemical analyses of both the forest floor and mineral soil were carried out. Forest floor and mineral soil (visually estimated to rooting depth) physical and chemical properties were examined and sampled separately at four sampling points selected at random. The methods prescribed by Ballard and Carter (1986) and used by Klinka *et al.* (1989), Carter and Klinka (1990), and Klinka and Carter (1990) for the sampling, and the physical and chemical analysis of forest floor and mineral soil were used in this study. Composite samples of forest floor and composite bulk samples of the mineral soils were taken at each point. The bulk density of both forest floor and mineral soil was measured near the point from which each soil sample was collected by cutting out a core, measuring its volume (by measuring the volume of glass beads required to fill the resulting hole lined with a thin plastic sheet), and measuring its mass after oven-drying at 105° C to constant weight.

There were 102 total plots available for this study. Sixty-one comprised the original data set, and an additional 41 plots were added for possible use as a test data set. For the original data set, samples were taken from 3 sides of an approximate 1 m X 1 m soil pit from a depth based on a subjective weighted ocular estimate of rooting depth. For the test data set, soil samples were taken from three points of an equilateral triangle (2 m on a side), and from a depth of 0-30cm.

Although most studies of nutrient availability examine only the upper mineral soil (Binkley and Hart 1989), the decision to sample to rooting depth was based on some conflicting results of nitrogen mineralization with depth and extractable phosphorus with depth. For the former, typically mineralization in forests generally decreases with depth, although major

exceptions occur (Binkley and Hart 1989). Binkley (1983) found that in a Douglas-fir plantation, the nitrogen mineralized during anaerobic incubations actually increased with depth. The same is noted for sampling phosphorus where Ballard (1980) noted that in published reports the surface layer of soil is generally better correlated to yield or foliar phosphorus. Contrary to this, Webber (1974) found that sampling from the upper or the entire profile did not effect results appreciably.

Because of these conflicting results, it was decided to allow the fine root location determine where nutrients were being taken up, thus determining the sampling depth. Fine roots (i.e., those below 1-2 mm diameter) are the main agents in ion uptake together with mycorrhizae (Bowen 1984). Roots in higher plants have been noted to be opportunistic in discovering and growing towards locally rich patches of water or nutrients (Cook 1983; Santantonio 1985). Experiments in solution culture have demonstrated a localized stimulation of root growth to local concentrations of nutrients with barley (Drew *et al.* 1973; Drew 1975; Drew and Saker 1975, 1978) and with Sitka spruce seedlings (Coutts and Philipson 1976; Philipson and Coutts 1977). Field experiments also concur with this localized stimulation of root growth, termed "tropism for nutrients" by St. John (1983). Powers (1984) noted that the distribution of fine roots seem to parallel the mineralizable nitrogen profile, Kimmins and Hawkes (1978) concluded that the distribution of fine roots is strongly correlated with vertical variations in soil fertility and organic matter, and Coopersmith (1986), using in-growth bags, found that nutrient rich growth materials stimulated fine root production. For western hemlock specifically, studies of root excavations (Eis 1974, 1987) have shown that organic material seems to stimulate root branching, and explains why the greatest concentration of

fine roots in western hemlock is associated with organic matter. Therefore, the portion of the soil profile that was to be sampled was subjectively chosen in proportion to the amount of fine roots visually estimated in the soil profile.

Horizontal variability in morphological characteristics was recognized and noted, especially in western hemlock sites. Also recognized was the accompanying variability in forest floor and mineral soil chemical properties (Quesnel and Lavkulich 1980; Courtin *et al.* 1983). However, Carter and Lowe (1986) reported that analyses of composite forest floor samples were highly correlated with the mean values for individual samples. They concluded that for most purposes, composite samples appeared to provide an adequate estimate of the mean value of samples analyzed individually. Thus, composite sampling of both forest floor and mineral soil was carried out in this study. Temporal variability was minimized by confining sampling to late spring and summer, although for total nutrients variability was expected to be small because the annual fluctuations in total nutrients are very small relative to the total pool (Binkley and Hart 1983). Successional temporal differences of an ecosystem's nutrient retention properties (Vitousek and Reiners 1975) were minimized by confining the ages to mainly mid-successional stages. It was recognized that the anaerobic technique is also temperature-dependent, with field soil temperature having a strong bearing on the interpretation of the laboratory test (Powers 1980). However, by confining the study to one variant, soil temperature differences due to climate or elevation were minimized.

3.4 Soil Chemical Analysis

All soil samples were air-dried to a constant weight in the laboratory

and then subsamples for each plot were composited. For chemical analysis, forest floor samples were ground in a Wiley mill to pass through a 2-mm sieve, while mineral soil samples were passed through a 2-mm sieve to separate coarse fragments. Soil pH was measured with a pH meter using a 1:1 suspension in water for mineral soil and a 1:5 suspension for forest floor material. Total carbon was determined using a Leco Induction Furnace (Bremner and Tabatabai 1971). Total nitrogen was determined by semimicro-Kjeldahl digestion followed by colorimetric estimation of ammonium (NH_4) (Bremner and Mulvaney 1982) using a Technicon Autoanalyzer (Anonymous 1976). Mineralizable nitrogen was determined by an anaerobic incubation procedure modified from Waring and Bremner (1964). Released NH_4 was determined colorimetrically by use of a Technicon Autoanalyzer. Total phosphorus in the forest floor was measured by a digestion procedure (Bray and Kurtz 1945) followed by a colorimetric determination of the phosphorus in the digest. Mineral soil available phosphorus was measured by the extraction procedure of Mehlich (1978). Total sulphur analyses in the forest floor material were conducted using a Fisher Model 475 Sulphur Analyzer (Lowe and Guthrie 1981). Available $\text{SO}_4\text{-S}$ was determined by ammonium-acetate extraction (Bardsley and Lancaster 1960, 1965) whereupon the extracted sulphate was reduced to sulphide by HI (Johnson and Nishita 1952) and the sulphide thus liberated was determined by the bismuth sulfide colorimetric procedure (Kowalenko and Lowe 1972). Available potassium, magnesium, and calcium were determined by extraction with Morgan's solution of sodium acetate at pH 4.8 (Greweling and Peech 1960). The extracted cations were then measured by atomic absorption spectrophotometry. Pyrophosphate-extractable iron and aluminium in the B horizon were extracted overnight at 25°C using

sodium pyrophosphate solution as described by Bascombe (1968). Extracted iron and aluminium were then determined by atomic absorption spectroscopy (Lavkulich 1978). Soil laboratory analysis was carried out by Pacific Soil Analysis Incorporated which, based on past performance (R.E. Carter pers. comm.¹), had met the criteria for laboratory selection as outlined in Ballard and Carter (1986).

Anaerobic incubation for mineralizable nitrogen was chosen as suggested by Powers (1980), mineral soil available phosphorus was determined using the new Mehlich method as suggested by Curran (1984), and Morgan's solution for available cations was used as suggested by Klinka *et al.* (1980).

Soil nutrient variables were expressed as concentrations on a dry mass basis as opposed to the traditional use of mass per area basis. The latter calculation uses bulk density corrected for coarse fragment content and represents mass of nutrient per hectare in the forest floor and the mineral soil. Concentrations were used in this study because

- (i) in many cases the accuracy of field estimates of bulk density and soil depth in soils derived from tills was hindered due to the preponderance of coarse fragments and boulders. Mass per area calculations were attempted but the depth and bulk density introduced considerable extra "noise" into the data;
- (ii) with western hemlock where deep mor humus forms are common, an expression in kg/ha for total nitrogen, for example, will give undue emphasis to the storage of nutrients in the more slowly decomposing thick mor humus forms, versus the relatively high

¹ R.E. Carter, Resource Analysis/Evaluation Forester Timberlands and Forests, Fletcher Challenge Canada, Vancouver, B.C.

availability of rapidly decomposing, thus very thin, mull humus forms containing little nitrogen on a kg/ha basis;

- (iii) appreciating the view of Mehlich (1972) in proposing a uniform system for calculating and reporting soil analytical results for agricultural soils, the vastly differing humus depth mentioned previously and vastly differing soil depth, from organic matter over bedrock to deep alluvial soils, does not lend itself to the agricultural concept of a "cultivated plow layer" with a uniform 20 cm or 30 cm depth;
- (iv) one objective of this study is to compare the soil chemical measures to the field derived SNRs. The heuristic field procedure used mineral soil depth greater than 30 cm and coarse fragment content in deriving SNRs. Mass per area calculations also use both depth and coarse fragment content. Soil nutrient measures expressed as concentrations on a dry mass basis are completely independent of the heuristic field key to which they are being compared.

3.5 Vegetation Data Analysis

For investigating vegetation relationships, the data collected by the author (61 plots) in 1988 were combined with data collected in 1987 (21 plots) by Kabzems(1988). Study plots were classified into vegetation associations using the methods described by Pojar *et al.* (1987) and Klinka *et al.* (1989). This vegetation classification is based on the Zürich-Montpellier Tradition, using the tabular analysis method of Braun-Blanquet (Braun-Blanquet 1932; Becking 1957; Poore 1955; Shimwell 1971; Mueller-Dombois and Ellenberg 1974; Westhoff and van der Maarel 1980) modified

for use within the BEC system (Krajina 1969; Pojar *et al.* 1987). Since the Braun-Blanquet method is, in a sense, conceptually between the organism viewpoint of Clements (1916) and the individualistic viewpoint of Gleason (1926), what Mueller-Dombois and Ellenberg (1974) have termed the "systematic viewpoint", both classification into communities and the use of ordination techniques can be used.

The relevés were compiled and sorted into floristically similar groups and classified into a hierarchy of vegetation units using the computerized tabling program VTAB (Emanuel 1989). Cluster analysis, using Ward's error sum of squares method (Ward 1963) with the ordering procedure of Gruvaeus and Wainer (1972), and the reciprocal averaging technique (Hill 1973) using a strategy of progressive data set fragmentation (Peet 1980) was used to aid in identifying groups and hierarchies. To independently examine the strength of the derived hierarchy, and as an hypothesis supporting technique, species were analyzed with centred, non-standardized principal components analysis (PCA) ordination (Pearson 1901; Hotelling 1933; Nichols 1977; Dillon and Goldstein 1984; Pielou 1977, 1984). The coordinates of the first and second axes were graphed, elliptical outlines centred on the group means, oriented in the direction of maximum variation and drawn to encompass 80% of the plotted points of the respective groups, were overlain and then the entire pattern visually inspected. Elliptical outlines were used as polygons and constructed using a variation of confidence ellipse construction (Jolicoeur and Mosiman 1960; Owen and Chimielewski 1985) where bivariate normality was not assumed; therefore, without statistical inference (Crovello 1970). This technique gave objectivity to the method of using polygons of various sizes and shapes.

To see if the derived hierarchy represented some sort of gradient of

underlying environmental factors, spectral histograms of indicator species were constructed for each group in the derived hierarchy. Percent frequency was calculated for an indicator species group (ISG) for a site attribute k (e.g. soil nutrients), and is calculated according to (Klinka *et al.* 1989):

$$F_{(k)j} = \sum_{i=1}^n C_{(kj)i} / \left(\sum_{j=1}^m \sum_{i=1}^n C_{(kj)i} \right)$$

$F_{(k)j}$ = percent frequency for site attribute k and ISG j

C_{kji} = is the midpoint percent cover for indicator species i for ISG j for a site attribute k

i = indicator species

j = Indicator Species Group

k = site attribute

n = number of indicator species in ISG j

m = number of ISGs for attribute k

The derived spectra for each group were then compared to see the trends of underlying environmental factors.

In order to describe soil chemical relationships with the vegetation and vegetation units, canonical correlation analysis (CCA) (Gittins 1979, 1985; Dillon and Goldstein 1984; Tabachnick and Fidell 1989) was used for the former and canonical discriminant analysis (Gittins 1979, 1980; SAS 1985) for the latter. The objective of CCA is to find a linear combination of independent variables that maximally correlates with a linear combination of dependent variables. A check for multivariate normality was done by plotting the normalized Mahalanobilis distance D^2 to the power $1/3$ against their expected order statistics for a chi-squared distribution with v d.f., where v is the number of variables (Healy 1968; Campbell 1980; Seber 1984). It should be recognized that this analysis is for descriptive purposes

only, so no distributional assumptions are required (Dillon and Goldstein 1984); however, the analysis is enhanced (i.e., the description is capturing as close as possible the "true" relationship) if the assumptions are met (Tabachnick and Fidell 1989). No attempt was made to apply a multivariate transformation to normalize the data since the analysis is used primarily for descriptive purposes. If a transformation were to be made, it was felt that the parameters associated with the transformed data would not be as meaningful as those with the original data (Seber 1984). However, it is informative to plot the set scores of the CCA to demonstrate graphically how the sets differ from one another (Pielou 1977).

Before the relationship between the vegetation and soil chemical properties could be examined, the large number of species and chemical property variables had to be reduced. This was done by performing centred PCA on the vegetation covariance matrix and the forest floor chemical correlation matrix to express the overall vegetation composition of the sites and the overall nutrient status of the forest floor. Canonical R^2 and redundancy were inspected to determine the correlation between the vegetation and forest floor sets.

To describe the relationship between the vegetation units derived from the hierarchy and the soil chemical measures, canonical discriminant analysis was used. This procedure is a canonical analysis where the vegetation units are in the form of binary valued "dummy" variables. To reduce the number of soil chemical property variables, PCA was carried out on the correlation matrix. Soil chemical properties correlated with the most important canonical variates were noted through correlations with the respective PCA axes. Canonical variates of the important axes were plotted and elliptical outlines drawn to encompass 80% of the plots in the

respective vegetation units and visually inspected.

3.6 Soil Nutrient Regime/Soil Moisture Regime Analysis

SNRs and SMRs of the study plots were identified based on a heuristic evaluation of physical properties of the plot and augmented by the indicator plants using the method described by Pojar *et al.* (1987) and Klinka *et al.* (1989). Plots were then assigned to a site series using the method of Banner *et al.* (1990). Of the 61 plots originally collected, 6 plots consisting of humus forms over bedrock were eliminated since mineral soil chemical properties were non-existent. The remaining 55 plots formed one set to derive relationships. A second data set was available for model validation consisting of 21 plots collected by Kabzems (1988) and 20 plots from a fertilizer study collected in 1989. These test plots were similar in stand and site characteristics to the original plots, although collected from a different area.

In order to explore whether SNRs as derived from the field heuristic procedure prescribed by the BEC system were related to direct measures of soil nutrients, PCA was first used for exploratory purposes followed by canonical discriminant analysis and discriminant analysis as a confirmatory procedure. To view the structure of the original data set, PCA was carried out on the correlation matrix. The PCA scores of the important axes were plotted and elliptical outlines were drawn to encompass 80% of the plots, and then visually inspected. Loadings of the soil chemical measures with the PCA scores were inspected and the ones having the strongest correlation were chosen for further analysis.

Canonical discriminant analysis was then carried out on this reduced set and the canonical variates of the important axes plotted and elliptical

outlines drawn to encompass 80% of the plots in the respective SNRs and visually inspected. This display reveals the shape and extent of the scatter of each group, as well as the extent of the overlap or separation between the groups (Gittins 1985). The soil chemical measures correlated with the canonical variates were then chosen to be used in a discriminant analysis to see how well these specific soil chemical properties can be used to predict field derived SNRs. The data were checked for outliers by a visual examination of plotted PCA scores, the multivariate normality checked as described previously, and the equality of group dispersions checked using a multivariate generalization of Bartlett's test of homogeneity of K population variances (Tatsuoka 1988). Since discriminant analysis is a confirmatory procedure (Tukey 1980; Williams 1983), transformations to normality were made when needed. Additionally, if the data exhibit multivariate normality, but lacks homogeneity of within covariance matrices, then Smith's (1947) quadratic function was used as the optimum rule to predict group membership, otherwise Fisher's (1936) linear discriminant function was used. Since prior probabilities influence the forms of discriminant functions (Williams 1983), and the priors were not known, the discriminant analysis was run first assuming equal prior probabilities and then with priors assigned based on ancillary experience and knowledge. The validation set was used with the two discriminant functions to test the portability of the results.

The rationale behind the above procedure was that if the field derived SNRs are meaningful in terms of actual measured soil chemicals, PCA, as an exploratory technique, will indicate which chemical measures show the largest variation. Canonical discriminant analysis will describe the relationship of the most meaningful chemical measures with the SNRs.

Finally, discriminant analysis and the subsequent testing of the discriminant function on a validation data set will provide evidence, as a confirmatory procedure, that the field derived SNRs are related to the actual soil chemical measures chosen.

Since comprehensive information gathered from an extensive soil water measurement program was not available, the comparison of SMRs, derived by the heuristic method of Banner *et al.* (1990), was made against the results of a simulation model. The Energy-Soil Limited (ESL) water balance model (Spittlehouse 1981; Spittlehouse and Black 1981) was used to calculate the actual evapotranspiration and growing season water-deficit in order to estimate actual SMR of water-deficient (excessively dry through slightly dry) and fresh sites. The depth to the soil gleyed horizon or the water table was used to estimate the actual SMR of moist through wet sites.

The ESL water balance model is driven by solar radiation, temperature and precipitation and uses soil depth and texture data to calculate available water storage capacity. The coefficients used in the model were derived by Giles *et al.* (1985) for use in immature stands of coastal Douglas-fir in the Eastern Very Dry Maritime variant of the CWH zone. This model is energy-limited until approximately 60% of the available soil water has been utilized, when it becomes increasingly soil-water-limited. Actual evapotranspiration was calculated as monthly totals during the growing-season (April-September) and as a growing-season total.

The ESL model has several limitations as outlined in Carter and Klinka (1990). Further, calibration of the model has not been carried out in the biogeoclimatic variant used in this study for immature stands of western hemlock. However, the model results compared to field derived SMRs is useful as a preliminary estimate.

3.7 Analysis of Productivity Relationships

The investigation of site index relationships was divided into two groups, the first using vegetation measures and the second using environment measures. The relationship of site index with the vegetation measures was subdivided into two indirect measures: (1) categorical: vegetation units; and (2) analytical: PCA scores on vegetation, and frequency of indicator species groups. The environment measures were subdivided into an indirect measure and a direct measure, which were respectively: (1) categorical: SMR, SNR, SMR & SNR, and site series; and (2) analytical: soil nutrient measures.

The relationship of site index to the plant associations was examined using "dummy" variable regression, where the independent variables were plant associations and binary β_j coefficients equaled 1 if the site index belonged to plant association j , and 0 otherwise (Suits 1957; Chatterjee and Price 1977; Ott 1988). The 67 plots used in the diagnostic vegetation table derivation were used. The residuals were then investigated for normality by a visual inspection of a normal probability plot of the residuals (Chambers *et al.* 1983), and homogeneity of variances were visually examined by a plot of the residuals.

To investigate how the individual species were related to site index, regression analysis was carried out. To reduce the number of independent variables from 120 species, PCA scores, which are a linear combination of all species, were used instead of individual species. Only those axes whose eigenvalues were greater than one were used in a backward stepwise regression. The rationale behind this rule of thumb is that any component should account for more variance than any single variable (Dillon and

Goldstein 1984). The respective loadings of the resulting regression equation were analyzed to ascertain the individual species relationships. This type of analysis has been referred to as principal components regression. Although a statistically biased procedure (Jolliffe 1986; Chatterjee and Price 1977), it was appropriate for this type of exploratory and descriptive use.

To investigate the relationship between site index and the frequency of indicator species groups (ISGs) (Klinka *et al.* 1989), species having an indicator value for moisture or nitrogen were grouped into ISGs and the frequency values were used as independent variables in a regression analysis.

SNRs and SMRs of study plots were identified based on a heuristic evaluation of physical properties of the plot, augmented by the indicator plants using the method described by Pojar *et al.* (1987) and Klinka *et al.* (1989). Plots were then assigned to a site series using Banner *et al.* (1990). Site index was used as a dependent variable in "dummy" variable regression to examine its relationship to site units derived from soil moisture regimes (SMRs) and soil nutrient regimes (SNRs). SMRs and SNRs were used in combination and separately, with the magnitude of coefficients examined, to determine the amount of influence each had upon site index. The residuals were then investigated for normality by a visual inspection of a probability plot of the residuals (Chambers *et al.* 1984), and homogeneity of variances was visually examined by a plot of the residuals. For this analysis, all 102 plots were combined into one data set to fill in some noted gaps in the site units within the edatopic grid.

To investigate the relationship between site index and soil chemical measures, multiple regression was used on the primary data set of 55 plots

(the original 61 plots minus 6 plots of forest floor over bedrock which did not have mineral soil chemical properties). The remaining 41 plots were reserved as a validation test data set. Because of suspected multicollinearity, three tests were carried out as suggested by Neter *et al.* (1990): bivariate correlation coefficients were examined, variance inflation factors translated into tolerance indices were examined, and a PCA was performed followed by inspection of eigenvalues. An all combinations multiple regression approach was then carried out with equations having relatively high R^2 and relatively low SEE noted. A "best fit" equation was chosen from inspection of all combinations based on higher adjusted R^2 and lower SEE, and factors that made "ecological sense". A 5% level of significance was required in all model development. As an additional test of model performance, the resulting equation was used to classify the original data into classes. Predictions within 3 m of the recorded site index were considered correctly classified. Predictions between 3 m and 6 m of the recorded site index were considered one class off, and so on. The equation was validated in the same manner on the test data set.

Further, to supplement the all combinations multiple regression, PCA regression (Chatterjee and Price 1977; Jolliffe 1986; Morzuch and Ruark 1991) was used. Loadings of the actual soil chemical measures with significant PCA axes scores derived from a backward stepwise procedure were investigated to determine the soil chemical measures most highly correlated with site index.

Additionally, an all combinations regression was done to explore the relationship between site index and forest floor chemical measures only. This was performed since the roots of western hemlock have been noted to occur mainly in the forest floor. Finally, a regression was done to relate site

index to mineral soil pyrophosphate extractable iron and aluminium, and total carbon. Although these three chemical measures are not nutrients, their amount in the B horizon has been reported to reflect the degree of podzolization (Lowe and Klinka 1981).

For all multivariate statistical analysis and the all combinations regression technique, the SAS statistical package (SAS 1985) was used. SYSTAT (Wilkinson 1990) was used for univariate statistical testing and graphics.

4. RESULTS AND DISCUSSION

4.1 Vegetation Classification

Preliminary use of cluster analysis and reciprocal averaging ordination failed to produce obvious groupings of relevés. This indicated that the vegetation derived from these second growth, mostly closed canopy, forests were relatively homogeneous (besides the small number of outliers). Therefore, the vegetation demonstrated low between plot species diversity, termed low β diversity by Whittaker (1975) (Figure 4.1). Tabular analysis without the use of further ordination was then employed following the traditional Braun-Blanquet classification procedure based primarily on the user's judgment and experience (Shimwell 1971).

Four alliances and fourteen plant associations were distinguished and characterized in a diagnostic table (Table 4.1). A major portion of the relevés were concentrated in four major associations, the *Gaultheria*, *Gaultheria-Polystichum*, *Polystichum*, and *Rubus* plant associations having 14, 11, 30 and 10 relevés respectively. Only 1 to 3 relevés were located in each of the remaining plant associations.

To test the strength of this derived hierarchy, and as an hypothesis supporting technique, all species were analyzed with centred non-standardized PCA ordination. The first and second axes of PCA scores were graphed, elliptical outlines were overlain and then the entire pattern visually inspected (Figure 4.2). Points in associations having 1 or 2 plots only were plotted without elliptical outlines.

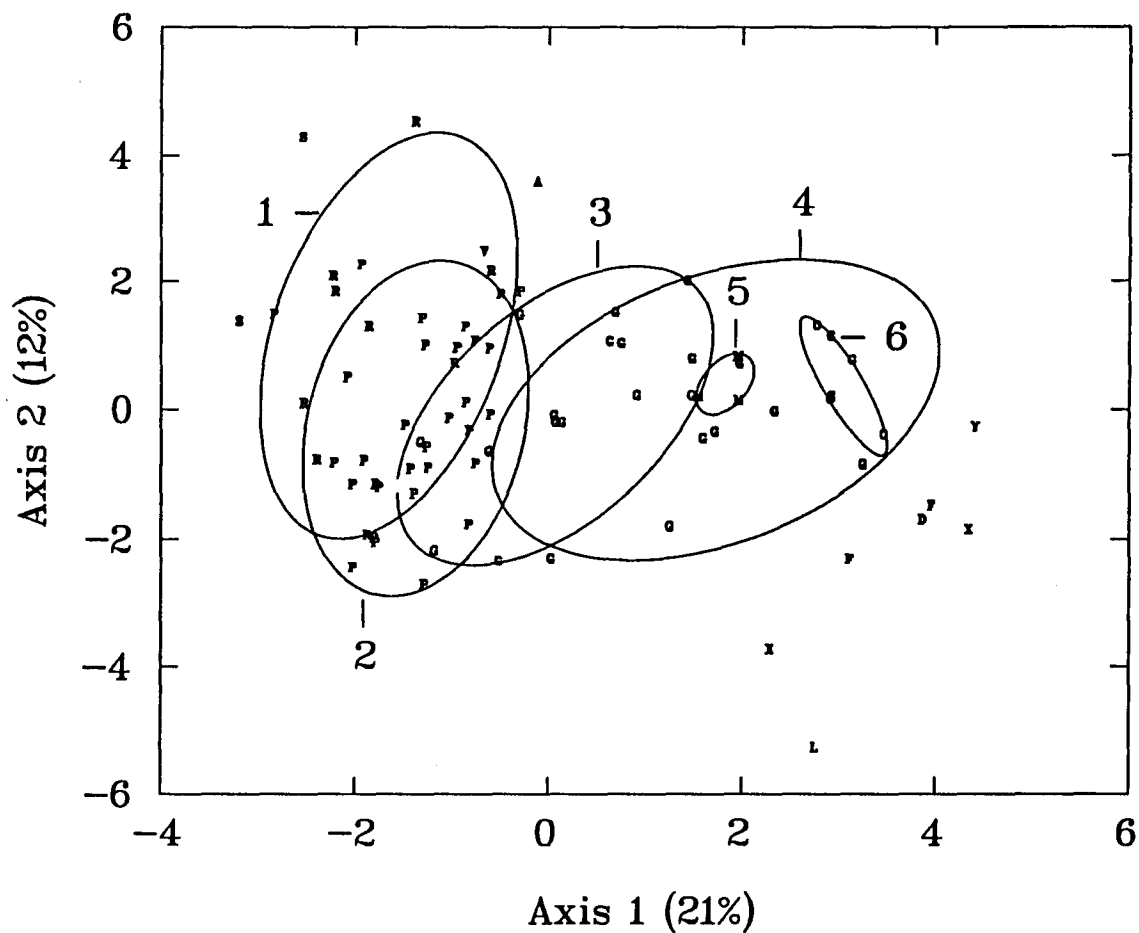
The first PCA axis explained 21% of the total variation and the second PCA axis a further 12%. The elliptical outlines showed an ordered



Figure 4.1. Immature western hemlock stand characterized by a closed canopy and lack of understory vegetation.

Table 4.1 (continued)

Vegetation unit		13	14
Number of plots	Diagnos	12	13
Vegetation units and species	value	1	1
Presence class and mean species significance			
TH-Gaultheria all.			
<i>Gaultheria shallon</i>	(dd)	5 3	5 3
TH-Mahonia sall., a.			
<i>Achlys triphylla</i>	(d)		
<i>Linnaea borealis</i>	(d)		
<i>Mahonia nervosa</i>	(d,c)		
<i>Pinus monticola</i>	(d,c)		
TH-Thuja sall.			
<i>Thuja plicata</i>	(d,cd)	5 6	5 4
TH-Racomitrium a.			
<i>Cladina</i> sp.	(d)		
<i>Dicranum</i> sp.	(d,c)		
<i>Pinus monticola</i>	(d,c)		
<i>Pleurozium schreberi</i>	(d,c)		5 6
<i>Racomitrium canescens</i>	(d,c)		
TH-Vaccinium(ovatum) a.			
<i>Vaccinium ovatum</i>	(dd)		
TH-Gaultheria a.			
TH-Gaultheria-Polystichum a.			
<i>Polystichum munitum</i>	(d,c)		
TH-Chamaecyparis a.			
<i>Chamaecyparis nootkatensis</i>	(d,c)		
<i>Tsuga mertensiana</i>	(d,c)	5 3	
<i>Vaccinium alaskaense</i>	(d,cd)	5 5	
TH-Malus a.			
<i>Alnus rubra</i>	(d,c)	5 1	
<i>Malus fusca</i>	(d,c)		5 +
<i>Taxus brevifolia</i>	(d)		
TH-Polystichum all.			
<i>Blechnum spicant</i>	(d,c)		
<i>Polystichum munitum</i>	(d,cd)		
TH-Polystichum sall., a.			
TH-Rubus all.			
<i>Rubus spectabilis</i>	(d,cd)		
<i>Tiarella trifoliata</i>	(d)		
TH-Achlys a.			
<i>Abies amabilis</i>	(d,c)		
<i>Achlys triphylla</i>	(d,cd)		
<i>Alnus rubra</i>	(d,c)	5 1	
<i>Aruncus dioicus</i>	(d,c)		
<i>Linnaea borealis</i>	(d,c)		
<i>Mahonia nervosa</i>	(d,c)		
<i>Trientalis latifolia</i>	(d,c)		
TH-Rubus a.			
TH-Sambucus a.			
<i>Hypnum circinale</i>	(d)		
<i>Rubus parviflorus</i>	(d)		
<i>Sambucus racemosa</i>	(d,cd)		
TH-Veratrum a.			
<i>Athyrium filix-femina</i>	(d,c)		
<i>Gymnocarpium dryopteris</i>	(d,c)		
<i>Ranunculus</i> sp.	(d,c)		
<i>Trautvetteria carolinensis</i>	(d,cd)		
<i>Veratrum viride</i>	(d,c)		
<i>Viola</i> sp.	(d,cd)		
TP-Sphagnum all., a.			
<i>Drosera rotundifolia</i>	(d,c)	5 +	
<i>Fauria crista-galli</i>	(d,cd)	5 5	
<i>Lysichiton americanum</i>	(d,cd)	5 6	
<i>Menziesia ferruginea</i>	(d,c)	5 4	
<i>Sphagnum girgensohnii</i>	(d,cd)	5 7	
<i>Sphagnum squarrosum</i>	(d,cd)	5 7	
TP-Ledum all., a.			
<i>Aulacomnium palustre</i>	(dd)	5 +	5 5
<i>Empetrum nigrum</i>	(d,cd)		5 8
<i>Ledum groenlandicum</i>	(d,cd)		5 8
<i>Pleurozium schreberi</i>	(d,cd)		5 6
<i>Vaccinium oxycoccos</i>	(d,cd)		5 5



Vegetation Associations:

R=Rubus; P=Polystichum; T=Gaultheria-Polystichum; G=Gaultheria;
 S=Sambucus; M=Mahonia; V=Vaccinium(ovatum); C=Chamaecyparis;
 X=Rhacomitrium; V=Veratrum; L=Ledum; D=Sphagnum; F=Malus;
 A=Achlys

Figure 4.2: Ordination of plots along the first two axes of PCA on all species showing 80% elliptical outlines for major plant associations *Rubus* (1), *Polystichum* (2), *Gaultheria-Polystichum* (3), *Gaultheria* (4), *Mahonia* (5), and *Vaccinium ovatum* (6).

transition of the four major associations along the first component from the *Rubus* association, grading into the *Polystichum*, *Polystichum-Gaultheria* associations, and into the *Gaultheria* association. Along the second axis, the *Rubus* association shows a separation from the *Polystichum* association. Only those species which had scores that correlated significantly ($p < 0.01$) and equalled or exceeded a "rule of thumb" correlation coefficient of 0.3 (i.e. approximately 10% of the variation accounted for) were taken into account and presented in Table 4.2. In total, 35 species met this criteria, with 10 correlated to the first PCA axis and 18 to the second PCA axis. Five species were correlated to both axes 1 and 2. *Gaultheria shallon* and *Polystichum munitum*, the two species defining the two major alliances, were noted to have the greatest positive and negative loadings on the first axis respectively. On this axis, generally, those species in the *Gaultheria* alliance had positive correlations, and those in the *Polystichum* alliance had negative correlations. On the second axis this trend is repeated, except for the addition of the group of species having a correlation of -0.35 which occur primarily in the *Ledum* plot. This was the lowest point on the vegetation PCA graph (Figure 4.2), located in the lower right quadrant. Of the 35 species correlated with the first 2 axes, 24 were included in a pre-edited diagnostic table and 15 were included in the final diagnostic table.

Although the first two PCA axes combined only account for 33% of the variation, this did provide for an independent and objective technique that supports the subjectively derived hierarchy. In general, the PCA of all vegetation supported the results of the vegetation table derived from traditional Blaun-Blanquet techniques. This is especially noteworthy considering the depauperate vegetation in second growth western hemlock stands.

Table 4.2: Correlation values ($r_{0.01} = 0.29$) of species and associated PCA scores on the first 2 PCA axis showing the respective nitrogen and moisture indicator values (Klinka *et al.* 1989).

Symbols mean: P=poor, M=medium, R=rich, FVM=fresh to very moist, VMW=very moist to wet, MDF=moderately dry to fresh, WWV=wet to very wet.

n=82 SPECIES	LOADINGS		NITROGEN INDICATOR VALUE	MOISTURE INDICATOR VALUE
	AXIS1	AXIS2		
<i>Gaultheria shallon</i>	0.86	-0.11	P	
<i>Tsuga heterophylla</i>	-0.64	0.25		
<i>Thuja plicata</i>	0.57	-0.11		
<i>Chamaecyparis nootkatensis</i>	0.44	-0.02		
<i>Blechnum spicant</i>	-0.40	0.28	P	FVM
<i>Plagiothecium undulatum</i>	-0.39	-0.18	P	FVM
<i>Menziesia ferruginea</i>	0.39	0.03	P	FVM
<i>Cornus canadensis</i>	0.38	-0.03	P	
<i>Tsuga mertensiana</i>	0.37	-0.12		
<i>Dryopteris expansa</i>	-0.31	0.07	M	FVM
<i>Hylocomium splendens</i>	0.69	0.34	P	
<i>Polystichum munitum</i>	-0.65	0.47	R	
<i>Pinus contorta</i>	0.42	-0.43		
<i>Rubus spectabilis</i>	-0.40	0.50	R	VMW
<i>Kindbergia oregana</i>	-0.31	0.57		MDF
<i>Pleurozium schreberi</i>	0.30	-0.45	P	
<i>Rhytidiadelphus loreus</i>	0.15	0.72	P	FVM
<i>Maianthemum dilatatum</i>	-0.21	0.42	R	VMW
<i>Vaccinium parvifolium</i>	0.26	0.38	P	
<i>Tiarella laciniata</i>	-0.09	0.37	R	FVM
<i>Rosa nutkana</i>	-0.11	0.37	R	FVM
<i>Rubus parviflorus</i>	-0.16	0.37	R	
<i>Tiarella trifoliata</i>	-0.13	0.36	R	FVM
<i>Aulacomium palustre</i>	0.16	-0.35	M	WWV
<i>Empetrum nigrum</i>	0.16	-0.35	P	
<i>Rhytidiadelphus triquetrus</i>	0.16	-0.35	M	
<i>Vaccinium oxycoccus</i>	0.16	-0.35	P	WWV
<i>Ledum groenlandicum</i>	0.16	-0.35		WWV
<i>Galium triflorum</i>	-0.16	0.33	R	FVM
<i>Vaccinium ovalifolium</i>	-0.05	0.33	P	FVM
<i>Polytrichum alpinum</i>	-0.15	0.32		
<i>Trautvetteria caroliniensis</i>	-0.13	0.32	R	FVM
<i>Rubus ursinus</i>	-0.07	0.32		
<i>Plagiochila asplenioides</i>	-0.08	0.30		
<i>Viola orbiculata</i>	-0.08	0.30	M	MDF

Of interest also was whether the axes represented some sort of gradient of underlying environmental factors as indicated either by the vegetation associations and/or by the individual plants. It was mentioned previously that there was a definite trend along the first PCA axis (Figure 4.2) with four major associations. Spectra showing the distribution and frequency of nitrogen ISGs for each of these four associations are given in Figure 4.3. Proceeding along the first PCA axis from the *Rubus* association to the *Gaultheria* association, the spectral histograms changed also. The frequency of indicators of nitrogen-rich soils (Table 4.3) decreased from the *Rubus* association to the *Gaultheria* association. The location of the associations with increasing scores along the first PCA axis showed that there was a concurrent decrease in the occurrence of nitrogen-rich indicator species. Comparing these frequencies to the proposed standard spectra for soil nutrient regimes for Coastal British Columbia (Klinka *et al.* 1989), the *Rubus* association was rich to very rich, the *Polystichum* association medium, the *Gaultheria-Polystichum* association poor and the *Gaultheria* association very poor. Therefore, the first PCA axis captured an inferred soil nutrient gradient, based on the frequencies of nitrogen-rich indicator species for the four major plant associations, from rich to very poor. The actual relationship between species and soil chemical measures are reported later.

Spectra of soil moisture regimes (Figure 4.4) showed a predominance of moderately dry to fresh and fresh to very moist ISGs. This suggested that an inferred soil moisture gradient, based on frequencies of moisture indicator species for the four major plant associations, did not exist.

The trend of the association between plants and an inferred nutrient gradient was also shown, but only in a general way, by looking at

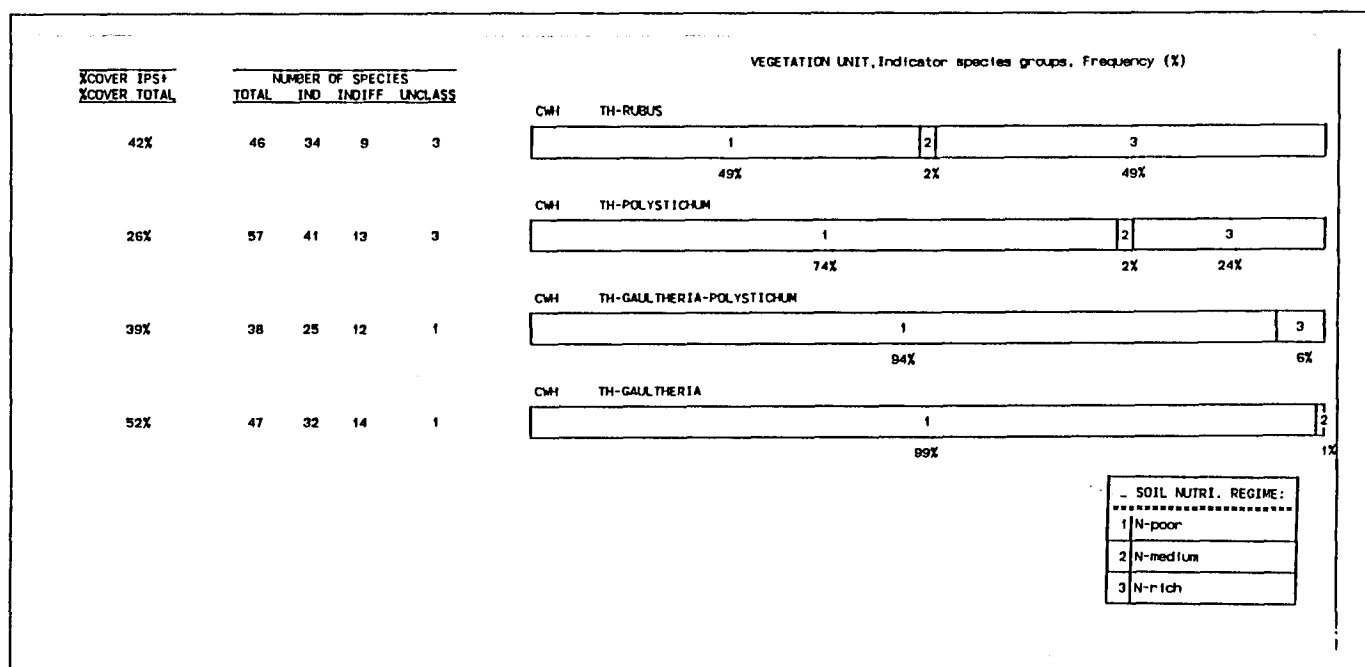


Figure 4.3. Spectra histograms, based on percentage of total cover of indicator species of soil nitrogen and expressed as % frequency, for four of the plant associations.

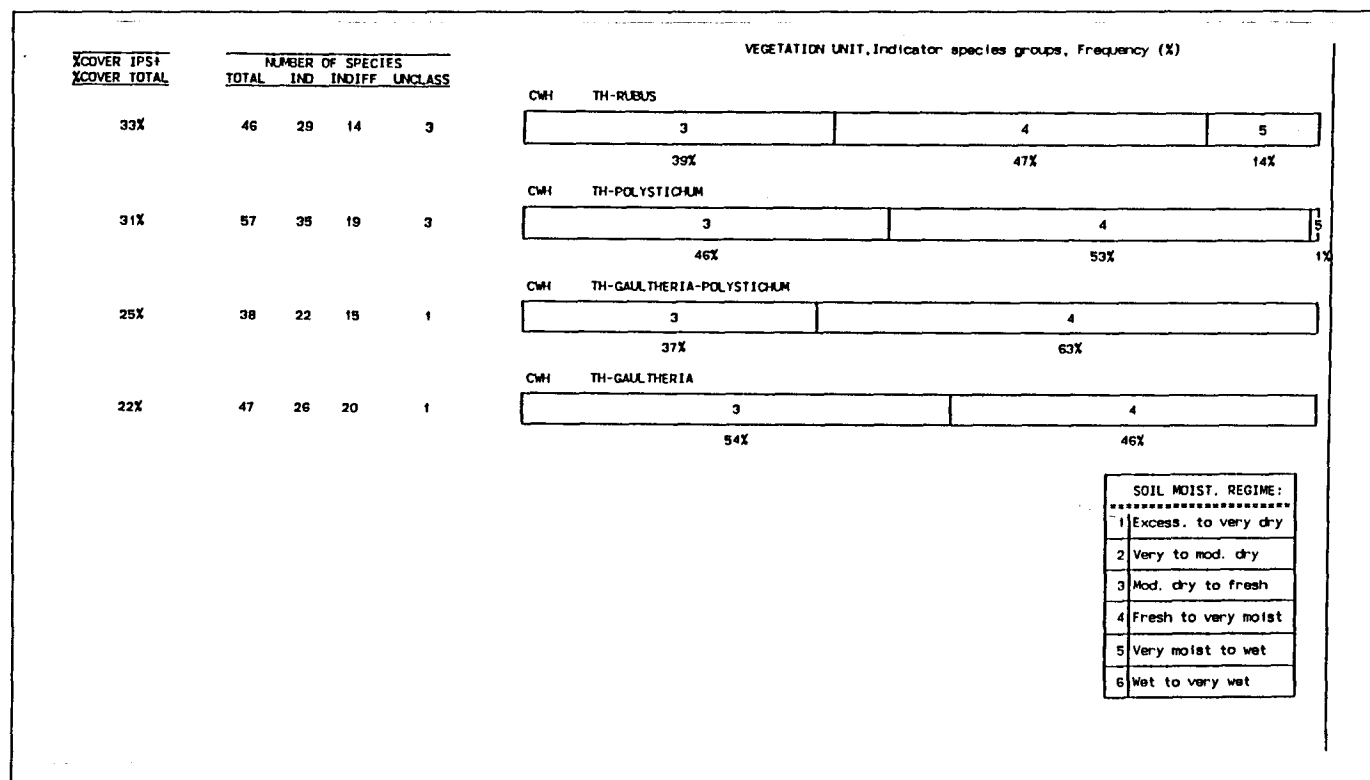


Figure 4.4. Spectra based on percentage of total cover of indicator species of soil moisture and expressed as % frequency. Spectra presented for four plant associations.

correlations of individual species with each of the PCA axis scores and the associated species diagnostic nutrient value (Klinka *et al.* 1989) (Table 4.2). Of the 16 species which were correlated with PCA axis 1, two were indicators of nitrogen rich soils, one of nitrogen medium soils and seven of nitrogen poor soils. Negatively correlated with PCA axis 1 were two nitrogen rich indicators, the one nitrogen medium indicator and two nitrogen poor indicators. Positively correlated with PCA axis 1 were five nitrogen poor indicators. The two nitrogen poor indicators negatively correlated with axis 1 confound the negative correlation of the two nitrogen rich indicators.

However, five of the seven nitrogen poor indicators had positive correlations with axis 1. Based on these species, PCA axis 1 conformed only in a general way with that of the vegetation associations, indicating that the first PCA axis scores increased along a species gradient of decreasing nitrogen indicator values. Similarly, trends in environmental elements as indicated by plant species were noted for PCA axis 2. Of the 25 species correlated with this axis, nine were nitrogen-rich indicators and were all positively correlated with PCA axis 2. Of the three nitrogen-medium indicators that were correlated, one was positive and two were negative. Of the seven poor-nitrogen indicators, five were positively correlated and two were negatively correlated. This trend was due to the concentration of the extreme non-forested plant communities in the bottom right quadrant (Table 4.3).

Using the soil moisture indicator value, the wet to very wet indicators were negatively correlated with the second axis. This too was attributed to four very poor, wet to very wet non-forested plant communities in the bottom right quadrant. Also in this quadrant were two non-forested ecosystems whose soils were classified as folisols over rock.

Table 4.3. Frequencies of nitrogen indicator species for the four major plant associations.

Plant Association	Frequency (%) of ISGs		
	N-rich	N-medium	N-poor
<i>Rubus</i>	49	2	49
<i>Polystichum</i>	24	2	74
<i>Gaultheria-Polystichum</i>	6		94
<i>Gaultheria</i>		1	99

In general, PCA axis 1 seemed to be negatively correlated with nitrogen-rich indicators and axis 2 seemed to be positively correlated with nitrogen-rich indicators. Both axes were not related to soil moisture indicators in a strong fashion.

Further to investigating the relationship between the plant associations and the measured soil chemicals, canonical discriminant analysis was used. Only the five major plant associations with enough plots were used for this analysis (*Gaultheria*, *Gaultheria-Polystichum*, *Polystichum*, *Rubus* and *Sambucus*). To reduce the number of chemical variables and to address the multicollinearities in the data, centred PCA of the soil chemical correlation matrix was used. Nine components were found to account for 94.6% of the total variance. These components were considered to adequately characterize the soil chemical domain and accordingly were used as one set of variables in the canonical analysis. The five plant associations in the form of a constant and four binary valued "dummy" variables composed the second set of variables. This gave a ratio of plots to variables of sixty-seven to twelve which was above the minimum ratio of five to one as suggested by Tabachnick and Fidell (1989).

The ecological objectives were to describe and account for the structure of the soil chemicals, expressed as PCA scores of linear combinations of soil chemical measures, and in doing so, investigate their

relationships to the plant associations. The results of the analysis are summarized in Table 4.4. All four canonical axes had squared canonical correlations of greater than 0.1, thus they explained greater than 10% of their respective proportion of the variance in the soil chemical domain.

To examine the relationships among the soil chemicals, plots of different combinations of canonical axes were examined. Only the first two showed a reasonable distinct visual separation on a scattergram. Figure 4.5 displays the samples in the space of canonical variates 1 and 2 of the soil chemical PCA scores domain with elliptical outlines, drawn to encompass 80% of the plotted points in the respective group, overlain.

There appeared to be no clear separation of the four vegetation units, with canonical axis 1 showing a gradation from the *Gaultheria*, through the

Table 4.4: Correlation of the soil chemical PCA scores with the canonical variate scores showing relationships between soil chemical PCA axes with five plant associations.

n=67 Canonical variate	Loadings U ₁	U ₂	U ₃	U ₄	h ² _w
<u>PCA axis of chemical variables</u>					
Axis1	0.867	-0.035	0.059	0.155	0.781
Axis2	-0.334	-0.254	0.627	0.142	0.589
Axis3	0.194	0.410	0.541	-0.276	0.575
Axis4	0.154	0.068	0.274	0.478	0.331
Axis5	-0.091	0.699	-0.204	0.340	0.655
Axis6	0.030	-0.385	-0.075	0.621	0.540
Axis7	0.059	-0.222	0.177	-0.129	0.101
Axis8	0.247	-0.215	-0.035	-0.346	0.228
Axis9	-0.019	0.168	0.396	0.120	0.200
Squared Canonical Correlation	0.533	0.264	0.146	0.101	

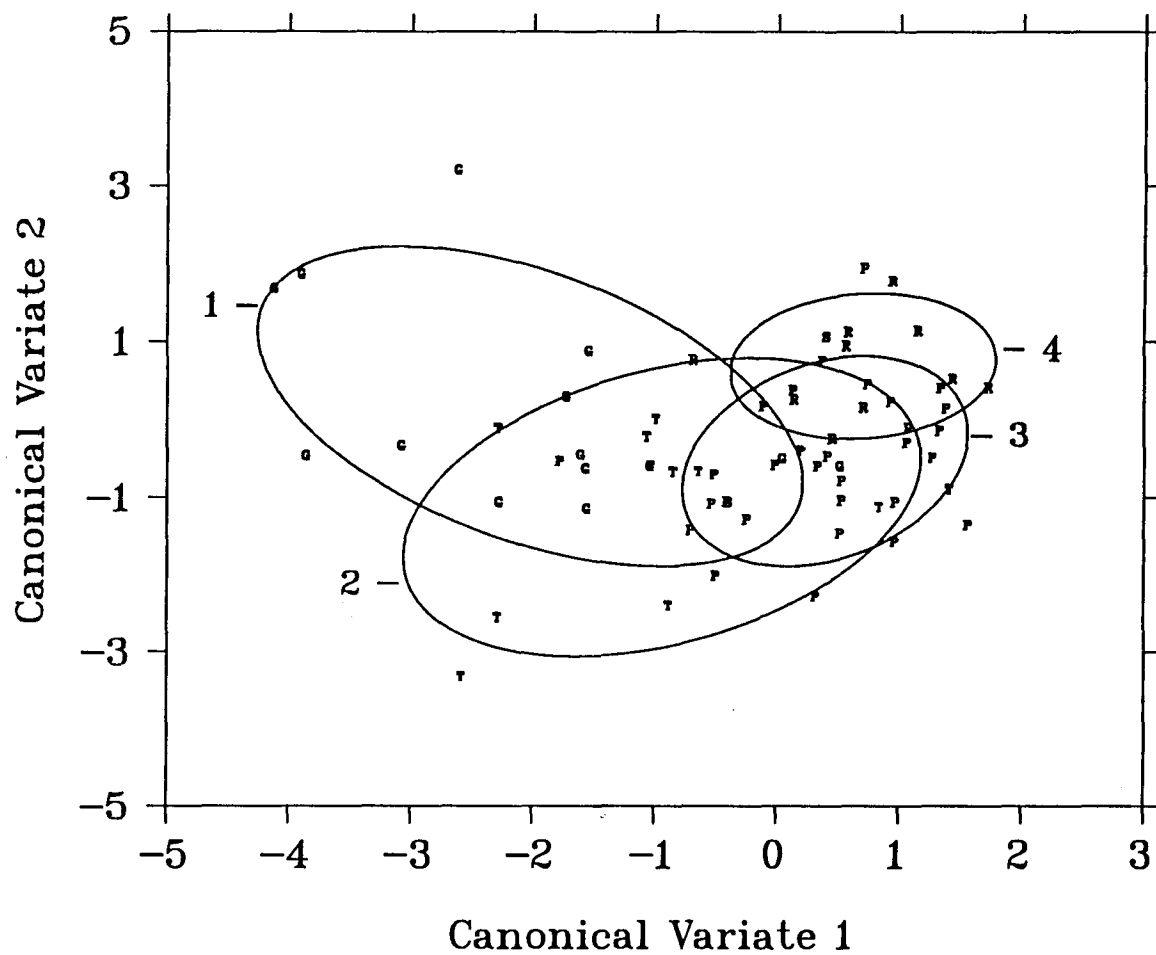


Figure 4.5. Canonical discriminant analysis plot of the first two canonical variates showing 80% elliptical outlines for plant associations *Gaultheria*(1), *Gaultheria-Polystichum*(2), *Polystichum*(3), and *Rubus*(4). Plot labels are G=*Gaultheria*, T=*Gaultheria-Polystichum*, P=*Polystichum*, R=*Rubus* and S=*Sambucus*.

Gaultheria-Polystichum, the *Polystichum* and to the *Rubus* plant association. The *Gaultheria* plant association was clearly separated from the *Rubus* plant association. Canonical axis 2 further separated the *Polystichum* from the *Rubus* plant association. The two plots of the *Sambucus* plant association did not separate from the *Rubus* plant association; therefore, they appeared to be chemically indistinguishable.

Correlations between the canonical axes and the soil chemical PCA scores (Table 4.4) indicated that there were strong positive correlations between canonical axis 1 with PCA axis 1, and canonical axis 2 with PCA axis 5. The first PCA axis was dominated by a high positive association with forest floor and mineral soil nitrogen (both total and mineralizable), and strong negative correlations with forest floor C:N ratio and available potassium (Table 4.5). PCA axis 5 showed a strong positive correlation with mineral soil carbon-nitrogen ratio and moderate positive correlations with forest floor pH and available potassium (Table 4.5). Hence, the underlying nutrient gradient from the plant associations *Gaultheria*, *Gaultheria-Polystichum* to *Polystichum* and *Rubus* appeared to be associated positively with nitrogen and negatively with forest floor C:N ratio and potassium. The gradation along canonical axis 2 appeared U-shaped, with both *Gaultheria* and *Rubus* associations correlated positively with forest floor available potassium, and mineral soil C:N ratio.

To investigate the relationship of soil nutrients with individual species, canonical correlation analysis (CCA) was performed. Only the original data set of 61 plots was used for this analysis because different laboratory methods were used for sulphur and phosphorus in the two data sets. The aim of the following application of CCA was to clarify relationships between species' abundance and associated soil chemical characteristics.

Before embarking on the CCA, it was necessary to re-express the data in a form better suited to analyses of this kind. The obvious need was to reduce the large number of species and chemical variables, and to address the problem of multicollinearity in the variables (Gittins 1979). To reduce the number of species from 120, only the 43 diagnostic species were used. Additionally, only the 10 forest floor chemicals were used, since during field sampling the roots of the vegetation were noted to occur predominantly in the forest floor. The roots located in the top portion of the mineral soil were mainly those of the overstory tree species. Klinka *et al.* (1990) also found that the structures of the humus form and vegetation data sets were strongly related.

Centred PCA performed on the vegetation covariance matrix, and

Table 4.5: Correlation of PCA scores used in canonical discriminant analysis with soil nutrient properties.

Chemical n=67	Axis 1 Loadings	Axis 2	Axis 3	Axis 5	Axis6
Forest Floor					
pH	-0.209	-0.158	0.741	0.414	-0.098
total carbon (%)	-0.078	-0.097	-0.635	0.037	0.459
total nitrogen (%)	0.846	-0.109	-0.236	0.284	0.122
mineralizable N (ppm)	0.675	-0.434	0.070	0.230	0.395
carbon-nitrogen ratio	-0.798	0.090	-0.196	-0.206	0.165
available calcium (ppm)	-0.018	-0.445	0.609	0.120	0.349
available magnesium (ppm)	-0.014	0.278	-0.167	0.066	-0.348
available potassium (ppm)	-0.764	0.210	0.017	0.438	-0.016
Mineral Soil					
pH	0.350	-0.678	0.267	-0.151	-0.106
total carbon (%)	0.454	0.756	-0.056	0.083	0.121
total nitrogen (%)	0.731	0.532	-0.023	0.146	-0.097
mineralizable nitrogen (ppm)	0.637	0.590	0.086	0.118	-0.122
carbon-nitrogen ratio	-0.466	0.081	-0.115	0.594	-0.030
available calcium (ppm)	-0.073	0.556	0.575	-0.344	0.229
available magnesium (ppm)	0.069	0.791	0.296	-0.124	0.078
available potassium (ppm)	-0.354	0.772	0.041	0.110	0.296

performed on the forest floor chemical correlation matrix was used to express the overall vegetational composition of the sites and the overall nutrient status of the forest floor in relation to the ten forest floor nutrient properties. In order to maintain a minimum ratio of plots to variables of five to one, eight vegetation PCA components and four chemical PCA components were used. The eight vegetation components were found to account for 80% of the total variance, and the four forest floor chemical components accounted for 87% of the variance. These components were considered to adequately characterize the vegetation and forest floor chemicals and accordingly, were used as the two sets of variables in the canonical analysis. The ecological objective was to achieve a preliminary understanding of the relationship between the diagnostic species with the forest floor nutrient properties measured.

Table 4.6 indicates that the variance of the vegetation PCA scores domain explained by the four canonical axes is 0.53, with axis 1 only explaining 0.13 of the variation. Therefore, canonical axis 1 was a rather weak component of the vegetation scores domain. Although the variance explained between the first two variates was 0.62 (Canonical R^2), the redundancy or raw variance of the vegetation PCA scores explained by the chemical PCA scores was only 0.08. This indicated a weak relationship between the diagnostic vegetation and the forest floor nutrient properties.

However, the vegetation relationships were dominated by six major diagnostic species at the alliance level. These individual species comprised one set of variables in a further canonical analysis. Preliminary analysis showed total sulphur was highly correlated with total nitrogen and that total phosphorus was unimportant in the canonical correlations. Consequently, both soil chemicals were omitted, which allowed the two data sets to be

combined for a total of 82 plots. Thus, eight forest floor chemicals comprised the second set with the ratio of variables to plots of 5.9:1.

The ecological objective of this analysis was to identify the connections between the six diagnostic species and the eight forest floor chemicals, and, in doing so, draw attention to the difference in magnitude between the effects of soil chemicals on the species. Since the ecological interest in this study was confined to the possible effects of the forest floor soil chemical variables on species' abundance, the analysis is directed in

Table 4.6: Canonical redundancy analysis of the species PCA scores and forest floor chemical PCA scores.

Their own Canonical Variables			The opposite Canonical Variables		
Variate	Proportion	Cumulative Proportion	Canonical R^2	Proportion	Cumulative Proportion
1	0.1313	0.1313	0.6219	0.0816	0.0816
2	0.0913	0.2226	0.3514	0.0321	0.1137
3	0.1231	0.3457	0.1647	0.0203	0.1340
4	0.1803	0.5260	0.0929	0.0168	0.1508

nature. The analysis was confined to the species and directed to looking at the variance of the species explained by the chemicals. The results of the CCA are summarized in Table 4.7.

Only the squared canonical correlation coefficients associated with the first four canonical axes exceeded 0.10 in magnitude. It therefore appeared that four dimensions was sufficient to fully account for the relationship between the variables and consequently, discussion will involve these four pairs of variates only.

Table 4.7: Canonical Correlation Analysis showing relationships between six diagnostic species and eight forest floor chemical properties: loadings, cross loadings and redundancy.

N = 82	Loadings					Cross loadings				
Canonical variates	U ₁	U ₂	U ₃	U ₄	h ² _w	V ₁	V ₂	V ₃	V ₄	h ² _b
<u>Species</u>										
<i>Blechnum spicant</i>	-0.370	-0.013	0.339	0.244	0.311	-0.281	-0.007	0.180	0.098	0.121
<i>Polystichum munitum</i>	-0.515	0.624	0.240	0.533	0.996	-0.391	0.374	0.127	0.214	0.355
<i>Gaultheria shallon</i>	0.971	-0.172	0.094	0.137	1.000	0.737	-0.103	0.050	0.055	0.559
<i>Thuja plicata</i>	0.551	0.339	0.324	-0.497	0.771	0.418	0.203	0.172	-0.199	0.285
<i>Rubus spectabilis</i>	-0.359	0.103	0.810	0.068	0.800	-0.273	0.062	0.429	0.027	0.263
<i>Tiarella trifoliata</i>	-0.341	-0.369	0.507	0.299	0.599	-0.259	-0.221	0.269	0.120	0.203
Variance extracted	0.487	0.111	0.121	0.117	0.837	0.281	0.040	0.034	0.019	0.374

Canonical variate	Loadings				h ² _w
	V ₁	V ₂	V ₃	V ₄	
<u>Forest floor chemical</u>					
pH	0.215	0.211	0.814	-0.189	0.789
total carbon (%)	0.187	0.371	-0.389	-0.318	0.425
total nitrogen (%)	-0.529	0.500	-0.170	0.219	0.603
mineralizable nitrogen	-0.647	0.422	-0.206	-0.268	0.711
carbon-nitrogen ratio	0.618	-0.143	-0.151	-0.193	0.462
available calcium	-0.060	0.510	0.280	-0.682	0.808
available magnesium	0.462	0.235	0.293	-0.042	0.356
available potassium	0.885	-0.135	-0.019	-0.118	0.816
Variance extracted	0.270	0.121	0.134	0.096	0.621
<u>Squared Canonical</u>					
Correlation	0.576	0.360	0.281	0.161	
Redundancy R ² _{y x}	0.281	0.040	0.034	0.019	0.374

The four species canonical variates (U_k) accounted for 84% of the variance in the species domain. Of the three, U_1 was by far the strongest, accounting for 49% of the total variance; U_2 , U_3 and U_4 accounted for some 11, 12, and 12 % respectively. The loadings on the first component indicated that all six species had moderate (>0.3) to strong (>0.7) correlations with this axis. The greatest correlation was with *Gaultheria shallon*, followed by moderate associations with *Polystichum munitum*, *Thuja plicata*, *Blechnum spicant*, *Rubus spectabilis*, and *Tiarella trifoliata*. *G. shallon* and *T. plicata* had a positive association with U_1 while the remaining four had a negative correlation. The second component (U_2) is characterized by a strong positive correlation with *P. munitum*, and a moderate positive and negative correlation with *T. plicata* and *T. trifoliata*, respectively. The third component (U_3) was mainly an expression of a strong positive correlation with *R. spectabilis* and moderate positive correlations with *T. plicata*, *T. trifoliata* and *B. spicant*. The fourth component (U_4) was characterized by a moderate positive correlation with *P. munitum* and a moderate negative correlation with *T. plicata*.

Considering the correlations between the original forest floor chemical variables and the canonical variates, V_k , defined on them, most chemical variables contributed positively to V_1 with the exception of total nitrogen, mineralizable nitrogen and available calcium,. Available potassium had a high correlation with this variate (0.89), and total and mineralizable nitrogen, C:N ratio, and available magnesium had moderate correlations with this variate. V_1 therefore, seemed to be a strong expression of potassium and moderate one of magnesium and C:N ratio in the positive direction, and a moderate expression of total and mineralizable nitrogen in the negative direction. The correlations with V_2 were all moderate and

positive with total carbon, total and mineralizable nitrogen and available calcium. Variate V_3 was predominantly a strong positive expression of pH along with a weaker negative expression of total carbon. V_4 had a moderate negative correlation with available calcium and total carbon. V_1 extracted 27% of the total variance of soil variables, V_2 12%, V_3 13% and V_4 10%. Together the four V_k canonical variates accounted for 62% of the variance of the forest floor chemical domain.

The intraset communalities (h^2_w) of the species variables for the rank 4 model indicated that U_k accounted for substantial proportions of the variances of each of the species. The equivalent forest floor chemical communalities showed that V_k also accounted for sizeable proportions of the chemical variances. Figure 4.6 shows U_1 and V_1 plotted against each other.

From the redundancies, it is clear that canonical variate V_1 accounted for most of the explained variance of the species examined. The redundancy in the species domain generated by the canonical variate V_1 was 0.28 -- thus the actual forest floor chemicals explained roughly 28 % of the variance in the species domain. The chemical variates V_2 , V_3 , and V_4 explained 4%, 3% and 2% additional variance respectively. A rank 4 model seems to be satisfactory to provide the necessary combination of fit, insight, and parsimony. The four forest floor chemical variates explained 37% of the variance of the species domain. As pointed out by Gittins (1979), in general when the ratio of predictor to criterion variables is in the order of 1:1, it is expected that the percentage of predictable variance will fall compared to multiple regression. Gittins demonstrated that canonical analysis was able to efficiently recover relationships of ecological interest between two sets of variables if about 40% of the variance of the variable-set of interest was

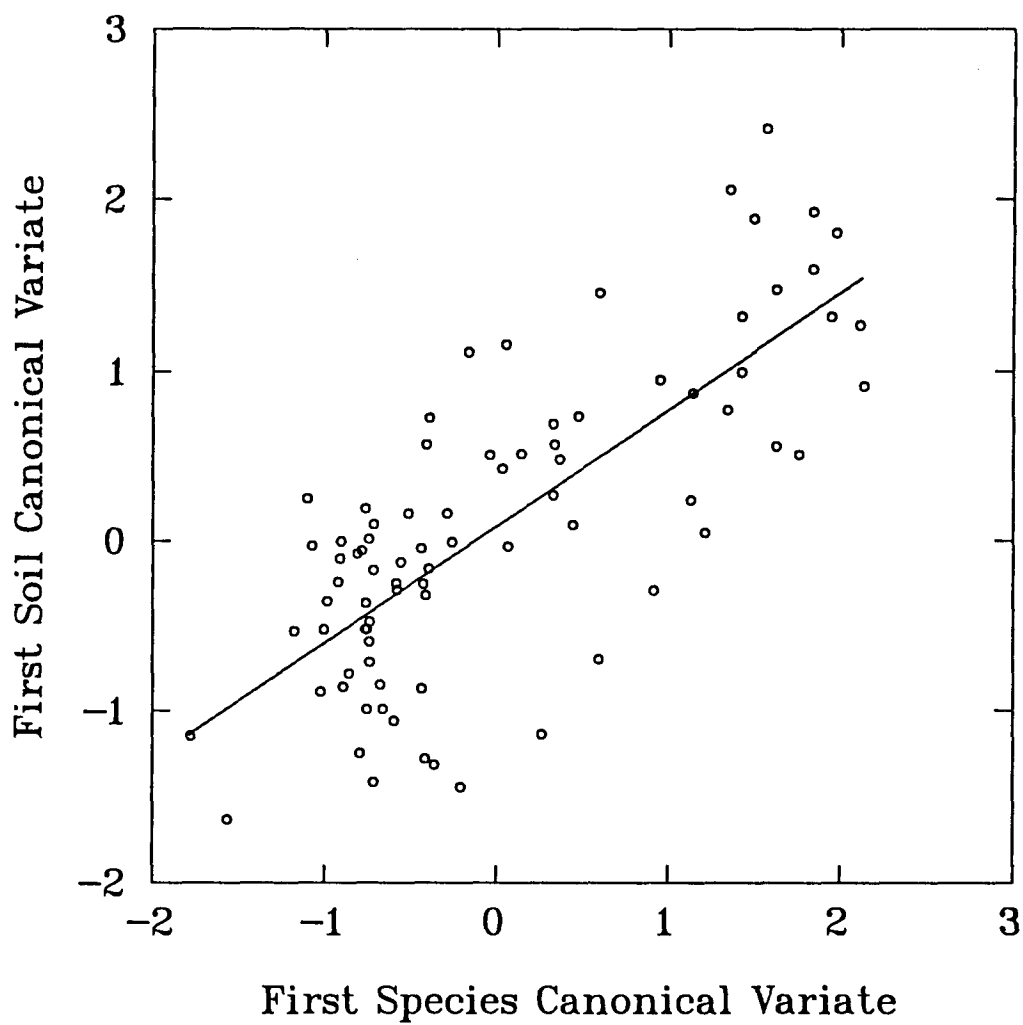


Figure 4.6. Relationships between the six diagnostic species and the eight forest floor chemical properties using the first canonical variate pair.

explained.

The preceding canonical correlation analysis suggested which of the forest floor nutrient properties were correlated with the six species (summarized in Table 4.8). The main correlations occurred on the first pair of variates where *G. shallon* and *T. plicata* varied negatively with total nitrogen, mineralizable nitrogen and positively with C:N ratio, potassium and magnesium. *B. spicant*, *P. munitum*, *R. spectabilis*, and *T. trifoliata* varied oppositely. Supplementary relationships also existed. *B. spicant*, *T. plicata*, *R. spectabilis*, and *T. trifoliata* had a positive relationship with forest floor pH, *B. spicant*, *R. spectabilis*, and *T. trifoliata* had a negative correlation with total carbon, *T. plicata* had a positive correlation with calcium, and *T. trifoliata* showed an inverse relationship with calcium.

The six predominant species distinguishing the major associations showed a trend in correlation, using CCA, with some of the forest floor chemical properties measured. In agreement with Klinka *et al.* (1989) *Gaultheria shallon*, considered an oxylophytic species, was negatively correlated with forest floor total and mineralizable nitrogen. *Polystichum munitum*, *Rubus spectabilis*, and *Tiarella trifoliata*, considered nitrophytic species, were positively correlated with mineralizable nitrogen. *Blechnum spicant* showed a positive correlation with nitrogen; this is opposite to what would be expected since it is considered an oxylophytic species. However, the sites were noted to have a large variation in the amount of decaying wood which, when combined with the low number of species, could result in such a disagreement.

These six species were dominant in defining four major associations in the diagnostic table; therefore, the trend exhibited by the soil chemical properties with the four plant associations reflected the relationship found

Table 4.8: Summary of positive and negative correlation of six diagnostic species with eight forest floor chemical properties. Large font size are from the first Canonical variate pair, small font size are from supplementary Canonical variate pairs.

Forest floor Chemical	pH	total C	total N	mineral N	C:N	avail Ca	avail Mg	avail K
<u>Species</u>								
<i>Blechnum spicant</i>	+	-	+	+	-		-	-
<i>Polystichum munitum</i>			+	+	-		-	-
<i>Gaultheria shallon</i>			-	-	+		+	+
<i>Thuja plicata</i>	+		-	-	+	+	+	+
<i>Rubus spectabilis</i>	+	-	+	+	-		-	-
<i>Tiarella trifoliata</i>	+	-	+	+	-	-	-	-

for individual species. There was an overlapping gradation of soil chemical properties from the *Gaultheria*, through the *Gaultheria-Polystichum*, *Polystichum*, to the *Rubus* Association. Considering that the plant associations themselves showed the same overlapping gradation, this same trend with the six major diagnostic species was expected. As with the total individual species, this gradation was correlated positively with both forest floor and mineral soil nitrogen (both total and mineralizable), and negatively correlated with forest floor C:N ratio and available potassium. Thus, the gradation of the four plant associations was associated with an increase of nitrogen availability which is correlated with an decrease in the C:N ratio and available potassium of the forest floor.

When examining the relationship between the six species and the plant associations with potassium, it should be kept in mind that the nutrients are based on a concentration basis. The negative correlation between the nitrogen measures and potassium may simply be due to a dilution effect (i.e., the increase in supply of other nutrient elements on the

sites with more nitrogen is proportionately greater than the presumed increase in supply of potassium).

4.2 Soil Nutrient Regimes

The primary data set of 55 plots was used to explore the relationship between the field derived SNRs (hereafter referred to as simply "SNR") and the soil chemical measures. The most promising individual soil chemical measures showing a relationship with SNRs are listed in Table 4.9. Figure 4.7 shows this relationship using a series of box plots. Although there are definite trends, the variation within each SNR is very wide with considerable overlap between SNRs.

To further explore the relationship between the field derived SNRs and the actual soil chemical measures, a PCA ordination was carried out on both the forest floor and mineral soil chemical measures. The first two axes, accounting for 32% and 18% of the variation respectively, were graphed and elliptical outlines were overlain (Figure 4.8). The elliptical outlines showed a definite gradation from the very poor SNR to the rich SNR. There was only one very rich plot and it was not considered further in the analysis. The very poor and rich SNRs showed a distinct separation but the poor and medium overlapped substantially with each other, and with the very poor and rich SNRs.

The correlations between PCA axes 1 and 2, and the soil chemical measures appear in Table 4.10. PCA axis 1 showed a highly positive correlation with forest floor and mineral soil total and mineralizable nitrogen, and total sulphur. Highly negative correlations were found with forest floor and mineral soil carbon:nitrogen ratios, and forest floor available potassium. PCA axis 2 showed moderately positive correlations with forest

Table 4.9: Means and standard deviations of selected soil chemical properties and their relationship to SNRs.

Chemical	Very Poor Mean Concentration	Poor Mean Concentration	Medium Mean Concentration	Rich	Very Rich
Forest Floor					
Number of plots	19	11	21	9	1
mineralizable N (ppm)	168 (59)	205 (74)	258 (75)	285 (104)	250
C:N	48 (6)	43 (7)	39 (10)	30 (6)	31
available K (ppm)	801 (245)	577 (226)	492 (182)	367 (128)	270
Mineral Soil					
Number of plots	13	11	21	9	1
pH	3.7 (0.4)	4.2 (0.3)	4.5 (0.3)	4.6 (0.3)	4.2
mineralizable N (ppm)	23 (12)	38 (29)	37 (22)	55 (27)	115
C:N	44 (9)	33 (7)	29 (6)	22 (2)	25
available K (ppm)	63 (35)	33 (15)	22 (7)	23 (9)	57

floor available magnesium and mineral soil available calcium. Also, highly positive correlations were found with mineral soil magnesium and potassium, and a highly negative correlation with mineral soil pH.

The very poor SNR was most associated with low forest floor and mineral soil nitrogen, low forest floor sulphur, high forest floor and mineral soil carbon-nitrogen ratio, high forest floor available potassium, low mineral soil pH and high mineral soil available cations. The opposite relationships were found with the rich SNR. The poor and medium SNRs fell between

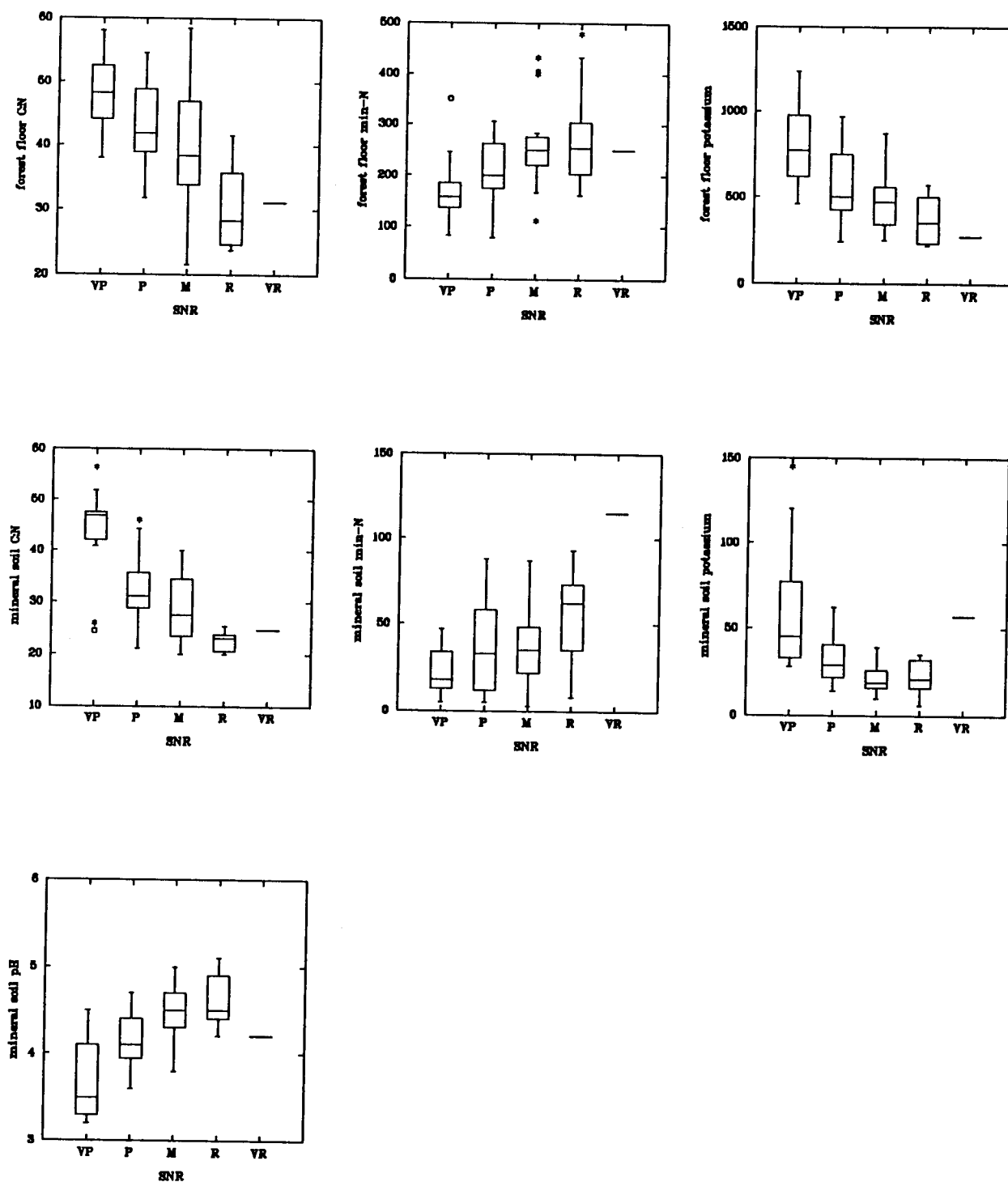


Figure 4.7. Box plots of selected soil chemical properties showing their relationship to SNRs. The symbols are very poor (VP), poor (P), medium (M), rich (R) and very rich (VR)

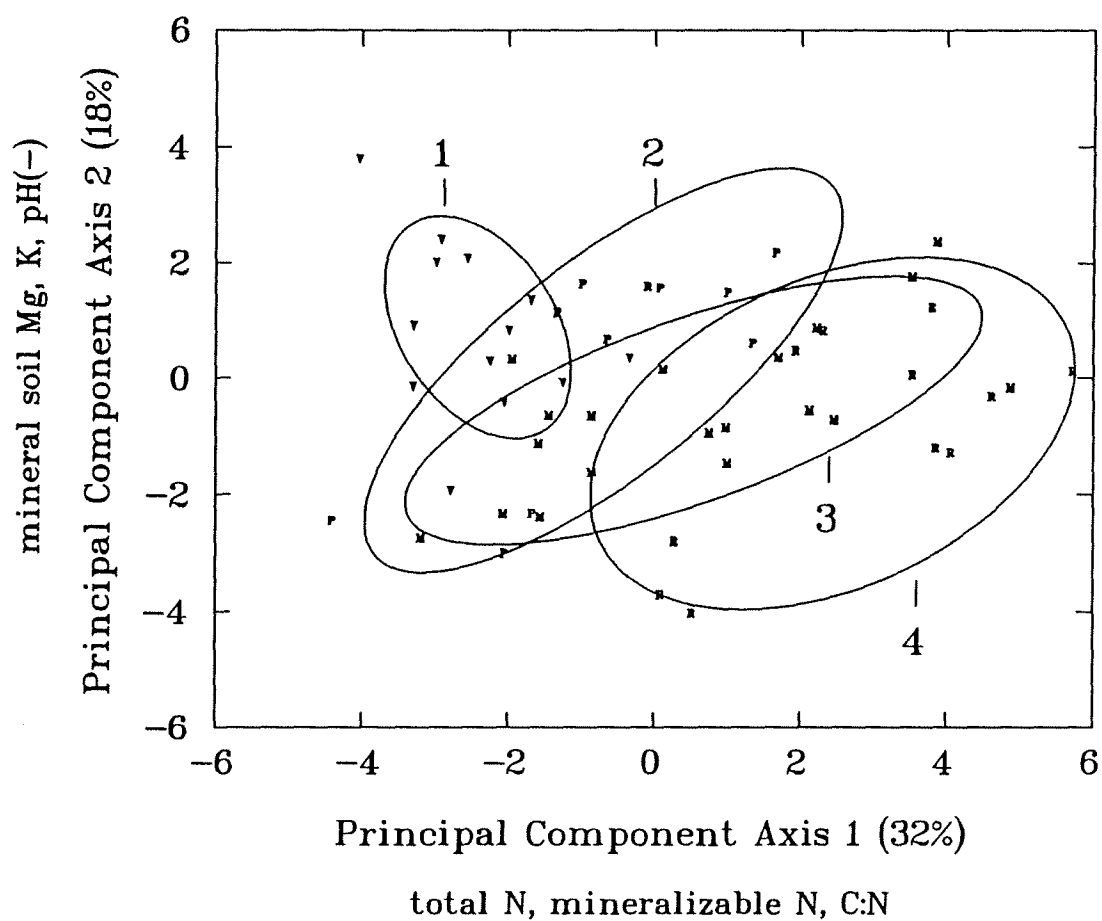


Figure 4.8. Plot of the first two PCA axes of the soil chemical measures with 80% elliptical outlines separating SNRs very poor (1), poor (2), medium (3), and rich (4).

Table 4.10: Correlation values ($r_{0.01} = 0.34$) of actual soil chemical properties with PCA axes 1 and 2.

Chemical	Axis 1 (32%)	Axis 2 (18%)
n=55	Loadings	
<u>Forest Floor</u>		
pH	-0.257	-0.221
total nitrogen (%)	0.871	0.018
mineralizable nitrogen (ppm)	0.779	-0.106
C:N	-0.855	0.289
total phosphorus (%)	0.246	-0.361
total sulphur (%)	0.818	0.075
available calcium (ppm)	-0.210	-0.280
available magnesium (ppm)	0.048	0.561
available potassium (ppm)	-0.724	0.110
<u>Mineral Soil</u>		
pH	0.319	-0.757
total nitrogen (%)	0.811	0.343
mineralizable nitrogen (ppm)	0.783	0.374
C:N	-0.784	0.258
available phosphorus (ppm)	-0.515	0.008
available sulphur (ppm)	-0.508	-0.190
available calcium (ppm)	-0.094	0.528
available magnesium (ppm)	0.150	0.733
available potassium (ppm)	-0.323	0.748

these two extremes and did not show definite associations. However, the strongest trend existed along the first PCA axis which was most correlated with the nitrogen forest floor and mineral soil measures. This trend also agreed with knowledge that nitrogen is considered to be the most limiting nutrient in many forest ecosystems (Jenny 1941; Viets 1965; Heilman 1979; Ballard and Carter 1986). Previous studies involving characterization of SNRs of the BEC system also supported the use of nitrogen as a criterion for defining SNRs (Kabzems and Klinka 1987; Courtin *et al.* 1989).

Consequently, the six forest floor and mineral soil nitrogen measures were used in a CDA to explore the relationship of nitrogen with SNRs. Since there was only one plot in the very rich SNR, this plot and the very rich SNR

were dropped from further analysis. Thus, the six nitrogen measures comprised one set of variables, and four SNRs, in the form of a constant and three binary valued "dummy" variables, composed the second set of variables. With fifty-four plots, there was a ratio of plots:variables of 5.4:1. The ecological objectives were to describe and account for the structure of the soil chemical measures, and in doing so, investigate their relationships to the field-derived SNR's.

Of the three CDA axes, the first accounted for 81%, the second 11%, and the third 8% of the variation. Figure 4.9 displays the samples in the space of canonical variates 1 and 2. The first two axes were plotted with outlines of ellipses which encompass 80% of the plotted points of the respective groups. Although the outlines showed somewhat more distinct groupings than with PCA, there still was substantial overlap between the poor and medium SNRs. The correlations between CDA axes 1 and 2, and the soil chemical measures appear in Table 4.11. CDA axis 1 showed a highly positive correlation with forest floor mineralizable nitrogen, and moderately positive correlations with forest floor total nitrogen, and mineral soil total and mineralizable nitrogen. This axis was highly negatively correlated with forest floor and mineral soil carbon:nitrogen ratio.

As a validation procedure to investigate how well the nitrogen measures are related to the field derived SNRs, discriminant analysis was conducted to test the ability of the six nitrogen chemical measures to differentiate among the four SNRs. Prior to analysis, a check of multivariate normality showed that the distribution was not normal. To achieve a multivariate normal distribution, five of the six variables were transformed using the common logarithm. Only the forest floor carbon:nitrogen ratio was left in the original units. A test of equality of the dispersion matrices

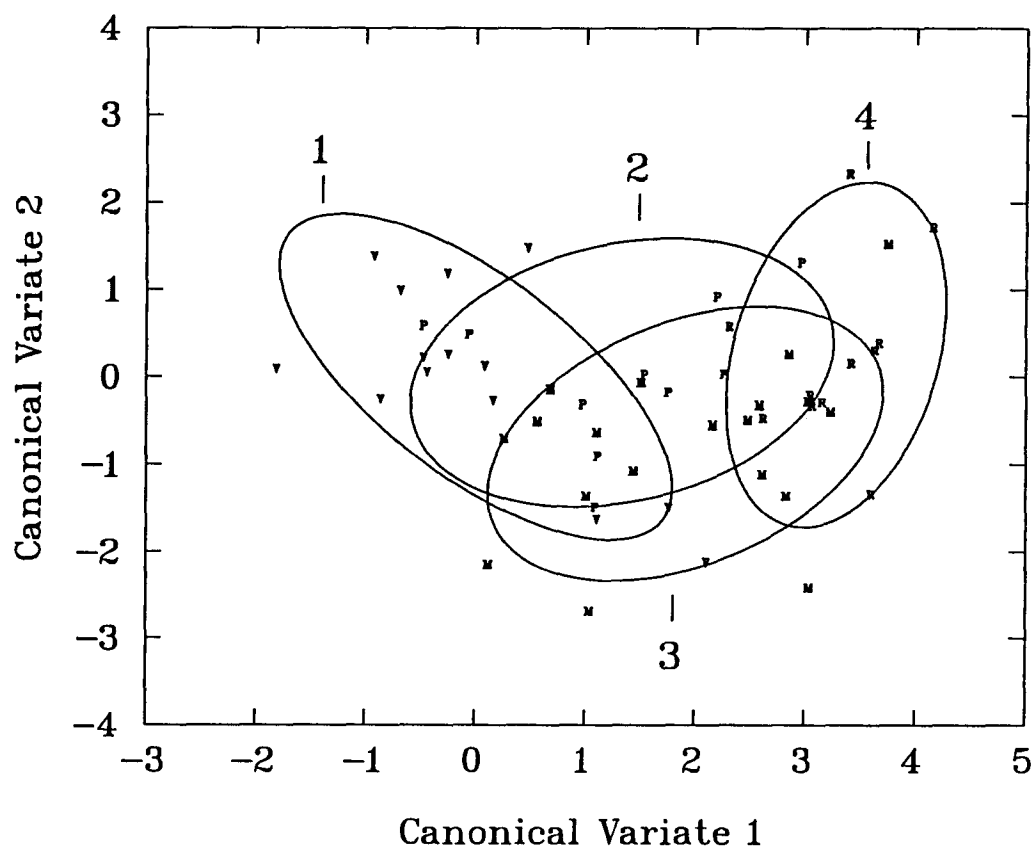


Figure 4.9. Plot of the first 2 canonical variates, derived from the soil nitrogen measures, with 80% elliptical outlines separating SNRs very poor (1), poor (2), medium (3), and rich (4).

Table 4.11: Canonical Discriminant Analysis showing correlations between the three CDA axes and six soil nitrogen measures.

n=54 Canonical variate	loadings U ₁	U ₂	U ₃
Forest floor chemical measures			
total nitrogen	0.670	-0.028	0.923
mineralizable nitrogen	0.706	-0.008	0.504
C:N	-0.882	-0.327	-0.127
Mineral soil chemical measures			
total nitrogen	0.639	-0.046	0.317
mineralizable nitrogen	0.584	0.187	0.008
C:N	-0.957	0.200	0.185
Squared Canonical Correlation	0.581	0.159	0.127

resulted in a test chi-square value significant at $p < 0.1$; therefore, the within covariance matrices were used in the discriminant function. For this analysis, equal prior probabilities were used. A validation data set of 41 plots was available, and was collected from similar areas. Comparison of the nitrogen measures between the two sets (Table 4.12) showed that the two sets were comparable, but did have some differences in means and ranges. The validation set also lacked very poor SNRs.

Discriminant analysis correctly classified 91% of the plots into their source groups (Table 4.13). Of the five plots that were misclassified, all were only wrong by one class. However, this high success rate was not repeatable; on the validation data set, the discriminant function correctly classified only 54% of the plots (Table 4.14). None of the poor plots and only half of the rich plots were correctly classified, although misclassification was only one soil nutrient class off.

Discriminant analysis was again carried out on the original data set but with prior probabilities thought to reflect the actual level based on

Table 4.12: Comparison of soil nitrogen measures between the original data set of 54 plots and a validation data set of 41 plots.

Forest floor measure	original data			validation data		
	mean	sd	range	mean	sd	range
total N (%)	1.09	0.28	0.65-2.06	1.09	0.22	0.59-1.53
mineralizable N (ppm)	230	86	79-479	303	113	89-586
C:N	41	10	21-58	42	9	31-78
Mineral soil measure						
total N (%)	0.19	0.12	0.03-0.47	0.21	0.08	0.08-0.42
mineralizable N	37	25	3-93	39	21	15-111
C:N	32	10	20-56	26	4	19-40

Table 4.13 Confusion matrix showing the percentage of plots identified by discriminant analysis in the source SNRs on the basis of forest floor and mineral soil log(total N), log(mineralizable N), forest floor C:N ratio and mineral soil log(C:N ratio). This matrix was derived from the original data set.

SNR	Percent correct	Number of plots identified in SNR			
		Very Poor	Poor	Medium	Rich
Very Poor	93	13	0	1	0
Poor	90	1	9	0	0
Medium	84	0	0	16	3
Rich	100	0	0	0	11
Total	89	14	9	17	14

Table 4.14 Confusion matrix showing the percentage of plots identified using the discriminant function derived from the original data set on a validation data set in the source SNRs on the basis of forest floor and mineral soil log(total N) and log(mineralizable N), forest floor C:N ratio and mineral soil log(C:N ratio).

SNR	Percent correct	Number of plots identified in SNR			
		Very Poor	Poor	Medium	Rich
Poor	0	1	0	6	0
Medium	71	1	5	17	1
Rich	50	0	0	5	5
Total	54	2	5	28	6

knowledge of the area. The priors for the SNRs were changed to .05 for very poor, 0.35 for poor, 0.45 for medium and 0.15 for rich. This reflected the proportion of the respective SNRs actually existing in the area. The results were only slightly different from using equal prior probabilities of 0.25 for all four SNRs. The function this time correctly classified 89% of the plots in the original data set, and once again, 54% for the validation data set.

The discriminant function then, captured the within site variability of the original data set but failed to capture between site variability with an independent test data set. This result may partly be attributed to the multicollinearities between the variables chosen. Multicollinearity can lead to unstable discriminant functions and is known to be a problem (Gittins 1985). Also, a substantial portion of the test data set was sampled from different geographical areas than the original data set. This included the following differences: (i) the original data set included non-forested, extreme very poor sites, (ii) the soil parent material of the original data set was predominantly of volcanic origin while the test data set included volcanic, granitic and limestone parent materials¹, and (iii) the test data set included areas on northern Vancouver Island, which had forest floors up to approximately one meter deep. Thus, the discriminant function derived from the original data set may only have use within the limited area and/or conditions that it was derived from. Further study on a wider geographic area is needed to assess whether a more general function can be derived, or whether a different function is required for smaller regions.

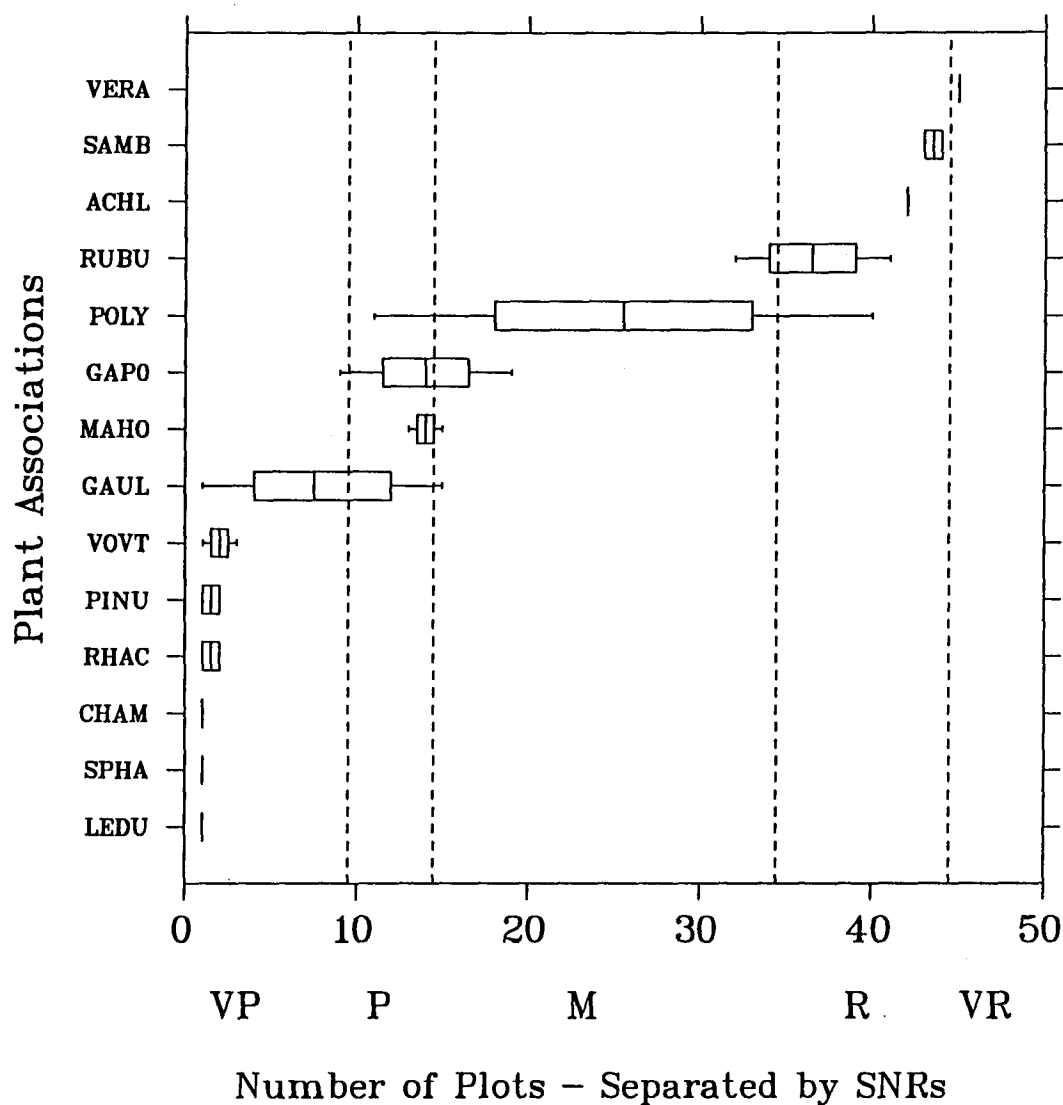
The use of multivariate analysis has its strength in pattern analysis, but the traditional univariate statistical analysis has its strength in actual

¹ Although, Heilman and Gass (1974) suggested that the influence of parent materials on chemical properties in the upper soil horizons (organic layers to B22) is small.

hypothesis testing (Gauch 1986). Therefore, if it is accepted that nitrogen is the major nutrient representing a SNR gradient, then the next step would be to statistically test for differences. However, the laboratory chemical analysis methods used in this study were chosen with pattern analysis in mind. Thus for instance, the anaerobic incubation procedure for mineralizable nitrogen, originally developed for "routine analysis of soils" (Waring and Bremner 1964), was used. Because laboratory estimates of nitrogen availability are insensitive to site environmental factors that are known to influence the nitrogen supplying power of soil, several investigators have chosen *in situ* assays (Raisin *et al.* 1987; Hart and Firestone 1989; Adams *et al.* 1989). Aber and Melillo (1984) also suggested that increased accuracy may come from the use of an *in situ* incubation procedure. A measure of the on-site nitrogen mineralization potential, which includes measurements of nitrate, can be viewed as reflecting an overall decomposition rate.

4.3 Relationship Between Plant Associations and SNRs

Both the vegetation classification and the site classification of edatopes were related, since understory species were used in supplementing the heuristic procedure to derive a SNR. However, the relationship was not exact, as shown in Figure 4.10 where several plant associations overlap with the SNRs. In this study, sites chosen were second growth hemlock stands which were characterized by a closed canopy resulting in depauperate vegetation. However, the use of even-aged second-growth stands ensured that the top height trees were not suppressed beyond breast height, which is necessary for site index estimates. It would be expected that the relationship between field derived SNRs and plant associations would be



LEDU=Ledum; SPHA=Sphagnum; CHAM=Chamaecyparis;
 RHAC=Racomitrium; PINU=Pinus; VOVV=Vaccinium(ovatum)
 GAUL=Gaultheria; MAHO=Mahonia; GAPO=Gaultheria-Polystichum;
 POLY=Polystichum; RUBU=Rubus; ACHL=Achlys; SAMB=Sambucus;
 VERA=Veratrum
 VP=Very Poor; P=Poor; M=Medium; R=Rich; VR=Very Rich

Figure 4.10. Box plots of the number of plots showing the relationship of plant associations to SNRs. The numbers on the x-axis represent the number of plots within each SNR.

stronger using ecosystems showing a better expression of vegetation.

4.4 Soil Moisture Regimes

The Energy-Soil Limited (ESL) water balance model (Spittlehouse 1981; Spittlehouse and Black 1981) was used to calculate the growing season water-deficit in order to estimate actual SMRs of water deficient (moderately dry through slightly dry) and fresh sites. The definitions of moderately dry, slightly dry and fresh sites as defined in Klinka *et al.* (1990) are given in Table 4.15.

However, even the driest non-forested ecosystem, with only 1 cm of soil, showed no water deficit upon using the model. Despite the high amount of rainfall associated with this variant (Table 4.16), this result does not seem reasonable. The occurrence of *Cladina* sp. and *Rhacomitrium canescens*, which are reported to occur on moisture deficient sites (Klinka *et al.* 1989), suggests that these extreme sites, even in this wet variant, do experience moisture deficits. Consideration must be given to the fact that the coefficients used in running the model were those of Giles *et al.* (1985) which were derived from a different biogeoclimatic subzone (CWHxm1) for Douglas-fir using daily data. It seems probable that the model needs calibration in the CWHvm1 variant, and for western hemlock. Spittlehouse

Table 4.15 Key to tentative soil moisture regimes for coastal British Columbia for moderately dry, slightly dry and fresh sites (from Klinka *et al.* 1989).

Soil moisture characteristic	Soil moisture regime
Water deficit > 1.5 but ≤ 3.5 months or AET/PET ¹ ≤ 90 but > 60%	moderately dry
Water deficit > 0 but ≤ 1.5 months or AET/PET > 90%	slightly dry
Utilization (and recharge) occurs (current need for water exceeds supply and soil-store water is used)	fresh

AET - actual evapotranspiration, PET - potential evapotranspiration

Table 4.16. Thirty year precipitation normals (1951-1980) from the climate station located at Tahsis, B.C. (Anonymous 1982).

	April	May	June	July	August	Sept	Oct	Yearly total
Precipitation (mm)	254.7	142.1	119.6	91.0	114.5	269.9	482.4	3828.8

(1981) stated that measurements at more forest sites and with different species are required to test the generality of this model. Also, Wang (1991) pointed out that coefficient calibration and model validation are required when applying the model to other ecosystems with different characteristics (under different regional climate or with different tree species).

Despite the need for model calibration and validation, it was still surprising that the model results showed no water deficit modelled on this extreme shallow soil site. There are three possible reasons why water deficits may not be detected, assuming that the ESL water balance model and the coefficients used are at least somewhat accurate. The first reason, stated by Carter and Klinka (1990), was that the monthly time-step used in the calculations likely resulted in an underestimation of soil water-deficits. Secondly, water deficits may occur in periods of weeks as opposed to months. The thirty year averages suggest that there is considerable precipitation in all months throughout the growing season. However, a model run with daily averages may detect shorter term deficits which may play an important role in western hemlock ecosystems. Daily averages also eliminate the effect of uniform distribution of precipitation over the whole month. The third possibility is that years of abnormally high rainfall were forcing the thirty year average monthly rainfall up, giving the impression that rainfall occurs throughout the growing season every year. To overcome

this, rather than using thirty year averages in the model, yearly values could be used and water deficits calculated yearly for the same thirty year period. The water deficits could then be averaged, eliminating the large influence of heavy rainfall years.

It is recommended for further use of this model in the very wet Coastal Western Hemlock Subzone that (i) model calibration and validation be first carried out, (ii) that daily averages separated by years be used for calculations, and the deficit periods averaged over the thirty-year data collection period¹, and (iii) for western hemlock ecosystems, an approach to modelling the effect of the thick humus layers is needed.

4.5 Relationships Between Site Index and Indirect Measures of Ecological Site Quality

In order to visually summarize the distribution of plots and the relationship between site index with plant associations, box plots of site index values (Tukey 1977; McGill *et al.* 1978; Chambers *et al.* 1983) are shown in Figure 4.11. Despite the wide variation, there was a trend of increasing site index from the *Ledum* to the *Polystichum* plant association, where it then leveled off.

To mathematically relate site index to the plant associations, "dummy" variable regression was used with the resulting full equation:

$$SI = 2.5 + 0.45(PA2) + 1.1(PA3) + 5.5(PA4) + 6.4(PA5) + 8.1(PA6) + 9.2(PA7) + 13.7(PA8) + 17.6(PA9) + 24.7(PA10) + 27.5(PA11) + 30.7(PA12) + 33.1(PA13) + 33.2(PA14)$$

$$\text{Adjusted } R^2 = 0.78 \quad F\text{-ratio} = 22.86 \quad SEE = 5.3 \text{ m} \quad N = 82$$

¹ Thus, despite the statement in the instructions to "SWBED1: Program to calculate simple water balances" (programmed by D.L. Spittlehouse 1987), that daily or monthly averages may be used it is suggested that daily averages only be used.

Dummy variables representing various vegetation associations (assn):
 Constant=*Ledum* Assn; PA2=*Rhacomitrium* Assn; PA3=*Sphagnum*
 Assn; PA4=*Malus* Assn; PA5=*Vaccinium(ovatum)* Assn; PA6=*Veratrum*
 Assn; PA7=*Chamaecyparis* Assn; PA8=*Gaultheria* Assn; PA9=*Mahonia*
 Assn; PA10=*Gaultheria-Polystichum* Assn; PA11=*Achlys* Assn;
 PA12=*Polystichum* Assn; PA13=*Rubus* Assn; PA14=*Sambucus* Assn.

A check of the residuals showed a lack of homogeneity of variance, mainly due to the few plots in several vegetation units. This weakens the analysis, if confidence or prediction intervals are required. However, heteroscedasticity does not invalidate the analysis since the linear relationship between variables is still captured (Tabachnick and Fidell 1989). A probability plot of residuals indicated that the error distribution was near normal. One outlier in the *Gaultheria* Association was detected but was difficult to explain, except perhaps by the depauperate vegetation. This plot was classified into the *Gaultheria* Association mainly on the presence of 2.3 to 5.0 % presence cover of *Gaultheria shallon* and lack of other diagnostic species.

From the box plots, it is apparent that there may not be a significant difference in site index among the *Gaultheria*, *Gaultheria-Polystichum*, *Polystichum*, *Rubus*, and *Sambucus* plant associations. The regression coefficients indicated only approximately a 3 meter difference between the *Polystichum*, *Rubus* and *Sambucus* associations.

To test whether these five major plant associations, which consist of 67 of the plots sampled, had significantly ($p < 0.05$) different mean site indexes, a Tukey-Kramer multiple range test (Ott 1988) was carried out on the *Gaultheria*, *Gaultheria-Polystichum*, *Polystichum*, and *Rubus* combined with *Sambucus* plant associations. The *Sambucus* unit and *Rubus* unit were combined since the former only had two plots, had *Rubus spectabilis* as a major component, represents very similar site conditions to the latter,

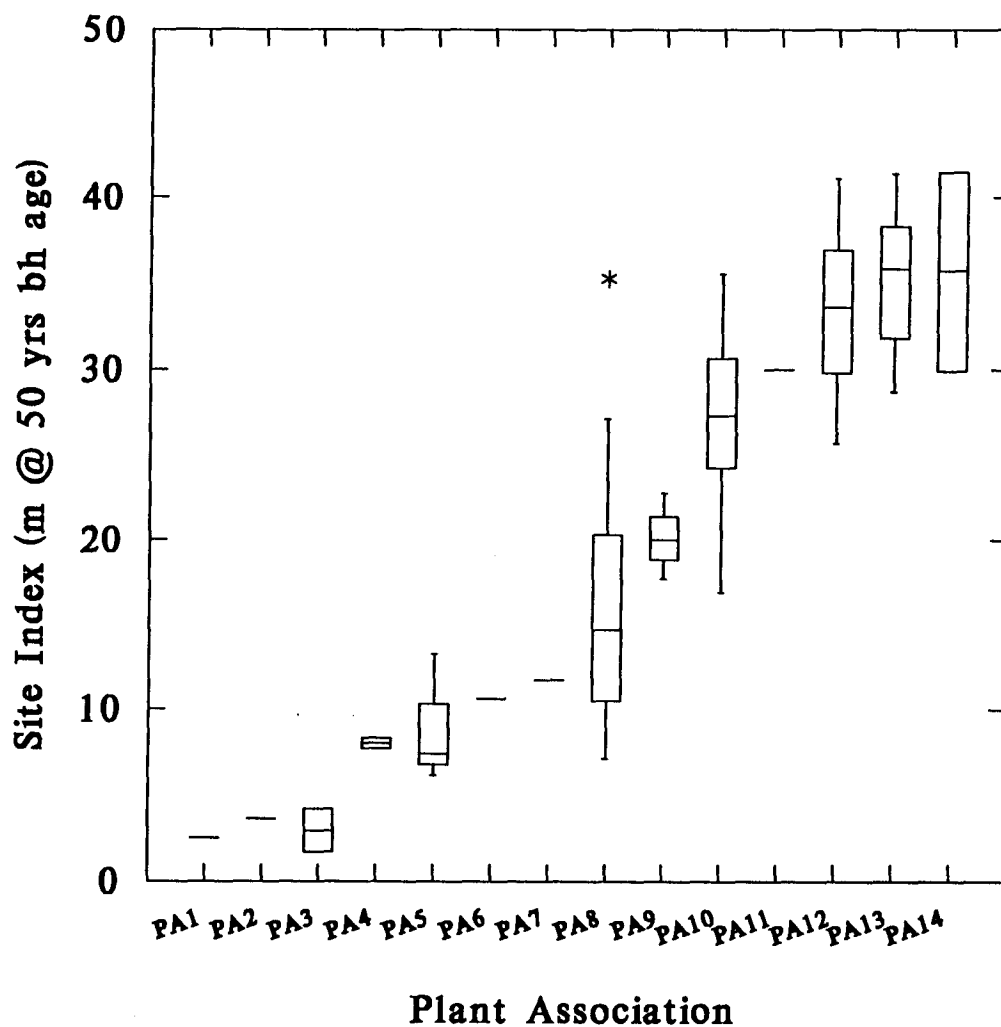


Figure 4.11. Box plots of site index and plant associations *Ledum* (PA1), *Sphagnum* (PA2), *Rhacomitrium* (PA3), *Malus* (PA4), *Vaccinium(ovatum)* (PA5), *Veratrum* (PA6), *Chamaecyparis* (PA7), *Gaultheria* (PA8), *Mahonia* (PA9), *Gaultheria-Polystichum* (PA10), *Achlys* (PA11), *Polystichum* (PA12), *Rubus* (PA13), and *Sambucus* (PA14).

and had a mean site index almost identical to the latter. An initial Bartlett test for homogeneity of the four group variances indicated significant ($p < 0.05$) differences between them. However, after eliminating the outlier discussed previously, differences were not significant. Bartlett's test is noted to be unduly sensitive to departures from normality in the data (Sokal and Rohlf 1981), an effect that can be caused by outliers. Based on a normal probability plot of site index, it was visually judged that the assumption of normality had been met. As Table 4.17 indicates, there was

Table 4.17. Results of a Tukey-Kramer multiple comparison for the plant associations *Gaultheria* (PA8), *Gaultheria-Polystichum*(PA10), *Polystichum*(PA12), and *Rubus-Sambucus*(PA13+PA14)

Matrix of Pairwise Comparison Probabilities				
	PA8	PA10	PA12	PA13+PA14
PA8	1.000			
PA10	0.220	1.000		
PA12	0.025	0.622	1.000	
PA13+PA14	0.032	0.465	1.000	1.000

no significant ($p < 0.05$) difference between the *Gaultheria* and *Gaultheria-Polystichum* units and none between the *Gaultheria-Polystichum*, *Polystichum*, and *Rubus-Sambucus* units. The only significant difference was between the *Gaultheria* and both the *Polystichum* and *Rubus-Sambucus* units.

The outlier in the *Gaultheria* group was noted previously. However, none of the relationships changed at the $p < 0.05$ significance level when it was removed, although the Bartlett's test for equal variances did become

non significant.

A similar relationship between plant associations and site index of western hemlock was described by Eis (1962). Three plant communities reported were similar to the ones in this study. The "Salal" plant community had the lowest site index value, with the "Blechnum" plant community somewhat larger, and the largest was the "Polystichum" plant community.

To investigate how the individual species were related to site index, PCA was first performed on the data set of 120 species. Eigenvalues indicated that 68 PCA axes contributed to the explained variance in some manner with the 68th axis accounting for only 0.0001% of the variance. Only the first eighteen axes accounted for greater than 1% of the variance and cumulatively explained 92 % of the variation. These axes were then used in a backward stepwise multiple regression with the resulting equation:

$$SI = 25.5 - 4.3(Axis1) + 0.8(Axis2) - 1.2(Axis7) - 1.4(Axis9) + 1.0(Axis13)$$

$$\text{Adjusted } R^2 = 0.78 \quad F\text{-ratio} = 58.05 \quad SEE = 5.1 \text{ m} \quad N = 82$$

Examination of the plot of residuals and the normal probability plot indicated a close to normal distribution and relative homogeneity of variances. Both the adjusted R^2 and SEE values were close to those obtained for the plant associations. This is expected when considering the close association shown previously between the first two PCA axes and the derived plant associations.

Of a total of 120 species, 62 were significantly ($p < 0.05$) correlated and had correlation coefficients greater than 0.3, with at least one of the five axes

(Table 4.18). Axis 7 mainly represented two plots on the extreme very wet sites - one is predominantly *Ledum groenlandicum*, and the other predominantly of *Sphagnum* species. Axis 13 mainly represented the former site only. Axis 9 most strongly represents one plot in a very wet/very rich site. Axes 1 and 2 captured, only in a general way, correlations with nitrophytic and oxylophytic species. The relationships were not very clear since higher site indexes generally occurred on sites with closed canopies, while the lower site indexes occurred on open-grown, and in extreme cases, non-forested, sites. In particular, *Tsuga heterophylla* presence was correlated negatively with the first axis, thus positively with site index. The decrease in site index associated with hemlock presence was simply a reflection of this canopy stand attribute. Conversely, the species *Hylocomium splendens* and *Rhytidiadelphus loreus* increased with increasing scores, with the higher scores coming from sites with decreased cover. This was again mainly attributable to the light conditions and not the site itself.

A multiple linear regression showed a weak relationship between site index and the frequency of indicator species groups, with the only significant variables being MOIST3 (moderately dry to fresh), MOIST4 (fresh to very moist) and NITR3 (nitrogen rich).

$$SI = -12.1 - 545.4(MOIST2) + 33.2(MOIST3) + 37.1(MOIST4) + 16.6(MOIST5) + 13.0(MOIST6) + 19.5(NITR2) + 19.2(NITR3)$$

Adjusted $R^2 = 0.35$

F-ratio = 7.19

SEE = 8.8 m

N = 82

constant = excessively dry to very dry and N-poor; MOIST2 = very dry to moderately dry; MOIST3 = moderately dry to fresh; MOIST4 = fresh to very moist; MOIST5 = very moist to wet; MOIST6 = wet to very wet; NITR2 = N-medium; NITR3 = N-rich.

Table 4.18. Correlation values ($r_{0.01} = 0.280$) of species that are significantly ($p > 0.01$) correlated and have $r > 0.3$ with PCA axes 1,2,7,9 and 13.

n=82 Species	Loadings				
	Axis1	Axis2	Axis7	Axis9	Axis13
<i>Gaultheria shallon</i>	0.86				
<i>Chamaecyparis nootkatensis</i>	0.44				
<i>Menziesia ferruginea</i>	0.39				
<i>Dryopteris expansa</i>	-0.31				
<i>Hylocomium splendens</i>	0.69	0.34			
<i>Polystichum munitum</i>	-0.65	0.47			
<i>Rubus spectabilis</i>	-0.40	0.50			
<i>Kindbergia oregana</i>	-0.31	0.57			
<i>Pinus contorta</i>	0.42	-0.43		0.35	
<i>Pleurozium schreberi</i>	0.30	-0.45	0.41	0.45	0.48
<i>Tsuga heterophylla</i>	-0.64		-0.39		
<i>Thuja plicata</i>	0.57		0.38		
<i>Blechnum spicant</i>	-0.40		-0.41		
<i>Cornus canadensis</i>	0.38		0.43		
<i>Tsuga mertensiana</i>	0.37		0.39		
<i>Plagiothecium undulatum</i>	-0.39			-0.33	
<i>Rhytidiadelphus loreus</i>		0.72			
<i>Vaccinium parvifolium</i>		0.38			
<i>Tiarella laciniata</i>		0.37			
<i>Vaccinium ovalifolium</i>		0.33			
<i>Polytrichum alpinum</i>		0.32			
<i>Rubus ursinus</i>		0.32			
<i>Plagiochila asplenioides</i>		0.30			
<i>Viola orbiculata</i>		0.30			
<i>Aulacomium palustre</i>		-0.35	0.46		0.72
<i>Empetrum nigrum</i>		-0.35	0.45		0.72
<i>Rhytidiadelphus triquetrus</i>		-0.35	0.45		0.72
<i>Vaccinium oxycoccus</i>		-0.35	0.45		0.72
<i>Ledum groenlandicum</i>		-0.35	0.45		0.72
<i>Maianthemum dilatatum</i>		0.42		0.47	
<i>Rosa nutkana</i>		0.37		0.41	
<i>Rubus parviflorus</i>		0.37		0.56	
<i>Galium triflorum</i>		0.33		0.56	
<i>Trautvetteria caroliniensis</i>		0.32		0.65	
<i>Tiarella trifoliata</i>		0.36		0.34	-0.32
<i>Coptis asplenifolia</i>			0.53		
<i>Sphagnum girgensohnii</i>			0.52		
<i>Sphagnum squarrosum</i>			0.51		
<i>Drosera rotundifolia</i>			0.42		
<i>Fauria crista-galli</i>			0.42		
<i>Lysichitum americanum</i>			0.42		
<i>Rhododendron albiflorum</i>			0.42		
<i>Sphagnum palustre</i>			0.42		
<i>Sphagnum rubra</i>			0.42		
<i>Chimaphila umbellata</i>			-0.33		
<i>Linnaea borealis</i>			-0.31		
<i>Myrica taylorii</i>			0.31	0.37	

<i>Nardia scalaris</i>	0.31	0.37	
<i>Ranunculus</i> sp.	0.31	0.37	
<i>Veratrum viride</i>	0.31	0.37	
<i>Viola</i> sp.	0.31	0.37	
<i>Gymnocarpium dryopteris</i>	0.31	0.37	
<i>Diplophyllum albicans</i>	0.31	0.37	
<i>Sambucus racemosa</i>		0.55	
<i>Mycelis muralis</i>		0.54	
<i>Pellia neesiana</i>		0.38	
<i>Dicranu</i> sp.		0.37	
<i>Bazzania denudata</i>		0.37	
<i>Rhacomitrium canescens</i>		0.36	
<i>Pinus monticola</i>		0.32	
<i>Cladina</i> sp.		0.31	
<i>Alnus rubra</i>			-0.31

Because of the lack of understory plants combined with the correlation of site index and canopy closure, the regression of site index with individual species, expressed through PCA scores or combined into indicator species groups, seems to be of limited value in this case. Second growth western hemlock stands do not have enough of an expression of understory species for use with individual species. However, the collective expression through plant associations seems to work to a certain extent.

A total of 102 plots was used in the investigation of the relationship between site index and SMRs and SNRs. A visual summary of the relationship of site index and field estimates of SMRs and SNRs is given in the 3 dimensional plot with orthogonal projections onto a SMR facet and SNR facet in Figure 4.12. Site index increased as the SNRs proceeded from very poor to rich, but showed a wide spread with changing SMRs. The low site indices on the SMR facet are due to the very poor SNR which extends across the SMR gradient. However, rich/dry and rich/wet sites do not support stands of western hemlock, thus maintaining an increase of site index on the SNR facet.

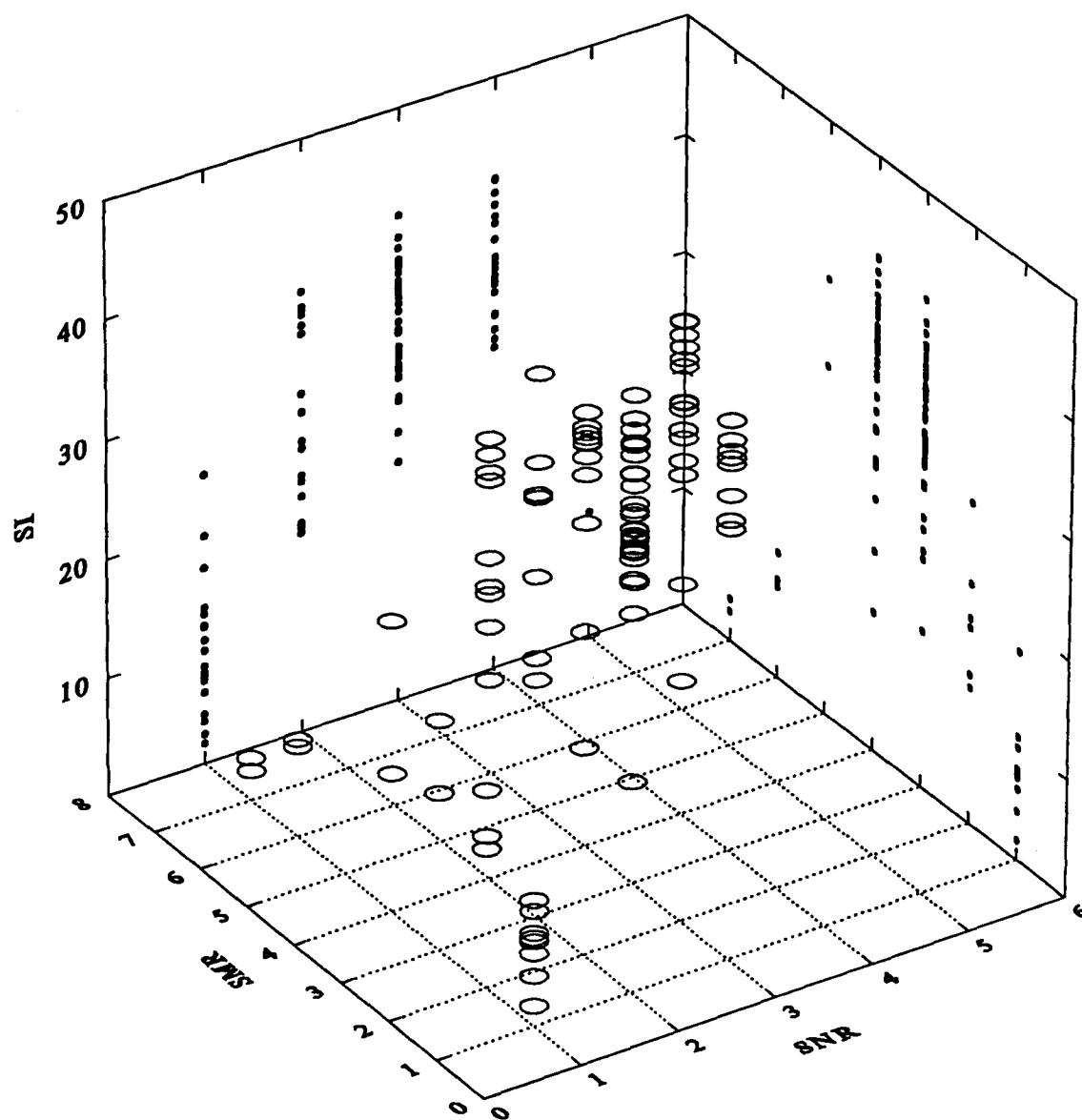


Figure 4.12. A 3 dimension plot of site indices on SNRs and SMRs with their orthogonal projections onto a SMR and SNR facet. SNR axis represents very poor (1), poor (2), medium (3), rich (4) and very rich (5). SMR axis represents moderately dry (1), slightly dry (2), fresh (3), moist (4), very moist (5), wet (6), and very wet (7).

Mathematically in a dummy variable regression, this relationship was expressed as:

$$SI = 5.7 + 4.2(MD) + 8.9(SD) + 14.3(F) + 16.2(MST) + 15.7(VM) + 4.9(W) - 2.6(VP) + 7.2(P) + 11.7(MED) + 13.2(R)$$

$$\text{Adjusted } R^2 = 0.81 \quad F\text{-ratio} = 43.7 \quad SEE = 4.5 \text{ m} \quad n = 102$$

Dummy variables representing combinations of SMR and simultaneously SNR: Constant=very wet or very rich; MD=moderately dry; SD= slightly dry; F=fresh; MST=moist; VM=very moist; W=wet; VP=very poor; P=poor; Med=medium; R=rich.

For the soil moisture gradient, the coefficients indicated that site index increased from moderately dry to slightly dry, leveled off at fresh and moist, then decreased slightly at very moist, and rapidly at wet and very wet sites. For the soil nutrient gradient, site index increased from very poor, and poor to medium where it leveled off between medium and rich and decreased at very rich SNRs.

The similar coefficients indicated that there may not be a significant difference in site index between fresh and moist SMRs and between poor, medium, and rich SNRs. Within the range of fresh to moist, poor to rich sites, there were 75 sample plots. Between these six units, Bartlett's test for homogeneity of group variances indicated that the variances could be significantly different ($p=0.06$). An analysis of variance (ANOVA) indicated that at least one of the means was significantly different ($p<0.05$). A Tukey-Kramer HSD test between the edaphic units within this range indicated that there was a significant difference ($p<0.05$) between the site indexes of moist/rich sites and either fresh/poor or moist/poor sites (Table 4.19), and no significant differences among the others.

A listing of mean site indexes on the edatopic grid is given in Figure

Table 4.19: Tukey-Kramer multiple comparison test matrix of pairwise comparison probabilities for combinations of SMR and SNR. Testing for differences in site index.

SMR/SNR	F/P	M/P	F/M	F/R	M/M	MR
Fresh/Poor	1.00					
Moist/Poor	1.00	1.00				
Fresh/Medium	0.62	0.39	1.00			
Fresh/Rich	0.73	0.61	1.00	1.00		
Moist/Medium	0.37	0.21	0.94	0.99	1.00	
Moist/Rich	0.04	0.01	0.13	0.48	0.87	1.00

4.13. Although site index increased until a maximum at Moist/Rich sites, the wide variation in site indexes for the site units is apparent. Although not enough samples were taken over the entire range, the dummy variable regression and the multiple comparison test indicated that the isolines of site index for a generalized edatopic grid of the submontane Very Wet Maritime Coastal Western Hemlock variant is as in Figure 4.14. This isoline graph was produced using a distance weighted least squares procedure with a tension of 0.2 (Wilkinson 1990).

Of interest also is how well just SMR or SNR alone would be in predicting site index. Dummy variable regression was used with the following results for SMRs:

$$SI = 5.1 + 5.2(MD) + 14.6(SD) + 27.7(F) + 29.0(MST) + 30.0(VM) + 5.8(W)$$

$$\text{Adjusted } R^2 = 0.69 \quad F\text{-ratio} = 38.0 \quad SEE = 5.8 \text{ m} \quad n = 102$$

Dummy variables representing combinations of SMR:

Constant=very wet or very rich; MD=moderately dry; SD= slightly dry; F=fresh; MST=moist; VM=very moist; W=wet.

**Submontane Very Wet Maritime
Coastal Western Hemlock variant (CWHvm1)**

		Soil nutrient regime				
		VP	P	M	R	VR
Actual soil moisture regime	MD	SI=7.2 sd=2.8 n=9	SI=17.7 n=1			
	SD	SI=13.6 sd=2.1 n=3	SI=22.3 sd=4.9 n=2	SI=20.3 n=1		
	F	SI=16.3 sd=3.1 n=2	SI=28.2 sd=6.5 n=5	SI=31.8 sd=4.3 n=31	SI=32.0 sd=3.1 n=8	
	M	SI=18.1 sd=6.4 n=2	SI=28.3 sd=6.7 n=9	SI=33.5 sd=2.6 n=9	SI=35.8 sd=4.1 n=13	
	VM			SI=32.6 sd=3.2 n=2		
	W	SI=8.0 sd=0.3 n=2				SI=10.6 n=1

Figure 4.13. Edatopic grid showing site index (m @ 50 years), standard deviations (m) and the number of plots for site units sampled.

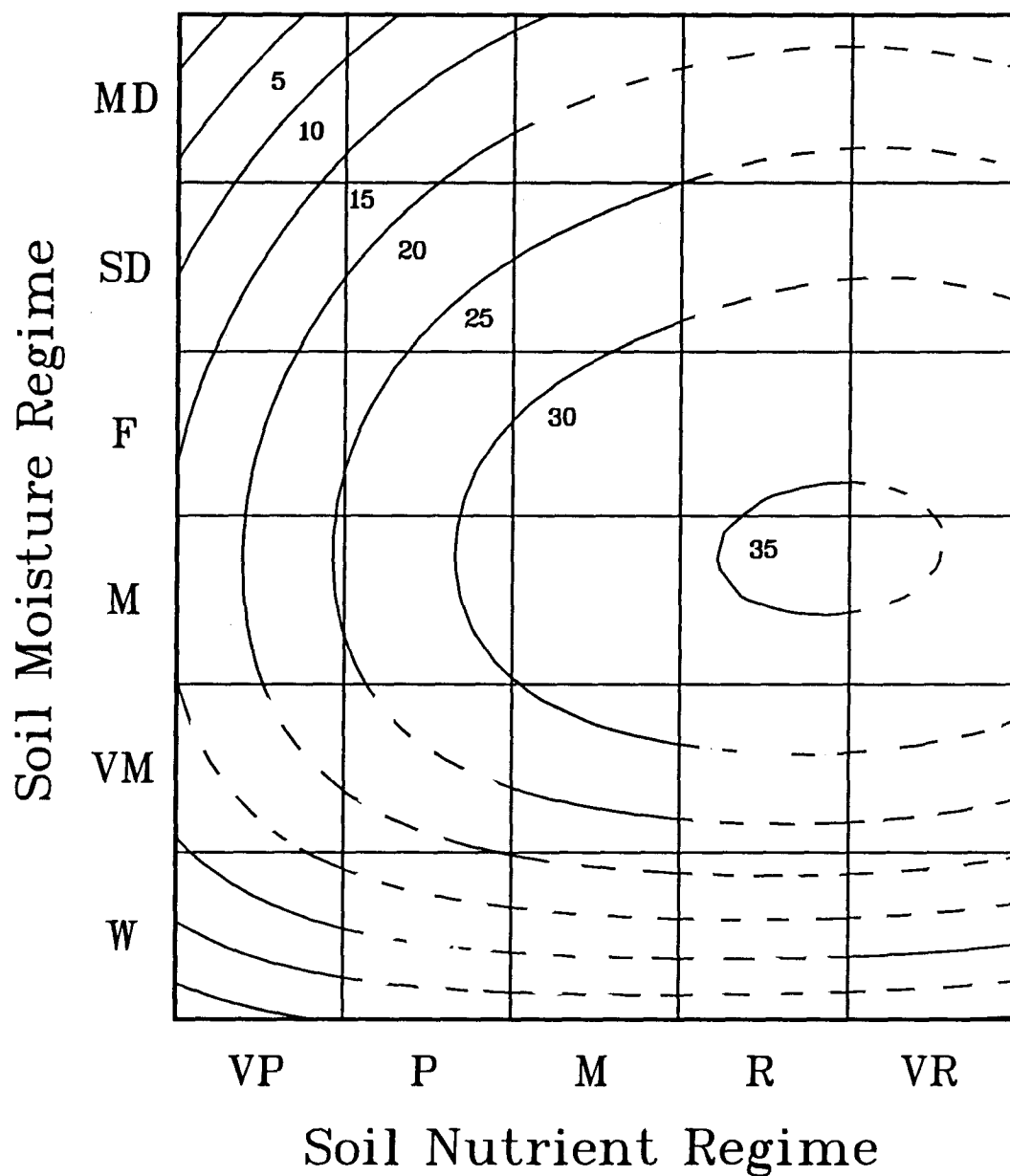


Figure 4.14. Edatopic grid with a site index isoline superimposed. This was calculated from actual mean site index values and extrapolated subjectively to areas lacking data (dashed lines).

The following were the results for SNRs:

$$SI = 10.6 - 0.8(VP) + 16.3(P) + 21.3(MED) + 23.7(R)$$

$$\text{Adjusted } R^2 = 0.75 \quad F\text{-ratio} = 77.3 \quad SEE = 5.2 \text{ m} \quad n = 102$$

Dummy variables representing combinations of SMR and simultaneously SNR:
Constant=very wet; VP=very poor; P=poor; Med=medium; R=rich.

Both equations had lower adjusted R^2 values and higher SEE values than the regression using both SNR and SMR. However, the equation using SNR alone had values that were close. There was a lack of slightly and moderately dry, and wet sites, with the majority of sites on fresh and moist moisture regimes, and this had the effect of holding SMR constant with a variable SNR gradient.

The relationship between site index and certain CWHvm1 site series is given in Figure 4.15 with accompanying standard deviations and sample sizes. Dummy variable regression gave the following result:

$$SI = 3.1 + 5.2(SS1) + 14.6(SS2) + 27.5(SS4) + 28.9(SS5) + 26.9(SS6) + 32.7(SS7) + 4.9(SS8) + 7.5(SS9)$$

$$\text{Adjusted } R^2 = 0.71 \quad F\text{-ratio} = 31.92 \quad SEE = 5.6 \text{ m} \quad n = 102$$

Dummy variables representing Site Series in the CWHvm variant:
Constant= very wet very poor site series; SS1 = HwPI-Cladina; SS2 = HwCw-Salal;
SS4 = HwBa-Blueberry; SS5 = BaCw-Foamflower; SS6 = HwBa-Deer Fern; SS7 =
BaCw-Salmonberry; SS8=PI-Spagnum; SS9 = CwSs-Skunk cabbage.

Five plots had large leverage; these were plots with the lowest site index and found on wet and very wet sites. In general, the plots had been categorized into units similar to the site units; however, the units based on site series combined poor and very poor SNRs. These two SNRs appeared to have large differences in site index for western hemlock. Also, sampling was

**Very Wet Maritime submontane variant
Coastal Western Hemlock (CWHvml)**

		Soil nutrient regime				
		VP	P	M	R	VR
Actual soil moisture regime	MD	① HwPl-Cladina SI=8.3 sd=4.1 n=10				
	SD	② HwCw-Salal SI=17.1 sd=5.5 n=6			CwHw-Sword Fern	
	F	④ HwBa-Blueberry SI=30.5 sd=5.8 n=38			⑤ BaCw-Foamflower SI=32.0 sd=3.1 n=8	
	M	⑥ HwBa-Deer Fern SI=29.9 sd=6.8 n=22			⑦ BaCw-Salmonberry SI=35.8 sd=4.1 n=13	
	VM					
	W	⑧ Pl-Sphagnum SI=8.0 sd=0.3 n=2		⑨ CwSs-Skunk Cabbage SI=10.6 n=1		

Figure 4.15. Site Series grid with site index values, standard deviations and number of plots indicated.

based on site units, thus there is over representation on the medium/fresh site units, which raises the mean site index for the HwBa-Blueberry site series relative to the others.

Krajina (1969) proposed that the most productive site for western hemlock would be a site index of 35 (meters @ 50 years) on a moist/poor site unit. This is different than what was found in this study where mean site index was at a maximum on moist/rich site units. However, there were no significant ($p < 0.05$) differences between poor-rich/fresh and poor-medium/moist site units, and between medium-rich/fresh and medium-rich/moist site units (Table 4.19). The only significant differences were between the moist/rich and fresh-moist/poor site units. Nevertheless, it is clear at least, that maximum site index does not occur on moist/poor sites.

Krajina based his proposal on the fact that western hemlock takes up nitrogen in the form of ammonium, and that nursery experiments indicated growth actually decreased in the presence of nitrate (Krajina *et al.* 1973). In this study, site index, in fact, followed an ammonium gradient; therefore, the site index relationship is not in conflict with Krajina (1969) based on ammonium. Maximum site index was found to be in the rich SNR, and the SNR gradient followed, among other nitrogen measures, ammonium, as measured by the anaerobic incubation procedure. Research is still needed to determine the nitrification potential across the SNRs, to investigate differences in western hemlock productivity with different levels of nitrate. Confounding this relationship was the association of western hemlock roots with decaying wood. The roots were noted, even on the rich sites, to be growing in rotten logs or old root channels. The complexity of the relationship between western hemlock and decaying wood, stated in the literature review, makes it difficult to assess western hemlock productivity

relationships with SNRs.

4.6 Relationship Between Site Index and Direct Measures of Soil Nutrient Regimes

To investigate the relationship of site index with the soil chemical properties, the primary data set of 55 plots was used. The relationships of mineral soil total carbon, pyrophosphate extractable iron and aluminium with site index was analyzed separately.

Strong pairwise correlations were identified between several of the variables (Table 4.20). As suggested by Neter *et al.* (1990), two more indicators of predictor variable multicollinearities were calculated. Variance inflation factors were transformed into tolerance indices (Table 4.21). All variables exhibit low tolerance values with forest floor total nitrogen, total sulphur, and mineral soil total nitrogen and potassium having values close to 0, indicating the presence of multicollinearity. As a third indicator, PCA was used and the eigenvalues examined. From table 4.22, it can be seen that the eigenvalues are far from equal and exhibit a strong trend of the first axes accounting for much of the variance in the data. These results support the fact that multicollinearity does exist. From knowledge of nutrient chemical behaviour, it is suggested that at least some of the collinearities are population-inherent. For example, there is an indication that nitrogen and sulphur in soil organic matter are mineralized at proportional rates (Bardsley and Lancaster 1960), and pH is known to effect several soil chemicals (Binkley and Richter 1987; Runge and Rode 1991).

Because of multicollinearity, independent variables alone in a regression equation may not improve the fit significantly, but they may when in combination with one or more additional variables. Since forward

Table 4.20. Pearson Correlation matrix of soil chemical properties showing the presence of several large bivariate correlations.

n=55										
	SI	Forest Floor PH	LOGTN	LOGMN	CN	TP	TS	CA	MG	K
SI	1.000									
FFPH	-0.224	1.000								
LOGFFTN	0.445	-0.270	1.000							
LOGFFMN	0.457	-0.056	0.735	1.000						
FFCN	-0.509	0.042	-0.791	-0.651	1.000					
FFTP	0.058	0.370	0.310	0.262	-0.426	1.000				
FFTS	0.403	-0.416	0.937	0.685	-0.649	0.161	1.000			
FFCA	0.008	0.552	-0.275	0.033	0.006	0.127	-0.346	1.000		
FFMG	-0.047	-0.081	0.104	0.020	0.141	-0.298	0.138	0.020	1.000	
FFK	-0.627	0.379	-0.481	-0.381	0.592	0.146	-0.498	0.090	0.058	1.000
MSPH	0.561	0.111	0.190	0.266	-0.423	0.281	0.152	0.240	-0.306	-0.432
LOGMSTC	0.231	-0.182	0.507	0.368	-0.274	0.096	0.493	-0.159	0.368	-0.318
LOGMSTN	0.458	-0.163	0.665	0.555	-0.542	0.155	0.600	-0.134	0.277	-0.524
LOGMSMN	0.426	-0.181	0.599	0.556	-0.451	0.006	0.552	-0.131	0.283	-0.541
MSCN	-0.648	0.037	-0.595	-0.614	0.736	-0.166	-0.469	0.019	0.066	0.619
MSP	-0.263	0.136	-0.415	-0.416	0.390	-0.014	-0.353	0.049	-0.246	0.332
MSS	-0.288	0.308	-0.285	-0.218	0.339	0.128	-0.236	0.275	-0.129	0.473
MSCA	-0.044	0.128	-0.180	-0.123	0.102	-0.332	-0.227	0.186	0.109	-0.079
MSMG	-0.046	0.033	0.093	0.075	-0.013	-0.170	0.039	-0.053	0.422	-0.054
LOGMSK	-0.511	0.086	-0.141	-0.203	0.298	0.029	-0.167	-0.072	0.313	0.434
	Mineral Soil MSPH	LOGTN	LOGMN	MSCN	MSP	MSS	MSCA	MSMG	LOGK	
MSPH	1.000									
LOGMSTN	0.014	1.000								
LOGMSMN	-0.102	0.878	1.000							
MSCN	-0.475	-0.592	-0.534	1.000						
MSP	-0.078	-0.359	-0.472	0.407	1.000					
MSS	-0.001	-0.395	-0.417	0.378	0.494	1.000				
MSCA	-0.308	0.122	0.226	0.059	0.177	-0.117	1.000			
MSMG	-0.423	0.390	0.430	-0.067	-0.081	-0.291	0.685	1.000		
LOGMSK	-0.764	0.246	0.220	0.458	0.061	0.086	0.294	0.464	1.000	

Table 4.21. Tolerance values for soil chemical properties, the low values indicating the presence of multicollinearity.

Forest Floor		Mineral Soil	
pH	0.353	pH	0.183
LOG(Total N)	0.040	LOG(Total N)	0.064
LOG(Min N)	0.293	LOG(Min N)	0.132
C:N	0.108	C:N	0.111
Total P	0.299	Available P	0.411
Total S	0.055	Available S	0.415
Available Ca	0.414	Available Ca	0.253
Available Mg	0.432	Available Mg	0.263
Available K	0.154	LOG(Available K)	0.074

Table 4.22. Eigenvalues and cumulative variation explained by soil chemical PCA axes

PCA Axis	Eigenvalue	Proportion	Cumulative
Axis1	6.11802	0.339890	0.33989
Axis2	3.34015	0.185564	0.52545
Axis3	1.98247	0.110137	0.62658
Axis4	1.67675	0.093153	0.72874
Axis5	1.09820	0.061011	0.78976
Axis6	0.87501	0.048612	0.83837
Axis7	0.54991	0.030551	0.86892
Axis8	0.53800	0.029889	0.89881
Axis9	0.43665	0.024259	0.92306
Axis10	0.32939	0.018300	0.94136
Axis11	0.27665	0.015369	0.95673
Axis12	0.23536	0.013075	0.96981
Axis13	0.15669	0.008705	0.97851
Axis14	0.14242	0.007912	0.98643
Axis15	0.12653	0.007029	0.99346
Axis16	0.06799	0.003777	0.99723
Axis17	0.02547	0.001415	0.99865
Axis18	0.02434	0.001352	1.00000

and backward stepwise procedures only consider the addition or deletion of variables by their individual effect, all combinations or setwise regression was used as suggested by Tabachnick and Fidell (1987) for multicollinear data. The top ten equations were inspected, but residual analysis indicated some nonlinearity and an outlier having large leverage. For the former problem, forest floor and mineral soil total nitrogen and mineralizable nitrogen, and mineral soil potassium were transformed into common logarithms. For the latter problem, the outlier was noted as being the one plot from a very rich and wet site. Thus, the nutrient levels were very high, but the site index relatively low. If there had been many plots in the wet SMR, dummy variables might have been used to separate the effects of a wet site. However, since this was the only plot in this SNR and SMR, it was deleted from further analysis. All combinations multiple regression was repeated after the transformations and deletion of the outlier, on a total of 54 plots.

The ten equations having the highest adjusted R^2 are listed in Table 4.23. Adjusted R^2 ranged from 0.56 to 0.69 and the SEE ranged from 5.4m to 6.5m. Although the maximum number of independent variables was three, there were eight different variables involved in different combinations forming the ten possible relationships. The effects of multicollinearity were evident, but generally pH, nitrogen and potassium reoccurred consistently in the equations. Site index leveled off with increasing nitrogen and decreasing potassium, as indicated by the log transformations.

The "best" fit equation, based on adjusted R^2 , and SEE was equation 1. However, this equation was rejected as exhibiting the most "ecological sense" since the effects of multicollinearity appeared to dominate the sulphur variable. The tolerance value of the sulphur variable was 0.52,

Table 4.23: Results of all combinations multiple regression on the primary data set.

Regression equation	R ²	Adj R ²	SEE(m)	Regression Coefficients of: Mineral soil chemical measures					Forest floor chemical measures		
				pH	log N	log minN	C:N	log K	pH	K	S
(1)	.70	.69	5.4		26.87			-26.22			-63.59
(2)	.68	.67	5.6		22.03			-23.67			
(3)	.66	.64	5.8	7.82		16.03		-11.25			
(4)	.65	.63	5.9	8.58	12.38					-0.01	
(5)	.63	.61	6.0	12.41		15.09					
(6)	.62	.60	6.2	4.90			-0.34			-0.01	
(7)	.60	.59	6.2			16.54		-22.63			
(8)	.60	.59	6.3	11.10	17.19						
(9)	.59	.56	6.5	7.0			-0.49		-7.51		
(10)	.57	.56	6.5				-0.42			-0.02	

indicating collinearity with the nitrogen variable which had a similar tolerance value. The standard error associated with the sulphur regression coefficient was 31.3, almost 50% of the value of its coefficient. The negative coefficient was opposite to that of simple correlation with site index, indicating that it is dependent on the other variables included or excluded from the equation (Neter *et al.* 1990). Thus, the "best" fit equation, based on adjusted R², SEE, and independent variables that made ecological sense, was:

$$SI = 76.7 + 22.0 [\text{Log}(\text{MSTN})] - 23.7 [\text{Log}(\text{MSK})]$$

Adjusted R² = 0.67

F-ratio = 54.21

SEE = 5.6 m N = 54

Variables representing:

Log(MSTN) = common logarithm of mineral soil total nitrogen; Log(MSK) = common logarithm of mineral soil available potassium.

The tolerance value of the two variables was 0.95, indicating that the two variables were nearly completely independent of each other. A three dimensional plot and contour plot of the logarithmic relations are given in Figure 4.16.

To test the portability of this equation, it was applied to the validation data set of 41 plots, which were sampled from the same biogeoclimatic variant. In both sets the same laboratory was used for soil chemical analyses. Comparison of the original and test data sets is given in Table 4.24. The site index range of the test data set indicated that this set only tested the upper portion of the equation. The results of the model test are summarized in Table 4.25.

The performance on the original data was not very good, with only 46% of the cases classified within 3 meters of the measured site index.

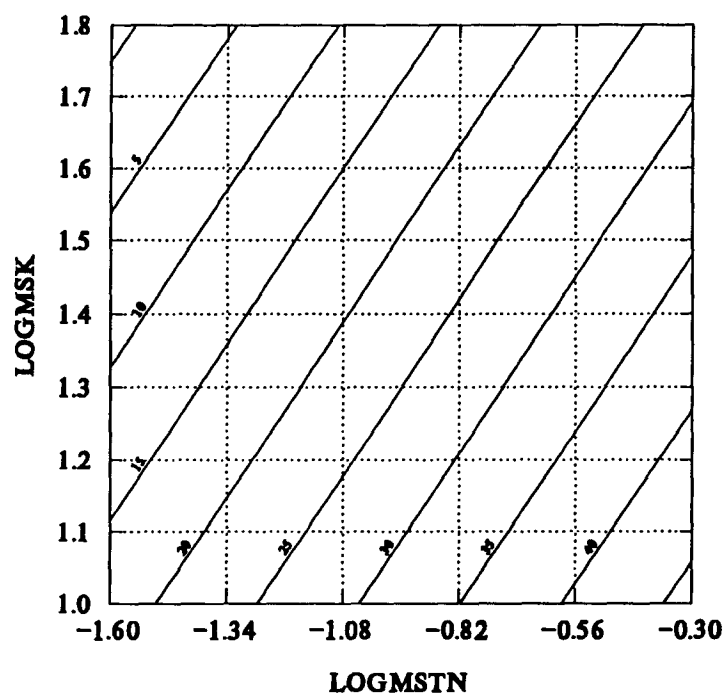
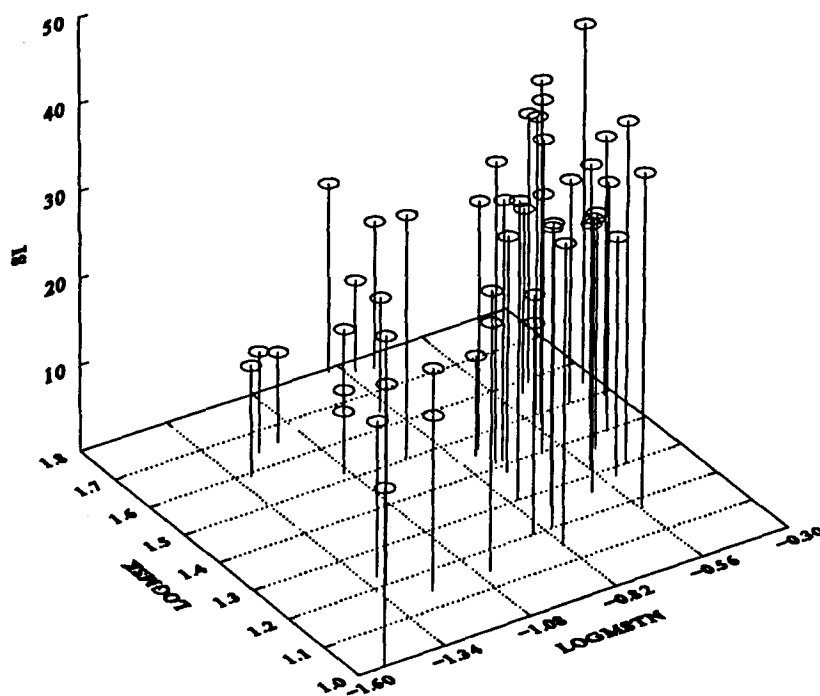


Figure 4.16. Three dimensional plot and contour plot of the logarithmic relations of mineral soil total nitrogen and available potassium with site index.

Table 4.24. Comparison of the mineral soil chemical measures used in the regression equation between the original data and test data sets.

	original data set (54 plots)			test data set (41 plots)		
	mean	SD	range	mean	SD	range
total nitrogen(%)	0.19	0.12	0.03-0.47	0.21	0.08	0.08-0.42
available potassium (ppm)	34	26	6-145	18	5	10-28
SI(ht @ 50 yrs bh age)	24.6	9.6	1.7-41.5	33.4	3.4	24.7-39.8

Table 4.25. Classification test of site index on the original and test data based on the soil chemical measures logarithm of mineral soil total nitrogen and available potassium.

	Number of cases classified (cumulative proportion in parentheses).	
	original data	test data
Correct ¹	25 (46)	27 (66)
1 class off	15 (74)	9 (88)
2 classes off	11 (94)	4 (98)
3 classes off	2 (98)	1 (100)
4 classes off	1 (100)	
TOTAL	54	41
% above correct	15 (28)	4 (10)
% below correct	14 (26)	10 (24)

¹ Correct within 3 m of measured site index; 1 class off within 3-6 m; 2 classes off within 6-9 m; 3 classes off within 9-12 m; 4 classes off within 12-15 m.

Twenty-six per cent of the cases were greater than 6 meters off. The performance of the equation on the test data, based on correct classification, was better, with 66% of the cases classified within 3 meters of the measured site index and 12% greater than 6 meters off. However, the equation underestimated site index on the test data by more than double the amount it did with the original data. The equation exhibits only a fair performance in predicting site index on the data from which it was derived. It appears to have some portability within the upper ranges of site index, but tends to underestimate site index.

The negative relationship of site index with mineral soil available

potassium was somewhat surprising since the parent material of the original plots was dominated by rocks of volcanic origin. Basalts generally contain plagioclase feldspars, whose chemical composition includes mainly sodium and calcium, as opposed to potassium, which is associated with the alkali feldspars of granite (Dietrich and Skinner 1979; Mengel 1985). Additionally, organic matter appears to exhibit a preference for divalent cations, such as Ca^{2+} and Mg^{2+} , over K^{+} (Naylor and Overstreet 1969; Jardine and Sparks 1984).

There are two possible reasons for this relationship. Mycorrhizae appear to enhance K^{+} uptake and storage in roots by increasing the vacuolar pool sizes, with this effect particularly evident for western hemlock seedlings (Ryglewicz and Bledsoe 1984). Potassium in the root vacuoles are not subject to leaching. When sieving forest floor samples, fine roots inevitably form part of the sample, and this may increase the concentration of K^{+} in the sample being analyzed. Additionally, the inverse correlation of potassium concentration with site index indicates that this element is not limiting tree growth. This inverse relationship may be explained by a dilution effect; the increase in supply of other nutrient elements on the better site (higher site index) is proportionately greater than the presumed increase in supply of potassium. The absolute quantities of potassium supplied annually on the sites with higher site index may well be higher than on the sites having lower site index, but these values can be determined only by the measurement on a mass per area basis.

In order to supplement the interpretations, PCA regression was used to overcome the problem of multicollinearity in the regression analysis. The PCA was carried out on the variables of the original data set used in the previous regression analysis. Transformed variables were maintained and

the outlier noted eliminated. Every axis that accounted for at least 1% of the variation was used in a backward stepwise regression procedure. Thus, the first 13 axes accounting for 96.3% of the variation were used with the following result:

$$SI = 24.5 + 2.65(\text{AXIS1}) - 1.31(\text{AXIS2}) - 2.33(\text{AXIS4}) + 3.07(\text{AXIS8})$$

$$\text{Adjusted } R^2 = 0.63 \quad F\text{-ratio} = 23.92 \quad \text{SEE} = 5.89 \quad n = 54$$

Examination of the residuals indicated that there was relatively homogeneous variance, and that a linear model was appropriate. A normal probability plot indicated that the residual distribution was close to normal.

Axis 1 was highly positively correlated ($r > 0.7$) with forest floor total nitrogen, mineralizable nitrogen, total sulphur and mineral soil total nitrogen, mineralizable nitrogen, and highly negatively correlated with forest floor C:N ratio and potassium (Table 4.26). Axis 1 was also moderately negatively correlated ($r > 0.5, r < 0.7$) with mineral soil available sulphur, available phosphorus and carbon to nitrogen ratio. Axis 2 was highly positively correlated with mineral soil magnesium and potassium, and highly negatively correlated with mineral soil pH. It was also moderately positively correlated with forest floor magnesium, and mineral soil available calcium. Axis 4 was moderately positively correlated with forest floor total phosphorus, and moderately negatively correlated with mineral soil available calcium. Finally, axis 8 showed a weak (< 0.5) negative correlation with the logarithm of forest floor mineralizable nitrogen and a weak positive correlation with the logarithm of forest floor total nitrogen. Axis 1 accounted for the majority of the variance (47%), with axes 2, 4 and 8 accounting for considerably less (9%, 4%, and 4% respectively). This indicates that the variables most associated with axis 1 have the strongest

Table 4.26. Correlation of PCA Scores with actual chemical values for the original data set.

Chemical	Loadings Axis 1	Axis 2	Axis 4	Axis 8
Forest Floor				
pH	-0.338	-0.190	-0.047	-0.105
Log (total nitrogen)	0.889	-0.030	0.334	-0.149
Log (mineralizable nitrogen)	0.774	-0.115	0.153	-0.330
C:N	-0.823	0.276	-0.022	0.072
total phosphorus (%)	0.174	-0.415	0.518	0.213
total sulphur (%)	0.831	-0.008	0.346	-0.165
available calcium (ppm)	-0.204	-0.210	-0.336	0.039
available magnesium (ppm)	0.126	0.602	0.057	0.076
available potassium (ppm)	-0.727	0.093	0.484	-0.196
Mineral Soil				
pH	0.317	-0.773	-0.317	0.177
Log (total nitrogen)	0.792	0.382	0.084	0.339
Log (mineralizable nitrogen)	0.758	0.471	-0.021	0.183
C:N	-0.795	0.228	0.266	-0.033
available phosphorus (ppm)	-0.569	-0.100	0.023	0.126
available sulphur (ppm)	-0.514	-0.266	0.333	-0.011
available calcium (ppm)	-0.084	0.588	-0.531	-0.163
available magnesium (ppm)	0.166	0.783	-0.202	-0.140
Log (Avail potassium)	-0.267	0.753	0.433	0.170

relationship with site index, while variables correlated to the remaining three axes have supplementary relationships. Thus, nitrogen, forest floor total sulphur and potassium were most strongly correlated with site index.

The PCA regression showed the multicollinear nature of this data set, with several soil chemical measures correlated with the axes in the resulting regression equation. This result provides evidence that the productivity of western hemlock is associated with a well balanced supply of nutrients. Further to the idea of a well balanced supply of nutrients, inspection of the forest floor carbon-nitrogen-sulphur-phosphorus ratios for different site index classes (Table 4.27) showed that nitrogen, sulphur and phosphorus are generally of the same ratio across site index classes. This ratio is also

Table 4.27. The total carbon-total nitrogen-total sulphur-total phosphorus ratio of the forest floor for different site index classes.

Site index (m @50 yrs) class	C:N:S:P
0-10	476 : 10 : 1.2 : 1.6
10-20	452 : 10 : 1.1 : 2.0
20-25	422 : 10 : 1.2 : 1.6
25-30	327 : 10 : 1.2 : 1.3
30-35	394 : 10 : 1.2 : 1.7
35-41	318 : 10 : 1.1 : 1.5
International average	140 : 10 : 1.3 : 1.3

similar to that reported for soil organic matter for an international average (Stevenson 1986). However, it should be emphasized that all direct nutrient relationships developed in this study are correlations, and may either be a cause or an effect, or even both.

Since the roots of western hemlock were noted to occur mainly in the forest floor, setwise regression was performed on the forest floor chemical measures only. The best fit regression was:

$$SI = 42.8 + 3.4 [\text{Log}(\text{FFMN})] - 0.21(\text{FFK})$$

$$\text{Adjusted } R^2 = 0.50$$

$$F\text{-ratio} = 27.14$$

$$SEE = 6.9 \text{ m}$$

$$n = 54$$

Variables representing:

Log(FFMN) = common logarithm of forest floor min-N; FFK = forest floor available potassium.

Once again nitrogen and potassium were involved in the final regression equation. In terms of adjusted R^2 and SEE, this regression was not as good as the best fit regression derived from both the mineral soil and forest floor chemical properties. However, in terms of knowledge of western hemlock rooting patterns, this equation seemed to have met biological expectation.

Pyrophosphate extractable iron and aluminium and total carbon of the mineral soil were also used in a backward stepwise regression with the following result:

$$SI = 28.4 + 18.6 [\text{Log(MSAI)}]$$

$$\text{Adjusted } R^2 = 0.45$$

$$F\text{-ratio} = 44.6$$

$$SEE = 7.2 \text{ m}$$

$$n = 54$$

Variables representing:

Log(MSAI) = common logarithm of pyrophosphate extractable aluminium.

Examination of the residuals indicated that there was relatively homogeneous variance, and that a linear model was appropriate. A normal probability plot indicated that the residual distribution was close to normal.

The correlation of site index with mineral soil pyrophosphate extractable aluminum is opposite in sign to that of Lowe and Klinka (1981). However, their correlation was with the soil chemical measure in the Bf horizon only. In this study, the sampling of the leached soil layer in the extreme organic matter over rock sites makes a direct comparison invalid.

The sites sampled in this study largely represented western hemlock ecosystems without a water deficit or water excess. Thus, the conceptual model of Kimmins *et al.* (1990), which is a presentation of the variation in the importance of moisture, nutrients, light, and soil aeration in determining net primary production under various combinations of site nutrient and moisture status, suggests that nutrients are the most limiting factor within most of the range sampled. This range effectively eliminates low site indexes that may occur in dry or wet nutrient rich sites. Dry and wet sites occurred mainly in the very poor and poor SNRs where the site index was low already. The one wet, very rich site was eliminated as an

outlier but this condition should be kept in mind -- i.e. that as the sites become wet, site index falls regardless of an increase in SNR, due to poor aeration.

The lack of sites with water deficits is due to the fact that western hemlock does not exhibit two mechanisms that contribute to drought tolerance -- stress avoidance mechanisms and stress tolerance mechanisms. Ballard and Dosskey (1984) found that water uptake by western hemlock from moderately dry soils is limited by higher needle water potential and higher uptake resistance compared to Douglas-fir. Western hemlock seedlings planted on a south-facing, high elevation clear-cut exhibited a failure to cope with drought because of lack of stress tolerance through osmotic adjustment to enable the seedlings to maintain turgor during dry periods (Livingston and Black 1987a,b).

Similarly, western hemlock is more adaptable to wet sites where water tables are more than fifteen centimeters below the surface (Minore and Smith 1971). Flooding during the growing season has a marked negative effect on survival and growth (Brink 1954; Minore 1968)

In the literature, site index regression relationships developed for western hemlock showed several possible soil chemical properties being correlated with site index (Table 4.28). The multicollinear nature of the soil chemical measures creating unstable regression equations is one possibility for explaining the different results. However, it is probable that over the large area in which western hemlock is found, which includes Oregon, Washington, Alaska and British Columbia, there are differences in growth limiting factors for western hemlock.

Table 4.28: Summary of site index regression relationships for western hemlock derived from the literature.

[1] $SI = f(-\text{exchangeable K})$

$R^2 = 0.58$ $N = 82$

Wooldridge (1961)

[2] $SI = f[+P \text{ (kg/ha)}, -\text{total N (kg/ha)}, +\text{sum of bases (kg/ha)}]$

$R^2 = 0.78$ $N = 14$ $SEE = 15.6 \text{ ft}$

Meurisse (1972, 1976).

[3] $SI = f(\text{total-N in the organic matter})$

$R^2 = 0.69$ $N = 25$

Stephens *et al* (1969) - (cited in Heilman 1976)

[4] $\text{Growth Class} = f(-\text{pyrophosphate extractable Fe} + \text{Al})$

$R^2 = 0.58$ $N = 26$

Lowe and Klinka (1981)

4.7 Site Index Relationships Discussion

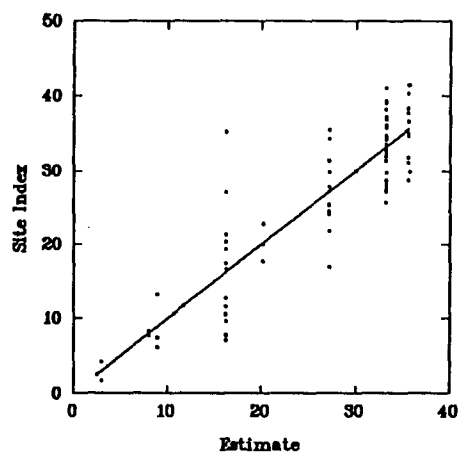
All regressions reported in this study were significant ($p < 0.05$) and, in most cases, had acceptable proportions of the variation in site index explained by the respective independent variables. The amount of variance explained was generally within the average range (65-85%) explained in successful soil-site models (Carmean 1975). For western hemlock specifically, Radwan and DeBell (1980a) felt that foliar chemical variables with correlation coefficients in the order of 0.85 (r^2 of 0.72) may be useful as

indicators to assess site index. Therefore, all regression models seemed to have successfully captured the pattern of mean site index response over the variables used.

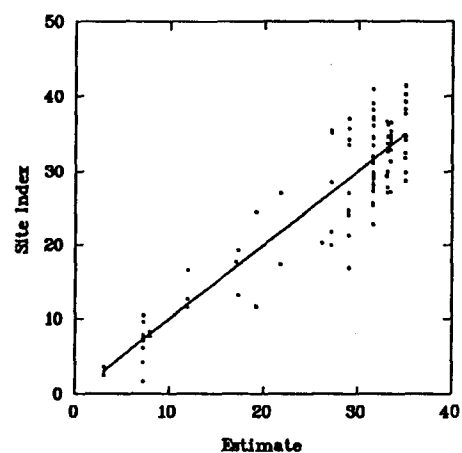
However, the relatively large standard error of estimates (SEE) indicated that there was still high variation in western hemlock site index for all regression models developed. Plots of the actual site index versus the estimated site index for some of the regression models (Figure 4.17) showed this variation. The effect of the large SEE was demonstrated on the equation that was tested against an independent data set. The equation failed to successfully predict the site index within three meters on 54% of the plots from the data set it was derived from.

This relatively large variation within similar sites (see Figures 4.12 and 4.13) and within similar nutrient levels (see Figure 4.16) is consistent with what is known about the nutrition of western hemlock (covered in the literature review). Soil-site studies involving western hemlock, reported site index to be correlated to several different soil physical and/or chemical measures. Moreover, fertilization studies, the most common criteria for defining nutritional status (Binkley 1986), are notorious for the inconsistency of the results, responses being positive, zero and negative.

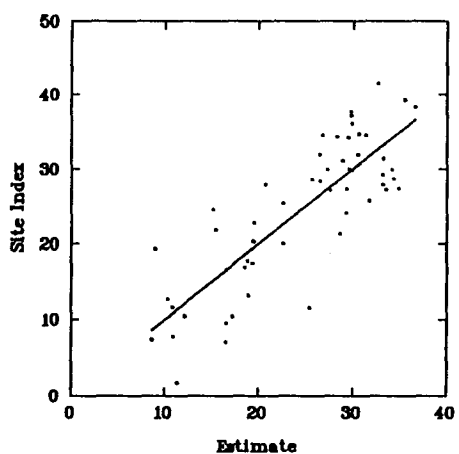
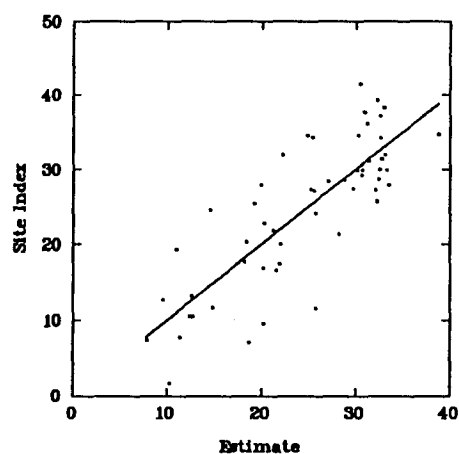
The causes for this variation about the regression model surfaces can be divided into two general categories -- (1) the nature of the data; and (2) the nature of western hemlock ecosystems. For the first category, it was noted during field collection that there was high variation in microsites, caused mainly by decaying wood. The presence of large amounts of decaying wood, even on sites designated as rich, is a confounding factor. For example, on a rich site with decaying wood present, the question arises whether the tree is growing on the rich site, or simply on rotten wood



[1] Plant Associations



[2] SMRs/SNRs

[3] $\log(\text{total N}) + \log(\text{available K})$ 

[4] Soil Chemical PCA Scores

Figure 4.17. Actual site indexes plotted against estimated site indexes for chosen regression models developed for western hemlock.

microsites?

The nature of western hemlock ecosystems was noted in the literature review, as being a complicated system of feedback, symbiosis and specialization. The rooting habit of western hemlock roots was reported to be primarily associated with decaying wood and mor humus forms (Figure 4.18). Even within the mineral soil profile, it was noticed that there was a proliferation of roots along root channels and buried wood. If roots are exploiting the area of maximum nutritional return, then mor humus forms and rotten wood seem to be most important for the nutrition of western hemlock. Associated with this organic matter are strong mycorrhizal relationships which, among other benefits, may enhance uptake of both nitrogen, especially in the form of ammonium, and phosphorus. There also exists evidence that mycorrhizae of some oxylophytic species have the ability to take up amino acids directly. Western hemlock is able to withstand relatively acid conditions which seems to be a condition favouring its mycorrhizal associates. Then, there is the suggestion that there are symbiotic nitrogen fixers associated with decaying wood and fungi. Finally, Major (1951) stated that it is the "plexus" of environmental factors which determine both vegetation and soil in a concomitant manner. However, with western hemlock this may include the suggestion that the vegetation and soil also seem to co-determine each other. That is, although acid parent materials in the humid climate of the west coast seem beneficial to western hemlock, western hemlock also is reported as influencing the site to cause more acid conditions.

Thus the nature of the western hemlock ecosystem itself may prevent plants or plant associations, an inferred nutrient/moisture gradient, or soil chemical measures from more precisely predicting site index. Considering



Figure 4.18. Soil profile illustrating the thick mor humus forms and associated decaying wood. The roots were noted to be predominantly in the organic layer.

the nature of western hemlock ecosystems, capturing the pattern of mean site index response, even though not as precise as what has been achieved for species such as Douglas-fir (see literature review), was considered a successful description of western hemlock productivity.

SUMMARY AND CONCLUSIONS

(1) Despite the lack of understory plants in second growth western hemlock ecosystems, the following relationships were found.

Based on the frequency of nitrogen indicator species groups, the four main plant associations, derived from the traditional Braun-Blanquet method, captured an inferred nitrogen gradient, from the nitrogen poor (based on the dominance of oxylophytic species) *Gaultheria* plant association to the nitrogen rich (based on the dominance of nitrophytic species) *Rubus* plant association.

An underlying nutrient gradient was supported through the use of canonical discriminant analysis on the PCA scores of the soil chemical measures on a concentration basis. A definite, but overlapping, trend was noted. There was generally an increase in both mineral soil and forest floor total and mineralizable nitrogen, a decrease in forest floor available potassium and a decrease in the carbon-nitrogen ratio in proceeding from the *Gaultheria* (oxylophytic) association to the *Rubus* (nitrophytic) association. Other supplementary soil chemical measure correlations with this nutrient gradient were also noted.

Analysis of the relationship between six predominant species, which distinguished the four major plant associations, with the forest floor chemical measures (on a concentration basis) was done using canonical correlation analysis. Four forest floor chemical canonical variates explained 37% of the variance of the species domain. Generally, species considered oxylophytic (Klinka *et al.* 1990) varied negatively with total and mineralizable nitrogen, and positively with available potassium and magnesium. The relationships with nitrophytic species were reversed.

Both the plant associations and the six diagnostic species were linked to an underlying nutrient gradient, despite the lack of understory plants. The nutrient gradient was generally correlated positively with nitrogen and negatively with potassium. Potassium was thought to be simply a result of a dilution effect on the nitrogen poorer sites rather than of a toxic nutrient status. Plant associations in the major variant sampled (CWHvm1), derived through the Braun-Blanquet method, may have use for management purposes to supplement the delineation and designation of an area to its soil nutrient status. However, the variation and overlapping of forest floor chemical CDA scores between plant associations, emphasizes the need for further study, especially using western hemlock ecosystems having a better expression of understory species. Five of the six individual species examined showed relationships with forest floor chemical measures which support their nutrient indicator values reported in Klinka *et al.* (1990).

(2a) The heuristic method of the BEC system, in conjunction with understory plants, was used to identify field estimated SNRs. A PCA ordination was carried out on both the forest floor and mineral soil chemical measures, expressed on a concentration basis. A plot of PCA axes 1 and 2, accounting for 32% and 18% of the variance respectively, captured a definite gradation, primarily with the first axis, of increasing scores as SNRs proceeded from very poor to rich. The very poor and rich SNRs showed a distinct separation but the poor and medium overlapped substantially. PCA axis 1 was highly positively correlated with forest floor and mineral soil total and mineralizable nitrogen, and total sulphur. Highly negative correlations were found with forest floor and mineral soil carbon-nitrogen ratios, and forest floor available potassium. Since this axis was most strongly

correlated with the nitrogen chemical measures (the four nitrogen measures and the two carbon-nitrogen ratios), these six soil chemical measures were used in a canonical discriminant analysis to further explore the relationship of nitrogen with SNRs. Plots of the first two canonical variates showed somewhat more distinct groupings than with PCA, but there still was substantial overlap between the poor and medium SNRs.

As a validation procedure to investigate how well the nitrogen measures are related to SNRs, discriminant analysis was conducted to test the ability of the six soil nitrogen chemical measures to differentiate among the four SNRs. To achieve a multivariate normal distribution, five of the six variables were transformed using common logarithms. Discriminant analysis correctly classified 91% of the plots into their source groups. However, this high success rate was not repeatable; on a validation data set, the discriminant function correctly classified only 54% of the plots. The discriminant function then, captured the within site variability of the original data set, but failed to capture between site variability with an independent test data set.

The results of this study provide evidence that supports the existence of a relationship between nitrogen measures, expressed on a concentration basis, and field derived SNRs. However, unlike the study by Kabzems and Klinka (1987), significant differences between SNRs, using either mineralizable or total nitrogen alone, could not be demonstrated. For further actual statistical testing, as opposed to pattern analysis, it is suggested that a technique, such as *in situ* incubation to determine mineralizable nitrogen, be chosen to distinguish or revise site units, or to revise the heuristic field identification procedure.

The success of the discriminant function in classifying the original

data into their source groups, and the lack of success in classifying an independent test data set, suggests that the relationship developed on the original data set was relative only. Consequently, there is a need for further study on a wider geographic area to assess whether a more general function can be derived, or whether a different function is required for smaller regions.

(2b) The Energy-Soil Limited water balance model was used to correlate the ratio of AET/PET with field derived SMRs. However, even the driest site, consisting of 1 cm of sand over bedrock, failed to show a moisture deficit. Even taking into account the fact that model validation and calibration for this variant and for western hemlock has yet to be done, this result was still considered unreasonable. It was suggested that in future runs of the ESL water balance model for the CWHvm1 variant, the following time periods should be used: (i) a shorter time period of weeks or days, to see if water deficits occur only through part of the month; and (ii) yearly measurements over the 30-year period from which climatic normals were derived. AET/PET could then be averaged, thus eliminating the over influence of years of very high growing season rainfall.

Model calibration and validation for this variant and for western hemlock needs to be carried out.

(3) A summary of the regression equations developed in this study is given in Table 5.1. All models developed demonstrated an increase in site index to a certain point and then levelling off relative to the respective independent variables. The SEEs of over 5 meters in all but model [4], showed that there was a relatively large variation around the regression response surface.

Table 5.1: Summary of relationships between site index and indirect and direct measures of ecological site quality. All variables are significant at $p < 0.05$.

Indirect Vegetation Measures of Ecological Site Quality

Categorical

$$[1] \text{ SI} = 2.5 + 0.45(\text{PA2}) + 1.1(\text{PA3}) + 5.5(\text{PA4}) + 6.4(\text{PA5}) + 8.1(\text{PA6}) + 9.2(\text{PA7}) + 13.7(\text{PA8}) + 17.6(\text{PA9}) + 24.7(\text{PA10}) + 27.5(\text{PA11}) + 30.7(\text{PA12}) + 33.1(\text{PA13}) + 33.2(\text{PA14})$$

$$\text{Adjusted } R^2 = 0.78 \quad \text{F-ratio} = 22.86 \quad \text{SEE} = 5.3 \text{ m} \quad n = 82$$

Dummy variables representing various plant associations:

Constant=*Ledum*; PA2=*Rhacomitrium*; PA3=*Sphagnum*; PA4=*Pinus(contorta)*;
 PA5=*Vaccinium(ovatum)*; PA6=*Veratrum*; PA7=*Chamaecyparis*; PA8=*Gaultheria*;
 PA9=*Mahonia*; PA10=*Gaultheria-Polystichum*; PA11=*Achlys*; PA12=*Polystichum*;
 PA13=*Rubus*; PA14=*Sambucus*.

Analytical

$$[2] \text{ SI} = 25.5 - 4.3(\text{PCA1}) + 0.8(\text{PCA2}) - 1.2(\text{PCA7}) - 1.4(\text{PCA9}) + 1.0(\text{PCA13})$$

$$\text{Adjusted } R^2 = 0.78 \quad \text{F-ratio} = 58.05 \quad \text{SEE} = 5.1 \text{ m} \quad n = 82$$

Variables representing vegetation PCA axis scores.

$$[3] \text{ SI} = -12.1 - 545.4(\text{MOIST2}) + 33.2(\text{MOIST3}) + 37.1(\text{MOIST4}) + 16.6(\text{MOIST5}) + 13.0(\text{MOIST6}) + 19.5(\text{NITR2}) + 19.2(\text{NITR3})$$

$$\text{Adjusted } R^2 = 0.35 \quad \text{F-ratio} = 7.19 \quad \text{SEE} = 8.8 \text{ m} \quad n = 82$$

constant = excessively dry to very dry and N-poor; MOIST2 = very dry to moderately dry;
 MOIST3 = moderately dry to fresh; MOIST4 = fresh to very moist; MOIST5 = very
 moist to wet; MOIST6 = wet to very wet; NITR2 = N-medium; NITR3 = N-rich.

Table 5.1: (continued)

Indirect Environmental Measures of Ecological Site Quality

Categorical

$$[4] \text{ SI} = 5.7 + 4.2(\text{MD}) + 8.9(\text{SD}) + 14.3(\text{F}) + 16.2(\text{MST}) + 15.7(\text{VM}) + 4.9(\text{W}) - 2.6(\text{VP}) + 7.2(\text{P}) + 11.7(\text{MED}) + 13.2(\text{R})$$

$$\text{Adjusted } R^2 = 0.81 \quad \text{F-ratio} = 43.7 \quad \text{SEE} = 4.5 \text{ m} \quad n = 102$$

Dummy variables representing SMRs and SNRs:

Constant=very wet or very rich; MD=moderately dry; SD= slightly dry; F=fresh; MST=moist; VM=very moist; W=wet; VP=very poor; P=poor; Med=medium; R=rich.

$$[5] \text{ SI} = 3.0 + 5.2(\text{MD}) + 14.6(\text{SD}) + 27.7(\text{F}) + 28.0(\text{MST}) + 30.0(\text{VM}) + 5.8(\text{W})$$

$$\text{Adjusted } R^2 = 0.69 \quad \text{F-ratio} = 38.0.4 \quad \text{SEE} = 5.8 \text{ m} \quad N = 102$$

Dummy variables representing SMRs:

Constant=very wet; MD=moderately dry; SD= slightly dry; F=fresh; MST=moist; VM=very moist; W=wet.

$$[6] \text{ SI} = 10.6 - 0.77(\text{VP}) + 16.3(\text{P}) + 21.3(\text{MED}) + 23.7(\text{R})$$

$$\text{Adjusted } R^2 = 0.75 \quad \text{F-ratio} = 77.3 \quad \text{SEE} = 5.2 \text{ m} \quad n = 102$$

Dummy variables representing and SNRs:

Constant=very rich; VP = very poor; p = poor; MED = medium; R = rich.

$$[7] \text{ SI} = 3.0 + 5.2(\text{SS1}) + 14.6(\text{SS2}) + 27.5(\text{SS4}) + 28.9(\text{SS5}) + 26.9(\text{SS6}) + 32.7(\text{SS7}) + 4.9(\text{SS8}) + 7.5(\text{SS9})$$

$$\text{Adjusted } R^2 = 0.71 \quad \text{F-ratio} = 31.92 \quad \text{SEE} = 5.6 \text{ m} \quad n = 102$$

Dummy variables representing Site Series in the CWHvm1 variant:

Constant= very wet/very poor; SS1 = HwPI-Cladina; SS2 = HwCw-Salal; SS4 = HwBa-Blueberry; SS5 = BaCw-Foamflower; SS6 = HwBa-Deer Fern; SS7 = BaCw-Salmonberry; SS8 = PI-Sphagnum; SS9 = CwSs-Skunk cabbage.

Table 5.1: (continued)

Direct Measures of Ecological Site Quality

Analytical

$$[8] \text{ SI} = 76.7 + 22.0[\log(\text{total N})] - 23.7[\log(\text{available K})]$$

Adjusted $R^2 = 0.67$ F-ratio = 54.21 SEE = 5.6 m n = 54

Variables representing soil chemicals:

$\log(\text{total N})$ = common log of mineral soil total nitrogen; $\log(\text{available K})$ = common log of mineral soil available potassium.

$$[9] \text{ SI} = 24.5 + 2.65(\text{AXIS1}) - 1.31(\text{AXIS2}) - 2.33(\text{AXIS4}) + 3.07(\text{AXIS8})$$

Adjusted $R^2 = 0.63$ F-ratio = 23.92 SEE = 5.9 m n=54

Variables representing PCA axis scores of forest floor and mineral soil chemicals.

$$[10] \text{ SI} = 42.8 + 3.4[\log(\text{mineralizable N})] - 0.21[\text{available K}]$$

Adjusted $R^2 = 0.50$ F-ratio = 27.14 SEE = 6.9 m n = 54

Variables representing soil chemicals:

$\log(\text{mineralizable N})$ = common log of forest floor mineralizable nitrogen; available K = forest floor available potassium.

$$[11] \text{ SI} = 28.4 + 18.6[\log(\text{MSAI})]$$

Adjusted $R^2 = 0.45$ F-ratio = 44.6 SEE = 7.2 m n = 54

Variables representing soil chemicals:

$\log(\text{MSAI})$ = common log of mineral soil pyrophosphate extractable aluminium.

In terms of adjusted R^2 and SEE, model [4] had the best fit, suggesting that the use of this model, which combines SNR and SMR, may produce the best prediction equation. This model suggests that the greatest productivity of western hemlock is associated with moist/rich sites. The difference in mean site index between fresh and moist rich sites compared to fresh and moist medium sites is not significant. The order of the difference is less than 3 meters, which is probably considered in the same site index class.

Significant relationships with site index were developed for plant associations and for individual species expressed in linear combinations through PCA. However, due to the lack of understory plants, these relationships may have questionable practical value. The use of plant associations with strong expressions of understory plants has a potential of being related to site index, considering these results with a poor expression of understory plants.

Of the direct analytical models, model [8] has the best fit. However, this model failed to predict successfully the site index of the data set from which it was derived. Only 46% of the plots were correctly predicted within 3 meters. The negative relationship with mineral soil potassium was thought to be due to weathering of the parent material. The PCA regression of mineral soil measures demonstrated the highly collinear structure of the data. Based on the loadings, a high proportion of the soil chemical measures are all related to site index.

Graphically, a depiction of the two major results is given by plotting site index against the first PCA axis of the soil chemical measures with SNRs indicated by elliptical outlines (Figure 4.18). The site index relationships show a logarithmic or asymptotic pattern, levelling of

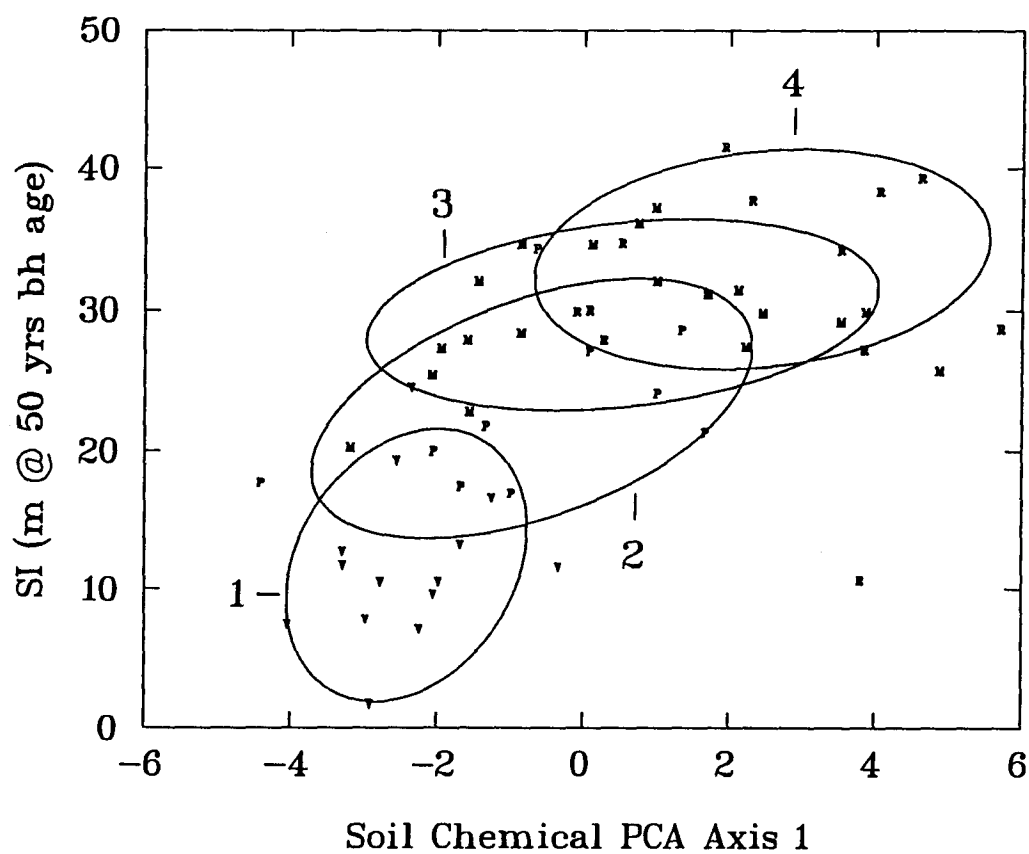


Figure 4.19. Plotted relationship of site index and soil chemical PCA axes 1 with 80% elliptical outlines indicating SNRs: 1 and V = very poor, 2 and P = poor, 3 and M = medium, 4 and R = rich.

somewhere around poor-medium sites or the soil chemical measure equivalent. The high variation associated with site index for all soil chemical levels or SNRs is shown by the relatively large width of the elliptical outlines. This relatively large variation within similar sites and within similar nutrient levels is consistent with what is known about the nutrition of western hemlock.

The relatively large variation in site index about the response surfaces may be due to a combination of the nature of the data and the nature of western hemlock ecosystems itself. The extreme heterogeneity of the site, especially with rotten logs, confounds the site factors used as independent variables. Finally, the interactions of western hemlock and its associates further complicate the system. Western hemlock seems to have a rooting preference for wood, which seems to be a preferred location for the associated mycorrhizae and some asymbiotic nitrogen fixers, since there is less competition. There is evidence that the mycorrhizae may provide the plant with increased ability to gain access to ammonium, phosphorus, and even amino acids containing nitrogen and phosphorus. Not only does western hemlock tolerate high acid conditions, but there is evidence that it also helps to maintain, or even, create it.

Thus, the nature of the western hemlock ecosystem itself may not allow plants, an inferred nutrient/moisture gradient, or soil chemical measures from more precisely predicting site index. Considering this nature, capturing the pattern of mean site index response, even though not as precisely as what has been achieved for species such as Douglas-fir, was considered to have successfully captured the character of western hemlock productivity.

(4) A final consideration to explain the large variation in site index associated with soil nutrients, is to question whether there is an adaptive advantage for western hemlock to increase height growth in response to increasing nutrient levels. For shade intolerant, early successional species a response in height growth would be an advantage. Since light becomes more limiting relative to an increase in nutrient levels, there is a selection pressure towards increased height growth in response to increased levels of nutrients (Tilman 1986). However, for a shade tolerant, climax species, such as western hemlock, this may not necessarily still hold. Instead, it may be expected that the selection advantage would be towards photosynthetic efficiency (as described by Kozlowski *et al.* 1991). Radwan and DeBell (1980) reported significant correlations ($p < 0.01$) between the site index of western hemlock with chlorophyll 'a' and total chlorophyll (extracted with 80% acetone) on a weight basis. The richer content of chlorophyll in chloroplasts of shade-adapted leaves may allow for more efficient light utilization (Boardman 1977). Thus increased nutrition may only be an advantage in its ability to enhance photosynthetic efficiency under shaded conditions. For shade tolerant species, further research is necessary to determine whether increasing nutrient levels effects both height growth and volume increment concomitantly, or predominantly just one of the two.

Additionally, since western hemlock is a climax species, there may also be an advantage to adapting to the nutritional soil characteristics of a mature ecosystem. Odum (1969) suggested that mature ecosystems have a greater capacity for nutrient retention, and that the selection pressure for species adapted to mature ecosystems would be towards this feedback control, as opposed to growth. Humification, a dominant process associated

with western hemlock (thus the development of thick mor humus forms), results in the removal of relatively simple organic compounds from the easily metabolized soil organic matter pool and their addition to the relatively stable soil organic matter fractions (Tate 1987). The accumulation of humus for nutrient retention may be important in the high rainfall climates associated with the distribution of western hemlock where there is pressure on the leaching of nutrient elements (podzolization being a dominant pedogenic force). Although resistant, humus remains subject to microbial decomposition but at a slow rate. Thus western hemlock may be adapted to this slow release of nutrients and, as suggested by Krajina (1969), may grow best with a well balanced supply of nutrients in small quantities.

Perhaps then, the key to western hemlock nutrition is the ability of the site to conserve nutrients, yet release them slowly. The soil chemical measure required to capture increasing western hemlock productivity may be one that not only tests the amount of nutrients, but also the capacity to conserve nutrients, and the ability to slowly release nutrients. Methods of evaluating organic matter, not only its chemical nature but also its chemical structure, need to be investigated as a possible influence on western hemlock nutrition.

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