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COMPARISON OF SOME GROWTH CHARACTERISTICS BETWEEN TWO DIFFERENT DOUGLAS-FIR ECOSYSTEMS OF THE SAME AGE AND SITE INDEX

by

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Diploma Forest Engineer, University of Munich, 1979

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Forestry)

We accept this thesis as conforming

to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April 1983

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ABSTRACT

This study compared growth characteristics of two naturally established, unmanaged, late-immature, Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] stands. Both stands were very similar in regards to age, site index, relative density and history, but represented two different ecosystems. The objective was to determine and explain differences in major growth characteristics between the two stands.

The ecosystems were identified at all levels of the biogeoclimatic ecosystem classification. The analysis of the ecosystems confirmed that the selected stands were considerably different in their ecotope. The stand in which Douglas-fir was moderately shade-tolerant had a warm and drier mesothermal climate. The other stand in which Douglas-fir was shade-intolerant had a cold and wetter mesothermal climate. Comparing edatopic differences, the site of the first stand was drier and had a poorer nutrient status than that of the second stand. The classification and site indices of Douglas-fir determined for the stands were in agreement with those predicted by Krajina (1969).

The stand in which Douglas-fir was moderately shade-tolerant had a multilayered stand structure and the associated growth characteristics resembled those of an uneven-aged stand of shade-tolerant tree species. The stand in which Douglas-fir was shade-intolerant had a uniform canopy and the associated characteristics were typical for an even-aged stand of shade-intolerant tree species. Adjusting for a six year difference in age, there was a 15 percent difference in volume in favour of the stand in which Douglas-fir was shade-intolerant. The analysis of stand structure and

relationship of density to a number of growth characteristics indicated consistent differences between the stands, which appeared to be correlated to shade tolerance of Douglas-fir.

Despite the similar site index and relative density index, it was concluded that there was a disparity in stand structure and volume production, which was related to ecological differences.

A small number of samples and unknown initial density levels however, limit the validity of conclusions reached. The described trends and relationships need to be verified by further integrated studies. If such studies can confirm the relationship between ecosystem taxa and growth characteristics as described in this study, the adoption of a selective ecosystem-specific approach to stand management and construction of yield tables for Douglas-fir should be recommended. This could help to fully utilize the production potential of a site and to accurately predict stand development.

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ACKNOWLEDGEMENTS

I wish to thank my supervisor Dr. K. Klinka for his thorough help and patience in the ecological part of the study, and for the generous amount of time and support during all phases of my study.

I wish to express appreciation to my Supervisory Committee, Dr. G. Weetman, Dr. K. Mitchell and Dr. J. Demaerschalk for advice and assistance.

I wish to acknowledge the help of the staff of the Research Section, Ministry of Forests, and the computer programmers at UBC, J. Emmanuel and B. Wong. Thanks also to C. Ray for assistance with the field work.

I am thankful for the financial support provided by a scholarship from the Canadian National Research Council, McPhee Fellowship and VanDusen Graduate Fellowship.

INTRODUCTION

The common approach of assessing site quality or forest productivity is to classify a stand according to its site index, that is, the expected height of a tree species at an index age. Once the stand has been classified a number of growth and yield characteristics, such as height, number of trees, basal area and volume per unit area, can be predicted from yield tables.

Assumptions inherent to yield tables based on site indices prescribe growth development as follows: even-aged stands with the same site index will have the same growth and yield characteristics at various ages, and at the end of the rotation period they will produce the same volume (Assman 1970). Foresters relate a stand to yield tables by determining its site index, and applying the yield tables, they make predictions and management decisions based upon the predicted values. If the above assumptions are not valid, the predicted values can be associated with errors of variable magnitude.

It has been accepted that site index alone is an inadequate measure to assess or explain site quality and to accurately predict stand development for the purpose of intensive silvicultural management. The rationale to consider other ecosystem properties was advanced by Franz (1965) as follows: "The yield level describes a complex of primary factors, which is based on site quality and plant physiological properties. Mensurational measurements summarize the effect of this complex, but cannot explain causal relationships. As a consequence, the mensurational attributes can only yield secondarily derived values."

The main purpose of the ecological program developed by the British Columbia Ministry of Forests is to classify forest lands and to elucidate environment-vegetation relationships. The intent is to provide an ecosystem-specific framework and interpretations for forest management. This program was not designed to provide detailed and reliable growth and yield characteristics for a multitude of forest stands found in different ecosystems. However, the information on the potential productivity of ecosystems for timber production and crop design is of particular importance to a forest manager. By comparing composition, structure and growth characteristics of fully-stocked, natural stands on a site-specific basis, information on the site-growth relationship can be obtained. This information is useful for the assessment of potential productivity of managed stands or for forest management in general (Franklin 1981). Ecologically based growth and yield studies should greatly enhance the value of the recognized ecosystem taxa and, in general, the understanding of site-specific, environmental- and community-growth relationships. Thus they should support current efforts of intensified silvicultural management.

Available information on the ecological characteristics of forest trees in British Columbia (Krajina 1969) makes it possible to conclude:

1. That significantly different ecosystems can support stands of the same species and forest productivity as expressed by site index and
2. that these stands may differ in some growth characteristics because of differences in the ecological characteristics of species and function of the ecosystems.

Recently, the Inventory Branch of the Ministry of Forests has initiated a program of classifying growth and yield plots using the biogeoclimatic classification system. The goal of this program is to determine the degree of relationship between the growth data and the recognized ecosystem syntaxa for the purpose of an accurate and integrated prediction of stand development.

This study is an attempt to characterize and compare some growth attributes of naturally developed, fully stocked, and nearly mature forest stands which are ecologically different. Specifically, the study tests the hypothesis that there is no difference in growth charateristics between two different Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] ecosystems of the same age, height - site index and history.

The first part of the study describes, classifies and compares the studied ecosystems, and suggests the compensating environmental factors responsible for the same height as expressed by site index.

In the second part of the study differences in basic growth and stand characteristics are identified, analyzed and related to the environmental properties of the ecosystems. It is assumed that the variations in these characteristics can be attributed to differences in the function of the ecosystems studied.

ECOLOGICAL FUNCTION OF DOUGLAS-FIR

Douglas-fir is one of the world's most important and valuable timber trees. It is native to Western North America, with the range of the coastal variety extending from central British Columbia (lat. 55°N) to the central coast of California (lat. 36°N) (Fowells 1965). This tree species has been introduced and grown for over 100 years in Europe, Great Britain and New Zealand. Its autecological characteristics have been reported in numerous studies from all these areas. On some important aspects most of the studies agree:

Douglas-fir grows in a cool, maritime climate with the precipitation ranging from 700 mm to 5000 mm in the Pacific Northwest (Shumway 1981). In central Europe, where the precipitation is evenly spread over the year Douglas-fir grows well with only 500 mm annual rainfall (Floehr 1958). The drought resistance of the species is rated intermediate in a comparison of the trees of the Pacific Northwest (Minore 1979).

Elevation and latitude interact in a way that Douglas-fir extends in its southern range (northern California) to 1800 m, whereas in its extreme northern range in British Columbia the upper altitudinal limit is 800 m (Fowells 1965). Douglas-fir is reported to be sensitive to wind on exposed sites in Great Britain, causing die-back and breakage of the leader (Darrah et al. 1965). Exposure is a limiting factor in New Zealand as well (New Zealand Forest Service 1971).

Early and late frosts are causing severe damage in young Douglas-fir plantations in Germany (Schober 1963). Kirkland (1971) reported similar problems for New Zealand. The general frost resistance of Douglas-fir in the Pacific Northwest is rated relatively high (Minore 1979).

When assessing the relative shade-tolerance of several tree species Minore (1971) rated the position of Douglas-fir intermediate. When compared with its most common associates, Douglas-fir rates very high on the scale of intolerance (Fowells 1965). In humid climates these associates, typically western hemlock, western redcedar and Pacific silver fir form the climax species. In drier areas, caused by topographic rain shade, soil and climatic characteristics pure Douglas-fir stands may exist as the climax stage and occasionally form uneven-aged stands (Williamson 1981). Under these conditions Douglas-fir apparently is tolerant to its own shade.

Douglas-fir occupies a wide variety of sites throughout its native habitat (Revell 1974). Good drainage and aeration of the root zone are important for the growth of Douglas-fir (Williamson 1980). It will not thrive on poorly drained soils or soils with an impervious layer near the surface (Fowells 1965). Heavy clay soils and podzols support unsatisfactory growth in New Zealand (New Zealand Forest Service 1971). Best growth of Douglas-fir in Germany was found on areas of glacial outwash till with clay influence, or morainic sites and on rich sandy sites (Floehr 1958). The best development of the species has been reported on soils with the pH between 5 and 5.5 (Fowells 1965). Floehr (1958) notes that in German Douglas-fir plantations the preferred pH range appears to be 5-6, with a decline in vigour for calcareous soils.

Krajina (1969) and, more recently, Krajina et al. (1982) presented autecological characteristics of forest trees in British Columbia. These characteristics were derived from the synecological studies carried out directly in the natural environment, experimental studies and field observations. As a result, this information can be related to specific sites where these trees may grow, thus providing a basis on which to describe the ecological function of every tree species. These sites or ecosystems, when including biocoenoses, are classified or identified using the taxonomic classification proposed by Krajina (1969, 1972, 1977). This classification system has several integration levels, with each level having several categories. In this study, syntaxa at the biogeocoenotic, biogeoclimatic, phytocoenotic and edatopic (functional) levels are applied.

The autecological characteristics of Douglas-fir were summarized by Krajina et al. (1982) as follows:

(a) geographic: Western North American; Pacific and Cordilleran Distribution in Western North America: central and south in the Pacific region; central and south in the Cordilleran region

(b) climatic: [subalpine boreal (Dfc) - boreal (Dfc) -] cool temperate (Dfb) - warm temperate (Dfa) - [semiarid (BSk)] - cold mesothermal (Cfc) - cool mesothermal (Csb, Cfb)

(c) orographic: submontane - montane (- subalpine)

(d) edatophic: (1) hygrotopes: (very xeric -) xeric - subxeric - submesic - mesic - subhygric - hygric

(2) trophotopes: (oligotrophic -) submesotrophic - mesotrophic - permesotrophic - subeutrophic to eutrophic; generalized nutritional type: subeutrophic eurytrophophyte

The scope of this study was limited to the central part of the Pacific region which supports the coastal population of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). In this area Douglas-fir is found growing in mesothermal climates (very rarely in a subalpine-boreal climate) from submontane to montane (very rarely subalpine) elevations and on a great variety of sites within the Coastal Douglas-fir (CDF) and Coastal Western Hemlock (CWH) (very rarely in the Mountain Hemlock) biogeoclimatic zones. The CDF and the CWH zones are characterized by a cool summer and a mild winter. A more complete climatic characterization of these zones is given by Krajina _et al_. (1982).

Frost resistance is not very high in the coastal variety which does not tolerate frost below -10°C for a period of more than about a week, even if the ground is well protected against freezing by snow.

Flood resistance of Douglas-fir is one of the lowest among the trees growing in British Columbia. This special characteristic is probably also reflected in the hydrosere gradient, because Douglas-fir does not grow on subhydric sites. It does not occur on recent floodplains because occasional flooding eliminates it completely.

Shade tolerance is considered to be moderate because the species is well adapted to subhumid or even dry climates. On mesic sites Douglas-fir is shade-tolerant only in the drier CDF subzones. In the wetter CDF subzones it is shade-tolerant only on very xeric to submesic sites, whereas on mesic sites it regenerates until the stands develop an open canopy. Krajina (1965) suggested that Douglas-fir in more humid climates becomes shade intolerant in many habitats, where it takes up more water than it is able to transpire, due to its leaf stomata being closed and in the shade.

In general, the nutritional requirements of Douglas-fir are moderate, but to achieve maximum growth nutritional requirements are considerable. Douglas-fir grows poorly on oligotrophic soils, where calcium, magnesium, nitrogen, phosphorus and potassium are in low supply. Phosphorus and potassium must be well balanced.

Krajina (1973) found in an experiment that Douglas-fir grows very poorly where it is dependent on ammonium compounds alone for its nitrogen supply. Root growth of Douglas-fir showed signs of intolerance towards pure ammonium nutrition (Bigg et al. 1978). Results of other experiments showed that the growth of Douglas-fir seedlings and young trees, fertilized with nitrogen was superior for the nitrate treatment versus the ammonium one (Garm 1958, Ebell et al. 1970, Radwan et al. 1971, Bigg et al. 1978). A study of van den Driessche (1971) where he grew Douglas-fir seedlings in a sand culture showed best growth for a combination of both the nitrate and the ammonium form. Gosz (1981) reviewed the various findings on this subject. Low nitrogen demanding species seem to prefer the nitrate form of nitrogen. Douglas-fir seems to be able to use both forms. He concluded that plants which have the ability to assimilate nitrate increase their level of nitrate reduction with increasing level of nitrate in the soil.

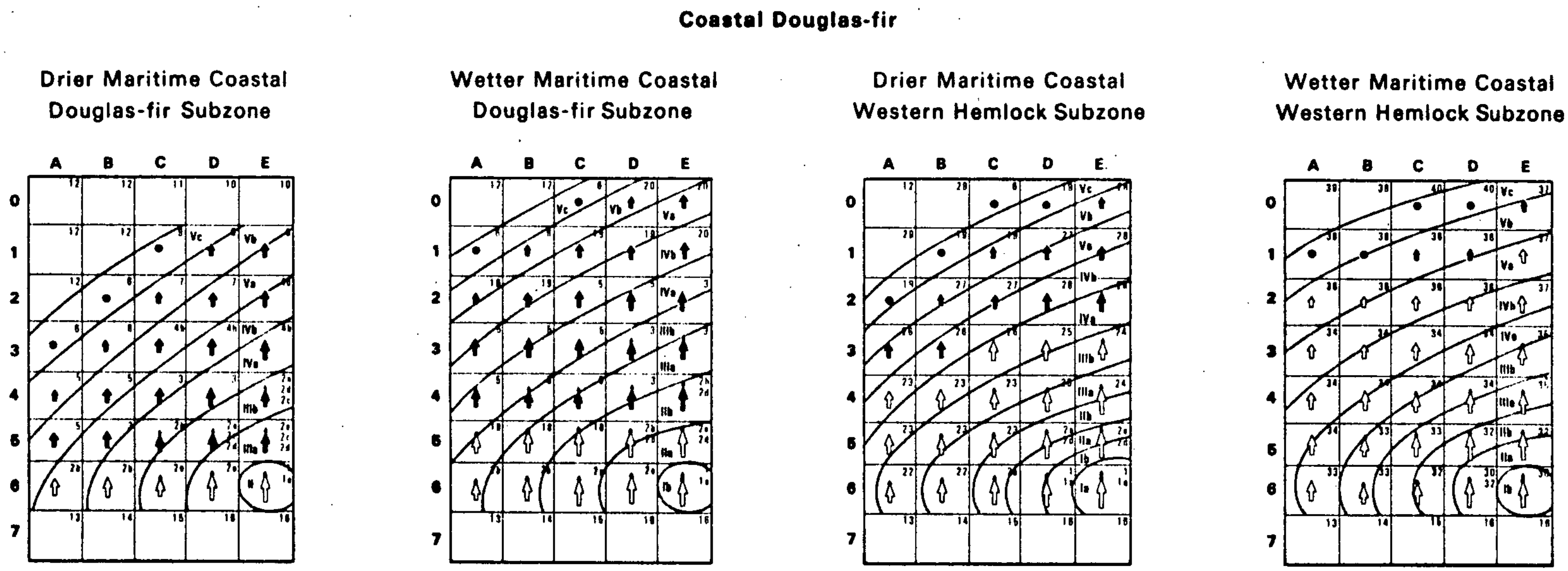
Havill et al. (1975) showed that calciphytic plants have a higher ability to produce nitrate reductase and therefore to utilize nitrate than calciphobic plants. Since nitrifying bacteria are dependent on a relatively high pH, nitrification is carried out mainly in Moders and Mulls of soils in which calcium is easily available and there is better growth of Douglas-fir in these than in acid Mors. The best growth of Douglas-fir was recorded on base-rich soils (Klinka et al. 1981a).

To indicate the ecological function of Douglas-fir it is necessary to integrate forest communities and site components of the ecosystems in which it grows. Krajina (1969) proposed a method by which the ecological characteristics of a tree species can be assessed together with its growth performance and shade tolerance in relation to a site. This method is based on the edatopic grid technique (Figure 1).

This technique uses a matrix which is composed of a moisture gradient (hygrotope) and a nutrient gradient (trophotope). The hygrotope is applied on a vertical axis and the trophotope is applied on a horizontal axis. Within the geographic limits of a biogeoclimatic subzone, forest ecosystems with the same or a similar hygrotope and trophotope as indicated by the similarity in their floristic composition, are grouped together into associations. Because each association is characterized by a range of values of hygrotope and trophotope in turn, these values can be used to identify the sites that are characteristic for an association or a group of closely related associations.

Coastal Douglas-fir is a component of various forest ecosystems classified into associations. The various associations supporting or having a potential to support the species, as well as all the other associations in the respective subzones, can also be shown on the edatopic grids. This is done by plotting the associations into individual cells (edatopes) according to the identified values of hygrotope and trophotope. Arabic numerals in the upper right corner of the grid cells identify these associations. On this basis tree species can be related to their sites or ecosystems.

A tree symbol can be drawn in the individual cells indicating under which particular climatic and edatopic conditions coastal Douglas-fir grows or may grow. The symbol may be modified to indicate the species productivity and shade tolerance or any other chosen silvical attribute. The size of the symbols in Figure 1 indicates the species growth class (i.e. site index class); solid black symbols represent tolerance of shade



Explanatory notes

Hygrotopes (vertical axis): 0 - very xeric, 1 - xeric, 2 - subxeric, 3 - submesic, 4 - mesic, 5 - subhygric, 6 - hygric, 7 - subhydric

Trophotopes (horizontal axis): A - oligotrophic, B - submesotrophic, C - mesotrophic, D - permesotrophic, E - subeutrophic to eutrophic

Tree symbols and their sizes according to growth classes (site indices m/100 yrs) and tolerance to shade:

Ia(>54) Ib(51) IIa(48) IIb(45) IIIa(42) IIIb(39) IVa(36) IVb(33) Va(30) Vb(22) Vc(<15)

Shade-requiring or shade-tolerant

Shade-intolerant

Figure 1. Edatopic grids showing isolines of site indices and shade tolerance for coastal Douglas-fir in the biogeocoenotic associations or types of four mesothermal biogeoclimatic subzones (after Krajina 1969). Small arabic numbers in the right upper corners refer to associations or types named in Krajina (1969, p.41-44).

while clear symbols represent intolerance of shade. Isolines are then drawn between cells with the same site index.

The diagrams presented in Figure 1 inform about the ecological function of coastal Douglas-fir in forest ecosystems of four mesothermal biogeoclimatic subzones. Forest ecosystems in these subzones were studied by Krajina and Spilsbury (1952, 1953), Sczawinski (1953), McMinn (1957, 1960, 1965), Krajina (1959, 1965), Mueller-Dombois (1959, 1965), Lesko (1961), Orloci (1961, 1964, 1965), Eis (1962), Kuramoto (1965), Wade (1965), Cordes (1969), Kojima (1971), Kojima and Krajina (1975), Klinka (1976) and Klinka and Krajina (1983). Based on these studies a brief summary of the function and productivity of this tree species in biogeoclimatic syntaxa relevant to this study follows.

Coastal Douglas-fir Zone

This is the driest mesothermal zone of British Columbia. It is found along the eastern side of Vancouver Island, on the Gulf Islands and on the adjacent coastal mainland between 48° and 50° 20' N latitude. Elevation may range from sea level to 150 m in the north and to 450 m in the south. This zone extends south into Washington and Oregon.

Douglas-fir is the most common tree species in the forest stands of this zone. It can regenerate under the canopy of mature and partly open forest stands on most sites. Western redcedar (*Thuja plicata* Donn *ex* D. Don *in* Lamb.), grand fir [*Abies grandis* (Dougl. *ex* D. Donn) Lindl.], Pacific madrone (*Arbutus menziesii* Pursh), and Garry oak (*Quercus garryana* Dougl. *ex* Hook.) may frequently accompany Douglas-fir, depending on the soil moisture and nutrient regime of the site. Predominance of smaller shrubs (Gaultheria shallon and Mahonia nervosa), low presence of herbs and mosses, and the moderate shade tolerance of Douglas-fir are characteristic floristic features of zonal ecosystems. Moder to weak Mor formation, melanization, weak laterization, and weak leaching were described by Krajina (1959, 1965, 1969, 1978) as the characteristic soil processes. The soils of zonal ecosystems are Dystric Brunisols with medium base saturation grading with increasing precipitation into Humo-Ferric Podzols with Moders or friable Mors. The high potential for forest production is limited by a summer water deficit.

Wetter Maritime CDF (CDFb) Subzone

This subzone is characterized by a moderate soil moisture deficiency, and hence has a higher forest productivity than the drier subzone. The effect of greater rainfall is noticeable especially in the ability of Douglas-fir to become established on very xeric sites. Douglas-fir is shade-requiring only on very xeric and xeric sites and shade-tolerant on subxeric and submesic sites. On mesic sites it is moderately shade-tolerant, i.e. it can establish in an overmature stage after the stand canopy has opened. On subhygric and hygric sites Douglas-fir is shade-intolerant. The most productive stands found on hygric and subeutrophic sites have a site index in the range from 49.6 to 52.5 m/100yrs.

Coastal Western Hemlock Zone

This is the wettest mesothermal zone of British Columbia. It covers much of Vancouver Island and the Coast Mountains. Upper elevations of the zone are 900 m on the windward and 1100 m on the leeward side of mountains in southwestern British Columbia. Outside of the rainshadow area, it extends to sea level. Like the CDF Zone, the CWH Zone continues along the Pacific coast into Washington and Oregon.

Western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] is usually the most common species in the forest cover. It regenerates in abundance under the canopy of forest stands on zonal sites and elsewhere if there is enough accumulation of acid humus materials or decaying wood on the forest floor. Throughout the zone, Douglas-fir and western redcedar occur frequently, while amabilis fir [*Abies amabilis* (Dougl. *ex* Loud.) Forbes] and yellow-cedar [*Chamaecyparis nootkatensis* (D.Don) Spach] are common only in the wetter CWH subzones. The predominance of several moss species (*Hylocomium splendens*, *Rhytidiadelphus loreus*, and *Plagiothecium undulatum*) along with the low presence of herbs and a high species significance of western hemlock are the characteristic floristic features of zonal ecosystems. Accumulation of acid decomposition products on the forest floor, leaching, eluviation, illuviation, and gleization were described by Krajina (1959, 1965, 1969, 1978) as the characteristic soil forming processes. The soils of zonal ecosystems are Humo-Ferric Podzols with Mors grading with increasing precipitation into Ferro-Humic Podzols with Mors.

Wetter Maritime CWH (CWHb) Subzone

In this subzone, which is the wettest biogeoclimatic unit of British Columbia, Douglas-fir is less productive than in the CWHa Subzone, due to the effective leaching of the soils caused by high precipitation. As a result, the loss of nutrients by leaching is detectable even on the most productive (subhygric to hygric/subeutrophic) sites which feature a site index in the range from 49.6 to 52.5 m/100yrs. Pacific Silver Fir, Sitka spruce [Picea sitchensis (Bong.) Carr.], western hemlock and yellow-cedar however, have the most productive growth in the CWHb Subzone. Douglas-fir is shade tolerant only on very xeric and xeric sites; on all other sites it is shade-intolerant. It does not grow on very xeric/oligotrophic and subhydric sites.

Figure 1 shows the predicted site indices for coastal Douglas-fir in different edatopes of different associations occurring in different biogeoclimatic subzones. Krajina (1969) admitted that the curves are idealized and need to be tested. It can be observed that:

1. The forest productivity (as measured by site index) of coastal Douglas-fir ecosystems of the same edatopes increases from the CDFa to CDFb or CWHa subzone, and then decreases in the CWHb subzone.
2. Within the same hygrotope the site index increases with increasing trophotope.
3. The same site index may be found for several ecosystems of different edatopes in the same or different biogeoclimatic subzones. The site index remains the same providing that the decrease in hygrotope is compensated by an increase in trophotope.

If these predictions are valid, then it should be possible to find comparable Douglas-fir stands with the same site index but with contrasting combination of climate, hygrotope and trophotope. Considering the described variations in tolerance to shade it is likely that along with site differences one can expect corresponding differences in the composition and development of the stands, such as in stocking or density, horizontal and vertical structure, and perhaps even in volume production.

THE STUDY AREA

Location

The study was carried out in two stands located in southwestern British Columbia - on Vancouver Island, near Ladysmith and in the Lower Mainland, near Chilliwack (Figure 2). The Douglas-fir stand on Vancouver Island was located about five km southwest of Ladysmith on the eastern side of Banon Creek and about five km north of the point where the creek joins the Chemainus River (48° 56' N latitude and 123° 49' W longitude). The Douglas-fir stand on the Lower Mainland was located on the western slopes of the Tamihi Creek Valley, about three km south from where the Tamihi Creek joins the Chilliwack River (49° 03' N latitude and 121° 48' W longitude).

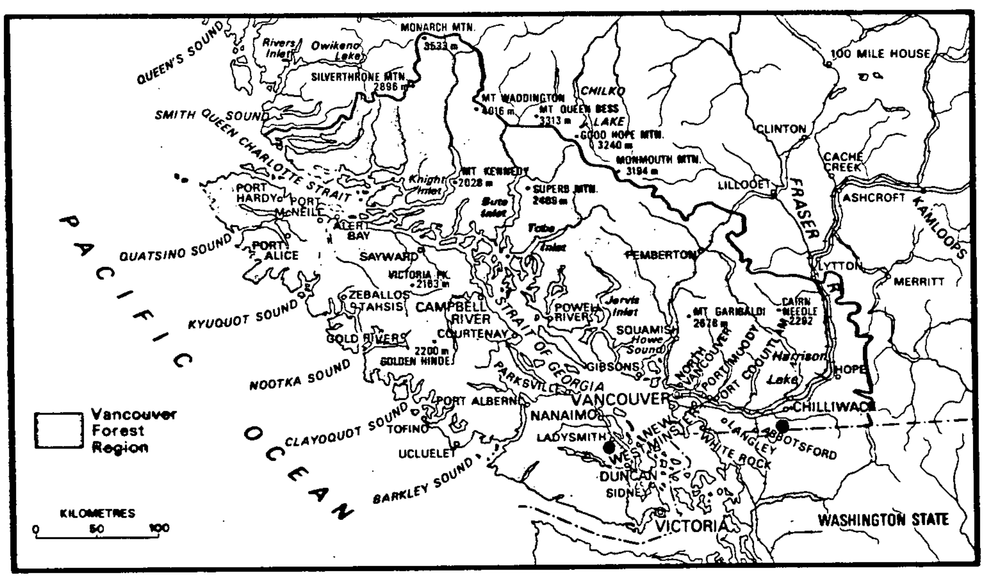


Figure 2. Location of the two study areas.

Climate

At the general level the climate of the study area is described as mesothermal (C) climate - a mild, rainy climate; the mean temperature of the coldest month is between 0°C and 18°C, the mean temperature of the warmest month is over 10°C after Koppen and Trewartha (Trewartha 1968 as modified by Krajina et al. 1982).

At the regional level however, there are profound climatic differences between the study areas. The following characterization of climates is based on Courtin et al's. (1983) summary for biogeoclimatic units in southwestern British Columbia.

The regional climate of the Ladysmith area is described as transitional between wetter Csb and drier Cfb - a cool mesothermal climate with no distinct dry season, precipitation of the driest month greater than 30 mm, grading to that with dry summer, precipitation of the driest month of summer less than 30 mm (the mean value for the area is 32 mm), and the mean monthly temperature of the warmest month below 22°C. A long growing season with low precipitation is characteristic of this climate.

The regional climate of the Chilliwack area is described as a milder Cfc - a cold mesothermal climate with no distinct dry season, precipitation of the driest month greater than 30 mm, and fewer than 4 months have a mean temperature greater than 10°C. A short, cold and wet growing season is characteristic of this climate.

Physiography

The Ladysmith study area is located within the eastern Vancouver Island Ranges, which belong to the Insular Mountains of the Outer Mountain Area (Holland 1964). The study stand is predominantly flat and is situated 190 m above sea level.

The Chilliwack study area is located within the Skagit Range which belongs to the Cascade Mountains (Holland 1964). The study stand is situated on the upper part of a steep, west facing slope with a slope gradient of 67 percent, at an elevation of 680 metres above sea level.

Soil Parent Materials

The Ladysmith area lies on a glaciofluvial terrace adjacent to Banon Creek. The materials are over 1 m thick and vary in particle size and content of coarse fragments from sandy in the upper solum to sandy-skeletal in the lower solum. Angular coarse fragments derived from volcanic rocks are predominant. The underlying bedrock is a sicker volcanic formation, consisting of hornblende-argite andesite (Geological Survey of Canada 1918).

The Chilliwack area lies within the Chilliwack series, consisting of argillite, quartzitic sandstone, and limestone, with interbeds of grit and conglomerate (Geological map of the North American Cordillera 1913). The surficial material in the area is a loamy-skeletal colluvial veneer underlain at a depth of about 1 m by a weathered shale bedrock which is oriented at nearly right angles to the slope. The content of thin and flat (shale derived) coarse fragments is over 60 percent.

History

It is estimated that the old (more than 250 years) growth forest in both study areas was logged about 80 years ago. The Ladysmith area was apparently a part of timber exploitation which occurred within the limits of the Esquimalt-Nanaimo Grant on eastern Vancouver Island. The forest in the Chilliwack area was likely within the area of logging operations which included forested lands on Vedder Mountain and easily accessible parts of the Chilliwack River Valley.

Identification of the remaining stumps and left-over cut timber indicates that western redcedar was a significant component of the tree species composition of old growth forest in both study areas (Figure 3). Charcoal on the stumps and timber debris and in the surface organic layer gave evidence of post-logging fire, but the degree of burning remains unknown.

The present forest was established by natural regeneration within a relatively short period following the fire and has not been managed. A considerable amount of small, undecomposed wood debris in the Ladysmith area suggests continuing mortality up to the present developmental stage. In contrast there are no signs of recent wood debris on the forest floor in the Chilliwack area. It could be concluded that either this forest stand had initially an open spacing or that mortality occurred in the very early stage of stand development due to the shade-intolerance of Douglas-fir in the climatic environment of the area.

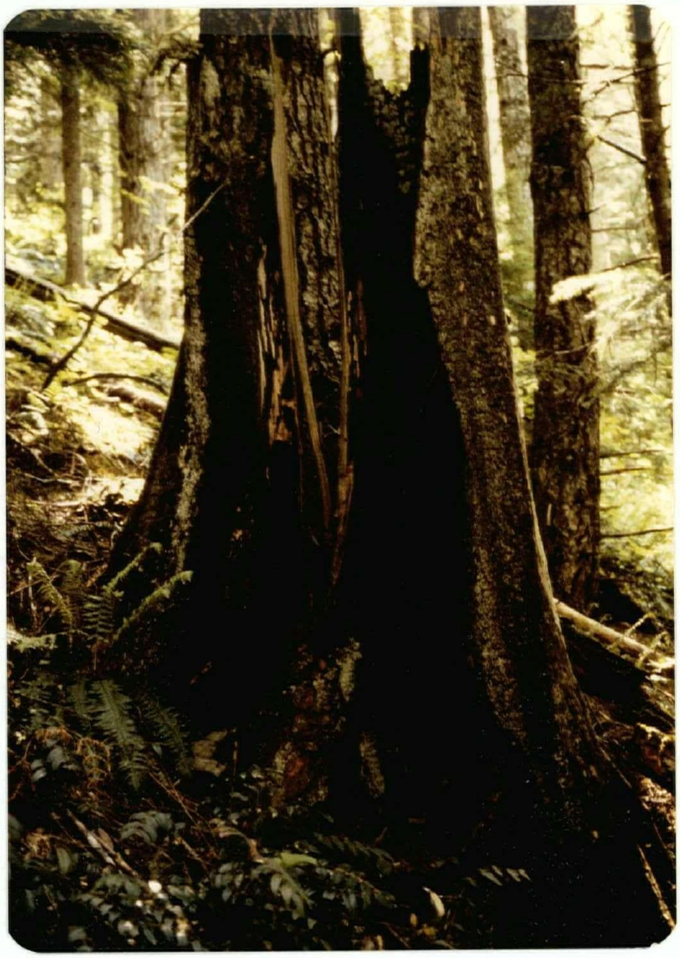


Figure 3. Charcoal on a remaining stump of western redcedar in the Chilliwack study area.

METHODS

Selection of Ecosystems and Sample Plots

To achieve the described objective of the study it was essential, to locate two stands of the same site index, but of contrasting sites. Specifically, the stands were required to be uniform in the following characteristics:

1. Age (preferably within the range from 60 - 100 years)
2. Height (based on the average height of the 100 largest diameter Douglas-fir trees per hectare)
3. Tree species composition (Douglas-fir comprising 90 percent or more of the total basal area)
4. Crown coverage (greater than 80 percent),
5. Vegetation and environment characteristics
6. History

An additional requirement was to select stands large enough to allow the establishment of 10 sample plots. The sample plot size of 25 x 25 m or 0.0625 ha was chosen to contain a minimum of 30 trees.

Ecologically, the objective was to select two stands that would represent two strongly contrasting ecosystems, i.e each being within a different biogeoclimatic subzone. The stand selection was done by using biogeoclimatic and forest cover maps of the Ministry of Forests and ground checks. Preliminary measurements were taken in selected stands to obtain information on the age and the site index.

Methods of Ecosystem Analysis

This study employed an approach and methods which were described by Brooke et al. (1970), Kojima and Krajina (1975), Inselberg et al. (1982) and Krajina et al. (1982).

Each sample plot used for stand analysis was also used for the ecosystem analysis. Each stand represented a sample of an individual ecosystem. On each plot the vegetation was analyzed by phytosociological techniques. The vegetation analysis included the listing of all vascular plants, bryophytes and lichens present on the plot, as well as evaluation of species significance and vigor according to vegetation strata (Inselberg et al. 1982). A list of all plant species recorded in the two ecosystems is given in Appendix I.

Sites (habitats) were described in terms of elevation, slope, exposure and parent materials. Description of soil pedons was limited to one selected plot in each stand. The description of the pedons sampled is given in Appendix II. Soil sampling and classification followed practices and terminology of the Canadian Soil Survey Committee (CSSC 1978). Classification of humus forms was done according to Klinka et al. (1981).

Samples of individual soil horizons were collected and prepared for chemical analysis. Analyses were made for soil pH in $CaCl_2$, total carbon by dry combustion, total nitrogen by Kjeldahl digestion and cation exchange capacity and exchangeable cations by NH_4OAC (pH 7.0) extraction. The analytical methods employed were those described by Lavkulich (1981).

Methods of Ecosystem Synthesis

Synthesis of Environmental and Vegetation Data

Following an analysis of vegetation and its environment, the lists of obtained values for each plot were compared for similarities and differences, using a tabular method (Klinka and Phelps 1979). Applying these methods, standardized tables and a differentiating table (Table 6) for the two ecosystems studied were prepared to supplement the description given. Principal component analysis (PCA) was used to complement the tabular methods. The PCA used a covariance matrix based on species coverage values altered by centering (Gauch 1977).

Synthesis of the data revealed consistency of plots in each ecosystem studied - from these, the taxa at the biogeoclimatic, biogeocoenotic, phytocoenotic and functional level were identified. The identification was based mainly on the floristic attributes of ecosystems, i.e. on the characteristic combination of species proposed for the recognized taxa by various workers and on the indicative values of plants in relation to selected environmental factors, as interpreted by Krajina et al. (1983).

The characteristic combination of species was defined by Braun-Blanquet (1928) as a combination of plants more or less unique to a particular taxon. Thus, the taxa can be differentiated or identified by the presence (as well the absence) of these mutually exclusive combinations. A detailed discussion on this topic, including the principles for selection and the criteria used to assign a differentiating value, in relation to the biogeoclimatic classification was given by

Inselberg *et al*. (1982) (Table 1).

Species Importance and Ecological Spectra

In all synecological studies, the question arises as to objective and reliable identification of the recognized taxa in order to permit their successful application for further ecosystem studies or practical application. In general, this question has been resolved by determining differentiating characteristics (usually a combination of environmental and floristic attributes of ecosystems) for the taxa or by taxonomic mapping or by a combination of both. The former approach, combined frequently with dichotomous keys, assumes that any random plot located in the classified area will fall into a described taxon or can be readily assigned to an intermediate position between two of the described taxa (McVean and Ratcliffe 1962). The latter approach fulfills directly the identification task, furthermore, it portrays a pattern of ecosystems in the landscape. Both approaches however, have weaknesses that may result in difficulties in identification. In general, the differentiation of ecosystem taxa predominantly on the basis of floristic characteristics may be difficult and result in inconsistencies, where the flora is species-poor or where the vegetation pattern is found to reflect varying successional stages. Similar problems may be encountered in mapping; moreover, because of cartographic considerations, each map tends to generalize. This is the case at large map scales in particular.

Of a special interest to forest management practitioners is the use of indicator plant species for the assessment of site quality. The plant

Table 1. Criteria for differentiating values of plant species in characteristic combination of species[1] [after Inselberg *et al.* (1982)].

Symbol	Name	Description
e	exclusive	A plant species whose distribution is exclusively or almost exclusively restricted to a particular taxon; presence class $\geq$ IV, species significance is variable.
s	selective	A plant species whose distribution indicates a strong association with a particular taxon, but may be infrequently associated with other taxa; presence class $\geq$ IV, species significance is variable.
p	preferential	A plant species whose distribution indicates a definite association with a particular taxon but may be associated with several other taxa; presence class $\geq$ IV, species significance is variable.
d	differential	A plant species which has qualified or may qualify as a character species at a higher level of generalization but at a lower level of generalization its distribution shows a definite association with a particular taxon. Presence class $\geq$ IV, in other taxa under comparison, presence class is lower by two or more classes, species significance may be variable. The same species may be used as differential in more than one characteristic combination of species providing it differentiates a particular taxon from other taxa under comparison.
cd	constant dominant	A plant species which has presence class V and mean species significance $\geq$ 3.0; the species which is constant dominant in all or nearly all taxa under comparison should be selected and designated as constant dominant or otherwise at the higher level of generalization.
c	constant	A plant species which has presence class V and mean species significance < 3.0; the species which is constant in all or nearly all taxa under comparison should be selected and designated as constant or otherwise at the higher level of generalization.
ic	important companion	A plant species that does not meet the above criteria but its distribution indicates an affinity to a particular taxon; presence class $\geq$ III, species significance is variable.
-	unimportant companion	A plant which does not meet the above criteria; the species should not be selected into a characteristic combination of species.

[1] Species with exclusive, selective and preferential values are referred to as character species, species with differential values as differential species, and the species with constant dominant, constant and important companion values are referred to as a companion species.

species are precise indicators of the integrated effects of environmental and biotic factors affecting the ecosystems (Major 1969). Various indicative values for plants of the regional flora have been proposed for this purpose, e.g. Mezera (1952), Aichinger (1967), Pliva and Prusa (1969), Ellenberg (1974), Landolt (1977), Bakusis (1978), and Krajina et al. (1983). Indicator plant species have been employed to assess hygrotope and trophotope of forest sites in the "Guide for Tree Species Selection and Prescribed Burning in the Vancouver Forest District" by Klinka (1977). The major weakness in consistently assessing forest sites has been the lack of an easily applied method integrating different indicative values of the plant species.

To address these weaknesses a concept of species importance and ecological spectra has been applied and tested in this study in an attempt to provide a more explicit method to identify ecosystem taxa and to assess site quality.

In the system of biogeoclimatic ecosystem classification, vegetation data are recorded and presented in a tabular form. The tables presented for taxa usually contain presence (constancy) class and mean species significance for each species listed. Several workers proposed scales that combined both presence or presence class, abundance (density) and dominance (coverage) (the latter two characteristics being combined in the Domin-Krajina species significance scale in a single value), referred to as a species importance value (Pliva and Prusa 1969), or as an importance value index (Curtis and McIntosh 1951). In this study the approach using species importance was adapted to fit the species significance scale (Table 2). The species importance value is derived from a matrix featuring

Table 2 a. Species importance scale - combined values of species significance and presence (exponential/linear scales)(Jaeger and Klinka).

Species significance		Presence (class symbol and nominal value)				
Class symbol	Corresponding cover value (%)	I 10	II 30	III 50	IV 70	V 90
+	0.2	2	6	10	14	18
1	0.7	7	21	35	49	63
2	1.6	16	48	80	112	144
3	3.6	36	108	180	252	324
4	7.5	75	225	375	525	675
5	17.5	175	525	875	1775	1575
6	29.0	290	870	1450	2030	2610
7	41.0	415	1245	2075	2905	3735
8	62.5	625	1875	3125	4375	5625
9	87.5	875	2625	4375	6125	7875

Table 2 b. Species importance scale - combined values of species significance and presence (exponential scales)(Jaeger and Klinka).

Species significance		Presence (class symbol and nominal value)				
Class symbol	Corresponding cover value (%)	I 1	II 3	III 9	IV 27	V 81
+	0.2	0.2	0.6	1.8	5.4	16.2
1	0.7	0.7	2.1	6.3	18.9	56.7
2	1.6	1.6	4.8	14.4	43.2	129.6
3	3.6	3.6	10.8	32.4	97.2	291.6
4	7.5	7.5	27.5	67.5	202.5	607.5
5	17.5	17.5	52.5	157.5	472.5	1417.5
6	29.0	29.0	87.0	261.0	783.0	2349.0
7	41.0	41.0	124.4	373.5	1120.5	3361.5
8	62.5	62.5	187.5	562.5	1687.5	5062.5
9	87.5	87.5	262.5	787.5	2362.5	7087.5

products of multiplication between species significance (mid-points of corresponding cover values) and nominal values assigned to presence classes. The latter values were rated in two ways:

1. By using the mid-point values of presence classes yielding an exponential/linear scale (Table 2a).
2. By using values of the geometric expansion scale yielding exponential scales (Table 2b).

The preliminary testing indicated only minor differences when evaluating ecological spectra obtained from the scales. Because the cover values increase exponentially and the exponential scale accentuates the presence of species more than the linear scale, the geometric expansion scale (Table 2b) was consistently applied.

When the presence class and species significance values of the species present in a series of plots or in a single study plot are transformed to species importance values, it then becomes possible to:

1. Characterize each taxon by the distribution of ecological species groups, each group indicating a certain set or sets of environmental factors,
2. to assess affinity of a plot or plots to the recognized taxa in the classification system, and
3. to assess quality of a site in relation to a number of environmental factors.

This is done by computing the relative species importance values (the proportions of the species importance value of a species or a group of species to that of the plot, series of plots or taxon as a whole). The computed percentages may be expressed graphically in a variety of histograms referred to as ecological spectra. The ecological spectra were used in this study to identify and compare the ecosystems studied.

Methods of Stand Analysis

Ten plots, each 25 x 25 m in size were established in each stand. In the Chilliwack area the slope distance of the uphill plot boundaries was calculated to equal the horizontal distance of 25 m. On each plot all live and dead trees with a diameter at height 1.3 m (dbh) greater than 7.5 cm were numbered. For each live tree the following parameters were measured: dbh, height of the lowest dead branch, and location using a coordinate system, whereby the plot boundaries were the x- and y- axes. Crown class (dominant, codominant, intermediate and suppressed) was estimated for each tree present on a plot. Dbh and location of dead trees were recorded providing they were higher than 1.3 m and their bark was intact. Heights of the seven largest diameter trees per plot to derive a top stand height and seven to ten more heights were also measured for height over diameter regressions. In addition, for all these trees the height of the live crown base was measured. In one of the plots in each stand the branch extensions of each tree into four cardinal directions was determined. On a 10 x 100 m strip in each stand, dbh, height, base of live crown and location of each live and dead tree were measured. On five plots in each stand increment cores were taken for the ten largest diameter trees. The increment cores were analysed on a tree-ring measuring instrument, which recorded the width of the earlywood and latewood for each ring.

Methods of Stand Synthesis

Age, Top Height and Site Index

The stand age was derived as the arithmetic mean of ages of the ten largest diameter trees from five plots in each stand. Six years were added to the mean based on increment borings at a height of 1.3 m applying the Ministry of Forests (1981) age-correction tables. The top height was defined as the arithmetic mean of the heights of the 100 largest diameter trees/ha, corresponding to the seven largest diameter trees per plot.

Using the stand age and height two different site indices were derived according to King's (1966) and B.C. Ministry of Forests (Hegyi et al. 1979) tables; King's tables use age at breast height and an index age of 50 years; the B.C. Ministry of Forests tables use the mean height, total age and an index age of 100 years. Mean height is defined as the arithmetic mean of the heights of 10 dominant and codominant trees (in a ratio 3:7).

In this study the site index derived from King's tables was used as a measure of forest productivity for the following reasons:

1. Many plots did not feature dominant trees.
2. To preclude subjectivity in selecting dominant and codominant trees.
3. In research studies the top height is thought to be least influenced by the initial stand density, thus providing the best expression of site (ecosystem) productivity (Assman 1961, Braathe 1957).
4. King's site index uses the age at breast height of the site trees; this prevents errors which may result from the use of age-correction tables.

Height/Diameter Regression Curves

For Douglas-fir in each stand a separate height/diameter regression curve was fitted to predict height values for the diameters measured. Firstly, the measured heights were plotted over the respective diameters. The scattergram suggested that three different curvilinear equations would yield a close fit. To decide which one would give the closest fit, the components of these three equations were combined into one equation. Through a procedure of stepwise elimination, using the MIDAS command REGRESSION this equation was reduced, until all remaining independent variables were significant at the 0.05 level. The final equation was tested logically by plotting it into the scattergram and statistically by plotting the residual values over the predicted values (Table 3). For western hemlock and western redcedar one height/diameter regression equation for each stand was derived applying the same procedure (Table 3).

Basal Area and Volume

The basal area for each plot was calculated as a sum of basal areas of all tree species present. The volume (total volume of entire stem, inside bark, including stump and top, without allowance for defect, trim or breakage) for each plot was computed as a sum of volumes of all trees present using the derived height/diameter regression equations and the volume equations of the B.C. Ministry of Forests (1976). The volume for red alder was derived applying the height/diameter regression equation for Douglas-fir and the volume equation for red alder of the B.C. Ministry of Forests.

Table 3. Relationships between height and diameter for Douglas-fir, western hemlock and western redcedar in the two stands studied.

Tree species	Regression equation	Equation statistics R^2	SE
The Ladysmith stand:			
Df	$h = -30.229 - 0.0989\ dbh + 43.108\ \log dbh$	.93	2.0
Hw and C	$h = 5.7135 + 0.0155\ dbh^3$	.80	0.82
The Chilliwack stand:			
Df	$h = -0.9778 + 1.2033\ dbh - 0.0089\ dbh^2$	.92	2.49
Hw and C	$h = 1.2641 + .6834\ dbh$	.86	1.54

explanation of symbols:

F = Douglas-fir, Hw = western hemlock, C = western redcedar
h = height, dbh = diameter at breast height
R^2 = coefficient of determination, SE = standard error.

Crown Maps and Stand Profiles

A crown map is a horizontal projection of the crown extension to show crown size, crown size in relation to crown class, distribution of crown classes, clustering patterns, overshaded areas and deviations of crown shape.

A stand profile is a vertical projection (cross-section) of a stand complementing the crown map. It shows the layering, crown extension and length of live crown and reveals clustering patterns.

A crown map was plotted for the plot no. 1 and plot no. 17 using branch extension measurements and location of each tree in a selected plot. Two stand profiles were plotted using location, height and base of live crown of trees in a 10 x 100 m strip.

Statistical Methods and Computing Techniques

Additional stand properties (stems per hectare, mean diameter, diameter of the stem of mean basal area stem) and descriptive statistics were computed for each plot and stand. All plot data were converted into per hectare values by multiplication with the factor 16 (625 m^2 x 16 = 1 ha). All per hectare figures given refer to the horizontal projection.

Statistical methods used in the study included basic statistics, t-tests, analysis of variance and simple and multiple regressions. These methods were used to compare descriptive growth characteristics of the stands and to determine the extent of differences in individual growth parameters. A principal component analysis was applied to the vegetational data set to identify clustering of the plots and to separate the two ecosystems.

The statistical analysis was carried out at the University of B.C. Computing Centre, which is equipped with an AMDAHL 470V18 computer and a Houston plotter.

The statistical package Midas (Fox *et al*. 1970) was used to compute descriptive statistics, t-tests and regressions. Ordiflex (Gauch 1977), an ordination program was used for the principle component analysis. Environment-vegetation tables were printed using the program described by Klinka and Phelps (1979). Crown mapping and all other calculations and plottings were performed with Fortran programs written by John Emmanuel and Barry Wong, Faculty of Forestry, University of B.C.

RESULTS AND DISCUSSION

Characterization of the Ecosystems

The locations of two ecosystems suitable for conducting the study were selected after two months of survey work in the Vancouver Forest Region. Environmental and stand characteristics of the selected ecosystems approached very closely the specified requirements but the reqirement of the same age was not satisfied. The six year difference in age notwithstanding, it is believed that the ecosystems finally chosen were satisfactory to meet the objective of this study.

The ecosystems studied have developed under the influence of different climates, soil parent materials and physiography (relief). As a result they exhibit differences in their floristic composition and structure despite similarities in age, composition, density and some aspects of the history of the forest cover. Basic information about the location, climate, soil parent materials, physiography and history was given earlier. Standardized vegetation-environment tables are included in the text, while some detailed information on vegetation and soils of the ecosystems is given in Appendices.

Description

The Ladysmith Ecosystem (Table 4; Figure 4 and 5; Appendix II; Appendix III, Table 1; Appendix IV).

This ecosystem was found on a flat fluvial terrace and the adjacent,

Table 4. Selected environmental and vegetation data for the study plots.

Study area Number of sample plots	Ladysmith 10	Chilliwack 10
Biogeoclimatic subzone	CDFb	(CWHa-) CWHb
Elevation (m)	190	680
Slope gradient (%)[1]	1	67
Aspect (degrees azimuth)[1]	flat(- 198)	250
Particle size (CSSC 1978)	Sandy	Fine loamy-skeletal
Volume of coarse fragments (%)	30	75
Soil subgroup (CSSC 1978)	Orthic Dystric Brunisol	Orthic Humo-Ferric Podzol
Parent materials (landform)	Alluvial terrace	Colluvial veneer
Lithology	Mixed (mainly basaltic)	Shale
Soil moisture regime	Mesic (-subhygric)	Submesic
Soil nutrient regime	Mesotrophic	Eutrophic
Thickness of the LFH layer (cm)	5	3
Humus form	Orthileptomoder	Mineroleptomoder
pH ($CaCl_2$) of the LFH layer	3.6	5.0
Total C (%) of the LFH layer	38.5	33.7
C/N ratio of the LFH layer	44.3	33.0
pH ($CaCl_2$) of the B horizon[1]	5.0	5.1
Total C (%) of the B horizon[1]	0.95	2.69
C/N ratio of the B horizon[1]	22.5	20.7
Base saturation (%) of the B horizon[1]	7.2	17.9
Site index of Douglas-fir (m/100 yrs)[1]	43	42
Strata coverage (%) A layer[1]	83	81
B layer[1]	75	47
C layer[1]	19	39
D layer[1]	59	74
Ground coverage (%) Humus[1]	83	89
Mineral soil[1]	-	-
Decaying wood[1]	16	11
Rocks & stones[1]	1	-
Total number of plant species	41	65

[1] The values are means or weighted means.

Figure 4. The understory vegetation of the forest community in the Ladysmith ecosystem (plot no. 3).

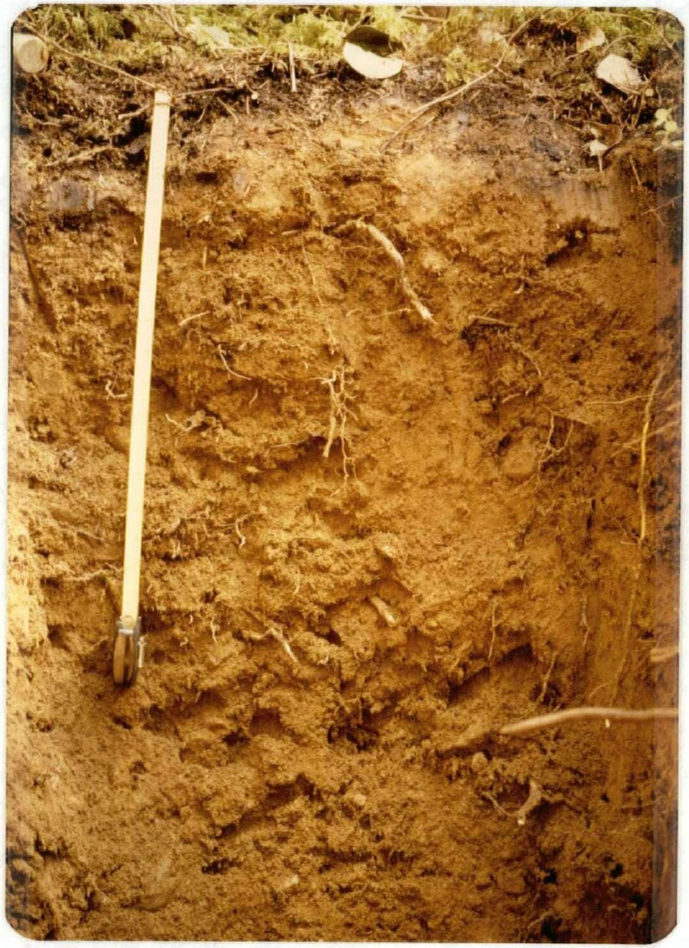


Figure 5. The representative pedon sampled in the Ladysmith ecosystem (plot no. 3).

very gently sloping flanks of a moraine blanket (till) at an elevation of 190 m above sea level. The tree layer had an average cover of 83 percent with minor canopy openings. Douglas-fir was the only tree species present in the tree layers - a feature indicating moderate shade-tolerance of the species and hence, a moderate vertical differentiation of the stand canopy. Red alder and western hemlock occurred sporadically in the A_3 layer. A few individuals of western redcedar, western hemlock and Douglas-fir were found scattered in the upper shrub layer. Vigor of western hemlock was poor - many individuals had dead tops. In contrast, vigor of western redcedar in the upper and lower shrub layer was good. Charcoaled stumps of western redcedar and Douglas-fir were conspicuous on the Ladysmith ecosystem. The lower shrub layer was very well developed with an average cover of 65 percent. It was dominated by Gaultheria shallon. Mahonia nervosa and Vaccinium parvifolium were the associated constant species. Average cover of the herb layer was only 19 percent and the most prominent species were Achlys triphylla, Polystichum munitum, Pteridium aquilinum and Linnaea borealis. The moss layer on humus substrate had a coverage of 59 percent, forming a discontinuous carpet on the forest floor. Hylocomium splendens was dominant; the associated species were Kindbergia[1] oregana, Rhytidiadelphus loreus and Rhytidiadelphus triquetrus. A total of 41 plant species were identified, suggesting a moderate floristic diversity which is characteristic for amphimesic forest communities.

Reconnaissance of the soil component indicated that with the exception of the uppermost layer the soils are morphologically uniform. The

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[1]A new name for the genus Stokesiella (Kind.) Robins., hom. illeg. (Ochyra 1981).

thickness of the LFH layer varied (the mean was 5 cm) as well as the presence of decaying wood both on the forest floor and within the organic surface layer. Based on morphological features, the humus form was identified as an Orthileptomoder; however, the high acidity and carbon/nitrogen ratio measured are more characteristic for Mors than for Moders. The incipient and discontinuous A horizon, either as an Ah, or Ae or both was present in the solum. The uppermost part of the master B horizon was identified as the podzolic Bf subhorizon; the remaining layer was formed by a series of brunisolic Bm subhorizons. The master B horizon contained less than 10 percent coarse fragments. The C horizon consisted of granular, coarse fragments and coarse sand and contained no roots. The pedon examined was identified as a sandy Orthic Dystric Brunisol, developed from fluvial (alluvial over glaciofluvial) materials. These materials contained both basaltic and granitic coarse fragments with the former prevailing over the latter. Considering both external and internal attributes, the hygrotope and trophotope were assessed as mesic and mesotrophic, respectively.

The Chilliwack Ecosystem (Table 4; Figure 6 and 7; Appendix II; Appendix III, Table 2; Appendix IV).

This ecosystem was found on a steep, west facing slope at the elevation of 680 m above sea level. The tree layer in all plots sampled had an average cover of 81 percent. Douglas-fir dominated the canopy and in most plots, western hemlock and occasionally red alder were found in the lower tree layers. The coverage of the A_2 layer was much greater than

Figure 6. The understory vegetation of the forest community in the Chilliwack ecosystem (plot no. 17).

that of the A_1 and A_3 layers. The lack of Douglas-fir in the A_3 and lower layers was attributed to its shade-intolerance in this ecosystem. In the moderately developed shrub layers the average cover was 47 percent. Mahonia nervosa, Tsuga heterophylla and Acer circinatum were constant dominant species; other frequently occurring species were Vaccinium parvifolium, Rosa gymnocarpa and Holodiscus discolor. Western hemlock was the only tree species found to regenerate on decaying wood under the stand canopy. Charcoaled stumps and cut timber debris of western redcedar and Douglas-fir were common in the Chilliwack ecosystem. Many ericaceous species and western hemlock have established on, or in the proximity of these materials. The diverse composition and well developed herb layer were the characteristic floristic features of the plots. A total of 65 plant species were recognized in the sample plots with 54 percent being in the herb layer. The constant dominant species were Polystichum munitum, Achlys triphylla, Pteridium aquilinum and Smilacina stellata. The coverage of the moss layer on humus was high (the average value was 74 percent) but discontinuous. Hylocomium splendens, Kindbergia oregana and Rhytidiadelphus triquetrus were the constant dominant species.

The associated soils were described using a pedon in the plot no. 17 (Figure 7). The forest floor varied in total thickness and thickness of

Figure 7. The representative pedon sampled in the Chilliwack ecosystem (plot no. 17).

individual organic horizons however, Mineroleptomoder was the prevailing humus form. The loose to friable H horizon featured a large amount of dropping residues and incorporated inorganic materials. The colour of the master podzolic B horizon, especially of the uppermost subhorizon, was reddish brown due to a high content of organic matter. All recognized subhorizons were identified as podzolic. The pedon examined was identified as fine loamy-skeletal (with 75 percent coarse fragments) Orthic Humo-Ferric Podzol developed from colluvial veneer derived from and over shale bedrock. Based on both external and internal properties, the hygrotope and trophotope were assessed as submesic and eutrophic, respectively.

Classification

Following synthesis of environmental and vegetation data, the sample plots were classified as successional stages (variations) at the category of association and then identified, using the recognized taxa at the biogeoclimatic, biogeocoenotic, phytocoenotic and functional integration levels. A synopsis of the taxa is given in Table 5.

The study plots fell into two successional associations: the Hylocomium - Gaultheria - PM in the Ladysmith area and the Hylocomium - Mahonia - (TH) - PM in the Chilliwack area. Both tabular and numerical analyses were carried out to determine similarities, differences, and relationships between these associations. The two types of analysis gave very similar results. From Table 6 it appears that the associations have a large number of both common and differential species. The former species suggest ecological relationships to be addressed at higher levels of

Table 5. Synopsis of ecosystem taxa using four integration levels of the biogeoclimatic classification system[1].

Study area	Ladysmith	Chilliwack
Biogeocoenotic level:		
Successional association	Hylocomio (splendentis) - Gaultherio (shallonis) - PM	Hylocomio (splendentis) - Mahonio (nervosae) - (TH) - PM
Climax association	Mahonio (nervosae) - Gaultherio (shallonis) - TP & PM	Mahonio (nervosae) - Polysticho (muniti) - TH & TP
Functional level:		
Hygrotope/trophotope	Mesic (-subhygric)/mesotrophic	Submesic/eutrophic
Biogeoclimatic level:		
Biogeoclimatic subzone	Wetter Maritime Coastal Douglas-fir Subzone (CDFb)	Wetter Maritime Coastal Western Hemlock Subzone [CWHb, the lowest limit of the montane ($CWHb_7$) variant]
Phytocoenotic level:		
Plant alliance	Mahonio (nervosae) - Thujo (plicatae) & Pseudotsugion menziesii	Polysticho (muniti) - Thujion plicatae
Plant order	Gaultherio (shallonis) - Pseudotsugatalia menziesii	Polysticho (muniti) - Thujetalia plicatae

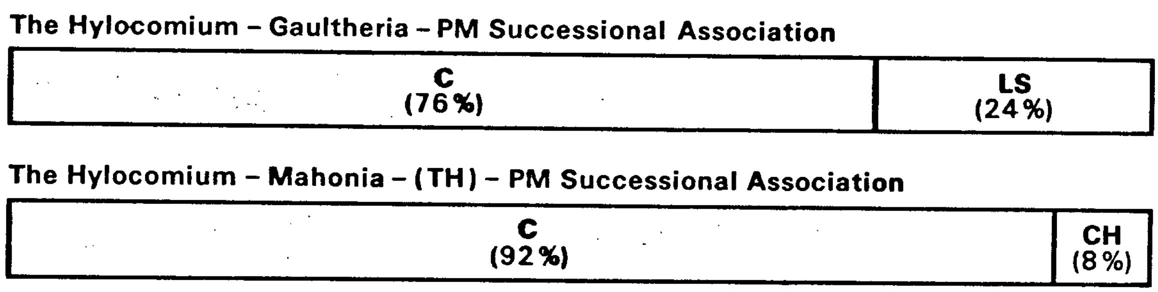
[1] The tree species component in the nomenclature for associations is expressed by two capital letters. The following abbreviations are used: PM - *Pseudotsuga menziesii*, TH - *Tsuga heterophylla*, TP - *Thuja plicata*. The complete names are derived by modifying species names according to standard phytosociological practice. In the text, for convenience, the anglicized names of biogeocoenotic and phytocoenotic taxa are used: tree species are abbreviated by two capital letters as described above and other species are referred to by their generic names.

Table 6. Common and differential combinations of species for the study plots[1].

Study area	Ladysmith	Chilliwack
Biogeoclimatic subzone	CDFb	CWHb
Edatope	4/C	3/E
Number of plots	10	10
Plant species	Presence class and mean species significance	
1. The combination of species common to both study areas:		
Achlys triphylla	IV 4.8	V 4.9
Adenocaulon bicolor	IV 2.0	III 1.3
Galium triflorum	IV 1.8	V 2.2
Hylocomium splendens	V 8.1	V 8.2
Mahonia nervosa	V 5.1	V 6.6
Polystichum munitum	V 3.0	V 5.7
Pseudotsuga menziesii	V 8.5	V 8.5
Pteridium aquilinum	V 4.3	V 3.2
Rhytidiadelphus loreus	V 2.2	IV 1.4
Rhytidiadelphus triquetrus	IV 1.6	V 3.6
Rosa gymnocarpa	III 1.9	V 2.5
Rubus ursinus	V 2.8	V 2.0
Kindbergia oregana	V 4.6	V 5.0
Tsuga heterophylla	V 2.7	V 5.3
Vaccinium parvifolium	V 4.4	IV 3.2
2. The differential combination of species for the Ladysmith study plots [the Hylocomio (splendentis) - Gaultherio (shallonis) - PM Successional Association]:		
Festuca subuliflora	III 1.3	I +.0
Gaultheria shallon	V 7.9	-
Linnaea borealis	V 3.2	III +.9
Listera cordata	III +.8	-
Thuja plicata	IV 2.3	-
Tiarella trifoliata	III 1.4	-
3. The differential combination of species for the Chilliwack study plots [the Hylocomio (splendentis) - Mahonio (nervosae) - (TH) - PM Successional Association]:		
Acer circinatum	-	V 3.5
Actaea rubra	-	IV 1.3
Aruncus dioicus	-	IV 2.1
Chimaphila menziesii	II +.0	IV 1.3
Disporum hookeri	-	V 2.2
Goodyera oblongifolia	II +.0	IV 1.2
Holodiscus discolor	-	IV 3.0
Mycelis muralis	III +.4	V 2.3
Rhytidiopsis robusta	-	V 2.4
Ribes lacustre	-	III 1.2
Smilacina racemosa	-	IV 1.2
Smilacina stellata	-	V 3.2
Symphoricarpos albus	-	IV 1.4
Trientalis latifolia	-	V 2.2
Trillium ovatum	II +.6	V 1.6
Viola orbiculata	-	III 2.0
Viola sempervirens	II +.2	IV 2.6

[1] These combinations include only the species that have presence class ≥ III, and whose presence class is greater by 2 or more than that for the same species in the other unit under comparison.

generalization while the latter species provide for a distinct differentiation of one association from another. Transforming presence class and mean species significance of the species listed to species importance values, the sums of the importance values for each combination and associations are expressed on a relative basis in Figure 8. The plot of ecological spectra indicates a considerable similarity and a minor difference in the floristic composition between the two associations. There were differential species present in both ecosystems which belonged to the opposite association, but their species significance values were so low, that the corresponding relative importance values were below 0.00 percent.



Explanation of symbols:

C - the combination of species common to both study areas
LS - the differential combination of species for the Ladysmith study plots
CH - the differential combination of species for the Chilliwack study plots

Figure 8. Ecological spectra indicating floristic affinity between successional associations.

The result of a principle component analysis is presented in Figure 9. The ordination of the plots showed two groups the centroids of which were significantly different along the second axis which expressed approximately

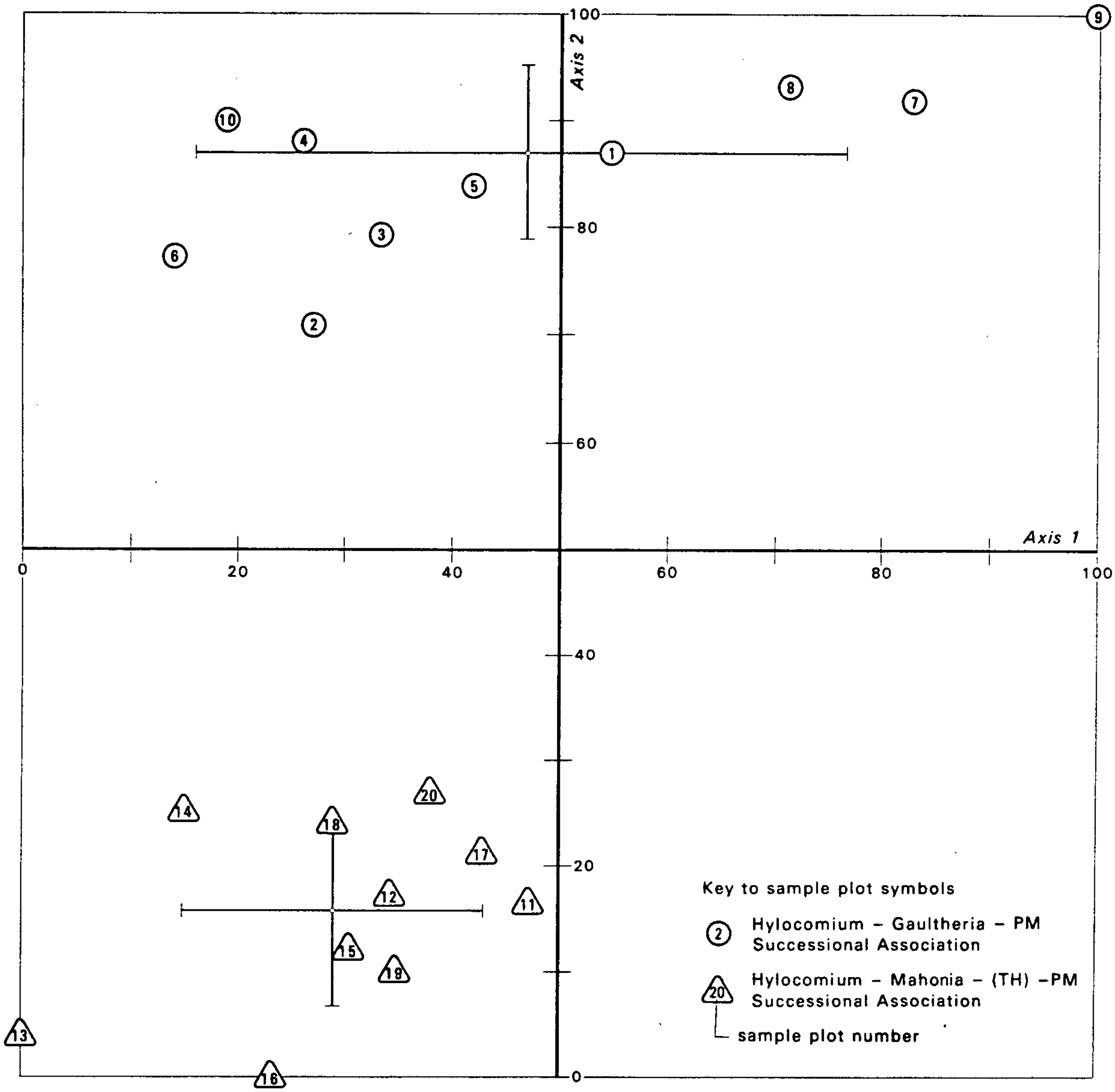


Figure 9. Ordination of the study plots using principle component analysis. The centroids and standard deviations for the associations are indicated.

10 percent of the variation in the data. The two groups and affinities recognized by this analysis are parallel to those derived by tabular analysis.

To proceed with identification of ecosystem taxa beyond the category of successional association it is logical to follow with the assessment of hygrotopes and trophotopes (i.e. edatopes) of the ecosystems. Tentative assessment of edatopes was done earlier on the basis of soil properties (Table 4). In the following discussion assessment of edatopes will be done on the basis of indicator plant analysis.

The occurrence of a plant species signals that it has competed successfully in a certain environment. The integrated effect of environmental and biotic factors in an ecosystem must be then within the tolerance limits of the species. Many plant ecologists have been using plant species as indicators of various properties of ecosystems. Recently, Krajina et al. (1983) compiled a matrix of vascular plants and some bryophytes, liverworts and lichens of British Columbia showing their affinities to selected ecosystem attributes. In relation to edatope, each species included was characterized by the range of hygrotope and trophotope using nominal relative scales of the edatopic grid. Grouping of species with the same or similar values of hygrotope or trophotope or both in a plot or set of plots makes it possible to characterize these plots or ecosystem taxa by a pattern of these groups, referred to as ecological or indicator species groups. The patterns of indicator species groups should assist (within certain geographic limits) to assess the edatope and taxonomic affinity of ecosystems.

The indicator plant analyses for the study plots in relation to hygrotope and trophotope are presented in Tables 7 and 8, respectively. The tables include only species that have the presence class $\geq$ III for one of the associations. Many species in nearly all indicator species groups were found to be common to both associations. The absence of some species in the Ladysmith ecosystem can be partly explained either by their intolerance of a drier (Csb) mesothermal climate (e.g. *Rhytidiopsis robusta*) or their geographic range (e.g. *Acer circinatum*), but most of the species are absent because of the edatopic quality of the site. The content of the tables is complemented by ecological spectra presenting relative importance values of the indicator species groups (Figure 10 and 11). Evidently, each association displays a distinctly different pattern of these groups suggesting a corresponding difference in their edatopes. The absence of calibrated spectra precludes however, identification of edatopes on a relative basis, i.e. relative to a biogeoclimatic subzone. Therefore, the examination of ecological spectra will be done on an absolute basis which is thought to be more meaningful for the purpose of this study.

The main difference between the Ladysmith and Chilliwack ecosystem in relation to hygrotope was found to be between the pattern of xero- to mesophytes and hygrophytes. The importance of the former group decreased from 47 to 28 percent, and that of the latter group increased from 5 to 27 percent. This change in pattern suggests that in absolute terms, the Chilliwack ecosystem has a substantially higher supply of available water than the Ladysmith ecosystem. The presence of three indicator species groups comprising mesophytes, which account for 95 percent of the spectrum, suggests an intermediate or mesic hygrotope of the Ladysmith ecosystem.

Table 7. Combinations of plant indicator species from the study plots in relation to hygrotope.

Group of indicator species	Xero- to mesophytes		Mesophytes		Meso- to hygrophytes		Hygrophytes	
Study area[1]	LS	CH	LS	CH	LS	CH	LS	CH
Species	Presence class and mean species significance							
1. Xero- to mesophytes:								
Chimaphila menziesii	II +.0	IV 1.3						
Gaultheria shallon	V 7.9	-						
Holodiscus discolor	-	IV 3.0						
Mahonia nervosa	V 5.1	V 6.6						
Rhytidiopsis robusta	-	V 2.4						
Rosa gymnocarpa	III 1.9	V 2.5						
Kindbergia oregana	V 4.6	V 5.0						
2. Mesophytes:								
Goodyera oblongifolia			II +.0	IV 1.2				
Linnaea borealis			V 3.2	III +.9				
Listera cordata			III +.8	-				
Pteridium aquilinum			V 4.3	V 3.2				
Rhytidiadelphus triquetrus			IV 1.6	V 3.6				
Rubus ursinus			V 2.8	V 2.0				
Trientalis latifolia			-	V 2.2				
Vaccinium parvifolium			V 4.4	IV 3.2				
Viola orbiculata			-	III 2.0				
Viola sempervirens			II +.2	IV 2.6				
3. Meso- to hygrophytes:								
Adenocaulon bicolor					IV 2.0	III 1.3		
Hylocomium splendens					V 8.1	V 8.2		
Rhytidiadelphus loreus					V 2.2	IV 1.4		
Ribes lacustre					-	III 1.2		
Smilacina racemosa					-	IV 1.2		
Smilacina stellata					-	V 3.2		
Symphoricarpos albus					-	IV 1.4		
4. Hygrophytes:								
Acer circinatum							-	V 3.5
Achlys triphylla							IV 4.8	V 4.9
Actaea rubra							-	IV 1.3
Aruncus dioicus							-	IV 2.1
Disporum hookeri							-	V 2.2
Festuca subuliflora							III 1.3	I +.0
Galium triflorum							IV 1.8	V 2.2
Mycelis muralis							III +.4	V 2.3
Polystichum munitum							V 3.0	V 5.7
Tiarella trifoliata							III 1.4	-
Trillium ovatum							II +.6	V 1.6

[1]The symbol LS refers to the Ladysmith study plots, the symbol CH refers to the Chilliwack study plots.

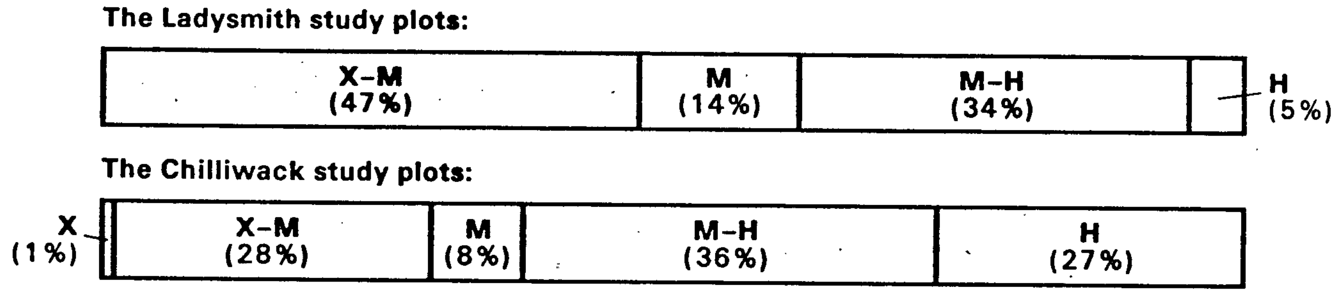
Table 8. Combinations of plant indicator species from the study plots in relation to trophotope.

Group of indicator species	Oxylophytes		Mesotrophytes		Eutrophytes	
Study area[1]	LS	CH	LS	CH	LS	CH
Species	Presence class and mean species significance					
1. Oxylophytes:						
Gaultheria shallon	V 7.9	-				
Goodyera oblongifolia	II +.0	IV 1.2				
Hylocomium splendens	V 8.1	V 8.2				
Listera cordata	III +.8	-				
Rhytidiadelphus loreus	V 2.2	IV 1.4				
Rhytidiopsis robusta	-	V 2.4				
Rosa gymnocarpa	III 1.9	V 2.5				
Vaccinium parvifolium	V 4.4	IV 3.2				
Viola orbiculata	-	III 2.0				
2. Mesotrophytes:						
Chimaphila menziesii			II +.0	IV 1.3		
Holodiscus discolor			-	IV 3.0		
Linnaea borealis			V 3.2	III +.9		
Mahonia nervosa			V 5.1	V 6.6		
Pteridium aquilinum			V 4.3	V 3.2		
Rubus ursinus			V 2.8	V 2.0		
Kindbergia oregana			V 4.6	V 5.0		
Trientalis latifolia			-	V 2.2		
Viola sempervirens			II +.2	IV 2.6		
3. Eutrophytes:						
Acer circinatum					-	V 3.5
Achlys triphylla					IV 4.8	V 4.9
Actaea rubra[2]					-	IV 1.3
Adenocaulon bicolor[2]					IV 2.0	III 1.3
Aruncus dioicus[3]					-	IV 2.1
Disporum hookeri					-	V 2.2
Festuca subuliflora					III 1.3	I +.0
Galium triflorum[3]					IV 1.8	V 2.2
Mycelis muralis[3]					III +.4	V 2.3
Polystichum munitum[3]					V 3.0	V 5.7
Rhytidiadelphus triquetrus					IV 1.6	V 3.6
Ribes lacustre[2]					-	III 1.2
Smilacina racemosa[3]					-	IV 1.2
Smilacina stellata[3]					-	V 1.3
Symphoricarpos albus					-	IV 1.4
Tiarella trifoliata[2]					III 1.4	-
Trillium ovatum[3]					II +.0	IV 0.6

[1] The symbol LS refers to the Ladysmith study plots, the symbol CH refers to the Chilliwack study plots.

[2] The suffix 2 denotes a nitrophyte.

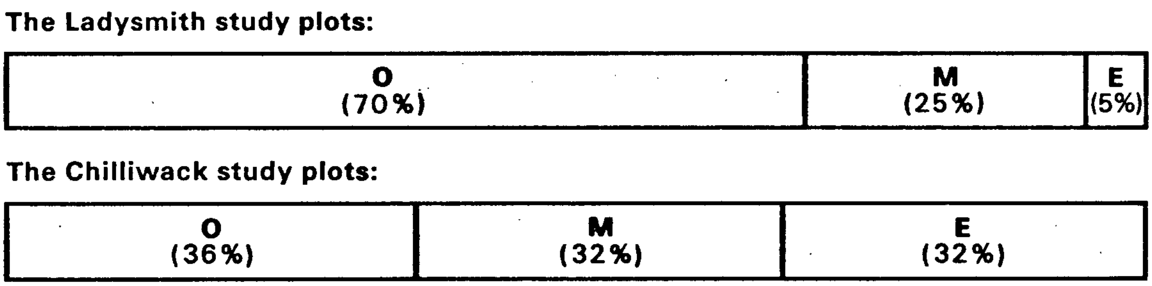
[3] The suffix 3 denotes a species with nitrophytic inclinations.



Explanation of symbols:

X - xerophytes
X-M - xero- to mesophytes
M - mesophytes
M-H - meso- to hygrophytes
H - hygrophytes

Figure 10. Ecological spectra indicating floristic affinity of the study plots to hygrotope.



Explanation of symbols:

O - oxylophytes; the species found on strongly acid, base-poor soils with Mors.
M - mesophytes; the species found on moderately acid and base saturated soil with Mors or Moders.
E - eutrophytes; the species found on weakly acid to circumneutral, base-rich, melanized soils providing a balanced supply of nutrients with Moders to Mulls; this group includes also nitrophytes and nitrophytic species found on soils with a high availability of nitrogen.

Figure 11. Ecological spectra indicating floristic affinity of the study plots to trophotope.

The considerable importance of xero- to mesophytes in the Chilliwack ecosystem suggests that the presence of hygrophytes could be partly due to a high nutrient supply. In relation to other ecosystems in the CWHb Subzone, the presence of three groups comprising mesophytes with the importance value of 73 percent suggests an amphimesic (submesic to mesic) hygrotope.

The difference between the associations in relation to trophotope was found to be even more pronounced than that for the hygrotope. The importance of oxylophytes decreased from 70 to 36 percent and that of eutrophytes increased from 5 to 32 percent, when comparing the Ladysmith and Chilliwack ecosystem. Along with the increase of eutrophytes, there was a corresponding increase in the importance of nitrophytes and nitrophytic species. The relative percentage of these species increased from 12 percent in the Ladysmith to 88 percent in the Chilliwack ecosystem. This suggests that the Chilliwack ecosystem has a substantially higher supply of available nutrients than the Ladysmith ecosystem. The relatively high importance of oxylophytes for an eutrophic trophotope is somewhat surprising. It should be noted that Hylocomium splendens accounts for the major part of the oxylophyte group in the Chilliwack ecosystem. This may be due to the presence of acidic microsites (e.g. decaying wood accumulation) on the forest floor.

The plant indicator analysis suggests that the Chilliwack ecosystem is considerably wetter and more nutrient rich than the Ladysmith ecosystem. Due to the lack of calibrated spectra for edatopes in different biogeoclimatic subzones, the analysis could not verify hygrotope and trophotope on the relative scales, but gave some support to their identification inferred from the soil properties.

Based on published biogeoclimatic maps (Klinka et al. 1979, Courtin et al. 1983), the study plots fell into two biogeoclimatic subzones: those in the Ladysmith area belonged to the CDFb Subzone, and those in the Chilliwack area belonged to the lowest limits of the CWHb Subzone, montane variant ($CWHb_7$). The identification was verified by a reconnaissance in the climax zonal ecosystems found in adjacent areas, using the differentiating characteristics for the subzones described by several workers.

To complement the above identification, floristic affinities to CDF and CWH zones were evaluated using the ecological spectra, despite the fact that the study plots featured non-climax vegetation and the Chilliwack plots were azonal. Plant species, which are members of the characteristic combinations of species for the two zones, and their differentiating values were compiled in Table 9. The species listed included only those ones which were present in the study plots. Transforming presence class and mean species significance to species importance values, the sums of the importance values for each combination (with and without Douglas-fir) and study area were plotted in Figure 12. The spectra for the Ladysmith ecosystem display a strong affinity to the CDF Zone. This could be substantiated by the zonal character of the Ladysmith ecosystem, and a significant proportion of Douglas-fir in the tree species composition of climax stands on mesic and mesotrophic sites. The Chilliwack ecosystem displays a similar pattern. However, the increased importance of species characteristic for the CWH Zone is of significance. In this case one must consider firstly, a great difference in vegetation between climax and

Table 9. The plant species from the study plots found in characteristic combinations for the CDF and CWH zones[1].

Study area	Ladysmith	Chilliwack
CDF Zone:		
Acer macrophyllum (p)	I +.0	I +.0
Cornus nuttallii (p)	-	I +.0
Gaultheria shallon (p, cd)	V 7.9	-
Holodiscus discolor (p)	-	IV 3.0
Mahonia nervosa (p, cd)	V 5.1	V 6.6
Pseudotsuga menziesii (p, cd)	V 8.5	V 8.5
Rhytidiadelphus triquetrus (ic)	IV 1.6	V 3.6
Rosa gymnocarpa (p)	III 1.9	V 2.5
Rubus ursinus (p, c)	V 2.8	V 2.0
Kindbergia oregana (p, cd)	V 4.6	V 5.0
Trachybryum megaptilum (p)	-	I +.0
Vaccinium parvifolium (cd)	V 4.4	IV 3.2
CWH Zone:		
Abies amabilis (d)	-	I +.0
Clintonia uniflora (d)	-	I +.0
Dryopteris expansa (ic)	I +.0	I +.0
Menziesia ferruginea (ic)	-	II +.9
Oplopanax horridus (ic)	-	I +.0
Plagiothecium undulatum (p)	I +.1	I +.0
Rhytidiadelphus loreus (p, cd)	V 2.2	IV 1.4
Rhytidiopsis robusta (d)	-	V 2.4
Tsuga heterophylla (p, cd)	V 2.7	V 5.3

[1] The source is Krajina (1959), Kojima and Krajina (1975), Klinka et al. (1979), Courtin et al. (1983) and Klinka and Krajina (1983).

Figure 12a. Ecological spectra indicating floristic affinity of the study plots to the mesothermal biogeoclimatic zones.

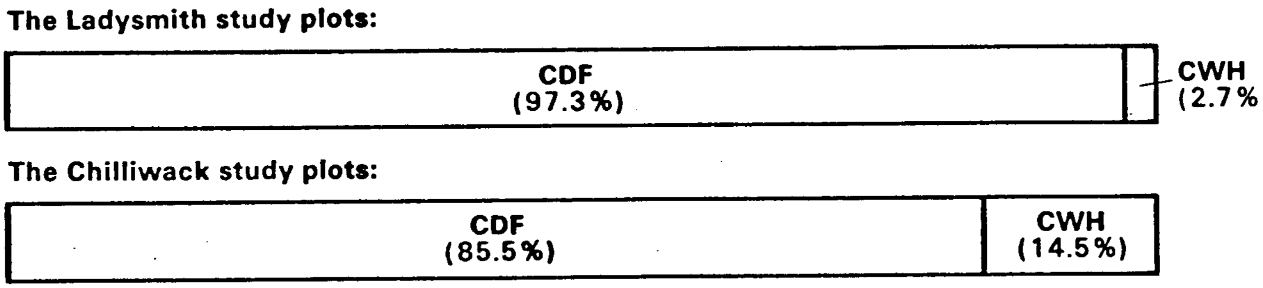
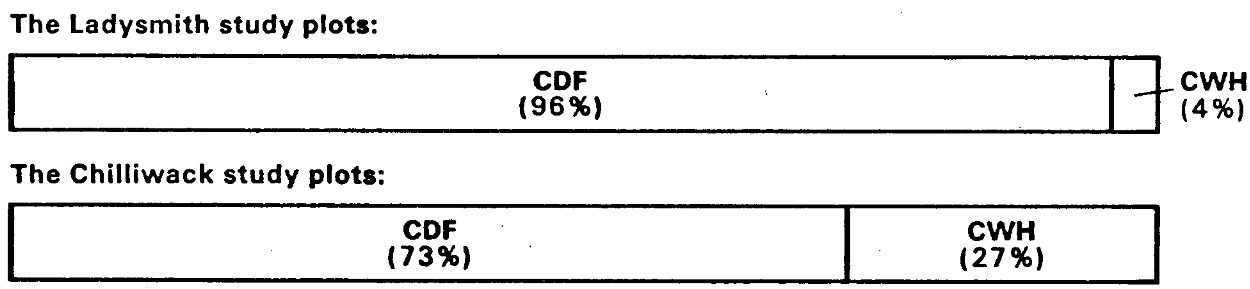


Figure 12b. Ecological spectra indicating floristic affinity of the study plots to the mesothermal biogeoclimatic zones when Douglas-fir is excluded.



Explanation of symbols:

CDF - refers to the species listed in the characteristic combination of species for the CDF Zone.

CWH - refers to the species listed in the characteristic combination of species for the CWH Zone.

non-climax forest communities in the CWHb Subzone and secondly the non-zonal character of the ecosystem. As a result, it was not surprising that the seral vegetation present in the Chilliwack ecosystem did not reveal a strong affinity to the CWH Zone. The change of tree species composition to western hemlock , western redcedar and amabilis fir (Orloci 1964, Krajina 1969, Klinka 1976) in the near-climax successional stage will result in profound changes in the composition of understory vegetation which then should express stronger affinity to CWH than to the CDF Zone.

The identification of edatopes and biogeoclimatic subzones allows the relation of successional associations to the phytocoenotic taxa and climax associations. The successional associations are likely members of one of the three plant orders: Gaultheria - PM[1], Rhytidiadelphus - TH[2] or Polystichum - TP[3] (Table 10). Using the available information, characteristic combinations of species for these orders were compiled and those species found in the study plots and listed in the combinations are presented in Table 10. Thus, the presented combinations are incomplete, i.e. they do not include all the species listed. Also, it should be noted that the presence and/or mean species significance of some species do not meet the specified differentiating values shown in parenthesis. Complementary ecological spectra in Figure 13 show the pattern of three combinations of

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[1]n.n.; Krajina (1969), Kojima (1971, 1975), Klinka and Krajina in Klinka (1976), Klinka and Krajina (1983).

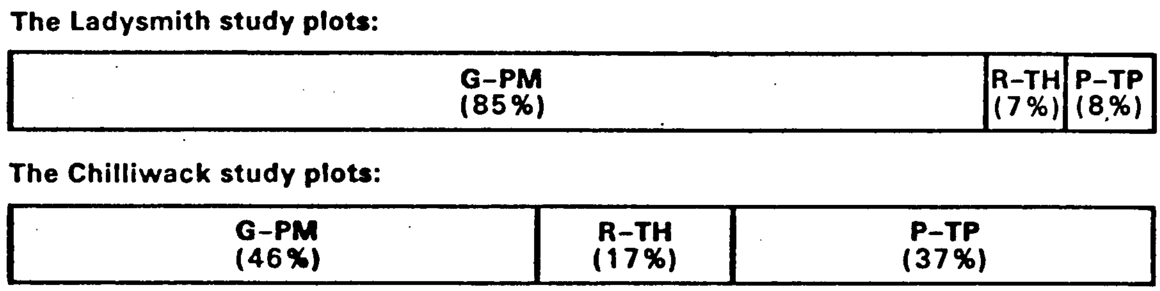
[2]n.n.; Krajina (1969), Kojima and Krajina in Kojima (1971), Kojima and Krajina (1975), Klinka and Krajina in Klinka (1976), Klinka and Krajina (1983), Klinka *et al*. (1980).

[3]n.n.; Krajina in Brooke (1965), Krajina (1965), Brooke et al. (1970), Klinka and Krajina in Klinka (1976), Klinka and Krajina (1983), Klinka *et al*. (1980, 1981), Inselberg *et al*. (1982).

Table 10. The plant species from the study plots found in characteristic combinations for three orders.

Study area	Ladysmith	Chilliwack
Gaultheria - PM Order		
Chimaphila umbellata (ic)	-	I +.0
Gaultheria shallon (p, cd)	V 7.9	-
Holodiscus discolor (p)	-	IV 3.0
Mahonia nervosa (ic)	V 5.1	V 6.6
Pseudotsuga menziesii (p, cd)	V 8.5	V 8.5
Rhytidiadelphus triquetrus (p)	IV 1.6	V 3.6
Rosa gymnocarpa (p)	III 1.9	V 2.5
Rubus ursinus (p, c)	V 2.8	V 2.0
Kindbergia oregana (p, cd)	V 4.6	V 5.0
Trachybryum megaptilum (s)	-	I +.0
Vaccinium parvifolium (cd)	V 4.4	IV 3.2
Rhytidiadelphus - TH Order		
Dryopteris expansa (ic)	I +.0	I +.0
Goodyera oblongifolia (ic)	II +.0	IV 1.2
Linnaea borealis (ic)	V 3.2	III +.9
Listera cordata (ic)	III +.8	-
Menziesia ferruginea (ic)	-	II +.9
Plagiothecium undulatum (p, c)	I +.1	I +.0
Rhytidiadelphus loreus (p, cd)	V 2.2	IV 1.4
Rhytidiopsis robusta (ic)	-	V 2.4
Tsuga heterophylla (p, cd)	V 2.7	V 5.3
Polystichum - TP Order		
Achlys triphylla (p)	IV 4.8	V 4.9
Festuca subuliflora (s)	III 1.3	-
Galium triflorum (s, c)	IV 1.8	V 2.2
Leucolepis menziesii (s)	-	I +.0
Mycelis muralis (p)	III +.4	V 2.3
Plagiomnium insigne (s)	-	I +.0
Polystichum munitum (p, cd)	V 3.0	V 5.7
Rhytidiadelphus triquetrus (ic)	IV 1.6	V 3.6
Thuja plicata (p, cd)	III 2.4	-
Tiarella trifoliata (s, c)	III 1.4	I +.0
Trillium ovatum (p)	II +.6	V 1.6

Figure 13. Ecological spectra indicating floristic affinity of the study plots to plant orders.



Explanation of symbols:

G-PM - plants of the characteristic combination of species for the Gaultheria - PM Order

R-TH - plants of the characteristic combination of species for the Rhytidiadelphus - TH Order

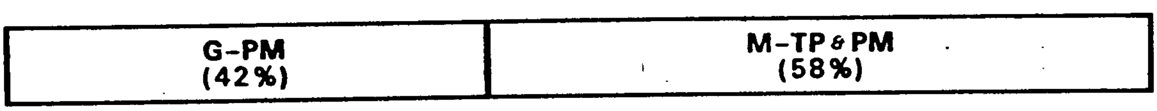
P-TP - plants of the characteristic combination of species for the Polystichum - TP Order

species for the orders. To reduce inherent problems arising from the successional character of ecosystems, Douglas-fir was excluded from the spectra for both ecosystems. The spectrum for the Ladysmith ecosystem shows overwhelming preponderance of species characteristic for the Gaultheria - PM Order, while that for the Chilliwack ecosystem displays a different pattern: The importance of characteristic species of the Polystichum - TP and Rhytidiadelphus - TH orders increased while that for the Gaultheria - PM Order decreased but is still accounting for the major part of the spectrum. It could be concluded that the Ladysmith ecosystem is a member of the Gaultheria - PM Order, however, for the Chilliwack ecosystem this analysis did not indicate a definitive taxonomic affinity either to Gaultheria - PM or Polystichum - TP Order. The lack of calibrated data might have prevented a proper interpretation.

Considering the tabular information and the change in spectral pattern, but mainly the identified edatopes and biogeoclimatic subzones, this ecosystem was identified as a member of the Polystichum - TP Order. On submesic and eutrophic sites in the CWHb Subzone, Douglas-fir is shade-intolerant, therefore the major species in climax stands will be western redcedar as it had been in the past, along with some amabilis fir. Such ecosystems in the maritime climate environment are considered to be members of the Polystichum -TP Order.

The membership of the Ladysmith study ecosystem in one of the two alliances of the Gaultheria - PM Order is examined in Table 11 and Figure 14. Both tabular and spectral analysis indicated that this ecosystem belongs to the Mahonia - TP & PM Alliance but showed a considerable affinity to the Gaultheria - PM Alliance, both being tentative taxa. Using the floristic data and edatope these study plots are identified as members of the Mahonia - Gaultheria - TP & PM Climax Association (n.n., Krajina 1969).

Figure 14. The ecological spectrum indicating floristic affinity of the Ladysmith study plots to two alliances of the Gaultheria - PM Order.



Explanation of symbols:

G-PM - plants of the characteristic combination of species for the Gaultheria - PM Alliance

M-TP - plants of the characteristic combination of species for the Mahonia - TP & PM Alliance

Table 11. The plant species from the Ladysmith study plots found in characteristic combinations for two alliances of the Gaultheria - PM Order.

Plant alliance	Presence class and mean species significance
The Gaultheria - PM Alliance:	
Gaultheria shallon (p, cd)	V 7.9
Goodyera oblongifolia (ic)	II +.0
Kindbergia oregana (p, cd)	V 4.6
Linnaea borealis (cd)	V 3.2
Mahonia nervosa (ic)	V 5.1
Pseudotsuga menziesii (p, cd)	V 8.5
Rhytidiadelphus loreus (ic)	V 2.2
Rhytidiadelphus triquetrus (p)	IV 1.6
Rosa gymnocarpa (p)	III 1.9
Rubus ursinus (p, c)	V 2.8
Vaccinium parvifolium (cd)	V 4.4
The Mahonia - TP & PM Alliance:	
Achlys triphylla (d)	IV 4.8
Gaultheria shallon (p, cd)	V 7.9
Goodyera oblongifolia (ic)	II +.0
Hylocomium splendens (cd)	V 8.1
Kindbergia oregana (p, cd)	V 4.6
Linnaea borealis (cd)	V 3.2
Mahonia nervosa (ic, cd)	V 5.1
Polystichum munitum (cd)	V 3.0
Pseudotsuga menziesii (p, cd)	V 8.5
Rhytidiadelphus loreus (ic)	V 2.2
Rhytidiadelphus triquetrus (p)	IV 1.6
Rosa gymnocarpa (p)	III 1.9
Rubus ursinus (p, c)	V 2.8
Thuja plicata (ic, cd)	III 2.3
Vaccinium parvifolium (cd)	V 4.4

The membership of the Chilliwack ecosystem in one of the two alliances of the Polystichum - TP Order is examined in Table 12 and Figure 15. Both tabular and spectral analysis suggest that they belong to the Polystichum - TP Alliance (n.n.; Kojima and Krajina 1971 in Kojima 1971, Kojima and Krajina 1975; Klinka and Krajina in Klinka 1976, Klinka and Krajina 1983; Inselberg *et al*. 1982). The presence of *Mahonia nervosa* (cd,ic), *Trientalis latifolia* (ic) and *Tsuga heterophylla* (cd) identified the study plots as members of the Mahonia - Polystichum - TH & TP Climax Association (n.n.; Klinka and Krajina in Klinka 1976, Klinka and Krajina 1983; Inselberg *et al*. 1982).

Figure 15. The ecological spectrum indicating floristic affinity of the Chilliwack study plots to two alliances of the Polystichum - TP Order.

P-TP (71%)	T-TP (29%)

Explanation of symbols:

P-TP - plants of the characteristic combination of species for the Polystichum - TP Alliance

T-TP - plants of the characteristic combination of species for the Tiarella - TP Alliance

Productivity and Functional Relationships

A comparison of taxa and site indices for Douglas-fir of this study and those predicted by Krajina (1969) is given in Table 13. It is concluded that the Mahonia - Gaultheria - TP & PM Climax Association is

Table 12. The plant species from the Chilliwack study plots found in characteristic combinations for two alliances of the Polystichum - TP Order.

Plant alliance	Presence class and mean species significance
The Polystichum - TP Alliance:	
Acer macrophyllum (ic)	I +.0
Achlys triphylla (p)	V 4.9
Chimaphila menziesii (ic)	IV 1.3
Galium triflorum (s, c, cd)	V 2.2
Goodyera oblongifolia (ic)	IV 1.2
Leucolepis menziesii (s, cd)	I +.0
Mycelis muralis (p)	V 2.3
Plagiomnium insigne (s)	I +.0
Polystichum munitum (p, cd)	V 5.7
Pseudotsuga menziesii (d, cd)	V 8.5
Rhytidiadelphus triquetrus (ic)	V 3.6
Ribes lacustre (ic)	III 1.2
Stokesiella oregana (cd)	V 5.0
Tiarella trifoliata (s, c)	I +.0
Trillium ovatum (p)	V 1.6
The Tiarella - TP Alliance:	
Achlys triphylla (p)	V 4.9
Adenocaulon bicolor (ic)	III 1.3
Galium triflorum (s, cd)	V 2.2
Leucolepis menziesii (s, cd)	I +.0
Mycelis muralis (p)	V 2.3
Plagiomnium insigne (s)	I +.0
Polystichum munitum (p, cd)	V 5.7
Rhytidiadelphus triquetrus (ic)	V 3.6
Rubus parviflorus (ic)	I +.0
Streptopus amplexifolius (ic)	I +.0
Tiarella trifoliata (s, cd)	I +.0
Trillium ovatum (p)	V 1.6

Table 13. Comparison of biogeocoenotic taxa and site indices for Douglas-fir between the study plots and those predicted by Krajina (1969).

Climax association	Edatope	Site index (m/100yrs)
The Ladysmith study plots, CDFb Subzone		
1. Present study:		
Mahonia - Gaultheria - TP & PM	mesic(-subhygric)/mesotrophic	43
2. Krajina (1969):		
Eurhynchium - Mahonia - Gaultheria - PM (biogeocoenotic unit no.5)	mesic(-subhygric)/mesotrophic	42 (40.6-43.5)
The Chilliwack study plots, CWHb Subzone		
1. Present study:		
Mahonia - Polystichum - TH & TP	submesic/eutrophic	42
2. Krajina (1969):		
Rhytidiadelphus - Rhytidiopsis - Vaccinium - PM - AA - TP (biogeocoenotic unit no.35)	submesic/eutrophic	39 (37.6-40.5)
	mesic/eutrophic	42 (40.6-43.5)

synonymous with Krajina's biogeocoenotic unit no. 5. The reconstruction of past tree species composition and advanced regeneration in the Ladysmith ecosystem suggests that western redcedar has been a significant component in the association's floristic composition (Figure 16). The role of western redcedar is believed to increase gradually in the course of secondary succession. Thus, the inclusion of western redcedar into this association's climax composition and into the other ones related to permesotrophic and eutrophic trophotopes is considered to be a viable interpretation. The site index determined for the Ladysmith ecosystem is

Figure 16. Western redcedar of good vigor is common in the shrub layer of the Ladysmith ecosystem.

within the limits of growth class IIIa (40.6 to 43.5 m/100yrs).

The Chilliwack ecosystem can be related to Krajina's (1969) taxa through its edatopic and climatic characteristics. The edatopic grid in Figure 1 indicates that the submesic to mesic/eutrophic edatope in the CWHb Subzone is related to the biogeocoenotic unit no. 35. The corresponding unit in the CWHa Subzone is the biogeocoenotic unit no. 25: Hylocomium - Mnium - Achlys - Polystichum - PM - TP. On the basis of comparing constant dominant species, it appears that the recognized Mahonia - Polystichum - TH - TP Climax Association cannot be readily assigned to any of these units. This conclusion is supported by two special circumstances; firstly the Chilliwack ecosystem is climatically transitional, and secondly it is one of the ecosystem series developed on steep colluvial slopes. These ecosystems were classified into a special series of associations (Klinka 1976, Klinka and Krajina 1983), which has not yet been included in the grids. Thus, the identified climax association has an intermediate position between the unit 35 and 25. For both units the predicted site index on submesic edatopes is 39 (37.6-40.5) m/100yrs which is lower than that found on the study plots.

The preceding discussion established that the Douglas-fir ecosystems studied differed in a number of properties but the estimated site index was similar. In consequence, the total effect of environmental factors controlling forest growth must also be similar but because of compensation, the individual factors responsible for this effect may be different in each ecosystem.

Following a general characterization, selected data for regional climates affecting each ecosystem are presented in Table 14. As stated

Table 14: Selected climatic data for the study area.[1]

Study area	Ladysmith		Chilliwack	
Biogeoclimatic unit	CDFb		CWHb7	
	Mean	Minimum/ Maximum	Mean	Minimum/ Maximum
Number of data sets	19		12	
Climate (Koppen/Trewartha)	wetter <u>Csb</u>-<u>Cfb</u>		wetter (<u>Cfb</u>)-<u>Cfc</u>	
Mean annual prec. (mm)	1305	958/1936	2236	1422/3774
Mean prec. April-Sept. (mm)	301	227/ 422	615	425/ 939
Mean prec. of driest month (mm)	32	22/ 45	62	51/ 89
Mean annual temperature (°C)	9.1	8.0/ 9.8	5.6	4.6/ 6.5
Mean temp. of coldest month (°C)	1.5	0.1/ 2.8	-2.4	-4/ -1
Mean temp. of warmest month (°C)	16.9	15.9/17.8	13.6	12.4/14.4
Number of months with mean temperature less than 0°C	0	0 / 0	2.3	1 / 3
Number of months with mean temperature larger than 10°C	5.2	5 / 6	3.8	3 / 4
Frost free period (days)	187	133/ 250	139	104/ 181
Effective growing-degree days	980	881/1137	776	460/ 944
Potential evapotranspiration (mm)	424	355/ 549	334	298/ 378
Actual evapotranspiration (mm)	341	308/ 439	334	298/ 378
Actual evapotranspiration/ potential evapotranspiration	.81	.67/ .99	1.0	1.0/ 1.0
Water surplus (mm)	961	626/1540	1902	1123/3462
Water deficit (mm)	82	5/ 160	0	0/ 0

[1]The source is Courtin <u>et</u> <u>al</u>. (1983).

earlier each ecosystem was under the influence of different regional climate. Employing potential (PET) and actual (AET) evapotranspiration as indices of zonal plant activity under natural conditions as suggested by Major (1963), the potential for plant growth appears to be much greater in the CDF Subzone than in the $CWHb_7$ variant. The reasons are the warm temperature and long growing season of a wetter Csb - drier Cfb climate (Figure 17 and 18). However, due to the low summer precipitation in the CDFb Subzone a significant period of soil moisture deficiency is usually encountered. As a result only 81 percent of the PET is realized in the mesic ecosystem of this subzone. In contrast, there is no difference between PET and AET in the index ecosystem for the CWHb Subzone suggesting that all potential heat is used for plant growth because precipitation is more than adequate to cover PET. The difference of 7 mm between PET and AET is insignificant.

On the flat, mesic and mesotrophic Ladysmith ecosystem the local physiography does not modify regional climate; however, the steep slope gradient and aspect, along with the soil properties of the Chilliwack ecosystem will likely be influential in modifying regional climate.

The slope of 70% gradient and somewhat southerly aspect (250° azimuth) may be responsible for a minor increase in PET. The steep slope and a high volume of coarse fragments could result in a reduction of available soil water but the plant indicator analysis rejects this possibility; in fact, it rather suggests that the Chilliwack ecosystem has a higher soil water supply than the Ladysmith ecosystem. The same analysis also assessed the former ecosystem to have a richer nutrient regime than the latter. A high pH, high C/N ratio and high values of total carbon and base saturation of

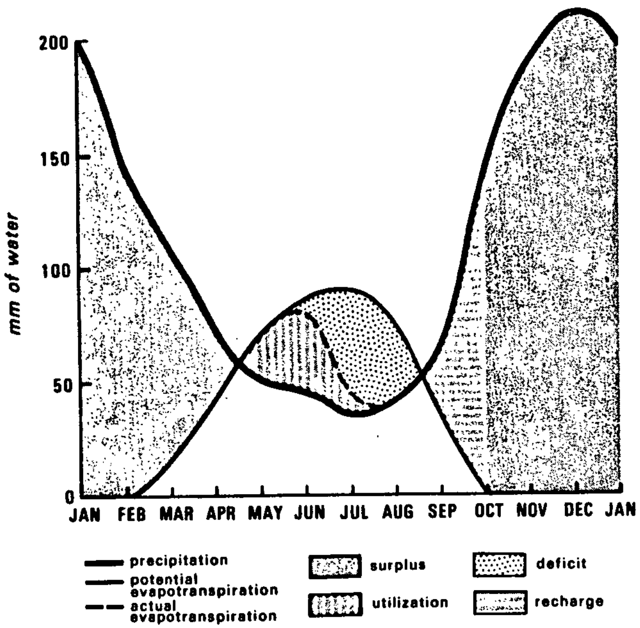


Figure 17. Annual water balance for the mesic ecosystems in the CDFb Subzone (after Courtin _et al_. 1983).

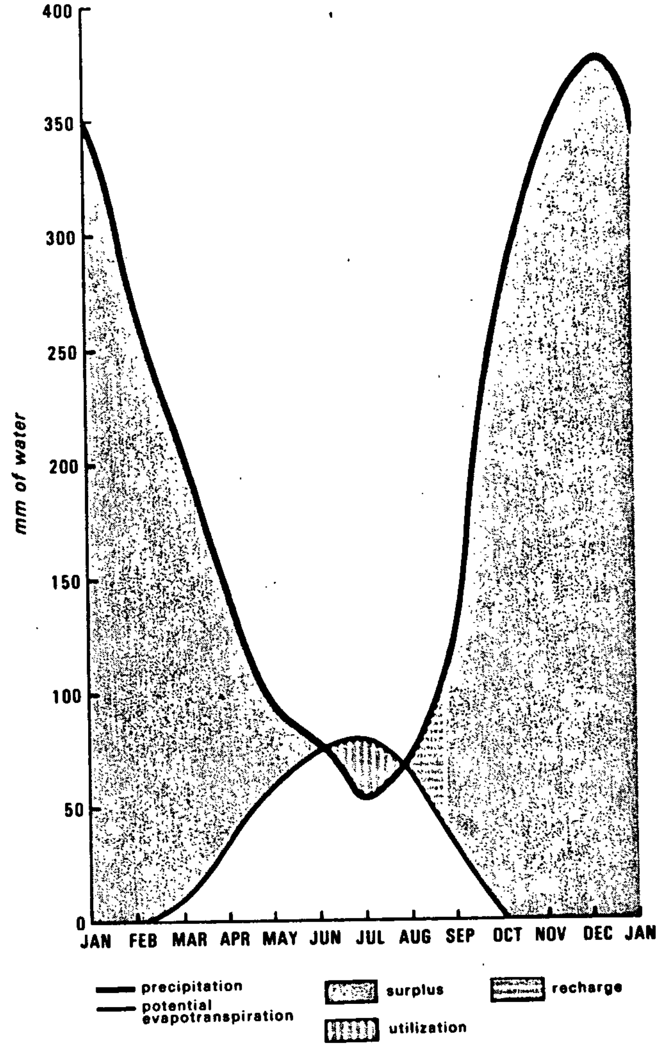


Figure 18. Annual water balance for the mesic ecosystems in the CWHb Subzone (after Courtin _et al_. 1983).

master B horizon determined for the Chilliwack ecosystem support this assessment.

Thus, the more humid climate and greater availability of nutrients, particularly of nitrogen, of the Chilliwack ecosystem compensate for the warmer climate and longer growing season of the Ladysmith ecosystem. The longer growing season of the latter ecosystem appears to be reflected in its radial growth pattern. The tree-ring analysis showed that the mean latewood/totalwood ratio was greater for the Ladysmith plots than for the Chilliwack plots. Although the difference between the plots is small, it was found to be highly significant ($p < 0.01$)(Table 15).

Table 15. Mean values obtained from a tree-ring analysis for the selected study plots. Standard deviations in parenthesis.

Study area	Latewood (cm)	Totalwood (cm)	Latewood/ Totalwood
Ladysmith	5.43 (0.97)	18.10 (3.29)	0.30 (0.02)
Chilliwack	5.57 (0.65)	20.66 (3.02)	0.27 (0.02)

Characterization of the Stands

While the analytical results will be presented and discussed from a number of viewpoints later in this section, major features of the stand analysis can be noted at this point.

Selected growth properties for the study plots and the mean values for each stand are summarized in Table 16. All parameters listed are given for Douglas-fir only and for all tree species found in the study plots including red alder, western hemlock and western redcedar. A small difference in age results in a 1.9 m difference in site index on a 50 year basis between the two stands. Major differences between the stands were found in number of stems/ha, diameter, basal area and volume characteristics. Because density and structure are the key factors determining growth characteristics of a stand, their characterization and relationship were the focus of stand analysis.

Age, Top Height and Site Index

The arithmetic mean age was 72 years and 78 years for the Ladysmith and Chilliwack stands, respectively, with a significant difference ($p < 0.01$) of six years. This difference will affect to a certain degree a variety of growth characteristics, and therefore will be accounted for where possible.

Both stands had an identical mean top height (height of the 100 largest diameter trees) of 39.6 m, with nearly identical ranges of 36.9 m to 41.5 m in the Ladysmith and 36.9 m to 41.1 m in the Chilliwack stand.

Table 16. Basic growth characteristics of the study plots and stands.

Plot no.	Age (yrs)	Top height (m)	Site index (m/50yrs)	Douglas-fir Dbh (cm) Mean	Douglas-fir Dbh (cm) Min.	Douglas-fir Dbh (cm) Max.	Douglas-fir NT/ha	Douglas-fir BA (m^2/ha)	Douglas-fir Volume (m^3/ha)	All species Dbh (cm) Mean	All species Dbh (cm) Min.	All species Dbh (cm) Max.	All species NT/ha	All species BA (m^2/ha)	All species Volume (m^3/ha)
The Ladysmith study plots:															
1	72	38.5	33.2	32.2	15.4	71.3	672	61.9	755	31.2	8.0	71.3	704	62.2	756
2	70	41.4	36.6	31.1	10.3	65.9	816	73.5	900	29.4	8.2	65.9	896	74.8	908
3	72	40.9	35.4	32.9	7.8	73.4	656	74.5	946	30.6	7.8	73.4	736	75.4	951
4	72	38.4	33.2	28.2	13.2	56.4	864	62.9	745	25.8	7.7	56.4	992	63.8	748
5	73	36.9	31.7	28.0	7.5	57.7	816	60.2	717	25.3	7.5	57.7	960	61.3	721
6	72	38.5	33.2	28.9	10.1	52.0	928	68.3	804	25.7	7.5	52.0	1120	69.9	811
7	72	39.5	34.1	31.9	11.5	66.0	608	58.4	723	30.6	10.5	66.0	656	60.5	728
8	72	39.1	33.8	31.6	7.1	61.0	816	76.2	937	31.6	7.1	61.0	816	76.2	937
9	72	37.3	32.3	28.7	8.5	63.1	976	72.8	864	27.8	8.0	63.1	1024	73.3	868
10	72	41.5	36.0	29.6	12.8	69.5	1008	84.9	1035	27.1	7.5	69.5	1152	86.1	1040
Mean	72	39.2	34.0	30.3	10.4	73.4	816	69.4	843	28.5	8.0	63.6	906	70.4	847
The Chilliwack study plots:															
11	78	39.3	32.3	41.2	14.0	70.1	461	70.8	875	33.2	9.4	70.1	723	79.0	939
12	77	38.9	32.3	39.7	18.2	62.5	569	76.3	920	32.4	10.3	62.5	846	83.5	972
13	78	39.1	32.3	41.4	15.1	65.0	496	75.4	931	33.0	8.7	65.0	720	79.5	955
14	78	36.9	30.5	38.6	21.2	54.6	544	68.0	809	28.6	8.0	54.6	944	75.9	856
15	78	41.2	34.1	44.6	16.8	65.5	448	76.4	952	33.3	8.6	65.5	736	82.7	992
16	79	38.3	31.4	43.5	18.8	69.3	512	83.2	1026	36.2	9.8	69.3	704	87.6	1054
17	78	39.1	32.0	48.8	24.4	75.7	400	80.0	1012	45.6	16.0	75.7	448	81.4	1021
18	78	39.6	32.3	38.4	9.0	69.4	592	78.9	943	35.0	9.0	69.4	704	81.7	962
19	80	38.5	29.9	42.0	13.5	76.3	533	83.8	1095	34.1	7.8	76.3	957	92.4	1167
20	78	41.1	33.8	46.8	27.7	71.1	464	85.6	998	46.8	27.7	71.1	464	85.6	998
Mean	78	39.2	32.1	42.5	17.9	76.3	502	77.9	956	35.8	11.5	68.0	725	82.9	992

The site index according to King (1966) is derived from the 10 largest diameter trees out of 50 sample trees, thus the number of site trees selected is not related to an area but to a fixed number of trees. Since number of trees per ha and stand structure are different for each stand the trees selected may be incompatible in relation to crown class. If, for instance, trees with a relatively lower crown class were included this would result in a lower site index for the Ladysmith stand. Adopting King's approach in this case would result in the site height as the average height of the 10 (ranging from 8 to 12) largest diameter trees per plot in the Ladysmith stand, being compared to the site height as the average height of the 6 (ranging from 5 to 8) largest diameter trees per plot in the Chilliwack stand.

To derive a more comparable site index, an area-related site height (i.e. the top height of the 100 largest diameter stems/ha) was used. This gave values identical to King's site height at a fixed density of 500 trees/ha. Using this approach, site indices of 34.0 and 32.1 m/50yrs were derived for the Ladysmith and the Chilliwack stands, respectively, and applied in further analysis. The predicted site heights at age 100 are 48.6 m and 46.1 m, respectively.

Curtis et al. 1974 examined whether the site index curves by McArdle et al. (1961) and King (1966) which were developed on the database of lowland Douglas-fir are applicable for high elevation Douglas-fir stands in western Oregon and northern Washington. They derived height growth and site index estimation curves from stem analysis of Douglas-fir trees in high-elevation stands and found that the resulting height growth pattern differs from that of low-elevation Douglas-fir; the height/age curve of high-elevation Douglas-fir has the culmination point at a higher age, declines before the intersection point with Kings's site index curve and exceeds the growth of the low-elevation stand afterwards.

Height over age growth could not be examined in this study to test the results of Curtis et al. According to their classification criteria (altitude) however, the Chilliwack stand belongs to these high-elevation forests. The site index curve for the site index of 42 m (reference age of 100 yrs) intersects King's site index curve at age 90. In consequence we can expect King's and Curtis et al's. site index values to be similar for the Chilliwack stand. The Curtis et al. site index was calculated for the Chilliwack stand as being 45.7 m/100yrs. Kings's predicted height value for age 100 was 46.1 m/100yrs. To compare growth and yield characteristics of the two stands at their present stage it was safe to apply King's site index for both stands. To compare the development of these parameters over time, King's site index is not applicable for the Chilliwack stand.

Applying the site index curves of the B.C. Ministry of Forests (Hegyi et al. 1981) site indices of 43 and 42 m/100yrs were derived for the Ladysmith and Chilliwack stands, respectively. Since not all plots featured dominant trees, the top height as defined above was applied to derive the site height. In comparison with King's and Curtis et al's. predictions for the site height at age 100, the site index curve of the B.C. Ministry of Forests seems to underestimate the site index. A single site index curve set for coastal Douglas-fir must lead to erroneous conclusions for growth and yield characteristics if the results of Curtis et al. are applicable in British Columbia.

In summary, the stands compared do not have the same site index as was

was desired for the objective of this study. The difference of 1.9 m (SI/50yrs) or 1.0 m (SI/100yrs) is due to the difference in age. Considering this relatively small difference in relation to exactness of measurements taken and the purpose of the study, it is thought that its influence on comparing the majority of growth characteristics will be insignificant, and whenever possible, appropriate adjustments could account for the difference.

Stand Structure

The stand composition is the arrangement of the elements constituting a forest stand. It is usually described in terms of species, age, structure and origin. The structure or the structural (spatial) composition of a stand refers to the horizontal and vertical distribution of trees (occasionally of other plant species) in a forest stand. The horizontal distribution is expressed either quantitatively by diameter distribution and crown coverage or qualitatively by a stand map showing location, diameter and crowns of individual trees. The vertical distribution or layering is expressed either quantitatively by coverage of layers (stories, strata), height distribution, crown class distribution, or graphically by stand map and stand profile.

The structure of a stand is the result of the species' silvical characteristics, site quality and management practices under which the stand originated and developed. Despite some uncertainty in stand history, the differences in stand structure between the two stands will be related to the different ecological function of Douglas-fir in the two ecosystems.

The different ecological function likely resulted in a significant difference in the number of Douglas-fir trees between the two stands. However, variations in stand density and initial stand density might be also responsible for much of these differences in stand structure.

The section on stand structure will describe structural differences between the stands and relate them to the ecological function of Douglas-fir. In the chapter on the influence of stand density some spacing and thinning studies, which show causative effects of density on some stand characteristics, will be reviewed, and the relationship between stand density and various stand characteristics will be examined.

Stand Map

To demonstrate the horizontal stand structure with elements of crown structure, size, shape and distribution, one representative plot in each stand was selected for stand mapping. Computer-plotted maps are presented in Figure 19 and 20. The maps are complemented by photographs of the canopy taken in each stand (Figure 21 and 22).

The four solid interconnecting lines on the margins represent the plot boundaries. The crown class identified for each tree is printed inside its diameter ring using arabic numerals from 1 to 4. The four points of branch extension are connected - for Douglas-fir with solid lines and for western hemlock with dashed lines - to give a rough shape of crown circumference. The trees with stems located outside the plot boundaries were included providing their branches extended into the plot.

The characteristic features of the horizontal stand structure for the

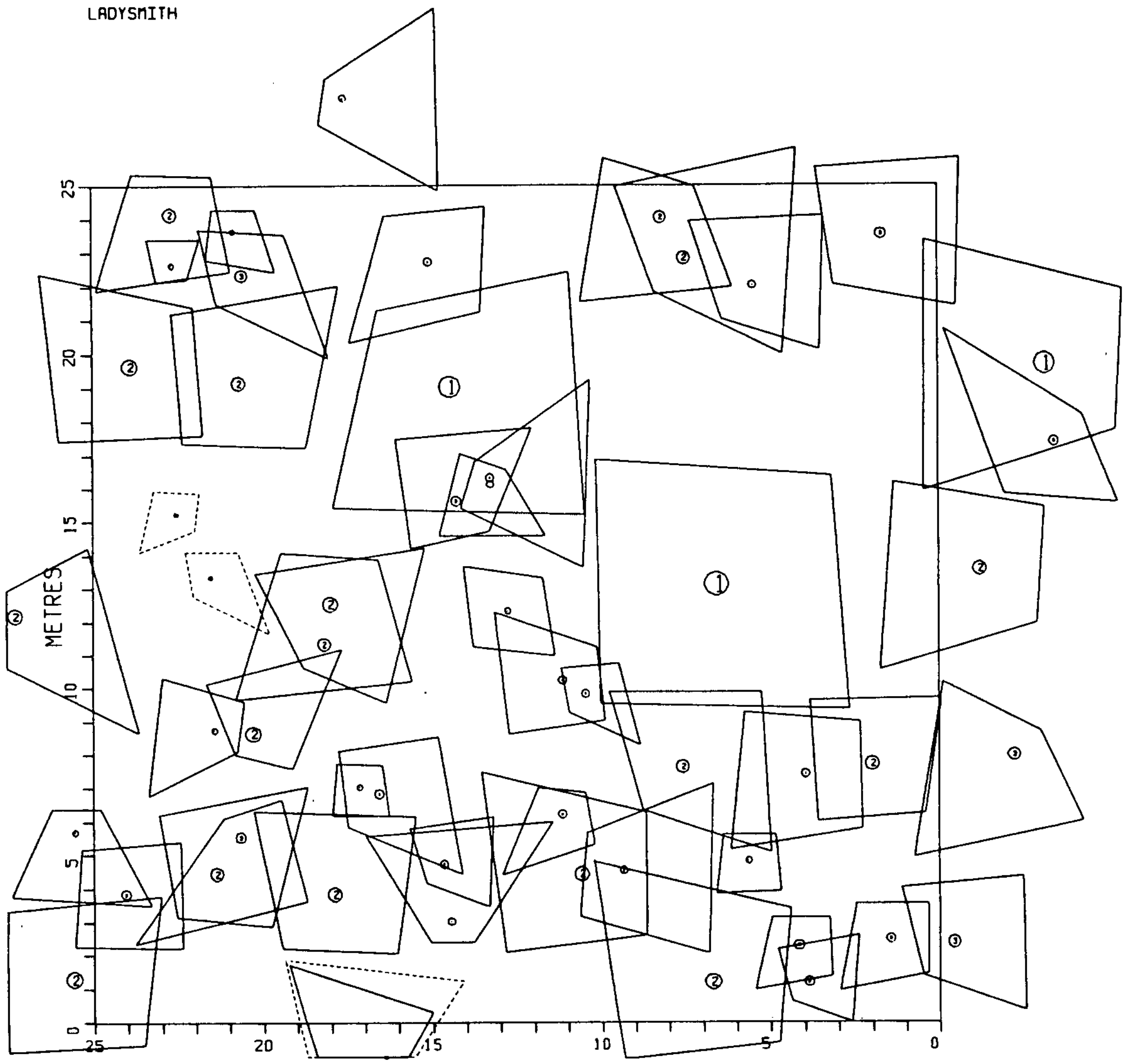


Figure 19. The stand map of the plot no.1 in the Ladysmith stand at the scale 1:222.

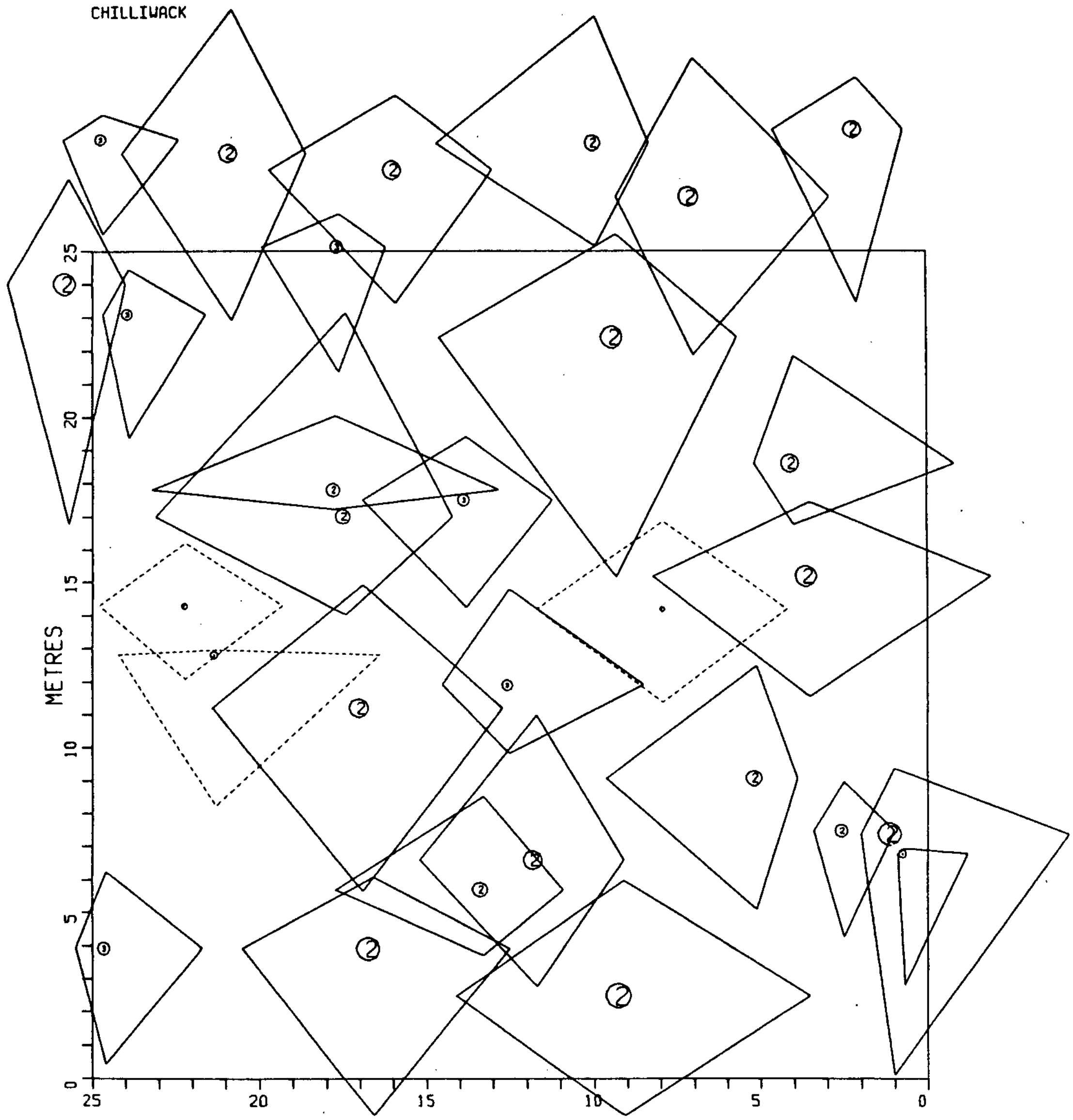


Figure 20. The stand map of the plot no.17 in the Chilliwack stand at the scale 1:222.

Figure 21. A representative view of the horizontal structure of the Ladysmith stand showing an uneven canopy with scanty crowns.

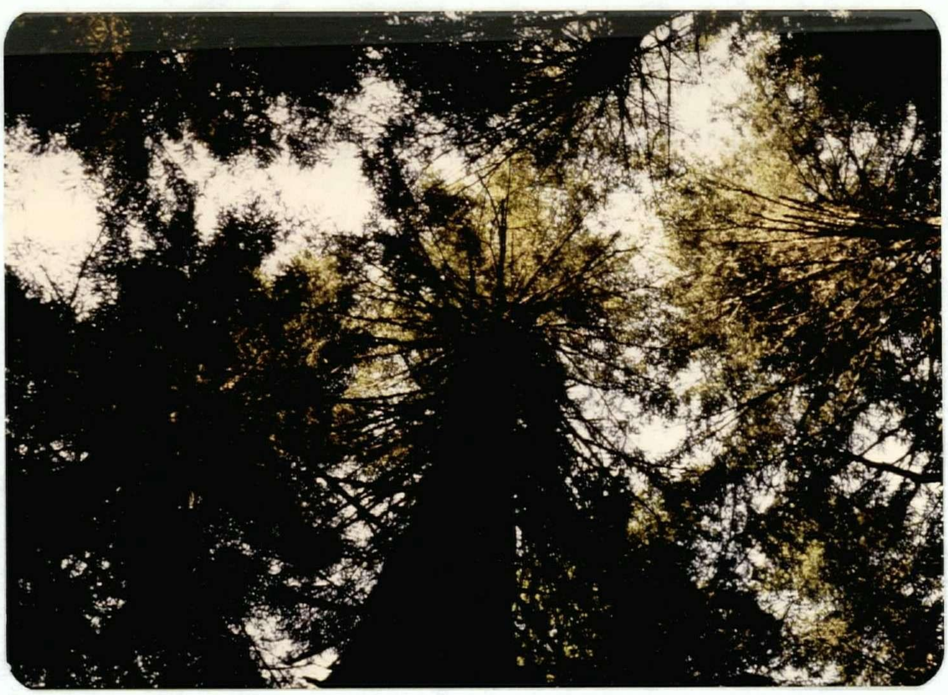


Figure 22. A representative view of the Chilliwack stand showing the horizontal structure of an uniform canopy with dense crowns.

Ladysmith stand are summarized as follows:

a. the two dominant trees are free of competition for space from codominant trees.
b. the codominant trees tend to form clusters, hence their crowns overlap but living branches are maintained.
c. the intermediate and suppressed trees appear to be evenly distributed
d. the crown shape is more or less a square.

The characteristic features of the horizontal stand structure for the Chilliwack stand are summarized as follows:

a. there are no dominant trees present.
b. the codominant trees are evenly distributed and no overlapped crowns are apparent.
c. there are very few intermediate and no suppressed Douglas-fir trees; those present are relatively little overshaded.
d. all trees tend to have a pronounced branch extension in the downslope direction as described earlier by Mitscherlich (1970).

Stand Profile

To illustrate the vertical structure of the stands a representative profile of each stand was plotted (Figure 23 and 24). Quantitatively, the differences between the stands in the coverage of the A_1, A_2, A_3 and B_1 layers were discussed earlier when describing the floristic composition and structure of forest communities. Although the relationship

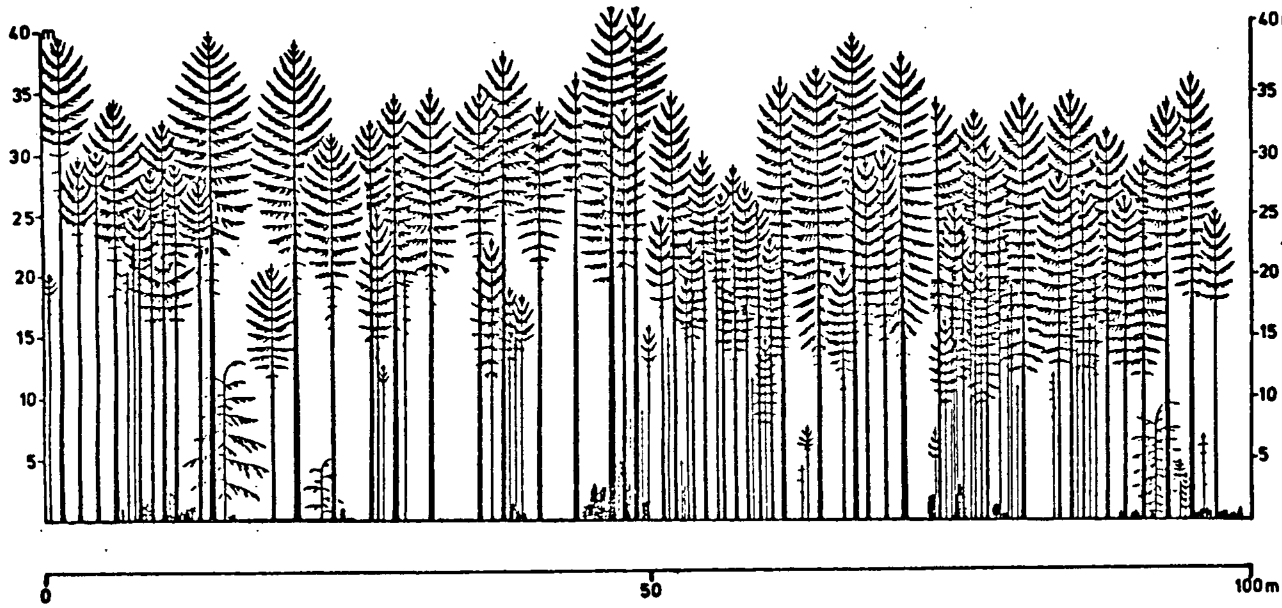


Figure 23. The stand profile representative of the Ladysmith stand, (the horizontal scale is 1:606, the vertical scale is 1:606).

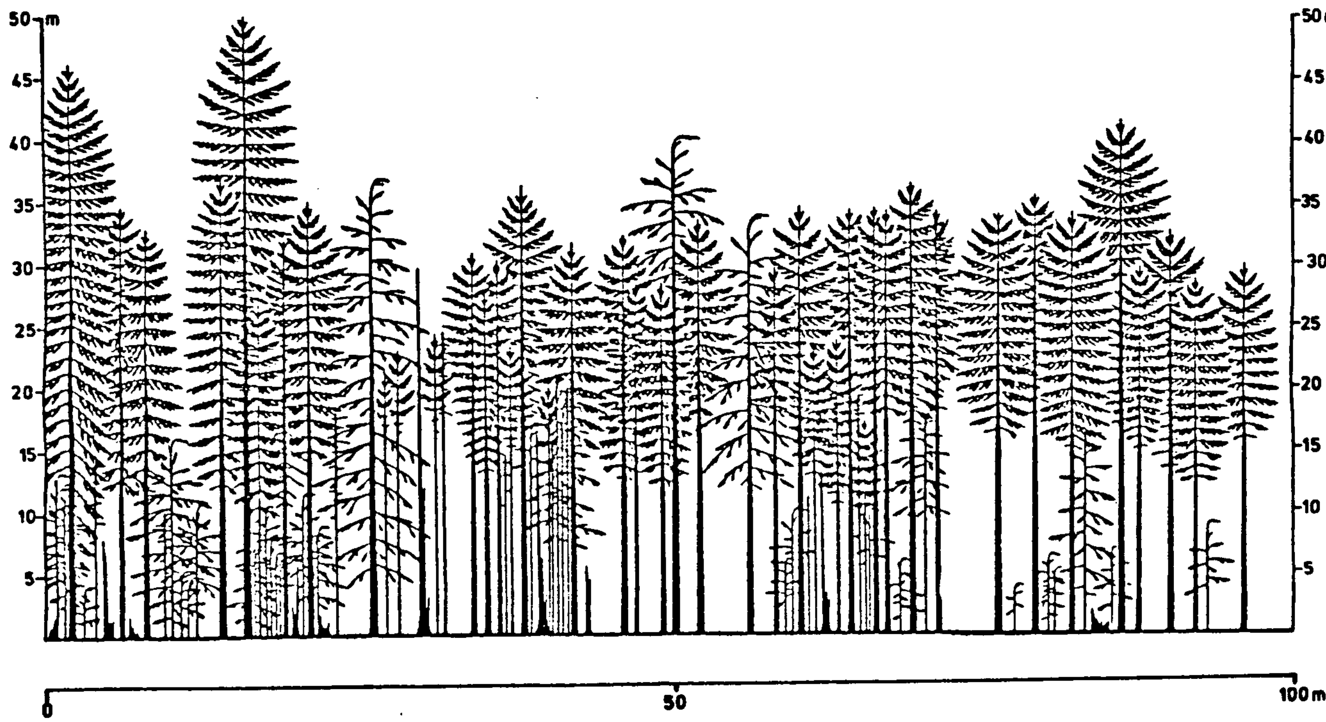


Figure 24. The stand profile representative of the Chilliwack stand (the horizontal scale is 1:606, the vertical scale is 1:606).

 = Douglas-fir;  = western hemlock

between crown classes and the above layers is only approximate the apparent differences in layering between the stands are complementary to those described for the stand maps. For an even-aged stand the Ladysmith stand exhibits a considerably diversified vertical structure. A high number of suppressed trees in the A_3 and B_2 layers and a large difference between heights of dominant and suppressed trees are the most characteristic features of this stand.

In contrast, the Chilliwack stand has an uniform structural pattern which is characteristic for an even-aged stand of a shade-intolerant species. This pattern features the dominant A_2 layer comprised mainly of codominant trees, the A_3 layer is lacking or very poorly developed comprising both intermediate and suppressed trees. There is only a small difference between heights of dominant and suppressed trees.

Crown Class Distribution

The relative distribution of crown classes either in relation to number of stems or basal area is one of the quantitative indicators of stand structure used in the study. Distribution histograms are presented in Figures 25 and 26. The role of density with respect to crown class distribution will be discussed in the chapter on the influence of density on various stand parameters.

The comparison of the distribution of crown classes in relation to number of trees revealed a contrasting pattern. In the Ladysmith stand the frequency increases in the order from crown class I to IV; in the Chilliwack stand, when omitting crown class I, the frequency decreased.

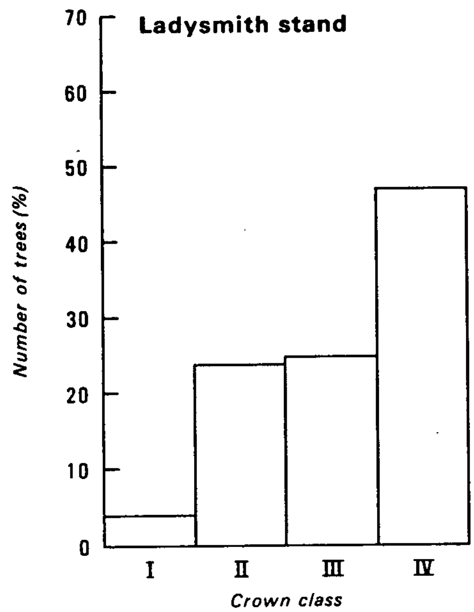


Figure 25a

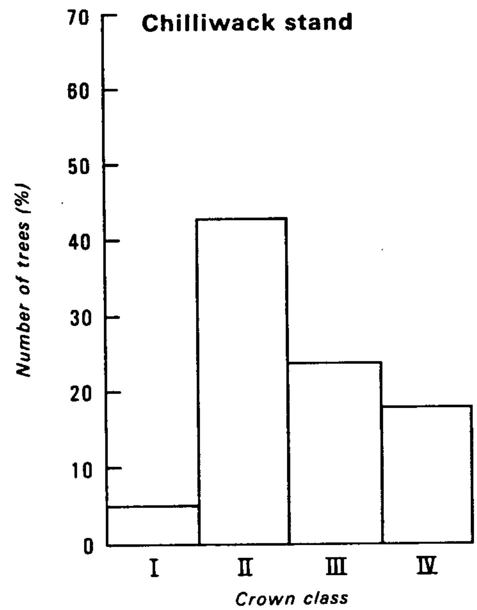


Figure 25b

Figure 25a and b. Distribution of crown classes in relation to number of trees for the Ladysmith stand (Fig. 25a) and the Chilliwack stand (Fig. 25b).

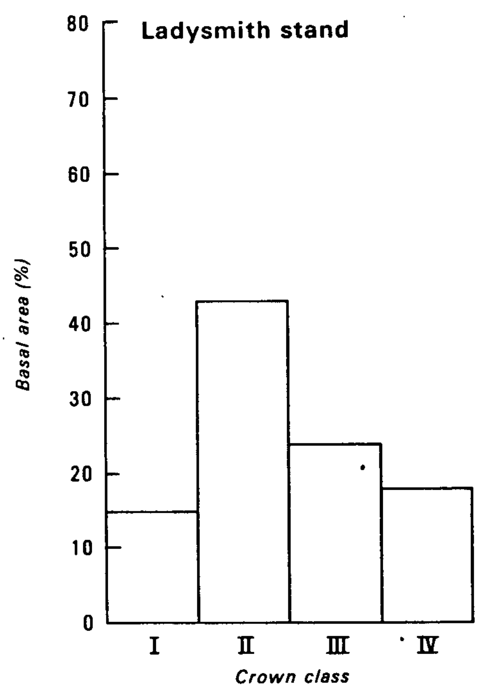


Figure 26a

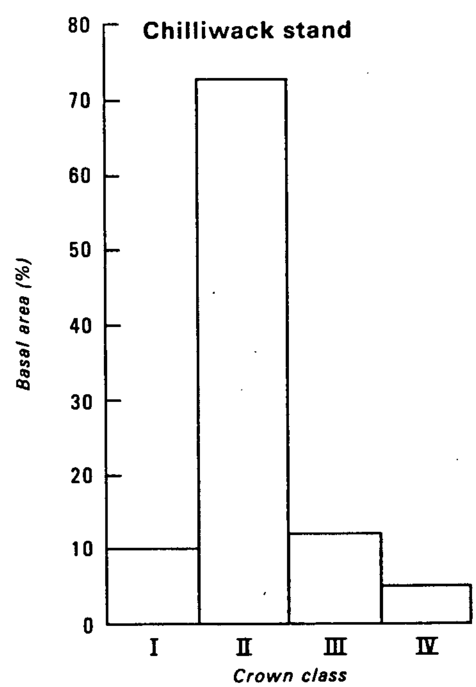


Figure 26b

Figure 26a and b. Distribution of crown classes in relation to basal area for the Ladysmith stand (Fig. 26a) and the Chilliwack stand (Fig. 26b).

The suppressed class is most frequent for the Ladysmith stand whereas the codominant class is most frequent for the Chilliwack stand.

Somewhat different but informative patterns emerged in relation to basal area. The codominant trees accounted for 73% of the basal area in the Chilliwack stand which is nearly twice the value for the same class in the Ladysmith stand. The combined basal area for crown classes III and IV in the Ladysmith stand was nearly as large as that for class II. Thus, a large number of intermediate and suppressed trees remain alive under the main canopy and contribute considerably to the stand basal area, substantially more than in the Chilliwack stand.

It could be safely inferred from the crown class distribution that crown competition is severe in the Chilliwack stand, particularly for the codominant component. The likely result of shading is early mortality because the frequency of intermediate and suppressed classes stays at a low level. On the other hand, the crown competition in the Ladysmith stand is believed to be less severe. There are fewer dominant and codominant trees to compete with the lower canopy layer and restrict the availability of light.

Length of Live Crown-Total Height Relationship

The form and size of live crown is considered to be an expression of vigor and shade-tolerance of a tree species. Vigorously growing trees, such as those in the uppermost tree layer, and shade-tolerant tree species tend to have long and large crowns in relation to their total height (Worthington _et al_. 1961, Mitscherlich 1970). To assess the difference in shade tolerance of Douglas-fir in the two stands, the relationship between the ratio of length of live crown to total height (LCTH) and total height (TH) was examined (Figures 27,28 and 29).

When comparing the plotted data, a high dispersion for the Ladysmith stand is apparent (Figure 27 and 28). Trees with very short live crowns persist in nearly all canopy layers. In contrast, in the Chilliwack stand there are very few living trees with the LC/TH ratio below 0.26; furthermore these trees belong exclusively to the lower canopy. The corresponding value of the LC/TH ratio in the Ladysmith stand is approximately 0.13. These values, shown in Figure 27 and 28 as parallel lines with the x-axis, are suggested to represent the upper limit of zones of imminent mortality (Drew and Flewelling 1979).

To evaluate the extent and significance of these trends two separate linear regressions are given (Figure 29). In comparison the slope of the regression for the Chilliwack stand is considerably steeper than that for the Ladysmith stand. This indicates that the decrease of total height is related to a rapid decrease of the LC/HT ratio. The short live crown of shorter trees predisposes low vigor and mortality of the shade-intolerant Douglas-fir in this ecosystem.

The regression line for the Ladysmith stand lies in the range from 12 to 37 m of total height well above that for the Chilliwack stand. Thus within this range, including suppressed, intermediate and some of the codominant components, trees possess relatively long live crowns, a high stand density notwithstanding. On a relative basis, the capability of Douglas-fir to maintain a longer live crown, especially in the lower tree layers, is interpreted as the expression of a greater shade-tolerance.

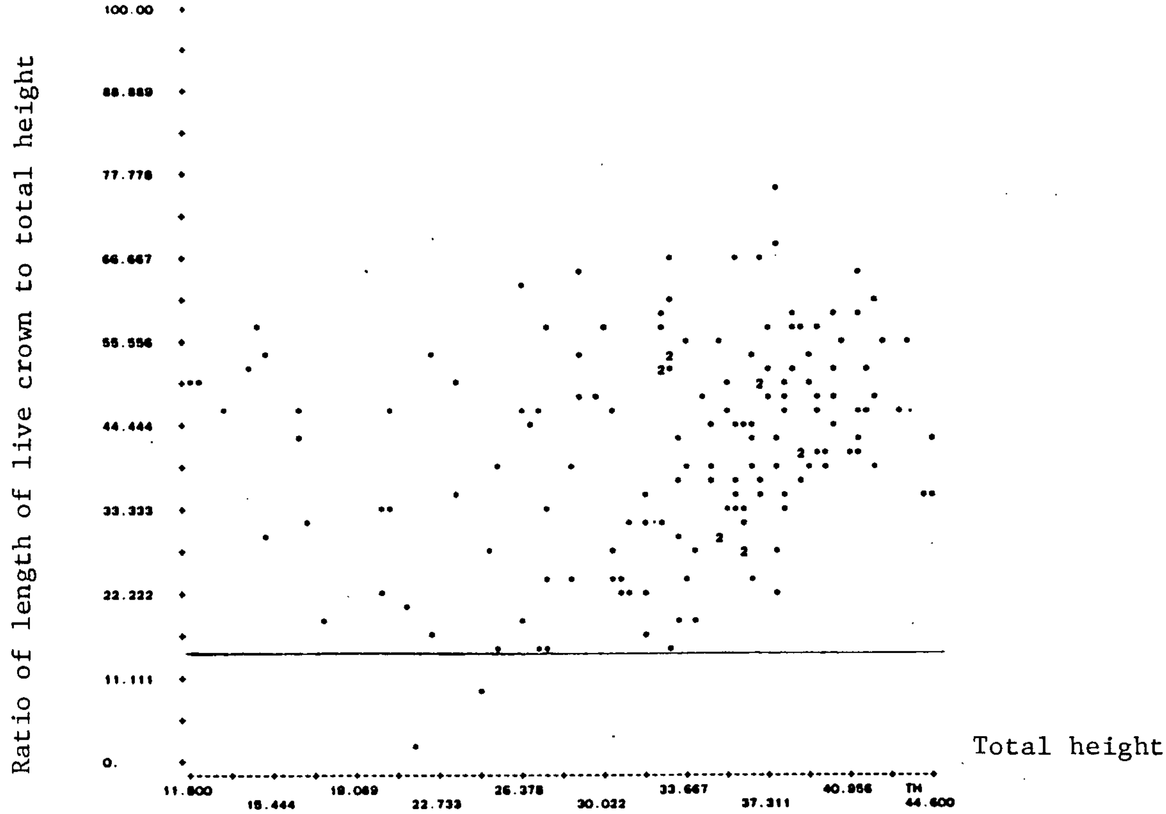


Figure 27. Relationship between the ratio of length of live crown to total height and total height for the Ladysmith stand.

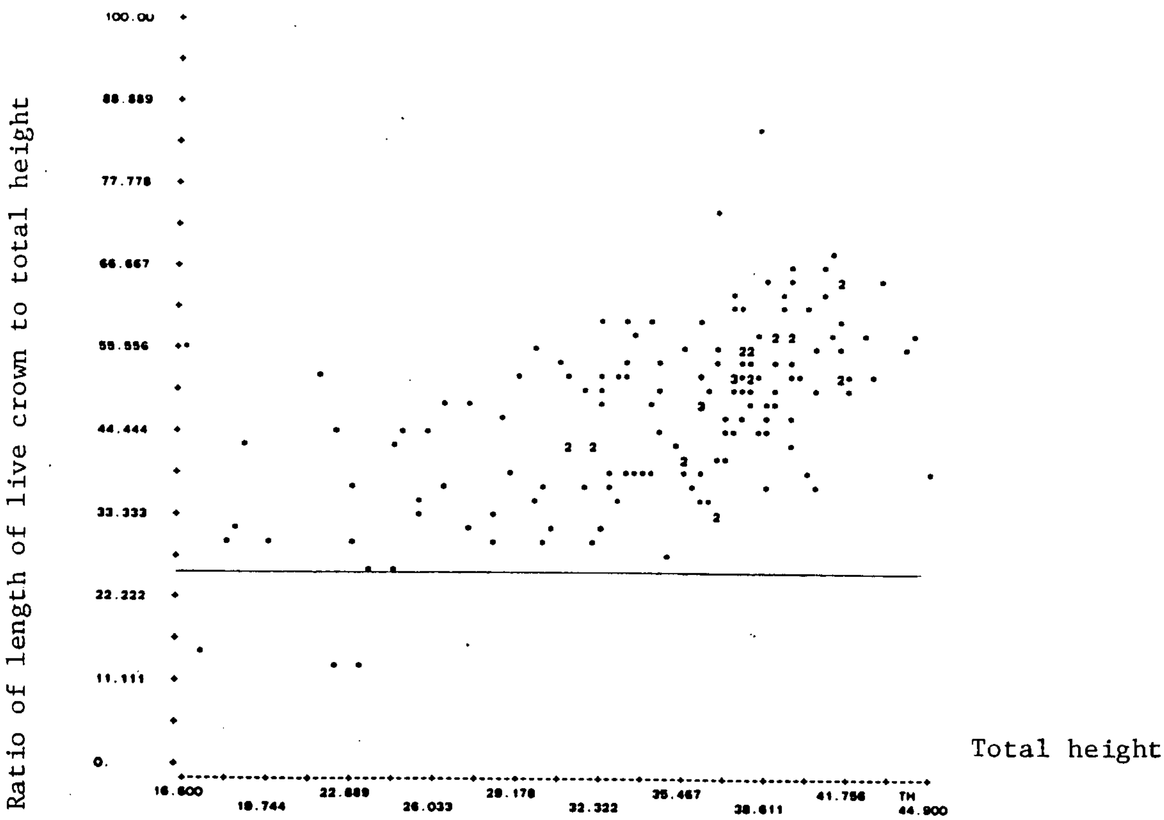


Figure 28. Relationship between the ratio of length of live crown to total height and total height for the Chilliwack stand.

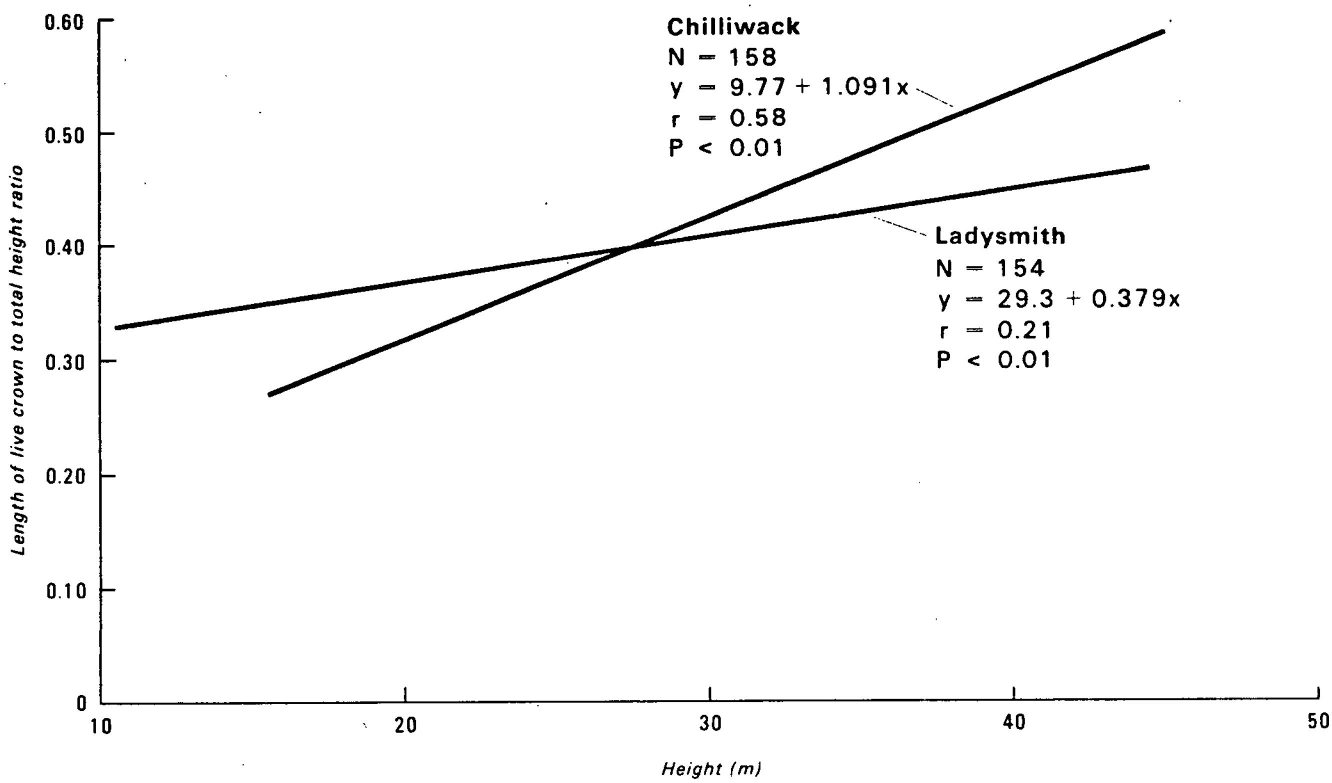


Figure 29. Linear regressions showing relationships between the ratio of length of live crown to total height and total height for the stands.

Within the height range of 30 to 45 m most trees in the Chilliwack stand belong to the codominant crown class. In that crown class position trees have relatively more space than in an intermediate or suppressed position, and therefore their live crown ratio is relatively higher (Worthington _et al_. 1961). Within this same height range many trees in the Ladysmith stand have an intermediate crown class position (Fig. 25). As a result, the regression line of the Chilliwack stand lies above the one of the Ladysmith stand within that range. ack stand lies above the one of the Ladysmith stand within that range.

Diameter Characteristics

Several mean diameters were computed for each plot (Table 17):

1. The arithmetic mean diameter of Douglas-fir and of all species.
2. The diameter of the mean basal area stem as the diameter of the (theoretical) tree with the arithmetic mean basal area for Douglas-fir only. This mean basal area stem is commonly preferred because in even-aged and uniform stands its diameter corresponds approximately to that of the stem with the mean volume (Gehrhardt 1901). This was applied when deriving Reineke's stand density index.
3. The arithmetic mean diameter of the 100 largest diameter stems/ha.

As could be expected on the basis of diameter-density relationships, all diameter characteristics for the Chilliwack stand have significantly greater values ($p < 0.01$) than those of the Ladysmith stand. The possible effect of density will be discussed in the section on the influence of density on stand structure and parameters.

Table 17. Diameter characteristics of the stands studied.

Stand	Ladysmith	Chilliwack
Diameter	(cm)	
The mean dbh of Douglas-fir	30.3	42.5
The mean dbh of all species	28.5	35.8
The dbh of the mean basal area stem	32.9	44.5
The mean dbh of the 100 largest diameter trees	53.7	60.1

Diameter and Basal Area Distribution

Distribution of diameters was the third quantitative analysis conducted to characterize structural differences between the stands (Figures 30 and 31). This analysis was complemented by the distribution of basal area showing number of trees in 0.02 m^2 classes (Figures 32 and 33).

Contrasting distribution patterns were expected on the basis of crown class distribution. The Ladysmith stand features a pattern which is strongly skewed to the left. A significant preponderance of the small diameter component in the Ladysmith stand is interpreted as the expression of the moderate tolerance to shade of Douglas-fir. The Chilliwack stand seems to approximate a normal distribution pattern, which is slightly skewed to the right. Since the basal area is a function of the squared diameter, a tree with a smaller diameter at the left side of the diameter distribution has a relatively smaller basal area than a tree with a larger diameter. In consequence, the basal area ranging from 0.01 to 0.03 m^2 comprises all trees with a diameter of 11.2 to 19.5 cm, whereas the basal area class ranging from 0.41 to 0.43 comprises the trees with the diameter between 72.3 and 74.0 cm. In consequence the culmination point of the basal area distribution is skewed to the left in relation to the diameter distribution. A large number of small trees in the Ladysmith stand explains a nearly J-shaped basal area distribution which further accentuates the distinct culminating pattern as seen in the diameter distribution. In contrast, the basal area distribution of the Chilliwack stand reveals an even distribution pattern throughout the range of the basal area.

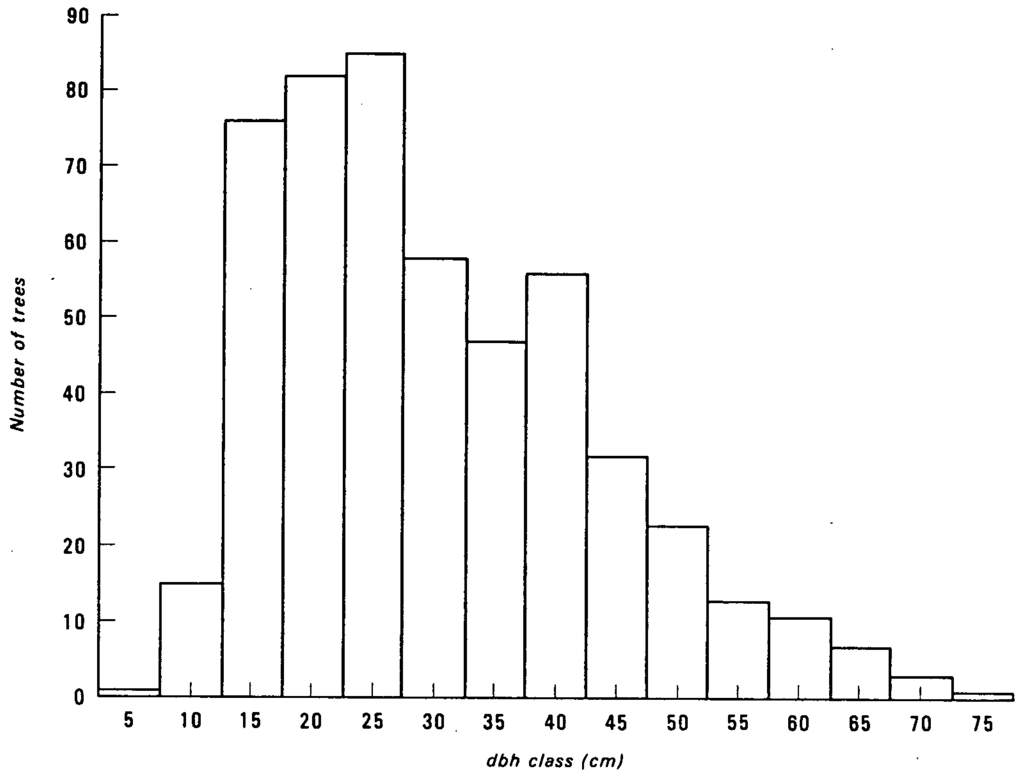


Figure 30. Diameter distribution for Douglas-fir in the Ladysmith stand.

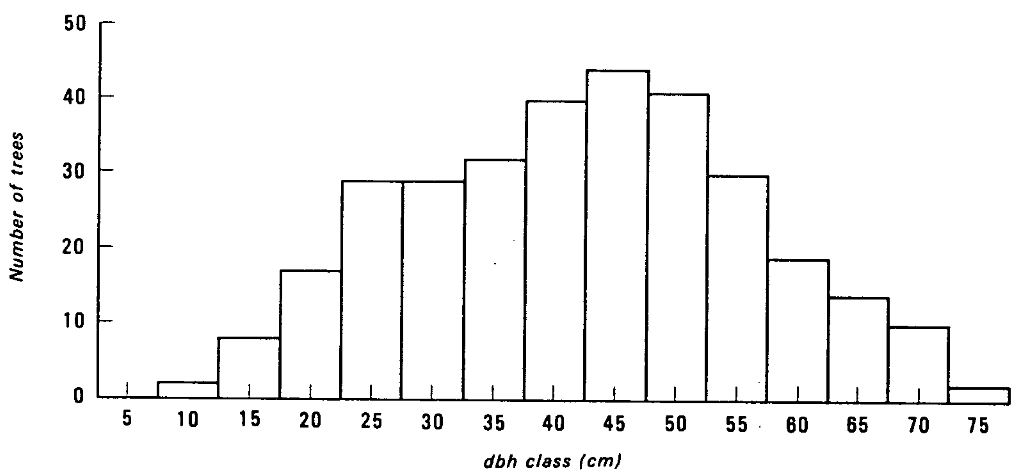


Figure 31. Diameter distribution for Douglas-fir in the Chilliwack stand.

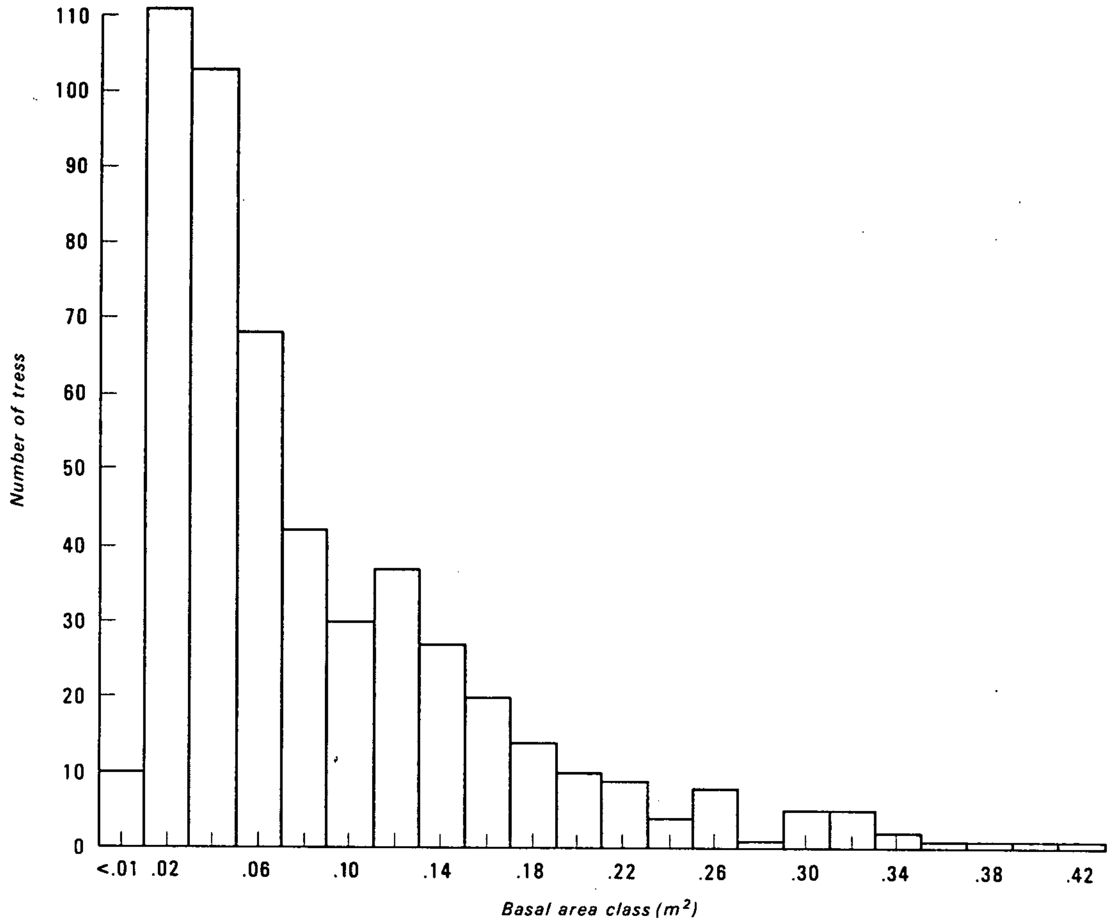


Figure 32. Basal area distribution for Douglas-fir in the Ladysmith stand.

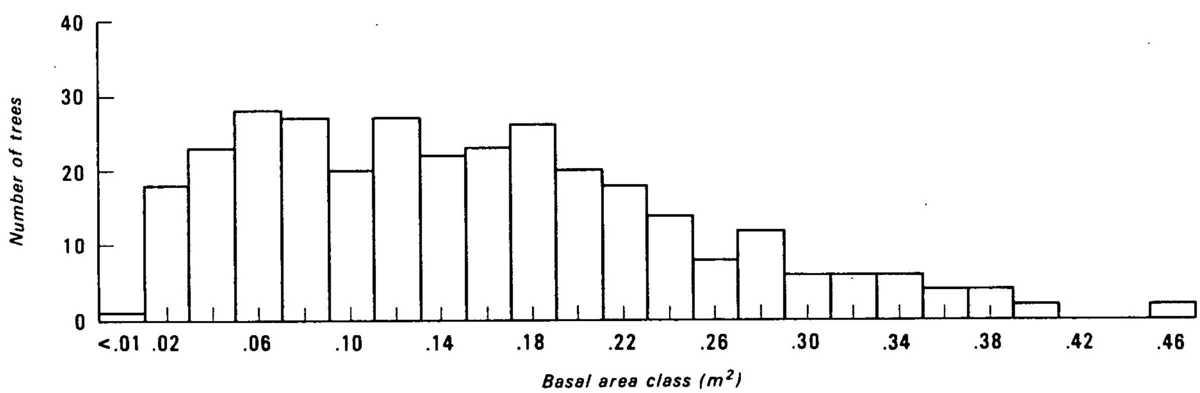


Figure 33. Basal area distribution for Douglas-fir in the Chilliwack stand.

Height-Diameter Relationship

The two stands studied had an identical top height but the corresponding diameters were consistently different. Therefore, height/diameter (h/d) ratios must be also different for each stand. Interpreting height-diameter relationships (Figure 34), the regression curve for the Ladysmith stand is located on the average about 2 m above that for the Chilliwack stand. In consequence, the h/d ratios for the Ladysmith stand must be consistently higher than those for the Chilliwack stand.

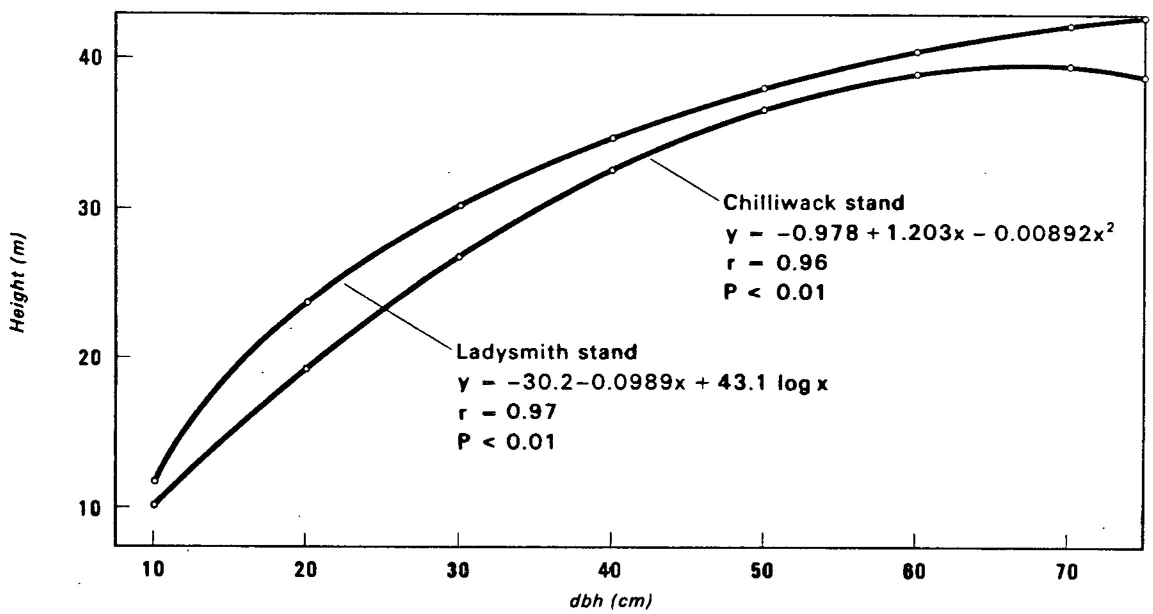


Figure 34. Relationship of height to diameter for Douglas-fir in the study plots.

The h/d ratio was calculated for all trees for which heights had been measured. For short trees the h/d ratio was in the range from 1.0 to 1.5 (the latter value refers to a tree with the dbh of 13.5 cm). The mean h/d ratio for the 100 largest diameter trees in the Ladysmith stand was 0.74

(ranging from 0.64 to 0.80). The corresponding values for the Chilliwack stand were significantly lower than those above; the mean h/d ratio was 0.65 (ranging from 0.57 to 0.70) and the highest ratio of 1.2 was calculated for a tree with dbh of 18.8 cm. In this stand h/d ratios equal to or greater than 1 were rare.

The h/d ratio is commonly used in Europe as an indicator of shade tolerance, taper and windfirmness. On a relative basis, shade-tolerant species tend to form high density stands (Mayer 1970). At high density levels diameter growth decreases in relation to height growth, hence the h/d ratio for shade-tolerant species is higher than that for less shade-tolerant or shade-intolerant species. The above results corroborate further the converging evidence on tolerance to shade as the underlying cause of structural differences found in the studied stands.

Under low density levels diameter growth increases in relation to height growth. It has been documented that the diameter increment at breast height is larger in relation to that higher on the stem (Assman 1970). In consequence, there is a corresponding increase in taper. Since trees in low density stands have also relatively low h/d ratios, taper and this ratio are negatively correlated. Thus, the h/d ratio is expected to be different between the two stands. In this respect the application of volume equations using a single value for taper may result in a considerable systematic error. Further study determining the variation of different ecosystems could be informative.

Windfirmness of even-aged stands is a desirable silvicultural attribute. A well developed root system is one of the several factors influencing windfirmness. In general, the development of root systems is inhibited by dense spacing. Large crowns and diameters develop under competition-free density levels, which are indicated by relatively low h/d ratios. Critical values of h/d ratios have been derived in Europe to guide stand density management in areas and for species prone to windthrow.

The qualitative and quantitative differences in horizontal and vertical structure described above suggest a distinct structural pattern for each stand: the diversified structure is characteristic for the Ladysmith stand while uniform structure is characteristic for the Chilliwack stand. In this respect the Ladysmith stand resembles an uneven-aged stand of a shade-tolerant species whereas the Chilliwack stand is typical for an even-aged stand of a shade-intolerant species. These structural arrangements are believed to reflect Douglas-fir activity in relation to local heat and water supply (cf. Major 1963).

The strongly vertically diversified structure of the Ladysmith stand is attributed to a moderate shade-tolerance of Douglas-fir in this climatic and edaphic environment. As a result, a multilayered canopy with scanty crowns has developed in which the lower tree layers are relatively free of shading. In contrast, the slightly vertically diversified structure of the Chilliwack stand is attributed to the shade-intolerance of Douglas-fir in this more humid and edaphically wetter environment. Thus, it is not surprising that a nearly single-layered canopy with dense crowns has developed in which shading causes a rapid reduction of live crown and mortality. These interpretations agree with the varying shade tolerance of Douglas-fir in different ecosystems discussed earlier. It was suggested that Douglas-fir in humid and perhumid climates and on sites where it takes up more water than it requires must not be shaded if the excess water is to be removed effectively by transpiration (Krajina 1965, Krajina et al. 1982). It is concluded that the tolerance of Douglas-fir to shade has been the main factor determining the structure of the stands studied.

Density

Number of Stems

Approximately 90 percent of the total number of stems/ha, 99 percent of the total basal area and 100 percent of the total volume in the Ladysmith study plots are constituted by Douglas-fir; the corresponding values for the Chilliwack study plots are 69, 94 and 96 percent, repectively.

The relatively high percentage of other tree species in the Chilliwack study plots is due to a large number of western hemlock trees in the upper shrub layer and the lower tree layer. However, they contribute only 6% to the total basal area and 4% to the total stand volume. The western hemlock component is considerably uneven-aged and young as it has followed the pattern of secondary succession. If it was included in the following analyses where density is correlated with other stand characteristics, the results might be distorted. It is suggested that this minor and subordinate component has had relatively little influence on the growth characteristics of the major Douglas-fir component. Therefore some analyses e.g. those involving number of stems/ha, are concerned with Douglas-fir only.

The comparison of number of trees per hectare (NT/ha) produced an overwhelming difference between the stands. The values of NT/ha for plots and stands were given in Table 16. Comparing the Douglas-fir component only, the difference between the stand means was found significant at $p < 0.01$ level; when all trees were considered this difference was found also significant at $p < 0.05$ level.

These results are consistent with respect to the overwhelming role of shade tolerance on the structure of the stands as discussed above. Under relatively dry conditions, considering interaction of climate and hygrotope, both shade-tolerant and shade-intolerant tree species grow in high density stands (Assman 1961). In relation to the shade-tolerance of a species, the shade-intolerant species however, grow in less dense stands than the shade-tolerant species (Mayer 1970). It is concluded that the number of trees in relation to the structure reported for each stand reflects approximately the maximum density level at this developmental stage.

Stand Density Indices

An important parameter, which determines yield characteristics is the stand density. Quantitative information on stand density is therefore important in relation to tree size and stand yield. Various workers have developed a number of density indices, whereby a given stand is compared to a reference stand, either at crown closure or in maximum stocking conditions. Curtis (1970) reviewed these indices and concluded that they have approximately equal utility.

A simple density index was proposed by Reineke (1933). It is based on the relationship between the maximum number of trees/ha (Nmax/ha) (this maximum number of stems/ha refers to his database from plantations) and the corresponding mean diameter (meandbh).

$$\log \text{Nmax/ha} = -\ 1.605 \log(\text{meandbh}) + \underline{k}$$

This relationship is believed to be independent of age and site index, the constant k is species-specific and was computed from Reineke's reference curve for Douglas-fir as 5.02928. This value for k and the mean diameter (Table 17) were entered into the above equation to solve it for Nmax/ha. The percentage stocking value was derived as the ratio between the actual number of stems/ha (N/ha) and the Nmax/ha. This calculation resulted in a percentage stocking value of 0.74 and 0.78 for the Ladysmith and the Chilliwack stands, respectively, with a relative difference of 5%.

Using the diameter of the mean basal area stem which corresponds closely to that of the stem with the mean volume instead to derive the percentage stocking value resulted in an identical percentage stocking value of 0.84 for both stands.

The corresponding stand-density index is 500 for both stands. This stand-density index refers to the number of trees per acre at the intersection of a line parallel to the reference curve with the 10-inch ordinate.

The reference curve as given by Reineke to derive the density index is valid only for even-aged stands of a single species. Therefore if all species were included to derive the percentage stocking value it should be interpreted with caution. To get an overall percentage stocking value for the two stands however, it was calculated. Applying the diameter of the mean basal area stem resulted in percentage stocking values of 0.87 and 0.95 for the Ladysmith and Chilliwack stands, respectively, this is a difference of 9%.

Drew and Flewelling (1979) proposed a relative stand density index, defined as the ratio of actual stand density to the maximum stand density attainable in a stand with the same mean tree volume. This index is independent of age, site quality and other factors. Applying the value of mean tree volume and number of Douglas-fir trees/ha to the diagram of relative density indices for Douglas-fir (cf. Drew and Flewelling, p. 525), the identical value of 0.74 was determined for both stands. The corresponding values, if all species are included, are 0.80 and 0.84 for the Ladysmith and the Chilliwack stands, respectively. This also implies that both stands are under conditions of imminent competition mortality (cf. Drew and Flewelling, p. 521).

The derived relative density indices are of considerable significance in indicating the same relative density, and hence comparability, for the stands studied. This is supportive of the previous conclusion suggesting that the present density levels of the stands approximate the carrying capacity of each site. The implied imminent competition mortality appears to be predicted correctly for shade-intolerant Douglas-fir in the Chilliwack stand. However, the agent for mortality is believed to be the density itself by causing excessive shading. In the Ladysmith stand mortality appears to be an environmental agent, which affects primarily the suppressed tree component having a reduced vigor. To elucidate the influence of density on stand structure the relationship of density to crown class, top height, diameter and volume were examined.

Relationship between Density and some Stand Characteristics

Crown Class-Density Relationship

The dominant and codominant component comprises the crop trees produced in a stand. Thus, the information on the influence of density on this stand component and stand structure could be useful for stand management. Using basal area, the ratio of crown class I and II to all crown classes was calculated for each plot and applied as an independent variable in a regression analysis. The results are given in Figure 35.

In general, the basal area of the upper canopy component decreases with increasing stand density. This suggests that a highly competitive environment in high density plots has suppressed the growth of dominant and codominant trees. Under the same density conditions dominant and codominant trees in the Chilliwack stand contribute consistantly more to basal area than those in the Ladysmith stand. This is to be expected in view of differences in stand structure discussed above.

However, the differential rate of this relationship is of considerable significance. The slope of the regression line for the Ladysmith stand is steeper than that for the Chilliwack stand (0.0509 and 0.0164, respectively). Therefore, increasing density in the Ladysmith stand does not result in an increase in mortality, but in an increase of the lower canopy component apparently due to the shade-tolerant nature of Douglas-fir. Growth of the upper canopy component is suppressed, its advantageous position notwithstanding, mainly due to the available water supply being shared by all trees present in the stand. In contrast, an increase in density in the

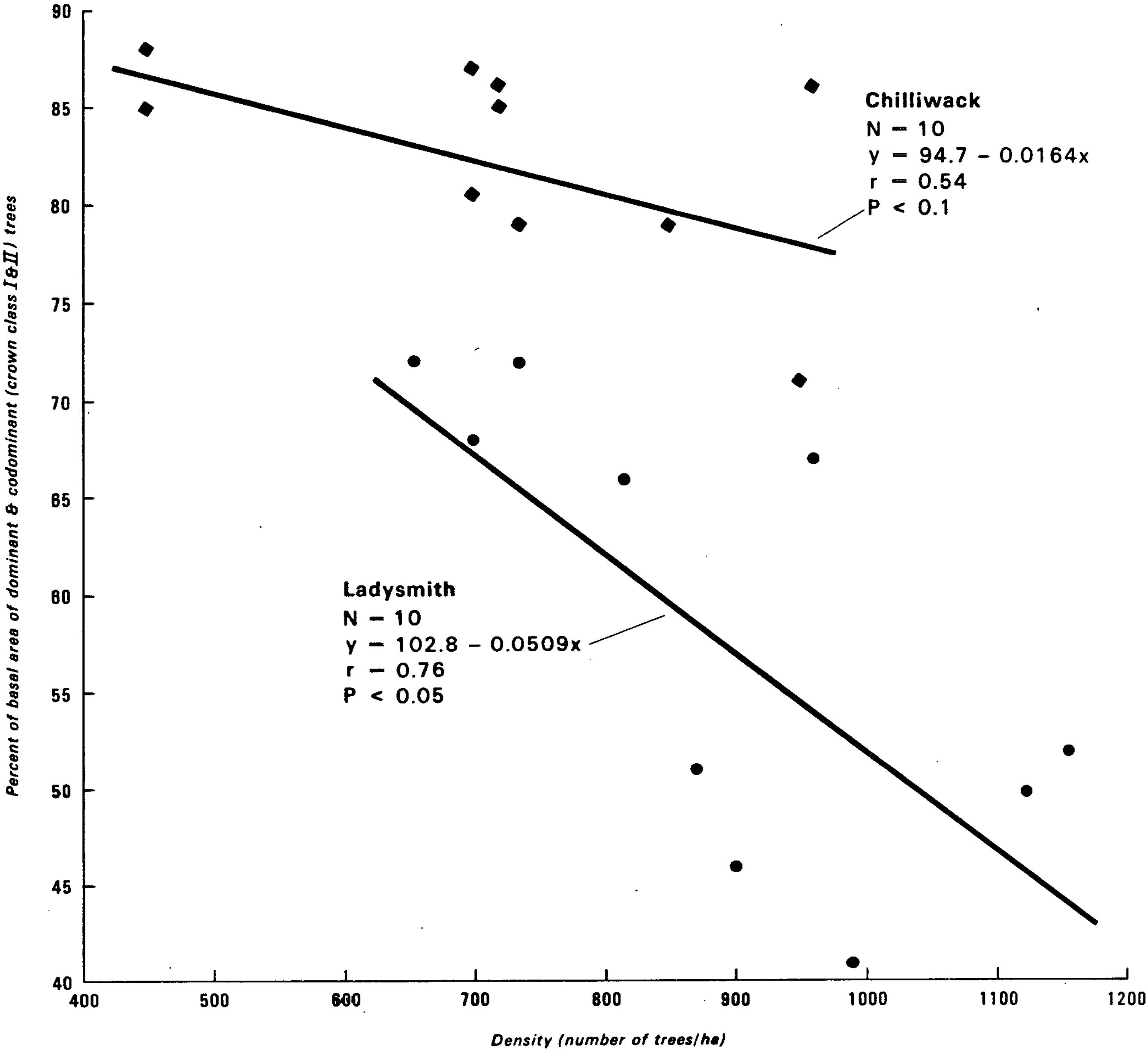


Figure 35. Relationship between the percent of basal area of dominant and codominant trees and density.

Chilliwack stand has relatively little influence on the contribution of the upper canopy component to the stand's basal area. High density conditions however, appear to reduce diameter growth of dominant and codominant trees.

With respect to the shade-intolerant nature of Douglas-fir, an increase in density results in an increased mortality, hence a poorly differentiated vertical stand structure. The suppressed and in part intermediate stand component is comprised mainly of shade-tolerant western hemlock whose contribution to the stand's basal area is negligible.

Effect of Density on Height

Braathe (1957), Sjolte-Jorgensen (1967) and Evert (1971,1973) reviewed literature on the effect of initial spacing on height, diameter, basal area and volume growth. Results from spacing experiments in Norway spruce plantations in Europe indicated that differing spacing had little influence on the height growth of trees (Braathe 1957). Sjolte-Jorgensen (1967) concluded, that for many studies he cited, in experiments with *Picea abies*, *Pinus* ssp. and other conifers, the mean height of the stand increased with increasing spacing. The spacing trials for which he showed this influence of spacing on height were generally denser than the ones Braathe referred to. Both authors agree that on dry and poor sites the development of height appears to be retarded by high initial spacing. However, most of the studies refer to mean height, which can be expected to be lower in denser stands with a larger number of small and suppressed trees. They also define mean height in various ways, and therefore results may vary according to the definition applied. Consequently caution is necessary when drawing conclusions about the effect of initial spacing on height growth and site index.

Summarizing results of a fity-year Douglas-fir spacing trial on a poor site (site index IV), Reukema (1979) reported that increasing number of stems/unit area had a definite negative impact on the height growth. The resulting site index (height of the 100 largest trees per acre) was found to be 50% higher at the widest spacing than at the dense spacing. Analyzing data from an 11-year-old Douglas-fir spacing trial in France, Bartoli et al. (1971) did not find any influence of spacing on top height. Results from the 20-year-old Douglas-fir spacing trial in the U.B.C. research forest on a high-quality site (SI is 55m/age 100) show no difference in total height and height growth for the plots ranging from 0.9 m to 4.60 m in initial spacing (Smith 1977).

An increase in height growth after thinning on a poor site (top height of 21 m at age 50) was reported in the Shawnigan Lake Experiment (Barclay et al. 1982), whereby trees in the smallest and largest diameter classes had the highest relative height increase. First results of a cooperative levels-of-growing-stock study show no difference in height growth between thinned plots and control plots (Williamson 1976, Berg et al. 1979). 21 years of repeated thinning had no effect on height growth in the Voight Creek study (Reukema 1972).

From a review of yield tables (1972) Curtis concluded, excluding lodgepole and ponderosa pine, that the effect of stand density on height growth and site index estimates is usually small. In contrast Reukema and Bruce (1977) suggested that a high initial spacing causes a reduction in height growth and consequently affects the site index.

It can be expected that additional results of Douglas-fir spacing trials in Germany (Abetz 1971), France (Bartoli et al. 1971) and the Pacific Northwest (Warrack 1964, Warrack et al. 1964, Revell 1970, Diggle 1972, Smith 1977) will show a variable reaction of Douglas-fir to initial density. In summary, no general statement about the influence of density on height can be made. The influence of variables like stand age, site quality and envionmental factors has to be assessed to allow valuable predictions about the interaction of spacing and height growth.

Top Height-Density Relationship

Comparability of the two stands measured in terms of site index is essential to the study. If the stand density in either of the two stands has influenced height growth, then the site index as a measure of the productivity potential of a site will be affected. For this purpose, the top height-density relationships were examined (Figure 36 and 37). Linear regression lines were derived for both data sets and drawn into the scattergrams. The linear regression for the Ladysmith plots was not significant and the slope coefficient was close to zero (0.00023). Thus it can be concluded that the density is not correlated with the top height in the Ladysmith stand. The regression line for Chilliwack however, is significant ($p < 0.1$), 34 percent of the total variation in the top height is explained by the regression. The trend of the regression line (slope coefficient is 0.00434) indicates that the top height decreases with increasing density. When the number of Douglas-fir was used as the independent variable in another regression analysis, a steeper slope coefficient of 0.00893 was obtained, but the regression analysis was not significant.

The variable density could be a result of differing site quality, whereby a better site is correlated with less trees/ha and a poorer site with a higher density. To examine this hypothesis site index was used

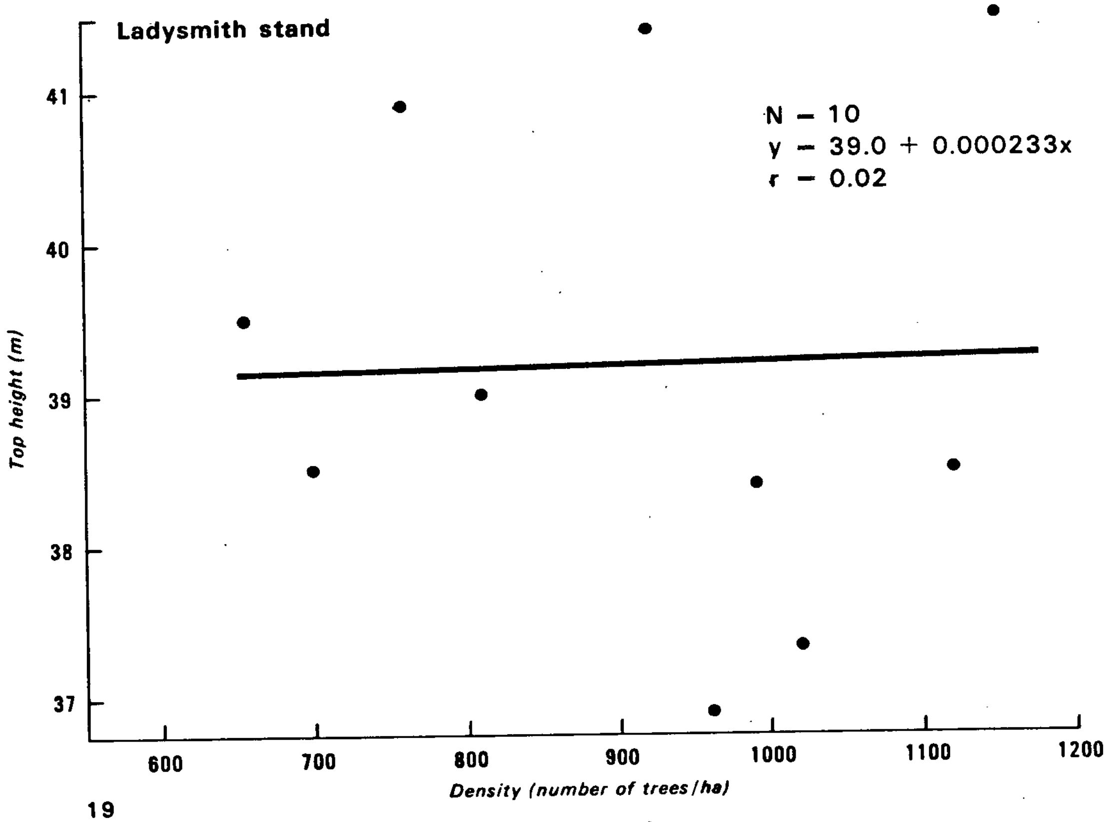


Figure 36. Relationship between top height and density (all species) in the Ladysmith stand.

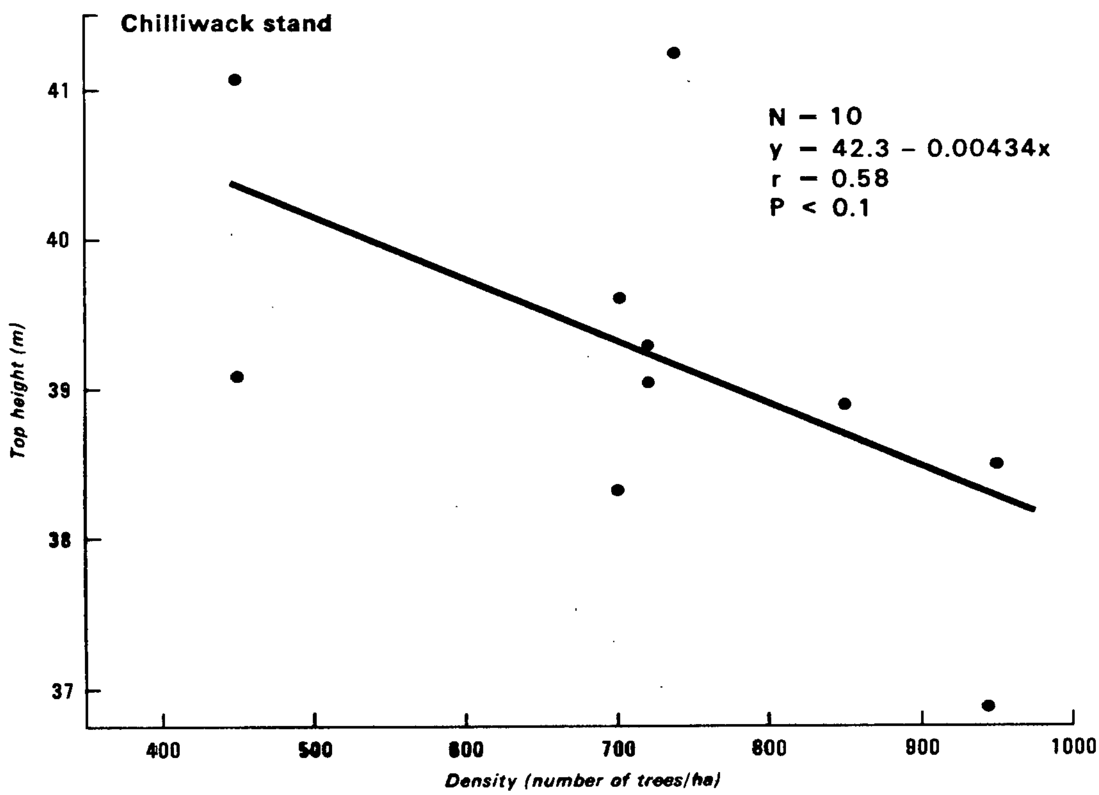


Figure 37. Relationship between top height and density (all species) in the Chilliwack stand.

instead of height as the dependent variable in another set of regression analyses. The resulting equations, r-values and significance were similar to the ones where height was used. No correlation between site index and density was found for the Ladysmith stand, with either Douglas-fir/ha or total stems/ha as the independent variable. For the Chilliwack stand, using the total number of stems/ha resulted in a significant ($p < 0.1$) relationship between this parameter and site index with a slope coefficient of 0.00466. Again this slope was steeper (0.00887) when the number of Douglas-fir/ha was used, but this regression was not significant. These results indicate that when trees on the more productive sites in the Chilliwack stand become taller, the smaller trees, left with less light, cannot survive. However, no correlation between site index and density is apparent in the Ladysmith stand. Therefore, if some trees on better sites become taller, the smaller trees manage to stay alive in a suppressed position - an indication for their relative shade-tolerance.

If however, the difference found in top height is not due to a variable site quality and, if the variability in stand density (stems/ha) as measured in this study reflects differences in initial spacing, then the lower spacing could have resulted in greater heights in the Chilliwack stand.

Because of the contrasting relationships found in this study I propose the hypothesis, that the top height of some tree species may be affected under certain conditions by stand density. It is suggested that this could be a function of shade tolerance of a species, which may vary in relation to regional climate and hygrotope (Krajina _et al_. 1982). In the Ladysmith stand where Douglas-fir is moderately shade-tolerant the dominant and codominant trees have crowns relatively free of shading. Even if the lower crowns of these trees are shaded, the shading is believed to have a minor effect on height growth and a slow effect on mortality. In the Chilliwack ecosystem however, where Douglas-fir functions as a shade-intolerant tree, increased stand density results in excessive shading of large parts of the live crowns of dominant but mainly codominant trees causing in this case a rapid reduction of live crown, and hence growth.

Effect of Density on Diameter

A stimulating effect of low initial spacing on the diameter growth rate has been reported in all spacing trials cited by Braathe (1957). Sjolte-Jorgensen (1967) confirms these results for young stands. In comparison initial spacing did not influence the diameter increment of a stand between age 29 and age 62. The difference in mean diameter at breast height (dbh) of plots with varying spacing did not increase after age 28 and therefore was due to the differing diameter increment during the first 28 years. Sjolte-Jorgensen concludes for conifers that the poorer the site, the longer it will take until the difference in mean dbh may be considered to remain constant with increasing age. Evert (1971) shows a similar effect of age in a graph (cf. Figure 13), where the mean dbh increment for a 5-year period is plotted over spacing for four stands at different ages. The steepness of slope for this relationship decreases with stand age.

For an 11-year-old Douglas-fir stand Bartoli et al. (1971) reports an increased mean dbh for the plots at wider spacing. In the Wind River spacing trial (Reukema 1970, Reukema 1979) the mean dbh was found to be twice as large at wider spacing as at denser spacing. The analysis of the U.B.C. spacing trial showed the mean dbh to be twice as large for the 4.60 m spacing as for the 0.9 m spacing, and the respective dbh increment eight times as large (Smith 1977). While sampling a wide range of spacing levels in unthinned plantations in New Zealand, James et al. (1974) reported that the mean ring width (defined as the mean dbh divided by age) decreased linearly with increasing spacing up to a spacing level of 1000 trees per hectare. For higher densities however, mean ring width and spacing were not correlated.

In various thinning trials the mean dbh and dbh increment were reported to increase for the thinned plots in comparison with the control plots and furthermore to increase with heavier thinning levels (James et al. 1974, Barclay et al. 1982). A considerable part of the increase in mean dbh however, may be due to the removal of trees with diameters smaller than the average dbh. The thinning rules for the "levels-of-growing-stock" studies (Williamson 1976, Berg et al. 1979) try to avoid this "false" effect by prescribing that the quadratic mean dbh of cut trees should approximate that of trees available for cutting. Since crop trees (usually the largest diameter trees!) are excluded from cutting, there will remain some small difference between the mean dbh before and after thinning, which is not due to growth. The reported differences in the mean dbh between the different thinning levels are however much larger than could be attributed to this effect. In the McClearly Experiment Forest thinning trial larger than average trees were removed during the initial thinning. After 15 years the residual trees were not appreciably larger in the thinned stand than in the unthinned stand, in spite of the fact that the 15-year dbh increment of the residual trees in the thinned stand was measured to be 29% greater (Reukema et al. 1973). In the Voight Creek study the removal of trees in all diameter classes did not result in an increase in the mean dbh (Reukema 1972). Miller et al. (1977) did not find an increased dbh increment in the thinned stands versus the control stands during a five-year observation period.

The growth of future crop trees (a specified largest number of trees per unit area) is of particular importance to forest managers. Therefore some studies additionally assess the influence of spacing on the mean dbh of these crop trees. In the spacing trials the mean dbh of the 100 largest trees/ha (Bartoli et al. 1971) and 250 largest trees/ha (Reukema 1979) was significantly greater. It is interesting to note that in the Wind River spacing trial the difference between the mean diameter growth of wider and denser spaced plots was slightly decreasing in the last 10-year period (Reukema 1979).

From some thinning trials an increase in mean dbh for crop trees in the thinned stands in comparison with the control plots is reported (Worthington 1966, Berg et al. 1979, Barclay et al. 1982). Dbh increment of the 100 largest diameter trees per hectare was not significantly greater in thinned stands than in unthinned stands in the Voight Creek study (Reukema 1972). Therefore the mean diameter of these crop trees did not increase for the thinned plots. Some authors note that thinning seems to favor the growth of intermediate and suppressed trees rather than dominant trees (Miller et al. 1974, Miller et al. 1979, Barclay et al. 1982).

In summary the stimulation of diameter increment by low stocking levels is a generally accepted fact. The degree of this impact however, seems to vary. This is graphically shown in Figure 3 of Sjolte-Jorgensen's (1967) report. The mean diameter as the dependent variable is plotted over spacing as the independent variable and regression lines are drawn. The slopes of this regressions differ for trials with the same tree species (Picea abies). This indicates that other factors, possibly age and site quality, initial stocking and kind and degree of thinning may influence this relationship.

As a consequence of larger diameter growth per tree the diameter distribution of low stocking plots is shifted to the right. In general the height-diameter regression curves of wider spaced plots tend to lie above the ones for closer spacing, because at low stocking levels height does not at all or slightly increase while the diameter increment increases considerably. Both effects can be observed in a comparison between the two stands (Figures 30,31 and 34).

Diameter-Density Relationship

To test whether density has a similar effect on the mean diameter, mean diameter/density regressions were computed for each stand (Figure 38 and 39).

A clear relationship for both stands emerged: the mean diameter decreases with an increasing number of Douglas-fir/ha. In addition there is a marked difference in the steepness of slope between the two ecosystems. The slope coefficient for the Chilliwack stand is more than five times as steep as that for the Ladysmith stand. This indicates that the Chilliwack stand responds to a change in density with a relatively

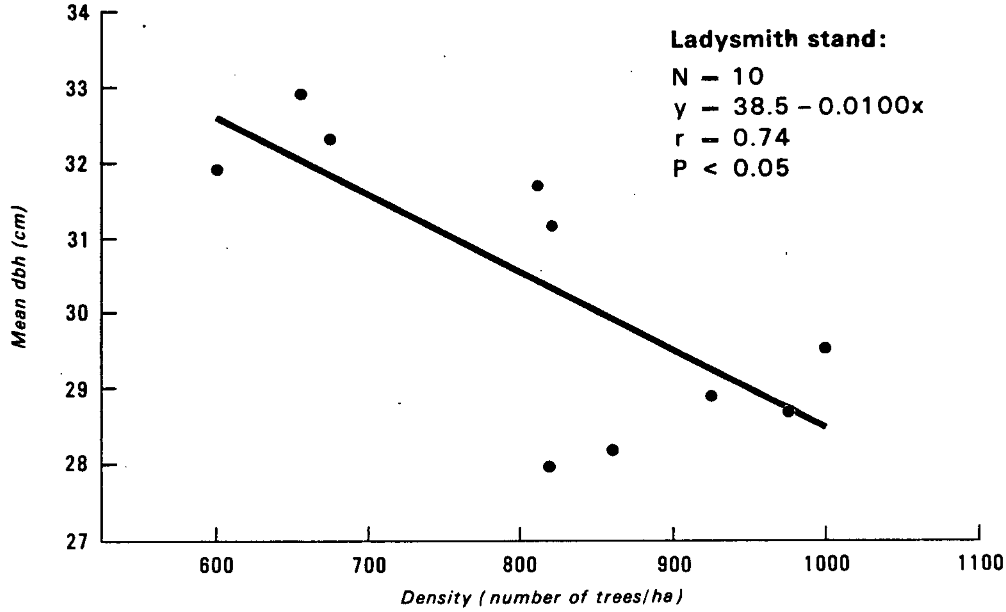


Figure 38. Relationships between mean dbh and number of trees/ha of Douglas-fir in the Ladysmith stand.

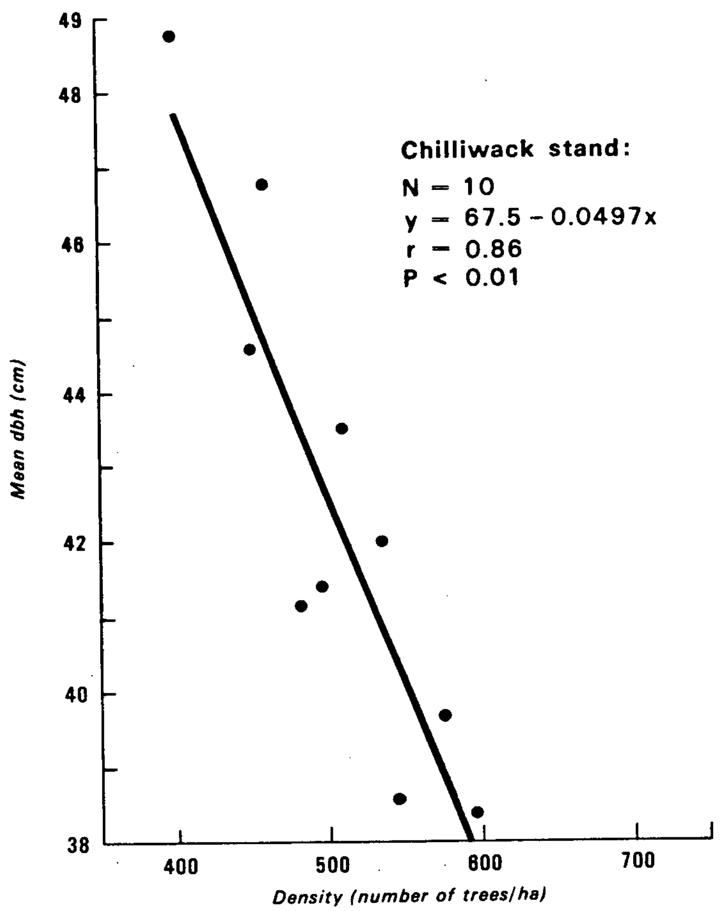


Figure 39. Relationships between mean dbh and number of trees/ha of Douglas-fir in the Chilliwack stand.

larger change in the mean diameter than the Ladysmith stand. If these trends could be confirmed then it would be safe to conclude that the same increase in diameter growth in response to decrease in stand density cannot be expected for the Ladysmith stand.

Since the density ranges in the above figures do not overlap, it must be questioned whether the relationship between mean dbh and density is adequately represented by a linear regression. Therefore, two more regressions including all species were calculated (Figure 40). Both regressions were again significant ($p < 0.01$) and a threefold difference in steepness of slope remained. Examining the scattergram it may be possible that the relationship between the two variables is curvilinear, e.g. a hyperbola. But since there are no datapoints between the values of 450 and 650 stems/ha in either stand, this can only be a speculation. If a hyperbolic relationship was established, then the curve for the Chilliwack stand would still lie a considerable distance above the one for the Ladysmith stand.

When all species were included the relative density index for the Chilliwack stand was somewhat above that for the Ladysmith stand. The decrease in slope steepness of the Chilliwack stand from the first regression analysis to the second one is likely due to this higher density. At the same relative density the mean diameter measured for the Chilliwack stand seems to be much greater than can be attributed to the small difference in age.

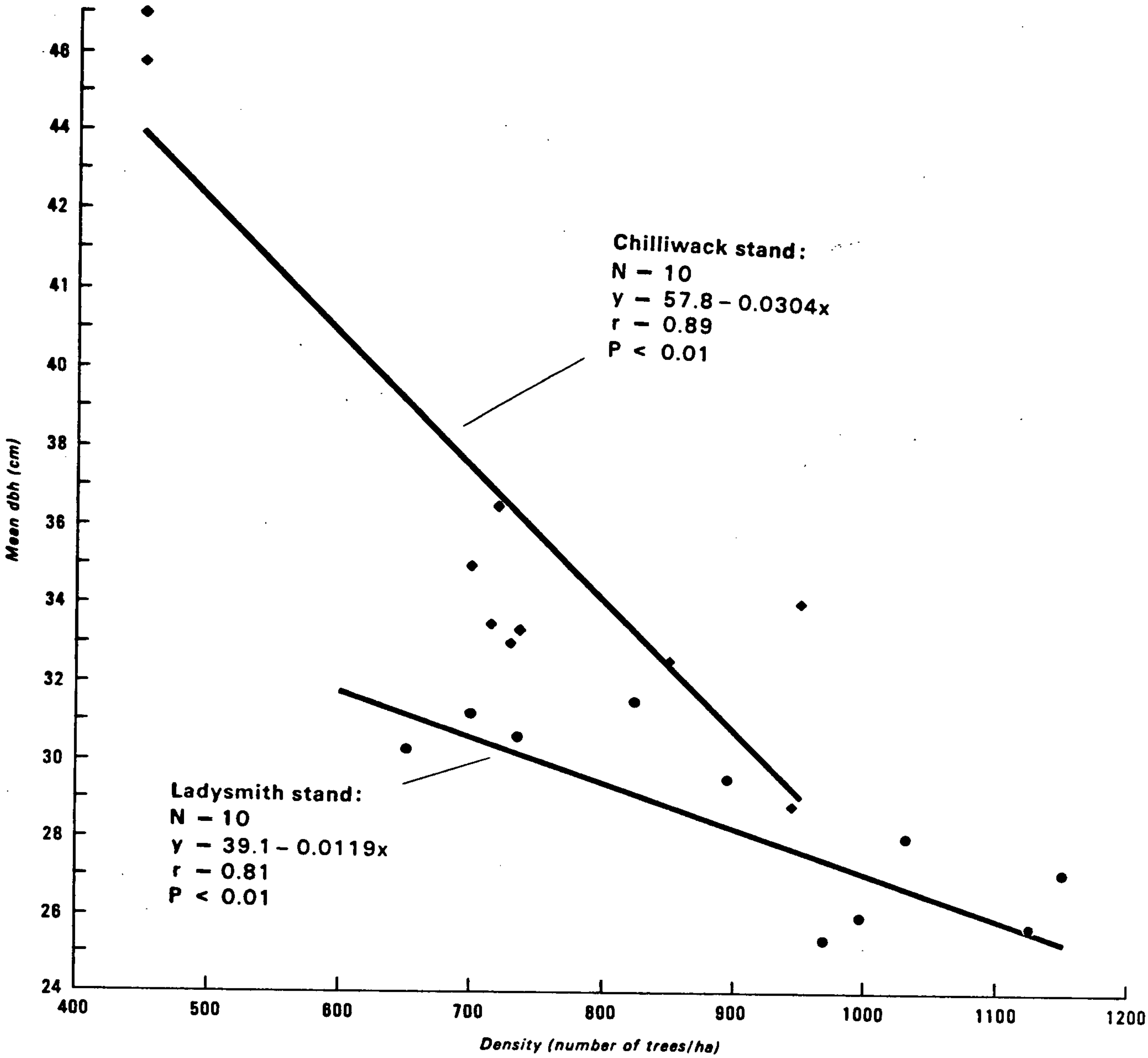


Figure 40. Relationship between mean dbh and number of trees/ha including all species in the Ladysmith and Chilliwack stand.

Effect of Density on Volume Production

Three growth parameters referred to in this chapter have to be clearly distinguished: Total production as the accumulated growth throughout stand age, growth as the increment per unit area for a specific time period and growth percent as the increment per unit of growing stock (residual growing stock) for a given time period. Whenever the term "gross" is used, mortality is included, "net" indicates that mortality is not considered. To test the response of thinning the following ratio maybe derived for any growth parameter: Thinned stand/thinned stand growing stock divided by control stand/control stand growing stock. A ratio of one or below means no response or depression of growth, a ratio greater than one indicates a positive response. The terms "growth" and "increment" are used interchangeably in this chapter.

It was previously shown that diameter increment increased with increasing spacing in most studies cited. The number of trees producing however decreases with increasing spacing. The growth per unit area, which is dependent on both, the number of trees and the increment per tree, will be reduced, if the basal area increment of these fewer trees (or the residual trees in the case of thinning) does not compensate. In general, basal area growth and volume growth will be similar, if height is not influenced by spacing.

In almost all experiments reviewed by Braathe (1957), Sjolte-Jorgensen (1967) and Evert (1971,1973) total basal area and volume production somewhat decreased with increasing spacing. Braathe (1957) explained this by the incomplete utilization of the soil space up to the period of crown closure, which occurs latest for the widest spacing. With increasing age, the difference in total production decreases (Evert 1971). Fries (1978) concluded for Norway spruce that increased spacing at the time of establishment and lowered density of the stand due to random effects will decrease the production; furthermore lowered density caused by selective low thinning has little impact on the volume production at least up to a difference in basal area of 40% (a reduction by means of thinnings down to 60% of the maximum basal area). Evert (1971) summarizes the influences of spacing on basal area and volume growth and growth percent. While growth percentage increased with increasing initial spacing in all studies he reviewed, the basal area and volume growth has sometimes increased and sometimes decreased.

Results of the 11-year-old spacing trial in France (Bartoli et al. 1971) and the 20-year-old U.B.C. trial (Smith 1977) show decreasing volume growth and decreased total volume production with increasing spacing. In contrast, the widest spaced plots at age 53 in the Wind River spacing trial (Reukema 1979) grew at double the rate of the more densely spaced plots, and their total volume production was nearly double as high. This superiority of the wider spacing levels however, is solely due to the considerably better height growth in these plots, while the basal area production is only loosely associated with spacing.

Miller et al. (1979) summarized some recent short-term results of thinning and fertilizing trials in the Pacific Northwest. The stands ranged from 15 to 68 years in age and from site II to IV in site quality. In all cases but one the volume growth per unit area was reduced. The percentage growth per unit growing stock increased in all cases. When including studies which observe the growth response for an extended period of time, we can summarize: There seems to be a general tendency that growth after thinning is initially reduced (Williamson _et al_. 1971, Reukema 1972, Reukema _et al_. 1973, Williamson 1976, Berg _et al_. 1979, Miller _et al_. 1979, Barclay _et al_. 1982). Thinning opens the crown canopy and trees are essentially free growing for a short period of time. During these years the growth of the thinned stand seems to be nearly proportional to the reduced thinning stock. After the canopy closes and the space is fully utilized the volume growth of unthinned stands approaches that for thinned stands (Williamson _et al_. 1971, Reukema _et al_. 1973, Miller _et al_. 1979, Barclay _et al_. 1982, Williamson 1982). Length of time for this process depends on the age and growth rate of the stand (site index), and on the amount of growing stock removed during thinning. This is illustrated by the 30-year growth response of a 60-year-old stand on a site IV, as reported by Worthington (1966). In the first 15-year period the lightly thinned stand (31-37% of initial basal area removed) grew 82% of the control stand's volume increment, in the second 15-year period the volume growth was equal for thinned and unthinned stands. In contrast the respective figures for the heavily thinned stand (44-50% of initial basal area removed) are 66% and 82% of the control stand's growth.

Comparison of various studies on thinning trials however, indicates that there is additional variability in basal area and volume growth rate which becomes evident when trials with similar age, site index and treatment are compared. Thus comparing thinning series in various geographical areas Braathe concludes: The results imply that the nature of the basal area growth differs somewhat with the length of growing season and climate.

Basal Area and Volume of the Studied Stands

Earlier it was suggested that the initial density in the Chilliwack stand was relatively lower than in the Ladysmith stand. Considering the reviewed studies on the effect of initial spacing and differences in the stocking level, we would expect the Ladysmith stand with a higher number of Douglas-fir/ha than the Chilliwack stand to have a somewhat higher total basal area and volume production. Since past mortality is unknown however, the total production cannot be assessed. The increment cores showed that the diameter growth for dominant trees was nearly identical for both stands. Therefore it is unlikely that the Ladysmith stand grew under extremely dense conditions which could have resulted in a considerable mortality. Thus the standing basal area and volume (net) are expected to be higher for the stand with the higher number of stems.

Testing the basal areas and volumes of the two stands for differences, they were found to be significantly different. Opposite to what was expected the Chilliwack stand exceeded the Ladysmith stand by 18% in basal area and 17% in volume when including all trees ($p < 0.01$) or by 12% in basal area and 13% in volume when including Douglas-fir only ($p < 0.05$).

To account for the difference in site index, the site index for the Ladysmith stand was adjusted by excluding the three highest site index plots. The resulting average volume is 796 m^3. A draft copy of the interim managed stand yield tables for coastal Douglas-fir (Tass-simulation model, Mitchell et al. 1982) was used to estimate the volume increment in the Ladysmith stand for the next 6 years. The model predicted for a comparable stand a volume increment of approximately 67 m^3/ha for the period between age 72 and age 78. Thus at age 78 the mean volume would be 863 m^3/ha, reducing the volume difference to 15% in favor of the Chilliwack stand.

A considerable variability in the volume production of stands with the same site index has been reported by Assmann (1961), Bradley et al.(1966), King (1970) and Chambers (1971). Assman defined the "yield level" of a stand as the total crop yield achieved for a given height and showed that the yield level varied considerably within one site index. This variability is due to a differing maximum basal area production of stands. The capability of producing and maintaining a certain basal area throughout the life time of a tree species is site-specific. It is also an expression for site quality not accounted for by the site index. King (1970) studied the variability in basal area production of Douglas-fir stands on permanent growth and yield plots in the Pacific Northwest. He developed a set of "Growing Stock Index" curves to account for this variability. With the additional knowledge of the yield level or the growing stock index of a site more accurate predictions of forest productivity and the expected yields at the end of a rotation period are possible. Fries (1978) showed that beside the site index, from all factors studied vegetation explained most of the variability in volume production.

The differences in basal area and volume production of the stands are small but significant. The 'shade-intolerant' Chilliwack stand, receiving an adequate moisture and nutrient supply seems to have a higher basal area growth and therefore higher volume production than the stand with a suspected moisture deficiency and relatively poorer nutrient supply. Decreased diameter growth with increased water stress (measured as soil water deficit) has been reported by Zaerr (1970) and Spittlehouse (1982) for studies in the CDF Biogeoclimatic Zone.

Since the volume lost through mortality which has occured prior to this study is not known, the mean annual increment can only be computed using the present volume (as measured). It is 11.2 m^3/ha for the Ladysmith and 12.7 m^3/ha for the Chilliwack stand.

The contrasting pattern for the basal area distributions of the two stands was shown earlier (Figure 32 and 33). When computing tree volumes, the basal area of each tree in the Chilliwack stand is multiplied by a slightly smaller height value than that of a tree with the same basal area in Ladysmith (Figure 34). In consequence the volume distribution shifts slightly to the left for the Chilliwack stand in comparison to that of the Ladysmith stand. The basic shape of the volume distribution however, resembles the corresponding basal area distribution closely for both stands.

Volume-Density Relationship

Scattergrams were plotted to examine the relationship between volume and density. To account for a possible influence of the site index, this parameter was included in a multiple regression analysis with the volume as the dependent and site index and Douglas-fir/ha as the independent variables. The regression analysis for the Chilliwack stand was not significant, in a stepwise backward selection both variables were excluded. With an R^2 value of 0.04 these two variables explain practically no variation of the volume. In contrast the multiple regression analysis for the Ladysmith stand was significant ($p < 0.05$), site index and density accounted for 66% of the variation in volume, whereby the addition of density accounted for 20%. The average value for the site index was entered into the equation to standardize the effect of site index. With increasing density the volume clearly increased. The resulting range of predicted volume values was between 770 m^3 at a density of 608 Douglas-fir/ha and 914 m^3 at a density of 1008 Douglas-fir/ha.

A comparison of the two stands, considering the different trend for the volume-density relationship and the difference in slope of the mean diameter-density relationship, suggests that with increasing density in the Chilliwack stand the growth of a smaller number of dominant Douglas-fir trees is sufficient to compensate for less trees producing. In contrast, in the Ladysmith stand it appears that lower density is correlated with less volume, and the mean diameter does not increase as rapidly as in the Chilliwack stand.

A possible explanation for this is given in the results of a study by Black (1980) on the effects of understory removal on the soil surface energy balance in a thinned Douglas-fir stand. The study stand of Black (1980) was younger than the Ladysmith stand, but comparable in all other vegetation and environmental properties. It was reported that after the stand was thinned, salal growth became very vigorous. About one half of the extractable soil moisture was consumed by the salal understory, while the thinned stand density was slightly less than one-half that of the unthinned stand, the diameter growth rate in the thinned stand was only slightly greater than that in the unthinned stand. Consequently the total volume production of the thinned stand was below that of the unthinned stand. Turner (1979) analyzed the relationship beween salal biomass and the biomass of the overstory stand and found that the amount of foliar biomass clearly decreased with increasing salal biomass.

A similar explanation could be provided by the results of a study by Lin (1982) in which the effect of 4 different spacing levels on the growth of the remaining trees was tested. The plots in which competing trees were removed but trees smaller than 1.3 m were left showed a significantly larger percentage height growth than the other spacing levels and the control plots.

When low initial spacing and precommercial thinning are suggested for management the common assumption is that this will result in the concentration of growth onto trees which will reach merchantable size (Reukema and Bruce 1977). If the above results are valid however, this assumption does not apply, or only apply to a certain degree for stands similar to the Ladysmith stand of this study. In this case fewer trees would not compensate for lower stand density by increases in dimeter growth and some loss in total volume production would be expected.

Timber Quality

Douglas-fir has been used mainly for lumber and related products. In order to produce high quality products, it is imperative that logs are clear and free from defects (e.g. excessive number of coarse knots).

The conspicuous difference observed between the stands was in the pattern of dead branches on the lower stem. To determine consistency and extent of this pattern, the height of the lowest dead branch was measured. In the Chilliwack stand the mean value was 50 cm (ranging from 33 to 65 cm), whereas that for the Ladysmith stand was 150 cm (ranging from 133 to 180 cm). The means were found statistically different ($p < 0.01$). Although a one meter difference does not appear to be impressive, one should consider that the lowest dead branch in the Chilliwack stand was usually a part of the whorl of branches extending for a considerable distance downslope. Most trees in this stand did not feature clear lower stems (Figure 41).

Figure 41. The downslope oriented pattern of dead branches on the lower stem of a dominant tree in the Chilliwack stand.

Such a pattern seems to be characteristic for shade-intolerant species on steep, south facing slopes, perhaps also provoked by a low initial density level (Mitscherlich 1970). In contrast, in the Ladysmith stand the lowest dead branch was usually a single branch or a short stub. However, most stems were clear of branches for several meters. The described branching patterns may have an impact on the quality of lumber produced.

SUMMARY

The purpose of this study was to examine growth characteristics of two different Douglas-fir ecosystems of the same age and site index. The underlying objective was to test the hypothesis that there are no significant growth differences between such ecosystems.

Two naturally established, unmanaged, late-immature stands of Douglas-fir, each representing a different ecosystem in coastal southwestern British Columbia were selected for the study. Both stands were nearly of the same age (72 and 78 years, respectively), identical top height (39.2 m), relative density and similar history; they were different in climatic and edatopic characteristics. The methods used for ecosystem analysis and synthesis (sensu Krajina) included an indicator plant analysis.

The ecosystems studied were identified at all levels of the biogeoclimatic ecosystem classification (sensu Krajina). The climate of one ecosystem was drier and warmer mesothermal (Csb - Cfb) whereas that of the other ecosystem was colder and perhumid mesothermal (Cfc). A comparison of edatopes indicated that the former ecosystem was relatively drier and had a poorer nutrient status than the latter ecosystem. Tolerance of Douglas-fir to shade was also found to be different between the ecosystems: Douglas-fir was shade-tolerant in the ecosystem with the Csb - Cfb climate but shade-intolerant in that with the Cfc climate. This difference in shade- tolerance was identified as the major underlying factor responsible for the described disparity in the growth and yield characteristics of the two stands.

The stand structure was described using stand maps, stand profiles and distribution patterns of crown classes, diameter and basal area; live crown-total height and height-diameter relationships were also examined.

Despite the similar site index and relative density index, there was a disparity in most of the growth characteristics examined. For the purposes of a full utilization of site productivity and accurate prediction of stand development it is recommended that a selective, ecosystem-specific approach to stand management and construction of yield tables for Douglas-fir be adopted.

This analysis is based on 20 samples in two stands only. General conclusions must therefore be tentative. Further studies involving random sampling of a larger amount of plots per ecosystem should be conducted to assess whether the shown differences and their suggested relationship with the ecological function of Dougals-fir will be consistent.

CONCLUSIONS

Based on the results of this study the following conclusions have been reached:

1. Indicator plant analysis was found helpful in quantifying ecological attributes and relationships. It confirmed the identification of hygrotope, trophotope and taxonomic units.
2. Krajina's predictions of biogeocoenoses, ecological function and site indices for Douglas-fir were found to agree with those of this study.
3. Despite an identical density index the two stands had a very different number of stems/ha. Independent of whether this may be due to differing initial regeneration density or due to mortality of trees in the initial stage I suggest that the difference in shade-tolerance of Douglas-fir would have resulted in any circumstance in some difference in number of stems/ha.
4. Considerable structural differences were found between the stands correlated apparently to shade-tolerance of Douglas-fir. The stand in which Douglas-fir was moderately shade-tolerant had a multilayered vertical structure and the associated characteristics resembled those of uneven-aged stands of a shade-tolerant species. The stand in which Douglas-fir was shade-intolerant had a uniform canopy, and the associated characteristics were typical for even-aged stands of a shade-intolerant species.
5. After adjusting for the difference in age and site index, there was a 15% difference in gross volume in favor of the 'shade-intolerant' stand.

6. While the top height in the moderately shade-tolerant stand was independent of density, it seemed to be negatively correlated with density in the other stand. It is suggested that high density levels result in excessive shading, which leads to the death of the lower live crown and then possibly to a reduction of height growth.
7. If it is implied that managed stands in which the density is regulated by initial spacing and thinning behave like the lower density plots in this study, then stands at lower density in a similar ecosystem as the Ladysmith one will have a smaller mean diameter than stands in conditions like the Chilliwack stand. This makes it questionable whether a corresponding increase in the mean diameter in the shade-tolerant stand can be expected, if stand density is decreased by management.
8. As a result of this difference in the diameter-density relationship,a contrasting pattern for the density-volume relationship was found. While in the shade-intolerant stand volume and density were not correlated, in the shade-tolerant stand basal area and volume seemed to increase with increasing density.

A small number of samples and unknown initial density levels however, limit the validity of these conclusions. Further studies are needed to verify these relationships.

Considering the trends described and the ecological relationships involved, in relation to stand management it appears that the 'shade-intolerant' ecosystem possesses a self-regulating mechanism producing the maximum gross volume attainable on a site in a stand with mainly large trees. In contrast, such a mechanism appears to be absent in the moderately 'shade-tolerant' stand. Trees of a small individual size will comprise a significant component of the volume produced in the course of natural development. However, it is uncertain whether lower density levels will result in greater growth of dominant and codominant trees with respect to the limited supply of soil water during the growing season, particularly where there is an effective competitor for soil water.

Despite the similar site index and relative density, there was a disparity in most of the growth characteristics examined. The described relationships should be examined in further research. If these studies verify the conclusions I have reached, then it is recommended that a selective, ecosystem-specific approach to stand management and construction of yield tables for Douglas-fir be adopted. Such an approach would assist in accurately predicting stand development as well as utilizing site productivity.

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APPENDIX I

List of Plant Species[1]

Abies amabilis (Dougl. *ex* Loud.) Forbes
Acer circinatum Pursh
Acer glabrum Torr.
Acer macrophyllum Pursh
Achlys triphylla (Sm.) DC.
Actaea rubra (Ait.) Willd.
Adenocaulon bicolor Hook.
Alnus rubra Bong.
Aruncus dioicus (Walt.) Fern.
Asarum caudatum Lindl.

Calypso bulbosa (L.) Oakes in Thomps.
Chimaphila menziesii (R. Br. *ex* D. Don) Spreng.
Chimaphila umbellata (L.) Barton
Circaea alpina L.
Claytonia sibirica L.
Clintonia uniflora (Schult.) Kunth
Corallorhiza maculata Raf.
Cornus nuttallii Audub. *ex* Torr. & Gray

Disporum hookeri (Torr.) Nicholson
Dryopteris assimilis (Jacq.) Woynar   Scheinz & Thell

Festuca subuliflora Scribn. in Macoun
Fragaria vesca L.

Galium triflorum Michx.
Gaultheria shallon Pursh
Goodyera oblongifolia Raf.

Hieracium albiflorum Hook.
Holodiscus discolor (Pursh) Maxim.
Hylocomium splendens (Hedw.) B.S.G.

Ilex aquifolium L.

Kindbergia oregana (Sull.) Ochyra

Leucolepis menziesii (Hook.) Steere *ex* L. Koch
Lilium columbianum Hanson *ex* Baker
Linnaea borealis L.
Listera cordata (L.) R. Br. in Ait.
Lonicera ciliosa (Pursh) DC.

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[1]Nomenclature of the vascular plants follows Krajina <u>et al</u>. (1983), Schofield (1968) for mosses and liverworts, and Hale and Culberson (1970) for lichens.

APPENDIX I (Continued)

Mahonia nervosa (Pursh) Nutt.
Menziesia ferruginea Sm.
Mycelis muralis (L.) Dumort

Oplopanax horridus (Sm.) Miq.
Orthilia secunda (L.) House
Osmorhiza chilensis Hook. & Arn.

Pinus monticola Dougl. *ex* D. Don in Lamb.
Plagiomnium insigne (Mitt.) Koponen
Plagiothecium undulatum (Hedw.) B.S.G.
Platanthera obtusata (Banks *ex* Pursh) Lindl.
Polystichum munitum (Kaulf.) Presl
Pseudotsuga menziesii (Mirb.) Franco
Pteridium aquilinum (L.) Kuhn in Decken
Pyrola asarifolia Michx.
Pyrola picta Sm. in Rees

Ranunculus uncinatus D. Don in G. Don.
Rhytidiadelphus loreus (Hedw.) Warnst.
Rhytidiadelphus triquetrus (Hedw.) Warnst.
Rhytidiopsis robusta (Hedw.) Broth.
Ribes lacustre (Pers.) Poir.
Rosa gymnocarpa Nutt. in Torr. & Gray
Rubus parviflorus Nutt.
Rubus spectabilis Pursh
Rubus ursinus Cham. & Schlecht.

Smilacina racemosa (L.) Desf.
Smilacina stellata (L.) Desf.
Spiraea betulifolia Pall.
Streptopus amplexifolius (L.) DC.
Symphoricarpos albus (L.) Blake

Taxus brevifolia Nutt.
Thuja plicata Donn *ex* D. Don in Lamb.
Tiarella laciniata Hook.
Tiarella trifoliata L.
Tolmiea menziesii (Pursh) Torr. & Gray
Trachybryum megaptilum (Sull.) Robins.
Trientalis latifolia Hook.
Trillium ovatum Pursh
Tsuga heterophylla (Raf.) Sarg.

Vaccinium parvifolium Sm. in Rees
Viola orbiculata Geyer *ex* Hook.
Viola sempervirens Greene

APPENDIX II

Description of the Pedons Sampled

Plot no.: 03
Location: Ladysmith
Soil taxon: Sandy Orthic Dystric Brunisol with Orthileptomoder

Horizon	Depth (cm)	Description
L,F & H	5 - 0	coniferous litter (1cm) underlain by a thin (1cm), discontinuous F horizon containing yellow-grayish mycelia; H horizon is mainly granular with commonly occurring worms and arthropods, yellow and white mycelia and abundant charcoal fragments; abrupt, wavy boundary.
Bf	0 - 8	dark brown (7.5YR 4/4); sandy loam; moderate, fine, subangular blocky; 5% gravel; very friable; abundant, very fine, fine and medium roots; clear, irregular boundary.
Bm1	8 - 43	dark yellowish brown (10YR 3/6); loamy sand; moderate, fine to medium, subangular blocky; 5% gravel; very friable; abundant, very fine, fine and medium roots; many dead root channels; abrupt, wavy boundary.
Bm2	43 - 73	dark yellowish brown (10YR 4/6); medium sand; weak, very fine to fine granular; 5% gravel; very friable; few, fine, very fine and medium roots within peds; abrupt, wavy boundary.
Bmj	73 - 85	light olive brown (2.5Y 5/4); coarse sand; 60% gravel, 10% cobbles; abrupt, wavy boundary.
II C	85 - 100+	light olive brown (2.5Y 5/4); coarse sand; 25% gravel, 30% cobbles, 30% stones; massive when undisturbed, single grain when disturbed; firm, when undisturbed, loose when disturbed, weak cementation by silica - possibly an incipient "duric" horizon partly restricting water movement and roots penetration; very few, medium roots.

APPENDIX II (Continued)

Plot no.: 17
Location: Chilliwack
Soil taxon: Fine-Loamy-Skeletal Orthic Humo-Ferric Podzol with Mineroleptomoder.

Horizon	Depth (cm)	Description
L,Fa & Hi	3 - 0	loose, discontinuous coniferous litter (1cm); underlain by a thin (0.5cm), discontinuous loose, Fa horizon containing very few mycelia but numerous droppings; loose, Hi horizon (2.5cm) is granular, very friable and contains 10% coarse fragments; abrupt, wavy boundary.
Bf1	0 - 15	dark reddish brown (5YR 3/3-4); laom; moderate, fine to medium granular to subangular blocky; 65% shale; very friable; abundant, very fine to fine roots; clear, wavy boundary.
Bf2	15 - 38	reddish brown (5YR 4/4); loam; weak, very fine, granular; 75% shale; very friable; abundant, very fine to fine roots; gradual, wavy boundary.
Bf3	38 - 56	yellowish red (5YR 4/6); loam; weak, very fine to fine, granular; 75% shale; very friable; plentiful, very fine to medium roots; gradual, wavy boundary.
Bf4	56 - 76+	yellowish red (5YR 4/6); loam; weak fine, subangular blocky; 90% shale; very friable; plentiful, very fine to medium roots, in cracks many fungi mycelia; clear, irregular boundary.

Appendix III, Table 1. Environment-vegetation table for the Ladysmith study plots, part 2.

Climax association: Mahonio (nervosae) - Gaultherio (shallonis) - TP & PM

Successional association: Hylocomio (splendentis) - Gaultherio (shallonis) - PM

Plot number					001	002	003	004	005	006	007	008	009	010
St. No.	Species	P	MSS	RS	SPECIES SIGNIFICANCE AND VIGOR									
A1														
1	*Pseudotsuga menziesii*	100.0	5.3	4-5	4.3	5.2	5.2	5.2	4.2	5.2	4.2	5.2	5.3	5.2
A2														
	Pseudotsuga menziesii	100.0	8.5	8-8	8.2	8.2	8.2	8.2	8.2	8.2	8.2	8.2	8.2	8.2
A3														
	Pseudotsuga menziesii	100.0	5.6	5-7	5.1	5.+	5.2	5.1	5.2	5.1	5.2	5.1	7.1	5.2
B1														
	Tsuga heterophylla	90.0	4.6	0-6	1.+	4.1	3.2	4.2	4.2	6.2	3.2	.	4.2	5.2
4	*Thuja plicata*	60.0	2.4	0-4	1.2	1.2	4.2	.	3.2	.	2.2	.	2.2	.
B2														
	Gaultheria shallon	100.0	7.9	3-9	7.2	3.2	8.2	7.2	7.2	6.2	8.3	9.3	9.3	7.2
7	*Mahonia nervosa*	100.0	5.1	3-6	5.2	3.2	5.2	5.2	6.2	3.2	3.2	3.2	3.2	5.2
	Vaccinium parvifolium	100.0	4.4	2-5	4.2	4.2	5.2	4.3	4.2	4.2	3.2	2.1	4.2	3.2
	Tsuga heterophylla	100.0	2.7	1-3	1.1	3.1	2.2	2.1	2.1	3.2	2.2	3.2	1.1	2.2
8	*Rubus ursinus*	90.0	2.8	0-3	2.1	2.2	2.2	3.2	3.2	3.2	2.1	.	1.1	3.2
	Thuja plicata	80.0	2.3	0-3	2.1	2.2	3.2	1.1	.	2.1	2.2	.	1.1	3.2
9	*Rosa gymnocarpa*	60.0	1.9	0-3	1.1	1.2	3.2	2.2	.	.	.	2.1	.	2.2
C														
15	*Pteridium aquilinum*	100.0	4.3	3-5	3.2	5.2	3.2	3.2	4.2	3.2	4.2	4.2	3.2	4.2
16	*Linnaea borealis*	100.0	3.2	1-4	2.2	4.2	3.2	3.2	2.2	3.2	3.2	2.2	1.1	3.2
17	*Polystichum munitum*	90.0	3.0	0-3	2.2	3.2	3.2	3.2	2.2	3.2	2.2	2.2	.	3.2
18	*Achlys triphylla*	80.0	4.8	0-5	5.2	4.2	4.2	4.2	5.2	5.2	1.1	.	.	5.2
19	*Adenocaulon bicolor*	70.0	2.0	0-3	1.1	3.2	1.2	2.2	2.2	1.2	.	.	.	2.2
20	*Galium triflorum*	70.0	1.8	0-2	1.2	2.2	2.2	1.2	2.2	2.2	.	.	.	2.2
21	*Tiarella trifoliata*	60.0	1.4	0-2	1.2	.	1.2	2.2	1.1	2.2	.	.	.	1.2
22	*Listera cordata*	60.0	+.8	0-1	1.2	.	.	.	1.2	+.2	1.2	+.1	+.+	.
23	*Festuca subuliflora*	50.0	1.3	0-2	.	2.2	1.2	2.2	1.2	.	.	.	.	1.2
24	*Mycelis muralis*	50.0	+.4	0-1	.	+.1	.	1.1	1.2	+.1	+.3	.	.	.
25	*Tiarella laciniata*	40.0	1.7	0-3	1.2	3.2	.	1.2	.	3.2	.	.	.	.
26	*Trillium ovatum*	40.0	+.6	0-1	1.2	1.1	.	1.2	.	+.2	.	.	.	.
27	*Viola sempervirens*	30.0	+.2	0-1	1.1	.	.	1.1	.	+.1	.	.	.	.
28	*Goodyera oblongifolia*	30.0	+.0	0-1	.	.	.	1.2	.	+.1	+.1	.	.	.
29	*Chimaphila menziesii*	30.0	+.0	0-+	.	.	+.+	.	.	.	+.1	+.+	.	.
DH														
37	*Hylocomium splendens*	100.0	8.1	3-9	8.3	8.2	5.2	9.2	8.2	8.2	5.2	9.2	3.2	8.2
38	*Kindbergia oregana*	100.0	4.6	2-5	4.2	5.2	4.2	4.2	3.1	5.2	4.2	2.2	3.2	4.2
39	*Rhytidiadelphus loreus*	100.0	2.2	1-3	3.+	1.2	2.2	2.2	1.+	1.2	2.2	1.2	1.2	2.2
40	*Rhytidiadelphus triquetrus*	70.0	1.6	0-2	1.2	1.2	2.2	.	1.2	2.2	2.2	1.2	.	.

		SPORADIC SPECIES WITH PRESENCE ≤ 20%													
A3															
	2	*Alnus rubra*	20.0	1.0	0-2	.	.	2.2	.	.	.	.	.	.	2.2
	3	*Tsuga heterophylla*	20.0	1.0	0-2	.	2.1	.	.	.	.	.	.	2.1	.
B1															
		Pseudotsuga menziesii	20.0	1.5	0-3	.	.	3.2	.	.	.	.	3.2	.	.
	5	*Vaccinium parvifolium*	20.0	+.6	0-2	2.2	.	.	.	.	.	.	.	.	1.3
	6	*Gaultheria shallon*	10.0	+.0	0-1	.	1.3	.	.	.	.	.	.	.	.
B2															
	10	*Pinus monticola*	20.0	+.1	0-1	1.1	.	.	.	.	.	.	.	.	1.1
	11	*Lonicera ciliosa*	20.0	+.0	0-1	1.+	.	.	.	.	+.+	.	.	.	.
	12	*Acer macrophyllum*	10.0	+.0	0-1	1.1	.	.	.	.	.	.	.	.	.
	13	*Rubus spectabilis*	10.0	+.0	0-1	1.1	.	.	.	.	.	.	.	.	.
	14	*Taxus brevifolia*	10.0	+.0	0-1	.	.	.	.	.	1.2	.	.	.	.
C															
	30	*Corallorhiza maculata*	20.0	+.0	0-1	.	.	.	.	.	.	+.2	.	1.1	.
	31	*Tiarella unifoliata*	10.0	1.0	0-3	.	3.2	.	.	.	.	.	.	.	.
	32	*Circaea alpina*	10.0	+.0	0-1	1.+	.	.	.	.	.	.	.	.	.
	33	*Claytonia sibirica*	10.0	+.0	0-1	.	.	.	1.2	.	.	.	.	.	.
	34	*Dryopteris assimilis*	10.0	+.0	0-1	.	.	1.2	.	.	.	.	.	.	.
		Lonicera ciliosa	10.0	+.0	0-1	.	.	.	.	.	.	.	.	.	1.+
	35	*Pyrola asarifolia*	10.0	+.0	0-1	1.2	.	.	.	.	.	.	.	.	.
	36	*Ranunculus uncinatus*	10.0	+.0	0-+	.	.	.	.	+.1	.	.	.	.	.
DH															
	41	*Plagiothecium undulatum*	20.0	+.1	0-1	.	.	.	1.2	.	.	.	.	.	1.2

Appendix III, Table 2. Environment-vegetation table for the Chilliwack study plots, part 2.

Climax association: Mahonio (nervosae) - Polysticho (muniti) - TH & TP

Successional association: Hylocomio (splendentis) - Mahonio (nervosae) -(TH)- PM

Plot number					011	012	013	014	015	016	017	018	019	020
St. No.	Species	P	MSS	RS	SPECIES SIGNIFICANCE AND VIGOR									
A1														
1	*Pseudotsuga menziesii*	30.0	3.3	0-5	4.2	.	.	5.2	.	.	.	4.2	.	.
A2														
	Pseudotsuga menziesii	100.0	8.5	7-9	8.2	8.2	8.2	8.2	8.2	8.2	9.2	7.2	8.2	8.3
A3														
	Pseudotsuga menziesii	100.0	5.0	2-6	3.1	5.2	4.1	5.2	4.2	2.1	4.2	6.2	4.2	4.1
	Tsuga heterophylla	70.0	4.1	0-5	5.1	4.2	4.1	4.2	4.1	2.1	.	.	4.2	.
	Alnus rubra	30.0	2.3	0-4	3.1	.	.	.	.	3.2	.	4.2	.	.
B1														
	Tsuga heterophylla	100.0	5.3	1-7	4.2	5.2	6.1	5.1	7.1	5.2	4.2	3.1	4.2	1.1
4	*Acer circinatum*	60.0	3.6	0-5	2.2	.	4.2	.	.	3.2	.	5.3	4.2	2.2
	Pseudotsuga menziesii	30.0	+.9	0-2	.	.	.	.	.	.	1.2	2.+	.	1.1
B2														
6	*Mahonia nervosa*	100.0	6.6	5-7	5.2	6.2	7.2	6.2	6.2	5.2	6.2	7.2	7.2	6.1
	Tsuga heterophylla	100.0	3.7	1-5	3.2	2.2	2.1	2.2	2.1	5.2	1.2	4.2	3.2	3.1
	Acer circinatum	100.0	3.5	1-4	2.2	3.2	3.1	2.2	3.2	3.2	3.2	4.2	4.2	1.2
7	*Rosa gymnocarpa*	100.0	2.5	1-3	1.1	2.2	2.1	2.2	2.2	3.2	1.2	2.2	1.+	3.2
8	*Rubus ursinus*	90.0	2.0	0-2	1.+	.	2.+	1.1	2.1	2.+	2.2	1.+	2.2	1.+
	Vaccinium parvifolium	80.0	3.2	0-4	3.2	3.2	3.1	3.2	2.2	.	3.2	3.2	.	4.2
9	*Holodiscus discolor*	80.0	3.0	0-3	2.2	.	3.2	1.2	.	3.2	3.2	3.2	3.2	3.2
10	*Symphoricarpos mollis*	70.0	1.4	0-2	1.+	1.2	1.+	1.+	2.2	2.1	.	.	.	1.1
11	*Ribes lacustre*	60.0	1.2	0-2	2.1	.	.	.	1.1	1.2	.	1.1	1.2	1.2
12	*Lonicera ciliosa*	30.0	+.9	0-2	.	.	.	.	.	.	2.3	1.1	1.+	.
13	*Menziesia ferruginea*	30.0	+.9	0-2	1.2	.	.	.	.	2.3	.	.	.	1.2
14	*Acer glabrum*	30.0	+.2	0-1	.	.	.	1.1	.	1.1	.	.	.	+.1
C														
22	*Polystichum munitum*	100.0	5.7	4-7	7.2	5.2	6.2	5.2	5.2	7.2	6.2	4.2	4.2	4.2
23	*Achlys triphylla*	100.0	4.9	3-5	3.2	4.2	4.2	4.2	3.2	4.2	5.2	5.2	4.2	5.2
24	*Pteridium aquilinum*	100.0	3.2	+-5	+.+	1.2	2.1	2.2	2.2	2.2	3.2	1.1	2.2	5.2
25	*Smilacina Stellata*	100.0	3.2	1-4	2.1	4.2	2.1	2.2	3.2	3.2	3.2	2.2	1.2	3.2
26	*Mycelis muralis*	100.0	2.3	+-4	+.+	1.1	1.1	1.1	1.2	1.1	2.2	1.2	1.2	4.2
27	*Disporum hookeri*	100.0	2.2	+-3	1.2	1.1	2.1	+.+	2.2	2.1	1.2	2.1	2.2	3.2
28	*Galium triflorum*	100.0	2.2	1-3	2.2	2.2	2.2	3.2	1.2	1.1	1.2	1.2	1.2	2.2
29	*Trientalis latifolia*	100.0	2.2	1-2	1.1	1.2	1.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2
30	*Trillium ovatum*	100.0	1.6	1-2	1.2	1.2	1.2	1.2	1.2	1.1	1.2	2.2	1.2	1.2

	31	*Viola sempervirens*	80.0	2.6	0-3	.	2.2	3.2	.	2.2	2.2	2.2	2.2	3.2	3.2
	32	*Chimaphila menziesii*	80.0	1.3	0-2	1.1	.	1.+	2.2	+.1	1.1	.	1.2	1.2	+.1
	33	*Goodyera oblongifolia*	80.0	1.2	0-1	1.2	1.2	1.2	.	+.2	1.2	1.2	1.2	.	1.2
	34	*Aruncus dioicus*	70.0	2.1	0-3	+.+	1.2	3.2	2.2	2.2	3.2	1.2	.	.	.
	35	*Actaea rubra*	70.0	1.3	0-2	.	1.2	.	2.2	+.2	1.2	1.2	.	+.1	2.2
	36	*Smilacina racemosa*	70.0	1.2	0-1	1.2	1.2	.	1.2	1.2	.	1.2	.	1.2	1.2
	37	*Viola orbiculata*	60.0	2.0	0-3	2.2	2.2	2.2	3.2	2.2	1.2	.	.	.	.
	38	*Adenocaulon bicolor*	60.0	1.3	0-3	.	+.1	.	.	+.2	1.2	.	+.1	1.2	3.2
	39	*Linnaea borealis*	50.0	+.9	0-1	.	+.2	.	1.2	.	.	.	1.2	1.2	1.2
	40	*Calypso bulbosa*	30.0	+.2	0-1	+.1	.	.	1.2	.	.	.	1.2	.	.
	41	*Claytonia sibirica*	30.0	+.2	0-1	1.2	.	.	.	+.2	.	1.2	.	.	.
	42	*Osmorhilo chilenis*	30.0	+.6	0-2	.	.	.	.	.	.	1.1	.	.	2.2
DH															
	57	*Hylocomium splendens*	100.0	8.2	6-9	6.2	9.2	8.2	7.2	8.2	7.2	8.2	8.2	8.2	7.2
	58	*Kindbergia oregana*	100.0	5.0	3-7	3.1	3.2	4.2	4.2	4.2	7.2	3.2	4.2	4.2	5.2
	59	*Rhytidiadelphus triquetrus*	100.0	3.6	2-4	3.2	3.2	4.2	3.2	2.2	3.2	2.2	3.2	3.2	4.2
	60	*Rhytidiopsis robusta*	100.0	2.4	1-3	1.1	1.2	2.2	3.2	2.2	2.2	2.2	1.2	1.2	3.2
	61	*Rhytidiadelphus loreus*	70.0	1.4	0-2	2.2	.	2.2	1.1	.	1.2	1.2	1.2	1.2	.

SPORADIC SPECIES WITH PRESENCE ≤ 20%

A2														
	2	*Alnus rubra*	10.0	1.0	0-3	.	.	.	.	3.2	.	.	.	.	.
	3	*Tsuga heterophylla*	10.0	1.0	0-3	.	.	.	.	.	.	.	.	3.2	.
B1															
	5	*Vaccinium parvifolium*	10.0	+.0	0-+	.	+.2	.	.	.	.	.	.	.	.
B2															
	15	*Oplopanax horridus*	20.0	+.0	0-1	.	.	.	1.2	.	.	.	+.+	.	.
	16	*Acer macrophyllum*	20.0	+.0	0-+	.	.	.	.	+.+	.	+.+	.	.	.
	17	*Abies amabilis*	10.0	+.0	0-1	.	.	.	1.+	.	.	.	.	.	.
	18	*Cornus nuttallii*	10.0	+.0	0-+	.	.	.	.	.	.	.	.	.	+.1
	19	*Ilex aquifolium*	10.0	+.0	0-+	.	.	.	+.1	.	.	.	.	.	.
	20	*Rubus parviflorus*	10.0	+.0	0-+	.	.	.	.	.	.	.	.	.	+.+
	21	*Spiraea betulifolia*	10.0	+.0	0-+	.	.	.	.	.	+.+	.	.	.	.
C															
	43	*Fragaria vesca*	20.0	+.1	0-1	.	.	.	.	.	.	.	1.2	.	1.1
	44	*Asarum caudatum*	20.0	+.0	0-1	.	.	.	.	.	1.2	.	.	.	+.1
	45	*Festuca subuliflora*	20.0	+.0	0-1	.	.	1.1	+.1	.	.	.	.	.	.
	46	*Lilium columbianum*	20.0	+.0	0-+	+.+	.	.	.	+.2	.	.	.	.	.
	47	*Streptopus amplexifolius*	20.0	+.0	0-+	.	.	.	.	.	.	.	+.2	.	+.1
	48	*Tiarella trifoliata*	20.0	+.0	0-+	+.+	.	.	.	.	.	.	.	.	+.1
	49	*Dryopteris assimilis*	10.0	+.2	0-2	2.2	.	.	.	.	.	.	.	.	.
	50	*Chimaphila umbellata*	10.0	+.0	0-+	.	.	.	+.2	.	.	.	.	.	.
	51	*Clintonia uniflora*	10.0	+.0	0-+	+.+	.	.	.	.	.	.	.	.	.
	52	*Hieracium albiflorum*	10.0	+.0	0-+	.	.	.	.	.	.	.	.	.	+.1

53	*Orthilia secunda*	10.0	+.0	0-+	.	.	.	+.1	.	.	.	.	.	.
54	*Platanthera obtusata*	10.0	+.0	0-+	.	+.1	.	.	.	.	.	.	.	.
55	*Pyrola asarifolia*	10.0	+.0	0-+	.	.	.	.	.	.	.	+.2	.	.
56	*Pyrola picta*	10.0	+.0	0-+	.	.	.	+.2	.	.	.	.	.	.
	Rubus parviflorus	10.0	+.0	0-+	.	+.+	.	.	.	.	.	.	.	.
DH														
62	*Plagiothecium undulatum*	20.0	+.0	0-1	.	.	.	1.2	.	.	.	.	.	+.2
63	*Trachybryum megaptilum*	20.0	+.0	0-1	.	+.2	.	.	1.2	.	.	.	.	.
64	*Plagiomnium insigne*	10.0	+.0	0-1	1.2	.	.	.	.	.	.	.	.	.
65	*Leucolepis menziesii*	10.0	+.0	0-+	.	.	.	.	.	.	+.1	.	.	.

APPENDIX IV

Summary Vegetation Table

Study area Number of plots	Ladysmith 10	Chilliwack 10
Species	Presence class and mean species significance	
Abies amabilis	-	I +.0
Acer circinatum	-	V 3.5
Acer glabrum	-	II +.2
Acer macrophyllum	I +.0	I +.0
Achlys triphylla	IV 4.8	V 4.9
Actaea rubra	-	IV 1.3
Adenocaulon bicolor	IV 2.0	III 1.3
Alnus rubra	I 1.0	II 2.3
Aruncus dioicus	-	IV 2.1
Asarum caudatum	-	I +.0
Calypso bulbosa	-	II +.2
Chimaphila menziesii	II +.0	IV 1.3
Chimaphila umbellata	-	I +.0
Circaea alpina	I +.0	-
Claytonia sibirica	I +.0	II +.2
Clintonia uniflora	-	I +.0
Corallorhiza maculata	I +.0	-
Cornus nuttallii	-	I +.0
Disporum hookeri	-	V 2.2
Dryopteris assimilis	I +.0	I +.2
Festuca subuliflora	III 1.3	I +.0
Fragaria vesca	-	I +.1
Galium triflorum	IV 1.8	V 2.2
Gaultheria shallon	V 7.9	-
Goodyera oblongifolia	II +.0	IV 1.2
Hieracium albiflorum	-	I +.0
Holodiscus discolor	-	IV 3.0
Hylocomium splendens	V 8.1	V 8.2
Ilex aquifolium	-	I +.0
Kindbergia oregana	V 4.6	V 5.0
Leucolepis menziesii	-	I +.0
Lilium columbianum	-	I +.0
Linnaea borealis	V 3.2	III +.9
Listera cordata	III +.8	-
Lonicera ciliosa	I +.0	II +.9

APPENDIX IV (Continued)

Study area Number of plots	Ladysmith 10	Chilliwack 10
Species	Presence class and mean species significance	
Mahonia nervosa	V 5.1	V 6.6
Menziesia ferruginea	-	II +.9
Mycelis muralis	III +.4	V 2.3
Oplopanax horridus	-	I +.0
Orthilia secunda	-	I +.0
Osmorhiza chilensis	-	I +.6
Pinus monticola	I +.1	-
Plagiomnium insigne	-	I +.0
Plagiothecium undulatum	I +.1	I +.0
Platanthera obtusata	-	I +.0
Polystichum munitum	V 3.0	V 5.7
Pseudotsuga menziesii	V 8.5	V 8.5
Pteridium aquilinum	V 4.3	V 3.2
Pyrola asarifolia	I +.0	I +.0
Pyrola picta	-	I +.0
Ranunculus uncinatus	I +.0	-
Rhytidiadelphus loreus	V 2.2	IV 1.4
Rhytidiadelphus triquetrus	IV 1.6	V 3.6
Rhytidiopsis robusta	-	V 2.4
Ribes lacustre	-	III 1.2
Rosa gymnocarpa	III 1.9	V 2.5
Rubus parviflorus	-	I +.0
Rubus spectabilis	I +.0	-
Rubus ursinus	V 2.8	V 2.0
Smilacina racemosa	-	IV 1.2
Smilacina stellata	-	V 3.2
Spiraea betulifolia	-	I +.0
Streptopus amplexifolius	-	I +.0
Symphoricarpos albus	-	IV 1.4
Taxus brevifolia	I +.0	-
Thuja plicata	IV 2.3	-
Tiarella laciniata	II 1.7	-
Tiarella trifoliata	III 1.4	I +.0
Tolmiea menziesii	I 1.0	-
Trachybryum megaptilum	-	I +.0
Trientalis latifolia	-	V 2.2
Trillium ovatum	II +.6	V 1.6
Tsuga heterophylla	V 2.7	V 5.3
Vaccinium parvifolium	V 4.4	IV 3.2
Viola orbiculata	-	III 2.0
Viola sempervirens	II +.2	IV 2.6