

EARLY GROWTH AND DEVELOPMENT OF DOUGLAS-FIR IN
RELATION TO INTERSPECIFIC COMPETITION

By

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THESIS ABSTRACT

An interlocking group of studies was carried out to address the concept of the free-to-grow seedling. This term is an attempt to define plantation establishment in a manner cognizant of early hazards from brush competition and other stresses. The studies were carried out on one- to five-year old Douglas-fir plantations on moist, rich sites in coastal British Columbia. Data were generated from field measurements and harvest sampling of the planted trees and their associated competing vegetation.

On these productive sites, tree growth appears sensitive to interference from neighbouring brush species. An index implying competitive shading was derived and proved a useful measure of stress on the planted trees, particularly when measured as a relative production rate. Growth losses varied with the light environment at specific crown positions. Therefore, height growth was not affected by competition until the terminal leader was shaded. This allows height growth to remain independent of competition level until the tree is overtopped on these sites.

The trees studied showed great ability to acclimate and survive relatively heavy shading by competing vegetation. After competition release treatment, trees were generally able to re-acclimate the current seasons growth to the increased light intensity. Growth following competition release was significantly improved by a chemical brush control treatment, while mechanical brushing resulted in little net change in competition levels after one year. The growth on these trees in the year following release from competition was also best measured as a relative production rate.

The vegetation on untreated areas followed a strong successional trend during the period studied. The trend was a function of differences in height growth patterns between species modified by leaf area index. In general, woody species tend to succeed geophytes and microphanerophytes on these sites.

A proposed free-to-grow definition in biological terms states that a tree must be free from competitive shading on the terminal leader and increasing in height relative to the competing vegetation. The free-to-grow status can be assessed by on a threshold value of the competition index and a predictive model for the comparative height increment of the tree and its competitors.

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CHAPTER ONE

Introduction to the Research Program

INTRODUCTION

Compared with many areas of the world, forest management practices in British Columbia are still in a developmental stage. While the industrial base is still firmly entrenched in the harvest of old-growth timber, the day is rapidly drawing near when the harvest will be based on artificial or man-made forests. When this occurs, significant changes in both the quantity and quality of timber harvested on each hectare will occur.

There is the opportunity, however, through insightful analysis of world markets and carefully targetted silvicultural expenditures to develop new forests which are tailored to produce high value, high demand products. The forest management programs must revolve around the regeneration or establishment phase, where these future opportunities originate. Conversely, the silvicultural activities chosen must have both short and long-term objectives so they are not operating in a vacuum.

For too long, forest regeneration has been looked on as a public relations issue, with hectares planted displayed in annual reports beside hectares logged. The key criteria for our silvicultural programs have not been addressed - species regenerated, stocking, density, growth, and health. An important step in this direction has been the introduction of the concept of the free-to-grow plantation as a benchmark for regeneration success.

This study aims to explore the biological basis for the free-to-grow concept and to make recommendations for a formalization of both the definition and associated assessment criteria. An interlocking group of studies is used to examine specific aspects of plantation establishment which affect the attainment of free-to-grow status. These studies were carried out on moist, rich sites in coastal British Columbia where productivity for coniferous growth is the highest in Canada. The problem of severe interspecific competition also makes plantation establishment on these sites among the most risk-prone to problems of suppression and mortality.

This thesis is arranged in chapters addressing the information obtained in each of the

studies. This procedure allows specific discussion of the results of the individual analyses and hopefully makes the material accessible to the reader interested in a specific aspect of the problem. While the studies are reported in separate chapters, an attempt has been made to avoid repetition or overlap in the introduction and methods sections of the various chapters and to keep an underlying theme or purpose throughout the document. The final discussion chapter addresses the free-to-grow concept directly, and draws on the material gained in chapters 2 through 5 to substantiate the recommendations.

BACKGROUND INFORMATION

THE FREE-TO-GROW SEEDLING CONCEPT

A vast majority of the forest land in Canada is managed under the sustained yield philosophy. The annual harvest reflects a moderate drawdown on old-growth timber which is intended to carry the industry until maturation of the "second-growth" or disturbance originated forests. As these new forests grow they produce increment which also can be harvested from the pool of old growth timber. This results in the common basis for determining an allowable annual harvest within a forest unit - inventory drawdown and annual increment.

During the early period of harvesting in British Columbia, the increment generated on immature stands was insignificant compared with the volume of mature timber. However, during the 1940's and 1950's the harvest continued to expand and concern was expressed that harvest rates would have to be significantly curtailed if new stands were not properly established after harvest or other denudation (Sloan 1945, Sloan 1956). Programs of reforestation commenced which have been continually increasing in magnitude since. Most recently, the recognition that the change to second-growth harvest is nearing has created worries of a "fall-down effect" when lower volumes of timber are harvested from younger stands (Pearse 1976). This concern has renewed interest in applying silvicultural measures to minimize the declining allowable annual harvest rate (B. C. Ministry of Forests 1979, Reed 1978).

A further problem which has come to light over the past two or three decades is the accuracy of the projections of increment based on the second growth forests. In British Columbia, this increment has been based on volume-age relationships derived by fitting curves to measurements of stands of various ages. After areas were planted, they were surveyed during the following year or two, and if survival was adequate, they were assigned to a given volume-age curve based on species composition and site quality. It is clear, however, that problems such as prolonged planting check, browsing, insect damage, and brush competition are preventing the attainment of projected yields on many sites.

This has led to the proposed concept of the free-to-grow plantation (Armson et al. 1980). The term is based on the need to determine a point at which the yields from a regenerated area can be entered into the allowable cut calculation with some veracity. It confronts problems such as prolonged planting check, off-site planting, browsing, insect damage, and most significantly brush competition. It also forces recognition that in many cases establishment of regeneration requires more than replanting to be successful.

Administratively, the free-to-grow concept is useful in three ways. First, by acting as a standard for re-entering denuded areas into the allowable cut calculation, it removes much of the potential for overestimating increment on improperly established areas. Second, as governments turn over an increasing responsibility for silviculture to the forest industry, it is an effective performance standard. Finally, as an objective for reforestation efforts, it gives focus to vegetation management or other management prescriptions.

To date, the free-to-grow standard has been adopted by three Canadian provinces (British Columbia, Ontario, and New Brunswick). The general definition requires the seedling to be of acceptable species for the site and with growth not impeded by brush competition. Usually this definition is coupled with stocking standards to produce free-to-grow plantation criteria. In other provinces, either informal definitions are in place or the term is not used. The provincial government of Alberta presently only requires that regeneration be "established". In Saskatchewan, Prince Albert Pulpwood Ltd., the major licensee, defines the term informally much as do the governments of British Columbia and Ontario. Quebec considers that a plantation is free-to-grow if it has reached an age of eight years and does not need further release treatments.

The important transition between a definition of the free-to-grow seedling in administrative terms and the biological understanding of the concept still seems to be a problem. Assessment techniques presently in use measure height growth on crop trees and describe tree condition and damaging influences subjectively. While these surveys allow a decision on free-to-grow status, they are no more than subjective estimates. This makes the

administration and implementation of the concept difficult.

CONCEPTS OF TREE GROWTH AND COMPETITION

Proper understanding of the process of plantation establishment and early growth requires application of the basic concepts of tree growth and competition to the conditions found in the field. Like agricultural crops, a tree seedling needs to overcome considerable changes in microenvironment during its early development. The basic microsite influences are modified by the dynamic development of competing species. To the forest manager, the influence of competition introduces variation into the crop, as uneven mortality and as an increase in the range of individual tree sizes.

Trees, like other autotrophs, fix energy through photosynthesis, trapping solar energy into the chemical bonds of carbon based molecules. Dry matter production results as the difference between gains from photosynthesis and losses through respiration, shed tissues, and other processes. In trees, the growth based on net carbon fixation is allocated to shoots, leaves, and root tips via primary growth, and to wood production by secondary growth. Allocation is controlled by relationships among sources (foliage) and sinks (areas of growth or respiration) mediated by hormonal action (Zimmerman and Brown 1971, Kramer and Kozlowski 1979).

The photosynthetic production of a seedling is a function of the total amount of foliage carried and the rate of photosynthesis per unit of foliage (Brix 1983). The rate of photosynthesis is influenced by the many environmental variables which make up the microsite of the plant. In particular, basic site conditions can be translated into the influences of light, moisture, nutrition, and temperature (cf. Zedaker 1982). If the site conditions change, as through competitive diminuation of resources, the efficiency of production is reduced and dry matter production slows. As production declines, there is a preferential maintenance of certain sinks, and changes to certain developmental characteristics which acclimate the tree to the new environmental conditions. By this process, the tree is able to compete and/or survive under a range of conditions.

To study the changing efficiency and acclimation strategy of plants in different environments, many techniques have evolved. Particularly useful are those methods available in the field of growth analysis. The scope of this methodology is broadly defined as the separation of growth into component processes to study the effect of endogenous and exogenous influences (Ledig 1974). The specific techniques have been fully described elsewhere (Evans 1971, Hunt 1978, Hunt 1982), particularly as they apply to agricultural crops or other herbaceous plants. In trees, these techniques often give insight into the origins of improvement in growth after silvicultural treatment (Brix and Mitchell 1983), difference in growth between species (Farmer 1980), or response to environmental change (Kohyama 1980). Growth analysis techniques have been developed to study the growth of different tree components, to quantify morphological changes, to study crown architecture (Halle et al. 1978, Tomlinson 1983), and to compare trends in demography or allometry of growth (Maillette 1983, Grier et al. 1984). These methods together provide a powerful tool to analyze the effects of environmental changes on tree growth.

During the regeneration phase of a forest stand, tree seedlings are unable to fully utilize all the site resources available to them. Many faster growing plants, shrubs, or pioneer trees quickly occupy the site. These species often have different growth characteristics to most commercial tree species which often allows for an advantage in development. For example, species with indeterminate shoot growth and sylleptic branching are able to rapidly develop large effective leaf areas (Farmer 1980). There are also differences in assimilation rate between species which can lead to differences in growth rates (Ledig 1969, Krueger and Ruth 1967).

The net result of competition is a modification in the quantity of resources available to the tree. Depending on site characteristics, the competition may reduce availability of light, moisture, or nutrients to the crop species (Nambiar and Zed 1980, Carter et al. 1984, Zedaker 1982). On a specific site it is difficult to determine the specific influences of light, moisture and nutritional competition on the growth response of the tree. The overall effect of

competition on the growth of the crop species will be a function of the initial supply of resources available on the site and the degree to which their availability is changed by the competing vegetation.

Light intensity changes have been modelled through various canopies. There is generally an exponential decline in light intensity as leaf area index increases (Monsi and Saeki 1953, Monteith 1965), although leaf angle, reflectance, size, and shape are also determinants. Soil moisture availability has been shown to decline under competition, particularly on xeric sites (Wilde 1971, Schmidt 1978, Zedaker 1982). In general, competition causes moisture deficits to occur sooner in the rooting zone, effectively shortening the growing season where summer droughts are common. Nutrient availability is related strongly to soil moisture, and this can be reduced by moisture depletion. A specific reduction in the availability of nutrients is difficult to quantify (e.g. Carter et al. 1984) but may be a factor on some sites. Conversely, some species may actually improve nutrition on degraded or nutritionally impoverished sites (e.g. *Alnus* species).

RESEARCH STRATEGY

As the early development of coniferous plantations and the associated competing vegetation is a dynamic process, both components of vegetation must be studied over time. Concurrently, the interaction of different levels of brush competition with the growth and development of tree seedlings must be identified. The study of this dynamic interaction requires information on tree growth and development, brush community growth, and the influence of brush competition on the tree growth.

Many studies of competition or of the interaction of resource factors on growth have identified light interception as being of primary importance (Magnussen 1983, Magnussen and Peschl 1981, Reed *et al.* 1983, Eissenstat and Mitchell 1983). This study was carried out on very productive sites in coastal British Columbia, where soil moisture and nutrients are plentiful. Therefore, it is hypothesized that decreasing light levels caused by competition from neighbouring vegetation results in growth suppression of the crop species. For this reason, competition was measured as indices of light interception. These measures also could be indirectly related to below-ground competition which may also occur.

In order to quantify both the inherent tree establishment pattern and sensitivity to competition, eleven measures of growth were tested on the study sites. These measures were of height, basal area, and foliage weight. They were formulated as both absolute and relative measures. Use of these different measures was to test the hypothesis that relative measures of growth would have greater sensitivity to environmental change than absolute measures. At the same time, growth of the foliage component was studied demographically by crown position to determine whether the effects on total tree growth were based on a balanced or unbalanced decline in the growth at different crown positions. The hypothesis was that the vigour of a branch would be a function of its particular crown position and not of the average light environment of the whole tree.

As a secondary study to the growth effects, a quantification of changes in morphology, architecture, and allometric relationships was undertaken. This study also was designed to

test the hypothesis that declining growth could be attributed to the reduction in light intensity. Many developmental variables have been related to light intensity under controlled laboratory conditions (Bjorkman and Holmgren 1963, Brix 1967, Brix 1970, Drew and Ferrell 1977) and it was hypothesized that developmental changes would be linearly related to increasing competitive shading.

The growth and development of the competing vegetation was studied in terms of both absolute canopy characteristics (leaf area index, height, percent cover) and derived indices (dominance, competitiveness). The aim was to derive trends in canopy development (as height vs. age) and vegetation succession based on biological measures. In this case the hypothesis was that species can be subdivided into different competitive strategies based on life form (Ellenberg and Mueller-Dombois 1967) and that these different strategies would be important to vegetation succession.

A final study was undertaken to determine the response of the plantation and competing vegetation to two different competition release treatments. Chemical (N-phosphonomethyl glycine) and manual (hand clearing) treatments were applied and first year results were determined in terms of tree growth response and brush species redevelopment. It was hypothesized that chemical treatment would result in more effective control by reducing the redevelopment of the vegetation canopy. It also was hypothesized that relative measures of growth would prove more sensitive for determination of improvements in growth by released trees.

The information gathered by these studies allows some generalizations on plantation development and interspecific competition. The objective was to test the broad hypothesis that the free-to-grow status of plantations is definable in biological terms and that an assessment-projection model could be formulated

EXPERIMENTAL DESIGN

A detailed description of the specific data collection and laboratory procedure is included with each of the four following chapters. This is to allow the reader to better determine how the methodology related to specific study objectives. There was, however, an underlying design framework within which all studies can be described.

An effort was made to select similar sites in terms of climate, soil moisture availability during the growing season, and nutritional status. Further, the specific site type was selected to remove moisture or nutritionally related constraints to growth. Other aspects of the sites are more fully discussed in later chapters. The site locations were in the foothills of the Cascade Mountains, surrounding the Fraser River valley (Figure 1).

The six sites selected represented an overlapping age sequence with similar silvicultural history. This allowed the sites to act as a chronosequence, thereby inferring changes over time. The experiment was a double sample blocked by site with an uneven number of experimental units per block. Each site (block) was stratified into areas of suitable hygrotone and a series of sample points were established systematically from random starting points. At each sample point, the nearest tree free from browsing or mechanical damage was selected as a sample tree for 1983, while another nearby tree was selected for use as a 1984 harvest tree. On two sites a third tree was selected for treatment with either a herbicide or hand clearing release. This third tree was also staked for 1984 sampling.

In order to remove much of the variability between the trees in the individual pairs of 1983 and 1984 sample trees, the 1984 tree was selected as a companion (c.f. Evans 1972). That is, it had a similar level of brush competition to the 1983 sample tree. From 8 to 12 sample trees per year were selected on each site. On sites where a treatment was carried out, an additional treated companion was selected for each 1983 tree. The total sample size was 62 control trees in 1983, 62 control trees in 1984, and 21 treated trees in 1984, for a total of 145 samples. Analysis was unbalanced due to the differences in the number of samples per site and the number of samples per growing season. The major analysis used measures of growth and

competition as covariates while age, site, and year of sampling were levels. The competition-growth relationship was analyzed as a random effect. Analyses comparing the influence of differences in age, site, or year of sampling were generally analyzed as fixed effects. The latter influences were confounded, as the growing seasons sampled varied from site to site.

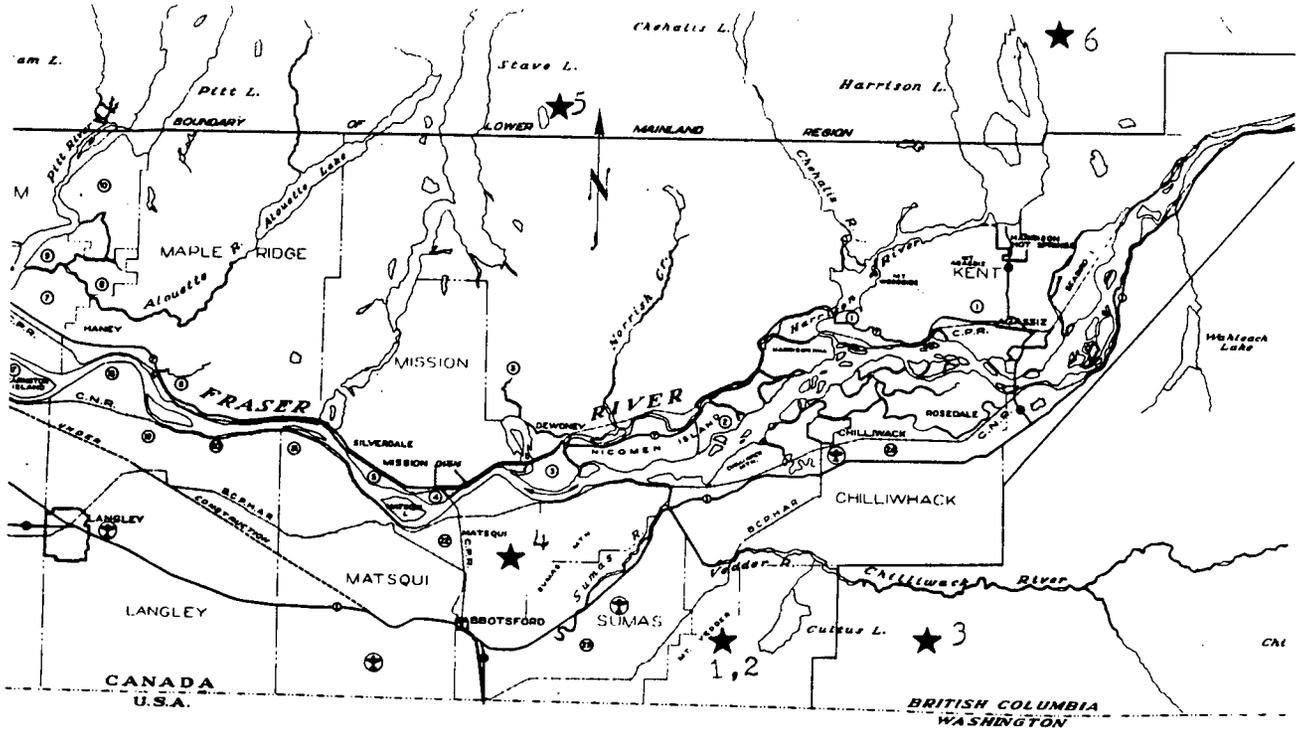


Figure 1. Location of study sites used in the experiment. Numbering corresponds to Table

1.

CHAPTER TWO

Growth of Douglas-fir in Relation to Indices
of Interspecific Competition.

ABSTRACT

The effects of interspecific competition on the growth of trees in one- to five-year-old Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) plantations were studied. A model of brush competition inferring light interception around the tree is proposed and tested against various measures of seedling growth. The relative production rates of foliage and new shoot biomass were the measures best explained by competition indices, followed by relative basal area growth rate and relative height growth rate. Foliage growth declined most rapidly in the lower crown as competition levels increased. Until overtopped, growth of the terminal leader and upper crown positions was unaffected by competition. This explains the reduced sensitivity of height measures to competition effects. The occurrence of lammas growth influenced the sensitivity of height and basal area measures more than foliage measures by increasing the variability in these quantities. Although absolute growth measures were strongly correlated with brush competition characteristics, the relationships do not appear to be causal in nature.

The relative growth measures followed a well-defined pattern from year to year for all characteristics tested. This pattern consisted of first season transplanting shock, second season re-establishment, and a decline towards a stable annual growth increment in the third to fifth seasons. It is proposed that plantation performance should be viewed against relative, rather than absolute growth measures. Competition indices show good potential for assessing interspecific competition problems, although they must be combined with a knowledge of the dynamics of competing species to be effective for predictive purposes.

INTRODUCTION

The moist, rich sites of coastal British Columbia are considered to have the highest potential productivity for forest growth in Canada (Krajina 1965). The establishment of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) plantations on these sites is hampered by severe competition from fast-growing brush species. Without effective plantation maintenance or brush control, these plantations are often overgrown, resulting in excessive regeneration delay and poorly stocked stands (Ruth 1956, Newton and White 1983, Howard and Newton 1984).

To date, foresters have used their experience with various site types and treatment regimes to make plantation management decisions, rather than using quantitative assessment techniques. However, as plantation maintenance programs are often becoming the source of public controversy due to their dependence on herbicides, prescriptions are proving difficult to defend. With the introduction to some Canadian provinces of the concept of the "free-to-grow" plantation, there is a second, administrative need for an improved measure of plantation performance and competition levels. The commonly accepted definition of a "free-to-grow" plantation requires that areas be sufficiently stocked with seedlings showing acceptable growth, which are free from unacceptable brush competition (B.C. Ministry of Forests 1984). This definition implies a need for standards to determine acceptable tree growth and unacceptable levels of brush competition. Further, the measure of growth must be one which is sensitive to competition.

The most frequently used indicator of growth is tree height. Both absolute height and rate of height growth have been used as a dependant variable in studies of plantation performance (e.g. Vincent 1954, Ruth 1956, Oxenham 1983, Howard and Newton 1984, Newton and White 1983). The biological basis for using height as a sensitive indicator of tree responses to environmental change is not particularly sound. The tendency to preferentially maintain height growth has been demonstrated by Farrar (1961) and Bormann (1965) for shade intolerant species. The impact of browsing can also also prove a major problem in the use of height

measurements. Other, potentially more sensitive measures of growth such as basal area, stem volume, foliage dry weight, or total dry weight have been tested sparingly in plantation conditions (Peterson and Newton 1983, Zedaker 1982). This is likely due to the ease of measurement of height, and the necessity for destructive sampling to determine these other variables.

While the choice of variable is important, so also is the measure of growth used to describe that variable. Using the example of height, performance can be measured as total height (an absolute measure of growth), height increment (a growth rate), relative height growth (a relative growth rate), or as a ratio between the production in successive growing seasons (a relative production rate). Therefore, not only must a researcher find a sensitive variable, he must present it in its most meaningful formulation. In the case of brush competition in forest plantations, it does not appear that different variables and measures of growth have been systematically tested to determine the optimum indicator of crop tree performance.

In order to carry out a test of different growth measures, the independent variables of brush competition must also be quantified effectively. Studies on inter-tree competition have variously used measures of crown overlap (Arney 1972), relative stem diameter (Bella 1971, Hegyi 1974), relative crown width or radius (Ek and Monserud 1974), and relative tree height (Ek and Monserud 1974). Most studies of brush competition in plantations, however, have used subjective estimates of competition such as "moderate" or "severe" (e.g. Vincent 1956, Eis 1981, Oxenham 1983). Recently, attempts have been made to quantify the competitive influence or index of competition affecting a given tree (Wagner 1982, Howard and Newton 1984). These indices are generally based on the proximity and relative height of competing vegetation to the planted trees. In order to be suitable, an index of this sort should be applicable through the range of plantations to be tested, relative to the tree affected, and measurable or quantifiable.

This study investigates the interaction of measures of absolute and relative growth rates

of height, basal area, and foliage weight with indices of interspecific competition. The objective is to determine what measure of tree growth is most sensitive to competition, and what measure of competition most strongly influences tree growth. Further, the competition-growth rate interaction is examined both temporally over two growing seasons, and demographically through the crown.

METHODS

Study Sites

In order to remove possible variability in growth between climatic zones or slope positions, a series of sites with similar soil moisture and climatic conditions were selected. The site type selected was considered to be optimum for Douglas-fir growth in British Columbia (Klinka and Carter 1980). These sites are characterized as being within the Pacific Ranges Drier Maritime Coastal Western Hemlock Biogeoclimatic Subzone (Krajina 1965, Klinka *et al.* 1979). They are classed as being of subhygric hydrotape, and mesotrophic to subeutrophic trophotope. All sites selected have been logged, site prepared by broadcast burning or scarification, and planted in the following spring to Douglas-fir seedlings. Each site was sampled in each of two growing seasons, resulting in the series of overlapping sequences mentioned in Chapter 1 (Table 1).

These study sites have deep, loamy soils derived from glacial or alluvial materials. Due to the effects of slope position, soil texture and depth, and the humid climate, these soils retain moisture throughout the growing season, despite low summer precipitation common to the area (Klinka 1976). These good growing conditions promote the vigorous development of naturally established deciduous species, shrubs, and ferns.

Table 1. Summary of study sites.

Location	Plots/ year	Preparation method and year	Year planted	Stock type*	Ages sampled
1. Vedder Mtn.	10	Broadcast burn 1982	1983	Plug+1	1,2
2. Vedder Mtn.	11	Broadcast burn 1981	1982	2+0 BR	2,3
3. Tamihi Ck.	10	Scarification 1981	1982	2+0 BR	2,3
4. Sumas Mtn.	12	Scarification 1980	1981	PSB 313	3,4
5. Davis Lake	11	Broadcast burn 1979	1980	2+0 BR	4,5
6. Cogburn Ck.	8	Broadcast burn 1979	1980	2+0 BR	4,5

*Plug+1 -transplanted for one year after grown as PSB 313

2+0 BR -two year old seedling grown in nursery bed

PSB 313 -plug grown in styroblock container

The study sites selected, despite pre-planting preparation, showed development of a varied community of Alnus rubra Bong., Rubus parviflorus Nutt., Rubus spectabilis Pursh, Pteridium aquilinum (L.) Kuhn var. pubescens Underw., Acer macrophyllum Pursh, Acer circinatum Pursh, and Epilobium angustifolium L. The degree of competition around individual trees varied with microtopographical position. On dry positions, or where surrounded by rotting wood, trees were relatively open-grown. In moist depressions, brush density was high, with values of up to 5.0 found for leaf area index. Each site allowed the measurement and harvest of sample trees varying from completely open-grown to severely suppressed

Field Procedures

A two year harvest sampling procedure was devised to collect information on the growth of the planted Douglas-fir and certain characteristics of the competing vegetation. Sampling was carried out from August 10 to September 9, 1983 and from August 6 to September 5, 1984. This period of the growing season was selected as the most stable with regards to vegetation foliage development and cessation of seedling growth. Some lammas and proleptic shoot growth occurred during the sampling period, but this was generally minor compared with the initial flush of growth.

The sample tree location and establishment are discussed in Chapter 1. At each sample tree, a 1/1600th hectare circular plot (1.41 metre radius) was established, centred on the seedling root collar. This plot size represented the area allocated to each tree by the planting density used on all sites (6.25 m²). Using a measuring cord, a plot map was prepared showing the brush species present and the area of the plot covered by the foliage of each. The average height of the canopy of each brush species also was measured. In the first sampling period (1983), in situ measurement was followed by manually removing and bagging the foliage from all major competing species for laboratory determination of leaf area. In the second season leaf area was not determined due to its lack of significance as a competition component in the analysis of the first season data.

The sample tree was measured for total height and height increment from each of the three previous years. Then, the tree was harvested by systematic branch clipping, with shoots stratified by crown position and season of production into cohorts. Each cohort is defined by unique location (whorl) and year of production. This was designed to allow a demographic analysis of growth (Bazzaz and Harper 1977, Hunt and Bazzaz 1980), which separates total plant growth into the sum of the growth of different crown positions. After clipping of shoots was completed, the remaining stem was cut at the root collar and bagged for transport to the laboratory. In total, 124 sample trees were used for this study. Treated trees were not included in the following analyses.

Laboratory Procedures

In the laboratory, leaf area determination was carried out for a subsample of the foliage, by species, of the competing vegetation from the 1983 plots using a LI-3000 (Lambda Instruments) leaf area meter. These samples and the remaining foliage were dried at 65° C for 48 hours to determine dry weight. Correction factors were developed from these subsamples to calculate the total leaf area by species in each plot.

The shoots collected from the sample trees also were dried at 65° C for 48 hours. The present year shoots were then stripped of foliage and the two components of stem and foliage weighed separately. The shoots from the previous growing season were also stripped and foliage weight determined. Stem weights were not determined for the previous growing season due to the difficulty in stratifying the weight of the twigs into current and previous years' production. Root collar sections were sanded and rubbed with zinc oxide paste to distinguish the growth rings. These segments were then measured for ring widths.

From the above measurements a data set of primary values was generated for each sample plot. This included a series of measurements of the competing brush community and the planted tree (Table 2).

Table 2. Summary of basic data for each sample

Component	Symbol	Measure
Seedling	LWijk	Foliage weight produced at position k of tree i in year j.
	SWijk	Shoot weight produced at position k of tree i in year j.
	HTi	Total height of tree i
	HTij	Height increment of tree i in year j.
	BATi	Total basal area of tree i.
	BAij	Basal area increment of tree i in year j.
	RTi	Crown radius of tree i.
Brush	*Lij	Leaf area of species j in plot i.
	HBij	Mean height of foliar canopy of species j in plot i.
	%Cj	% of plot i covered by species j.
	RB	Average distance to inner edge of foliage of any species from centre of crown of tree i.

*1983 harvest only.

Determination of Analytical Variables

From the primary values listed in Table 2, a set of variables were derived to indicate various measures of tree growth and characteristics of the competing vegetation. Methods for studying plant growth are well-documented (Evans 1972, Hunt 1978, 1982) and this work will use the standards of nomenclature devised in plant growth analysis.

Two measures of absolute growth and two measures of relative growth were used. Further, a demographic partitioning of the growth by crown position was carried out. The absolute measures were total growth (or total size) and growth rate (annual increment). While these measures may be related to productivity, the relationship is indirect. Differences in absolute growth are generally more a function of plant size than of exogenous influences (Ledig 1974). Using relative growth measures diminishes the effect of plant size as a determinant of performance. The relative measures used were the relative growth rate and the relative production rate. The relative growth rate has the drawback of an inherent decline over time in perennial plants due to the accumulation of non-productive supportive tissues. The relative production rate measures current increment as a function of the growth in the preceding period of the same length. The formula for each of these measures is shown in Table 3.

Table 3 -- Derived variables of growth and competition tested.
(refer to Table 2 for definition of basic terms).

Measure	Generalized equation	Variables tested (growth measures)
Total growth		Height, basal area,
Absolute growth rate	$G = (W_2 - W_1) / (T_2 - T_1) \dagger$	Foliage Wt., height, basal area
Rel. growth rate	$R = \ln(W_2 / W_1) / (T_2 - T_1)$	Height, basal area
Rel. prodn. rate	$RPR = \frac{(W_3 - W_2) / (T_3 - T_2)}{(W_2 - W_1) / (T_2 - T_1)}$	#Shoot Wt., foliage Wt., height, basal area
Partial prodn. rate	see text p. 25	Foliage weight

Inverse proximity	$Invprox = [(RB/RT) + 1]^{-1}$	
Relative height	$H_{trel} = [\sum(HB_j * \%C_j) / n] / HT$	
Percent cover	$Percov = \sum \%C_j$	
Foliage density#	$LAI = \sum L_j / 62,500$	

#Rel. Shoot Production Rate is calculated as the current shoot weight divided by the previous season foliage weight.

#LAI values are calculated for 1983 harvest only.

†T₂-T₁ = change in time (i.e. one year).

The measures of whole-tree foliage growth can be partitioned into partial growth rates at each whorl in the tree crown. These partial production rates can be separated and examined in terms of their contribution to the growth of the tree as a whole. This is done by separating the total foliage weight of the tree into cohorts (Bazzaz and Harper 1977):

$$[1] \quad LW_i = \sum lw_{ij}$$

Where LW_i is the total foliage produced in a given growing season and lw_{ij} is the weight of foliage produced in year i at position j of the tree crown. The total relative foliage production rate is also subdividable amongst the different crown positions:

$$[2] \quad LW_2/LW_1 = (lw_{21}/LW_1) + (lw_{22}/LW_1) + \dots + (lw_{2n}/LW_1)$$

Giving a proportional allocation of the total relative foliage production to each crown position. Dividing each term by the total production rate gives the partial production rate at each position:

$$[3] \quad 1.0 = (lw_{21}/LW_1)/(LW_2/LW_1) + (lw_{22}/LW_1)/(LW_2/LW_1) + \dots \\ + ((lw_{2n}/LW_1)/(LW_2/LW_1))$$

Which can be simplified as the proportion of current dry weight at each position:

$$[4] \quad 1.0 = (lw_{21}/LW_2) + (lw_{22}/LW_2) + \dots + (lw_{2n}/LW_2)$$

The partial production rates in [2] are relative growth measures while the percentage production rates are a proportional allocation of absolute increments. The partial production rates can be considered yield components, and indicate the proportion of the total growth of the tree attributable to each whorl.

The characteristics of the competing vegetation around each sample tree were divided into four separate indices. These are representative of proximity, height of the brush canopy relative to the total tree height, percent of the plot covered by the brush foliage, and the

leaf area index of the brush foliage over the plot (Table 3). While these four measures may be indicators of the light interception around the tree, they more generally indicate the level of total competition influencing the trees growth. The light interception basis for competition may be inferred from studies (Magnussen and Peschl 1981, Zedaker 1981, Eissenstat and Mitchell 1983, Reed *et al.* 1983, Magnussen 1983) which have looked at the interactions of light, moisture, and nutrients with tree growth.

The proximity term is based on the average horizontal distance from the tree stem to the brush foliage (RB) as a ratio to the radius of the tree crown (RT). The inverse of this ratio is used so that the value increases exponentially as the brush foliage approaches the tree. The constant is added to prevent extremely large values where RB approaches zero. The relative height term is the ratio of the weighted mean height of the brush canopy compared to the sample tree. The percent cover is the sum of the plot area covered by the various competing species. The leaf area index is the total surface area of brush foliage divided by the total plot area (6.25 m²).

RESULTS

Absolute Growth

Trends in mean total height and mean total basal area (inside bark) for the six sites listed are shown in Figure 2. Reconstruction of trends was carried out using stem internode and ring width measurements. From Figure 2, differences between sites are apparent, likely due to the different stock types planted on sites 1 and 4. The transplant stock on site 1 was the largest at the time of planting and remained so through the first two growing seasons in terms of both height and basal area. The smaller plug stock shows the least total growth after the fourth season. The bare root stock on the remaining four sites seems to show similar height and basal area at a given age from planting.

Trends in the annual increments of height, basal area, and foliage dry weight are shown in

Figure 3. By removing previous growth and concentrating on current growth increment, a better representation of the vigour of the tree at each age is gained. For example, the graph of annual height increment shows a transplanting shock on all sites more clearly than does total height in Figure 2. While the three variables of height, basal area, and foliage weight show similar trends over time, the basal area and foliage measures seem to increase at a faster rate than height.

Comparing the performance of trees on different sites, the pattern is similar in the graphs of Figures 2 and 3. The larger trees of site 1 show the highest growth rate of the three variables. The plug stock planted on site 4 shows comparable performance in height and foliage weight measures to the bareroot stock as a growth rate. This indicates that the major difference in size between the plug and bareroot stock in Figure 2 was due to the initial difference at the time of planting.

Relative Growth Measures.

Differences in absolute growth between the plug, bareroot, and transplant stock types in Figures 2 and 3 was due to the influences of initial tree size at outplanting. By using relative measures, the influences of tree size is diminished (Figures 4 and 5). Trends in relative growth were constructed for individual trees using annual increments of height, basal area, and foliage weight.

The trends in relative growth rate of height and basal area shown in Figure 4 reflect the performance of the trees more dynamically than the absolute growth measures. High relative growth rates in the nursery are followed by a very sharp decline in the year of outplanting due to transplanting shock. As the trees root systems become re-established, there was a renewed high relative growth rate of both height and basal area in the second growing season. The third to fifth seasons show a general decline in relative growth due partly to the continual increase in total height and basal area respectively for the two graphs.

In Figure 4 the relative performance of the larger and smaller stock types on sites 1 and

4 is now reversed from Figures 2 and 3. This indicates that the superior absolute growth of the trees on site 1 is a function of their larger size, rather than inherently superior vigour.

A more subtle difference in the use of absolute and relative growth measures is seen in the comparison of height growth of trees on sites two and three. In Figures 2 and 3 a reversal of the performance ranking occurs in the third season. Using the relative growth measures (Figures 4 and 5) this reversal occurs earlier, in the second season. The earlier sensitivity suggests that relative growth rate is a better indicator of the real vigour of the sample trees.

While relative growth rate seems to be a more sensitive indicator of vigour than absolute growth measures, it too is linked to tree size. The accumulation of height and basal area on the trees represented in Figure 4 causes an inherent decline in the relative growth rate, most noticeably in the third to fifth growing seasons. The trends in the relative production rate of height, basal area, foliage dry weight, and current shoot dry weight shown (Figure 5) indicate most effectively the current vigour of the growth of the trees. The shoot production rate is slightly different from the other relative production rates, being calculated as the total weight of current year shoots divided by the previous years foliage dry weight production. The general trends in relative production rates are similar to those of the relative growth rates (Figure 4). The transplanting shock is still very evident as a sharp drop in the first growing season. The fourth and fifth growing seasons do not decline as sharply in the relative production rate graphs as do the relative growth rate graphs.

The relative production rates of height and basal area seem to stabilize (approach a value of 1.0) more rapidly than the shoot and foliage measures. This stabilization, particularly of height growth may be the earliest point at which the site quality is expressed as a limiting factor.

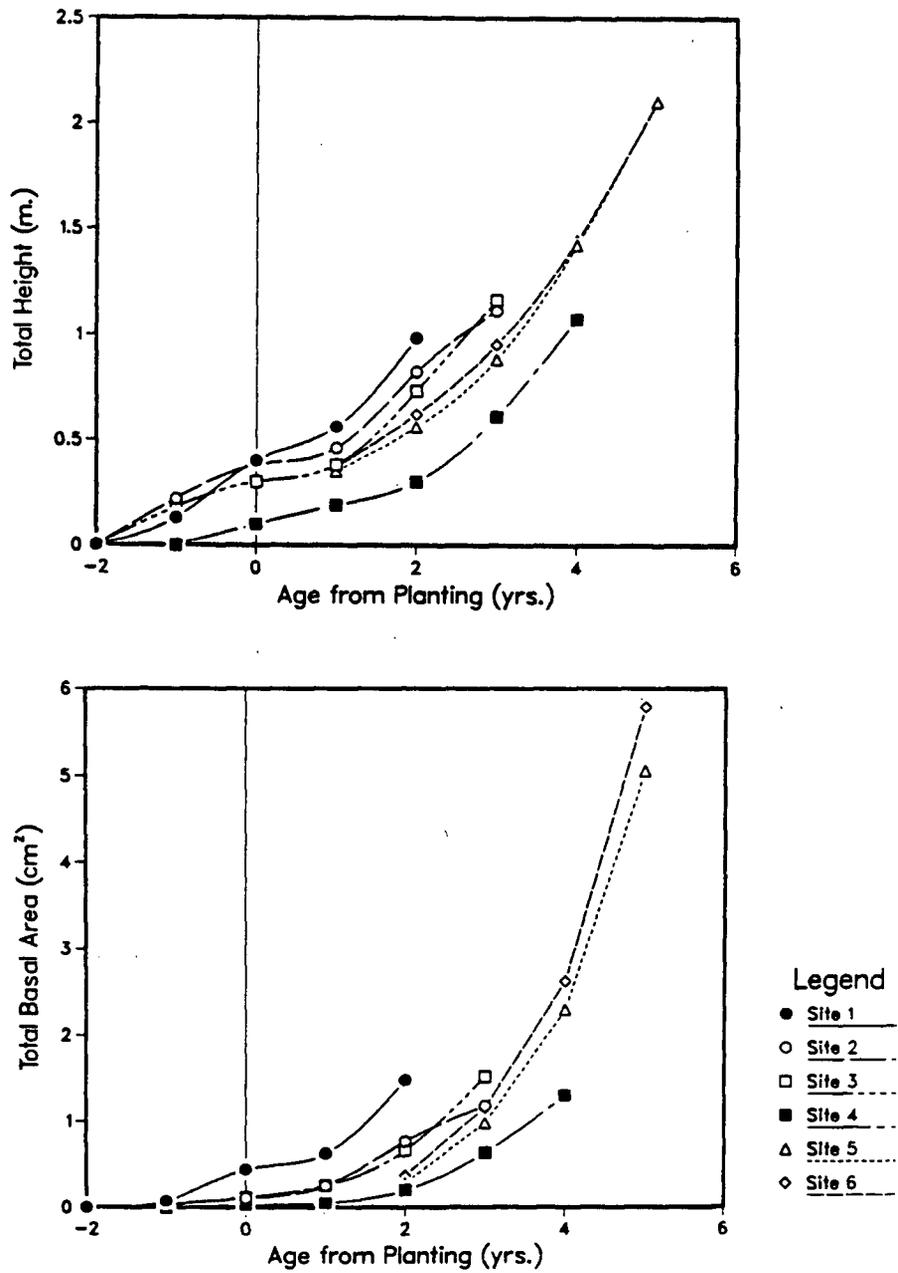


Figure 2. Trends in mean total height and mean total basal area on the six study sites.

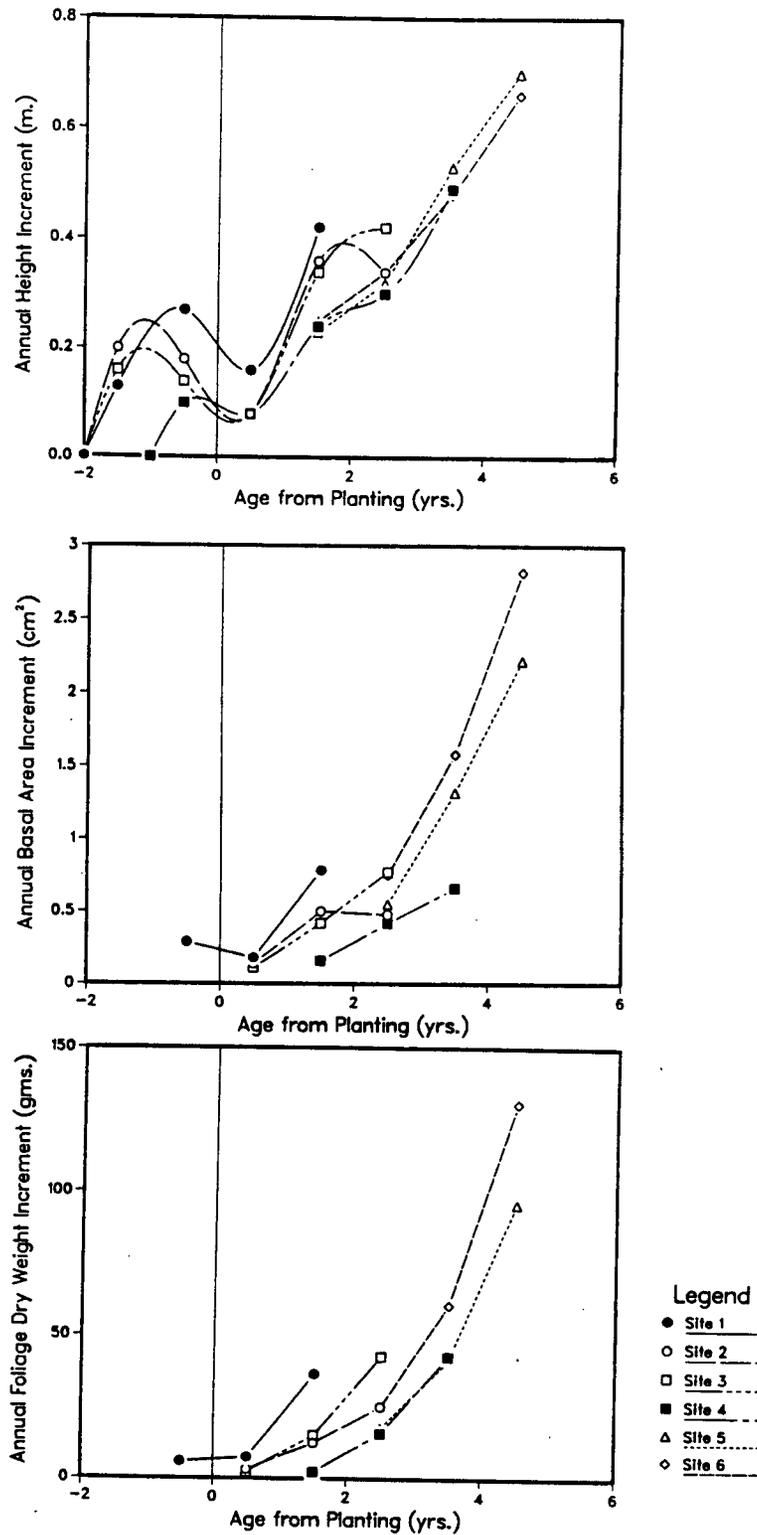


Figure 3. Trends in mean height increment, mean basal area increment, and mean foliage dry weight increment on the six study sites. Measures are of the form $y=dx/dt$, where dt is one year.

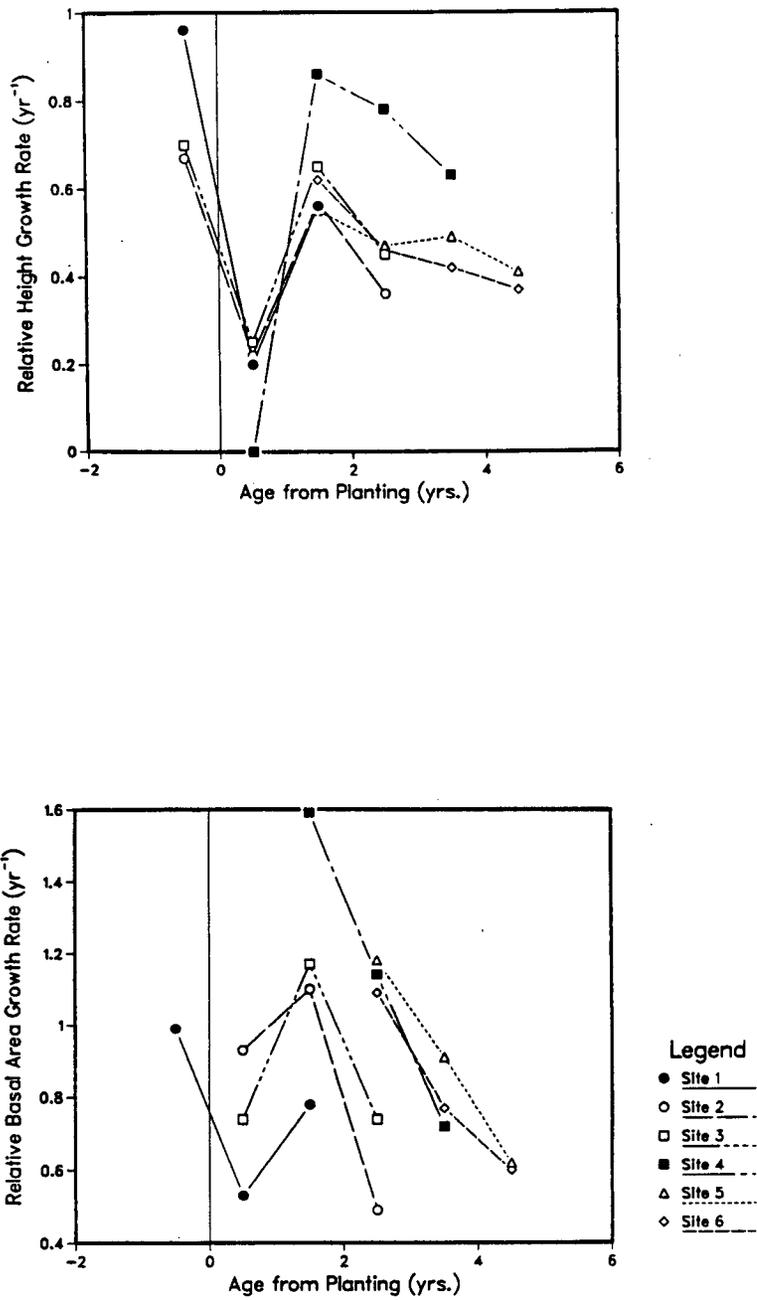


Figure 4. Trends in mean relative height growth rate and mean relative basal area growth rate on the six study sites. Measures are of the form $y=(1/x)(dx/dt)$

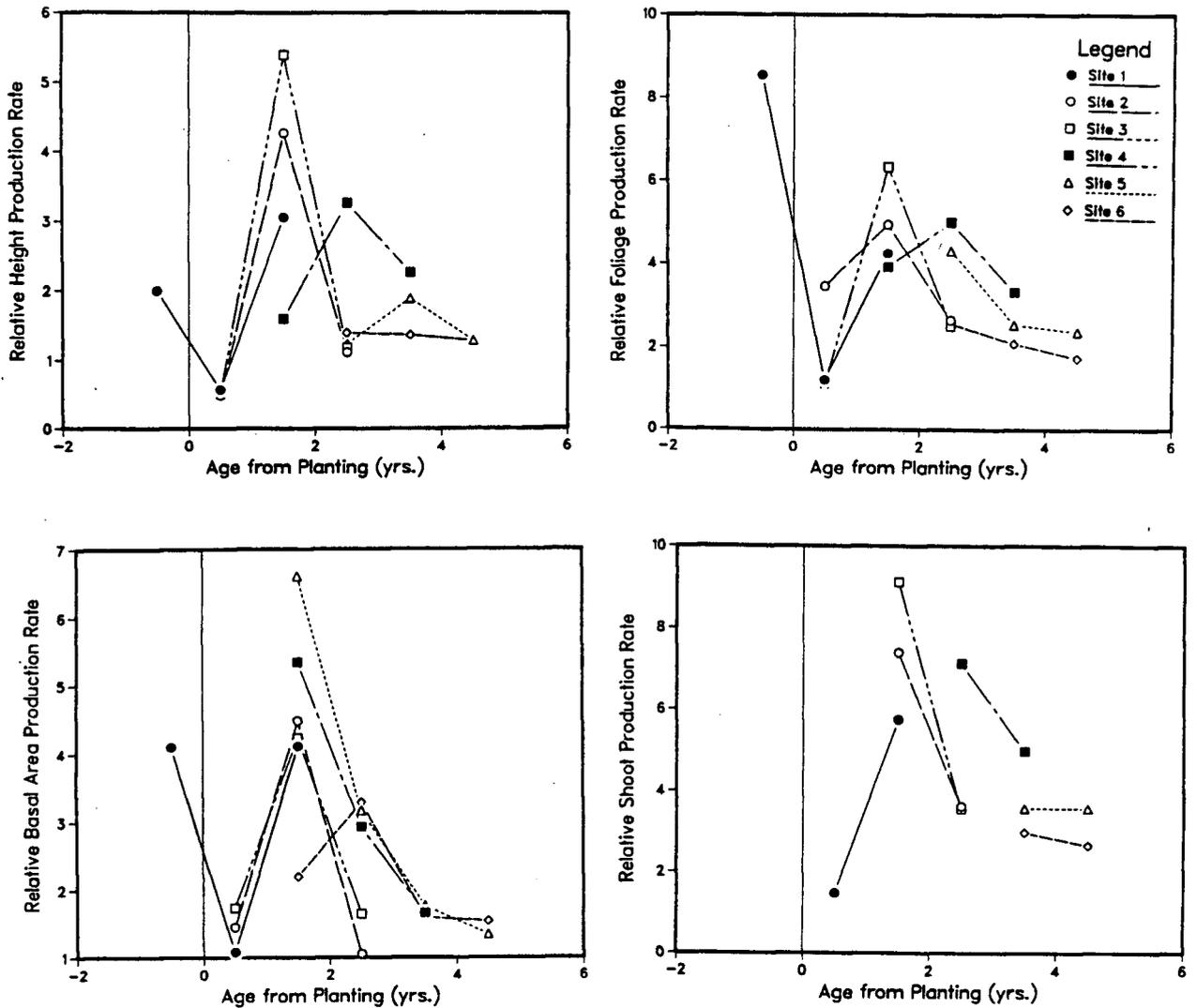


Figure 5. Trends in mean relative height production rate, mean relative basal area production rate, mean relative foliage production rate, and mean shoot production rate on the six study sites. Measures are in the form $y=(dx_2/dt_2)/(dx_1/dt_1)$ where dx_2/dt_2 and dx_1/dt_1 are growth rates in succeeding years.

Demographic Analysis of Growth

The growth in foliage weight, partitioned into the leader and the six uppermost whorls is shown in Figure 6a. The curves were generated using the data from the trees planted as 2 + 0 bareroot. As each tree carried at least two years of foliage at each crown position, and each site was measured in two growing seasons, the individual data points represent the mean values of up to four sites. From Figure 6a, a more thorough understanding of the distribution of growth is gained. Each whorl is born at the point where it originates from the x-axis, produces an annual increment, and eventually will die, rejoining the x-axis. In Figure 5 the relative foliage production rate was still at a value of almost 2.0 in the fifth growing season, indicating that the annual foliage weight increment is still increasing. From Figure 6a, it can be seen that this increase is attributable to both an increase in the number of living whorls and the increment produced on a given whorl over time.

The total relative foliage production rate in each growing season can also be allocated on a proportional or percentage basis to each crown position. An example of this for the data in Figure 6a is shown in Figure 6b. The contribution of each whorl peaks earlier as a percentage production rate rather than as an absolute increment. As these trees age and develop, the contribution of the leader and uppermost whorl declines. The second and third whorl increase, accounting for over 60% of the total relative foliage production rate by the fourth and fifth growing seasons.

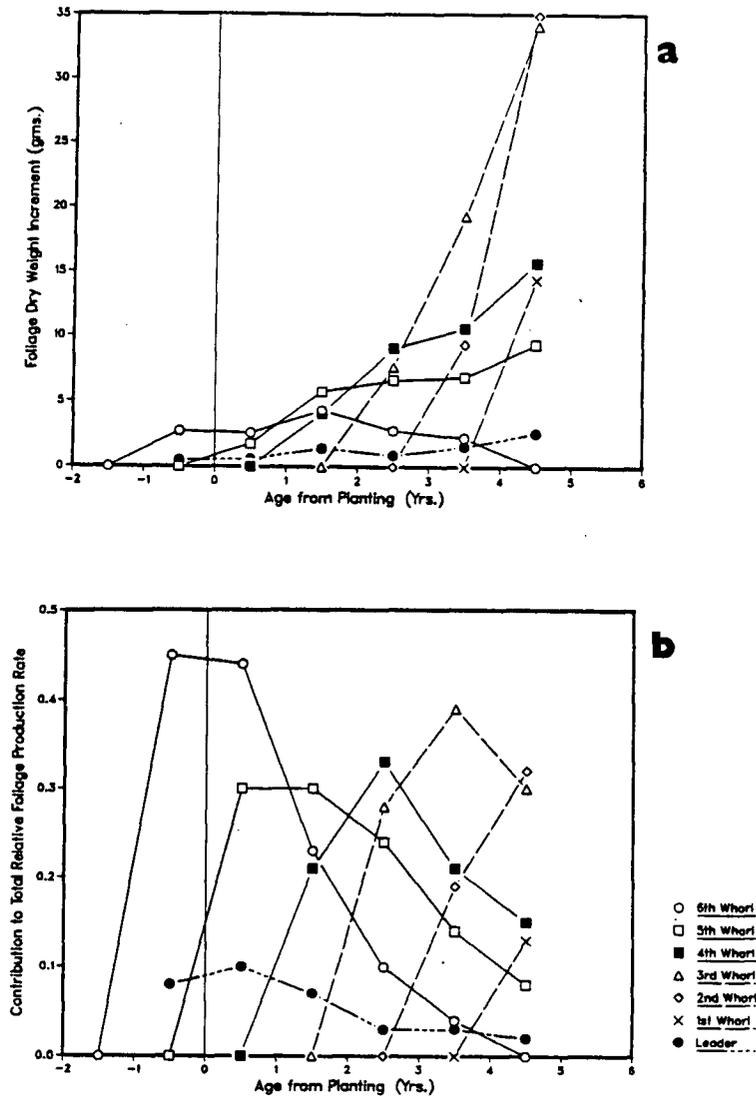


Figure 6. (a). Demographic analysis of foliage dry weight increment on 2 + 0 bareroot seedlings. Individual curves represent the development of the whorls on a mean tree in the fifth growing season. Whorls are numbered from the top down. (b) Demographic analysis of the proportional allocation of the production rate of foliage dry weight of a mean 2 + 0 bareroot seedling. At each growing season the sum of the whorls present is 1.0. The whorls are numbered based on their status on a mean tree in the fifth growing season and are numbered from the top down.

Derivation of a Competition Model

The foregoing results have presented the trends of the mean values of different tree growth measures over time. The relative performance of similarly aged trees on different sites appears to change depending on the measure of growth used. The determination of brush competition influences also may be affected by the choice of growth measure. It is now intended to account for variation among different growth measures on each site under varying intensities of competition.

Correlation of Growth Measures with Competition Characteristics

In Table 4, the simple linear correlation coefficients between growth measures and competition characteristics are presented (the indices in Table 4 will be discussed later). Each measure of plantation growth includes a great deal of variation not directly attributable to competition (i.e. trends over time, differences between sites, genetic variation). Nevertheless, differences in the relationship between specific growth measures and competition characteristics are visible in Table 4.

Looking first at the classes of growth measures, it appears that relative production rates and absolute growth rates are more sensitive to competition than relative growth rates and total growth respectively. Both relative measures are most strongly related to the proximity term, while both absolute measures are better correlated to the relative height term. Since absolute growth measures are largely a function of plant size (Figures 2-5), the correlation of absolute growth measures to the relative height term may not indicate a causal relationship. For example, it was shown that the shorter trees on site 4 (plug stock) had lower absolute growth rates because they were of smaller initial size. These trees also have higher values of the relative height term associated with a given brush canopy because of their short stature. Therefore, in the case of absolute growth measures, shorter or smaller trees may be negatively related to the relative height term because they are smaller, rather than because the taller brush has caused them to grow less vigorously.

Table 4. Simple linear correlation coefficients for measures of tree growth and brush competition characteristics.

Growth variable	Competition variable			Competition		
	Cover	Rel. Ht.	Inv. LAI*	index		
	(%)	(cm/cm)	Prox.	#1	#2	
Rel. Foliage Prodn. Rate	-.38	-.40	-.53	-.32	-.55	-.56
Rel. Shoot Prodn. Rate	-.36	-.42	-.50	-.31	-.56	-.57
Rel. Height Prodn. Rate	-.09	-.09	-.21	-.16	-.16	-.16
Rel. B. A. Prodn. Rate	-.20	-.10	-.25	-.03	-.19	-.22
Rel. Height Growth Rate	-.21	-.16	-.33	-.30	-.28	-.33
Rel. B. A. Growth Rate	-.31	-.21	-.41	-.19	-.36	-.41
Abs. Growth Rate-Foliage	-.40	-.71	-.34	-.17	-.68	-.66
Abs. Growth Rate-Height	-.15	-.63	-.16	-.03	-.51	-.49
Abs. Growth Rate-B. A.	-.37	-.65	-.31	-.10	-.61	-.61
Total Height	-.04	-.58	+.03	+.20	-.39	-.33
Total B. A.	-.30	-.62	-.22	-.05	-.54	-.52

n=121 df=119 p(.05)=0.178 p(.01)=0.233

*for LAI values n=61, df=59, p(.05)=0.257, p(.01)=0.333

aIndex #1=(Rel. Ht.)X(Inv.Prox.)

Index #2=(Rel. Ht.)X(Inv.Prox.)X(Cover)

Further evidence that relative measures of growth are more causally affected by competition than absolute measures is the significant relationship of the relative foliage production rate measure to all characteristics ($p < .01$) of the competing vegetation. There is particular improvement in the correlation of these relative measures with the proximity term. As the relative measures are not measures of size, they better indicate changes in vigour.

There seems to be a hierarchy among the characteristics of growth (i.e. foliage weight, basal area, height) in terms of sensitivity to competition. Foliage measures (including the shoot production rate) generally have the highest correlation with competition characteristics followed by basal area measures and height measures. The individual growth term that is most strongly related to competition is the absolute foliage weight growth rate. This is likely due to the abovementioned non-causal relationship of tree size with the relative height term and an indirect expression of some decline in vigour being translated into actual reduction in absolute growth.

2. Multiple Regression Models

While the correlation matrix gives an overview of the relationship between two variables, it does not allow insight into the effects of more than one independent variable on a dependent variable. It also gives little insight into whether the independent variables are complementary or simply explaining the same variation in the dependant variable. For these reasons, multiple linear regression equations were developed for each measure of tree growth as a function of the competition characteristics that proved significant (Table 5).

Table 5. Multiple linear regression models for growth estimators as a function of competition characteristics.

Growth estimator	Equation*	n	r ²
Rel. foliage prod. rate	$\ln(y)=1.90-0.23H_{trel}-0.94Invprox$	123	.57
Rel. shoot prod. rate	$\ln(y)=2.27-0.29H_{trel}-0.88Invprox$	123	.56
Rel. b. a. prod. rate	$\ln(y)=0.97-0.56Invprox$	119	.25
Rel. height prod. rate	$\ln(y)=0.92-0.49Invprox$	124	.21
Rel. height growth rate	$\ln(y)=-.48 - .42Invprox$	124	.33
Rel. b. a. growth rate	$\ln(y)=-0.61Invprox$	120	.41
Ab. growth rate-foliage	$\ln(y)=4.26-1.53H_{trel}$	124	.71
Ab. growth rate-height	$\ln(y)=-0.55+.005Percov-0.63H_{trel}$	124	.65
Ab. growth rate-B. A.	$\ln(y)=0.70-1.21H_{trel}$	120	.64
Total height	$\ln(y)=0.31-0.56H_{trel}+0.53Percov$	124	.65
Total basal area	$\ln(y)=1.29-1.09H_{trel}$	120	.62

*Percov=% cover H_{trel} =relative height $Invprox$ =inverse proximity
(c.f. Table 3)

Leaf area index (measured on a 61-tree subsample) and percent cover were non-significant in all but one equation. The models of absolute growth largely reflect the negative correlation of tree size with the relative height term discussed above. The models constructed for the relative production rate of foliage and shoot weight show improved correlation coefficients over the individual terms in Table 4. This infers that the proximity and relative height terms have additive influences in the relative foliage or shoot production rate measures of growth. The proximity term is still the most important determinant in the decline of relative growth rates. The percent cover and leaf area index terms may be estimating proximity, but less effectively than the direct measurement of that term, and thus do not contribute to these models.

The equations derived in Table 5, while clarifying the relative importance of the different competition characteristics, are still of limited utility for predictive purposes. Individual regressions are needed for each growing season on each site to isolate the validity of these models. Equations were derived in this manner, but the problems of chance correlations, changes in sign by variables from year to year, and variation in the significance of various terms from year to year became evident. In general, multiple linear regression did not lead to the construction of a single model with consistent terms.

3. Competition Indices

In an attempt to overcome the problems of model-fitting with multiple regression, single term competition indices were constructed. Competition indices combine the individual competition characteristics, developing a single modified term. Examples of these types of indices are seen in the work of Wagner (1982), Hegyi (1974), and Bella (1971). The benefits of indices are ease of use, removal of variability from more than one source if the variation is in some way additive or synergistic, and reduction of anomalies in individual terms (such as the height-relative height interaction discussed earlier).

Two indices were constructed to act as models of competition around individual trees. The

relationships of the indices with the growth measures is displayed alongside the individual terms in Table 4. The first index (#1) is a function of the relative height term multiplied by the inverse proximity term. The second index (#2) is produced from the first index multiplied by the percent cover term for each sample tree.

Of the two indices, the second seems best correlated with relative growth, while neither improves on the relative height characteristic in determining absolute growth (Table 4). The predictability of relative production rates of foliage and shoot dry weight benefit most strongly from the use of an index. This follows from their multiple regression equations in Table 5, where both relative height and proximity were significantly negative terms. The ability of the percent cover term, added in index #2, to improve the correlation coefficient when applied to relative growth measures is due to a relatively small number of plots where brush was present only very close to the tree. In these instances the cover term acts to reduce the index value. In most other plots it followed similar trends to the proximity term and did not have a large influence.

4. Significance of the Competition Index within Specific Sites

To be successful, the competition index should be consistently applicable through the range of sites tested. This would allow the index to be useful in ranking competition problems on different sites or in estimating growth losses on sites similar to those studied here.

Table 6 presents a matrix of the significance of individual regressions between competition index #2, the growth measures, and the sites sampled by growing season. It seems that the relative foliage production rate and relative shoot production rate are the most consistently sensitive growth measures. The other foliage based measure (foliage growth rate) also was sensitive. The lowest significance of the regressions of foliage and shoot production rates versus the competition index is on site 1 in 1983, likely due to an over-riding influence of planting shock. A review of the data for this site also shows a somewhat coincidental correlation between absolute growth measures (foliage growth rate, basal area growth rate,

total height, total basal area) and the competition index. This is because two smaller than average trees were sampled in the heaviest brush on site 1 in the year of outplanting.

The very poor correlation of the individual regressions of relative height and basal area production rates in Table 6 is due to two factors. The 1983 season had a significant second flush (lammas and proleptic growth) on all sites. In the 1984 season a second flush was less prevalent, resulting in considerable variation in these relative production rates not attributable to site, age, or competition effects. The second factor was an improvement in the techniques used in determining proximity in the 1984 sampling season. Preliminary analysis of the 1983 data had shown the importance of this measure, and in 1984 the measurements of crown width and distances to the brush foliage were made on more axes and averaged to improve accuracy. Both these forms of variation could be minimized by operational methodology. Lammas growth could be ignored and standards produced for proximity measurements.

It is desirable to look beyond the significance of these regressions and determine what effect the variation in competition level has on the different growth measures within the sites. The final column of Table 6 lists the percentage of the total variation between trees on the sites which is attributable to the competition index. This is determined by covariance analysis; removing the variation between the sites and between the 1983 and 1984 sampling periods. If the proportion of the remaining variation explained is considered an indication of the sensitivity of the measure to competition index #2, the foliage and shoot production rates would be considered the most successful relative growth measures, while the foliage or basal area increment would be the best absolute measures. The absolute measures, while highly correlated to the indices, still contain non-causal relationships with the competition index.

Table 6. Probability($p < 0.0x$) levels of individual regressions between measures of growth and the competition index* for each site by growing season. Right hand column indicates the percentage of the total variation within sites which is attributable to competition influences (from covariance analysis).

Measure	Sample												%
	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		
	'83	'84	'83	'84	'83	'84	'83	'84	'83	'84	'83	'84	
RFPR	.08	.00	.00	.01	.00	.00	.01	.04	.10	.00	.00	.00	54
RSPR	.09	.00	.01	.00	.00	.00	.02	.02	.07	.00	.00	.00	57
RHPR	.09	.50	.17	.15	.08	.18	.63	.30	.31	.01	.10	.24	12
RBAPR	.26	.00	.87	.46	.22	.54	.97	.32	.49	.15	.46	.56	9
RHGR	.43	.01	.17	.07	.01	.04	.89	.72	.86	.01	.12	.03	15
RBAGR	.28	.01	.03	.01	.03	.83	.10	.03	.25	.06	.09	.01	23
HGR	.11	.00	.02	.00	.01	.05	.12	.17	.74	.01	.11	.00	47
FGR	.00	.00	.00	.00	.00	.00	.01	.04	.15	.00	.03	.00	62
BAGR	.00	.00	.02	.02	.02	.04	.02	.00	.07	.36	.10	.01	70
Htot	.00	.01	.03	.00	.41	.08	.02	.03	.73	.89	.38	.00	43
BAtot	.00	.00	.04	.00	.05	.07	.03	.00	.15	.63	.14	.02	55

*Competition index = (Rel. Ht.)X(Inv. Prox)X(% Cover)

RPR=Relative production rate RGR=Relative growth rate

GR=absolute growth rate tot=total growth F=foliage weight

H=height BA=basal area S=shoot weight

5. Predicting Growth Losses from Competition

The competition index appears successful as a measure of stress on the relative foliage production rate in Table 6. It is therefore desirable to formulate the competition index in a way which will estimate the growth losses on a site similar to those tested. To do this, the x-axis intercept value of the individual regressions in Table 6 were set at 1.0 by dividing all points by their corresponding b_0 values. Now the relationship is predicting percentage growth loss due to the increasing levels of the competition index. This form of model was produced for the influence of competition index #2 on the percentage relative foliage production rate of trees on all sites. Due to the overbearing effects of planting shock in the first growing season, only the second to fifth season data were used. The equation estimating growth losses is:

$$[5] \quad \% \text{ maximum RFPR} = 100 - 0.332(\text{Competition Index})$$

$$(n=112, r^2=.51)$$

It can be seen that where the competition value is 0, the mean production rate is 100%. A competition value of 100, which might indicate complete coverage of the plot with brush of equal height to the tree, indicates about a one-third lower production rate than an open-grown tree. Figure 7 shows the scatter of individual trees used to produce this relationship. The relationship is based on estimating growth losses for individual trees, which is rarely necessary operationally. Using a mean competition value from a plantation sample would produce an estimation of the average growth loss of an entire plantation.

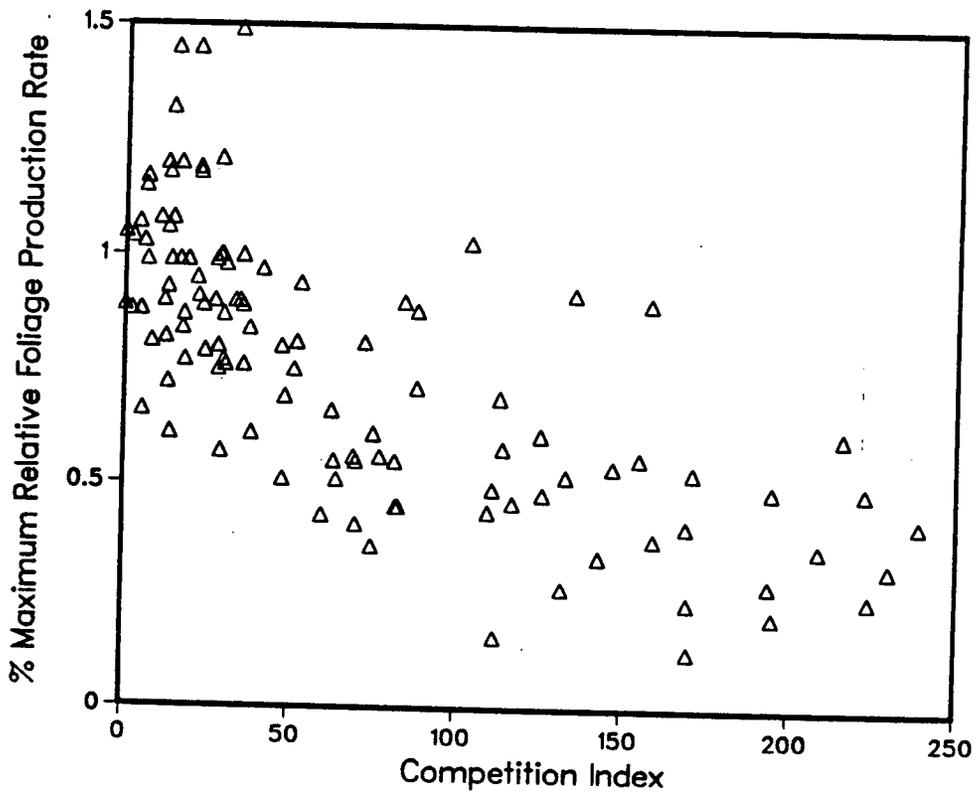


Figure 7. Percentage of mean maximum relative foliage production rate against the competition index ($y = 1.0 - .00332(\text{Competition Index})$).

Demographic Analysis of Growth Losses

To gain further insight into how increasing competitive stress is translated into a reduced relative foliage production rate, a demographic analysis was carried out. The objective was to determine whether a declining relative foliage production rate is due to an even reduction in growth through the crown, or due to an imbalanced redistribution of growth. This analysis does not take into account the many changes in morphology of foliage which also occur in shaded conditions.

Two statistical tests were undertaken which highlight the trend in foliage demography as the value of competition index #2 increases. A regression analysis was used to see the influence of brush competition on the partial production rate at each crown position (see Equation [2]). The competition index did not significantly influence the partial production rate of the terminal leader or the lowest whorl of the crown (Table 7). The first to fourth whorl of branches (counting down from the top) were significantly negatively related to the competition index. The relationship was strongest in the second and third whorls of branches. As the leader's partial production rate was unrelated to competition, it follows that height growth will not be as sensitive as foliage weight growth to competition. The decline in significance of competition on the partial production rate of the lower whorls is due to the self-shading in the lower crown.

Using the regressions derived for each crown position (Table 7), the whorl where the maximum partial production rate occurs can be calculated for any level of the competition index. For example, at a competition index value of 0, the maximum production rate is at the second whorl (1.57). As the competition value increases, however, the first whorl (and theoretically the leader) will contribute an increasing proportion of growth to total production. However, total production will be less under competition than for open-grown trees (i.e. competition index=0).

Table 7. Effect of competition index #2 (C.I.) on the partial production rates of the leader and five uppermost whorls.

Position	n	equation	F-stat	signif.
Leader	123	n.s.	0.01	n.s.
1st whorl	123	$y = 1.07 - .003(\text{C.I.})$	9.70	*
2nd whorl	121	$y = 1.57 - .0056(\text{C.I.})$	14.77	*
3rd whorl	121	$y = 1.21 - .0052(\text{C.I.})$	13.84	*
4th whorl	81	$y = 0.41 - .0018(\text{C.I.})$	12.59	*
5th whorl	36	n.s.	2.73	n.s.

C. I. = (Relative Height X Inverse Proximity X % Cover)

*significant ($p < .01$)

The second analysis was undertaken to reinforce these results. Regressions carried out to determine the effect of competition on the percentage production rate (Equation [4]) were non-significant except at the terminal leader. The percentage production rate of the leader is strongly ($F=43.3$, $n=123$) positively correlated with the competition index. This again indicates that growth is being preferentially maintained in the uppermost part of the tree as the competition index value increases.

Projecting Future Growth from Current Competition Index Values

Thus far, the analyses have concentrated on the relationship between measures of competition and current tree growth. However, it is equally important to determine whether the level of competition is increasing, decreasing, or static over time. In order to address this question, the study incorporated a two-year measurement of individual sites of different ages.

As the sites were of similar characteristics and had similar silvicultural history, trends may be evident over time both within individual sites from year to year, and between different sites of different ages. Table 8 shows the mean values of the relative foliage production rate and competition index #2. These two quantities appear acceptable indicators of the vigour of the planted trees, and the influence being exerted by the competing species. It can be seen that within a site both the growth measures and competition index are highly variable. However, the trends in growth presented in Figures 4 and 5 can be seen. Site 1 shows the planting shock in 1983, followed by establishment in 1984. Sites 2 through 6 show an inherently declining trend not attributable to increasing competition. The competition index, in fact, is generally stable from year to year on a given site. The only exception is on site 2 where the mean value of the competition index increased by 30% from 1983 to 1984. The maintenance of a stable competition index value over time on the other sites indicates that the growth of the trees is balanced by the growth of the brush community. This does not, however, infer that the competition level influencing individual trees is static over time.

Table 8. Mean values for relative foliage production rate and competition index #2 on each site for the two growing seasons sampled (standard deviations are shown adjacent).

site	n/	ages	RFPR		Competition Index	
			1983	1984	1983	1984
1	10	1/2	1.22±0.62	4.26±2.02	72.8±95.4	70.0±90.9
2	11	2/3	4.97±2.55	2.66±1.28	71.1±59.2	94.1±75.3
3	10	2/3	6.34±3.32	2.52±0.97	68.0±78.0	65.9±25.8
4	12	3/4	5.02±1.80	3.35±0.95	58.8±57.3	52.2±59.5
5	11	4/5	2.56±0.71	2.39±0.63	52.2±47.9	54.2±55.3
6	8	4/5	2.11±0.80	1.76±0.62	96.0±85.2	90.5±100.2

Table 9. Covariance analysis of 1984 season growth based on 1983 competition level. Variation between means is the difference in growth due to variation between sites of different ages. The regression analysis for specific year to year trends is shown in the lower portion of the table.

Source	df	Sum sqrs.	Mean square	F-stat	Signif.
Between means	3	34.14			
Competition	1	27.74	27.74	29.7	.0000
Error	56	52.36	0.935		
total	60	114.24			

Individual relationships for each age sequence ($y=a-bx$)

Season	Constant	Slope	R ²	Signif.
1-2	5.29	.014	.45	.03
2-3	3.38	.011	.41	.00
3-4	3.53	.003	.04	.52
4-5	2.63	.007	.50	.00

To test whether the future growth of individual trees is predictable, the paired "companion trees" on each site were used. Each tree harvested in 1983 had a companion staked for 1984 harvest which was of similar size and had a similar brush competition level. Using the 1983 competition index and the 1984 relative foliage production rate, a covariance analysis was undertaken to determine whether the current competition index would predict future growth. Table 9 shows that the current competition level is significantly related to the next seasons growth ($F=29.7$). The lower portion of Table 9 summarizes the regression equations for each 2 year trend studied. The competition index is significantly related to the following years growth in three of the four cases. However, in the third to fourth year trend, the site was overgrown by red alder (Alnus rubra Bong.) in some areas, causing large changes in the status of some trees. On sites where shrub competition (ie thimbleberry (Rubus parviflorus Nutt.)) was the leading competitor, growth seemed more predictable. In general, it appeared that competition models could not predict dynamic changes in the relationship of competition indices to tree growth. This is because the height growth of the tree and brush are species specific and independent.

DISCUSSION

On the sites used for this study, the early growth of the planted seedlings and their interactions with the competing species are dynamic processes. The interactions with the brush species (interspecific interference) cause changes in the productivity of the seedlings, and thus changes in their growth. These changes in productivity are not equally distributed throughout the tree, as with increasing competition there were changes in allocation of growth. As the early development of a plantation can strongly influence the final stocking, stem size variability, and rotation length of the stand, it is important for foresters to understand these interactions. This study has been aimed at quantifying both the level of competition affecting a tree seedling, and the seedling response under varying levels of interspecific competition.

The competition characteristics studied in this work were designed to indicate light interception around the tree crown. As they were relatively successful in explaining variation in tree growth, there is some implication that light is the factor most strongly limited by brush competition. Studies by Magnussen (1983), Eissenstat and Mitchell (1983), Magnussen and Peschl (1981), Reed *et al.* (1983), and Drew and Ferrell (1977) have shown that light abundance is the dominant factor in control of tree growth, even where moisture and/or nutrients are also limiting. The four characteristics inferring competitive light interception were positively correlated with each other, but negatively correlated with measures of growth. Therefore, they all influence growth, but are describing the same phenomenon. Combining the terms into an index of competition gives a single variable which is applicable to a range of sites over the ages and conditions tested.

The competition index developed here is based on a tree centred approach, like those of Howard and Newton (1984) or Wagner (1982). The utility of the index seems biologically meaningful. The relative height and proximity measures effectively describe the degree to which competing brush foliage directly overtops a tree, thereby intercepting the maximum amount of radiation. The percent cover variable serves to modify the index, particularly where brush is light or scattered.

The strength of the correlation between the index and seedling growth varies depending on the growth measure and variable used. In this study various measures of height, basal area, foliage weight, and current shoot weight were used, although any number of other characteristics are possible. These best indicated the variables of interest to the forester. The general trend in sensitivity was shoot measures > foliage measures > basal area measures > height measures. Height growth was determined by the annual extension of the terminal leader and was shown to be preferentially maintained over the lower crown growth, probably because of its improved light climate, apical dominance, or etiolation effects. Sapwood basal area and foliage measures generally were well-correlated (Shinozaki *et al.* 1964a,b, Kaufmann and Troendle 1981, Waring *et al.* 1982); possibly due to a functional relationship between

transpiration and cross-sectional conducting area. However, in this study, foliage measures were more sensitive to light interception than basal area measures. The difference may be attributable to false ring development associated with lammas growth that caused more variation in the basal area measures. Also, basal area measures were taken at root collar rather than at the base of the live crown as recommended by Waring *et al.* (1982). The shoot measure was the most sensitive because of the increased tendency of new shoots to preferentially maintain foliage growth over twig growth in low light situations (Kellomaki 1981).

Comparing different growth measures of the variables tested shows some of the inherent problems in assessing plantation performance. Absolute measures, whether used as total growth or growth rates, correlate strongly with the relative height of the brush canopy to the tree. In most cases this correlation is not combined with a concurrent sensitivity to proximity measures. The relative measures on the other hand, were more sensitive to proximity, but tended to correlate significantly with all competition measures. This demonstrates a major problem with absolute growth measures -- they are a measure of size rather than productivity or vigour. When assessing performance, relative measures of growth prove superior due to their sensitivity to environmental conditions, and their ability to diminish the effects of size.

Relative growth rates or relative production rates also must be used with caution. The effect of planting shock, and inherent trends in these measures overshadow competitive effects. This study has shown that within a specific site over half of the total variability in the growth of the trees can be attributed to vegetation competition effects. Estimating the growth loss in a plantation, therefore, can be carried out with a fair degree of accuracy. Projecting growth forward is more difficult, as the particular competing species have very different capacities for development over time.

The inherent trend in relative growth rate of Douglas-fir is somewhat predictable from the plantations studied. The pattern was initial planting shock lasting one year, followed by establishment and rapid increase in relative growth, followed in turn by a decline towards a stable annual growth rate. The pattern is followed for all characteristics studied, but in the

case of height growth, the annual growth seems to stabilize sooner; as early as age 5. This stabilization point in height growth is of interest as it is the earliest expression of limitations due to site quality. Foliage and basal area growth do not reach a maximum until later (c.f. Ford 1979), and are more dependent on stocking levels.

CONCLUSION

Some conclusions can be made from the data generated in this study. Caution must be used in extrapolating results outside of Douglas-fir plantations on these rich, moist sites in the coastal western hemlock biogeoclimatic subzone where light interception may be acting as the major limitation to tree growth

The growth of Douglas-fir is reduced by brush competition. However, the growth of foliage or new shoot biomass is most significantly affected, measured as a relative annual production rate. Basal area and height growth also are sensitive to competition levels, particularly as relative growth rates. In these cases the best measure of competition is a function of the proximity, cover, and relative height of the brush species around a given tree. A competition index derived from these measures was suitable for assessing growth losses during the establishment phase of plantations.

Douglas-fir plantations seem to follow a fairly well-defined relative growth trend in their early years. The effect of brush competition is superimposed on this trend, modifying the growth rate downwards on a given site in a given growing season.

CHAPTER THREE

Early Morphological, Architectural, and Allometric
Development of Planted Douglas-fir.

ABSTRACT

Variables relating to the development of planted Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were measured on a series of sites in Southwestern British Columbia. These variables; including morphology and nutritional status of foliage, crown architecture, and allometric relationships, were analyzed for their sensitivity to interspecific competition from non-commercial brush. The influence of tree vigour, age or size, and crown position on these developmental variables also were considered. As competition by brush species increases, tree foliage becomes thin and nitrogen concentration increases, height growth is maintained preferentially to basal area growth, foliage production increases relative to shoot stem production, and branches become more horizontal and set fewer buds. This acclimation to shade is overlaid on the inherent developmental pattern of the establishing seedling.

INTRODUCTION

The successful establishment of forest plantations requires both acceptable survival and growth. Most survival problems occur in the first or second year after outplanting and are due to moisture stress from poor root regeneration (Sutton 1968). Assessment of the growth and development of plantations is more difficult, as site quality, interspecific competition, planting shock, and seedling size (age) all interact to produce the annual increment of a tree. When assessing plantation growth, there is a need to sort out the factors influencing performance so that the appropriate silvicultural practices are implemented.

Assessment of developmental variables separately from growth may be useful in determining what factors are important in a particular situation. If two trees of the same size, growing at a similar rate in widely different environments are assessed based on growth alone, the specific constraints on each may not be evident. Therefore, adding the use of diagnostic developmental variables such as those of morphology, architecture, or allometric ratios, will improve performance assessment by identifying factors influencing growth.

Many of these variables have been described as they pertain to individual stresses or limitations to growth. Planting shock, a major problem of white spruce (*Picea glauca* (Moench) Voss), has been characterized by the presence of dwarf chlorotic needles (Richards 1968), a lack of root growth (Sutton 1968), shortened leaf internode lengths (Burdett et al. 1984) and poor shoot extension. These characteristics are even more evident when compared with the developmental pattern produced on the same tree in the nursery prior to outplanting.

A major determinant of growth is tree size. It is difficult to separate growth from vigour, as growth is often most strongly related to tree size, while vigour should be a measure of productivity. For example, Burdett et al. (1984) considered the leaf internode length and total number of internodes produced on the terminal leader of white spruce to be indicative of vigour. Paterson and Fayle (1984) showed that needle length and terminal leader characteristics are useful for projecting early performance of planted red pine (*Pinus resinosa* Ait.) There do not, however, appear to be studies relating developmental variables to relative

growth rates or relative production rates of plantation trees.

Sorting out the influences of tree size and planting shock for particularly important for assessment of the effects of brush competition on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations. On the moist, rich sites of coastal British Columbia, brush competition appears to act largely through interception of solar radiation around trees. Controlled laboratory and greenhouse studies have shown that growth reductions due to light limitation are accompanied by concurrent developmental changes (Brix 1968, 1970, Drew and Ferrell 1976, Reed et al. 1983). In Douglas-fir seedlings, this acclimation includes differential maintenance of height growth over diameter growth, extended leaf internodes, and much thinner foliage (ie. increased specific leaf area). These and other changes are attributable to photomorphogenesis, but have not been fully assessed in young plantations.

The present study aims to quantify these morphological, architectural, and allometric variables in Douglas-fir plantations. The objective is to relate changes in these measures to brush competition, while considering the interaction with tree productivity and tree size or age. Coupling these measures with those of growth should improve plantation performance assessment techniques for Douglas-fir.

METHODS

Experimental Material

Chapters 1 and 2 have outlined the sites used in this study. Briefly, the experimental material for this study were operationally planted Douglas-fir seedlings. The site type selected was considered to be optimum for the growth of Douglas-fir in B. C. (Klinka and Carter 1982). These sites are within the Drier Maritime Coastal Western Hemlock biogeoclimatic subzone (Krajina 1965) and are classed as having a subhygric hygrotape and a mesotrophic to subeutrophic soil nutrient regime. The sites are summarized in Table 1 of chapter 2.

On each site, the area of suitable soil moisture was determined and trees were selected

with a systematic sampling technique using a randomized starting point. Trees which had been browsed or otherwise damaged were rejected. In total, 124 of the sample trees were used in this study, 62 from each of the 1983 and 1984 sampling periods. Treated trees were not included in the following analyses.

Field Procedures

A series of in situ measurements were made on the sample trees in order to study and describe the development of the architectural characteristics of the seedling crown. The brush community which surrounded each tree also was measured to provide data which would allow development of a competition index for each tree. As this study forms part of a larger study of early plantation growth, further details of sampling procedures can be found in Chapter 2.

Each sample tree was measured for total height and annual height increment from the current and two previous growing seasons. Branch elongation was similarly determined by measuring length increments on sample shoots from the same three year period. Where occurring, lammis growth was not differentiated, thus giving total height or length produced in each growing season. A sample shoot for measurement was selected from each annual node and each internodal position. The branch selected was of average size for the nodal or internodal position concerned. The result was a matrix of branch lengths from different crown positions and growing seasons for each tree.

The total branch production at each nodal and internodal crown segment was counted by year of development. The sample branches from the nodal positions and the terminal leader also had bud production determined. Nodal branches which were still growing had their angle of incidence to the mainstem and maximum branching order determined.

In order to study the influence of interspecific competition for solar radiation on the tree characteristics, a series of measures were made of the surrounding brush species at each sample tree. The percent ground cover, proximity, height, and leaf area index (1983 samples only) were determined by species and used to derive a competition index for each tree (Chapter

2). This index was determined as in [1]:

$$[1] \text{ C.I.} = (\text{Hb}/\text{Ht}) \times [((\text{Rb}/\text{Rt}) + 1)^{-1}] \times \%C$$

where Hb=mean height of brush canopy

Ht=sample tree height

Rb=mean distance to brush foliage from tree stem

Rt=tree crown radius

%C=% cover of competing species around tree

After the in situ measurements were completed each tree was harvested, with shoots sorted by crown position and year of origin.

Laboratory Procedure

In the laboratory, the leader and a sample branch from each node of each tree were selected for analysis of specific leaf area. From the sample branch, ten needles from the central portion of the shoot were removed, measured for length and leaf area. Determination of projected leaf area was undertaken by fixing the needles into glass slides and running them through a LI-COR 3000 leaf area meter. After leaf area calculation, the 10-needle subsamples were dried and used to determine the specific leaf area for each crown position. Previous foliage dry weight was also determined for use in determining the relative foliage production rate (RFPR), a measure of seedling vigour (Chapter 2).

$$[2] \text{ RFPR} = [\text{LW}_n/\text{LW}_{(n-1)}]/(t_2-t_1)$$

where LW_n=current season foliage dry weight increment

LW_(n-1)=previous season foliage dry weight increment

(t₂-t₁)=change in time (one year)

Table 10. Summary of the variables tested and the factors used for analysis.

1. Variables	A. Foliar	i. Leaf length
		ii. Leaf area
		iii. Specific leaf area
		iv. Leaf internode length
		v. Foliar N (%)
		vi. 10-needle N Content
	B. Allometric	i. BA ¹ inc.:foliage wt. inc.
		ii. Height:basal area
		iii. Foliage:shoot weight
	C. Architectural	i. Branch length increment
		ii. Rel. branch extension rate
		iii. Nodal:internodal length
		iv. Bifurcation rate
		v. Bud production
		vi. Branch angle
		vii. Maximum branch order
2. Factors	A. Age from planting	
	B. Crown position	
	C. Competition index	
	D. Tree vigour(RFPR)	
	E. Year (1983/1984)	

¹Basal area

The leader segments from the present and previous growing season were also analyzed for leaf internode lengths. A three centimetre section was taken from the centre of the stem segment, and the total number of needles and leaf scars were counted and divided by three to give the number of stem units per centimetre. The foliage from a 70-tree subsample of paired 1983-1984 trees was also analyzed for foliar nitrogen concentration. A summary of the variables tested is shown in Table 10.

RESULTS

Foliage Morphology, Arrangement, and Nutritional Status

Measures analyzed were the length, area, and thickness of needles from different crown positions, the frequency of stem units on the terminal leader, and the concentration and content of nitrogen in current season foliage. Analysis included the determination of trends over the five-year establishment period studied, and changes due to competition, crown position, and tree vigour (measured as relative foliage production rate).

From Table 11, the influence of crown position, tree productivity, and competition levels on are morphological features is presented. There are decreases in leaf length and blade area with depth in the crown and with increasing levels of brush competition. The production rate measure is the most strongly correlated with these measures of needle size. This can be explained by the determinate nature of Douglas-fir, stem units being set in the bud the summer prior to their expansion. Therefore, if conditions deteriorate, as is the case when nursery stock is lifted and outplanted, needles expanded are small and production rates are low. This trend is shown in Figure 8.

Table 11. Simple linear correlation coefficients between variables of foliage morphology and indicators of crown position, competition level, and tree vigour.

n=535 df=533

	Leaf Length	Leaf Area	Specific Leaf Area
Competition index	-.158	-.149	+.584
Crown position	-.068	-.136	+.223
Relative foliage production rate	+.216	+.279	-.153

r at .01=.111

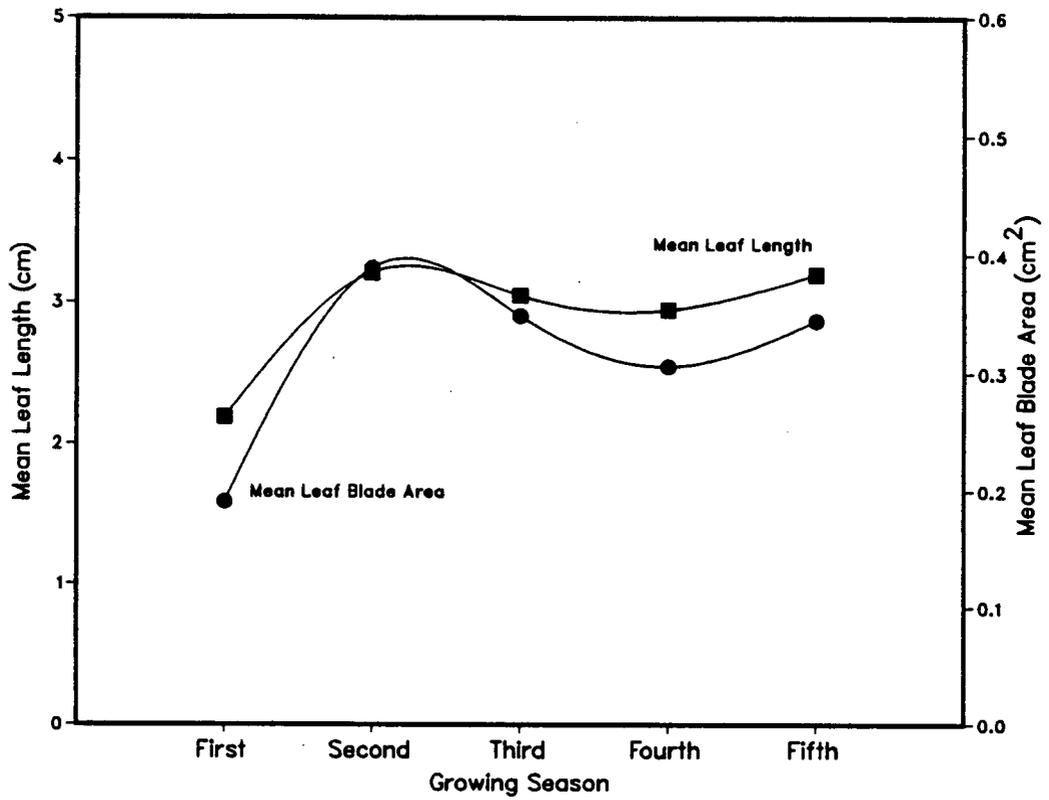


Figure 8. Trends in mean leaf length and mean leaf blade area during the first five years after outplanting.

The most commonly used measure of needle thickness and morphology is specific leaf area, measured as square centimetres of leaf area per gram of leaf weight. From Table 11, the significant correlation of specific leaf area to crown position, competition level, and tree vigour can be seen. The strong control of light intensity on the specific leaf area of foliage has been shown before (Brix 1967, Drew and Ferrell 1977, Lewandoska and Jarvis 1977, Del Rio and Berg 1979, Kellomaki and Oker-Blom 1981). As declining light intensity also affects growth rates (see Chapter 2) in these plantations, the correlation of specific leaf area to production rate is likely indirect. Of interest was a marginally significant difference between the mean specific leaf area in 1983 samples and 1984 samples, which correlates with a large difference in the hours of bright sunlight in July of the two years (Figure 9).

The leaf internode length was analyzed as both an absolute measure of internode frequency per centimetre, and as a relative measure of current to previous year leaf internode frequency. Figure 10 shows that the mean number of needles per centimetre increases dramatically during the year of planting, then declines sharply in the following year. There is also an indication that the leaf internode frequency decreases slightly over time in the second to fifth growing seasons.

Although an increase in leaf internode length of Douglas-fir with decreasing light intensity has been reported from controlled studies (Drew and Ferrell 1977), there was no significant correlation of leaf internode length to brush competition level found in this study. The frequency of internodes, however, was significantly related to the relative foliage production rate, with more vigorous trees showing more widely spaced needles. The relative internode frequency between current and previous stem segments on a tree was also most strongly related to tree vigour. It appears that the etiolation of the stem in shade is counterbalanced by a reduction in relative production rate, accounting for the poor correlation with the competition index.

Table 12. Changes in foliar nitrogen concentration as a percentage of dry weight and 10-needle content between 1983 and 1984.

Site	Growing 1983 Samples			Growing 1984 samples		
	season	10-needle content	%N	season	10-needle content	%N
Vedder II	1	.19	1.37	2	.60*	1.92*
Vedder I	2	.74	1.55	3	.69	1.34
Sumas Mtn.	3	.63	1.63	4	.66	1.56
Davis Lake	4	.57	1.39	5	.69	1.55

*significantly different from 1983 value ($p < 0.01$)

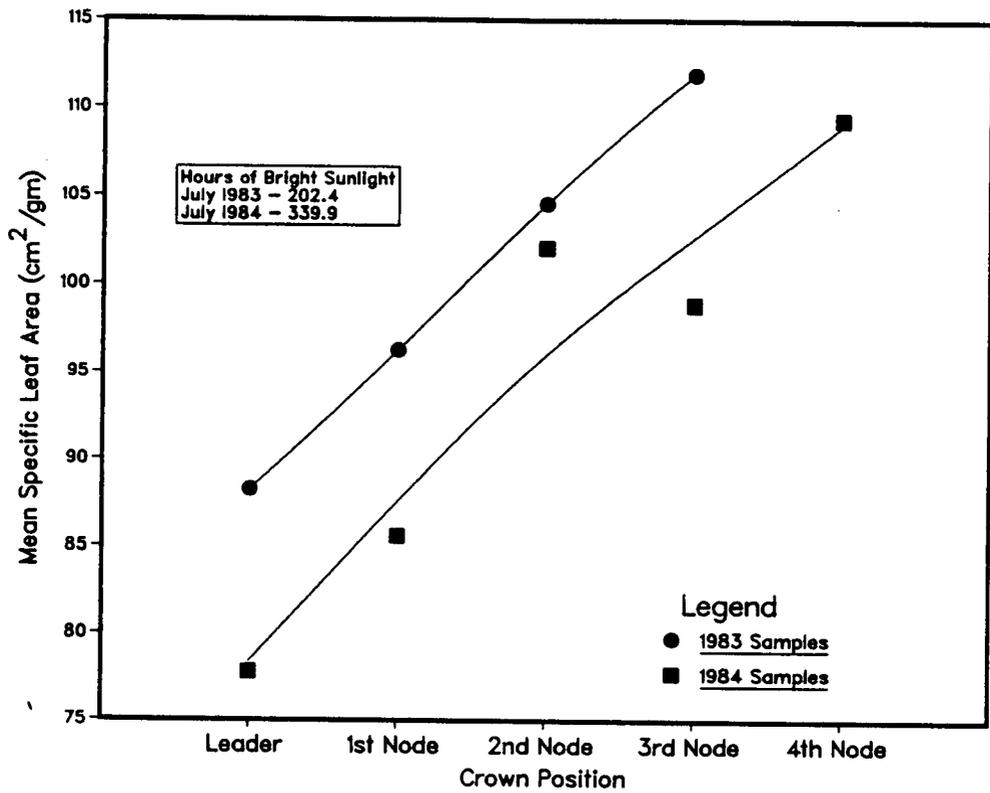


Figure 9. Comparison of specific leaf area values from different crown positions for trees sampled in 1983 and 1984. Inset is the hours of sunlight received at Abbotsford airport in July of the two years.

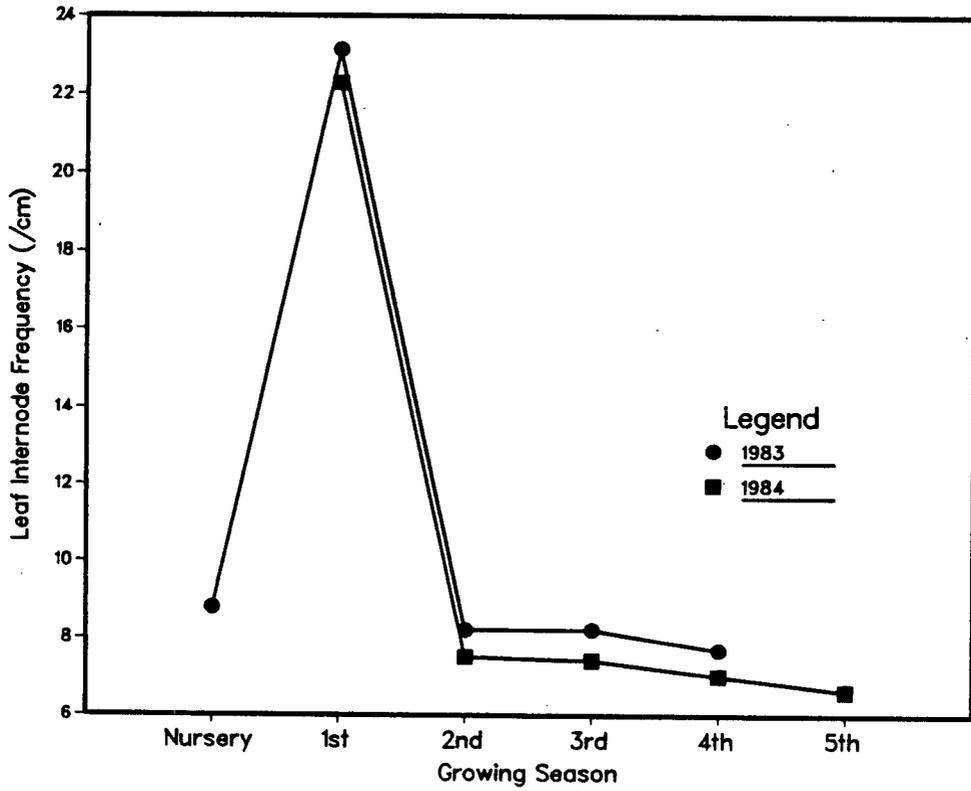


Figure 10. Mean leaf internode frequency during the five year period studied. Nursery values are from analysis of previous internodes on the first season outplants.

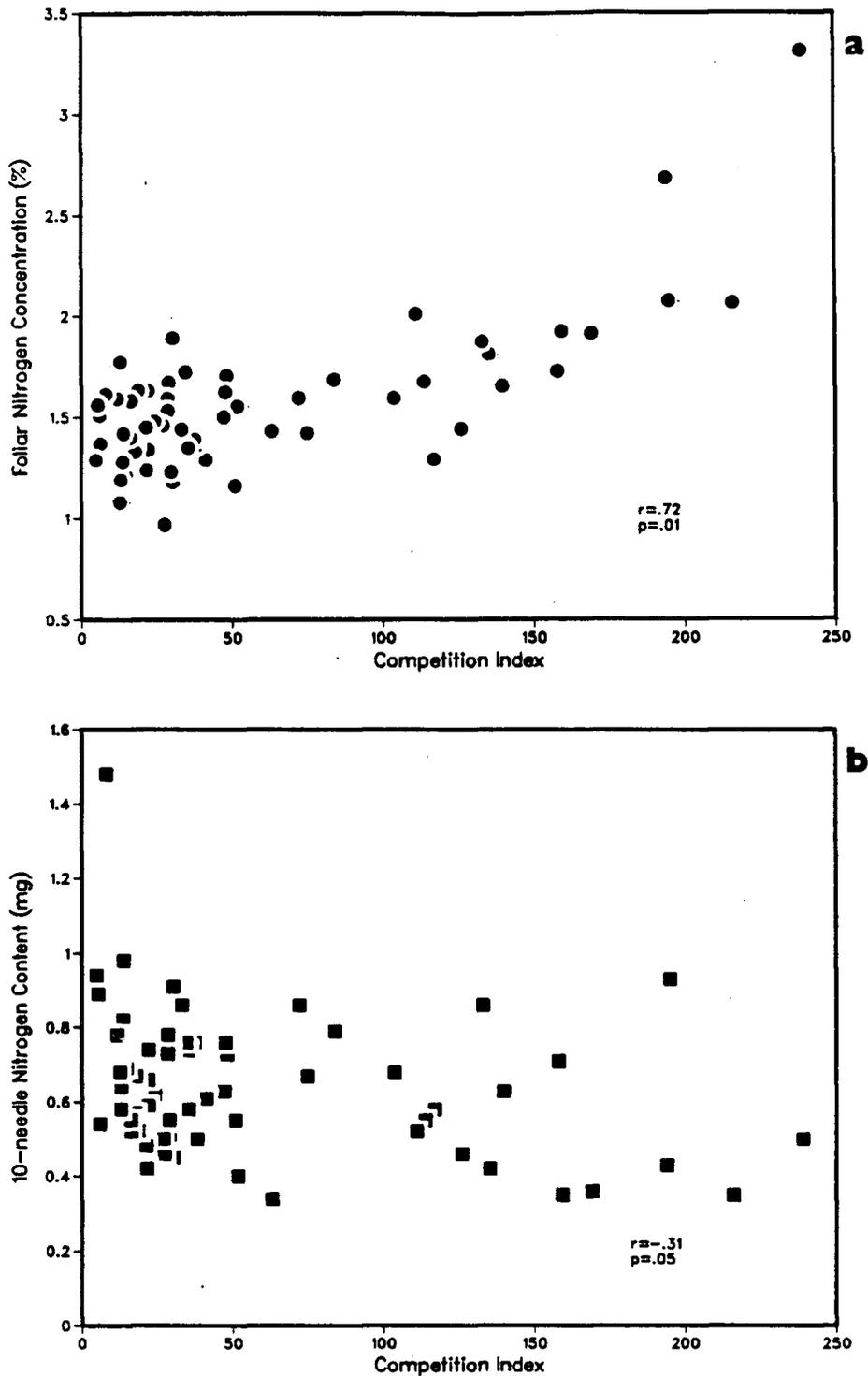


Figure 11. (a). Foliar nitrogen concentration for individual sample trees compared with the competition index calculated for each. (b). 10-needle nitrogen content for individual sample trees compared with the competition index calculated for each.

Foliar nitrogen concentration and 10-needle content for the sampled trees are summarized in Table 12. The only significant difference is between nitrogen content in 1983 and 1984 on the Vedder II site. This can be attributed to a reduced nitrogen uptake during first season planting shock. Nitrogen concentration was positively correlated with increasing competition levels, while nitrogen content was less negatively related to this index (Figure 11a,b). The apparent discrepancy can be attributed to declining needle weight in shade, enrichment of nitrogen-rich compounds in shaded needles, and a possible interaction of brush competition with rich microsites (cf. Ballard, T. 1984. Nutrition of planted white spruce. Contract Res. Rep. to Research Branch, B. C. Ministry of Forests, Victoria, B. C. 23 pp.) The negative relationship between nitrogen concentration and competition levels was particularly strong in the second growing season, as two extremely suppressed trees had very high concentrations of nitrogen in their foliage. There was also a positive correlation between needle nitrogen content and the relative foliage production rate of the tree, likely due to the increased needle size of trees with higher productivity. These results are similar to those of Bjorkman and Holmgren (1963) with Solidago virgaurea L.

Allometric Relationships

Allometry is the study of the relationship between different tissues or quantitative measures within plants. Allometric ratios have frequently been used to study the response of trees or other plants to environmental change. In this study, three specific ratios were used; foliage weight increment to basal area increment, total height to total basal area, and current year shoot foliage weight to shoot twig weight. Biologically these ratios indicate imbalances in growth caused by stress or environmental changes. These relationships were analyzed against tree size, vigour, competition level, and in the cases of the shoot allocation measure, crown position.

The relationship between total foliage biomass and total sapwood cross-sectional area has been studied extensively (Shinozaki et al. 1964a, b, Grier and Waring 1974, Snell and Brown

1978, Granier 1981, Kaufmann and Troendle 1981, Waring et al. 1982, Brix and Mitchell 1983). In this study the current foliage dry weight increment was strongly related to the basal area increment ($r^2=0.95$, $n=120$). Investigation of the effects of competition and tree vigour on this ratio showed that competition favours foliage weight increment slightly over basal area increment, but that tree vigour is apparently not a determinant of this ratio. There was some indication that trees on dry microsites favoured stem increment over foliage increment, but this could not be validated. Figure 12 shows that there appears to be a significant decline in this ratio due to first season planting check, and an apparent slight decline in the later years from a peak in the second growing season. This observation also may point to moisture stress being an important determinant of this ratio, as planting shock is believed to be a moisture limitation. The later decline indicates that foliage production rates are declining more rapidly than basal area production rates in the five year period studied.

Many studies have shown that height growth of intolerant conifers is maintained preferentially to diameter growth as competition increases and light intensity decreases (Farrar 1961, Bormann 1965, Brix 1970, Drew and Ferrell 1977). This demonstrated by the Douglas-fir studied here, as the height to basal area relationship was positively correlated with increasing values of the competition index. Over time there was a trend towards a decline in this ratio, attributable to the production rate of height growth stabilizing more rapidly than that of basal area (Figure 12). Table 13 shows the variation in this ratio attributable to the competition index and the age from planting. It can be seen that there are significant influences due to both factors, but that competition effects are a stronger influence. The significant interaction term indicates that the slope of the relationship between the competition index and the height:basal area ratio differs between growing seasons.

Table 13. Analysis of variance for the influences of competition and growing season on the ratio of total height:total basal area

ANOVA

Source	df	SS	MS	F-stat	Signif.
Between ages	4	12.22	3.05	9.27	.00
Competition index	1	40.85	40.85	124.04	.00
Interaction	4	6.20	1.55	4.70	.00
Error	109	35.90	0.33		
Total	118	95.53			

Table 14. Variation in allocation of current season shoot growth between foliage and shoot stem* due to crown position and brush competition

ANOVA

Source	df	SS	MS	F-stat	Signif.
Crown position	5	1414.3	282.85	105.26	.00
Competition index	1	72.8	72.81	27.10	.00
Interaction	5	16.9	3.38	1.26	.28
Error	554	1488.8	2.69		
Total	565	2963.4			

*measured as foliage dry weight/twig dry weight

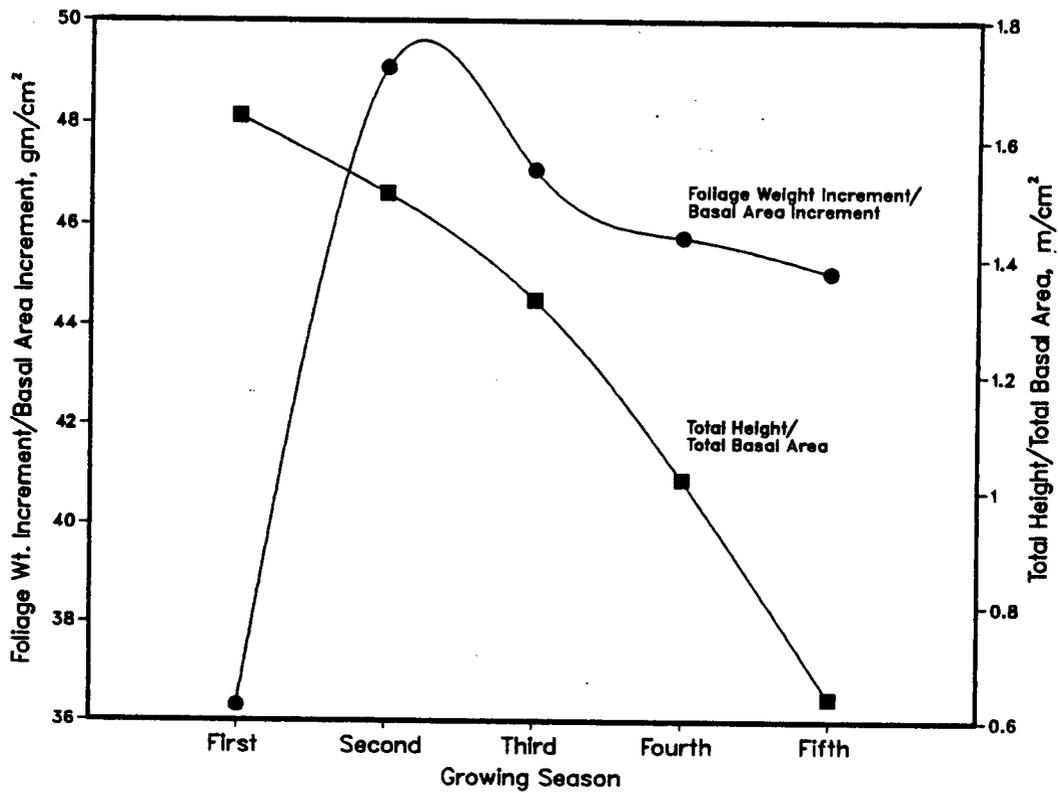


Figure 12. Trends in two allometric ratios over the first five growing seasons from outplanting.

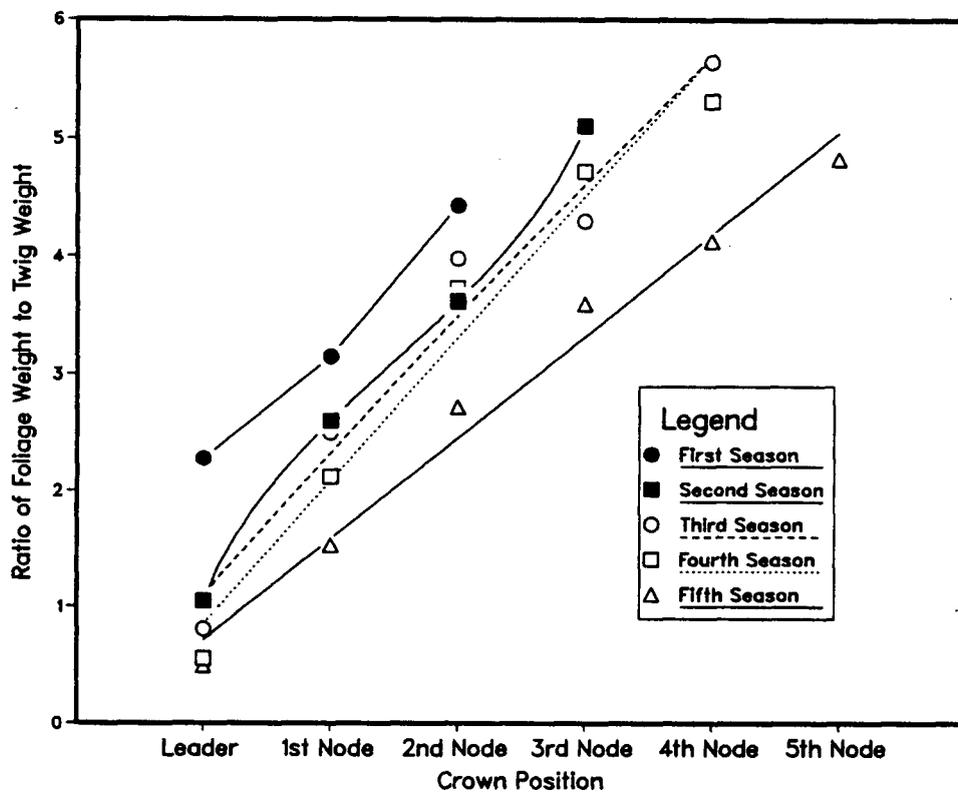


Figure 13. Trends in the allometric ratio of current foliage weight to current twig weight at different crown positions. Individual curves represent mean values for different aged trees from outplanting.

The allocation of dry matter in current season shoots between foliage and structural tissues can vary with crown position and stand density in Scots pine (*Pinus sylvestris*) (Makela *et al.* 1980, Kellomaki 1980, Kellomaki 1981). Table 14 indicates that lower crown positions and increased interspecific both cause significant increases in foliage weight relative to shoot-stem weight. Analyzing the effect of brush competition on individual crown positions showed that the most significant effect occurred on the terminal leader. With increasing depth in the tree crown, the competition index became a decreasingly important influence, becoming non-significant at the third branch whorl and below. Within each crown position the proportional allocation of growth to foliage declines over time (Figure 13). It appears that shading promotes allocation to foliage, while the inherent development of the tree tends towards increasing investment in structural tissues.

Crown Architecture

Components of crown architecture have been separated and analyzed individually. The measures studied are the absolute and relative extension rate of branches at different crown positions, the bifurcation rate and current bud production through the crown, and the branch angle and maximum branch order of each whorl.

The relationship between the degree of extension of branches at various crown positions has a large influence on the crown form of trees (Kozlowski and Ward 1961, Stiel 1962). Figure 14 shows the mean extension rate of the terminal leader and second order nodal shoots from different crown positions by growing season. It can be seen that branch extension at a given crown position increases over time and decreases with depth in the crown. The nodal shoots generally extended by about 50% more than the internodal shoots below them. Competition affected the absolute growth of both nodal and internodal shoots, although the variation in growth due to differences between crown position was a stronger influence (Table 15). The competition effects were equally strong on the leader and first two whorls of branches. Below the second whorl, while still significant, the relationship is not as strong, likely due to the

increasing effects of self-shading.

The relative extension rate on axes two years or older was determined as the current season length increment divided by the previous season length increment. This relative measure declined over time on a given branch, and declined through the crown, being highest on the terminal leader. Nodal and internodal branches at a given crown position had similar values. This measure seems a good indicator of tree vigour, as values were greatly depressed by planting shock, high in the second growing season, then declined slowly over the following three seasons. Although competition levels had a significant negative influence on relative extension of branches, it was not as strong as crown position, growing season, or tree productivity (Table 15). Multiple regression equations incorporating relative extension of several branch axes showed good predictive value for current tree vigour, as would be expected. The most important determinants of productivity in these equations were the uppermost whorls.

Although relative extension rate of nodal and internodal branches was similar, the smaller initial size of internodal branches results in an increasing discrepancy in absolute size between the two classes. This ratio between nodal and internodal branch lengths was not affected by age, or competition. There was only a slight negative correlation with tree vigour, indicating that longer internodal branches may be somewhat beneficial to a tree.

Table 15. Simple linear correlation coefficients for relationships between absolute and relative branch extension and factors of brush competition, tree productivity, crown position, and age

n=461 df=459

	absolute extension	relative extension
	rate	rate
Competition index	-.25	-.18
RFPR	+.07	+.61
Crown position	-.64	-.37
Growing season	+.25	-.28
r at .01 = .120		

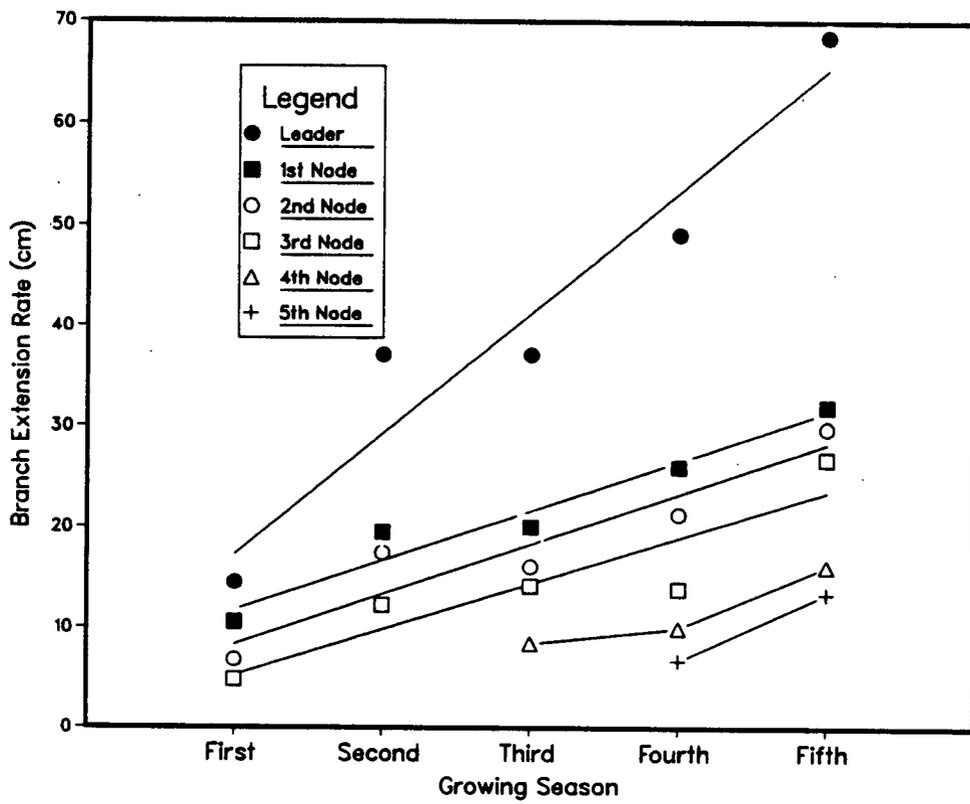


Figure 14. Mean extension rate of branches at specific crown positions over the first five growing seasons from outplanting.

A second component of crown architecture is bifurcation, or increase in the number of axes of growth. In this study, past branching was measured as a bifurcation rate, or ratio of the current number of shoots produced divided by the number of previous season shoots which produced them. The trends in this bifurcation rate nodally and internodally are shown in Figure 15 a and b. It can be seen that while there are initially more internodal branches produced, they have a lower bifurcation rate, and as a result nodal branches dominate in the middle to lower crown. The depression due to planting shock can be seen, this likely due to bud abscission. There is also some reduction in second year branching which can be attributed to reduced budset on the short axes of the tree in shock. The tendency towards increasing bifurcation in the upper crown is due to increased budset on the longer individual branches.

Bifurcation is significantly related to brush competition, tree age, and crown position (Table 16). The positional differences are due to the increasing branch order and poorer light climate of shoots lower in the crown. Competition effects were most strongly felt on nodal shoots, although the influence was not as strong as that of position. Increasing bifurcation was also significantly related to tree productivity, but only through the third to fifth whorls. The bifurcation rate in the top two nodes is not related to productivity, likely due to the influence of previous year productivity on budset.

The number of buds on a branch will indicate the potential for production of new axes in the next year. This study looked at influences on the number of buds set on the terminal leader and a second order branch at each node. Figure 16 shows that the number of buds produced per branch declines with depth in the crown. Based on the decline in branch lengths with depth in the crown, it appears that the length of the axis is a principal determinant of budset. A multiple linear regression also indicates this (Table 17). The branch length and crown position are the most significant determinants of budset, followed by competition effects.

Table 16. Simple linear correlation coefficients between measures of crown architecture and the influences of brush competition, tree productivity, crown position, and plantation age.

n=346 df=344

	Branch order	Branch angle	Bifurcation rate
Competition index	-.29	+.18	-.28
RFPR	+.12	-.02	+.13
Crown position	+.55	+.38	-.40
Growing season	+.15	-.06	+.14

r at .01 = .138

Table 17. Multiple linear regression analysis of determinants to bud production by a branch

Variable	Partial coefficient of determination	Coefficient	t-stat	Signif.
Constant		9.46	11.81	.00
Branch length	.31	0.164	7.94	.00
Crown position	-.31	-1.76	-7.76	.00
Competition index	-.21	-0.0364	-5.20	.00
LengthXposition	.12	0.0268	3.02	.00
LengthXcompetition	.11	0.00069	2.60	.01
PositionXcompetition	.14	0.00654	3.33	.00
PosnXcompnXlength	-.10	-0.00027	-2.43	.02

(n=588, $r^2=.74$, S.E.=3.16)

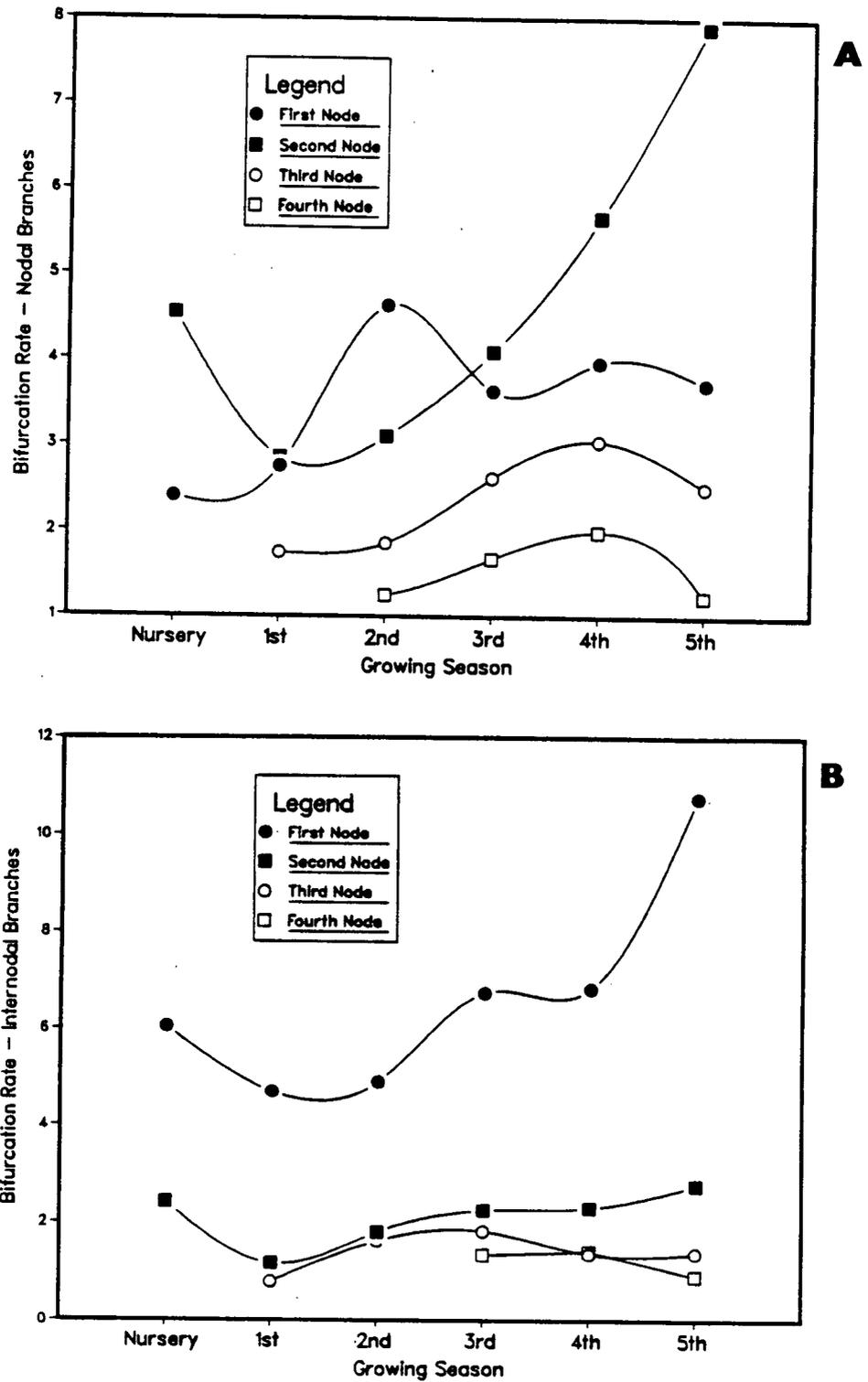


Figure 15. Trends in bifurcation rate at different crown positions over time (a) at nodal crown positions and (b) at internodal crown positions.

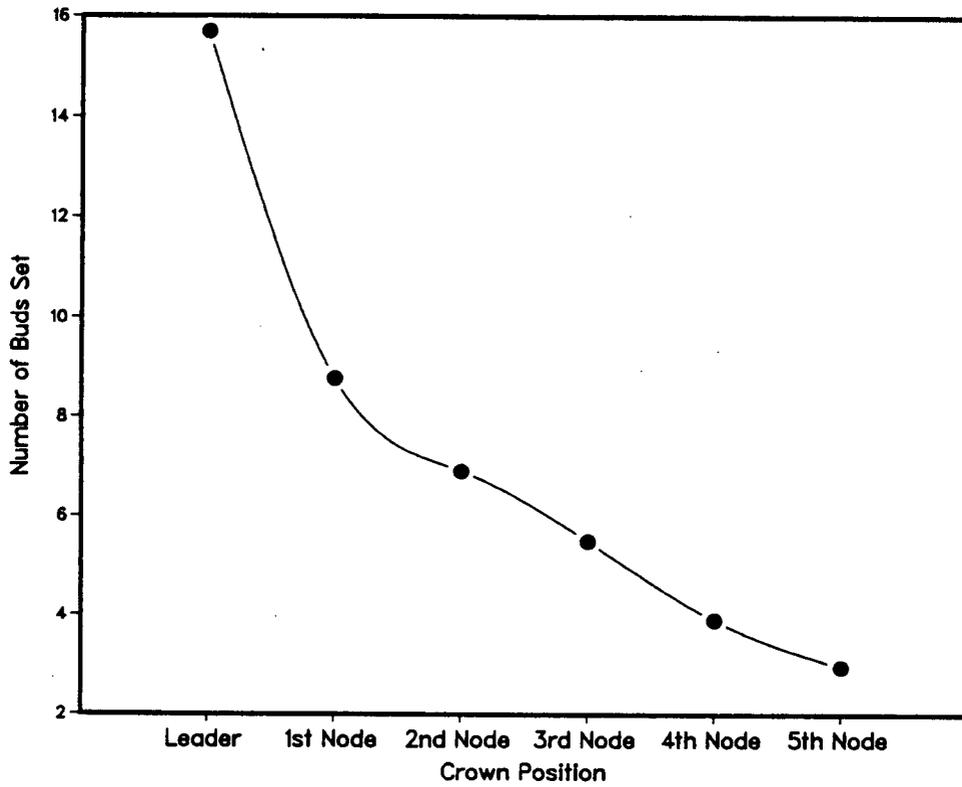


Figure 16. Trends in bud production on the terminal leader and a second order sample branch at each node.

Continual branching leads to the generation of increasing branch orders at a given crown position. Figure 17 shows that branch order increases to a peak, then drops off in the lowermost whorls. The generation of higher branch orders than the age of a given crown position is due to lammas growth occurring on some trees. In general Douglas-fir tends to have a maximum fourth branch order. Only one sample tree was regularly branched to the fifth order. There was a tendency for branching order to decline with increased competition, with the effects most strongly felt at the third whorl. There is apparently a peak influence between the lack of effect on the low inherent branch orders of the upper crown and the heavy self-shading in the lower crown. Increasing branch orders also correlated with increasing tree productivity in the middle and lower crown, although this may be secondary, relating to the competition effects.

A final architectural variable which may show developmental sensitivity is branch angle. Figure 17 shows that there is a steady increase in branch angle with depth in the crown. Whether this increase is due to epinastic effects or increasing weight is not known, but it does tend to improve light interception in shaded crown positions. There was a general tendency towards higher branch angle with increasing competition (Table 16). This increase was most significant in the two uppermost whorls and appeared due to poor lignification of branches in suppressed trees.

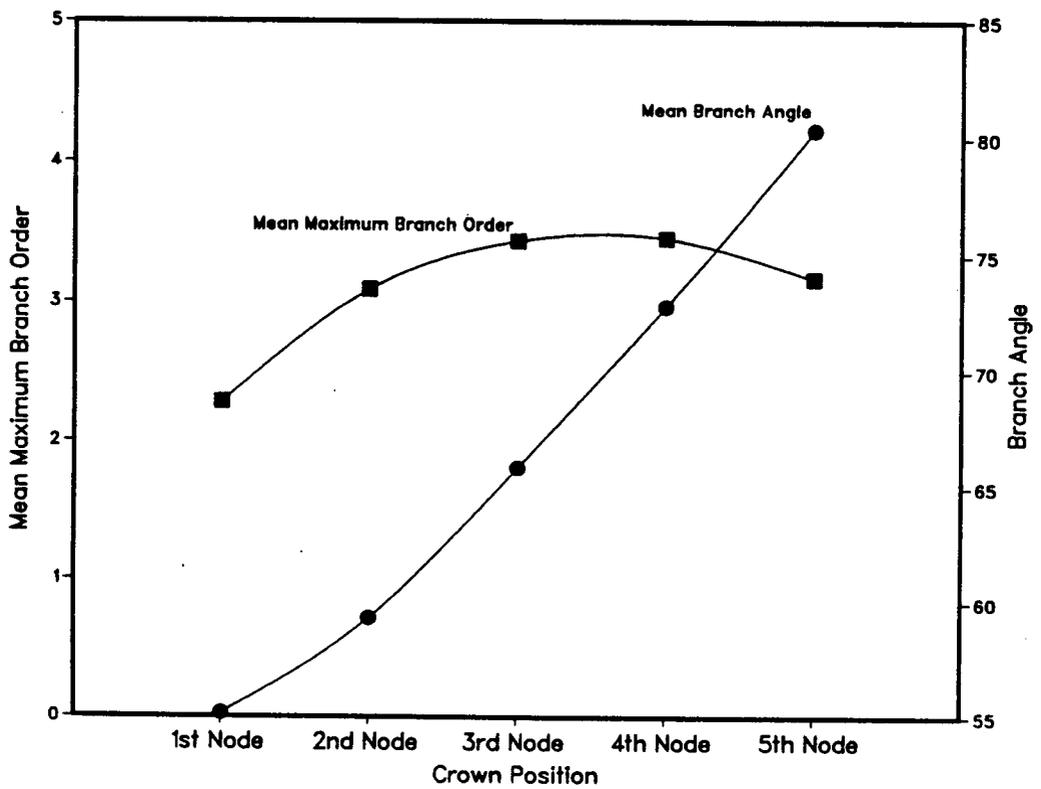


Figure 17. Trends in branch angle of nodal shoots from the mainstem and maximum branch order through the crown.

DISCUSSION

In this study, the development of planted Douglas-fir seedlings was followed on an age sequence of similar sites. The period studied was the first to fifth growing seasons from outplanting. During this initial period of establishment these plantations are most risk-prone, being susceptible to partial or complete failure due to severe interspecific competition from brush species. For this reason there has been considerable interest to date in attempting to determine and quantify brush competition influences on plantation survival and growth (Ruth 1956, Eis 1981, Conard and Radosevich 1982, Wagner 1982, Oxenham 1983, Newton and White 1983, Howard and Newton 1984).

Concurrently to this, studies of tree development in controlled conditions have been undertaken to quantify responses to variation in solar radiation, moisture, and nutrition (Brix 1967, 1970, Drew and Ferrell 1977, Magnussen 1983, Reed *et al.* 1983). These studies have shown that solar radiation is the most important factor controlling growth, and that as light levels diminish, the developmental pattern of young trees also changes. Although most studies in the field have only looked at total growth, there have been indications that similar morphogenetic variation may occur in plantations (Lewandoska and Jarvis 1977, Del Rio and Berg 1979, Kellomaki 1980, Kellomaki and Oker-Blom 1981, Zedaker 1981).

The results of this study show that there are significant developmental changes in Douglas-fir plantations which may indicate light interception by competing species. Among foliar measures, the significant increases in specific leaf area and nitrogen concentration can be attributed to reduced investment in cell walls and cuticular waxes by leaves grown in lower light intensities. The other foliar measures tested (leaf blade area, leaf length, and leaf internode frequency) do not appear to be strongly controlled by light intensity, but rather indicate overall tree vigour. The reported tendency of shading to promote lower leaf unit frequency on the main stem (Drew and Ferrell 1977) was not seen here. The lack of a strong correlation between competition and leaf size (length or area) seems similar to Brix's (1970) work which showed that peak leaf size is reached at about 50% of full sunlight.

Changes in allometric relationships reflect differences in the relative growth rates or relative production rates of the quantities compared. In chapter 2, it was shown that the relative growth rates of height, basal area, and foliage dry weight follow inherently different trends in young Douglas-fir plantations, with absolute annual height growth peaking (ie. reaching a relative production rate of 1.0) earliest. Production of foliage increment is related to basal area increment, as seen in the strong linear relationship between the absolute growth of the two over time. As both the relative foliage production rate and the relative basal area production rate are more strongly influenced by competition than relative height production rates, a change in the allometric relationships due to competition would be expected. This is borne out in this study, as increasing competition strongly correlates with preferential maintenance of height growth over basal area growth. As both basal area and foliage weight are influenced by competition, the ratio of these two quantities is not sensitive to light intensity. Due to the increase in specific leaf area of shaded trees, the relationship between leaf area increment and basal area increment would not be as constant in changing light intensity.

The allocation of current shoot growth between foliage and twig or stem tissue appears strongly controlled by light intensity. Even on the terminal leader, where height growth is being maintained to a large degree, stem weight declines more significantly than foliage weight. This is similar to the results of Kellomaki (1981) with Scot's pine.

The study of tree architecture has developed into a large area of research with specific terminology and classification schemes (Halle et al. 1978, Tomlinson 1983). Studies have compared the architecture of trees with their successional status (Boojh and Ramakrishnan 1982) and their modification in shade (Kohyama 1980, Greis and Kellomaki 1980, Kellomaki 1980). It is apparent that early successional species have crowns which are more efficient in high light intensities, and when shaded, attempt to compete for light while acclimating to shade. Late successional, shade tolerant species have more efficient crown structures for low light intensities (Horn 1971) and acclimate to shade by becoming increasingly conservative and

tolerant.

The Douglas-fir in this study maintained high productivity in full sunlight, while competing strongly via rapid height growth. Branches are arranged in several layers, with upper whorls having more acute angle. This arrangement tends to keep many layers of foliage near to the light compensation point and to maximize whole tree net productivity. Under moderate levels of competition, Douglas-fir maintains height growth, potentially improving the light environment of the tree, while the crown development acclimates to shade. Fewer buds are set on shaded branches, resulting in reduced bifurcation rates and lower maximum branch orders. New shoots developing in shade are of higher branch angle, producing the more flattened branch whorls characteristic of shaded trees.

The expression of the acclimation strategy to shade is overlain on the basic development of the plant. For example, a tree in planting shock which is grown under brush shows the characteristics of both stresses. The small needles and high leaf internode frequencies of trees in shock are combined with high specific leaf area values, reduced stem and twig growth relative to height growth and foliage growth respectively, and higher branch angles from the mainstem. Also, as trees increase in size and age, the absolute values of some variables change. Leaf internode frequency declines, allometric relations change, and absolute extension of various axes increases to a maximum. Similarly to the work of Lewandoska and Jarvis (1977), the trees in this study showed dynamic crown development, with a given branch being a function of its light climate. Lower in the crown, self-shading results in naturally high specific leaf area, branch angle, and foliage:twig weight ratios. Competition effects appear additive to self shading, having most significant effects on the development of branches in the upper crown. The development of the tree, then, is a function of the influences of vigour, size, and competition on a dynamic structure.

The possibility of using diagnostic measures to improve assessment of plantation performance seems practical. In fact, the characteristics of planting shock and suppression by competitive shading are apparent without sophisticated analyses and are inherently used by

field personnel. Improved quantification of these variables will assist in setting threshold competition levels for plantation maintenance, and in identifying situations where brush competition is not the limiting factor to growth. Also, in agricultural research, these developmental variables have been instrumental in breeding programs to improve yields (Murata and Matsushima 1975). Looking beyond measures of growth alone, to growth and development, will improve insights into the origins of plantation yield and the limitations to those yields.

CONCLUSION

This chapter has quantified the trends in the variation of morphological, architectural, and allometric measures of Douglas-fir development. These measures are influenced by tree size and age, environmental variation, and tree vigour. The use of these or other diagnostic variables may have potential in assessing factors limiting growth in plantations.

CHAPTER FOUR

Characteristics and Dynamics of Competing
Vegetation in Douglas-fir plantations.

ABSTRACT

A study was made of competing brush species found associated with Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) plantations on a chronosequence of moist, rich sites in the drier coastal western hemlock biogeoclimatic subzone. Species were compared spatially and temporally in terms of frequency, dominance, and canopy characteristics.

It was found that different brush communities can develop on sites with similar soil moisture and nutrient regimes. These differences can possibly be explained by differences in humus form, microclimate, and site preparation.

There was a strong trend over time in the relative dominance of different species groups. Rhizomatous canes and low woody brush which regenerate by sprouting are the major species in the initial two or three years. Colonizing herbaceous species show a peak dominance in the second season after disturbance, then decline as they are shaded out by phanerophytes. Taller woody species begin to establish in the second growing season, and steadily increase in dominance over time.

Three different strategies were noted in the species studied. They were, respectively, rapid colonization and continual dissemination; persistence by exclusion of competitors; and rapid height growth. An index of competitiveness is proposed to analyze the ability of different brush species to exclude later successional species. Rubus parviflorus Nutt. is the most effective early competitor on these sites, although Alnus rubra Bong. and other deciduous tree species eventually succeed them, particularly on scarified sites.

INTRODUCTION

On the highly productive sites of coastal British Columbia, as much as fifteen or twenty cubic metres of wood can be grown annually on each hectare. However, the historical lack of proper forest management on these sites has left a legacy of mixed deciduous cover over thousands of hectares of former Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) forests. It has become clear that if these sites are to be managed for coniferous production (particularly of Douglas-fir) the establishment phase of silviculture must be practiced as an interlocking regime of site preparation, planting, and plantation maintenance (Cleary and Kelpas 1981).

With implementation of sophisticated regeneration programs come increased needs for information on the growth and development of planted trees and brush species, and the comparative efficacies of different treatment regimes. In particular, controversies over herbicide use and questions about the administration of free-to-grow standards for various tenures have resulted in the need to quantify and project the development of brush competition in plantations.

Many indices have been developed to estimate the degree of competition occurring in a stand or around an individual tree. Most have involved measures of the proximity of competitors and their absolute or relative size (Moore et al. 1973, Alemdag 1978, Ganzlin and Lorimer 1983, Lorimer 1983, Howard and Newton 1984). While these indices prove valuable in assessing the current effect of competition on various measures of tree growth, they do not allow prediction of whether the presently open-grown tree will be able to maintain its competitive advantage. As vegetation management decisions must be made before suppression occurs, it is important to gain an understanding of the growth habit and successional patterns of the competing species involved.

Pioneering work in this field was carried out by Mueller-Dombois (1960, 1965), who described the changes and development of secondary succession after logging various biogeoclimatic associations on Vancouver Island. Dyrness (1973) followed vegetation

development in the Oregon Cascades, showing that species significance changed over time and with differences in site preparation. These studies were mainly concerned with identifying species associations and relationships with pre-disturbance communities. They were not designed to study the development of competitors in plantations. Some studies have recently begun to address this question. Bormann and Likens (1979) carried out an exhaustive study of the secondary succession of a northern hardwood forest in terms of the growth strategies of competing species. Eis (1981) studied vegetation development on different site types in the interior of British Columbia, demonstrating differences in successional patterns due to site type and the stocking of the preceding stand. He produced height over age comparisons for brush and planted trees, highlighting situations where interspecific competition problems were likely. Harrington *et al.* (1983) developed predictive models for the development of woody sprouting species based on the diameter of the parent stump. Harrington and Deal (1982) have determined height over age curves for Sitka alder (*Alnus sinuata* (Regel) Rydb.) and compared them with those of planted Douglas-fir. In combination, these studies point out the different competitive characteristics of individual species.

The purpose of this study was to describe the development of various brush species on a relatively common site type. Further, the study was designed to determine successional patterns and differences in competitive characteristics between species or species groups which might influence vegetation management decision-making.

METHODS

Study Sites

This study was carried out on plantations in the Pacific Ranges variant of the Drier Western Hemlock Biogeoclimatic subzone (Klinka *et al.* 1979). The sites were selected based on their silvicultural history and their hygrotome and trophotope. The silvicultural history was broadcast burning or scarification followed by immediate planting (i.e. the following spring). This silvicultural regime was necessary to produce an age sequence, as it diminished the

variability in development of the brush community in year zero. This silvicultural regime is also widely recommended on the site type selected (Klinka and Carter 1982, Green *et al.* 1984).

The target site ecologically was of moist (4-5), rich (D-E) edatope, preferably with deep loamy soils. These sites are characteristic of the highest forest productivity in Canada when growing Douglas-fir (Krajina 1970). They are also subject to severe brush problems, necessitating intensive early plantation maintenance in order to assure successful regeneration programs for Douglas-fir.

Using the B. C. Ministry of Forests History of Crop Establishment and Stand Tending record system twelve candidate sites were selected. After site inspection and classification, six sites were determined to be acceptable for the purposes of the study. They are briefly described in Table 18.

Field Sampling

The data collection commenced in early August and was completed in the second week of September in each year. Plots were established systematically on the study sites described above. Each plot was centred on a planted Douglas-fir. All plots were sampled for the height and percent cover of each species of competing vegetation. The 1984 plots also included estimated canopy height increment for each phanerophytic species.

Height was measured at an estimated average point in the cover of the species. Percentage cover was sketched using a plot cord and sweeping the plot area. The foliage cover of each species was then calculated from the diagram. Identification of species was based on Lyons (1965) and Hitchcock and Cronquist (1973).

Table 18. Summary of some characteristics of the study sites

Location	# plots	Preparation method & year	Growing* seasons	Edatopic position	Aspect
Vedder Mtn	20	Broadcast burn 1982	1,2	3-5/D-E	S
Vedder Mtn	22	Broadcast burn 1981	2,3	4-5/D	SSE
Tamihi Ck.	20	Scarification 1981	2,3	4-5/D-E	Neu.
Sumas Mtn.	24	Scarification 1980	3,4	3-5/C-E	NW
Davis Lake	22	Broadcast burn 1979	4,5	3-5/D-E	NW
Cogburn Ck	16	Broadcast burn 1978	4,5	3-5/C-E	S

*sites were sampled in late summer 1983 and 1984.

In addition, on 1983 plots, all foliage was manually stripped by species and bagged. Bags from each plot were held in a larger plastic bag until transported to the laboratory for leaf area calculation. Certain species were not determined for leaf area. These were species having low percent cover, species with a low growth habit (i.e. Rubus ursinus Cham. & Schlect.) and species where leaf area determination was difficult (i.e. Bromus spp., Cirsium spp.)

Laboratory Procedure

In the laboratory, a subsample of the foliage from each species in each plot was run through a LI-3000 leaf area meter (LAMBDA Instruments). Then the subsamples and remaining foliage were dried at 65° C. for 48 hours to determine dry weights. The subsample leaf area to dry weight ratios were then used to determine the total leaf area by species for each plot.

The calculated leaf areas for each plot allowed the determination of the total leaf area index of the plot, and the leaf area index for the area occupied by each species. The data set generated for each sample is described in Table 18.

Table 19. Data set for brush community analysis

Symbol	Measure
PCij	Percent of plot area covered by foliage of species i in plot j.
HBij	Mean height of canopy or individuals of species i in plot j.
HIBij	Current year canopy increment of phanerophytic species (1984 samples only)
LAIj	Leaf area calculated for species i in plot j.
LAIij	Leaf Area Index of species i in plot j. ($LAI_{ij} = \{LAI_{ij}/PC_{ij}\}/62500$)(1983 samples only)

RESULTS

VEGETATION COMPOSITION

The presence of an individual on a plot is largely a chance event based on the sprouting of a previously established rhizome or stump, or the availability of an appropriate seedbed for germination. Over a number of plots the relative frequencies of occurrence of various species indicates the general favorability of the area for their respective growth. The competing species found on the study sites are listed in Table 20, along with their presence class on each site by sampling period. In general, a species was only used for this analysis if it was one of the four or five most abundant species on the plot and had a percent cover of greater than one percent. The result tends to lower the frequency of herbs or scattered species, such as Achlys triphylla (Smith) DC. or Dicentra formosa (Andr.) Walp., which while often present, are of less practical significance than more predominant species. The competing species present on a plot also reflect site characteristics, previous vegetation, and successional development.

There is variation between the sites (Table 20). This variation is possibly due to differences in site characteristics, preparation method, and age or successional stage. Several differences are immediately noticeable. The Sumas and Davis Lake blocks differ from the others in a reduced presence of thimbleberry (Rubus parviflorus Nutt.), an abundance of salmonberry (Rubus spectabilis Pursh), and more bracken (Pteridium aquilinum (L.) Kuhn). The Davis Lake site also has more vine maple (Acer circinatum Pursh), and includes a minor component of red huckleberry (Vaccinium parviflorus Smith), willow (Salix spp.), and cascara (Rhamnus purshiana DC.). These differences appear to be related to site and microclimate, as both these two blocks are of a cooler northerly aspect. The Davis Lake site also has a coarser soil texture than the other sites, indicating a slightly drier moisture regime.

Table 20. Frequency of competing brush species on study sites.

Species	Vedder II 83,84	Vedder I 83,84	Tolmies Ranch 83,84	Sumas Mtn. 83,84	Davis Lake 83,84	Cogburn Creek 83,84
1. Herbs						
<i>Epilobium angustifolium</i>	- , I	III, III	- , -	- , -	III, II	I, I
<i>Anaphalis margaritacea</i>	- , II	I, II	II, I	- , III	I, I	II, I
<i>Lactuca</i> spp.	I, I	- , -	- , -	- , -	- , -	- , -
<i>Cirsium</i> spp.	- , II	- , -	- , I	- , -	- , -	- , -
<i>Aruncus sylvester</i>	- , -	- , -	- , -	- , -	- , I	- , I
<i>Stachys ciliata</i>	I, -	- , -	- , -	- , -	- , -	- , -
<i>Erigeron strigosus</i>	- , I	- , -	- , -	- , -	- , -	- , -
<i>Verbascum thapsus</i>	I, I	- , -	- , -	- , -	- , -	- , -
2. Grasses						
<i>Poa pratensis</i>	I, I	I, I	I, -	I, -	I, -	- , -
<i>Bromus</i> spp.	- , I	- , I	- , -	- , -	- , -	- , -
<i>Elymus</i> spp.	- , -	- , -	- , I	- , I	- , -	- , -
3. Ferns						
<i>Pteridium aquilinum</i>	I, II	- , III	II, II	IV, III	III, IV	I, II
<i>Athyrium felix-femina</i>	- , -	- , -	II, I	I, III	- , -	- , -
<i>Polystichum munitum</i>	- , -	- , -	- , -	- , I	I, -	I, II
4. Canes						
<i>Rubus parviflorus</i>	IV, V	V, V	V, V	- , -	I, III	IV, IV
<i>Rubus spectabilis</i>	- , -	- , -	I, II	IV, IV	IV, IV	- , -
<i>Rubus leucodermis</i>	- , -	- , -	- , -	- , -	- , -	II, -
<i>Rubus laciniatus</i>	- , -	- , -	- , II	I, -	- , -	- , -
<i>Ribes lacustre</i>	- , -	- , -	- , -	- , -	- , -	- , -
<i>Sambucus pubens</i>	- , -	- , -	- , -	- , -	- , -	I, II
<i>Sambucus racemosa</i>	I, II	I, I	- , II	I, -	- , I	- , -
5. Low woody shrubs						
<i>Vaccinium parviflorus</i>	- , -	- , -	- , -	- , -	I, I	- , -
<i>Symphoricarpus albus</i>	I, -	- , -	- , -	- , -	- , -	- , -
6. Naturally established conifers						
<i>Tsuga heterophylla</i>	- , -	- , -	- , -	- , I	I, I	- , I
<i>Pseudo. menziesii</i>	- , -	- , -	- , -	- , -	- , -	- , I
7. Tall woody - sprouting						
<i>Acer macrophyllum</i>	- , -	I, -	- , -	- , -	I, I	I, II
<i>Acer circinatum</i>	I, I	- , III	- , -	I, I	III, III	- , -
8. Tall woody - non-sprouting						
<i>Alnus rubra</i>	- , -	I, I	II, IV	IV, III	I, -	- , -
<i>Betula papyrifera</i>	- , I	- , I	- , -	- , II	I, II	I, II
<i>Salix</i> spp.	- , -	- , -	I, -	- , -	I, I	- , -
<i>Prunus emarginata</i>	- , -	- , -	- , -	- , -	- , I	I, I
<i>Rhamnus purshiana</i>	- , -	- , -	- , -	- , -	I, I	- , -

Frequency scale: I < 21% II 21-40% III 41-60% IV 61-80% V > 80%

The two scarified blocks, Tolmies Ranch and Sumas Mountain, showed the most vigorous development of red alder (Alnus rubra Bong.) and the unique presence of lady fern (Athyrium felix-femina (L.) Roth.), blackberry (Rubus laciniatus Willd.) and disturbance related rushes (ie. Juncus spp.). They also showed a marked lack of fireweed (Epilobium angustifolium L.), and a general reduction in woody sprouting species.

Some indication of trends over time can be inferred from the year to year changes on individual sites. Similarly to Eis' (1981) study in the interior of British Columbia, there was not much colonization by invading species such as Epilobium angustifolium or pearly-everlasting (Anaphalis margaritacea (L.) B. & H.) until the second growing season. From the third season on, these species declined, being steadily relegated to landings and waste patches. The cane species expanded most rapidly in the second and third seasons, with salmonberry and/or thimbleberry becoming ubiquitous by the second season. The woody species such as red alder begin to emerge during the second growing season, and achieve substantial frequency on scarified sites. The burned sites also develop an increasing presence of woody species, but more slowly than on the scarified areas.

CHARACTERISTICS OF COMPETING SPECIES

Knowledge of the composition of the plant community on an area allows certain inferences to be made about the characteristics of the site and climate. However, a listing of plant species and their presence or frequencies is only one of the descriptive tools available for analysis. Practical applications of vegetation management require information on the relative dominance of species, the potential size they can attain, and their ability to compete with other species (i.e. successional tendencies).

1. Dominance

Measures of dominance are used to indicate the degree to which a species occupies the plot or area under consideration. Recent studies (c.f. Inselberg et al. 1982) estimate dominance

using a 10 or 11 point scale adopted from Krajina (1933). This scale is largely based on the percent cover where the species is abundant or the number of individuals where scarce.

In this study, dominance was calculated empirically as the percent cover of the species multiplied by its height. This approach was used to suit the purposes of the study, which required information on the actual size trends of the brush. The Domin-Krajina technique concentrates on separating out the dominance values in the low end of the scale. This is because many scattered individuals may be useful indicators of site characteristics, despite never achieving a high percentage ground cover. For vegetation management, it is more important to study the relative dominance of the more common or continuous species.

The height times cover measure relates to the competition index developed in Chapter 2, where the proximity and relative height of the brush to the planted trees were the most important indicators of competition intensity. The dominance measure still allows comparison between plots or sites, although the comparison is of an empirical nature.

The calculated dominance values for each species are shown in Appendix 1. In using this data it must be remembered that dominance values are also influenced by the frequency of a species on a given site. Species such as broadleaf maple (Acer macrophyllum Pursh) have very high dominance values on localized areas, but are moderated when calculated on a whole site basis. Also, these dominance values are absolute rather than relative. A relative dominance can be calculated by dividing the dominance value of an individual species by the sum of the dominance values for that site (c.f. Curtis and Cottam 1962).

Table 21. Absolute* and relative* dominance of species groups by age since disturbance.

Group	Dominance measure	Years from disturbance				
		1	2	3	4	5
Herbs	Absolute	4.0	15.3	2.3	2.3	6.0
	Relative	8.2	22.4	3.0	2.3	3.7
Grasses	Absolute	7.0	1.0	1.3	0.7	0.0
	Relative	14.3	1.5	1.7	0.7	0.0
Ferns	Absolute	6.0	10.3	16.3	20.3	16.5
	Relative	12.2	15.1	21.0	20.2	10.3
Canes	Absolute	31.0	36.7	36.7	42.7	42.5
	Relative	63.2	53.7	47.1	42.4	26.5
Low shrub	Absolute	1.0	0.0	0.0	0.3	4.5
	Relative	2.0	0.0	0.0	0.3	2.8
Conifers	Absolute	0.0	0.0	0.0	0.3	1.5
	Relative	0.0	0.0	0.0	0.3	0.9
Woody-sprouting	Absolute	0.0	2.3	4.3	13.3	60.5
	Relative	0.0	3.4	5.5	13.2	37.7
Woody-seeded	Absolute	0.0	2.7	17.0	20.7	29.0
	Relative	0.0	4.0	21.8	20.6	18.1
Total	Abs. Dominance	49.0	68.2	77.9	100.6	160.5

Absolute Dominance = (% cover * height of species)

Relative Dominance = (Absolute dominance of species i)/(Sum of absolute dominance values for site).

In Table 21, the absolute and relative dominance of several species groups is shown. Species were grouped based on their growth habit. This grouping has allowed some analysis of trends over time, because different species are filling similar ecological niches on the different sites. The salmonberry/thimbleberry dichotomy, for example, is generally considered an indication of whether the microclimate of a site is under a cool, moist influence, or a warm, dry influence. Both Sumas Mountain and Davis Lake are on northerly aspects, and are the westernmost sites of the study. This may explain the relative abundance of salmonberry on these two areas.

Table 21 shows that specific trends occur in the different species groups, despite considerable variation in the actual species from site to site. It is apparent that a species must continually increase in absolute dominance over time in order to maintain the same relative dominance. Species which are limited in the ability to compete in height growth tend to decline over time as they are overtopped. Table 21 demonstrates that early treatment of cane species may simply unveil the greater emerging problem from woody species.

Figures 18 and 19 graphically depict these trends for the three major classes of competing vegetation, the geophytes (including grasses, ferns, and herbaceous plants), the canes and other low brush, and the woody species. The general increase in total dominance is apparent. The differing trends by the three classes of species are also apparent. Comparing the absolute dominance values with the relative dominance curves, confirms that the vegetation community is dynamic. Species increasing in absolute dominance may still be overtopped by more vigorous woody brush and actually decline in relative dominance.

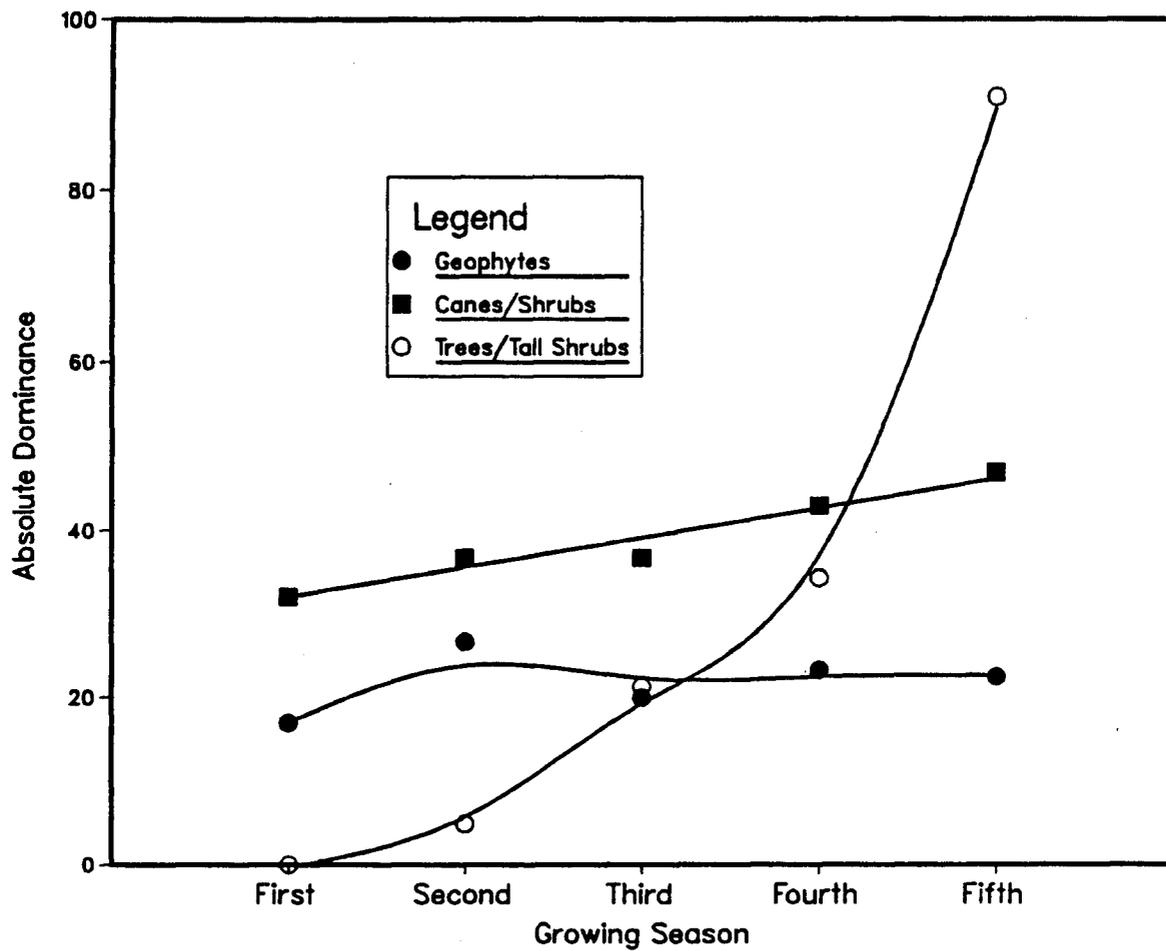


Figure 18. Trends in absolute dominance (mean height X % cover) for the three main species groups over the first five years after disturbance.

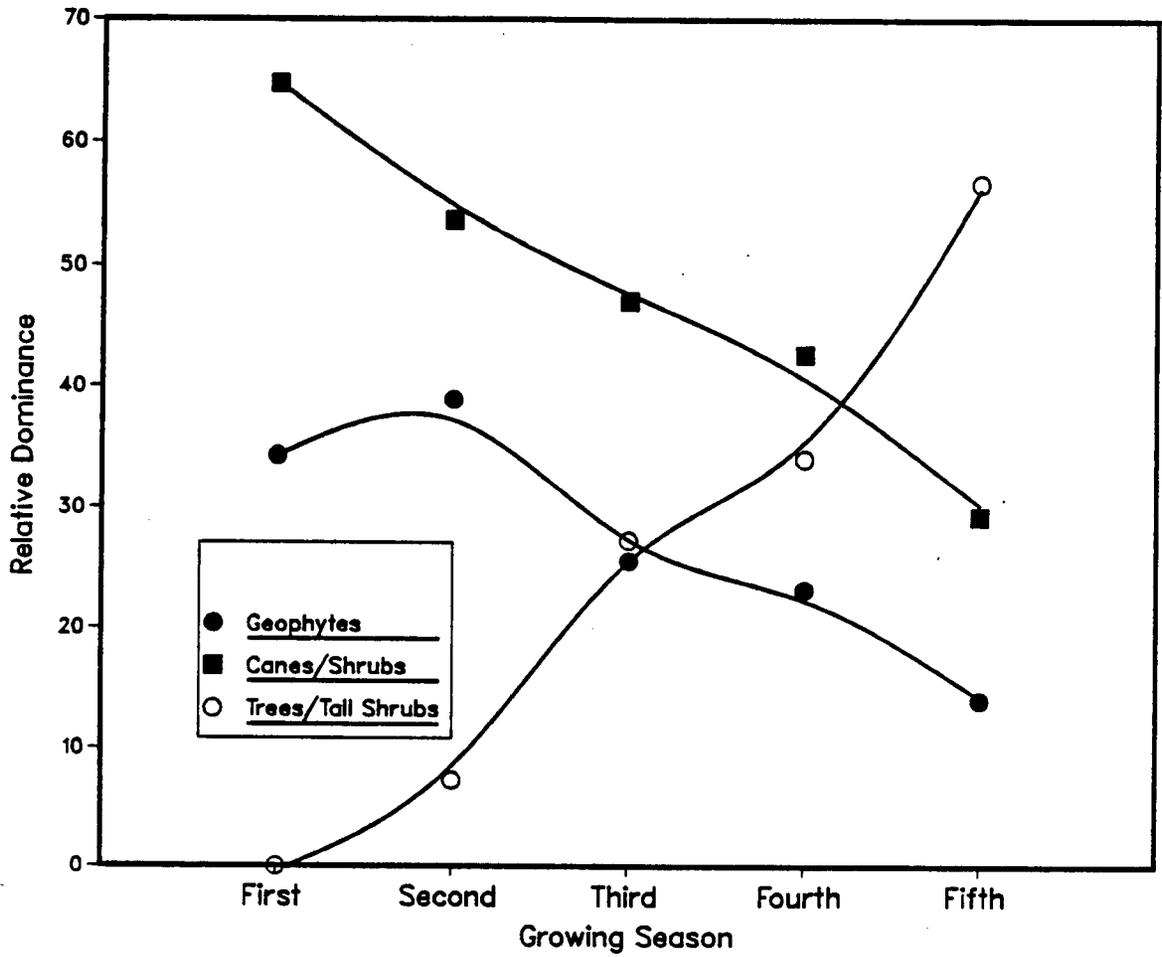


Figure 19. Trends in relative dominance for the three main species groups over the first five years after disturbance.

2. "Competitivity"

In order to understand why some species colonize a site only transiently, while others persist, and still others expand, characteristics other than the measure of dominance used above are necessary. There appear to be three different strategies of survival or continuance operating among the species studied. The first strategy is to produce large amounts of easily disseminated seed, thereby continually colonizing available habitats but not maintaining cover on a specific area for any amount of time. The second is to produce rapid height growth thereby outcompeting rival species and eventually shading them out. The third strategy is to form dense continuous canopies of foliage which prevent the colonization of other species. Another strategy, unimportant here, is not to actively compete at all and simply to live in a shaded environment (c.f. Grime 1979).

There is considerable cross-over between the three types of competing plants discussed above. For example, broadleaf maple (Acer macrophyllum Pursh) not only grows rapidly in height, but also forms a dense foliar canopy. In terms of brush competition, the second and third categories representing species able to persist over time, and those able to rapidly grow in height are the most important.

The species present on the study sites were assessed for their ability to produce persistent foliage canopies using an index of "competitivity". This measure is determined as the leaf area index of the plant multiplied by its percent cover. While not an accurate model of light diminuation potential, leaf area index is a large determinant of the depth of shade caused by a canopy (Monsi and Saeki 1953, Monteith 1965). The percent cover modifies this for edge effects, as canopies covering continuous areas will prove more impenetrable to succeeding species. It should indicate species which will persist on a site, and which may cause the greatest mortality to planted trees. Table 22 shows the calculated values for several common species from this study.

Table 22. Mean competitiveness* values for some brush species.

Species	Common name	Competitivity
<i>Epilobium angustifolium</i>	Fireweed	17.4
<i>Anaphalis margaritacea</i>	Pearly Everlasting	1.8
<i>Pteridium aquilinum</i>	Bracken	59.5
<i>Rubus parviflorus</i>	Thimbleberry	105.7
<i>Rubus spectabilis</i>	Salmonberry	35.8
<i>Acer macrophyllum</i>	Broadleaf Maple	96.6
<i>Alnus rubra</i>	Red Alder	19.8

*Competitivity = LAI X % cover for species (where present).

Looking at these species, it is relatively easy to sort them into the three strategies discussed above. The fireweed and pearly-everlasting are light-seeded species which are able to colonize disturbed sites readily. They persist via underground rhizomes, sending up new shoots each year. However, they do not produce dense canopies, and often exist in small groups or as individuals. Other species tend to grow over them, shading them out within the first two or three years.

Red alder represents the second category. These species do not develop dense canopies, but grow as individuals. They tend to have low initial cover values, but as they eventually overtop shorter species, they are able to gain dominance.

The bracken, thimbleberry, and to a certain degree salmonberry, have limited height development. They form continuous cover of relatively dense foliage, thereby overtopping the new shoots of herbaceous species and preventing the development of woody species. Thimbleberry in particular has an effective canopy of large leaves, closely arranged. This allows little direct or diffuse light penetration, and hampers the development of a shade intolerant species such as alder.

3. Projecting Height Growth of Competing Vegetation

The concepts of dominance and competitiveness outlined above are useful in describing the successional tendencies and canopy characteristics of brush communities. However, the major factor in determining the impact of a given brush canopy on a planted tree is the relationship between the height development of the two neighbours.

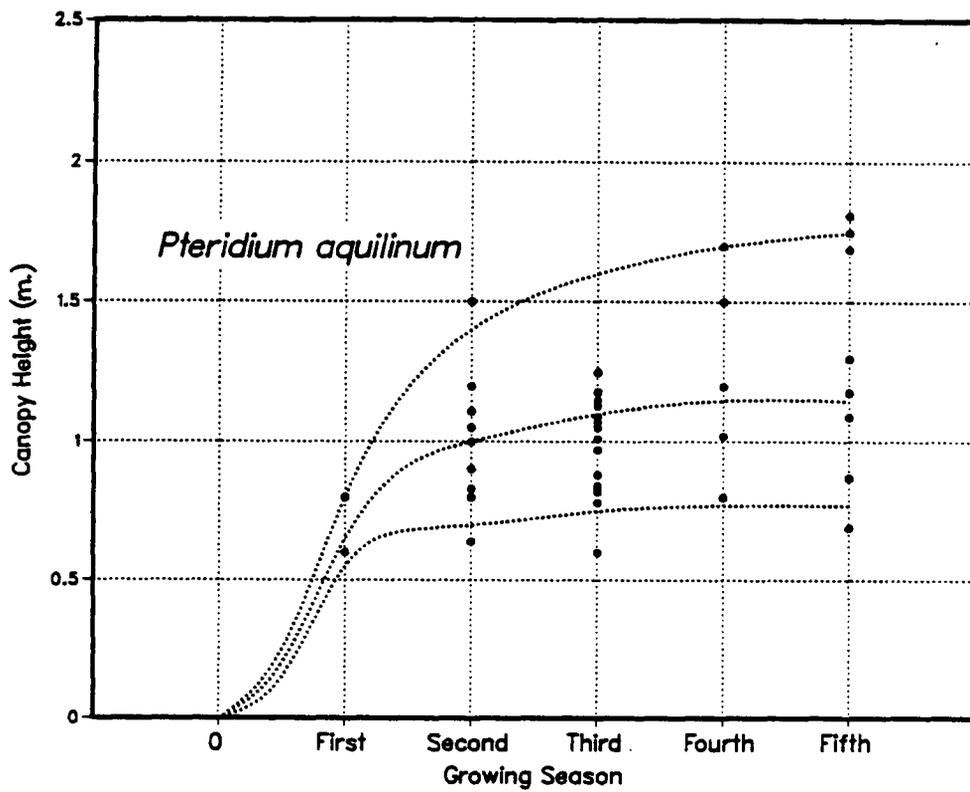


Figure 20. Projected height growth trends for bracken (*Pteridium aquilinum* (L.) Kuhn.) canopies in the initial five year period following disturbance. Individual curves represent drier, mesic, and moister microsites.

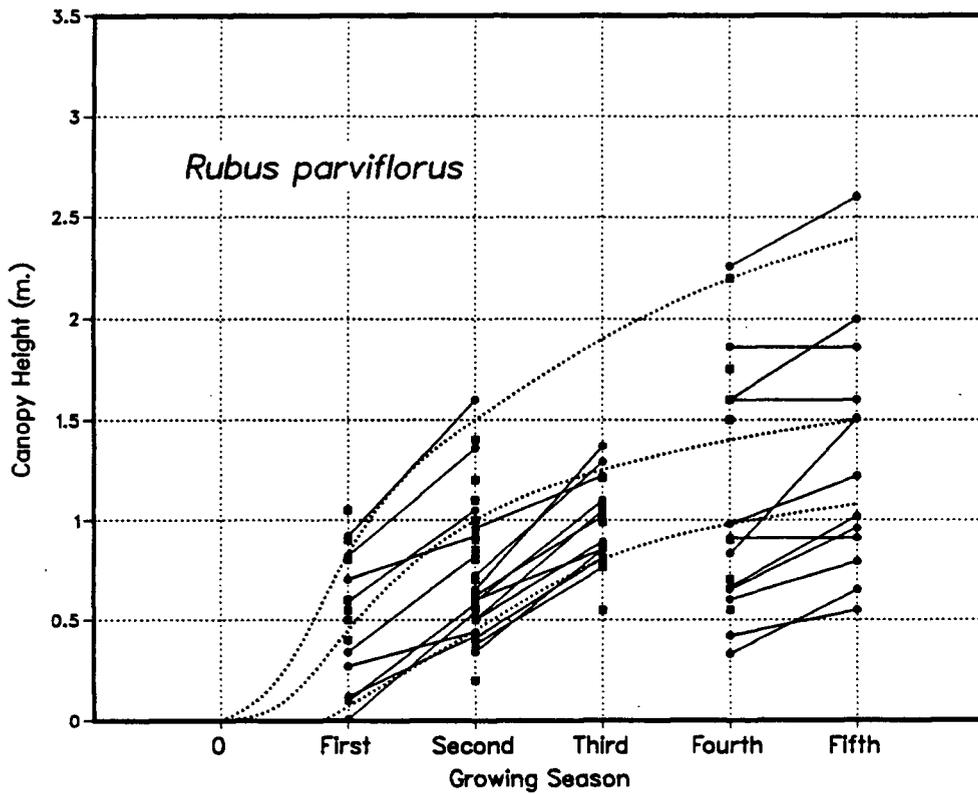


Figure 21. Projected height growth trends for thimbleberry (Rubus parviflorus Nutt.) canopies in the initial five year period following disturbance. Upper curves represent sprout originated canopies, while the lowermost represents seed originated canopies.

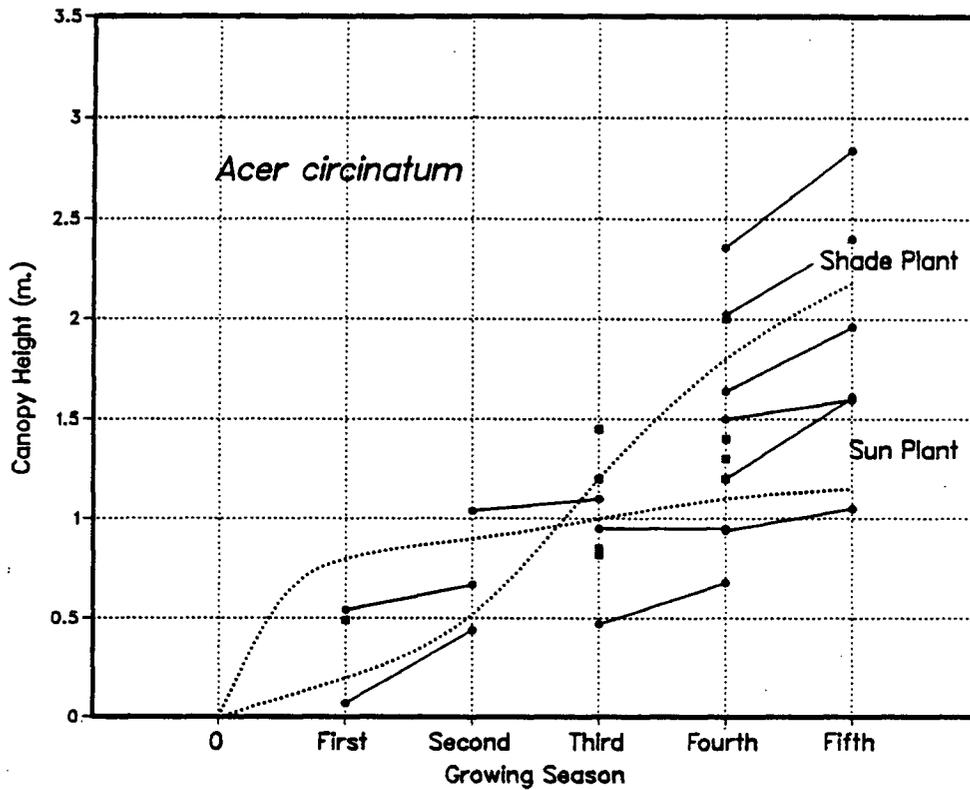


Figure 22. Projected height growth trends for vine maple (*Acer circinatum* Pursh) canopies in the initial five year period following disturbance. Note different trends followed by shade vs. sun plants.

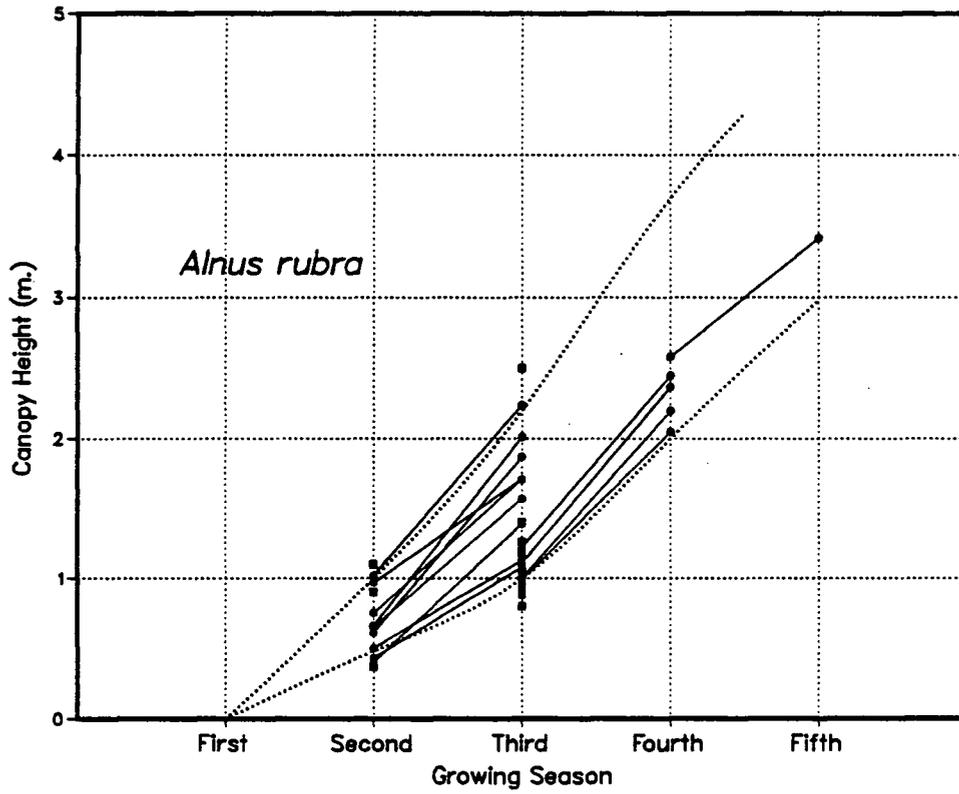


Figure 23. Projected height growth trends for red alder (*Alnus rubra* Bong.) in the initial five year period following disturbance.

Figures 20 through 23 project height growth for the four most common brush species in this study. These four species illustrate the trends in canopy height growth which characterize geophytes (Pteridium aquilinum), canes (Rubus parviflorus), and woody species (Alnus rubra, Acer circinatum). The Pteridium aquilinum curves indicate a range of growth habits from dry to moist microsites. The trend for rapid early attainment of maximum canopy height agrees with the work of Cody and Crompton (1975). The cane species illustrated by figure 21 show a more gradual attainment of maximum canopy height, but still become asymptotic by about the fifth growing season. Rubus parviflorus is often present on a site prior to disturbance. This allows sprout regeneration (as in the two upper curves) which provides more rapid height growth. The lower curve represents the slower height growth of seed established individuals.

The curves for Acer circinatum show two differing growth strategies. This is because vine maple is a very shade tolerant species (Krajina et al. 1982) which forms a compact shrub in full sun. Where the surrounding brush is as tall and conditions are shaded, the upper height growth curves seems to be followed. Alnus rubra, on the other hand, is a shade tolerant species which has very rapid height development. The curves shown are compatible with those of Newton et al. (1968) which show red alder to have maximum growth in the third and fourth season, reaching up to 10 metres of height by age 10.

Comparing these curves with the height growth of open Douglas-fir plantations must be done with caution. As the brush canopy will affect the height growth of the planted tree, a simple comparison of the two height over age curves can be misleading (c.f. Harrington and Deal 1982). Often the early competition from species such as bracken and thimbleberry slow the height growth of the conifers, allowing woody species to gain greater height advantage in later years.

DISCUSSION

The ability to project vegetation development either prior to or immediately after logging or site preparation is an important tool in plantation management. Studies carried out in coastal British Columbia and the adjacent Pacific Northwest of the United States

(Mueller-Dombois 1965, Kellman 1969, Dyrness 1973) have shown that the characteristic or indicator species of the previous undisturbed forest associations are still present in the secondary vegetation. They are supplemented, however, by additional species which either expand from other associations or invade as shade-intolerant weeds.

While the original character species can still be found in the years following disturbance, they are often in "refugea" within the area, and often show poorer vigour than in their original habitat. In this study, sword fern (Polystichum munitum (Kaulf.) Presl), for example, was only found in shady spots, such as under broadleaf maple sprout clumps. Kellman (1969) noted that many of the primary species (those present in undisturbed forest) were only found in unburned patches of third and fourth year cutovers. Species of this type found in the present study included Polystichum munitum, Achlys triphylla, and Dicentra formosa.

A second class of vegetation, called semi-tolerant forest weeds by Mueller-Dombois (1965), are present in the undisturbed forest, but expand in both dominance and range after disturbance. These species, as a class, are the most persistent and strongest competitors to establishing plantations. The most important of these species in this study were Rubus parviflorus, Rubus spectabilis, Rubus leucodermis Dougl., Acer macrophyllum, Acer circinatum, Pteridium aquilinum, and Alnus rubra. Rubus spectabilis and Alnus rubra spread from wet sites onto drier sites after disturbance. In the case of Rubus spectabilis, this observation may be due to the presence of a nutrient flush on sites with decomposing organic matter. Alnus rubra was found in the wet association of mature forests due to the more open canopy (Mueller-Dombois 1965), but after logging, the species spreads onto dry areas of exposed mineral soil.

Other species are present in the mature forest in shade forms or in small canopy openings, but achieve substantial increases in dominance after disturbance. Pteridium aquilinum, Rubus parviflorus, Acer macrophyllum and Acer circinatum are examples from this study. These species show greatly improved vigour after canopy removal, increasing in height, cover, and leaf area index.

The invading or secondary species (Kellman 1969) are composed of shade intolerant plants

which cannot survive in the shaded conditions of the mature forest. They are generally light-seeded, rapidly developing plants, which are able to colonize vacant ground space after burning. These plants tend to be fairly ubiquitous with respect to soil moisture, although they may have optimum conditions under a certain hygrotape. Epilobium angustifolium and Anaphalis margaritacea are the most common species of this class on the sites studied.

The present study was aimed at moist, rich sites in the Drier Western Hemlock biogeoclimatic subzone. These sites are the "sword fern" association of Mueller-Dombois (1960), the Orthic Polystichum and Degraded Polystichum of Orloci (1964), and the Moss-Polystichum Western Redcedar and Tiarella-Polystichum Western Redcedar of Klinka (1976). Orloci used as a distinguishing feature the presence of a forest floor with the Degraded Polystichum association; possibly due to a cooler microclimate. Klinka separated his "alliances" based on duration of seepage water and humus form.

These differences may be reflected in the post-disturbance brush community also. There are indications of two distinctive brush associations on the sites chosen for this study. One is characterized by the dominance of *Rubus spectabilis*, *Pteridium aquilinum*, and *Acer circinatum* (Davis Lake and Sumas Mountain), and the other by the dominance of *Rubus parviflorus* (Vedder, Tamih, and Cogburn). Klinka *et al.* (1984. Classification of seral ecosystems at the University of British Columbia research forest [submitted to Can. J. For. Res.]) have also recognized two distinct associations of seral vegetation, one dominated by *Rubus spectabilis* and *Epilobium angustifolium*, and another by *Rubus parviflorus*. These communities appear to be separable by the humus form of the preceding stand, in turn a function of the amount of seepage present (Klinka 1976) and the soil temperature.

The different brush communities and where they occur must be studied along with their development in time. Succession occurs among species most rapidly in the early years after disturbance. Looking at the sites in this study there may be a trend in the relative dominance of different species groups over time. In the first year after burning, vegetation is largely sprouts from rhizomes or root collars. In the second year, these sprout colonies increase in

size and cover, while the light-seeded species are invading on areas of open ground. Slowly the cover of the highly competitive species such as bracken fern, thimbleberry, and salmonberry overtop these herbaceous species. Woody species such as red alder in turn succeed these low brush species wherever they gain dominance. Without silvicultural intervention the eventual result is a deciduous canopy.

This generalized trend must be considered in brush control decisions. The control objective may require that "later successional" species such as red alder be removed even when present in small amounts. This can be a particular concern where selective herbicides are proposed. For example, a bracken fern treatment may promote more long-term red alder problems.

CONCLUSION

This study has looked at the vegetation of different aged sites over two growing seasons. Although the individual species differ between sites, there are successional trends related to classes of vegetation. These successional trends are a function of differing ecological strategies based on reproductive and canopy characteristics. Projection of the development of competing vegetation in plantations requires knowledge of these trends, and the interaction of the height development of the planted trees with the brush canopy.

CHAPTER FIVE

A Comparison of Manual and Chemical Release Treatments:
Crop Tree Growth Response and Control of Competing Vegetation.

ABSTRACT

This chapter presents results from a comparative study of mechanical and chemical release treatments after one season. Mechanical treatment neither significantly improved seedling growth performance nor significantly reduced competition levels from that on control plots. Glyphosate application at 2.0 kg. a. i. per hectare significantly reduced competition levels resulting in a significant improvement in crop tree growth measured as foliage or basal area based relative production rates. Changes in developmental variables (specific leaf area, allometric relationships) and lack of changes to foliar nitrogen status suggests growth response may be related to improved light conditions. Damage to crop trees by the glyphosate application appears due to late season lammas growth during treatment. This damage did not appear to cause a reduction in the vigour of the released trees.

INTRODUCTION

The importance of vegetative competition as a major limiting factor in young plantations has been shown by many authors (Ruth 1956, Baskerville 1961, Tucker et al. 1968, Eis 1981, Conard and Radosevich 1982, Oxenham 1983, Howard and Newton 1984). Without silvicultural intervention many plantations develop into mixed stands with low stocking of crop species and wide ranging individual tree sizes (Stiell 1976).

Recent evidence indicates that early release treatments can significantly improve total volume production and reduce the range in height and diameter of individual stems much later in the rotation (MacLean and Morgan 1983). Vegetation management principles and techniques have been reviewed by Newton and Knight (1981) and Cleary and Kelpsas (1981). The two major classes of vegetation control activity are chemical and mechanical treatments. Although both methods have proven successful in various circumstances (Turpin 1977), the chemical option has been most widely touted (Sutton 1978, Newton and Knight 1981).

In British Columbia, the use of herbicides has been strictly controlled, with a lengthy permit process required for all forestry uses. This is due to the need to protect fisheries resources and also due to a general public apprehension of the widespread use of biocides. The result is that manual release treatments are frequently proposed as an alternative to chemical treatments (Horowitz 1977). Studies which have compared chemical and manual treatments (MacLean and Morgan 1983, Sutton 1978, 1984) show that herbicides are more effective in controlling the rapid sprouting of competing species and are thus a more viable practice. Studies by Roberts (1977, 1980) also point out that there are problems of crop tree damage, rapid canopy redevelopment, and high costs associated with mechanical brush control treatments.

Herbicide treatments also have drawbacks. Bigley and Kimmins (1984) report large losses of nitrates to groundwater after herbicide application. They attributed this to a lowered C/N ratio of killed vegetation and to changes in microclimate. Sutton (1984) reports that outplanted white spruce were more heavily frost damaged after complete release by highly effective herbicide treatments. Direct damage to crop trees also can occur if applications are

made at improper periods of the growing season or if late season lammas growth has not completely hardened off (Radosevich *et al.* 1980, Sutton 1984).

The most recent chemical to be registered for forestry use in British Columbia is glyphosate (N-phosphonomethyl glycine). This herbicide has several salient features including low toxicity to fish and mammals, low soil mobility, good translocation in target species, and effective control of woody brush, shrubs, herbs, and grasses (Ashton and Crafts 1981, Weed Science Society of America 1979, Anonymous 1984). Operational use of glyphosate in British Columbia commenced in 1983.

This study aimed to determine the efficacy of glyphosate in terms of brush control and promotion of growth on residual conifers. The experiment also is designed to compare herbicide treated relative to control and manually treated areas. Damage to conifers attributable to glyphosate also was assessed.

METHODS

Two of the study sites described earlier were selected to assess the influence of a brush control treatment on seedling growth and development and brush competition levels. The two sites were at the end of the second growing season, and were relatively similar in seedling size and competition levels.

Both sites had been sampled in the 1983 season for data used in the previous sections of this study. For each tree sampled in 1983, however, two companions were staked for 1984 measurement, a treatment and a control. The treatment consisted of an operational herbicide application on the Vedder I site, and a mechanical clearing on the Tolmie site. The herbicide used was glyphosate, applied with backpack sprayers at an approximate rate of 2.0 kilograms of active ingredient per hectare. The manual treatment was carried out with hand clippers in a 2.5 metre radius surrounding the individual staked trees. An attempt was made to keep the mechanical release treatment to operational standards. That is, brush was clipped to about 30 centimetres of residual height, and slash left scattered within the plot.

In the 1984 sample, the treatment and control trees were harvested as has been outlined earlier. The only additional assessment was a written description of damage to conifers from the glyphosate application.

RESULTS

1. Trends in Vegetation Composition and Dominance.

The two treatments appear to differ in both the qualitative (compositional) and quantitative (dominance) responses they create. The Vedder Mountain site was far more severely disturbed than the Tolmie site, with dead canes and woody shoots continuous across the treated area. The manually treated plots on the Tolmie site were far less conspicuous, being almost indistinguishable from the surrounding vegetation after one year. The competing vegetation on the control and treated plots is summarized in terms of frequency class and dominance in Table 23.

The glyphosate killed all woody species on the Vedder site, effectively reducing competition to the level it had been at immediately after the initial site preparation burn. After treatment, the most dominant species group was the herbaceous species, particularly fireweed. Grasses also increased in dominance from their pre-treatment levels. The most important competitor on this site prior to treatment had been thimbleberry. It was effectively controlled by the herbicide, with ground cover reduced from 55% of the site to 6% and canopy height from 0.8 to 0.5 metre. On the control plots, thimbleberry coverage remained at about 50%, while canopy height increased to an average of 0.9 metre. Figure 24 shows the heavy thimbleberry canopy on the untreated area. In the background the radically different composition of the treated area is visible.

Table 23. Frequency and dominance values for competing species

	Vedder Mountain			Tolmie's Ranch		
	1983	1984	Roundup	1983	1984	Mech.
	Control	Control		Control	Control	

1. Herbs						
<i>Epilobium angustifolium</i>	III, 17	III, 4	III, 3	- , -	- , -	- , -
<i>Anaphalis margaritacea</i>	I , 1	II, 3	I , 1	II, 1	I , -	II, 1
<i>Lactuca canadensis</i>	- , -	- , -	II, 1	- , -	- , -	- , -
<i>Cirsium arvense</i>	- , -	- , -	I , -	I , 2	- , -	III, 3
<i>Erigeron canadensis</i>	- , -	- , -	I , 1	- , -	- , -	- , -
<i>Hypochaeris radica</i>	- , -	- , -	I , -	- , -	- , -	- , -
<i>Lathyrus nevadensis</i>	- , -	- , -	I , -	- , -	- , -	- , -

2. Grasses						
<i>Poa pratensis</i>	I , -	I , -	II, 4	I , 1	- , -	- , -
<i>Bromus vulgaris</i>	- , -	I , 2	I , 1	- , -	- , -	II, 3
<i>Elymus</i> spp.	- , -	- , -	I , -	- , -	I , 1	I , -

3. Ferns						
<i>Pteridium aquilinum</i>	- , -	III, 7	II, -	II, 14	II, 14	III, 16
<i>Athyrium felix-femina</i>	- , -	- , -	- , -	II, 15	I , -	1 , -

4. Canes						
<i>Rubus parviflorus</i>	V , 44	V , 45	IV, 3	V , 24	V , 40	V , 21
<i>Rubus spectabilis</i>	- , -	- , -	- , -	I , 3	II, 3	II, 10
<i>Rubus laciniatus</i>	- , -	- , -	- , -	- , -	II, 1	I , 1
<i>Sambucus racemosa</i>	I , 3	I , 2	- , -	- , -	II, -	II, 4

5. Shrubs						
<i>Cytisus scoparius</i>	- , -	- , -	I , 2	- , -	- , -	- , -

6. Tall Woody-Sprouting						
<i>Acer circinatum</i>	- , -	III, 13	- , -	- , -	- , -	- , -
<i>Acer macrophyllum</i>	I , 3	- , -	- , -	- , -	- , -	- , -

7. Tall Woody-Seed Origin						
<i>Alnus rubra</i>	I , 3	I , 5	- , -	II, 4	IV, 29	II, 7
<i>Betula papyrifera</i>	- , -	I , 1	- , -	- , -	- , -	- , -
<i>Salix</i> spp.	- , -	- , -	- , -	I , -	- , -	I , -
<i>Populus trichocarpa</i>	- , -	- , -	- , -	- , -	- , -	I , 1

Total Dominance	71	82	16	64	88	67

Frequency Classes I-1-20 II-21-40 III-41-60 IV-61-80 V-81-100
 Dominance=(mean height*percent cover)



Figure 24. Heavy thimbleberry competition on Vedder 1984 control plot. Note glyphosate-treated area in background is free from thimbleberry.



Figure 25. a) Plot immediately after manual clearing of brush in 1983 and b) one year later in 1984.

The results of the manual treatment were far less significant. The species composition is similar for the treatment and control plots, although there appears to be an enrichment of thistles, grasses, and ferns relative to the canes and woody species. This may indicate that geophytic species which are able to take advantage of the lower initial canopy of the phanerophytic species are slightly favoured by the mechanical treatment. The bracken fern, for example, increased from 13% to 15% cover and from 1.1 to 1.3 metres canopy height after treatment, while on the control it remained static. The cane species, despite rapid resprouting, were diminished by the treatment. Thimbleberry developed on the control from 34% to 40% cover and 0.7 to 1.0 metre canopy height. The treated plots showed 24% cover and 0.88 metre canopy height for thimbleberry after one year. After cutting, the thimbleberry responded by resprouting an average of 0.6 metre, compared with a canopy increment of only 0.4 metre for the control plots. Figure 25a and b shows a plot immediately after treatment in 1983 and rephotographed after one year in 1984.

2. Influences of Treatment on Seedling Performance and Competition Level after one Growing Season.

The average growth of the plantation is compared in Table 24 for the treatment and control plots on each site. Eleven different growth measures are compared, including absolute and relative measures. The mean competition index value for the sample trees on each site also is shown.

Table 24. Summary of Growth Measures for Treatment and Control Plots in 1984, one year after treatment. Bracketed values indicate one standard deviation.

Growth Measure	Vedder		Tolmie	
	Control	Glyphosate	Control	Mechanical
Total Height	1.11(0.36)	1.22(0.30)	1.16(0.21)	1.14(0.27)
Total Basal Area	1.18(0.85)	2.54(2.53)	1.52(0.65)	1.84(1.28)
Height Increment	0.32(0.14)	0.41(0.18)	0.42(0.11)	0.44(0.15)
Basal Area Increment	0.48(0.36)	1.33(1.25)	0.77(0.32)	0.93(0.72)
Foliage Wt. Increment	25.5(23.5)	59.5(67.0)	42.8(30.2)	46.3(43.0)
Rel. Ht. Growth Rate	0.35(0.07)	0.46(0.16)	0.46(0.12)	0.48(0.13)
Rel. BA Growth Rate	0.48(0.16)	0.81(0.22)	0.72(0.11)	0.69(0.19)
Rel. Ht. Productn Rate	1.12(0.35)	1.32(0.73)	1.19(0.29)	1.45(0.44)
Rel. BA Productn Rate	1.05(0.31)	2.27(1.49)*	1.65(0.33)	1.98(1.20)
Rel. Fol. Productn Rate	2.66(1.28)	6.22(2.74)*	2.52(0.97)	3.41(1.33)
Rel. Shoot Productn Rate	3.62(1.68)	8.96(4.09)*	3.56(1.33)	4.69(1.73)
Competition Index	94.1(75.3)	3.9(3.2)*	65.9(25.8)	56.2(48.8)

*Treatment is significantly different from control ($p < .01$)

The significant impact of the herbicide treatment on the competition index value can be seen. The mechanical treatment indicates some success in reducing the competition level, but the difference is not statistically significant. Due to the high degree of variation among the individual sample trees, the majority of growth measures did not show significant improvement after treatment. There was, however, a general trend towards improved growth due to both treatments. The significant improvements were in the relative production rates of basal area, foliage, and shoot dry weight after the glyphosate treatment. These relative production rates were shown earlier to be the most sensitive growth measures to the competition index, and it follows that they would best demonstrate changes in tree vigour due to competition release.

In Figure 26, the two treatments are compared graphically in terms of their effects on the competition index and the seedling performance as relative foliage production rate. The vectors show both the treatment and control trends over the first year after treatment. Both treatments result in a trend towards declining competition and improved growth, but the herbicide treatment showed a far greater magnitude of response. It appears that the Vedder site was tending to heavier competition levels without treatment, while the Tolmie controls seemed to have a more static competition level in the two growing seasons sampled.

3. Influence of Treatment on Foliage Morphology and Allometric Relationships within trees.

It was shown earlier that the tree foliage can be a sensitive indicator of tree vigour and stress from competitive shading. A comparison was undertaken to determine the influence of the two treatments on leaf blade length, leaf blade area, and specific leaf area at different crown positions. The results are summarized in Table 25.

The manual treatment did not result in statistical differences in either the size or specific leaf area of foliage. Although there was a general trend towards larger needles and lower specific leaf area values, the differences were not sufficiently large to be significant. This is similar to the results in Table 24, where there appears to be only a slight trend towards increased vigour and reduced competition a year after mechanical release.

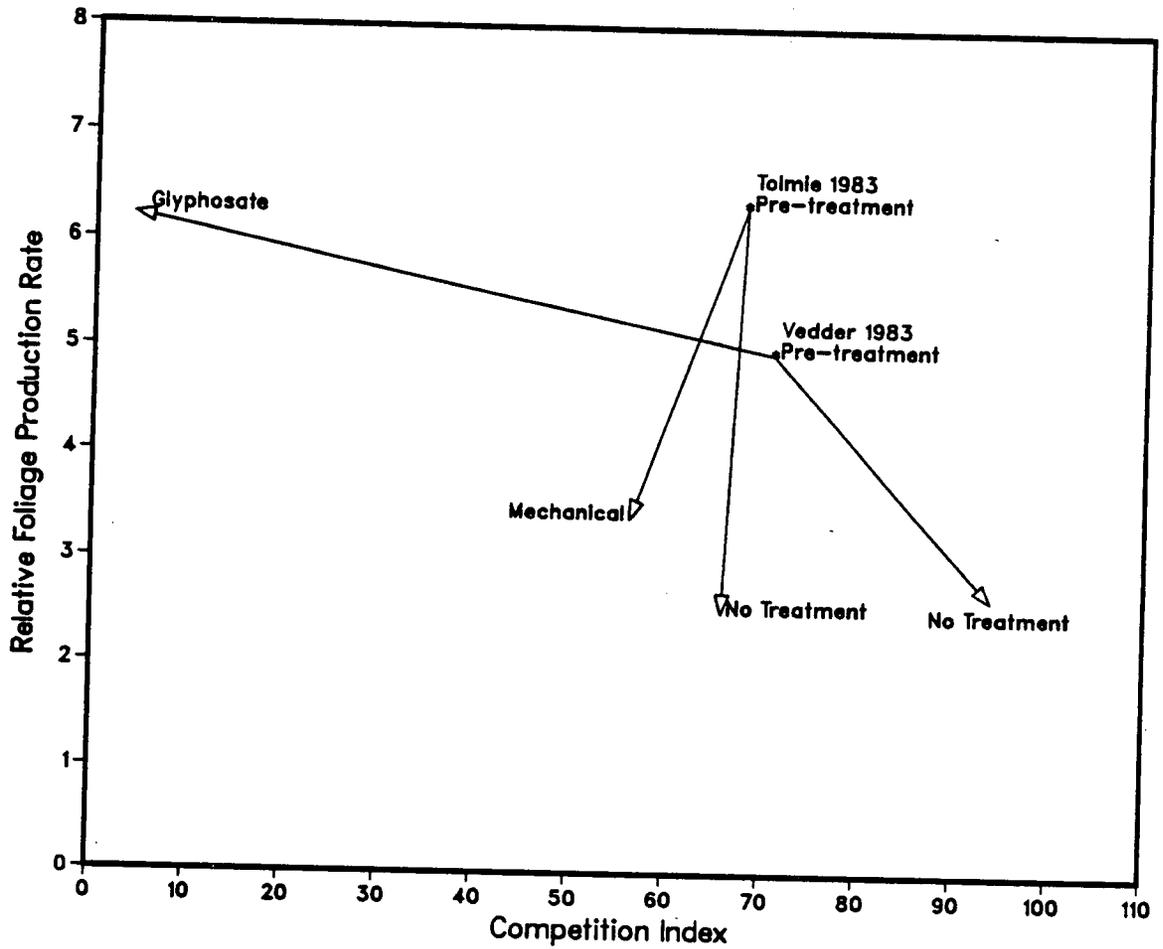


Figure 26. Graphical depiction of the trends in the mean relative production rate of the planted trees and the mean competition index for pre-treatment conditions, 1984 control, and 1984 post-treatment plots.

Table 25. Mean values for leaf length, leaf blade area, specific leaf area, and foliar nitrogen status for control and treated plots on the two sites. Mean values for treated plots differing significantly from 1984 control plots are indicated ($p < .05$, $*p < .01$).

Character	Position	Vedder			Tolmie		
		1983 Control	1984 Control	1984 Chem.	1983 Control	1984 Control	1984 Mech.
Leaf Length (cm.)	Leader	3.40	3.00	3.11	3.30	3.15	3.27
	1st Whorl	3.01	2.89	3.20 _a	2.79	3.11	3.18
	2nd Whorl	3.10	3.09	3.49	3.04	3.23	3.29
	3rd Whorl	2.67	2.97	3.62*	2.92	3.05	3.40
	4th Whorl		2.51	3.24		2.88	3.22
Leaf Area (10 needles) (mm ²)	Leader	4.55	3.48	4.19 _a	4.25	3.96	4.19
	1st Whorl	3.71	3.29	3.90*	3.28	3.72	3.92
	2nd Whorl	3.77	3.22	4.18*	3.61	3.63	3.74
	3rd Whorl	3.33	3.18	4.60*	3.30	3.52	3.98
	4th Whorl		2.58	3.88		3.25	3.54
Specific Leaf Area (cm ² /gm)	Leader	81.5	87.2	60.4 _a	92.0	71.3	67.6
	1st Whorl	87.1	91.9	64.4 _a	99.9	75.6	72.4
	2nd Whorl	101.7	107.8	66.0 _a	101.7	85.1	84.9
	3rd Whorl	114.6	138.3	65.8*	119.8	96.1	91.5
	4th Whorl		164.3	66.6		118.5	108.6
Foliar Nitrogen†	Conc. (%) Content (mg)	1.55 0.74	1.34 0.69	1.34 0.84			

†-calculated on a 100-needle basis; foliage from uppermost whorl

The glyphosate application showed more determinable differences in all foliar measures. There was a strong trend towards increasing leaf blade size and decreasing specific leaf area. This would indicate that the trees had responded to the reduction in competition with both morphological re-acclimation and increased vigour. The most significant improvements were in the middle to lower crown, where brush influences tend to be strongest on the control trees. An analysis of the foliar nitrogen status of half of the trees on the Vedder site showed no significant differences in either nitrogen concentration or content. There was some indication, however, that concentration was stable, while content increased with leaf size after treatment. This may lend support to the earlier assumption that competition for nitrogen is not a limiting factor on this site.

The influence of the two treatments on three allometric ratios also was determined. Ratios of height to basal area and foliage weight increment to basal area increment were determined on a whole tree basis, while foliage weight to twig weight ratios were determined for current shoots from each crown position. The results are shown in Table 26.

The manual treatment did not result in statistically significant changes to allometric measures. The glyphosate treated plots showed a significant improvement in basal area growth relative to height growth. This follows from Table 24, where basal area measures showed greater differences between treated and control plots than height measures. The ratio of current foliage dry weight increment to basal area increment was not affected by either treatment, although release seemed to promote basal area growth slightly relative to foliage growth. This is somewhat counter to the results of Brix and Mitchell (1983), who found that thinning caused a relative increase in the foliage component of this ratio.

Table 26. Allometric relationships for treated and control plots on the two study sites. Significant differences between 1984 control and treated plots are noted ($\alpha < .05$, $*p < .01$)

Ratio	Position	Vedder			Tolmie		
		1983 Control	1984 Control	Chem	1983 Control	1984 Control	Mech.
Height:BA (m/cm ²)	Whole Tree	1.59	1.43	0.75 ^a	1.54	0.85	1.00
Foliage:BA (gms/cm ²)	Whole Tree	59.4	48.7	40.6	45.5	52.2	48.3
Foliage:Twig	Leader	0.94	0.97	1.12	0.94	0.50	0.99
Weight (gm/gm)	1st Whorl	2.75	3.01	2.21*	1.98	2.04	2.57
	2nd Whorl	4.40	4.56	2.84*	2.95	3.48	4.10
	3rd Whorl	5.75	5.40	3.23*	4.49	3.32	4.43
	4th Whorl		6.65	3.45		5.12	6.17

BA=basal area

The ratio of foliage to twig weight growth in current shoots was significantly changed through much of the crown by the herbicide release treatment. The increased allocation to structural tissue may be attributable to increased light levels. This change in the glyphosate plots can be considered as acclimation to full light levels, similarly to the specific leaf area effects seen above.

4. Herbicidal Damage to Crop Trees

In order to produce optimum brush control with minimal crop tree damage, glyphosate is applied after current season vegetative growth of conifers has ceased, but while brush species are still active. In many growing seasons, however, Douglas-fir plantations will develop a second flush of lammas or proleptic growth. Not wanting to delay the herbicide application, foresters are often faced with the prospect of applying the herbicide before the second flush is fully hardened off. This was the situation in 1983 and the treatment, while effectively controlling the competing vegetation, also caused damage to the planted trees.

Five of the eleven sample trees were damaged to the extent that the terminal leader did not flush normally. In three cases, the previous leader was completely killed back and a nodal shoot from the uppermost living whorl assumed dominance. In the other two cases, the leader was not completely killed and an internodal bud assumed dominance. Of the six trees which continued height growth normally, half sustained other damage to non-terminal shoots. The three remaining trees which were undamaged had been under heavy competition, and may not have been directly exposed to the spray. At this stage, after one growing season, it was difficult to project whether long-term damage to form would result on any of the five terminal-damaged trees. In three cases, no single branch had regained sole terminal dominance. Figure 27 illustrates a case where a single nodal shoot has assumed dominance after the previous leader was completely killed.



Figure 27. Response to herbicidal injury. Previous season nodal shoot has assumed terminal dominance after glyphosate damage to former leader.

DISCUSSION

This experiment compared the effects of manual and chemical conifer release treatments on plantation growth and development and competition levels one year after treatment. The chemical competition release treatment significantly improved growth, measured as a relative production rate of basal area, foliage biomass, or shoot biomass, and significantly reduced competition levels. The manual release treatments resulted in neither significantly improved growth nor reduced competition levels.

The improved control of competing vegetation by chemical means over manual methods is similar to the results of Sutton (1978, 1984) in boreal forest conditions, MacLean and Morgan (1983) in Atlantic Canada, and Lewis and Higdon (1977) in Oregon. The improved herbicide efficacy in this study may be attributable to the translocation of glyphosate, resulting in complete plant kill. The manual control, however, does not directly damage the root systems, allowing the rapid sprouting found in this and other studies (Roberts 1977, 1980, Turpin 1977, Bernstein 1977).

Based on comparison with control plots and field notes, the glyphosate successfully killed thimbleberry, elderberry, red alder, birch, vine maple, bigleaf maple, and willow. Herbaceous species, including fireweed, pearly everlasting, and thistle, were killed but rapidly reseeded. In comparison with the results of other reported herbicide treatments on these species (ie. Gratkowski 1971, Stewart 1974), glyphosate shows very high potential as a wide spectrum control measure at 2.0 kilograms per hectare. The mechanical treatment, while not significantly changing the total level of competition, did seem to cause a greater decline in the woody species relative to the herbaceous. There also appeared to be an enrichment in the more shade tolerant salmonberry (Barber 1976) relative to the thimbleberry. These trends may be due to rapid early season development of ferns and herbaceous species causing reduced vigour in the sprouting woody plants and thimbleberry.

The improved growth on the herbicide treated area to indicates that the trees were able to respond immediately to brush removal. The growth response appeared best, however, where trees

had not been completely suppressed prior to release treatment. There appeared to be a release shock on two or three trees which had been extremely suppressed. This phenomenon has been reported in other species and site conditions (e.g. Gordon 1973). These shock symptoms may be due to damage from high radiation loads (Conard and Radosevich 1982) or poor control of evaporative water losses by the shade-adapted foliage (Keller and Tregunna 1976).

The current growth in the herbicide released area showed a re-acclimation to high light intensities on all trees. This included increased specific leaf area and an increasing allocation of growth to structural tissues. The manually released trees showed little change in foliage morphology or allometric relationships. The lack of significant changes in foliar nitrogen status also may indicate the controlling influence of light, as brush control did not appear to result in improved nitrogen uptake.

This study adds further evidence to the value of measuring growth as a relative production rate. First season differences in growth were not detectable as absolute measures after glyphosate treatment. The production rates of foliage and basal diameter increment did, however, show significant improvement. This can be attributed to the ability of this measure to detect year-to-year changes in productivity. Absolute growth measures require more time for these changes in vigour to develop into significant changes in size.

In this study the herbicidal damage to crop trees can be attributed to the late season lammas growth of 1983. This damage did not appear to influence tree vigour, and would likely be much less prevalent in years where lammas growth did not occur. The mechanical treatment here did not result in any crop tree damage, although it has been reported that operational treatments with power saws regularly cause 30% of crop trees to be damaged (Bernstein 1977, Roberts 1980).

CONCLUSION

The general conclusion from this work is that chemical release treatments with glyphosate give improved control of competing vegetation on the moist, rich sites of coastal British Columbia relative to manual treatments. If manual treatments are to be used repeated removal of the vegetation need occur for a considerable period of time. There is some evidence that improved growth after competition release involves response to improved light intensity around the seedlings and a rapid re-acclimation of foliage to these improved conditions.

CHAPTER SIX

Discussion of the Concept of the Free-to-Grow Seedling

INTRODUCTION

The preceding chapters have looked at different aspects of plantation establishment and interspecific competition, with the larger goal of an improved understanding of the biological basis for the concept of the free-to-grow seedling. The following discussion utilizes this biological information to form a conceptual model of interspecific competition during plantation establishment. While influences other than competition also may limit achievement of free-to-grow status (i.e. browsing, insect damage of trees), these will not be considered here. Nevertheless, competition has been implicitly recognized as the major problem limiting establishment of plantations in British Columbia (B. C. Ministry of Forests 1984).

This study has quantified the competition level around individual trees, and analyzed the seedlings response in terms of both growth and development. The measurements were not static, being made at the end of the growing season in each sampling period. Therefore, trends in the growth of the planted Douglas-fir and the competing species have been developed. It is important to quantify both the interactions among neighbouring plants and the trends of the species through time. A free-to-grow projection must use the trends in the crop tree and its competing species to project the dynamics of the interaction of the two.

The basis for the projection of free-to-grow status is that a tree will be considered free-to-grow if it is below some threshold of maximum competition and the current competition index value is projected to decline in the following growing season. This predictive definition requires a threshold level of competition which is biologically acceptable, and the ability to project both the future growth of the crop trees and the future growth of the competing vegetation. The following discussion will elaborate on how projections of this nature can be developed without including the detailed mathematical formulation or verification.

MEASURING PLANTATION GROWTH AND COMPETITION LEVEL

The two basic components of any forest growth simulation or projection system are the measure of growth used and the quantification of the competition influence. The essential characteristic of a successful growth measure is sensitivity to changes in resource availability which affect tree vigour (c.f. Newton 1973). The essential quality of a competition measure is that it directly or indirectly describes the degree to which resources have been diminished. The free-to-grow projection also must incorporate these measures. Finally, the free-to-grow assessment should be based on relatively simple, non-destructive field measurements.

The four major growth measures available are total growth, current increment, relative growth rate, and relative production rate. The first two are absolute measures and are the most commonly used variables for assessing plantations (i.e. Knight 1957, Arnott 1976, Smith 1975, Howard and Newton 1984). Occasionally studies have reported the influence of competition on relative growth rates (i.e. Ford 1979, Zedaker 1982), while relative production rate measures have not been previously tested.

The results of this study show the relative production rate to be promising as a measure of tree vigour or productivity. It has the benefits of being independent of the variation in tree size which plagues the use of absolute growth measures and is free from the artificial decline in relative growth rate due to the accumulation of non-productive tissues. The decline in relative production rates during early plantation growth is likely caused by a real decline in vigour, since the respiratory drain on the carbon fixed by photosynthesis may slowly increase with tree size. The second demonstrable benefit of the relative production rate seems to be an improved sensitivity to environmental changes. This benefit is due to the concentration of this measure on recent growth, removing the influence of size or cumulative past growth. An example of the merits of relative production rates as an indicator of growth response to environmental change is shown by the data in Table 24 (Chapter 5).

The improved performance of the trees released by glyphosate application was evident only as a relative production rate of basal area or foliage weight. Finally, in competition studies relative growth measures (including both relative growth rates and relative production rates) remove fallacious correlation between competition indices and absolute growth measures. Many studies demonstrate that small trees have large competition indices and slow growth without proving a causal relationship. This situation is not the case with relative growth measures, since the measure of growth is independent of the measure of size used in the competition index.

The different possibilities for competition measures were initially classified for forest stand modelling purposes by Munro (1974). Munro's (1974) classes (whole stand distance independent, individual tree distance independent, and individual tree distance dependent) can also be applied to early plantation conditions. An example of whole plantation models would be the work of Fiske (1982) who uses competition indices based on the crown volume of competing brush or competing biomass per hectare. These models are only useful in assessing impacts on the average growth of the plantation and are unable to determine the range of conditions operating. Individual tree distance dependant models are scarce in very young plantations. These models generally project growth of trees in different size classes based on whole stand conditions. In young plantations, however, it is difficult to apply uniform conditions to all trees. It may be possible to derive a model of this sort, applying relative growth trends to a given distribution of individual tree sizes.

By far the most commonly used method in young plantations, however, is the individual tree distance dependent model. The most basic technique is the subjective assessment, where competition conditions around each tree are estimated as light, moderate, or severe (e.g. Oxenham 1983). More quantifiable techniques have been developed, however. Howard and Newton (1984) recommend using the overlap by competing vegetation through a projected inverse cone above the base of the terminal leader. Wagner (1982) and Radosevich and Wagner (1983) have proposed a formula based on the height, cover, and distance to the competing vegetation from

individual trees. Both of these competition measures are problematic if used in modelling. The inverse cone assessment (Howard and Newton 1984) only recognizes adjacent, overtopping vegetation, with all levels of competition below this assigned a value of zero. The empirical model (Wagner 1982) does not assess the relative status of the brush species and the crop tree. Thus, a large tree with short competitors may have the same competition index value as a small, overtopped tree. This leads to an inability to directly estimate the influence of a given competition level on tree development.

The competition index derived in this work is somewhat similar to a competition index proposed by Ek and Monserud (1974) for interspecific competition in hardwood stands. It is based on a relative measure of proximity and a relative measure of the size of the crop tree and competitors. The use of relative measures gives several advantages to this index. It is effective through a range of conditions and tree sizes, it is sensitive to all levels of competing vegetation, and it can be used to compare conditions on different sites or on the same site over several growing seasons.

The competition index proved fairly successful in explaining differences in vigour through the range of young sites and ages sampled. The index generally explained 40% to 60% of the variation in relative foliage production rate on individual sites. Relative basal area production rate also was significantly related to the index, but not as strongly as the foliage measure. Height proved to be least dependent on competition, which is similar to work with other species (e.g. Martin and Ek 1984). The portability of the relationship between sites and ages indicates that there is good possibility for its use as a predictive tool.

DEFINING A MAXIMUM ACCEPTABLE THRESHOLD OF COMPETITION

The implementation of a projection-based free-to-grow assessment requires the determination of a maximum acceptable threshold of competition. This threshold would be the point at which growth losses, declining potential for competition release, and increasing potential for mortality make projected growth increments invalid. Trees which fall below this

threshold undergo radical acclimation to shade and convert to a more conservative, stress-tolerant strategy of growth. While in many cases these trees emerge from the competing vegetation after many years, they are generally smaller than the main body of the crop and not likely to contribute significantly to final yields.

The acclimation of Douglas-fir to implied changes in light intensity (and perhaps spectral quality) was addressed in chapter 3. The foliage is most notably affected, with the change towards a shade leaf morphology linearly related to the competition index. The increasing nitrogen concentration of the foliage also reflects this change, indicating less development of cell walls in the leaf under shaded conditions. The limited growth under influence of competition is allocated increasingly to the foliage component of the new shoots. These shaded shoots are also more horizontally oriented, produce fewer buds, and have lower orders of branching than those in well-lit positions.

Acclimation varies within the tree based on the light conditions. Branches produced above the vegetation canopy can have completely different morphology, architecture, and allometry from those found lower in the same tree. The result is that height growth is preferentially maintained in the trees, compared to production of foliage biomass or basal area. It is not until the terminal leader is overtopped that height growth begins to slow significantly. It is proposed that the threshold level of competition be defined as the point at which the inherent ability of the tree to compete is reduced. This occurs when the height growth of the tree is affected by the competing vegetation. As the growth of the upper crown has been shown to be unaffected until overtopped, the threshold level will be set as a competition index value of 100. This level infers that the brush canopy is of equal height to the tree and covers the entire plot.

In a modelling or projection context, the threshold level rejects trees from free-to-grow status without considering growth potential. The basis for rejection is an uncertainty as to the degree to which the tree will maintain height growth in shaded conditions. However, these "threshold-rejected" trees represent a pool of increased stocking on a site if competition

release treatments are applied. The objective of the free-to-grow survey of plantation establishment is to minimize the number of trees which will cross the threshold into suppression.

PROJECTING FREE-TO-GROW STATUS

Trees currently growing below the maximum competition level, discussed above, prove most difficult for foresters to deal with. Such trees must be maintained in a vigorous state, and therefore require vegetation management decisions be made before they become suppressed. At the same time, if it can be projected that the competition level is declining, the trees can begin contributing yield in the calculation of the increment for the forest unit concerned.

The major competition characteristic influencing the productivity of trees appears to be the horizontal proximity to the competing vegetation. However, height development is the more important factor in determining whether the tree is escaping or succumbing to competition. Therefore, the most important factor in a free-to-grow projection is estimation of the height increment for the tree and for the competitors. If the height growth of the tree exceeds that of the brush, for example, the proximity effects become less important (i.e. the competition index declines). Even if the proximity is increasing and the model underestimates the future competition index by not projecting this increase adequately, it is not important, as the tree is growing out of the brush.

The estimation of future height growth for the tree is best carried out using a generalized trend of relative height production rate (Figure 28). After the second growing season, height increment continues to increase from year to year, but the increase is proportionately smaller each year, eventually reaching a stable annual rate of constant height increment (ie. 1.0). Using the current production rate as a basis for the production rate for the following growing season can be estimated as:

$$[1] \text{ Future Relative Height Production Rate} = (1 + \text{Current Relative Height Production Rate})/2$$

This formula acts as an exponential approach to a stable height increment, but is based on the actual conditions in the stand being assessed. The relative height production rate should be based on the initial flush of growth only; excluding lammas increment. Future height increment is then calculated as:

$$[2] \text{ Future Height Increment} = \text{Future Relative Height Production Rate} \times \text{Current Increment}$$

This equation should give a usable estimate of height increment, but will not include any contingency for lammas growth which may occur. This is necessary, because lammas growth does not occur in every growing season, and therefore cannot be counted on as potential increment.

The estimation of the height increment of the competing vegetation must take into account the different growth habits of the various species. It is proposed that there are three main classes of height development curves which are followed (c.f. Figures 20-23, Chapter 4). The geophytic competitors die back to the ground each winter and regrow from rhizomes in the spring. As a general rule, the height of these species (i.e. fireweed, pearly-everlasting, bracken) stabilizes by the third growing season. Therefore, if a tree is below the threshold of competition (i.e. not overtopped) by the third growing season, it should be free-to-grow if geophytes are its only competitors.

The second group of competing species can be classed as the microphanerophytes (from Ellenberg and Mueller-Dombois 1967). These species do not die back to the ground each year, but leave a perenniating aerial shoot system 0.5 to 5.0 metres tall. In this study these species include thimbleberry, salmonberry, elderberries, and huckleberries. Their growth habit is asymptotic, with height growth limited after the third season. Their future increment could be estimated in two ways. Either as a function of current year height increment (e.g. 50%) or as a function of current canopy height (e.g. 20%). The former method is preferable as it ties into the current increment of the canopy. The current canopy increment is estimated by comparing the height of current shoot tips to dead tips from the previous season.

The third group of competitors are the mesophanerophytes, which are the long-term

competitors. On these sites red alder, willows, birch, bigleaf maple, and bitter cherry are examples. These species, like Douglas-fir should be projected with a relative height production rate technique. This requires the ability to assess the height increment on the plant from the previous two seasons, which is sometimes difficult. In general, current increment is either foliated, or with determinable recent leaf scars. The previous increment must be determined with differences in bark shade and leaf scar characteristics. Sprouting species will often approach the stable production rate value from the opposite direction (i.e. a lessening decline), but still suit this technique.

From the height models, the competing class of vegetation with the greatest projected future height will be the competitor on which to base the free-to-grow decision. For example, this allows an initially shorter red alder to succeed fireweed competition if it produces sufficient height increment. The model, therefore, projects growth within the constraints of the species characteristics and vigour on a specific site.

The final free-to-grow projection, then, will calculate a new relative height component for the competition index, and determine if this causes the index to increase in the following season. In certain cases an increase in the competition index will not warrant release. For example, if the tree is 2.5 metres tall and its competitor, while increasing in relative height, is not able to achieve sufficient canopy height to overtop the crop tree.

The free-to-grow assessment can then be tied into yield projection tools such as the density management diagram for Douglas-fir (Drew and Flewelling 1979) to project potential yields from the current stocking of free-to-grow trees. This also will identify the estimated time at which interspecific competition will commence on the site.

In summary, the free-to-grow model proposed initially sorts trees into suppressed and non-suppressed categories using a competition threshold. Trees currently non-suppressed can be classed as free-growing if their total height, relative to their competitors, is increasing. The entire plantation is free-growing if sufficiently stocked with free-growing trees.

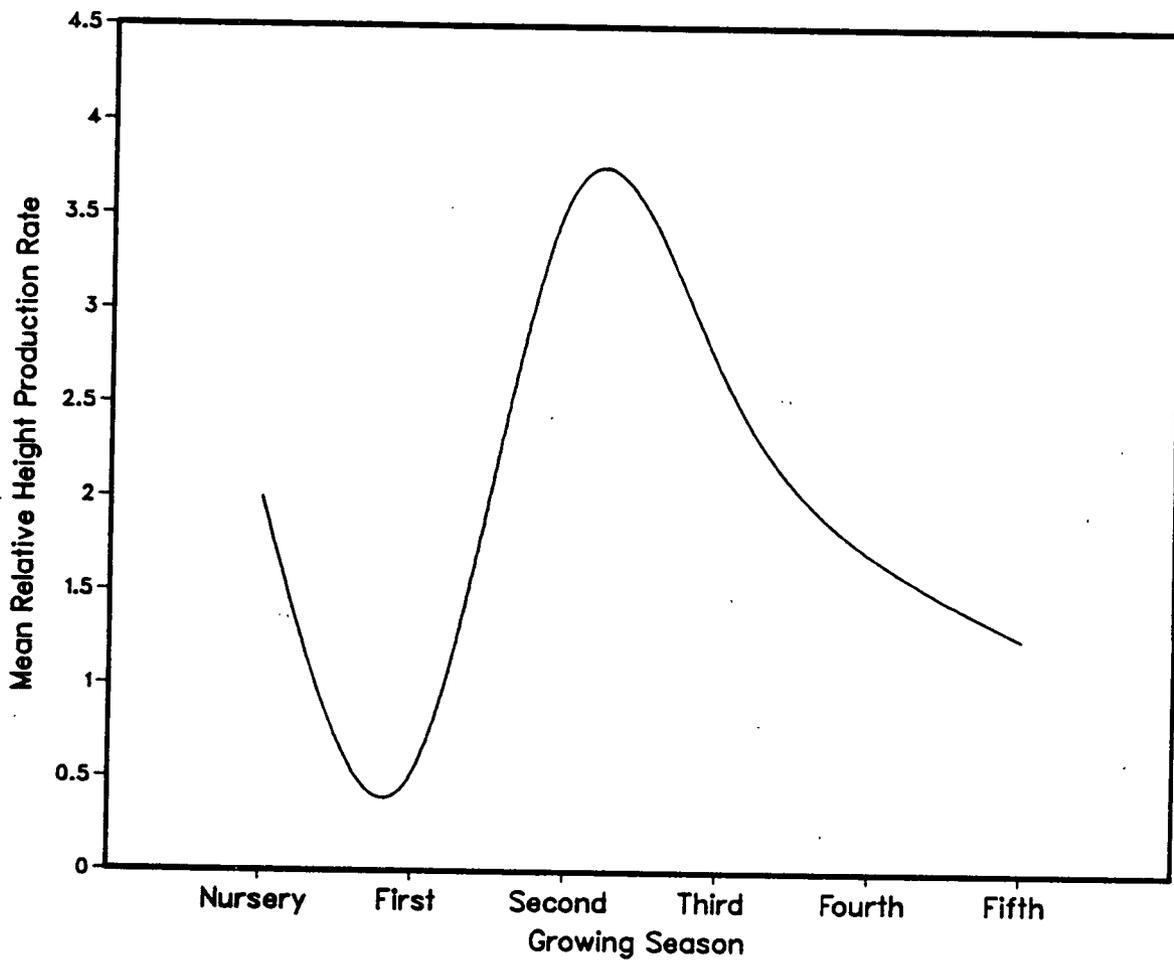


Figure 28. A hypothetical trend in relative height production rate based on averaging the data from the six sites studied.

SETTING FREE-TO-GROW STANDARDS FOR OTHER SITES

The current study has determined a biologically-based definition and assessment technique for the free-to-grow status of Douglas-fir plantations on moist, productive sites. It addresses the specific establishment problems created by interspecific competition. On other sites, the competition influence may act on the tree differently or other establishment risks may be more important.

The establishment risks which influence regeneration can be considered in two classes - those which are based on resource limitations (e.g. planting shock and brush competition) and those from damaging agents (insects, browsing, flooding, frost, root rots). In terms of a free-to-grow classification some of these hazards are more or less treatable, while others preclude the use of certain species on a site. It is important that all these cases be fitted into a biological free-to-grow definition if it is to have widespread applicability as a standard.

By slightly reworking the definition presently in use, a free-to-grow seedling definition which accomodates all the types of hazards above can be produced. The tree must meet all three criteria below:

1. Acceptable species for the site in terms of potential productivity and security from epidemic or catastrophic risks.
2. Presently acceptable growth within the limitations of the site for the species concerned.
3. Projected continued access to sufficient site resources and ability to maintain acceptable growth.

Using this definition non-treatable problems (e.g. flood hazard, frost hazard) make a species unsuitable for the site conditions. Other problems such as root rots may require preparation techniques to remove inoculum before the site is acceptable for a species. Treatable risks or hazards must also fulfill the final two criteria. For a given risk on a

site, a free-to-grow standard should include a threshold value for (2) and a method of projecting whether the threshold will be exceeded (3). The threshold value and projection system does not have to use similar variables for different hazards. For example, an area with browsing problems may require a total height standard while an area influenced by competing vegetation may use a maximum competition index value. Different thresholds simply reflect the different nature of the stresses involved.

By setting free-to-grow standards for major site types and establishment risks, regeneration programs will have better short-term focus. The free-to-grow goal forces recognition of many persistent problems in Canadian reforestation practice. Future work should place other site types and establishment problems within the framework discussed in this study.

CONCLUSIONS

This study has derived a biological basis for the concept of the free-to-grow seedling. It has used a specific site type where light limitation due to interspecific competition is believed to be the most important determinant to plantation establishment. Six sites with operationally planted Douglas-fir formed an overlapping chronosequence representing the first five growing seasons after outplanting. Specific experiments were undertaken on these sites to determine trends in the growth of Douglas-fir, trends in the development of competing vegetation, and the interaction between brush competition and the performance of the planted trees. Secondary studies analyzed morphological, architectural, and allometric acclimation of Douglas-fir to competitive shading, and the response of both the planted trees and brush community to different competition release treatments.

Several conclusions can be made:

1. On the sites studied, growth was strongly limited by competing vegetation. Competitive effects were quantified, but could not be specifically related to reduction in light, moisture, or nutritional availability to the trees.
2. Growth, measured as a relative production rate, was most sensitive to environmental change. The shading from brush limited the relative production rate of foliage weight most significantly on these sites. The relative production rate of basal area was the next most sensitive measure of growth. Height growth was least sensitive to measures of competition in any formulation.
3. The reduction in relative foliage production rate due to competition varies through the crown depending on the apparent light climate of each branch. Growth of the terminal leader was least affected by competition, resulting in a preferential maintenance of height growth.
4. Changes in foliage morphology, crown architecture, and allometric relationships were comparable to controlled studies on the influence of varying light intensity on seedling

growth. Many variables, however, interact with influences of establishment stresses, crown position, and tree size.

5. Competing vegetation appears to follow a fairly strong trend of succession during the five-year period studied. The woody mesophanerophytes appear to be the most important long-term competitors due to their logistic height growth pattern.
6. Competition release had superior long-term benefits if carried out with herbicides rather than manually on these sites. The major benefit of the glyphosate treatment in this case was prevention of the rapid sprouting by phanerophytes.
7. Response to competition release treatments was best measured as a relative production rate. Foliage and diameter-based measures were more responsive than height-based measures.
8. A free-to-grow definition in biological terms states that a tree must be free from shading on the terminal leader and increasing in height relative to the competing vegetation.
9. Free-to-grow assessment can be based on a threshold competition index and predictive models of tree height increment and competing vegetation canopy increment.

LITERATURE CITED

- Alemdag, I. S. 1978. Evaluation of some competition indexes for the prediction of diameter increment in planted white spruce. Inf. Rep. FMR-X-108, Can. Forest Manag. Inst., Ottawa, Ont. 39 pp.
- Anonymous. 1984. Roundup herbicide Q & A. Monsanto Canada Inc., Streetsville, Ont. 4 p.
- Armson, K. A., F. C. Robinson, and J. E. Osburn. 1980. Forest management manual for the province of Ontario. Ontario Ministry of Natural Resources, Toronto, Ont.
- Arney, J. D. 1972. Computer simulation of Douglas-fir tree and stand growth. Ph. D. thesis, Oregon State Univ., Corvallis, Oreg. Univ. Microfilms 72-20, 742.
- Arnott, J. 1976. Effects of stock size on field performance. Part I. Coastal species. British Columbia Min. of Forests, Reforestation Notes Vol 3(1): 14-16.
- Ashton, F. M. and A. S. Crafts. 1981. Mode of Action of Herbicides. John Wiley and Sons, Toronto.
- Barber, H. W., Jr. 1976. An autecological study of salmonberry (Rubus spectabilis Pursh) in western Washington. Ph. D. Thesis, Univ. of Washington, Seattle, Wash. 154 p.
- Baskerville, G. L. 1961. Response of young fir and spruce to release from shrub competition. Canada Dept. Forestry, Forest Res. Div. Tech. Note No. 98. 14 p.
- Bazzaz, F. H., and J. L. Harper. 1980. Demographic analysis of Linum usitatissimum. New Phytol. 78, 193-208.
- Bella, I. E. 1971. A new competition model for individual trees. Forest Science, 17, 364-372.
- Bernstein, A. 1977. Seven immediate impact consequences of the use of a chainsaw to control brush. Proc. 1977 Western Forestry Conf., Western Forestry and Cons. Assn., Portland, Or., p.

100.

- Bigley, D. and J. P. Kimmins. 1984. Herbicide effects on ecosystem nitrogen loss. Proc. Soc. Am. Foresters 1982 Annual Conv., Soc. Am. Foresters, Washington, D. C. [in press].
- Binkley, D. and P. Reid. 1984. Long-term response of stem growth and leaf area to thinning and fertilization in a Douglas-fir plantation. *Can. J. For. Res.* 14: 656-660.
- Bjorkman, O. and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiol. Plant.* 16: 889-914.
- Boojh, R. and P. S. Ramakrishnan. 1982. Growth strategy of trees related to successional status. I. Architecture and extension growth. *For. Ecol. Manag.* 4: 359-374.
- Bormann, F. H. 1965. Changes in the growth pattern of white pine trees undergoing suppression. *Ecology* 46: 269-277.
- Bormann, F. H. and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York. 253 pp.
- British Columbia Ministry of Forests. 1979. Forest and Range Resource Analysis Technical Report. Prov. of B. C., Ministry of Forests, Information Services Branch, Victoria, B. C. 802 p.
- British Columbia Ministry of Forests. 1984. Basic silviculture, monitoring performance. B. C. Ministry of Forests, Ministry Draft Proposal, Sil-XXX-4.
- Brix, H. 1967. An analysis of dry matter production of Douglas-fir seedlings in relation to temperature and light intensity. *Can. J. Bot.* 45: 2063-2072.
- Brix, H. 1970. Effect of light intensity on growth of western hemlock and Douglas-fir seedlings. *Can. Dept. of Fisheries and Forestry, Bi-Monthly Res. Notes.* 26(4): 1-2.

- Brix, H. 1983. effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. *Can. J. For. Res.* 13: 167-175.
- Brix, H. and A. K. Mitchell. 1983. Thinning and nitrogen fertilization effects on sapwood development and relationships of foliage quantity to sapwood area and basal area in Douglas-fir. *Can. J. For. Res.* 13: 384-389.
- Burdett, A. N., L. J. Herring, and C. F. Thompson. 1984. Early growth of planted spruce. *Can. J. For. Res.* 14: 644-651.
- Carter, G. A., J. H. Miller, D. E. Davis, and R. M. Patterson. 1984. Effects of vegetative competition on the moisture and nutrient status of loblolly pine. *Can. J. For. Res.* 14: 1-10.
- Cleary, B. D., and B. R. Kelpsas. 1981. Five steps to successful regeneration planning. Oregon State University School of Forestry. Forest Research Lab. Special Pub. 1. Corvallis, OR.
- Cody, W. J., and C. W. Crompton. 1975. The biology of Canadian weeds. 15. Pteridium aquilinum (L.) Kuhn. *Can. J. Plant. Sci.* 55: 1059-1072.
- Conard, S. G. and S. R. Radosevich. 1982. Growth responses of white fir to decreased shading and root competition by montane chaparral shrubs. *For. Sci.* 28: 309-320.
- Curtis, J. T., and G. Cottam. 1962. Plant ecology workbook. Burgess Publishing Co., Minneapolis, Minn. 193 pp.
- Del Rio, E. and A. Berg. 1979. Specific leaf area of Douglas-fir reproduction as affected by light and needle age. *For. Sci.* 25: 183-186.
- Drew, A. P. and W. K. Ferrell. 1977. Morphological acclimation to light intensity in Douglas-fir seedlings. *Can. J. Bot.* 55: 2033-2042.

- Drew, J. T. and J. T. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. *For. Sci.* 25: 518-532.
- Dyrness, C. T. 1973. Early stages of plant succession following logging in the Western Cascades of Oregon. *Ecology*, 54: 57-69.
- Eis, S. 1981. Effect of vegetative competition on regeneration of white spruce. *Can. J. For. Res.* 11: 1-8.
- Eissenstat, D. M., and J. E. Mitchell. 1983. Effects of seeding grass and clover on growth and water potential of Douglas-fir seedlings. *For. Sci.* 29: 166-179.
- Ek, A. R. and R. A. Monserud. 1974. Trials with program FOREST: Growth and reproduction simulation or mixed species forest stands. In Fries, J. (ed.) 1974. Growth models for tree and stand simulation. Res. Note No. 30, Dept. of Forest Yield Research, Royal College of Forestry, Stockholm, pp. 56-73.
- Ellenberg, H. and D. Mueller-Dombois. 1967. Tentative physiognomic-ecological classification of plant formations of the earth. *Ber. geobot. Inst. ETH, Stiftg. Rubel, Zurich*, 37: 21-55.
- Evans, G. C. 1972. The quantitative analysis of plant growth. Blackwell Scientific Publications, Oxford.
- Farmer, R. E. Jr. 1980. Comparative analysis of 1st-year growth of six deciduous tree species. *Can. J. For. Res.* 10: 35-41.
- Farrar, J. L. 1961. Longitudinal variation in the thickness of the annual ring. *For. Chron.* 37: 323-330.

- Fiske, J. N. 1982. Evaluating the need for release from competition from woody plants to improve conifer growth rates. [in] Proceedings of the Third Annual Forest Vegetation Management Conf., Redding, Calif.
- Ford, E. D. 1979. An ecological basis for predicting the growth and stability of plantation forests. [in] Ford, E. D., D. C. Malcolm, and J. Attenson. 1979. The ecology of even-aged forest plantations. Institute of Terrestrial Ecology, Cambridge, U.K.
- Ganzlin, W. K. and C. G. Lorimer. 1983. Tests of a rapid field method for evaluating competition around individual trees. Univ. Wisconsin, Dept. of Forestry, Forestry Res. Notes No. 253. 6 pp.
- Gordon, D. T. 1973. Released advance reproduction of white fir ... growth, damage, mortality. United States Dep. Agric. Forest Serv. Pac. S.W. Forest and Range Exp. Sta., Res. Pap. PSW-95, 12 p.
- Granier, A. 1981. Etude des relations entre la section du bois d'aubier et la masse foliaire chez le Douglas (Pseudotsuga menziesii Mirb. Franco). Ann. Sci. For. 38: 503-512.
- Gratkowski, H. 1971. Midsummer foliage sprays on salmonberry and thimbleberry. United States Dept. Agric. Forest Serv. Pac. N.W. Forest and Range Exp. Sta. Res. Note PNW-171, 5 p.
- Green, R. N., P. J. Courtin, K. Klinka, R. J. Slaco, and C. A. Ray. 1984. Site diagnosis, tree species selection, and slashburning guidelines for the Vancouver Forest Region. Province of B. C. Ministry of Forests, Land Management Handbook No. 8, 143 p.
- Greis, I. and S. Kellomaki. 1981. Crown structure and stem growth of Norway spruce undergrowth under varying shading. Silva Fenn. 15: 306-322.
- Grier, C. C., K. M. Lee, and R. M. Archibald. 1984. Effect of urea fertilization on allometric relations in young Douglas-fir trees. Can. J. For. Res. 14: 900-904.

- Grier, C. C. and R. H. Waring. 1974. Conifer foliage mass related to sapwood area. *For. Sci.* 20: 205-206.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, Toronto.
- Halle, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. *Tropical trees and forests: An architectural analysis*. Springer-Verlag, New York. 441 pp.
- Harrington, C. A., and R. L. Deal. 1982. Sitka alder, a candidate for mixed stands. *Can. J. For. Res.* 12: 108-111.
- Harrington, J. B., J. C. Tappeiner II, and J. C. Walstad. 1983. Predicting leaf area and biomass of Tanoak [Lithocarpus densiflorus (Hook. and Arn.)Rehd.] and Pacific Madrone (Arbutus menziessii Pursh) sprout clumps. *Can. J. For. Res.* 14:
- Hegy, F. 1974. A simulation model for managing jack pine stands. {in} Fries, J. (ed.) 1974. *Growth models for tree and stand simulation*. Research Notes #30, Department of Forest Yield Research, Royal College of Forestry, Stockholm. pp. 74-90.
- Hitchcock, C. L. and A. Cronquist. 1973. *Flora of the Pacific Northwest*. Univ. Washington Press, Seattle. 730 pp.
- Horn, H. S. 1971. *The adaptive geometry of trees*. Monographs in Population Biology 3, N. J. Univ. Press, Princeton. 144 pp.
- Horowitz, H. 1977. Manual Alternatives to herbicides - four case studies. *Proc. of the 1977 Western Forestry Conf., Western Forestry and Cons. Assn., Portland, Or.* p. 96.
- Howard, K. M. and M. Newton. 1984. Overtopping by successional coast range vegetation slows Douglas-fir seedlings. *J. For.* 82: 178-180.
- Hunt, R. 1978. *Plant growth analysis*. Studies in biology No. 96. Edward Arnold, London.

Hunt, R. 1982. Plant growth curves. Edward Arnold, London.

Hunt, R. and F. A. Bazzaz. 1980. The biology of Ambrosia trifida L. V. Response to fertilizer, with growth analysis at the organismal and suborganismal levels. *New Phytol.* 84: 113-121.

Inselberg, A. E., K. Klinka, and C. Ray. 1982. Ecosystems of MacMillan Park on Vancouver Island. Province of British Columbia, Ministry of Forests. Land Management Report 12. 113 pp.

Kaufmann, M. R. and C. A. Troendle. 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest species. *For. Sci.* 27: 477-482.

Keller, R. A. and E. B. Tregunna. 1976. Effects of exposure on water relations and photosynthesis of western hemlock in habitat forms. *Can. J. For. Res.* 6: 40-48.

Kellomaki, S. 1981. Growth dynamics of young Scots pine crowns. *Comm. Inst. For. Foun.* 98(4): 1-50.

Kellomaki, S. 1981. Effect of the within-stand light conditions on the share of stem, branch, and needle growth in a twenty-year old Scots pine stand. *Silva Fenn.* 15: 130-139.

Kellomaki, S. and P. Oker-Blom. 1981. Specific needle area of Scots pine and its dependence on light conditions inside the canopy. *Silva Fenn.* 15: 190-198.

Kellman, M. C. 1969. Plant species inter-relationships in a secondary succession in coastal British Columbia. *Syesis* 2: 201-212.

Klinka, K. 1976. Ecosystem units, their classification, interpretation, and mapping in the University of British Columbia Research Forest. Ph. D. thesis, Faculty of Forestry, Univ. of British Columbia, Vancouver, B. C. 622 p.

- Klinka, K. and R. E. Carter. 1980. Ecology and silviculture of the most productive ecosystems for growth of Douglas-fir in Southwestern British Columbia. Land Management Rep. No. 6, B. C. Ministry of Forests, Victoria, B. C. 12 pp.
- Klinka, K., F. C. Nuzsdorfer, and L. Skoda. 1979. Biogeoclimatic units of central and southern Vancouver Island. Prov. of B. C., Ministry of Forests, Victoria, B. C. 120 pp.
- Knight, H. 1957. Growth and survival of experimental plantations of Douglas-fir. British Columbia Dept. Lands and Forests, Forest Service, Res. Notes No. 33.
- Kohyama, T. 1980. Growth pattern of *Abies mariessii* saplings under conditions of open-grown and suppression. Bot. Mag. Tokyo. 93: 13-24.
- Kozlowski, T. T. and R. C. Ward. 1961. Shoot elongation characteristics of forest trees. For. Sci. 7: 358-368.
- Krajina, V. J. 1933. Die Pflanzengesellschaften des Mylnica-Thales in der Vysoke Tatry (Hohe tatra) mit besonderer Beruechsichtigung der oekologischen Verhaeltnisse. Sonderdruck aus den beiheften zum Botanischen Zentralblatt, Band L., Abtlg. II (1. Teil), Band L., Abtlg. II (2. Teil).
- Krajina, V. J. 1965. Biogeoclimatic zones and classification of British Columbia. [in] Krajina, V. J. (ed.) 1965. Ecology of Western North America. Vol. 1: 1-17. Dept. of Botany, Univ. of B. C., Vancouver, B. C.
- Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of Western North America 2(1): 1-146.
- Krajina, V. J., K. Klinka, and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. University of British Columbia, Faculty of Forestry. Vancouver, B. C. 131 pp.

- Kramer, P. J. and T. T. Kozlowski. 1979. *Physiology of Woody Plants*. Academic Press, New York. 811 p.
- Krueger, K. W. and R. H. Ruth. 1968. Comparative photosynthesis of red alder, Douglas-fir, Sitka spruce, and western hemlock. *Can. J. Bot.* 47: 519-527.
- Ledig, F. T. 1974. Concepts of growth analysis. [in] Reed, C. P. P., and G. H. Feschner. (eds). 1974. *Proceedings of the third North American forest biology workshop*. Colorado State University, Fort Collins, Co. pp. 166-182.
- Lewandowska, M. and P. G. Jarvis. 1977. Changes in chlorophyll and carotenoid content, specific leaf area, and dry weight fraction in Sitka spruce, in response to shading and season. *New Phytol.* 79: 247-256.
- Lewis, R. and J. Higdon. 1977. Effect of brush cutting for site preparation and release. *Proc. of the 1977 Western Forestry Conf., Western Forestry and Cons. Assn., Portland, Or.* p. 97.
- Lorimer, C. G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manag.* 6: 343-360.
- Lyons, C. P. 1965. *Trees, shrubs, and flowers to know in British Columbia*. J. M. Dent & Sons, Vancouver, B. C. 194 pp.
- MacLean, D. A. and M. G. Morgan. 1983. Long-term growth and yield responses of young fir to manual and chemical release from shrub competition. *For. Chron.* 59: 177-183.
- Magnussen, V. S. 1983. [Influences of shading grand fir seedlings under different moisture and nutrient regimes] *Allg. Forst- u Jagdztg.* 154: 10-20 [Ge, Eng Summary].

- Magnussen, S., and A. Peschl. 1981. [The influence of shading on the photosynthesis and transpiration of silver and grand fir seedlings.] *Allg. Forst- u. Jagdztg.* 152: 82-92. [Ge. Eng. summary].
- Maillette, L. 1982. Needle demography and growth pattern of Corsican pine. *Can. J. Bot.* 60: 105-116.
- Makela, A., S. Kellomaki, and P. Hari. 1980. Eco-physiological studies on young Scots pine stands. III. Photosynthate allocation for needle growth and wood formation in current year shoots. *Silva Fenn.* 14: 258-263.
- Martin, G. L. and A. R. Ek. 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *Forest Sci.* 30: 731-743.
- Monsi, M. and T. Saeki. 1953. Uber den Lichtsaktor in den Pflanzengesellschaften und seine bedeutung fur die stoffproduction. *Jpn. J. Bot.* 14: 22-52.
- Monteith, J. L. 1965. Light distribution and photosynthesis in field crops. *Ann. Bot.* 29: 17-37
- Moore, J. A., C. A. Budelsky, and R. C. Schlesinger. 1973. A new index representing individual tree competitive status. *Can. J. For. Res.* 3: 495-500.
- Mueller-Dombois, D. 1960. The Douglas-fir forest associations on Vancouver Island in their initial stages of secondary succession. Ph. D. thesis, Dept. of Biology and Botany, University of British Columbia. 570 pp.
- Mueller-Dombois, D. 1965. Initial stages of secondary succession in the coastal Douglas-fir and western hemlock zones. *Ecol. of Western North America.* 1: 38-41.

- Munro, D. D. 1974. Forest stand growth models - A prognosis. [in] Fries, J. (ed.). 1974. Growth models for tree and stand simulation. Res. Notes #30, Dept. Forest Yield Research, Royal College of Forestry, Stockholm.
- Murata, Y. and S. Matsushima. 1975. Rice. [in] Evans, L. T. 1979. Crop Physiology: Some Case Histories. Cambridge Univ. Press, Cambridge.
- Nambiar, E. K. S. and P. G. Zed. 1980. Influence of weeds on the water potential and growth of young radiata pine. Aust. For. Res. 10: 279-288.
- Newton, M. 1973. Environmental management for seedling establishment. For. Res. Lab., Sch. For., Oreg. St. Univ., Corvallis, Res. Paper 16, 5 p.
- Newton, M., B. A. el Hassan, and J. Zavitkovski. 1968. Role of alder in Western Oregon forest succession. IN Biology of alder, ed. Trappe, J. M., et. al. USDA For. Serv., Pac. N. W. For. Range Expt. Sta. 292 pp.
- Newton, M. and F. B. Knight. 1981. Handbook of weed and insect control chemicals for forest resource managers. Timber Press, Beaverton, Or. 213 p.
- Newton, M. and D. E. White. 1983. Effect of salmonberry on growth of planted conifers. Proceedings, West. Soc. Weed Sci. 36: 59-64.
- Orloci, L. 1964. Vegetational and environmental variations in the ecosystems of the Coastal Western Hemlock zone. Ph. D. thesis, University of B.C.
- Oxenham, R. 1983. A study of the effect of competing vegetation and browsing on early plantation performance. Forest Tech. Rep. 5, Nova Scotia Dept. Lands and Forests, Truro, N. S. 6 pp.
- Paterson, J. M. and D. C. F. Fayle. 1984. Early prediction of plantation performance for red pine. For. Chron. 60: 340-344.

- Pearse, P. H. 1976. Timber Rights and Forest Policy in British Columbia. Report of the Royal Commission on Forest Resources, Peter H. Pearse Commissioner. K. M. MacDonald, Victoria, B. C.
- Peterson, T. D. and M. Newton. 1983. Growth of Douglas-fir following release from snowbrush and forbs in the Oregon Cascades. Proceedings, Western Society of Weed Science. 36: 58-59 (Abstr.).
- Radosevich, S. R., E. J. Roncoroni, S. G. Conard, and W. B. McHenry. 1980. Seasonal tolerance of six coniferous species to eight foliage active herbicides. For. Sci. 26: 3-9.
- Radosevich, S. R. and R. G. Wagner. 1983. Interspecific competition indices for vegetation management decisions in young Douglas-fir stands on the Siuslaw National Forest. CRAFTS study plan, Ore. State Univ., College of Forestry, Corvallis. Or.
- Reed, F. L. C. 1978. Forest management in Canada. Env. Canada, Canadian Forestry Service, Forest Management Inst. Inf. Rep. FMR-X-102-1.
- Reed, K. C., J. S. Shumway, R. B. Walker, and C. S. Bledsoe. 1983. Evaluation of the interaction of two environmental factors affecting Douglas-fir seedling growth: Light and nitrogen. For. Sci. 29: 193-203.
- Richards, N. A. 1968. Spruce seedling establishment over a range of soil conditions in an old field at Heiberg Forest. Abstr. of Thesis, [in] TAPPI 51: 372.
- Roberts, C. 1977. Vegetative response to manual brush control. Proc. of the 1977 Western Forestry Conf., Western Forestry and Cons. Assn., Portland, Or. p. 97.
- Roberts, C. 1980. Second year report. Cooperative brush control study. Cathy Roberts, Reforestation Consultant, Corvallis, Or. (Unpub. Doc.) 29 p.

- Ruth, R. H. 1956. Plantation survival and growth in two brush threat areas of coastal Oregon. Pac. NW For. and Range Expt. Sta., USDA For. Serv., Corvallis, Or.
- Schmidt, W. C. 1978. Some biological and physiological responses to forest stand density. Paper presented at the Eighth World Forestry Congress, Jakarta, Indonesia.
- Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964a. A quantitative analysis of plant form - the pipe model theory. I. Basic analysis. *Jap. J. Ecol.* 14: 97-105.
- Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964b. A quantitative analysis of plant form - the pipe model theory. II. Further evidence of the theory and its application in forest ecology. *Jap. J. Ecol.* 14: 133-139.
- Sloan, G. M. 1945. Report of the Commissioner, Hon. Gordon McG. Sloan, relating to the Forest Resources of British Columbia. Charles F. Banfield, Victoria, B. C. 195 p.
- Sloan, G. M. 1956. Report of the Commissioner, Hon. Gordon McG. Sloan, ... Relating to the Forest Resources of British Columbia. Don McDiarmid, Victoria, B. C. 416 p.
- Smith, J. H. G. 1975. Effects of spacing and other factors on growth of planted trees. British Columbia Min. of Forests, Reforestation Notes, Vol 2(2): 8-12.
- Snell, J. A. and J. K. Brown. 1978. Comparison of tree biomass estimators - DBH and sapwood area. *For. Sci.* 24: 455-457.
- Stewart, R. E. 1974. Foliage sprays for site preparation and release from six coastal brush species. U. S. Dept. Agric. Forest Serv. Pac. N. W. Forest and Range Exp. Sta. Res. Pap. PNW-172, Portland, Or., 18 p.
- Stiell, W. M. 1976. White spruce: Artificial regeneration in Canada. Can. Forestry Service, Forest Management Inst. Information Rep. FMR-X-85, 275 p.

- Stiell, W. M. 1969. Crown development in white spruce plantations. Forestry Branch, Can. Dept. of Fisheries and Forestry, Pub. No. 1249. 12 pp.
- Sutton, R. F. 1968. Ecology of young white spruce (Picea glauca (Moench) Voss). Ph. D. thesis, Cornell, Univ. Microfilms, Ann Arbor, Mich.
- Sutton, R. F. 1978. Glyphosate herbicide: An assessment of forestry potential. For. Chron. 54: 24-28.
- Sutton, R. F. 1984. Plantation establishment in the boreal forest: Glyphosate, hexazinone, and manual weed control. For. Chron. 60: 283-287.
- Tomlinson, P. B. 1983. Tree architecture. Am. Scientist. 71: 141-149.
- Tucker, R. E., J. M. Jarvis, and R. M. Waldron. 1968. Early survival and growth of white spruce plantations, Riding Mountain National Park, Manitoba. Ministry of Forestry and Rural Dev., Forestry Branch, Dept. Pub. 1239.
- Turpin, T. 1977. Hand release of young seedlings. Proc. of the 1977 Western Forestry Conf., Western Forestry and Cons. Assn., Portland, Or., p. 97.
- Vincent, A. B. 1954. Release of balsam fir and white spruce reproduction from shrub competition. Department of North. Affairs and Nat. Resources, Silviculture Leaflet No. 100.
- Wagner, R. G. 1982. A method for assessing severity of weeds in young plantations. Paper presented at: The use of herbicides in forest vegetation management. CRAFTS, Univ. of Oregon, Dept. For. Sci., Corvallis, Ore. 13 pp.
- Waring, R. H., P. F. Schroeder, and R. Oren. 1982. Application of the pipe-model theory to predict canopy leaf area. Can. J. For. Res. 12: 556-560.

Weed Science Society of America. 1979. Herbicide Handbook, 4th ed. Weed Science Soc. of America, Champagne, Ill. pp. 224-228.

Wilde, S. A. 1971. Weeds and treeplanting. Treeplanters Notes 21(1): 24-26.

Zedaker, S. M. 1982. Growth and development of young Douglas-fir in relation to intra- and inter-specific competition. Ph. D. Thesis, Oregon St. Univ., Univ. Microfilms, Ann Arbor, Mich.

Zimmermann, M. L. and C. L. Brown. 1971. Trees Structure and Function. Springer-Verlag, New York. 336 p.

Erigeron strigosus	Pres.	- , I	- , -	- , -	- , -	- , -	- , -	- , -
	Height	- , 0.8	- , -	- , -	- , -	- , -	- , -	- , -
	LAI	- , -	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , 1	- , -	- , -	- , -	- , -	- , -	- , -
	Dom.	0 , 1	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0
Verbascum thapsus	Pres.	- , I	- , -	- , -	- , -	- , -	- , -	- , -
	Height	- , 1.4	- , -	- , -	- , -	- , -	- , -	- , -
	LAI	- , -	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , 0	- , -	- , -	- , -	- , -	- , -	- , -
	Dom.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0

 II Grasses

Poa Spp.	Pres.	I , I	I , I	I , -	I , -	I , -	- , -
	Height	0.8, 0.5	0.7, 0.7	0.7, -	0.8, -	0.3, -	- , -
	LAI	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	9, 2	0, 1	2, -	2, -	5, -	- , -
	Domin.	7, 1	0, 0	1, -	1, -	1, -	- , -
	Compet.	- , -	- , -	- , 0	- , 0	- , 0	0 , 0
Bromus spp.	Pres.	- , I	- , I	- , -	- , -	- , -	- , -
	Height	- , 0.6	- , 0.9	- , -	- , -	- , -	- , -
	LAI	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , 2	- , 2	- , -	- , -	- , -	- , -
	Domin.	0 , 1	- , 2	0 , 0	0 , 0	0 , 0	0 , 0
	Compet.	0 , -	0 , -	0 , 0	0 , 0	0 , 0	0 , 0
Elymus spp.	Pres.	- , -	- , -	- , I	- , I	- , -	- , -
	Height	- , -	- , -	- , 1.4	- , 1.6	- , -	- , -
	LAI	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , -	- , -	- , 1	- , 1	- , -	- , -
	Domin.	0 , 0	0 , 0	0 , 1	0 , 1	0 , 0	0 , 0
	Compet.	0 , 0	0 , 0	0 , -	0 , -	0 , 0	0 , 0

 III - Ferns

Pteridium aquilinum	Pres.	I , II	- , III	II , II	IV, III	III, IV	I , II
	Height	0.7, 0.7	- , 1.1	1.1, 1.1	0.9, 0.9	1.3, 1.4	0.8, 0.6
	LAI	1.3, -	- , -	1.2, -	1.3, -	1.7, -	- , -
	% Cover	9, 3	- , 6	13, 13	24, 24	27, 22	1, 1
	Domin.	6, 2	0, 7	14, 14	22, 22	35, 31	1, 1
	Compet.	54, -	0, -	51, -	48, -	85, -	- , 0
Polystichum munitum	Pres.	- , -	- , -	- , -	- , I	I , -	I , II
	Height	- , -	- , -	- , -	- , 0.6	0.6, -	0.6, 0.6
	LAI	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , -	- , -	- , -	- , 2	1, -	0, 2
	Domin.	0 , 0	0 , 0	0 , 0	0 , 1	0 , 0	0 , 1
	Compet.	0 , 0	0 , 0	0 , 0	0 , -	- , 0	- , -
Athyrium felix-femina	Pres.	- , -	- , -	II , I	I , III	- , -	- , -
	Height	- , -	- , -	1.3, 0.7	1.0, 1.0	- , -	- , -
	LAI	- , -	- , -	1.3, -	1.0, -	- , -	- , -
	% Cover	- , -	- , -	12, 1	5, 3	- , -	- , -
	Domin.	0 , 0	0 , 0	15, 0	5, 3	0 , 0	0 , 0
	Compet.	0 , 0	0 , 0	49, -	38, -	0 , 0	0 , 0

IV - Canes

Rubus	Pres,	IV, V	V, V	V, V	- , -	1, III	IV, IV
parviflorus	Height	0.7, 0.9	0.8, 0.9	0.7, 1.0	- , -	0.7, 1.0	1.4, 1.6
	LAI	2.0, -	1.7, -	1.7, -	- , -	2.1, -	3.2, -
	% Cover	33, 38	55, 50	34, 40	- , -	9, 11	49, 29
	Domin.	23, 34	44, 45	24, 40	0 , 0	6, 11	69, 46
	Compet.	82, -	92, -	57, -	0 , 0	90, -	207, -
Rubus	Pres.	- , -	- , -	I , II	IV, IV	IV, IV	- , -
spectabilis	Height	- , -	- , -	0.5, 0.8	0.7, 1.1	0.9, 1.1	- , -
	LAI	- , -	- , -	1.2, -	1.5, -	1.5, -	- , -
	% Cover	- , -	- , -	2, 4	20, 25	14, 8	- , -
	Domin.	0 , 0	0 , 0	3, 3	14, 27	13, 9	0 , 0
	Compet.	0 , 0	0 , 0	31, -	47, -	30, 0	0 , 0
Rubus	Pres.	- , -	- , -	- , -	- , -	- , -	II, -
leucodermis	Height	- , -	- , -	- , -	- , -	- , -	1.6, -
	LAI	- , -	- , -	- , -	- , -	- , -	1.7, -
	% Cover	- , -	- , -	- , -	- , -	- , -	4, -
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	6, 0
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	17, 0
Rubus	Pres.	- , -	- , -	- , II	I , -	- , -	- , -
laciniatus	Height	- , -	- , -	- , 1.1	1.2, -	- , -	- , -
	LAI	- , -	- , -	- , -	0.6, -	- , -	- , -
	% Cover	- , -	- , -	- , 1	1, -	- , -	- , -
	Domin.	0 , 0	0 , 0	0 , 1	1, 0	0 , 0	0 , 0
	Compet.	0 , 0	0 , 0	0 , -	1, 0	0 , 0	0 , 0
Ribes	Pres.	- , -	- , -	- , -	- , I	- , -	- , I
lacustre	Height	- , -	- , -	- , -	- , 0.7	- , -	- , 2.8
	LAI	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , -	- , -	- , -	- , 1	- , -	- , 2
	Domin.	0 , 0	0 , 0	0 , 0	0 , 1	0 , 0	0 , 4
	Compet.	0 , 0	0 , 0	0 , 0	0 , -	0 , 0	0 , -
Sambucus	Pres.	- , -	- , -	- , -	- , -	- , -	I , II
pubens	Height	- , -	- , -	- , -	- , -	- , -	2.3, 2.3
	LAI	- , -	- , -	- , -	- , -	- , -	0.6, -
	% Cover	- , -	- , -	- , -	- , -	- , -	2, 6
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	6, 14
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	11, -
Sambucus	Pres.	I , II	I , I	- , II	I , -	- , I	- , -
racemosa	Height	1.1, 1.4	1.4, 1.8	- , 1.4	0.7, -	- , 1.5	- , -
	LAI	1.2, -	1.8, -	- , -	0.3, -	- , -	- , -
	% Cover	7, 2	2, 1	- , 2	2, -	- , 1	- , -
	Domin.	8, 3	3, 2	0 , 3	1, 0	0 , 1	0 , 0
	Compet.	41, -	35, -	0 , -	6, 0	0 , -	0 , 0

V - Low Woody Shrubs

Vaccinium parvifolium	Pres.	- , -	- , -	- , -	- , -	- , -	I , I	- , -
	Height	- , -	- , -	- , -	- , -	- , -	1.1, 1.5	- , -
	LAI	- , -	- , -	- , -	- , -	- , -	2.5, -	- , -
	% Cover	- , -	- , -	- , -	- , -	- , -	1, 6	- , -
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	1, 9	0 , 0
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	25, -	0 , 0
Symphoricarpus albus	Pres.	I , -	- , -	- , -	- , -	- , -	- , -	- , -
	Height	0.6, -	- , -	- , -	- , -	- , -	- , -	- , -
	LAI	0.3, -	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	1, -	- , -	- , -	- , -	- , -	- , -	- , -
	Domin.	1, 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0
	Compet.	2, 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0

VI. Naturally Established Conifers

Tsuga heterophylla	Pres.	- , -	- , -	- , -	- , I	I , I	- , I
	Height	- , -	- , -	- , -	- , 1.0	0.7, 0.8	- , 3.0
	LAI	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , -	- , -	- , -	- , 0	1, 0	- , 1
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	1, 0	0 , 3
	Compet.	0 , 0	0 , 0	0 , 0	0 , -	- , -	0 , -
Pseudotsuga menziesii	Pres.	- , -	- , -	- , -	- , -	- , -	- , I
	Height	- , -	- , -	- , -	- , -	- , -	- , 2.8
	LAI	- , -	- , -	- , -	- , -	- , -	- , -
	% Cover	- , -	- , -	- , -	- , -	- , -	- , 2
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 6
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , -

VI - High Woody Shrubs - Sprouting

Acer macrophyllum	Pres.	- , -	I , -	- , -	- , -	I , I	I , II
	Height	- , -	1.5, -	- , -	- , -	1.1, 7.0	4.0, 4.0
	LAI	- , -	3.6, -	- , -	- , -	2.5, -	3.1, -
	Percent	- , -	2, -	- , -	- , -	1, 6	6, 14
	Domin.	0 , 0	3, 0	0 , 0	0 , 0	2, 42	24, 56
	Compet.	0 , 0	90, 0	0 , 0	0 , 0	25, -	139, 0
Acer circinatum	Pres.	I , I	- , III	- , -	I , I	III, III	- , -
	Height	0.5, 0.6	- , 1.1	- , -	0.8, 0.8	1.4, 1.9	- , -
	LAI	0.4, -	- , -	- , -	3.0, -	3.6, -	- , -
	% Cover	0, 3	- , 11	- , -	0, 1	9, 12	- , -
	Domin.	0, 2	0 , 13	0 , 0	0, 1	13, 23	0 , 0
	Compet.	2, -	0 , -	0 , 0	15, -	72, -	0 , 0

VII - High Woody Shrubs - Non-Sprouting

Alnus rubra	Pres.	- , -	I , I	II, IV	IV, III	I , -	- , I
	Height	- , -	1.1, 1.8	0.9, 1.7	1.1, 2.0	1.8, -	- , 3.4
	LAI	- , -	1.9, -	1.5, -	1.3, -	1.8, -	- , -
	% Cover	- , -	3, 3	4, 15	15, 20	1, -	- , 2
	Domin.	0 , 0	3, 5	4, 29	16, 40	2, 0	0 , 7
	Compet.	0 , 0	16, -	16, -	28, -	18, 0	0 , -
Betula papyrifera	Pres.	- , I	- , I	- , -	- , II	I , II	I , II
	Height	- , 2.4	- , 1.4	- , -	- , 0.9	1.5, 1.7	2.2, 2.6
	LAI	- , -	- , -	- , -	- , -	0.3, -	0.8, -
	% Cover	- , 0	- , 1	- , -	- , 2	1, 2	3, 4
	Domin.	0 , 0	0 , 1	0 , 0	0 , 2	2, 4	7, 9
	Compet.	0 , -	0 , -	0 , 0	0 , -	0, -	20, -
Salix spp.	Pres.	- , -	- , -	I , -	- , -	I , I	- , -
	Height	- , -	- , -	1.0, -	- , -	1.0, 0.9	- , -
	LAI	- , -	- , -	0.4, -	- , -	0.4, -	- , -
	% Cover	- , -	- , -	0, -	- , -	0, 0	- , -
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0
	Compet.	0 , 0	0 , 0	6 , 0	0 , 0	0 , -	0 , 0
Prunus emarginata	Pres.	- , -	- , -	- , -	- , -	- , I	I , I
	Height	- , -	- , -	- , -	- , -	- , 4.0	3.5, 5.0
	LAI	- , -	- , -	- , -	- , -	- , -	1.2, -
	% Cover	- , -	- , -	- , -	- , -	- , 3	2, 4
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 12	7, 20
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , -	24, -
Rhamnus purshiana	Pres.	- , -	- , -	- , -	- , -	I , I	- , -
	Height	- , -	- , -	- , -	- , -	2.1, 2.9	- , -
	LAI	- , -	- , -	- , -	- , -	0.7, -	- , -
	% Cover	- , -	- , -	- , -	- , -	1, 2	- , -
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	2, 6	0 , 0
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	7, -	0 , 0

note: presence classes - I 0-20% II 21-40% III 41-60% IV 61-80
V 81-100%

VII - High Woody Shrubs - Non-Sprouting

Alnus rubra	Pres.	- , -	I , I	II, IV	IV, III	I , -	- , I
	Height	- , -	1.1, 1.8	0.9, 1.7	1.1, 2.0	1.8, -	- , 3.4
	LAI	- , -	1.9, -	1.5, -	1.3, -	1.8, -	- , -
	% Cover	- , -	3, 3	4, 15	15, 20	1, -	- , 2
	Domin.	0 , 0	3, 5	4, 29	16, 40	2, 0	0 , 7
Betula papyrifera	Compet.	0 , 0	16, -	16, -	28, -	18, 0	0 , -
	Pres.	- , I	- , I	- , -	- , II	I , II	I , II
	Height	- , 2.4	- , 1.4	- , -	- , 0.9	1.5, 1.7	2.2, 2.6
	LAI	- , -	- , -	- , -	- , -	0.3, -	0.8, -
	% Cover	- , 0	- , 1	- , -	- , 2	1, 2	3, 4
Salix spp.	Domin.	0 , 0	0 , 1	0 , 0	0 , 2	2, 4	7, 9
	Compet.	0 , -	0 , -	0 , 0	0 , -	0 , -	20, -
	Pres.	- , -	- , -	I , -	- , -	I , I	- , -
	Height	- , -	- , -	1.0, -	- , -	1.0, 0.9	- , -
	LAI	- , -	- , -	0.4, -	- , -	0.4, -	- , -
Prunus emarginata	% Cover	- , -	- , -	0, -	- , -	0, 0	- , -
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0	0 , 0
	Compet.	0 , 0	0 , 0	6 , 0	0 , 0	0 , -	0 , 0
	Pres.	- , -	- , -	- , -	- , -	- , I	I , I
	Height	- , -	- , -	- , -	- , -	- , 4.0	3.5, 5.0
Rhamnus purshiana	LAI	- , -	- , -	- , -	- , -	- , -	1.2, -
	% Cover	- , -	- , -	- , -	- , -	- , 3	2, 4
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	0 , 12	7, 20
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	0 , -	24, -
	Pres.	- , -	- , -	- , -	- , -	I , I	- , -
Rhamnus purshiana	Height	- , -	- , -	- , -	- , -	2.1, 2.9	- , -
	LAI	- , -	- , -	- , -	- , -	0.7, -	- , -
	% Cover	- , -	- , -	- , -	- , -	1, 2	- , -
	Domin.	0 , 0	0 , 0	0 , 0	0 , 0	2, 6	0 , 0
	Compet.	0 , 0	0 , 0	0 , 0	0 , 0	7, -	0 , 0

note: presence classes - I 0-20% II 21-40% III 41-60% IV 61-80
V 81-100%