

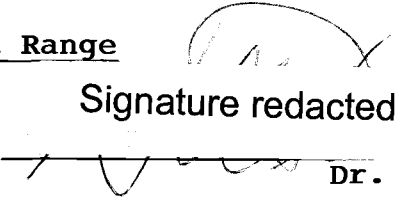
AN ABSTRACT OF THE THESIS OF

Elisabeth H. Kaiser for the degree of Master of Science
in Forest Science presented on May 30, 1986.

Title: The Influence of Stand Structure and Topography
on Growth, Leaf Area, and Efficiency of Young Douglas-fir
in the Oregon Coast Range

Signature redacted for privacy.

Abstract approved:


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The relative influences of stand structure and topographic variation on volume growth, photosynthetic surface area, and stem growth efficiency were determined for six 17 to 23 year old well stocked stands in the central Oregon Coast Range. Plots were assigned to topographic classes (aspect, slope steepness, and slope position), by which stand density, stand growth and efficiency, and individual tree size and growth were compared. Plots were also assigned to classes according to the hardwood content and the same characteristics compared. In addition, individual trees were assigned to and compared by crown dominance classes. Multiple regression analyses were performed to show correlations of growth and efficiency variables with stand structure and topography variables.

Results showed that not only stocking levels but also stand structure influence both stand and individual tree volume growth and efficiency. At a given Relative

Density, stands with a lower stem density of large trees grew more volume and were more efficient than stands with many small trees. In addition, stands with more variation in tree size were more efficient than were more uniformly sized stands. The effect of stand structure overrode the effect of topography on growth and efficiency with two exceptions: stand volume growth and efficiency were higher on southerly than on northerly aspects and in areas of higher rainfall. In these areas, stands of a given density carried more leaf area, which may help to explain why growth was better there.

In the regression analyses, stand volume growth correlated positively with Douglas-fir stand basal area, average annual rainfall, Relative Density, and an aspect variable that indicated better growth on southerly aspects. Stand volume growth correlated negatively with stem density of Douglas-fir. Stand leaf area correlated positively with stand basal area, average annual rainfall, stem density, and south aspects. Stand stem growth efficiency (volume growth per unit of leaf area) correlated positively with Relative Density, individual tree size variance, and southerly aspects, and correlated negatively with stem density and leaf area.

Individual tree growth was mostly determined by the tree basal area, although there was a small negative

effect of increasing stand basal area. The more dominant a tree was in a stand the greater was its growth, but suppressed trees were the most efficient, whether efficiency was calculated in terms of stem volume growth per unit individual tree leaf area or basal area growth per unit individual tree basal area.

The presence of hardwoods of the small size and low densities in this study had no effect on absolute growth, however Douglas-fir grew more efficiently in pure stands than when mixed with hardwoods.

The Influence of Stand Structure and Topography
on Growth, Leaf Area and Efficiency
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by

Elisabeth H. Kaiser

A THESIS

submitted to

Oregon State University

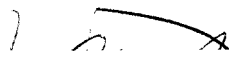
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THE INFLUENCE OF STAND STRUCTURE AND TOPOGRAPHY ON GROWTH,
LEAF AREA, AND EFFICIENCY OF DOUGLAS-FIR IN THE
OREGON COAST RANGE

INTRODUCTION

Mountainous terrain presents a range of microclimates that can vary in a complex manner over short distances. Forest vegetation responds to these variations through changes in composition and probably in productivity, although the influence of local site variation on the latter has seldom been documented. Forest productivity clearly varies over broad environmental gradients and is likely to respond to local differences among microclimates as well.

For this study I related leaf areas and volume growth of stands and individual trees to stand structure and topographic variables on one National Forest district in the Oregon Coast Range. I also examined growth variables between stands with and without hardwoods and among size classes of Douglas-fir within a given stand.

My objectives were to determine a) whether growth differs by topography (aspect, slope, slope position) and if so, whether differences in leaf area and/or efficiency of leaf use are responsible; b) whether differences can be explained by expected effects of site differences on tree physiology; and c) whether effects of topography can be

separated from those of stand structure.

I hypothesized that growth would be affected by topography differently according to whether water or light is more limiting. If water is more limiting than light, better growth on north aspects and in lower slope positions is expected, and possibly on gentle slopes if soils are deeper and less rapidly drained there. No aspect * slope interaction is expected.

If light is the most important limiting factor, better growth on south slopes is expected, and aspect * slope interaction is likely. More variability in tree and crown sizes may result in increased efficiency of leaf use. Lower slopes are expected to grow less.

I also hypothesized that, over the range of leaf areas studied, annual growth per hectare would not differ, and stand growth efficiency would correlate negatively with leaf area.

The productivity of a forest site depends in part on its ability to accumulate leaf area (Schroeder et al. 1982, Tappeiner et al. 1982, Binkley and Reid 1984) and, when expressed in terms of stem volume growth, on the amount of photosynthate allocated to stemwood (Keyes and Grier 1981). The generally positive relationship between stem volume growth and stand leaf area, found both in comparisons of different sites and of different treatments on similar sites, indicates that the forest

photosynthetic capacity is the ultimate determinant of growth. The amount of leaf area carried by a fully stocked stand has been related to the developmental stage (Turner and Long 1975) and to various environmental factors : site water balance, air temperatures (Gholz et al. 1976, Grier and Running 1978, Gholz 1982), and available nutrients (Waring 1983).

Nitrogen in particular often limits forest leaf area, which is demonstrated when leaf area increases substantially after stands are fertilized (Brix 1981, Binkley and Reid 1984). In one study in which young Scots pine were fertilized annually with nitrogen, after 6 years treated stands held up to twice as much needle dry weight as did control stands (Albrektson 1977).

Seasonal moisture stress causes potential photosynthesis to fall below that predicted by annual cumulative radiation and temperatures, even on the west side of the Coast Range (Fujimori 1971, Emmingham and Waring 1977). Stemwood production is affected even more: in one study, an increase in water stress decreased the rate of photosynthesis but had an even greater effect on diameter growth, indicating a change in allocation from stemwood to roots (Brix 1972).

Because stem growth is a low priority for carbon allocation (Gordon and Larson 1968), the ratio of stem growth to leaf area is a reflection of environmental

harshness and/or competition. This ratio, known as stem growth efficiency, is therefore a valuable index of environmental conditions, especially when the effects of competition can be eliminated.

Changes in growth and efficiency that occur in a uniform environment as a result of different stocking levels (and therefore leaf areas) were demonstrated in a study on the east side of the Oregon Coast Range (Waring et al. 1981). At low stand leaf areas individual tree growth and efficiency were high but total stand growth was below its potential. At increasingly higher stem and leaf area densities, individual growth and efficiency decreased linearly while total stand growth increased, then leveled off. At very high densities net stand growth fell off in the control stands due to mortality. Thus the effect of increasing stocking was to divide the stands' production over more individuals while total growth remained fairly constant over a range of stocking. Constant yields over a wide range of stocking, a phenomenon known variously as the "law of constant final yield" or (in forestry) as Langsaeter's relation, have been widely documented both in agronomic plants and in trees (Harper 1977, Perry 1985).

The response of trees and stands to increasing competition has recently been demonstrated with the Relative Density Index (Drew and Flewelling 1979). The

value of the index is the ratio of actual stand density to the theoretical maximum that is attainable by a stand with the same mean tree volume. Important stages of Douglas-fir stand development correspond to values of the index as follows: crown closure occurs around Relative Density of density but individual tree growth declines; between .40 and .55 stand growth is independent of density and individual tree growth continues to decline; and above .55 net growth may decline because of mortality. Recommended densities for managed stands are between .40 and .55.

Topographic Influences on Environment and Stand Character

Topography affects microclimate through differences in radiant energy, precipitation, soil depth, and air and soil temperatures. These factors influence the type of vegetation growing on an area, which in turn determines the substrate quality of detritus and thus the rate of nutrient cycling (Fogel and Cromack 1977, Charley and Richards 1983). Differences in nutrient cycling may cause further divergence of the vegetation (Lee and Sypolt 1974, Keyes and Grier 1981, Hicks and Frank 1984). Soils of uniform origin may differ by topography. Steep slopes often have shallow, rocky soil with low nutrient content and water-holding capacity, whereas flat areas tend to

have deeper, more fertile soil which has been deposited there due to erosion of steep areas. Soil may also differ by aspect. In a study of a mixed hardwood forest in West Virginia, Hicks and Frank (1984) found that the upper soils on north slopes were richer in nutrients made available through decomposition, while south slopes had more of those made available through soil weathering. They reasoned that the litter stayed moister and therefore decayed faster on the north slopes. On south slopes, where the litter dried out and built up, weathering was the more active process. The standing biomass and species importance of trees in these sites correlated well with aspect.

In another West Virginia study, Lee and Sypolt (1974) found that the soil at 15 cm depth on south slopes was cooler during the day and warmer at night than that on the north slopes. They speculated that this was due to the insulating properties of the built-up litter, and that greater growth on north slopes was due to better moisture availability (even though rainfall is frequent during the growing season) and lower canopy temperatures, so water stress on north slopes was lower. Similar studies have not been done in western North America. Grier and Logan (1977) found forest floor thickness to be strongly influenced by topography and vegetation in old-growth

Douglas-fir in the Oregon Cascades but there was no simple relationship to aspect, although soil temperatures were greater on south aspects year round and air temperatures were greater on south aspects in summer. Litter was thin on very steep slopes simply because it rolled onto flatter areas below. Fogel and Cromack (1977) found that the rate of litter decomposition correlated negatively with maximum plant moisture stress and temperature growth index in old-growth Douglas-fir in the Oregon Cascades, indicating that moisture limits microbial activity on these sites.

The difference in effective radiation between north and south slopes is not simple to estimate. At the latitude of stands in this study, steep north slopes get no direct winter sun at noon, while moderate south aspects get the most direct radiation year round (Lee 1978). Moderate south slopes here receive about twice as much direct solar radiation annually as north slopes of the same inclination, and the difference increases with increasing steepness (Buffo et al. 1972). Differences in actual energy input are closer than this, however, because of diffuse sky radiation, which is incident on all aspects equally. In cloudy oceanic climates, such as those of this study, it can be a high proportion of the total radiation received by a site, reducing the effect of aspect on vegetation (Bannister 1976). For example, during summer in England diffuse light accounts for about 60 per

cent of the total light falling on a horizontal surface in the open (Hughes 1966). Geiger (1966) reports an experiment done in Germany in which comparisons were made of total radiation, including diffuse, and direct radiation expected from sun position and slope angle of the ground. In December, north slopes with a slope of 66 per cent were expected to receive 2 per cent and in June about 73 per cent of the radiation on an equivalent south slope. Actual measurements showed values of about 32 per cent in winter and 94 per cent in summer. Because it is also more uniformly distributed through the canopy than direct radiation, canopy photosynthetic rates are higher for a given flux density of diffuse radiation than for an equal level of direct radiation (Sinclair 1975).

In forests that are structurally similar the effect of net radiation on transpiration and evaporation is small because they are most affected by the regional vapor pressure deficit, which does not differ greatly by aspect (Kaufmann 1983, McNaughton and Jarvis 1983). The respiration rate of leaves, however, correlates closely with the mean illumination they receive (Kira et al. 1969) and so may be quite different on different aspects during some periods. In Grier and Logan's (1977) study of old-growth Douglas-fir communities, an estimated 70 per cent of the plant communities' respiration came from foliage.

The build-up of respiratory tissue causes a significant reduction in a site's productivity as maintenance costs become higher (Waring and Schlesinger 1985).

A study of thermal emissions from stands in the Andrews Experimental Forest in the Oregon Cascades, where data were taken at mid-day on a clear July day, showed Douglas-fir stands 13 to 25 years old had 3.5 degrees C higher heat emittance from south slopes than from north slopes, the emittance from east and west slopes being intermediate (Sader 1984). Flat areas were about 3 degrees cooler than slopes greater than 15% slopes. This indicates that the canopies of young stands approaching maximum leaf area do heat up more on sloping south aspects, which probably affects their respiration rates.

A number of studies have been done in the Pacific Northwest relating forest growth to site factors including topography, soil characteristics, and precipitation. In these studies Site Index (height of dominant trees at a given age) has been the most commonly used measure of site quality, rather than total yield, for several reasons, among these that height growth tends to vary much less with stocking level than does diameter growth, and that height growth of most conifers correlates with total volume growth of fully stocked stands (Urie 1959).

Results of Site Index : site factor studies have usually shown Site Index to be higher on north aspects

than on south, although Site Index tends to be more variable on south aspects (Lemmon 1955, Urie 1959, McArdle et al. 1961, Youngberg and Ellington 1982). Hill et al. (1948) found that north aspects were only superior on certain soil types. A study of soil-site relationships was carried out on the Mapleton Ranger District (the locale of my study) by Youngberg and Ellington (1982). They found a rather loose relationship between height growth and site factors; in regressions in which topographic factors were included as independent variables, only 25 per cent of the observed variation in Site Index was explained. In their regression equations, aspect and elevation each had negative coefficients, indicating lower Site Index on south slopes and at higher elevations. Soil series and understory plant community were the best predictors of Site Index, accounting for about 40 per cent of the observed variation.

Studies in other areas of North America have shown Site Index of various species to decrease with increasing slope steepness on south aspects, and not to differ or to increase with increasing slope steepness on north aspects (Stage 1976, Tajchman 1983). Site Index correlated positively with slope steepness in one study in the Oregon Coast Range (Urie 1959) and negatively in a study in the Willamette Basin (Lemmon 1955). Steep slopes

and south aspects cause decreased growth when they combine with shallow soil that has poor moisture retaining capabilities. Soil depth was found to correlate positively with Site Index in several studies in the Pacific Northwest (Hill 1948, Carmean 1954, Lemmon 1955, McArdle et al. 1961, Youngberg and Ellington 1982), while Tarrant (1950) found that, within a soil type in one county in Washington state, height growth was better on concave than on convex topography. However, flat and concave areas where drainage is poor support stands of lower Site Index in the Oregon Coast Range (Urie 1959). Site Index is often high in lower slope positions, probably because of water and nutrient input from upslope, also, nitrogen levels may be high in these positions due to the presence of alder.

The optimum aspect for basal area growth may be different than that for height growth. In the Rocky Mountain region, Stage (1976) reported that, although height growth of several species, including Douglas-fir, was best on northeast aspects, diameter growth was best on southerly aspects. In Youngberg and Ellington's (1982) study on the Mapleton Ranger District, both of the basal area growth indexes they used indicated better basal area growth on south aspects, although the effect was not statistically significant. In a previous study that included 5 of the 6 stands used in my study (Perry 1984), the ratio of current to previous basal area growth (a

measure of the change in growth over time) was analyzed with respect to topography. In plots that had never been thinned the variable correlated positively with adjusted aspect, indicating that growth was better on south aspects. There was a negative correlation with aspect X slope interaction, which probably means that there is a reduction in growth on very steep south aspects.

Leaf Area : Sapwood Area Relationships

Accurate estimates of leaf areas are needed in order to study the physiological basis of forest productivity. Because direct sampling is time consuming and requires destructive methods, indirect methods have been sought. A linear relationship between leaf area and sapwood cross-sectional area has been found for a number of tree species, and several authors have suggested that, although the relationship differs by species, a single leaf area : sapwood area ratio may apply for a species over a variety of sites and treatments (Grier and Waring 1974, Kaufmann and Troendle 1981, Whitehead et al. 1984, Blanche et al. 1985). These generalized relationships have been used in numerous studies to estimate leaf areas from sapwood areas, most often calculated from cores taken at breast height.

Water flow theory, however, suggests that the

leaf area : sapwood area relationship may well differ under different environmental conditions, and possibly by individual tree dominance status, as a physiological balance is maintained between available water and transpiration demand within the tree (Whitehead 1978, Whitehead and Jarvis 1981). In some cases it appears the relationship may vary by site and stand treatment (Brix and Mitchell 1983, Albrektson 1984, Espinosa 1985) and therefore the use of a universal leaf area : sapwood area relationship may lead to errors (Binkley 1984). It is usually assumed that a single relationship holds well for different trees on a given site but this has not been well tested. Snell and Brown (1978) found in one area that regressions for large trees greatly overestimated leaf areas for small trees. The inclusion of sapwood permeability into the relationship may help to normalize between-site and even between-species differences (Whitehead et al. 1984).

Estimating leaf area from sapwood area at the base of the live crown, as I did, rather than at breast height eliminates errors due to sapwood taper (Long et al. 1981, Waring et al. 1982) but probably doesn't correct for different relationships caused by environmental differences. Because I used a single equation to calculate leaf areas and efficiency in this study,

differences between sites on different topography may be either obscured or overemphasized.

STUDY AREA

The study was conducted on the Mapleton District of the Siuslaw National Forest, on the west slope of the Oregon Coast Range at about 44 degrees north latitude. Winters are mild and wet while summers are warm and dry. Elevation of the units ranges from about 50 to 460 m. Plot locations, along with isolines of average annual precipitation, are shown in Figure 1. Average annual rainfall, more than 90 per cent of which falls from September to May, increases from about 220 cm at lower elevations to 270 cm at higher elevations (Franklin and Dyrness 1973, Hemstrom and Logan 1984). Soils tend to be deep on gentle slopes and benches and may be shallow and rocky on steep slopes. Soils are generally well drained except where slumps have disrupted subsurface drainage, causing water to accumulate on benches in wet periods.

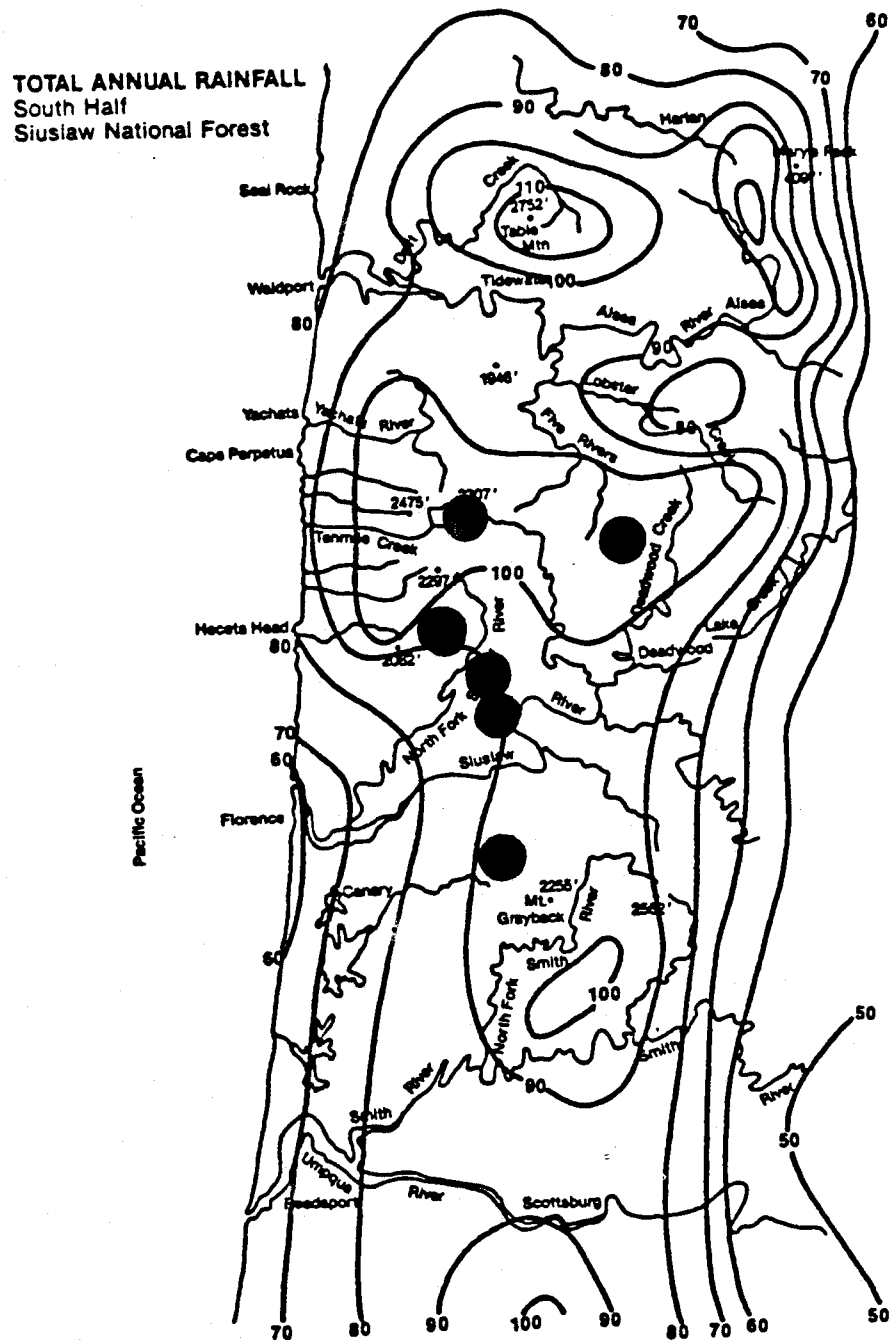


Figure 1. Annual total precipitation (in inches), Siuslaw National Forest (U.S. Dept. of Commerce), and plot locations

METHODS

Stand and Plot Selection

Selection of stands for use in this study was made with the help of Forest Service personnel. The requirements were that the stands be unthinned, around 20 years old, and overstocked (which for this purpose meant that there were more than about 700 trees per hectare, which is the density that would be left after thinning to Forest Service stocking guidelines in a stand with trees the size of these). Six stands were selected, five of them north of the Siuslaw River and one south of the river. Records on the Forest Service TRI system list the stands north of the river as Site Class 2 and the stand south of the river as Site Class 3. Stands were planted after the original stands were clearcut and burned, with the exception of one which was aeriually seeded. Stand ages range from 17 to 23 years from seed.

For purposes of a future study, plots were established in pairs on uniform topography so that the two members of each pair were as similar to each other as possible with regard to aspect, slope per cent, and slope position. One plot in each pair was thinned.

Potential plot sites within the selected stands were identified from aerial photos. Areas well-stocked

with conifers, with few hardwoods, and with terrain uniform enough to fit a pair of plots were identified as potential plot sites. These were then checked on the ground, and plots installed on suitable sites. Disease pockets and large canopy openings were avoided. A total of 68 plots, or 34 plot pairs, were established.

Field Procedures

Square 1/120 hectare plots were established during the summer of 1984. Diameter at breast height (1.4 m) was measured on each tree on the plot. Crop trees were selected on each plot as though it would be thinned to a spacing that would leave approximately 500 to 700 trees per hectare, which equalled 4 to 6 crop trees per plot. Two increment cores, 90 degrees from one another, were taken at breast height from each crop tree and 5 randomly chosen noncrop trees ("excess trees") on the plot. (Trees smaller than 7.5 cm were only cored once.) We recorded sapwood radius, current radial growth, yearly growth for the past 5 years, and complete wood radius of each core. The sapwood radius was determined using a 10% ferric chloride stain, which turns the heartwood black (Kutscha and Sachs 1962).

Sapwood radii at the base of the live crown were measured on trees felled on thinned plots in order to

establish a relationship between sapwood area at breast height and at the base of the live crown (defined as the first whorl in which the live crown extended at least three quarters of the way around the bole). The distance from the ground to the bottom of the live crown was estimated to the nearest meter on all cored trees.

Plot locations were chosen to minimize the number of hardwoods (red alder, Alnus rubra Bong.; cascara buckthorn, Rhamnus purshiana DC.; and bitter cherry, Prunus emarginata, (Dougl.) Walpers) within or adjacent to the plot boundaries. It was impossible to avoid them completely though, and 42 of the 68 plots had some hardwood component. Plots with and without hardwoods were analyzed separately and growth compared.

Data Analysis

Average stand rainfall was estimated using a map of rainfall isolines from the U.S. Department of Commerce, reprinted in Hemstrom and Logan (1984). Plot elevations were taken from contour maps provided by the Forest Service.

A transformation was used to convert azimuth to a more biologically meaningful continuous variable, which I called adjusted aspect. The formula used was:

$$180 - (\text{Absolute value of } (180 - \text{azimuth})).$$

This transformation collapses the azimuth along a vertical axis, giving due north a value of zero, south a value of 180, and both east and west the value of 90. The transformation that is more commonly used in studies of topography and site productivity is one that gives minimum and maximum values to northeast and southwest respectively (Beers et al. 1966). That transformation was tried on this data and correlated less with growth and efficiency than did the transformation used.

Basal Area and Leaf Area Calculations

Basal area inside bark was calculated from DBH using an equation derived for Douglas-fir in the Willamette Valley (Ritchie and Hann 1984).

Two sapwood radii at breast height were measured on 645 Douglas-fir. From these, heartwood basal area was calculated, and sapwood basal area was taken as the difference between total basal area inside bark and heartwood area (Whitehead 1978). On the 204 Douglas-fir with no sapwood measurement, sapwood area at breast height was estimated from the following linear regressions (derived from the measured trees):

For trees with basal area inside bark less than 30 sq. cm, sapwood area = (basal area inside bark * .918) + .616; $r^2 = .88$,

$p < .001$.

For trees with basal area inside bark greater than 30 sq. cm, sapwood area = (basal area inside bark * .597) + 18.456; $r^2 = .91$, $p < .001$.

Sapwood radii at the bottom of the live crown were measured on 134 Douglas-fir. On 511 trees for which the height to the live crown was known, sapwood area at breast height was converted to sapwood area at the base of the crown using a taper equation in Bennett and Swindel (1972). For the remaining 204 trees, crown height sapwood basal area was estimated by regression on breast height sapwood basal area. Projected leaf area was calculated from sapwood area at the base of the live crown using the equation of Waring et al. (1982) for Douglas-fir.

Sapwood radii at breast height were measured on 5 western hemlock. Only 2 of the measured trees were smaller than 8 cm in diameter, while most of the unmeasured trees were below this size, so the 2 small trees were used to generate an equation for sapwood area from basal area which was applied to the other 13 hemlock. Projected leaf area was calculated from sapwood basal area at breast height using the equation of Waring et al. (1982) for hemlock.

Foliage weights for the 30 red alder, 18 cascara,

and 20 bitter cherry were calculated from diameters using the equation for alder in Snell and Little (1983). This was converted to projected leaf area using a conversion constant for alder from Smith (1977 cited in Bormann 1981).

Stand leaf areas were developed by totaling individual tree leaf areas on the plot and expanding to a per-hectare basis. They are reported as leaf area index (LAI), square meters of projected leaf area per square meter of ground surface.

Volume Calculations

Douglas-fir volumes were calculated from DBH and height using equations developed for second-growth Douglas-fir by Bruce and Demars (1974). Heights were estimated using the following equation from an earlier study in these and similar stands in the same area (Perry 1984), in which there were no significant differences in height or height growth by aspect class, slope class, or slope position class.

$$\text{Height (m)} = (\text{diameter (cm)} * \text{age}^2 (\text{years from seed}) * 0.000832) + 7.557$$

$$\text{Adjusted } R^2 = .73$$

Data from the previous year's study (Perry 1985) were used to estimate annual height growth. Stepwise forward regression was used to determine that height growth was related to tree DBH, but the relationship was very loose; the coefficient of determination from regression of annual height growth on DBH was .08. Among all but a few of the trees sampled there was only about 1/3 meter of variation in height growth. Scatter plots showed that the very small trees in the sample had a smaller average annual height growth than did the others. For these reasons I divided the trees in my stands into two size classes and used a single height growth value for all trees in each size class.

Size classes and annual height growth were as follows:

Trees ≤ 9 m, annual height growth = .84 m.
SE = 0.033 m

Trees > 9 m, annual height growth = 1.03 m.
SE = 0.013 m

Statistical Analysis

Single and multiple variable regressions were done using the SYSTAT statistical software package (Wilkinson 1984). Forward stepwise regression was used to choose appropriate variables (those with p value $< .05$) and then multiple regression was used to obtain coefficients.

The adjusted coefficient of multiple determination is reported (Neter et al. 1983).

At the stand level, current volume growth (the year prior to sampling), 5 year volume growth, LAI, and annual volume growth per unit LAI were each regressed against the following variables: trees per hectare, basal area per hectare, Douglas-fir basal area per hectare, LAI, Douglas-fir LAI, Relative Density, variance and coefficient of variation of individual tree basal areas, variance and coefficient of individual tree leaf areas, slope per cent, slope position, adjusted aspect, plot elevation, and average annual rainfall.

Individual tree growth variables (current volume growth and 5 year volume growth) were each regressed against individual tree size variables (basal area, leaf area, and volume) as well as the topographic and stand density and variance variables listed above.

Analysis of variance was performed using the Statistical Analysis System (SAS) to compare means of variables by topographic class, hardwood component class, and crown class. Where the overall F was significant in the comparison of three or more means, Scheffe's multiple comparison test for unbalanced designs was used to determine whether means were significantly different at the .05 level of probability (Steel and Torrie 1960).

RESULTS

Plot Frequencies by Topographic Class

Table 1 shows plot frequencies by topographic class and hardwood component. Thirty-nine of the plots, about 60 per cent, were on northerly aspects (less than 90 degrees azimuth or greater than 270 degrees azimuth) and 25 plots were on southerly aspects (greater than 90 and less than 270 degrees azimuth). Four plots which faced due east or west or were on completely flat ground were not included in the analysis by aspect class.

Plots were distributed fairly evenly between slope steepness classes. There were 25 plots on gentle slopes (defined as less than 30 per cent slope), 17 plots on moderate slopes (30 to 60 per cent slope), and 26 plots on steep slopes (greater than 60 per cent slope).

Slope position classes were defined as follows: upper slopes included ridgetops and the top one-third of the distance from main ridgetops to draws; mid-slopes were the middle one-third of the slopes, and lower slopes included the lower one-third and bottoms of draws. There were 20 plots on upper slopes, 42 on mid-slopes, and 6 on bottom slopes. Many potential plot sites in lower slope positions were not included in the study because of high hardwood stocking.

There were 26 plots containing only Douglas-fir, 24 with Douglas-fir and cherry and/or cascara, and 10 with Douglas-fir and alder. The remaining 8 plots contained hemlock or a combination of hardwood species and were not used in the analysis by hardwood component class.

Table 1. Frequency tables for plots

	<u>Aspect</u>			
	<u>North</u> (271-89)	<u>South</u> (91-269)	<u>East,</u> (90	<u>West, or Flat</u> or 270)
No. plots	39	25		4

	<u>Slope Steepness</u>		
	<u>Gentle</u> (<30%)	<u>Moderate</u> (30-60%)	<u>Steep</u> (>60%)
No. plots	25	17	26

	<u>Slope Position</u>		
	<u>Top 1/3</u>	<u>Middle 1/3</u>	<u>Bottom 1/3</u>
No. plots	20	42	6

	<u>Hardwood Component</u>			
	<u>Douglas-fir</u> <u>only</u>	<u>Douglas-fir,</u> <u>cascara, and/or</u> <u>cherry</u>	<u>Douglas-fir</u> <u>and alder</u>	<u>Mixed</u> <u>Species</u>
No. plots	24	26	10	8

Table 2 shows two-way plot frequencies by topographic class. Slope classes were fairly evenly distributed by aspect except for somewhat fewer moderate slopes than gentle or steep slopes on south aspects. On both north and south aspects the majority of plots were in middle slope positions. Of the gentle slopes, about 70 per cent were in mid-slope positions and none were in bottom slope positions. In middle slope positions only about 15 per cent were of moderate steepness, with the remaining 85 per cent about evenly divided between gentle and steep slopes. The plot distribution cannot be considered to be random but it does reflect the physiography of the Coast Range, where the slopes tend to be steep, broken by gentle benches where slumps have deposited soil.

Table 2. Two-way frequency tables for plots by topographic class

	<u>Aspect X Slope</u>			Total
	Gentle (<30%)	Moderate (30-60%)	Steep (>60%)	
	Number of plots			
North (271-89)	13	12	14	39
South (91-269)	9	5	11	25
East or West (90 or 270)	2	0	1	3
No aspect	1	0	0	1
Total	25	17	26	68

	<u>Aspect X Slope Position</u>			Total
	Top 1/3	Middle 1/3	Bottom 1/3	
	Number of plots			
North (271-89)	12	25	2	39
South (91-269)	8	13	4	25
East or West (90 or 270)	0	3	0	3
No aspect	0	1	0	1
Total	20	42	6	68

	<u>Slope X Slope Position</u>			Total
	Top 1/3	Middle 1/3	Bottom 1/3	
	Number of plots			
Gentle (<30%)	7	18	0	25
Moderate (30-60%)	6	7	4	17
Steep (>60%)	7	17	2	26
Total	20	42	6	68

Average Stand Characteristics

General stand characteristics and their ranges are shown in Table 3. Plots averaged 1646 trees (range 957 to 3110) and 36.1 square meters basal area (18.1 to 54.4) per hectare. Average projected leaf area index was 8.0 (4.6 to 12.4). Douglas-fir made up 91 per cent of the stems, 96 per cent of the basal area, and 99 per cent of the leaf area. The average individual Douglas-fir had 51.0 square meters of projected leaf area.

Relative Density Index of sample plots ranged from .19 to .59, and averaged .39. This average is at the lower limit of density recommended by Drew and Flewelling (1979) for managed stands, and the range extends from just beyond crown closure (RD = .15) to the point at which density-dependent mortality would be expected (roughly RD = .60).

Table 3. Average values and ranges for stocking, basal area, leaf area, and Relative Density of sample plots

	Mean	Range
All trees:		
Trees per hectare	1646	957 - 3110
Basal area per hectare, m ²	36.1	18.1 - 54.4
Leaf area index, m ² /m ²	8.0	4.6 - 12.4
Leaf area per tree, m ²	48.0	0.20 - 161.5
Douglas-fir only:		
Trees per hectare	1493	837 - 2392
Basal area per hectare, m ²	34.7	15.8 - 53.4
Leaf area index, m ² /m ²	7.9	4.6 - 11.6
Leaf area per tree, m ²	51.0	0.20 - 170.1
Relative Density	0.39	0.19 - 0.59

Density and Growth by Topographic PositionAspect

Stands on north aspects had higher basal area, both for all trees and for Douglas-fir only, and higher Douglas-fir Relative Density and stem volume than those on south aspects (Table 4). Trees per hectare and LAI did not differ significantly by aspect class but averaged somewhat higher on north aspects. Trees averaged about a year older and were larger on north than on south aspects, however average leaf area per tree was not significantly different.

Stem volume growth per hectare (current and 5 year) was about 15 per cent greater on north than on south aspects, but volume growth per unit LAI was not significantly different (Table 4). Current and 5 year volume growth of individual trees did not differ significantly between aspects.

Table 4. Stand characteristics and growth by aspect class

	North Aspects (271_to_89_)	South Aspects (91_to_269_)	Probability that means do not differ at .05_level		
Number of Plots	39	25			
<u>All Trees</u>	\bar{x}	(SE)	\bar{x}	(SE)	p
Per Hectare:					
Number of trees	1705	(76)	1588	(82)	.318
Basal area (m2)	37.9	(1.2)	31.8	(1.5)	.003
LAI (m2*m-2)	8.2	(0.2)	7.4	(0.3)	.070
Variances of basal areas (cm2)	20943	(1363)	23932	(1771)	.182
<u>Douglas-fir Only</u>					
Per Hectare:					
Number of trees	1573	(63)	1401	(76)	.091
Basal area (m2)	36.9	(1.2)	29.7	(1.5)	.000
LAI (m2)	8.1	(0.2)	7.4	(0.3)	.056
Relative Density	0.41	(0.01)	0.33	(0.02)	.001
Standing volume (m3)	233.7	(10.6)	172.5	(9.9)	.000
Current stem volume growth (m3)	27.3	(0.8)	24.2	(1.2)	.027
5 year stem volume growth(m3)	134.7	(4.4)	115.3	(5.5)	.007
Volume growth per unit LAI(m3)	3.37	(0.04)	3.29	(0.06)	.278
Individual Trees:					
	2				
Mean basal area (cm)	234.3	(6.7)	212.0	(9.1)	.044
(Quadratic mean DBH (cm))	(17.3)		(16.4)		
Leaf area (m2)	50.3	(1.4)	49.3	(2.1)	.681
Stem volume (m3)	.149	(.005)	.123	(.006)	.002
Current stem volume growth(m3)	.017	(.001)	.017	(.001)	.924
5 year volume growth (m3)	.086	(.003)	.082	(.004)	.482
Age (years from seed)	21.0	(0.1)	19.7	(0.1)	.000

Slope Steepness

Average stand ages were 19.3, 20.7, and 22.0 years respectively on gentle, moderate, and steep slopes, and average tree size correlated with stand age (Table 5).

Although there were no significant differences between stands in the various slope steepness classes, there was a trend toward lower stocking density and higher basal area as slopes became steeper, as well as a trend toward greater stand volume growth and efficiency on steep slopes. Stand leaf area and Relative Density were similar between slope classes. Average individual tree size, leaf area, and volume growth were significantly greater on steep slopes than on gentle slopes, probably because of age differences.

Table 5. Stand characteristics and growth by slope class

Means followed by the same letter do not differ
at the .05 level of probability

	<30%		30-60%		>60%	
Number of Plots	25		17		26	
<u>All trees</u>	\bar{x}	(SE)	\bar{x}	(SE)	\bar{x}	(SE)
Per Hectare:						
Number of trees	1746	(84) a	1625	(114) a	1564	(91) a
Basal area (m ²)	35.1	(1.6) a	36.6	(1.9) a	36.8	(1.8) a
LAI (m ² *m ⁻²)	7.9	(0.4) a	8.0	(0.4) a	8.1	(.3) a
Variance of basal areas (cm ²)	20982	(1666) a	20303	(1410) a	24380	(1931) a
<u>Douglas-fir only</u>						
Per Hectare:						
Number of trees	1593	(80) a	1449	(98) a	1426	(73) a
Basal area (m ²)	33.5	(1.6) a	34.9	(2.1) a	35.7	(1.8) a
LAI (m ² *m ⁻²)	7.8	(0.3) a	7.8	(0.4) a	8.0	(0.3) a
Relative Density	0.37	(0.02) a	0.39	(0.02) a	0.40	(0.02) a
Standing volume (m ³)	193.1	(13.4) a	218.0	(15.9) a	237.0	(14.6) a
Current stem volume growth(m ³)	25.6	(1.2) a	25.9	(1.3) a	28.0	(1.2) a
5 year stem volume growth(m ³)	123.4	(6.1) a	127.2	(7.1) a	138.0	(6.2) a
Current stem volume growth/LAI(m ³)	3.28	(0.05) a	3.31	(0.07) a	3.47	(0.06) a
Individual Trees:						
	2					
Mean basal area (cm)	210.3	(8.2) a	240.8	(10.1) ab	250.1	(9.3) b
(Quadratic mean DBH (cm))	(16.4)		(17.5)		(17.8)	
Leaf area (m ²)	47.1	(1.8) a	51.6	(2.1) ab	54.8	(2.0) b
Stem volume (m ³)	.121	(.005) a	.150	(.007) b	.166	(.007) b
Current stem volume growth (m ³)	.016	(.001) a	.018	(.001) ab	.020	(.001) b
5 year stem volume growth (m ³)	.077	(.003) a	.088	(.004) ab	.097	(.004) b
Age (years from seed)	19.3	(0.1) a	20.7	(0.2) b	22.0	(0.1) c

Slope Position

Average tree ages were 20.1, 20.8, and 21.8 on top, middle and lower slope positions respectively. Statistics by slope position class are given in Table 6.

Stands on different slope positions did not differ significantly in basal area per hectare or in LAI, either considering all trees or Douglas-fir only, but the values for lower slopes averaged less than those for top and mid-slope positions. The number of Douglas-fir per hectare was significantly lower on bottom slope positions than on top, perhaps because of greater age. Relative density, standing volume, volume growth, and growth efficiency averaged higher on midslopes than on upper and lower slopes, however differences were not significant. Individual tree size, leaf area, and stem growth trended toward lower values on upper slopes, with similar values on mid- and lower slopes. However only top and mid-slope positions differed significantly.

Table 6. Stand characteristics and growth
by slope position class

Means followed by the same letter do not differ
at the .05 level of probability

	Top_1/3	Middle_1/3	Bottom_1/3
Number of Plots	20	42	6
<u>All trees</u>	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)
Per Hectare:			
Number of trees	1836 (109) a	1572 (63) a	1535 (194) a
Basal area (m ²)	35.8 (1.8) a	36.8 (1.3) a	31.7 (3.8) a
LAI (m ² m ⁻²)	8.2 (0.4) a	8.0 (0.3) a	7.1 (0.7) a
Variance of basal areas (cm ²)	22537 (2542) a	21279 (1114) a	25526 (1902) a
<u>Douglas-fir only</u>			
Per Hectare:			
Number of trees	1680 (89) a	1450 (56) ab	1176 (121) b
Basal area (m ²)	34.2 (1.7) a	35.8 (1.3) a	28.6 (4.0) a
LAI (m ² m ⁻²)	8.2 (0.4) a	7.9 (0.2) a	6.9 (0.6) a
Relative Density	0.38 (0.02) a	0.39 (0.01) a	0.33 (0.05) a
Standing volume (m ³)	201.4 (13.3) a	227.5 (11.6) a	185.2 (29.5) a
Current stem volume growth (m ³)	26.9 (1.2) a	27.0 (0.9) a	23.0 (2.4) a
5 year stem volume growth (m ³)	128.0 (5.9) a	133.4 (4.9) a	111.8 (13.6) a
Volume growth per unit LAI (m ³)	3.27 (.07) a	3.41 (.04) a	3.33 (.17) a
Individual Trees:			
	2		
Mean basal area (cm ²)	203.7 (9.2) a	246.7 (6.8) b	243.4 (19.4) ab
(Quadratic mean DBH (cm))	(16.1)	(17.7)	(17.6)
Leaf area (m ²)	46.8 (2.0) a	53.1 (1.4) b	52.7 (4.2) ab
Stem volume (m ³)	.119 (.006) a	.157 (.005) b	.157 (.014) ab
Current stem volume growth (m ³)	.016 (.001) a	.019 (.001) b	.020 (.002) ab
5 year stem volume growth (m ³)	.076 (.004) a	.092 (.003) b	.095 (.008) ab
Age (years from seed)	20.1 (0.1) a	20.8 (0.1) b	21.8 (0.1) c

Growth Efficiency Among Crown Classes

The 698 crop trees were grouped into standard dominance classes by relative crown height within the canopy (Daniel, Helms and Baker 1977). The classes decreased significantly in both size and growth from dominant through codominant, intermediate, and suppressed trees (Table 9, Figure 2). Growth efficiency, in terms of each tree's stem volume growth divided by its leaf area, was significantly higher in suppressed trees than in the other crown classes (Figure 3). Dominants and codominants did not differ significantly in efficiency, and intermediates were the least efficient. Relative growth rate (basal area growth per unit basal area) was significantly higher in suppressed trees than in codominant and intermediate trees, and dominants had a significantly higher rate than intermediates (Figure 4). Dominants and suppressed trees did not have significantly different relative growth rates although the relative growth of the suppressed trees averaged somewhat higher.

Table 7. Individual tree characteristics by crown class

Means followed by the letter do not differ
at the .05 level of probability

	Dominant	Codominant	Intermediate	Suppressed
Number of trees	76	343	179	58
<u>Tree size:</u>	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)
Mean basal area (cm ²) (Quadratic mean DBH (cm))	456.0 (12.5) a (24.1)	320.5 (5.8) b (20.2)	138.2 (5.4) c (13.3)	37.1 (3.2) d (6.9)
Volume (m ³)	.297 (.012) a	.205 (.005) b	.079 (.004) c	.018 (.002) d
Leaf area (m ²)	99.8 (2.76) a	69.3 (1.17) b	31.0 (1.17) c	7.3 (0.77) d
<u>Growth:</u>				
Current stem volume growth (m ³)	.039 (.001) a	.025 (.001) b	.010 (.000) c	.002 (.000) d
5 year stem volume growth (m ³)	.186 (.006) a	.124 (.003) b	.046 (.002) c	.013 (.001) d
<u>Efficiency:</u>				
Volume growth/leaf area (m ³ m ⁻² 1000)	.389 (.007) a	.362 (.003) a	.319 (.007) b	.467 (.053) c
Relative growth (cm ² cm ⁻²)	.072 (.003) ab	.063 (.002) bc	.058 (.003) cd	.085 (.008) a
Age (years from seed)	20.4 (0.2) a	21.0 (0.1) a	20.9 (0.2) a	20.4 (0.3) a

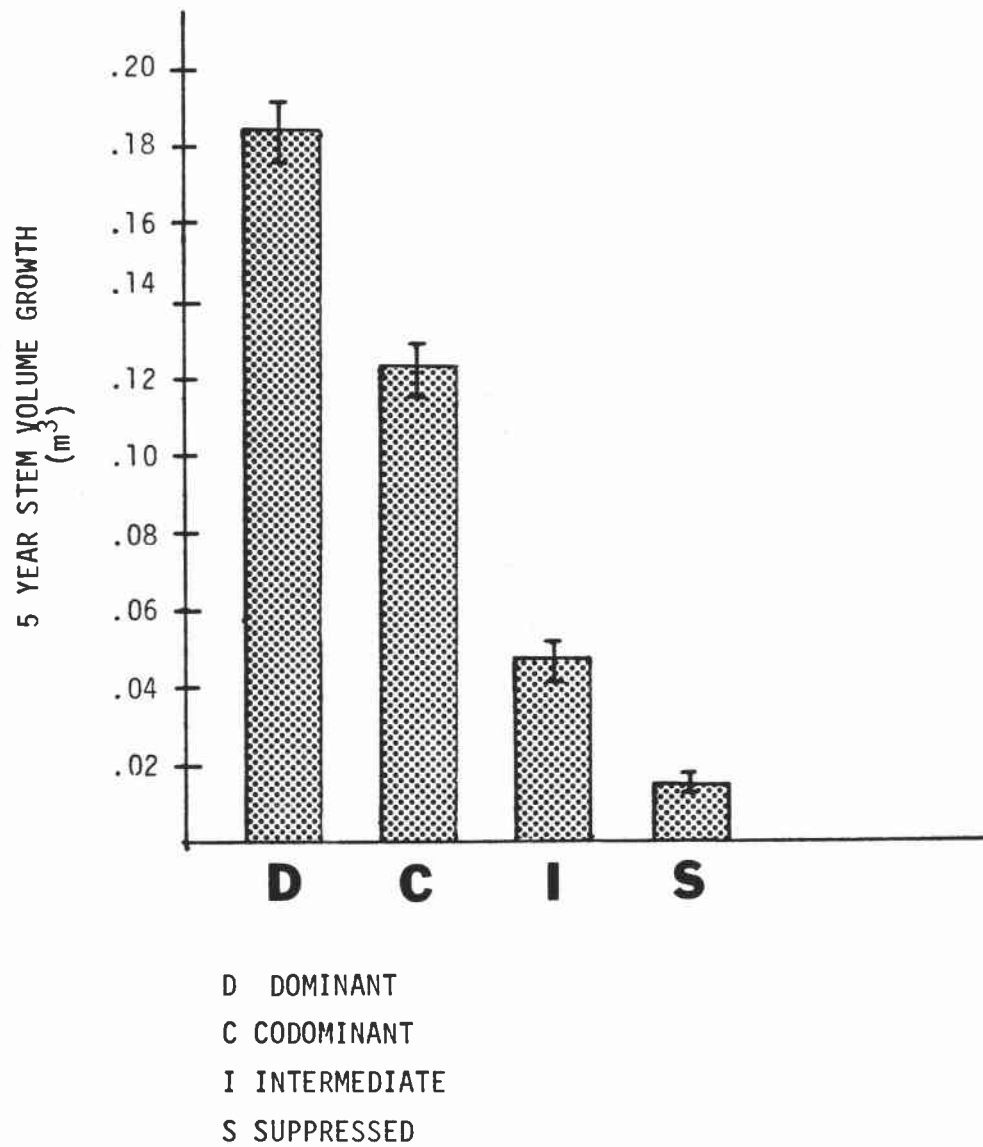


Figure 2. Mean 5 year stem volume growth by crown class

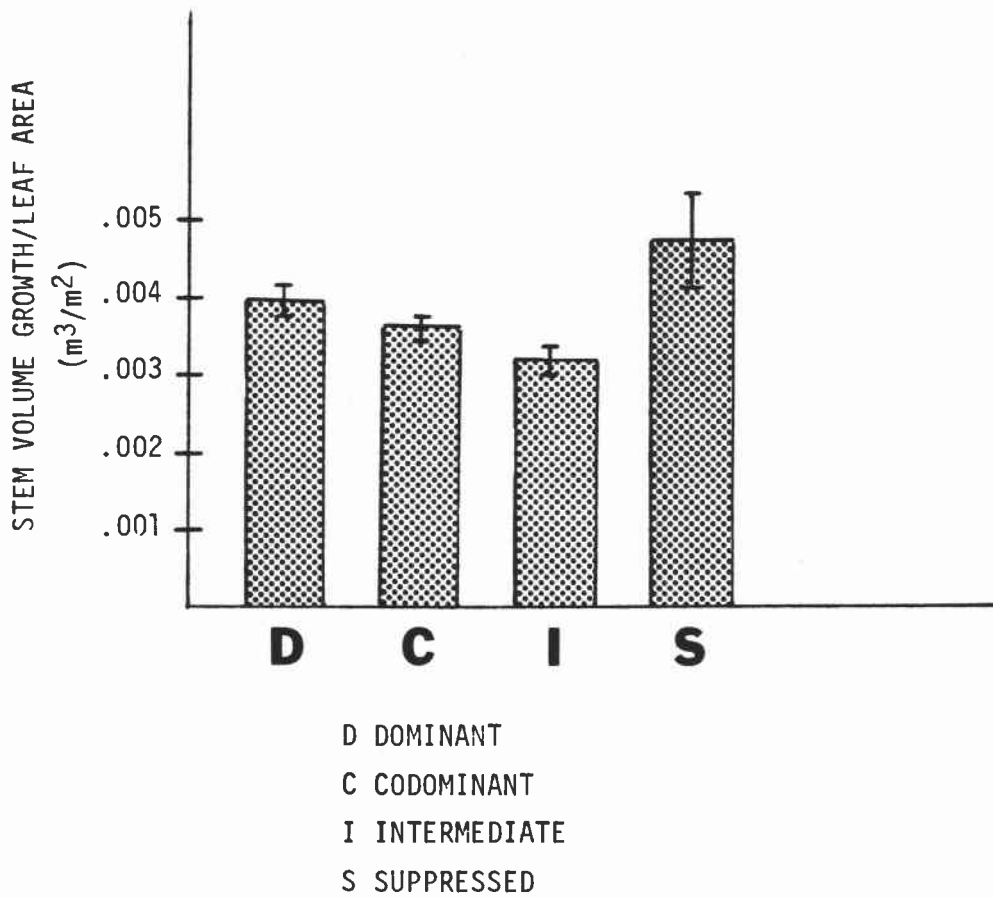


Figure 3. Mean stem growth efficiency by crown class

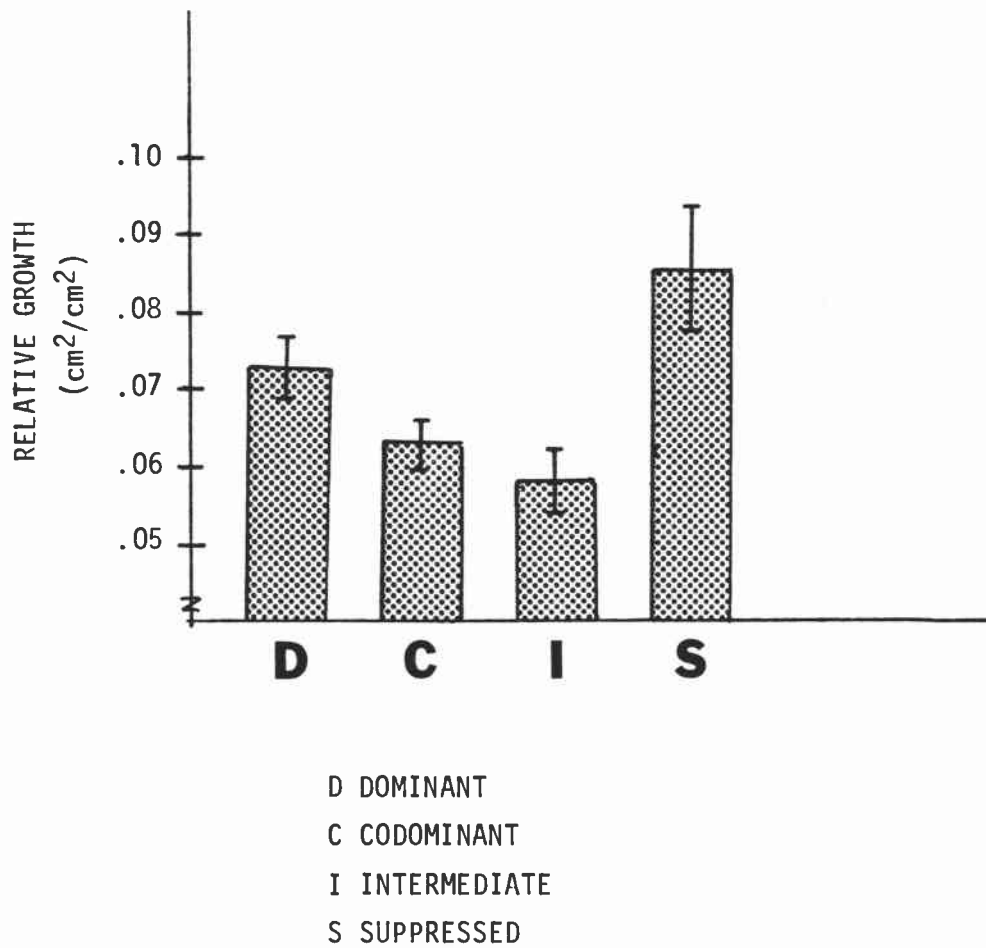


Figure 4. Mean Relative Growth by crown class

Comparison of Plots With and Without Hardwoods

Plots with Douglas-fir and cherry and/or cascara averaged 229 hardwood trees per hectare, and plots with Douglas-fir and alder averaged 191 trees of that species per hectare. The average diameter of cascara was 6.1 cm (range 3.8 - 9.4); of cherry, 9.2 cm (range 5.1 - 16.5); and of red alder, 12.6 cm (3.8 - 19.3). Statistics for plots with and without hardwoods are shown in Table 7, and locations of plots in hardwood component classes by topographic class are shown in Table 8.

Number of trees per hectare was significantly higher in plots with cherry and cascara than in plots with Douglas-fir only; plots with alder had average density between these two. For the Douglas-fir component only, stocking density, basal area, LAI, Relative Density, stem volume, and volume growth all averaged highest on cherry\cascara plots and lowest on alder plots. No differences were significant, however. Douglas-fir volume growth efficiency was significantly lower on alder than on pure Douglas-fir plots, whether calculated on the basis of total LAI or Douglas-fir LAI. The growth of individual Douglas-fir did not differ by hardwood component class.

Table 8. Stand characteristics and growth
in stands with and without hardwoods

Means followed by the same letter do not differ
at the .05 level of probability

	Douglas-fir		
	Douglas-fir only	with cherry and/ or cascara	Douglas-fir with alder
Number of plots	24	26	10
<u>All trees</u>	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)
Per Hectare:			
Number of trees	1495 (78) a	1794 (81) b	1614 (124) ab
Basal area (m ²)	35.8 (1.7) a	39.5 (1.5) a	34.7 (2.1) a
LAI (m ² *m ⁻²)	7.8 (0.3) a	8.6 (0.3) a	7.5 (0.5) a
Variance of basal areas (cm ²)	20550 (1501) a	24138 (977) a	22728 (4706) a
<u>Douglas-fir only</u>			
Per Hectare:			
Number of trees	1495 (78) a	1565 (79) a	1423 (105) a
Basal area (m ²)	35.8 (1.7) a	38.0 (1.5) a	31.4 (1.9) a
LAI (m ² *m ⁻²)	7.8 (0.3) a	8.4 (0.3) a	7.5 (0.5) a
Relative Density	0.39 (0.02) a	0.42 (0.02) a	0.35 (0.02) a
Stem volume (m ³)	225.5 (15.3) a	240.0 (13.1) a	187.1 (14.7) a
Current stem volume growth (m ³)	27.3 (1.1) a	28.5 (1.0) a	24.4 (2.0) a
5 year stem volume growth (m ³)	133.9 (6.2) a	140.5 (5.4) a	117.7 (8.2) a
Current stem volume growth/LAI (m ³)	3.48 (0.05) a	3.32 (0.05) ab	3.22 (0.09) b
Current stem volume growth/ Douglas-fir LAI (m ³)	3.48 (0.05) a	3.38 (0.05) ab	3.24 (0.08) b
Individual Trees:			
	2		
Mean basal area (cm ²)	239.8 (8.7) a	242.9 (8.6) a	220.3 (14.7) a
(Quadratic mean DBH (cm))	(16.7)	(17.5)	(17.6)
Leaf area (m ²)	52.4 (1.8) a	52.3 (1.8) a	48.6 (3.1) a
Stem volume (m ³)	.151 (.006) a	.153 (.006) a	.131 (.010) a
Current stem volume growth (m ³)	.018 (.001) a	.018 (.001) a	.017 (.001) a
5 year stem volume growth (m ³)	.089 (.004) a	.090 (.004) a	.083 (.006) a
Age (years from seed)	20.6 (0.1) a	20.8 (0.1) a	20.2 (0.2) a

Table 9. Two-way frequency tables for plots with and without hardwoods

Hardwood Class X Topographic Cell

Hardwood Class X Aspect

	Douglas-fir only	Douglas-fir, cascara, and/or cherry	Douglas-fir and alder	Mixed Species	Total
	Number of plots				
North (271-89)	15	18	4	2	39
South (91-269)	9	4	6	6	25
East or West (90 or 270)	2	1	0	0	3
No aspect	0	1	0	0	1
Total	26	24	10	8	68

Hardwood Class X Slope

	Douglas-fir only	Douglas-fir, cascara, and/or cherry	Douglas-fir and alder	Mixed Species	Total
	Number of plots				
Gentle (< 30%)	10	8	6	1	25
Moderate (30-60%)	6	7	1	3	17
Steep (>60%)	10	9	3	4	26
Total	26	24	10	8	68

Hardwood Class X Slope Position

	Douglas-fir only	Douglas-fir, cascara, and/or cherry	Douglas-fir and alder	Mixed Species	Total
	Number of plots				
Top 1/3	7	7	4	2	20
Middle 1/3	19	17	6	0	42
Bottom 1/3	0	2	0	4	6
Total	26	26	10	6	68

Results of Regression Analysis

Stand Volume Growth

Stepwise regression showed four variables to be significantly correlated with current stand volume growth. The variables came into the regression as follows:

1. Douglas-fir basal area per hectare (m^2),
 $R^2=.89$, $p<.001$
2. Adjusted aspect (degrees), $R^2=.92$, $p=.002$
3. Average annual rainfall (cm), $R^2=.93$, $p<.001$
4. Douglas-fir trees per hectare, $R^2=.94$,
 $p=.003$

The multiple regression equation resulting from these variables was:

Annual volume growth per hectare = $-12.110 + (0.707 * \text{Douglas-fir basal area per hectare}) + (0.015 * \text{adjusted aspect}) + (0.066 * \text{annual rainfall}) - (0.002 * \text{Douglas-fir trees per hectare})$.

Adjusted $R^2=.93$

The regression of five-year stand volume growth on stand and site variables resulted in a slightly different model than that for one year's growth. Stepwise

regression included these variables in the model:

1. Douglas-fir basal area per hectare (m^2),
 $R^2=.93$, $p<.001$
2. Douglas-fir trees per hectare, $R^2=.95$,
 $p<.001$
3. Average annual rainfall (cm), $R^2=.96$, $p=.002$
4. Relative Density, $R^2=.97$, $p<.001$
5. Adjusted aspect (degrees), $R^2=.98$, $p<.001$

The multiple regression equation resulting from these variables was:

Five year stand volume growth = $-28.215 +$
 $(2.046 * \text{Douglas-fir basal area per hectare}) -$
 $(0.016 * \text{Douglas-fir trees per hectare}) +$
 $(0.178 * \text{annual rainfall}) + (168.003 * \text{Relative Density}) + (0.068 * \text{adjusted aspect}).$

Adjusted $R^2=.97$

Leaf Area Index

The regression of LAI (m^2 per m^2) on stand density, variance and topographic variables brought in 4 variables:

1. Basal area per hectare (m^2), $R^2=.87$,
 $p<.001$
2. Average annual rainfall (cm), $R^2=.90$, $p=.008$

3. Trees per hectare, $R^2=.92$, $p<.001$
4. Adjusted aspect (degrees), $R^2=.93$, $p=.031$

The multiple regression equation was:

LAI= $-2.656 + (0.175 * \text{basal area per hectare}) + (0.013 * \text{annual rainfall}) + (0.001 * \text{trees per hectare}) + (0.003 * \text{adjusted aspect})$.

Adjusted $R^2=.92$

Stand Volume Growth per Unit Leaf Area

Stepwise regression of current stand volume growth per unit LAI (m^3) brought in these variables:

1. Douglas-fir trees per hectare, $R^2=.33$, $p<.001$
2. Relative Density, $R^2=.51$, $p<.001$
3. Variance of individual tree basal areas (cm^2),
 $R^2=.57$, $p=.004$
4. Douglas-fir LAI, $R^2=.64$, $p<.001$
5. Adjusted aspect (degrees), $R^2=.66$, $p=.029$

The resulting multiple regression was:

Volume growth per unit LAI= $3.431 - (.000341 * \text{trees per hectare}) + (3.845 * \text{Relative Density}) + (.0000085 * \text{variance of individual tree basal areas}) - (0.164 * \text{Douglas-fir LAI}) + (0.001 * \text{adjusted aspect})$.

Adjusted $R^2 = .64$

Figure 5 shows solutions to the stand efficiency model, plotted onto a Stand Density Management Diagram for Douglas-fir (Drew and Flewing 1979). Basal area variance and adjusted aspect are held constant at 21000 and 90 degrees, respectively, and LAI is calculated as a function of trees per hectare and Relative Density. Points of equal efficiency (stand volume growth per unit LAI) are connected.

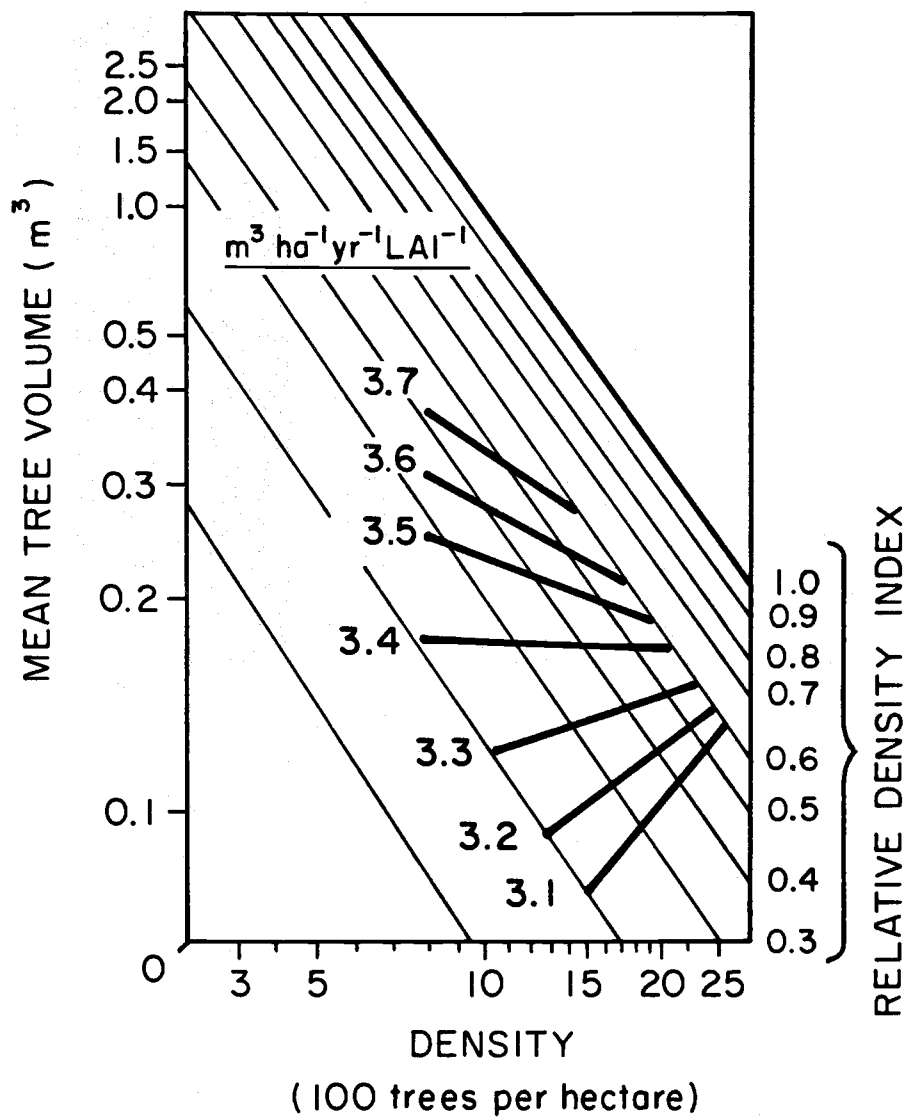


Figure 5 Isolines of constant stand volume growth per unit LAI, at various levels of Relative Density

Individual Tree Volume Growth

Stepwise regression of current individual tree volume growth per year on tree size and topographic variables brought in:

1. Individual tree basal area (cm^2),
 $R^2 = .94$, $p < .001$
2. Douglas-fir basal area per hectare (m^2),
 $R^2 = .95$, $p < .001$

The multiple regression equation was:

Annual volume growth = $.0024 + (.000086 * \text{individual tree basal area}) - (.000126 * \text{Douglas-fir basal area per hectare})$.

Adjusted $R^2 = .95$

Stepwise regression of 5 year individual tree volume growth ($\text{m}^3 * 1000$) on tree size and stand variables brought in the same two variables:

1. Individual tree basal area (cm^2),
 $R^2 = .97$, $p < .001$
2. Douglas-fir basal area per hectare (m^2),
 $R^2 = .98$, $p = .001$

The multiple regression equation was:

5 year volume growth = .00355 + (.000418 *
individual tree basal area) - (.00384 *
Douglas-fir basal area per hectare).

Adjusted R² = .97

DISCUSSION

Influence of Tree Size and Stand Density on Douglas-fir Growth

Growth, leaf area and growth efficiency of both stands and individual trees consistently correlate most strongly with tree size and stand density in this study. Although significant in some cases, topographic effects are relatively small. Topography probably has a greater effect on vegetation in climates where water or nutrients are more limiting than in these highly productive Coast Range sites.

Individual tree volume growth is mostly related to tree size, as has been found previously in young stands of this type (Perry 1984, 1986). There is a small negative effect of stand basal area on individual tree growth, indicating that competition among trees is intensifying within the range of sampled basal areas (18 to 54 m² per hectare).

Both current and five year stand volume growth correlate positively with the stand basal area of Douglas-fir, but negatively with the number of Douglas-fir per hectare; five year volume growth also correlates positively with Relative Density. Volume growth of western conifers usually correlates positively with some measure

of site occupation such as leaf area or basal area (Schroeder et al. 1982, Tappeiner et al. 1982, Binkley and Reid 1984). My results indicate that stand structure plays a role as well - at a given basal area, growth is better with a few large trees than it is with many small trees. Similar results were found in a western Washington study of Douglas-fir stands thinned to various structures within prescribed densities (Oliver and Murray 1983). In my study growth efficiency also correlates negatively with tree density and positively with Relative Density, indicating that better growth of stands with few large trees is due to more efficient use of leaves. This cannot be an effect of tree size since, since in the absence of competition, small trees are more efficient than large (Perry 1985). Higher efficiency may be due to better distribution of light in the elongated crowns that are retained in stands at wider spacing. Crowns in densely stocked stands tend to become shortened and concentrated into the tops of the trees, with a high surface : volume ratio (Curtis and Reukema 1970, Whitehead 1978, Binkley 1984). The consequent compactness of stand leaf area probably limits diffusion of light within the canopy. In addition, there is evidence that mid-day carbon dioxide depression and heat buildup occur in dense canopies, perhaps causing stomatal closure and / or increased respiration (Kira et al. 1969).

In support of the above, growth efficiency of our stands correlates positively with the variance of individual tree basal areas. A higher value for variance of basal areas implies the establishment of a dominance hierarchy, which leads to differentiation of crown classes and more use of vertical space by needles.

The negative correlation of stand efficiency with LAI means that a unit increase in LAI produces less than a unit of increase in stand volume growth, so efficiency of the leaves becomes smaller at higher densities due to self shading (Waring 1984). This effect has been previously shown for individual tree efficiency, which decreased relative to increasing LAI (Waring et al. 1981), and for stand growth efficiency (Schroeder et al. 1982).

Several of the efficiency relationships that apply to the young stands in this study are illustrated in Figure 5: a) at a given density in trees per hectare, stand efficiency is higher at higher Relative Density; b) at a given Relative Density, stand efficiency is higher at lower stem density; c) according to the model, at high densities a thinning that removed the smaller trees and left trees with equal or greater mean tree size would leave a more efficient stand. At lower densities, a thinning that left the same mean tree size would leave a less efficient stand, whereas a thinning that left a

greater mean tree size would leave an equally efficient stand. The adjusted coefficient of multiple determination (R^2) of the regression equation for stand growth efficiency is 0.64, so less than two-thirds of the variation in stand volume growth per unit leaf area index is accounted for by the stand density and topographic variables included in this study. Therefore the model should not be considered predictive for any given stand, but the trends suggested are noteworthy.

Influence of Crown Class on Individual Tree Growth

Growth efficiency of trees in different crown classes has been expressed in various ways. Kellomaki and Hari (1980) expressed efficiency of Scots pine in terms of growth (height, radial, and needle) per unit needle biomass. By these criteria, suppressed trees were more efficient than trees in other crown classes. Using volume growth per unit of crown projection area as a measure of efficiency, Hamilton (1969) found that Sitka spruce trees in the upper canopy were more efficient than those in lower canopy positions. With efficiency represented as either basal area growth per unit sapwood basal area or volume growth per unit leaf area, Waring et al. (1980) found that suppressed Douglas-fir were less efficient than were trees in other crown classes. When data from this

study are expressed in terms of basal area growth per unit basal area (relative growth rate) or volume growth per unit leaf area, suppressed trees were the most efficient. This may reflect the developmental stage of these stands. Ford (1975) and Perry (1986) found that the smaller trees in a stand have higher relative growth rates than larger trees until competition becomes strong, at which point the smaller trees' relative growth rate falls below that of the larger trees.

Suppressed trees may be efficient in their use of leaf area because they have proportionately less respiratory biomass than larger trees (branches and possibly roots) and because their shade-adapted leaves have a lower weight : surface ratio, and therefore less respiring tissue (Larcher 1983).

Influence of Topography on Douglas-fir Growth

Although in this study stands on north slopes were growing more volume per year than those on south slopes, the positive correlation of volume growth and LAI with the transformed aspect variable indicates that, at a given basal area, leaf area is higher and stand stem volume growth is better on south slopes. (Because the relationship between diameter and height was assumed constant over topography in this study, calculated volume

growth is proportional to basal area growth.) Stage (1976) and Youngberg and Ellington (1982) also observed higher basal area growth on south aspects, even though Site Index was higher on north aspects in both of their studies, and Grier and Logan (1977) found higher biomass of old-growth Douglas-fir on south than on north aspects in the Oregon Cascades.

Stand growth efficiency also correlates positively with transformed aspect in the regression equations. This means that, with equal stocking, LAI, and Relative Density, volume growth per unit leaf area is higher on south than on north aspects. This could be because a) slower nutrient cycling on cool north slopes leads to greater allocation of carbohydrates belowground (Keyes and Grier 1981), or b) the smaller amount of direct radiation on north slopes restricts photosynthesis. Trees in low light environments allocate proportionately more growth to height than to diameter than do those in full sunlight, radial growth being more dependent on the supply of photosynthates than is height growth (Kellomaki and Kanninen 1980). Since stands on south aspects probably receive substantially more total radiation than those on north, it may be that they photosynthesize more per unit leaf area and therefore allocate more carbohydrates to radial growth than do stands on north aspects.

The fact that the individual trees are growing

significantly faster with increasing slope steepness can probably be explained by tree size differences. Individual tree basal area was greater on steep slopes; in the regression equations, this is responsible for most of the variation in individual growth.

The plots for this study were laid out so that their areas were all the same when projected onto a horizontal plane, i.e. the lengths of the plot boundaries were increased to compensate for the slope. On very steep slopes this increases the ground surface area of each plot by as much as 20 per cent over flat areas, which confounds the effects of slope steepness on stand growth by including more trees per plot, thereby increasing all the density and stand growth values. Efficiency and individual growth values should not be affected. McArdle et al. (1961) suggest that cubic volume on 30 to 50 per cent slopes is about 10 per cent higher than on flat areas with the same stocking.

The increasing individual tree growth going from top toward lower slope positions can probably be explained by the larger tree size and lower stocking on lower slopes. Stand level volume growth does not differ significantly by slope position class, although it is slightly lower on lower slopes, following the lower stand basal area there.

Stand volume growth and leaf area correlate positively with estimated annual rainfall. Other studies have found rainfall to have a less important effect on these characteristics than does some measure of evaporative demand. Over a range of climates across Oregon, stand leaf area was positively related to annual precipitation but was more strongly related to a water balance index that included growing season evaporation (Grier and Running 1978). In a similar study Gholz (1982) found the same results, and also that net primary production and standing biomass in mature stands were more strongly related to growing season evaporation than to annual precipitation.

Within a much less extensive area, such as that covered by the current study, evaporative demand may be fairly constant at any given time. Transpiration rates, probably a good index of evaporative demand in fully stocked stands, are similar among different topographic features within a forest (Kaufmann 1983, McNaughton and Jarvis 1983). With a uniform evaporative demand an increase in rainfall represents a real increase in available water. Site Index has also been found to increase with rainfall within one county in western Washington (Hill 1948).

Because there were not many stands available that met the requirements for this study, it was impossible to

sample stands of the same age in each of the topographic divisions, and stands in different topographic positions differed significantly in average age. These stands are in a stage of rapid growth so the maximum difference of 1.7 years could be the reason for significant differences in basal area per hectare. Since stand volume growth, LAI, and stand efficiency are all positively correlated with stand basal area and/or Relative Density, and individual growth is negatively correlated with stand basal area, the differences in age alone may account for some of the observed differences by topographic feature. However, the inclusion of stand age in the regression equations did not increase the accuracy of the models.

Influence of Hardwoods on Douglas-fir Growth

The small number of hardwoods present in these stands do not represent significant competition to the Douglas-fir. Neither is there any evidence that the alder present in some plots is supplying enough nitrogen to the conifers to increase their leaf areas or their efficiency. The constant conversion from sapwood area to leaf area, however, could conceal an effect of this type. In Youngberg and Ellington's (1982) study in the same area, more than half of their plots contained less than 40 ppm available nitrogen, the amount below which nitrogen is

thought to be a limiting factor for Douglas-fir. In the current study, however, none of the plots was located on the less productive soils that were included in their study.

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