2099

Effects of Residual Trees on Growth of Young to Mature Douglas-fir and Western Hemlock in the Western Central Oregon Cascades

by

Eric K. Zenner

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed February 23, 1995
Commencement June 1995

58p.

Master of Science thesis of Eric K. Zenner presented on February 23, 1995.

APPROVED:

Co-Professor, representing Forest Science

Co-Professor, representing Forest Science

Head of Department of Forest Science

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Eric K. Zenner, Author

ACKNOWLEDGEMENTS

I would like to thank Ted Thomas, Bob Sanders, Dave Leach, Jim Mayo, Pam Skeels, Gene Skrine, Ginny Tennis, Gary Marsh, John DeWitz, Ray Rasmussen, Bill Porter, Cathy McGrath, Coulter Rose, Bibit Traut, and Matthew Goslin for their help with site selection. Joshua Edwards and A.J. Helgenberg provided invaluable assistance with the fieldwork. The statistical analyses were improved greatly by the advice of Tom Sabin. For her loving support I wish to thank JeriLynn E. Peck. Finally, I must thank my major advisors Dr. William H. Emmingham and Dr. Steven A. Acker for providing considerable guidance throughout this project. The project was funded under a cooperative agreement between the Pacific Northwest Research Station and the Department of Forest Science, Oregon State University.

TABLE OF CONTENTS

Page

Introduction 1

Literature Review 3
- Microenvironmental Factors 3
- Stand Density and Plant Competition 4
- Simulation Studies 6
- Empirical Studies 7

Study Area 9

Methods 11
- Site Selection 11
- Plot Locations 11
- Plot Design and Measurements 13
- Demographic Analyses 14
- Statistical Analyses 17

Results 19
- Description of Stands Sampled 19
- Relationships Between Response and Independent Variables 26
- Results of Paired T-Tests 30
- Results of Multiple Linear Regressions 31
- Summary 41

Discussion 42
- Understory Stand Dynamics 43
- Individual Tree Dynamics 46
- Residual Trees 48
- Management Implications 49

References 50

LIST OF FIGURES

Figure		Page
1	Selected stand characteristics across all stands	23
2	Understory trees and basal area per hectare	24
3	Volume per hectare	25
4	Relationships between dbh, BAL, and 5-year growth of DBH and BA of the young cohort	26
5	Relationship of dq, BA, volume, and height of dominant understory trees to residual tpha, understory tpha, age, and dq of the young cohort	27
6	Relationship of basal area of dominant, codominant, intermediate, and suppressed understory trees to density of residual and understory tpha	28
7	Diameter distribution of Douglas-fir and western hemlock	31
8	Stand growth reductions	39
9	Predicted 5-year diameter and basal area growth reductions	40

LIST OF TABLES

Table		Page
1	Plot locations	11
2	Nonlinear regression formulae for tree volumes	16
3	Characteristics of the residual tree component	20
4	Characteristics of the young cohort	21
5	Characteristics of the young cohort and volume of residual trees	22
6	Periodic and mean radial increment for Douglas-fir and western hemlock in different canopy classes	29
7	Ratio of basal area and density in Z to R stands by crown class	30
8	Selected stand level regression models	32
9	Selected individual tree regression models	33
10	Stand growth reductions (in %)	38
11	Five-year diameter and basal area growth and understory height reductions (in %) for a tree of DBH 40cm	38

AN ABSTRACT OF THE THESIS OF

Eric K. Zenner for the degree of Master of Science in Forest Science presented on February 23. 1995. Title: Effects of Residual Trees on Growth of Young to Mature Douglas-fir and Western Hemlock in the Western Central Oregon Cascades.

Abstract approved: _____
William H. Emmingham

_____
Steven A. Acker

The purpose of this study was to assess how growth of young to mature Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sar.) in mixed stands was influenced by the presence of residual trees. Fourteen paired plots with and without residual trees were examined in a retrospective study on the Willamette National Forest, Oregon. Growth was analyzed at the stand level, and at the individual tree level, contrasting growth behavior of Douglas-fir and western hemlock. Stands were generally highly stocked with relative densities between 0.38 and 1.05 and age ranged between 55 and 121 years.

Results indicate that both understory and residual tree densities had a major influence on average tree size and growth and yield of the young cohort. At the stand level, residual trees and high understory densities reduced volume, basal area, and the mean squared diameter of the young cohort, while understory mortality increased. The influence of residual tree density on total understory and Douglas-fir volume and basal area was best fit by a negative logarithmic function. After accounting for understory density effects, the decrease of understory volume and basal area per individual residual tree decreased with increasing residual tree density. With 5 to 50 residual trees/ha, total understory volume reduction was 22 and 45%, respectively, averaging 2.4 and 1.5% per residual tree, respectively. In mixed

stands, Douglas-fir volume and basal area declined more rapidly than the volume and basal area of the entire young cohort, when residual tree density exceeded 15 trees/ha. This was probably due to the relative shade-intolerance of Douglas-fir. Douglas-fir volume and basal area on southerly aspects was more than double the values on northerly aspects.

Examination of quadratic mean diameters and radial growth rates by crown class revealed that the average size and growth rates of dominant Douglas-fir were not reduced by residual trees. However, the number and basal area of understory trees, particularly dominant and codominant Douglas-fir, declined with increasing residual tree densities. Understory volume was highest in stands that had lowest understory densities. High understory stocking levels were associated with reduced growth and high mortality rates of the young cohort, suggesting stands were undergoing self-thinning.

At the individual tree level, basal area growth and diameter growth of trees increased with increasing size and dominance. The marginal effect of residual trees declined with increasing numbers of residual trees per hectare. No residual tree effects on heights of dominant Douglas-fir was found, perhaps because the few dominant Douglas-firs may have been located sufficiently far from residual trees to minimize interaction.

Due to high stocking levels in the young cohort, results from this study only apply to stands with relative densities above 0.38. In addition, leave-trees in managed stands may be younger, smaller, and may have different growth rates from residual trees in this study, thus affecting the young cohort differently. Finally, due to the observational nature of this study, cause-and-effect relationships cannot be established. However, since understory volume was highest in stands with low understory densities, understory density management may reduce growth losses from self-thinning of the young cohort and competition from leave-trees.

EFFECTS OF RESIDUAL TREES ON GROWTH OF YOUNG TO MATURE DOUGLAS-FIR AND WESTERN HEMLOCK IN THE WESTERN CENTRAL CASCADES OF OREGON

INTRODUCTION

In recent decades, timber management in the Pacific Northwest has been dominated by clearcutting and short rotations (i.e. 40-80 years, Scott 1980), leading to concerns that ecological functions and biological diversity may not be maintained in managed forest ecosystems. In contrast to clearcutting, natural disturbances often do not result in complete stand mortality (Agee 1991, Stewart 1986, Morrison and Swanson 1990, Teensma 1987). Biological legacies of natural disturbances, such as large live residual trees and coarse woody debris are structural components of old-growth forests (Spies and Franklin 1988, 1989, 1991) that may be essential for forest ecosystem complexity, biodiversity, and resiliency (Franklin 1989, Hopwood 1991, Swanson and Berg 1991, Shaw *et al.* 1993). Live residual trees moderate microclimate (Chen *et al.* 1993), provide structural diversity, habitat for mycorrhizal fungi and epiphytic lichens (Harmon *et al.* 1986, Esseen *et al.* 1992, McCune 1993), and serve as a source of future snags (Spies and Franklin 1988). Mycorrhizae and epiphytic cyanolichens make a significant contribution to nutrient cycling and biomass production (Pike 1978, Denison 1973, Trappe and Luoma 1992). Snags provide a suitable habitat for many late-seral species, such as cavity nesting birds and mammals (Carey *et al.* 1991, Gilbert and Allwine 1991 a,b, Thomas *et al.* 1993).

The retention of structural components as part of timber harvest operations has recently become a focal point of forest management (Swanson and Franklin 1992, Shaw *et al.* 1993). Current management plans for the matrix of public forests outside of habitat reserves within the range of the Northern Spotted Owl (*Strix occidentalis caurina*) call for retention of 15 % of the volume of each cutting unit (FEMAT 1993 a,b). However, although recent simulation studies (Long and Roberts 1992, Birch and Johnson 1992, Garman *et al.*

1992) showed a reduced timber production due to green tree retention, information from field studies to confirm or refute results of the simulation studies is generally lacking and effects of green tree retention on biodiversity and timber production are still speculative (Swanson and Berg 1991, DeBell and Curtis 1993).

In the absence of long-term experimental records of understory growth in green tree retention units, a retrospective approach can be used to determine understory growth response since initiation of the young cohort. This approach depends on the assumption that past residual trees left by patchy natural disturbances are analogues for leave-trees in green tree retention cuts, but does not permit to infer causation between residual tree density and growth of the young cohort. Nevertheless, retrospective studies are a timely method to predict likely results of different harvest regimes (Thomas *et al.* 1993), which would take several decades to materialize in controlled experiments.

This retrospective study was undertaken to better understand the quantitative relationships between density of large residual trees and growth of understory trees. Growth responses were compared between Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sar.) that were located in plots with scattered residual trees, and adjacent plots where residual trees were absent. Specific objectives included:

1. To determine to what extent residual trees affect the volume of 60-120-year old stands that have regenerated beneath them;
2. To determine to what extent the density of large residual trees affect the most recent five-year diameter at breast height (dbh) and basal area (BA) growth of individual 60-120-year old Douglas-fir and western hemlock understory trees that have regenerated beneath the residual trees.

The implications for forest management are also briefly discussed.

LITERATURE REVIEW

MICROENVIRONMENTAL FACTORS

While macroenvironmental factors such as slope, aspect, elevation, soil parent material, precipitation, and geographic location determine the general temperature-moisture-nutrient regime (Tesch and Mann 1991), microenvironmental factors such as light, heat, water, nutrients, and biotic factors such as understory vegetation favor or inhibit establishment and growth of plants according to their physiological requirements (Atzet and Waring 1970, Sorensen and Ferrell 1973, Drew and Ferrell 1979, Atzet 1981). Microenvironmental factors may be influenced by the structure of forests. For instance, in contrast to clearcut areas, retaining overstory trees creates a different microenvironment (Childs *et al.* 1985), altering light intensity, ambient air and soil temperature, wind speed, and vapor pressure deficit in the air (Tucker and Emmingham 1977, Vanderwaal and Holbo 1984, Waring and Schlesinger 1985, Radosevich and Osteryoung 1987).

Given the importance of shade tolerance in forest succession, the light environment will affect stand composition of green tree retention stands. Effects of light on seedling survival and growth depend on a combination of intensity, duration, and quality (Tesch and Mann 1991). Temperature and moisture conditions also affect seedling survival (Krueger and Ferrell 1965). Within a given temperature-moisture-nutrient regime, the light intensity required for seedling survival varies by species. In the Siskiyou Mountains of southern Oregon, the minimum light threshold for white fir was <2% of full sunlight, 2-10% for Douglas-fir, and 20-30% for ponderosa pine. Survival of all species increased at higher light intensities (Atzet and Waring 1970). The highest survival rates for Douglas-fir were found on shaded portions of clearcuts (Isaac 1938). Seedlings exhibited greatest height growth where the midday maximum was 20% of full light (Isaac 1943). Williamson (1973) found best survival of

seedlings on south-facing slopes at approximately 50% shade. As light intensity increased up to full sunlight, growth rates of established understory trees improved (Emmingham and Waring 1973, Williamson and Ruth 1976).

Although self-shading and competition among plants make light a limiting resource (Norman and Jarvis 1974), other environmental factors may be important. Reduced temperatures at the soil-air interface and in the soil, for example, improved survival of germinants where soil surface temperatures are high (Williamson 1973, Helgerson *et al.* 1982, Childs and Flint 1987). Childs (1985) showed that the amount of soil water available to the understory decreased markedly with increased overstory basal area. For example, an overstory of 10 m^2/ha (44 ft^2/acre) basal area used an estimated 20% of the plant-available seasonal water and an overstory basal area of 39.5 m^2/ha (174 ft^2/acre) used an estimated 50% of the plant-available seasonal water.

STAND DENSITY AND PLANT COMPETITION

Although residual trees may influence growth and composition of the understory by shading and the use of site-specific resources, this effect may be confounded with understory density. As plants grow, competition for site-specific limiting growth factors, such as light, water, and nutrients intensifies, resulting in decelerating individual plant growth. Growth reduction due to competition has been characterized by the Self-Thinning Rule or the -3/2-power rule (Yoda *et al.* 1963, Westoby 1984, Lloyd and Harms 1986, Zeide 1987). The model describes reciprocal changes in the average plant mass, w, and the number of plants per unit area, N, during the development of a monospecific even-aged stand with complete crown closure according to the formula:

$$w = kN^{-3/2} \quad (1)$$

where k is a species-specific coefficient and -3/2 is a constant independent of species, location, age, initial density, and site quality (Zeide 1987).

Like the Self-Thinning Rule, Reineke's (1933) stand density index (SDI), is related to the concept of a maximum size-density relationship. SDI is based on a predictable relationship between quadratic mean diameter (dq) (diameter of tree of average basal area) and the number of trees per hectare (tpha). SDI is computed according to the formula (Daniel and Sterba 1980):

$$SDI = tpha\ (dq/25)^{1.605}. \quad (2)$$

Plotting the logarithm of tpha against the logarithm of dq of fully stocked stands shows a linear relationship. The intercept of the size-density line varies among species (Reineke 1933), while the same slope could be used to define the limits of maximum stocking. This negatively sloping line is expressed by:

$$\log tpha = -1.605 \log dq + k \quad (3)$$

where k is a species dependent constant. Although SDI and the -3/2 rule were developed in even-aged stands, residual tree stocking may limit the amount of biomass accumulation in the understory of multiple-layered stands.

Other measures of stand density and indicators of competition include BA, tpha, (Curtis *et al.* 1981, Holdaway 1984, Ritchie and Hann 1985, Wensel *et al.* 1987, Dolph 1988, Hann and Larsen 1991), or indicators of the relative canopy position of a tree such as crown class and basal area larger (BAL) (Wykoff *et al.* 1982, Wykoff 1986, Ritchie and Hann 1985, Dolph 1988). BAL estimates competition faced by individual trees and is defined as the sum of basal area of trees larger than the subject tree. The largest diameter tree in the stand would therefore have a BAL value of zero, while the smallest-diameter tree would have a BAL value near the total basal area of the stand.

SIMULATION STUDIES

From a variety of simulation studies, it appears that green tree retention reduces understory growth in comparison to clearcutting. Long and Roberts (1992) used the PROGNOSIS growth and yield model (Wykoff *et al.* 1982) to simulate stand development of a mixed-conifer stand in Northern Idaho with abundant grand fir (*Abies grandis* (Dougl.) Forbes) and western hemlock in the understory, and Douglas-fir and a few mature (150+ years) western red cedar in the overstory. Compared to a clearcut, retention of 5-35 trees/acre (12-87 tpha) resulted in a growth reduction in the understory between 26-56% after an 80-year rotation. The marginal effect on understory growth decreased from 5.1 to1.6% per leave-tree as the number of leave-trees increased. When growth and mortality of leave-trees were included in the yield calculation, Long and Roberts estimated a long-term growth reduction of 20%.

Garman *et al.* (1992) used the forest succession model ZELIG (Urban 1990), which simulates the annual establishment, diameter growth, and mortality of individual trees, to evaluate timber production and animal-habitat diversity. A scenario of clearcutting and replanting of Douglas-fir every 70 years, without retaining any overstory and dead wood, was compared to a scenario with clearcutting every 125 years and retaining 40 overstory tpha over the entire rotation. They concluded that after 375 years clearcutting yielded about twice the BA of the second scenario due to shading effects.

Birch and Johnson (1992) used the ORGANON growth and yield model (Hann 1989) to simulate understory growth over 60- and 90-year rotations with a Douglas-fir overstory (5-50 tpha) on a site of average productivity (50-yr King's SI of 105). During the rotation, a 10% blow-down for leave-trees was assumed and 2.5-5 snags/ha were created every 30 years. Compared to a clearcut, they found a 5-38% decline in understory growth rates depending on the number of trees left, their size, and the rotation age of future stands. The marginal effect

on understory and total stand growth decreased as the number of leave-trees increased and as the rotation increased. When leave-trees were included in the yield calculation, green tree retention between 5-50 tpha resulted in an overall growth reduction between 8-25%.

EMPIRICAL STUDIES

In the German pine region, Baader (1941) compared the volume production of a Scots pine (*Pinus silvatica* L.) reserve tree system, with the potential yield of a clearcut system on a rotation of 80-100 years. A reserve system is characterized by overstory "reserve" trees, that are retained on the site for a second rotation. The number of reserve trees dropped from 50 to 20 tpha during the rotation. Crown cover was about 12-15% and BA 4-6 m^2 throughout the rotation. Increment loss in the pine understory was examined on nested circular plots around a reserve tree with radii of 5, 7.5, 10, 15, and 20m. Growth reduction in the innermost plot increased markedly with age. Beyond 15m BA there was no influence and reductions beyond 7.5m were generally not apparent beyond the age of 60 years. By the age of 80 years Baader found a 19% volume reduction in the understory and a 2-4% lower volume yield when growth of the reserve trees was taken into account.

Mang (1955) investigated the volume production of a Scots pine reserve tree system with more shade tolerant species in the understory in southern Germany. The understory was a mixed-conifer stand with 20% Scots pine and 80% white fir (*Abies alba* L.) and Norway spruce (*Picea abies* (L.) Karst.). He determined volumes and volume increments of all individual understory trees on 7 paired, concentric plots, each of 0.0314 hectares (10m radius) with and without reserve trees. Mang (1955) found that the average increment reduction of the understory was 10% for the whole rotation of 80-100 years, beginning with 60 reserve tpha (12% ground cover) and finishing with 45 reserve tpha (16% ground cover), but that it was spatially highly variable. Including reserve trees into the volume calculation

resulted in total volume yields between -14 and +10% compared to stands without reserve trees.

Few studies have been conducted to assess the spatial scale over which residual trees affect the development of the new stand. McDonald (1976) calculated height growth loss for seedlings in a California ponderosa pine (*Pinus ponderosa* Dougl.) stand where 4,8, and 12 seed trees/acre (10, 20, and 30 tpha, respectively) were left for 9 years following harvest. He found that overstory seed trees exhibited effects on the understory up to at least 40 feet (12m). Compared to seedlings grown in the open, seedlings less than 20 feet (6m) from a seed tree suffered an equivalent of 6.8 years of loss in height growth after 9 years and 10.6 years of loss after 13 years.

Volume reduction of second growth over an entire rotation due to old-growth trees was investigated in mixed-age, mixed-species stands in the western Oregon Cascades (USFS, Willamette NF, 1988). Plots were located in a 90-year-old Douglas-fir understory and in a 75-year-old understory with noble fir (*Abies procera* Rehd.), western hemlock, Douglas-fir and sparse grand fir and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) using old-growth trees as plot centers. From each old-growth tree transects of 50 feet were taken at a cardinal direction and every understory tree within 10 feet of the transect line was measured for diameter and distance. Within a 25 foot distance to an overstory tree understory tree growth was heavily reduced. Over the whole rotation a 3.2 and 2.9% volume reduction per residual tree of the Douglas-fir and the mixed-species understory was estimated, respectively.

Hoyer (1993) examined the effect of overstory trees on understory tree height. He found understory height to be a function of distance to overstory trees. At distances beyond 25 feet understory trees attained 80-84% of the height of site trees for understory ages between 10 to 60 years and for site index 110. Trees over 45 feet from the overstory exceeded 92% at understory age 60. Beyond 60ft (18.3m), understory trees achieved 98% of the height of site trees.

STUDY AREA

This study was conducted in the physiographic province of the Western Central Oregon Cascade Range (Franklin and Dyrness 1973) in the Willamette National Forest (43° 45' to 44° 45' N latitude and 122° 22' to 121° 52' W longitude). This province consists of Tertiary (Oligocene and Miocene) basaltic lava flow and pyroclastic rock parent material (Franklin and Dyrness 1973), which formed the mountainous, steep, deeply dissected western slope of the range (Peck *et al.* 1964).

Soils can be divided into two groups according to parent material. Soils derived from pyroclastic parent materials (tuffs and breccias) are often deep, fine textured, but poorly drained on gentle slopes (Haploxerults), and less-developed, stony and gravelly clay loams (Haplumbrepts and Xerumbrepts) on steeper slopes. Soils derived from basic igneous rocks (basalt and andesite) are well-drained, stony, and coarse textured (Agrixerolls, Haplohumults, or Xerumbrepts) (Franklin and Dyrness 1973).

The climate is maritime and is characterized by moderate temperatures, abundant rainfall, cool and wet winters, and dry summers (Franklin 1979). Precipitation shows a distinct seasonal distribution pattern with 72% occuring between November and March and 6-9% between June and September (Franklin and Dyrness 1973) and ranges from about 1500 to 2500mm (Oregon Climate Service 1993). The local climate is affected by elevation and topography. Precipitation and snowfall increase with elevation. Temperatures decrease with elevation. Mean annual and mean July temperatures in the Western Cascades range from 9-10°C and 17-19°C, respectively (Franklin and Dyrness 1973). Plant moisture stress seldom exceeds 15 bars during the growing season (Zobel *et al.* 1976, Hemstrom *et al.* 1987).

Plots were located in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). This zone is the most extensive vegetation zone in the Douglas-fir of western Oregon and Washington and the most important for timber production (Franklin 1979). In the Western

Central Cascades the elevational range of this zone is from 150-1000 m (Franklin 1979). *Pseudotsuga menziesii - Tsuga heterophylla* forests occupy a wide range of environments and vary markedly in composition, structure, and productivity along moisture and temperature gradients (Zobel *et al.* 1976, Franklin 1988). Some variation within the zone regarding seral and climax species exists. Douglas-fir typically dominates young forests, often forming pure stands (Franklin 1988). However, depending on available seed, mixed-species stands may develop following disturbance (Franklin and Dyrness 1973). In the absence of disturbance, there is a tendency for western hemlock to replace Douglas-fir (Munger 1940, Hansen 1947, Cooper 1957, Barrett 1962, Franklin and Dyrness 1973). On environmentally moderate sites, western hemlock appears to be the sole climax species, while Douglas-fir can be the climax species on dry sites. Western red cedar is common on wet to very wet sites (Franklin and Dyrness 1973).

METHODS

SITE SELECTION

Study sites were selected during the spring and summer of 1993 after initial screening (see Acknowledgements) and field reconnaissance of sites that were identified from recent aerial photographs and topographic maps. Aerial photographs were used to assess stand structure and degree of disturbance, and topographic maps to assess elevation. Sites were selected according to the following criteria:

1. Presence of two-aged stands with mature to old-growth residual trees over well-stocked young tree cohorts and an adjacent area without residual trees. All stands originated after disturbance, which killed most of the overstory trees in the two-aged stands, and all of the overstory stands in the control plots. This permitted the establishment of paired plots.
2. To minimize variation in macroenvironment, disturbance, and establishment history, and aspect, slope, and topographic position within a pair, sites were located entirely on one topographic feature. No major slope breaks, drainages, or other obvious soil differences were allowed within individual plots.
3. Stands with shrub dominance or excessive recent mortality of the young cohort were excluded from the study to eliminate understocked stands.

PLOT LOCATIONS

A total of 14 stands (Table 1) were found on the Detroit, Sweet Home, Blue River, McKenzie, and Lowell Ranger Districts and sampled during the summer of 1993. Stands ranged in elevation from 520 to 850 m and were located in the western hemlock/dwarf Oregon grape (TSHE/BENE), western hemlock/dwarf Oregon grape-salal (TSHE/BENE-

GASH), and western hemlock/ rhododendron-dwarf Oregon grape (TSHE/RHMA-BENE) (Hemstrom *et al.* 1987) plant associations.

Table 1. Plot locations.

Pair #	Ranger District	R/Z[1]	Elev. (m)	Slope (%)	Slope-Pos.[2]	Aspect (azim)	Latitude (degrees)	Longitude (degrees)	Plant Association from Hemstrom *et al.* (1987)
1	Blue River	R	823	85	B	14	44°13'52"	122°17'21"	TSHE/BENE
	Blue River	Z	823	60	B	29			
2	Blue River	R	823	75	B	350	44°14'02"	122°17'01"	TSHE/BENE--
	Blue River	Z	823	80	B	343			TSHE/RHMA-BENE
3	Blue River	R	671	75	T	210	44°11'24"	122°16'48"	TSHE/BENE
	Blue River	Z	671	68	T	217			
4	Blue River	R	853	73	T	225	44°05'12"	122°12'49"	TSHE/BENE
	Blue River	Z	853	77	T	230			
5	Detroit	R	640	30	M	143	44°43'00"	122°06'13"	TSHE/BENE
	Detroit	Z	640	40	M	153			
6	Lowell	R	731	62	T	128	43°58'41"	122°27'11"	TSHE/BENE-GASH
	Lowell	Z	731	55	T	120			
7	Lowell	R	701	28	T	102	43°48'26"	122°38'49"	TSHE/BENE
	Lowell	Z	701	17	T	110			
8	Lowell	R	701	50	T	288	43°48'11"	122°38'37"	TSHE/BENE
	Lowell	Z	701	35	T	282			
9	Lowell	R	518	62	T	128	43°48'53"	122°36'51"	TSHE/BENE-GASH
	Lowell	Z	518	17	T	142			
10	Lowell	R	792	60	T	124	43°48'02"	122°39'09"	TSHE/BENE-GASH
	Lowell	Z	792	57	T	112			
11	McKenzie	R	701	32	T	220	44°11'53"	122°12'28"	TSHE/BENE-GASH
	McKenzie	Z	701	32	T	230			
12	McKenzie	R	671	33	M	180	44°11'40"	122°12'32"	TSHE/BENE-GASH
	McKenzie	Z	571	25	M	193			
13	SweetHome	R	671	53	T	181	44°23'54"	122°14'21"	TSHE/BENE
	SweetHome	Z	671	70	T	172			
14	SweetHome	R	640	30	M	194	44°23'50"	122°14'49"	TSHE/RHMA-BENE
	SweetHome	Z	640	30	M	199			

[1]- R=plots with large residual trees, Z=plots without residual trees
[2]- Position on slope: B=Bottom third, M=Middle third, T=Top third

The TSHE/BENE type, the most common western hemlock series on the Willamette National Forest, occurs on warm, well-drained, moderately-productive soils on all aspects below 1000 m elevation and on southerly aspects above 1000 m (Hemstrom *et al.* 1987). The canopy is dominated by Douglas-fir, western hemlock, and western red cedar. Dwarf Oregon grape (*Berberis nervosa* Pursh) and vine maple (*Acer circinatum* Pursh) dominate the shrub layer. Salal (*Gaultheria shallon* Pursh) joins the shrub layer in the TSHE/BENE-GASH

association, which occurs on well-drained soils, usually below 1000 m elevation and indicates slightly drier conditions. Western red cedar and Pacific yew (*Taxus brevifolia* Nutt.) are often well represented in the TSHE/RHMA-BENE association. It occurs on north-facing slopes between 600 and 1400 m elevation (Hemstrom *et al.* 1987). The environment is warm to moderately cool with moderate summer droughts.

PLOT DESIGN AND MEASUREMENTS

Paired plots were established to compare stands with residual trees over well-stocked young cohorts with nearby stands without residual trees. Concentric, fixed-radius plots were nested to create a "buffer" between the inner or "detection plot" and the outer plot, that either had large residual trees ("residual plot") or did not have residual trees ("zero-residual plot"). The response variables were assessed in the "detection plot," which had a slope-corrected radius of 12.6m or an area of 500m^2 (1/8 acre). The larger plot had a radius of 30.9m or an area of 3000m^2 (3/4 acre) in which residual density was similar to that in the detection plot. A "buffer" width of 18.3m (60 ft) was chosen based on Hoyer's (1993) findings that the influence of residual trees on growth rates in the new stand was minimal beyond 18.3m. Residual trees in this study consisted of large survivors of the disturbance event that initiated the new stand (generally fire), which were still alive at the present time. Residual trees were measured within the larger plot.

In the detection plot, species, dbh to the nearest centimeter, canopy class, and whether the tree was alive or dead were recorded for all trees over 5cm dbh. Measurements of tree height and height to the base of the crown were taken on all residual trees and at least two representative, undamaged trees for each combination of species and canopy class (see pg. 32) among the young cohort. Canopy class for the young cohort was determined

relative to the general canopy layer formed by all trees in the young cohort. The decay class of dead trees was recorded after Cline *et al.* (1980).

Increment cores of at least 100 years were obtained for living residual trees and a subsample of live understory trees in the detection plot. Cores were taken on the up-slope side at breast height of all trees. Data on slope, aspect, and topographic position were collected in each of the paired plots. Elevations were obtained from topographic maps. A transformation was used to convert aspect to a more biologically meaningful continuous variable, which gives north a value of 0, south a value of 180, and east and west a value of 90 according to the following formula (Kaiser 1986):

$$\text{adjusted aspect} = 180 - |\,180 - \text{azimuth}\,| \qquad (4)$$

DEMOGRAPHIC ANALYSES

Tree ages and radial tree growth

Ages of understory trees were determined on 552 increment cores that contained the pith or were jugded to be within less than 10 years from the pith. Stand age was defined as the average of the breast-height age of dominant and codominant trees.

Ignoring the current year's growth, past 5-year diameter increment was measured with the aid of a dissecting microscope to the nearest 1/10th of a millimeter on all but one residual trees and a subsample of 718 Douglas-fir, 343 western hemlock, 6 western redcedar, and 40 hardwoods in the young cohort that were alive 5 years ago. Past 5-year radial growth was estimated for 451 trees from which either no cores were obtained because trees were rotten, or cores were of such a poor quality that exact growth measurements could not be performed. Because most of these trees were suppressed, the mean 5-year growth increment for suppressed trees was computed for each plot and species and applied to trees without useable cores.

The periodic 5-year mean radial increment (PRI) was calculated on an annual basis for all measured understory trees. PRI was compared with the mean radial increment (MRI). MRI, defined as one-half of a tree's dbh divided by its age, was calculated for trees with known age.

Tree heights and volumes

Heights were measured on 303 Douglas-fir, 158 western hemlock, 13 western redcedar, 8 bigleaf maple, 7 Pacific dogwood (*Cornus nuttallii* Audubon), 22 giant chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.), 1 Pacific yew, 3 Pacific madrone (*Arbutus menziesii* Pursh), and 5 incense-cedar (*Libocedrus decurrens* Torr.). All heights of dominant and codominant Douglas-fir trees measured in zero-residual plots were used to compute King's (1966) site index (SI). Within a paired plot, SI was assumed to be the same. Because the method for obtaining SI was different from the method described by King (1966), calculated site indices probably underestimate the site potential. SI is given for site description but was not used in further analyses because heights and ages varied substantially within any given plot.

After regressing dbh, BAL, and BA of each species against measured tree heights, individual tree heights were estimated for 420 Douglas-fir, 296 western hemlock, 10 giant chinkapin, 3 Pacific dogwood, 2 bigleaf maple, 1 western red cedar, and 1 Pacific yew; lacking height measurements. This permitted estimation of total stand volume (wood volume without bark) by using a nonlinear regression formula for each species (Means *et al.* 1994, Michener *et al.* 1990) (Table 2).

Table 2. Nonlinear regression formulae for tree volumes.

Species	Volume equation	Source
Douglas-fir	$0.2346*(dbh/100)^2$ *height	Michener *et al.* 1990
Western hemlock	$0.2961*(dbh/100)^2$ *height	Michener *et al.* 1990
Giant chinkapin	$0.0001169607*(dbh/100)^{2.02232}$ *height$^{0.68638}$	Means *et al.* 1994
Pacific dogwood	$\exp(5.60842 + 2.09759*\log(dbh))/100^3$	Means *et al.* 1994
Bigleaf maple	$0.0000718042*(dbh/100)^{2.22462}$ *height$^{0.83458}$	Means *et al.* 1994
Western redcedar	$0.2180*(dbh/100)^2$ *height	Michener *et al.* 1990
Pacific yew *)	$0.2961*(dbh/100)^2$ *height	Michener *et al.* 1990

*) due to lack of eqn. for TABR, TSHE coefficient was used as a substitution.

Understory density and tree position

Understory tree mortality, defined as the number of trees that died within the last five years, was estimated by assuming that trees of decay class 1 died within the previous five years. Backdating dbh and tpha to the start of the previous 5-year growth period allowed calculation of several tree position and stand density variables at the start of the previous 5-year growth period. This permitted regression of dbh and BA growth on tree position (BAL) and stand density variables (BA, tpha) to assess the influence of competition on growth and to develop predictive equations for future growth rates (Hann and Larsen 1991). However, backdating dbh and tpha can introduce measurement errors and potential bias of parameters, if measurement errors are correlated with the error of the residuals (Hann and Larsen 1991). The only solution to this potential problem lies in repeated measurements from permanent plots, but measures to determine whether errors are correlated are not readily available. Therefore, potential problems introduced by backdating were ignored, as is usually the case (Hann and Larsen 1991).

STATISTICAL ANALYSES

Stepwise variable selection was used to determine which independent variables were included in multiple linear regression models (SAS Institute, Inc. 1987). In this method, the order of variable selection does not determine which predictor explains more of the variance. At the individual tree level, 5-year dbh and BA growth, and height of Douglas-fir and western hemlock (dependent variables) were regressed against the number of residual tpha, understory tpha, BAL, total understory BA, dbh, age, elevation, and adjusted aspect (independent variables). Only measured trees were used in the regression. Differences between Douglas-fir and western hemlock were assessed through use of a categorical variable. At the stand level, the number of understory tpha, understory mortality, dq, understory BA, Douglas-fir BA, understory height, understory volume, and Douglas-fir volume (dependent variables) were regressed against the same independent variables.

The best model was the one that minimized the residual mean squared error, came closest to meeting the assumptions for a linear regression, and characterized the relationship between independent and dependent variables in a biologically meaningful way. Multicollinearity diagnostics were computed to examine the adequacy of the models. Multicollinearity is defined as a high degree of correlation among several independent variables. Predicted values were plotted against observed values for residual inspection. In all selected models, mean residuals were centered around zero and no systematic trends were detected.

Where indicated, natural logarithmic transformation was applied to dependent and independent variables to linearize regression models. In similar studies the residuals of the log-transformation were not normally distributed because of their skewness and kurtosis statistics (Hann and Larsen 1991). Standard log-bias correction procedures (Flewelling and Pienaar 1981) then produce mean residuals that are not zero and Furnival's (1961) index of

fit will be higher than for alternative regression methods. The use of weighted, nonlinear regression has been proposed over the use of log-transformed equations as it better fits the data (Zumrawi and Hann 1993). However, Cole and Stage (1972) compared dbh and BA increment equations as well as logarithmic transformations of each and concluded that the log of BA growth best met the regression assumptions of normally distributed residuals and constant variance. West (1980) concluded from a similar study that there was no *a priori* justification for choosing one over the other.

The standard errors in the individual tree models in this study were computed under the assumption that each tree was randomly selected from the population. Because all trees on a plot were measured, their selection was not truly random. Therefore their measurements are probably correlated with each other and standard errors may be underestimated (Dolph 1988, Hann and Larsen 1991).

The multiple linear regression analysis in this study did not explicitly use the paired plot design. All 28 plots were treated as independent samples that covered a range of residual tree densities with many data-points at zero-residual density.

Paired t-tests were performed to test for differences in age and dq between Douglas-fir and western hemlock. Only stands in which each species accounted for at least 10% of tpha were used in the analysis.

RESULTS

DESCRIPTION OF STANDS SAMPLED

Young cohorts were fully stocked and had high densities of Douglas-fir and western hemlock. In most cases stands without residual trees had higher understory and Douglas-fir basal areas and volumes than stands with residual trees.

Age of the young cohorts ranged from 55-121 years (Table 4). Thus stands were young to mature (Spies and Franklin 1991). Dq ranged from 19-47cm (Table 4). Understory tree density ranged from 440-1920 tpha (Table 4); densities of 17 of 28 stands exceeded those of fully stocked normal stands given in Bulletin 201 (McArdle *et al.* 1961). RD varied between 0.38-1.05 (Table 4). Thirteen of 14 paired plots had a higher RD in stands without residual trees. Stands with residual trees had a residual tree density between 3-57 tpha (Table 3). Residual trees accounted for 81-795m^3/ha in volume, understory volumes ranged from 311-1164m^3/ha and total stand volumes ranged from 443-1275m^3/ha (Table 5). Residual tree BA ranged from 5-52m^2/ha (Table 3). Understory BA was from 36-87m^2/ha (Table 4). The proportion of Douglas-fir BA was between 0-100% and 14 of 28 stands had above 90% (Table 4). Western hemlock was between 0-99% of BA and 14 of 28 stands had less than or equal to 1% (Table 4). In most cases, present understory BA was lower than 5 years ago due to mortality (Table 4). Comparison of paired stands indicates that understory BA was higher in 13 of 14 stands without residual trees (Table 4); total understory and Douglas-fir volume were higher in 12 of 14 stands without residual trees (Table 5). The two stands with residual trees that had higher Douglas-fir volume had the lowest residual densities. After including BA of residual trees, 10 of 14 pairs had higher total stand BA in stands with residual trees (Fig. 2D). When volumes of residual trees were included, 10 of 14

pairs had a higher volume in stands with residual trees (Table 5). For each stand, residual and understory tree characteristics are summarized in Tables 3-5 and Figs. 1-3.

Table 3. Characteristics of the residual tree component.

Plot	Dq (cm)	dbh Range (cm)	Live BA (m^2/ha) 1993	Live BA (m^2/ha) 1988	Live Residual tpha	Snags/ha	Mean Height * (m)	Height Range * (m)	Height SD[1] *
BR07R	97.6	72-127	24.9	24.6	33.3	17.1	41.3	30.9-53.9	7.2
BR08R	73.1	44-104	23.8	23.2	56.7	6.0	36.2	29.5-46.2	4.8
BR09R	122.5	81-150	15.7	15.5	13.3	10.3	41.2	19.7-54.8	15.0
BR17R	120.5	100-136	26.8	26.5	23.3	5.7	47.3	35.8-60.8	8.9
DE06R	103.1	88-126	13.9	13.7	16.7	0	45.4	36.5-50.1	5.2
LO01R	95.0	66-136	26.0	25.2	36.7	0	50.1	41.4-61.7	6.5
LO05R	107.8	72-128	51.7	50.5	53.3	0	50.3	34.8-58.9	5.9
LO06R	171.0	119-203	23.0	22.7	10.0	0	61.8	57.7-65.2	3.8
LO07R	136.4	102-151	19.5	19.3	13.3	1.9	45.2	27.8-59.5	13.1
LO08R	155.4	134-170	19.0	18.8	10.0	0	48.3	36.5-57.2	10.6
MC03R	132.0	132	4.6	4.5	3.3	0	66.7	N/A	N/A
MC04R	110.5	83-123	9.6	9.4	10.0	0	43.0	33.6-59.7	14.5
SH09R	116.0	100-130	7.0	6.8	6.7	0	37.0	31.0-43.1	8.6
SH13R	129.9	113-157	17.7	17.5	13.3	6.0	43.0	38.3-49.9	4.9

* live residual trees

[1] standard deviation

Table 4. Characteristics of the young cohort.

Plot	Age 1993 (years)	Dq[a] 1993 (cm)	Dq 1988[g] (cm)	Tpha[b] 1993	Tpha 1988	BA[c] 1993 (m^2/ha)	BA 1988 (m^2/ha)	PSME-%[d] 1993	TSHE-%[e] 1993	RD[f] 1993
BR07R[h]	104	22.96	20.12	860	1140	35.6	38.2	0	99	0.38
BR07Z	121	27.11	24.04	1380*	1680	79.7	79.8	65	28	0.99
BR08R	110	19.19	16.88	1480*	1880	42.8	44.9	23	65	0.54
BR08Z	111	20.12	17.19	1920*	2440	61.0	61.1	39	61	0.79
BR09R	62	26.93	23.26	900	1120	51.3	49.4	99	0	0.70
BR09Z	76	36.76	31.27	600	780	63.7	63.9	100	0	0.77
BR17R	65	25.70	21.64	900 *	1200	46.7	45.7	100	0	0.65
BR17Z	58	27.85	23.45	1040*	1480	63.3	64.8	92	0	0.84
DE06R	90	34.63	29.79	680 *	900	64.0	66.1	99	0	0.79
DE06Z	67	31.87	27.26	860	1220	68.6	72.2	100	0	0.88
LO01R	61	23.25	17.78	940	1620	39.9	42.2	64	36	0.52
LO01Z	55	24.07	19.27	1240*	1780	56.4	58.7	91	1	0.79
LO05R	83	32.48	28.37	460	600	38.1	39.7	35	57	0.40
LO05Z	84	31.07	27.67	860 *	1020	65.2	67.6	78	22	0.79
LO06R	84	35.42	31.20	480	620	47.3	49.7	48	49	0.50
LO06Z	87	30.12	27.23	920 *	1020	65.6	64.6	55	45	0.76
LO07R	92	30.24	25.57	660 *	920	47.4	48.8	84	16	0.59
LO07Z	94	36.14	34.10	800 *	880	82.0	82.6	66	29	0.91
LO08R	81	27.74	24.45	860 *	1080	52.0	51.9	85	15	0.67
LO08Z	85	37.34	31.87	680 *	880	74.5	77.3	100	0	0.89
MC03R	84	47.39	41.48	480	540	84.7	82.0	100	0	0.92
MC03Z	73	41.55	38.57	440	480	59.7	57.7	99	0	0.68
MC04R	87	34.68	30.39	620 *	760	58.6	58.9	98	1	0.72
MC04Z	95	38.57	35.10	740 *	840	86.5	85.5	99	0	1.02
SH09R	80	33.48	28.70	860	1040	75.7	75.2	97	1	0.94
SH09Z	81	32.51	29.12	1000 *	1160	83.0	82.3	100	0	1.05
SH13R	74	22.38	20.63	1200 *	1380	47.2	46.9	68	30	0.64
SH13Z	76	29.86	26.59	860	1000	60.2	58.9	84	14	0.76

[a] - mean squared diameter (Dq) (cm)

[b] - trees/ha (Tpha)

[c] - basal area (m^2/ha)

[d] - Douglas-fir proportion of basal area/ha (PSME-%)

[e] - western hemlock proportion of basal area/ha (TSHE-%)

[f] - relative density (RD) of the young cohort. Relative density was calculated by dividing Reineke's (1933) SDI by the maximum SDI value for a species (1450 tpha for Douglas-fir, and 1950 tpha for western hemlock) (Long 1985). Actual maximum SDI values were weighted according to the portion of Douglas-fir and western hemlock BA. Because hardwood BA in each stand was generally small (between 0 and 10% of total understory BA), hardwoods were given the maximum SDI value for Douglas-fir.

[g] - all 1988 values are estimates (see Methods)

[h] - residual plot (R), zero-residual plot (Z)

*- stocking above normal levels of Bulletin 201 (McArdle *et al.* 1961)

Table 5. Characteristics of the young cohort and volume of residual trees.

Plot	Height 1993[i] (m)	Height Range[i] (m)	Height SD	SI[j] (King)	Volume 1993 (m^3)	PSME Volume (m^3)	Residual Volume (m^3)[k]	Stand Volume (m^3)
BR07R	27.2	23.1-28.9	2.1	74 (5)	321.8	0	309.8	631.5
BR07Z	33.4	30.1-36.6	2.7		728.0	493.5		728.0
BR08R	28.3	24.7-30.0	1.8	59 (5)	311.4	74.2	289.6	601.0
BR08Z	25.9	23.1-30.5	2.7		443.7	179.6		443.7
BR09R	29.4	26.6-31.7	2.5	98 (3)	448.1	445.7	213.1	661.2
BR09Z	37.8	32.0-41.0	4.2		698.2	698.2		698.2
BR17R	30.4	23.9-35.5	4.2	89 (4)	431.8	430.4	435.4	862.2
BR17Z	29.5	20.8-39.7	6.8		596.8	551.8		596.8
DE06R	36.6	29.9-39.9	3.9	100 (3)	651.3	643.8	191.0	842.3
DE06Z	36.0	32.7-37.6	2.2		651.6	651.3		651.6
LO01R	31.5	24.4-36.4	4.2	102 (3)	378.2	245.3	409.2	787.4
LO01Z	33.1	29.9-37.2	2.5		510.3	456.4		510.3
LO05R	36.6	24.8-44.3	5.7	96 (3)	479.6	140.2	795.2	1274.8
LO05Z	38.1	33.9-41.4	2.5		723.3	559.7		723.3
LO06R	42.5	36.4-48.2	5.3	106 (3)	617.6	274.7	430.2	1047.8
LO06Z	43.5	41.1-47.4	1.9		821.0	457.0		821.0
LO07R	37.6	30.1-46.8	5.9	96 (3)	529.7	469.7	267.6	797.3
LO07Z	40.7	32.6-50.4	5.8		964.1	607.0		964.1
LO08R	37.7	31.9-41.9	3.2	96 (3)	545.1	478.6	281.2	826.3
LO08Z	38.8	36.1-44.5	2.9		809.6	809.6		809.6
MC03R	42.0	31.7-53.0	7.4	110 (3)	1164.9	1163.8	90.9	1255.8
MC03Z	41.4	34.5-45.3	4.7		733.6	729.3		733.6
MC04R	41.4	36.5-44.9	3.2	96 (3)	669.6	666.6	128.4	798.0
MC04Z	40.8	34.5-50.0	5.7		1021.8	1020.2		1021.8
SH09R	33.8	31.9-39.1	2.8	82 (4)	784.3	767.2	81.2	865.5
SH09Z	32.5	29.6-35.9	2.4		754.9	754.9		754.9
SH13R	32.2	22.5-42.2	5.9	80 (4)	421.8	290.0	227.6	649.4
SH13Z	30.2	25.4-33.3	3.1		580.1	498.8		580.1

[i] - Mean height of all dominant and codominant understory trees

[j] - Site Index (in feet) after King (1966), with Site Index Class given in parentheses, SI assumed to be the same for R and Z within each pair.

[k] - Equations for calculation of volume of residual trees are based on intact trees. Since many of the residual trees had broken tops, trees have less taper than assumed in the volume equations. Therefore, the volume of residual trees is probably underestimated.

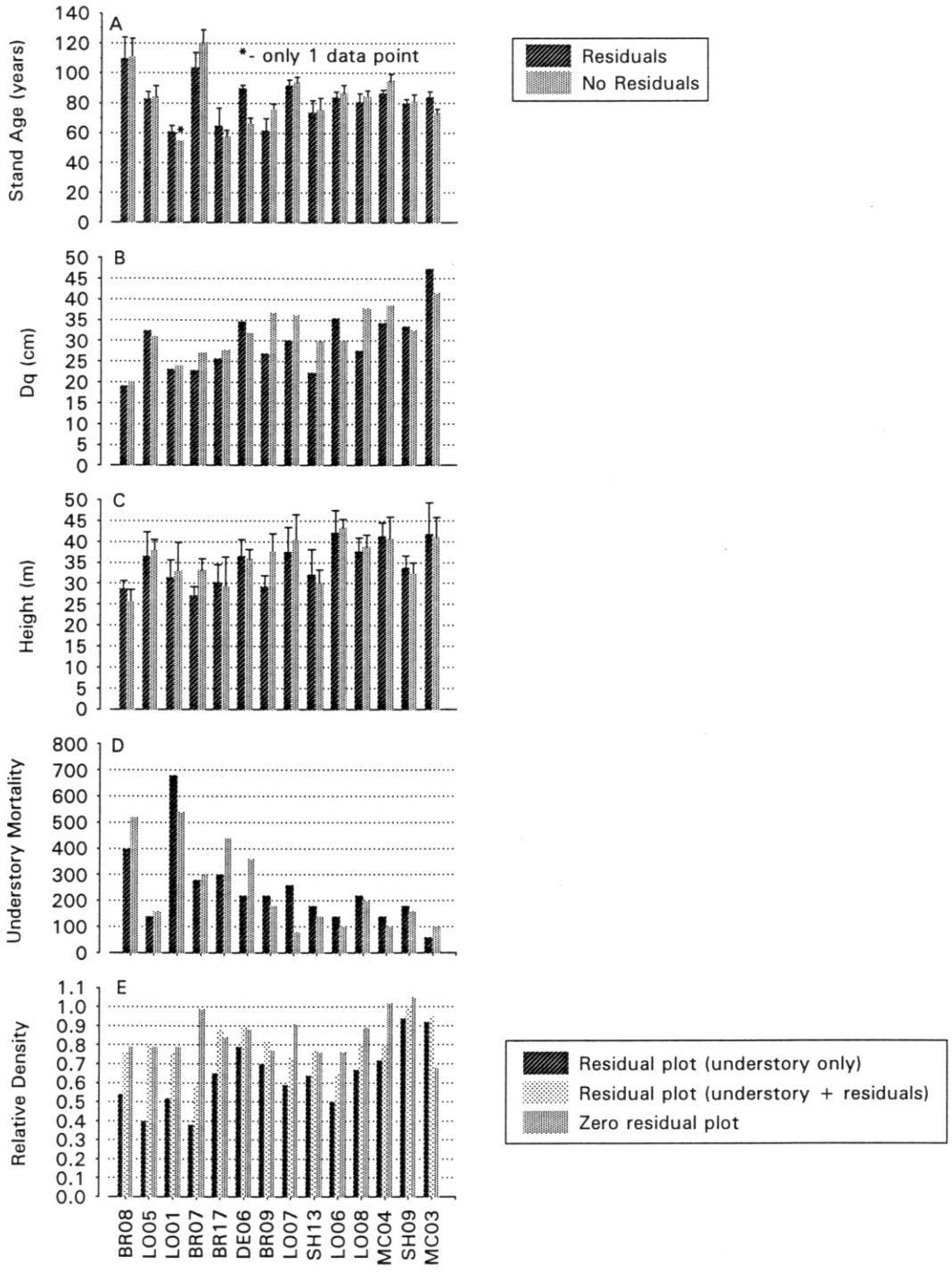


Figure 1. Selected stand characteristics across all stands. (A) Mean stand ages (with 1 SD), (B) Mean squared diameter, (C) Mean heights of dominant trees (with 1 SD), (D) 5-year stand mortality (tpha), (E) Relative Density. Stands are ordered by decreasing residual tree density.

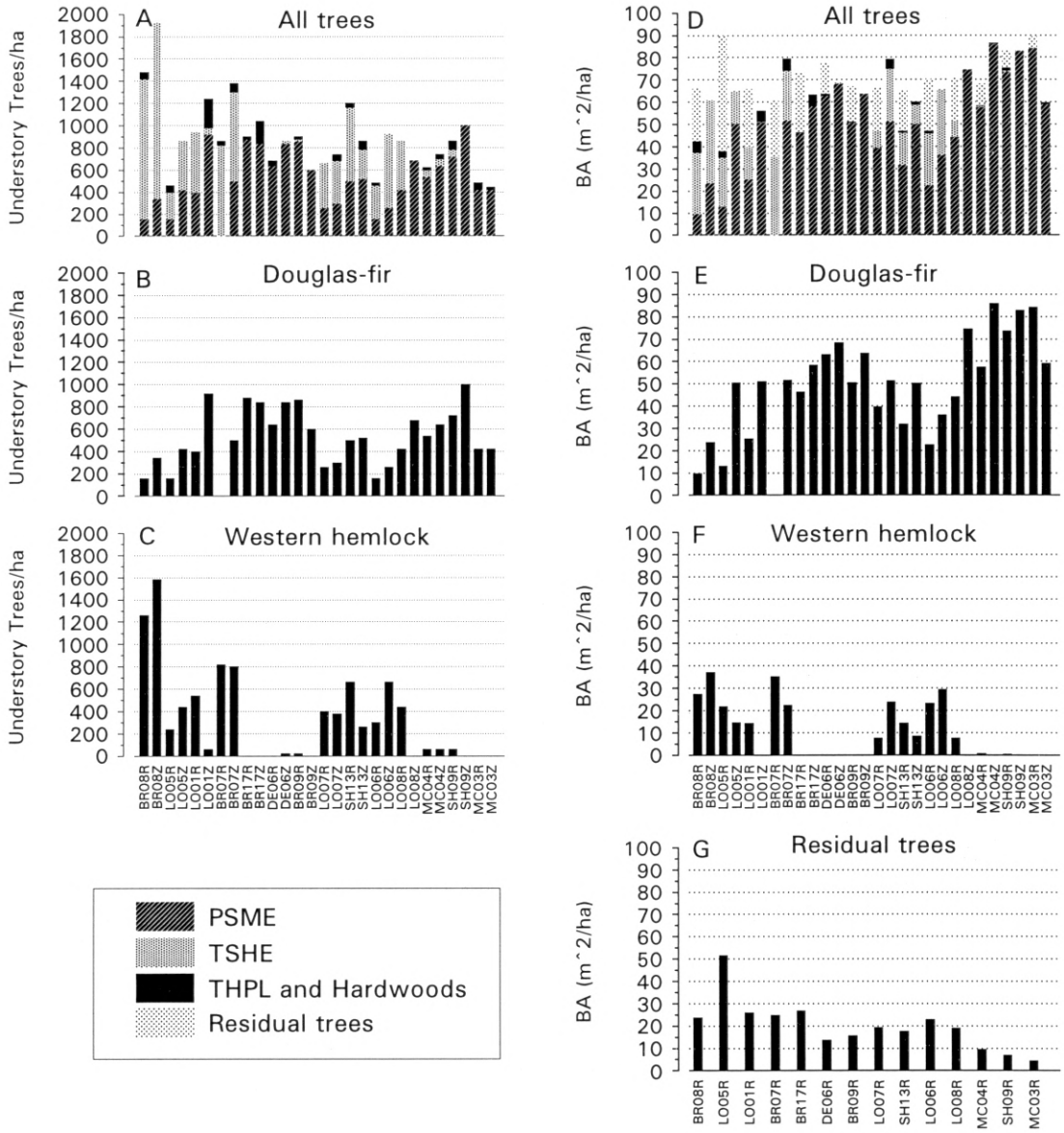


Figure 2. Understory trees and basal area per hectare. (A) All trees, (B) Douglas-fir, (C) Western hemlock, (D) BA of all trees, (E) BA of Douglas-fir, (F) BA of western hemlock, (G) BA of residual trees. Stands are ordered by decreasing residual tree density.

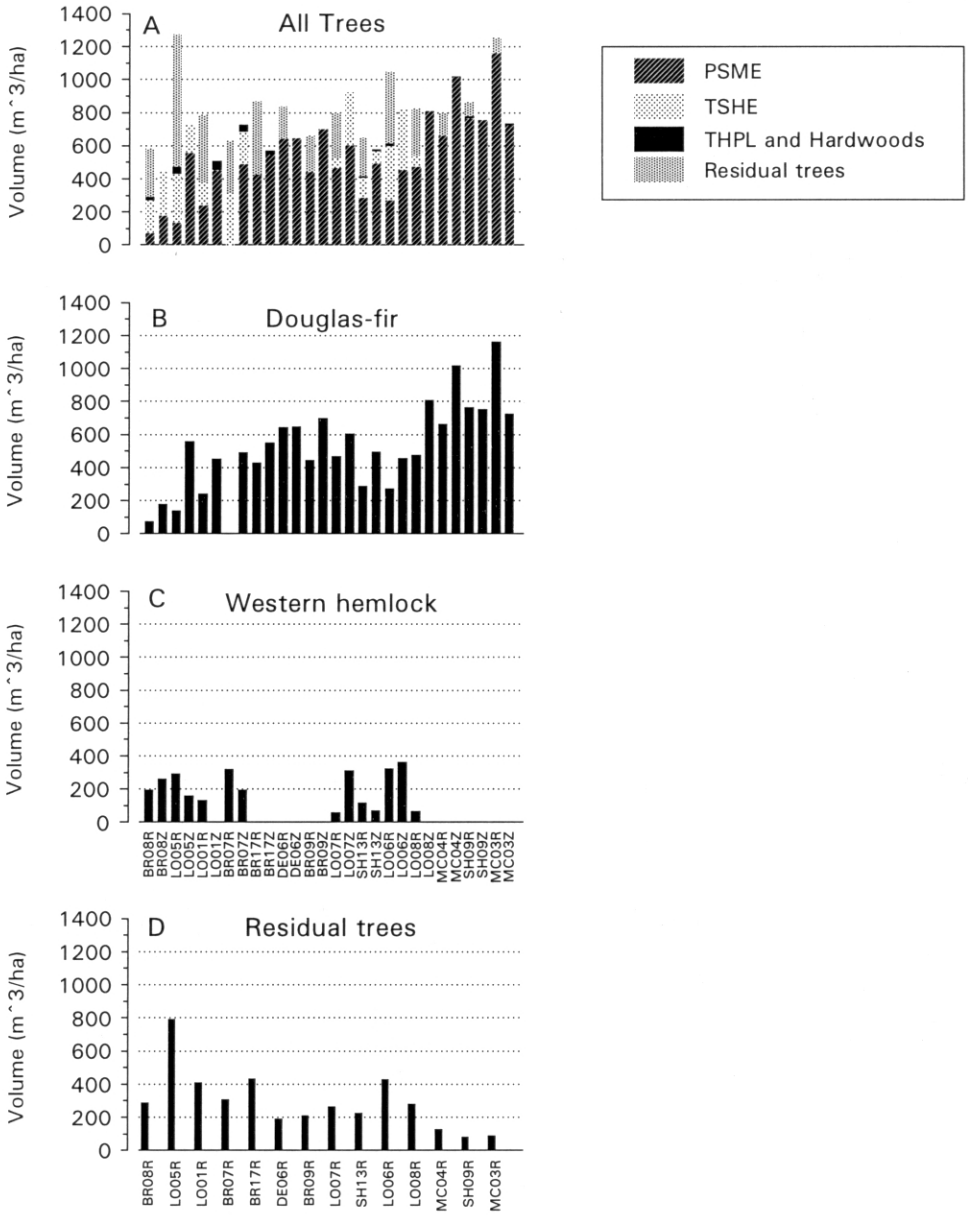


Figure 3. Volume per hectare. (A) All trees, (B) Douglas-fir, (C) Western hemlock, (D) Residual trees. Stands are ordered by decreasing residual tree density.

RELATIONSHIPS BETWEEN RESPONSE AND INDEPENDENT VARIABLES

Original data were plotted to explore relationships between dependent and independent variables. In Figure 4 dbh- and BA-growth data are plotted against dbh (size) and BAL (position). It shows that as the dbh increased and subsequently BAL decreased, radial growth of understory trees increased. Although the relationships showed a distinct pattern, there was a large amount of variation in the data.

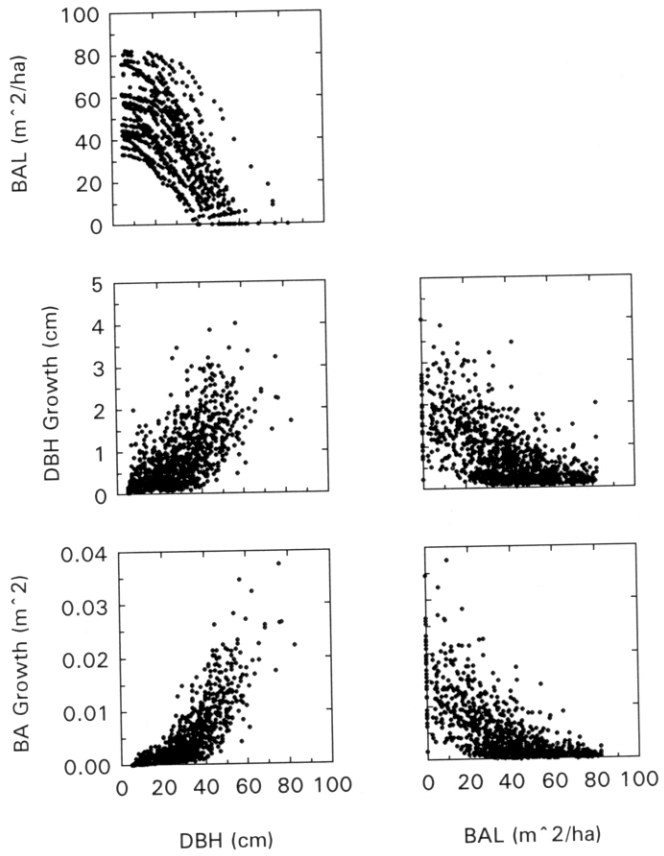


Figure 4. Relationships between dbh, BAL, and 5-year growth of DBH and BA of the young cohort.

The relationships of dq, BA, volume, and height of dominant and codominant understory trees to density of residual and understory trees, dq, and age of the young cohort were plotted for the original data in Fig. 5.

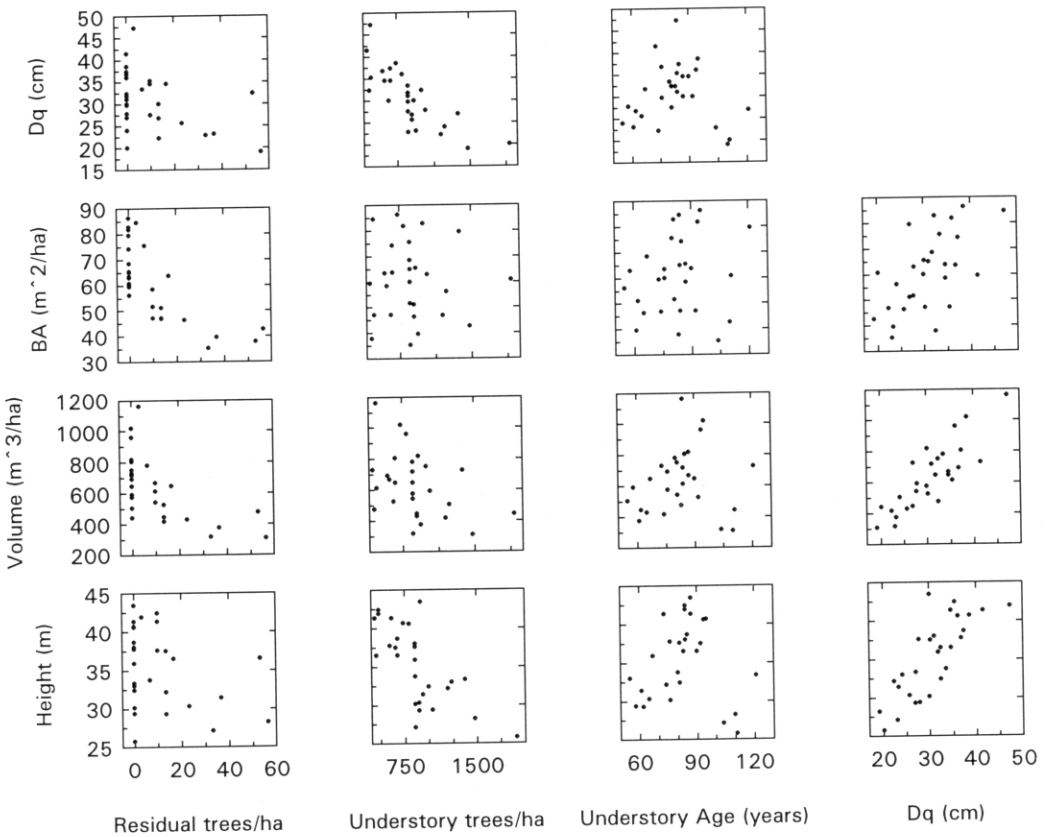


Figure 5. Relationship of dq, BA, volume, and height of dominant understory trees to residual tpha, understory tpha, age and dq of the young cohort.

The plot of residual tpha versus height of dominant understory trees did not show a clear pattern. In contrast, the data suggested a negative association between residual tpha and BA, and volume of the young cohort. There was a weak negative association between residual tpha and dq. Understory density showed a negative association with height of dominant understory trees, dq, and volume. However, the data did not suggest a relationship between understory tpha and understory BA. The data showed no clear pattern for

associations between age of the young cohort and dq, volume, and height due to the four oldest stands. It should be noted that these four outliers all had a high western hemlock component in the young cohort. Furthermore, no clear pattern existed for understory age and BA of the young cohort. Dq seemed to have a strong positive association with BA, volume, and height of the young cohort.

Figure 6 shows the association between BA and residual and understory tpha plotted for all canopy classes. Residual tpha seemed to be negatively associated with BA of dominant, codominant, and intermediate canopy classes, though the relationship was weak for codominant and intermediate canopy classes. Suppressed trees showed a weak positive association with residual trees. The data suggested a week negative association between understory tpha and BA of dominant and codominant canopy classes. No clear pattern seemed to exist between density of the young cohort and BA of the intermediate canopy class. The BA of suppressed class was positively associated with the density of the young cohort.

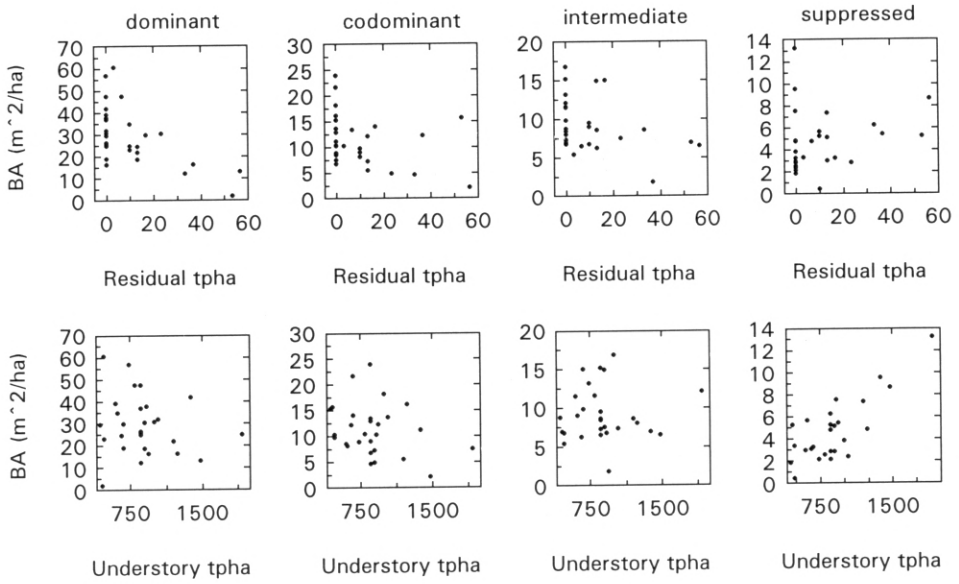


Figure 6. Relationship of basal area of dominant, codominant, intermediate, and suppressed understory trees to density of residual and understory tpha.

Periodic mean radial increment (PRI) and mean radial increment (MRI) were different for Douglas-fir and western hemlock. Both PRI and MRI differed among canopy classes and decreased from dominant to suppressed trees (Table 6). Note that MRI>PRI, suggesting slowing of radial growth and that culmination of radial growth has occurred. PRI of dominant western hemlock was higher in stands without residual trees. Dominant and intermediate Douglas-fir had higher PRI in stands with residual trees.

Table 6. Periodic and mean radial increment for Douglas-fir and western hemlock in different canopy classes.

Species	R/Z	CC[1)]	% BA	N	dq (cm)	PRI (cm/yr)	SE[2)] PRI	N	MRI (cm/yr)	SE MRI
PSME	R	dom	46.0	87	48.5	0.36	0.016	71	0.62	0.018
PSME	Z	dom	45.8	119	47.2	0.30	0.011	93	0.59	0.016
PSME	R	cod	15.0	51	36.1	0.18	0.015	42	0.47	0.015
PSME	Z	cod	18.6	87	35.2	0.21	0.013	52	0.46	0.014
PSME	R	int	12.7	79	26.8	0.10	0.011	41	0.38	0.014
PSME	Z	int	14.3	113	27.1	0.08	0.007	52	0.37	0.011
PSME	R	sup	4.6	65	17.7	0.05	0.004	28	0.29	0.013
PSME	Z	sup	3.2	62	17.3	0.07	0.009	28	0.28	0.015
TSHE	R	dom	5.9	18	38.3	0.32	0.026	17	0.44	0.033
TSHE	Z	dom	6.6	22	41.8	0.35	0.032	13	0.49	0.036
TSHE	R	cod	3.7	13	35.6	0.28	0.025	11	0.46	0.033
TSHE	Z	cod	1.9	11	31.5	0.25	0.030	9	0.34	0.033
TSHE	R	int	3.7	25	25.5	0.16	0.020	12	0.32	0.029
TSHE	Z	int	1.6	16	24.2	0.15	0.013	7	0.30	0.038
TSHE	R	sup	5.1	111	14.2	0.08	0.006	37	0.22	0.012
TSHE	Z	sup	3.9	115	14.0	0.07	0.006	30	0.18	0.009

[1)] Canopy classes (Young Cohort):
dominant: crown emerges from the general canopy layer, and so receives light from the top and the sides
co-dominant: crown extends to the top of the general canopy layer, and so receives light from the top, but not much from the sides
intermediate: crown extends into the lower portion of the general canopy layer, and so receives mostly filtered light from the top and the sides
suppressed: crown completely beneath the general canopy layer
[2)] Standard Error

Table 6 shows that the proportion of the understory BA of dominant and codominant canopy classes was approximately the same in R and Z stands. However, the basal area and density of dominant and codominant Douglas-fir (Table 7) were higher when no residual trees were present. For example, the basal area and density of dominant and codominant

trees was 29 and 39%, and 34 and 53% higher in stands without residual trees, respectively (Table 7).

Table 7. Ratio of basal area and density in Z to R stands by crown class.

	BA ratio Z/R	density ratio Z/R
dominant	1.34	1.29
codominant	1.53	1.39
intermediate	1.50	1.26
suppressed	1.21	0.96
overall	1.21	1.27

RESULTS OF PAIRED-T-TESTS

Differences in mean breast-height age between Douglas-fir and western hemlock was assessed in 13 stands in which both species accounted for at least 10 % younger cohort tpha. Mean breast-height age of Douglas-fir was 87.9 years (SD= 17.5 years, range from 55 to 121 years) and western hemlock was 79.9 years (SD=15.3 years, range 36 to 102 years). Breast-height age differences varied between 1 and 20 years, with a mean age difference of 9 years (H_0:diff=0, $p<0.0001$).

In the same stands dq of Douglas-fir and western hemlock was 35.9cm (SD=6.1cm) and 21.3cm (SD=6.2cm), respectively. Except for one stand, Douglas-fir had a greater dq than western hemlock. Differences in dq ranged from -1.6 to 28.5cm with a mean difference of 14.6cm ($p<0.0001$).

Diameter distributions across all stands showed more western hemlock in the diameter range between 5 and 15cm than Douglas-fir. For diameters over 20cm Douglas-fir was more abundant than western hemlock. This resulted in an inversed J-shape distribution for western hemlock and a positively skewed normal distribution for Douglas-fir (Fig. 7).

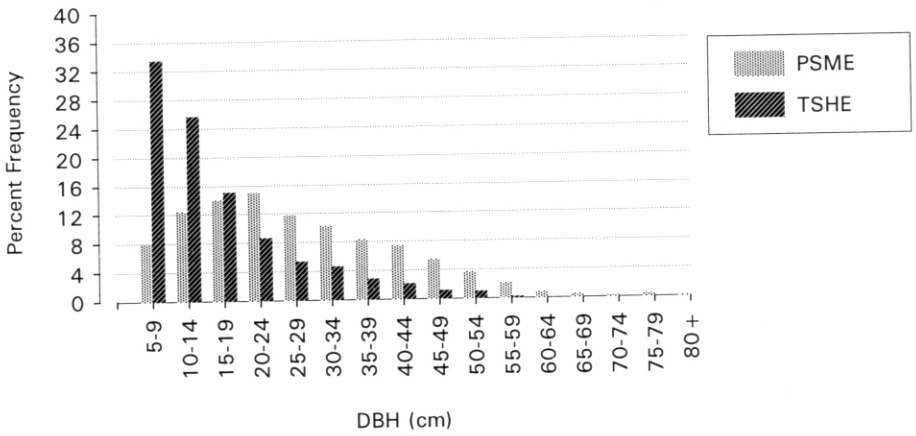


Figure 7. Diameter distribution of Douglas-fir and western hemlock.

RESULTS OF MULTIPLE LINEAR REGRESSIONS

The models resulting from multiple linear regrsssion are presented in Tables 8 and 9. All but one independent variables for the stand level and individual tree regression models were statistically significant at the α=0.05 level. Regression coefficients, standard errors, degrees of freedom, the value of the F-statistic, the value of the dependent mean, and the coefficient of determination are given in Tables 8 and 9. Also reported are the square root of the error mean square (root MSE) and the coefficient of variation (CV). Root MSE estimates the standard deviation of the error. CV is defined as the ratio of root MSE to the mean of the dependent variable, expressed as a percentage, and is a measure of relative variation. This coefficient is sometimes used as a standard to judge the relative magnitude of the random error.

Predictions from selected models are shown in Tables 10 and 11. Response surfaces generated from the models are displayed in Figures 8 and 9.

Table 8. Selected stand level regression models. Measurements backdated to the start of the previous 5-year growth period are denoted with a subscript 1.

Parameter	Estimate	Standard Error	T for H0: Param=0	Pr > |T|	Partial R^2	
Total understory volume						
Intercept	7.076	0.116	60.7	0.0001		[Mean ln(Vol)=6.40, df=25,
ln(Residual tpha)	-0.152	0.024	-6.20	0.0001	0.415	F=26.50, C.V.=3.04,
understory tpha	-0.0005	0.0001	-4.54	0.0001	0.264	Root MSE=0.70, R^2=0.68]
Douglas-fir volume						
Intercept	6.367	0.298	21.4	0.0001		[Mean ln(PSME-Vol)=6.15,
Residual tpha	-0.026	0.003	-7.84	0.0001	0.577	df=23, F=43.35, C.V.=4.10,
understory tpha	-0.0005	0.0002	-3.01	0.0062	0.059	Root MSE=0.25, R^2=0.85]
adjusted aspect	0.004	0.001	3.07	0.0055	0.213	
Total understory basal area						
Intercept	3.800	0.146	26.1	0.0001		[Mean ln(BA)=4.08, df=25,
ln(Residual tpha)	-0.106	0.018	-5.75	0.0001	0.595	F=31.30, C.V.=3.43,
ln(dq)	0.014	0.004	3.23	0.0036	0.119	Root MSE=0.14, R^2=0.71]
Douglas-fir basal area						
Intercept	2.958	0.255	11.6	0.0001		[Mean ln(PSME-BA)=3.82,
Residual tpha	-0.020	0.003	-6.46	0.0001	0.603	df=23, F=39.10, C.V.=6.09,
adjusted aspect	0.005	0.001	4.35	0.0002	0.207	Root MSE=0.23, R^2=0.84]
dq	0.015	0.008	1.89	0.0716	0.025	
Understory density						
Intercept	8.436	0.163	51.60	0.0001		[Mean ln(tph)=6.72, df=25,
Residual tpha	-0.100	0.021	-4.85	0.0001	0.169	F=56.99, C.V.=2.43,
ln(dq)	-0.051	0.005	-10.58	0.0001	0.631	Root MSE=0.16, R^2=0.82]
Understory mortality						
Intercept	-4.959	1.177	-4.21	0.0003		[Mean ln(mort)=5.29, df=25,
ln(understory $tpha_1$)	1.452	0.169	8.61	0.0001	0.701	F=39.79, C.V.=6.37,
Residual $tpha_1$	0.009	0.004	2.460	0.0215	0.046	Root MSE=0.34, R^2=0.76]
Mean squared diameter (dq)						
Intercept	6.855	0.301	22.75	0.0001		[Mean ln(dq)=3.40, df=25,
ln(Residual tpha)	-0.006	0.001	-6.14	0.0001	0.200	F=81.84, C.V.=2.43,
ln(understory tpha)	-0.503	0.045	-11.26	0.0001	0.668	Root MSE=0.08, R^2=0.87]

Table 9. Selected individual tree regression models. Measurements backdated to the start of the previous 5-year growth period are denoted with a subscript 1.

Parameter	Estimate	Standard Error	F-Value	Pr > F	Partial R^2
		Five-year dbh growth			
Intercept	-2.155	0.195		0.0001	
Ln(dbh_1) x species			132.89	0.0001	0.114
Douglas-fir	0.660	0.048		0.0001	
Western hemlock	0.759	0.047		0.0001	
Ln(Residual $tpha_1$) x species			28.44	0.0001	0.079
Douglas-fir	-0.083	0.017		0.0001	
Western hemlock	-0.138	0.019		0.0001	
BAL_1 x species		208.32		0.0001	0.322
Douglas-fir	-0.027	0.001		0.0001	
Western hemlock	-0.020	0.002		0.0001	
adjusted aspect	0.004	0.0004	112.41	0.0001	0.038
Mean ln(Dgro) = -0.72, df = 1169, F = 279.84, C.V. = -80.50, Root MSE = 0.58, R^2 = 0.626.					
		Five-year BA growth			
Intercept	-7.978	0.230		0.0001	
ln(dbh_1) x species			239.29	0.0001	0.024
Douglas-fir	1.144	0.052		0.0001	
Western hemlock	1.247	0.061		0.0001	
BAL_1	-0.027	0.002	261.26	0.0001	0.383
ln(Residual $tpha_1$) x species			43.33	0.0001	0.142
Douglas-fir	-0.129	0.021		0.0001	
Western hemlock	-0.188	0.023		0.0001	
Mean ln(BAgro) = -5.68, df = 1171, F = 461.47, C.V. = -13.52, Root MSE = 0.77, R^2 = 0.663.					
		Understory height			
Intercept	1.091	0.056		0.0001	
DBH	0.155	0.005	812.71	0.0001	0.665
DBH^2	-0.003	0.0002	347.84	0.0001	0.172
DBH^3	0.00002	0.000001	184.77	0.0001	0.044
Ln(Residual tpha) x species			3.61	0.0278	0.001
Douglas-fir	-0.004	0.007		0.5536	
Western hemlock	-0.022	0.008		0.0077	
understory tpha x species			20.67	0.0001	0.012
Douglas-fir	-0.0002	0.00003		0.0001	
Western hemlock	-0.0001	0.00003		0.0001	
Median ln(ht) = 3.19, df = 455, F = 543.96, C.V. = 5.84, Root MSE = 0.19, R^2 = 0.893.					

Stand-level models

Total understory volume was largely explained by residual tree density (R^2=0.415) and understory tpha (R^2=0.264). Residual tree density was more strongly correlated with overall understory volume than understory density (r=-0.64, and r=-0.43, respectively). Total understory volume decreased logarithmically with increasing residual tree density, resulting in decreasing effects per residual tree as residual tree density increased. Doubling the number of residual trees was associated with a reduction in median volume by a multiplicative factor of 0.90 (95% confidence interval 0.869 to 0.932). Increasing the number of understory trees from 500 tpha was associated with a reduction in median overall understory volume by a multiplicative factor of 0.95 (95% CI 0.927 to 0.972) per 100 understory trees.

Douglas-fir volume was best explained by residual tree density (R^2=0.577), adjusted aspect (R^2=0.213), and understory tpha (R^2=0.059). The effect of each additional residual tree was a reduction in median Douglas-fir volume by a multiplicative factor of 0.974 (95% CI 0.968 to 0.981). An increase in understory density from 500 tpha was associated with a reduction in median Douglas-fir volume by a factor of 0.948 (95% CI 0.914 to 0.983) per 100 understory trees. Correlations between Douglas-fir volume and understory tpha (r=-0.48) were weaker than with residual tpha (r=-0.78). In comparison, western hemlock volume was not significantly correlated to density of either residual trees or understory (r=0.35, p=0.12 and r=0.25, p=0.28, respectively).

Douglas-fir and total understory volume were positively correlated with more southerly aspects (r=0.65 and r=0.43, respectively), while western hemlock volume was negatively correlated with southerly aspects (r=-0.58). Differences in Douglas-fir volume between southerly and northerly aspects were 109.6%. This effect was the same at all understory and residual tree densities.

Total understory and Douglas-fir basal area showed similar relationships as total understory and Douglas-fir volume. Total understory basal area was best explained by residual tree density (R^2=0.595) and the average understory tree size (R^2=0.119). Again, per tree residual tree effects declined as the density of residual trees increased. Doubling the number of residual trees was asssociated with a reduction in median basal area by a multiplicative factor of 0.928 (95% CI 0.905 to 0.954).

Douglas-fir basal area was significantly associated with residual tree density (R^2=0.603), marginally with the average understory tree size (R^2=0.025), and, as Douglas-fir volume, with adjusted aspect (R^2=0.207). Residual tree effects resulted in a decline in median Douglas-fir basal area by a multiplicative factor of 0.980 (95% CI 0.973 to 0.986) per additional residual tree. Neither total understory, nor Douglas-fir basal area were correlated with understory tpha (r=-0.03, p=0.89 and r=-0.32, p=0.10, respectively). In contrast, understory density was positively correlated with western hemlock basal area (r=0.44). Correlations between adjusted aspect and total understory, Douglas-fir, and western hemlock basal area were r=0.36, r=0.65, and r=-0.63, respectively. Differences in Douglas-fir basal area between southerly and northerly aspects were 136.6% at all understory and residual tree densities.

Understory tpha was negatively associated with the average understory tree size (R^2=0.631) and with the density of residual trees (R^2=0.169). The effect of each additional residual tree was a decline in median understory density by a multiplicative factor of 0.933 (95% CI 0.906 to 0.959). Stand density was negatively correlated with southerly aspects (r=-0.38).

Understory mortality was positively associated with both understory (R^2=0.701) and residual tree density (R^2=0.046). The effect of each additional residual tree was an increase in median mortality by a multiplicative factor of 1.076 (95% CI 1.013 to 1.139). Mortality was highest in stands with highest understory densities.

The average understory tree size (dq) decreased logarithmically with increasing understory (R^2=0.668) and residual tree densities (R^2=0.200). Dq was more strongly correlated with understory density (r=-0.82) than with residual tree density (r=-0.35). Doubling the density of residual trees was associated with a decrease in median understory tree size by a multiplicative factor of 0.994 (95% CI 0.992 to 0.996).

Individual-tree-level model

Five-year growth of dbh and BA were largely explained by BAL, and to a lesser extent by dbh, residual tpha, and the adjusted aspect. Dbh and BA growth had an exponential relationship with the dbh at the beginning of the growth period ($p<0.0001$). Bigger dbh's resulted in higher growth rates. However, for the same dbh, growth rates depended also on the intensity of competition from the understory, expressed as BAL of trees in the same stand ($p<0.0001$). A BAL near zero would suggest that a tree is in a dominant position. Dominant trees had highest growth rates because the impact of the understory (BAL) was minimal (correlation between dbh and BAL was r=-0.64). Suppressed trees had lowest growth rates. BAL reduced basal area growth of western hemlock and Douglas-fir similarly. Dbh growth of Douglas-fir was more strongly limited by BAL tree than was western hemlock ($p<0.0001$). Increasing BAL by 1 m^2 resulted in a reduced growth of the median Douglas-fir dbh by a multiplicative factor of 0.973 (95% CI 0.971 to 0.976) and western hemlock by 0.98 (95% CI 0.976 to 0.983). Median basal area growth reduction per 1 m^2 increase in BAL was by a multiplicative factor of 0.973 (95% CI 0.970 to 0.976) for both species.

Competition from residual trees exponentially decreased both dbh and BA growth and limited western hemlock growth more strongly than Douglas-fir. Doubling the residual tree density resulted in a decrease in median dbh and BA growth of Douglas-fir by a multiplicative

factor of 0.944 (95% CI 0.923 to 0.966) and 0.914 (95% CI 0.888 to 0.941), respectively. This reduction was by a multiplicative factor of 0.909 for dbh (95% CI 0.885 to 0.933) and 0.878 for BA (95% CI 0.850 to 0.906) for western hemlock.

Diameter growth was significantly greater at more southern aspects ($p<0.0001$). Regardless of understory and residual tree density diameter growth the difference between a northerly and southerly aspect was 101.1%.

Understory height was associated with dbh, residual tree, and understory density. Understory height increased in a sigmoid fashion with increasing dbh ($p<0.0001$). Height of western hemlock was more strongly limited by understory tpha than Douglas-fir. Increasing the density of understory trees resulted in a decrease of median Douglas-fir height by a multiplicative factor of 0.987 (95% CI 0.982 to 0.993) and a decrease of median western hemlock height by a factor of 0.983 (95% CI 0.978 to 0.988) per 100 understory trees. Residual tree density significantly reduced the height of western hemlock ($p=0.0077$), while Douglas-fir was not significantly affected ($p=0.5537$). Doubling the number of residual trees resulted in a decrease of median Douglas-fir height by a multiplicative factor of 0.997 (95% CI 0.987 to 1.010) and in a decrease of median western hemlock height by 0.985 (95% CI 0.974 to 0.996).

Predictions of the models

The effect of each independent variable in these regression models can be illustrated by defining values of independent variables that maximize the dependent variables and examining response surfaces as independent variables depart from the maximal values. Setting residual tree density to 0 tpha, understory density to 500 tpha, BAL to 0, and the adjusted aspect to 180° determines maximal growth given the ranges of these independent variables in this study. Departures from these values result in reductions of predicted growth.

Examples are given in Tables 10 and 11 and in Figures 8 and 9. Examples for the individual tree level are based on a tree of 40cm dbh (Table 11 and Figure 9).

Table 10. Stand growth reductions (in %). Baseline is 0 residual and 500 understory tpha.

	Volume	Douglas-fir Volume	BA	Douglas-fir BA	tpha	mort (increase)	dq
Residual tpha							
5	21.7	12.1	15.7	9.7	14.9	18.4	1.0
15	33.7	32.2	25.1	26.3	23.8	32.9	1.6
50	44.8	72.6	34.0	69.1	32.5	50.8	2.3
Understory tpha							
600	5.0	5.2					8.8
1000	22.8	23.4					29.5

Table 11. Five-year diameter and basal area growth and understory height reductions (in %) for a tree of dbh 40 cm.

	5-yr. dbh growth		5-yr. BA growth		Understory height	
	Douglas-fir	western hemlock	Douglas-fir	western hemlock	Douglas-fir	western hemlock
Residual tpha						
5	12.5	19.9	18.9	26.1	0.7	3.5
15	20.1	31.2	29.6	39.9	1.2	5.8
50	27.6	41.8	39.5	52.2	1.7	8.2
BAL						
10	23.6	18.7	24.0			
20	41.7	33.9	42.1			
50	74.0	64.5	74.7			
Understory tpha						
600					1.3	1.7
1000					6.2	8.2

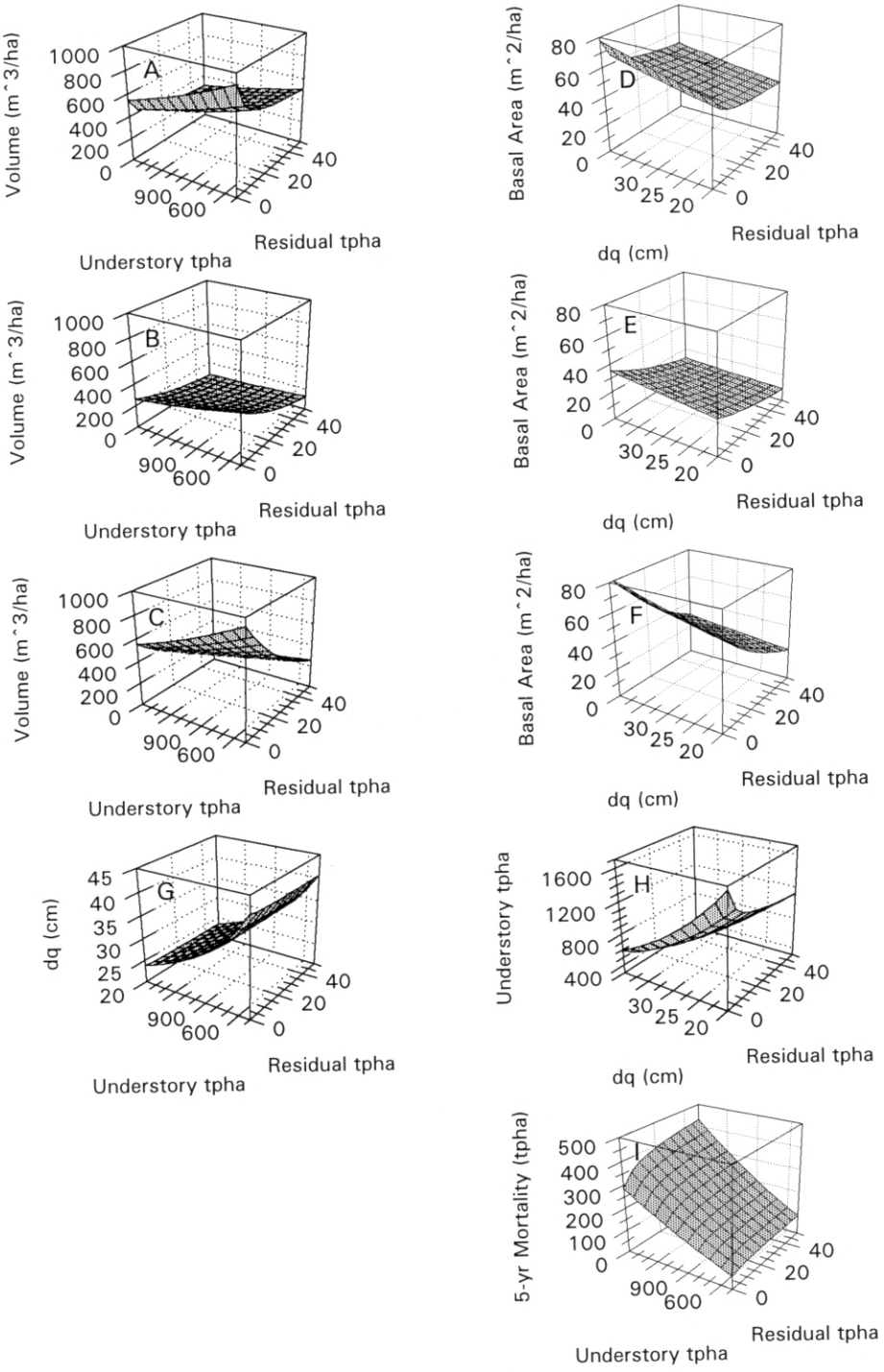


Figure 8. Stand growth reductions. (A) Total understory volume, (B), (C) Douglas-fir volume (aspect=180° and 0°), (D) Overall understory basal area, (E), (F) Douglas-fir basal area (aspect=180° and 0°), (G) Dq, (H) Understory tpha, (I) 5-yr. mortality.

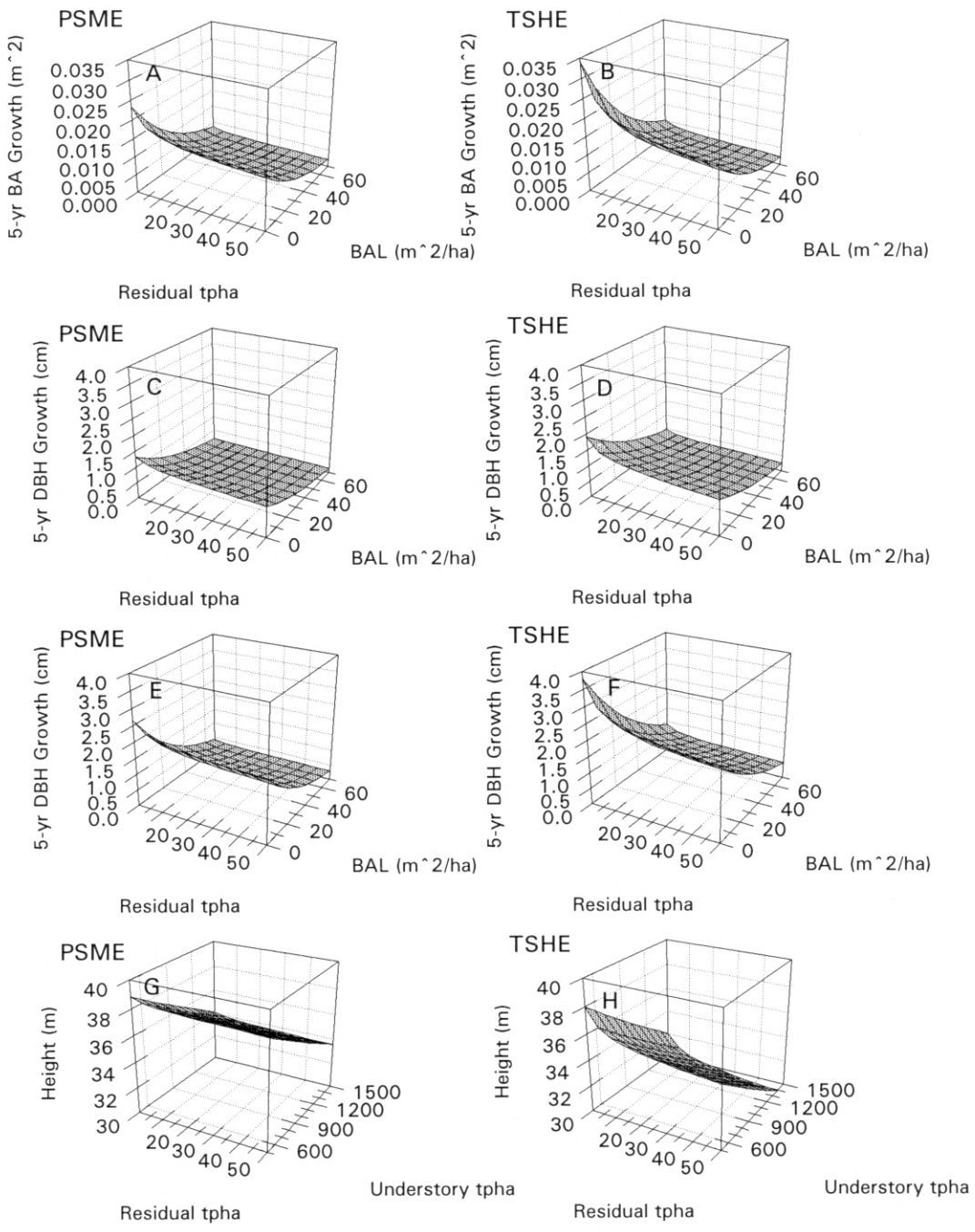


Figure 9. Predicted 5-year diameter and basal area growth reductions for a tree of 40cm dbh. (A), (B) 5-yr. BA growth of Douglas-fir (PSME) and western hemlock (TSHE), (C), (D) 5-yr. dbh growth of Douglas-fir and western hemlock (aspect=180°), (E), (F) 5-yr. dbh growth of Douglas-fir and western hemlock (aspect=0°), (G), (H) height of Douglas-fir and western hemlock.

SUMMARY

Growth of both individual understory trees and the entire young cohort was strongly affected by 1) understory competition, i.e., understory basal area or understory density; 2) overstory competition, i.e. basal area or residual tree density; and 3) adjusted aspect.

At the stand level, both total understory basal area and volume were correlated with the mean squared diameter, which was reduced by high understory and residual tree densities. Total understory basal area and volume were negatively affected by increasing residual tree and understory densities. The sharpest reduction of total understory basal area and volume per residual tree occurred at lower residual tree densities. This was also found for Douglas-fir basal area and volume. However, Douglas-fir basal area and volume were reduced to lower levels than was the total understory basal area and volume when the residual tree density exceeded 15 tpha. Douglas-fir basal area and volume were higher on south than on north aspects.

Growth rates of individual trees in the understory depended on the tree's dbh and competition from understory and residual trees. Understory growth was higher on south than on north aspects. Differences in growth between north and south aspects were primarily associated with a tendency of Douglas-fir to perform better on south aspects.

DISCUSSION

Although simulation studies suggest green tree retention may reduce timber production (Long and Roberts 1992, Garman *et al.* 1992, Birch and Johnson 1992), few field studies have investigated the relationship between retained trees and understory growth. The aim of this study was to determine whether and to what extent residual trees affect timber production, i.e. the volume of the young cohort. Therefore, it is necessary to understand how residual tree density affects understory tree dynamics. Volume is a function of a stand's basal area and the height of the trees. Furthermore, basal area and height may be associated with density of the young cohort and mortality within that cohort. To what extent do residual trees modify understory tree dynamics, and, ultimately, understory volume?

It is important to remember that understory tree and stand dynamics may be the result of interaction between residual trees and the understory since initiation of the understory. Present stand characteristics reflect a response integrated over time, of both residual trees and the young cohort, to environmental factors. Differences between residual and zero-residual stands may thus be due to environmental conditions at the time of stand initiation as well as factors related to stand development thereafter. However, the importance of these environmental factors since the time of stand initiation can not be determined from a retrospective study of growth responses. It is therefore not possible to infer causation between residual tree density and the dynamics of the young cohort. Nevertheless, accounting for the effect of understory density and quantifying the influence of residual trees on individual tree and stand dynamics may provide valuable information for management of forest ecosystems.

UNDERSTORY STAND DYNAMICS

Within the stands examined in this study, total understory and Douglas-fir basal area and volume showed a negative logarithmic relationship with both understory and residual tree densities. There were substantial volume reductions at higher understory and residual tree densities. Residual tree density was more strongly (negatively) correlated with total understory and Douglas-fir basal area and volume than was understory density. Residual trees seemed to exhibit their greatest influence per tree at low densities. This supports findings by Birch and Johnson (1992) that the marginal effect of leave-trees on understory and total stand growth decreased with increasing numbers of leave-trees. With 5 to 50 leave-trees/ha they found a 8-25 % decline in total stand growth and a 5-38 % decline in understory growth only, averaging between 1.6 and 0.75% growth reduction per leave-tree, respectively. In this study, after accounting for understory density effects, with 5 to 50 residual trees/ha, the models predicted a total understory volume reduction between 22 and 45%, averaging between 4.3 and 0.9% per residual tree. For Douglas-fir, this effect varied between 2.4 and 1.5% per residual tree. At residual tree densities over 15 trees/ha understory Douglas-fir volume and basal area declined faster than overall understory volume and basal area. The reason for this may be the increasing abundance of shade-tolerant western hemlock.

Together with understory and residual tree densities, aspect affected Douglas-fir basal area and volume in this study. Douglas-fir volume was significantly greater on southerly than northerly aspects. Similar findings on the influence of aspect have been reported in previous research. Douglas-fir is more commonly present on south slopes in the northern part of its range (Williamson and Twombly 1983). Stage (1976) and Youngberg and Ellington (1982) observed higher basal area growth on southerly aspects. Grier and Logan (1977) found higher biomass of old-growth Douglas-fir on southerly than northerly aspects in the Oregon Cascades. Greater Douglas-fir basal area and volume on more southerly aspects may be

due to light availability, moisture availability, or both. The amount of light received in the understory is probably higher on south aspects. This would favor Douglas-fir, since light is one of the major growth constraints for Douglas-fir (Minore 1979). With high stocking on south slopes there may be less available soil moisture. This would discriminate against western hemlock, which was negatively correlated with south aspects. Death of western hemlock due to a loss of hydraulic conductivity tends to occur at higher water potentials than Douglas-fir (Brix 1978). Furthermore, the stomata of western hemlock tend to close at 10mb vapor pressure deficit (Marshall and Waring 1984), whereas Douglas-fir closes its stomata at 20mb (Waring and Franklin 1979).

Once the extent to which residual trees and understory density affect understory volume has been established, there is the question of which understory volume characteristics have been influenced by residual trees.

Understory density and five-year mortality in this study were correlated with two factors: the average size of understory trees and the residual tree density. In turn, the average size of understory trees was influenced by the densities of understory and residual trees. This is not surprising as such a relationship has been described in competition-density and self-thinning theories (Reineke 1933, Kira *et al.* 1953, Yoda *et al.* 1963), which relate the number of trees per hectare to the average tree size in a stand. Given that there is a species-specific upper limit on the number of trees that can exist in a given area (Reineke 1933), an increase in the average tree size requires a reduction in the number of surviving individuals once a forest reaches maximum leaf area (Mohler *et al.* 1978). This usually occurs through differentiation and mortality (McFadden and Oliver 1988).

Although the exact time of death of trees of decay class 1 in this study is uncertain and could have resulted in over-estimates of death rates, calculated mortality was highest in stands with highest understory densities. This may be because most stands were over-stocked and had relative densities between 0.38 and 1.05 (excluding residual trees). Tree

growth has been shown to decline at relative densities of 0.40 to 0.55 (Long 1985). Drew and Flewelling (1979) showed that self-thinning appears to occur above relative densities of 0.55. Stands undergoing self-thinning have reduced net stand growth (Long 1985, Waring *et al.* 1981), which appears to be related to a decrease in maximum leaf area if stand densities are high (Bormann and Godron 1984). In this study, 23 of 28 stands had relative densities above 0.55. Self-thinning may explain why the basal area of most stands declined during the previous 5-year growth period.

Since understory tree density was lower, and understory mortality was higher, in stands with residual trees, it would follow from the competition-density theory that the average size of understory trees in stands with residual trees would be higher. Comparing periodic mean and mean radial growth rates by species and crown class revealed that the average size and growth rates of dominant Douglas-fir and were indeed highest in stands with residual trees. The reason for this appears to be the lower density of dominant and codominant trees in stands with residual trees. Oliver and Larson (1990) reported that residual trees tend to cause flatter crowns in understory trees experiencing high shade. Understory trees, and particularly dominant and codominant trees would thus require more lateral room free of side shade to maintain a larger live crown than without high shade, which may explain the lower density of dominant and codominant trees in stands with residual trees. A higher understory basal area and density of dominant and codominant understory trees in stands without residual trees may therefore have resulted in more competition among and lower growth rates of dominant Douglas-fir in these stands. Consequently, the association between dominant and codominant Douglas-fir and residual trees was not a reduction in growth rates, but rather a reduction in density of dominant and codominant crown classes. Across all crown classes and both species, residual trees had a negative logarithmic association with the average size of understory trees. Since dominant and codominant Douglas-fir represented most of the

basal area and volume in the stands, residual trees may affect timber production by reducing the density of large, dominant trees.

Once the relationship between residual trees and understory stand dynamics has been established, scaling down to the individual tree level provides an opportunity to confirm that both understory and residual tree densities determine stand growth.

INDIVIDUAL TREE DYNAMICS

Within the stands examined in this study individual tree growth was related to several measures of understory and residual tree competition. In particular, diameter and basal area growth of understory trees were correlated with dbh, BAL, and the density of residual trees. Understory height was correlated with dbh, understory tree density, and residual tree density. While a tree's diameter is an integrated response to past competition, BAL, understory tree density, and residual tree density are measures of current competition.

Independent of residual trees, larger trees had greatest radial growth rates and heights, and given the same dbh, trees that experienced less competition grew best. Radial growth rates were more strongly influenced by larger than by smaller understory trees, as larger trees contributed a greater proportion to BAL and radial growth rates of understory trees declined with increasing BAL. This is consistent with reported higher diameter growth rates of dominant versus suppressed trees (Kramer and Kozlowski 1979), and an inverse relationship between radial growth rates and BAL (Wykoff *et al.* 1982). Height of understory trees declined with increasing understory density, which is consistent with an inverse relationship between height growth and stand density (Curtis *et al.* 1981, Harrington and Reukema 1983, Reukema 1979). These growth reductions have been related to a decrease in light availability for smaller trees due to shading effects (Oliver and Larson 1990). A decrease in light availability has been shown to result in smaller net assimilation rates

(Waring *et al.* 1981), a reduction in cambial activity and root growth (Kramer and Kozlowski 1979), and a reduction in photosynthesis and diameter growth in slower growing trees (Oliver and Larson 1990). The more dominant a tree is, the longer its annual period of growth (Kramer and Kozlowski 1979); furthermore, larger trees tend to produce more photosynthate (Hamilton 1969). Due to larger crowns and an extended annual period of growth, trees have greater individual growth when grown at wider spacings (Curtis and Reukema 1970, Oliver *et al.* 1986, O'Hara 1988). Growth is proportional to a tree's crown size (Ker 1953) and available growing space (Oliver and Larson 1990). Hence, dominant trees with greater growing space, have enhanced potential for future growth (Yoda *et al.* 1957, Oliver and Murray 1983, O'Hara 1988).

The logarithmic decrease of mean radial understory tree growth with increasing residual tree density indicates that the greatest reduction per residual tree occured at low densities of residual trees. A possible explanation may be that as the density of residual trees increased, residual trees competed with each other and limit one another's crown area. As Oliver and Larson (1990) reported, compared to trees in clumps, free-grown conifers did not prune their lower branches and generally had a denser crown and therefore cast more shade. Further studies are needed to investigate whether the marginal decrease in growth reduction due to residual trees is the result of the logarithmic decrease of light penetration as residual tree density increases.

In contrast to Hoyer's (1993) findings, no residual tree effect on heights of dominant Douglas-fir was found in this study. This is not surprising, however, since the few dominant Douglas-firs in stands with residual trees may have been located sufficiently far from residual trees that interaction was minimal.

In this study adjusted aspect was positively related to diameter growth of Douglas-fir and western hemlock. Given the same stand characteristics, diameter growth of all understory trees on south slopes doubled that on northern aspects. This would suggest that

light availability may have been an important growth limiting factor. This result contrasts with studies in more moisture limited interior environments where conifer growth was poorest on south slopes (Stage 1976, Ferguson *et al.* 1986).

RESIDUAL TREES

Within the range of residual tree densities from 0 to 57 trees/ha the greatest growth reduction per residual tree seemed to occur at low residual densities. However, the negative effects of residual trees on growth of the young cohort may have been underestimated in this study for the following reasons. First, the influence of snags, which were alive at least for some time since initiation of the young cohort, was ignored due to great uncertainty about the time of their death. Second, in some of the zero-residual plots, residual trees that were beyond the buffer-zone of 18.3m from the plot center may have had an effect on the young cohort. The distance of 18.3m was chosen based on Hoyer's (1993) findings that the influence of residual trees on understory height was minimal beyond 18.3 m. However, since height does not reflect competition as well as diameter (Oliver and Larson 1990), an 18.3m buffer radius beyond the detection plot may not have been sufficient to exclude possible effects of residual trees on the understory of zero-residual plots. It may therefore be concluded that these estimates of the effect of residual trees is conservative.

Residual trees were large (dbh ranged from 75- 203 cm), and generally slow-growing (1-3 mm per year). When current basal area and volumes of residual trees were included in the yield calculation, most residual tree stands had higher overall stand basal area and volume. However, it cannot be concluded from this study that residual trees provide for additive stand growth as it was not possible to estimate volume growth of residual trees since initiation of the young cohort.

MANAGEMENT IMPLICATIONS

In this study, both understory tree density and residual tree density influenced understory volume and basal area, as well as height and diameter growth of the young cohort. Since trees in the young cohort grow and differentiate slowly in partial shade (Oliver and Larson 1990), understory density control may accelerate growth of the young cohort and prolong the time before culmination of the mean annual increment. All stands in this study had high relative densities and stand volume was highest for stands that had lowest understory densites. Therefore, understory density management should be of paramount importance when managing with green tree retention.

Characteristics of retained trees in green tree retention harvest units are likely to be different than the residual trees in this study. Retained trees in managed stands may be younger and smaller and thus may have higher growth rates than residual trees in this study. If many trees are retained in managed stands they will contribute a substantial amount to the relative density of a stand, and their importance over time is likely to increase as they continue to grow and expand their contribution to the relative stand density. However, since they are likely to be smaller than residual trees in this study, their influence at the outset will probably be much smaller than was shown for residual trees in this study.

Whether residual trees should be retained in an aggregate or dispersed fashion is beyond the scope of this study. It appears, however, that when aggregated, through competition with one another, residual trees may have a lower leaf area and cast less shade per tree. Thus, aggregated retained trees may cause less reduction of understory growth than dispersed retained trees. The final decision about the spatial arrangement, however, may be primarily influenced by windfirmness and stability of residual trees, harvest logistics, aesthetics, and landscape ecology.

REFERENCES

Agee, J.K. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. *In*: Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey and M.M. Huff, tech. coords. General Technical Report PNW-GTR-285. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 25-33.

Atzet, T. 1981. Operational environment and factors limiting reforestation in the Siskiyou Mountains. *In* Proceedings, Workshop on reforestation of skeletal soils. *Edited by* S.D. Hobbs and O.T. Helgerson. Forest Research Laboratory, Oregon State University, Corvallis. pp 6-10.

Atzet, T., and Waring, R.H. 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. Canadian Journal of Botany **48**: 2163-2167.

Baader, J. 1941. Der Kiefernüberhaltbetrieb. Frankfurt, Germany.

Barrett, J.W. 1962. Regional Siviculture of the United States. Ronal Press Co., New York, USA. 610p., illus.

Birch, K.R., and Johnson, K.N. 1992. Stand-level wood-production costs of leaving live, mature trees at regeneration harvest in coastal Douglas-fir stands. Western Journal of Applied Forestry **7**:65-68.

Bormann, B.T., and Godron, J.C. 1984. Stand density effects in young red alder plantations: Productivity, photosynthate partitioning, and nitrogen fixation. Ecology **65**: 394-402.

Brix, H. 1978. Effects of plant water stress on photosynthesis and survival of four conifers. Canadian Journal of Forest Research **9**:160-165.

Carey, A.B., Hardt, M.M., Horton, S.P., and Biswell, B.L. 1991. Spring bird communities in the Oregon Coast Range. *In*: Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey and M.M. Huff, tech. coords. General Technical Report PNW-GTR-285. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 128-142.

Chen, J., Franklin, J.F., and Spies, T.A. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth forests. Agricultural and Forest Meteorology **63**: 219-237.

Childs, S.W. 1985. Soil and microclimate considerations. *In* Proceedings, Workshop on the shelterwood management system. *Edited by* J.W. Mann and S.D. Tesch. Forest Research Laboratory, Oregon State University, Corvallis. pp 9-13.

Childs, S.W., and Flint, L.E. 1987. Effect of shadecards, shelterwoods, and clearcuts on temperature and moisture environments. Forest Ecology and Management **18**: 205-217.

Childs, S.W., Holbo, H.R., and Miller, E.L. 1985. Shadecard and shelterwood modification of the soil temperature environment. Soil Science Society of America Journal **49**: 1018-1023.

Cline, S.P., Berg, A.B., and Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management **44**: 773-786.

Cole, D.M., and Stage, A.R. 1972. Estimating future diameters of lodgepole pine trees. Research Paper INT-131. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Station. 20p.

Cooper, W.S. 1957. Vegetation of the Northwest-American Province. Proceedings. Eighth Pacific Scientific Congress **8**: 133-138.

Curtis, R.O., Clendenen, G.W., and DeMars, D.J. 1981. A new stand simulator for Douglas-fir - DFSIM user's manual. General Technical Paper PNW-128. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 79p.

Curtis, R.O., and Reukema, D.L. 1970. Crown development and site estimates in a Douglas-fir plantation spacing test. Forest Science **16**: 287-301.

Daniel, T.W., and Sterba, H. 1980. Zur Ansprache der Bestandesdichte. Allgemeine Forstzeitung **91**: 155-157.

DeBell, D.S., and Curtis, R.O. 1993. Silviculture and new forestry in the Pacific Northwest. Journal of Forestry **91**: 25-30.

Denison, W.C. 1973. Life in tall trees. Scientific American **228**: 74-80.

Dolph, K.L. 1988. Prediction of periodic basal area increment for young-growth mixed conifers in the Sierra Nevada. Research Paper PSW-190. Berkeley, California: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 20p.

Drew, A.P., and Ferrell, W.K. 1979. Seasonal changes in the water balance of Douglas-fir *(Pseudotsuga menziesii)* seedlings grown under different light intensities. Canadian Journal of Botany **57**: 666-674.

Drew, T.J., and Flewelling, J.W. 1979. Stand density management: An alternative approach and its application to Douglas-fir planatations. Forest Science **25**: 518-532.

Emmingham, W.H., and Waring, R.H. 1973. Conifer growth under different light environments in the Siskiyou Mountains of southwestern Oregon. Northwest Science **47**: 88-99.

Esseen, P.A., Ehnstrom, B., Ericson, L., and Sjoberg, K. 1992. Boreal forests - the focal habitats of Fennoscandia. *In*: Ecological Principles of Nature Conservation. Application in Temperate and Boreal Environments. *Edited by*: L. Hansson. Elsevier App.

Ferguson, D.E., Stage, A.R., and Boyd, R.J. 1986. Predicting regeneration in the grand fir-cedar-hemlock ecosystem of the northern Rocky Mountains. Forest Science Monographs 26.

Flewelling, J.W., and Pienaar, L.V. 1981. Multiplicative regression with lognormal errors. Forest Science **7**: 337-341.

Forest Ecosystem Management Assessment Team (FEMAT). 1993a. Forest ecosystem management: an ecological, economic, and social assessment. U.S.D.A., U.S.D.I. [and others]. U.S. Government Printing Office, Portland, Oregon. (irregular pagination).

Forest Ecosystem Management Assessment Team (FEMAT). 1993b. Draft supplemental environmental impact statement on management of habitat for late successional and old-growth forest related species within the range of the northern spotted owl. U.S.D.A., U.S.D.I. [and others]. U.S. Government Printing Office, Portland, Oregon.

Franklin, J.F. 1979. Vegetation of the Douglas-fir region. *In*: Forest soils of the Douglas-fir region. *Edited by* P.E. Heilman, H.W. Anderson and D.M. Baumgartner. Pullman. Washington State University Cooperative Extension: 93-112.

Franklin, J.F. 1988. Pacific Northwest Forests. *In*: North American Terrestrial Vegetation. *Edited by* M.G. Barbour and W.D. Billings. Cambridge University Press: 103-130.

Franklin, J.F. 1989. Toward a new forestry. American Forests: **95**: 37-44.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Corvallis. Oregon State University Press.

Furnival, G.M. 1961. An index for comparing equations used in constructing volume tables. Forest Science **7**: 281-289.

Garman, S.L., Hansen, A.J., Urban, D.L., and Lee, P.F. 1992. Alternative silvicultural practices and diversity of animal habitat in western Oregon: A computer simulation approach. *In*: Proceedings of the 1992 Summer Simulation Conference, The Society for Computer Simulation. *Edited by* P. Luker. pp 777-781.

Gilbert, F.F., and Allwine, R. 1991a. Spring bird communities in the Oregon Cascade Range. *In*: Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey and M.M. Huff, tech. coords. General Technical Report PNW-GTR-285. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 145-158.

Gilbert, F.F., and Allwine, R. 1991b. Terrestrial amphibian communities in the Oregon Cascade Range. *In*: Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey and M.M. Huff, tech. coords. General Technical Report PNW-GTR-285. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 319-324.

Grier, C.C., and Logan, R.S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs **47**: 373-400.

Hamilton, G.J. 1969. The dependence of volume increment of individual trees on dominance, crown dimensions, and competition. Forestry **42**: 133-144.

Hann, D.W. 1989. User's manual for ORGANON. Department of Forest Resources, Oregon State University, Corvallis. 95p.

Hann, D.W., and Larsen, D.R. 1991. Diameter growth equations for fourteen tree species in southwest Oregon. Forest Research Laboratory, Oregon State University, Corvallis. 18p.

Hansen, H.P. 1947. Postglacial forest succession, climate, and chronology in the Pacific Northwest. Am. Philos. Soc. Trans. New Ser., vol 37, part 1. 130p., illus.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *In*: A. MacFayden, E.D. Ford *(eds.)*. Advances in ecological research **15**: 133-302. New York, USA.

Harrington, C.A., and Reukema, D.L. 1983. Initial shock and long-term stand development following thinning in a Douglas-fir plantation. Forest Science **29**: 33-46.

Helgerson, O.T., Wearstler, K.A. Jr., Brucker, W.K. 1982. Survival of natural and planted seedlings under a shelterwood in southwest Oregon. Forest Research Laboratory, Oregon State University, Corvallis. 4p.

Hemstrom, M.A., Logan, S.E., Pavlat, W. 1987. Plant association and management guide for the Willamette National Forest.R6-Ecol-257-1986. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 312p.

Holdaway, M.R. 1984. Modelling the effects of competition on tree diameter growth as applied in STEMS. General Technical Report GTR-NC-94. St. Paul, Minnesota: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 8p.

Hopwood, D. 1991. Principles and practices of New Forestry. British Columbia Ministry of Forestry, Victoria, British Columbia, Canada.

Hoyer, G.E. 1993. The influence of Douglas-fir overstory on understory tree height growth in coastal forests of Washington. Washington Department of Natural Resources. FLMRC Contribution 348.

Isaac, L.A. 1938. Factors affecting establishment of Douglas-fir seedlings. Circ. No. 486. Washington, D.C.: U.S. Department of Agriculture, Forest Service. 45p.

Isaac, L.A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Forestry Foundation, Washington D.C. 107p.

Kaiser, E.H. 1986. The influence of stand structure and topography on growth, leaf area, and efficiency of young Douglas-fir in the Oregon Coast Range. Oregon State University, Corvallis. 70p. M.S. thesis.

Ker, J.W. 1953. Growth of immature Douglas-fir by tree classes. Forestry Chronicle **29**: 367-373.

King, J.E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser Company, Forest Research Center, Centralia, Washington. Weyerhaeuser Forestry Paper 8. 49p.

Kira, T., Ogawa, H., and Sakazaki, N. 1953. Intraspecific competition among higher plants: I. Competition-density-yield interrelationship in regularly dispersed populations. Journal of the Institute of Polytechnics, Osaka City University **4**: 1-16.

Kramer, P.J., and Kozlowski, T.T. 1979. Physiology of woody plants. Academic Press. New York, USA. 811p.

Krueger, K.W., and Ferrell, W.K. 1965. Comparative photosynthesis and respiratory responses to temperature and light by *Pseudotsuga menziesii* var. *menziesii* and var. *glauca* seedlings. Ecology **46**: 794-800.

Lloyd, F.T., and Harms, W.R. 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. Annals of Botany **57**: 681-688.

Long, J.N. 1985. A practical approach to density management. Forestry Chronicle **61**: 23-27.

Long, J.N., and Roberts, S.D. 1992. Growth and yield implications of a "New Forestry" silvicultural system. Western Journal of Applied Forestry **7**: 6-9.

Mang, K. 1955. Der Föhrenüberhaltbetrieb im Forstamt Lindau. Dissertation, Universität München, Germany.

Marshall, J.D., and Waring, R.H. 1984. Conifers and broadleaf species: stomatal sensitivity differs in western Oregon. Canadian Journal of Forest Research **14**:905-908.

McArdle, R.E. Meyer, W.H., and Bruce, D. 1961. The yield of Douglas-fir in the Pacific Northwest. Washington D.C.: U.S. Department of Agriculture, Forest Service. Technical Bulletin 201. 74p.

McCune, B. 1993. Gradients in epiphytic biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. Bryologist **96**: 405-411.

McDonald, P.M. 1976. Inhibiting effect of ponderosa pine seed trees on seedling growth. Journal of Forestry **74**: 220-224.

McFadden, G., and Oliver, C.D. 1988. Three-dimensional forest growth model relating tree size, tree number, and stand age: Relation to previous growth models and to self-thinning. Forest Science **34**: 662-676.

Means, J.E., Hansen, H.A., Koerper, G.J., Alabach, P.B., and Klopsch, M.W. 1994. Software for computing plant-biomass - BIOPAK users's guide. General-Technical-Report PNW-GTR-340. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Michener, W.K., Miller, A.B., and Nottrott, R. *(eds.).* 1990. Long-Term Ecological Research Network core data set catalog. Belle W. Baruch Institute for Marine Biology and Coastal Research. University of South Carolina, Columbia. 322p.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species - a literature review. General Technical Report PNW-87. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Mohler, C.L., Marks, P.L., and Sprugel, D.G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. Journal of Ecology **66**: 599-614.

Morrison, P.H., and Swanson, F.J. 1990. Fire history and pattern in a Cascade Range landscape. General Technical Report PNW-GTR-254. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Munger, T.T. 1940. The cycle from Douglas-fir to hemlock. Ecology **21**: 451-459.

Norman, J.M., and Jarvis, P.G. 1974. Photosynthesis in Sitka Spruce *(Picea sitchensis* [Bong.] Carr.*)*.III. Measurements of canopy structure and interception of radiation. Journal of Applied Ecology **11**: 375-395.

O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Canadian Journal of Forest Research **18**: 859-866.

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

Oliver, C.D., and Murray, M.D. 1983. Stand structure, thinning prescriptions, and density indexes in a Douglas-fir thinning study, western Washington, USA. Canadian Journal of Forest Research **13**: 126-136.

Oliver, C.D., O'Hara, K.L., McFadden, G., and Nagame, I. 1986. Concepts of thinning regimes. *In*: Douglas-fir: Stand management for the future. *Edited by:* C.D. Oliver, D. Hanley, and J.Johnson. College of Forest Resources. University of Washington, Seattle. Institute of Forest Resources Contribution No. 55. pp. 246-257.

Oregon Climate Service. 1993. Normal annual precipitation. State of Oregon (map).

Peck, D.L., Griggs, A.B., Schlicker H.G. and others. 1964. Geology of the central and northern parts of the western Cascade Range in Oregon. U.S. Geological Surv. Professional Paper 449, 56p.

Pike, L.H. 1978. The importance of epiphytic lichens in mineral cycling. The Bryologist **81**: 247-257.

Radosevich, S.R., and Osteryoung, K. 1987. Principles governing plant-environment interactions. *In* Forest vegetation management for conifer production. *Edited by* J.D. Walstad and P.J. Kuch. John Wiley & Sons, New York, USA. pp 105-156.

Reineke, L.H. 1933. Perfecting a stand density index for even-aged forests. Journal of Agricultural Research **46**: 627-638.

Reukema, D.L. 1979. Fifty-year development of Douglas-fir stands planted at various spacings. Research Paper PNW-253. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 21p.

Ritchie, M.W., and Hann, D.W. 1985. Equations for predicting basal area increment in Douglas-fir and grand fir. Forest Research Laboratory, Oregon State University, Corvallis. 9p.

SAS Institute Inc. 1987. SAS/STAT™ guide for personal computers. Version 6 ed. SAS Institute Inc., Cary, N.C., USA.

Scott, D.R.M. 1980. The Pacific Northwest region. *In* Regional silviculture of the United States, 2nd edition. *Edited by* J.W. Barrett. John Wiley and Sons, New York.

Shaw, D., Greenleaf, J., and Berg, D. 1993. Monitoring New Forestry. Environmental Monitoring and Assessment **26**: 187-193.

Sorensen, F.C., and Ferrell, W.K. 1973. Photosynthesis and growth of Douglas-fir seedlings when grown in different environments. Canadian Journal of Botany **51**: 1689-1698.

Spies, T.A., and Franklin, J.F. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal. **8**: 190-201.

Spies, T.A., and Franklin, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology. **70**: 543-545.

Spies, T.A. and Franklin, J.F. 1991. The structure of natural, young, mature, and old-growth Douglas-fir forests in Oregon and Washington. *In*: Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey and M.M. Huff, tech. coords. General Technical Report PNW-GTR-285. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 91-121.

Stage, A.R. 1976. An expression for the effect of aspect, slope, and habitat type on tree growth. Forest Science **22**: 457-460.

Stewart, G.H. 1986. Population dynamics in a montane conifer forest, western Cascade Range, Oregon, USA. Ecology **67**: 534-544.

Swanson, F.J., and Berg, D. 1991. The ecological roots of New Approaches to forestry. Forest Perspectives **1**: 6-8. World Forestry Center. Portland, Oregon.

Swanson, F.J., and Franklin, J.F., 1992. New Forestry principles from ecosystem analysis of Pacific Northwest forests. Ecological Applications **2**: 262-274.

Teensma, P.D.A. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Ph.D. dissertation, University of Oregon, Eugene.

Tesch, S.D. and Mann, J.W. 1991. Clearcut and shelterwood reproduction methods for regenerating Southwest Oregon forests. Forest Research Laboratory. Oregon State University, Corvallis. 43p.

Thomas, J.W., Raphael, M.G., Anthony, R.G., Forsman, E.D., Gunderson, A.G., Holthausen, R.S., Marcot, B.G., Reeves, G.H., Sedell, J.R., and Solis, D.M. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. Portland, Oregon: U.S. Department of Agriculture, Forest Service. 523p.

Trappe, J., and Luoma, D. 1992. The ties that bind: fungi in ecosystems. *In*: The Fungal Community - Its Organization and Role in the Ecosystem. *Edited by* G. Carrol, and D. Wicklow. Marcel Dekker, New York, USA. 17-27.

Tucker, G.F., and Emmingham, W.H. 1977. Morphological changes in leaves of residual western hemlock after clear and shelterwood cutting. Forest Science **23**: 195-203.

Urban, D.L. 1990. A versatile model to simulate forest pattern. A user's guide to ZELIG version 1.0 University of Virginia, Charlottesville, Virginia, USA.

U.S. Department of Agriculture, Forest Service, Willamette National Forest. 1988. Cost tradeoffs for Willamette National Forest wildlife trees. unpublished manuscript, Willamette National Forest, Eugene, Oregon.

Vanderwaal, J.A., and Holbo, H.R. 1984. Needle-air temperature differences of Douglas-fir seedlings and relation to microclimate. Forest Science **30**: 635-644.

Waring, R.H., and Franklin, J.F. 1979. The Evergreen Forests of the Pacific Northwest. Science **204**:1380-1386.

Waring, R.H., and Schlesinger, W.H. 1985. Forest ecosystems-concepts and management. Academic Press, New York, USA. 340p.

Waring, R.H., Newman, K., and Bell, J. 1981. Efficiency of tree crowns and stemwood production at different canopy leaf densities. Forestry **54**: 15-23.

Wensel, L.C., Meerschaert, W.J., and Biging, G.S. 1987. Tree height and diameter growth models for northern California conifers. Hilgardia **55**: 1-20.

West, P.W. 1980. Use of diameter increment and basal area increment in tree growth studies. Canadian Journal of Forest Research **10**: 71-77.

Westoby, M. 1984. The self-thinning rule. Advances in Ecological Research **14**: 167-225.

Williamson, R.L. 1973. Results of shelterwood harvesting of Douglas-fir in the Cascades of western Oregon. Research Paper PNW-161. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 13p.

Williamson, R.L., and Ruth, R.H. 1976. Results of shelterwood cutting in western hemlock. Research Paper PNW-201. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 25p.

Williamson, R.L., and Twombly, A.D. 1983. Pacific Douglas-fir. *In*: Silvicultural systems for the major forest types of the United States. *Edited by*: Burns, R.M. tech. compiler. Agriculture Handbook 445. Washington D.C.: U.S. Department of Agriculture, Forest Service.

Wykoff, W.R., Crookston, N.L., and Stage, A.R. 1982. User's guide to the stand prognosis model. General Technical Report INT-133. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 112p.

Wykoff, W.R. 1986. Supplement to user's guide for the stand prognosis model. Version 5.0. General Technical Report INT-208. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 36p.

Yoda, K., Kira, T., and Hozumi, K. 1957. Intraspecific competition among higher plants: IX. Further analysis of the competitive interactions between adjacent individuals. Journal of the Institute of Polytechnics, Osaka City University **8**: 161-178.

Yoda, K., Kira, T., Ogawa, H., and Hozumi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of the Institute of Polytechnics, Osaka City University, Series D **14**: 107-129.

Youngberg, C.T., and Ellington, W.B. 1982. Soil-site relationships, Siuslaw National Forest, Mapleton Ranger District, Mapleton, Oregon.

Zeide, B. 1987. Analysis of the 3/2 power law of self-thinning. Forest Science **33**: 517-537.

Zobel, D.B., McKee, A., Hawk, G.M., and Dyrness, C.T. 1976. Relationships of environment to composition structure and diversity of forest communities of the central western Cascades of Oregon. Ecological Monographs **46**: 135-156.

Zumrawi, A.A., and Hann, D.W. 1993. Diameter growth equations for Douglas-fir and grand fir in the western Willamette Valley of Oregon. Forest Research laboratory, Oregon State University, Corvallis. 6p.