

AN ABSTRACT OF THE THESIS OF

Timothy B. Harrington for the degree of Doctor of Philosophy in Forest Resources Management presented on May 5, 1989.

Title: Stand Development and Individual Tree Morphology and Physiology of Young Douglas-fir (*Pseudotsuga menziesii*) in Association with Tanoak (*Lithocarpus densiflorus*)

Abstract approved: Signature redacted for privacy.

John C. Tappeiner II

Effects of tanoak (*Lithocarpus densiflorus*) on early growth, morphology, and physiology of Douglas-fir (*Pseudotsuga menziesii*) were studied to determine developmental characteristics of young stands and mechanisms of competition. Growth, leaf area, and biomass of Douglas-fir, tanoak, and shrubs / herbs were monitored for six years after establishing a gradient of tanoak cover with and without suppression of shrubs / herbs. Growth trajectories for Douglas-fir and tanoak were related to initial tanoak cover, a variable that can be predicted using inventory data from the pre-harvest stand.

Morphology, duration, and relative rates of growth of Douglas-fir were studied for three growing seasons to

determine how the accumulating effects of competition caused tree size to vary. Tanoak competition reduced the size and number of buds, internodes, and needles for Douglas-fir shoots. In a given year, Douglas-fir growth was limited by competition in previous years via reduced potential growth (i.e., internode number for shoot growth and stem circumference for diameter growth) and by competition in the current year via reduced attainment of potential growth (i.e., expansion of internodes and basal area growth per unit stem circumference).

To describe mechanisms of competition, variables of microclimate (air / soil temperature, light, and soil water) and physiology (xylem pressure potential, conductance, and photosynthesis) were measured in each of eighteen consecutive months on Douglas-fir of different competitive status. Throughout the year, Douglas-fir shaded by tanoak had light-limited rates of photosynthesis. During the growing season, both shaded and unshaded Douglas-fir in tanoak-dominated areas experienced elevated leaf temperatures, lower relative humidities, and reduced soil water availability, resulting in limited rates of photosynthesis.

Stand Development and Individual Tree Morphology and
Physiology of Young Douglas-fir (Pseudotsuga menziesii)
In Association with Tanoak (Lithocarpus densiflorus)

by

Timothy B. Harrington

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TABLE OF CONTENTS

INTRODUCTION	1
I. USING STAND INVENTORIES TO PREDICT EARLY GROWTH AND DEVELOPMENT OF MIXED DOUGLAS-FIR / TANOAK STANDS IN SOUTHWESTERN OREGON	5
Abstract	5
Introduction	7
Methods	10
Site descriptions	10
Treatments	11
Douglas-fir growth measurements	13
Tanoak growth measurements	16
Measurements of understory species	17
Statistical analysis	18
Results and discussion	26
Effects of tanoak and understory vegetation on Douglas-fir growth	26
Predicting stand development	27
II. EFFECTS OF TANOAK COMPETITION ON MORPHOLOGY, DURATION, AND RELATIVE RATES OF GROWTH OF DOUGLAS-FIR SAPLINGS	57
Abstract	57
Introduction	59
Shoot growth processes	59
Cambial growth processes	60
Effects of competition on tree growth	61
Methods	63
Site description	63
Study treatments	64
Douglas-fir measurements	65
Statistical analysis	69
Results and discussion	71
Douglas-fir bud parameters	71
Douglas-fir height and basal area growth	74

TABLE OF CONTENTS (continued)

III. SEASONAL PHYSIOLOGY OF DOUGLAS-FIR SAPLINGS AS AFFECTED BY MICROCLIMATE IN YOUNG TANOAK STANDS	89
Abstract	89
Introduction	91
Methods	95
Site description	95
Experimental design	96
Measurements	98
Statistical analysis	106
Results and discussion	112
Microclimate	112
Plant physiology	116
Conclusions	130
CONCLUSIONS	172
CONSIDERATIONS FOR FUTURE RESEARCH	177
REFLECTIONS	178
BIBLIOGRAPHY	180

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
I. 1.	Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir diameter at Squaw.	40
I. 2.	Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir diameter at Fir Point.	41
I. 3.	Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir height at Squaw.	42
I. 4.	Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir height at Fir Point.	43
I. 5.	Relationship of the six-year exponential growth rate (R) for Douglas-fir diameter at Squaw and Fir Point with initial (1983) tanoak cover and level of understory vegetation (shrubs and herbs).	44
I. 6.	Relationship of the six-year exponential growth rate (R) for Douglas-fir height at Squaw and Fir Point with initial (1983) tanoak cover and level of understory vegetation (shrubs and herbs).	45
I. 7.	Relationship of the five-year growth rate (k) for tanoak cover at Squaw and Fir Point with initial (1983) tanoak cover and level of understory vegetation (shrubs and herbs).	46
I. 8.	Response surface for Douglas-fir diameter predicted for six years after treatment from initial (1983) tanoak cover at Squaw and Fir Point.	47
I. 9.	Response surface for Douglas-fir height predicted for six years after treatment from initial (1983) tanoak cover at Squaw and Fir Point.	48

LIST OF FIGURES (continued)

<u>Figure</u>	<u>Page</u>
I.10. Response surface of tanoak cover predicted for six years after treatment from initial (1983) tanoak cover at Squaw and Fir Point.	49
I.11. Predictions of growth trajectories for Douglas-fir diameter based on stand inventory data adapted from Tappeiner and McDonald (1984).	50
I.12. Predictions of growth trajectories for Douglas-fir and tanoak height based on stand inventory data adapted from Tappeiner and McDonald (1984).	51
I.13. Predictions of growth trajectories for tanoak cover based on stand inventory data adapted from Tappeiner and McDonald (1984).	52
I.14. Predictions of growth trajectories for leaf area index of tanoak, Douglas-fir, and understory vegetation (shrubs and herbs) based on stand inventory data adapted from Tappeiner and McDonald (1984).	53
I.15. Predictions of growth trajectories for leaf area index of Douglas-fir and understory vegetation (shrubs and herbs) following removal of tanoak at a stand age of 3 years.	54
I.16. Predictions of growth trajectories for aboveground biomass of tanoak, Douglas-fir, and understory vegetation (shrubs and herbs) based on stand inventory data adapted from Tappeiner and McDonald (1984).	55
I.17. Predictions of growth trajectories for aboveground biomass of Douglas-fir and understory vegetation (shrubs and herbs) following removal of tanoak at a stand age of 3 years.	56

LIST OF FIGURES (continued)

<u>Figure</u>	<u>Page</u>
II. 1. Relationship of ln(1987 basal area increment) to ln(1986 stem circumference) for individual Douglas-fir growing in the presence and absence of tanoak competition.	83
II. 2. Relationship of ln(1987 terminal shoot length) to ln(1986 bud diameter x length) for individual Douglas-fir growing in the presence and absence of tanoak competition.	84
II. 3. Mean relative rates of basal area growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Fir Point.	85
II. 4. Mean relative rates of basal area growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Squaw.	86
II. 5. Mean relative rates of height growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Fir Point.	87
II. 6. Mean relative rates of height growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Squaw.	88
III. 1. Diagram of causal relationships hypothesized to exist among variables of microclimate and tree physiology in young Douglas-fir / tanoak stands.	137
III. 2. Average maximum monthly air temperature at 1 m height for two conditions in young Douglas-fir / tanoak stands.	138
III. 3. Average minimum monthly air temperature at 1 m height for two conditions in young Douglas-fir / tanoak stands.	139

LIST OF FIGURES (continued)

<u>Figure</u>	<u>Page</u>
III. 4. Average soil temperatures at 15 cm depth for three conditions in young Douglas-fir / tanoak stands.	140
III. 5. Average monthly precipitation at Fir Point and Squaw for 1987.	141
III. 6. Average morning photosynthetically-active photon flux density (PPFD) measured for three conditions in young Douglas-fir / tanoak stands.	142
III. 7. Average afternoon photosynthetically-active photon flux density (PPFD) measured for three conditions in young Douglas-fir / tanoak stands.	143
III. 8. Average cumulative change in soil water potential (SWP) at 30 cm depth measured for two conditions in young Douglas-fir / tanoak stands.	144
III. 9. Average cumulative change in soil water potential (SWP) at 60 cm depth measured for two conditions in young Douglas-fir / tanoak stands.	145
III.10. Average morning leaf temperature for three conditions in young Douglas-fir / tanoak stands.	146
III.11. Total determination of morning leaf temperature by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD).	147
III.12. Average afternoon leaf temperature for three conditions in young Douglas-fir / tanoak stands.	148
III.13. Total determination of afternoon leaf temperature by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD).	149

LIST OF FIGURES (continued)

<u>Figure</u>	<u>Page</u>
III.14. Average morning relative humidity for three conditions in young Douglas-fir / tanoak stands.	150
III.15. Total determination of morning relative humidity by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD).	151
III.16. Average afternoon relative humidity for three conditions in young Douglas-fir / tanoak stands.	152
III.17. Total determination of afternoon relative humidity by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD).	153
III.18. Average base xylem pressure potential of trees growing in the three conditions in young Douglas-fir / tanoak stands.	154
III.19. Total determination of base xylem pressure potential by species and cumulative change in soil water potential (SWP) at 30-cm depth.	155
III.20. Average morning leaf conductance of trees growing in the three conditions in young Douglas-fir / tanoak stands.	156
III.21. Total determination of morning leaf conductance by species, photosynthetically-active photon flux density (PPFD), base xylem pressure potential (XPP), and relative humidity (RH).	157
III.22. Average afternoon leaf conductance of trees growing in the three conditions in young Douglas-fir / tanoak stands.	158

LIST OF FIGURES (continued)

<u>Figure</u>	<u>Page</u>
III.23. Total determination of afternoon leaf conductance by species, photosynthetically-active photon flux density (PPFD), base xylem pressure potential (XPP), and relative humidity (RH).	159
III.24. Average morning xylem pressure potential of trees growing in the three conditions in young Douglas-fir / tanoak stands.	160
III.25. Total determination of morning xylem pressure potential by species, base xylem pressure potential (XPP), and leaf conductance (G).	161
III.26. Average afternoon xylem pressure potential of trees growing in the three conditions in young Douglas-fir / tanoak stands.	162
III.27. Total determination of afternoon xylem pressure potential by species, base xylem pressure potential (XPP), and leaf conductance (G).	163
III.28. Average morning photosynthesis of trees growing in the three conditions in young Douglas-fir / tanoak stands.	164
III.29. Total determination of morning photosynthesis by species, leaf temperature (T), photosynthetically-active photon flux density (PPFD), and leaf conductance (G).	165
III.30. Average afternoon photosynthesis of trees growing in the three conditions in young Douglas-fir / tanoak stands.	166
III.31. Total determination of afternoon photosynthesis by species, leaf temperature (T), photosynthetically-active photon flux density (PPFD), and leaf conductance (G).	167

LIST OF FIGURES (continued)

<u>Figure</u>		<u>Page</u>
III.32.	Average basal area relative growth rate for Douglas-fir growing in the three conditions in young Douglas-fir / tanoak stands.	168
III.33.	Total determination of basal area relative growth rate for Douglas-fir by cumulative change in soil water potential (SWP) at 30 cm depth.	169
III.34.	Average height relative growth rate for Douglas-fir growing in the three conditions in young Douglas-fir / tanoak stands.	170
III.35.	Total determination of height relative growth rate for Douglas-fir by cumulative change in soil water potential (SWP) at 30 cm depth.	171

LIST OF TABLES

<u>Table</u>	<u>Page</u>
I. 1. Inventory data from two mature tanoak stands in southwestern Oregon (adapted from Tappeiner and McDonald, 1984).	35
I. 2. Regression equations for predicting $\ln(R)$ for Douglas-fir diameter and height.	36
I. 3. Regression equations for predicting k (tanoak cover model) and $\ln(R)$ for tanoak crown width and height.	37
I. 4. Regression equations for predicting $\ln(R)$ for Douglas-fir cover, LAI, and biomass.	38
I. 5. Regression equations for predicting fifth-year (1987) understory cover, LAI, and biomass from initial values (1983) of these variables and 1987 tanoak cover.	39
II. 1. Effects of tanoak competition on morphological parameters of Douglas-fir terminal shoots in 1987.	79
II. 2. Regression models describing relationships among Douglas-fir morphological parameters for 1987 terminal and lateral shoots.	80
II. 3. Effects of tanoak competition on size (beginning of growing season) and increment in Douglas-fir basal area and height for 1985-1987.	81
II. 4. Effects of tanoak competition on duration of Douglas-fir basal area and height growth in the 1985-1987 growing seasons.	82
III. 1. Parameters used to obtain average rates of whole-tree photosynthesis for the three conditions in young Douglas-fir / tanoak stands.	136

Stand Development and Individual Tree Morphology and
Physiology of Young Douglas-fir (Pseudotsuga menziesii)
In Association with Tanoak (Lithocarpus densiflorus)

INTRODUCTION

A variety of hardwood tree species are associated with Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) in southwestern Oregon and northwestern California, and the most common is probably the evergreen species, tanoak (Lithocarpus densiflorus (Hook. & Arn.) Rehd.).

Throughout the region, tanoak forms understories in mature and old-growth conifer stands (Tappeiner and McDonald, 1984). Following wildfire or stand harvest, tanoak can rapidly re-occupy a site through vigorous growth of basal stump sprouts (Tappeiner et al. 1984) -- a typical growth strategy of hardwood species in this region.

Since tanoak sprout clumps develop from previously-established root systems, they quickly assume a superior competitive status over many of the Douglas-fir in a plantation. The dense, evergreen canopy formed by a tanoak sprout clump can have a leaf area index of $7 \text{ m}^2/\text{m}^2$ (Harrington et al., 1984), allowing it to compete effectively for light and soil water. Further limits on soil water are imposed by the Mediterranean climate of the region, which is characterized by limited growing season precipitation and hot summer temperatures.

The following research was conducted to improve strategies for managing young Douglas-fir / tanoak stands in southwestern Oregon and northwestern California. Increasing reliance of society on forests of this region has prompted the need to manage conifer / hardwood stands for a variety of resources, including timber, wildlife, and aesthetics. Based on this and similar research, it appears that opportunities exist for manipulating characteristics of mixed stands to achieve a range of management objectives.

Three types of information could be used to further the technology for managing conifer / hardwood stands. First, to determine if silvicultural treatments, such as vegetation control, create the desired stand structure, a technique is needed to predict the course of young stand development for a range of conifer / hardwood mixtures. Second, because of the vigorously-competitive nature of tanoak and other hardwoods in the region, indicators of competitive stress for Douglas-fir are needed to prevent its suppression and mortality. Finally, a full understanding is needed of the competitive strategies of Douglas-fir and tanoak in mixture. Such information could be used to identify the critical treatments necessary to ensure conifer survival under low management intensities, or to promote maximum wood production under intensive management.

In the first phase of this research (Chapter I), the influences of competition from tanoak, shrubs, and herbs on Douglas-fir growth were quantified over a six-year period. Because tanoak sprout clump development is a function of parent tree size (Tappeiner et al. 1984), characteristics of the pre-harvest tanoak stand could be used to predict expected competition level from tanoak following stand harvest, and the resulting rate of Douglas-fir plantation development. This analytical approach was designed to provide a technique that could be used in planning and prioritization of silvicultural treatments.

The observed differences in Douglas-fir growth from its association with tanoak formed the basis for successive research on growth processes and mechanisms of competition. In the second phase of the research (Chapter II), morphology and activity of Douglas-fir growth were compared between extremes in a competition gradient to describe the growth processes that resulted in differences in tree size. The concepts of 'potential growth' and 'potential growth attainment' were developed to account for the accumulating influences of competition on Douglas-fir cambial and shoot growth. To characterize the competitive influences specific to a given year, the relative rates and duration of tree growth were

investigated.

Since net carbon assimilation ultimately determines biomass of Douglas-fir, competition must influence tree growth at the physiological level. The objective of the third phase of research (Chapter III) was to describe mechanisms of tanoak competition that could limit net carbon assimilation of Douglas-fir. Because of its dense evergreen canopy, it seemed likely that tanoak could impose limitations on Douglas-fir photosynthesis by restricting soil water availability during the growing season, and by restricting light availability throughout the year.

To dissect the mechanisms of tanoak competition, a two-level approach was used. First, a series of cause and effect relationships were hypothesized to link microclimate with tree physiological response. Second, the microclimate and physiology of Douglas-fir was characterized throughout the year for trees of various competitive statuses with tanoak. In analysis of the data, mechanistic pathways by which tanoak competition limited Douglas-fir photosynthesis were ranked according to their importance during specific periods of the year.

CHAPTER I

USING STAND INVENTORIES TO PREDICT EARLY GROWTH AND
DEVELOPMENT OF MIXED DOUGLAS-FIR (PSEUDOTSUGA MENZIESII) /
TANOAK (LITHOCARPUS DENSIFLORUS) STANDS

ABSTRACT

Early development of Douglas-fir (Pseudotsuga menziesii) / tanoak (Lithocarpus densiflorus) stands for a range of initial levels of tanoak cover was studied on two forest sites in southwestern Oregon during 1983-1988. Exponential growth rates (R) for diameter and height of Douglas-fir (Pseudotsuga menziesii) saplings declined significantly ($p < 0.005$) with increasing levels of tanoak cover. R values for Douglas-fir parameters varied as negative exponential functions of initial (1983) tanoak cover and understory level ($R^2 = 0.38$ to 0.72), permitting the development of predictive equations. Tanoak cover (%) development was described by a monomolecular growth function in which the rate of growth (k) was related linearly ($r^2 = 0.57$) to initial tanoak cover. Cover (%), leaf area index, and biomass of understory vegetation (herbs and shrubs) five years after treatment were related linearly to initial (1983) values for these parameters and current-year tanoak cover ($R^2 = 0.43$ to 0.74).

Using stand inventory data for several mature tanoak stands, tanoak cover for the recovering stand was predicted three years following a hypothetical disturbance, such as cutting or burning. Using these predicted values for initial tanoak cover, parameters describing subsequent development of a new Douglas-fir / tanoak stand on these sites were estimated, including average Douglas-fir growth, stand leaf area index, and biomass. This approach provides a technique for ranking pre-harvest tanoak stands according to their post-harvest potential to limit rates of Douglas-fir growth and determine the course of stand development.

INTRODUCTION

Evergreen hardwood trees, principally tanoak (Lithocarpus densiflorus (Hook. & Arn.) Rehd.) and Pacific madrone (Arbutus menziesii Pursh), are common associates of Douglas-fir in southwestern Oregon and northwestern California (Tappeiner and McDonald, 1984). After cutting or burning, these hardwoods sprout vigorously (Tappeiner et al. 1984), ensuring their presence in newly-developing conifer stands.

Competition from hardwood sprout clumps can impede growth (Radosevich et al. 1976; Roy, 1981; Tappeiner et al. 1987; Jaramillo, 1988; Hughes et al. (in press)) and morphological development (Chapter II) of Douglas-fir seedlings in southwestern Oregon and northwestern California. Therefore, young stand management typically includes control of hardwoods to improve survival and growth of planted conifer seedlings.

Current nursery and planting practices generally ensure effective plantation establishment in southwestern Oregon (Rost, 1988). However, there is little information to help managers anticipate early growth of conifers, shrubs, and hardwoods, and thus aid decision-making in young stand management. Such predictions would be most practical if they could be made before harvest, when opportunities are favorable for treatment planning and

scheduling.

Predictions of stand development would be particularly useful in the management of multiple resources if they described development of various stand components (conifers, hardwoods, and shrubs) for a range of hardwood densities. For example, it would be useful to know, prior to stand harvest, how hardwood density will affect early conifer growth, as well as production of wildlife browse and mast during development of the next young stand.

Predictions of tree growth based on empirical relationships often are limited to a given site or region. To be most relevant and generalizable to a range of conditions and sites, growth predictions should be based on mechanisms that govern plant response to competition. This would permit the analysis of outcomes in stand development that occur for various treatments, timings, and/or relative sizes and densities of hardwoods and conifers.

Effects of interspecific competition on conifer early growth often are evaluated by comparing tree responses among discrete levels of treatments or vegetation abundance. If such treatments are not relevant to current or future forestry practices, the research will have limited practical application. In addition, outcomes in

stand development observed in plant competition research are influenced heavily by treatment timing and the initial size, density, and proportion of each species (Radosevich, 1987).

The objectives of this study were: a) to determine the effects of various levels of tanoak on early growth of Douglas-fir, tanoak, and shrubs / herbs, and b) to develop a method for predicting early development of Douglas-fir / tanoak stands based on characteristics of the pre-harvest stand. An attempt was made to develop predictive information that could be generalized to a range of sites, plantation ages, and timing or type of treatment.

METHODS

SITE DESCRIPTIONS

The early growth and development of Douglas-fir / tanoak stands was studied at two sites in southwestern Oregon, Squaw and Fir Point, that are being managed for conifer wood production and other resources. Prior to study initiation, site histories included clearcut harvesting of the previous old-growth stands (1980), broadcast burning (spring, 1981), and planting with 2-year-old bare-root Douglas-fir seedlings (April, 1981 at Squaw; April, 1982 at Fir Point). Wide spacing of the Douglas-fir (3 m) probably minimized intraspecific competition for the duration of the study. Following broadcast burning, an even distribution of tanoak sprout clumps developed from the stumps of parent trees present in the pre-harvest stand.

The Squaw site is located near Cave Junction, Oregon (T39S R6W S21) at an elevation of 900 m, and has gravelly-loam soils of the Pollard/Beekman series (Meyer and Amaranthus, 1979). The Fir Point site is located near Glendale, Oregon (T32S R6W S17, 70 km south of Squaw) at an elevation of 800 m, and has clay-loam soils of the Josephine/Speaker series (Hubbard, 1980). Both sites receive approximately 130 cm of annual precipitation, and

site index₁₀₀ varies from 35 (Squaw) to 37 m (Fir Point). Site aspect is east/southeast (Squaw) or west/southwest (Fir Point), and slopes range from 30 to 65%.

TREATMENTS

In order to describe early growth and development for a range of initial stand conditions, the crown cover of both tanoak and understory vegetation (i.e., shrubs and herbs) were manipulated. Four levels (treatments) of tanoak, replicated three times in 20 x 20 m plots, were established at each site: 1) a high level of cover representing the site maximum, 2) a medium level (50% of the mean cover for treatment 1), 3) a low level (25% of the mean cover for treatment 1), and 4) zero tanoak cover. At Squaw, understory species were suppressed in an additional replicated set of the four tanoak levels, giving a total of 24 plots. At Fir Point, suppression of understory species was applied to an additional replication of treatment 4 only, giving a total of 15 plots.

Using a randomized complete block design, the plots were established in areas at each site having a relatively homogenous cover of tanoak sprout clumps. Sprout clumps in each plot were counted by 25-cm crown width classes in

March, 1983, at which time the tanoak were two years old. Multiplying crown-width class frequencies by respective class midpoints for crown area and summing these values gave an estimate of initial crown area per plot.

To ensure that high levels of tanoak competition were adequately represented in the study, subsets of six and ten plots were designated at Fir Point and Squaw, respectively, and treatment 1 was assigned randomly to these plots. Treatments 2 through 4 were assigned randomly to the remaining plots at each site. Suppression of understory species was assigned randomly to plots after designating the tanoak treatments.

The original size distribution for tanoak sprout clumps was maintained for each plot receiving treatments 2 and 3. To accomplish this, the number of sprout clumps to be removed for a given crown width class were calculated according to that class' proportion of the total plot crown area. The estimated number of sprout clumps per plot remaining after treatment was used to calculate tanoak spacing.

In April, 1983, individual tanoak in treatments 2 to 4 were removed to obtain the desired size distributions using a directed spray of triclopyr ester herbicide (2% in water with surfactant). The Douglas-fir were covered to protect them during herbicide application. In the years following the one-time herbicide application, recovering

tanoak sprouts in treatment 4 were manually removed.

Understory species were suppressed on plots receiving this additional treatment by broadcast application of glyphosate herbicide (2% in water) in April, 1983. Thereafter the effects from understory competition were minimized by manual removal and installation (March, 1985) of a 2 x 2 m square of porous polyester fabric (Terra-Mat E, Terra Enterprises, Inc., Moscow, ID) around individual Douglas-fir. Deer and elk damage was prevented by installing tubes of either rigid plastic (Squaw) or polyester fabric (Fir Point) (Terra Tech, Inc., Eugene, OR) in May, 1984 to protect each tree's terminal shoot.

DOUGLAS-FIR GROWTH MEASUREMENTS

The following variables were measured on fifteen systematically-selected Douglas-fir per plot at the end of each growing season from 1983-1988: stem diameter (mm) at a permanently-marked height of 15 cm, total height (cm), height increment (cm), and average crown width at the base of the tree (cm). Light availability to individual trees was estimated visually using an imaginary projection of an inverted 60° cone from the base of a tree's terminal shoot (Howard and Newton, 1984). A four-point scale was used to classify proportional occlusion of light, or

"overtopping", by shrubs and hardwoods above each tree.

Aboveground biomass was determined on a total of 72 Douglas-fir saplings that were harvested adjacent to the study plots during the dormant seasons of 1984 through 1988. The sample comprised a series of annual collections of open-grown trees (overtopping < 25%) encompassing a range of sizes for a given age. To determine if shaded trees exhibited different biomass relationships, five overtopped (> 75%) trees were harvested per site in March, 1988.

Each tree was cut at the root collar, and in the laboratory it was dried at 70° C to a constant weight. Woody and foliage components were separated and weighed to the nearest 0.1 g. Regression equations were developed for predicting total aboveground and foliage biomass of Douglas-fir:

$\ln(\text{aboveground biomass (g)}) =$

$$1.312 + 0.889(\ln(\text{STVOL}(\text{cm}^3)))$$

$$\text{adjusted } R^2=0.979 \quad s_{y.x} = 0.228 \quad n = 72$$

$\ln(\text{foliage biomass (g)}) =$

$$0.731 + 0.848(\ln(\text{STVOL}(\text{cm}^3))) - 0.249(\text{OT}>75\%)$$

$$\text{adjusted } R^2=0.955 \quad s_{y.x} = 0.327 \quad n = 72$$

where: $\text{STVOL} = \text{stem volume} = \pi (\text{diameter}/20)^2 \times (\text{height})/3$

$\text{OT}>75\% = 1$ if overtopping is greater 75% and 0 otherwise

Douglas-fir specific leaf area (cm^2 leaf area / g foliage dry weight) was estimated in October, 1986 and 1987 to provide a factor for converting foliage biomass to leaf area. A subsample of foliage was collected from 27 trees, and one-sided leaf area was measured to the nearest 0.1 cm^2 in the laboratory using a surface area meter (model Li-3100, Li-Cor Inc., Lincoln, NB). These samples were dried to a constant weight at 70°C and weighed to the nearest 0.01 g. Specific leaf areas were calculated by dividing sample leaf area by sample dry weight, and a regression equation was developed to predict this variable for individual trees from overtopping:

specific leaf area (cm^2/g) =

$$64.234 + 9.759(\text{SITE}) + 40.448(\text{OT}>50\%)$$

$$\text{adjusted } R^2=0.819 \quad s_{y.x} = 8.95 \quad n=27$$

where: SITE = 1 for Squaw and 0 for Fir point

OT>50% = 1 if overtopping is greater 50% and 0 otherwise

Plot values for Douglas-fir leaf area index (m^2/m^2) and aboveground biomass (kg/m^2) were estimated by multiplying the average leaf area or biomass of the 15 sample trees by a standard tree density of 1076/ha (436/A) and dividing by the plot area (400 m^2).

TANOAK GROWTH MEASUREMENTS

Five tanoak sprout clumps, representing a range of sizes, were selected per plot in treatments 1 to 3. At the end of each of the 1983-1988 growing seasons, average crown width (cm, mean of two directions) and maximum height (cm) were measured for each sprout clump. Tanoak crown area per plot was measured at the end of the 1983-1987 growing seasons using the previously-described methods, and dividing this value by the plot area x 100% gave percent cover. Plot values for tanoak LAI and aboveground biomass were calculated by multiplying sprout clump frequencies per 25 cm crown width class by class midpoint values obtained from the following regression equations that were refitted to data from Harrington et al. (1984):

$\ln(\text{aboveground biomass (kg)}) =$

$$1.137 + 0.965(\ln(\text{CRAREA}(\text{m}^2)))$$

$$\text{adjusted } R^2=0.838 \quad s_{y.x} = 0.421 \quad n = 143$$

$\ln(\text{leaf area (m}^2)) =$

$$1.988 + 0.966(\ln(\text{CRAREA}(\text{m}^2)))$$

$$\text{adjusted } R^2=0.838 \quad s_{y.x} = 0.421 \quad n = 143$$

where: CRAREA = sprout clump crown area =

$$\pi (\text{average crown width}/200)^2$$

MEASUREMENTS OF UNDERSTORY SPECIES

Five Douglas-fir seedlings per plot were systematically selected and used as reference points for estimating percent cover of understory species. In June of 1983, and 1985-1987, crown cover (%) for each species was estimated visually at the same location adjacent to each reference Douglas-fir using a 1 m² square frame.

In 1986 and 1987, cover was estimated visually as described above for one to three plants of each of 21 major shrub and herbaceous species. Aboveground portions of these plants were harvested, and at the laboratory, foliage from each plant was subsampled to estimate specific leaf area (cm² leaf area / g foliage dry weight). Woody or foliage components from each plant were separated, dried to a constant weight at 70° C, and weighed to the nearest 0.1 g.

Ratios of plant leaf area or aboveground biomass to crown area were calculated and averaged by species, and these values were applied to the percent cover data to estimate the leaf area and aboveground biomass of individual plants. Cover, LAI, and aboveground biomass values were summed for each 1 m² sample, and averaged to yield plot estimates for these variables.

STATISTICAL ANALYSIS

Effects of Competition on Douglas-fir Growth

Analysis of variance (ANOVA) was used to test the significance of tanoak and understory levels on the mean growth trajectories for height and diameter of Douglas-fir. Each variable was averaged by year x site x plot, and graphical analysis suggested that data for each plot conformed to the following general model of exponential growth:

$$\text{SIZE}_t = b_0 e^{Rt} \quad (1)$$

where: SIZE_t = tree size at time t

t = growing seasons since treatment - 1

b_0 = initial Douglas-fir size at $t = 0$

R = exponential growth rate for 1983-1988

Natural logarithmic transformations were applied to the average values for Douglas-fir diameter and height to linearize model (1). Linear regression of the six values for $\ln(\text{SIZE}_t)$ against t gave unbiased estimates of the parameters, b_0 and R , for each plot. In order for initial (1983) tree size to correspond to year 0, t was defined as shown above. R^2 values in these regressions averaged 0.97 and 0.96 for diameter and height, respectively, indicating that the error in estimating b_0 and R was small. The

estimated R for each plot is equal to an average annual relative growth rate (Evans, 1972).

A randomized block ANOVA, with tanoak and understory level arranged in a factorial design, was used to partition variation in the estimated values of b_0 and R for Douglas-fir diameter and height. A natural logarithmic transformation was applied to each dependent variable to improve the homogeneity of residual variation. Multiple comparisons of treatment means were performed using a protected LSD test at the 95% significance level (Snedecor and Cochran, 1980).

Equations for Predicting Stand Development

In a concurrent study (Chapter II), tanoak competition was found to reduce monthly relative growth rates for height and basal area of Douglas-fir during the 1986-1987 growing seasons. Based on these findings, exponential growth rates (i.e., R in model (1)) for Douglas-fir and tanoak were hypothesized to be functionally related to initial tanoak cover (1983) and understory level. Preliminary analyses suggested that variation in R was best described by a negative exponential function of initial tanoak cover and understory treatment:

$$R = B_0 \exp(-B_1 \text{TCOVER}_i - B_2 \text{UND}) \quad (2)$$

where: R = exponential growth rate for 1983-1988.

B_0 = maximum exponential growth rate (i.e., when tanoak and understory competition are zero)

B_1 = reduction in R per unit of initial tanoak cover

TCOVER_i = initial tanoak cover (1983)

B_2 = reduction in R from understory competition

UND = 0 for understory suppressed, = 1 understory not suppressed

R values were estimated for each plot using linear regression as described above for the following variables (average R^2 for these regressions follow each variable in parentheses): 1) Douglas-fir diameter (0.97), height (0.96), cover (0.92), LAI (0.96), and biomass (0.96), and 2) tanoak height (0.94) and crown width (0.93). A natural logarithmic transformation was applied to the plot estimates of R to linearize model (2), permitting the use of linear regression to estimate B_0 , B_1 , and B_2 for the combined data from both sites.

To quantify variation due to site differences, an indicator variable (SITE) was specified as equal to 1 for Squaw and -1 for Fir Point. This specification for the site indicator variable permits a given regression model to be generalized to average site conditions by setting the SITE parameter at its mean (0).

Stepwise linear regression (Wilkinson, 1988), using a

90% significance level for variable entry and removal, was utilized to select independent variables from the following list (see model (2) above): $TCOVER_i$, UND, $\ln(\text{initial tree size (1983)})$, SITE, $\text{SITE} \times TCOVER_i$, $\text{SITE} \times \text{UND}$, and $\text{SITE} \times \ln(\text{initial tree size})$. Graphical analysis of residuals was used to screen potential models. Incorporation of the site-specific variables into the stepwise regression analysis permitted the overall effects from tanoak and understory competition to be estimated with less error.

A monomolecular growth function (Draper and Smith, 1981) was used to describe the rate at which tanoak cover approaches its maximum value of 100%:

$$TCOVER_t = 100(1 - C_0 e^{-kt}) \quad (3)$$

where: $TCOVER_t$ = tanoak cover at time t

t = growing season since treatment - 1

$C_0 = 1 - (TCOVER_i/100)$; $TCOVER_i$ =
initial tanoak cover (1983)

k = growth rate

This growth function was selected because it provided a biologically-realistic description of the asymptotic development of tanoak cover. Least-squares nonlinear regression (Wilkinson, 1988) was used to estimate k (see model (3) above) from the five values of tanoak cover for each plot. An approximate R^2 value was calculated for

each plot's regression using asymptotic estimates of the regression and error sums of squares (Wilkinson, 1988). These approximate R^2 values averaged 0.99, indicating that error in estimating k probably was small.

Using combined data from both sites, an equation for predicting k was developed using stepwise linear regression to select among the following independent variables: $TCOVER_i$, UND , $SITE$, $SITE \times TCOVER_i$, and $SITE \times UND$. Variable entry/removal was controlled at the 90% significance level, and graphical analysis of residuals was used to screen potential models.

Within a given measurement year, the variables, understory cover, LAI, and biomass, were found to be linearly related to initial (1983) values of these variables and current-year tanoak cover. Equations for predicting fifth-year values for the understory variables were developed using stepwise linear regression and the model selection and screening criteria described above.

Predicting Young Stand Development from a Pre-harvest Stand Inventory

Tanoak sprout clump data from Tappeiner et al. (1984) and Harrington (1987) were combined into a comprehensive data set representing 32 sites in southwestern Oregon and northwestern California that spanned an age range of 1 to

15 years. Using these data, the following equation was developed to predict crown width of tanoak sprout clumps from their age and from characteristics of the parent tree(s) from which they originated:

$$\begin{aligned} \ln(\text{crown width (cm)}) = & 3.414 + 0.417(\ln(\text{DBH(cm)})) \\ & + 0.468(\ln(\text{AGE(years)})) \\ & + 0.335(\ln(\text{STEMNO})) \end{aligned}$$

where:

DBH = the quadratic mean diameter at breast height (1.37 m) of the parent tanoak tree(s) for a given clone

AGE = number of years since disturbance of the parent tree(s)

STEMNO = number of trees per tanoak clone

$$\text{adjusted } R^2 = 0.823 \quad s_{y.x} = 0.213 \quad n = 326$$

This equation was applied to tree diameter frequency data from two mature tanoak stands (stands 2 and 4 in Tappeiner and McDonald, 1984) to predict hypothetical values for tanoak percent cover three years after harvesting each stand (Table I.1). First, all sprout clumps were assumed to originate from single-stemmed parent trees. Second, the frequency of trees in each of six - 5 cm diameter classes was multiplied by the crown area (m^2) predicted from the class' midpoint d.b.h. value. Finally, crown area values were summed for each stand, divided by 10,000 m^2/ha , and multiplied by 100% to estimate 'initial' tanoak cover.

Assuming that each developing tanoak stand had a three-year-old Douglas-fir plantation similar to Squaw in 1983, data from this site were used to initialize Douglas-fir size, LAI, and biomass. The equations in Tables I.2-4 were applied to the initial values for tanoak cover and Douglas-fir variables to predict R and k for the following treatments: tanoak removal, tanoak removal with understory suppression, and no treatment. The correction factor, $\exp(0.5*s^2)$, was multiplied by estimates of R to correct for logarithmic bias in the predictions (Flewelling and Pienaar, 1981).

Douglas-fir and tanoak growth trajectories for five years following treatment were predicted by incorporating the estimates of R and k along with the initial stand values into models (1) and (3), respectively. Predicted values for tanoak cover in stands 2 and 4 were converted directly to LAI and biomass using the following equations:

$$\text{LAI (m}^2\text{/m}^2\text{)} = 0.078 * \text{tanoak cover (\%)}$$

$$\text{biomass (kg/m}^2\text{)} = 0.033 * \text{tanoak cover (\%)}$$

These equations were developed by regressing plot estimates for LAI or biomass (see methods above) from Squaw and Fir Point against values for cover ($r^2=0.99$ $n=234$). The regression intercept, which had little effect in reducing the error mean square, was not included in

these equations.

Understory cover, LAI, and biomass were initialized at 1983 mean values from Squaw and Fir Point using data for plots in which the understory was not treated. Fifth-year values for the understory variables were predicted using these initial values and the estimate of tanoak cover five years after treatment derived from the equations in Table I.5.

RESULTS AND DISCUSSION

EFFECTS OF TANOAK AND UNDERSTORY VEGETATION ON DOUGLAS-FIR GROWTH

Tanoak competition at each site significantly ($p < 0.005$) reduced the exponential growth rates (R) for Douglas-fir stem diameter in the six years following treatment, resulting in markedly different growth trajectories (Fig. I.1-2). Based on the ANOVA, suppression of understory vegetation (both sites) and the interaction of tanoak level x understory level (Squaw only) did not significantly ($p > 0.1$) influence diameter growth rates.

At Squaw, removal of tanoak resulted in significantly greater values for diameter growth rates versus all other tanoak levels (Fig. I.1). Differences in stem diameter due to tanoak level already existed at Squaw in 1983, the first year after treatment ($p = 0.055$). At Fir Point, diameter growth rates observed for no tanoak and low tanoak cover were significantly greater than for high tanoak cover (Fig. I.2). Diameter growth rates for low and medium tanoak cover did not differ at either site.

Exponential growth rates for Douglas-fir height were significantly ($p < 0.01$) less at each site for trees in high tanoak cover versus all other levels of tanoak cover

(Figs. I.3-4). Height growth rates did not differ significantly ($p > 0.05$) among the zero, low, and medium tanoak cover levels at either site, indicating that height growth rates were less sensitive to tanoak competition than those for diameter. As found for diameter, neither understory level (both sites) nor the interaction of tanoak level x understory level (Squaw only) significantly ($p > 0.1$) influenced height growth rates.

PREDICTING STAND DEVELOPMENT

Douglas-fir and Tanoak

Exponential growth rates (R) for both diameter and height of Douglas-fir were found to vary as negative exponential functions of initial (1983) tanoak cover and understory level (Fig. I.5-6 and Table I.2). These variables explained 72% and 38%, respectively, of the variation in R for diameter and height.

In contrast to the ANOVA, the regression analyses revealed that understory level limited R for Douglas-fir diameter ($p < 0.001$) and height ($p = 0.058$). The regression of diameter R on initial tanoak cover was over twice as steep as that for height R (Table I.2), emphasizing the different sensitivities of these parameters to competition. R for tanoak crown width also had a

negative exponential relationship ($r^2 = 0.51$) with initial tanoak cover; however, such a relationship was not significant ($p > 0.1$) for tanoak height R (Table I.3).

The k parameter for the tanoak cover model was linearly related ($r^2 = 0.57$) with initial tanoak cover (Fig. I.7 and Table I.3). This relationship indicates that the rate at which tanoak cover approaches its maximum (100%) was directly related to the amount of initial cover present. The k parameter was not significantly ($p > 0.1$) influenced by understory level.

R values for Douglas-fir cover, LAI, and biomass also had negative exponential relationships with initial tanoak cover and understory level (Table I.4). In these regressions, initial tanoak cover explained 51-65% of the variation, while understory level explained an additional 2-6% of variation.

Maximum R (B_0) for Douglas-fir biomass was 0.96 (Table I.4), suggesting that during early growth, Douglas-fir trees approximately double their biomass each year. Other research in the Oregon Coast Range has documented similar rates of biomass accumulation (M. Newton, unpublished data). Maximum R values for Douglas-fir cover (0.59) and LAI (0.64) indicated that annual growth rates for these variables were not as great as for biomass.

In each of the Douglas-fir regressions, additional

variation could be explained by including the site-specific variables for initial (1983) tree size and initial understory cover (Tables I.2 and I.4). For example, these variables explained an additional 13% of variation in diameter R, and an additional 34% in height R.

To ascertain the nature of relationships between R and initial tree size or understory cover, residuals were estimated for models not including these independent variables. A scatterplot of these residuals against initial tree size revealed that in the Fir Point data, diameter and height R increased with initial tree size, however the relationship was weakly negative for Squaw. Residuals for height R displayed a strong negative relationship with initial understory cover in the Fir Point data, but such a relationship was not evident in the Squaw data.

The site-specific variables for initial tree size and understory cover were included because they reduced the error associated with the parameter estimates for the factors, maximum R (B_0), initial tanoak cover, and understory level. When used for predictive purposes, these regression equations can be generalized to mean site effects by setting the SITE parameter at its mean (0).

The effects of initial tanoak cover on the growth trajectories for diameter and height of Douglas-fir and

cover of tanoak can be summarized using three-dimensional response surfaces (Figs. I.8-10). For Douglas-fir, the response surfaces were generated using the equations in Table I.2 to predict R for initial tanoak cover values ranging from 0 to 35% and understory level held constant at a mean level. A log-bias correction (Flewelling and Pienaar, 1981) was applied to the predictions of R. Tree size then was estimated by applying model (1) and an average initial tree size from Squaw in 1983 to the predicted R values.

For initial tanoak cover values greater than 25%, the growth trajectory for Douglas-fir diameter assumes a near-linear shape (Fig. I.8). With successive reductions in initial tanoak cover, the growth curve for diameter becomes a progressively steeper exponential function. The growth trajectories for Douglas-fir height also become steeper exponential functions with decreasing initial tanoak cover (Fig. I.9), but the trend is less pronounced than observed for diameter. The distribution of plotted data in Figs. I.8-9 indicate that Douglas-fir growth response to understory level was greatest for low values of initial tanoak cover.

For tanoak cover, the response surface (Fig. I.10) was generated by predicting k using the equation in Table I.3 for a range of initial tanoak cover values (5 to 35%).

Predicted k then was applied to model (3) to estimate tanoak cover. Figure I.10 illustrates that the rate at which a tanoak stand approaches its maximum cover (100%) is related to its initial cover. The monomolecular growth function assumes that as cover approaches 100%, the rate of approach declines asymptotically to zero. This function appears to adequately describe the rate of crown closure for a tanoak stand as intensity of intraspecific competition increases.

Understory Vegetation

Regression analyses indicated that cover, LAI, and biomass of understory vegetation in a given year were most strongly related to initial (1983) values for these variables. Table I.5 gives equations for predicting understory level five years after treatment (1987).

Application of glyphosate (April, 1983) caused a significant ($p < 0.04$) reduction in 1983 understory cover, LAI, and biomass relative to untreated plots. Such a reduction in understory level due to treatment was not detected in the 1985-1987 data, probably because treatment-related differences in understory level are explained by the initial (1983) values. Understory cover in 1986 and 1987 was negatively related ($p < 0.001$) to current-year tanoak cover, however this relationship was

not present in the 1983 and 1985 data. Site differences in the 1987 regression relationships were not detected.

The regression parameter for initial understory cover (Table I.5) indicated that understory cover in 1987 was 28% greater than that observed in 1983. In contrast, understory LAI and biomass increased 109-141% from 1983 to 1987. Using average values from 1983, the understory vegetation was estimated to have the following characteristics five years after removing tanoak: 48% cover, $0.79 \text{ m}^2/\text{m}^2$ LAI, and $0.20 \text{ kg}/\text{m}^2$ biomass. In the presence of 60% tanoak cover, understory development would be reduced by about half: 17% cover, $0.42 \text{ m}^2/\text{m}^2$ LAI, and $0.10 \text{ kg}/\text{m}^2$ biomass.

Predicting Stand Development from a Pre-harvest Tanoak Stand Inventory

The predicted developmental patterns for two Douglas-fir / tanoak stands demonstrate that the rates of exponential growth for Douglas-fir are affected by characteristics of the pre-harvest tanoak stands (Figs. I.11-12). Predicted Douglas-fir growth in the tanoak stand 2 was markedly less than that for stand 4, because the initial tanoak cover at three years age (22 and 7%, respectively) differed greatly for the two stands (Fig. I.13). The predictions suggest that average Douglas-fir

height does not exceed average tanoak height until stand ages of 8 to 9 years (Fig. I.12).

At an age of eight years, predicted LAI and biomass of tanoak in stand 2 exceeded that for Douglas-fir and understory vegetation by over tenfold (Figs. I.14 and I.16). Five years following removal of tanoak, predicted values for Douglas-fir LAI and biomass (Figs. I.15 and I.17) were still only 12-25% of that for the undisturbed tanoak stand (Figs. I.14 and I.16).

The predictions suggest that during the first seven years of stand development, Douglas-fir LAI and biomass are less than that for understory vegetation, regardless of tanoak level (Figs. I.14-17). These comparable values for site occupancy support the findings of other research on the strong competitive effects of shrubs and herbs on Douglas-fir growth (Tappeiner et al. 1987; White 1987; Newton and Preest, 1988).

It is important to recognize that a range of outcomes in Douglas-fir / tanoak stand development are possible if initial tanoak cover, treatment timing, or initial Douglas-fir size are varied. Since the models are based on size-dependent growth functions, they can be used within the age range of the data to estimate stand development for different initial tree sizes, a factor which can be directly manipulated by forest management.

For example, effective site preparation or the use of large planting stock can have a direct bearing on tree size at the time of a vegetation control treatment.

The predictive equations have the flexibility to simulate the effects of treatments that were not specifically included in this research. For example, the response of Douglas-fir to manual cutting of tanoak can be predicted as follows. Using frequency / stem diameter class data from an uncut tanoak stand, one-year-old crown widths could be predicted from parent tree size to simulate first-year recovery following manual cutting of tanoak sprout clumps. In combination, this initial tanoak cover and the size of the Douglas-fir at the time of treatment would then define subsequent growth trajectories for the various components in the stand.

TABLE I.1. Inventory data from two mature tanoak stands in southwestern Oregon (adapted from Tappeiner and McDonald, 1984).

Stand Number	D. B. H. Class (cm)					
	2-5	6-10	11-15	16-20	21-25	26-30
number of stems per ha						
2	1322	576	229	62	18	22
4	529	136	69	44	0	0

TABLE I.2. Regression equations for predicting $\ln(R)$ for Douglas-fir diameter and height.

Independent Variables	Dependent Variables	
	Douglas-fir diameter R (mm/mm/yr)	Douglas-fir height R (cm/cm/yr)
	Regression Coefficients	
intercept*	-0.998	-1.035
TCOVER _i *	-0.016	-0.007
UND*	-0.100	-0.047
SITE* x Y-INITIAL*	-0.087	-0.042
SITE x UCOVER _i *	0.010	0.007
Adjusted R ²	0.852	0.715
s _{y.x}	0.074	0.067
n	39	39

*intercept = $\ln(B_0)$ where B_0 = maximum R for zero competition

TCOVER_i = initial (1983) tanoak cover (%)

UND = 0 for understory suppressed; = 1 for understory not suppressed

SITE = 1 for Squaw; = -1 for Fir Point

Y-INITIAL = $\ln(\text{initial tree size})$

UCOVER_i = initial understory cover (%)

TABLE I.3. Regression equations for predicting k (tanoak cover model) and ln(R) for tanoak crown width and height.

Independent Variables	Dependent Variables		
	tanoak cover k parameter	tanoak crown width R (cm/cm/yr)	tanoak height R (cm/cm/yr)
intercept*	0.034	-1.829	-2.207
TCOVER _i *	0.004	-0.021	-----
SITE* x UCOVER _i *	-----	-----	0.007
Adjusted R ²	0.571	0.513	0.138
s _{y.x}	0.029	0.157	0.201
n	27	27	27

*intercept = $\ln(B_0)$ where B_0 = maximum R for zero competition

TCOVER_i = initial (1983) tanoak cover (%)

SITE = 1 for Squaw; = -1 for Fir Point

UCOVER_i = initial understory cover (%)

TABLE I.4. Regression equations for predicting $\ln(R)$ for Douglas-fir cover, LAI, and biomass.

Independent Variables	Dependent Variables		
	Douglas-fir cover R	Douglas-fir LAI R	Douglas-fir biomass R
	(proportion/yr)		
	Regression Coefficients		
intercept*	-0.521	-0.448	-0.043
TCOVER _i *	-0.010	-0.012	-0.012
UND*	-0.063	-0.076	-0.065
Y-INITIAL*	-0.185	-0.079	-----
SITE*	-----	-0.135	-0.187
SITE x UND	-0.045	-----	-----
SITE x UCOVER _i *	-----	0.008	0.008
Adjusted R ²	0.704	0.853	0.843
S _{y.x}	0.075	0.059	0.062
n	39	39	39

*intercept = $\ln(B_0)$ where B_0 = maximum R for zero competition

TCOVER_i = initial (1983) tanoak cover (%)

Y-INITIAL = \ln (initial Douglas-fir cover or LAI)

SITE = 1 for Squaw; = -1 for Fir Point

UCOVER_i = initial understory cover (%)

TABLE I.5. Regression equations for predicting fifth-year (1987) understory cover, LAI, and biomass from initial values (1983) of these variables and 1987 tanoak cover.

Independent Variables	Dependent Variables		
	Understory Cover	Understory LAI	Understory biomass
	(%)	(m ² /m ²)	(kg/m ²)
	Regression Coefficients		
Intercept	32.133	0.307	0.082
Initial (1983) understory value	1.280	2.089	2.412
1987 tanoak cover (%)	-0.506	-0.006	-0.002
Adjusted R ²	0.433	0.655	0.744
s _{y.x}	15.370	0.311	0.075
n	39	39	39

FIGURE I.1. Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir diameter at Squaw. Growth trajectories followed by the same letter are not significantly different (95% level).

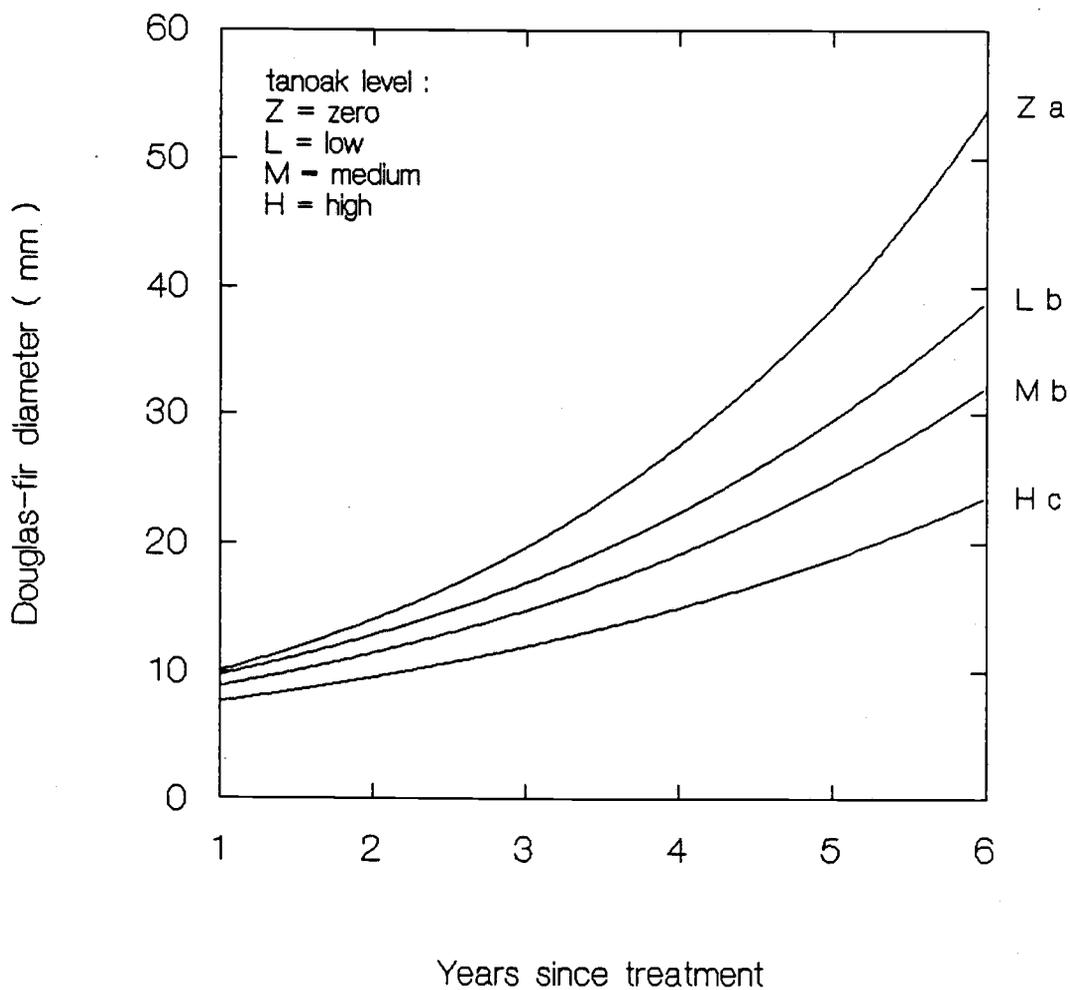


FIGURE I.2. Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir diameter at Fir Point. Growth trajectories followed by the same letter are not significantly different (95% level).

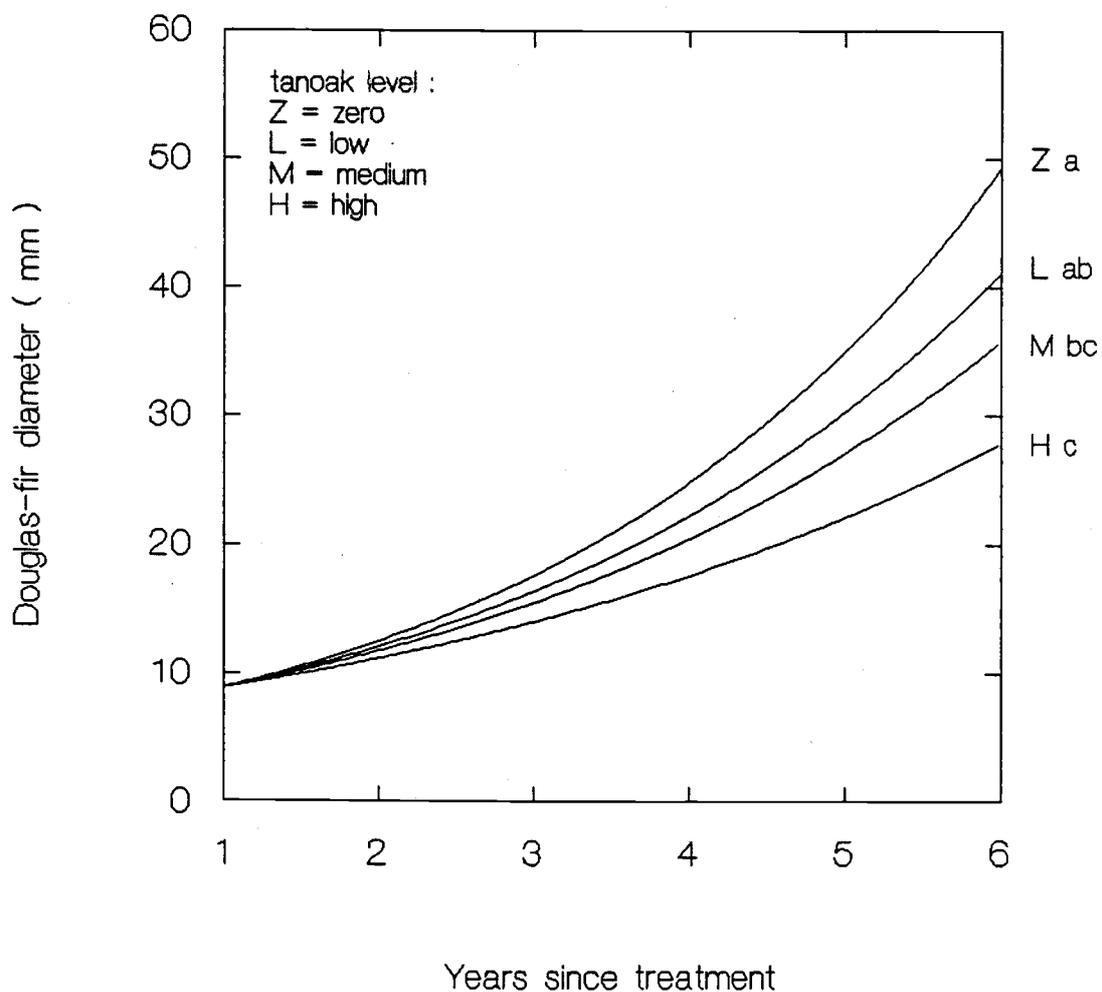


FIGURE I.3. Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir height at Squaw. Growth trajectories followed by the same letter are not significantly different (95% level).

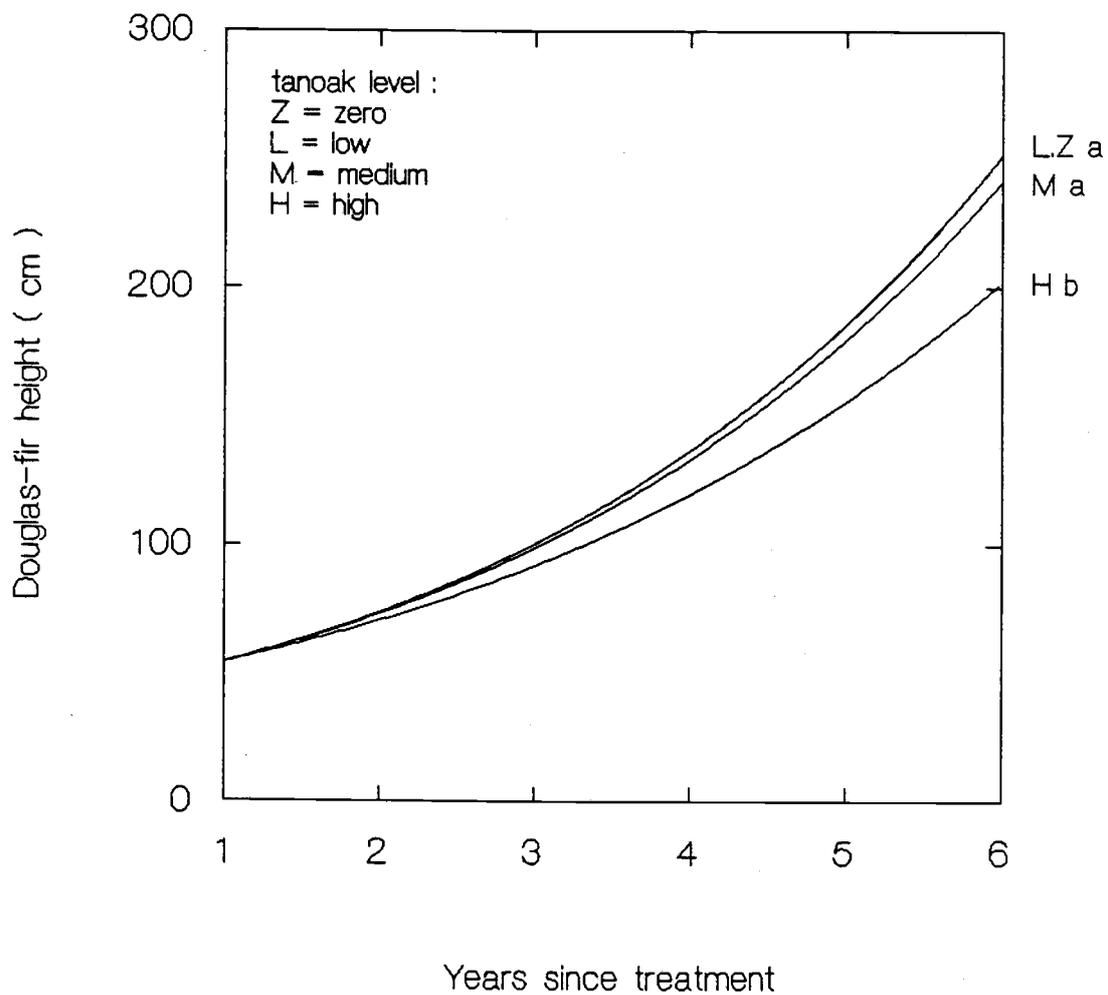


FIGURE I.4. Effects of tanoak level on six-year exponential growth trajectories for Douglas-fir height at Fir Point. Growth trajectories followed by the same letter are not significantly different (95% level).

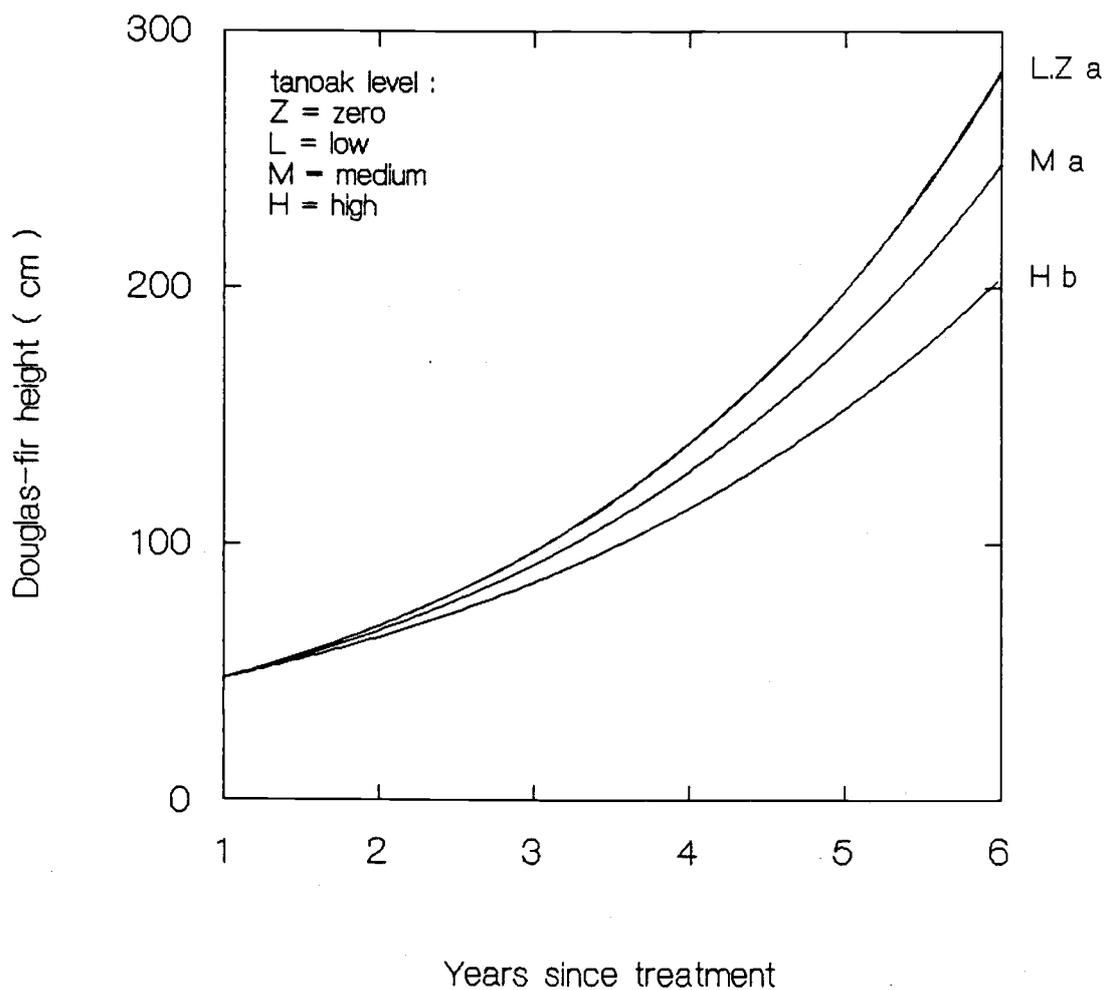


FIGURE I.5 Relationship of the six-year exponential growth rate (R) for Douglas-fir diameter at Squaw and Fir Point with initial (1983) tanoak cover and level of understory vegetation (shrubs and herbs).

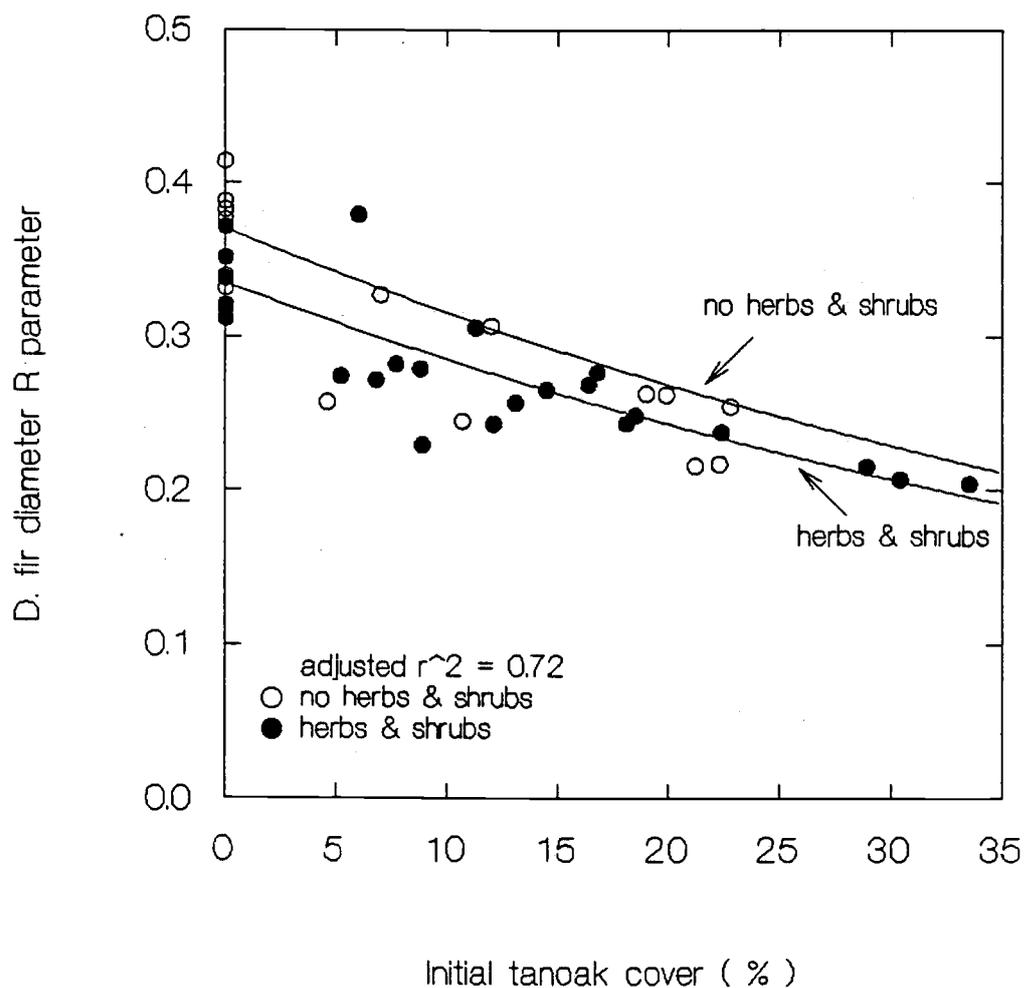


FIGURE I.6 Relationship of the six-year exponential growth rate (R) for Douglas-fir height at Squaw and Fir Point with initial (1983) tanoak cover and level of understory vegetation (shrubs and herbs).

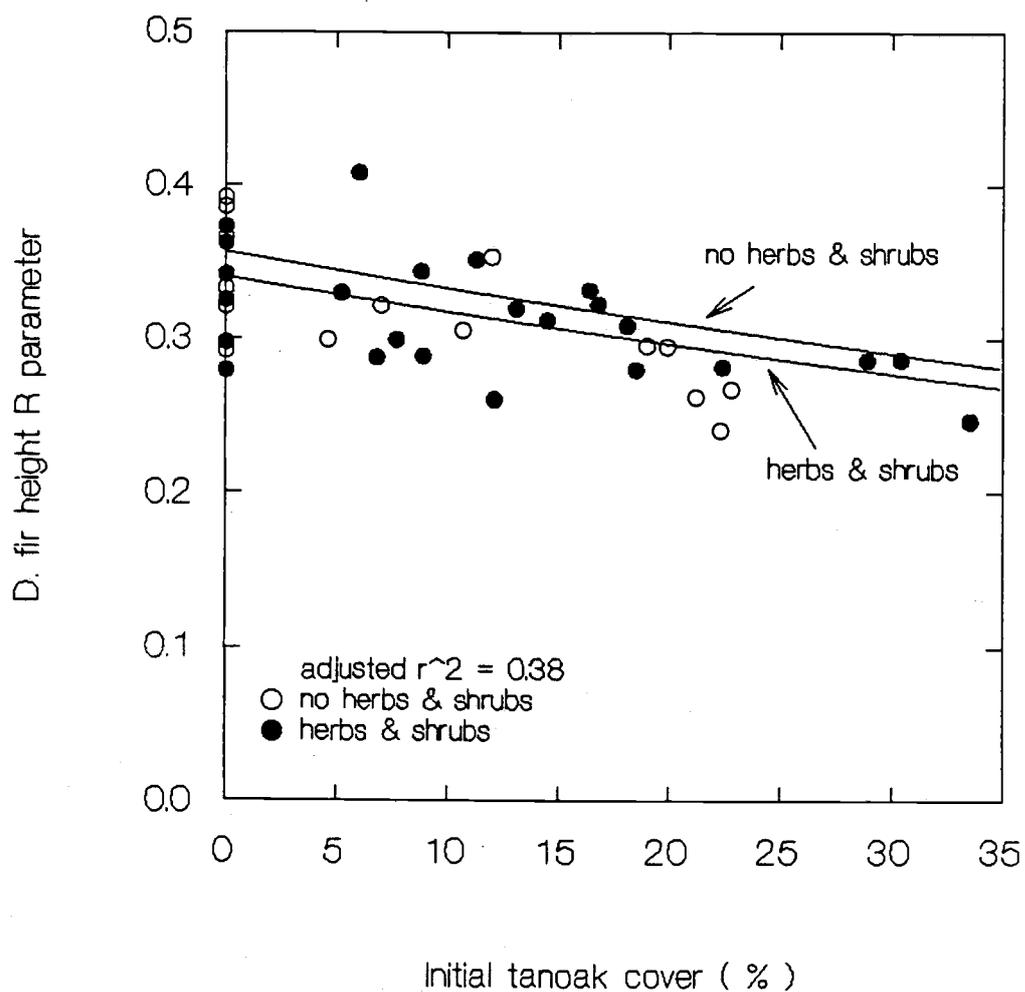


FIGURE I.7 Relationship of the five-year growth rate (k) for tanoak cover at Squaw and Fir Point with initial (1983) tanoak cover and level of understory vegetation (shrubs and herbs).

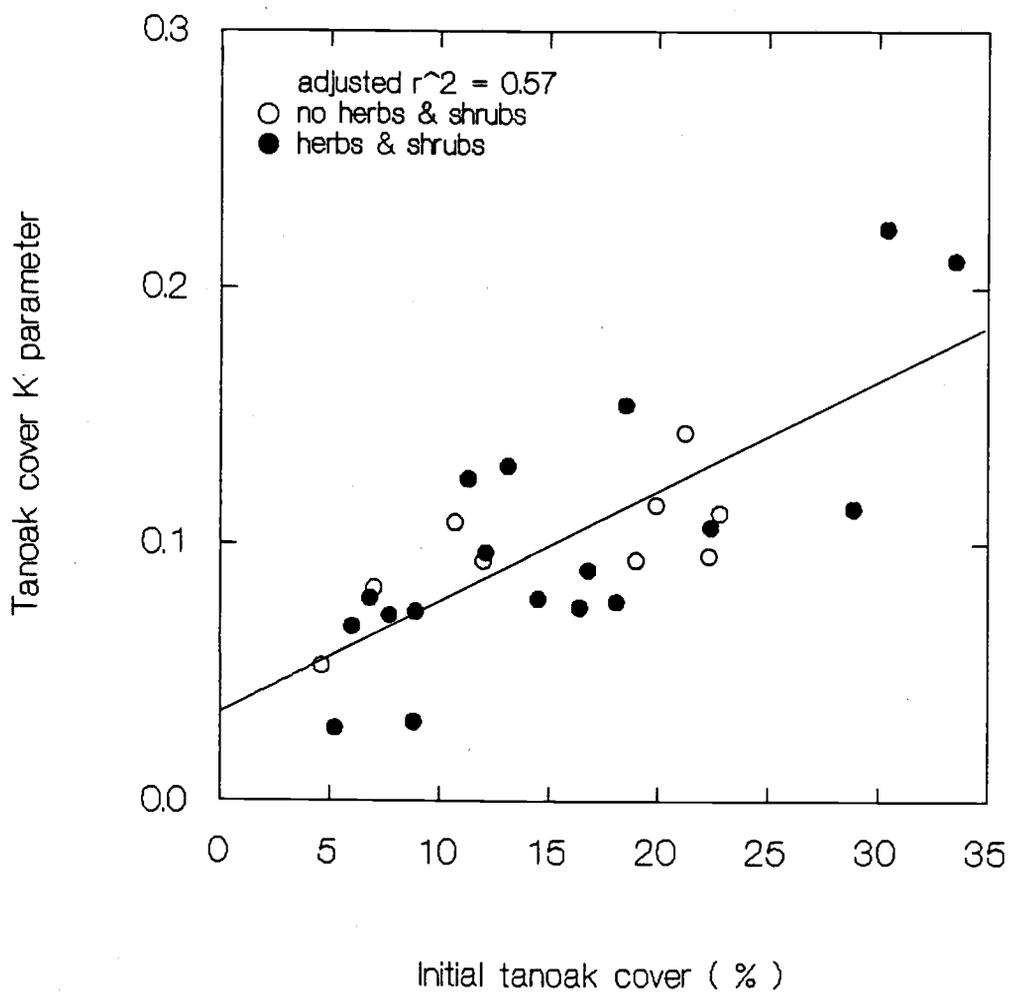


FIGURE I.8. Response surface for Douglas-fir diameter predicted for six years after treatment from initial (1983) tanoak cover at Squaw and Fir Point. Understory level was held constant at a midpoint value. Plotted points are observed values for mean Douglas-fir diameter per plot.

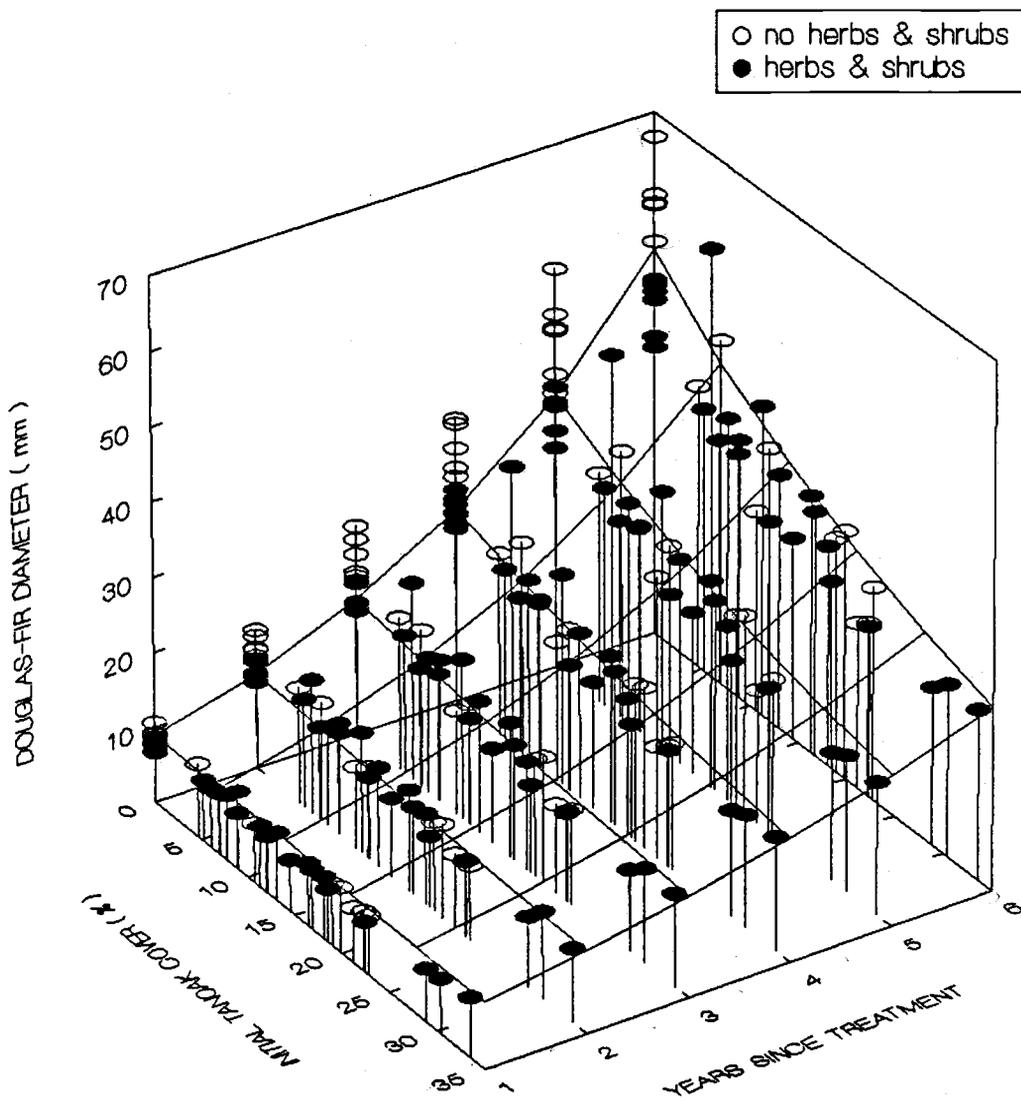


FIGURE I.9. Response surface for Douglas-fir height predicted for six years after treatment from initial (1983) tanoak cover at Squaw and Fir Point. Understory level was held constant at a midpoint value. Points on the surface are observed values for mean Douglas-fir height per plot.

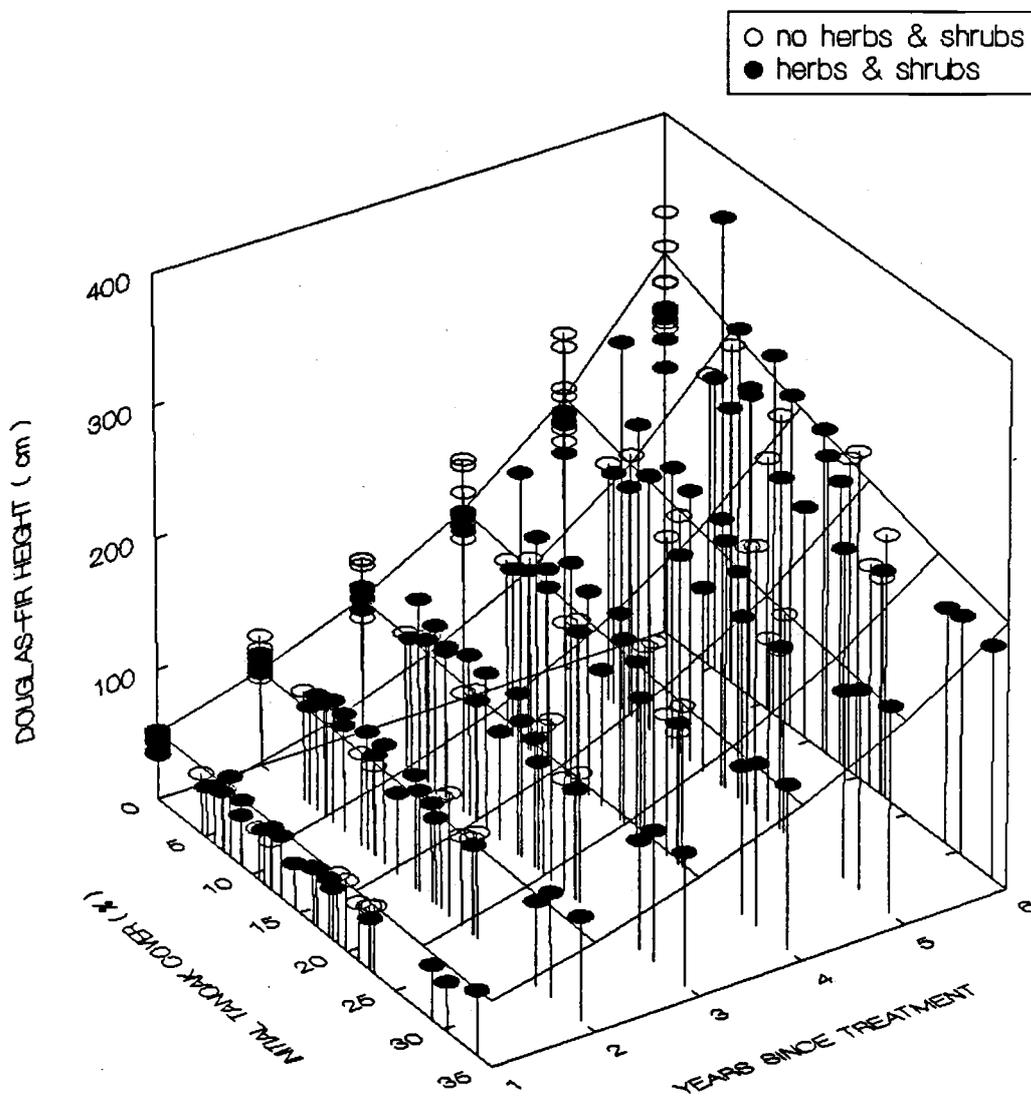


FIGURE I.10. Response surface of tanoak cover predicted for six years after treatment from initial (1983) tanoak cover at Squaw and Fir Point. Understory level was held constant at a midpoint value. Points on the surface are observed values for tanoak cover per plot.

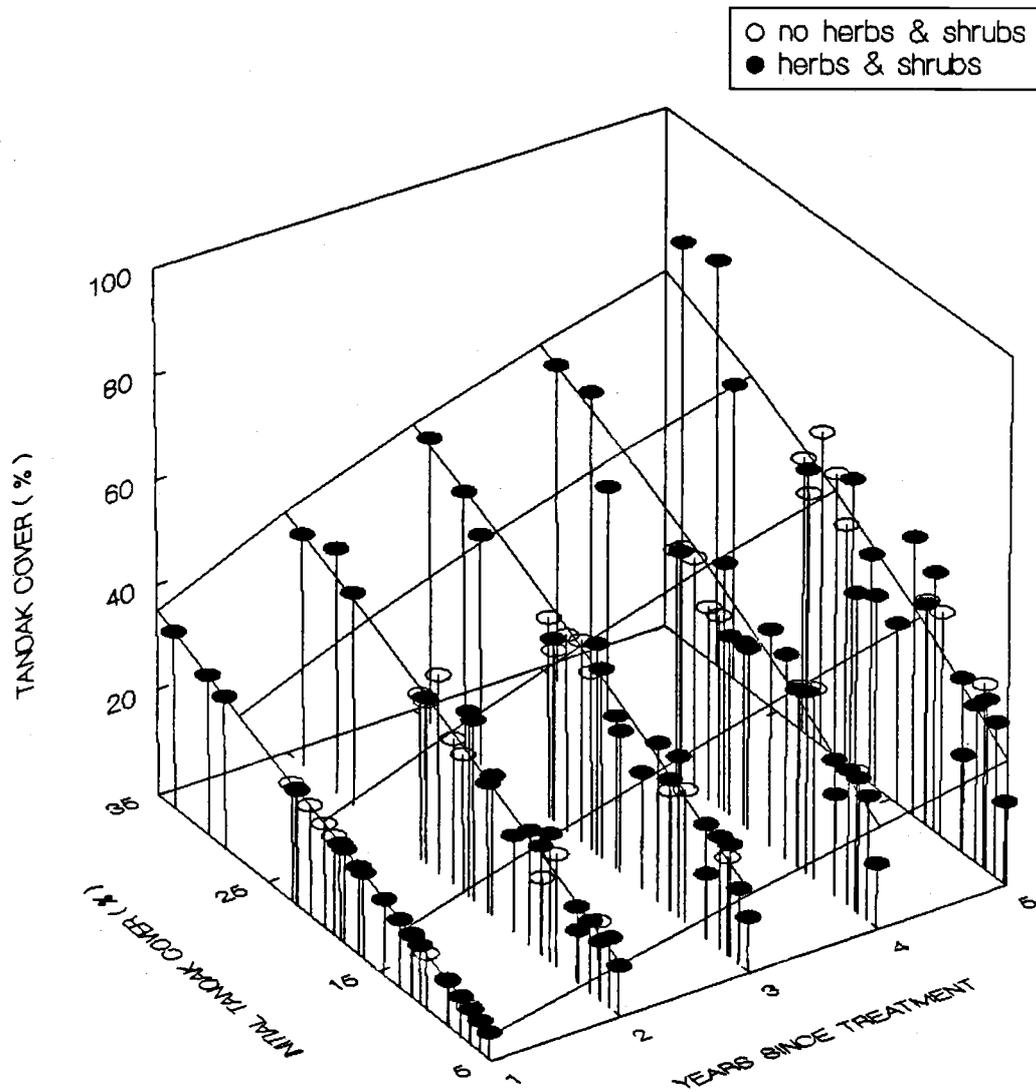


FIGURE I.11. Predictions of growth trajectories for Douglas-fir diameter based on stand inventory data adapted from Tappeiner and McDonald (1984). Growth trajectories for tanoak removal and/or suppression of shrubs / herbs assume that these treatments were applied at a stand age of 3 years.

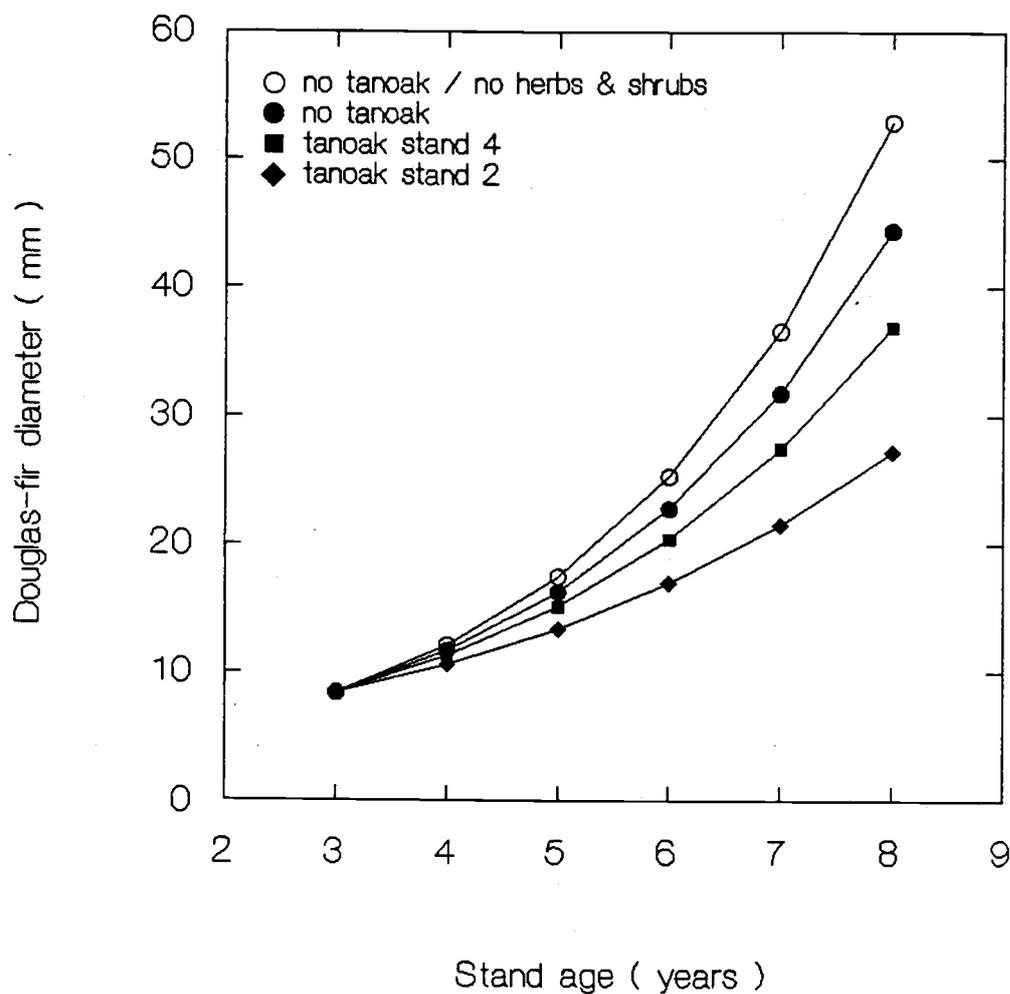


FIGURE I.12. Predictions of growth trajectories for Douglas-fir and tanoak height based on stand inventory data adapted from Tappeiner and McDonald (1984). Growth trajectories for tanoak removal and/or suppression of shrubs / herbs assume that these treatments were applied at a stand age of 3 years.

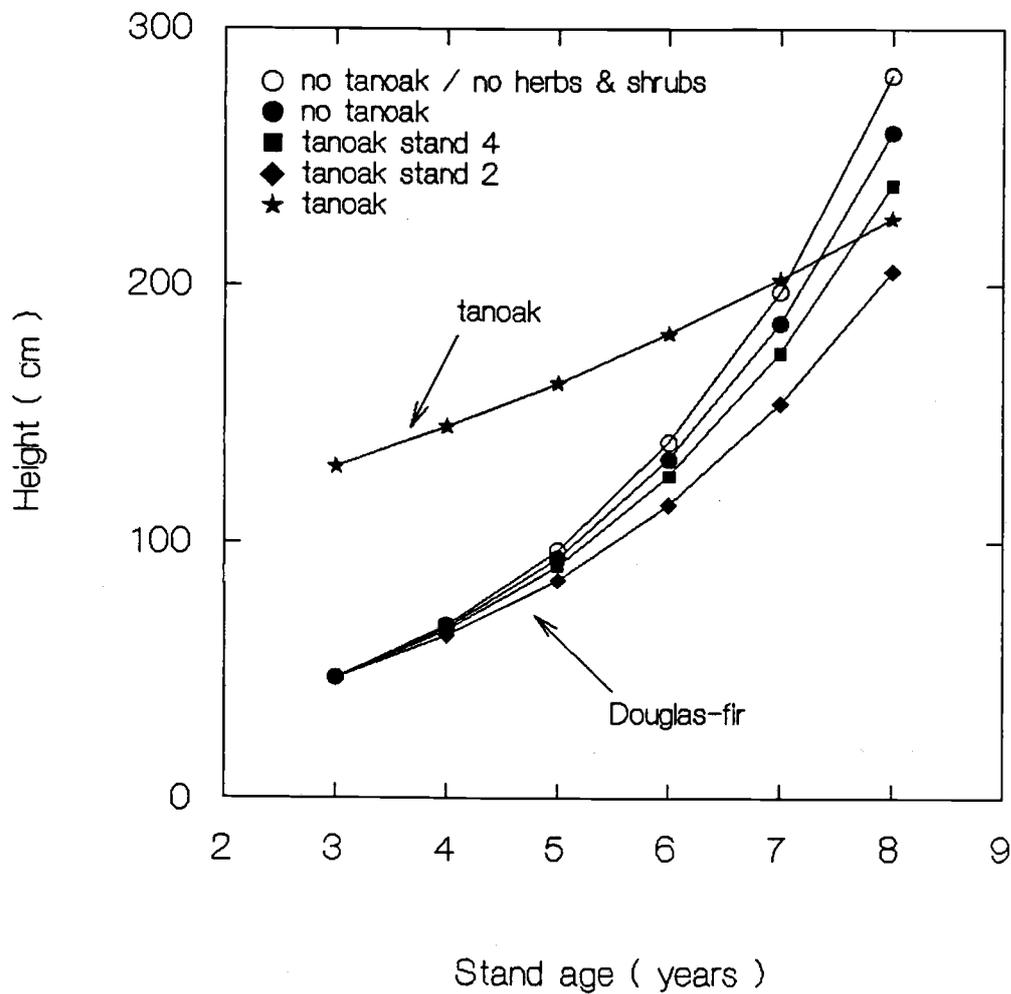


FIGURE I.13. Predictions of growth trajectories for tanoak cover based on stand inventory data adapted from Tappeiner and McDonald (1984).

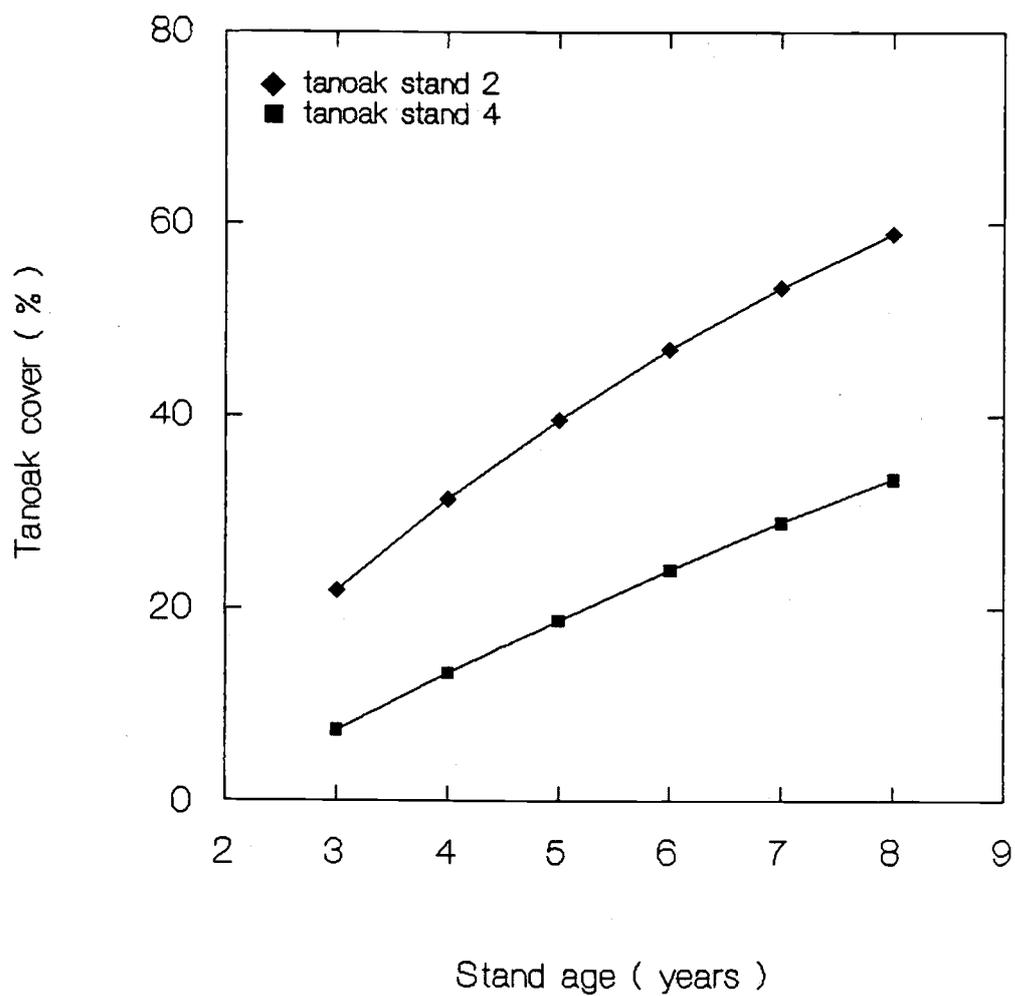


FIGURE I.14. Predictions of growth trajectories for leaf area index of tanoak, Douglas-fir, and understory vegetation (shrubs and herbs) based on stand inventory data adapted from Tappeiner and McDonald (1984).

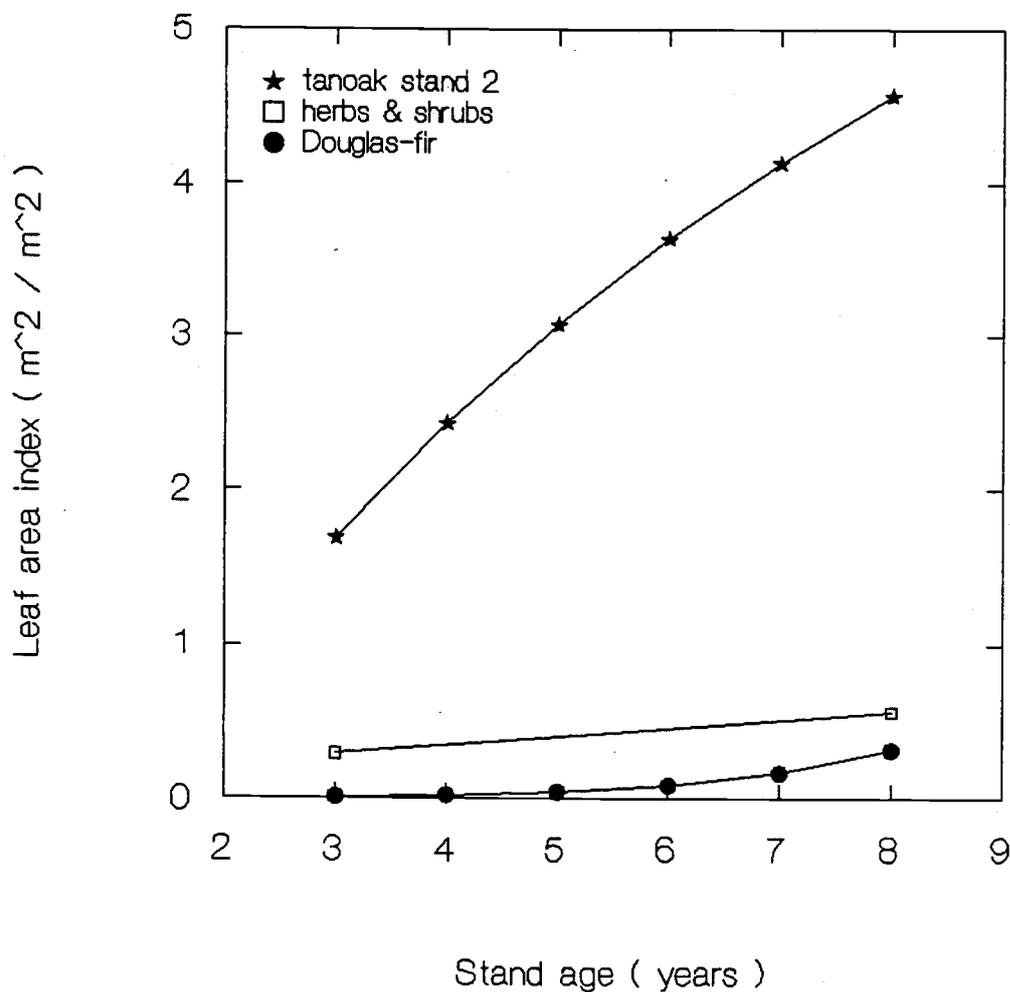


FIGURE I.15. Predictions of growth trajectories for leaf area index of Douglas-fir and understory vegetation (shrubs and herbs) following removal of tanoak at a stand age of 3 years.

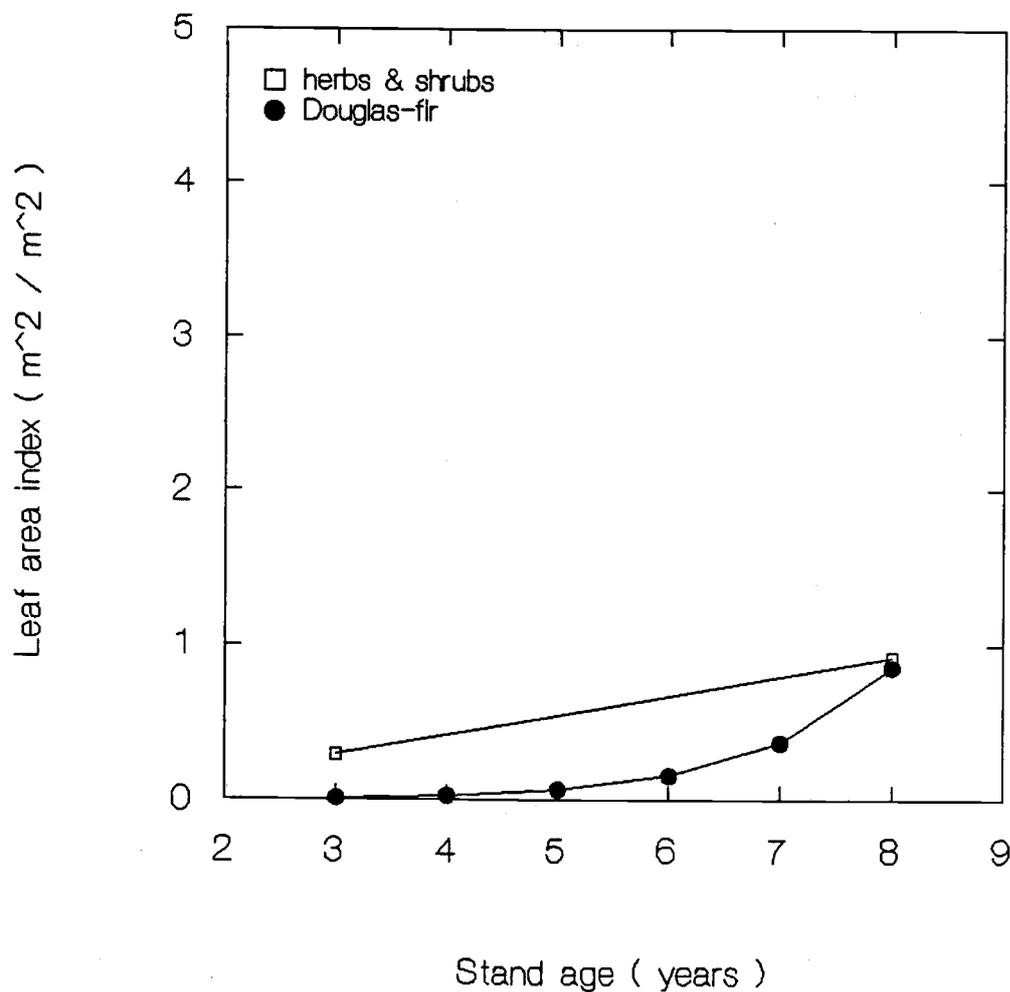


FIGURE I.16. Predictions of growth trajectories for aboveground biomass of tanoak, Douglas-fir, and understory vegetation (shrubs and herbs) based on stand inventory data adapted from Tappeiner and McDonald (1984).

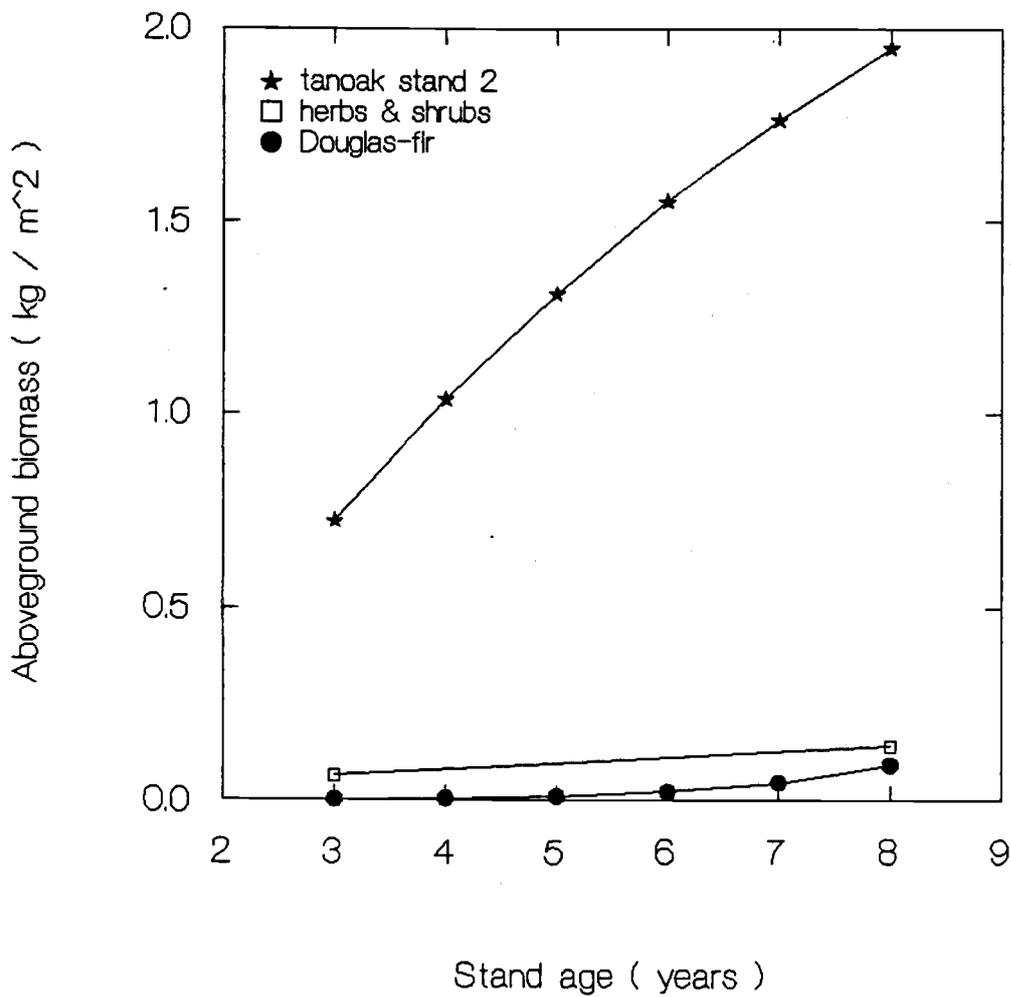
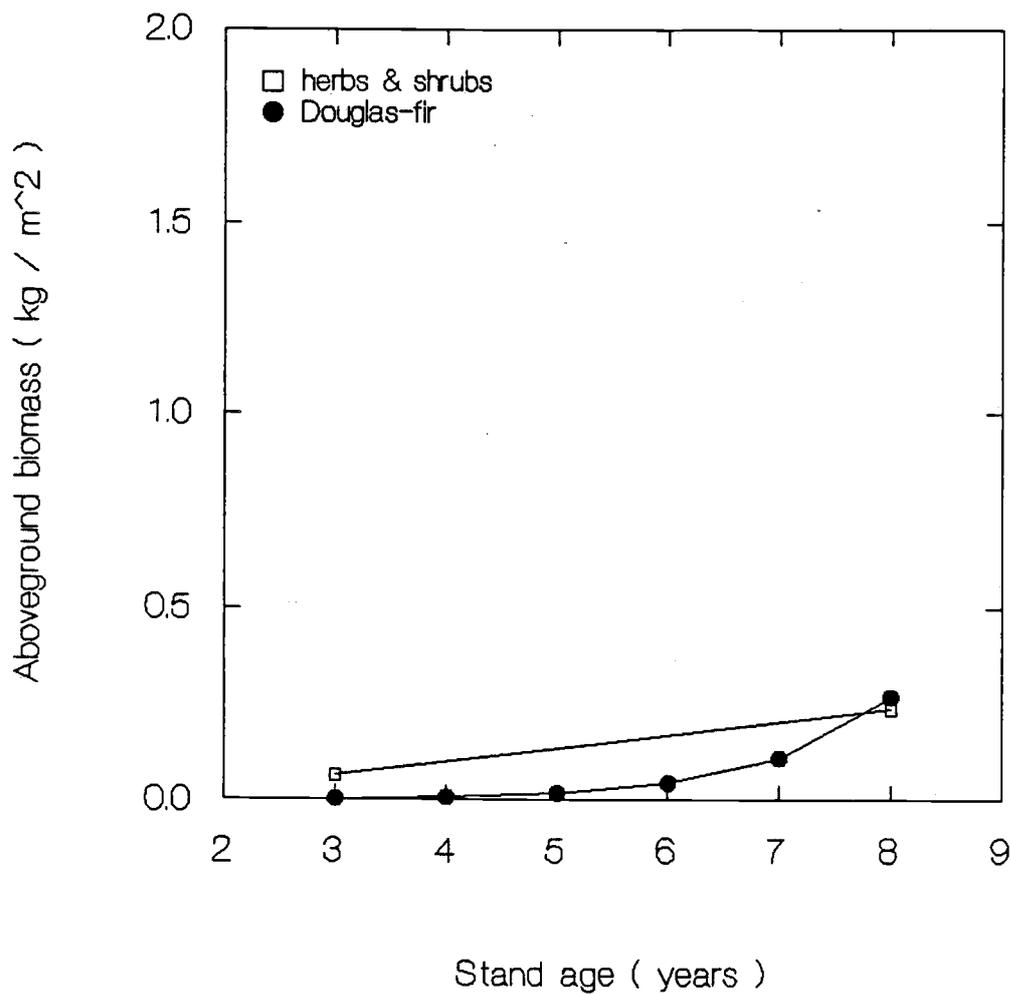


FIGURE I.17. Predictions of growth trajectories for aboveground biomass of Douglas-fir and understory vegetation (shrubs and herbs) following removal of tanoak at a stand age of 3 years.



CHAPTER II

EFFECTS OF TANOAK (LITHOCARPUS DENSIFLORUS) COMPETITION ON
MORPHOLOGY, DURATION, AND RELATIVE RATES OF GROWTH
OF DOUGLAS-FIR (PSEUDOTSUGA MENZIESII) SAPLINGS

ABSTRACT

Douglas-fir (Pseudotsuga menziesii) saplings were grown with and without competition from tanoak (Lithocarpus densiflorus) sprout clumps at two forest sites in southwestern Oregon. Tanoak competition significantly reduced (95% level) the following morphological parameters on Douglas-fir terminal and lateral shoots: number and size of buds; lengths of shoots, internodes, and needles; and biomass in foliage and wood. Number of internodes (or needles) on shoots was strongly related ($r^2=0.80$) to the size of the bud from which they developed. Competition resulted in differences in Douglas-fir biomass and shoot elongation; these differences were attributed to combined reductions in internode number and internode length (distance between needles), with internode number accounting for most (72-87%) of the variation. The cumulative effects of competition on Douglas-fir were described by partitioning the variation in growth of shoots and stem basal area into

that attributable to potential growth, or morphology, and that from current-year attainment of potential growth.

During the 1986 and 1987 growing seasons, tanoak competition limited both the rates and duration of growth in Douglas-fir basal area; for height, only the growth rates were reduced.

INTRODUCTION

Management of plantations of young Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) often includes prescribing silvicultural treatments to reduce the intensity of interspecific competition. Such treatments would be most effective if they were designed according to the processes by which competition affects tree growth. In this study, we describe some of the processes by which competition from a common hardwood, tanoak (Lithocarpus densiflorus (Hook. and Arn.) Rehd.), influences the growth and morphology of Douglas-fir. The following is an overview of growth processes in Douglas-fir, and potential influences of competition on these processes are discussed.

SHOOT GROWTH PROCESSES

Shoot growth of Douglas-fir is determinate, and results largely from the number of stem internodes that developed from cell division and differentiation within the bud in the previous year (Cannell et al. 1976). An internode is defined as the portion of stem between two successive nodes, and a node is the point of attachment for one or more lateral appendages (Critchfield, 1985). Internode initiation within newly-forming buds of Douglas-

fir occurs largely during the summer dry season common to the Pacific Northwest (Owens, 1968).

An additional component of Douglas-fir shoot growth is the current-year elongation of internodes, which involves the increase in cell number from intercalary meristems and the expansion of previous- and current-year cells (Cannell et al. 1976). Cell number usually accounts for more of the variation in final internode length than does cell elongation (Zimmermann and Brown, 1971).

Growth processes of Douglas-fir needles are similar to those for shoots in that most of the current-year elongation is attributable to expansion of cells that developed in the previous year (Owens, 1968). However, a portion of the growth is due to current-year mitosis from an intercalary meristem located at the base of the needle and to the subsequent expansion of the new cells (Owens, 1968).

CAMBIAL GROWTH PROCESSES

Unlike shoot growth, cambial growth is indeterminate; it is highly dependent on current-year resource availability (Kramer and Kozlowski, 1979). When soil water tensions drop to -0.1 to -0.2 MPa, cambial growth of many tree species is reduced, and relief from water stress

via irrigation or rainfall can cause cambial growth to resume (Kramer and Kozlowski, 1960). Generally for most tree species, cambial growth has a lower priority for photosynthate allocation than shoot growth (Waring, 1987). Thus, trees under environmental stress typically demonstrate reductions in cambial growth before shoot growth.

Given that the amount of stem tissue produced by the cambium is proportional to the number of cambial cells, a relationship should exist between the annual increment in cambial tissue and stem size. In 5- to 9-year-old Douglas-fir, significant correlations have been found between current-year diameter increment and stem diameter from previous years (Howard and Newton, 1984; Harrington and Wagner, unpublished data).

EFFECTS OF COMPETITION ON TREE GROWTH

Competition has a compounding influence on tree growth as a result of two interactive processes: a) it constrains tree morphological development (potential growth), and b) it limits the proportion of potential growth that is attained in a given growing season (potential growth attainment). Potential growth is defined as growth that is unimpeded by competition, thus it is strictly a function of the size and morphology of

the tree. Potential growth attainment is the proportion of potential growth realized in a given growing season, and it is governed by growth rate and duration.

Based on the previous discussion, variation in Douglas-fir shoot and cambial growth for a given growing season can be partitioned into two sources: a) potential growth, described by number of internodes or stem circumference, and b) potential growth attainment, described by elongation of internodes and increment in stem basal area.

The objectives of this study were, first, to evaluate the effects of tanoak competition on potential shoot growth of Douglas-fir by assessing differences in morphology. Second, in order to assess the cumulative effects of tanoak competition, variation in Douglas-fir shoot and stem basal area growth was partitioned into the components of potential growth and potential growth attainment. Finally, the mechanisms by which tanoak competition limits potential growth attainment were described by analyzing the duration (days) and relative rates of Douglas-fir height and basal area growth during several growing seasons.

METHODS

SITE DESCRIPTIONS

The study was conducted in two conifer plantations, Squaw and Fir Point, in southwestern Oregon that are being managed for wood production and other resources. Fir Point (T32S R6W S17) is located 70 km north of Squaw (T39S R6W S21). Prior to harvest in 1980, each site contained an old-growth conifer stand with an understory of tanoak. Tanoak is an evergreen hardwood tree that sprouts vigorously following a disturbance (Tappeiner et al. 1984), and the resulting sprout clumps limit the growth of planted conifers (Radosevich et al. 1976; Roy, 1981; Tappeiner et al. 1987; Jaramillo, 1988; Chapter I).

Both sites were broadcast-burned (spring, 1981) prior to planting with two-year-old bare-root Douglas-fir seedlings in April of 1981 (Squaw) and 1982 (Fir Point). Wide spacing of the Douglas-fir (3 m) probably minimized intraspecific competition for the duration of the study. Following broadcast burning, an even distribution of tanoak sprout clumps developed from the stumps of parent trees present in the pre-harvest stand. Elevations of the two study sites range from 800 to 900 m, and they receive approximately 130 cm of annual precipitation. Soils are composed of gravelly/clay loams of the Pollard-Beekman

series at Squaw (Meyer and Amaranthus, 1979) and the Josephine-Speaker series at Fir Point (Hubbard, 1980). Site index₁₀₀ varies from 35 (Squaw) to 37 m (Fir Point).

STUDY TREATMENTS

Douglas-fir morphology, duration, and relative rates of growth were studied at two extreme levels of competition: 1) untreated tanoak sprout clumps, representing the maximum cover for each site, and 2) absence of tanoak, where all sprout clumps were removed and the shrubs and herbs were controlled. At each study site, the two treatments were replicated three times in 20 x 20 m plots arranged in a randomized complete-block design.

In October of 1985-1987, tanoak cover (%) was estimated on each of the treatment 1 plots using crown diameter measurements of individual sprout clumps. The sum of sprout clump crown areas divided by the plot area x 100% gave percent cover. Shrub and herb cover was estimated from 5 - 1 m² subplots located randomly throughout each plot. In 1985-1987 the level of tanoak cover ranged from 40 to 63%, while shrub and herb cover averaged 14%. Visual estimates of percent overtopping by hardwoods and shrubs (Howard and Newton, 1984) in 1985-

1987 ranged from 18 to 20%, suggesting that light was readily available to the Douglas-fir in treatment 1.

In April, 1983, tanoak sprout clumps were removed in treatment 2 plots using triclopyr ester herbicide (2% concentration in water with surfactant). The Douglas-fir were covered to protect them during herbicide application. In the years following the one-time herbicide application, recovering tanoak sprouts were controlled by manual cutting.

Shrub and herbaceous cover on treatment 2 was reduced by a one-time application of glyphosate herbicide (2% in water) in April, 1983. Thereafter, competitive effects of shrubs and herbs were minimized by manual removal and by installation in March, 1985, of a 2 x 2 m piece of porous polyester fabric (Terra-Mat E, Terra Enterprises, Inc., Moscow, ID) around each Douglas-fir sapling. Thus, Douglas-fir on treatment 2 had essentially no competition from tanoak, shrubs, or herbs.

DOUGLAS-FIR MEASUREMENTS

Number and size of buds

On each site, five Douglas-fir were randomly selected from each of the three replicates of treatments 1 and 2 -- a total of 30 sample trees per site. Bud diameter and

length were measured to the nearest 1 mm on the terminal shoot and on a marked current-year whorl shoot (referred to hereafter as a lateral shoot). When growth was complete in October, lengths of shoots originating from the samples buds were measured to the nearest cm. In 1987, data on bud size (March) and shoot length (October) were collected at both sites. Interwhorl buds were counted (after Tappeiner et al. 1987) in March, 1987 and 1988 on each of the terminal and lateral shoots at both the Fir Point and Squaw sites.

Stem units

In October, 1986, internode length (i.e., the distance (cm) between needles) was estimated for each terminal and lateral shoot of the thirty trees at Fir Point as follows: the needles in a 30-mm section located at shoot midpoint were counted, this value was divided by 30, and its reciprocal was taken to give an estimate of internode length (mm). Needle length was measured to the nearest mm on five randomly selected needles per shoot.

In October, 1987, internode and needle length were measured on each terminal shoot at both sites, and a subsample (50%) of lateral shoots that had originated from a range of bud sizes. Number of internodes per shoot was

determined by counting the number of needles on each terminal shoot and on a subsample (30%) of lateral shoots that had originated from a range of bud sizes.

Shoot biomass

In October, 1987, each of the 30 lateral shoots per site were removed and taken to the laboratory for biomass determination. Terminal shoots were not collected from the sample trees. Instead, ten terminal shoots, representing a range of lengths (5 to 100 cm), were randomly selected at each site from trees located adjacent to the study plots. For each of the collected terminal shoots, number and length of internodes were estimated. Foliage and wood from harvested shoots were separated, dried to a constant weight at 70°C, and weighed to the nearest 0.01 g.

Douglas-fir growth

Douglas-fir stem diameter (mm) was measured at 15 cm aboveground; this point was permanently marked with tree paint. Stem basal area was calculated as πr^2 . Terminal shoot length was measured to the nearest cm.

In 1985, growth measurements were taken in 3-week

intervals from May (budbreak) through late July (budset) at both sites. In 1986, measurements were taken monthly from April through September at Fir Point only. To fully document the duration and rates of growth, monthly measurements were taken from January through December of 1987 at both sites. Annual tree growth was measured at each site during September-October of 1985-1987.

The duration of stem diameter or height growth in a growing season was computed by summing the number of days between successive measurements in which tree size increased. Thus, total days of active growth were estimated regardless of whether growth was continuous or intermittent.

Relative growth rates (RGR) for Douglas-fir basal area and height were calculated for each period between measurements during the 1985-1987 growing seasons using the following equation (Evans, 1972):

$$\text{RGR} = \frac{\ln(s_i) - \ln(s_{i-1})}{t_i - t_{i-1}}$$

where: s_i = measurement of tree size at the end of period i

t_i = julian (numerical) date at the end of period i

RGR expresses the rate of tree growth independent of size, thus it focuses our analysis on current-year effects of

competition.

STATISTICAL ANALYSIS

For variables measured in a single year, an analysis of variance (ANOVA) was performed on plot means from each site using a randomized complete block design with treatments (i.e., tanoak competition level, terminal versus lateral shoots) in a factorial arrangement.

A split plot design (Milliken and Johnson, 1984) was used in ANOVA of plot means from each site for variables measured in multiple time periods (years or months). This design partitioned variation into two sources: 1) 'main-plot' effects (e.g., tanoak, shoot type, tanoak x shoot type), and 2) 'split-plot' effects in time (e.g., year, tanoak x year, shoot type x year, tanoak x shoot type x year).

Parameters of Douglas-fir size and morphology were transformed to logarithms prior to ANOVA to improve the homogeneity of residual variances. Graphical analysis was used check the normality and distribution of residuals resulting from each ANOVA. To perform multiple comparisons of means (95% significance level), a protected LSD test was used (Snedecor and Cochran, 1980).

On the combined individual tree or shoot data from both sites, linear regression was used to analyze the

relationships among the various shoot morphology parameters and to partition Douglas-fir growth into potential growth and potential growth attainment. Natural logarithmic transformations were applied to both the dependent and independent variables to linearize the relationships and to improve the homogeneity of residual variances. Indicator variables were specified in the regressions to determine the amount of variation explained by differences in tanoak competition level, sites, and type of shoot (terminal versus lateral).

RESULTS AND DISCUSSION

DOUGLAS-FIR BUD PARAMETERS

In 1987, tanoak competition at each site significantly (95% level) reduced the following morphological parameters for Douglas-fir terminal and lateral shoots: number and size of buds; lengths of shoots, internodes, and needles; and biomass in foliage and wood (Table II.1). Similar results were found for the 1986 data from Fir Point (data not presented).

Internode number was significantly reduced by tanoak competition at Fir Point only. Values for each parameter of shoot morphology, except needle length, were significantly (95% level) greater for terminal shoots than for lateral shoots. The interaction of tanoak competition level and shoot type was significant (95% level) only for bud number at Fir Point. For this interaction, multiple comparisons of means indicated that bud numbers were significantly (95% level) greater for both terminal and lateral shoots on competition-free Douglas-fir versus that for trees subjected to competition.

As found by Tappeiner et al. (1987), a principal effect of hardwood and shrub competition in southwestern Oregon is to limit Douglas-fir bud production. This limitation has a compounding influence on future tree

growth, because it is chiefly through bud production that young conifers are able to multiply their leaf areas, and thus increase their production of photosynthates (Cannell et al. 1976).

Number of internodes per shoot was strongly related ($r^2=0.80$) to the diameter x length of the bud from which the shoot originated (Table II.2). This indicates that smaller buds contain fewer internodes, and therefore, less potential shoot growth. Shoot length and woody biomass each had strong linear relationships ($r^2=0.94$ to 0.95) with number X length of stem units (Table II.2). In these relationships, internode number accounted for 72% of the variation, and internode length explained an additional 22-23% of variation, yet these two variables were relatively independent ($r^2=0.06$). Shoot foliage biomass was strongly related to internode number X average needle length ($r^2=0.93$), with internode number accounting for 87% of the variation.

None of the relationships described in Table II.2 were strongly influenced by tanoak competition, shoot type (terminal versus lateral), or site differences ($r^2<0.02$). These results suggest that bud size, an index of internode number, can be used to assess potential elongation and biomass of shoots.

Limitations in Douglas-fir shoot growth resulted from

reductions in internode number (Fir Point only) and/or internode elongation (both sites), characteristics which can be attributed, respectively, to previous- and current-year effects of competition. Limitations in biomass development of Douglas-fir imposed by tanoak competition resulted principally from reductions in the number of buds and internodes. In addition, foliage biomass development, and presumably leaf area, were limited by reductions in average needle length.

Since overtopping by tanoak averaged only 18-20% during 1985-1987, light probably was not the factor limiting Douglas-fir shoot growth. Therefore it is likely that restrictions in soil water availability during shoot development, imposed by tanoak competition, limited the number and length of shoot internodes in Douglas-fir.

Sucoff (1971) found that excessive summer drought reduced both the rates and duration of internode initiation within shoot buds of red pine (*Pinus resinosa*). Clements (1970) found that soil water deficits from the previous year limited red pine shoot growth, and current-year watering treatments did not have a detectable effect. In contrast, research by Garrett and Zahner (1973) indicated that current-summer water stress affected shoot development of red pine by limiting elongation of internodes and needles.

DOUGLAS-FIR HEIGHT AND BASAL AREA GROWTH

Effects of competition

In 1985-1987, Douglas-fir subjected to competition from tanoak at both sites had significantly (95% level) smaller basal areas, versus trees growing free of competition (Table II.3). For each site, the interaction of tanoak competition level and year was significant. Multiple comparisons of means indicated that for competition-free Douglas-fir, basal area is diverging from that of trees influenced by tanoak competition in an exponential fashion (Table II.3).

Basal area increment was significantly ($p=0.01$) greater for competition-free Douglas-fir versus trees under competition during each of the 1985-1987 growing seasons at Fir Point; at Squaw, however, differences were not as prominent ($p=0.06$). Both height and height increment of Douglas-fir did not vary significantly ($p \geq 0.09$) by tanoak competition level at either site.

Potential growth and potential growth attainment

In 1987, Douglas-fir in competition with tanoak had smaller stem circumferences, suggesting a reduced potential for basal area growth (Fig. II.1). Stem

circumference accounted for 92% of the variation in basal area increment. The regression slope was significantly ($p < 0.001$) less for trees influenced by tanoak competition, and this parameter explained an additional 3% of variation in basal area increment. This result indicates that for trees under competition, basal area growth per unit stem circumference was less than for trees growing without competition. Basal area growth was related similarly to stem circumference and tanoak competition level in the 1985 ($r^2 = 0.70$) and 1986 ($r^2 = 0.85$) data.

Douglas-fir in competition with tanoak had smaller terminal bud sizes (bud diameter x length) in 1987, denoting fewer internodes, and therefore reduced potential for shoot growth (Fig. II.2). Bud size accounted for 65% of the variation in terminal shoot growth. For Douglas-fir influenced by tanoak competition, the regression intercept parameter was significantly ($p < 0.001$) smaller than for trees growing free of competition, and inclusion of this parameter explained an additional 6% of variation in terminal shoot length.

These results indicate that, regardless of bud size, potential shoot growth attained in 1987 was reduced by a constant amount for trees subjected to competition. Such a result would occur if elongation of internodes was restricted by a fixed amount. Similar relationships with

bud size were found for 1987 lateral shoots ($r^2 = 0.74$) and for 1986 terminal ($r^2 = 0.44$) and lateral shoots ($r^2 = 0.62$).

In the preceding relationships for basal area and shoot growth, site-specific parameters explained no more than 1% of additional variation, thus they did not greatly influence the regression analysis. Therefore, these variables were not retained in the final models.

Duration of growth

The average duration of growth in basal area was significantly (95% level) reduced 48 to 70 days for Douglas-fir influenced by tanoak competition at Fir Point in each of the 1985-1987 growing seasons (Table II.4). Differences in the duration of basal area growth attributable to tanoak competition were not as prominent at Squaw ($p=0.07$). In contrast to basal area, the duration of height growth was not influenced ($p>0.4$) by competition at either site during the 1985-1987 growing seasons.

In 1985, the period of basal area growth was particularly brief at Squaw (56-89 days), and for trees subjected to competition at Fir Point (50 days). Growing conditions may have been especially harsh in 1985, since January-June precipitation was the lowest in 25 years for

much of southwestern Oregon (McNabb, 1985).

Relative growth rates

During most of the 1987 growing season, relative rates of basal area growth were significantly (95% level) less at each site for Douglas-fir subjected to tanoak competition versus trees growing free of competition (Figs. II.3-4). Beginning in May, Douglas-fir under competition had a declining trend in basal area RGR that continued until growth cessation in September-October. In contrast, during this same period, trees free of competition had essentially no change in basal area RGR until August-September.

At Fir Point, relative rates of height growth were significantly reduced by tanoak competition in June and July during the 1987 growing season (Fig. II.5); however at Squaw, differences attributable to competition ($p=0.06$) were not as prominent (Fig. II.6).

The shape of the seasonal RGR curve for Douglas-fir height (Figs. II.5-6) differed strikingly from that for basal area (Figs. II.3-4). The seasonal progression of height RGR for the two levels of tanoak competition was either identical or parallel. Height RGR peaked at the same time (June) for both levels of tanoak competition;

however height RGR peaked at a higher value for trees growing free of competition.

During the 1985 growing season (data not presented), differences in Douglas-fir RGR attributable to tanoak competition were not significant for basal area ($p>0.08$) or height ($p>0.16$). However, results from the 1986 data (Fir Point only; data not presented) were almost identical to those from 1987. These results suggest that in exceptionally dry growing seasons, such as 1985, both the duration and rates of Douglas-fir growth are curtailed.

Since cambial growth is indeterminate, competition-imposed reductions in the duration and relative rate of basal area growth must denote the onset of resource limitations during a given growing season. As discussed earlier, soil water was probably the factor that limited basal area growth rates, since light availability did not vary greatly between the two treatments. In the following chapter (III), the relationship of soil water availability to Douglas-fir relative growth rate was tested using data that spanned a range of tanoak competition levels.

TABLE II.1. Effects of tanoak competition on morphological parameters of Douglas-fir terminal shoots in 1987.

Shoot Morphology Parameter	Fir Point		Squaw	
	Tanoak competition*			
	Present	Absent	Present	Absent
bud number	11.0a	18.0b	9.0a	14.0b
bud diameter (mm)	4.5a	5.5b	4.1a	4.8b
bud length (mm)	10.0a	11.4b	8.7a	10.4b
shoot length (cm)	37.0a	63.0b	32.0a	57.0b
internode no.	235.0a	313.0b	282.0a	366.0a
internode lgth. (mm)	12.2a	16.3b	13.5a	16.0b
needle length (mm)	25.3a	27.4b	25.8a	27.9b
foliage dry wt. (g)	1.5a	2.6b	1.1a	2.2b

*Means within each site followed by the same letter did not differ significantly (95% level) between tanoak competition levels.

TABLE II.2. Regression models describing relationships among Douglas-fir morphological parameters for 1987 terminal and lateral shoots. Each equation has the form: $\ln(Y) = B_0 + B_1(\ln(X_i))$.

Y	B ₀	B ₁	X _i [*]	n	s _{y.x}	R ²
Stem unit number	2.959	0.704	X ₁	74	0.160	0.80
Shoot length (cm)	0.140	0.976	X ₂	94	0.147	0.95
Foliage dry weight (g)	-9.364	1.478	X ₃	50	0.185	0.93
Wood dry weight (g)	-6.871	2.170	X ₂	37	0.435	0.94

*variables:

X₁ = bud diameter (mm) x bud length (mm)

X₂ = internode number x internode length (cm)

X₃ = internode number x needle length (cm)

TABLE II.3. Effects of tanoak competition on size (beginning of growing season) and increment in Douglas-fir basal area and height for 1985-1987.

Douglas-fir Parameter	Year	Fir Point		Squaw	
		Tanoak competition*			
		Present	Absent	Present	Absent
basal area (cm ²)	1985	1.4a	2.1b	0.9a	3.5b
	1986	1.8a	5.1b	1.3a	5.8b
	1987	2.6a	9.6b	1.9a	12.0b
basal area increment (cm ²)	1985	0.4a	1.9b	0.4a	2.3a
	1986	0.9a	4.3b	0.6a	6.2a
	1987	1.5a	8.7b	0.9a	7.7a
height (cm)	1985	76a	83a	70a	102a
	1986	90a	110a	85a	125a
	1987	119a	153a	111a	160a
height increment (cm)	1985	21a	40a	19a	29a
	1986	29a	43a	26a	35a
	1987	37a	55a	32a	57a

*Means within each site and year followed by the same letter did not differ significantly (95% level) between tanoak competition levels.

TABLE II.4. Effects of tanoak competition on duration of Douglas-fir basal area and height growth in the 1985-1987 growing seasons.

Parameter	Year	Fir Point		Squaw	
		Tanoak competition*			
		Present	Absent	Present	Absent
Duration of basal area growth (days)	1985	50a	120b	56a	89a
	1986	93a	141b	----	----
	1987	118a	172b	91a	163a
Duration of height growth (days)	1985	96a	86a	71a	79a
	1986	129a	123a	----	----
	1987	87a	84a	91a	91a

*Means within each site and year followed by the same letter did not differ significantly (95% level) between tanoak competition levels.

FIGURE II.1. Relationship of $\ln(1987$ basal area increment) to $\ln(1986$ stem circumference) for individual Douglas-fir growing in the presence and absence of tanoak competition.

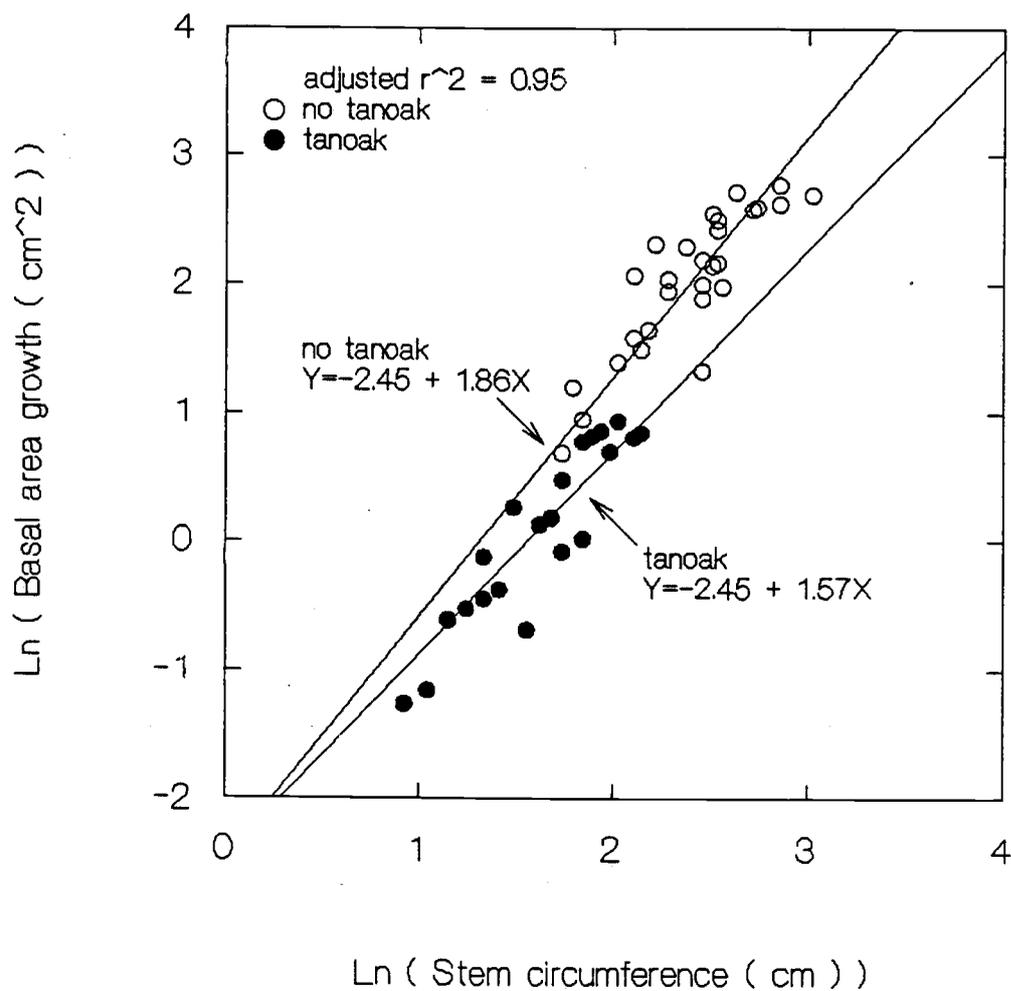


FIGURE II.2. Relationship of $\ln(1987 \text{ terminal shoot length})$ to $\ln(1986 \text{ bud diameter} \times \text{length})$ for individual Douglas-fir growing in the presence and absence of tanoak competition.

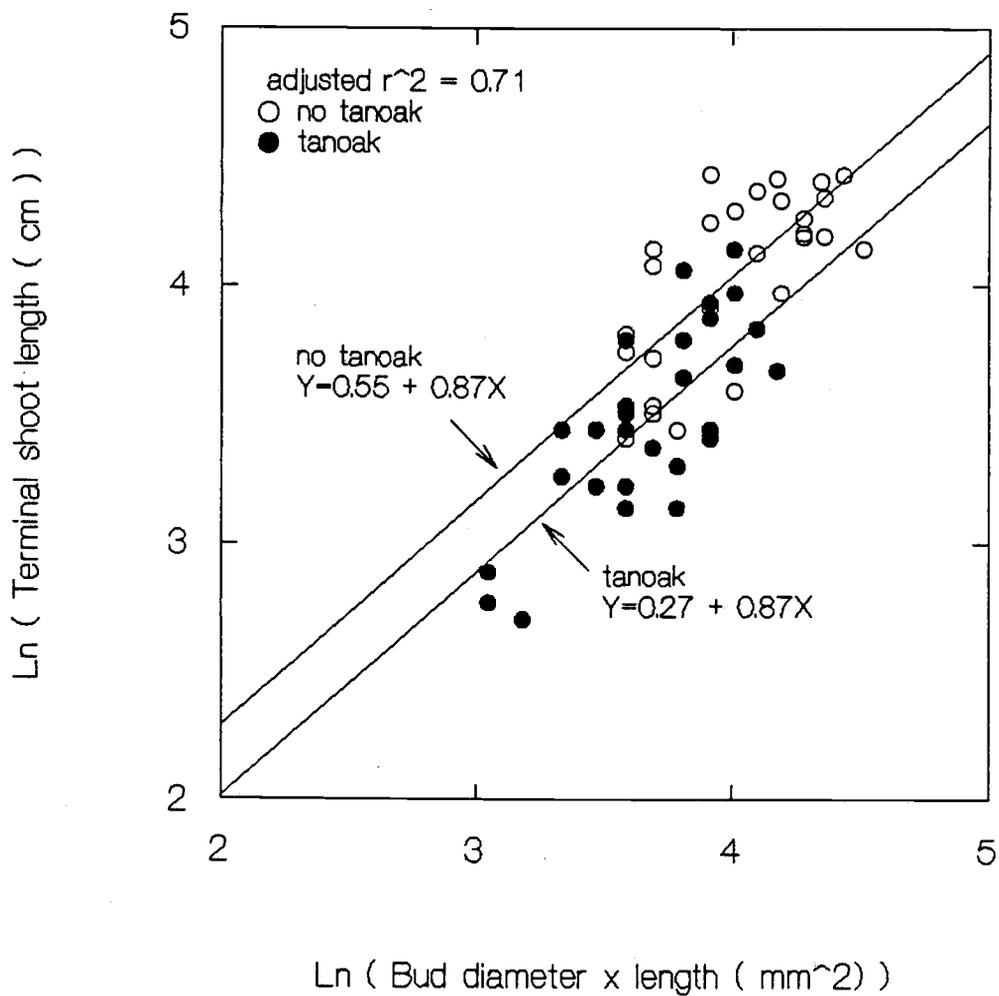


FIGURE II.3. Mean relative rates of basal area growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Fir Point. Asterisks denote dates in which growth rates differed significantly (95% level) between tanoak competition levels. Vertical bars indicate one standard error.

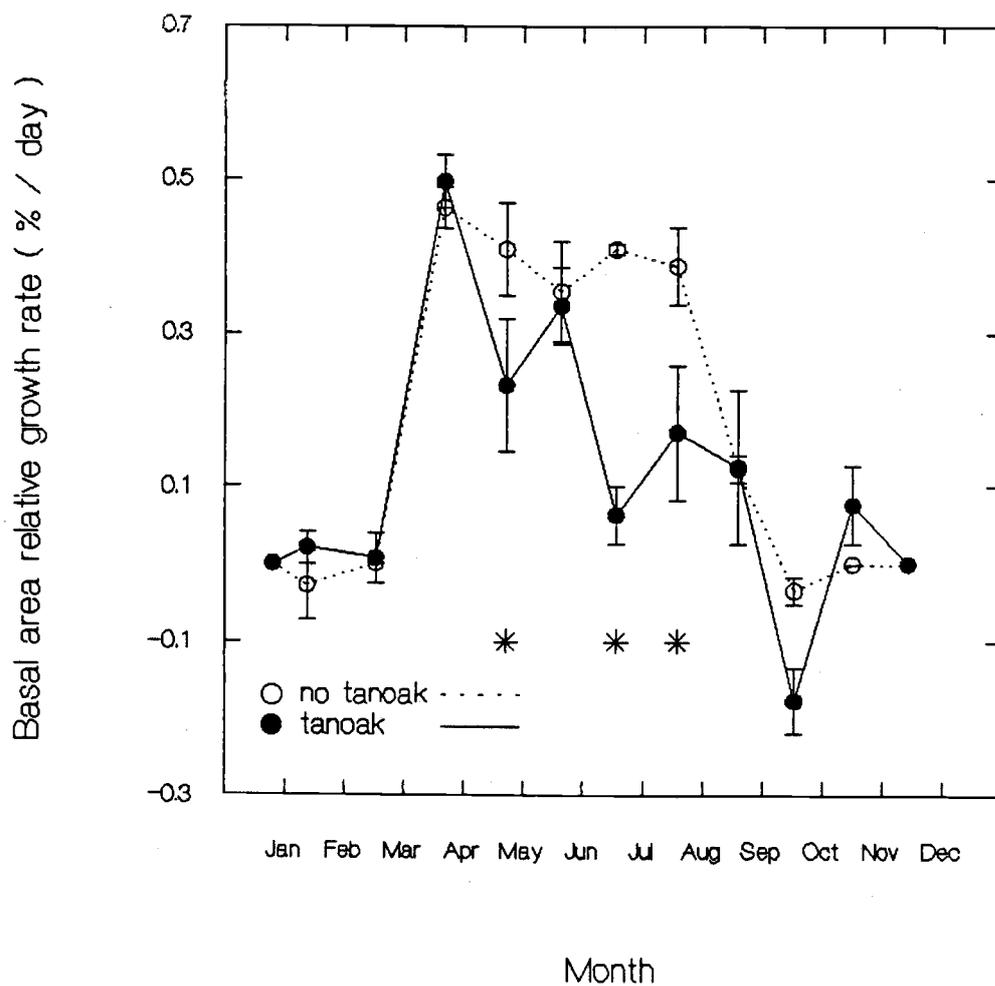


FIGURE II.4. Mean relative rates of basal area growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Squaw. Asterisks denote dates in which growth rates differed significantly (95% level) between tanoak competition levels. Vertical bars indicate one standard error.

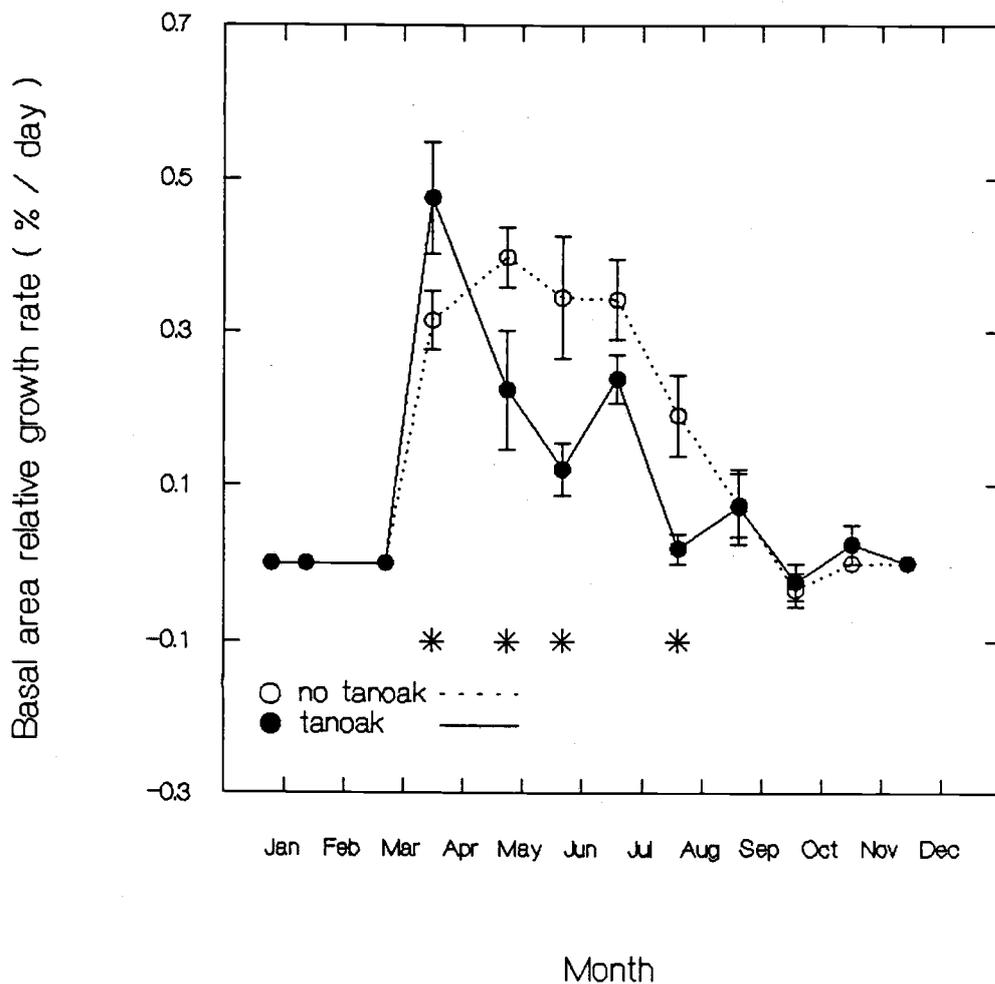


FIGURE II.5. Mean relative rates of height growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Fir Point. Asterisks denote dates in which growth rates differed significantly (95% level) between tanoak competition levels. Vertical bars indicate one standard error.

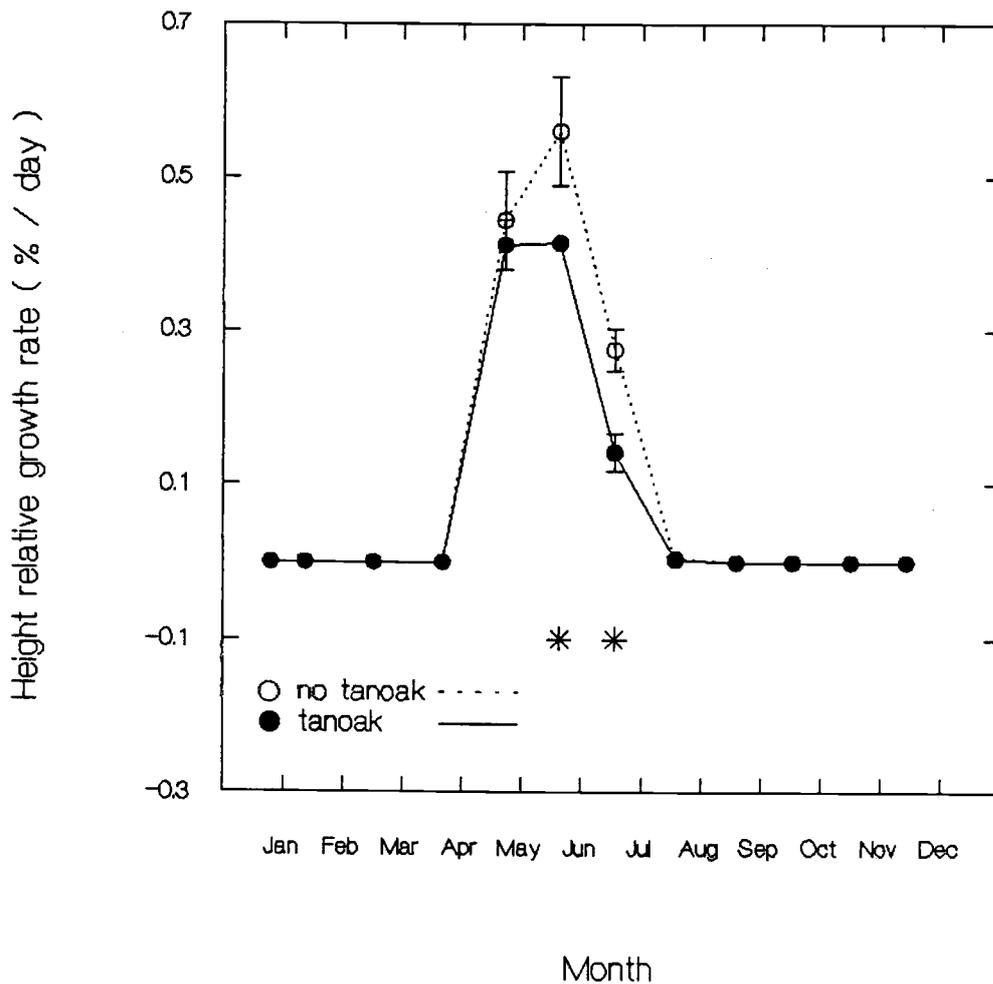
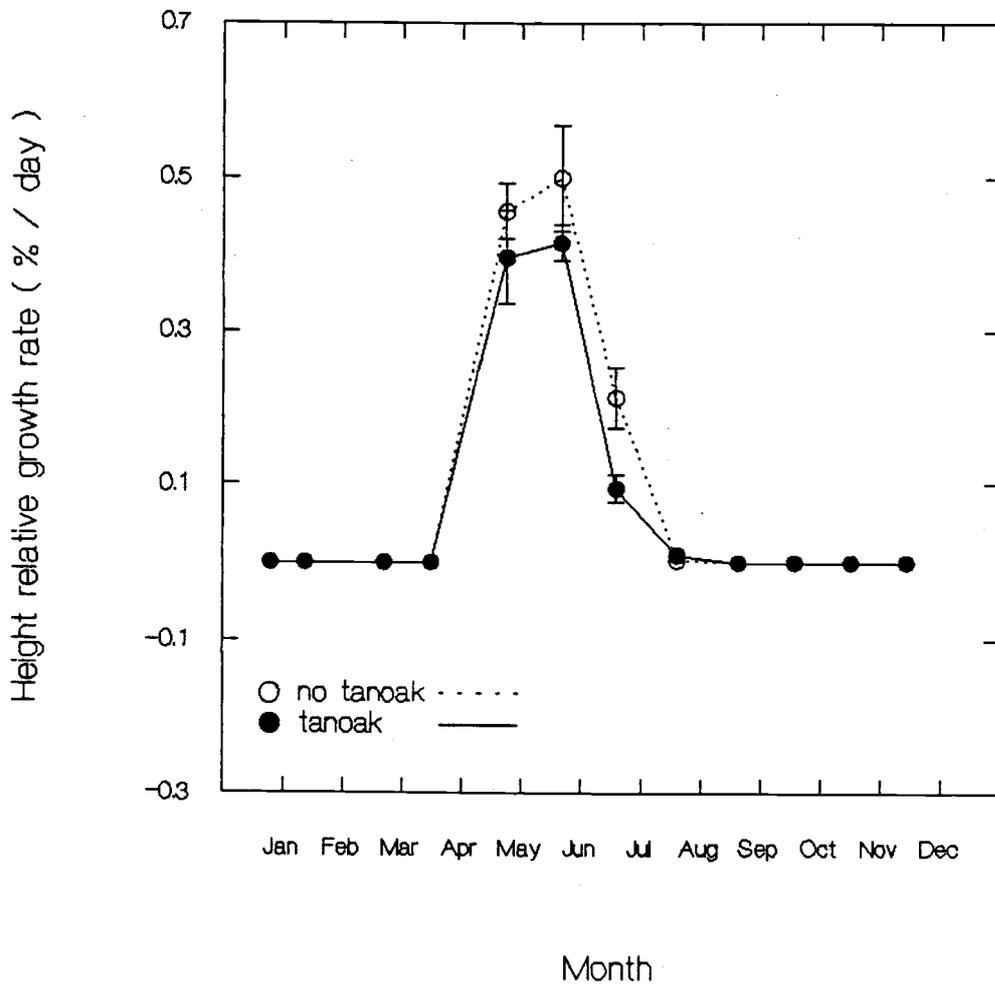


FIGURE II.6. Mean relative rates of height growth for Douglas-fir growing in the presence and absence of tanoak competition during 1987 at Squaw. Asterisks denote dates in which growth rates differed significantly (95% level) between tanoak competition levels. Vertical bars indicate one standard error.



CHAPTER III

SEASONAL PHYSIOLOGY OF DOUGLAS-FIR (PSEUDOTSUGA MENZIESII)
SAPLINGS AS AFFECTED BY MICROCLIMATE IN YOUNG TANOAK
(LITHOCARPUS DENSIFLORUS) STANDS.

ABSTRACT

Physiological responses (xylem pressure potential, leaf conductance, and photosynthesis) of Douglas-fir (Pseudotsuga menziesii) saplings were monitored monthly from May, 1986 to December, 1987 to describe influences of microclimate (light, soil water, temperature, and relative humidity) associated with young tanoak (Lithocarpus densiflorus) stands. Throughout most of the year, Douglas-fir shaded by tanoak had light-limited rates of photosynthesis. During the growing season, microclimatic conditions associated with the tanoak stand (reduced soil water availability, elevated leaf temperatures, and lower relative humidities) imposed a stomatal limitation on photosynthesis of Douglas-fir. Tanoak was able to maintain positive rates of photosynthesis throughout the summer drought period by using stomatal control to minimize its water stress. When expanded to a whole-tree basis, photosynthesis of Douglas-fir varied by over two orders of magnitude between shaded trees (0.1 umole

$\text{CO}_2/\text{m}^2/\text{s}$) and trees growing free of competition (13.3 $\mu\text{mole CO}_2/\text{m}^2/\text{s}$)--variation attributable to differences in tree leaf area and in the rates of photosynthesis per unit leaf area.

INTRODUCTION

During the dormant season for conifers, the Mediterranean climate of southwestern Oregon is characterized by mild temperatures and abundant precipitation--conditions which favor carbon assimilation by evergreen species. In similar climates, winter-time photosynthesis can account for a significant proportion of the total annual carbon assimilation by conifers (Kramer and Kozlowski, 1979; Bradbury and Malcolm, 1978).

In measurements of 38-year-old Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) growing in western Washington, Helms (1965) found winter rates of photosynthesis that were as high as any recorded during other seasons. He estimated that 5 to 15% of annual net assimilation occurred during winter. Using simulations for Douglas-fir growing in western Oregon, Emmingham and Waring (1977) estimated that photosynthesis during the entire dormant-season period accounted for 30 to 55% of annual net assimilation.

Low temperatures can have an important limiting influence on dormant-season photosynthesis of Douglas-fir, either directly via altered biochemical reactions, or indirectly through reduced leaf conductance. For example, Drew and Ferrell (1979) found that, following the first autumn frost, conductance of Douglas-fir seedlings

declined gradually to a wintertime minimum--a result they attributed to stomatal closure. Similarly, Babalola et al. (1968) attributed reduced rates of transpiration and photosynthesis in Monterey pine (Pinus radiata D. Don) seedlings to a stomatal limitation imposed by low soil temperatures. Their findings suggested that low soil temperatures increased water viscosity and reduced root permeability to water, leading to restricted rates of photosynthate translocation and ultimately causing stomatal closure.

In contrast, during the growing season, conifers in southwestern Oregon typically encounter limitations in soil water coupled with high evaporative demands. Associated hardwood and shrub species can further modify these climatic influences on Douglas-fir growth by competing for limited supplies of soil water.

Tanoak (Lithocarpus densiflorus (Hook. & Arn.) Rehd.) is a common hardwood tree associated with Douglas-fir in southwestern Oregon and northwestern California. Following cutting or burning, tanoak sprouts have rapid initial height growth (60 to 120 cm/yr) (Tappeiner et al. 1984), and the evergreen canopies of developing sprout clumps can have leaf area indices of over $7 \text{ m}^2 / \text{m}^2$ (Harrington et al. 1984). Competition from tanoak can reduce growth (Radosevich et al. 1976; Roy, 1981;

Tappeiner et al. 1987; Jaramillo, 1988; Chapter I) of young Douglas-fir, as well as limit their morphological development (Chapter II).

Current levels of atmospheric and soil moisture are known to actively influence leaf conductance and photosynthesis of Douglas-fir. For example, several studies have suggested that at xylem pressure potentials less than -1.5 MPa, stomatal closure begins to cause leaf conductance of Douglas-fir to decline to low or negligible values (Lopushinsky, 1969; Running, 1976; Drew and Ferrell, 1979; Johnson and Ferrell, 1983; White, 1987).

Stomata of Douglas-fir respond rapidly (0.5-2 minutes) to changes in atmospheric humidity, with sensitivity declining with increasingly negative xylem pressure potentials (Johnson and Ferrell, 1983). Running (1976) found that leaf conductance of Douglas-fir declined up to 50% in response to increased vapor pressure deficit. In contrast, declines in conductance of up to 90% were associated with increasingly-negative values of xylem pressure potential (Running, 1976). In contrast to conductance, net photosynthesis of Douglas-fir begins to decline as xylem pressure potential drops below -1.0 MPa (Brix, 1979).

Seasonal physiology of Douglas-fir as influenced by microclimate in young tanoak stands was studied in order to describe mechanisms of competition and to provide

insight into observed Douglas-fir growth reductions (Chapter I). The following microclimatic factors were hypothesized to limit photosynthesis of Douglas-fir in young tanoak stands: 1) reduced light availability throughout the year, 2) reduced soil water availability during summer and early fall (June-September), and 3) reduced air temperatures during the dormant season (October-March).

To test these hypotheses, Douglas-fir were selected that had different competitive status with tanoak, either as a result of natural stand development or removal of tanoak. Variables were measured for each tree to describe its microclimate (photosynthetically-active radiation, soil water potential, temperature, and relative humidity) and physiology (base and current xylem pressure potential, conductance, and net photosynthesis).

A network of causal relationships were hypothesized to link the variables of microclimate and physiology, and path analysis was used to assess seasonal trends in the strength of each relationship. As indicated above, microclimate refers to a specific subset of environmental conditions and levels of resource availability associated with individual Douglas-fir and tanoak.

METHODS

SITE DESCRIPTION

The study was conducted at two sites in southwestern Oregon, Squaw and Fir Point, that are being managed for Douglas-fir wood production and other resources. Following harvest (1980) of the previous old growth stands, these sites were broadcast-burned (spring, 1981) and planted with two-year-old bare-root Douglas-fir seedlings (April, 1981 at Squaw; April, 1982 at Fir Point). Wide spacing of the Douglas-fir (3 m) probably minimized intraspecific competition for the duration of the study. Following broadcast burning, an even distribution of tanoak sprout clumps developed from the stumps of parent trees present in the pre-harvest stand.

Fir Point, located near Glendale, Oregon (T32S R6W S17) at an elevation of 800 m, has clay-loam soils of the Josephine/Speaker series (Hubbard, 1980). Gravelly-loam soils of the Pollard/Beekman series (Meyer and Amaranthus, 1979) predominate at Squaw, which is located about 70 km south of Fir Point, near Cave Junction, Oregon (T39S R6W S21) at an elevation of 900 m. Both sites receive approximately 130 cm of annual precipitation, and site index_{100} varies from 35 (Squaw) to 37 m (Fir Point). Site aspect is west/southwest (Fir Point) or east/southeast

(Squaw), and slopes range from 30 to 65%.

EXPERIMENTAL DESIGN

Both the tanoak and shrub / herb vegetation were manipulated to create differing environmental conditions and resource levels. Within areas having an even distribution of two-year-old tanoak sprout clumps, 2 - 20 x 20 m plots were installed at each site in March, 1983. On a randomly-selected plot at each site, the tanoak were removed in April, 1983 using a 2% solution of triclopyr ester herbicide in water with surfactant. A broadcast spray of glyphosate herbicide (2% in water with surfactant) also was applied in April, 1983 to suppress herb and shrub vegetation. The Douglas-fir were shielded to protect them during herbicide applications. To eliminate shrub and herb competitive effects, this vegetation was manually removed in a 2-m radius around each sample Douglas-fir or tanoak for the duration of the study, beginning in May, 1986. In the additional plot at each site the tanoak were left undisturbed.

Experimental units were individual Douglas-fir saplings growing in the following conditions: 1) high light and soil water availability (tanoak removed), 2) high light and restricted soil water availability (full

exposure to sunlight in openings within the tanoak stand), 3) restricted light and soil water availability (fully shaded by tanoak).

Douglas-fir in conditions 2 and 3 (designated hereafter as C-2 and C-3, respectively) represent trees growing in microclimates that are typical of young plantations containing tanoak. Douglas-fir in condition 1 (designated hereafter as C-1) were studied to quantify their physiological responses in a microclimate that was not modified by tanoak.

In May, 1986 at Fir Point, three Douglas-fir were selected randomly to represent each condition, giving a total of nine sample trees. Selections of Douglas-fir were limited to trees having sufficient crown development to permit monthly collections of shoots for measurement of xylem pressure potential and photosynthesis. In addition, three tanoak sprout clumps were selected randomly that represented a range of sizes and that were growing with full exposure to sunlight (C-2). In January, 1987 a new set of nine sample Douglas-fir and three tanoaks were selected at each site using the selection criteria described previously.

Mean sizes of the Douglas-fir sample trees varied among conditions as a result of previous competitive effects from tanoak (Chapter I). At the end of the study (December, 1987), average values for Douglas-fir stem

diameter were 57 (C-1), 28 (C-2), and 14 mm (C-3), whereas average values for height were 275 (C-1), 182 (C-2), and 126 cm (C-3). For the sampled tanoak, December, 1987 values for mean crown width and height were 184 and 168 cm, respectively.

MEASUREMENTS

Sampling Frequency

Parameters of microclimate and tree physiology were measured monthly from May to December of 1986 at Fir Point, and from January to December of 1987 at both sites. In each month, physiological measurements were repeated in the morning (1000 to 1200 Pacific Standard Time (PST)) and afternoon (1330 to 1530 PST), with each set of measurements requiring 90 to 120 minutes.

At Fir Point, morning and afternoon physiological measurements were collected in the following order: C-1, C-2, tanoak, and C-3. At Squaw the sampling order was C-2, C-1, tanoak, and C-3. This sampling order best accomplished several experimental objectives. First, it allowed the Douglas-fir and tanoak in C-1 and C-2 to receive full sunlight for at least one-half hour prior to measurement. Plot aspect at Fir Point prevented full

sunlight from reaching both C-2 and tanoak until 1030 to 1100 PST during late fall to early spring, whereas such a constraint did not exist at Squaw. Second, this sampling order permitted reasonable comparisons of C-1 with C-2 and C-2 with tanoak that were relatively free of bias due to changing environmental conditions with time.

Microclimate

A sheltered thermometer located at 1 m height in each plot was used to record monthly minimum and maximum air temperatures (1987 only). Soil temperature at 15 cm depth was recorded during each monthly measurement just after sunrise from a thermometer probe placed 15 cm south of the main stem of each of 2 to 3 Douglas-fir in each condition.

A rain gauge (150 mm capacity) was installed at 1 m height in the tanoak-absent plot at each site to obtain a monthly estimate of precipitation (1987 only). To prevent evaporation between measurements, a thin layer of oil was added to each rain gauge.

A neutron soil moisture gauge (model 3225, Troxler, Inc., Sacramento, CA, U.S.A.), calibrated for the soils at each site, provided count-ratio data that was used to estimate gravimetric water content at 30- and 60-cm depths in each of three access tubes per plot.

The estimates of gravimetric water content were

collected monthly at Fir Point from June 1986 through December 1987, and at Squaw, from January 1987 through December 1987. Soil samples were collected near each access tube for pressure plate analysis, and the resulting data were used to predict soil water potential from gravimetric water content (Pabst and Tappeiner, unpublished data).

Photosynthetically-active photon flux density (PPFD) was measured with a quantum sensor (model Li-190S-1, Li-Cor Inc., Lincoln, NB) mounted on the cuvette used in the photosynthesis and conductance measurements (described below).

Relative humidity (RH) was measured using a Vaisala sensor located in the cuvette used in the photosynthesis and conductance measurements (described below). A chromel-constantan thermocouple in contact with the abaxial leaf surface gave measurements of leaf temperature (T). Air temperature was measured with a linearized thermistor located in the cuvette. Vapor pressure deficit (VPD) was predicted from leaf temperature and humidity using a regression equation based on data from Langhans (1978).

Since measurements of T were always within 1°C of air temperature, the latter measurement was considered redundant. Because of the similarities between

T and air temperature, in analysis of the data (described below) leaf temperature was defined as a microclimatic parameter rather than a physiological parameter.

Tree physiology

Rates of net photosynthesis (A) were measured on individual Douglas-fir and tanoak shoots using a closed-system portable infrared gas analyzer (model Li-6000, Li-Cor Inc., Lincoln, NB). Except during the period of active shoot elongation (May and June), sampled shoots were of current-year origin located on the south side of each Douglas-fir or tanoak at a height of 60-120 cm. In May and June, physiological measurements were conducted on previous-year shoots because current-year shoots had not completed their development.

A 3-4 cm terminal section of each shoot was enclosed in a 1-liter cuvette (model Li-6000-12, Li-Cor Inc., Lincoln, NB) for 1 minute, during which time ten separate measurements of CO₂ concentration were taken at consecutive intervals. The Li-6000 utilized linear regression of CO₂ drawdown versus time to compute an initial rate of CO₂ depletion (i.e., the regression intercept) that was representative of conditions at the beginning of the measurement.

To prevent the dilution of volumetrically-measured

CO₂ concentration within the cuvette resulting from transpired water vapor, a magnesium perchlorate desiccant was installed in the air flow path to provide a source of moisture-free air. The Li-6000's infrared gas analyzer (IRGA) was regularly calibrated in the laboratory using a gas of known CO₂ concentration. To adjust IRGA calibration during field measurements, a lime-soda scrubber was used to produce a reference gas having a CO₂ concentration of 0 ppm.

Similarly to photosynthesis, initial values for leaf conductance to water vapor (G) were estimated from linear regression of ten consecutive estimates of G versus time. These ten estimates of G were computed by the Li-6000 using a difference equation that included the variables, RH, T, and air temperature, averaged over a given measurement interval. By adjusting the flow of moisture-free gas entering the cuvette, relative humidity was maintained at ambient conditions ($\pm 1-4\%$) during each measurement. Because conductance could not be measured accurately on wet foliage, precipitation during data collection prevented some (July, 1987) or all (February, 1987) of the conductance measurements.

Base (pre-dawn) measurements of xylem pressure potential (XPP) were taken just before sunrise on each sample tree using a pressure chamber (PMS Inc., Corvallis,

OR). Winter-storm conditions during February, 1987 prevented measurement of base XPP at Squaw.

Immediately before or after taking cuvette measurements for a given condition, current XPP was measured on all respective sample trees except the shaded Douglas-fir, which were not sampled to minimize disturbance to their crowns. To maintain a close correspondence between measured XPP and values expected for the A/G sample shoots, shoots of similar branch order and crown location were collected, transported to the pressure chamber in moistened plastic bags, and their XPP measured within 2-4 minutes.

Following afternoon physiology measurements, each A/G sample shoot was clipped, and its projected leaf area was determined (nearest 0.1 cm^2) at the laboratory using a surface-area meter (model Li-3100, Li-Cor Inc., Lincoln, NB). Both Douglas-fir and tanoak are hypostomatous, having most or all their stomata on the lower (abaxial) leaf surface (Unterschuetz et al. 1974; King, 1976); therefore, values for G and A were adjusted for one-sided leaf area. After drying for 24 hours at 70°C , foliage samples were weighed to the nearest 0.01 g and specific leaf area values were calculated (cm^2 leaf area / g foliage dry weight).

Douglas-fir Growth

In 1987, Douglas-fir stem diameter (mm) was measured each month at a permanently-marked point 15 cm aboveground. Stem basal area was calculated as πr^2 . During the period of active shoot elongation in 1987, Douglas-fir terminal shoot length (cm) was measured each month. To provide a monthly measure of growth activity that was relatively independent of size, relative growth rates (RGR) were calculated for basal area and height using the following equation (Evans, 1972):

$$\text{RGR} = \frac{\ln(s_i) - \ln(s_{i-1})}{t_i - t_{i-1}}$$

where: s_i = measurement of tree size at end of period i

t_i = julian (numerical) date at end of period i

Whole-tree photosynthesis

In order to estimate an average rate of photosynthesis at the whole-tree level, the measurements of A were assumed to be applicable to current-year foliage located on the south-half of each tree's crown. Using the 18 Douglas-fir that were sampled in 1987, foliage biomass

of each tree before and after the 1987 growing season was predicted using measurements of tree size in the following equation (Chapter I):

$$\ln(\text{foliage biomass (g)}) = 0.731 + 0.848(\ln(\text{STVOL}(\text{cm}^3)) - 0.249(\text{SHADE}))$$

$$\text{adjusted } R^2 = 0.955 \quad s_{y.x} = 0.327 \quad n = 72$$

where: STVOL = stem volume = π (diameter/20)² X (height)/3

SHADE = 1 for fully shaded Douglas-fir (C-3) and 0 otherwise

Estimates of foliage biomass were multiplied by each tree's average specific leaf area for 1987 to give values for Douglas-fir leaf area before and after the 1987 growing season.

Similarly, for each of the 6 tanoak sprout clumps that were sampled in 1987, leaf area before and after the 1987 growing season was predicted by applying measurements of crown width (cm) to the following equation (Chapter I):

$$\ln(\text{leaf area (m}^2\text{)}) =$$

$$1.988 + 0.966(\ln(\text{CRAREA}(\text{m}^2)))$$

$$\text{adjusted } R^2 = 0.838 \quad s_{y.x} = 0.421 \quad n = 143$$

where: CRAREA = sprout clump projected crown area =

$$\pi (\text{crown width}/200)^2$$

Leaf area of each tree prior to the 1987 growing season was subtracted from the value predicted for after

the growing season to provide an estimate of current-year (1987) leaf area increment. Leaf area increment was multiplied by 0.5 to make it applicable to the south-half of a given tree's crown. The average rate of photosynthesis for each tree was calculated by multiplying the tree's 1987 mean value for A by the corresponding value for 50% of leaf area increment.

STATISTICAL ANALYSIS

Microclimate

The parameters, maximum and minimum air temperature and soil temperature, varied as periodic functions of time. To analyze the effect of condition (i.e., C-1, C-2, and C-3) on temperature, the data from both sites were pooled, and the periodic trends were linearized by expressing julian date in radians and applying a sine or cosine transformation. This approach was similar to that used by Ferguson et al. (1986) to model periodic trends in the effects of site aspect on conifer growth and survival.

Since regression models containing quadratic terms for sine and cosine improved the fit to the temperature data, selection of independent variables using stepwise regression (95% level for variable entry and removal) was based upon the following list: $\sin(x)$, $\sin^2(x)$, $\cos(x)$,

$\cos^2(x)$, and $\sin(x)*\cos(x)$, where x =julian date.

Indicator variables were assigned to denote sites and conditions. After incorporating the site indicator into the regression, the significance of adding condition indicators was assessed to determine their additive influence on each temperature variable.

The initial measurements of soil water potential in each of the 1986 and 1987 growing seasons gave values that were less negative than -0.1 MPa, suggesting that soils were at or near field capacity. To remove the sources of variation associated with individual neutron-probe access tubes (e.g., air pockets and accumulations of organic matter), a relative measure of soil water potential was calculated as the cumulative sum of changes between consecutive monthly estimates (designated hereafter as SWP).

Data for PPF and SWP that were common to each level of month and sampling period (morning versus afternoon) were pooled, giving 12 (SWP) or 24 (PPF) independent data sets. Using a similar approach to that described above, linear regression was used on each data set to determine if PPF and SWP differed among conditions after incorporating a site indicator.

Relative humidity (RH) was selected instead of vapor pressure deficit as the best variable to describe

atmospheric moisture level, because it consistently accounted for more variation in G. Since causal relationships existed among the variables, PPF, RH, and T, path analysis (described below) was used to analyze variation in RH and T.

Tree physiology

Using current research information, a series of causal relationships were hypothesized to link the measured parameters of microclimate and tree physiology (Fig. III.1). The arrows in this diagram denote the directional nature of cause and effect between connected variables. Figure III.1 was designed to provide an analytical framework for assessing the nature of the main causal relationships that determine tree physiological response to microclimate. Thus, this diagram does not encompass all possible inter-relationships among the variables, nor does it include all of the influences that can affect a given dependent variable.

Using the methods outlined by Li (1975), path analysis was used to partition the variation in a given dependent variable into components of "total determination" by other causal variables. Total determination by a causal variable equals its direct effect plus the sum of its joint effects as it operates

through other causal variables. Thus, total determination is expressed as a proportion of variation in the dependent variable determined by a given independent variable.

For example, in the causal relationship of light and photosynthesis (Fig. III.1), total determination by light is equal to its direct effect (path_G), plus the sum of its joint effects as it operates through the other causal variables, conductance (path_{HM}) and leaf temperature (path_{CF}). Since the variation in a dependent variable often is shared jointly by several causal variables, negative determination is possible and implies a redundancy in the causal scheme.

Data for Douglas-fir and tanoak common to a given month and sampling period (morning or afternoon) were pooled for the parameters, A, G, base XPP, current XPP, T and RH. This created 24 independent data sets (12 months x 2 sampling periods) in which to test the causal network of relationships hypothesized in Figure III.1.

Graphical analysis was used to determine if the relationships among variables were linear--an implicit assumption in path analysis. Only the relationship of G to base (pre-dawn) XPP consistently demonstrated non-linearity. Logarithmic transformation of G was found to linearize this relationship, as suggested by previous research (Emmingham and Waring, 1977; Johnson and Ferrell,

1983).

Variation in T was partitioned into portions of total determination attributable to PPF_D and PST (Pacific standard time). PST was included as a causal variable to account for differences in T attributable to changing environmental conditions during a given sampling period. Similarly, variation in RH was partitioned into that determined by T and PST.

Variation in base XPP was partitioned into portions of total determination attributable to SWP and an indicator variable denoting species. Variation in current XPP was partitioned into portions of total determination attributable to base XPP, G, and species. The direction of causality was assumed to operate from leaf conductance to current XPP, since for much of the data, current XPP was less negative than the observed threshold for stomatal closure (-2 MPa) (Lopushinsky, 1969; Running 1976; Johnson and Ferrell, 1983). In addition, work by Drew and Ferrell (1979) supports the contention that the direction of causality is from G to current XPP.

Variation in G was partitioned into portions of total determination attributable to PPF_D, RH, base XPP, and species. Variation in A was partitioned into portions of total determination attributable to G, T, PPF_D, and species. Because the sample size for G in February and July was limited by weather conditions, this variable was

not included in the path analyses for current XPP and A in these months.

RGR was used as an indicator of growth activity in individual Douglas-fir, thus, in the path analysis it was treated similiarly to other indicators of physiological response. For each month the proportion of variation in RGR that was attributable to SWP was determined. In preliminary analyses, RGR was found to be related to SWP at 30-cm depth, and not to SWP at 60-cm depth.

RESULTS AND DISCUSSION

MICROCLIMATE

Air and soil temperatures

Maximum monthly air temperatures were over 2° C higher ($p=0.005$) in plots where tanoak was present, versus those where it had been removed (Fig. III.2). Conard and Radosevich (1981) found similar results in which maximum air temperatures were 2 to 3° C higher within versus above a shrub canopy composed of snowbrush (Ceanothus velutinus Dougl. ex. Hook.) and greenleaf manzanita (Arctostaphylos patula Greene). The tanoak canopy did not have a significant ($p>0.10$) influence on minimum monthly air temperatures (Fig. III.3). This result contrasts with Conard and Radosevich's (1981) findings of lower minimum air temperatures within versus above a shrub canopy.

Soil temperatures at 15 cm depth were approximately 2° C lower ($p<0.001$) for Douglas-fir in C-3 versus trees in C-1 and C-2 (Fig. III.4). Emmingham and Waring (1977) predicted that conductance of Douglas-fir would be at 100, 50, and 0% of maximum values when soil temperatures were 5, 0 and -2° C, respectively. Thus, in the current study soil temperature probably had a minimal influence on conductance, because soil temperatures were above 5° C for

every monthly measurement except January and December, when minimum values were 3 to 4° C.

Precipitation

During April through September, the period of active shoot and/or cambial growth for Douglas-fir (referred to hereafter as 'growing-season' months), monthly precipitation in 1987 was less than 50 mm (Fig. III.5). Monthly precipitation in September and October was negligible (< 5 mm) during the prolonged summer drought of 1987. The first significant precipitation following the growing season occurred in early November.

Photosynthetically-active photon flux density

In 9-10 of the 12 monthly measurements, C-3 had significantly ($p=0.001$ to 0.03) lower values for photosynthetically-active photon flux density (PPFD), in both the morning (Fig. III.6) and afternoon (Fig. III.7), versus C-1 and C-2. Overcast or stormy conditions during February, March, June, and July caused PPFD levels to drop dramatically, leading to smaller and less significant ($p>0.1$) differences among conditions.

Overtopping shade from tanoak reduced light

availability to levels that were less than 25% of full sunlight. In a controlled study, Chan (unpublished data) found that, at high levels of soil water availability, limitations in light availability similar to those observed in C-3 restricted growth and morphological development of Douglas-fir.

Soil water potential

During June through September, values for the cumulative change in soil water potential (SWP) at 30 cm depth were significantly more negative ($p=0.03$ to 0.001) for C-2 than for C-1 (Fig. III.8). SWP at 30 cm became most negative in September, when values averaged -0.6 and -0.2 MPa for C-2 and C-1, respectively. In contrast, SWP at 60-cm depth was less negative during July through October for C-2 than for C-1 (Fig. III.9); however, these differences were found to approach statistical significance only in September ($p=0.10$) and October ($p=0.055$).

Leaf temperature

Morning and afternoon values for leaf temperature (T) were 2 to 6° C higher in C-2 and C-3 versus C-1 throughout the growing-season months (Figs. III.10 and III.12).

During this period, PST determined most of the variation in T, except in June and July, when PPF had the predominate influence (Figs. III.11 and III.13). In the dormant-season months, PPF had the greater influence on morning values for T, while for afternoon values, PST was more important.

Because both PPF and PST were similar for C-1 and C-2, observed differences in T between these conditions during growing-season months are presumed to result from restricted air flow and subsequent heating within the tanoak canopy. This same effect probably caused higher maximum air temperatures to occur in C-2 and C-3 versus C-1.

Relative humidity

Relative humidity (RH) varied greatly among the monthly measurements because of differences in prevailing weather patterns; however, in general, RH was lower during the growing-season months (Figs. III.14 and III.16). A July, 1987 storm caused mean values for RH to be elevated relative to those in June and August. For C-1, RH was up to 10% higher in August and September than measured for C-2 and C-3.

For most of the measurements, T was the factor

determining the bulk of the variation in morning and afternoon RH (Figs. III.15 and III.17). Thus, the observed differences in relative humidity among conditions during growing season months were attributable, in part, to the elevated leaf temperatures associated with the tanoak canopy. In September through December, PST had a more influential role than T in determining variation in afternoon RH values. This high degree of determination by PST occurred because, during late fall and early winter, RH values increased rapidly with time with the approach of sunset.

PLANT PHYSIOLOGY

Base xylem pressure potential

Two separate phenomena caused measurable declines in base (pre-dawn) xylem pressure potential (XPP) of Douglas-fir and tanoak (Figs. III.18). First, in the dormant-season months, base XPP values became more negative as air temperatures dropped below 0° C, especially for C-1 and C-2 (i.e., open-sky conditions). For example, when pre-dawn temperatures were -1 to -4° C in December 1987, base XPP values for Douglas-fir ranged from -0.9 to -2.7 for C-1 and C-2, and from -0.8 to -2.2 for C-3.

Second, during growing-season months, depletion of

soil water from evaporation and/or transpiration by tanoak and Douglas-fir, resulted in increasingly-negative base XPP values. Summertime base XPP became most negative in September, at which time Douglas-fir in C-2 and C-3 had values ranging from -1.0 to -1.8, while values for trees in C-1 ranged from -0.6 to -0.8. Regardless of seasonal conditions, base XPP for tanoak always was less negative than or equal to the least negative values for Douglas-fir.

The highly-negative values for base XPP observed in some of the winter months may be attributable to reduced water uptake resulting from both decreased permeability of roots to water and increased water viscosity (Kramer and Kozlowski, 1979). In addition, as a result of errors associated with pressure-chamber measurements on frozen tissues, base XPP values can be artificially negative (Evans and Reid, 1974). The results from the February data were not presented because, as a result of missing observations for base XPP, the regression contained only two levels of the independent variable, SWP.

SWP at 30-cm depth was the main determinant of variation in base XPP for Douglas-fir and tanoak (Fig. III.19). Base XPP was not significantly ($p > 0.10$) related to SWP at 60-cm depth. As soil water supplies became depleted from evapotranspiration, determination of base

XPP by SWP steadily increased each month from May ($r^2=0.05$) through October ($r^2=0.59$). Precipitation in November caused determination of base XPP by SWP to plummet ($r^2<0.01$).

At maximum soil water depletion, base XPP of Douglas-fir in C-3 averaged -0.2 MPa more negative than trees in C-2. Drew and Ferrell (1979) found that, for a range of soil water potentials, Douglas-fir grown under reduced light intensities had more negative values for current XPP than trees grown in full sunlight, and as a result such trees were less able to maintain open stomata.

Determination of base XPP by the species indicator also increased each month from June ($r^2=0.10$) through September ($r^2=0.38$). This increasing level of determination resulted because, throughout the growing-season months, base XPP values for tanoak were less negative than for Douglas-fir, after accounting for SWP. In November, following the first fall precipitation, the species indicator determined 76% of the variation in base XPP because tanoak recovered to less negative XPP values (-0.2 MPa) than Douglas-fir (-0.5 to -0.6 MPa).

These results demonstrate a direct link between tree water status and soil water availability at 30 cm depth, suggesting that root systems of young tanoak and Douglas-fir rely on soil water at shallow depths. Ahrens and Newton (unpublished data) found that 65% of fine root (<2

mm diameter) biomass for tanoak in 2- to 9-year-old stands occurred in the top 30 cm of soil. For Douglas-fir growing in a young Pacific madrone stand, base XPP values also were related to soil water availability at 30-cm depth (Pabst, Tappeiner, and Newton, unpublished data).

Leaf Conductance

For Douglas-fir in C-2, morning values for conductance (G) peaked in April, followed by a continual monthly decline to a minimum value in September (Fig. III.20). For Douglas-fir in C-3, G declined gradually from March through July, and then dropped to a negligible value in September, indicating near closure of the stomata. In contrast, both tanoak and Douglas-fir in C-1 maintained moderate to high levels of morning G throughout the year; however, for tanoak, these values were about 30% lower than for Douglas-fir. Following fall precipitation, morning G peaked again in November for all Douglas-fir and tanoak.

Two factors were found to determine most of the variation in morning G: base XPP and RH (Fig. III.21). PPFD had a noticeable influence on morning G only in April, May, and September. Since during these months other potentially-limiting factors were at similar levels

for Douglas-fir in C-2 and C-3, PPF_D was the additional factor limiting G for shaded trees.

During periods when base XPP was not limiting G (e.g., May, November, and December), RH was the most influential variable on morning G (Fig. III.21). The species indicator determined moderate amounts of variation in morning G in March, April, and November, during which times G was less for tanoak than for Douglas-fir, after accounting for the other factors.

Independent of the conditions (C-1, C-2, or C-3), afternoon G followed similar periodic trends for Douglas-fir and tanoak, with maximum values occurring in spring and fall, and minimum values occurring in late summer (Fig. III.22). During most of the year, afternoon G for tanoak was lower than for Douglas-fir.

RH influenced afternoon G from June through October, however the proportion of variation it explained declined in September and October as base XPP began to exert its overriding influence (Fig. III.23). These results are similar to those of Johnson and Ferrell (1983), who found for Douglas-fir that sensitivity of G to atmospheric humidity decreased with increasingly negative values of current XPP.

The species indicator accounted for moderate amounts of variation in afternoon G throughout winter and spring,

during which times G was less for tanoak than for Douglas-fir, after accounting for other factors (Fig. III.23). Afternoon G was not greatly affected by PPF. The low degree by which PPF determined variation in both morning and afternoon G may have resulted because, during most of the monthly measurements, PPF exceeded the threshold value ($300 \text{ umole} / \text{m}^2 / \text{s}$) considered necessary for full stomatal aperture of conifers (Jarvis, 1980).

In addition to the factors identified here as controlling G, several researchers have shown that cold soil temperatures (Babalola et al. 1968) and below-freezing air temperatures during the previous night (Neilson and Jarvis, 1976; Drew and Ferrell, 1979; Kaufmann, 1982; Graham and Running, 1984) can reduce daytime transpiration and conductance of conifer species. Drew and Ferrell (1979) attributed the reduced conductance of Douglas-fir seedlings during winter to stomatal closure, rather than to highly-negative XPP.

Current xylem pressure potential

Current XPP was influenced by a combination of ambient conditions and soil water availability (Figs. III.24 and III.26). For Douglas-fir in C-1 and C-2, current XPP averaged -1.5 and -2.3 MPa, respectively, when values reached their most negative extent. At its most

negative value, current XPP for tanoak averaged -1.7 MPa. In general, values for tanoak were equal to or less negative than that for Douglas-fir in C-1.

For the growing-season months, much of the variation (20 to 68%) in current XPP was determined by base XPP (Fig. III.25 and III.27). However, variation also was determined by species and G, especially during the dormant-season months. For example, November values for current XPP of Douglas-fir were -1.8 to -2.0 MPa in the morning and afternoon, respectively, compared to values of -0.6 to -0.8 MPa for tanoak. This species difference probably resulted because, in November, tanoak had both less negative values for base XPP (Fig. III.18) and lower values for G when compared to Douglas-fir (Fig. III.20 and III.22).

In September, despite the development of current XPP values that were more negative than the threshold value (-2.0 MPa) (Figs. III.24 and III.26) commonly reported to cause stomatal closure in Douglas-fir (Lopushinsky, 1969; Running, 1976; Drew and Ferrell, 1979; White, 1987), G values for trees in C-2 ranged from 0.05 to 0.1 cm/s (Figs. III.20 and III.22). In similar field research on Douglas-fir seedlings, Livingston and Black (1987) were unable to identify a discrete threshold value for turgor potential which would cause stomatal closure.

Photosynthesis

Morning values for Douglas-fir A followed a similar seasonal progression (Fig. III.28) to that observed for morning G (Fig. III.20). Tanoak and Douglas-fir in C-1 and C-2 maintained relatively stable morning values for A throughout the year, with trees in C-1 demonstrating consistently higher rates.

Variation in morning A was determined largely by G and PPFD (Fig. III.29). G was the factor most influencing A during the growing season, and its total determination increased steadily from May ($r^2=0.13$) through October ($r^2=0.62$). PPFD consistently determined moderate amounts of variation (10-37%) in morning A for 10 of the 12 monthly measurements. This variation explained by PPFD can be attributed to the low values in A measured for the shaded Douglas-fir (C-3).

In June, T determined 21% of the variation in morning A. During this measurement, leaf temperature averaged 2° C higher for C-2 and C-3 than for C-1; however, only trees in C-3 had depressed values for A. Since variation in A attributable to G, PPFD, and species already had been accounted for, the effect of T in June was probably the result of increased rates of respiration or photorespiration for the shaded Douglas-fir.

Species differences explained 20% of the variation in

morning A during December, when values for tanoak were equal to those for the shaded Douglas-fir (C-3). In general, species differences did not appear to have a strong influence on variation in morning A, after accounting for the other factors.

Afternoon rates for A declined in mid-summer for Douglas-fir and tanoak in each of the conditions (Fig. III.30). Except for shaded trees (C-3), afternoon values for A peaked during spring (April and May) and fall (November) months for Douglas-fir and tanoak. For shaded trees, the spring maximum occurred earlier, in March, following which A declined to negligible values for the remainder of the year.

In August and September, assimilation rates for the shaded Douglas-fir (C-3) were less than zero, during which times leaf temperatures ranged from 30 to 35° C. These measurements of 'negative' photosynthesis probably resulted from elevated respiration rates, and possibly photorespiration, since the latter is often associated with high temperatures (Kramer and Kozlowski, 1979).

As found for morning A, G and PPFD determined most of the variation in afternoon A throughout the year (Fig. III.31). G influenced afternoon A for most of the year (April through December) during which times it explained 18 to 85% of the variation in afternoon A. In

contrast, PPF_D explained variation (14 to 36%) in afternoon A largely in the dormant-season months, because during this period of low PPF_D, light has a greater limiting influence than G on A. Similar to the results observed for morning A, species differences only determined a minor amount of the variation in afternoon A.

The following three findings are evidence that differences in A between species are due largely to the greater stomatal control of tanoak: 1) values of tanoak G generally were less than or equal to the lowest values measured for Douglas-fir growing in similar microclimatic conditions (C-2), 2) in comparison to Douglas-fir in C-1, tanoak had similar values for base XPP, but less negative values for current XPP, and 3) the species indicator was not important in determining variation in A after accounting for the other factors. Thus, photosynthesis rates for tanoak were found to be similar to those for Douglas-fir, after adjusting for conductance. Through stomatal control, it appears that tanoak is able to prevent the development of highly negative values for current XPP that would cause complete stomatal closure.

Another explanation, aside from stomatal control, could account for the observed similarity in base XPP values for tanoak versus Douglas-fir growing without competition (C-1), despite differences in their competitive environments. Research by Ahrens and Newton

(unpublished data) suggests that sprout clump stands of tanoak retain at least half of the fine (< 2 mm diameter) root biomass present in the pre-disturbance stand. These extensive residual root systems may impart to tanoak sprout clumps access to soil water supplies that remain available throughout the growing season (i.e., at soil depths of 60 cm or greater).

The "water conserving" strategy of tanoak differs greatly from the "water using" strategy observed for several Arctostaphylos species. White (1987) found that stomatal closure of whiteleaf manzanita (Arctostaphylos viscida Parry) did not occur until current XPP became more negative than -3.0 MPa. Similarly, the onset of stomatal closure was not detectable when current XPP of greenleaf manzanita (Arctostaphylos patula Greene) was -2.2 MPa (Shainsky and Radosevich, 1986; Conard and Radosevich, 1981).

Douglas-fir relative growth rates

Douglas-fir growth activity, as measured by RGR, was confined to the months of April through September for basal area growth, and May through August for height growth (Fig. III.32). In general, basal area RGR was relatively variable, and maximum values occurred in April

and July with two months of reduced or zero RGR in May and June.

Both the rates and duration of basal area growth were greater for Douglas-fir in C-1 than for trees in C-2 and C-3. Height RGR was greater in July for trees in C-1 than for C-2 and C-3, however the duration of height growth did not vary among conditions, as found in Chapter II (Fig. III.34). From July through September, SWP at 30 cm determined 39 to 69% of the variation in basal area RGR (Fig. III.33); however, only 18 to 34% of the variation in height RGR was determined by SWP (Fig III.35).

In Chapter II, tanoak competition was found to reduce monthly values for basal area RGR of Douglas-fir when light was fully available (i.e., overtopping shade was less than 20%), suggesting that growth was limited by soil water availability. Although these results indicate that soil water availability was not severely restricted by tanoak competition (i.e., SWP at 30 cm never became more negative than -0.9 MPa), soil water potentials of only -0.1 to -0.2 MPa have been shown to reduce cambial growth rates of some tree species (Kramer and Kozlowski, 1960).

Whole tree photosynthesis

Average 1987 values for specific leaf area (SPLA) of Douglas-fir were similar for C-1 and C-2 (6.30 and 6.68

m^2/kg , respectively); however, SPLA was higher ($9.17 \text{ m}^2/\text{kg}$) for trees in C-3 (Table 1). Del Rio and Berg (1979) found similarly that Douglas-fir SPLA decreased linearly with increasing exposure to full sunlight. The mean SPLA value for tanoak ($5.10 \text{ m}^2/\text{g}$) was lower than any of the values for Douglas-fir.

Average 1987 leaf area increment varied widely for Douglas-fir, ranging from 0.23 m^2 for trees in C-3 to 5.41 m^2 for trees in C-1 (Table III.1). The differences in leaf area increment of Douglas-fir among conditions probably resulted from the combination of differences in bud numbers produced per tree and needle numbers produced per bud. Tanoak competition can limit each of these parameters of Douglas-fir morphology (Tappeiner et al. 1987; Chapter II). Tanoak leaf area increment (4.34 m^2) was similar to that for Douglas-fir in C-1.

Average values for A spanned a wide range from 0.65 (Douglas-fir in C-3) to $4.98 \text{ umole CO}_2/\text{m}^2/\text{s}$ (Douglas-fir in C-1) (Table III.1). Average per-tree photosynthesis rates (i.e., for the south-half of a tree's crown) provide an indication of the huge differences in net assimilation that result from the combined differences in leaf area increment and A (Table III.1). The highest per-tree rate was that of Douglas-fir in C-1 (13.32 umole/s), which was about twice the value for tanoak (6.67 umole/s). The

ratios of per-tree photosynthesis rates for Douglas-fir
were 190:25:1 for C-1 : C-2 : C-3.

CONCLUSIONS

Tanoak exerts a strong influence on the microclimate of young stands, creating conditions that severely limit photosynthesis of associated Douglas-fir. Year-round limitations in Douglas-fir photosynthesis were associated with the microclimate of tanoak shade, while mainly growing-season limitations occurred for trees growing in openings of the tanoak stand.

The following scenario, which draws on the causal paths shown Figure III.1, describes the expected progress of microclimatic limitations imposed by tanoak on Douglas-fir photosynthesis during a typical year. Since the scope of this scenario is limited to the causal relationships that were studied, it does not include other potentially-important microclimatic variables, such as soil temperature, days since the last frost, and nutrient availability.

In spring, when conditions are most favorable for Douglas-fir photosynthesis (i.e., when both light and soil water are at peak levels), shaded trees are receiving less than 25% of full sunlight. Under these conditions, Douglas-fir photosynthesis rate is inhibited directly via reduced incoming photosynthetically-active radiation (in Fig. III.1, $path_{AG}$), and indirectly through reduced stomatal aperture ($path_{AHM}$). The latter effect appears to

be less important, because generally even the shaded trees receive the light needed for maximum conductance ($300 \mu\text{mole} / \text{m}^2 / \text{s}$). In previous physiological research on mechanisms of shrub and hardwood competition, light availability was not emphasized as a factor limiting growth of young conifers (Conard and Radosevich, 1981; Shainsky and Radosevich, 1986; Lanini and Radosevich, 1986; Petersen et al. 1988).

In addition to the direct physiological limitations imposed by reduced light availability (i.e., reduced photosynthetic rate and stomatal aperture), the foliage of shaded Douglas-fir probably has a lower photosynthetic capacity than that for unshaded trees (Boardman, 1977), as indicated by the differences in specific leaf area (Table III.1). In comparison to 'sun' foliage, 'shade' foliage has a mesophyll region composed of fewer layers of shorter palisade cells (Nobel, 1983). As a result of this restricted mesophyll development, for a given leaf area, shade leaves have a lower total volume of chlorophyll and less mesophyll surface area for CO_2 absorption than sun leaves.

For trees growing in openings within the tanoak stand, light limitations are not nearly as severe as for the shaded trees, but depending on their exposure to the sun, the duration of full sunlight they receive may be

limited by tanoak, especially during the dormant season. In this study, sampling order of Douglas-fir in C-2 was restricted because the tanoak stand delayed the arrival of full sunlight on trees during the winter months.

An added limitation to photosynthesis begins to occur in early summer, when leaf temperatures become elevated for trees growing with tanoak, especially the shaded trees (path_{ACF}). Presumably this occurs when air becomes trapped and heated within the dense canopy of tanoak. As a result, respiration and photorespiration rates begin to equal assimilation rates. In addition, with each increase in leaf temperature, a decrease in relative humidity follows, causing reduced stomatal aperture of Douglas-fir, and limiting their rates of photosynthesis (path_{ACEKM}).

By late summer, tanoak has consumed much of the available soil water, and the base xylem pressure potentials of the associated Douglas-fir are becoming increasingly negative (-1.2 to -1.8 MPa). During a given day, Douglas-fir growing with tanoak quickly reach values of xylem pressure potential that limit their stomatal aperture (-2.0 MPa), often by mid-morning. This is especially true for the shaded trees, which have poorer stomatal control (Drew and Ferrell, 1979). For the remainder of the day, fixed carbon is lost through respiration and photorespiration. Thus, an additional mechanism of tanoak competition limits late-summer

photosynthesis of Douglas-fir--stomatal closure imposed by water stress (path_{BDIM}).

In contrast, for Douglas-fir growing without tanoak competition, the major factor limiting their growing season rates of photosynthesis appears to be the low relative humidities typical during afternoons in mid- to late-summer (path_{ACEKM}).

Individual tanoak appear to have lower rates of photosynthesis than Douglas-fir throughout the most of the growing season. Their strategy for coping with the microclimatic limitations imposed by the tanoak stand is to maintain a favorable water status via stomatal control. Without encumbering highly-negative levels of water stress, individual tanoak are able to maintain positive rates of photosynthesis throughout the growing season.

In autumn, microclimatic conditions become similar to those of spring, and a second peak in photosynthesis rates occurs for Douglas-fir and tanoak. The shaded Douglas-fir, however, do not demonstrate a fall peak, presumably because of light limitations (path_{AG}). In addition, a residual effect of summer drought continues to limit photosynthesis of all Douglas-fir growing with tanoak. Despite similarities in soil water availability to trees growing in the absence versus presence of tanoak, the latter have lower photosynthesis rates during the fall.

During the winter, photosynthesis rates of all Douglas-fir and tanoak become limited from the reduced levels of light (path_{AG}) and air temperature (path_{ACF}); however, rates comparable to those observed in the growing season are possible during periods of mild weather. Shaded Douglas-fir continue to be at a disadvantage because of their light-limited photosynthesis rates (path_{AG}). Low soil temperatures, which occur throughout the winter, have a common limiting influence on photosynthesis of all trees by reducing their conductance.

When annual averages of photosynthesis rate are expanded to the whole-tree level, differences among the Douglas-fir and tanoak span a huge range. Because both their leaf areas and average rates of photosynthesis can have similar magnitudes, tanoak and Douglas-fir growing without tanoak competition demonstrate similar whole-tree photosynthesis rates. For Douglas-fir growing with tanoak, a combination of restricted leaf area development and reduction in the average rate of photosynthesis limit whole-tree photosynthesis rates by over two orders of magnitude relative to Douglas-fir growing without tanoak. As found in Chapter II, the rate of Douglas-fir leaf area development depends greatly on the size and number of buds produced in previous years.

The results from this study demonstrate that tanoak competition can severely limit annual assimilation of

Douglas-fir. The extremely low rates of assimilation for the shaded Douglas-fir appear to account for their slow growth rates and reduced vigor. Similar factors appear to account for growth reductions of trees that occur in openings within the tanoak canopy.

TABLE III.1. Parameters used to obtain average rates of whole-tree photosynthesis for the three conditions in young Douglas-fir /tanoak stands. Each value (standard error below in parentheses) represents the mean of 6 Douglas-fir or tanoak.

Parameter	conditions for Douglas-fir			tanoak
	1	2	3	
specific leaf area (m ² /kg)	6.30 (0.07)	6.68 (0.15)	9.17 (0.36)	5.10 (0.04)
tree leaf area increment (m ²)	5.41 (0.73)	1.00 (0.16)	0.23 (0.06)	4.34 (2.74)
average net photosynthesis rate (umole CO ₂ /m ² /g)	4.98 (0.16)	3.32 (0.20)	0.65 (0.31)	2.74 (0.57)
tree net photosynthesis rate (umole CO ₂ /s)	13.32 (1.58)	1.72 (0.36)	0.07 (0.03)	6.67 (4.62)

FIGURE III.1. Diagram of causal relationships hypothesized to exist among variables of microclimate and tree physiology in young Douglas-fir / tanoak stands. In the text, 'paths' of cause-and-effect among variables are referenced by the letters for a given series of connected arrows.

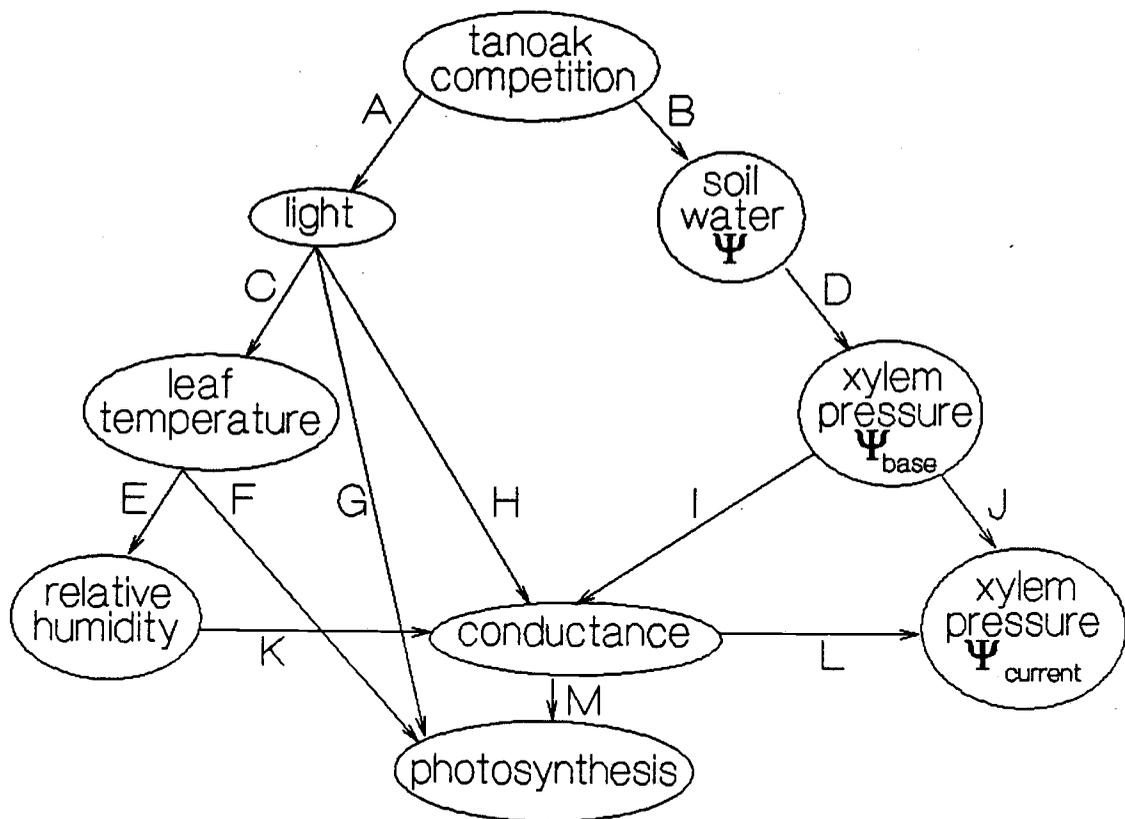


FIGURE III.2. Average maximum monthly air temperature at 1 m height for two conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 2 observations measured in 1987.

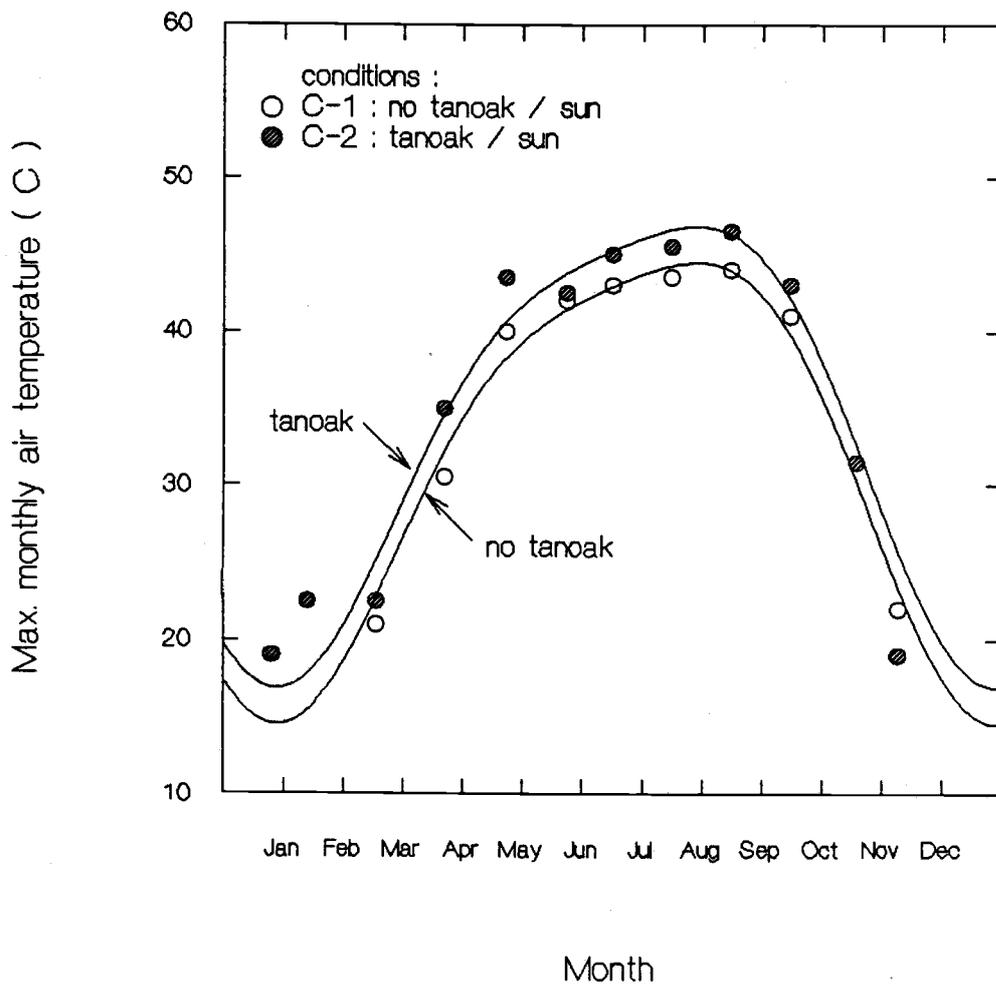


FIGURE III.3. Average minimum monthly air temperature at 1 m height for two conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 2 observations measured in 1987.

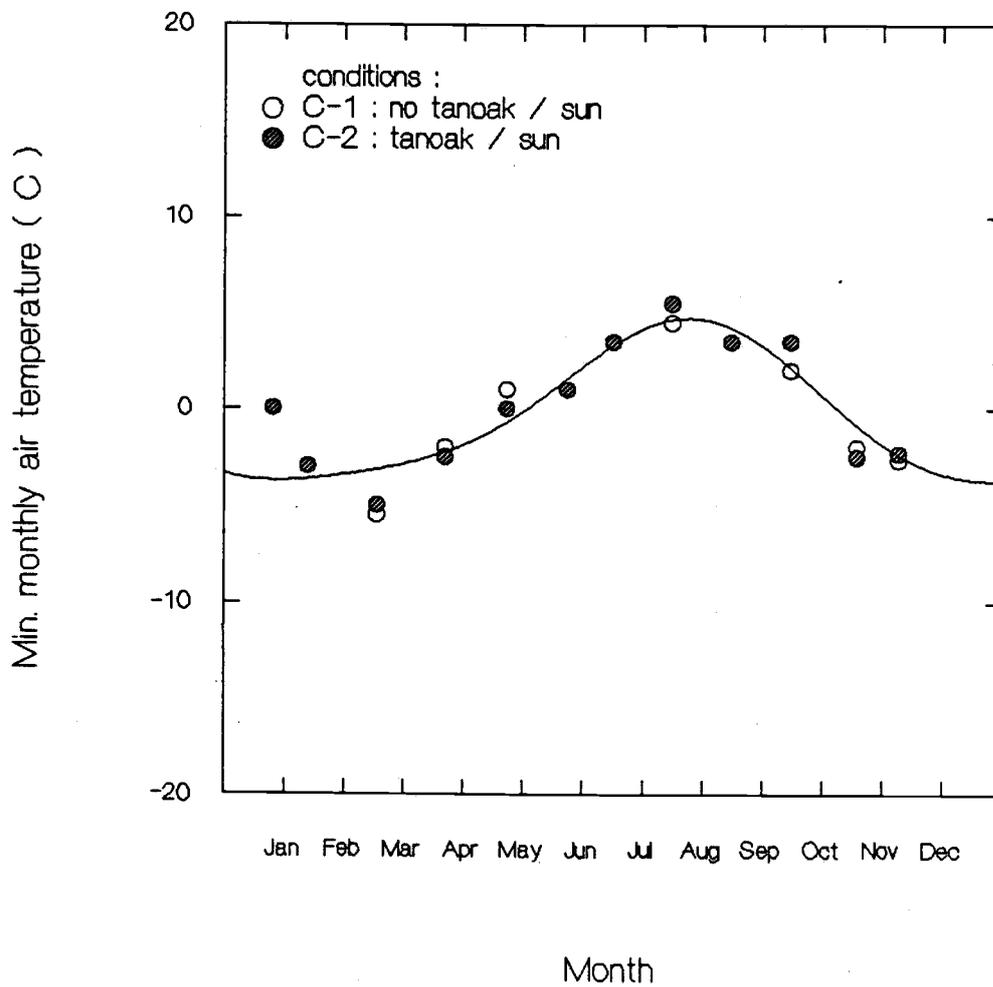


FIGURE III.4. Average soil temperatures at 15 cm depth for three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 4 to 7 observations measured in 1986 and 1987.

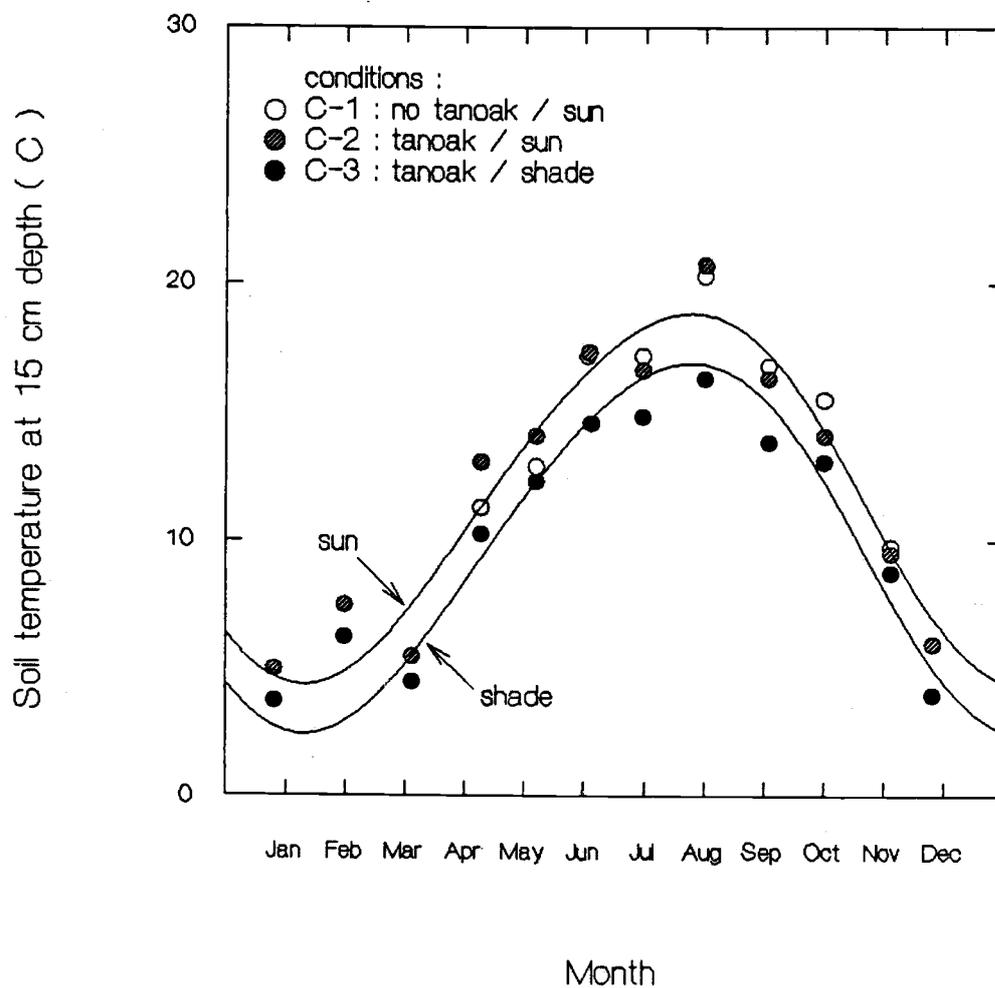


FIGURE III.5. Average monthly precipitation at Fir Point and Squaw for 1987.

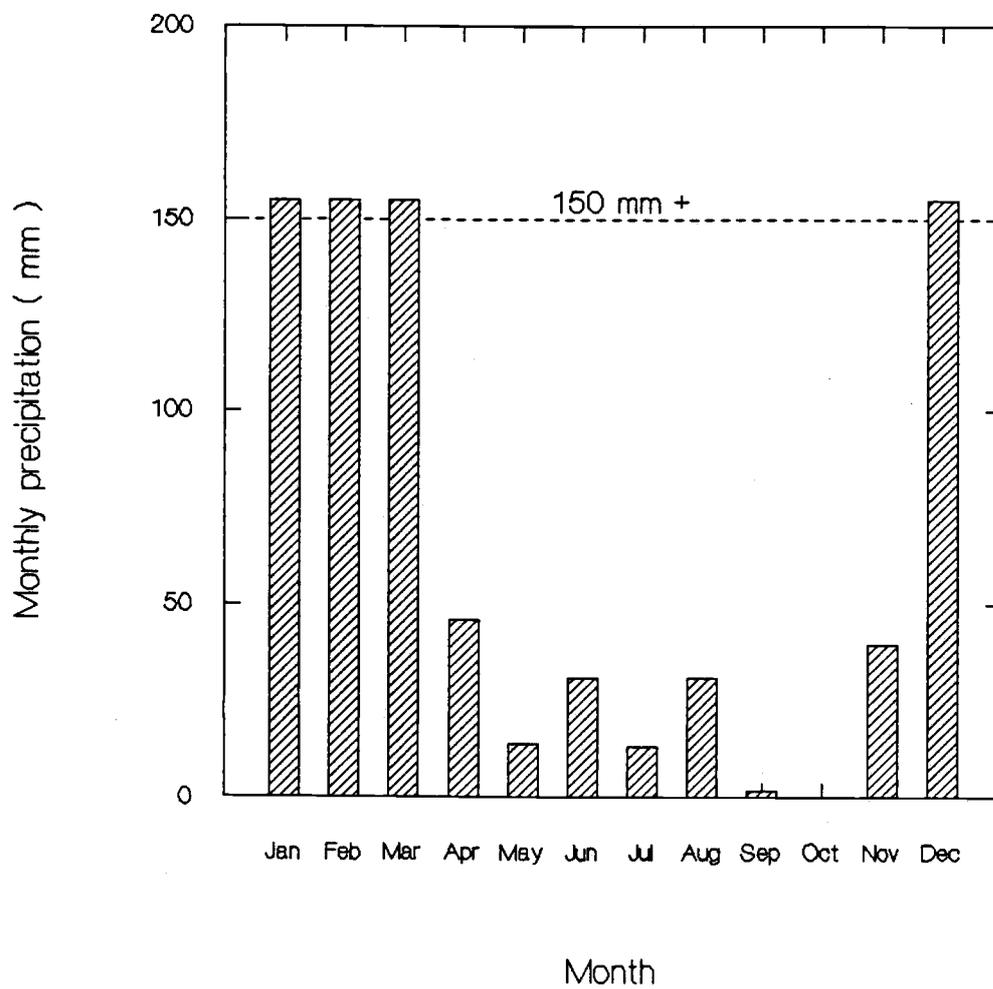


FIGURE III.6. Average morning photosynthetically-active photon flux density (PPFD) measured for three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 18 observations measured in 1986 and 1987. During months indicated by an '*', PPFd differed significantly (95% level) among conditions.

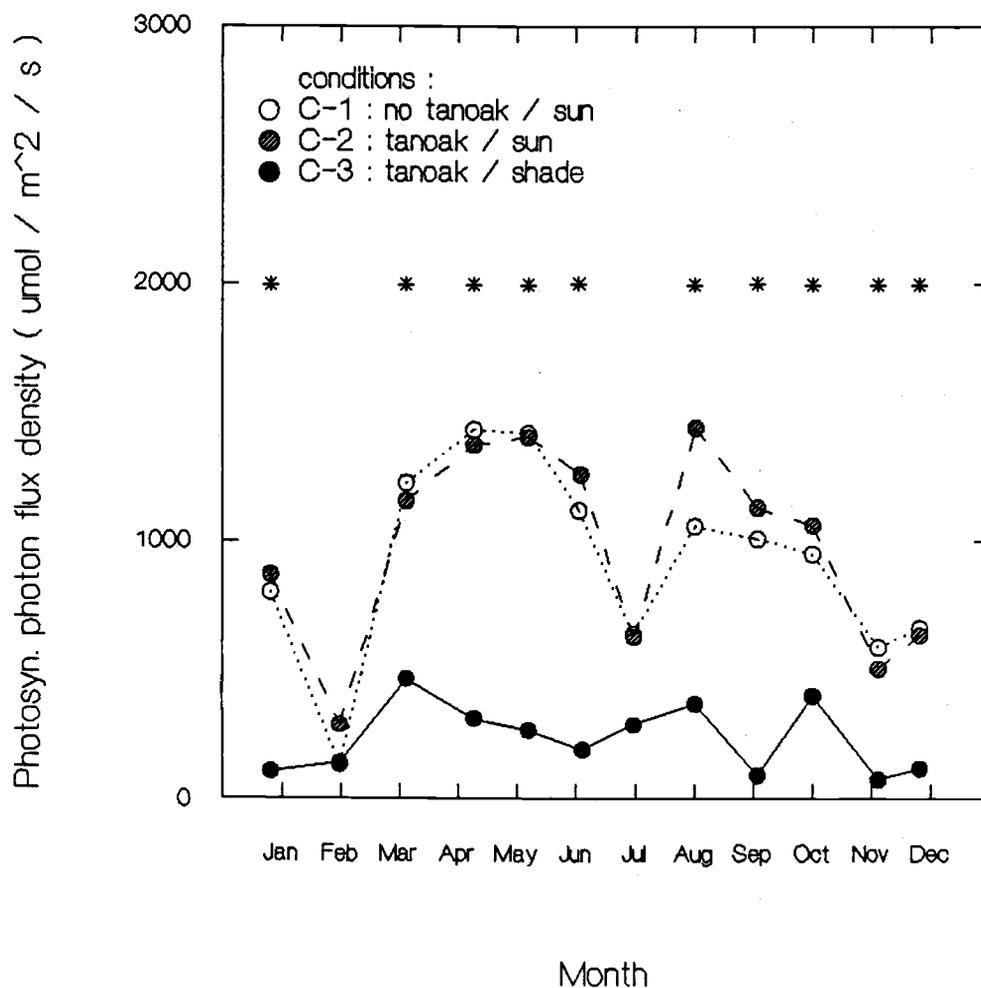


FIGURE III.7. Average afternoon photosynthetically-active photon flux density (PPFD) measured for three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 18 observations measured in 1986 and 1987. During months indicated by an '*', PPFd differed significantly (95% level) among conditions.

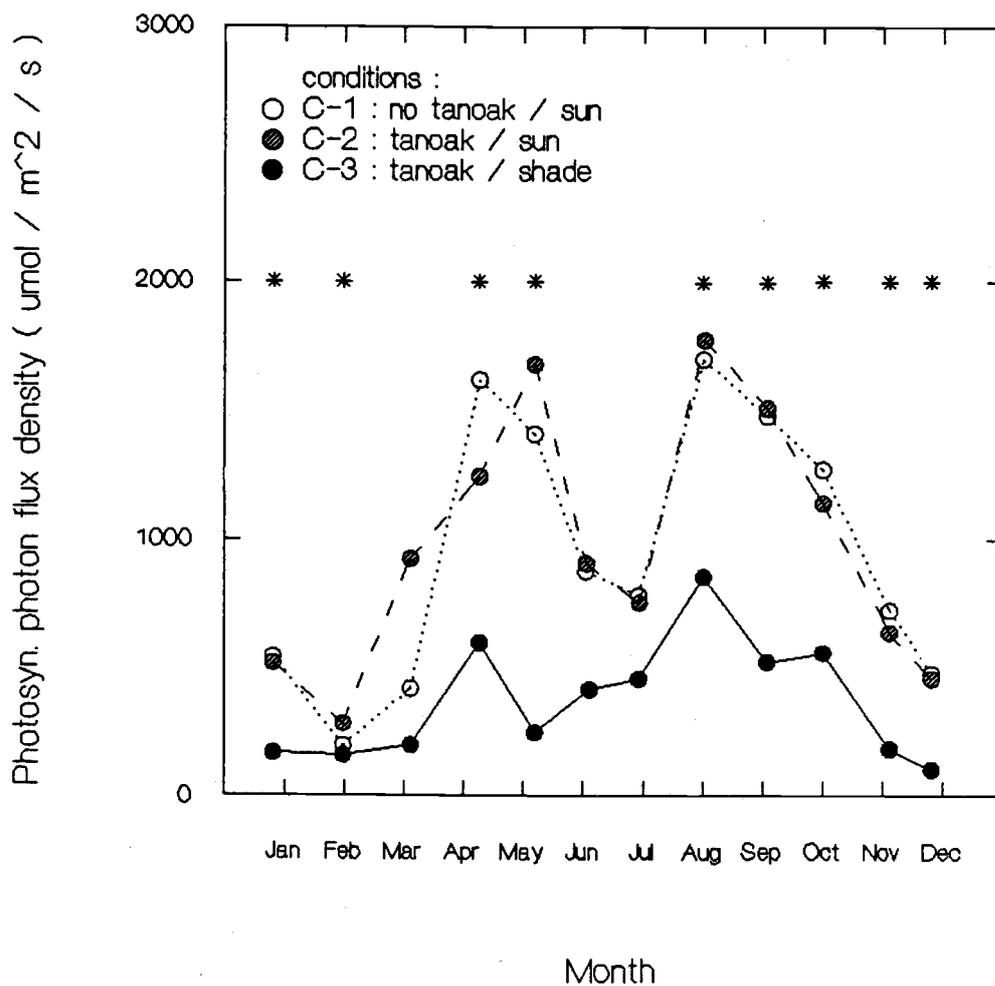


FIGURE III.8. Average cumulative change in soil water potential (SWP) at 30 cm depth measured for two conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987. During months indicated by an '*', SWP differed significantly (95% level) among conditions.

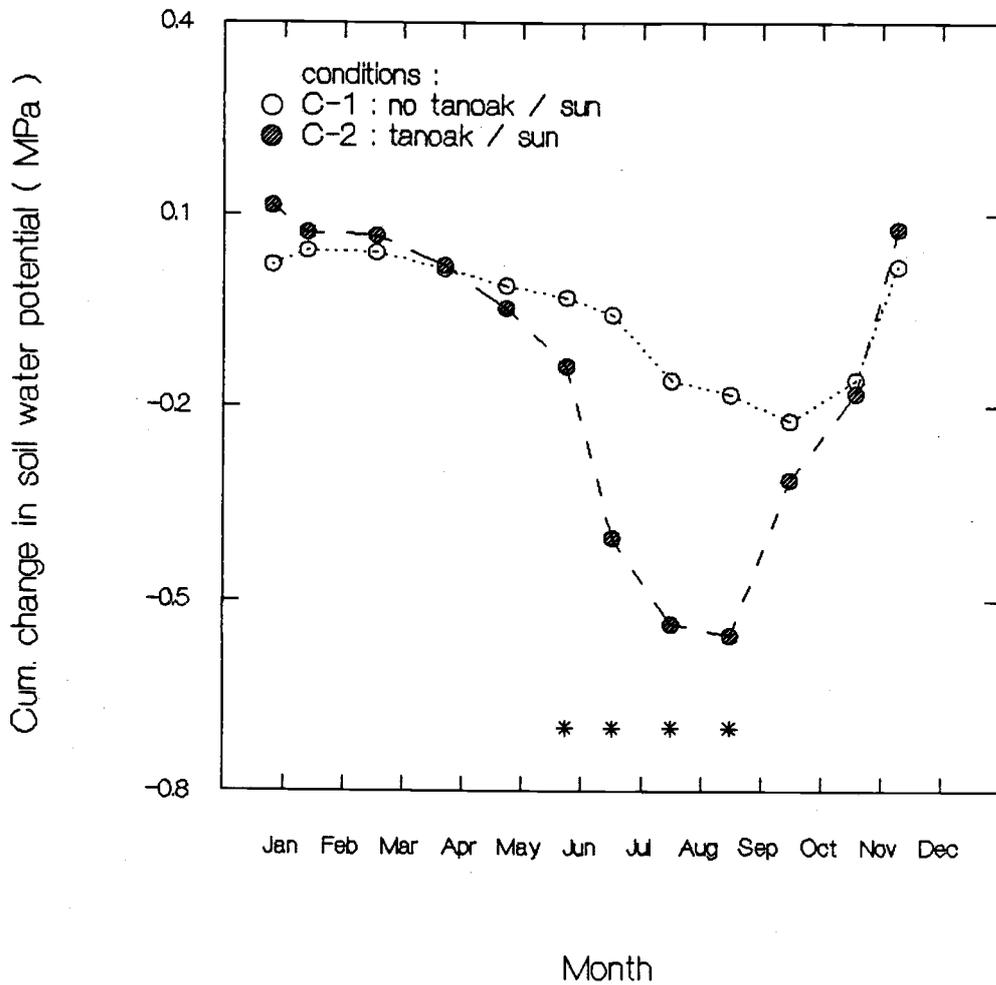


FIGURE III.9. Average cumulative change in soil water potential (SWP) at 60 cm depth measured for two conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987. During months indicated by an '*', SWP differed significantly (95% level) among conditions.

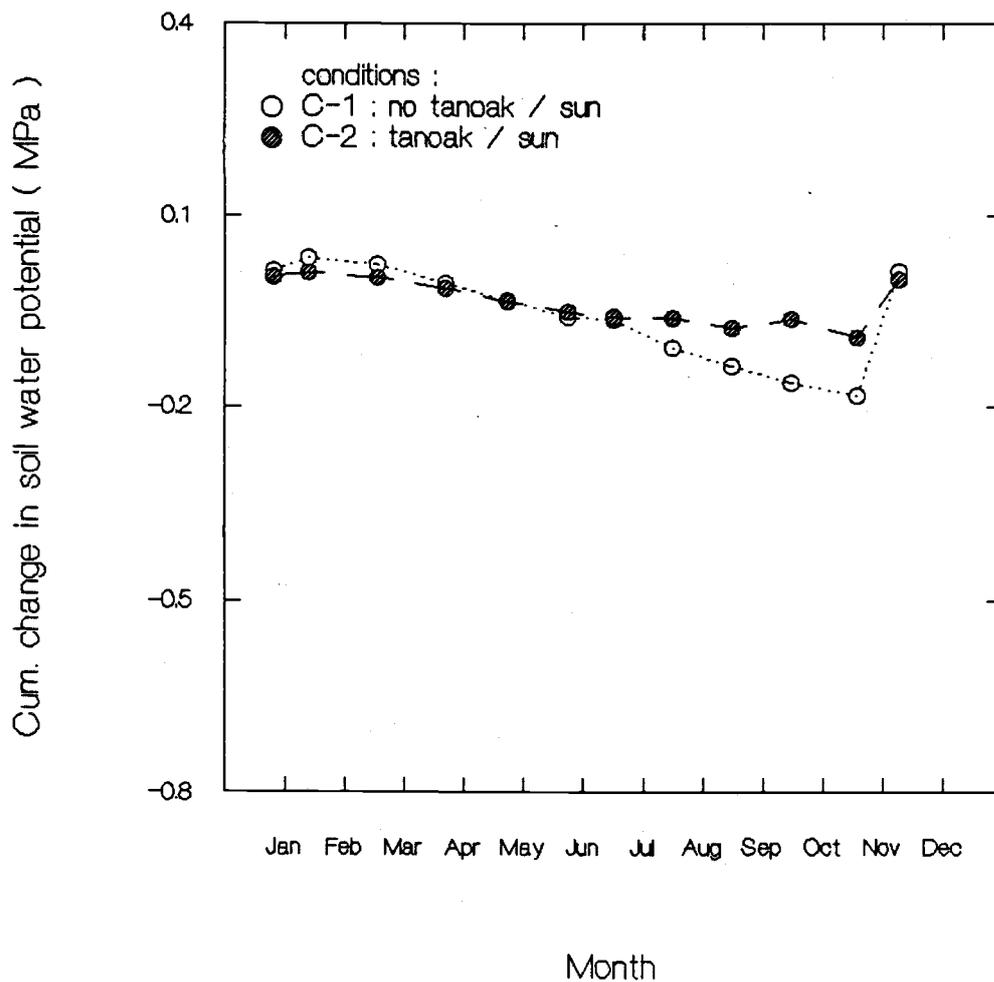


FIGURE III.10. Average morning leaf temperature for three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 18 observations measured in 1986 and 1987.

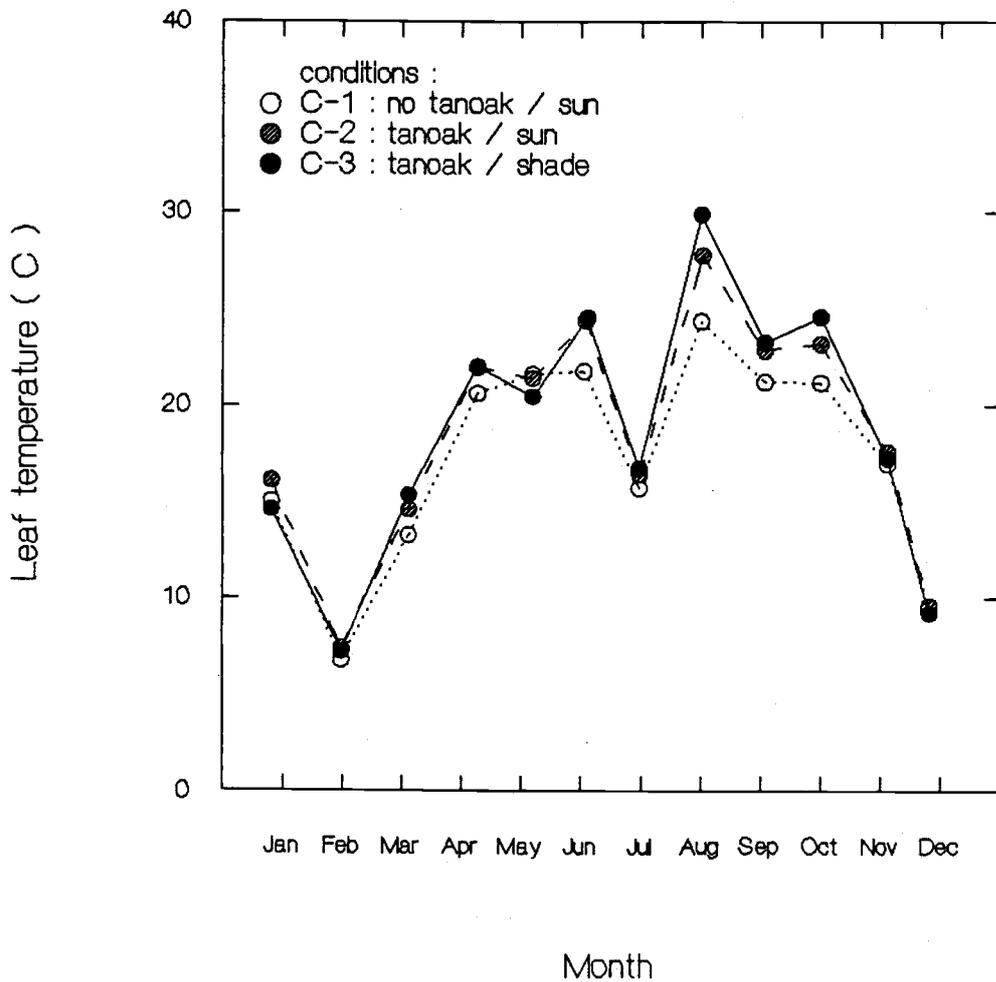


FIGURE III.11. Total determination of morning leaf temperature by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD). Each point in represents the mean of 6 to 18 observations.

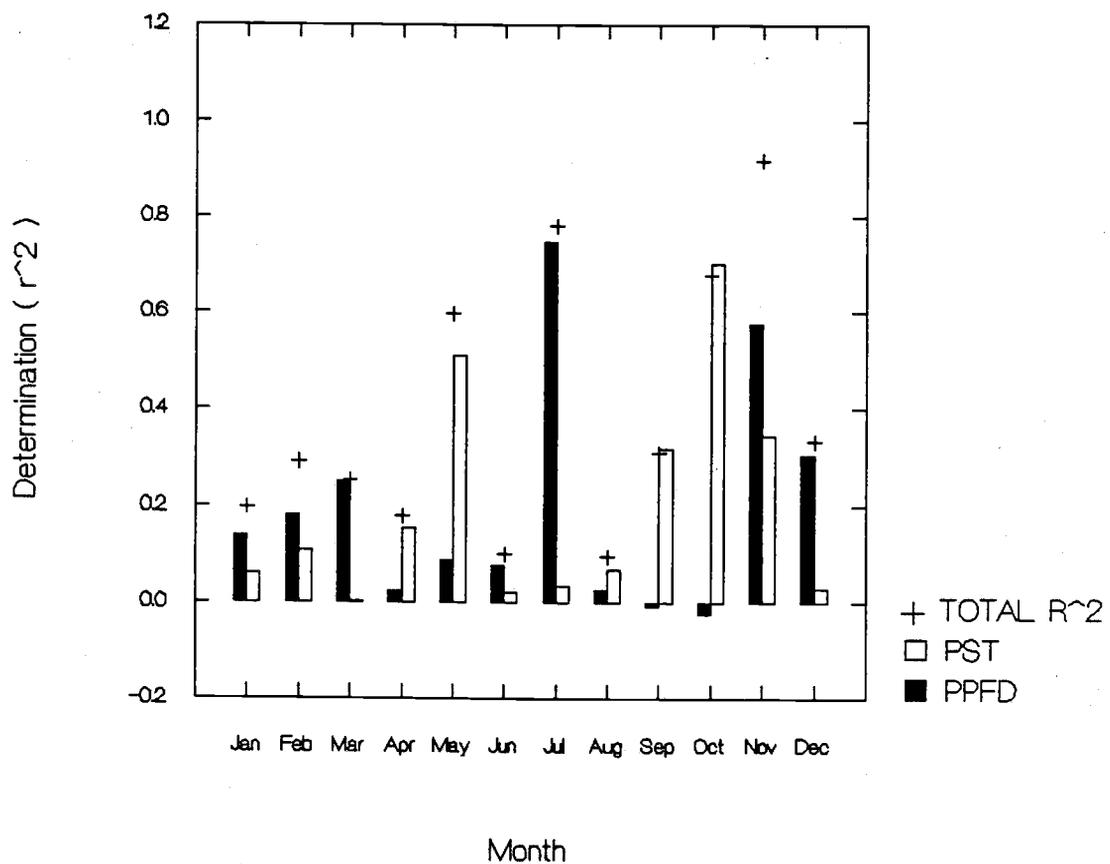


FIGURE III.12. Average afternoon leaf temperature for three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 18 observations measured in 1986 and 1987.

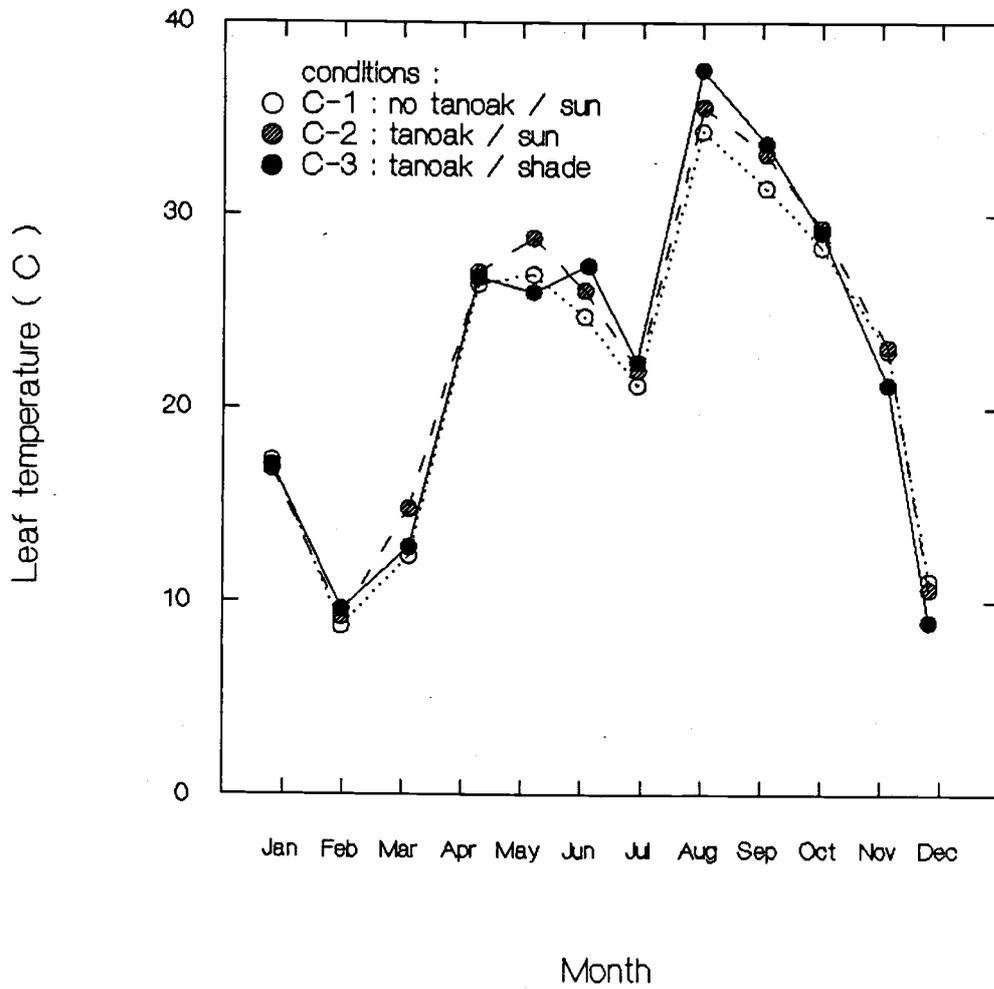


FIGURE III.13. Total determination of afternoon leaf temperature by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD).

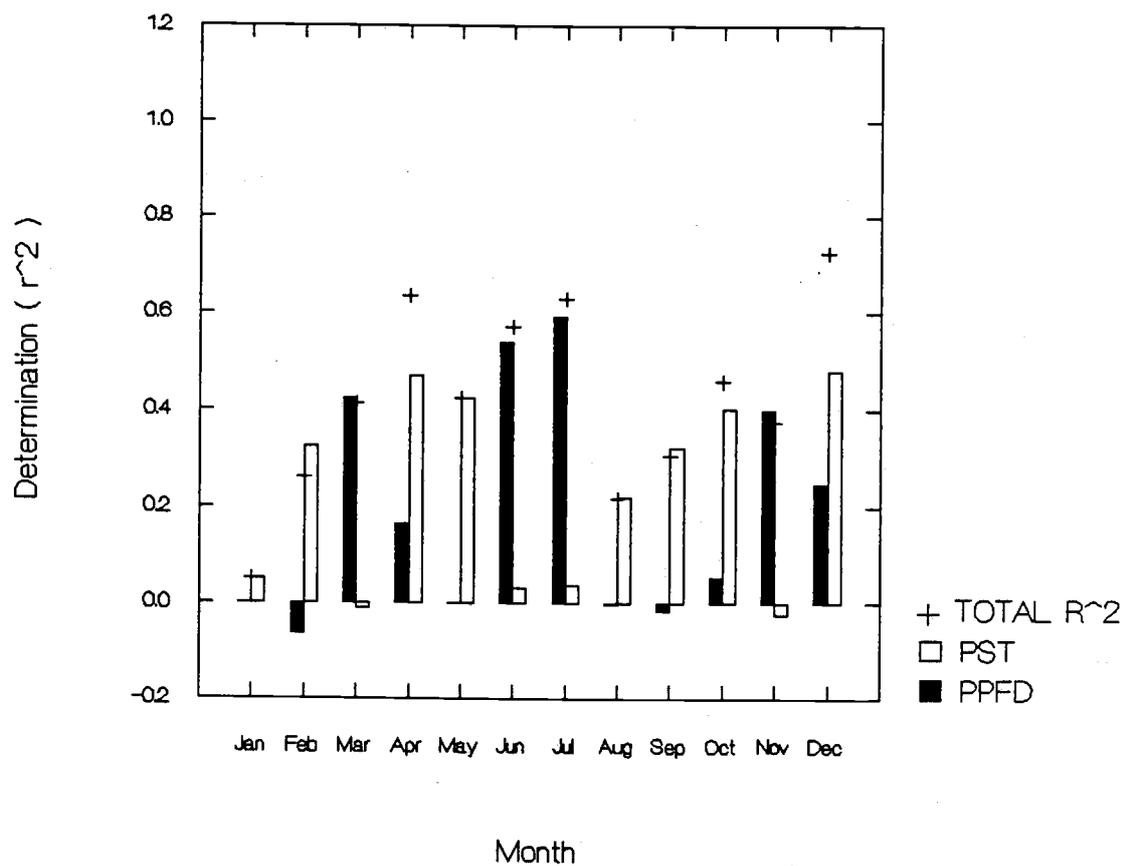


FIGURE III.14. Average morning relative humidity for three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 18 observations measured in 1986 and 1987.

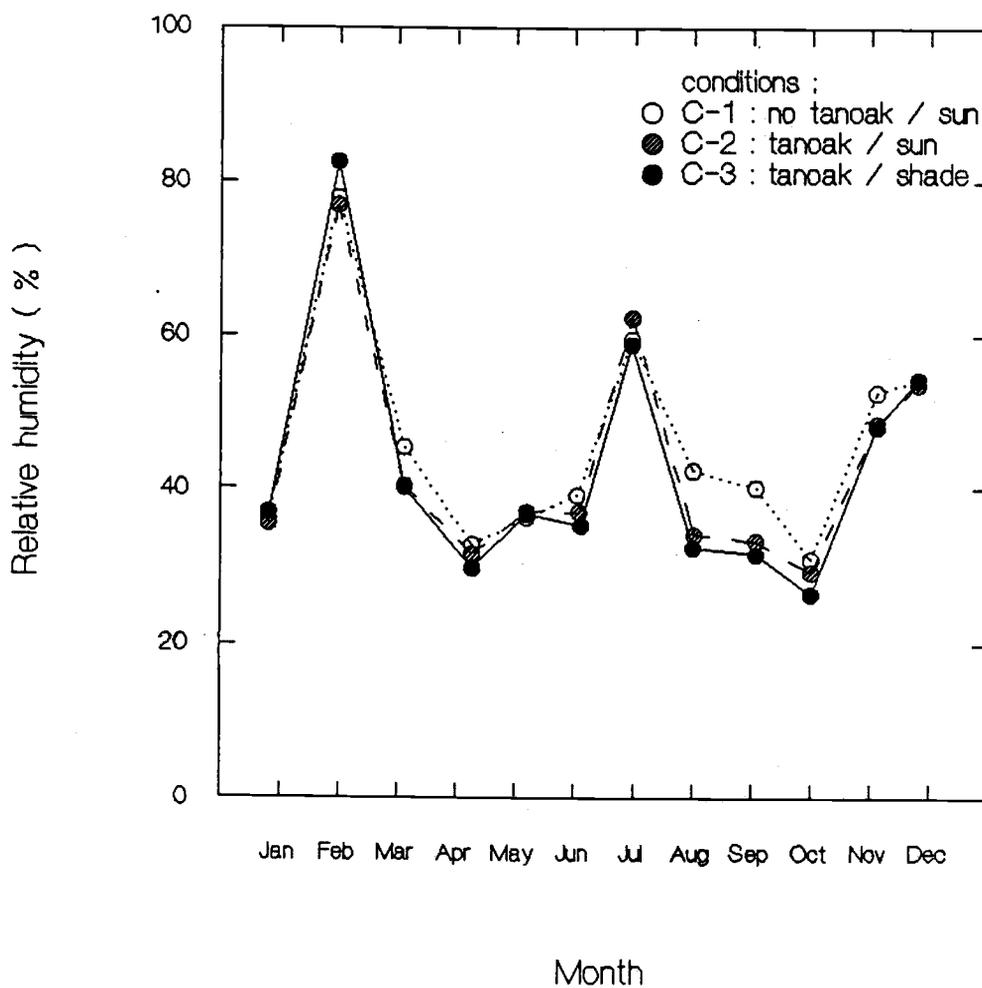


FIGURE III.15. Total determination of morning relative humidity by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD).

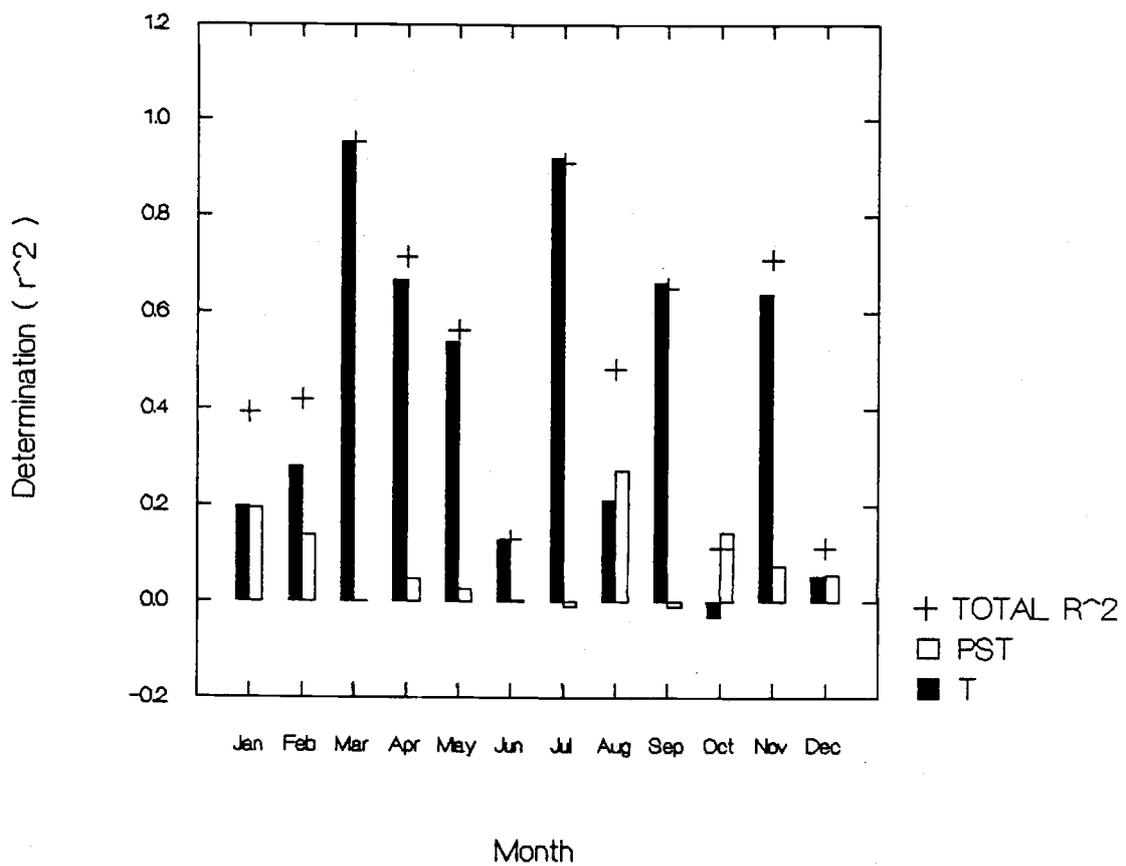


FIGURE III.16. Average afternoon relative humidity for three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 18 observations measured in 1986 and 1987.

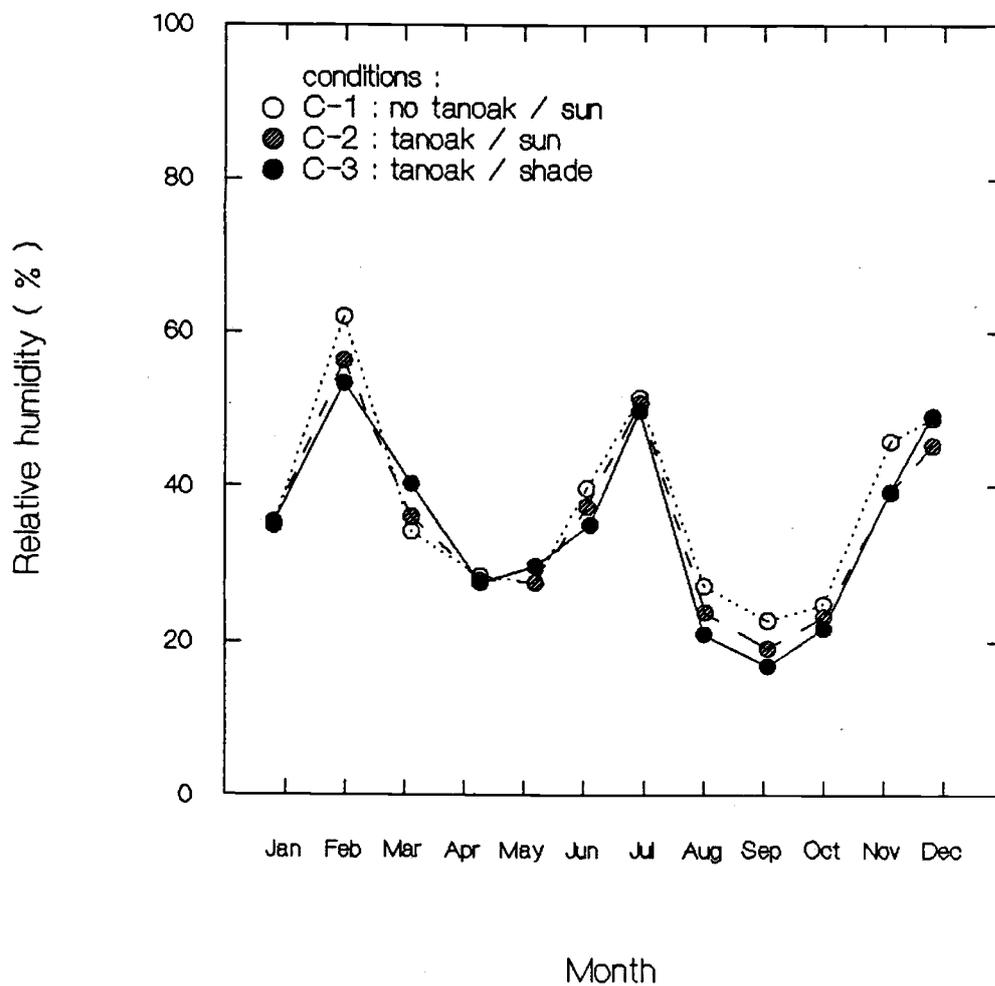


FIGURE III.17. Total determination of afternoon relative humidity by Pacific standard time (PST) and photosynthetically-active photon flux density (PPFD).

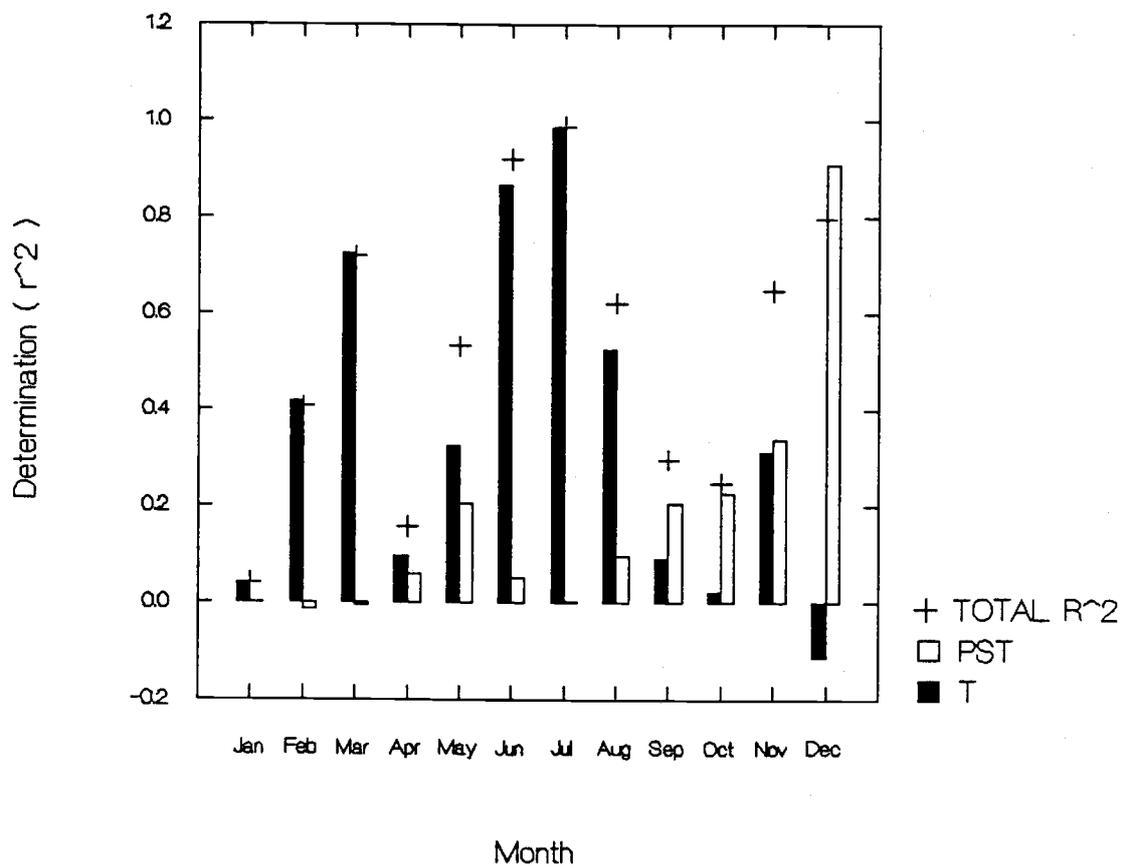


FIGURE III.18. Average base xylem pressure potential of trees growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987.

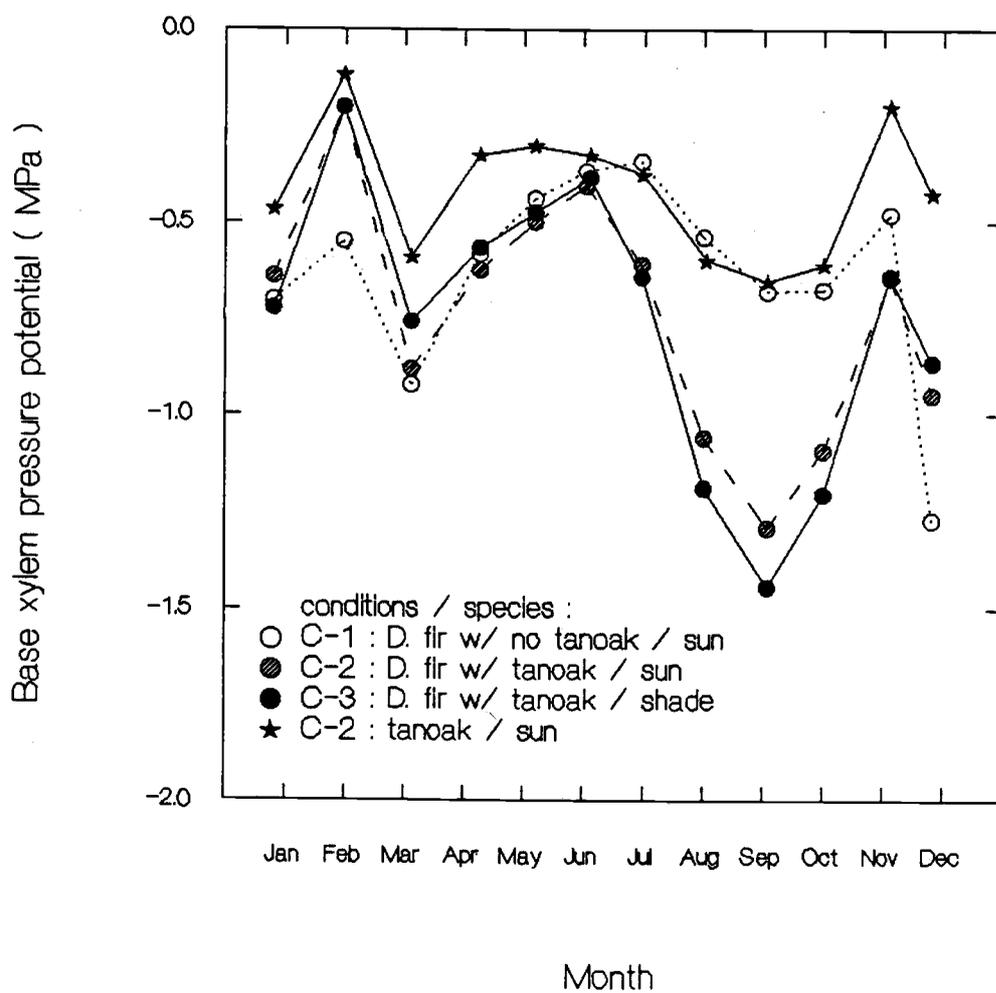


FIGURE III.19. Total determination of base xylem pressure potential by species and cumulative change in soil water potential (SWP) at 30-cm depth.

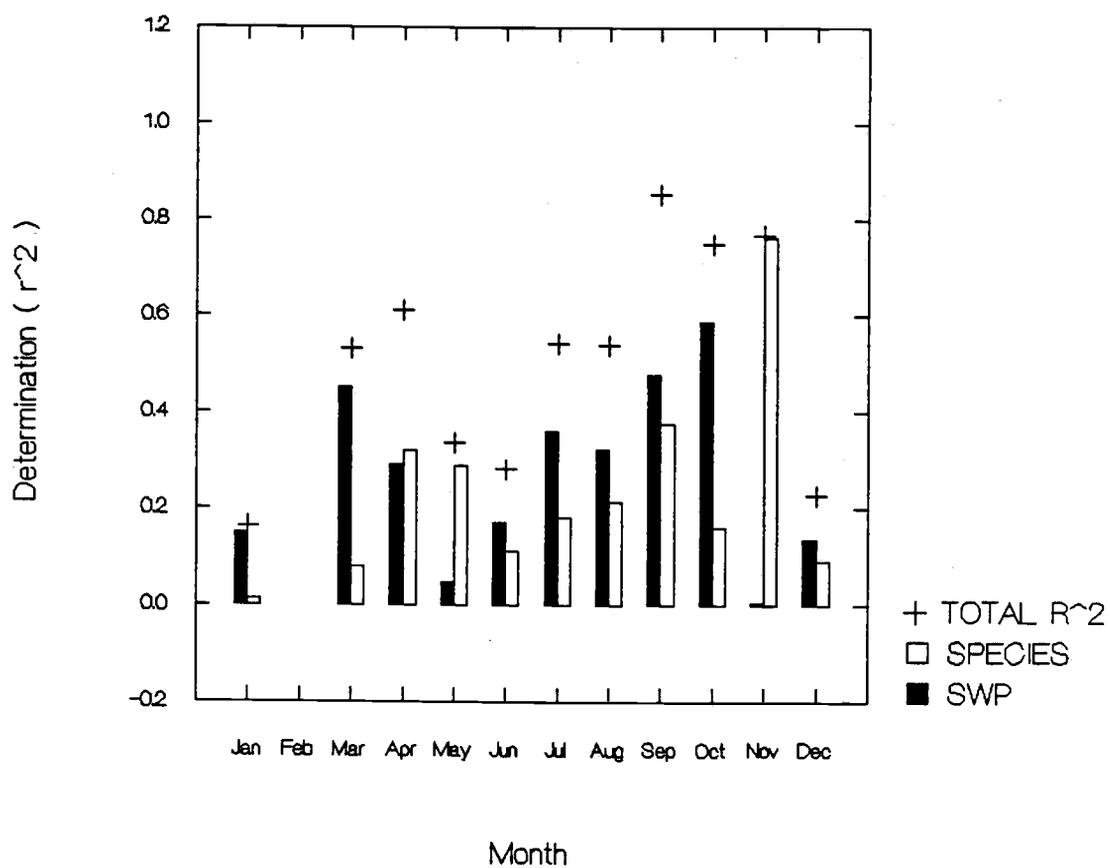


FIGURE III.20. Average morning leaf conductance of trees growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987.

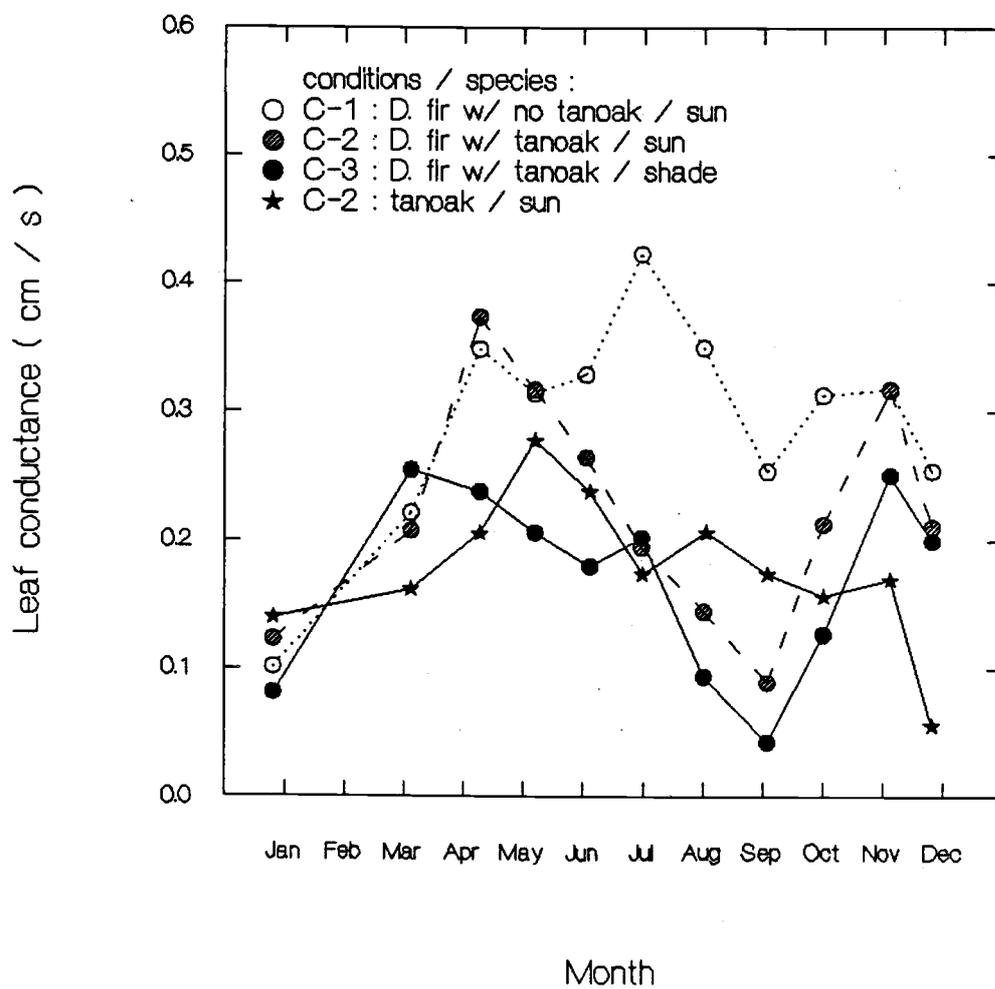


FIGURE III.21. Total determination of morning leaf conductance by species, photosynthetically-active photon flux density (PPFD), base xylem pressure potential (XPP), and relative humidity (RH).

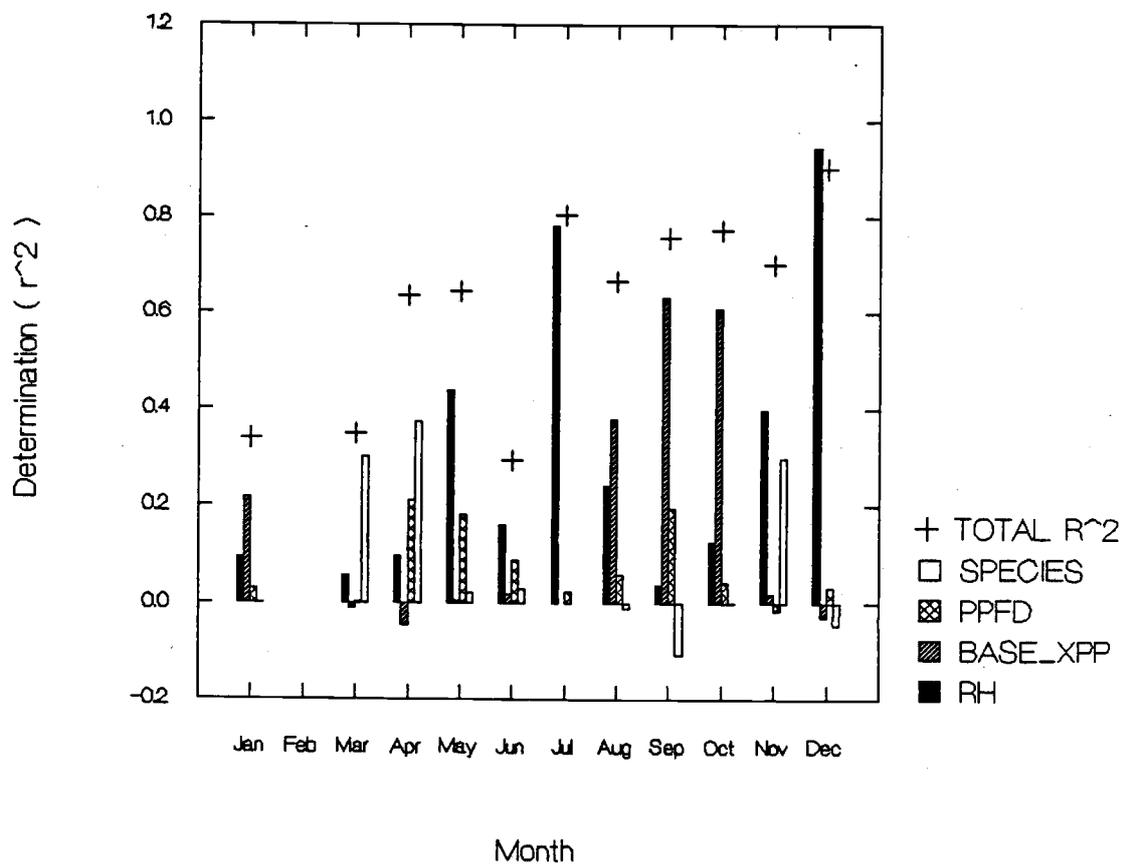


FIGURE III.22. Average afternoon leaf conductance of trees growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987.

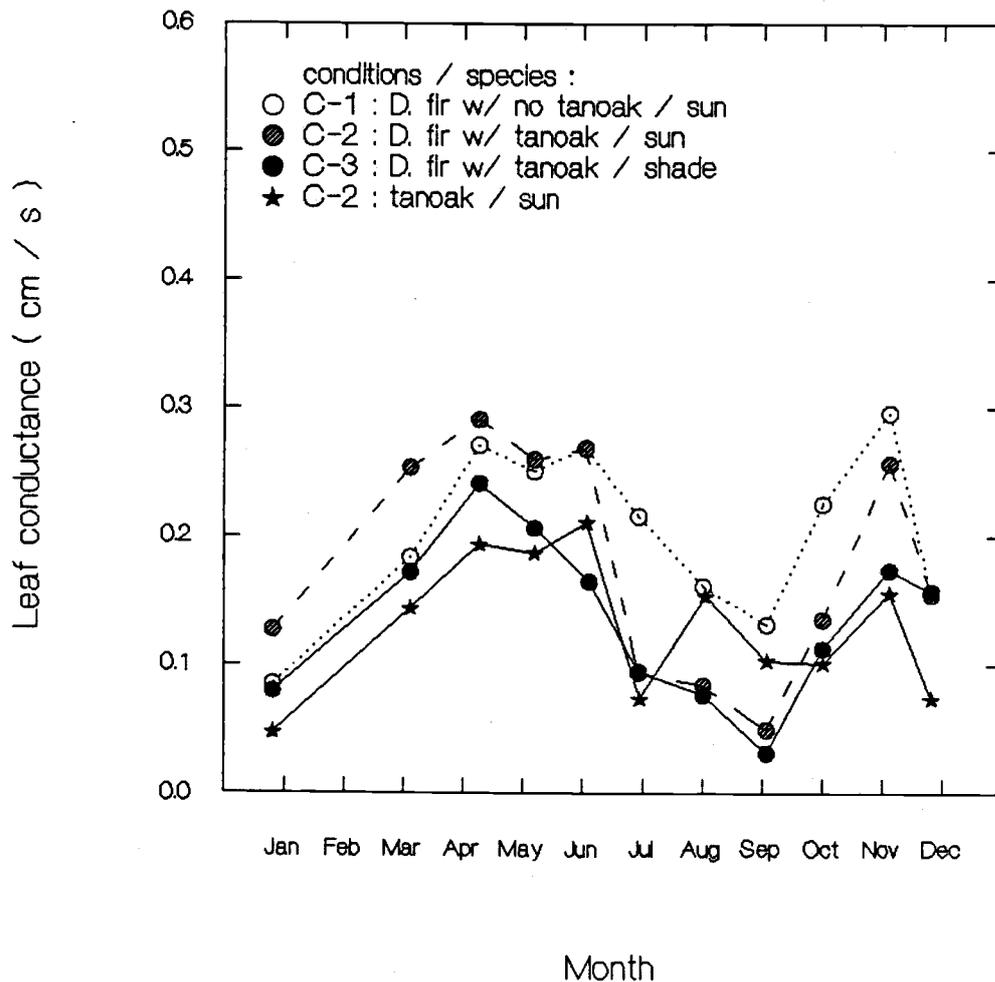


FIGURE III.23. Total determination of afternoon leaf conductance by species, photosynthetically-active photon flux density (PPFD), base xylem pressure potential (XPP), and relative humidity (RH).

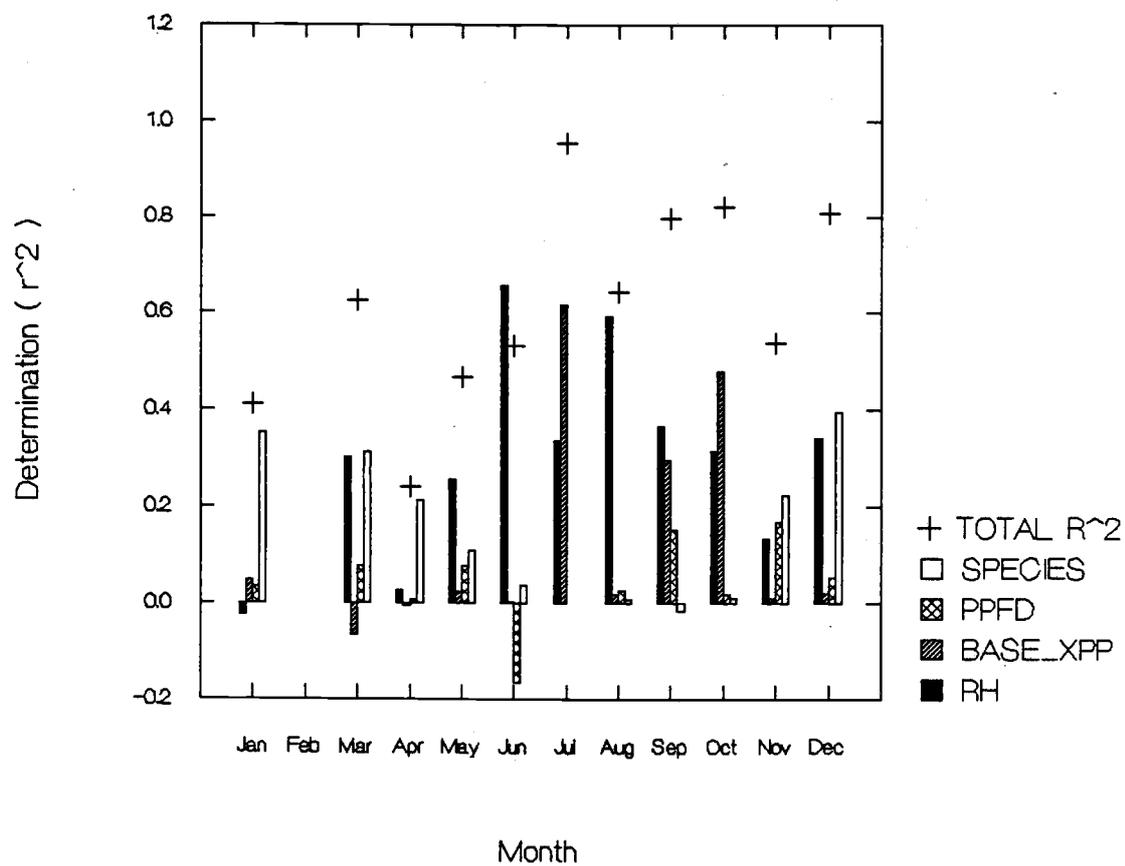


FIGURE III.24. Average morning xylem pressure potential of trees growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987.

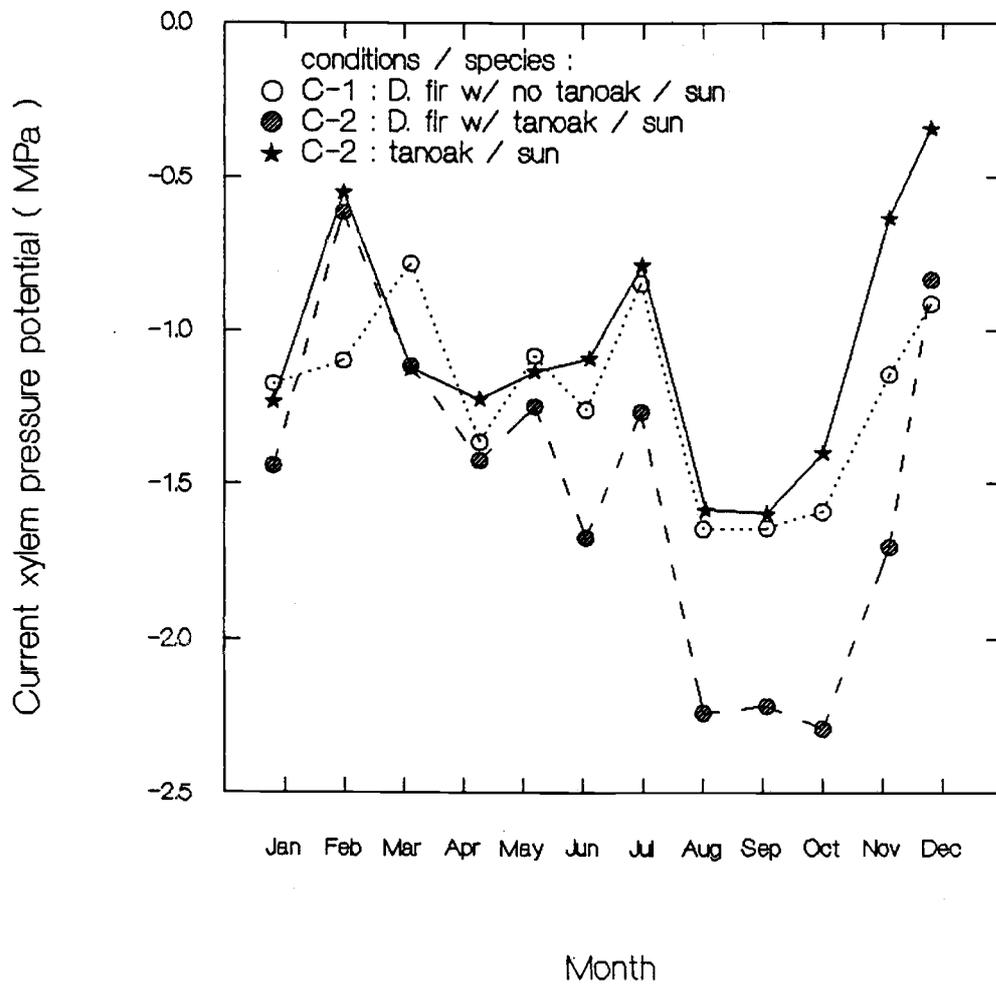


FIGURE III.25. Total determination of morning xylem pressure potential by species, base xylem pressure potential (XPP), and leaf conductance (G).

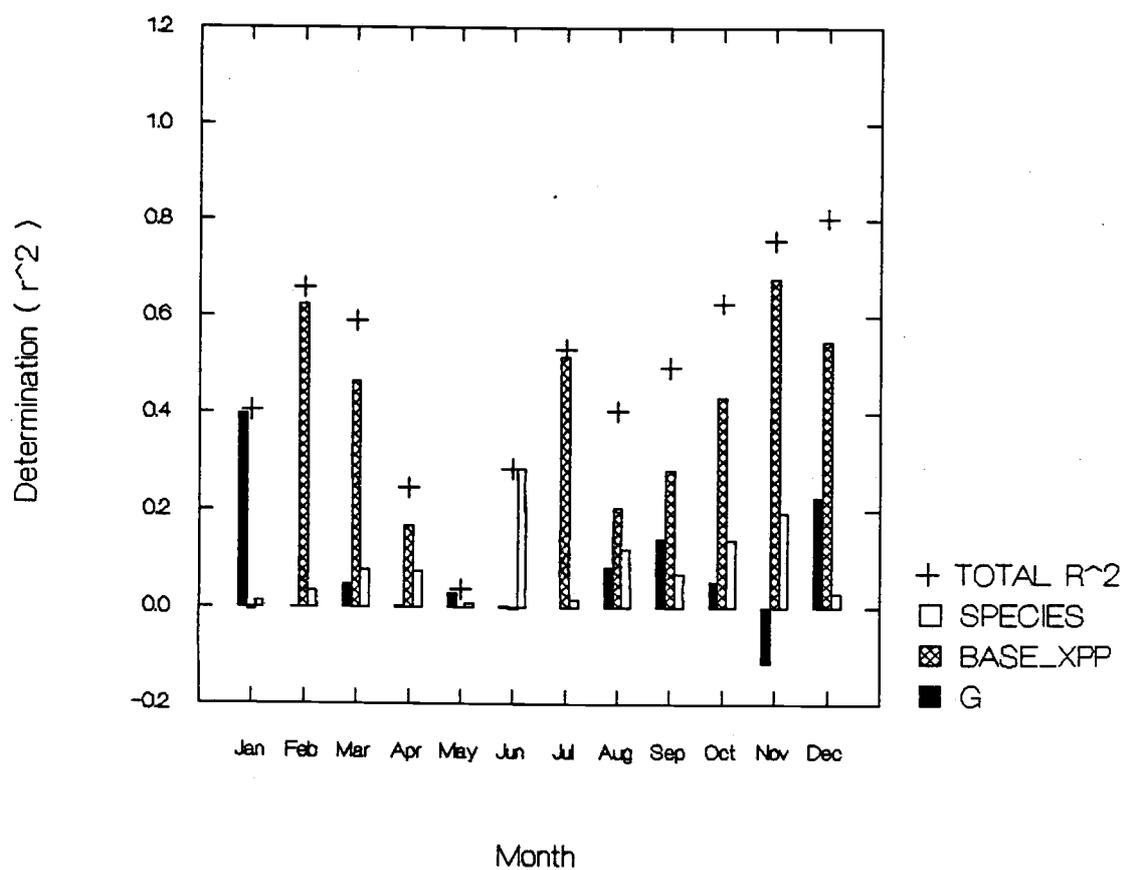


FIGURE III.26. Average afternoon xylem pressure potential of trees growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987.

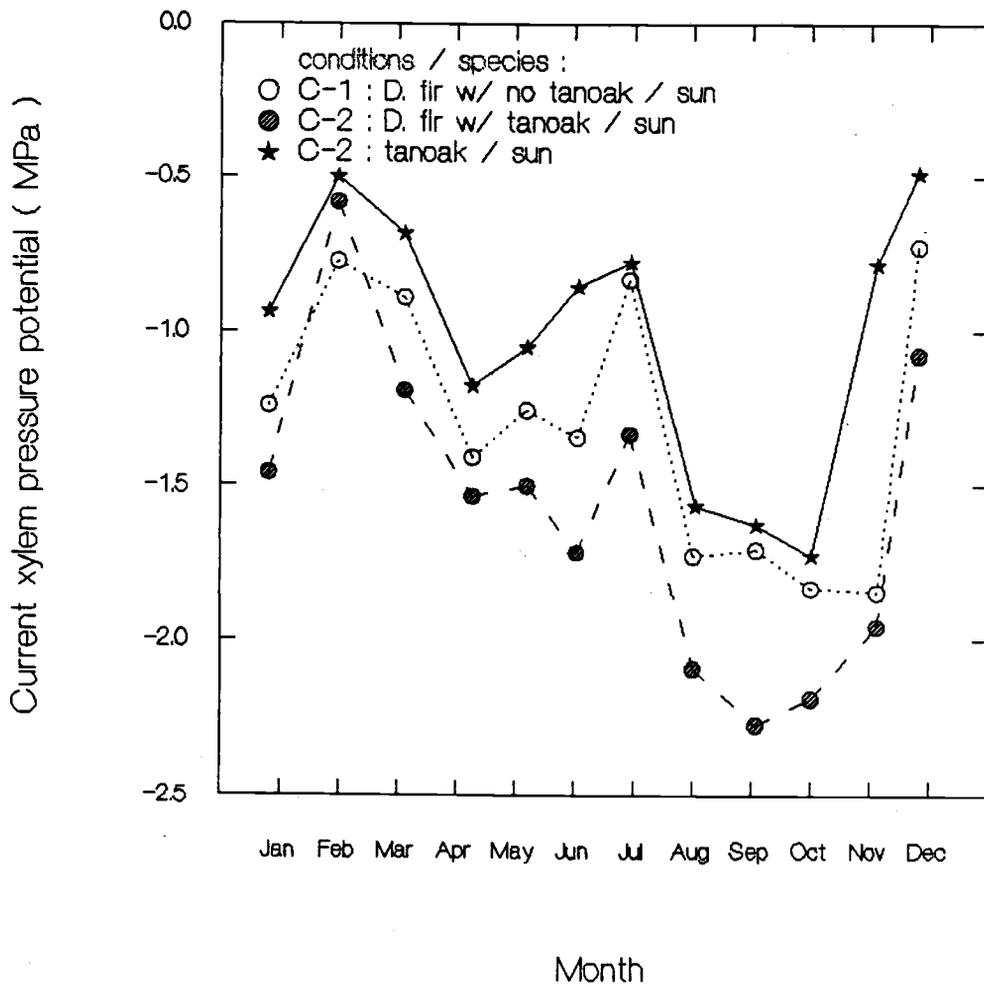


FIGURE III.27. Total determination of afternoon xylem pressure potential by species, base xylem pressure potential (XPP), and leaf conductance (G).

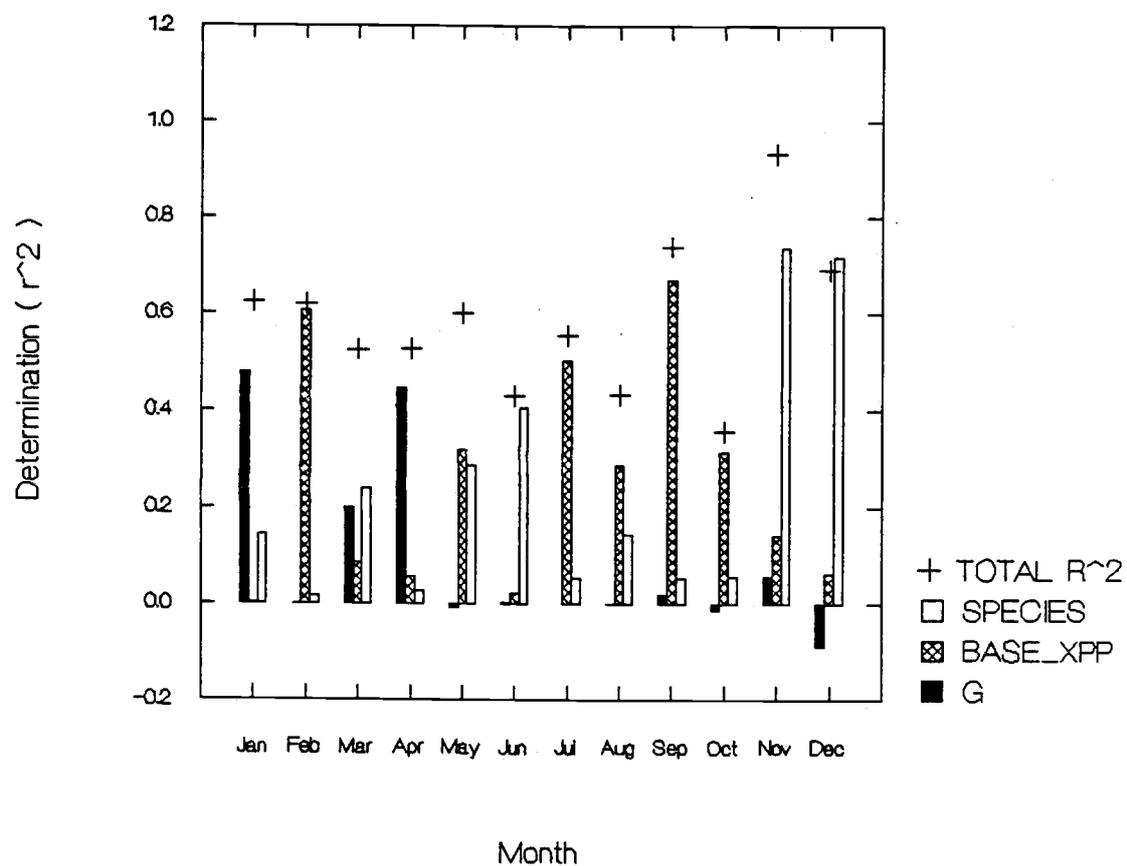


FIGURE III.28. Average morning photosynthesis of trees growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987.

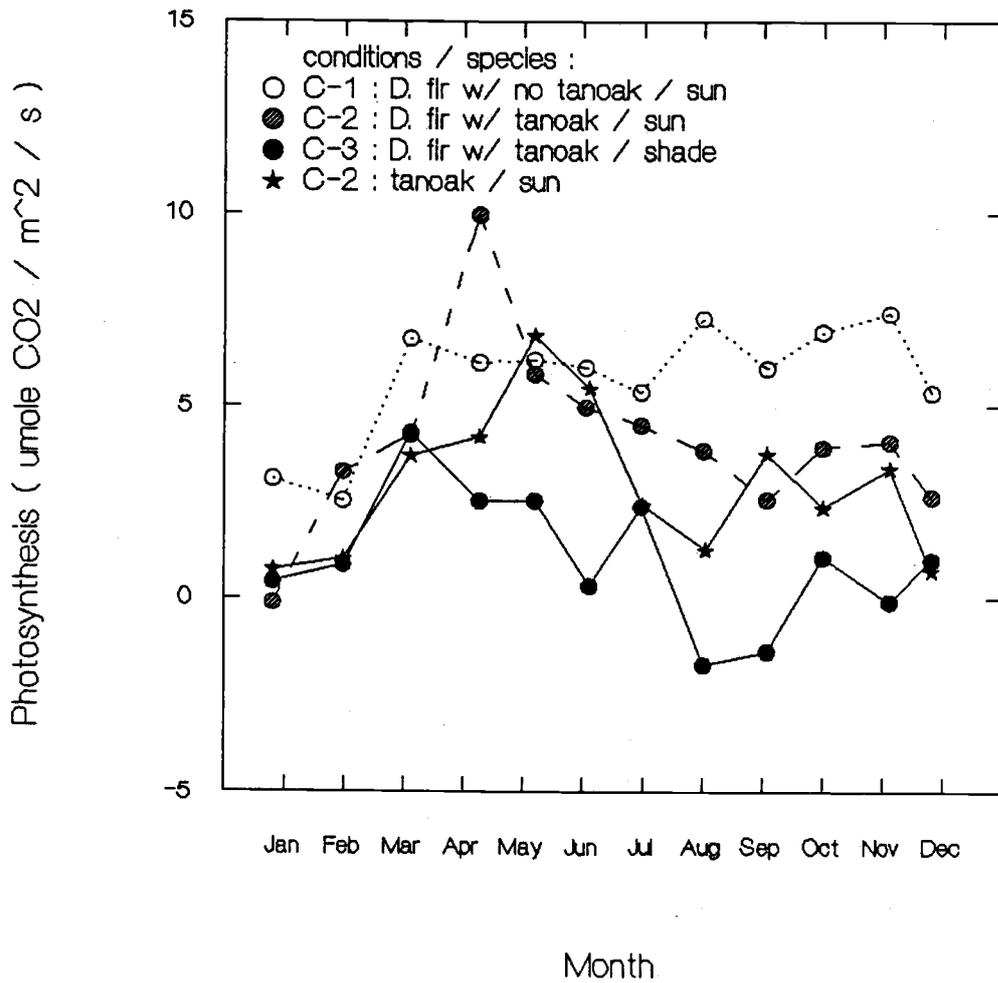


FIGURE III.29. Total determination of morning photosynthesis by species, leaf temperature (T), photosynthetically-active photon flux density (PPFD), and leaf conductance (G).

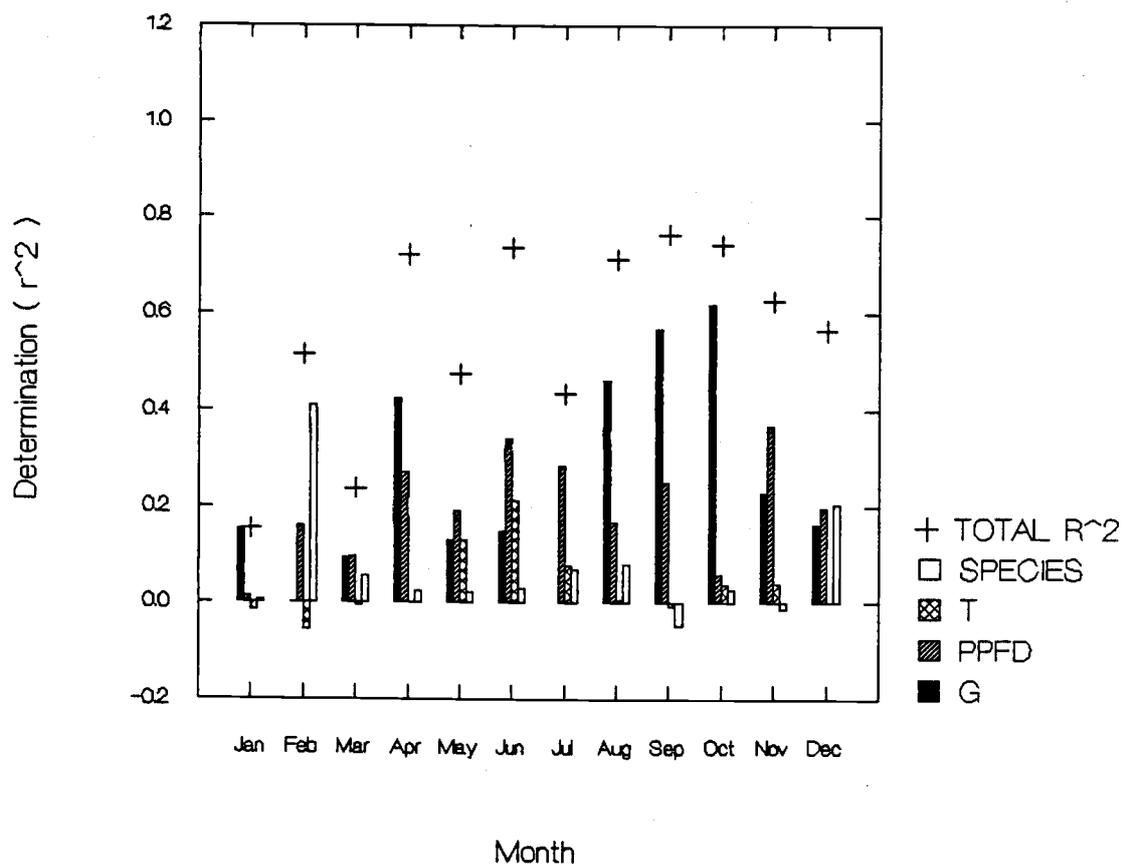


FIGURE III.30. Average afternoon photosynthesis of trees growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 to 9 observations measured in 1986 and 1987.

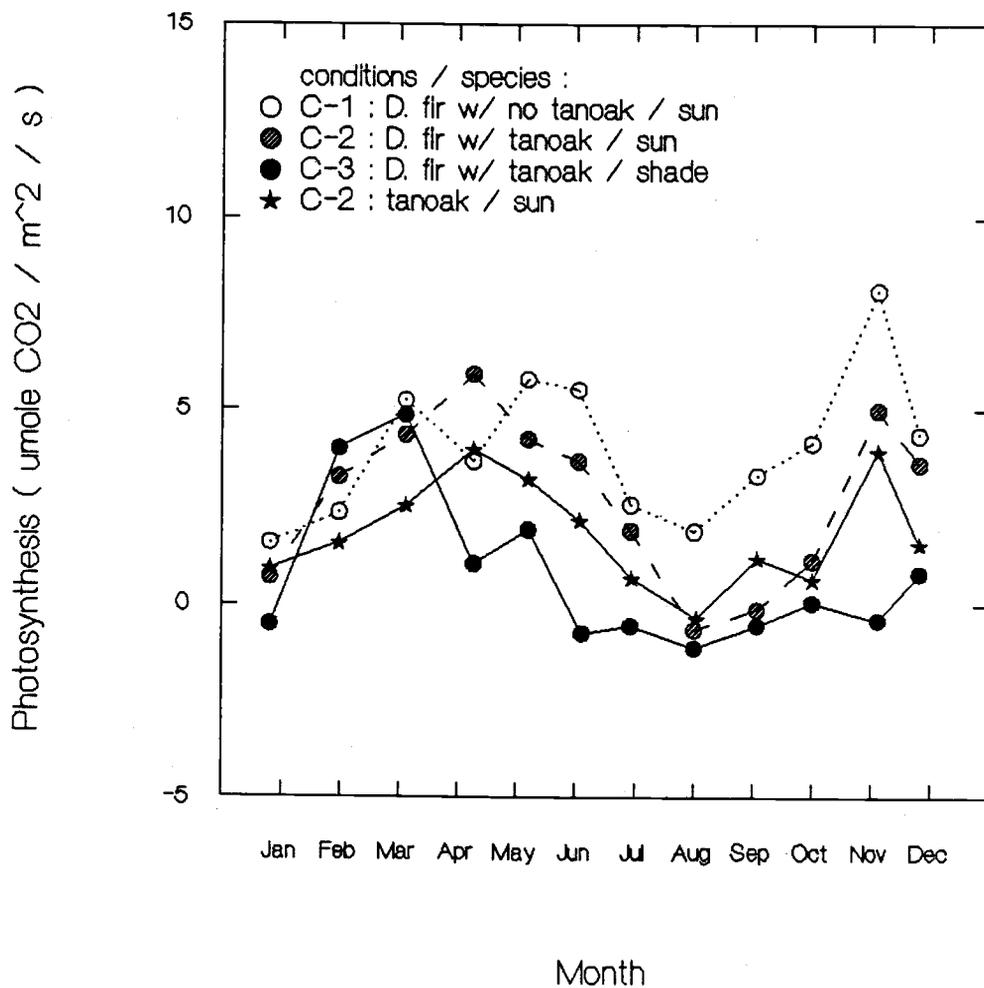


FIGURE III.31. Total determination of afternoon photosynthesis by species, leaf temperature (T), photosynthetically-active photon flux density (PPFD), and leaf conductance (G).

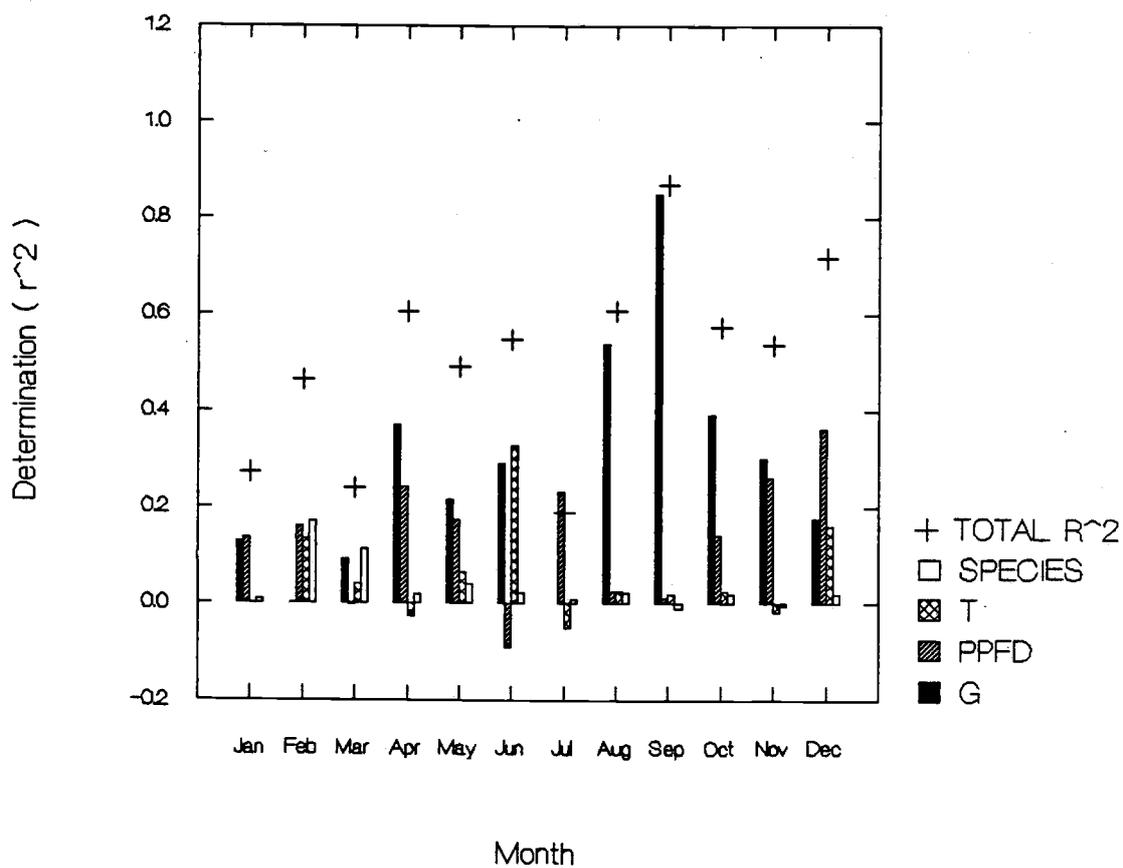


FIGURE III.32. Average basal area relative growth rate for Douglas-fir growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 observations measured in 1987.

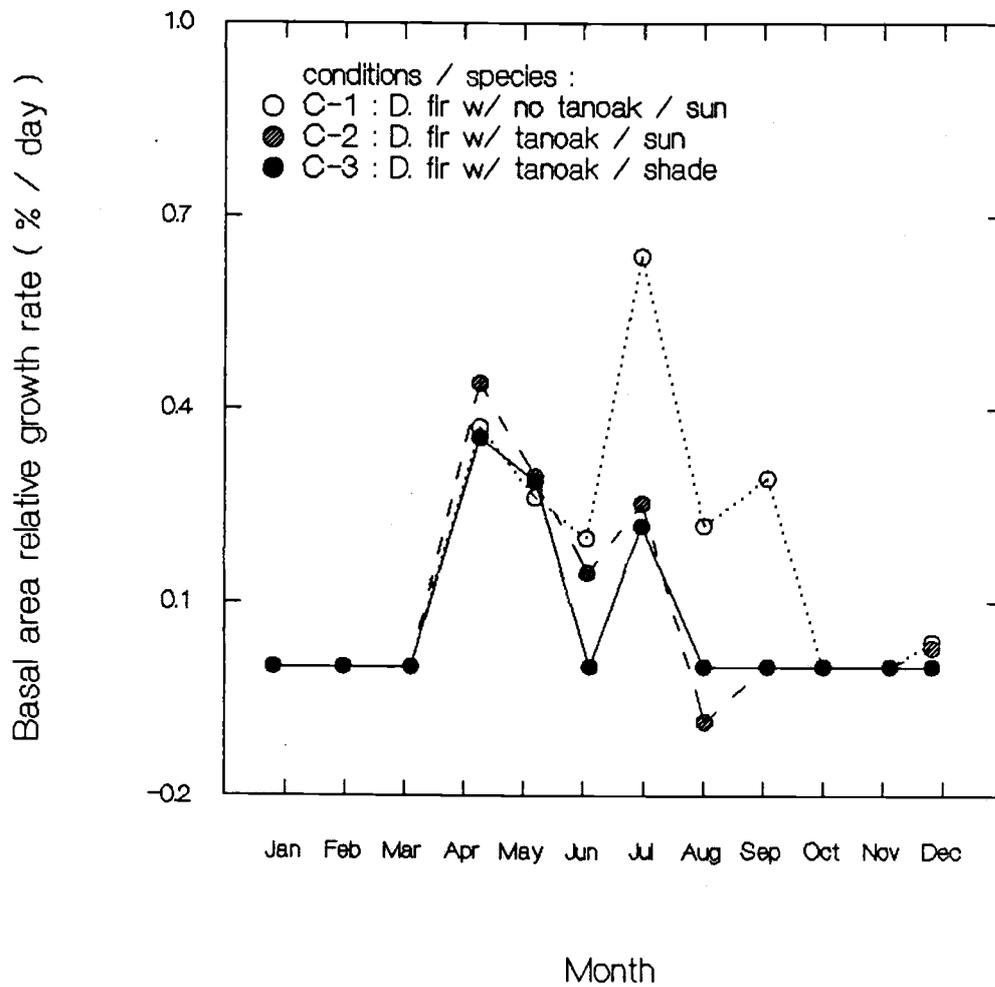


FIGURE III.33. Total determination of basal area relative growth rate for Douglas-fir by cumulative change in soil water potential (SWP) at 30 cm depth.

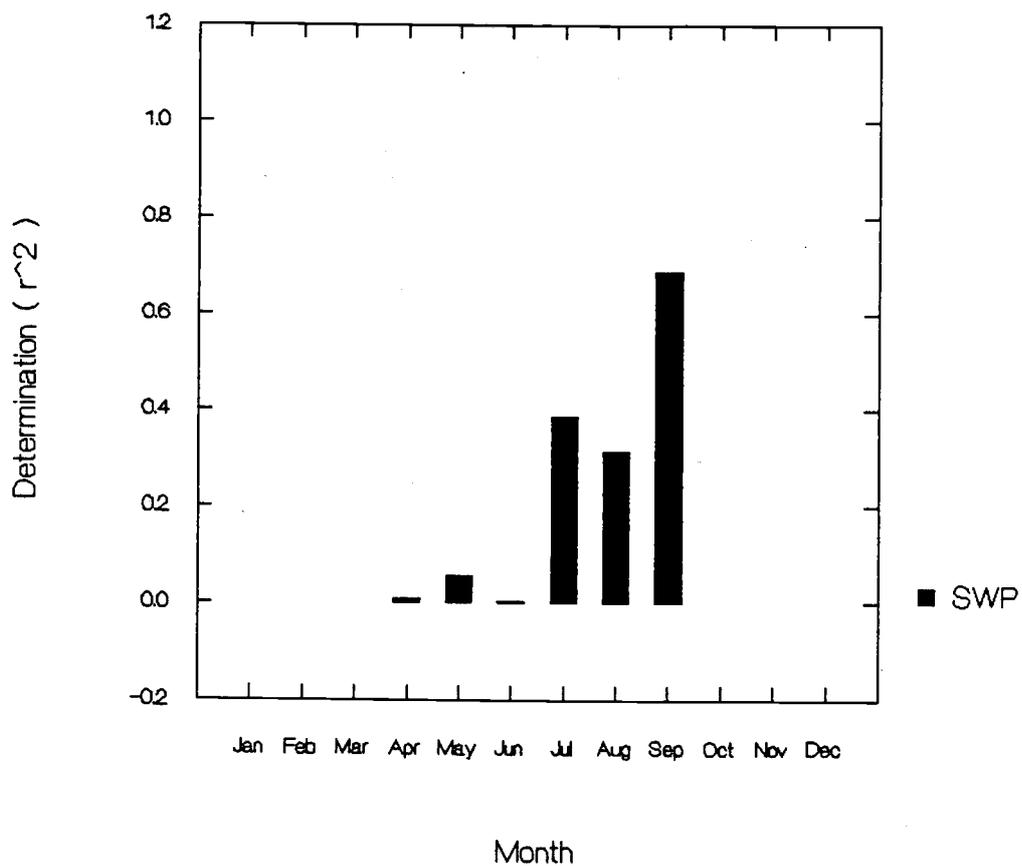


FIGURE III.34. Average height relative growth rate for Douglas-fir growing in the three conditions in young Douglas-fir / tanoak stands. Each point represents the mean of 6 observations measured in 1987.

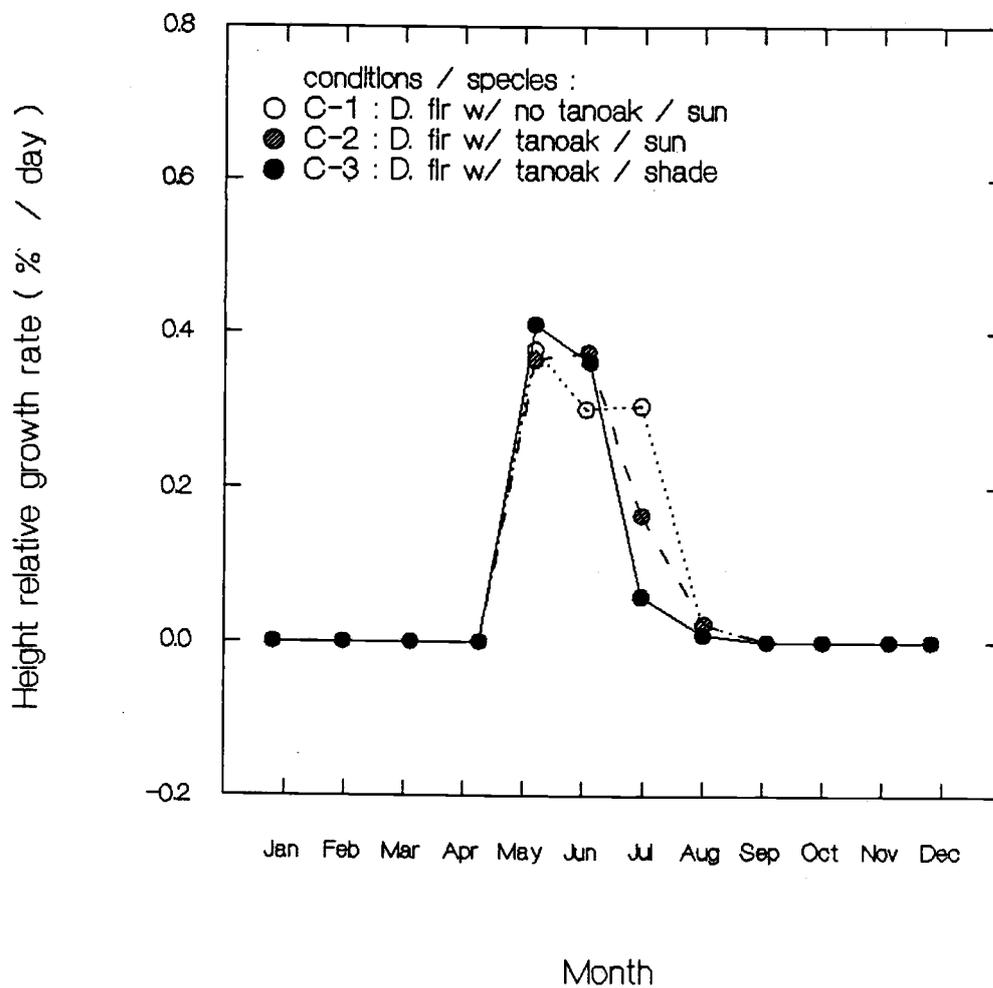
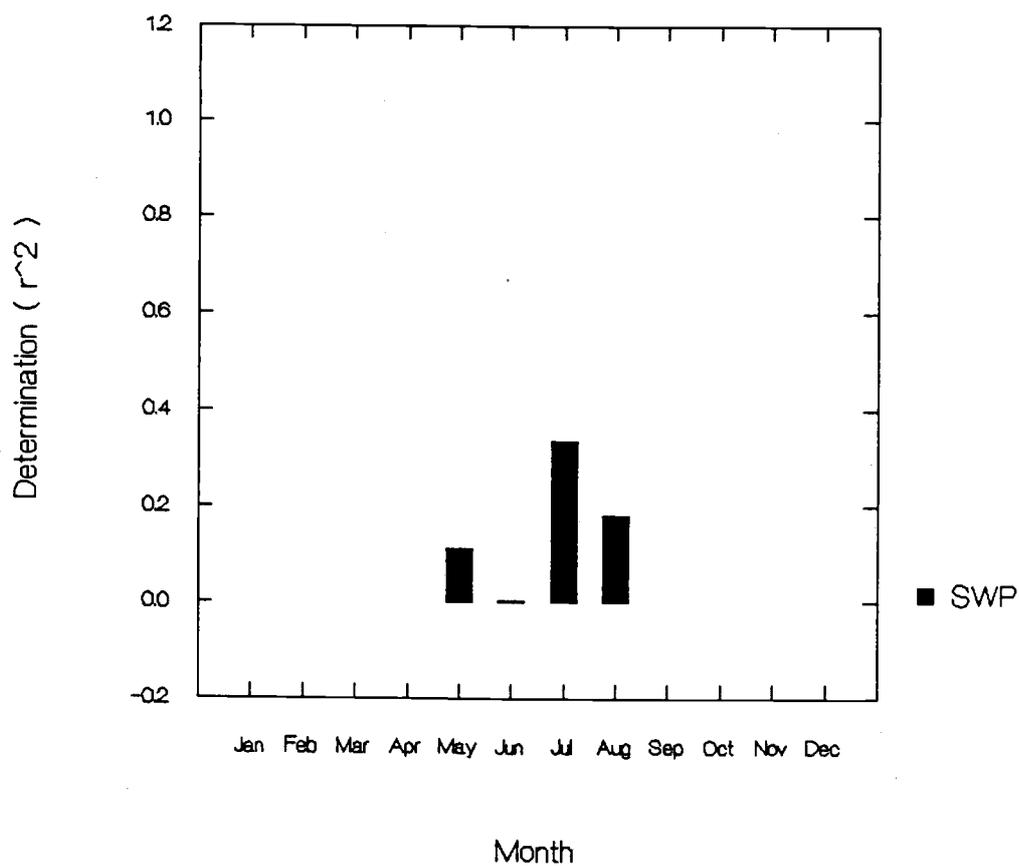


FIGURE III.35. Total determination of height relative growth rate for Douglas-fir by cumulative change in soil water potential (SWP) at 30 cm depth.



CONCLUSIONS

Early stand development of Douglas-fir and tanoak largely was determined by the level of tanoak competition present at an early age (3 years). Initial (1983) tanoak cover had a less-pronounced effect in reducing the steepness of the growth trajectory for Douglas-fir height than for diameter. Presence of shrubs and herbs had an additional limiting influence on Douglas-fir growth trajectories, especially at low or zero levels of tanoak competition, where this vegetation reached its maximum development.

Cover, leaf area, and biomass of shrubs and herbs were described by linear functions of initial (1983) values for these parameters and current-year tanoak cover. Thus, future development of understory vegetation can be predicted early in stand development, and it can be managed through manipulation of tanoak cover.

Inventory data from a pre-harvest tanoak stand were used to predict its post-harvest competitive effects on plantation development of Douglas-fir. Examples of stand projections demonstrated that expected levels of tanoak competition can vary greatly depending on the stocking and size of the pre-harvest stand. If Douglas-fir seedling size and the rate of tanoak cover development were varied through management prescriptions, a range of

outcomes in stand development are possible.

This study identified the following parameters as indicators of competitive stress in Douglas-fir: bud number, bud size, internode number, internode length, and needle length. When expressed in multiplicative combinations, these parameters accounted for over 90% of the variation in the length and biomass of Douglas-fir shoots. Of these indicators, bud number is probably the most indicative of future crown development of Douglas-fir, because it has strong limiting influence on the rate at which growing points are initiated for production of leaf area.

By using the concepts of potential growth and potential growth attainment, it was possible to partition the effects of competition into previous- and current-year influences. Competition limited Douglas-fir shoot growth in a given year by reducing both the number of internodes initiated within buds during the previous year (potential growth) and the expansion of these internodes in the current year (potential growth attainment).

Likewise, basal area growth of Douglas-fir in a given year was limited because competitive effects from previous years resulted in smaller stem circumferences (potential growth), and competitive effects in the current year limited basal area increment per unit circumference

(potential growth attainment).

Current-year competitive effects on Douglas-fir growth were attributed to differences in both the duration of cambial growth and the relative rates of cambial and shoot growth. The fact that duration of shoot growth was not influenced by competition could account for its lower sensitivity in comparison to cambial growth.

Rates of photosynthesis for Douglas-fir were most sensitive to the microclimatic limitations associated with tanoak shade. Of these limitations, reduced light availability from tanoak's evergreen foliage probably had the greatest influence because it represented a year-round limitation in photosynthetic rate.

During the growing season, Douglas-fir growing in tanoak shade encountered additional photosynthetic limitations as result of elevated leaf temperature, reduced relative humidity, and restricted soil water availability. Throughout much of the summer, the compounding influences associated with these photosynthetic limitations caused zero or negative rates of carbon assimilation to occur for shaded trees. Douglas-fir growing in openings within the tanoak stand experienced similar growing-season limitations in photosynthetic rate, with the exception of reduced light availability, however the magnitude of their limitations generally was less than for shaded trees.

In contrast, stand-grown tanoak and Douglas-fir growing without tanoak had much smaller seasonal fluctuations in their rates of photosynthesis. Under these conditions, both species demonstrated minimal levels of water stress, which permitted conductance and photosynthesis to occur with minimal impedance for much of the growing season. The higher soil water availabilities associated with tanoak removal kept water stress levels low for the Douglas-fir growing under these conditions, whereas, tanoak maintained low levels of water stress by restricting its water losses through stomatal control.

When expressed on a whole-tree basis, average rates of photosynthesis varied by over two orders of magnitude. Because tanoak and Douglas-fir growing without tanoak had similar leaf area increments and average rates of photosynthesis, their whole-tree rates were similar. Growing season limitations caused whole-tree rates of photosynthesis for Douglas-fir growing in openings within the tanoak stand to be 4% of that for trees growing without tanoak. Because of the additional suppressive effects of tanoak shade on both leaf area increment and average photosynthetic rate, shaded Douglas-fir had whole-tree rates that were only 0.5% of that for trees growing without tanoak.

Whole-tree rates of photosynthesis have provided a

meaningful synthesis of the research findings from this project, because they accurately represent the compounding effects of tanoak competition as a multiplication of differences in both morphology (leaf area production) and physiology (net assimilation rate) of Douglas-fir.

CONSIDERATIONS FOR FUTURE RESEARCH

- 1) Controlled laboratory study on Douglas-fir seedlings to determine the influence of different levels and combinations of light, water, and temperature on:
 - a) cambial growth and shoot elongation
 - b) initiation of needle primordia
 - c) initiation of interwhorl buds
 - d) photosynthetic capacity
- 2) Repeat 1) (above), but first expose seedlings to a pre-conditioning level of constant environmental regime, then impose gradual changes in combinations and levels of light, water, and temperature.
- 3) Germination and development of shrub species following control of sprouting hardwoods.
- 4) Silvicultural strategy for sites receiving low management inputs: plant extra trees to ensure that enough will survive in tanoak stand openings where they can become crop trees.
- 5) The effect of plant canopy structure and season on air temperature.
- 6) Wintertime photosynthesis of Douglas-fir as affected by time since the last frost.
- 7) Changes in nutrient availability associated with control of sprouting hardwoods.

REFLECTIONS

Entry

Sometime after arrival
You will realize where you are
Amidst forested wonder
Under a sky so real.

Fir Point - a soothing surprise -
Has me thinking
And disagreeing
But nonetheless - completing.

I stood at this point
Where the fir had grown thick
And thought of another great trick:
Return to Squaw after two slow years
See the Mountain and enter.

Upon entry you will dream
Of rich, dank forests
Brimming over with life
Rockery amidst rockery
Music's soul residing.

Remember those years
Keep track of 'yer blues
Add up truth correctly
Wander the slopes
In search of news.

Bring back the sphere
And return it -
Where?...a valley town
Just may not suffice.
Because crystalline livelihood
Enlivens the spice,
Step lightly - but remember
The colors
 when you return.

Squaw Song

The wind is in the trees
The sky has 'yer blues
I can't tell if fall or spring
Has come to spread the news.

Sing a song of a man all alone
With days in the unit
of Squaw.

Temperatures effect:
Recall hot and cold mornings
and afternoons.

Sublime effect?
Could be that it's the realizing
That got me here
Again, at the Squaw site.

Were it the water more important
Then we'd be forgetting
the sun.

Wake up, realize, there's work
to be done.

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