

AN ABSTRACT OF THE THESIS OF

Zhengqi Wang for the degree of Master of Science
in Forest Science presented on March 18, 1991.

Title: Effects of Bedrock Water Availability on
Growth and Ecophysiology of Douglas-fir (*Pseudotsuga*
menziesii) and Pacific Madrone (*Arbutus menziesii*)
Saplings in Southwest Oregon.

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Effects of bedrock water availability on growth and ecophysiology of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and Pacific madrone (*Arbutus menziesii* Pursh) were studied in southwest Oregon in 1990. Bedrock physical features, including bulk density, water holding capacity, and available water capacity, were examined at different depths from 1.0 to 3.0 m. Bulk density increased with an increase of soil/rock depth, whereas water holding capacity and available water capacity decreased with an increase of bulk density, i.e., increase of depth.

The soil/rock water depletion patterns for three treatments, no-, medium-, and high-madrone density, was measured by using a neutron-probe soil water meter from

March to September. The cumulative water used by both Douglas-fir and madrone was calculated. There was no significant difference on total water used from June to September among three treatments. However, species in high madrone density plots depleted more water in June than others, whereas in plots of 10-year-old Douglas-fir only, rock water depletion was the least. Medium madrone densities were depleted to an intermediate degree. Douglas-fir in no-madrone plots did not use the soil/rock water as rapidly as the rate of depletion in high- and medium-madrone density plots.

Root distributions for both madrone and mature Douglas-fir were measured. Madrone roots can penetrate as deep as 3.5 m or even deeper, whereas root systems of old growth Douglas-fir can only penetrate down to 2.0 to 2.5 m in bedrock.

Plant xylem pressure potentials in predawn and midday for both Douglas-fir and madrone were measured from July to September. Madrone had lower plant xylem pressure potentials both in predawn and midday than those of Douglas-fir; these may be adaptive characteristics for madrone in this area.

Growth of 10-year-old Douglas-fir and madrone was monitored in September, 1990, including height and basal diameter. Basal diameter growth of Douglas-fir was

affected by madrone density. Douglas-fir height growth in high madrone density plots was significantly less than those in medium madrone density plots and Douglas-fir only plots.

Effects of Bedrock Water Availability on Growth
and Ecophysiology of Douglas-fir (Pseudotsuga
menziesii) and Pacific Madrone (Arbutus menziesii)
in Southwest Oregon

by

Zhengqi Wang

A THESIS

Submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Master of Science

Completed March 18, 1991

commencement June 1991

ACKNOWLEDGMENT

I would like to express my gratitude to my major professor Dr. M. Newton for his kind assistance to develop experimental procedure, field work, consultant, encouragement, financial support, and countless corrections in this manuscript.

I am indebted to Dr. John Tappeiner II for his critical review of this manuscript. Thanks also to the members of my committee: Dr. Donald Zobel and Dr. Steven Knapp for their very good suggestion and review of this manuscript.

I also thank to Rob Pabst for his frequent assistance, many helpful discussions, and providing many helpful information. Thanks also to Jennifer Nelson and Mike Cloughesy for their successful cooperation for collecting data.

I take this opportunity to thank to professors and students in the Department of Forest Science, Oregon State University for their good suggestion, discussion, and encouragement.

My special thanks to Dr. Marshall English for his kind assistance and encouragement. Special thanks also to an unknown professor for his financial support.

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Effects of Bedrock Water Availability on Growth and Ecophysiology of Douglas-fir (*Pseudotsuga menziesii*) and Pacific Madrone (*Arbutus menziesii*) Saplings in Southwest Oregon

INTRODUCTION

Southwest Oregon is an area of seasonally dry climate and shallow soils where competition for water defines the survival and growth of forest vegetation. This area is occupied by conifer forests with a strong mixture of sclerophyllous hardwoods and shrubs that has become more prominent after harvest of conifers. Extensive research is currently being conducted to quantify the physical and biotic environment for reforestation on the million ha of commercial forests in southwest Oregon. This effort was stimulated by a history of reforestation failures which are generally assumed to be due to heat or drought stress (Helgerson and Tesch, 1982). The Mediterranean climate of the region has high summer evapotranspiration demands and there is little water available other than that of soil storage (Flint and Childs, 1984). The Mediterranean climate requires that reforestation efforts be accomplished under the influence of hot, dry summers. Reforestation is further complicated by shallowness and rockiness of soils, transpirational water losses through seedling or sprouting brush, and by herbaceous vegetation (Helgerson and Tesch,

1982; White, 1987). Water, therefore, is the resource most limiting for conifers.

Seedling survival and growth depend on resources such as water, light and nutrients. Most resources are not unrestricted, and plants compete to get them. The species able to preempt the most resources in the long run will dominate a site. This dominance can be of long or short term, but in either event will affect the growth of other species. Newton's (1973) discussion of dominance demonstrated that the time of arrival, early growth, and economy of water use in droughty areas are very important in determining the species composition of seral vegetation.

Pacific madrone (Arbutus menziesii Pursh) is a common evergreen hardwood in the mixed conifer-hardwood forests of southwest Oregon and northern California. The harvesting and site preparation practices common in the area 15-30 years ago removed conifers and left madrone and other hardwoods and shrubs dominant (Tappeiner et al., 1986). Stump sprouts and seedlings have formed many well-stocked madrone stands. Many of these stands are being clearcut, slashed, and burned as site preparation before being planted with conifers. However, madrone sprouts vigorously after cutting and/or burning and is adapted to a cycle of frequent disturbance (McDonald, 1978). Rapidly

forming crowns of madrone sprouts affect the growth of conifers by competing for site resources, especially water, in this droughty area.

White et al. (1987) observed that most sclerophyll stands are found on shallow soils with total water storage capacities less than 10 cm between 0 and - 2 MPa water potential, and that shrubs continue to transpire long after June, when extractable soil water was exhausted. The question here is, from where do the woody plants get water? Newton et al. (1988) hypothesized that they may get water from bedrock, and verified that plants of various types depleted more or less of the bedrock water down to 150 cm.

The general hypothesis of this thesis is that bedrock provides a major reservoir of water beneath the soil that is available to plants. In order to improve our understanding of quantity and accessibility of rock-held water, this thesis poses these questions: (1) how much water can bedrock hold; (2) how much is available for plants; (3) why are some species more successful in extracting water from sources other than soil; and (4) what is the effect of bedrock water on the growth of conifers and madrone competing for water? Answers to these questions will lead to validation or rejection of the general hypothesis. They will also provide some guidance for

how to inventory and benefit from water held in bedrock.

LITERATURE REVIEW

Success in re-establishing conifers in the sclerophyll communities now occupying commercial forest sites will depend on sound knowledge and management of the soil water resource until conifers are dominant. Establishment of the bedrock as an additional reservoir will add greatly to the resources subject to manipulation. Recent studies (Newton et al., 1988) have stated that the rock probably plays an important role in primary production and competition interaction not only in southwestern Oregon, but also in the much larger area of California supporting sclerophyll vegetation.

Woody plants cannot grow actively during periods of water stress below -2.0 MPa (Brix, 1979). To avoid shutdown during the long, hot summer, they must either conserve water through stomatal closure (Scott and Geddes, 1979), adapt to extreme water deficit (White, 1987; Ortiz-Funez, 1989, unpublished data, Oregon State University), or penetrate and utilize deep sources of stored water. Where soils are shallow, water held in the soil proper may furnish only a minor fraction of the summer water deficit. In this situation, the growing season is effectively limited by the available stored water supply in combination

with the rate of transpirational loss (Newton, 1965). The ability of roots to augment the apparent water supply by penetrating bedrock and extracting water therefrom would increase the effective length of growing season. White (unpublished data, Oregon State University, 1986) noted that several shrub species continue to transpire rapidly after the available water in shallow, low water-holding capacity soil has been depleted. The above hypothesis has as its logical extension that the ultimate competition for water occurs in the deeper layers of the rock. However, few studies have specifically been designed to widen our understanding about the moisture stored in the rocks and its role in plant growth.

In most soil analyses it is conventional to consider only that part of the mineral soil that will pass a 2 mm sieve. Material larger than 2 mm in diameter is called "gravel" or "stone". The amount of gravel, or stone, when present in appreciable quantities, is often expressed as a percentage of the total amount of soil (< 2 mm and >2 mm) combined. The availability of water in rock is often, but not always (McNabb, 1989), considered negligible. This water, however, may play an important role in the water relations. Few articles concerning the water content of coarse fragments can be found in the literature.

There is some evidence indicating that woody species are able to utilize rock-held water with some efficiency. Previous studies have shown that rock fragments can hold substantial quantities of water which are available to plants (Coile, 1953; Hanson and Blevins, 1979).

Coile (1953) sampled each horizon of five representative soil series of the Piedmont region and plotted the moisture content of the 2 to 12.7 mm coarse fragments against the field moisture content of the total sample. Water content of the coarse fragments ranged from 10 to > 15% as compared with corresponding bulk sample water contents of 16 to 33%. From experiments in which oat plants were used to reduce the moisture content of soil and presaturated coarse fragment wilting percentage, Coile (1953) concluded that coarse fragments did contain available water, although the amounts varied with the size and type of coarse fragments.

Newton (1989) stated that "Flint and Childs (1984) have found that coarse fragments in soils may retain two-thirds the amount of extractable water of a comparable volume of clay loam soil. McNabb (1989) and DeLucia et al. (1988) have also reported that rocks have some water holding value but less than that of the displaced soil. Newton et al. (1988) have demonstrated that whiteleaf manzanita (Arctostaphylos viscida Parry) and ponderosa pine

(Pinus ponderosa L.) have the ability to extract more water from bedrock of metasedimentary origin where Douglas-fir appears unable to do so. They subsequently observed that the roots were extracting more water from rocks than from soil. By using diffusion porometry, they found that trees and evergreen shrubs growing on shallow soils with total extractable water storage capacities of 7 - 10 cm in 45 - 75 cm of soil water were still transpiring rapidly during the post-June summer drought when extractable soil water in the 0 - 75 cm zone was below -2.0 MPa.

DeLucia and others (1988) studied the water relations on hydrothermally altered rock (Serpentine) and its capacity to sustain Sierran conifers in the desert soils of the Great Basin in western Nevada. Although the authors neither measured the water content in the rock, nor tried to explain how the absorption process is carried out, they did focus on the reliance of conifer species on the moisture contained in the rocks for keeping their physiological processes working. Other workers have reported that Artemesia tridentata Nutt. maintains high conductance values and growth rates at very low soil water potentials and can strongly deplete soil water to a depth of 2 m in deep soils (Campbell and Harris 1977, Sturges 1977, Black and Mack 1986). The ability of shrubs to

maintain high conductances at low soil water potential would lead to depletion of water in the rooting zone of soils derived from unaltered rock (DeLucia et al., 1988). This would provide an adaptive advantage to such species.

Depth of rooting is both genetically and environmentally modified (Taylor and Klepper, 1978) and similar-sized trees may extend their root systems to different depths at the same site (Rutter, 1968).

Newton et al. (1988) noted that ponderosa pine, Douglas-fir, and whiteleaf manzanita under several competition levels showed differential moisture depletion patterns in the saprolyte and slightly weathered bedrocks. Conifer species have shown promising growth responses to shrub management on these extreme sites, especially ponderosa pine. One preliminary explanation is that pine and manzanita are able to absorb water from a large supply held by the rocks, and that manzanita control provides a longer growing season for the pine. Waring and Cleary (1967) emphasized the importance of rooting by demonstrating that in a 25 m tall Douglas-fir tree water potential fell to -2.0 MPa at midday, whereas a 1 m tall tree had a less extensive root system and storage volume, hence its water potential fell more rapidly. This implies a special importance of the bedrock reservoir when trees

have little storage volume in stems.

The morphology and growth rates of root systems differ considerably among plant species, and these differences may relate to the successful exploitation of any particular environment. However, there have been few quantitative studies showing that these differences in rooting are quantitatively important either for competition between plant species or for allowing one genotype to grow better than another at a specific location (Gregory, 1987).

This study focused on the effects of water availability in rock on the growth and ecophysiology of Douglas-fir and Pacific madrone, and their competition for water under different treatments in southwest Oregon. The specific objectives of the study are:

1. To describe the distribution and penetration of root systems of Douglas-fir and Pacific madrone in rocks.
2. To determine soil/rock physical properties in terms of water holding capacity, bulk density, water availability, and seasonal depletion pattern of soil/rock water.
3. To determine the effect of rock water availability on growth and ecophysiology of Douglas-fir and Pacific madrone in terms of basal diameter, height, leaf area index, and plant xylem pressure potential.

MATERIALS AND METHODS

SITE DESCRIPTION

Southwest Oregon is an area of seasonally dry climate and shallow soils where competition for water defines the survival and growth of forest vegetation. The study site occupies about 2 ha at an elevation of 720 m in the Klamath Mountains of southwest Oregon, about 10 km southwest of Canyonville (42.5 ° N, 123.2 ° W). Slopes face southwest to west and range from 15 - 60%. Winters are typically cool and wet; summers, warm and dry. Annual precipitation averages about 108 cm (Froehlich et al., 1982), but only 12% (about 13 cm) normally occurs from May through September (McNabb et al., 1982). High summer temperatures are normally in the vicinity of 35 ° C with a maximum of more than 40 ° C in July (Froehlich et al., 1982, White, 1987, and Tappeiner et al., 1986). This climate places critical demands on stored water, making it a limiting resource for plant survival and growth (Waring, 1969). Soils are generally shallow (25-50 cm), gravely loams or clay loams of the Vermisa and Beekman series (Bureau of Land Management, 1977) in this site. Parent material is slightly metamorphosed sandstone, siltstone,

and shale (Bureau of Land Management, 1977). Because these soils are shallow, high in coarse fragments and low in organic matter, they have low water-holding capacity. Water content of fine soil (< 2 mm: silt, sand, clay fraction) averaged 12.2% at -0.5 MPa and 7.2% at -1.5 MPa (permanent wilting point) (Soil Testing Laboratory, Oregon State University). Volumetric rock content (> 2 mm) ranged from 16-53% and averaged 26%. The average site index₁₀₀ of 200-year-old Douglas-fir in the stand adjacent eastern to the study area is 30.5 m (McArdle et al., 1961).

The site previously supported a mixed stand of Pacific madrone, Douglas-fir, sugar pine (Pinus lambertiana Dougl.), and canyon live oak (Quercus chrysolepis Liebm.). Following harvest in 1953, a stand of madrone sprouts and seedlings dominated the site. In early spring 1979, the madrone was slashed and burned to prepare the site for operational planting with 2-0 Douglas-fir stock at a spacing of about 2.5 x 2.5 m in September. Besides the madrone sprout clumps, woody species in the understory shrubs layer include poison oak (Rhus diversiloba Torr. and Gray), ocean-spray [Holodiscus discolor (Pursh) Maxim.], deerbrush (Ceanothus integerrimus Hook and Arn.), and canyon live oak. Grasses (Festuca myuros L. and Aira caryophyllea L.) and whipplevine (Whipplea

modesta Torr.) are important components of the herbaceous understory. Pabst et al. (1990) and Hughes et al. (1990) recently described the cover and its competitive status on the site.

STUDY DESIGN AND INSTALLATION

This work is superimposed on a 10-year-old experiment with Douglas-fir and madrone in various competitive relationships. A randomized, complete block design is being used in which each of these blocks has received eight treatments, each on a 0.04 ha plot. In 1982, four density levels of madrone were installed, two plots per level, in each block: high (H) averaged 2.7 x 2.7 m spacing; medium (M) was at 5.5 x 5.5 m spacing; low (L) had 7.9 x 7.9 m spacing; and complete removal (N) was essentially free of madrone. All spacings are approximately equidistant. All plots were originally well stocked with sprout clumps, and differences in density were created by chemical removal of excess clumps in 1982, at age 3, with follow-up maintenance in 1983. One of two plots at each density was chemically treated in 1982 (third growing season) to remove shrubs and herbs. Thus, there was a factorial design with four levels of madrone with and without herbs. This study utilized a

subset of that design in which the full range of competitive conditions could be observed at the bedrock level. Time sequence and details of treatment follow.

In 1979, the managed plant community began its current development after madrone was slashed and burned, and the 2-0 Douglas-fir seedlings from local seed source were planted with spacing of 2.5 x 2.5 m in spring, 1980. Madrone spacing was achieved by marking sprout clumps to be left and then treating the bases of all unmarked clumps with a 3% solution of 2,4-D in diesel applied from a backpack sprayer. To assess the effects of madrone relative to other vegetation on conifer seedling growth, understory shrubs, forbs, and grasses were treated in one plot per madrone density per block with a 2% solution of Roundup, a glyphosate product, in water, applied from a backpack sprayer. Thus, for each madrone density, the herb/shrub understory was treated on half the plots (T) and not treated on the other half (NT). To maintain control of the understory without further herbicide maintenance, a porous 2 x 2 m polyester fiber mat (Terra Enterprises, Inc., P.O. Box 9485, Moscow, ID 83843) was placed on the soil surface around the 15 Douglas-fir randomly selected per plot as sample seedlings. The mats effectively removed most vegetation beneath them.

ROCK PHYSICAL FEATURE MEASUREMENTS

On the site, neutron probe access tubes were installed with a pneumatic drill to a depth of 180 cm for use with a neutron-probe, soil water meter (Troxler, Model 3225) in each of three of the vegetation treatments (medium-, high-, and no-madrone density, respectively) in both blocks, for a total of 20 deep tubes. Over 70 neutron probe access tubes are in place, mostly limited in depth to the top of the bedrock layer, revealing that soil depth is consistently 24 - 55 cm, and uniform in texture and color. Deep access tubes are readable to 150 cm, of which the part below 55 cm is bedrock with an estimated < 1-5% fine material, decreasing with depth. Measurements of water depletion were made at depths of 30, 60, 90, 120, and 150 cm.

Description of the total soil/rock profile required the blasting of bedrock. Two pits were created to depths of 3 and 3.5 m. For each, vertical drill holes were spaced 50 cm apart to 180 cm depths to create a wall, and additional holes drilled at 2 per m² to loosen up rock to provide access to the profile. Each hole was charged with 2 - 200 g sticks of medium-velocity dynamite. All were detonated simultaneously. Rubble and soil were shoveled out by hand after which 180 cm holes were drilled in the bottom and the

hole blasted to full depth.

Specimens of rocks were removed from the profile headwalls at 50 cm intervals from surface to the bottom of the profile. These were used to determine bulk density and water holding capacity by using gravimetric methods (Flint and Childs, 1984 a and b). For measuring bulk density and water holding capacity, we put the rock sample into water under vacuuming condition (29") in three 10 min. cycles, and then recorded the saturated weight. After that, saturated samples were put in a tared beaker containing water without touching the bottom. The change of the recorded weight was expressed as volume of water. Bulk density and water holding capacity were calculated by following formulas:

$$BD = DW \times VOL^{-1}$$

Where: BD is the bulk density (g/cm^3), DW is dry weight (g), and Vol. is volume of rock (cm^3).

$$WHC = (SW - DW) \times VOL^{-1} \times 100$$

Where: WHC is the water holding capacity (g/cm^3) in percent by volume, SW is saturated weight (g) of rock samples, DW is the dry weight of rock samples, and VOL. is the volume of rock samples (cm^3).

Water availability was measured with a pressure plate and membrane. The water content of rock between -0.03 MPa (field water capacity) and -1.5 MPa (wilt point) was measured as available water for woody plants. The measurement was conducted in the Soil Physics Laboratory of the Soil Science Department at Oregon State University. The samples from different depths were sliced to about 2 cm and ground to a precise plane on the contact surface thickness so that the water would have equal distance of extraction movement to reach the membrane or plate. Five pressure levels (-0.01 , -0.03 , -0.1 , -0.5 , and -1.5 MPa) were used for measuring water availability. The measurements below -0.5 MPa were conducted with a pressure plate and higher pressure with the membrane.

Water availability was also measured in a greenhouse by using a simple bioassay method developed under guidance of Dr. Newton: saturated and weighed rock samples from different layers (1.0, 1.5, 2.0, 2.5, and 3.0 m) were embedded in pots of greenhouse soil, respectively, which had been pre-mixed with fertilizer. Grasses were sown in each pot so as to make a dense stand. After that, the pots were watered, and when grasses grew to about 30 cm, watering was stopped. As grasses approached the wilting point, the rocks were removed from soil, brushed off and weighed. Available water capacity was determined as following

equation:

$$AWC = (W1 - W2)/VOL$$

Where: AWC is available water content(g/cm³), W1 is the sample weight (g) at -0.03 bar, W2 is the sample weight (g) at -15 bars, and VOL is volume of sample (cm³).

ROOT MEASUREMENTS IN BEDROCK

The two soil/rock profiles were excavated to 3.0 to 3.5 m deep. The profiles were excavated with rock drilling equipment and low - velocity dynamite (Helix or torex water - gel) to reduce physical damage to rock under observation and the roots within it. The rocks were shoveled out , and all loosened or scattered rocks were removed from a vertical wall. The profiles were dug where only Douglas-fir or madrone grow so that their root systems can be identified.

Effective rooting depth was based on the presence or absence of roots and mycorrhizae. The rock samples were taken randomly from the headwalls of both Douglas-fir and madrone profiles at 50 cm intervals, and three samples were taken at each depth as replications. Roots on the sample surface and in fissures were taken carefully. Total length of roots for each sample was measured, and sample volume

was measured by using the method mentioned above. Estimates of root density were made at 50 cm intervals down the profiles. Root density was calculated by following formula:

$$\text{Root density} = \text{Root length} \times \text{Volume}^{-1}$$

The samples collected from the holes and used for measurements mentioned above were kept from evaporative water losses by making the analysis as soon as possible. Most of these data were collected only at the beginning of the study.

PLANT MOISTURE STRESS MEASUREMENTS

Predawn plant xylem pressure potential (PXPP) was measured monthly from July to September in 1990 with a PMS Model 600 portable pressure chamber (PMS Instrument Company, Corvallis, OR), by the method of Waring and Cleary (1967). Twigs from growth of the previous year were sampled in July, and hardened twigs from the current year were sampled in August and September. Twig samples (3 - 6 mm in diameter) were collected from exposed portions of mid-crown of both 10-year-old Douglas-fir and madrone. PXPP measurements were taken in three treatments (H, M, and N

madrone density) on both blocks, on the same day as soil moisture measurements. Each month, 3 of the Douglas-fir sample trees in each plot and the madrone clump nearest them were randomly selected and tagged with flagging for PXPP measurements. Pressure within the chamber was controlled at an increase rate of approximately 0.03 MPa/sec. until sap appeared on the cut surface. Midday PXPP was measured in September with the same procedure.

PLANT GROWTH MEASUREMENTS

White and Newton (1989), Ortiz (1989), Hughes et al. (1990) and Pabst et al. (1990) have done extensive studies on the primary production and competitive interactions of conifers and principal shrubs and hardwoods during eight years following devegetation by fire, logging, or bulldozer. The current study provides data for the site reported by Pabst et al. (1990), to age 10, and provides insight into the water resources involved in community development.

Growth of Douglas-fir and madrone is carrying them toward full site occupancy. Responses of Douglas-fir and the madrone to increasing competition were evaluated by measuring height, basal diameter at the height of 15 cm

aboveground, understory vegetation cover percent and mortality rate.

Total height from the ground surface to the tip of the tree was measured by using a 6.5 m measuring rod. For the madrone, the tallest shoot was measured as the total height of clumps.

Basal diameter was defined as the diameter at 15 cm above ground for both Douglas-fir and madrone. Calipers and diameter tapes were used for measurement.

Madrone leaf area index and biomass were estimated with the data of height and basal diameter by the equations from Harrington et al. (1984) as follows:

$$Y = 0.197X - 0.05 \quad \begin{array}{l} r^2 = 0.96 \\ s = 0.27 \end{array} \quad n = 70$$

Where Y is leaf area (m^2), and X (cm^2) is sprout basal area.

$$Y = 0.117X - 0.108 \quad \begin{array}{l} r^2 = 0.97 \\ s = 0.13 \end{array} \quad n = 70$$

Where Y is biomass (kg), and X (cm^2) is sprout basal area.

All conifers were measured within each of 10 plots. Douglas-fir was tagged after measurement to prepare for repeated measurement. So, in total about 735 Douglas-fir

plus 90 groups of madrone formed the data base.

Douglas-fir aboveground biomass was estimated with the data of height and basal diameter by the equation from Harrington (1989) as following:

$$\ln[\text{aboveground biomass (g)}] = 1.312 + 0.889\{\ln[\text{STVOL}(\text{cm}^3)]\}$$

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

where STVOL is the stem volume.

DATA ANALYSIS

SOIL/ROCK PHYSICAL FEATURES

The data were evaluated with a descriptive statistical methods (Peterson, 1985). Bulk density, water holding capacity, and available water content were described for each depth, with standard error. One-way analysis of variance was used to compare the difference in soil/rock physical features among different layers.

VEGETATION GROWTH AND MOISTURE RESPONSE

First of all, an analysis of variance was carried out to note the differences in conifer growth associated with

the different competition treatments. The data from growth of Pacific madrone were analyzed in the same way. Differences between means of tree dimensions were assessed by comparison with Duncan's multiple range analysis computed for the indicated value of $P = 0.05$.

Regression was used to show cumulative plant growth as a function of cumulative water used. Subsets included rock water used and total water use. The means were used in a stepwise procedure in giant-sized regression to fit a curve to rock water and total water as independent variables. So the index of fitness for each step or each independent variable serves to assess its utility to improve the overall fit of the curve (Draper and Smith, 1981).

Relationship between xylem pressure potential and soil/rock water content for two species was examined with simple linear regression.

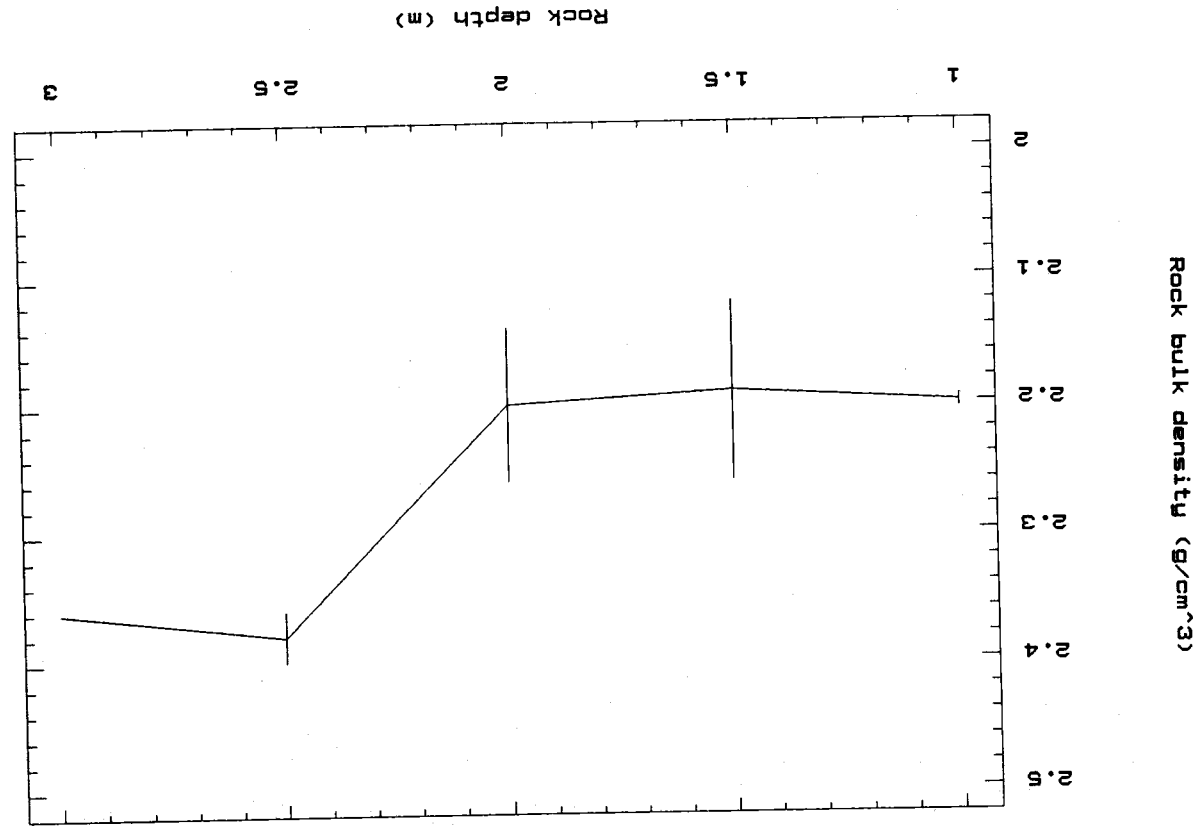
RESULTS

ROCK PHYSICAL FEATURES

On the Douglas-fir site, the rock was moderately hard, and bulk density ranged from 2.2 - 2.38 g/cm³ at 50 cm intervals from 1.0 to 3.0 m depth (Fig. 1). With an increase of soil/rock depth below 1.5 m, rock water holding capacity decreased (Fig. 2); it ranged from 0.237 g/cm³ to 0.103 g/cm³. In contrast to water holding capacity, bulk density increased with increase of soil/rock depth, reflecting decreasing degrees of weathering. Bulk density was inversely related to water holding capacity ($r = 0.70$). Based on analysis of variance, there were significant differences between depths with respect for water holding capacity ($P = 0.004$), but there were no significant differences between depths for bulk density ($P = 0.26$).

On the madrone site, bulk density and water holding capacity showed the same trends as on the Douglas-fir site (Fig. 3,4). The bulk densities were 2.29 (2.0 m), 2.48 (2.5 m), and 2.43 g/cm³ (3.0 m), respectively, which were higher than those of Douglas-fir profile at the same depth. Water availability again decreased with depth (Table 1). The similarity between profiles suggests that the available

Fig. 1 Changes of rock bulk density among depth zones in Douglas-fir profile



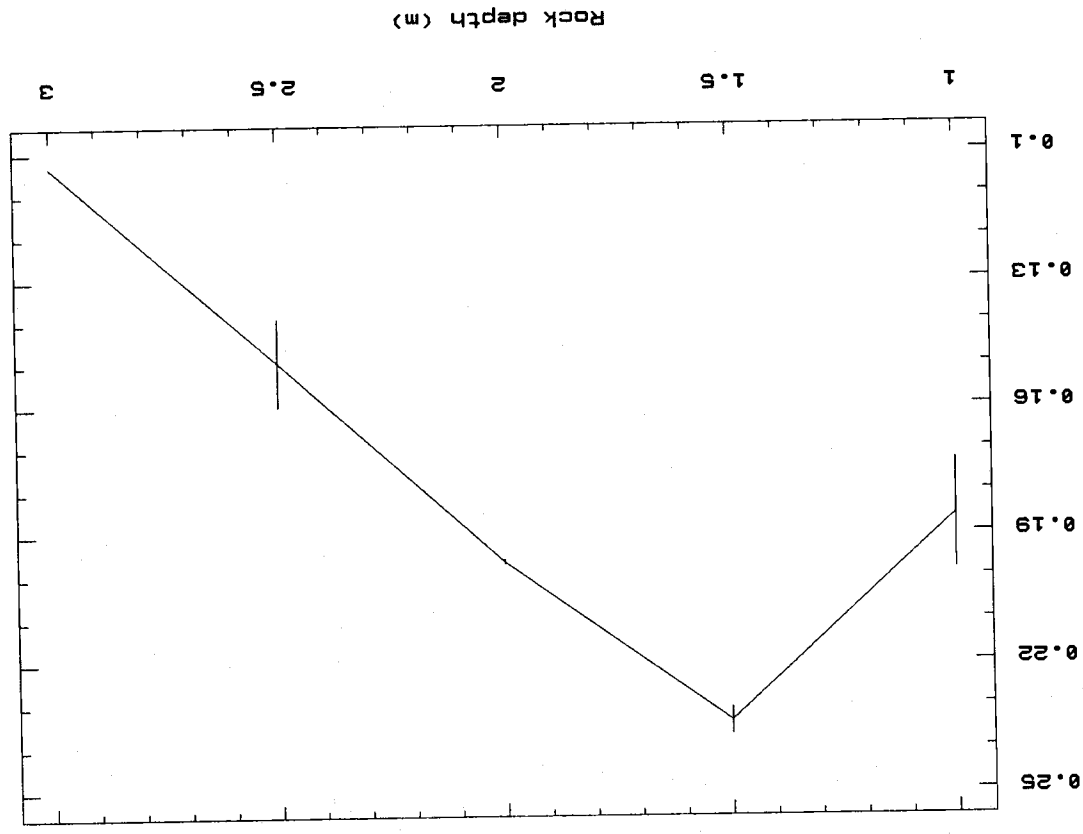
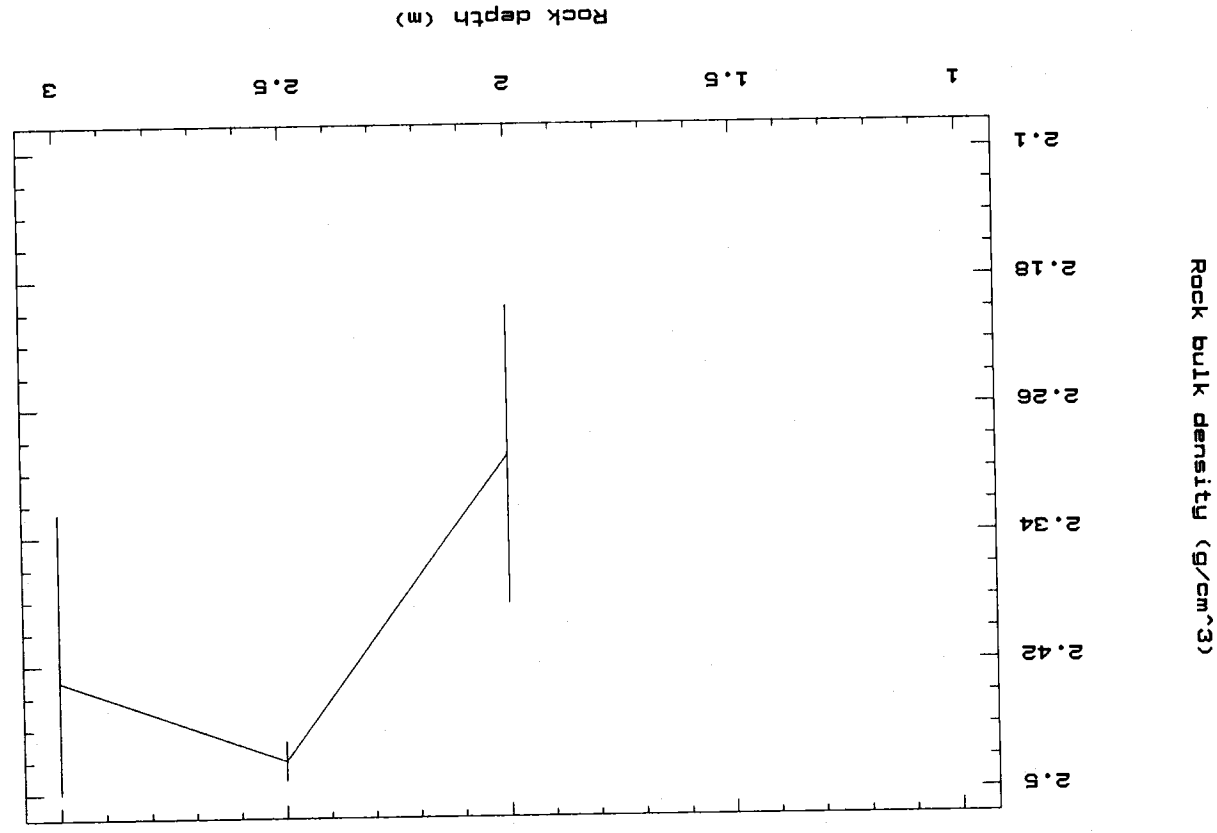
Rock water holding capacity (g/cm³)

Fig. 2 Changes of water holding capacity of rock among depths in Douglas-fir

Fig. 3 Rock bulk density among rock depth zones in madrone profile.



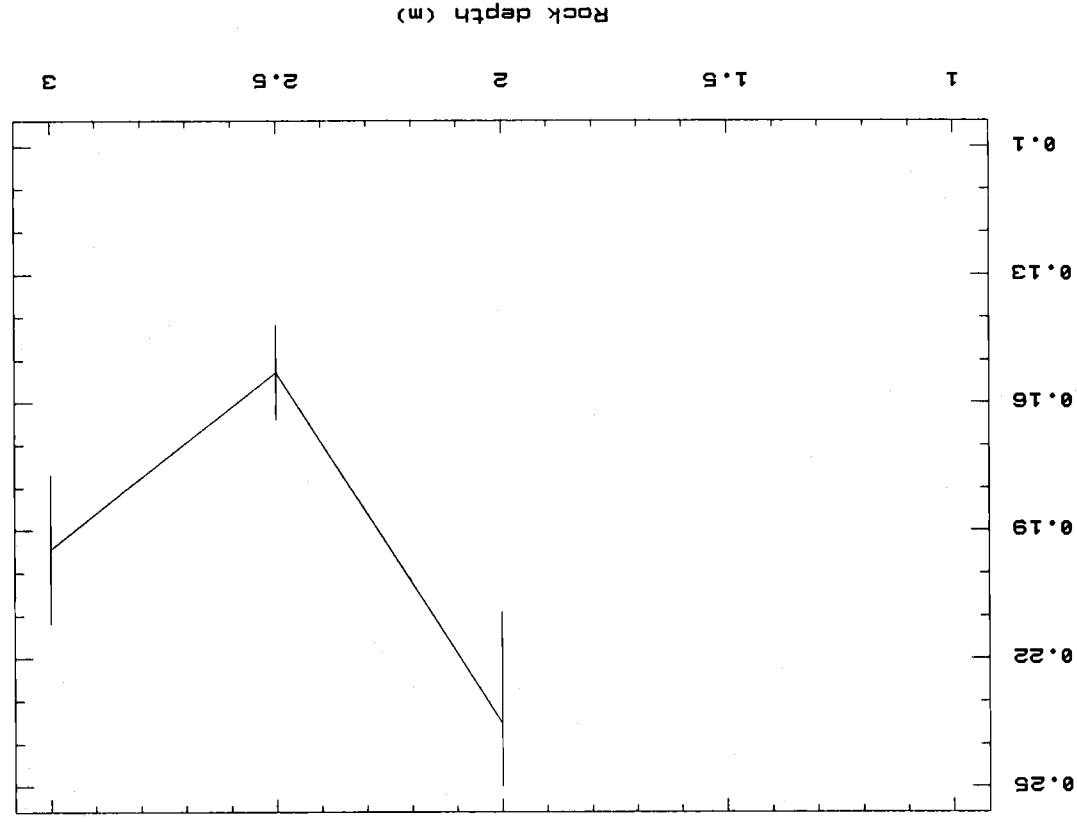
Rock water holding capacity (g/cm³)

Fig. 4 Rock water holding capacity among rock depth zones in madrone porfille.

water content probably decreases consistently with increasing sampling depth.

When grasses are used as a mechanism for extraction of water from rocks under madrone, there appeared to be significant differences among available water contents from different depths (Table 2). Available water content of rock from beneath madrone showed that AWC at the depth of 2.0 m was much higher than that of 2.5 m and 3.0 m.

Table 1. Available water content of rock in madrone profile measured by using pressure plate. Values with the same letter are not significantly different at the level of $P=0.05$.

Sampling depth (m)	AWC (%)	water content -0.3 bar -15 bar (g/g DWT)		VOL. (cm ³)	DWT (g)
2.0	3.0a	13.47	11.46	145.74	66.1
2.5	1.3a	12.50	11.43	194.95	84.6
3.0	0.2a	11.08	10.91	275.20	111.0

* AWC - Available water content.

VOL. - Rock volume.

DWT - Rock dry weight.

Table 2. Available water content of sample rocks in Douglas-fir profile measured in greenhouse. Values with the same letters are not significantly different at the level of $P=0.05$.

Sampling depth (m)	SWT (g)	DWT (g)	VOL (cm ³)	WPWT (g)	AWC (%)
1.0	1058.2	958.2	424.6	1012.0	7.3a
1.5	1211.6	1112.5	508.0	1160.0	7.4b
2.0	1129.9	1057.4	480.6	1089.9	6.2c
2.5	1132.6	1073.7	436.4	1109.1	4.3d
3.0	313.2	300.4	116.0	308.2	3.7e

* SWT - Saturated weight.

DWT - Dry weight.

VOL - Volume.

WPWT - Weight at wilt-point.

AWC - Available water content of rock.

AWC data from the greenhouse were different from those of the pressure membrane and pressure plate. AWCs estimated from greenhouse study are much higher than the laboratory, and trends for two procedures are different.

DOUGLAS-FIR ROOT SYSTEM IN BEDROCK

Root systems of Douglas-fir mainly occurred between 0 - 1.5 m (Fig. 5). Root density of Douglas-fir ranged from 0.14 to 0.76 cm/cm³ and decreased with depth below 1.5 m (Table 3). There were a few roots at a depth of 2.0 m and no roots existed below 2.5 m.

MADRONE ROOT SYSTEM IN BEDROCK

Different from Douglas-fir roots, madrone root systems penetrated substantially deeper and they were present in the deepest strata. The root systems mainly occurred within 0 - 1.5 m. However, roots still can be found at 3.0 m. It appeared that root systems of madrone can penetrate as deep as 3.5 m, and deeper roots may have occurred beyond reach.

The root densities of madrone ranged from 0.11 to 0.71 cm/cm³ between 3.0 m and 1.0 m (Table 4). This is a slightly wider range and somewhat greater density than that of Douglas-fir (Fig. 5). Root density of madrone was correlated with bulk density of rock ($r = 0.73$) and water holding capacity ($r = 0.59$) (Table 5).

Mycorrhizae were found on roots from all layers. They were readily visible on surfaces of rock chunks from nearly soil-free fracture planes at the deeper layers.

Fig. 5 Root density distribution of old growth Douglas-fir and madrone among rock depth zones.

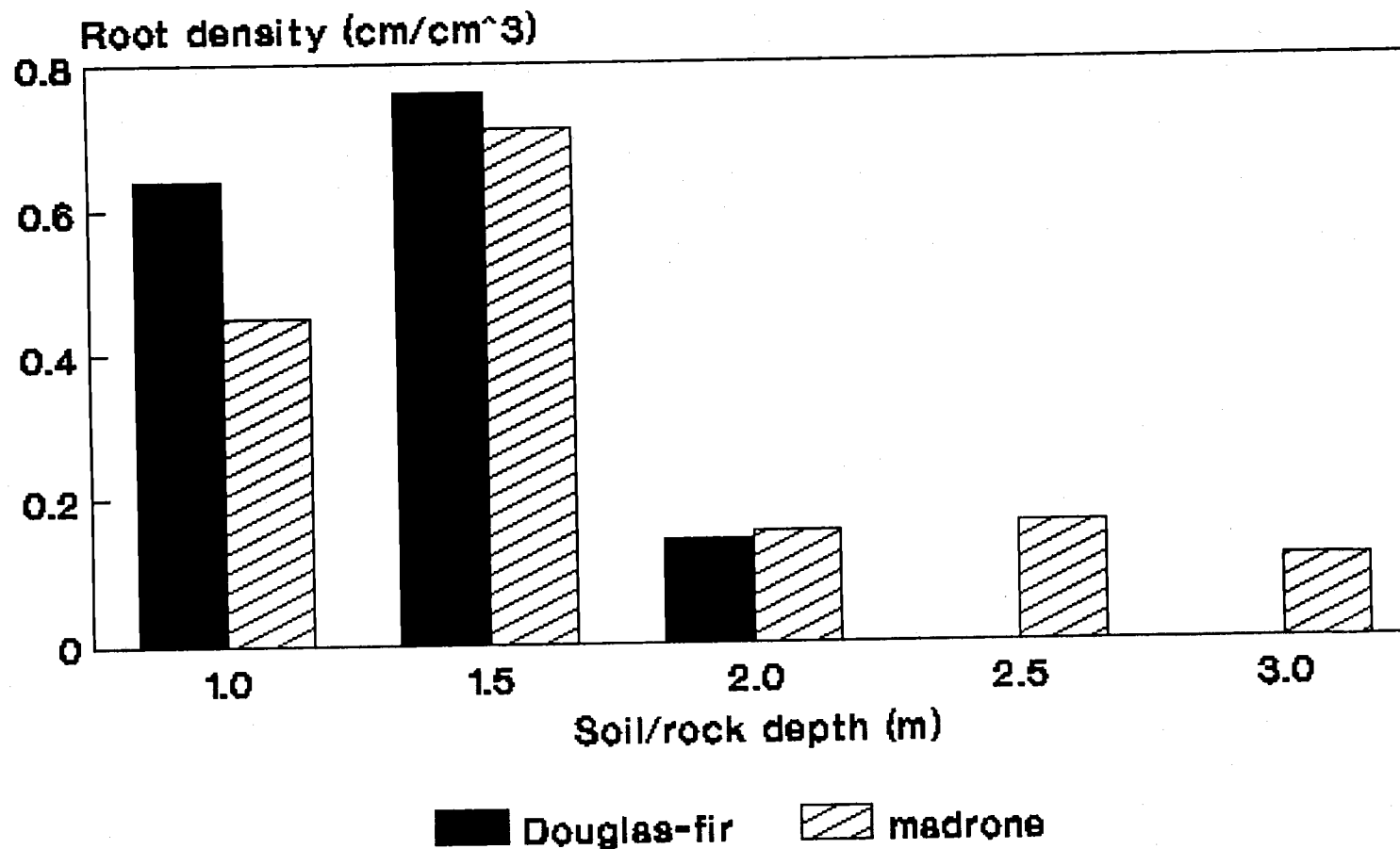


Table 3. Old growth Douglas-fir root density among soil/rock depth zones. Values with the same letter are not significantly different at the level of $P = 0.05$.

Sampling depth (m)	Rock volume (cm ³)	Root length (cm)	Root density (cm/cm ³)
1.0	692.0 (366.8)	423.0 (192.9)	0.64a (0.19)
1.5	453.9 (46.5)	323.3 (236.5)	0.76a (0.59)
2.0	546.0 (163.8)	66.7 (106.9)	0.14b (0.23)
2.5	0	0	0*
3.0	0	0	0

* -- A few roots were found between 2.0 and 2.5 m.

Table 4. Madrone root density along soil/rock depth zones (with standard error).

Sampling depth (m)	Rock volume (cm ³)	Root length (cm)	Root density (cm/cm ³)
1.0	871.4 (496.9)	311.9 (53.8)	0.45 (0.32)
1.5	590.0 (297.0)	375.0 (28.3)	0.71 (0.31)
2.0	591.9 (177.7)	91.8 (43.9)	0.15 (0.03)
2.5	402.1 (53.6)	61.1 (6.5)	0.16 (0.04)
3.0	266.0 (86.3)	25.8 (13.8)	0.11 (0.08)

Table 5. Regression models describing relationships between root density of madrone and rock water holding capacity and bulk density at different depths.

Y	Intercept (a)	Slope (b)	Xi	P-value	R ²
Root density	5.0766	-2.0726	X1	0.06	0.73
	-0.3395	0.0385	X2	0.13	0.59

X1 - Bulk density of rock in madrone profile.

X2 - Water holding capacity of rock in madrone profile.

SEASONAL WATER DEPLETION PATTERN IN SOIL/ROCK

Soil/rock water depletion patterns for the different competition treatments are quite different from March to September (Fig. 6). After onset of the dry season, soil/rock water contents in all treatments tended to decrease. All vegetation classes depleted between 28 - 47 mm of water from the top 1.5 m as rains ceased, between March and June. In the following month, dense madrone drew 50 mm of water from this layer, whereas the other treatments were in the range of 15 - 28 mm demand. Whereas dense madrone depleted its available water early, medium density madrone had a maximum withdrawal later in the summer, but the non-madrone, supporting mostly sapling Douglas-fir depleted little water after July.

The above soil/rock water depletion pattern only shows the picture for the integrated 1.5 m profile. Further information is contained in soil/rock water depletion amount at each depth zone. From June to July, plots with high madrone density apparently depleted more water than those of other two treatments at all depths, whereas water depletion for plots without madrone decreased with increasing soil/rock depth (Fig. 7).

From July to August, water depletion pattern changed

36

**Fig. 6 Soil/rock water depletion pattern
under three madrone density treatments
from March to September in 1990.**

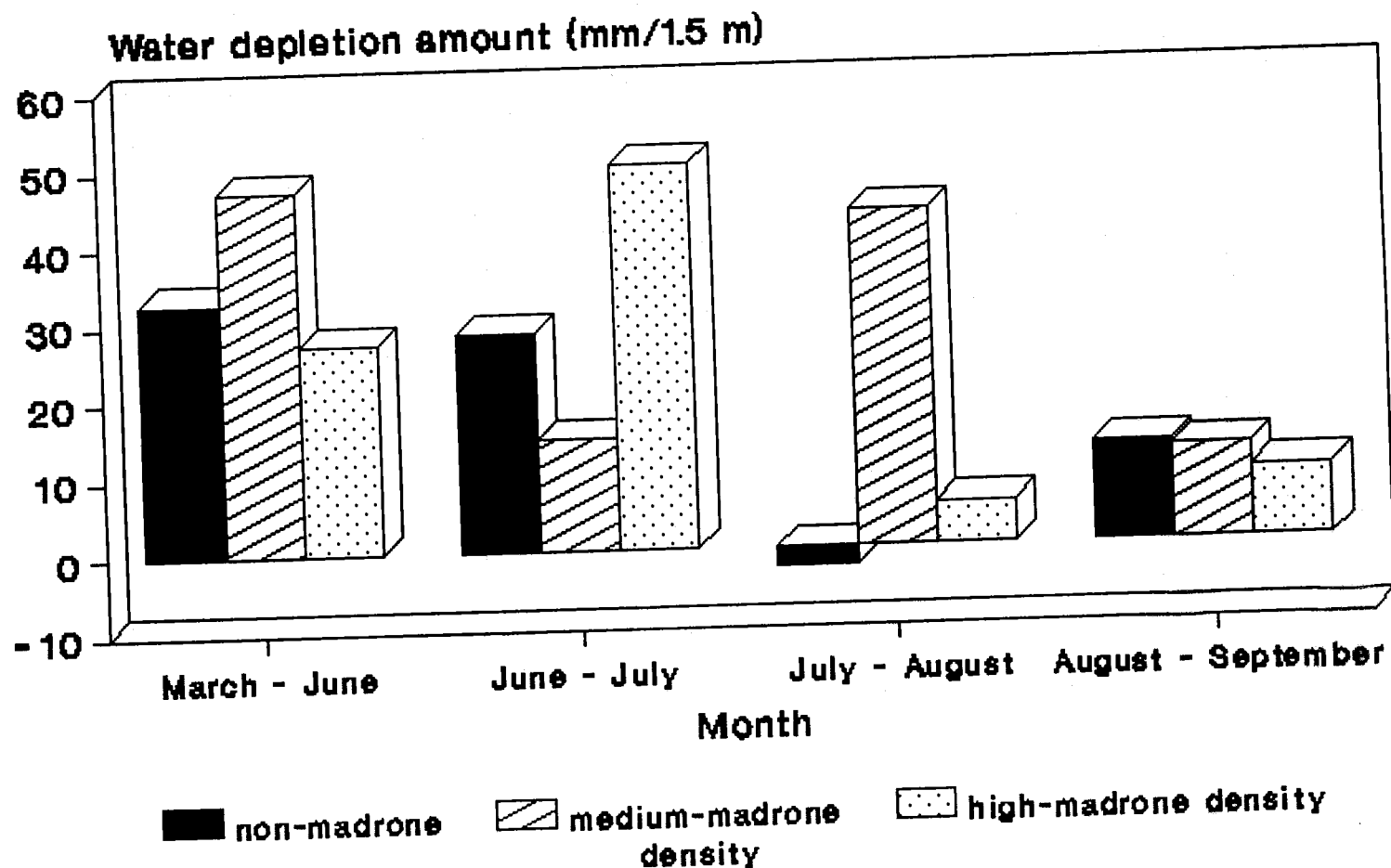
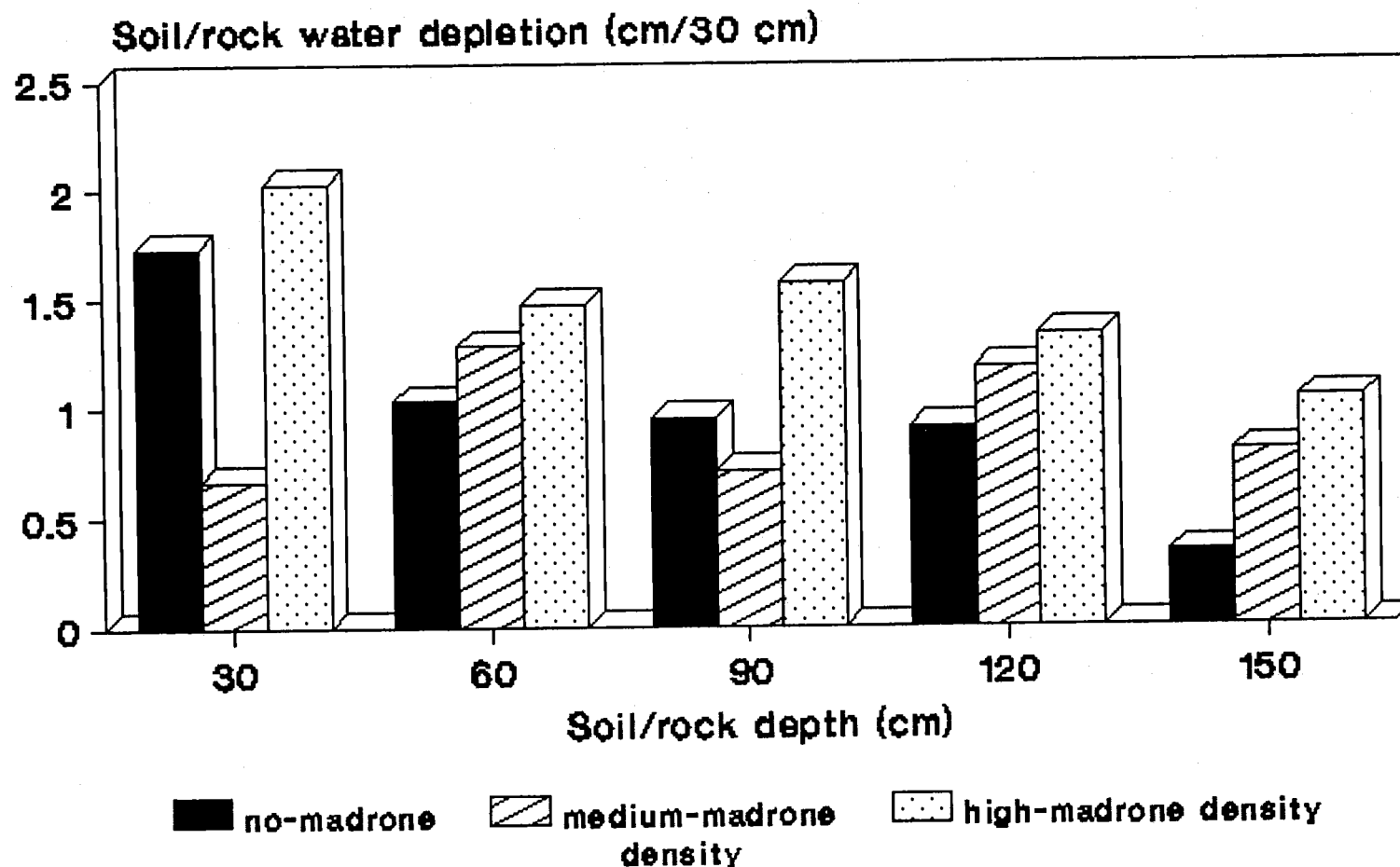


Fig. 7 Soil/rock water depletion pattern at different depths from June to July in 1990.



greatly comparing with previous period (Fig. 8). The plots with medium madrone density depleted more water at all depth zones than no-madrone and heavy madrone plots, whereas there was less moisture lost for no-madrone and heavy madrone plots.

Soil/rock water depletion increased again from August to September (Fig. 9) for both no- and high-madrone density treatments. Apparently, at top 30 cm layer, plots with high madrone density depleted the least amount of water and the most in 60 - 90 cm depth than the others. However, medium madrone density plots depleted more water from deeper layers (120-150 cm). Here may seen the value of the deep, rock-held water, which appears in late summer to furnish more than the depleted surface soil.

PLANT MOISTURE STRESS

In July, 1990, predawn xylem pressure potentials (PXPP) for all treatments were not significantly different for Douglas-fir ($P = 0.64$), but for madrone, differences were pronounced between high and medium density ($P = 0.03$) (Fig. 10 and 11). In August, PXPP of Douglas-fir for all madrone-free plots were significantly higher than those of other treatments ($P < 0.0001$). However, PXPP of madrone were about the same regardless of density ($P = 0.28$), but

Fig. 8 Soil/rock water depletion pattern at different depths from July to August in 1990.

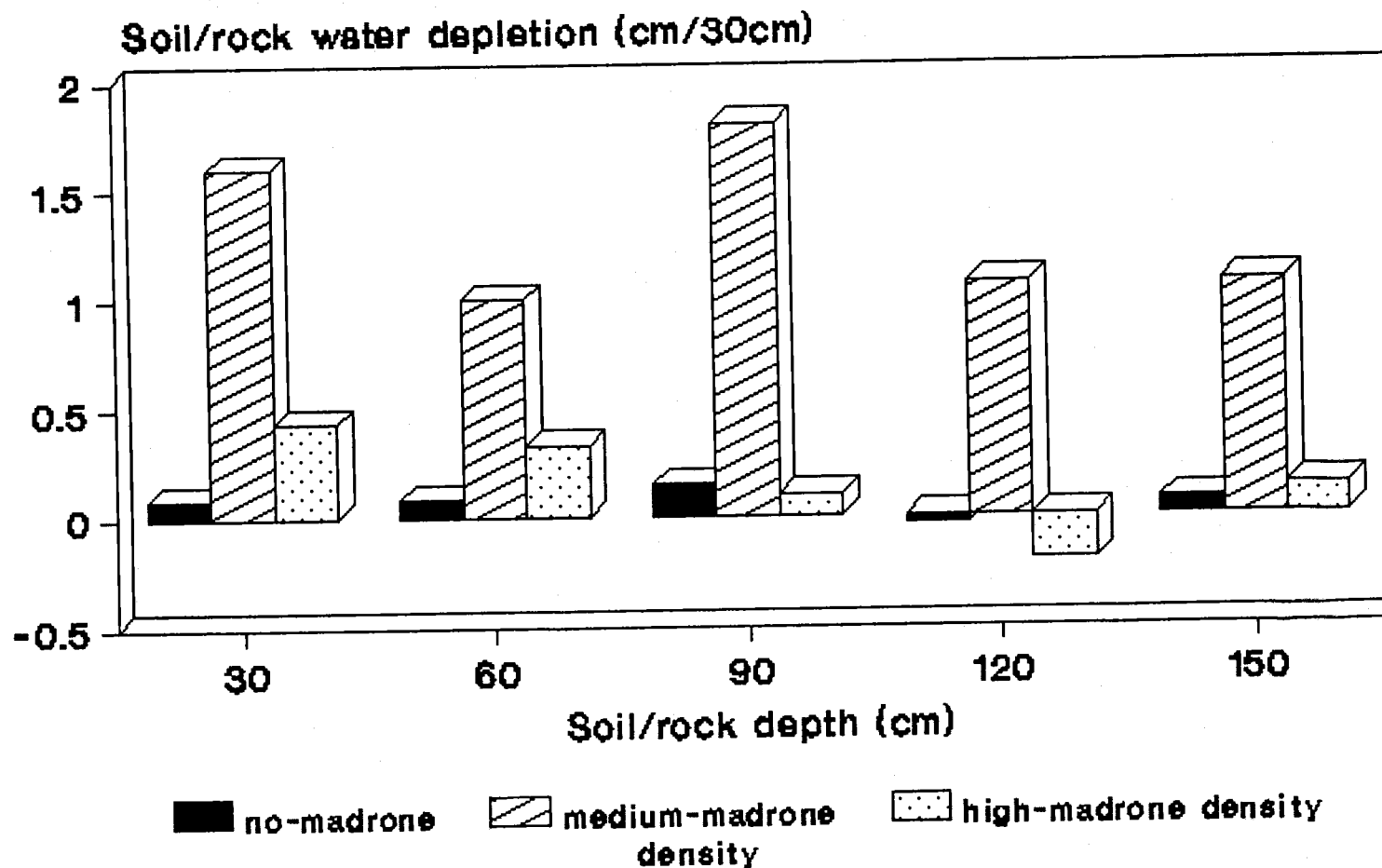


Fig. 9 Soil/rock water depletion pattern at different depths from August to September in 1990.

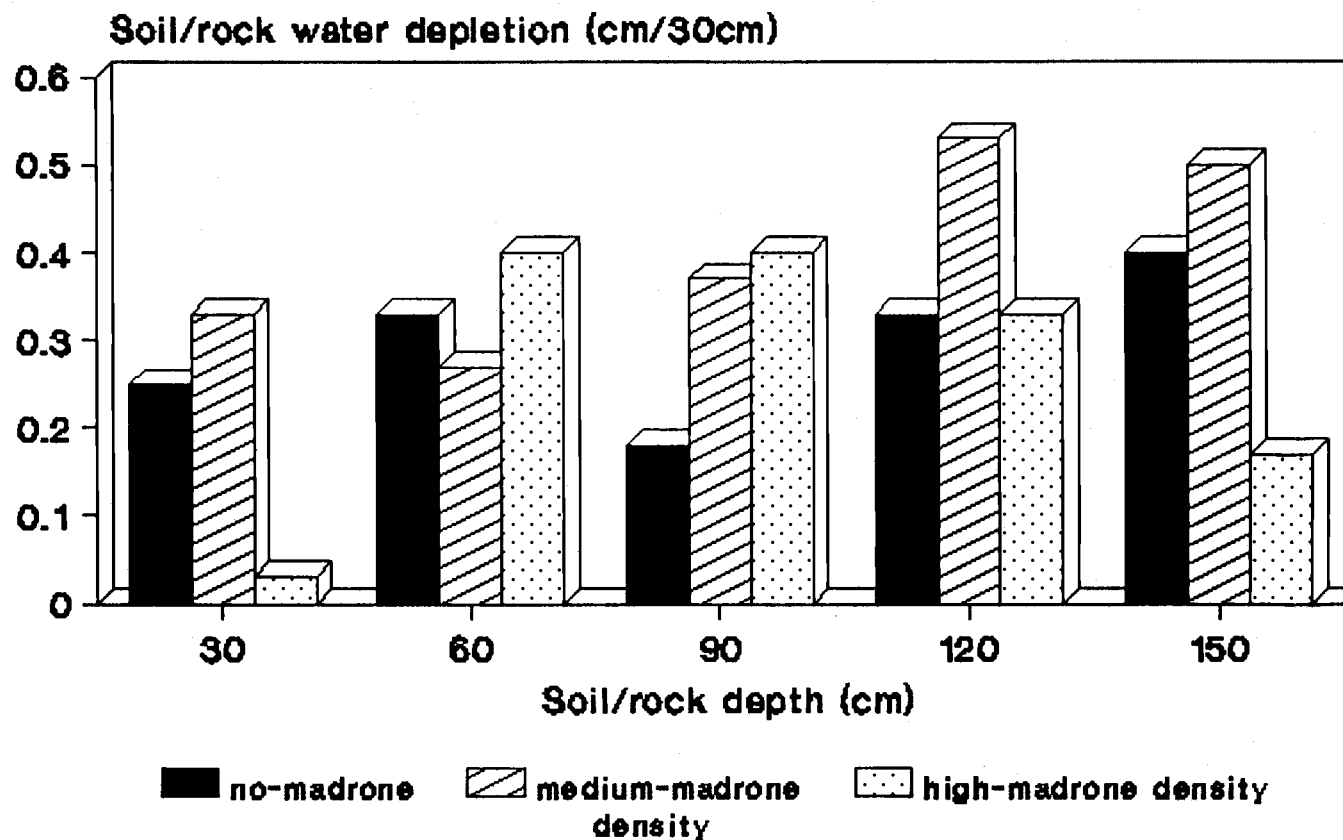


Fig. 10 Predawn xylem pressure potential of Douglas-fir from July to September.

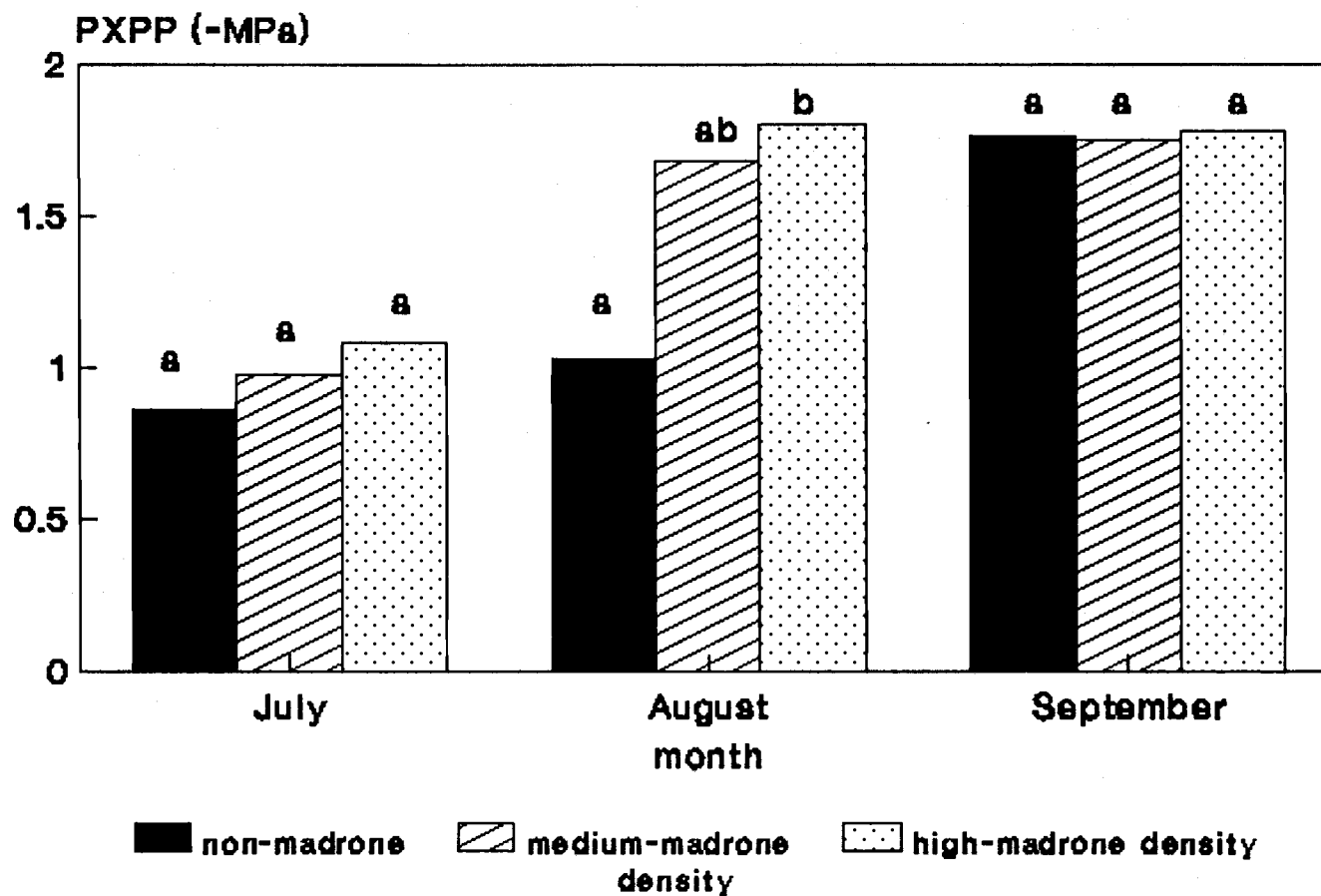
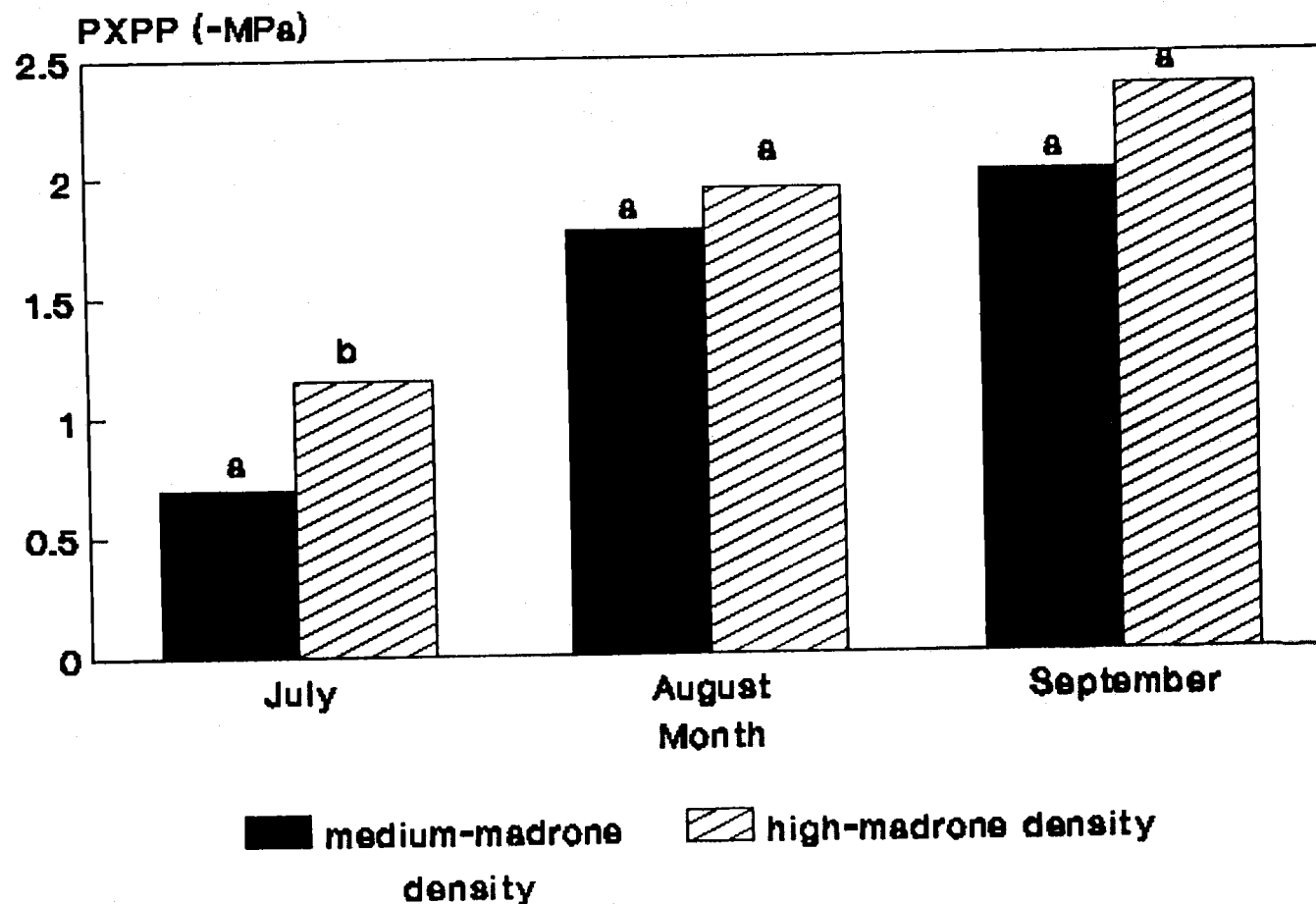


Fig. 11 Predawn xylem pressure potential of madrone from July to September.



stress was much higher than in July. In September, PXPP for both Douglas-fir and madrone showed no significant differences among treatments.

Comparing PXPP of Douglas-fir with that of madrone, we can find that PXPPs of madrone were significantly higher in July and August than in September; for those Douglas-fir with medium or no madrone, PXPPs of Douglas-fir were higher in July than that of in August and September.

PXPP of madrone at high density was higher in July than later ($P < 0.0001$), but did not differ significantly between August and September.

The midday PXPPs of Douglas-fir measured in September were -2.1 to -2.2, and -2.1 MPa, respectively, in all classes of competition; madrone reached -2.8 MPa to -2.9 MPa. There were no significant differences on midday PXPP in Douglas-fir or madrone from different treatments.

DOUGLAS-FIR AND MADRONE GROWTH

Douglas-fir growth

Both madrone sprout growth and understory vegetation affected Douglas-fir growth. For basal diameter, the plots without madrone and understory vegetation had higher average basal diameters, 64.7 cm, than did other

treatments (Table 6). The effects of madrone density on Douglas-fir basal diameter growth were significant ($P < 0.0001$). Douglas-fir basal diameter was inversely related to the density of madrone ($P < 0.05$). The effects of understory vegetation, where left uncontrolled, were not significant.

The effect of madrone density on Douglas-fir height was significant ($P = 0.002$) although the medium density alone did not produce significant suppression, despite the significant volume reduction (Table 6). Madrone is consistently taller than Douglas-fir in all plots.

Douglas-fir height was not correlated with madrone LAI, SWC, and PXPP, but was marginally and negatively correlated with madrone biomass (Table 7). On the same plots, Douglas-fir height was also not correlated with seasonal soil tension relief, seasonal moisture stress relief and madrone LAI in 1985 and 1987 (Pabst et al. 1990).

Douglas-fir diameter growth was not related to SWC, madrone LAI, and PXPP in July, but PXPP in August and September ($r^2 = 0.88$) (Table 7). In 1985 and 1987, Douglas-fir basal diameter growth was correlated with seasonal soil tension relief ($r^2 = 0.62$), seasonal moisture stress relief ($r^2 = 0.76$), and madrone LAI ($r^2 = 0.78$) (Table 8).

Table 6 Average size characteristics (and standard error) of Douglas-fir saplings with different madrone density treatments. Values with the same letter are not different significantly at the level of $P = 0.05$.

Treatment	Height (cm)	Basal diameter (mm)	Tree/plot	aboveground biomass (kg/tree)
no madrone	365.6a (14.1)	64.7a (3.1)	85 (14)	7.59a (1.56)
medium madrone density	367.9a (27.8)	52.3b (3.6)	65 (10)	4.24b (0.99)
high madrone density	336.7b (45.4)	39.0c (3.8)	70 (34)	2.78b (0.83)

Table 7. Regression models describing relationships between growth parameters of Douglas-fir and PXPP, soil/rock water content, and madrone LAI and biomass. Equations are of the form: $Y = a + bX_i$.

Y	Intercept (a)	Slope (b)	X_i	P-value	R^2
D-fir height	525.186	-10.2106	X1	0.15	0.27
	524.965	-16.8266	X2	0.20	0.22
	365.763	-6.5548	X3	0.82	0.02
	40.4126	1.2199	X4	0.53	0.07
	402.840	-0.0057	X5	0.16	0.53
Basal Diameter	154.756	-61.958	X1	0.0006	0.88
	66.4331	-1.3753	X2	0.78	0.01
	59.7614	-7.7289	X3	0.10	0.64
	-41.6719	0.3758	X4	0.36	0.12
	52.8772	-0.0007	X5	0.43	0.22

X1 -- Predawn xylem pressure potential of Douglas-fir in August and September.

X2 -- Predawn xylem pressure potential of Douglas-fir in July.

X3 -- Madrone leaf area index (LAI).

X4 -- Soil/water content.

X5 -- Madrone biomass.

Table 8. The linear relationship of Douglas-fir diameter growth to seasonal soil tension relief (SSTR), seasonal moisture stress relief (SMSR), and madrone leaf area index (LAI) for N, M and H in a mixed conifer-hardwood stand in southwestern Oregon in 1985 and 1987 (n = 8).*

Y	Year	Intercept (a)	Slope (b)	Xi	P-value	R ²
	1985	6.06	-0.88	X1	0.03	0.5

D-fir diameter growth	1987	13.0	-1.9	X1	0.0004	0.87
		-2.0	0.23	X2	0.03	0.51
		-13.0	0.5	X3	0.002	0.81

* -- Table is adapted from Pabst and others (1990)

X1 -- Madrone leaf area index.

X2 -- SSTR.

X3 -- SMSR.

Madrone growth

Madrone sprout clumps grew rapidly. Eight years after density treatment, the height of the 12-year-old sprout clumps ranged from 4.2 - 4.9 m and did not differ significantly between plots (Table 9) regardless understory vegetation.

Madrone density affected the madrone LAI and biomass. Madrone LAI with high density was apparently higher than on medium-density ($P = 0.045$), which were 2.5 and 1.3 m/m for high- and no-madrone plots, respectively. Comparing with past several years, the trend of madrone LAI in 1990 did not increase continuously and kept no apparent change. Madrone biomass was also affected by density significantly ($P < 0.05$).

Madrone biomass with high density was significantly greater than that of in medium-madrone density plots ($P < 0.0016$), and the trend of madrone biomass for both densities is still increaseing comparable to past several years. Madrone biomass was not correlated with soil/rock water content, Douglas-fir height, and basal diameter growth, but was correlated with predawn PXPP in July ($r^2 = 0.73$), in August and September ($r^2 = 0.70$), and correlated marginally with midday PXPP ($r^2 = 0.53$) (Table 10).

Table 9. Average characteristics of madrone sprout clumps with different density treatments. Values with the same letter are not different significantly at the level of $P = 0.05$.

Treatment	Height (cm)	LAI (m^2/m^2)	Clumps/ha	Biomass (kg/ha)
medium	465.0a (36.0)	1.33a (0.12)	330	7732.1a (568.33)
high	423.0a (5.6)	2.50b (0.69)	1322	14644.3b (4152.67)

Table 10. Regression models describing relationships between madrone biomass and soil/rock water content, Douglas-fir growth, and plant xylem pressure potential with two madrone density treatments.

Y	Intercept	Slope	Xi	P-value	² R
Madrone biomass	21032.9	-39.8491	X1	0.880	0.01
	15927.9	-13.7702	X2	0.816	0.02
	26750.7	-341.034	X3	0.217	0.35
	-2937.8	1647.19	X4	0.143	0.73
	-33989.7	2283.03	X5	0.164	0.70
	-78480.4	3182.44	X6	0.273	0.53

- X1 -- Soil/rock water content through growth season.
 X2 -- Douglas-fir height.
 X3 -- Douglas-fir basal diameter.
 X4 -- Predawn xylem pressure potential of madrone in July.
 X5 -- Predawn xylem pressure potential of madrone in August and September.
 X6 -- Midday xylem pressure potential of madrone in September.

Madrone LAI was not correlated with soil/rock water content and Douglas-fir growth, but PXPP in July ($r^2 = 0.79$) and in August and September ($r^2 = 0.71$), midday PXPP ($r^2 = 0.59$) (Table 11). Madrone biomass on different treatments had the same result.

Douglas-fir biomass in no madrone and medium density plots was significantly higher than those of in high madrone density plots ($P = 0.02$) (Table 6). Our result also indicated that Douglas-fir biomass was not correlated with total soil/rock water depletion from June to September ($r^2 = 0.17$), madrone LAI and biomass, but marginally with the density of Douglas-fir ($r^2 = 0.51$) (Fig. 12).

Table 11. Regression models describing relationships between madrone LAI and Douglas-fir growth, and xylem pressure potential of madrone in two madrone density treatments.

Y	Intercept (a)	Slope (b)	Xi	P-value	R ²
madrone LAI	2.7175	-0.0023	X1	0.82	0.02
	4.5574	-0.0579	X2	0.212	0.35
	-0.5678	0.2884	X3	0.113	0.79
	-5.7705	0.3882	X4	0.159	0.71
	-14.0788	0.5672	X5	0.224	0.59

X1 -- Douglas-fir height.

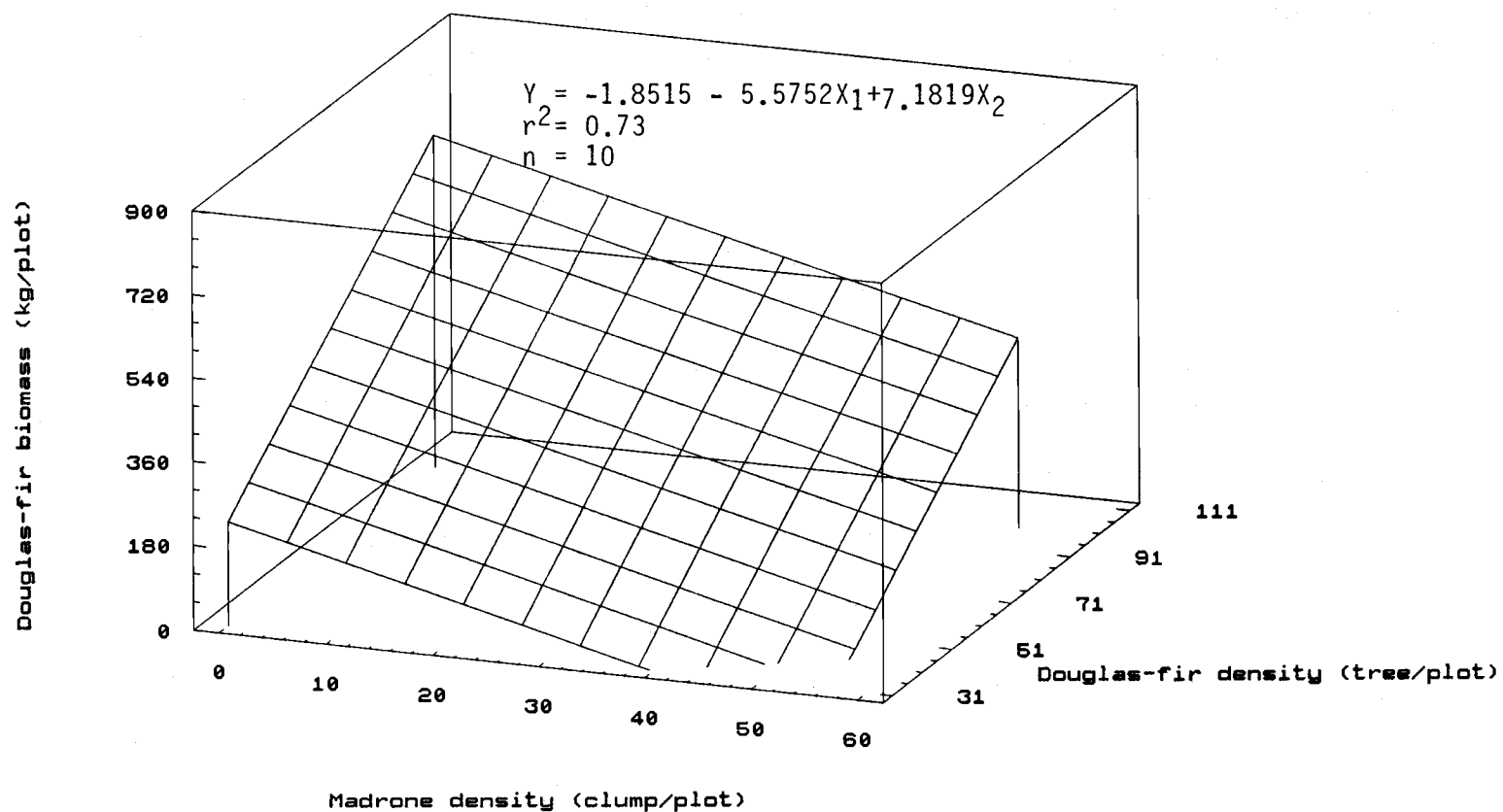
X2 -- Douglas-fir basal diameter.

X3 -- Predawn xylem pressure potential of madrone in July.

X4 -- Predawn xylem pressure potential of madrone in August and September.

X5 -- Midday xylem pressure potential of madrone in September.

Fig.12 Changes of D-fir biomass as the function of madrone and D-fir densities.



DISCUSSION

ROLE OF BEDROCK IN TREE GROWTH

The evidence relating to rock physical features, bulk density, water holding capacity, and available water content support the hypothesis that the solid phase of bedrock can hold substantial quantities of water which is available to plants.

Bulk density of rock is variable, and inversely related to natural porosity. Our data showed that bulk density was related to water holding capacity with a negative correlation ($r^2 = 0.70$) (Fig. 13). The result indicates that the water holding capacity would decrease with the increase of bulk density, presumably because of the decrease in porosity.

The bulk density of 2.2 to 2.38 in the Douglas-fir profile indicates that rock in this site has been weathered substantially from 2.65 at the depths measured.

Figure 14 shows that within a 3.0 m profile, the range of rock bulk density is very narrow, whereas water holding capacity changed greatly at the same depth range, indicating that a relatively minor change in bulk density may lead to great change in water holding capacity. This

Fig.13 Relationship between bulk density and water holding capacity of rock.

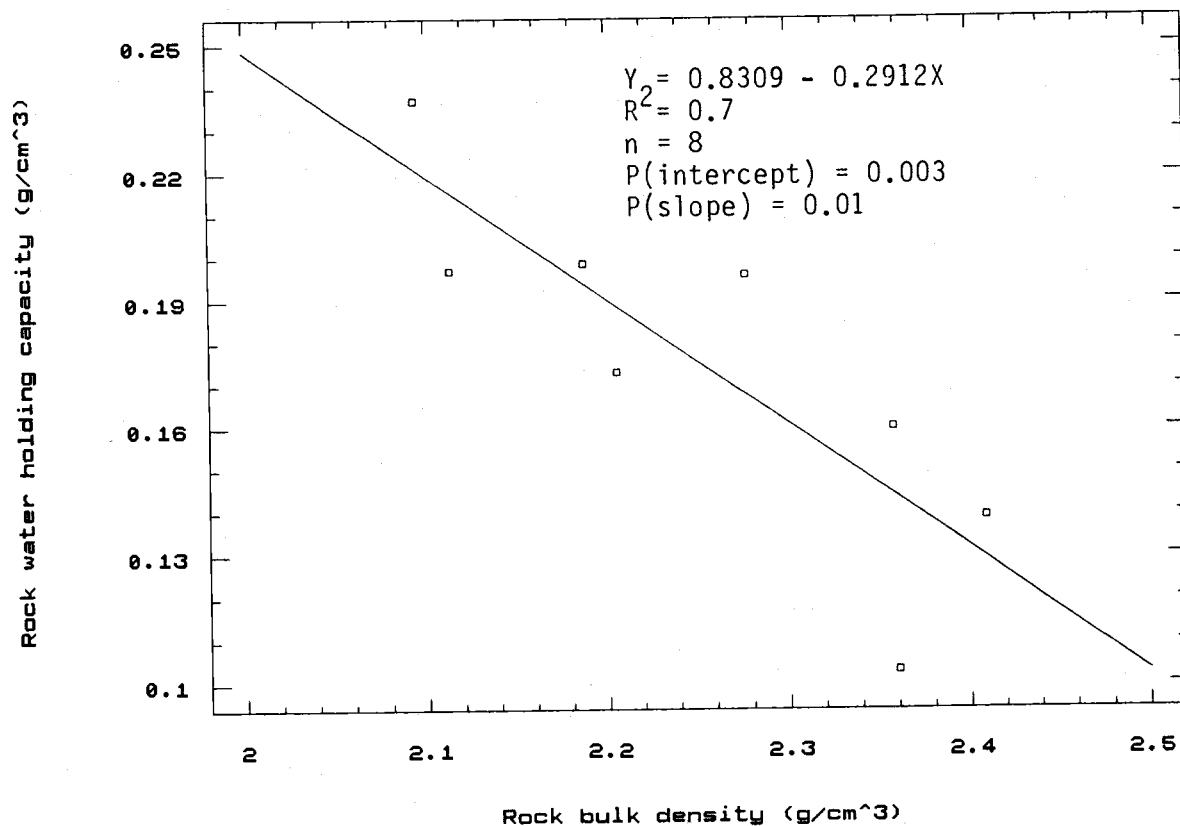
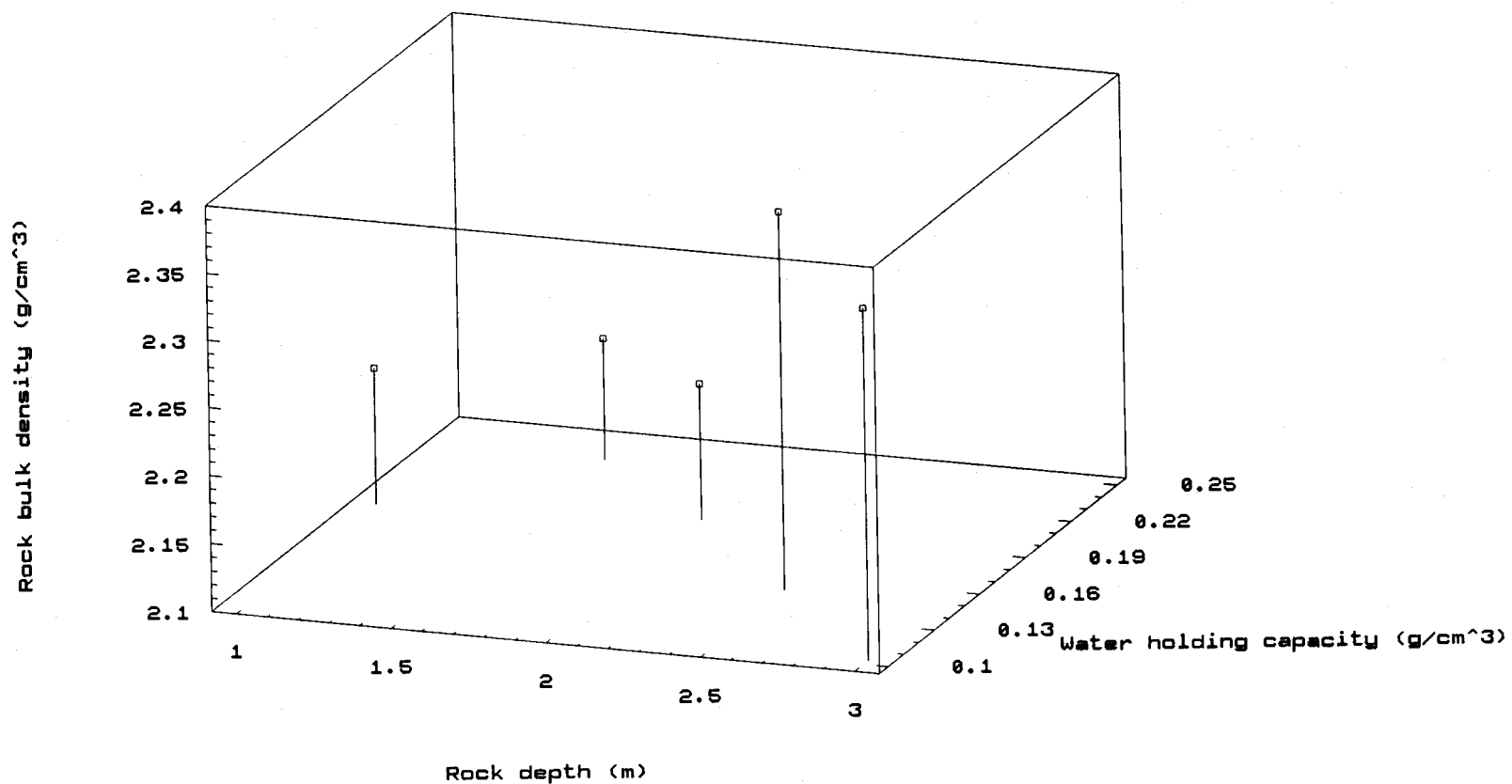


Fig.14 Changes of water holding capacity and bulk density of rock among depths.



phenomenon is the result of large proportional increase in pore space with relatively small decreases in density in the range of 2.2+. I.e. there is twice as much pore space at 2.2 as at 2.42, yet only 31 percent further increase between 2.2 and 2.0 densities. Thus, the greatest relative increments in water holding capacity occur early in the weathering process. Drainage from large pores probably limits extension of this phenomenon.

Evidence of available water determinations in the Douglas-fir profile indicated that the rock between 1.0 - 1.5 m contained 7.4% available water, on a volume basis. There was 6.2% in rock at 2.0 m, and approximately 4.0% for the rock between 2.5 to 3.0 m. The reason for the difference of available water content between depth zones is that rock in upper layer is less dense, hence more porous. The increased porosity provides more micropore space for water in surface rocks than in deeper layers. The rock in upper layers has been most heavily exposed to weathering conditions (Hanson and Blevins, 1979), hence the gradient in density with depth.

Generally, permanent wilting is considered as around - 1.5 MPa. It was measured by Slatyer (1957) with sunflower and other similar species. He also found that the permanent wilting for some species occurred at the water potential as low as -7.0 MPa. Thus, our measurement of

available water capacity does not necessarily reflect the true value of available water capacity. Presumably permanent wilting points for both Douglas-fir and madrone are lower than -1.5 MPa, and madrone may have a much lower permanent wilting point than that of Douglas-fir in view of its ability to transpire freely at low potentials. Therefore, the available water holding capacity of rocks may be more than we measured, if we put to the maximum demand.

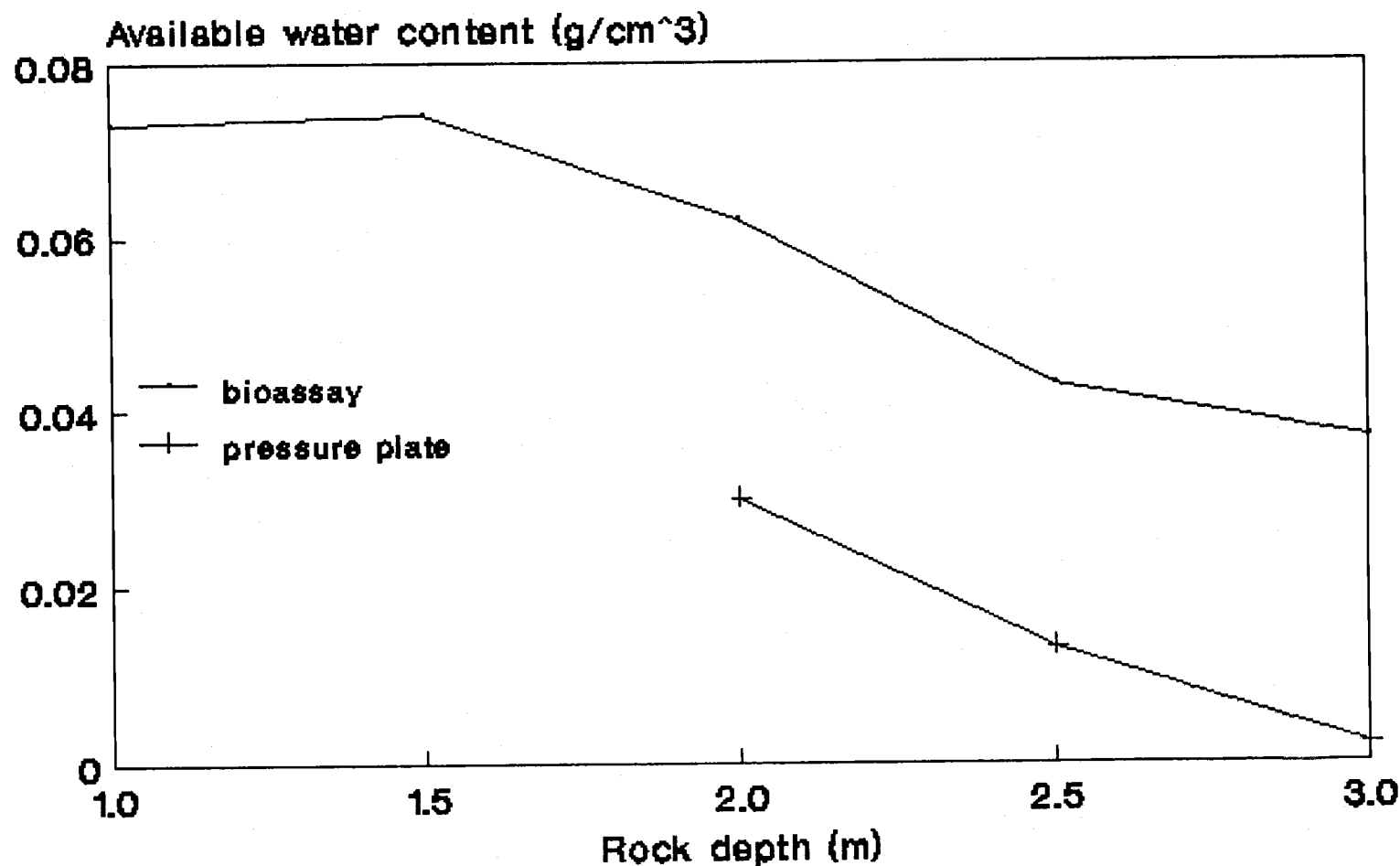
Southwest Oregon is very dry and hot at low elevations during summers. Water held in soil proper is typically depleted by mid-June (White, 1987; Ortiz, 1989). Plants on such site may absorb water from deeper bedrock layers if roots can reach it. From our results, available water content in rocks at -1.5 MPa or less ranged from 7.4 to 3.7% by volume. The average available water content for rock between 1.0 to 3.0 m was approximately 6.0% by volume. The depth of surface soil in the site is about 50 cm or less containing up to 6 cm available water. The rock layer from 0.5 to 3.0 m adds 15.0 cm of available storage capacity to that of the surface soil. Thus, our results suggest that the bedrock can hold about four-fifths of all available water between 0 and 3.0 m, plus any additional extractable water at lower potentials. Flint and Childs (1984) demonstrated that coarse fragments in soils may

retain two-thirds the amount of extractable water of a comparable volume of clay loam soil. Presumably these represent the most completely weathered parts of bedrock, in which case their data are in close agreement with our findings.

The results from the pressure plate and membrane showed much lower available water contents than those observed with wilting point bioassays of analogous rocks (Fig. 15). The difference can be caused by the rock size, stages of weathering, kind (soil series), and concentration of rock. Coile (1953) discussed the differences caused by these factors. He pointed out that the effect of size of stone on the permanent wilting percentage is not the same for stones from different soil series. None of the above work was conducted with solid rock free of soil and ground to fit the pressure membrane surface. Nevertheless, even when fitted perfectly to a semi-permeable membrane, air pressure does not force out much water. Fortunately water depletion observed in the access tubes in the field provided corroborative support for the bioassay method, and it appears that this approach is reliable. The failure of pressure equipment to perform on fitted rocks may be an indication that such equipment gives erroneous data on soils containing any significant content of rock fragments.

Rock bulk density, which we assume to be correlated

Fig. 15 Comparison of available water content by using two different procedures.

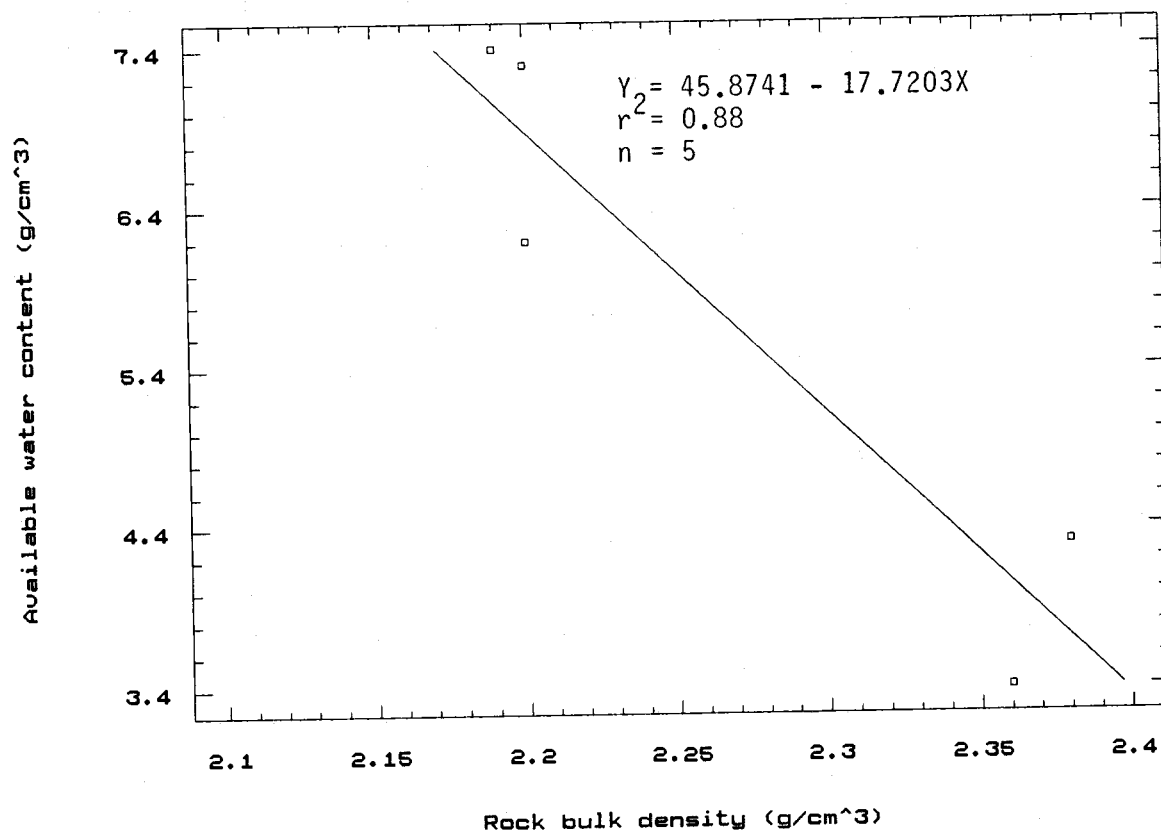


with porosity is very important to water retention and total available water stored in rock. Our findings indicated that bulk density is so highly correlated with available water content ($r^2 = 0.88$) (Fig. 16) that it is probably the most reliable indicator of the value of rock as a water storage medium. Accessibility is another matter, and this concept needs to be validated with a variety of rock strata and vegetation types, as evidenced by difference between Douglas-fir and madrone.

ROOT SYSTEM COMPARISON BETWEEN DOUGLAS-FIR AND MADRONE

The root systems of plants compete for soil resources such as moisture. Yet, apart from depletion, the manner in which these root systems interact and compete is neither obvious nor well studied (Caldwell, 1987). Competition among roots for resources can result in one of two patterns: either roots of one plant deplete the soil resources more quickly than roots of another hence prioritize allocation, or roots of the more successful competitor deplete resources to levels below the capacity of other plant roots, thereby using water not available to others (Tilman, 1982).

Fig.16 Relationship between bulk density and available water content of rock.



The distribution of root systems is very important because the species with high penetrating and branching ability can absorb more water from a given volume of soil than those with shallow root systems (Kozlowski, 1972), but roots with much elongating ability and sparsely branched may gain access to more total volume. Regarding root depth distribution, the root systems of madrone can penetrate below 3.5 m, since we still can find a few scattered roots at that depth. Madrone roots up to 2 mm in diameter penetrated the major fractures in the surface two meters. Finer roots penetrated to a greater depth than our 3.5 m hole. Diameter of roots did not taper greatly between the upper layer of rock (50 cm) and 1.5 m deep in our madrone profile, but tapered below 1.5 m. Fine madrone roots followed the fine fissures between major fissures so that there were few volumes of rock more than a cubic dm with no roots, even at a depth of 3 m. Thus, the entire rock profile examined was characterized by moderately short distances along gradients between stored water and the roots available to exploit it, even though root density was much lower than in soil. Absolute density of roots decreased with depth; this coincides with the distribution of available water content, but also with increasing rock density. Few roots were found where density was much over 2.4 g/cm^3 .

In contrast to madrone, root systems of Douglas-fir penetrated only to less than 2.5 m. Mature Douglas-fir main and branch roots were restricted to depth of less than 1.5 m, and there were lots of roots > 2 mm at 1.5 m. They appeared to have lifted much of the upper 0.5 m of bedrock in a layer of cobbles with some fine material. The fine roots of Douglas-fir were found in fissures where some soil had formed. Few roots < 1 mm in diameter were found more than 50 cm from large roots (> 10 cm). Over-all roots were short and prolifically branched, in striking contrast to the thread like, seldom-branched madrone roots below 2.0 m.

The distribution of root systems of madrone and Douglas-fir indicated that madrone root systems can penetrate deeper than those of Douglas-fir. They therefore have more ability to reach water resources later in the growing season.

The distribution of madrone root density in our site showed that root densities are comparable in surface rocks, but madrone was alone in deep rock. After soil moisture is depleted in upper soil layers, water absorption by roots deeper in the profile becomes more important. The ability of plants to meet the majority of their needs while exploiting favorable soil zones is well documented (Russell, 1977; Kramer and Kozlowski, 1979).

Root density of madrone was correlated with bulk density² ($r = 0.59$) and water holding capacity² ($r = 0.73$) (Table 5), showing that roots penetrate the rock most readily in low bulk density zones (low resistance) and higher water content conditions. Gregory (1987) demonstrated that roots grow when the turgor pressure inside the elongating cells is sufficient to overcome the constraint imposed by the cell walls and any external constraint caused by the soil matrix. Thus, at equilibrium

$$P = \psi_i - \psi_s - W$$

where P is the pressure (root growth pressure) exerted by the root against the soil, ψ_i is the water potential of the cell, ψ_s is the water potential of the soil, and W is the pressure exerted by the cell walls.

It was found that roots of Douglas-fir were suberized even near root tips. In response to seasonal drought, roots of pine (*Pinus halepensis*, *P. resinosa*) cease extension and become 'metacutinized' (Wilcox, 1968). The ability of the growing root tips to withstand water stress is likely to depend on different properties from those required by older parts of the root systems (Drew, 1987).

The total water depletion rate at both 30 and 60 cm depths was similar. This suggests that the entire soil

profile was occupied, probably almost fully, including presence of shrubs and herbs complementing madrone density. This, in turn, could explain the low linear correlation between monthly total depletion rate with madrone density. The high depletion rate found in the plots under dense vegetation regimes, coupled with lower tree growth, indicates that water is being used fully, regardless of composition at age 11.

Mycorrhizae were found on all Douglas-fir and madrone roots. We did not examine mycorrhizae quantitatively.

RESPONSE OF TREE XYLEM PRESSURE POTENTIAL TO WATER STRESS IN SOIL/ROCK

Soil moisture decreased rapidly from June to July in the plots with high madrone density (Fig. 6). For those plots with high madrone density, water in the upper layer of soil (30 cm) was depleted more rapidly and more fully than deeper layers. In 1985 and 1987, soil water potential in dense madrone plots was significantly less than in three treatments of lower density or non-madrone in this site (Pabst et al., 1990). This result indicated that under high madrone density, soil moisture stress would be more severe during the dry season in the early years of development.

From July to August, when the temperature was highest and the depletion potential was also high, plots with high madrone density showed much less water depletion than the others. The reason may be that water was already depleted, hence the dense madrone could only deplete deeper layers (below 1.5 m).

For high madrone density plots, July depletion mainly was greatest in upper layer (30 cm) (Fig. 7), indicating that there was still some water available at upper layer. Nevertheless, water depletion at all other layers was still apparently higher than in plots with less madrone. From July to August, soil water depletion decreased dramatically at all depths (Fig. 8). From August to September, the soil/rock moisture conditions were more severe at this time hence opportunities for depletion were limited. But our results seem to suggest that steady slow depletion continues in all depths through September.

For all plots measured, soil moisture at a depth of 90 - 120 cm was higher than those at other layers, whereas that root distribution is related to soil/rock moisture distribution. The neutron probe also "see" roots as if water. Hence there is some possibility of data confounding at this point, lack of fluctuation suggests this is probably occurring to some degree.

Water depletion by madrone with high leaf area appeared to decrease predawn xylem pressure potential more than elsewhere, indicating that madrone with high density may induce a level of stress that limits its own development.

Predawn xylem pressure potentials of madrone were higher than those of Douglas-fir in July and then were lower than Douglas-fir in August and September. This indicates that soil/rock water condition become severe gradually, and with temperature increased and almost no rainfall added, madrone was able to continue to absorb water from soil and rock as its pressure potential decreased.

In order to keep functioning under dry condition, plants must maintain water potential lower than that of soil water potential so that a gradient along soil-plant-atmosphere continuum maintained for water movement in the system. Our madrone xylem pressure potentials both in predawn and midday were lower than those of Douglas-fir from August to September. This may be an indication that the osmotic concentration of madrone is also greater than Douglas-fir. Under dry conditions, hydrostatic pressure becomes more negative. In this case, madrone were lower in pressure than Douglas-fir. This may explain driving force for water absorption and movement from soil through plant and finally to atmosphere. Thus, madrone's ability to maintain

open stomata and still function until around -3.0 MPa, is an indication that madrone is more adapted to this area than Douglas-fir in terms of its physiological characteristics alone.

Douglas-fir PXPP was not related to soil/rock water content in madrone-free plots (Table 12). The same was reported by Pabst and others (1990).

In medium madrone density plots, predawn PXPP of Douglas-fir was related to soil/rock water content ($r^2 = 0.84$) (Fig. 17) from July to September, and there was no correlation between predawn PXPP of Douglas-fir and soil/rock water content in dense madrone plots ($r^2 = 0.07$). If we further analyze the relationship between rock water content among depth zones and Douglas-fir PXPP, we found that Douglas-fir PXPP in dense plots was also not related to rock water content at any depths from 30 to 150 cm (Table 13). The reason for this result may be that with high madrone density, both Douglas-fir and madrone had been under stress already since June, and that this integrated the whole profile equally. From Fig. 7, we can find that from June to July, soil/rock moisture was depleted more rapidly in high-madrone plots than in others, especially in the upper layers (0-30 cm; 30-60 cm). As a result, their PXPP was not the function of soil/rock moisture in the upper layer, but perhaps of a layer deeper

Fig. 17 Relationship between soil water content and D-fir PXPP in M plots.
(x 0.01)

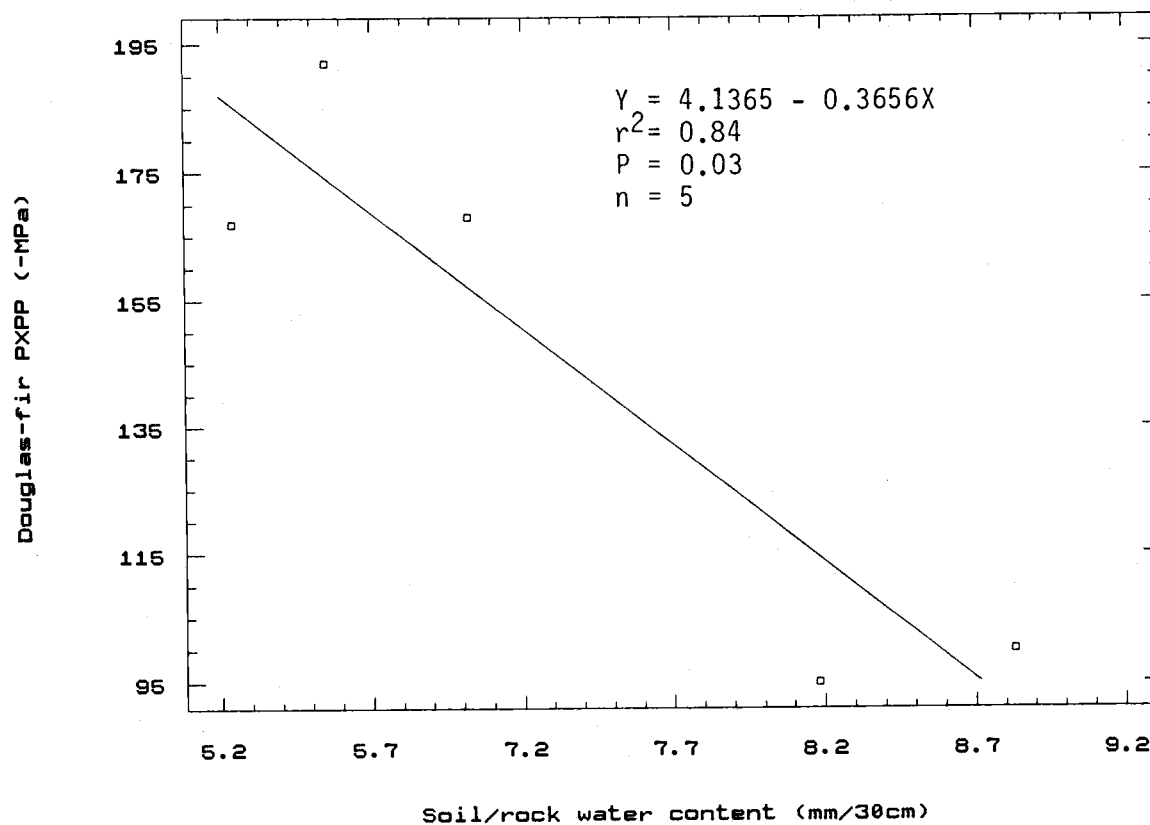


Table 12. Regression model describing relationship between Douglas-fir xylem pressure potential (-bar) and soil moisture in no-madrone plots from July to September.

Y	intercept (a)	slope (b)	X	n	R^2
D-fir PXPP	45.4428	4.3870	soil moisture	6	0.23

Table 13. Regression model describing relationship between Douglas-fir xylem pressure potential (-bar) and soil moisture in high-madrone density plots from July to September.

Y	intercept (a)	slope (b)	X	n	R^2
D-fir PXPP	38.3295	3.8115	soil moisture	6	0.03

than those of record.

The strength of these relationships and similarity in predawn response of Douglas-fir and madrone suggest that in these shallow, rocky soils a concentration of fine roots of all species in the surface 30 cm of soil is competing for soil water, especially in early summer (Pabst, et al. 1990). But for deeper water held by rocks, depletion progresses somewhat more slowly than in surface soil, and it is tapped largely by madrone. Deep rock apparently hold substantial water which can be a big reservoir of water for use largely for growth. However, it is notable that depletion in all zones follows the same pattern. There is no evidence that water held in rock is available only after other resources are exhausted. Such could be the case below 150 cm, but data are not available now even though this study has identified that there is a major storage capacity reachable only by madrone.

A study by White (1987) indicated that Douglas-fir had lower stomatal conductance and higher PXPP than whiteleaf manzanita, suggesting that manzanita may have access to more soil moisture, probably through larger, deeper root systems than Douglas-fir. Our results showed the similar trend and confirmed her finding.

Adaptations of madrone have been observed elsewhere to

place it at a competitive advantage over Douglas-fir, especially on poor sites (McDonald, 1981). Vigorous madrone sprouts can produce a 90% cover 3 - 4 m tall and basal area of 20+ m²/ha in 5 - 7 years. Stomatal control in madrone is linked closely with available soil moisture (Morrow and Mooney, 1974), and the thick leaf cuticle of madrone helps minimize non-stomatal moisture loss (McDonald, 1981). Pabst and others (1990) found that although madrone consistently reached lower midday levels of moisture stress (< -2.5 MPa), it recovered to predawn levels similar to those of Douglas-fir, except in dense madrone in June and September.

The midday PXPP of madrone was lower than that of Douglas-fir. Douglas-fir stomata closure occurs around -2.3 MPa (White, 1989), whereas the stomatal conductance of madrone seems to function until midday PXPP was around -3.0 MPa. This suggests that madrone has less stomatal sensitivity to water stress and exhibits a "water user" strategy.

RESPONSE OF TREE GROWTH TO SOIL/ROCK WATER STRESS

Douglas-fir growth response

Douglas-fir growth was affected by both madrone presence

and dominance, and by understory vegetation. Basal diameter growth of Douglas-fir was significantly different among all three overstory treatments ($P < 0.0001$). Clearly, conditions for maximum Douglas-fir diameter growth on this site occurred where madrone was completely removed. Conditions for growth of Douglas-fir were relatively severe in medium- and high-density competition, where Douglas-fir experienced moderate to extreme levels of plant moisture stress and soil moisture depletion within reach of its relatively shallow roots.

Height growth of Douglas-fir seems only weakly affected by madrone density at this time in development. Hughes and others (1990) pointed out that as crowding and overtopping increase, conifers allocate relatively more resources to height growth than to diameter growth. They have observed that trees with ratios of height to diameter (H:D) in excess of 70 experience a rapid decline in height growth, often leading to suppression and death. This suggests a poor future growth potential for Douglas-fir on high density, and possibly medium-density, plots, especially if it has limited access to the reservoir of water that helps maintain the competition.

Douglas-fir height growth was not correlated with madrone LAI, soil water content, or plant xylem pressure

potential, but was inversely related to madrone biomass² ($r = 0.62$) (Table 7), agreeing with the earlier report by Pabst et al. (1990) and also Hughes et al (1990).

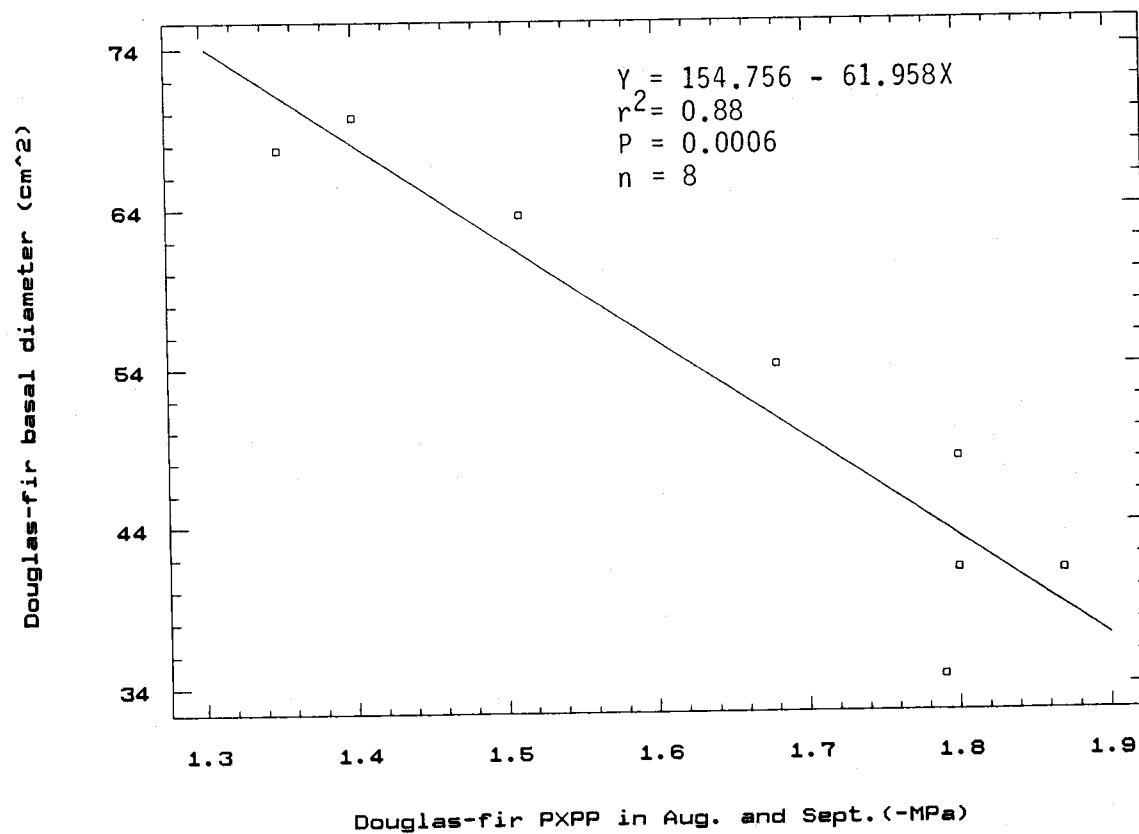
Douglas-fir height growth was not correlated with seasonal soil tension relief, seasonal moisture stress relief and madrone LAI at the same site in 1985 and 1987.

Douglas-fir basal diameter growth was related to predawn xylem pressure potential in August and September² ($r = 0.88$) (Fig. 18), indicating that Douglas-fir basal diameter growth was sensitive to water stress in high density madrone plots; with a decrease in madrone density, Douglas-fir diameter growth appears to increase. Although water status of Douglas-fir is affected by soil available water content and vapor pressure deficit, this effect is confounded with shading by madrone inextricably.

Douglas-fir biomass per ha was affected by the densities of both madrone and Douglas-fir² ($r = 0.73$) (Fig. 12). With an increase in madrone density and a decrease of Douglas-fir density, Douglas-fir biomass decreased dramatically, even though decreasing madrone density increased Douglas-fir individual tree size.

Douglas-fir-only plots did not use the soil/rock available moisture as rapidly as the high and medium madrone plots did. Douglas-fir and madrone in high density

Fig. 18 Relationship between Douglas-fir basal diameter and PXPP in Aug. and Sep.



madrone plots depleted the soil/rock moisture from 28.9% in June down to 22.5% in September, and in non-madrone plots soil/rock moisture decreased only 3.8% between June and September. Douglas-fir in madrone-free plots apparently had 26 mm more moisture for their use. This suggests that conifers had more nearly adequate moisture, leading to a higher growth rate.

Comparing soil/rock moisture consumption in medium plots to that in dense plots, we found that their total depletion amounts were about the same. However, soil/rock moisture depletion in dense plots occurred earlier than that in medium plots, 49.8 mm and 14.4 mm by July, respectively, indicating that madrone with high density depleted much moisture in upper soil layers in mid-summer, and then they relied on water from deeper layers, where some water was apparently available for them.

Ortiz (1989) found that depletion rate is most rapid from the upper layer during May and June, and that depletion is slightly more evenly distributed through the spring and summer for the 60 cm depth. This suggests the additive role of surface evaporation in early seasonal water loss.

Madrone growth response

Madrone sprout clumps grew rapidly, both in height and

basal diameter. Madrone growth has not been severely affected by the presence of Douglas-fir. That is, Douglas-fir at 800 - 2500 trees/ha at age 10 did not cause major mortality or loss of growth in madrone; in high madrone density plots, some small stems were dead as the result of self crowding. In contrast with Oliver's observation (1984) that dense pine failed to decrease brush cover, should Douglas-fir emerge as a dense canopy above madrone, the dark, dense shade would reduce madrone to a minor presence, as indicated in the mature Douglas-fir stand of this study.

Both madrone biomass and LAI were related to madrone moisture stress from July to September (Table 10 and 11). In this site, soil moisture is the major limiting factor for plant growth. Clearly, madrone at high density depleted its water resources most rapidly and encountered stress more severe than those with lower density. There was an complementary relation between madrone and other shrub densities, however, that illustrates the compensatory effects of the other species. Historical soil moisture stress can explain much of the difference of current growth parameters between different treatments, especially in terms of growth/water relations in earlier years before compensatory understory was fully developed.

Compared with the growth in 1988, madrone LAI and

biomass in 1990 appeared to have decreased (Table 9). It is not clear whether this apparent paradox is real or because of a potential difference in sampling procedures. But madrone LAI did seem to decrease in high density plots, presumably because Douglas-fir stocking is heavy enough to offer some competition. Otherwise, madrone growth in high density plots appears to have reached their growth peak and their growth was partially limited by density. Because of their rapid growth rates, dense madrone stands are capable of reaching the stem-exclusion stage of plant succession (Oliver 1981) in less than 8 years.

There is abundant literature on self-thinning and competition exclusion, and these data are not in conflict with the main body of reports. This work merely adds the dimension that a previously unexploited source of plant resources is more available to one species group than another, and that this resource may have a pivotal role in the long-term successful pattern where madrone occurs in high densities soon after disturbance.

SUMMARY AND CONCLUSIONS

Bedrock can hold great quantity of water which is available to plants. In our site, available water capacity ranged from 3.6% to 7.4% by volume in a layer that extends soil depth from 50 to 300 cm or more, indicating that the bedrock can hold about four-fifth of all available stored water. It is very important for tree growth because evergreen tree species still transpire after upper soil moisture has been depleted in mid-June. Available water capacity is affected by bulk density of bedrock, i.e., higher bulk density would lead to low available water capacity and vice versa.

The root systems for Douglas-fir and madrone showed quite different distribution patterns. Roots of madrone can penetrate as deep as 3.5 m or even deeper, whereas roots of old growth Douglas-fir can penetrate to 2.0 to 2.5 m deep, and young trees are probably shallower. Thus, madrone can absorb more water through its deeper root systems than Douglas-fir can.

Among madrone densities, there was no significant difference on total soil/rock moisture depletion between 0 - 1.5 m from June to September; this layer was fully occupied by one form of vegetation or another. Madrone and Douglas-fir in high madrone density plots consumed more

soil/rock water in June, relative to those in no madrone and medium madrone density plots, and, thereafter, depletion rate decreased rapidly. Our results suggest that rate of soil/rock water depletion depended on madrone density. Soil/rock moisture depletion rate in no-madrone plots was less over-all than in plots with medium and high madrone densities, suggesting that Douglas-fir saplings are less able to deplete deep water than madrone sprout clumps of the same age.

Madrone had lower midday xylem pressure potentials than those of Douglas-fir, and recovered to predawn levels similar to those of Douglas-fir. Madrone had less stomatal sensitivity to water stress and exhibits a "water user" strategy, while Douglas-fir stomata closure occurs around 2.3 MPa. Thus, physiological advantages of madrone place it at a competitive advantage over Douglas-fir in this area that it might not have if bedrock did not offer the water reservoir.

Basal diameter growth of Douglas-fir was affected significantly by madrone density. On the other hand, basal diameter growth of Douglas-fir is reflected by availability of soil/rock resources, and would decrease greatly if growing with any strong competitor. Early dominance of competitors before Douglas-fir dominates the site has the potential for suppressing or eliminating most of the

Douglas-fir.

Height growth of Douglas-fir showed less effect from madrone density. Douglas-fir allocates relatively more resources to height growth than to diameter growth when subjected to shade, but not herb competition. Thus the elevated H/D ratios in these plots show that shade adds to water depletion as a major competitive mechanism, and indication that the problem is long-term.

Madrone sprout clumps grew rapidly, both in height and basal diameter. Madrone growth has not been severely affected by the presence of Douglas-fir. However, madrone LAI and biomass in 1990 were decreased relative to that in past several years. It is obvious that Douglas-fir in no-madrone and low-madrone plots will dominate the site after a few years, perhaps to the exclusion of the better-adapted madrone. It appears that the adaptability of madrone for successful domination of such sites is dependent, in part, on high density and early crown closure.

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