

AN ABSTRACT OF THE THESIS OF

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Title: Seasonal and Diurnal Trends of Leaf Water Potential  
and Stomatal Conductance of Red Alder (Alnus rubra Bong)  
Growing Along a Density Gradient in Western Oregon

Abstract approved: Signature redacted for privacy.  
/ Joe B. Zaerr

Three Nelder plots of 3-year-old red alder (Alnus rubra Bong) were used for this study at the Cascade Head Experimental Forest, Oregon in the growing season of 1988 at an elevation of 330 meters. Each Nelder plot represented a range of densities from 238 to 101,219 trees per hectare. The objectives of this study were to describe the seasonal and diurnal trends in leaf water potential and stomatal conductance of red alder growing at different densities, and how environmental parameters affect these physiological measures of plant water relations. The following results were observed: (1) Predawn leaf water potential and noontime stomatal conductance of red alder growing at high densities were lower than that of red alder growing at lower densities in the late part of the growing season. This reduction became severe as the

season progressed. (2) Tree density did not seem to affect leaf water potential of red alder during the daytime. (3) The optimum temperature for red alder stomatal conductance was from 18 to 27°C. Stomata remained widely open when photosynthetically active radiation levels were as low as 100  $\mu\text{E m}^{-2}\text{s}^{-1}$ . Stomatal conductance was related to vapor pressure deficit differently at different times during the growing season. Stomatal conductance increased as VPD increased early in the growing season, but decreased as vapor pressure deficit increased from 0.6 to 2.0 KPa later in the growing season. (4) Leaf water potentials did not seem to limit plant stomatal conductance in the early of the growing season. But plants responded to close their stomata further when leaf water potential was lower than -1.2 MPa in the late part of the growing season. (5) Leaf water potential and stomatal conductance could be predicted from each other, and could be predicted from environmental parameters of which vapor pressure deficit was the most effective.

Seasonal and Diurnal Trends of  
Leaf Water Potential and Stomatal Conductance of  
Red Alder (Alnus rubra Bong) Growing Along  
a Density Gradient in Western Oregon

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SEASONAL AND DIURNAL TRENDS OF  
LEAF WATER POTENTIAL AND STOMATAL CONDUCTANCE OF  
RED ALDER (Alnus rubra Bong) GROWING ALONG  
A DENSITY GRADIENT IN WESTERN OREGON

INTRODUCTION

Red alder (Alnus rubra Bong) is commonly found at low elevations from southern California to southern Alaska in a wide range of soil types and site conditions. It is the major hardwood tree that has proliferated as a result of past logging practices in the Douglas-fir region of the Pacific Northwest (Hibbs, et al., 1989). About 1.14 million ha, or 12% of the forest land base in this region, supported this species in 1975 (Gedney, 1987). Red alder has been described as a pioneer species of vigorous juvenile growth after some disturbance, having a growth rate after establishment that is extremely rapid (DeBell and Turpin, 1983). Another important reason for the increased interest in this species is its potential for efficient nitrogen fixation (Borman and DeBell, 1981; Binkley, 1981). In addition to its unique biological role in forest establishment and management, red alder has high commercial value (Resch, 1980, 1988). The total hardwood log consumption by primary industries such as sawmills, veneer plants, pulpmills, and board mills for 1976 was

65.1 MM bf Scribner net in western Oregon. Approximately 90 percent of these hardwood were red alder (Resch, 1980). All of these characteristics of red alder point towards its potential value in intensively managed forests. There is therefore increasing interest in understanding the biological characteristics of red alder and the factors which influence its growth.

Lack of water is one of the most important factors which limits plant growth. Plants cannot maintain adequate turgor without sufficient water. Cell turgor is essential to plant growth. Above a threshold turgor pressure, the cell wall will deform irreversibly, enlarging the cell (Boyer, 1988). Plants also respond to inadequate water by closing their stomata. This response closes the path by which plants absorb  $\text{CO}_2$  from the atmosphere, causing photosynthesis to be inhibited or reduced (Vu and Yelenosky, 1988), thereby reducing plant growth. For example, Conard and Radosevich (1981) reported that leaf conductance less than  $2.0 \text{ mm s}^{-1}$  limited photosynthesis in white fir. Undoubtedly, plant growth rate can be significantly reduced when plants are under water stress. Zaerr (1970, 1971) and Cleary (1971) demonstrated that diameter growth of Douglas-fir was greater in irrigated trees than in non-irrigated or lightly irrigated trees. Perhaps this difference resulted from the effects of water stress on plant photosynthesis.

Density of plants is an important factor which affects water availability of red alder. Plants compete with each other for natural resources, including water. Plants growing at high density have less chance to obtain water than do scattered trees, especially on dry sites and in dry seasons. The total amount of water consumption of plants growing at high density is more than that of plants growing at low density. For example, Brix and Mitchell (1986) found that thinning treatments of 24 year-old Douglas-fir forest increase soil water potential in the growing season by as much as 1 MPa. Also, the total water reserve in thinned stands was higher than in the control. In the same species, Aussenac and Granier (1988) reported that soil moisture, transpiration, and predawn water potential of a thinned stand of 19-year-old Douglas-fir was higher than that of an unthinned stand. Tarrant et al. (1983) reported that trees in a 12-year-old red alder plantation on the Oregon coast averaged 5.4 inches in diameter whereas trees in unmanaged natural stands do not normally reach this size until age 20.

Because of the desirable characteristics of red alder, it is of interest for reforestation purposes. Information concerning water relations and interactions between water availability and density is needed for intensive management of this species. Unfortunately, such information is not currently available. Little is known

about water relations of red alder, or how trees of this species utilize water when they are grown in different densities. This study was designed to provide information on plant water potential and stomatal conductance of red alder trees growing at different densities. This information will help us understand how density affects plant water relations, and will help foresters manage red alder stands. The specific objectives of this study are:

(1) To describe the effects of density on seasonal and diurnal trends of leaf water potential and stomatal conductance of red alder.

(2) To determine the effects of environmental factors on leaf water potential and stomatal conductance of red alder.

This research was focused on the above ground portion of red alder trees in a 3-year-old plantation in western Oregon.

## LITERATURE REVIEW

### (I). DIFFERENT SENSITIVITIES OF PLANTS TO WATER STRESS

Plant sensitivity to water stress varies with species. Lopushinsky (1969) studied stomatal closure in response to leaf moisture stress in conifer seedlings. He found that in grand fir (Abies grandis (Dougl.) Lindl.) and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), a decline in transpiration rate in response to drought was associated with a relatively small reduction in size of stomatal aperture as compared with ponderosa pine (Pinus ponderosa Laws.), Lodgepole pine (Pinus contorta Dougl.), and Engelmann spruce (Picea engelmannii Parry). The mesophyll resistance may have been a significant factor limiting transpiration in the firs.

Drivas and Everett (1988) compared leaf water potential and conductance of singleleaf pinyon (Pinus monophylla), low sagebrush (Artemisia arbuscula), and basin big sagebrush (Artemisia tridentata ssp. tridentata). They found that singleleaf pinyon seedlings had an apparent threshold water potential (-2.3 to -3.0 MPa) which resulted in stomatal closure and enabled pinyon seedlings to maintain a seasonally stable water potential. But low sagebrush and basin big sagebrush did not have an apparent threshold. Their water potentials were highly correlated with soil water potential ( $r=0.82$ ) which led to

a very low predawn water potential (-3.5 to -5.5 MPa) for low sagebrush by late summer. Thus, pinyon seedlings appear to be more sensitive to water stress than these two brush species, and it has a more efficient means for controlling water use during drought condition.

Colquhoun (1984) described 3 types of stomatal control of Eucalyptus plants. Eucalyptus marginata and E. calophylla exhibited little stomatal control of water loss, and leaf resistance remained low throughout the study period. E. maculata, E. resinifera, and E. saligna exhibited marked stomatal regulation during summer days when xylem pressure potentials fell below -2.0 MPa. E. wandoo also controlled water loss but developed xylem pressure potentials far lower than all other species tested.

Bachelard (1986) studied the effect of soil moisture stress on the growth of seedlings of 3 Eucalyptus species. He found that E. pilularis and E. maculata seedlings 'sensed' drought sooner than E. sieberi seedlings. This enabled seedlings of the two species to survive a more severe drought.

Buxton et al. (1985) compared 3 northern conifer species: black spruce (Picea mariana (Mill) Britt.), white spruce (Picea glauca (Moench) Voss.), and jack pine (Pinus banksiana Lamb). The highest resistance to turgor loss



and the maximum adjustment to moisture stress were observed in white spruce.

Even within the same species, trees from different origins respond differently to water stress. Newville and Ferrell (1980) found that Douglas-fir seedlings from xeric and mesic environments transpired similarly during the first drought cycle. During the second drought cycle, however, seedlings originating from a xeric site closed their stomata at a higher level of plant moisture stress in the second cycle than in the first cycle, while mesic seedlings remained unchanged during the second cycle.

Bongarten and Teskey (1986) reported that loblolly pine (Pinus taeda L.) seedlings growing in a moist regime had greater mean leaf conductance (0.30 versus 0.13 cm s<sup>-1</sup>) and greater response to absolute humidity deficit than seedling growing in a dry regime.

## (II). SEASONAL AND DIURNAL TRENDS

Various studies showed a similar diurnal trend of leaf water potential: The highest value was at predawn, but this value decreased rapidly from early morning, reaching a minimum in the midday, then increasing slightly to mid-afternoon, and finally recovering by evening. This pattern was observed in Pyrus communis L. var Williams' Bon Chretien and Prunus armeniaca L. var Trevatt (Klepper, 1968), Douglas-fir (Zaerr, 1971), several species of

Eucalyptus (Carbon, Barlet, and Murphy, 1981), chamise (Adenostoma fasciculatum H. and A.) (Hart and Radosevich, 1987), and red alder and black cottonwood (Pezeshki and Hinckley, 1988).

However, leaf water potential and stomatal conductance can be variable for different species at different times and environments. Leaf conductance of Douglas-fir was quite different in different times of the year at 5 habitat types (Murphy and Ferrell, 1982).

A study on highbush blueberry (Vaccinium corymbosum L. cv. Bluecrop) revealed that the most negative value of water potential was usually reached by 10:00 in the morning, and was maintained until late afternoon. Leaf stomatal conductance values were high in the early morning, remained high throughout the day, and decreased in late evening (Boyer et al., 1988).

In African locust bean (Parkia biglobosa (Jacq.) Benth) stomatal conductance was high early in the day, but decreased sharply by midday. There was no significant increase in stomatal conductance late in the day (Sonubi and Facehum, 1987). In Eucalyptus behriana and E. microcarpa, stomata were opened in the early morning, and maximum leaf conductance was observed at midday (Myers and Neales, 1984).

Zhou and Zhou (1984) described a double peak of

transpiration rate, while leaf stomata remained open throughout the whole day in locust (Robinia pseudoacacia).

Seasonal trends of leaf water potential may be correlated with precipitation. In ponderosa pine, the lowest value of leaf water potential was observed in the dry season (Vance, 1985).

Maximum stomatal conductance was recorded early in the season when soil moisture was greatest in Celtis occidentalis, Quercus macrocarpa and Q. muehlenbergii (Abrams and Knapp, 1986).

Ginter-whitehouse et al. (1983) reported that leaf water potential was greatest during the early growing season. Seasonal maximum leaf conductance was observed in Quercus alba, Juniperus virginiana, and Juglans nigra during the period between June 1 and July 4.

In Douglas-fir, water potential and leaf conductance were low during summer drought, but leaf conductance was high during the fall and spring (Murphy and Ferrell, 1982).

### (III). THE RELATIONSHIP BETWEEN LEAF WATER POTENTIAL, STOMATAL CONDUCTANCE, AND ENVIRONMENTAL PARAMETERS

Hinckley and Scott (1971) found there was no significant correlation between solar radiation, air temperature and sap flow when Douglas-fir saplings were

under low soil water conditions. However, high correlations were observed after soil moisture recharge had occurred.

Teskey et al. (1987) found that night temperatures below 0°C reduced maximum leaf conductance the following day in proportion to the temperature in loblolly pine (Pinus taeda L.). Environmental conditions of the following day seemed to have little effect on leaf conductance after freezing.

Myers and Neales (1984) studied the seasonal changes in the water relations of Eucalyptus behriana and E. microcarpa in the field. Xylem water potential was associated with rainfall. A single peak of xylem water potential in 1982 was measured after 10.33 mm of rainfall in the previous 6 days.

Vance and Running (1985) reported that water stress recovery may occur within 3 hours of sufficient precipitation in Pinus ponderosa.

Waring and Running (1976) stated that when equilibrium condition are approached just before dawn, there is a predictable relationship between plant water potential and maximum possible leaf conductance when the stomata first open.

Running (1975) found a linear regression of maximum

leaf stomatal conductance on predawn water potential in six conifer species. Leaf stomatal conductance was high when predawn recovery was completed. He also found that leaf stomatal conductance was reduced to near zero when water potential dropped to -2.0 MPa in Douglas-fir, and -1.8 MPa in ponderosa pine.

Water stress significantly decreased stomatal conductance and relative water contents at zero turgor for two subspecies of Eucalyptus: E. globulus Labill subsp. globulus and E. globulus subsp. bicostata grown in soil in pots in the greenhouse (Wang, Bachelard and Banks, 1988). Hinckley et al. (1975) reported hydroactive stomatal closure began as xylem pressure potential decreased below -2.1 and -2.5 MPa in shade and sun leaves respectively. Stomatal response appeared to be light saturated at 0.16 to 0.18 cal cm<sup>-1</sup>min<sup>-1</sup> in sun leaves, and 0.2 to 0.22 cal cm<sup>-1</sup>min<sup>-1</sup> in shade leaves in white oak (Quercus alba).

In Pinus contorta the progression of maximum leaf conductance prior to water stress development appeared to follow the seasonal temperature trends, and maximum leaf conductance was highly correlated with previous night minimum temperature. In the summer, leaf conductance decreased in a trend similar to that of predawn water potential (Graham and Running, 1984).

Lafleur (1988) studied leaf conductance of sedge (Carex paleacea) and 3 woody species (Alnus rugosa, salix bebbianna, and salix discolor). He found that leaf conductance in the three woody species were influenced by solar irradiance, air temperature, and atmospheric vapor pressure deficit. A continuous curve depicting the boundary line is given to represent the ideal stomatal response when all other factors are nonlimiting. Light saturation for all species occurred at about 180 to 220  $\text{W m}^{-2}$ . Maximum conductance for the woody species occurred between 22 to 24°C. All species demonstrated the trend of decreasing conductance with increasing atmospheric vapor pressure deficit. He suggested that knowledge of leaf water potential was probably an important factor for prediction of leaf conductance.

The difference in vapor pressure between leaf and air is a very important parameter, because it drives transpiration and directly affects stomatal conductance. Plants have developed a mechanism to regulate conductance directly in response to humidity to avoid excessive rate of water loss and desiccation. Schulze (1986b) found that leaf conductance and transpiration of larix decidua X leptolepis in a dense stand increased after sunrise, but decreased later in the morning when the leaf-to-air vapor pressure difference increased to more than 5 MPa.

Schulze (1986a) suggested a number of possible

interactions between stomatal response, transpiration, and leaf water potential during changes of leaf-to-air vapor pressure ( $dW$ ): 1. At constant leaf conductance, transpiration is proportional to  $dW$  and leaf water potential is inversely related to  $dW$ ; 2. If stomata respond to  $dW$  in leaf transpiration in such a way as to minimize further decrease in leaf water potential, it is expected that transpiration would initially increase but then level off at a constant maximum in dry air. In this case, leaf conductance would show a curvilinear response approaching a minimum value, and leaf water potential would decrease in a curvilinear fashion to reach a corresponding constant minimum value in dry air. This type of control is referred to as feedback control; And 3. If epidermal water loss and turgor of the epidermis determine stomatal aperture independent of stomatal transpiration and mesophyll water status, then it is expected with increasing evaporative demand that leaf transpiration would reach a maximum and then decrease, whereas leaf water potential would reach a corresponding minimum and then increase. This type of response is referred to as feedforward control.

#### (IV). THINNING EFFECTS ON WATER AVAILABILITY

Thinning can increase water availability in many stands. In a 18 year-old pure red pine (*Pinus resinosa*) stand, soil moisture above 46 cm was always higher, so

needle water potential was usually higher in the thinned plots than in the control plots (Sucoff and Hong, 1974).

Aussenac and Granier (1988) investigated thinning effect in a 19-year-old Douglas-fir stand for 5 years. They found that thinning has an important effect on water balance. The increase of soil water potential led to a lower duration and level of water stress in the thinned plots. Predawn water potentials of plants in the thinned plot was higher than in the control plot. Donner and Running (1986) found that leaf water potential of Pinus contorta in the late summer was significantly higher (0.17 to 0.35 MPa) in the thinned stand than in the control.

After studying soil moisture in stands of Pinus radiata in deep Pinaki sands, Jackson et al. (1983) found that soil moisture content in lower density stands (density ranged from 2224 stem/ha of most dense to 741 stem/ha of most scattered) was greater than that in higher density stands during late summer and autumn within the surface meter of the soil profile in the first 3 years, but became insignificant after 5 years.

Reduction in stand density by thinning has often been shown to increase diameter growth and soil water content in the residual stand (Stogsdill 1986). But Creg (1986) studied the effects of thinning on water relations of a loblolly pine plantation and found that stocking



reductions did not significantly decrease the xylem pressure potential of the trees in the residual stand. Mean daily conductance and transpiration per unit leaf area were also relatively unaffected by thinning.

#### (V). NEIGHBORING VEGETATION EFFECTS ON WATER AVAILABILITY

Neighboring shrubs and grasses in the community also affect plant water availability.

In ponderosa pine stands, Shainsky and Radosevich (1986) created five mixtures of ponderosa pine and manzanita (Arctostaphylos patula Greene) shrubs. They found that increasing the proportion of manzanita in the mixture resulted in depressed predawn water potentials of pine seedlings. This depression became more severe as the dry season progressed from June to September. Leaf stomatal conductance of the pine declined throughout the growing season, while the conductance for the trees in a pure pine stand remained constantly high.

Peterson and Maxwell (1987) obtained the same results in ponderosa pine but with different shrubs. The predawn needle water potential of pine planted along a density gradient ranged from -0.5 MPa when competing foliage was near zero to less than -3.0 MPa when competing foliage was more extensive.

Lanini and Radosevich (1986) found that both predawn

and midday water potential of ponderosa pine and white fir (Abies concolor (Gord. and Glend).Lindl.) was lower when growing on a site with high shrub canopy volume than with lower shrub canopy volume.

In Douglas-fir stands mixed with ceanothus velutinus and forbs, Peterson et al. (1988) created three stands: control, partial weeds, and pure Douglas-fir. The soil water potential of the control plots declined much faster and earlier than the pure Douglas-fir and partial weeds plots at 10 cm depth. Soil water potential during late summer was less than -1.5 MPa at 10, 40, and 100 cm depths in the control and partial weeds. In the absence of shrubs and forbs, the soil water potential at 100 cm was near capacity level throughout the growing season.

Newton and Preest (1988) studied the growth and water relations of Douglas-fir seedlings under different weed control regimes. They found that vegetation contributed an important modification on soil water depletion. Xylem water potential on both irrigated and nonirrigated plots was consistently highest on the devegetated plots. Predawn xylem water potential of trees in the mixed-vegetation plots was -0.7 to -0.8 MPa for much of the summer, while that of trees in plots containing only broadleaf plants or grasses was -0.5 to -0.6 MPa. Seedling stem volume at 5 years after transplanting was linearly related ( $r=0.77$ ) to the sum of water stress

relief during the first three growing seasons after transplanting.

In Pinus radiata, Sanda and Nambiar (1983) found weed presence in the dry season depressed pine water potential and increased stomatal resistance. This effect was stronger on young trees than on old trees.

In loblolly pine (Carter et al., 1983) and Pinus sylvestris (Whitehead, 1984), water potential and stomatal conductance were usually lower in stands competing with weeds than in stands without weeds.

#### **(VI). DIRECT DENSITY EFFECTS ON PLANT WATER RELATIONS**

Cole and Newton (1986) used Nelder plots with 3 treatment: Douglas-fir only, Douglas-fir and grass, and Douglas-fir and red alder. They found that predawn water potentials of Douglas-fir were similar among treatments at the beginning of the growing season, but deviated later on. The highest stress (most negative water potentials) values were from the Douglas-fir growing at high density in the Douglas-fir and red alder treatment. For each treatment, stress was highest at high density.

Shainsky (1989) studied the effect of different densities of Douglas-fir and red alder on their plant water relations. For both species, she found that density significantly influenced soil moisture content during the

1986 growing season. Soil moisture depletion over the growing season was highly correlated with total stand leaf area. Predawn leaf water potential of red alder became more negative with increasing density, and became more negative as the season progressed. Red alder density had twice as much influence as Douglas-fir on plant water status. Red alder density affected leaf water potential measured during the day less severely than it did predawn leaf water potential. The correlation between predawn leaf water potential and soil moisture content was weak for red alder, but the correlation between predawn leaf water potential of Douglas-fir and soil moisture content at 90 cm depth was highly significant.

#### (VII). WATER RELATIONS OF RED ALDER

Koo (1989) reported that leaf water potentials of red alder seedlings during a five-day drought cycle decreased from -0.7 MPa on the first day to -0.92 MPa at the third day, and then to -1.5 MPa by the fifth day. Stomatal conductance decreased from  $0.36 \text{ cm s}^{-1}$  on the first day to  $0.22 \text{ cm s}^{-1}$  on the third day, and then to  $0.04 \text{ cm s}^{-1}$  by the fifth day.

Pezeshki and Hinckley (1982) studied the diurnal course of stomatal conductance and xylem water potential of red alder and cottonwood (Populus trichocarpa Torr. & Gray). Leaf stomatal conductance increased as

photosynthetically active radiation (PAR) increased in the morning, and reached the highest value near mid-day. Water potential was highest just before sunrise and lowest around midday. Compared to cottonwood, stomata of red alder remained more open under dry conditions. They also found that soil drought had a pronounced effect on reducing stomatal conductance. There were several periods of rain in 2 days, and soil water potential recovered from -0.13 to -0.05 MPa during that time. Lower predawn water potentials resulted in lower stomatal conductance. They used the boundary line analysis technique, and reported that the saturation PAR was around  $400 \text{ } \mu\text{mol m}^{-2}\text{s}^{-1}$  in the morning. Stomata did not begin to close until the light decreased below  $80 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ . The threshold of leaf xylem water potential for stomatal closure was lower than -1.1 MPa.

In a later study, Pezeshki and Hinckley (1988) found that leaf age and drought exposure of red alder influenced its osmotic potential. There appeared to be continued decrease in osmotic potential in red alder during the growing season. They concluded that red alder exhibited slight to moderate capacity to survive exposure to low leaf water potential and moderate to excellent capacity to survive stomatal closure conditions potentially leading to lower water potential.

Cole and Newton (1986) compared Douglas-fir and red

alder, and found that red alder seemed capable of preempting water resources or tapping water resources that were unavailable to Douglas-fir. Predawn measurements recorded for red alder trees in the Douglas-fir and red alder mixture were 0.00 to 0.4 MPa higher than those for Douglas-fir.

## MATERIALS AND METHODS

### RESEARCH SITE

This study was conducted at a site about 5 kilometers east of the Cascade Head Experiment Forest Headquarters, which is 15 kilometers northeast of Lincoln City, Oregon. The following data were reported for the Cascade Head Experiment Forest Headquarters (Greene, 1982):

Mean annual temperature	13.3°C (50.6°F)
Mean January temperature	5.3°C (41.5°F)
Mean July temperature	15.3°C (59.6°F)
Mean January minimum temperature	2.2°C (35.9°F)
Mean July maximum temperature	20.9°C (69.7°F)
Average annual precipitation	2496 mm (98.26 in.)
June through August precipitation	163 mm (6.42 in.)

Temperature and precipitation from May to October, 1988 were:

Mean July maximum temperature	22.96°C (73.32°F)
Mean July temperature	15.79°C (60.42°F)
Total precipitation	486.41 mm (19.15 in.)
June through August precipitation	150.37 mm (5.92 in.)

Summer fog is a common phenomenon in this area. The precipitation shown above does not reflect the effects of fog drip.

The study site is at an elevation of 330 meters above

sea level and is part of a larger study. For this study, three type 1a Nelder plots were used. All the trees in these 3 plots were planted in the spring of 1986 after the original forest was clear-cut and burned. Plot #1 is 300 meters from Plots #2 and #3 and is on a gentle southwest facing slope. Plot #2 is on a steep slope facing southeast and plot #3 is level. The average height and diameters of trees on the three Nelder plots before the growing season of 1988 were:

Basal diameter	2.81 cm
DBH	1.25 cm
Height	257.49 cm

The original forest is Sitka spruce (Picea sitchensis (Bong.) Carr) and western hemlock (Tsuga heterophylla (Raf.) Sarg) (Greene, 1982). The area falls in-between the Picea sitchensis zone and Tsuga heterophylla zone of Franklin and Dyrness (1973). Much of the area has been logged or burned during the last 150 years. Douglas-fir (Pseudotsuga menziesii) is usually a dominant in this area. Other tree species include red alder, western redcedar (Thuja plicata Donn), and bigleaf maple (Acer macrophyllum).

The soil type of these sites is predominantly of a moderately deep to shallow soil derived primarily from residuum. Surface layers are thin loams and subsoils are thin to moderately thick silt loams and silty clay loams.



Vegetation other than red alder was mechanically removed from these 3 plots throughout the experimental period.

#### **NELDER PLOT DESIGN**

Nelder plot design has several advantages over other plot designs (Nelder, 1962). Less area is required, fewer guard trees are required, and different and continuous densities appear in the same plot. A Nelder type 1a plot design was used to investigate absolute density in red alder in this study. Spacing ranged from 30 cm to 6 m in each plot. One Nelder plot consists of 15 concentric circles and 24 spokes (Fig. 1). Each plot represents a density ranging from 238 to 101,219 trees per hectare. Table 1 shows the density for each circle. The most interior circle is #1, and the most exterior is #15 (lowest density). Each plot was divided in half by a line perpendicular to the contour of the slope. One half was chosen at random to receive fertilizer, while the other half serves as control and was used in this study. To avoid possible influence of fertilizer, the 4 middle boundary spokes adjacent to the fertilized half were not used.

#### **MEASUREMENT METHODS**

Leaf water potential was measured with a pressure chamber apparatus (PMS Instrument Co., Corvallis, OR) (Scholander, 1965). A single leaf was used for each

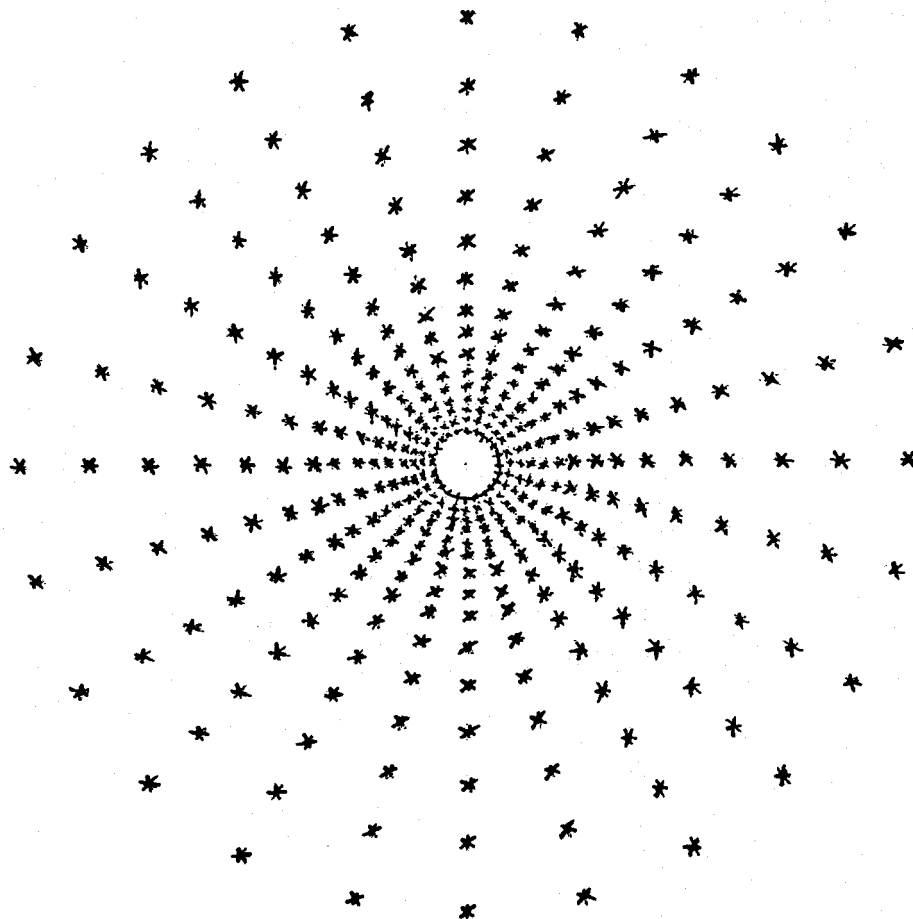


Fig.1. Diagram of a type 1a Nelder plot

A Nelder plot consists of 15 concentric circles and 24 spokes. Each point indicates one red alder tree in the Nelder plot

Table 1. Density at each arc in the Nelder plots

arc #	area per tree (M <sup>2</sup> /tree)	tree per hectare (tree/ha)
1 *	0.10	101,219
2	0.10	101,219
3	0.15	64,627
4	0.26	37,864
5	0.43	23,016
6	0.73	13,623
7	1.24	8,048
8	2.10	4,759
9	3.57	2,804
10	6.02	1,660
11	10.17	984
12	17.13	584
13	28.99	345
14	41.99	238
15 *	41.99	238

\* Arcs 1 and 15 are borders and were not used

sample. One instrument was used for most of the measurements, and when another instrument was used, it was calibrated with the first one. Sample leaves were taken at random for night measurements and from the south side of the mid-crown in the daytime (Klepper, 1968; Tobiessen et al., 1971). The rate of pressure increase was kept at about  $0.68 \text{ atm s}^{-1}$  (Waring and Cleary, 1967). Only one person operated the instrument to avoid errors between operators.

Stomatal conductance was measured with a LI-1600 steady state porometer (Li-Cor inc., Lincoln, Nebraska, USA). The same instrument was used for all measurements. It was calibrated in the Department of Soil Science in Oregon State University in April, 1988. Nondestructive measurements were conducted only on mature and healthy leaves (Harrington, 1987). Because solar radiation shows strong correlation with transpiration of leaves (Baker, 1984), only leaves which were exposed to the sun in the upper crown of the trees were used. The same person conducted all of the measurements.

#### DATA COLLECTION

Figure 2 shows the configuration of seasonal and diurnal measurements conducted.

Seasonal data was collected biweekly from May 1 to October 9, 1988. Predawn Leaf water potential was measured

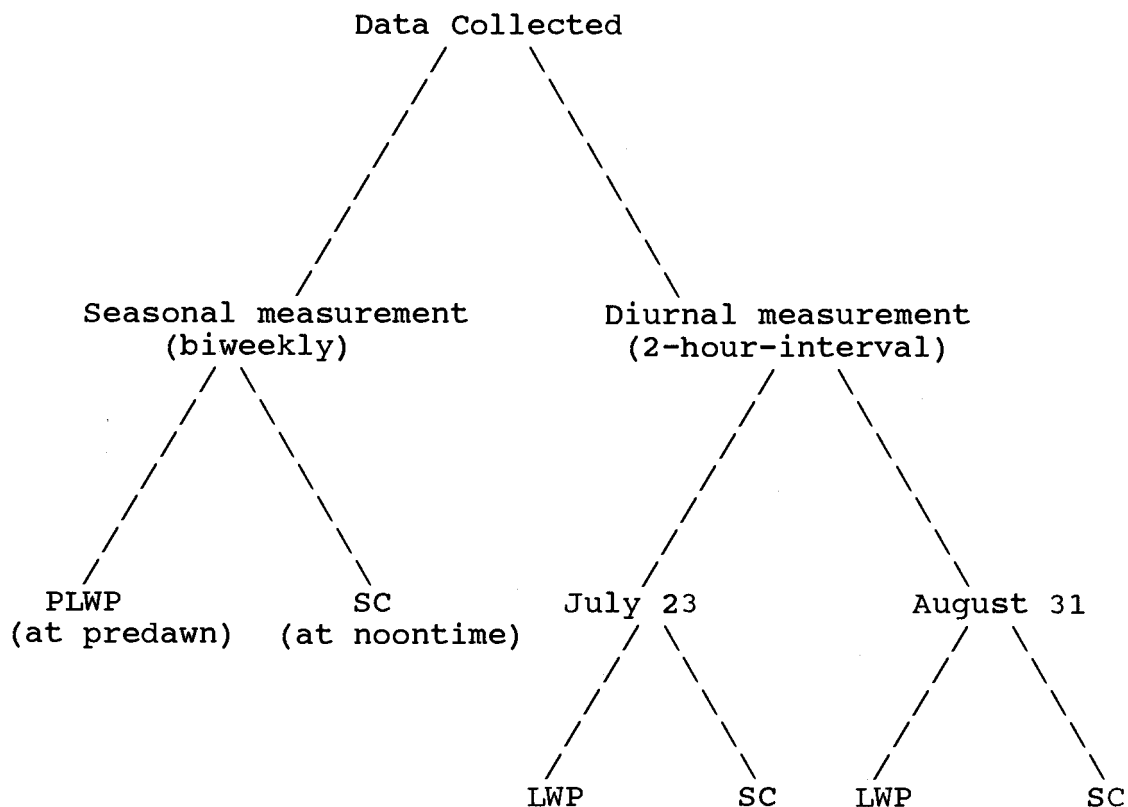


FIG. 2. The configuration of seasonal and diurnal measurements of red alder at Cascade Head Experiment Forest in 1988.

LWP: Leaf water potential

PLWP: Predawn leaf water potential

SSC: Seasonal stomatal conductance

between 4:00 and 6:00 am on trees from 6 densities (arcs 2, 4, 6, 9, 12, and 14). All three plots were used. Three sample trees were randomly chosen from each arc in each plot. Stomatal conductance was measured at noontime on the same day the predawn leaf water potential measurements were made provided the weather was clear. If the weather was cloudy, stomatal conductance was measured on the next clear day. Four densities (arcs 4, 6, 9, and 12) were selected for measurement of stomatal conductance. Only plot #1 was used for stomatal conductance measurements. The same trees used for predawn leaf water potential measurements were used for these measurements. Two leaves were sampled from each tree. Air temperature, photosynthetically active radiation, and relative humidity were also recorded at the same time.

Diurnal measurements were conducted on two days: July 23 and August 31, 1988. Both were warm and clear with gentle wind. July 23 represented the early days with no water limitation, while August 31 represented the driest days in the late summer. Only plot #1 was used. Sample trees were different from those used for biweekly measurements. Five densities (arcs 2, 4, 6, 9, and 12) were used for diurnal leaf water potential measurements, while 4 densities (arcs 4, 6, 9, and 12) were used for diurnal stomatal conductance measurements. Arc 2 was not used because there were insufficient leaves facing the sun

in that density. Four sample trees were used from each density. One leaf water potential measurement and two stomatal conductance measurements were recorded from each tree. The diurnal leaf water potential measurements were started at 4:00 am and terminated at 2:00 am on the following day. Leaf water potentials were measured over a 24-hour cycle, while diurnal stomatal conductance measurements were conducted from 8:00 am to 6:00 pm on the same day. Leaf water potential and stomatal conductance were measured every 2 hours. Leaf water potential was measured first, followed by the stomatal conductance measurement. For each sampling period, leaf water potential measurements took about 25 min., and stomatal conductance measurements about 20 min..

Annual precipitation and temperature data were obtained from the Cascade Head Experimental Forest Headquarters. Soil water content was obtained from another study that used the same Nelder plots in 1988 (T. Harrington, personal communication).

Table 2 shows the number of samples taken for predawn leaf water potential (PLWP), seasonal stomatal conductance (SSC), diurnal leaf water potential (DLWP), and diurnal stomatal conductance (DSC) measurements on each date.

#### DATA ANALYSIS

SAS software (Cody and Smith, 1987) was used for

Table 2. Number of samples of seasonal and diurnal measurements on each date

	Measurement			
	PLWP	SSC	DLWP	DSC
# of plots	3	1	1	1
# of densities/plot	6	4	5	4
# of trees/density	3	3	4	4
# of samples/tree	1	2	1	2
total # of samples /density	9	6	4	8

PLWP: Predawn leaf water potential  
 SSC: Seasonal stomatal conductance  
 DLWP: Diurnal leaf water potential  
 DSC: Diurnal stomatal conductance



analysis of variance, separation of means, and regression analysis. A randomized block design was used for analysis of variance. Least Square difference, Waller, and Duncan test methods were used for the separation of means. Since date in seasonal data and time in diurnal data interacted with density treatment, the analysis of variance and mean separations were conducted on each date and time. A significance level of 0.05% was used in this study. The stepwise method was used for multiple regression, and only the parameters with significant coefficients ( $p < 0.05$ ) were included in the model.

STATGRAPHICS software (STSC, Inc, 1988) was used for graphs. Means for each density on each date or at each time were used for seasonal and diurnal courses of leaf water potential and stomatal conductance. Individual measurements from seasonal and diurnal data were used to develop the limitation lines of temperature, radiation, and vapor pressure deficit on stomatal conductance using the boundary-line analysis techniques (Webb, 1972). But means from diurnal measurements were used to develop limitation lines of leaf water potential on stomatal conductance.

Seasonal data were used for seasonal courses of Predawn leaf water potential and stomatal conductance, analysis of variance, mean separation, and regressions of predawn leaf water potential and stomatal conductance on

density, maximum and minimum temperature, precipitation, and vapor pressure deficit at noontime. Diurnal data (on July 23, August 31, 1988) were used for diurnal courses of leaf water potential and stomatal conductance, analysis of variance, mean separation, and regression of leaf water potential and stomatal conductance on air temperature, radiation, and vapor pressure deficit.

Vapor pressure deficit was converted from relative humidity and air temperature (Waring and Schlesinger, 1985). The equation of saturated vapor pressure ( $VP_S$ ) is:

$$VP_S = 6.1078(17.269T/237 + T)$$

Where T is temperature in degree of Celsius. The vapor pressure deficit (VPD) calculated as:

$$VPD = VP_S - (VP_S) \cdot (RH)$$

Where RH is relative humidity.

## RESULTS

### SEASONAL TRENDS OF PREDAWN LEAF WATER POTENTIAL (PLWP)

The PLWP of trees at lower densities (2,804, 584 and 238 trees/ha) remained relatively constant throughout the entire growing season (Fig.3 A). On the other hand, the PLWP of trees growing at higher densities decreased during the dry season. The curves of these two groups did not diverge before day 74 (measurements started from May 1, 1988). But plants growing at higher densities (101,219, and 37,864) had much lower PLWP than those growing at lower densities (2,804, 584, and 238 trees/ha) from day 88 to day 162 (table 3).

Precipitation appeared to affect the PLWP strongly (Fig.3 A.C). A series of rains before day 74 appeared to increase the PLWP of all trees to -0.04 MPa. A rain of 20 mm on day 108 apparently continued to affect the PLWP of plants growing at the 4 highest densities on day 115. The lowest PLWP (-1.05 MPa) occurred on day 137 (September 14, 1988) which was in the driest period before the fall rains. The maximum PLWP (-0.03 MPa) occurred on day 74 (July 14).

A period of hot days seemed to correlate with lower PLWP (Fig.3 A.B). A continuous series of high maximum temperatures from day 80 to day 100 preceded the lower

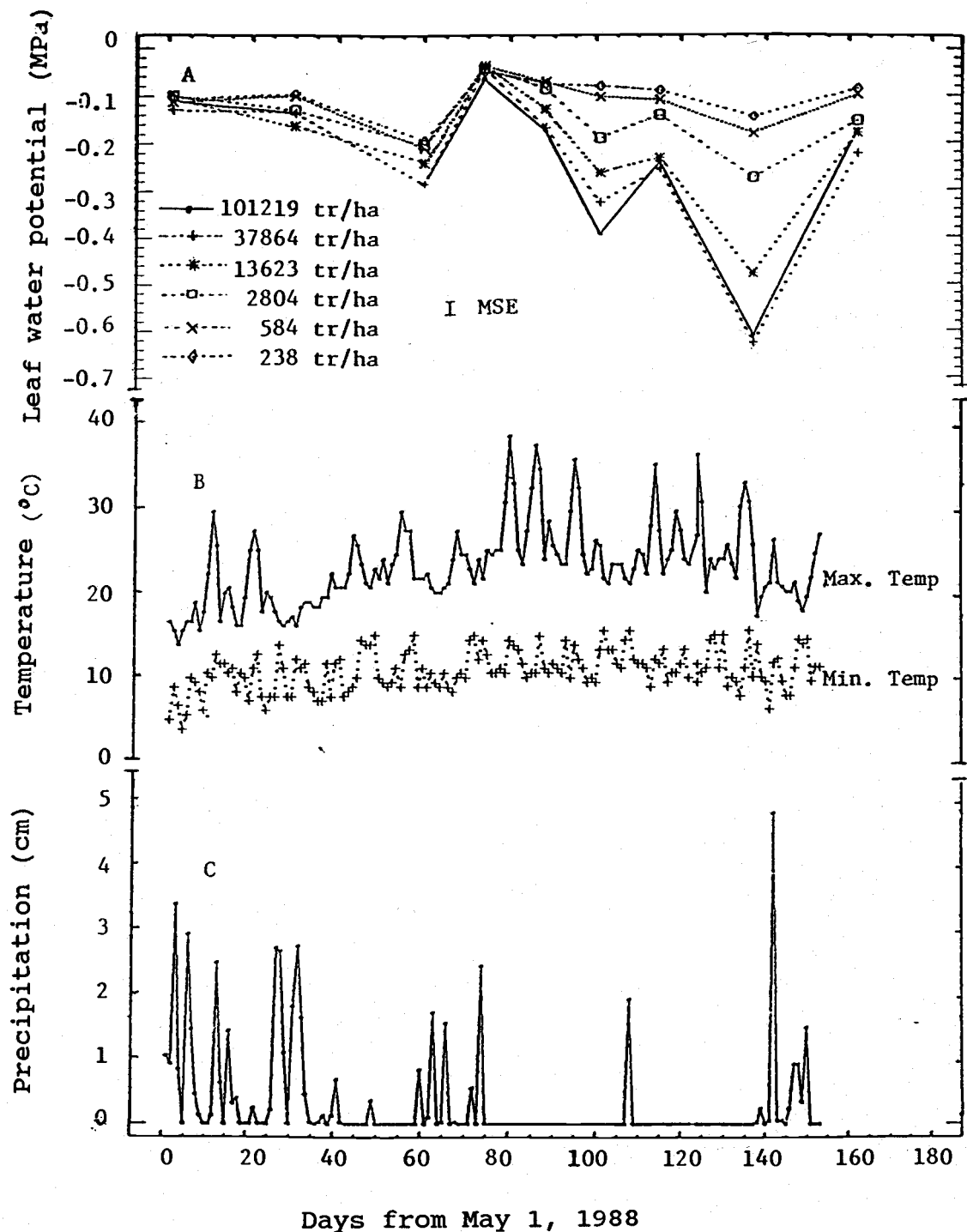


FIG.3. Seasonal trends of predawn leaf water potential of red alder growing at different densities (A). Each point in each line is the mean of 9 measurements. Seasonal trends of maximum and minimum temperature (B). Seasonal trend of precipitation (C).

Table 3. Mean difference analysis of predawn leaf water potentials (MPa) in different densities (n = 9)

Density trees/ha	Days from May 1, 1988				
	1	30	60	74	88
<hr/>					
101219 *	-0.110 a	-0.134 a	-0.286 a	-0.065 a	-0.174 a
37864	-0.128 a	-0.134 a	-0.286 a	-0.043 a	-0.167 a
13623	-0.097 a	-0.161 a	-0.241 ab	-0.037 a	-0.127 ab
2804	-0.098 a	-0.128 a	-0.203 b	-0.043 a	-0.084 b
584	-0.112 a	-0.099 a	-0.210 b	-0.037 a	-0.071 b
238	-0.105 a	-0.095 a	-0.193 b	-0.050 a	-0.073 b

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101	115	137	162	
<hr/>				
-0.392 a	-0.238 a	-0.610 ab	-0.174 b	
-0.324 ab	-0.252 a	-0.626 a	-0.224 a	
-0.262 bc	-0.230 ab	-0.478 b	-0.180 b	
-0.188 c	-0.140 bc	-0.274 c	-0.154 c	
-0.103 d	-0.108 c	-0.180 c	-0.099 c	
-0.080 d	-0.088 c	-0.145 c	-0.087 c	

\* For each day, means followed by the same letters are not significantly different ( $p < 0.05$ ).

PLWP on day 101. And a series of hot days from day 110 to day 137 preceded the lowest PLWP on day 137.

#### SEASONAL TRENDS OF STOMATAL CONDUCTANCE AT NOONTIME

Seasonal variation in stomatal conductance of red alder for all densities was large (Fig.4 A). The highest conductance ( $1.05 \text{ cm s}^{-1}$ ) was measured on day 88, and the lowest ( $0.08 \text{ cm s}^{-1}$ ), on day 136 in the densities of 2,804 and 37,864 trees per hectare, respectively. The over-all mean for all densities was  $0.676 \text{ cm s}^{-1}$  ( $n=216$ ). The maximum value was recorded in the early season when soil water was nonlimiting. The minimum was found in late summer when the soil was dry.

Precipitation was closely related to plant stomatal conductance (Fig.4 A.C) during most of the growing season. A series of rains preceded the highest stomatal conductance on day 88, and a long dry period (before day 140) was related to the lowest value on day 136. Greater stomatal conductance resumed after the fall rains.

Mean stomatal conductance of plants in different densities were not significantly different from each other early in the season. But plants growing at low density (584 tree/ha) had significantly higher mean stomatal conductance than plants at the 3 higher densities after day 88 (Table 4). In general, plants growing at lower densities had greater stomatal conductance than those

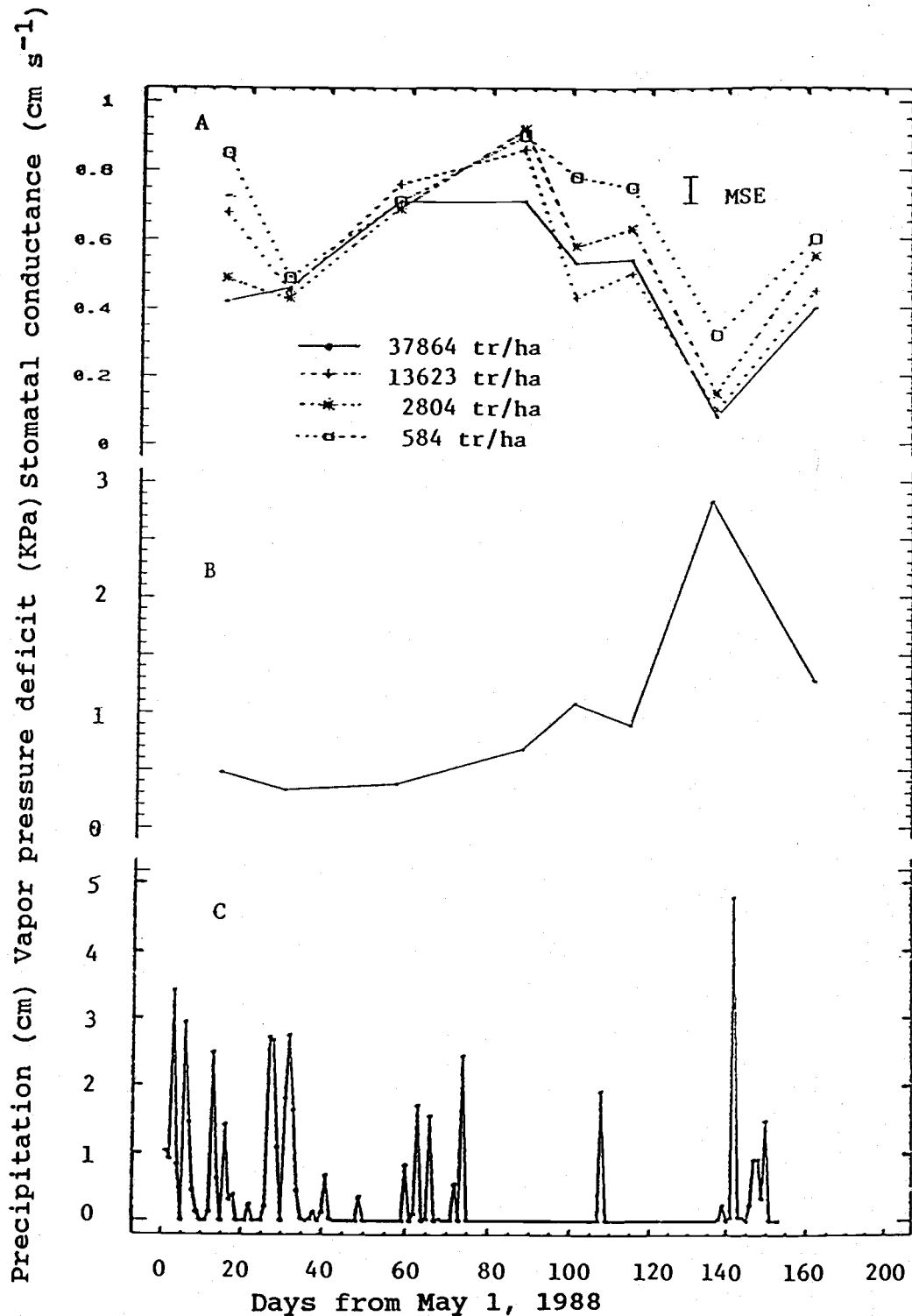


FIG.4. Trends of seasonal stomatal conductance of red alder in different densities (A). Each point in each line is the mean from 6 measurements. Seasonal trend of vapor pressure deficit (B). Seasonal trend of precipitation (C).

Table 4. Mean difference analysis of stomatal conductance ( $\text{cm s}^{-1}$ ) of red alder growing at different densities measured at noontime (n=6)

DENSITY	Days from May 1, 1988				
TREE/HA	14	30	57	84	88
<hr/>					
<sup>*</sup>					
37,864	0.42 a	0.46 a	0.71 a	2.08 a	0.71 a
13,623	0.68 ab	0.45 a	0.76 a	1.49 a	0.86 a
2,804	0.49 a	0.43 a	0.69 a	1.52 a	0.92 a
584	0.85 b	0.49 a	0.71 a	1.65 a	0.90 a
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	101	115	136	162	
	<hr/>				
	0.53 ab	0.54 a	0.08 a	0.40 a	
	0.43 a	0.50 a	0.10 ab	0.45 ab	
	0.58 b	0.63 ab	0.15 b	0.55 bc	
	0.78 c	0.75 b	0.32 c	0.60 c	
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\* For each day Means followed by the same letters are not significantly different ( $P < 0.05$ ).



growing at higher densities in the dry season.

Stomatal conductance appeared to parallel evaporation demands for all plants in the early season (Fig. 4 A.B) before day 84, but that relationship disappeared, and VPD negatively related to stomatal conductance in the later part of the growing season. High evaporation demand apparently related to low stomatal conductance from day 88 to day 162.

#### DIURNAL TRENDS OF LEAF WATER POTENTIAL

Two days were selected for diurnal measurements of leaf water potential and stomatal conductance: July 23, which followed a series of rains in the early growing season; and August 31, which was in the dry season in the latter part of the growing season.

The general trends of leaf water potential were the same for both days (Fig. 5 and 6). Plant leaf water potential maintained high values before sunrise, then changed rapidly in early morning from high (predawn values) to low values (midday value), and plants maintained a low leaf water potential from 10:00 am to 4:00 pm. Leaf water potential gradually increased after 4:00 pm. There are some differences between these two diurnal courses. Plants had a larger difference between the highest and the lowest leaf water potential value, and plants recovered more quickly on July 23 than on August

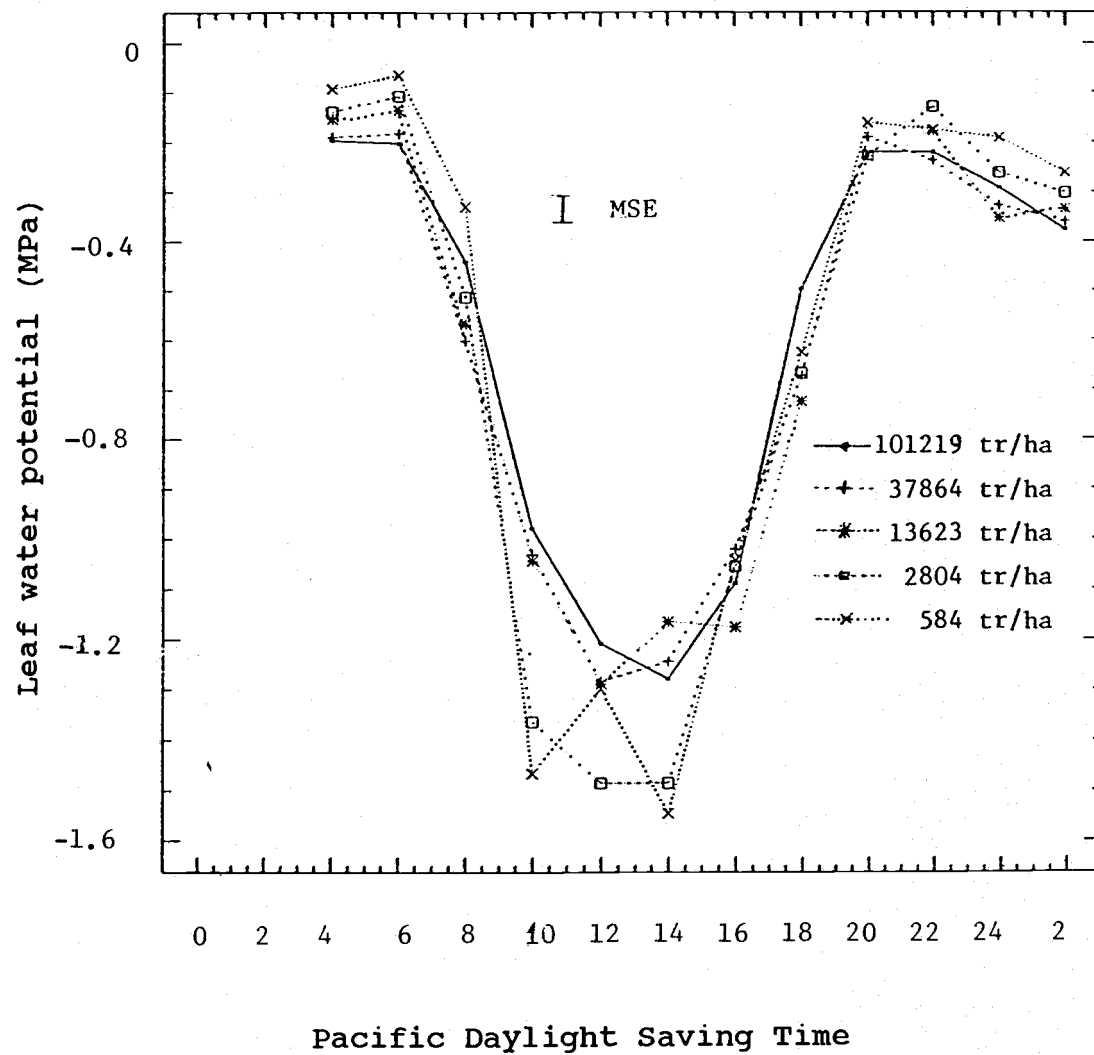


Fig. 5. Trends of diurnal leaf water potential of red alder growing at different densities on July 23, 1988. Each point is the mean of 4 measurements

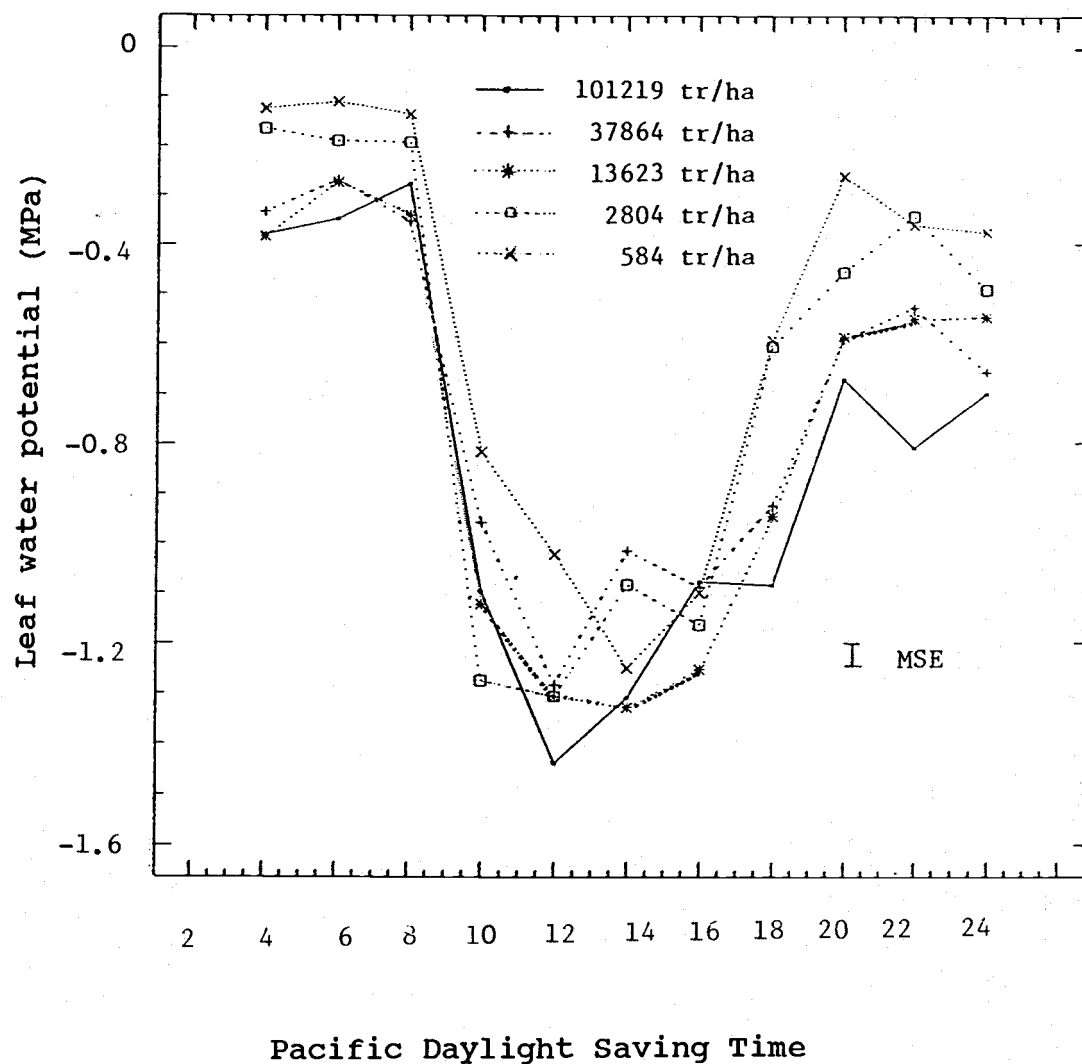


Fig. 6. Trends of diurnal leaf water potential of red alder growing at different densities on August 31, 1988. Each point is the mean of 4 measurements

31. There were larger differences in leaf water potential between different densities at night on August 31 than on July 23. Plants also maintained a lower leaf water potential for a longer time during the day on August 31 than on July 23. At night on August 31, Plants growing at higher densities had significantly lower leaf water potential than those growing at lower densities. During the day, however, there were no significant differences in leaf water potential between plants growing at different densities (Tables 5 and 6) for both days.

#### DIURNAL TRENDS OF STOMATAL CONDUCTANCE

Plant stomatal conductance increased from early morning to a maximum value by 10:00 am, then maintained that high value for the rest of the day even though the solar radiation was very low by 6:00 pm on July 23 (Fig.7). The changes in temperature and vapor pressure deficit value seemed to parallel the diurnal trends of stomatal conductance.

Stomatal conductance of plants in different densities were not significantly different for most of the day on July 23 (Table 7) although the mean stomatal conductance of plants at high density (37,864 tree/ha) was always higher than that found in plants at lower densities. The differences were not significant statistically due to large variation of stomatal conductance in trees at the

Table 5. Mean difference analysis of diurnal leaf water potential (MPa) of red alder on July 23, 1988 (N=4)

DENSITY		Pacific daylight saving time				
TREE/HA		4:00	6:00	8:00	10:00	12:00
<hr/>						
	*					
101,219		-0.198a	-0.203a	-0.440a	-0.978a	-1.208a
37,864		-0.190ab	-0.183ab	-0.600a	-1.033a	-1.283a
13,623		-0.155bc	-0.138bc	-0.565a	-1.043a	-1.288a
2,804		-0.140c	-0.108cd	-0.513a	-1.363b	-1.485a
584		-0.093d	-0.065d	-0.330a	-1.465b	-1.298a
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						**
14:00	16:00	18:00	20:00	22:00	24:00	2:00
<hr/>						
-1.278a	-1.000a	-0.588a	-0.220a	-0.220a	-0.293a	-0.378a
-1.242a	-1.020a	-0.620a	-0.190a	-0.238a	-0.328a	-0.360a
-1.165a	-1.175a	-0.722a	-0.230a	-0.178ab	-0.353a	-0.335ab
-1.485a	-1.055a	-0.665a	-0.228a	-0.130b	-0.263a	-0.303ab
-1.545a	-1.043a	-0.622a	-0.163a	-0.175ab	-0.193a	-0.263b
<hr/>						

\* For each time, means followed by the same letters are not significantly different ( $P < 0.05$ ).

\*\* 2:00 am on July 24, 1988

Table 6. Means difference analysis of diurnal leaf water potential (MPa) of red alder measured at different times on August 31, 1988 (n=4)

DENSITY TREE/HA	Pacific daylight saving time					
	4:00	6:00	8:00	10:00	12:00	14:00
	*					
101,219	-0.383a	-0.350a	-0.278ab	-1.098ab	-1.438a	-1.308a
37,864	-0.307ab	-0.257ab	-0.333a	-0.93b	-1.227a	-1.067a
13,623	-0.385a	-0.275ab	-0.343a	-1.123ab	-1.305a	-1.328a
2,804	-0.167bc	-0.190bc	-0.193ab	-1.275a	-1.305a	-1.083a
584	-0.100c	-0.110c	-0.140b	-0.920b	-1.047a	-1.250a
	16:00	18:00	20:00	22:00	24:00	
	-1.078a	-1.085a	-0.670a	-0.808a	-0.700a	
	-1.237a	-0.983a	-0.620a	-0.550b	-0.557ab	
	-1.253a	-0.945a	-0.585ab	-0.550b	-0.548b	
	-1.163a	-0.905a	-0.455b	-0.343b	-0.493b	
	-1.100a	-0.457a	-0.273c	-0.347b	-0.363b	

\* For each time, means followed by the same letters are not significantly different ( $P < 0.05$ ).

Table 7. Mean difference analysis of diurnal stomatal conductance ( $\text{cm s}^{-1}$ ) of red alder on July 23, 1988 (N=8)

Density		Pacific daylight saving time				
Tree/ha	8:00	10:00	12:00	14:00	16:00	18:00
*						
37,864	0.99a	1.83a	2.08a	2.18a	2.03a	1.80a
13,623	0.83ab	1.57a	1.49a	1.76a	1.56b	1.72a
2,804	0.72ab	1.64a	1.52a	1.85a	1.47b	0.96b
584	0.45b	1.12a	1.65a	1.65a	1.30b	1.35ab

\* For each time, means followed by the same letters are not significantly different ( $P < 0.05$ ).

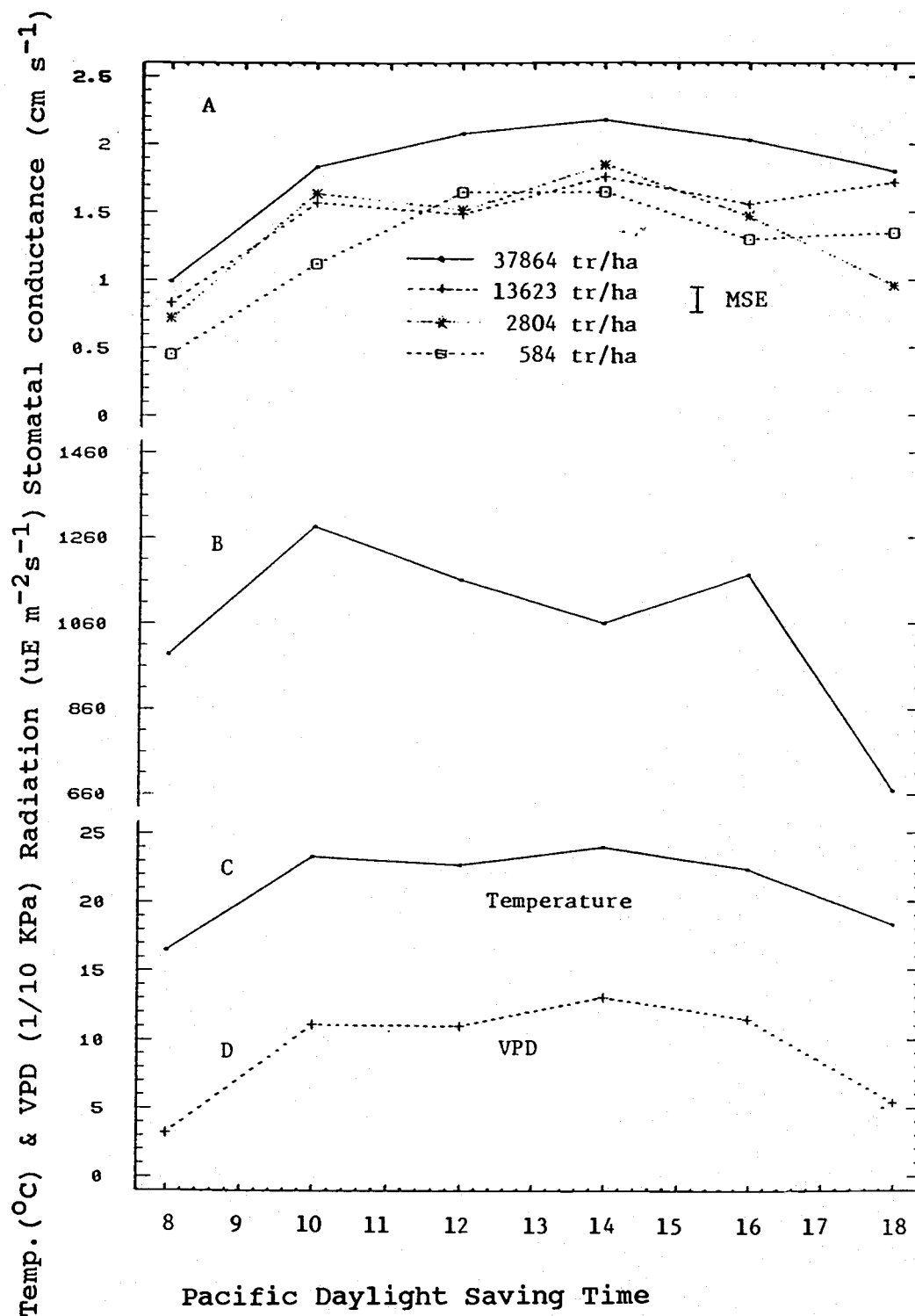


Fig. 7. Trends of diurnal stomatal conductance of red alder in different densities (A) on July 23, 1988. Each point in each line is from 8 measurements. Diurnal trend of solar radiation (B). Diurnal trend of temperature (C). Diurnal trend of vapor pressure deficit (D).



density of 37,864 trees per hectare.

On August 31, stomatal conductance of plants at low density (2,804 and 584 trees/ha) remained high from 8:00 am until 4:00 pm, then decreased to near zero by 6:00 pm (Fig.8). But plants at high density (37,864 and 13,623 trees/ha) seemed to close their stomata by 10:00 am. The highest and average values on August 31 (0.69 and 0.414 respectively) were much smaller than those found on July 23 (2.18 and 1.503 respectively). Temperature and vapor pressure deficit did not seem to affect stomatal conductance on August 31 the same way as on the earlier date. Trees at high density closed their stomata as the vapor deficit increased to greater than 6 mb.

Stomatal conductance of plants growing at lower densities (2,804 and 584 tree/ha) was significantly higher than that of plants growing at higher densities (37,864 and 13,623 tree/ha) most of the day on August 31 (Table 8).

#### RESPONSES OF STOMATAL CONDUCTANCE

The boundary lines in Figures 9, 10, 11, 12, and 13 represent the upper limit of stomatal conductance responses to air temperature, vapor pressure deficit, solar radiation, and plant leaf water potential separately over the conditions of the data set.

The upper limit of stomatal conductance as a function

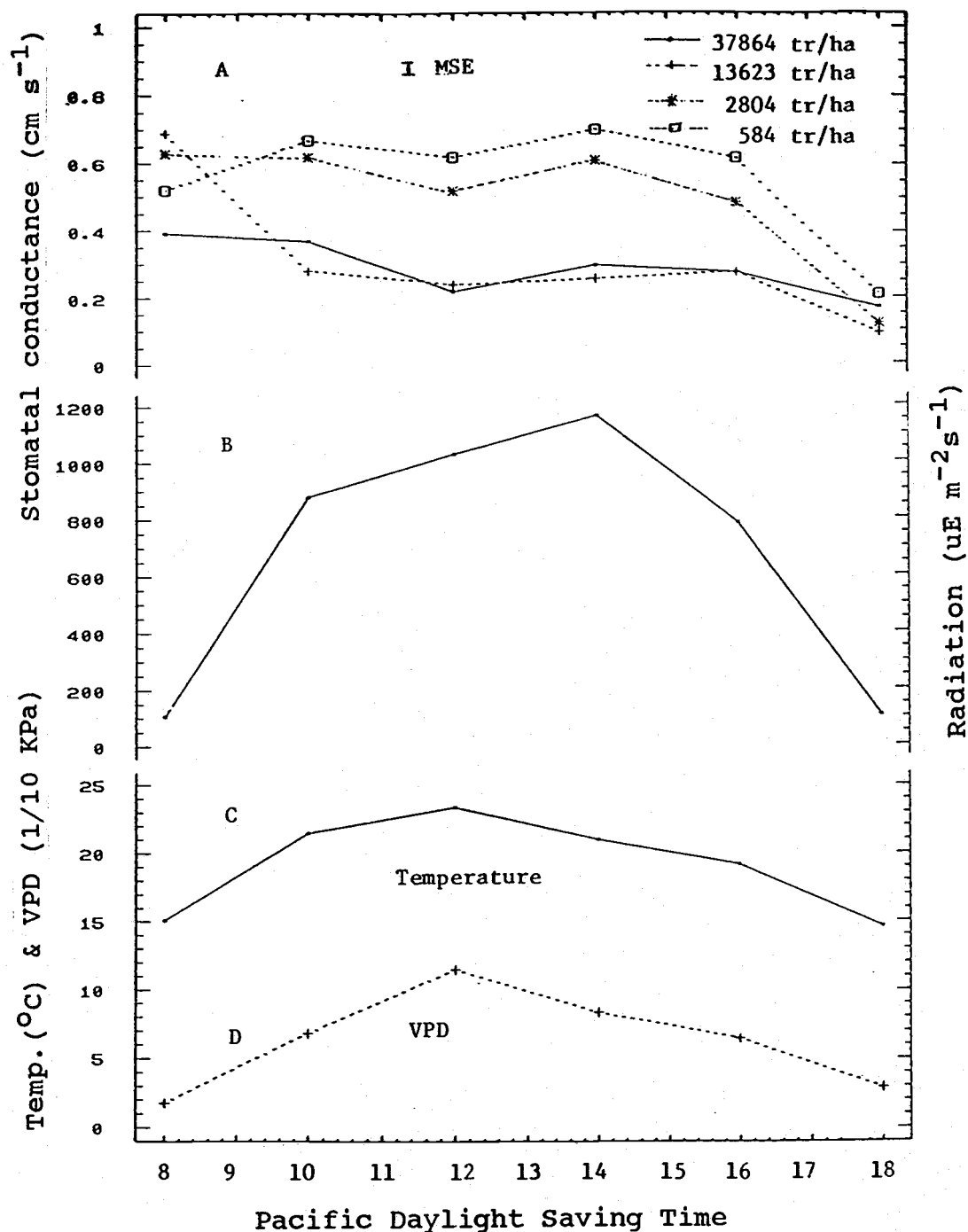


Fig. 8. Trends of diurnal stomatal conductance of red alder in different densities (A) on August 31, 1988. Each point in each line is from 8 measurements.  
 Diurnal trend of solar radiation (B).  
 Diurnal trend of temperature (C).  
 Diurnal trend of vapor pressure deficit (D).

Table 8. Mean difference analysis of diurnal stomatal conductances ( $\text{cm s}^{-1}$ ) of red alder on August 31, 1988 (N=8)

Density		Pacific daylight saving time				
Tree/ha	8:00	10:00	12:00	14:00	16:00	18:00
<hr/>						
37,864	0.39a	0.37a	0.22a	0.30a	0.27a	0.17a
13,623	0.69a	0.28a	0.24a	0.26a	0.28a	0.09a
2,804	0.63a	0.62b	0.52b	0.61b	0.49b	0.12a
584	0.52a	0.67b	0.62b	0.74c	0.62b	0.21a
<hr/>						

\* For each time, means with the same letters are not significantly different ( $P < 0.05$ ).

of air temperature was bell-shaped (Fig.9). Stomatal conductance increased as temperature increased at the range of temperature less than 23°C, then stomatal conductance decreased as the temperature continued to rise. The optimum temperature for stomatal conductance ranged from 18 to 27°C. The stomatal conductances in this range were all larger than 85% of the maximum values.

The response line of stomatal conductance at noontime to vapor pressure deficit (VPD) in the early growing season was positively associated (Fig. 10). Increasing VPD also increased stomatal conductance. In the late summer, stomatal conductance was curvilinearly associated with VPD over the range of VPD less than 3.0 KPa using the pooled data from seasonal and diurnal measurements (Fig.11). Stomatal conductance decreased as VPD increased from 0.6 to 2.0 KPa, While stomatal conductance seemed to increase as VPD increase in the range less than 0.6 KPa, and stomatal conductance leveled off in the range of VPD higher than 2.0 KPa.

The responses of stomatal opening seemed to require a low level of solar radiation. A solar radiation level of 100  $\mu\text{E m}^{-2}\text{s}^{-1}$  corresponded to a stomatal conductance which was 80% of the maximum value. Stomatal conductance closed rapidly as the solar radiation decreased from 100 to 0  $\mu\text{E m}^{-2}\text{s}^{-1}$ , the saturation point (Fig.12) was less than 1,200  $\mu\text{E m}^{-2}\text{s}^{-1}$ . Stomatal conductance remained at the highest

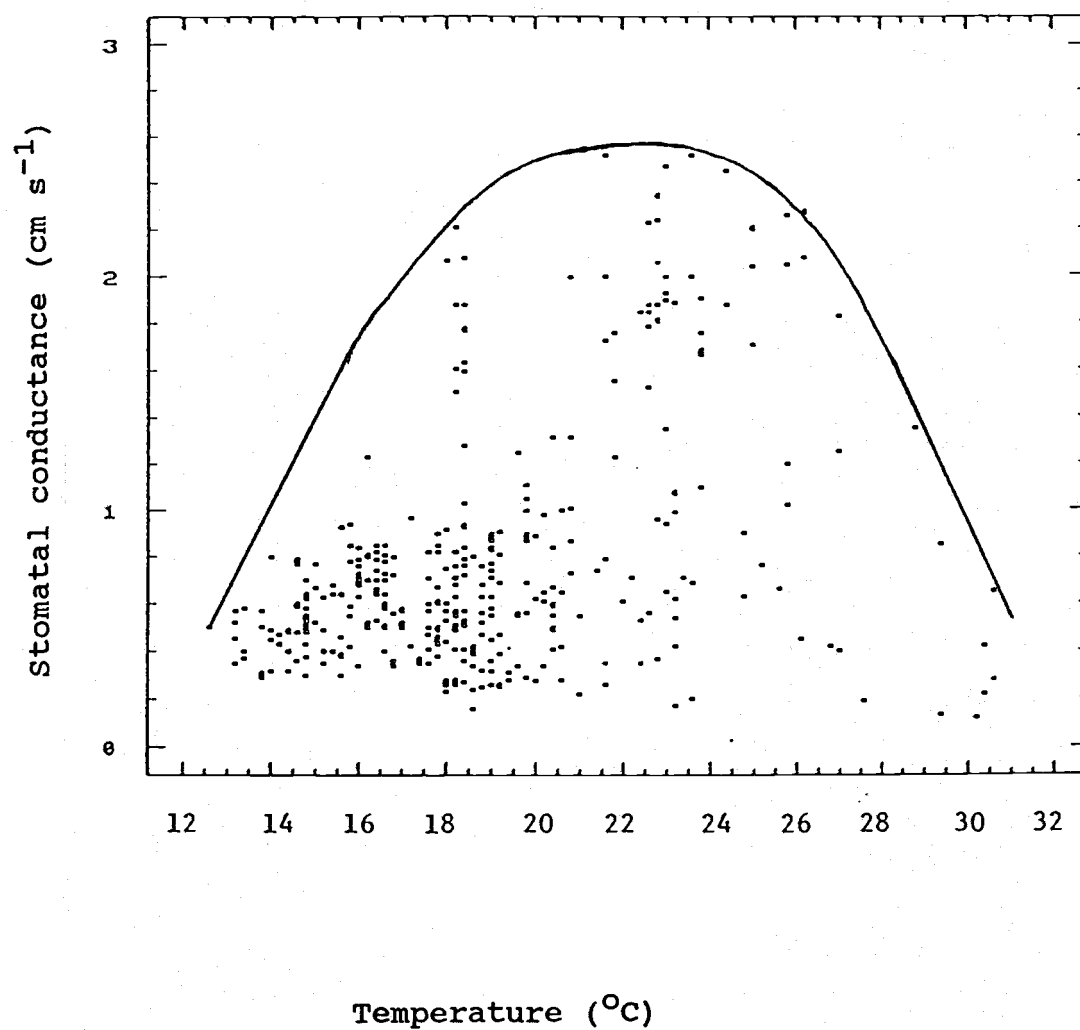


Fig. 9. Boundary-line of stomatal conductance to air temperature (N=368). The continuous line represents the upper limit of stomatal conductance response to air temperature.

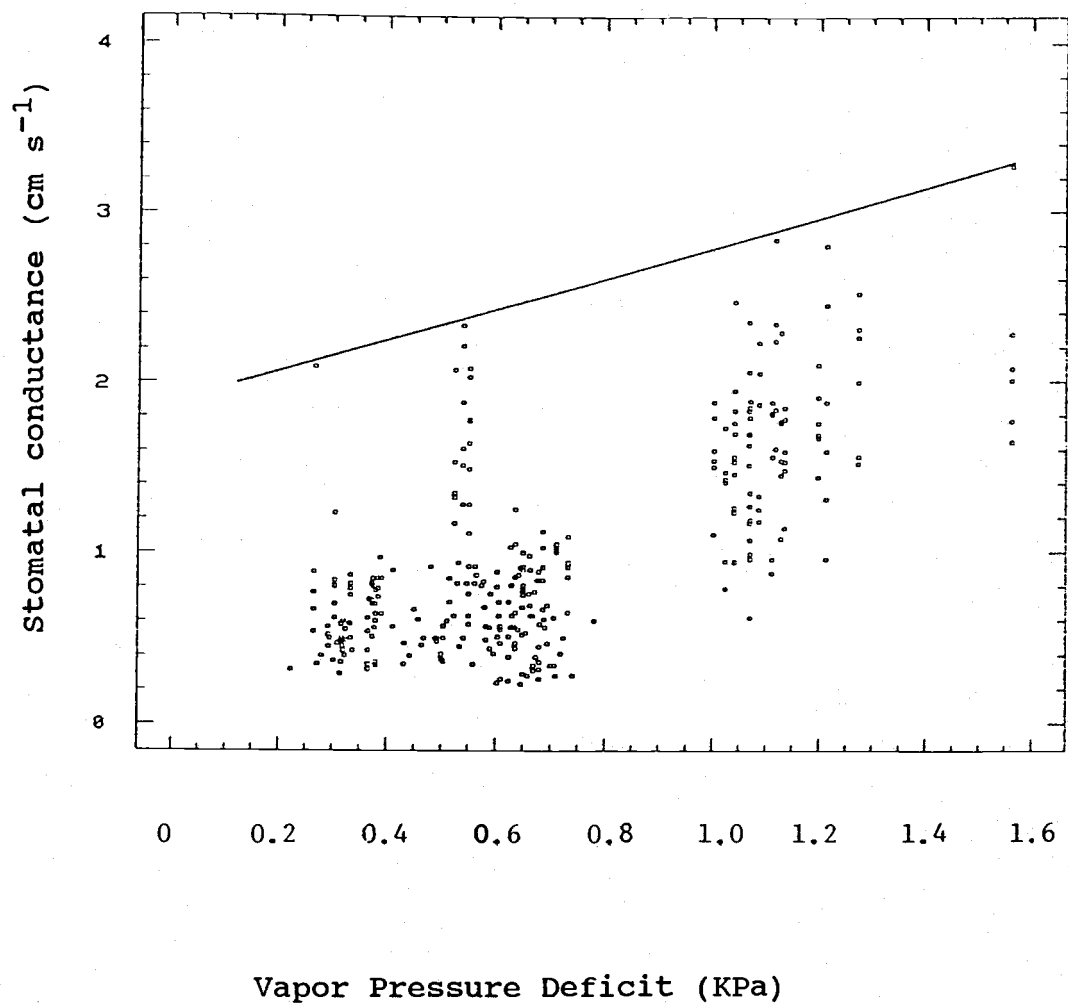


Fig. 10. Boundary-line of stomatal conductance to vapor pressure deficit of the pooled seasonal data (before day 88) and diurnal data (July 23) in the early growing season (N=320). Data are from 4 trees from each of the 4 densities: 37864 tr/ha, 13623 tr/ha, 2804 tr/ha, and 584 tr/ha.

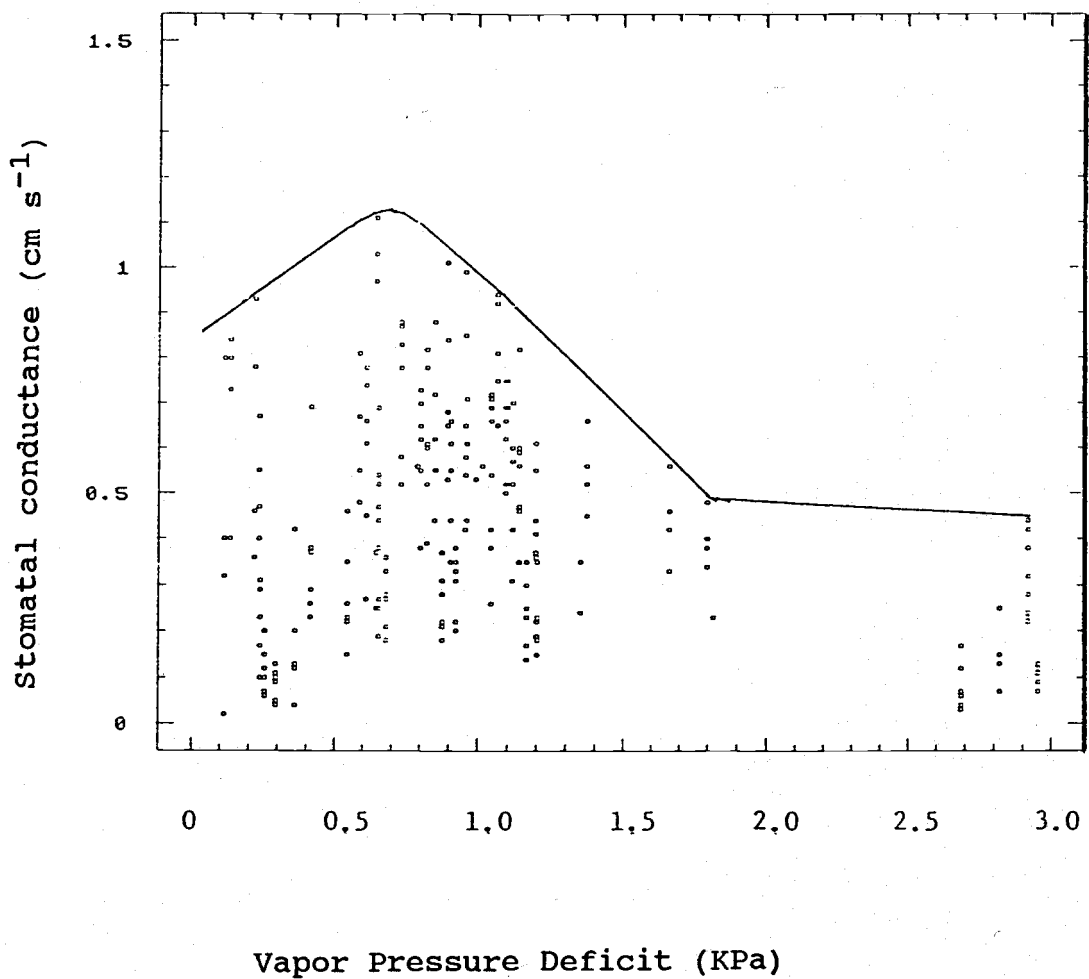


Fig 11. Boundary-line of stomatal conductance to vapor pressure deficit of the pooled data collected from day 88 to end of the season, and diurnal data on August 31. Densities used are the same as in Fig. 10.

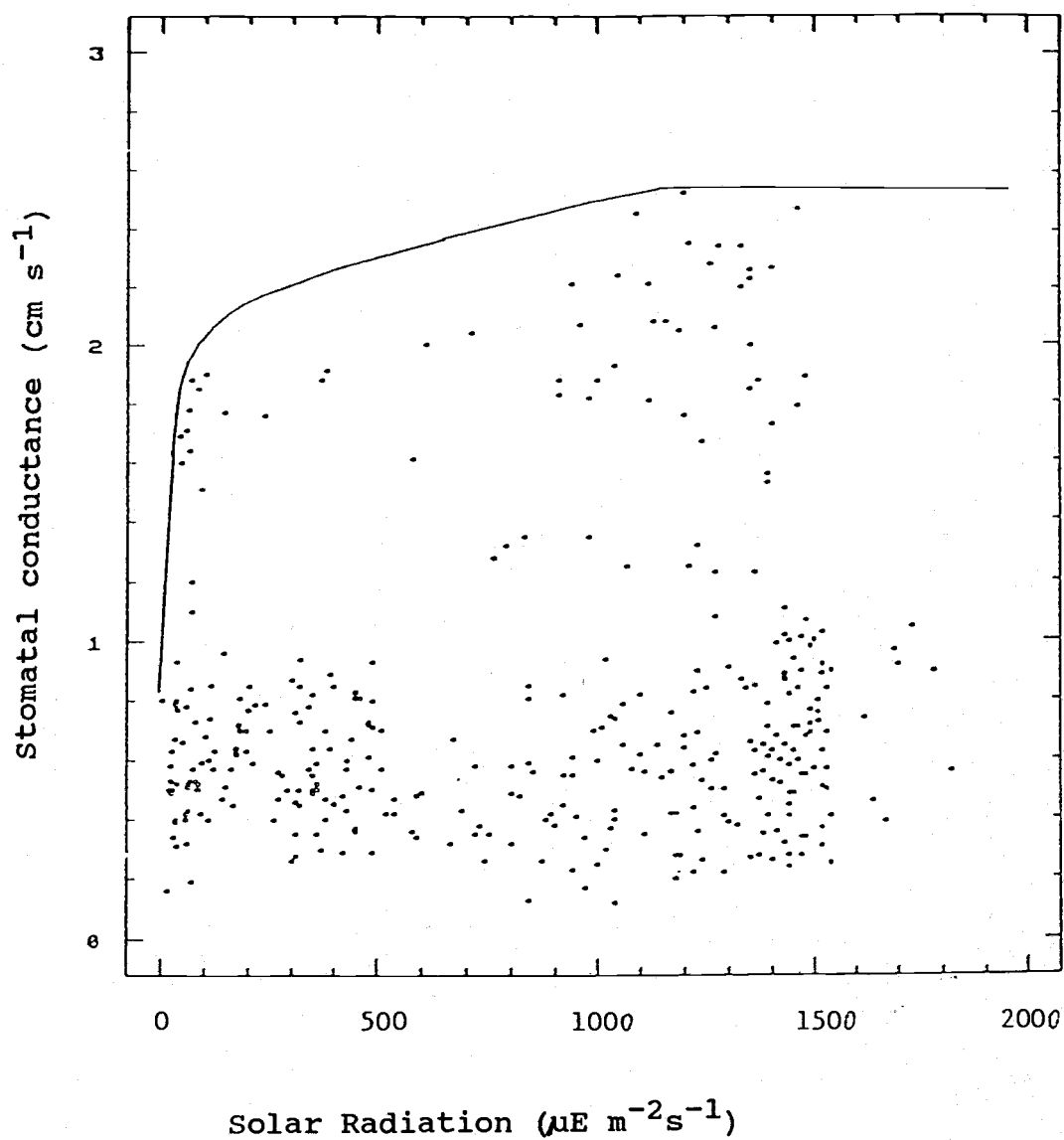


Fig 12. Boundary-line of stomatal conductance to solar radiation (N=368). The continuous line represents the upper limit of stomatal conductance response to solar radiation.



level when solar radiation was above  $1200 \text{ uE m}^{-2}\text{s}^{-1}$ .

Stomatal conductance did not seem to decrease as leaf water potential decreased in the early of the growing season. But in the late part of the growing season, plants responded by closing their stomata further when leaf water potential was greater than  $-1.2 \text{ MPa}$ . Figure 13 shows the response pattern of stomatal conductance to leaf water potential in the late part of the growing season.

There were no significantly different responses of stomatal conductance to the above factors in trees growing at different densities.

#### REGRESSION OF LEAF WATER POTENTIAL AND STOMATAL CONDUCTANCE

A. Regressions of seasonal predawn leaf water potential (PLWP) and regressions of stomatal conductance at noontime (SSC) were computed from seasonal data.

Table 9 shows the simple regressions of mean predawn leaf water potential on the following variables: mean stomatal conductance at noontime, density ( $\text{M}^2/\text{tree}$ ), vapor pressure deficit at noontime (VPD), maximum temperature ( $T_{\text{max}}$ ), minimum temperature ( $T_{\text{min}}$ ), and the sum of precipitation two weeks before the day of measurement (Precip). Stomatal conductance at noontime predicted PLWP very well ( $R^2 = 0.804$ ). Tree density was also a good predictor for PLWP in the late part of the growing season.

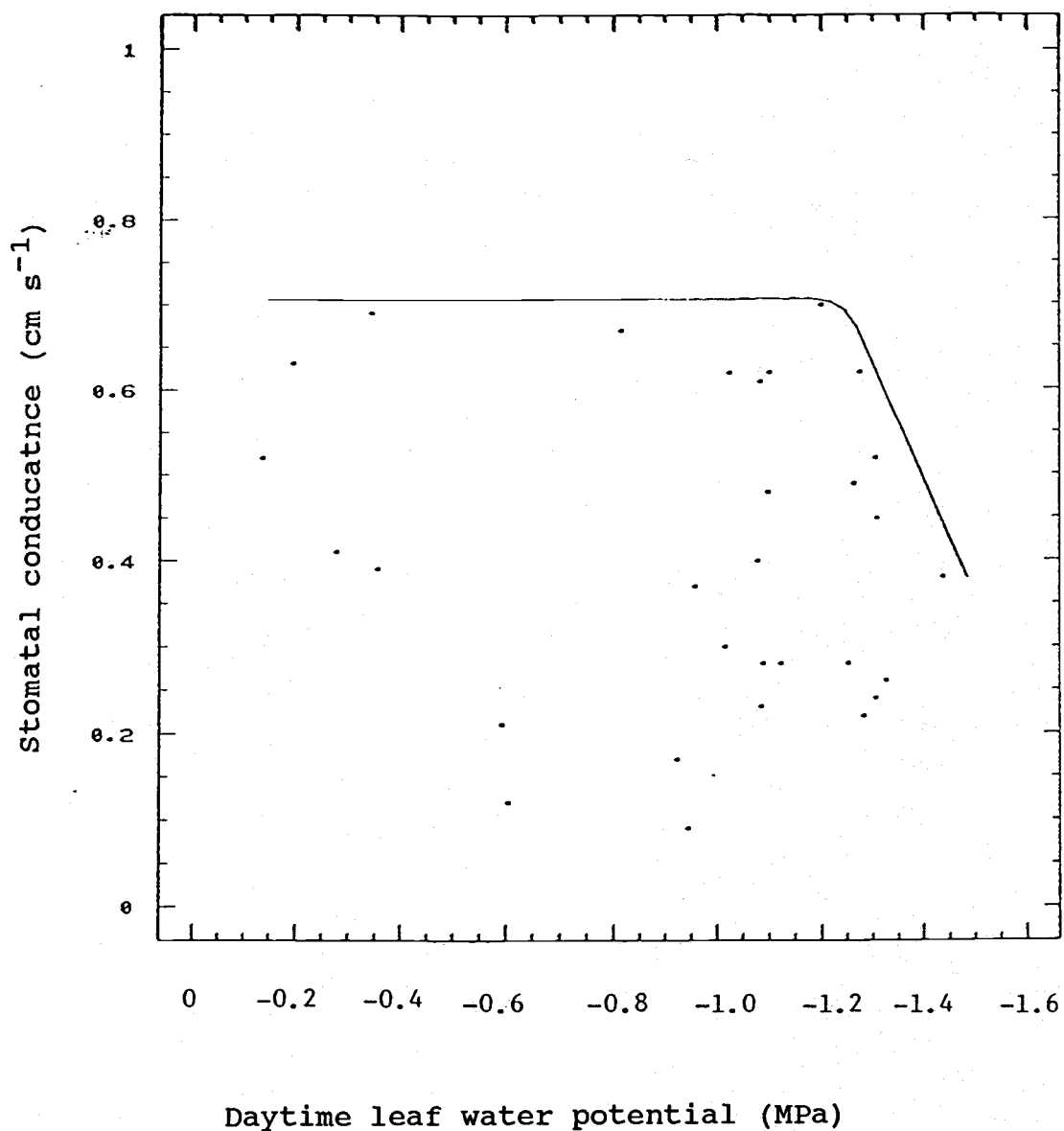


Fig.13. Boundary-line of stomatal conductance to leaf water potential (N=59). The continuous line represents the upper limit of stomatal conductance to leaf water potential from diurnal data collected on August 31, 1988. Densities used are the same as Fig.10.

Table 9. Simple regressions of predawn leaf water potential (n=54)

Equation	intercept (a)	slope (b)	P-value	R <sup>2</sup>
PLWP = a + b X ln(SSC)	0.0738	-0.1751	0.0001	0.804
* PLWP = a + b X (Dense)	0.0831	-0.0184	0.0001	0.571
PLWP = a + b(VPD)	0.1011	0.0904	0.0001	0.392
PLWP = a + b(Tmax)	-0.1070	0.0141	0.001	0.299
PLWP = a + b(Precip)	0.2470	-0.0218	0.001	0.279
PLWP = a + b(Tmin)	0.0163	0.0197	0.005	0.234

\* Data were from seasonal measurement in late summer  
(after day 88) (n=30)

PLWP: mean predawn leaf water potential (-MPa)  
 SSC: mean seasonal stomatal conductance (cm s<sup>-1</sup>)  
 Dense: density (M<sup>2</sup>/tree)  
 VPD: vapor pressure deficit (KPa)  
 Tmax: maximum temperature (°C)  
 Tmin: minimum temperature (°C)  
 Precip: precipitation (cm)

The multiple regression of PLWP on other variables are shown in table 10. Stomatal conductance at noontime, density, precipitation, and noon-time VPD significantly affected PLWP, but maximum and minimum temperature did not improve the fitness of the regression.

Table 11 shows the simple regressions of stomatal conductance at noontime on PLWP, VPD. Density, precipitation, maximum and minimum temperatures are not good predictors for stomatal conductance at noontime because the  $R^2$  is too low (less than 0.20). The multiple regression of SSC on PLWP, VPD, and precipitation is shown in table 12. Other variables did not improve the fitness of the regression.

B. Regressions of leaf water potential at daytime (DLWP) and regressions of stomatal conductance at daytime (DSC) were computed from diurnal measurements.

Stomatal conductance, VPD, and air temperature predicted leaf water potential at daytime very well (Table 13). Density seemed to predict mean leaf water potential during the day very poorly because the  $R^2$  is less than 0.10 in the simple regression.

Vapor pressure deficit, air temperature, and DLWP seemed to predict stomatal conductance during the daytime very well (Table 14). Solar radiation, and density seemed not to be good single predictors for stomatal conductance

Table 10. Multiple regression of mean predawn  
leaf water potential (-MPa) (n=54)

predictor	coefficient	P-value
constant	0.2073	0.0001
ln(SSC)	-0.2206	0.0001
ln(Dense)	-0.0127	0.03
Precip	-0.0250	0.0001
VPD	-0.089	0.005

R-square = 0.871

Model:

$$PLWP = a + \ln(SSC) + \ln(Dense) + Precip + VPD$$

ln: natural LOG.

SSC: seasonal stomatal conductance ( $\text{cm s}^{-1}$ )

Dense: density ( $\text{m}^2/\text{tree}$ )

Precip: precipitation (cm)

VPD: vapor pressure deficit (KPa)

Table 11. Simple regressions of Mean seasonal stomatal conductance (n=32)

Equation	intercept (a)	slope (b)	P-value	R <sup>2</sup>
SSC = a + b ln(PLWP/10)	0.7764	-0.3862	0.0001	0.669
SSC = a + b (VPD)	0.7452	-0.1870	0.0001	0.482

SSC: mean seasonal stomatal conductance (cm s<sup>-1</sup>)

PLWP: mean predawn leaf water potential (-MPa)

VPD: vapor pressure deficit (KPa)

Table 12. Multiple regression of mean seasonal stomatal conductance ( $\text{cm s}^{-1}$ ) (n=32)

predictor	coefficient	p-value
constant	1.0460	0.0001
ln(PLWP)	-0.2530	0.0001
VPD	-0.2070	0.0001
Precip	-0.0510	0.0001

R-sqaure = 0.844

Model:

$$\text{SSC} = a + \ln(\text{PLWP}/10) + \text{VPD} + \text{Precip}$$

SSC: seasonal stomatal conductance ( $\text{cm s}^{-1}$ )

ln: Natural LOG

PLWP: mean predawn leaf water potential (-MPa)

VPD: vapor pressure deficit (KPa)

Precip: precipitation (cm)

Table 13. Simple regressions of mean diurnal  
leaf water potential (n=24)

Equation	intercept (a)	slope (b)	R <sup>2</sup>
DLWP = a + b(VPD)	0.3102	0.7596	0.664
DLWP = a + b(Tair)	-0.8155	0.0849	0.618
DLWP = a + b(DSC)	0.2571	0.5105	0.664
DLWP = a + b(solar radiation)	0.4150	0.0006	0.278

DLWP: Mean diurnal leaf water potential (-MPa)  
DSC: Mean diurnal stomatal conductance (cm s<sup>-1</sup>)  
Tair: Air temperature (°C)



Table 14 Simple regressions of mean diurnal  
stomatal conductance (n=24)

Equation	intercept (a)	slope (b)	R <sup>2</sup>
DSC = a + b(VPD)	0.7141	0.8390	0.561
DSC = a + b(Tair)	-0.4077	0.0882	0.462
DSC = a + b(DLWP)	0.7482	0.7370	0.376

DSC: mean diurnal stomatal conductance (cm s<sup>-1</sup>)  
DLWP: mean diurnal leaf water potential (-MPa)  
Tair: air temperature (°C)

during daytime ( $R^2$  less than 0.20).

There was no multiple regression found to be superior to the simple regressions for predicting leaf water potential and stomatal conductance during daylight hours.

## DISCUSSION

### SEASONAL TRENDS OF PLWP AND STOMATAL CONDUCTANCE

Predawn leaf water potential (PLWP) and stomatal conductance at noontime were measured biweekly from May 1 to October 9, 1988. Predawn leaf water potential was measured just prior to dawn and was assumed to be the minimum value for the day. This daily minimum was used as an indicator of day-to-day changes of plant water status. The seasonal changes of stomatal conductance measured at noontime served as an indicator of seasonal changes of stomatal conductance.

Figures 3 and 4 show the seasonal courses of PLWP and stomatal conductance at noontime of plants growing at different densities. Generally speaking, values of PLWP and noontime stomatal conductance were higher in the early season before day 88 than in the late growing season. The maximum values of PLWP and stomatal conductance at noontime were recorded in the early summer, while the minimum values were found late in the growing season. As the season progressed, both PLWP and stomatal conductance at noontime decreased. The most likely reason for these decreases are that the soil water content decreased and the vapor pressure deficit increased as the season progressed (Fig 14). Plants could not absorb adequate

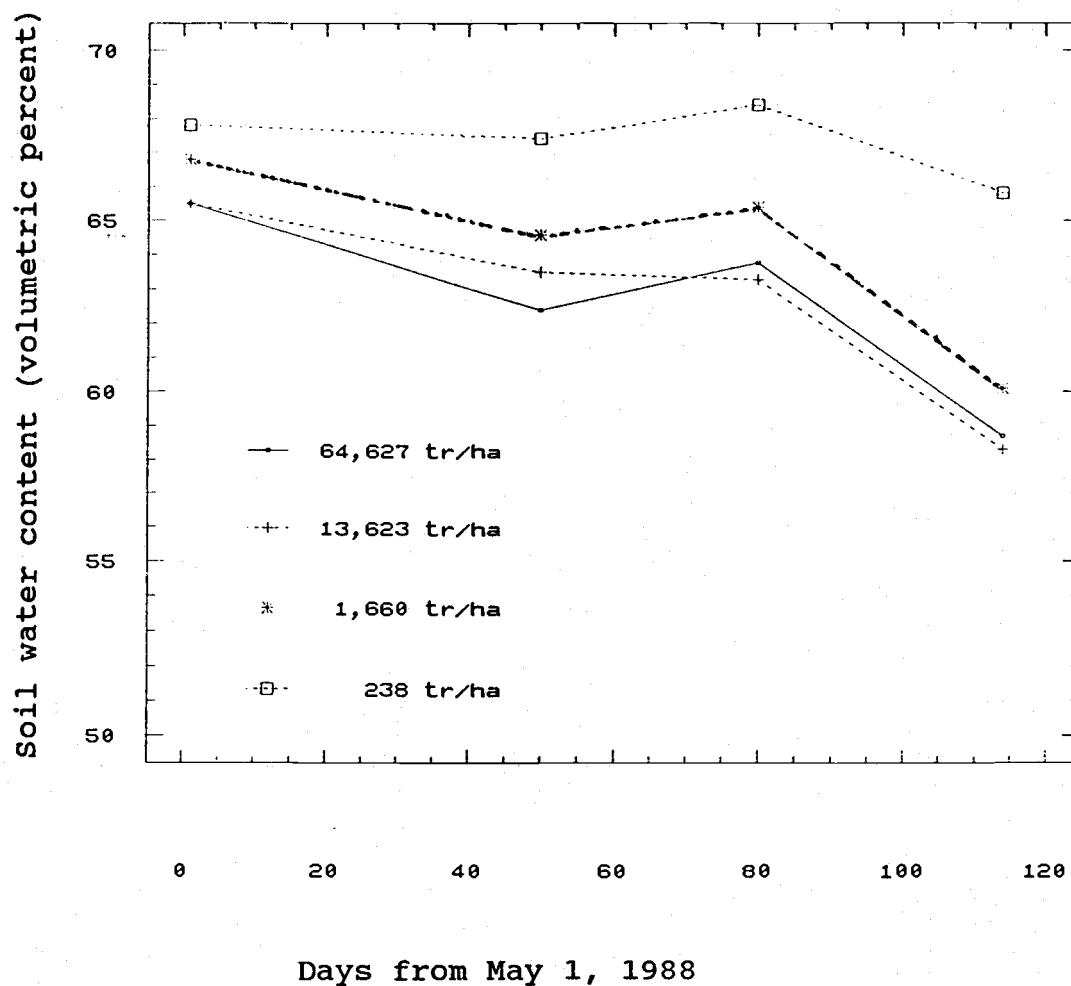


Fig. 14. Seasonal trends of soil moisture content in the area of different red alder densities in the Nelder plots at Cascade Head (T. Harrington, unpublished data).

water from soil in the late summer as readily as in the early season. When loblolly pine seedlings were grown in a moist regime, they had greater mean leaf conductance and osmotic potential than seedlings grown in a dry regime (Bongarten and Teskey, 1986). Leaf conductance of five subspecies of Alnus glutinosa decreased as water stress changed from moist to moderate to severe in a controlled environment study (Hennesey and Lorenzi, 1987).

Evaporative demand also increased as the season became warmer and drier (Fig.4). Plants responded by reducing their stomatal aperture as a certain VPD level was reached in the late summer (Fig.11). A negative relationship between humidity and stomatal conductance was found in white oak, eastern red cedar and black walnut (Ginter-whitehouse et al., 1983), and in various Eucalyptus species (Carbon et al., 1981). Precipitation affected PLWP and SSC profoundly. This effect was also observed in Ponderosa pine (Vance and Running, 1985) and Eucalyptus behriana, and in E. microcarpa (Myers and Neales, 1984).

Low stomatal conductance on day 30 (Fig.4), probably was caused by low air temperature and vapor pressure deficit. The average temperature was 14.32 °C on day 30 which is lower than 17.53 °C on day 14 and 16.71 °C on day 57. Stomatal conductance increased with increasing air temperature up to 23°C (Fig.9).

Several hot days seemed to be related to low PLWP during the growing season (Fig.3). In the early summer, this result was probably caused by a high transpiration rate during the day due to high evaporative demand. The high demand occurred in early summer when stomatal conductance increased as VPD increased. In late summer, on the other hand, lower PLWP was probably a result of the low soil water content.

High VPD was related to high stomatal conductance in the early summer, but to lower stomatal conductance later in the summer (Fig.4). Pezeshki and Hinckley (1988) reported that red alder stomatal aperture response to VPD differently in predrought and drought periods. In the present study, increasing VPD in the early season also increased stomatal conductance, but decreased stomatal conductance in the higher VPD range (6 to 20 mb) in the late summer (Fig.10, 11).

Predawn leaf water potential and noontime stomatal conductance of plants growing at different densities were not significantly different in the early season before day 88 (Fig.3, 4). But in the late summer, plants at high density had lower PLWP and stomatal conductance than plants at low density. Plants grown at high density were clearly under greater water stress in late summer. Other studies have shown that thinned stands are under less water stress a few years after thinning (red pine, Sucoff

and Hong, 1974; Pinus contorta, Donner and Running, 1986; Pinus radiata, Jackson et al., 1983; and Douglas-fir, Brix and Mitchell, 1986). Many studies have shown that increasing competing vegetation increases water stress in late summer (Petersen et al., 1988; Newton and Preest, 1988; Lanini and Radosevich, 1986; and Sands and Nambiar, 1983). In Douglas-fir tree, high density increased water stress (Shainsky, 1989). In red alder, a similar result was reported (Shainsky, 1989; Cole, 1984).

Peterson and Maxwell (1987) found that soil water content decreased linearly in relation to the amount of foliage in ponderosa pine. Increasing density also increased leaf area index in red alder (Cole, 1984; Shainsky, 1989). Table 15 shows the leaf area index in late of the 1988 growing season in the Nelder plots used in the present study (Giordano, 1988). Plants growing at high density had more leaf area in the same unit of land than plants growing at low density. The greater plant water stress of trees grown at high density are most likely caused by the greater water consumption per unit land.

Plants growing at high density are under greater water stress than plants growing at low density in the dry period of the growing season. Also, plants growing under a dry regime grow less than plants growing under a moist regime (Zaerr, 1970. 1971). For these reasons,

Table 15. Leaf area index of red alder trees growing at different densities at Cascade Head in late summer, 1988 (P. Giordano, 1989)

ARC #	Density (M <sup>2</sup> /tree)	* leaf area index
2	0.10	5.97
4	0.26	2.70
6	0.73	2.70
9	3.57	1.70
12	17.13	0.50
14	41.99	0.16

\* Young leaves were not included



plants growing at a high density would be expected to grow at a slower rate than plants growing at a low density. This was the case in the Nelder plots used in the present study (Fig.15 and Fig.16. P. Giordano, Personal communication). The same Nelder plots were used in Giordano's measurements, and the measurements were conducted on the same dates as the present study. Plants at the two highest density (101,219 and 37,864 trees/ha) ceased their height growth earlier in the growing season (when PLWP was less than  $-0.3$  MPa) than did the plants at low density (584 and 238 trees/ha) (Fig.15). The diameter increment of plants at high density (101,219 and 13,623 trees/ha) seemed to increase very slowly throughout the season, and the trees at a density of 13,623 trees/ha seemed to stop growing in the middle of the growing season (when PLWP was less than  $-0.3$  MPa). The diameter increment of plants at low density (2,804, 584, and 238 trees/ha) continued even in late summer (Fig.16). Trees in the two highest densities seemed to be too crowded for optimal individual tree growth. The density of 13,623 trees per hectare seemed not to be limiting to both height and diameter growth. The seasonal trends of PLWP and noontime stomatal conductance (Fig.3 and Fig.4) also indicate that plants growing at the two highest densities were under greater water stress; stomatal conductance was reduced during the driest part of the growing season. This response may have limited diffusion of  $\text{CO}_2$ , and in turn reduced plant

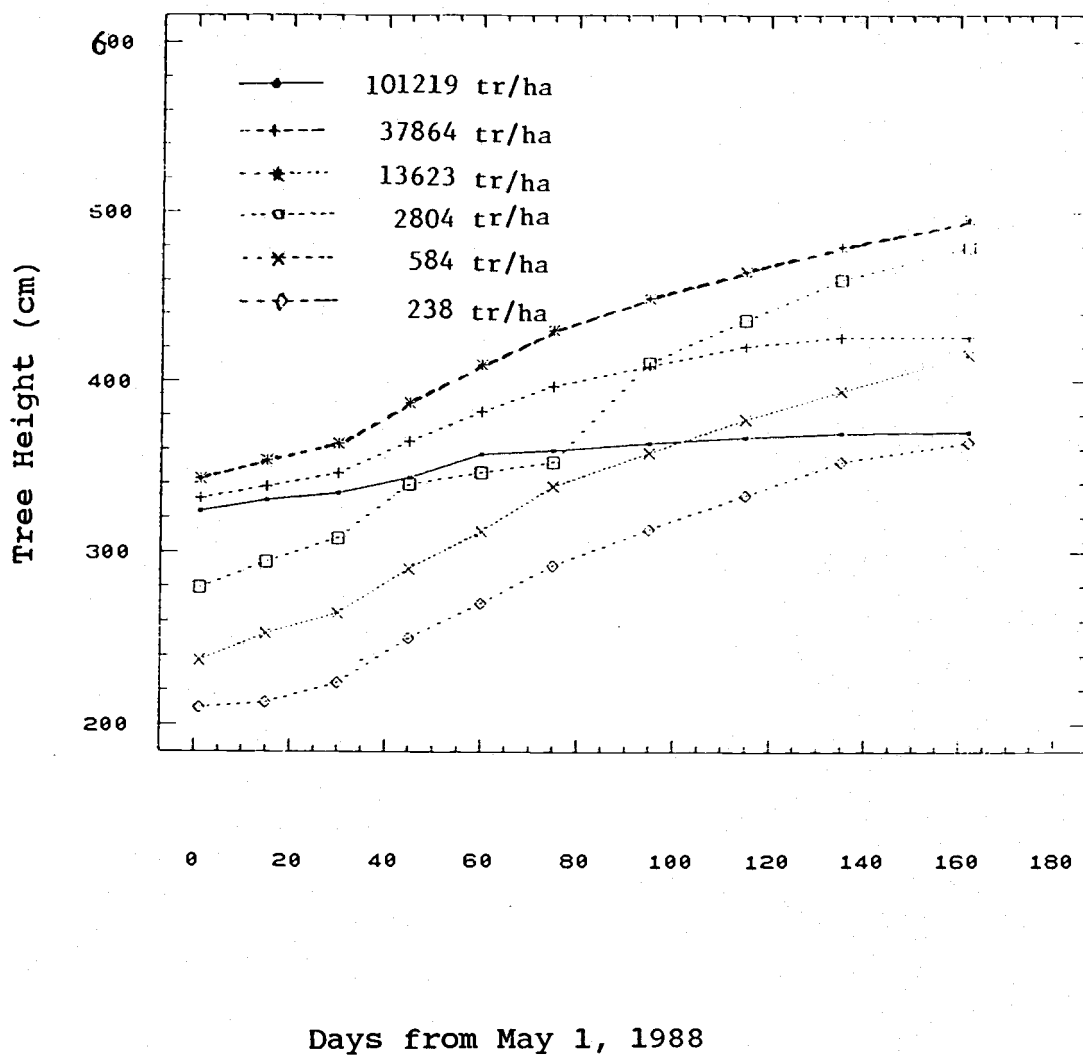


Fig. 15. Seasonal trends of height growth of red alder growing at different densities at Cascade Head (P. Giordano, personal communication)

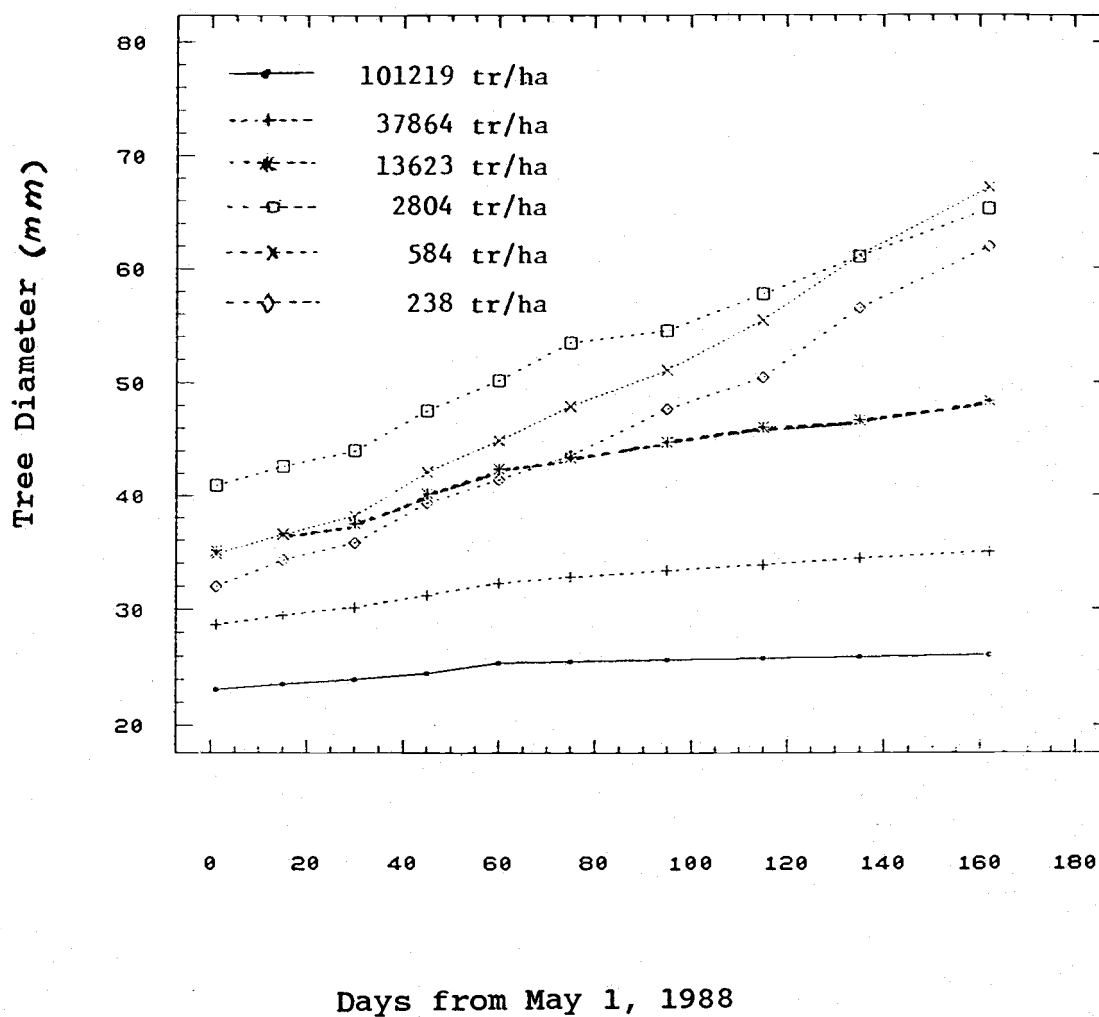


Fig. 16. Seasonal trends of diameter growth of red alder growing at different densities at Cascade Head (P. Giordano, personal communication)

photosynthesis. The three lowest densities therefore seemed well suited for maximum growth of individual tree on this site for the 1988 growing season.

#### DIURNAL TRENDS OF LEAF WATER POTENTIAL

Both days on which measurements of leaf water potential were conducted were warm, and clear with a gentle wind and a high evaporative demand (Table 16). July 23 represented a day with high soil water content, and August 31 represented the peak of the driest season.

The general trends of LWP were the same on both days: LWP was high before predawn, and the lowest at midday (Fig.6 and Fig.7). A similar pattern was also found in Douglas-fir (Murphy and Ferrell, 1982; Zaerr, 1971), highbrush blueberry (Byer et al., 1988), eucalypt (Carbon et al., 1981), hackberry, bur and chinquapin oak (Abrams and Knapp, 1986), white fir (Conard and Radosevich, 1981), and Pinus monophylla (Drivas and Everett, 1985).

The climatic condition and leaf water potential value range were roughly the same on both days (Table 16), except VPD was lower on August 31 than on July 23. Soil water content was very low on August 31, 1988, but minimum leaf water potential on August 31 was still the same as on July 23. This result may have been because red alder can regulate stomata closing at some threshold level of water potential (Fig.13) in late summer. This threshold was

Table 16. Weather conditions and leaf water potential and stomatal conductance

Day	July 23	August 31
* Max.Temp.	76°F	75°F
* Min.Temp.	45°F	44°F
Minimum VPD	15.62 mb	20.56 mb
Min.LWP	-1.79 Mpa	-1.85 Mpa
Max.LWP	-0.05 Mpa	-0.07 Mpa
Mean LWP	-0.61 Mpa	-0.71 Mpa
Max.conduct.	2.84 cm/s	0.99 cm/s
Min.conduct.	0.32 cm/s	0.04 cm/s
Mean conduct	1.503 cm/s	0.414 cm/s

\* Data from Cascade Head Experimental Forest  
Headquarters

-1.2 MPa in the present study. Pezeshki and Hinckley (1982) found a similar threshold at -1.1 MPa in the same species.

There were no statistically significant differences among leaf water potentials at different times during the night on July 23. Plants apparently recovered from water deficit by dark (8:00 pm). On the other hand, DLWP did not reach the highest value until midnight on August 31. One reason for that difference could be that the temperature at night was warmer on August 31 than on July 23, causing transpiration to continue longer into the night. Another possible reason is that the soil was very dry in August, so that plants needed a longer time to absorb enough water from the soil for recovery from the soil. Furthermore, because of the low soil moisture, plants might not have recovered to the same level on September 1 as on August 31. As a matter of fact, there were no significant differences among leaf water potentials at times 20, 22, and 24, and between times 4, 6, and 8 on August 31, but there was a significant difference ( $P < 0.05$ ) between these two groups.

There were no significant differences between leaf water potential of plants growing at high density and leaf water potential of plants growing at low density during the daytime. The most likely explanation for this result is that stomatal aperture response to leaf water potential is the same (-1.2 MPa) for plants growing at different

densities.

#### DIURNAL TRENDS OF STOMATAL CONDUCTANCE

The typical course of stomatal conductance when soil water is not limiting is as follows: stomatal conductance increases during the morning to the highest value before noontime, maintains a high value until mid-afternoon, then decreases gradually. This pattern was reported in many studies (Carbon et al., 1981; Murphy and Ferrell, 1982; Abrams and Knapp, 1986). The pattern on July 23 was similar to the typical course reported in the literature except that stomata closed very late in the afternoon. The stomatal conductance reached the highest value in the early morning on August 31, and maintained a high value until later afternoon in the lower densities. But plants growing at high densities reduced their stomatal conductance at 10:00 am and maintained a lower value the rest of the day. A possible reason for this difference is that the soil in the area of high density was drier than where plants were at low density. Plants may have regulated their stomatal aperture in response to soil moisture (Schulze, 1986).

The stomatal conductance on August 31 was generally lower than on July 23 (Table 16). The stomatal conductance value at 8:00 am on both days did not differ significantly. But stomatal conductance did not increase

on August 31 as on it did July 23, while leaf water potential was roughly the same. Plant stomatal conductance was reduced less and maintained a higher value on July 23 than on August 31. The most likely reason that stomatal conductance was higher on July 23 than on August 31 when LWP was about the same is that the stomata responded to VPD differently early and late in the season (Fig.11). Increasing VPD increased stomatal conductance early in the season, but decreased stomatal conductance late in the summer.

No significant differences in stomatal conductance of plants growing at different densities were found on July 23, perhaps because no significant soil water differences existed. But plants at high density had lower stomatal conductance than those grown at lower density on August 31. The weather conditions and PLWP were roughly the same on both days (Table 16). The reason for this difference is unclear. But soil in the high plant density areas might have been more dry than soil in areas of low plant density, and stomata could have been responding to a signal from the roots when soil moisture was low (Schulze, 1986).

It is still unclear what caused the leaf water potential to recover in the early afternoon while stomatal conductance maintained high levels on these 2 days.



## RESPONSES OF STOMATAL CONDUCTANCE

If an adequate number of measurements were taken to fill a space, the upper limit (boundary-line) of a scatter diagram would show the response of the dependent variable when other independent variables were at optimum (Webb, 1972; Pezeshki and Hinckley, 1982). Boundary-line analysis technique is therefore an efficient way to find optimum conditions and critical values.

The stomatal conductance increased as temperature increased until an optimum point was reached (Fig.9), then decreased as temperature increased further. The optimum temperature range for stomatal conductance was from 18 to 27°C. Similar results have been reported for other species. For example, Lafleur (1987) found that maximum leaf conductance occurred between 22 to 24°C for 3 woody species (Alnus rugosa, Salix bebbiana, and S.discolor) using the same technique. A similar result was also observed by Fanjul and Barradas (1985) and Beadle et al. (1985). The low value of stomatal conductance at low temperature may be related to an overall decrease in metabolic functioning. Low stomatal conductance values at high temperature may be caused by low plant leaf water status since high temperature (>27°C) only occurred in late summer when it was very dry. Another reason that low stomatal conductance occurred at high temperature may be related to high VPD which is directly related to low

stomatal conductance in the late part of the growing season.

Stomatal conductance was related curvilinearly to VPD in the range of VPD from 0 to 2.0 KPa in the late part of the summer (Fig.11). Stomatal conductance decreased as increasing evaporative demand in the range from 0.6 to 2.0 KPa. A similar pattern was reported in Eucalypts (Myers and Neales, 1984). A linear relationship between stomatal conductance and vapor pressure deficit has been reported in Pinus sylvestris (Whitehead et al., 1984) and in Pinus radiata (Dean and Sands, 1983). In the range of VPD larger than 2.0 KPa, the stomatal conductance seemed to level off as VPD increased, plants seemed not to be able to regulate further water loss beyond this value. But the data were not adequate to discern that effect in this study. In the early growing season, increasing VPD also increased stomatal conductance (Fig.10). The differential responses of red alder during different drought periods were also reported by Pezeshki and Hinckley (1988) in the same species. In the early season, stomatal conductance increased with increasing VPD (Fig.10). In this study this relationship is probably because increasing VPD in this range was also related to increasing temperature which in turn was related to increasing stomatal conductance (Fig.9).

Because of heavy dew in the morning on both days,

measurements were commenced at 8:00 am. Therefore, only the stomatal closure response to photosynthetically active radiation was observed. Apparently, stomata remained open at very low PAR values ( $100 \text{ uE m}^{-2}\text{s}^{-1}$ ) (Fig 12). Light saturation (PAR) was at least less than  $1200 \text{ uE m}^{-2}\text{s}^{-1}$ , but more than  $100 \text{ uE m}^{-2}\text{s}^{-1}$ . The data were not sufficient over this range of PAR from 100 to  $1200 \text{ uE m}^{-2}\text{s}^{-1}$  to pinpoint the saturated light level. It seemed clear that plants closed their stomata when PAR was less than  $100 \text{ uE m}^{-2}\text{s}^{-1}$ . Stomatal conductance decreased sharply when PAR was less than this critical point. Pezeshki and Hinckley (1982) reported that light saturation was  $400 \text{ uE m}^{-2}\text{s}^{-1}$  and stomatal closure point,  $80 \text{ uE m}^{-2}\text{s}^{-1}$  in red alder.

Leaf water potential did not seem to limit stomatal conductance in the early of the growing season. But in the late part of the growing season, plants responded to close their stomata further when LWP was lower than a certain threshold value ( $-1.2 \text{ MPa}$ ) even when the stomatal conductance was very low. The threshold values has been reported in many species (Table 17). The threshold was  $-1.2 \text{ MPa}$  in this study (Fig.13) which is slightly different from the value reported by Pezeshki and Hinckley (1982) ( $-1.1 \text{ MPa}$ ). This difference may be due to a different seed source, environment, or experimental error.

#### REGRESSIONS OF LEAF WATER POTENTIAL AND STOMATAL CONDUCTANCE

Table 17. Threshold values of leaf water potential  
on stomatal conductance

species	* threshold (-MPa)	Reference
Douglas-fir	2.0	Running, 1976
Poderosa pine	1.8	Running, 1976
Scots pine	1.6	Whitehead, 1980
Radiata pine	1.1	Rook <i>et al.</i> , 1978
<u>Picea sitchensis</u>	1.6-2.7	Beadle <i>et al.</i> , 1978
<u>Pinus monophylla</u>	2.3-3.0	Drivas <i>et al.</i> , 1988
Red alder	1.1	Pezeshki <i>et al.</i> , 1982

\* The values of leaf water potential below which stomatal conductance is limited by stomatal closure.

#### A. Regressions from seasonal data

Mean seasonal stomatal conductance was significantly related to mean predawn leaf water potential. The  $R^2$  for the simple regression is 0.804 which is very high considering only one variable was included. Plant density in the late part of the growing season, VPD at noontime, and total precipitation the previous two weeks all significantly improved the fitness of the multiple regression of predawn leaf water potential (Table 10).

Mean predawn leaf water potential significantly affected the seasonal stomatal conductance (Table 11). A similar result was reported by Running (1975) in six conifer species. Vapor pressure deficit is another factor which affected the seasonal stomatal conductance. Precipitation summed over the two previous weeks, along with the above two variables, successfully predicted seasonal stomatal conductance (Table 12).

#### B. Regression from diurnal data

Stomatal conductance, VPD and air temperature were the 3 best predictors for DLWP (table 13). All the  $R^2$  were high. Mean diurnal leaf water potential, air temperature, and VPD predicted DSC well (Table 14). There was no improvement by including more than one variable to predict either DLWP and DSC. Compared to seasonal stomatal conductance and predawn leaf water potential,

diurnal stomatal conductance and leaf water potential varied more, and were more difficult to predict.

Examining all the simple and multiple regressions, it appears that leaf water potential and stomatal conductance related to each other significantly in both seasonal and diurnal cases. Lower predawn leaf water potential limited the possible maximum stomatal conductance (Waring and Running, 1976). Vapor pressure deficit is the most important climatic factor which significantly affected both seasonal and diurnal leaf water potential and stomatal conductance. Precipitation was also an important factor which affected leaf water potential and stomatal conductance. Density seemed not to affect leaf water potential at day-time and stomatal conductance. But we can predict PLWP in the late part of the growing season by using density as a single predictor.

#### **THE POSSIBLE APPLICATION OF THE RESULTS**

According to this study of 3-year-old red alder growing at different densities in the Cascade Head Experiment Forest Station during 1988, the following guidelines are suggested for the intensive management of young red alder forests:

Plants growing at high density were under greater water stress at night than those growing at low density, especially in the dry season. Density is an important

factor to consider for optimum tree growth.

The density of 3-year-old red alder forest should be less than 13,623 stems per hectare, or higher than  $0.73 \text{ M}^2$  per tree, or leaf area index should be less than 2.70. For maximum individual tree growth, the optimum density is from 238 to 2,804 trees per hectare in the density range tested in this study.

Predawn leaf water potential can be used as an indicator of plant water stress in the growing season. For a young red alder forest (3-year-old), predawn leaf water potential should be maintained above  $-0.30 \text{ MPa}$ , perhaps by irrigation.

The best growth can be expected where the temperature is from  $18$  to  $27^\circ\text{C}$ , and VPD is less than  $2.0 \text{ KPa}$ . Light generally does not limit maintenance of stomatal opening and diffusive conductivity of  $\text{CO}_2$  by red alder trees in this area although light competition may occur in trees growing in high density.

Predawn leaf water potential and noontime stomatal conductance, daytime leaf water potential and stomatal conductance can be predicted from each other, and can be predicted from the environmental parameters of which VPD is the most effective one.

### SUMMARY

The present study was conducted in the Cascade Head Experimental Forest Headquarters during the growing season in 1988. The 3-year-old red alder trees in a 1a type Nelder plot were used. The general objective of this study was to investigate the plant water potential and stomatal conductance of red alder growing at different densities. The following results were obtained:

1. The leaf water potential and stomatal conductance of red alder over the course of seasonal and diurnal time periods were described.

2. Predawn leaf water potential of red alder growing at lower densities remained constant throughout the entire growing season, while PLWP of red alder growing at high densities was depressed as the season progressed. Plants growing at higher density were usually under greater water stress at night than those growing at lower density, especially during the dry season.

3. Stomatal conductance of red alder growing at high densities was reduced more than for plants growing at low densities during the dry season.

4. Different density treatments affected predawn leaf water potential in the late part of the growing season



only. They did not seem to affect diurnal leaf water potential during the day.

5. The optimum temperature for red alder stomatal conductance is from 18 to 27°C. Stomatal conductance remained high when photosynthetically active radiation level was as low as 100  $\mu\text{E m}^{-2}\text{s}^{-1}$ . The Light saturation point was from 100 to 1200  $\mu\text{E m}^{-2}\text{s}^{-1}$ . Stomatal conductance was related to VPD differently in different parts of the growing season. Stomatal conductance increased as VPD increased over the range of VPD up to 1.5 KPa early in the growing season, but decreased as VPD increased in the VPD range from 0.6 to 2.0 KPa. Red alder trees seemed not to be able to regulate further water loss by further closing their stomata when VPD was greater than 2.0 KPa in the late part of the growing season. Leaf water potential seemed not to limit stomatal conductance in the early of the growing season. But plants responded to close their stomata further when leaf water potential was lower than -1.2 MPa in the late part of the growing season.

6. Predawn leaf water potential and noontime stomatal conductance, daytime leaf water potential and stomatal conductance can be predicted from each other, and can be predicted from environmental parameters. Vapor pressure deficit is the most efficient predictor of these parameters.

## BIBLIOGRAPHY

- ABRAMS, M. D., and A. K. KNAPP. 1986. Seasonal water relations of three gallery forest hardwood species in Northeast Kansas. *For. Sci.* 32(3): 687-696.
- AUSSENAC, G., and A. GRANIER. 1988. Effects of thinning on water stress and growth in Douglas-fir. *Can. J. For. Res.* 18: 100-105.
- BACHELARD, E. P. 1986. Effects of soil moisture stress on the growth of seedlings of three Eucalypt species. II. Growth effects. *Aust. For. Res.* 16: 51-61.
- BAKER, D. A. 1984. Water relations. IN: *Advanced Plant Physiology*. By Malcolm B. Wilkins, ED. Pitman Press, Bath. pp. 297-319.
- BEADLE, C. L., N. C. TURNER, and P. G. JARVIS. 1978. Critical water potential for stomatal closure in Sitka spruce. *Physiol. Plant.* 43: 160-165.
- BEADLE, C. L., P. G. JARVIS, H. TALBOT, and R. E. NEILSON. 1985. Stomatal conductance and photosynthesis in a mature Scots pine forest. II. Dependence on environmental variables of single shoots. *J. Appl. Ecol.* 22: 573-586.
- BINKLEY, D. 1981. Nodule biomass and acetylene reduction rates of red alder and Sitka alder on Vancouver Island, B. C. *Can. J. For. Res.* 11: 281-286.
- BONGARTEN, B. C., and R. O. TESKEY. 1986. Water relations of loblolly pine seedlings from diverse geographic origins. *Tree physiology* 1: 265-276.
- BORMANN, B. T., and D. S. DEBELL. 1981. Nitrogen content and other soil properties related to age of red alder stands. *Soil Sci. Soc. Am. J.* 45: 428-432.
- BOYER, J. S. 1988. Cell enlargement and growth-induced water potentials. *Physiol. Plant.* 73: 311-316.
- BOYER, P. L., J. N. MOORE, and H. D. SCOTT. 1988. Plant-water relations of young highbush blueberry plants. *HortScience* 23(5): 870-873.
- BRIX, H., and A. K. MITCHELL. 1986. Thinning and nitrogen fertilization effects on soil and tree water stress in a Douglas-fir stand. *Can. J. For. Res.* 16: 1334-1338.

- BUXTON, G. F., D. R. CRY, E. B. DUMBROFF, and D. P. WEBB. 1985. Physiological responses of three northern conifers to rapid and low induction of moisture stress. *Can. J. Bot.* 63: 1171-1176.
- CARBON, B. A., G. A. BARTLE, AND A. M. MURRAY. 1981. Patterns of water stress and transpiration in Jarrah Forest. *Aust. For. Res.* 11: 191-200.
- CARTER, G. A., J. A. MILLER, D. E. DAVIS, and R. M. PETTERSON. 1984. Effect of vegetative competition on the moisture and nutrient status of loblolly pine. *Can. J. For. Res.* 14: 1-9.
- CLEARY, B. D. 1971. The effect of plant moisture stress on the physiological and establishment of planted Douglas-fir and Ponderosa pine seedlings. Ph.D. dissertation. Oregon State Univ., Corvallis, Oregon.
- Cody, R. P., J. K. Smith. 1987. Applied statistics and SAS programming language. Second Edition. North-Holland.
- COLE, E. C. 1984. Fifth-year growth responses of Douglas-fir to crowding and other competition. Master Thesis. Oregon State Univ., Corvallis, Oregon.
- COLE, E. C., and M. NEWTON. 1986. Fifth-year responses of Douglas-fir to crowding and nonconiferous competition. *Can. J. For. Res.* 17: 181-186.
- COLE, E. C., and M. NEWTON. 1986. Nutrient, moisture, and light relations in 5-year-old Douglas-fir plantations under variable competition. *Can. J. For. Res.* 16: 727-732.
- COLQUHOUM, I. J., R. W. RIDGE, D. T. BELL, W. A. LONERAGAN, and J. KUO. 1984. Comparative studies in selected species of Eucalyptus used in rehabilitation of the Northern Jarrah Forest, Western Australia. I. Patterns of xylem pressure potential and diffusive resistance of leaves. *Aust. J. Bot.* 32: 367-373.
- CONARD, S. D., and S. R. RADOSEVICH. 1981. Photosynthesis, Xylem pressure potential, and leaf conductance of three Montane Chaparral species in California. *Forest Sci.* 27(4): 627-639.
- CREGG, B. M. 1986. The effects of precommercial thinning on water relations and wood quality in loblolly pine. M.S. Thesis, Oklahoma State Univ., Stillwater, OK.
- DEAN, D. A., and R. SANDS. 1983. Stomatal response to

- evaporative demand and soil water status in families of radiata pine. Aust. For. Res. 13: 179-182.
- DEBELL, D. S., and T. C. TURPIN. 1983. Red alder. Agricultural handbook, USDA, Washington. 445. Rev. pp 26-28.
- DONNER, B. L., and S. W. RUNNING. 1986. Water stress response after thinning Pinus conrta stands in Montana. Forest Sci. 32 (3): 614-625.
- DRIVAS, E. P. and R. L. EVERETT. 1988. Water relations characteristics of competing singleleaf pinyon seedlings and sagebrush nurse plants. For. Ecol. Manage., 23: 27-37.
- FANJUL, L., V. L. BARRADS. 1985. Stomatal behavior of two heliophile understory species of a tropical deciduous forest in Mexico. J. Appl. Ecol. 22: 943-954.
- FRANKLIN, J. F., C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S.D.A., Forest Service, Pacific Forest and Range Experiment Station. 417 p.
- GEDNEY, D. R. 1987. Timber resource statistics for non-federal forest land in west-central Oregon. USDA For. Serv. Resour. Bull. PNW-RB-143. 26p.
- GINTER-WHITEHOUSE, D. L., T. M. HINCKLEY, and S. G. PALLARDY. 1983. Spatial and temporal aspects of water relations of three species with different vascular anatomy. For. Sci. 29(2): 317-329.
- GIORDANO, P. A. 1989. Growth and carbon allocation of red alder seedlings grown over a density gradient. Master thesis. Oregon State University, Corvallis, Oregon.
- GRAHAM, J. S., and S. W. RUNNING. 1984. Relative control of air temperature and water status on seasonal transpiration of Pinus contorta. Can. J. For. Res. 14: 833-838.
- GREEN, S. E. 1982. Neskowin Crest Research Natural Area. Supplement No. 13. Forestry Sciences Laboratory, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon.
- HARRINGTON, C. A. 1987. Responses of red alder and black cottonwood seedlings to flooding. Physiol. Plantum. 69: 35-48.
- HART, J. J., and S. R. RADOSEVICH. 1987. Water relations

- of two california chaparral shrubs. Amer. J. Bot. 74(3): 371-384.
- HENNESSEY, T. C., and E. M. LORENZI. 1987. Stomatal conductance and growth of five Alnus glutinosa clones in response to controlled water stress. Can. J. For. Res. 18: 421-426.
- HIBBS, D. E., W. H. EMMINGHAM, and M. C. BONDI. 1989. Thinning red alder: Effects of method and spacing. Forest Sci. 35(1): 16-29.
- HINCKLEY, T. M., and D. R. M. SCOTT. 1971. Estimates of water loss and its relation to environmental parameters in Douglas-fir saplings. Ecol. 52(3): 520-524.
- HINCKLEY, T. M., M. O. SCHROEDER, J. E. ROBERTS, and D. N. BRUCKERHOFF. 1975. Effect of several environmental variables and xylem pressure potential on leaf surface resistance in white oak. For. Sci. 21: 201-211.
- JACKSON, D. S., E. A. JACKSON, and H. H. GIFFARD. 1983. Soil water in deep Pinaki sands: some interactions with thinned and fertilized Pinus radiata. N. Z. J. For. Sci. 13(2): 183-196.
- KLEPPER, B. 1968. Diurnal pattern of water potential in woody plants. Plant Physiol. 43: 1931-1934.
- KOO, C. D. 1989. Effects of water stress on ectomycorrhiza and nodule formation, N-fixation and growth of red alder seedlings. PH. D thesis. Oregon State University, Corvallis, Oregon.
- LAFLEUR, P. 1988. Leaf conductance of four species growing in a Subarctic marsh. Can. J. Bot. 66: 1367-1375.
- LANINI, W. T., and S. R. RADOSEVICH., 1986. Response of three conifer species to site preparation and shrub control. Forest Sci. 32(1): 61-77.
- LOPUSHINSKY, W. 1969. Stomatal closure in conifer seedlings in response to leaf moisture stress. Bot. Gaz. 130(4): 258-263.
- MURPHY, E. M., and W. K. FERRELL. 1982. Diurnal and seasonal changes in leaf conductance, xylem water potential, and abscisic acid of Douglas-fir in five habitat types. Forest Sci. 28(3): 627-638.
- MYERS, B. A., and T. F. NEALES. 1984. Seasonal changes in the water relations of Eucalyptus behriana F. Muell and

- E. microcarpa (Maiden) Maiden in the field. Aust. J. Bot. 32: 495-510.
- NELDER, J. A. 1962. New kinds of systematic designs for spacing experiments. Biometrics. 18(3): 283-307.
- NEWTON, M., and D. S. PREEST. 1988. Growth and water relations of Douglas-fir seedlings under different weed control regimes. Weed Science. 36: 653-662.
- NEWVILLE, E. G., and W. K. FERRELL. 1980. Abscissic acid levels and stomatal behavior during drought and recovery in Douglas-fir. Can. J. Bot. 58: 1370-1375.
- OSONOB, O., and F. E. FASEHUM. 1987. adaptations of soil drying woody seedlings of african locust. Tree physiology. 3: 321-330.
- PETERSON, T. D., and B. D. MAXWELL. 1987. Water stress of Pinus ponderosa in relation to foliage density of neighboring plants. Can. J. For. Res. 17:1620-1622.
- PETERSON, T. D., and M. NEWTON. 1988. Influence of Ceanothus velutinus and associated forbs on the water stress and stemwood production of Douglas-fir. Forest Sci. 34(2): 333-343.
- PEZESHKI, S. R., and T. M. HINCKLEY. 1982. The stomatal response of red alder and black cottonwood to changing water status. Can. J. For. Res. 12: 761-771.
- PEZESHKI, S. R., and T. M. HINCKLEY. 1988. Water relations characteristics of Alnus rubra and Populus trichocarpa: responses to field drought. Can. J. For. Res. 18: 1159-1166.
- RESCH, H. 1980. Utilization of red alder in the Pacific Northwest. Forest Products Journal. 30(4): 21-26.
- RESCH, H. 1988. Red alder: opportunities for better utilization of a resource. Special publication 16. Forest Research Lab. Oregon State University. Corvallis, Oregon, USA.
- ROOK, D. A., R. H. SWANSON, and A. M. CRANAWICK. 1978. Reaction of radiata pine to drought. pp 55-68. In: proceeding of the soil and plant water symposium. Palmerston North, New Zealand.
- RUNNING, S. W. 1976. Environmental control of leaf water conductance in conifers. Can. J. For. Res. 6: 104-112.

- SANDS, R., and E. K. S. NAMBIAR. 1984. Water relations of Pinus radiata in competition with weeds. Can. J. For. Res. 14: 233-237.
- SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, and E. A. HEMMINGSEN. 1965. Sap pressure in vascular plants. Science 148: 339-46.
- SCHULTE, P. J., T. M. HINCKLEY, and R. F. STETTLER. 1986. Stomatal response of populus to leaf water potential. Can. J. Bot. 65: 255-260.
- SCHULZE, E. D. 1986a. Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. Ann. Rev. Plant Pgysiol. 37: 247-74.
- SCHULZE, E. D. 1986b. Whole-plant responses to drought. Aust. J. Plant physiol. 13: 127-41.
- SHAINSKY, L. J., and S. R. RADOSEVICH. 1986. Growth and water relations of Pinus ponderosa seedlings in competitive regime with Arctostaphylos patula seedling. J. Appl. Ecol. 23: 957-966.
- SHAINSKY, L. J. 1989. Competitive interaction between Douglas-fir and Red alder seedlings: growth analysis, resource use, and physiology. Ph.D thesis. Oregon State University, Corvallis, Oregon.
- STOGSDILL, W. R. 1986. The effects of precommercial thinning on soil moisture and throughfall in loblolly pine. M. S. Thesis. Oklahoma State Univ. Stillwater, OK.
- STSC, Inc. 1988. Statgraphics statistical graphics system. User's Guide. STSC Inc. 2115 East Jefferson Street, Rochville, Maryland 20852, USA.
- SUCOFF, E. and S. G. HONG. 1974. Effects of thinning on needle water potential in red pine. Forest Sci. 20(1): 25-29.
- TARRANT, R. F., B. T. Bormann, D. S. DeBell, and W. A. Atkinson. 1983. Managing red alder in the Douglas-fir region: some possibilities. Journal of Forestry. 81(12): 787-792.
- TESKEY, R. O., B. C. BONGARTEN, B. M. CREGG, P. M. DOUGHERTY, and T. C. HENNESSEY. 1987. Physiology and genetics of tree growth response to moisture and temperature stress: an examination of the

- characteristics of loblolly pine. Tree physiology. 3: 41-61.
- TOBIESSEN, P., P. W. RUNDEL, and R. E. STECKEY. 1971. Water potential gradient in a tall Sequoiadendron. Plant Physiol. 48: 303-304
- VANCE, N. C., and S. W. RUNNING. 1985. Summer climatic influences on Pinus ponderosa planted on mined lands in eastern Montana, Reclam. Reveg. Res. 4: 129-143.
- VU, J. C. V., and G. YELENOSKY. 1988. Water deficit and associated changes in some photosynthetic parameters in leaves of 'Valencia' orange (Citrus sinensis (L.) Osbeck). Plant Physiol. 88: 375-378.
- Wang, D., E. P. BACHELARD, and J. C. G. BANKS. 1988. Growth and water relations of seedlings of two subspecies of Eucalyptus globulus. Tree Physiology. 4: 129-138.
- WARING, R. H., and B. D. CLEARY. 1967. Plant moisture stress: Evaluation by pressure bomb. Science. 155: 1248-1254.
- WARING, R. H. and S. W. RUNNING. 1976. Water uptake, storage and transpiration by conifer: a physiological model. In Ecological studies. Analysis and synthesis. Vol.19. Water and Plant Life. Edited by O. L. Lange, L. Kappen, E. D. Schulze. Springer-verlag Berlin Heidelberg New York.
- WARING, R. H., and W. H. SCHLESINGER. 1985. Forest ecosystem. concept and management. pp. 84. Academic Press, Inc.
- WEBB, R. A. 1972. Use of the boundary line analysis of biological data. J. Hort. Sci. 47: 309-319.
- WHITEHEAD, D. 1980. Assessment to water status in trees from measurements of stomatal conductance and water potential. N. Z. J. FOR. SCI. 10(1): 159-165.
- Whitehead, D., P. G. JARVIS, and R. H. WARING. 1984. Stomatal conductance, transpiration, and resistance to water uptake in a Pinus sylvestris spacing experiment. Can. J. For. Res. 14: 692-700.
- ZAERR, J. B. 1970. Effects of plant moisture stress on growth of Douglas-fir trees. In: Tree ring analysis with special reference to Northwest America. Univ. of B. C. Faculty of Forest. Bull. #7.



ZAERR, J. B. 1971. Moisture stress and stem diameter in young Douglas-fir. Forest Sci. 17(4):466-469.

ZHOU, N. G., and J. L. ZHOU. 1984. Transpiration measurements in locust trees. Forest Sci. Tech. Shaanxi. 1:1-29.