

AN ABSTRACT OF THE THESIS OF

Barbara J. Yoder for the degree of Master of Science in

Botany and Plant Pathology presented on November 14, 1983.

Title: Comparative Water Relations of Abies grandis, Abies concolor and their hybrids.

Abstract approved: Signature redacted for privacy.

Donald B. Zobel

Comparisons were made of the tissue water relations, stomatal conductance and growth of grand fir (Abies grandis), white fir (Abies concolor) and their hybrids growing in a western Oregon plantation. The grand fir were naturally-regenerated trees native to the study site. White fir and hybrids were the progeny of controlled crosses between white fir from the Rocky Mountains of Colorado and the Sierra Nevada Mountains of California and grand fir from the northern California coast.

Osmotic potentials of all trees, at both full and zero turgor, were lowest in March (averaging -2.05 MPa and -2.73 MPa, respectively), highest in June (averaging -1.18 MPa and -1.54 MPa), and intermediate in August (averaging -1.73 MPa and -2.34 MPa in August, 1981, and -1.65 MPa and -2.22 MPa in August, 1982). August, 1981, was hotter and drier than August, 1982; the lower osmotic potentials in 1981 may be a response to more severe stress. Osmotic potentials decreased more than water potentials between June and August; thus,

turgor pressure increased through the summer. Bulk turgor of twigs averaged 0.71 MPa before dawn in June, 1982, and 0.87 MPa before dawn in August, 1982. In the mid-morning, twig turgor averaged 0.30 MPa in June and 0.40 MPa in August, 1982.

The trees that grew most rapidly on the study site, hybrids between Colorado white fir and California grand fir, had lower stomatal conductance throughout the year than slower growing white fir. The fastest growing hybrids also had the least negative osmotic potential at full and zero turgor and the lowest twig turgor in August. Thus, rapid growth rate did not correlate with either high conductance or high turgor. More rapid growth may be partly explained by higher leaf area. Needle longevity of the fastest growing hybrids averaged 5.3 years, compared with 2.8 years for the slowest growing white fir. It is speculated that rapidly growing trees may also allocate a greater percentage of photosynthate to production of new needles.

Comparative Water Relations of
Abies grandis, Abies concolor and Their Hybrids

by

Barbara J. Yoder

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed November 14, 1983

Commencement June 1984

ACKNOWLEDGEMENT

I received a great deal of help producing this thesis. Dr. David Thomas suggested methods of statistically analyzing my data, and Ms. Susan Stafford helped me as I implemented those techniques. Dr. Philip Rundel provided a copy of the computer program used in his laboratory to analyze pressure-volume curves. Dr. Rundel also has been a long-term source of inspiration and encouragement. He sparked my interest in physiological plant ecology many years ago, he helped me learn to have confidence in my scientific capabilities, and when I contemplated returning to graduate school to become an "older-than-average" student, he convinced me I had a "few good years left". I am also very grateful to Dr. Richard Waring for his encouragement and advice. Dr. Waring advised using the "water-release" technique to develop pressure-volume curves, and he suggested several alternate approaches for interpreting my data. He also helped me believe this work was worthwhile.

My major professor, Dr. Donald Zobel, planted the experimental trees on my study site. Some of the data reported here are from his measurements of those trees. Dr. Zobel was very helpful providing resources, references, and much-needed critical feedback. He forced me to think, often a painful procedure, and helped me develop order out of muddled thinking.

One's spouse is generally an indispensable aid in an undertaking such as this, and mine was no exception. Bill recorded data on

uncomfortably hot afternoons at my study site. He became a "single parent" many times as I deserted my family to work on this project. He altered our family budget to finance my educational "hobby". And he gave me more encouragement than I probably deserved. But Bill's assistance went far beyond financial and emotional support. He borrowed an impressive array of Hewlett-Packard computer equipment for me, transporting disc drives, printers, plotters and word processors between the H-P Corvallis plant and our home time and time again. He was my tutor for each new piece of equipment, and suffered through countless interruptions as I called him at work for help. I couldn't have completed this project without his help.

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
LITERATURE REVIEW	4
Water Relations	4
Water Potential	5
Turgor Maintenance and Osmotic Adjustment	7
Measurement: Psychrometry and Pressure-Volume Curves	9
Leaf Conductance	13
Control of Stomatal Movement	13
Leaf Conductance in Relation to Photosynthesis and Transpiration	16
<u>Abies grandis</u> and <u>Abies concolor</u>	17
Taxonomy	17
Ecology and Distribution	19
STUDY SITE, METHODS AND MATERIALS	22
The Study Site	22
Experimental Populations	23
Sampling Technique	24
Conductance Measurement	26
Measurement of Water Potential Components	30
Measurement of Leaf Area and Growth of Branches	36
RESULTS AND DISCUSSION	39
Height Growth	39
Leaf Conductance	39
Needle Age and Conductance	39
Diurnal Variation of Conductance	42
Relationships between Diurnal Conductance and Water Potential	49
Seasonal Variation of Conductance	55
Conductance and Growth	59
Variation in the Components of Water Potential	60
Osmotic Potential	61
Seasonal Variation	61
Variation among Varieties	67
Xylem Water Potential	67
Seasonal Variation	67
Variation among Varieties	70

	<u>Page</u>
Turgor Pressure	71
Seasonal Variation	71
Variation among Varieties	74
Water Potential Components and Leaf Conductance	75
Growth and Estimated Leaf Area of Branches	77
Phenology	82
GENERAL DISCUSSION	83
CONCLUSIONS	88
REFERENCES	91
APPENDICES	97
1. A summary of the parentage of experimental trees	98
2. Arrangement of experimental trees on the study site	99
3. A summary of the eight blocks used in sampling and data analysis	100
4. A comparison of leaf temperatures of the five varieties	101
5. A sample data output from the computer program analyzing "Water-Release" curves	102
6. Typical "Water-Release" curves	105

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1.	An example of a type of "Pressure-Volume" curve	11
2.	Mean height growth from 1976 to 1980 of the five varieties	40
3.	Diurnal air temperature and vapor pressure deficit on July 15, 1981	43
4.	Diurnal air temperature and vapor pressure deficit on July 29, 1981	44
5.	Diurnal leaf conductance on July 15, 1981	45
6.	Diurnal leaf conductance on July 28, 1981	46
7.	Twig water potential on July 15, 1981	51
8.	Twig water potential on July 28, 1981	52
9.	The annual mean "maximum" conductance of the five varieties	56
10.	Osmotic potential at full turgor in August, 1981 and March, June and August, 1982	64
11.	Osmotic potential at zero turgor in August, 1981 and March, June and August, 1982	65
12.	Pre-dawn water potentials of trees used in "Water-Release" analysis	68
13.	Water potentials of trees used in "Water-Release" analysis at time of "maximum conductance"	69
14.	Pre-dawn turgor in August, 1981 and June and August, 1982	72
15.	Turgor pressure in August, 1981 and March, June and August, 1982, at time of "maximum" conductance	73

LIST OF TABLES

<u>Tables</u>		<u>Page</u>
I.	Variation of conductance with needle age	41
II.	Maximum leaf conductance in July, 1981, relative to Ψ , time of day, temperature and vapor pressure deficit	53
III.	Mean "maximum" conductance: supplementary information for Figure 9	57
IV.	Mean values of water potential components from "water-release" curves	62
V.	Correlations between leaf conductance and the components of water potential, June 1982	76
VI.	Branch growth, basal sapwood area, and specific needle area	78
VII.	Needle longevity	81
VIII.	Mean growth rates of leaders, 1980	85

COMPARATIVE WATER RELATIONS OF
ABIES GRANDIS, ABIES CONCOLOR AND THEIR HYBRIDS

INTRODUCTION

Lack of water frequently limits plant growth and survival (Pallardy 1981) and has been a major selective force in plant evolution (Hanson and Hitz 1982). Accordingly, the morphological and physiological characteristics that influence the water economy of plants vary both among and within species. Comparative studies of the water relations of closely related plants can provide information about the adaptive importance of particular characteristics (Zobel 1975, Pallardy 1981). In this study, I compared the water relations of two common true fir species of the western United States, Abies grandis (Doug. ex D. Don) Lindl. (grand fir) and Abies concolor (Gordon and Glend. ex Hildebr.) Lindl. (white fir), and hybrids between the two species.

A large number of physiological and morphological characteristics may affect a plant's water status. In some cases, adjustment of leaf area may be of primary importance (Kozlowski 1973); by shedding leaves or producing smaller leaves, a plant may limit its water loss. Stomatal movement provides another important mechanism for modifying water loss (Jarvis 1981, among others), and has been extensively studied. Depth and extensiveness of roots, xylary resistance to water flow, storage of water in plant tissues, thickness of the leaf

cuticle -- these and many other traits determine a plant's ability to stabilize internal water status despite a changing external water regime, or its ability to avoid drought.

A plant's drought resistance depends on both avoidance and tolerance of drought (Kramer 1980, Hinckley et al. 1982). Drought tolerance is the ability to survive periods of low water potential. Little is known of the physiological processes that confer drought tolerance (Parker et al. 1982), but attention has focused recently on adjustment of the concentration of solutes in cell vacuoles as a mechanism of maintaining cell turgor as plant water potential fluctuates (Cheung et al. 1975, Hsiao 1976, Roberts et al. 1980, Hanson and Hitz 1982, among others).

My goal was to compare characteristics of grand fir and white fir which confer both drought tolerance and drought avoidance and to assess the adaptive significance of particular characteristics. I gave primary attention to seasonal trends of turgor and osmotic potentials and of stomatal conductance. But characteristics of organisms are not necessarily adaptive simply because they differ. I evaluated the importance of individual characteristics by relating them to differences in tree growth; if a trait is very important to trees growing on a particular site, tree growth should be correlated with that trait.

The specific objectives of this study were to:

1. Describe the water relations of grand fir, white fir and their hybrids, including pre-dawn values and diurnal

changes of water potential, osmotic potential and bulk turgor, in spring, early summer, and late summer.

2. Determine whether there is evidence of internal regulation of osmotic potential and whether varieties have different capabilities for osmotic adjustment and maintenance of turgor.
3. Test the hypotheses that the fastest growing varieties maintain higher leaf conductance and higher turgor than other varieties.
4. Verify previous indications that trees morphologically more like A. concolor maintain higher stomatal conductance at low water potentials than do trees which closely resemble A. grandis.
5. Evaluate the relative drought resistance of the species and hybrids based on values of water potential components and stomatal characteristics.

LITERATURE REVIEW

Water Relations

Plant water status is most frequently evaluated in terms of the plant water potential, which measures the capacity of water at a given point in the plant to do work compared with pure, free water at the same temperature and at sea level gravity (Nobel 1974). The water potential is usually described by units of pressure, most commonly atmospheres (1 atmosphere = 1.013×10^6 dynes/cm²), bars (1 bar = 10^6 dynes/cm²) and megaPascals (MPa, 1 MPa = 10^7 dynes/cm² = 10 bars). MegaPascal units are used here since the Pascal has been adopted as the Standard International unit of pressure.

Plant water potential is commonly split into three components as follows:

$$\Psi = \Psi_p + \Psi_\pi + \Psi_\tau$$

where Ψ is the water potential, Ψ_p is hydrostatic pressure, Ψ_π is the osmotic or solute potential and Ψ_τ is the matric potential. The plant is considered under equilibrium conditions when Ψ is the same at all points (Nobel 1974); when plants are growing in natural conditions, equilibrium conditions are most closely approximated just before dawn. Even at equilibrium, the distribution of the water potential into components varies with plant parts. In the xylem, osmotic and matric components are small, usually less than 0.3 MPa (Ritchie and Hinckley 1971), and $\Psi \approx \Psi_p$. There is negative hydro-

static pressure, or tension, in the xylem. Cell vacuoles contain few colloidal surfaces or interfaces, so vacuolar Ψ_{τ} is negligible. But solutes in vacuoles generally create significant osmotic pressure. In turgid cells, vacuolar Ψ_{π} is lower than Ψ . The positive hydrostatic pressure which results from low Ψ_{π} in vacuoles gives rise to cellular turgidity (Nobel 1974).

Water Potential

The water potential is relatively easy to estimate with a pressure chamber. Plant tissue is placed in the chamber with the cut end of the xylem protruding through an airtight seal and the chamber is pressurized until water just begins to emerge from the cut xylem. The pressure in the chamber at which the xylem surface first becomes wet is called the "balance pressure" (Tyree et al. 1978). The balance pressure is the opposite of the water tension or negative hydrostatic pressure in the xylem. Since $\Psi \cong \Psi_p$ in the xylem, balance pressure is assumed to approximate $-\Psi$.

Much work has been done to analyze plant water potential as it varies through space and time and as it affects other plant processes, because it is easy to measure and because of the importance of water to plant growth and distribution. Hinckley and others (1979) provide an excellent review of work on forest trees. Here I will simply summarize some of the concepts that have come out of this work. (Except where noted, the following information is from Hinckley et al. 1979).

Water potential varies diurnally, seasonally, from one side of a tree to another (Ritchie and Hinckley 1971), and with increasing tree height. Leaf water potential is highest (least negative) before dawn, drops during the day as more water is lost through transpiration than is taken in by roots, and rises again later in the day. With increasing water vapor deficit and decreasing soil moisture availability, recovery occurs later in the day, and eventually the difference between pre-dawn and mid-day potential decreases due to lower stomatal conductance. Pre-dawn water potential of conifers often is not correlated with soil water potential, although there is a close correlation in hardwoods. In some cases, the difference between types of trees may be related to substantial leaf conductance in the dark in conifers, which prevents the tree from reaching equilibrium with the soil overnight. Higher xylem resistance to water flow, due to conifers' small tracheids, may also inhibit overnight equilibrium, so pre-dawn conifer water potential may be significantly lower than soil water potential.

Most studies of the seasonal course of water potential are limited to the summer months. In general, as soils dry through the summer, plant water potential decreases. But trees seem to equilibrate with "wet" areas of the soil (Hinckley and Bruckerhoff 1975), and as the growing season progresses the "wet" zones become progressively deeper (Krygier 1971). Cold soils in winter can lower plant water potential by greatly increasing root resistance. Murphy and Ferrell (1982) also found low winter water potential in Pseudotsuga

menziesii on a mild, coastal site, possibly the result of heavy transpirational water loss.

Plant water potential has been used extensively as an indicator of plant moisture stress. Recently, however, turgor has been suggested as a better criterion of plant water status than total water potential (Cheung et al. 1975, Hsiao 1976, Jackson and Spomer 1979, Roberts et al. 1980). Turgor may directly affect stomatal opening (although bulk turgor may be different from guard cell turgor), and the effects of changing water status on cell metabolism have been attributed to small changes in turgor (Hsiao 1976, Zimmerman 1978).

Turgor Maintenance and Osmotic Adjustment

The turgor at any given water potential depends on the osmotic potential and the elasticity of the cell walls. Low osmotic potential and highly elastic cells aid in maintaining cell turgor. Water deficits induce inconsistent alterations in elasticity; generally elasticity decreases, but sometimes it increases with decreasing water potential (Turner and Jones 1980). There is considerable evidence that osmotic potential drops substantially as water potential decreases. In some circumstances, solute concentration increases beyond that attributable simply to water loss. This osmotic adjustment, or osmoregulation, is viewed as a mechanism by which the plant maintains turgor as water potential drops.

The most detailed and conclusive evidence for osmoregulation is for crop plants (Turner and Jones 1980). Work on forest trees is limited, but several studies do suggest osmoregulation in response to drought. Cline and Campbell (1976) noted that the osmotic potential of twigs of Acer glabrum, Pinus monticola, Alnus sinuata and Physocarpus malvaceus decreased from June through August, followed by an increase in September. Jackson and Spomer (1979) found similar summer-season decreases in Pinus ponderosa, Pseudotsuga menziesii, Abies grandis, and Thuja plicata, as did Roberts and others (1980) in Acer rubrum, Liriodendron tulipifera, Cornus florida, and Ilex opaca.

There is also evidence that drought tolerant species are able to achieve a lower osmotic potential than less tolerant species when subjected to conditions of low soil moisture (Tyree et al. 1970, Jackson and Spomer 1979, Nilsen et al. 1981, among others). Similar differences occur among provenances of a single species. Kaplan (1974) found Eucalyptus camaldulensis from hot, dry habitats achieved lower osmotic potentials and had higher turgor during drought than did trees of the same species from a more mesic habitat.

Documentation of diurnal osmotic adjustment is more limited. Wenkert (1981) demonstrated substantial diurnal osmotic change in corn beyond that attributable to water loss alone. Many other attempts to document diurnal osmoregulation have failed, leading Tyree and Karamanos (1981) to conclude that diurnal osmotic changes are usually passive. Nilsen et al. (1981) concur that ecologically significant diurnal osmoregulation is probably rare.

Apparently, the nature of the compounds responsible for increased osmotic potential has been explored only in crop species. Sugars, potassium and amino acids are responsible for osmotic regulation in wheat; in addition, chloride ions and carboxylic acids are involved in sorghum. High proline levels have also been noted in stressed tissues (Hanson and Hitz 1982). There is no indication that new biochemical pathways or syntheses of new compounds are involved in osmotic adjustment (Turner and Jones 1980, Hansen and Hitz 1982).

Turgor maintenance by osmotic adjustment is not always sufficient to maintain physiological processes fully. Decreased growth rates (in soybeans) and decreased stomatal conductance (in wheat) occur with decreased xylem water potential despite maintenance of turgor (Turner and Jones 1980).

Measurement: Psychometry and Pressure-Volume Curves

Osmotic potential is sometimes measured by freezing tissue, squeezing cell sap and collecting it on a paper disc, and measuring the osmotic potential with a thermocouple psychrometer (Cline and Campbell 1979). Since this technique combines cell sap with xylem water, a small amount of dilution of cell solutes will occur.

Water potential parameters can be estimated more simply by pressure-volume (P-V) analysis (Scholander et al. 1966, Tyree and Hammel 1972). This technique relates Ψ , estimated with a pressure chamber,

to some measure of water content in desiccating tissue. The relationship is usually plotted with $1/\Psi$ on the ordinate; water content (expressed as a proportion of the total water in fully turgid tissue), water deficit ($1 - \text{water content}$), or the total volume of water lost from the tissue is usually plotted on the abscissa (Figure 1). Less frequently, Ψ is plotted directly against water content (Jackson and Spomer 1979), or the inverse of the water content is plotted against Ψ (Hinckley et al. 1979).

The inverse transformation of either Ψ or water content is useful because it separates curves fitted through data points into two distinct portions. Data points obtained from turgid tissue fall on a curved line, while points obtained after turgor is lost fall on a straight line. The linear relationship between $1/\Psi$ and water content occurs because of the Van't Hoff relationship between osmotic potential and the volume of symplastic water. Simplified, this relationship is (Richter et al. 1981):

$$\Psi_{\pi} * V = \text{constant} \quad (1)$$

where V is volume of symplastic water and the constant is the product of the number of moles of dissolved solute, Kelvin temperature, and the gas constant (R). Rearranging the equation:

$$1/\Psi_{\pi} = V * 1/\text{constant} \quad (2)$$

Since $\Psi_{\pi} = \Psi$ at zero turgor,

$$1/\Psi = V * 1/\text{constant} \quad (3)$$

Equation (3) describes the linear relationship between $1/\Psi$ and volume of symplastic water after turgor loss. Water content and water

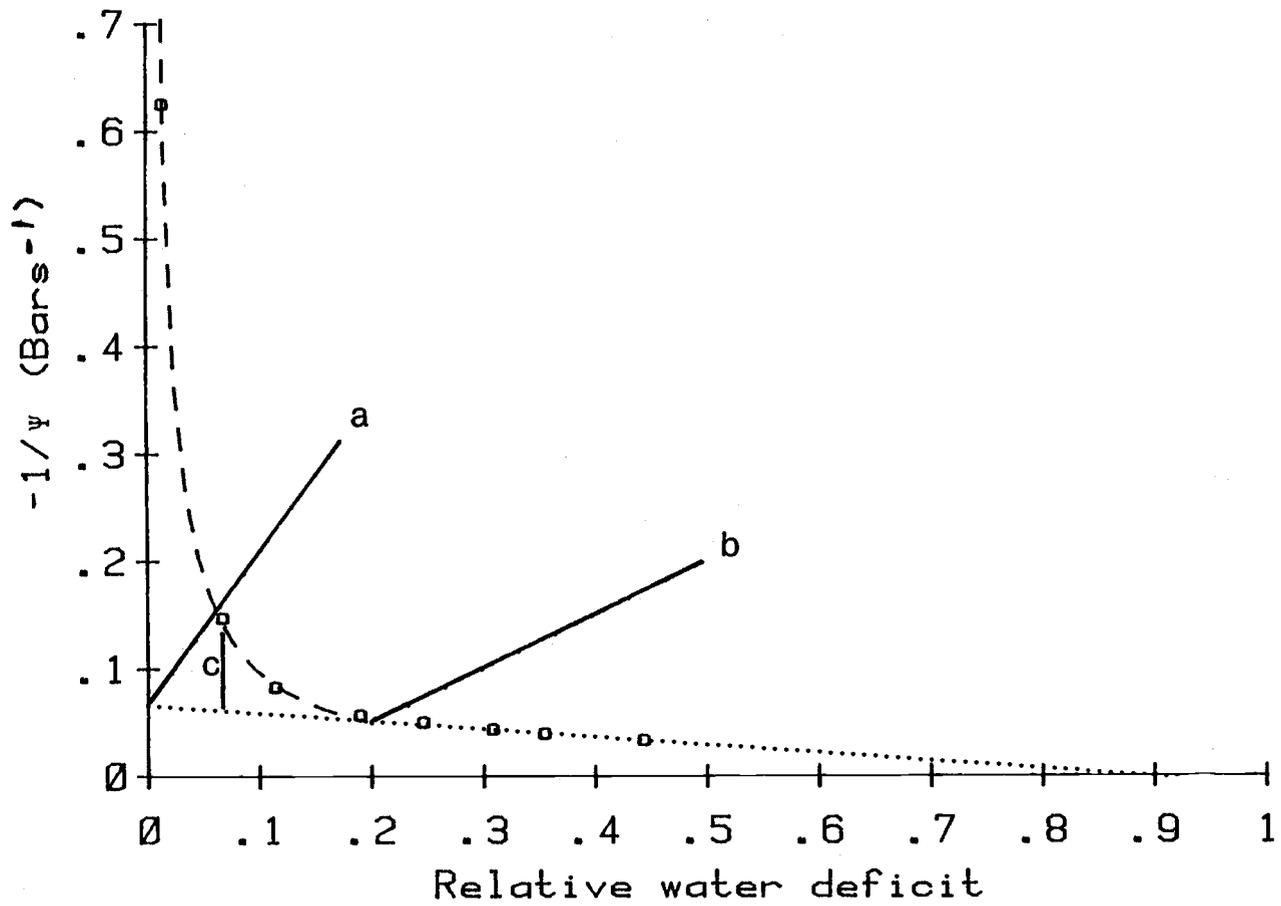


Figure 1. An example of one type of "Pressure-Volume" curve. See text for explanation of notations.

deficit are proportional to the volume of symplastic water, so there is also a linear relationship between $1/\psi$ and these parameters after turgor loss.

The osmotic potential at full turgor ($\psi_{\pi_{100}}$) is a measure of solute concentration at zero water potential. The reciprocal of $\psi_{\pi_{100}}$ can be obtained by extrapolation of the straight line segment of P-V curve to the ordinate (Figure 1, point a). The osmotic potential at the turgor loss point (ψ_{π_0}) is determined from the value of $1/\psi$ at the intersection of the straight and curved portions of the plot (Figure 1, point b). The bulk turgor (or volume-averaged turgor, Tyree and Hammel 1972) at a particular water potential or water deficit may also be estimated from the pressure-volume curve. At each value of water deficit, the bulk turgor is equal to the difference between ψ_{π} , indicated by the straight line, and ψ , indicated by the curved line (Figure 1, point c) (Tyree and Hammel 1972). P-V curves may also be used to estimate the volumes of symplastic water and apoplasmic water at full turgor, the relative water content at a given water potential, and the bulk elasticity of the cell walls (Tyree et al. 1978, Wilson et al. 1979).

Good correlation has been found between the values of osmotic potential at full and zero turgor obtained by psychrometry and those from the pressure-volume technique, but for other parameters (bound water, bulk elasticity, relative water content at zero turgor) the two techniques yield different results (Wilson et al. 1979).

Leaf Conductance

Leaf conductance is a measure of the permeability of a leaf to gas flow (Nobel 1974). It relates gas flow into or out of a leaf to the driving force existing between the leaf and the bulk air. In the case of water vapor (Jarvis 1981):

$$F = c * \Delta q * \rho \quad (4)$$

where F is the transpirational flux of water vapor ($\text{g cm}^{-2} \text{ sec}^{-1}$), Δq is the difference in specific humidity between the leaf and air (g g^{-1}), ρ is the density of air (g cm^{-3}), and c is the conductance (cm sec^{-1}).

Gas exchange can occur both across the waxy leaf cuticle and through stomatal pores. For most leaves cuticular flux is almost inconsequential compared with stomatal flux, so leaf conductance is generally considered synonymous with conductance through stomata (Jarvis 1981). Conductance of carbon dioxide and water through a leaf can profoundly affect many important physiological parameters in a plant, including leaf temperature (and, indirectly, enzymatic activity), cell turgor, photosynthetic activity, and transport in the phloem and xylem. Stomatal movement is an important mechanism for balancing a plant's internal physiology, and stomatal movement is controlled by many internal and external factors.

Control of Stomatal Movement

The major factors known to influence stomatal conductance are irradiance, leaf water status, ambient humidity, leaf temperature and

carbon dioxide concentration (Hall et al. 1976). Typically, conductance will decrease at radiation levels below 10% full sunlight (Hinckley et al. 1979). This is a relatively low threshold, but beneath a forest canopy such low levels of radiation are not uncommon even on a bright day (Zobel and Hawk 1980). Stomata also respond to the quality of light and show more rapid responses in blue rather than red light (Bannister 1976). Although stomata generally close in the dark, some evidence suggests that Pseudotsuga menziesii under optimal water status may not close stomata even in total darkness (Running 1975). Some, though not all, shade tolerant species open stomata faster and at lower radiation levels than intolerant species (Hinckley et al. 1979).

The relationship of stomatal conductance to leaf water potential has been extensively studied. Maximum conductance during a day has been directly correlated with pre-dawn xylem water potential, and mid-day stomatal closure is often closely related to a threshold water potential. Threshold values generally range between -1.2 and -2.5 MPa; different species have different threshold levels (Hinckley et al. 1979). Many reviewers conclude that stomata do not respond to decreasing water potentials until the threshold level is reached (e.g. Tibbits 1979), but Hall and others (1976) contend that this conclusion may be an artifact of comparing leaf resistance rather than conductance with leaf water potential. Resistance responses are curvilinear, increasing dramatically at "threshold" values, while conductance varies more linearly with water potential. Stomatal

sensitivity to leaf water potential is often interpreted as inducing drought resistance (e.g. Minore 1979).

Low atmospheric moisture (high vapor pressure deficit) can cause stomatal closure, but it is often difficult to separate the effects of humidity from those of other variables. Leaf conductance in Picea sitchensis decreased linearly with increasing vapor pressure deficit (VPD) between 1 and 12 mb (Watts et al. 1976). But different species respond very differently to increasing VPD. In some cases stomatal aperture and transpiration increase with increasing VPD (Tibbits 1979). In many cases stomatal movement related to VPD may be due to changes in leaf water potential, but in some cases water potential is clearly not involved. For example, Chamaecyparis stomata opened as humidity rose even at low xylem water potentials (Zobel and Liu 1980). Leaf water potential and vapor pressure deficit can act synergistically. When leaf water potential is low due to limited soil moisture, stomata are more sensitive to sudden changes in VPD (Tibbits 1979).

The primary effect of temperature on stomata is probably to alter their sensitivity to other factors. Leaf water potential has a greater influence on stomatal conductance at extreme temperatures (Hinckley et al. 1979).

Intracellular carbon dioxide has been well-studied as a stomatal regulator, although the precise mechanism is not clear. With increasing CO₂ concentration, stomata close. Stomatal conductance can oscillate under constant environmental conditions, which has been

attributed to fluctuations in internal CO₂ concentration, although fluctuations in the plant's hydraulic system may also be responsible (Raschke 1975).

Stomatal responses to osmotic pressure and turgor have not been studied well, although, as mentioned earlier, it has been widely speculated that high turgor might allow stomata to remain open despite low water potential. Turgor pressure regulates the *kdp* operon in the bacterium Escherichia coli; this operon controls potassium ion transport through the cell membrane (Laimins et al. 1981). This demonstration of direct control of gene expression by turgor pressure may have important implications for higher plants, particularly because stomatal movement occurs in response to K⁺ movement across guard cell membranes. Hsiao (1973) documented a close relationship between turgor, stomatal activity and cell elongation.

Leaf Conductance in Relation to Photosynthesis and Transpiration

Carbon dioxide and water vapor diffuse passively in and out of a leaf. The flux, or rate of flow, was described earlier; it is driven by the concentration gradient of the CO₂ or H₂O and mediated by tissue conductivity. The "conductance" parameter is generally used to describe diffusion through stomata. Its reciprocal, "resistance", is used more frequently when more complex diffusive pathways are described. In this situation, resistance is easier to manipulate mathematically; the total resistance along a diffusive pathway is equal to the sum of resistances of its individual parts.

The diffusive pathway of CO₂ includes the resistances along the H₂O pathway (boundary layer, stomata, intercellular air space) in addition to a series of resistances within the mesophyll. The additional resistances are sometimes described by the single term "mesophyll resistance", but it is more accurate to distinguish the "carboxylation resistance", due to enzymatic action of photosynthesis, from "mesophyll resistance", the CO₂ pathway from the intercellular air space to the site of CO₂ fixation in the chloroplast (Farquhar and Sharkey 1982).

Farquhar and Sharkey point out two common but incorrect assumptions in the literature: 1) stomata impose a large limitation on the rate of CO₂ assimilation and 2) the stomatal limitation is more severe when plants are stressed. They maintain that stomatal limitation of photosynthesis is usually small; minimizing water loss is a far more important role of stomatal movement. Jarvis (1981) agrees, and suggests that photosynthesis regulates stomata far more than stomata regulate photosynthesis.

Obviously, open stomata do permit CO₂ entry and subsequent photosynthesis. But since stomata regulate H₂O more than CO₂, stomatal movement provides a mechanism for modifying water use efficiency, the amount of water lost relative to carbon dioxide fixed.

Abies grandis and Abies concolor

Taxonomy

Abies grandis and Abies concolor have a history of taxonomic

confusion. Various authors have described them as one, two and even three separate species (Daniels 1969). Two problems have caused the confusion. First, both grand fir and white fir are polytypic, so it is difficult to give a definitive description of either species. Second, although "typical" grand fir and "typical" white fir are clearly distinct, trees that appear intermediate between the two types grow across a broad area from northwestern California through southwestern to northeastern Oregon and into central Idaho (Daniels 1969). After extensively sampling the trees across their combined ranges, Daniels concluded that the morphologically intermediate types are the result of introgression -- hybridization followed by repeated backcrossing to Abies grandis.

Other investigations corroborate Daniels' hypothesis. The two species readily hybridize in plantations (Klaehn and Winieski 1962), and hybrids are morphologically intermediate between parent types. Seedlings in a common garden, grown from seed collected across the range of the species-complex, maintain many morphological and growth differences (Hamrick and Libby 1972), indicating a genetic basis for intermediate characters.

White fir in the Rocky Mountains is morphologically different from white fir in the Sierra Nevada Mountains of California, leading some authors to classify the Rocky Mountain firs as a species (A. concolor) distinct from their more western relatives (A. lowiana) (Steinhoff 1965). After a detailed survey of trees in a common garden, Hamrick and Libby (1972) recommended classifying all white

firs as a single species, but they recognized trees from southern California and the Rocky Mountains as subspecies A. concolor var. concolor and Sierra Nevada trees as subspecies A. concolor var. lowiana.

Ecology and Distribution

Both Abies concolor and A. grandis are common and widespread in the western United States and grow in a wide variety of sites. Grand fir is common in the valleys and lower slopes from southern British Columbia to northern Idaho, western Montana, Oregon, and on the north coast of California. It grows best on deep, moist, porous soils of bottomlands, in some cases reaching heights of over 250 feet (Sudworth 1908). But the trees also grow well on shallow, exposed soils of mountain slopes and ridges in favorable moisture conditions (Daniels 1969).

The climatic conditions across the range of grand fir vary widely, but may be generally described as relatively cool summers, mild winters, and rather gradual changes in temperature. Annual precipitation ranges from as low as 50 to over 250 cm per year. Typically, there is little or no rainfall in July or August. The growing season ranges from less than 100 days in northern Idaho to longer than 185 days in western Washington and Oregon (Daniels 1969).

The range of white fir covers two main areas (Hopkins 1981). The western portion stretches from the southern Cascades and Coast Ranges of Oregon through the Klamath, Siskiyou, and Sierra Nevada

Ranges to the Coast Ranges of southern California. The interior portion of the range extends from southern Idaho south through Utah, eastern Nevada, southern Colorado, Arizona and New Mexico to northern Mexico. White fir grows over a wide range of elevations, from 3,000 feet on the west side of the California Coast Range to as high as 10,000 feet in the San Bernardino Mountains of Southern California (Hopkins 1981).

The relative drought resistance of grand fir and white fir is not clear. Grand fir generally grows on moist sites (Sudworth 1908, Steinhoff 1978), but Steinhoff added that it has the lowest moisture requirements among the moist-site species. Also, Zobel (1974) noted that grand fir on the west side of the Oregon Cascades had relatively low water potentials before dawn in late summer (about -2.5 to -3.0 MPa) compared with those of trees on the east side of the Cascades (-0.9 to -1.1 MPa). The eastern Cascade trees had stomatal characteristics more similar to white fir. White fir is generally associated with drier forests than is grand fir (Hopkins 1981), but despite the more xeric vegetation associated with it, Minore (1979) ranked white fir below grand fir in drought resistance. Annual precipitation across the range of white fir, 50 to 225 cm (Hopkins 1981), is broad and similar to that of grand fir. Zobel (1975) noted, though, that white fir occurs in areas with both less and much more summer rainfall (about 1 to 25 cm) than that of areas where grand fir occurs (about 3 to 10 cm).

White fir grows more slowly than grand fir. Hopkins (1981) considered it extremely shade tolerant compared with other conifers, though Minore (1979) ranked white fir below grand fir in shade tolerance. Minore's ranking put white fir slightly higher than grand fir in frost tolerance.

STUDY SITE, METHODS AND MATERIALS

The Study Site

This study was conducted in McDonald Forest, part of the eastern foothills of the Oregon Coast Range, about 13 km northwest of Corvallis, Oregon. Annual rainfall is about 115 cm, with over 75 percent of that precipitation occurring between early November and late April (Sprague and Hansen 1946). Temperatures are moderate, and the frost free season averages about 170 days.

The study site, a steep north-facing slope, has a mean elevation of 440 m. Soils on the site are a silty clay loam of the Price series, with a Douglas fir site index of 115.¹ Originally the site supported an old-growth Douglas-fir forest; it was clear cut in 1970. Juday (1976) extensively surveyed the vegetation of a similar old-growth stand, also on a north-facing slope, about 1 km north of this site. He denoted the association as Pseudotsuga menziesii - Acer macrophyllum/Corylus cornuta var. californica/Adenocaulon bicolor -- the most widespread and abundant of all old-growth community types in his Willamette Valley margin zone. Abies grandis was a common understory component of the original stand.

¹U.S. Department of Agriculture - Soil Conservation Service Interpretation Record 7-81 for Benton County, Oregon.

Experimental Populations

Trees for this project were obtained from the Institute of Forest Genetics of the Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, located in Placerville, California. These trees were all F1 hybrids resulting from a variety of crosses between white fir from Colorado and white fir and grand fir from California (Appendix 1). Several naturally regenerated grand fir were also included in the study. It is important to clarify that the grand fir in the study are not parents of the grand fir x white fir hybrids; grand fir parents for the crosses were from the northern California coast. Also, since the grand fir saplings used in this study resulted from natural regeneration in the forest understory, differences between these trees and the other varieties reflect both their history and genotype.

Progeny from ten crosses were planted on the site. Including the local grand fir, then, eleven types were available for this investigation. The eleven types represent five general "varieties", based on the species and geographic origin of parents:

1. Colorado white fir x Colorado white fir (CO x CO w.f)
2. Colorado white fir x California white fir (CO x CA w.f.)
3. Colorado white fir x California grand fir (CO x CA hybrid)
4. California white fir x California grand fir (CA x CA hybrid)
5. Native grand fir (Native g.f.)

I chose these five "varieties" as the units for comparison in this study. In sampling and data analysis, I made no attempt to differentiate among the specific parentage of crosses within each "variety". It was difficult to sample enough trees to establish differences among five varieties; it would have been impossible to distinguish among all eleven progenies. The types within each variety were very similar morphologically, while the five varieties were quite distinct both in morphology and growth.

The seven progenies included in the white fir varieties and the Colorado x California hybrids were planted on April 9, 1970, as 2-0 seedlings. They were planted on two contiguous grids, each with seven north-south columns by eighteen east-west rows (Appendix 2). The arrangements of trees across each row were independently randomized. In many cases the trees were set out in pairs of the same genotype, but by the time of this study only one tree of the pair survived in most cases.

The three progenies of California x California hybrid trees were planted as 2-0 seedlings in the spring of 1971 in the spaces where trees planted the previous year had not survived.

Sampling Technique

I was not able to make physiological measurements on all trees, but choosing an adequate sample proved a taxing problem. Preliminary measurements revealed that stomatal activity and water potential varied considerably, depending on the location in the study site as

well as time of day and genotype. Also, the varieties were unequally represented on the site: there were only six native grand fir trees, and only seven Colorado x Colorado white fir were healthy enough to use.

I needed a sample that would:

1. be small enough to measure in an hour or less.
2. be large enough to establish statistically meaningful differences among varieties.
3. take into account location on the study site.
4. use the few available trees of the rare varieties.

I chose an uneven block design, with each block centered around a tree of the less common varieties. At least four of the five tree varieties were represented in each block. Trees in each block were physically close to each other, minimizing the problem of environmental variability within the sample. Also, I could make water potential and leaf conductance measurements on a block in less than an hour.

I started with six blocks in August, 1981, and increased the sample size to eight blocks including thirty-six trees in June, 1982 (Appendix 3). I did not always measure all blocks in any single measurement period, but I always measured all trees in a particular block.

To analyze the data statistically, I used a multiple linear regression with indicator variables for blocks and genotypes. This is a cumbersome technique; each data point is represented by up to

eleven independent indicator variables (5-1 varieties + 8-1 blocks, Neter and Wasserman 1974). The mean square error of the regression is used to compare means by standard t-tests. This type of analysis accomodates unequal representation of varieties in blocks: the array of indicator variables for the missing variety is simply skipped. If entire blocks are missing from a data set, the total number of independent variables is decreased accordingly. I used Hewlett-Packard 75 and 85 microcomputers to perform statistical analyses, using statistics software packages developed by Hewlett-Packard.

My sample sizes were relatively small, determined by the maximum number I could accurately measure, not the minimum required for good statistical differentiation. Because of small sample size and my statistical techniques, I have probably failed to identify some true differences between genotypes, but it is not likely that I identified differences which really do not exist.

Conductance Measurement

I measured leaf diffusive resistance (the inverse of conductance) with a LiCor 1600 steady state porometer fitted with a 4 cm² square conifer chamber. I followed the manufacturer's recommended procedures for using the porometer, which include thoroughly drying the dessicant before each day's use. The LiCor 1600 is elegantly simple to use, but because of its simplicity it is easy to overlook many important precautions necessary for accurate measurement.

The porometer must be in equilibrium with ambient temperature. Resistance calculations depend on accurate measurement of absolute humidity, which in turn is a function of the relative humidity and leaf or air temperature. It may take 20 minutes or more to establish an equilibrium if the porometer is taken from room temperature to hot or cold field conditions.

A related problem occurs when the porometer cuvette heats as it is exposed to intense solar radiation for more than a few minutes, for example, during a hot summer afternoon. I attempted to shade the sensor head with my body as I took measurements. A single measurement takes about a minute, and it is unlikely that stomata will respond significantly to decreased light in that time.

Accurate leaf temperature measurements are also necessary for resistance calculations, and the LiCor 1600 is equipped with a thermocouple designed to touch the leaf surface and measure leaf temperature. The thermocouple seems to work quite well with broad leaves, but it is nearly impossible to be sure that the thin wire makes contact with fir needles in the chamber. For the sake of consistency, I bent back the thermocouple so that it always measured cuvette air temperature. This introduces an error into resistance calculations, but I preferred this consistent error to an inconsistent error, since my primary purpose was to compare performances of different varieties, not to assess absolute performance of individual varieties. If leaf temperature of all varieties deviated from air temperature in

exactly the same way, their relative resistance is not much affected by assuming $T_{\text{leaf}} = T_{\text{ambient}}$.

Unfortunately, needle temperatures may not always be the same for all varieties. My preliminary measurements suggest that white fir needles can be as much as 2 °C cooler than hybrid or grand fir needles on hot summer days (Appendix 4), probably because of the waxy white surface of the white fir needles and possibly because of more evaporative cooling of faster transpiring white fir. Bending back the thermocouple (i.e. assuming $T_{\text{leaf}} = T_{\text{ambient}}$) causes white fir needle conductance to be underestimated relative to that of hybrids and grand fir. My data will show that the white fir had higher conductance than other trees on summer afternoons. If leaf temperature differences shown in Appendix 4 occur consistently, true differences are probably slightly more pronounced than my data indicate.

To calculate resistance, it is necessary to determine the surface area of needles enclosed in the cuvette. In order to harvest precisely the same needles I placed in the cuvette, I removed three or four needles on either side of the measured needles. I did this at least 24 hours before porometer measurements, to allow time for restabilization of the water balance.

Harvested needles were carefully cut to exclude those parts which had been outside the cuvette aperture, then placed inside a piece of folded acetate. Projected needle area was determined by running the needles through a LiCor 3100 leaf area meter from four to ten times, depending on the consistency of the measurements. The

accuracy of the area meter, determined with known areas of paper cut in the shape of needles, was \pm about 5%.

The LiCor 1600 porometer is programmed to assume a 0.15 sec cm^{-1} boundary layer resistance in leaf resistance calculations. The manufacturer recommends adjusting for the boundary layer when resistance measurements are adjusted for leaf area, according to the following equation:²

$$R = [(R_d + 0.15) * (\frac{A_t}{A})] - R_b \quad (5)$$

R = true diffusive resistance, R_d = displayed diffusive resistance, 0.15 = assumed boundary layer resistance, A_t = true leaf area, A = assumed leaf area, and R_b = true boundary layer resistance.

In this study, $A = 1 \text{ cm}^2$, A_t was usually about 2 cm^2 , and R_b was probably between 0.1 and 0.3 sec cm^{-1} (from the formula, $R_b = 1.3$ [leaf dimension in direction of wind flow/wind speed]^{1/2} and a wind speed of about 80 cm sec^{-1} in the cuvette).²

So, in the average situation:

$$R = 2(R_d) + 2(0.15) - 0.2 \quad (6)$$

$$= 2(R_d) + 0.1 \quad (7)$$

Since R_d is generally 10 to 100 times greater than the 0.1 cm sec^{-1} boundary layer adjustment term, I chose to ignore it and use the simpler formula:

$$R = R_d (A_t)$$

²Equations are from the LiCor 1600 operator's manual.

The simplified approach will cause a slight error at low resistance (high conductance). After resistance was adjusted for leaf area, conductance was calculated as its reciprocal.

Unless otherwise noted, stomatal conductance measurements were made only on one-year-old needles. Stomatal conductance may vary with conifer needle age (Kozlowski 1971, Running 1975), but the purpose of this study was to assess differences among varieties, not to determine the absolute performance of individual varieties. It was assumed that one-year-old needles represent differences occurring in all age classes. Through the summer of 1981, I harvested needles at the end of each measurement day. In the early spring of 1982 I established two measurement areas on southern exposed branches of each tree. All 1982 porometry measurements were made on the same needles. Measurements in 1981 and 1982 were made on cloudless days on needles that had not been shaded for at least one hour.

Measurement of Water Potential Components

Throughout this study I used a PMS pressure chamber to estimate twig water potential. I generally followed the procedure and precautions that Cleary and Zaerr (1980) recommend, although I did use a sharp razor blade to cut a very thin slice off the end of twig samples after inserting them in corks. This cut greatly facilitated seeing the endpoint, and should not significantly affect measurements on conifer twigs, with their small tracheids (Scholander et al. 1965).

The twigs used in water potential measurements included the current year's flush of growth and usually the complete previous year's segment. I generally clipped the samples about 1 m from the ground (except when trees were too small) and chose samples exposed to full sunlight close to the twigs used for porometry studies, but on a different branch. Water potentials of the fully exposed twigs were as much as 0.3 MPa less than shaded twigs on the same tree. Twigs were placed in the pressure chamber within two minutes of removal from the tree.

I determined the components of the water potential (solute potential and turgor pressure) by running modified versions of "pressure-volume" (P-V) curves on twig samples taken back to the laboratory. The technique I used does not involve measurement or calculation of volumes, so it is not completely accurate to call it a "pressure-volume" technique. Jackson and Spomer (1979) use a more precise designation, "water-release curve". But "pressure-volume" curves have become well-known recently, and the term is useful for communicating the general nature of several related techniques that yield similar information.

The theoretical basis for analyzing P-V curves, first described by Scholander et al. (1965) and later refined by Tyree and Hammel (1972), can be directly applied to the "water release" technique. As described in my LITERATURE REVIEW section, a P-V curve is frequently plotted as the reciprocal of the water potential in a drying leaf or twig against the water deficit. In water-release analysis, the water

deficit is computed on the basis of weight loss from a leaf or twig sample as it dries. In the classic P-V analysis, water deficit is calculated from the volume of sap exuded from the cut end of a twig sample placed in a pressure chamber.

The "water-release" method is simpler to use than the classic "pressure-volume" technique; it is much easier to weigh samples periodically than to collect sap carefully. One may evaluate many more samples in one measurement period when using the "water-release" technique. In the "pressure-volume" technique a sample remains in the pressure chamber for the entire measurement period, so sample number is limited by the number of pressure chambers available. Some researchers use the two techniques interchangeably (P.W. Rundel, personal communication). There is currently insufficient evidence to determine which of the two techniques is the more accurate, though Ritchie (1983) recently reported obtaining different results using the two techniques on Pseudotsuga menziesii twigs.

I cut twig samples for "water-release" analysis just after taking pre-dawn water potential readings. I placed stems in jars containing about 5 cm of distilled water, and then recut the stems under water. After sealing the jars tightly in plastic bags, I placed them in a refrigerator. Samples remained cold and dark for approximately 24 hours before analysis began, to allow tissue to become fully turgid. According to Nilsen et al. (1981), sclerophyllous leaves may be kept in the cold and dark for up to a week with no influence on components of water potential.

Samples were removed from jars one at a time to begin analysis. The stem was recut and inserted into a pre-weighed rubber cork. Excess water was carefully blotted away and the initial weight determined. The sample was immediately placed in a pressure chamber, the balance pressure was noted, and the sample was removed and allowed to air dry. At regular intervals, initially every 20 minutes but increasing to periods of 5 hours or more, samples were reweighed and the balance pressure again determined. The procedure continued until the balance pressure exceeded 3.0 MPa (the limit of the pressure chamber was 4.0 MPa). The result is a set of 7-20 data pairs for each sample. The procedure took less than 20 hours in March, but some samples took up to 50 hours to dry adequately in June.

A few precautions are necessary with the technique. Pressurization dehydrates the sample unevenly, and time must be allowed between measurements for redistribution of water (equilibration) within the sample (Tyree et al. 1978). Initially equilibration requires 20-30 minutes, and the time increases as the analysis proceeds. Incomplete equilibration causes balance pressure readings to be lower (balance pressure is a positive value, xylem tension is negative) than they ought to be. It is even possible for consecutive readings to show a decreased rather than an increased chamber pressure at the balance point if tissue is not equilibrated.

It is difficult to get a precise measurement of the initial turgid tissue weight. During preparation, samples may lose significant water. Alternatively, the initial weight may be higher than the

true turgid weight if moisture remains on the needles. When pressure is plotted against water deficit (as in Figure 1), underestimating turgid weight causes the curve to be shifted to the left. This shift lowers the intercept on the $1/\psi$ axis, which results in overestimation of $\psi_{\pi_{100}}$. The magnitude of the error increases as the slope of the linear portion of the curve increases. In one sample trial I found that an error of 0.2 g in turgid weight resulted in a 0.4 MPa error in the osmotic potential at full turgor. Turgid weight errors will not displace the curve vertically, so ψ_{π_0} is not affected.

I resolved the turgid weight problem by inferring turgid weight (Campbell et al. 1979). There is a nearly linear relationship among the first few data points (ψ , weight) after $\psi < -0.3$ MPa. I determined the linear regression equation through these points and evaluated the equation at zero ψ to estimate the initial turgid weight. In nearly all cases the correlation coefficient of these regressions was more than 0.95; usually it was greater than 0.98.

A final problem occurs because each time a sample is pressurized, tissues are subjected to high temperatures, and when pressure is released, tissues cool. The rapid temperature changes can damage tissue (Puritch and Turner 1973). Slow pressure changes (0.2 - 0.3 MPa min^{-1}) have been suggested to minimize damage. I generally increased pressure slowly; however, I took no precautions to decrease pressure slowly since I was unaware of the problem until after I finished collecting the data reported here. The effect of temperature change on results is unknown, but I do not believe it is

significant. If significant tissue damage occurred during measurement, one would expect subsequent data points to deviate from patterns established by initial data points. Such deviation did not occur. Regression equations through data points (described below) had high coefficients of correlation, generally over 0.98, and curves were smooth; visual examination of curves revealed no sudden changes.

I analyzed P-V curve data on a Hewlett-Packard 87 microcomputer with software developed at the University of California at Irvine; hard copies of the program are available (E. T. Nilsen, P. W. Rundel and M. R. Sharifi, Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717). A power regression is fit to describe points in the curved portion of the P-V plot, using the model $\ln(1/\Psi) = \ln(a) + (b) \ln(WD)$, where WD is the water deficit and a and b are constants. Linear regressions are determined for the last three points, then the last four, and so on until all data points are included. The best fit line is chosen as the line with the highest correlation coefficient; this is the osmotic potential line. I modified the original program to include a graphic display of the P-V curve data points and the two regression lines. Visual examination of the output is necessary to verify that regression lines appropriately represent the overall curves. It is possible, for example, for the linear regression through the last three data points to have a higher correlation coefficient than the last five, even though the last five may be a better representation of the linear portion of the curve. In this situation, I substituted

the line I deemed more representative for the line with the best fit regression.

The computer program also calculates water relations components for a theoretical Hoffler diagram. Starting with a relative water deficit of 0.02 and increasing at increments of 0.02 until the point of incipient plasmolysis (the intersection of the linear and power regressions), water potential (from the power regression), osmotic potential (from the linear regression), and turgor pressure (the difference between the first two components) are evaluated. The Hoffler analysis allows a very convenient method for determining turgor pressure at any given water potential or water deficit.

A sample data output from the computer program is shown in Appendix 5.

Measurement of Leaf Area and Growth of Branches

In October, 1982, one entire branch was removed from each of the 36 study trees (see SAMPLING TECHNIQUE). Branches were four- or five-years-old and contained one of the two "leaf areas" used for leaf conductance measurement during 1982.

The cross-sectional area of sapwood at the base of each branch was measured to estimate relative leaf area. Cross-sectional area of sapwood in the crown of conifer boles is an accurate indicator of canopy leaf area, and the regression equation relating sapwood area to leaf area is nearly the same for grand fir and grand fir x white fir hybrids (Waring et al. 1982). I assumed that basal sapwood area

of branches is likewise related to total branch leaf area, and that the relationship between sapwood area and leaf area is the same for all of the tree varieties studied here. Given these assumptions, relative sapwood area approximates relative leaf area. The assumptions have not been tested, and results of this analysis should be considered preliminary.

I harvested branches with clippers, which compressed stems and distorted the cross-sectional area. I then removed a section about 2 cm long from the cut end of each branch with a fine-toothed saw and determined the sapwood area of the saw-cut surface. I measured the smallest and largest diameters across the xylem of each stem to the nearest 0.01 cm. I placed the section under a dissecting microscope and measured the smallest and largest diameters inside the most recent growth ring. I computed areas from the average of the squares of the longest and shortest radii, and then subtracted the area inside the most recent growth ring from the total cross-sectional area to determine the cross-sectional area of the current-year increment of wood.

I clipped all current-year growth from the ends of twigs and dried it to constant weight. This I have defined "appendant" growth, to distinguish it from total annual growth of branches, which also includes the sapwood increment on stems produced in previous years.

I removed ten one-year-old needles at random from each branch and determined projected area as described earlier. I dried these

needles to constant weight and calculated the weight to area ratio of the needles.

RESULTS AND DISCUSSION

Height Growth

The California grand fir x Colorado white fir hybrid clearly outgrew all other varieties on the study site (Figure 2). Trees with two Colorado white fir parents grew quite poorly. In 1980 the differences between the fastest- and slowest-growing varieties increased. The change may indicate that competition among the trees and between trees and shrub cover was becoming important in 1980. Nearly all of the slow-growing Colorado white fir experienced significant shading by the time this study was initiated in 1981, and most trees with intermediate growth were subjected to at least partial shading by other trees and shrubs.

It is important not to interpret the data in Figure 2 as a provenance test. The trees planted on the study site all resulted from artificial crosses, some between very distantly related trees, and they do not necessarily reflect adaptations to a particular environment. Inferences between performance on this site and adaptations to other climatic conditions can be made only in a general sense.

Leaf Conductance

Needle Age and Conductance

In a September, 1982, survey of conductance vs. needle age in

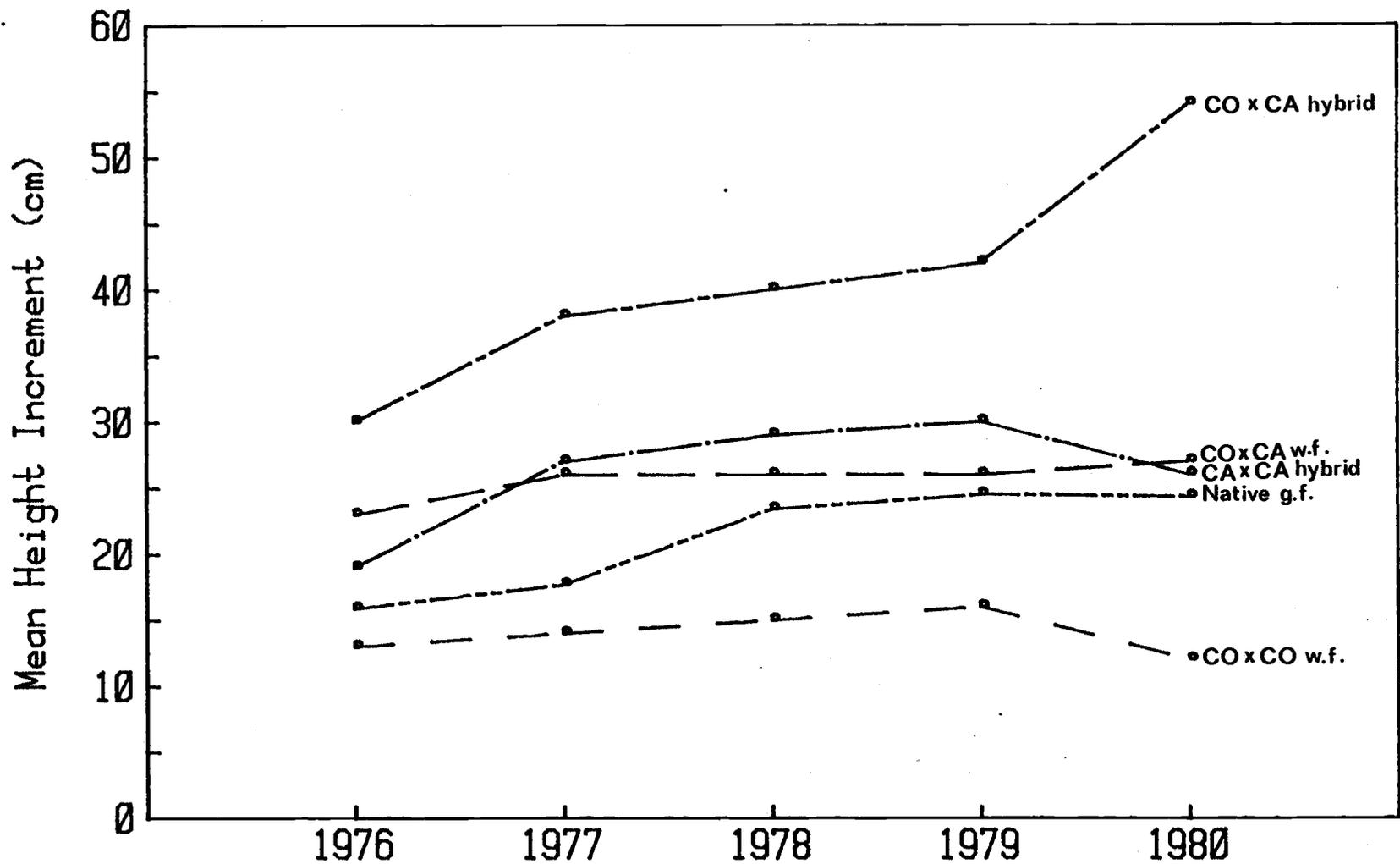


Figure 2. Mean height growth from 1976 to 1980 of the five varieties. Data points are mean values of all members of each variety on the study site. Increments were determined by measuring lengths between whorls. Data for 1976-1979 are from D.B. Zobel.

two varieties (Table I), age generally had only a slight effect on conductance. Although the differences among varieties were large, as shown in my other measurements, differences among age classes of a single variety were not significant. The lack of significant differences is due in part to large variability among older needles. The mean values do indicate declines with age.

Because of large variability, it is also not possible to validate the assumption that needle age affects conductance similarly in all varieties (see METHODS). But since differences among varieties are generally much larger than differences among needle age classes, it is unlikely that conclusions reached in this research are biased by measuring a single age class.

TABLE I. Variation of conductance with needle age. Values are in cm sec^{-1} and represent the means of measurements on four trees. Measurements were made on September 11, 1982 between 12:00 and 13:00.

Needle Age	Variety	
	CO x CA white fir	CO x CA hybrid
Current-year needles	0.239 \pm 0.026	0.087 \pm 0.018
One-year-old needles	0.261 \pm 0.063	0.076 \pm 0.034
Two-year-old needles	0.185 \pm 0.054	0.078 \pm 0.057

Diurnal Variation of Conductance

Both July 15 and 28, 1981, were hot, moderately dry days (Figures 3 and 4). Conductance measurements made on these days reveal different responses of the five varieties to high temperature and vapor pressure deficits (Figures 5 and 6). One tree of each variety was measured on each day, but a different set of trees was measured on the two days.

With the exception of the Colorado x Colorado white fir, the varieties exhibited consistent differences in conductance. Conductance of the grand fir and the two grand fir x white fir hybrid varieties peaked in the mid- to late morning, declined to a minimum in mid-afternoon, and sometimes recovered slightly later in the day (Figures 5 and 6). This pattern is typical of many northwestern conifers during the summer months (Hinckley *et al.* 1979). The grand fir always had lower mid-afternoon conductance than the other trees. The Colorado x California white fir trees, in contrast, had much higher maximum conductance, the peak conductance occurred two or more hours after the other trees, and higher conductance was maintained through the afternoons.

Performance of the Colorado x Colorado white fir probably reflected the trees' poor condition more than their genetic potential. Most of these trees were chlorotic; none appeared healthy. Some trees had a conductance similar to the Colorado x California white fir, others had very low summer afternoon conductance. It is reasonable to conclude that the Colorado x Colorado white fir have

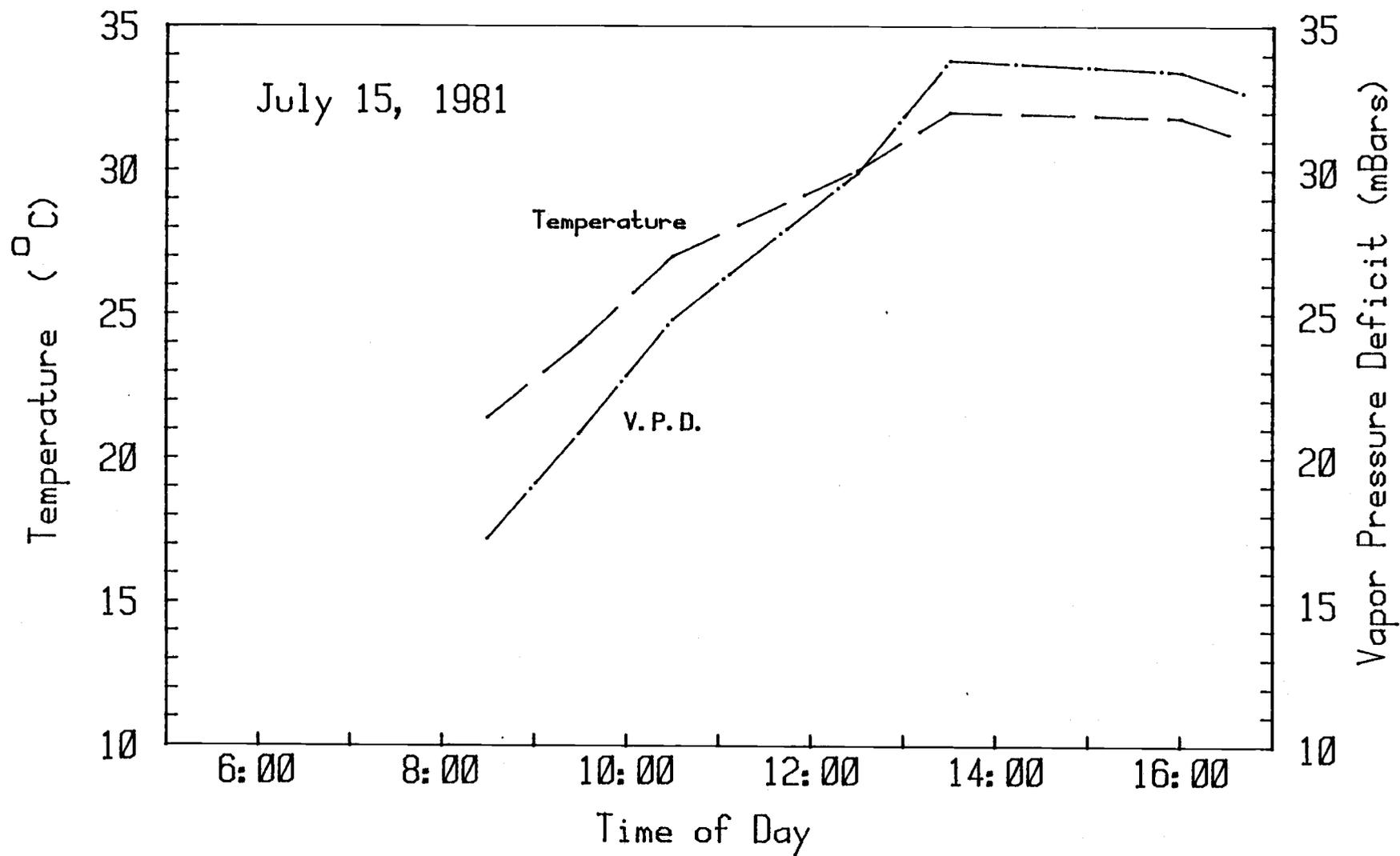


Figure 3. Diurnal air temperature and vapor pressure deficit on July 15, 1981. Measurements were made with the LiCor 1600 porometer.

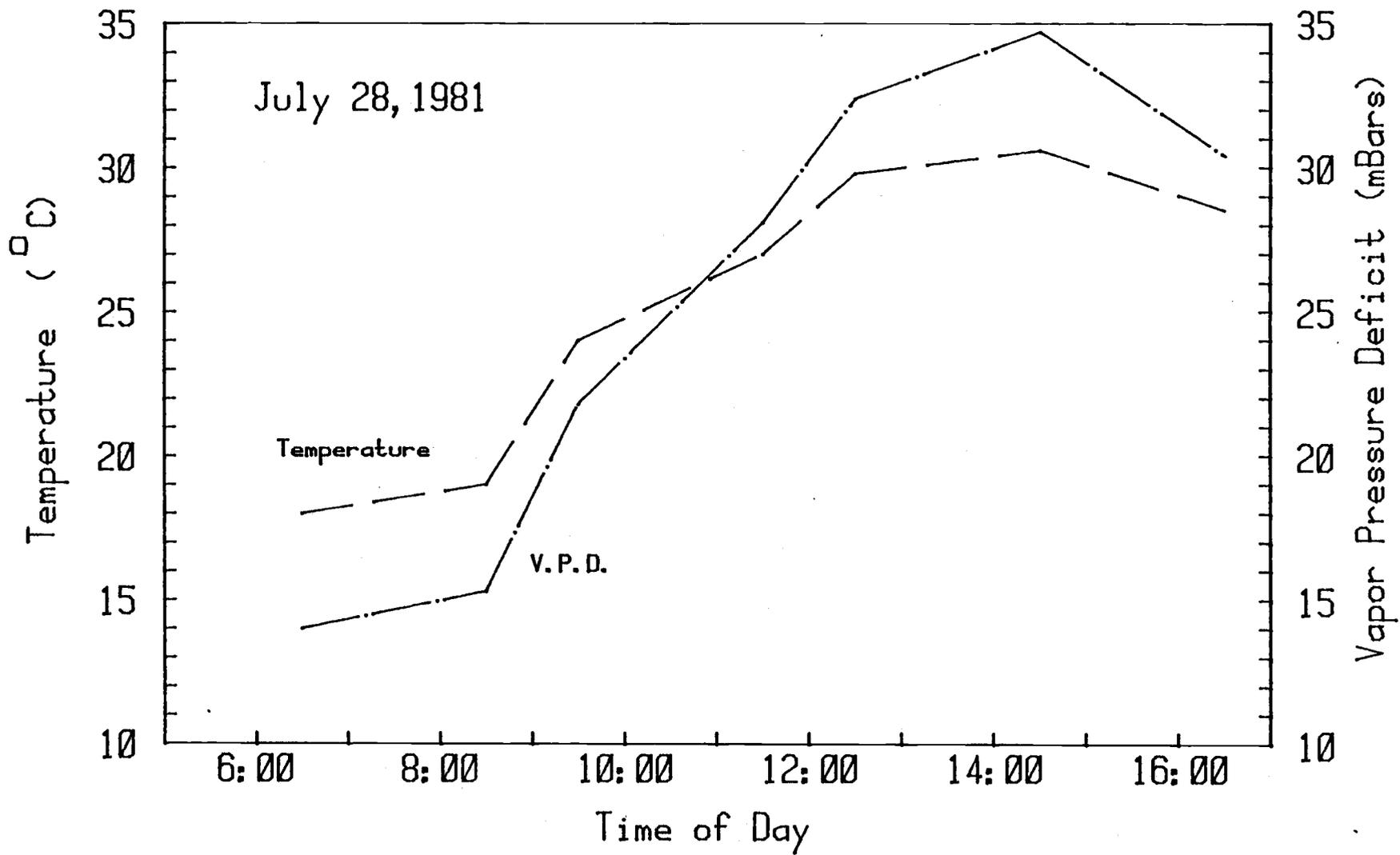


Figure 4. Diurnal air temperature and vapor pressure deficit on July 28, 1981. Measurements were made with the LiCor 1600 porometer.

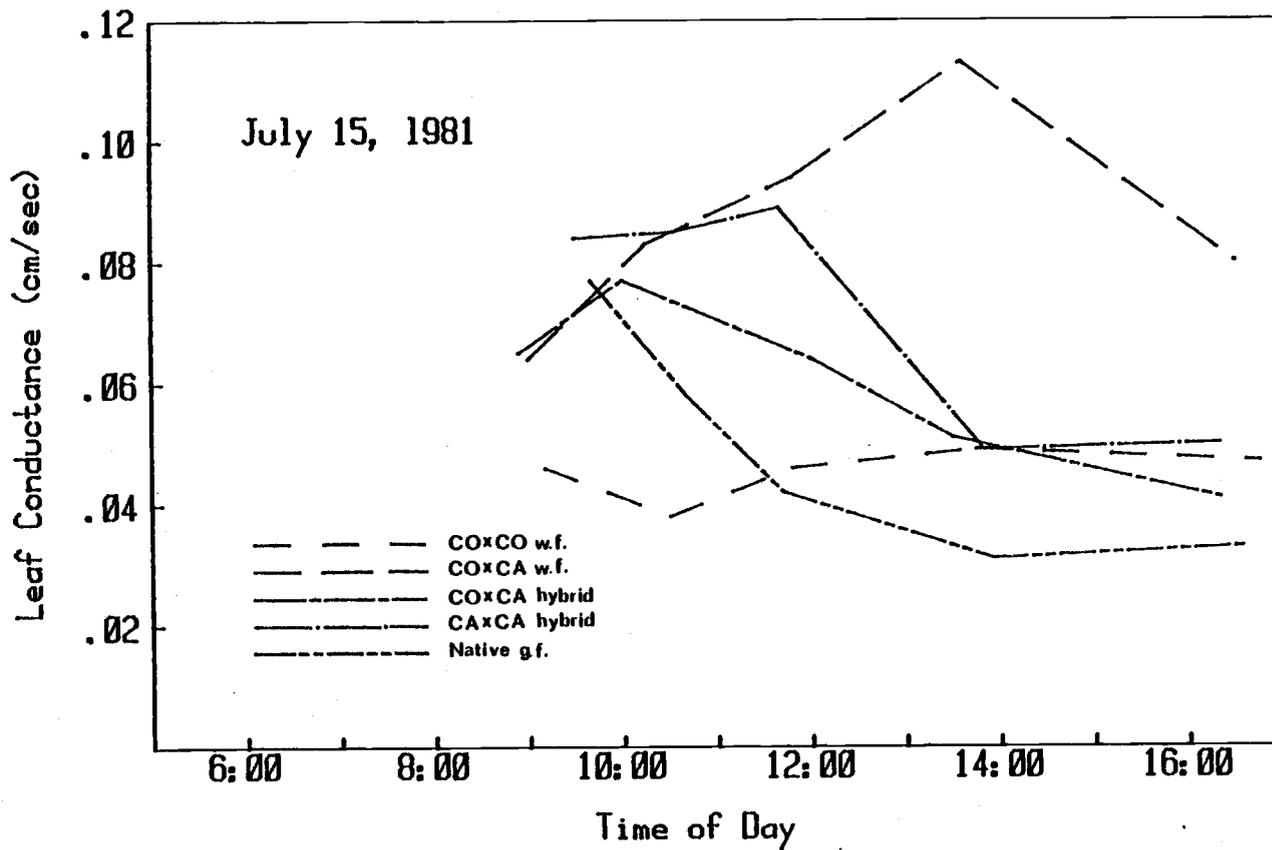


Figure 5. Diurnal leaf conductance on July 15, 1981. Data points represent single measurements.

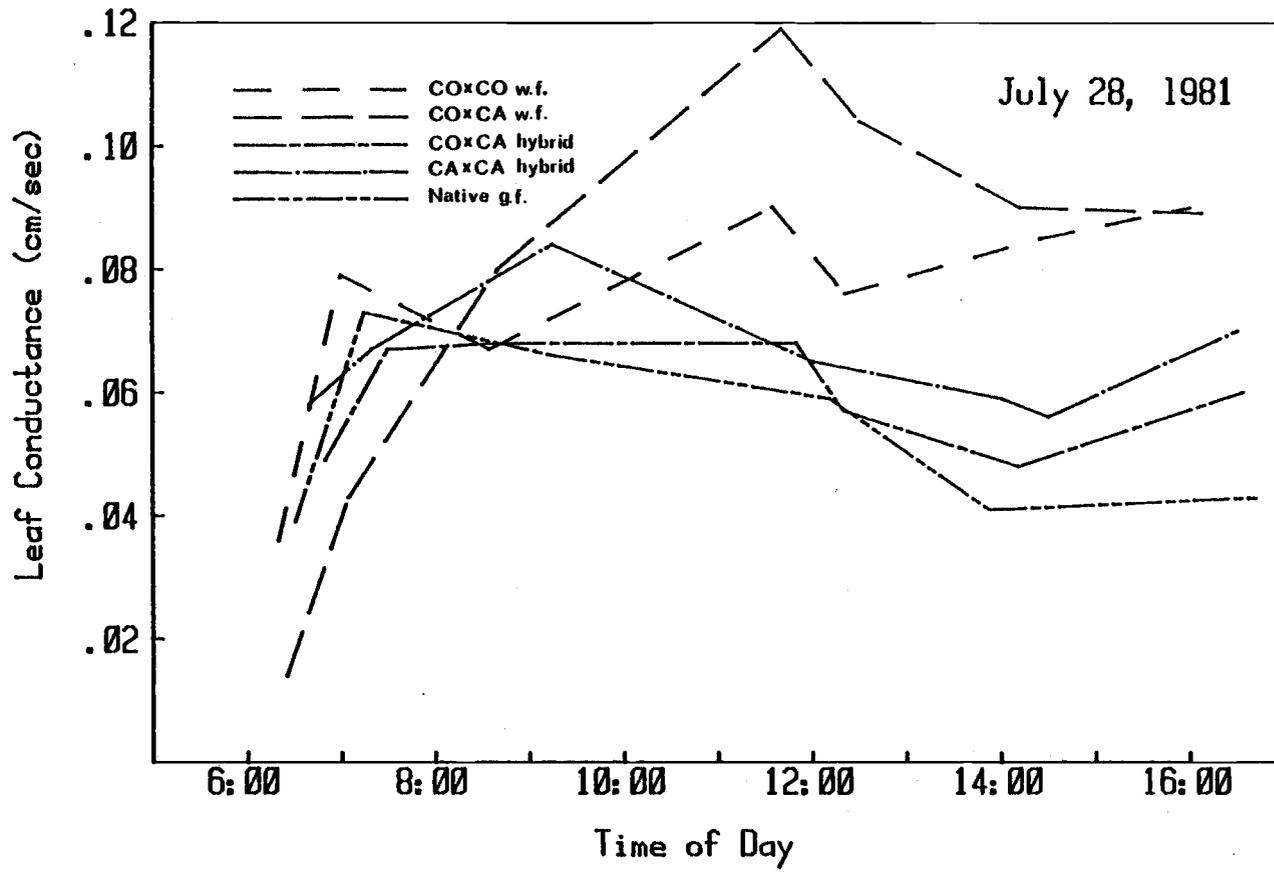


Figure 6. Diurnal leaf conductance on July 28, 1981. Data points represent single measurements.

the potential to maintain relatively high conductance, but poor condition reduced the conductance of some of them.

It is important to interpret these data cautiously. Although the trees are closely related, differences in needle morphology may affect the relationship between leaf conductance and stomatal aperture. White fir needles have stomata covering adaxial surfaces, whereas hybrids have only a small group of adaxial stomata near the needle tip, and grand fir have no stomata on the upper surface of needles. Since white fir presumably have more stomata per cm^2 leaf surface, the white fir stomata would be relatively more closed than grand fir stomata at equal conductances. Leaf conductance differences do not necessarily reflect stomatal aperture differences among the tree varieties.

There is considerable variation among other reports of grand fir and white fir leaf conductance. According to Running (1976), the seasonal daylight minimum for grand fir is $0.003 \text{ cm sec}^{-1}$. I never measured a daylight conductance value less than 0.03 cm sec^{-1} . Many factors may contribute to these different values. Measurement is less accurate at very low conductance, and different instrumentation could yield different results. Running used both an aspirated "Turner" porometer and a null-balance porometer; he does not describe cuvette types or differences in results from the two porometers. Minimum conductance differences could also result from genetic differences between the grand fir in this study and Running's

study. Running measured trees at several Oregon sites and does not identify which had the lowest conductance.

Jackson and Spomer (1975) estimated a maximum potential conductance of $0.068 \text{ cm sec}^{-1}$ for grand fir; Running (1976) evaluated a much higher maximum conductance of $0.192 \text{ cm sec}^{-1}$ for grand fir during the growing season. In my study, the daily maximum conductance for grand fir during July drought averaged around $0.060 \text{ cm sec}^{-1}$ and frequently exceeded $0.080 \text{ cm sec}^{-1}$, higher than Jackson and Spomer's maximum but well below Running's. Conductance well below the maximum potential might be expected during summer drought. Jackson and Spomer estimated maximum conductance on detached branches in October. Conductance of several age classes of needles will be averaged with this technique, which may partly explain their low maximum. Also, maximum conductance of conifers may vary with season (Murphy and Ferrell 1982). A single measurement in October probably would not represent the annual or seasonal maximum conductance.

A study by Radosevich et al. (1980) included three diurnal conductance curves for northern California white fir. The conductance of their four-year-old, plantation-grown trees was considerably higher in July than that of the trees in this study, ranging from about 0.13 to 0.21 cm sec^{-1} , perhaps because temperatures were cooler (about 23° C maximum) and plant water potential higher (predawn xylem pressure potential was -0.39 MPa). Considering these differences, diurnal conductance of white fir in

this study compares reasonably well with that reported by Radosevich et al.

These data confirm summer differences in stomatal behavior between grand fir and white fir indicated by previous studies. Keys (1976) measured higher stomatal infiltration pressure (indicating smaller aperture, therefore lower conductance) on trees with foliage similar to grand fir than on trees with foliage similar to white fir, when trees were growing in the same plantations. In several populations in the central Oregon Cascades, Zobel (1974) reported higher afternoon infiltration pressure among trees more similar to grand fir; the difference became more pronounced in late summer. Considering the combined data from this and earlier studies, it may be concluded that white fir have the genetic potential to maintain higher leaf conductance than grand fir during summer. F1 hybrid trees appear to be intermediate, although more like grand fir than white fir.

Relationships Between Diurnal Conductance and Water Potential

Leaf conductance during hot, dry conditions has been correlated with plant water potential by many investigators. Maximum diurnal conductance of conifers is sometimes a function of pre-dawn water potential (Running 1976). Stomatal closure is often closely correlated with a critical water potential; in conifers the critical point ranges between -1.2 and -2.5 MPa (Hinckley et al. 1979).

The diurnal conductance (Figures 5 and 6) and water potential data (Figures 7 and 8) in this study are insufficient for a detailed analysis of their interaction, but some relationships may be noted. First, although Colorado x Colorado white fir leaf conductance was much higher than hybrids or grand fir during the afternoon, water potentials were similar. Similarly, the two hybrid varieties had slightly higher leaf conductance than grand fir during the afternoon, while the hybrids' water potential was equal to or less than that of grand fir. It has been noted previously that trees more similar to white fir maintain more open stomata at a given water potential during the summer than trees more similar to grand fir (Zobel 1974, 1975, Keys 1976). These data confirm such differences during summer afternoons.

These data also suggest a relationship between leaf conductance and water potential that is not variety-specific. Conductance peaked and began to decline (presumably due to stomatal closure) when water potentials reached about -1.3 MPa in most cases (Table II). The grand fir and Colorado x Colorado white fir on July 28 were exceptions, but as mentioned earlier the latter were in poor condition and responded erratically. The apparent relationship between water potential and stomatal closure may simply be a coincidence resulting from small sample sizes; further testing is needed to verify whether these Abies varieties have a common or similar "critical" water potential at which stomata begin to close.

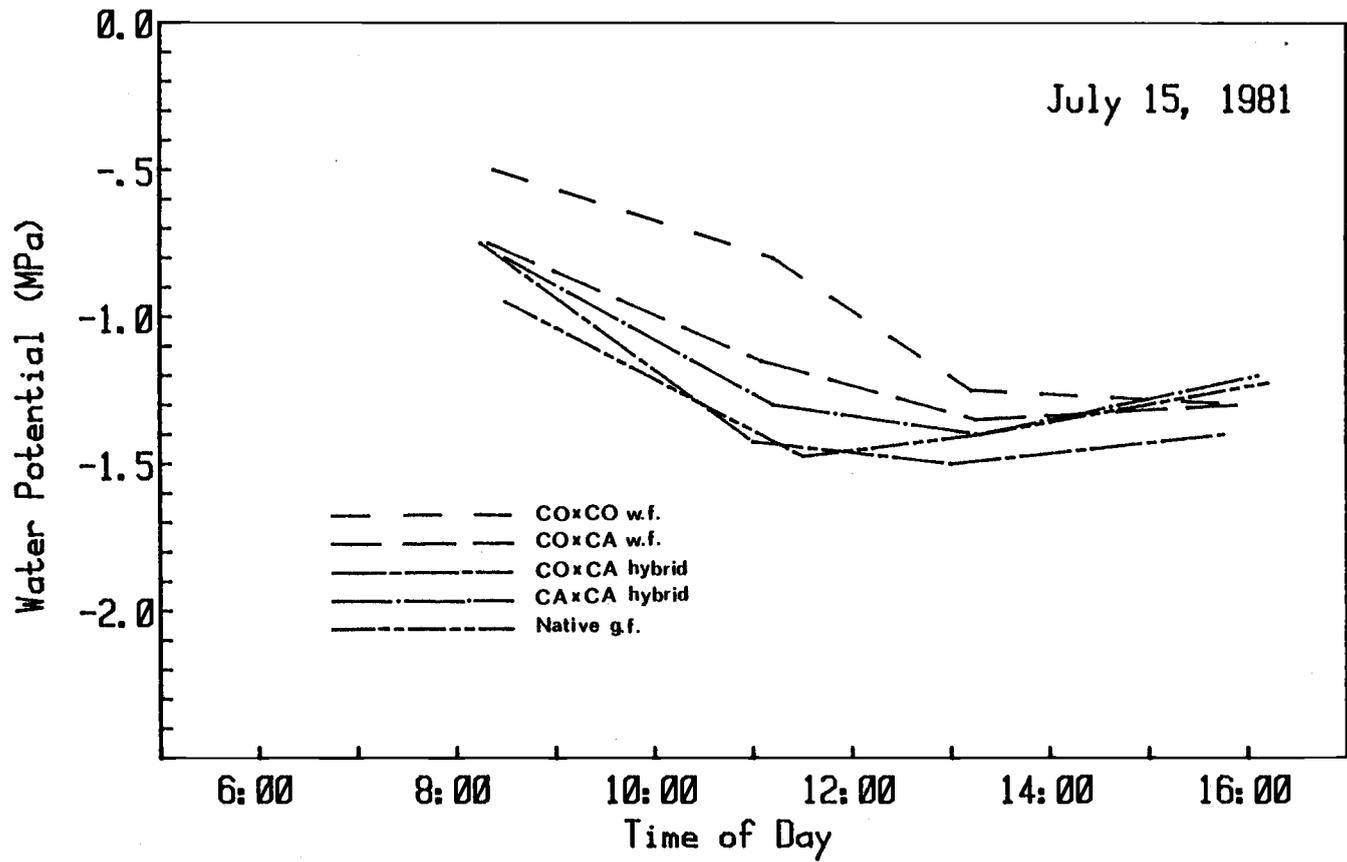


Figure 7. Twig water potential on July 15, 1981. Data points represent single measurements.

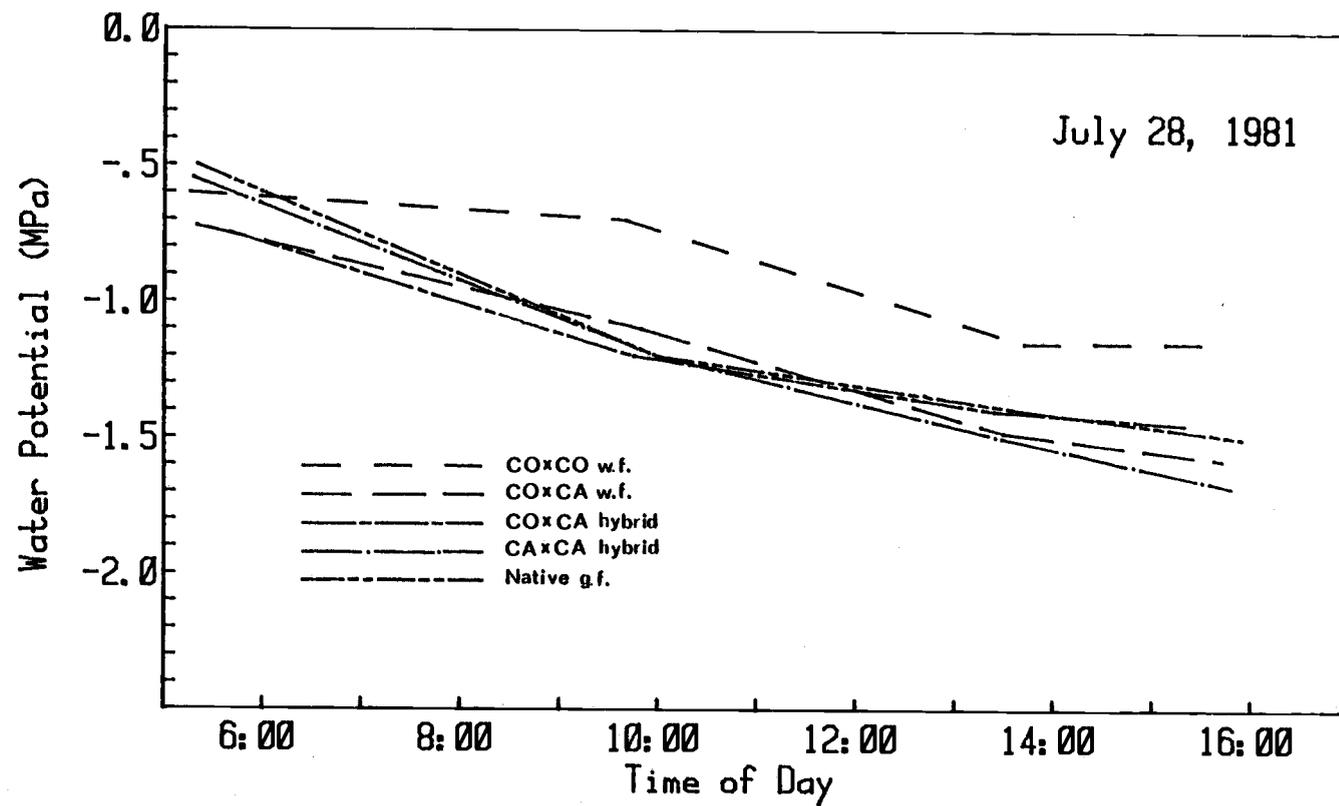


Figure 8. Twig water potential on July 28, 1981. Data points represent single measurements.

TABLE II. Maximum leaf conductance in July, 1981, relative to Ψ , time of day, temperature and vapor pressure deficit. Ψ , air temperature and vapor pressure deficit at maximum conductance were estimated from Figures 2, 3, 6 and 7 by determining values of each parameter at the time of maximum conductance.

	Variety				
	CO x CO w.f.	CO x CA w.f.	CO x CA hybrid	CA x CA hybrid	NATIVE g.f.
July 15, 1981					
Max. leaf con- ductance (cm sec ⁻¹)	0.049	0.113	0.077	0.089	0.078
Ψ (MPa) at max. conduc- tance.	-1.28	-1.32	-1.25	-1.32	-1.20
Air temperature (° C) at max. conductance.	32	32	25.5	29.5	21.5
Vapor pressure deficit (mBars) at max. conductance.	33.5	33.5	24.8	28.5	24.5
Time of day at max. conductance	13:45	13:40	10:00	11:40	9:30
July 28, 1981					
Max. leaf con- ductance (cm sec ⁻¹)	0.090	0.120	0.068	0.084	0.073
Ψ (MPa) at max. conduc- tance.	-0.90	-1.28	-1.30	-1.28	-0.85
Air temperature (° C) at max. conductance	27.5	27.5	26.5	24.0	18.5
Vapor pressure deficit (mBars) at max. conductance	29.0	29.0	27.0	22.0	14.5
Time of day at max. conductance.	11:35	11:40	9:00 - 11:00	9:20	7:15

Water potential thresholds for stomatal closure have been noted previously for many coniferous species (Hinckley et al. 1979). Lopushinsky (1969) reported a threshold for grand fir of -2.5 MPa, but his value refers to the water potential at which stomata were entirely closed, not the potential at incipient closure, as noted here. Puritch (1973) reported transpiration declines in four Abies species (A. balsamea, A. lasiocarpa, A. amabilis and A. grandis) beginning at similar water potentials, ranging from -1.0 to -1.1 MPa (my inference from Puritch's graph). Puritch's results correspond fairly well with the -1.3 MPa "critical" point indicated by my study; his results also support the idea of similar "critical" water potentials at incipient stomatal closure among Abies.

The water potentials of white fir reached the apparently critical -1.3 MPa later in the day than those of hybrids or grand fir. Differences were most obvious on July 15 (Figure 7), but also occurred on July 28 (Figure 8). This seems curious, since the afternoon leaf conductance of the Colorado x California white fir was much higher than that of grand fir and grand fir x white fir hybrids. Why does the white fir not suffer lower water potential from its apparently greater water loss? There are several possible explanations. First, relatively high conductance does not necessarily imply relatively high water loss for whole trees or branches. The transpirational water loss of the entire canopy is the product of leaf conductance, concentration gradient of water vapor, and leaf area. If the white fir have a significantly lower leaf area, they could be

maintaining higher leaf conductance while losing significantly less water than the other varieties.

Maintenance of higher water potential by white fir could also result from more effective root systems or greater water storage capacities. White fir tend to be more deeply rooted than grand fir (Hinckley et al. 1982), and their root system may be more extensive. The water storage capacities of these species have not been compared, but water storage in other coniferous species is known to buffer the effects of diurnal water loss from transpiration. Water storage in Pinus contorta needles plays an important role in stomatal movement by affecting leaf water potential (Running 1980), and stored water in sapwood allowed P. contorta trees to maintain stable leaf water potential for 33 days after trees were cut. Waring and Running (1978) estimated that water storage in a stand of old-growth Pseudotsuga menziesii was equivalent to 16 days of transpiration.

Seasonal Variation of Conductance

Conductance through the annual cycle varies among the five tree varieties (Figure 9). Each data point represents a mean of 2-8 values (Table III) rather than a single measurement. Measurements were made when near-maximum conductance would be expected (Table III); because a diurnal series of measurements was not made, the values do not represent absolute maxima.

Although sample sizes on several sampling dates were not sufficient for statistical discrimination among means, general differences

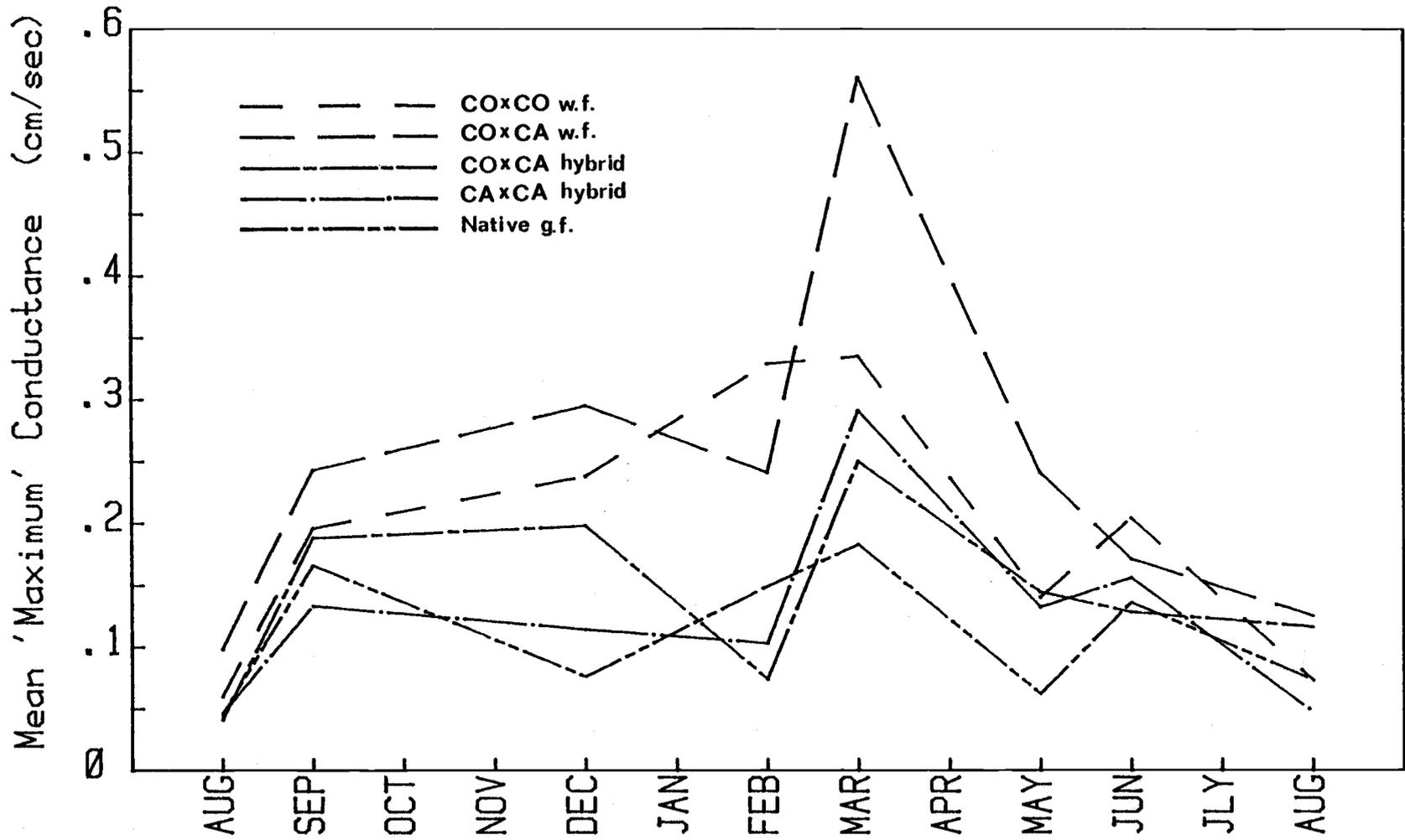


Figure 9. The annual mean "maximum" conductance of the five varieties. See Table III for additional information.

TABLE III. Mean "maximum" conductance: supplementary information for Figure 9. Statistical comparisons were computed with a one-tailed t-test of the differences between means, testing the null hypotheses that the Colorado x California white fir conductance is less than each of the hybrids and the grand fir. Tests used a family error mean square obtained from a multiple linear regression using indicator variables, as described in the METHODS. The September and December measurements occur out of chronological sequence to create a single annual cycle.

Date	Time	Mean Temp. ($^{\circ}$ C)	Mean Relative Humidity (%)	Blocks Measured	Significant Differences ($\alpha = 0.05$)
8/20/81	9:00-11:00	23	23	4, 5, 7	NONE
9/11/82	10:00-12:30	18	39	5,6,7,8	COxCA wf \neq COxCA hybrid, CAxCA hybrid and native g.f.
12/27/82	13:00-14:00	4.5	47	1, 2	NONE
2/7/82	13:30-14:30	3.5	29	2, 5	NONE
3/23/82	13:30-15:00	18	35	2,4,5,6,7	COxCA wf \neq COxCA hybrid, and native g.f.
5/6/82	13:30-14:30	24	33	2, 5, 7	COxCA wf \neq COxCA hybrid, CAxCA hybrid and native g.f.
6/10/82	8:00-11:00	25.5	38	1,2,3,4 5,6,7,8	COxCA wf \neq COxCA hybrid, CAxCA hybrid and native g.f.
8/25/82	9:00-11:00	22	45	1,2,3,4	NONE

are quite clear, both from the overall annual patterns (Figure 9) and from the four measurement periods that did yield statistically significant differences. In all measurement periods, one of the white fir varieties, usually the Colorado x California white fir, had higher conductance than both hybrids and grand fir. Hybrids usually had somewhat higher conductance than the grand fir, although the differences were statistically significant only in March (Table III).

Since these data represent approximate maximum conductances on selected days and not mean or total conductance, there is a bias introduced. All measurements were made on cloudless days with relatively low humidity, a rare occurrence during winter on this site. The differences in conductance among varieties may be less pronounced or perhaps even reversed under the more prevalent humid, low light conditions of winter. But since both absolute conductance as well as relative differences among varieties was highest in March and May, when clear days are more common, it is probably safe to conclude that the white fir have higher average annual conductance than the grand fir or hybrids.

All varieties attained much higher leaf conductance in winter and spring than in summer. This is consistent with other studies. Murphy and Ferrell (1982) reported higher leaf conductance of Douglas-fir in January and February than in July, August, October or May at sites throughout Oregon. Douglas-fir on moist sites achieved conductances of about 0.40 cm sec^{-1} , somewhat higher than winter values for the true firs in this study.

Conductance and Growth

One of the objectives of this study was to test the hypothesis that the fastest-growing varieties maintained higher winter and early spring conductance than other trees. As discussed earlier, previous studies (Zobel 1974, 1975, Keys 1976) showed that trees more similar to white fir have more open stomata during the summer than trees more similar to grand fir. The diurnal conductance curves for July reported here confirm this difference. But Colorado x California hybrid trees grew much faster than the white fir, despite lower leaf conductance during the summer. The hypothetical higher winter leaf conductance of the Colorado x California hybrids could help explain their superior growth. Emmingham and Waring (1977) predicted that 30-55 percent of the total annual carbon fixation of Douglas-fir in the Pacific Northwest occurs between October and May. Grand fir typically occur at lower elevations than do white fir, and they encounter milder winters. Higher winter leaf conductance might be expected for grand fir x white fir hybrids than for white fir.

The data fail to support this hypothesis (Figure 9). Although Colorado x California white fir have higher conductance, the Colorado x California hybrids grow faster. I suggested earlier that a smaller leaf area could account for white fir maintaining higher summer afternoon conductance without suffering from decreased water potential. Leaf area differences (or different allocation of photosynthate to leaf area) could similarly help to account for growth differences.

Faster-growing hybrid trees might compensate for low leaf conductance with greater overall leaf area. Estimated leaf areas of branches are given later in these RESULTS.

Another possible explanation, not mutually exclusive with the first, is greater carbon fixation per unit water loss (a higher water use efficiency) in faster-growing trees. Puritch (1973) showed that photosynthesis of A. grandis was about 65 percent of maximum when transpiration was at 30 percent maximum. A. lasiocarpa, A. amabilis and A. balsamea had about 50, 45 and 35 percent maximum photosynthesis at 30 percent transpiration. These results suggest relatively high water use efficiency in A. grandis during water stress. But Puritch does not give actual values for photosynthesis and transpiration, so carbon fixation per unit water loss cannot be directly compared, and his study did not include A. concolor. The water use efficiencies of A. grandis, A. concolor and their hybrids should be compared.

Variation in the Components of Water Potential

I evaluated "water-release" (= "pressure volume") relationships on detached twigs in August, 1981, March, 1982, June, 1982 and August, 1982. A few samples were not included in analysis because of technical problems such as needle loss during sampling; 112 curves were analyzed. "Water-release" curves for a representative Colorado x California white fir and a Colorado x California hybrid individual at each measurement period are in Appendix 6.

Most pressure-volume analyses either report data from single individuals, or there is no indication of sample size, but water potential components can vary considerably even among twigs from the same tree sampled at the same time (Nilsen et al. 1981). The sample sizes used in this study permit statistical verification of some differences between varieties (Table IV).

Osmotic Potential

Seasonal Variation

Although there were differences among varieties during some seasons, the seasonal variation of $\Psi_{\pi_{100}}$ and Ψ_{π_0} was much greater than the variation among varieties in any single season (Figures 10 and 11; Table IV).

The very low $\Psi_{\pi_{100}}$ and Ψ_{π_0} in early spring (indicating a high concentration of osmotically active material in vacuoles) probably resulted from conversion of starch to sugar (Ericsson 1979). Osmotic potentials rose rapidly (i.e. became less negative) between March and June, possibly due to depletion of sugar reserves during early growth. In all cases, measurements were made on the flush of twigs at the end of a branch. Phenology affects solute potential independently of environment; immature leaves can have much higher osmotic potential than mature leaves on the same plant at the same time (Nilsen et al. 1981). So the sharp increase found in this study between March and June could reflect tissue age.

TABLE IV. Mean values of water potential components from "water-release" curves. Values are in MPa. Statistical comparisons between means were made with a two-tailed t-test using a family error mean square obtained from a multiple linear using indicator variables, as described in METHODS. Sample size (n) is indicated in parentheses.

	Variety					Significant Differences ($\alpha = 0.05$)
	COxCO w.f. ("1")	COxCA w.f. ("2")	COxCA hybrid ("3")	CAxCA hybrid ("4")	Native g.f. ("5")	
Aug. 20, 1981						
$\Psi_{\pi_{100}}$	-1.70 (n=4)	-1.86 (n=5)	-1.59 (n=5)	-1.74 (n=4)	-1.92 (n=3)	1 \neq 3,5 2 \neq 3 3 \neq 4,5
Ψ_{π_0}	-2.38 (n=4)	-2.39 (n=5)	-2.19 (n=5)	-2.38 (n=4)	-2.39 (n=3)	NONE
Pre-dawn Turgor	1.05 (n=4)	1.13 (n=5)	0.81 (n=5)	0.93 (n=4)	1.43 (n=3)	1 \neq 3,5 2 \neq 3,5 3 \neq 5 4 \neq 5
Mid-AM Turgor	0.68 (n=1)	0.65 (n=2)	0.44 (n=2)	0.45 (n=2)	0.62 (n=1)	NONE
March 5, 1982						
$\Psi_{\pi_{100}}$	-2.10 (n=4)	-1.99 (n=5)	-2.11 (n=5)	-1.92 (n=4)	-2.13 (n=4)	NONE
Ψ_{π_0}	-2.86 (n=4)	-2.77 (n=5)	-2.64 (n=5)	-2.54 (n=4)	-2.87 (n=4)	4 \neq 1,5
Mid-PM Turgor	1.47 (n=4)	1.31 (n=5)	1.30 (n=5)	1.13 (n=4)	1.20 (n=4)	1 \neq 4

TABLE IV Continued

	COxCO w.f. ("1")	COxCA w.f. ("2")	COxCA hybrid ("3")	CAxCA hybrid ("4")	Native g.f. ("5")	Signifi- cant Dif- ferences ($\alpha = 0.05$)
June 11, 1982						
$\Psi_{\pi_{100}}$	-1.11 (n=5)	-1.22 (n=8)	-1.21 (n=7)	-1.18 (n=8)	-1.17 (n=5)	NONE
Ψ_{π_0}	-1.47 (n=5)	-1.54 (n=8)	-1.57 (n=7)	-1.57 (n=8)	-1.55 (n=5)	NONE
Pre-Dawn Turgor	0.64 (n=5)	0.72 (n=8)	0.67 (n=7)	0.76 (n=8)	0.72 (n=5)	NONE
Mid-AM Turgor	0.33 (n=5)	0.38 (n=8)	0.25 (n=7)	0.27 (n=8)	0.27 (n=5)	2 \neq 3
Aug. 25, 1982						
$\Psi_{\pi_{100}}$	-1.66 (n=7)	-1.71 (n=8)	-1.58 (n=8)	-1.66 (n=7)	-1.75 (n=6)	2 \neq 3 3 \neq 5
Ψ_{π_0}	-2.18 (n=7)	-2.26 (n=8)	-2.19 (n=8)	-2.30 (n=7)	-2.28 (n=6)	NONE
Pre-dawn Turgor	0.82 (n=7)	0.85 (n=8)	0.75 (n=8)	0.81 (n=7)	1.16 (n=6)	2 \neq 3 1,2,3,4 \neq 5
Mid-AM Turgor	0.57 (n=2)	0.38 (n=4)	0.22 (n=2)	0.38 (n=2)	0.39 (n=3)	NONE
Mid-PM Turgor	0.47 (n=4)	0.31 (n=4)	0.36 (n=4)	0.33 (n=3)	0.40 (n=4)	1 \neq 2,3,4,5

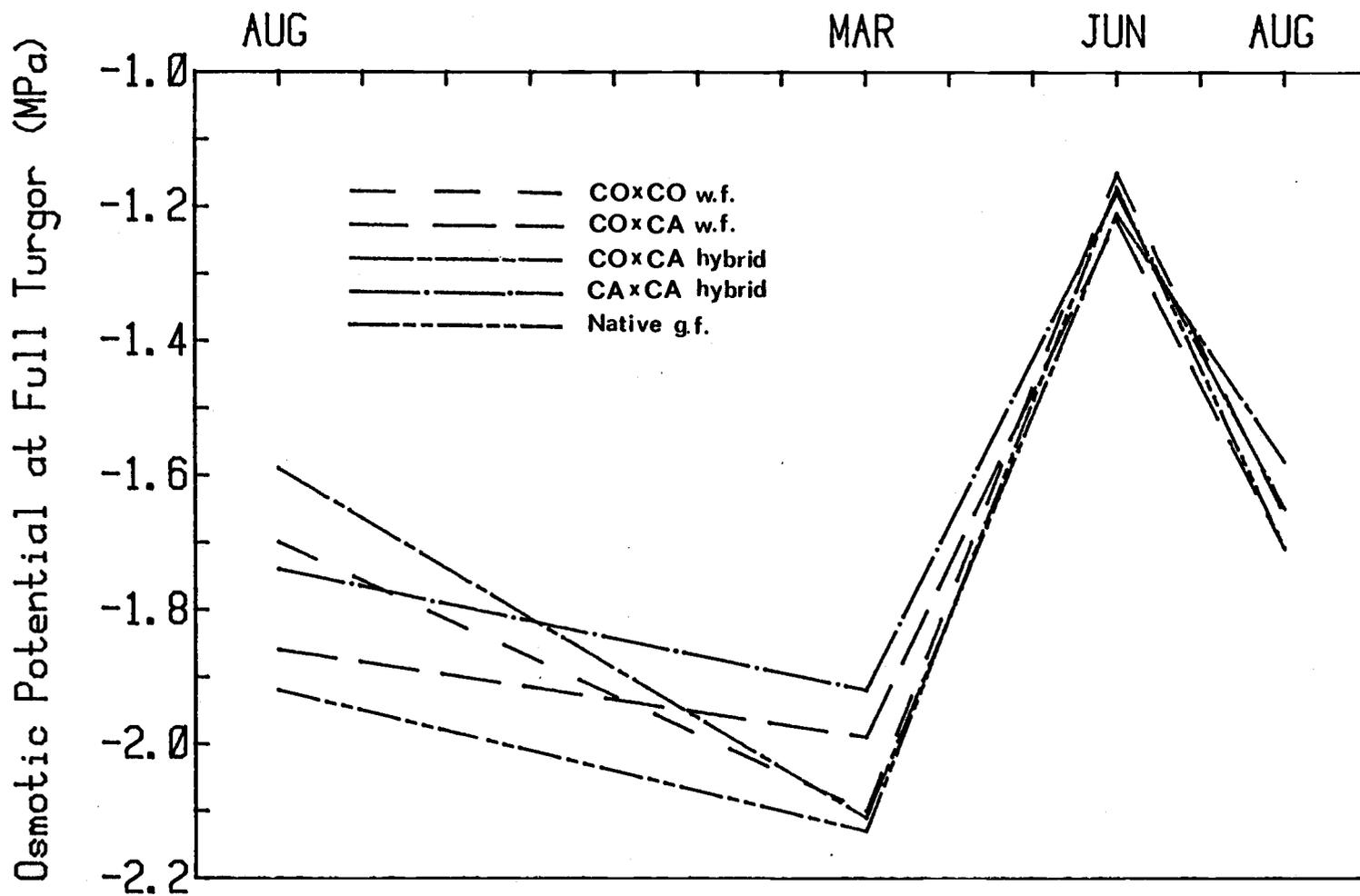


Figure 10. Osmotic potential at full turgor in August 1981, and March, June and August, 1982. See Table IV for additional information.

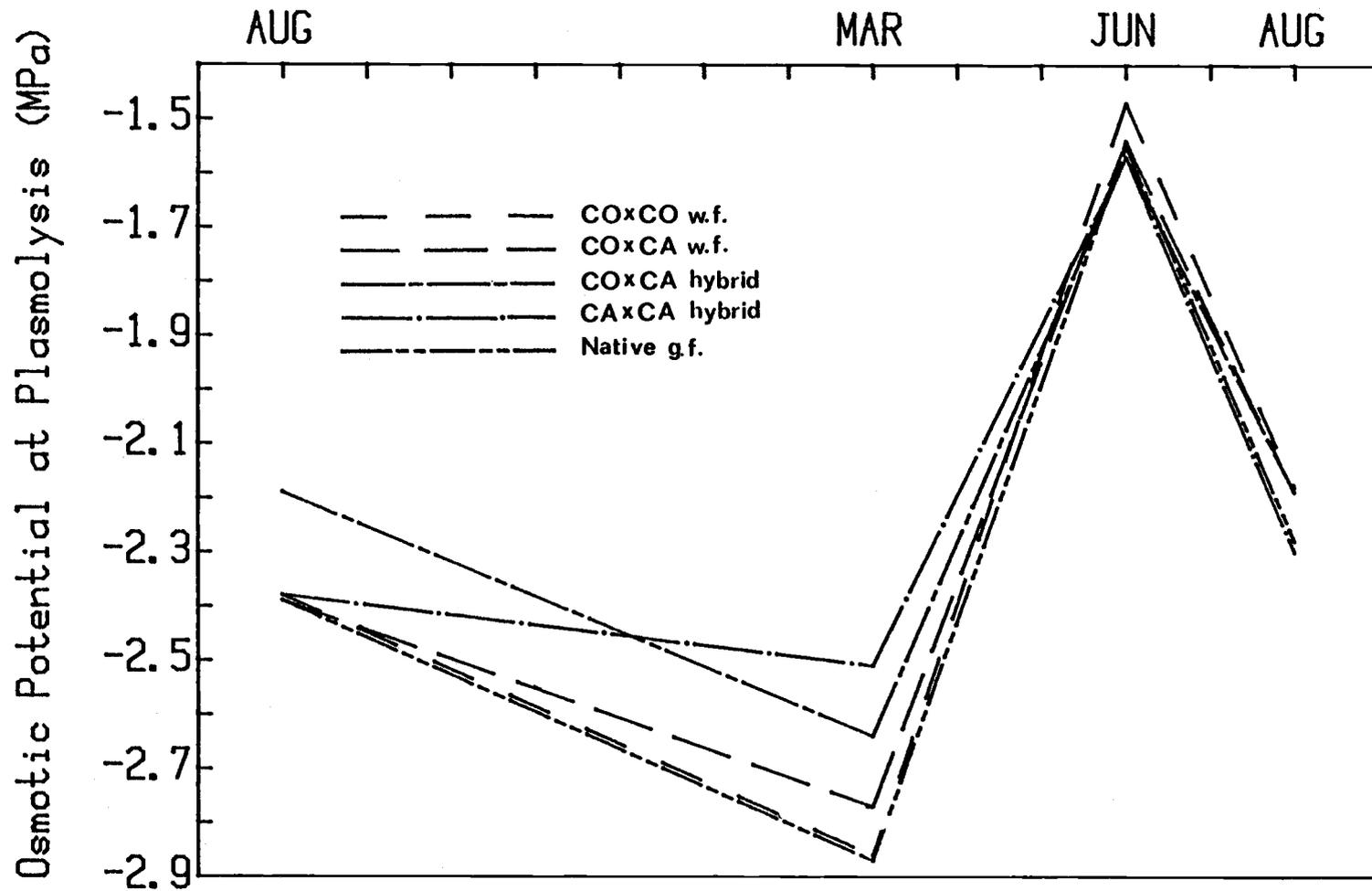


Figure 11. Osmotic potential at zero turgor in August 1981, and March, June and August, 1982. See Table IV for additional information.

$\Psi_{\pi_{100}}$ and Ψ_{π_0} of all varieties dropped sharply between June and August. This is consistent with other studies (Jackson and Spomer 1979, Roberts et al. 1980, Nilsen et al. 1981), although Jackson and Spomer reported lower values for grand fir from northern Idaho. Their reported $\Psi_{\pi_{100}}$ values ranged from -2.0 MPa in June to -2.1 MPa in August; their Ψ_{π_0} values ranged between -2.3 MPa and -2.4 MPa. The discrepancy might result from differences in ecotype, site, or tissue age.

The range of osmotic potentials in this study (-1.1 to -2.9 MPa) is within the range that has been reported for other mesophytic species (Roberts et al. 1980), but much higher than values reported for species from xeric or saline environments, which may be less than -5.0 MPa.

The decreasing osmotic potential between June and August noted here may result partly from changes due to leaf development, but there is good reason to believe that low August values are at least in part an osmoregulatory response. $\Psi_{\pi_{100}}$ and Ψ_{π_0} were lower in August of 1981 than August of 1982 for all varieties (Figures 10 and 11; Table IV). In 1981, hotter, drier conditions prevailed for several weeks before measurement than in 1982. August 20, 1981, when twigs were harvested for water-release analysis, was a fairly warm, dry day (Table III). A light rain the day before ended three weeks of very hot, dry weather (afternoon temperatures generally over 30^o C). The 1982 harvest date, August 25, was also warm but more humid (Table III). Two very hot days immediately preceded harvest in

1982, but followed two weeks of generally mild, overcast weather (afternoon temperatures generally less than 27° C).

Variation Among Varieties

Pronounced differences in $\Psi_{\pi_{100}}$ and Ψ_{π_0} occurred among varieties in August of both years. Most differences were not significant in March or June (Table IV).

The fastest-growing trees, the Colorado x California hybrids, had the highest $\Psi_{\pi_{100}}$ and Ψ_{π_0} (indicating lower solute concentration) in August of both years. Differences among other types are less conclusive, especially in August, 1982, but the native grand fir appear to have consistently low August osmotic potentials, with other varieties intermediate.

Xylem Water Potential

Seasonal Variation

Pre-dawn and midday Ψ , estimated the same day that twig samples were harvested for water-release analysis, dropped between June and August (Figures 12 and 13). Midday water potentials dropped between March and June (pre-dawn measurements were not made in March), but the decrease was not so large as the summer decrease. This seasonal decline reflects depletion of soil water reserves through the spring and summer (Hinckley et al. 1979). All varieties had higher pre-dawn and midday Ψ in August, 1981 than August, 1982, possibly because of the light rain the day before measurement in 1981.

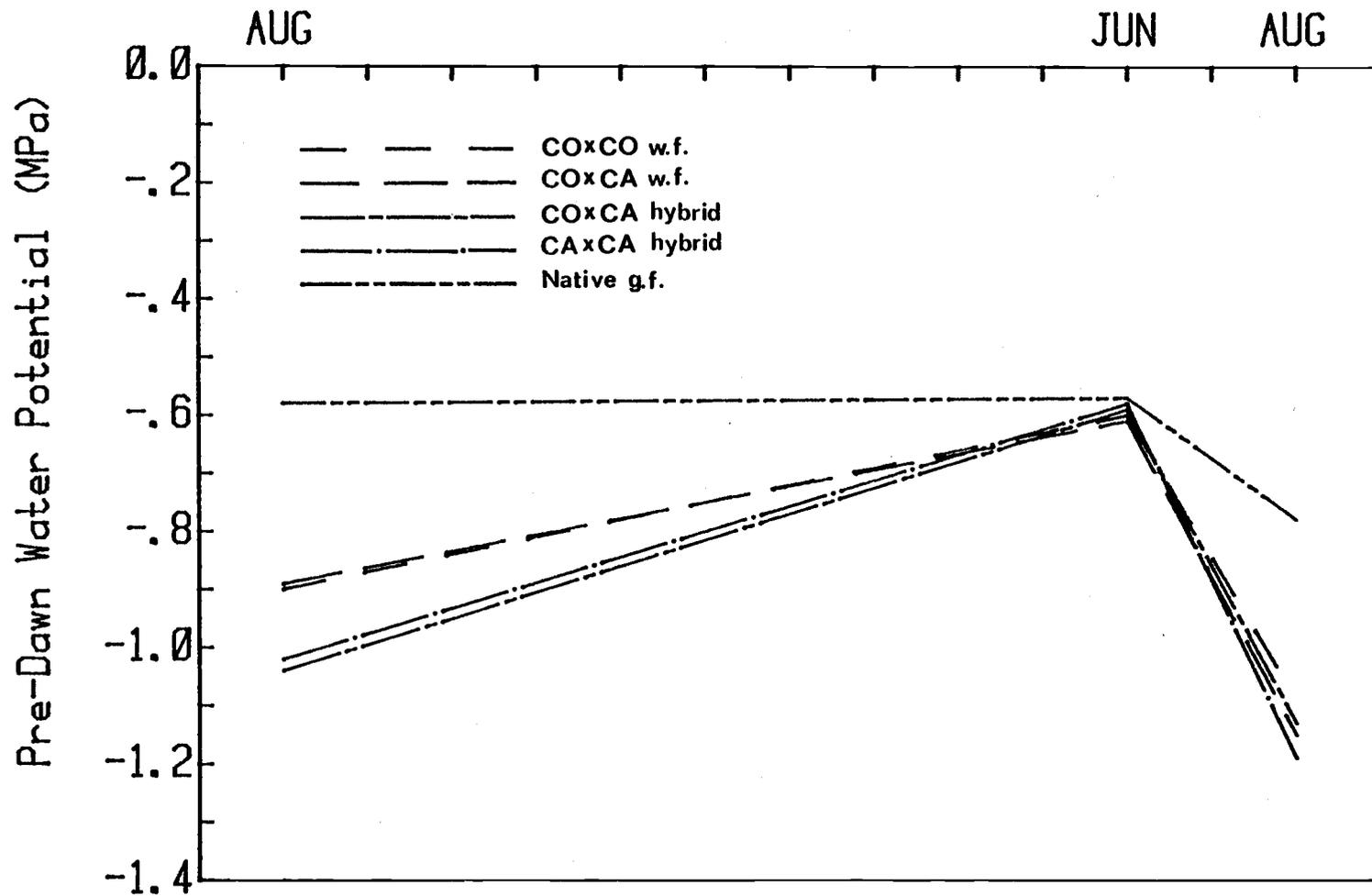


Figure 12. Pre-dawn water potentials of trees used in "Water-Release" analysis. See Table IV for sample sizes.

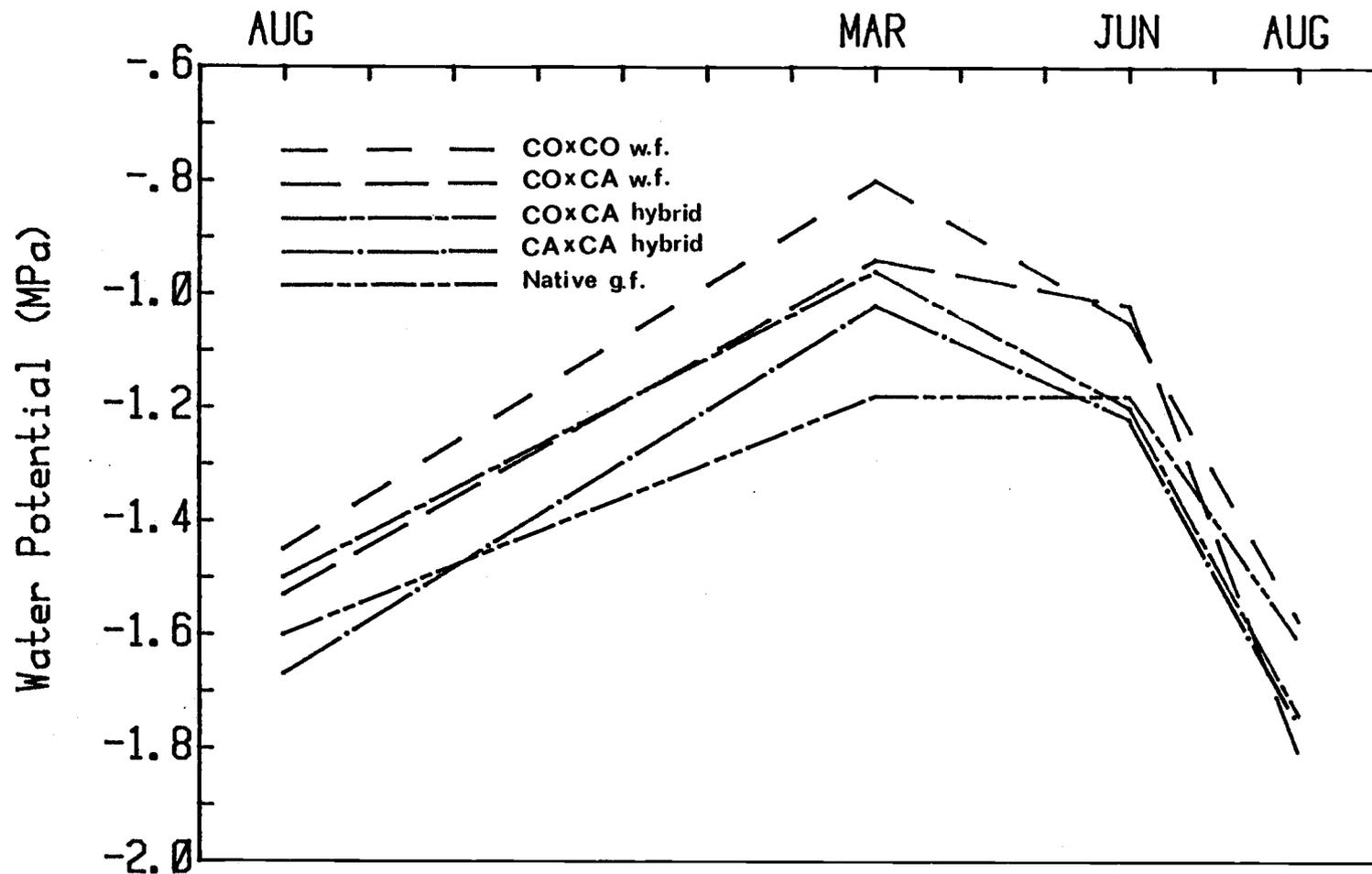


Figure 13. Water potentials of trees used in "Water-Release" analysis at time of "maximum" conductance. See Table IV for sample sizes and Table III for time of day.

Variation Among Varieties

A survey of pre-dawn water potentials of 49 trees on August 13, 14 and 15, 1981, yielded the following results:

	Pre-dawn Ψ (MPa)	Sample Size
Colorado x Colorado white fir	-0.904 \pm 0.151	6
Colorado x California white fir	-0.919 \pm 0.175	15
Colorado x California hybrid	-0.963 \pm 0.147	15
California x California hybrid	-1.033 \pm 0.134	7
Native grand fir	-0.667 \pm 0.192	6

Native grand fir trees consistently had higher pre-dawn water potentials in August than other varieties, which may indicate that the grand fir are more deeply rooted than other trees. Hybrids appear to have slightly lower pre-dawn water potentials than white fir, but the difference was not statistically verifiable.

The water potentials in Figure 13 are from the time of presumed "maximum conductance" (see Table III for details). In addition, a mid-afternoon survey on August 25, 1982, illustrates approximate minimum water potentials for each variety on this site:

	Mid-PM Ψ (MPa)	Sample Size
Colorado x Colorado white fir	-1.69 \pm 0.12	7
Colorado x California white fir	-2.01 \pm 0.07	8
Colorado x California hybrid	-1.85 \pm 0.14	8
California x California hybrid	-1.81 \pm 0.14	7
Native grand fir	-1.76 \pm 0.12	6

Variability was fairly high, but a few generalizations can be made. It is interesting that the slowest-growing Colorado x Colorado white fir, which visually appeared quite stressed, had the most "favorable" summer afternoon water status. The Colorado x California white fir had the opposite response, with significantly lower (0.05 level of confidence) Ψ than the grand fir or the other white fir. The relatively low Ψ of the Colorado x California white fir on this date contrasts with diurnal measurements in July, 1981, when white fir Ψ was nearly equal to or greater than that of other varieties.

I found no relationship between pre-dawn and afternoon Ψ . Grand fir, despite high pre-dawn Ψ , had intermediate Ψ during the day.

Turgor Pressure

Seasonal Variation

The differences in turgor between July and August were unexpected (Figures 14 and 15; Table IV). Both Ψ and Ψ_{π} dropped sharply between June and August, as noted above. But since osmotic potential changed more than water potential, pre-dawn and mid-day bulk turgor actually rose through the summer months in all but one variety. Most varieties accomplished nearly 40% of total height growth during June (see RESULTS, Phenology) and turgor is the driving force of tissue expansion and growth. It seems odd that rapidly-growing young tissue in June had lower turgor than slower-growing tissue in August.

To my knowledge there is no precedent for these results, and my attempt to explain them is tentative. High bulk turgor in August

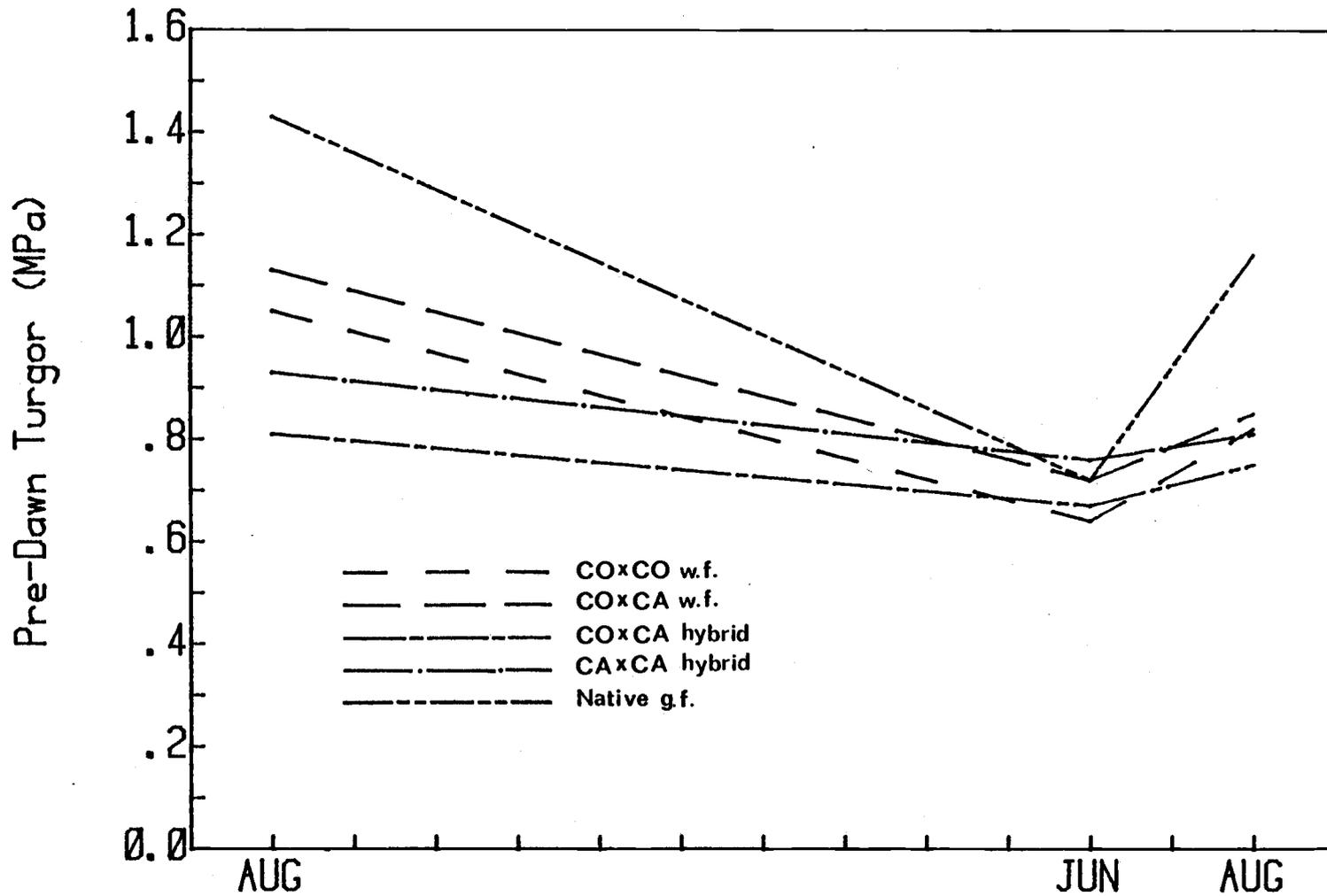


Figure 14. Pre-dawn turgor in August 1981 and June and August, 1982. See Table IV for additional information.

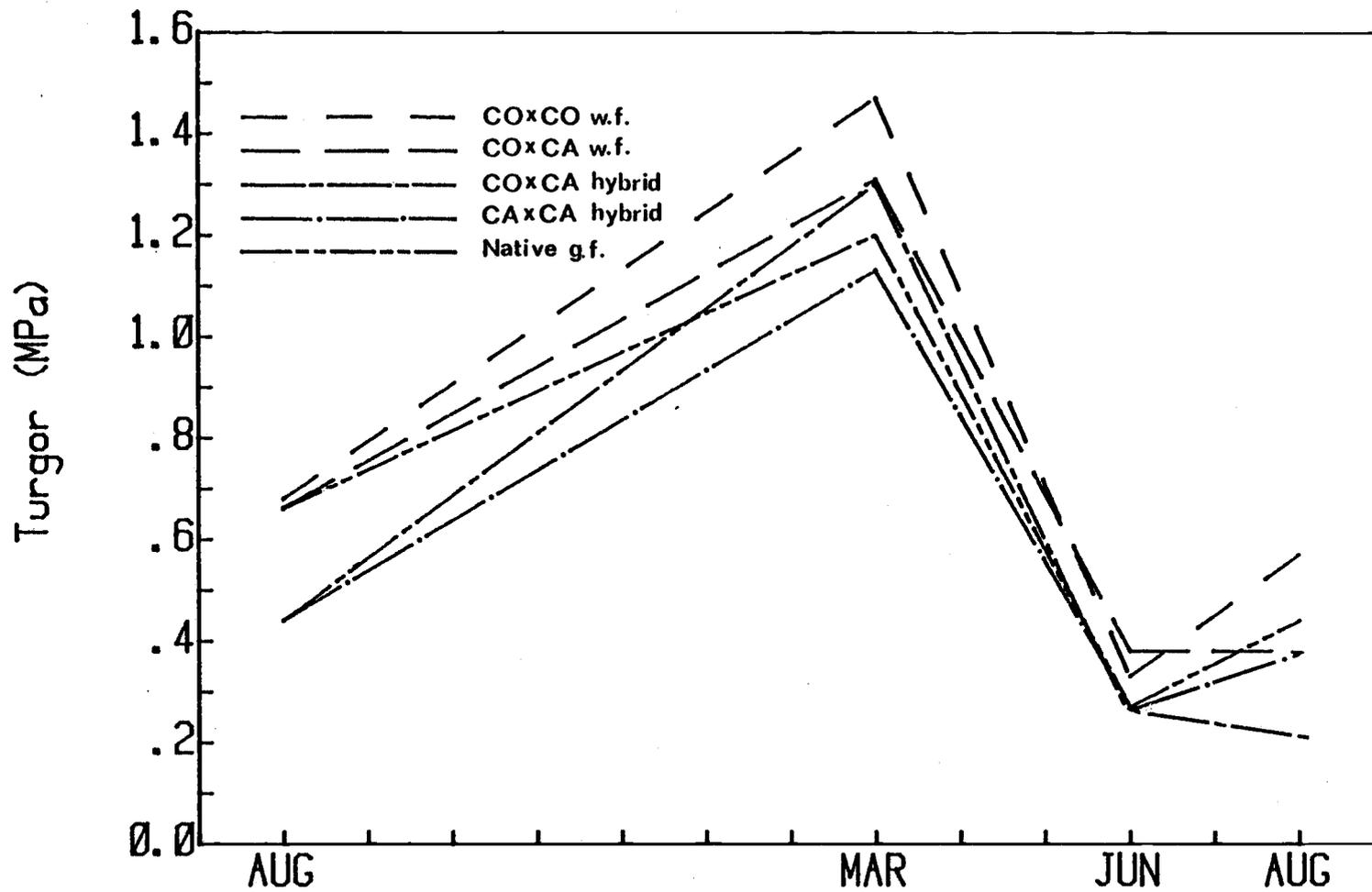


Figure 15. Turgor pressure in August, 1981 and March, June and August, 1982, at time of "maximum" conductance. See Table III for time of day and Table IV for additional information.

might be interpreted as the result of a kind of metabolic "drought insurance". Perhaps the trees maintain very low Ψ_{π} through the late summer as a protection in the case of severe drought. In the absence of severe drought, turgor would be relatively high. But there must be a metabolic cost or "premium" for this drought insurance. Low osmotic potential could affect enzyme activity and phloem transport, and osmotically active material in vacuoles ties up energy that might be used for growth. In June, when there is little possibility of severe drought, maintaining low Ψ_{π} would be wasteful.

Variation among Varieties

There was a nearly inverse relationship between growth rate and turgor. The fastest-growing variety, the Colorado x California hybrids, had lower pre-dawn turgor than any other type in August of both years (Figure 14; Table IV). The grand fir, which grew relatively slowly, had the highest pre-dawn turgor. The high grand fir turgor before dawn resulted from relatively high Ψ as well as low Ψ_{π} . Turgor differences were not so pronounced during the day in August, but no variety had lower turgor than the Colorado x California hybrids in the mid-morning (Figure 15; Table IV).

The inverse relationship between growth and turgor was not perfect, but at almost every measurement period, regardless of month, time of day or year, either the slowest-growing variety (the Colorado x Colorado white fir) had relatively high turgor or the fastest-

growing variety (the Colorado x California hybrid) had relatively low turgor (Figures 14 and 15; Table IV). One objective of this research was to test the hypothesis that faster-growing trees maintain higher turgor than other varieties. The data do not support this hypothesis; in fact, the fastest growing trees demonstrated the least osmoregulation during the summer and had the lowest turgor in five of the eight measurement periods.

Water Potential Components and Leaf Conductance

There was no close correlation between maximum leaf conductance and pre-dawn water potential, concurrent water potential, pre-dawn turgor, or concurrent turgor for any variety in June, 1982 (Table V). Thorough analysis was not attempted for other measurement periods, but there appeared to be no relationships between conductance and water relations components at other times, either.

It was not a major purpose of this research to identify factors affecting stomatal closure, and measurement techniques were not designed test correlations between stomatal activity and other factors; analysis is more for the sake of interest since the data are available. "Maximum conductance" is defined loosely for the purpose of comparing varieties -- values do not necessarily represent absolute maxima. "Concurrent" conductance and water potential were sometimes measured up to an hour apart. The lack of correlations certainly does not imply that none exist. Indeed, on a seasonal scale, it is clear that "maximum" conductance does decrease coincidentally with

TABLE V. Correlations between leaf conductance and the components of water potential, June, 1982. "Maximum" conductance is approximate; "concurrent" water potential parameters reflect conditions within one hour of measurement of conductance. No correlation coefficient was significant at $\alpha = 0.05$

	Sample	Coefficient of Correlation
1. "Maximum" conductance and pre-dawn Ψ :		
Co x Co white fir	7	0.70
Co x Ca white fir	7	0.33
Co x Ca hybrid	7	0.11
Ca x Ca hybrid	6	0.02
Native grand fir	5	0.19
All varieties	32	0.16
2. "Maximum" conductance and concurrent Ψ :		
Co x Co white fir	7	0.27
Co x Ca white fir	7	0.10
Co x Ca hybrid	7	0.26
Ca x Ca hybrid	6	0.46
Native grand fir	5	0.12
All varieties	32	0.03
3. "Maximum" conductance and pre-dawn turgor:		
Co x Co white fir	6	0.00
Co x Ca white fir	7	0.44
Co x Ca hybrid	7	0.00
Ca x Ca hybrid	6	0.43
Native grand fir	4	0.01
All varieties	30	0.07
4. "Maximum" conductance and concurrent turgor:		
Co x Co white fir	6	0.00
Co x Ca white fir	7	0.14
Co x Ca hybrid	7	0.46
Co x Ca hybrid	6	0.00
Native grand fir	4	0.03
All varieties	30	0.10

pre-dawn water potential between June and August, an effect that has been noted previously (Zobel 1974, Running 1975, Hinckley et al. 1979). Interestingly, stomatal conductance was not correlated with turgor even on a broad, season-to-season scale. Turgor rose as "maximum" conductance decreased between June and August.

The most definitive relationship between leaf conductance and Ψ or its components indicated by my data is the possible "critical" level of Ψ , about -1.3 MPa, for initiating stomatal closure, noted earlier.

Growth and Estimated Leaf Area of Branches

As mentioned earlier, results reported in this section are preliminary. Interpretation depends on two assumptions: sapwood area at the base of a branch is proportional to leaf area on that branch, and the proportionality constant relating sapwood area to leaf area is similar for all varieties (see METHODS).

Given these assumptions, there were large differences among the leaf areas of branches from the five varieties (Table VI). Most of the differences were statistically significant. Branches from the fastest-growing Colorado x California hybrids had more than four times the leaf area of branches from the slowest-growing Colorado x Colorado white fir.

I speculated earlier that relatively high allocation of resources to leaf area could help explain the rapid growth of the Colorado x California hybrids despite their relatively low leaf

TABLE VI. Branch growth, basal sapwood area, and weight per area ratios of needles. Statistical comparisons between means were made with a two-tailed t-test using a family error mean square obtained from multiple linear regression using indicator variables, as described in METHODS. Measurements were made on 4- to 5-year-old branches harvested in October, 1982. "Appendant" growth is defined as all new needles and supporting twigs produced in the current growth year.

	Variety					Significant differences ($\alpha = 0.05$)
	COxCO w.f. ("1")	COxCA w.f. ("2")	COxCA hybrid ("3")	CAxCA hybrid ("4")	Native g.f. ("5")	
Basal sapwood area (cm ²)	0.247	0.587	1.122	0.445	0.638	1 \neq 2,3,4,5 2 \neq 3,4 3 \neq 4,5 4 \neq 5
1982 "append- dant" growth (g dry wt.)	6.2	17.2	54.3	9.07	20.2	Not Analyzed
"Appen- dant" growth/ sapwood area (g/cm ²)	24.7	30.8	52.2	32.6	40.1	1 \neq 3,4,5 2 \neq 3 3 \neq 4
Current- year sapwood area (cm ²)	0.075	0.138	0.334	0.111	0.112	Not Analyzed
Current/ total sapwood (cm ² / cm ²)	0.213	0.234	0.308	0.265	0.195	3 \neq 1,2,5

TABLE VI. Continued

	Variety					Significant Differences ($\alpha = 0.05$)
	COxCO w.f. ("1")	COxCA w.f. ("2")	COxCA hybrid ("3")	CAxCA hybrid ("4")	Native g.f. ("5")	
Needle weight/ needle area (g dry wt/ cm ²)	0.019	0.020	0.016	0.013	0.012	1 \neq 4,5 2 \neq 3,4,5 3 \neq 4,5
Sample size	6	8	8	6	6	

conductance. Leaf area differences could also explain why the white fir do not experience relatively low twig water potentials during summer afternoons when their leaf conductance is high. The results in Table VI are consistent with my speculations, but do not prove them. Leaf area differences could be more a consequence of rapid growth than a cause. Still, there is some evidence of differential resource allocation. White fir needles have relatively high weight per unit area (Table VI); for a given amount of carbon allocated to leaves, the hybrids and grand fir will have greater leaf area.

Greater leaf area may result from longer needle retention as well as greater allocation of resources to leaf area. Grand fir on the study site retained needles much longer than white fir; hybrids were intermediate (Table VII).

It seems likely that higher leaf area, whether due to needle longevity, "less expensive" needles, or greater proportional allocation of resources to needles, may partly explain more rapid growth. But leaf area differences cannot explain growth differences entirely. When growth of branches is adjusted for leaf area, the Colorado x California hybrids still grew much more in 1982 than any other variety. The ratio between "appendant" growth and sapwood area, a rough index of relative extension growth per unit of leaf area, is far higher for the faster-growing hybrids than for other varieties (Table VI). The ratio between the cross-sectional area of the current growth ring and total sapwood area may be used as an indicator

of wood growth per unit of leaf area.³ Again, the fast-growing Colorado x California hybrids appear to be more "growth-efficient" per unit of leaf area than are other varieties.

TABLE VII. Needle longevity. Trees were surveyed on January 25, 1983, and the age of the oldest needles that still appeared in good condition was noted for each tree. Statistical comparisons between means were made with a two-tailed t-test using a family error mean square obtained from multiple linear regression using indicator variables, as described in METHODS.

Variety	Mean age of oldest healthy needles	Number of trees Sampled	Significant Differences ($\alpha = 0.05$)
CO x CO w.f. ("1")	2.8 \pm 0.8	6	\neq 2, 3, 4, 5
CO x CA w.f. ("2")	4.0 \pm 0.5	8	\neq 1, 3, 5
CO x CA hybrid ("3")	5.3 \pm 0.5	8	\neq 1, 2, 5
CA x CA hybrid ("4")	4.8 \pm 1.6	6	\neq 1, 5
Native g.f. ("5")	7.2 \pm 0.4	6	\neq 1, 2, 3, 4

³Waring, Thies and Muscato (1980) proposed that stem growth per unit of total canopy leaf area could be used to evaluate tree vigor, and Waring, Newman and Bell (1981) suggested that the ratio between stemwood increment and total sapwood area could be used to estimate the net assimilation rate of a whole tree. It is not reasonable to use these interpretations here, since one must assume that there are no genetically-determined resource allocation differences among trees that are compared.

Phenology

There is a weak relationship between total growth and timing of growth; varieties which grew the most accomplished a greater proportion of their growth later in the season. These results correspond with those of Libby and others (1980), who found that yearly growth of white fir provenances was highly correlated with late-season growth but not with early flushing.

TABLE VIII. Mean growth rates of leaders, 1980. Data are from D. B. Zobel.

	Variety				
	COxCO w.f.	COxCA w.f.	COxCA hybrid	CAxCA hybrid	Native g.f.
4/21/80					
Total length (mm)	2	2	5	2	4
% total growth	2	1	1	1	2
4/28/80					
Total length	4	3	9	4	5
% total growth	3	1	2	2	2
5/12/80					
Total length	14	9	28	10	10
% total growth	12	3	5	4	4
5/26/80					
Total length	53	41	96	49	59
% total growth	45	15	18	19	25
6/30/80					
Total length	100	182	270	153	155
% total growth	84	67	50	59	67
9/22/80					
Total length	119	273	536	260	233
Number of trees	21	91	195	13	5

GENERAL DISCUSSION

Despite several problems associated with the experimental trees, as discussed below, some very interesting conclusions are possible, especially when attention is focused on the Colorado x California hybrids and the Colorado x California white fir. In the following discussion I will concentrate primarily on these varieties.

Many of the results were contrary to my expectations. The slower-growing white fir had much higher leaf diffusive conductance on a year-round basis than the faster-growing hybrids. Conductance is not necessarily a good indicator of photosynthesis (Jarvis 1981), but higher conductance should allow greater carbon fixation, especially since the conductance of white fir appears to be nearly double that of the hybrids on a yearly basis.

An important lesson from these results is that comparative studies of leaf conductance need to be interpreted cautiously. Porometer measurements indicate stomatal movement, but do not necessarily indicate the total carbon dioxide and water fluxes through a tree. Total flux is dependent on leaf area, and in the case of these true firs it appears that low leaf conductance may be offset by high leaf area.

The techniques I used to evaluate relationships between leaf area, conductance and growth were crude and need to be confirmed by further study. But the results do suggest that the Colorado x California hybrids maintained much higher leaf area than the white fir and also that branch growth per unit of leaf area was higher for

hybrids. There are two possible explanations for the apparently greater growth per unit of leaf area of the hybrids: 1) White fir have higher mesophyll and carboxylation resistances than hybrids, and/or 2) white fir and hybrids have very different carbon allocation patterns. The white fir might allocate a smaller proportion of resources to photosynthesizing tissue and support for that tissue; possibly more resources are used to support a more extensive root system or more rapid turnover of root tissue. In either case the differences must be large. My results suggest that branch growth per unit of leaf area of the Colorado x California hybrids was 1.6 times that of the Colorado x California white fir (Table VI). Differences of this magnitude seem surprising between such closely related trees; several of them had a common Colorado white fir parent (Appendices 1, 2, and 3).

Turgor potentials also yielded interesting and unexpected results. The faster-growing trees had the lowest turgor during August, both before dawn and in mid-morning. Also, all trees had higher turgor in August than June. Finally, despite the higher turgor in August, stomatal conductance decreased between June and August in all varieties. I know of no other work for comparison with these results.

The lack of correlation between stomatal conductance and turgor indicates that although osmoregulation does occur, it does not directly affect stomatal conductance of these trees, as it does for other plants. A more important role of osmoregulation may be

protecting a tree from injury due to complete turgor loss, or plasmolysis, at very low plant water potentials.

One of the objectives of this research was to integrate the data I collected for each variety and evaluate relative drought resistance based on these data. White fir are considered to be less drought resistant than grand fir (Minore 1979). Drought resistance arises from both ability to tolerate drought and ability to avoid drought. Since osmotic adjustment permits turgor maintenance at low plant water potentials, it contributes to drought tolerance. In this study, white fir appeared more drought tolerant than hybrids. Osmotic potentials were lower and turgor higher for white fir in August than for hybrids. But these data defy simple interpretation, since osmotic potentials of native grand fir were relatively low in August; they, too, appeared more drought tolerant than hybrids.

I have no consistent evidence that any of the varieties have better capability to avoid drought, or maintain water potential, than any others. As explained earlier, high pre-dawn water potentials of grand fir in August were probably the result of differences in tree age. It does appear, though, that the different varieties avoid drought by different mechanisms. Hybrids and grand fir apparently maintain water potential by reducing stomatal conductance, and grand fir do so to a greater extent than hybrids. White fir, on the other hand, seem to employ more non-stomatal mechanisms to avoid drought. I've already suggested that relatively low leaf area could be one way that white fir avoid drought. It is also possible that white fir

have higher water storage capacity, allowing trees to maintain water potential as they lose water through transpiration. Another possibility is that the white fir maintain a more extensive root system and thus are able to tap water from a greater volume of soil. A larger root system could also contribute to the lower growth per unit of leaf area, as discussed earlier.

Unfortunately, a number of problems beyond my control limited the conclusions I can draw from this work. The grand fir, which were growing naturally on the study site, probably had much deeper roots than other types and were reaching equilibrium with moister soil. This may explain their high August pre-dawn xylem water potentials, over 0.3 MPa higher than hybrid trees. It is unlikely that the difference is strictly genetic, especially since grand fir is reputed to be more shallow-rooting species than white fir (Hinckley *et al.* 1981). Deeper roots are more likely a consequence of tree age. Thus the grand fir cannot be strictly compared with the other types.

The Colorado x Colorado white fir trees were growing very slowly, and there was no way to be sure whether their poor condition was the result or the cause of observed stomatal and water relations characteristics. Since data from these trees were more variable in many cases than other varieties, there is reason to believe that their poor condition influenced my results.

Finally, the California x California hybrid trees were a year younger than other trees and had been planted in spaces left after other trees died, possibly less desirable microsites. These trees

did not grow as well as the Colorado x California hybrids, but again there is no way to be sure whether genotype or experimental factors were primarily responsible for differences in performance.

The trees in this investigation resulted from artificial crosses between parents that would never produce progeny naturally. Therefore these results cannot be directly applied to naturally-growing populations. But these results are not consistent with the suggestion that white fir are less drought resistant than grand fir. In fact, compared with hybrids, white fir appear to have more drought tolerance characteristics.

The results of this study indicate that a large number of morphological and physiological characteristics are responsible for regulating water balance and controlling growth. It may be misleading to evaluate the significance of individual characteristics out of the context of their interaction with other characteristics.

CONCLUSIONS

The specific objectives of this study were to:

1. Describe the water relations of grand fir, white fir and their hybrids, including pre-dawn values and diurnal changes of water potential, osmotic potential and bulk turgor, in spring, early summer, and late summer.

Descriptions have been given (Figures 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15; Tables III and IV).

2. Determine whether there is evidence of internal regulation of osmotic potential and whether varieties have different capabilities for osmotic adjustment and maintenance of turgor.

Osmotic potentials at full and zero turgor varied markedly with the time of year, being lowest in March and highest in June. Osmotic potentials dropped between June and August, and it appears that the decrease may be a response to drought since all varieties had lower osmotic potentials in August, 1981 than in the moister, cooler August, 1982. There were significant differences among the osmotic potentials of the varieties, especially in August. Hybrids between Colorado white fir and California grand fir had less negative osmotic potentials at full turgor than white fir or grand fir.

3. Test hypotheses that the fastest-growing varieties maintain higher leaf conductance and higher turgor than other varieties.

These data contradict the hypotheses that high turgor and high stomatal conductance are closely related to rapid growth on the study site. Maintaining turgor above a certain level may be energetically wasteful. High allocation of resources to leaf area and perhaps low mesophyll resistance and carboxylation resistance may be more important than high stomatal conductance for rapid growth.

4. Verify previous indications that trees morphologically more like A. concolor maintain higher stomatal conductance at low water potentials than do trees which more closely resemble A. grandis.

Maximum conductance of white fir is much higher than maximum conductance of grand fir or hybrids, but the water potentials of white fir are usually equal to or higher than those of grand fir and hybrids during the summer. So these data confirm earlier indications that white fir tend to maintain higher stomatal conductance at a given water potential than do grand fir. In June, all varieties in this study appeared to have a similar critical water potential that initiated stomatal closure, about -1.3 MPa.

5. Evaluate the relative drought resistance of the species and hybrids based on values of water potential components and stomatal characteristics.

Although white fir has been designated less drought resistant than grand fir, the white fir in this study exhibited more drought resistance characteristics than grand fir or hybrids. White fir and grand fir both maintained lower osmotic potentials and higher turgor than hybrids, evidence of drought tolerance. White fir employed more non-stomatal mechanisms of drought avoidance than grand fir or hybrids.

REFERENCES

- Bannister, P. 1976. Introduction to physiological plant ecology. John Wiley and Sons, New York. 273 p.
- Campbell, G.S., R.I. Papendick, E. Rabie and A. Shayongowi. 1979. A comparison of osmotic potential, elastic modulus, and apoplastic water in leaves of dryland winter wheat. *Agron. J.* 71:31-36.
- Cheung, Y.N.S., M.T. Tyree, and J. Dainty. 1975. Water relations of single leaves obtained in a pressure bomb and some ecological interpretations. *Can. J. Bot.* 53:1342-1346.
- Cleary, B.D. and J.B. Zaerr. 1980. Water status and carbon dioxide exchange studies. Part C. Pressure chamber techniques for monitoring and evaluating seedling water status. *New Zeal. J. For. Sci.* 10:133-141.
- Cline, R.G. and G.S. Campbell. 1976. Seasonal and diurnal water relations of selected forest species. *Ecology* 57:367-373.
- Daniels, J.D. 1969. Variation and intergradation in the grand fir-white fir complex. Ph.D. Thesis, Univ. Idaho, Moscow, Idaho.
- Emmingham, W.H. and R.H. Waring. 1977. An index of photosynthesis for comparing forest sites in western Oregon. *Can. J. For. Res.* 7:165-174.
- Ericsson, A. 1979. Effects of fertilization and irrigation on the seasonal changes of carbohydrate reserves in different age-classes of needles on 20-year-old Scots Pine trees (*Pinus sylvestris*). *Physiol. Plant.* 45:270-280.
- Farquhar, G.D. and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis. *Ann. Rev. Plant Physiol.* 33:317-345
- Hall, A.E., E.-D. Schulze and O.L. Lange. 1976. Current perspectives of steady-state stomatal response to environment. IN: *Water and Plant Life*. O.L. Lange, L. Kappan, and E.-D. Schulze, eds. Springer-Verlag, Berlin. 536 p.
- Hamrick, J.L. III and W.J. Libby. 1972. Variation and selection in western U.S. montane species. I. White fir. *Silvae Genetica* 21:29-35.
- Hanson, A.D. and W.D. Hitz. 1982. Metabolic responses of mesophytes to plant water deficits. *Ann. Rev. Plant Physiol.* 33:163-203.

- Hinckley, T.M. and D.M. Bruckerhoff. 1975. The effects of drought on water relations and stem shrinkage of Quercus alba. Can. J. Bot. 53:62-72.
- Hinckley, T.M., J.P. Lassoie, and S.W. Running. 1979. Temporal and spatial variations in the water status of forest trees. Forest Science Monograph 20.
- Hinckley, T.M., R.O. Teskey, R.H. Waring and Y. Morikawa. 1982. The water relations of true firs. IN: True Fir. Proceedings of the biology and management of true fir in the Pacific Northwest symposium. D.O. Chadwick and R.M. Kenady, eds. USDA Forest Service, Portland, OR. 344 p.
- Hopkins, W.E. 1982. Ecology of white fir. IN: True Fir. Proceedings of the biology and management of true fir in the Pacific Northwest symposium. D.O. Chadwick and R.M. Kenady, eds. USDA Forest Service, Portland, OR. 344 p.
- Hsaio, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570.
- Hsaio, T.C., E. Acevedo, E. Fereres and D.W. Henderson. 1976. Stress metabolism, water stress, growth and osmotic adjustment. Phil. Trans. R. Soc. Land. B. 273:479-500.
- Jackson, P.A. and G.G. Spomer. 1979. Biophysical adaptations of four western conifers to habitat water conditions. Bot. Gaz. 140:428-432.
- Jarvis, P.G. 1981. Stomatal conductance, gaseous exchange and transpiration. IN: Plants and their atmospheric environment. J. Grace and E.D. Ford, eds. 21st Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford. 419 p.
- Juday, G.P. 1976. The location, composition, and structure of old-growth forests of the Oregon Coast Range. Ph.D. Dissertation, Oregon State University, Corvallis, OR.
- Kaplan, J. 1974. The ecology of Eucalyptus camaldulensis Dehn. in Israel. La-Yaaran 24:1-2.
- Keys, S.C. 1976. Stomatal activity patterns of provenance plantations of Abies concolor and Abies grandis. M.S. Thesis, Oregon State University, Corvallis, OR.
- Klaehn, F.V. and J.A. Winieski. 1962. Interspecific hybridization in the genus Abies. Silvae Genetica 11:130-142.

- Kozlowski, T.T. 1971. Growth and development of trees, Vol. 1. Academic Press, N.Y. 443 p.
- Kozlowski, T.T. 1973. Extent and significance of shedding of plant parts. IN: Shedding of plant parts. T.T. Kozlowski, ed. Academic Press, N.Y. 560 p.
- Kramer, P.J. 1980. Drought, stress, and the origin of adaptations. IN: Adaptation of plants to water and high temperature stress. N.C. Turner and P.J. Kramer, eds. John Wiley and Sons, New York. 482 p.
- Krygier, J.T. 1971. Comparative water loss of Douglas-fir and Oregon white oak. Ph.D. Dissertation, Oregon State University, Corvallis, OR.
- Laimins, L.A., D.B. Rhoads and W. Epstein. 1981. Osmotic control of kdp operon expression in Escherichia coli. Proc. Natl. Acad. Sci. 78:464-468.
- Libby, W.J., I. Kani, and J.B. King. 1980. Variation in flushing time among white fir population samples. Annales Forestales 8:123-138.
- Lopushinsky, W. 1969. Stomatal closure in conifer seedlings in response to leaf moisture stress. Bot. Gaz. 130:258-263.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species -- A literature review. USDA Forest Service Gen. Tech. Rep. PNW-87. 72 p.
- Murphy, E.M. and W.K. Ferrell. 1982. Diurnal and seasonal changes in leaf conductance, xylem water potential, and abscisic acid of Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] in five habitat types. Forest Sci. 28:627-638.
- Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Ill. 842 pp.
- Nilsen, E.T., P.W. Rundel and M.R. Sharifi. 1981. Ecological perspectives on pressure-volume analyses for evaluating plant water relations: a case study with woody desert phreatophytes. Unpublished manuscript, Department of Ecology and Evolutionary Biology, University of California, Irvine, CA.
- Nobel, P.S. 1974. Introduction to biophysical plant physiology. W.H. Freeman and Co., San Francisco. 488 p.

- Pallardy, S.G. 1981. Closely related woody plants. IN: Water deficits and plant growth, Vol. VI. Woody plant communities. T.T. Kozlowski, ed. Academic Press, N.Y.
- Parker, W.C., S.G. Pallardy, T.M. Hinckley and R.O. Teskey. 1982. Seasonal changes in tissue water relations of the Quercus-Carya forest type. Ecology 63: 1259-1267.
- Puritch, G.S. 1973. Effect of water stress on photosynthesis, respiration and transpiration of four Abies species. Can. J. For. Res. 3:293-298.
- Puritch, G.S. and J.A. Turner. 1973. Effects of pressure increase and release on temperature within a pressure chamber used to estimate plant water potential. J. Exp. Bot. 24:342-348.
- Radosevich, S.R., S.G. Conard and E.J. Roncoroni. 1980. Comparative physiology and growth of five conifer species planted on an exposed site. Unpublished manuscript, Univ. of Calif., Davis.
- Raschke, K. 1975. Stomatal Action. Ann. Rev. Plant Physiol. 26:309-340.
- Richter, H., F. Duhme, G. Glatzel, T.M. Hinckley, and H. Karlic. 1981. Some limitations and applications of the pressure-volume curve technique in ecophysiological research. IN: Plants and their atmospheric environment, J. Grace and E.D. Ford, eds. 21st Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford. 419 p.
- Ritchie, G.A. 1983. Comparison between two methods of generating pressure-volume curves. Abstract #28, Northwest Scientific Association, 56th Annual Meeting, Olympia, WA.
- Ritchie, G.A. and T.M. Hinckley. 1971. Evidence for error in pressure-bomb estimates of stem xylem potentials. Ecology 52:534-535.
- Roberts, S.W., B.R. Strain, and K.R. Knoerr. 1980. Seasonal patterns of leaf water potential in four co-occurring forest tree species: parameters from pressure-volume curves. Oecologia 46:330-337.
- Running, S.W. 1975. Environmental control of leaf water conductance in conifers. Can. J. For. Res. 6:104-111.
- Running, S.W. 1980. Relating plant capacitance to the water relations of Pinus contorta. Forest Ecology and Management 2:237-252.

- Scholander, P.F., H.T. Hammel, E.D. Bradstreet and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* 148:339-346.
- Sprague, F.L., and H.P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon. *Northwest Science* 20:89-97.
- Steinhoff, R.J. 1978. Distribution; ecology, silvicultural characteristics and genetics of the Abies grandis-Abies concolor complex. Proc. of the IUFRO joint meeting of working parties, Vol. 1: background papers and Douglas-fir provenances. B.C. Ministry of Forests, Vancouver, B.C. Canada.
- Sudworth, G.B. 1908. Forest trees of the Pacific slope. Government Printing Office, Washington D.C. 441 p.
- Tibbits, T.W. 1979. Humidity and plants. *Bioscience* 29:358-363.
- Turner, N.C. and M.M. Jones. 1980. Turgor maintenance by osmotic adjustment: A review and evaluation. IN: Adaptation of plants to water and high temperature stress, N.C. Turner and P.J. Kramer, eds. John Wiley and Sons, New York.
- Tyree, M.T. and H.T. Hammel. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure bomb technique. *J. Exp. Bot.* 23:267-282.
- Tyree, M.T. and A.J. Karamanos. 1981. Water stress as an ecological factor. IN: Plants and their atmospheric environment. J. Grace and E.D. Ford, eds. 21st Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford. 419 p.
- Tyree, M.T., Y.N.S. Cheung, M.E. MacGregor, and A.J.B. Talbot. 1978. The characteristics of seasonal and ontogenetic changes in the tissue-water relations of Acer, Populus, Tsuga and Picea. *Can. J. Bot.* 56:635-647.
- Tyree, M.T., M.E. MacGregor, A. Petrov and M.I. Upenieks. 1978. A comparison of systematic errors between the Richards and Hammel methods of measuring tissue-water relations parameters. *Can. J. Bot.* 56:2153-2161.
- Waring, R.H. and S.W. Running. 1978. Sapwood water storage: its contribution to transpiration and effects upon water conductance through the stems of old growth Douglas-fir. *Plant Cell Env.* 1:131-140.

- Waring, R.H., K. Newman and J. Bell. 1981. Efficiency of tree crowns and stemwood production at different canopy leaf densities. *Forestry* 54:129-137.
- Waring, R.H., W.G. Thies and D. Muscato. 1980. Stem growth per unit of leaf area: A measure of tree vigor. *Forest Sci.* 26:112-117.
- Waring, R.H., P.E. Schroeder and R. Oren. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* 12:556-560.
- Waring, R.H., H.L. Gholz, C.C. Grier and M.L. Plummer. 1977. Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms. *Can. J. Bot.* 55:1474-1477.
- Watts, W.R., R.E. Neilson and P.G. Jarvis. 1976. Photosynthesis in Sitka spruce (*Picea sitchensis* [Bonq.] Carr.). VII. Measurements of stomatal conductance and $^{14}\text{CO}_2$ uptake in a forest canopy. *J. Appl. Ecol.* 623-639.
- Wenkert, W. 1981. The behaviour of osmotic potential in leaves of maize. *Envir. Exper. Bot.* 21:231-239.
- Wilson, J.R., M.J. Fisher, E.-D. Schulze, G.R. Dolby, and M.M. Ludlow. 1979. Comparison between pressure-volume and dewpoint hygrometry techniques for determining the water relations characteristics of grass and legume leaves. *Oecologia* 41:77-88.
- Zimmerman, U. 1978. Physics of turgor and osmoregulation. *Ann. Rev. Plant Physiol.* 29:121-148.
- Zobel, D.B. 1974. Local variations in integrading Abies grandis-Abies concolor populations in the central Oregon Cascades. II. Stomatal reaction to moisture stress. *Bot. Gaz.* 135:200-210.
- Zobel, D.B. 1975. Local variation in integrading Abies grandis-Abies concolor populations in the central Oregon Cascades. III. Timing of growth and stomatal characteristics in relation to environment. *Bot. Gaz.* 136:63-71.
- Zobel, D.B. and G.M. Hawk. 1980. The environment of Chamaecyparis lawsoniana. *Amer. Midl. Nat.* 103:280-297.
- Zobel, D.B. and V.T. Liu. 1980. Effects of environment, seedling age, and seed source on leaf resistance of three species of Chamaecyparis and Tsuga chinensis. *Oecologia* 46:412-419.

APPENDICES

APPENDIX 1. A summary of the parentage of experimental trees.

A. Parent trees

<u>Code</u>	<u>Species</u>	<u>Place of Origin</u>
N5	<u>A. concolor</u>	Monument Nursery, Colorado
V5	<u>A. concolor</u>	Monument Nursery, Colorado
V6	<u>A. concolor</u>	Monument Nursery, Colorado
V7	<u>A. concolor</u>	Plumas National Forest, California
U	<u>A. grandis</u>	Irish Beach, Manchester, California
V	<u>A. grandis</u>	Irish Beach, Manchester, California
W	<u>A. grandis</u>	Navarro River, Manchester, California
Eld-4.1	<u>A. concolor</u>	Wright's Lake, Eldorado National Forest, California
Eld-4.2	<u>A. concolor</u>	Wright's Lake, Eldorado National Forest, California

B. Progeny

	<u>"Variety"</u>	<u>Parental Crosses</u>
1.	Colorado x Colorado white fir	V6xV5
2.	Colorado x California white fir	N5xV7, V5xV
3.	Colorado x California hybrid	V6xV, V5xV, V6xW, V5xW
4.	California x California hybrid	Eld-4.1xV, Eld-4.2xU, Eld-4.2xW

	COLUMN													
	N	M	L	K	J	I	H	G	F	E	D	C	B	A
1	V6V5	V5W	V6W	4.2W	N5V7	V5V	V5V7	V5W	N5V7	V5V7	V5V	V6W	V6V	V6V5
2	N5V7	V5V7	4.1V	V6V	V6W			V6W	4.2U		V5W	V6V		V5V
3	V5V	V5W	V6V5	N5V7	V6W	V5V7	V6V		V5V	V6W		V6V		V5V7
4	V5V7	V6W	V5V		N5V7	4.2W	V6V	V6W	V6V5	V6V	V5V	V5V7	N5V7	V5W
5	V6V5	V6V	V5V7	V5V	V6W	N5V7	V5W	V6V	V6W	V5V7	V6W	V5V	V6V5	N5V7
6	V6V5	V6W		V5V		V5V7	N5V7	V6V5	V5V7	V5W	V5V	V6W	N5V7	
7	N5V7	V6W	V6V5		V5W	V5V		V5W	V5V	V6W	V5V7	N5V7	V6V	V6V5
8		V6V5	V6W	V5V	N5V7	V6V			4.2W	V6W	V6V5	N5V7	4.2W	
9	V6V5	V6V			V5V	V6W	N5V7	V6V	V6W	N5V7	4.2W	V6V5	V5V7	V5W
10	V6W		N5V7	V5V7	4.2W				N5V7					
11	V6V5	V5V	V5W	V6W	V5V7				V6V	N5V7	V6V	V5V	V5V7	
12	N5V7	V6W	4.2W	V5W	4.1V			V5V7	V6V5	V5V	V6V	V5W	N5V7	V6W
13	V5V		V5V7	4.2U	4.2W	V6W	V6V	V5W	V6W	V6V5	V6V	V5V	V5V7	N5V7
14	V6W	V5V7	V5V	V5W	V6V	N5V7	V6V5	V5V7	N5V7	V6W	V6V	V5V		V6V5
15	V6W	V5V7		V6W	V6V5	V6V	N5V7	N5V7	V5W	V6V5	V5V	V5V7	V6V	V6W
16		V5V7	V5W	V6V	V6W	V5V	N5V7	V5V7		V5W	N5V7	V6V		V6W
17	V5W	V6V	V6W	N5V7	V5V7	V6V5			V5W	V5V	V6V	N5V7	V6W	V5V7
18	V6V		4.1V	V5V	V5V7	V6W	N5V7	N5V7	4.2W	V6V	V5V	V5V7	V6W	V6V5

APPENDIX 2. Arrangement of experimental trees on the study site. See Appendix 1 for explanation of symbols. Blank spaces are shown where no tree survived as of 1979.

APPENDIX 3. A summary of the eight "blocks" of experimental trees used in sampling and data analysis. Each entry in the table indicates the row and column of one tree, as shown in Appendix 2. Native grand fir are indicated by the location of the nearest planted tree.

	COxCO w.f.	COxCA w.f.	COxCA hybrid	CAxCA hybrid	Native g.f.
BLOCK 1	15J	17K	17L	18L	(18N)
BLOCK 2	17I	17J	16J	13K	(17I)
BLOCK 3	18A	18C	18B	18F	(18H)
BLOCK 4	14A	12B	12A		(12A)
BLOCK 5	8D	9E	9F	9D	
BLOCK 6	5B	6B	6C	8B	(8B)
BLOCK 7	4F	1H	1G	2F	
BLOCK 8		1J	2K	1K	(1J)

APPENDIX 4. A comparison of leaf temperatures of the five varieties on June 24, 1981 between 14:20 and 15:30. Air temperature was approximately 27°C. Values given are temperatures (°C) registered by the thermocouple on the LiCor 1600 porometer that is designed to measure leaf temperature, but in many cases there may not have been contact between the thermocouple and needle surface. Subsequent to these measurements the thermocouple was bent back and registered air temperature rather than leaf temperature (see METHODS). Each value is the mean of four measurements, two per tree and two trees per variety.

CO x CO white fir	26.6 ± 1.8
CO x CA white fir	27.1 ± 2.1
CO x CA hybrid	28.8 ± 2.0
CA x CA hybrid	28.6 ± 0.8
Native grand fir	30.1 ± 2.0

APPENDIX 5. A sample data output from the computer program analyzing "Water Release" curves.

=====

WATER RELEASE CURVE RELATIONSHIPS FOR 12B 6/82

WATER RELEASE CURVE RAW DATA:

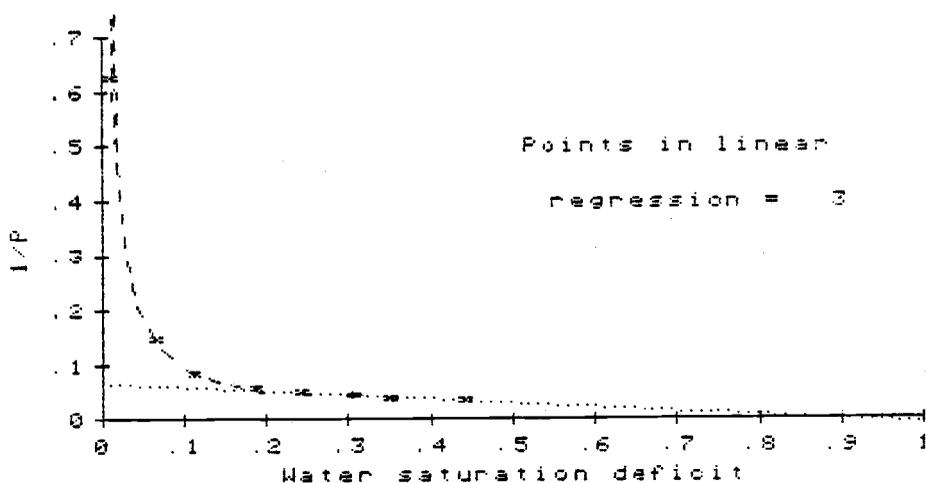
WT (grams)	P (bars)	1/P	WD	RWC
8.20100	1.60000	.62500	.01406	.98594
7.90300	6.80000	.14706	.06712	.93288
7.63900	12.10000	.08264	.11430	.88570
7.21400	17.60000	.05682	.18978	.81022
6.89700	20.00000	.05000	.24622	.75378
6.54800	23.00000	.04348	.30835	.69165
6.28800	25.40000	.03937	.35464	.64536
5.79000	29.90000	.03344	.44330	.55670

TURGID WEIGHT = 8.28
 TOTAL WATER = 5.617
 DRY WEIGHT = 2.663

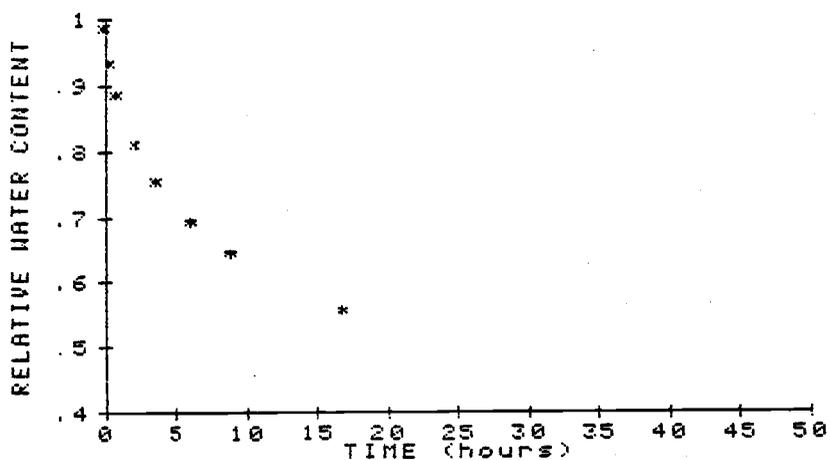
The best fit linear equation is $1/P = A + B(WD)$ with:
 A = 6.58128927337E-2
 B = -7.33495976985E-2
 R = .994363035168
 N = 3

The best fit power equation is $\text{LN}(1/P) = \text{LN}(A) + B(\text{LN}(WD))$ with:
 $A = 1.06785090662E-2$
 $B = -.956653515248$
 $R = .998900981954$
 $N = 3$

 Here is a graphic display of the data and the best regression lines



 Rate of Water Loss:



General water relations components

P2: BEST DATA PTS

Osmotic potential at full turgor (OP100) = -15.1945911882

Osmotic potential at zero turgor (WPO) = -20.082476507

Volume of osmotically active water (VO) = 5.03985066155

Water deficit at incipient plasmolysis (WDO) = .2

Water deficit at zero osmotically active water (F*) = .897249539176

Water relation components for a Hoffer diagram

WD	LWP (bars)	SP (bars)	TP (bars)	MP (bars)
.02000	-2.29167	-15.57733	13.32197	-.03632
.04000	-4.45847	-15.97947	11.59688	-.07588
.06000	-6.58556	-16.40251	9.93597	-.11903
.08000	-8.69070	-16.84810	8.32351	-.16612
.10000	-10.78269	-17.31806	6.75296	-.21759
.12000	-12.86709	-17.81440	5.22123	-.27391
.14000	-14.94803	-18.33939	3.72700	-.33563
.16000	-17.02886	-18.89553	2.27003	-.40337
.18000	-19.11260	-19.48562	.85084	-.47782
.20000	-20.67261	-20.11282	0.00000	-.55979
.22000	-21.43087	-20.78066	0.00000	-.65021

WD = Water deficit
 LWP = Leaf water potential
 SP = Solute potential
 TP = Turgor potential
 MP = Matric potential

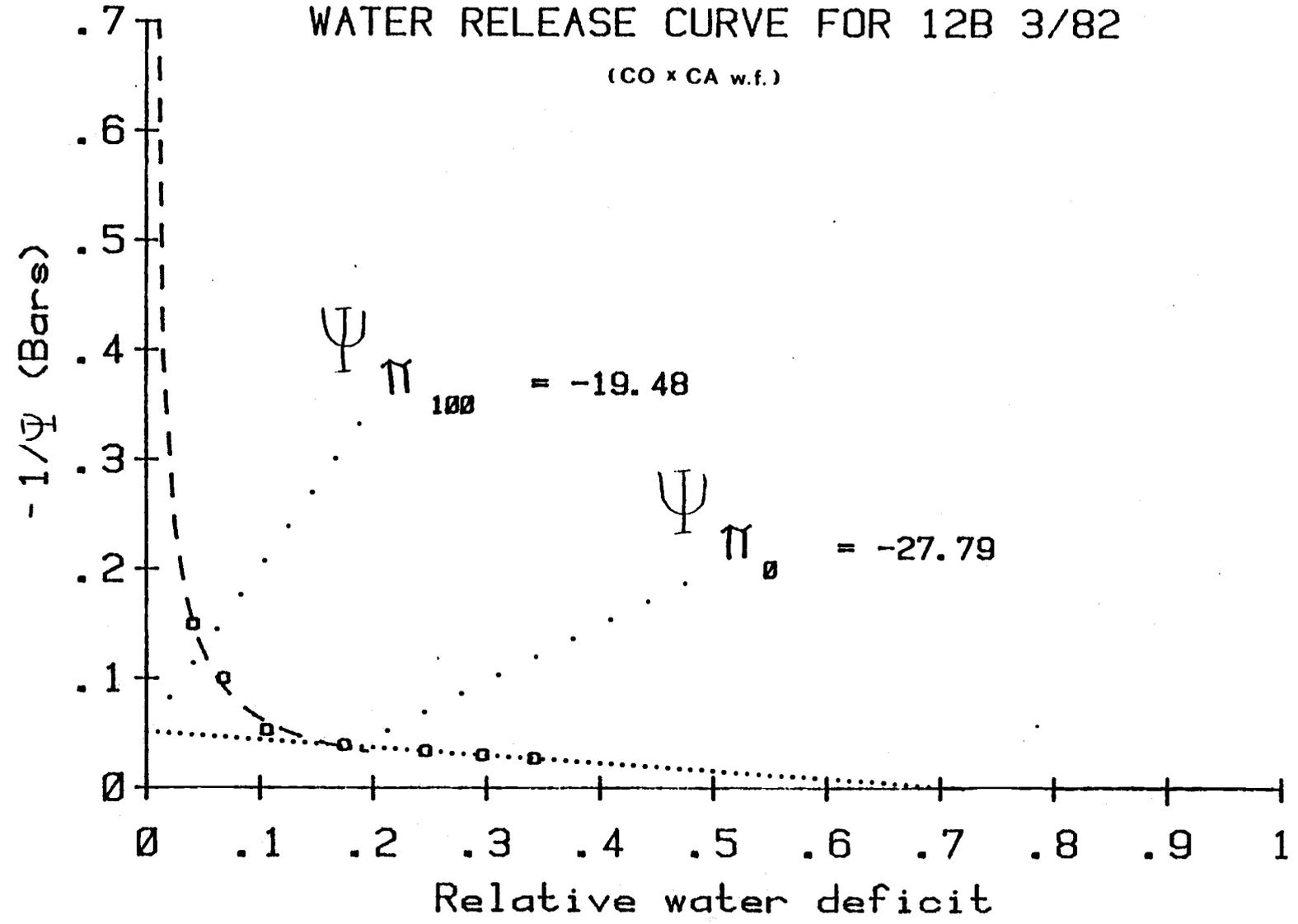
WD	RSWC	EM
.02000	.97771	0.00000
.04000	.95542	-93.65815
.06000	.93313	-91.55561
.08000	.91084	-90.21639
.10000	.88855	-89.23347
.12000	.86626	-88.45791
.14000	.84397	-87.81812
.16000	.82168	-87.27411
.18000	.79939	-86.80125
.20000	.77710	-86.38332
.22000	.75481	-86.00905

WD = Water deficit
 RSWC = Relative symplastic water content
 EM = Elastic modulus

APPENDIX 6. Typical "Water-Release" curves of a Colorado x California white fir and a Colorado x California hybrid in March, June and August, 1982. The units of water potential are bars in these figures, 10 bars = 1 MPa.

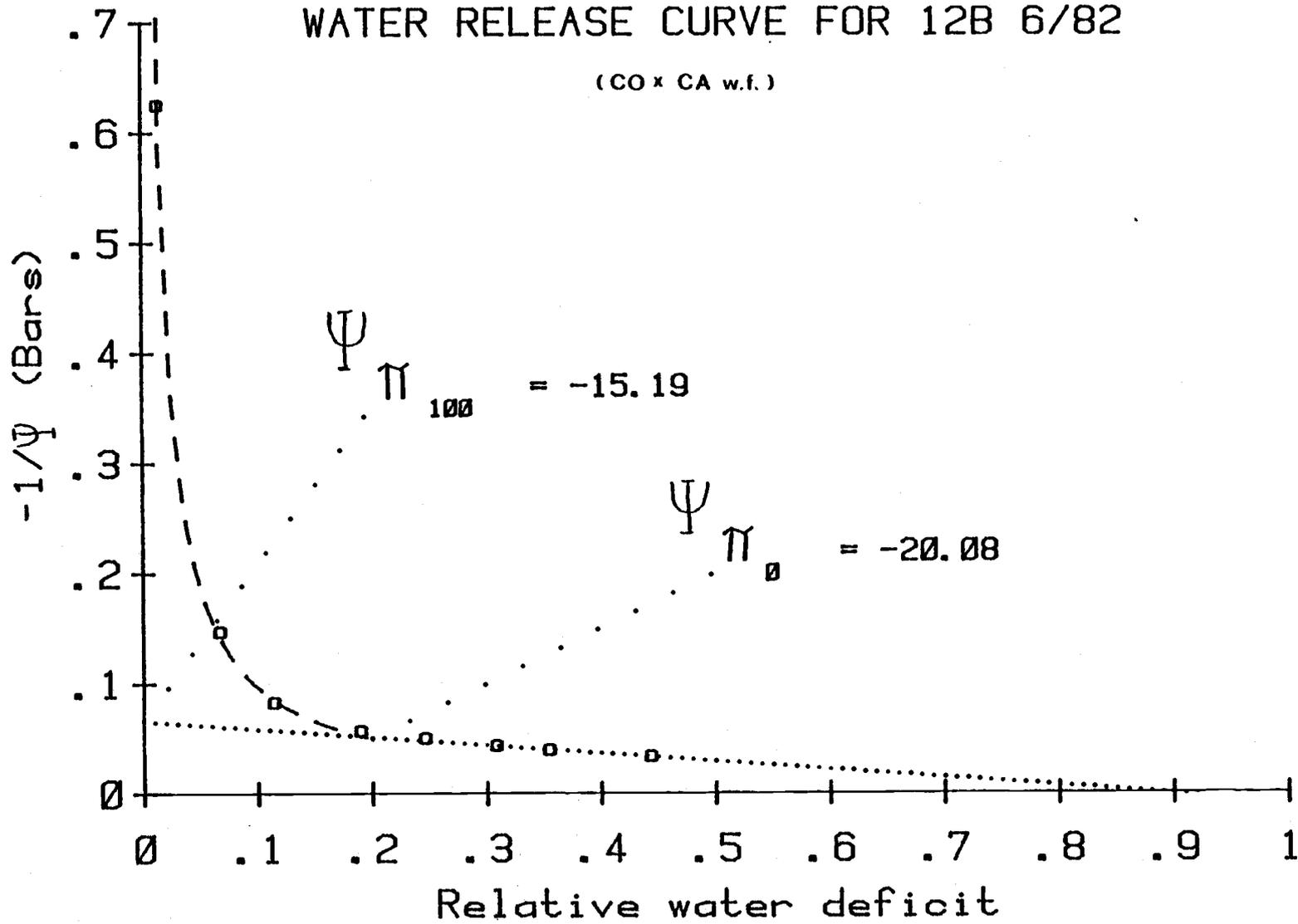
WATER RELEASE CURVE FOR 12B 3/82

(CO x CA w.f.)



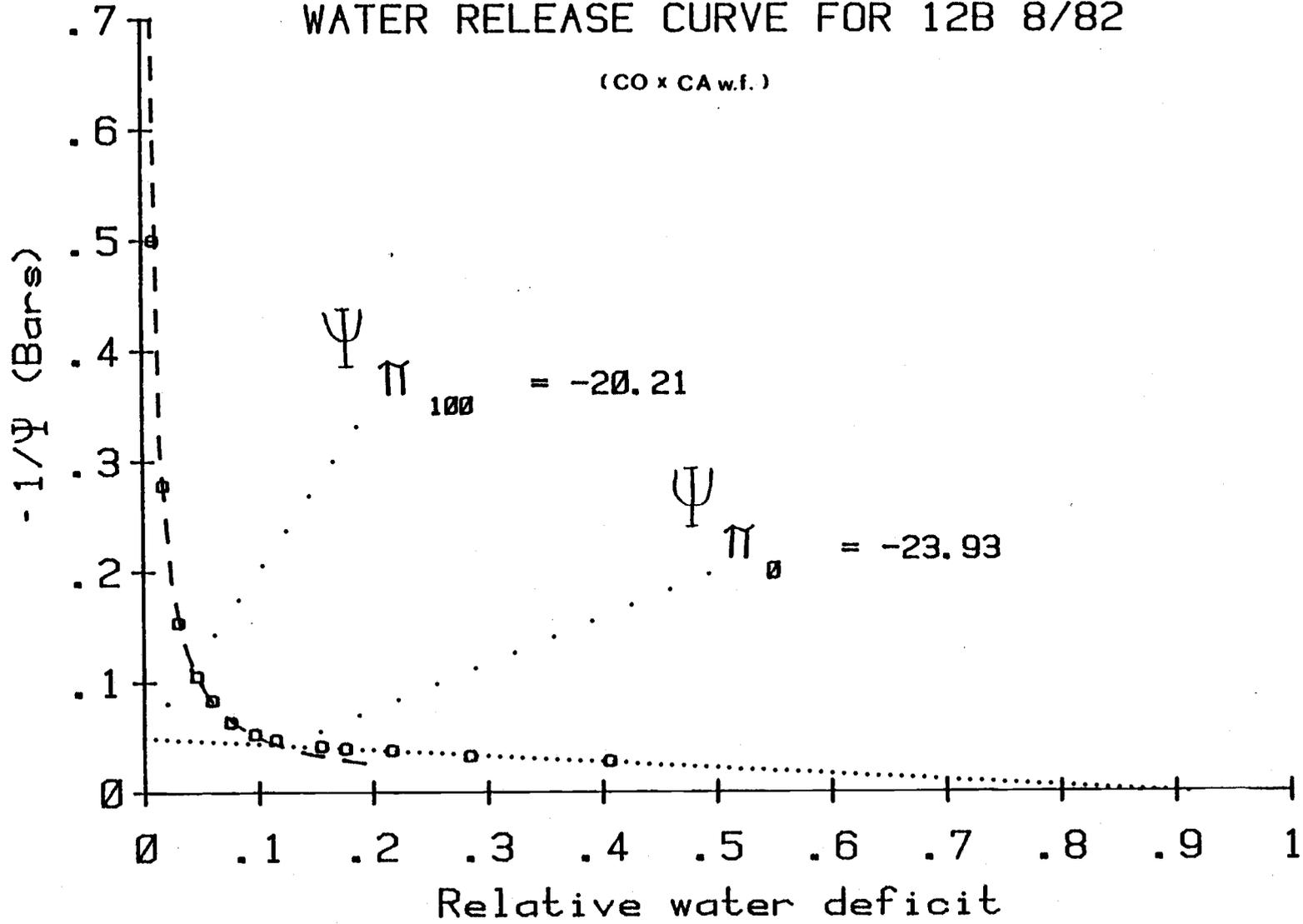
WATER RELEASE CURVE FOR 12B 6/82

(CO x CA w.f.)



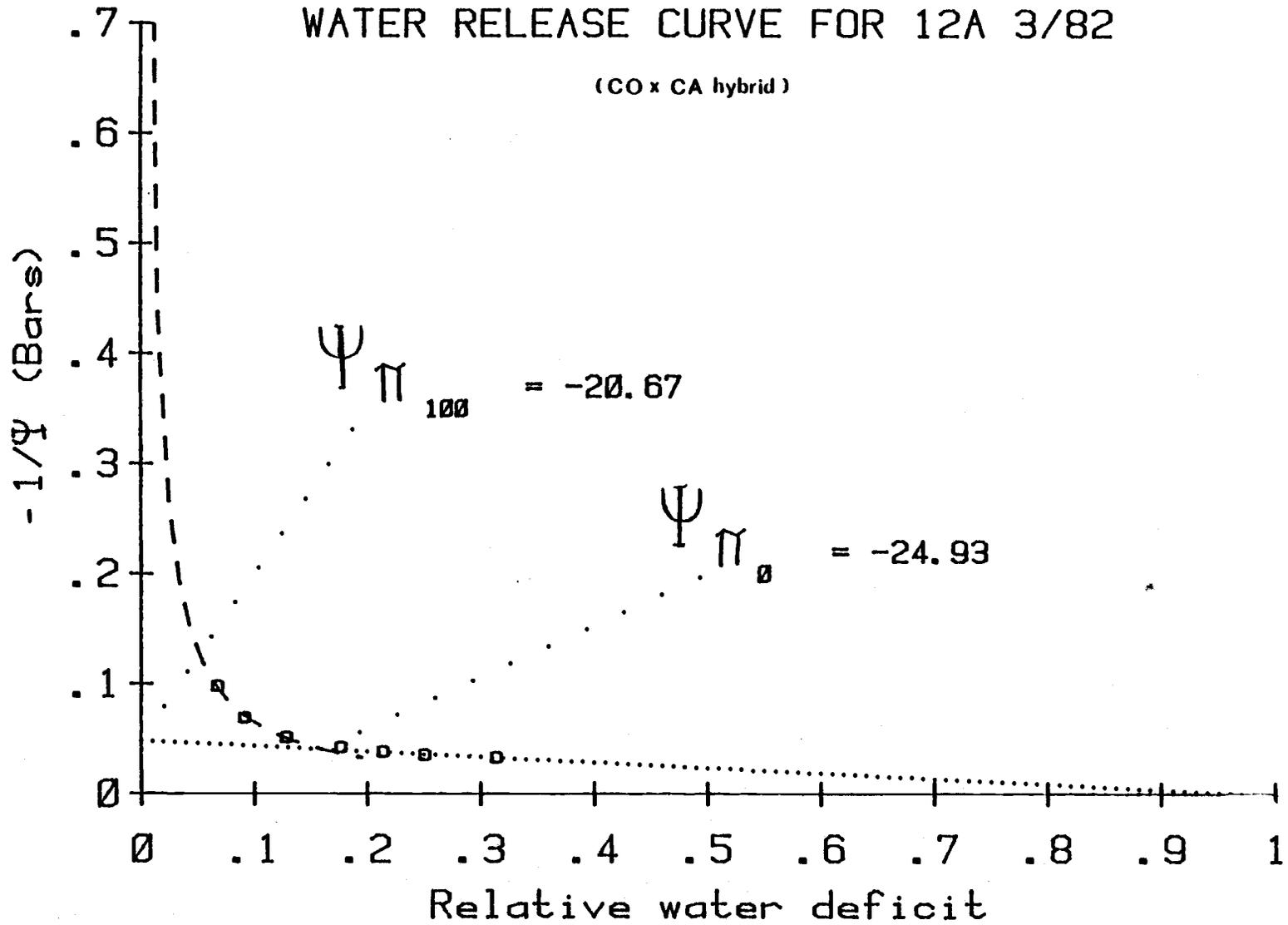
WATER RELEASE CURVE FOR 12B 8/82

(CO x CA w.f.)



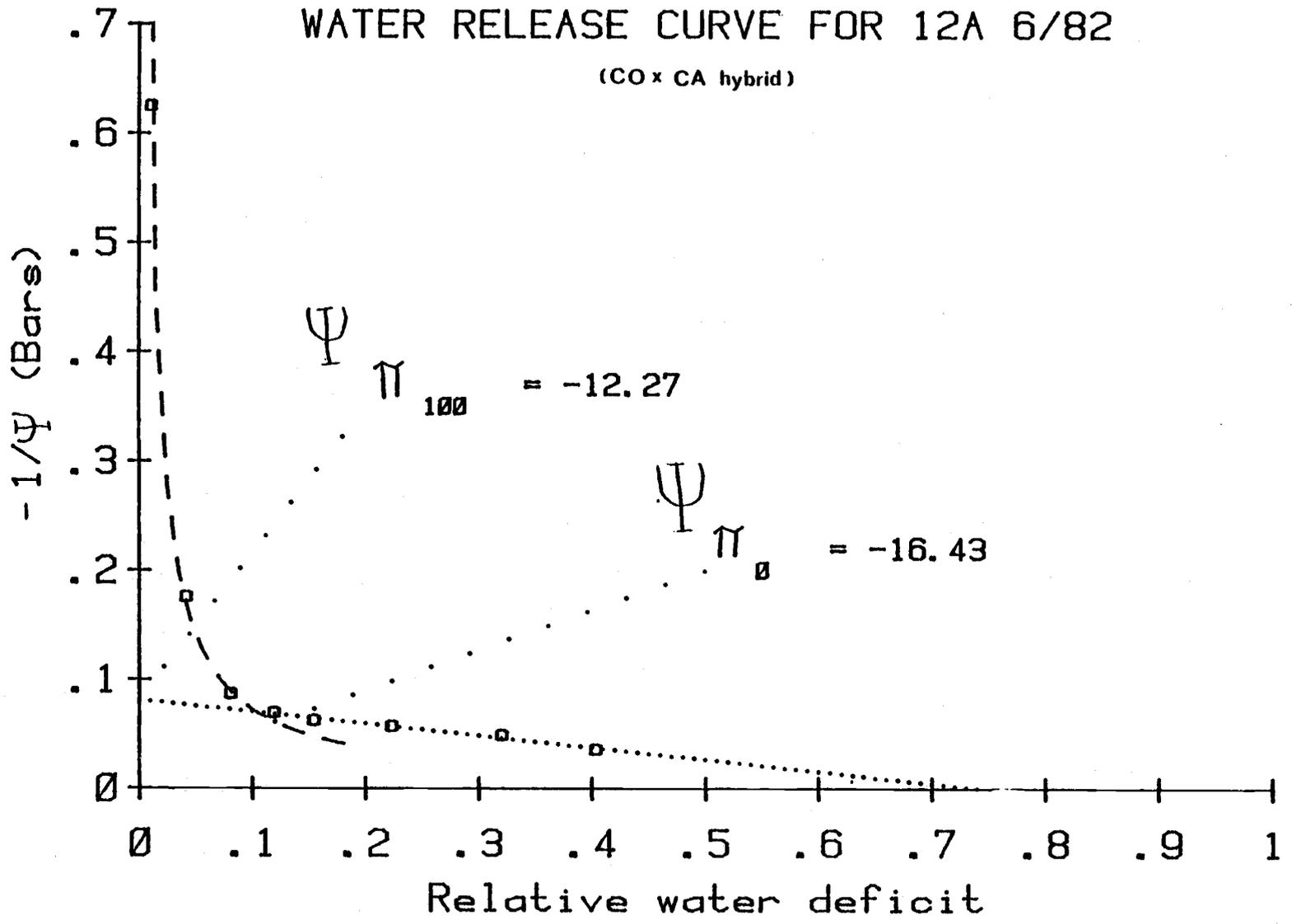
WATER RELEASE CURVE FOR 12A 3/82

(CO x CA hybrid)



WATER RELEASE CURVE FOR 12A 6/82

(CO x CA hybrid)



WATER RELEASE CURVE FOR 12A 8/82

(CO x CA Hybrid)

