

AN ABSTRACT OF THE THESIS OF

Kent J. Davis for the degree of Master of Science in Botany and Plant Pathology presented on April 22, 2005.

Title: Comparison of the Water Relations Characteristics of Woody Plants in Western Oregon.

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Abstract approved:

Donald B. Zobel

I studied the water relations traits, twig conductivity, C<sup>13</sup> isotopic composition, and wood density of three conifer and five angiosperm species in western Oregon. This study took place from spring 2002 to fall 2003 on four sites. Species were selected to represent the diversity of drought tolerance of woody plants in western Oregon. The objectives of this work were to describe the seasonal variation and species' response to the dry season and to determine suites of functional traits that vary in a similar manner across species. Pre-dawn ( $\Psi_{pd}$ ) and mid-day ( $\Psi_{md}$ ) water potentials decreased throughout both summers for most species; however, the diurnal change ( $\Delta\Psi$ ) in water potential decreased for conifers and increased for angiosperms during the same time. *Quercus garryana* and *Arbutus menziesii* reached the lowest  $\Psi_{md}$  and the forest species had the highest values. Stomatal conductance ( $g_w$ ) was highest, and remained high during the summer, for *Q. garryana*, consistently lowest for *Acer macrophyllum* and *Corylus cornuta* in the forest, and intermediate for *A. menziesii*. Osmotic potentials at full ( $\Psi_{sf}$ ) and zero turgor ( $\Psi_{sz}$ ) decreased from early to late summer, and increased from late summer to spring for the four evergreen species sampled.  $\Psi_{sf}$  and  $\Psi_{sz}$  were lowest for *Pseudotsuga menziesii*, *Q. garryana*, and *A. menziesii* and highest for the forest species. The index of elasticity (IE) also increased (i.e., tissue elasticity decreased)

summer, and continued to increase for most species from late summer to spring. Throughout the summer, *A. macrophyllum* and *C. cornuta* had the most elastic tissue (low IE), while the more drought resistant species had less elastic tissue. The twig cross-sectional area/leaf area ratio (Huber Value) was, in general, lowest for the conifers, *C. cornuta*, and *A. macrophyllum* and highest for *Q. garryana* and *A. menziesii*, and did not change much with season. The specific conductivity ( $k_s$ ) of twigs was lowest for conifers, intermediate for *C. cornuta* and *A. menziesii* and highest for *Q. garryana*, *A. menziesii*, *A. macrophyllum*, and *Fraxinus latifolia* in the mid-summer and changed little during the summer. The leaf-specific conductivity ( $k_l$ ) was lowest for conifers, intermediate for angiosperms in the forest and *F. latifolia*, and highest for *Q. garryana* and *A. menziesii*. During the summer, there were few significant changes in  $k_l$  for most of the species. In spring,  $k_l$  was very high for two deciduous species due to their small, immature leaves.  $\delta^{13}\text{C}$  values were lower for forested species than clear-cut species and indicated that, within each habitat, intrinsic water use efficiency (WUE) was higher for conifers than for the co-occurring angiosperms. Wood density was lowest for *A. macrophyllum* (high percentage of pith resulted in an underestimation of wood density in this species), highest for *Q. garryana*, and intermediate for the remaining species.

The eight species in this study shared common relationships between leaf water potentials, wood density, osmotic potential, cell wall elasticity, and expressions of conductivity, despite their differences in drought resistance. Among the five angiosperms,  $\Psi_{sz}$  and  $\Delta\Psi$  decreased as maximum  $g_w$  increased and the maximum  $g_w$  increased as the Huber value,  $k_l$  and tissue elasticity decreased, across species. For species in the forest and clear-cut,  $\delta^{13}\text{C}$  increased with decreasing early summer  $\Psi_{md}$  and

increasing  $\Delta\Psi$ . Across all species and seasons,  $\Psi_{md}$  decreased with decreasing  $\Psi_{pd}$ ; however, the slope of decrease was greater for ring-porous species than for diffuse porous or conifer species. Tissue elasticity decreased with decreasing minimum  $\Psi_{sz}$  for all species except *Q. garryana*, which had higher tissue elasticity than would be predicted based on the other species. Across all species except *A. macrophyllum*, mean  $k_s$  and mean  $k_l$  increased with increasing wood density. Decreasing  $\Psi_{md}$ ,  $\Psi_{sf}$ , and  $\Psi_{sz}$  were associated with increasing wood density. The maximum  $\Delta\Psi$  increased with increasing  $k_s$  and  $k_l$ , while the minimum  $\Psi_{sz}$  decreased with increasing Huber Value.

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Comparison of the Water Relations Characteristics of Woody Plants in Western Oregon

by  
Kent J. Davis

A THESIS

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Master of Science thesis of Kent J. Davis presented on April 22, 2005.

APPROVED: *Redacted for Privacy*

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Dean of the Graduate School

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Kent J. Davis, Author

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## CONTRIBUTION OF AUTHORS

Kent Davis collected and analyzed all data except for carbon isotope and nitrogen content data (which was analyses were purchased from the Idaho Stable Isotopes Laboratory) and wrote the first draft of this manuscript. Dr. Donald Zobel, Dr. Frederick Meinzer, and Dr. Mark Patterson provided editing and research advice throughout this project.



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## LIST OF ABBREVIATIONS

$\delta^{13}\text{C}$	The ratio between $^{13}\text{C}/^{12}\text{C}$ between the sample and standard material (‰)
$\Delta\Psi$	The difference between $\Psi_{\text{pd}}$ and $\Psi_{\text{md}}$ (MPa)
$\Psi$	Total water potential (MPa)
$\Psi_{\text{g}}$	Gravitational potential (MPa)
$\Psi_{\text{m}}$	Matric potential (MPa)
$\Psi_{\text{md}}$	Mid-day water potential (MPa)
$\Psi_{\text{p}}$	Hydrostatic pressure or pressure potential (MPa)
$\Psi_{\text{pd}}$	Pre-dawn water potential (MPa)
$\Psi_{\text{s}}$	Osmotic or solute potential (MPa)
$\Psi_{\text{sf}}$	Osmotic potential at full turgor (MPa)
$\Psi_{\text{sz}}$	Osmotic potential at zero turgor (MPa)
$g_{\text{w}}$	Stomatal conductance ( $\text{mmol m}^{-2} \text{sec}^{-1}$ )
$g_{\text{wAM}}$	Morning stomatal conductance ( $\text{mmol m}^{-2} \text{sec}^{-1}$ )
$g_{\text{wPM}}$	Afternoon stomatal conductance ( $\text{mmol m}^{-2} \text{sec}^{-1}$ )
IE	Index of elasticity (inversely proportional to tissue elasticity) (MPa)
J	Water flux ( $\text{kg sec}^{-1}$ )
K	Hydraulic conductance ( $\text{kg sec}^{-1} \text{MPa}^{-1}$ )
$k_{\text{h}}$	Hydraulic conductivity ( $\text{kg m sec}^{-1} \text{MPa}^{-1}$ )
$k_{\text{l}}$	Leaf-specific conductivity ( $\text{kg m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ )
$k_{\text{s}}$	Specific conductivity ( $\text{kg m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ )
P-V curve	Pressure-volume curve
RWC	Relative water content (%)
$\text{RWC}_{\text{z}}$	Relative water content at zero turgor (%)
VPD	Vapor pressure deficit (kPa)
$W_{\text{d}}$	Wood density ( $\text{g cm}^{-3}$ )
WUE	Water-use efficiency ( $\text{mmol mol}^{-1}$ )

## DEDICATION

This thesis is dedicated to Chantel, someone who loved to write.

# Comparison of the Water Relations Characteristics of Woody Plants in Western Oregon

## CHAPTER ONE: INTRODUCTION AND LITERATURE REVIEW:

### **Introduction:**

In many climates, water availability controls the distribution and physiological functioning of plants (Kramer and Boyer 1995). Most plant processes (e.g., respiration, growth, photosynthesis) are affected directly or indirectly by water availability. In climates with dry seasons, trees often experience water deficits that cause major changes in physiology and morphology, such as loss of turgor pressure, arrested cell elongation, stomatal closure, and reduced photosynthesis. Physiological adjustments to water deficits include changes in a wide range of water relations attributes. For example, low water potential may develop in response to increasing drought or decreasing water availability and be correlated with reduced stomatal conductance, reduced osmotic potential and tissue elasticity, and reduced xylem hydraulic conductivity for drought resistant species (Larcher 1995). However, despite the large range of individual “suites” of water relations attributes for individual species or groups of species, water transport properties and leaf level characteristics appear to covary in a similar manner across species, demonstrating generality in plant processes and indicating the trade-offs among traits (Bucci et al 2004).

In general, the Pacific Northwest has dry, warm summers and cool, wet winters. However, the climate is extremely diverse, with steep gradients of rainfall and temperature across the region. Although the landscape in the Pacific Northwest is dominated by dense coniferous forests, broadleaf evergreen and deciduous species are

important components in some parts of the vegetation (Waring and Franklin 1979). The summer dry period undoubtedly controls the distribution of plant species and, to a lesser extent, cold temperatures may also affect species distribution patterns (Zobel et al 1976, Lassoie et al 1985). Locally, the vegetation bordering the Willamette valley is composed of coniferous stands dominated by *Pseudotsuga menziesii* with *Abies grandis* and *Acer macrophyllum* being important shade-tolerant components (Franklin and Dyrness 1973). A common successional sequence for this vegetation consists of the replacement of grasslands with *Quercus garryana* savanna, and later, oak forest. *P. menziesii* often replaces *Q. garryana*, which, in turn, is replaced by *A. grandis*, *A. macrophyllum* or *A. macrophyllum/P. menziesii* forests (Franklin and Dyrness 1973). *Q. garryana* and *Arbutus menziesii* are present in pioneering stands and are often the first tree species to establish in grasslands following removal of fire or grazing. *A. menziesii* and *A. macrophyllum* can also invade openings alongside *Q. garryana* in certain situations (Franklin and Dyrness 1973).

There have been many water relations studies in the Pacific Northwest (Lassoie et al 1985). Most, however, involve the commercially important conifers and few have concurrently examined several species that differ in drought resistance, distribution pattern, and growth form, and few have included species of minor importance in the vegetation.

The purpose of this study was to quantify and compare the seasonal variation and range of water relations characteristics of a diverse group of woody species, to determine how species vary in their adaptations to drought in the Pacific northwest climate, and to



determine relationships among different water relations characteristics within that group of species.

The specific objectives of this study were to:

1. Describe and compare seasonal variation in water relations traits for species representing major growth forms in western Oregon and determine “suites” of water relations characteristics that characterize individual species.
2. Identify suites of functional traits that covary in a similar manner across species and compare these relationships to those of species from other locations.

Here I report patterns of shoot water potential, shoot osmotic potential and tissue elasticity; aspects of twig hydraulic conductivity; stomatal conductance; stable carbon isotope ratios and % N concentration of leaves; and twig wood density for eight species at four sites near Corvallis, Oregon, during two years. The eight species were selected to represent the taxonomic and growth form diversity and range of drought tolerance for woody plants in western Oregon.

#### **Literature Review:**

Water moves from the soil into the roots, through xylem, and transpires out of plants through stomatal pores in leaves. The driving force behind water movement through plants is a water potential gradient, from highest in soil to lowest in the atmosphere. Living plant cells contain solutes that create osmotic potential. Lowering osmotic potential induces water uptake by cells, producing turgor pressure (Nobel 1991). In order for cells to remain turgid, osmotic potential inside cells must remain lower than water potential of the surrounding tissue. As cells lose water, the osmotic potential decreases due to the reduction in cell (and water) volume and subsequent concentration

of solutes. In order for turgor to be maintained, mid-day water potential may be controlled by reducing stomatal conductance and, therefore, transpiration. The ability of xylem to transport water also affects mid-day water potential. Therefore, species with lower osmotic potential and a greater ability to transport water can maintain turgor even while they experience lower mid-day water potentials, which allows higher stomatal conductance (Tyree and Ewers 1991). Stomatal conductance can also be reduced during water stress, from reduction of water transport in the xylem due to cavitation of the water column in xylem cells, which render xylem conduits non-conductive (Tyree and Sperry 1989, Tyree and Zimmermann 2002, Sperry et al 2002).

#### Water Relations:

The water status of plants is most often expressed in terms of water potential ( $\Psi$ ), a measure of the potential energy of plant water as compared to pure, free water at atmospheric pressure (Kramer and Boyer 1995).  $\Psi$  is usually described in terms of pressure in units of MegaPascals (MPa) and, in plants, is usually negative. The total  $\Psi$  in plants is composed of four components, as follows:

$$\Psi = \Psi_p + \Psi_s + \Psi_m + \Psi_g$$

Where  $\Psi$  is the total water potential,  $\Psi_p$  is the hydrostatic pressure or pressure potential,  $\Psi_s$  is the osmotic or solute potential,  $\Psi_m$  is the matric potential, and  $\Psi_g$  is gravitational component.  $\Psi_m$  is commonly ignored in plant water studies but is important in soils and  $\Psi_g$  is ignored when dealing with cells because it only becomes significant at heights over 1 m (Kramer and Boyer 1995). The components of  $\Psi$  can vary in different plant parts.

The  $\Psi$  can be quickly and easily estimated with a pressure chamber. The pressure chamber measures a “balance pressure” that is assumed to be equal, but of opposite sign,

to the  $\Psi$  in the plant tissue under examination (Scholander et al 1965). Although there is longstanding debate about whether the balance pressure is equal to  $\Psi$  or to  $\Psi_p$  in the xylem of transpiring tissue (Canny 1995, Canny 1998, Canny 2001, Melcher et al 2001, Zimmermann et al 2002), for this study I assumed that balance pressure equals  $-\Psi$  (Turner 1981). Although it may be inappropriate to use transpiring tissue to determine xylem  $\Psi$ , because high resistance can cause a large difference in water potential between twig xylem and leaves during times of transpiration (Melcher et al 2001), plant water potential has been measured on transpiring tissue in many studies. Plant  $\Psi$  measured with the pressure-chamber has been used to explain species distribution patterns and to evaluate plant moisture stress (Waring and Cleary 1967). Plant  $\Psi$  is most often measured before dawn ( $\Psi_{pd}$ ), which has been extensively used to represent the  $\Psi$  of the soil ( $\Psi_{soil}$ ) (Pallardy et al 1991, Lassoie and Hinckley 1991, Hinckley et al 1979); however, this may not always be the case. This assumption is based on the expectation that leaves rehydrate during night and that no transpiration takes place (Donovan et al 2001). However, differences greater than 0.5 MPa between  $\Psi_{pd}$  and  $\Psi_{soil}$  have been reported for many species, including some from this study, and that nighttime transpiration could contribute to significant discrepancies in from the assumption that  $\Psi_{pd}$  represents  $\Psi_{soil}$  (Donovan et al 2001). Plant water potential was also measured during the middle of day ( $\Psi_{md}$ ), which represents plant  $\Psi$  when the water deficit is likely to be the largest. The difference between these two measurements ( $\Psi_{pd} - \Psi_{md}$ ) is important in understanding the extent of stomatal control of water loss, thus,  $\Psi$  during the day.

Much work has shown that plant  $\Psi$  and its components vary with time and space and affect plant processes, such as photosynthesis, cell growth, stomatal aperture and

water transport (Kramer and Boyer 1995). It is beyond the scope of this review to highlight all findings; rather I will focus on trends for trees in the Pacific Northwest. In general, plant  $\Psi$  varies diurnally, seasonally, within a tree from one side to another, and declines with height in the tree (Waring and Cleary 1967, Ritchie and Hinckley 1971). Studies on a wide range of species and in many habitats have shown that the  $\Psi$  in leaves is highest (closest to zero) before dawn and drops during the day with the onset of transpiration, increasing vapor deficit, and increasing leaf and air temperature.  $\Psi$  has also been shown to vary between sun and shade foliage for conifers and angiosperms (Waring and Cleary 1967, Ritchie and Hinckley 1971). Both  $\Psi_{pd}$  and  $\Psi_{md}$  tend to be highest during the early spring, decrease as the dry summer progresses, and increase with the return of precipitation during the fall and winter.

In the Pacific Northwest,  $\Psi$  decreased during the onset of summer for *A. grandis* in the central Cascades (Zobel 1974) and in the Coast Range of Oregon (Yoder 1983), *P. menziesii* in Washington state (Ritchie and Shula 1984), and *Q. garryana* in Oregon (Hibbs and Yoder 1993), and for *A. menziesii* and *P. menziesii* in southwestern Oregon (Pabst et al 1990). Hickman (1970) found that both  $\Psi_{pd}$  and  $\Psi_{md}$  decreased from July to September for most plants on Iron Mountain in the Western Cascade Range in Oregon.

#### Turgor Maintenance and Osmotic and Cell Wall Elasticity Adjustment:

Maintenance of turgor at low water potentials depends on the osmotic potential and elasticity of cell walls. This is because as cells lose water, cell volume and water potential decrease until the turgor-loss point is reached, which depends on the cell wall elasticity (Lambers et al 1998). Cells with elastic walls contain more water at full turgor than those with rigid cell walls. In tissue with rigid cell walls,  $\Psi_p$  will drop faster, with a

small amount of water loss in comparison to tissue with elastic cell walls. Therefore, tissue with rigid cell walls will develop lower  $\Psi$ , maintaining a larger gradient of  $\Psi$ , between the soil and leaf (Abrams 1988). However, elastic tissue can experience greater changes in volume while maintaining  $\Psi_p$  at lower  $\Psi$ s and low water content (Abrams 1988, Abrams 1990, Niinemets 2001). Although rigid cell walls do not allow turgor maintenance at low water content, rigid cell walls provide the advantage of increased integrity during rehydration (Clifford et al 1998) but may limit growth of expanding cells during leaf expansion (Lambers et al 1998).

Usually elasticity decreases with decreasing  $\Psi$ ; however, it can also increase (Turner and Jones 1980, Abrams 1988). Either an increase or decrease in cell wall elasticity can be viewed as advantageous during decreasing water availability, depending on adjustments in osmotic potential during the same time (Abrams 1988, Lambers et al 1998). Many studies have provided evidence that wall elasticity may increase or decrease with the development of drought, so there does not appear to be a universal solution. Some studies show that species that increase elasticity in cell walls are inherently more drought tolerant (Fan et al 1994), but for many species increased elasticity is not associated with decreases in  $\Psi$ s (Nunes et al 1989, Evans et al 1992, Fan et al 1994). However, other studies show that a combination of a decrease in elasticity and a reduction of  $\Psi$ s is an effective means of surviving drought. There is much evidence that  $\Psi_s$  drops with decreasing  $\Psi$  (Roberts et al 1980, Parker et al 1982, Meinzer et al 1986, Kloeppel et al 1994, Myers et al 1997, Nguyen-Queyrens and Bouchet-Lannat 2003) and that a reduction of  $\Psi$ s is important in maintaining cell elongation, stomatal opening, photosynthesis, and survival of dehydration during times of water stress (Turner

and Jones 1980). The adjustment in  $\Psi_s$ , in coordination with adjustments in cell wall elasticity, is one mechanism that aids to maintain turgor as plant  $\Psi$  decreases.

#### Measurement of Osmotic Potential and Cell Wall Elasticity:

Components of  $\Psi$  can be determined using the technique of pressure-volume analysis (P-V curve) (Scholander et al 1965, Tyree and Hammel 1972, Koide et al 1989, Pallardy et al 1991). I used an approach outlined by Pallardy et al (1991). P-V curve analysis relates the bulk water potential ( $\Psi$ ), measured using a pressure-chamber, to the relative water content (RWC) of the tissue under study. The relationship of  $\Psi$  and RWC is plotted as  $1/\Psi$  on the y-axis and RWC on the x-axis. This transformation of  $\Psi$  is necessary to show clearly the inflection point when bulk tissue turgidity is lost. The osmotic potential at full turgor ( $\Psi_{sf}$ ) is the solute concentration at zero balance pressure (full turgidity and RWC=100%) and is found by extrapolating the straight-line portion of the relationship to the y-axis. The water potential at zero turgor ( $\Psi_{sz}$ ) is the turgor loss point and is the inverse of  $\Psi$  at the intersection of the straight and curved portions of the P-V relationship. The P-V analysis can also be used to determine the elasticity of the cell walls. Elasticity is inversely related to the index of elasticity (IE), which is given by the slope of all  $\Psi_p$  values above the turgor loss point, plotted over RWC on the abscissa.

Although there is much discussion concerning experimental and calculation procedures in P-V curve analysis (Meinzer et al 1986, Parker and Pallardy 1987, Kubiske and Abrams 1991, Parker and Columbo 1995, Zobel 1996), most of the controversy concerns the rehydration of samples before determination of the P-V curve. Rehydration of plant tissue may cause excessive uptake of water into the apoplastic region, resulting in an overestimate of the initial weight of the sample and a shift of the P-V curve to the

right. This shift causes estimates of osmotic potentials at full turgor to be less negative, and RWC and IE to be lower than for non-rehydrated tissue. However, the effects of rehydration may be larger for xeric than for mesic species. For example, hydration caused  $\Psi_{sz}$  to increase as much as 3.0 MPa in *Larrea tridentata* from the upper Sonoran Desert (Meinzer et al 1986) and increased  $\Psi_{sz}$  and  $\Psi_{sf}$  by about 0.4-0.6 MPa for two xeric oak species (Kubiske and Abrams 1990). However, rehydration caused no significant difference in osmotic potentials for oak and hickory in the Midwest (Parker et al 1982). In addition, rehydration caused little difference in osmotic potentials for *Quercus rubra* and *Fraxinus americana*, two mesic valley species in central Pennsylvania (Kubiske and Abrams 1990).

Rehydration time appears to have little effect on  $\Psi_s$ .  $\Psi_s$  for *Q. rubra* and *F. americana* did not differ between 12 and 24 hours of rehydration (Kubiske and Abrams 1990). In a study of 12 southern Appalachian species, 24 additional hours of rehydration caused a difference in  $\Psi$  in only 4 of 52 cases (Zobel 1996) and an additional day of rehydration did not change P-V analysis results for oak and hickory in Missouri (Parker et al 1982).

For non-rehydrated tissue, it is necessary to estimate the initial weight from a graph of tissue weight and leaf  $\Psi$ . Because non-rehydrated tissue often has low initial  $\Psi$  values, it appears that not rehydrating may result in inadequate estimates of the initial weight of the tissue. However, there may be a strong linear relationship between the tissue weight and the  $\Psi$  above the  $\Psi_{sz}$  (Kubiske and Abrams 1990). Proponents of rehydration state that rehydration is necessary to ensure sufficient data above  $\Psi_{sz}$  (Kubiske and Abrams 1994). The best balance may be to rehydrate each sample only

long enough to allow recovery to full turgor; however, rehydration time to full turgor varies with species (Pallardy et al 199) rendering this technique difficult for studies involving several species.

#### Stomatal Conductance:

Transpiration is the loss of water out of plants to the atmosphere. Water diffuses out of epidermal cells, into the substomatal cavities, through the stomatal pores and boundary layer. Total conductance measures the permeability of a leaf surface and the boundary layer (a thin layer of air above the leaf surface) to water vapor diffusion (Nobel 1991, Pearcy et al 1989); however, measuring total stomatal conductance in a ventilated porometer disrupts the boundary layer and, thus, measurements of conductance represent the leaf conductance, which includes the cuticle and stomatal conductances ( $g_w$ ) (Pearcy et al 1989).  $g_w$  relates the rate of water vapor loss by a leaf to the driving force, the difference in specific humidity between the leaf and the atmosphere (Pearcy et al 1989). The boundary layer conductance is mainly a function of leaf shape and size and wind speed (Jones 1994). Maximum  $g_w$  varies widely among species, but in general is usually higher in light adapted deciduous forest trees ( $250-370 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) than evergreen conifers ( $140-170 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) (Larcher 1995). Nevertheless,  $g_w$  is strictly a function of stomatal aperture size, stomatal density, stomatal cavity depth, and boundary layer thickness (Kramer and Boyer 1995). For example, in still air a large change in stomatal aperture will facilitate a smaller change in transpiration than the same change in stomatal aperture in moving air that increases boundary layer conductance. For most leaves, conductance of water vapor through the cuticle is very small compared to that through stomata; therefore,  $g_w$  is often considered to represent stomatal conductance.



Conductance of water through stomata affects the internal water balance of plants, which influences basic physiological processes such as photosynthesis and cell growth (Kramer and Boyer 1995, Lambers et al 1998).  $g_w$  can be measured in a variety of ways, although steady-state diffusion porometers are the most widely used (Percy et al 1989).

The major factors controlling  $g_w$  are light, intercellular carbon dioxide concentrations, leaf water status, humidity, and temperature (Kramer and Boyer 1995). However, seldom is  $g_w$  clearly related to a single plant or environmental factor, and plots of  $g_w$  and one factor often result in a non-significant relationship (Hinckley et al 1979). It has been suggested that, when many measurements are taken, the response of  $g_w$  to a factor may be represented with a boundary line analysis (Hinckley et al 1979).  $g_w$  usually increases with increasing light levels (Kramer and Boyer 1995, Jarvis 1980) and maximal  $g_w$  also begins to decrease at light levels below about 10% of that of full sunlight (Hinckley et al 1979). The relationship between  $g_w$  and  $\Psi$  has been studied for many species. In the Northwest,  $g_w$  decreases throughout the day as  $\Psi$  decreases; stomata close at critical values ranging from  $-1.5$  MPa to  $-2.5$  MPa in many species of conifers (Hinckley et al 1979, Lassoie et al 1985). Aside from this general diurnal trend,  $g_w$  increases with increasing irradiance in the morning even though  $\Psi$  may be declining. The relationship between declining  $g_w$  and increasing vapor pressure deficit (VPD) is very clear; however, the response of  $g_w$  depends on species, growing conditions and plant water status (Jones 1994, Jarvis 1980). *Picea sitchensis* in the Northwest (Hinckley et al 1979) and a few major conifers and deciduous trees in the Northwest (Waring and Franklin 1979) showed this relationship.

### $\delta^{13}\text{C}$ Isotope Composition:

There are two naturally occurring stable isotopes of carbon,  $^{12}\text{C}$  and  $^{13}\text{C}$ , with  $^{12}\text{C}$  being the most abundant, and lightest. The ratio of  $^{12}\text{C}/^{13}\text{C}$  is greater in plant tissue than in ambient  $\text{CO}_2$ . This difference is caused by the enzymatic and physical discrimination against the heavier and less abundant  $^{13}\text{C}$  (Farquhar et al 1989, Lajtha and Marshall 1994). The isotopic composition of plant material is expressed as the difference in ratios of  $^{13}\text{C}/^{12}\text{C}$  between the sample (Rp) and the standard material (Rs) and has the units of per mil (‰) (Farquhar et al 1989, Lajtha and Marshall 1994)

$$\delta^{13}\text{C} = (\text{Rp}/\text{Rs}-1)1000$$

Differences in  $\delta^{13}\text{C}$  among plants are due to differences in the diffusion of  $\text{CO}_2$  through the stomata and boundary layer and carboxylation by rubisco. For  $\text{C}_3$  plants, values of  $\delta^{13}\text{C}$  range from  $-25\text{‰}$  to  $-35\text{‰}$  (Farquhar et al 1989, Lajtha and Marshall 1994).

Discrimination against  $\delta^{13}\text{C}$  can be expressed as:

$$\Delta = \delta_{\text{source (air)}} - \delta_{\text{plant}}$$

and does not depend on the isotopic composition of the standard and ambient air.

Diffusion of  $\text{CO}_2$  through stomata and the boundary layer account for a  $\Delta$  value of about  $4.4\text{‰}$ , rubisco discriminates at about  $27\text{‰}$ , and  $\delta^{13}\text{C}$  of the  $\text{CO}_2$  in the atmosphere is about  $8\text{‰}$  (Lajtha and Marshall 1994). Therefore, if all of the  $\text{CO}_2$  that entered the leaf was fixed,  $\delta^{13}\text{C}$  would be about  $-12\text{‰}$  ( $-8-(4.4)$ ). However, if rubisco did not fix any  $^{13}\text{C}$ ,  $\delta^{13}\text{C}$  values would be about  $-35\text{‰}$  ( $-8-(27)$ ). In reality,  $\Delta$  is a function of diffusion and enzymatic processes.

One of the most common uses of  $\delta^{13}\text{C}$  values is as an index of long-term water use efficiency (WUE) (Farquhar et al 1989, Lajtha and Marshall 1994). WUE is defined as the ratio of net photosynthesis to transpiration (A/E) and can be expressed as

$$\delta^{13}\text{C}_{\text{leaf}} = \delta^{13}\text{C}_{\text{atm}} - a - (b - a) (c_i/c_a)$$

where  $\delta^{13}\text{C}_{\text{atm}}$  is about  $-8 \text{ ‰}$ ,  $a$  is the discrimination due to diffusion ( $4.4 \text{ ‰}$ ),  $b$  is the discrimination due to carbon fixation ( $27 \text{ ‰}$ ), and  $c_i/c_a$  is the ratio of intercellular and ambient concentration of  $\text{CO}_2$  (Lajtha and Marshall 1994). WUE is related to  $c_i$  as:

$$\text{WUE} = A/E = (c_a - c_i) / (1.6(\text{VPD}))$$

Therefore, assuming constant VPD (kPa), WUE varies with  $c_i$  as does  $\delta^{13}\text{C}_{\text{leaf}}$ . For example, when stomata are closed, water loss and  $c_i$  are reduced, which increases WUE and results in less discrimination of  $^{13}\text{C}$  (more positive values of  $\delta^{13}\text{C}$ ).

#### Xylem Hydraulic Conductivity:

Water transport through plants takes place in xylem of roots, stems, and leaves and is driven by a gradient in  $\Psi$  between the root and atmosphere. This relationship is described by

$$J = K(\Psi_{\text{root}} - \Psi_{\text{leaf}})$$

Where  $J$  is the water flux through the plant,  $K$  is the conductance of water through the plant, and  $(\Psi_{\text{root}} - \Psi_{\text{leaf}})$  is the difference in water potential between the root and leaf. This relationship ignores capacitance, i.e., the storage and release of water by plant tissues; therefore, it is most applicable at the twig level where water storage is small (Tyree and Ewers 1991). Because in woody plants most of the pressure difference occurs in small twigs (Gartner 1995), it is important to consider the hydraulic conductivity at the twig level. The hydraulic conductivity ( $k_h$ ) is given by

$$k_h = J / (d\Psi/dx),$$

Where  $(d\Psi/dx)$  represents the pressure difference across a twig segment of a given length. Because  $k_h$  increases with twig diameter, it is necessary to scale it by the cross-sectional area of the active xylem, yielding the specific conductivity ( $k_s$ ) and a measure of water transport efficiency per unit xylem area that can be compared among twigs.

Normalizing  $k_h$  by the leaf area supported by the twig segment yields the leaf-specific conductivity ( $k_l$ ), a measure of sufficiency of the twig to supply water to the leaves downstream (Tyree and Zimmerman 2002). In addition, the relationship between the xylem cross-sectional area and the leaf area supplied by twigs (Huber value) can be calculated from size measurements alone, and may be informative when comparing species (Tyree and Zimmerman 2002). Assuming that all xylem is conductive, the relationship between the Huber value,  $k_s$ , and  $k_l$  is given by

$$k_l = \text{Huber Value } k_s$$

These xylem hydraulic attributes vary among and within plants and have been used in many studies to compare one species growing in different conditions, different species growing in different conditions, and different species growing under the same conditions. In general,  $k_l$  and  $k_s$  of twigs are smaller for conifers than angiosperms (Tyree and Zimmerman 2002). In the Pacific Northwest, these xylem attributes have been studied in *P. menziesii* (Spicer and Gartner 1998a, Spicer and Gartner 1998b, Kavanagh et al 1999, Bond and Kavanagh 1999), *Pinus ponderosa* (Hubbard et al 1999, Hubbard et al 2002, Stout and Sala 2003), *Tsuga heterophylla* (Meinzer et al 2004), *Rhododendron macrophyllum* (Cordero and Nilsen 2002) and *Q. garryana* (Phillips et al 2003). In general, conductivity or conductance is related to stomatal conductance or photosynthetic

ability (Hubbard et al 1999, Hubbard et al 2001, Stout and Sala 2003). Xylem hydraulic attributes have also been studied in many other species from contrasting habits. For example, Cavender-Bares and Holbrook (2001) studied the hydraulic properties of 17 oaks from Florida, Stratton et al (2000) examined 6 Hawaiian forest species, Santiago et al (2004) measured xylem conductivity in 20 Panamanian forest trees, Poudyal et al (2004) studied 5 Himalayan tree species while Gorkoti et al (2000) and others (unpublished) examined 11 Himalayan species. In general, these studies also concluded that conductivity was related to soil moisture status, transpiration, and CO<sub>2</sub> assimilation rates. Despite the correlation between xylem conductivity and many physiological attributes and numerous comparative studies in other habitats, comparisons among a wide variety of species in a single location in the Pacific Northwest are virtually non-existent.

#### Relationships of Water Relations Traits to Plant Adaptations:

Because water transport is related to the hydraulic conductivity (ignoring water storage) and the pressure gradient, species with high hydraulic conductivity can maintain high  $g_w$  without increasing the pressure gradient from soil to leaf (i.e., mid-day bulk leaf water potentials may stay high enough so that stomata remain open and photosynthesis can continue). Conversely,  $g_w$  may be lower in species with low hydraulic conductivity. Therefore, patterns among pre-dawn and mid-day water potential, leaf conductance, and xylem conductivity attributes should differ for plants adapted to different growing conditions. Different patterns, or suites, of water relations attributes have been described for a variety of co-occurring species adapted to different conditions. There is much evidence that drought resistant species achieve lower  $\Psi_s$  and higher tissue elasticity than less tolerant species (Lambers et al 1998); however, this pattern does not always hold.

For example, dry site *Quercus* species had lower osmotic potentials, lower elasticity and higher leaf conductance than did the moist site species *Acer saccharum*, and *Cornus florida* in a central Missouri oak-hickory forest (Bahari et al 1985). Sala and Tenhunen (1994) found that *Q. ilex* at a dry site experienced lower  $\Psi_{pd}$ , lower  $g_w$ ,  $\Psi_{sf}$ ,  $\Psi_{sz}$  and lower tissue elasticity during mid-summer than trees of the same species in a wetter environment. *P. ponderosa* had lower  $\Psi_s$  and lower elasticity than *P. menziesii* (Jackson and Spomer 1979). Adaptation for many tree species also occurs seasonally by reducing osmotic potential during dry periods (Cline and Campbell 1976, Tyree et al 1978, Jackson and Spomer 1979, Roberts et al 1980, Lassoie et al 1985).

In the Pacific northwest, the vegetation is primarily made up of conifers, atypical of other northern temperate regions of the world (Franklin and Waring 1979). The three significant reasons for the dominance of conifers are that they can perform photosynthesis during wet, cool times of the year, the hot, dry season limits photosynthesis for deciduous species, and conifers have high nutrient use efficiency (Lassoie et al 1985). In general, stomata of conifers open rapidly with increasing light levels, but have lower stomatal conductance than deciduous trees at similar levels of VPD (Franklin and Waring 1979, Lassoie et al 1985). Substantial osmotic adjustment has been documented for many conifers in the northwest and may partially explain successional and distribution patterns among forest trees (Lassoie et al 1985, Smith 1985).

#### Wood Density:

Density of sapwood ranges from  $<0.2 \text{ g/cm}^{-3}$  in balsa to  $>1.0 \text{ g/cm}^{-3}$  in ebony and appears to be important in water relations. The density is a function of the size and number of different kinds of cells (Panshin and de Zeeuw 1980). Fibers are particularly

important because of their small cross section and variation in cell wall thickness (Panshin and de Zeeuw 1980). For example, woods with thin-walled and large diameter fibers have low wood density. Density is related to the specific gravity and the two are equal for oven-dry wood. The strength and stiffness of wood increases with increasing specific gravity (Haygreen and Bowyer 1996). Wood density varies within a species due to many environmental and topographic factors (Haygreen and Bowyer 1996). Wood density is also a good predictor of water transport properties in the stems of trees. Hacke et al (2001) showed that the xylem tension required to produce a 50% loss of specific conductivity by cavitation increased with wood density and was different for conifers and angiosperms. For a given wood density, conifers required more negative xylem tensions than angiosperm species to cause a 50 % loss of conductivity, providing evidence that conifers are inherently more resistant to reduction in conductivity from water stress.

#### Functional Convergence:

Enormous variation of osmotic potential, tissue elasticity, stomatal conductance, xylem transport properties, and wood density has been reported for tree species from different habitats. This variation is thought to represent adaptation to a variety of environmental conditions. Historically, species or groups of species have been grouped by a particular combination or “suite” of characteristics. Little attention has been given to the identification of relationships among leaf level, xylem transport properties, and wood density that covary in a similar manner across species. However, if similar combinations of characteristics occur in unrelated species in adaptation to similar environmental conditions, it would indicate that water relations are constrained to converge into common relationships. Because many water relations attributes are linked

physiologically to one another, relationships among different species should converge into functional relationships, with individual species operating over distinct ranges along a common relationship. However, the recognition of functional convergence in plants has long been obscured because physiological and morphological measurements, which are usually taken at the plant organ scale, are thought to represent whole-plant properties (Meinzer 2003). The recognition of unifying relationships among water relations characteristics serves to highlight trade-offs that determine the species specific “suites” or strategies of water relations characteristics among a wide range of plant species.

Wood density is related to a wide range of water relations attributes, including stem water storage capacity, xylem hydraulic properties (Huber value,  $k_s$ ,  $k_l$ ), leaf  $\Psi$ ,  $g_w$ , and osmotic potential across taxonomically and morphologically diverse species (Stratton et al 2000, Meinzer 2003, Gartner and Meinzer 2004, Bucci et al 2004, Santiago et al 2004). For example, wood density was related to  $\Psi_{md}$ ,  $k_s$  and  $k_l$ , leaf:sapwood area ratio, stomatal conductance, specific leaf area, and  $\Psi_{sf}$  for six Brazilian savanna woody species (Bucci et al 2004). Increasing wood density was associated with increasing  $\Delta\Psi$  for 21 mostly tropical trees (Meinzer 2003) and decreasing  $\Psi_{sz}$  for 12 Hawaiian dry forest, Sonoran desert, North Carolina piedmont, and tropical species (Gartner and Meinzer 2004). For 20 Panamanian species, increasing wood density was associated with decreasing saturated water content, minimum  $\Psi$ ,  $CO_2$  assimilation rate,  $k_l$  (Santiago et al 2004) and in Hawaii, higher wood density predicted decreasing saturated water content,  $k_s$ , and  $k_l$  (Stratton et al 2000). In general, these studies indicate the convergence of leaf level characteristics, transport properties, and wood density. These relationships suggest



that certain traits, such as wood density, act to confine the range of other water relations traits, such as water transport.

Aside from relationships with wood density, other water relations traits are also interrelated and appear to covary in similar ways. For example, minimum annual  $\Psi$  was related to  $\Psi_{sz}$  and  $k_l$  was related to hydraulic efficiency, minimum annual  $\Psi$  and  $\Delta\Psi$  for 6 evergreen Hawaiian species (Stratton et al 2000). Increasing  $k_l$  was associated with increasing whole plant conductance for Brazilian species (Bucci et al 2004) and increasing  $g_w$  and  $CO_2$  assimilation rates in Panamanian species (Santiago et al 2004). These studies imply that species with large  $k_l$  experience low  $\Delta\Psi$ , high minimum  $\Psi$ , increased maximum  $g_w$ , and that species with high minimum  $\Psi_{md}$  experience high  $\Psi_{sz}$ .

Although the studies above outline convergence of water relations traits in many species in diverse habitats, in almost all cases the species studied are diffuse-porous angiosperms. There is little study for temperate North American tree species. More research is needed to determine if water relations attributes in North American tree species and conifers follow similar convergence patterns as tropical species.

This study presents water relations characteristics for several conifer and angiosperm species that co-occur but have different drought resistance and seeks to learn how species-specific “suites” of characteristics may contribute to adaptation and successional patterns in the Willamette valley of Oregon. This study also provides evidence that water transport properties, wood density and leaf level traits co-vary for woody species in western Oregon.

## CHAPTER TWO: MATERIALS AND METHODS

This study took place over a two-year period from spring 2002 to fall 2003, using eight species of woody plants on clear-cut, forested, meadow and creek-bottom sites in western Oregon.

### **Species:**

The eight study species were selected to represent the diversity and range of drought tolerance of woody plants in western Oregon. The species studied were the broad leaf evergreen *Arbutus menziesii* Pursh (Pacific Madrone, Ericaceae); the deciduous *Quercus garryana* Dougl. (Oregon White Oak, Fagaceae), *Corylus cornuta* Marsh. (Hazel, Betulaceae), *Acer macrophyllum* Pursh (Big Leaf Maple, Aceraceae), and *Fraxinus latifolia* Benth. (Oregon Ash, Oleaceae); and the evergreen conifers *Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii* (Douglas-fir, Pinaceae), *Abies grandis* (Dougl.) Forbes (Grand Fir, Pinaceae), and *Pinus ponderosa* Dougl. (Ponderosa Pine, Pinaceae). Nomenclature follows Hitchcock and Cronquist (1973). I sampled five trees of each species at each site where it was sampled. Trees were selected so that all individuals within a species at each site were of similar size and age, and experienced similar environmental conditions (Table 2.1).

Table 2.1. Mean age for each species on each site. The clear-cut and forest sites were used during year 1 and the meadow and creek bottom sites during year 2.

Site	Species	Mean Age (years)
Clear-Cut	<i>A. menziesii</i>	ND <sup>x</sup>
	<i>Q. garryana</i>	Sprouted from stumps <sup>y</sup>
	<i>P. menziesii</i>	10
	<i>P. ponderosa</i>	9
Forest	<i>A. macrophyllum</i>	ND
	<i>C. cornuta</i>	Multiple stems <sup>z</sup>
	<i>A. grandis</i>	17
Meadow	<i>Q. garryana</i>	32
	<i>A. macrophyllum</i>	23
	<i>P. menziesii</i>	13
Creek Bottom	<i>Q. garryana</i>	20
	<i>F. latifolia</i>	33

<sup>x</sup> ND= no data

<sup>y</sup> these trees sprouted from stumps of trees cut during clear-cutting

<sup>z</sup> this species does not form a single stem; rather, it has a multiple stem shrub habit.

The geographic distribution varies greatly among the species studied. The range of *Q. garryana* spans from Vancouver Island in Canada south nearly to Los Angeles County, California, in a narrow band beginning about 50 km and ending about 100 km from the Pacific Ocean in Oregon (Stein 1990). *Q. garryana* grows on a variety of sites ranging from sea level to 1160 m but is most common on droughty sites with full exposure. However, *Q. garryana* can also grow in very wet areas such as flood plains. The distribution of *A. menziesii* ranges from Vancouver Island, Canada, south to San Diego County, California, and east from the Pacific coast to the eastern slopes of the Cascade Range (McDonald and Tappeiner 1990). *A. menziesii* grows on a variety of sites from near sea level to 915 m elevation in northwestern Oregon and seems to be most abundant on soils with good internal drainage and low moisture retention during summer. The distribution of *F. latifolia* is nearly the same as that of *A. menziesii*, but *F. latifolia* occupies habitats with poorly drained soils (Owston 1990). The distribution of *A.*

*macrophyllum* runs in a 150 km wide band inland from the Pacific Ocean and from Port Hardy on Vancouver Island, Canada, south to within 16 km of San Francisco Bay, California (Minore and Zasada 1990). In Oregon, *A. macrophyllum* grows from moist creek bottom sites to dry hillsides as an understory tree or in full exposure, from sea level to approximately 350 m elevation. *C. cornuta* is widespread at low elevations as an understory shrub on well drained soil from British Columbia south to California and east to western Montana (Hitchcock and Cronquist 1973). In Oregon, *C. cornuta* occurs mainly west of the Cascade Mountains (Peck 1941). The distributions of *A. grandis* and *P. menziesii* are very similar over a wide range of conditions and soils; they include much of western Oregon and Washington north into Canada and the northern half of Idaho and western Montana (Foiles et al 1990, Hermann and Lavender 1990). Although these species have a similar geographic range, *P. menziesii* grows in extensive pure stands over much of its range while *A. grandis* is a dominant species over little of its range (Foiles et al 1990, Hermann and Lavender 1990). At our sites, *A. grandis* does not establish in full sun while *P. menziesii* does. The distribution of *P. ponderosa* covers much of the drier parts of Oregon, Washington, Idaho, Montana and California (Oliver and Ryker 1990). *P. ponderosa* historically grew in the Willamette Valley of Oregon, but probably not in the study area.

In the Willamette valley, some of these species are involved in common successional patterns. *Q. garryana* often invades into open meadows, providing a favorable environment for the establishment of *P. menziesii* (Franklin and Dyrness 1973). *P. menziesii* stands may be replaced by the shade-tolerant *A. grandis* and *A. macrophyllum*.

**Study Periods and Water Relations Characters:**

This study was conducted in four sites. Trees in the clear-cut and forest sites were studied from July 2002 to April 2003. Trees in the meadow and creek-bottom were studied from June 2003 to August 2003. The aim of the first year was to quantify the full range of water relations characteristics. During the first year, sampling was conducted during the early (early July, 2002), mid- (mid-August, 2002) and late summer (mid-September, 2002), winter (late December, 2002), and spring (March/April, 2003). The sampling periods lasted less than two weeks except for the spring sampling, which was split into two periods four weeks apart. During the first summer, I measured pre-dawn ( $\Psi_{pd}$ ) and mid-day ( $\Psi_{md}$ ) water potential, stomatal conductance ( $g_w$ ) in the morning and afternoon, pressure-volume (P-V) curves, and xylem conductivity attributes (the Huber Value, specific conductivity [ $k_s$ ], and leaf-specific conductivity [ $k_l$ ]) on all species. During the winter and spring sampling, I measured the previous water relations characteristics except for the Huber value,  $k_l$ ,  $g_w$ , and P-V curves for the deciduous species. During the second summer, sampling took place during the early (mid-June, 2003) and mid-summer (mid-August, 2003) and I measured all characteristics on all species, but the Huber value,  $k_s$ , and  $k_l$  and  $g_w$  were measured two weeks after P-V curves were determined during the mid-summer sampling period.  $\delta^{13}C$  for all trees was determined from tissue removed in late summer sampling in the clear-cut and forest sites.

During the second summer, I sampled *Q. garryana* at two new sites to compare data with the *Q. garryana* trees that had sprouted from stumps in the clear-cut site and to compare non-sprouted *Q. garryana* to naturally establishing *P. menziesii* in the meadow. I also compared *Q. garryana* with *F. latifolia* (both ring-porous species that often occupy

different microenvironments) with *A. macrophyllum*. I sampled *A. macrophyllum* growing in full exposure, so that direct comparisons could be made for this species growing in the forest and in the open. Finally, *P. menziesii* was selected to represent conifers in the different locations.

### **The Study Area:**

The four study sites (Table 2.2) were located within 2 km of each other in the McDonald-Dunn Research Forest 10 km N of Corvallis, Oregon. The McDonald-Dunn Research Forest is managed by Oregon State University's College of Forestry and consists of about 4452 ha of forested land in the foothills along the western edge of the Willamette Valley. The forest site was located just outside the eastern boundary of the Research Forest; the clear-cut site was adjacent to the forest site and had been burned and planted with *P. menziesii* and *P. ponderosa* about 10 years previously. The meadow and creek-bottom were located about 2 km south of the other sites. The forest, clear-cut, and creek bottom sites support vegetation representing the *Abies grandis/Rubus ursinus-Rhus diversiloba* plant association (ABGR/RUUR-RHDI) (Hubbard 1991). This association has a high coverage of *Rhus diversiloba* and *Rubus ursinus* and is considered very species rich (Hubbard 1991). This association occurs in the mesic to dry environments in the forest and may contain many dry-site species (Leavell 1991, Hubbard 1991). The meadow site is very open with *P. menziesii*, *A. macrophyllum*, and *Q. garryana* invading from the adjacent forest.

Table 2.2. Location, slope, aspect, and elevation of the four sites used during this study.

Site	NAD 27 State Plan Coordinates		Slope (°)	Aspect (°)	Elevation (m)
	North	East			
Clear-Cut	1273595	363420	40	187	333
Forest	1273785	363559	20	150	305
Meadow	1272563	358608	20	157	153
Creek Bottom	1273528	357725	10	2	137

Soils at the clear-cut, meadow, and creek bottom sites are classified as Witzel, Philomath, and Dupee types, respectively (Soil Type, McDonald-Dunn Forest, 2001). Witzel and Philomath series consist of shallow, well-drained soils, while Dupee soils are deep, moderately well drained soils in swales and depressions (Knezevich 1975). The soils of the forest site are in the Ritner-Price complex series (Knezevich 1975). The Ritner-Price series consists of moderately deep, well-drained soils located in the foothills (Knezevich 1975).

#### **Climate During the Study:**

Twenty-year mean monthly maximum temperature ranges from 7 °C to 27 °C at the Corvallis OSU Hyslop Farm weather station, located about 6 km east (44 ° 38' N, 123 ° 12' W) of the study sites at 69 m elevation. Mean annual precipitation at the Hyslop Farm is 108.5 cm, with a dry season from June through September. During 2002 and 2003, annual precipitation was 110.4 and 119.0 cm, respectively; however, the summer months were drier and warmer than the 20-year mean for both years (Figure 2.1, 2.2). In both years, the lowest average monthly minimum air temperature occurred

during January and December of 2002 and December 2003 and the highest average monthly maximum air temperature occurred during July (Figure 2.1).

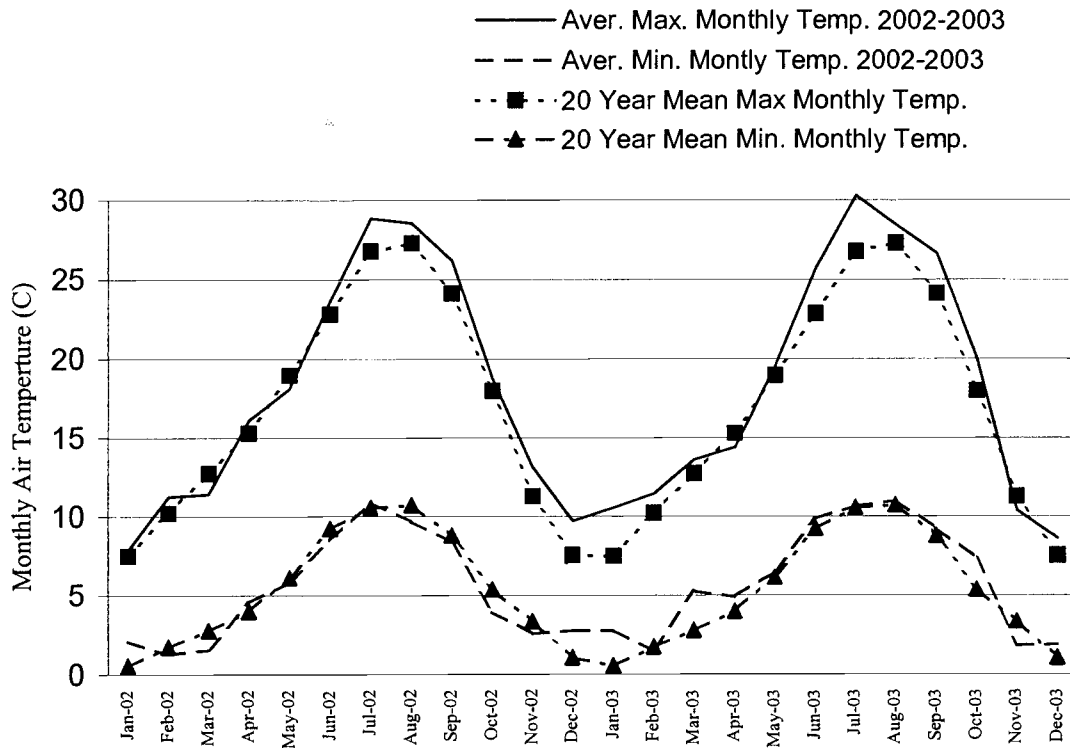


Figure 2.1. Mean monthly maximum and minimum temperature during 2002-2003 (lines) and long-term average maximum and minimum monthly temperatures (lines with symbols) at the Corvallis OSU Hyslop Farm weather station about 6 km East of the study sites.



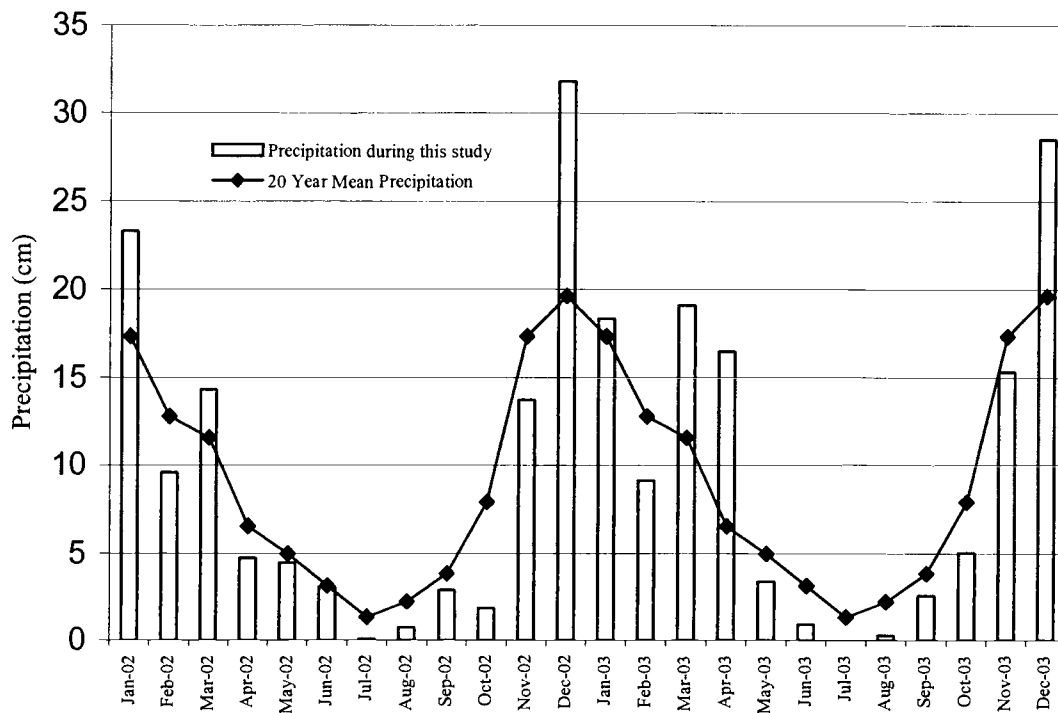


Figure 2.2. Precipitation during 2002-2003 (bars) and the 20-year mean precipitation (line with symbols) at the Corvallis OSU Hyslop Farm weather station.

### Methods Used to Determine Water Relations Characteristics:

#### Plant Water Potential:

I used a pressure chamber (Model 1000, PMS Instruments, Corvallis, OR, 4.0 MPa maximum) to measure  $\Psi_{pd}$  and  $\Psi_{md}$  and for the development of the P-V curves.  $\Psi_{pd}$  and  $\Psi_{md}$  were measured on all trees on the same day within sites currently under study. On days when  $\Psi_{pd}$  and  $\Psi_{md}$  were measured, I calculated the diurnal change in  $\Psi$  ( $\Delta\Psi$ ) as the difference between  $\Psi_{pd}$  and  $\Psi_{md}$ . Samples for  $\Psi_{pd}$  measurements were taken from the north side of each tree, while samples for  $\Psi_{md}$  measurement were taken from branches on the south sides of trees in full sunlight, where sunlit branches were

available. Samples for  $\Psi_{pd}$  and  $\Psi_{md}$  usually contained current and one previous year's growth. I did not measure water potential on leafless twigs during winter.

Stomatal Conductance:

In general, I measured stomatal conductance on the broad leaf species on the same days that I measured  $\Psi_{pd}$  and  $\Psi_{md}$ , using a LI-COR Model 1600 steady state porometer fitted with a 2 cm<sup>2</sup> aperture (LI-COR, Lincoln, Nebraska). I followed the manufacturer's procedures closely, which included using thoroughly dried dessicant and setting the atmospheric pressure for the elevation. With each reading, I also recorded photosynthetically active radiation (PAR), relative humidity, leaf temperature, and cuvette temperature. These parameters were measured between 900 and 1100 hours and between 1200 and 1600 on 3 leaves of each tree. I measured only leaves that were receiving maximum sunlight. I calculated  $g_w$  (cm sec<sup>-1</sup>) for morning ( $g_wAM$ ) and afternoon ( $g_wPM$ ) from the reciprocal of leaf resistance and transformed the units to mmol m<sup>-2</sup> s<sup>-1</sup> by using the following formula:

$$g_w (\text{mmol m}^{-1} \text{ s}^{-2}) = 1000 \times g_w (\text{cm s}^{-1}) \times 0.446 \times (273 / (T + 273)) \times (P / 101.3)$$

where  $g_w$  (cm s<sup>-1</sup>) is the leaf conductance, T is the air temperature (°C), and P is the atmospheric pressure (kPa) (Percy et al 1989). The mean for each tree was calculated from the three or four leaf values.

Vapor pressure deficit (VPD) was calculated for each measurement based on the following formula

(<http://lawr.ucdavis.edu/coopextn/biometeorology/biomet/VPD/vpd.htm>, March 6, 2005):

$$\text{VPD(kPa)} = 0.6108e^{(17.27 \cdot T/T + 237.3)} - \{ \text{RH}/100 \times 0.6108e^{(17.27 \cdot T/T + 237.3)} \}$$

where T is the leaf temperature (C) and RH in the relative humidity (%). The mean for each tree was then calculated and all relationships used tree mean values. The soil/leaf hydraulic efficiency was calculated for early, mid-, and late summer for angiosperms in the clear-cut and forest and for early and mid-summer for the angiosperms in the meadow and creek-bottom. The soil/leaf hydraulic efficiency is  $g_w \text{PM}/\Delta\Psi$  and represents the whole-plant hydraulic conductance (Meinzer et al 1990).

#### Leaf Osmotic Potential, Elasticity, and Relative Water Content:

I derived P-V curves and calculated tissue water relations characteristics for the evergreen species during each sampling session, but for the deciduous species only when leaves were present. I collected and analyzed samples from one site at a time. For example, I collected samples from the forested site one afternoon, and processed these samples the second day; then I collected samples from the clear-cut the second afternoon, and ran the remaining samples the third day. On a few occasions, I was not able to collect samples on the second day because the processing time exceeded 12 hours or the required measuring frequency would not allow my absence to collect samples. In these cases, I would collect samples from the second site on the third day and process them on the fourth day.

I employed the free transpiration method (Pallardy et al 1991). Briefly, I secured a clear plastic bag around the sample before cutting it from the tree. Samples were re-cut under water and left to rehydrate overnight. The next morning, I randomly selected one sample from the species that would require the longest time to complete the curve.

Depending on the species, the development of a P-V curve took from 8 hours (A.

*macrophyllum*) to as much as 30 hours (*P. ponderosa*). A linear regression line through the first 4 or 5 balance pressure readings and sample masses was used to obtain the precise initial mass of the turgid sample. Curves were checked for plateaus and corrected if necessary. This resulted in an initial weight that was used to calculate the following water-relations characteristics: osmotic potential at zero ( $\Psi_{sz}$ ) and full ( $\Psi_{sf}$ ) turgor. The index of elasticity (IE) was calculated as the slope of a linear regression of all non-zero values of pressure potential over relative water content (RWC). RWC at zero turgor ( $RWC_z$ ) was defined by solving the equation of this line for the inverse of balance pressure equal to zero.

$\delta^{13}\text{C}$  and % N Concentration:

Nitrogen concentration and  $\delta^{13}\text{C}$  were determined on leaves from P-V curve samples taken from the forested and clear-cut sites in late summer 2002. Samples were dried at 70 C for 48 hours and stored in closed paper envelopes until processing in early January 2003. A small sample of tissue was taken from the current year's foliage (on deciduous species, a random sample of tissue was taken from the collection) and was ground to a fine consistency by shaking the sample in an epitube with 3 mm glass beads. This procedure worked well on all species and samples except *P. ponderosa*, which did not pulverize effectively. I requested that *P. ponderosa* samples be ground by the isotope laboratory. Samples were then sent to the Idaho Stable Isotopes Laboratory for % N composition and  $^{13}\text{C}$  isotope analysis (Department of Forest Resources, College of Natural Resources, University of Idaho, Moscow, ID).

### Xylem conductivity:

#### *Collection and Storage:*

Samples for twig xylem conductivity attributes were collected from trees when other water relations attributes were measured. I used these twigs to determine Huber Value (cross-sectional xylem area/leaf area), leaf-specific conductivity ( $k_l$ ) ( $k_h$ /leaf area), and specific conductivity ( $k_s$ ) ( $k_h$ /active xylem cross-sectional area) of the twig xylem. In order to reduce xylem embolism, long branches were cut from the south side of trees and quickly put into a sealed black plastic bag. I collected twigs from all trees in the forested and clear-cut sites in one trip; however, branches were collected and processed from the meadow and creek-bottom sites separately. Twigs were quickly transferred to a large tub of cold tap water and transported to the laboratory. Twigs were stored in room temperature tap water for no longer than four days before being processed.

#### *Hydraulic Conductivity Measurement:*

I determined hydraulic conductivity ( $k_h$ ) according to Sperry et al (1988). No effort was made to remove emboli; therefore, this method measures native conductivity. Leafless stem segments were cut from the middle of branches, leaves distal to the stem segment were stored (for conifers, one half of the needles on the segment were included in the leaf sample), and segments were attached to an apparatus designed to measure  $k_h$  under approximately a  $8.0 \times 10^{-3}$  MPa pressure gradient. The flow rate was measured using filtered ( $0.22 \mu\text{m}$ ) 0.5% oxalic acid for all species for several one-minute periods and the mean flow rate was used to calculate  $k_h$ . Once the measurement of flow rate was completed, I removed the sample from the apparatus and measured the diameter of the xylem and the pith on both ends along two perpendicular axes. With these

measurements, I calculated an average xylem area for each twig and calculated  $k_h$ .

Samples were then stored in water until staining.

*Xylem Staining:*

Samples were attached to an apparatus similar to the one used to measure the flow rate that was equipped with branching tubes to allow simultaneous staining of up to 15 samples. After samples were attached, a solution of filtered (0.22  $\mu\text{m}$ ) 0.1% safranin O was passed through the samples until it appeared that xylem was completely stained (8-10 hours in conifers, 3-4 hours for angiosperms). Once staining was complete, the sample was dried at room temperature and transverse sections were examined to determine the percentage of xylem cross-section at the middle of the sample that was stained. I used this percentage to calculate the effective xylem area for each twig.

*Leaf Area:*

Leaf area was determined using two methods. For the angiosperms, I used a LI-COR Model 3100 leaf area meter (LI-COR, Lincoln, NE). However, a test using pieces of paper cut to similar dimensions as conifer needles showed that the LI-COR 3100 leaf area meter was not accurate for needles. To determine the projected area of conifer needles, I employed ImageJ software (National Institutes of Health, NIH, downloaded from <http://rsbweb.nih.gov/ij/>, July 1, 2002) to analyze images scanned with a Scanmaker 4800 scanner (Microtek, Carson, CA). Because these conifer samples were quite large, I measured the projected leaf area from a sub-sample (approximately 20%-30% of the total) from both the old and new needles. This sub-sample was carefully arranged on the bed of the scanner to minimize overlap and a black and white (150 dpi) digital image was captured. A simple test using small pieces of paper revealed that this procedure produced

less than 5% error. The error in assuming that projected area is close to  $\frac{1}{2}$  of total leaf area is probably small for *A. grandis* and *P. menziesii* needles, but quite large for *P. ponderosa* needles because these needles are three-sided. Therefore, I used a formula (courtesy of Barbara Bond, Oregon State University):

$$\text{Total leaf area of } P. \textit{ ponderosa} = \text{projected leaf area of } P. \textit{ ponderosa} * 2.36$$

The leaf area for *P. ponderosa* used in this study is the total leaf area, not projected area, which was used for the remaining species.

Once the sub-samples were scanned, they were carefully transferred to small paper envelopes and dried with the remainder of the sample at 70 C for 48 hours. After drying, the samples were weighed. I used the weight and projected area of the subsamples to estimate the area of the entire weighed sample.

#### Wood Density:

I determined the wood density ( $W_d$ ) on twigs that were very similar to those used for P-V curve analysis, cut from trees on all sites in early November 2003. After twigs were cut from branches, leaves were removed and the twigs were transported to the laboratory, where they were stored submerged in water. I removed the bark and used the displacement method (Haygreen and Bowyer 1996) to determine the volume of each sample. The samples were dried at 70 C for 48 hours and weighed to determine dry mass.  $W_d$  was calculated as the dry mass/volume of the wet sample twig and is expressed in  $g/cm^3$ . Although wood density is often expressed when the mass and volume are at the same moisture content, I felt that dry mass was more appropriate because this created consistency across species. No attempt was made to subtract pith volume; therefore,  $W_d$

was underestimated for species for which the pith makes up a large percentage of the cross-sectional area of the twig (*A. macrophyllum*).

Statistical Analysis:

Before statistical analysis, variables were tested for normality and transformed, if possible, to a normal distribution. Analysis of variance (ANOVA) was used to determine significance of differences among species, date, tree number, and the species x date interaction for each year's data. Means and standard errors for each water relations characteristic were calculated for each sampling date for each species. Tukey's multiple range test was used to separate significant differences for IE and  $\Psi_{sf}$  adjustment, %N,  $\delta^{13}\text{C}$ ,  $W_d$  and  $g_w$ . Multiple linear regression was used to relate VPD and light to  $g_w$ .



CHAPTER 3: RESULTS-SEASONAL TRENDS AND COMPARISONS:

**Sources of Variation of Water Relations Parameters:**

Analysis of variance (ANOVA) revealed a significant difference among species for all water relations parameters in the clear-cut, forest, and meadow sites, but often there was not a significant difference between *Q. garryana* and *F. latifolia*, the only species at the creek bottom site (Table 3.1). All parameters, except xylem conductivity attributes, usually varied significantly with sampling date (Table 3.1). Parameters seldom varied significantly among trees within species at a site; however, the species x date interaction was often significant (Table 3.1).

Table 3.1. Probability values for sources of variation in ANOVA of water relations parameters analyzed for each site involved in the study. Bold indicates p values <0.05.

Parameter	Source	Site			
		Clear-Cut	Forest	Meadow	Creek Bottom
$\Psi_{pd}^I$	Species	<0.0001	<0.0001	<0.0001	0.069
	Date	<0.0001	<0.0001	<0.0001	<0.0001
	Tree number	0.140	0.287	0.197	<b>0.033</b>
	Species x date	<0.0001	<0.0001	<0.0001	0.286
$\Psi_{md}$	Species	<0.0001	<0.0001	<b>0.0003</b>	0.083
	Date	<0.0001	<0.0001	<0.0001	<0.0001
	Tree number	0.318	<b>0.0409</b>	0.233	0.063
	Species x date	<0.0001	0.209	<0.0001	<b>0.033</b>
$\Delta\Psi$	Species	<0.0001	<0.0001	<0.0001	<b>0.007</b>
	Date	<b>0.0059</b>	<b>0.002</b>	<0.0001	<0.0001
	Tree number	0.199	0.087	0.140	<b>0.017</b>
	Species x date	<0.0001	0.067	<0.0001	<0.0001
$\Psi_{sf}$	Species	<0.0001	<b>0.0021</b>	<0.0001	<0.0001
	Date	<0.0001	0.133	<b>0.001</b>	<0.0001
	Tree number	0.820	<b>0.050</b>	0.418	0.064
	Species x date	<0.0001	0.479	<0.0001	0.682
$\Psi_{sz}$	Species	<0.0001	<0.0001	<0.0001	<0.0001
	Date	<0.0001	<0.0001	<0.0001	<0.0001
	Tree number	0.776	0.378	0.454	<b>0.036</b>
	Species x date	<0.0001	0.068	<b>0.0004</b>	0.988

Table 3.1 continued

Parameter	Source	Site			
		Clear-Cut	Forest	Meadow	Creek Bottom
IE	Species	<0.0001	<0.0001	<0.0001	<b>0.027</b>
	Date	<0.0001	<b>0.01</b>	0.969	<b>0.0003</b>
	Tree number	0.228	0.478	0.101	0.371
	Species x date	<0.0001	0.310	<b>0.001</b>	0.483
RWC <sub>z</sub>	Species	<0.0001	<0.0001	<0.0001	0.108
	Date	<b>0.007</b>	0.115	<0.0001	<b>0.033</b>
	Tree number	0.233	0.679	0.532	0.864
	Species x date	<b>0.005</b>	<0.0001	<b>0.0003</b>	0.219
Huber Value	Species	<0.0001	<b>0.005</b>	0.105	0.165
	Date	0.204	<0.0001	0.933	0.806
	Tree number	0.507	0.664	0.419	0.188
	Species x date	<b>0.012</b>	<0.0001	0.287	0.140
k <sub>s</sub>	Species	<0.0001	<0.0001	<b>0.0005</b>	<b>0.032</b>
	Date	0.168	<b>0.034</b>	0.701	0.398
	Tree number	0.161	0.467	0.697	<b>0.037</b>
	Species x date	0.184	<b>0.048</b>	0.840	0.069
k <sub>l</sub>	Species	<0.0001	<b>0.0024</b>	<b>0.009</b>	0.169
	Date	0.795	<b>0.0002</b>	0.372	0.899
	Tree number	0.265	0.776	0.566	0.947
	Species x date	0.882	<b>0.0011</b>	0.569	0.866

<sup>1</sup>Symbols:  $\Psi_{pd}$ , pre-dawn water potential;  $\Psi_{md}$ , mid-day water potential;  $\Delta\Psi$ , diurnal change in water potential;  $\Psi_{sf}$ , osmotic potential at full turgor;  $\Psi_{sz}$ , osmotic potential at zero turgor; IE, Index of elasticity; RWC<sub>z</sub>, relative water content at zero turgor; Huber, the Huber value; k<sub>s</sub>, specific xylem conductivity; k<sub>l</sub>, leaf-specific xylem conductivity.

### Water Relations Characteristics:

#### Plant Water Potential:

Tree  $\Psi_{pd}$  varied significantly with species, date of sampling and the species x date interaction for the clear-cut, forest, and meadow sites and only for date and tree number at the creek bottom site (Table 3.1). Tree  $\Psi_{md}$  varied with species, date, and the species x date interaction at the clear-cut and meadow sites; with species, date and tree number at the forest site; and with date and the species x date interaction at the creek bottom site (Table 3.1).  $\Psi_{pd}$  was highest for all species during the spring followed by

early summer (Figure 3.1A).  $\Psi_{md}$  was, in general, highest during the early summer and lowest during the mid- and late summer for all species (Figure 3.1B). Both  $\Psi_{pd}$  and  $\Psi_{md}$  decreased throughout the summer for all species, and increased throughout the winter and spring for those species sampled (Figure 3.1A, B).  $\Psi_{pd}$  was  $< -1.0$  MPa during the mid- and later summer for the evergreens; for other sampling times and species,  $\Psi_{pd}$  was  $\geq -1.0$  MPa, indicating little water stress (Figure 3.1A). During mid- and later summer,  $\Psi_{pd}$  was lower for the evergreens than for the deciduous angiosperms (Figure 3.1A). However, the pattern differed for  $\Psi_{md}$  (Figure 3.1B). During mid- and late summer,  $\Psi_{md}$  was highest for angiosperms in the forested site and *F. latifolia*, intermediate for the conifers, and lowest for *Q. garryana* (Figure 3.1B).

The diurnal change in tree water potential ( $\Delta\Psi = \Psi_{pd} - \Psi_{md}$ ) was calculated during early, mid- and later summer.  $\Delta\Psi$  varied significantly with species and date and for the species x date interaction at the clear-cut and meadow sites; with species and date at the forest site; and with all sources at the creek bottom site (Table 3.1).  $\Delta\Psi$  was greatest for *P. menziesii* and *P. ponderosa* during early summer and decreased throughout the summer; however, it did not change for *A. grandis* during the summer. For the angiosperms,  $\Delta\Psi$  was lowest during early summer, increased to mid-summer and decreased slightly during late summer; but did not change for *A. macrophyllum* in the meadow between early and mid-summer (Figure 3.1C).

Figure 3.1. Mean values of  $\Psi_{pd}$  (A),  $\Psi_{md}$  (B) and  $\Delta\Psi$  (C) for conifers (left) and angiosperms (right) at all four sites and all dates of sampling. Error bars are one standard error of the mean for each species for each sampling date.

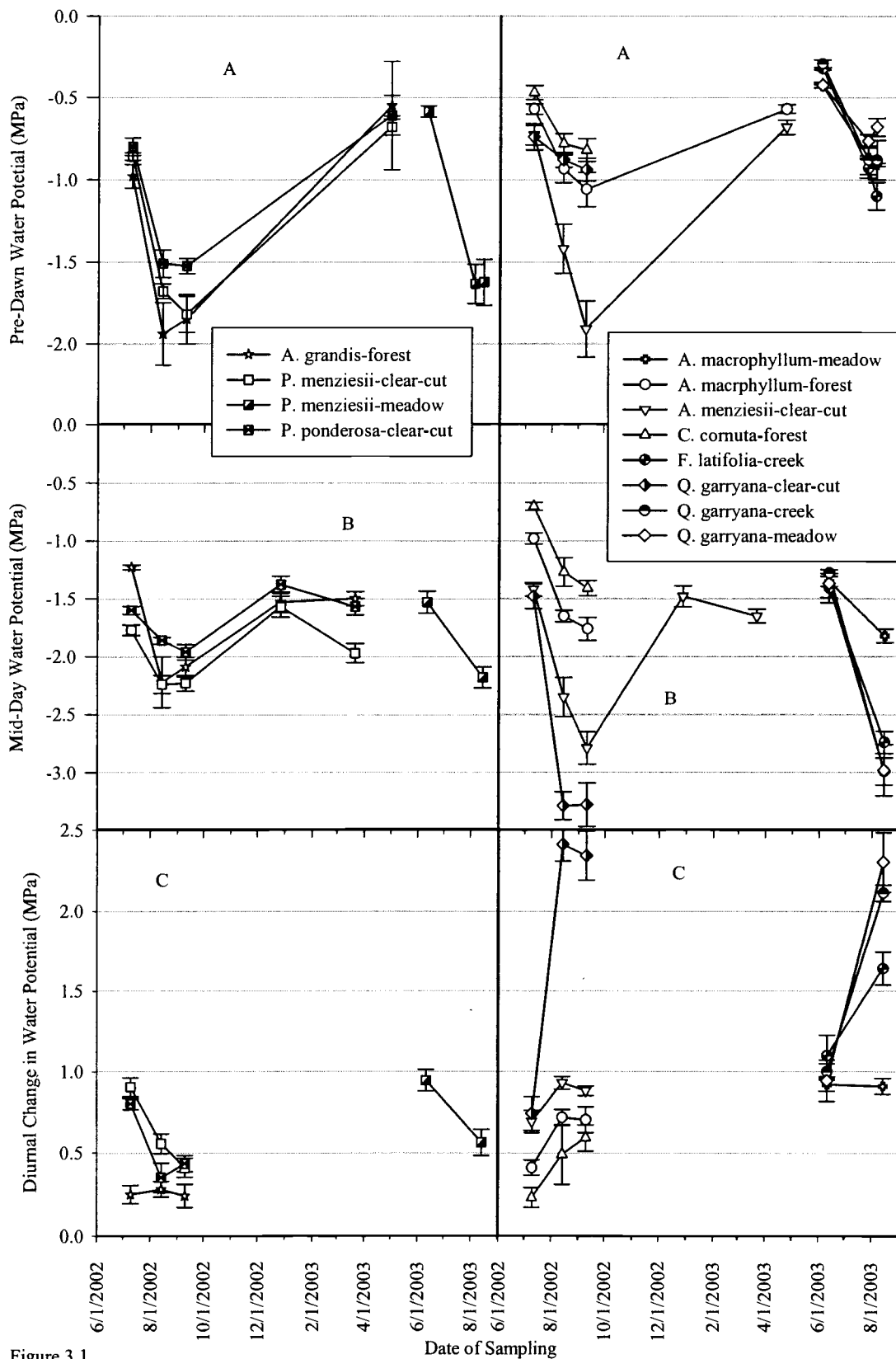


Figure 3.1

### Stomatal Conductance:

Mean values of angiosperm leaf conductance ( $g_w$ ) ranged from  $12 \text{ mmol m}^{-2} \text{ sec}^{-1}$  for *A. menziesii* in the clear-cut during the afternoon in the late summer to  $510 \text{ mmol m}^{-2} \text{ sec}^{-1}$  for *Q. garryana* in the meadow during the afternoon in mid-summer (Figure 3.2). Mean  $g_w$  decreased for all species throughout the summer, except for the oak, for which it was lower in mid-summer than early or late summer and for *C. cornuta*, for which mean  $g_{wAM}$  was higher in late summer than mid-summer (Figure 3.2). Mean  $g_{wPM}$  was higher in the spring for *A. menziesii* than for any other sampling date (Figure 3.2). In general, mean  $g_w$  was highest for the oak and *F. latifolia*, intermediate for *A. menziesii* and *A. macrophyllum* in the meadow, and lowest for the remaining species (Figure 3.2). Mean  $g_{wPM}$  was lower than mean  $g_{wAM}$  for *A. macrophyllum*, *C. cornuta*, and *A. menziesii*; however, it was higher for *Q. garryana* and *F. latifolia* (Figure 3.2).

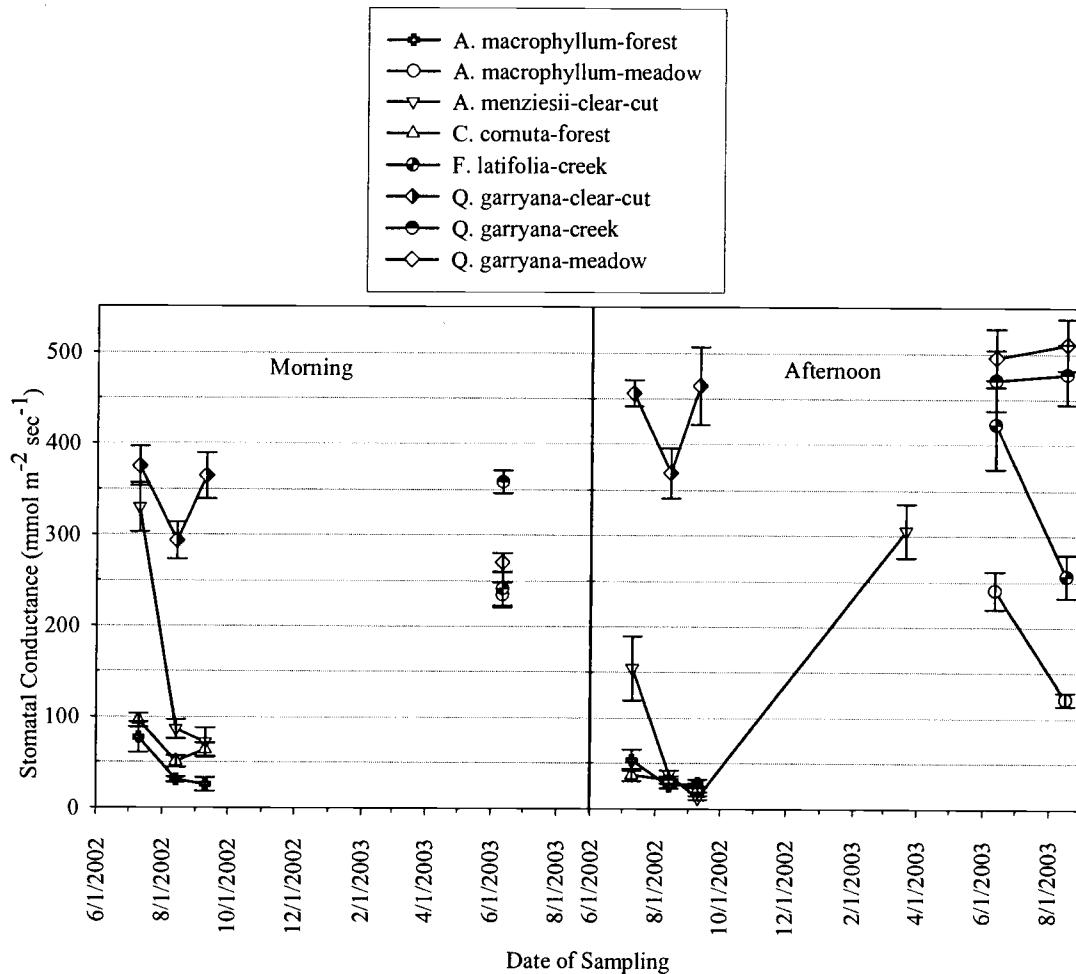


Figure 3.2. Mean values of  $g_w$  for morning ( $g_{wAM}$ ) and afternoon ( $g_{wPM}$ ) of angiosperms at all four sites. Error bars are one standard error of the mean for each species for each sampling date.

#### Shoot Osmotic Potential, Index of Elasticity, and Relative Water Content:

$\Psi_{sf}$  and  $\Psi_{sz}$  varied significantly with species, date, and the species x date interaction at the clear-cut and meadow sites (Table 3.1).  $\Psi_{sf}$  varied significantly with species and tree number at the forest site and with species and date at the creek bottom site (Table 3.1).  $\Psi_{sz}$  varied with species and date at the forest site and with species, date and the species x date interaction at the creek bottom site (Table 3.1).  $\Psi_{sf}$  and  $\Psi_{sz}$

decreased throughout the summer for all species except that  $\Psi_{sf}$  remained constant for *P. menziesii* in the meadow, and  $\Psi_{sf}$  and  $\Psi_{sz}$  remained constant for *A. macrophyllum* in the meadow (Figure 3.3A, B). For the evergreens,  $\Psi_{sf}$  increased only for *P. menziesii* from late summer to winter while  $\Psi_{sz}$  remained constant (Figure 3.3A, B). From the winter to spring, changes in  $\Psi_{sf}$  and  $\Psi_{sz}$  varied among species (Figure 3.3A, B). During most sampling periods,  $\Psi_{sf}$  and  $\Psi_{sz}$  were lowest for *Q. garryana* and *A. menziesii* and highest for *A. macrophyllum* in the forest (Figure 3.3A, B).

IE varied significantly with species, date, and the species x date interaction at the clear-cut, with species and date at the forest and creek bottom, and with species and the species x date interaction at the meadow site (Table 3.1). IE increased throughout the summer for all species except for *Q. garryana* in the clear-cut and *A. macrophyllum* in the forest, for which it decreased and for *P. menziesii* in the meadow, for which it remained constant (Figure 3.4A). From late summer to winter, IE increased for *A. grandis* only; however, from winter to spring, IE decreased for *A. grandis*, increased for *A. menziesii* and remained constant for the other species (Figure 3.4A). During the summer, IE was lowest for *A. macrophyllum* and *C. cornuta* in the forest, intermediate for conifers and species at the creek bottom site, and highest for *Q. garryana* and *A. menziesii* in the clear-cut, except during the late summer, when IE was highest for *P. menziesii* in the clear-cut and *A. menziesii* (Figure 3.4B).



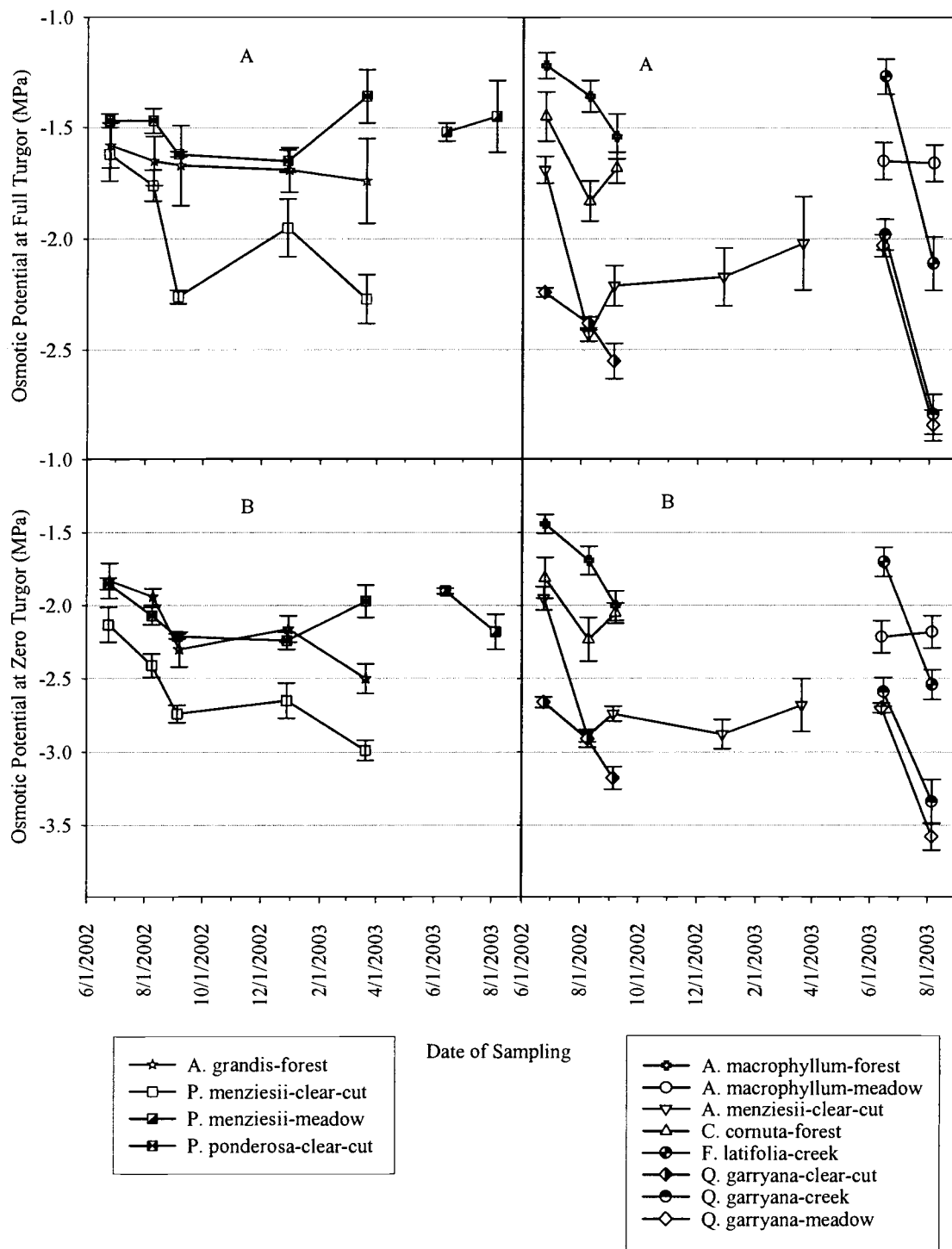


Figure 3.3. Mean values of osmotic potential at full ( $\Psi_{sf}$ , A) and zero turgor ( $\Psi_{sz}$ , B) for conifers (left) and angiosperms (right) at all sites and all dates sampled. Error bars are one standard error of the mean for each species for each sampling date.

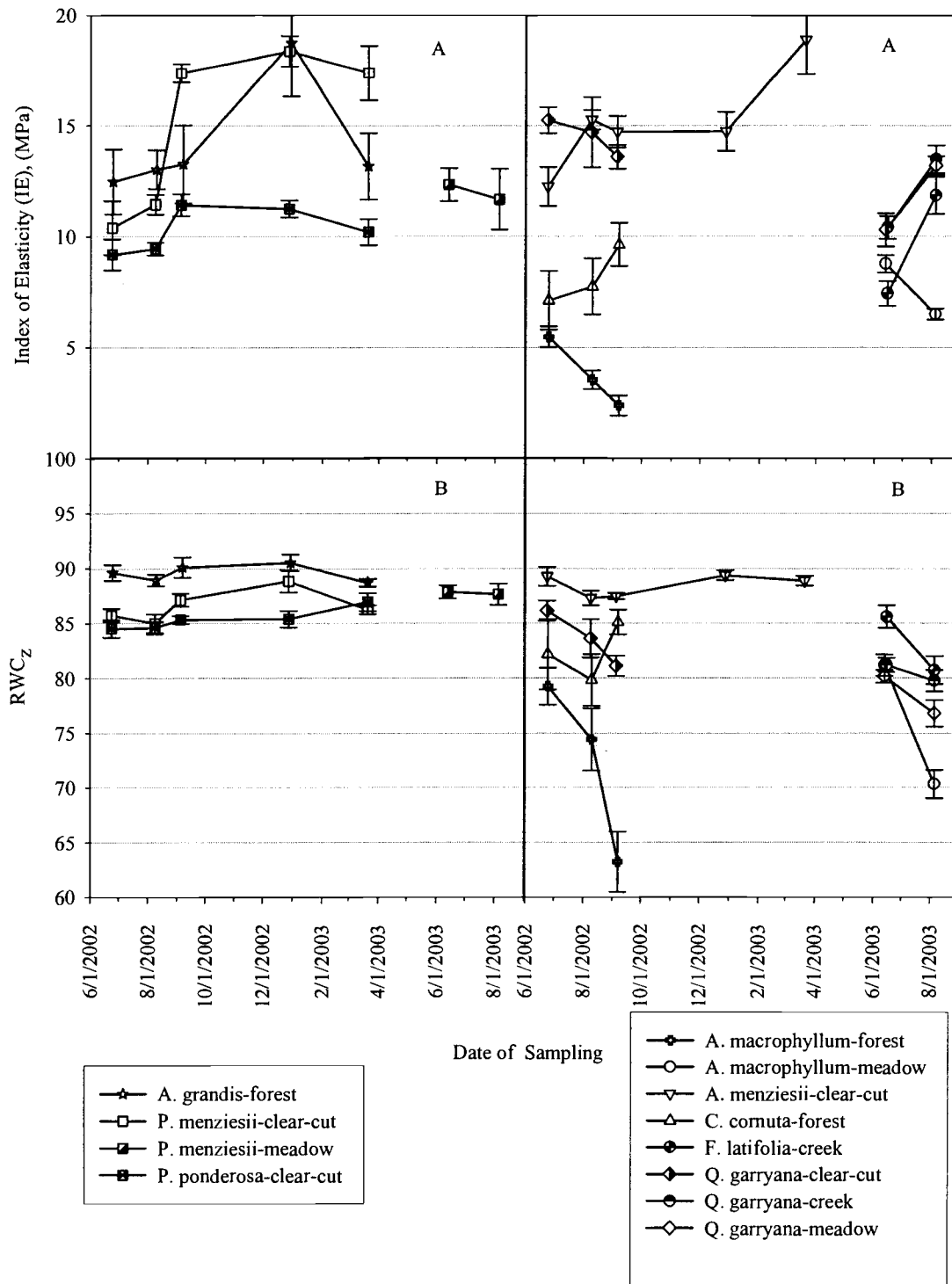


Figure 3.4. Mean values of index of elasticity (IE, A) and relative water content at zero turgor (RWC<sub>z</sub>, B) for conifers (left) and angiosperms (right) at all sites and all dates sampled. Error bars are one standard error of the mean for each species for each sampling date.

RWC<sub>z</sub> varied significantly with species, date and the species x date interaction at the clear-cut and meadow, with species and date at the forest, and with date only at the creek bottom site (Table 3.1). There was little change in RWC<sub>z</sub> except for *A. macrophyllum*, *Q. garryana* at the clear-cut and meadow, and *F. latifolia*, for which RWC<sub>z</sub> decreased over the summer (Figure 3.4B). RWC<sub>z</sub> increased from mid-summer to late summer to winter for *P. menziesii*, then decreased to early summer levels in the spring (Figure 3.4B). RWC<sub>z</sub> increased from mid-summer to late summer for *C. cornuta* (Figure 3.4B). Throughout the study, RWC<sub>z</sub> was highest for *A. grandis* and *A. menziesii* and lowest for *A. macrophyllum* and *Q. garryana* in the meadow during the mid-summer (Figure 3.4B).

The osmotic adjustment varied with species (Table 3.2). It was greatest for *A. menziesii*, *Q. garryana* at the creek bottom and meadow, *F. latifolia*, *P. menziesii* in the clear-cut and *C. cornuta*, intermediate for *A. macrophyllum* in the forest and *Q. garryana* in the clear-cut, and least in the remaining conifers and *A. macrophyllum* in the meadow (Table 3.2).

The adjustment in IE varied among species (Table 3.2). The adjustment was positive for all species (i.e., tissue became less elastic) except *A. macrophyllum*, *P. menziesii* in the meadow and *Q. garryana* in the clear-cut (Table 3.2). The adjustment was greatest for *A. grandis*, *A. menziesii*, and *P. menziesii* in the clear-cut (Table 3.2).

Table 3.2. Mean values of osmotic ( $\Psi_{sf}$ ) and index of elasticity (IE) adjustment.  $\Psi_{sf}$  adjustment is defined as the difference between the highest and lowest  $\Psi_{sf}$  during the year. IE adjustment was calculated as the difference between the highest and lowest IE during the year and the early summer. Species with the same letter do not differ significantly (LSD,  $p=0.05$ ).

Species	Site	$\Psi_{sf}$ Adjustment (MPa)	IE Adjustment (MPa)
<i>A. grandis</i>	Forest	0.15abc	6.23cde
<i>A. macrophyllum</i>	Forest	0.32bcd	-3.15a
<i>A. macrophyllum</i>	Meadow	0.01ab	-2.25a
<i>A. menziesii</i>	Clear-cut	0.73e	6.63de
<i>C. cornuta</i>	Forest	0.47cde	2.52b
<i>F. latifolia</i>	Creek Bottom	0.67de	3.54bcde
<i>P. menziesii</i>	Clear-cut	0.64de	6.97e
<i>P. menziesii</i>	Meadow	0.06a	-0.51ab
<i>P. ponderosa</i>	Clear-cut	0.14abc	2.23b
<i>Q. garryana</i>	Clear-cut	0.31bcd	-1.64a
<i>Q. garryana</i>	Creek Bottom	0.82e	3.09bcd
<i>Q. garryana</i>	Meadow	0.82e	2.89bc

#### Xylem Conductivity Attributes:

The Huber value varied significantly with species and the species x date interaction at the clear-cut and with species, date, and the species x date interaction at the forest site, but there were no significant differences at the other sites (Table 3.1). For most species, the Huber value did not change much throughout the seasons, exceptions being *C. cornuta* and *A. macrophyllum* during the spring (Figure 3.5A). In general, the Huber value was lowest for the conifers, *C. cornuta* and *A. macrophyllum* and highest for *Q. garryana* and *A. menziesii* (Figure 3.5A).

The specific conductivity of twig xylem ( $k_s$ ) varied with species at all sites; in addition it varied with date and the species x date interaction in the forest, and with tree number at the creek bottom site (Table 3.1). Throughout the summer,  $k_s$  did not change for the conifers, except that it increased for *P. menziesii* in the meadow (Figure 3.5B).

From late summer to winter,  $k_s$  decreased for *P. ponderosa* and from winter to spring,  $k_s$  increased; however,  $k_s$  did not change for the remaining conifers (Figure 3.5B). During the summer,  $k_s$  decreased significantly for the oak in the creek-bottom and meadow and increased from early to mid-summer and decreased from mid-summer to late summer for *A. macrophyllum* only; for the remaining species it remained constant (Figure 3.5B). During the rest of the year,  $k_s$  decreased from late summer to winter for *C. cornuta*, *A. macrophyllum* in the forest and *A. menziesii* (Figure 3.5B). From winter to spring,  $k_s$  increased for *C. cornuta* and *A. macrophyllum* and decreased for *Q. garryana* in the clear-cut (Figure 3.5B). The large standard error occludes other significant changes, especially for *Q. garryana* and *F. latifolia*. In general,  $k_s$  was lowest for the conifers, intermediate for *C. cornuta* and *A. menziesii*, and highest for *A. macrophyllum* and *Q. garryana* and *F. latifolia* in the mid-summer (Figure 3.5B).

The leaf-specific conductivity ( $k_l$ ) varied only with species at the clear-cut and meadow sites and with species, date and the species x date interaction in the forest (Table 3.1). As with  $k_s$ , there were few significant changes in  $k_l$  throughout the seasons (Figure 3.5C). However,  $k_l$  did decrease from late summer to winter for *P. ponderosa*, from mid-summer to late summer for *A. macrophyllum*, and from late summer through winter and spring for *A. menziesii* (Figure 3.5C). The large changes in *A. macrophyllum* and *C. cornuta* between late summer and spring occurred for the Huber Value and  $k_l$  because sampling was conducted when leaves were not fully expanded. Otherwise, throughout the study,  $k_l$  was lowest for the conifers, intermediate for angiosperms in the forest and *F. latifolia*, and highest for *Q. garryana* and *A. menziesii* (Figure 3.5C).

Figure 3.5. Mean values of the Huber Value (A),  $k_s$  (B) and  $k_l$  (C) for conifers (left) and angiosperms (right) at all sites and all dates sampled. Error bars are one standard error of the mean for each species for each sampling date.

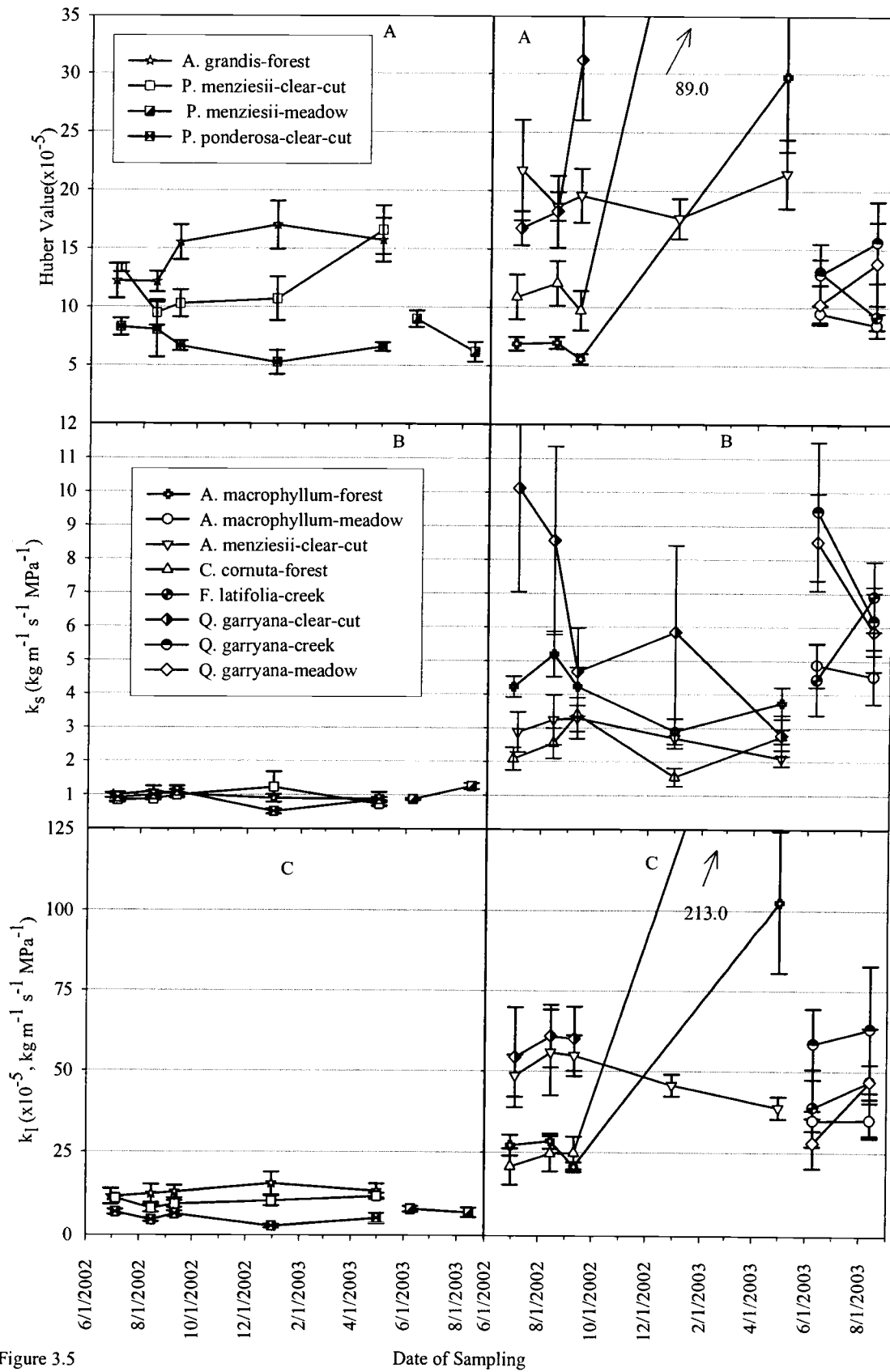


Figure 3.5

Date of Sampling

$\delta^{13}\text{C}$  and % Leaf Nitrogen Concentration:

For leaf samples taken during the late summer 2002,  $\delta^{13}\text{C}$  varied significantly with species (Table 3.3).  $\delta^{13}\text{C}$  was lowest for species in the forest, intermediate for *Q. garryana*, and highest for the evergreens in the clear-cut (Table 3.3). Evergreen species had the lowest % N, while deciduous species had the highest values (Table 3.3).

Table 3.3. Mean values of  $\delta^{13}\text{C}$  and %N composition for conifers and angiosperms. Within a column, species with the same letters do not differ significantly (Tukey's honestly significant difference,  $p = 0.05$ ).

Species	Site	$\delta^{13}\text{C}$	% N
<i>Q. garryana</i>	Clear-cut	-29.26c	1.66b
<i>A. macrophyllum</i>	Forest	-31.11ab	3.19c
<i>C. cornuta</i>	Forest	-31.93a	1.84b
<i>A. menziesii</i>	Clear-cut	-27.96d	0.96a
<i>P. menziesii</i>	Clear-cut	-27.50d	1.10a
<i>P. ponderosa</i>	Clear-cut	-26.08e	1.16a
<i>A. grandis</i>	Forest	-30.41b	0.98a

Wood Density:

Wood density ( $W_d$ ) sampled in November 2003 varied among species (Table 3.4).  $W_d$  was lowest for *A. macrophyllum* in the forest, highest for *Q. garryana*, and intermediate for the remaining species (Table 3.4).



Table 3.4. Mean values of wood density,  $W_d$ , ( $\text{g}/\text{cm}^3$ ). Species with similar letters do not differ significantly (Tukey's Honestly significant difference,  $p=0.05$ ).

Species	Site	Wood Density, $W_d$ ( $\text{g}/\text{cm}^3$ )
<i>A. grandis</i>	Forest	0.52c
<i>A. macrophyllum</i>	Forest	0.28a
<i>A. macrophyllum</i>	Meadow	0.42b
<i>A. menziesii</i>	Clear-cut	0.51c
<i>C. cornuta</i>	Forest	0.53c
<i>F. latifolia</i>	Creek Bottom	0.53c
<i>P. menziesii</i>	Clear-cut	0.52c
<i>P. menziesii</i>	Meadow	0.49bc
<i>P. ponderosa</i>	Clear-cut	0.43bc
<i>Q. garryana</i>	Clear-cut	0.66d
<i>Q. garryana</i>	Creek Bottom	0.65d
<i>Q. garryana</i>	Meadow	0.62d

#### Comparisons of Species Among Sites:

In this section, comparisons are made for oak growing in the clear-cut, meadow and creek bottom sites, *P. menziesii* at the clear-cut and meadow sites, and *A. macrophyllum* at the forest and meadow sites. Measurements were taken at the clear-cut and forest sites during the summer of 2002 and at the meadow and creek-bottom during the summer of 2003. These comparisons are meant to highlight similarities and differences in water relations characteristics that change depending on where the species grows.

There were clear differences in many of the water relations attributes for *Q. garryana* and *A. macrophyllum* growing in different locations, but no clear patterns were present for *P. menziesii*. *Q. garryana* experienced slightly lower mid-summer  $\Psi_{md}$ ,  $g_w$ PM,  $\Psi_{sf}$  adjustment and IE adjustment and higher  $\Psi_{sf}$ ,  $\Psi_{sz}$ , IE, Huber value,  $k_s$ , and  $k_i$  at the clear-cut than at other locations (Figure 3.1, 3.2, 3.3, 3.4, 3.5, Table 3.2). *A.*

*macrophyllum* experienced lower mid-summer  $\Psi_{md}$ ,  $\Psi_{sf}$ ,  $\Psi_{sz}$ , and  $\Psi_{sf}$  adjustment and IE adjustment in the meadow and higher  $g_w$ PM and IE than in the forest (Figure 3.1, 3.2, 3.3, 3.4, 3.5, Table 3.2).

### **Overall Patterns of Water Relations:**

Throughout the summer sampling periods, oak differed distinctly from the other species in its suite of water relations properties. The oaks and *A. menziesii* usually had the lowest osmotic potential and usually the highest xylem conductivity attributes and leaf conductance in early summer (Figure 3.2, 3.3, 3.4, 3.5). However, the oaks never experienced extremes of  $\Psi_{pd}$  or  $\Psi_{md}$  (except high  $\Psi_{pd}$  at the creek-bottom), or the values were not significantly different from other species. Although this early summer pattern is vague for some characteristics, the pattern becomes clearer for mid-summer values.

During the mid-summer, the oaks, *A. menziesii* and *F. latifolia* had the lowest  $\Psi_s$  and, in general, the highest IE (except for *P. menziesii*), Huber Value, and  $k_1$  (Figure 3.3, 3.4, 3.5). However, the oaks and *F. latifolia* clearly had higher  $k_s$  during the mid-summer than the other species (Figure 3.5). The oak also had high  $g_w$  and  $W_d$  (Figure 3.2, Table 3.4).

During the early summer, the conifers in the open had low  $\Psi_{md}$ , high  $\Delta\Psi$ , intermediate  $\Psi_{sz}$  and IE, and low  $k_s$  and  $k_1$  (Figure 3.1, 3.3, 3.4, 3.5). The conifers had intermediate  $W_d$  and  $\delta^{13}C$  (Table 3.3, 3.4). During the mid-summer, the conifers had intermediate values of  $\Psi_{md}$  and  $\Delta\Psi$ , relatively high values of  $\Psi_{sz}$ , intermediate values of IE, and low values of  $k_s$  and  $k_1$  (Figure 3.1, 3.3, 3.4, 3.5)

For the remaining angiosperm species, during the early summer, *A. macrophyllum* in the forest had the highest  $\Psi_s$  and lowest IE, Huber value, and  $g_w$  (Figure 3.2, 3.3, 3.5). *C. cornuta* was similar to *A. macrophyllum* but, in some cases, had slightly lower or higher values (Figure 3.1, 3.2, 3.3, 3.5). *A. menziesii* was much like the oaks during the mid-summer with respect to  $\Psi_s$ ,  $k_s$  and  $k_l$ , but not during other sampling periods.

Little attempt was made to compare averages of water relations traits from different sites because sites typically contained different species; however, mean  $\Psi_{pd}$ , an indicator of water availability, was lower for the clear-cut than the forest and mean  $\Psi_{pd}$  was lower for the meadow than the creek-bottom site.

### **Relationships Among Water Relations Characteristics:**

#### Relationships Among Stomatal Conductance, Environment, Leaf Characteristics, and Xylem Conductivity:

Stomatal conductance ( $g_w$ ) responded differently to light levels and VPD for the five angiosperm species (Figure 3.6, 3.7).  $g_w$  was higher for *Q. garryana* and *A. menziesii* than for the other species over the same range of light (Figure 3.6). The upper limit of  $g_w$  appeared to increase as light increased for *Q. garryana* and *A. menziesii*, but not for the other species (Figure 3.6).  $g_w$  appeared to respond to VPD for many of the species, although  $g_w$  was higher for *Q. garryana* and *A. menziesii* than the other species over the same range of VPD (Figure 3.7). However, both  $g_{wPM}$  and  $g_{wAM}$  increased with increasing light level and decreased with increasing VPD for all species considered together (Spearman Rank Correlation, 0.43, 0.42; -0.40, -0.28;  $p < 0.05$ , respectively).

Figure 3.6. The relationship between stomatal conductance (afternoon and morning) and light for 5 species of angiosperms in this study in the four sites.

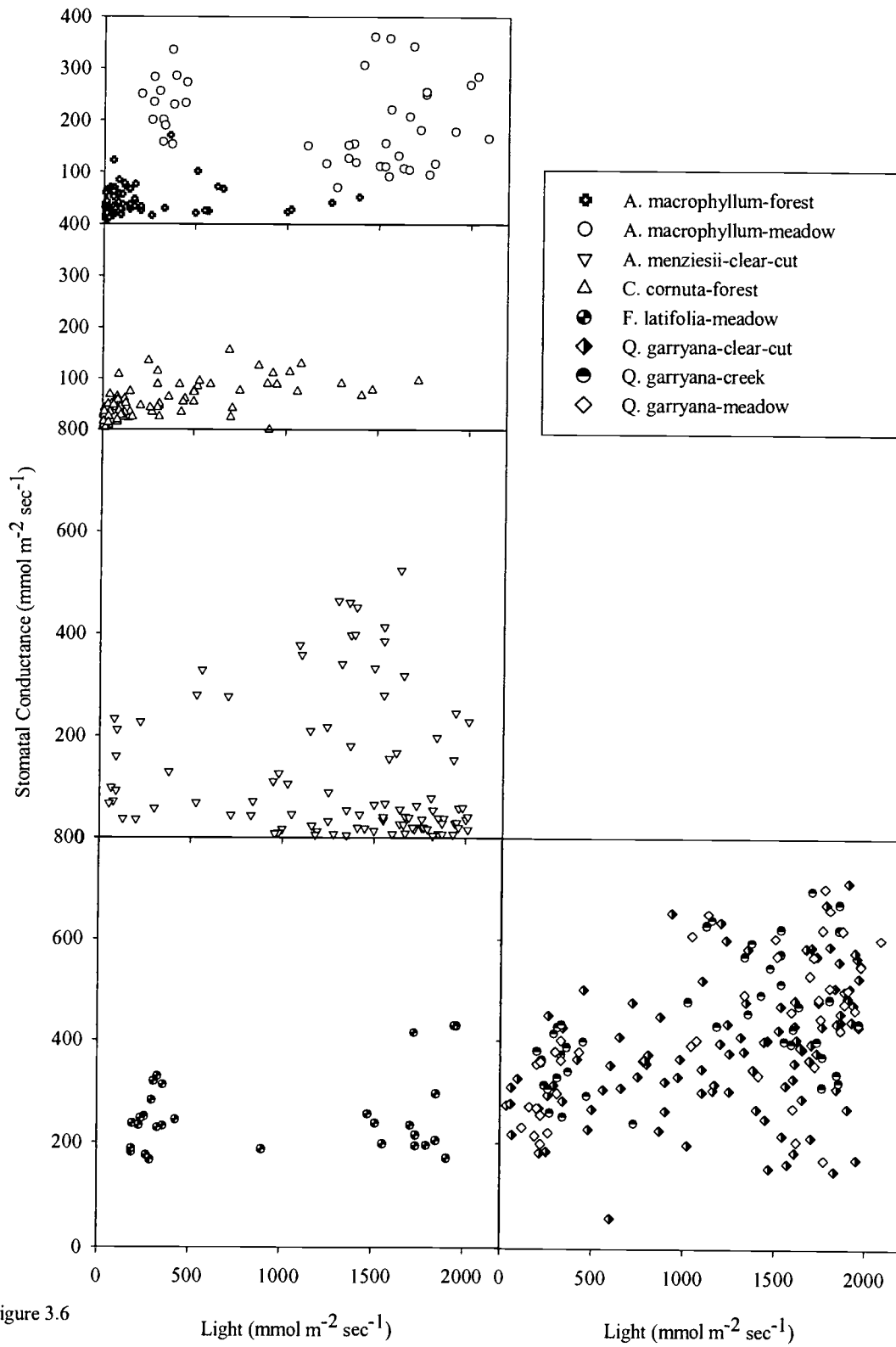


Figure 3.6

Figure 3.7. The relationship between stomatal conductance (afternoon and morning) and VPD for 5 species of angiosperms in this study in the four sites.

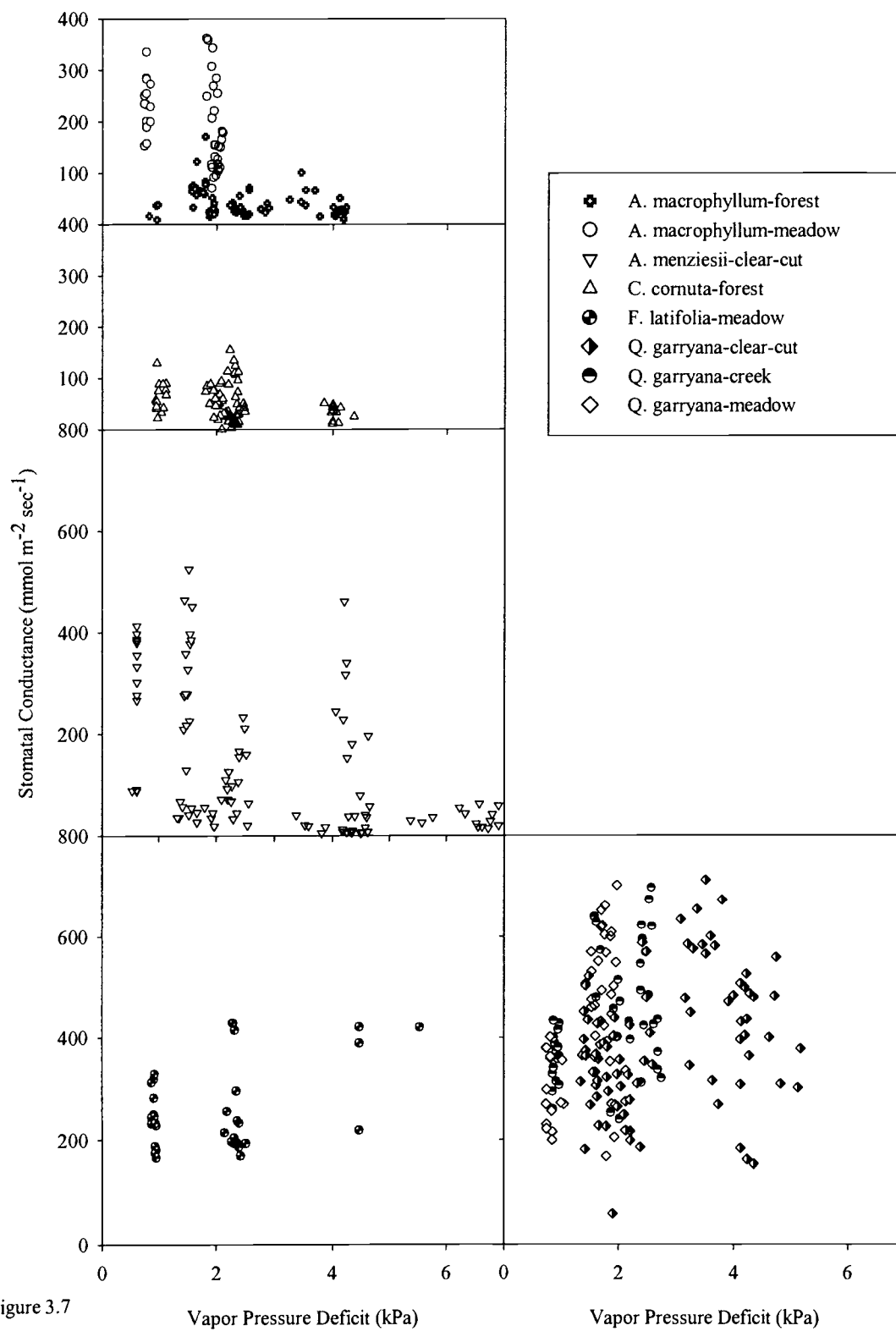


Figure 3.7

Considering both parameters, multiple linear regression explained  $g_w$ PM better than  $g_w$ AM ( $r^2=0.40$  versus  $r^2=0.20$ ); however, the terms were not significant by themselves.

Among the angiosperms, maximal stomatal conductance was related to leaf level traits and xylem conductivity attributes. Maximum conductance experienced for each species in each site decreased with increasing  $\Psi_{sz}$ , but increased with increasing IE (Figure 3.8A, D). The maximum afternoon stomatal conductance also increased with increasing  $\Delta\Psi$  (Figure 3.8B). The relationship was not linear;  $\Delta\Psi$  increased slower at lower  $g_w$  than at higher  $g_w$  (Figure 3.8B). Maximum stomatal conductance also increased with increasing Huber value and  $k_l$  (Figure 3.8C, E). The maximum soil/leaf hydraulic efficiency increased with increasing  $k_s$  (Figure 3.8F); there are two groups: the oaks, with large vessels, and the other species.

Among species from the forest and the clear-cut,  $\delta^{13}\text{C}$  decreased with increasing early summer  $\Psi_{md}$  and increased with early summer  $\Delta\Psi$  (Figure 3.9). For species in these two locations, lower  $\Psi_{md}$  and large difference between  $\Psi_{pd}$  and  $\Psi_{md}$  were associated with decreased isotope discrimination and increased intrinsic water use efficiency.



Figure 3.8. Relationships between the maximum mean stomatal conductance of 5 angiosperm species and leaf level characteristics and xylem conductivity attributes. Error bars are one standard error of the mean for the maximum stomatal conductance and other characteristics for each species. Maximum mean stomatal conductance and other attributes were taken from the same sampling date.

- |   |                        |
|---|------------------------|
| ✱ | A. macrophyllum-forest |
| ○ | A. macrophyllum-meadow |
| ▽ | A. menziesii-clear-cut |
| △ | C. cornuta-forest      |
| ● | F. latifolia-creek     |
| ◆ | Q. garryana-clear-cut  |
| ● | Q. garryana-creek      |
| ◇ | Q. garryana-meadow     |

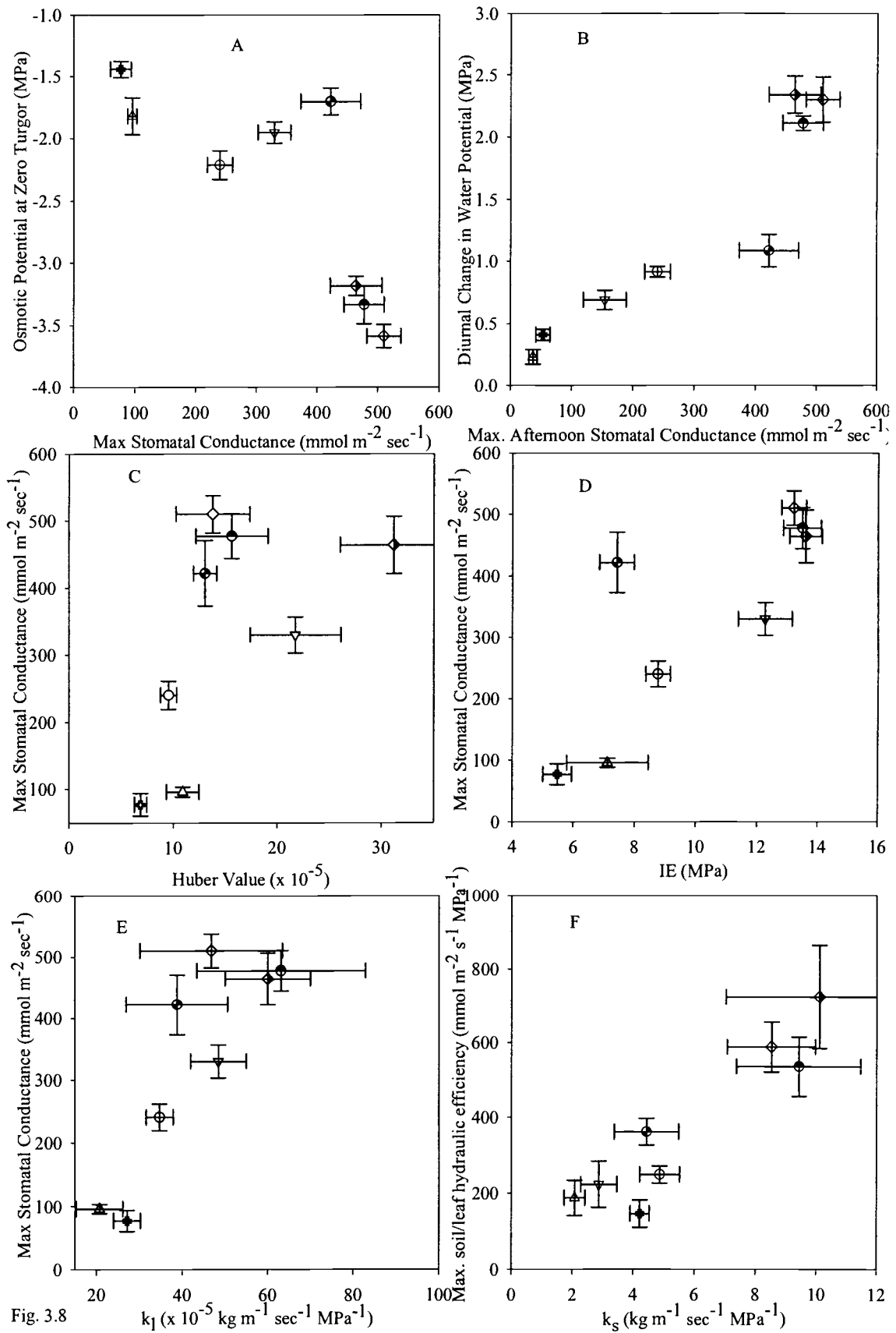


Fig. 3.8

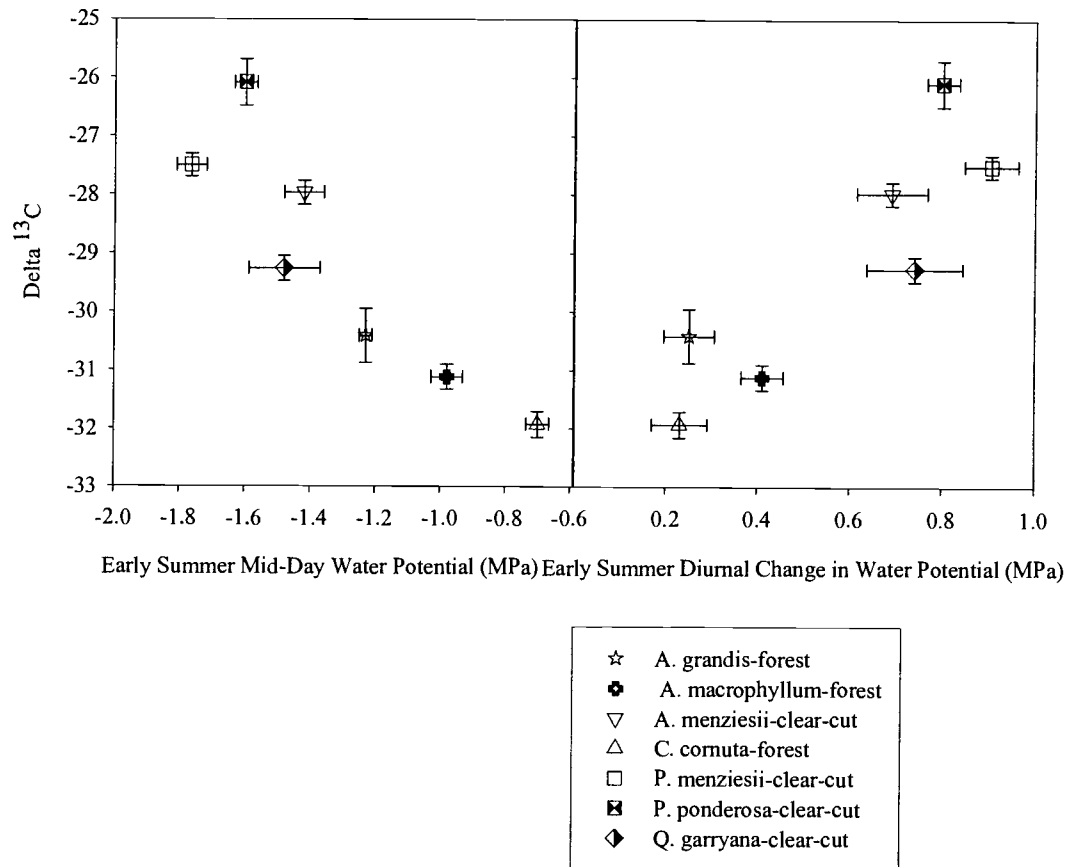


Figure 3.9. The relationship between  $\delta^{13}\text{C}$  and the early summer  $\Psi_{\text{md}}$  and  $\Delta\Psi$  of species located at the clear-cut and forest sites. Tissue was collected in late summer for  $\delta^{13}\text{C}$  analysis. Error bars are on standard error of the mean for  $\delta^{13}\text{C}$  and the early summer  $\Psi_{\text{md}}$  and  $\Delta\Psi$  for each species.

#### Relationships Among Leaf Attributes:

In general,  $\Psi_{\text{md}}$  decreased with decreasing  $\Psi_{\text{pd}}$ ; however, the slope was highest for ring-porous angiosperms, intermediate for diffuse-porous angiosperms, and lowest for the conifers (Figure 3.10A).  $\Psi_{\text{sz}}$  also decreased with decreasing  $\Psi_{\text{md}}$  (Figure 3.10B). Sometimes  $\Psi_{\text{sz}}$  was higher than  $\Psi_{\text{md}}$  (species that lie the above 1:1 line), suggesting that during the summer a few individuals of most of the species may have experienced turgor loss in field conditions (Figure 3.10B). This occurred throughout the summer, not just

during the hottest day of sampling. There was also an association between minimum  $\Psi_{sz}$  and IE, especially when the oaks were excluded (Figure 3.10C). In general, species with lowest  $\Psi_{sz}$  had the highest IE (excluding *Q. garryana*), indicating the trade-off between osmotic potential and tissue elasticity (Figure 3.10C). This relationship would be very strong if not for *Q. garryana*, which exhibited lower IE than the relationship determined from the other species, indicating that this species, with very low  $\Psi_{sz}$  had *more* elastic tissue than expected for its  $\Psi_{sz}$ .

#### Relationships Among Wood Density and Water Relations Traits:

Among the seven species sampled at four sites (*A. macrophyllum* was not included in this analysis because  $w_d$  was underestimated due to the pith occupying a large percentage of the twig volume), increasing  $w_d$  was also associated with increasing mean  $k_l$ , and mean  $k_s$ . The variation in xylem conductivity attributes was large in comparison to the change in  $w_d$  (Figure 3.11A, C). The minimum seasonal  $\Psi_{md}$ , and  $\Psi_{sz}$  decreased linearly with increasing  $w_d$  (Figure 3.11B, D). Although not shown,  $\Psi_{sf}$  and  $\Psi_{sz}$  responded similarly to increasing  $w_d$ .

#### Relationships Among Leaf Characteristics and Xylem Conductivity Attributes:

The maximum  $\Delta\Psi$  increased curvilinearly with increasing  $k_s$  and  $k_l$  (Figure 3.12A, B). The log minimum  $\Psi_{sz}$  (the transformation was the log of the absolute value of the minimum  $\Psi_{sz}$ ) experienced by each species increased with increasing Huber value (Figure 3.12C).

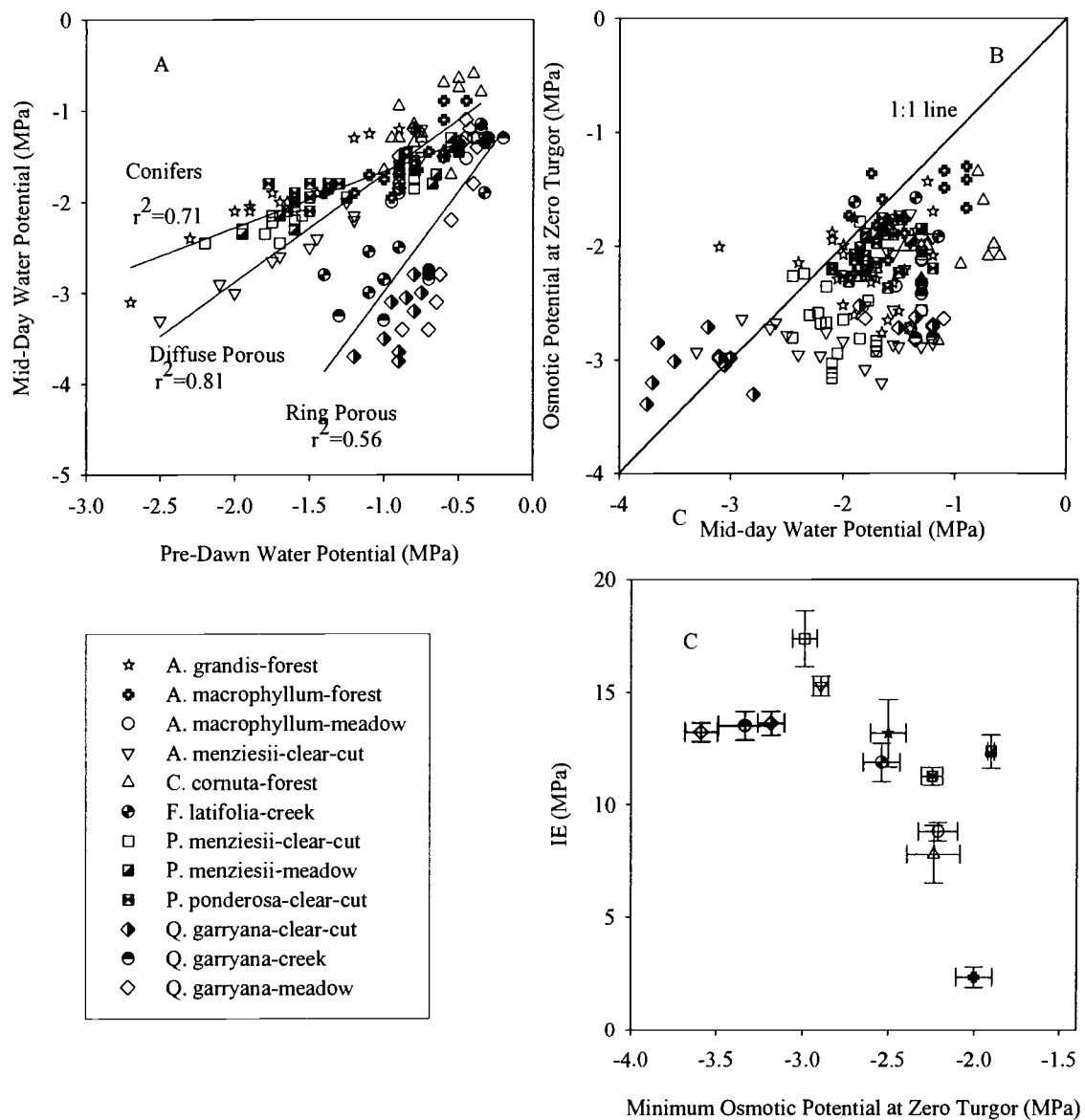
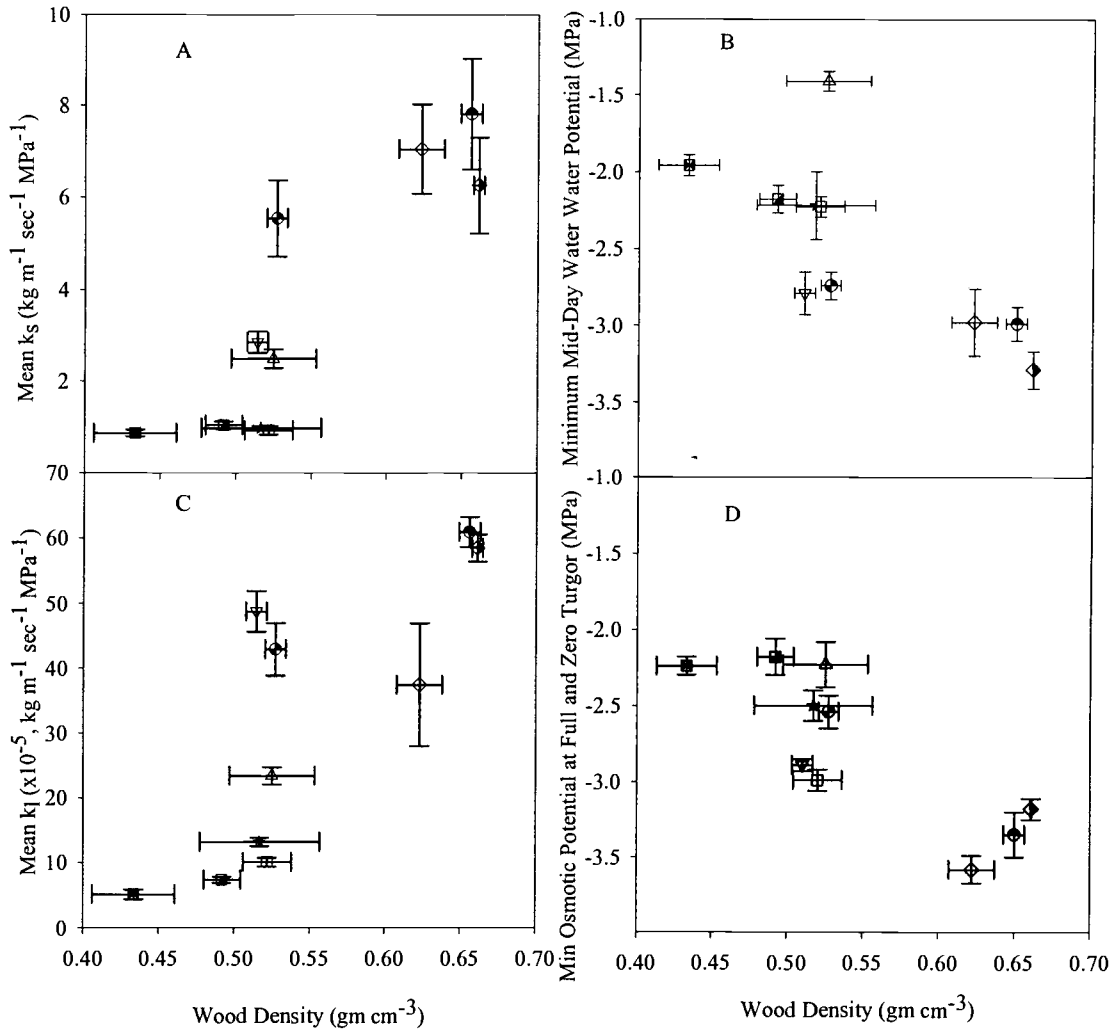


Figure 3.10. Relationships among leaf level characteristics for the species in this study. Each point in A, B, and C are values for an individual tree for all sampling dates. Each point in D is the mean for  $\Psi_{sz}$  and IE when the minimum  $\Psi_{sz}$  occurred. Error bars are one standard error for that sampling date.

Figure 3.11. Relationship between  $w_d$  and mean  $k_s$  (A), mean  $k_l$  (C), and, minimum  $\Psi_{md}$  (B), and  $\Psi_{sz}$  (D). Points are the mean of each characteristic during the date when the minimum value of that characteristic occurred. Error bars of one standard error of the mean for the two characteristics for each species. *A. macrophyllum* was not used in this analysis because of the error introduced in calculating  $w_d$  in this species.



- ☆ A. grandis-forest
- ◆ A. macrophyllum-forest
- A. macrophyllum-meadow
- ▽ A. menziesii-clear-cut
- △ C. cornuta-forest
- F. latifolia-creek
- P. menziesii-clear-cut
- P. menziesii-meadow
- ▣ P. ponderosa-clear-cut
- ◇ Q. garryana-clear-cut
- Q. garryana-creek
- ◇ Q. garryana-meadow

Figure 3.11

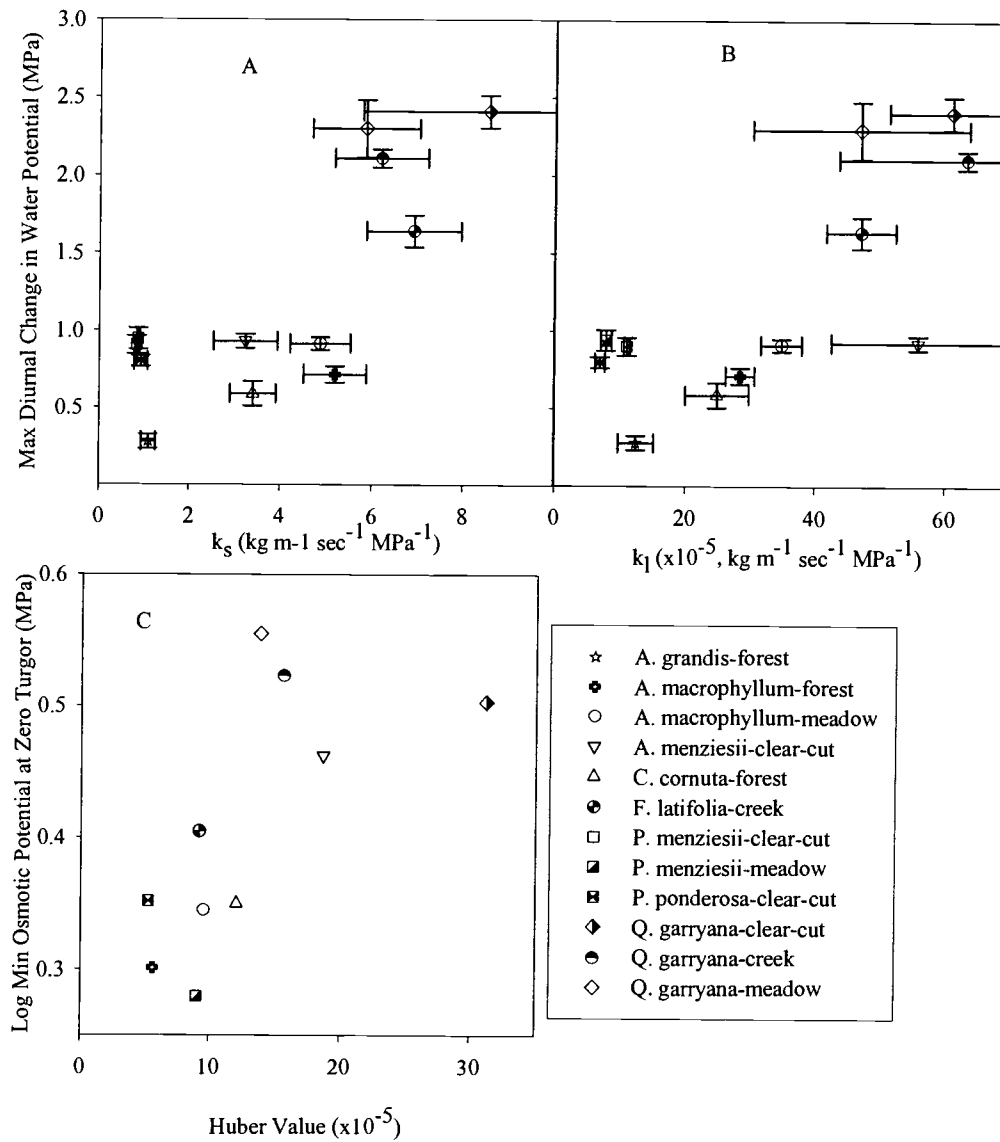


Figure 3.12. Relationships between  $k_s$  and maximum  $\Delta\Psi$  (A); between  $k_1$  and maximum  $\Delta\Psi$  (B); and between the Huber value and log of the minimum absolute value of  $\Psi_{sz}$  (C). Error bars are one standard error of the mean for each species for the dates with the minimum or maximum characteristic.



## CHAPTER 4: DISCUSSION:

### **Comparison of Water Relations Properties and Seasonal Variation:**

#### Plant Water Potential:

As expected, pre-dawn water potential ( $\Psi_{pd}$ ) was high during early summer, decreased throughout the summer and increased in the spring (Figure 3.1A) for most species. The three conifers, *A. menziesii*, and *F. latifolia* experienced low ( $<1.0$  MPa) predawn water potential ( $\Psi_{pd}$ ) during some part of the summer (Figure 3.1A). The lowest  $\Psi_{pd}$  for conifers in this study were within the range for the same species from other locations in Oregon (Waring 1969, Zobel et al 1976, Zobel and Hawk 1980, Pabst et al 1990, Maherali and DeLucia 2000, Zobel et al 2001, Stout and Sala 2003). The lowest  $\Psi_{pd}$  for our oak was higher than other reported values for oaks. For example, extreme values of  $\Psi_{pd}$  ranged from  $-2.5$  to  $-3.8$  MPa for 3 oak species in the Mediterranean and  $-2.2$  to  $-2.4$  MPa for *Q. agrifolia* and *Q. douglasii* in California (Griffin 1973, Acherar and Rambel 1992, Sala and Tenhunen 1994). However, the  $\Psi_{pd}$  of *Q. garryana* in this study was comparable to values from other locations in the Willamette Valley of Oregon (Hibbs and Yoder 1993, Phillips et al 2003). Extreme  $\Psi_{pd}$  was about 0.5 MPa lower for *A. menziesii* in this study than in the Klamath Mountains (Pabst et al 1990). Therefore, I conclude that our species experienced  $\Psi_{pd}$  values similar, if not lower than, the same species in other habitats.

Also as expected, mid-day water potential ( $\Psi_{md}$ ) decreased during the summer, increased from late summer to winter and decreased in the spring (Figure 3.1B) for all species at all sites. Extreme values of  $\Psi_{md}$  for *P. menziesii* were lower than  $-2.1$  MPa reported by Hubbard et al (1999), but similar to young trees in the Wind River Basin in

southern Washington (Phillips et al 2002).  $\Psi_{md}$  for *P. ponderosa* was similar to *P. ponderosa* in the eastern Sierra Nevada and Great Basin (Maherali and DeLucia 2000) and near Black Butte, Oregon (Hubbard et al 1999).  $\Psi_{md}$  during early summer for *A. grandis* in this study were similar to young trees in the area (Yoder 1983). Our oaks experience  $\Psi_{md}$  higher than oaks in the Mediterranean (Tognetti et al 1999) and in California (Griffin 1973), while *A. menziesii* experienced  $\Psi_{md}$  similar to the same species in the Klamath Mountains of Oregon (Pabst et al 1990).

The diurnal change in water potential ( $\Delta\Psi$ ) decreased for the conifers, but increased for the angiosperms during the summer (Figure 3.1C) for most species at all sites. Mean  $\Delta\Psi$  never exceeded 1 MPa except for *Q. garryana* and *F. latifolia*.  $\Delta\Psi$  for *P. ponderosa* was about half that of *P. ponderosa* found in the eastern Sierra Nevada and Great Basin (Maherali and DeLucia 2000). The maximum  $\Delta\Psi$  for our oak was similar to Mediterranean oaks (Rambal 1992).

#### Stomatal Conductance:

Stomatal conductance ( $g_w$ ) declined throughout the summer for *A. menziesii*, *C. cornuta*, *F. latifolia* and *A. macrophyllum*, but not for *Q. garryana* (Figure 3.2).  $g_w$  was consistently highest for *Q. garryana*, intermediate for *F. latifolia*, *A. menziesii*, and *A. macrophyllum* in the open, and lowest for *A. macrophyllum* and *C. cornuta* in the forest.  $g_w$  for *Q. garryana* ranged from about 300 to just over 500  $\text{mmol m}^{-2} \text{sec}^{-1}$ , high compared to other oaks under similar  $\Psi_{pd}$  conditions (Table 4.1).

Table 4.1. Stomatal conductance and  $\Psi_{pd}$  for a variety of oak species across different habitats.

Species	Location	$\Psi_{pd}$ (MPa)	$g_w$ (mmol m <sup>-2</sup> sec <sup>-1</sup> )	Reference
<i>Q. afares</i>	Mediterranean	-0.85	200-300	Acherar and Rambal, 1992
<i>Q. ilex</i>	Mediterranean	-1.0	150	Sala and Tenhunen, 1994
<i>Q. lanata</i>	Nepal	Approx. -1.8	150-350	Poudyal et al, 2004
<i>Q. floribunda</i> , <i>Q. leucotrichophora</i>	India	-1.0 to -1.5	50-200	Garkoti et al, 2000
<i>Q. rubra</i> , <i>Q. prinus</i> , <i>Q. ilicifolia</i>	Pennsylvania	--	50-200	Abrams et al, 1990
<i>Q. garryana</i>	Oregon	-0.5 -0.75	300-500	This study

A positive association between  $g_w$  and  $\Psi_{pd}$  has been reported often for oaks and other species (Lassoie et al 1985, Reich and Hinckley 1989, Abrams et al 1990, Acherar and Rambal 1992, Oliveira et al 1992, Castell and Terradas 1995, Tognetti et al 1999, Terwari 2000). Throughout the summer, both  $\Psi_{pd}$  and  $g_w$  decreased for all species except for *Q. garryana* (Figure 3.1A, 3.2). *Q. garryana* did not experience low  $\Psi_{pd}$  during this study, which could explain its different behavior. Even though other species in the clear-cut site experienced low  $\Psi_{pd}$ , the oaks had sprouted from stumps with a well-established, deep root system that apparently accessed an adequate water supply. The oak trees in the other sites were also trees, apparently with deep roots that protected against low  $\Psi_{pd}$ . Apparently, critical values of  $\Psi_{pd}$  were not reached for *Q. garryana* in this study, even though I sampled the species in a very dry site during hot, dry weather. However,  $\Psi_{pd}$  for *A. menziesii* did decrease to levels below other species in the clear-cut

(*P. ponderosa* and *P. menziesii*), suggesting the lack of deep roots, which could explain why its  $g_w$  declined during the summer. This trend was also present for the forest species, not as distinctly, however, as for *A. menziesii* in the open.

Although I lack  $g_w$  values for the conifers in this study, all conifers reached  $\Psi_{pd}$  that should have triggered significant stomatal closure during the summer. Initial stomatal closure occurred in *A. grandis* at  $-0.9$  MPa and complete closure at  $-2.4$  MPa (Running 1976, Lassoie et al 1985, Zobel 1974). *A. grandis* in this study reached  $\Psi_{pd}$  values within this range. Stomatal conductance begins to decrease at  $\Psi$  of  $-1.0$  to  $-2.0$  MPa and complete stomatal closure appears to occur in *P. menziesii* at  $\Psi_{md}$  of  $-2.0$  to  $-2.5$  MPa (Running 1979, Lassoie et al 1985, Bond and Kavanagh 1999), values experienced by trees in this study. Threshold values of  $-1.5$  to  $-1.7$  MPa have been reported for *P. ponderosa* (Lassoie et al 1985), which is well within the range experienced by trees in this study.

#### Shoot Osmotic Potential, Tissue Elasticity, and Relative Water Content:

In general, mean osmotic potential at full ( $\Psi_{sf}$ ) and zero turgor ( $\Psi_{sz}$ ) decreased during the summer, exceptions being  $\Psi_{sf}$  in *A. grandis*, *A. macrophyllum*, and *P. menziesii* in the meadow (Figure 3.3A, B). The reduction of  $\Psi_{sf}$  and  $\Psi_{sz}$  during the summer is a widespread trend for both deciduous and evergreen species (Zobel 1996) and contributes to drought resistance in many annual and woody plants (Osonubi and Davies 1978, Turner and Jones 1980, Morgan 1984). The reduction of osmotic potential allows plants to maintain turgor while experiencing low water potentials. The extent of osmotic adjustment varied for the species in this study but was not  $>1.0$  MPa for any species (Table 3.2). For example, osmotic adjustment of  $0.14$  and  $0.16$  MPa for *P. ponderosa*

and *A. grandis*, respectively, was much lower than 1.0 MPa reported for hybrids of *A. grandis* with *A. concolor* (Yoder 1983). Osmotic adjustment for our oak in the clear-cut was low, but oaks in the meadow and creek-bottom compared to other North American oaks (Parker et al 1982). Reasons for not detecting osmotic adjustment on par with other reported values may include not sampling during conditions leading to extreme values of  $\Psi_{sf}$  and  $\Psi_{sz}$ . I conclude that most of our species displayed some degree of osmotic adjustment throughout the growing season, which probably contributed to their drought resistance; however, the apparently most drought resistant species did not display more adjustment than less resistant species.

The conifers in this study had values of  $\Psi_{sf}$  and  $\Psi_{sz}$  similar to other regional conifers. For example,  $\Psi_{sf}$  from -2.0 MPa to -2.5 MPa and  $\Psi_{sz}$  from -3.25 to -3.5 MPa were reported for *P. menziesii* shoots during the summer (Ritchie and Shula 1984) and values of  $\Psi_{sf}$  from -1.1 MPa to -2.1 MPa and  $\Psi_{sz}$  values from -1.5 MPa to -2.8 MPa throughout the year for *A. grandis* (Yoder 1983).

By the end of the summer,  $\Psi_{sf}$  for *Q. garryana* ranged from -2.0 MPa to -2.75 MPa and  $\Psi_{sz}$  from -2.6 to -3.25 MPa, lower than many other oaks. In a review of 25 *Quercus* species from a wide geographical range,  $\Psi_{sf}$  ranged from -0.76 MPa to -3.25 MPa with only two oak species below -2.35 MPa and  $\Psi_{sz}$  ranged from -0.99 MPa to -3.10 MPa (not all values were listed for all species, Abrams 1990). *Q. ilex*, an evergreen oak in the Mediterranean, had  $\Psi_{sf}$  between -1.63 to -2.17 MPa and  $\Psi_{sz}$  between -2.85 to -3.40 MPa (Sala and Tenhunen 1994). I am not aware of any reports of  $\Psi_{sf}$  and  $\Psi_{sz}$  for *F. latifolia*: However,  $\Psi_{sf}$  and  $\Psi_{sz}$  of -1.56 and -1.92 MPa, respectively, have been reported for *F. pennsylvanica* from Ontario (Abrams 1988), well within the range of *F.*

*latifolia*. Likewise, I could find no values for *A. macrophyllum*; however, many *Acer* species have been studied elsewhere, with values of  $\Psi_{sf}$  and  $\Psi_{sz}$  similar to ours (Abrams 1988). No values could be found for related species of *C. cornuta*, or *A. menziesii*. I conclude that my species developed  $\Psi_{sf}$  and  $\Psi_{sz}$  values similar to or lower than related species studied elsewhere.

Tissue index of elasticity for oaks in this study ranged from 10 to 15.5 MPa (Figure 3.4A), moderate values for North American oaks, which range from about 4 to 23 MPa (Abrams et al 1971, Bahari et al 1985, Abrams 1990). Elasticity for *A. macrophyllum* was also within the range reported for other *Acer* species (Niinemets 2001); likewise, elasticity of *F. latifolia* was similar to that reported for *F. americana* in Pennsylvania (Kubiske and Abrams 1991). However, elasticity for *P. ponderosa* was higher than reported for this species elsewhere (Vance and Zaerr 1991) but elasticity for *P. menziesii* was in the range reported for seedlings of this species (Ritchie and Shula 1984). Apparently, the species in this study had tissue elasticity similar to related species elsewhere.

In this study, *C. cornuta* and *A. macrophyllum* in the forest had the most elastic leaf tissue (low IE). Cells with elastic walls shrink as water is lost, maintaining turgor pressure, but not volume. In contrast, stiff cell walls allow  $\Psi$  to drop sharply as water is lost, maintaining the  $\Psi$  gradient between soil and leaf (Abrams 1988, Lambers et al 1998). The species in the open had the most rigid cell walls, which may have increased the  $\Psi$  gradient and allowed the development of lower  $\Psi_{md}$ .

Leaf tissue became more rigid (i.e., IE increased) throughout the summer for all species except *Q. garryana* in the clear-cut and *A. macrophyllum* (Figure 3.4A), for

which tissue became more elastic during the summer (IE decreased). In a review of 25 North American *Quercus* species, elasticity decreased for most species (Abrams 1990). In this study, elasticity increased for *Q. garryana* at the clear-cut, but decreased at the other two sites (Table 3.2). The increases and decrease in elasticity for the oak in this study was near the lowest reported for North American species (Abrams 1990).

#### Xylem Hydraulic Conductivity:

In most of the species in this study, there was no clear reduction in the specific conductivity ( $k_s$ ) or leaf-specific conductivity ( $k_l$ ) of twig xylem as the summer progressed, but the Huber value did change significantly for many species (Figure 3.5A). The Huber value represents the ratio of the supply capacity in relation to leaf area (Tyree and Ewers 1991). Our species fall into three general groups in terms of the Huber value: lowest for the conifers, intermediate for forest angiosperms, and highest for the oaks, *F. latifolia* and *A. menziesii* (Figure 3.1A). Our conifers fall within the range reported for other gymnosperms (Tyree and Zimmerman 2002), but the Huber value of *P. menziesii* in this study was lower than that reported for this species by Spicer and Gartner (1998a, 1998b). The Huber Values for the angiosperms in this study were also well within the range reported for angiosperms in general (Tyree and Zimmerman 2002). The Huber values for the oak in this study were higher than other deciduous and white oaks from Florida (Cavender-Bares and Holbrook 2001), but similar to two evergreen oaks in Nepal (Poudyal et al 2003).

The  $k_s$  is a measure of the efficiency of water transport in twig xylem (Tyree and Zimmerman 2003). Again, our data indicate three groups of species; the conifers had the lowest  $k_s$ ; *C. cornuta* and *A. menziesii*, intermediate  $k_s$ ; and *Q. garryana*, *A.*

*macrophyllum*, and *F. latifolia*, the highest  $k_s$  (Figure 3.5B). The  $k_s$  of *P. menziesii* in this study is similar to that reported on the same species by Spicer and Gartner (1998a), but  $k_s$  for *Q. garryana* was much higher than deciduous oaks in Vermont (3.14 and 2.84  $\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ , respectively; Cavender-Bares and Holbrook 2001) and higher than two oaks from Nepal (Poudyal 2003).

$k_j$  represents the sufficiency of water transport to leaves (Tyree and Zimmerman 2003). The conifers had the lowest  $k_j$ ; *A. macrophyllum* and *C. cornuta* in the forest, intermediate values; and *Q. garryana*, *A. macrophyllum* in the meadow and *F. latifolia*, the highest values (Figure 3.5C). The mean values for our oaks were slightly higher than those reported for deciduous and white oaks from Vermont (Cavender-Bares and Holbrook 2001) and those reported for oaks in Nepal (Poudyal et al 2003), but within the range of 3 oaks from India (Zobel, unpublished). Spicer and Gartner (1998a, b) found similar  $k_j$  for *P. menziesii*.

#### $\delta^{13}\text{C}$ and % Leaf Nitrogen Concentration:

$\delta^{13}\text{C}$  varied among species in this study (Table 3.3).  $\delta^{13}\text{C}$  is correlated with intrinsic long-term water-use efficiency (WUE), which is ratio of net photosynthesis to transpiration (Lajtha and Marshall 1995).  $\delta^{13}\text{C}$  values suggest that for trees in the clear-cut, the conifers had the highest WUE, *A. menziesii*, intermediate values, and *Q. garryana* the lowest WUE (Table 3.3). In the forest, *A. grandis* had the highest  $\delta^{13}\text{C}$ , indicating high WUE, while *A. macrophyllum* had an intermediate value, and *C. cornuta* the lowest (Table 3.3), but all were higher than in the clear-cut.

Leaf nitrogen composition is strongly related to photosynthetic capacity (Field and Mooney 1983) The evergreens in this study had the lowest levels of %N, implying



that their rates of photosynthesis were lowest, *Q. garryana* and *C. cornuta* had intermediate values, and *A. macrophyllum*, the highest values of N (Table 3.3).

Among the angiosperms of this study, *Q. garryana* consistently had the highest  $g_w$  and lowest WUE of trees in the clear-cut; based on leaf N values, I infer moderate levels of photosynthesis. The evergreen *A. menziesii* had slightly higher WUE, lower  $g_w$ , and low inferred photosynthetic rates. In the forest, *A. macrophyllum* and *C. cornuta* both had low WUE, but much different inferred photosynthetic rates and  $g_w$ .

### **Suites of Water Relations Properties and Plant Adaptation:**

When one considers combinations of water relations traits, several trends appear among these eight species of northwest trees. Different combinations, or “suites”, of water relations traits have been described for co-occurring tree species. Trees that experience more extreme environments may possess lower osmotic potentials and more rigid cell walls than trees growing in less extreme environments (Bahari et al 1985, Sala and Tenhunen 1994). Adaptation in northwest trees has focused on stomatal behavior and osmotic adjustment (Lassoie et al 1985, Minore 1979). *Q. garryana* and *A. menziesii* can establish and survive in extreme microenvironments because they possess a suite of water relations traits that maintains physiological activity during hot, dry weather. In this study, oak had the lowest  $\Psi_{md}$ ,  $\Psi_{sf}$ , and  $\Psi_{sz}$ , moderate elasticity, high  $g_w$ , high  $\Delta\Psi$ , and the highest values of hydraulic conductivity (Figure 3.1, 3.2, 3.3, 3.4, 3.5). During times of low water availability, high  $g_w$  can be maintained with deep roots that can access water and high xylem conductivity must be present. Even with these characteristics, oak developed large  $\Delta\Psi$ . Low  $\Psi_s$  allows turgor to be maintained despite a large  $\Delta\Psi$ . Although not as clear, this strategy is also present for *A. menziesii*, another tree found in

sites that experience very dry conditions. This species did not experience  $\Psi_{md}$  as low as *Q. garryana* nor were the  $\Delta\Psi$  or  $g_w$  as great; however, *A. menziesii* did develop  $\Psi_{sf}$ ,  $\Psi_{sz}$ , and cell wall elasticity similar to oak. The Huber Value and  $k_l$  were similar between the two species, although  $k_s$  was lower for *A. menziesii*. Although it appears that both species could resist dry conditions well, *Q. garryana* seedlings re-sprout after fire, grazing, and cutting, whereas *A. menziesii* seedlings die after such damage. Responses to soil type also probably contribute to their different importance and distribution patterns (McDonald and Tappeiner 1990).

In the Willamette Valley, *Q. garryana* often establishes in open grasslands, forming oak savanna and eventually oak forest, and is considered one of the most drought resistant tree species in the northwest (Franklin and Dyrness 1973, Minore 1979). Although *A. menziesii* behaves similarly and is considered very drought resistant, it is restricted to well drained soils (Minore 1979, McDonald and Tappeiner 1990). *Q. garryana* has deep tap roots, a very extensive lateral root system, can tolerate moist soil, and has copious acorn production (Stein 1990). Hydraulic redistribution has been shown to occur in blue oak in California (Ishikawa and Bledsoe 2000), and may also occur in *Q. garryana*. This behavior probably accounts for the species ability to establish and survive in open habitat. *A. menziesii*, on the other hand, does not develop nearly as deep roots, can not tolerate moist soil, and has low survival of seedlings, which probably explains most of the differences in local distribution (McDonald and Tappeiner 1990). Another factor that contributes to the establishment of *A. menziesii* in the open is its evergreen habit, which presumably facilitates photosynthesis (inferred from high  $g_w$ ) during times of low water stress in the spring and winter when oak is leafless.

The conifers in this study possessed intermediate values of  $\Psi_{sf}$ ,  $\Psi_{sz}$ , elasticity, and Huber Values and low values of  $k_s$  and  $k_i$  throughout most of the summer (Figure 3.3, 3.4, 3.5). The conifers also had intermediate values of  $\Psi_{md}$  during mid-summer, but had relatively low  $\Psi_{pd}$  and, except for early summer, low  $\Delta\Psi$  (Figure 3.1). I do not have  $g_w$  for the conifer trees in this study, but other studies have shown it to be low (12-20 mmol  $m^{-2} sec^{-1}$ ) for conifers in the northwest (Lassoie et al 1985, Hubbard et al 1999, Phillips et al 2002), compared to angiosperms in this study. Within the conifers, *A. grandis* had low  $\Psi_{pd}$  and  $\Psi_{md}$  and low  $\Delta\Psi$  throughout most of the summer; however, the species had moderate  $\Psi_{sf}$ ,  $\Psi_{sz}$  and elasticity (except for late summer). *A. grandis* had high Huber Values and  $k_i$  during certain periods of the summer, but  $k_s$  was similar for all of the conifers (Figure 3.5).

Even though conifers don't possess extreme values of many water relations traits that could help to explain presence in summer dry locations, they are dominant in the Pacific Northwest. Evergreens are favored in summer dry climates with mild winters because the presence of leaves allows for photosynthesis during wet times of year. (Waring and Franklin 1979). Conifers also have an advantage during the summer because needles stay cooler than broadleaves, thus reducing respiration and transpiration, although both conifers and deciduous species experience reduced photosynthesis in summer (Waring and Franklin 1979). Because adult conifers can be large and have a high proportion of sapwood, they can store more water relative to hardwoods of the region, which can supply up to half the daily water needs of a large *P. menziesii* (Waring and Franklin 1979). Conifers have lower requirements for nutrients than deciduous

species and most decomposition occurs during the wet seasons, which favors conifers over hardwood species (Waring and Franklin 1979).

In the Willamette Valley, in the absence of fire, *Q. garryana* establishes in prairies, and then often provides favorable conditions for the establishment of *P. menziesii* seedlings even on south facing slopes (Franklin and Dyrness 1973). Apparently, from a water relations point of view, *P. menziesii* does not have a suite of characteristics that allow the species to withstand the conditions in the open on drier sites during the seedling stage. Although considered moderately drought resistant, the species undoubtedly takes advantage of the moderated conditions under *Q. garryana* during the dry summers, but performs a large portion of its yearly photosynthesis during the winter (Waring and Franklin 1979, Minore 1979). In contrast to *P. menziesii*, *A. grandis* seldom establishes in open habitat and in the Valley, but often partially replaces *P. menziesii* in later successional stages (Franklin and Dyrness 1973). *A. grandis* is not considered drought resistant, but little in the way of water relations traits from this study point to the differences in behavior between *P. menziesii* and *A. grandis*- the species has comparable values of many traits to *P. menziesii*. The difference probably lies in characteristics that were not measured in this study such as sensitivity of stomatal conductance to water potential and environmental conditions. Running (1976) found  $g_w$  was lower for *A. grandis* than *P. ponderosa* and Korol (2001) showed that maximum  $g_w$  and assimilation rates were lower for *A. grandis* than most other conifers in the inland Northwest. Yoder (1983) reported a critical value of  $-1.3$  MPa for stomatal closure in *A. grandis*, a value the trees in this study experienced consistently. Maximum leaf conductance is lower for *A. grandis* than for many other conifers and may have a lower potential for acclimation to

drought (Jackson and Spomer 1979). Photosynthesis was higher in shade than under sunny conditions (Hodges 1967), which may also explain why *A. grandis* prefers shady sites. Stomatal closure in *A. grandis* at water potentials higher than for *P. menziesii* could explain the inability of *A. grandis* to establish, survive, and compete in environments which pose little threat to other conifers.

Although *P. ponderosa* does not historically play a successional role where this study was conducted, it is important in southwestern Oregon and in the southern Willamette Valley along river channels (Franklin and Dyness 1973). In this study, *P. ponderosa* had the highest  $\Psi_{sz}$  and  $\Psi_{sf}$ , and intermediate values of cell wall elasticity, Huber Value, and  $k_1$ . Although, from this suite of characteristics and the fact that it is often ranked more drought resistant than *P. menziesii*, the species should be important in dry sites (Franklin and Dyness 1973, Minore 1979). The species does not compete well with other conifers, which could act to limit its co-occurrence with other conifers (Oliver and Ryker 1990). Throughout its range the species is found on drier sites with coarse textured soils, so the difference in behavior could be explained by factors other than the water relations traits measured during this study. For example, *P. ponderosa* had greater  $g_w$ , lower osmotic potential, and less elastic cell walls than a few other conifers (Jackson and Spomer 1979) and has the ability to grow deep tap roots (Oliver and Ryker 1990), all of which may contribute to the species' ability to exist on extreme sites.

In this study, *C. cornuta* and *A. macrophyllum* had high values of  $\Psi_{sf}$ ,  $\Psi_{sz}$ , and tissue elasticity, and low values of  $g_w$ , Huber Value, and  $k_1$  for the angiosperms. This suite of water relations traits suggests that both species should be restricted to less severe conditions. *C. cornuta* and *A. macrophyllum* are both important as understory species

during late succession in the Willamette Valley (Franklin and Dyness 1973). *A. macrophyllum* often establishes in forests of *P. menziesii* along with *A. grandis* (as at the forest site in this study), but develops best on moist sites (Franklin and Dyness 1973). *A. macrophyllum* can also succeed on open sites alongside *Q. garryana* (the meadow site in this study) and on hot, dry hillsides in many locations (Minore and Zasada 1990). In this study, when *A. macrophyllum* grew in the open, it developed slightly lower  $\Psi_{sf}$  and  $\Psi_{sz}$ , more rigid cell walls, and higher Huber Value and  $k_i$  than when growing as an understory tree (Figure 3.3, 3.4, 3.5). Although these values are not on par with *Q. garryana* and *A. menziesii*, it appears that flexibility in these traits allow *A. macrophyllum* to establish in openings. Although establishment on dry sites probably occurs only on limited soil types, it is important on hillsides in southwestern Oregon and on the western Cascade Range (Minore and Zasada 1990).

In this study, *F. latifolia* had water relations traits that made it difficult to classify. For example, during early summer,  $\Psi_{sf}$ ,  $\Psi_{sz}$  and cell wall elasticity were similar to *A. macrophyllum* in the forest, but by mid-summer these characteristics were closer to *P. menziesii* and *A. menziesii* (Figure 3.3, 3.4). Similarly, the Huber Value was comparable to *Q. garryana* in the clear-cut in early summer but much lower than the other oaks by mid-summer.  $k_s$  was about the same as *A. macrophyllum* in the forest during the early summer, but rose to levels of *Q. garryana* by mid-summer. Although not extreme either way, the suite of traits of *F. latifolia* should allow it to resist some level of drought (as indicated by mid-summer values). In the Willamette Valley, the species is mostly found along streams in soils that experience seasonal flooding and summer drying (Owston 1990). These locations could provide moderate early summer conditions, which become

droughty sites by late summer. The water relations traits from this study suggest that *F. latifolia* adjusts to increasing water stress by decreasing osmotic potential (the  $\Psi_{sz}$  adjustment was similar to *A. menziesii* and *Q. garryana*, Table 3.2), decreasing cell wall elasticity, and closing stomata. The suite of characteristics from this study does not explain why this species is not more important in other habitats, but its behavior may be related to the lack of deep roots, and the need for moist, wet, high organic matter soils for seedling establishment (Owston 1990).

Turgor pressure maintenance during periods of low  $\Psi_{md}$  depends on  $\Psi_s$  and cell wall elasticity. Usually elasticity decreases (increasing IE) with decreasing  $\Psi$ ; however, elasticity can also increase and either pattern may be advantageous in resisting periods of drought in coordination with decreasing osmotic potential (Turner and Jones 1980, Abrams 1988). Elastic cell walls can assist in maintaining turgor at low water contents, while tissue with relatively rigid cell walls helps to create a large difference in water potential between soil and leaf (Abrams 1988). The species in this study appear to use both strategies to survive dry summers. Throughout the summer, osmotic potential decreased for all species except *A. macrophyllum* in the open and tissue elasticity decreased (increasing IE) except for *Q. garryana* in the clear-cut and for *A. macrophyllum*. Apparently, as water stress increased (as indicated by decreasing  $\Psi_{pd}$ ), most species adapted by decreasing  $\Psi_s$  and tissue elasticity (cell walls became more rigid). *Q. garryana* (except at the clear-cut) and *A. menziesii*, both very drought resistant species, had the greatest  $\Psi_{sf}$  adjustment (decreased during summer, Table 3.2); however tissue became more elastic for *Q. garryana* and less so for *A. menziesii*. Thus even in the most drought resistant species, changes in elasticity differed. Perhaps because  $\Psi_s$  was

low for oak, it could afford the advantage of increased elasticity. In contrast, tissue elasticity decreased for oak at the creek bottom, even though oaks in meadow and creek bottom had similar  $\Psi_{pd}$ .

Decreases in tissue elasticity are more often associated with decreasing  $\Psi_s$  than is increasing elasticity (Nunes et al 1989, Evans et al 1992, Fan et al 1994). However, dry site species often have relatively elastic cell walls, which contribute to turgor maintenance in the same way as low  $\Psi_s$  (Lambers et al 1998). Assuming rigid cell walls are related to drought resistance for these species, our data suggest that *P. menziesii*, *Q. garryana*, and *A. menziesii* are the most drought resistant of the species studied. These are also the species with the lowest  $\Psi_s$ . This pattern also suggests that *A. macrophyllum* as an understory tree and *C. cornuta* are the least drought resistant. Similar ranking have been proposed by Minore (1979) and Lassoie et al (1985).

#### **Relationships Among Water Relations Characteristics:**

The eight species that I studied shared similar functional relationships between leaf water potential attributes, wood density, osmotic potential and cell wall elasticity, and xylem conductance attributes despite taxonomic diversity and different distributional ranges. In some cases, relationships were strengthened by examining conifers, diffuse-porous angiosperms, and ring-porous angiosperms separately. Thus, rather than differing in some uncoordinated way, species characteristics appeared to converge along response curves dictated by high level taxonomic divisions and their wood anatomy. This is the first study that I know of that identifies these relationships for Pacific Northwest tree species, although such relationships have been described for trees in other ecosystems



(Stratton et al 2000, Meinzer 2003, Gartner and Meinzer 2004, Bucci et al 2004, Santiago et al 2004).

Relations Among Stomatal Conductance, Environment, Leaf Characteristics and Hydraulic Conductivity:

In this study, boundary line analysis revealed that  $g_w$  increased with increasing radiation for *A. macrophyllum* and *C. cornuta* in the forest, *Q. garryana*, and *A. menziesii* (Figure 3.6). Data were too few to determine  $g_w$  response to radiation for *F. latifolia* at the creek bottom and *A. macrophyllum* in the meadow. This response of  $g_w$  is common and has been reported for a variety of forest tree species (Hinckley et al 1979).

Maximum  $g_w$  was reached at light levels of about  $500 \text{ mmol m}^{-2} \text{ sec}^{-1}$  in *A. macrophyllum* and *C. cornuta*, whereas maximum  $g_w$  was reached at about  $1500 \text{ mmol m}^{-2} \text{ sec}^{-1}$  for *A. menziesii*.  $g_w$  continued to increase beyond  $2000 \text{ mmol m}^{-2} \text{ sec}^{-1}$  for *Q. garryana*. *A. macrophyllum* in the forest reached maximum values of  $g_w$  at lower light levels than the same species in the open. In general, species in the open reach maximum values of  $g_w$  at higher light levels than species in shade (Hinckley et al 1979). The species in this study appeared to conform to expectations concerning shade tolerant and open grown trees.

The species in this study also responded to vapor pressure deficit (VPD) but the level of response differed (Figure 3.7).  $g_w$  for *A. menziesii* and *Q. garryana* decreased at higher levels of VPD than did *C. cornuta* and *A. macrophyllum*. Again, this is a common response of  $g_w$  to increasing VPD (Hinckley et al 1979).

Among the 5 species of angiosperms in this study, the maximum  $g_w$  was higher in species with low  $\Psi_{sz}$ , rigid cell walls, high xylem/leaf ratio, and high  $k_l$  (Figure 3.8). In addition,  $\Delta\Psi$  increased with increasing maximum afternoon  $g_w$ . Maximum soil/leaf

hydraulic efficiency increased with rising  $k_s$  (Figure 3.8). On sampling dates when *Q. garryana* had the highest  $g_w$ , it also had the lowest  $\Psi_{sz}$ , most rigid cell walls, and highest Huber value and  $k_1$  (Figure 3.8). *A. macrophyllum* in the forest and *C. cornuta* were consistently on the opposite end of these relationships from oak (Figure 3.8). Apparently, among these species a high Huber value and a high  $k_1$  facilitate high rates of water loss (high  $g_w$ ). In plants that display high  $g_w$ ,  $k_1$  (a measure of the sufficiency of hydraulic supply to leaves) needs to be high facilitate to high rates of water loss. Turgor is maintained in these species with low  $\Psi_s$ .

Among the species in the clear-cut and forest,  $\delta^{13}C$  decreased as early summer  $\Psi_{md}$  increased and early summer  $\Delta\Psi$  decreased (Figure 3.9). Among species in the open, *Q. garryana* and *A. menziesii* had similar  $\Psi_{md}$  and  $\Delta\Psi$  and the lowest intrinsic WUE (inferred from low  $\delta^{13}C$ ), while the conifers had lower  $\Psi_{md}$  and higher WUE. Although the angiosperms had presumably higher  $g_w$  than the conifers, which would contribute to low WUE, they did have lower  $\Psi_{md}$  and  $\Delta\Psi$ . Among the species in the forest, *A. grandis* had lower  $\Psi_{md}$  and higher WUE than the other forest species. Again, assuming the angiosperms had higher  $g_w$  than *A. grandis*, their  $\Psi_{md}$  was higher and WUE was lower.

#### Relationships Among Leaf Level Attributes:

Among the eight species in this study,  $\Psi_{md}$  declined with declining  $\Psi_{pd}$ ; however, rates differed for conifers, diffuse porous and ring porous species (Figure 3.10). At any given value of  $\Psi_{pd}$ ,  $\Psi_{md}$  was lowest for ring porous species, intermediate for diffuse porous species and highest for conifers, except when  $\Psi_{pd}$  was above  $-1.0$  MPa. In general, the xylem of ring porous species has higher conductivity than that of diffuse porous species,

which is higher than conifers (Sperry and Sullivan 1992). The ring porous species also had the highest  $g_w$ , which acted to lower  $\Psi_{md}$  in these species. For the most part, the diffuse porous species had low values of  $g_w$  and did not experience low  $\Psi_{md}$ . Although, I do not have  $g_w$  values for the conifers, it was probably lower than the angiosperms.

A number of individuals appeared to experience turgor loss in field conditions (Figure 3.10B). This condition occurred in six species and at various times of the summer. All of samples for P-V curve analysis were rehydrated during this study, which can produce less negative estimates of  $\Psi_{sf}$  and  $\Psi_{sz}$  than for non-rehydrated tissue (Meinzer et al 1986, Kubiske and Abrams 1991). The effects of rehydrating tissue appear to be greater for species growing in drier conditions than for mesic species (Parker et al 1982, Kubiske and Abrams 1991). In this study, *Q. garryana*, frequently a dry site species, experienced  $\Psi_{md}$  lower than  $\Psi_{sz}$  often and commonly by as much as 0.5 MPa (Figure 3.10B). On a few occasions, *A. menziesii*, *P. menziesii*, *A. grandis* and *A. macrophyllum* also experienced  $\Psi_{md} < \Psi_{sz}$ . These data suggest that, based on the number of occurrences of turgor loss and magnitude of difference, rehydration probably did result in less negative estimates of  $\Psi_{sz}$  for *Q. garryana*, but not for the other species. Alternately, if rehydration did not effect estimates of  $\Psi_{sz}$ , the oak reached zero turgor often during mid-day.

Among the species in this study, there appears to be a tradeoff between minimum  $\Psi_{sz}$  (usually during late summer for forest and clear-cut species, and mid-summer for the others) and cell wall elasticity, except for the oak (Figure 3.10C). Excluding the oak, drought resistant species had the lowest  $\Psi_{sz}$  and the most inelastic tissue, while the less drought resistant species had higher  $\Psi_{sz}$  and more elastic tissue. Contrary to the

suggestion that elastic cell walls are important in drought resistant trees (Fan et al 1994, Lambers et al 1998), the resistant species in this study appeared to have cell walls that are more rigid. *Q. garryana* diverged from this pattern. It had slightly more elastic cell walls than would be expected from the relationship established from the other species. This suggests that because the oak did experience more extreme  $\Psi_{md}$  than the other species, it did require slightly more elastic cell walls to maintain turgor at such low water potentials.

#### Relationships Among Wood Density and Xylem Conductivity:

Among the species in this study, increasing wood density was associated with decreasing mean values of  $\Psi_{md}$ ,  $\Psi_{sf}$  and  $\Psi_{sz}$ , and increasing mean values of  $k_1$  and  $k_s$  (Figure 3.11). For these 7 species, wood density varied from about 0.43 to 0.67 gm cm<sup>-3</sup> while the minimum  $\Psi_{md}$  decreased from about -2.0 to -3.4 MPa and the  $\Psi_{sf}$  and  $\Psi_{sz}$  decreased over a similar range (Figure 3.11B, D). Similar relationships between wood density and  $\Psi_{md}$  and  $\Psi_s$  have been shown to exist for Brazilian (Bucci et al 2004), Hawaiian (Meinzer 2003), and Panamanian species (Santiago et al 2004), but tropical species show the inverse relationship between wood density and  $k_1$  and  $k_s$ . Denser wood can withstand more negative xylem water potentials before implosion of conduits or cavitation of the water column (Hacke et al 2001) and may be associated with drought resistant species. For the angiosperms in this study (excluding *A. macrophyllum*), the oaks had the highest  $W_d$  and experienced the lowest  $\Psi_{md}$  but, also, had low  $\Psi_{sf}$  and  $\Psi_{sz}$  to maintain turgor. However, *A. menziesii*, also a drought resistant species, had low  $W_d$  among the angiosperms but did not experience as negative  $\Psi_{md}$  as oak. The conifers

also conformed to a similar relationship; however, interpretation is confounded owing to high  $W_d$  in *A. grandis*, which is not considered especially drought resistant.

In this study, wood density was a good predictor of  $k_l$  and  $k_s$  (Figure 3.11A, C). However, this is opposite from what appears to occur in Hawaiian dry forests and tropical savanna trees (Bucci et al 2004, Stratton et al 2000). In these studies, increasing  $W_d$  was associated with decreasing  $k_l$  and  $k_s$ . The species in these studies were all diffuse porous species. Wood density within diffuse porous species is a function of the trade-off between vessel and fiber density: dense wood has fewer vessels and more fiber per cross-sectional area. Hence, dense wood would be expected to have low conductivity. The ring porous species in my study have much larger vessels than the diffuse porous species (Panshin and de Zeeuw 1980), and conductivity is a function of the radius<sup>4</sup>, which could explain the high conductivity of oak and ash. Conifer xylem is mostly tracheids, which limit conifers to low conductivity. Therefore, an increase in conductivity with increasing wood density across conifers, diffuse, and ring-porous species is a consequence associated with changes in dimension of conductive xylem elements.

#### Relationships Among Leaf Level Characteristics and Xylem Conductivity:

Among the species in this study, as  $k_s$  and  $k_l$  increased, the maximum  $\Delta\Psi$  increased (Figure 3.12A, B). This behavior was different from 6 species of trees in Hawaii where  $\Delta\Psi$  decreased with increasing  $k_l$  (Stratton et al 2000). Hawaiian species with high  $k_l$  also had high  $\Psi_{pd}$  and  $\Psi_{md}$ , which would account for low  $\Delta\Psi$ . Because  $\Delta\Psi$  is the result of water loss exceeding uptake, the Hawaiian species may have had better access to water (i.e., deep roots) than the species in this study. In contrast, the species in my study that possessed high  $k_s$  and  $k_l$  maintained a high  $g_w$ , which produced high  $\Delta\Psi$ .

High Huber Values were also associated with low  $\Psi_{sz}$  (Figure 3.12C). High Huber Value allows a high  $g_w$  (Figure 3.8C), which leads to low  $\Psi_{md}$ . Turgor maintenance during times of low  $\Psi_{md}$  depends on low  $\Psi_s$ , which explains the relationship between a high sapwood/leaf area ratio and high  $g_w$ .

### **Conclusions:**

This study examined water relations traits, twig xylem conductivity, and wood density of three conifer and five angiosperm species that vary in drought resistance in western Oregon. Predawn and mid-day water potential, stomatal conductance, osmotic potential, and cell elasticity decreased throughout the summer for most of the species. However, there were few changes in the sapwood/leaf area ratio, leaf-specific, or twig specific-xylem conductivity during the summer. In general, the plants in this study were not extreme one way or another compared to similar species studied elsewhere, except that stomatal conductance for *Q. garryana* was high compared to other oaks. In this study, *A. macrophyllum*, *Q. garryana*, and *P. menziesii* were studied at multiple sites. Of these three species, *A. macrophyllum* showed the most plasticity in its suite of water relations traits, probably because the two sites where it was studied were much different (forest versus open meadow). Most drought resistant species in this study lower osmotic potentials and decrease cell wall elasticity during the development of the summer dry season and they also had the lowest osmotic potentials throughout the summer. Suites of water relations traits helped to explain successional patterns in the Willamette Valley for *Q. garryana*, *A. menziesii*, and *P. menziesii*. In the Pacific Northwest, evergreen conifers have a distinct advantage over winter deciduous species because they can perform photosynthesis during wet seasons. *Q. garryana*, a deciduous, open habitat, drought

resistant species, posed traits such as low osmotic potential and sustained high stomatal conductance that allows it to persevere in this climate. Other deciduous species without these traits are limited as understory trees or shrubs where microenvironmental conditions are mediated.

This study identified convergent suites of functional traits that co-varied across species. Among the angiosperms of the study, stomatal conductance was inversely related to osmotic potential and positively correlated with diurnal change in water potential. The sapwood/leaf area ratio, leaf specific and specific conductivity were also positively correlated with increasing maximum stomatal conductance, and, although correlated indirectly, decreasing cell wall elasticity was related to increasing stomatal conductance. These relationships highlight the tradeoffs between the requirement for a low turgor loss point, morphological properties of twigs, and efficiency and sufficiency of water transport to facilitate stomatal conductance and the resulting diurnal change in leaf water status. Changes in water status throughout the day were also correlated with wood anatomy. Mid-day water potential in ring-porous species decreased faster than for diffuse porous species or for conifers because of differences in water transport ability among the groups. Wood density, which was lowest for the conifers, intermediate for diffuse porous and highest for ring-porous species, was also positively correlated with specific and leaf-specific conductivity of twig xylem, but inversely related to minimum mid-day water potential and osmotic potential. Xylem transport properties were also positively correlated with maximum diurnal change in leaf water potential. Again, xylem conductivity properties are traded-off against turgor loss and minimum mid-day water potential.

Literally hundreds of studies have examined water relations of plants from a number of different locations. This study is unique because it examines xylem transport properties, leaf level water relations traits, and wood density for 8 species that regionally co-occur, but have varying drought resistance. Although, some of the species have been studied before, some have not, and no study has presented the trade-offs that occur among xylem transport, leaf water relations, and wood density for this range of species from the Pacific Northwest.



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APPENDICES

## Appendix A- Sampling Date Details

Table A1. Dates, air temperature, and relative humidity for sampling periods for year 1. ! indicates data taken from Corvallis OSU Hyslop Farm weather station 6 km east of the study sites. ND indicates that no data were collected during this date

Site	Characteristic	Date	Air temp (C) (Mid-day/Pre-dawn)	Relative Humidity (%) (Mid-day/Pre-dawn)
<b>Clear-Cut</b>				
	$\Psi_{md}$ , $\Psi_{pd}$	7-10-02	36.6/22.2	45/31
	P-V curves	6-24-02	32.4/10!	32/ND
	Huber value,	7-05-02-		ND
	$k_s$ , $k_l$	7-11-02		
	$g_w$	7-10-02	36.6/14!	ND
<b>Forest</b>				
	$\Psi_{md}$ , $\Psi_{pd}$	7-10-02	35.2/22.2	43/44
	P-V curves	6-25-02	26.4/10!	40/ND
	Huber value,	6-30-02-		ND
	$k_s$ , $k_l$	7-02-02		
	$g_w$	7-10-02	35.2/141	ND
<b>Clear-Cut</b>				
	$\Psi_{md}$ , $\Psi_{pd}$	8-14-02	38/24	17/38
	P-V curves	8-9-02	29!/11.6!	ND
	Huber value,	8-15-02-		ND
	$k_s$ , $k_l$	8-16-02		
	$g_w$	8-14-02	39.8/13.3!	17/ND
<b>Forest</b>				
	$\Psi_{md}$ , $\Psi_{pd}$	8-14-02	34/25	23/37
	P-V curves	8-10-02	31.7!/13.3!	ND
	Huber value,	8-15-02-		ND
	$k_s$ , $k_l$	8-17-02		
	$g_w$	8-14-02	34.2/13.3!	25/ND
<b>Clear-Cut</b>				
	$\Psi_{md}$ , $\Psi_{pd}$	9-10-02	33//16	24/67
	P-V curves	9-5-02	23.3!/3.9!	ND
	Huber value,	9-11-02-		ND
	$k_s$ , $k_l$	9-15-02		
	$g_w$	9-10-02	33//16	24/67
<b>Forest</b>				
	$\Psi_{md}$ , $\Psi_{pd}$	9-10-02	26/16.9	35/64
	P-V curves	9-7-02	23.3!/5.5!	ND
	Huber value,	9-11-02-		ND
	$k_s$ , $k_l$	9-15-02		
	$g_w$	9-10-02	26/16.9	35/64

Site	Characteristic	Date	Air temp (C) (Mid-day/Pre-dawn)	Relative Humidity (%) (Mid-day/Pre-dawn)
Clear-Cut	$\Psi_{md}$ , $\Psi_{pd}$	12-27-02	12.2!/4.4!	ND
	P-V curves	12-28-02	11.1!/5!	ND
	Huber value, $k_s$ , $k_l$	12-31-02-1-03-03		ND
Forest	$\Psi_{md}$ , $\Psi_{pd}$	12-27-02	12.2!/4.4!	ND
	P-V curves	12-30-02	8.9!/1.7!	ND
	Huber value, $k_s$ , $k_l$	12-31-02-1-03-03		ND
Clear-Cut	$\Psi_{md}$ , $\Psi_{pd}$	3-21-03	25.5/7.2!	ND
	P-V curves	3-21-03	25.5/7.2!	ND
	$g_w$	Sampled for ARME only		ND
Forest	$\Psi_{md}$ , $\Psi_{pd}$	3-21-03	21.1/7.2!	ND
	P-V curves	3-21-03	21.1/7.2!	ND
Clear-Cut	$\Psi_{md}$ , $\Psi_{pd}$	4-30-03	18.9!/12.2	ND/63
	Huber value, $k_s$ , $k_l$	5-01-03-5-03-03		ND
	Forest	$\Psi_{md}$ , $\Psi_{pd}$	4-30-03	18.9!/9.9
Huber value, $k_s$ , $k_l$		5-01-03-5-03-03		ND

Table A2. Dates, air temperature, and relative humidity for sampling periods for year 2. ! indicates data taken from Corvallis OSU Hyslop Farm weather station 6 km east of the study sites. ND indicates that no data were collected during this date

Site	Characteristic	Date	Air temp (Mid-day/Pre-dawn)	Relative Humidity (Mid-day/Pre-dawn)
<hr/>				
Meadow	$\Psi_{md}$ , $\Psi_{pd}$	6-11-03	25.6/13	50/75
	P-V curves	6-13-03	19.4!/11.1!	ND
	Huber value, $k_s$ , $k_l$	6-9-03	30.5!/6.7!	ND
	$g_w$	6-11-03	25.6/13	50/75
Creek Bottom	$\Psi_{md}$ , $\Psi_{pd}$	6-11-03	25/13	41/75
	P-V curves	6-15-03	22.2!/6.11	ND
	Huber value, $k_s$ , $k_l$	6-9-03	30.5!/6.7!	ND
	$g_w$	6-11-03	25/13	41/75
<hr/>				
Meadow	$\Psi_{md}$ , $\Psi_{pd}$	8-04-03	26.7!/9.4!	ND
	P-V curves	8-05-03	28.9!/12.2!	ND
Creek Bottom	$\Psi_{md}$ , $\Psi_{pd}$	8-04-03	26.7!/9.4!	ND
	P-V curves	8-05-03	28.9!/12.2!	ND
<hr/>				
Meadow	$\Psi_{md}$ , $\Psi_{pd}$	8-14-03	28.3!/12.8!	ND
	Huber value, $k_s$ , $k_l$	8-13-03/ 8-15-03	26.7!/10!	ND
	$g_w$	8-16-03	26.7!/9.4!	ND
Creek Bottom	$\Psi_{md}$ , $\Psi_{pd}$	8-14-03	28.3!/12.8!	ND
	Huber value, $k_s$ , $k_l$	8-13-03/ 8-15-03	26.7!/10!	ND
	$g_w$	8-16-03	28.8/ND	34/ND

Appendix B-Correlations between water relations traits

Table A3. Spearman-rank correlation coefficients of all water relations characteristics. Bold indicates statistically significant correlations. Symbols: \*\*\* =  $p < 0.001$ ; \*\* =  $0.001 < p < 0.01$ ; and \* =  $0.01 < p < 0.05$ .

Character	Character	All Species	<i>Q. garryana</i>	<i>F. latifolia</i>	<i>A. macrophyllum</i>	<i>C. cornuta</i>	<i>A. menziesii</i>	<i>P. menziesii</i>	<i>P. ponderosa</i>	<i>A. grandis</i>
$\Psi_{pd}$	$\Psi_{md}$	<b>0.58***</b>	<b>0.73***</b>	<b>0.92*</b>	<b>0.77***</b>	0.51 ns	<b>0.97***</b>	<b>0.90***</b>	<b>0.77**</b>	<b>0.96***</b>
	$\Delta\Psi$	<b>0.35***</b>	<b>-0.55**</b>	-0.67 ns	0.00 ns	-0.18 ns	-0.39 ns	<b>0.84***</b>	<b>0.85**</b>	0.31 ns
	$\Psi_{sf}$	0.07 ns	<b>0.52**</b>	0.69 ns	-0.02 ns	0.13 ns	<b>0.63**</b>	<b>0.53**</b>	0.29 ns	-0.32 ns
	$\Psi_{sz}$	0.13 ns	<b>0.42*</b>	0.69 ns	-0.2 ns	0.17 ns	<b>0.65**</b>	<b>0.70**</b>	<b>0.71**</b>	0.12 ns
	$\Psi_{amp}$	-0.20 ns	0.24 ns	-0.21 ns	0.11 ns	-0.20 ns	<b>-0.73**</b>	-0.24 ns	<b>-0.82**</b>	-0.47 ns
	IE	<b>-0.34***</b>	<b>-0.54**</b>	-0.67 ns	<b>0.62**</b>	-0.16 ns	-0.49 ns	-0.33 ns	-0.45 ns	0.19 ns
	RWC <sub>z</sub>	<b>-0.39***</b>	-0.03 ns	<b>0.86*</b>	<b>0.59**</b>	0.06 ns	0.51 ns	-0.01 ns	-0.14 ns	-0.27 ns
	Huber	-0.07 ns	<b>-0.54**</b>	0.29 ns	0.34 ns	-0.01 ns	-0.14 ns	0.22 ns	0.15 ns	-0.11 ns
	k <sub>s</sub>	<b>0.45***</b>	0.29 ns	0.12 ns	-0.02 ns	0.02 ns	-0.16 ns	-0.15 ns	0.01 ns	0.15 ns
	k <sub>l</sub>	<b>0.32***</b>	-0.29 ns	0.12 ns	0.39 ns	0.08 ns	-0.29 ns	0.27 ns	0.16 ns	0.24 ns
	g <sub>w</sub> AM	<b>0.34**</b>	0.08 ns	<b>0.88***</b>	<b>0.88**</b>	0.42 ns	<b>0.95***</b>			
	g <sub>w</sub> PM	<b>0.39***</b>	0.33 ns	0.49 ns	<b>0.70**</b>	0.10 ns	<b>0.89***</b>			
	$\delta C^{13}$	<b>0.58***</b>								
	W <sub>d</sub>	0.23 ns								

Table A3 (Continued)

		All Species	<i>Q.</i> <i>garryana</i>	<i>F.</i> <i>latifolia</i>	<i>A.</i> <i>macrophyllum</i>	<i>C.</i> <i>cornuta</i>	<i>A.</i> <i>menziesii</i>	<i>P.</i> <i>menziesii</i>	<i>P.</i> <i>ponderosa</i>	<i>A.</i> <i>grandis</i>
$\Psi_{md}$	$\Delta\Psi$	<b>-0.46***</b>	<b>-0.93***</b>	<b>-0.79*</b>	<b>-0.60**</b>	<b>-0.89**</b>	<b>-0.53*</b>	<b>0.68**</b>	0.49 ns	0.18 ns
	$\Psi_{sf}$	<b>0.46***</b>	<b>0.66***</b>	0.62 ns	0.39 ns	0.03 ns	<b>0.55**</b>	0.22 ns	-0.09 ns	0.02 ns
	$\Psi_{sz}$	<b>0.49***</b>	<b>0.66***</b>	0.62 ns	<b>0.41*</b>	0.09 ns	<b>0.39*</b>	0.21 ns	0.05 ns	0.12 ns
	$\Psi_{amp}$	<b>-0.23**</b>	0.10 ns	<b>1.0***</b>	-0.28 ns	-0.08 ns	-0.07 ns	-0.07 ns	-0.35 ns	-0.16 ns
	IE	<b>-0.33***</b>	<b>-0.44*</b>	-0.59 ns	0.19 ns	-0.25 ns	-0.31 ns	0.06 ns	0.10 ns	0.07 ns
	RWC <sub>z</sub>	0.07 ns	0.13 ns	<b>0.86 *</b>	<b>0.52 *</b>	-0.09 ns	<b>0.60**</b>	0.19 ns	0.23 ns	-0.16 ns
	Huber	<b>-0.19**</b>	<b>-0.57**</b>	0.40 ns	-0.04 ns	0.13 ns	-0.13 ns	0.08 ns	0.21 ns	-0.03 ns
	k <sub>s</sub>	-0.06 ns	<b>0.42*</b>	0.05 ns	0.07 ns	-0.52 ns	-0.19 ns	-0.22 ns	<b>-0.41 *</b>	-0.10 ns
	k <sub>l</sub>	-0.11 ns	-0.28 ns	0.02 ns	0.11 ns	-0.11 ns	-0.28 ns	0.10 ns	-0.34 ns	0.06 ns
	g <sub>w</sub> AM	-0.09 ns	0.00 ns	0.47 ns	0.44 ns	<b>0.65*</b>	<b>0.92***</b>			
	g <sub>w</sub> PM	-0.16 ns	<b>0.39*</b>	0.48 ns	0.23 ns	0.22 ns	<b>0.88***</b>			
	$\delta C^{13}$	<b>0.46**</b>								
W <sub>d</sub>	<b>-0.53**</b>									



Table A3 (Continued)

	All Species	<i>Q. garryana</i>	<i>F. latifolia</i>	<i>A. macrophyllum</i>	<i>C. cornuta</i>	<i>A. menziesii</i>	<i>P. menziesii</i>	<i>P. ponderosa</i>	<i>A. grandis</i>	
$\Delta\Psi$	$\Psi_{sf}$	<b>-0.35***</b>	<b>-0.55**</b>	0.5 ns	-0.43 ns	0.08 ns	<b>-0.60*</b>	<b>0.70**</b>	0.22 ns	<b>-0.80**</b>
	$\Psi_{sz}$	<b>-0.36***</b>	<b>-0.61**</b>	0.50 ns	<b>-0.55**</b>	0.07 ns	<b>-0.65*</b>	<b>0.76**</b>	<b>0.69**</b>	0.45 ns
	$\Psi_{amp}$	<b>0.20*</b>	0.12 ns	<b>-1.0!</b>	<b>0.65*</b>	-0.05 ns	<b>0.52*</b>	-0.32 ns	<b>-0.93***</b>	-0.32 ns
	IE	<b>0.17*</b>	0.25 ns	0.44 ns	<b>0.41*</b>	0.29 ns	0.43 ns	-0.38 ns	-0.30 ns	<b>0.53 *</b>
	RWC <sub>z</sub>	<b>-0.38***</b>	-0.26 ns	-0.41 ns	-0.10 ns	0.20 ns	-0.08 ns	-0.08 ns	0.05 ns	-0.41 ns
	Huber	<b>0.24**</b>	<b>0.44*</b>	-0.64 ns	<b>0.47**</b>	0.03 ns	-0.44 ns	0.33 ns	0.15 ns	0.06 ns
	k <sub>s</sub>	<b>0.50***</b>	-0.33 ns	0.24 ns	-0.13 ns	<b>0.61*</b>	0.20 ns	-0.23 ns	-0.06 ns	0.19 ns
	k <sub>l</sub>	<b>0.53***</b>	0.17 ns	0.24 ns	0.28 ns	0.28ns	-0.09 ns	-0.30 ns	-0.00 ns	0.25 ns
	g <sub>w</sub> AM	<b>0.47***</b>	-0.10 ns	0.3 ns	0.33 ns	<b>-0.66*</b>	-0.35 ns			
	g <sub>w</sub> PM	<b>0.53***</b>	-0.33 ns	0.09 ns	<b>0.52**</b>	-0.17 ns	-0.38 ns			
	$\delta C^{13}$	-0.16 ns								
	W <sub>d</sub>	0.23 ns								

Table A3 (Continued)

	All Species	<i>Q. garryana</i>	<i>F. latifolia</i>	<i>A. macrophyllum</i>	<i>C. cornuta</i>	<i>A. menziesii</i>	<i>P. menziesii</i>	<i>P. ponderosa</i>	<i>A. grandis</i>	
$\Psi_{sf}$	$\Psi_{sz}$	<b>0.93***</b>	<b>0.91***</b>	<b>1.0 ***</b>	<b>0.93***</b>	<b>0.76**</b>	<b>0.89***</b>	<b>0.89 ***</b>	<b>0.88***</b>	<b>0.68***</b>
	$\Psi_{amp}$	<b>-0.21**</b>	-0.12 ns	0.42 ns	<b>-0.61**</b>	-0.14 ns	-0.05 ns	0.01 ns	-0.11 ns	0.24 ns
	IE	<b>-0.63***</b>	<b>-0.45**</b>	<b>-0.97 **</b>	-0.39 ns	-0.26 ns	<b>-0.65**</b>	<b>-0.67***</b>	<b>-0.57**</b>	<b>-0.54***</b>
	RWC <sub>z</sub>	0.09 ns	<b>0.38*</b>	0.64 ns	0.23 ns	-0.07 ns	<b>0.50*</b>	0.26 ns	0.28 ns	0.31 ns
	Huber	<b>-0.48***</b>	-0.22 ns	0.59 ns	-0.36 ns	-0.15 ns	-0.13 ns	-0.29 ns	0.07 ns	-0.33 ns
	k <sub>s</sub>	<b>-0.25***</b>	0.14 ns	-0.05 ns	-0.05 ns	-0.21 ns	0.03 ns	0.32 ns	<b>0.53*</b>	-0.13 ns
	k <sub>l</sub>	<b>-0.41***</b>	-0.16 ns	0.15 ns	-0.29 ns	-0.23 ns	-0.07 ns	-0.13 ns	<b>0.55**</b>	-0.33 ns
	g <sub>w</sub> AM	<b>-0.40***</b>	-0.09 ns	-0.35 ns	-0.28	-0.09 ns	<b>0.69**</b>			
	g <sub>w</sub> PM	<b>-0.42***</b>	0.24 ns	0.37 ns	<b>-0.55*</b>	0.17 ns	0.46 ns			
	$\delta C^{13}$	0.26 ns								
	W <sub>d</sub>	<b>-0.73***</b>								
$\Psi_{sz}$	$\Psi_{amp}$	<b>-0.53***</b>	<b>-0.47**</b>	<b>0.42*</b>	<b>-0.84***</b>	<b>-0.53*</b>	<b>-0.40*</b>	<b>-0.37*</b>	<b>-0.54**</b>	<b>-0.49*</b>
	IE	<b>-0.60***</b>	-0.32 ns	<b>-0.97**</b>	-0.33 ns	0.14 ns	<b>-0.56**</b>	<b>-0.65 ***</b>	<b>-0.51*</b>	-0.29 ns
	RWC <sub>z</sub>	0.09 ns	<b>0.46**</b>	0.64 ns	0.34 ns	0.31 ns	0.39*	0.21 ns	0.30 ns	0.21 ns
	Huber	<b>-0.44***</b>	-0.22 ns	0.59 ns	-0.29 ns	-0.07 ns	0.02 ns	-0.28 ns	0.27 ns	<b>-0.48*</b>
	k <sub>s</sub>	-0.17*	0.21 ns	-0.05 ns	-0.07 ns	-0.21 ns	0.00 ns	<b>0.38*</b>	<b>0.46*</b>	0.09 ns
	k <sub>l</sub>	<b>-0.33***</b>	-0.09 ns	0.14 ns	-0.27 ns	-0.16 ns	-0.01 ns	-0.09 ns	<b>0.58**</b>	-0.22 ns
	g <sub>w</sub> AM	<b>-0.37**</b>	0.09 ns	-0.21 ns	-0.27	-0.09 ns	<b>0.69**</b>			
	g <sub>w</sub> PM	<b>-0.43***</b>	0.22 ns	0.37 ns	<b>-0.61**</b>	0.10 ns	0.49 ns			
	$\delta C^{13}$	<b>0.37*</b>								
	W <sub>d</sub>	<b>-0.74***</b>								

Table A3 (Continued)

		All Species	<i>Q. garryana</i>	<i>F. latifolia</i>	<i>A. macrophyllum</i>	<i>C. cornuta</i>	<i>A. menziesii</i>	<i>P. menziesii</i>	<i>P. ponderosa</i>	<i>A. grandis</i>
$\Psi_{amp}$	IE	0.17 ns	-0.22 ns	-0.39 ns	0.27 ns	<b>-0.7**</b>	0.15 ns	-0.05 ns	0.15 ns	-0.17 ns
	RWC <sub>z</sub>	-0.02 ns	-0.22 ns	0.00 ns	-0.29 ns	<b>-0.87**</b>	0.13 ns	-0.13 ns	-0.14 ns	0.08 ns
	Huber	0.03 ns	<b>-0.50**</b>	<b>0.59**</b>	0.21 ns	-0.31 ns	-0.16 ns	-0.19 ns	-0.42 ns	0.35 ns
	k <sub>s</sub>	-0.05 ns	-0.21 ns	-0.14 ns	0.09 ns	-0.14 ns	0.05 ns	-0.01 ns	-0.12 ns	-0.16 ns
	k <sub>l</sub>	-0.06 ns	-0.22 ns	0.09 ns	0.25 ns	-0.32 ns	-0.02 ns	-0.25 ns	-0.31 ns	-0.10 ns
	g <sub>w</sub> AM	0.24 ns	-0.26 ns	-0.5 ns	0.09 ns	0.09 ns				
	g <sub>w</sub> PM	<b>0.39**</b>	-0.11 ns	-0.08 ns	<b>0.60*</b>	-0.13 ns				
	$\delta C^{13}$	<b>0.39*</b>								
	W <sub>d</sub>	0.23 ns								
IE	RWC <sub>z</sub>	<b>0.58***</b>	<b>0.46**</b>	-0.56 ns	<b>0.59**</b>	<b>0.93**</b>	-0.07 ns	<b>0.41*</b>	<b>0.48*</b>	0.22 ns
	Huber	<b>0.52***</b>	0.39 ns	-0.70 ns	<b>0.73***</b>	-0.01 ns	0.20 ns	0.13 ns	0.15 ns	0.21 ns
	k <sub>s</sub>	<b>-0.19**</b>	-0.12 ns	0.22 ns	-0.21 ns	0.25 ns	-0.25 ns	-0.24 ns	<b>-0.41*</b>	0.07 ns
	k <sub>l</sub>	0.10 ns	0.30 ns	0.02 ns	<b>0.52*</b>	0.19 ns	-0.09 ns	0.21 ns	<b>-0.43*</b>	0.23 ns
	g <sub>w</sub> AM	<b>0.45***</b>	0.00 ns	<b>0.94***</b>	<b>0.94**</b>	0.00 ns	-0.48 ns			
	g <sub>w</sub> PM	<b>0.33**</b>	-0.14 ns	-0.35 ns	<b>0.85***</b>	-0.31 ns	-0.34 ns			
	$\delta C^{13}$	<b>0.41*</b>								
	W <sub>d</sub>	<b>0.54**</b>								
RWC <sub>z</sub>	Huber	<b>0.33***</b>	0.22 ns	0.14 ns	0.30 ns	0.08 ns	-0.14 ns	-0.27 ns	0.19 ns	0.03 ns
	k <sub>s</sub>	<b>-0.48***</b>	0.00 ns	0.09 ns	-0.15 ns	0.09 ns	-0.13 ns	0.11 ns	-0.02 ns	-0.11 ns
	k <sub>l</sub>	<b>-0.19**</b>	0.19 ns	0.07 ns	0.21 ns	0.15 ns	-0.18 ns	-0.06 ns	-0.08 ns	-0.16 ns
	g <sub>w</sub> AM	0.23 ns	-0.02 ns	<b>0.77**</b>	<b>0.77**</b>	0.19 ns	0.49 ns			
	g <sub>w</sub> PM	-0.03 ns	0.03 ns	0.72 ns	0.25 ns	-0.23 ns	0.39 ns			
	$\delta C^{13}$	0.19 ns								
	W <sub>d</sub>	-0.07								

Table A3 (Continued)

		All Species	<i>Q.</i> <i>garryana</i>	<i>F.</i> <i>latifolia</i>	<i>A.</i> <i>macrophyllum</i>	<i>C.</i> <i>cornuta</i>	<i>A.</i> <i>menziesii</i>	<i>P.</i> <i>menziesii</i>	<i>P.</i> <i>ponderosa</i>	<i>A.</i> <i>grandis</i>
Huber	$k_s$	0.02 ns	<b>-0.62***</b>	-0.45 ns	-0.33 ns	-0.05 ns	<b>-0.58 **</b>	<b>-0.67***</b>	0.09 ns	0.22 ns
	$k_l$	<b>0.51***</b>	0.19 ns	-0.24 ns	<b>0.51*</b>	0.54 ns	0.09 ns	<b>0.70***</b>	-0.08 ns	<b>0.70***</b>
	gw AM	<b>0.36**</b>	0.13 ns	<b>0.69**</b>	<b>0.73**</b>	-0.07 ns	-0.25 ns			
	gw PM	0.15 ns	-0.33 ns	-0.26 ns	<b>0.52*</b>	0.25 ns	0.05 ns			
	$\delta C^{13}$	0.03 ns								
	$W_d$	<b>0.58***</b>								
$k_s$	$k_l$	<b>0.80***</b>	0.15 ns	<b>0.95*</b>	<b>0.52*</b>	<b>0.64 *</b>	<b>0.70 ***</b>	-0.16 ns	<b>0.90***</b>	<b>0.74***</b>
	gwAM	<b>0.28*</b>	0.02 ns	<b>-0.51*</b>	-0.34	-0.34 ns	-0.04			
	gwPM	<b>0.42***</b>	0.20 ns	-0.03 ns	0.05 ns	0.00 ns	-0.39 ns			
	$\delta C^{13}$	<b>0.46**</b>								
	$W_d$	0.21								
$k_l$	gwAM	<b>0.33**</b>	0.05 ns	0.46 ns	0.45 ns	-0.13 ns	-0.31 ns			
	gwPM	0.17 ns	-0.28 ns	-0.09 ns	<b>0.59**</b>	0.08 ns	-0.35 ns			
	$\delta C^{13}$	<b>-0.35*</b>								
	$W_d$	<b>0.37**</b>								