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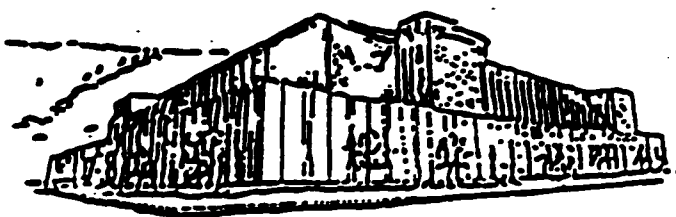
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**EVEN-AGED AND MULTIAGED PONDEROSA PINE:
A PHYSIOLOGICAL COMPARISON OF STAND STRUCTURE
AND PRODUCTIVITY**

by

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B.S. South Dakota State University, Brookings, SD 1994

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for the degree of

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Even-aged and multiaged ponderosa pine: A physiological comparison of stand structure and productivity

Director: Kevin L. O'Hara

**ABSTRACT**

Physiological and leaf structural characteristics were investigated in even-aged and multiaged stand structures of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) in western Montana and central Oregon. No differences in net photosynthesis (A_{net}), stomatal conductance (g_s), transpiration (E), instantaneous water use efficiency (WUE) or Ψ_{leaf} were observed in June in Oregon. As a whole, even-aged plots appeared to be more water-stressed than multiaged plots that were able to maintain higher rates of E in July in Montana.

In a seasonal comparison of one plot-pair in Montana in June, A_{net} was positively related to PAR, T_{air} , VPD and Ψ_{leaf} . In July and August, A_{net} and g_s decreased linearly with increasing T_{air} , VPD, and Ψ_{leaf} . The strongest correlation between A_{net} and these environmental variables occurred in August when water stress was greatest. In July, average daily transpiration (E) was significantly greater for multiaged trees. Multiaged trees also maintained higher rates of A_{net} , g_s , and E for a longer period of the day in July, suggesting less of a water limitation than in the even-aged stand structure.

Both A_{area} and A_{mass} were relatively constant with canopy depth in both stand structures. N_{area} and N_{mass} decreased with increasing canopy depth in the even-aged but not in the multiaged stand structures. SLA tended to increase with increasing canopy depth, although this relationship was significant only in the multiaged stand structures. N_{area} was highly correlated to SLA in both even-aged and multiaged stand structures. These data suggest that leaf structure and nitrogen investment are adjusted in ponderosa pine such that photosynthesis is maximized in comparable ways throughout the canopies of both types of stand structure.

It is concluded that water-limiting conditions found later in the growing season in both Montana and Oregon may influence diurnal gas exchange patterns in a way that could result in lower productivity in even-aged stand structures. These findings support the notion that multiaged stand structures of ponderosa pine have the physiological potential to produce similar amounts of wood volume as even-aged stand structures.

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LIST OF SYMBOLS

Symbol	Meaning	Units
A	photosynthetic rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{area}	net photosynthesis expressed on a leaf area basis	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{mass}	net photosynthesis expressed on a leaf mass basis	$\text{nmol m}^{-2} \text{s}^{-1}$
A_{max}	maximum photosynthesis rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{net}	net photosynthesis	$\mu\text{mol m}^{-2} \text{s}^{-1}$
E	transpiration	$\text{mmol m}^{-2} \text{s}^{-1}$
E_{max}	maximum transpiration rate	$\text{mmol m}^{-2} \text{s}^{-1}$
g_s	stomatal conductance	$\text{mol m}^{-2} \text{s}^{-1}$
$g_{s\text{-max}}$	maximum rate of stomatal conductance	$\text{mol m}^{-2} \text{s}^{-1}$
LI-6200	infrared gas exchange system made by Li-Cor, Inc.	
N_{leaf}	leaf nitrogen	g m^{-2}
N_{area}	leaf nitrogen expressed on a leaf area basis	g m^{-2}
N_{mass}	leaf nitrogen expressed on a leaf mass basis	mg g^{-1}
PAR	photosynthetically active radiation (400-700 nm)	nm
relative height	height of sample / height of tallest tree on the plot	unitless
SLA	specific leaf area	$\text{cm}^2 \text{g}^{-1}$
T_{air}	temperature of the air	$^{\circ}\text{C}$
VPD	vapor pressure difference	kPa
WUE	water use efficiency, A/E	$(\text{mmol CO}_2)/$ $(\text{mol H}_2\text{O})$
$\delta^{13}\text{C}$	stable carbon isotopic composition	$^{13}\text{C} : ^{12}\text{C}$
Ψ_{leaf}	xylem leaf water potential	MPa
Ψ_{predawn}	predawn xylem leaf water potential	MPa

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CHAPTER ONE

Diurnal fluctuations of gas exchange and water potential in different stand structures of *Pinus ponderosa* Dougl. ex Laws.

ABSTRACT

Leaf-level gas exchange and leaf water potential (Ψ_{leaf}) measurements were made over a diurnal time-course in multiaged and even-aged stand structures of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in central Oregon (June) and western Montana (July) to test for differences in physiological performance due to stand structure. Total site occupancy was similar between the geographical regions as measured by basal area, leaf area index, and stand density index. No differences in net photosynthesis (A_{net}), stomatal conductance (g_s), transpiration (E), instantaneous water use efficiency (WUE) or Ψ_{leaf} were observed in June in Oregon. As a whole, even-aged plots appeared to be more water-stressed than multiaged plots that were able to maintain higher rates of E in July in Montana. There were no differences in WUE between multiaged and even-aged stand structures in Montana, but because both A_{net} and E tended to be less in even-aged trees, overall productivity and efficiency of foliage may be less than in multiaged stand structures. It is concluded that under environmental conditions that are not limited by water, patterns in gas exchange and water use are unaffected by stand structure. Water-limiting conditions found later in the growing season in both Montana and Oregon may influence diurnal gas exchange patterns in a way that could result in lower productivity in even-aged stand structures.

INTRODUCTION

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is a widely distributed western North American conifer that has occurred historically in both even-aged and multiaged stand structures (Cooper 1960, White 1985, Habeck 1990, Arno et al. 1995, Harrod et al. 1999). Even-aged forest structures are usually considered to produce more volume than multiaged stand structures (Helms and Lotan 1988), but this depends on what type of merchantable product is desired (Guldin and Baker 1988, Guldin and Fitzpatrick 1991). Greater volume production could result if even-aged stands have higher site occupancy than multiaged stands (Baker et al. 1996). This is not necessarily the case in ponderosa pine if leaf area index (LAI) of overstory vegetation is assumed to represent site occupancy (O'Hara 1996, Valappil 1997).

Multiaged stand structures of ponderosa pine in Oregon have been shown to produce more volume per unit leaf area than even-aged stand structures (O'Hara 1996). O'Hara (1996) found that growth efficiency, defined as biomass or volume production per unit leaf area, also increased as the number of cohorts present in the stand increased (O'Hara 1996). This has been attributed to greater efficiency of the crowns of trees in multiaged stand structures, suggesting that foliage arrangement in different stand structures affects physiological performance and/or efficiency of foliage in individual tree crowns. Canopy position as dictated by stand structure becomes an important factor that influences resource allocation and competition within and between even-aged and multiaged stand structures and is an attribute that can be controlled through silvicultural intervention.

Growth efficiency of individual tree crowns tends to decline with increasing stand age (Long and Smith 1990, Long and Smith 1992, Yoder et al. 1994, Shi and Cao 1997), but these trends have been observed primarily in even-aged stand structures. Increasing sapwood respiration in larger trees has been hypothesized as an explanation for decreased growth efficiency, but this has recently been disputed (Ryan and Waring 1992, Ryan et al. 1997). Increased stand density may cause a decline in growth efficiency of individual trees if an optimum stand leaf area is exceeded (Waring et al. 1981, Oren et al. 1987, Roberts et al. 1993). There also appears to be an interaction between size, density, and canopy characteristics where growth efficiency of lodgepole pine (*Pinus contorta* Dougl.) declined with increasing canopy depth of even-aged stands (Smith and Long 1989).

The complexity of a forest structure, whether it consists of a single stratum as in an even-aged stand or multiple strata in a multaged stand, may affect biophysical properties such as precipitation, radiation, wind speed, temperature, and humidity (Parker 1995). Photosynthesis is regulated by many factors that work simultaneously, including direct and indirect effects of environmental factors (light, water, temperature, and CO₂ concentration), and structural characteristics of leaves and canopies (Stenberg et al. 1994, Stenberg et al. 1995, Teskey et al. 1995). The way leaves of trees in different stand structures respond to their environment influences the overall productivity of a stand. The functional relationship between stand structure and physiological performance of a given species with similar site occupancy in different stand structures is largely unknown.

The objectives of this study were: (1) to identify diurnal gas exchange and leaf water potential patterns in even-aged and multiaged stand structures of ponderosa pine; (2) to assess the influence of stand structure on limitations to gas exchange, including possible

water limitations in older trees of multiaged stand structures; and (3) to identify trends between the physiological parameters measured. By understanding the relationships between physiological performance in relation to structural variations in resources (light, water, and nutrients) we may better understand why similar production in terms of woody biomass is obtained from different stand structures.

MATERIALS AND METHODS

Study sites - This experiment was implemented in stands of ponderosa pine in two different geographic locations: western Montana and central Oregon. Study sites in Montana were located on the Bitterroot and Lolo National Forests, and on Lubrecht Experimental Forest. Sites in Oregon were located south of Bend, OR on the Deschutes National Forest. Pure stands of ponderosa pine (>95% ponderosa pine conifer composition) were selected, with individual plot pairs of even-aged and multiaged stand structures placed in areas that were close in proximity and deemed to be of the same or similar site quality based on slope, aspect and vegetation characteristics. Circular plots 0.1 ha in size were implemented in fully stocked stands, trying to avoid any differences in density both within plot pairs and between plot pairs within each geographical region. Habitat types (Pfister et al.1977) in Montana and plant associations in Oregon (Volland 1988) were identified for each plot, and were similar within each geographic region (Tables 1.1 and 1.2). Plot numbers followed by an E refer to even-aged plots; plot numbers followed by an M refer to multiaged plots (Tables 1.1 and 1.2)

Tree measurements - Each tree breast height (1.37 m) and taller was counted and measured. Total tree height and height to the base of the live crown were measured with a clinometer or a height pole, and diameter was measured at breast height. Two increment cores at right angles were taken from each tree 12.7 cm (5 in) and greater in breast height diameter to obtain age at breast height. The age range for the even-aged plots in Oregon was 37 to 85 years old (breast height age, Table 1.1). Average age of even-aged plots in Montana was 82 years, with the exception of plot 18 that was 11 years (breast height age, Table 1.2). Trees from the multiaged plots ranged from 5 to 211 years in Oregon, and 10 to 152 years in Montana. Bark thickness was measured with a bark-gauge to the nearest mm directly below the location of each core on each tree. Sapwood length was measured on the increment cores in the field, and later used to compute sapwood basal area. Leaf area per tree was computed using equations that relate sapwood basal area with leaf area of individual trees (O'Hara and Valappil 1995) in these two geographical areas. This concept is based on the pipe model theory to predict canopy leaf area presented by Waring et al. (1982). Sapwood basal area of trees less than 12.7 cm in diameter was assumed to be basal area minus the bark. Leaf area of each tree was computed, summed, and divided by the area of the plot to get leaf area index (LAI). Stand density index (SDI) was computed for each plot, using the formula:

$$SDI = \Sigma(DBH_i/10)^{1.6}$$

where DBH_i is the diameter of the i th tree in the stand (Long and Daniel 1990). For this study, there were four even-aged and three multiaged plots identified in Montana, and three even-aged and three multiaged plots in Oregon. Plots 14E and 18E at the Lubrecht site in Montana are two even-aged plots at different stages of stand development that are

compared to multiaged plot 13M for physiological measurements described below (Table 1.2).

Sample tree selection - For each even-aged plot, three trees were sampled at mid-canopy. Crown classification of individual trees was made following the definitions of Oliver and Larson (1996). Even-aged stands of ponderosa pine typically maintain one uniform canopy layer. All trees in the even-aged stand structures were classified as the B-stratum (upper continuous canopy layer) in this study. For each multiaged plot, four to five trees were sampled, encompassing the range of ages and sizes to represent the number of cohorts. Emergent trees belonging to the oldest cohort were classified as the A-stratum. Trees belonging to the middle cohort were considered the B-stratum, and because of their age and size, are the most comparable to those found in the even-aged plots. Two trees belonging to the B-stratum were typically sampled from the multiaged plots. Trees belonging to the youngest cohort were classified as the C-stratum (lower stratum beneath the B-stratum), and ranged from seedlings to saplings. All trees sampled were co-dominant within their respective strata.

Predawn xylem water potential - Predawn xylem leaf water potential (Ψ_{predawn}) was measured during the growing season of 1998 in both Oregon (June) and Montana (July). Previous studies have shown no difference in measured Ψ_{predawn} throughout tree canopies (Valappil and O'Hara 2000), so mid-canopies were chosen for consistent sampling and comparisons. One branch was excised from each sample tree, placed in a plastic ziplock bag, and put on ice until all samples were obtained. After all samples were gathered, Ψ_{predawn} was measured using a pressure chamber. Two fascicles of each branch were measured, in the order that the samples were obtained. These two measurements were

averaged to obtain an average Ψ_{predawn} for that branch. If the two fascicles measured were not within 0.2 MPa, a third fascicle was measured, and the two closest values were averaged to get the Ψ_{predawn} for that branch. As a check, the first branch measured was kept on ice and re-measured after all other samples to ensure that there was no effect of time since cutting on the measured Ψ_{leaf} .

Gas exchange - A field portable closed gas exchange system (LI-6200, Li-Cor Inc., Lincoln, NE) was used to measure net photosynthesis (A_{net}) and stomatal conductance (g_s) with a 1/4-l cuvette. Two one-year-old fascicles were excised from each branch and measured by placing the mid-portion of the fascicles inside the cuvette. Measurements were made every hour from 0800 to 1600 in Montana, and from 0900 to 1600 in Oregon. Early-morning temperatures in June in Oregon made calibrating the LI-6200 difficult, so measurements commenced at 0900. Samples were obtained with a 4-m tall platform and a pole pruner, or with a 12-gauge shotgun for larger trees. One sample from mid-canopy of each of the previously identified sample trees was obtained and measured at each hour. Measurements were completed within three minutes of detachment from the tree. Preliminary measurements found no difference in gas exchange when detached branches were measured within three minutes. Due to intermittent clouds in June in Oregon, a QED light source (Quantum Devices, Inc., Barneveld, WI) with a peak wavelength of 670 nm was used to supply additional light (at a rate of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$) to ensure that photosynthesis was not light-limited. All measurements were made on either sunny or mostly sunny days in both Montana and Oregon. Gas exchange measurements were taken on the same day for plots 3M and 4E, 11M and 12E, 14E and 18E, and 301M and 302E. Other combinations of plot pairs (13M, 14E and 18E, 303M and 304E, and 307M

and 308E) were measured on consecutive days because the proximity of the plots to each other made it impossible to measure each pair on the same day.

Computations of transpiration (E) and WUE - Transpiration (E) and water use efficiency (WUE) were computed using stomatal conductance and photosynthesis values obtained with the LI-6200. Immediately before each pair of fascicles was placed in the cuvette, the temperature of the air, T_{air} , (simulated by using the chamber temperature measured by the LI-6200) and relative humidity were recorded. Vapor pressure difference (VPD) was computed as:

$$VPD = (e_{sat}(T_{air}) - e_{air}) / \text{pressure (mb)}, \text{ where}$$

$$e_{sat} = 6.1078 * \exp((17.269 * T_{air}) / (237.3 + T_{air})), \text{ and}$$

$$e_{air} = e_{sat} * (RH/100)$$

following Campbell and Norman (1998). Transpiration was then computed as:

$$E = VPD * g_s * 1000$$

WUE was computed as photosynthesis/transpiration (A/E).

Ponderosa pine has three-needled fascicles with stomata on all surfaces. All physiological data are expressed on an all-sided leaf area basis. After gas exchange measurements, the width of the fascicles was measured to the nearest 0.1 mm, and multiplied by the width of the cuvette to obtain projected leaf area. Since the middle portion of the fascicles were measured, the area of ponderosa pine needles was assumed to be a right cylinder divided into thirds. It follows that the conversion factor from projected leaf area to all-sided leaf area is 2.36 (Rundel and Yoder 1998).

Data analysis – Diurnal patterns of photosynthesis (A_{net}), stomatal conductance (g_s), transpiration (E), WUE, and xylem leaf water potential (Ψ_{leaf}) are expressed as actual

values, even though mean values represent measurements taken on different days. It is likely that there were daily variations in temperature and VPD that influenced gas exchange. However, light was saturating to gas exchange for all measurements taken in Oregon and Montana. For the multiaged plots in Montana, diurnal values of A_{net} , g_s , E , WUE , and Ψ_{leaf} for each strata were weighted for the proportion of leaf area each strata represented in each plot. The proportions for the multiaged plots in Montana were as follows: Plot 3M: $A = 0.42$, $B = 0.55$, $C = 0.03$; Plot 11M: $A = 0.22$, $B = 0.77$, $C = 0.01$; Plot 13M: $A = 0.26$, $B = 0.51$, $C = 0.23$. Diurnal patterns of A_{net} , g_s , E , WUE , and Ψ_{leaf} are presented as structural means (even-aged and multiaged) with associated standard errors. An additional line is present representing the data weighted in the fashion just described for the multiaged plots (this is labeled as “multiaged weighted”). The diurnal data in Oregon could not be weighted because the A-stratum was not measured consistently on all plots, which resulted in an incomplete dataset. All even-aged trees were grouped together separately for Oregon and Montana regardless of measurement day or plot.

Mean daily values reported and tested are unweighted for both Oregon and Montana. Two-sample t-tests were used to compare differences between even-aged and multiaged means. One-way ANOVA was used to determine differences in stand structure where strata A, B, and C were tested against each other and the even-aged trees, and for tests between plots 13M, 14E, and 18E. Fischer’s LSD pair-wise comparison was used where ANOVA produced a significant effect. All differences were tested at the $\alpha = 0.05$ level. Linear regression was conducted on E and Ψ_{leaf} values separately for even-aged and

multiaged samples for both Oregon and Montana. All analyses were conducted with SYSTAT (SPSS Inc.).

RESULTS

Basal area, sapwood basal area, and LAI were greater for two of the three multiaged plots when compared to their even-aged counterparts in Oregon (Table 1.1). The reverse was generally true for the Montana plots (Table 1.2). Stand density index (SDI) was greater for all the even-aged plots in Montana as compared to the multiaged plots (Table 1.2), while two of the three multiaged plots in Oregon had greater SDI than the even-aged (Table 1.1).

Predawn leaf water potential (Ψ_{predawn}) measurements were lower in even-aged stand structures than their multiaged counterparts in July 1998 in Montana (Figure 1.1). Plot-level mean predawn Ψ_{predawn} ranged from -0.86 to -0.97 MPa in Montana and from -0.60 to -0.87 MPa in Oregon. There were no significant differences in Oregon between stand structures for Ψ_{predawn} measured in June, 1998.

Oregon physiology - Multiaged and even-aged stand structures followed a similar diurnal pattern for all physiological measurements (Figure 1.2a – 1.2d). Maximum photosynthetic rates (displayed as A_{net} in Figure 1.2a) appear to have been reached in mid-morning, and persisted into the afternoon. Average A_{net} never dropped below 50% of its maximum through the measurement period for either stand structure, suggesting few limitations to photosynthesis. Stomatal conductance (g_s) followed a similar pattern as A_{net} (Figure 1.2b), with no significant differences in average A_{net} , A_{max} , g_s , or $g_{s\text{-max}}$ between stand structures (Table 1.3).

Transpiration (E) reached its maximum at 1200 for even-aged trees, and 1400 for multiaged trees (Figure 1.2c), and did not decrease markedly through the measurement period. Water use efficiency ($WUE = A/E$) appeared higher for multiaged trees than even-aged trees for the middle portion of the diurnal time-course measured, with WUE decreasing throughout the day in both stand structures (Figure 1.2d). In general, Ψ_{leaf} was lower for even-aged trees throughout the measurement period, with average lowest values (-1.76 MPa) reached at 1100 (Figure 1.3). Lowest Ψ_{leaf} for multiaged trees (-1.70 MPa) was reached at 1300. There were no significant differences between daily means for any of the physiological measurements between stand structures in Oregon (Table 1.3).

Montana physiology – Net photosynthesis (A_{net}) in July on the Montana sites followed a similar trajectory for both stand structures in the early part the day (Figure 1.4a). After a peak around 1000-1100, the even-aged stand structures tended to decrease photosynthetic activity, while multiaged trees decreased at a lesser rate, forming a plateau of activity throughout the day. Integration under the diurnal curves from 0800 to 1600 showed that A_{net} was an average 22 and 25% less for even-aged trees as compared to weighted and unweighted mean diurnal values for multiaged trees. Stomatal conductance (g_s) peaked in the early morning for both stand structures, and followed a similar pattern as A_{net} , but decreased more steadily for both stand structures through the course of the day (Figure 1.4b). Overall mean A_{net} , g_s , and g_{s-max} were significantly greater for multiaged trees as compared to even-aged trees ($P < 0.05$, Table 1.4).

Transpiration (E) remained low in the early part of the day for both even-aged and multiaged stand structures, reached a plateau during the mid-portion of the day, and dropped off steadily during the late afternoon hours (Figure 1.4c). Integration under the

curves showed E to be an average 25 and 29% less for even-aged trees as compared to weighted and unweighted mean values for multiaged trees for the diurnal course. Maximum transpiration rates (E_{\max}) and average daily E were significantly lower for even-aged trees than multiaged trees ($P < 0.01$, Table 1.4). WUE followed the same pattern for both stand structures diurnally (Figure 1.4d). WUE was highest during the early part of the day when A_{net} was high but E was low due to low vapor pressure difference (VPD). WUE remained fairly constant during the mid-portion of the day when A_{net} , g_s , and E decreased steadily. This diurnal pattern mirrors that of the Oregon measurements (Figure 1.3d).

Leaf water potential (Ψ_{leaf}) started out more negative for even-aged trees, and remained lower than multiaged trees throughout the day with the exception of the last measurement period (Figure 1.5). Overall mean Ψ_{leaf} and lowest (minimum) Ψ_{leaf} was more negative for even-aged trees than multiaged trees ($P < 0.01$, Table 1.4). Multiaged trees in the middle (B) and lowest strata (C) had significantly higher mean Ψ_{leaf} than even-aged trees ($P < 0.05$ and $P < 0.01$ respectively, Table 1.4).

There were no significant differences in gas exchange between even-aged and multiaged trees at the Larry Creek site (plots 11M and 12E, Table 1.5), which was the first site measured in July in Montana. E was significantly higher on the multiaged plot at the Tarkio site (plots 3M and 4E, Table 1.5), but there was no significant difference between any other physiological variables. There were significant differences between both even-aged plots (14E and 18E) and the multiaged plot (13M) at the Lubrecht site for all physiological measurements (Table 1.5). The multiaged trees measured at Lubrecht

had greater gas exchange (A_{net} , A_{max} , g_s , $g_{s\text{-max}}$, E , and E_{max}) as well as overall higher Ψ_{leaf} .

E and Ψ_{leaf} - The relationship between Ψ_{leaf} reached at different transpiration rates was significant for both even-aged and multiaged stand structures in both Oregon and Montana (Figure 1.6). (Note that only plots 301M and 302E are shown in Oregon because those are the only two plots where Ψ_{leaf} was measured, and plots 3M and 4E in Montana because that is the only plot-pair where Ψ_{leaf} was measured on the same day). E was greater and Ψ_{leaf} less negative in Oregon for both stand structures as compared to Montana (Tables 1.3 and 1.4). In both Montana and Oregon, multiaged trees showed overall higher E than the even-aged trees, while the even-aged trees showed more negative Ψ_{leaf} than the multiaged trees (Tables 1.3 and 1.4, and Figure 1.6).

DISCUSSION

Plants have evolved various means for avoiding or tolerating water stress. The fastest way for plants to avoid excessive water loss is through stomatal control (Cowan 1982). Plants essentially exchange H_2O for CO_2 , and stomatal conductance plays a role in regulating photosynthesis and transpiration (Cowan 1982). Ponderosa pine is generally thought to be a water use efficient conifer (Franklin and Dyrness 1988, Anthoni et al. 1999), and its physiology appears to be influenced by stand age and forest structure (Yoder et al. 1994, Valappil 1997). In the present study, greater photosynthetic rates in multiaged trees in Montana suggest foliage of these trees is performing better than foliage of trees in even-aged stand structures. Water appears to be less limiting in these multiaged stand structures as shown by higher water potentials throughout the day

combined with greater transpiration rates. Maximum rates of photosynthesis and stomatal conductance (shown as A_{net} and g_s in Figures 1.4a and 1.4b) were similar in magnitude and peaked at the same time for both stand structures in Montana. As the day progressed, differences in the rate of decline could lead to considerable differences in overall productivity of these stands, with even-aged trees showing a greater decline in gas exchange. Overall, multiaged trees achieved higher levels of g_s and E, with these higher levels being maintained for a longer period in the day.

It is difficult to quantify and compare densities of even-aged and multiaged stands to determine whether they are occupying a site to an equal degree. SDI allows comparison of stand density between stand structures by giving each tree on the plot a value that represents the degree of site occupancy it would have as compared to a tree 25.4 cm (10 in) in diameter (Long and Daniel 1990). Comparisons of SDI gave more distinct differences between even-aged and multiaged stand structures than other measures of site occupancy used in this study (LAI and basal area) in both Oregon and Montana (Tables 1.1 and 1.2). SDI differed by 11-31% in Oregon and by 9-23% in Montana between even-aged and multiaged plots. Therefore, it is difficult to conclude that density did not influence physiological performance between different stand structures of ponderosa pine in this study. LAI was greater for the multiaged plot at Tarkio (3M), as well as the multiaged plot at Lubrecht (13M) as compared to the younger even-aged plot (Table 1.2). Leaf-level gas exchange tended to be higher in both of these multiaged plots as compared to their even-aged counterparts (Table 1.5), despite the greater LAI, further suggesting an influence of stand structure on leaf physiology.

A number of studies have investigated physiology of various sized trees and in forest stands of varying growing stock levels, including some in ponderosa pine. Water potential is assumed to be a measure of plant moisture stress, representing an integration of soil and internal plant water status (Running 1976). Water potential might be expected to be higher (less negative) in stands of lower density, as there would be more water available to each tree. Higher predawn water potentials have been observed with decreasing density (37 to 78% reduction in initial density) in lodgepole pine (Donner and Running 1986) and ponderosa pine (Stone et al. 1999). Schmid et al. (1991) found decreases in predawn and midday Ψ_{leaf} with increasing density in ponderosa pine in the Black Hills (density ranged from 13.8 to 40 $\text{m}^2 \text{ha}^{-1}$), but the influence of seasonal variation was also present and significant. Kolb et al. (1998) showed a consistent decrease in predawn and midday Ψ_{leaf} with increasing basal area (ranging between 6.9 to 78.2 $\text{m}^2 \text{ha}^{-1}$). Basal area in the present study was comparable to the intermediate stand density reported by Kolb et al. (1998). The range in stand density in the present study is also relatively small (21.8 to 25.62 $\text{m}^2 \text{ha}^{-1}$ in Montana with the exception of plot 18E, and 17.2 to 17.8 $\text{m}^2 \text{ha}^{-1}$ in Oregon). Therefore, the range in stand density found in this study should not be a significant factor between plots when considering water relations, although stand density was not tested.

Small differences in Ψ_{predawn} suggests trees of both stand structures were equally able to replenish water storage at night, resulting in the same water status at the beginning of each day. Water potential variation diurnally suggests a different pattern in water usage and may influence subsequent physiological functions. Average midday and lowest Ψ_{leaf} reached differed significantly between multiaged and even-aged trees on the Montana

sites (Table 1.4), suggesting some influence of water status on physiologic function between stand structures. There were no differences in Ψ_{leaf} between stand structures in Oregon, but Ψ_{leaf} was measured on only two plots. Running (1976) identified two major influences of water potential on g_s ; the first is the assumption that Ψ_{predawn} controls the maximum g_s obtainable, and the second is the notion of a threshold Ψ_{leaf} . Others have identified a threshold Ψ_{leaf} with which major declines in gas exchange are observed. For ponderosa pine, this is typically assumed to be between -1.3 and -1.8 MPa (Cleary 1971, Lopushinsky 1969, Bunce 1979). Lopushinsky and Klock (1974) claimed ponderosa pine operates at only 12% of its maximum E when soil water potentials reach -1.0 MPa (under controlled experimental conditions). In a growth chamber study, ponderosa pine exhibited an exponential decrease in g_s and a linear decrease in A_{net} as Ψ_{leaf} decreased under water-stressed and well-watered conditions (Zhang et al. 1997). In this study, there was a significant relationship between E and Ψ_{leaf} for both even-aged and multiaged stand structures in Oregon and Montana (Figure 1.6). This relationship, combined with the diurnal differences in Ψ_{leaf} , E, and g_s between trees of varying canopy positions (Tables 1.3 and 1.4) suggest trees in the C and B strata in the multiaged stand structures are the optimum size and in the best canopy position for maintaining high levels of gas exchange for longer periods of the day. This implies that trees in a multiaged stand structure may be growing under more favorable conditions that may result in higher levels of overall productivity as compared to trees in a single canopy stratum in an even-aged stand structure. It is important to note that the trees that were sampled in this study were

codominant within their representative strata, meaning that they were not overtopped or suppressed by neighboring trees within the same stratum.

The above assertion contradicts the notion that the top strata in a multiaged forest canopy will have the fastest growth rate, and presumably the highest rates of gas exchange due to its superior position where resources such as light would not be limiting (O'Hara 1996). Recently, it has been argued that foliage from older trees operates at lower levels of gas exchange due to increasing hydraulic resistance with increasing height (Yoder et al. 1994, Mencuccini and Grace 1996, Hubbard et al. 1999). Lower predawn and midday Ψ_{leaf} in tall trees has also been observed in large trees (Yoder et al. 1994, Bauerle et al. 1999). Although the sample size for the oldest cohort of trees measured in the present study was small, no differences were observed in midday Ψ_{leaf} , or any other physiological parameter measured when compared to other canopy locations or even-aged trees. This neither supports nor disproves the hydraulic limitation theory of Ryan and Yoder (1997), but it would appear that foliage from tall trees (although sampled only at mid-canopy in this study) was not limited in any way differently than foliage from other strata in the canopy.

Pinus species tend to have high WUE when compared to other sympatric coniferous or deciduous species (Marshall and Zhang 1994, Rundel and Yoder 1998). High WUE results from either high photosynthesis, low transpiration or both (Zhang et al. 1997), and is often associated with lower carbon assimilation due to the greater resistance of CO_2 in comparison to H_2O (Cowan 1982). Previous research comparing long-term WUE in even-aged and multiaged stand structures of ponderosa pine based on stable-carbon isotope discrimination suggests that trees in even-aged stand structures are more water

use efficient than in multiaged, further implying lower overall productivity of foliage in even-aged stands (Valappil and O'Hara 2000). Zhang et al. (1997) concluded that a drought avoidance strategy is more important for growth than high (instantaneous) WUE. In the case of populations of ponderosa pine that differed in drought tolerance, having plasticity to photosynthesize at higher rates when conditions were favorable with the ability to close stomates to reduce water loss under water-stressed conditions resulted in the best drought avoidance strategy (Zhang et al. 1997). Instantaneous WUE, as computed in this study, did not differ between stand structures or with crown position. Since WUE is a ratio of carbon fixed to water lost, and given that even-aged trees showed both lower A_{net} and E overall, then the ratios of A/E may be the same for both stand structures. Collectively, even-aged stands may be less productive because of overall lower rates of photosynthesis, explaining why integrated WUE may be higher in even-aged stands, as shown in previous work (Valappil and O'Hara 2000). It is concluded that trees in certain crown positions in multiaged stand structures may be more productive because of greater rates of gas exchange and not necessarily because of differences in instantaneous WUE.

This study looked at physiological performance of pure ponderosa pine stands in two ecologically different geographic areas at two different points in time during the growing season. The measurements in Oregon were done in late June when soil moisture is still generally available. Therefore, the trees were measured when water was less limiting than later in the growing season. In Montana, July can be quite dry, presenting more severe water limitations than earlier in the growing season. Daily maximum temperatures may also contribute to limitations in gas exchange by increasing the VPD

between leaves and the air. Therefore, measurements taken in July under growing conditions that involved a limitation due to water stress may be elucidating differences in stand structure that are not present under non-limiting conditions. The Larry Creek site was sampled earliest in July, and although the density of these plots was comparable to other plots, maximum rates of photosynthesis (A_{\max} , Table 1.5) were the highest when compared to all other plots in Montana. Transpiration rates were highest on the multiaged plot in Lubrecht (plot 13M) even though that plot was measured latest in July. The most significant differences in physiology between plots occurred at the Lubrecht site, where the multiaged plot had greater A_{net} , g_s , E and higher Ψ_{leaf} as compared to both even-aged plots at Lubrecht. The even-aged plots (plots 14E and 18E) had similar densities with no differences in these physiological variables, while the multiaged plot (plot 13M) had lower stand density and significantly greater gas exchange. These results must be interpreted with some caution, as gas exchange and Ψ_{leaf} at the multiaged plot was measured two days after the even-aged plots at the Lubrecht site. There was a total of 18 mm of precipitation recorded at Lubrecht Experimental Forest for the month of July, but none of that occurred between measurement days from this study (precipitation was recorded on July 1, 4, 16, 17, and 24). Still, there appears to be a difference in water status between plots in July as the average Ψ_{leaf} measured at hour 0800 on the multiaged plot was -0.95 MPa while the even-aged were -1.40 and -1.25 MPa for plots 14E and 18E respectively. Even though these values do not necessarily reflect Ψ_{predawn} , they probably provide a fair representation of plant water status. Air temperature and vapor pressure difference (VPD) followed a very similar trajectory throughout each measurement period (data not shown). Differences in physiology between the multiaged

and even-aged plots at Lubrecht are therefore possibly the result of differences in site occupancy, plant water status as influenced by soil water availability, or due to physiological differences as influenced by stand structure.

The fact that no differences were detected between stand structures in Oregon, while significant differences were found in Montana could be explained by various reasons other than increasing water stress associated with the growing season. The first could be a difference in stand structure and ecophysiology of ponderosa pine between Oregon and Montana, although it is the same variety in both areas (*Pinus ponderosa* var. *ponderosa*, Read 1980). The second reason could be an overall difference in climate between the two regions, and differences in site related to soil characteristics. It is also possible that pairs of even-aged and multiaged plots were not matched up in the same way (due to density, site characteristics (habitat type, plant association, soil, or microclimate differences) or some other factor). Since multiple comparisons were not done in each area, it is impossible to attribute the difference in findings to any particular reason. Differences in time of measurement (growing season) certainly played a major role in the water dynamics of each stand structure, and probably greatly influenced physiological performance.

As mentioned previously, density between even-aged and multiaged plots was measured in terms of basal area, SDI, and LAI. LAI can be viewed as the amount of photosynthetic machinery present in a stand. Greater LAI may contribute to greater gross production potential because of greater photosynthetic material on the site, but may also suggest that the machinery present may be less efficient due to limitations posed to individual trees by greater site occupancy leading to greater competition for limited

resources or increased respiration. Thus, productivity of a stand could be viewed as a function of the amount of photosynthesizing material (LAI) and the rate of carbon assimilation (A_{net}). There were no clear trends in LAI or basal area between even-aged and multiaged plots in this study (Tables 1.1 and 1.2), but if a stand has a lower A_{net} with greater LAI than a stand with less LAI but higher A_{net} , net productivity of the stands might be similar. Therefore, in order to draw clear conclusions from the research presented, one would need to take into account both rates of productivity and some measure of site occupancy. Higher growth efficiency in multiaged stands (O'Hara 1996) combined with greater rates of gas exchange observed in this study add to the evidence that multiaged stand structures have the ability to out-perform even-aged stand structures physiologically when both stand structures have comparable LAI.

In conclusion, the present study conducted in a small number of stands gives evidence toward differential rates of carbon assimilation that appear to be related to site water balance and perhaps canopy position within different stand structures. Under environmental conditions that are not limited by water, patterns in gas exchange and water use appear unaffected by stand structure. Water-limiting conditions influence diurnal gas exchange patterns in a way that could result in lower productivity of even-aged stand structures. Because this study was not conducted throughout an entire growing season, it is impossible to speculate on the contributions of other parts of the growing season to overall productivity in different stand structures. A combination of site occupancy, previous growth, and physiological performance will best represent the functional differences between stand structures.

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Table 1.1. Plot attributes for Oregon plots. Plots were circular and 0.1 ha in size. Plant associations follow those identified by Volland (1988). Abbreviations: PIPO = *Pinus ponderosa* Dougl. ex Laws., PUTR = *Purshia tridentata* (Pursh) DC., ARTR = *Artemisia tridentata* Nutt., FEID = *Festuca idahoensis* Elmer, ARPA = *Arctostaphylos patula* Greene, CEVE = *Ceanothus velutinus* Dougl.

Plot No.	Plot Type	Location	LAI (all-sided)	Average Age or Age Range at BH	Trees per Hectare	Basal Area (m ² ha ⁻¹)	Sapwood Basal Area (m ² ha ⁻¹)	SDI	Plant Association
301M	multiaged	LaPine	4.94	51-211	240	22.77	15.52	377	PIPO/PUTR/FEID
302E	even-aged	LaPine	5.30	85	350	24.99	16.65	453	PIPO/PUTR-ARTR/FEID
303M	multiaged	Bend	4.43	5-110	660	19.55	13.92	347	PIPO/PUTR-ARPA/FEID
304E	even-aged	Bend	4.32	58	220	17.80	13.59	310	PIPO/PUTR-ARPA/FEID
307M	multiaged	Wickiup	5.06	18-146	470	25.26	15.91	434	PIPO/PUTR-CEVE/FEID
308E	even-aged	Wickiup	3.81	37	330	17.21	11.96	326	PIPP/PUTR-CEVE/FEID

Table 1.2. Plot attributes for Montana plots. Plots were circular and 0.1 ha in size, except plot 18E which was 0.01 ha. Habitat types follow those identified by Pfister et al. (1977). Abbreviations: PSME = *Pseudotsuga menziesii* (Mirbel) Franco., PIPO = *Pinus ponderosa* Dougl. ex Laws., CARU = *Calamagrostis rubescens* Buckl., CAGE = *Carex geyeri* Boott, ARUV = *Arctostaphylos uva-ursi* (L.) Spreng., AGSP = *Agropyron spicatum* (Pursh) Scribn. & Smith.

Plot No.	Plot Type	Location	LAI (all-sided)	Average Age or Age Range at BII	Trees per Hectare	Basal Area (m ² ha ⁻¹)		SDI	Habitat Type	
						Basal Area	Sapwood Basal Area			
3M	multiaged	Tarkio Road	5.63	20-132	350	21.76	14.38	384		PSME/CAGE
4E	even-aged	Tarkio Road	5.53	81	410	24.22	14.13	470		PSME/CAGE
11M	multiaged	Larry Creek	5.42	10-126	620	23.76	13.76	441		PSME/CAGE
12E	even-aged	Larry Creek	5.49	86	720	23.28	13.90	491		PSME/CAGE
13M	multiaged	Lubrecht	5.53	34-152	450	21.90	14.10	398		PSME/CARU/ARUV
14E	even-aged	Lubrecht	6.29	79	620	25.62	16.01	518		PSME/CARU/ARUV
18E	even-aged	Lubrecht	5.38	11	2700	15.11	12.97	436		PSME/CARU/ARUV

Table 1.3. Daily means for physiological measurements in Oregon. There were no significant differences. Standard errors are given in parentheses. Water potential (Ψ_{leaf}) was measured on plots 301M and 302E only (N = 5 and N = 4, respectively). Under structure type, A, B, and C refer to canopy strata. Data are unweighted.

Structure Type	N	A_{net} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	g_{s-max} ($\text{mol m}^{-2} \text{s}^{-1}$)	E ($\text{mmol m}^{-2} \text{s}^{-1}$)	E_{max} ($\text{mmol m}^{-2} \text{s}^{-1}$)	WUE ($\text{mmol CO}_2 / \text{mol H}_2\text{O}$)	Ψ_{leaf} (MPa)	min Ψ_{leaf} (MPa)
Multi-A	2	3.88 (0.44)	6.28 (0.26)	0.061 (0.005)	0.085 (0.010)	0.92 (0.36)	1.48 (0.54)	5.33 (2.41)	--	--
Multi-B	8	4.89 (0.29)	6.35 (0.30)	0.072 (0.004)	0.093 (0.007)	1.32 (0.13)	2.11 (0.18)	5.12 (0.85)	--	--
Multi-C	4	5.32 (0.22)	7.04 (0.10)	0.074 (0.004)	0.101 (0.009)	1.35 (0.19)	1.90 (0.23)	4.96 (1.26)	--	--
Even-B	12	4.89 (0.32)	6.57 (0.23)	0.068 (0.004)	0.088 (0.004)	1.17 (0.08)	1.71 (0.11)	5.01 (0.51)	--	--
Multi	14	4.87 (0.22)	6.54 (0.19)	0.071 (0.003)	0.094 (0.005)	1.27 (0.10)	1.96 (0.14)	5.10 (0.63)	-1.58 (0.01)	-1.78 (0.01)
Even	12	4.89 (0.32)	6.57 (0.23)	0.068 (0.004)	0.088 (0.004)	1.17 (0.08)	1.71 (0.11)	5.01 (0.51)	-1.66 (0.04)	-1.81 (0.05)

Table 1.4. Daily means for physiological measurements in Montana. Significant differences ($\alpha = 0.05$) are denoted by letters that are not the same. Standard errors are given in parentheses. N for water potential values (Ψ'_{leaf}) are as follows: A = 2, B = 3, C = 3, Multi = 8, Even = 8. Under structure type, A, B, and C refer to canopy strata. Data are unweighted.

Structure	N	A_{net} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	$g_{s,max}$ ($\text{mol m}^{-2} \text{s}^{-1}$)	E ($\text{mmol m}^{-2} \text{s}^{-1}$)	E_{max} ($\text{mmol m}^{-2} \text{s}^{-1}$)	WUE ($\text{mmol CO}_2/$ ($\text{mol H}_2\text{O}$)	Ψ'_{leaf} (MPa)	min Ψ'_{leaf} (MPa)
Multi-A	3	3.83 (0.78) ^a	5.50 (1.13) ^a	0.045 (0.010) ^a	0.068 (0.015) ^a	1.02 (0.13) ^a	1.60 (0.06) ^a	4.34 (0.22) ^a	-1.56 (0.02) ^{ab}	-1.81 (0.06) ^a
Multi-B	5	4.37 (0.48) ^a	5.89 (0.59) ^a	0.052 (0.008) ^a	0.061 (0.008) ^a	1.14 (0.12) ^a	1.71 (0.16) ^a	4.73 (0.17) ^a	-1.55 (0.09) ^a	-1.85 (0.08) ^a
Multi-C	5	5.14 (0.45) ^a	6.57 (0.29) ^a	0.063 (0.008) ^a	0.077 (0.004) ^a	1.43 (0.19) ^{ab}	2.16 (0.31) ^{ab}	4.40 (0.18) ^a	-1.44 (0.03) ^a	-1.83 (0.04) ^a
Even-B	12	3.45 (0.33) ^a	5.57 (0.34) ^a	0.037 (0.005) ^a	0.055 (0.004) ^a	0.82 (0.08) ^{ac}	1.23 (0.11) ^{ac}	4.57 (0.12) ^a	-1.73 (0.04) ^b	-1.98 (0.06) ^a
Multi	13	4.54 (0.32) ^a	6.06 (0.35) ^a	0.054 (0.005) ^a	0.069 (0.005) ^a	1.22 (0.10) ^a	1.86 (0.14) ^a	4.51 (0.11) ^a	-1.51 (0.04) ^a	-1.83 (0.03) ^a
Even	12	3.45 (0.33) ^b	5.57 (0.34) ^a	0.037 (0.005) ^b	0.055 (0.004) ^b	0.82 (0.08) ^b	1.23 (0.11) ^b	4.57 (0.12) ^a	-1.73 (0.04) ^b	-1.98 (0.06) ^b

Table 1.5. Mean values from physiological measurements for individual trees on plots in Montana. Data are unweighted. Standard errors are given in parentheses. Significant differences ($\alpha = 0.05$) within each plot pair are denoted by letters that are different. N for water potential values (Ψ_{leaf}) are as follows: Plot 3M = 3, Plot 4E = 2, Plot 13M = 5, Plot 14E = 3, Plot 18E = 3.

Plot Number	Tarkio		Larry Creek		Lubrecht		
	3M	4E	11M	12E	13M	14E	18E
Plot type	multiaged	even-aged	multiaged	even-aged	multiaged	even-aged	even-aged
Date	7/14/99	7/14/99	7/8/99	7/8/99	7/22/99	7/20/99	7/20/99
N	4	3	4	3	5	3	3
A_{net} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	3.06 (0.27) ^a	2.31 (0.43) ^a	5.27 (0.23) ^a	5.13 (0.07) ^a	5.13 (0.29) ^a	3.05 (0.18) ^b	3.31 (0.27) ^b
A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	4.23 (0.57) ^a	4.76 (0.70) ^a	6.97 (0.08) ^a	6.99 (0.16) ^a	6.64 (0.10) ^a	5.20 (0.54) ^b	5.43 (0.42) ^b
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	0.031 (0.003) ^a	0.022 (0.003) ^a	0.062 (0.002) ^a	0.062 (0.002) ^a	0.067 (0.006) ^a	0.029 (0.002) ^b	0.035 (0.003) ^b
$g_{s,max}$ ($\text{mol m}^{-2} \text{s}^{-1}$)	0.047 (0.006) ^a	0.040 (0.004) ^a	0.08 (0.004) ^a	0.075 (0.000) ^a	0.077 (0.005) ^a	0.045 (0.006) ^b	0.060 (0.003) ^b
E ($\text{mmol m}^{-2} \text{s}^{-1}$)	0.88 (0.06) ^a	0.56 (0.08) ^b	1.24 (0.05) ^a	1.22 (0.04) ^a	1.48 (0.17) ^a	0.66 (0.03) ^b	0.84 (0.17) ^b
E_{max} ($\text{mmol m}^{-2} \text{s}^{-1}$)	1.49 (0.10) ^a	0.80 (0.13) ^b	1.73 (0.02) ^a	1.59 (0.04) ^a	2.25 (0.29) ^a	1.14 (0.09) ^b	1.40 (0.29) ^{ab}
WUE [(mmol CO ₂)/ (mol H ₂ O)]	4.26 (0.17) ^a	4.54 (0.30) ^a	4.52 (0.03) ^a	4.35 (0.28) ^a	4.70 (0.24) ^{ab}	5.04 (0.09) ^a	4.34 (0.04) ^b
Ψ_{leaf} (MPa)	-1.58 (0.07) ^a	-1.89 (0.08) ^a	--	--	-1.47 (0.03) ^a	-1.73 (0.03) ^b	-1.65 (0.04) ^b
min Ψ_{leaf} (MPa)	-1.88 (0.07) ^a	-2.20 (0.10) ^a	--	--	-1.80 (0.03) ^a	-1.93 (0.03) ^b	-1.87 (0.02) ^{ab}
max Ψ_{leaf} (MPa) (0800 hr)	-1.21 (0.08) ^a	-1.30 (0.10) ^a	--	--	-0.95 (0.08) ^a	-1.40 (0.06) ^b	-1.25 (0.09) ^b

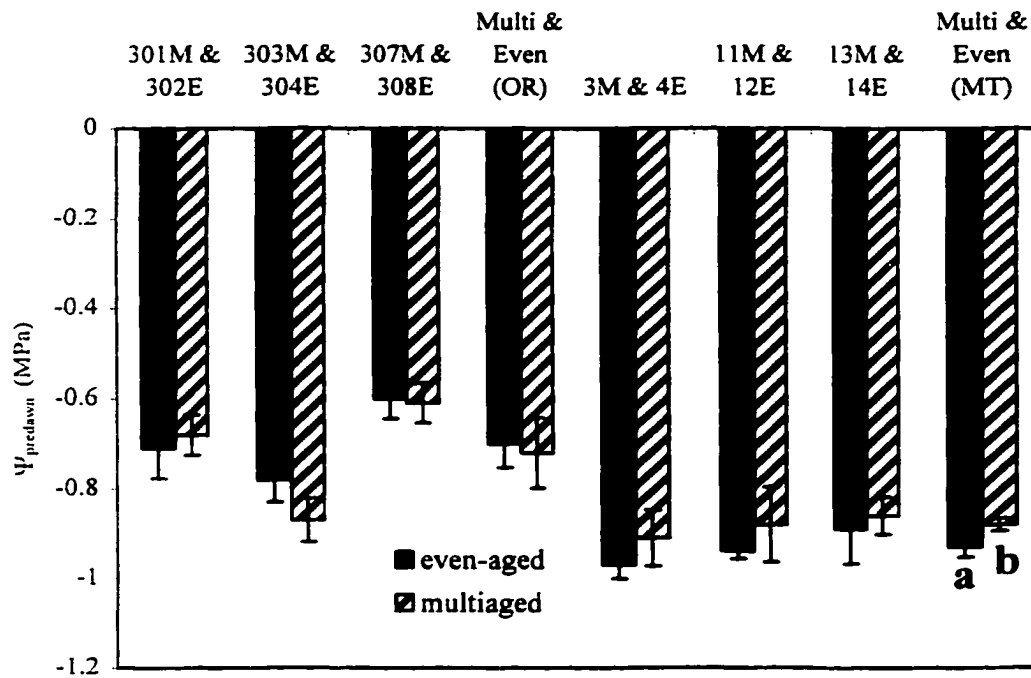


Figure 1.1. Predawn leaf water potential (Ψ_{predawn}) values measured in Oregon (June 1998) and Montana (July 1998). Error bars represent +/- one standard error. $N = 3$ for each even-aged bar, $N = 5$ for each multiaged bar. Letters that are different within each pair denote significant differences at the $\alpha = 0.05$ level. Data are unweighted.

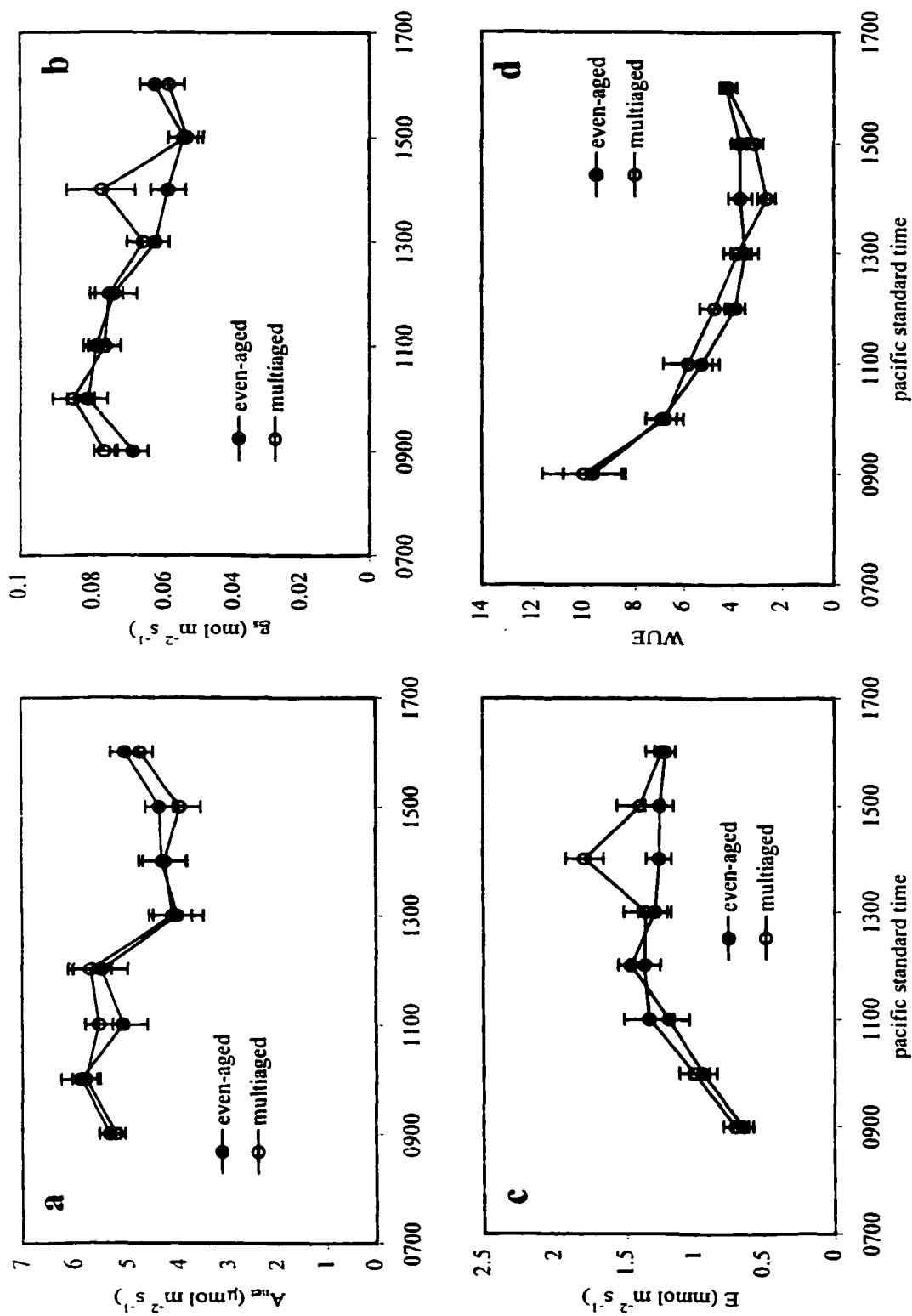


Figure 1.2. Diurnal patterns of gas exchange measured in June 1999 in Oregon: (a) photosynthesis (A_{net}), (b) stomatal conductance (g_s), (c) transpiration (E), and (d) water use efficiency (WUE). Error bars represent \pm one standard error. Data are unweighted.

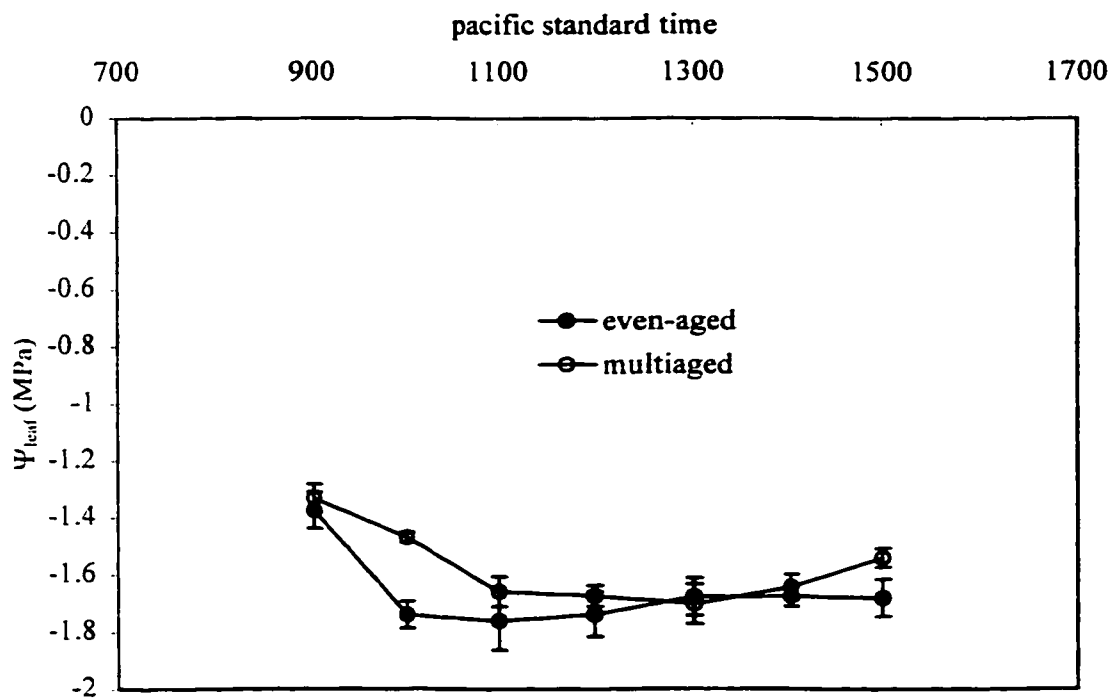


Figure 1.3. Diurnal pattern of leaf water potential (Ψ_{leaf}) in June (1999) for plots 301M and 302E in Oregon. Data are unweighted.

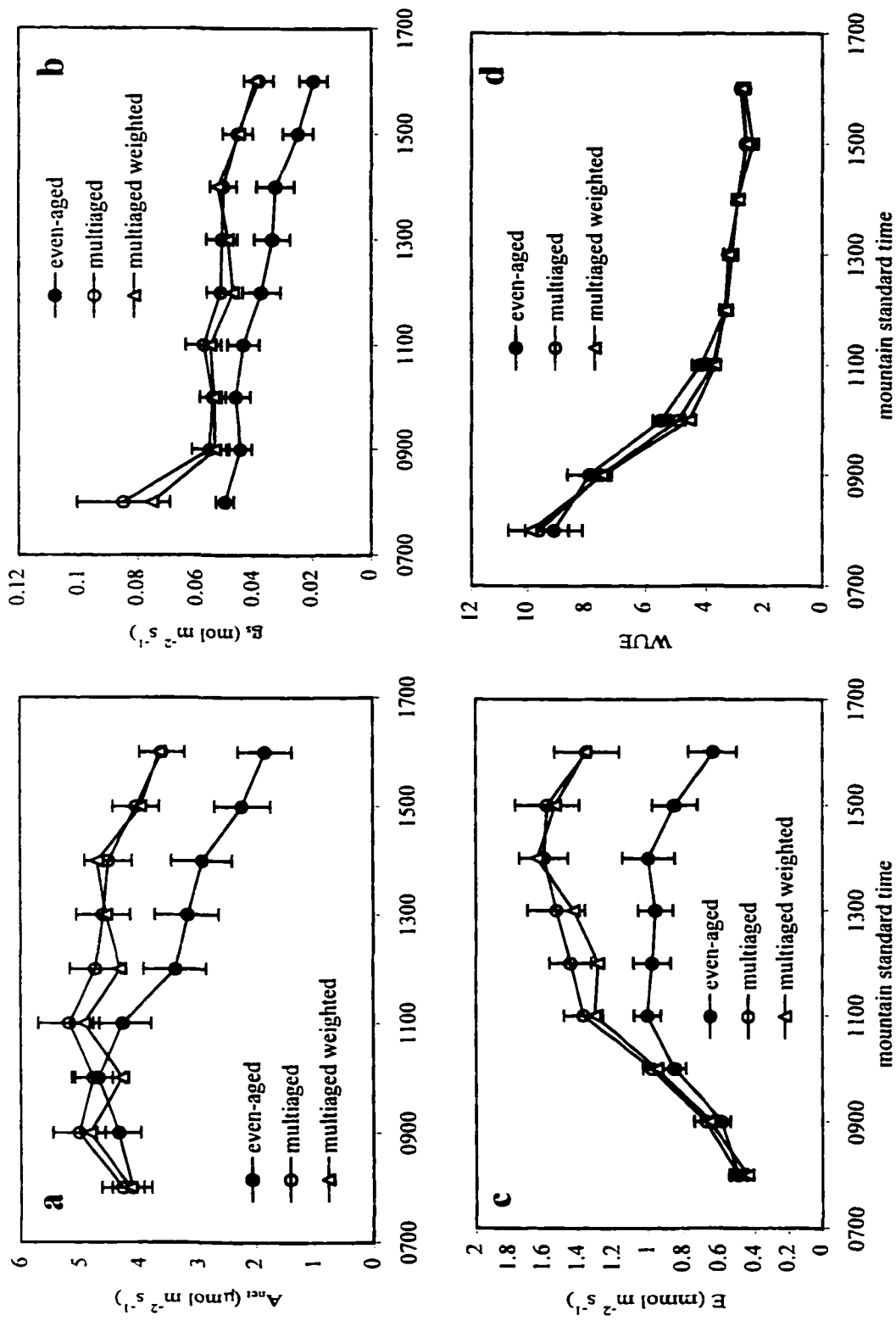


Figure 1.4. Diurnal patterns of gas exchange measured in July 1999 in Montana: (a) photosynthesis (A_{net}), (b) stomatal conductance (g_s), (c) transpiration (E), and (d) water use efficiency (WUE). Error bars represent +/- one standard error. Multiaged weighted refers to the data being weighted for the amount of leaf area present within each strata.

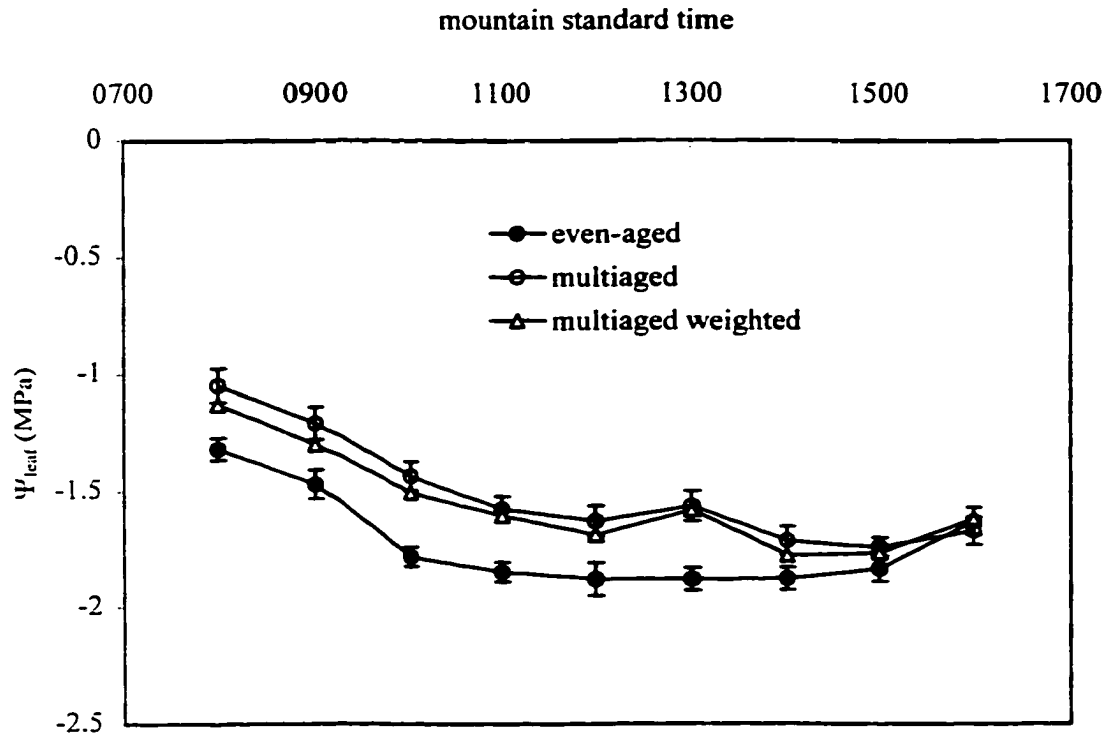


Figure 1.5. Diurnal pattern of leaf water potential (Ψ_{leaf}) in July (1999) for plots 3M, 4E, 13M, 14E, and 18E in Montana. Multiaged weighted refers to the data being weighted for the amount of leaf area present within each strata.

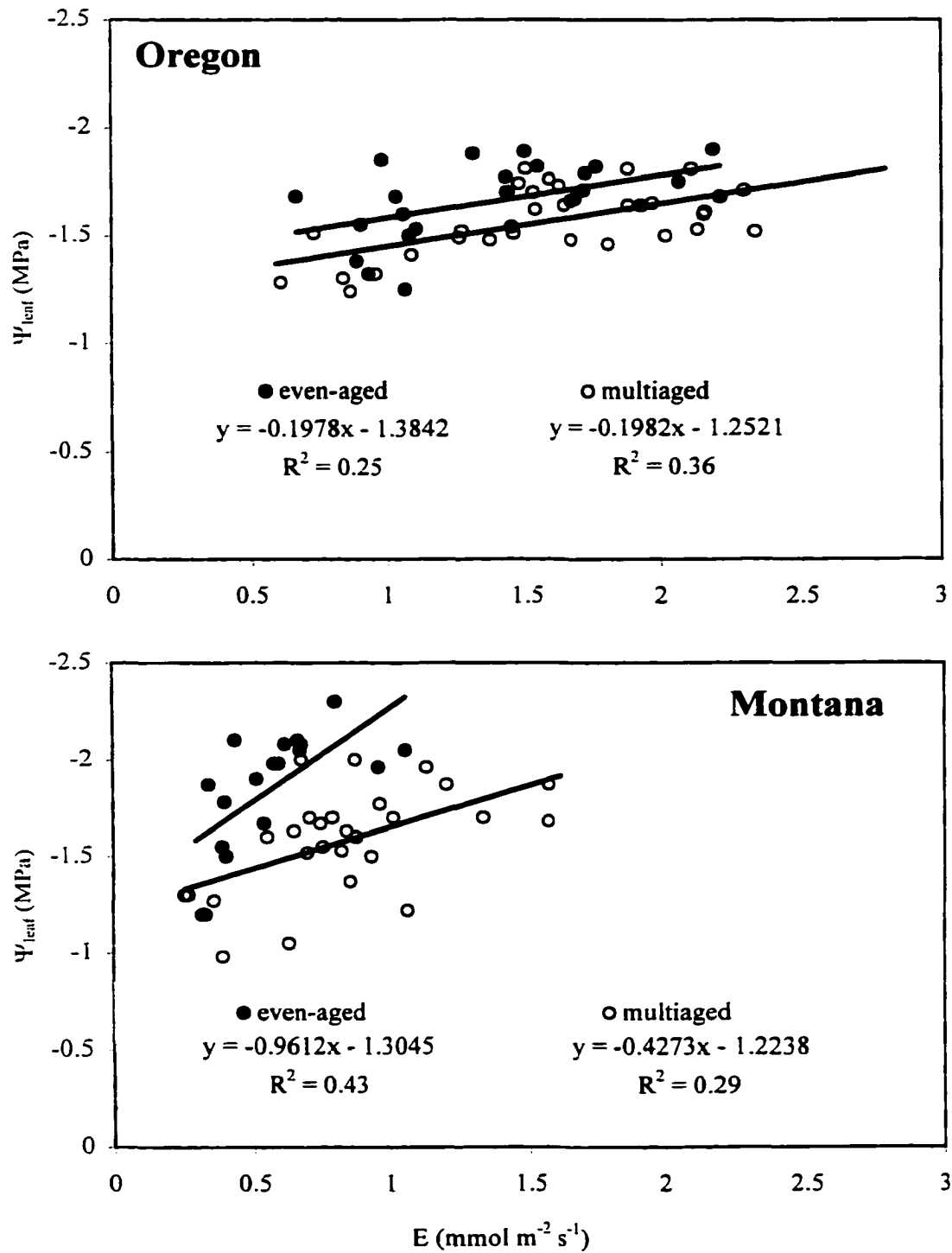


Figure 1.6. Relationship between water potential (Ψ_{leaf}) and transpiration (E) for plots 301M and 302E in Oregon and plots 3M and 4E in Montana.

CHAPTER TWO

Seasonal variation in physiological function of even-aged and multiaged

Pinus ponderosa Dougl. ex Laws. stand structures

ABSTRACT

Diurnal gas exchange and leaf water potential (Ψ_{leaf}) of an even-aged and multiaged stand structure of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) were measured in June, July and August in Montana. Photosynthetically active radiation (PAR), air temperature (T_{air}), and vapor pressure difference (VPD) were measured simultaneously to test for the effect of each environmental variable seasonally. In June, net photosynthesis (A_{net}) was positively related to PAR, T_{air} , VPD and Ψ_{leaf} . In July and August, A_{net} and g_s decreased linearly with increasing T_{air} , VPD, and Ψ_{leaf} . The strongest correlation between A_{net} and these environmental variables occurred in August when water stress was greatest. In July, average daily transpiration (E) was significantly greater for multiaged trees. Multiaged trees also maintained higher rates of A_{net} , g_s , and E for a longer period of the day in July, suggesting less of a water limitation than in the even-aged stand structure. Maximum rates of A_{net} , g_s , and E were reached in June, while WUE (A/E) increased from June to August. Environmental variables exhibited varying levels of control over gas exchange throughout the season, with possible implications for carbon gain in different forest structures.

INTRODUCTION

Gas exchange varies seasonally, spatially and temporally in forest canopies. Net photosynthesis is determined primarily by the water balance of the leaf and by environmental factors (Campbell and Norman 1998). The driving force for water transport through the soil-plant-atmosphere continuum is evaporation, and is described by available radiant energy, the humidity deficit, air temperature and wind speed in the Penman-Monteith equation (Passioura 1980). Seasonal photosynthetic rates are influenced by developmental stage and environmental conditions that influence stomatal aperture (Holbrook and Lund 1995). Light, CO₂ concentration, evaporative demand of the air and soil water content are important factors that influence stomatal control (Jarvis 1980, Dang et al. 1997).

Environmental conditions, including incident radiation, moisture availability, and temperature, vary throughout the growing season, and exert a varying degree of control over gas exchange depending on season. The Intermountain West is characterized by moderate annual precipitation and a dry growing season. Moisture is often limiting to gas exchange as the growing season progresses. A shift in the environmental factors that control stomatal conductance at different times during the growing season have been observed in conifers (Helms 1972, Maier and Teskey 1992) and appear to be related to the degree of water stress present.

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is a widely distributed conifer in North America, and often forms a transition between grasslands and mixed coniferous forests (Franklin and Dyrness 1988). Ponderosa pine is characterized by high water use efficiency (WUE, photosynthesis/transpiration), and often has higher WUE than other

sympatric conifers (Marshall and Zhang 1994). Pure stands of ponderosa pine grow in even-aged and multiaged stand structures as the result of natural and human-caused disturbance. Forest structure affects biophysical properties such as precipitation, radiation, wind speed, temperature, and humidity (Parker 1995). Even-aged and multiaged stand structures of ponderosa pine may exhibit differences in gas exchange and water relations as a result of the influence of structure on biophysical properties and physiological functions.

This study was designed to investigate some of the environmental variables that control physiological functions at different times of the growing season and to investigate the effect of stand structure on gas exchange diurnally. The specific objectives for this study were as follows: (1) to identify the diurnal course of environmental variables, gas exchange, and leaf xylem water potential in June, July and August in even-aged and multiaged stand structures of ponderosa pine; and (2) to identify the influence of environmental controls on gas exchange for each seasonal measurement.

MATERIALS AND METHODS

Study sites - This experiment was implemented in pure stands of ponderosa pine on the Lolo National Forest in Montana that contained both multiaged and even-aged stand structures. One circular plot 0.1 ha in size was installed in a fully stocked stand of each structure, trying to avoid any differences in density between the two plots. Habitat type was characterized as *Pseudotsuga menziesii* (Mirbel) Franco./*Calamagrostis rubescens* Buckl. (Pfister et al. 1977). Each tree breast height (1.37 m) and taller was counted and measured. Total tree height and height to the base of the live crown were measured with

a clinometer or a height pole, and diameter was measured at breast height. Two increment cores at right angles were taken from each tree 12.7 cm (5 in) and greater in breast height diameter to obtain age at breast height. Bark thickness was measured with a bark-gauge to the nearest mm directly below the location of each core on each tree. Sapwood length was measured on the increment cores in the field, and later used to compute sapwood basal area. Leaf area per tree was computed using equations that relate sapwood basal area with leaf area of individual trees (O'Hara and Valappil 1995). Sapwood basal area of trees less than 12.7 cm in diameter was assumed to be basal area minus the bark. Leaf area of each tree was computed, summed, and divided by the area of the plot to get leaf area index (LAI). Stand density index was computed for each plot, using the formula:

$$SDI = \Sigma(DBH_i/10)^{1.6}$$

where DBH_i is the diameter of the i th tree in the stand (Long and Daniel 1990). The plots had similar basal area, sapwood basal area, and LAI (Table 2.1). Trees per hectare and SDI were slightly greater for the even-aged plot (Table 2.1).

Sample tree selection – Even-aged stands of ponderosa pine typically have bell-shaped diameter distributions, while multiaged stands have more irregular distributions. Multiaged stands can typically be divided into cohorts of trees that have arisen after a common disturbance (O'Hara 1996, see Figure 2.1 for the diameter distributions of the even-aged and multiaged plots for this study). All diameter classes (5 cm) were represented in the multiaged stand, with a maximum dbh of 51 cm. The multiaged plot has a heterogeneous canopy layer with numerous strata and with leaf area present from the top of the canopy to the forest floor (Figure 2.2b). Three cohorts were recognized in

this stand based on both ages and sizes of trees: cohort one is comprised of the diameter class 2.5 cm, cohort two encompassed the diameter classes 7.5-37.5 cm (resembling the bell-shaped curve in the even-aged stand), and cohort three consisted of diameter classes 42.5-52.5 cm (Figure 2.1). The mean diameter of the even-aged plot was 27 cm (10.6 in), and all trees were considered to be one cohort. Even-aged stands of ponderosa pine typically maintain a continuous, uniform canopy layer.

Crown classification of individual trees was made following the definitions of Oliver and Larson (1996). All trees in the even-aged plot were considered to be the B-stratum. Three trees in the even-aged plot were sampled at mid-canopy, and are denoted in Figure 2.2a with an asterisk. For the multiaged plot, four representative trees were sampled: one from cohort one, two from cohort two, and one from cohort three. Emergent trees belonging to the oldest cohort were classified as the A-stratum. The upper continuous canopy layer was composed of the middle cohort, and was considered the B-stratum. Trees belonging to the B-stratum are the most comparable to trees in the even-aged plot because of similar ages and sizes. Trees belonging to the youngest cohort were classified as the C-stratum (lower stratum beneath the B-stratum), and ranged from seedlings to saplings. All trees sampled were co-dominant within their respective strata, and were sampled at mid-canopy (see Figure 2.2b for sample tree selection). The average crown ratio was 0.69 for the multiaged stand structure and 0.55 for the even-aged.

Predawn xylem water potential - Predawn xylem leaf water potential (Ψ_{predawn}) was measured during the growing season of 1998. Previous studies have shown no difference in measured Ψ_{predawn} throughout tree canopies of ponderosa pine (Valappil 1997), so mid-canopies were sampled for consistent sampling and comparisons. One branch was

excised from each sample tree, placed in a plastic ziplock bag, and put on ice until all samples were obtained. After all samples were gathered, Ψ_{predawn} was measured using a pressure chamber. Two fascicles of each branch were measured in the order that the samples were obtained. These two measurements were averaged to obtain an average Ψ_{predawn} for that branch. If the two fascicles measured were not within 0.2 MPa, a third fascicle was measured, and the two closest values were averaged to get the Ψ_{leaf} for that branch. As a check, the first branch measured was kept on ice and re-measured after all other samples to ensure that there was no effect of time since cutting on the measured Ψ_{predawn} .

Soil water content - On June 10 (even-aged), June 14 (multiaged), and July 15 (both structures), soil samples were collected for soil water content calculations. On each plot, ten points were randomly selected and soil samples between 15 and 20 cm from the top of the soil surface were collected. It is generally assumed that most of the fine roots of trees and understory vegetation occur within the top 30 cm of soil (Brady and Weil 1999). The soil samples were placed in soil tins, brought back to the lab, weighed to the nearest g, dried for 48 hours at 80° C, and weighed again to the nearest g. Water content (% by weight) was calculated as ((wet-dry)/dry)*100.

Gas exchange - A field portable closed gas exchange system (LI-6200, Li-Cor Inc., Lincoln, NE) was used to measure net photosynthesis (A_{net}) and stomatal conductance (g_s) with a 1/4-l cuvette. Two fascicles were excised from each branch and measured by placing the mid-portion of the fascicles inside the cuvette. Measurements were made every hour beginning at 0700-0900 and continued until 1600. Samples were obtained with a 4-m tall platform and a pole-pruner, or with a 12-gauge shotgun for larger trees.

One sample from mid-canopy of each of the previously identified sample trees was obtained and measured at each hour. Branches excised were fully sunlit at the time of sampling. Measurements were completed within three minutes of detachment from the tree. Preliminary measurements found no difference in gas exchange when detached branches were measured within three minutes. Due to intermittent high clouds in August, a QED light source (Quantum Devices, Inc., Barneveld, WI) with a peak wavelength of 670 nm was used to supply additional light (at a rate of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$) to ensure that photosynthesis was not light-limited. All other measurements were made on sunny days. Ambient photosynthetically active radiation (PAR, 400-700 nm) was measured with a quantum sensor (Li-Cor Inc., Lincoln, NE) attached to the tripod where the leaf chamber was mounted. The June 16 gas exchange measurements ceased at 0200 due to an equipment failure.

Computations of transpiration (E) and WUE - Transpiration (E) and water use efficiency (WUE) were computed using stomatal conductance and photosynthesis values obtained with the LI-6200. Immediately before each pair of fascicles was placed in the cuvette, the temperature of the air (simulated by using the chamber temperature measured by the LI-6200) and relative humidity were recorded. Vapor pressure difference (VPD) was computed as:

$$\text{VPD} = (e_{\text{sat Air}} - e_{\text{air}})/\text{pressure (mb)}, \text{ where}$$

$$e_{\text{sat Air}} = 6.1078 * \exp((17.269 * T_{\text{air}})/237.3 + T_{\text{air}}), \text{ and}$$

$$e_{\text{air}} = e_{\text{sat Air}} * (\text{RH}/100)$$

following Campbell and Norman (1998). Transpiration was then computed as:

$$E = \text{VPD} * g_s * 1000$$

WUE was computed as photosynthesis/transpiration (A/E).

Ponderosa pine has three-needled fascicles with stomata on all surfaces. All physiological data presented here are expressed on an all-sided leaf area basis. After gas exchange measurements, the width of the fascicles was measured to the nearest 0.1 mm, and multiplied by the width of the cuvette to obtain projected leaf area. Since the middle portion of the fascicles was placed in the cuvette, the area of ponderosa pine needles was assumed to be a right cylinder divided into thirds. It follows that the conversion factor from projected leaf area to all-sided leaf area is 2.36 (Rundel and Yoder 1998).

Data analysis - All even-aged trees were averaged together for each measurement day, as were all multiaged trees to look at mean values of A_{net} , g_s , E , WUE, and Ψ_{leaf} diurnally or across daily periods for both structures. Additionally, the multiaged leaf physiology data for each strata were weighted for the proportion of leaf area each strata represented in the plot. The proportions for the multiaged plot were as follows: A = 0.42, B = 0.55, C = 0.03. Diurnal patterns of A_{net} , g_s , E , WUE, and Ψ_{leaf} are presented as structural means (even-aged and multiaged) with associated standard errors. An additional line is present representing the data weighted in the fashion just described for the multiaged plot (this is labeled as “multiaged weighted”).

Significant differences ($\alpha = 0.05$) in mean daily values between stand structures were determined by two sample t-tests. Linear regression was used to describe the relationships between A_{net} and g_s with VPD and T_{air} , with no separation between structures. Even-aged and multiaged plots were treated separately to test for differences in the A_{net} versus Ψ_{leaf} relationship. Differences in slope between even-aged and

multiaged measurements were tested with a general linear model procedure. All analyses were conducted using SYSTAT (SPSS Inc.).

RESULTS

Predawn leaf water potential (Ψ_{leaf}) and soil water content – There were no differences in $\Psi_{predawn}$ between even-aged and multiaged plots for any measurement period in 1998 (Figure 2.3). Soil water content (% by weight) was significantly greater for the even-aged plot in both June and July in 1999 (Figure 2.4). It is important to note that for the June measurement, the even-aged plot was sampled on June 10 and the multiaged plot was sampled on June 14. The effect of time on the amount of water in the soil cannot be quantified.

Environmental conditions – Photosynthetically active radiation (PAR, 400 – 700 nm) followed a similar trajectory for all three measurement days (Figure 2.5a). PAR was variable on the August date as intermittent high clouds caused PAR to drop below 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Light saturation for photosynthesis in ponderosa pine generally occurs between 800 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Hadley 1969, Bond et al. 1999). Vapor pressure difference (VPD) and air temperature (T_{air}) were very similar between measurement days (Figure 2.5b and 2.5c). Highest T_{air} and VPD were reached in August.

Gas exchange – The time when net photosynthesis (A_{net}) was at its daily maximum was different for each measurement date (Figure 2.6). Photosynthesis was maximized at 1100 for both even-aged and multiaged plots in June. The highest photosynthetic rates achieved in July and August were at the beginning of the measurement period (between the hours of 0800-0900) with a steady decline as the day progressed (Figure 2.6).

Stomatal conductance (g_s) was generally at its maximum early in the day, with the exception of the even-aged trees in June (Figure 2.7). Late in the afternoon in August, g_s was severely depressed (Figure 2.7), corresponding to the depression in A_{net} (Figure 2.6). Average daily A_{net} (averaged over each measurement day for each structure) and average A_{max} (the average maximum photosynthetic rate for each plot on each day) declined from June to August, while g_s and g_{s-max} showed a variable pattern (Table 2.2).

Transpiration rates (E) were highest in June, decreasing in July and August (Figure 2.8). Average daily E and average E_{max} were significantly greater for the multiaged plot as compared to the even-aged in July only (Table 2.2). The depressed transpiration rates in August correspond to the lower rates of g_s and A_{net} (Figure 2.8). Early morning Ψ_{leaf} was highest in June and lowest in August for both stand structures (Figure 2.9). Average Ψ_{leaf} tended to stay above -2.0 MPa, with no individual measurement less than -2.1 except for one measurement in July (-2.3 MPa midday on the even-aged plot). The average lowest Ψ_{leaf} achieved was highest for June and lowest for July (Table 2.2). There were no significant differences in water use efficiency ($WUE = A/E$) for any measurement date, but average WUE generally increased from June to August for both stand structures (Table 2.2).

A distinct pattern in physiological measurements is apparent when comparing all data together over all measurement periods. Trends in diurnal patterns are very similar between even-aged and multiaged structures in June and August, while there are distinctly different patterns in A_{net} , g_s , E, and Ψ_{leaf} in July between even-aged and multiaged plots (Figures 2.6, 2.7, 2.8 and 2.9). The multiaged trees demonstrated higher

photosynthesis, stomatal conductance, transpiration and lower Ψ_{leaf} for the majority of the July measurement day.

Relationship of A_{net} and g_s with environmental variables – In early summer (June), net photosynthesis (A_{net}) increased with increasing PAR, VPD, and T_{air} , but in July and August, A_{net} decreased with increasing VPD and T_{air} (Table 2.3, Figures 2.10a and 2.11a). There was a steeper decline in A_{net} with VPD in August than in July ($P < 0.001$). There was not a positive relationship between A_{net} and PAR in July and August (Table 2.3). There was a significant linear relationship for all dates between A_{net} and T_{air} (Figure 2.11a), with the strongest correlation occurring in August. Stomatal conductance (g_s) decreased linearly with increasing VPD (Figure 2.10b) and T_{air} (Figure 2.11b) for all three dates. The strongest correlation between g_s and VPD and g_s and T_{air} was in August ($R^2 = 0.70$ and $R^2 = 0.71$, Table 2.3).

Relationship between A_{net} and Ψ_{leaf} – Net photosynthetic rates (A_{net}) increased with decreasing Ψ_{leaf} in June (Figure 2.12) producing a significant relationship for the multiaged stand structure ($R^2 = 0.38$, $P = 0.006$) but not the even-aged ($R^2 = 0.20$, $P = 0.107$). In July, A_{net} generally decreased with decreasing Ψ_{leaf} (Figure 2.12), although only the even-aged stand structure exhibited a significant relationship ($R^2 = 0.22$, $P = 0.049$ for the even-aged structure; $R^2 = 0.08$, $P = 0.158$ for the multiaged stand structure). The relationship between A_{net} and Ψ_{leaf} was strongest in August for both stand structures ($R^2 = 0.66$, $P < 0.001$ for the multiaged stand structure; $R^2 = 0.40$, $P = 0.001$ for the even-aged stand structure) with A_{net} decreasing with decreasing Ψ_{leaf} (Figure 2.12).

DISCUSSION

Seasonal differences in gas exchange and water relations have been observed and described in many different coniferous tree species (Teskey et al. 1984, Maier and Teskey 1992, Yoder et al. 1994, Kloeppel et al. 1995, Dang et al. 1997), including ponderosa pine (Hadley 1969, Helms 1972, Cregg 1993). One advantage of being evergreen is the ability to fix carbon during any part of the year that conditions are favorable (Matyssek 1986, Man and Lieffers 1997). Even so, the summer months provide the most optimal growth conditions and remain the most important season for carbon gain (Troeng and Linder 1982a, Teskey et al. 1984, Maier and Teskey 1992, references within Teskey et al. 1994). Carbon assimilation is affected by environmental influences differently at various times in the season (Helms 1972, Maier and Teskey 1992). Early in the growing season (May – June), irradiance presents the greatest limitation to maximum carbon assimilation (Helms 1972). As the season progresses, water typically becomes limiting. As a result, the evaporative demand of the air (as described by vapor pressure difference, VPD) and air temperature become more important factors in controlling gas exchange (Helms 1972).

In the Intermountain West, precipitation occurs in fall, winter, and spring, with much of the growing season receiving little precipitation (Pfister et al. 1977). Ponderosa pine is especially well adapted to areas with high temperatures and low moisture availability (Franklin and Dyrness 1988), and often is the first conifer encountered on the edge of grasslands (Pfister et al. 1977, Franklin and Dyrness 1988). In this study, season influenced the relationship between the environment and physiological performance. In June, it appears that water was not limiting to gas exchange as net photosynthesis (A_{net})

increased with increasing VPD, T_{air} , and decreasing Ψ_{leaf} (Figures 2.10a, 2.11a, and 2.12). The strongest decreases in A_{net} with increasing VPD and T_{air} and decreasing Ψ_{leaf} occurred in August, when water typically becomes most limiting in western Montana. All environmental parameters measured (PAR, VPD, and T_{air} , Figure 2.5) were comparable between measurement days. These data alone suggest no obvious differences in the level of environmental stress as the season progressed. The Ψ_{predawn} data from 1998 (Figure 2.3) and the decreasing soil water content in 1999 (Figure 2.4) suggest that soil water depletion throughout the season likely causes a water limitation later in the growing season. The lowest Ψ_{leaf} values occurred in even-aged trees in July, and instantaneous WUE increased from June to August (Table 2.2), implying physiological adjustment by individual trees in response to their environment. This data contributes to the argument that ponderosa pine is a drought tolerant species, as it possesses the ability to thrive when water is adequate while avoiding water loss when water becomes limiting.

Others have shown a stronger correlation between carbon assimilation and VPD and T_{air} as water becomes more limiting later in the growing season. Helms (1972) found that light level explained most of the variation in photosynthetic rates under low stress conditions, with air temperature and relative humidity becoming more important as the level of environmental stress increased. Kaufmann (1982) found that photosynthetic photon flux density (PPFD) and absolute humidity difference (DAH) were the most important environmental variables in predicting stomatal conductance for any season using data from three subalpine conifers and one angiosperm. In this study, there was a significant but weak ($R^2 = 0.35$) positive linear relationship between ambient PAR and A_{net} in June only (Table 2.3). Maier and Teskey (1992) reported strong correlations of

A_{net} and g_s with absolute humidity deficit at predawn xylem pressure potentials less than -1.0 MPa, but no correlation above -1.0 MPa for eastern white pine. Vapor pressure difference and temperature regulated photosynthesis and mesophyll conductance (g_m) in *Picea mariana* (Mill.) B.S.P. and *Pinus banksiana* Lamb., with stomatal limitations more apparent later in the growing season (Dang et al. 1997). From the data presented in this study, it is evident that water availability plays an increasing role in controlling gas exchange as the season progresses, with a similar effect in both the even-aged and multiaged stand structures.

Stomatal closure in relation to water potential has been observed in other coniferous species (*Pseudotsuga menziesii* (Mirbel) Franco. - Running 1976, *Larix occidentalis* Nutt. - Kloeppe et al. 1995). Stomata tend to be unaffected by a wide range in Ψ_{leaf} , with a linear or curvilinear decline after a threshold Ψ_{leaf} is reached (Ludlow 1980). The possibility of ponderosa pine exhibiting a linear decrease in A_{net} and g_s in response to a threshold xylem water potential has been extensively studied, with observed threshold values ranging between -1.0 and -1.5 MPa (Cleary 1971, Lopushinsky and Klock 1974, Bunce et al. 1979). Threshold water potentials have been observed in other conifers, including *Pseudotsuga menziesii* (Mirbel) Franco. (-2.0 MPa, Running 1976), *Pinus banksiana* Lamb. and *Picea mariana* (Mill.) B.S.P. (-1.3 and -2.5 MPa, Dang et al. 1997), and *Pinus halepensis* Mill. (-0.8 MPa, Melzack et al. 1985). Ψ_{leaf} in this study consistently remained between -0.90 and -2.1 MPa for each diurnal measurement period. The largest decline in A_{net} with decreasing Ψ_{leaf} occurred in August for both even-aged and multiaged stand structures (Figure 2.12), with no negative effect of Ψ_{leaf} on A_{net} in June. From this data, there also appears to be a minimum leaf water potential (-2.0 to $-$

2.1 MPa) that ponderosa pine needles would not go below for all three measurement dates (Figure 2.9). A lethal water potential (no recovery of photosynthesis) of -2.2 MPa has previously been identified in ponderosa pine under controlled experimental conditions (Bunce et al. 1979). An important point to note from this study – in comparison to others – is that different varieties of ponderosa pine as well as different populations and sizes of individuals within varieties were investigated. It is therefore impossible to rule out genotypic or phenotypic variation in water relations with regard to gradients in the environment within ponderosa pine (in particular, influences of VPD and water availability on g_s and A_{net}).

All rates of gas exchange tended to decrease from June to August in this study, while WUE increased (Table 2.2, Figures 2.6, 2.7 and 2.8). A decrease in carbon assimilation with season has been observed previously in ponderosa pine (Helms 1972, Cregg 1993), although one early study demonstrated maximum rates of photosynthesis occurring in autumn and cool summer days (Hadley 1969). Furthermore, the time of the day when maximum rates of photosynthesis were reached changed with each measurement period, but was similar between the different stand structures. Early in the growing season, A_{net} reached a maximum rate during mid-day, while later in the season, A_{net} was maximized during the earliest measurement periods (between 0800 and 0900, Figure 2.6) which may actually have presented a light limitation to CO_2 assimilation at the time of sampling (see diurnal PAR, Figure 2.5). This emphasizes the importance of determining the time of day where gas exchange is being least limited when measuring CO_2 assimilation in experimental studies, as various environmental parameters limit photosynthesis at

different times of the day during different times of the season (Helms 1972, Running 1976).

Previous physiological studies in ponderosa pine have identified temperature optima for photosynthesis to be between 17 and 35 °C (Hadley 1969, Helms 1972, Monson and Grant 1989). Helms (1972) identified different temperature optima during the growing season depending on the level of environmental stress, with optimum temperature increasing with greater stress. Helms (1972) also showed that as environmental stress increased, the relationship between photosynthesis and air temperature decreased. That was not the case in this study, where the relationship was strongest for the August measurements (Figure 10). The data analysis done by Helms (multiple regression with data transformation) was different than in this study (simple linear regression), which may contribute to differences in the results and conclusions of each study. Nevertheless, it is difficult to discern a temperature optimum from the data presented here, but it would appear that temperatures above 30 °C are not favorable for photosynthesis (Figure 2.11a). In this study, as in any field experiment, it is difficult to determine the true effect of temperature on gas exchange because increases in temperature are accompanied by changes in VPD (Helms 1976, Jarvis 1980).

The differences observed in soil water content (Figure 2.4) could be due to a number of factors. Since soil water content and predawn water potentials were not measured during the same growing season, it is impossible to test for a correlation between them, or to conclude that the patterns observed in water availability were the same for both growing seasons. The stand structure of multiaged ponderosa pine tends to be somewhat open as compared to even-aged stand structures (Figure 2.2) despite both structures

having similar LAI. As a result, incident radiation often reaches the forest floor in multiaged stands. The two plots in this study were similar in leaf area, trees per hectare, basal area, sapwood basal area, and SDI (Table 2.1), and can be considered comparable in terms of site occupancy. If the multiaged structures allow for more light penetration, then the microclimate within the stand would certainly be different, including air temperature and VPD as the result of greater turbulence and mixing of the air. As a result, there may be increased evaporation from the soil in the multiaged structures, contributing to decreased soil water content. The multiaged structure may also be using more water as suggested by the higher transpiration rates in July. This would deplete the soil water resources, but Ψ_{leaf} values tended to be higher for the multiaged trees than the even-aged trees (Figure 2.9). This suggests that the multiaged site was equally able to support the gas exchange demands of the foliage present, especially considering total leaf area was similar for both plots. Ponderosa pine reportedly develops a taproot (Jackson and Spomer 1979), and it is likely that roots of larger trees are reaching into a source of water well beneath the upper soil surface. Multiaged stand structures, because of the varying sizes of trees present, may be more efficient at extracting water from different depths of the soil than trees in even-aged stand structures. This may result in a more efficient partitioning of water use throughout the canopy.

Instantaneous WUE was not different between structures (Table 2.2), but did increase as the season progressed in both structures. The data indicates no difference in the way trees in the two stand structures are using water (carbon produced per unit water lost), but the soil water content and gas exchange data suggest there are differences. As demonstrated earlier in chapter one (Nagel 2000), instantaneous WUE was not different

between structures in either June in Oregon or July in Montana. The magnitude of A_{net} and E were different between structures in chapter one, suggesting no difference in WUE, but a difference in the magnitude of each process. This appears to be the case in this study, as well (Figures 2.6 and 2.8). Multiaged trees maintained higher Ψ_{leaf} with higher rates of A_{net} and E , suggesting less stomatal limitation as compared to the even-aged trees. In August, there appears to be a water limitation for both structures as A_{net} decreases significantly with Ψ_{leaf} (Figure 2.12) coinciding with suppressed g_s and E in both structures (Figures 2.7 and 2.8).

Long-term WUE (as determined by stable carbon isotope discrimination, $\delta^{13}\text{C}$) has previously been found to be higher in even-aged stands of ponderosa pine when compared to multiaged stands (Valappil and O'Hara 2000). Lower Ψ_{predawn} was also observed in even-aged stands. If trees in even-aged stand structures are forced to close stomates sooner in the day in response to increased environmental stress, there may be less discrimination of $\delta^{13}\text{C}$, resulting in a higher long-term WUE, while instantaneous WUE may be the same between stand structures. Greater WUE in even-aged stands could also be partially attributed to greater site occupancy of even-aged structures, creating greater water stress for individual trees (Valappil and O'Hara 2000). In a progeny study involving ponderosa pine parents from coastal and interior varieties (var. *ponderosa* and var. *scopulorum*), Monson and Grant (1989) concluded that ponderosa pine exhibits greater WUE and lower transpiration rates at the expense of lower maximum rates of photosynthesis. Zhang et al. (1997), however, found no relationship between drought tolerance and high WUE between three populations of ponderosa pine. Phenotypic acclimation or genotypic changes in the ratio of sapwood basal area to leaf

biomass have been observed in desert vs. montane stands of ponderosa pine in Nevada (var. *ponderosa*), with a higher ratio of sapwood basal area to leaf area in desert stands (Callaway et al. 1994). This phenomenon was not accompanied by a decrease in photosynthetic rate due to higher stem respiration partly because of a higher leaf nitrogen investment in the desert pines (Carey et al. 1998). Greater $\delta^{13}\text{C}$ composition in desert stands was attributed to a greater evaporative demand in the desert environment, and not to greater WUE due to greater photosynthesis or lower transpiration (Carey et al. 1998). In the even-aged stand sampled in this study, it appears that greater water stress in the even-aged structure has resulted in lower rates of carbon assimilation for at least part of the growing season, with no apparent effect on instantaneous WUE. Implications for long-term WUE are unknown, but results from Valappil and O'Hara (2000) suggest lower long-term WUE in even-aged stand structures of ponderosa pine.

From this study, it is clear that environmental conditions controlled gas exchange in various ways throughout the months of June, July and August. Different environmental controls were important depending on the amount of water stress present. Although the effects of PAR, T_{air} , VPD, and Ψ_{leaf} were tested separately, it is most likely that there is an interaction of environmental controls, especially later in the season where more stress is apparent (Helms 1972). This must certainly be the case where an increase in PAR is accompanied by an increase in VPD and T_{air} , resulting in a negative relationship between PAR and A_{net} in July and August (Table 2.3). Only fully sunlit, one year-old foliage from the middle portion of individual trees was sampled in this study, with a limited number of trees from each plot. Rates of photosynthesis and stomatal conductance tend to decrease with canopy depth in both evergreen and deciduous tree species (Beadle et al.

1985, Hollinger 1989, Ellsworth and Reich 1993). Often times, there is more variation in photosynthesis and stomatal conductance within a tree crown than between individual trees of the same canopy (Troeng and Linder 1982b, Beadle et al. 1985). Variation is caused mainly by differences in light intensity, biochemical capacity of leaves to fix CO₂, and water loss associated with CO₂ uptake (Holbrook and Lund 1995). Maximum rates of photosynthesis occur in needles of various ages in conifers, but currently developing leaves through two year-old leaves are generally the most productive (two-year-old needles in *Pinus ponderosa* - Helms 1970, current-year needles in *Pseudotsuga menziesii* (Mirb.) Franco - Woodman 1971, one-year-old needles in *Abies amabilis* (Dougl.) Forbes- Teskey et al. 1984, current- to one-year-old in *Pinus strobus* L., depending on season - Maier and Teskey 1992, one- to four-year-old in *Pinus contorta* Dougl. - Schoettle and Smith 1999). Therefore, it is likely that not all the variation between even-aged and multiaged stand structures of ponderosa pine was captured by the data presented here, and it would therefore be inappropriate to make inferences about all potential factors influencing productivity between these two stand structures of ponderosa pine.

In conclusion, values of VPD, T_{air} , and Ψ_{leaf} can have very different implications on gas exchange depending on the time of year. The relationships between photosynthesis and stomatal conductance and any one environmental variable are not constant throughout the growing season. These different relationships need to be considered when predicting plant growth using environmental variables as drivers in mechanistic growth models. The importance of determining the time of day when carbon assimilation is at its peak is tremendously important when making field observations, especially as the level of water stress increases. It appears that physiological performance may be different

between even-aged and multiaged stand structures of ponderosa pine, but the implication for overall productivity is still unknown.

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Table 2.1. Plot-level characteristics for the multiaged and even-aged plots. Plots were circular and 0.1 ha in size.

	Multiaged	Even-aged
LAI	5.63	5.53
age range	20-132	81
trees per hectare	350	410
basal area (m ² ha ⁻¹)	21.76	24.22
sapwood basal area (m ² ha ⁻¹)	14.38	14.13
SDI	382	458

Table 2.2. Daily means for physiological measurements between multiaged and even-aged plots. Data area unweighted. Significant differences ($\alpha = 0.05$) within each measurement date are denoted by letters that are not the same. Standard errors are given in parentheses.

Structure Type	N	Average A_{net} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Average A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Average g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	Average g_{s-max} ($\text{mol m}^{-2} \text{s}^{-1}$)	Average E ($\text{mmol m}^{-2} \text{s}^{-1}$)	Average E_{max} ($\text{mmol m}^{-2} \text{s}^{-1}$)	Ave WUE ((mmol CO ₂)/(mol H ₂ O))	Average Ψ_{leaf} (MPa)	Average min Ψ_{leaf} (MPa)
June multi	3	3.59 (0.24) ^a	5.10 (0.84) ^a	0.056 (0.008) ^a	0.069 (0.009) ^a	1.04 (0.04) ^a	1.55 (0.09) ^a	3.63 (0.27) ^a	-1.37 (0.05) ^a	-1.79 (0.11) ^a
June even	2	3.73 (0.21) ^a	5.61 (0.08) ^a	0.052 (0.001) ^a	0.067 (0.006) ^a	0.88 (0.07) ^a	1.49 (0.06) ^a	4.76 (0.08) ^b	-1.41 (0.10) ^a	-1.82 (0.07) ^a
July multi	4	3.06 (0.27) ^a	4.23 (0.57) ^a	0.031 (0.003) ^a	0.047 (0.006) ^a	0.88 (0.06) ^a	1.49 (0.10) ^a	4.26 (0.17) ^a	-1.58 (0.07) ^a	-1.88 (0.07) ^a
July even	3	2.31 (0.43) ^a	4.76 (0.70) ^a	0.022 (0.003) ^a	0.040 (0.004) ^a	0.56 (0.08) ^b	0.80 (0.13) ^b	4.54 (0.30) ^a	-1.89 (0.08) ^a	-2.20 (0.10) ^a
August multi	4	2.07 (0.26) ^a	4.18 (0.42) ^a	0.022 (0.003) ^a	0.052 (0.011) ^a	0.38 (0.04) ^a	0.54 (0.05) ^a	5.50 (0.18) ^a	-1.59 (0.07) ^a	-1.80 (0.03) ^a
August even	3	1.96 (0.25) ^a	4.45 (0.96) ^a	0.021 (0.002) ^a	0.045 (0.004) ^a	0.36 (0.05) ^a	0.62 (0.07) ^a	5.29 (0.31) ^a	-1.72 (0.01) ^a	-1.88 (0.02) ^a

Table 2.3. Relationship between net photosynthesis (A_{net}) and stomatal conductance (g_s) and photosynthetically active radiation (PAR), vapor pressure difference (VPD), and air temperature (T_{air}). SEE = standard error of the estimate. N for each date: June = 34, July = 64, and August = 56.

Relationship	Date	B_0	B_1	R^2	SEE	P
A_{net} vs. PAR	June	2.266	0.001	0.35	1.162	< 0.001
	July	5.213	-0.002	0.36	1.016	< 0.001
	August	4.577	-0.002	0.38	1.149	< 0.001
A_{net} vs. VPD	June	2.647	0.511	0.17	1.313	0.016
	July	5.015	-0.769	0.42	0.968	< 0.001
	August	4.322	-0.983	0.75	0.761	< 0.001
A_{net} vs. T_{air}	June	0.912	0.118	0.26	1.239	0.002
	July	6.830	-0.159	0.38	1.001	< 0.001
	August	8.460	-0.243	0.73	0.790	< 0.001
g_s vs. PAR	June	0.068	< -0.001	0.31	0.012	0.001
	July	0.046	< -0.001	0.26	0.010	< 0.001
	August	0.052	< -0.001	0.38	0.013	< 0.001
g_s vs. VPD	June	0.071	-0.008	0.45	0.011	< 0.001
	July	0.045	-0.006	0.30	0.010	< 0.001
	August	0.050	-0.011	0.70	0.009	< 0.001
g_s vs. T_{air}	June	0.088	-0.001	0.39	0.011	< 0.001
	July	0.060	-0.001	0.28	0.010	< 0.001
	August	0.097	-0.003	0.71	0.009	< 0.001

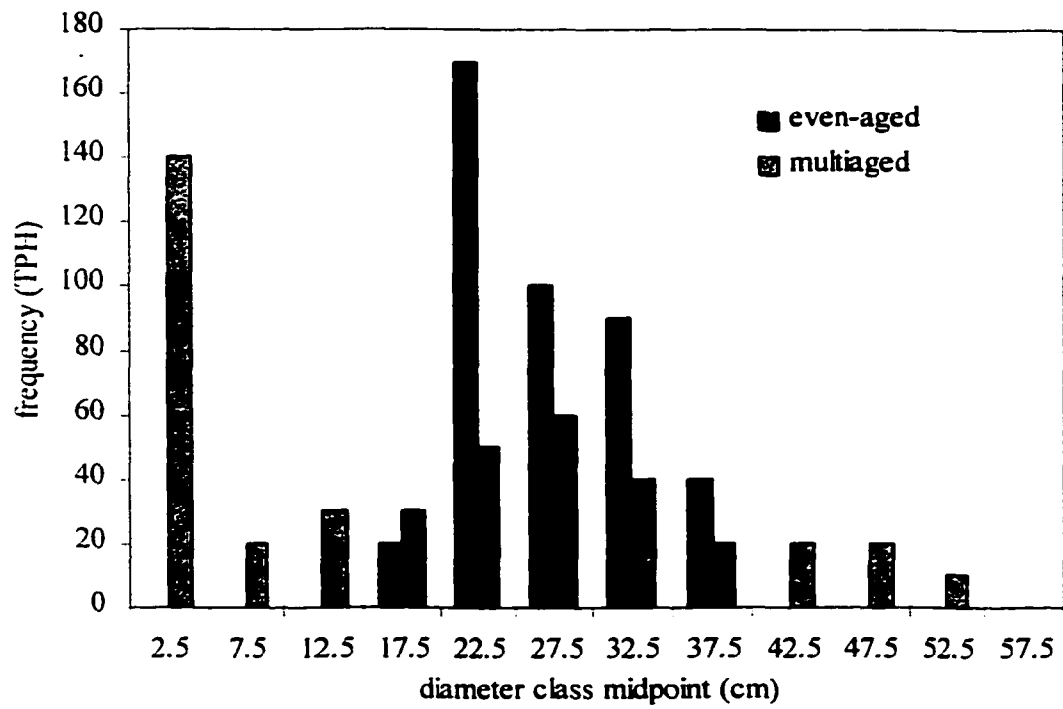


Figure 2.1. Diameter distribution for the even-aged and multiaged stand structures.

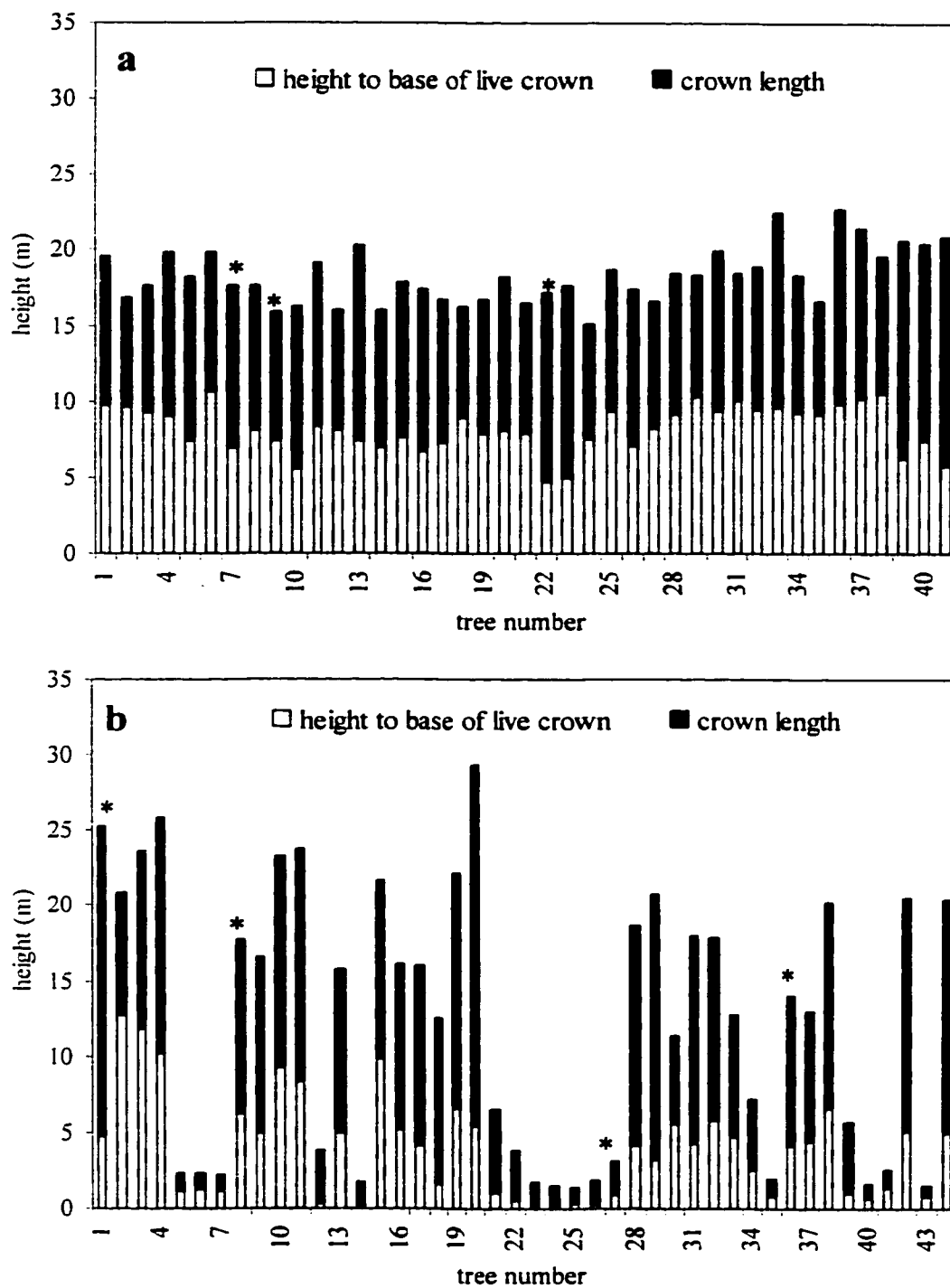


Figure 2.2. Total height and crown length of the even-aged (a) and multiaged (b) stand structures. Each bar represents the total height of individual trees with the darker shading denoting crown length. Trees that were sampled for physiological measurements are marked with an asterisk.

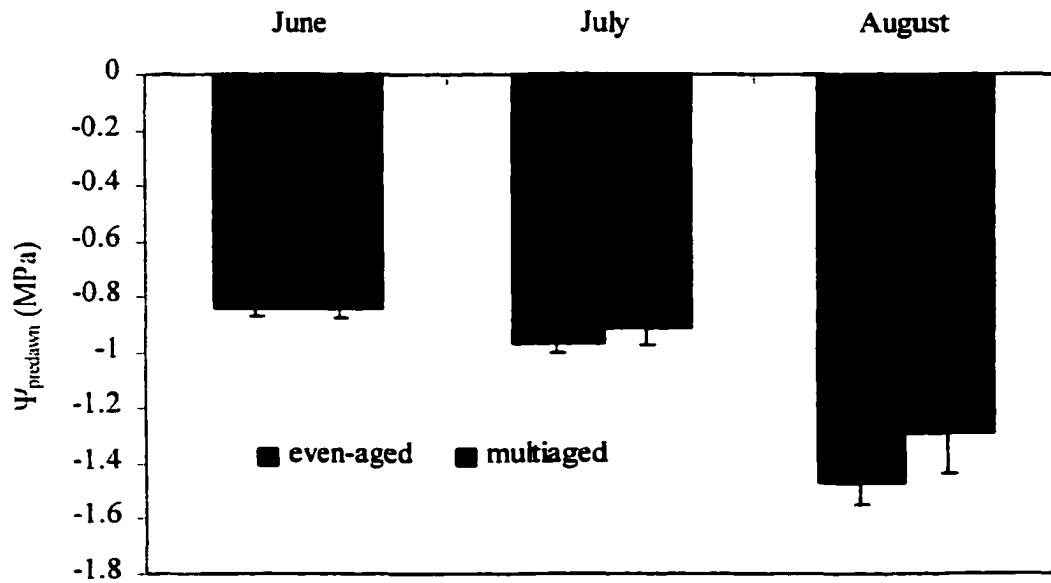


Figure 2.3. Predawn leaf water potential (Ψ_{predawn}) values measured in 1998. Data are unweighted. Error bars represent +/- one standard error. N = 3 for even-aged, N = 5 for multiaged.

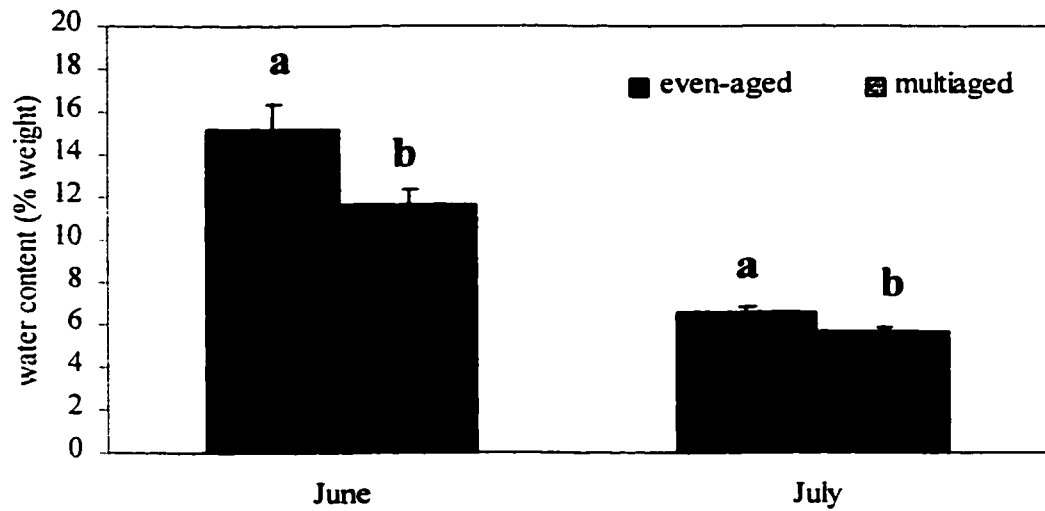


Figure 2.4. Soil water content (% by weight) for June and July 1999. Note that the even-aged samples were taken on June 10 and the multiaged on June 14. Both structures were re-sampled on July 15. Letters that are different denote significant differences. Error bars represent +/- one standard error. N = 10.

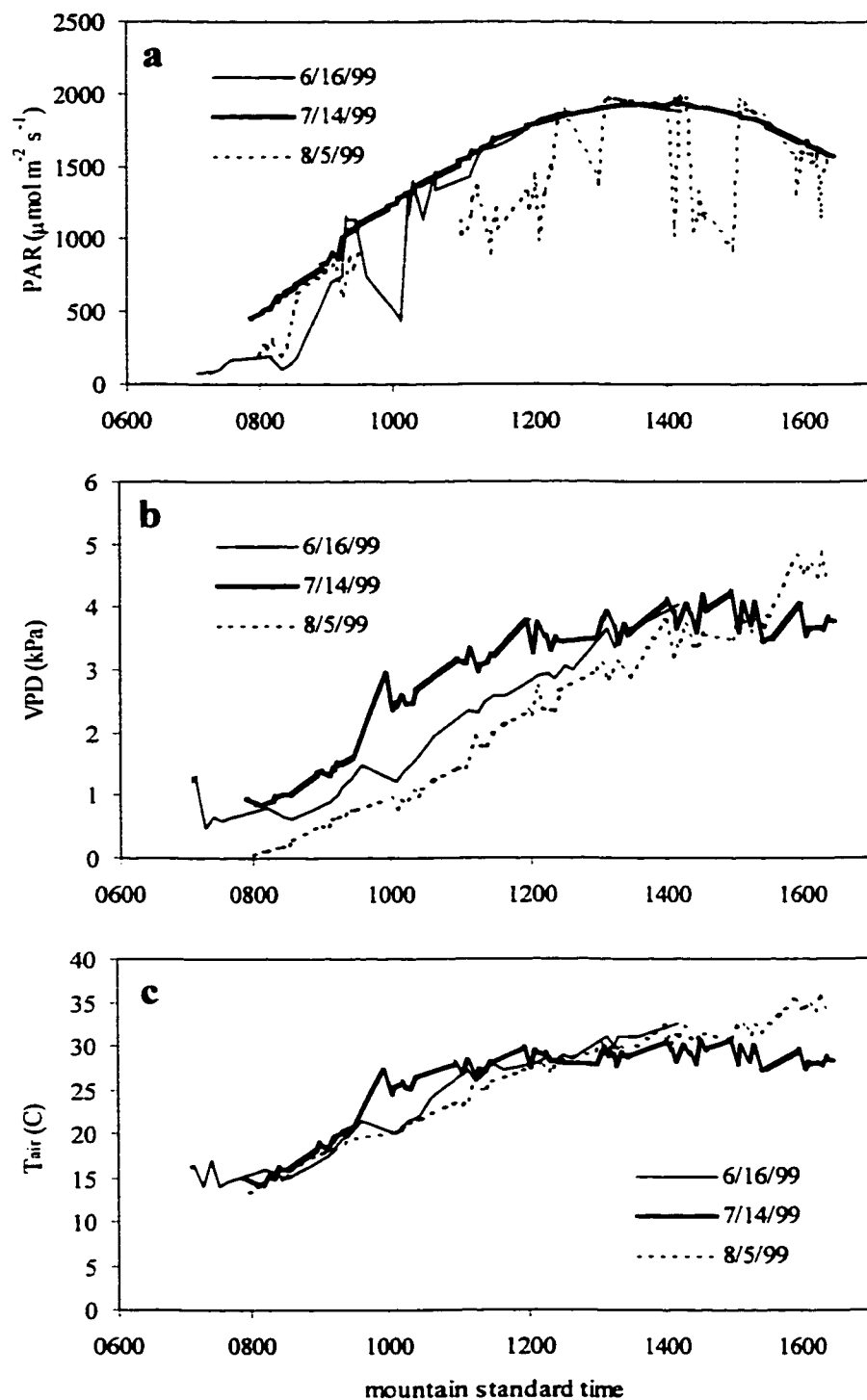


Figure 2.5. Diurnal pattern of environmental variables for the three measurement dates: (a) PAR, (b) VPD, and (c) T_{air} .

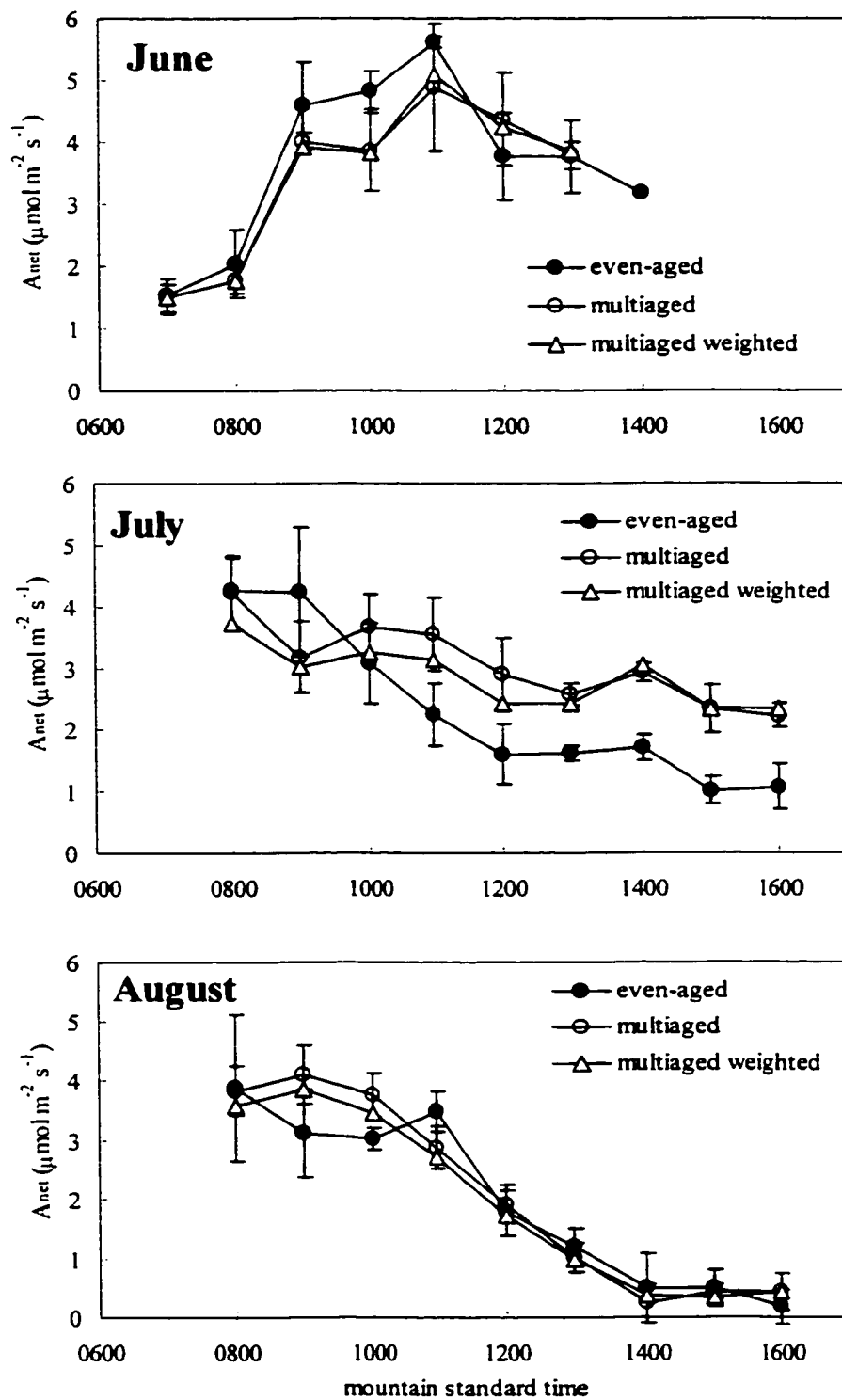


Figure 2.6. Mean diurnal net photosynthesis (A_{net}) rates for June, July, and August for even-aged and multiaged plots. Error bars represent \pm one standard error. Multiaged weighted refers to the data being weighted for the amount of leaf area present within each strata.

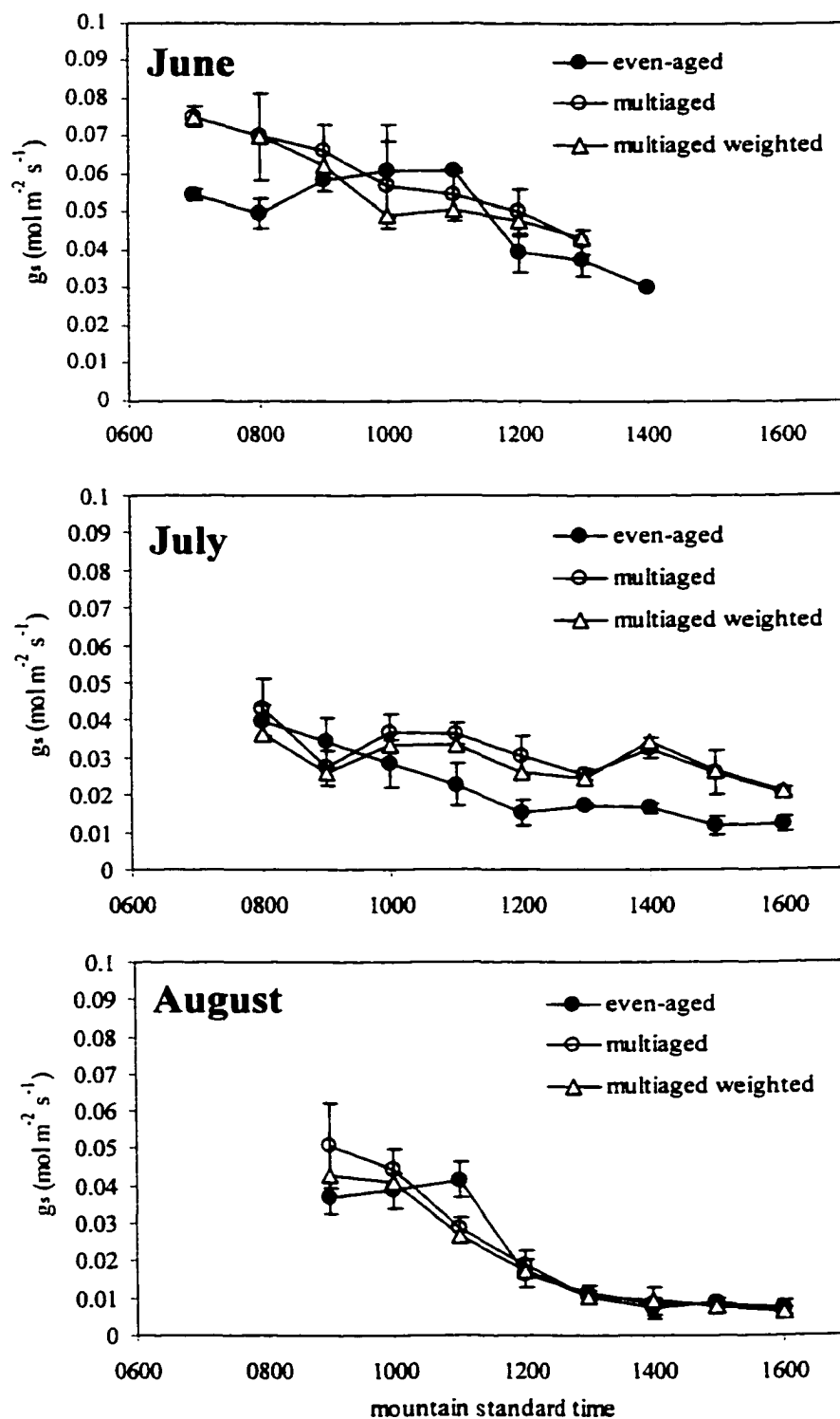


Figure 2.7. Mean diurnal stomatal conductance (g_s) for June, July, and August for even-aged and multiaged plots. Error bars represent \pm one standard error. Multiaged weighted refers to the data being weighted for the amount of leaf area present within each strata.

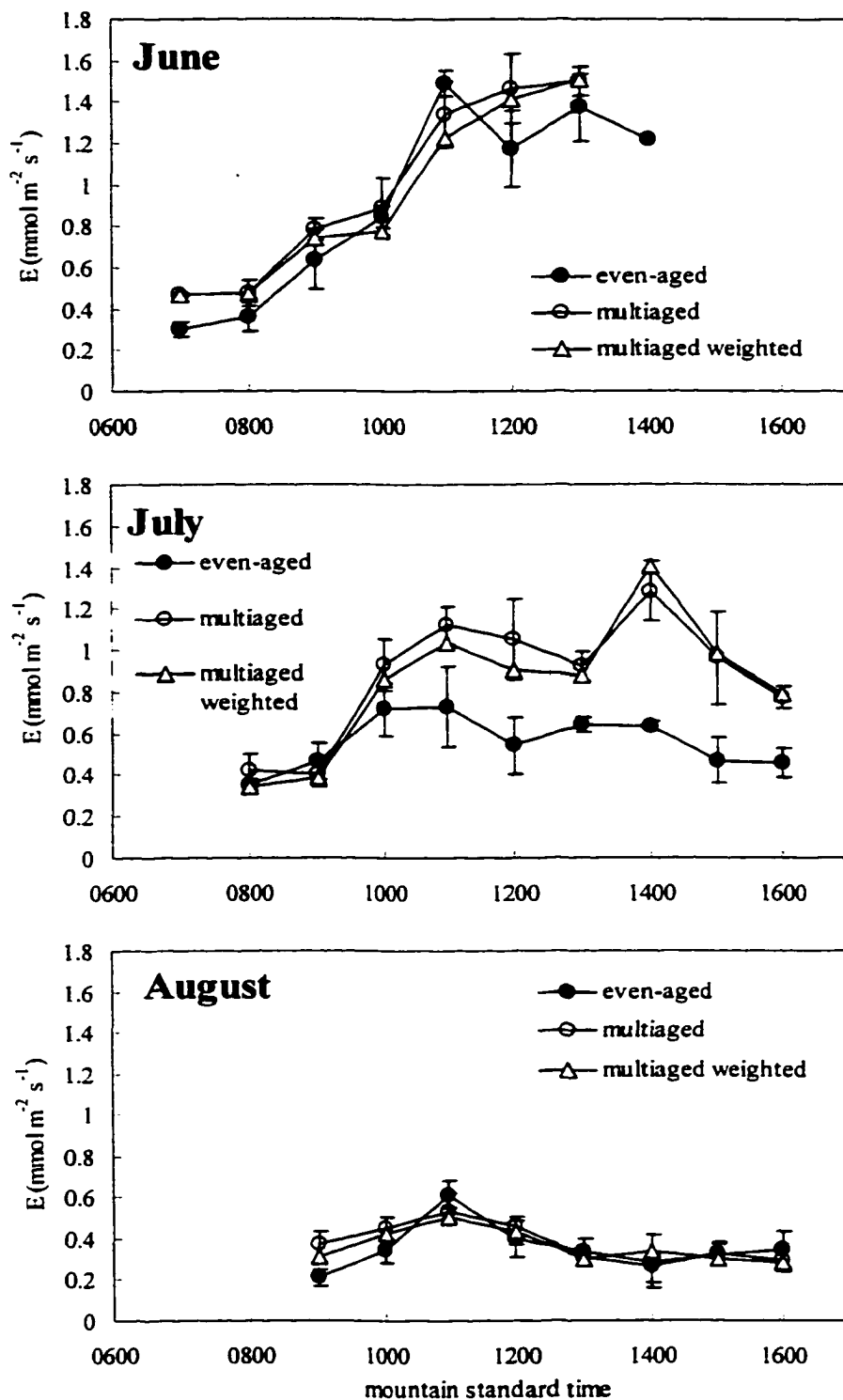


Figure 2.8. Mean diurnal transpiration (E) rates for June, July, and August for even-aged and multiaged plots. Error bars represent \pm one standard error. Multiaged weighted refers to the data being weighted for the amount of leaf area present within each strata.

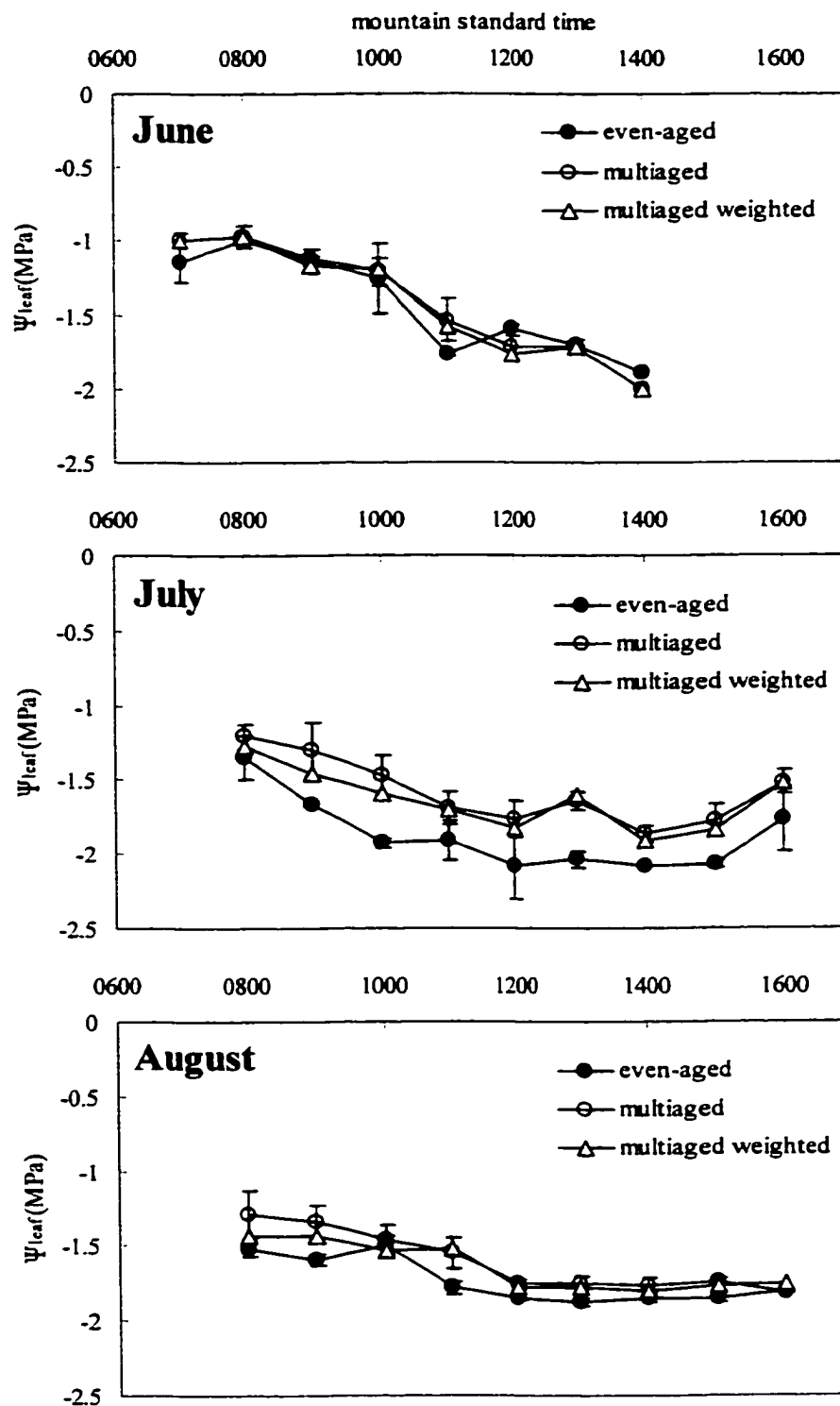


Figure 2.9. Mean diurnal leaf water potential (Ψ_{leaf}) patterns for June, July, and August for even-aged and multiaged plots. Error bars represent \pm one standard error. Multiaged weighted refers to the data being weighted for the amount of leaf area present within each strata.

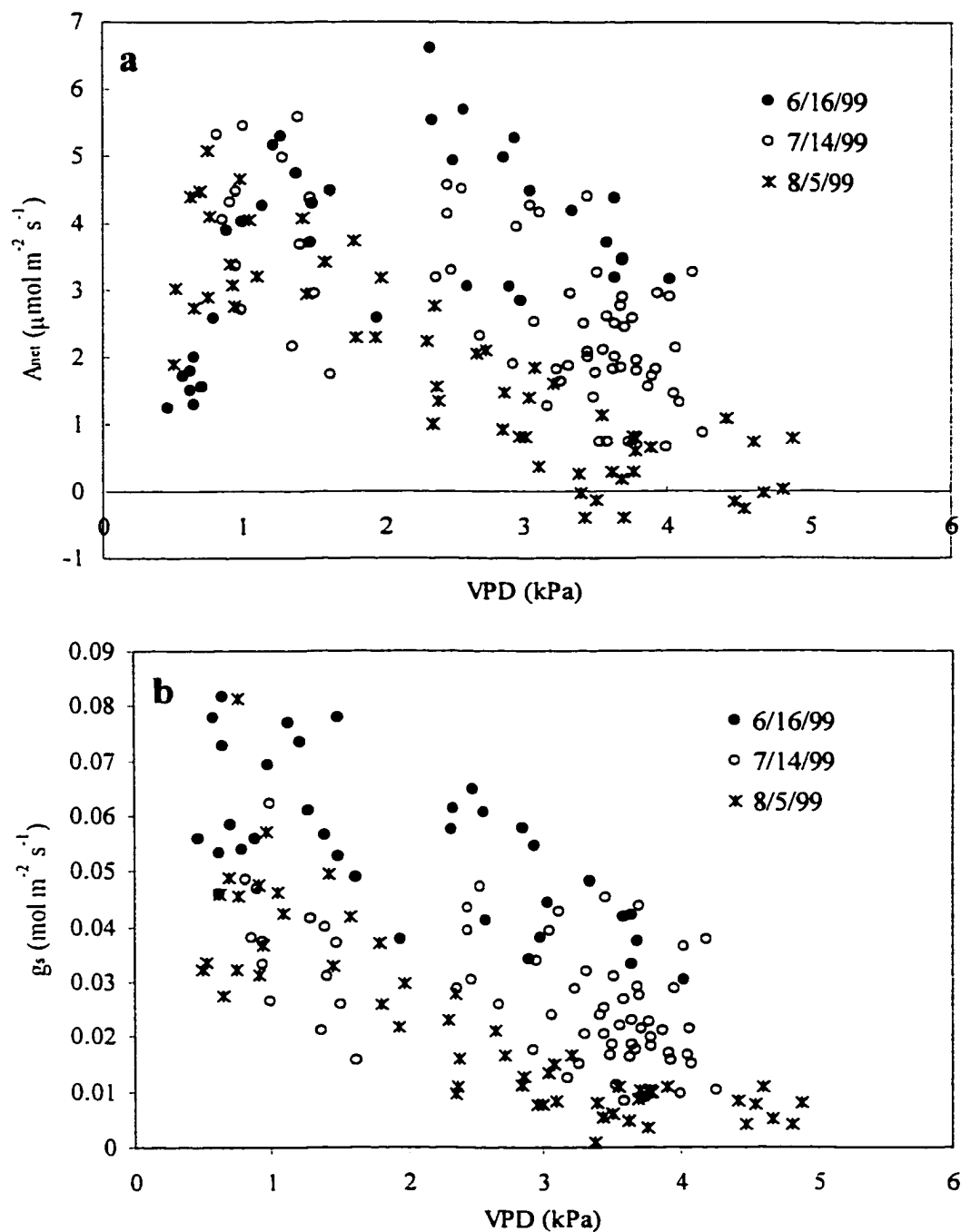


Figure 2.10. The relationship between A_{net} (a) and g_s (b) to vapor pressure difference (VPD) for the three measurement dates. Correlation coefficients for A_{net} vs. VPD are: 6-16-99 $R^2 = 0.17$, $P = 0.016$; 7-14-99 $R^2 = 0.42$, $P < 0.001$; 8-5-99 $R^2 = 0.75$, $P < 0.001$. Correlation coefficients for g_s vs. VPD are: 6-16-99 $R^2 = 0.45$, $P < 0.001$; 7-14-99 $R^2 = 0.30$, $P < 0.001$; 8-5-99 $R^2 = 0.70$, $P < 0.001$.

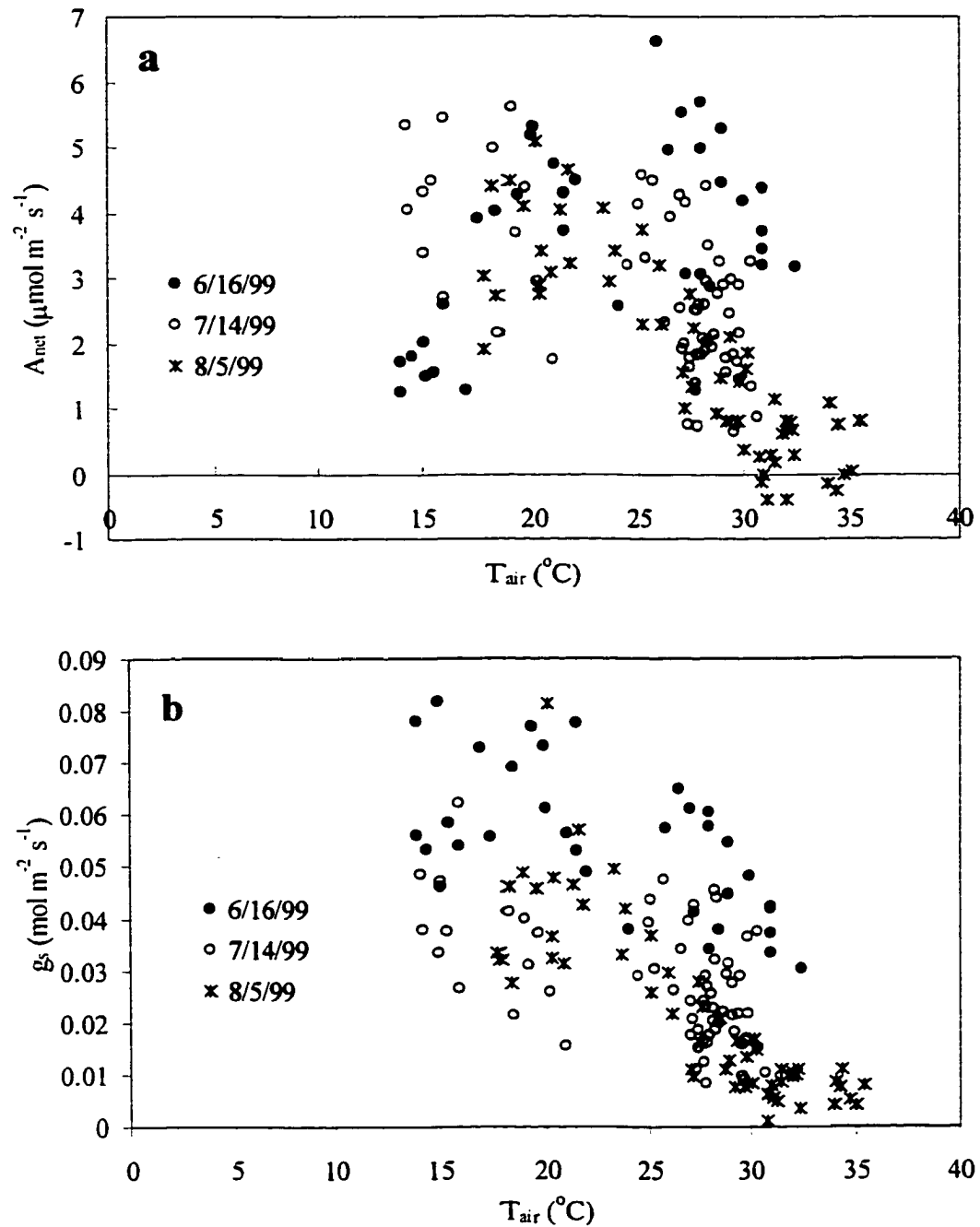


Figure 2.11. The relationship between A_{net} (a) and g_s (b) to air temperature (T_{air}) for the three measurement dates. Correlation coefficients are for A_{net} vs. T_{air} : 6-16-99 $R^2 = 0.26$, $P = 0.002$; 7-14-99 $R^2 = 0.38$, $P < 0.001$; 8-5-99 $R^2 = 0.73$, $P < 0.001$. Correlation coefficients for g_s vs. T_{air} : 6-16-99 $R^2 = 0.39$, $P < 0.001$; 7-14-99 $R^2 = 0.28$, $P < 0.001$; 8-5-99 $R^2 = 0.71$, $P < 0.001$.

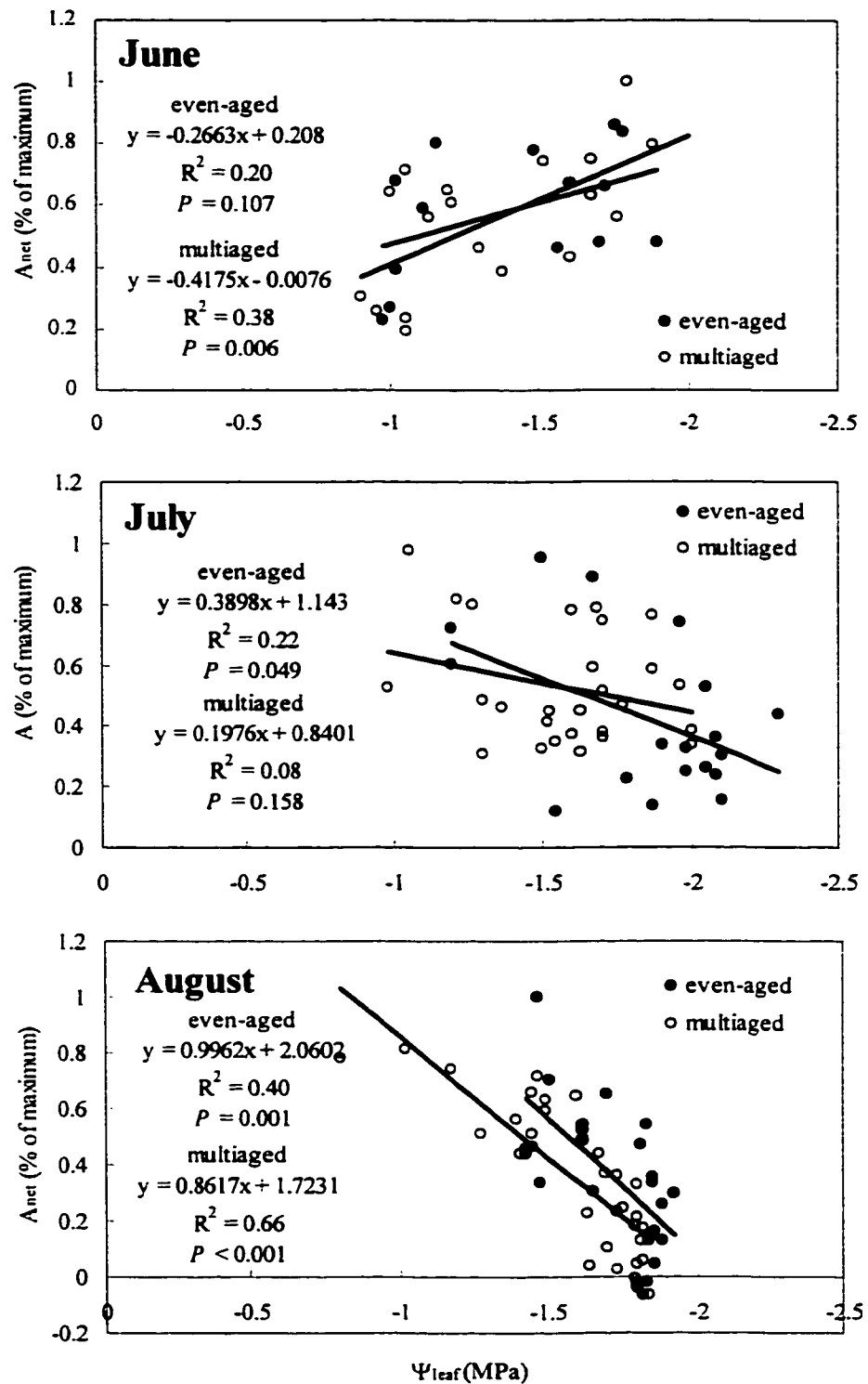


Figure 2.12. Relationship between leaf water potential (Ψ_{leaf}) and % maximum A_{net} for June, July, and August for even-aged and multiaged plots.

CHAPTER THREE

Does stand structure influence productivity potential in shade intolerant *Pinus ponderosa* Dougl. ex Laws.?

ABSTRACT

The relationships between canopy depth and area-based (A_{area}) and mass-based (A_{mass}) maximum photosynthetic rates, specific leaf area (SLA), and area-based (N_{area}) and mass-based (N_{mass}) leaf nitrogen were investigated for even-aged and multiaged stand structures of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). The primary structural difference between stand structures involves greater canopy depth in the multiaged stand structures as compared to the even-aged, possibly resulting in different light relations within each canopy. Both A_{area} and A_{mass} were relatively constant with canopy depth in both stand structures. N_{area} and N_{mass} decreased with increasing canopy depth in the even-aged stand structures but not in the multiaged stand structures. SLA tended to increase with increasing canopy depth, although this relationship was significant only in the multiaged stand structures. The typical linear relationship observed for many species between photosynthetic rate and leaf nitrogen was not present in either stand structure on either an area- or a mass-basis. N_{area} was highly correlated to SLA in both even-aged and multiaged stand structures ($R^2 = 0.66$ and $R^2 = 0.52$, respectively). These data suggest that leaf structure and nitrogen investment are adjusted in ponderosa pine such that photosynthesis is maximized in comparable ways throughout the canopies of both types of stand structure. This finding, along with similar levels of leaf area index (LAI) and basal area growth efficiency (BAGE), support the notion that multiaged stand structures of ponderosa pine have the physiological potential to produce similar amounts of wood volume as even-aged stand structures.

INTRODUCTION

The primary growth factor that determines the distribution of photosynthetic surfaces within forest canopies is light (Holbrook and Lund 1995). The amount of intercepted photosynthetically active radiation (PAR, 400-700 nm) is highly correlated to measures of growth and productivity in both agricultural and tree species (Monteith 1981, Oker-Blom et al. 1989, Dalla-Tea and Jokela 1991, Law et al. 1992). Canopy light interception is influenced by the amount of light received at the top of the plant canopy, the total amount of foliage (leaf area index, LAI), the vertical distribution of leaf area within the canopy, leaf angle, the optical properties of the leaves, and canopy architecture (Kuuluvainen and Pukkala 1989, Dalla-Tea and Jokela 1991, Chen et al. 1994). Crown shape and canopy structure primarily determine the spatial pattern of leaf display, which influences self-shading and efficiency of radiation interception (Kuuluvainen and Pukkala 1989, Stenberg et al. 1994).

The maximum or optimum amount of foliage a given species can support on a given site is determined by many factors, including site water balance (Grier and Running 1977), climate (including evaporative demand, Gholz 1982, Vose et al. 1994), soils, and shade tolerance (Vose et al. 1994, Oliver and Larson 1996). Shade intolerant conifers typically show less plasticity in physical leaf properties in response to light environment than do relatively more shade tolerant evergreen coniferous or broadleaf deciduous tree species (Abrams and Kubiske 1990, Smith et al. 1991). This trend is related to leaf-life longevity and is accompanied by a decrease in SLA, A_{\max} , and leaf nitrogen with increasing leaf-life span (Reich et al. 1995, Reich et al. 1997).

Photosynthetic performance of foliage is often related to leaf structural properties in many forest species. A strong relationship between leaf nitrogen (N_{leaf}) and maximum photosynthetic rates (A_{max}) has been observed across a diverse range of species (Field and Mooney 1986, Evans 1989, Reich et al. 1991, Reich et al. 1992). This relationship appears to be strongest in life-form groups that grow in environments rich in resources. Further, the $A_{\text{max}}-N_{\text{leaf}}$ relationship appears stronger in broad-leaved deciduous trees than in evergreen conifers (Reich et al. 1998).

Specific leaf area (SLA, leaf area per unit dry leaf biomass) is a relationship that describes the distribution of leaf biomass in relation to leaf area of a plant canopy (Pierce et al. 1994). Species exhibiting high SLA are able to support a large leaf area with a small carbon investment (Matyssek 1986). Species with high SLA often have relatively high photosynthetic rates, partly because of a higher nitrogen investment (Matyssek 1986, Reich et al. 1992, and Reich et al. 1997). Broadleaf deciduous trees generally have higher SLA than evergreen conifers (Abrams and Kubiske 1990, Kloeppel et al. 1995, Reich et al. 1998) with most *Pinus* species exhibiting low SLA relative to other coniferous species (Rundel and Yoder 1998). There are indications that deciduous tree species with a high SLA may exhibit lower water use efficiency (WUE = mmol CO₂ fixed in photosynthesis / mol H₂O lost through transpiration) than evergreen trees that have lower SLA, lower nitrogen investment, and lower overall photosynthetic capacity (Matyssek 1986).

Leaf structure and physiology vary with canopy depth in many forest species primarily due to vertical gradients in light. Total dry mass of plant canopies is arranged in a manner that maximizes photosynthetic rates (Gutschick and Wiegand 1988). Plants

generally have lower SLA in parts of the canopy where direct solar radiation is received (the top of the canopy where primarily “sun” leaves occur) and higher SLA where leaves may be shaded (Gutschick and Wiegel 1988, Klinka et al. 1992, Chen et al. 1996). This trend corresponds to sun leaves typically being thicker with higher photosynthetic capacity than shade leaves (Bjorkman and Holmgren 1963, Boardman 1977, Bjorkman 1981). Others have shown an increase in SLA and a decrease in leaf nitrogen content and photosynthetic capacity of leaves with increasing depth in deciduous and evergreen forest canopies (Hollinger 1989, Ellsworth and Reich 1993). Variations in these leaf properties, along with a decrease in leaf inclination angle with canopy depth, results in a more uniform distribution of PAR through the canopy and thus greater carbon gain than a forest with randomly distributed properties (Hollinger 1989).

Most *Pinus* species are classified as being relatively shade intolerant as compared to other coniferous evergreens (Daniel et al. 1979). Various forms of even-aged management are usually used for shade intolerant species because of their management efficiency and ease of regenerating intolerant species like most *Pinus*. Even-aged management usually results in a uniform canopy structure composed of one stratum. There is currently a growing desire to diversify stand structures across the landscape to meet a diverse array of objectives (O'Hara 1998), including timber production. Stand structure and stand development influence the vertical arrangement of LAI (Vose et al. 1994), further influencing light gradients throughout the canopy. In an intolerant *Pinus* species, enhancing the light environment for a greater portion of leaf area within the canopy could affect potential productivity of foliage and may influence overall stand productivity. Theoretically, a species on a given site should be able to support an

optimum amount of leaf area regardless of the distribution of the foliage under various stand structures.

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is a common conifer in western North America that is intensively managed for timber production as well as for its aesthetic value to the public. Ponderosa pine historically occurred in both even-aged and multiaged stand structures as the result of disturbance patterns that included high frequency, low intensity fire (White 1985, Habeck 1990, Arno et al. 1995, Harrod et al. 1999). Not much is known about optimum stocking levels, but there is some indication of differences in productivity of foliage (in terms of volume growth per unit of leaf area) of ponderosa pine under different stand structures (O'Hara 1996, Valappil 1997). This is quite possibly related to stand structural characteristics that influence light absorption. Ecophysiological traits (such as gas exchange, N_{leaf} and SLA) of individual species under specific stand structures have been studied for many forest species. The relationship of these variables for a given species under different stand structures, however, is unknown. The mechanisms that contribute to differences in stand productivity of ponderosa pine in different stand structures also remain unknown, and may be explained by physiological variation in the foliage as a direct effect of the light environment. This study was implemented to test the relationships between site occupancy, light interception, leaf structural properties, and gas exchange throughout the canopies of different stand structures of ponderosa pine to elucidate possible differences in these relationships that may explain observed differences in stand productivity.

MATERIALS AND METHODS

Study sites - This experiment was implemented in stands of ponderosa pine in western Montana. Study sites were located on the Bitterroot and Lolo National Forests, on Lubrecht Experimental Forest, and on land managed by the Montana Department of Natural Resources and Conservation. Pure stands of ponderosa pine (>95% ponderosa pine conifer composition) were selected, with individual plot pairs of even-aged and multiaged stand structures placed in areas that were close in proximity and deemed to be of the same or similar site quality based on slope, aspect and vegetation characteristics. There was a total of five plot pairs (five even-aged plots and five multiaged plots) installed. Circular plots 0.1 ha in size were established in fully stocked stands with minimal differences in density within plot pairs and between plot pairs. Habitat types (Pfister et al.1977) were identified for each plot (Table 3.1). Plot numbers followed by an E refer to even-aged plots; plot numbers followed by an M refer to multiaged plots (Table 3.1).

Tree measurements - Each tree breast height (1.37 m) and taller was counted and measured. Total tree height and height to the base of the live crown was measured with a clinometer or a height pole, and diameter was measured at breast height. Two increment cores at right angles were taken from each tree 12.7 cm (5 in) and greater in breast height diameter to obtain age at breast height. Average age of even-aged plots was 83 years (breast height age). Trees from the multiaged plots ranged from 10 to 152 years (Table 3.1). Bark thickness was measured with a bark-gauge to the nearest mm directly below the location of each core on each tree. Sapwood length was measured on the increment cores in the field, and later used to compute sapwood basal area. Leaf area per tree was

computed using equations that relate sapwood basal area with leaf area of individual trees (O'Hara and Valappil 1995). This concept is based on the pipe model theory to predict canopy leaf area presented by Waring et al. (1982). Sapwood basal area of trees less than 12.7 cm in diameter was assumed to be basal area minus the bark. Leaf area of each tree was computed, summed, and divided by the area of the plot to get leaf area index (LAI). Stand density index (SDI) was computed for each plot, using the formula:

$$SDI = \Sigma(DBH_i/10)^{1.6}$$

where DBH_i is the diameter of the i th tree in the stand (Long and Daniel 1990). Crown diameter was measured for each tree on each plot in a north-south and east-west orientation. Crown width was assumed to be equal to the point where the end of the longest branch extended from the bole of the tree in each direction. The distance was estimated as the distance from the bole of the tree as if a plumb-line was extended to the ground from the branch. Projected crown area was computed for each tree as a function of average crown width, summed across the plot, and divided by the plot area to obtain percent canopy cover.

Basal area increment was computed for each tree that was cored. Previous five-year radial growth was measured on each core and averaged for each tree. Basal area growth was computed as current basal area – basal area of the tree 5-years previous. Annual basal area growth (BAGR, $m^2 ha^{-1}$) was computed by dividing 5-year basal area growth by 5. Basal area growth efficiency (BAGE) was computed as BAGR/leaf area of individual trees ($mm^2 m^{-2}$). Total BAGR and average BAGE were computed for each plot.

Sample tree selection – Even-aged stands of ponderosa pine typically exhibit a bell-shaped diameter frequency distribution, while multiaged stands can typically be divided into cohorts of trees that have arisen after a common disturbance (O'Hara 1996, see Figure 3.1, plots 8E and 7M). Leaf area in the even-aged plots is concentrated in one canopy stratum (Figure 3.2a, Figure 3.3). The multiaged structures have a heterogeneous canopy layer with numerous strata, and leaf area located from the top of the canopy to the forest floor (Figure 3.2b, Figure 3.3).

For each even-aged plot, three trees were sampled for physiological measurements and leaf collection. Crown classification of individual trees was made following the definitions of Oliver and Larson (1996). The uniform canopy layer of all the even-aged stands sampled in this study was considered to be the B-stratum. For each multiaged plot, four to five trees were sampled, encompassing the range of ages and sizes that represent the number of cohorts present in each stand. Emergent trees belonging to the oldest cohort were classified as the A-stratum. The upper continuous canopy layer was composed of the middle cohort in each stand, and was considered the B-stratum. Trees belonging to the B-stratum are the most comparable to trees in the even-aged plot because of similar ages and sizes. Trees belonging to the youngest cohort were classified as the C-stratum (lower stratum beneath the B-stratum), and ranged from seedlings to saplings. All trees sampled were co-dominant within their respective strata.

Light interception – Measurements of below-canopy PAR (Q_z) were made on each plot using a Sunfleck Ceptometer (Decagon Devices, Pullman, WA, USA) following the procedures of Pierce and Running (1988). Measurements were made on cloud-free days one hour \pm solar noon. A complete plot pair was measured on the same day to avoid day-

to-day variations in light conditions. Before and after each plot was measured, open conditions were measured, recorded, and later averaged to obtain a value for open PAR (Q_o) conditions. A 576 m² square grid was placed on the 0.1 ha circular plots centered on plot center. Measurements began at the northwest corner of the grid, and were made at 3-m intervals from west to east along the first transect, from east to west along the second transect, and so forth. Each measurement point is the average of four readings taken in the four cardinal directions. Measurements were taken at a total of 81 points within each plot.

The Beer-Lambert Law was used to compute a canopy light extinction coefficient, k :

$$k = \frac{\ln(Q_z/Q_o)}{LAI}$$

The extinction coefficient was computed in two ways: as a point-based measure and as a plot-average. In the point-based method, k was computed for each point on the plot, and then averaged to obtain one k for the plot. In the plot-average method, all values of Q_z were averaged, and one k was computed for the plot. A PAR-ratio was computed as below canopy PAR divided by total incoming PAR (PAR ratio = Q_z/Q_o). A low PAR-ratio indicates more light absorption by the plant canopy relative to a high PAR-ratio.

Gas exchange - A field portable closed gas exchange system (LI-6200, Li-Cor Inc., Lincoln, NE) was used to measure photosynthesis and stomatal conductance with a 1/4-l cuvette during the summer of 1999. Two fascicles were excised from each branch and measured by placing the mid-portion of the fascicles inside the cuvette. Gas exchange measurements were made within a one- to two-hour period that was centered over the peak in leaf gas exchange activity identified one day prior to measurement of each plot

pair. The peak period for all measurement days in July fell between the hours of 0830 and 1100. The maximum rate of photosynthesis (A_{\max}) is assumed to be photosynthesis that occurs under non-limiting conditions (water, light, temperature, CO_2 , etc.). By identifying the peak in leaf gas exchange activity, photosynthetic rates obtained with the LI-6200 under these conditions are being reported as rates of A_{\max} .

Samples were obtained with a 4-m tall platform and a pole pruner, or with a 12-gauge shotgun for larger trees. Two or three branches at varying heights were sampled on each previously identified sample tree. Gas exchange measurements were completed within three minutes of detachment from the tree. Preliminary measurements found no difference in gas exchange when detached branches were measured within three minutes. Supplemental light from a QED light source (Quantum Devices, Inc., Barneveld, WI) with a peak wavelength of 670 nm was used to supply additional light (at a rate of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$) for all measurements to ensure light saturating conditions for photosynthesis. All measurements were made on either sunny or mostly sunny days. Gas exchange measurements were taken on the same day for plots 1M and 2E, 3M and 4E, 7M and 8E, and 11M and 12E. The Lubrecht plot pair (13M and 14E) was measured on July 21 and 23 respectively, because the proximity of the plots to each other made it impossible to measure both plots on the same day.

Ponderosa pine has three-needled fascicles with stomata on all surfaces. All gas exchange data are expressed on an all-sided leaf area basis (A_{area}) or a mass basis (A_{mass}). After gas exchange measurements, the width of the fascicles was measured to the nearest 0.1 mm, and multiplied by the width of the cuvette to obtain projected leaf area. Since the middle portion of the fascicles were measured, the area of ponderosa pine needles

was assumed to be a right cylinder divided into thirds. It follows that the conversion factor from projected leaf area to all-sided leaf area is 2.36 (Rundel and Yoder 1998).

Specific leaf area and leaf nitrogen – After each gas exchange measurement, five fascicles from the same branch were collected for measurement of specific leaf area (SLA) and leaf nitrogen (N_{leaf}). The fascicles were kept on ice until they were analyzed in the lab after gas exchange measurements were completed in the field. Length of each needle was measured to the nearest 0.5 mm. The five fascicles were placed in water, and the volume of water displacement was measured. Following the procedures of Johnson (1984) for three-needled pines, the equation:

$$A = 2l [1 + \pi/n] * \text{sqrt} (V n/\pi l)$$

was used to compute all-sided leaf area collectively for the five fascicles, where A is the total surface area (cm^2), V is the displaced volume of the needle sample (cm^3), n is the number of needles per fascicle, and l is the cumulative needle length of the needles in the sample (cm). Needles were then dried at 70 °C for 48 hr, and weighed to the nearest g. SLA was computed as all-sided leaf area (cm^2) divided by dry weight (g). Leaves were ground through a 40-size mesh using a Wiley Mill and analyzed for nitrogen content using an elemental gas analyzer. Leaf nitrogen is expressed on a mass (N_{mass}) and an area (N_{area}) basis.

The height of each branch sampled for physiological measurements and leaf structural analysis (both were measured on the same branch) was recorded at the time of sampling. To test the relationship of A_{area} , A_{mass} , N_{area} , N_{mass} , and SLA with canopy depth, a relative height for each sample in each plot was computed as follows:

$$\text{relative height} = \text{height of sample (m)} / \text{height of the tallest tree on the plot (m)}.$$

The average relative height of the even-aged samples was 0.49 and ranged from 0.26 to 0.76. The average relative height of the multiaged samples was 0.34 and ranged from 0.06 to 0.81.

Statistical Analysis – Plot-level means (tph, basal area, sapwood basal area, LAI, SDI, % canopy cover, and crown ratio) for even-aged and multiaged plot pairs were tested for significant differences using paired t-tests. Paired t-tests were also used to test for statistical significance in the light extinction coefficient (k) and PAR-ratio between even-aged and multiaged stand structures. Relationships between A_{\max} , N_{leaf} , SLA, and relative height were analyzed with linear regression techniques using SYSTAT (SPSS Inc.). All differences were tested at the $\alpha = 0.05$ level.

RESULTS

Growing space occupancy and light relations – Basal area (m^2/ha) and stand density index (SDI), both diameter-based measures of site occupancy, were significantly greater in the even-aged plots as compared to their multiaged pairs (Table 3.2). The range in basal area for even-aged plots was 23.3 to 25.6 $\text{m}^2 \text{ha}^{-1}$ compared to a range of 20.2 to 23.8 $\text{m}^2 \text{ha}^{-1}$ for multiaged plots (Table 3.2). Sapwood basal area (m^2/ha) and LAI were not significantly different between stand structures (Table 3.2), indicating both structures supported the same amount of water-conducting tissue and the same amount of leaf area. Even-aged plots had significantly greater % canopy cover and significantly lower crown ratio on average as compared to multiaged plots (Table 3.2). Mean annual basal area growth (BAGR) and basal area growth efficiency (BAGE) were not significantly different between stand structures (Table 3.3). The range in mean BAGR was very

similar for both stand structures, ranging from 0.15 to 0.34 $\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$ for the even-aged plots and from 0.15 to 0.35 $\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$ for the multiaged plots. Mean plot-level BAGE ranged from 4.46 to 6.96 $\text{mm}^2 \text{m}^{-2}$ for the even-aged plots and 3.60 to 8.28 $\text{mm}^2 \text{m}^{-2}$ for the multiaged plots (Table 3.3).

There were no significant differences in the average light extinction coefficient (k) for the point-based or the plot-average based measure between stand structures (Table 3.4). Multiaged plots had a greater PAR-ratio overall as compared to even-aged plots, indicating the even-aged stands absorbed more light resulting in less light being measured under the canopy of the even-aged plots as compared to the multiaged plots (Table 3.4).

A_{max} , N_{leaf} , and SLA – Relationships were variable between A_{max} , N_{leaf} , and SLA between stand structures and between methods of comparison. These relationships, as well as the relationship between A_{max} , N_{leaf} and SLA with canopy height are summarized in Table 3.5. There were few significant relationships of A_{max} with any other variable. SLA was correlated best with mass-based A_{max} (A_{mass}), area-based N_{leaf} (N_{area}), and relative height. There was no relationship in either stand structure between A_{mass} or A_{area} with relative height of sample within each structure (Figure 3.4a-d). Leaf nitrogen exhibited a positive linear relationship with increasing relative height when expressed on a mass (N_{mass}) and an area (N_{area}) basis in the even-aged plots (Figure 3.5a and 3.5b), with no trend in the multiaged plots (Figure 3.5b and 3.5d). There was a tendency for N_{mass} to increase with increasing relative height in the multiaged plots (Figure 3.5b). Specific leaf area (SLA) tended to decrease with increasing height in both structures, with only the multiaged stand structure exhibiting a significant linear relationship (Figure 3.6a and 3.6b, Table 3.5).

There was no relationship between mass-based photosynthesis (A_{mass}) and mass-based leaf nitrogen (N_{mass}) or between area-based photosynthesis (A_{area}) and area-based leaf nitrogen (N_{area}) for either stand structure (Figure 3.7a-d, Table 3.5). A_{mass} was not correlated with SLA in the even-aged stand structure (Figure 3.8a), however A_{mass} showed a weak positive linear relationship with SLA in the multiaged stand structure (Figure 3.8b). There was no relationship between A_{area} and SLA for either stand structure (Figure 3.8c and 3.8d). Leaf nitrogen on a mass basis (N_{mass}) and SLA were not correlated for even-aged or multiaged stand structures (Figure 3.9a and 3.9b). Leaf nitrogen on an area basis (N_{area}) was strongly correlated with SLA for both the even-aged and the multiaged stand structures (Figure 3.9c and 3.9d).

DISCUSSION

Multiaged stand structures comprised of pure ponderosa pine supported comparable amounts of leaf area as even-aged stand structures in this study (Table 3.2). Basal area growth efficiency (BAGE) tended to be greater (although not significant) for multiaged stands, but overall annual basal area growth (BAGR) was similar (Table 3.3). Basal area growth does not account for volume increment related to height, and may underestimate the wood production of large trees because of the relationship between basal area increment and tree size. The stands investigated in this study show the same trends in site occupancy and overall growth efficiency as stands sampled by O'Hara (1996) and Valappil and O'Hara (2000a and 2000b) in similar locations in western Montana. The current study further supports the notion that different stand structures of ponderosa pine can support similar amounts of leaf area and can produce similar amounts of wood

volume. Diameter-based measures of density, including basal area and stand density index (SDI), may not be adequate descriptors of site occupancy of complex stand structures such as the multiaged stand structures sampled in this study. More physiologically-based measures of site occupancy such as LAI (O'Hara 1988) and sapwood basal area may better represent the potential productivity of a site because they better represent first principle processes (water use and light capture) that occur within a forest stand structure (O'Hara and Valappil 1999).

The relationship between sapwood basal area and foliage biomass or leaf area of individual trees has been well established for many coniferous species of western North America (Grier and Waring 1974, Snell and Brown 1978, Waring et al. 1982, O'Hara and Valappil 1995). This relationship, known as the pipe model theory, states that a given amount of transpiring foliage must be supplied with water by a proportional amount of water conducting tissue (Margolis et al. 1995). Total site occupancy between and within northern coniferous forests as described by LAI is strongly related to site water balance (Grier and Running 1977). In the present study, sapwood basal area and LAI are comparable between homogenous canopy layers of even-aged stands and stratified canopy layers of multiaged stands, allowing for the examination of leaf- and canopy-level physiological differences related to stand structure. Instantaneous gas exchange measurements combined with measures of leaf structural attributes that estimate longer-term leaf productivity allow for investigation of potential differences in the physiology of leaf area as related to stand structure.

There are often inconsistencies in the literature involving the expression of A_{\max} and leaf nitrogen. A reason for expressing A_{\max} on an area-basis is that light interception

within the canopy is related to projected leaf area. *Pinus* species, however, have stomata on all surfaces (Rundel and Yoder 1998), and therefore conduct gas exchange on all leaf surfaces even though light absorption occurs on only a projected leaf area basis. SLA of *Pinus* species and coniferous evergreens in general can be highly variable between species (Rundel and Yoder 1998), suggesting that expression on a mass-basis might take into account variations in A_{\max} due to variations in leaf structure. The range in A_{mass} was similar for both stand structures, ranging from 21.18 to 60.78 $\text{nmol g}^{-1} \text{s}^{-1}$ for even-aged trees and 18.23 to 64.54 $\text{nmol g}^{-1} \text{s}^{-1}$ for multiaged trees. A_{mass} and A_{area} were highly correlated with each other for both stand structures ($R^2 = 0.84$ for the even-aged plots and $R^2 = 0.85$ for the multiaged plots, data not shown), suggesting relationships (if they do exist) between A_{\max} and other variables (leaf nitrogen, SLA, or canopy depth) should be similar regardless of the method of expression.

The lack of any trend in photosynthetic rates with increasing canopy depth along with similarities in the rate of light absorption at the canopy level suggests light is not limiting to the foliage in either stand structure at any point within the canopy. Ponderosa pine is a relatively shade intolerant conifer that exhibits an open canopy structure (Harlow et al. 1996). Foliage is typically shed when irradiance reaches 10% full sunlight (Bond et al. 1999). Although even-aged stand structures had greater mean percent canopy cover, the rate with which the foliage absorbed incoming radiation was not different from the multiaged stand structures as indicated by similar light extinction coefficients (Table 3.4). PAR-ratios, however, indicate that even-aged stand structures were able to absorb 16% more radiation than multiaged stand structures (Table 3.4).

The shade intolerance of ponderosa pine may have contributed to the relatively small range in leaf nitrogen content for both stand structures (N_{mass} ranged from 11 to 15.3 mg g⁻¹ for even-aged trees and from 10.3 to 16.8 mg g⁻¹ for multiaged trees while N_{area} ranged from 1.17 to 2.07 g m⁻² for even-aged and 1.16 to 2.22 g m⁻² for multiaged trees). SLA also exhibited a relatively small range in values for both structures (68.17 to 100.87 cm² g⁻¹ for even-aged and 62.26 to 97.21 cm² g⁻¹ for multiaged trees). The amount of variation in SLA (increasing 32% in the even-aged and 36% in the multiaged with canopy depth) is similar to other reports of a 50% increase in SLA with canopy depth in ponderosa pine (Bond et al. 1999) and a 22% increase in a 25-year old even-aged stand of *Pinus pinaster* Ait. (Porte and Loustau 1998). Other more shade tolerant evergreen species often exhibit greater changes in SLA (up to several times higher) with increasing canopy depth (Hollinger 1989, Ellsworth and Reich 1993, Bond et al. 1999). The upper 20% of the canopies in both the even-aged and multiaged stand structures were not sampled in this study due to the restrictions associated with the sampling procedure implemented (the height of the platform used and the range of the ballistic sampling device). Because of the small range observed in the other 80% of the canopy, it is unlikely that sampling the very top of the canopy would have captured a significant amount of additional canopy-level variation.

As leaves exhibit greater SLA within a plant canopy, leaf thickness tends to decrease and leaf area increases (Chabot et al. 1979, Kellomaki and Oker-Blom 1981). At the top of the canopy, where productivity of the foliage is expected to be the greatest within the canopy because of the greatest amount of incident radiation, SLA will tend to be lower because of greater leaf thickness and less leaf area (Gutschick and Wiegell 1988). Greater

SLA is more efficient at capturing light when light is limiting because greater leaf area will receive more incident radiation. This may be accompanied by lower stomatal density, which may further result in greater water use efficiency due to increased transpiration resistance (Chen et al. 1996). On a mass-basis, leaf nitrogen may be similar throughout a given plant canopy because the nitrogen investment per unit of leaf mass will be the same regardless of the leaf structure or leaf location within the canopy. Mass-based photosynthesis (A_{mass}) will also tend to be similar throughout the canopy partly due to the strong relationship exhibited between nitrogen content of leaves and the significant role nitrogen plays in photosynthetic processes. Nitrogen is the primary constituent of proteins of the Calvin cycle and is strongly related to chlorophyll content of leaves (Evans 1989). Previous studies have shown relative constancy in N_{mass} and A_{mass} with canopy depth (Ellsworth and Reich 1993, Bond et al. 1999). On an area-basis, however, a strong relationship between leaf nitrogen and photosynthetic rates may be expected within any given plant canopy. Strong relationships between SLA, N_{area} and A_{area} have been observed in a broadleaf deciduous forest (*Acer saccharum*, Marsh., sugar maple), with significant gradients in these leaf properties with canopy depth (Ellsworth and Reich 1993). N_{mass} and A_{mass} did not show any trend with vertical canopy depth in the maple forest.

Broad-leaved deciduous trees tend to show stronger relationships between A_{max} and leaf nitrogen and exhibit higher SLA than evergreen conifers (Reich et al. 1995, Reich et al. 1998). Other studies have demonstrated greater variations in SLA and leaf thickness in deciduous broadleaf trees than in coniferous trees when comparing sun- and shade-type leaves (Abrams and Kubiske 1990). Further, shade tolerant conifers (*Abies amabilis*

(Dougl. ex Loud.) Forbes, *Abies lasiocarpa* (Hook.) Nutt., *Picea engelmannii* Parry ex Engelm., and *Pseudotsuga menziesii* (Mirbel) Franco.) tend to exhibit more plasticity in SLA as the percent incident above canopy radiation decreases than more shade intolerant conifers (*Pinus contorta* Dougl. ex Loud. and *Pinus ponderosa* Dougl. ex Laws., Klinka et al. 1992, Chen et al. 1996, Chen 1997).

In the present study, there was a negative linear relationship between SLA with increasing canopy depth for the multiaged stand structures, with a similar tendency in the even-aged stand structures (Figure 3.6). The correlation between SLA and relative height was relatively low ($R^2 = 0.07$ for even-aged and $R^2 = 0.20$ for multiaged) and the range in values of SLA was small. Therefore, it can be concluded that SLA changed in the expected way with increasing canopy depth, but the rate of change was relatively small in both even-aged and multiaged stand structures. Because ponderosa pine is a relatively shade intolerant pine, the light environment may be fairly constant from the top to the bottom of the canopy, resulting in the small range and lack of change in SLA with canopy height in both stand structures. Both A_{area} and A_{mass} were also relatively constant within the canopies of both the even-aged and the multiaged stand structures sampled in this study (Figure 3.4).

With a strong gradient in SLA with increasing canopy depth, area-based measures of leaf nitrogen and photosynthetic rates would be expected to vary with canopy depth also. There was a significant linear relationship between N_{area} with canopy depth for the even-aged structures but not for the multiaged stand structures (Figure 3.5c and 3.5d). The lack of relationship of photosynthetic performance with canopy depth resulted in no distinct relationships between photosynthesis and leaf nitrogen (Figure 3.7). The only

significant relationship between photosynthesis and SLA was for A_{mass} in the multiaged stand structures (Figure 3.8b). The observed trend (increasing A_{mass} with increasing SLA) is the opposite of what might be expected in a plant canopy where a light gradient exists.

N_{mass} did not vary with SLA (Figures 3.9a and 3.9b) because the nitrogen investment per unit of leaf mass was the same regardless of canopy depth, stand structure, or SLA. N_{area} however was highly correlated with SLA in both stand structures (Figure 3.9c and 3.9d). This trend indicates that at lower SLAs (where leaf area per unit leaf mass is less), nitrogen investment is greater on an area basis. This would correspond to sun-type leaves in canopies where light gradients are prevalent. Since there was no relationship between A_{area} and SLA or between A_{area} and canopy depth in this study, the strong relationship between N_{area} and SLA suggests that leaf structural properties have changed within the canopy so that photosynthetic rates are maximized in comparable ways throughout the canopies in both even-aged and multiaged stand structures.

Many factors determine photosynthetic capacity within a given forest canopy. It is well established that light environment influences leaf structural attributes and photosynthetic performance. It is also possible that gradients in temperature, vapor pressure difference, leaf water potential and CO_2 concentrations exist within a given canopy and may be different between diverse canopy structures. In the present study, only fully sunlit one-year-old foliage was sampled, decreasing the total variation sampled within the canopies. Other studies have shown decreasing nitrogen content, photosynthetic rates, and SLA with increasing leaf age (Schoettle and Smith 1999, Valappil and O'Hara 2000b). Gas exchange measurements were conducted during

previously identified peaks in July, which occurred most commonly between the hours of 0830 and 1100 (see chapters one and two, Nagel 2000a and 2000b). Light is often not saturating to photosynthesis at this time (at 0830, PAR is usually $< 500 \mu\text{mol m}^{-2} \text{s}^{-1}$). Even though gas exchange measurements occurred under supplemental light ensuring light-saturating conditions for photosynthesis, some samples may have been clipped in environments experiencing light-limiting conditions at the time of measurement. All of these uncontrolled and unmeasured variables must be recognized when extrapolating findings from this study to other situations, especially where the ecophysiology of a given species is quite different from ponderosa pine.

CONCLUSIONS

Canopy-average SLA is sometimes used in ecosystem process models to compute LAI from foliage biomass (Running and Gower 1991, Aber and Federer 1992, Landsberg and Waring 1997). SLA demonstrates significant plasticity within plant species, is often closely related to leaf nitrogen and photosynthetic capacity, and can be predicted from LAI (Pierce et al. 1994). Individual tree models designed to predict growth in response to manipulations in stand structure could incorporate leaf structural properties as they relate to gradients in the light environment within a forest canopy. The results from this study show that canopy-level light is attenuated similarly through the even-aged and multiaged stand structures sampled here. This resulted in a similar amount of variation in gas exchange and leaf structural properties of fully sunlit one-year-old foliage in both stand structures. The effect of stand structure on the physiology of newly developing foliage, foliage greater than one-year-old, or foliage not fully exposed to sunlight was not

quantified, and may play a significant role in overall stand-level productivity.

Therefore, the relationships between stand structure, light environment, water relations, leaf-level structure and physiology are quite complex and are influenced by many factors. Canopy-level growth models that do not take into account variations in leaf-level gas exchange in relation to stand structure may not adequately represent vegetation response to silvicultural manipulation.

The relative constancy in leaf physiology and leaf structure observed in both the even-aged and multiaged stand structures of ponderosa pine may not hold true for other coniferous forest types. Broadleaf deciduous forests are also more likely to show different relationships because they typically exhibit greater variations in leaf structure and physiology in response to light environment as related to stand structure. This study, along with previous studies that have investigated production efficiency in ponderosa pine (O'Hara 1996, Valappil and O'Hara 2000a and 2000b) indicate that multiaged stand structures can be as productive as even-aged stand structures. Overall site occupancy, arrangement of foliage by size classes of trees, and spatial arrangement of stems as well as site quality act together in yielding a given stand productivity. We now have more evidence that complex stand structures can meet productivity objectives while meeting many other societal objectives.

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Table 3.1. Plot attributes for even-aged and multiaged plots in Montana. Plots were circular and 0.1 ha in size. Habitat types follow those identified by Pfister et al. (1977). Abbreviations: PSME = *Pseudotsuga menziesii* (Mirbel) Franco., PIPO = *Pinus ponderosa* Dougl. ex Laws., CARU = *Calamagrostis rubescens* Buckl., CAGE = *Carex geyeri* Boott, ARUV = *Arctostaphylos uva-ursi* (L.) Spreng., AGSP = *Agropyron spicatum* (Pursh) Scribn. & Smith.

Plot No.	Plot Type	Location	Average Age or Age Range at BH	Slope (%)	Aspect	Habitat Type
1M	multiaged	Swency Creek	27-133	11	NE	PSME/CARU/PIPO
2E	even-aged	Sweeney Creek	82	13	NE	PSME/CARU/PIPO
3M	multiaged	Tarkio Road	20-132	3	N/NW	PSME/CAGE
4E	even-aged	Tarkio Road	81	5	S/SW	PSME/CAGE
7M	multiaged	Tarkio Road	20-119	9	SW	PSME/CAGE
8E	even-aged	Tarkio Road	85	7	SW	PSME/CAGE
11M	multiaged	Larry Creek	10-126	4	E	PSME/CAGE
12E	even-aged	Larry Creek	86	9	E	PSME/CAGE
13M	multiaged	Lubrecht	34-152	10	W	PSME/CARU/ARUV
14E	even-aged	Lubrecht	79	5	SW	PSME/CARU/ARUV

Table 3.2. Comparisons of different density measures for even-aged and multiaged plots in Montana. Plots were circular and 0.1 ha in size. Significant differences ($\alpha = 0.05$) as detected by a paired t-test are denoted by letters that are not the same. Means are +/- one standard error.

Plot No.	Plot Type	Location	Trees per Hectare	Basal Area ($\text{m}^2 \text{ha}^{-1}$)	Sapwood Basal Area ($\text{m}^2 \text{ha}^{-1}$)	LAI (all-sided)	SDI	% Canopy Cover	Crown Ratio
1M	multiaged	Sweeney Creek	280	22.5	12.8	5.00	384	64	0.56
2E	even-aged	Sweeney Creek	380	25.2	15.5	6.00	470	74	0.49
3M	multiaged	Tarkio Road	350	21.8	14.4	5.63	382	66	0.69
4E	even-aged	Tarkio Road	410	24.2	14.7	5.53	458	83	0.55
7M	multiaged	Tarkio Road	480	20.2	12.4	4.89	378	61	0.68
8E	even-aged	Tarkio Road	450	25.3	15.5	6.07	485	74	0.54
11M	multiaged	Larry Creek	620	23.8	13.8	5.42	441	66	0.67
12E	even-aged	Larry Creek	720	23.3	13.9	5.49	491	71	0.53
13M	multiaged	Lubrecht	450	21.9	14.1	5.53	398	51	0.59
14E	even-aged	Lubrecht	620	25.6	16.0	6.29	517	66	0.49
Means	multiaged		436 (58) ^a	22.0 (0.6) ^a	13.5 (0.4) ^a	5.29 (0.15) ^a	397 (12) ^a	62 (3) ^a	0.64 (0.03) ^a
	even-aged		516 (66) ^a	24.7 (0.4) ^b	15.1 (0.4) ^b	5.88 (0.16) ^a	484 (10) ^b	74 (3) ^b	0.52 (0.01) ^b
P - value			0.071	0.044	0.057	0.084	0.002	0.005	0.001

Table 3.3. Annual basal area growth (BAGR) and basal area growth efficiency (BAGE) for even-aged and multiaged plots. Means are +/- one standard error.

Plot No.	Plot Type	Basal Area Growth (m² ha⁻¹ yr⁻¹)	Basal Area Growth Efficiency (mm² m⁻²)
1M	multiaged	0.24	6.31
2E	even-aged	0.28	4.46
3M	multiaged	0.31	7.88
4E	even-aged	0.34	6.31
7M	multiaged	0.24	4.03
8E	even-aged	0.30	5.90
11M	multiaged	0.15	3.60
12E	even-aged	0.15	5.23
13M	multiaged	0.35	8.28
14E	even-aged	0.27	6.96
Means	multiaged	0.26 (0.034) ^a	6.02 (0.96) ^a
	even-aged	0.27 (0.032) ^a	5.77 (0.43) ^a
P - value		0.704	0.778

Table 3.4. Light extinction coefficient (k) and PAR-ratio for even-aged and multiaged plots. Means are +/- one standard error. Means followed by different letters are significantly different ($\alpha = 0.05$).

Plot No.	Plot Type	Location	k point-based	k plot average	PAR-ratio
1M	multiaged	Sweeney Creek	-0.52	-0.33	0.49
2E	even-aged	Sweeney Creek	-0.46	-0.33	0.44
3M	multiaged	Tarkio Road	-0.43	-0.28	0.52
4E	even-aged	Tarkio Road	-0.49	-0.40	0.39
7M	multiaged	Tarkio Road	-0.48	-0.34	0.49
8E	even-aged	Tarkio Road	-0.47	-0.37	0.38
11M	multiaged	Larry Creek	-0.40	-0.26	0.55
12E	even-aged	Larry Creek	-0.42	-0.33	0.47
13M	multiaged	Lubrecht	-0.40	-0.28	0.52
14E	even-aged	Lubrecht	-0.34	-0.28	0.48
Means	multiaged		-0.45 (0.024) ^a	-0.30 (0.016) ^a	0.51 (0.011) ^a
	even-aged		-0.44 (0.027) ^a	-0.34 (0.020) ^a	0.43 (0.020) ^b
P - value			0.689	0.127	0.009

Table 3.5. Linear relationships ($y = B_0 + B_1 x$) between photosynthesis (A_{area} and A_{mass}), leaf structural attributes (N_{area} , N_{mass} , and SLA), and relative height (RH) for even-aged and multiaged stand structures. SEE = standard error of estimate. N = 41 for even-aged and N = 52 for multiaged.

Relationship	Structure	Figure	B_0	B_1	R^2	SEE	P
A_{mass} vs. RH	even-aged	3.5a	37.69	4.37	0.00	9.65	0.694
	multiaged	3.5b	41.85	-11.82	0.03	10.60	0.204
A_{area} vs. RH	even-aged	3.5c	4.16	1.21	0.02	1.14	0.362
	multiaged	3.5d	4.71	-0.09	0.00	1.18	0.930
N_{mass} vs. RH	even-aged	3.6a	11.69	2.93	0.15	0.98	0.012
	multiaged	3.6b	13.91	-2.29	0.07	1.36	0.058
N_{area} vs. RH	even-aged	3.6c	1.27	0.63	0.17	0.20	0.007
	multiaged	3.6d	1.57	0.22	0.02	0.25	0.318
SLA vs. RH	even-aged	3.7a	91.34	-14.59	0.07	7.74	0.106
	multiaged	3.7b	88.43	-22.87	0.20	7.52	0.001
A_{mass} vs. N_{mass}	even-aged	3.8a	43.65	-0.29	0.00	9.67	0.843
	multiaged	3.8b	53.61	-1.20	0.03	10.64	0.265
A_{area} vs. N_{area}	even-aged	3.8c	3.20	0.99	0.03	1.14	0.251
	multiaged	3.8d	5.84	-0.70	0.02	1.17	0.295
A_{mass} vs. SLA	even-aged	3.9a	21.49	0.22	0.03	9.51	0.259
	multiaged	3.9b	-7.75	0.57	0.19	9.67	0.001
A_{area} vs. SLA	even-aged	3.9c	7.51	-0.03	0.05	1.13	0.154
	multiaged	3.9d	3.97	0.01	0.00	1.18	0.656
N_{mass} vs. SLA	even-aged	3.10a	15.38	-0.03	0.04	1.04	0.206
	multiaged	3.10b	13.32	0.00	0.00	1.41	0.923
N_{area} vs. SLA	even-aged	3.10c	3.41	-0.02	0.66	0.13	<0.001
	multiaged	3.10d	3.37	-0.02	0.52	0.17	<0.001

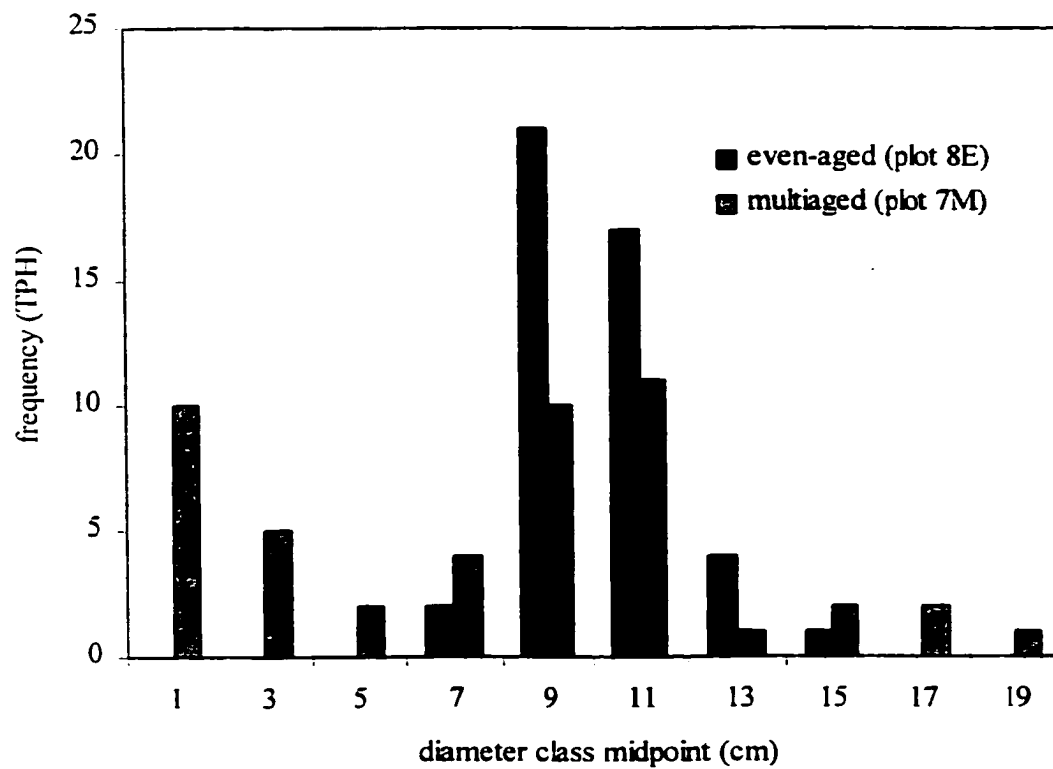


Figure 3.1. Diameter distribution for a representative even-aged (8E) and multiaged (7M) stand structure.

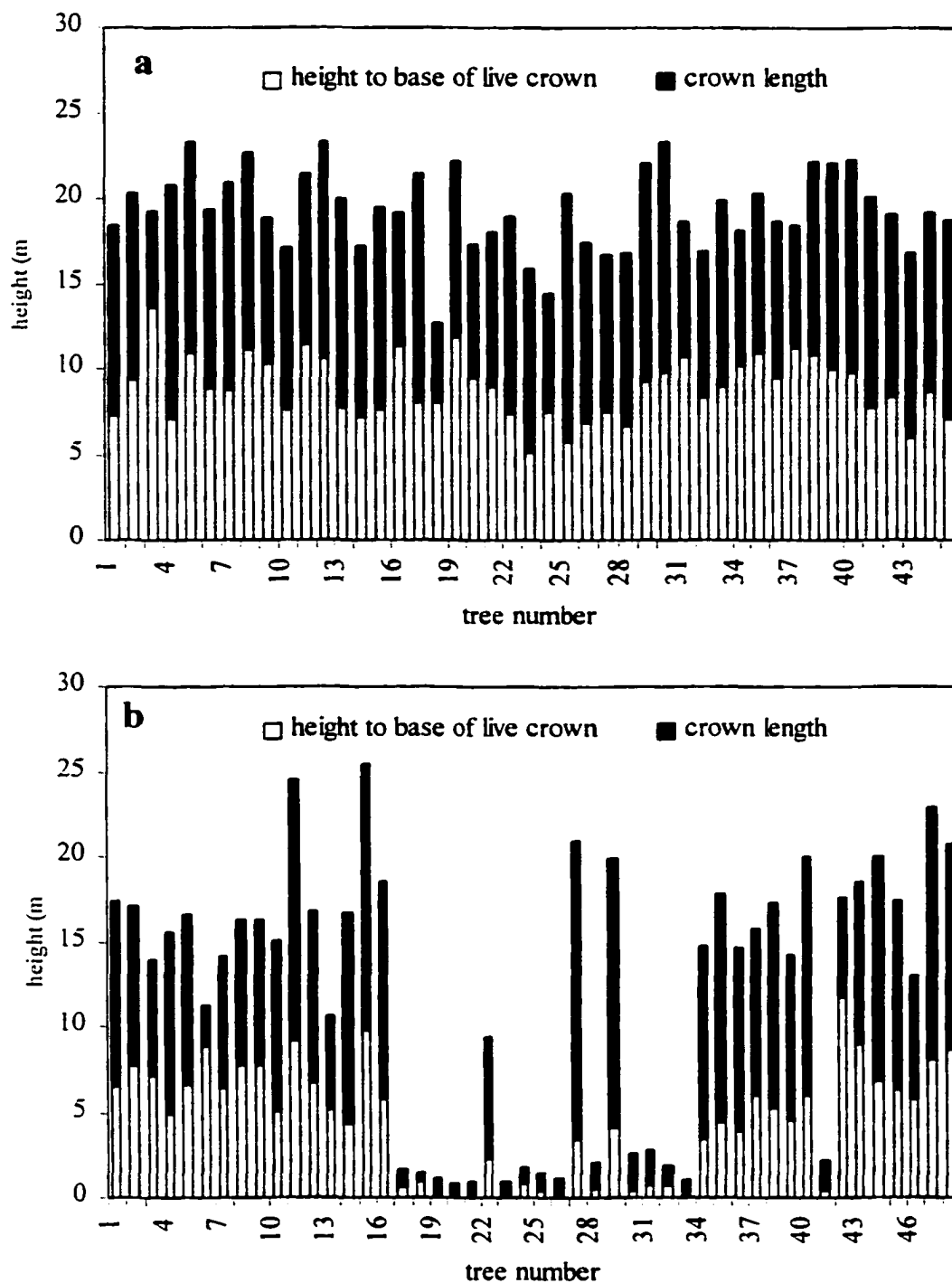


Figure 3.2. Total height and crown length of a representative even-aged (a) and multi-aged (b) plot. Each bar represents the total height of individual trees with the darker shading denoting crown length.

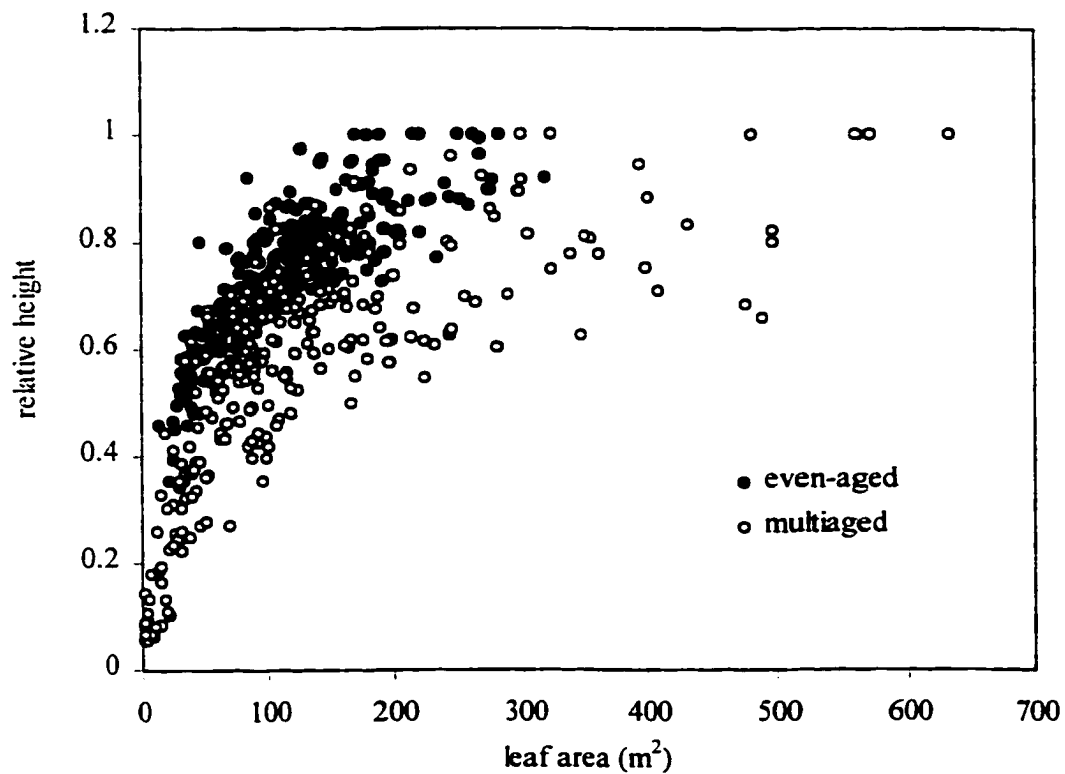


Figure 3.3. Individual tree leaf area distribution with canopy depth for all even-aged and multiaged plots. Each point on the figure represents an individual tree. Relative height refers to height of each tree / height of the tallest tree on each plot. A relative height of 1.0 denotes the top of the canopy.

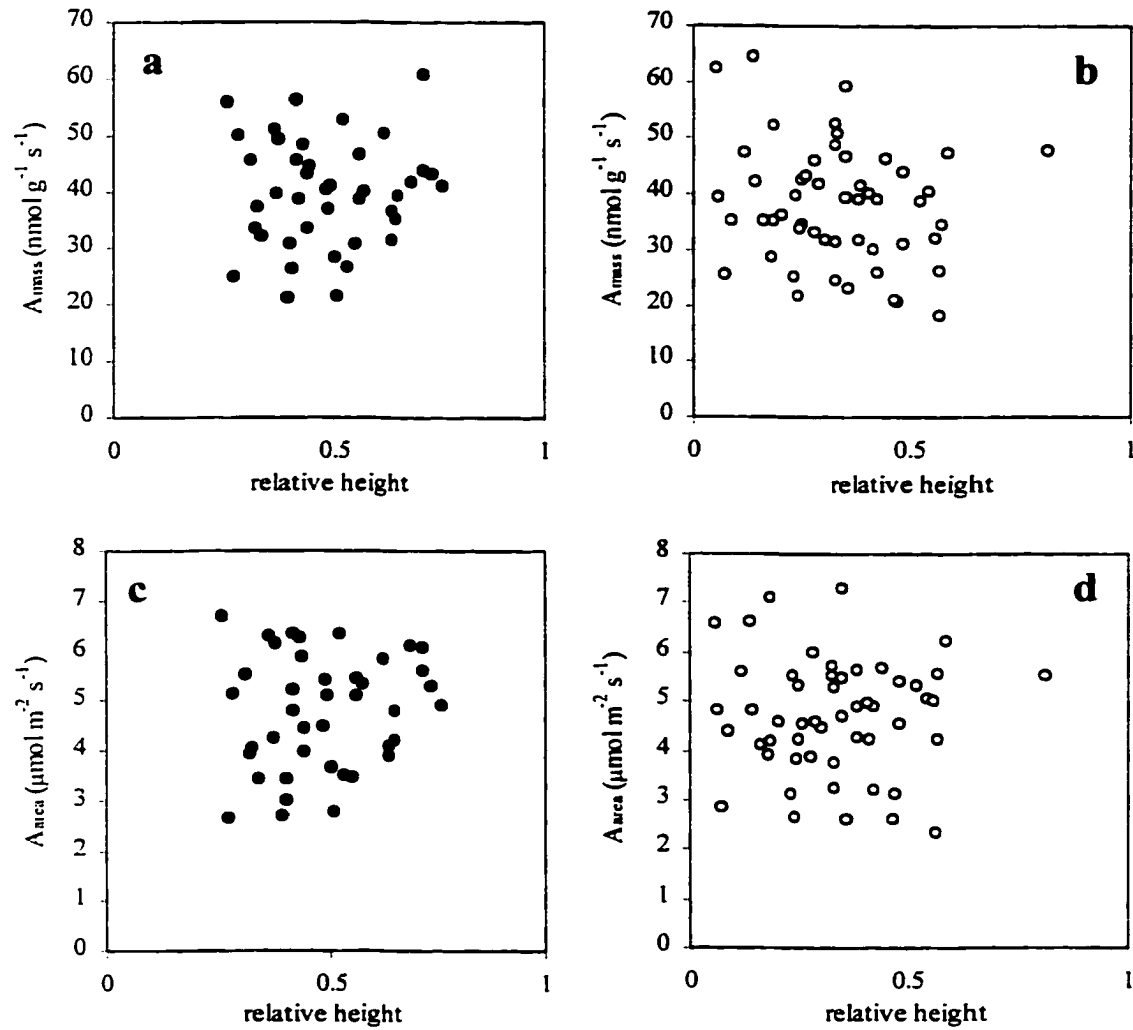


Figure 3.4. Relationship between A_{mass} and relative height, and A_{area} and relative height in even-aged (a and c) and multiaged (b and d) plots in Montana. See Table 3.5 for linear regression relationships.

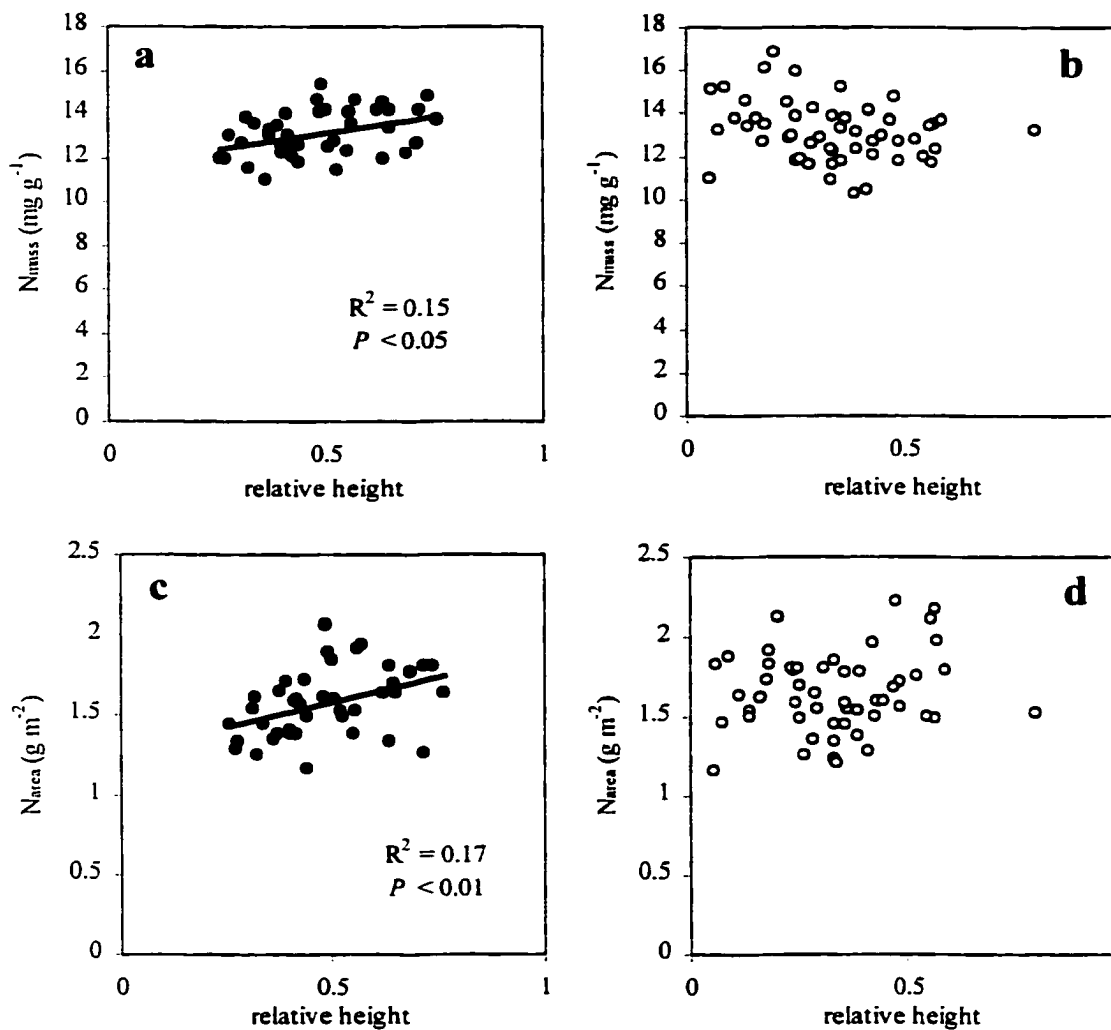


Figure 3.5. Relationship between N_{mass} and relative height, and N_{area} and relative height in even-aged (a and c) and multiaged (b and d) plots in Montana. See Table 3.5 for linear regression relationships.

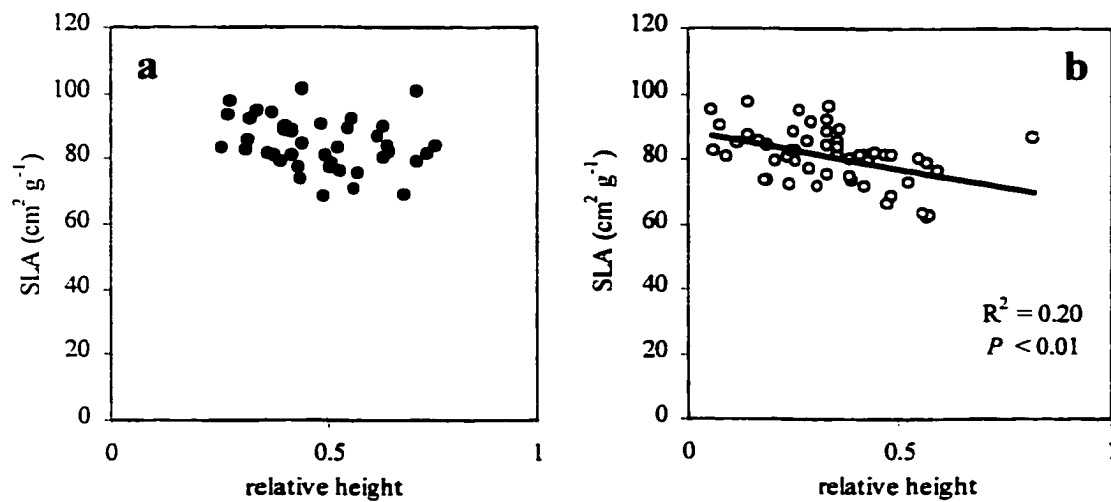


Figure 3.6. Relationship between SLA and relative height of sample in even-aged (a) and multiaged (b) plots in Montana. See Table 3.5 for linear regression relationships.

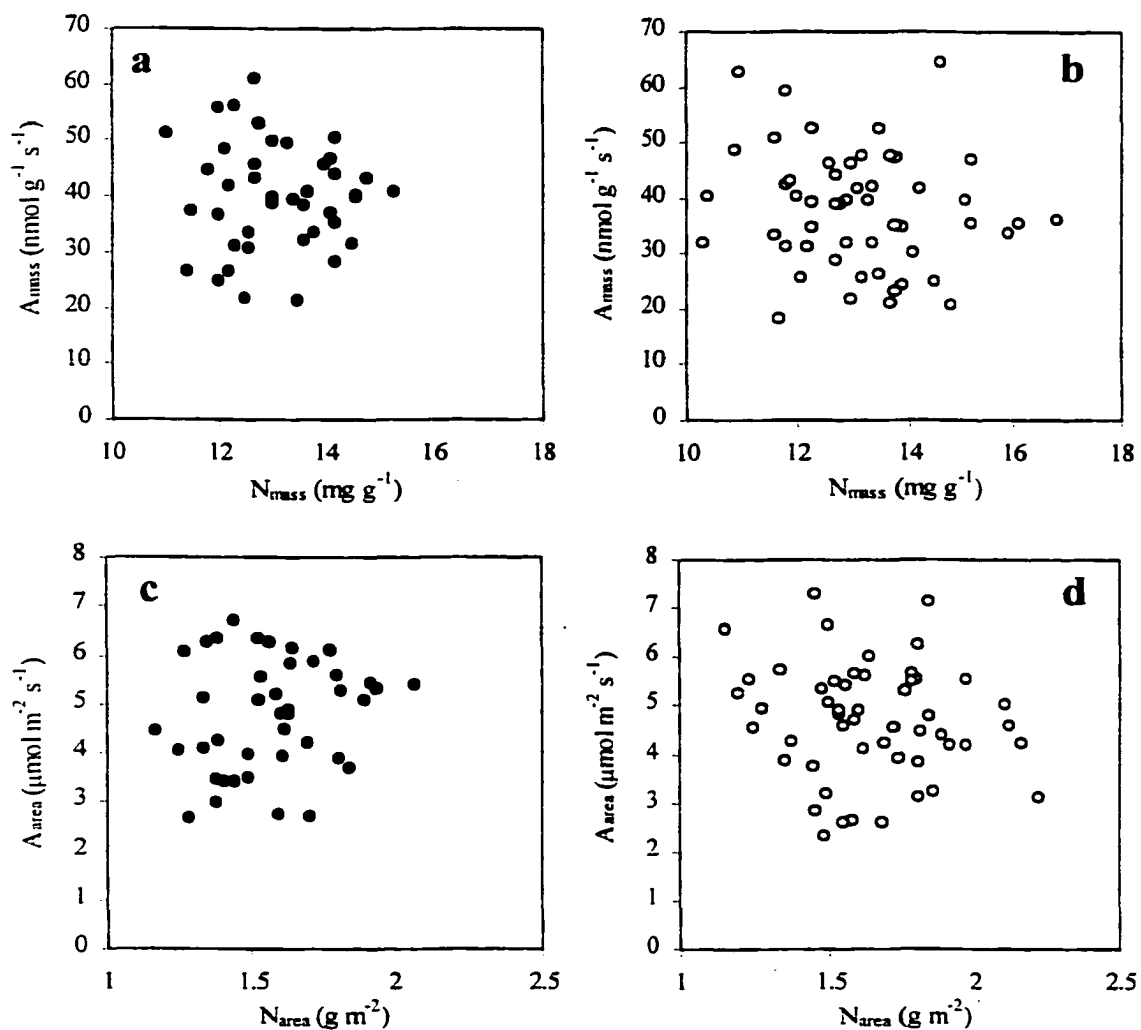


Figure 3.7. Relationship between A_{mass} and N_{mass} , and A_{area} and N_{area} for even-aged (a and c) and multiaged (b and d) plots. See Table 3.5 for linear regression relationships.

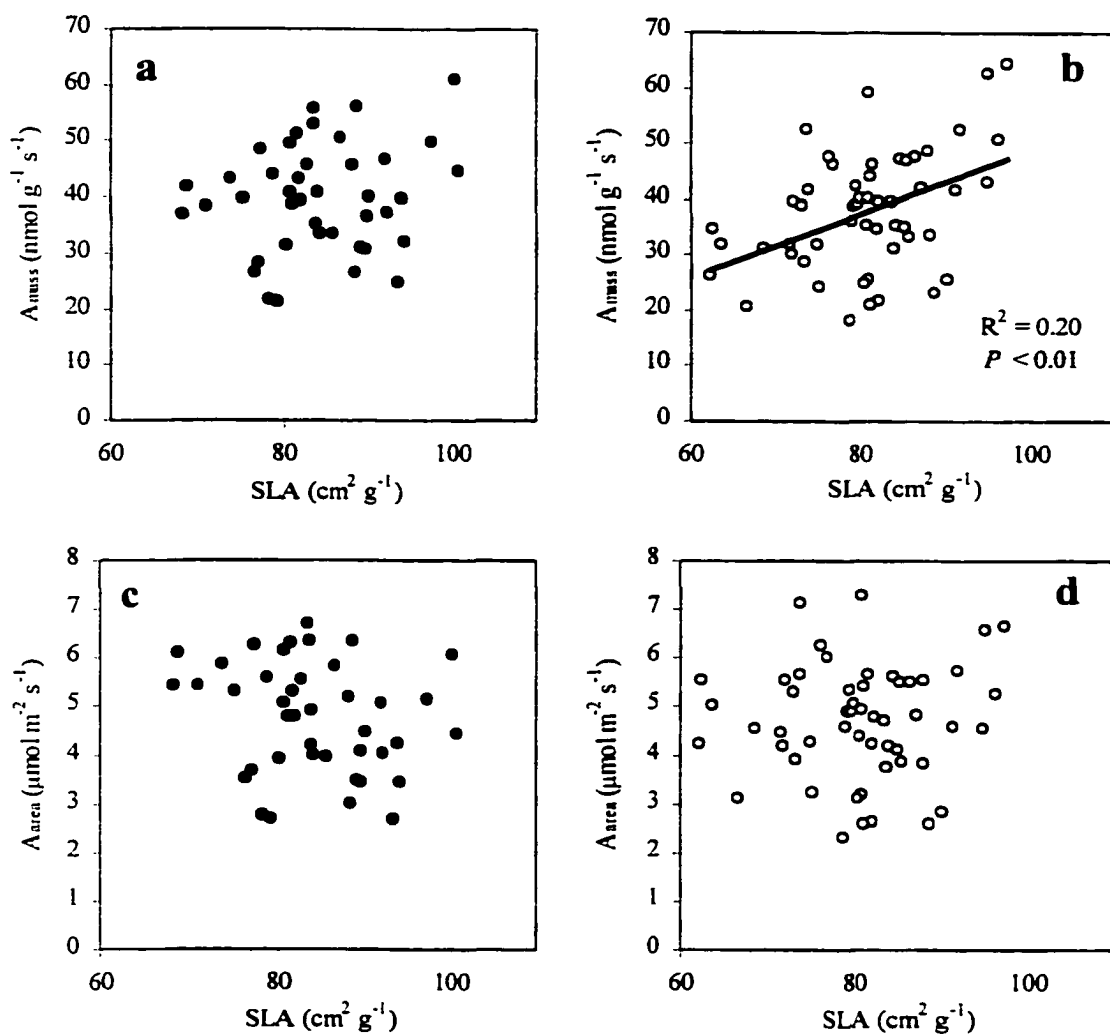


Figure 3.8. Relationship between A_{mass} and SLA, and A_{area} and SLA for even-aged (a and c) and multiaged (b and d) plots. See Table 3.5 for linear regression relationships.

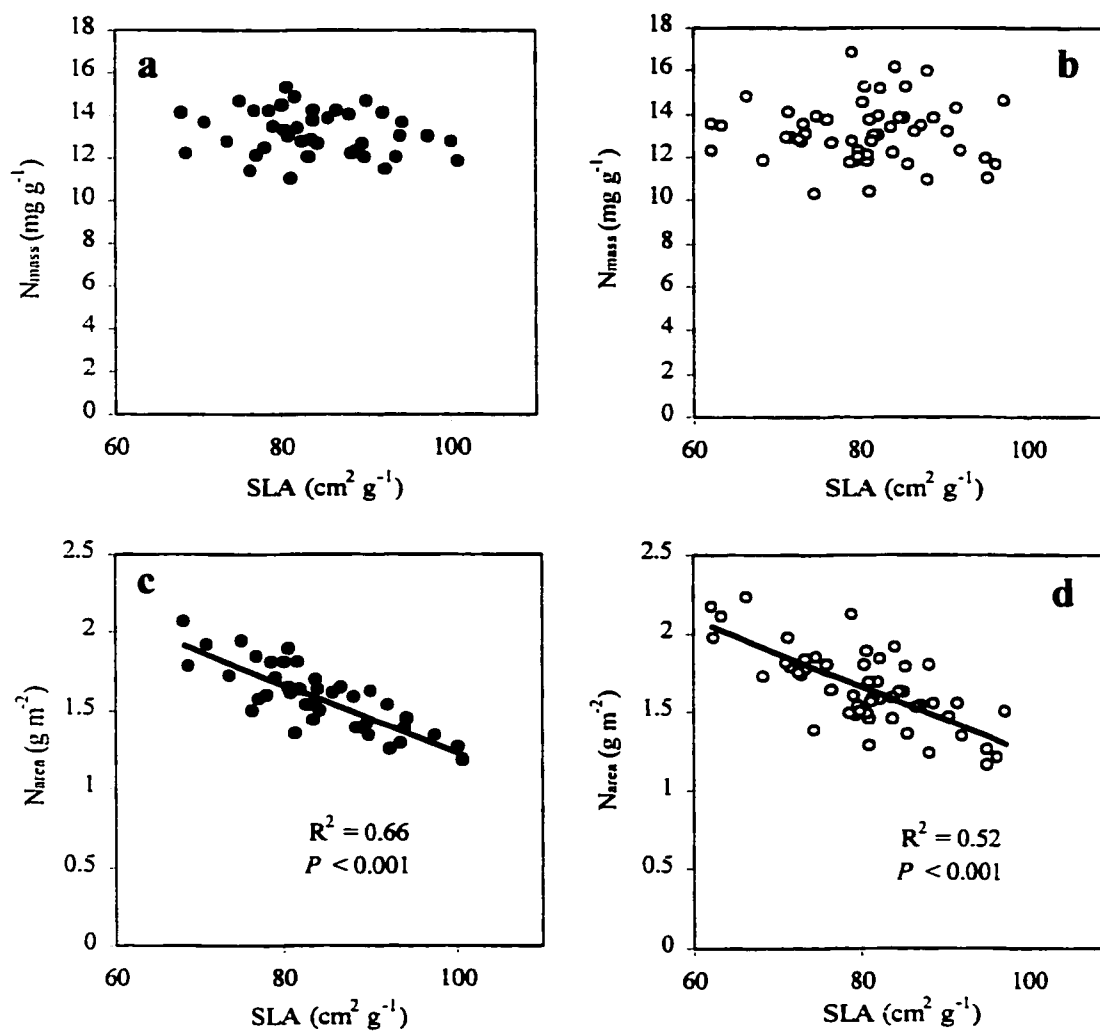


Figure 3.9. Relationship between N_{mass} and SLA, and N_{area} and SLA for even-aged (a and c) and multiaged (b and d) plots. See Table 3.5 for linear regression relationships.