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A physiologically-based comparison of even- and multi-aged ponderosa pine stand productivity

Narayanan Illath Valappil
The University of Montana

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A PHYSIOLOGICALLY-BASED COMPARISON OF EVEN- AND MULTI-AGED PONDEROSA PINE STAND PRODUCTIVITY

by

Narayanan Illath Valappil

School of Forestry

B.Sc., Kerala Agricultural University, Thrissur, India, 1986
M.Sc., Kerala Agricultural University, Thrissur, India, 1989

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for the degree of

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The University of Montana

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Approved by:

Chairman, Board of Examiners

Dean, Graduate School

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A Physiologically-Based Comparison of Even- and Multi-aged Ponderosa Pine Stand Productivity

Director: Kevin L. O'Hara

ABSTRACT

The productivity of natural even- and multi-aged ponderosa pine (*Pinus ponderosa*) stand structures was compared based on leaf level physiological factors responsible for production. Leaf area index (LAI), stem volume increment, specific leaf area, leaf nitrogen, and leaf water potential were compared between the stand structures in western Montana and central Oregon. LAI and mean annual volume increment were relatively higher in the even-aged stands, suggesting higher growing space occupancy compared to multi-aged stands.

Specific leaf area and leaf nitrogen content were significantly different between the top and bottom crown thirds in even-aged stands. Smaller ranges in specific leaf area and leaf nitrogen content between top and bottom thirds in multi-aged stands suggest higher foliage production efficiencies throughout the crowns compared to those in even-aged stands. Higher vertical stratification of crowns in multi-aged stands enhance the three-dimensional growing space availability and also reduced the stand-level competition for light and moisture.

Pre-dawn leaf water potential was comparatively higher in multi-aged structures than in even-aged throughout the growing season. A late summer pre-dawn leaf water potential lower than -1.6 MPa, in even-aged stands indicate that trees might have very limited photosynthesis due to moisture limited stomatal closure. Higher water stress in even-aged stands could be a combined effect of stand density and structure. The long-term water-use efficiency estimated from carbon isotope discrimination suggest the top third of crowns in even-aged stands were more water-use efficient compared to multi-aged structures. Prolonged periods of water stress, lower than -1.6 MPa, could result in decreased foliage and tree productivity in even-aged stands despite their higher water-use efficiency.

Results from this study suggest that stand structure is an important factor influencing stand productivity. Diverse vertical stratification of tree crowns in stands reduce the competition for available growing space, especially light and soil moisture and could result in enhanced leaf, tree, and stand productivity.

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Chapter 1

Introduction

Traditionally, land managers have practiced even-aged silviculture to increase wood production in a short rotation period which is perceived to be simpler and cheaper compared to multi-aged silviculture. Even-aged and multi-aged silviculture produces diverse stand structural characteristics. Multi-aged stand (stand with two or more age classes) structures can meet a variety of resource management objectives not met by even-aged structures (O'Hara 1996). In the recent past, public preference for multi-aged stand structures has increased due to many reasons such as visual qualities, better wildlife habitat, recreational demands, and continuous site protection, etc. The comparative productivity in terms of wood production per unit area of even-aged and uneven-aged silvicultural systems is a controversial issue. Although most comparative studies have indicated that even-aged structures were more productive, virtually no studies reported any causal mechanism why such difference exists. In an era of ecosystem management, the paradigms regarding the relative merits of traditional even-aged and multi-aged structures need to be justified with some physiological basis for long-term sustainability of these management systems rather than based on empirical comparisons of volume productivity.

Ponderosa pine is a species that can be managed in pure even-aged as well as multi-aged structures. In many parts of the northwest, due to past selection harvesting, many existing ponderosa pine stands have multi-aged structures and could be easily managed for meeting a variety of structure-related objectives. The suitability of a particular stand structure to increase productivity has to consider the climate and physiographic conditions of a site.

Soil and climate are the most important factors governing primary production on a site. The potential site productivity (amount of carbon fixed per unit area) depend on the available growing space and is generally represented and quantified by maximum leaf area index (O'Hara 1988). The leaf area index of a stand can be influenced by stand structure. Therefore managing stand structure could directly influence the productivity of a site.

In this dissertation research, pure even-and multi-aged ponderosa pine stand structures were compared in terms of leaf level physiological attributes affecting tree and stand production which are directly modified by stand structures. The study was conducted in two different geographical areas to address the following major objectives: 1) Leaf area, crown structure and aboveground primary production in even- and multi-aged ponderosa pine stands growing on similar site conditions were compared to examine whether the total aboveground primary production (stored carbon) is different in these two stand structures; 2) To estimate the variation in specific leaf area and leaf nitrogen within and between tree crowns growing in even- and multi-aged stand structures to examine whether the foliage production efficiencies are different under varying structures; 3) To compare the differences in soil water status and foliage water-use efficiencies in even- and multi-aged ponderosa pine stands to relate the influence of stand structure on tree and stand productivity.

The overall study objectives are examined in detail in three separate chapters and a general conclusion based on these results is presented in chapter 5. The results from the study have many potential benefits especially to provide the land managers with an insight regarding the important factors to be considered while managing stands for varying structures in ponderosa pine ecosystems.

Literature Cited

O'Hara, K. L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can. J. For. Res. 18:859-866.

O'Hara, K. L. 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. For. Sci. 42: Monograph 33. 34 p.

Chapter 2

Stand Structure and Its influence on Leaf Area Index and Productivity in Ponderosa Pine Stands

ABSTRACT

Climate-related physiological and stand structural characteristics are important factors that influence the production efficiency of trees. The productivity in terms of stem volume increments, basal area increments and total aboveground biomass was compared between even- and multi-aged ponderosa pine stands (unmanaged) in western Montana and central Oregon. Stand density and canopy cover percentage were higher, mean tree crown projection area and live crown percentage were slightly lower in the even-aged stands. Leaf area index (LAI) and mean annual stem volume increments were not significantly higher in the even-aged stands on sites of a medium aridity index (t-tests, $\alpha = 0.05$). On better quality sites (high aridity index) the even-aged stands had significantly higher LAI and mean annual volume increments, suggesting the multi-aged stands on better sites were not occupying the site's full growing space compared to the even-aged stands. With similar LAI, the foliage production efficiency measured in terms of stem volume growth per unit leaf area (volume growth efficiency) was higher in multi-aged stands compared to even-aged stands. Basal area growth efficiency (basal area growth per unit leaf area) was lower in multi-aged stands. The different trend between volume and basal area growth efficiencies for the multi-aged stands was due to variation in the distribution and tree sizes. The mean aboveground tree biomass was higher in multi-aged stands in western Montana but not in central Oregon. The understory vegetation biomass was generally higher in multi-aged stands. The influence of stand structure related factors to enhance leaf, tree and stand productivity was described using a conceptual model.

Keywords: stand structure, even-aged, multi-aged, leaf area index, growth efficiency, production efficiency.

2.1. INTRODUCTION

Stand structure, or the physical and temporal distribution of trees in a stand (Oliver and Larson 1996), is an important parameter for stand production and utilization. Generally, trees in a stand arrange their foliage to maximize solar energy harvest, at minimum, to balance the maintenance respiration costs. Manipulating stand structure for increased canopy light interception increases leaf and stand productivity (biomass or volume growth) in stands where light is limited. O'Hara (1989, 1996) found large differences in stand growth efficiency due to stand structure or the arrangement of tree sizes. The total production per unit leaf area or growth efficiency (Waring and Schlesinger 1985; O'Hara 1988) of a tree varies depending upon its relative crown position compared to its neighbors. The gross primary production in a stand is the product of stand leaf area (leaf area index) and leaf production efficiency. In addition to stand volume or biomass production, stand structure also influences wildlife habitat, aesthetics, recreational, and hydrological recharges in a forest.

In this chapter, total leaf area and net aboveground primary production in even- and multi-aged ponderosa pine stand structures (unmanaged) on similar site conditions were compared to determine the influence of stand structure on productivity of pure, shade-intolerant species. Total stand aboveground productivity in terms of stem volume and basal area increments, live crown biomass, total aboveground tree- and understory biomass were compared between the even- and multi-aged stands in two study locations. Stand structure related factors that influence leaf-level physiological attributes to enhance leaf, tree, and stand production efficiencies were discussed using a conceptual model.

2.1.1. Leaf Area Index

Leaf area index (LAI) represents the foliage area (m^2) per land area (m^2) on a site, and is directly influenced by the climate, soil, and other edaphic factors. The total leaf area on a site is an important variable determining stand production, because of its relation to light interception (Cannell et al. 1987). Total stand leaf area also represents the limiting factors in stand growth relationships (Waring 1983; Binkley and Reid 1984; Oren et al. 1987; O'Hara 1988, 1989; Long and Smith 1992). The total available, three-dimensional growing space on a site can also be interpreted to be represented by the maximum (potential) leaf area (O'Hara 1988). Stands continue to increase leaf area toward the maximum until they reach a state of equilibrium (Moller 1947; Marks and Bormann 1972; Grier and Running 1977; Long and Smith 1984, 1992), which is also described as the potential LAI. LAI, less than its potential is considered as occupied growing space (O'Hara 1988, 1996). The potential leaf area on a site also depends on species composition, but should be constant across similar site qualities for a given composition. O'Hara (1996) found that multi-aged ponderosa pine stands carry slightly lower LAI and slightly higher growth efficiency compared to even-aged stands. However, studies to explore the potential/occupied leaf area in multi-aged stand structures are of recent origin (O'Hara et al. (in press), Kollenberg 1997).

2.1.2. Production Efficiency of Foliage

The production efficiency of foliage can be defined as the amount of carbon produced per unit leaf area. This is also known as growing space efficiency (O'Hara

1988, 1989), and can be used as an index to compare the growth and vigor of trees in a stand. O'Hara (1988) used leaf area based growth efficiency to compare various thinning treatments in even-aged stands. Growth efficiency was also used to compare the competition of understory vegetation (Oren et al. 1987), silvicultural and managemental treatments like selection harvesting (O'Hara 1996; Kollenberg 1997) and fertilization etc. (Binkley and Reid 1984).

Trees allocate photosynthate to different sinks: production of new foliage, branches, roots, stems, and reproductive organs on a priority basis (Waring and Running 1998). Generally, stem diameter growth is a low priority compared to other sinks. During periods of stress, trees produce comparatively little stem diameter growth. This sometimes makes it difficult to quantify the leaf production efficiency in instances where production of protective chemicals became the priority due to forest health reasons. The term production efficiency is a measure of gross primary production without respiration requirements per unit leaf area. An accurate measurement of this efficiency index is difficult on a stand-level basis for comparative studies, hence growth or growing space efficiency (stem volume increment or basal area growth per unit leaf area) is used as an alternative index for comparison (O'Hara 1988).

One of the major factors influencing foliage production efficiency is the amount of absorbed photosynthetically active radiation (Doley 1982). The potential absorbed radiation differs greatly due to differences in physiographic and structural characteristics (Kaufmann and Ryan 1986). Manipulation of stand structure using silvicultural tools like thinning, partial harvesting, etc., increases available growing space to remaining trees in a stand. The increased available growing space, if fully utilized, can enhance the canopy photosynthesis of the residual trees in a stand.

Stand production directly depends production efficiency of component trees and their foliage. The production efficiency (growth efficiency) can be also determined indirectly by measuring specific leaf area (leaf area per unit dry biomass) of needles. Specific leaf area (SLA) is closely related to leaf photosynthetic capacity (Gutschick and Wiegel 1988). The increased availability of radiation at the canopy top increases the leaf biomass concentration per unit area. The availability of light, water, and nutrients during leaf expansion is an important determinant of SLA (Tucker and Emmingham 1977). Mooney et al. (1978) and Specht and Specht (1989) reported that canopy average SLA decreases with increasing aridity.

Site water potential is another important factor which affects the physiology and production efficiency of leaves on a stand. The production efficiency of conifers in the northwest largely depends on the availability of water, mainly because northwest conifers grow in water limited ecosystems, especially during late summer months (Running 1976). The environmentally driven water translocation from soil to atmosphere through plants is an important ecosystem processes. Increased site and plant moisture availability results in increased photosynthesis, provided other factors are optimal.

Stand density significantly influences leaf water potential. Higher stand density results in increased leaf area and decreased water potential. Low water potential results in decreased photosynthesis. Donner and Running (1986) reported that water potential increased in thinned lodgepole stands compared to the controls, and could result in 21%

greater seasonal photosynthesis (using an ecosystem simulation model).

Plants generally optimize leaf nitrogen to maximize photosynthesis (Field and Mooney 1986; Evans 1989). Canopy average leaf nitrogen per unit area is highly correlated to canopy transmittance (Pierce et al. 1994). Trees translocate nitrogen differently through different seasons. Pierce et al. (1994) reported that leaf nitrogen was higher during August-September compared to March-June. Leaf nitrogen content is directly related to photosynthetic capacity because of its requirement in the construction of essential enzymes in the Calvin Cycle, which is mainly concentrated in the thylakoids of leaves (Evans 1989). There is a strong relationship between nitrogen and RuBp carboxylase (Ribulose 1,5-bisphosphate carboxylase) and chlorophyll. Changes in the leaf nitrogen content mainly influence the RuBp carboxylase and the rate of photosynthesis. Increased nitrogen fertilization has found increased growth in plants due to higher rates of photosynthesis in nitrogen limited ecosystems (Linder and Troeng 1980; Brix 1981; Sheriff et al. 1986; Linder 1987; Gower et al. 1993).

In addition to these physiological factors, leaf arrangement, orientation, and density are other important structural characteristics influencing leaf and tree production efficiencies. Manipulation of canopy structure could lead to morphological and physiological changes in leaves due to variations in canopy light and moisture availability.

2.2. METHODS

2.2.1. Site Selection

The study was conducted in western Montana and central Oregon during the summers of 1995 and 1996. In western Montana, stands were sampled on the Lolo National Forest (Ninemile and Lolo Ranger Districts), on State lands near Florence and Tarkio, the University of Montana's Lubrecht Experimental Forest, and a nearby private holding (**Figure 2.1**). Pure multi-aged stands are common in drier habitat types in western Montana, but due to fire suppression for the past several decades, interior Douglas-fir has come increasingly abundant both in understory and overstory composition on many sites (Arno et al. 1995). Study plots were located at elevations from approximately 850 to 1250 m, and from 46° 37′ to 47° 06′N latitude, and 113° 23′ to 114° 47′W longitude. The stands were located primarily on *Pseudotsuga menziesii* climax series (Pfister et al. 1977). Stands were predominantly pure ponderosa pine with an occasional inclusion of interior Douglas-fir. All the sample plots were located on south to southeast aspects with slopes ranging from 2 to 30% (**Table 2.1**).

In central Oregon, stands were sampled on Deschutes, Fremont, and Winema National Forests (**Figure 2.1**). The elevations ranged from 1330 to 1540 m , latitudes from 43° 13′ to 43° 52′N, and longitudes from 121° 8′ to 121° 48′ W. The sample plots were selected on *Pinus ponderosa* plant associations on pumice soils as part of the High Cascades Province (Franklin and Dyrness 1973). Many of the ponderosa pine stands in central Oregon were seriously defoliated by pandora moths' outbreak (*Coloradia pandora* Blake) during 1992-95. Special attention was given to selection of stands which were attacked at a minimal level by examining the stand/trees for the number of needle age classes. Stands with trees less than 4 year's needles were not selected. The plant associations were identified as per the guides by USDA Forest Service for each sampling area (Hoplins 1979a, 1979b, Volland 1988). The sample plots were located on all aspects on slopes ranging from 2 to 12% **(Table 2.1).**

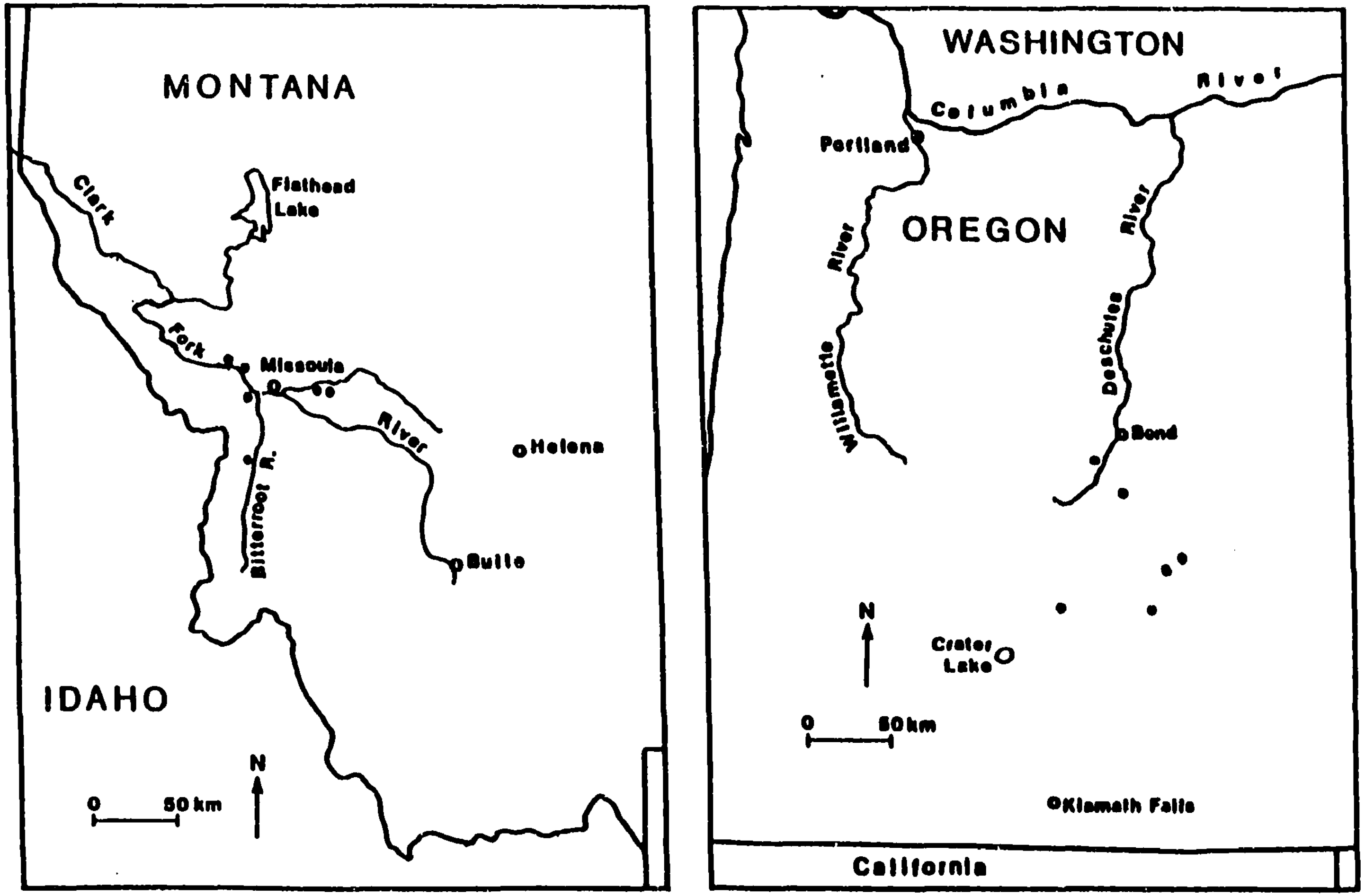


Figure 2.1. Maps showing the general location of study plots in western Montana and central Oregon. Each dot represents a pair of even- and multi-aged plot selected at closer proximity.

Table 2.1. Characteristics of the even-aged and multi-aged sample plots selected in different locations in western Montana and central Oregon. Habitat types for western Montana were identified as per Pfister et al. (1977) and for central Oregon USDA Forest Service for each plant association and published in guides for sampling area by Hopkins (1979a, 1979b) and Volland (1988).

Location	Plot	Size(ha)	Habitat type	Elevation (m)	Aspect	Slope%	# of trees
Sweeny Creek Rd, MT	1E	0.1	PSME/FEID	1105	E	2	58
Sweeny Creek Rd, MT	1M	0.1	PSME/FEID	1106	E	3	26
Tarkio, MT	2E	0.1	PSME/CAGE	855	S	2	57
Tarkio, MT	2M	0.1	PSME/CAGE	855	S	2	34
Ninemile Rd, MT	3E	0.1	PIPO/FEID-FESC	975	SE	4	183
Ninemile Rd, MT	3M	0.1	PIPO/FEID-FESC	975	SE	7	89
Lubrecht, MT	4E	0.1	PSME/SYAL-SYAL	1230	S	30	114
Lubrecht, MT	4M	0.1	PSME/VACA	1256	SE	11	70
Blue Mountian, MT	5E	0.1	PIPO/FEID-FESC	1130	S	20	61
Blue Mountian, MT	5M	0.1	PSME/CARU-AGSP	1145	SE	28	50
Potter's Ranch, MT	6E	0.1	PSME/CARU-PIPO	1200	S	5	314
Potter's Ranch, MT	6M	0.1	PSME/CARU-PIPO	1205	S	2	94
Bend-Ft. Rock, OR	101M	0.1	PIPO/PUTR-ARPA/STOC	1290	E	5	55
Bend-Ft. Rock, OR	101E	0.04	PIPO/PUTR-ARPA/STOC	1295	E	10	45
Paulina Lake Rd, OR	102M	0.1	PIPO/PUTR-ARPA/STOC	1444	W	7	47
Paulina Lake Rd, OR	102E	0.04	PIPO/PUTR-ARPA/STOC	1438	S	11	41
Chemult, OR	103M	0.1	PIPO/PUTR/STOC	1457	S	8	42
Chemult, OR	103E	0.04	PIPO/PUTR/STOC	1463	S	12	32
Fremont, OR	104M	0.1	PIPO/PUTR/FEID	1436	SE	2	51
Fremont, OR	104E	0.04	PIPO/PUTR/FEID	1436	SE	3	31
Silver Lake Rd, OR	105M	0.1	PIPO/PUTR-ARTR/SIHY	1356	N	3	16
Silver Lake Rd, OR	105E	0.04	PIPO/PUTR-ARTR/SIHY	1378	N	4	14
Silver Lake Rd, OR	105EO	0.1	PIPO/PUTR-ARTR/SIHY	1359	N	2	17
Silver Lake Rd, OR	106M	0.1	PIPO/PUTR/ARAR/FEID	1402	NW	5	11
Silver Lake Rd, OR	106E	0.04	PIPO/FEID	1387	N	3	35

Key to species abbrevations: PSME = *Pseudotsuga menziesii* var. *glauca*; FEID = *Festuca idahoensis*; CAGE = *Carex geyeri*; PIPO = *Pinus ponderosa*; FESC = *Festuca scabrella*; SYAL = *Symphoricarpos albus*; VACA = *Vaccinium caespitosum*; CARU = *Calamagrostis rubescens*; AGSP = *Agropyron spicatum*; PUTR = *Purshia tridentata*; ARPA = *Arctostaphylos patula*; STOC = *Stipa occidentalis*; ARTR = *Artemisia tridentata* var. *tridentata*; SIHY = *Sitanion hystrix*; ARAR = *Artemisia arbuscula*. Plot symbols E = Even-aged, M = Multi-aged, EO = Even-aged old growth.

2.2.2. Site Water Balance and Aridity Index

The long-term average climatic data from nearby weather stations were used to calculate the site water balance for the study sites in western Montana and central Oregon. Site specific annual average precipitation data for the selected sites in central Oregon was estimated from the precipitation map developed for the state of Oregon using PRISM model (Daly et al. 1994). Site water balance is expressed as aridity index, which is the ratio of precipitation (P) to potential evaporation (PE). The potential evaporation (PE) was computed using the methodology reported by Linacre (1977) as follows

$$PE\ (\text{mm day}^{-1}) = 700\ T_m / (100 - A) + 15\ (T - T_d) / (80 - T)$$

Where $T_m = T + 0.006h$, h is elevation (m); T = mean temperature; A = latitude; T_d = mean dew point temperature.

Table 2.2. A summary of the long-term average climatic data for the study sites in western Montana and central Oregon.

Location of study sites	Base weather station	Mean annual precip. (cm)	Annual temp. (°F) Min.	Max.	Aridity Index
Sweeny creek	Stevensville, MT	33	30.9	58.3	0.22
Ninemile	Missoula, MT	33	32.2	56.4	0.25
Lubrecht	Lubrecht, MT	45	26.2	52.8	0.35
Tarkio	Superior, MT	41	32.5	59.6	0.29
Bend-Ft. Rock	Bend, OR	45	32.3	60.4	0.28
Pauline Lake Rd..	Bend, OR	50	31.0	60.4	0.31
Fremont	Fremont, OR	30	24.4	60.4	0.19
Silver Lake Rd..	Fremont, OR	30	24.4	60.4	0.19
Chemult	Chemult, OR	65	26.2	58.2	0.43

2.2.3. Plot-Level Sampling

The general stand selection criteria included fully stocked, pure even-aged and multi-aged ponderosa pine stands (unmanaged) at close proximity with similar site quality. The stands were not treated for past 15 years from the year of sampling to eliminate bias in stand productivity estimation. Six pairs of even- and multi-aged stands were selected in each region. The even-aged plots were sampled in second-growth ponderosa pine stands in both locations. In central Oregon, an old-growth even-aged stand was also sampled in addition to the six second-growth even-aged stands. The multi-aged stands were created by the past selection cutting treatments on most sites. A 0.1 ha size circular sample plot (17.8 m radius) was located in each stand. In central Oregon, the even-aged plots were 0.04 ha (11.3 m radius). The reduction in sample plot size in even- aged stands is due to approximately similar variances in LAI in even-aged plots of sizes 0.1 ha and 0.04 ha. Larger plot size (0.1 ha) was selected in multi-aged stands due to higher structural and spatial heterogeneity.

2.2.4. Tree Measurements

Within each sampled plot, each tree was measured for its total height (m) and the height up to live crown base (m) using a clinometer. From these two heights, live crown percentage (LCP) for each tree was calculated. Each tree was assigned a stratum and crown class using the procedure described by Smith (1986) and Oliver and Larson (1996). Trees in the uppermost canopy layer of multi-aged stands were assigned as stratum A, which are also called as emergents, and those in the main canopy layer as stratum B. Subsequent layers below the stratum B are called stratum C and D. In the even-aged stands, most of the trees were grouped in stratum B and assigned a crown class based on its crown position in that stratum. The crown classes were dominant, co-dominant, intermediate, and suppressed. The diameter at breast-height (dbh) was measured at 1.37 m height from ground level. Trees with dbh≥3 cm on each plot were cored on north and east sides. The cores were projected to sunlight to distinguish the sapwood and the heartwood boundaries. The sapwood radius was measured on each core to the nearest 0.5 mm from the heart wood boundary to the tip of previous year's growth. Trees taller than breast-height, but below 3 cm dbh, were cored only on the north side. The diameter and sapwood radius of trees shorter than 1.37 m were measured immediately below the lower-most branch forming the live crown. The bark thickness on each tree was measured using a bark gauge to the nearest mm at points closer to sapwood measurements. The number of bark measurements and their positions followed the guidelines for sapwood estimation.

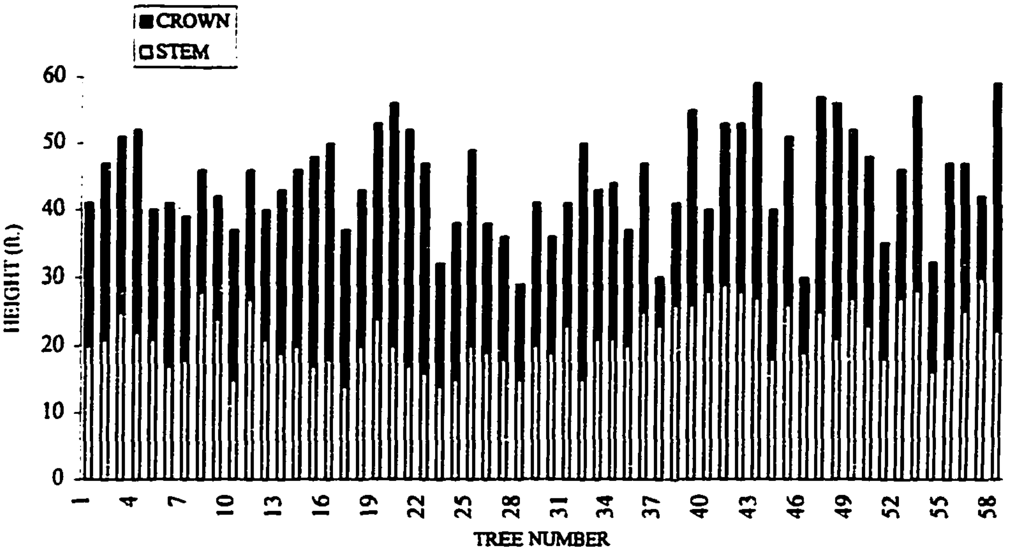
Breast-height age was determined from ring counts made in the field on cores which extended to the pith. In general, the ages of trees of different sizes and clumps/cohorts in multi-aged, and on fewer trees in even-aged were determined to know the bounds of age classes in each stand. In western Montana 27% of trees in the multi-aged plots were cored for age compared to 5% in the even aged. Approximately 47% of trees in the multi-aged and 30% in the even-aged were aged in central Oregon. Cohort number was assigned to each tree in a plot from tree ages following the method described by O'Hara (1996). Stand density measures in terms of total basal area per ha

(m^2/ha), trees per ha, and quadratic mean diameters (cm) were calculated for both structures. Stand density index (SDI) was also calculated for all stands using an equation from Long and Daniel (1990) to avoid bias in non-normal diameter distributions.

2.2.5. Crown Projection Area Estimation

The crown radius of each tree in the sampled plots was measured on north and east direction from the tree base. The crown projection area was then calculated from the average crown radius for each tree and added to calculate the canopy cover percentage in both structures.

The vertical stratification of tree heights and crown lengths in a typical even-aged and multi-aged stand sampled in western Montana (**Figure 2.2**) and central Oregon (**Figure 2.3**) was diagramed using the graphic capability of the TSTRAT computer program developed by Latham et al. (in press).



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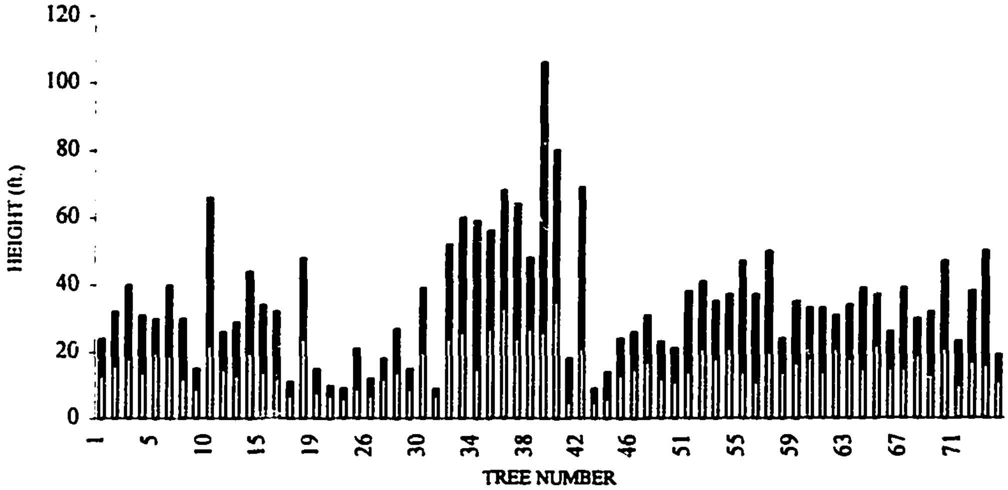


B

Figure 2.2. The vertical stratification of tree heights and crown lengths in ponderosa pine stands in western Montana (A: Even-aged, B: Multi-aged).

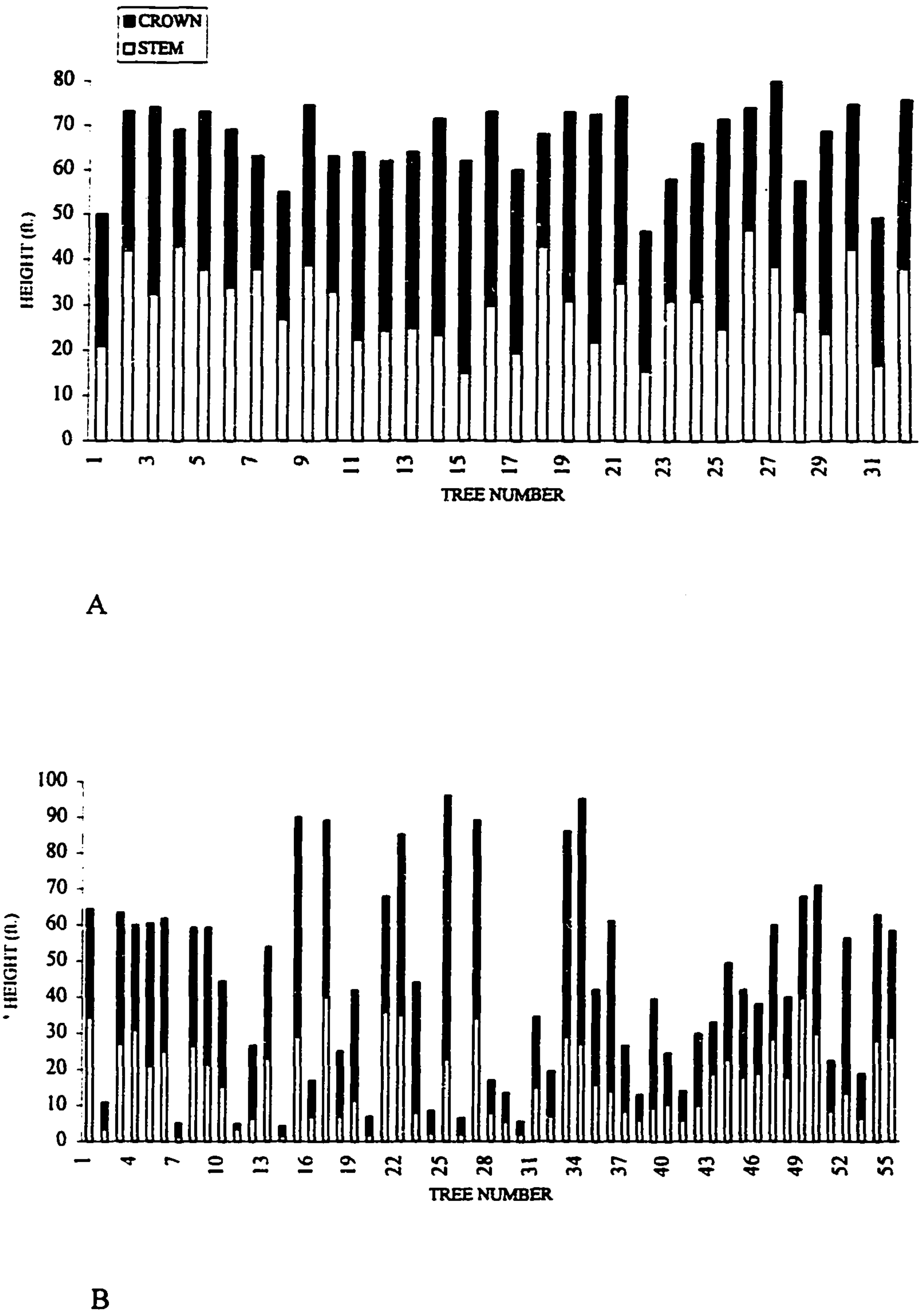


Figure 2.3. The vertical stratification of tree heights and crown lengths in ponderosa pine stands in central Oregon (A: Even-aged, B: Multi-aged).

2.2.6. Leaf Area Estimation

The sapwood area (cm^2) at breast-height was determined for each tree from the average length of two sapwood measurements taken from the cores from each tree. The individual tree leaf area (m2) was estimated from sapwood area using sapwood-leaf area prediction equations developed by O'Hara and Valappil (1995) for western Montana and central Oregon. Plot- and stand-level all-sided LAI was determined from individual tree leaf area. The sapwood-leaf area prediction equation may under-predict leaf area for larger sized trees due to smaller sapwood area increments at breast-heights compared to smaller sized trees, whereas leaf area may be overestimated for smaller diameter sized class trees (O'Hara 1996).

2.2.7. Tree Volume Estimation

2.2.7.1. Models for Past Five years Height Growth

Five years height (cm) and radial growth (0.5mm) were measured on trees destructively sampled for developing sapwood-leaf area prediction equations for western Montana and central Oregon (O'Hara and Valappil 1995). In Montana, an additional 8 trees were destructively sampled during 1996 to increase the sample size to a total of 56 trees. These trees ranged in dbh from 1.2 cm to 46.7cm. A total of 62 trees ranging from 1.6 cm to 34.8 cm was sampled in central Oregon. Multiple linear regression equations to predict the past 5-year height increment were developed separately for western Montana and central Oregon.

2.2.7.2. Total Stem Volume

The total stemwood volume (ft^3) was estimated from diameter and height for the measurement year and for the five years previous using generalized volume equations. and then converted to cubic meters. In western Montana, unpublished volume equations for trees greater than 80 yr of age and trees less 80 yr of age developed by Champion International Corporation were used. In central Oregon the volume equation published by DeMars and Barrett (1987) were used. Average annual stem volume increment during a period of 5 years was used for productivity comparisons.

2.2.8. Growth Efficiency

The growth efficiency in terms of stem volume increment per unit leaf area was compared between the structures as a measure for tree and stand production efficiency. Basal area growth per unit leaf area (basal area growth efficiency) was also compared between the structures. Compared to basal area growth efficiency, volume growth efficiency is a more meaningful estimate for comparison of tree growth efficiency because it incorporates height and diameter growth. Individual tree volume and basal area increments were estimated in cm^3 and mm^2, respectively.

2.2.9. Stand Biomass Estimation

2.2.9.1. Tree biomass

Total tree biomass in both locations was estimated using a general equation for ponderosa pine by Gholz (1982). Total live crown biomass was calculated by adding the total foliage and branch biomass estimated using separate equations. Total stem biomass was the sum of estimated total stem wood biomass and total stem bark biomass. The sum of total live crown biomass and total stem biomass was the total tree biomass. Location specific equations with certain limitations were also used to compare the live crown biomass under both structures. In western Montana, the live crown biomass in even-and multi-aged stands was estimated using two separate equations for crown classes developed by Brown (1978). In central Oregon, separate equations for total foliage and total live branch biomass developed by Cochran (1984) for thinned second-growth ponderosa pine stands were used for estimating the live crown biomass. Total stem volumes estimated using location specific equations together with live crown biomass were compared between the even- and multi-aged stands in both locations.

2.2.9.2. Understory Vegetation Biomass

The understory vegetation biomass was sampled between the last week of July and first week of August 1996 in western Montana and central Oregon respectively. In both even- and multi-aged stands, the understory vegetation was sampled on 2 m^2 circular sub-plots. Three 2 m^2 sub-plots, each at 120, 240, and 360 ^{0} azimuth were established at distances of 9, 13.5, and 4.5 m respectively from the plot center in the even-aged plots in western Montana. Whereas in central Oregon, the distances from the plot center were 6, 9, and 4.5 m on 120, 240, and 360 ^{0} azimuths respectively. The reduction in distance from the plot center to the sub-plots at each azimuth in even-aged stands in central Oregon was due to a smaller sample plot radius compared to western Montana. For multi-aged stands in both locations, six 2 m^2 sub-plots each at 60, 120, 180, 240, 300 and 360 ^{0} azimuth were established at distances of 6 and 12 m alternatively starting from 60 ^{0} azimuth. On each sub-plot, all the aboveground vegetation excluding trees were clipped and dried at 70 ^{0} for 2 days. Plot-level total understory vegetation biomass was calculated by adding all the sub-plots biomass. The total biomass per ha in both structures were estimated by summing the overstory tree biomass and understory vegetation biomass for each plot.

2.2.10. Data Analysis

T-tests with $\alpha = 0.05$ were used to test the difference in the means for stand and tree variables between even- and multi-aged stands. Difference in means between the two study locations was also compared using t-tests. A significance level of $\alpha = 0.05$ was used to determine the selection of independent variables for the multiple regression models.

2.3. RESULTS

2.3.1. Stand Density

Stand density was higher in the even-aged stands in both study locations. The trees per hectare ranged from 570 to 3140 in even-aged and from 260 to 940 in multi-aged stands in western Montana. In central Oregon, it ranged from 160 to 1100 in even-aged and from 100 to 540 in multi-aged stands (**Table 2.3A & B**).

Table 2.3(A & B). Trees per hectare (TPH), Quadratic mean diameter (QMD), Basal area per hectare (BA) m2/ha, Stand density index (SDI), and Canopy cover percentage (CC) in even- and multi-aged stands. E = Even-aged, M = Multi-aged, EO = Even-aged Old-growth. A: western Montana, and B: central Oregon.

A

Plot No.&ID	TPH	QMD (cm)	BA(m²/ha)	SDI	CC (%)
1E	580	21.5	21.0	445	69
1M	260	39.3	31.6	506	70
2E	570	27.7	34.5	659	54
2M	340	32.6	28.5	499	59
3E	1830	15.1	32.7	764	78
3M	890	20.7	30.0	587	79
4E	1140	20.4	37.2	794	94
4M	700	20.4	22.9	451	66
5E	610	25.6	31.5	625	71
5M	500	29.1	33.1	593	69
6E	3140	11.9	34.8	918	82
6M	940	21.0	32.4	636	67

B

Plot No. &ID	TPH	QMD (cm)	BA (m²/ha)	SDI	CC (%)
101E	1100	23.9	50.6	1019	76
101M	540	28.0	34.0	586	64
102E	1025	22.2	39.8	838	65
102M	420	24.8	18.9	358	36
103E	800	28.5	50.9	970	53
103M	420	35.0	40.4	646	54
104E	750	23.0	32.3	656	42
104M	510	24.9	24.9	455	34
105E	350	33.2	30.4	546	32
105EO	160	46.9	32.9	517	37
105M	160	37.2	17.4	274	25
106E	875	23.4	38.7	764	47
106M	100	43.1	16.0	261	21

The mean basal area was higher but not significant for even-aged stands (31.9 m^2/ha) compared to multi-aged (29.8 m^2/ha) stands in western Montana. In central Oregon, the even-aged stands had a significantly higher mean basal area (39.4 m^2/ha) compared to the multi-aged (25.3 m^2/ha) stands. The mean stand density index (SDI) for even- and multi-aged stands in western Montana was 701 and 545, respectively. In central Oregon, the mean SDI was 759 for even-aged stands compared to 430 for multi-aged stands.

2.3.2. Age Classes

The mean breast-height age for the second-growth even-aged stands was higher in western Montana (85) compared to central Oregon (68). In central Oregon, the average breast-height-age in the old-growth even-aged stand was 124 years. For multi-aged stands in western Montana and in central Oregon, the mean breast-height age for the different cohorts ranged from 35 to 280, and from 23 to 254 years, respectively.

Table 2.4. Number of trees, mean age at breast-height (1.37 m), mean total height, mean live crown percentage (LCP), mean leaf area per tree, and mean tree growing space efficiency (GSE) per year (cm^3/m^2) for even- and multi-aged plots in western Montana. E = Even-aged, C = Cohort, C1 = oldest and C4 = youngest.

	PLOT 1					PLOT 2				PLOT 3		
	E	Multi-aged				E	Multi-aged			E	Multi-aged	
		C1	C2	C3	C4		C1	C2	C3		C1	C2
No. of trees	58	5	7	10	4	57	13	12	9	183	2	87
Mean Age (bh)	80	178	132	80	45	81	153	79	63	88	219	80
Mean Height (m)	13.6	24.0	22.1	17.5	8.4	20.3	26.8	17.7	14.4	11.5	22.0	11.5
Mean LCP	51.5	66.0	58.5	60.0	56.4	41.6	61.7	51.9	47.6	32.9	68.4	46.8
Mean LA (m^2)	80	513	305	147	41	128	282	112	65	36	301	58
Mean Tree GSE (cm^3/m^2)	68.5	48.3	61.8	79.3	37.6	92.0	82.6	115	75.7	50.3	101	49.6

(cont.)

	PLOT 4				PLOT 5			PLOT 6			
	E	Multi-aged			E	Multi-aged		E	Multi-aged		
		C1	C2	C3		C1	C2		C1	C2	C3
No. of trees	114	1	9	60	61	40	10	314	2	83	9
Mean Age (bh)	76	280	71	35	84	85	35	99	150	81	49
Mean Ht (m)	14.5	32.3	17.9	9.3	16.1	17.9	4.6	9.0	27.4	13.6	8.1
Mean LCP	0.5	75.5	57.3	50.3	50.7	54.4	48.0	33.7	63.2	41.1	40.2
Mean LA (m^2)	68	839	197	50.4	126	188	11.3	24.3	535	62.9	19
Mean Tree GSE (cm^3/m^2)	67.9	83.3	75.6	70.9	66.6	76.5	42.1	45.3	72.3	57.6	38.5

Table 2.5. Number of trees, mean breast-height age, mean total height, mean live crown percentage (LCP), mean leaf area per tree, and mean growing space efficiency(GSE) per tree per year (cm^3/m^2) for even- and multi-aged plots in central Oregon. C = Cohort, C1 = oldest and C5 = youngest. E = Even-aged, EO = Even-aged Old-growth.

	PLOT 101				PLOT 102					PLOT 103					
	E	Multi-aged			E	Multi-aged				E	Multi-aged				
		C1	C2	C3		C1	C2	C3	C4		C1	C2	C3	C4	C5
No. of trees	44	9	34	11	41	1	1	26	14	32	3	1	14	21	3
Mean Age (bh)	58	122	51	32	55	247	206	48	23	57	247	175	90	45	23
Mean Ht (m)	16.3	25.1	13.6	3.5	14.7	31.7	23.3	14.0	4.1	20.3	32.2	33.5	22.7	10.8	1.9
Mean LCP	44.2	65	59.5	63.1	54	60.1	71.2	65.3	74.4	54.5	70.9	82.7	63	70	66.8
Mean LA (m^2)	88.3	457	84.1	5.9	77.4	860	390	93	18.9	127	797	717	254	57	1.9
Mean Tree GSE (cm^3/m^2)	74.6	97.2	81.0	61.0	78.3	105	117	86.6	96.7	99.9	87.6	118	117	104	---

	PLOT 104					PLOT 105							PLOT 106				
	E	Multi-aged				E	EO	Multi-aged					E	Multi-aged			
		C1	C2	C3	C4			C1	C2	C3	C4	C5		C1	C2	C3	C4
No. of trees	30	1	14	21	15	14	16	1	1	5	8	1	35	1	2	6	1
Mean Age (bh)	75	180	100	58	44	86	124	254	115	95	79	53	78	175	151	72	43
Mean Ht (m)	11.8	27.1	16.3	9.4	3.9	15.2	22.4	30.5	21.8	17	10.7	7.5	11.4	36	24.2	9.1	4.3
Mean LCP	58	78	66	59	57	57	61	60	70	67	60	49	49	79	76	69	64
Mean LA (m^2)	77	755	177	58	8.5	157	369	847	302	149	80	33	74	1712	507	57	12
Mean Tree GSE	70.5	62.4	88.4	68.3	51.5	81.9	81.9	104	82	98.7	82	88	71.2	77	77.4	98.6	73.7

2.3.3. Canopy Cover Percentage

Stand level canopy cover estimated using individual tree crown projection area was generally higher in even-aged stands in both locations (**Table 2.3A & B**). In western Montana, the mean canopy cover was higher for even-aged (75 %) stands but not significantly different compared to multi-aged stands (68 %) (t-tests, $P = 0.325$). In central Oregon, the even-aged stands (50 %) had higher canopy cover compared to the multi-aged (39 %) stands ($P = 0.240$). The mean canopy cover for all even-aged stands was not significantly higher compared to multi-aged stands for both locations combined (t-tests, $\alpha = 0.05$).

2.3.4. Crown Projection Area

Compared to multi-aged stands, the individual tree crown projection area was smaller in even-aged stands. The mean crown radius of trees in even-aged stands was significantly lower compared to those in multi-aged stands (t-tests, $\alpha = 0.05$) in both locations (**Table 2.6**).

2.3.5. Live Crown Percentage

The mean live crown percentage was smaller for even-aged stands (Montana = 37 %, Oregon = 53 %) compared to multi-aged stands (Montana = 49 %, Oregon = 64 %). The even- and multi-aged stands had significantly ($P < 0.005$) different LCP in western Montana and central Oregon (**Table 2.6**). An analysis with the data collected for a previous study published by O'Hara (1996) also indicated the mean LCP for even-aged stands was significantly lower (48 %) compared for the multi-aged stands (52 %) in western Montana (t-tests, P < 0.001).

Table 2.6. Mean leaf area (m^2), mean live crown percentage, and mean crown radius in even- and multi-aged stands in western Montana and central Oregon. Means followed by different letters for each location were significantly different (t-tests, $\alpha = 0.05$).

	W. Montana		C. Oregon	
	Even-aged	Multi-aged	Even-aged	Multi-aged
No of trees	787	363	212	215
Min. Leaf area (m^2)	1.71	1.44	1.92	1.92
Leaf area (m^2)	**52.95**	**102.78**	**113.84**	**135.25**
Max. Leaf area (m^2)	344.51	839.39	785.24	1712.31
LCP	**37^a**	**49^b**	**53^a**	**64^b**
Crown Radius (m)	**1.20^c**	**1.66^d**	**1.43^c**	**1.59^d**

The vertical stratification of crown lengths from a typical even- and multi-aged stand sampled in western Montana (**Figure 2.2**) and central Oregon (**Figure 2.3**) indicates the crowns in multi-aged stands are widely stratified compared to those in even-aged stands.

2.3.6. Leaf Area

The average leaf area per tree in even-aged stands was significantly lower in western Montana (53 m^2) compared to central Oregon (114 m^2). Whereas in multi-aged stands, the average tree leaf area was higher in central Oregon (135 m^2) than in western

Montana (103 m^2) **(Table 2.6)**. In both locations, the mean tree leaf area in even-aged stands was lower compared to multi-aged stands. The average tree leaf area in multi-aged stands tends to vary greatly depending on the percentage of smaller sized trees (younger cohorts) in the stands. The oldest cohort had the highest mean leaf area in western Montana (262 m^2) and central Oregon (667 m^2) **(Table 2.4 &2.5)**. In general, the cohorts leaf area in multi-aged stands decreased with reduction in cohort age.

2.3.7. Leaf Area Index

In western Montana and central Oregon all-sided leaf area index was higher but not significant for the even-aged stands compared to the multi-aged ones (t-tests, $P > 0.05$) **(Table 2.7)**. Higher LAI in the even-aged stands compared to the multi-aged stands were also reported by O'Hara (1996), but the mean LAI was slightly lower for both structures excepting the even-aged stands in central Oregon.

Table 2.7. Mean all-sided LAI comparison between even- and multi-aged stand structures in western Montana and central Oregon (t-tests, $\alpha = 0.05$).

Structure	Study Area	LAI	SD	n	P-value
W. Montana	Even-aged	7.0	1.2	6	0.265
	Multi-aged	6.3	0.8	6	
C. Oregon	Even-aged	7.4	1.9	7	0.053
	Multi-aged	4.9	2.2	6	

The comparison of LAI between the two study locations for even- and multi-aged stands indicated that the mean LAIs for even-aged (P = 0.18) or multi-aged stands (P = 0.66) were not significantly different between western Montana and central Oregon. The large difference in aridity index values among the sites in central Oregon compared to western Montana resulted in a wide difference in mean LAI for the even- and multi-aged stand structures in central Oregon. In central Oregon, 50 % of the sites were on drier sites (aridity index < 0.20) and one pair (about 16 %) on a wet site (aridity index > 0.40). All sites in western Montana were medium aridity (aridity index > 0.20 and < 0.40).

2.3.8. Estimation of Past Height Increment

The regression model for predicting past 5-year height growth (cm) for western Montana used radial growth (mm) as the independent variable, whereas for central Oregon the model used live crown percentage, radial growth (mm), and natural logarithm of total height as independent variables.

Table 2.8. Leaf area index, mean annual volume increment, basal area growth, volume and basal area growth efficiencies for ponderosa pine stands. WM = western Montana, CO = central Oregon, E = Even-aged, M = Multi-aged, EO = Even-aged Old-growth, MAV = Mean annual volume increment, BAGR = Basal area growth, VGE = Volume growth efficiency, and BAGE = Basal area growth efficiency.

Location	Plot	ST	Size (ha)	Trees	LAI	MAV (m^3/ha)	BAGR (m^2/ha)	VGE (cm^3 /m^2)	BAGE (mm^2/m^2)
WM	1	E	0.1	54	4.7	3.5	0.37	76	8
WM	1	M	0.1	25	6.3	3.9	0.24	62	4
WM	2	E	0.1	57	7.3	7.4	0.57	101	8
WM	2	M	0.1	34	5.6	5.3	0.37	94	7
WM	3	E	0.1	183	6.6	3.9	0.43	58	6
WM	3	M	0.1	89	5.9	3.6	0.30	61	5
WM	4	E	0.1	114	7.8	5.8	0.57	75	7
WM	4	M	0.1	70	5.6	4.2	0.43	74	8
WM	5	E	0.1	61	7.7	5.2	0.47	67	6
WM	5	M	0.1	50	7.7	5.5	0.43	72	6
WM	6	E	0.1	314	7.6	4.1	0.59	53	8
WM	6	M	0.1	94	6.5	4.5	0.38	70	6
CO	101	E	0.04	44	9.7	7.4	0.68	76	7
CO	101	M	0.1	54	7.0	5.8	0.41	81	6
CO	102	E	0.04	41	7.9	6.1	0.65	77	8
CO	102	M	0.1	42	4.0	3.6	0.36	91	9
CO	103	E	0.04	32	10.1	11.3	0.91	112	9
CO	103	M	0.1	42	7.9	7.7	0.54	98	7
CO	104	E	0.04	30	5.8	3.9	0.44	67	8
CO	104	M	0.1	51	4.6	3.2	0.31	71	7
CO	105	E	0.04	14	5.5	3.7	0.37	67	7
CO	105	EO	0.1	16	5.9	4.5	0.23	76	4
CO	105	M	0.1	16	2.6	2.1	0.16	80	6
CO	106	E	0.04	35	6.5	4.4	0.47	67	7
CO	106	M	0.1	10	3.1	2.2	0.11	71	4

The model explained 59 and 75% of the variation in 5-year height growth for all trees in western Montana and central Oregon, respectively. Separate regression models to predict past 5-year height growth for upper and lower canopy strata trees did not improve the predictive power in terms of R^2 and standard error compared to the overall model for both locations.

2.3.9. Growth Efficiency

2.3.9.1. Volume Growth Efficiency

The volume growth efficiency (VGE) measured in terms of annual volume increment (cm^3) per unit leaf area (m^2) was higher in 50% of the even-aged stands in western Montana and 15% in central Oregon (**Table 2.8**). The overall mean VGE for even-aged and multi-aged stands was similar (72 $cm^3/ m^{2)}$ in western Montana. For central Oregon the mean VGE for even-aged stands was 78 compared to 82 cm^3/ m^2 in multi-aged stands.

2.3.9.3. Basal Area Growth Efficiency

The mean basal area growth efficiency (BAGE) was lower in multi-aged compared to even-aged stands in both locations (**Table 2.8**). In western Montana, the mean BAGE for even- and multi-aged stands was 7 and 6 mm^2 /m^2, respectively. In central Oregon, the mean BAGE for even-aged stands was 8 mm^2 /m^2 compared to 6 mm^2 /m^2 for multi-aged stands.

2.3.10. Tree Volume and Biomass

2.3.10.1. Stem Volume Increment

The mean annual stem volume increment was higher, but not significant for even-aged stands (5.5 m^3/ha) compared to multi-aged stands (4.6 m^3/ha) on medium aridity sites (t-tests, $P = 0.18$) from both locations combined. The mean values for even- and multi-aged stands in western Montana were 4.5 and 5.0 m^3/ha, respectively (t-test, $P = 0.49$). On drier sites (aridity index < 0.20) the mean was higher for even-aged stands (4.1 m^3/ha) than multi-aged stands (2.5 m^3/ha).

2.3.10.2. Total Stem Volume

The mean stem volume per ha was higher in multi-aged stands compared to even-aged stands in western Montana (**Table 2.9**). In central Oregon, the mean volume was low in multi-aged stands than in even-aged stands. For both locations combined, the mean stem volume was higher in even-aged (220 m^3/ ha) compared to multi-aged stands (207 m^3/ha).

2.3.10.3. Live Crown Biomass

The live crown biomass calculated using site specific equations indicated the multi-aged stands in western Montana had higher mean crown biomass (39 tonne ha^{-1}) compared to the even-aged stands (27 tonne ha^{-1}) (**Table 2.9**). In central Oregon the even-aged stands (49 tonne ha^{-1}) had comparatively higher live crown biomass than the multi-aged stands (33 tonne ha^{-1}).

Table 2.9. Total stem volume, live crown biomass, and tree biomass in even- and multi-aged stands in western Montana and central Oregon. WM = Western Montana, CO = Central Oregon, SS = Stand Structure, E = Even-aged, M = Multi-aged, EO = Even-aged Old-growth.

Location	Plot No	SS	Separate equations for both location		Gholz's equation (kg/ha)	
			Total stem volume (m^3/ha)	Live crown biomass (kg/ha)	Live crown biomass	Total biomass
WM	1	E	122.6	20435	16912	57948
WM	1	M	248.9	45854	38142	138412
WM	2	E	275.3	26718	31938	111864
WM	2	M	243.3	37024	30060	107249
WM	3	E	189.2	20739	23729	79970
WM	3	M	205.7	31050	28548	100521
WM	4	E	235.5	28302	30013	102929
WM	4	M	165.6	26736	22439	79428
WM	5	E	205.3	31361	27528	95576
WM	5	M	244.1	41610	34287	122016
WM	6	E	162.5	18425	21609	70669
WM	6	M	235.7	31073	31654	111960
WM	**All**	**E**	**198.4**	**24330**	**25286**	**86493**
WM	**All**	**M**	**223.9**	**35558**	**30855**	**109930**
CO	101	E	318.3	62278	43315	150288
CO	101	M	257.2	41869	38069	137026
CO	102	E	214.0	45718	32184	110366
CO	102	M	127.7	21377	18893	67055
CO	103	E	394.1	68072	47174	165188
CO	103	M	343.9	52022	50718	185080
CO	104	E	146.1	33137	27516	95397
CO	104	M	139.3	26520	26017	92778
CO	105	E	151.8	31781	30269	107101
CO	105	EO	245.0	38157	41645	152258
CO	105	M	121.6	19056	23213	85427
CO	106	E	184.7	39692	34480	120508
CO	106	M	145.1	19185	25630	96045
CO	**All**	**E**	**237.8**	**44244**	**37536**	**132882**
CO	**All**	**M**	**189.1**	**30005**	**30424**	**110569**

The mean crown biomass estimated using Gholz (1982) generalized equation had similar trend for even- and multi-aged stands. The means for even-aged stands in western Montana and for multi-aged stands in central Oregon had similar live crown biomass using both methods of calculation.

2.3.10.4. Total Tree Biomass

Total tree aboveground biomass for the even- and the multi-aged stands followed the same pattern for live crown biomass in both locations (**Table 2.9**). The total tree biomass for even-aged stands was 95 and 146 tonne ha^{-1} in western Montana and central Oregon, respectively. The values for multi-aged stands were 121 and 122 tonne ha^{-1} in western Montana and central Oregon, respectively. The overall mean aboveground tree biomass for both locations combined was similar (121 tonne/ha) for even- and multi-aged stands.

2.3.11. Understory Vegetation Biomass

In general, the understory vegetation biomass was higher in multi-aged stands than even-aged stands (**Table 2.10**).

Table 2.10. Understory vegetation biomass in even- and multi-aged ponderosa pine stands. WM = Western Montana, CO = central Oregon. E = Even-aged, M = Multi-aged.

Location	Plot No	Understory biomass (kg/ha)	
		Even-aged	Multi-aged
WM	1	294	744
WM	2	1387	1392
WM	3	202	526
WM	4	688	1261
WM	5	959	636
WM Mean		**706**	**912**
CO	101	27	1123
CO	102	28	2476
CO	103	377	686
CO	104	168	372
CO	105	518	458
CO Mean		**224**	**1023**

The overall mean for multi-aged stands (967 kg/ha) was almost double compared to even-aged stands (464 kg/ha). There was very little relationship between LAI and understory biomass ($r = 0.09$) in western Montana, whereas in central Oregon a negative linear relationship between LAI and understory biomass ($r = -0.41$) was evident. For all stands, there was a linear negative relationship ($r = -0.30$) between LAI and understory biomass (**Figure 2.4**).

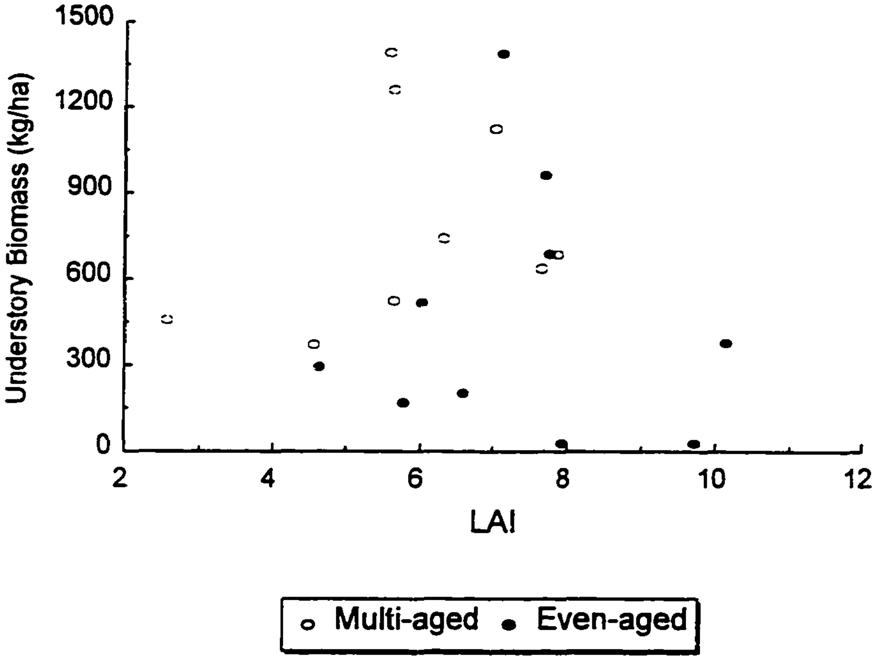


Figure 2.4. Relationship between LAI and understory biomass for even- and multi-aged ponderosa pine stands in western Montana and central Oregon.

2.4. DISCUSSION

Higher stand density in terms of trees per ha in the natural even-aged stands, was characterized with low live crown percentage, leaf area, crown projection area, and crown biomass, indicating higher levels of competition for growing space. The basal area and total sapwood area in even-aged stands were very similar to multi-aged stands due to higher stand densities. Reduction in stand density in the even-aged stands may increase the available growing space, which would have improved the average tree characteristics similar to those in multi-aged stands. In the even-aged lodgepole pine (*Pinus contorta*) stands, Long and Smith (1984) reported that the average crown diameter and depth increased with mean tree size and decreased with stand density. The mean tree leaf area for multi-aged stands was greatly influenced due to the variations in size structure and age classes. Leaf area on trees with similar ages but from different stand structures indicated that trees from even-aged stands carry comparatively lower leaf area than those from multi-aged stands (**Table 2.4&2.5**). This could mainly be due to stand density related competition, which is greater in the even-aged than the multi-aged stands. In central Oregon, most of the multi-aged stands had lower stocking density, but the proportion of larger sized trees was higher compared to western Montana. The distribution of trees by diameter and height classes in the multi-aged stands is an important factor to be considered for stand comparison, even though both structures have similar basal area or SDI.

The mean canopy cover in even-aged stands was higher compared to multi-aged stands in both locations. Higher stocking densities in the even-aged stands compared to the multi-aged stands resulted in higher mean canopy cover. A large sized tree or an old-growth tree generally occupies more growing space compared to small and medium sized trees. Higher proportions of old-growth or larger sized trees in a stand could sometimes result in lower canopy cover and tree density. This may be the reason for lower canopy cover and TPH for the even-aged old-growth stand in central Oregon. The comparison between old-growth and second-growth even-aged stands on a similar site in central Oregon indicated that both stands carry similar LAI but different TPH, QMD, SDI, and canopy cover percentage.

Similar LAI in even- and multi-aged stands indicates the maximum LAI that could be supported on similar quality sites is not significantly different between even- and multi-aged structures. Slightly higher mean LAI for the even-aged stands in central Oregon could be due to higher potential growing space in few sites with high aridity index compared to western Montana. The LAI on a site directly depends on the site growing space, which is limited by climatic and edaphic factors. The stands at Chemult (plot 103), had the highest aridity index and also had the highest LAI for even-aged and multi-aged stands in central Oregon.

In central Oregon, 50% of the stands were on relatively drier habitat types (aridity index < 0.20). The multi-aged stands on those drier sites were characterized with some old-growth and second-growth trees and practically no regeneration. The understory vegetation was abundant with antelope bitterbrush (*Purshia tridentata*), and basin big sagebrush (*Artemisia tridentata)*. Competition for growing space, especially for soil moisture might have been the limiting factor for lack of new regeneration on those sites.

Low stand LAI on drier (arid) sites brought down the overall mean LAI for the multi-aged stands in central Oregon.

In western Montana, the even-aged stands had comparatively higher LAI than the multi-aged stands. This could be due to lower stand density in older cohorts and higher in younger cohorts (cohorts 3 & 4) in the multi-aged stands. The trees belongs to younger cohorts in the multi-aged stands may not be fully utilizing the growing space created from past stand treatments (examples: Plot 2, 4, and 6 in western Montana and Plot 101, 102, 103, and 104 in central Oregon). Whereas the corresponding, even-aged plots had higher numbers of second-growth trees, resulted in larger sapwood area and LAI. A proportionally larger number of trees in older cohorts and fewer in younger cohorts might result in higher LAI in the multi-aged stands compared to the even-aged stands (Plot 1, **Table 2.4**). A multi-aged stand with four times more larger-sized trees compared to young second-growth trees had similar LAI as in the corresponding even-aged stand (Plot 5, **Table 2.4**). The comparison between stand structures with similar LAI on similar sites describes more clearly the effect of canopy architecture on tree and stand productivity.

The diverse pattern in volume growth efficiency between even- and multi-aged stands could be for different reasons. For example, the multi-aged stand in Plot 1 in western Montana had several large-sized trees, resulting in a higher sapwood and LAI. For a larger sized tree, the annual radial increment at breast-height might be very small. The smaller radial growth would predict a lower 5-year height increment from the height-growth model, where the height growth model depends on 5-year radial growth increments. This resulted in a lower stand volume increment and volume growth efficiency. In contrast, if the even-aged stand was fully stocked with medium sized trees, this would have resulted in a higher radial growth, 5-year height growth, stand volume increment, volume and basal area growth efficiencies. This could be the reason for higher VGE and BAGE for the even-aged stand in the Sweeny Creek site in western Montana.

A comparison between even- and multi-aged stands with similar LAI indicated that multi-aged stands tend to produce higher stand volume increment and VGE (Plot 5). Overstocked even-aged stands tend to have smaller radial growth because height growth becomes the highest priority over diameter growth on trees competing heavily for growing space. Small radial growth results in low 5-year height growth (predicted), and therefore low volume increment and volume growth efficiency (Plot 3E and 6E). However, the stand basal area growth efficiency in even-aged could be higher due to high stand densities compared to multi-aged stands. The even-aged stand in Plot 103 in central Oregon was fully stocked with reasonably good radial growth. The mean annual radial growth was about 1 mm and had the highest VGE and BAGE compared to other even-aged stands in central Oregon. In general, depending on the size structure of trees in a stand, the VGE could change considerably between stands with similar LAI.

In western Montana, the mean total stem volume was higher for multi-aged stands due to many large sized trees compared to even-aged stands. In central Oregon, 50 % of the multi-aged stands were understocked (low LAI), resulted in a lower mean total stem volume and volume increments for the multi-aged stands. Even though the mean basal area was similar for even- and multi-aged stands in western Montana, higher tree heights in multi-aged stands resulted in larger stem volumes.

In western Montana, the mean live crown biomass was higher for multi-aged stands, even though the mean basal area was slightly lower compared to even-aged stands. At the same time, the mean leaf biomass was lower in the multi-aged stands compared to even-aged stands. This indicates that the total branch biomass should be higher in multi-aged stands compared to even-aged stands. So the estimated VGE based only on the stem volume increments may not indicate the actual tree volume increments per unit tree leaf area. By taking into consideration the total branch volume increments, together with stem volume increments, the multi-aged stands might have larger volume increments per leaf area compared to even-aged stands.

The comparison between live crown biomass using Gholz's and Cochran's equations for central Oregon indicated that Cochran's equations estimated comparatively higher live crown biomass for both even- and multi-aged stands, except for the stands from drier habitat types. For the stands in drier habitat types, Gholz's equations produced higher live crown biomass. This could be due to two reasons: 1) Gholz's and Cochran's equations were developed from ponderosa pine stands growing in two different geographical regions; 2) Cochran's equation was developed from second-growth ponderosa pine trees of sizes ranging between 5.3 cm and 38.7 cm dbh. The multi-aged stands in drier habitat types of central Oregon had many large-sized old-growth trees and relatively lower estimated live crown biomass. Despite the differences, both equations had a general trend for a higher mean live crown biomass for the even-aged stands compared to multi-aged stands. The mean live crown biomass for multi-aged stands in central Oregon was lower due to lower stand densities. In western Montana, both Gholz's and Brown's equations estimated approximately similar amounts of live crown biomass. The mean live crown biomass estimated using Gholz's equation was slightly higher for even-aged stands and about 13% less for multi-aged stands compared to Brown's equations.

The mean total overstory trees biomass estimated using Gholz's equation indicates that in central Oregon the even-aged stands had higher tree biomass. This is due to higher mean basal area and LAI for the even-aged stands in central Oregon compared to western Montana. This could also be due to differences in water balance between the two locations. The multi-aged stands in central Oregon had lower basal area than in western Montana, but the mean total tree biomass for multi-aged stands was similar in both locations. This may be because, in central Oregon, the majority of the stands' basal area was from large sized trees compared to western Montana.

The trees allocate more biomass for stem and branch production in multi-aged stands due to different canopy structure. In multi-aged stands, trees produce more lateral branches to capture maximum available 3-dimensional growing space, whereas the trees in even-aged stands are limited to explore the horizontal growing space due to higher density related competition from neighbor trees. Higher levels of competition for horizontal growing space may favor height growth over lateral branches on trees in even-aged stands. Silvicultural treatments like thinning increases growing space availability (light and soil moisture) in stands. A reduction in stand density also increases soil moisture due to enhanced canopy interception of rainfall and snow. Higher light and soil moisture levels increases gross photosynthesis if other growth factors like soil nutrients status are not limited. Improved light and moisture availability also results in lower needle specific leaf area (cm^2/gm). Leaves with lower specific leaf area have comparatively more volume of mesophyll tissues containing chlorophyll (Waring 1985) and more carboxylase per unit area (Jones 1992). Shade leaves or leaves with higher SLA have markedly reduced capacity for electron transport through photosystems, when expressed on a chlorophyll basis, Boardmann et al. (1975) reported that about 14 times higher electron transport in chloroplasts extracted from sun plants than those from shade plants. Several studies have reported the negative relationship between specific leaf area and photosynthesis in plant species. Manipulation of stand structure to increase the foliage production efficiency (low SLA) may also result in higher tree- and stand-level productivity (**Figure 2.5**).

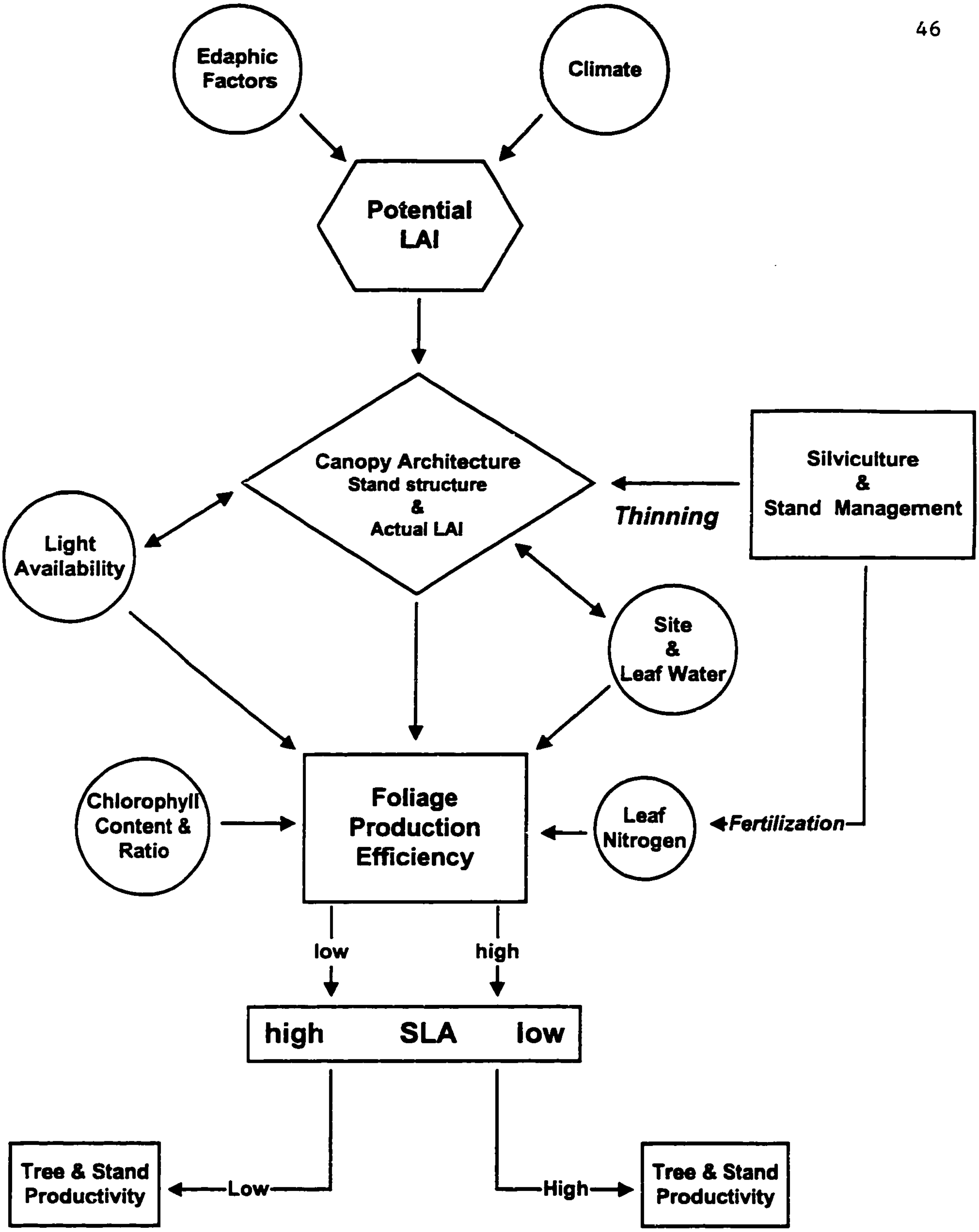


Figure 2.5. A conceptual model describing factors that regulate leaf to stand level productivity

The multi-aged stands had comparatively lower LAI and higher understory vegetation biomass on both locations. The overall negative linear relationship (r = -0.30) between LAI and understory vegetation biomass indicates that a reduction in overstory biomass or canopy cover increases the understory vegetation biomass due to higher available growing space for the understory species. This could also suggest that distribution pattern of biomass between perennial overstory trees and seasonal understory vegetation is directly related to its overstory stand structure.

2.5. CONCLUSIONS

Leaf area index (LAI) in the even- and multi-aged stands largely depends on the climate and edaphic factors on that site. The total stand biomass production on a site is related to its LAI. The production efficiency of foliage in a stand is related to available growing space and stand structure. The production efficiency of foliage in terms of stem volume growth per unit leaf area was higher in multi-aged stands. Trees with similar ages, but from different stand structures, had significantly different leaf area, live crown percentage, crown projection area, and growing space efficiency, suggesting that trees in multi-aged structures have increased available growing space compared to those in even-aged stand structures. The increased growth factors for the trees in multi-aged stands could be attributed to lower stocking level and diverse vertical stand structure.

Several other factors also influence the production efficiency of leaves. Creating more available growing space in a stand increases individual tree production. At the same time, low stocking levels decrease stand-level volume growth/production. This could be the main reason for low LAI and mean stem volume increments in the multi-aged stands. When LAI is similar for the even- and multi-aged stands, the influence of stand structure on production became more obvious. On good quality sites (ex: high aridity index), when soil moisture is not a limiting factor, stand LAI and stem volume increments tend to increase in the even-aged stands. On water limited sites, the even-aged stand structure could result in higher levels of competition for soil moisture, and may reduce individual tree as well as stand production. Even though most of the study sites in western Montana were on sites with relatively medium aridity index, the low LAI and stem volume increments for few of the multi-aged stands were mainly due to low stocking levels compared to the adjacent even-aged stand. Relatively lower stocking in multi-aged stands provide higher understory vegetation biomass compared to even-aged stand structure. Higher understory biomass may increase the wildlife carrying capacity. Diverse crown stratification in multi-aged stands may have different above- and belowground biomass allocation patterns compared to single strata even-aged stands. Total biomass including both above- and belowground components should be taken into consideration while comparing the net productivity in multi-aged vs. even-aged structures.

Literature Cited

Arno, S. F., J. H. Scott, J. H. and Hartwell, M. G., 1995. Age-class structure of old growth ponderosa pine /Douglas-fir stands and its relationship to fire history. USDA For. Serv. Res. Pap. INT-RP- 481, 25 pp.

Binkley, D. and Reid, P., 1984. Long-term responses of stem growth and leaf area to thinning and fertilization to a Douglas-fir plantation. Can. J. For. Res., 14:656-660.

Boardmann, N. K., Bjorkman, O., Anderson, J. M., Goodchild, D. J. and Thorne, S. W., 1975. Photosynthetic adaptation of higher plants to light intensity: relationship between chloroplast structure, composition of the photosystems and photosynthetic rates. In: M. Averon (Editor), Proceedings of the third international congress on photosynthesis, Amesterdam, Elsevier, pp. 1809-1827.

Brix, H., 1981. Effects of nitrogen fertilizer source and application rates on foliar nitrogen concentration, photosynthesis, and growth of Douglas-fir. Can. J. For. Sci., 15:189-196.

Brown, J. K., 1978. Weight and density of crowns of Rocky Mountain conifers. USDA For. Serv. Res. Pap. INT-197, 56 pp.

Cannell, M. G. R., Milne, R., Sheppard, L. J. and Unsworth, M .H., 1987. Radiation interception and productivity of willow. J. Appl. Ecol., 24:1261-1313.

Cochran, P. H., Jennings, J. W. and Youngberg, C. T., 1984. Biomass estimators for thinned second-growth ponderosa pine trees. USDA For. Serv. Pac. Northwest For. and Range Exp. Station. Research Note. PNW-415, 6 pp.

Daly, C., Neilson, R. P. and Phillips, D. L., 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Appl. Meteorol., 33:140-158.

DeMars, D. J., and J. W. Barrett. 1987. Ponderosa pine managed-yield simulator: PPSIM users guide. USDA For. Serv. Gen. Tech. Rep. PNW-203, 36 pp.

Donner, B. L. and Running, S. W., 1986. Water stress response after thinning *Pinus contorta* stands in Montana. For. Sci., 32:614-625.

Doley, D., 1982. Photosyntetic productivity of forest canopies in relation to solar radiation and nitrogen cycling. Aust. J. For. Res., 12:245-261.

Evans, J. R., 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. Ecology, 78: 9-19.

Field, C. and Mooney, H. A., 1986. The photosynthesis-nitrogen relationships in wild plants. In: T. J. Givinish (Editor), On the Economy of Plant Form and Function, Cambridge University Press, New York, 717 pp.

Franklin, J. F. and Dyrness, C. T., 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, 417 pp.

Gholz, H. L., 1982. Environmental limits on aboveground net primary production, leaf area and biomass in vegetation zones of the Pacific Northwest. Ecology, 63:469-481.

Gower, S. T. , Haynes, B. E., Fassnacht, K. S., Running, S. W. and Hunt Jr. E. R., 1993. Influence of fertilization on the allometric relations for two pines in contrasting environments. Can. J. For. Res., 23:1704-1711.

Grier, C. C. and Running, S. W., 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology, 58:893-899.

Gutschick, V. P., and Wiegel, F. W., 1988. Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. Am. Nat., 132:67-86.

Hopkins, W. E., 1979a. Plant associations of the Fremont National Forest. USDA For. Serv. Pac. Northwest Reg. R6-Ecol-79-004, 106 pp.

Hopkins, W. E., 1979b. Plant associations of the south Chiloquin and Klamath Ranger Districts-Winema National Forests. USDA For. Serv. Pac. Northwest Reg. R6-Ecol-79-005, 96 pp.

Jones, H. G., 1992. Plants and microclimate-A quantitative approach to environmental plant physiology. Second edition, Cambridge University Press, 428 pp.

Kaufmann, M. R. and Ryan, M. G., 1986. Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine trees. Tree physiol., 2:47-59.

Kollenberg, C. L. 1997. Leaf area dynamics and stocking relationships of multi-aged lodgepole pine stands in western and central Montana. Master's thesis, The Uni. of Montana, Missoula, 77 pp.

Latham, P. A., Zuuring, H. R. and Coble, D. W., 1998. A method for quantifying vertical forest structure. For. Ecol. Mange., (In press).

Linacre, E. T., 1977. A simple formula for estimating evaporation rates in various climates, using temperature data alone. Agric. Meteorol., 18:409-424.

Linder, S. 1987. Response to water and nutrients in coniferous ecosystems. In: E.D.Schulze and H. Zwolfer (Editors), Potentials and limitations in ecosystem analysis. Springer, Berlin Heidelberg New York Tokyo, pp. 180-202.

Linder, S. and Troeng, E., 1980. Photosynthesis and transpiration of 20 -year-old Scots pine. In: T. Persson (Editor), Structure and function of northern coniferous forests - an ecosystem study. Ecol. Bull., Stockholm 32: 165-181.

Long, J. N. and Daniel, T. W., 1990. Assessment of growing stock in uneven-aged stands. West. J. Appl. For., 5:93-96.

Long, J. N. and Smith, F. W., 1984. Relation between size and density in developing stands: a description and possible mechanism. For. Ecol. Manage., 7:191-206.

Long, J. N. and Smith, F. W., 1992. Volume increment in *Pinus contorta* var. *latifolia*: The influence of stand development and crown dynamics. For. Ecol. and Manage., 53:53-64.

Marks, P. L. and Bormann, F. H., 1972. Revegetation following forest cutting: Mechanism for return to steady-state nutrient cycling. Science, 176:914-915.

Moller, C., 1947. The effect of thinning, age, and site on foliage, increment, and loss of dry matter. J. For., 45:393-404.

Mooney, H. A., Ferrar, P. J. and Slayter, R. O. 1978. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. Ocecologia 36:103-111.

O'Hara, K. L., 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can. J. For. Res., 18:859-866.

O'Hara, K. L., 1989. Stand growth efficiency in a Douglas-fir thinning trial. Forestry, 62:409-418.

O'Hara, K. L. and Valappil, N. I., 1995. Sapwood/leaf area prediction equations for multi-aged ponderosa pine stands in western Montana and central Oregon. Can. J. For. Res., 25:1553-1557.

O'Hara, K. L., 1996. Dynamics and stocking-level relationship of multi-aged Ponderosa Pine stands. For. Sci., 42: Monograph 33, 34 pp.

O'Hara, K. L., Valappil, N. I. and Kollenberg, C. L. (in press). Stocking control in multi-aged stands using a leaf area allocation approach. In: Uneven-aged silviculture, Proceedings of the IUFRO interdisciplinary uneven-aged silviculture symposium, Sept. 15-19, 1997, Corvallis, Oregon.

Oliver, C. D. and Larson, B.C., 1996. Forest stand dynamics, update edition, Wiley, New York, 520 pp.

Oren, R., Waring, R. H., Stafford, S. G. and Barrett, J. W., 1987. Twenty-four years of ponderosa pine growth in relation to canopy leaf area and understory competition. For. Sci., 33:538-547.

Pfister, R. D., Kovalchik, B. L., Arno, S. F. and Presby, R. C., 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34, 177 pp.

Pierce, L. L. and Running, S. W., 1994. Regional-scale relationship of leaf area index to specific leaf area and leaf nitrogen content. Ecol. Appl., 4:313-321.

Running, S. W., 1976. Environmental control of leaf water conductance in conifers. Can. J. For. Res., 6:104-112.

Sheriff, D. W., Nambiar, E. K. S. and Fife, D. N., 1986. Relationship between nutrient status, carbon assimilation, and water use efficiency in *Pinus radiata* (D. Don.) needles. Tree Physiol., 2:73-88.

Smith, D. M., 1986. The Practice of Silviculture. 8th edition, John Wiley & Sons, New York, 527 pp.

Specht, R. L. and Specht, A., 1989. Canopy structure in *Eucalyptus*-dominated communities in Australia along climatic gradients. Oecologia Plantarum, 10:191-213.

Tucker, G. F. and Emmingham, W. H., 1977. Morphological changes in leaves of residual western hemlock after clear and shelterwood cutting. For. Sci., 23:95-203.

Volland, L. A., 1988. Plant associations of the central Oregon pumice zone. USDA For. Serv. Pac. Northwest Reg., R6- ECOL-104-1985, 138 pp.

Waring, R. H., 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Adv. Ecol. Res., 13:327-354.

Waring, R. H. and Schlesinger, W. H., 1985. Forest ecosystems: Concepts and management. Academic Press, Inc., New York, 340 pp.

Waring, R. H. and Running, S. W., 1998. Forest ecosystems: Analysis at multiple scales. Academic Press, Inc., San Diego, (in press).

Chapter 3

Specific Leaf Area and Leaf Nitrogen Measures for Comparative Productivity in Even- and Multi-aged Ponderosa Pine Stands

ABSTRACT

Leaf level physiological differences due to stand structures were examined in even- and multi-aged ponderosa pine (*Pinus ponderosa*) stands in western Montana and central Oregon. Leaf area and its arrangement are important factors determining tree and stand productivity. Specific leaf area (cm^2/gm) and leaf nitrogen content were examined at different crown heights on trees in even- and multi-aged stands. Trees belonging to different strata in even- and multi-aged structures were selected and one- to three-year-old needle samples were collected from top, middle, and bottom crown thirds to determine the specific leaf area (SLA). SLA for the top third was lowest and increased down through the crown in both structures. Multi-aged stands were characterized by lower SLA at different crown thirds compared to even-aged stands. The range between top and bottom third mean SLA was the greatest for even-aged stands, even though the live crown percentage was the lowest. Two- and three-year-old needles had the lowest SLA in western Montana and central Oregon respectively. Compared to the even-aged stands, multi-aged stands had the lowest PAR interception, indicating higher levels of PAR beneath the canopy. Leaf nitrogen content (area basis) was the highest in top crown third and decreased down through the crown. In western Montana, two-year-old needles had the highest leaf nitrogen content in both structures, whereas three-year-old needles in even-aged stands had the highest leaf nitrogen in central Oregon. Low SLA and high leaf nitrogen content indicate physiologically more productive needles. A negative linear relationship between volume increment and SLA indicates low SLA leads to increased production. Comparatively lower SLA for crown thirds in multi-aged stands is not an age factor, but rather an age-related structural phenomena. These results suggest that managing stands with diverse vertical structure is an important factor to increase tree and stand productivity.

Keywords: ponderosa pine, specific leaf area, leaf nitrogen, needle age, even-aged, multi-aged, photosynthetically active radiation, stand structure, stand productivity.

3.1. INTRODUCTION

Stand productivity of even- and multi-aged (stands with two or more age classes) structures or stands has always been a subject of controversy. Most previous studies were based on empirical yield reports. Comparative studies emphasizing physiological factors responsible for stand productivity under these silvicultural systems has not been made in the past. Soil and climate are the most important biophysical factors limiting plant growth and productivity. If the variation in these factors is minimal, stand production efficiency in terms of carbon fixed per unit leaf area depends on the degree of site occupancy and stand structure. Stand structure is the physical and temporal distribution of trees and other components of a forest (Oliver and Larson 1996).

Total stand production depends on the production efficiency of trees in a stand and the number of trees. Stand structure modifies the micro-climate controlling the physiological functioning of a stand. It has been found that stands with many age groups and diverse vertical structure have slightly greater growth efficiency compared to even-aged stands (O'Hara 1996). Leaf area index (LAI) has been used as a measure of occupied growing space on a site (O'Hara 1988). On similar sites, stands having similar LAI but varied vertical crown structure can result in different leaf level physiological characteristics that leads to changes in tree and stand productivity. Specific leaf area (leaf area per unit dry biomass) and leaf nitrogen content are two important physiological surrogates for available growth factors: light, temperature, water, and nutrients in a stand.

In this paper, comparative differences in leaf-level physiological characteristics like specific leaf area (SLA) and leaf nitrogen content were examined within the crowns of even- and multi-aged stand structures to relate the differences in these foliar measurements to tree- and stand- level productivity. Ponderosa pine (*Pinus ponderosa*), a light-demanding tree species, is managed under both even- and multi-aged stand structures. The objectives of the study were: 1) To test whether specific leaf area (SLA), a surrogate measure for photosynthetic efficiency, varies significantly between crowns in even-aged and multi-aged ponderosa pine stands; 2) To examine the range in SLA between crown thirds of trees in these stand structures; 3) To measure the photosynthetically active radiation (PAR) available at 1 m above ground level and its influence on distribution of SLA and productivity in even- and multi-aged ponderosa pine stands; 4) To determine the difference in total leaf nitrogen content between and within crowns of trees in even- and multi-aged ponderosa pine stands; and 5) To examine the relationship between tree mean SLA and volume increment, SLA and crown height, and SLA and leaf nitrogen in both even- and multi-aged stands.

3.2. BACKGROUND

3.2.1. Specific Leaf Area and Photosynthesis

Leaf area per unit dry biomass (cm^2/gm) in a plant is arranged to maximize solar energy harvest and photosynthesis. SLA describes the concentration of plant leaf biomass relative to its area within a plant canopy (Janecek et al. 1989; Pierce and Running 1994), and it acts as an important link between the stored carbon and water cycle within a plant. SLA has been found to be closely related to canopy photosynthetic capacity (Gutschick and Wiegel 1988; Ellsworth and Reich 1993). Studies have reported that upper canopy parts of trees are more productive compared to others (Ellsworth and Reich 1993). Generally, the top section of a tree crown receives maximum solar radiation compared to middle and lower sections. Therefore, a similarity in SLA within a tree's crown indicates approximately equal crown productivity, suggesting SLA can be used as to compare the production potential of trees in different stand structures.

Plants grown in water limited environments typically have reduced SLA in comparison to the same species grown in non-water limited environments (Pierce and Running 1994; Jose and Gillespie 1997). Hollinger (1989) demonstrated that SLA increased as canopy depth and Amax (light saturated photosynthetic rate under non-limiting environmental conditions) decreased. SLA varies largely within and between plants (Mooney et al. 1978; Norman and Campbell 1989) depending on species, age, and light environments (Fitter and Hay 1987; Nobel and Hartsock 1981). Farnsworth and Ellison (1996) found that in red mangrove (*Rhizophora mangle*) the leaf anatomy was insensitive to light environments, but leaf length, width, specific leaf area, and summer maximum photosynthetic rates varied between sun and shade leaves in the neo-tropical mangrove forests at Wee Wee Cay, Belize. Increasing SLA and decreasing total biomass were found when increasing shade levels in loblolly pine (*Pinus taeda*), white pine (*Pinus strobus*) by Groninger et al. (1996). But they also reported that quantum efficiency, dark respiration, and light compensation points were not reduced in trees under shade treatments. Intra-specific variation of SLA reflects the phenotypic plasticity of *Quercus ilex* in different habitats and demonstrated the ability of plants to respond adequately to changing environmental factors by altering leaf morphology (Gratani 1996). In beech

(*Fagus sylvatica*) seedlings, Larsen and Buch (1995) reported that mesophyll thickness and stomata density were significantly varied among provenances due to differences in light.

Ducrey (1994) found higher maximum photosynthesis of sun-grown seedlings than shade-grown seedling in seven tropical rain forest species from Guadeloupe (French West Indies). He also reported a reduction in maximum photosynthesis and an increase in apparent quantum yield with higher SLA (when plants were more shaded). Grace et al. (1987) used SLA for modeling canopy net photosynthesis in *Pinus radiata* stands to account for the variation in rates of net photosynthesis due to physiological and morphological state of individual shoots throughout the canopy. Klinka et al. (1992) reported a decreased growth in terms of height increment, lateral branch growth, and growth at the base of the current leader, and higher SLA due to lower levels of irradiance in Pacific silver fir (*Abies amabilis*) and subalpine fir (*A. lasiocarpa*) forests in northwestern North America. In Finland, Nygren and Kellomaki (1983) reported that shading increased SLA and decreased the leaf mesophyll thickness in young birches such as *Betula pendula* and *B. Pubescens*. They also reported the maximum photosynthetic rate and light intensity for photosynthetic saturation were decreased in shading, and were associated with an increase in SLA and a decrease in chlorophyll amount per unit of leaf area.

3.2.2. Leaf Age

Borghetti et al. (1986) reported a decrease in SLA with leaf age and from base to apex of the crown in an unthinned 25 yr old Douglas-fir plantation in Florence, Italy. Shelton and Switzer (1984) reported that within the canopy of loblolly pine stands, the SLA was greatest for current fascicles in the lower canopy and least for older fascicles in the upper canopy. Gilmore et al. (1995) reported significantly different SLA between foliage age classes showing a decreasing trend with an increase in leaf age in *Abies balsamea* trees in the Penobscot River Valley, Maine. In Scots pine in The Netherlands, Hees et al. (1993) reported that SLA decreased with needle age and increased with crown depth. Pereira et al. (1992) reported that the differences between the photosynthetic capacity of adult and juvenile leaves of *Eucalyptus globulus* seedlings in optimal water, nutrients, and in non-irrigated, unfertilized control treatments were largely explained by the lower SLA of adult leaves.

3.2.3. Stand Structure, Light Intensity and Canopy Extinction Coefficient (k)

Tree foliage intercepts most of the light captured by the canopy and increased foliage area increases light interception (Cannell et al. 1987). The availability of light in a canopy determines the amount of net photosynthesis (PSN) under non-limited moisture and nutrient environments. Stand structure, tree species, stem density, leaf morphology, leaf density, and leaf orientation affect the availability of solar radiation at different canopy heights. When light passes through a canopy, some of the incident radiation gets absorbed by the canopy and the rest is reflected. A good portion of the unabsorbed radiation filters down through the canopy layers. The rate at which foliage absorbs radiation depends on the type of species. This rate is known as the light extinction coefficient 'k'. The k varies due to types of canopies as well as due to variations in vertical distribution of canopy foliage (Sampson and Smith 1993). Several studies have found low extinction coefficients associated with increased canopy depth and LAI (McIntyre et al. 1990; Gholz et al. 1991; Smith et al. 1991). In the simplest approach, the penetration of visible light through an accumulated layer of foliage (a uniform spongy medium of chlorophyll) approximates the Beer-Lambert law (Waring 1985).

The extinction coefficient k can be considered an efficiency coefficient because, for each unit of LAI, a canopy with a higher k will intercept more light (Oker-Blom and Kellomaki 1983). The difference in extinction coefficients in two stand structures with different LAI can be calculated using this method assuming that light attenuation occurs through a homogeneous media of foliage with a specific depth and property (Campbell 1977). Light transmission within the canopy is influenced by leaf properties and canopy structure or LAI (Ross 1981; Campbell and Norman 1989). In many instances, the canopy heterogeneity due to structure, stem surface area, sun angle, and foliage clumping, cause more complexity in estimation of k. At maximum solar elevation, the value of k for conifers varies between 0.40 to 0.65 (Jarvis and Leverens 1983).

3.2.4. SLA, PAR, and Leaf Nitrogen

For evergreen conifers, mass-based Amax was less correlated with leaf nitrogen compared to broad leaved deciduous trees, whereas on an area basis there was no correlation in the evergreen conifers (Reich et al. 1995). It was also reported that both leaf N and Amax on a mass basis were correlated with SLA; in contrast, area-based leaf

N scaled tightly with SLA, but area-based Amax did not because of low Amax per unit N in the evergreen conifers. They also stated that trees with lower SLA and longer leaf life spans tend to have lower Amax per unit leaf N and a lower slope and higher intercept of Amax-N relation than do species with shorter leaf life span and higher SLA. Midgley (1995) reported an inverse relation in SLA and leaf nitrogen with rainfall in South African forest species. In a thinning study in British Columbia, Wang et al. (1995) reported that increased PAR and foliar nitrogen concentration and decreased SLA for lower stand density levels compared to very high density of paper birch (*Betula papyrifera*).

3.3. METHODS

3.3.1. Site Selection

The study was conducted in western Montana and central Oregon to examine the influence of stand structure related variations in leaf physiology in ponderosa pine. In western Montana, the study plots were located at elevations of approximately 850 to 1250 m. The latitude and longitude ranged from 46° 37′ to 47° 06′N and 113° 23′ to 114° 47′W, respectively. The long-term average climatic data for the sites were given in **Table 2.2.** The stands were located primarily on *Pseudotsuga menziesii* climax series (Pfister et al. 1977), and were predominantly pure ponderosa pine with an occasional inclusion of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) less than 5%. All the sample plots were located on south to southeast aspects between a slope of 2 to 30%. The even-aged stands were primarily on second growth ponderosa pine forests.

In central Oregon the study plots were located at elevations between 1330 to 1540 m. The latitude and longitudes of the study locations range from 43° 13′ to 43° 52′N and 121° 8′ to 121° 48′ W, respectively. The long-term average climatic data from nearby weather stations were used to characterize the study sites (**Table 2.2**). The sample plots were selected on *Pinus ponderosa* plant associations on pumice soils as part of the High Cascades Province (Franklin and Dyrness 1973). Many of the central Oregon stands were seriously defoliated by pandora moth outbreak (*Coloradia pandora* Blake) during 1992-95. Special attention was given to choose the sample plots on stands which were attacked at a minimal level by examining the stand/trees for the number of years' needle whorls. Stands with trees less than 4 year's needles were not selected. Pure multi-aged ponderosa pine stands are common in central Oregon due to partial cutting and deliberate selection silviculture. The plant associations were identified as per the guides by USDA Forest Service for each sampling area (Hoplins 1979a, 1979b, Volland 1988). The sample plots were located on all aspects between slopes ranging from 2 to 12%.

3.3.2. Plot Selection

Pure paired even- and multi-aged ponderosa pine stands at closer proximity (for similar site condition) were selected in both study locations. The selected stands were not treated for 15 years prior to the year of sampling to eliminate bias in stand productivity. In western Montana, six pairs of even and multi-aged plots were identified, whereas in central Oregon five pairs. A 0.1 ha size circular sample plot (17.8 m radius) was selected randomly on all the identified stands in western Montana and central Oregon except the even-aged stands in central Oregon. The plot size in the even-aged stands in central Oregon was 0.04 ha (11.3 m radius). This is due to approximately similar variances in estimated LAI between plot sizes 0.1 ha and 0.04 ha in even-aged stands. Larger plot size was selected in multi-aged stands due to higher structural and spatial heterogeneity.

3.3.3. Tree Measurements

Within each sampled plot, the trees were measured for their diameter (dbh) in cm at 1.37 m from ground level, total height (m), and the height up to live crown base (m). From the two heights, live crown length and live crown percentage for each tree was calculated. In each stand, the trees were grouped into different canopy strata based on their total heights and their relative position in the canopy. Generally, in even-aged stands most of the trees were grouped into a single stratum in both locations. But in western Montana, for SLA analysis, a few shorter trees were grouped as EV-2 (lower stratum) in addition to the major group EV-1. In multi-aged stands there were up to four strata levels which were designated MA-1, MA-2, MA-3, and MA-4 representing the tallest to the shortest, respectively. Each tree was also assigned a crown class using the procedure described by Smith (1986).

Trees were cored at breast height on their north and east sides. The radial growth for the past five years was measured to the nearest 0.5 mm on both increment cores to calculate mean annual volume increments (methodology described in Chapter 2) on all trees. Breast height age was determined from ring counts made in the field on cores which extended to the pith. Based on tree age classes identified in each stand, cohort number was also assigned to trees in each plot using the method described by O'Hara (1996).

3.3.4. PAR Measurements

PAR was measured in both structures using a Decagon Sunfleck Ceptometer (model SF-80, Decagon Devices, Incorporated) during June and July of 1996 in western Montana and central Oregon, respectively. The measurements were made on clear, sunny days between ± one hour of solar noon. In western Montana and central Oregon a total of eight pairs of even and multi-aged stands were sampled for PAR measurements. In each stand, a 400 m^2 (20 m x 20 m) square plot with grids at 2 m intervals was used. PAR was measured on points marked on each grid line at an interval of 4 m. The measurements were taken from east to west following a boustrephedon sampling design to avoid time related bias between adjacent measurement points. At each point, the PAR was taken as an average of eight readings between 0 to 360^0 at 45^0 interval. A total of 66 measurements were taken for each plot and completed on the same day in both stands. An average "open condition" PAR was determined for each stand from two measurements taken, right before and soon after the measurements inside the canopy. The ratio of PAR inside the canopy to open were calculated for each stand. The canopy light extinction coefficient 'k' was estimated using the Beer-Lambert equation.

$$\text{(Eq. 3.1)} \qquad -k = \ln(I_z/I_0)/\Sigma LAI$$

Where I_0 = PAR outside the canopy (open condition), I_z = PAR measured beneath (inside) the canopy, and ΣLAI is the (projected) leaf area index. The projected LAI for each stand was approximated by dividing the all-sided LAI by a factor 3.2 (Johnson 1984). The 'k' was calculated in two methods: In the first method, k was calculated at each measurement point and averaged for the stand. But in the second method, average stand PAR ratio and stand projected LAI were used.

3.3.5. Leaf Level Measurements

In western Montana and central Oregon, five codominant trees belonging to different strata classes were selected from each multi-aged plot for leaf level physiological measurements. Three codominant trees per plot were selected in even-aged structure due to smaller variation in tree height and age compared to multi-aged stands.

The live crowns of trees selected for leaf level measurements were divided into equal thirds: top, middle, and bottom. In western Montana during the first week of August 1995, a fully exposed 1-2 cm thickness terminal twig with a minimum three year's needle whorls was shot down from each crown third. Needles from each twig were immediately separated into age classes and stored on ice before taken to the laboratory. All-sided needle surface area was calculated using a geometric technique developed by Johnson (1984). SLA for each crown third, as well as for each needle age class from crown thirds, was determined using the method described by O'Hara and

Valappil (1995). In western Montana, the needle samples from all the plots were collected within the first week of August 1995 to reduce the variation in SLA due to time/seasonal changes and the same procedure was repeated in central Oregon during the third week of July 1996.

3.3.6. Leaf Nitrogen Estimation

Leaf nitrogen content was determined in needle samples used for SLA estimation. A total of 15 trees from three study sites in western Montana and 10 trees from two sites in central Oregon were chosen for leaf nitrogen analysis. Three multi-aged and two even-aged trees from each study site were selected. The dried needle samples were ground to 40 mesh size in a Wiley Mill and about 10 mg each were wrapped in tin boats and fed into an elemental gas analyzer. Total leaf nitrogen content was estimated from a linear regression equation developed from standards of known nitrogen percentage used for calibration. The samples were replicated twice and the average leaf nitrogen concentration was expressed in mols/m^2 using all-sided leaf area.

3.3.7. Data Analysis

Analysis of variance was used to compare the mean SLA and leaf nitrogen content between crown thirds and needle age classes. Scheffe's multiple range test was used when the ANOVA hypothesis of no difference was rejected. The mean range in SLA between top and bottom thirds was compared between even- and multi-aged stands using t-tests ($\alpha = 0.05$). Two sample t-tests were used to test the differences in PAR ratios and canopy extinction coefficients between even- and multi-aged stands. Simple linear regression equations were developed to predict SLA and leaf nitrogen from crown heights (different heights from tree base within a crown). Multiple regression procedures were used to predict leaf nitrogen content (mols/m^2) from independent variables like SLA, leaf age, total height (m), crown height (m), and crown sections. Simple linear regression was used to develop a predictive model for volume increment from mean crown third SLA. A significance level with $\alpha = 0.05$ was used to determine the selection of independent variables in regression model building.

3.4. RESULTS

3.4.1. Stand Characteristics

The even-aged stands had higher stand density compared to the multi-aged stands in western Montana and central Oregon. In western Montana, the trees per ha (TPH) ranged from 570 to 3140 in even-aged and from 260 to 940 in multi-aged stands. The TPH ranged from 160 to 1100, and from 100 to 540 for even- and multi-aged stands in central Oregon, respectively. The mean basal area for even-aged stands (31.9 m^2/ha), was not significantly higher compared to multi-aged (29.8 m^2/ha) stands in western Montana, but in central Oregon, the even-aged stands had significantly higher mean basal area (39.4 m^2/ha) than the multi-aged stands (25.3 m^2/ha). The higher mean basal area in even-aged stands is due to higher stand density compared to multi-aged stands.

The mean breast height age for the second-growth even-aged stands was higher in western Montana (95) compared to central Oregon (71). The mean age of the trees selected from the different canopy strata in multi-aged stands in western Montana and central Oregon is given in **Table 3.1**. Trees in strata MA-3 and MA-4 had similar mean breast height age in western Montana, whereas in central Oregon, trees in different strata followed a distinct age pattern or cohort class. The mean LCP was significantly larger in multi-aged stands compared to even-aged stands in both locations (t-tests, $P < 0.05$). At the same time, the mean LCP for even-aged stands in western Montana (40) was significantly lower compared to central Oregon (56) stands. For multi-aged stands the mean LCP was 59 and 67 for western Montana and central Oregon, respectively. In both locations, the trees belong to each strata in multi-aged stands had LCP higher than 50%. In western Montana, the upper most strata had the highest LCP, whereas in central Oregon, the third strata (MA-3) had the highest LCP.

Table 3.1. Mean age, height, leaf area, live crown percentage (LCP), volume increment, and basal area for trees sampled for SLA analysis in even- and multi-aged stands in western Montana and central Oregon. The means were based on strata classes identified in each plot.

	Western Montana					Central Oregon				
	Even-aged	Multi-aged				Even-aged	Multi-aged			
Strata	EV-1	MA-1	MA-2	MA-3	MA-4	EV-1	MV-1	MV-2	MV-3	MV-4
Number of Tree	18	7	6	7	7	12	5	6	5	2
Mean Age	95	115	83	56	55	71	179	113	62	39
Mean Strata Height (m)	14	25	19	12	9	17	29	21	12	6
Mean LCP	40	67	58	55	55	56	68	68	72	60
Mean Leaf Area (m^2)	67.4	492.0	148.3	51.0	40.4	120.9	670.5	245.7	109.7	32.7
Mean Volume Increment (cm^3)	4463	29547	13862	3331	2836	10745	68759	25020	10254	2842
Mean Tree Basal Area (cm^2)	303	2348	716	218	179	638	3871	1305	561	189

3.4.2. Specific Leaf Area (SLA)

The mean SLA decreased with increasing crown third heights for both even- and multi-aged stands in western Montana and central Oregon (**Figure 3.1A&B**). The standard errors were approximately equal for all crown thirds. In both locations, the mean SLA for top, middle, and bottom crown thirds was significantly different in even-aged stands (ANOVA, $P < 0.01$).

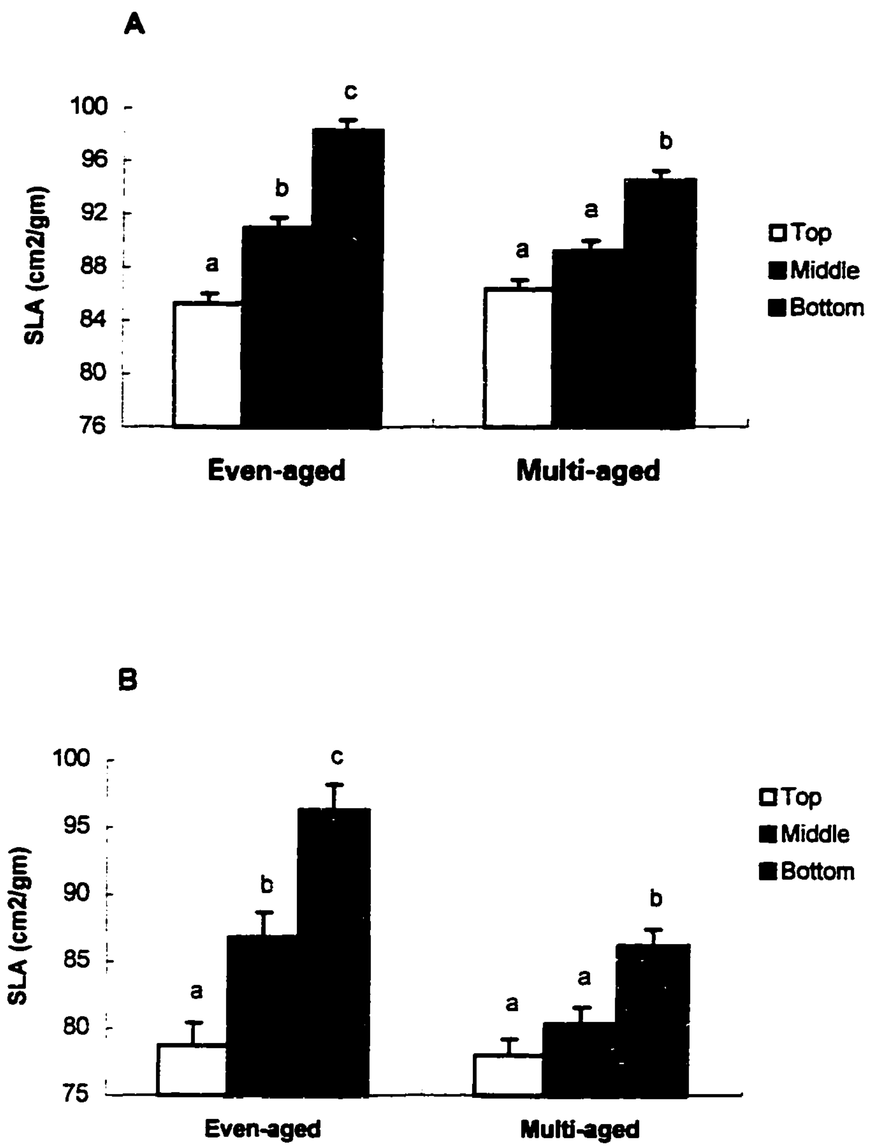


Figure 3.1. Distribution of mean SLA (cm^2/gm) within the crown thirds in even- and multi-aged ponderosa pine stands (A: western Montana, B: central Oregon). Error bars represent 1SE. Bars with same letter within each structure are not significantly different (P < 0.01).

Multiple comparisons of mean SLA for crown thirds failed to reject the null hypothesis that mean SLA varies more within the crown thirds of trees in even-aged stands due to differential radiation environments. In both locations, mean SLA in multi-aged stands was significantly different only between top and bottom thirds ($P < 0.005$) and between middle and bottom thirds ($P < 0.01$). The mean SLA for top and middle thirds was not significantly different ($P > 0.01$).

3.4.3. SLA Range

The range in mean SLA between top and bottom thirds in even-aged stands was 15 and 17 cm^2/gm in western Montana and central Oregon, respectively (**Table 3.2**). In multi-aged stands, the range was 10 and 9 for western Montana and central Oregon, respectively. The even-aged stands had a significantly larger range in mean SLA between top and bottom thirds than multi-aged stands in both study locations (t-tests; $P < 0.01$). The standard deviations were similar for each structure in both locations.

In western Montana, the mean SLA for top thirds in even-aged stands was slightly lower than multi-aged stands (**Figure 3.1**). But the middle and bottom thirds in even-aged had higher mean SLA than multi-aged stands. In central Oregon, multi-aged stands had lower SLA for all crown thirds than corresponding thirds in even-aged stands. The differences between corresponding thirds in even- and multi-aged stands were larger in central Oregon than in western Montana.

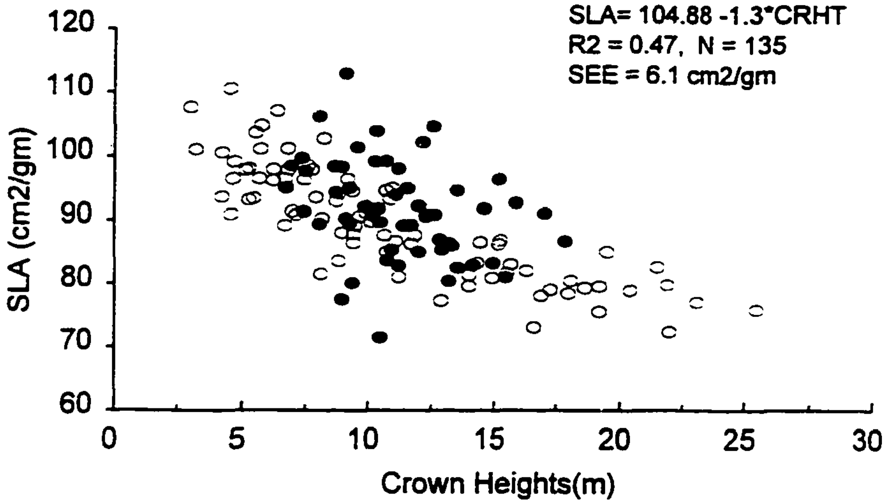
Table 3.2. Descriptive statistics for the range in mean SLA (cm^2/gm) from top to bottom thirds of trees in even- and multi-aged stands in western Montana and central Oregon. Means followed by different letters for each location were significantly different (t-tests, $\alpha = 0.05$).

	Western Montana		**Central Oregon**	
	Even-aged	Multi-aged	Even-aged	Multi-aged
No of trees	18	29	13	19
Minimum	3.6	1.3	3.2	0.1
Mean SLA	**15.0**^{a}	**9.5**^{a}	**17.3**^{b}	**8.9**^{b}
Maximum	30.4	21.3	26.7	18.7
SD	6.8	5.7	7.2	5.4

3.4.4. SLA and Crown Heights

A negative linear relationship was evident between the crown heights and mean SLA for all trees in both structures combined (**Figure 3.2A**). The overall model for western Montana had a better predictive power in terms of R^2 compared to that in central Oregon (**Figure 3.2B**). Regression models to predict mean SLA at different crown heights were more robust in multi-aged stands than even-aged structure in both locations (**Figure 3.3, 3.4**). The model for multi-aged structure in western Montana explained 72% of the variation in mean SLA using natural logarithm of crown heights (m), whereas in central Oregon an untransformed model explained 45% of the variation in SLA from crown heights. In both locations, the even-aged structure did not yield a good predictive model.

A



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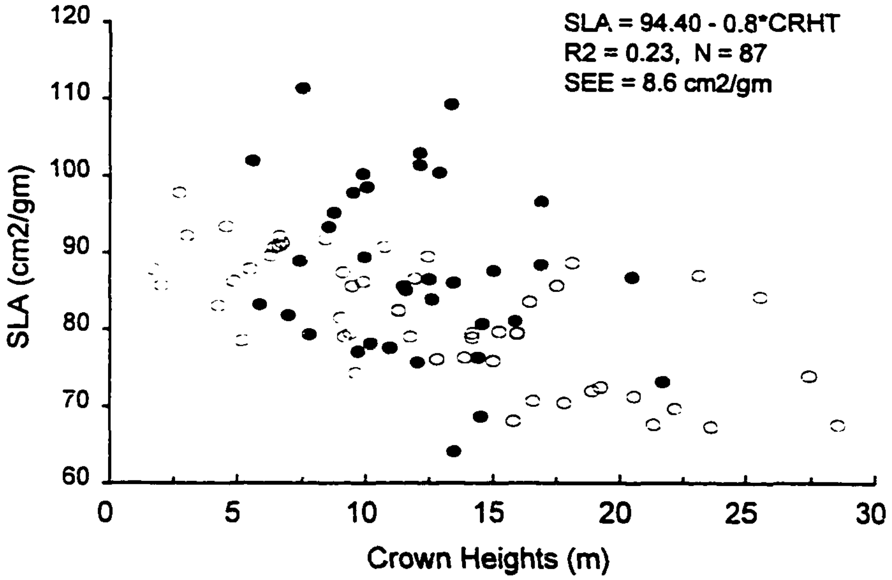


Figure 3.2. Relationship between crown heights and mean SLA for both even- and multi-aged stands. A: western Montana, B: central Oregon. ● Even-aged ○ Multi-aged.

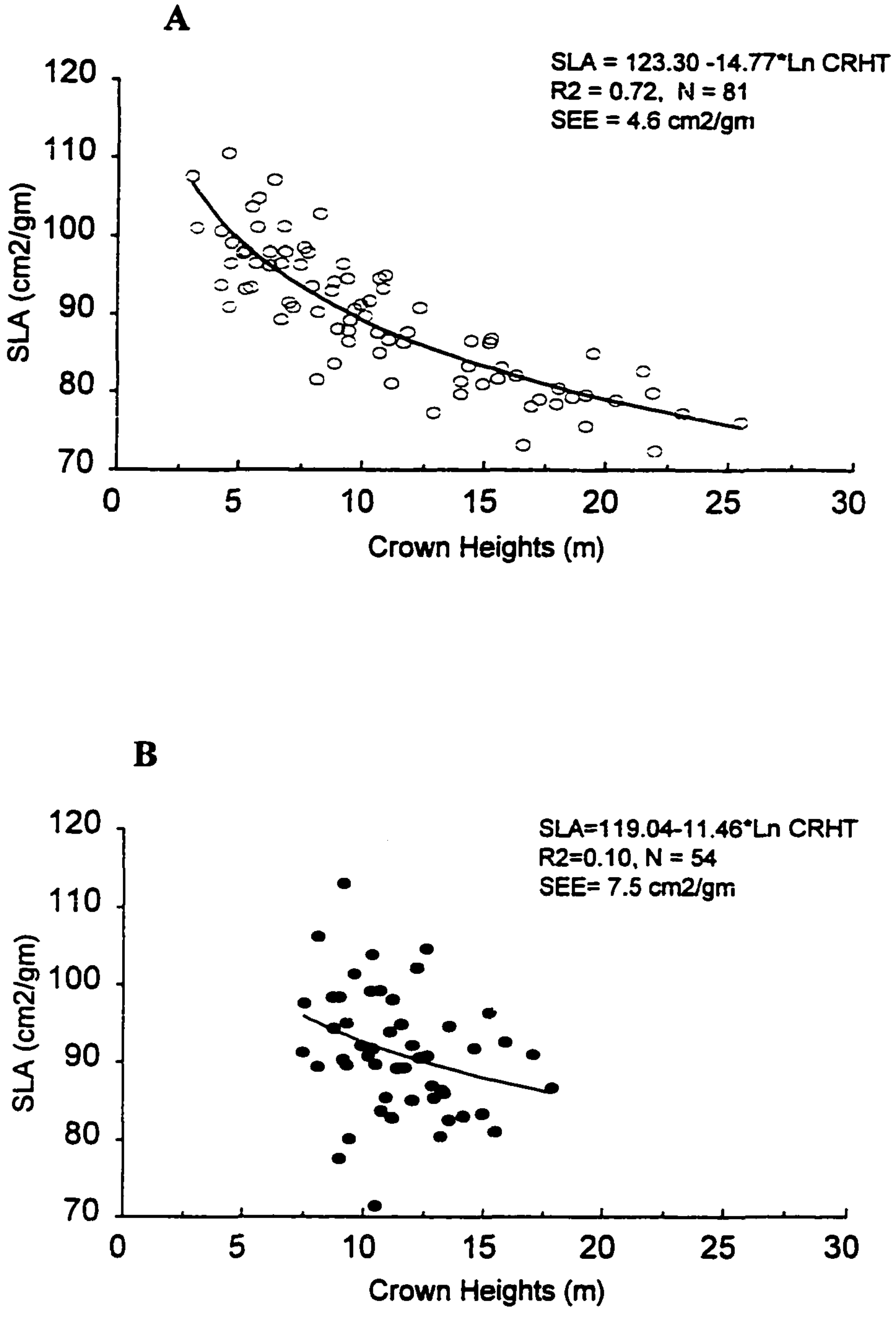
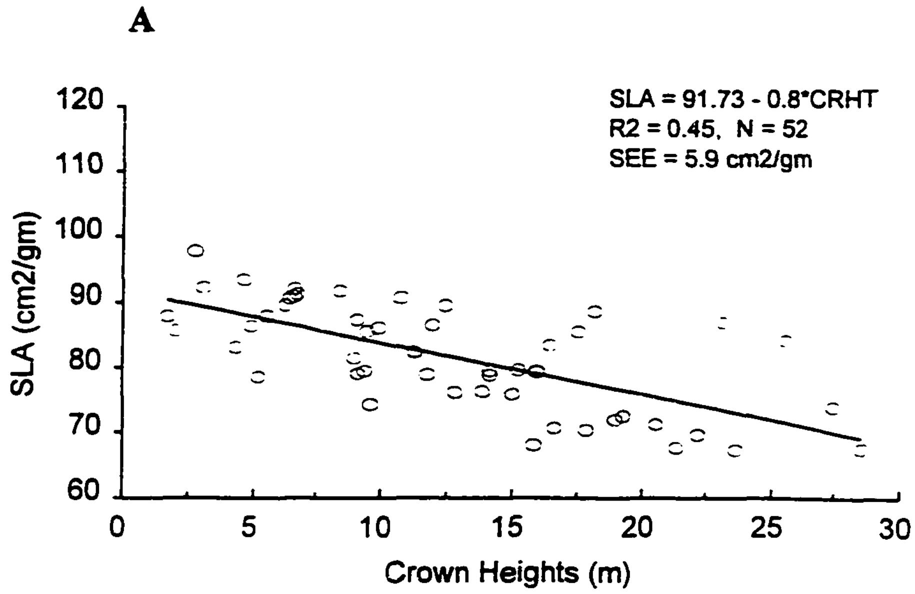


Figure 3.3. Relationship between crown height and mean SLA in western Montana (A: Multi-aged stands, B: Even-aged).



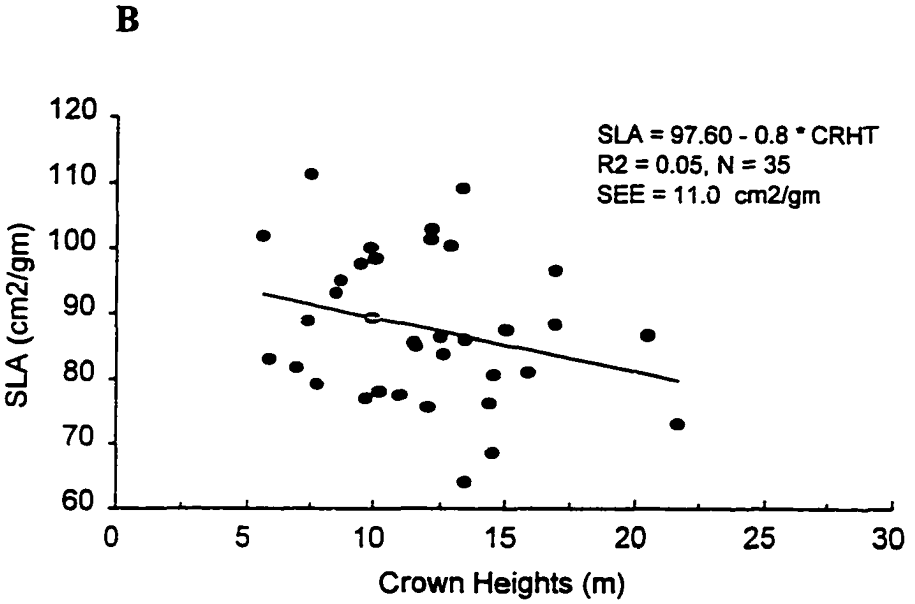


Figure 3.4. Relationship between crown height and mean SLA in central Oregon (A: Multi-aged, and B: Even-aged).

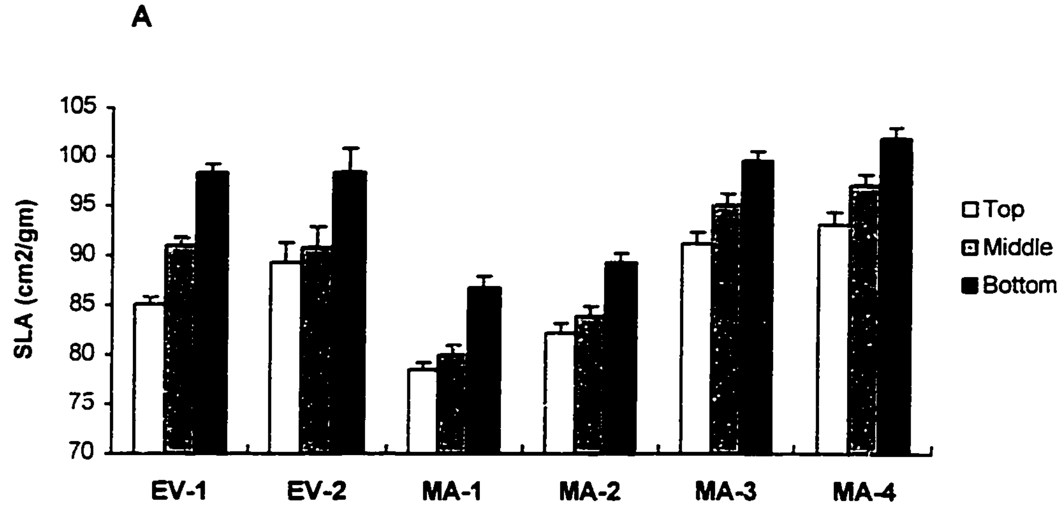
3.4.5. SLA and Crown Strata

The mean SLA distribution within crowns of various strata was compared without considering cohort class in both study locations (**Figure 3.5A & B**). The even-aged stands in western Montana had two canopy strata (EV-1, EV-2) based on their total height distribution, even though they belong to a single cohort class. Both strata had similar SLA for middle and bottom thirds (**Figure 3.5A**). However, for the top third, the upper stratum (EV-1) had low SLA compared to the lower strata (EV-2). The SLA for the top crown third in the lower stratum was very similar to the middle thirds in both strata of the even-aged stands. The bottom thirds in both strata had almost identical SLA.

The four canopy strata identified in the multi-aged stands in western Montana had a decreasing trend in SLA with increasing strata heights (**Figure 3.5A**). In both locations, the mean SLA for the top third in MA-1 and MA-2 were lower than the top third in the even-aged stands. However, in western Montana, the bottom third SLA in MA-3 and MA-4 was higher than the bottom third in even-aged stands. Relatively high standard error for the means in central Oregon was due to smaller sample size.

3.4.6. SLA and Needle Age

The SLA for different needle age groups was examined without considering variations in SLA due to crown positions. Most of the ponderosa pine trees retained up to three years needle whorls and sometimes four to five years on more productive sites.



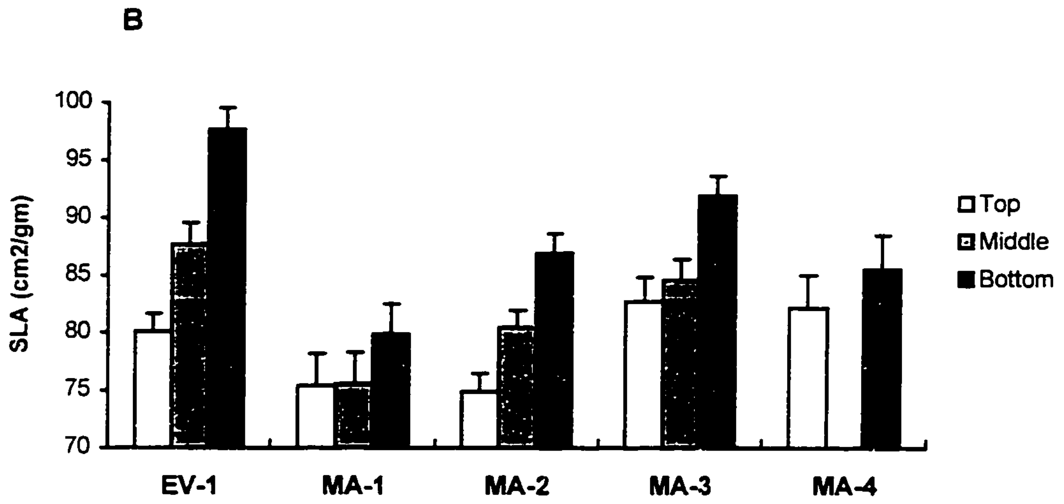


Figure 3.5. Distribution of mean SLA (cm^2/gm) within the crown thirds for different strata on even- and multi-aged ponderosa pine stands. A: western Montana, B: central Oregon. EV-1 and EV-2 are the upper and lower strata in even-aged stands. MA-1, MA-2, MA-3, and MA-4 represent four different strata levels from upper most to lowest in the multi-aged stands. Error bars represent 1SE.

Needle ages from one to three years were compared across all the sites in both structures. One-year-old needles had the highest SLA for even- and multi-aged stands in both locations (**Figure 3.6**). In western Montana, the lowest SLA was for two-year-old (Age 2) needles compared to other age groups. In central Oregon, the SLA decreased with an increase in needle age in both structures.

3.4.7. Canopy Extinction Coefficient 'k'

The mean canopy extinction coefficient k estimated using plot-level average method was significantly higher in even-aged stands compared to multi-aged stands (t-tests, P = 0.026). In central Oregon, the mean k was higher in even-aged stands using both methods (**Table 3.3**). When calculated for each measurement point, k was higher in both structures compared to plot-level average method. Generally, the mean k is higher in even-aged stands compared to multi-aged stands using both methods.

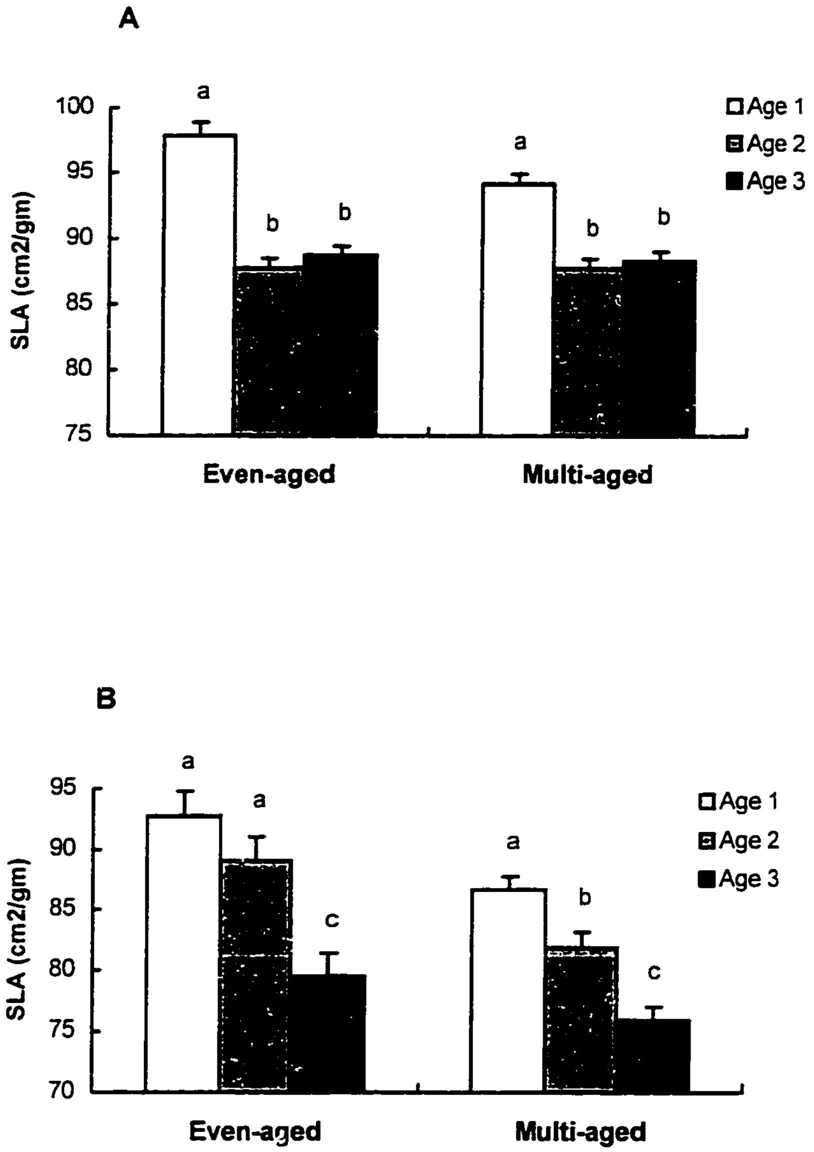


Figure 3.6. Distribution of mean SLA (cm^2/gm) within the needle age groups in even- and multi-aged ponderosa pine stands. A: western Montana, B: central Oregon. Error bars represent 1SE. Bars with same letters within each structure are not significantly different ($P < 0.01$).

3.4.8. PAR Ratio

The PAR ratio, (PAR beneath the canopy divided by "open" PAR) was significantly higher in multi-aged stands compared to even-aged stands in central Oregon (**Table 3.3**). In western Montana, the ratio was higher in multi-aged stands, but was not significant. When the mean ratio was compared between structures in both locations together, multi-aged stands had significantly higher PAR ratios (0.55) than even-aged (0.41) stands.

Table 3.3. Mean extinction coefficient (k) and mean PAR ratio calculated for even- and multi-aged stands in western Montana (MT) and central Oregon (OR). Different letters for structures within a location indicate significantly different means.

	Mean Extinction Coefficient (k)				**Mean PAR Ratio**	
	Point based		Plot level		Plot level	
	Even-aged	Multi-aged	Even-aged	Multi-aged	Even-aged	Multi-aged
MT	-0.53	-0.53	-0.43	-0.38	0.41	0.48
OR	-0.56	-0.51	-0.36^{a}	-0.31^{b}	0.41^{a}	0.61^{b}
All	-0.54	-0.52	-0.40^{a}	-0.34^{b}	0.41^{a}	0.55^{b}

3.4.9. Leaf Nitrogen

Mean leaf nitrogen content was the highest for top thirds, and the lowest for bottom thirds in even and multi-aged stands in both locations. Leaf nitrogen content was not significantly different between crown thirds in multi-aged stands in either study location (**Table 3.4**). However, it varied significantly between top and bottom thirds in

Table 3.4. Descriptive statistics for leaf nitrogen content for top, middle, and bottom crown thirds in even- and multi-aged stands in western Montana. Leaf nitrogen content was expressed in mols/m^2. Different letters within a structural group denote significantly different means (ANOVA; $P < 0.01$).

	Top		Middle		Bottom	
	Even-aged	Multi-aged	Even-aged	Multi-aged	Even-aged	Multi-aged
n	17	27	18	27	18	27
Min. N	65.0	56.1	63.3	60.5	62.4	61.0
Max. N	103.0	119.0	92.8	127.5	94.2	115.0
Mean N	89.4^{a}	**86.3**	84.0	**84.3**	79.6^{b}	**80.1**
SD	7.9	15.1	8.2	16.0	8.2	13.8

Table 3.5. Descriptive statistics for leaf nitrogen content for top, middle, and bottom crown thirds in even- and multi-aged stands in central Oregon. Leaf nitrogen was content expressed in mols/m^2. Different letters within a structural group denote significantly different means (ANOVA; $P < 0.05$).

	Top		Middle		Bottom	
	Even-aged	Multi-aged	Even-aged	Multi-aged	Even-aged	Multi-aged
n	12	18	9	18	12	18
Min. N	91.7	75.2	81.4	80.8	73.5	75.0
Max. N	107.2	116.1	95.8	125.2	97.0	124.2
Mean N	**99.6^{a}**	**96.8**	**89.6^{b}**	**96.8**	**81.8^{c}**	**90.7**
SD	5.9	13.0	3.7	12.7	6.8	14.8

even-aged stands in western Montana (ANOVA; $P < 0.01$). In central Oregon it decreased significantly from top to bottom thirds in the even-aged stands (ANOVA, $P < 0.05$). The mean leaf nitrogen content at the top crown third was higher in even-aged stands than multi-aged stands. The nitrogen content decreased about 11% between top and bottom in even-aged stands, whereas in multi-aged stands it decreased by 7%.

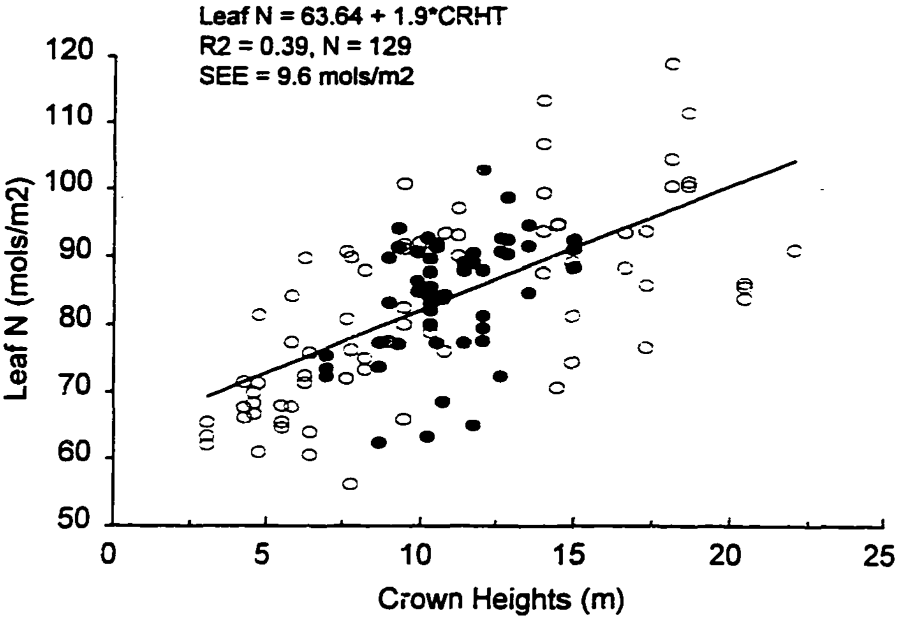
3.4.10. Leaf Nitrogen and Needle age

The mean leaf nitrogen content was higher for two-year-old needles (Age 2) in both even and multi-aged stands in western Montana (**Table 3.6**). Whereas three-year-old needles (Age 3) had the lowest amounts of nitrogen among all ages. In central Oregon, three-year-old needles from even-aged stands had the highest leaf nitrogen, whereas for multi-aged stands, leaf nitrogen content decreased as age increased (**Table 3.7**). However, in both locations, the means were not significantly different between the age groups (P = 0.05) in both structures, indicating that all ages had relatively similar leaf nitrogen content.

Table 3.6. Descriptive statistics for leaf nitrogen content for three needle age classes (Age 1, Age 2, and Age 3) in even- and multi-aged stands in western Montana. Leaf nitrogen content was expressed in mols/m^2. The means were not significantly different between age groups in both even- and multi-aged stands (ANOVA; P > 0.05).

	Age 1		Age 2		Age 3	
	Even-aged	Multi-aged	Even-aged	Multi-aged	Even-aged	Multi-aged
n	18	27	17	27	18	27
Min. N	72.3	62.0	75.4	63.3	62.4	56.1
Max. N	98.8	127.5	94.7	119.0	103.0	106.9
Mean N	**83.9**	**85.6**	**87.5**	**85.5**	**81.5**	**79.6**
SD	7.2	14.5	6.0	15.3	11.9	15.0

A



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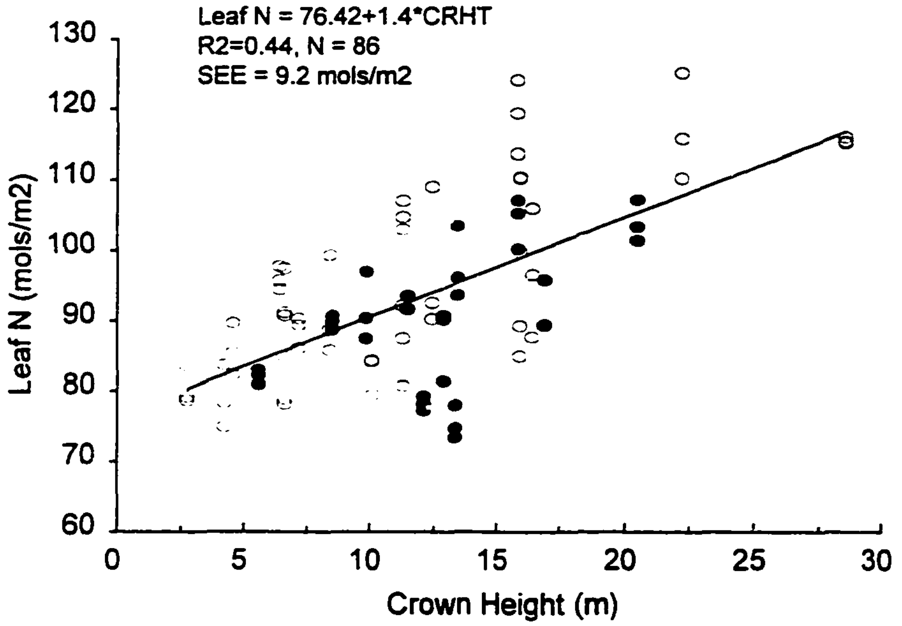


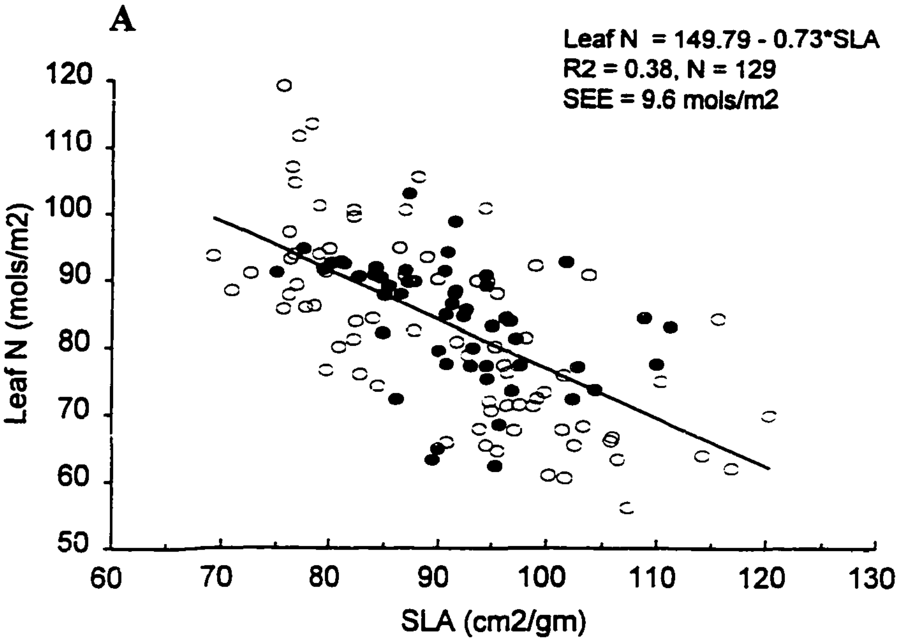
Figure 3.7. Relationship between crown height and leaf nitrogen content (area basis) for trees both in even- and multi-aged stands in A: western Montana, B: central Oregon.
● Even-aged ○ Multi-aged.

Table 3.7. Descriptive statistics for leaf nitrogen content for three needle age classes (Age 1, Age 2, and Age 3) in even- and multi-aged stands in central Oregon. Leaf nitrogen content was expressed in mols/m^2. The means were not significantly different between age groups in even- and multi-aged stands (ANOVA; P > 0.05).

	Age 1		Age 2		Age 3	
	Even-aged	Multi-aged	Even-aged	Multi-aged	Even-aged	Multi-aged
n	11	18	11	18	11	18
Min. N	73.5	75.0	77.3	78.5	74.8	75.2
Max. N	107.2	115.2	105.3	125.2	107.1	119.5
Mean N	**90.0**	**96.7**	**89.6**	**95.0**	**91.6**	**92.6**
SD	9.3	12.7	9.4	14.9	10.7	13.6

3.4.11. Leaf Nitrogen and Crown height

A positive linear relationship between crown height and leaf nitrogen content was evident from all trees in western Montana (**Figure 3.7A**) and central Oregon (**Figure 3.7B**). The simple linear regression model to predict leaf nitrogen content at various crown heights in western Montana was similar ($R^2 = 0.39$, SEE = 9.6) to central Oregon ($R^2 = 0.44$, SEE = 9.2) in terms of R^2 and SEE. The predictive power of the overall models in terms of R^2 was lower due to poor correlation between crown heights and leaf nitrogen, in even-aged stands than in multi-aged stands. Separate models for multi-aged stands to predict leaf nitrogen content from SLA had higher predictive power than overall models in both locations. For western Montana and central Oregon the R^2 and SEE for the multi-aged stands were 0.44, 10.6 and 0.56, 8.9, respectively.



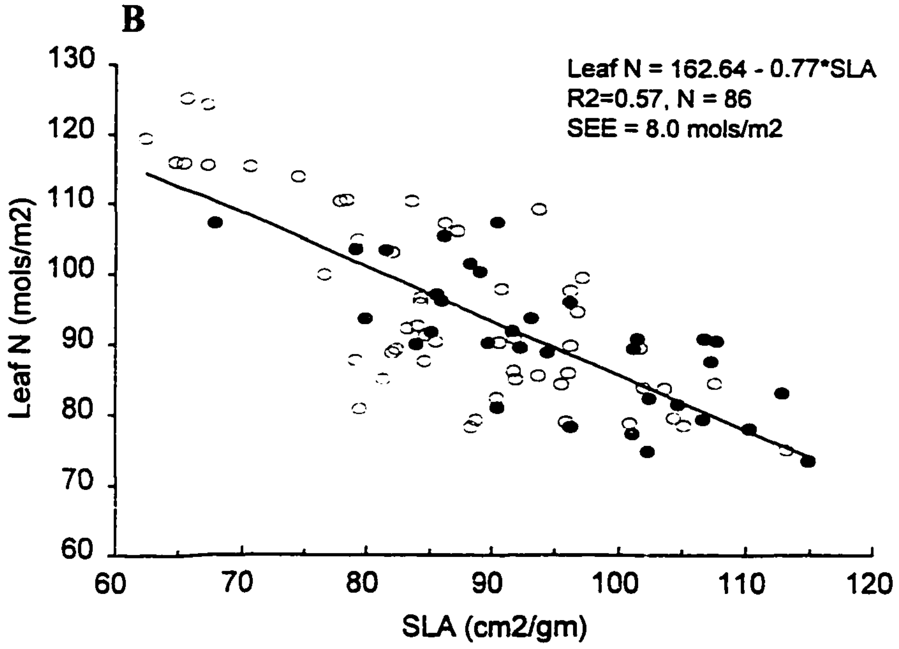


Figure 3.8. Relationship between SLA and leaf nitrogen content (area basis) for trees in both even- and multi-aged stands in A: western Montana, B: central Oregon. ● Even-aged ○ Multi-aged.

3.4.12. Leaf Nitrogen and SLA

A negative linear relationship was observed between SLA and leaf nitrogen (area basis) for all trees under both structures. Simple linear regression model had lower predictive power (R^2= 0.38, SEE = 9.6) in western Montana (**Figure 3.8A**) than in central Oregon (R^2 = 0.57, SEE = 8.0; **Figure 3.8B**). A separate model for multi-aged stands had higher R^2 compared to the overall models in both locations (western Montana: R^2 = 0.46, SEE = 10.4 and central Oregon R^2 = 0.58, SEE = 8.7). Poor relationship between SLA and leaf nitrogen content resulted in low coefficient of determination (R^2) for even-aged stands.

The stepwise procedure to develop multiple regression models to predict leaf nitrogen from SLA, crown height, stand structure, total stand height, live crown height, crown sections, and leaf age, identified SLA and leaf age as the independent variables in western Montana (**Table 3.8**). In central Oregon, models with independent variables like SLA, leaf age, crown length (m), and total height (m) resulted in the best predictive model for all structures as well as for individual structures.

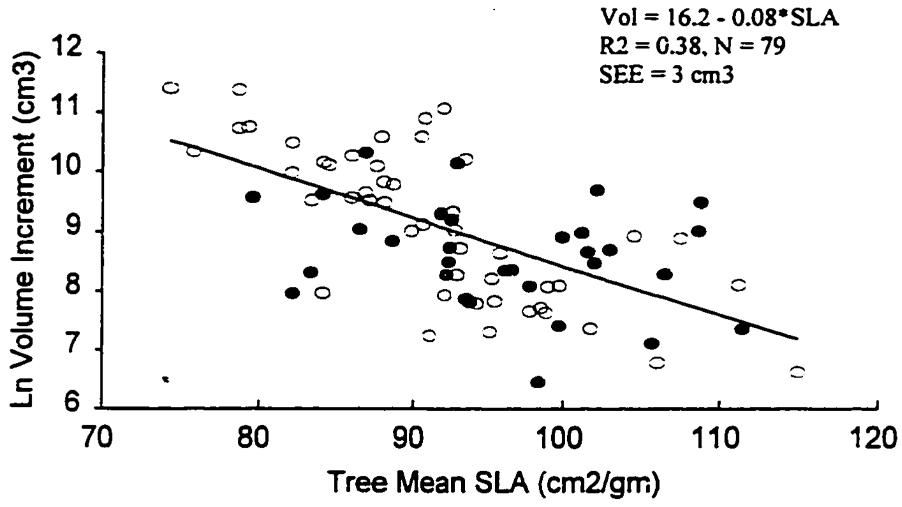


Figure 3.9. Relationship between mean tree SLA and annual volume increment (cm^3) for all trees in even and multi-aged stands in western Montana and central Oregon. ● Even-aged ○ Multi-aged.

Table 3.8. Multiple regression models for predicting leaf nitrogen content (mols/m^2) from different independent variables for even-, multi-aged, and for all structures. MT = western Montana, OR = central Oregon, ALL = both structures combined MA = multi-aged, EA = even-aged, CLM = crown length (m), THM = total height (m).

Location	ST	N(mols/m^2) =	R^2	SEE	n
MT	ALL	173.20-5.46*AGE-0.87*SLA	0.50	8.6	129
MT	MA	175.53-5.61*AGE-0.90*SLA	0.55	9.5	76
MT	EA	162.67-4.82*AGE-0.75*SLA	0.32	7.3	53
OR	ALL	188.87-6.55*AGE-0.93*SLA-1.5*CLM+1.0*THM	0.72	6.5	87
OR	MA	170.53-5.83*AGE-0.75*SLA-2.8*CLM+2.0*THM	0.71	7.3	54
OR	EA	220.25-6.14*AGE-0.92*SLA-6.7*CLM+1.9*THM	0.81	4.2	33

3.4.13. SLA and Volume Increment

A linear negative relationship between annual volume increment and mean tree SLA was observed for all trees (**Figure 3.9**) in both locations. The relationship was stronger in multi-aged stands (**Figure 3.10**). For all trees, the model predicted 38% of the variation in volume increment (transformed to natural logarithm) from their mean tree SLA (R^2 = 38%, SEE = 3 cm^3). In multi-aged stands, the model had relatively a higher predictive power (R^2 = 53%, SEE = 2 cm^3) than even-aged stands. The lower R^2 of the overall model was due to poor relationship between SLA and volume increment in even-aged stands.

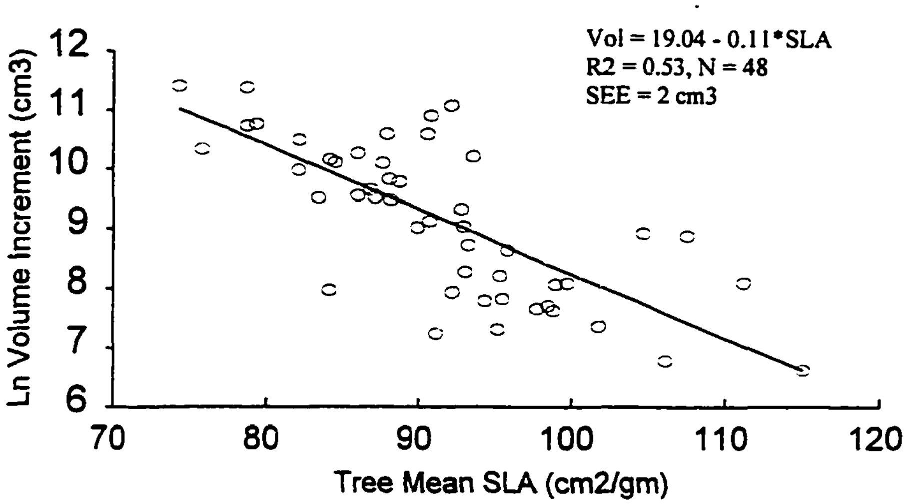


Figure 3.10. Relationship between mean tree SLA and tree annual volume increment (cm^3) for multi-aged stands in western Montana and central Oregon.

3.5. DISCUSSION

The lowest SLA for top crown thirds in both even- and multi-aged stands is due to higher interception of unlimited solar radiation compared to other part of the crown. Increasing SLA as crown height decreases (from top to bottom crown thirds) indicates that the incident radiation at the top of the canopy gets attenuated while passing down through the canopy layers. Comparatively lower radiation at bottom thirds resulted in higher SLA than top thirds in both structures. Hager and Sterba (1985) also reported variations in SLA within a crown at various heights due to different expositions to light in the canopy. Ellsworth and Reich (1993) reported that LMA (Leaf Mass Area), which is the opposite of SLA, decreased continuously by over twofold from upper to lower canopies in closed deciduous forests of sugar maple (*Acer saccharum*) in southwestern Wisconsin, USA. They also reported that light attenuation in the forest occurred primarily in the upper and middle portions of the canopy. This explains the highest SLA for bottom crown thirds in even- and multi-aged stands. In multi-aged stands, because of higher live crown ratios, the trees carry longer live-crowns compared to the even-aged stands. The mean SLA for the bottom third in multi-aged stands was lower than even-aged stands in both locations despite shorter live crowns in even-aged stands. This could be due to relatively similar radiation loads even at the bottom thirds of the crowns in multi-aged stands. This is also supported by higher PAR ratios at breast height in the multi-aged compared to the even-aged stands. The lower canopy extinction coefficient in multi-aged stands also confirms these findings, indicating higher light environments beneath the live crowns in multi-aged stands. This could be due to: 1) The multi-aged stands have relatively lower LAI; and 2) Lower stand density in terms of stems per ha resulted in larger canopy gaps. Generally, the crown thirds in multi-aged stands were larger compared to even-aged stands. The similarity between the top and middle third SLA indicated that the trees were not mutually shaded even at their mid-crown positions. Comparatively lower PAR ratios in even-aged stands is due to canopy structure and LAI distribution within a canopy.

In western Montana, the mean SLA for crown thirds in both even- and multi-aged structures was comparatively higher than in central Oregon due to differences in climate and soil between the study regions. Compared to western Montana, 50 % of the sampled trees in central Oregon were on relatively less arid sites (aridity index < 0.20). It has been reported that higher soil moisture availability increases leaf thickness, resulting in lower SLA (Pierce and Running 1994; Jose and Gillespie 1996).

Trees with shorter crown lengths are assumed to have less variation in SLA between top and bottom crown thirds. But a larger range in SLA between the top and the bottom thirds in even-aged stands compared to multi-aged stands indicates significantly lower light environments at the bottom thirds. This could be due to increased mutual shading in the canopy in the even-aged structures. A larger range in SLA despite shorter live crown ratios in even-aged stands also indicates higher competition for available light and moisture compared to multi-aged structures. Increased competition for these growth factors resulted in thinner leaves.

In western Montana, the mean SLA for top thirds was slightly lower in even-aged stands than in multi-aged stands, indicating maximum light interception at the top layers of the even-aged canopy. The continuous canopy layer from crowns of similar height trees may function like a uniform (spongy) leaf surface, and the percentage of light absorbed might be relatively higher compared to the discontinuous canopies in multi-aged stands. Generally, most of the direct incident radiation gets absorbed by the continuous canopy, and some gets reflected back due to differences in needle morphology and orientation (Jones 1992). Due to less vertical stratification of crowns, the trees might mutually shade at the middle and bottom thirds of the crowns in even-aged structures, resulting in thinner leaves (higher SLA). The multi-aged stands characterized by wider distribution of crowns in the vertical dimension, and larger canopy gaps might result in higher irradiance across the crowns compared to even-aged structures. This could also be the reason for comparatively lower SLA for bottom thirds in multi-aged than in even-aged stands.

The linear negative relationship between mean SLA and crown height may exist only in stands where trees are competing for available light. In open grown stands, due to unlimited radiation environments, the relationship may not be as strong as in closed stands. The poor relationship between mean tree SLA and crown heights in even-aged stands may be attributed to continuous canopy layers in even-aged structures, considerably reducing the available light beneath the top layer. A large variation in SLA in even-aged stands at similar crown heights could also result in poor predictive relationship.

The strata level comparison also indicates that generally, the upper strata tend to have the lowest crown SLA, and the bottom strata the highest. In multi-aged stands, a higher mean SLA for trees in the lower canopy strata (MA-3 and MA-4) compared to those from upper strata also indicates lower production potentials. The lower growth efficiency (production potential) for the trees in the lower canopy strata also supports the findings by O'Hara (1996) that the youngest cohorts are the least efficient in single species multi-cohort stands.

The lowest SLA for Age 2 needles in western Montana indicates that two-year-old needles in ponderosa pine are physiologically more productive (photosynthetically efficient) compared to other needle age groups. A comparative study on the effect of needle age on photosynthesis in ponderosa pine by Helms (1970) found that two-year-old needles was more photosynthetically efficient than current, three-year-old or four-year-old needles. The lowest SLA in central Oregon was for three-year-old needles (Age 3), which may be due to differences in climate and soil conditions compared to western Montana. In comparatively drier climates of western Montana, ponderosa pine trees tend to retain a lower number of leaf whorls (ages) than in central Oregon. Multi-aged structures had higher LCP in both study locations. Higher tree leaf area (due to higher LCP) in multi-aged stands could also result in a higher number of two-year-old needles per tree. This could also contribute to higher photosynthesis in multi-aged stands compared to even-aged stands. In even-aged stands, due to closed canopies and relatively shorter crown lengths, the trees may be competing more for incident radiation. Whereas in multi-aged stands the competition for available light at various crown positions may be lower due to longer crowns and higher vertical arrangements of foliage. This illustrates that three dimensional structural variation in even and multi-aged stands are important determinants of distribution of SLA within tree crowns. Therefore, the distribution and the range in mean tree SLA could be used as a strong variable to predict the production potentials of crowns in different stand structures.

A higher level of leaf nitrogen content at the top crown third also indicates higher production potentials, because leaf nitrogen content is a strong correlate of photosynthetic capacity in C_3 plants (Field and Mooney 1986; Evans 1989). The leaf nitrogen content influences the availability of N-based enzymes in photosynthetic activities in leaves. The general trend in decreasing leaf nitrogen (area basis) from top to bottom thirds was similar to that in SLA. These results are very similar to those reported by Ellsworth and Reich (1993), and Hollinger (1989). A smaller range in leaf nitrogen content between top and bottom crown thirds in multi-aged trees also indicates a similar production efficiency for all thirds of a crown. Compared to multi-aged stands, trees in even-aged stands might be translocating maximum leaf nitrogen to the top thirds to maximize net photosynthesis. Presence of higher radiation loads and leaf nitrogen contents might increase the photosynthesis in the top third of crowns compared to other thirds in even-aged stands. This is also supported by lower SLAs for top thirds in even-aged stands. Higher leaf nitrogen content as well as lower SLAs for two-year-old needles in western Montana suggests that two-year-old needles are the most productive needle age group.

Leaf nitrogen content and crown heights were more related in multi-aged stands than in even-aged. The negative linear relationship between SLA and leaf nitrogen content (area based) indicates higher leaf nitrogen for lower SLA. This relationship was not very strong in even-aged stands, where SLA varied significantly from top to bottom thirds. Multi-aged stands characterized by lower SLAs and higher leaf nitrogen contents could have higher tree level photosynthetic capacity compared to even-aged stands. Ellsworth and Reich (1993) also reported a positive linear relationship between LMA and leaf nitrogen contents. The poor relationship between SLA and leaf nitrogen in even-aged stands indicates that a change in SLA (due to difference in light availability) may not be proportionally affecting the leaf nitrogen content in the middle and bottom crown thirds. A moderate relationship between SLA and volume increments for trees from all structures indicate that the variations in volume increments may not be exclusively predicted from a change in mean tree SLA due to the poor relationship between SLA and volume increments in even-aged stands. However, a stronger relationship between these variables in multi-aged stands suggests that the volume increments can be better predicted in multi-aged stands than in even-aged stands due to lower variations in tree mean SLA.

3.6. CONCLUSIONS

The results of the study suggest that the distribution of specific leaf area and leaf nitrogen content within a tree crown is closely related to the canopy light environments. LAI and stand structure are two major factors governing light distribution inside a canopy. Trees in multi-aged stand structures have lower SLA at the top, middle, and bottom crown thirds due to similar radiation environments. In even-aged stand structure, the SLA for crown thirds tends to differ significantly due to high variability in canopy light levels. Higher vertical stratification of live crowns and a relatively low stand LAI, in multi-aged stands increases the PAR beneath the canopy. Unlimited availability of soil moisture and nutrients in stands with structures which permit more uniform light levels could result in higher leaf and tree productivity. Significantly lower SLA and higher leaf nitrogen content in two-year-old needles in ponderosa pine indicates that they are more productive compared to other needle age groups. Therefore, stand structures with higher proportion of two-year-old needles could also result in higher tree and stand productivity. The closed canopies of even-aged stands are characterized by trees with comparatively shorter live crowns due to higher competition for incident radiation than in multi-aged stands. Whereas higher vertical stratifications in multi-aged structures provide increased light availability and higher production potentials, indicated by low SLAs.

Higher photosynthetic efficiency reported in needles with low SLA suggests that SLA could be used an index for foliage production efficiency. Higher foliage and tree-level production efficiencies indicated by low SLA is not necessarily an age factor, rather an age related structure. By manipulating the crown structures for higher light interception at different canopy layers, the gross primary production (amount of photosynthate produced) per unit leaf area can be increased in stands with different structures.

Literature Cited

Borghetti, M., Vendramin, G. G., and Giannini, R. 1986. Specific leaf area and leaf area index distribution in a young Douglas fir plantation. Can. J. For. Res. 16: 1283-1288.

Campbell, G. S. 1977. An Introduction to Environmental Biophysics. Springer-Verlag, New York.

Campbell, G. S., and Norman, J. M. 1989. The description and measurement of canopy structure. *In* Plant canopies: their growth-form and function. Cambridge University Press, Cambridge. pp 1-20.

Cannell, M. G. R., Milne, R., Sheppard, L. J. and Unsworth, M .H. 1987. Radiation interception and productivity of willow. J. Appl. Ecol. 24: 1261-1313.

Ducrey, M. 1994. Influence of shade on photosynthetic gas exchange of 7 tropical rain forest species from Guadeloupe (French West Indies). Annales des Sciences Forestieres 51: 77-94.

Ellsworth, D. S., and Reich, P. B. 1993. Canopy structure and vertical pattern of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96: 169-178.

Evans, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants, Ecology 78: 9-19.

Farnsworth, E. J., and Ellison, A. M. 1996. Sun-shade adaptability of the red mangrove, *Rhizophora mangle* (Rhisophoraceae): changes through ontogeny at several levels of biological organization. Am. J. Bot. 83: 1131-1143.

Field, C. B., and Mooney, H. A. 1986. The photosynthesis-nitrogen relationships in wild plants. *In* On the Economy of Plant Form and Function. *Edited by* T. J. Givinish. Cambridge University Press, Cambridge. pp. 25-55.

Fitter, A. H., and Hay, R. K. 1987. Environmental physiology of plants. 2nd edition. Academic Press.

Franklin, J. F., and Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8-417.

Gholz, H. L., Vogel, S. A., Cropper, W. P. Jr., McKelvey, K., Ewel, K.C., Teskkey, R.O. and Curran, P. J. 1991. Dynamics of canopy structure and light interception in *Pinus elliottii* stands, north Florida. Ecol. Monogr. 61: 33-51.

Gilmore, D. W., Seymour, R. S., Halteman, W. A., Greenwood, M. S. 1995. Canopy dynamics and the morphological development of *Abies balsamea*: effects of foliage age on specific leaf area and secondary vascular development. Tree Physiol. 15: 47-55.

Grace, J. C., Rook, D. A., and Lane, P. M. 1987. Modeling canopy photosynthesis in *Pinus radiata* stands. New Zealand journal of Forestry Science. 17: 210-228.

Gratani, L. 1996. Leaf and shoot growth dynamics of *Quercus ilex* L. *Acta-* Oecologia. 17: 17-27.

Groninger, J. W., Seiler, J. R., Peterson, J. A., and Kreh, R.E. 1996. Growth and photosynthetic response of four Virginia Piedmont tree species to shade. Tree Physiol. 16: 773-778.

Gutschick, V. P., and Wiegel, F. W. 1988. Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. Am. Nat. 132: 67-86.

Hager, H., and Sterba, H. 1985. Specific leaf area and needle weight of Norway spruce (*Picea abies*) in stands of different densities. Can. J. For. Res. 15: 389-392.

Hees AFM van, Bartelink, H. H., and Van Hees AFM. 1993. Needle area relationships of Scots pine in the Netherlands. For. Ecol. Manage. 58: 19-31.

Hollinger, D. Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. Functional Ecology 3: 53-62.

Helms, J. A. 1970. Summer net photosynthesis of ponderosa pine in its natural environment. Photosynthetica 4: 243-253.

Hopkins, W. E. 1979a. Plant associations of the Fremont National Forest. USDA For. Serv. Pac. Northwest Reg. R6-Ecol-79-004.

Hopkins, W. E. 1979b. Plant associations of the south Chiloquin and Klamath Ranger Districts-Winema National Forests. USDA For. Serv. Pac. Northwest Reg. R6-Ecol-79-005.

Janacek, A., G. Benderoth, Ludeke, M. B. K., and Kinderman, J. 1989. Model of the seasonal and perennial carbon dynamics in deciduous-type forests controlled by climatic variables. Ecological Modelling 49: 101-124.

Jarvis, P. G., and Leverenz, J. W. 1983. Productivity of temperate, deciduous and evergreen forests. *In* Encyclopedia of plant physiology. *Edited by* O. L. Lange, P.S. Nobel, C. B. Osmond, and H. Ziegler. Springer-Verlag. Berlin Heidelberg New York, New Series, vol 12D. pp. 233-280.

Johnson, J. D. 1984. A rapid technique for estimating total surface area of pine needles. For. Sci. 30: 913-921.

Jones, H. G. 1992. Plants and microclimate-A quantitative approach to environmental plant physiology. Second edition, Cambridge University Press, New York.

Jose, S. and Gillespie, A. R. 1997. Leaf area-productivity relationships among mixed-species hardwood forest communities of the Central Hardwood Region. For. Sci. 43: 56-64.

Klinka, K., Wang, Q., Kayahara, G. J., Carter, R. E., and Blackwell, B.A. 1992. Light-growth response relationships in Pacific silver fir (*Abies amalbilis*) and subalpine fir (*Abies lasiocarpa*). Can. J. Bot. 70: 1919-1930.

Larsen, J. B., and Buch, T. 1995. The influence of light, lime, and NPK-fertilizer on leaf morphology and early growth of different beech provenances (*Fagus sylvatica* L.). Forest and Landscape Research 1: 227-240.

McIntyre, B. M., School, M. A., and Sigmon, J. T., 1990. A quantitative description of a deciduous forest canopy using a photographic technique. For. Ecol. Manage. 7: 191-206.

Midgley, J. J., Wyk.-GR-van, Everard, D.A., and Van-Wk.-GR. 1995. Leaf attributes of South African forest species. African Journal of Ecology 33: 160-168.

Mooney, H. A., Ferrar, P. J. and Slayter, R. O. 1978. Photosynthetic capacity and carbon allocation patterns in diverse forms of Eucalyptus. Oecologia 36: 103-111.

Nobel, P. S., and Hartsock, T. L. 1981. Development of leaf thickness for *Plectranthus parviflorus*-Influence of photosynthetically active radiation. Physiol. Plant. 51: 163-166.

Norman, J. M., and Campbell, G. S. 1989. Canopy structure. *In* Plant physiological ecology: Field methods and Instrumentation. Chapman and Hall, New York. pp. 301-325.

Nygren, M., and Kellomaki S. 1983. Effect of shading on leaf structure and photosynthesis in young birches, *Betula pendula* Roth. and *B. Pubescens* Ehrh. For. Ecol. Manage. 7: 119-132.

O'Hara, K. L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can. J. For. Res. 18: 859-866.

O'Hara, K. L., and Valappil, N. I. 1995. Sapwood-leaf area prediction equations for multi-aged ponderosa pine stands in western Montana and central Oregon. Can. J. For. Res. 25: 1553-1557.

O'Hara, K. L. 1996. Dynamics and stocking-level relationship of multi-aged ponderosa pine stands. For. Sci. 42: Monograph 33.

Oliver, C. D., and Larson, B. C. 1996. Forest stand dynamics, update edition. Wiley, New York.

Oker-Blom, P., and Kellomaki, S. 1983. Effect of grouping of foliage on the within-stand and within-crown light regime: comparison of random and grouping canopy models. Agric. For. Meteorol. 28: 143-155.

Pereira, J. S., M. M. Chaves, F. Fonseca, M. C. Arau'jo and F. Torres. 1992. Photosynthetic capacity of leaves of *Eucalyptus globulus* (Labill.) growing in the field with different nutrient and water supplies. Tree Physiology. 11: 381-389.

Pfister, R. D., Kovalchik, B. L., Arno, S. F., and Presby, R. C. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34.

Pierce, L. L., and Running, S. W. 1994. Regional-scale relationship of leaf area index to specific leaf area and leaf nitrogen content. Ecol. Appl. 4:313-321.

Reich, P. B., Kloeppel, B. D., Ellsworth, D. S., and Walters, M. B. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia. 104: 24-30.

Ross, J. 1981. The radiation regime and architecture of plant stands. The Hauge.

Sampson, D. A., and Smith, F. W. 1993. Influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta* va. Latifolia) forests. Agric. For. Meteorol. 64: 63-79.

Shelton, M. G., and Switzer, G. L. 1984. Variation in the surface area relationships of loblolly pine fascicles. For. Sci. 30: 355-363.

Smith, D. M. 1986. The Practice of Silviculture. 8th ed. John Wiley & Sons, Inc., New York.

Smith, F. W., Sampson, D. A., and Long, J. N. 1991. Comparison of leaf area index estimates from tree allometric and measured light interception. For. Sci. 37: 1682-1688.

Volland, L. A. 1988. Plant associations of the central Oregon pumice zone. USDA For. Serv. Pac. Northwest Reg. R6-ECOL-104-1985.

Waring, R. H., and Schlesinger, W. H. 1985. Forest Ecosystems: Concepts and Management. Academic Press, New York.

Wang, J. R., Simard, S. W., and Kimmins, J. P. 1995. Physiological responses of paper birch to thinning in British Columbia. For. Ecol. Manage. 73: 177-184.

Chapter 4

Water Stress and Carbon Isotope Discrimination in Even- and Multi-aged Ponderosa pine Stand Structures

ABSTRACT

Plant water status is one of the major factors controlling leaf level gas exchange in conifers. Moisture limitation could result in significantly lower leaf, tree, and stand productivity. The influence of stand structure on leaf-water potential was examined on ponderosa pine trees growing in the even- and multi-aged structures. Pre-dawn leaf water potential was measured on a few selected trees under both structures using the pressure chamber technique during the growing season of 1995 and 1996. Long-term water-use efficiency of the needles was estimated from the stable carbon isotope discrimination analysis. The even-aged stands were under relatively higher water stress than the adjacent multi-aged stands during the earlier part of the growing season. Whereas during the later part, the water stress in the even-aged stands was significantly higher compared to the multi-aged stands ($P < 0.05$). Trees from the even-aged stand structures discriminate significantly less compared to those from the multi-aged structures. The top thirds of the crown in the even-aged stands (17.58 ‰) had the lowest discrimination, suggesting the top portions of crowns were more water-use efficient. Comparatively higher water stress in the even-aged stands due to higher leaf area indices might induce a selective pressure for high water-use efficient crowns in the even-aged stands than the adjacent multi-aged stands. Prolonged periods of water stress, lower than -1.6 MPa during the growing season could result in low tree and stand productivity in the even-aged structures despite its higher water-use efficiency. Despite the difference in stocking level, diverse crown arrangement and structure-related ecophysiolgical advantages could also be a possible reason for lower water stress in the multi-aged stands compared to the even-aged stands growing on similar site conditions.

Keywords: ponderosa pine, pre-dawn leaf water potential, carbon isotope discrimination, water-use efficiency, stand structure, leaf area index.

4. 1. INTRODUCTION

Ponderosa pine (*Pinus ponderosa*) has been considered a drought resistant species due to its ability to grow in drier climates. The drought resistance is partly attributed to its desiccation resistance and partly from water retention (Bassman 1988). Ponderosa pine stores considerable amounts of water in both heartwood and sapwood (Parker 1954). The presence of similar amounts of water in heartwood and sapwood in ponderosa pine gives an advantage in water storage compared to many other gymnosperms (Parker 1969. Stewart 1967). Loupshinsky (1975) reported that the stomates of ponderosa pine close completely in the dark compared to other western conifers like Douglas-fir. which remained open and transpiring about 26% to 42% of day time values. The maximum leaf conductance reported in ponderosa pine was 0.32 cm s^{-1} (Korner et al. 1979). and showed no difference between needle age classes (Running 1976).

The water potential decreases by late summer in many ponderosa pine habitat types in the northern Rocky Mountains due to longer periods with fewer summer precipitations. During the periods of high water stress, stand density and structure become an important factor affecting photosynthesis and productivity. Donner and Running (1986) reported significantly higher leaf water potential in the thinned lodgepole pine stands than in the unthinned controls in Montana. The ecosystem simulation model. DAYTRANS/PSN produced 21% greater seasonal photosynthesis due to higher plant water potential and additional solar radiation available in the thinned stands. In another study in ponderosa pine in the Black Hills of South Dakota, Schmid et al. (1991) reported no significant differences in water potential among different levels of stand density.

During late summer in northwestern Montana, Petersen and Maxwell (1987) found decreasing soil water content in relation to the total foliage of herbs and shrubs in the ponderosa pine stands. Pothier and Margolis (1990) reported higher pre-dawn water potentials in the thinned stands of balsam fir and paper birch than the unthinned controls. Many thinning studies have reported higher water potential in thinned stands due to reduced leaf area and increased canopy interception for snow and rainfall than unthinned controls (Donner and Running 1986).

Generally, even-aged stands are maintained to fully occupy the site potential growing space, whereas the merchantable portions of uneven-aged stands are maintained at less than full occupancy for regeneration (Baker et al. 1996). This could sometimes result in comparatively higher tree density in even-aged stands than multi-aged stands. Most of the natural even-aged stands sampled in western Montana and central Oregon were developed on multi-aged stands after past selection cuttings. The stands established after a major disturbance regime support many small to medium size even-aged trees. Whether from higher stand density or from full site occupancy by fewer trees, the even-aged stands may experience higher water stress relatively earlier in the growing season than the multi-aged stands, especially in water-limited environments of the northern Rockies. Comparatively less stratification of crowns in even-aged stands could result in higher competition for many of the site resources like: light, water, and nutrients than in multi-aged stands. The difference in the arrangement of tree crowns in even-aged and multi-aged stand structures could modify the micro-environments inside the canopies, which could also result in different canopy moisture demands and gas exchange rates.

Ponderosa pine has been well studied in terms of many physiological attributes relating to its drought resistance (Bassman 1988). Most of the studies were focused at tree-level physiology, growth, and establishments. Influence of stand structure on various physiological attributes has not been studied in the past. In this chapter, the dynamics of water stress and the long term water-use efficiencies on trees in even-aged and multi-aged stand structures were examined: 1) to determine whether trees in both stand structures could continue normal rates of gas exchange throughout the growing season in the water limited environments of the northern Rockies; and 2) to examine the long-term water-use efficiency relationships of trees in even-aged and multi-aged stand structures using carbon isotope discrimination analysis.

4.2. BACKGROUND

4.2.1. Water-Related Physiology in Ponderosa Pine

Physiological adjustments in water-relations and photosynthesis determine the relative drought resistance in ponderosa pine (Bassman 1988). The drought resistance in a species is attributed to its morphological and physiological adaptations. The rooting depth and the amount of rhizosphere are other important factors related to plant moisture status. In addition to great rooting depths in ponderosa pine, presence of numerous sinker roots (Parker 1969) also contribute to water absorption during droughts.

The stomata controls the movement of water from plants to the atmosphere. The rate of water loss directly depends on stomatal conductance. A gradient in absolute humidity between the needles and the air immediately surrounding the needles is a major factor controlling the stomatal conductance (Running 1976; Kaufmann 1982; Jones 1992). The lower the gradient, the higher the stomatal conductance. The total leaf conductance is dependent on xylem pressure potential, soil water status, atmospheric humidity and the air and leaf temperatures (Jones 1992).

The rates of stomatal conductance and transpiration are different for species, and primarily depend on soil and plant water status. Plant moisture stress is assumed to represent an integration of soil and internal plant water status (Running 1976). Transpiration rates in Scots pine (*Pinus sylvestris*) decreased considerably with an increase in soil moisture tension of one to two bars (Rutter and Sands 1958; Jarvis and Jarvis 1963). In ponderosa pine, Lopushinsky and Klock (1974) reported a reduction in transpiration (% of maximum) of 38, 12 and 2.5 for decreased soil water potential of -0.5, -1.0, -2.0 MPa, respectively. Lopushinsky (1969) observed that stomates of ponderosa pine close at a threshold xylem pressure potential of -1.65 MPa. Wambolt (1973) reported a high correlation between leaf xylem pressure potential and stand density, elevation, percentage sand, temperature, relative humidity and vapor pressure deficit in ponderosa pine stands. In the planted ponderosa pine seedlings, Baldwin and Barney (1976) reported a high correlation between leaf water potential and air temperature, vapor pressure deficit, soil moisture, and aspect.

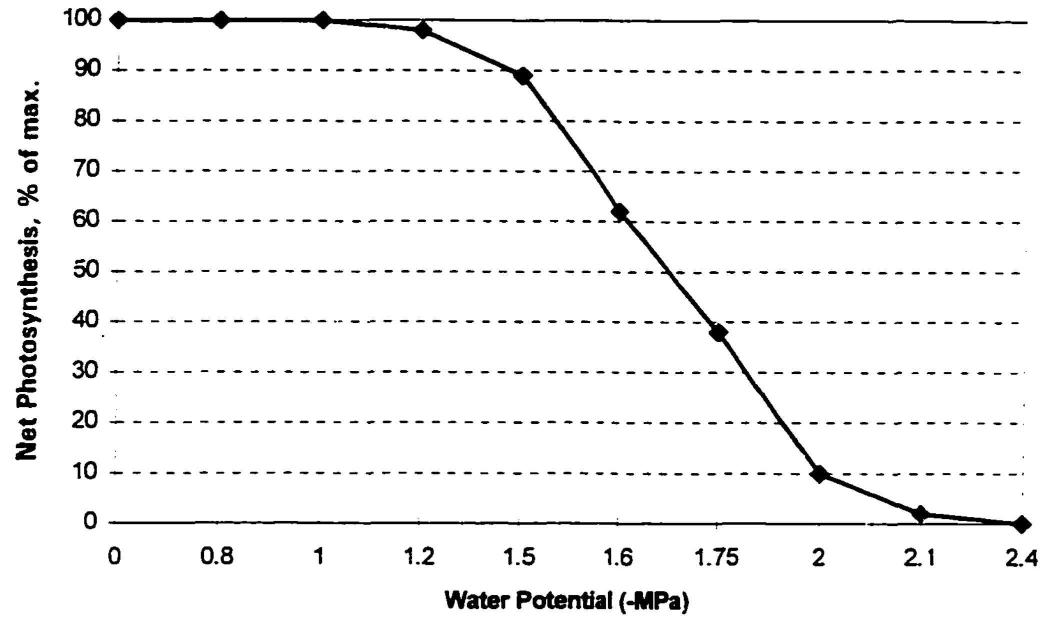


Figure 4.1. Relative changes in photosynthesis of ponderosa pine in response to decreasing soil water potential (redrawn from Cleary 1971).

Many studies have reported the direct relationship between leaf water status and rate of photosynthesis. Puritch (1973) reported a decline in net photosynthesis in four Abies species native to Canada due to water stress. In ponderosa pine, Cleary (1971) reported rapid decline in photosynthetic rates with decreases in xylem pressure potentials beyond -1.5 MPa (**Figure 4.1**).

4.2.2. Carbon Isotope Discrimination and Water-Use Efficiency

Leaf-level instantaneous water-use efficiency (WUE) has been defined as ratio of photosynthetic carbon produced to transpirational water loss, and the long-term WUE is the total plant dry matter produced to total amount of water used over the same period. In simpler terms, WUE is the ratio of assimilation rate to transpiration rate (A/E). In water limited environments, plants are thought to be under selective pressure for higher water-use efficiency (Cowan 1982; Passioura 1982; Donovan and Ehleringer 1994). WUE is considered an important factor of drought tolerance (Sun et al. 1996), which is directly related to leaf conductance (g).

Instantaneous measurements of WUE vary within and between plant species over time (Cowan 1988). Long-term water use efficiency estimation from stable carbon isotope ratios in plant organic matter has been a relatively recent approach (Farquhar et al. 1982; Farquhar and Richards 1984; Hubick and Farquhar 1987; Johnson et al. 1990; Knight et al. 1994; Sun et al. 1996). In ponderosa pine, Monson and Grant (1989) suggested that ponderosa pine has acquired improved water-use efficiencies and lower transpiration rates at the expense of reduced maximum photosynthesis rates to adapt in drier habitat types. Sun et al. (1996) reported a positive correlation between carbon isotope ratio ($\delta^{13}C$) and long term water-use efficiency and productivity in white spruce (*Picea glauca* (Moench) Voss) seedlings. A strong negative correlation between carbon isotope discrimination (Δ) and traditional measures of WUE was reported by Farquhar et al. (1989 reviewed); and Zhang and Marshall (1994).

It has been found that plants with C_3 photosynthetic pathway discriminate against the stable isotope ^{13}C as they fix CO_2 (Zhang and Marshall 1994). Farquhar et al. (1982, 1989) reported a linear relationship between Δ and the ratio of intercellular CO_2 (C_i) to atmospheric CO_2 (C_a) concentration. Since the carbon incorporated in the needles is the integrated assimilation over a period of time, the Δ provides the long-term average estimates of C_i/C_a, and therefore is a long-term indicator of plant metabolism. Plants with higher capacity for CO_2 assimilation by their mesophyll tissue could result in decreased amounts of CO_2 in the intercellular air spaces of leaves (C_i). This could also be considered as high CO_2 assimilation per unit of water transpired or high water-use efficiency (WUE). Therefore, a low C_i/C_a ratio indicates high WUE and lower discrimination.

Genetic variation and population differences in terms of WUE using carbon isotope discrimination were examined in many native conifers of the north-central Rockies (Marshall and Zhang 1994; Zhang et al. 1993; Zhang and Marshall 1994). But the relationship between carbon isotope discrimination (Δ), WUE and dry matter production under different stand structures has not been examined in the past.

4.3. METHODS

4.3.1. Study Area

The study was primarily conducted in western Montana, but a one-time pre-dawn leaf water status was measured during July 1996 in central Oregon. Even- and multi-aged (stands with two or more age classes) ponderosa pine stands selected for stand-level productivity comparison (Chapters 2 and 3) was used for water potential measurements in both locations. Five pairs of even- and multi-aged plots were sampled in western Montana, whereas four pairs in central Oregon. The site characteristics are presented in **Table 4.1**. The long-term climatic data for the study sites were given in **Table 2.2**.

4.3. 2. Leaf Water Potential

In western Montana, a total of five trees from each multi-aged stand belonging to different crown strata/cohort classes were selected for pre-dawn leaf water potential measurements. Three representative trees were only selected from even-aged stands due to less variation in the crown strata. Trees belonging to codominant crown class were only selected from both structures to reduce the influence of tree vigor in leaf water status. The selected trees were measured for their diameter (cm) at breast height (dbh, 1.37 m), total height (m), height to the base of live crown (m), using standard forest inventory equipments.

Table 4.1. General stand characteristics of the even- and multi-aged plots sampled in western Montana and central Oregon. Habitat types for western Montana were identified as per Pfister et al. (1977) and for central Oregon as per USDA Forest Service for each plant association and published in guides for sampling area by Hopkins (1979a, 1979b,) and Volland (1988).

Location	Plot	Habitat type	Elev(m)	Aspect	Slope%	LAI	TPH	BA(m^2/ha)
Sweeny Creek Rd, MT	1E	PSME/FEID	1105	E	2	4.7	580	21.0
Sweeny Creek Rd. MT	1M	PSME/FEID	1106	E	3	6.3	260	31.6
Tarkio, MT	2E	PSME/CAGE	855	S	2	7.3	570	34.5
Tarkio, MT	2M	PSME/CAGE	855	S	2	5.6	340	28.5
Ninemile Rd, MT	3E	PIPO/FEID-FESC	975	SE	4	6.6	1830	32.7
Ninemile Rd, MT	3M	PIPO/FEID-FESC	975	SE	6	5.9	890	30.0
Lubrecht, MT	4E	PSME/SYAL-SYAL	1230	S	30	7.8	1140	37.2
Lubrecht, MT	4M	PSME/VACA	1256	SE	11	5.6	700	22.9
Blue Mountain, MT	5E	PIPO/FEID-FESC	1130	S	20	7.7	610	31.5
Blue Mountain, MT	5M	PSME/CARU-AGSP	1145	SE	28	7.7	500	33.1
Bend-Ft. Rock, OR	101M	PIPO/PUTR-ARPA/STOC	1329	E	5	9.7	540	34.0
Bend-Ft. Rock, OR	101E	PIPO/PUTR-ARPA/STOC	1335	E	10	7.0	1100	50.6
Chemult, OR	103M	PIPO/PUTR/STOC	1533	S	8	7.9	420	40.4
Chemult, OR	103E	PIPO/PUTR/STOC	1539	S	12	10.1	800	50.9
Fremont, OR	104M	PIPO/PUTR/FEID	1475	SE	2	4.6	510	24.9
Fremont, OR	104E	PIPO/PUTR/FEID	1475	SE	3	5.8	750	32.3
Silver Lake Rd, OR	105M	PIPO/PUTR-ARTR/SIHY	1396	N	3	2.6	160	17.4
Silver Lake Rd, OR	105E	PIPO/PUTR-ARTR/SIHY	1417	N	4	5.5	350	30.4
Silver Lake Rd.OR	105EO	PIPO/PUTR-ARTR/SIHY	1399	N	2	5.9	160	32.9

Key to species abbreviations: PSME = *Pseudotsuga menziesii* var. *glauca*; FEID = *Festuca idahoensis*; CAGE = *Carex geyeri*; PIPO = *Pinus ponderosa*; FESC = *Festuca scabrella*; SYAL = *Symphoricarpos albus*; VACA = *Vaccinium caespitosum*; CARU = *Calamagrostis rubescens*; AGSP = *Agropyron spicatum*; PUTR = *Purshia tridentata*; ARPA = *Arctostaphylos patula*; STOC = *Stipa occidentalis*; ARTR = *Artemisia tridentata* var. *tridentata*; SIHY = *Sitanion hystrix*; ARAR = *Artemisia arbuscula*. Plot symbols E = Even-aged, M = Multi-aged. EO = Even-aged Old-growth.

Pre-dawn leaf water potential measurements were taken at monthly intervals during the last week of June, July, August and September 1995 in western Montana. In central Oregon, one time measurement was taken from the selected sites during the middle of July 1996. In western Montana, three of the study sites previously sampled during 1995 were revisited during the last week in July and August 1996 to confirm the pattern in pre-dawn water potential measurements between the structures. During each month, the measurements from all plots were completed within a period of three days to avoid the variations in pre-dawn water potential due to changes in time and weather conditions.

A sample twig from the middle of the selected tree's crown was removed using a shot gun. Generally a well exposed/extended twig was chosen to determine the maximum level of water stress. A fully intact needle was randomly selected from the twig for pre-dawn measurement. A pressure chamber was used for determination of leaf water potential using standard techniques (Ritchie and Hinckley 1975). In case of large difference in the pre-dawn water potential measured in two needle samples, a third sample was used to confirm the measurements.

4.3.3. Carbon Isotope Discrimination

The needle samples from western Montana were only used for carbon isotope analysis. Plots with different stand densities and mean mid summer pre-dawn water potentials were selected for sample collection. One-year-old needles from the top and bottom crown thirds were used for the isotope ratio analysis. A pilot study using the needle samples from top, middle and bottom crown thirds of trees from both structures indicated a significant difference in carbon isotope ratios between top and bottom thirds (ANOVA; $P = 0.05$) but the means between top and middle or middle and bottom were not significantly different in both structures. A total of 48 samples from 24 trees were analyzed for the carbon isotope ratios.

The needles without their fascicles were oven-dried at 70° C for 48 hours and ground in a Wiley Mill to a size 40 mesh. The samples were analyzed for the relative abundance of ^{13}C and ^{12}C using an isotope ratioing mass spectrometer at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah, Salt Lake City. Stable carbon isotope ratio (δ^{13} C) of the plant sample was expressed as the ratio relative to PeeDee Belemnite standard (Craig 1957). The absolute isotopic composition of the plant sample was measured by the mass spectrometer as the deviation of the isotopic composition of the plant material from the standard (PeeDee Belemnite).

(Eq. 4.1)
$$\begin{aligned}\delta_p\ (^{o}/_{oo}) &= (R_p - R_s) / R_s{*}1000 \\ &= (R_p / R_s - 1)\ {*}1000\end{aligned}$$

where δ_p is the carbon isotopic ratio of the plant material, R_p is the molar abundance ratio ($^{13}C/^{12}C$) of the plant material, R_s is the molar abundance ratio ($^{13}C/^{12}C$) of the standard.

The carbon isotope discrimination (Δ, $^{o}/_{oo}$) in the needle samples was calculated using the following equation.

(Eq. 4.2)
$$\Delta = \delta_a - \delta_p / 1{+}\delta_p$$

where δ_a is the carbon isotopic ratio of air (assumed to be -8 $^o/_{oo}$).

The ratio of intercellular (C_i) to atmospheric (C_a) concentration of CO_2 in the needle samples were calculated from the quantitative relationship proposed by Farquhar et al. (1982).

(Eq. 4.3) $$\Delta = a + (b - a)\, C_i / C_a$$

where a (= 4.4$^o/_{oo}$) is the fractionation occurring due to diffusion in air and b (= 27$^o/_{oo}$) is the net fractionation caused by ribulose- 1,5-bisphosphate carboxylase oxygenase (Rubisco).

4.3.4. Data Analysis

The mean pre-dawn water potential for the even- and multi-aged stands for each site as well as for the different months was compared using paired t-tests at $\alpha = 0.05$ significance level. The carbon isotope ratio and discrimination (Δ) were also compared using t-tests. Significance of stand structure and crown position to carbon isotope discrimination were examined using a two-way analysis of variance (P = 0.05). The stepwise procedure in multiple regression technique was used to develop models to predict carbon isotope discrimination from the possible independent variables. A significance level of P = 0.05 was used as the criteria for selecting independent variables for model building. Pearson's correlation method was used to detect the relationship between SLA and carbon stable isotope discrimination (Δ) for both stand structures.

4.4. RESULTS

4.4.1. Pre-Dawn Leaf Water Potential

Pre-dawn leaf water potentials for the different months of the growing season during 1995 indicated that water stress was low during the last week of June in both even- and multi-aged stands. The overall mean values for the even- and multi-aged stands in western Montana were -0.42 and -0.49 MPa, respectively (**Figure 4.2**). Water stress was significantly higher in the even-aged stands compared to the multi-aged stand (t-tests, $P < 0.05$) at the Ninemile study site in western Montana (**Table 4.2**). The even-aged stand at the Lubrecht site had the highest basal area, leaf area (**Table 4.1**) and water stress compared to other stands. However, the multi-aged stand also had similar water potential despite its lower LAI and stand density compared to the even-aged.

The water potentials in most of the study sites were about -1.00 MPa during the last week in July. The even- and multi-aged stands had significantly different water potentials. The lowest water potential (the highest stress) was measured at the Blue Mountain study site. The mean July water potential for the even-aged stand was -1.83 MPa and for the multi-aged stand -1.67 MPa.

Table 4.2. Mean pre-dawn leaf water potentials during June, July, August, and September 1995 for the even- and multi-aged stands at various locations in western Montana. The water potential is expressed in negative Mega Pascals (-MPa). All monthly pre-dawn water potentials between the structural types at each location are significantly different except for those indicated with the letter 'a' (t-tests, $\alpha = 0.05$).

LOCATION	STRUCTURE	JUNE 95	JULY 95	AUGUST 95	SEPTEMBER 95
Sweeney Creek	Even-aged	0.39a	1.07	1.49	0.95a
	Multi-aged	0.51a	0.96	1.29	0.91a
Tarkio	Even-aged	0.45a	1.23	1.66	0.87a
	Multi-aged	0.41a	1.09	1.36	0.91a
Ninemile	Even-aged	0.69	1.54	1.65	1.22a
	Multi-aged	0.44	1.42	1.37	1.07a
Lubrecht	Even-aged	0.73a	1.12	1.66	0.98
	Multi-aged	0.69a	0.85	1.35	0.65
Blue Mtns.	Even-aged	0.34a	1.83	1.72	0.85a
	Multi-aged	0.29a	1.67	1.44	0.82a

According to Lopushinsky (1969) and Cleary (1971) the ponderosa pine trees in both structures might have completely stopped the gas exchange due to stomatal closures. The stand level July average for the even- aged (-1.36 MPa) structure was significantly higher compared to the multi-aged (-1.16 MPa) stands in western Montana (t-tests, $P = 0.006$).

The second sets of measurements taken from three study sites during July 1996 had similar pattern in pre-dawn water potential for July 1995 (**Figure 4.2, Table 4.3**). The mean for the even- and multi-aged stands was -1.24 and -0.93 MPa, respectively. The even-aged stands had significantly higher water stress compared to the multi-aged stands (t-tests, $P < 0.001$).

During the last week in August 1995, 1996 the stands were at their peak in water stress in both structures. Similar to the trends in previous months, the even-aged stands had higher mean water stress compared to the multi-aged stands. The mean water potentials for 1995 and 1996 were -1.64 MPa, -1.36 MPa (t-tests, $P < 0.001$) and -1.62 MPa, -1.17 MPa (t-tests, $P < 0.001$), respectively for the even-, multi-aged stands in western Montana.

The measurements taken during the late growing season (September) indicated comparatively lower water stress in both structures. The mean pre-dawn water potential for the even- and multi-aged stands was -0.96 MPa and -0.85 MPa, respectively (t tests, $P = 0.015$).

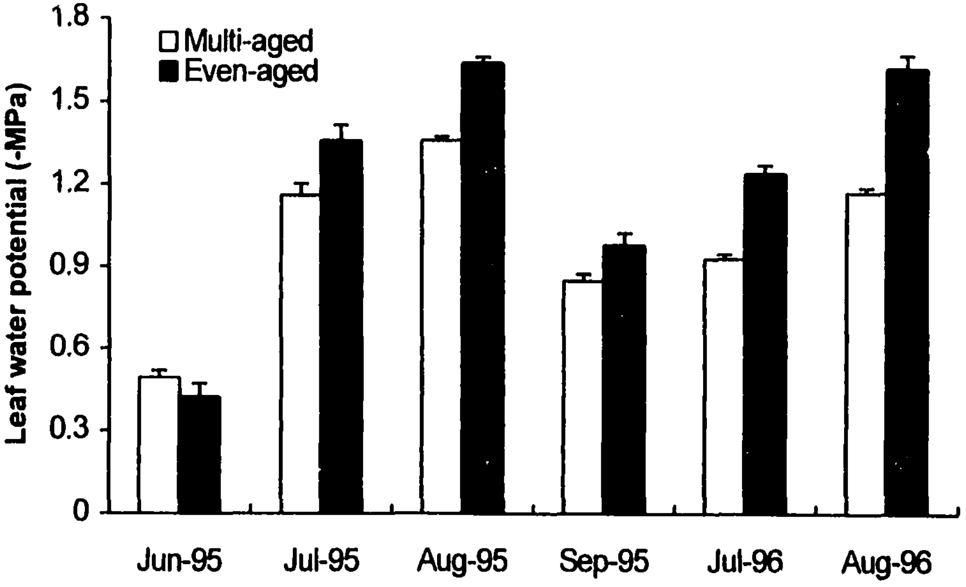


Figure 4.2. The mean pre-dawn leaf water potential measured from June to September 1995 and for July and August 1996 in western Montana. The 1995 mean is from five locations and for 1996 the mean was from three locations. The bars represent the mean and one standard error for each month.

Table 4.3. Mean pre-dawn leaf water potential measurements during July, August 1996 for even- and multi-aged stands at three locations in western Montana. The water potential is expressed in negative Mega Pascals (-MPa). All monthly pre-dawn water potentials between structural types at each location are significantly different except for those indicated with letter 'a' (t-tests, $\alpha = 0.05$).

LOCATION	STRUCTURE	JULY 96 (-MPa)	AUGUST 96 (-MPa)
Ninemile	Even-aged	1.22	1.72
	Multi-aged	1.04	1.16
Lubrecht	Even-aged	1.13	1.50
	Multi-aged	0.89	1.24
Blue Mountain	Even-aged	1.38	1.68
	Multi-aged	0.88	1.09

The overall comparison between the structures for all the sites indicated comparatively higher water stress in the even-aged stands than multi-aged stands. During July 1995, both even- and multi-aged stands in the Sweeny Creek study site had reasonably higher water potential compared to other sites in western Montana. Similarly, during the last week in September 1995 both even- and multi-aged stands had approximately equal water potentials, except the stands at the Lubrecht site.

The pre-dawn leaf water potential measured during the middle of July 1996 at the four sites in central Oregon indicated that the stands were not experiencing water stress compared to the sites in western Montana (**Figure 4.3**). The plot level averages for water potential in the even and multi-aged stands were not significantly different at $\alpha = 0.05$ level (t-tests). The even-aged stand at the Chemult (Plots 103) study site had comparatively low water potentials than its corresponding multi-aged stand. However, there was a difference in slope between the even- and the multi-aged stands, which might have influenced in the soil water status in those study plots. The study site at the Fremont National Forest (Plot 104) had similar but the highest mean water potential (-0.50 MPa) among the other sites. The mean pre-dawn water potential for the even (-0.70 MPa) and multi-aged (-0.71 MPa) stands in central Oregon during July 1996 was substantially lower compared to the mean values in western Montana during both July 1995 and 1996.

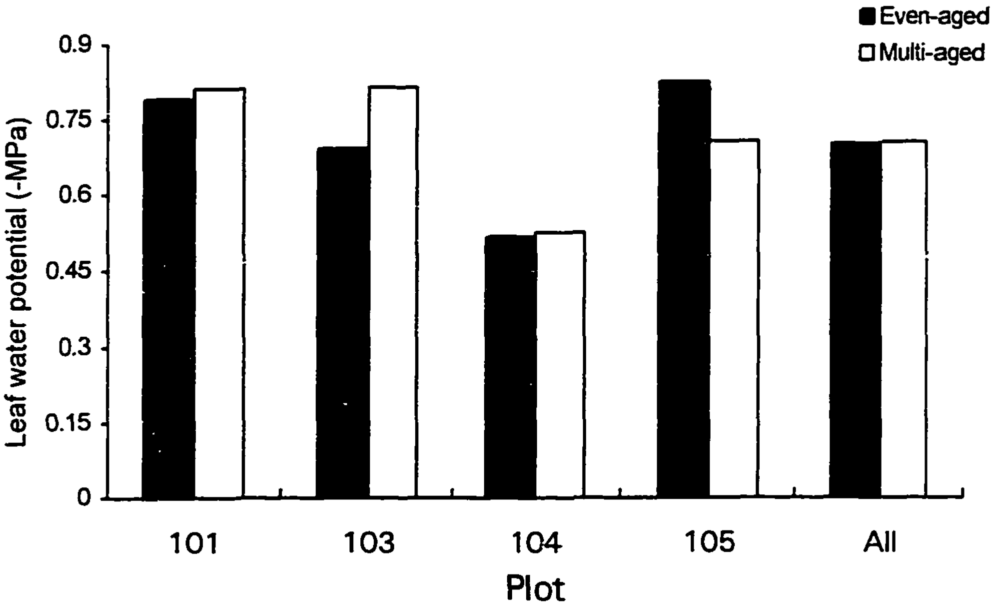


Figure 4.3. The mean value for pre-dawn leaf water potential measured during the middle of July 1996 in central Oregon in different study plots.

4.4.2. Carbon Isotope Discrimination and WUE

The carbon isotope discrimination ratio analysis indicated that trees in the even-aged stands discriminate significantly less compared to the multi-aged stands at 95 percent confidence level (t-tests). The comparison between the top and bottom crown thirds indicated that in even-aged stands, the top thirds discriminate significantly lower than the bottom thirds (**Table 4.4**). Whereas in the multi-aged stands, the discrimination was also higher for the bottom thirds, but not significantly different than the top thirds. The mean **Δ** values for the top and bottom thirds in the even-aged stands were 17.58 $^{0}/_{00}$ and 18.06 $^{0}/_{00}$, respectively. Whereas the mean for the multi-aged stands were 17.97 $^{0}/_{00}$ and 18.26 $^{0}/_{00}$ for the top and bottom thirds, respectively. The whole tree crown comparison in both structures indicated significantly higher discrimination in the multi-aged stands compared to the adjacent even-aged stands.

Table 4.4. Mean carbon isotope discrimination (Δ) and Ci/Ca for top and bottom crown thirds in the even- and multi-aged ponderosa pine stands in western Montana. Means followed by different letters for a structure were significantly different (t-tests).

Structure	**Crown Third**	**n**	**Δ ($^0/_{00}$)**	**Ci/Ca**
Even-aged	Top	12	17.58a	0.58a
	Bottom	12	18.06b	0.60b
Multi-aged	Top	12	17.97a	0.60a
	Bottom	12	18.26a	0.61a
Even-aged	Whole Crown	24	17.82a	0.59a
Multi-aged	Whole Crown	24	18.12b	0.61b

Table 4.5. Two-way analysis of variance table for isotope discrimination of needles by stand structure (even- and multi-aged) and crown sections (top and bottom thirds) in western Montana during summer 1995.

Source of Variation	df	Sum of Square	Mean-Square	F-ratio	Probability
Stand Structure (SS)	1	1.033	1.033	5.303	0.026
Crown Section (CS)	1	1.733	1.733	8.900	0.005
SS*CS	1	0.114	0.114	0.586	0.448
Error	44	8.567	0.195		

The results from two-way analysis of variance indicated that, at 0.05 level of significance, trees from both structures and their crown thirds significantly discriminate the carbon isotopes (**Table 4.5**). It was also found that the interaction between stand structure and crown thirds had no significant effect on discrimination.

Higher carbon isotope discrimination in the even-aged compared to multi-aged stand structures, indicated that the trees in the even-aged stands were more water-use efficient compared to the multi-aged stands. Lower discrimination for top thirds compared to bottom thirds also indicated that top thirds of the crowns were water-use efficient. Relatively higher discrimination for top and bottom thirds of the crown in multi-aged stands than in even-aged stands also suggested that the amount of carbon produced per water transpired in the needles from top and bottom crown thirds in the multi-aged stands were comparatively lower than in even-aged stands.

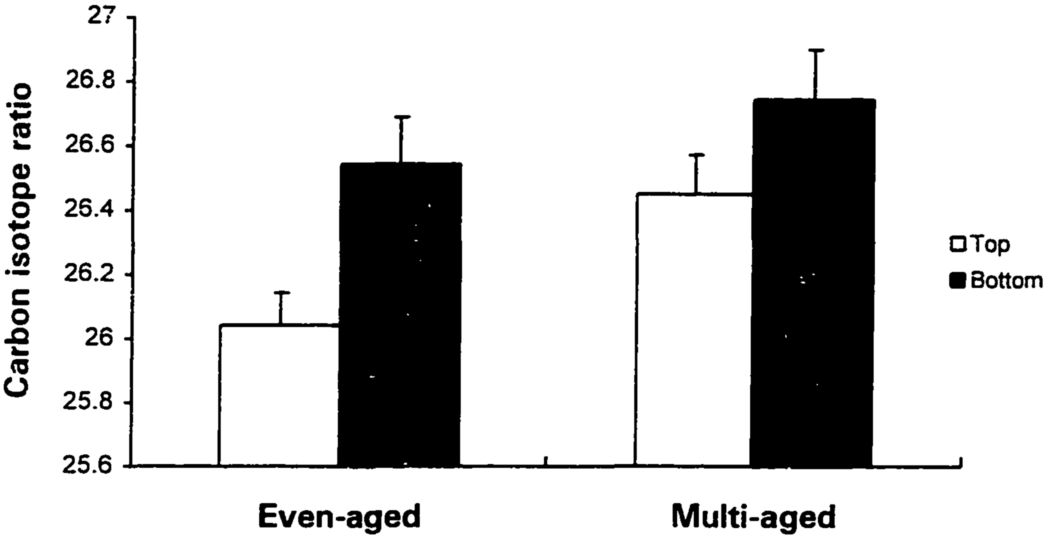


Figure 4.4. Mean and one standard error for the carbon isotope ratio for top and bottom crown thirds of even- and multi-aged stands in western Montana (n = 12).

Pairwise comparison of similar crown thirds between even- and multi-aged structures indicated that the top thirds in the even-aged stands were significantly higher water-use efficient compared to multi-aged stands. However, the water-use efficiency for bottom thirds in even- and multi-aged stands were not significantly different, even though the bottom thirds in the even-aged stands had slightly higher water-use efficiencies.

Comparatively higher C_i/C_a ratios for the bottom thirds also indicates lower WUE than top thirds in both structures. The pattern was the same as indicated by **Δ** values (**Table 4.4**). The carbon isotope ratio in the needle sample also indicated higher mean values for bottom thirds in both structures and followed the pattern in Δ (**Figure 4.4**).

A negative linear relationship between SLA and needle δ^{13} C isotope (fractionation) ratios ($^0/_{00}$) was evident in both structures (**Figure 4.5**). The relationship was stronger for even-aged stands compared to multi-aged stands. Pearson's correlation coefficient calculated separately for both even- and multi-aged stands indicated that the SLA and needle isotope ratio for even-aged stands was higher (-0.64) compared to multi-aged stands (-0.48).

A multiple linear regression model to predict carbon isotope discrimination Δ ($^0/_{00}$) was developed using SLA, July water potential and stand structure as independent variables.

The model: $\Delta\ (^0/_{00}) = \mathbf{15.05 + 0.67{*}July\ \psi_n + 0.03{*}SLA - 0.44{*}\ ST}$

Where ψ_n = Pre-dawn needle water potential (-MPa), SLA = Specific leaf area for the crown thirds, ST = Stand structure. $R^2 = 0.44$, $n = 36$, and SEE = 0.42.

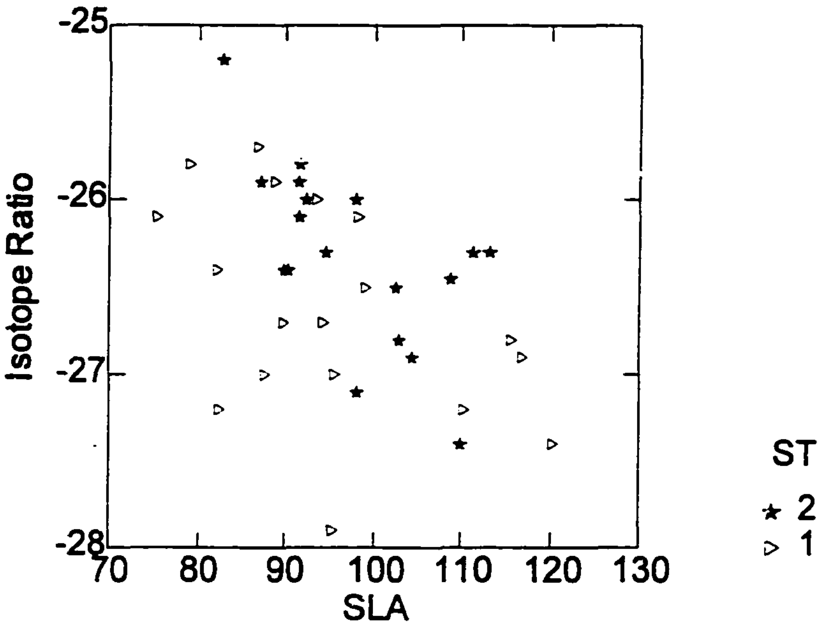


Figure 4.5. Needle δ^{13} C isotope ratios ($^0/_{00}$) and SLA (top and bottom thirds) for trees in the even-and multi-aged ponderosa pine stands in western Montana.

The predictive power (R^2) of the model was not high due to comparatively low relationship between the variables used for multi-aged stands.

4.5. DISCUSSION

4.5.1. Pre-dawn Water Potential

The results from the pre-dawn leaf water potential measurements indicated that both even- and multi-aged stands were not water-stressed during the earlier part of the growing season. The difference in LAI between the even- and multi-aged stands could result in varying soil and plant water potentials primarily due to evapo-transpiration loss. This could be the reason for significantly different moisture stress in the even- and multi-aged stands in the Ninemile site during the last week of June 1995. The LAI and stand density were higher in the even-aged stands in Ninemile and Lubrecht compared to their adjacent multi-aged stands (**Table 4.1**), which probably resulted in higher pre-dawn leaf water stress. Pre-dawn water potentials lower than -1.5 MPa during the middle of the summer (growing season) in the even-aged stands indicate that the trees in those stands might be closing their stomata sometime earlier than the multi-aged stands due to limitations in soil moisture. Similarly, the even and multi-aged stands in the Blue Mountain site might also have reduced rates of gas exchange by the last week in July. Comparatively higher water stress in the Blue Mountain study site could be due to several possible reasons: 1) High LAIs; 2) Comparatively high basal area (> 30 m^2/ha); and 3) Slopes > 20 percent. Similar to the findings by Donner and Running (1986) in a thinning study in lodgepole pine (*Pinus contorta*) stands in Montana, the results from this study also indicates that lower transpirational surface area and higher canopy interception for snow and rainfall could be the possible reason for significantly higher pre-dawn water potentials in the multi-aged stands compared to the even-aged stands on similar site conditions. They have also discussed that a reduction in root mass by thinning to low stand density could increase the availability of underground growing space for the residual trees on a stand. Similar trends in the underground root surface area/ biomass due to different stand structure could also be another possible reason for significantly high pre-dawn water potentials in the multi-aged stands. Baldwin and Barney (1976) reported that the air temperature, aspect, vapor pressure deficit and soil moisture were highly correlated with leaf water potential in the planted and natural ponderosa pine and lodgepole pine stands. Comparatively steeper slopes for the Blue Mountain study sites than the other study sites might be a factor for the significantly high water stress in both structures on this site. Slopes at about 20 to 30 percent on a southernly aspect may result in higher irradiance, soil, and air temperatures. This could considerably increase the evaporative demand of a stand compared to the one on relatively flat terrains, with similar LAIs. In general, comparatively higher water stress during the months of July and August in all the even-aged stands than the adjacent multi-aged stands was primarily attributed to their high LAIs and stand structural characteristics.

Pre-dawn leaf water potentials lower than -1.6 MPa in most of the even-aged stands during the last week of August in 1995 and 1996 indicated that the trees during the days might have very minimal photosynthesis due to moisture limited stomatal closure. Lopushinsky (1969) and Cleary (1971) reported that ponderosa pine trees close their stomata at leaf water potentials in the range of -1.4 to -1.7 MPa, and their net photosynthesis would fall to almost zero. Comparatively higher leaf water potential for the trees in the multi-aged stand structures suggests that, they could carry out at least a few hours of photosynthesis compared to the trees in adjacent even-aged stands. Presence of few summer rain showers during September 1995 reduced the water stress below -1.0 MPa in all the stands except those at the Lubrecht site. This could be due to the erratic pattern of rainfall during the measurement period. Comparatively higher water potential in both stand structures during the end of September was due to several rainfall events and could also be partly due to increased nighttime periods compared to the previous months of the growing season. Increased nighttime hours·allows enough duration for soil moisture recharge. The second sets of pre-dawn leaf water potential measurements taken during 1996 from three sites in western Montana were lower due to comparatively more summer rainfall during July and August 1996 than for the same period in 1995.

The variations in climate and soil between western Montana and central Oregon could be the probable reason for relatively low pre-dawn water stress during the middle of July 1996 for all the sites in central Oregon. Due to the void in pre-dawn water potential data for other periods of the growing season, it is difficult to tie the influence of stand structure on water stress in central Oregon stands, where water may not be a limiting factor for production. Plot level comparison of pre-dawn water potential indicated that Plot 104 at the Fremont National Forest had the lowest water stress in central Oregon. A probable reason could be due to low stand foliage area. Even though the sapwood area estimated average LAIs for these stands, the actual transpiring leaf area was lower in the even- and multi-aged stands due to severe pandora moth (*Coloradia pandora* Blake) outbreaks.

4.5.2. Water-Use Efficiency

The long-term WUE estimated from needle carbon isotope discrimination (Δ) on trees from both structures indicates totally opposite pattern compared to the pre-dawn leaf water potential measurements. But the pattern in WUE measures was very similar to many other studies on water limited environments. High water stress in the even-aged stands resulted in partial closure of their stomata often during the second half of the growing season, but at the same time their respiration loads (due to high LAI and SLA) were higher compared to the multi-aged stands. To be successful, the trees have to increase their photosynthesis, which could only be attained either by increased water availability or water-use efficiency. The WUE inferred from the carbon isotope discrimination (Δ) was the highest for the top thirds of the crowns in the even-aged stands compared to the multi-aged stands. This suggests that the trees in the even-aged structures overcome the limitations in water primarily by increasing their gas exchange efficiency. The results from the SLA (specific leaf area) analysis described in the previous chapter (Chapter 3) also indicated that SLA was the highest for top crown thirds in the even-aged stands. High radiation loads at the top of the canopy, and increased limitations in soil moisture induce the even-aged trees to have more efficient and productive top crown thirds to sustain in water limited environments. Comparison of

Ci/Ca also indicates that the intercellular CO_2 concentration was lower in the needles from top thirds of the crowns. Cowan (1982), and Passioura (1982) suggested that plants are thought to be under selective pressure for water-use efficiency in water limited environments. Similarly, In two populations of western larch (*Larix occidentalis*) seedlings with two different water treatments, Zhang and Marshall (1994) also reported a lower carbon isotope discrimination (Δ) and a higher water-use efficiency for the water-stressed seedlings compared to the well-watered ones. The results from this study supports the previous findings and suggests that the ponderosa pine trees growing in a water limited environment or stand structure may be under an induced selective pressure to be more water-use efficient.

4.6. CONCLUSIONS

Significantly different pre-dawn leaf water potentials in the even- and multi-aged ponderosa pine stands on similar sites, suggest that stand structure in water limited environments plays a major role in temporary conversion of a site to be a water-limited one during parts of the growing season. Several interrelated factors influence a particular stand structure to be limited in soil moisture. One of the main factors is the pattern of air turbulence inside the canopy of stands with different structures. The even-aged stand structure may have a totally different air turbulence pattern compared to those in the multi-aged structure, where the canopy is widely distributed on a vertical scale. During periods of higher air temperature, the vapor pressure deficit becomes larger, and the trees shut down their stomata to reduce the transpiration loss. The less diverse and more homogenized crowns in even-aged stand structure could have different canopy dynamics than multi-aged stands. With low wind, the air mass surrounded by the needles of the trees in even-aged stands tends to be relatively in a state of still. Less frequent displacement of air through the canopy, retains the humidity in the air from evapo-transpiration. This could reduce the moisture gradient between the leaf and the air immediately surrounding the needles. Low vapor pressure gradient with adequate irradiance and air temperature could increase the stomatal conductance and gas exchanges. Higher stomatal conductance could result in increased transpiration loss during gas exchange. These structurally modified micro-environments might induce increased moisture loss from trees in even-aged structures compared to multi-stratified multi-aged stands.

In addition to the aboveground structure-related differences in plant moisture status, the ratio of the live root surface area to the total transpiring foliage surface area might also be different in stands with varying aboveground stand structures. Stands with different size and age structures, but similar LAIs could have different root biomass and rhizoshpere to maximize water harvest to meet the moisture demands of the aboveground sinks. If this ratio is found different between stand structures with similar LAIs and ages, then the total biomass production and its allocation pattern for both above- and below-ground components have to be considered for better comparison of net primary production in different stand structures.

Literature Cited

Baldwin, V. C. and C. W. Barney. 1976. Leaf water potential in planted ponderosa and lodgepole pines. For. Sci. 22:344-350.

Baker, J. B., M. D. Cain, J. M. Guldin, P. A. Murphy, and M. G. Shelton. 1996. Uneven-aged silviculture for the loblolly and shortleaf pine forest cover types. USDA For. Serv. Gen. Tech. Rep. SO-118. 65 pp.

Bassman, J. H. 1988. Photosynthesis and water relations of ponderosa pine. *In* Ponderosa pine: The species and its management. Eds. D. M. Baumgartner and J. E. Lotan. Coop. Extension, Wash. St. Univ., Pullman, USA, pp 45-58.

Cleary, B. D. 1971. The effect of plant moisture stress on the physiology and establishment of planted Douglas-fir and ponderosa pine seedlings. Ph.D. Dissertation, Oregon State University, Corvallis, OR, USA.

Cowan, I. R. 1982. Regulation of water use in relation to carbon gain in higher plants. *In* Water relations and carbon assimilation. Encyclopedia in plant physiology, new series, Vol. 12B. Eds. O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler. Springer-Verlag, New York, pp 589-613.

Cowan, I. R. 1988. Stomatal physiology and gas exchange in the field. *In* Flow and transport in the natural environment. Ed. O.T. Denmead. Springer-Verlag, New York, pp 160-172.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correlation factors for mass-spectrometric analysis of carbondioxide. Geochimica. Cosmochim. Acta, 12:133-149.

Donovan, L. A. and J. R. Ehleringer. 1994. Potential for selection on plants for water-use efficiency as estimated by carbon isotope discrimination. Am. J. Bot. 81:927-935.

Donner, B. L. and S. W. Running. 1986. Water stress response after thinning *Pinus contorta* stands in Montana. For. Sci., 32:614-625.

Farquhar, G. D., M. H. O'Leary and J. A. Berry. 1982. On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9:121-137.

Farquhar, G. D., K. T. Hubick, A. G. Coindon, R.A. Richards. 1989a. Carbon isotope fractionation and plant water-use efficiency. *In* Stable isotopes in ecological Research. Eds. P. W. Rundel, J. R. Ehleringer, K.A. Nagy. Springer-Verlag, New York, pp 21-40.

Farquhar, G. D., and R. A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust. J. Plant Physiol. 11:539-552.

Hopkins, W. E. 1979a. Plant associations of the Fremont National Forest. USDA For. Serv. Pac. Northwest Reg. R6-Ecol-79-004, 106 p.

Hopkins, W. E. 1979b. Plant associations of the south Chiloquin and Klamath Ranger Districts-Winema National Forests. USDA For. Serv. Pac. Northwest Reg. R6-Ecol-79-005, 96 p.

Hubick, K. T. and G. D. Farquhar. 1987. Carbon isotope discrimination-selecting for water use efficiency. Aust. Cotton Growers 8:66-68.

Jarvis, P. G., and M. S. Jarvis. 1963. The water relations of tree seedlings. II. Transpiration in relation to soil water potential. Physiol. Plant. 16:236-253.

Jones, H. G. 1992. Plants and microclimate-A quantitative approach to environmental plant physiology. Second edition, Cambridge University Press. 428 p.

Johnson, D. A., K. H. Assay, L. L. Tieszen, J. R. Ehleringer and P. G. Jefferson. 1990. Carbon isotope discrimination: potential in screening cool-season grasses for water-limited environments. Crop Sci. 30: 38-343.

Kaufmann, M. R. 1968. Evaluation of the pressure chamber technique for estimating plant water potential of forest tree species. For. Sci. 14:369-374.

Kaufmann, M. R. 1982. Leaf conductance as a function of photosynthetic photon flux density and absolute humidity difference from leaf to air. Plant Physiol. 69:1023-1026.

Knight, J. D., N. J. Livingston and C. Van Kessel. 1994. Carbon isotope discrimination and water-use efficiency of six crops grown under wet and dry land conditions. Plant Cell Environ. 17:173-179.

Korner, C. H., J. A. Scheel and H. Bauer. 1979. Maximum leaf diffusive conductance in vascular plants. Photosynthetica 13:45-82.

Lopushinsky, W. 1969. Stomatal closure in conifer seedlings in response to leaf moisture stress. Bot. Gaz. 130:258-263.

Lopushinsky, W. and G. O. Klock. 1974. Transpiration of conifer seedlings in relation to soil water potential. For. Sci. 20:181-186.

Lopushinsky, W. 1975. Water relations and photosynthesis in lodgepole pine. *In* Proc. Management of lodgepole pine ecosystem. Ed. D. Baumgartner. Coop. Ext. Serv., Washington State University, Pullman, WA, USA, pp 135-153.

Marshall, J. D. and J. W. Zhang. 1994. Carbon isotope discrimination and water use efficiency in native plants of the north-central Rockies. Ecology 75:1887-1895.

Monson, R. K. and M. C. Grant. 1989. Experimental studies on ponderosa pine. III. Differences in photosynthesis, stomatal conductance, and water-use efficiencies between two genetic lines. Am. J. Bot. 76:1041-107.

Parker, J. 1954. Available water in stems of some Rocky Mountain conifers. Bot. Gaz. 115:380-385.

Parker, J. 1969. Further studies of drought resistance in woody plants. Bot. Rev. 35:317-371.

Passioura, J. B. 1982. Water in the soil-plant-atmosphere continuum. *In* Water relations and carbon assimilation. Encyclopedia in plant physiology, new series, Vol. 12B. Eds. O. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler. Springer-Verlag, New York, pp 589-613.

Petersen, T. D. and B. D. Maxwell. 1987. Water stress of *Pinus ponderosa* in relation to foliage density of neighboring plants. Can. J. For. Res. 17:1620-1622.

Pfister, R. D., B. L. Kovalchik, S. F. Arno and R. C. Presby. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34, 177 p.

Pothier, D., and H. A. Margolis. 1990. Changes in the water relations of balsam fir and white birch saplings after thinning. Tree Physiol. 6:371-380.

Puritch, G. S. 1973. Effect of water stress on photosynthesis, respiration, and transpiration of four Abies species. Can. J. For. Res. 3:293-298.

Ritchie, G. A. and T. M. Hinckley. 1975. The pressure chamber as an instrument for ecological research. Adv. Ecol. Res. 9:165-264.

Running, S. W. 1976. Environmental control of leaf water conductance in conifers. Can. J. For. Res. 6:104-112.

Rutter, A. J. and K. Sands. 1958. The relation of leaf water deficit to soil moisture tension in *Pinus sylvestris* L. I. The effect of soil moisture on diurnal changes in water balance. New Phytol. 57:50-65.

Sands, R. and E. K. S. Nambiar. 1984. Water relations of *Pinus radiata* in competition with weeds. Can. J. For. Res. 14:233-237.

Schmid, J. M., S. A. Mata, R. K. Watkins and M. R. Kaufmann. 1991. Water potential in ponderosa pine stands of different growing-stock levels. Can. J. For. Res. 21:750-755.

Sun, Z. J., N. J. Livingston, R. D. Guy and G. J. Ethier. 1996. Stable carbon isotopes as indicator of increased water use efficiency and productivity in white spruce (*Picea gluace* (Monech) Voss) seedlings. Plant, Cell and Environment 19, 887-894.

Stewart, C. M. 1967. Moisture content of living trees. Nature 214:138-140.

Volland, L. A. 1988. Plant associations of the central Oregon pumice zone. USDA For. Serv. Pac. Northwest Reg., R6- ECOL-104-1985, 138 pp.

Wambolt, C. F. 1973. Conifer water potential as influenced by stand density and environmental factors. Can. J. Bot. 51: 333-2337.

Zhang, J. W., J. D. Marshall and B. C. Jaquish. 1993. Genetic differentiation in carbon isotope discrimination and gas exchange in *Pseudotsuga menziesii*: a common garden experiment. Oecologia 93:80-87.

Zhang, J. W. and J. D. Marshall. 1994. Population differences in water-use efficiency of well-watered and water-stressed western larch seedlings. Can. J. For. Res. 24:92-99.

Chapter 5

Conclusions

In this study, I explored the influence of stand structure on leaf level physio-morphological attributes which can lead to variable production efficiencies. The study was undertaken to provide some physiological basis for management decisions to select even- and multi-aged stand structures for different landscapes.

Stem volume increment per unit leaf area was found higher in multi-aged stands due to increased availability of light and moisture. Diverse vertical structures in multi-aged stands resulted in lower canopy specific leaf area and higher leaf water potentials. In multi-aged stands the size and distribution of trees along with stand density, are recognized as important factors influencing stand leaf area index and aboveground net productivity. Proportionally larger number of old-growth or younger sized trees in multi-aged stands tend to influence stand LAI, volume growth, and other stand productivity measures based on LAI, such as stem volume and basal area growth efficiencies. However, with similar LAI, multi-aged stands have equal or higher stem volume increment compared to even-aged stands on identical sites.

Most of the natural, even-aged stands in both western Montana and central Oregon have higher trees per ha compared to regulated even- or uneven-aged stands. The relatively uniform structure of even-aged stands leads to higher competition for many important growth factors like light and soil moisture. For example, even-aged stands were under higher water stress during mid-late growing season, indicating lower stand photosynthesis and production compared to multi-aged stands. The above-ground productivity was higher in even-aged stands growing in relatively non-water limited sites in central Oregon. A comparison of even- and multi-aged stand structures in two different climatic regions (western Montana and central Oregon) suggests that the decision to select a particular stand structure for a specific ecosystem should be based on the climate and other-related physiographic conditions prevailing on that site. Adopting a uniform stand structure (even-aged or multi-aged) throughout the landscape without considering the various climate-related physiological processes for stand growth will result in poor stand productivity on certain sites.

Tree crowns in multi-aged stands are characterized by relatively equal production potentials, indicated by similar crown third specific leaf area and leaf nitrogen content. Recent studies in ponderosa pine indicated that old-growth trees are not physiologically efficient in production due to their reduced diurnal photosynthesis and stomatal conductance compared to younger trees (Yoder 1994) and hydraulic limitations (Ryan and Yoder 1997). Even though net dry matter production is less in old-growth trees, the park-like structures in which these trees are typically found provide many other values besides carbon fixation and storage.

In water-limited ecosystems, maintaining higher stand densities in natural, even-aged ponderosa pine stands increases the competition for moisture, light, and nutrients, which may increase many forest health problems. For example, poor stand growth due to water limitations could reduce the resistance in ponderosa pine to mountain pine beetle (*Dendroctonus ponderosae* Hopk.) attack. Relatively high amounts of understory biomass due to increased light and soil moisture levels in multi-aged stands may improve the habitat types for many wildlife species compared to even-aged stands.

Manipulating stand structures to expand the vertical and horizontal growing space could enhance foliage-, tree-, and stand-level productivity in natural even-aged ponderosa pine stands.

Literature Cited

Ryan, M. G. and B. J. Yoder. 1997. Hydraulic limits to tree height and tree growth - what keeps trees from growing beyond a certain height? BioScience 47:235-242.

Yoder, B. J., M.G. Ryan, R.H. Waring, A. M. Schoettle, and M. R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40:513-527.

IMAGE EVALUATION
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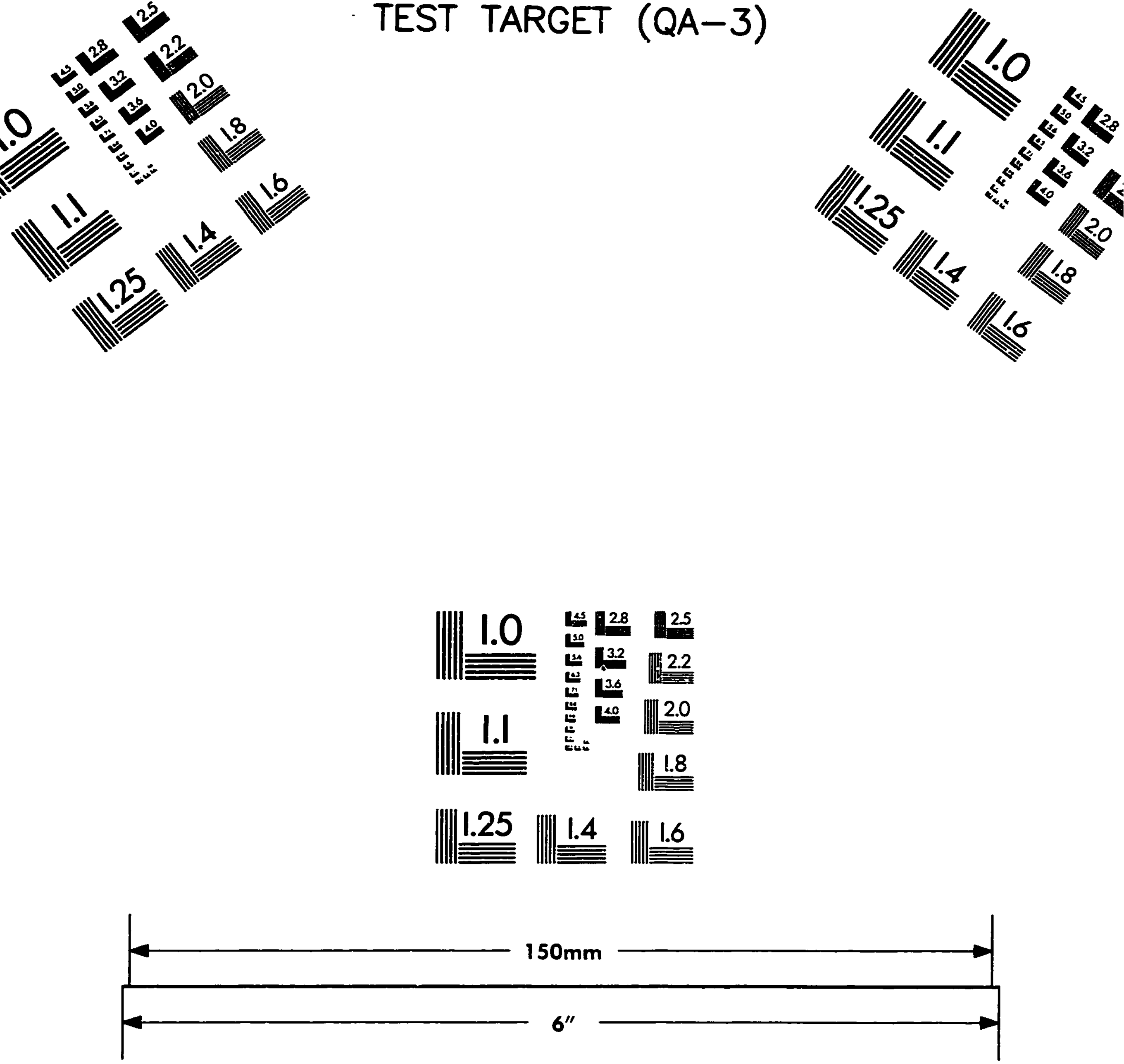

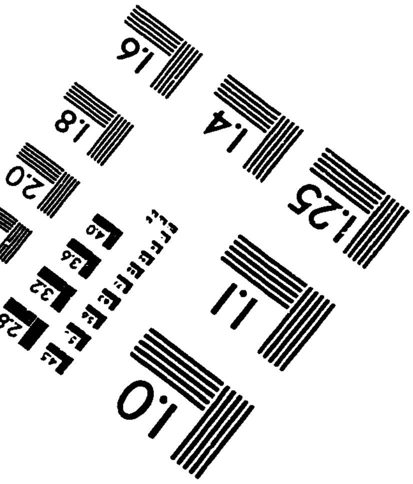

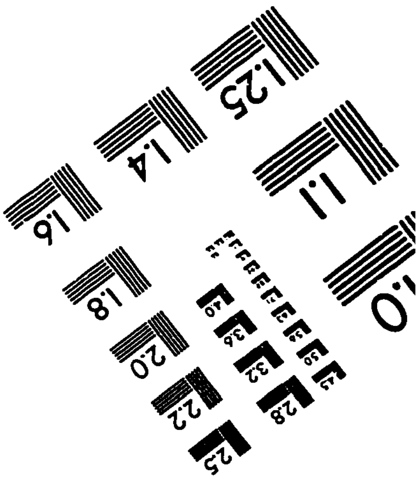

APPLIED IMAGE . Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989