AN ABSTRACT OF THE THESIS OF

<u>Adam O. Burke</u> for the degree of <u>Master of Science</u> in <u>Sustainable Forest Management</u> presented on <u>June 5th, 2015</u>.

Title: <u>Distribution of Live Biomass, Herbivory and Foliar Retention in Central Oregon Lodgepole</u>

<u>Pine (*Pinus contorta ssp. murrayana*) Crowns.</u>

Abstract approved:

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Stephen A. Fitzgerald

        Lodgepole pine (*Pinus conorta*) is a widely distributed forest type across western North America. Central Oregon lodgepole pine forests are ecologically unique when compared to other lodgepole pine ecosystems. Sierra lodgepole pine (Pinus contorta *ssp. murrayana)* is the dominant variety and often exists as the climax species on pumice soils, while in most other regions lodgepole pine is an early successional species. Most lodgepole pine research has been conducted at high elevations in the Rocky Mountains. Research findings from other geographic locations may not by applicable to central Oregon lodgepole pine ecosystem.

        Forest and tree biomass distribution and utilization is currently of interest in the northwestern United States due to large outbreaks of MPB, changes in fuel distribution, and the desire utilize lodgepole pine for wood products and biomass. Understanding natural stand

dynamics and responses to disturbance on individual tree physiology and canopy biomass distribution requires detailed studies on the structural differences of central Oregon lodgepole pine ecosystems. Little is currently known about the influence of vertical position and crown aspect within the canopy and their effect on the distribution of canopy biomass, herbivory and foliage retention in central Oregon lodgepole pine.

This thesis describes the influence of both vertical crown position and crown aspect on the distribution of live biomass, herbivory and foliage retention in central Oregon lodgepole pine crowns.

We randomly selected and sampled 33 trees within a stand in the Deschutes National Forest in central Oregon. We systematically sampled 36 branches from each tree, from which we measured total biomass, the percentage of consumed leaf area (visually estimated) and the foliage retention in years of each branch. Linear mixed models (LMMs) were used for this study to describe the responses of crown structure attributes to live biomass distribution, herbivory distribution and foliar retention distribution. A nested experimental design was used, where plots were nested within the stand to account for the differing levels of between plot variability.

We found strong evidence that the vertical position of the branch within the tree crown has a significant effect on the distribution of total biomass per branch, percentage of consumed leaf area and needle longevity. We also found that crown aspect has a significant influence on the distribution of branch biomass, but does not have a significant effect on herbivory or foliage retention. The biomass findings were consistent with findings in previous Rocky Mountain lodgepole pine studies; however there were inherent differences present with needle longevity and the distribution of the foliage retention. There are differences between lodgepole pine ecosystems in the intermountain west and central Oregon, which need to be accounted for when further studying crown architecture and canopy structure.

Distribution of Live Biomass, Herbivory and Foliar Retention in Central Oregon Lodgepole Pine
(*Pinus contorta ssp. murrayana*) Crowns

by

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Adam O. Burke, Author

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CONTRIBUTION OF AUTHORS

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Introduction

Forests are complex ecosystems that are the product of many differing biome characteristics such as species biodiversity (Cardinale et al 2000), stand productivity and structure, (Mainwaring and Maguire 2004), disturbance and succession processes, elevation and hydrologic processes and geographic location. These characteristics all impact ecosystem structure and individual tree physiology in significant, yet very different ways.

Lodgepole pine (*Pinus conorta*) is a widely distributed forest type across western North America (Lotan and Critchfield 1990). Throughout the range of lodgepole pine many physiologic traits differ as a result of genetic drift (Latta et al 1997), the historical fire regime (Gauthier et al 1996), and the physical landscape and its corresponding characteristics (Franklin et al 1973). Across North America there are two varieties of lodgepole pine *Pinus contorta ssp. murrayana* (Sierra lodgepole pine) and *Pinus contorta ssp. latifolia* (Rocky Mountain lodgepole pine) that differ from each other slightly.

Central Oregon lodgepole pine forests are ecologically unique when compared to other lodgepole pine ecosystems, as two varieties of lodgepole pine intersect (Lotan and Critchfield 1990). Sierra lodgepole pine is the dominant variety within the central and southern Oregon Cascade Range, however Rocky Mountain lodgepole can also be found from the central Oregon Cascades and north into Washington. Central Oregon lodgepole pine stands often exist as the climax species, in uneven aged stands (Simpson 2007), while in most other regions lodgepole pine is an early successional species that grows primarily in even-aged cohorts (Lotan and Critchfield 1990).

Forest and tree biomass distribution and utilization is currently of much interest in the northwestern United States, especially with how it relates to utilization and its impacts of forest fire and fire ecology within the dry pine systems (Cambero et al 2014; Stidham and Simon-Brown 2011; Stocks and Kauffman 1997). Due to natural stand dynamics and responses to unique

environmental conditions on individual tree physiology and biomass distribution, more research needs to be conducted on the structural differences of the central Oregon lodgepole pine ecosystem. To best understand these relationships and processes (e.g., disturbance and succession) one should consider the habitat type or plant association as these processes change across gradients in environmental conditions (Garber and Maguire 2005).

One fundamental aspect of stand structure that has a direct influence on stand productivity is the vertical distribution of foliage (Garber and Maguire 2005). Studies show that tree structure and function are fundamentally governed by the vertical distribution of leaf area (Weiskittel et al 2009). Closely tied to the vertical distribution of foliage throughout the tree crown is the distribution of overall biomass within the live-crown portion of the tree. From previous research it has been shown that leaf area is well correlated with branch diameter and location within the crown (Kershaw and Maguire, 1995, Godfree et al 2002). Also associated with stand productivity and vertical biomass distribution is the distribution of biomass within individual lodgepole pine crowns by aspect. The importance of crown architecture in determining sunlight interception and tree productivity has been discussed by numerous studies and expressed in many independent models (Horn 1971). Most of these models assume random leaf distribution throughout the crown, however conifer leaves are generally not randomly distributed, rather clustered on shoots (Schoettle and Smith 1991).

Another factor of crown structure in lodgepole pine is needle retention and leaf longevity. Schoettle and Smith (1991) showed that there was a positive correlation with needle longevity and vertical distribution within Rocky Mountain lodgepole pine where the upper crown has lower needle retention. These patterns of biomass and leaf longevity have been shown to differ across contrasting lodgepole pine forests within the Rocky Mountains (Pearson et al 1984), however the general influence of vertical position and crown aspect remain significant (Garber and Maguire 2005; Schoettle and Smith 1991).

Within tree crowns there are competing environmental factors that can impact the overall biomass and leaf area. It has been shown that the presence of dwarf mistletoe within lodgepole pine forests can have a significant impact on biomass distribution (Godfree et al 2002). In addition to the impact of dwarf mistletoe, other biotic factors may have an impact of crown physiology. Arthropod herbivory has been shown to be highly stratified within deciduous tree crowns (Ulyshen 2011), however there is little known about the stratification of herbivory within pines (Lowman 1995; Rinker and Lowman 2004; Schowalter 1989).

There are relatively few lepidopteran defoliators present in coniferous forests, with the most prevalent being the Douglas fir Tussock Moth, the Pandora Moth, and the Pine Butterfly. These species have been shown to have a very low impact on defoliation during endemic levels (Mason et al. 1998). The defoliation patterns present within the lepidopteran defoliators in pines has been observed to be cyclical between the endemic state and epidemic states, with epidemic herbivory being very heavy and sometimes leading to tree mortality (Shaw et al. 2006; Speer et al. 2001; Evenden 1940). Conifers are also shown to have increased phloem thickness and resin flow, along with a high needle toughness, which may impact the preferences of arthropods. (Chen et al. 2002; Kolb et al.1997).

The objective of this study was to describe the effects of vertical location and crown aspect on the distribution of biomass, arthropod herbivory and foliar retention within unmanaged central Oregon lodgepole pine forests. The specific research questions that I addressed were:

1. How does vertical position and crown aspect, within central Oregon lodgepole pine crowns, affect the distribution of live biomass?

2. How does vertical position and crown aspect, within central Oregon lodgepole pine crowns, affect the distribution of arthropod herbivory?

3. How does vertical position and crown aspect, within central Oregon lodgepole pine crowns, affect the distribution of foliar retention?

Methods

Study Area

The study took place within a single lodgepole pine stand within the Deschutes National Forest in Central Oregon. The stand is located 0.5km North-East of the Edison Butte Sno-Park (Appendix A, Table 1). This site was within the lodgepole pine/bitterbrush/western needlegrass (*Pinus contorta/Purshia tridentate/Stipa occidentalis*) plant association that is restricted to ash/pumice influenced areas (Volland 1988). Predominate vegetation on this site included 70-90 year-old lodgepole pine, with an understory comprised of bitterbrush, wax currant (*Ribes cereum*), western needlegrass, Ross's sedge (*Carex rossii*), and squirreltail (*Sitanion hystrix*). Soils consist primarily of air-fall ash/pumice or pyroclastic flow pumice (Simpson 2007). The soil texture is typically loamy course sand to sandy loams. The mean annual precipitation varies between 27.9cm and 99cm with an average of 63.5cm (WRCC 2015). The majority of the precipitation comes in the form of snowfall. Temperatures range from an average of 3.3° C to 6.1° C (WRCC 2015). The elevation is approximately 1537m.

Experimental Design

Within the stand four rectangular belt transects were randomly located using aerial photography. A 100-box grid was placed over the aerial photograph with each box being labeled one through one hundred. A random number generator was then used to choose the starting point of each transect. The random number generator was also used to randomly select the azimuth of the belt transect, but had several constraints. The belt transect had to fall completely within the stand, and could not overlap an adjacent transect. If the azimuth that was randomly generated failed to meet either of these two constraints, another random azimuth was generated until all constraints were satisfied.

The belt transects were 100 meters long by 10 meters wide, 5 meters to the left and right of the center line (Figure 1). Within each belt transect a stem map was then created for all trees ≥6 centimeters in diameter at breast height (4.5 feet) (DBH). The stem map recorded the distance in meters of each tree from transect start along the transect centerline, followed by the distance in meters to the right or left of the centerline. The stem map was created to calculate tree averages for different tree attributes, specifically: tree species, total tree height (m), tree diameter at breast height (cm), and estimated crown width (m).

The study focused on the average co-dominate lodgepole pine tree within the selected stand. A co-dominate tree is commonly defined as a tree with a crown at the general canopy level that receives full light from above but is generally restricted from the sides (Appendix A, Table 2).The average co-dominate lodgepole pine tree for this study was defined as a tree that fell within 2 standard deviations of the individual transect averages of total height (m), DBH (cm) and estimated crown width (m). The stem map of each transect allowed for the average trees to be designated for sampling.

After establishing the number of trees within each transect, ten trees within each transect were sampled based on a set of pre-determined constraints. In the event that there were more than ten trees that met all of the sampling constraints within each transect, each tree was given a number, after which a random number was generated to select which trees would be sampled.

Ethics Statement

No permits were required for this study. All sampled trees were on US Forest Service land and permission was obtain from land managers to conduct this study. Sampling methods were designed to minimize tree damage. No endangered or threatened species were present.

Tree Selection

Only co-dominate crown class trees were to be sampled to maintain consistency within the crown shape and characteristics. All trees that were sampled had to be well spaced and have spatially distinguishable tree crowns to prevent the sampling of intermediate or suppressed crown class trees. The selected trees were spatially independent from their neighbors in an effort to minimize the effects of shading on crown growth (Garber and Maguire 2005). The spacing also allowed room for the sampling method to be implemented (see *Sampling Protocol*).

No trees taller than 16.5 meters were to be sampled due to height restrictions with the sampling methods (see *Sampling Protocol*). There were several co-dominate trees within the sample range that were not able to be sampled due to their total height. This limits the scope of heights within the sampled co-dominate trees within the study.

For this study we utilized Hawksworth's 6-class mistletoe rating system. The mistletoe rating system classifies the prevalence of mistletoe within North American pines and ranges from 0-6, with 0 being no mistletoe present to 6 being completely infested (Hawksworth, 1977) (Figure 2) throughout the crown. For this study the mistletoe rating within each sampled tree had to be equal to or less than 3. Past studies have shown that the biomass of trees is not affected by mistletoe until individual tree rating is greater than 3 (4-6) (Hawksworth, 1977). Therefore, when selecting trees that had a mistletoe ratings from 0-3, I assumed there should not be a measurable difference in biomass due to mistletoe (Godfree et al 2002).

No trees with a forked top were sampled. Trees with forked tops typically contain more live biomass than trees with a singular bole, and were not deemed as average for this study (Adu-Bredu et al. 2008)

Sampling Protocol

Individual Tree Sampling

After trees were selected within each transect, the trees were sampled using a semi non-destructive sampling method. A mobile scaffold system (9m tall) was used to reach the crowns of the selected trees. From the top of the scaffolding a pole saw (5m long) was used in conjunction with hand tools to reach the sampled branches throughout the selected trees. Due to the limited height of the scaffold and pole saw combination; no trees above 16.5m could be sampled for this study.

Prior to sampling branches, several tree attributes were measured, including canopy base height (m), canopy length (m), and tree diameter (cm). Tree diameter was measured at base height, crown base, and ideally mid-crown (as high as could be reached, if below mid-crown height). In several cases, depending on the overall tree height and crown length, mid-crown was located above 10 meters, which prohibited mid-crown measurement. Tree cores were also taken at DBH, crown base and mid-crown to determine tree age in years, diameter inside bark (cm), diameter outside bark (cm), sapwood radius (cm), and the core wet weight (g).

Within each tree the live tree crown was divided into three horizontal strata: lower crown, middle crown and upper crown. Each strata was then divided into thirds, resulting in nine total horizontal strata distributed throughout the live tree crown: lower lower crown, lower middle crown, lower upper crown, lower middle crown, middle middle crown, middle upper crown, lower upper crown, middle upper crown, and the upper upper crown (Figure 3).

In addition to dividing the tree crown into horizontal strata, they were also divided vertically by aspect, resulting in a North, South, East and West vertical quadrants. The vertical division resulted in 32 unique sections throughout the live tree crown (north lower lower, south lower lower, east lower lower, west lower lower etc.). All of the branches within each of the 32

sections were tallied in order to later scale the biomass estimates up to the tree level. After all the branches were tallied, one branch was sampled from each section within the live tree crown.

An average branch was selected and removed from each unique section throughout the live crown. An ocular evaluation was used to determine the average branch, taking into account branch length, foliated length and foliated width as compared to the other branches within that section. These branches were not randomly selected due to limitations with measuring and selecting branches that were out of reach. The height and aspect of each branch was recorded before it was cut using either a 100m tape that ran from 9m high to the base of the tree, or a laser height finder for branches over 9m. If there was no live branch within a unique section, no branch was sampled.

Each branch was removed from the tree using either hand pruners or a pole saw as close to the tree bole as possible. After the branches were removed they were measured for total branch length (m), foliated length (m), and foliated width (m). The branches were then labeled with index cards and placed in plastic bags for transport back to Oregon State University to be processed in the lab.

Lab Analysis

Once at Oregon State University, the branches were stored in a refrigerated room (-10 C) until ready to process in order to maximize foliage retention. Initial measurements were taken on the branches, including needle retention in years, ocular estimate of needle herbivory recorded as a percentage of overall branch foliage consumed (Schowalter 1995), presence of lichen, and the presence of mistletoe (Appendix B). Any insects that were found on branches were collected to be processed at a later date.

The individual branches were then separated by the following attributes: foliage, flowers, cones, and branches. After a branch had been separated, the wet weight (g) was taken for each attribute. After weighing, the samples were placed in paper bags and put into the drying ovens,

which were set at 50° C. The samples were weighed after three days in the oven, and then

reweighed after an additional three days to establish a dry weight. If the dry weight was not

established after six days, the samples remained in the oven for an additional two days, and then

reweighed. Once there was no significant change in the biomass (<5g) between measurements, the

resulting dry weight for each attribute was added together to establish biomass value for each

branch.

Model Selection and Data Analysis

Linear mixed models (LMMs) were used for this study to describe the characteristics of

crown structure attributes to distribution, herbivory distribution and foliar retention distribution.

A nested experimental design was used, where plots were nested within the stand to account for

the differing levels of between plot variability. There were no stand or tree level covariates that

were identified as potential sources of variation within the stand that could impact the responses of

crown structure to the distribution of live woody biomass, herbivory and foliar retention beyond

random variation within the plots and the random variation between the trees themselves. Since all

of the trees were located within one stand with a common stand density, stand structure, site

productivity, and insect and disease prevalence those factors were not accounted for in the model.

In order to ensure that final models captured the relationships between the variables of

interest while maintaining the simplest level of parsimony within the regression, we used the

Bayesian Information Criterion (BIC) to select the most appropriate model. (Appendix A, Tables 3-

9). Models were fitted using the maximum likelihood method for each response (Burnham and

Anderson 2002). BIC was selected over other information criteria options as it performs well when

there are redundant explanatory variables in the candidate models, (Ramsey and Schaffer 2013).

BIC was also chosen as it penalizes model complexity more heavily, resulting in the selection of the

simplest model possible (Dziak et al. 2012). The model with the lowest BIC value (ΔBIC of 0) was considered to be the most appropriate model.

Assumptions of equal variance and normality were tested for each potential model using standard diagnostics prior to model selection (Ramsey and Schafer 2013). We used a log-transformation on the response variables of biomass and herbivory to correct for violations of the constant variance assumption. The foliage retention response variable was fitted with a linear mixed model, but was not log-transformed. Linear mixed models were used to model all of the response parameters to keep the analysis methods consistent.

Models with p-values below an α-level of 0.05 were interpreted to have strong evidence of a linear relationship. Models with $P < 0.10$ were interpreted to have suggestive but inconclusive evidence of a linear relationship to lower the probability of making a Type II error (Ramsey and Schafer 2013). All analyses were performed using the program R, version 2.12.0 (R Development Core Team 2009).

Results

The sample design limited the number of potential environmental covariates between each plot as stand density, crown class, diameter and crown spacing were all parameters of the initial tree selection. As such all thirty-three trees, across the four plots (10 from plot 1, 10 from plot 2, 10 from plot 3, 3 from plot 4) were pooled together to characterize the spatial distribution of biomass, herbivory and foliar retention throughout the lodgepole pine crowns. Spatial distribution within the crown was characterized in two distinct categories, vertical distribution by crown thirds and distribution by crown aspect.

Distribution of Live Biomass

In order to avoid violating the assumptions of variance and normality, the response variable, biomass, was log transformed. After the model selection using the BIC, an analysis of variance (ANOVA) was performed to analyze the differences among the different group medians. A resulting p-value of <.0001 indicated a significant impact of the horizontal strata on the volume of biomass per branch (Appendix A, Table 10). The log biomass estimates were then back-transformed, reported in the median values of each strata and aspect. The volume of live biomass per branch decreased with increasing height within the crown (Table 1). This pattern followed a strong linear relationship with a R^2 = 0.9811 (Figure 4). The distribution of live biomass by crown aspect also showed a significant difference on biomass allocation, although it was not a linear relationship (Figure 5). A p-value of <.0001 indicated at an α-level of 0.05 the South aspect was significantly different than other aspects (Appendix A, Table 11).

Table 1. Crown characteristics of 70-90 year-old lodgepole pine trees by branch. Values of total biomass and foliar herbivory are medians, as the data was originally on the logarithmic scale and then back-transformed. The values for foliar retention are means as they were never log-transformed. The values for all three attributes were pooled across 33 trees sampled within the four plots. The influence of crown third was not affected by crown aspect so the data is shown in separate pools. Values followed by different letters were significantly different at an α-level of 0.05.

Crown Location	Sample Size (# branches)	Total Biomass (g/branch)	Foliar Herbivory (% leaf area /branch)	Foliar Retention (years)
Crown Third:				
Upper	*380*	*113.58 a*	*0.97 a*	*5.46 a*
Middle	*328*	*153.38 b*	*1.06 b*	*5.90 b*
Lower	*216*	*177.76 c*	*1.29 c*	*5.68 c*
Crown aspect:				
North	*205*	*132.42*	*1.025*	*5.63*
South	*261*	*177.37 a*	*1.102*	*5.65*
East	*231*	*127.22*	*1.047*	*5.67*
West	*227*	*122.57*	*1.088*	*5.70*

Distribution of Herbivory

In order to avoid violating the assumptions of variance and normality, the response variable, herbivory, was log transformed. After the model selection using the BIC, an analysis of variance (ANOVA) was performed to analyze the differences among the different group medians. A resulting p-value of <.0001 indicated a significant relationship of the horizontal strata on the percentage of herbivory per branch (Appendix A, Table 12). The log herbivory estimates were then back-transformed, reported in the medians of each strata and aspect. The percentage of herbivory per branch decreased with increasing height within the crown (Table 1). This pattern followed a strong linear relationship with a $R^2 = 0.940$ (Figure 6). The distribution of herbivory by crown aspect did not show a significant difference on the distribution of herbivory (Figure 7). A p-value of 0.5189 indicated at an α-level of 0.05 crown aspect did not have a significant impact on the distribution of herbivory. (Appendix A, Table 13).

Influence of Crown Location on Foliar Retention

After the model selection using the BIC, an analysis of variance (ANOVA) was performed to analyze the differences among the different group means. A resulting p-value of 0.0023 indicated a significant relationship of the vertical strata on the foliage retention per branch (Appendix A, Table 14). The age of the foliage that was retained was significantly different in the upper crown than the middle, or lower crown (Table 1). The middle crown had the highest retention of foliage, however it was not significantly different that the retention in the lower crown (Figure 8). The crown aspect did not result in a significant difference on foliage retention (Figure 9). A p-value of 0.9741 indicated at an α-level of 0.05 crown aspect did not have a significant impact on foliar retention. (Appendix A, Table 15).

Cumulative Crown Biomass and Herbivory Estimates

Using the total number of branches per tree section, the branch biomass (Table 2) and herbivory estimates (Table 3) were extrapolated from the branch scale to the tree crown scale. The number of branches per vertical strata increased with increasing height. The middle crown third reported the highest level of biomass, followed by the lower crown and ultimately the upper crown (Table 2). The estimated volume of herbivory decreased as height increased within the tree crown. The percentage of leaf area consumption when each vertical strata was pooled over the 22 sampled trees within the four plots was 1.13% (Table 3).

Table 2. Crown Characteristics of 70-90 year-old lodgepole pine trees. Values of total biomass are medians that were derived over the average number of branches within each vertical strata pooled over the 33 sampled trees within the four plots. The median values per branch were extrapolated to each vertical strata based on the average total number of branches present within each vertical strata across all 33 trees.

Crown Location	Average # of Branches	Estimate of Total Crown Biomass (g)
Crown Third:		
Upper	*57.4*	*6522.25*
Middle	*49.4*	*7571.39*
Lower	*40.1*	*7126.56*
Total	*146.9*	*21220.20*

Table 3. Crown Characteristics and herbivory of 70-90 year-old lodgepole pine trees. Values of average foliage per strata were derived over the average number of branches within each vertical strata pooled over the 33 sampled trees within the four plots. The values for the percentage of foliar herbivory per branch are medians that were also pooled across all 33 trees within the four plots.

Crown Location	Average # of Branches	Average Foliage per Branch (g)	Estimate of Foliage per strata (g)	Foliar Herbivory (%/branch)	Estimate of Consumed Foliage (g)
Crown Third:					
Upper	*57.4*	*69.92*	*4013.20*	*0.97*	*38.93*
Middle	*49.4*	*74.37*	*3674.00*	*1.06*	*38.94*
Lower	*40.1*	*74.57*	*2990.29*	*1.29*	*38.57*
Total	*146.9*		*10677.50*	*1.13*	*116.45*

Discussion

Effects of Vertical Position and Crown Aspect on Live Biomass Distribution

We found that as the vertical position of a branch within the tree crown increases the total biomass of that branch decreases linearly (Table 1; Figure 4). We also found that crown aspect had a significant effect on live biomass distribution, with the South aspect containing a significant amount more than the other aspects (Table 1). Both of these findings were consistent with previous work (Garber and Maguire 2005; Schoettle and Smith 1991; Oker-Blom and Kellomaki 1982), however this study is unique in that it was performed in a single-species stand with many of the confounding environmental factors controlled for. It has been shown that stand density (Xu and Harrington 1998), species composition (Garber and Maguire 2005), tree health (Weiskittel 2003) and stand age (Jerez et al 2005) are influential factors in individual tree vertical distribution of leaf area. The study took place within a single stand of lodgepole pine with a common stand density, species composition and in a single aged cohort, which controlled for the random effects of these confounding variables within this site.

The biomass estimates were derived from the combination of the woody branch, foliage, cone and flower biomass that was separated and dried within the lab. The study was consistent with previous studies in that branch size decreased as vertical position within the crown increased, which was the ultimate driver of biomass distribution (Garber and Maguire 2005). Although the average number of branches per vertical strata increased with increasing vertical location, the overall biomass per branch decreased with increasing vertical location. This pattern of vertical distribution is tied closely to the distribution of branch diameter (Garber and Maguire 2005; Van Pelt and Nadkarni 2004). This pattern has been shown to be a function of crown spacing and light interception throughout the crown (Oker-Blom et al 1991).

The importance of crown architecture on sunlight interception has been discussed by Horn (1971), Schoettle and Smith (1991) and others. My study found that there was a significant difference in the biomass distribution by crown aspect, with the south aspect exceeding the others. This finding is consistent with those found in previous work with Rocky Mountain lodgepole pine (Schoettle 1991; Oker-Blom et al 1991). The increased sunlight availability on the south aspect of the tree promotes increased biomass distribution over the competing aspects. All trees within this study were chosen to be spatially independent from one another, which may have had an impact on the ability for sunlight to penetrate the stand. This pattern of biomass distribution is an important facet of crown architecture as it has been shown to have a direct impact on sunlight interception, influences the allocation of foliage (Schoettle and Smith 1991) and ultimately influences the tree's ability to grow (Jahnke and Lawrence 1965; Oker-Blom and Kellomaki 1983).

Effects of Vertical Position and Crown Aspect on Herbivory Distribution

My results show that with increasing vertical position within lodgepole pine crowns there was a negative linear relationship with the percentage of leaf area that was consumed (Figure 6). The overall leaf area consumption ranged from <1% in the upper crown to ~1.3% in the lower crown, demonstrating a low level of consumption overall. The study also found that crown aspect had no significant impact on leaf area consumption, with all values being around 1% (Figure 7). Both of these finding were novel when compared to the relatively limited data available for the distribution of arthropod herbivory within individual pine tree crowns.

There has been a significant amount of work done on the effect of vertical strata within deciduous trees. Ulyshen (2011) found that predation and changes in foliage characteristics impact the presence and abundance of arthropods in deciduous trees, of which some patterns may be relevant to coniferous trees. For example, it has been shown that the vertical arrangement of leaves within both deciduous and coniferous trees vary physiologically (Clancy et al. 2004), which may be

tied to light interception and photosynthesis contribution. Upper canopy, sun exposed leaves are thicker, tougher and more chemically defended in both deciduous and coniferous forests (Ulyshen 2011; Bond et al. 1999). These differences in leaf physiology may contribute to the distribution of insect taxa throughout the crown (Schowalter and Ganio 1998). Vertical position may also have an impact on the predation rate of herbivores within the tree crown, as it has been shown that both birds and ants impact the survival of some endemic herbivores, especially in the larval state (Campbell et al. 1983; Campbell et al. 1984)

In previous work done in coniferous forests it has been shown that the herbivory averages were <3% for *Pseudotuga menziesii, Tsuga heterophylla, Abies grandis*, and *Thuja plicata* (Schowalter and Ganio 1998). Other work in coniferous forests, predominantly *Pseudotuga menziesii,* has shown that individual trees are estimated to have a leaf area consumption of <2% (Shaw et al. 2006; Schowalter 1989; Schowalter and Ganio 1998). The study found similar levels of leaf area consumption in pines as other coniferous species, however the linear relationship of vertical crown position and herbivory is novel. Tree canopies are complex and many factors may impact and perpetuate this relationship. Canopy height likely affects the presence of different arthropod taxa that are sensitive to vertical gradients of light, foliage quality, and potential microclimate (Schowalter and Ganio 1998). These different gradients all interrelate and potentially impact each other differently on a tree level as dictated by the overall stand structure and complexity. The relationship that was found within this study was specific to an even-aged stand of 70-90 year-old lodgepole pine with little stand-level canopy heterogeneity.

In addition to the impact of crown height on herbivory, the arthropods themselves play an important role in the impact of herbivory within the crown. Depending on the taxa present within the tree canopy, different resources (nutrients, protection, moisture availability, etc.) are required that may be associated with different canopy levels (Schowalter and Ganio 1998). This allocation of resources within the canopy could drive arthropod distribution; for example insects that feed on

cones in the upper crown would not be expected to be present in the lower crown. Temperate

coniferous forests have also been noted to have the lowest level of herbivory out of all forest types

(Shaw et al. 2006). One potential reason for the low herbivory rate in coniferous trees may be due

to the low abundance of lepidopteran defoliators within these coniferous crowns (Shaw et al.

2006). The Douglas fir Tussock Moth, the Pandora Moth, and the Pine Butterfly are the three main

lepidopteran defoliators of pines, of which all three typically defoliate in a cyclical cycle with

generally low levels of endemic herbivory and epidemic defoliation events (Mason et al. 1998;

Speer et al. 2001; Evenden 1940). The literature states that as trees become larger in diameter and

height they have increased phloem thickness and resin flow, which may impact the trees defense

against insect attack (Davis and Hofstetter 2014; Baumgartner et al. 1985). Pines have a high level

of resin and monoterpenes when compared to deciduous trees, which decreases the level of foliar

herbivory (Chen et al. 2002; Kolb et al.1997).

The impact of crown aspect on herbivory, unlike vertical position, showed no significant

difference or pattern (p-value= 0.5189). Currently little is known about the relationship between

herbivory and crown aspect as the current literature on this topic for pine ecosystems is scant.

There is no evidence that needle physiology contains different levels of nutrients or photosynthetic

capability as it relates to crown aspect. Rather the influence of crown position and light interception

influences the growth of additional foliage on the South aspect of the crown (Schoettle and Smith

1991, Pearson et al. 1984), which is not unique in tree physiology. Since the percentage of

consumed leaf area in this study is being reported at an individual branch level, there was no

impact of the additional biomass found in the southern-crown aspect.

Effects of Vertical Position and Crown Aspect on Foliar Retention

Foliar retention and the distribution of leaf area within the tree crown is influenced by

stand structure, solar radiation interception and penetration, and the social standing (e.g., crown

classes) of the tree itself within the stand (Vose et al, 1994; Garber and Maguire 2005; Horn 1971). Retention and leaf area are tied closely to one another as areas that have a higher leaf area index tend to also maintain foliage for longer periods. My study found that vertical position within the crown had a significant relationship (p-value=0.0023) on needle longevity, with the mid-crown retaining needles the longest, followed by the lower crown and ultimately the upper crown (Table 1). In contrast, we did not find any significant influence (p-value=0.9741) of crown aspect on foliar retention, with all aspects retaining an average of ~6.7 years of foliage.

The vertical distribution of foliage age and leaf area index has been an area of interest for many prior studies (Schoettle and Smith 1991; Vose et al. 1994; Garber and Maguire 2005; Jahnke and Lawrence 1965). Vertical distribution of foliage is strongly tied to the abundance of solar radiation interception and penetration (Vose et al. 1994), which is a function of stand structure and age. As coniferous forests mature, canopy closure coincides with reduced penetration of radiation and the tree's ability to intercept that radiation. The impact of the trees social standing within the canopy when closure occurs impacts the distribution of leaf area, and ultimately foliage retention (Vose et al. 1994; Garber and Maguire 2005).

In even-aged stands stand density and age affect foliage distribution (Gary 1978). In young, open stands more foliage tends to be distributed in the lower portion of the crown, as shading and competition are not a limiting factor in radiation interception (Vose et al. 1994). As the stand matures and the canopy closes, the leaf area shifts upward toward the middle of the crown leading to leaf area that is normally distributed across the canopy. At higher stand densities the leaf area tends to shift into the middle to upper crown in an effort to maximize radiation interception. Even though the study occurred in an even-aged lodgepole pine stand, the sampled trees had spatially independent crowns where crown overlap was minimal, which could have allowed increased radiation penetration within the canopy. The greater level of radiation could have impacted the distribution of biomass into the middle crown, as opposed to upper crown.

While there is little published information about the relationship of crown aspect on foliar retention in lodgepole pine, my study found no significant effect (p-value=0.9741) of crown aspect on needle retention which contradicts previous research by Schoettle and Smith (1991). Their work showed a significant difference between the north and south aspects in Rocky Mountain lodgepole pine found in Colorado and Wyoming. One potential reason for the differences found in my study and the Schoettle and Smith (1991) study could be the effect of elevation. Higher elevation lodgepole pine needles have longer lifespans than lower elevation lodgepole pine trees (Reich et al. 1992), which may be an influence of a combination of lower temperatures, a shorter growing season and less available nutrients (Reich et al. 1995). This response has been found to be a largely phenotypic response (Reich et al. 1995), which could also influence the distribution of the leaf area index and ultimately impact the differences seen in needle lifespan throughout the crown.

Conclusions

The vertical position within tree crowns of central Oregon lodgepole pine has a significant impact on the distribution of total biomass per branch, the level of arthropod herbivory and needle longevity. Crown aspect has an influence on the distribution of total biomass, but no significant influence on herbivory or needle retention. My findings show that there are similarities between the lodgepole pine in central Oregon and the Rocky Mountains in biomass distribution throughout the tree crown, however there are also inherent differences present with needle retention and the distribution of that retention. I also found a linear pattern of herbivory within lodgepole pine crowns that has not been previously documented.

While the results here confirm some known relationships within pine crowns, there are several limitations with this study. All research took place within a single stand, which limits the scope of inference. The study was focused on the unique pumice plateau ecosystem of central

Oregon, which limits the ability for these results to be applied to other lodgepole pine ecosystems. The study also focused on the average co-dominant tree within the stand, which excluded much of the stand heterogeneity between trees (crown classes); this limitation limits the scope of the study to a specific subset of the actual stand population. Due to the inability to secure destructive sampling permits, all trees were sampled from a scaffold system which increased the potential error in calculating heights and total branch counts.

This work supports the body of knowledge that both vertical location and crown aspect have an influence on the distribution of biomass within the crown of lodgepole pine forests. This study could potentially have an impact on what is known about individual tree net primary production, radiation interception and how they interplay with biomass distribution in pines. More work should be done to gain a better understanding of the pattern of herbivory distribution throughout coniferous tree crowns. While the overall consumption of leaf area is low (at the time of sampling), there could be management implications of knowing how herbivory is distributed throughout a tree crown under both endemic and epidemic levels of defoliation. Finally there is an opportunity to further explore the effect of crown aspect on needle longevity and the impact that this may have on overall crown architecture and tree growth.

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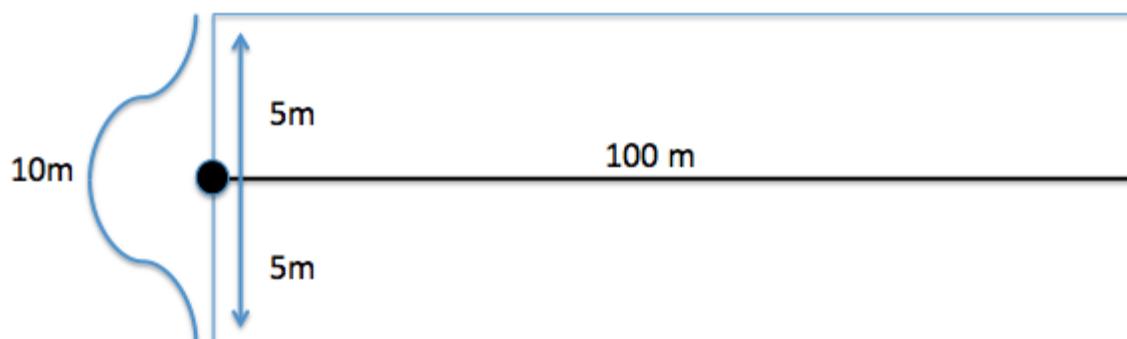
Figures

Figure 1. Diagram of belt transect (100 meters long by 10 meters wide, 5 meters to the left and right of the center line).

Vertically divide live crown into thirds

Give each third a rating of 0, 1, or 2 according to the following guidelines:
0 – no visible infections
1 – less than 50% of the branches are visibly infected
2 – over 50% of the branches are visibly infected

Add ratings for the thirds to obtain overall rating for the tree

The example tree would be rated a 0 in the top third, a 1 in the middle third, and a 2 in the bottom third, for an overall DMR of 3.
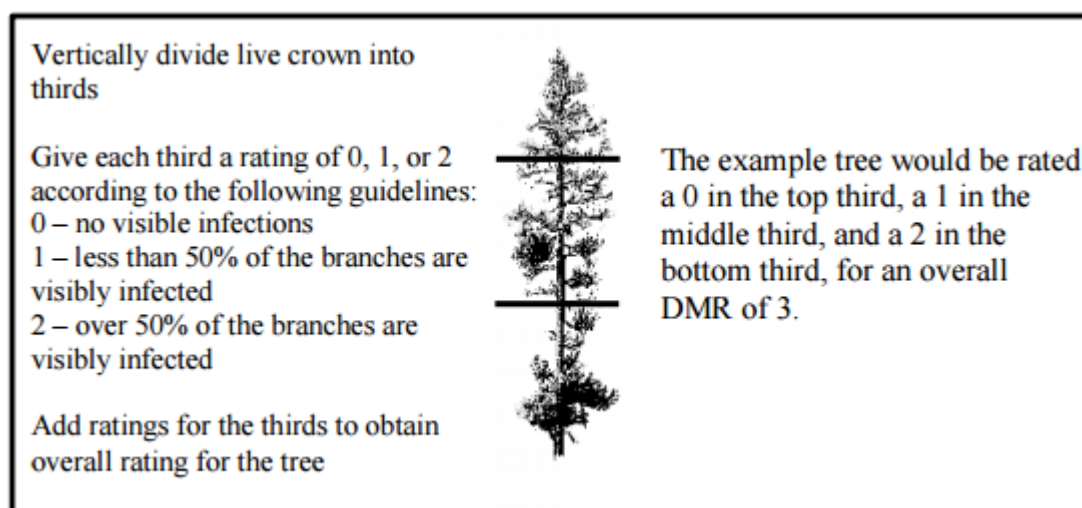
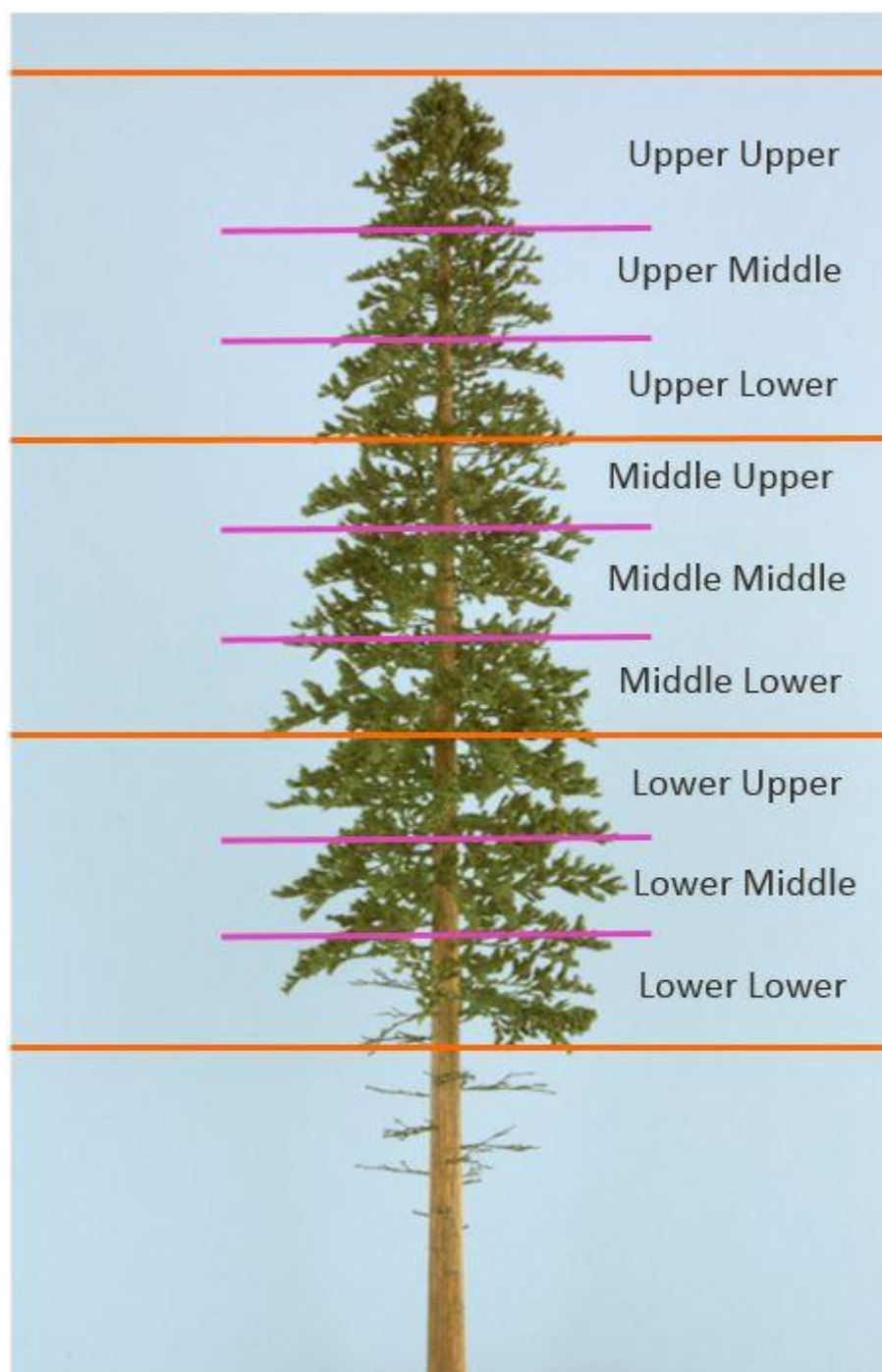Figure 2. Hawksworth's 6-class mistletoe rating system diagram (Hawksworth, 1977).

Figure 3. Diagram of vertical strata crown divisions. The crown was systematically divided into thirds, followed by thirds again to create nine distinct vertical strata.
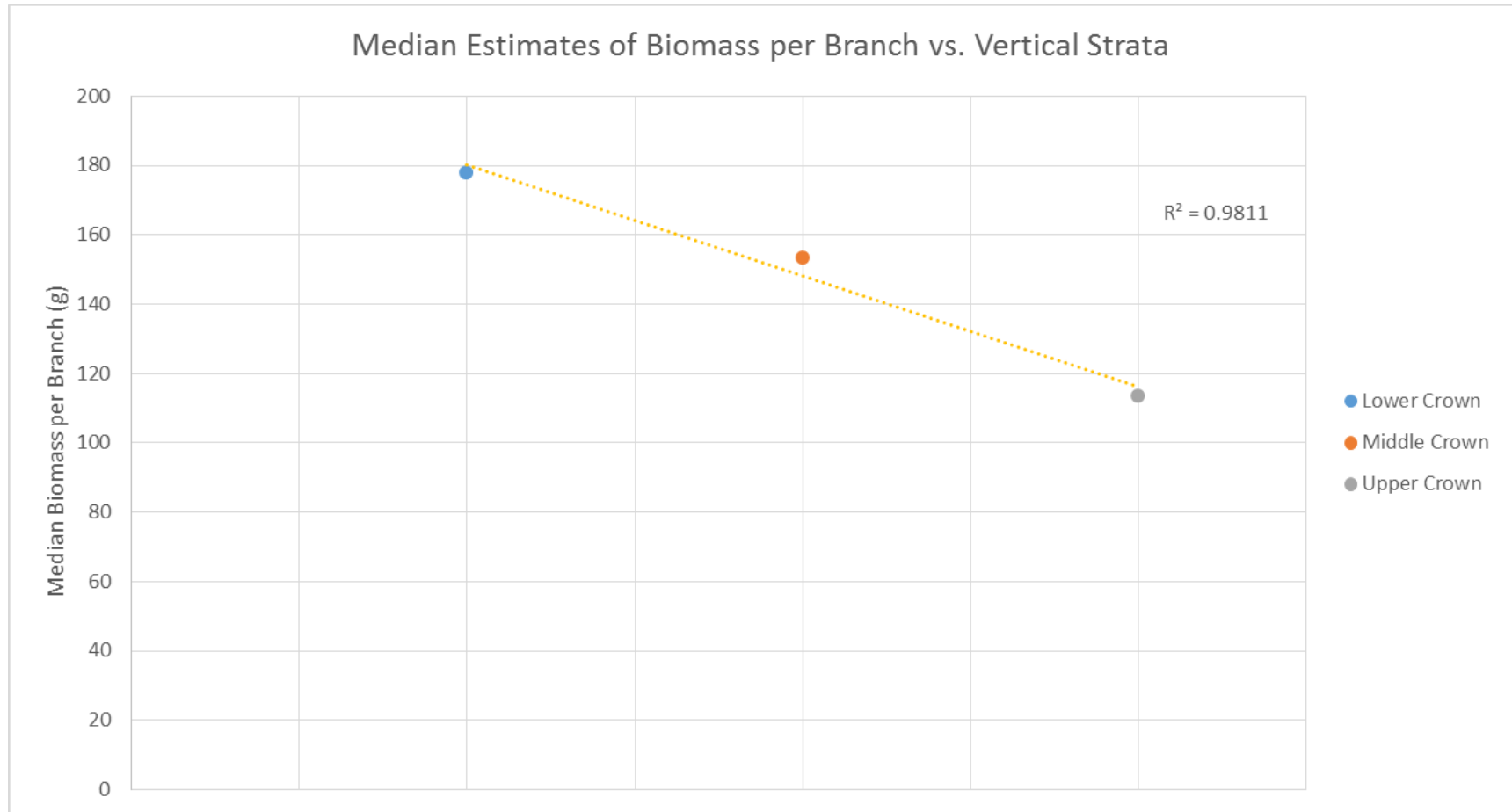
Figure 4. Graph showing the linear relationship of the median estimates of biomass per branch (g) compared to the vertical location of the branch within the lodgepole pine tree crown. There is a strong linear relationship present with an R^2 = 0.9811 indicating that the total volume of biomass per branch decreases as height within the tree crown increases.
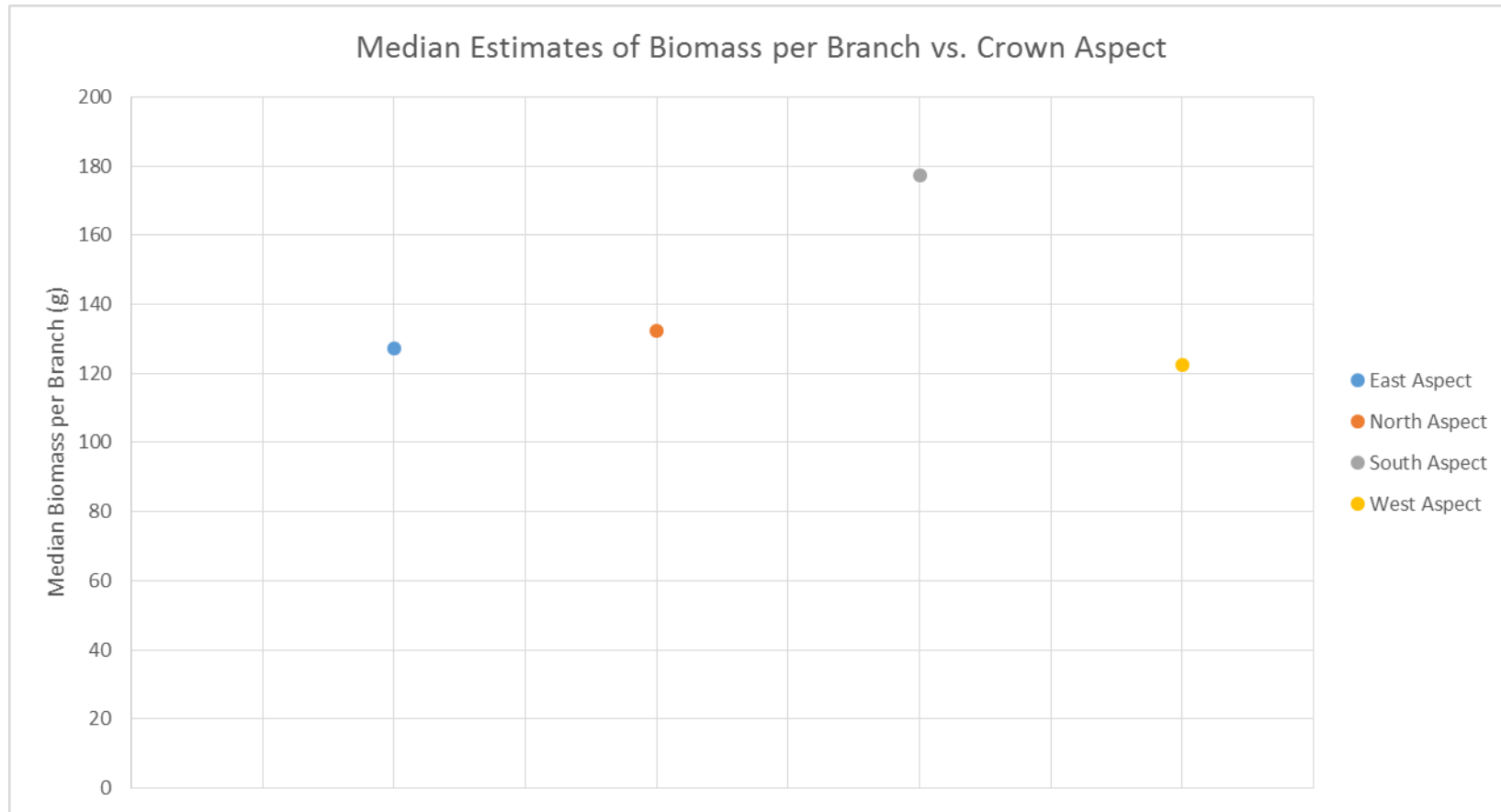
Figure 5. Graph showing the relationship of the median estimates of biomass per branch (g) compared to the crown aspect of the branch within the lodgepole pine tree crown. The south facing aspect is significantly different at an α-level of 0.05 containing a higher level of biomass than the other crown aspects.
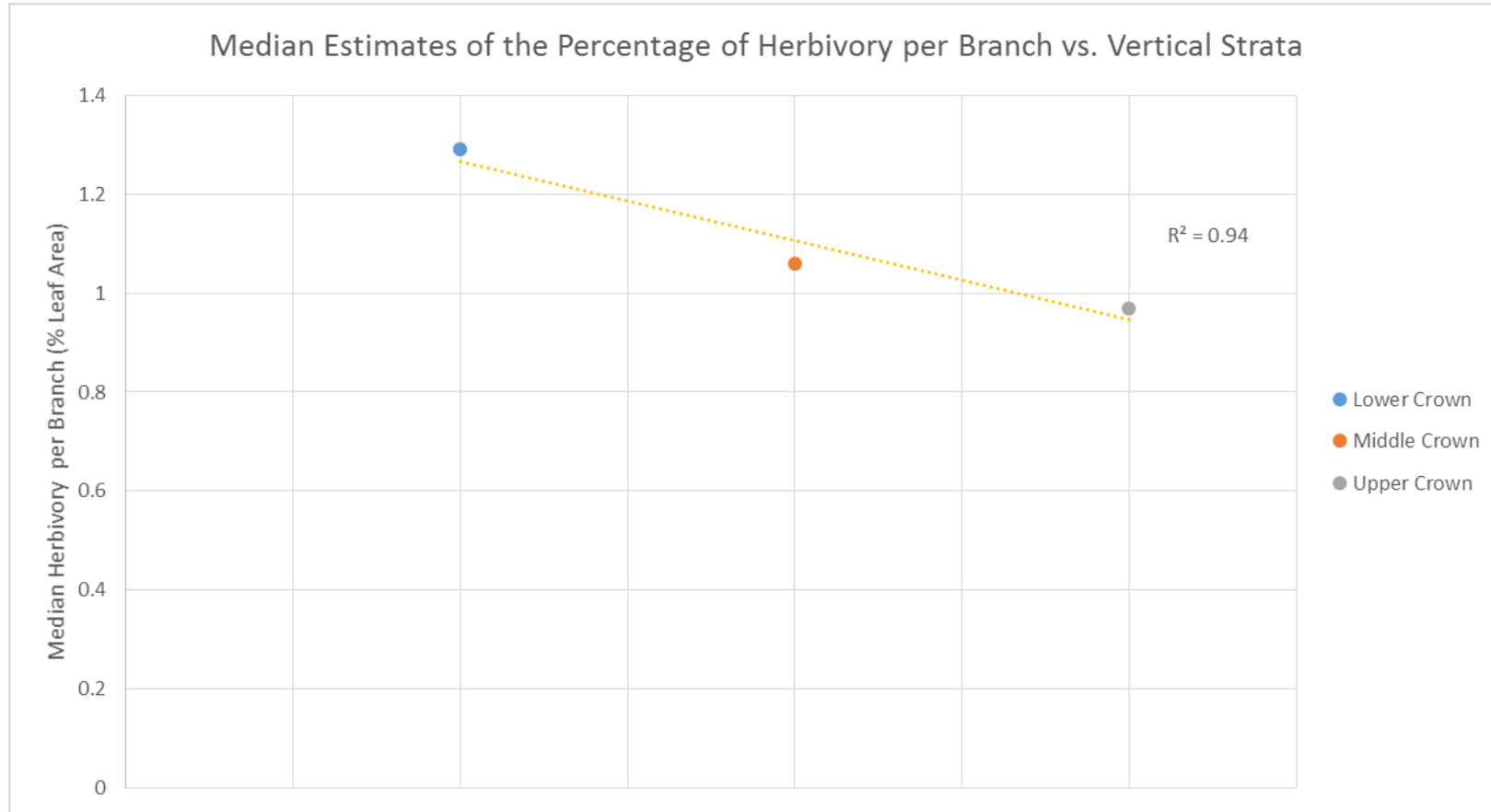
Figure 6. Graph showing the linear relationship of the median estimates of the percentage of consumed leaf area per branch compared to the vertical location of the branch within the lodgepole pine tree crown. There is a strong linear relationship present with an R^2 = 0.940 indicating that the total percentage of consumed leaf area per branch decreases as height within the tree crown increases.
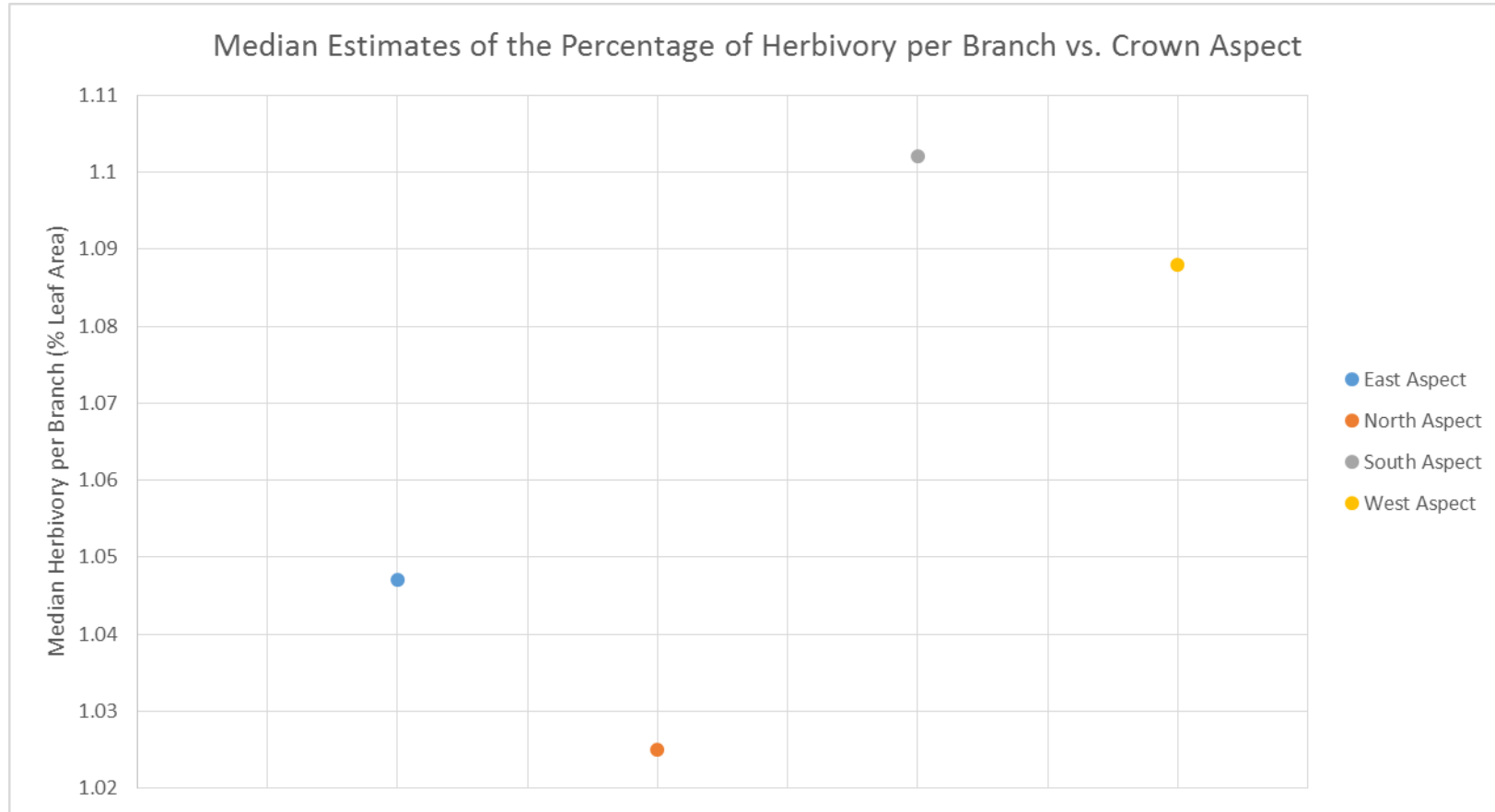
Figure 7. Graph showing the relationship of the median estimates of the percentage of consumed leaf area per branch compared to the crown aspect of the branch within the lodgepole pine tree crown. None of the values were found to be significantly different from one another with an ANOVA p-value of 0.5189.
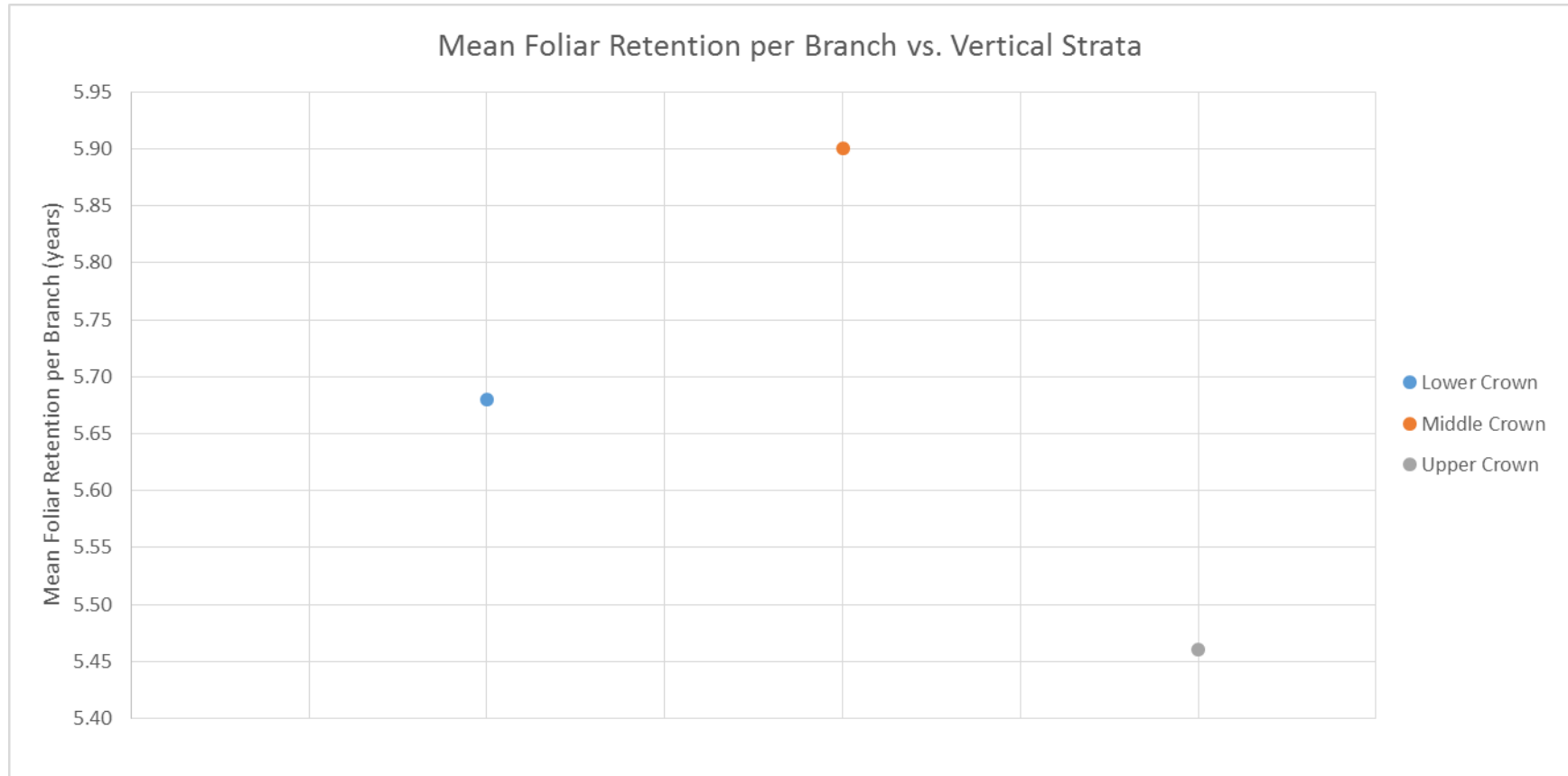
Figure 8. Graph showing the relationship of the mean estimates of foliar retention per branch (years) compared to the vertical location of the branch within the lodgepole pine tree crown. There was not a strong linear relationship between the vertical strata, however with an α-level of 0.05 the values were significantly different from one another.
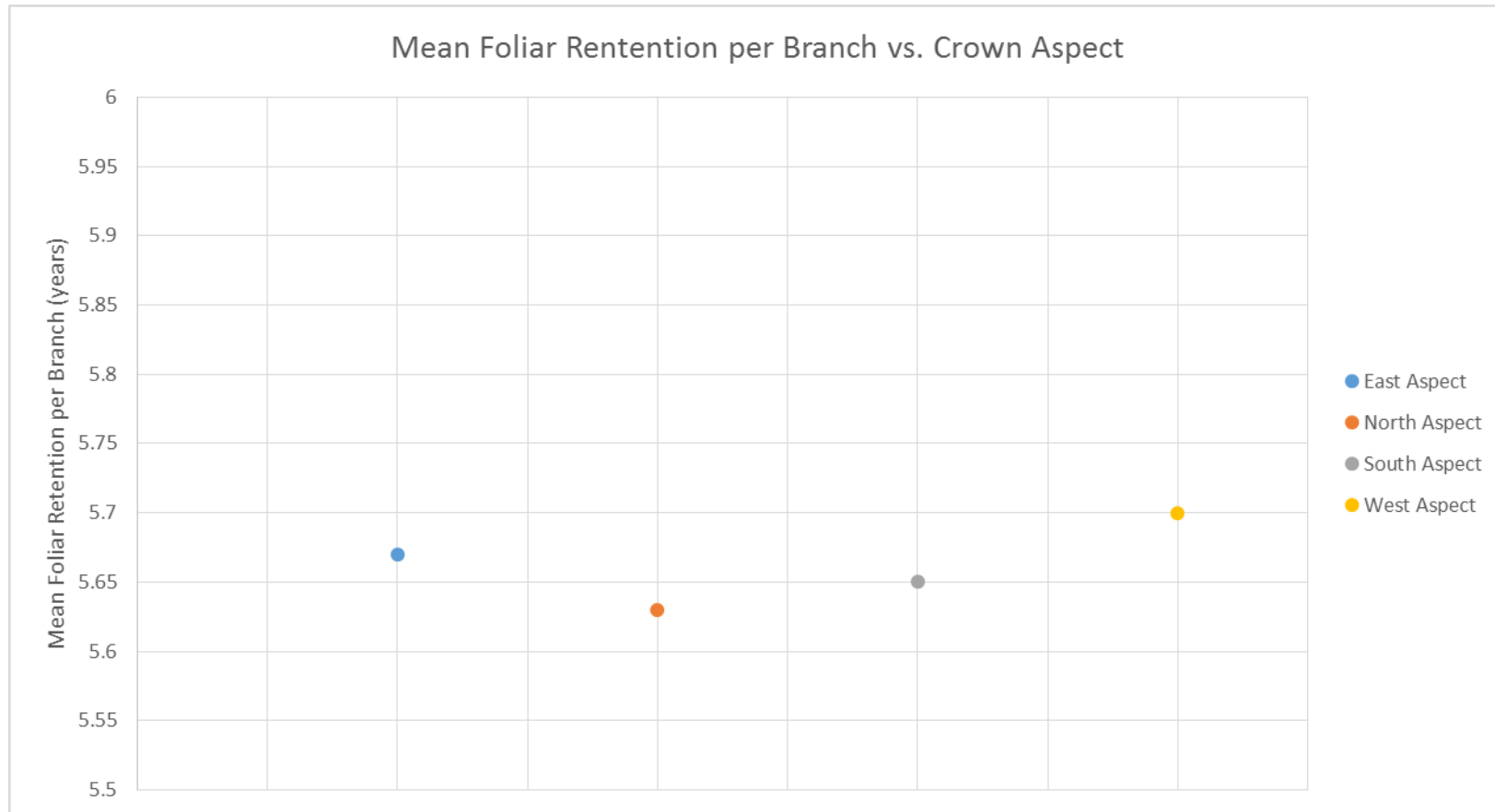
Figure 9. Graph showing the relationship of the mean estimates of foliar retention per branch (years) compared to the crown aspect of the branch within the lodgepole pine tree crown. None of the values were found to be significantly different from one another with an ANOVA p-value of 0.9741.

APPENDIX A

Tables

Table 1. Plot coordinates for all four belt transects located within the Deschutes National Forest in central Oregon.

Transect #		Plot Coordinates	
Transect 1	*Start*	*43°56'04.2581" N*	*121°35'34.4078" W*
	End	*43°56'06.4152" N*	*121°35'31.0459" W*
Transect 2	*Start*	*43°56'04.4629" N*	*121°35'35.3878" W*
	End	*43°56'01.5905" N*	*121°35'33.2774" W*
Transect 3	*Start*	*43°56'03.5222" N*	*121°35'33.2774" W*
	End	*43°56'00.3883" N*	*121°35'37.3334" W*
Transect 4	*Start*	*43°56'05.6651" N*	*121°35'38.4423" W*
	End	*43°55'59.8146" N*	*121°35'35.5861" W*

Table 2. Crown classification system used for the classification of live tree selection.

Class	Definition
Dominant	Trees with crown extending above the general level of the crown cover and receiving full light from above and partly from the sides. These trees are taller than the average trees in the stand and their crowns are well developed, but they could be somewhat crowded on the sides. Also,these are trees whose crowns have received full light from above and from all sides during early development and most of their life. Their crown form or shape appears to be free of influence from neighboring trees.
Codominant	Trees with crowns at the general level of the crown canopy. Crowns receive full light from above, but little direct sunlight penetrates their sides. Usually they have medium-sized crowns and are somewhat crowded from the sides. In stagnated stands, co-dominant trees have small-sized crowns and are crowded on the sides.
Intermediate	Trees that are shorter than dominants and codominants, but their crowns extend into the canopy of codominant and dominant trees. They receive little direct light from above and none from the sides. As a result, intermediates usually have small crowns and are very crowded from the sides.
Suppressed	Trees with crowns entirely below the general level of the crown canopy that receive no direct sunlight either from above or the sides.

Table 3. Table of codes used to describe the model inputs within the BIC candidate models. Codes are used in Tables 4-9.

Code	Description
lbio	*Log response of biomass per branch*
lhrb	*Log response of herbivory per branch*
age	*Response of foliar retention per branch*
plot	*Control for variability between plots*
tree	*Control for variability between individual trees*

Table 4. BIC table for the vertical distribution of biomass model. *lbio* represents the biomass, while *random = ~1|plot* accounts for the random variability within the plot, and *random = ~1|plot/tree* accounts for the random variability within both the individual tree and the plot. Note that the lower AIC and BIC values for model2 indicate that model2 provides a better fit than model1 when controlling for the variation at both the plot and tree level.

Model	DF	AIC	BIC	ΔBIC	
model1 = lme(lbio ~ Strata, random = ~1|plot, data=biomass)	917	2601.64	2625.76	124.38	
model2 = lme(lbio ~ Strata, random = ~1|plot/tree, data=biomass)	888	2472.43	2501.38	0	**

Table 5. BIC table for the distribution of biomass by crown aspect model. *lbio* represents the biomass, while *random = ~1|plot* accounts for the random variability within the plot, and *random = ~1|plot/tree* accounts for the random variability within both the individual tree and the plot. Note that the lower AIC and BIC values for model2 indicate that model2 provides a better fit than model1 when controlling for the variation at both the plot and tree level.

Model	DF	AIC	BIC	ΔBIC	
model1 = lme(lbio ~ Azim., random = ~1|plot, data=biomass)	916	2609.56	2638.5	114.254	
model2 = lme(lbio ~ Azim., random = ~1|plot/tree, data=biomass)	887	2490.48	2524.25	0	**

Table 6. BIC table for the distribution of herbivory by vertical strata model. *lhrb* represents the herbivory, while *random = ~1|plot* accounts for the random variability within the plot, and *random = ~1|plot/tree* accounts for the random variability within both the individual tree and the plot. Note that the lower AIC and BIC values for model2 indicate that model2 provides a better fit than model1 when controlling for the variation at both the plot and tree level.

Model	DF	AIC	BIC	ΔBIC	
model1 = lme(lhrb ~ Strata, random = ~1|plot, data=biomass)	917	1658.6	1682.72	22.328	
model2 = lme(lhrb ~ Strata, random = ~1|plot/tree, data=biomass)	888	1631.44	1660.39	0	**

Table 7. BIC table for the distribution of herbivory by crown aspect model. *lhrb* represents the herbivory, while *random = ~1|plot* accounts for the random variability within the plot, and *random = ~1|plot/tree* accounts for the random variability within both the individual tree and the plot. Note that the lower AIC and BIC values for model2 indicate that model2 provides a better fit than model1 when controlling for the variation at both the plot and tree level.

Model	DF	AIC	BIC	ΔBIC	
model1 = lme(lhrb ~ Azim., random = ~1|plot, data=biomass)	916	1695.38	1724.32	20.814	
model2 = lme(lhrb ~ Azim., random = ~1|plot/tree, data=biomass)	887	1669.74	1703.5	0	**

Table 8. BIC table for the arrangement of foliar retention by vertical strata model. *Age* represents foliar retention, while *random = ~1|plot* accounts for the random variability within the plot, and *random = ~1|plot/tree* accounts for the random variability within both the individual tree and the plot. Note that the lower AIC and BIC values for model2 indicate that model2 provides a better fit than model1 when controlling for the variation at both the plot and tree level.

Model	DF	AIC	BIC	ΔBIC	
model1 = lme(age ~ Strata, random = ~1|plot, data=biomass)	917	3766.33	3790.45	124.14	
model2 = lme(age ~ Strata, random = ~1|plot/tree, data=biomass)	888	3637.36	3666.31	0	**

Table 9. BIC table for the arrangement of foliar retention by crown aspect model. *Age* represents foliar retention, while *random = ~1|plot* accounts for the random variability within the plot, and *random = ~1|plot/tree* accounts for the random variability within both the individual tree and the plot. Note that the lower AIC and BIC values for model2 indicate that model2 provides a better fit than model1 when controlling for the variation at both the plot and tree level.

Model	DF	AIC	BIC	ΔBIC	
model1 = lme(age ~ Azim., random = ~1|plot, data=biomass)	916	3778.67	3807.61	120.774	
model2 = lme(age ~ Azim., random = ~1|plot/tree, data=biomass)	887	3653.07	3686.84	0	**

Table 10. ANOVA results showing a significant p-value of <.0001 for the impact of horizontal strata biomass volume per branch.

	numDF	denDF	F-Value	p-value	
(Intercept)	1	888	1718.8423	<.0001	
Strata	2	888	20.2387	<.0001	**

Table 11. ANOVA results showing a significant p-value of <.0001 for the impact of crown aspect on biomass volume per branch.

	numDF	denDF	F-Value	p-value	
(Intercept)	1	887	1742.5682	<.0001	
Azimuth	3	887	8.9736	<.0001	**

Table 12. ANOVA results showing a significant p-value of <.0001 for the impact of Strata on the percentage of herbivory per branch.

	numDF	denDF	F-Value	p-value	
(Intercept)	1	888	3.968332	0.0467	
Strata	2	888	17.674	<.0001	**

Table 13. ANOVA results showing a non-significant p-value of 0.5189 for the impact of crown aspect on the percentage of herbivory per branch.

	numDF	denDF	F-Value	p-value
(Intercept)	1	887	3.939263	0.0475
Azimuth	3	887	0.756095	0.5189

Table 14. ANOVA results showing a significant p-value of 0.0023 for the impact of Strata on the Foliar Retention (years).

	numDF	denDF	F-Value	p-value	
(Intercept)	1	888	1240.0647	<.0001	
Strata	2	888	6.1222	0.0023	**

Table 15. ANOVA results showing a non-significant p-value of 0.9741 for the impact of crown aspect on foliar retention (years).

|	numDF	denDF	F-Value	p-value
(Intercept)	1	887	1244.8367	<.0001
Azimuth	3	887	0.0736	0.9741

APPENDIX B

Stem and Branch Sample Processing

Stem and Branch Sample Processing (Lab) (Woolley et al. 2012)

Branch processing Steps

1. Remove samples from plastic bags.
2. **From secondary lateral branch (Figure below) determine foliage retention**

- **Foliage Retention (yrs.**) – The # of years of foliage remaining on a representative branch lateral shall be recorded to the nearest 0.1

year.
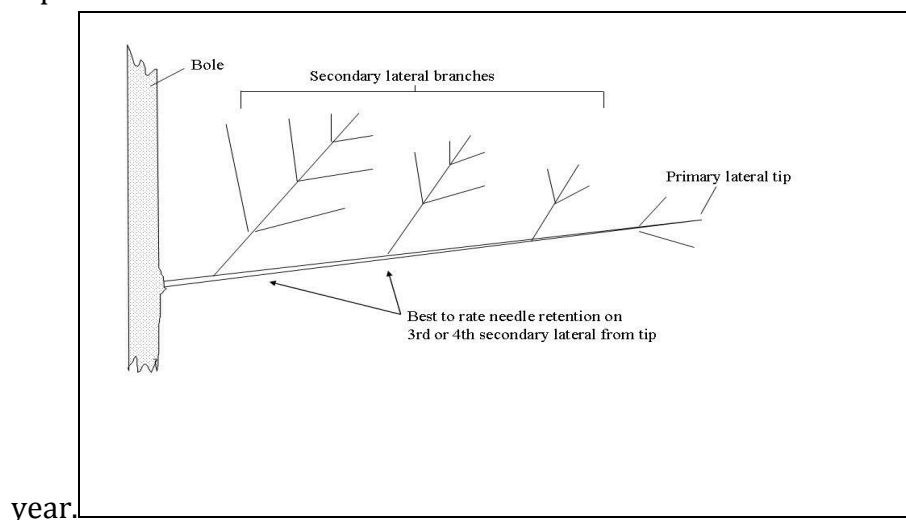
Figure 3

Examine secondary lateral branches on each sub-sampled branch and estimate the average number of annual needle compliments present. A *secondary lateral* is a branch that comes off the side of the main branch (Figure 2). Do not score the primary tip of the lateral for needle retention because it often loses foliage excessively and does not represent overall needle retention. **Estimate the number of annual needle compliments present for each branch to at least the nearest 0.1 year as per the following examples**:

0.5 = 50 % of one-year-old needles (1998) remain, all older needles gone
1.0 = All one-year-old needles remain, older needles gone
1.2 = One-year-old needles plus 20 % of two year old needles remain
1.6 = One-year-old needles plus 60 % of two year old needles remain
2.0 = One- and two-year-old needles remain, older needles gone
2.5 = One- and two-year-old needles remain, plus 50% three year old needles remain
3.0 = All one-, two-, and three-year old needles remain....
...and so on up to **6.0**.

3. Estimate **% Herbivory** of foliage on entire branch.

4. Using bud scars and branch color characteristics, separate foliage and foliated branches into annual age classes

   a. Cut branch segments at the top of bud scar, leaving bud scar as previous year's growth
   b. Use plates/frisbee to organize and keep track of age classes

5. All material that is LIVE and cannot be determined to have an age class will go into OTHER branch or OTHER foliage categories and bagged separately and label "**FO**" or "**BO**".
6. For dead secondary lateral branches, separately bag, and label as **DEAD**.
7. Label bags with information from note card and appropriate age classes of branches and foliage

   a. EXAMPLE: **EFR3-3-6-17 F1 (SITE-PLOT-TREE-BRANCH, FOLIAGE AGE 1)**
   b.

8. Bag foliage/branches by age classes, OTHER, and DEAD separately and bag accordingly.
9. If an entire branch is bagged separately and labeled brown, red, or **DEAD** with foliage, treat the same as live branches but label appropriately from information on notecard.
10. Staple bags.
11. Place in 55° C oven
    a. Check weights every day
12. Remove from oven once weights have stabilized(approx. 1 week)
13. Remove dried samples from bag onto tare plate
14. Weigh dried samples to nearest 0.01 gram.
15. Record weight on data sheet
    a. For **OTHER** foliage and branches label "**O**" on data sheet
16. *FOR BRANCH SAMPLES*
    a. Once branches are weighed by age class re-sort and separate woody branches into size classes and re-weigh

       Size classes

1.	0-3 mm	3.	6-10 mm
2.	3-6 mm	4.	10-25 mm
5.	25-50 mm	6.	50-75+ mm