DISSERTATION

CROWN CHARACTERISTICS OF INTERIOR WESTERN U.S. CONIFERS WITH

IMPLICATIONS FOR CANOPY FIRE HAZARD EVALUATION

Submitted by

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ABSTRACT

CROWN CHARACTERISTICS OF INTERIOR WESTERN U.S. CONIFERS WITH

IMPLICATIONS FOR CANOPY FIRE HAZARD EVALUATION

Tree crown characteristics are important determinants of forest stand features such as their potential to sustain canopy fire. There are characteristic differences between crowns of shade tolerant and shade intolerant conifer species: shade tolerant conifers generally have longer, fuller crowns than intolerant species. In this work, I investigated the response of vertical foliage distribution to stand density for a suite of western U.S. conifer species of varying shade tolerance and interpreted results in terms of canopy fire hazard evaluation. In addition, I evaluated whether diameter-based foliage area allometries differ between geographic areas in the interior western U.S. in order to gain insight into the extent that local allometries can be applied outside their area of origination. I found shade tolerant tree species maintained a greater proportion of their foliage in low light environments than intolerant species. This was consistent with lesser sensitivity of crown ratio to increasing stand density for tolerant compared to intolerant conifers. Regardless of species shade tolerance or stand density, the center of foliage mass within crowns was nearly always above the crown midpoint. Foliage mass was shifted upward and concentrated in closed-canopy forest stands compared to open-canopy woodland stands, which is consistent with greater light competition in closed-canopy stands. Foliage area allometries differed between geographic areas, and differences were species-specific. Using realistic depictions of the vertical distribution of crown fuels in a canopy fire hazard evaluation procedure resulted in dramatic increases in

estimated canopy bulk density for stands, with associated increases in estimated potential fire behavior.

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INTRODUCTION

Reduction of canopy fire hazard through fuels reduction treatments is a central focus of

forest management in western U.S. conifer forests. Fuels treatments consist of thinning to reduce

stand density, which in turn reduces the continuity of fuels in the canopy. Most assessments of

canopy fire hazard for forests in the interior western U.S. rely on characterizations of the canopy

fuels complex and predictions of potential fire behavior obtained using the Fire and Fuels

Extension to the Forest Vegetation Simulator (FFE-FVS [Rebain et al. 2010]). The Fire and

Fuels extension to FVS predicts two types of canopy fire behavior based on stand structure, fuel

moisture and wind speed – passive and active crown fire (Scott and Reinhardt 2001). Passive

crown fire occurs when there is sufficient connectivity between surface and canopy fuels to

spread surface fire vertically into the main canopy at a given wind speed. The readiness with

which fire can transition from surface to canopy fuels is dependent to a large degree on canopy

base height (CBH). Active crown fire occurs when there is sufficient horizontal continuity of

fine fuels (e.g. foliage and twigs) at any height in the canopy to carry fire from tree to tree at a

given wind speed. The density (kg m^{-3}) of needles and small branches in a given volume of space

is used to quantify canopy fuel continuity and is called canopy bulk density (CBD).

Accurate estimation of the amount and vertical distribution of canopy fuel is critical for

prediction of the likelihood of passive or active crown fire. The Fire and Fuels Extension to FVS

uses diameter-based crown biomass allometries to predict crown mass. Most allometries

incorporated in FFE-FVS were developed by Brown (1978) using data obtained from trees in

northern Montana and Idaho. These models, therefore, may not represent the full range of

variation in allometric relationships across the interior western U.S. Furthermore, FFE-FVS

assumes fuel (foliage and half of 1-hr fuel [Bradshaw et al. 1983]) is distributed uniformly within individual crowns, which is unrealistic (Reinhardt et al. 2006; Keyser and Smith 2010). Inaccurate crown mass estimation and unrealistic vertical crown profiles may result in underestimates of CBH and CBD from FFE-FVS and therefore produce inaccurate estimates of potential fire behavior.

A measure of 'effective' CBD is generated in FFE-FVS by summing the crown mass of individual trees by 0.3 m (1.0 ft) height intervals across the canopy and then dividing by the volume of the height interval extended over an area of 0.4 ha (1.0 ac). The greatest running mean interval CBD is indicative of the potential for canopy fire contagion and is thus taken as an estimate of CBD for the canopy as a whole. Keyser and Smith (2010) found using a local crown fuel biomass allometry in combination with a non-uniform vertical fuel distribution assumptions resulted in a 78% increase in estimated CBD on average over estimates from the production version of FFE-FVS for Black Hills ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). Forty-seven percent of the increase came from using the local biomass allometry, while the remainder was attributable to relaxing the assumption of uniformity for vertical crown fuel distribution. This suggests predictions of likely crown fire behavior from FFE-FVS are in error, resulting in incorrect evaluations of CBD response to fuel treatments. In Keyser and Smith (2010), only two of 16 stands evaluated had CBD estimates > 0.10 kg m^{-3} (the CBD threshold for active crown fire [Keyes and O'Hara 2002]) from the production version of FFE-FVS. The number increased to 12 when the local allometry and non-uniform fuel distribution were used.

The above results are consistent with results from Reinhardt et al. (2006), who found that current procedures for estimating CBD based on a uniform vertical distribution of canopy fuel (e.g., dividing the sum of the biomass of individual tree crowns by canopy depth) were not

accurate when compared to CBD empirically determined by felled tree measurements in five dense stands across the western U.S. This suggests that canopy fire hazard evaluation using FFE-FVS is likely to lead to insufficient density reduction in fuels treatments and overestimation of the duration of treatment effectiveness.

This dissertation describes investigations into the nature of variation in crown biomass configuration for conifer species in the interior western U.S., the generality of diameter-based allometric relationships derived from data collected in discrete geographic areas, and the impact of these factors on canopy fire hazard assessment using FFE-FVS. Chapter 1 details an empirical test of predictions from a conceptual model that postulates the distribution of foliage within crowns is dictated in part by the capacity of a given species to retain foliage in low light environments. Chapter 2 describes an investigation of whether diameter-based foliage area allometries differ between geographic areas in the interior western U.S. corresponding to the areas sampled in Brown (1978) and more southerly locations where the allometries developed in Brown (1978) are routinely applied, and whether differences between allometries depend on choice of predictor variables. Chapter 3 characterizes the range of variation in the vertical distribution of crown biomass across forest types (closed- versus open-canopy forests), species, stands and trees within stands, and assesses the predictability of biomass distribution from stand density and species' shade tolerance. Finally, Chapter 4 describes an investigation of the impact of incorporating realistic crown biomass distributions in FFE-FVS on canopy fire hazard assessment.

CHAPTER 1: AN EMPIRICAL TEST OF PREDICTED TRENDS IN CROWN

HOLLOWING AND SELF-PRUNING WITH RESPECT TO SHADE TOLERANCE

FOR SYMPATRIC CONIFER SPECIES

1.1 Introduction

The term 'crown hollowing' describes the development of non-uniform foliage

distributions in conifer crowns. Once crowns grow large, foliage is densest near their exteriors;

interiors are 'hollow' by comparison (p. 111, Assmann 1970). 'Self-pruning' is a related

phenomenon where the lowest branches in crowns die and eventually abscise in crowded

growing environments (Sorrensen-Cothern, Ford, and Sprugel 1993). The phenomena of crown

hollowing and self-pruning are presumed to be plastic responses of crown architecture to light

competition. Consequently, shade tolerant tree species, which exercise conservative resource use

strategies to enhance fitness in low light environments (Wright et al. 2004), tend to have fuller,

longer crowns than intolerant species. In this study, we compare light extinction and foliage

occurrence for crowns and canopies of two conifer species to ascertain whether characteristic

differences between species are attributable to differences in their tolerance to shade.

It is generally accepted that crown hollowing arises from self-shading in evergreen

conifer crowns (Xu and Harrington 1998; Duursma et al. 2010). Annual foliage production is

concentrated in active growth zones near branch tips and in upper crowns. This new growth

shades older foliage in crown interiors, which eventually dies. The effect is most apparent in the

crowns of large trees, where self-shading is advanced (Porté et al. 2000). The minimum quantity

of photosynthetically active radiation (PAR) required for foliage to maintain a positive net

carbon balance in its growing environment has been termed the ecological light compensation

point (ELCP [Schoettle and Fahey 1994]). There is evidence that PAR at the inner boundary of live foliage on conifer shoots is constant for a given species and site (Schoettle and Smith 1991; Han et al. 2003). This constant value of PAR presumably reflects the ELCP of foliage in crowns.

Self-pruning is thought to result from diminished PAR near crown bases in crowded growing environments (Mäkelä and Vanninen 1998). Like crown hollowing, self-pruning is likely the result of foliage death when PAR falls below the ELCP. Individual branches within crowns are largely independent in terms of growth and survival (Kawamura 2010). Branches die and are eventually shed as PAR at the crown base declines over time as a result of increased shading from growth of the crown and of neighboring trees. This interpretation of the self-pruning relationship is supported by modeling work that shows realistic representations of tree crowns can be created by simulating self-pruning as a response to light competition (Sorrensen-Cothern, Ford, and Sprugel 1993). Empirical results are consistent with modeling work, showing self-pruning is accelerated in crowded stands with greater shading of lower crowns relative to the rate of self-pruning in less crowded stands (Baldwin Jr et al. 2000).

Shade tolerance has been called the whole-plant light compensation point (Baltzer and Thomas 2007). Tree species that are tolerant of shade are able to survive at lower levels of PAR than intolerant species (Valladares and Niinemets 2008). Shade tolerance is associated with conservative growth resource use strategies that involve tradeoffs with respect to potential growth and resource acquisition (Ameztegui and Coll 2011). Intolerant species may produce more biomass than tolerant species at a given level of PAR, but tolerant species are able to persist at lower levels of PAR because the baseline level of photosynthesis required for survival is lower (Reich et al. 2003). Some research suggests shade tolerant species have lower leaf-level

light compensation points than intolerant species (Craine and Reich 2005), though the evidence for this is mixed (Reich et al. 2003).

Shade tolerant conifers typically have fuller, longer crowns than intolerant species (Canham et al. 1994). While crown architecture is the product of numerous factors, including genetically-programmed modular growth rules and hormone-mediated interactions between semi-independent branches in heterogeneous light environments (Kawamura 2010) as well as external factors such as mechanical damage, a simple conceptual framework developed to explain differences in foliage retention times between *Pinus* species can be extended to explain characteristic differences between the crowns of tolerant and intolerant conifers (Schoettle and Fahey 1994). Schoettle and Fahey (1994) maintained variation in foliage retention time between species was related to tree growth rates. Foliage is retained in crowns until self-shading from annual foliage production reduces available light below the ELCP. Faster growth thus translates into more self-shading and shorter foliage retention times. This conceptual model has since been substantiated by in-situ forest fertilization experiments and common garden studies (Reich et al. 1996; Balster and Marshall 2000). It follows that shade tolerant species have fuller crowns because they have lower ELCPs than intolerant species, permitting more layers of foliage to accumulate in crowns before PAR is sufficiently reduced to initiate crown hollowing. Similarly, tolerant species with low ELCPs can maintain longer crowns than intolerant species because self-pruning initiates at lower levels of PAR, allowing tolerant species to form deeper canopies with more layers of foliage.

This paper describes empirical tests of predictions based on the conceptual model of Schoettle and Fahey (1994). We tested predictions by evaluating trends in crown hollowing and self-pruning with respect to light availability for conifer species of differing shade tolerance.

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Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) frequently co-occur in interior western U.S. forests. Of the two species, Douglas-fir is considered more tolerant of shaded growing environments (Burns and Honkala 1990). Leaf-level light compensation points of ~80 μmol m^{-2} s^{-1} have been measured for ponderosa pine (Zhang et al. 1997), compared to <50 μmol m^{-2} s^{-1} for Douglas-fir (Lewis, Olszyk, and Tingey 1999; Lewis et al. 2000). We tested two specific predictions in this study: foliage is retained at lower levels of PAR in the crowns of Douglas-fir trees than in the crowns of ponderosa pine trees on the same site, and; self-pruning is associated with lower levels of light availability in Douglas-fir canopies than in ponderosa pine canopies.

1.2 Methods

Ponderosa pine and Douglas-fir are important tree species in interior western U.S. conifer forests. These species often coexist at elevations between ~2,000-3000 m, bound at lower elevations by xeric woodlands, shrublands and grasslands, and at higher elevation by subalpine conifer forests (Peet 1981). However, they are also frequently intermixed with other tree species outside of the elevation range in which they are dominant cover types. Ponderosa pine occupies somewhat drier sites than Douglas-fir. This means it can be a late-successional species at lower elevations, while it is usually seral to Douglas-fir and other shade tolerant conifers at higher elevations (Eyre 1980; Burns and Honkala 1990).

We investigated the relationship between foliage occurrence, light availability and shade tolerance at two levels of organization: individual tree crowns and canopies consisting of many crowns. For crowns, we measured PAR in the crowns of several under-story trees in one stand and also obtained branch-level foliage distribution data through destructive sampling; this enabled us to correlate foliage occurrence with light availability. By accounted for light

attenuation of over-story trees using a light extinction equation (p. 118, Landsberg and Sands 2011), we were able to compare ponderosa pine and Douglas-fir in terms of the proportion of above canopy light that reaches crown interiors as well as in terms of the proportion of total crown foliage in various within-crown light environments (ranging from ~1-40% of above canopy light availability). We collected crown-level data from trees growing in the same stand because there is evidence species ELCP varies between sites (Schoettle 1990). Consequently, site-related differences in ELCP could obscure differences between species if ponderosa pine and Douglas-fir trees were sampled from different sites.

We evaluated light attenuation through canopies by developing light extinction profiles for two-dozen stands using canopy foliage profiles. To develop canopy foliage profiles, we first estimated total canopy foliage area from inventory data using allometric foliage area estimators, and then distributed foliage vertically using empirically derived statistical distributions. We converted foliage profiles to light extinction profiles using the same light extinction equation incorporated in our crown-level analysis. This allowed us to compare species in terms of the proportion of above canopy light that reaches the canopy base as well as in terms of canopy base height at a given level of light availability, which reflects the extent of self-pruning. We accounted for potential between-site variation in ELCP in this analysis by sampling a multitude of stands, allowing us to investigate patterns of light availability and foliage occurrence across a range of sites for each species.

1.2.1 Crown-level Methodology

We collected crown-level data from three Douglas-fir and four ponderosa pine trees in the understory of a stand of larger trees. Understory trees were sampled because their short stature allowed us to access upper crowns for PAR measurement with a stepladder, and because

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preliminary evaluation of potential sample trees suggested crown hollowing had not yet occurred in similarly sized open-grown Douglas-fir trees. All sample trees were growing singly in the understory and had symmetric crowns. Our study site was located on the Canyon Lakes Ranger District of the Arapahoe-Roosevelt National Forest near the town of Red Feather Lakes, Colorado. The stand was typical of Foothill *Pinus ponderosa-Pseudotsuga* Forest (Peet 1981). Mean annual precipitation at the study site is ~47 cm, most of which falls during the growing season (WRCC 2014). The location is ~2,550 m in elevation, and experiences warm summers and freezing winters.

Above-branch PAR measurements were collected at the midpoint of every 10 cm increment from the bole to the branch tip for 20 branches of each sample tree. Branches were selected by dividing crowns vertically into five equal sections, then choosing the four major whorl branches in each section that were oriented closest to each of the four cardinal directions. We measured PAR using a paired sensor technique. A quantum sensor was mounted level at a height of 3.5 m on a pole adjacent to each sample tree crown to collect outside-crown PAR measurements. Within-crown measurements were collected using a 10 cm array of eight photosensors on a leveled probe (Decagon Devices Inc. 2006-2010). Simultaneous readings of radiation in the range 400-700 nm were collected from above- and within-crown sensors, yielding measures of light extinction through the crown at every measurement location. The quantum sensor was calibrated at the beginning of the field season, and the array of sensors on the probe was calibrated using the quantum sensor each day prior to sampling. Instantaneous PAR measurements were collected between 10:00-14:00 under overcast skies during the first two weeks of August, 2013. Similar methodologies have been shown to yield PAR values that are moderately correlated with growing season PAR (Gendron, Messier, and Comeau 1998).

We sampled foliage using methodology similar to that described by Kershaw and Maguire (1996). Branches were pruned after PAR measurement and were laid on a sheet on which we had drawn concentric circles in 10 cm radial increments so that cut ends of branches were at 0 cm (similar to Fig. 1 in Kershaw and Maguire [1996]). We used the concentric circles as guides to strip foliage from branches in 10 cm increments of crown radius from boles to branch tips. Foliage for each increment of every branch was weighed to the nearest 0.1 g in the field using a portable balance. In total, we measured PAR and weighed foliaged for 435, 10 cm segments of crown radius for four ponderosa pine trees, and for 387 segments for three Douglas-fir trees (Table 1.1).

We inventoried the stand from which we collected crown-level data using 0.05 ha fixed-radius plots centered on each sample tree. Inventory plot size was chosen so that the radius of plots approximately corresponded to the height of the tallest trees in the stand. Our inventory thus in-effect accounted for all neighbors within a tree-length of each sample tree. We recorded diameter at breast height (DBH [breast height = 1.37 m]), height, crown base height, species, and status (live or dead) for each tree ≥ 1 cm DBH in fixed-radius plots.

Table 1.1 Summary data for crown-level sampling. Ponderosa pine is PIPO and Douglas-fir is PSME. CBH is crown base height and N is the number of paired foliage weights and PAR measurements for each sample tree. TPH (trees ha^{-1}), BA (basal area) and LAI (leaf area index of trees > 3.5 m tall) were estimated from inventory data from fixed-radius plots centered on each sample tree.

Spp.	DBH (cm)	Height (m)	CBH (m)	N	TPH	BA (m^2 ha^{-1})	LAI
PIPO	8.1	5.2	1.5	141	620	23.9	2.7
	9.7	5.3	2.3	125	560	22.2	2.6
	5.5	3.4	0.6	107	660	22.0	2.6
	2.0	1.9	0.4	62	580	15.9	1.8
PSME	5.9	3.9	0.5	136	920	22.8	2.7
	6.1	3.8	0.0	143	860	24.5	3.0
	3.1	2.5	0.0	108	600	16.5	1.7

Our field measurements of PAR for crowns were in-effect estimates of light extinction through sample tree crowns; they did not account for light extinction by larger neighbors because the reference PAR sensor was positioned below the canopy. It was thus necessary to estimate light attenuation by the canopy above each of our sample trees. We accomplished this by estimating the foliage area above each sample tree using point-specific stand inventory data and DBH-based foliage area allometries, and then calculating percent PAR extinction using a published equation (p. 118, Landsberg and Sands 2011).

Foliage area allometries were developed for ponderosa pine and Douglas-fir using destructively-sampled data (described below in canopy-level methods). Allometries were of the form:

(Model 1.1) $$y = b_0 * x_1{}^{b_1} * x_2{}^{b_2}$$

where y is foliage area (m^2), x_1 is DBH (cm), x_2 is the distance from breast height to the center of the live crown (m), and the b's are estimated parameters. We chose this form because allometries based on DBH and some measure of crown size have been shown to yield good estimates of foliage area (Tobin et al. 2006), and because nonlinear allometries of the same form that use sapwood instead of DBH for x_1 have been shown to be unbiased by site quality, stand density and tree size (Long and Smith 1988, 1989; Ex and Smith 2014). Allometric models were fit using an iterative, derivative-free algorithm with DBH^{-3} as a weighting factor to satisfy assumptions of homoscedasticity as described by Keyser and Smith (2010).

We used Model 1.1 to estimate projected foliage area of inventory trees, then converted foliage area to leaf area index (LAI [a dimensionless measure of projected foliage area per unit ground area]) of only those trees with heights greater than 3.5 m (the height of the quantum

sensor adjacent to crowns). We used this value to estimate PAR above the main canopy based on our below canopy measurements using:

(Equation 1.1) $$I_0 = \frac{I_z}{e^{-kL_z}}$$

where I_0 is above canopy PAR (μmol m^{-2} s^{-1}), I_z is measured PAR at the quantum sensor (μmol m^{-2} s^{-1}), k is an extinction coefficient assumed to be 0.5, and L_z is LAI (p. 118, Landsberg and Sands 2011). Photosynthetically active radiation measurements from within crowns were converted to percentages of above canopy PAR (% PAR) by dividing them by I_0 and then multiplying by 100.

We compared curves describing foliage accumulation versus % PAR for ponderosa pine and Douglas-fir to evaluate the relationship between foliage occurrence, light availability and shade tolerance at the crown level. Foliage weights for all branch segments, branches and trees were combined for each species, ranked by the % PAR value associated with each sample weight, and then plotted against % PAR. Species curves were then compared to evaluate differences in PAR extinction through crowns (minimum values of % PAR for each species), and distribution of foliage mass relative to light availability.

1.2.2 Canopy-level Methodology

Canopy-level data was derived from 117 destructively sampled trees and 1,050 inventory trees from 24 pure, even-aged stands (Table 1.2). For both ponderosa pine and Douglas-fir, six stands representing ranges of stand density and average tree size were selected from corresponding south (Colorado, Utah, New Mexico and southern Idaho) and north (Wyoming, Montana and northern Idaho) populations (Appendix 1). Stands were chosen to be free of disease and any sign of disturbance within the previous 20 years. We did not attempt to control-for or investigate the potential effects of site quality.

Our field sampling methodology for canopies closely followed Keyser and Smith (2010). Briefly, we selected five trees for sampling in each stand that represented the range of tree sizes present in the main canopy. Trees with two tops, asymmetric crowns, or other obvious abnormalities were not sampled. Trees were felled and crowns were divided into 10 equal length sections. All live branches were removed from each section in turn and foliated twigs were clipped and weighed to the nearest g in the field by crown section using a hanging scale. Subsamples (~300 g) of foliated twigs from each section were then collected and weighed to the nearest 0.1 g using a portable balance, dried to constant weight, separated into woody and foliage components, and re-weighed for development of ratio estimators to determine total biomass of foliage for each crown section. Sampling and material processing methodologies are described in greater detail in Keyser and Smith (2010). We also performed point inventories in each stand using a single fixed-radius plot sized to include at least 30 overstory trees. All live trees ≥ 1 cm DBH (including sample trees) were tallied and species, DBH, height, and crown base height were recorded.

Table 1.2. Summary sample data for canopy level sampling. Species are as described for Table 1.1. N is # sample stands followed by # destructively sampled trees in parentheses. All other columns are means followed by minimum and maximum values in parentheses. DBH applies to destructively sampled trees only, while BA, QMD (quadratic mean diameter) and LAI are based on inventory data from fixed-radius plots. On average, LAI was greater for Douglas-fir stands than for ponderosa pine stands, and for north population stands than for south population stands.

Spp.	Pop.	N	DBH (cm)	BA (m^2 ha^{-1})	QMD (cm)	LAI
PIPO	North	6 (28)	26.7 (4.6, 55.4)	33.1 (14.1, 61.3)	26.9 (8.1, 43.7)	2.8 (1.7, 4.2)
	South	6 (29)	30.4 (8.1, 54.4)	26.9 (13.0, 39.6)	27.6 (14.5, 43.2)	2.1 (1.4, 3.4)
PSME	North	6 (30)	22.1 (6.1, 56.1)	43.4 (16.9, 62.0)	21.2 (14.7, 33.6)	5.7 (3.9, 9.4)
	South	6 (30)	22.9 (4.3, 54.6)	34.0 (11.5, 54.4)	21.3 (13.5, 34.0)	3.6 (2.4, 4.4)

In addition to the sampling described in Keyser and Smith (2010), we collected a foliage sample from the top, middle and bottom of each sample tree crown for determination of specific

leaf area (projected foliage area per unit of foliage mass). Specific leaf area was determined strictly for the purpose of estimating whole tree foliage area from foliage mass and was not analyzed further. Foliage area samples were placed in plastic bags and packed in ice upon collection, then frozen until they were processed in the lab. Processing consisted of scanning samples using a platen scanner, estimating projected area of scanned samples using digital image analysis software, drying samples to constant weight, and finally weighing samples to the nearest 0.01 g. This allowed us to develop ratios to convert foliage mass of crown sections to projected foliage area.

We constructed light extinction profiles for canopies by first developing cumulative vertical foliage area distributions for each stand, and then calculating light extinction using Equation 1 (similar to Fig. 3f. in Lieffers et al. [1999]). We used an iterative, derivative-free algorithm to fit foliage area of sample tree crown sections to a two-parameter cumulative Weibull distribution individually for each destructively-sampled tree in our dataset as described by Keyser and Smith (2010). The form of the model was:

(Model 1.2)
$$y = 1 - e^{\left[-\left(\frac{x}{\beta}\right)^{\alpha}\right]}$$

where y is the cumulative percentage of foliage area at x, and x is depth into the crown expressed as a percentage of total crown length. The estimated shape parameter α represents the degree to which foliage area is skewed upward or downward in crowns, while the estimated scale parameter β represents the degree to which foliage area is concentrated in a few sections versus spread evenly throughout crowns. After estimating α and β for each destructively sampled tree, we used Model 1.1 to estimate foliage area for all trees in canopy inventory plots and then used Model 1.2 with species average values of α and β to build vertical foliage area distributions. We then interpolated foliage area distributions of crowns to correspond to 0.5 m canopy layers and

summed foliage area of inventory trees for each layer. Diving this value by inventory plot size

yielded estimates of LAI for each 0.5 m canopy layer. Finally, we estimated percent light

availability for each canopy layer by setting I_0 in Equation 1.1 to 100 and solving for I_z.

We interpreted light extinction curves for stands of Douglas-fir and ponderosa pine to

evaluate the relationship between self-pruning, light availability and shade tolerance at the

canopy level. Light extinction curves reveal minimum values of light availability under canopies

of each species. Furthermore, because curves are derived from foliage profiles, the lower bound

of extinction curves can be interpreted as canopy base height, which is indicative of the extent of

self-pruning at a given level of light extinction. To prevent extinction curves from extending to

the lowest single live branch in stands (which was often well below the canopy base), we

developed curves using the uppermost 95% of foliage in stands.

1.3 Results

1.3.1 Crown-level Results

The ponderosa pine trees we sampled were somewhat larger on average than the

Douglas-fir trees (Table 1.1). LAI in the canopy above sample trees spanned similar ranges for

the two species. For each species, the smallest sample tree was growing in an open environment

relative to larger sample trees, with over-story LAI < 2 (Table 1.1). All estimated parameters for

Model 1 were significant at $\alpha = 0.05$ for both species (Table 1.3). There were no patterns in

residual error with respect to predicted values, DBH, or tree crown ratio.

Table 1.3. Parameter estimates and fit statistics for Model 1.1. Values are followed by estimated standard error in parentheses. Species are as described for Table 1.1. RMSE is root mean squared error. Bias is observed – predicted foliage area.

Spp.	b_0	b_1	b_2	RMSE (m^2)	Bias (m^2)
PIPO	0.03 (0.01)	2.84 (0.16)	-0.82 (0.15)	16.5	0.2
PSME	0.14 (0.05)	2.38 (0.20)	-0.69 (0.16)	20.5	-0.4

Douglas-fir crowns extinguished a greater proportion of above-canopy PAR than ponderosa pine crowns. We recorded % PAR values as small as ~1 in Douglas-fir crowns (Fig. 1.1). In contrast, the smallest % PAR values measured in ponderosa pine crowns were ~6. Proportionally more foliage was in low light environments in Douglas-fir crowns than in ponderosa pine crowns. Approximately 37% of Douglas-fir foliage mass was in locations where % PAR was < 10 (Fig. 1.1). By comparison, only ~6% of ponderosa pine foliage mass was growing at % PAR < 10. The disparity in proportional foliage distribution lessened as % PAR increased. ~90% of total foliage mass for both species was in locations with % PAR ≤ 22 (Fig. 1.1).
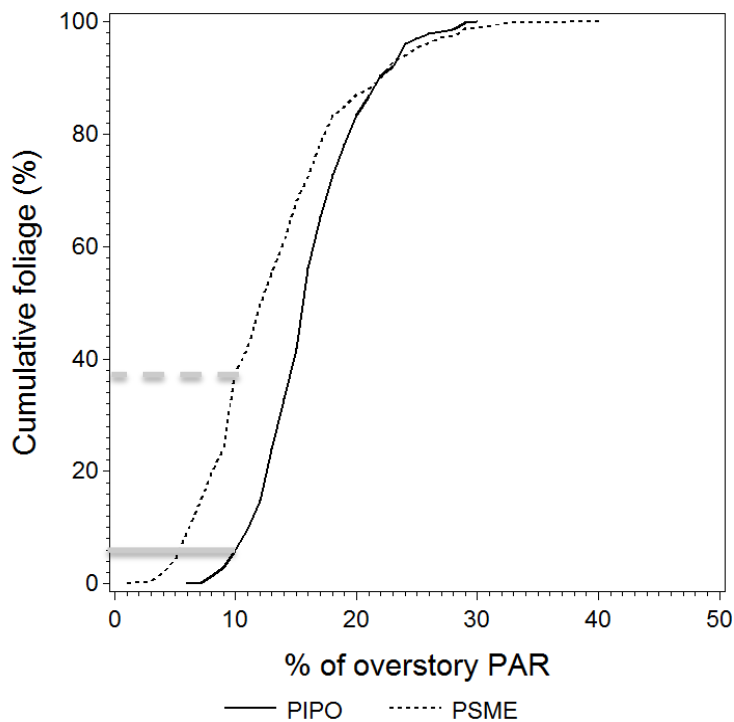

Figure 1.1. Foliage occurrence in crowns with respect to % PAR. Horizontal lines show almost 40% of foliage in Douglas-fir crowns occurs in locations that receive < 10% of above canopy PAR, compared to < 10% of foliage in ponderosa pine crowns.

1.3.2 Canopy-level Results

The average LAI of Douglas-fir stands (~4.7) was almost twice that of ponderosa pine

stands (~2.5). Leaf area index was also greater on average for stands in north populations than

stands in south populations for both species (2.8 versus 2.1 for ponderosa pine and 5.7 versus 3.6

for Douglas-fir [Table 1.2]). Mean Model 1.2 parameters were nearly the same for ponderosa

pine and Douglas-fir (Table 1.4). All Model 1.2 parameters were significant at $\alpha = 0.05$.

Table 1.4. Estimated Model 1.2 parameters for each species (as described for Table 1.1).
Minimum and maximum values follow means in parentheses.

Spp.	α	β
PIPO	2.5 (1.6, 3.8)	62.4 (49.0, 85.1)
PSME	2.4 (1.6,4.2)	59.1 (29.6, 81.5)
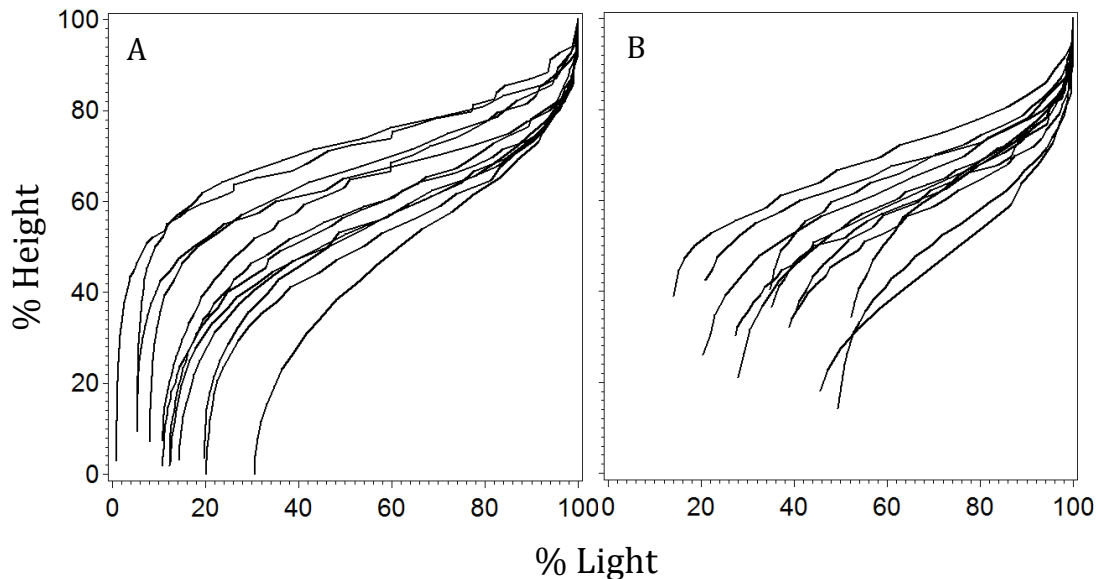
Figure 1.2. Estimated light extinction profiles for (A) Douglas-fir and (B) ponderosa pine
canopies. Lower extremes of profiles are canopy base height for each stand. Almost every
Douglas-fir canopy extinguished >~80% of above canopy light; the opposite was true for
ponderosa pine canopies.

Because Douglas-fir stands had greater LAI, they extinguished more light than ponderosa

pine stands on average. The densest Douglas-fir canopy extinguished ~99% of above canopy

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light, compared to a maximum of ~86% for ponderosa pine (Fig. 1.2). Foliage was concentrated higher in the canopy profile for ponderosa pine than for Douglas-fir. A comparison of Douglas-fir and ponderosa pine stands of similar LAI suggested self-pruning occurs at higher light availabilities for ponderosa pine than for Douglas-fir. At ~80% light extinction, canopy base height in a ponderosa pine stand was ~40% of stand height, while canopy base height in a comparable Douglas-fir stand was only ~4% of stand height (Fig. 1.3).
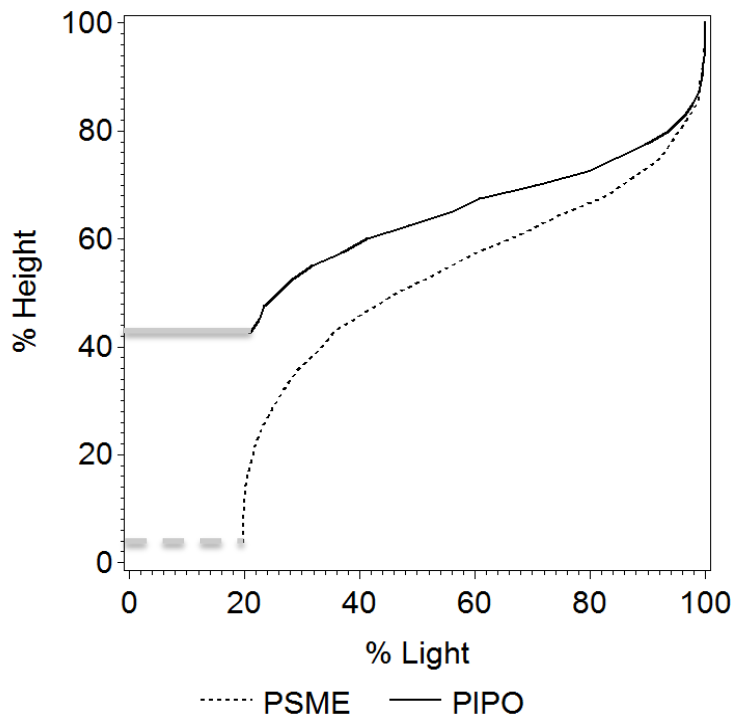
Figure 1.3. Typical estimated light extinction profiles for Douglas-fir and ponderosa pine stands with similar LAI. At ~20% light availability, the ponderosa pine stand has self-pruned to 43% of stand height, while canopy base of the Douglas-fir stand is only 4% of stand height

1.4 Discussion

Our objective in this study was to test whether relationships between foliage occurrence, light availability and shade tolerance at crown and canopy levels were consistent with predictions based on a conceptual model that postulates foliage distribution is a product of ELCP and changing light availability in growing crowns and canopies (Schoettle and Fahey 1994).

While factors besides light availability clearly play a role in foliage distribution (see reviews by Cannell and Dewar 1994; Lacointe 2000), our results suggest the phenomena of crown hollowing and self-pruning are related to declining light availability as tree growth leads to increased shading of older foliage. Crown hollowing was evident in both Douglas-fir and ponderosa pine crowns: there were low-light environments in the crowns of both species of trees in which there was no living foliage. However, Douglas-fir crowns extinguished a greater proportion of above canopy PAR than ponderosa pine crowns and a greater proportion of Douglas-fir foliage mass was growing in poor light environments (Fig. 1.1). These results are consistent with the conceptual model, which predicted intermediate tolerant Douglas-fir would retain foliage at lower light levels than ponderosa pine, reflecting a lower ELCP.

Ponderosa pine crowns extinguished > 90% of above canopy PAR. Previous studies that measured PAR extinction through crowns of intolerant *Pinus* species reported only ~75% extinction (Schoettle and Smith 1991; Han et al. 2003). This could reflect species differences in ELCP; however methodological differences between studies may account for the disparity. We collected PAR measurements throughout crown interiors, while both Schoettle and Smith (1991) and Han et al. (2003) focused their sampling on foliated shoots near crown exteriors. Our focus on the hollow crown interior thus led us to measure PAR in darker portions of crowns. It is also likely we over-estimated canopy light extinction using Equation 1.1. Our methodology makes the implicit assumption that foliage is distributed randomly throughout the canopy, when in actuality it is clustered in tree crowns. Making this assumption has been shown to inflate estimates of light extinction (Kim et al. 2011). These methodological issues have no bearing on our comparison of light extinction in Douglas-fir and ponderosa pine crowns because we used the same techniques

for the two species, but they necessitate the use of caution when comparing our results to those from other studies.

Canopy bases, measured as a proportion of stand height, were much lower on average in Douglas-fir stands than in ponderosa pine stands (Fig. 1.2). This suggests self-pruning initiates at higher levels of light availability for ponderosa pine. Despite up to 99% light extinction by Douglas-fir canopies, canopy base height was typically less than 10% of stand height. In contrast, canopy base heights in ponderosa pine stands were 20-40% of stand height despite maximum canopy light extinction of only 86%. These results indicate Douglas-fir foliage is retained in lower light environments than foliage of ponderosa pine, suggesting this species has a lower ELCP.

The extent of light extinction through canopies we observed was broadly similar to that previously reported for conifer stands (Messier 1996). However light extinction through Douglas-fir canopies was comparable to that reported for species usually considered more shade tolerant (Messier 1996). This could result from our use of Equation 1.1 to estimate light extinction, as described above. It is possible our canopy-level comparison of Douglas-fir and ponderosa pine was affected by differences between species in the distribution of foliage within crowns (Thérézien et al. 2007). These differences would have manifested as species-specific values of k in Equation 1.1. k values of 0.48 have been reported for Douglas-fir, and values from 0.40 to 0.62 for various *Pinus* species that did not include ponderosa pine (p. 249, Jarvis and Leverenz 1983). Repeating our analyses using a range of k values from 0.40 to 0.60 for ponderosa pine shifted light extinction curves, but did not affect our interpretation of results. Furthermore, the effect of within-crown foliage distribution on canopy light attenuation is most evident in low density stands (Kim et al. 2011), while our interpretation of results hinges on the

large differences we observed between species in the light profiles of the densest stands in our dataset.

1.5 Conclusion

Our results suggest crown hollowing and self-pruning are precipitated by deteriorating light environments in crowns and canopies. Characteristic differences in the crown characteristics of shade tolerant and shade intolerant tree species are related to species' ability to retain foliage in poor light environments (their ELCP). Douglas-fir retained foliage at lower light levels in both crowns and canopies, suggesting this species has a lower ELCP than ponderosa pine, other factors held constant. The lower ELCP of Douglas-fir explains why crowns of this species appear fuller than ponderosa pine crowns: because foliage is retained at lower light levels, crown hollowing is retarded relative to ponderosa pine, meaning more layers of foliage can accumulate in Douglas-fir crowns. Douglas fir canopies are deeper than ponderosa pine canopies for the same reason: foliage is retained at lower light levels, which allows more layers of foliage to accumulate in canopies before self-pruning of lower branches causes canopy bases to rise.

CHAPTER 2: GENERALITY OF FOLIAGE AREA ALLOMETRIES FOR THREE

INTERIOR WESTERN U.S. CONIFERS

2.1 Introduction

Good estimates of the projected foliage area of trees are critical for investigations of production ecology in forests (e.g. Ex and Smith [2014]). Allometries based on breast-height stem diameter (DBH) or cross-sectional sapwood area (BHSA) are applied over large geographic areas in production ecology research, yet there is evidence these relationships vary between sites (e.g. Gilmore and Seymour 2004). In this work, we investigate the stability of a suite of diameter and sapwood-area based foliage area allometries across geographic areas to determine whether accounting for sapwood taper enhances their generality.

The conceptual foundation for diameter and sapwood area-based foliage area allometries is the pipe model theory, which postulates cross-sectional sapwood area is proportional to the foliage area that it supports (Shinozaki et al. 1964). Strong support for the pipe model theory has been amassed over decades of study (see Schneider et al. [2011] for a recent review). The conceptual model has been refined over time to account for sapwood taper (Waring, Schroeder, and Oren 1982), permeability (Whitehead, Edwards, and Jarvis 1984) and capacitance (McCulloh et al. 2014). Sapwood-based foliage area allometries have been shown to vary with tree height, stand density and site quality. This results from the influence of these factors on sapwood amount and taper and potentially reduces the generality of allometries and, by extension, their applicability across different sites (e.g. Long and Smith 1988, 1989). The cross-sectional area of sapwood at the base of the live crown (CBSA) is considered a good index of

total crown foliage area because it minimizes inflation of the sapwood area estimate from sapwood taper along the crown-free bole (Maguire and Batista 1996).

Tree height is thought to affect allometries based on BHSA because sapwood conductance decreases as path length increases, which means greater BHSA is required to support a given foliage area for a tall tree than would be required to support an equal amount of foliage area for a shorter tree (McDowell et al. 2002). Stand density has been shown to influence allometries by acting on sapwood taper via self-pruning: crown lift in crowded stands increases the distance between breast height and the base of the live crown, which has the effect of increasing BHSA relative to foliage area by increasing the distance over which sapwood tapers along the bole (Maguire and Batista 1996; McDowell et al. 2006). Site quality (in particular moisture availability) potentially affects foliage area allometries based on CBSA as well as those based on BHSA: the ratio of sapwood area to foliage area has been shown to increase as moisture availability decreases regardless of sapwood measurement location, which reflects increased conducting capacity or capacitance in dry environments (Callaway, DeLucia, and Schlesinger 1994; Mencuccini and Grace 1995; Barnard et al. 2011).

Including a taper term in BHSA-based allometries can eliminate systematic differences between allometries from different sites (Long and Smith 1988, 1989); using CBSA instead of BHSA would presumably have a similar effect (Monserud and Marshall 1999; but see Callaway, DeLucia, and Schlesinger 1994). The implication is that foliage area allometries that account for sapwood taper or allometries based on CBSA are more transportable in general than allometries based solely on breast-height measurements because they are less affected by site-related variation in sapwood taper below live crowns.

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This paper describes an investigation of the stability of foliage area allometries across geographic areas in the interior western U.S. for lodgepole pine (*Pinus contorta* Douglas ex Loudon), ponderosa pine (*P. ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). We compared allometries based on DBH, BHSA, BHSA + a taper term, and CBSA for trees from two populations of each species from different geographic areas to assess whether allometries that accounted for sapwood taper (those based on BHSA + taper or CBSA) were more similar across populations than allometries that did not (those based on DBH or BHSA). In doing this, we determined whether allometries that account for sapwood taper are sufficiently constant for a given species (akin to a species-specific Huber value [p. 146, Tyree and Zimmermann 2002]) that they can be applied over broad geographic areas without introducing substantial bias into foliage area estimates.

2.2 Methods

2.2.1 Data Collection

We investigated foliage allometries for multiple conifer species because prior work has shown the dynamics of sapwood area-foliage area relationships can vary dramatically between species (DeLucia, Maherali, and Carey 2000; McDowell et al. 2002). Douglas-fir, ponderosa pine and lodgepole pine are widely distributed tree species that comprise a substantial component of forest cover in the interior western U.S. (Eyre 1980). Both pines are shade intolerant early-seral species; ponderosa pine typically occurs at lower elevations than lodgepole and often transitions to late-successional roles on sites that are too dry for more shade tolerant competitors. Douglas fir is a later-successional intermediate shade tolerant species that occurs at mid elevations; it is frequently intermixed with both ponderosa pine and lodgepole pine (Burns and Honkala 1990). To permit comparison of sapwood area-foliage area relationships from

different geographic areas, we collected data for Douglas-fir and ponderosa pine from each of two populations located in the south (New Mexico, Utah, southern Idaho and Colorado) and north (Wyoming, Montana and northern Idaho) central Rocky Mountains (Appendix 1). We also re-analyzed previously-published data in order to compare foliage area allometries for lodgepole pine trees from the Bear River Mountains in northern Utah (Dean and Long 1986) to those for trees from the Snowy Mountains in southern Wyoming (Long and Smith 1988).

We selected stands of ponderosa pine and Douglas-fir for sampling such that they spanned ranges of tree size and density (Table 2.1). Our approach was to first, destructively sample trees to obtain measurements of sapwood area and foliar biomass; foliar biomass was then converted to projected foliage area using ratio estimators. Our field sampling methodology closely followed Keyser and Smith (2010). Briefly, we selected five trees for sampling in each stand that represented the range of tree sizes present in the main canopy. Trees with two tops, asymmetric crowns, or other obvious abnormalities were not sampled. Trees were felled and all foliage was weighed in the field. Foliage subsamples were collected from each crown, weighed, dried to constant weight, re-weighed and used to develop ratio estimators, which we then used to convert field measurements of green foliage weight to total crown foliage biomass. Sampling and material processing methodologies used to estimate foliage biomass are described in greater detail in Keyser and Smith (2010).

To convert foliage biomass to projected foliage area, we collected a foliage sample from the top, middle and bottom of each sample tree crown for determination of specific leaf area (projected foliage area per unit of foliage mass). Specific leaf area was determined strictly for the purpose of estimating whole-crown foliage area and was not used as an analysis variable. Foliage area samples were placed in plastic bags and packed in ice upon collection, then frozen until they

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were processed in the lab. Processing consisted of scanning samples using a platen scanner, estimating projected area of scanned samples using digital image analysis software, drying samples to constant weight, and finally weighing samples to the nearest 0.01 g. This allowed us to develop ratios to convert crown foliage mass to projected foliage area. We measured BHSA and CBSA for each sample tree by cutting thin discs at breast height and canopy base height, using a marker to trace the boundary between translucent sapwood and opaque heartwood, then estimating sapwood area by subtracting heartwood area from inside-bark basal area calculated using πr^2 where heartwood and total cross-section radii were averages of radii along the major and minor axes of ellipses superimposed on cross-sections. Finally, we performed point inventories in each stand using a single fixed-radius plot sized to include at least 30 over-story trees. All live trees with diameter at breast height (DBH) $\geq$ 1 cm (including sample trees) were tallied and species, DBH, height, and crown base height were recorded.

Table 2.1. Summary of tree and stand-level data used to develop foliage area allometries. PICO is lodgepole pine, PIPO is ponderosa pine and PSME is Douglas-fir. N is number of sample locations followed by number of destructively sampled trees in parentheses. All other columns are means followed by minimum and maximum values in parentheses. Diameter at breast height (DBH) applies to destructively sampled trees only, while basal area (BA) and quadratic mean diameter (QMD) were calculated from stand inventory data.

Spp.	Pop.	N	DBH (cm)	BA (m^2 ha^{-1})	QMD (cm)
PICO	Wyoming	17 (78)	10.4 (3.6, 27.6)	34.7 (9.1, 56.9)	9.8 (3.4, 29.3)
	Utah	1 (20)	14.7 (6.0, 31.4)	62.8	13.6
PIPO	North	6 (26)	26.7 (4.6, 55.4)	33.1 (14.1, 61.3)	26.9 (8.1, 43.7)
	South	6 (28)	30.4 (8.1, 54.4)	26.9 (13.0, 39.6)	27.6 (14.5, 43.2)
PSME	North	6 (27)	22.1 (6.1, 56.1)	43.4 (16.9, 62.0)	21.2 (14.7, 33.6)
	South	6 (29)	22.9 (4.3, 54.6)	34.0 (11.5, 54.4)	21.3 (13.5, 34.0)

Previously published lodgepole pine data were obtained from the authors of the prior work. Details of data collection and processing are described in Dean and Long (1986) and Long and Smith (1988). Lodgepole pine data were not originally sampled as comparable datasets from

different geographic areas; the one stand sampled in Utah was considerably denser with larger

trees on average than the 17 stands sampled in Wyoming (Table 2.1). Wyoming sampling is

described in Long and Smith (1988), who present data for 10 stands. Data from the seven

additional stands used in the present study were collected as part of the earlier work but were not

used for the analysis described in Long and Smith (1988).

2.2.2 Data Analysis

We developed foliage area allometries based on DBH, BHSA and CBSA for each species

and geographic area. In each case, we first used an iterative, derivative-free algorithm to fit a

general allometric model of the form:

(Model 2.1) $$y = b_0 x_1{}^{b_1}$$

(Monserud and Marshall 1999), where y is projected foliage area (m^2), x_1 is DBH (cm), BHSA

(cm^2) or CBSA (cm^2) and the b's are estimated parameters. We then interpreted b_1 to determine

whether a simpler linear model could be used instead: if b_1 was not statistically different from

one, we used a linear model of the form:

(Model 2.2) $$y = b_0 + b_1 x_1$$

instead of Model 2.1 (Monserud and Marshall 1999). For Douglas-fir and ponderosa pine, we

also fit a second nonlinear model of the form:

(Model 2.3) $$y = b_0 x_1{}^{b_1} x_2{}^{b_2}$$

where x_1 is BHSA and x_2 is a variable that accounts for sapwood taper, either the distance

between breast height (1.37 m) and crown base height in m (Mäkelä, Virtanen, and Nikinmaa

1995), or the distance between breast height and the center of the live crown (Long and Smith

1989). All nonlinear models were fit using DBH^{-3} as a weighting factor to satisfy regression

assumptions (Keyser and Smith 2010). We were unable to fit Model 2.3 for lodgepole pine

because we did not have access to the necessary height data.

After estimating parameters for foliage allometries, we tested for statistical differences

between parameters from different populations for each species. Linear relationships were

considered equivalent if there were no statistical differences between populations in the slope or

intercept of regression lines. This was indicated by non-significance ($\alpha = 0.05$) of the categorical

variable 'population' as well as of the interaction between population and the continuous

predictor variable in a generalized linear model. We compared nonlinear model parameters

between populations by setting all estimated parameters except b_1 to mean parameter values for

the species (estimated by combining trees from both populations), then estimating b_1

independently for each population; nonlinear models were deemed equivalent if the 95%

confidence intervals for b_1 overlapped between populations. To evaluate the potential impact of

transporting foliage area allometries between geographic areas on foliage area estimates, we

estimated foliage area for all of the sample trees for each species using the parameters for each

population and then graphically interpreted differences in estimates from allometries for different

populations.

2.3 Results

Our analysis data were derived from 54 ponderosa pine trees from 12 locations, 56

Douglas-fir trees from 12 locations and 98 lodgpole pine trees from 18 locations (Table 2.1).

There was no difference in average sample tree DBH between populations of Douglas-fir or

ponderosa pine (2-sample t-test; $p = 0.82$, df $= 54$ for Douglas-fir; $p = 0.41$, df $= 52$ for

ponderosa pine). Lodgepole pine trees sampled from Wyoming were on average about four cm

smaller in DBH than those from Utah (2-sample t-test; $p < 0.01$, df $= 96$). There was no

difference in average quadratic mean diameter or basal area between north and south populations of Douglas-fir or ponderosa pine (2-sample t-test; p > 0.35, df = 10 for all comparisons). We did not make statistical comparisons of stand level variables for lodgepole pine because trees from Utah were sampled in from only one stand (Table 2.1).

The relationship between DBH and projected foliage area was curved for all species and populations (Fig. 2.1). The 95% confidence interval for b_1 overlapped for different populations of Douglas-fir and ponderosa pine when b_0 was held constant, so we fit DBH-based allometries for these species using trees from both populations combined (Table 2.2). The same was not true for lodgepole pine; the relationship between foliage area and DBH was shaped differently for trees from Wyoming and Utah (Fig. 2.1). Although the 95% confidence interval for b_1 overlapped for lodgepole populations when we held b_0 constant, there was pronounced bias in residual error from models with a common b_0. This reflects the large difference in estimated b_0 between lodgepole populations (Table 2.2). We consequently did not fit a common DBH-based foliage area allometry for lodgepole pine.

Relationships between foliage area and BHSA were curved for lodgepole pine and for the south population of Douglas-fir and were linear for ponderosa pine and for the north population of Douglas-fir (Fig. 2.1). The intercepts of all linear relationships in this study were non-significant and were set to zero. Without exception, linear models had $r^2 > 0.90$ and unbiased residual error distributions. There was no overlap in the 95% confidence intervals for b_1 for lodgepole from Wyoming and Utah because there was more curvature in the relationship for trees from Utah (Fig. 2.1). For ponderosa pine, the slope of the linear relationship between foliage area and BHSA was significantly steeper for trees from the south population than for trees from the north population (Fig. 2.1). We did not make a statistical comparison of allometric

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model parameters for different populations of Douglas-fir because the relationship was curved

for the south population and linear for the north population (Fig. 2.1). We took this to be

sufficient evidence of the inappropriateness of fitting a common model for Douglas-fir.
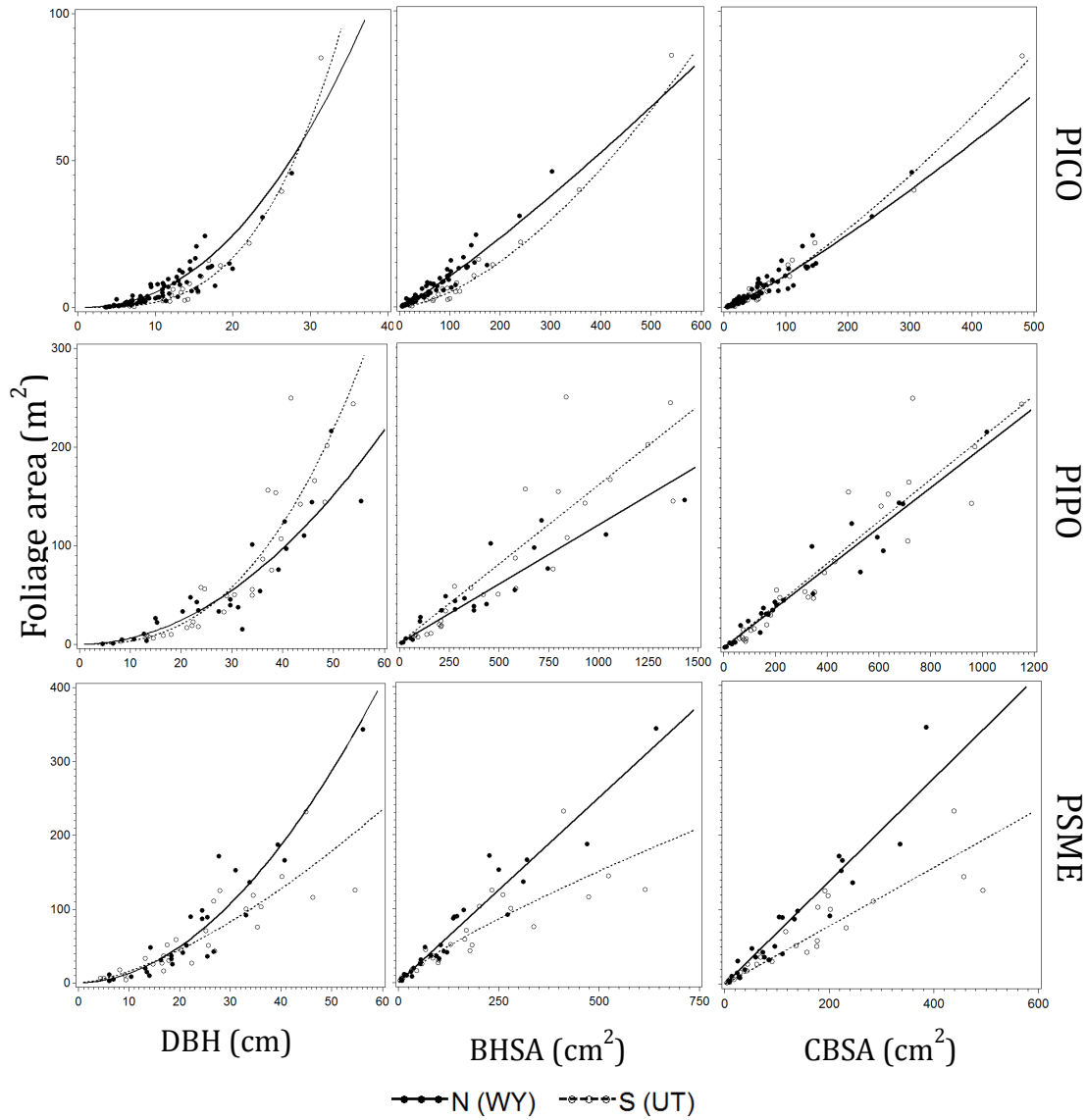
Figure 2.1. Relationships between total crown foliage area and predictor variables. Species are as described for Table 2.1. Parameters for fitted lines are in Table 2.2. Solid lines and filled circles are the north populations of ponderosa pine and Douglas-fir and the Wyoming population of lodgepole pine. Dashed lines and open circles are the south populations of ponderosa pine and Douglas fir and the Utah population of lodgepole pine. There are no statistical differences between lines describing the CBSA relationship for lodgepole pine and ponderosa pine, or for lines describing the DBH relationship for ponderosa pine and Douglas-fir.

Table 2.2. Estimated parameters (b's) and fit statistics for allometries that predict total crown foliage area in m^2. Species are as described for Table 2.1. Estimates are followed by standard errors in parentheses. X's are the predictor variables used in allometries where DBH is in cm, BHSA and CBSA are in cm^2, and other variables are in m; CB is the distance between breast height and the crown base, and MC is the distance between breast height and the center of the live crown. In rows where no population is specified, parameter estimates are for both populations of the species combined, and there are no significant differences in average parameter values between populations for that allometry

Spp.	Pop.	b_0	b_1	b_2	x	Model	RMSE
PICO	-	0.05 (0.01)	1.20 (0.03)	-	CBSA	2.1	2.26
	WY	0.03 (0.01)	2.24 (0.11)	-	DBH	2.1	2.99
		0.05 (0.01)	1.16 (0.04)	-	BHSA	2.1	1.77
		0.05 (0.01)	1.17 (0.04)	-	CBSA	2.1	2.12
	UT	0.001 (0.001)	3.25 (0.15)	-	DBH	2.1	2.63
		0.003 (0.001)	1.61 (0.06)	-	BHSA	2.1	1.99
		0.03 (0.01)	1.28 (0.05)	-	CBSA	2.1	2.40
PIPO	-	0.03 (0.01)	2.27 (0.14)	-	DBH	2.1	29.27
		0.07 (0.03)	1.22 (0.07)	-0.41 (0.09)	BHSA+CB	2.3	25.35
		-	0.20 (0.004)	-	CBSA	2.2	19.95
	N	0.06 (0.04)	1.99 (0.16)	-	DBH	2.1	22.23
		-	0.12 (0.01)	-	BHSA	2.2	49.58
		0.08 (0.04)	1.23 (0.10)	-0.50 (0.12)	BHSA+CB	2.3	12.36
		-	0.20 (0.01)	-	CBSA	2.2	13.42
	S	0.01 (0.01)	2.60 (0.22)	-	DBH	2.1	30.46
		-	0.16 (0.01)	-	BHSA	2.2	34.99
		0.05 (0.03)	1.26 (0.11)	-0.33 (0.15)	BHSA+CB	2.3	32.42
		-	0.21 (0.01)	-	CBSA	2.2	27.92
PSME	-	0.31 (0.10)	1.68 (0.10)	-	DBH	2.1	32.93
	N	0.15 (0.08)	1.93 (0.16)	-	DBH	2.1	25.19
		-	0.50 (0.02)	-	BHSA	2.2	28.48
		0.50 (0.16)	1.27 (0.11)	-0.60 (0.21)	BHSA+MC	2.3	20.61
		-	0.69 (0.03)	-	CBSA	2.2	24.85
	S	0.50 (0.17)	1.50 (0.11)	-	DBH	2.1	28.17
		1.00 (0.19)	0.81 (0.04)	-	BHSA	2.1	27.25
		0.98 (0.36)	1.18 (0.14)	-0.88 (0.32)	BHSA+MC	2.3	23.32
		-	0.39 (0.03)	-	CBSA	2.2	26.47

We chose variables for x_2 in Model 2.3 by comparing corrected Akaike's information

criteria (AICc [p. 66, Burnham and Anderson 2010]) of versions of Model 2.3 where x_2 was

either the distance between breast height and the center of the live crown (MC) or the distance between breast height and the crown base (CB). The variable MC most improved allometries for Douglas-fir, while CB was better for ponderosa pine (Table 2.2). For ponderosa pine, the statistical difference in b_1 between populations disappeared when x_2 was added to the model. In contrast, the 95% confidence intervals for b_1 did not overlap for Douglas-fir populations whether x_2 was in the model or not.

The relationship between foliage area and CBSA was linear for ponderosa pine and Douglas-fir and curved for lodgepole pine (Fig. 2.1). There were no differences in b_1 between populations of either pine (Table 2.2). However, the relationship between foliage area and CBSA was significantly steeper for Douglas-fir trees from the north population compared to those from the south (Fig. 2.1).

The magnitude of difference between populations in foliage area estimates depended on the average crown size of the species. The smallest differences in estimates between populations were for lodgepole pine trees, which had much less foliage area than trees of other species on average (Fig. 2.1). Generally speaking, there was little difference between estimates from population-specific foliage area allometries whose estimated parameters were not significantly different, but only when the difference was expressed as a percentage of observed foliage area (Fig. 2.2). This was because allometric relationships tended to diverge for large trees (Fig. 2.1), meaning the absolute difference in predictions from different allometric models tended to be small for small trees and though larger for large trees, still small relative to the amount of foliage area carried by large trees (Fig. 2.2). Large differences between pine populations in estimates from BHSA-based allometries all but disappeared when CBSA was used instead (Fig. 2.2).

Douglas-fir was unique in that differences in estimated foliage area were more pronounced for

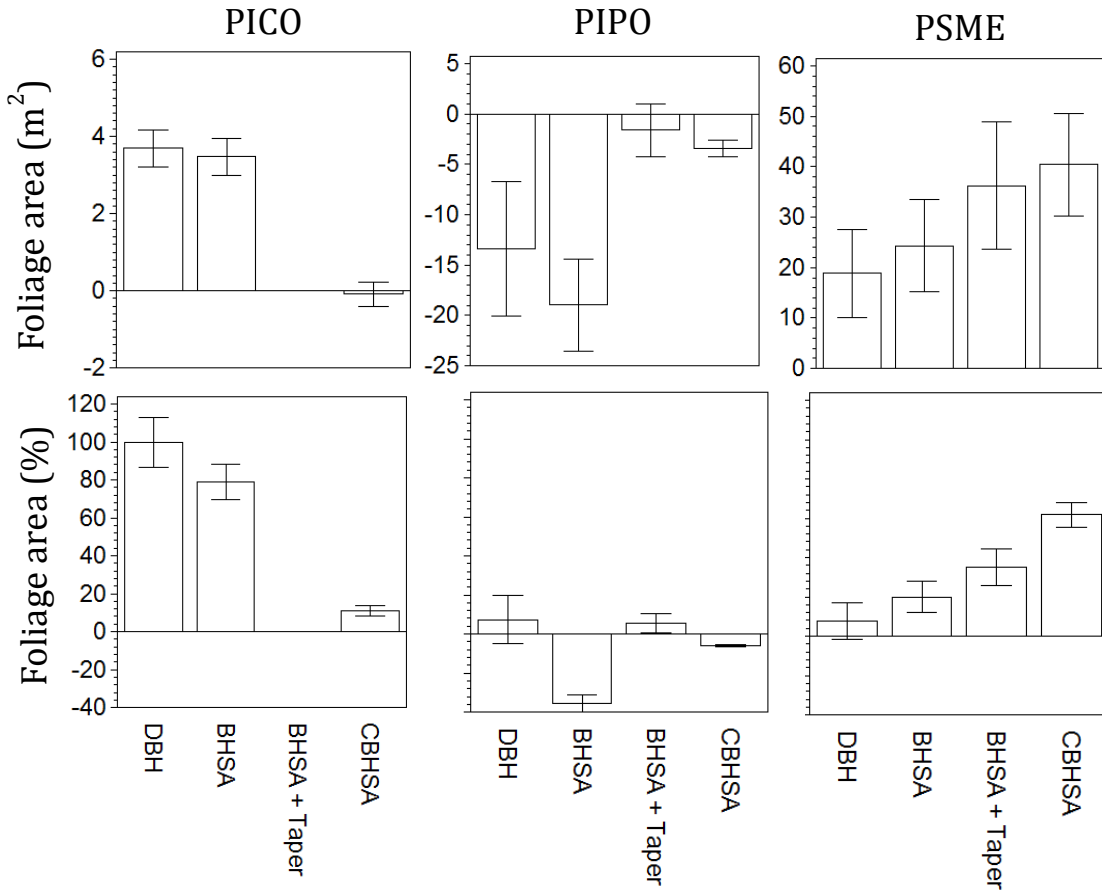allometries that accounted for sapwood taper (Fig. 2.2).

Figure 2.2. Mean difference in foliage area estimates from all four population-specific allometries. Top panels are north population estimates – south population estimates for ponderosa pine and Douglas-fir (Wyoming population estimates – Utah population estimates for lodgepole pine). Bottom panels are the same differences divided by observed foliage area. Species are as described for Table 2.1. Accounting for sapwood taper reduced differences in estimates from population-specific allometries for the pines, yet it increased differences for Douglas-fir.

2.4 Discussion

We set out to investigate the stability of pipe model-based foliage area allometries across

geographic areas for three interior western U.S. conifer species. Our results showed that the

degree to which allometric relationships differ between geographic areas depends on whether

allometric models account for sapwood taper, however the nature of this dependence was species-specific (Fig. 2.1). For the pine species we investigated, the most general allometries (as indicated by small differences in estimated foliage area from allometries for different populations) were based on CBSA or BHSA and a term that accounted for sapwood taper (Fig. 2.2). In contrast, the most general allometry for Douglas-fir was based on DBH, and allometries that accounted for sapwood taper were not general for this species (Fig. 2.2).

Allometries based on CBSA were stable across populations for both pine species, as evidenced by non-significant differences between populations in their parameters. For ponderosa pine, the relationship between CBSA and foliage area was linear with a zero intercept. Callaway, DeLucia, and Schlesinger (1994) found the slope of the relationship between foliage area in m^2 and CBSA in cm^2 varied from about 0.1 for ponderosa pine trees in desert environments to about 0.2 for trees in montane environments (their Fig. 1). Our results are consistent with their montane population. This suggests that, while the relationship between foliage area and CBSA may vary across steep moisture gradients, merely multiplying CBSA by 0.20 (akin to a Huber value [p. 146, Tyree and Zimmermann 2002]) may be adequate for estimating foliage area of ponderosa pine trees on non-desert sites in the interior western U.S.. In this study, CBSA * 0.2 predicted foliage area for ponderosa pine trees with lower RMSE than nonlinear models based on DBH and BHSA + CB (Table 2.2).

The relationship between foliage area and CBSA was curved for lodgepole pine. However, a single model worked equally well for trees from Wyoming and Utah. This is striking because there were substantial differences between populations in tree size and stand density (Table 2.1). These results are consistent with prior work based on the same data that suggests

site-related differences in the foliage area – sapwood area relationship for lodgepole pine

primarily result from sapwood taper below the live crown (Long and Smith 1988).

Foliage area allometries based on BHSA alone were substantially different between

populations for both pine species (Fig. 2.1), but including a term that accounted for sapwood

taper virtually eliminated this difference for ponderosa pine (Fig. 2.2). Accounting for taper

would probably have had a similar effect for lodgepole pine (Long and Smith 1988). These

results are consistent with prior work that found the relationship between foliage area and BHSA

is variable between sites for pines (O'Hara and Valappil 1995; McDowell et al. 2006), but that

differences can be eliminated by accounting for sapwood taper or indexing sapwood area at the

base of the live crown (Shelburne, Hedden, and Allen 1993; Mäkelä, Virtanen, and Nikinmaa

1995). Our findings suggest that sapwood-based foliage area allometries need to account for

taper (or be based on CBSA) to be stable across geographic areas for ponderosa pine and

lodgepole pine.

There was no difference in DBH-based allometries between north and south populations

of ponderosa pine and Douglas-fir trees. However, relationships between foliage area and DBH

were substantially different between populations of lodgepole pine (Fig. 2.1). This could indicate

a difference between species (implying DBH-based allometries are more stable for ponderosa

pine and Douglas-fir than for lodgepole pine), but it more likely reflects the fact that there were

substantial tree size and stand density differences between populations of lodgepole pine but not

between populations of the other species (Table 2.1).

All sapwood-based foliage area allometries were population-specific for Douglas-fir (Fig.

2.1). The differences between predictions from population-specific models were greatest for the

allometries that accounted for sapwood taper. Like ponderosa pine, CBSA-based allometries

were linear with non-significant intercepts, however relationships for Douglas-fir populations did not converge on a common 'Huber value' like ponderosa pine (Table 2.2). Consequently, there were substantial differences in predicted foliage area from CBSA-based allometries. Allometries based on DBH were most stable across geographic areas for Douglas-fir (Fig. 2.2). This implies the mechanical relationship between foliage area and DBH (the necessity of a large diameter bole to physically support a large crown) is more general than the hydraulic relationship between foliage area and conducting sapwood area for this species.

Why were pipe model-based allometries more stable for ponderosa pine than for Douglas-fir? Our results imply the amount of sapwood area required to support a given amount of foliage area is more variable between sites for Douglas-fir than for ponderosa pine. This was borne-out by the data: the range in average ratios of foliage area to CBSA for Douglas-fir stands (0.49) was more than three times that for ponderosa pine stands (0.14). This could reflect a more conservative hydraulic strategy for the pine species we investigated compared to Douglas-fir. Ponderosa pine trees typically occur on drier sites than Douglas-fir trees, and are more susceptible to xylem cavitation during drought (Stout and Sala 2003). Lodgepole pine trees are also more susceptible to xylem cavitation than Douglas-fir trees (Piñol and Sala 2000). The relative constancy of foliage area – sapwood area relationships for these species could thus reflect adaptive strategies that involve maintaining a substantial margin of safety in conducting capacity or capacitance for a given amount of foliage area that renders the foliage area – sapwood area relationship comparatively insensitive to site conditions. In contrast, Douglas-fir is typically found on wetter sites and is less vulnerable to xylem cavitation, so the adaptive strategy for this species may involve minimizing the maintenance cost of living sapwood tissue by

operating with a smaller hydraulic buffer. This would explain why the foliage area – sapwood area relationship was more variable between sites for Douglas-fir than for the pine species.

2.5 Conclusion

This work showed the stability of foliage area allometries across geographic areas in the interior western U.S. depends on whether allometric models account for sapwood taper as well as on the hydraulic dynamics of tree species. The most general allometries for the pine species we examined were those that accounted for sapwood taper; this reflects the constancy of the foliage area – sapwood area across sites for these species. Accounting for between-site variation in sapwood taper increased the generality of foliage area allometries for ponderosa pine and lodgepole pine. In contrast, allometries that accounted for sapwood taper were least general for Douglas-fir because the foliage area – sapwood area relationship varied widely between sites for this species. Generality was reduced by accounting for sapwood taper for Douglas-fir because accounting for sapwood taper in-effect indexed a relationship that was site-specific.

Our results and others suggest foliage area allometries based on BHSA and a term that accounts for taper could be applied broadly for ponderosa pine and lodgepole pine in the interior western U.S. with little risk of bias. Allometries based on CBSA were also stable across geographic areas for the pine species examined in this study, however CBSA is more difficult to measure than BHSA, so BHSA-based allometries may be more practical. For Douglas-fir, DBH-based allometries are likely to yield better results than sapwood-based allometries when applied across broad geographic areas because the foliage area – sapwood area relationship is highly variable for this species. Allometries based on BHSA alone were not general for any of the species we investigated, suggesting this technique of foliage area estimation should only be used when local relationships are available.

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CHAPTER 3: CHARACTERIZING CANOPY FUELS FOR INTERIOR WESTERN

U.S. CONIFER FORESTS

3.1 Introduction

Managers of western U.S. conifer forests are challenged with addressing fuel buildup from fire suppression, increasingly large and frequent forest fires and the growth of the wildland-urban interface. Management responses such as fuel treatments and fire suppression are informed by canopy fire hazard assessments, especially by whether active spread of fire through the canopy is expected given certain weather conditions (see Affleck, Keyes, and Goodburn [2012] for a recent review). Most methods of predicting potential fire behavior rely heavily on estimates of canopy bulk density (CBD) for stands (Van Wagner 1977). Standard procedures for estimating CBD have been shown to be sensitive to the vertical distribution of crown fuels (usually defined as foliage and some proportion of fine branches [Call and Albini 1997]), yet in practice fuel is almost always assumed to be uniformly distributed within crowns (Keyser and Smith 2010). The assumption of uniform vertical crown fuel distribution is a matter of convenience and is unrealistic. To our knowledge, investigations of vertical distributions of foliage (or fuels, of which foliage is the major constituent) in conifer crowns report non-uniformity without exception, with biomass typically concentrated near the center of the live crown (e.g. Reinhardt et al. 2006; Tahvanainen and Forss 2008; Keyser and Smith 2010). In this paper, we describe an investigation of the nature of variation in vertical distributions of crown fuels with respect to stand density and shade tolerance. Specifically, we assess whether there are systematic differences between tolerant and intolerant conifers in within-crown fuel distribution

response to increasing stand density that are analogous to differences between tolerant and intolerant species in the response of crown ratio to stand density.

It is well documented that crown ratio, the proportion of total tree height which supports live foliage, declines with increasing stand density (p. 72, Oliver and Larson 1996). However crown ratios of shade tolerant species decline less than those of intolerant species (p. 183, Smith et al. 1997), meaning shade tolerant species tend to have longer crowns than intolerant species at a given stand density, presumably because they are able to maintain foliage in more shaded environments. Shade tolerance may also bear on within-crown foliage distributions: the center of foliage mass is usually lower in the crowns of shade tolerant species than in the crowns of intolerant species (Garber and Maguire 2005; Weiskittel et al. 2009), which appears analogous to trends in crown ratio.

There is considerable evidence showing foliage is shifted upward within crowns in dense stands relative to its distribution in open stands, which presumably reflects the plastic response of crown architecture to light competition from neighbors (Brix 1981; Xu and Harrington 1998; Garber and Maguire 2005; Keyser and Smith 2010; but see Stephens 1969; Weiskittel et al. 2009). Upward-shifted foliage distributions are also frequently reported for trees in subordinate social positions, which is likely a similar response to light competition (Stephens 1969; Maguire and Bennett 1996; Gilmore and Seymour 1997; Xu and Harrington 1998; Mäkelä and Vanninen 2001; Garber and Maguire 2005; but see Weiskittel et al. 2009; Keyser and Smith 2010).

Evidence is mixed with regard to whether the center of foliage mass is consistently located above or below the middle of conifer crowns, or whether its location depends on growing environment and species shade tolerance. A study of five interior western U.S. conifer species showed the center of crown fuel mass resided above the middle of crowns

for all species (Reinhardt et al. 2006), which is consistent with work showing foliage mass was concentrated in upper crowns of ponderosa pine trees (*Pinus ponderosa* Lawson & C. Lawson [Keyser and Smith 2010]) as well as Norway spruce (*Picea abies* [L.] Karst.) and Scots pine (*P. sylvestris* L. [Tahvanainen and Forss 2008]) regardless of stand density. Vose (1988) found the center of foliage area was at or above the midpoint of loblolly pine (*P. taeda* L.) crowns, which suggests foliage mass was centered in upper crowns because the distribution of foliage mass tends to be shifted upward relative to the distribution of foliage area as a result of height-related trends in specific leaf area (Maguire and Bennett 1996). In contrast, foliage biomass has been shown to be concentrated in lower crowns of loblolly pine ([Gillespie, Allen, and Vose 1994; Xu and Harrington 1998]) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco [Maguire and Bennett 1996]). Other work suggests the center of foliage mass can shift above or below the middle of crowns depending on stand density, social position of trees and species shade tolerance (Garber and Maguire 2005).

This paper describes an investigation of within-crown biomass distribution for several important interior western U.S. conifer species. We assembled a comprehensive dataset spanning ranges of species shade tolerance and stand density in order to evaluate the effect of these factors on the vertical distribution of fuel within conifer crowns. Our objectives in this work were to: develop non-uniform vertical crown biomass distributions for conifer stands representing different forest types (open-canopy woodlands versus closed-canopy forests), as well as ranges of species shade tolerance and stand density; ascertain the degree to which distribution parameters vary among individual trees, stands and species; and ascertain whether within-crown biomass distribution is predictable from shade tolerance and stand density in a similar manner as crown ratio. To meet these objectives, we destructively sampled almost

200 trees at dozens of locations across the interior western U.S. and re-analyzed data from four

additional studies conducted over the past three decades.

3.2 Methods

3.2.1 Data Collection

We used detailed crown biomass data from a total of 394 trees of seven conifer species to

meet our objectives (Table 3.1). 'Woodland' species two-needle pinyon (*P. edulis* Engelm.) and

Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) are short-statured trees usually found on

xeric sites that do not typically form closed canopies, while 'forest' species subalpine fir (*Abies*

lasiocarpa (Hook.) Nutt.), lodgepole pine (*P. contorta* Douglas ex Loudon), Engelmann spruce

(*Picea engelmannii* Parry ex Engelm.), ponderosa pine and Douglas-fir are taller trees found on

comparatively wetter sites that form closed-canopy stands. Forest tree species were selected to

represent a shade tolerance gradient. Lodgepole and ponderosa pine are considered intolerant,

Douglas-fir is considered intermediate, and subalpine fir and Engelmann spruce are considered

tolerant of shaded growing environments (Burns and Honkala 1990). Our data come from a total

of 75 relatively pure, even-aged stands located throughout Colorado, New Mexico, Utah, Idaho,

Montana, South Dakota and Wyoming that were selected to span ranges of mean tree size and

stand density (Table 3.1). Stands that showed evidence of disturbance within the previous ~20

years were not sampled.

Our field sampling methodology closely followed Keyser and Smith (2010). Briefly, we

selected five trees for destructive sampling at each location that represented the range of tree

sizes present in the main canopy. Trees with two tops, lopsided crowns, or other obvious

abnormalities were avoided. Sample trees were felled and crowns were divided into 10 equal

length sections. All branches were removed from each section in turn, sorted into live and dead

categories, divided into time-lag classes (Bradshaw et al. 1983), and weighed in the field using a

hierarchical sampling scheme. Subsamples were then collected and dried to constant weight for

development of ratio estimators to determine total biomass of foliage and each time lag class of

live and dead woody material in each crown section. Hierarchical sampling and material

processing methodologies are described in detail in Keyser and Smith (2010).

Table 3.1. Summary sample data. ABLA is subalpine fir, JUSC is Rocky Mountain juniper, PICO is lodgepole pine, PIED is two-needle pinyon pine, PIEN is Engelmann spruce, PIPO is ponderosa pine and PSME is Douglas-fir. N is number of sample locations followed by number of sample trees in parentheses. All other columns are means followed by minimum and maximum values in parentheses. BA is basal area, SDI is as described in methods, QMD is quadratic mean stand diameter, and dia. is diameter of destructively sampled trees. Diameter-based variables were calculated using DBH except where noted.

Spp.	N	BA (m^2 ha^{-1})	SDI	QMD (cm)	Dia. (cm)
ABLA[*]	9 (49)	48.4 (23.3, 93.8)	0.73 (0.29, 1.32)	15.6 (8.6, 25.4)	17.0 (5.6, 40.6)
JUSC[**]	3 (15)	27.0 (16.6, 43.8)	0.77 (0.48, 1.20)	19.6 (15.5, 23.3)	20.4 (6.3, 41.8)
PICO	17 (90)	34.7 (9.1, 56.9)	0.62 (0.19, 0.98)	9.8 (3.4, 29.3)	10.0 (2.9, 27.6)
PIED[**]	3 (15)	27.0 (16.6, 43.8)	0.58 (0.37, 0.91)	19.6 (15.5, 23.3)	19.1 (6.2, 33.5)
PIEN	6 (30)	56.2 (25.1, 101.5)	0.74 (0.37, 1.24)	16.9 (10.0, 23.5)	23.4 (6.6, 48.8)
PIPO	28 (135)	28.0 (5.8, 61.3)	0.51 (0.13, 1.12)	25.3 (8.1, 43.7)	26.9 (4.6, 58.0)
PSME	12 (60)	38.7 (11.5, 62.0)	0.54 (0.18, 0.87)	21.3 (13.5, 34.0)	22.5 (4.3, 56.1)

[*] Stand-level data from two small (< 0.01 ha) inventory plots sampled by Long and Smith (1989) indicated SDI values > 1.5. We presumed this reflected sampling bias and excluded these data when summarizing BA and SDI as well as from regression analyses that used SDI.
[**] JUSC and PIED were sampled together in three stands where they co-occurred. All diameter-based variables for these species were calculated using diameter at the root crown.

We performed point inventories at each location using a single fixed-radius plot sized to

include at least 30 overstory trees. All trees > 1 cm dbh (including sample trees) were tallied and

species, dbh, height, and crown base height were recorded. Crown base height was designated as

the base of the compact live crown by 'moving up' the lowest live branches until at least three

were accumulated, thus constituting a full whorl.

In addition to the sampling effort described above, we also re-analyzed several previously

published datasets. We were able to directly incorporate data collected from ponderosa pine

stands in South Dakota's Black Hills by Keyser and Smith (2010) because we duplicated their protocols exactly. Long and Smith (1988) sampled lodgepole pine in Wyoming and Long and Smith (1989) sampled subalpine fir in Utah using protocols that deviated from our methodology such that their data (hereafter the 1980's data) required interpolation prior to incorporation into our dataset.

The 1980's data were collected using fixed-length vertical sections (either 1 m or 0.5 m depending on tree size) that started at ground level and continued to the top of each tree, where the top section was a fraction of the length of other sections such that all section lengths added together would equal the total tree height. Consequently, the number of crown section divisions for the 1980's data depended on crown length, and section lengths within tree crowns were unequal. In order to seamlessly integrate the 1980's data, we interpolated by first defining crown base height as the height of the bottom of the lowest section that contained foliage, dividing the crown into 10 equal length sections, and then assigning material to sections based on the fraction of original sections that corresponded to the new, equal length sections. For example, to interpolate data from a tree with a 15 m crown which had 15, 1 m sections, we would assign 100% of material from the lowest 1 m crown section and 50% of material from the next lowest 1 m section to the bottom tenth (1.5 m) of the crown, and so on.

Branch biomass was not subdivided into time lag classes in the 1980's datasets, so we developed ratio estimators to assign branch biomass to classes. For subalpine fir, the 1980's data supplemented contemporary sampling, so we were able to derive ratios of time lag class biomass to total branch biomass for different crown sections and size classes of trees from data collected using the methodology described above and in Keyser and Smith (2010). For lodgepole pine, we collected data specifically for development of time lag class ratios from nine trees in three pure,

even-aged stands of varying average tree size near Foxpark, Wyoming. At each location, we felled three sample trees that represented the range of tree sizes in the main canopy, divided live crowns into five equal sections, and then collected the three nearest live and one nearest dead branch to the midpoint of each crown section. Branches were stripped of foliage and woody material was divided into time lag classes before being weighed in the field. A sample of each time lag class of live and dead material was collected from each section of every tree, dried to constant weight, and used to develop ratios of time lag class biomass to total branch biomass for different sections and size classes of lodgepole pine trees from the 1980's data.

3.2.2 Data Analysis

We developed vertical fuel distributions by using an iterative, derivative-free algorithm to fit a two-parameter cumulative Weibull distribution for foliage and 1-hr fuel biomass of crown sections individually for each tree in our dataset as described by Keyser and Smith (2010). The Weibull distribution has been used extensively to characterize the spatial arrangement of biomass in conifer crowns (e.g. Gillespie, Allen, and Vose 1994; Kershaw and Maguire 1996; Weiskittel et al. 2009); our use of it here permits comparison of our parameter estimates to those from other studies. The form of the model was:

(Model 3.1) $$y = 1 - e^{[-\left(\frac{x}{\beta}\right)^{\alpha}]}$$

where y is the cumulative proportion of biomass at x, and x is depth into the crown expressed as a proportion of total crown length. The estimated shape parameter α represents the degree to which biomass is skewed upward or downward in crowns, while the estimated scale parameter β represents the degree to which biomass is concentrated in a few sections versus spread evenly throughout crowns. We used estimates of α and β from Keyser and Smith (2010) as starting values for nonlinear regression.

We investigated the nature of variation in crown fuel distribution by interpreting and analyzing estimates of α and β for trees, stand, species and characteristic forest types (forests versus woodlands). The Weibull distribution is nearly symmetric when the α parameter is ~3.6. In this study, α > ~3.6 indicates biomass is shifted below the crown midpoint, while α < ~3.6 indicates biomass is shifted above the midpoint (Mori and Hagihara 1991). Small values of the β parameter reflect concentration of biomass in a small portion of the vertical crown profile. Large β values indicate biomass is spread more evenly throughout the crown. We compared the magnitude of within-stand ranges in parameter values to within-species ranges and also compared average parameter values for species and characteristic forest types. In addition, we used linear regression techniques to evaluate whether α and β were predictable from stand density and shade tolerance in a manner similar to crown ratio. Stand density was quantified using stand density index (SDI [Reineke 1933]) expressed as a proportion of species maximum SDI (maximum values from J.N. Long [pers. comm.]). Stand density index is calculated using tree size and density, and can be thought of as a measure of a given stand's proximity to the '-3/2 self-thinning line' that describes equivalent maximum combinations of size and density for species (Shaw and Long 2010).

3.3 Results

We estimated α and β for each destructively sampled tree using Model 3.1 and averaged parameter values for species and forest types (Table 3.2). In some cases biomass distributions were bimodal or otherwise poorly approximated by the Weibull distribution. In these cases, the derivative-free algorithm used for nonlinear regression usually did not converge on a solution so no estimates were obtained. We also discarded pairs of estimated parameters when either

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Table 3.2. Average parameter values for species and characteristic forest types. Species are as described for Table 3.1. Forest types are described in methods. Estimate is the mean parameter value followed by the standard deviation in parentheses. Stand and species ranges are within-stand and species ranges of parameter estimates.

Spp.	Component	Parm.	Estimate	Stand range	Spp. range
ABLA	Foliage	α	2.55 (0.41)	0.89	1.70
		β	0.54 (0.07)	0.14	0.27
	1 Hr fuel	α	2.51 (0.38)	0.84	1.82
		β	0.67 (0.05)	0.13	0.22
JUSC	Foliage	α	3.39 (0.74)	1.88	2.56
		β	0.78 (0.05)	0.09	0.17
	1 Hr fuel	α	3.96 (0.88)	2.20	2.66
		β	0.81 (0.06)	0.11	0.21
PICO	Foliage	α	2.30 (0.39)	0.85	1.96
		β	0.46 (0.10)	0.19	0.43
	1 Hr fuel	α	2.37 (0.49)	1.04	2.95
		β	0.59 (0.07)	0.16	0.39
PIED	Foliage	α	2.91 (0.84)	1.97	3.42
		β	0.69 (0.07)	0.15	0.25
	1 Hr fuel	α	3.23 (1.08)	2.51	4.57
		β	0.73 (0.07)	0.14	0.26
PIEN	Foliage	α	2.08 (0.45)	1.00	1.83
		β	0.56 (0.09)	0.19	0.39
	1 Hr fuel	α	2.30 (0.58)	1.11	2.37
		β	0.64 (0.08)	0.17	0.34
PIPO	Foliage	α	2.44 (0.44)	0.87	2.27
		β	0.61 (0.07)	0.13	0.35
	1 Hr fuel	α	3.91 (1.86)	2.39	10.84
		β	0.75 (0.14)	0.14	0.73
PSME	Foliage	α	2.40 (0.47)	0.92	2.36
		β	0.57 (0.11)	0.23	0.53
	1 Hr fuel	α	2.49 (0.57)	1.06	3.09
		β	0.61 (0.12)	0.24	0.54
Forest	Foliage	α	2.38 (0.45)	-	-
		β	0.56 (0.10)	-	-
	1 Hr fuel	α	2.88 (1.30)	-	-
		β	0.66 (0.12)	-	-
Woodland	Foliage	α	3.14 (0.82)	-	-
		β	0.73 (0.08)	-	-
	1 Hr fuel	α	3.58 (1.04)	-	-
		β	0.77 (0.07)	-	-

parameter was not significant ($p > 0.05$) or when Hougaard's skewness index was > 1, which indicates potential for substantial bias in parameter estimates (Ratkowsky 1990).

With the exception of 1-hr fuel for Rocky Mountain juniper and ponderosa pine, α was $<$ ~3.6 on average for all combinations of species and crown fuel component, meaning biomass of foliage and 1-hr fuel was shifted above crown midpoints (Table 3.2). The center of foliage mass was above the crown midpoint for 97% of our sample trees; the center of 1-hr fuel mass was above the crown midpoint for 85%. On average, the range of parameter values for trees in a given stand was about half the total range of values for the species, indicating within-crown foliage distributions varied widely between trees in the same stand. The ratio of average within-stand parameter range to total parameter range was smallest for ponderosa pine, averaging 0.29 for all parameters, and largest for Rocky Mountain juniper, averaging 0.65. Ratios for all other species were between 0.40 and 0.60 (Table 3.2).

There was no obvious trend in foliage parameter values with respect to shade tolerance for forest species (Fig. 3.1). Parameters for 1-hr fuel tended to be similar to foliage parameters (Table 3.2), and are not shown in Fig. 3.1. α and β for foliage distributions were smaller on average for forest trees than for woodland trees when trees were grouped into characteristic forest types (Fig. 3.1 [$p < 0.01$, $df > 30$, Satterthwaite's approximate t-test to account for unequal variance]). This indicates foliage was shifted upward and more concentrated in the crowns of forest trees than in crowns of woodland trees (Fig. 3.2).

The relationship between crown ratio and SDI was not significantly different for tolerant subalpine fir and Engelmann spruce and intermediate tolerant Douglas-fir (the interaction between shade tolerance and SDI was not statistically significant in a generalized linear model [$p > 0.80$, $df = 47$]), so Douglas-fir was grouped with tolerant tree species for regression analysis.

SDI was a statistically significant predictor of crown ratio for both tolerant and intolerant tree

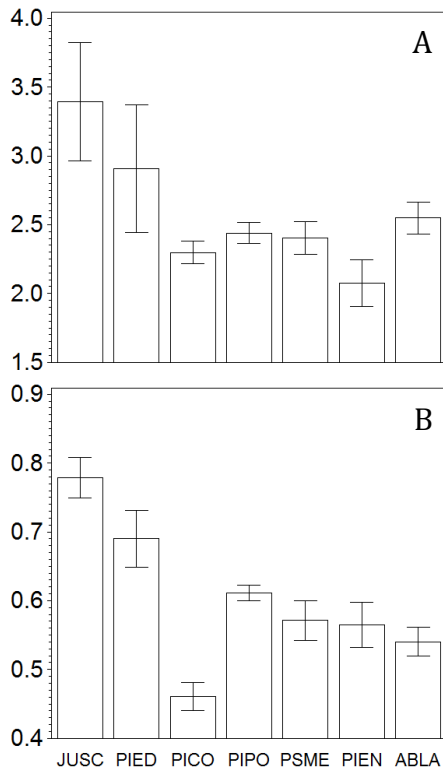species (Fig. 3.3, Table 3.3). However, SDI explained a much greater proportion of the variation

Figure 3.1. Mean α (A) and β (B) foliage distribution parameters for species. Error bars are 95% confidence intervals of means. Species are as described for Table 3.1. Woodland species are the leftmost two bars. PICO and PIPO are intolerant, PSME is intermediate-tolerant, and PIEN and ABLA are tolerant of shaded growing conditions. There is no apparent trend in values of α with respect to shade tolerance.

in crown ratio for intolerant species (65% versus 19%), and crown ratio decreased much more

rapidly with increasing SDI for intolerant species (slope of -0.49 compared to -0.19). This

dichotomy between tolerant and intolerant species was not evident for relationships between

within-crown foliage distribution and SDI. The relationship between α and SDI for tolerant
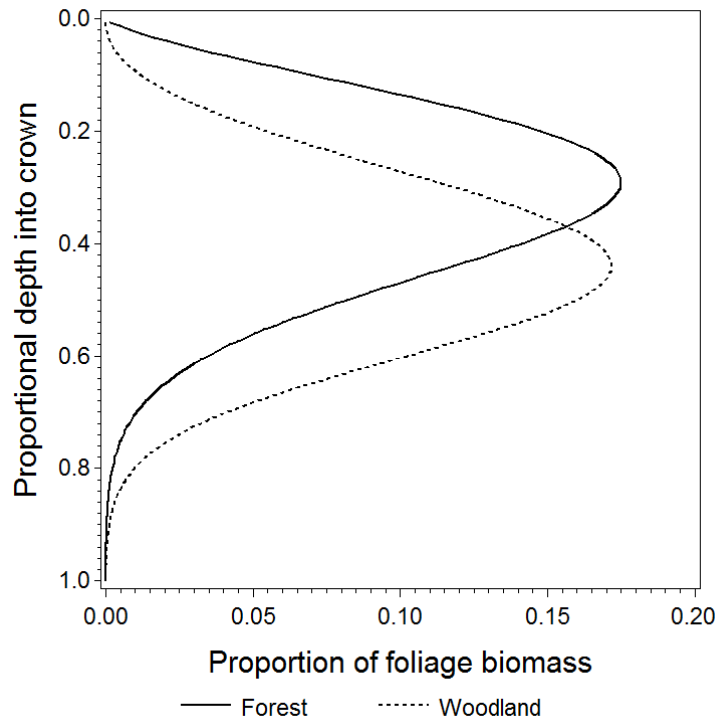
Figure 3.2. Characteristic foliage biomass distributions for forest and woodland trees. Curves were generated using mean parameter values for characteristic forest types (Table 3.2). Foliage was shifted upwards and concentrated in forest tree crowns relative to the crowns of woodland trees.

species was only marginally significant when evaluated on its own (Fig. 3.3, Table 3.3).

However, there were no differences between tolerant and intolerant species in the relationship between α and β and SDI when SDI, shade tolerance and their interaction were evaluated using a generalized linear model ($p > 0.30$, df $= 49$ for the interaction between shade tolerance and SDI for both parameters). SDI was a significant predictor of α and β when tolerant and intolerant species were combined (Fig. 3.3, Table 3.3), which suggests foliage is shifted upward and concentrated in upper crowns at high stand densities.
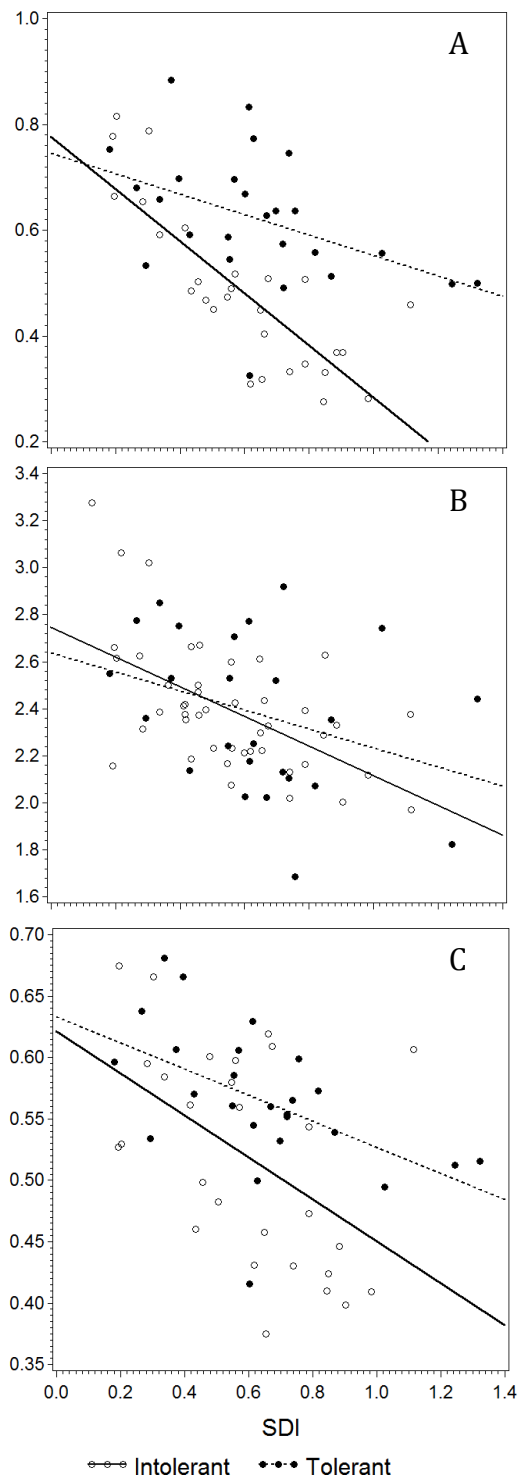
Figure 3.3. Relationships between crown ratio (A), α (B) and β (C) and SDI for tolerant and intolerant conifers. There are no statistical differences between regression lines for tolerant and intolerant species in B and C, meaning there is no difference between tolerant and intolerant species in within-crown distribution of foliage with respect to stand density.

Table 3.3. Estimated slopes and intercept for regression lines in Figure 3.3. Parameter estimates are followed by p-values in parentheses. Estimates followed by the same letter are not significantly different for tolerant and intolerant species at $\alpha = 0.05$. Fits for tolerant species had 23 degrees of freedom, intolerant species had 26, and combined had 51. The slope of the relationship between crown ratio and stand density was substantially different for tolerant and intolerant species.

	Tolerance	Intercept	Slope	r^2
Crown ratio	Tolerant	0.75 (<0.01) a	-0.19 (0.03) a	0.19
	Intolerant	0.78 (<0.01) a	-0.49 (<0.01) b	0.65
α	Tolerant	2.64 (<0.01) a	-0.40 (0.10) a	0.11
	Intolerant	2.55 (<0.01) a	-0.33 (0.04) a	0.15
	Tol. + Intol.	2.59 (<0.01)	-0.36 (0.01)	0.12
β	Tolerant	0.63 (<0.01) a	-0.11 (0.01) a	0.27
	Intolerant	0.62 (<0.01) a	-0.17 (0.01) a	0.24
	Tol. + Intol.	0.62 (<0.01)	-0.13 (<0.01)	0.19

3.4 Discussion

Our objectives in this work were to characterize within-crown vertical fuel distributions for interior western U.S. conifers species and evaluate whether distribution parameters were predictable from stand density and species shade tolerance. We found foliage and 1-hr fuel was nearly always concentrated above the midpoint of live crowns. This held for five conifers that represented a broad spectrum of shade tolerance as well as two characteristic forest types: closed-canopy forests and open-canopy woodlands, which suggests it is generally true for interior western U.S. conifers. Rocky Mountain juniper and ponderosa pine were exceptional in this regard, as the center of 1-hr fuel mass was often below crown midpoints for these species. This could reflect a tendency for woody biomass to be centered lower in crowns than foliage biomass for these species (Tahvanainen and Forss 2008). However, we observed during field sampling that the smallest live twigs of ponderosa pine trees were often slightly larger than the 6.4 mm diameter threshold that delineates 1- and 10-hr fuels (Bradshaw et al. 1983). Thus, they

were not counted as 1-hr fuel. This could account for downward-shifted 1-hr fuel distributions for ponderosa pine: distributions would be shifted toward the crown base if 1-hr fuel consisted of predominantly dead twigs in lower crowns that had died and shrunk to < 6.4 mm diameter.

Our results indicate foliage biomass shifts upward and becomes more concentrated in upper crowns in high-density stands, much as crown ratio decreases at high stand densities (Fig. 3.3). This likely reflects redistribution of foliage into favorable light environments in response to shading by neighbors in crowded stands. Our results are consistent with a substantial body of evidence that suggests foliage distributions in tree crowns respond dynamically to varying light environment across ranges of stand density and canopy position (e.g. Garber and Maguire 2005). Our interpretation of results is informed by characteristic differences between forest and woodland species in within-crown foliage biomass distributions (Fig. 3.2). In open-canopy woodlands, foliage was shifted only slightly above crown midpoints on average ($\alpha = 3.14$) and was spread relatively evenly throughout crowns ($\beta = 0.77$). In contrast, foliage in crowns of trees in closed-canopy forests was shifted upward to a greater degree on average ($\alpha = 2.38$), and was more concentrated within crowns ($\beta = 0.56$). These results suggest light competition plays a greater role in shaping crown characteristics in closed-canopy forests than in open-canopy woodlands because competition is more intense in closed-canopy stands.

There was substantial tree-to-tree variation in crown characteristics within stands, which presumably reflects small-scale heterogeneity of the light environment. On average, α and β varied within stands over about half the range of values for species (Table 3.2). This suggests within-crown fuel distribution may depend as much on whether trees are in openings or crowded or whether they are taller than adjacent trees as on overall stand density.

Crown ratios of shade intolerant species were more responsive to increasing SDI than those of tolerant species (Fig. 3.3). However, the same was not true for the relationship between the parameters of within-crown foliage distributions and SDI (Fig. 3.3). Nonetheless, within-crown foliage distribution and crown ratio are almost certainly expressions of the same process: foliage redistribution in crowded growing environments. Partitioning this phenomenon into components is a matter of convenience; crown ratio is usually considered independently because it is much more easily observed and quantified than within-crown foliage distribution. We characterized foliage and 1-hr fuel using a two-parameter Weibull distribution where the location of the distribution was fixed between crown base and the tops of trees. Had we instead used a three-parameter distribution in which crown base height was also estimated as a location parameter (p. 100, Clutter et al. 1983), we likely would have detected differences between tolerant and intolerant species in the response of the location parameter to SDI. The implication is that most of the variation with respect to shade tolerance in foliage distribution response to stand density is expressed in the crown ratio relationship. This is a critical finding for canopy fire hazard assessment; it suggests species-specific relationships for the response of canopy fuel distributions to stand density are not necessary for realistic characterization of the canopy fuels complex. It is sufficient to account for species-specific relationships between crown ratio and stand density.

3.5 Conclusion

This study suggests the distribution of foliage within crowns is, like crown ratio, an expression of foliage redistribution into favorable light environments in crowded growing conditions. Foliage and 1-hr fuel were nearly always concentrated in upper crowns where light availability is high. The degree to which foliage was concentrated in upper crowns was greater

for closed-canopy forest species than for open-canopy woodland species, which was expected given the assumption that trees in closed-canopy stands experience more shading from neighbors. The extent of upward skew and concentration of foliage in crowns of forest species was predictable from stand density. However, unlike crown ratio, the response of within-crown foliage distribution to increasing density was the same for shade tolerant and intolerant species. Because foliage accounts for the bulk of canopy fuels, our results suggest there is no need to develop species-specific within-crown fuel distribution models to characterize fuels complexes of western U.S. conifer forests. Simply relaxing the assumption of uniform fuel distribution within crowns in favor of an upward-skewed distribution substantially improves the realism of canopy fuels characterization. Distribution parameters could be adjusted to account for stand density. However, substantial within-stand variation in parameter estimates suggests accurate prediction of distribution parameters requires accounting for growing environments of individual trees (e.g. canopy gaps and distance to neighbors).

CHAPTER 4: EFFECT OF FUEL DISTRIBUTION ASSUMPTIONS ON CANOPY FIRE

HAZARD ASSESSMENT USING THE FIRE AND FUELS EXTENSION TO THE FOREST

VEGETATION SIMULATOR

4.1 Introduction

Large, destructive wildfires and expansion of the wildland-urban interface have catapulted canopy fire hazard assessment to the forefront of management priorities for conifer forests in the western U.S. (Radeloff et al. 2005; Stephens and Ruth 2005). In Colorado alone, the 2012 and 2013 wildfire seasons each saw hundreds of homes destroyed, with insurance claims totaling hundreds of millions of dollars (Chaykowski 2013). Canopy fire hazard assessment entails using models to predict potential fire behavior based on the canopy fuels complex (Scott and Reinhardt 2001). This type of assessment is used to prioritize stands for treatment, to compare alternative fuel treatment options in terms of their anticipated effects on crown fire behavior, to evaluate treatment effectiveness after the fact and to assess potential risk to firefighters during suppression activities (Cruz and Alexander 2010).

Most fire behavior models rely on two key canopy fuel metrics to predict fire behavior: canopy bulk density (CBD) is a measure of how tightly fuels are packed in space, and is a critical variable for predicting fire spread through canopies; while canopy base height (CBH) is an important determinant of the readiness with which fire transitions from surface fuels into canopies (Van Wagner 1977). Canopy fuel is generally considered to consist of foliage and some portion of small twigs (Call and Albini 1997). The amount and spatial arrangement of canopy fuels change over time as trees grow and competitively interact, driving structural development of canopies. Because canopy fuels are dynamic, effective fire hazard assessment requires

forecasting changes in CBD and CBH over time in addition to characterization of the current canopy fuels complex.

The Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS) is widely-used for canopy fire hazard assessment because it accommodates fire behavior and forest growth in a common, distance-independent modeling framework (Rebain et al. 2010). Thus, it can be used to predict canopy fire behavior based on current and future canopy fuels characteristics. The Fire and Fuels Extension to FVS calculates a measure of "effective CBD" as the largest running mean CBD of horizontal canopy layers of fixed depth that collectively account for the entire vertical canopy profile (Scott and Reinhardt 2001). Canopy bulk density is calculated for each layer by summing the contribution of individual crowns to canopy fuel mass for that layer and then dividing by the volume of the layer (Sando and Wick 1972). Canopy base height is defined in FFE-FVS as the height at which CBD exceeds 13.6 kg 0.4 ha-0.3 m^{-1} (30 lbs ac-ft^{-1} [Scott and Reinhardt 2001]). Canopy bulk density and CBH are used by FFE-FVS to generate two fire behavior indices: crowning index (CI) is an estimate of the minimum wind-speed necessary to propagate fire from tree-to-tree through canopies, while torching index (TI) is an estimate of the minimum wind-speed necessary for fire to transition from surface fuels into the canopy (Scott and Reinhardt 2001). Generally speaking, CI decreases as CBD increases because canopy fuel connectivity is higher at large values of CBD, thus lower wind-speeds are necessary for fire to spread (e.g. Fulé et al. 2001). Torching index tends to increase with CBH because greater surface fire behavior is required to ignite canopy fuels that are further from the forest floor; however other factors such as surface fuel characteristics are also influential in the TI calculation.

Like nearly all fire behavior models, the FFE-FVS modeling framework assumes fuel is distributed uniformly through the vertical crown profiles of individual trees (Rebain et al. 2010;

Parsons, Mell, and McCauley 2011). Yet, the assumption of uniform vertical crown fuel distribution is unrealistic (Reinhardt et al. 2006; Keyser and Smith 2010). Furthermore, incorporating non-uniform vertical biomass distributions in FFE-FVS has been shown to increase CBD estimates by 31% for even-aged stands of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) in South Dakota's Black Hills (Keyser and Smith 2010). If ponderosa pine is indicative of other conifers, the assumption of uniform crown fuel distribution may result in systematic misdiagnosis of canopy fire hazard by FFE-FVS through underestimation of CBD and, by extension, CI. Torching index may also be affected by virtue of CBH's dependence on CBD in the FFE-FVS modeling framework. The assumption of uniform crown fuel distribution therefore represents a potentially serious flaw in current canopy fire hazard assessment methodology, as the consequences of underestimating canopy fire hazard could be severe (Cruz and Alexander 2010).

In this work, we evaluated the effect of relaxing the assumption of uniformity of vertical crown fuel distribution on predictions of crown fuel characteristics and fire behavior indices from FFE-FVS for seven widely distributed interior western U.S. conifer species. We developed non-uniform fuel distributions using data that were obtained by destructively sampling hundreds of trees at dozens of locations across the region. We then worked with FVS staff (Dixon 2002) to incorporate non-uniform distributions into a stand-alone executable version of FFE-FVS and generate estimates of CBD, CBH, CI and TI for comparison with estimates from the production version of FFE-FVS.

4.2 Methods

<u>4.2.1 Data Collection</u>

We collected detailed crown biomass data from tree species that represented two characteristic interior western U.S. conifer forest types in order to develop non-uniform crown fuel distributions. Two-needle pinyon pine (*P. edulis* Engelm.) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) are short-statured trees usually found on xeric sites that typically occur in open-canopied 'woodlands'. In contrast, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*P. contorta* Douglas ex Loudon), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), ponderosa pine (*P. ponderosa* Lawson & C. Lawson), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are taller trees found on comparatively wetter sites that usually form closed-canopy 'forest' stands. For each forest species, we sampled trees from relatively pure, even-aged stands that were selected to span ranges of mean tree size and stand density; woodland species were sampled in mixed stands (Table 4.1). Stand density was quantified using Stand Density Index (SDI [Reineke 1933]), expressed as a proportion of species maximum SDI (maximum values from J.N. Long [pers. comm.]). Stands that showed evidence of harvest within the previous ~20 years were not sampled.

Our field sampling methodology closely followed Keyser and Smith (2010). Briefly, we selected five trees for sampling at each location that represented the range of tree sizes present in the main canopy (Table 4.1). Trees with two tops, lopsided crowns, or other obvious abnormalities were avoided. Sample trees were felled and crowns were divided into 10 equal length sections. All branches were removed from each section in turn, sorted into live and dead categories, separated into foliage and fuel time lag classes (Bradshaw et al. 1983) and weighed in the field using a hierarchical sampling scheme. Subsamples were then collected and dried to

constant weight for development of ratio estimators to determine total fuel (foliage and 1-hr fuel,

hereafter referred-to collectively as 'fuel') biomass for each crown section. Hierarchical

sampling and material processing methodologies are described in detail in Keyser and Smith

(2010). We also inventoried each stand using a single fixed-radius plot sized to include at least

30 over-story trees. All live trees > 1 cm DBH (including sample trees) were tallied and species,

DBH, height, and crown base height were recorded. Plot sizes ranged from 0.007 ha to 0.5 ha

(median size = 0.05 ha). Crown base height was designated as the base of the compact live

crown by 'moving up' the lowest live branches until at least three were accumulated, thus

constituting a full whorl.

Table 4.1. Summary sample data. ABLA is subalpine fir, JUSC is Rocky Mountain juniper, PICO is lodgepole pine, PIED is two-needle pinyon pine, PIEN is Engelmann spruce, PIPO is ponderosa pine and PSME is Douglas-fir. N is number of sample stands followed by number of sample trees in parentheses. All other columns are means followed by minimum and maximum values in parentheses. BA is basal area, SDI is as described in methods, QMD is quadratic mean stand diameter, and dia. is diameter of destructively sampled trees. Diameter-based variables were calculated using DBH except where noted.

Spp.	N	BA (m^2 ha^{-1})	SDI	QMD (cm)	Dia. (cm)
ABLA[*]	9 (49)	48.4 (23.3, 93.8)	0.73 (0.29, 1.32)	15.6 (8.6, 25.4)	17.0 (5.6, 40.6)
JUSC[**]	3 (15)	27.0 (16.6, 43.8)	0.77 (0.48, 1.20)	19.6 (15.5, 23.3)	20.4 (6.3, 41.8)
PICO	17 (90)	34.7 (9.1, 56.9)	0.62 (0.19, 0.98)	9.8 (3.4, 29.3)	10.0 (2.9, 27.6)
PIED[**]	3 (15)	27.0 (16.6, 43.8)	0.58 (0.37, 0.91)	19.6 (15.5, 23.3)	19.1 (6.2, 33.5)
PIEN	6 (30)	56.2 (25.1, 101.5)	0.74 (0.37, 1.24)	16.9 (10.0, 23.5)	23.4 (6.6, 48.8)
PIPO	28 (135)	28.0 (5.8, 61.3)	0.51 (0.13, 1.12)	25.3 (8.1, 43.7)	26.9 (4.6, 58.0)
PSME	12 (60)	38.7 (11.5, 62.0)	0.54 (0.18, 0.87)	21.3 (13.5, 34.0)	22.5 (4.3, 56.1)

[*] Stand-level data from two small (< 0.01 ha) inventory plots sampled by Long and Smith (1989) indicated SDI values > 1.5. We presumed this reflected sampling bias and excluded these data when summarizing BA and SDI.
[**] JUSC and PIED were sampled together in three stands where they co-occurred. All diameter-based variables for these species were calculated using diameter at root crown.

We combined data from the sampling effort described above with three previously

published datasets. We were able to directly incorporate data collected from ponderosa pine

stands in South Dakota's Black Hills by Keyser and Smith (2010) because we duplicated their

protocols exactly. Long and Smith (1988) sampled lodgepole pine in Utah and Wyoming and Long and Smith (1989) sampled subalpine fir in Utah using protocols that deviated from our methodology such that their data (hereafter the 1980's data) required interpolation prior to incorporation into our dataset.

The 1980's data were collected using fixed-length vertical sections (either 1 m or 0.5 m depending on tree size) that started at ground level and continued to the top of each tree, where the top section was a fraction of the length of other sections such that all section lengths added together would equal tree height. Consequently, the number of crown section divisions for the 1980's data depended on crown length, and the uppermost section was always a different length than lower sections. In order to seamlessly integrate the 1980's data, we interpolated by first defining crown base height as the height of the bottom of the lowest section that contained foliage, dividing the crown into 10 equal length sections, and then assigning material to sections based on the fraction of original sections that corresponded to the new, equal length sections. For example, to interpolate data from a tree with a 15 m crown which had 15, 1 m sections, we would assign 100% of material from the lowest 1 m crown section and 50% of material from the next lowest 1 m section to the bottom tenth (1.5 m) of the crown, and so on.

One-hr fuel was not subdivided from branch biomass in the 1980's datasets, so we estimated 1-hr fuel biomass from branch biomass using ratios developed from contemporary data. Subalpine fir stands were sampled by the authors for this study as well as in the 1980's, so we were able to derive ratios of 1-hr fuel biomass to total branch biomass for different sections and size classes of trees from data collected using the methodology described above and in Keyser and Smith (2010). For lodgepole pine, we collected data specifically for development of 1-hr fuel ratios from nine trees in three pure, even-aged stands of varying average tree size near

Foxpark, Wyoming. At each location, we felled three sample trees that represented the range of tree sizes in the main canopy, divided live crowns into five equal sections, and then collected the three nearest live and one nearest dead branch to the midpoint of each crown section. Branches were stripped of foliage and 1-hr fuel was separated from larger material before all woody material was weighed in the field. Samples of 1-hr fuel and larger woody material were collected from each section of each tree, dried to constant weight, and used to develop ratios of 1-hr fuel biomass to total branch biomass for different sections and size classes of lodgepole pine trees from the 1980's data.

All told, our analysis dataset was based on destructive sampling of 394 trees from 75 stands (Table 4.1). One-hundred nineteen were sampled by Long and Smith (1988, 1989), 76 were sampled by Keyser and Smith (2010) and 199 were sampled by the authors in 2011 and 2012. Sampling locations were widely distributed throughout Colorado, New Mexico, Utah, Idaho, Wyoming, South Dakota and Montana.

4.2.2 Data Analysis

We fit a two-parameter Weibull distribution to foliage and 1-hr fuel biomass data individually for each tree in our dataset using an iterative, derivative-free algorithm as described by Keyser and Smith (2010). The form of the model was:

(Model 4.1) $$y = 1 - e^{\left[-\left(\frac{x}{\beta}\right)^{\alpha}\right]}$$

where y is the cumulative proportion of biomass at x, x is depth into the crown expressed as a proportion of total crown length and α and β are estimated parameters. We used estimates of α and β from Keyser and Smith (2010) as starting values for nonlinear regression. In some cases biomass distributions were bimodal or otherwise poorly approximated by the Weibull distribution. In these cases, the derivative-free algorithm used for nonlinear regression usually

did not converge on a solution so no parameter estimates were obtained. We also discarded pairs of estimated parameters when either parameter was not significant ($p > 0.05$) or when Hougaard's skewness index was > 1, which indicates potential for substantial bias in parameter estimates (Ratkowsky 1990). We obtained average values of α and β for each characteristic forest type by averaging tree values for stands, stand values for species, and finally averaging species values for each type. This process prevented parameter values for species with large sample sizes from dominating overall averages for forest types (Table 4.1).

After estimating crown fuel distribution parameters, we worked with FVS staff to develop stand-alone executable versions of FFE-FVS in which crown fuel (in FFE-FVS, foliage and half of 1-hr fuel biomass) was distributed non-uniformly using average values of α and β for forest and woodland species. We then compared estimates of CBD, CBH, CI and TI for our stands from versions of FFE-FVS with uniform and non-uniform crown fuel distributions to assess the effect of relaxing distribution assumptions on fire hazard evaluation for each species. We used default settings for surface fuels and fire weather, specified the appropriate FVS Variant for each stand (either Central Rockies or Inland Empire depending on stand location), and used no keywords apart from those required to write fire and fuels reports to an output database. Because Rocky Mountain juniper and two-needle pinyon pine were sampled in mixed stands, they were considered together as pinyon-juniper stands for this analysis. We were unable to obtain inventory data for stands sampled by Keyser and Smith (2010), so FFE-FVS outputs were not evaluated for these stands.

4.3 Results

Foliage and 1-hr fuel were concentrated in upper crowns of both forest and woodland tree species. The center of foliage mass was located at a greater height in crowns than the center of 1-

hr fuel mass on average; both foliage and 1-hr fuel were concentrated higher in the crowns of

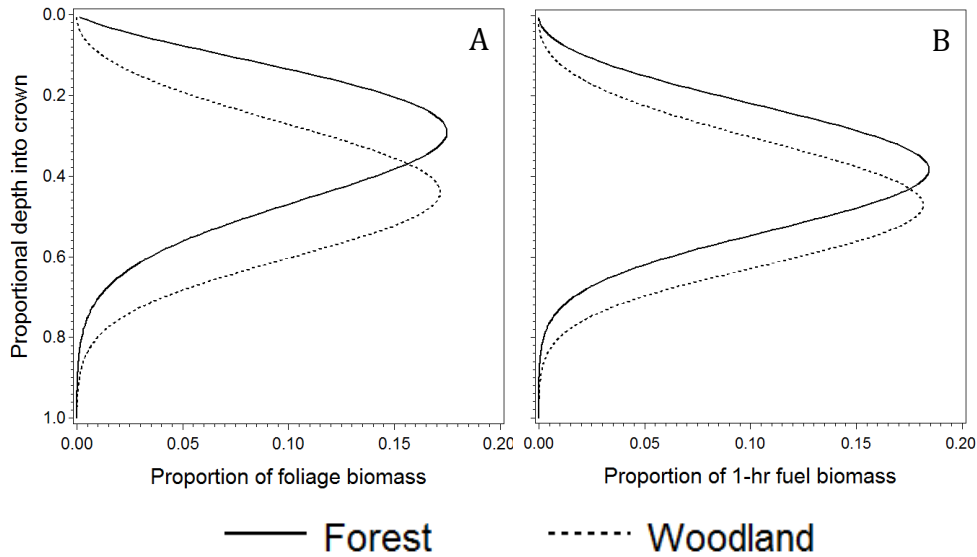forest species than in the crowns of woodland species (Fig. 4.1). Relaxing the assumption of

Figure 4.1. Average vertical distributions of foliage (A) and 1-hr fuel (B) biomass for forests and woodlands. Curves are probability density functions of Model 4.1. Foliage distribution parameters are $\alpha = 2.38$, $\beta = 0.56$ (forest) and $\alpha = 3.14$, $\beta = 0.73$ (woodland). One-hr fuel distribution parameters are $\alpha = 2.88$, $\beta = 0.66$ (forest) and $\alpha = 3.58$, $\beta = 0.77$ (woodland). Foliage and 1-hr fuel were skewed upward and concentrated in forests compared to woodlands.

uniform vertical crown fuel distributions in FFE-FVS resulted in nontrivial increases in

predictions of CBD and CBH for stands of all tree species. Average CBD increases ranged from

17% for pinyon-juniper to 112% for subalpine fir stands, while average CBH increases ranged

from 111% for lodgepole pine to 367% for pinyon-juniper (Figs. 4.2 and 4.3). Absolute increases

in CBD were greatest for stands of shade-tolerant species (subalpine fir, Engelmann spruce),

least for stands of intolerant species (pinyon-juniper, ponderosa pine, lodgepole pine) and

intermediate for Douglas-fir, which is somewhat shade tolerant (Fig. 4.2 [see Burns and Honkala

(1990) for species silvics]). Percentage changes in CBD did not closely track absolute increases

because relatively small increases in CBD sometimes represented large proportional increases

for stands with low CBD. For example, although the average absolute increase in CBD for ponderosa pine was smaller than for all other species save pinyon-juniper, it represented the second-largest average percentage increase because ponderosa pine stands had the smallest average estimated CBD from the production version of FFE-FVS (Table 4.2, Fig. 4.2).

Figure 4.2. Mean absolute (A) and percentage (B) difference in CBD and CI (C) predictions from the production version of FFE-FVS versus predictions from a version of FFE-FVS that incorporated non-uniform vertical crown fuel distributions (Fig. 4.1). Species are as described for Table 4.2. Error bars are 95% confidence intervals of means. Canopy fire was predicted at lower wind-speeds when non-uniform distributions were used.
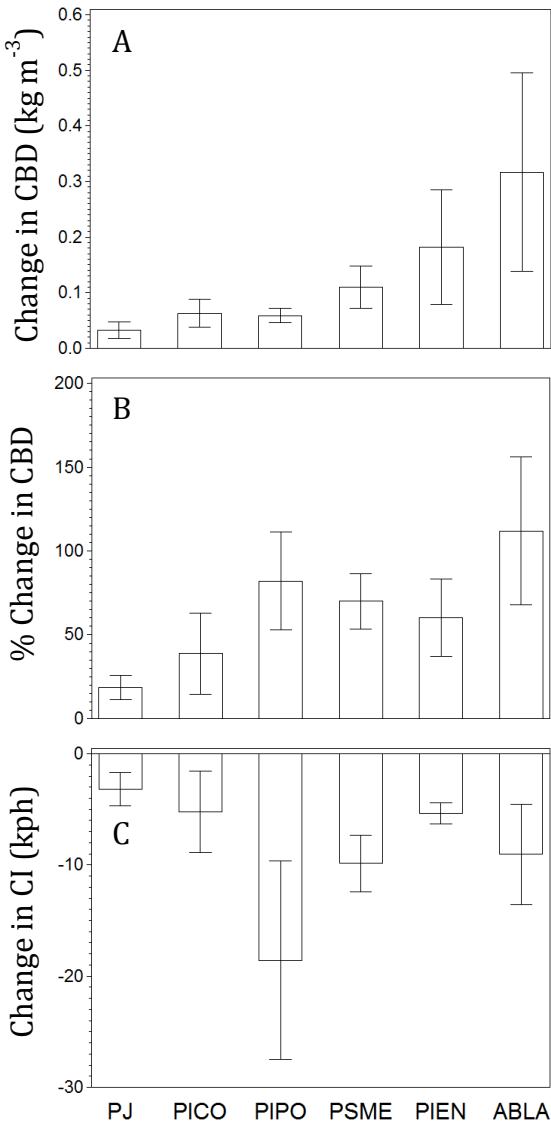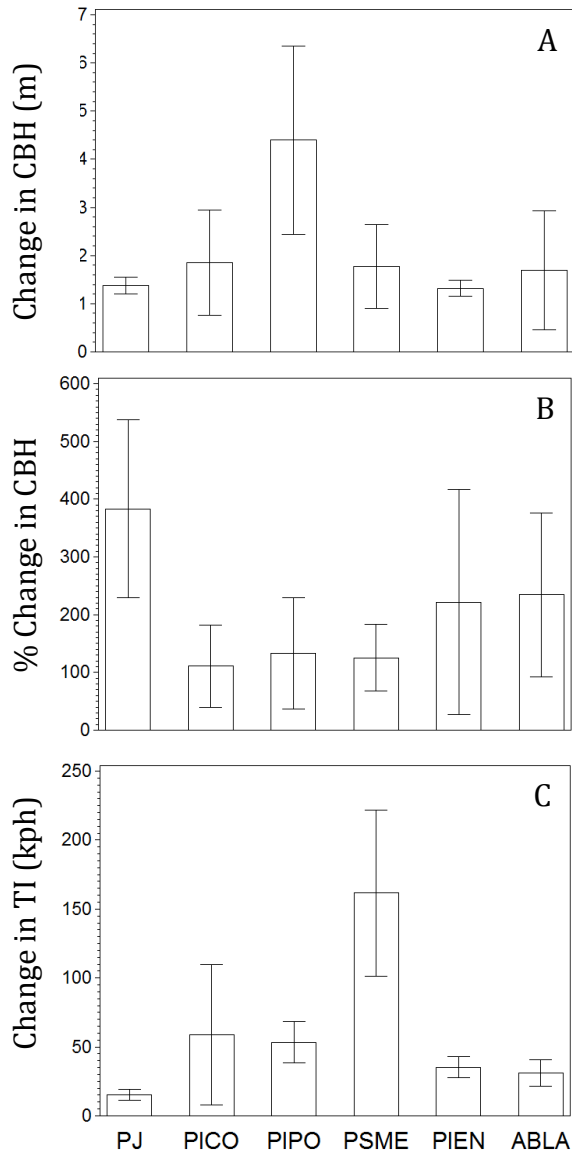
Figure 4.3. Mean absolute (A) and percentage (B) difference in CBH and TI (C) predictions from the production version of FFE-FVS versus predictions from a version of FFE-FVS that incorporated non-uniform vertical crown fuel distributions (Fig. 4.1). Panels are otherwise as described for Fig. 4.2. Using non-uniform distributions increased predictions of the amount of wind required to initiate canopy fire.

While using non-uniform vertical crown fuel distributions in FFE-FVS led to increases in estimated CBH on average for all species, by far the greatest average absolute increase was observed for ponderosa pine (Fig. 4.3). However, pinyon-juniper stands showed the greatest average percentage increase in CBH even though the average absolute increase for these stands

was comparatively small (Fig. 4.3). This reflects a 10-fold difference in average estimated CBH

between ponderosa pine and pinyon-juniper stands; the average percentage CBH increase was

greater for pinyon-juniper stands because they had much lower CBH's to begin with (Table 4.2).

Table 4.2. Estimates of CBD (kg m^{-3}), CBH (m), CI (km hr^{-1}) and TI (km hr^{-1}) from FFE-FVS using uniform and non-uniform crown fuel distributions. Species are as described for Table 4.1 except here JUSC and PIED are combined (PJ). Values in columns are estimates followed by standard deviations in parentheses. Canopy bulk density and CBH increased, CI decreased and TI increased when non-uniform distributions were used.

Spp.	Estimate	Uniform	Non-uniform
ABLA	CBD	0.28 (0.10)	0.60 (0.31)
	CBH	1.08 (0.84)	2.78 (2.22)
	CI	20 (11)	11 (6)
	TI	11 (12)	42 (13)
PICO	CBD	0.23 (0.10)	0.29 (0.10)
	CBH	2.51 (1.99)	4.36 (3.34)
	CI	23 (11)	18 (6)
	TI	87 (142)	145 (228)
PIEN	CBD	0.29 (0.07)	0.47 (0.16)
	CBH	1.07 (0.77)	2.39 (0.81)
	CI	17 (3)	12 (3)
	TI	18 (21)	53 (26)
PIPO	CBD	0.10 (0.07)	0.16 (0.08)
	CBH	4.47 (3.17)	8.87 (5.85)
	CI	49 (24)	31 (11)
	TI	60 (51)	113 (65)
PSME	CBD	0.16 (0.09)	0.27 (0.14)
	CBH	1.75 (0.89)	3.53 (1.60)
	CI	30 (11)	21 (8)
	TI	200 (152)	362 (186)
PJ	CBD	0.15 (0.08)	0.18 (0.09)
	CBH	0.41 (0.18)	1.73 (0.18)
	CI	27 (9)	24 (8)
	TI	0 (0)	15 (4)

For all species, relaxing the assumption of uniform vertical crown fuel distribution

resulted in decreased CI and increased TI. Torching index was more sensitive to distribution

assumptions than crowning index; TI increased by 67 kph on average for all species, while CI decreased by nine kph on average (Table 4.2). However, TI was not as closely related to CBH as CI was to CBD. Decreases in CI were essentially mirror images of percentage increases in CBD. Generally speaking, decreases in CI were inversely proportional to increases in CBD (Fig. 4.2). The same was not true for TI and CBH. By far the greatest average increase in TI was observed for Douglas-fir, yet CBH increases of Douglas-fir stands were merely average (Fig. 4.3).

4.4 Discussion

Our objective in this work was to assess the effect of relaxing crown fuel distribution assumptions on fire hazard evaluation using FFE-FVS. We found replacing uniform crown fuel distributions with non-uniform distributions resulted in substantial increases in estimated CBD and CBH for all of species we investigated; this led to decreases in CI and increases in TI (Figs 4.2 and 4.3). Large values of CBD indicate a high degree of canopy fuel connectivity, which accounts for observed decreases in CI. Other factors held constant, increasing CBH decreases connectivity between surface and canopy fuels; this was the source of observed increases in TI.

4.4.1 Effect on CBD and CI

Canopy bulk density increased because distributing crown fuel using non-uniform distributions in-effect concentrated fuel near crown midpoints. As the trees in our even-aged stands were similar in terms of height and crown ratio, peaks in vertical crown fuel distributions (Fig. 4.2) tended to overlap those of other trees, creating zones of high fuel concentration in canopy fuel profiles. This had the effect of increasing CBD of canopy layers near canopy midpoints. Because FFE-FVS estimates stand CBD as the maximum running of horizontal canopy layer CBDs (Scott and Reinhardt 2001), increasing maximum canopy layer CBD in the canopy profile also increased estimates of CBD for stands. These results suggest the magnitude

of potential increase in CBD from relaxing the assumption of uniform vertical crown fuel distribution is partly a function of stand structure. The greatest potential for increased CBD is in managed even-aged stands, such as plantation stands, where tree heights and crown ratios are very similar, leading to a high degree of overlap between fuel distribution bodies. In contrast, the potential for CBD increase is smaller in stands with more complex structures where tree heights and crown ratios are more variable.

The largest absolute increases in CBD were in stands of shade-tolerant species (Fig. 4.2). Stands of shade tolerant conifers typically support more foliage area than stands of intolerant species (p. 32, Assmann 1970), which implies they contain more foliar biomass. Because foliage constitutes the majority of canopy fuel, it is likely stands of shade-tolerant species saw large absolute increases in CBD simply because they contained more canopy fuel biomass than stands of intolerant species.

Changes in CI mirrored percentage changes in CBD (Fig. 4.2). This highlights the sensitivity of the CI calculation to CBD and underscores the importance of accurately quantifying CBD for canopy fire hazard assessment. Our results suggest CBD estimation methodologies used by FFE-FVS and nearly all other fire behavior models systematically underestimate connectivity of canopy fuels in even-aged stands by failing to account for concentration of fuel above crown midpoints. This directly impacts canopy fire hazard assessment by inflating estimates of the amount of wind necessary to propagate fire through canopies. Misdiagnosing canopy fire hazard in this fashion could have serious consequences, including compromised firefighter safety, and ineffective fuel treatment implementation (Cruz and Alexander 2010).

4.4.2 Effect on CBH and TI

Estimates of CBH increased because using non-uniform distributions in-effect shifted fuel away from crown bases. Because CBH is defined by FFE-FVS using a CBD threshold (Scott and Reinhardt 2001), this had the effect of increasing CBH by reducing fuel mass in lower canopies and increasing the height at which the threshold was met. While upward skew in fuel distributions no doubt contributed to increases in estimated CBH, any realistic representation of fuel concentration near crown midpoints would have had a similar effect. For example, the distribution of 1-hr fuel was only slightly skewed for woodland tree species, yet there was nonetheless very little 1-hr fuel in the bottom 20% of crowns (Fig. 4.1). Unlike increases in CBD, increases in CBH would probably be apparent regardless of stand structure. While CBD increased in our even-aged sample stands as a result of overlapping crown fuel distributions of similarly sized trees, CBH increased because crown fuel was shifted away from crown bases for all trees regardless of their similarity to neighbors.

There were large differences between species in the degree to which relaxing the assumption of uniform crown fuel distribution affected estimates of CBH. The average absolute increase in CBH for ponderosa pine stands was more than double that for any other species (Fig. 4.3). This likely reflects the small average CBD of ponderosa pine stands (Table 4.2). It appears that bulk densities of lower canopy layers in ponderosa pine stands were sufficiently small that shifting fuel distributions toward crown centers caused many lower canopy layers to fall below the CBD threshold used to delineate CBH. In contrast, the absolute increase in CBH was relatively small or pinyon-juniper stands, but the percentage increase was large because estimated CBH from the production version of FFE-FVS was small (Table 4.2, Fig. 4.3).

Therefore, even relatively small absolute increases in CBH represented large percentage changes for pinyon-juniper stands.

Unlike the close relationship between CI and CBD, changes in TI did not necessarily mirror changes in CBH (Figs 4.2 and 4.3). Canopy fuel connectivity (i.e. CBD) is the major determinant of CI if slope and fuel moisture are held constant, as they were in this study. In contrast, CBH only partly accounts for the connectivity of surface and canopy fuels; TI also depends on surface fuel characteristics, particularly those that bear on surface flame lengths. Changes in TI therefore depended not only on increase in CBH, but also on the size of the increase relative to potential surface flame lengths. To illustrate: average increase in CBH was similar for stands of Douglas-fir and subalpine fir, however TI increased much more for Douglas-fir (Fig. 4.3). This reflects that fact that Douglas-fir stands were assigned low surface fuel loads (generally fire behavior model eight) in FFE-FVS simulation compared to subalpine fir stands (generally fire behavior model 10 [Anderson 1982]). Other factors held constant, greater surface fuel loads usually translate to longer surface flame lengths. Consequently, increases in TI for subalpine fir stands, while considerable, were tiny compared to increases for Douglas-fir stands because CBH increases in Douglas-fir stands were large relative to potential flame lengths. The relationship between TI and CBH may also have been muddied by TI's dependency on canopy wind reduction, which is calculated using CBD in FFE-FVS (Rebain et al. 2010).

It is important to point-out that the increases we observed in estimated CBH are an artifact of the CBH estimation methodology used in FFE-FVS and probably do not reflect actual conditions in stands. The CBD threshold used to define CBH in FFE-FVS is arbitrary (Cruz and Alexander 2010), and was selected to yield realistic predictions of torching behavior under the

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assumption of uniformly-distributed crown fuel. Relaxing fuel distribution assumptions without adjusting the threshold therefore resulted in unrealistically large estimates of CBH. This highlights the need to adjust the CBD threshold used to delineate CBH in FFE-FVS to accommodate non-uniform crown fuel distributions. Alternatively, CBH could be delineated using a methodology that is less sensitive to CBD, such as mean crown base height. However, average values may not be meaningful for structurally complex stands (Cruz and Alexander 2010).

4.5. Conclusion

This work showed that using realistic crown fuel distribution assumptions in FFE-FVS caused substantial increases in estimates of CBD and CBH for stands of interior western U.S. conifer species; this decreased estimates of CI by 9 kph on average, and increased estimates of TI by 67 kph. The implication is that the assumption of uniform vertical crown fuel distribution currently made by FFE-FVS and nearly all other fire behavior models results in systematic underestimation of the connectivity of canopy fuels (CBD) in even-aged stands. This in turn impacts fire hazard assessment by inflating estimates of CI, causing underestimation of the potential for fire to spread laterally through canopies. Canopy base height is an important determinant of the readiness with which fire transitions from surface fuels into canopies. Estimates of CBH were sensitive to crown fuel distribution assumptions; however, this was an artifact of the methodology used to estimate CBH in FFE-FVS.

Our results argue for adopting non-uniform fuel distributions in fire behavior models for interior western U.S. conifer stands. This would correct a tendency to underestimate the potential for crown fire spread that arises from the current unrealistic assumption that crown fuel is uniformly distributed through crowns. Underestimating potential fire behavior is a critical flaw

for fire behavior models because it could have potentially severe consequences (i.e. increased

risk to firefighters). Adopting non-uniform crown fuel distributions in FFE-FVS would require

altering the current CBH estimation methodology. However, this could be accomplished by

changing the value of a single arbitrary constant.

CONCLUSION

This work was an investigation of the nature of variation in the distribution of fuel within conifer crowns in the interior western U.S., the generality of diameter-based allometries, and the potential impact of these factors on canopy fire hazard assessment using the Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS). This study was precipitated by the observation that the current, unrealistic, assumption of uniform within-crown fuel distribution made by FFE-FVS and almost all other fire behavior models could lead to underestimation of potential fire behavior by misrepresenting the degree of horizontal connectivity of canopy fuels (Reinhardt et al. 2006; Keyser and Smith 2010). Furthermore, estimates of crown fuel biomass for areas across the western U.S. rely heavily on allometric estimators developed from trees in northern Idaho and Montana (Brown 1978), which have been shown to underestimate crown fuel mass for trees in South Dakota's Black Hills (Keyser and Smith 2010). This study was designed to yield insights into the generality of findings from Keyser and Smith (2010), and to develop management recommendations for improving canopy fire hazard evaluation methodology based on our results.

Chapter 1 detailed an investigation into the relationship between light availability, foliage occurrence and shade tolerance in conifer crowns and canopies. This provided the conceptual foundation for subsequent chapters. Chapter 1 showed the distribution of foliage (which is the major constituent of crown fuel) in conifer crowns and canopies is predictable from light availability, and that this relationship is mediated by species' shade tolerance. Light availability is decreased in the interiors of large tree crowns and under the canopies of high density stands, which accounts for 'hollowing' of the interiors of lower crowns and self-pruning of lower

branches in crowded stands. Shade tolerant species are able to maintain foliage in lower light environments than intolerant species, which allows them to maintain longer and fuller crowns. It is clear from Chapter 1 that in order to characterize the distribution of canopy fuel, it is necessary to account for both stand density and species shade tolerance.

In Chapter 2, I described an investigation of whether sapwood- and diameter-based foliage area allometries developed from trees in northern Idaho, Montana and Wyoming (roughly the same geographic area represented by allometries in Brown [1978]) were interchangeable with allometries developed from trees in more southerly locations (southern Idaho, Utah, Colorado and New Mexico). I also evaluated whether accounting for factors known to vary between sites (in this case, sapwood taper) increased the generality of allometries. This work showed allometric relationships based on diameter at breast height (DBH) were broadly similar across geographic areas when tree datasets spanned similar ranges of stand density and tree size. However, relationships were dissimilar for sets of trees that differed in average size and stand density, and tended to diverge for large trees regardless of the degree of similarity between sets of trees. Accounting for sapwood taper eliminated differences between allometries from different geographic areas for two species of pine, but increased differences for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). This suggests the characteristics of allometric models that confer the property of generality are species-specific. For the pine species we investigated, sapwood-based allometries that accounted for sapwood taper were most general, implying the relationship between foliage area and hydraulic capacity is broadly stable for these trees. In contrast, a DBH-based allometry was most general for Douglas-fir, which suggests the mechanical relationship between the DBH required to support a crown of given size was more stable for this species.

Chapter 3 described an investigation of the nature of variation in within-crown distributions of crown fuel for seven conifer species that represented a broad range of shade tolerance. This work showed the center of within-crown fuel mass is almost without exception located above the crown midpoint, and that fuel is shifted upward and concentrated in upper crowns in crowded stands compared to open stands. These results are consistent with the findings described in Chapter 1, which lends credence to a conceptual model that posits foliage distribution is largely a product of the light environment in crowns and canopies (Schoettle and Fahey 1994). Importantly, this work showed the effect of species shade tolerance on fuel distribution is primarily expressed as differences between species in the response of crown ratio to stand density, not in differences in the response of within-crown biomass to stand density. Thus, a 'generic' model of within-crown biomass response to stand density combined with species-specific crown ratio responses appears to adequately characterize the canopy fuels complex.

Finally, in Chapter 4 I described the impact of relaxing the assumption of uniform vertical distribution of crown fuel on canopy fire hazard evaluation using FFE-FVS. The standard methodology used by FFE-FVS and almost all fire behavior models to estimate canopy bulk density (CBD) is to interpret the maximum running mean CBD of discrete canopy layers (CBD is calculated for layers as the sum of fuel biomass in each layer divided by the volume of the layer) as 'effective' CBD, thought to indicate the degree of horizontal connectivity of canopy fuels (Sando and Wick 1972). Using realistic, upward-skewed crown fuel distributions instead of uniform distributions thus increased estimates of CBD because the uniform distributions did not accurately represent the concentration of fuels in upper crowns and canopies; accounting for this concentration of fuels increased the maximum running mean CBD of canopy layers and, by

extension, effective CBD. The implication is that the current CBD estimation methodology underestimates the connectivity of canopy fuels and thus potential fire behavior.

Based on the four lines of investigation described above, I conclude the distribution of fuels in interior western U.S. conifer forest canopies can be described using stand density and species shade tolerance, in accordance with the conceptual model of Schoettle and Fahey (1994). Crown fuel biomass is best estimated using locally developed allometries. Estimates from non-local models may be substantially biased, especially for large trees. Further research is needed to identify allometric model forms that are generally applicable across geographic areas, as this work showed model characteristics that confer the property of generality for some species may reduce it for others. Methods of characterizing crown fuels for canopy fire hazard assessment are sensitive to fuel distribution assumptions. It should be expected that incorporating more realistic within-crown fuel distributions into CBD estimation methodology will result in revisions of fire behavior predictions, and that revisions will generally entail predictions of canopy fire under less extreme weather conditions than predicted from the current methodology.

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APPENDIX 1

Table A.1. Sampling location details. Species are as described for Table 4.2. Lat. and Long. are in decimal degrees. Elevation is in m, plot is plot size (ha), N is number of trees, TPH is trees ha^{-1}, BA is basal area (m^2 ha^{-1}) and QMD is quadratic mean diameter (cm).

Spp.	Pop.	Lat.	Long.	Elev.	Plot	N	TPH	BA	QMD
PSME	N	45.50278	113.98398	1401	0.050	45	900	30.6	20.8
		44.47524	111.23428	2081	0.050	35	700	62.0	33.6
		45.51271	111.11829	2025	0.020	36	1800	34.7	15.7
		46.84480	110.28700	1554	0.020	35	1750	55.0	20.0
		47.00694	114.36237	998	0.040	40	1000	16.9	14.7
		45.38531	109.76966	1934	0.020	31	1550	61.3	22.4
	S	40.25027	105.41234	2338	0.050	50	1000	27.1	18.6
		41.92290	111.46561	2372	0.050	30	600	54.4	34.0
		38.72308	105.92911	3014	0.020	46	2300	40.8	15.0
		38.98664	105.17760	2769	0.100	67	670	24.8	21.7
		39.91459	110.61682	2419	0.050	40	800	11.5	13.5
		42.55767	111.30388	2246	0.050	46	920	45.5	25.1
PIEN		39.44107	106.68606	3024	0.020	47	2350	101.5	23.5
		44.80067	107.65738	2746	0.050	122	2440	65.5	18.5
		42.20846	111.60381	2394	0.050	133	2660	61.0	17.1
		38.29993	108.13495	2812	0.033	42	1273	25.1	15.9
		39.35906	106.06605	3500	0.020	47	2350	49.5	16.4
		43.70162	109.95863	2568	0.007	30	4478	34.8	10.0
PJ		36.14552	106.70399	2384	0.100	61	610	16.6	15.5
		37.90044	105.20096	2532	0.100	104	1040	43.8	23.3
		37.40763	108.37051	2269	0.100	65	650	20.5	20.1
PIPO	N	46.84410	110.28976	1566	0.020	34	1700	61.3	21.4
		46.74451	111.76291	1425	0.013	63	5040	26.2	8.1
		46.58345	114.13956	1124	0.200	32	160	24.0	43.7
		46.99791	113.67889	1274	0.067	74	1104	14.1	12.8
		44.82067	107.32828	1787	0.100	34	340	35.5	36.5
		45.52516	113.98338	1488	0.100	32	320	37.5	38.6
	S	40.84964	105.56982	2504	0.020	46	2300	38.2	14.5
		37.49297	108.39046	2407	0.050	35	700	39.6	26.8
		38.23915	108.13876	2475	0.250	34	136	19.9	43.2
		36.06808	105.80710	2466	0.500	90	180	13.0	30.3
		37.87432	105.27293	2530	0.100	34	340	25.6	31.0
		38.68283	105.87185	2863	0.050	41	820	25.2	19.8
ABLA		40.64112	105.70811	3178	0.010	55	5500	32.2	8.6
		40.10225	107.29864	3144	0.050	52	1040	46.3	23.8
		43.90071	110.97530	2390	0.100	46	460	23.3	25.4
		39.26501	106.45385	3363	0.040	83	2075	35.6	14.8