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ARTICLE

Characterizing crown fuel distribution for conifers in the interior western United States

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Abstract: Canopy fire hazard evaluation is essential for prioritizing fuel treatments and for assessing potential risk to firefighters during suppression activities. Fire hazard is usually expressed as predicted potential fire behavior, which is sensitive to the methodology used to quantitatively describe fuel profiles: methodologies that assume that fuel is distributed uniformly throughout crowns have been shown to predict less severe fire behavior than those that assume more realistic nonuniform fuel distributions. We used crown fuel data from seven interior western United States conifer species to characterize within-crown fuel distributions. Fuel was shifted upward and concentrated in crowns in crowded stands compared with crowns in open stands, which suggests that the vertical distribution of fuel is shaped by foliage concentration in favorable light environments near the top of crowns and echoes the predictable relationship between crown ratio and stand density. However, unlike crown ratio, the relationship between within-crown foliage distribution and stand density was independent of the shade tolerance of a species. This implies that there is a general relationship between stand density and within-crown fuel distribution for conifers and that species differences in fuel profiles related to shade tolerance are expressed primarily in the relationship between stand density and crown ratio.

Key words: fire hazard, canopy bulk density, canopy fuel profile, relative density, shade tolerance.

Résumé : L'évaluation des risques de feu de cime est essentielle pour prioriser les traitements des combustibles et évaluer les risques potentiels pour les pompiers lors d'activités de suppression. L'expression du risque d'incendie prend habituellement la forme d'une prédiction du comportement potentiel du feu, qui est sensible à la méthodologie utilisée pour décrire de façon qualitative le profile des combustibles. On a démontré que les méthodologies qui assument que les combustibles sont répartis uniformément dans les cimes prédisent un comportement moins sévère du feu que celles qui assument de façon plus réaliste que les combustibles ne sont pas uniformément répartis. Nous avons utilisé des données portant sur les combustibles de cime de sept espèces continentales de conifères de l'ouest des États-Unis pour caractériser la répartition des combustibles à l'intérieur de la cime. Les combustibles étaient concentrés dans le haut des cimes dans les peuplements denses comparativement aux peuplements clairs, ce qui indique que la répartition verticale des combustibles est déterminée par la concentration du feuillage dans les endroits où la lumière est favorable près du sommet des cimes et rappelle la relation prévisible entre le rapport de cime et la densité du peuplement. Cependant, contrairement au rapport de cime, la relation entre la répartition du feuillage à l'intérieur de la cime et la densité du peuplement était indépendante de la tolérance à l'ombre de l'espèce. Cela implique qu'il existe une relation générale entre la densité du peuplement et la répartition des combustibles à l'intérieur de la cime chez les conifères; et que les différences interspécifiques dans le profile des combustibles reliés à la tolérance à l'ombre sont exprimées principalement dans la relation entre la densité du peuplement et le rapport de cime. [Traduit par la Rédaction]

Mots-clés : risque d'incendie, densité apparente du couvert, profile des combustibles dans le couvert forestier, densité relative, tolérance à l'ombre.

Introduction

Canopy fire hazard has become a central management consideration in many conifer forests. Widespread fire suppression in dry, fire-adapted forests of the interior western United States (US) has promoted ladder fuel development and increased canopy bulk density (CBD), factors that have been implicated in large, high-severity crown fires (Peterson et al. 2005). In addition, expansion of the wildland–urban interface increasingly necessitates fuel treatments even in forests adapted to infrequent stand-replacing fire that have not experienced fuel buildups (Theobald and Romme 2007). Decisions to treat fuels or to suppress fires using direct attack techniques frequently hinge on assessment of canopy fire hazard (see Affleck et al. (2012) for a recent review). Fire hazard assessment often consists of evaluating whether active canopy fire behavior is expected under a set of reference fire weather conditions (Scott and Reinhardt 2001). Most methods of predicting potential canopy fire behavior rely heavily on estimates of CBD (Van Wagner 1977). Standard procedures for estimating CBD (more correctly described as "effective" CBD (Scott and Reinhardt 2001)) 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 nonuniformity without exception,

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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).

Increasing the realism of crown fuel characterization is necessary to enhance managers' ability to assess canopy fire hazard and also to support the development of physics-based fire behavior models (e.g., Mell et al. 2009) that make explicit assumptions about the distribution of fuel within the crowns of individual trees. In this paper, we describe an investigation of the nature of variation in the vertical distribution of fuel in conifer crowns with respect to stand density and shade tolerance. Specifically, we assess whether there are systematic differences between shade-tolerant and shade-intolerant (hereafter, tolerant and intolerant, respectively) conifers in the response of within-crown fuel distribution to increasing stand density that are analogous to differences in the response of crown ratio (CR) to stand density for the same set of species.

It is well documented that CR, the proportion of total tree height that supports live foliage, declines predictably with increasing stand density (Oliver and Larson (1996), p. 72). The CRs of tolerant species typically decline less than those of intolerant species (p. 183, Smith et al. (1997)), meaning that 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 affect the distribution of foliage within crowns: the vertical distribution of foliage within the crowns of intolerant conifers has been shown to be more sensitive to stand density than the distribution of foliage within the crowns of tolerant species (Garber and Maguire 2005). This suggests that trends in within-crown foliage distribution with respect to shade tolerance and stand density may be analogous to trends in CRs with respect to the same factors.

There is considerable evidence indicating that within-crown foliage distributions arise in part from the plastic response of crown architecture to light competition from neighbors. Foliage is typically shifted upward in crowns growing in dense stands relative to its distribution in crowns growing in open stands (e.g., Brix 1981; Garber and Maguire 2005; Keyser and Smith 2010; but see Stephens (1969)). This effect presumably arises from the increased shading of lower branches in dense stands. Similarly, upward-shifted foliage distributions are frequently reported for trees in subordinate social positions (e.g., Maguire and Bennett 1996; Gilmore and Seymour 1997; Mäkelä and Vanninen 2001; Garber and Maguire 2005; Jiménez et al. 2013; but see Weiskittel et al. (2009)). This is likely a similar plastic response of within-crown foliage distribution to light competition.

The center of foliage mass typically resides near the midpoint of the vertical crown profile in conifers; however, its exact location appears to depend on the growing environment and the shade tolerance of the species. A study of five interior western US conifer species with differing levels of shade tolerance showed that the center of crown fuel mass was consistently located above the middle of crowns for all species (Reinhardt et al. 2006). Similarly, the center of foliage mass was found to reside above crown midpoints for Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), although the centers of total crown biomass were lower (Tahvanainen and Forss 2008). Vose (1988) found that the center of foliage area was located at or above the midpoint of loblolly pine (*Pinus taeda* L.) crowns, which suggests that the 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). Conversely, other studies have shown foliage biomass to be consistently concentrated in lower crowns of loblolly pine (Gillespie et al. 1994; Xu and Harrington 1998) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Maguire and Bennett 1996). Some researchers have concluded that the center of foliage mass shifts between the middle and lower portions of crowns depending on the stand density, social position of trees, and species shade tolerance (Garber and Maguire 2005).

This paper describes an investigation of within-crown distributions of foliage and twigs for several common interior western US conifer species. We assembled a dataset that spans broad ranges of stand density and tree size for species with different levels of shade tolerance to evaluate the effect of these factors on the vertical distribution of fuel within conifer crowns. Our objectives in this work were to (*i*) develop nonuniform vertical crown fuel distributions for conifers that occur in different forest types (open-canopy woodlands versus closed-canopy forests), as well as for trees with different levels of shade tolerance; (*ii*) ascertain the degree to which distribution parameters vary among individual trees, stands, and species; and (*iii*) determine whether within-crown fuel distribution is predictable from shade tolerance and stand density in a similar manner as CR. To meet these objectives, we destructively sampled almost 200 trees at dozens of locations across the interior western US and reanalyzed data from three additional studies, which were conducted over the past three decades.

Methods

Data collection

We used detailed crown biomass data from a total of 394 trees of seven conifer species to meet our objectives (Table 1). "Woodland" species two-needle pinyon (*Pinus edulis* Engelm.) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) are short-statured trees that are usually found on xeric sites that do not typically form closed canopies. "Forest" species subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* Douglas ex Loudon), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), and Douglas-fir are taller trees found on comparatively wetter sites and form closed-canopy stands. Forest tree species were selected to represent various levels of shade tolerance. Lodgepole and ponderosa pines are considered intolerant, Douglas-fir is considered intermediately tolerant, 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 the states of Colorado, New Mexico, Utah, Idaho, Montana, South Dakota, and Wyoming. Stands were selected to represent broad ranges of density and mean tree size (Table 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 (Supplementary Table S1[1]) from across the range of tree sizes present in the main canopy. We subjectively chose "normal" trees, and individuals 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. For every other section, foliage and live twigs ≤ 2.54 cm in diameter were weighed together. Otherwise, foliage was combined only with live twigs ≤ 0.64 cm in diameter. Subsamples were then collected from three sections near the top, bottom, and midpoint of crowns and dried to constant mass for development of ratio estimators to determine the total biomass of foliage and each time-lag class of live and dead woody material in each crown section. Hierarchical sampling and material process-

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0503.

Table 1. Summary sample data.

Species	N	Basal area ($m^2 \cdot ha^{-1}$)	RD	Quadratic mean diameter (cm)	Diameter (cm)
Subalpine fir	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)
Rocky Mountain juniper	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)
Lodgepole pine	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)
Two-needle pinyon	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)
Engelmann spruce	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)
Ponderosa pine	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)
Douglas-fir	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)

Note: The number of sample locations (*N*) followed by the number of sample trees in parentheses. All other columns are means followed by minimum and maximum values in parentheses. RD, relative density of stands (described in Methods); diameter, diameter of destructively sampled trees. Twenty-nine subalpine fir trees were sampled by Long and Smith (1989), all lodgepole pine trees were sampled by Long and Smith (1988), and 76 ponderosa pine trees were sampled by Keyser and Smith (2010). For subalpine fir, stand-level data from two small (<0.01 ha) inventory plots sampled by Long and Smith (1989) indicated RD > 1.5, and we presumed that this reflected sampling bias and excluded these data when summarizing BA and RD, as well as from regression analyses that used RD. Rocky Mountain juniper and two-needle pinyon were considered "woodland" tree species in this study and 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.

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

We inventoried trees surrounding those selected for destructive sampling at each location using a single fixed-radius plot sized to include at least 30 overstory trees. Species, diameter at breast height (dbh, 1.37 m), height, and crown base height were recorded for all trees with a dbh > 1 cm (including sample trees). Diameter at breast height was measured to the nearest 0.1 cm using a dbh tape, and height and crown base height were measured to the nearest 0.1 m using a laser hypsometer. Crown base height was designated as the base of the compact live crown by "moving up" the lowest live branches until at least three branches were accumulated. We chose three branches to represent a full whorl, because although we assumed whorls for most trees would have four branches (one in each of four quadrants), we felt it would be inappropriate to "move up" a nearly complete whorl consisting of three branches.

In addition to the sampling effort described above, we also reanalyzed several previously published datasets (Table 1). We were able to directly incorporate data collected from ponderosa pine stands in Black Hills, South Dakota, by Keyser and Smith (2010), because we duplicated their protocols exactly. We also reanalyzed a lodgepole pine dataset from Wyoming collected by Long and Smith (1988) and a subalpine fir dataset from Utah collected by Long and Smith (1989). Branch biomass was not subdivided into time-lag classes in these datasets (hereafter the 1980s data), so we developed ratio estimators to assign branch biomass to classes. For subalpine fir, the 1980s 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 mean 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 branches 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 mass, 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 1980s data.

Data analysis

We developed vertical fuel distributions by using an iterative, derivative-free least-squares algorithm to fit a two-parameter cumulative Weibull distribution separately for the biomass of foliage and live and dead twigs < 0.64 cm in diameter for each tree in our dataset. Ten data points (one per crown section) were used to fit distributions for most trees; however, the number of crown sections per tree (and consequently, data points per tree) in the 1980s data ranged from 4 to 14. Nonlinear regression was used for parameter estimation, because this analysis could be performed easily using statistical software (SAS version 9.3, SAS Institute, Inc., Cary, North Carolina). We defined fuel as foliage and live and dead twigs < 0.64 cm in diameter to maintain consistency with crown fuel characterization in the Fire and Fuels Extension to the Forest Vegetation Simulator (Rebain et al. 2010), which is often used to plan fuel treatments. The Weibull distribution has been used extensively to characterize the spatial arrangement of biomass in conifer crowns (e.g., Gillespie et al. 1994; Keyser and Smith 2010); our use of it here permits comparison of our parameter estimates with those from other studies. The form of model 1 was

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

where y is the cumulative proportion of total biomass 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 biomass is skewed upward or downward in crowns, whereas the estimated scale parameter β represents the degree to which biomass is concentrated in a few sections versus spread evenly throughout crowns. We opted to estimate parameters using the cumulative Weibull distribution instead of the probability density function, because the cumulative function can be expressed as a closed-form expression, which is simpler than the probability density function (p. 100, Clutter et al. (1983)). We used estimates of α and β from Keyser and Smith (2010) as starting values for nonlinear regression. Pairs of estimated parameters were discarded when either parameter was not significant ($p > 0.05$) or when Hougaard's index was greater than 1 ((Ratkowsky 1990), p. 26). We used Hougaard's index to filter out parameter estimates with highly skewed residual error distributions. This allowed us to construct symmetric confidence intervals around the estimates. Characterizing the vertical distribution of fuel within crowns instead of over total tree height allowed us to use a two-parameter distribution instead of estimating the location of crown base height with a third parameter.

We investigated the nature of variation in crown fuel distribution by interpreting and analyzing estimates of α and β for trees, stands, species, and characteristic forest types (forests or woodlands; Table 1). The Weibull distribution is nearly symmetric when $\alpha \approx 3.6$. As it is used here, values of $\alpha > \sim 3.6$ indicate negatively skewed biomass distributions, whereas values of $\alpha < \sim 3.6$ indicate positively skewed distributions (Mori and Hagihara 1991). Small β values reflect the concentration of fuel in the vertical crown profile. Large β values indicate that material is spread more evenly throughout the crown. We compared the magnitude of within-stand ranges in parameter values with within-species ranges to ascertain the degree to which distributions varied within stands relative to their variation between stands of similar composition. We also compared mean foliage distribution parameter values of species that occurred in forests with species that occurred in woodlands (Table 1), using t tests to assess whether there were differences between distributions for stands of dissimilar composition and type. We accounted for the uncertainty of estimated parameter values for this comparison and for the construction of confidence intervals by adding the mean standard errors of parameter estimates for a species or type (forest or woodland) to the standard deviations of the mean parameter estimates. Finally, we used linear regression techniques to evaluate whether α and β were predictable from stand density and shade tolerance in a manner similar to CR, as well as whether they were related to canopy position of trees (tree height expressed as a proportion of mean stand height). Stand density was quantified using relative density (RD), expressed as the stand density index (SDI; Reineke 1933) divided by an estimate of the maximum SDI of the species (maximum values from J.N. Long, personal communication, 20 May 2013). Relative density 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).

Results

We estimated α and β for each destructively sampled tree using model 1 and then averaged parameter values for species and forest types (Table 2). In some cases, biomass distributions were bimodal and thus poorly approximated by the Weibull distribution. In these cases, the derivative-free algorithm used for nonlinear regression did not converge on a solution, so no estimates were obtained. With the exception of twigs for Rocky Mountain juniper and ponderosa pine, α was $< \sim 3.6$, on average, for all combinations of species and crown fuel component (Table 2). For foliage, α was $< \sim 3.6$ for 97% of our sample trees, and for twigs, α was $< \sim 3.6$ for 85% of our sampled trees. On average, the range of parameter values for trees in a given stand was about one-half the total range of values for the species (ratio of average within-stand parameter range to total parameter range ≈ 0.5), indicating that within-crown foliage distributions varied widely between trees in the same stand. The ratio of within-stand to within-species range was smallest for ponderosa pine, averaging 0.29 for all parameters, and largest for Rocky Mountain juniper, averaging 0.65 for all parameters. Ratios for all other species were between 0.40 and 0.60 (Table 2). When we used linear regression techniques to investigate whether observed within-stand variation in parameter values was related to the canopy position of individual trees, we found that relationships were, in most cases, nonsignificant ($p > 0.5$). The exceptions were significant negative relationships between β (foliage) and canopy position for Douglas-fir ($p < 0.01$, degrees of freedom (df) = 58, $r^2 = 0.14$) and for Engelmann spruce ($p = 0.05$, df = 28, $r^2 = 0.13$). This indicates that for these species, foliage was more concentrated within the vertical crown profile of trees in subordinate canopy positions compared with trees in better canopy positions.

There was no obvious relationship between foliage distribution parameter values and shade tolerance (Fig. 1). Parameters for twig distributions tended to be similar to those for foliage distributions (Table 2) and are not shown in Fig. 1. The α and β values for foliage distributions were smaller, on average, for forest trees than for woodland trees when trees were grouped into characteristic forest types (Fig. 1) (α: $p < 0.01$, df = 29.91, Satterthwaite's approximate t test to account for unequal variance; β: $p < 0.01$, df = 315, two sample t test). In open-canopy woodlands, foliage was only slightly skewed on average ($\alpha = 3.27$) and was spread relatively evenly throughout crowns ($\beta = 0.74$). In contrast, foliage in crowns of trees in closed-canopy forests was shifted upward to a greater degree ($\alpha = 2.37$) and was more concentrated within crowns ($\beta = 0.54$). This indicates that foliage was shifted upward and was more concentrated in the crowns of forest trees compared with the foliage of woodland trees (Fig. 2).

The relationship between CR and RD was not significantly different for tolerant subalpine fir and Engelmann spruce and intermediately tolerant Douglas-fir (the interaction between shade tolerance and RD was not statistically significant in a multiple linear regression; $p = 0.86$, df = 21), so Douglas-fir was grouped with tolerant tree species for regression analysis. Relative density was a statistically significant predictor of CR for both tolerant and intolerant tree species (Fig. 3; Table 3). However, RD explained a much greater proportion of the variation in CR for intolerant species (65% versus 19%, respectively), and CR decreased much more rapidly with increasing RD for intolerant species (slope of –0.49 compared with a slope of –0.19, respectively). This dichotomy between tolerant and intolerant species was not evident for relationships between within-crown foliage distribution parameters and RD. The relationship between α and RD was significant for intolerant species and nonsignificant for intolerant species when shade tolerance groups were evaluated individually (Fig. 3; Table 3). However, there were no differences between tolerant and intolerant species in the relationship between α or β and RD when RD, shade tolerance, and their interaction were evaluated using a multiple linear regression ($p > 0.30$, df = 49 for the interaction between shade tolerance and RD for both parameters). Relative density was a significant predictor of α and β when tolerant and intolerant species were combined (Fig. 3; Table 3).

Discussion

In this work, we characterized within-crown vertical fuel distributions for the predominant conifer species in the interior western US and evaluated whether distribution parameters were predictable from RD and species shade tolerance. We found that vertical biomass distributions of foliage and twigs were nearly always positively skewed and that the degree of skewness increased with stand density, suggesting that the center of foliage and twig mass is shifted upward in dense stands. This held for five species that represented three levels of shade tolerance, as well as two characteristic forest types, i.e., closed-canopy forests and open-canopy woodlands. Rocky Mountain juniper and ponderosa pine were exceptional in this regard, as twig biomass distributions were often negatively skewed for these species. This implies that fine woody biomass is centered lower in crowns than foliage biomass for these species, which has also been demonstrated for Norway spruce and Scots pine in Europe (Tahvanainen and Forss 2008).

Our results (Fig. 2) appear to be consistent with previous work that suggests that the center of crown fuel mass generally resides above the crown midpoint for interior western US conifer species that occur in closed-canopy forests (Reinhardt et al. 2006). However, this finding appears to be at odds with other work that found that the center of foliage mass was located below the crown midpoint for some of the same species (Maguire and Bennett 1996; Garber and Maguire 2005). Although there are methodological differences between studies that preclude direct comparison of results (Maguire and Bennett (1996) and Garber and Maguire (2005) used a

Table 2. Mean Weibull distribution parameter values for species and characteristic forest types (forest and woodland).

Component	RMSE	Coeficient of determination	Parameter	Estimate	Stand range	Species range
Subalpine fir						
Foliage	0.01–0.06	0.9786–0.9986	α	2.55 (0.55)	0.89	1.70
			β	0.54 (0.08)	0.14	0.27
Twigs	0.01–0.08	0.9671–0.9986	α	2.51 (0.60)	0.84	1.82
			β	0.67 (0.07)	0.13	0.22
Rocky Mountain juniper						
Foliage	0.05–0.08	0.9381–0.9858	α	3.64 (1.71)	1.88	2.56
			β	0.79 (0.08)	0.09	0.17
Twigs	0.03–0.09	0.9173–0.9945	α	4.07 (1.53)	2.20	2.66
			β	0.81 (0.08)	0.11	0.21
Lodgepole pine						
Foliage	<0.01–0.08	0.9638–>0.9999	α	2.30 (0.56)	0.85	1.96
			β	0.46 (0.11)	0.19	0.43
Twigs	0.01–0.11	0.9296–0.9999	α	2.38 (0.74)	1.04	2.95
			β	0.59 (0.09)	0.16	0.39
Two-needle pinyon						
Foliage	0.04–0.08	0.9260–0.9899	α	2.91 (1.18)	1.97	3.42
			β	0.69 (0.09)	0.15	0.25
Twigs	0.04–0.08	0.9473–0.9900	α	3.23 (1.47)	2.51	4.57
			β	0.73 (0.09)	0.14	0.26
Engelmann spruce						
Foliage	0.01–0.09	0.9303–0.9998	α	2.08 (0.59)	1.00	1.83
			β	0.56 (0.10)	0.19	0.39
Twigs	0.01–0.08	0.9264–0.9998	α	2.30 (0.76)	1.11	2.37
			β	0.64 (0.10)	0.17	0.34
Ponderosa pine						
Foliage	0.01–0.07	0.9561–0.9991	α	2.46 (0.58)	0.87	2.27
			β	0.60 (0.08)	0.13	0.35
Twigs	0.02–0.13	0.8269–0.9985	α	3.91 (2.51)	2.39	10.84
			β	0.75 (0.16)	0.14	0.73
Douglas-fir						
Foliage	0.01–0.10	0.8821–0.9994	α	2.40 (0.62)	0.92	2.36
			β	0.57 (0.12)	0.23	0.53
Twigs	0.01–0.08	0.9411–0.9993	α	2.49 (0.78)	1.06	3.09
			β	0.61 (0.13)	0.24	0.54
Forest						
Foliage	<0.01–0.10	0.8821–>0.9999	α	2.37 (0.59)	—	—
			β	0.54 (0.12)	—	—
Twigs	0.01–0.13	0.8269–0.9999	α	2.86 (1.68)	—	—
			β	0.66 (0.14)	—	—
Woodland						
Foliage	0.04–0.08	0.9260–0.9899	α	3.27 (1.52)	—	—
			β	0.74 (0.10)	—	—
Twigs	0.03–0.09	0.9173–0.9945	α	3.65 (1.58)	—	—
			β	0.77 (0.09)	—	—

Note: Foliage and twigs are the crown fuel component to which parameters apply. The nonlinear regression coefficient of determination (calculated as 1 – (residual SS/corrected total SS)) is presented for comparison of model fits and does not reflect the proportion of variation explained by the model. Estimates are the mean parameter values followed by the sum of the mean standard error of the estimated parameter and the standard deviation of the mean value in parentheses. Mean within-stand and within-species ranges in estimated parameter values for individual trees.

β distribution instead of a Weibull distribution to characterize crowns), it is likely that there were real differences between studies in the distribution of foliage within crowns of sample trees, because both β and Weibull distributions would be strongly influenced by the location of the center of mass within crowns.

The variability of crown biomass distributions within real stands is almost certainly greater than suggested by our results. In this study and in every other similar study that we are aware of, trees were subjectively selected for sampling such that "abnormal" characteristics such as lopsided crowns and double tops were avoided. Given that trees with these features are commonplace in forests, it is likely that any characterization of crowns based on "normal" trees systematically misrepresents crown biomass distributions for many real trees (e.g., biomass may be shifted upward or downward in abnormal crowns). The nature of this misrepresentation is uncertain.

The failure of the Weibull distribution to decline to zero at the crown base (Fig. 2) suggests that a right-truncated Weibull distribution would be a highly appropriate choice for characterizing crown biomass, as has been previously reported for foliage area

Fig. 1. Mean values of α and β for within-crown foliage distribution for each species, arranged by canopy type (woodland (W.land) and forest) and shade-tolerance category (Intol., intolerant; Int., intermediate; Tol., tolerant). Error bars are 95% confidence intervals of means calculated using the sum of the mean standard error of the estimated parameter and the standard deviation of the mean value. Abbreviations on x axis are for species common names (for definitions, see Table 1).

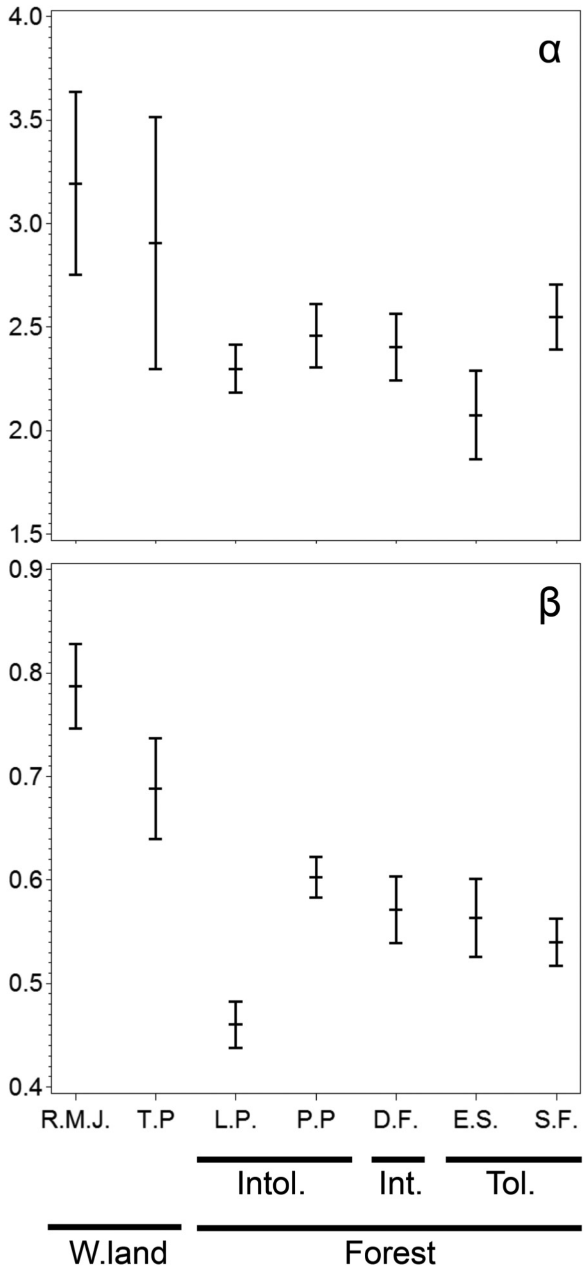
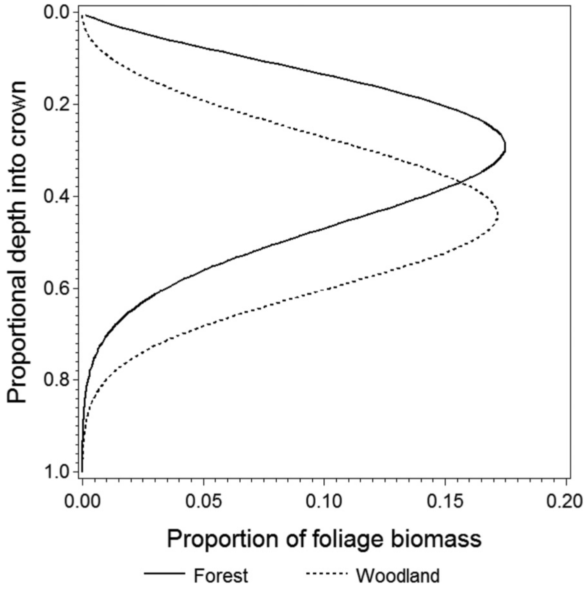


Fig. 2. Characteristic foliage biomass distributions for forest and woodland trees indicate that foliage is shifted upwards and concentrated in forest tree crowns relative to the crowns of woodland trees. Curves were generated using mean parameter values for characteristic forest types (Table 2).



(Weiskittel et al. 2009). Unlike the β distribution, the Weibull distribution is not constrained to the interval 0–1, so it is possible for the right tail of the distribution to extend below the crown base. It is therefore necessary to truncate the distribution such that all biomass is located above the base of the crown to properly describe the vertical distribution of fuel in crowns. Although the β distribution correctly distributes all biomass above the crown base, the failure of the Weibull distribution to decline to zero suggests that predictions from the β distribution would have been biased near crown bases for the trees in this study.

This study shows that foliage shifts upward and becomes more concentrated in upper crowns in high-density stands, much as CR decreases at high stand densities (Fig. 3). This likely reflects the redistribution of foliage into favorable light environments in response to shading by neighbors in crowded stands. Our findings are consistent with a substantial body of evidence that suggests that foliage distributions in tree crowns respond dynamically to varying light environments 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. 2). These patterns suggest that 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. Although contrasting patterns of foliage distribution in forests and woodlands are consistent with the intensity of light competition as a driver of within-crown foliage distribution, it is important to note that forests and woodlands in this study were comprised of wholly different sets of species. Thus, species composition also could have factored into differences in within-crown foliage and twig distribution parameters (Weiskittel et al. 2009).

There was substantial tree-to-tree variation in crown characteristics within stands, which presumably reflects small-scale heterogeneity of the light environment. Numerous studies have concluded that within-crown foliage distribution is affected by canopy position: foliage is generally found to be skewed upward in crowns of subordinate trees compared with dominant trees in the same stand (e.g., Xu and Harrington 1998). Our results did not lead us to the same conclusion. We found that α and β varied within an average stand over about one-half the range of values for species (Table 2), but we did not find a significant relationship between α and canopy position, as suggested by prior studies (e.g., Garber and Maguire 2005), for any of the species we investigated. This suggests that stand-level measurements such as RD may not be adequate to predict characteristics of individual crowns. Within-crown fuel distribution may depend as much on whether trees are in openings or crowded as on stand density.

Fig. 3. Linear relationships between CR, α, β, and RD. There are no statistical differences between regression lines in the lower two panels. Open circles, intolerant; closed circles, tolerant + intolerant.

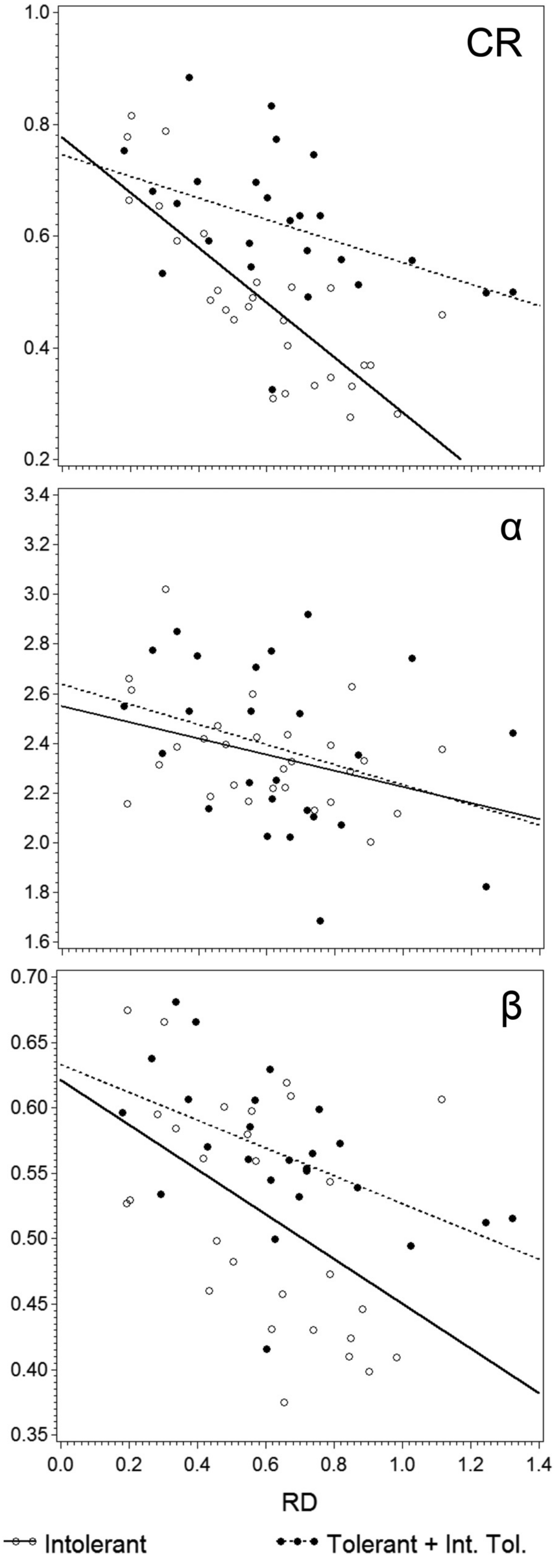


Table 3. Parameter estimates followed by *p* values in parentheses for estimated slopes and intercepts of regression lines in Fig. 3.

Shade tolerance	Intercept	Slope	r^2
CR			
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
Tolerant + intolerant	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
Tolerant + intolerant	0.62 (<0.01)	−0.13 (<0.01)	0.19

Note: For the intercept and slope, degrees of freedom are as follows: 23, tolerant species; 26, intolerant species; 51, tolerant + intolerant species. Estimates followed by the same lowercase letter are not significantly different for tolerant and intolerant species at α = 0.05.

Crown ratios of intolerant species were more responsive to increasing RD than those of tolerant species (Fig. 3). However, the same was not true for relationships between α or β and RD (Fig. 3). Nonetheless, within-crown foliage distribution and CR are almost certainly expressions of the same process: vertical redistribution of foliage in crowded growing environments. Partitioning this phenomenon into whole-tree (CR) and within-crown (α and β) components is a matter of convenience. We characterized foliage and twigs using a two-parameter Weibull distribution that started at the top of the crown and extended downward toward the crown base. Had we instead used a three-parameter Weibull distribution that started at the crown base and extended upward, we would have also needed to estimate crown base height as a location parameter (Clutter et al. (1983), p. 100). This would likely have led us to detect differences between tolerant and intolerant species in the response of the location parameter to RD (although the failure of the Weibull distribution to decline to zero suggests that predictions would have been biased near the base of crowns). The implication is that most of the difference between species of varying shade tolerance in foliage distribution response to RD is expressed in the CR relationship. This is of critical importance for canopy fire hazard assessment; it suggests that it is not necessary to account for species-specific relationships between α or β and RD to realistically characterize the canopy fuels complex. Canopy fuels can be adequately characterized using a general average crown fuel distribution, provided that species-specific relationships between CR and RD are accounted for.

Conclusion

Our results suggest that the distribution of foliage within crowns is, like CR, an expression of foliage redistribution into favorable light environments in crowded growing conditions. The degree to which foliage distributions were positively skewed 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 positive skew and concentration of foliage in crowns of forest species was predictable from RD. However, unlike CR, the response of α and β for foliage distributions to increasing RD was no different for tolerant and intolerant species. Because foliage accounts for the bulk of canopy fuels, our results suggest that it is not necessary to develop species-specific within-crown fuel distribution models to realistically characterize fuel complexes of western US conifer forests (i.e., to estimate effective CBD). Simply relaxing the assumption of uniform fuel distribution within crowns in favor of a positively skewed distribution substantially enhances the realism of canopy fuels characterization. Estimates of α and β can be improved by accounting for RD. However, substantial within-stand variation in parameter estimates implies that accurate prediction of distribution parameters requires accounting for growing environments of individual trees (e.g., crowding expressed as the distance to neighbors and their heights). This would necessitate spatially explicit data (e.g., stem maps) that are generally unavailable to forest managers.

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