



Tree species influence woodland canopy characteristics and crown fire potential



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ABSTRACT

Differences in canopy structure and biomass of trees are due to evolved morphologies particular to each species, interactions with neighboring trees during stand development, and environmental constraints on growth. In this paper we examine, how foliage shape and size coupled with distribution within the canopy are important theoretical factors affecting crown fire rate of spread. To accomplish this, we sampled leaves and measured leaf area index within woodland canopies dominated by four tree species (*Juniperus ashei*, *Quercus buckleyi*, *Quercus fusiformis*, and *Quercus sinuata* var. *brevifolia*). We found that mean leaf mass per unit area (*LMA*) of the four species were significantly different affecting maximum estimated canopy mass ranging in value between 41.61 and 85.46 g m⁻² for *Q. buckleyi* and *J. ashei*, respectively. We found no evidence that *LMA* was affected by whether a tree was grown with same species or different species indicating that this was an intrinsic, species character. Canopy mass, and therefore fuels, was calculated by multiplying *LMA* and leaf area index at different levels within the canopies. From this we found significant differences between the species measured, particularly *Q. buckleyi* and *J. ashei* ranging between 208.2 and 572.2 g m⁻² and canopy bulk density (*CBD*) ranging between 15.21 and 26.06 g m⁻³, respectively. Using a canopy fire behavior model, we found that all canopies could potentially sustain active crown fires based on recent average wind speeds (1997–2015); however a large range in critical wind speed values for these fires was found with *J. ashei* having the lowest value of 14.8 km h⁻¹ and *Q. buckleyi* the highest, 44.4 km h⁻¹ indicating importance of the dominance of different species in the canopy. Current management of these woodlands may be increasing dominance of *J. ashei* thereby impacting potential crown fire behavior.

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1. Introduction

Crown fire initiation and rate of spread are affected by forest species composition as a function of leaf morphology, foliar distribution in the canopy, and growth form of individual trees (Fulé et al., 2004). Foliage morphology is typically characterized by leaf mass per unit area (*LMA*; g m⁻²), which is the ratio of the dry matter mass of a leaf and its projected surface area. The inverse of *LMA* is the specific leaf area (*SLA*; m² g⁻¹) that was originally derived to capture differences in leaf expansion to mass accumulation rates (Hughes, 1959). Changes in *LMA* within a plant canopy are generally associated with light transmission with leaf shape changing in response to the plant balancing photosynthetic gain

through radiation interception and carbon allocation (Givnish, 1988). Plant species with higher variable *LMA* within their canopies have higher canopy-level photosynthetic rates (Gutschick and Wiegel, 1988).

Leaf area index (*LAI*; m² leaf area m⁻² ground area) is a well-established plant biophysical trait which is defined as the ratio of foliar area per unit ground area represents an individual tree or stand canopy leaf surface area available for interception of radiation (Watson, 1947), water (Carlisle et al., 1967), and gas exchange (Monteith, 1965). The correspondence of *LAI* and *LMA* vertically within a canopy profile has been demonstrated for single and mixed-species forests indicating the ability of plants to adjust foliar shape under differing light regimes (White and Scott, 2006). Typically, total aerial fuels (*TAF*; g m⁻²) and canopy bulk density (*CBD*; g m⁻³) are canopy components that are important for assessing fire behavior in tree canopies (Van Wagner, 1977; Keane et al., 2005; Dickinson et al., 2007). These essential fuel characteristics can be derived by taking measurements of *LAI* and *LMA* at different height intervals in a canopy

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$$CM_i = LAI_i \times LMA_i \quad (1)$$

where crown mass (CM ; g m^{-2}) is at each calculated at each interval (i) in the canopy then summed:

$$TAF = \sum CM_i \quad (2)$$

to calculate TAF . Because evergreen, coniferous tree species have high and deciduous broad-leaved species have low average LMA values as evolutionary adaptations to different light, water, and nutrient requirement (Niinemets, 2007), forest species composition may affect TAF . Stand TAF may also vary with site productivity, microsite differences, and disturbance regimes (Riaño et al., 2004; Cruz et al., 2010).

The volumetric distribution of foliar mass within canopies is represented by CBD (g m^{-3}) calculated by:

$$CBD = TAF/CL \quad (3)$$

where CL is the canopy length in meters (Cruz et al., 2005). Stand CBD represents the live fuel per unit volume of a canopy and is used to determine the likelihood of torching and rate of crown fire spread (Scott and Reinhardt, 2001). CBD has been also used to determine whether enough live fuel is available to sustain a crown fire (Van Wagner, 1977; Scott, 2006) and the intensity of an active crown fire (Rothermel, 1972). Species interaction and composition of a stand may also affect LMA and CBD . Crown shapes of individual trees are affected by canopy crowding, as a function of initial density of trees, indicating individual growth effects among species influenced by differences in shade tolerance (Canham et al., 2004). Canopy crowding increases physical interaction of branches among adjacent trees leading to abrasion as branches collide during wind events that results in asymmetrically-formed canopies as species differ in growth of terminal stems, regrowth of damaged tissues, and hardness of branch material (Hajek et al., 2015). In contrast, stands with species that have different crown shapes due from inherent growth habits (e.g. determinant, indeterminate) have reduced interactions with each other by filling space through complementary geometry (Pretzsch, 2014).

Population viability of individual tree species within a forest is sustained across environmental gradients where multiple species are present (Grumbine, 1994) may increase resilience to endogenous disturbances (Knocke et al., 2008), and buffer climate-change influences on ecosystem services (Ford et al., 2011). Management of multiple species within forests may be needed to balance objectives for wildlife, watershed protection, carbon accumulation, and fire risk (Hansen et al., 1991; Bullock et al., 2011). However, because wildfires may modify habitat (Yao et al., 2012), remove canopies to increase soil erosion (Yao et al., 2014), and consume site carbon (Sommers et al., 2014), addressing fire risk precedes consideration of all other management goals. Characterizing canopy fuel is an important first step for assessing fire risk because crown fire spread prediction may be predicted based on total canopy mass (Dickinson et al., 2007) and mass density (Van Wagner, 1977). Coarse estimates of canopy fuels and structure may be derived from measurement of leaf area that when coupled with averaged LMA provide stand level values. Stand species composition potentially influences variation in fire-related canopy characteristics due to intrinsic differences in foliage shape and mass. More information is necessary to understanding the linkage between tree species and canopy characteristics that potentially affect crown fire behavior.

2. Materials and methods

2.1. Site description

The Balcones Canyonlands National Wildlife Refuge (BCNWR) (Lat. 30.32°N, Long. 97.73°W) and the Balcones Canyonlands Conservation Preserve (BCCP) (Lat. 30.63°N, Long. 98.04°W) are located in the central Texas hill country of the Edward's Plateau Region. The BCNWR is managed by the U.S. Fish and Wildlife Service (USFWS) and is comprised of 6500 ha. The BCCP is comprised of 5300 ha and is managed jointly by the City of Austin, Texas and Travis County, Texas. Both of these preserves are comprised of land tracts that are actively managed for endangered species. The refuges serve as breeding grounds for two federally listed endangered species of birds: the golden-cheeked warbler (*Setophaga chrysoparia*), and the black-capped vireo (*Vireo atricapilla*) (USFWS, 1992). The refuge tracts are interspersed within private lands, primarily comprised of grazing operations surrounding BCNWR, and urban development for BCCP creating a definitive wildland urban interface.

The geology of the Balcones region is dominated by outcropping of the Glen Rose (upper Cretaceous), Walnut (lower Cretaceous), and Edwards (lower Cretaceous) limestone formations. Well-drained, clay loam soils have developed from this parent material that covers a distinctive plateau and valley topography with over 300 m of relief. The valleys are dominated by grasslands comprised of *Andropogon gerardii*, *Bouteloua gracilis*, *Schizachyrium scoparium*, and the introduced invasive *Bothriochloa ischaemum*. Riparian forests are found in creek bottoms composed of by tree species including: *Quercus buckleyi*, *Prunus serotina* var. *eximia*, *Juglans major*, *Ulmus crassifolia*, *Juniperus ashei*, and *Quercus fusiformis*. *J. ashei* and *Q. fusiformis* are found on mid-slopes on most aspects, with north-facing slopes dominated by the deciduous oaks *Q. buckleyi* and *Quercus sinuata* var. *brevifolia*, including sub-dominant species such as *P. serotina* var. *eximia*, *Diospyros texana*, *U. crassifolia*, *Celtis laevigata*, and *Ilex vomitoria*. The plateaus are partially covered by short, scrubby *J. ashei* groves (colloquially known as cedar brakes), grasslands (with same species as in the valleys), *Opuntia* spp. thickets, shrubby *Q. sinuata* var. *brevifolia* stands, and/or and bare limestone.

Four dominant woodland tree species were examined for this study including: *J. ashei*, *Q. fusiformis*, *Q. buckleyi*, and *Q. sinuata* var. *brevifolia*. *J. ashei* is a scaled-leaf evergreen conifer that grows to around 10 m in height, tolerates drier soils, and is probably shade intolerant (Adams, 1977; Diamond, 1997). This species does not resprout following fire or cutting and reproduces by large crops of berries dispersed by mammals and birds. *Q. fusiformis* is an evergreen broad-leaved oak that can grow 12 m, can tolerate dry slopes, and is moderately shade tolerant (Lin et al., 2001). It regrows vigorously post-fire from lateral root-sprouting. *Q. buckleyi* is a deciduous, broad-leaved oak that grows to around 12 m, grows rapidly in large canopy gaps (shade intolerant) (Murray et al., 2013a), prefers well-watered, loamy soils, and sprouts vegetatively from the root ball following fire (Andruk et al., 2014). *Q. sinuata* var. *brevifolia* is a deciduous, broad-leaved oak that is shade and competition intolerant (Reemts and Hansen, 2008). It can grow to height of 12 m in deeper soils or form a copse that is less than 4 m (known as shinneries) in shallow soils.

2.2. Canopy measurement

For this study, we measured mature, healthy dominant, trees located in forested stands with contiguous canopy cover (>80%) and were separated from other sampled trees by a minimum distance of 30 m. Individual crowns of trees sampled were considered

to represent the local canopy for an area 114 m² surrounding the tree based on optical estimates of *LAI* described later. Sampling locations were randomly selected among available forest stands on the BCNWR and BCCP properties. Trees sampled were selected in a stratified random manner to achieve highest number of species possible. For each tree species, canopy height (*h*), canopy base height (*CBH*), and *CL* were measured in meters. Canopy base height was defined as the height from the ground to the lowest part of the canopy that contained live foliage. Canopy length was calculated as the tree height minus the *CBH*. Geographic location and descriptions of the trees within the canopy were noted.

Each tree sampled was considered to represent a portion of the canopy with an approximate projected area of 100 m² surrounding the tree based on the viewing area of the LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, Nebraska) instrument used. The canopy *LAI* derived from the LAI-2000 assumes that light transmission is related to contact frequency by randomly distributed leaves in is derived by:

$$LAI = 2 \sum \{[-\ln(\varphi_{in}/\varphi_{out})] \cos \theta \sin \theta d\theta\} \quad (4)$$

where φ_{in} is the radiant flux density measured within the stand at the base of the canopy, φ_{out} is the radiant flux density outside of the stand, and θ is zenith angle of the incident radiation. For the LAI-2000, radiation is measured across 5 zenith angles ranging from 7° to 68° from nadir. A 45° mask cap was fitted to the ocular of the LAI-2000 to block the tree bole and to emphasize measurement of tree foliage. All zenith angles of the LAI-2000 optics were used for analysis because the distribution of foliage in these forests was nearly continuous from the ground upward. At ground level, the maximum viewing area of the LAI-2000 with the 45° mask cap for a 12 m canopy was estimated at 114 m². To assess vertical *LAI* distribution through the canopy, we mounted the LAI-2000 on a 10 m telescopic pole with sequential measurements of cumulative values of *LAI* from the top of canopy to the ground in 1 m intervals. Because we obtained *LAI* within closed canopies, sampling height was not considered at factor in our measurements.

Following measurement of *LAI*, 5–20, healthy leaves were clipped from the tree at each 1 m intervals from the top of the canopy to ground level using a pole pruner for an average 50 leaves per tree. Leaf samples by interval were stored in plastic bags and kept cool and moist to maintain leaf vigor. Leaf samples were returned to the lab within one day of collection. Sample projected leaf area of all collected leaves was first imaged with a flatbed digital scanner (Microtek Lab, Fontana, California). Digital images were collected as black and white silhouettes with pixel area converted to cm² using Adobe Photoshop (Adobe Systems Incorporated, San Jose, California). Imaged leaves were then dried at 60 °C for 48 h and weighed to 0.01 g. Total leaf dry mass was divided by calculated leaf area for each sample to compute interval values of *LMA* (*LMA_i*) at different heights within the canopy.

Interval values of *LAI* (*LAI_i*) were calculated as the difference in the *LAI* measured at a given depth in the canopy minus the *LAI* measured for the interval directly above. Prior to calculation of canopy fuels, the raw *LAI_i* values were adjusted to account for: (1) leaf clumping and (2) stem (i.e. twig) components. For leaf clumping, the *LAI_i* data were multiplied by a constant value 1.58 which has been shown to be a reliable estimate of shoot-level leaf clumping for mixed species forests derived from the LAI-2000 instrument (White et al., 1997). Originally, we excluded twigs from our field sampling due to a lack of standard methodology to account for sampled material from the a trees (i.e. defining a twig as tapered stem distinguished from the leaves). However, to account for twigs as a live fuel component, we multiplied our *LMA_i* values by a constant 1.21 based on robust foliar to twig mass ratios reported by Sun et al. (2006). These adjusted *LAI_i* and *LMA_i* values

where then used to calculate *CM_i* and subsequently *TAF* for each tree and associated canopy. Because the distribution of foliage in the canopy is generally clumped at a particular height thus affecting fuel level (Keane et al., 2005), the maximum canopy *CBD* value (*CBD_{Max}*) was derived from:

$$CBD_{Max} = \text{Max}(CM_i)/l \quad (5)$$

where *l* is the distance of the interval length measured between depths in the canopy (1 m) and *Max*(*CM_i*) is the maximum value of *CM* determined for each tree canopy layer (*i*).

To assess relative accuracy of our measured *CBD* and *CBD_{Max}* values, we compared our values with those derived from the U.S. Forest Service's LANDFIRE Project database (Reeves et al., 2006). Data for this analysis were acquired from the online portal (<http://landfire.cr.usgs.gov/viewer/>) for Region 35 and included the LANDFIRE 2012 (LF 1.3.0) Forest Canopy Bulk Density dataset representing the latest release (version 1.3). The original units of these data were in 100 (kg m⁻³) that we converted into g m⁻³. Using geographic locations of trees sampled, we extracted LANDFIRE *CBD* pixel values for comparison.

2.3. Statistical assessment

Data were compiled and analyzed using IBM SPSS ver. 22.0 (IBM Corp., Armonk, New York). Normality of data was initially assessed by the Shapiro–Wilkes test. Comparisons between two samples were accomplished using unpaired student's *t*-tests. For comparisons of multiple groups, data were analyzed with a univariate ANOVA with a post hoc Tukey's Honest Significant Differences (HSD) used to determine differences between tests. Correlation among variables, by species, was assessed by calculating the Pearson's coefficient (*r_{xy}*).

We considered *CBD* and *TAF* to be the most important canopy attributes due to: (1) their relationship to ecosystem and fire management and (2) difficulty obtaining accurate values over large areas (Keane et al., 2005). Therefore, we derived predictive models of *CBD* and *TAF* using the other canopy variables (e.g. *LMA*, *CBH*, *LAI*, etc.) as independent variables using a step-wise linear regression with an *F* value threshold for entering variables set to ≤0.05. Significance of results was assessed using $\alpha = 0.05$ for all analyses.

2.4. Crown fire behavior analysis

We assessed potential crown fire behavior using a simplified method to first predict the rate of active crown fire spread rate (*R_a*; m/min) based on a regression model by Cruz et al. (2005):

$$R_a = (11.02 \cdot U_{10})(CBD^{0.19})(\exp^{-0.17 \cdot EFFM}) \quad (6)$$

where *U₁₀* is the wind speed 10 m above surrounding vegetation (km h⁻¹), *EFFM* is the estimated dead fine fuels moisture content in percent, with *CBD* expressed in units of kg m⁻². The value of *EFFM* was set to 10% representing a typical dry mid-summer fine fuel condition for this region (C. Schwoppe, personal communication). The threshold rate of spread for sustaining crown fire (*R'_a*) was calculated by:

$$R'_a = \frac{3.0}{CBD} \quad (7)$$

where 3.0 is an estimated critical mass-flow rate (kg m⁻² min⁻¹) (Scott, 2006). Derived values of mean *CBD* from this study were then input to calculate values of *R_a* for a range of *U₁₀* from 0 to 60 km hr⁻¹. Both values of *R_a* and *R'_a* were calculated from mean *CBD* values for each species. A critical *U₁₀* necessary to sustain a crown fire was derived analytically as the value where *R_a* = *R'_a*. For comparison, mean and maximum gust wind speeds were

derived from meteorological data from the Austin, Texas, Bergstrom airport for 1997–2015 (National Climatic Data Center site #13904).

3. Results

For BCNWR, we sampled 60 trees and 49 trees at BCCP. No differences in canopy attributes between these two refuges properties were detected, therefore stands and species were considered to be from the same population. Overall mean canopy attribute values for this study are found in Table 1.

Average LMA values were found to differ among the four dominant tree species with *J. ashei* leaves having a significantly higher mean LMA value (257.1 g m^{-2}) followed by *Q. fusiformis* (141.1 g m^{-2}), *Q. sinuata* var. *brevifolia* (95.7 g m^{-2}), and then *Q. buckleyi* (81.1 g m^{-2} ; Table 2). The mean LAI were significantly higher for *Q. sinuata* var. *brevifolia* compared to *Q. fusiformis*. Different TAF values were also found with *Q. buckleyi* having the least amount of canopy fuel loading (208.2 g m^{-2}) than the other species with *J. ashei* having the highest amount (572.2 g m^{-2}). Mean canopy CBD were also different with all the oak species having significantly lower values than *J. ashei* (202.9 g m^{-3}). For CBD_{Max} , *Q. buckleyi* and *Q. sinuata* var. *brevifolia* had significantly lower values of 160.0 and 245.1 g m^{-3} , respectively, than *J. ashei* (538.4 g m^{-3}). In addition, the mean CBD_{Max} for *Q. fusiformis* was also significantly lower (277.6 g m^{-3}) than *J. ashei*, but not different than *Q. sinuata* var. *brevifolia*. Comparison of canopies without and with multiple species showed that only CL of *Q. buckleyi* was lower when other species were present in the canopy (4.5 vs. 6.7 m).

Analysis of CM distributions within canopies showed varying degrees of foliage clumping that differed by height and species (Fig. 1). For example, the highest CM value was found between 0 and 4 m for *J. ashei* that also had a distinct bi-modal distribution of CM. In comparison, *Q. fusiformis*, and *Q. buckleyi* had largest masses in the upper portion of the crown with CM increasing monotonically with height. For *Q. sinuata* var. *brevifolia*, CM was bi-modally distributed with largest masses between 10 and 12 m.

Canopy variables were correlated among structural (e.g. height, CL, etc.) and mass characteristics (e.g. TAF, CBD) (Table 3). The degree of correlation and the number of correlated variables differed between species. *J. ashei* had the lowest number of correlated variables but had high correlation ($r_{xy} = 0.91$) between CBD and CBD_{Max} . Generally higher, positive correlation between TAF and CBD_{Max} was found for all species. LAI was also positively correlated with TAF, but only for the broad-leaved species.

Stepwise linear regression modeling showed that three variables, CL, LMA, and LAI, were found to consistently best predict CBD and TAF (Table 4). For *J. ashei*, *Q. fusiformis* and *Q. sinuata* var. *brevifolia*, correlation was relatively high for both dependent variables with R^2 values ranging from 0.91 to 0.98 for these species. For *Q. buckleyi*, model correlation values were low for CBD and TAF, with R^2 values of 0.57 and 0.37, respectively; however the independent variables selected, CL and LAI, were significant. Using all canopy data showed high correlation for predicting CBD and TAF with R^2 values of 0.88 and 0.90, respectively.

The fire behavior variables R_a and R'_a were calculated using species mean CBD values of 202.9 , 67.6 , 100.9 , and 85.0 g m^{-3} for *J. ashei*, *Q. buckleyi*, *Q. fusiformis* and *Q. sinuata* var. *brevifolia*, respectively. Values of R_a for the range of U_{10} are shown in Fig. 2 where R_a was found to be highest for *J. ashei* and lowest for *Q. buckleyi*. Derived values of R'_a for *J. ashei*, *Q. buckleyi*, *Q. fusiformis* and *Q. sinuata* var. *brevifolia* were 16.8 , 36.9 , 27.5 , and 31.1 m min^{-1} , respectively. Estimated critical U_{10} values were 14.8 , 44.4 , 29.7 , and 35.3 km h^{-1} for *J. ashei*, *Q. buckleyi*, *Q. fusiformis* and *Q. sinuata* var. *brevifolia*, respectively. For comparison, the mean annual wind

Table 1

Sample sizes and attributes of all trees sampled. All values given are mean \pm one standard deviation. Variables shown are height (m), canopy base height (CBH; m), canopy length (CL; m), leaf area index (LAI; $\text{m}^2 \text{ m}^{-2}$), total areal fuels (TAF; g m^{-2}), canopy bulk density (CBD; g m^{-3}), and maximum CBD (CBD_{Max} ; g m^{-3}).

Parameter	Combined
Trees sampled	109
By species	
<i>Juniperus ashei</i>	25
<i>Quercus buckleyi</i>	37
<i>Quercus fusiformis</i>	21
<i>Quercus sinuata</i> var. <i>brevifolia</i>	19
<i>Prunus serotina</i> var. <i>eximia</i>	2
<i>Ilex vomitoria</i>	1
<i>Celtis laevigata</i>	1
<i>Ulmus crassifolia</i>	1
<i>Juglans major</i>	1
<i>Diospyros texana</i>	1
Height (m)	7.6 ± 2.1
CBH (m)	2.5 ± 1.8
CL (m)	6.1 ± 1.9
LAI ($\text{m}^2 \text{ m}^{-2}$)	3.6 ± 1.0
TAF (g m^{-2})	328.6 ± 183.8
CBD (g m^{-3})	112.2 ± 71.6
CBD_{Max} (g m^{-3})	297.4 ± 217.9

Table 2

Comparison of mean (\pm one standard deviation) foliage and canopy attributes by species. The symbols ^{a,b,c,d} indicate that groupings of significant differences based on the ANOVA and the post hoc Tukey's HSD analysis. Variables shown are leaf mass area (LMA; g m^{-2}), height (m), canopy base height (CBH; m), canopy length (CL; m), leaf area index (LAI; $\text{m}^2 \text{ m}^{-2}$), total areal fuels (TAF; g m^{-2}), canopy bulk density (CBD; g m^{-3}), and maximum CBD (CBD_{Max} ; g m^{-3}).

Species	<i>J. ashei</i>	<i>Q. buckleyi</i>	<i>Q. fusiformis</i>	<i>Q. sinuata</i> var. <i>brevifolia</i>
LMA (g m^{-2})	257.1 ± 25.8^a	81.1 ± 10.6^b	141.1 ± 14.8^c	95.7 ± 18.8^d
Height (m)	7.1 ± 1.7	8.3 ± 2.1	7.6 ± 2.3	6.9 ± 2.1
CBH (m)	2.5 ± 1.8	2.6 ± 1.6	2.8 ± 2.0	1.9 ± 1.1
CL (m)	5.6 ± 1.4	6.7 ± 2.3	5.8 ± 1.9	6.1 ± 1.5
LAI ($\text{m}^2 \text{ m}^{-2}$)	3.5 ± 0.9	3.7 ± 1.1	3.1 ± 1.0^a	3.9 ± 0.8^b
TAF (g m^{-2})	572.2 ± 176.0^a	208.2 ± 76.0^b	300.6 ± 103.7^c	253.4 ± 60.3^{bc}
CBD (g m^{-3})	202.9 ± 67.3^a	67.6 ± 45.8^b	100.9 ± 32.5^b	85.0 ± 28.1^b
CBD_{Max} (g m^{-3})	538.4 ± 290.2^a	160.0 ± 66.2^b	277.6 ± 112.4^c	245.1 ± 70.8^{bc}
n	25	37	21	19

speed for the study area was 15.1 km h^{-1} with a maximum gust speed of 59.6 km h^{-1} recorded at the Bergstrom airport.

4. Discussion

The canopy attributes presented here are some of the first for these woodlands and species. We found the canopy attributes we measured were generally intermediate in value between those reported for shrub and forest ecosystems. Cruz et al. (2010) found TAF values ranged from 610 to 1400 g m^{-2} with CBD values ranging from 180 to 320 g m^{-3} for western montane U.S. forest species such as *Pinus ponderosa* and *Pseudotsuga menziesii*. For pure *Pinus sylvestris* stands, TAF values have been shown to range from 650 to 2430 g m^{-2} with CBD values ranging from 140 to 560 g m^{-3} (Riaño et al., 2004). For shrublands, foliar TAF have been found to range from 145 to 416 g m^{-2} (Cowan and Ackerly, 2010) with CBD values ranging from 18 to 116 g m^{-3} (Lindenmuth and Davis, 1973).

When measured CBD values were compared with those extracted from the LANDFIRE (ver. 1.3), ours were lower with $CBD = 246 \text{ g m}^{-3}$ and $CBD_{Max} = 328 \text{ g m}^{-3}$, compared to 276 g m^{-3}

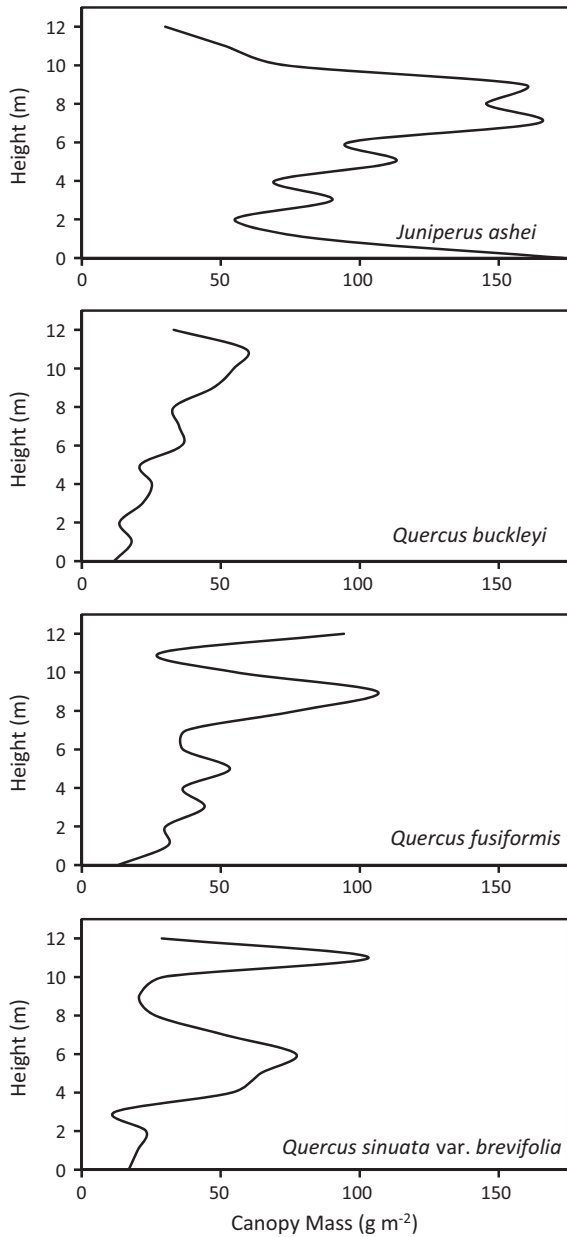


Fig. 1. Mean canopy mass values (g m^{-2}) derived for each species by height. Each species is shown in separate graphs for clarity.

from the LANDFIRE database. Point accuracy of *CBD* was low (Fig. 3) likely due to assumptions regarding how *CBD* values in LANDFIRE are assigned based on vegetation type. For example, the *CBD* values for some broad-leaved species in LANDFIRE are automatically set to a minimum value of 10 g m^{-3} . This could account for underestimated LANDFIRE values, especially for canopies dominated by *Q. buckleyi*. However, the range of values for our canopies was $51\text{--}1378 \text{ g m}^{-3}$ for *CBD* and 66 to 1764 g m^{-3} for *CBD*_{Max} compared to $0\text{--}340 \text{ g m}^{-3}$ for LANDFIRE data. These range differences are likely due to values averaged over a map grid cell with a spatial resolution of $30 \times 30 \text{ m}$. We note that the mean value of *CBD*_{Max} of 328 g m^{-3} were similar to the maximum LANDFIRE *CBD* value of 340 g m^{-3} for our study sites.

Canopy *LMA* is an important stand characteristic as an indicator of fire behavior because species with higher *LMA* values were found to require lower wind speeds to sustain potential crown fire (Fig. 2). *LMA* also indicates the potential for live foliage ignition as

Table 3

Pearson's correlation analysis by species. Variables shown are leaf mass area (*LMA*; g m^{-2}), height (m), canopy base height (*CBH*; m), canopy length (*CL*; m), leaf area index (*LAI*; $\text{m}^2 \text{ m}^{-2}$), total areal fuels (*TAF*; g m^{-2}), canopy bulk density (*CBD*; g m^{-3}), and maximum *CBD* (*CBD*_{Max}; g m^{-3}). Values shown are those with $P < 0.05$; dashes indicate non-significant results. Only half of the correlation matrices are shown for clarity.

	<i>LMA</i>	Height	<i>CBH</i>	<i>CL</i>	<i>LAI</i>	<i>TAF</i>	<i>CBD</i>	<i>CBD</i> _{Max}
<i>Juniperus ashei</i>								
<i>LMA</i>	-	-	-	-	-	-	-	-
Height	-	-	-	0.84	-	-	-	-
<i>CBH</i>	-	-	-	-	-	-	-	-
<i>CL</i>	-	-	-	-	-	-	-	-
<i>LAI</i>	-	-	-	-	-	-	0.68	0.62
<i>TAF</i>	-	-	-	-	-	-	0.81	0.76
<i>CBD</i>	-	-	-	-	-	-	-	0.91
<i>CBD</i> _{Max}	-	-	-	-	-	-	-	-
<i>Quercus buckleyi</i>								
<i>LMA</i>	-	-	-	-	-	-	-	-
Height	-	-	-	0.72	0.48	0.55	-	-
<i>CBH</i>	-	-	-	-0.55	-	-0.54	-	-
<i>CL</i>	-	-	-	-	0.41	0.84	-	0.36
<i>LAI</i>	-	-	-	-	-	0.65	0.46	0.55
<i>TAF</i>	-	-	-	-	-	-	0.42	0.61
<i>CBD</i>	-	-	-	-	-	-	-	0.62
<i>CBD</i> _{Max}	-	-	-	-	-	-	-	-
<i>Quercus fusiformis</i>								
<i>LMA</i>	-	0.53	0.67	-	-	0.59	-	-
Height	-	-	0.57	0.55	0.60	0.53	-	-
<i>CBH</i>	-	-	-	-	-	-	-	-
<i>CL</i>	-	-	-	-	-	0.75	-	0.45
<i>LAI</i>	-	-	-	-	-	0.59	-	-
<i>TAF</i>	-	-	-	-	-	-	0.76	0.88
<i>CBD</i>	-	-	-	-	-	-	-	0.85
<i>CBD</i> _{Max}	-	-	-	-	-	-	-	-
<i>Quercus sinuata</i> var. <i>brevifolia</i>								
<i>LMA</i>	-	-	-	-	-	-	-	-
Height	-	-	0.87	0.85	-	-	-	-
<i>CBH</i>	-	-	-	-	-	-	-	-
<i>CL</i>	-	-	-	-	-	-	-	-
<i>LAI</i>	-	-	-	-	-	0.65	0.75	0.73
<i>TAF</i>	-	-	-	-	-	-	0.62	0.69
<i>CBD</i>	-	-	-	-	-	-	-	0.92
<i>CBD</i> _{Max}	-	-	-	-	-	-	-	-

species with high *LMA* (e.g. *Juniperus*) are less likely to lose water and become flammable compared to species with lower *LMA* (e.g. *Quercus*) (Dimitrakopoulos and Papaioannou, 2001). Species differences in *LMA* reflect the plasticity of this trait in response to intercepted solar irradiance that is particular to each species (White and Scott, 2006; Thomas, 2009). The hypothesis that *LMA* is an intrinsic growth characteristic species is supported by our finding that *LMA* did not change between canopies with single and multiple species. Only *CL* for *Q. buckleyi* was found to be reduced with other species present in the canopy likely due to the shade intolerance of this species.

Like *LMA*, the distribution of *CM* appeared to differ between species (Fig. 1). For *J. ashei*, canopy growth is highly deterministic, like most conifers, leading to an ellipsoid to ovoid shaped canopy in this environment. This is reflected in the larger amount of canopy mass near the ground for *J. ashei* with tapering with height. This species shows little self-pruning, therefore maintains branches for the entire length of the bole with varying support of live foliage. Distribution of *CM* for the broad-leaved species generally reflected a canopy form described as inverted cone with *Q. buckleyi* having the highest fidelity to this shape. This crown shape is likely due to combined indeterministic meristematic growth of the broad-leaved species. Also, competition-induced canopy base height increases in closed canopies (Ishii and McDowell, 2002) coupled with inter-tree mechanical abrasion mechanisms (Hajek

Table 4

Multiple linear step-wise regression analysis of canopy bulk density (CBD; g m^{-3}) and total areal fuels (TAF; g m^{-2}) by species. Selected independent variables included average leaf mass area (LMA; g m^{-2}), canopy length (CL; m), leaf area index (LAI; $\text{m}^2 \text{m}^{-2}$). Unstandardized model coefficient values, significance values, coefficient of determination (R^2) and standard error of the estimate ($S_{Y|X}$) are shown.

	Variable	Coefficient	p-value	R^2	$S_{Y X}$
<i>Juniperus ashei</i>					
CBD	Intercept	53.450		0.91	21.69
	CL	-26.664	<0.01		
	LMA	0.403	0.029		
	LAI	56.412	<0.01		
TAF	Intercept	-527.252		0.97	30.78
	LMA	1.962	<0.01		
	LAI	171.556	<0.01		
<i>Quercus buckleyi</i>					
CBD	Intercept	84.862		0.57	19.18
	CL	-11.035	<0.01		
	LAI	14.136	<0.01		
	LMA	14.136	<0.01		
TAF	Intercept	45.136		0.37	61.01
	LMA	1.962	<0.01		
	LAI	171.556	<0.01		
<i>Quercus fusiformis</i>					
CBD	Intercept	-20.017		0.90	10.93
	CL	-14.149	<0.01		
	LMA	0.642	<0.01		
	LAI	34.802	<0.01		
TAF	Intercept	-270.557		0.98	30.167
	LMA	1.792	<0.01		
	LAI	98.404	<0.01		
<i>Quercus sinuata</i> var. <i>brevifolia</i>					
CBD	Intercept	53.254		0.93	8.09
	CL	-15.097	<0.01		
	LMA	0.618	<0.01		
	LAI	16.082	<0.01		
TAF	Intercept	-173.163		0.95	14.252
	LMA	2.002	<0.01		
	LAI	59.103	<0.01		
<i>All species</i>					
CBD	Intercept	-14.372		0.88	27.07
	CL	-15.550	<0.01		
	LMA	0.742	<0.01		
	LAI	32.010	<0.01		
TAF	Intercept	-309.789		0.90	59.61
	LMA	2.221	<0.01		
	LAI	90.035	<0.01		

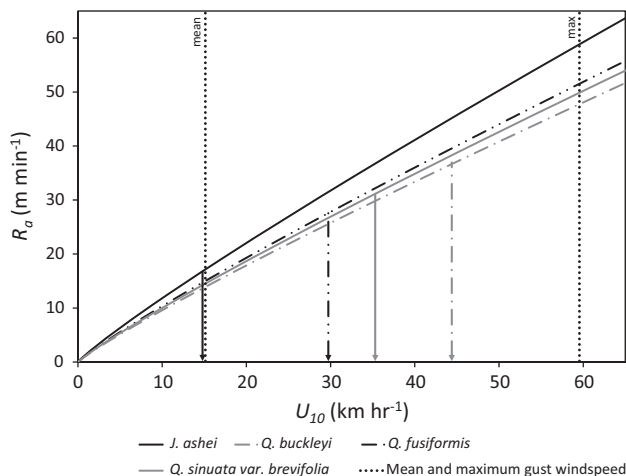


Fig. 2. Predicted rate of fire spread in the canopy (R_a ; m min^{-1}) by wind speed above the canopy (U_{10} ; km h^{-1}) calculated for each species based on mean CBD values. The arrows indicate the critical rates of spread (R'_a ; m min^{-1}) associated with wind speeds required to sustain the crown fire. The wind speed data (km h^{-1}) were derived from climatic data for Austin's Bergstrom airport (National Climatic Data Center site #13904).

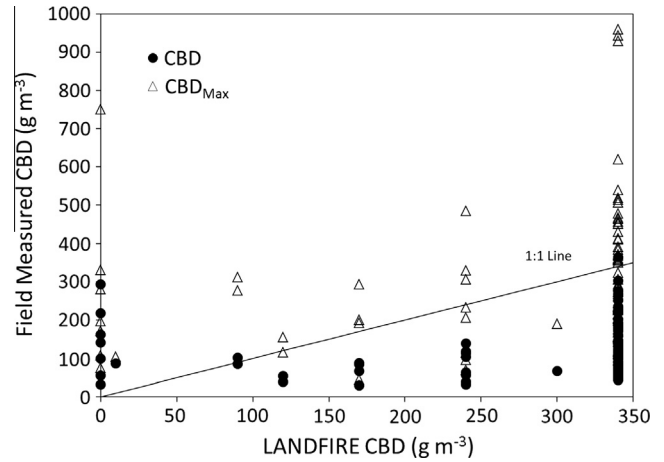


Fig. 3. Comparison of field measured CBD and CBD_{Max} with values derived from the LANDFIRE CBD database (version 1.3; <http://landfire.cr.landfire.gov>). The 1:1 line is shown for reference.

et al., 2015) affecting individual tree crown morphology. Our finding of different CM distribution for individual species supports the hypothesis of Pretzsch (2014) that canopy space may be optimized by complementary geometries. However, whether this complementary-driven organization is ontogenic or a result of individual crown morphogenesis during stand development, influenced by inter-tree interactions, is still questionable.

Despite canopies having similar overall structural characteristics such as canopy height and lengths, we found different canopy fuel loads for the tree species studied. The range of mean canopy fuels characteristics including TAF and CBD, between species were mostly due to differences in the amount of foliage represented by LAI, particularly for the broad-leafed species (Table 2). Foliage sampled were from mature trees, therefore differences between individuals of each species reflect vigor of each tree growing in a particular environment. Each of the four dominant species can grow in any location within the study area; however some of the species are more tolerant of water stress induced by topographic position. The species relative tolerance of xeric to mesic conditions rank *J. ashei* followed by *Q. fusiformis*, *Q. sinuata* var. *brevifolia*, with *Q. buckleyi* found most in the wettest locations (Gehlbach, 1988). Higher correlation, particularly between LAI and canopy fuel characteristics found for the broad-leafed species likely indicate a higher sensitivity and growth response of these species to site water availability. High correlation between LAI and fuel characteristics such as CBD and TAF (Table 4) indicated a broad association between displayed canopy foliage and the expression of fuel as mass in the crown.

Prediction of CBD and TAF appear to be highly related to CL, LMA, and LAI (Table 4). Canopy structural attributes such as *h*, *CBH*, and *CL* are directly detectable from waveform light detection and ranging (lidar) sensors (Lefsky et al., 2002; Wulder et al., 2012). Stand level traits including mean LMA and LAI may be obtained indirectly from spectral vegetation indices (Lymburner et al., 2000; White et al., 1997). Combining these remote sensing data provide an improved method for distributed mapping of canopy fuels with potential increased accuracy in spatially-explicit fire behavior prediction.

The canopy fire modeling portion of this study assumed that surface fuel conditions produced the energy necessary for canopy ignition. Previous fire behavior research using the FARSITE model (Finney, 2004) has been conducted for this study area using field-measured inputs of dead surface fuels of 28.44, 318.5, and 319.9 g m^{-2} for 1 h, 10 h, and 100 h fuel loadings, respectively

(Thomas, 2009). These simulations projected a mean predicted fireline intensity (I_s) of 3261.7 kW m⁻¹ under dry summer, windy conditions (wind speed = 48 km h⁻¹). The low *CBH* measured across all stands is important for lowering the critical threshold of fireline intensity required to initiate crown fire (I'_s). Using a mean *CBH* of 2 m and a foliar moisture content of 70%, a critical value important for canopy ignition common for *Juniperus–Quercus* woodlands (Alexander and Cruz, 2013), we calculated an I'_s value of 305.5 kW m⁻¹ (*sensu* Van Wagner, 1977). Because $I'_s < I_s$ from this analysis, crown fires are possible in canopies of some of the species studied but likely only sustained under extreme wind conditions (Fig. 2). This is consistent with theoretical modeling of active crown fires for canopies with relatively low *CBD*, compared to other forested ecosystems (Scott and Reinhardt, 2001), and the observation of relative infrequency of crown fires in these mixed juniper woodlands (Reemtsma and Hansen, 2008; Murray et al., 2013a). Surface fuels measured across the same locations as the canopy samples in a related study varied by time since disturbance rather than species dominance (Yao et al., 2012). Therefore, crown fire activity in our study area may be constrained most by the canopy attributes of the dominant species.

The use of the Van Wagner (1977) crown fire model in this study has its limitations given that the original energy transfer functions and empirical constants were derived from observations of fires coniferous North American montane species. Our application here is meant to highlight the potential differences that may exist in canopy fire behavior based on the different canopy fuel characteristics of the species we studied. Because crown fire behavior research in these type of woodlands is completely lacking, first-principle based models such as FIRETEC (Pimont et al., 2011) may be more appropriate to use for deriving accurate rates of crown fire spread. However, these physics models are computationally intensive and may require more detailed information such as actual tree positions within a simulation landscape.

Crown fire modeling also showed that sustaining active crown fire is a potentially lower where *Q. buckleyi* dominates based on the critical U_{10} value we derived of 44.4 km h⁻¹. The low *CBD* of *Q. buckleyi* canopies values observed likely indicates active crown fires for canopies dominated this species are rare, rather individual tree torching more likely. Therefore, canopies where this species is prevalent could potentially change canopy fire activity under certain conditions. However in the Edward's Plateau, *Q. buckleyi* has been declining as a constituent of woodland canopies due to potential mechanisms including the infection of a deleterious fungal pathogen (Appel, 1995), increased deer browsing (Russell and Fowler, 2004), acorn recruitment failure (Russell and Fowler, 2002), and ironically, reduced surface fires (Murray et al., 2013a). With regard to surface fires, Murray et al. (2013a) found that stand recruitment of *Q. buckleyi*, primarily from root sprouting, was associated with increased fires during a drought that occurred throughout the study area in the 1950s. Persistence of *Q. buckleyi* in the past seems to be associated with patchy crown disturbance by fire with less evidence for large stand-replacing fires (Murray et al., 2013b) that are more typical of western North American conifer forests. Surface fire exclusion shifts species dominance and increases fuel accumulation, such as from *J. ashei* dominance in this case (Fuhlendorf et al., 1996). In eastern U.S. temperate forests, fire suppression has been attributed with decreased oak recruitment and composition in canopies (Abrams, 1992; Iverson et al., 2008; DeSantis et al., 2010). Oak recruitment can be increased by combining different management activities such as prescribed burning (surface) and thinning (Albrecht and McCarthy, 2006) however success may still be limited where herbivory is high (Andruk et al., 2014).

5. Conclusions

Tree species contribute to mean canopy differences in fuel loadings including *LMA*, foliar distribution in the canopy, and *LAI*. Environmental effects on species growth affect foliage biomass accumulation influencing canopy fuels. Differences in foliage distribution through the canopy also were found to be affected by species, such as *J. ashei* which lacks self-pruning, where canopy shape and foliage distribution that appears to be sensitive to some form of competitive inhibition. Based on simple crown fire modeling using derived canopy inputs, particularly *CBD*, we found differences in rate of crown fire spread among species indicating managing fire risk includes management of individual tree species.

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