



ORIGINAL RESEARCH

Open Access



# Branching out: species-specific canopy architecture limits live crown fuel consumption in Intermountain West USA conifers

Elliott T. Conrad<sup>1\*</sup> , W. Matt Jolly<sup>1</sup>, Tegan P. Brown<sup>1</sup> and Samuel C. Hillman<sup>1</sup>

## Abstract

**Background** Accurate estimates of available live crown fuel loads are critical for understanding potential wildland fire behavior. Existing crown fire behavior models assume that available crown fuels are limited to all tree foliage and half of the fine branches less than 6 mm in diameter (1 h fuel). They also assume that this relationship is independent of the branchwood moisture content. Despite their widespread use, these assumptions have never been tested, and our understanding of the physiochemical properties that govern live crown flammability and consumption remains limited. To test these assumptions, we sampled branches from 11 common Intermountain West USA conifers and determined the corrected available fuel estimates using physiochemical measurements, diameter subsample class distributions, and a bench-scale consumption experiment. Additional branches were air-dried to explore interaction between moisture content and consumption. Corrected available live crown fuel was compared to existing models across species and then used to determine potential differences in crown fire energy release.

**Results** Across the 11 common conifers, distinct patterns of sub 1 h fuel distributions were strong predictors of whether the existing available live crown fuel models overestimated, approximately correctly estimated, or underestimated available live fuel. Fine branchwood distributions generally fell into three archetypes: fine skewed, normally distributed, and coarse skewed. Based on our corrected estimates, existing models overestimated the potential canopy energy by 34% for an average-sized western larch and underestimated it by 18.8% for western hemlock. The critical fine branchwood consumption diameter varied with species and moisture content. Larger proportions of fine branches were consumed as the branchwood dried, and nearly all the 1 h fuel was consumed when the branches were completely dry.

**Conclusions** These results suggest that available live canopy fuel load estimates should consider species and moisture content to accurately assess and map fuel loads across landscapes. This work has implications for forest and fire management in conifer-dominated forests throughout western North America, and in other similar forests worldwide.

**Keywords** Live fuel, Crown fuels, Fire behavior, Fuel consumption, Fuel moisture content, Ignition probability, Physical fuel properties, Surface area-to-volume ratio, Conifer

\*Correspondence:

Elliott T. Conrad  
elliott.conrad@usda.gov

Full list of author information is available at the end of the article



This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2024. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## Resumen

**Antecedentes** La estimación precisa de la carga de combustibles en copas vivas de árboles es crítica para entender el comportamiento potencial del fuego. Los modelos existentes de comportamiento de fuegos de copas suponen que los combustibles en las copas están limitados a todo el follaje del árbol y a ramas finas menores a 6 mm de diámetro (combustibles de 1 h.). También suponen que esta relación es independiente del contenido de humedad que tengan esas ramas. A pesar de su extendido uso, estas suposiciones nunca fueron probadas, y a nuestro entender, las propiedades fisicoquímicas que gobiernan la inflamabilidad y el consumo de las copas por el fuego (o coronas de los árboles) son aún muy poco comprendidas. Para probar esas suposiciones, muestreamos ramas de 11 coníferas comunes de la región intermontana de los EEUU y determinamos la correcta disponibilidad de estimaciones usando mediciones fisio-químicas, distribución en subclases de tamaños, y realizamos un experimento de consumo a escala de laboratorio. Ramas adicionales fueron secadas al aire para explorar la interacción entre humedad del combustible y el consumo por el fuego. Los cálculos disponibles corregidos de combustible en copa viva fueron comparados con modelos disponibles de las especies muestreadas, y luego usados para determinar las diferencias potenciales en la energía liberada por el fuego en estas copas.

**Resultados** Entre las 11 coníferas muestreadas, los distintos patrones de distribución de combustibles menores de 1 h. fueron muy fuertes predictores de cómo los modelos de combustibles de copas vivas disponibles sobreestimaban, estimaban aproximadamente de manera correcta, o subestimaban el combustible vivo disponible. La distribución de las ramas finas generalmente respondió a tres arquetipos: finamente sesgadas, normalmente distribuidas, y gruesamente sesgadas. Basados en nuestras correctas estimaciones, los modelos existentes sobrestimaron la energía potencial del dosel en un 34% para un alerce occidental (*Larix occidentalis*) de tamaño medio, y subestimaron en un 18.8% para la tsuga del Pacífico (*Tsuga heterophylla*). El diámetro crítico para el consumo de ramas finas varió de acuerdo a las especies y su contenido de humedad. Una gran proporción de ramas finas fueron consumidas a medida que iban secándose, y casi todas las ramas de 1 h. fueron consumidas cuando éstas estaban completamente secas.

**Conclusiones** Estos resultados sugieren que la estimación de los combustibles disponibles en los doseles debe considerar las especies y el contenido de humedad de las ramas para determinar exactamente y poder mapear las cargas de combustibles a través de los paisajes. Este trabajo tiene implicancias para los bosques y el manejo del fuego en las regiones dominadas por coníferas en el oeste de Norteamérica, y también para otros bosques similares alrededor del mundo.

## Background

Wildfires are a common global disturbance that interact with climate to shape vegetation patterns and the terrestrial carbon balance (Bowman et al. 2009). Although essential for the proper functioning of many ecosystem processes, fires can negatively impact society by endangering life, damaging property and community infrastructure, and threatening ecosystems (Doerr and Santín 2016). Fire behavior is a product of weather, topography, and available fuel, which for wildland fires can include living and dead organic matter between the upper soil layer and forest canopy (Duff et al. 2017). Live fine canopy fuels include foliage and small-diameter branchwood, which are important sources of available fuel for wildfires (Nolan et al. 2022) and the basis for crown fire initiation, spread, and erratic fire behavior (Wagner 1977; Fernández-Alonso et al. 2013). Despite the importance of live crown fuels in fire behavior, it is difficult to quantify the available live crown fuel loads and their associated variability across tree species, and they remain poorly evaluated across the range of fire-prone global forest types.

Accurate estimates of the available live crown fuel load are critical for understanding potential fire behavior, which informs the modelling of carbon pool fluxes (Stenzel et al. 2019; Ottmar 2014), smoke emissions (Drury et al. 2014), and biodiversity impacts (Haslem et al. 2011). This information can also be used in assisting land managers in planning fuel reduction activities and quantifying community risk from wildfires (Prichard et al. 2017). In existing fire behavior models that incorporate canopy fuel loads, crown fuel availability has been estimated as a function of the size of the fuel element and an approximation of foliar moisture content (Scott 2001; Wagner 1977, 1993). Fuel size classes were originally developed for dead fuels, describing the size class (diameter) of fuel that would reach an equilibrium moisture content under ambient conditions for 1 h, 10 h, and 100 h (Fosberg and Deeming 1971), which correspond roughly to fuel diameter classes of  $\leq 6$  mm,  $> 6$  mm to 26 mm, and  $> 26$  mm to 72 mm, respectively. Fuels with smaller diameters have larger surface area-to-volume ratios (SVR) per unit mass, which promote faster

ignition (Santoni et al. 2014). SVR has long been an indicator of fuel flammability (Brown 1970).

When live crown fuels were integrated into fire models (Scott 2001; Wagner 1977, 1993), the fuel size classes and reference diameters ascribed to dead fuels were used as default values to classify the fraction of crown biomass that could be consumed in a wildfire (Deeming et al. 1977). Allometric equations are routinely used to accurately estimate the living crown biomass for a wide range of species (Brown 1978; Nolan et al. 2022). However, the criteria used to determine the amount of biomass that would be consumed in a fire, that is, the available crown fuel, are poorly defined and vary widely between studies and across different tree species (Brown and Bradshaw 1994; Call and Albin 1997; Reinhardt 1997; Reinhardt et al. 2006; Cruz et al. 2003). Some current fire-spread models assume that live crown fuel loads are the sum of all foliage and half of the 1 h fuel class canopy biomass (fine branchwood) (Reinhardt et al. 2006). These total available crown fuel estimates are then divided by the crown volume to calculate the crown bulk density or scaled to the plot level to represent the canopy bulk density. None of the 10 h or 100 h live fuels are considered available to burn in the flaming front of a crown fire. Within these models, the embedded assumption is that fuels are normally distributed with respect to the mean diameter of the fuel class. Therefore, half the 1 h fuel implies that all crown branchwood fuels less than 3 mm in diameter are completely consumed in a crown fire. However, this assumption has never been tested in the laboratory or explored in a variety of tree species.

To date, there have been relatively few empirical studies on which to base crown available fuel estimates because crown fire experiments are costly and require rigorous planning. The exception is the International Crown Fire Modelling Experiment (1997–2000) in Canada's Northwest Territories. During these high-intensity fires in black spruce and jack pine forests, empirical data report that that almost all canopy fuels less than 10 mm were consumed in the fire (Stocks et al. 2004). The complex nature of crown fires means that the results can be highly variable owing to the moisture conditions of crown fuels and other environmental factors affecting fire behavior; thus, results vary across the literature (Taylor et al. 2004). Call and Albin (1997) reported that the crown fuel consumption in immature jack pine experimental fires was 65% of fuels between 0 and 6 mm at 100% moisture. In *Pinus pinaster* stands, Molina et al. (2014) found that all foliage, 87.6% of the 1 h, and 62.8% of the 10 h crown fuel were available for burning. Brown and Bradshaw (1994) reported a percentage of crown fuel consumption of 100% for foliage and between 30% and 60% for

fine branchwood (0–6 mm diameter) in conifer forests. However, these estimates seem to be largely based on the authors' experience with these forest types, rather than empirical data. The lack of empirical observations means that many authors arbitrarily designate the diameter at which crown fuels will be consumed. Fernández-Alonso et al. (2013) designated all crown fuels < 0.5 mm as available to sustain the spread of crown fires. In another study, the available fuel load of the crown was estimated from live foliage only because fine branch data were not available (Cruz et al. 2003).

The lack of empirical data on available live crown fuels highlights three key knowledge gaps pertinent to crown fires in diverse forested stands which are currently assumptions in many crown fire models:

- The fine branchwoods of different tree species may not always be normally distributed around the mean diameter of the fuel size class.
- Three millimeters (3 mm), that is, the midpoint diameter of the 1 h fuel class, may not be the critical diameter for fine branchwood consumption across different tree species.
- Tree death leads to a natural decline in branchwood moisture content and, therefore, potentially promotes branchwood that is easier to ignite and be consumed at larger diameters.

Although generalizations are a necessary component of modelling complex natural landscapes, these assumptions have received limited empirical evaluation and may overestimate or underestimate the available live crown fuel and potential energy output. In developing a new experimentally derived crown consumption model for boreal forests, de Groot et al. (2022) report that varying the model using species, height, diameter at breast height (DBH), and stand density were key to the improved reliability of their model. However, these experiments have not been replicated across a broader range of intermountain tree species common in the Western US. Underestimating the available live crown fuel could result in unexpected fire behavior, fire effects, and smoke emissions. Meanwhile, overestimation could falsely inform public policies that regulate carbon storage in forests or over-state potential fire impacts to forest communities with inherent fire resistance (Stevens et al. 2020). These oversimplifications are exacerbated by the lack of experimental data directly relating physical fuel properties with ignition behavior. Without specific knowledge of the properties affecting ignition and consumption, we cannot accurately estimate the available crown fuel or model the fire behavior of living plants.

Here, we explored and tested the assumption that all foliage and half of the live 1 h fuel were available to burn in a crown fire across a range of intermountain tree species in the Western US. We described the physical live fuel properties and estimated the available fuel for eleven North American conifers that span a range of fire regimes (Stevens et al. 2020) using laboratory physiochemical measurements and a bench-scale ignition experiment. We examined how species differences in crown fuel distribution across size classes and live fuel moisture

variation could influence the available crown energy load and potential fire behavior. We have also shown how the estimates of available canopy fuels can change when branchwood moisture content declines.

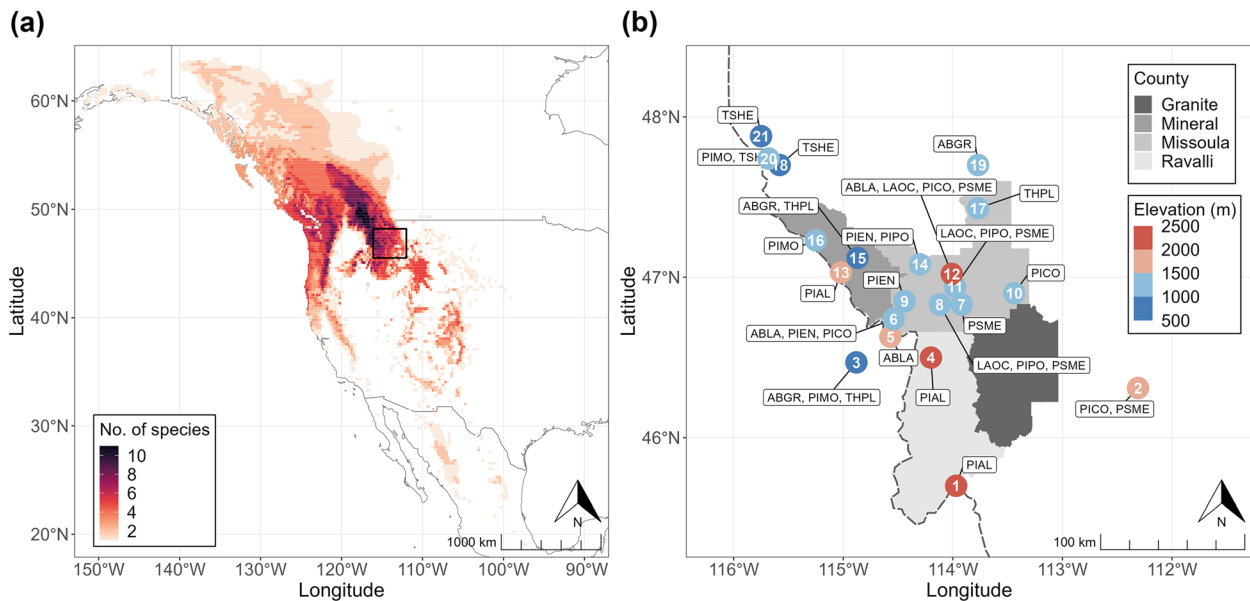
**Materials and methods**

**Field sampling**

Eleven coniferous tree species were chosen to represent potential crown fuels. These species span a large geographical range across the Intermountain West

**Table 1** The species, abbreviation, and number of branches sampled in this study

Species	Common name	Abbreviation	Branches
<i>Abies grandis</i> (Douglas ex D. Don) Lindl.	Grand fir	ABGR	4
<i>Abies lasiocarpa</i> (Hook.) Nutt.	Subalpine fir	ABLA	4
<i>Larix occidentalis</i> Nutt.	Western larch	LAOC	4
<i>Picea engelmannii</i> Parry ex Engelm.	Engelmann spruce	PIEN	4
<i>Pinus albicaulis</i> Engelm.	Whitebark pine	PIAL	4
<i>Pinus contorta</i> Douglas ex Loudon var. <i>latifolia</i> Engelm.	Lodgepole pine	PICO	5
<i>Pinus monticola</i> Douglas ex D. Don	Western white pine	PIMO	4
<i>Pinus ponderosa</i> Lawson & C. Lawson var. <i>scopulorum</i> Engelm.	Ponderosa pine	PIPO	4
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>glauca</i> (Beissn.) Franco	Rocky Mountain Douglas-fir	PSME	5
<i>Thuja plicata</i> Donn ex D. Don	Western redcedar	THPL	4
<i>Tsuga heterophylla</i> (Raf.) Sarg.	Western hemlock	TSHE	4



**Fig. 1** Maps depicting (a) the distribution extent of the 11 conifer species sampled in this study. The color ramp represents the concentration of species per cell. The black box in a describes the focus area of this study. The enlarged map (b) depicts the field sites where branch samples were collected across Montana and Idaho, USA. The elevation gradient of each site is shown in four categories, from blue (500–1000 m), light blue (1000–1500 m), pink (1500–2000 m), and red (2000–2500 m). The branches sampled at each site are listed via the abbreviations, which are available in Table 1. The grey scale depicts the counties that were used as boundaries to extract Forest Inventory Analysis (FIA) data. Spatial data for a were extracted from a digitized version of Little and Viereck (1971)

USA and a range of fire adaptive traits (Stevens et al. 2020). Intact branches were collected from June to September in 2014, 2015, and 2022 across western Montana and central Idaho (Table 1, Fig. 1). Branches were selected from healthy trees at sunlit edges and cut at a node. First-order branches, that is, those that were branching directly from the main stem, were preferred. However, second-order branches were occasionally selected because of processing time limitations. The cut branches were stored in plastic bags and kept in the shade for transport to the laboratory.

**Laboratory analyses**

**Moisture content and physical fuel properties**

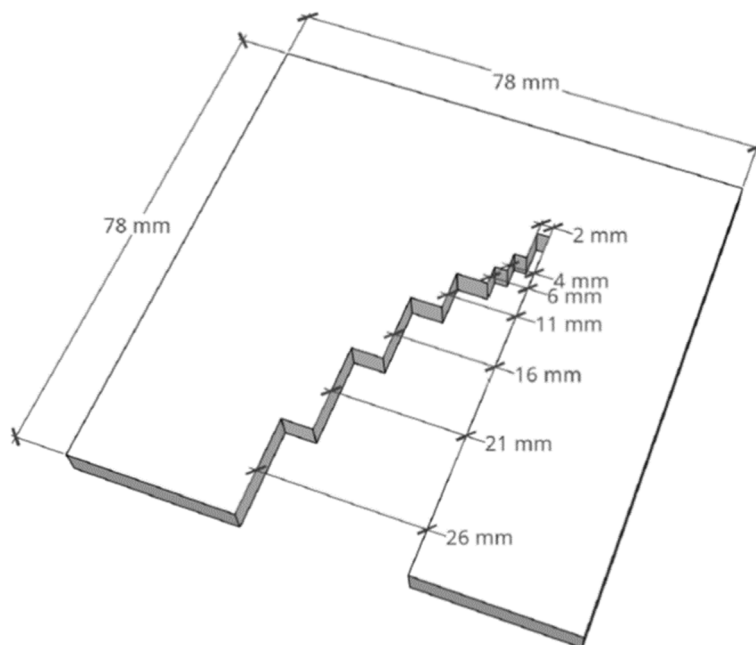
The entire branch was sorted into size classes. To better assess the available live crown fuel, the traditional fuel size classes of 1 h ( $\leq 6$  mm) and 10 h ( $> 6$ –26 mm) were divided into smaller experimental groups, that is, 0.1–2 mm, 2.1–4 mm, and 4.1–6 mm (1 h fuels) and 6.1–11 mm, 11.1–16 mm, 16.1–21 mm, and 21.1–26 mm (10 h fuels). The foliage was divided into new (current year) and old (all previous years) growth, and each foliage group was weighed to the nearest 0.1 mg. Defoliated branches were cut at the nodes, and a custom handheld gauge (Fig. 2) was used to divide the branchwood by size class. Internodal sections representing more than one size class were further divided at size class transition points. Each size class was weighed to the nearest

0.1 g. Dead fuels were not considered in this study and any dead branchwood was not included in the size class totals. Fresh branchwood and foliage samples were randomly selected from each branch from each size class. For up to 12 samples per size class, if present on a branch, the diameter ( $\phi$ ) and length were recorded. The fresh mass (FW) was weighed to the nearest 0.1 mg. Volume and density ( $\rho$ ) were determined using a balance density determination kit (Ohaus, Parsippany, NJ, USA). All the samples were oven-dried at 70 °C for at least 72 h and then reweighed to determine the dry mass (DW).

Surface area (SA) was measured on single needles of fresh foliage and oven-dried branch sections using wax dipping methods adapted from Veal et al. (2010). Branchwood and foliage samples were weighed, dipped briefly in 70 °C paraffin (Paraplast, Leica Biosystems, Richmond, IL), and then reweighed to determine wax deposition. Wax was removed from the end faces of the branch segments prior to reweighing. A calibrated regression was created using dowels, wood blocks, and cardstock of a known surface area. The regression was applied to calculate the total fuel surface area based on the weight of the deposited wax. The surface area-to-volume ratio (SVR) was calculated by dividing the surface area by the volume.

**Branch ignition and consumption**

Ignition and consumption tests were conducted on all the branches sampled in 2014 and 2015. The SVR measurements were destructive. Therefore, each size class was



**Fig. 2** The handheld gauge used to sort 1 h and 10 h branchwood into smaller divisions

subsampled once more for the ignition and consumption tests using as many branch segments available from a size class up to  $n = 12$ . If only one branch section remained in a size class, it was divided into nonadjacent segments to allow for multiple tests. Sustained ignition and consumption were measured on 4 cm branch segments, avoiding end pieces where excessive drying may have occurred during weighing. Ignition and consumption tests were performed in a temperature-controlled laboratory. The segments were placed in a wire mesh basket and introduced 16 cm above an open-flame burner (Fig. 3) as described in Jolly et al. (2016). The apparatus was built specifically for the rapid heating and ignition of live fuel samples and is composed of a pre-mixed propane open flame burner, a sample holder and timer. Flow rates were set at  $0.48 \text{ mol min}^{-1}$  for fuel and  $6.47 \text{ mol min}^{-1}$  for air. This yielded a rich flame similar to wildland flames that was partially pre-mixed and partially diffuse and a convective heating environment that was conducive to very rapid heating. Gas temperatures measured at the sample location for four minutes at 10 Hz using a 2-mm K-type thermocouple had an inner-quartile range of  $355\text{--}616 \text{ }^\circ\text{C}$  with a mean gas temperature of  $480 \text{ }^\circ\text{C}$ , a minimum of  $108 \text{ }^\circ\text{C}$ , and a maximum of  $1099 \text{ }^\circ\text{C}$ . This falls within the average and extreme temperatures measured for crown fires (Butler et al. 2004). The time to self-sustained ignition ( $t_{ig}$ ) was measured. The branch segment was held over the burner until it exhibited flame attachment, even after removal from the ignition source.



**Fig. 3** A photo of the open flame burner used to conduct ignition and consumption tests. Branchwood segments were held over the flames in a wire basket while time to ignition was measured

Once all the flaming and smoldering had ceased, the branch segment was scored for fuel consumption on a yes/no basis. Samples turning completely to crumbly white ash following sustained ignition were scored “yes.” All other samples, including those that were partially ashed, were scored “no.” Fuel consumption was assessed visually and by tapping the sample with a pair of forceps to assess material integrity. For foliage samples, sustained ignition ( $n = 20/\text{species}$ ) was assessed with the following adjustments. Entire fascicles of *Pinus* and *Larix* and single needles of all other genera were used with no adjustment to length. The samples were sent over the burner attached to the fascicle or needle base with an alligator clip rather than in an open basket.

Given that fuel availability is a function of fuel size and moisture content, we also assessed the effect of moisture content on fuel consumption using live branches separately harvested from *PICO*, *PIPO*, and *PSME*. Branchwood samples (*PICO*:  $n = 144$ , *PIPO*:  $n = 53$ , *PSME*:  $n = 74$ ) were ignited on the burner. The moisture content was measured on a paired adjacent sample. The branches were sampled over 2 weeks as they were air-dried in the laboratory and once more after oven-drying.

**Data analysis**

The fuel moisture content (FMC) as a percentage of dry weight was calculated using Eq. 1:

$$FMC(\%) = 100 \times \frac{(FW - DW)}{DW} \tag{1}$$

The mean and standard deviation (SD) for FMC, SVR,  $\rho$ , and  $t_{ig}$  were weighted to account for varying sample numbers per branch. SVR,  $\rho$ , and  $t_{ig}$  were reported (Table S1) for all experimental size classes. The branch proportional biomass distribution on a dry weight basis was calculated between the different size classes for each species. In 2014 and 2015, the size classes were subsampled for ignition and other tests prior to obtaining the final dry mass. Therefore, the total dry mass for each size class was calculated from the fresh mass and average FMC using Equation 2. In 2022, the dry mass of each size class was directly weighed. The proportional dry mass of each size class of each branch ( $p_{mass}$ ) was averaged for each species.

$$DW_{sizeClassTotal} = \frac{100 \times FW_{sizeClassTotal}}{FMC + 100} \tag{2}$$

Species were assigned to 1 h fuel distribution archetypes based on the size class with the largest proportion of biomass, that is, 0–2 mm, fine skewed; 2.1–4 mm, normal; 4.1–6 mm, coarse skewed. We quantified degree of coarse

or fine skew using a version of Pearson mode skewness, modified to account for data in three ordered bins:

$$skewness = X \times \frac{x_2 - \max(x_1, x_2, x_3)}{\sigma} \tag{3}$$

where

$$X = \begin{cases} -1 & \text{if } \max(x_1, x_2, x_3) = x_1 \\ 1 & \text{otherwise} \end{cases} \tag{4}$$

In this case,  $x_1$ ,  $x_2$ , and  $x_3$  were the biomass proportions in the 0–2, 2.1–4, and 4.1–6 mm size classes, respectively, and  $\sigma$  was their standard deviation. This metric does not quantify skewness for distributions where the maximum value is in the middle bin. Species in that category were considered normally distributed.

**Probability of consumption**

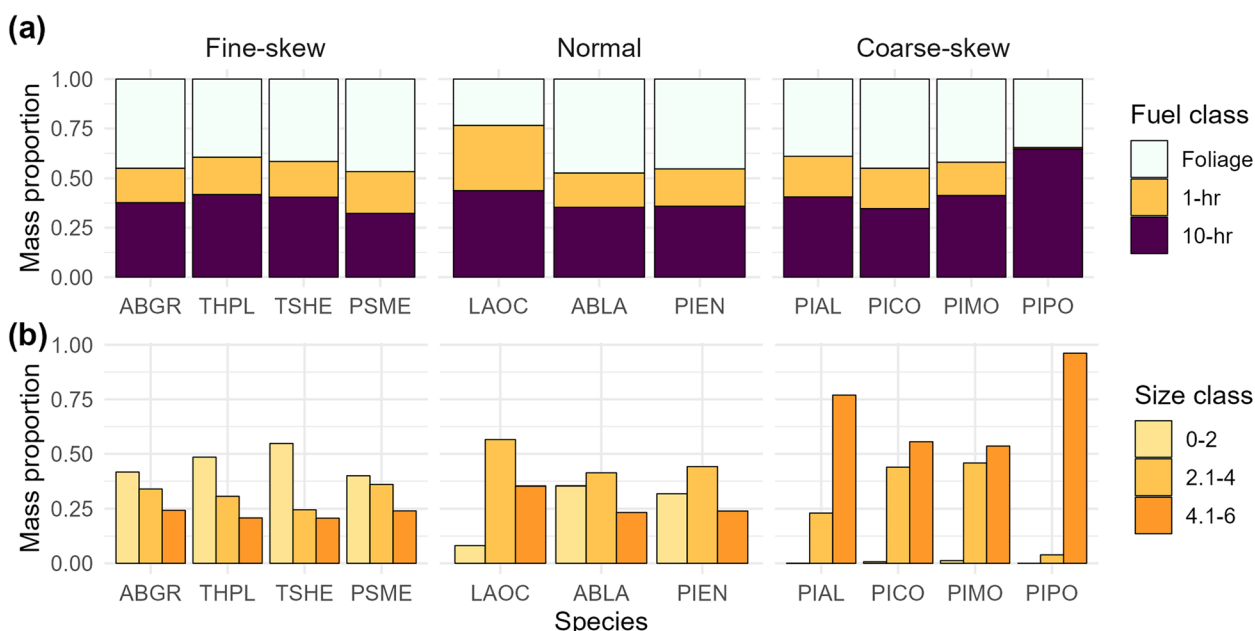
The probability of consumption was modelled as a function of diameter ( $\phi$ ) using generalized linear binomial logistic regression with the *stats* package in R 4.2.2 (R Core Team 2021), with species and consumption as predictive variables. Fuel consumption was predicted using a 50% threshold. The threshold diameter ( $\phi_{th}$ ) at which the consumption probability was 50% was calculated for each species. The significance of moisture content on the probability of consumption was modeled

using binomial logistic regression with moisture content as an additional predictive variable.

Linear relationships were fitted between the cumulative biomass values of the three size classes to determine an experimentally corrected value for the available live fuel for each species. The appropriate line was evaluated at  $\phi_{th}$  to predict the total proportion of 1 h biomass likely to be consumed for each species. This value was normalized to the total 1 h branchwood plus foliage mass and compared with the estimates of available fuel using all foliage plus half of the 1 h branchwood. A paired *t*-test was used to determine the significance of the differences between the models by species.

**Live crown available energy**

The difference in available crown energy between the assumed (foliage + half 1 h) and corrected available live crown fuel loading was calculated by multiplying the species-specific heat content values (HC, MJ/kg) by the crown mass and the proportion of the crown available to burn for each scenario. The HC for foliage and 1 h wood for each species was measured using a calorimeter (C200, IKA-Works, Staufen, Germany). Crown mass for each species was modelled using diameter at breast height (DBH) data from the USDA Forest Service, Forest Inventory and Analysis (FIA) program averaged across the Western Montana survey unit, and allometric equations from FuelCalc Appendix D (Lutes 2020). The DBH



**Fig. 4** A bar chart showing species biomass proportions for **a** existing conventional fuel classes and **b** experimental fuel classes for 1 h fuels only. The colors correspond to foliage (light green), 1 h fuels (orange), and 10 h fuels (purple). The color of **b** is scaled from 0–2 mm (light orange) to 4.1–6 mm (darker orange). The order of species (x-axis) reflects the emergent distribution patterns within the 1 h size class

and HC data used in the calculations are listed in Table 4. Assumed available fuel was calculated using the 50% proportion of the crown mass, whereas the corrected available fuel was calculated using the experimentally derived proportion of 1 h fuel available from the results (Table 2).

## Results

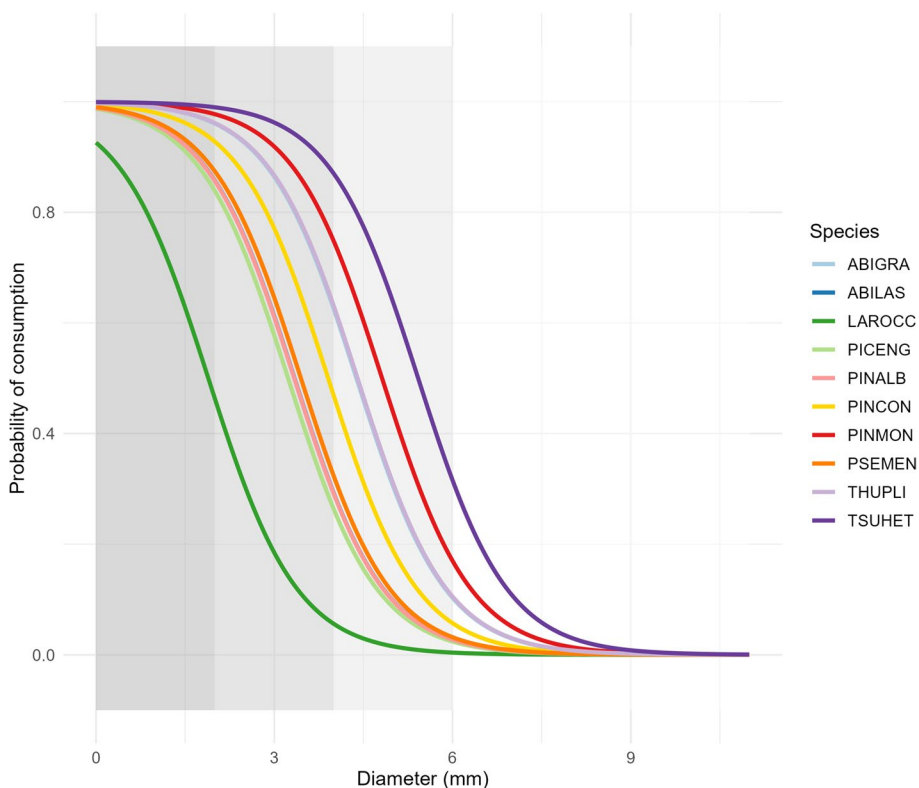
### Linking physical fuel properties to available live crown fuel

Despite similar normalized biomass distributions between the foliage, 1 h, and 10 h fuel classes with the exception of LAOC and PIPO (Fig. 4a), distinct patterns of biomass distribution emerged within the 1 h experimental classes (0–2 mm, 2.1–4 mm, 4.1–6 mm) of the 11 conifers studied (Fig. 4b). These patterns could be grouped into three primary archetypes, that is, fine skewed, approximately normally distributed, and coarse skewed (Table 2). All pine species had coarse-skewed 1 h fuels. ABGR, PSME, THPL, and TSHE were fine skewed, and ABLA, LAOC, and PIEN were approximately normally distributed. Table 2 provides a measure of relative skewness between species.

We conducted a series of ignition and consumption tests across species and fuel classes to empirically derive fuel availability from the physical fuel properties

measured. Across all species, foliage was completely consumed in all tests. In contrast, the 10 h fuels were never completely consumed after sustained ignition. The probability of consumption model demonstrated that consumption varies by species and the largest change in ignition behavior occurred in the 1 h fuel class (Fig. 5). Species-specific logistic regression models were generated to determine the probability of consumption as a function of diameter (Table 2). These performed well across all species tested with a predictive accuracy of 83.0% and area under curve of 83.8%. Using the species-specific probability of consumption models, Table 2 shows the threshold diameters of consumption at 50% probability ( $\phi_{th}$ ) for 1 h fuels, highlighting the substantial differences across species and archetype groups ( $\phi_{th}$ , Table 2).  $\phi_{th}$  ranged from 5.89 mm (TSHE fine skew) to 1.98 mm (LAOC normal) (Table 2).  $\phi_{th}$  for PIPO was unavailable because there were not enough 1 h fuel samples to conduct ignition tests.

The species-specific distributions of 1 h fuel (Fig. 4) and  $\phi_{th}$  were combined to determine the corrected available fuel (1 h avail, Table 2). Compared with the assumption that half of the 1 h fuel was available for each species, we found that corrected 1 h available live crown fuel varied

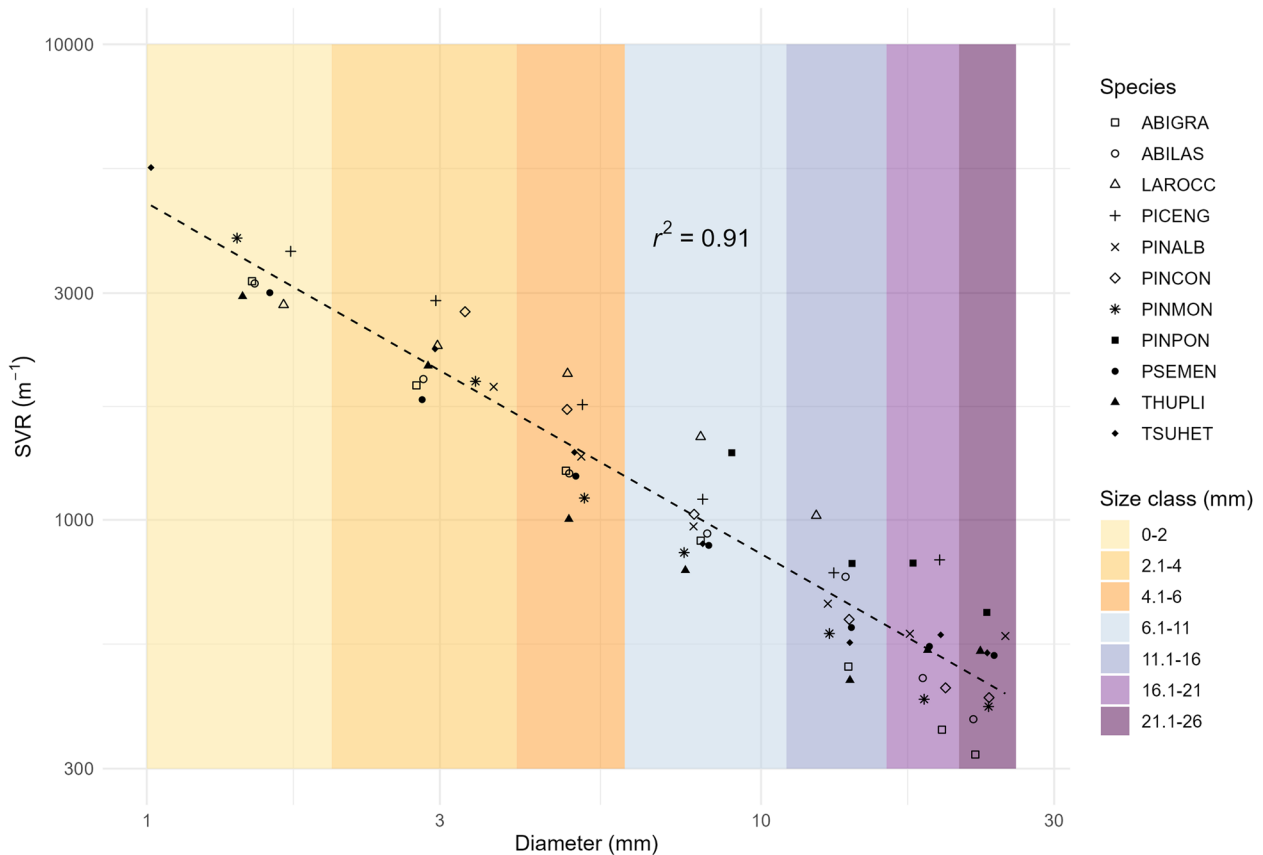


**Fig. 5** Probability of branchwood consumption predicted for branchwood diameter by species. Grey boxes indicate 1 h size classes. PINPON is not included because it lacked 1 h fuel

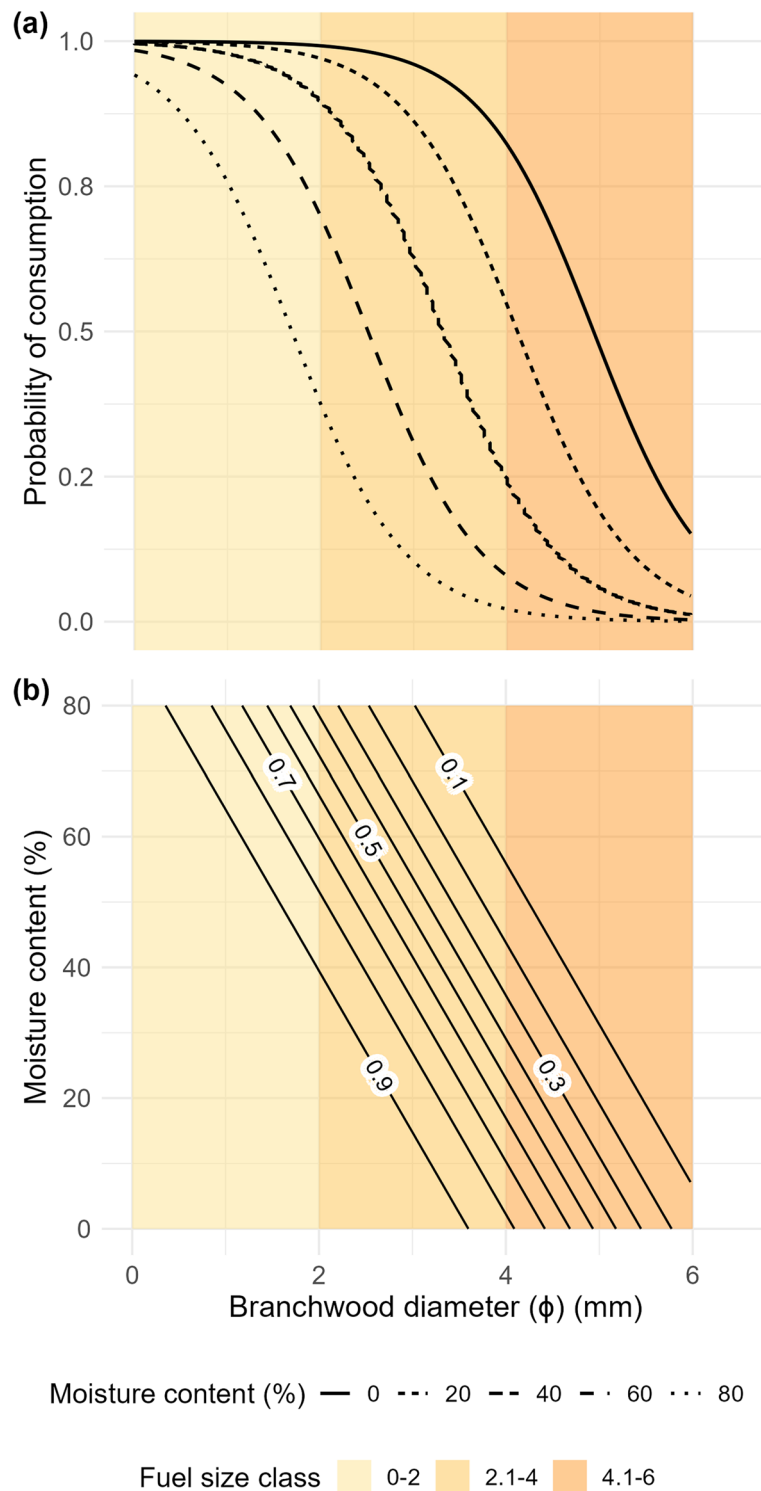


**Table 2** Fuel characteristics and fuel class proportions for each species.  $\phi_{th}$  is the branchwood diameter below which fuel has a 50% likelihood of being consumed;  $SVR_{th}$  is the corresponding crown threshold surface area to volume ratio. Branchwood available as fuel (1 h avail) is shown as a proportion of total 1 h biomass. Biomass proportions within the 1 h fuel class are shown as well as foliage, 1 h, and 10 h fuel as a proportion of the average measured branch. Proportions are on a dry mass basis; 1 h skew is the skewness of the biomass distribution within the 1 h fuel class

1-h dist.	Species	Fuel characteristics			1-h branchwood			1-h skew	Total branch proportions		
		$\phi_{th}$	$SVR_{th}$	1-h avail	0.1–2	2.1–4	4.1–6		Foliage	1-h	10-h
		mm	$m^{-1}$	$\hat{p}$	$\hat{p}$				$\hat{p}$		
Fine skew	ABGR	4.38	1560	0.80	0.42	0.34	0.24	0.87	0.45	0.17	0.38
	TSHE	5.89	1332	0.99	0.55	0.25	0.21	1.62	0.42	0.18	0.40
	THPL	4.38	1560	0.84	0.48	0.31	0.21	1.27	0.39	0.19	0.42
	PSME	3.44	1864	0.65	0.40	0.36	0.24	0.47	0.47	0.21	0.32
Normal	LAOC	1.98	2915	0.08	0.08	0.57	0.35	0	0.23	0.33	0.44
	ABLA	3.39	1906	0.64	0.35	0.41	0.23	0	0.47	0.17	0.35
	PIEN	3.33	1952	0.61	0.01	0.44	0.56	0	0.45	0.20	0.35
Coarse skew	PIAL	3.28	1906	0.15	0.32	0.44	0.24	-1.37	0.45	0.19	0.36
	PICO	3.80	1696	0.41	0.00	0.23	0.77	-0.40	0.39	0.20	0.41
	PIMO	4.79	1459	0.73	0.01	0.46	0.54	-1.70	0.42	0.17	0.41
	PIPO	-	-	0.00	0.00	0.08	0.96	-0.27	0.35	0.01	0.65



**Fig. 6** A log-log plot of branchwood diameter and SVR, which were measured independently. Data points represent the species average for each experimental size class, and each shape depicts one species. Colors equate to the experimental fuel classes, from 0–2 mm (1 h, light orange) to 21.1–26 mm (10 h, dark purple). Linear least squares fit of the log transformed data resulted in  $r^2 = 0.91$  and  $p < 2.2e - 16$



**Fig. 7** Figures depicting the probability of branchwood being fully consumed relative to branchwood diameter ( $\phi$ ). **a** depicts the probability of consumption as a function of moisture content, while **b** depicts the relationship as a contour plot. Logistic regression models for each moisture content were derived from the ignition and consumption of branchwood segments ( $n = 271$ ) harvested from a branch allowed to dry in the lab

widely, ranging from low values of 0% and 8% (PIPO and LAOC, respectively) to 99% (TSHE) of fuels within the 1 h category.

In the present study, branchwood diameter and SVR were strongly correlated (Fig. 6), although these two values were measured independently. Using the model depicted in Fig. 6, the threshold surface area-to-volume ratio ( $SVR_{th}$ ) for crown consumption was calculated for each species.  $SVR_{th}$  ranged from 1332 (TSHE) to 2915  $m^{-1}$  (LAOC), highlighting the different amounts of available live crown fuel required for 50% probability of crown consumption.  $SVR_{th}$  was not available for PIPO in the 1 h fuel category. The relationship between probability of consumption and diameter varied with species

(Table 2) and moisture content (Fig. 7). The diameter at which fine fuels were consumed increased as the moisture content decreased. Between 80% (fully alive) and 0% (oven-dry) moisture content,  $\phi_{th}$  nearly tripled (Fig. 7).

**Live crown available energy**

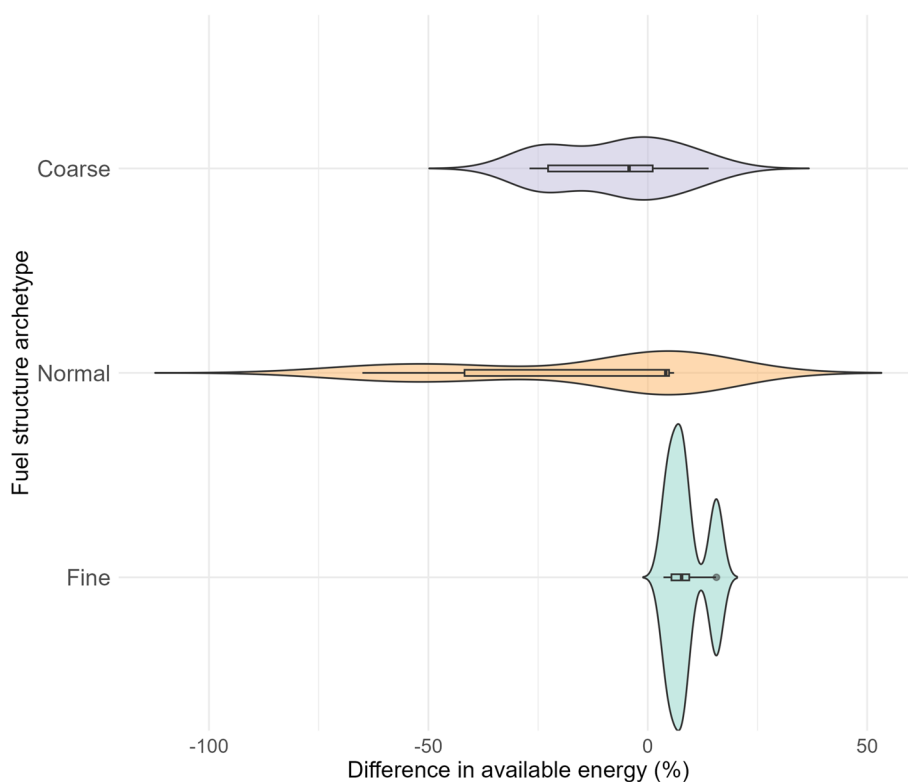
Assumed and corrected values for the available live crown energy were determined by multiplying the proportion of crown mass available for burning (Table 2) by the foliage and branchwood species-specific heat content (Table 4). Differences in crown available energy between the assumed and measured values varied by species (Table 3) and included overestimates and

**Table 3** Difference between available live fuel calculated as available energy

1-h distribution	Species	Crown biomass proportion		Total crown weight	Crown available energy	Δ Energy between 1/2 1-h and modeled available fuel	
		fol	1-h	kg	MJ	MJ	%
Fine skew	ABGR	0.52	0.19	76.9	1057.3	85.3	8.8
	THPL	0.54	0.12	42.4	573.3	33.8	6.3
	TSHE	0.36	0.18	145.6	1620.1	256.1	18.8
	PSME	0.40	0.19	95.5	1051.0	54.7	5.5
Normal	LAOC	0.23	0.30	63.1	319.2	- 164.1	- 34.0
	ABLA	0.45	0.22	63.7	816.2	41.2	5.3
	PIEN	0.43	0.23	130.5	1473.9	68.2	4.9
Coarse skew	PIAL	0.38	0.30	56.3	507.2	- 124.2	- 19.7
	PICO	0.41	0.26	46.4	513.0	- 24.5	- 4.6
	PIMO	0.42	0.22	51.9	615.0	52.5	9.3
	PIPO	0.32	0.02	205.3	1399.4	- 55.0	- 3.8

**Table 4** Diameter at breast height (DBH) and heat content (HC) were used to calculate the energy release of assumed and measured available fine live fuel. DBH statistics were gathered from the USDA Forest Service, Forest Inventory and Analysis (FIA) program for the counties where each species was collected. HC was measured in our laboratory

Species	DBH (in)				Heat content (MJ/kg)	
	1Q	Median	3Q	N	Foliage	1-h
ABGR	4.1	6.6	10	7153	20.988	19.488
ABLA	5.1	6.7	9.2	8557	21.939	20.71
LAOC	6.4	9.1	14.1	2614	19.55	20.479
PIAL	6	8.2	11.2	2557	21.469	20.705
PICO	5.7	7.2	9.1	15703	21.491	21.255
PIEN	6	9.4	14.4	3111	19.923	20.055
PIMO	5.75	8	12.8	54	20.579	20.365
PIPO	7.3	11.45	16.6	2931	21.045	22.085
PSME	5.9	8.7	12.8	16386	21.073	20.179
THPL	2.3	5.75	9	1141	21.354	19.9
TSHE	7.7	11.4	17.1	16	21.089	19.708



**Fig. 8** Fuel archetype and percent difference available energy for all species between assumed and corrected available live crown fuel, including foliage and 1 h fuel

underestimates. For LAOC, the assumption that all foliage plus half of the 1 h fuel was available to burn overestimated the available energy by 34% (164.1 MJ). In contrast, the available live crown energy was underestimated for TSHE trees by 18% (256 MJ). The smallest changes in available energy between the assumed (existing) model and our corrected results were for PIPO, where the available energy was overestimated by 3.8%, and ABLA where the available energy was underestimated by 5.3%.

The 1 h fuel structure archetypes showed distinct differences in available energy, shown in Fig. 8 as a percent difference between assumed and corrected available fuel. On average, the corrected available fuel for fine-skewed species led to around 8% more energy, while coarse-skewed species had about 5% less. Species with normally distributed 1 h fuels averaged 5% more energy except for LAOC, whose fuel structure and fuel availability differed significantly from those of the other species.

**Discussion**

**Testing assumptions by linking physical fuel properties and ignition behavior**

Our results have demonstrated that the assumption that all foliage and half of the 1 h fuel were available to burn

in a crown fire leads to substantial overestimation and underestimation of actual available live crown fuel for 11 widespread conifer species common to the Intermountain West, USA (Fig. 8). All crown foliage was typically available and 10 h fuels were rarely available, suggesting that the existing framework was well suited to these fuel classes. However, the 1 h fuel class alone may not have been an appropriate delineator of the branch material available as fuel. Of the conifers sampled, branchwood distributions within the 1 h fuel class were either fine skewed, normal, or coarse skewed (Fig. 4), which typically corresponded to underestimation, appropriate estimation, or overestimation of available live crown fuel (Fig. 8). This finding has strong implications for quantifying the available live crown fuel load because of the interaction between the 1 h fuel distributions and  $\phi_{th}$ , the threshold branchwood diameter for 50% probability of consumption.

In the present study,  $\phi_{th}$  varied widely across the eleven conifers tested (Table 2), ranging from 1.98 mm (LAOC) to 5.89 mm (TSHE). Although they are independent metrics for characterizing live crown fuel availability,  $\phi_{th}$  interacts on species 1 h branchwood distributions to shift the amount of fuel above and below this critical threshold for consumption. 1 h LAOC (western larch) fuel falls

within the “normal” archetype, with a relatively small proportion of branchwood in the 0–2 mm experimental fuel category (Fig. 4). Coupled with a relatively small  $\phi_{th}$  value, our results suggested that only 8% of LAOC live crown fuels could be considered available in a crown fire. In contrast, species with larger  $\phi_{th}$  values, such as TSHE (western hemlock), had a greater amount of branchwood distributed below  $\phi_{th}$ ; thus, a large proportion (99%) was available to burn in a crown fire.

Our results have further highlighted the substantial impact of fuel moisture content on fuel availability through its role in determining the threshold diameter of consumption ( $\phi_{th}$ ) of fuels in the 1 h class. Although we were not able to assess the moisture effects for all species, ignition tests for PICO, PIPO, and PSME samples with decreasing moisture content highlighted that lowered live fuel moisture conditions could increase the amount of fuel available within a tree crown, which aligns with other crown fire research findings related to dead crown fuel moisture content (Cruz et al. 2004).

#### Implications for modelling and fire effects

The physical and chemical factors measured in this study have linked live crown fuels to ignition behavior. This has allowed us to calculate the amount of energy available to burn in a fire (Table 3) (Fig. 8). The quantification of the available live crown fuel at these scales has facilitated a deeper understanding of crown fire potential and fire effects. Crown fire behavior models form an integral part of fire simulations used by fire managers in the Northern Hemisphere (Finney 1998). Initiation (Wagner 1977) and propagation models (Wagner 1993) rely on descriptions of the canopy base height, crown foliage ignition energy, live fuel moisture content, and canopy bulk density. Bulk density was estimated for the canopies by dividing the crown mass (load) by the volume, with the load derived from the assumed fuel availability. In the modelling environment, crown fire behavior is sensitive to the bulk density (Wagner 1977). Therefore, a modest adjustment in the available live fuel load may produce considerable variations in the modelled fire behavior. Figure 8 illustrates this, presenting the percentage difference in energy released during a crown fire between assumed and corrected models. For coarse-skewed and approximately normally distributed species, the assumed method typically overestimated the crown available energy (Fig. 8). This suggests that modelled fire behavior metrics, such as the rate of spread or consumption, may also be overestimated in forests dominated by these species. This may have an impact on the modelling of carbon storage or incorrectly predict fire spread where it may not occur. By contrast, the corrected values of the available live crown fuel have shown that the assumed method

typically underestimates crown available energy for fine-skewed species. Underestimating the available live crown fuel is particularly important for fire managers because it can result in unexpected fire behavior, smoke emissions, and fire effects. The amount of available live crown fuel in the western hemlock (TSHE) indicates that the energy released when TSHE burns in a crown fire increases  $\approx 19\%$  between the assumed and corrected models (Fig. 8). While TSHE is the upper limit, on average, the assumed available live crown fuel models underestimated the energy that the fine-skewed species could release during a crown fire by  $\approx 10\%$ .

Our research has suggested that crown fire models should also consider metrics describing how 1 h fuels are distributed within the crown volume. Although branchwood diameter and SVR are theoretically correlated, our empirical data have demonstrated the strength of this relationship across species and fuel size classes (Fig. 6). Using this relationship, we calculated the threshold SVR values per species for a 50% probability of fuel consumption (Table 2), which demonstrated a relatively high range at this probability. The mass input to crown bulk density does not explicitly differentiate between tree crowns where the branchwood is concentrated into fewer coarse branches, such as PIPO, or many fine branches, such as TSHE. However, the range in threshold SVR observed across species ( $1332 \text{ m}^{-1}$  (TSHE)– $2915 \text{ m}^{-1}$  (LAOC)) and the role that SVR plays in the rate of fuel consumption has suggested that this is an important parameter that future crown fire behavior models should capture in addition to bulk density. More accurate fuel load estimates and the distribution of that load across fuel size classes will improve crown fire behavior model outputs and also enhance our understanding of potential ecological fire effects (Dickman et al. 2023). Such improvements to the inputs underpinning crown fire models will then enable more accurate wildfire risk assessment and mapping products, improved operational decision making, and more useful wildfire risk information provided to communities.

A more accurate quantification of the available live crown fuel will also increase our understanding of the mechanisms driving fire effects and our ability to model these across different species and landscapes. Heat damage to foliage, buds, or branches, collectively referred to as crown scorch, is a common outcome of prescribed and wildland fire, which can result in tree mortality (Dickinson MB 2001). While it has been well established that small diameter branches are more sensitive to high temperatures (Kozlowski et al. 1991), modelling temperature flux within tree crowns is difficult and remains a priority area of research for fire ecologists (Varner et al. 2021). Our research has filled a knowledge gap by describing the

physical and chemical properties of available live crown fuel across 11 conifers common to the Intermountain West. The findings may explain the differing fire effects across species given uniform heat exposure and also provide a physical link between plant functional traits and prevailing fire regimes (Stevens et al. 2020). Understanding tree crown architecture, available energy, and potential fire behavior at the scale of our study enhances the linkages between fire behavior and fire ecology, which is currently a key challenge in the field (O'Brien et al. 2018).

Other forms of canopy damage and tree mortality include beetle kill, which is widespread in conifer-dominated forest systems (Berner et al. 2019; Hicke et al. 2012; Jenkins et al. 2013). Beetle-killed trees represent a unique fire management challenge because they retain the architecture of a living tree but typically have a much lower moisture content (Jolly et al. 2012) and altered foliage chemical composition as the foliage dies (Page et al. 2012). Figure 7 illustrates the interactions between moisture content, diameter, and probability of consumption, with substantial differences in the probability of consumption observed between fuels of 0–80% moisture content. Page et al. (2012) report similar findings, noting that yellow and red Lodgepole pine foliage had significantly lower time to ignition and temperature of ignition compared to green foliage. Although some research has found that beetle-kill has limited effects on wildfire area burned (Hart et al. 2015) or severity (Harvey et al. 2013), others report significant impacts of this disturbance type on fire activity (Lynch et al. 2006; Schoennagel et al. 2012). In a summary of the beetle-kill literature, Hicke et al. (2012) detail the panoply of interactions that influence beetle-kill effects on fire, such as weather conditions, and highlight that the potential for crown fire behavior in beetle-killed areas is an important area for continued research.

As moisture content decreased, branches with larger diameters were more likely to be consumed. At the scale of a crown fire, this means that there is a lot more fuel available in a dead or dying tree, because  $\phi_{th}$  increases, bringing more branchwood into an available state. Our research also has important implications for quantifying carbon pool fluxes, emissions from wildland and prescribed fires, and smoke production, because they all require fuel consumption as an input. A more accurate quantification of fuel availability and actual consumption would enhance our capacity to model these fluxes in the context of fire effects in forested regions.

#### Limitations and future research

Our estimates of the available live crown fuels were conservative. The bench ignition tests required sustained ignition without additional heat inputs, whereas actual

crown fire benefits from the energy released by the combustion of surface and adjacent fuels. In addition, we only scored completely consumed samples, although most samples exhibited some degree of partial consumption. Maximum fuel consumption during a crown fire is also a function of fire intensity (Whight and Bradstock 1999), so greater consumption would be expected in high intensity fires. Our study adds to the experimental crown fire literature by empirically deriving a lower bound for fuel consumed during a crown fire.

The fuel distribution archetypes fit some species more strongly than others, as illustrated by the data spread in Fig. 8. Individual pine branches were overwhelmingly coarse skewed, whereas PSME ( $n = 5$ ) had three fine-skewed branches, one normally distributed branch, and one with approximately even branchwood proportions in the 1 h fuel class. We grouped LAOC as normal. However, it may represent its own category. LAOC was the only deciduous species assessed here and was the only species in which the fine branchwood mass exceeded the foliage mass (Fig. 4). The branchwood distribution presented in the present study represented a limited sample of the study area. In the future, additional measurements covering a broader range of tree replicates and species are required to better capture intra- and inter-species variations. Overall, branchwood distribution archetypes are a useful way of grouping species based on whether the available live crown fuel is likely to be under, over, or appropriately estimated using the existing framework. However, future iterations of crown fire models should incorporate inputs for species-specific fuel arguments rather than using generalized groupings.

The method presented here for quantifying crown fuel is straightforward and requires limited equipment beyond calipers (or a handheld gauge) and an ignition source. We used a purpose-built burner, but any apparatus that can ignite the fuel samples to a self-sustaining state is sufficient. In this experiment, we separated the branches into foliage, 1 h, and 10 h fuel classes. However, because branches in the 10 h fuel class could not burn, simply separating the foliage and 1 h fuels would be sufficient to repeat this experiment. While this study focused on coniferous gymnosperms, future research could expand this experimental approach to include angiosperms to quantify the available live crown fuel across a greater range of species throughout forested regions.

#### Conclusions

In this study, we presented a method to determine the corrected available live crown fuel and apply this method to 11 conifer species common to the Intermountain West USA. We demonstrated that the

assumptions embedded in existing models of available live crown fuel led to overestimation and underestimation of available fuel. This resulted in substantial differences in the amount of energy available to fuel a crown fire. Our results have strong implications for fire behavior modelling in conifer-dominated forests. We have presented a simple method for calculating the corrected available live crown fuel that can be used by other researchers and land managers to gain a deeper understanding of potential fire behavior.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-024-00261-3>.

### Supplementary Material 1.

## Acknowledgements

Not applicable.

## Authors' contributions

ETC, WMJ, and TPB conceptualized and developed the methodology for the study. WMJ provided supervision. ETC and TPB collected and analyzed the data. ETC, TPB, and SCH visualized the data and prepared the original draft. All authors were involved in the writing, reviewing, and editing of the final manuscript.

## Funding

Funding for this study was provided by DOD SERDP Grant #RC19-C1-1092.

## Availability of data and materials

Data available upon request.

## Declarations

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

The authors declare no competing interests.

## Author details

<sup>1</sup>Missoula Fire Sciences Laboratory, Rocky Mountain Research Station, USDA Forest Service, 5775 Highway 10 W, Missoula 59808, MT, USA.

Received: 23 August 2023 Accepted: 27 February 2024

Published online: 15 March 2024

## References

- Berner, L., B. Law, A. Meddens, and J. Hicke. 2019. Tree mortality from fires and bark beetles at 1-km resolution, Western USA, 2003–2012. ORNL DAAC, Oak Ridge, Tennessee, USA.
- Bowman, D.M., J.K. Balch, P. Artaxo, W.J. Bond, J.M. Carlson, M.A. Cochrane, C.M. D'Antonio, R.S. DeFries, J.C. Doyle, S.P. Harrison, et al. 2009. Fire in the earth system. *Science* 324 (5926): 481–484.
- Brown, J.K. 1970. Ratios of surface area to volume for common fine fuels. *Forest Science* 16 (1): 101–105.
- Brown, J.K., and L.S. Bradshaw. 1994. Comparisons of particulate-emissions and smoke impacts from presettlement, full suppression, and prescribed natural fire period in the selway-bitterroot wilderness. *International Journal of Wildland Fire* 4 (3): 143–155.
- Brown, J.K. 1978. *Weight and density of crowns of Rocky Mountain conifers*, Volume 197. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station
- Butler, B., J. Cohen, D. Latham, R. Schuette, P. Sopko, K. Shannon, D. Jimenez, and L. Bradshaw. 2004. Measurements of radiant emissive power and temperatures in crown fires. *Canadian Journal of Forest Research* 34 (8): 1577–1587.
- Call, P.T., and F.A. Albin. 1997. Aerial and surface fuel consumption in crown fires. *International Journal of Wildland Fire* 7 (3): 259–264.
- Cruz, M., M. Alexander, R. Wakimoto, et al. 2003. Assessing canopy fuel stratum characteristics in crown fire prone fuel types of Western North America. *International Journal of Wildland Fire* 12 (1): 39–50.
- Cruz, M.G., M.E. Alexander, and R.H. Wakimoto. 2004. Modeling the likelihood of crown fire occurrence in conifer forest stands. *Forest Science* 50 (5): 640–658.
- Deeming, J.E., R.E. Burgan, and J.D. Cohen. 1977. *The national fire-danger rating system, 1978*, Volume 39. US Department of Agriculture, Forest Service, Intermountain Forest and Range.
- de Groot, W.J., C.C. Hanes, and Y. Wang. 2022. Crown fuel consumption in Canadian boreal forest fires. *International Journal of Wildland Fire* 31 (3): 255–276.
- Dickinson MB, J.E. 2001. Fire effects on trees. In *Forest fires: behavior and ecological effects*, ed. E.A. Johnson, K. Miyanishi, et al., 477–525. San Diego: Academic Press.
- Dickman, L.T., A.K. Jonko, R.R. Linn, I. Altintas, A.L. Atchley, A. Bär, A.D. Collins, J.L. Dupuy, M.R. Gallagher, J.K. Hiers, et al. 2023. Integrating plant physiology into simulation of fire behavior and effects. *New Phytologist* 238 (3): 952–970.
- Doerr, S.H., and C. Santín. 2016. Global trends in wildfire and its impacts: perceptions versus realities in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1696): 20150345.
- Drury, S.A., N.S. Larkin, T.T. Strand, S. Huang, S.J. Strenfel, E.M. Banwell, T.E. O'Brien, and S.M. Raffuse. 2014. Intercomparison of fire size, fuel loading, fuel consumption, and smoke emissions estimates on the 2006 tripod fire, Washington, USA. *Fire Ecology* 10 (1): 56–83.
- Duff, T.J., R.E. Keane, T.D. Penman, and K.G. Tolhurst. 2017. Revisiting wildland fire fuel quantification methods: the challenge of understanding a dynamic, biotic entity. *Forests* 8 (9): 351.
- Fernández-Alonso, J., I. Alberdi, J. Álvarez-González, J. Vega, I. Cañellas, A. Ruiz-González, et al. 2013. Canopy fuel characteristics in relation to crown fire potential in pine stands: analysis, modelling and classification. *European Journal of Forest Research* 132 (2): 363–377.
- Finney, M.A. 1998. *Farsite, fire area simulator—model development and evaluation*. Technical report, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula, MT, USA.
- Fosberg, M. and J. Deeming. 1971. *Derivation of the one-and ten-hour timelag fuel moisture calculations for fire-danger rating*. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station
- Hart, S.J., T. Schoennagel, T.T. Veblen, and T.B. Chapman. 2015. Area burned in the western united states is unaffected by recent mountain pine beetle outbreaks. *Proceedings of the National Academy of Sciences* 112 (14): 4375–4380.
- Harvey, B.J., D.C. Donato, W.H. Romme, and M.G. Turner. 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane douglas-fir forests. *Ecology* 94 (11): 2475–2486.
- Haslem, A., L.T. Kelly, D.G. Nimmo, S.J. Watson, S.A. Kenny, R.S. Taylor, S.C. Avitabile, K.E. Callister, L.M. Spence-Bailey, M.F. Clarke, et al. 2011. Habitat or fuel? implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* 48 (1): 247–256.
- Hicke, J.A., M.C. Johnson, J.L. Hayes, and H.K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management* 271: 81–90. <https://doi.org/10.1016/j.foreco.2012.02.005>.
- Jenkins, M.J., J.B. Runyon, C.J. Fettig, W.G. Page, and B.J. Bentz. 2013. Interactions among the mountain pine beetle, fires, and fuels. *Forest Science* 60 (3): 489–501. <https://doi.org/10.5849/forsci.13-017>.
- Jolly, W.M., R.A. Parsons, A.M. Hadlow, G.M. Cohn, S.S. McAllister, J.B. Popp, R.M. Hubbard, and J.F. Negron. 2012. Relationships between moisture,

- chemistry, and ignition of *pinus contorta* needles during the early stages of mountain pine beetle attack. *Forest Ecology and Management* 269: 52–59.
- Jolly, W.M., J. Hintz, R.L. Linn, R.C. Kropp, E.T. Conrad, R.A. Parsons, and J. Wintterkamp. 2016. Seasonal variations in red pine (*pinus resinosa*) and jack pine (*pinus banksiana*) foliar physio-chemistry and their potential influence on stand-scale wildland fire behavior. *Forest Ecology and Management* 373: 167–178. <https://doi.org/10.1016/j.foreco.2016.04.005>.
- Kozłowski, T.T., P.J. Kramer, and S.G. Pallardy. 1991. *The Physiological Ecology of Woody Plants*. Elsevier Science.
- Little, E.L., and L.A. Viereck. 1971. *Atlas of United States Trees: Conifers and important hardwoods*, vol. 1. Washington, D.C.: US Government Printing Office.
- Lutes, D.C. 2020. Fuelcalc 1.7. Technical report, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula, MT, USA.
- Lynch, H.J., R.A. Renkin, R.L. Crabtree, and P.R. Moorcroft. 2006. The influence of previous mountain pine beetle (*dendroctonus ponderosae*) activity on the 1988 yellowstone fires. *Ecosystems* 9: 1318–1327.
- Molina, J.R., F. Rodríguez y Silva, E. Mérida, and M. Ángel Herrera. 2014. Modeling available crown fuel for *pinus pinaster* ait. stands in the “cazorla, segura and las villas natural park” (spain). *Journal of Environmental Management* 144: 26–33. <https://doi.org/10.1016/j.jenvman.2014.05.003>.
- Nolan, R.H., O.F. Price, S.A. Samson, M.E. Jenkins, S. Rahmani, and M.M. Boer. 2022. Framework for assessing live fine fuel loads and biomass consumption during fire. *Forest Ecology and Management* 504: 119830.
- O’Brien, J., J. Hiers, J. Varner, C. Hoffman, M. Dickinson, S. Michaletz, E. Loudermilk, and B. Butler. 2018. Advances in mechanistic approaches to quantifying biophysical fire effects. *Current Forestry Reports* 4: 161–177.
- Ottmar, R.D. 2014. Wildland fire emissions, carbon, and climate: modeling fuel consumption. *Forest Ecology and Management* 317: 41–50.
- Page, W.G., M.J. Jenkins, and J.B. Runyon. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Canadian Journal of Forest Research* 42 (8): 1631–1647.
- Prichard, S., M. Kennedy, C. Wright, J. Cronan, and R. Ottmar. 2017. Predicting forest floor and woody fuel consumption from prescribed burns in southern and western pine ecosystems of the united states. *Forest Ecology and Management* 405: 328–338.
- R Core Team. 2021. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Reinhardt, E.D. 1997. First order fire effects model: Fofem 4.0, user’s guide. Technical report, Intermountain Forest and Range Experiment Station, Forest Service, US.
- Reinhardt, E., J. Scott, K. Gray, and R. Keane. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. *Canadian Journal of Forest Research* 36 (11): 2803–2814.
- Santoni, P., P. Bartoli, A. Simeoni, and J. Torero. 2014. Bulk and particle properties of pine needle fuel beds-influence on combustion. *International Journal of Wildland Fire* 23 (8): 1076–1086.
- Schoennagel, T., T.T. Veblen, J.F. Negron, and J.M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, colorado, usa. *PLoS ONE* 7 (1): e30002.
- Scott, J.H. 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. Technical Report 29, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula, MT, USA.
- Stenzel, J.E., K.J. Bartowitz, M.D. Hartman, J.A. Lutz, C.A. Kolden, A.M. Smith, B.E. Law, M.E. Swanson, A.J. Larson, W.J. Parton, et al. 2019. Fixing a snag in carbon emissions estimates from wildfires. *Global Change Biology* 25 (11): 3985–3994.
- Stevens, J.T., M.M. Kling, D.W. Schwilk, J.M. Varner, and J.M. Kane. 2020. Biogeography of fire regimes in western us conifer forests: a trait-based approach. *Global Ecology and Biogeography* 29 (5): 944–955.
- Stocks, B., M. Alexander, B. Wotton, C. Steffner, M. Flannigan, S. Taylor, N. Lavoie, J. Mason, G. Hartley, M. Maffey, et al. 2004. Crown fire behaviour in a northern jack pine black spruce forest. *Canadian Journal of Forest Research* 34 (8): 1548–1560.
- Taylor, S., B. Wotton, M. Alexander, and G. Dalrymple. 2004. Variation in wind and crown fire behaviour in a northern jack pine black spruce forest. *Canadian Journal of Forest Research* 34 (8): 1561–1576.
- Varner, J.M., S.M. Hood, D.P. Aubrey, K. Yedinak, J.K. Hiers, W.M. Jolly, T.M. Shearman, J.K. McDaniel, J.J. O’Brien, and E.M. Rowell. 2021. Tree crown injury from wildland fires: causes, measurement and ecological and physiological consequences. *New Phytologist* 231 (5): 1676–1685.
- Veal, C., M. Carmi, M. Fine, and O. Hoegh-Guldberg. 2010. Increasing the accuracy of surface area estimation using single wax dipping of coral fragments. *Coral Reefs* 29: 893–897.
- Wagner, C.V. 1977. Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research* 7 (1): 23–34.
- Wagner, C.V. 1993. Prediction of crown fire behavior in two stands of jack pine. *Canadian Journal of Forest Research* 23 (3): 442–449.
- Whight, S., and R. Bradstock. 1999. Indices of fire characteristics in Sandstone heath near Sydney, Australia. *International Journal of Wildland Fire* 9 (2): 145–153.

## Publisher’s Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.