RESEARCH ARTICLE

BIOMASS AND BURNING CHARACTERISTICS OF SUGAR PINE CONES

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ABSTRACT

We investigated the physical and burning characteristics of sugar pine (*Pinus lambertiana* Douglas) cones and their contribution to woody surface fuel loadings. Field sampling was conducted at the Yosemite Forest Dynamics Plot (YFDP), a 25.6 ha mapped study plot in Yosemite National Park, California, USA. We developed a classification system to describe sugar pine cones of different sizes and decay conditions, and examined differences among cone classes in biomass, bulk density, flame length, burning time, consumption, and relative contribution to surface fuel loads. Sugar pine cones comprised 601 kg ha^{-1} of surface fuels. Mature cones comprised 54 % of cone biomass, and aborted juvenile cones accounted for 44 %. Cone biomass, diameter, and bulk density differed among cone condition classes, as did burning characteristics (one-way ANOVA, $P < 0.001$ in all cases). Flame lengths ranged from 5 cm to 94 cm for juvenile cones, and 71 cm to 150 cm for mature cones. Our results showed that the developmental stage at which sugar pine cones become surface fuels determines their potential contribution to surface fire behavior in Sierra Nevada mixed-conifer forests. Sugar pine cones burn with greater flame lengths and flame times than the cones of other North American fire-tolerant pine species studied to date, indicating that cones augment the surface fire regime of sugar pine forests, and likely do so to a greater degree than do cones of other pine species.

Keywords: fuel loading, mixed-conifer, *Pinus lambertiana,* Sierra Nevada, surface fuel, Yosemite National Park

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INTRODUCTION

The composition, structure, and spatial heterogeneity of seasonally dry western North American mixed-conifer forests are largely determined by fire (Sugihara *et al*. 2006, Scholl and Taylor 2010, Larson and Churchill 2012). Land managers are increasingly seeking to restore active fire regimes in mixed-conifer forests following the period of fire exclusion in the twentieth century (e.g., Keane *et al.* 2006, Miller *et al.* 2012, van Wagtendonk *et al.* 2012), but reintroducing fire to landscapes in which it has been excluded requires understanding fire behavior and effects. In turn, sound fire management decisions require understanding of surface fuel properties and loads (van Wagtendonk *et al*. 1996, van Wagtendonk *et al*. 1998*a*, Stephens *et al*. 2004, Keifer *et al*. 2006, Hiers *et al*. 2009).

Surface fuel quantities and accumulation rates in the Sierra Nevada have long been recognized as high, with high forest productivity, low rates of decay in the absence of fire, and the long period of fire exclusion in the twentieth century playing a role (Keifer *et al.* 2006 and references therein). Components of the surface fuel complex in the Sierra Nevada have unique burning characteristics (e.g., Agee *et al.* 1978), and differences in the relative energy content, fuel bed properties, and physical characteristics among different fuel types has long been recognized (van Wagtendonk *et al.* 1996; 1998*a, b*). Additionally, species-specific differences in surface litter and duff fuel bed properties such as bulk density (Stephens *et al.* 2004) and conifer needle flammability (Fonda *et al.* 1998, Fonda 2001) are well known.

Pine cones are a unique woody surface fuel and relatively little is known about their contribution to surface fire behavior, although recent studies have begun to address this issue. Van Wagtendonk *et al.* (1998*b*) were apparently the first to recognize cones as a distinct fuel component with their study of heat contents of 19 Sierra Nevada conifer species. More recently, Fonda and Varner (2004) examined the burning characteristics of cones of eight North American pine species, finding that pine cones can flame for up to 15 minutes, smolder for over 80 minutes, and develop maximum flame lengths in excess of 80 cm.

Pine cones contribute to surface fire behavior and effects, possibly including mortality of large-diameter trees. The combustible nature and relatively large maximum flame lengths of cones of some tree species, particularly the larger cones that fall to the ground intact (Figure 1), suggest that they could be locally important to surface fire behavior (Mitchell *et al.* 2009) and may possibly spread fire to ladder fuels (Fonda and Varner 2004). Smoldering cones are thought to be vectors for duff ignition, especially when mixed with forest floor litter (Mitchell *et al*. 2009, Hood 2010). Pine cone combustion may be indirectly linked to fire mortality of large-diameter trees (Hood 2010), insomuch as it may act as an ignition vector for litter and duff around tree boles (Varner *et al.* 2009, Nesmith *et al.* 2010).

The cones of sugar pine (*Pinus lambertiana* Douglas) are among the largest of all conifers, reaching 56 cm long (Kinloch and Scheuner 1990). Sugar pine cones are a locally abundant component of the surface fuel bed in middle elevation mixed-conifer forests of the Sierra Nevada (Figure 1). Sugar pine cones were investigated by van Wagtendonk *et al.* (1998*b*) and reported to have an ash free heat content of 21.82 MJ kg^{-1}. The burning characteristics of sugar pine cones (*sensu* Fonda and Varner 2004), however, are unknown. Despite their large size and local abundance, sugar pine cones remain one of the least-understood components of the surface fuel complex in Sierra Nevada mixed-conifer forests.

Sugar pine cone production takes two years and cone crops can sustain high rates of spontaneous abortion during the first year of development (Kinloch and Scheuner 1990). The sugar pine cone beetle (*Conophthorus lambertianae*) can cause very high (up to

Figure 1. A site in Yosemite National Park, California, USA, illustrates the potential contribution of sugar pine cones to the surface fuel bed in Sierra Nevada mixed-conifer forests (26 June 2012 composite photo stitched from three originals by A.J. Larson). This site experienced surface fire on 2 September 2009 during the Big Meadow Fire.

93 %) rates of cone loss (Bedard 1968, Kinloch and Scheuner 1990), suggesting that aborted juvenile cones could be an episodically important component of litter fall. Additionally, Douglas-squirrel (*Tamiasciurus douglasii* Bachman) activity can result in high levels of cone litter fall, and squirrel activity also visibly changes the morphology and, presumably, burning characteristics of cones (Tevis 1953). Sugar pines growing in pure stands deposited cones into the surface litter at a rate of 336 kg ha^{-1} yr^{-1}, but with high levels of interannual variability (290 kg ha^{-1} yr^{-1}; van Wagtendonk and Moore 2010). Average deposition rate for sugar pine cones in a mixed-conifer stand was 435 kg ha^{-1} yr^{-1}, accounting for up to 10 % of total annual litter fall (Stohlgren 1988). These studies only sampled recently fallen cones, however, and the relative contribution of fresh aborted first-year cones,

fresh mature cones, and older partially decomposed cones (*sensu* Varner *et al.* 2009) to surface fuel loads is unknown.

The physical attributes, abundance, and burning characteristics of sugar pine cones on the forest floor constitute an important knowledge gap in the basic fire ecology of western North American mixed-conifer forests. Our field observations caused us to predict that the abundance and biomass of aborted juvenile and partially decomposed cones on the forest floor would be substantial. Further, we hypothesized that the burning characteristics of partially decomposed, fresh aborted, and fresh mature cones would differ because of the striking changes in cone morphology that occur during maturation and decomposition. We followed these predictions with three research questions:

1) What differences exist among mean cone biomass, diameter, and bulk density based on cone condition class (a combination of developmental stage and decomposition status)?
2) How abundant are sugar pine cones of different condition classes on the floor of an old-growth mixed-conifer forest?
3) How do burning characteristics differ among cone condition classes and relate to cone physical characteristics?

To the extent that sugar pine cones constitute a unique fuel type, with burning characteristics that vary with cone developmental stage or decomposition status, their presence could contribute to fire behavior different from that predicted with our current fuel models.

METHODS

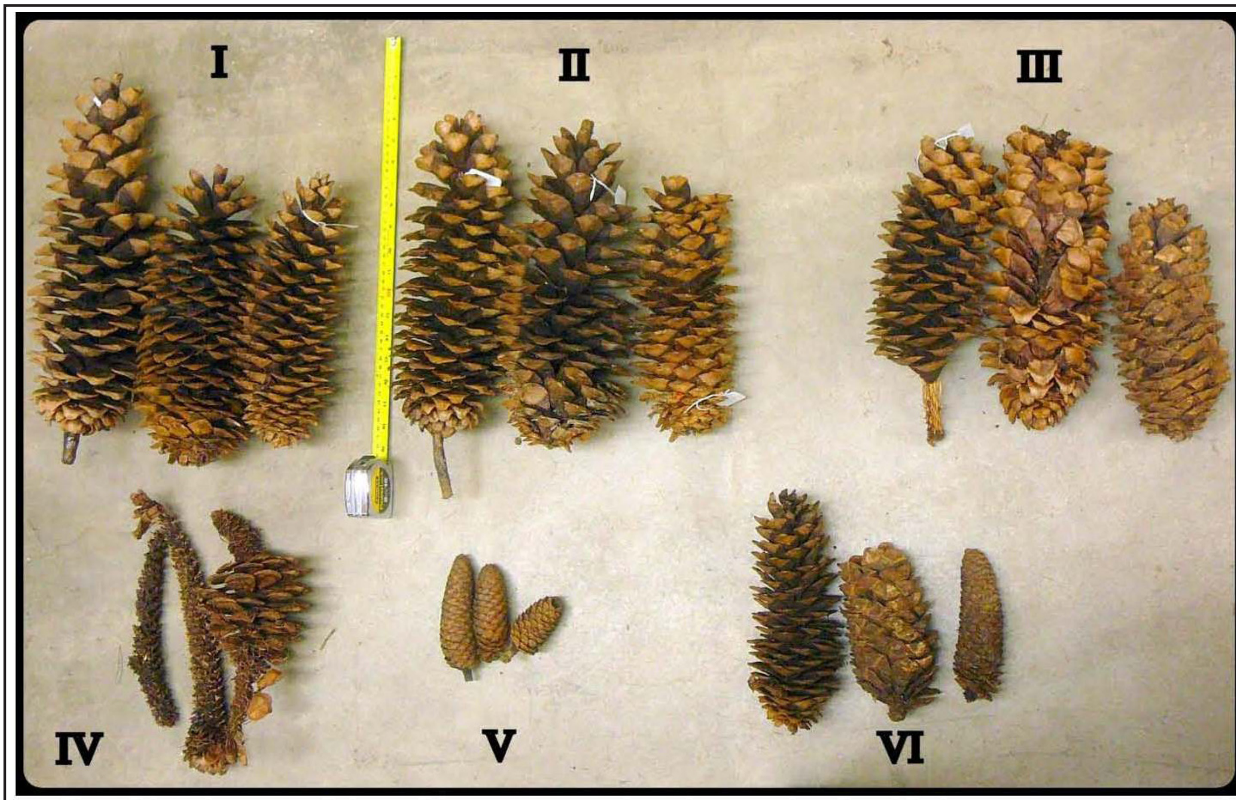
Study Site and Field Sampling

The study site was the Yosemite Forest Dynamics Plot (YFDP), a 25.6 ha study area situated at 1860 m elevation near Crane Flat in Yosemite National Park, California, USA (Lutz *et al*. 2012). Trees ≥1 cm dbh had been tagged, mapped, and measured using permanent monuments, providing a foundation of data for related studies. Fire has been excluded from the study site for at least 80 years, allowing deep litter and duff layers to accumulate (Lutz *et al*. 2012).

The YFDP is located in the white fir mixed-conifer forests of Yosemite National Park (Fites-Kaufman *et al.* 2007) and is typical of the white fir-sugar pine forest alliance in the Sierra Nevada (Keeler-Wolf *et al.* 2012). White fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) is the most abundant tree species (376 trees ha^{-1} ≥10 cm dbh), with sugar pine second in abundance (85 trees ha^{-1}). White fir and sugar pine have equivalent basal area (29 m^2 ha^{-1} each) and together comprise 90 % of the basal area of the forest, with sugar pine constituting a greater proportion (69 %) of trees ≥100 cm dbh (Lutz *et al.* 2012). Sugar pine is a long-lived, fire-tolerant species that regenerates readily following fire, but also can establish in moderate shade. The current forest densities at the YFDP are assumed to be much higher than those prevailing prior to the period of fire exclusion (Scholl and Taylor 2010), with fire exclusion and the introduced pathogen white pine blister rust (*Cronartium ribicola*) assumed to be affecting current levels of regeneration, but having little effect on cone producing trees (van Mantgem *et al.* 2004). Along with white fir and sugar pine, canopy dominants include, in decreasing abundance, incense cedar (*Calocedrus decurrens* [Torr]) Florin), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), red fir (*Abies magnifica* A. Murray bis) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). California black oak (*Quercus kelloggii* Newberry) and Pacific dogwood (*Cornus nuttallii* Audubon ex Torr. & A. Gray) are abundant in the lower canopy on xeric and mesic sites, respectively.

We developed a cone condition classification system based on cone size and condition attributes that could be easily estimated in the field. Categories were determined using a combination of cone developmental stage, length, and degree of decomposition (Figure 2). Cones were assigned to a condition class by simultaneously assessing size, developmental stage, and level of decomposition or animal damage. Length thresholds (Figure 2), which do not include the pedicel, were applied at a tolerance of ±20 %. The critical difference between cone classes I and II was degree of weathering and presence of resin on the scales of Class I cones, which we expected would lead to different burning characteristics (Figure 2).

To inventory cones by condition class, we placed ninety 9 m^2 quadrats at randomly located points throughout the YFDP during late June 2011. Within each sample quadrat, we recorded the number of cones by condition class. We counted cones only when a portion of their volume protruded above surface litter and when >50 % of their volume lay inside the quadrat. To measure cone physical and burn-



Condition class	Diagnostic attributes
I	Scales reflexed and rigid; resinous; no weathering; >25 cm long.
II	Scales reflexed; partially weathered; 70 % to 100 % scales attached; >25 cm long.
III	Scales flexible; partially decomposed; 10 % to 70 % scales attached; >25 cm long.
IV	Scales removed by rodents; <30 % of scales attached; >25 cm long.
V	Scales imbricate; 5 cm to 15 cm long.
VI	Scales imbricate to reflexed; 15 cm to 25 cm long.

Figure 2. Sugar pine cone classification system including diagnostic attributes and three example cones from each condition class. The tape measure is extended to 50 cm.

ing characteristics, we collected five cones in each condition class from six randomly located points across the YFDP.

Laboratory Experiments and Statistical Analysis

We measured cone biomass and experimentally determined their burning characteristics at the Missoula Fire Sciences Laboratory, Missoula, Montana, USA, closely adhering to the methods of Fonda and Varner (2004). We measured maximum cone length, excluding pedicel, and diameter at the widest point of the cones. We dried the cones for at least 72 hours at 100 °C, and weighed them to obtain dry biomass. We used length and diameter measurements to estimate cone volume using the equation for the volume of a prolate spheroid,

$$V = \frac{4}{3}\pi\left(\frac{d}{2}\right)^2 L, \qquad (1)$$

where V is cone volume, d is cone diameter at the widest point, and L is cone length along the central axis, excluding the pedicel. We then combined the estimate of cone volume with measured cone biomass to estimate the bulk density of individual cones.

We evaluated cone flammability, fire sustainability, and consumption (*sensu* Fonda and Varner 2004) using a brick surface burn table ventilated by a fume hood. We weighed each cone before placing it on three kerosene-soaked cotton strings cut to the length of the cone. The strings were laid parallel on a metal tray, spaced evenly relative to cone diameter. We measured the weight of the tray, kerosene-soaked strings, and cone before ignition. We ignited the kerosene-soaked strings with a propane torch and started two timers upon cone ignition. Following Fonda and Varner (2004), we stopped the first timer when flames disappeared. The second timer measured total burning time and ran until smoke or embers were no longer visible, whichever was later. Pilot observations indicated that some combustion continued for several hours after smoke and embers ceased to be visible, but the mass loss was minimal (1 % to 2 %) so we adhered to the burning time protocol of Fonda and Varner (2004).

The mass of the tray, cone debris, and unconsumed string after burning was used to calculate total mass loss (the unconsumed string was a small portion of total mass). We subtracted flaming time from total burning time to calculate smoldering time. Flame length (flame height) was ocularly estimated using a metal ruler (with major graduations in inches) placed behind the flaming combustion zone as a reference. Maximum flame lengths were recorded for each burn.

This study used a completely randomized design. We conducted one-way ANOVA and *post hoc* pairwise comparisons (Tukey's HSD) to test for differences in cone physical characteristics (oven dry mass, diameter, and bulk density) and of the burning characteristics (flaming time, smoldering time, burning time, flame length, percent mass loss, and mass loss rate) among the six cone condition classes. The interrelationships of cone bulk density and flame length, burning time, and percent mass loss were assessed with Spearman rank correlation.

RESULTS

Physical Characteristics

We measured physical characteristics of 177 cones (Table 1). One-way ANOVA revealed differences among cone classes for the biomass, diameter, and bulk density ($P < 0.001$ in all cases). *Post-hoc* analysis showed that the two most intact mature cone condition classes (I and II) did not differ significantly from each other (Table 1). Cone physical characteristics differed significantly between mature and aborted cone condition classes, however (Table 1). Bulk density in small, aborted cones (Class V) was approximately four times

Table 1. Mean dry biomass, length, diameter, and bulk density of sugar pine cones collected from the Yosemite Forest Dynamics Plot in 2011. Values that share a superscript within columns are not significantly different. Cone length was not statistically analyzed because it is a principal discriminating attribute in the cone classification system (Figure 2).

Cone condition class	*n*	Dry biomass (g)		Length (cm)		Diameter (cm)		Bulk density (g cm^{-3})	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
I	30	216.2[a]	12.8	34.1	6.3	12.8[a]	0.3	0.073[a]	0.002
II	33	195.3[a]	11.2	32.6	5.3	12.0[a]	0.3	0.080[ab]	0.003
III	30	88.4[b]	7.3	26.6	4.8	10.0	0.4	0.066[a]	0.005
IV	29	40.4[cd]	3.9	28.6	4.9	5.2[b]	0.4	0.120[b]	0.013
V	29	26.7[c]	1.9	9.1	2.3	3.9[b]	0.1	0.374	0.018
VI	26	64.1[bd]	2.9	19.4	3.7	7.1	0.7	0.181	0.019

higher than intact mature cones (classes I through III), reflecting the open structure of mature cones.

Abundance and Biomass

Cone density at the YFDP exceeded 10 000 cones ha^{-1}, and biomass exceeded 600 kg ha^{-1} (Table 2). Aborted juvenile cones (classes V and VI) were 44 % of cone biomass on the forest floor while mature cones (classes I, II, and III) accounted for another 54 % (Table 2). Squirrel-eaten cones comprised the remaining 2 % of cone biomass on the forest floor.

Table 2. Density (cones ha^{-1}) and biomass (kg ha^{-1}) of sugar pine cones for six condition classes at the Yosemite Forest Dynamics Plot in 2011.

Cone condition class	Cones	Biomass	
		Mean	SE
I	235	51	3
II	815	159	9
III	1 358	120	10
IV	296	12	1
V	7 099	190	13
VI	1 086	70	3
Total	10 889	601	40

Burning Characteristics

Significant differences among cone classes were apparent for all burning characteristics investigated (one-way ANOVA, $P < 0.001$ in all cases). Recently deposited mature cones (Class I) flamed significantly longer than all other cone classes, which did not differ from each other (Table 3). Smoldering time exhibited a strikingly different pattern compared to flaming time, however, with classes I through III all smoldering for *ca.* 2250 s; smoldering duration was 2 to 10 times shorter for juvenile and squirrel-eaten cones (Table 3). Total burning time did not differ significantly between intact, mature cone classes (classes I through III). Total burning time was significantly longer for mature cones (classes I through III) than for aborted and squirrel-eaten cones. Juvenile aborted cones (Class VI) had the highest variance of all cone condition classes for the burning characteristics flame length, percent fuel combusted, smoldering time, and burning time, but not flaming time.

Flame length, percent mass loss, and mean rate of mass loss depended on cone condition class (one-way ANOVA, $P < 0.001$ in all cases). Intact mature cones (classes I and II) burned vigorously in the laboratory. Mature cone classes I and II did not differ significantly from one another in terms of burning time,

Table 3. Burning characteristics of sugar pine cones of six different condition classes from the Yosemite Forest Dynamics Plot. Values that share a superscript (within columns) are not significantly different.

Cone condition class	*n*	Flaming (s)		Smoldering (s)		Total (s)	
		Mean	SE	Mean	SE	Mean	SE
I	15	383	57	2213[a]	201	2596[a]	207
II	14	238[a]	21	2317[a]	241	2554[a]	235
III	13	217[a]	41	2242[a]	316	2460[a]	303
IV	14	166[a]	18	269[bc]	61	435[bc]	66
V	15	113[a]	16	117[b]	25	230[b]	28
VI	15	160[a]	21	1140[c]	397	1300[c]	407
Cone condition class	***n***	**Flame length (cm)**		**Consumption (%)**		**Loss rate (mg s^{-1})**	
		Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
I	15	114[a]	5	95.3[a]	0.4	98[a]	11
II	14	111[a]	6	96.2[a]	0.4	89[a]	10
III	13	48[bc]	7	76.8[a]	6.7	28[b]	5
IV	14	29[bd]	4	33.0[b]	4.5	84[a]	17
V	15	17[d]	2	13.3[b]	2.1	34[b]	6
VI	15	28[cd]	7	34.1[b]	9.9	27[b]	4

flame length, or percent mass loss (Table 3, Figure 3), but aborted and squirrel-eaten cones differed significantly from the mature cones. Mean flame length for recently deposited mature cones was nearly 5 times that of aborted cones. Mass loss approached 100 % for recently dropped, mature cones, but combustion was significantly less for aborted and squirrel-eaten cones, with mass loss <34 % (Figure 3).

Spearman rank correlation analysis confirmed an inverse relationship between cone bulk density (Figure 3) and burning time ($\rho = -0.58$, $P < 0.001$), flame length ($\rho = -0.62$, $P < 0.001$), and percent mass loss ($\rho = -0.68$, $P < 0.001$).

DISCUSSION

The cone condition class model captured the variation of sugar pine cone physical characteristics. Cone length and diameter increase substantially during cone growth (Figure 2). Cone morphology also changes—small, immature cones have a closed structure of imbricate scales forming a dense shell, resulting in higher bulk density. During maturation, cone scales separate from one another as they reflex away from cone stems, resulting in higher cone volume and lower bulk density (Table 1). These changes in cone morphology alter cone surface area to volume ratio, an important determinant of fuel combustion (van Wagtendonk 2006) for which our cone bulk density measurements serve as a proxy. As a result, bulk density and length explain most of the variation in sugar pine cone structure.

The 601 kg ha^{-1} of sugar pine cone biomass found in this study is close to reported deposition rates of 336 kg ha^{-1} yr^{-1} in pure stands (van Wagtendonk and Moore 2010) and 435 kg ha^{-1} yr^{-1} in a mixed conifer stand (Stohlgren 1988). Our one-time measurement integrates, but does not fully capture, interannual variation in cone deposition, which varied from 200 kg ha^{-1} yr^{-1} to 800 kg ha^{-1} yr^{-1} in a mixed-conifer forest in Sequoia National Park,

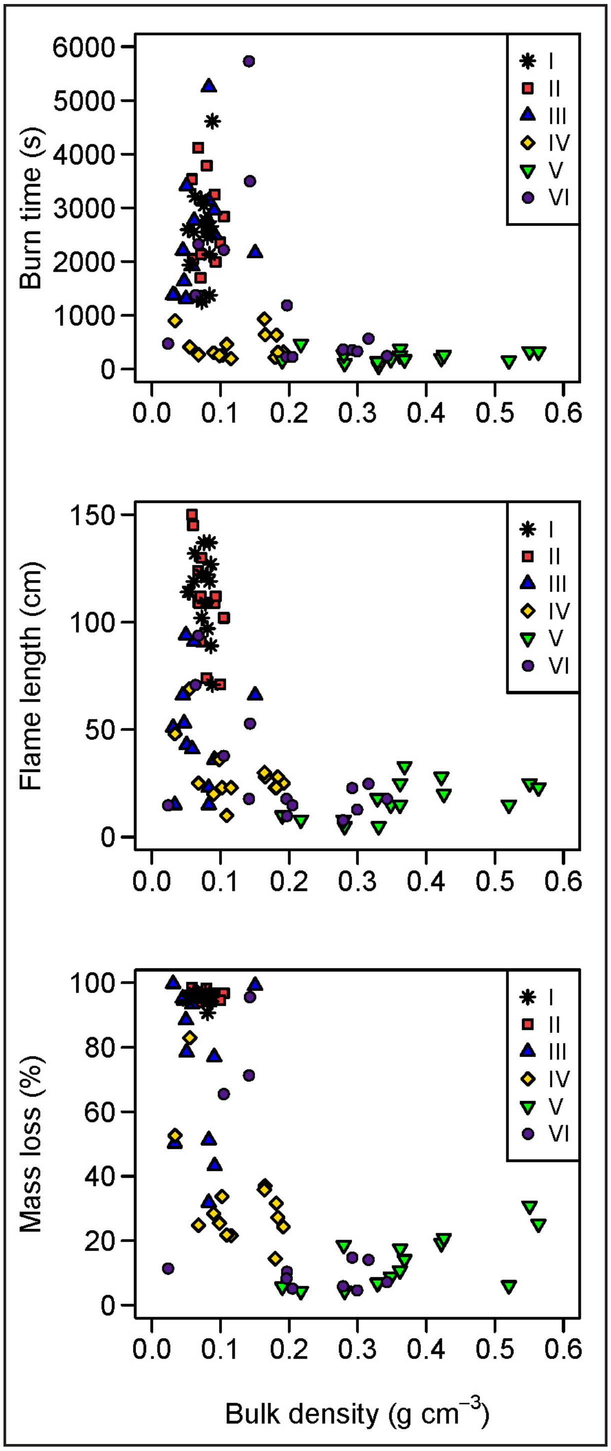


Figure 3. Relationships among cone bulk density and burning time, flame length, and percent mass loss for sugar pine cones collected from the Yosemite Forest Dynamics Plot in 2011.

California, USA (Stohlgren 1988). Given reported cone deposition rates (Stohlgren 1988, van Wagtendonk and Moore 2010), our estimates of total cone biomass stocks suggest that cones decay rapidly once on the forest floor. Based on our observations in the field, physical fragmentation appears to be an important process driving the apparently rapid decomposition of cones.

Sugar pine cones comprised 1.3 % of the total forest floor fuel (duff, litter, and woody fuels <10 cm in diameter) mass in the YFDP (Lutz *et al.* 2012). On sites with active frequent fire regimes, sugar pine cones may comprise a larger fraction of the surface fuel load that is more in line with their relative representation in annual litterfall inputs (up to about 10 %; Stohlgren 1988): frequent fires preclude development of a deep duff layer, which should increase the proportional representation of apparently rapidly decaying pine cones in the surface fuel bed in an active fire regime (Figure 1). In addition, fire may stimulate cone production. For example, thinning alone, and in combination with prescribed fire, increased ponderosa pine cone production (Peters and Sala 2008).

Burning characteristics of sugar pine cones depended on developmental stage and degree of decomposition, supporting our initial hypothesis. Changes in cone physical structure associated with maturation—increasing cone mass and decreasing cone bulk density—precipitate accompanying changes in how cones function as surface fuels. Bulk density shares an inverse relationship with flame length, burning time, and percent mass loss (Figure 3): as cones mature they become increasingly flammable, consistent with previous work on bulk density (Burgan and Rothermel 1984). The low bulk density and high flammability of mature cones likely results from the open structure of mature cones, which increases the surface area to volume ratio, allowing for more rapid heating and drying during combustion compared to that for aborted juvenile cones.

Only flaming time differed significantly between Class I and Class II cones; other burning characteristics did not differ between these cone classes. The difference of flaming time was substantial, however, with Class I cones flaming 1.5 times longer than Class II cones. Initial weathering and loss of resin likely explain the longer flaming time of Class I compared to Class II cones. Resin has an energy content of 35.3 MJ kg^{-1} (Agee 1993), much higher than the 21.8 MJ kg^{-1} of cone tissue (van Wagtendonk *et al.* 1998*b*). The resin-sealed serotinous cones of Monterey pine (*Pinus radiata* D. Don) and knobcone pine (*Pinus attenuata* Lemmon) flamed on average for 605 s and 740 s, respectively (Fonda and Varner 2004), despite their closed structure and presumably high bulk density, consistent with resin being an important determinant of pine cone flaming time.

Our laboratory measurements of cone burning characteristics implicate sugar pine cones as contributors to the surface fire regime created by litterfall in Sierra Nevada mixed-conifer forests (*sensu* Fonda and Varner 2004). Sugar pine cones burn with greater flame lengths and longer flaming times than cones of ponderosa pine and Jeffrey pine (*Pinus jeffreyi* Balf.), two other pine species that commonly co-occur with sugar pine. Maximum flame length and flame duration for mature sugar pine cones exceeded previously reported values for ponderosa pine and Jeffrey pine by *ca.* 58 cm and 120 s (Fonda and Varner 2004). The relatively greater potential contribution of sugar pine cones to surface fire behavior compared to cones of ponderosa pine and Jeffrey pine becomes more apparent when burning characteristics of cones are considered alongside those of conspecific foliage. Maximum flame lengths of ponderosa pine and Jeffrey pine needles were similar to maximum flame lengths of conspecific cones (Fonda *et al.* 1998). Maximum flame lengths of sugar pine cones, however, were twice that of sugar pine needles, in addition to cones having longer flaming time and smoldering time compared to needles (Fonda *et al.* 1998). Thus, it appears that sugar pine cones can be relatively greater contributors to surface fire behavior than cones of ponderosa pine or Jeffrey pine. By enhancing the flammability of the surface fuels, sugar pine cones may play an important role in the fuel dynamics of in mixed-conifer forests that lack a significant ponderosa pine or Jeffrey pine component, such as the YFDP.

Mature sugar pine cones, with flame lengths >1 m and flame duration of 3 min to 6 min, clearly have the potential to contribute to surface fire behavior and spread (Fonda and Varner 2004). Under some circumstances, flaming mature cones might also ignite shrubs and tree saplings. Burning cones also contribute to fire spread when they roll downhill beyond the fire perimeter, part of the reason for the practice of cup-trenching fire lines on steep terrain. Cones that smolder for long periods, such as the approximately 35 min smoldering times observed here for classes I through III, become potential ignition sources in the litter and duff layers with negative consequences for large tree survival (Hood 2010). Our laboratory measurements did not examine differences in burning characteristics due to different moisture contents or due to admixtures of cones and needles (*sensu* Taylor and Fonda 1990, Fonda and Varner 2004). A combination of laboratory and field experiments would provide insights into the role of sugar pine cones as a flame and heat vector for surface and ladder fuel ignition, or as a vector for duff ignition.

Although sugar pine cones do not necessarily drive surface fire dynamics throughout the forest, at small spatial scales they are locally abundant (Figure 1) and likely influence fire behavior and effects at such scales. Microtopography, down coarse woody debris, and the spatial arrangement of large diameter cone-producing trees cause the abundance of sugar pine cones on the forest floor to vary spatially. Accumulations of sugar pine cones that may increase the severity of surface fire locally could, for example, contribute to the small-scale (15 m to 20 m) spatial heterogeneity observed in these mixed-conifer forests (e.g., Larson and Churchill 2012, Lutz *et al.* 2012) through increased mortality of smaller trees. Fonda and Varner (2004) advanced a similar hypothesis, noting that cones of ponderosa pine and Jeffrey pine are frequently aggregated around tree bases and therefore may contribute to maintenance of a low-competition environment in the immediate tree neighborhood when they burn. Further study is warranted, given the vigorous burning characteristics of individual sugar pine cones in the laboratory, of spatial patterns of cone accumulation on the forest floor and the burning characteristics of aggregations of cones.

Conclusion

We discovered that sugar pine cones burn with greater flame lengths and flaming times than the cones of other North American resister pines (*sensu* Agee 1993) studied to date. Sugar pine cone flaming times were only exceeded by the resin-coated serotinous cones of knobcone pine and Monterey pine (Fonda and Varner 2004). Sugar pine cones burned with greater flame length, flaming time, smoldering time, and mass loss than sugar pine foliage (Fonda *et al.* 1998), indicating that cones augment surface fire behavior of sugar pine forests, and likely do so to a greater degree than do cones of other resister pine species (Fonda 2001, Fonda and Varner 2004). Finally, we found that flammability of sugar pine cones varied dramatically and was dependent on degree of cone maturation and post-deposition decomposition. Our results indicate that the developmental stage at which cones become surface fuels and the time since deposition exert strong control over the contribution of sugar pine cones to surface fire behavior.

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