R. W. Fonda[1], Biology Department, Western Washington University, Bellingham, Washington 98225-9160

and

J. M. Varner[2], School of Natural Resources and Environment, University of Florida, Gainesville, Florida 32611-8526

Burning Characteristics of Cones from Eight Pine Species

Abstract

This experiment studied burning characteristics of pine cones as a separate fuel component. Cones of fire resisters ponderosa pine, Jeffrey pine, longleaf pine, and south Florida slash pine, and cones of fire evaders Monterey pine, knobcone pine, sand pine, and pond pine were burned in a fire chamber. The experiment tested fire adaptive strategy (resisters vs. evaders), geographic region (western vs. eastern U.S.A.), and interactions between those two factors in a 2x2 factorial experiment. Jeffrey pine, longleaf pine, and south Florida slash pine supported the longest flames, smolder times, and burn times; they also lost >89% of cone mass. Monterey pine and knobcone pine sustained flames that lasted >10 min. Cones of Monterey pine, sand pine, and pond pine lost <50% cone mass. Resisters significantly exceeded evaders in all burning categories except flame time and mean rate of weight loss. Western pines significantly exceeded eastern pines in all burning categories except flame length and percent fuel combusted. Significant interactions between fire adaptive strategy and geographic region existed for all burning characteristics except mean rate of weight loss. The interaction was accounted for by cones of eastern evaders, which had the lowest mean values for most characteristics. Only recently have cones been regarded as a separate fuel component, yet they contribute more to fire regimes in their communities than previously thought. Fire models might be more accurate if they incorporate the contributions of cones to fire regimes. Furthermore, smoke emitted by smoldering cones is an important smoke management concern.

Introduction

The typical pine life cycle described in botany textbooks depicts cones opening and releasing seeds in the second growing season after cones are formed. Species with serotinous cones, however, are an exception. These cones commonly remain closed on the tree, impregnated with resin and sealed shut until heat from a stand-replacing fire opens them. The seeds are released to germinate on the postfire landscape, forming the next forest.

Depending on which strategy they use to adapt to repeated fires in their environment, pines are classified into two groups. Species that use a strategy of cone serotiny are evaders (Rowe 1983, Agee 1993, Fonda et al. 1998, Fonda 2001), and forests they dominate are termed fire-resilient (Fonda et al. 1998, Fonda 2001). These forests typically support high intensity crown fires and occasional surface fires, in which the entire stand is killed (Abrahamson 1984, Myers 1985, Vogl et al. 1988, Harms 1996, Schwilk and Ackerly 2001).

Continued dominance of pines depends heavily on the success of seed in the serotinous (closed) cones. Except for a few species that resprout, such as pond pine (*Pinus serotina*) (Fowells 1965), most parent trees do not survive the fire. The importance of cone serotiny as an evolutionary strategy for fire evaders is demonstrated by the significant negative correlation that exists between cone serotiny and self-pruning, leaf length, needle density, twig thickness, and minimum reproductive age (Schwilk and Ackerly 2001). Cone serotiny represents a co-evolution strategy with traits that typify fire evaders (Schwilk and Ackerly 2001). Because evaders maintain cones in the canopy for many years, only occasionally dropping them, litter layers in fire-resilient forests are sparsely populated with fallen cones (Figure 1). Often these cones are attached to twigs that have broken from parent trees.

The other group of pines comprises species that have developed different strategies to resist and survive fire, and their cones have few to no fire adaptive values (Schwilk and Ackerly 2001). In this article, we will refer to these pine cones with reflexed cone scales as open cones, to contrast with closed serotinous cones. Species for which cones are fire-neutral are resisters (Rowe 1983, Agee 1993, Fonda et al. 1998, Fonda 2001),

[1] Author to whom correspondence should be addressed. Current address: 1646 Sudden Valley, Bellingham, WA, 98229. E-mail:richfonda@comcast.net

[2] Current address: Department of Forestry and Watershed Management, Humboldt State University, Arcata, CA, 95521

Figure 1. Cones of pond pine, a fire evader, scattered in the stand.

Figure 2. Cones of Jeffrey pine, a fire resister, around tree bases.

and forests they dominate are termed fire-stable (Fonda et al. 1998, Fonda 2001). Typically, fire-stable forests support low intensity surface fires in highly flammable fine fuels (Sweeney 1967, Vogl 1967, Williamson and Black 1981, Arno and Peterson 1983, van Wagtendonk 1983, Myers 1985, Agee 1994). Continued survival of resister species depends on thick bark, fire-resistant bark, self-pruning, or thick needle clusters that protect meristems and aerial portions of the trees. Because resisters shed cones frequently, litter layers in fire-stable forests are heavily populated with downed cones (Figure 2).

Reviews of wildland fire ecology focus on fire regimes, behavior, severity, effects, history, and management (Agee 1993, Pyne et al. 1996). These books, which summarize the existing body of fire ecology knowledge, contain no references to cones as a fuel source. The fuel model is one of the main components of any fire behavior model, and several fuel model descriptions and classifications exist (Rothermel 1972, Albini 1976, Anderson 1982, Andrews and Chase 1989, Andrews and Bradshaw 1997). None of these identifies cones as a separate fuel component. Perhaps those who should be most aware of cones as a fuel source are involved with fire suppression, however, a typical publication for wildland firefighters (Teie 1994) has no text on how cones relate to fire suppression efforts. Cones are essentially the invisible fuel.

Cone fuels have been considered in fire science, albeit predominantly in passing. Brown et al. (1982) include cones in the litter layer for purposes of calculating fuel loadings. Cones, however, were not specifically isolated as a separate fuel component, and in the example given in Brown et al. (1982) the contribution of cones to the 0.09 kg m^{-2} fuel loading in the litter layer of a lodgepole pine (*P. contorta*) forest is not identified. Clements (1976) investigated firebrands (long-distance embers that cause spot fires) for fuels in the eastern United States. He studied cones of six pine species, including longleaf (*P. palustris*), slash (*P. elliottii*), and pond pine, measuring their terminal velocity and burn out times. He concluded that cones represented significant firebrand fuels, but placed no more emphasis on cones than any of the other 25 firebrand fuels (Clements 1976).

In a study of 19 Sierra Nevada conifers van Wagtendonk et al. (1998) identified cones as a fuel component separate from the common categories used in most fire behavior models. Mean heat contents of the 19 species varied narrowly from 21.22 MJ kg $^{-1}$ with ash to 21.64 MJ kg $^{-1}$ without ash, but differences among species were not significant. Because these heat contents were not substantially different from heat contents calculated for foliage, duff, and woody fuels, contributions of cones to fireline intensity should be considered in fuel calculations for wildland fires. The values for Sierra Nevada fuel components were higher than standard values used in fuel models to predict fire behavior, which could predict lower fireline intensities than actually encountered. Cone fuels contributed to these overall values. To our knowledge, van Wagtendonk et al. (1998) is the only reference that recognizes cones as a separate fuel component.

The burning characteristics of needles from eight species of pines were investigated recently to examine aspects of flammability, and to compare fire resisters with fire evaders and western pines with eastern pines (Fonda 2001). Differences existed among the eight species, between resisters and evaders, and between western and eastern pines. Significant interactions existed between fire adaptive strategy and geographic region for all burning characteristics except mean rate of weight loss. The interaction was accounted for primarily by differences between western evaders, which had high values for most burning characteristics, and eastern evaders, which had some of the lowest values. In this study, we examined pond pine and all but jack pine (*P. banksiana*) of the eight species studied by Fonda (2001) to determine how their cones contribute to the same aspects of flammability examined previously for pine needles.

The eight pines studied here (Table 1) were an ideal group to investigate the relationship between flammability of cones and fire adaptive strategies in fire-stable and fire-resilient communities. The research was designed to compare 1) differences among the eight pine species, 2) four resisters with four evaders, 3) four western pines with four eastern pines, 4) two western resisters with two eastern resisters, 5) and two western evaders with two eastern evaders, and to analyze the interaction between fire adaptive strategy and geographic region.

Methods

Experimental Design

We used the same basic method described in Fonda et al. (1998) and Fonda (2001), burning 10 cones of each species for a total of 80 burns. The research was a 2x2 factorial experiment in a completely randomized design (CRD) ANOVA, with the significance level set at P=0.05 before the research began. This design allowed us to designate species as a treatment effect, and to test for significant differences according to a basic CRD analysis. The two main factors (A: fire adaptive strategy and B: geographic region) combined to contribute four treatments: western resisters, eastern resisters, western evaders, and eastern evaders. These combinations, the main factors, and the interactions between the main factors were tested for significant differences for each burning characteristic by standard factorial analysis (Zar 1999). Significant differences among more than two treatments for each burning characteristic were judged by a Newman-Keuls multiple range

TABLE 1. Species sampled, fire adaptive strategy, and collection sites. Resister (R) or evader (E) designations are based on information from Rowe (1983) and Agee (1993).

Common name	Latin name	Strategy	Collection site	Principal distribution
Jeffrey pine	*P. jeffreyi*	R	Tahoe Basin, CA	Sierra Nevada, Basin and Range forests
Ponderosa pine	*P. ponderosa*	R	Kyburz, CA	Sierra Nevada, Cascade, Rocky Mountain forests
Longleaf pine	*P. palustris*	R	Ocala, FL	Atlantic, Gulf coastal plain forests
South Florida slash pine	*P. elliottii* var. *densa*	R	Lake Placid, FL	South Florida sandhill, flatwood stands
Knobcone pine	*P. attenuata*	E	Gold Run, CA	Central California, southern Oregon small stands
Monterey pine	*P. radiata*	E	Point Lobos, CA	Monterey Peninsula forests
Pond pine	*P. serotina*	E	Ocala, FL	Southeastern pocosins, wettest flatwood forests
Ocala sand pine	*P. clausa* var. *clausa*	E	Ocala, FL	Central Florida scrub forests

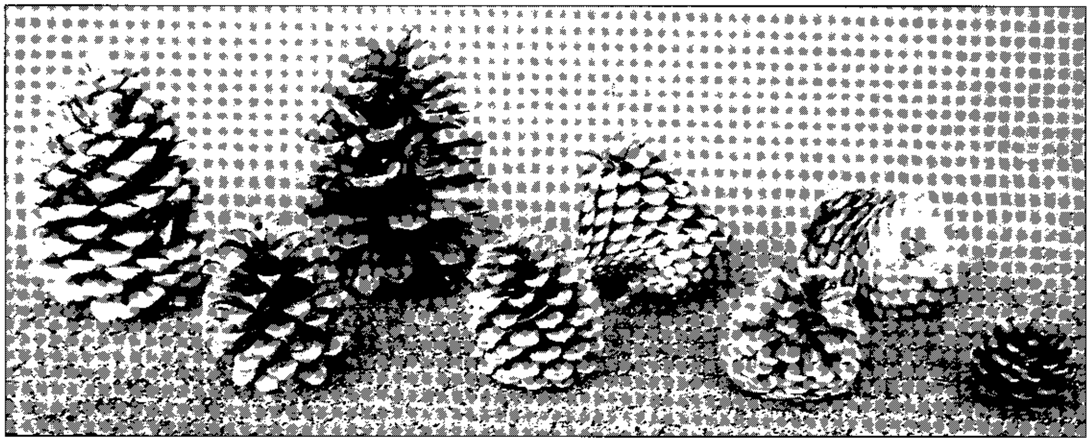

Figure 3. Cones of species used in this study. Front row, from left: ponderosa pine, south Florida slash pine, pond pine, sand pine. Back row, from left: Jeffrey pine, longleaf pine, Monterey pine, knobcone pine.

test (MRT). Data for percent fuel combustion were transformed by arcsin before analysis.

Field Collections

Cones from the litter layer were collected in August-October 2002 at several locations from sites on which only the targeted pine species grew (Table 1). Only cones that fell before summer 2002, and that showed no signs of decomposition, were collected. At least 15 cones were collected from each location and taken to Western Washington University, from which 10 were randomly chosen to be burned. We did not knowingly collect more than one pine cone from a given parent tree. The cones of each species were allowed to air dry, then oven dried for at least 72 hr at 100°C. Cones were removed from the oven, allowed ~20 min for weight to stabilize, then weighed. Mean fuel moisture at the time of burning ranged from 0.3% (Monterey pine) to 2.3% (ponderosa pine). Equilibrium fuel moisture during fire weather is on the order of 1-3% (Agee 1993), and we elected to burn all cones at approximately those values.

Burning Characteristics

We used a fire chamber to study burning characteristics of cones from these eight pine species (Figure 3) as indicators of flammability for this fuel component. Flammability has four components: ignitability, combustibility (intensity) and consummability of the fuel, and sustainability of the fire (Martin et al. 1994). This work relates to intensity (flame length), sustainability (flame time, smolder time, and burn time), and consummability (percent fuel combustion and mean rate of weight loss), as defined by Fonda et al. (1998) and Fonda (2001).

The fire chamber was 1 m^2 x 3 m tall, with a four-story exhaust chimney. Excessive draw from the chimney over the fire bed was prevented by a series of baffles in the chimney, and air movement was controlled by a fan in the chimney. Mean air velocity over the fuel bed was 9.9 cm sec^{-1} (Fonda et al. 1998, Fonda 2001).

Each cone was placed on the floor of the fire chamber on three 15-cm xylene-soaked strings. Strings were ignited, and two timers were started when fuels first ignited. Maximum flame length was compared against a 2-m rule on the rear wall of the fire chamber. This 5-cm wide steel rule, with prominent 1-cm markings, was machined specifically for this fire chamber. Distance between the flames and the steel rule was ~30 cm. After flame length was recorded, room lights were turned off for judging flame and burn times. We used a mirror to observe flames, embers, and smoke on the back side of the cones.

The first timer was stopped when all flames were extinguished, the second when the last ember was extinguished or when smoke no longer was emitted, whichever came last. The first timer measured flame time, the second measured burn time, and the difference between the two was smolder (ember) time. For cones of sand pine and pond pine, which smoked during the smoldering period, we used a flashlight beam to highlight the smoke against the mirror. In cases for which we were unsure if smoke was no longer being emitted, a third timer was started at the time we suspected smoldering had ended while we continued to watch the cone for at least 60 sec to be certain. This extra time was subtracted from the second timer once we stopped the two timers.

Unburned string was removed, and unconsumed ashes were weighed. Percent fuel combusted was calculated by dividing consumed weight by initial weight. Mean rate of weight loss was calculated as mg lost over burn time.

Because cone weights varied widely across the eight species, all data were analyzed to identify burning characteristics that correlated significantly with cone weight.

In nature, cones are embedded in the needle layer on a forest floor. We wanted to know how burning characteristics would differ if the cones were ignited by the needle litter, rather than by string. Means ± SE were calculated for cone weights for each species, based on the 80 cones we burned individually. One unburned cone of each species within ±2 SE of the mean (i.e., not significantly different from the mean weight) was selected to be burned on 15 g of ponderosa pine needles (i.e., the fuel source was constant). These cones and needles were oven-dried at 100°C for 72 hr, then burned according to the same protocol as previously. Values for each burning characteristic for the cones burned with needles were compared to mean values of the same burning characteristics derived from individual cones in a paired t-test, wherein each species was a pairing factor.

Results

Burning Behavior

Among the resisters, longleaf pine and Jeffrey pine cones burned nearly completely to white ash. The cones glowed red as soon as flames began, and white ash appeared well before flames were extinguished. Longleaf pine was the only species for which we heard an audible whooshing sound as the cones caught fire. South Florida slash pine cones also glowed red with flames, and emitted dense smoke when flames were extinguished. These cones burned nearly as completely as Jeffrey pine and longleaf pine, but some blackened cone scales remained. Ponderosa pine cones never created white ash; all ended the burn period with heavily blackened cones.

Serotinous cones burned incompletely, and finished the burn period with heavily charred cone scales. All closed cones in this study had dense whorls of thick cone scales at their bases (Figure 3). All four species emitted flames from the basal whorl, but none of the scales was consumed. Only the distal, slightly open, scales glowed red and were consumed by flames and smoldering. Knobcone and Monterey pine cones smoldered with abundant embers and little smoke, in contrast to sand and pond pine cones for which flames and embers were extinguished simultaneously. The smolder times for these cones were judged by smoke emissions.

Burning Characteristics of Individual Species

Mean maximum flame length was significantly greater for longleaf pine than all other species, and all test burns exceeded 80 cm. Jeffrey pine had significantly longer mean maximum flame lengths than the other six species (Table 2), but only one cone supported flames as long as 80 cm. Mean maximum flame length did not differ significantly between south Florida slash pine and ponderosa pine, between Monterey pine and knobcone pine, and between sand pine and pond pine. Sand pine and pond pine had the shortest flames.

TABLE 2. Means of cone weight and burning characteristics from 10 test burns for each pine species. Values in a row with identical letters are not significantly different.

	Jeffrey	Ponderosa	Longleaf	SF slash	Knobcone	Monterey	Sand	Pond
Maximum flame length (cm)	69.3	57.5^{a}	87.1	57.6^{a}	49.3^{b}	50.1^{b}	44.4^{c}	42.7^{c}
Flame time (sec)	262^{b}	250^{b}	208^{b}	207^{b}	740^{a}	605^{a}	207^{b}	328^{b}
Smolder time (sec)	4412	864^{b}	2958^{a}	2388^{a}	1262^{b}	1652^{b}	178^{c}	188^{c}
Burn time (sec)	4674	1114	3166	2595^{a}	2002^{a}	2257^{a}	385^{b}	516^{b}
Fuel combusted (%)	89.0^{a}	78.9	93.8^{a}	88.8^{a}	68.0	44.0^{b}	49.3^{b}	43.6^{b}
Weight loss (mg/sec)	19.1^{b}	24.9^{ab}	17.1^{b}	7.9	28.8^{a}	18.8^{b}	13.3	18.0^{b}
Cone weight (g)	96.6^{a}	24.2^{b}	56.1	22.2^{b}	70.0	88.1^{a}	10.3	19.8^{b}

Mean flame times for Monterey pine and knobcone pine were not significantly different, and both species flamed significantly longer than all other species (Table 2). There were no significant differences among the remaining six species. Maximum/minimum flame times were 1094/533 sec for knobcone pine and 935/339 sec for Monterey pine. The next two longest flame times among the other six species were 910 and 504 sec (Jeffrey pine). Every species had at least one cone that flamed for ≥300 sec, and 40 of the 80 burned cones flamed for ≥300 sec.

Smolder times are the noteworthy burning characteristic for these pine species. Jeffrey pine cones smoldered significantly longer than all other species (Table 2). Four Jeffrey pine cones smoldered for >5000 sec. Longleaf pine and south Florida slash pine did not differ significantly, nor did Monterey pine, knobcone pine, and ponderosa pine. Of the 20 cones burned for longleaf pine and south Florida slash pine, 11 smoldered for longer than 2500 sec. Of the 30 cones burned for Monterey, knobcone, and ponderosa pine, three exceeded 2500 sec. Pond pine and sand pine were not significantly different, and had the shortest smolder times of the eight species.

Mean burn times followed the same order as smolder times, although more differences were significant for this burning characteristic (Table 2). Jeffrey pine and longleaf pine ranked first and second, and both were significantly longer than the other species. Two Jeffrey pine cones had total burn times >6000 sec. Maximum burn time for longleaf pine was 3755 sec. Differences among south Florida slash pine, Monterey pine, and knobcone pine were not significant. As with smolder time, sand pine and pond pine were not significantly different, and had significantly shorter burn times than the other species. Maximum burn times for these species were <650 sec.

Mean percent fuel combusted did not differ significantly among longleaf pine, Jeffrey pine, and south Florida slash pine, for which at least 88% of the fuel was consumed. (Table 2). These species were significantly greater than any others. Ponderosa pine cones lost nearly 80% of their mass. Knobcone pine had the highest percent combustion of the closed cone pines, but significantly lower than ponderosa pine. Percent combustion among sand pine, Monterey pine, and pond pine did not differ significantly; all were <50% combusted.

Mean rate of weight loss provides little information on which to separate the species (Table 2). South Florida slash pine had a significantly lower rate than other species, and sand pine was next lowest. The others were mostly not significantly different, and the overlap between knobcone pine and ponderosa pine indicates that a gradient of rates existed among these cones. All lost weight at values between 17 and 29 mg sec^{-1}.

Mean cone weights for Jeffrey pine and Monterey pine were not significantly different from each other, and they were significantly heavier than the other species (Table 2). Knobcone pine and longleaf pine were each significantly different from all others, and significantly heavier than the remaining four species. Mean weights of these above four species all exceeded 50 g. Mean weights of the remaining four species were <25 g. Ponderosa pine, south Florida slash pine, and pond pine did not differ significantly. Sand pine had significantly lighter cones than any other species. Cone weights correlated significantly with three burning characteristics. Heavier cones had longer flame lengths, smolder times, and burn times. No other characteristics correlated significantly with cone weights.

Values in Table 2 are based on individual cones burning on the floor of the burn chamber. For cones burned with pine needles as the ignition source, smolder times were significantly longer by 1302 sec, burn times were significantly longer by 1338 sec, and percent combusted was significantly greater by 8.3%. Mean rate of weight loss was significantly lower by 9.3 mg sec^{-1}. The most important effect for cones burned with pine needles was longer smolder times, which led to longer burn times and greater fuel consumption. The greater heat created by the pine needle bed involved more of the core of the cone in combustion.

Treatments Combining Fire Adaptive Strategy and Geographic Region

Flame length is a measure of fire intensity. Eastern resisters had significantly longer flames than all other combinations, followed by western resisters (Table 3); both groups exceeded 60 cm. Flame lengths for western evaders and eastern evaders were not significantly different; both groups were <50 cm.

For measures of fire sustainability (flame, smolder, and total burn time), western evaders

TABLE 3. Means of cone weight and burning characteristics from 20 test burns per group to compare factors. Values in a row with identical letters are not significantly different.

	Western resisters	Eastern resisters	Western evaders	Eastern evaders
Maximum flame length (cm)	63.4	72.4	49.7^{a}	43.6^{a}
Flame time (sec)	256^{a}	207^{a}	672	268^{a}
Smolder time (sec)	2638^{a}	2673^{a}	1457	183
Burn time (sec)	2894^{a}	2880^{a}	2129	451
Fuel combusted (%)	91.3	84.0	56.1	46.4
Weight loss (mg/sec)	22.0^{a}	12.5^{b}	23.8^{a}	15.6^{b}
Cone weight (g)	60.4	39.2	79.1	15.0

supported significantly longer flame times than all other combinations, among which there were no significant differences (Table 3). Western resisters and eastern resisters had significantly longer smolder times and burn times than other groups. Eastern evaders had the shortest smolder and burn times (Table 3). Western evaders were significantly longer, by a considerable difference, in both categories than eastern evaders.

For measures of consummability, percent fuel combusted differed significantly among all groups (Table 3). Western resisters lost over 90% of cone mass, followed by eastern resisters. Western evaders lost >50% of cone mass, whereas eastern evaders lost <50% of cone mass. Mean rate of weight loss did not differ significantly between western resisters and western evaders, nor between eastern resisters and eastern evaders (Table 3). Western resisters and western evaders had significantly higher rates of weight loss than eastern resisters and eastern evaders.

Mean cone weights differed significantly across all groups (Table 3). Western evaders had the heaviest cones, followed by western resisters and eastern resisters. The lightest cones in the experiment were eastern evaders.

Main Effects of Fire Adaptive Strategy and Geographic Region

For the main effects of fire adaptive strategy, resisters had significantly greater flame lengths, smolder time, burn time, and percent fuel combusted (Table 4). Evaders had significantly longer flame times. The differences between resisters and evaders for mean rate of weight loss and cone weight were not significant. Of the top four species for flame length, smolder time, burn time, and percent fuel combusted at least three were resisters, whereas the three top species for flame time were evaders (Table 2). Except for flame time, resisters had higher values for characteristics relating to intensity, sustainability, and consummability.

For the main effects of geographic region, western species had significantly larger values for flame time, smolder time, burn time, mean rate of weight loss, and cone weight (Table 5). The differences between western and eastern

TABLE 4. Means of cone weight and burning characteristics from 40 test burns per group to compare the main effects of fire adaptive strategy. Values in a row with identical letters are not significantly different.

	Resisters	Evaders
Maximum flame length (cm)	67.9	46.6
Flame time (sec)	232	470
Smolder time (sec)	2656	820
Burn time (sec)	2888	1290
Fuel combusted (%)	87.6	51.3
Weight loss (mg/sec)	17.2^{a}	19.7^{a}
Cone weight (g)	49.8^{a}	47.0^{a}

TABLE 5. Means of cone weight and burning characteristics from 40 test burns per group to compare the main effects of geographic region. Values in a row with identical letters are not significantly different.

	Western	Eastern
Maximum flame length (cm)	55.6^{a}	58.0^{a}
Flame time (sec)	464	238
Smolder time (sec)	2048	1428
Burn time (sec)	2512	1666
Fuel combusted (%)	70.0^{a}	68.8^{a}
Weight loss (mg/sec)	22.9	14.1
Cone weight (g)	69.7	27.1

pines for maximum flame length and percent fuel combusted were not significant. Western species had significantly higher values for all characteristics relating to intensity, sustainability, and consummability.

Factor Interaction

Significant interactions between fire adaptive strategy and geographic region existed for all burning characteristics except mean rate of weight loss (Figure 4). The midpoints on the lines connecting

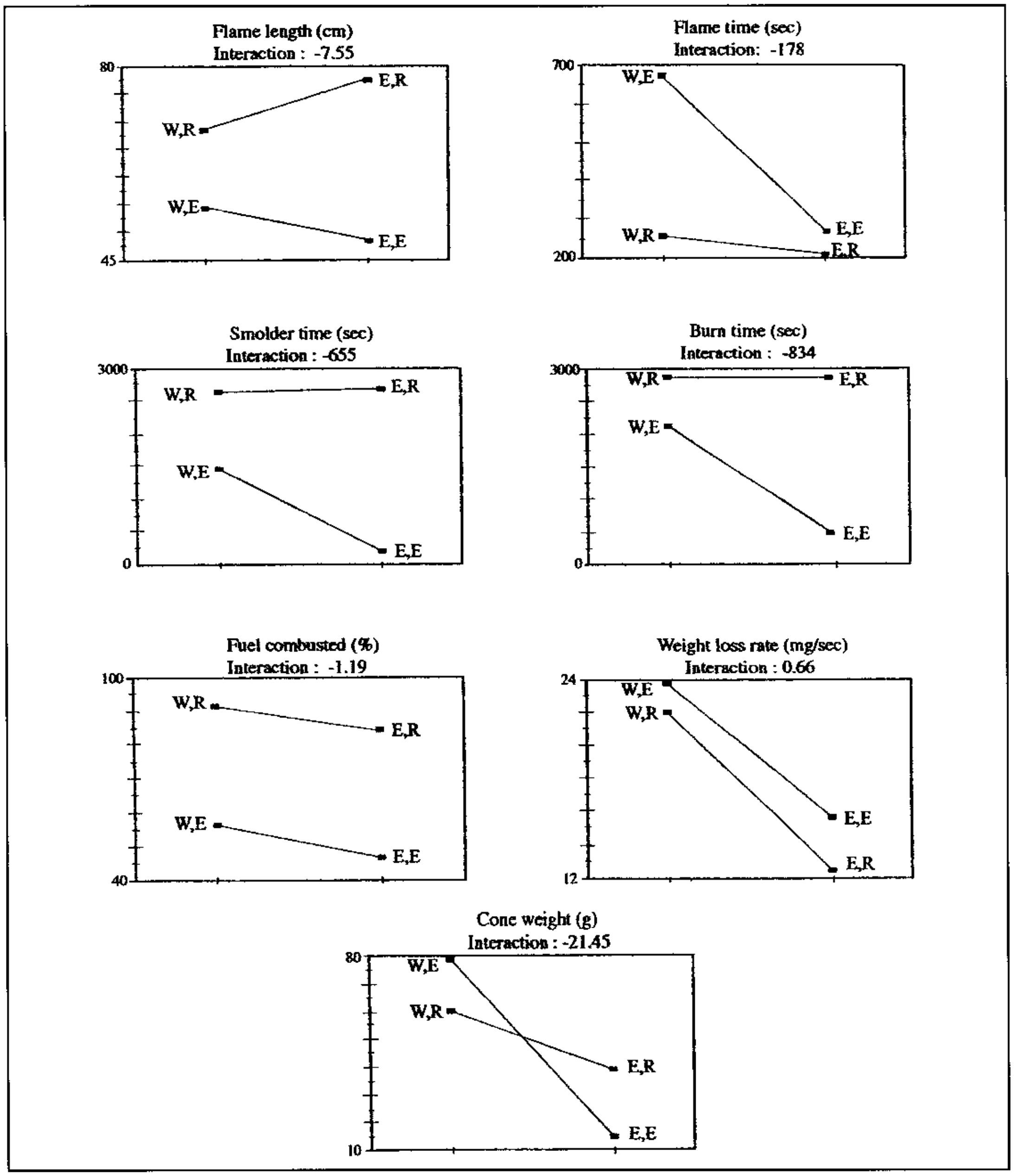

Figure 4. Interactions between fire adaptive strategy and geographic region, based on the data in Table 3. All interactions were significant, except weight loss rate. W,R: western resisters; W,E: western evaders; E,R: eastern resisters; E,E: eastern evaders.

the W,R-E,R and W,E-E,E pairs represent the central tendencies of the groups, and the vertical difference between the two midpoints identifies the magnitude of the interaction. For instance, the midpoints for weight loss are extremely close, thus the interaction of 0.66 is not significant. Conversely, the midpoints for all other burn characteristics are widely separated and significant. The main effects of the factors for each burning characteristic (Tables 4, 5) were affected significantly by the interactions, which are reciprocal within the burning categories. Strategy contributed strongly to every interaction except cone weight. Region contributed strongly to cone weight, flame, smolder, and burn times, but contributed only slightly to the interactions involving flame lengths and percent fuel combusted. In general, interactions were driven by responses from eastern evaders, which had the lowest mean values for most characteristics (Figure 4). Only for flame time were western evaders the top-ranked group.

Discussion

The data from this study exemplify differences in cones relative to fire adaptive strategies. Resisters burned for a long time and to white ash, with high values for percent fuel consumption (Table 4). Evaders (particularly Monterey pine and knobcone pine) supported flames for significantly longer times than resisters, but otherwise resisters had higher values in all burn categories. The constant characteristic among the evaders was the low percentage of cone mass combusted by fire (Tables 2-4). Differences between open and closed cones drove the significant interactions in this study. Regional differences centered on the timed characteristics, for which the western species had significantly higher values (Table 5). Flame lengths and percent fuel combusted did not differ significantly between eastern and western species. Cone serotiny is negatively correlated with several traits associated with fire in pines (Schwilk and Ackerly 2001). The long flame times of knobcone pine and Monterey pine for the cones (Table 2) and needles (Fonda et al. 1998, Fonda 2001) are strategies that should enable crown fires. Forests dominated by these species typically have abundant ladder fuels when they are fire-prone, so that flames from the cones and needles should ignite the ladder fuels, leading to a crown fire. The cones and needles of sand pine and pond pine (Figure 1), however, are less likely to ignite ladder fuels.

These eight pines are prominent in communities for which fire is an important environmental factor, and virtually all authors of papers exploring fire relationships mention their highly flammable fine fuels. We compared mean values for each burning characteristic for cones (Table 2) against needles (Fonda 2001; Table 6) by paired t-tests. Cones had significantly longer flame, smolder, and burn times, whereas needles had significantly greater flame length, percent combusted, and rates of weight loss. It is also noteworthy that flame times of cones (Table 2) were not significantly different from total burn times of needles (Fonda 2001). Cones are clearly an important fuel component in pine forest fire regimes, especially when combined with needles. These two components should ensure fire sustainability and consummability in ecosystems dominated by resisters, and they should help preheat and ignite ladder fuels in forests dominated by western evaders.

Smoke production has become an important consideration in wildland fire. The data for these cones (Tables 2-5) indicate that burning and smoldering cones contribute to the smoke environment for time periods that cannot be ignored. Except for eastern evaders, the other groups produced smoke for well over 30 min (Table 3). Jeffrey pine averaged > 1 hr of smoke production (Table 2).

Regardless of geographic location, all four resisters dominate communities in which surface fires are common, and their burning characteristics demonstrate that they produce highly flammable cones (Table 2). Jeffrey pine and ponderosa pine had the most flammable needles of 13 western conifers (Fonda et al. 1998). Longleaf pine and south Florida slash pine had some of the longest flames from needles (Fonda 2001). The cones of these four species clearly augment the surface fire regime created by the needles (Figure 2), yet their role has been unrecognized. Surface fires that might be carried poorly by minimal fine fuel loads should move more dependably when cones fill in gaps in the fuel bed and are an additional flame source. Cone fuels may also maintain competition-free environments surrounding resister pines in a kill thy neighbor strategy (sensu Bond and Midgley 1995). Taylor and Fonda (1990) noted that fuels in a ponderosa pine stand were not concentrated near trees, ignoring the clustered cones that are so common in these stands. Ponderosa pine and Jeffrey pine cones had longer flame, smolder, and burn times than needles, although cones had shorter flame lengths. Rather than being fire-neutral, these pines have invested the same kind of highly flammable strategies in cones that they invested in needles.

Western evaders dominate forests in which surface and crown fires are common. Their needles are highly flammable, with long flames, long flame times, and the longest burning times (Fonda et al. 1998, Fonda 2001). Their cones contribute to the fuel layer, although they are less concentrated on the forest floor than cones from resisters. The heavy cones of Monterey pine and knobcone pine supported flames for >10 min (Table 2), and they had longer burn times than the eastern evaders (Table 3). The combination of high needle flammability and long flame and ember times of cones ensures that surface fuels ignite ladder fuels and initiate the crown fires on which seed release depends. Abundant cones in the canopies should help sustain fire in the crowns, as suggested by Clements (1976). Even with these high values for flammability, it is significant that cones were only ~50% combusted (Tables 2, 3). The strategy to protect seeds against fire by developing cones that resist consumption is paramount with these evaders.

In contrast to western evaders, forests dominated by eastern evaders generally do not support surface fires (Myers 1985). Crown fires are characteristic of fires in sand pine (Myers 1990), less so in pond pine communities (Harms 1996). Jack pine needles were burned by Fonda (2001), and they proved to be among the least flammable pine needles. Because we used pond pine cones in this test, we wanted to know how needle flammability differed between these two species, which would provide more information on how cones and needles relate to fire behavior in forests dominated by eastern evaders. Ten 15-g samples of pond pine needles were burned according to the above protocol and compared to jack pine data (Fonda 2001). Pond pine needles were more flammable than jack pine and sand pine, except that pond pine flame times were significantly shorter (Table 6). Pond pine needles produced flames that were significantly longer than any pine species tested previously (Fonda et al. 1998, Fonda 2001), which might be a factor in initiating surface fires in the dense pond pine understory. Although the short burn times for pond pine and sand pine did not differ significantly for either needles or cones (Tables 2, 6), sand pine needles had longer flame times whereas pond pine needles had longer ember times. As with western evaders, fuel consumption was low for eastern evader cones (Tables 2, 3). Perhaps most importantly, these cones smoldered with no glowing embers, and total burn time was ~450 sec (Table 3). All of these data argue that needles and cones are unlikely to contribute sufficient fire to ignite a crown fire in eastern evader communities, especially compared to western evader communities.

TABLE 6. Means of burning characteristics from 10 test burns for needles from three eastern evaders. Values in a row with the same letter are not significantly different. Data for jack pine and sand pine are from Fonda (2001).

	Pond	Jack	Sand
Maximum flame length (cm)	87.2	46.4	50.3
Flame time (sec)	89.1	167.8	195.4
Ember time (sec)	213.2	69.9	124.6
Burn time (sec)	302.3[a]	237.6	319.9[a]
Fuel combusted (%)	88.5	60.7[a]	61.6[a]
Mean rate of weight loss (mg/sec)	45.6[a]	39.3[a]	29.1

Only recently have cones been regarded as a separate and distinct fuel component (van Wagtendonk et al. 1998). Heat contents of foliage, duff, woody fuels, and cones of Sierra Nevada conifers were about equal, but they were higher than standard values commonly used in fuel models (van Wagtendonk et al. 1998). Although they did not study cones, Williamson and Agee (2002) demonstrated that foliar heat contents of three interior Pacific Northwest conifers also were higher than standard values. These authors demonstrated that models that ignored the different heat contents of these fuel components were liable to underestimate fireline intensity, and van Wagtendonk et al. (1998) further implied that ignoring cones would result in miscalculations. Indeed, heat content with ash varied narrowly among knobcone pine, Jeffrey pine, and ponderosa pine cones in the Sierra Nevada (20.73-22.52 MJ kg^{-1}), yet the cones of each species burned quite differently (Table 2).

Fire behavior models should incorporate the diversity in flammability of fuels with similar shapes, sizes, and heat contents (i.e., their burning characteristics), and also their placement in the fuel bed. The burning characteristics of these eight pine species (Tables 2-5) indicate that they contribute more to fire regimes of their communities than previously thought. Closed cones and open cones respond differently to fire, as do western and eastern species. Models for forests in which the dominant species are resisters, whether east or west, should account for the burn times of the cones (Tables 2, 3) and their ability to ignite fine fuels to sustain surface fires. Furthermore, because cones in resister-dominated forests invariably are distributed evenly throughout the fuel layer, they sustain surface fires and serve as vectors of ground fires when they are abundant.

Models for evader-dominated forests should differ according to eastern and western species. The large cones of western evaders supported flames for a mean of >11 min (Table 3). Although these cones are scarcer in the fuel layer compared to resisters, they still are capable of igniting abundant fine fuels that characterize mature western evader-dominated forests. These cones are also likely to ignite in the tree canopies, further enhancing the likelihood of a crown fire. On the other hand, our data argue that models for eastern evader-dominated forests would not benefit from recognizing cones as a significant contributor to the fire environment. All of their burning characteristics are unimportant in starting or carrying ground fires.

Although differences in the importance of cone fuels exist among fire-adaptive strategies (i.e., cone serotiny) and geographic region, it is evident that future models should better incorporate these factors and begin to recognize the role of cones, heretofore an invisible wildland fuel.

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