Research Article

The Effects of Conifer Encroachment and Overstory Structure on Fuels and Fire in an Oak Woodland Landscape

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ABSTRACT

The role of fire in the maintenance of oak-dominated ecosystems is widely recognized. Fire exclusion results in structural and compositional shifts that alter fuelbed composition and structure, together influencing fire behavior and effects. To clarify the influence of overstory structure on fuels and fire intensity in oak woodlands and savannas, we examined fuelbeds across a gradient from open grassland to Douglas-fir- (*Pseudotsuga menziesii* (Mirb.) Franco) invaded Oregon white oak (*Quercus garryana* Douglas ex Hook.) woodland in the Bald Hills of Redwood National Park, California, USA. Herbaceous mass decreased markedly from a high in grasslands (3.38 Mg ha^{-1}) to a low in invaded woodlands (0.03 Mg ha^{-1}), whereas leaf litter and woody fuel mass increased substantially along this gradient. Mean fire temperatures at 30 cm height ranged from 74.7 °C in invaded woodland up to 207.9 °C in grassland. Highly flammable grassland and savanna communities maintain heavy herbaceous mass, but low woody mass, favoring quick-spreading, relatively high-intensity fires. The encroachment of Douglas-fir into grasslands and oak-dominated communities dampens flammability through changes in fuelbed composition and structure (e.g., the replacement of herbaceous fuels with woody fuels), underscoring the necessity for ecological restoration efforts that focus on fuelbed structure in addition to other common restoration goals.

Keywords: Bald Hills, ecological restoration, flammability, niche construction, *Quercus garryana*, savannas

Citation: Engber, E.A., J.M. Varner III, L.A. Arguello, and N.G. Sugihara. 2011 The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. Fire Ecology 7(2): 32-50. doi: 10.4996/fireecology.0702032

INTRODUCTION

Fire influences the structure and composition of savanna and woodland ecosystems worldwide (e.g., Higgins *et al*. 2000, Peterson and Reich 2001, Hoffmann and Solbrig 2003, Bond and Keeley 2005). Past research has focused on potential mechanisms dictating the distribution and structure of woody and herbaceous vegetation in these ecosystems, most notably, fire (Scholes and Archer 1997, Hoffman 1999, Beckage *et al*. 2009). Where fire is excluded from woodlands and savannas, substantial changes occur (Grossmann and Mladendoff 2007, Hiers *et al*. 2007, Peterson *et al*. 2007). Frequently, increases in woody stem densities and advancement of forest boundaries lead to shading of herbaceous layers (Hoffman *et al*. 2003, Devine *et al*. 2007) and development of organic forest floor horizons (Varner *et al*. 2005, Hiers *et al*. 2007), two processes that not only threaten biodiversity but alter fuel structure and characteristics of fire regimes.

In the Pacific Northwest region of the US, fire exclusion has resulted in a suite of structural and compositional changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) woodlands and other plant communities. Increases in stand density (Thilenius 1968), advancement of woody vegetation into adjacent grasslands (Sugihara and Reed 1987, Magee and Antos 1992, Fritschle 2008), and changes in stand structure (Hunter and Barbour 2001, Peterson and Hammer 2001) have been reported throughout the region. Of notable concern is the success with which a native conifer, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), has invaded oak woodlands and grasslands in the absence of frequent fire (Sugihara *et al*. 1987, Agee 1993, Barnhart *et al*. 1996, Tveten and Fonda 1999, Devine *et al*. 2007, Fritschle 2008). Douglas-fir encroachment shifts understory composition toward shade tolerant species (Thysell and Carey 2001, Devine *et al*. 2007), alters understory microclimate (Devine and Harrington 2007), and importantly, changes fuelbed structure (Figure 1). In stands where Douglas-fir becomes dominant, the shorter stature and shade intolerant oaks are shaded, leading to crown retreat and eventual oak mortality (Devine and

Figure 1. Typical Douglas-fir invaded (A) and intact (B) Oregon white oak woodland illustrating differences in understory vegetation and fuels, Redwood National Park, California, USA.

Harrington 2006), eliminating a primary fuel source, Oregon white oak leaf litter.

While the exclusion of fire from Oregon white oak woodlands leads to significant structural and compositional shifts, the implications for fire regimes and the underlying mechanisms affecting differential flammability have been widely overlooked in past research. Changes in species composition and community structure affect fuelbed properties such as fuel mass, moisture, and bulk density, each influencing fire behavior (Rothermel 1983). The interaction between plant traits and flammability has gained interest since Mutch (1970) hypothesized that some fire-adapted plants evolved flammable traits to exclude invading, fire-sensitive species. Though some authors have criticized the hypothesis in part—citing the potential for flammable traits to be confounded by other selection pressures, and its implication of group, as well as individual, selection (Snyder 1984, Troumbis and Traubad 1989, Bond and Midgley 1995)—numerous works still entertain the idea that flammable plant traits offer enhanced fitness in fire-prone environments (Bond and Midgley 1995, Fonda 2001, Schwilk and Kerr 2002, Gagnon *et al*. 2010). Prominent examples of fire-facilitating plant communities include longleaf pine (*Pinus palustris* Miller)-oak in the southeastern United States (Glitzenstein *et al*. 1995), Gambel oak (*Quercus gambelii* Nutt.)-ponderosa pine (*Pinus ponderosa* C. Lawson) in the southwestern United States (Abella and Fulé 2008), savannas of northeastern South Africa (Govender *et al*. 2006), and Brazilian cerrado (Hoffman 1999), among others. Plant modifications to their immediate environment that lead to differential flammability has been termed niche construction (Schwilk 2003), and recruitment of fire-sensitive species in these fire-prone environments may be mediated by fire intensity generated by flammable fuels provided by fire-facilitating species (e.g., Rebertus and Burns 1997, Fonda 2001, Hoffman *et al*. 2003, Kane *et al*. 2008, Beckage *et al*. 2009). Species with less flammable leaf litter or that suppress understory herbaceous fuels may inhibit fire spread in their proximity, lengthening fire return intervals and altering species composition and structure (Kane *et al*. 2008). To date, few studies have quantified the underlying mechanisms affecting differential flammability in woodlands and savannas, and no studies have addressed this question in structurally heterogeneous Oregon white oak ecosystems.

One example of a landscape where fire shapes community composition and structure is the Bald Hills of Redwood National Park, characterized by a structural gradient from forest-woodland-savanna-grassland (Figure 2). Our primary research objective was to understand the pattern of fuelbed change across this structural gradient, shedding light on the mechanisms driving differences in flammability, a hypothesized mechanism responsible for the maintenance of community structure. To accomplish this, we sought: 1) to quantify fuelbed mass of herbaceous, woody, and litter components; 2) to compare fuelbed bulk density and fuel moisture; and 3) to estimate fire temperature heterogeneity across the structural gradient. With these data, we tested the following hypotheses: 1) fuelbed components will differ significantly across the structural gradient, leading to differences in flammability; 2) differences in flammability will result in differences in measured fire temperature (a proxy for fire intensity) across the structural gradient; and 3) Douglas-fir invasion will result in decreases in herbaceous fuel mass and increases in woody load and bulk density, resulting in dampened flammability (niche construction) when compared with the other structural communities. Findings of this study offer particular relevance to managers faced with the invasion of fire-sensitive species in fire-prone ecosystems, documenting how community structure alters fuelbeds and, therefore, the ability of managers to meet restoration objectives with managed fire.

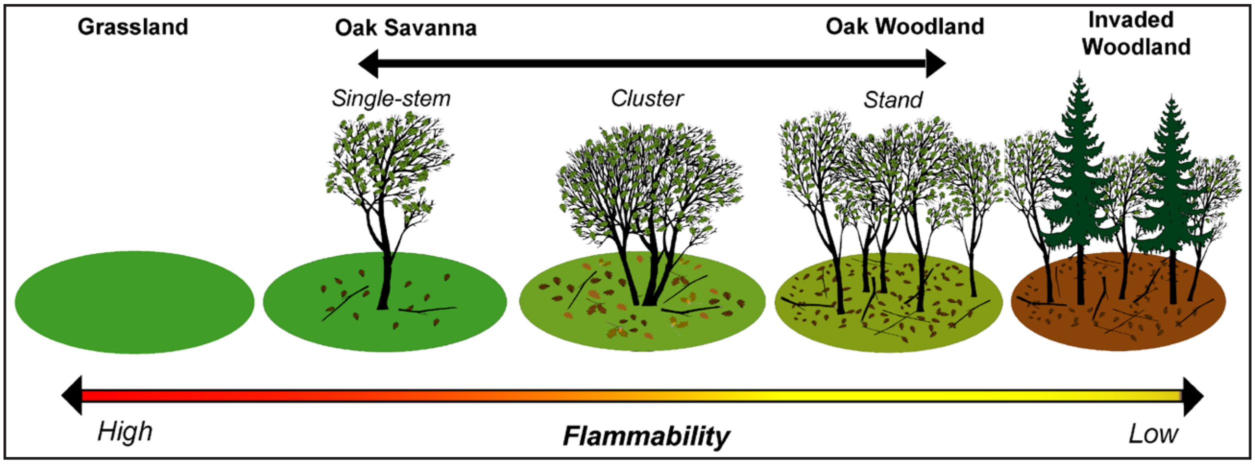

Figure 2. Conceptual diagram depicting oak woodland structures studied and relative flammability of each. Leaf litter and woody fuels increase with overstory density, while herbaceous fuels become increasingly sparse.

METHODS

Site Description

We located study sites in the Bald Hills of Redwood National Park, an area encompassing approximately 1700 ha of Oregon white oak woodlands and grasslands that divide the Redwood Creek and Klamath River drainages in northwestern California, USA. Since 1993, park managers have instituted a robust prescribed fire program in the Bald Hills, burning 202 ha to 809 ha annually, with an approximate 3 yr to 5 yr fire return interval for individual sites. Primary objectives of this burn program include control of Douglas-fir invasion in oak woodlands and grasslands and maintenance of native herbaceous species richness (Underwood *et al*. 2003). The Bald Hills are dominated by Oregon white oak woodlands intermixed with grasslands, with Douglas-fir-tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehder) forests occurring at woodland and grassland margins. Douglas-fir-tanoak forest historically occurred on relatively mesic sites in the Bald Hills (lower slopes, drainages, and north aspects), but has expanded dramatically since 1900 following removal of Native American tribes, widespread fire exclusion, and anthropogenic activities (Underwood *et al*. 2003, Fritschle 2008).

We established plots in the Schoolhouse Peak, Copper Creek, and Coyote Creek burn units as they were prioritized for prescribed burning during the fall of 2008 and 2009. Copper Creek and Coyote Creek units had been burned three times since 1993, while Schoolhouse Peak had been burned five times. Both the Schoolhouse Peak and Copper Creek units were grazed by cattle until 1980, and the Coyote Creek unit was grazed until 1991 when it was added to Redwood National Park. Under park management, many of the fire-resistant Douglas-fir that established during fire-free periods have been removed from these burn units by felling and or girdling; therefore, most of the invaded plots (8 out of 10) were located adjacent to units (but within the park boundary) in order to capture more natural fuelbeds. The age of encroaching Douglas-fir was approximately 80 yr to 100 yr in the Copper Creek plots, but only 30 yr to 50 yr old in the Schoolhouse Peak and Coyote Creek plots (L. Arguello, National Park Service, personal communication). Overstory basal area for invaded plots averaged 62 m^2 ha^{-1} with Douglas-fir comprising 25% to 56% of the total basal area.

Burn units were systematically surveyed and sites representing five structural community types including grassland (n = 25), oak savanna (n = 11), oak cluster (n = 15), oak woodland (n = 15), and invaded woodland (n = 10) were randomly selected for analysis (Figure 2). Plots were selected in areas where managers anticipated heading fires (fires moving with the slope and in the direction of surface winds) to minimize variation in fire intensity independent of fuels. The five structural communities were selected because they appeared to differ in fuelbed composition and structure, and past research has questioned the prevalence of various stand structures (e.g., single-stem vs. cluster) in the Bald Hills under varying fire regimes (Sugihara and Reed 1987). In addition to the five structural communities, we established eight plots in oak woodland with an understory dominated by California fescue (*Festuca californica* Vasey), a notably flammable native grass (Hastings *et al*. 1997). Values for herbaceous mass from the fescue plots were included in the analysis of herbaceous mass across all structural community types. Across all plots, slopes averaged 30% (SE = 1.2%), while aspects ranged from SE to NW (mode = SW). Rocky outcrops, seeps, water courses, slumps, and areas of concentrated rodent (e.g., gophers [*Thomomys* spp.] and voles [*Microtus* spp.]) activity (with correspondingly reduced herbaceous vegetation) were avoided to minimize variation in site factors influencing fuelbed metrics.

Fuelbed Sampling

Fuels were sampled in four strata, including woody, leaf litter, total herbaceous (live and dead combined), and shrub surface fuels over two field seasons (2008 and 2009). Rainfall recorded by the Schoolhouse Peak Remote Automated Weather Station (http://raws.wrh.noaa.gov/roman/) as of 1 June 2008 was 120.9 cm but slightly less on the same date in 2009 (107.6 cm). Sampling occurred after 1 August during both seasons to allow herbaceous species time to cure. Schoolhouse Peak and Copper Creek burn units were sampled in season one, while Coyote Creek was sampled in season two (no plots were re-sampled). A plot consisted of three 25 cm × 50 cm subplots located at a random azimuth, approximately 1 m to 2 m from an oak stem (unless in grassland). Grassland plots were located using a random azimuth approximately 5 m from adjacent oak crowns. The three subplots were averaged at the plot level for all analyses. Herbaceous, shrub, and litter mass within each subplot was clipped approximately 1 cm from ground level and removed, bagged in polypropylene bags, and transported to the lab for drying and weighing. Fuels were dried in a convection oven at 70 °C for 72 hours. One hour and 10 h (<2.54 cm diameter) woody fuels were destructively sampled from subplots in the first sampling season, while the planar intercept method (Brown 1974) was employed to estimate 1 h, 10 h, 100 h, and 1000 h woody fuel loading in the second sampling season. Sampling planes were located to intersect each subplot; fuel time-lag classes including 0 cm to 2.54 cm (1 h and 10 h), 2.54 cm to 7.62 cm (100 h), and >7.62 cm (1000 h) diameter woody fuels were sampled from 0 m to 2 m, 0 m to 4 m, and 0 m to 11.3 m along each sampling plane, respectively. Specific gravity and mean particle diameter for 1 h and 10 h woody fuels were measured on a subsample (1 h: n = 26; 10 h: n = 18) of fuels to provide species-specific values for coefficients used in calculations (Brown 1974).

To estimate fuelbed bulk density (kg m^{-3}), fuel depths were measured in each subplot prior to any destructive sampling to estimate fuelbed volume (25 cm × 50 cm frame area × measured fuelbed depth). Herbaceous fuel depth was estimated following methods of Brown (1981) at six systematically placed points in each subplot. Fuelbed bulk density was calculated in two ways: herbaceous mass divided by fuelbed volume (ρ_b h), and a combination of herbaceous, shrub, 1 h and 10 h woody fuels, and litter mass divided by fuelbed volume (ρ_b *tot*).

Given the importance of fuel moisture in surface fire spread and intensity (Rothermel 1983), live herbaceous and 10 h woody fuel moisture were sampled across the five structural communities (*n* = 5 replicates of each) on four afternoons in late summer, 2008. Herbaceous and woody fuel moistures were not sampled on the same sampling day due to time constraints. Live herbaceous fuel moisture was estimated by clipping a 20 g to 35 g (oven-dry weight) sample at ground level on the south side of tree stems, unless in grassland. Live herbaceous moisture was not sampled in invaded woodland since these sites harbored little to no herbaceous biomass. After clipping, samples were placed in sealed polypropylene bags and transported in a cooler back to the laboratory where they were weighed and placed in a convection oven at 70 °C for 72 h. Sampling occurred on two dates (29 August 2008 and 20 September 2008) between 1200 h and 1600 h to minimize variations in environmental conditions (Agee *et al*. 2002). Woody fuel moisture was estimated across all five structural communities with standard 10 h fuel moisture sticks (*n* = 5 replicates of each community type). Sampling occurred on two dates (16 September 2008 and 22 September 2008) between 1200 h and 1600 h.

To characterize important species contributing to fuelbed components at the study site, understory species cover was surveyed in a subsample of plots (grassland: *n* = 10; oak savanna: *n* = 6; oak cluster: *n* = 10; oak woodland: *n* = 10; invaded woodland: *n* = 5). Within each 25 cm × 50 cm subplot, two observers estimated percent cover for each species and bare ground (non-vegetated) using a modified Daubenmire (1959) cover scale with five cover classes (<10 %; 10 % to 25 %; 25 % to 50 %; 50 % to 75 %; >75 %). Cover class mid-point values were used for all analyses, assuming that actual values were symmetrically dispersed about midpoints (Bonham 1989). In all plots with an overstory present, diameter at breast height (1.37 m, dbh) was recorded for the plot tree (e.g., single-stem or cluster); in oak woodland and invaded woodland sites (where more than one individual tree was present), dbh was recorded for all stems greater than 5 cm in 0.04 ha circular plots.

Fire Temperature

Fire intensity (i.e., energy output; Alexander 1982) has been linked to fire effects on vegetation across a wide range of ecological studies (e.g., Gibson *et al*. 1990, Glitzenstein *et al*. 1995, Govender *et al*. 2006). Heterogeneity in fire intensity across plant communities is a potential mechanism influencing community composition and species demography (Moreno and Oechel 1993, Hoffman 1999). Fire temperatures obtained from thermocouples and pyrometers have been used as surrogates for fire intensity (Iverson *et al*. 2004, Kennard *et al*. 2005, Wally *et al*. 2006), although these devices actually reflect temperatures of the devices themselves. Thermocouples, opposed to pyrometers, provide temperature duration data, which are more relevant to fire effects than instantaneous maximum temperature (Bova and Dickinson 2008). Pyrometer data, however, have been shown to correlate well with mean and maximum temperatures recorded by thermocouples (60 % to 82 % of the variation; Kennard *et al*. 2005) and temperatures obtained from other devices (Iverson *et al*. 2004), and have great utility for comparison of temperature regimes within a site (Wally *et al*. 2006). We constructed metal pyrometers with 13 Omegalaq temperature-sensitive paints (Omega Engineering Inc., Stamford, Connecticut, USA; temperatures range from 79 °C to 649 °C) applied to thin copper tags (15 cm × 2.5 cm × 0.255 mm thick) in adjacent non-overlapping strips. Pyrometers were wired to metal conduit and erected 30 cm above ground, with four per plot. The four pyrometers were averaged at the plot level for all analyses. Manufacturer's protocols were followed to assess melting of paints, using two observers.

Prescribed burns were conducted by Redwood National Park managers in the fall of 2008 (Table 1). Prescribed fires in the Bald Hills are generally conducted in the fall due to the sensitivity of the California oatgrass (*Danthonia californica* Bol.) to spring burning (Arguello 1994). The Coyote Creek unit was scheduled for burning in fall 2009, but the burn was not accomplished because prescription weather was not met. Additionally, not all plots within burned units burned; these were removed from analysis, leaving a total of 112 pyrometers across 28 plots.

Data Analysis

Descriptive statistics were calculated at the structural community level for all measured fuelbed components. Individual one-way analysis of variance (ANOVA) tests were conducted to determine significant differences among structural communities for each fuelbed component measured: 1 h, 10 h, 100 h, 1000 h sound and rotten woody fuel; shrub, fern, herbaceous, and litter fuel mass; herbaceous and woody fuel moisture; herbaceous and total fuelbed bulk density; cover of bare ground; overstory basal area; and fire temperature. If differences were detected, the conservative Tukey-Kramer multiple comparison test was conducted to compare all pair-wise differences. Residual plots were examined to assess normality (normal probability plots) and homoscedasticity (residuals versus fitted value plots). If data failed to meet assumptions of normality or homoscedasticity, square root or logarithmic (log10) transformations were employed. If data persistently failed to meet assumptions for ANOVA despite transformations, a non-parametric Kruskal-Wallis test on ranks was employed, followed by a non-parametric Kruskal-Wallis multiple comparison *Z*-value test with a Bonferroni test value. General Linear Models ANOVA was employed to test for differences in herbaceous mass by structure, year, and the structure × year interaction. Individual two-sample *t*-tests (two-tailed) were used to test for differences in herbaceous mass for each structural community type by sampling year (2008 vs. 2009). Linear correlation analysis was conducted to determine associations between overstory basal area ($m^2 ha^{-1}$) and herbaceous, litter, and fine woody fuel mass (1 h and 10 h). Linear correlation analysis was also conducted with herbaceous mass (response) and litter mass (predictor), and with fire temperature (response) and individual fuelbed components (predictors). Statistical significance was assessed at $\alpha = 0.05$ and all analyses were performed using Statistical and Power Analysis Software (NCSS, Kaysville, Utah, USA).

RESULTS

Fuelbed Components

Fuelbed components varied markedly across the structural gradient from grassland to invaded woodland, with mean values differing

Table 1. Prescribed fire conditions and behavior in the Bald Hills of Redwood National Park, California, USA, 2008. FL = flame length; Temp. = ambient air temperature; RH = relative humidity.

Burn unit	Ignition type	Grassland FL (m)	Oak woodland FL (m)	Wind (gusts) km/h	Temp. (°C)	RH %	Date burned
Schoolhouse Peak	Strip and spot head fires	0.9 to 3.0	0.6 to 1.5	3 to 8 (22)	20 to 23	31 to 71	23-9-2008
Copper Creek	Strip and spot head fires	0.9 to 1.5	0.6 to 0.9	0 to 8 (16)	19 to 23	28 to 55	27-10-2008

significantly by structural community type for all fuelbed components ($P < 0.001$; Figures 3, 4), with the exceptions of shrub (Kruskal-Wallis; $\chi^2_4 = 5.27$, $P = 0.26$) and fern (Kruskal-Wallis; $\chi^2_4 = 6.99$, $P = 0.13$) strata. Herbaceous mass decreased substantially from grassland to invaded woodland ($F_{3,\,62} = 17.0$, $P < 0.001$), while leaf litter and woody mass increased along this gradient and were positively related to overstory basal area (Figure 5). Mean herbaceous mass ranged from 3.38 Mg ha^{-1} in grassland, to 1.8 Mg ha^{-1} in oak woodland, to only 0.03 Mg ha^{-1} in invaded woodland; mean values for savanna and grassland plots were not significantly different. Oak woodland with an understory dominated by California fescue had the greatest herbaceous mass of any structural community type, averaging 7.76 Mg ha^{-1}, more than double the grassland plots ($P < 0.001$). Herbaceous mass differed significantly by sampling year for oak cluster (year 1 = 2.69 Mg ha^{-1}, year 2 = 1.85 Mg ha^{-1}; $P = 0.02$), approached significance for savanna (year 1 = 3.05 Mg ha^{-1}, year 2 = 2.28 Mg ha^{-1}; $P = 0.05$), but did not differ for other structural community types ($P > 0.38$). Structure × year interac-

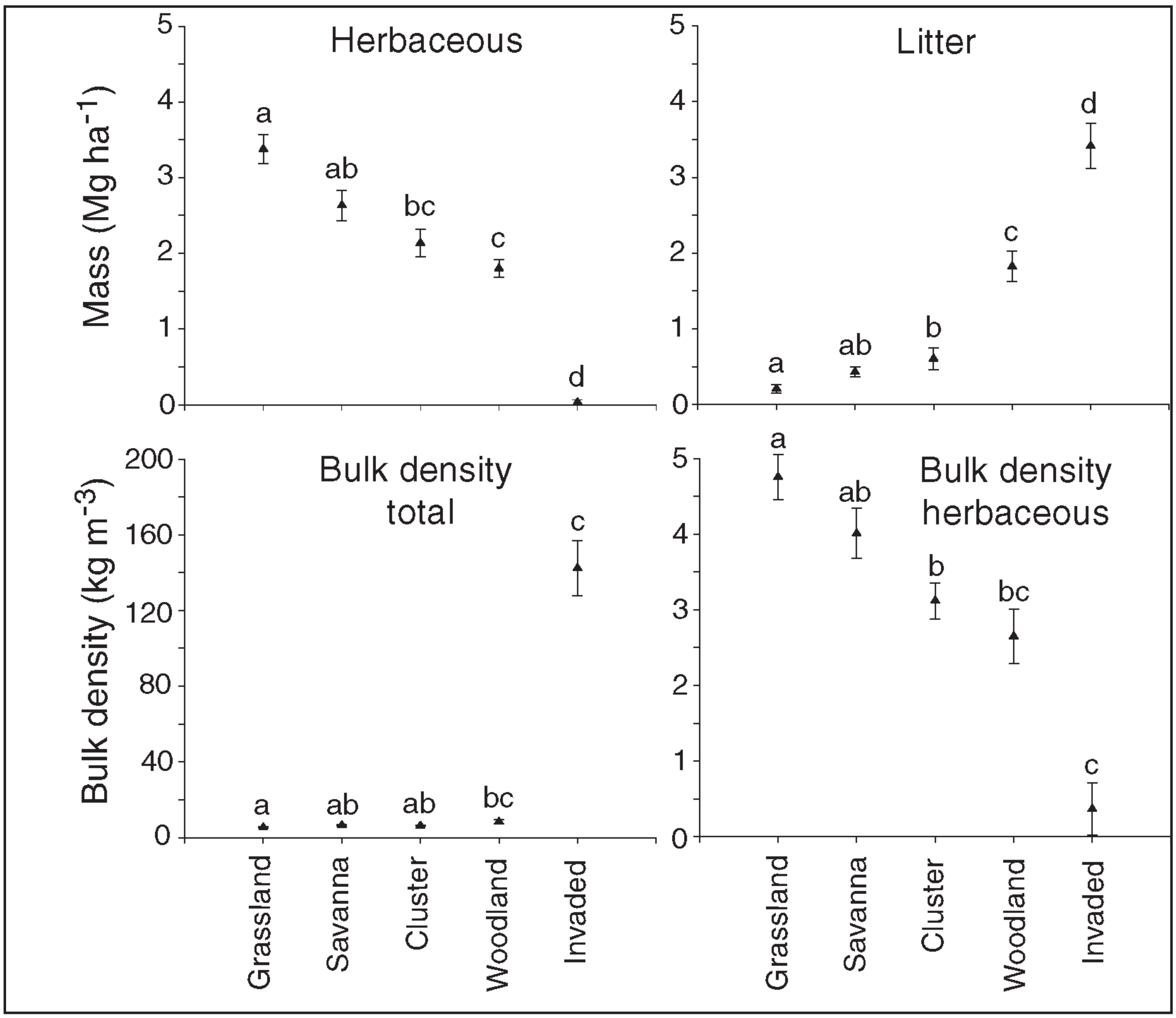

Figure 3. Herbaceous mass, litter mass, total bulk density, and herbaceous bulk density across a structural gradient in the Bald Hills of Redwood National Park, California, USA. Bars represent the standard error, while means with the same superscript are not significantly different.

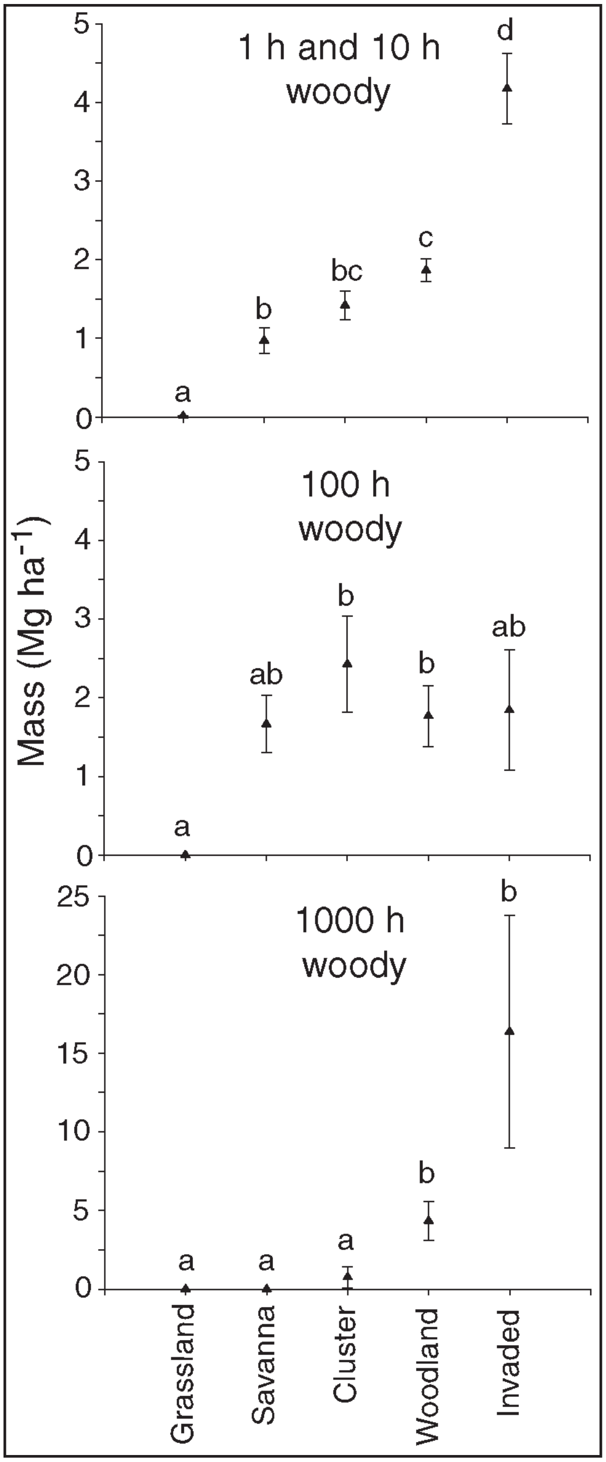

Figure 4. Woody surface fuels across a grassland-invaded woodland gradient in the Bald Hills of Redwood National Park, California, USA.

tions for herbaceous mass were not significant ($F_{3, 58}$ = 2.26, P = 0.09).

Live herbaceous fuel moisture was substantially drier in grassland (16% to 37% fuel moisture lower; Table 2) compared to oak woodland on both sampling dates (P = 0.005 and P = 0.01, respectively), although significant differences were not found among savanna, cluster, and woodland communities. Ten hour woody fuel moisture was slightly moister in invaded woodlands compared to grasslands (~1%) and differed significantly by community type on both sampling dates (P = 0.02 and P = 0.01, respectively) (Table 2).

Variability in cover was generally high for both native and non-native grasses. Herbaceous mass was dominated by non-native grasses, with dogtail (*Cynosurus echinatus* L.) (CV = 63%), tall oatgrass (*Arrhenatherum elatius* [L.] P. Beauv. ex J. Presl and C. Presl) (CV = 96%), and orchard grass (*Dactylis glomerata* L) (CV = 114%) being the most common, collectively comprising nearly 40% cover (Table 3). California brome (*Bromus carinatus* Hook. & Arn.) (CV = 132%) and blue wildrye (*Elymus glaucus* Buckley) (CV = 78%), the most frequently encountered native, perennial grasses, comprised less than 10% cover together. The non-native annual grass, dogtail, was present in all plots and at the highest cover, although it was lower in oak woodland (mean cover = 16.5% compared to 40.6% in grassland). Percent cover of bare ground (i.e., non-vegetated) increased drastically from grassland (11.2%) to invaded woodland (87.5%; $F_{4, 36}$ = 27.19, P < 0.001). Cover of bare ground in grassland differed significantly from all structural community types except savanna (P < 0.001).

Invaded woodland had the greatest woody fuel mass in the 1 h, 10 h, and 1000 h timelag categories (Figure 4), although variability was high for 1000 h sound (CV = 143.6%) and rotten (CV = 96.1%) logs. Leaf litter was nearly absent in grassland plots but heavy in invaded woodland. One-hour woody fuel loading did not differ among savanna, cluster, and woodland, but was substantially greater in invaded

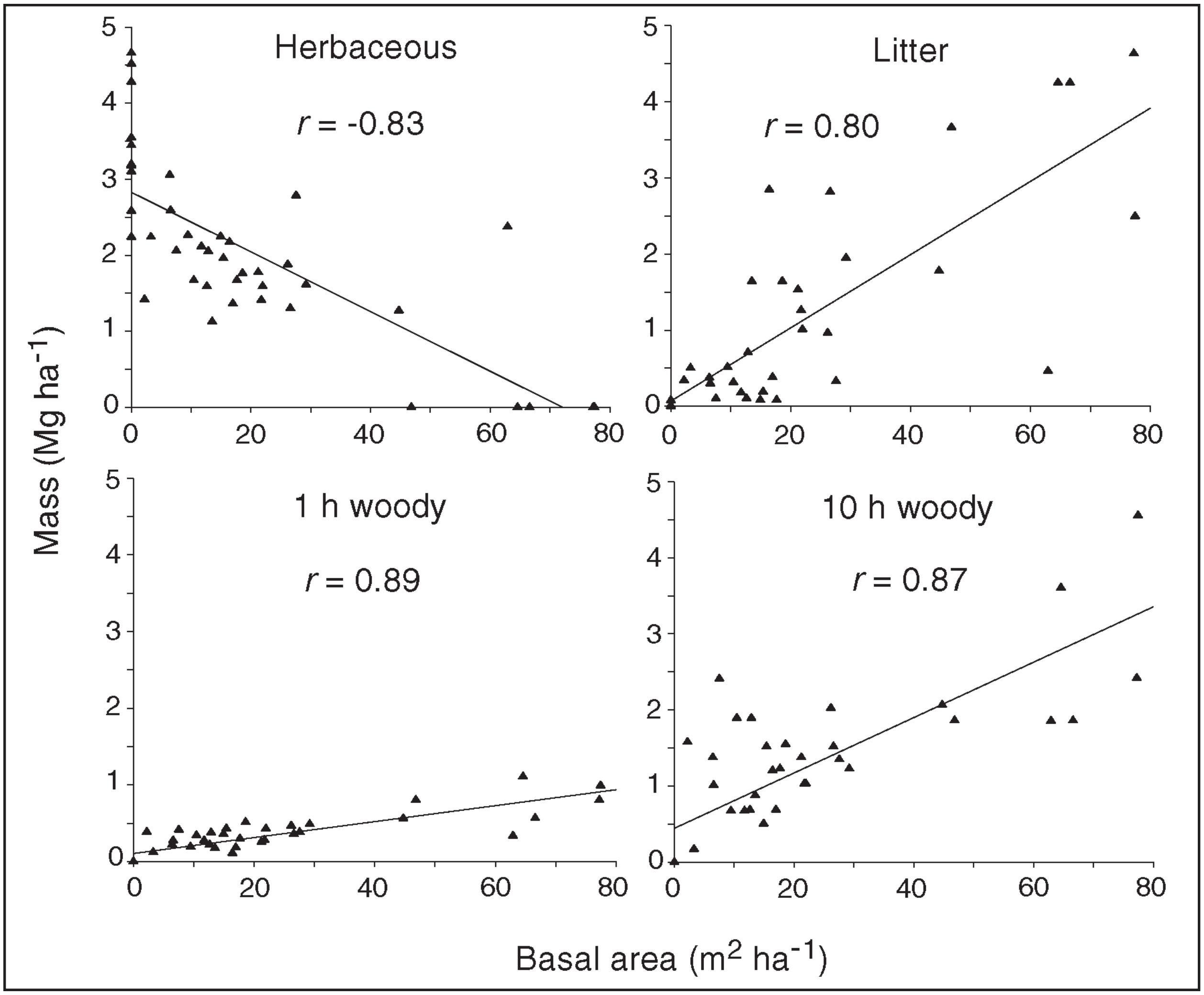

Figure 5. Relationships between overstory basal area and surface fuels across a grassland-invaded woodland gradient in the Bald Hills of Redwood National Park, California, USA.

woodland (Kruskal-Wallis *Z*-value test; $P < 0.001$). Ten-hour woody fuel loading was lower in savanna compared to woodland and invaded woodland, where it was greatest ($F_{3, 47} = 12.04$, $P < 0.001$). One-hundred-hour woody fuel loading was more variable than other woody classes and did not differ among tree-dominated plots ($F_{3, 27} = 0.45$, $P = 0.72$) (Figure 4). Large woody (>7.62 cm diameter) fuel loading was quite variable and did not differ significantly among tree-dominated plots, with the exception of 1000 h rotten logs, which had significantly more mass in invaded woodland than in all other communities (Kruskal-Wallis; $\chi^2_3 = 18.45$, $P < 0.001$).

Overstory basal area (m^2 ha^{-1}) differed by structural community type ($F_{4, 36} = 193.04$, $P < 0.001$) and was negatively correlated with herbaceous mass ($r = -0.83$, $P < 0.001$). Strong positive correlations were found between live overstory basal area and fuel mass in the litter ($r = 0.80$, $P < 0.001$), 1 h (r = 0.89, $P < 0.001$), and 10 h ($r = 0.87$, $P < 0.001$) woody fuel strata (Figure 5). Herbaceous mass was strongly negatively correlated with litter mass ($r = -0.85$, $P < 0.001$).

With few woody fuels and deep fuelbeds, grassland had the lowest values for total fuelbed bulk density (ρ_b *tot* = 5.44 kg m^{-3}), and greatest values for herbaceous fuelbed bulk density (ρ_b *h*

Table 2. Live herbaceous and 10-hour woody fuel moisture across structural community types on four dates during the 2008 fire season in the Bald Hills of Redwood National Park, California, USA. Means followed by the same letter (e.g., ABC) are not significantly different based on a Tukey-Kramer multiple comparison test. Values in parentheses represent the standard error.

Date	Overstory structure	*n*	Mean (%)	CV (%)	Range
	Live herbaceous fuel moisture				
29-8-2008	Grassland	5	33.25 (4.45) A	29.94	16.79t o43.73
	Savanna	5	51.87 (6.08) AB	26.20	33.63t o63.87
	Cluster	5	63.36 (7.74) B	27.30	42.77 to 89.12
	Woodland	5	70.23 (6.94) B	22.09	52.96 to 94.65
20-9-2008	Grassland	5	36.37 (4.09) A	25.14	27.97t o51.96
	Savanna	5	43.40 (4.10) AB	21.05	30.80t o56.42
	Cluster	5	53.28 (3.63) B	15.25	48.04 to 67.70
	Woodland	5	52.40 (1.83) B	7.82	45.70t o56.36
	10 hour woody fuel moisture				
16-9-2008	Grassland	5	4.96 (0.16) A	7.62	4.37 to 5.32
	Savanna	5	5.04 (0.29) A	12.68	4.12t o5.72
	Cluster	5	5.19 (0.23) AB	9.87	4.51 to 5.76
	Woodland	5	5.45 (0.18) AB	7.47	4.87t o5.91
	Invaded	5	5.98 (0.21) B	7.90	5.392t o6.44
22-9-2008	Grassland	5	10.95 (0.57) A	11.73	9.19t o12.78
	Savanna	5	10.37 (0.17) AB	3.82	9.85 to 10.94
	Cluster	5	10.81 (0.29) AB	6.12	9.89 to 11.76
	Woodland	5	10.95 (0.22) AB	4.60	10.15t o1 1.46
	Invaded	5	12.16 (0.16) B	2.86	11.65 to 12.53

= 4.76 kg m^{-3}) (Figure 3). Similar to other fuelbed components, bulk density did not differ between grassland and savanna communities. Total fuelbed bulk density increased substantially along the gradient from grassland to invaded woodland (Kruskal-Wallis; $P < 0.001$), with invaded woodland (ρ_b *tot* = 142.4 kg m^{-3}) having considerably greater values than all other structural communities. Herbaceous fuelbed bulk density decreased along the structural gradient from grassland (ρ_b *h* = 4.76 kg m^{-3}) to woodland (ρ_b *h* = 2.65 kg m^{-3}) to invaded woodland (ρ_b *h* = 0.36 kg m^{-3}) (Figure 3).

Fire Temperature

Results revealed a decreasing trend in fire temperatures, as approximated by pyrometers, across the gradient from grassland (207.9 ±19 °C) to savanna (202.1 ±62.9 °C), to cluster (184.9 ±29.3 °C), to woodland (190.4 ±31.5 °C), to invaded woodland (74.7 ±19.6 °C). However, due to limited replication and within-treatment variation in measured temperature (CV = 33 % to 54 %), differences among structural community types were not significant ($F_{4, 23} = 1.53$, $P = 0.23$) (Table 4.). We did find a positive, significant correlation between fire temperature and herbaceous fuel

Table 3. Percent cover and percent frequency by structural community type for important species encountered at the study sites in the Bald Hills of Redwood National Park, California, USA. Values in parentheses represent the standard deviation. Bold font = native species; asterisk = perennial grass.

Species		Grassland	Oak savanna	Oak cluster	Oak woodland
*Arrhenatherum elatius**	Cover	7.58 (5.81)	12.36 (13.03)	5.08 (3.69)	6.08 (4.92)
	Frequency	90	100	100	90
Bromus carinatus*	Cover	0.33 (0.70)	6.94 (7.42)	2.25 (3.04)	5.25 (3.35)
	Frequency	20	66.6	50	80
Cynosurus echinatus	Cover	40.58 (13.41)	23.61 (11.47)	33.41 (23.05)	16.50 (13.02)
	Frequency	100	100	100	100
*Dactylis glomerata**	Cover	0.58 (1.84)	2.50 (0.91)	3.83 (3.24)	5.08 (4.50)
	Frequency	10	100	80	100
Elymus glaucus*	Cover	7.08 (5.33)	5.83 (4.65)	3.76 (2.20)	5.75 (4.70)
	Frequency	80	100	90	70
*Holcus lanatus**	Cover	3.83 (9.66)	---	0.16 (0.52)	---
	Frequency	30	0	10	0
Lathyrus vestitus	Cover	---	---	---	3.08 (5.38)
	Frequency	0	0	0	50
Pteridium aquilinum	Cover	4.83 (9.20)	2.08 (5.10)	4.08 (8.20)	---
	Frequency	40	16.6	30	0
Rumex acetosella	Cover	4.83 (7.71)	0.97 (2.38)	1.58 (3.10)	---
	Frequency	50	16.6	20	0
Trifolium bifidum	Cover	15.25 (13.70)	2.49 (4.01)	0.16 (0.52)	---
	Frequency	90	33.3	10	0

Table 4. Descriptive statistics for pyrometer temperature across structural communities in the Bald Hills of Redwood National Park, California, USA. Means followed by the same letter (e.g., ABC) are not significantly different based on a Tukey-Kramer multiple comparison test. Values in parenthesis following the mean represent the standard error. N refers to the number of plots per community type, while *n* refers to the number of pyrometers per community type.

Structure	N (*n*)	Mean (SE) °C	CV (%)	Range
Grassland	13 (52)	207.9 (19.0) A	33.02	109.2 to 350.2
Savanna	3 (12)	202.1 (62.9) A	53.92	79.4 to 287.7
Cluster	5 (20)	184.9 (29.3) A	35.41	94.3 to 273.9
Woodland	5 (20)	190.4 (31.5) A	36.97	100.3 to 287.7
Invaded	2 (8)	74.7 (19.6) A	37.06	55.1 to 94.3

mass (r = 0.52, P = 0.004), as well as a negative correlation between fire temperature and 1 h and 10 h woody fuel mass (r = –0.47, P = 0.01) (Figure 6). Additional variation in measured fire temperature could not be explained by including more explanatory variables in a multiple regression model (e.g., live fuel moisture, 10 h fuel moisture, fuelbed bulk density, or slope).

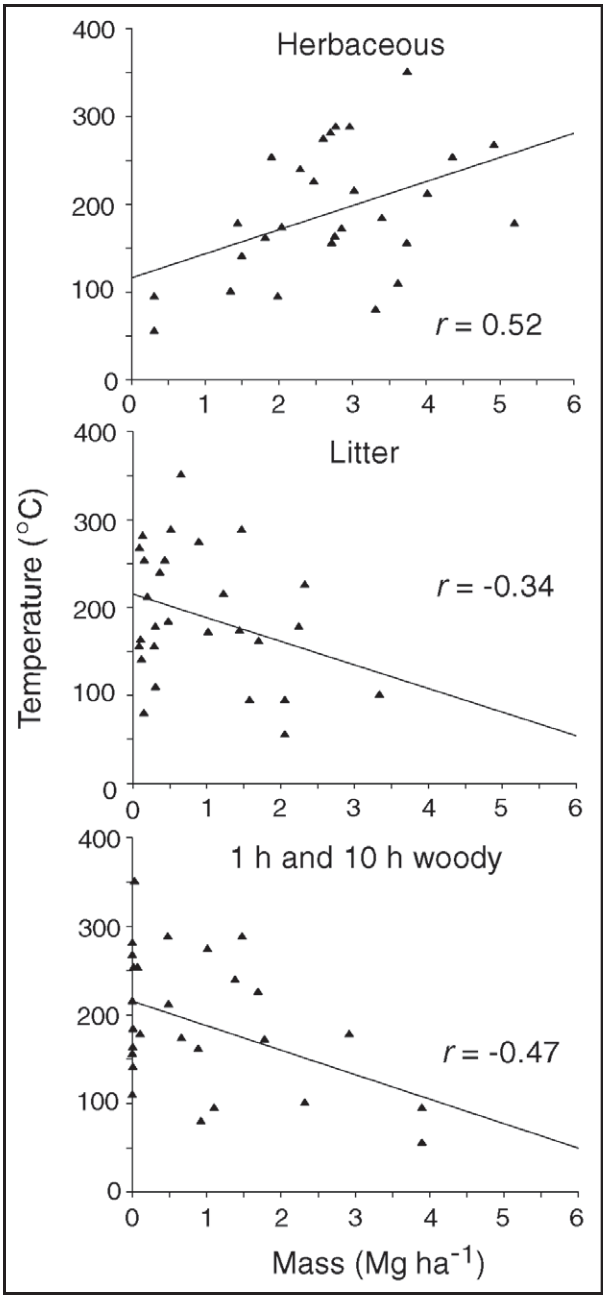

Figure 6. Scatter plots with estimated regression line for mean fire temperature (°C) on herbaceous, litter, and fine woody (one- and ten-hour) mass (Mg ha^{-1}) from two prescribed burns in the Bald Hills of Redwood National Park, California, USA, 2008.

DISCUSSION

Mechanisms of Community Flammability

While past research in Oregon white oak woodlands has documented changes in stand structure and conversion to Douglas-fir forest following fire exclusion (Sugihara and Reed 1987, Barnhart *et al*. 1996, Devine *et al*. 2007), the findings of this research highlight the importance of fuelbed-scale variation in community flammability following changes in community structure. Across the gradient from grassland to invaded woodland (Figure 2), the greatest fuelbed discrepancies were observed between the beginning (grassland) and end (invaded woodland) of the spectrum. Fuelbed characteristics typical of grasslands (low bulk density, heavy herbaceous mass, low fuel moisture) are inverted with Douglas-fir invasion, resulting in woody fuel recruitment, reduced herbaceous mass, and, ultimately, lower community flammability. Greater overstory shading, combined with the development of forest floor horizons (litter, fermentation, and humus), are notable mechanisms responsible for this change in many ecosystems that historically had frequent fire (Hiers *et al*. 2007). The fact that these communities occur adjacent to each other is intriguing, and underscores the importance of fire in shaping boundaries between the two. By maintaining fuelbeds that are very receptive to fire (i.e., niche construction), grassland fuel structures favor higher-frequency fire, ultimately limiting the recruitment of invading woody species into mature size classes (Higgins *et al*. 2000).

Fuelbed differences across the oak structural communities (savanna, cluster, woodland) were more subtle than those differentiating grassland from invaded woodland, but still have important implications for fire behavior. Grassland and savanna communities did not differ significantly for several fuelbed metrics, sharing high herbaceous mass, low fuelbed bulk density, and low fuel moistures, suggesting that both are fire-facilitating, flammable structural communities. Similarly, Jackson *et al*. (1990) found little difference in understory productivity beneath blue oaks (*Quercus douglasii* Hook and Arn.) compared to adjacent grassland in the foothills of the Sierra Nevada, California, USA. Clonal oak clusters were intermediate between savanna and woodland regarding herbaceous, litter, and fine woody fuel mass, differing significantly only from grassland and invaded woodland for most fuelbed components (Figures 3, 4). Differences in herbaceous mass among these communities (Figure 3) may be very important to variation in fire intensity, however, as indicated by the positive relationship between herbaceous mass and pyrometer temperature (Figure 6). Structural communities that enable greater herbaceous mass may promote elevated fire intensities; variation in fire temperature across this structural gradient could be understood in terms of a fire intensity regime (e.g., Govender *et al*. 2006) in which fuelbed-scale variability facilitates fire intensities that maintain specific vegetation structures. For example, elevated flammability exhibited in grassland and savanna structural communities could promote both frequent and relatively high intensity fire, thereby killing invading Douglas-fir seedlings and saplings.

Although fire temperature maxima did not differ significantly across structural community types in the Bald Hills (Table 4), observed trends are congruent with recent laboratory-based flammability research. Ganteaume *et al*. (2009) found grass fuelbeds to be significantly more flammable than tree and shrub litter beds (e.g., pine [*Pinus*], eucalyptus [*Eucalyptus*], oak [*Quercus*], arbutus [*Arbutus*], and holly [*Ulex*] species) in terms of ignition probability (greater), time to ignition (shorter), rate of spread (higher), rate of combustion (higher), and flame height (higher), suggesting that even small reductions in herbaceous mass result in substantially dampened flammability. Further, Douglas-fir litter ranked among the least flammable western USA conifers during laboratory burns conducted by Fonda *et al*. (1998). While fuelbed-scale differences observed across structural communities are important in understanding the mechanisms driving variation in fire behavior, the implications for community persistence are intriguing. For example, Guerin (1993) found that clonal oak domes in Florida lacked the well developed herbaceous and pine litter layers characteristic of surrounding longleaf pine-wiregrass (*Aristida stricta* Michx.) communities, making domes less likely to burn and more likely to persist in that community—a scenario somewhat analogous to Douglas-fir persistence in Oregon white oak woodlands.

Non-Native Plant Species Effects on Fuelbeds

Past work has shown that non-native species affect fuelbed properties (e.g., mass, moisture content, bulk density, structure) and fire regimes (Platt and Gottschalk 2001, Brooks *et al*. 2004); however, the role of non-native herbaceous species, in regard to fuelbed alteration, is an unknown in Oregon white oak woodlands. MacDougall and Turkington (2007) suggested that invasion of non-native grasses in Oregon white oak savanna in southwestern British Columbia, Canada, in conjunction with fire exclusion, increased grass litter fuel loads at their study site. Growth form of natives and non-natives must be considered in regard to fuel structure, however. Many native grasses in the Bald Hills are robust perennials (e.g., California brome, blue wildrye, California fescue), and if these have been replaced by wispy annuals (e.g., dogtail), fuel loads may be lighter, leading to lower fire intensities. In the Bald Hills, however, many of the non-native grasses are robust perennials (e.g., tall oatgrass, orchard grass) and contribute to heavy herbaceous fuel loading. That significant alterations of herbaceous mass occurred across structural communities, despite highly variable understory species composition and cover, suggests that overstory structure may be more important than species composition in terms of fuelbed flammability, at least at the structural community scale. An exception to this hypothesis would be oak woodlands with an understory dominated by California fescue, a species Hastings *et al*. (1997) found to be highly flammable. The substantially inflated fuel loads we observed in fescue fuels (7.67 Mg ha^{-1}) reveal a possible mechanism for this finding. The role of individual species in surface fire behavior is a topic that holds tremendous promise for further research, with obvious implications for ecological restoration and management (Kane *et al*. 2008).

Management Implications

Managers faced with grassland and woodland restoration in long-unburned ecosystems are challenged in using prescribed fire alone as a management tool (Peterson and Reich 2001). In the Bald Hills, fire weather prescriptions often ensure lower-intensity burns that result in little mortality of Douglas-fir taller than 3 m (Sugihara and Reed 1987), requiring mechanical removal of larger trees. Research by Tveten and Fonda (1999) and Regan and Agee (2004) suggest that prescribed fires result in little mortality of overstory Oregon white oaks as well. Therefore, if managers desire to restore Douglas-fir invaded stands similar to those studied here (e.g., dominant Douglas-fir in the oak canopy) or to reduce oak densities, thinning or similar silvicultural treatments may be required to remove fire-resistant individuals. Thinning would expose the forest floor to sunlight, promoting lower afternoon fuel moistures and the eventual establishment of an herbaceous fuelbed (Devine *et al*. 2007), although it is unclear how long the residual effects of the Douglas-fir overstory (i.e., organic forest floor fuels) will persist. Where prescribed fires are used to maintain oak woodlands and grasslands from invading Douglas-fir saplings, fireline intensities need to be elevated, particularly in areas with greater overstory basal area and lower herbaceous mass. Fire effects could be manipulated by altering firing patterns, changing season of burn, and conducting burns under more favorable fire weather scenarios (e.g., lower relative humidity, higher wind). Overstory structure must be considered in burn prescriptions, however, as results reveal that single prescriptions generate differential behavior across the diverse community structures.

In managed ecosystems such as the Bald Hills, where lightning ignitions are rare and fragmented landscapes prevent spread of these rare ignitions, managers are tasked with the maintenance of fire-facilitating ecosystems via prescribed fire and rare wildfires. Given the region-wide lapse in fire during the twentieth century and subsequent replacement of oak woodlands and grasslands with Douglas-fir forest, a substantial amount of restoration will be required to reestablish grasslands, lower density oak woodlands, and savannas. Initial efforts focused on the restoration of stand and fuel structure may be a prerequisite for longer-term management goals aimed at maintaining native species richness.

ACKNOWLEDGMENTS

Funding for this research was provided by the National Park Service Klamath Network Monitoring and Assessment Program and Redwood National Park. We appreciate the field and lab assistance provided by L. Quinn-Davidson, E. Banwell, B. Mueller, C. Benson, J. Wheeler, C. DaSilva, H. Kuljian, M. Cocking, D. Matheson, P. Cigan, and E. Johnson. Thoughtful comments on experimental design and statistical analysis were provided by C. Edgar. We are grateful to managers at Redwood National Park (J. McClelland, R. Young, and J. Beck) for providing access to burn units and supplemental site information.

LITERATURE CITED

Abella, S.R., and P.Z. Fulé. 2008. Fire effects on Gambel oak in southwestern ponderosa pine-oak forests. USDA Forest Service Research Note RMRS-RN-36, Fort Collins, Colorado, USA.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Agee, J.K., C.S. Wright, N. Williamson, and M.H. Huff. 2002. Foliar moisture content of Pacific Northwest vegetation and its relation to wildland fire behavior. Forest Ecology and Management 167: 57-66. doi: 10.1016/S0378-1127(01)00690-9

Alexander, M.E. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60: 349-357. doi: 10.1139/b82-048

Arguello, L.A. 1994. Effects of prescribed burning on two perennial bunchgrasses in the Bald Hills of Redwood National Park. Thesis, Humboldt State University, Arcata, California, USA.

Barnhart, S.J., J.R. McBride, and P. Warner. 1996. Invasion of northern oak woodlands by *Pseudotsuga menziesii* (Mirb.) Franco in the Sonoma Mountains of California. Madroño 43: 28-45.

Beckage, B., W.J. Platt, and L.J. Gross. 2009. Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. American Naturalist 174: 805-818. doi: 10.1086/648458

Bond, W.J., and J.E. Keeley. 2005. Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution 20: 387-394. doi: 10.1016/j.tree.2005.04.025

Bond, W.J., and J.J. Midgley. 1995. Kill thy neighbor—an individualistic argument for the evolution of flammability. Oikos 73:79-85. doi: 10.2307/3545728

Bonham, C.D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons, New York, New York, USA.

Bova, A.S., and M.B. Dickinson. 2008. Beyond "fire temperatures": calibrating thermocouple probes and modeling their response to surface fires in hardwood fuels. Canadian Journal of Forest Research 38: 1008-1020. doi: 10.1139/X07-204

Brooks, M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, J.M. Di'Tomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. Bioscience 54: 677-688. doi: 10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service INT-GTR-16. Intermountain Forest and Range experiment Station, Ogden, Utah, USA.

Brown, J.K. 1981. Bulk densities of nonuniform surface fuels and their application to fire modeling. Forest Science 27: 667-683. doi: 10.1126/science.6256857

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33: 43-64.

Devine, W.D., and C.A. Harrington. 2006. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook) following release from overtopping conifers. Trees 20: 747-756. doi: 10.1007/s00468-006-0089-8

Devine, W.D., and C.A. Harrington. 2007. Release of Oregon white oak from overtopping Douglas-fir: effects on soil water and microclimate. Northwest Science 81: 112-124. doi: 10.3955/0029-344X-81.2.112

Devine, W.D., C.A. Harrington, and D.H. Peter. 2007. Oak woodland restoration: understory response to removal of encroaching conifers. Ecological Restoration 25: 247-255. doi: 10.3368/er.25.4.247

Fonda, R.W., L.A. Belanger, and L.L. Burley. 1998. Burning characteristics of western conifer needles. Northwest Science 72: 1-9.

Fonda, R.W. 2001. Burning characteristics of needles from eight pine species. Forest Science 47: 390-396.

Foster, J.R., and S.E. Shaff. 2003. Forest colonization of Puget lowland grasslands at Fort Lewis, Washington. Northwest Science 77: 283-296.

Fritschle, J.A. 2008. Reconstructing historic ecotones using the public land survey: the lost prairies of Redwood National Park. Annals of the Association of American Geographers 98: 24-39. doi: 10.1080/00045600701734018

Gagnon, P.R., H.A. Passmore, W.J. Platt, J.A. Myers, C.E.T. Paine, and K.E. Harms. 2010. Does pyrogenicity protect burning plants? Ecology 91: 3481-3486. doi: 10.1890/10-0291.1

Ganteaume, A., C. Lampin-Maillet, M. Guijarro, C. Hernando, M. Jappiot, T. Fonturbel, P. Pérez-Gorostiaga, and J.A. Vega. 2009. Spot fires: fuelbed flammability and capability of fire brands to ignite fuelbeds. International Journal of Wildland Fire 18: 951-969. doi: 10.1071/WF07111

Gibson, D.J., D.C. Hartnett, and G.L.S. Merrill. 1990. Fire temperature heterogeneity in contrasting fire prone habitats: Kansas tallgrass prairie and Florida sandhill. Bulletin of the Torrey Botanical Club 117: 349-356. doi: 10.2307/2996832

Glitzenstein, J.S., W.J. Platt, and D.R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65: 441-476. doi: 10.2307/2963498

Govender, N., W.S.W. Trollope, and B.W. Van Wilggen. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. Journal of Applied Ecology 43: 748-758. doi: 10.1111/j.1365-2664.2006.01184.x

Grossman, E.B., and D.J. Mladenoff. 2007. Open woodland and savanna decline in a mixed-disturbance landscape (1938 to 1998) in the Northwest Wisconsin (USA) Sand Plain. Landscape Ecology 22: 43-55. doi: 10.1007/s10980-007-9113-7

Guerin, D.N. 1993. Oak dome clonal structure and fire ecology in a Florida longleaf pine dominated community. Bulletin of the Torrey Botanical Club 120: 107-114. doi: 10.2307/2996939

Hastings, M.S., S. Barnhart, and J.R. McBride. 1997. Restoration management of northern oak woodlands. USDA Forest Service General Technical Report PSW-GTR-160. Pacific Northwest Research Station, Portland, Oregon, USA.

Hiers, J.K., J.J. O'Brien, R.E. Will, and R.J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecological Applications 17: 806-814. doi: 10.1890/06-1015

Higgins, S.I., W.J. Bond, and W.S.W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88: 213-229. doi: 10.1046/j.1365-2745.2000.00435.x

Hoffman, W.A., and O.T. Solbrig. 2003. The role of topkill in the differential response of savanna woody species to fire. Forest Ecology and Management 180: 273-276. doi: 10.1016/S0378-1127(02)00566-2

Hoffman, W.A., B. Orthen, and P.K.V. Nascimento. 2003. Comparative fire ecology of tropical savanna and forest trees. Functional Ecology 17: 720-726. doi: 10.1111/j.1365-2435.2003.00796.x

Hoffman, W.A. 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology 80: 1354-1369. doi: 10.1890/0012-9658(1999)080[1354:FAPDOW]2.0.CO;2

Hunter, J.C., and M.G. Barbour. 2001. Through-growth by *Pseudotsuga menziesii:* a mechanism for change in forest composition without canopy gaps. Journal of Vegetation Science 12: 445-452. doi: 10.2307/3236996

Iverson, L.R., D.A. Yaussy, J. Rebbeck, T.F. Hutchinson, P.L. Long, and A.M. Prasad. 2004. A comparison of thermocouples and temperature paints to model spatial and temporal characteristics of landscape-scale prescribed fires. International Journal of Wildland Fire 13: 311-322. doi: 10.1071/WF03063

Jackson, L.E., R.B. Strauss, M.K. Firestone, and J.W. Bartolome. 1990. Influence of tree canopies on grassland productivity and nitrogen dynamics in deciduous oak savanna. Agriculture, Ecosystems & Environment 32: 89-105. doi: 10.1016/0167-8809(90)90126-X

Kane, J.M., J.M. Varner, and J.K. Hiers. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. Forest Ecology and Management 256: 2039-2045. doi: 10.1016/j.foreco.2008.07.039

Kennard, D.K., K.W. Outcalt, D. Jones, and J.J. O'Brien. 2005. Comparing techniques for estimating flame temperature of prescribed fires. Fire Ecology 1(1): 75-84. doi: 10.4996/fireecology.0101075

Ko, L.J., and P.B. Reich. 1993. Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. American Midland Naturalist 130: 31-42. doi: 10.2307/2426272

MacDougall, A.S., and R. Turkington. 2007. Does the type of disturbance matter when restorating disturbance-dependent grasslands? Restoration Ecology 15: 263-272. doi: 10.1111/j.1526-100X.2007.00209.x

Magee, T.K., and J.A. Antos. 1992. Tree invasion into a mountain-top meadow in the Oregon Coast Range, USA. Journal of Vegetation Science 3: 485-494. doi: 10.2307/3235805

Moreno, J.M., and W.C. Oechel. 1993. Demography of *Adenostoma fasciculatum* after fires of different intensities in southern California chaparral. Oecologia 96: 95-101. doi: 10.1007/BF00318035

Mutch, R.W. 1970. Wildland fires and ecosystems—a hypothesis. Ecology 51: 1046-1051. doi: 10.2307/1933631

Nelson Jr., R.M., and J.K. Hiers. 2008. The influence of fuelbed properties on moisture drying rates and timelags of longleaf pine litter. Canadian Journal of Forest Research 38: 2394-2404. doi: 10.1139/X08-078

Peterson, D.W., and P.B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11: 914-927. doi: 10.1890/1051-0761(2001)011[0914:PFIOSF]2.0.CO;2

Peterson, D.L., and R.D. Hammer. 2001. From open to closed canopy: a century of change in a Douglas-fir forest, Orcas Island, Washington. Northwest Science 75: 262-269.

Peterson, D.W., P.B. Reich, and K.J. Wrage. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. Journal of Vegetation Science 18: 3-12. doi: 10.1111/j.1654-1103.2007.tb02510.x

Platt, W.J., and R.M. Gottschalk. 2001. Effects of exotic grasses on potential fine fuel loads in the ground cover of south Florida slash pine savannas. International Journal of Wildland Fire 10: 155-159. doi: 10.1071/WF01016

Rebertus, A.J., and B.R. Burns. 1997. The importance of gap processes in the development and maintenance of oak savannas and dry forests. Journal of Ecology 85: 635-645. doi: 10.2307/2960534

Regan, A.C., and J.K. Agee. 2004. Oak community and seedling response to fire at Fort Lewis, Washington. Northwest Science 78: 1-11.

Rothermel, R.C. 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service General Technical Report INT-143. Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Scholes, R.J., and S.R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28: 517-544. doi: 10.1146/annurev.ecolsys.28.1.517

Schwilk, D.W. 2003. Flammability is a niche construction trait: canopy architecture affects fire intensity. American Naturalist 162: 725-733. doi: 10.1086/379351

Schwilk, D.W., and B. Kerr. 2002. Genetic niche-hiking: an alternative explanation for the evolution of flammability. Oikos 99: 431-442. doi: 10.1034/j.1600-0706.2002.11730.x

Snyder, J.R. 1984. The role of fire: Mutch ado about nothing? Oikos 43: 404-405. doi: 10.2307/3544161

Sugihara, N.G., L.J. Reed, and J.M. Lenihan. 1987. Vegetation of the Bald Hills oak woodlands, Redwood National Park, California. Madroño 34: 193-208.

Sugihara, N.G., and L.J. Reed. 1987. Vegetation ecology of the Bald Hills oak woodlands of Redwood National Park. Redwood National Park Research and Development Technical Report 21. Redwood National Park, Arcata, California, USA.

Thilenius, J.F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology 49: 1124-1133. doi: 10.2307/1934496

Thysell, D.R., and A.B. Carey. 2001. *Quercus garryana* communities in the Puget Trough, Washington. Northwest Science 75: 219-235.

Troumbis, A.Y., and L. Trabaud. 1989. Some questions about flammability in fire ecology. Acta Oecologica–Oecologia Plantarum 10: 167-175.

Tveten, R.K., and R.W. Fonda. 1999. Fire effects on prairies and oak woodlands on Fort Lewis, Washington. Northwest Science 73: 145-158.

Underwood, S., L. Arguello, and N. Siefkin. 2003. Restoring ethnographic landscapes and natural elements in Redwood National Park. Ecological Restoration 21: 278-283. doi: 10.3368/er.21.4.278

Varner, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: novel fire effects and consequences for long-unburned ecosystems. Restoration Ecology 13: 536-544. doi: 10.1111/j.1526-100X.2005.00067.x

Wally, A.L., E.S. Menges, and C.W. Weekly. 2006. Comparison of three devices for estimating fire temperatures in ecological studies. Applied Vegetation Science 9: 97-108. doi: 10.1111/j.1654-109X.2006.tb00659.x