

Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone

DANIEL C. DONATO,^{1,4} BRIAN J. HARVEY,¹ WILLIAM H. ROMME,² MARTIN SIMARD,³ AND MONICA G. TURNER¹

¹Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

²Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA

³Department of Geography and Centre for Northern Studies, Laval University, Pavillon Abitibi Price, 2405 de la Terrasse, Québec City, Québec G1V 0A6 Canada

Abstract. Consequences of bark beetle outbreaks for forest wildfire potential are receiving heightened attention, but little research has considered ecosystems with mixed-severity fire regimes. Such forests are widespread, variable in stand structure, and often fuel limited, suggesting that beetle outbreaks could substantially alter fire potentials. We studied canopy and surface fuels in interior Douglas-fir (*Pseudotsuga menziesii* v. *glauca*) forests in Greater Yellowstone, Wyoming, USA, to determine how fuel characteristics varied with time since outbreak of the Douglas-fir beetle (*Dendroctonus pseudotsugae*). We sampled five stands in each of four outbreak stages, validated for pre-outbreak similarity: green (undisturbed), red (1–3 yr), gray (4–14 yr), and silver (25–30 yr). General linear models were used to compare variation in fuel profiles associated with outbreak to variation associated with the range of stand structures (dense mesic forest to open xeric parkland) characteristic of interior Douglas-fir forest.

Beetle outbreak killed 38–83% of basal area within stands, generating a mix of live trees and snags over several years. Canopy fuel load and bulk density began declining in the red stage via needle drop and decreased by ~50% by the silver stage. The dead portion of available canopy fuels peaked in the red stage at 41%. After accounting for background variation, there was little effect of beetle outbreak on surface fuels, with differences mainly in herbaceous biomass (50% greater in red stands) and coarse woody fuels (doubled in silver stands). Within-stand spatial heterogeneity of fuels increased with time since outbreak, and surface-to-crown continuity decreased and remained low because of slow/sparse regeneration. Collectively, results suggest reduced fire potentials in post-outbreak stands, particularly for crown fire after the red stage, although abundant coarse fuels in silver stands may increase burn residence time and heat release. Outbreak effects on fuels were comparable to background variation in stand structure. The net effect of beetle outbreak was to shift the structure of mesic closed-canopy stands toward that of parklands, and to shift xeric parklands toward very sparse woodlands. This study highlights the importance of evaluating outbreak effects in the context of the wide structural variation inherent to many forest types in the absence of beetle disturbance.

Key words: *Dendroctonus pseudotsugae*; disturbance interaction; Douglas-fir beetle; fuel complex; fuel heterogeneity; fuel loads; fuel profiles; Greater Yellowstone Ecosystem, Wyoming, USA; lower montane forest; mixed-severity fire regime; *Pseudotsuga menziesii*; Rocky Mountain Douglas-fir.

INTRODUCTION

Outbreaks of native bark beetles (*Dendroctonus* spp.) have recently resulted in widespread tree mortality across tens of millions of hectares of forest in western North America (Raffa et al. 2008). The resulting areas of abundant dead trees have led to key management concerns regarding the potential for altered fire behavior and related effects on forest resources (Jenkins et al. 2008, 2012). Emerging research shows that beetle outbreaks can substantially change the arrangement, quantity, and composition of forest fuels (i.e., fuel profiles), but significant knowledge gaps remain with

respect to this disturbance interaction (Hicke et al. 2012). Reciprocal interactions between insect outbreaks and wildfires are increasingly important to understand, as warming climate is implicated in both recent and projected increases in both disturbances (Bentz et al. 2010, Westerling et al. 2011).

Although research has begun to address the effects of bark beetle outbreaks on fuels and fire behavior/effects (Bebi et al. 2003, Kulakowski and Veblen 2007, Page and Jenkins 2007a, b, DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011, Hoffman et al. 2012a, b, Schoennagel et al. 2012), studies to date have focused almost exclusively on forests with climate-driven, stand-replacing fire regimes. For example, bark beetle-induced mortality has been found to significantly alter fuel profiles in *Pinus contorta* and *Picea engelmannii* forests,

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Corresponding Editor: B. P. Wilcox.

⁴ E-mail: ddonato@wisc.edu

but it is acknowledged that such forests generally burn at high severity with or without prior beetle outbreaks (Klutsch et al. 2011, Schoennagel et al. 2012). In contrast, drier, lower montane forests with mixed-severity fire regimes have received almost no study in this regard, despite being among the most widespread fire regimes in the temperate zone (Halofsky et al. 2011). Highly variable in structure and typified by sensitive thresholds between surface and crown fire behavior, these systems can be comparatively fuel limited, so that changes in stand structure may have important influences on fire potentials (Perry et al. 2011). Drier forests are speculated to respond differently to bark beetle outbreaks due to more open conditions, greater herbaceous cover, lower biomass, or lower tree-crown base heights (Parker et al. 2006, Jenkins et al. 2008, Hicke et al. 2012); however this hypothesis has received little empirical study.

Interior Douglas-fir (*Pseudotsuga menziesii* v. *glauca*) forests provide a key example of lower montane, mixed-severity fire ecosystems affected by bark beetle (*Dendroctonus pseudotsugae*) outbreaks. Characterized by both surface and crown fires over time and space (Baker 2009), interior Douglas-fir forests often possess fuel structures more similar to dry *Pinus ponderosa* forests than to *Pinus contorta* or mixed-conifer types (Cruz et al. 2003). Additionally, Douglas-fir comprises an exceptionally broad range of stand structure and composition, from dense closed-canopy forests on mesic sites to open parklands on xeric sites—the latter often ecotonal with low-elevation grasslands (Fig. 1; Despain 1990, Barrett 1994, Heyerdahl et al. 2006). Because bark beetle impacts on fuel profiles vary strongly depending on the state of the system prior to outbreak (DeRose and Long 2009, Klutsch et al. 2011, Hicke et al. 2012), variable forests such as Douglas-fir likely respond differently not only from other forest types but also among stands within the forest type.

We conducted a field study to examine the effects of Douglas-fir beetle outbreaks on fuel profiles of Douglas-fir forests in the Greater Yellowstone Ecosystem (GYE). Epidemic outbreaks (large-scale “mass attacks” of healthy live trees) in the 1980s, 1990s, and 2000s afforded an opportunity to quantify fuel profiles in stands of differing time since outbreak, across a wide range of pre-outbreak stand structures. Stands with ongoing/recent (1–3 yr), intermediate-term (4–14 yr), and old (25–30 yr) outbreaks were compared to each other and to undisturbed forests in terms of stand structure and fuel characteristics. We addressed the following questions: (1) How do fuel profiles that affect fire potentials vary among stands of differing time since bark beetle outbreak? (2) How do variations in fuel profiles associated with outbreak compare to variations associated with the wide range of stand structures for which Douglas-fir forests are known (dense mesic forests to open xeric parklands; Baker 2009)?

Bark beetle outbreaks are expected to initially reduce stand-level foliar moisture via tree-crown deaths (briefly

increasing crown fire initiation and spread potential), then thin canopies via needle/branch drop (reducing crown-fire spread and energy-release potential), increase surface loading of both live and dead fuels via increased light availability and needle/branch drop (increasing potential surface fire intensity and torching into tree crowns), and, in later stages, increase ladder fuels via growth of regenerating trees (increasing torching potential) (Page and Jenkins 2007a, b, Jenkins et al. 2008, DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011, Hicke et al. 2012, Hoffman et al. 2012b, Schoennagel et al. 2012). We hypothesized that, compared to other studied systems, lower montane forests would exhibit greater increases in live herbaceous fuels, lesser increases in coarse woody fuels, and higher importance of canopy fuel reductions because of already abundant herbaceous understories and relatively sparse trees. We further hypothesized greater within-stand spatial heterogeneity in fuels after beetle outbreak and that outbreak effects on fuels would be larger than the variability in background conditions.

To our knowledge this study represents one of the most detailed field assessments of post-disturbance fuels conducted to date, and the first to specifically compare disturbance effects to background variation in stand structure. We build on the methods of Simard et al. (2011) and Schoennagel et al. (2012), comprehensively sampling fuels in a replicated series of stands validated for pre-outbreak similarity via dendrochronology. We expand on prior work by refining canopy fuel estimates in post-outbreak stands and by evaluating changes in within-stand heterogeneity in fuels, as the spatial arrangement (not just mean loading) of live and dead fuels could influence fire propagation. Our focus is on fuel profiles rather than modeled fire behavior because currently available models have known shortcomings in post-disturbance environments that are yet to be resolved, and thus only account for a portion of beetle effects on fuels (Jenkins et al. 2008, Cruz et al. 2010, Klutsch et al. 2011, Hicke et al. 2012); as such, fuel profiles effectively contain more comprehensive and reliable information than fire models for this application. We report the key variables that drive fire models plus several for which available models cannot currently account (e.g., dead-tree foliar moisture, changes in spatial heterogeneity).

METHODS

Study area

The Greater Yellowstone Ecosystem (GYE) is centered in northwest Wyoming, USA, comprising ~80 000 km² of mountains and plateaus associated with the Yellowstone super-volcano. The area is representative of the Middle Rocky Mountains ecoregion, which extends over 200 000 km² of interior, largely coniferous montane forests (Omernik 1987). Our study occurred in the Lamar River drainage in northern Yellowstone National Park (“north zone,” latitude/longitude 44°55' N, 110°15' E), and the upper Snake River drainage in and around Grand Teton

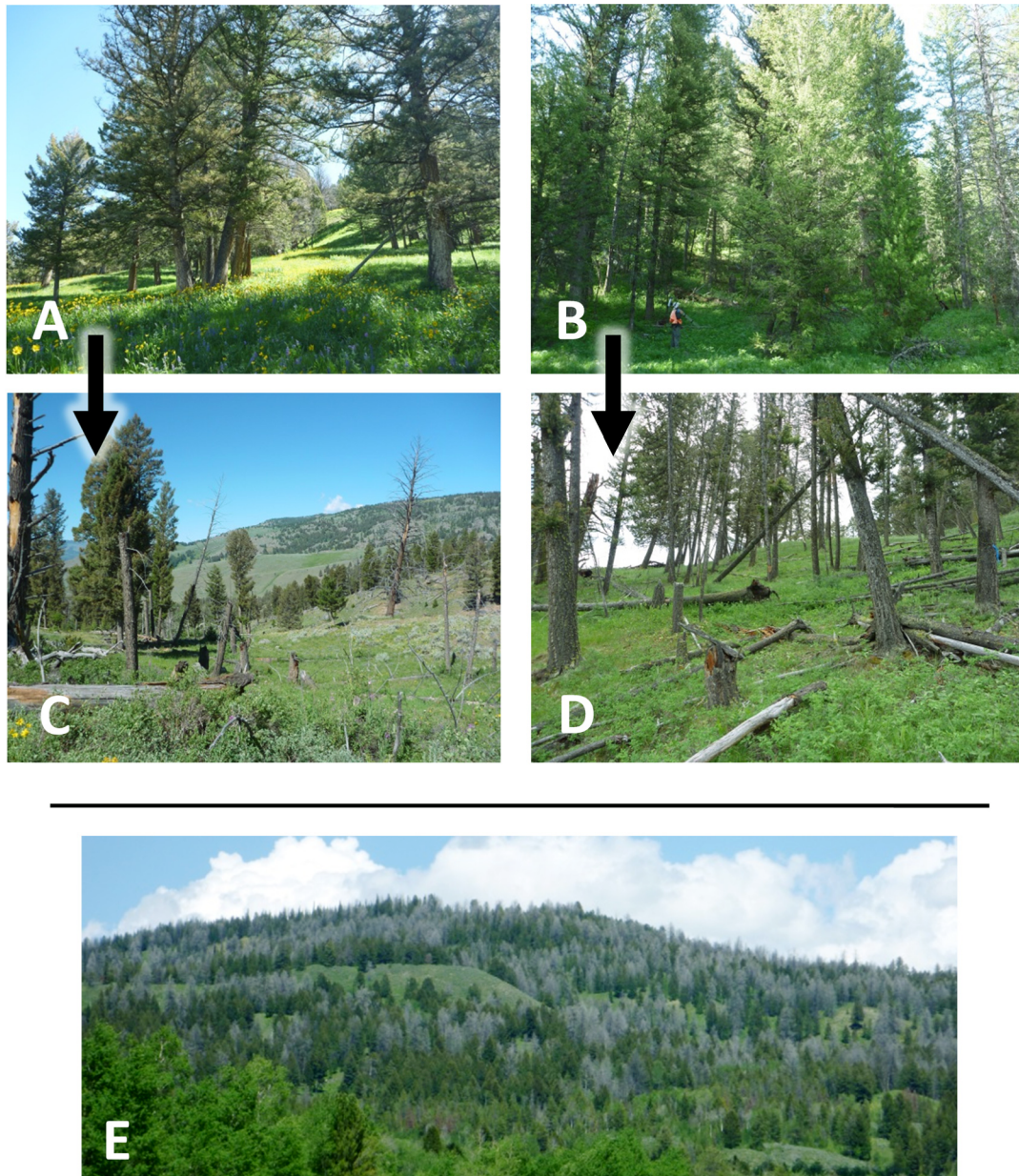


FIG. 1. Forest structures and bark beetle effects in Douglas-fir (*Pseudotsuga menziesii* v. *glauca*) forests of the Greater Yellowstone Ecosystem (GYE), Wyoming, USA. Undisturbed stands span a range of background conditions, from (A) low-basal-area parklands near the grassland (xeric) ecotone, to (B) high-basal-area forests in mesic sites. Stand structure after bark beetle outbreak varies widely between (C) low-basal-area and (D) high-basal-area stands (28 years post-outbreak in these examples). Douglas-fir beetle outbreaks in the GYE are typically (E) a partial disturbance at both stand and watershed scales. Photo credits: D. C. Donato.

National Park (“south zone,” 43°52′ N, 110°26′ E). Both zones are characterized by mean July high temperature of 25°C and mean January low of −15°C, while mean annual precipitation is 34 and 64 cm in the north and south zone, respectively (data *available online*).⁵ Slopes of study sites range between 10° and 30° (mean, 22°) on all aspects, at

elevations between 2000 and 2350 m. Soils are well drained and non-rhyolitic, derived from both sedimentary and volcanic/metamorphic parent materials.

Douglas-fir covers ~30% of the forested area of the GYE, typically occupying steep terrain at middle to low elevations. Common associates in mesic sites include lodgepole pine (*Pinus contorta* v. *latifolia*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies*

⁵ www.prism.oregonstate.edu

lasiocarpa); and in xeric sites include limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*). Abundant understories of tree regeneration, woody shrubs, and herbs are common in mesic sites, while open understories dominated by grasses and herbs are typical of xeric sites (Fig. 1). The fire ecology of interior Douglas-fir forests is poorly understood compared to other Rocky Mountain forest types, but the few published studies indicate a mixed-severity fire regime with small, low- to moderate-severity fires occurring at ~20–80 year intervals (prior to effective fire exclusion) and large or stand-replacing fire events occurring at longer intervals of perhaps 100–200 years (Houston 1973, Loope and Gruell 1973, Barrett 1994, Littell 2002, Korb 2005, Huerta et al. 2006, Baker 2009). The balance of these fire types almost certainly varies across the xeric–mesic gradient that Douglas-fir occupies, but such variation remains largely unstudied.

The Douglas-fir beetle is an important native disturbance agent in Douglas-fir forests, usually killing small groups of stressed or dying trees, but occasionally reaching epidemic population levels that mass-attack healthy live trees in outbreaks across large tracts of forest (Schmitz and Gibson 1996). Trees are attacked in early summer as adults bore under the bark and excavate galleries along which females oviposit (see Plate 1). Tree mortality occurs via girdling of the phloem layer by larvae and effects of associated fungi (Schmitz and Gibson 1996). After successful attack a tree's foliage turns red within a year, then drops from the canopy over the course of ~1–4 years. Stands are typically infested over the course of 4–6 years and only a portion of trees within a stand are killed (Negron 1998, McMillin and Allen 2003), generating a fine-scale mix of live trees and dead trees in varying stages of post-attack condition.

Sampling design

We measured forest fuels in 20 Douglas-fir stands that included undisturbed and up to 30-year post-outbreak conditions. Sampling was conducted in 2010 and included five stands in each of the following time-since-outbreak (TSO) classes commonly described in the literature (e.g., Simard et al. 2011): green (undisturbed); red stage (1–3 yr post-outbreak, with >50% of beetle-killed basal area retaining red needles and/or trees still being attacked); gray stage (4–14 yr post-outbreak, all beetle-killed trees with <50% needle retention, most fine branches still intact, no new attack occurring); and silver stage (25–30 yr post-outbreak, beetle-killed trees deteriorating structurally, also known as “old-attack”). Each class was sampled to span the continuum of Douglas-fir stand structures present in the GYE, from open xeric parklands to closed-canopy mesic forests (Fig. 1). Sample stands were multi-aged but had dominant trees ~150–200 years old; thus our data may be most relevant to forests of similar age, which are among the most commonly affected by *Dendroctonus* outbreaks. No signs of other recent disturbances were evident in the

field or in agency fire-history records. All stands within a class were separated by at least 1.7 km (mean 53 km apart), were interspersed with the other classes geographically, and were sampled in both the north and south zones. Abiotic characteristics of slope, aspect, elevation, and soil origin were all similar among the TSO classes (Table 1).

We used dendrochronological analysis (Appendix A) on 250 live-tree cores and 75 dead-tree samples to (1) reconstruct initial stand conditions and verify that all classes were similar prior to outbreak, and (2) verify the outbreak severity and timing of each TSO class (Johnson and Miyanishi 2008, Simard et al. 2011). In brief, stand reconstruction entailed subtracting post-outbreak growth and recruitment from the basal area of currently living trees, and adding in beetle-killed basal area after adjusting for falling, bark loss, and desiccation shrinkage (Appendix A). To establish outbreak timing, we cross-dated samples from beetle-killed trees against master chronologies constructed for each of the north and south sampling zones (Appendix A; Donato and Timme 2012). This analysis confirmed that all classes had similar pre-outbreak basal area (mean, 46.3 m²/ha), stem density (mean, 378 trees/ha), quadratic mean tree diameter (mean, 29.5 cm), and Douglas-fir dominance (mean 93%) (Table 1). Outbreak timing was confirmed to be 1–3 years prior to sampling for red stands, 4–14 years for gray stands, and 25–30 years for silver stands. Outbreak severity in beetle-affected stands was verified to be highly similar among TSO classes in both absolute and relative terms (Table 1).

Field measurements

We measured stand structure and fuels in a 0.25-ha (50 × 50 m) plot within each of the 20 stands. To assess canopy fuels, trees >1.4 m in height were surveyed in three parallel 6 × 50 m transects (300 m² each), spaced at 25-m intervals. For each live tree rooted in the transects, we recorded species, diameter at breast height (dbh; 1.4 m above ground), and total height and crown base height using a laser rangefinder/clinometer. Crown base height was considered to be at the lowest vertically contiguous green or red needles, usually the first full whorl. Dead trees were also recorded for standing or down status, broken-top presence and height, decay class (1–5, adapted from Harmon et al. (2011) to emphasize branch and bark loss), evidence of bark beetle attack (adult and larval galleries, exit holes, boring frass), and red needle retention level (100% retention/fading, >50% retention, 5–50% retention, or <5% retention). For needle-less dead trees that retained fine branches, which could still support transition to crown fire, we estimated crown base height using stand-specific outputs from a general linear model relating crown base height to dbh and stand for 1171 trees having both measurements ($R^2 = 0.60$) (Simard et al. 2011, Schoennagel et al. 2012). Trees with height <1.4 m were measured for species, live or dead status, height,

TABLE 1. Comparison of pre-outbreak forest stand characteristics and outbreak severity among the time-since-outbreak (TSO) classes (mean with SE in parentheses) from our study of *Dendroctonus pseudotsugae* beetle outbreaks in interior Douglas-fir (*Pseudotsuga menziesii* v. *glauca*) stands in Greater Yellowstone, Wyoming, USA.

Characteristic	Green (undisturbed)	Red (1–3 yr post-outbreak)	Gray (4–14 yr post-outbreak)	Silver (25–30 yr post-outbreak)	One-way ANOVA	
					$F_{3,16}$	P
Abiotic						
Slope (°)	20.6 ^a (2.6)	24.0 ^a (3.1)	24.2 ^a (3.1)	19.2 ^a (4.3)	0.56	0.65
Aspect (cosine transform)	1.12 ^a (0.29)	1.18 ^a (0.27)	1.01 ^a (0.26)	1.06 ^a (0.38)	0.06	0.98
Elevation (m)	2110 ^{ab} (38)	2234 ^a (38)	2246 ^a (43)	2041 ^b (49)	5.51	0.01†
Soil origin	volcanic/ metamorphic, sedimentary	volcanic/ metamorphic, sedimentary	volcanic/ metamorphic, sedimentary	volcanic/ metamorphic, sedimentary		
Biotic (pre-outbreak)‡						
Basal area (m ² /ha)	41.1 ^a (4.4)	56.8 ^a (6.7)	43.5 ^a (6.7)	43.6 ^a (6.8)	1.30	0.31
Overstory stem density§ (trees/ha)	427 ^a (73)	361 ^a (59)	341 ^a (31)	381 ^a (98)	0.28	0.84
Quadratic mean diameter (cm)	23.6 ^a (3.3)	37.5 ^a (5.6)	28.3 ^a (2.9)	28.6 ^a (2.4)	2.37	0.11
Douglas-fir dominance (% of basal area)	88.2 ^a (7.3)	91.0 ^a (6.6)	96.2 ^a (2.1)	96.2 ^a (2.7)	0.59	0.63
Disturbance severity¶						
Beetle-killed basal area (m ² /ha)	2.2 ^a (2.0)	31.4 ^b (2.7)	26.6 ^b (5.2)	26.2 ^b (5.4)	8.83	0.001
Outbreak severity (% basal area killed)	4.0 ^a (3.5)	57.2 ^b (6.3)	60.2 ^b (7.3)	59.8 ^b (5.4)	29.9	<0.001

Note: Superscript letters are results of Tukey-Kramer comparisons among TSO classes within a one-way ANOVA; entries with different lowercase letters are statistically different ($\alpha = 0.05$).

† Statistically but not biologically significant because of narrow elevation range sampled; we confirmed that elevation was not associated with pre-outbreak basal area ($P = 0.35$, $R^2 = 0.05$), stem density ($P = 0.33$, $R^2 = 0.04$), quadratic mean diameter ($P = 0.35$, $R^2 = 0.05$), or Douglas-fir dominance ($P = 0.52$, $R^2 = 0.02$).

‡ Reconstructed via dendroecological analysis.

§ All trees with dbh >15 cm.

¶ In this summary, live-but-fading “green attack” trees in red stands are classified as beetle-killed to reflect eventual outbreak severity.

and crown base height. Canopy cover was measured, using a spherical densiometer with one user, at 12 systematic points within each stand.

Surface fuels were measured along ten 20-m long planar intercept transects (Brown 1974) originating at regular intervals along the outer tree transects. Five surface fuel transects were oriented in the southwest–northeast direction, and five in the northwest–southeast direction. Down-wood particles <0.64 cm (1-h fuels) and 0.64–2.54 cm (10-h fuels) were tallied along a 2-m subsection of each sampling plane, particles 2.54–7.62 cm (100-h fuels) were tallied along a 5-m subsection, and particles >7.62 cm (1000-h fuels) were recorded for diameter, species, and decay class along the entire 20-m sampling plane. Depths of the litter (recognizable organic matter) and duff (decayed, unrecognizable organic matter) layers were recorded at two systematic points along each transect, and dead fuel depth (distance from bottom of litter layer to highest particle in plane) was recorded in three systematic 0.5-m intervals along each transect. Surface vegetation and ground cover characteristics were recorded in twenty 0.25-m² micro-plots, one at the start and end of each of the 10 planar intercept transects. We recorded percent cover and height of tall woody shrubs (>20 cm height), low shrubs, herbs, and graminoids, and percent cover of litter, wood, bryophytes, bare soil, and rock.

To assess the effects of beetle outbreak on surface temperatures and relative humidities during summer

(i.e., fire season) we deployed micrometeorological probes in three stands in each TSO class (iButton; Maxim Integrated Products, Dallas Semiconductor, Sunnyvale, California, USA). Measured stands spanned the range from cool to warm aspects in each class (Kruskal-Wallis test on cosine-transformed aspect vs. TSO class, $P = 0.87$, mean 1.0 out of possible range 0–2). In each stand an air temperature and relative humidity (RH) probe in a ventilated white PVC tube was installed on a tree at 1.5 m above ground level. Temperature probes were also installed at the litter–duff interface at three systematic locations in each stand. Temperature and RH were recorded every 2 h with a resolution of 0.5°C and 0.6%, respectively, between 10 July and 15 August 2010. For analysis we summarized temperature and RH data into daily mean and daytime hours (10:00–18:00 hours) mean values.

Fuel computations

We used field data to generate a comprehensive fuel profile for each stand. These data provide very similar inference as common fire models, as they include the main variables that drive model outputs, plus others for which models cannot currently account. Chief among the model-driving responses are canopy bulk density (amount of fuel per unit volume of canopy, a determinant of mass flow rate and spread potential of crown fire), available canopy fuel load (potential energy available for release from crown fuels), canopy base



PLATE 1. Bark beetle galleries on a recently killed Douglas-fir tree, Greater Yellowstone, USA. Photo credit: D. C. Donato.

height (vertical gap beneath the base of tree crowns, which affects the ability of fire to move vertically from the surface to the canopy), and surface fuel loads by size class and live/dead category (which affect fireline intensity, spread, and transition to crowns) (see Van Wagner 1977, Rothermel 1983, Cruz et al. 2003, Reinhardt and Crookston 2003, Reinhardt et al. 2006).

Crown fuel masses of foliage and 1-h, 10-h, and 100-h woody fuels were estimated for each tree using species-specific equations for Rocky Mountain conifers based on dbh, height, and/or crown length (Brown 1978). Following convention, we use the term “crown” for tree-level metrics and “canopy” for stand-level metrics (Cruz et al. 2003). For dead trees, each individual was corrected for loss of needle biomass based on a multiplier representing the midpoint of its red-needle retention level: 1.0, 0.75, 0.25, and 0.0, respectively, for the fading/100%, 50–100%, 5–50%, and <5% red-needle ratings. This approach allows for all red trees to retain all their needles if the outbreak is recent and synchronous. We similarly corrected for branch loss using the decay-class rating of each dead tree (adapted from Harmon et al. 2011): 1-h fuels were designated as 0% loss for decay class 1 and 100% loss for all other decay classes; 10-h and 100-h fuels were designated across decay classes 1–5 as 0%, 20%, 50%, 80%, and 100% loss, respectively. Broken-top trees had a fraction of their crown fuel deducted based on the ratio of remaining crown length to original crown length derived from a crown length : dbh regression for 1018 unbroken trees in our data set ($R^2 = 0.78$).

Available canopy fuel load (ACFL) was computed as the sum of live and dead foliage, plus 50% of the live 1-h

fuels and 100% of dead 1-h fuels, across all trees (Reinhardt et al. 2006). Vertical profiles of canopy fuels were generated by distributing available crown fuel for each tree along its crown length in 0.25-m vertical bins, and summing by bin across all trees in a stand. This approach is employed by the Fire and Fuels Extension of the Forest Vegetation Simulator (Reinhardt and Crookston 2003) and in several studies of canopy fuels (Reinhardt et al. 2006, Simard et al. 2011, Schoennagel et al. 2012). Although the method assumes a vertically uniform distribution of fuels along individual tree crowns, other crown-shape equations are not available for species in our study area and, most importantly, this method has been validated via independent field data to produce unbiased canopy bulk density (CBD) estimates and to accurately reflect actual canopy profiles in this region (Reinhardt et al. 2006). Effective CBD was computed as the maximum of a 3-m running mean of the profile within each stand (Reinhardt et al. 2006); however we also graphically present 1-m bins to better evaluate vertical heterogeneity in canopy fuels.

Effective canopy base height (CBH) was defined as the lowest height at which CBD (including both live and dead fuels) exceeded 0.04 kg/m^3 , a commonly used value that the few empirical validations have supported in terms of the ability to support crown fire initiation (Sando and Wick 1972, Cruz 2004; see also Mitsopoulos and Dimitrakopoulos 2007). Because no universal solution exists for assessing canopy base height (Cruz and Alexander 2010), we also compare CBH results using a threshold CBD of 0.011 kg/m^3 (Scott and Reinhardt 2001) and by using the mean of tree crown base heights within a stand (Cruz et al. 2003).

Evaluating canopy-level foliar moisture in outbreak stands is challenging due to the spatial mix of live and dead tree crowns, with high and low moisture content, respectively. Most fire-prediction frameworks require stand-level canopy moisture, but there are limitations to such spatial averaging, which may obscure patchy influences on fire behavior. We therefore took two complementary approaches. First, we estimated stand-level canopy foliar moisture by applying a standard assumption for live-needle moisture of 100%, and a reduced moisture for dead needles, then computing an abundance-weighted average within each stand. Estimates of dead-needle moisture are available for *P. contorta* (~10–20%; Jolly et al. 2012) but not for *P. menziesii*; we therefore applied a conservative estimate of 5%. Second, we summarized the separate abundances of live trees, dead trees with needles and fine branches, and dead trees with no needles and fine branches.

We computed the mass of surface woody fuels by size class using standard geometric scaling and species- and decay-class-specific wood density values (Brown 1974, Harmon and Sexton 1996). For coarse (1000-h) fuels, biomass was summarized separately for sound (decay class 1–3) and rotten (decay class 4–5) particles. Dry biomass of live understory fuels was estimated using percentage cover data and previously published allometric equations for the GYE (Turner et al. 2004, Simard et al. 2011). Biomass of shrubs was summed to obtain live woody fuel load; biomass of forbs, grasses, and sedges was summed to obtain herbaceous fuel load. All surface and canopy fuel data were slope-corrected to obtain estimates per hectare.

Data analysis

To evaluate beetle outbreak effects while accounting for the inherent variation in Douglas-fir stand structure (Fig. 1), we analyzed fuel responses within a general linear model (GLM) that included predictors of TSO class (categorical) and pre-outbreak basal area (continuous). Basal area was chosen as the integrative metric of pre-existing structure because of its well-established use as an indicator of forest stature and biomass density (Husch et al. 2003), its known strong correlations with canopy fuel characteristics including ACFL and CBD (Cruz et al. 2003), and its observed correspondence with the xeric-mesic gradient of Douglas-fir forests in the GYE (basal area increases from xeric to mesic stands; Fig. 1). In essence, our approach was to regress a given fuel metric against pre-outbreak basal area, then test for statistically significant shifts in the regression line among TSO classes. We did not formally evaluate interaction terms in the GLMs owing to insufficient available degrees of freedom (however, exploratory analyses with them included did not suggest important interactions; $P > 0.10$ for virtually all possible interaction terms). Pre-outbreak basal area was retained in all the GLMs for consistency and because, even when not significant (minority of cases), the sign of the basal area effect (+

or –) was ecologically sensible for both canopy and surface fuels (Appendix B). Residuals and model fits were checked using diagnostics described by Ramsey and Schafer (2002). Percentage data were logit-transformed prior to analysis (Ramsey and Schafer 2002).

For fuel and cover data, basal-area-corrected means and standard errors for each class were obtained by centering the regression on the grand mean basal area and extracting the intercept terms from the GLM (Ramsey and Schafer 2002). Bar graphs therefore represent the responses at the grand mean pre-outbreak basal area. To aid interpretation, we present family-wise Tukey-Kramer comparisons among TSO classes after accounting for pre-outbreak basal area. Because our field observations suggested wide natural variability in this system, we interpreted P below an α -level of 0.05 as strong evidence of differences, and $P < 0.10$ as suggestive/moderate evidence. This approach guards against missing ecologically meaningful effects because of modest sample size (i.e., Type II error).

We also used the GLM framework to compare the influence of beetle outbreaks to background variation associated with the xeric-mesic gradient. The background effect represented the range in a given fuel metric in undisturbed stands, obtained by extracting the slope term from the model (relationship between fuel metric and pre-outbreak basal area) and multiplying it by a representative range of basal area in undisturbed stands. The basal area range was obtained using reconstructed pre-outbreak basal area in all 20 stands. To be conservative, we used the 10th and 90th percentiles of basal area rather than the raw range in order to avoid influence of extremes; the resulting range was 31–61 m²/ha. For the beetle outbreak effect we considered the largest effect size possible, by computing the maximum difference in means between the undisturbed condition and any post-outbreak class.

The above GLM framework was only employed for fuels and cover data that are likely associated with pre-outbreak stand structure; for other responses such as estimated foliar moisture content and pre-outbreak validations, a one-way ANOVA among TSO classes was used. For microclimate data, we applied nonparametric Kruskal-Wallis tests due to smaller sample size. All analyses were conducted using the program R, version 2.12.0 (R Development Core Team 2009).

To assess changes in fine-scale heterogeneity of fuels within stands, we computed the coefficient of variation (CV) in fuels among transects within each plot (Fraterrigo and Rusak 2008). This approach still treats the stand as the experimental unit, with one value for each stand; however the response becomes the variation among subsamples within the plot, rather than their mean. We computed this within-stand CV for broad classes of surface fuels as well as canopy fuels in different strata. We computed heterogeneity in ACFL separately for the lower (<10 m height), middle (10–20 m), and top (>20 m) canopy strata. We additionally

TABLE 2. Post-outbreak stand structure in each of the time-since-outbreak (TSO) classes (data are means with SE in parentheses).

Characteristic	Green (undisturbed)	Red (1–3 yr post-outbreak)	Gray (4–14 yr post-outbreak)	Silver (25–30 yr post-outbreak)	One-way ANOVA	
					$F_{3,16}$	P
Basal area (m ² /ha)						
Live	35.5 ^a (2.7)	26.4 ^{ab} (5.2)	16.3 ^b (3.9)	14.5 ^b (4.1)	5.74	0.007
Dead	5.6 ^a (3.0)	29.0 ^b (5.8)	28.1 ^b (5.3)	21.1 ^{ab} (4.0)	7.78	0.002
Quadratic mean diameter (cm)						
Live	23.6 ^a (3.3)	32.7 ^a (6.7)	21.9 ^a (4.5)	24.0 ^a (3.0)	1.10	0.38
Dead	17.4 ^a (3.0)	40.0 ^b (4.4)	36.4 ^b (1.9)	31.9 ^b (3.3)	9.18	<0.001
Stem density in overstory (trees/ha)†						
Live	364 ^a (61)	198 ^{ab} (24)	181 ^{ab} (36)	164 ^b (63)	3.55	0.038
Dead (fine fuels attached)	19 ^a (14)	104 ^{ab} (10)	121 ^b (38)	36 ^{ab} (12)	5.32	0.010
Dead (fine fuels fallen)	45 ^a (21)	47 ^a (28)	61 ^a (38)	136 ^a (31)	2.06	0.146
Stem density in understory (trees/ha)						
Live	654 ^a (271)	289 ^a (165)	369 ^a (128)	183 ^a (70)	1.34	0.300
Dead (fine fuels attached)	45 ^a (19)	37 ^a (14)	23 ^a (21)	62 ^a (36)	0.49	0.693
Dead (fine fuels fallen)	35 ^a (9)	86 ^a (46)	61 ^a (28)	46 ^a (18)	0.59	0.632

Note: Superscript letters are results of Tukey-Kramer comparisons among TSO classes within a one-way ANOVA; entries with different lowercase letters are statistically different ($\alpha = 0.05$).

† The overstory–understory threshold is 15 cm dbh. Dead trees were classified as having fine fuels attached if they retained components that contribute to available canopy fuel load (foliage or twigs <0.64 cm diameter) (Reinhardt et al. 2006). In this summary, live-but-fading trees in red stands are classified as currently live to reflect actual stand conditions rather than eventual outbreak severity.

computed ACFL heterogeneity along the vertical dimension, using the CV among 1-m canopy layers.

RESULTS

Post-outbreak stand structure

Stand structure in each of the TSO (time-since-outbreak) classes reflected the partial and gradual nature

of Douglas-fir beetle outbreaks (Table 2, Fig. 2). Outbreak severity ranged between 38% and 83% of pre-outbreak basal area and did not differ among red, gray, and silver TSO classes (mean 59%, compared to the endemic level of 4% in green stands) (Tables 1–2, Fig. 2). Live basal area declined with time since outbreak, but remained at 14–16 m²/ha in gray and silver stands (Table 2, Fig. 2). Live stems were as

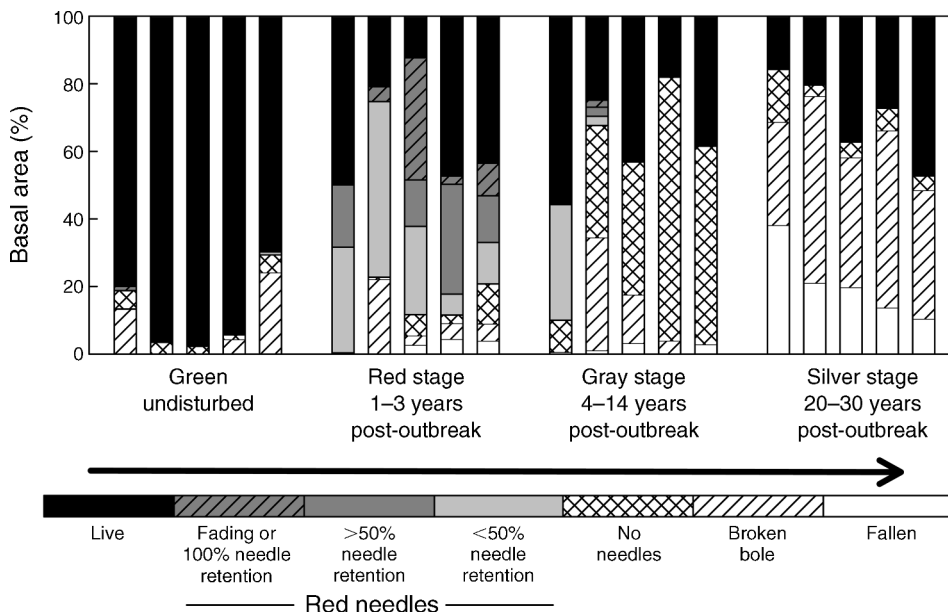


FIG. 2. Progression of stand structure with time since outbreak (TSO). Each column represents a sample Douglas-fir stand. Basal areas include trees standing at the time of outbreak. All stages contained a mix of live trees and beetle-killed trees with different levels of post-death fragmentation, reflecting the partial and gradual nature of the disturbance. Beetles typically killed ~40–80% (mean 59%) of basal area within stands. (See Methods: Sampling design for a description of the TSO classes.)

numerous as dead stems in all TSO classes, even in the overstory (Table 2).

The gradual nature of the outbreak is apparent in the structure of red stands (Fig. 2), which included a mix of fading trees (current attack), those of both high and low needle retention, and some trees with complete needle loss. Dendrochronological analysis also showed peak outbreak periods lasting 4–7 years (Appendix A). Minor amounts of stem breakage began in the gray stage, and by the silver stage 25–30 years after peak mortality, most beetle-killed stems were broken topped, with a lesser portion having fallen completely (Fig. 2).

Canopy fuels

After accounting for pre-outbreak basal area, there were significant reductions in available canopy fuel load and canopy bulk density with increasing time since outbreak (Figs. 3 and 4A, B). Total available canopy fuel load (ACFL) declined monotonically and was approximately halved by the silver stage (8.0 vs. 17.0 Mg/ha in green stands); however, the proportion dead was elevated in both the red and gray stages (Fig. 4A). Foliage biomass began declining in the red stage (8.0 Mg/ha vs. 12.1 Mg/ha in green stands; Fig. 4G). Canopy bulk density declined by ~30% in post-outbreak stands compared to green stands (0.10 kg/m^3 ; Fig. 4B); the initial decline in the red stage is significant at the $\alpha=0.10$ level. Effective canopy base height increased in post-outbreak stands and became significantly higher by the silver stage (3.4 m) compared to green stands (0.6 m) (Fig. 4C). Estimated stand-level foliar moisture content, the weighted average for all live and dead needle biomass, decreased significantly to 75% in red stands, from effectively 100% in green stands and other post-outbreak stages (Fig. 4H). See Appendix B for full statistical outputs from GLMs of all canopy fuel variables, including their live and dead subcomponents.

Pre-outbreak basal area was an important correlate with post-outbreak canopy fuel properties, confirming its use in representing the effect of preexisting stand structure. As a predictor within the GLMs, pre-outbreak basal area was significant for 14 of 18 canopy fuel metrics (see Appendix B). Ranges in canopy fuels in undisturbed stands, associated with the xeric–mesic gradient, were on par with beetle outbreak effects (Fig. 5).

The use of alternative methods for canopy fuel calculations only made a difference for canopy base height (CBH). Computing CBH using a threshold of 0.011 kg/m^3 (Reinhardt et al. 2006) resulted in much lower CBH values (mean, 0.5 m), while the simple-means method of Cruz et al. (2003) yielded similar absolute values as ours (mean, 2.6 m); both alternative approaches resulted in no significant differences in canopy base height among TSO classes. Computing canopy bulk density (CBD) via the method of Cruz et al. (2003) (dividing ACFL by canopy depth) yielded the same qualitative results as shown in Fig. 4B, with higher absolute values (mean 0.16 kg/m^3).

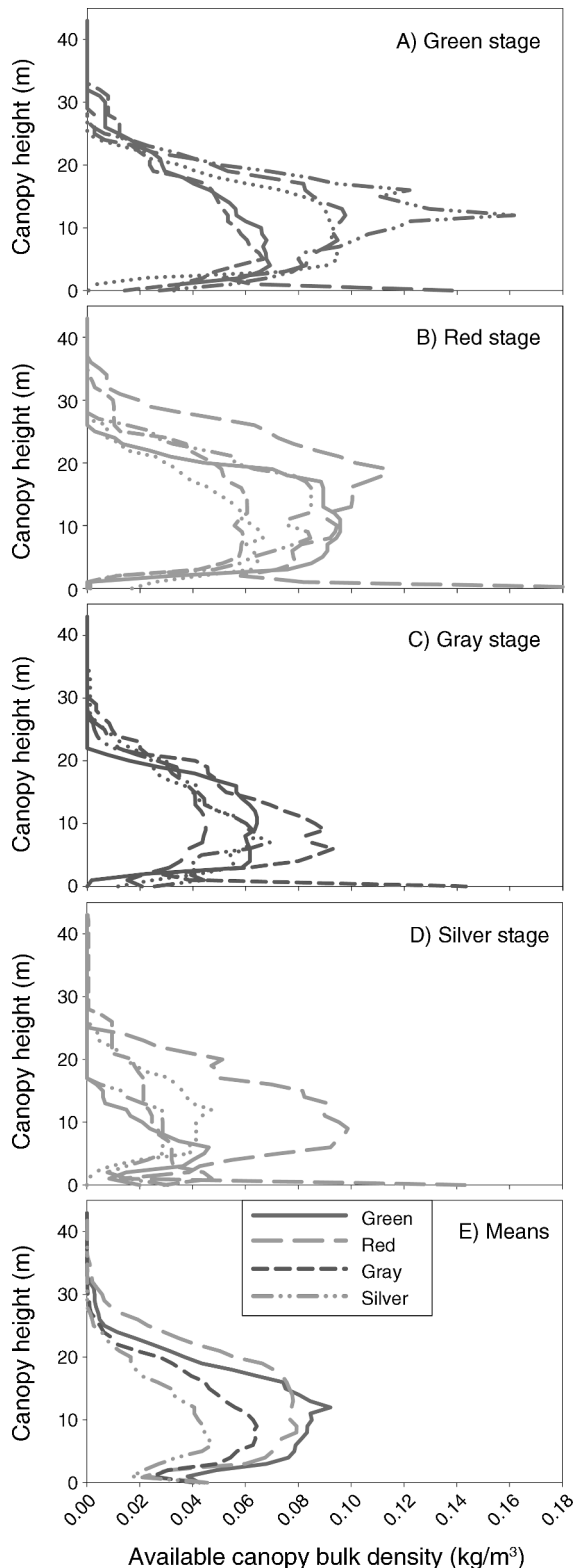


FIG. 3. Vertical profiles of available canopy fuel in each of the five stands within time-since-outbreak (TSO) class, and averaged by class. Classes are: green (undisturbed), red (1–3 yr), gray (4–14 yr), and silver (25–30 yr).

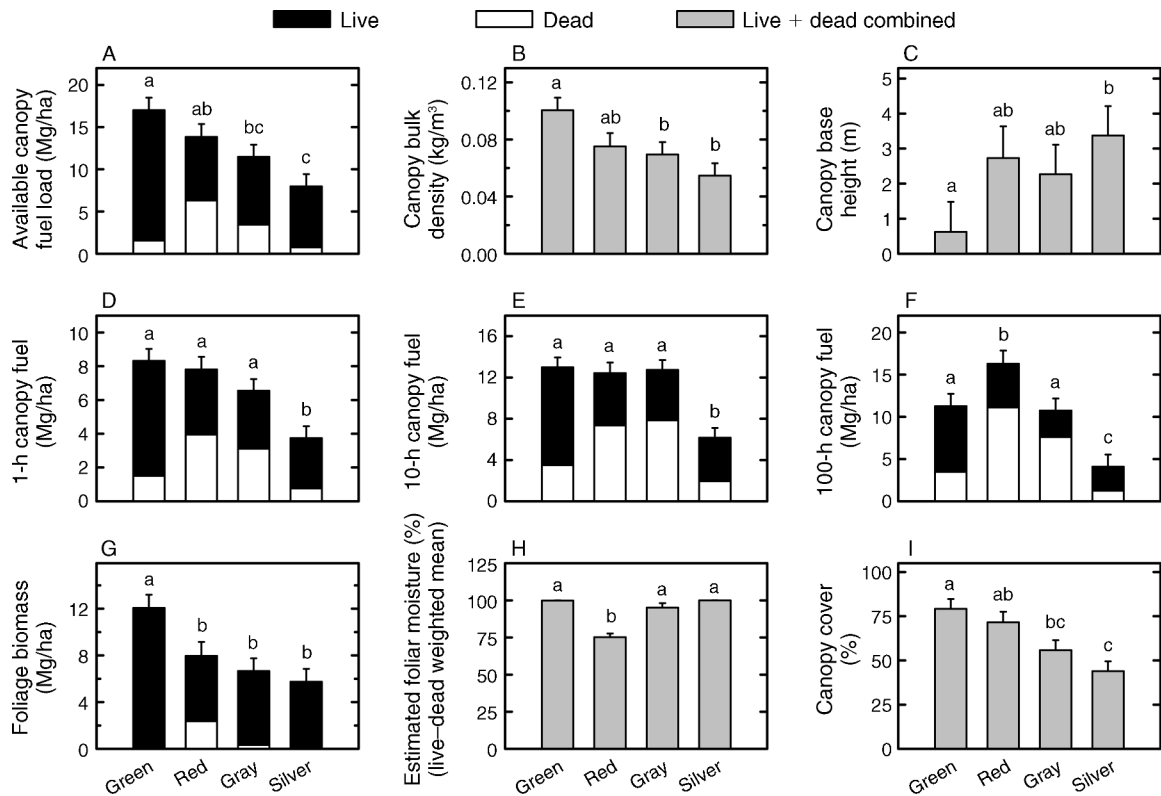


FIG. 4. Canopy fuels in each time-since-outbreak (TSO) class (green, red, gray, and silver). Bars represent basal-area-corrected mean values (i.e., the response value at the mean basal area) and standard errors from the general linear model (GLM). Lowercase letters are results of Tukey-Kramer pairwise comparisons among groups ($\alpha = 0.05$), after accounting for variation in pre-outbreak conditions (basal area). See Appendix B for full statistical outputs from the GLM for all variables, including live/dead subcomponents. Fuel size classes are standard time-lag classes: 1-h fuels, <0.64 cm diameter; 10-h fuels, 0.64 – 2.54 cm; 100-h fuels, 2.54 – 7.62 cm. Note that estimated canopy foliar moisture is a weighted average including all live and dead foliage within a stand; for separate abundances of live and dead tree crowns, see Table 2.

Surface fuels

There were few significant changes in surface fuels associated with beetle outbreak, after accounting for pre-existing variation in stand basal area (Fig. 6). Most size classes of surface woody fuels showed no trend with time since outbreak (Fig. 6A–E), except that silver stands had comparatively low levels of 1-h fuels and high levels of 1000-h sound fuels (see Appendix B for comparisons with $\alpha = 0.10$). The only other significant response was herbaceous biomass, which showed an increase in the red stage that was moderately significant (Fig. 6I; Appendix B). Full statistical outputs from GLMs for all surface fuel variables are in Appendix B.

Pre-outbreak basal area was an important correlate with post-outbreak surface fuel properties, with significant effects for 8 of 13 surface fuel metrics within the GLMs (Appendix B). Ranges in surface fuel loads in undisturbed stands, associated with the xeric-mesic gradient, were greater than the beetle outbreak effect for woody fuels and of similar or less magnitude for live herbaceous fuels and forest floor depth (Fig. 5).

Within-stand heterogeneity in fuels

Within-stand coefficients of variation (CV) showed increasing spatial heterogeneity with time since outbreak for several fuel components (Fig. 7). For canopy fuels, horizontal heterogeneity showed an increasing trend with time since outbreak in all of the top, middle, and lower canopy strata (Fig. 7A–C), with the effect most significant in the middle stratum. Absolute magnitudes of the CV tended to decrease from the heterogeneous top layer (Fig. 7A) to the more homogeneous bottom layer (Fig. 7C). Vertical heterogeneity in canopy fuels also increased significantly with time since outbreak (Fig. 7D). No significant trend was apparent for crown base heights, which had very low CVs in general (Fig. 7H). For surface fuels, spatial heterogeneity in forest floor depth (litter + duff) increased significantly with time since outbreak, mainly in silver stands compared to other classes (Fig. 7E). Trends were less clear and were not significant for heterogeneity of surface fine or coarse woody fuels (Fig. 7F, G).

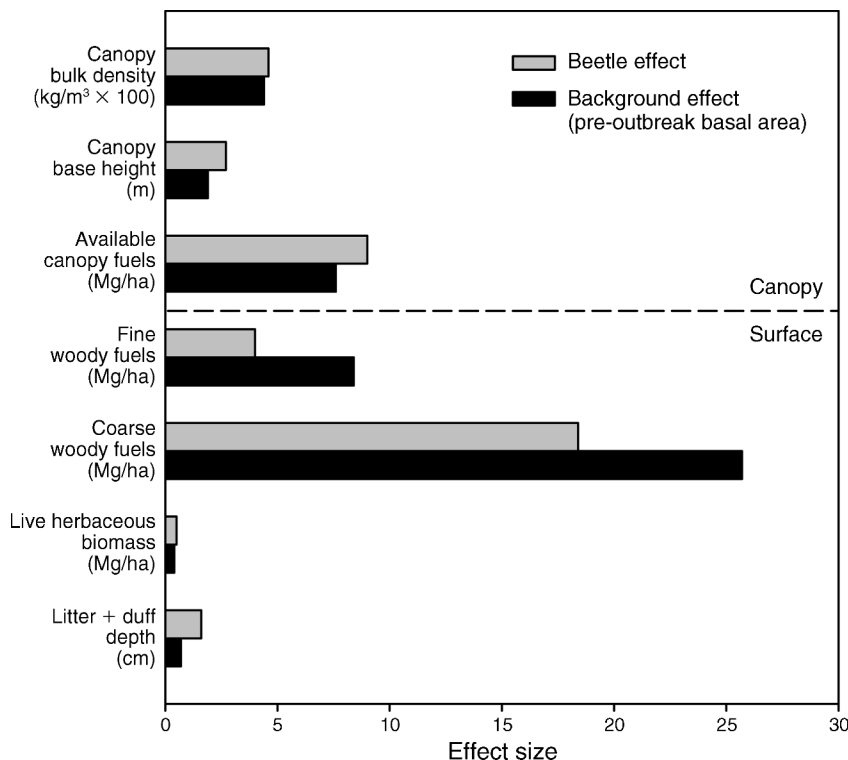


FIG. 5. Relative effect size on fuels of beetle outbreak (gray) vs. background variability in pre-outbreak conditions (black). Background variation value is the range present in undisturbed green stands, obtained by multiplying the basal area effect (regression slope from GLM) times a representative range of basal areas for undisturbed stands (10th and 90th percentiles to avoid influence of extremes, equating to 31–61 m²/ha). For the beetle outbreak, effect size is the maximum difference in means between any post-outbreak class and undisturbed green stands (Figs. 4 and 6; see also Appendix B). Fine woody fuels are those with 1–100-h particles (<7.6 cm); coarse woody fuels comprise all 1000-h particles (>7.6 cm).

Microclimate

We found few ecologically significant trends in microclimate. There were no significant associations with TSO class for relative humidity (RH) daily mean (Kruskal-Wallis $P = 0.82$; mean, 55%) or RH daytime-hours mean ($P = 0.40$; mean, 48%), nor for ground temperature mean ($P = 0.91$; mean, 13°C) or daytime-hours mean ($P = 0.87$; mean, 16°C). Air temperature daily mean was also not significant ($P = 0.16$; mean, 15°C), while daytime-hours air temperature was marginally significant ($P = 0.09$) but with a small effect size (gray stands 21°C vs. 20°C in other stands).

DISCUSSION

Douglas-fir beetle outbreak was associated with altered fuel profiles in Douglas-fir forests of Greater Yellowstone; however the magnitude and importance of these changes (and resulting stand structures) were comparable to the range of pre-outbreak stand conditions. The strongest effects of beetles were canopy thinning and increased spatial heterogeneity of fuels over post-outbreak time, whereas effects on surface fuels were generally minor after accounting for background variation. These results highlight how bark beetle impacts on fuel profiles may differ between lower

montane forests and other systems, as well as the importance of the gradual and partial nature of beetle disturbance in determining post-outbreak fuel dynamics.

Our study analyzed results in four stages after beetle outbreak in a stand: green (undisturbed), red (1–3 yr post-outbreak), gray (4–14 yr post outbreak), and silver (25–30 yr post-outbreak).

Beetle impacts in lower montane, mixed-severity fire forests

Canopy fuels.—Consistent with findings in *Pinus contorta* and *Picea engelmannii* forests (Page and Jenkins 2007a, DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012), a primary effect of beetles was to thin canopy biomass, culminating in 50% loss in silver stands (Fig. 4B, Appendix B). However, initial canopy bulk density in green Douglas-fir stands (0.10 kg/m³) was much lower than in more mesic forests (0.14–0.20 kg/m³; Page and Jenkins 2007a, b, Simard et al. 2011, Schoennagel et al. 2012, see also Cruz et al. 2003). Post-outbreak Douglas-fir stands (0.06–0.08 kg/m³) thus had lower absolute values than in other forest types (0.07–0.13 kg/m³). This finding is consistent with expectations in sparsely treed systems, and suggests that outbreaks lead to especially low

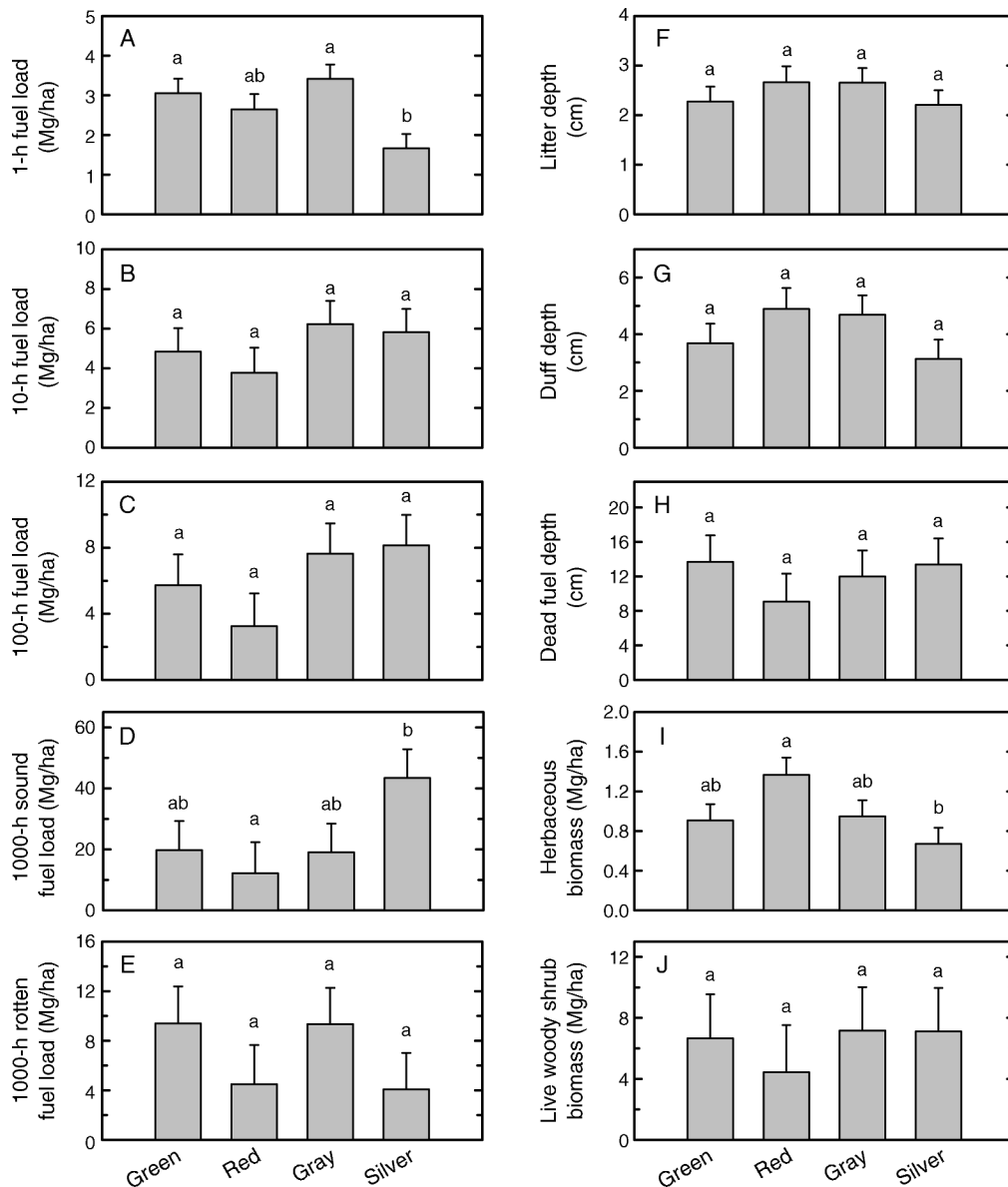


FIG. 6. Surface fuels in each time-since-outbreak (TSO) class. Statistical outputs are the results of general linear models (GLMs) with predictors of pre-outbreak basal area and time since outbreak. Bars represent basal-area-corrected mean values (i.e., the response value at the mean basal area) and standard errors from the GLM. Lowercase letters are results of Tukey-Kramer pairwise comparisons among groups ($\alpha = 0.05$), after accounting for variation in pre-outbreak conditions (basal area). See Appendix B for full statistical outputs from the GLM for all variables. Fuel size classes are standard time-lag classes: 1-h fuels, <0.64 cm diameter; 10-h fuels, 0.64–2.54 cm; 100-h fuels, 2.54–7.62 cm, 1000-h fuels, >7.62 cm.

crown-fire spread potential in these forests once needles and fine branches fall.

Significant foliage loss and reduction of canopy bulk density began even in the red stage (Fig. 4G; Appendix B), consistent with the few other empirical studies (Simard et al. 2011, Schoennagel et al. 2012). This trend is not incorporated in most conceptualizations of the red stage, which generally emphasize a reduction in canopy foliar moisture without significant needle drop. The

difference between predicted and observed patterns may be ascribed to the gradual nature of most *Dendroctonus* outbreaks, which usually occur over a period of 3–7 years (Appendix A; Negron 1998, McMillin and Allen 2003, Klutsch et al. 2011, Meigs and Kennedy 2011, Simard et al. 2011, DeRose and Long 2012). Initially, foliar moisture would be reduced for some trees before any needles drop, a 1–2 year window that has not yet been reported quantitatively; however by the classic

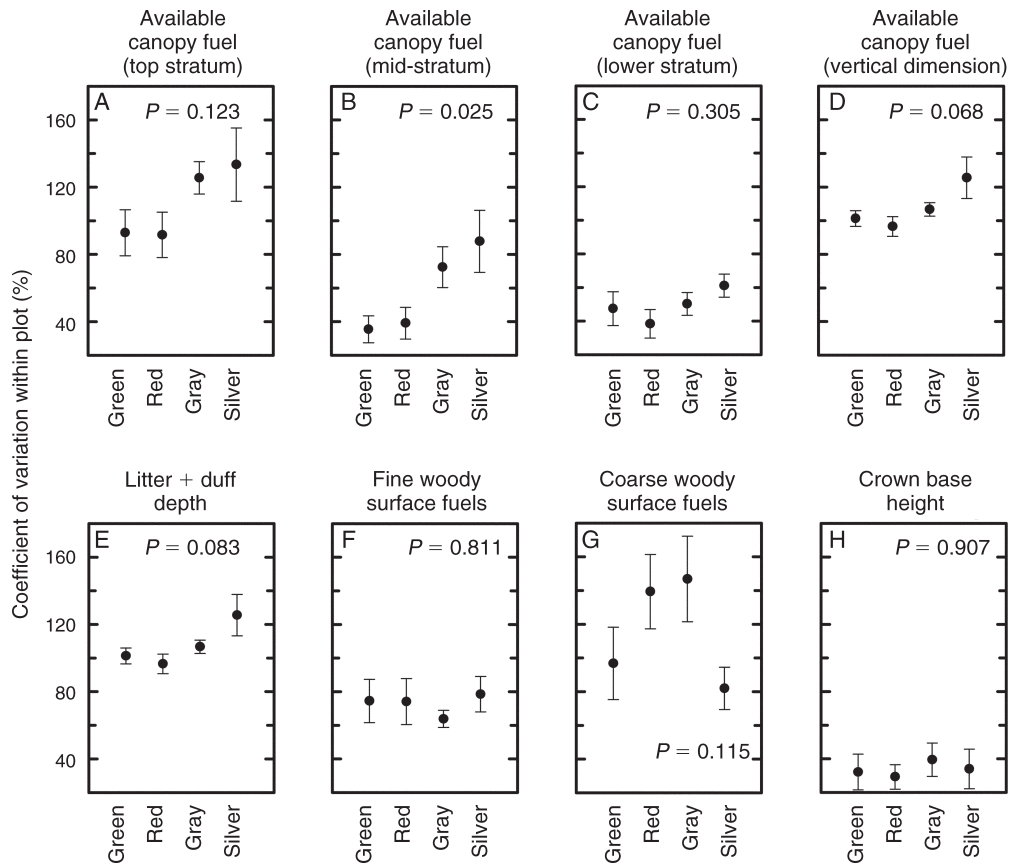


FIG. 7. Fine-scale (within-stand) spatial heterogeneity of fuels in each time-since-outbreak (TSO) class (data are means \pm SE). The coefficient of variation within each sample plot is derived by computing the standard deviation among subsamples (transects) and scaling by the plot mean, generating a single estimate of fine-scale heterogeneity for each stand (Fraterrigo and Rusak 2008). Horizontal heterogeneity in canopy fuels is shown for the (A) bottom (0–10 m height), (B) middle (10–20 m height), and (C) top (>20 m height) strata, as well as for the (D) vertical dimension (variation along z-axis among 1-m canopy layers). (E–G) Surface fuel variation is shown by aggregated size class (fine woody fuels are those with 1–100-h particles [<7.6 cm]; coarse woody fuels comprise all 1000-h particles [>7.6 cm]), and (H) crown base height includes live and dead trees. Statistical outputs are results of one-way ANOVA among TSO classes. Note that these within-plot CVs differ fundamentally from more traditional class-level (between-plot) CVs, which were generally $<50\%$ for canopy fuels and $<70\%$ for surface fuels (Figs. 4 and 5).

peak “red stage” (i.e., peak mortality and red-needle tree abundance), many trees have already begun losing needles (Figs. 2 and 4G; Simard et al. 2011, Schoennagel et al. 2012). Reduced canopy bulk density (CBD) in red stands occurred in our data despite the conservative assumption that 100% of fine twigs become available fuel upon death (vs. 50% when live), which could theoretically increase available fuel substantially as crowns die. This dynamic highlights the importance of clearly defining post-outbreak stages (Hicke et al. 2012); our red stands were “mid-stage,” a few years after outbreak initiation and thus including a range of post-mortality needle loss within stands (Fig. 2).

Gradual and partial disturbance also affected dynamics of estimated canopy foliar moisture. As expected, estimated canopy foliar moisture declined during the red stage, to 71–85% (weighted average of live and dead foliage within stands) (Fig. 4H). This dip was less than expected, but similar to other studies (e.g., 63–78%;

Simard et al. 2011). The stand-level average does not approach the pure dead-needle moisture for two reasons: mortality is partial within stands so significant live foliage remains present (Fig. 2), and needle drop reduces the contribution of dead needles to canopy metrics (Figs. 2 and 4G). Similarly, Page and Jenkins (2007a) reported that dead needles composed 17–29% of stand foliage during epidemic-stage outbreak in *Pinus contorta*. Nevertheless, spatial intermixing of live and dead crowns could be important for localized fire behavior such as individual tree torching. This effect is not captured in currently available fire models that assume homogeneous fuels, and has not been studied empirically.

Our expectation regarding increased ladder fuels in later post-outbreak stages was not supported, due to slow regeneration. Effective canopy-base height, a measure of resistance to fire transition into crowns (torching), increased from 0.6 m in green stands to 3.4 m in silver stands (Fig. 4C). This trend was due to canopy

biomass loss, such that the threshold CBD of 0.04 kg/m^3 occurred higher, where more trees became part of the canopy profile (Fig. 3). In contrast, studies in more mesic forests have found that, by ~ 25 years post-outbreak, the base of the canopy effectively decreases as growth and recruitment of sapling regeneration fills in the lower canopy with foliage, thereby increasing torching potential (Simard et al. 2011). In the drier system we studied, regeneration after disturbance often takes many decades (Baker 2009), and post-outbreak tree regeneration remains sparse even in silver stands (Table 2). Thus, beetle-triggered acceleration of succession (release and recruitment of advanced regeneration) and its effects on torching appear to be less of a factor in drier, lower montane systems.

Surface fuels.—There were surprisingly few significant effects of bark beetle outbreak on surface fuel loads, and some unique patterns relative to higher-elevation forests. As we hypothesized, herbaceous biomass increased in the red stage, and the increase of $\sim 50\%$ (0.5 Mg/ha) above green stands was at the high end of that reported for higher-elevation forests such as *Pinus contorta* (Page and Jenkins 2007a, Simard et al. 2011). The pattern of increase followed by a decline in later time-since-outbreak (TSO) classes may be due to an initial flush of light, soil moisture, and available nitrogen associated with red needle-fall, with nitrogen subsequently becoming immobilized within the system (Griffin et al. 2011, Griffin and Turner 2012).

Patterns of dead surface fuels suggested key differences from other ecosystems. The only significant effects that emerged over background variation were reduced 1-h fuels and increased 1000-h fuels in silver stands (Fig. 6A–H). Coarse (1000-h) fuel accumulation in silver stands is consistent with expectations of post-disturbance snag-fall and fragmentation (Fig. 2). As we hypothesized, coarse-fuel accumulation was much lower in Douglas-fir forests (2 times higher than in green stands) than that reported for higher-elevation forest types (3–8 times higher; Page and Jenkins 2007a, Simard et al. 2011, Schoennagel et al. 2012). The difference may be due to lower standing biomass in drier systems. Decreased 1-h fuels in silver stands has not been reported for other systems, and may be due to decreased inputs from a reduced and increasingly patchy overstory, an effect which is likely pronounced in sparsely treed lower montane systems.

Role of background variability

Our hypothesis that beetle effects would be much larger than background variation was generally not supported. For most categories of both canopy and surface fuels, effect sizes of the beetle outbreak were similar or even less than the range associated with background variability (Fig. 5). Partial R^2 values from the general linear models (GLMs) also showed similar explanatory power between pre-outbreak basal area and beetle outbreak for most variables. This comparison to an ecologically meaningful range of pre-outbreak stand

structure has important implications for interpreting beetle outbreak effects, in both ecological and management contexts.

Several studies have reported no detectable beetle outbreak effects for many (especially surface) fuel components (Page and Jenkins 2007a, b, Jorgensen and Jenkins 2011, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012), leading to understandable speculations that Type II error may be preventing detection of trends over background variation (Hicke et al. 2012). While sampling error likely does play a role in some studies, our analysis shows that weak or undetectable trends can be an ecological phenomenon and not simply a statistical one. First, in our study we validated pre-outbreak comparability of stands via extensive dendrochronological reconstructions, minimizing this common source of sampling error and helping compensate for modest sample size (Johnson and Miyanishi 2008, Simard et al. 2011). Perhaps more importantly, the GLM approach we used allowed us to explicitly account for background variation in fuel loads, a stronger analysis that aided in detecting several beetle effects. It also showed quantitatively that, while beetles may alter the fuel profile within a given stand, when viewed across stands these effects tend to be of similar magnitude to variation among stands in the absence of beetle disturbance. A similar pattern has also been suggested for *P. contorta* pine forests (Hicke et al. 2012). Although beetle outbreaks necessarily have an impact on fuel profiles (e.g., dead canopy biomass must fall to the surface and decay over time), the relative difficulty in detecting these effects across many studies suggests that the context of background variability is ecologically meaningful when interpreting the overall role of beetles.

Fuel-driven variations in fire behavior can be influenced by other processes as much or more than beetle outbreaks, which may underlie common findings of weak or equivocal outbreak effects in empirical studies of fires burning through recently beetle-affected landscapes (Bebi et al. 2003, Lynch et al. 2006, Kulakowski and Veblen 2007, Bond et al. 2009, Kulakowski and Jarvis 2011). Background variation may be especially important for lower montane systems which vary widely in structure, productivity, and fire regime (Baker 2009). By comparison, in higher-elevation systems with lower structural variation, fires are often climate driven, rendering bottom-up controls via fuels less important overall (Turner et al. 1994), whether from beetle outbreaks or other factors. For the management of wildland fuels in lower montane forests, the context of wide background variation suggests recognizing outbreaks as one of many factors influencing fuel profiles and fire potentials. Prioritization of treatments will benefit by considering which fuel components are uniquely affected by beetles (e.g., window of reduced canopy foliar moisture in initial outbreak stage), which components vary with similar magnitude in response to

beetles and other drivers (e.g., canopy fuel load and bulk density), and which components seem to vary less with beetles than with other drivers (e.g., most surface woody fuels) (Figs. 4–6).

Fuel decay dynamics: closing the loop

At first glance, a significant loss of canopy fuels but relatively few increases in surface fuels appears incongruent. Biomass clearly must fall from the canopy over time; however two factors explain why surface fuel accumulations may not be as large as expected: the gradual nature of beetle outbreaks and the key role of decomposition.

The multiyear outbreak produces a gradual input of needle litter to the forest floor, which allows time for decomposition to influence accumulation concurrently. The decay half-life of needle litter (3–8 yr; e.g., Keane 2008) is on the same order as the period of beetle outbreak (3–7 yr), which may explain why post-outbreak litter accumulation in more mesic forest types have varied from no change to slight increases that do not always mirror canopy loss (Page and Jenkins 2007a, b, DeRose and Long 2009, Simard et al. 2011, Schoennagel et al. 2012). Notably, another study of litter dynamics in GYE Douglas-fir forests also reported no significant change in litter depth or mass following bark beetle outbreak (Griffin and Turner 2012).

Gradual inputs and decomposition are also important for woody fuels. Disturbances that kill trees within a stand over multiple years lead to protracted dead-wood inputs, with 20–50% lower maximum accumulations relative to synchronous disturbance (Cobb et al. 2012). Thus, dead woody fuels following multi-year beetle outbreaks should be expected to exhibit a more gradual, flatter accumulation over time rather than a sharp spike consisting of all material at once.

The role of wood decomposition can be explored quantitatively with our data. Parameterizing standard negative exponential decay models ($Y_t = Y_0 e^{-kt}$; Harmon et al. 1986) with our field data using all pools (canopy + surface) for each fine fuel size class yields exponential decay constants of $k = 0.037$ for 1-h fuels, 0.014 for 10-h fuels, and 0.016 for 100-h fuels. These values are within ranges commonly reported for western conifers (Harmon et al. 1986, Keane 2008). In other words, changes in the total amounts of dead fuels over the time period spanned by our sample (red to silver stage, ~26 yr) are consistent with those predicted by known decay constants.

Spatial heterogeneity in fuels

Disturbance-driven changes in variability, rather than just means, are increasingly recognized as fundamental to understanding the effects of both single events and interactions between multiple disturbances (Fraterrigo and Rusak 2008). We found that within-stand spatial heterogeneity increased with time since beetle outbreak for several fuel components (Fig. 7), which may indicate

important fine-scale changes in fuel connectivity and fire propagation potential. Within-stand heterogeneity increased for canopy fuels in both the vertical and horizontal dimensions (Fig. 7A–D). Greater patchiness in the horizontal dimension was most pronounced in the mid-canopy layer (Fig. 7B), where available fuel loads generally peak and therefore determine effective canopy bulk density and crown-fire spread potential (Fig. 3; Reinhardt and Crookston 2003, Reinhardt et al. 2006). Combined with increased variation among vertical canopy layers (Fig. 7D), this pattern suggests reduced potential for both vertical (torching) and horizontal (spreading) crown-fire propagation, all other factors being equal. Changes in variability were less common for surface fuels, although silver stands had patchier litter and duff depths, which may also influence surface fire spread potential. Overall, increased spatial heterogeneity in fuels supports the notion that currently available fire models, which assume homogeneous fuel beds, are of decreased utility in post-outbreak environments, and that new models under development may be better suited to this question (see Hoffman et al. 2012b).

Implications for fire potentials

Applying known relationships between fuel profiles and the behavior of both surface (Rothermel 1983) and crown (Van Wagner 1977) fires, bark beetle outbreaks appear to have a number of implications for fire potentials in Greater Yellowstone Douglas-fir forests. In red stands, surface fire potential appears largely unchanged except for a slight increase in frontal flame length and fire line intensity associated with greater herbaceous biomass (Fig. 6). Coupled with reduced estimated canopy foliar moisture (Fig. 4), this effect suggests increased potential for torching into the canopy, while the potential for active crown-fire spread appears decreased due to lowered effective CBD but increased due to lower foliar moisture (Fig. 4). The net balance of these counteracting influences—especially the effect of dead foliage with <70% moisture and its patchy spatial distribution—has not been parameterized within most fire modeling frameworks (Jenkins et al. 2008, 2012, Hicke et al. 2012, but see Hoffman et al. 2012b). Reduced foliar moisture may be key in increasing crown fire potential during the red stage (Jenkins et al. 2012, Jolly et al. 2012); yet so far there is a lack of quantitative empirical studies on fire behavior in red stands to complement the visual observations reported to date. Especially needed are studies comparing how otherwise-similar red and green stands burn under a range of weather conditions.

In gray stands, surface fire potentials appear no different than in green stands (Fig. 6), while further thinning of the canopy in terms of mass, bulk density, and connectivity suggests substantially reduced potential for crown fire initiation and spread (Fig. 4). Most dead 1-h fuels remain in the canopy at this stage, and we conservatively included these in our calculations of canopy base height (CBH) and canopy bulk density

(CBD), but it is unknown the degree to which these can support crown fire when foliage is highly discontinuous. Increased spatial heterogeneity in canopy fuel mass becomes important by this stage, especially in the mid-canopy layer (Fig. 7).

By the silver stage, potential fire behavior appears substantially altered from that in undisturbed stands. Lower 1-h fuel mass and litter-plus-duff continuity suggest diminished surface fire spread and intensity, while higher coarse-fuel loading suggests potentially increased burn residence time and heat release (Fig. 5). Higher CBH (Fig. 4) and vertical heterogeneity (Fig. 7D) suggest reduced torching potential, and significantly lower CBD and connectivity suggest greatly reduced crown fire spread potential (Fig. 4). Potential mid-flame wind speeds are likely increased due to the open canopy (Reinhardt and Crookston 2003), while microclimatic effects (surface temperature and relative humidity) are within the range found in undisturbed forests.

In the context of the mixed-severity fire regime that characterizes many drier lower montane forests, even though outbreak effects may be less important relative to background structural variation than in other ecosystems, they may still influence the propensity for surface vs. crown fire. Mixed-severity fire regimes are considered to be more fuel limited than comparatively mesic high-elevation forest types (Halofsky et al. 2011), and beetle outbreaks appear to move the system toward still greater fuel limitation, particularly in older post-outbreak stages. Reduced vertical fuel continuity suggests a shift away from crown-fire behavior, and toward conditions more likely to support surface fires. Under moderate weather conditions, therefore, beetle outbreaks may result in lower-severity fire in terms of canopy mortality and fire-created openings, for perhaps several decades. These effects may vary among forest types with mixed-severity fire regimes, which themselves vary widely in structure and function.

The net effect for Greater Yellowstone Douglas-fir forests is that mesic closed-canopy stands affected by beetles shifted in character toward that of undisturbed xeric parklands (compare Fig. 1D to Fig. 1A), while xeric parklands affected by beetles shifted toward a very sparse woodland/savanna condition (Fig. 1C). The latter condition in particular appears very unlikely to support significant crown-fire activity. Thus, any management of fuels in post-outbreak stands may be better prioritized for denser stands in which crown fuels may still have a degree of continuity, and coarse woody fuels are more abundant (Fig. 1D).

Conclusion

We found evidence that the effects of bark beetle outbreak on fuel profiles in lower montane forests differ from those in higher elevation forests with stand-replacing fire regimes. Relatively low tree density and canopy biomass to begin with, as well as slow regeneration dynamics, were among the most important

differences; canopy thinning associated with beetle-caused tree mortality thus resulted in very low canopy fuel mass and continuity, with little recovery up to three decades post-outbreak. Changes in surface fuels were comparatively minor. Combined with increased spatial heterogeneity in fuels, these results suggest overall diminished fire potentials in post-outbreak stands, particularly for crown fire. A remaining uncertainty is how, in the red stage, the net effects of reduced foliar moisture, concurrent canopy thinning, and the patchy spatial distribution of live and dead biomass will influence crown fire potentials. The gradual and partial nature of outbreak was key in mediating changes to fuel profiles, resulting in less extreme fluctuations in estimated canopy foliar moisture (red stage) and coarse woody fuel accumulations (silver stage) than expected. Overall, effects of *Dendroctonus* outbreaks were generally on par with background variation in stand structure. In essence, formerly dense forests affected by outbreak became more like open parklands, while open parklands became more like woodland/savannas (Fig. 1). These results highlight the importance of evaluating outbreak effects within the context of the structural variation inherent to many forest types in the absence of beetle disturbance. For management of wildland fuels, this finding suggests that bark beetle outbreaks can be approached as but one of many influences structuring fuel profiles, and that treatments in beetle-affected landscapes could continue to address a variety of objectives rather than focusing singularly on beetle impacts. Although most important in structurally variable forests such as interior Douglas-fir, such context likely has relevance in other forested ecosystems affected by bark beetle outbreaks.

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SUPPLEMENTAL MATERIAL

Appendix A

Tree-ring analyses for chronosequence validation and stand reconstruction (*Ecological Archives* A023-001-A1).

Appendix B

Two tables providing statistical outputs from general linear models for all fuel variables (*Ecological Archives* A023-001-A2).