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Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests?

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Abstract. Disturbance interactions have received growing interest in ecological research in the last decade. Fire and bark beetle outbreaks have recently increased in severity and extent across western North America, raising concerns about their possible interactions. Although it is often presumed that bark beetle outbreaks increase probability of active crown fire by producing high loads of surface and canopy dead fuels, empirical data are scarce and results are ambivalent. We combined field measurements and modeling to address the following question: How do fuel characteristics, microclimate, and potential fire behavior change with time since a severe mountain pine beetle outbreak in *Pinus contorta* forests of Greater Yellowstone (Wyoming, USA)? We measured surface and canopy fuels, and soil surface temperature in a time-since-beetle-outbreak chronosequence ($n = 35$ sites) from undisturbed to 36 years post-outbreak, including stands in red- and gray-needle stages (respectively, 1–2 and 3–5 years post-outbreak). Field data were used to parameterize the fire behavior model NEXUS and predict potential fire behavior at each site.

Dead surface fuel loads of all size categories did not differ among undisturbed, red, and gray-stage stands. Compared to undisturbed sites, red and gray-stage sites had on average 53% lower canopy bulk density, 42% lower canopy fuel load, and 29% lower canopy moisture content, but had similar canopy base heights (3.1 m). In subsequent decades, coarse wood loads doubled and canopy base height declined to 0 m. Modeling results suggested that undisturbed, red, and gray-stage stands were unlikely to exhibit transition of surface fires to tree crowns (torching), and that the likelihood of sustaining an active crown fire (crowning) decreased from undisturbed to gray-stage stands. Simulated fire behavior was little affected by beetle disturbance when wind speed was either below 40 km/h or above 60 km/h, but at intermediate wind speeds, probability of crowning in red- and gray-stage stands was lower than in undisturbed stands, and old post-outbreak stands were predicted to have passive crown fires. Results were consistent across a range of fuel moisture scenarios. Our results suggest that mountain pine beetle outbreaks in Greater Yellowstone may reduce the probability of active crown fire in the short term by thinning lodgepole pine canopies.

Key words: bark beetles; chronosequence; compound disturbances; disturbance interactions; fire behavior modeling; fuel loads; Greater Yellowstone Ecosystem; insect–fire interactions; linked disturbances; lodgepole pine, Pinus contorta; *mountain pine beetle,* Dendroctonus ponderosae; *Rocky Mountains.*

Introduction

Disturbance interactions have received growing interest in ecological research (Paine et al. 1998, Kulakowski and Veblen 2007). Understanding of individual disturbances has greatly improved, and ecologists now recognize that many ecosystems are affected by different types of natural disturbances that may interact in surprising but important ways (Turner 2005). Interest in disturbance interactions is also driven by concerns about the effects of climate change and human impact on natural disturbance regimes, which might display nonlinear responses and unpredictable feedbacks that could possibly result in abrupt regime shifts (Paine et al. 1998, Scheffer et al. 2001, Apps and McGuire 2005). However, surprisingly few studies have explored the complex interactions between disturbances.

We distinguish two types of disturbance interactions. *Compound disturbances* (sensu Paine et al. 1998) take place when two disturbances occurring in a short period of time have a synergistic effect that cannot be predicted from the sum of the individual disturbances. By definition, compound disturbances have unpredictable effects on ecosystems and may result in regime shifts (Jasinski and Payette 2005). In contrast, a disturbance may interact with another by changing its extent, severity, or probability of occurrence (Kulakowski and Veblen 2007, Lynch and Moorcroft 2008), a concept that we call *linked disturbances*. Thus, the concept of compound disturbances emphasizes the unpredictable or qualitatively different ecological consequences of suc-

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cessive disturbance events, whereas that of linked disturbances focuses on changes in their probability of occurrence.

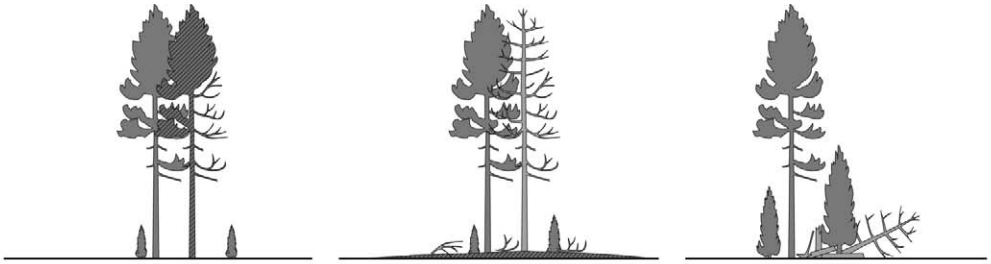
Linked disturbances may interact in two ways. One disturbance may amplify the second by increasing its likelihood or severity through a positive feedback, or alternatively, the first may dampen the second, reducing the frequency and impact of disturbances at the landscape scale. The relationship between linked disturbances may also vary over time, e.g., during succession or in conjunction with changing climate. Predicting when positive or negative feedbacks are most likely to occur between linked disturbances requires understanding the mechanisms underpinning their interactions. In this study, we investigate interactions between two primary disturbance agents in western North America, bark beetle outbreaks and wildfire.

Bark beetle outbreaks and forest fires have both increased in extent and severity during recent decades (Westerling et al. 2006, Raffa et al. 2008), raising concerns about their possible interactions (Negron et al. 2008). Native bark beetles of the genus *Dendroctonus* undergo episodic population outbreaks that result in widespread mortality of host trees through pheromone-mediated mass attacks (Wallin and Raffa 2004, Raffa et al. 2005). In the last 10 years, more than 47 million ha of subalpine and boreal forests have been affected by bark beetle outbreaks in the western United States and British Columbia, representing one of the largest outbreaks in recent history (Raffa et al. 2008). It is often presumed that bark beetle outbreaks increase the probability and intensity of active crown fire because they create great quantities of dead and ladder fuels (Hopkins 1909, Brown 1975, Amman and Schmitz 1988, McCullough et al. 1998). On the other hand, it has also been proposed that beetle outbreaks may reduce the probability of active crown fire by thinning the forests and reducing canopy fuel loads (Despain 1990, Schmid and Amman 1992). If bark beetle outbreaks amplify subsequent probability of active crown fire, then extensive regions of western North America could be at risk of high-severity fires, and carbon losses to the atmosphere, which are already substantial following beetle outbreak (Kurz et al. 2008), would be further increased in the short term. However, if fire disturbance is dampened, carbon losses may not accelerate so rapidly. In either case, this issue has important implications for forests at the wildland–urban interface and in remote areas, which are intensively managed to reduce a perceived increase in fire risk. Given the large extent of the forests currently affected by the recent bark beetle outbreak, understanding whether the probability of subsequent high-severity fire is elevated is increasingly important.

Previous empirical studies on linked bark beetle and fire disturbances have either used a retrospective approach, i.e., by comparing observed to expected patterns of area burned in a landscape that was previously affected by bark beetle outbreaks, or a prospective approach, by predicting potential fire behavior with fire behavior models and fuel data sampled in beetle-killed and undisturbed forests. These studies, which were carried out in different forest types (lodgepole pine [*Pinus contorta*], Engelmann spruce [*Picea engelmanii*]–subalpine fir [*Abies lasiocarpa*], and Douglas-fir [*Pseudotsuga menziesii*]), have yielded mixed results (Simard et al. 2008), with some analyses suggesting slightly increased probability or severity of fire following beetle outbreak (Bigler et al. 2005), and others showing no evidence for such a relationship (Bebi et al. 2003). In this study, we employ a prospective approach to quantify fuel dynamics and predict potential fire behavior during and for several decades after bark beetle outbreak. A few prospective studies have explored the relationship between beetle-caused changes in fuels and fire behavior, yet, to our knowledge, this is the first study to include detailed fuels, microclimate, and fire behavior data in a 35-year post-outbreak chronosequence replicated in space ($n =$ 35 sites) and time (1981 and 2007) and validated using extensive dendrochronological reconstruction of pre-outbreak stand conditions.

Bark beetle outbreaks potentially may amplify or dampen the critical components of fire behavior, including fire intensity, rate of spread and fire type (e.g., surface vs. crown fire). Active crown fires are especially threatening to human values because of their high intensity and rate of spread. Active crown fires develop when weather and fuel conditions allow both *torching* (when surface fire transitions to tree crowns when the vertical continuity of ladder fuels permits; Pyne et al. 1996) and *crowning* (when fire then spreads to nearby tree crowns). If canopy fuels are sparse or weather conditions are moderate, crown fires do not spread to nearby tree crowns, resulting in passive crown fires. Conditional crowning is predicted when conditions allow crowning but not torching; active crown fire could potentially occur if the canopy was ignited by a firebrand or by a crown fire from an adjacent stand (Scott and Reinhardt 2001). Thus, weather conditions can constrain the effects of stand structure (i.e., fuels) on fire behavior (Renkin and Despain 1992).

A linkage between bark beetle outbreaks and fire behavior could occur through several mechanisms related to the quantity and arrangement of live and dead fuels and to microclimate (Fig. 1). In the short term (approximately 1–2 years post-beetle, "red-needle stage"), the probability of torching and crowning may be increased because canopy foliar moisture is reduced but dead needles are retained in the canopy. When dead needles fall to the ground (approximately 3–5 yrs post-beetle, "gray-needle stage"), the reduction in canopy fuels may decrease the probability of crowning, but inputs of fine fuels from the canopy to the surface, and increased understory live fuel loads resulting from accelerated growth of grasses and shrubs might increase surface fire rate of spread. At longer time periods (10–40



	Red stage 1–2 years post-outbreak		Gray stage 3–5 years post-outbreak		Old attacks 10–40 years post-outbreak	
Effects of bark beetle outbreak on stand structure	Large trees killed by beetles Canopy dead needles dry out		Dead needles and twigs fall Shrub, grass biomass increases		Understory trees released Shrub, grass biomass increases Snags fall	
	Hypothesized beetle-caused changes	Hypothesized component of fire behavior affected	Hypothesized beetle-caused changes	Hypothesized component of fire behavior affected	Hypothesized beetle-caused changes	Hypothesized component of fire behavior affected
Fuel loads	No change	No change	↓Canopy fuels ↑Surface fine fuels and live understory fuels	↓ Crowning ↑ Surface fire RoS	↓Canopy fuels ↑Live understory fuels ↑Surface coarse fuels	↓Crowning ↑Surface fire RoS ↑Post-frontal combustion and soil heating
Fuel distribution	No change	No change	↑Fuel bed depth	↑ Surface fire RoS	↑Ladder fuels	↑ Torching
Microclimate	↑Surface temperature	↑Surface fire RoS	↑Surface temperature	↑ Surface fire RoS	↑ Surface temperature ↑ Mid-flame wind speed	↑Surface fire RoS ↑Surface fire RoS ↑ Torching ↑ Crowning
Fuel moisture content (MC)	↓Surface fuel MC ↓Canopy fuel MC ↓Evapotranspiration ↑Live understory fuels MC	↑Surface fire RoS ↑ Torching ↑ Crowning ↓Surface fire RoS	↓Surface fuel MC ↓Evapotranspiration ↑ Live understory fuels MC	↑Surface fire RoS ↓ Surface fire RoS	↓Surface fuel MC	↑Surface fire RoS

FIG. 1. Description of hypothesized mechanisms through which mountain pine beetle (*Dendroctonus ponderosae*) outbreak could affect fuel characteristics and potential fire behavior compared to undisturbed stands of *Pinus contorta* in Greater Yellowstone (Wyoming, USA). In the red stage, the hatched tree on the right is "red" and the tree on the left is green (live). In the gray stage, needles of the "red" tree have fallen to the ground (hatched). Abbreviations are: MC, moisture content; RoS, rate of spread. Upward arrows indicate increase; downward arrows indicate decrease.

years post-outbreak), understory tree growth may create ladder fuels that promote torching, and the opening of the stand could result in higher wind speeds and temperatures, and lower moisture content of surface fuels, which may increase surface fire rate of spread and possibly also increase torching, crowning, and overall fire intensity. Given the complexity of changes in stand structure and microclimate, the net effect of beetle outbreak on fire behavior is also complex and probably varies with time since the beetle outbreak (TSB).

We combined field studies and fire behavior modeling to determine whether bark beetle outbreaks and wildfire

are linked disturbances and whether this linkage results in amplification or dampening of post-beetle fire severity in Greater Yellowstone (Wyoming, USA). Specifically, we addressed the following question: How do fuel characteristics, microclimate, and likely fire behavior under a range of fire weather conditions change with time since a severe bark beetle outbreak in lodgepole pine (*Pinus contorta* var. *latifolia*) forests? We hypothesized that the disturbances would be linked, but that the nature of the linkage would change over time in response to changes in fuel characteristics and microclimate (Fig. 1), such that bark beetle outbreak would: (1) amplify probability of active crown fire in red-needle stands at about 1–2 years post-outbreak; (2) amplify intensity and rate of spread of surface fire but dampen probability of active crown fire in gray-needle stands at about 3–5 years post-outbreak; (3) amplify probability of torching and passive crown fires but dampen probability of active crown fire in stands 10–40 years post-outbreak as small surviving trees grow in the canopy. In this study, "lower probability" means that higher wind speeds and/or lower fuel moisture content are required to propagate fire, and "higher probability" means that the fire behavior component (torching, crowning, passive crown fire, and so forth) could happen at lower wind speeds and/or at higher fuel moisture content. Both terms are used to qualify fire behavior of a TSB class relative to the undisturbed stands.

Study Region

The lodgepole pine forest of Greater Yellowstone is a good system for studying bark beetle–fire interactions because it is a crown fire-driven ecosystem that is also prone to periodic outbreaks of the mountain pine beetle (MPB; *Dendroctonus ponderosae*), for which long-term (1960–present) records of activity are available (Lynch et al. 2006). The Greater Yellowstone Ecosystem, an 80 000-km^2 area straddling the states of Wyoming, Montana, and Idaho, represents one of the largest tracts of continuous forest in the conterminous United States. Yellowstone and Grand Teton National Parks form the core of this landscape and are surrounded by National Forests and other federal lands. Lodgepole pine is a dominant forest type in the region and grows on most xeric and nutrient-poor substrates, where they form both pioneer and late-successional stages (Despain 1990). On more mesic sites, postfire cohorts of lodgepole pine are succeeded by Engelmann spruce and subalpine fir, and also by whitebark pine (*Pinus albicaulis*), which can form monospecific stands at treeline. Douglas-fir is typically found at lower elevations and on slopes. The climate is cool with cold winters and dry summers. Mean annual temperature (Old Faithful weather station, 1971–2000) is 0.9°C (mean monthly temperatures for January and July are, respectively, −10.7°C and 13.7°C) and mean annual precipitation is 620 mm (Western Regional Climate Center 2007).

Fire reconstruction studies in Yellowstone National Park have documented mean fire return intervals ranging from about 160 years at low elevation (2100–2500 m) to more than 300 years at high elevation (2300–2600 m) (Romme and Despain 1989, Schoennagel et al. 2003). The MPB is an important biotic disturbance in the region, affecting mature stands of both lodgepole pine and whitebark pine across their distribution range (Raffa et al. 2008) (see Plate 1). Bark beetle colonization occurs during the summer, when female beetles excavate vertical J-shaped galleries in the phloem of the trees to lay eggs, a process that induces abundant production of tree resin that accumulates at the entrance of the galleries (i.e., "pitch tubes"). The developing larvae feed in horizontal galleries that girdle and kill the trees within weeks, although beetle-killed trees keep their green foliage until the end of the summer of the attack (also called "green attack stage"). One year after the initial attack, all the needles of the beetle-killed trees have turned red ("red-needle stage") and will remain on the trees for a few years, after which they will fall to the ground (about 3+ years post-beetle; "gray-needle stage"). The last previous major MPB outbreak in Greater Yellowstone occurred during the 1960s through early 1980s (Furniss and Renkin 2003, Lynch et al. 2006), and a current outbreak has been ongoing since about 2003 (USDA Forest Service 2008*a*, *b*).

Methods

We measured forest fuels in a time-since-beetle-outbreak (TSB) chronosequence from undisturbed to 36-year post-outbreak stands and used the field data to parameterize the fire behavior model NEXUS (Scott and Reinhardt 2001) and predict potential fire behavior at each site under similar abiotic conditions. Two different sets of field data were used. The first is a chronosequence of 25 sites that we established in 2007, where all components (canopy, understory, and surface) of fuels were measured. This chronosequence, which comprised undisturbed to 36-year-old post-outbreak stands, was supplemented by another chronosequence sampled in 1981 that included undisturbed to 18-year-old post-outbreak stands ($n = 10$) but only included surface fuel measurements. These two chronosequences did not share common stands and were selected, sampled, and validated using slightly different criteria, which are explained below. Combining these two independent data sets provided a way to cross-validate the chronosequences and verify that the trends observed were independent of sampling time. To our knowledge, this is the first post-beetle chronosequence study that is replicated in both space and time. Addition of the 1981 data set also helped fill a gap in the 2007 chronosequence between 4 and 26 years post-beetle.

2007 chronosequence

Site selection.—Based on aerial detection survey maps (U.S. Forest Service, 1999–2006; National Park

Service, 1960–1986) and current forest composition and successional stage maps, we identified potential sites that were either undisturbed or severely impacted by the MPB. All potential sites were visited and inspected for evidence of MPB activity from current (pitch tubes, J-shaped galleries, exit holes, and boring dust) or past (J-shaped galleries and pupation chambers on large downed logs) outbreaks. Pitch tubes, which are accumulations of tree resin at the entrance of boring holes, are a diagnostic sign of *Dendroctonus* bark beetle attack and persist for several years until the bark sloughs off the trees (Safranyik and Carroll 2006). J-shaped galleries and pupation chambers are also specific to *Dendroctonus* beetle feeding but can persist for decades because tree xylem is damaged. Final selection of sites was based on strict criteria to minimize variability in factors other than MPB activity. All sites were homogeneous, mature lodgepole pine-dominated (>90% basal area) stands (>1 ha in extent) growing on coarse-textured soils, and showed similar understory composition (mainly sedges, grasses, and shrubs such as *Vaccinium scoparium* and *Shepherdia canadensis*). In addition, all post-outbreak stands had high outbreak severity (>40% beetle-killed basal area), showed no evidence of other disturbances (including other outbreaks of the MPB) before or after the targeted MPB outbreak, and had approximately the same postfire stand age at the time of the outbreak (based on increment cores taken on-site and post-outbreak age from aerial detection survey maps).

To avoid pseudoreplication due to spatial autocorrelation, selected sites were separated by a minimum of 350 m, a distance at which variance was stabilized according to semivariance analysis of Landsat imagery (results not shown). Although the minimum distance between sites was 350 m, most sites were separated by more than 1 km, and some sites within the same TSB class were up to 33 km apart. Although bark beetle outbreaks can occur at broad scales (10–100 km), these beetles are poor dispersers, and tree mortality is very variable at fine scales (10–100 m) and strongly influenced by stand composition and local beetle population dynamics. Our sampling design, and the fact that the set of sites sampled in 1981 was spatially and temporally independent of the 2007 chronosequence, suggests that potential problems of pseudoreplication were minimized in this study.

Recently infested sites were classified in the red (TSB set at 2 years) or gray stage (TSB set at 4 years) if the proportion of gray tree basal area (relative to total beetle-killed basal area) was below or above 30%, respectively (Appendix A). In total, 25 sites were selected, with five replicates of each of the following TSB classes: undisturbed, red stage (1–2 years post-outbreak), gray stage (3–5 years post-outbreak), 25 years post-outbreak, and 35 years post-outbreak. All sites were selected and sampled during the summer of 2007.

Field sampling.—

1. *Trees and canopy fuels*.—At each site, we established a 50×50 m plot and noted its slope, aspect, and location (Trimble GeoExplorer 3 GPS; >500 readings differentially corrected, yielding a horizontal precision <2 m). Within each plot, we recorded canopy trees (i.e., >1.4 m in height) in three 200-m^2 subplots: a circular subplot in the center, and two 50×4 m subplots at the west and east sides of the plot (total area sampled = 600 m^2). For each tree rooted in the subplots, we recorded tree species, diameter at breast height (dbh; 1.4 m from the ground), status (live, dead standing, or dead downed), foliage condition (green, 0–50% red needles, 51–100% red needles, no needles), and signs of MPB presence (pitch tubes, J-shaped galleries, exit holes, and boring dust for recent outbreaks, and J-shaped galleries and pupation chambers for old outbreaks). In 1/4 of each subplot, tree saplings and seedlings (<1.4 m in height) were described using the same variables used for canopy trees, except that height (nearest 10 cm) was noted instead of dbh. In the West and East subplots, we recorded crown base height for each tree as the distance between the ground and the lowest green or red needles. Crown base height was recorded with a graduated pole (for heights $\leq$ 6 m) or an electronic clinometer (for heights > 6 m) with a 0.25-m precision from 0 to 1 m, a 0.5-m precision from 1 to 6 m, and a 1-m precision above 6 m.

2. *Surface fuels*.—Surface fuels were sampled in 10 transects, each 10 m long (preliminary tests showed no difference in mean or coefficient of variation in the amount of fuels between 10 and 20 transects), using Brown's planar intersect method (Brown 1974). We recorded dead surface fuels that intersected a 2 m high plane in the following diameter classes: 0–0.64 cm (1-h time lag fuels; tallied over the first 2 m of the transect), 0.64–2.54 cm (10-h time lag fuels; tallied over the first 2 m of the transect), 2.54–7.62 cm (100-h time lag fuels; tallied over the first 3 m of the transect), and >7.62 cm (1000-h time lag fuels; diameter measured and decay class recorded over the whole 10-m transect). Duff (organic layer between the mineral soil surface and the litter layer, composed of the fermentation and humus layers) depth and dead fuel depth (distance between bottom of litter layer to top of highest particle in plane) were recorded at two and three locations, respectively, within the first two meters of each transect. Fuel load per area was calculated for each diameter class following Brown (1974).

3. *Understory vegetation*.—Understory cover was visually estimated (0–5%, 5–10%, 10–20%, 20–30%, and so forth) in 20 circular microplots (0.25 m^2) using the following cover classes: grass, sedge, forb, shrub, tree seedling/sapling, tree trunk, litter, bare soil, and rock. When grass, sedge, or shrub cover was greater than 5%, mean height of these plant groups was also recorded in 10-cm classes.

4. *Tree-ring sampling*.—We used dendrochronology to determine the precise time since the beetle outbreak (TSB) and time since a stand-replacing fire, and to reconstruct stand conditions at time of outbreak in all chronosequence stands (Appendix B). In each undisturbed, red-, and gray-stage stand, an increment core was taken at 30 cm from the ground on 10 dominant live trees (Kipfmueller and Baker 1998), whereas in the 25- to 35-year post-outbreak stands, increment cores were sampled on 50 live trees and cross-sections were sampled on 20 downed trees showing MPB galleries. Tree cores were mounted on wood sticks, and all cores and cross-sections were finely sanded (400 grit), scanned (1200 dpi) and measured with a tree-ring measuring software (OSM 3, SCIEM, Brunn am Gebirge, Austria).

To determine year of beetle attack in the 25- and 35-year post-outbreak stands (Table 1), we cross-dated the 200 cross-sections taken from beetle-killed trees using master chronologies developed from live trees in each stand (chronologies had 6 to 20 tree-ring series, were 115 to 268 years long, and had an intercorrelation coefficient of 0.35 to 0.56) and the program COFECHA (Holmes 1983). Bark beetle outbreak year was identified at each site by a pulse of mortality within a 2-4 year window period that corresponded with published aerial survey data, and year of outbreak was defined as the year where cumulative basal area killed of sampled trees exceeded 50% (Appendix B). Postfire stand age was estimated using the earliest pith date of all tree cores and cross sections in each site. All sites showed a pulse of tree establishment in a relatively narrow time window (~10 years) during which tree growth was not suppressed, indicating synchronous establishment of a postfire cohort following a stand-replacing fire (Appendix B).

To verify the assumption that all chronosequence sites had similar stand conditions before the outbreak and sustained similar levels of insect damage (Johnson and Miyanishi 2008), we reconstructed pre-outbreak basal area by adding up the basal area of surviving trees minus the basal area grown since the outbreak, and the basal area of beetle-killed trees after adjusting for loss of bark and for shrinking due to loss of water content (Appendix C). Outbreak severity was calculated as the percentage of bark beetle-killed basal area relative to pre-outbreak basal area (see Appendix C for details).

5. *Microscale meteorology*.—To quantify the influence of MPB outbreak on microscale meteorology, we deployed temperature and relative humidity probes (iButton, Maxim Integrated Products, Dallas Semiconductor, Sunnyvale, California, USA) in three sites of each TSB class ($n = 15$ stands in total). At each site, one air temperature and relative humidity probe encased in a well-ventilated white PVC tube was installed on a tree at 1.5 m from the ground. In addition, temperature probes were installed at the litter–duff interface at three locations within each site. Temperature and relative humidity were recorded every hour with a resolution of 0.5°C and 0.6%, respectively, between 20 June and 3 August 2008 (the time period for which data were available for all sites). Data from the three litter–duff probes were averaged for each site, and then both air and litter–duff temperature time series were averaged to get average air and litter–duff temperature per site. To highlight the difference in temperature between air and the litter–duff interface, and to account for differences in local temperature between sites, we calculated the difference between litter–duff and air temperature.

1981 chronosequence

Site selection.—During the summer of 1981, potential chronosequence sites that were either undisturbed or severely affected by the MPB were identified using field surveys and annual reports of the National Park and Forest Service. As for the 2007 chronosequence, all sites were visited and carefully examined for evidence (or lack thereof) of MPB attack (see *2007 chronosequence*). Each site had to be located within a relatively homogeneous (>0.5 ha in extent), even-aged, lodgepole-pine-dominated (>75% of stand basal area in lodgepole pine) forest between 50 and 250 years old and show either low (<10% of total basal area affected) or high (>30%) mortality due to MPB for the undisturbed and post-outbreak stands, respectively. In total, two undisturbed stands and eight post-outbreak stands ranging in TSB from 0 to 18 years were selected and sampled in the summer of 1981 (Table 1). Time since a stand-replacing fire was determined from tree-ring dating of synchronous establishment dates of dominant trees, and TSB was determined from growth releases in tree rings of sub-canopy trees that survived the outbreak (Romme et al. 1986, Veblen et al. 1991).

Field sampling.—

1. *Trees and canopy fuels*.—At each site, three belt transects (one in the center and one on either side) were established within a ~0.5-ha plot to survey canopy and sub-canopy trees. Transects were 3 m wide and had a variable length (30 m to 120 m), depending on tree density. Within each belt transect, every canopy tree (dbh > 2.5 cm) was tallied, recording species, dbh, status (live, dead standing, dead downed), presence of MPB pitch tubes, and presence of red needles. Saplings (dbh < 2.5 cm and height > 0.3 m) were measured (to the nearest 30 cm) and described (same variables as above), and seedlings (<30 cm high) were counted in only one or in all three belt transects, depending on their density. At each site, average cover (%) and height (to the nearest 3 cm) of live ground fuels were also noted.

2. *Surface fuels*.—Dead surface fuels were described using the same method as outlined in the previous section, except that the number and length of transects varied between sites to account for variability in fuel loads. Twenty transects were established in all but one site where 30 transects were sampled. Across all sites, 1-hour and 10-hour time lag fuels were sampled in the first 1.8 to 4.6 m of each transect; 100-hour fuels were sampled in the first 3.7 to 15.2 m; and 1000-hour fuels

TABLE 1. Characteristics of the chronosequence stands ($n = 35$ sites) for assessing fuel characteristics, microclimate, and potential fire behavior with time since a severe mountain pine beetle outbreak in *Pinus contorta* forests of Greater Yellowstone (Wyoming, USA).

Site ID, by year	TSB (yr)†	TSB class‡	Stand age at time of beetle infestation (yr)	Live basal area (m^2/ha)	Live lodgepole pine basal area (%)	Basal area beetle-killed (m^2/ha)	Reconstructed pre-outbreak live basal area (m^2/ha)	Reconstructed outbreak severity (%)
1981								
B4		U	80	30.3	100	3.1	33.4	9
B8		U	250	12.0	99	1.3	13.3	10
B6	1	R	100	15.3	100	12.0	27.3	44
B1	4	G	100	11.2	99	19.9	31.1	64
B5	4	G	100	18.4	100	23.9	42.3	57
KK	4	G	100	18.5	100	14.4	33.0	44
YY	8	8–18	80	15.5	99	9.4	26.1	46
II	12	8–18	110	11.2	100	4.7	15.9	38
B3	16	8–18	80	6.3	69	14.3	23.6	78
B2	18	8–18	80	14.2	100	14.6	29.2	64
2007								
TSBU-1		U	120	35.6	100	0	35.6	0
TSBU-2		U	128	36.4	100	0	36.4	0
TSBU-3		U	230	36.9	98	0	37.0	0
TSBU-4		U	205	34.5	100	0	34.5	0
TSBU-5		U	213	60.4	100	0	60.4	0
TSBR-1	2	R	136	12.3	98	23.0	35.3	65
TSBR-2	2	R	155	8.8	98	29.3	38.1	77
TSBR-4	2	R	139	15.9	94	8.9	24.8	36
TSBR-3	2	R	153	10.8	100	19.0	29.8	64
TSBR-5	2	R	150	17.1	100	15.0	32.1	47
TSBG-1	4	G	150	15.6	82	19.9	35.5	56
TSBG-2	4	G	151	17.5	81	24.0	41.6	58
TSBG-3	4	G	260	23.1	100	17.1	40.2	43
TSBG-4	4	G	225	10.1	96	17.5	27.6	64
TSBG-5	4	G	173	9.6	97	14.1	23.8	59
TSB20-1	29	25	97	14.0	100	14.3	27.8	66
TSB20-2	27	25	89	9.3	100	5.8	13.8	54
TSB20-3	27	25	249	15.1	97	13.5	22.5	78
TSB20-4	27	25	173	18.8	100	10.2	26.4	50
TSB20-5	27	25	246	14.4	100	11.2	23.2	62
TSB30-1	36	35	160	17.5	94	24.5	38.7	82
TSB30-2	26	25	167	20.1	98	19.0	35.5	69
TSB30-3	26	25	173	21.5	100	11.8	33.5	45
TSB30-4	28	25	163	18.5	100	8.6	26.4	42
TSB30-5	36	35	177	16.4	96	17.0	29.3	75

† Time since the beetle outbreak; in the red and gray stages, TSB was set at 2 and 4 years, respectively, whereas in older attacks, it was determined from tree-ring analyses.

‡ Key to abbreviations: U, undisturbed; R, red; G, gray; 8–18, 8- to 18-yr-old stands; 25, 25-yr old stands; 35, 35-yr-old stands.

were sampled in the whole transects, which measured between 12.2 and 24.4 m. In all transects, duff depth and needle depth were noted to the nearest 0.5 cm at two to three locations.

Data pre-processing

Canopy fuel calculations.—Crown weight and the proportions of foliage, 1-hour, 10-hour, and 100-hour time lag fuels in the crown were estimated for individual stems using tree dbh measured in the field and allometric equations developed for Rocky Mountain conifers (Brown 1978). To account for loss of foliage in recently killed trees (red and gray stages), foliage mass was multiplied by 0.25 and 0.75 for trees in the 0–50% and 51–100% red needle classes, respectively. Available canopy fuel load was computed for each stand as the sum of foliar biomass plus 50% of the 1-hour time lag fuels, which are generally thought to be consumed during a crown fire (Reinhardt and Crookston 2003, Reinhardt et al. 2006).

Tree height was estimated from dbh using allometrics developed for lodgepole pine (Schlieter [1986], cited in Koch 1996:450) and used to calculate crown length (here and for the rest of the paper, crown is a tree-level attribute and canopy is a stand-level attribute). Vertical profiles of canopy bulk density were then developed for each stand by distributing available crown fuel along the crown of each tree in 0.25-m bins, and summing across trees; the vertical profiles were then smoothed with a 3-m running mean (Scott and Reinhardt 2001, Reinhardt et al. 2006). This method, which is implemented in the Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS; Reinhardt and Crookston 2003), assumes that canopy fuels are uniformly distributed along tree crowns. Unlike other methods however, it provides an unbiased estimate of canopy bulk density

and results in vertical profiles that accurately represent the observed profiles (Reinhardt et al. 2006). For each stand, effective canopy bulk density was calculated as the maximum value of available canopy bulk density, and effective canopy base height was defined as the lowest height in the profile where canopy bulk density exceeded 0.011 kg/m^3 (Reinhardt and Crookston 2003).

Although recently killed (gray stage) trees have less canopy fuels than live trees, their fine twigs (1-hour fuels) contribute to canopy bulk density. However because these trees did not bear foliage, their crown base height was not recorded. To circumvent this shortcoming and incorporate gray-attacked trees in the calculation of canopy bulk density, we developed regression equations between dbh and crown base height for all trees for which both variables were available ($n = 2438$). We used a linear model (PROC GLM; SAS Institute 2003) with ln(crown base height + 1) as the response variable, and ln(dbh + 1) and its interaction with site as explanatory variables ($R^2 = 0.69$, $F_{25,2413} = 543.05$, $P < 0.0001$). The resulting site-specific equations were then used to estimate missing crown base heights ($n = 101$ trees).

Understory fuel calculations.—Dry biomass of herbaceous and woody fuels were computed using percent cover data in each site and previously published (Turner et al. 2004) or new (*Shepherdia canadensis*) allometric equations. Equations for the dominant understory species were used to estimate biomass of each of the broad categories: *Calamagrostis canadensis* for grasses, *Carex geyeri* for sedges, *Arnica cordifolia* for forbs, and *Vaccinium scoparium* for shrubs smaller than 20 cm. Cover of shrubs taller than 20 cm were converted to biomass using new allometrics developed for *S. canadensis* ($R^2 = 0.97$). Biomass of grasses, sedges, and forbs was then summed to obtain live herbaceous fuel load, and that of *Vaccinium* and *Shepherdia* to obtain live woody fuel load.

Fire behavior modeling

We used the fuel data sampled in the field to parameterize the fire behavior model NEXUS and predict potential fire behavior at each site under similar abiotic conditions (e.g., wind, slope, fuel moisture).

NEXUS.—NEXUS is a nonspatial deterministic fire modeling system that uses fuel, weather, and topographic inputs to predict stand-level fire behavior and assist in decision making for fire management (Scott 1999, Scott and Reinhardt 2001). Its basic structure, which is shared among many other models (e.g., BehavePlus, FARSITE, and so forth; Scott 2006), includes (1) a surface fire spread module (Rothermel 1972), driven by surface fuel characteristics, slope, and wind speed; (2) a crown fire initiation module (Van Wagner 1977), which depends on surface fire intensity, canopy base height (ladder fuels), and foliar moisture; and (3) a crown fire spread module (Van Wagner 1977, Rothermel 1991*a*), which depends primarily on surface fire rate of spread, canopy bulk density, and wind speed. In these models, predictions are greatly influenced by fuel type and loads, in contrast with other models such as the Canadian Forest Fire Behavior Prediction System (Forestry Canada Fire Danger Group 1992), which are primarily driven by weather conditions. NEXUS assumes that fuels are homogeneously distributed horizontally, but uses simple metrics to describe their vertical distribution.

Outputs.—NEXUS predicts fire type, i.e., surface, passive crown, active crown, and conditional crown fire. Crown fraction burned represents the degree of crowning, i.e., the proportion of canopy fuels consumed in a fire. It ranges from 0 (surface fire) to 1 (crown fire or conditional fire), with intermediate values characterizing passive crown fires. Rate of spread (km/h) is the speed at which the flaming front moves forward in a direction perpendicular to the perimeter, and heat per unit area (kJ/m^2) is the total amount of energy released per area. Fire line intensity (kW/m), which is the rate of heat release in the flaming front per unit length of fire front, is the product of rate of spread and heat per unit area, and is related to flame length. In NEXUS, the overall rate of spread of the head fire is the average of the surface and crown fire rates of spread, scaled with the crown fraction burned. Because wind speed is highly variable and is a major driver of fire behavior, it can be used as a metric to evaluate thresholds for crown fire initiation and active crown fire spread, all other things being equal. NEXUS computes the Torching Index and the Crowning Index, which are the open wind speed at which torching and crowning respectively occur under a given set of fuel and moisture parameters.

Model parameterization and simulation experiments.—We used fuel field data to construct custom fuel models and canopy fuel profiles for each site. Parameters derived from field data included surface fuel loads, fuel bed depth, canopy fuel characteristics, and wind adjustment factor (Table 2). To focus specifically on the effects of stand structure on fire behavior, we kept the slope constant (0%). We simulated three different summer fuel moisture scenarios (Dry, Very Dry, and Extreme Drought) that span the range of weather conditions observed during fire events in the region (Table 2). The extreme drought scenario corresponds to the conditions experienced during the 1988 fires in Yellowstone National Park (Hartford and Rothermel 1991, Rothermel 1991*b*). Although moisture content of dead and live canopy fuels was constant within a given scenario, stand-level canopy moisture content was site specific, depending on the proportion of live and dead canopy biomass in a stand. Because wind speed is highly variable and can qualitatively change fire behavior, we studied a range of wind speed values (0 to 100 km/h). Finally, to determine the effects of surface fuels on surface fire behavior only, we performed simulation runs in a surface fire-only mode, using data from both data sets. This was necessary because in NEXUS, the overall rate of spread of the head fire (and thus also overall fire

TABLE 2. Parameters used for fire behavior modeling in *Pinus contorta* forests of Greater Yellowstone (Wyoming, USA).

Parameter	Units	Value
Surface fuels (custom fuel models)		
1-h time lag fuel load	Mg/ha	field
10-h time lag fuel load	Mg/ha	field
100-h time lag fuel load	Mg/ha	field
Live herbaceous fuel load	Mg/ha	field
Live woody fuel load	Mg/ha	field
1-h fuel surface area to volume ratio	m^2/m^3	6562†
Live herbaceous surface area to volume ratio	m^2/m^3	4921†
Live woody surface area to volume ratio	m^2/m^3	4921†
Fuel bed depth	m	field
Dead fuel moisture of extinction	%	25†
Dead fuel heat content	kJ/kg	18 622†
Live fuel heat content	kJ/kg	18 622†
Canopy fuel characteristics		
Canopy base height	m	field
Available canopy bulk density	kg/m^3	field
Available canopy fuel load	Mg/ha	field
Fuel moisture‡		
1-h time lag fuel moisture	%	3, 5, 7
10-h time lag fuel moisture	%	4, 6, 8
100-h time lag fuel moisture	%	5, 7, 9
Live herbaceous moisture	%	50, 70, 90
Live woody moisture	%	70, 100, 120
Foliar moisture, green foliage§	%	3, 5, 7
Foliar moisture, red foliage§	%	95, 100, 105
Weather		
Open wind speed (20 feet or 6.1 m)	km/h	0–100
Wind adjustment factor		0.1 to 0.2 (field)
Terrain		
Slope steepness	%	0

† From fuel model 10 (timber litter and understory; Anderson 1982).

‡ Values (percentage dry mass) are given for the extreme drought, very dry, and dry fire weather scenarios (see *Methods: Fire behavior modeling: Model parameterization and simulation experiments*).

§ Overall canopy moisture content is calculated as the average of red and green canopy moisture content, weighted by their respective biomass.

¶ Calculated from field-based measurements of canopy cover and lookup tables in NEXUS, which are based on Albini and Baughman (1979), Rothermel (1983), and Finney (1998).

line intensity) is the average of the surface and crown fire rates of spread, scaled with the crown fraction burned.

Statistical analyses

To test among-stand differences in stand conditions at the time of sampling (live and beetle-killed basal area) and at the time of beetle outbreak (pre-outbreak basal area, outbreak severity, and postfire stand age at time of outbreak), we used analysis of variance (ANOVA) on TSB class (undisturbed, red stage, gray stage, 8- to 18-year post-beetle stands, and 25- to 35-year post-beetle stands), data source (1981 vs. 2007 data), and their interaction.

We used two statistical approaches to analyze the fuels data. First, to test the short-term effects of beetle outbreak, we used ANOVA to compare the undisturbed, red, and gray stages of beetle outbreak. Because of the significant difference in stand age at time of beetle outbreak between the two chronosequences, we also tested for the effect of data source and its interaction with TSB class. Second, for a longer-term analysis, we used regression to relate fuel characteristics to TSB (as a continuous variable) in beetle-killed stands, while still accounting for data source and its interaction with TSB. We used a similar approach to analyze canopy fuel characteristics and fire behavior indices (torching index and crowning index), except that data source was not included because canopy data were only available for 2007. Because fire behavior response variables (crown fraction burned, head fire rate of spread, heat per unit area, and fire line intensity) were analyzed with a range of wind speed, we tested differences among TSB classes using ANOVA at four different wind speeds: 20, 40, 60, and 80 km/h. For all statistical analyses, we used a significance level of 5% and log-transformed the data when needed to meet the assumptions of statistical tests. For all ANOVAs, we used Duncan's multiple range test to identify differences among class means, but relied on the P value of the ANOVA to determine if these differences were significant (Sokal and Rohlf 1995).

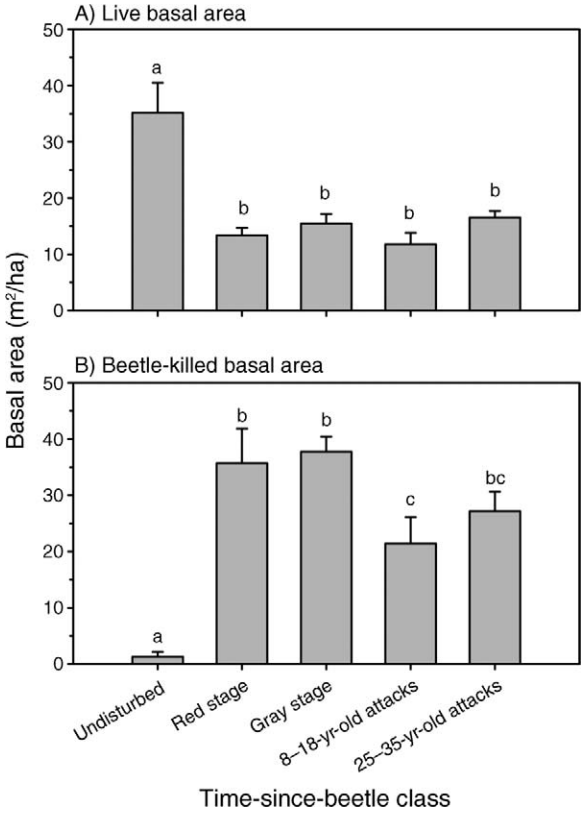


FIG. 2. (A) Live and (B) beetle-killed basal area (mean + SE) at time of sampling in the 2007 and 1981 chronosequence sites ($n = 35$). The classes 8–18- and 25–35-yr-old attacks refer to the number of years since the beetle attack. Lowercase letters above each bar indicate ANOVA results testing differences in means among classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 0.05$).

RESULTS

Time-since-beetle chronosequence

In total, 10 and 25 sites were sampled in 1981 and 2007, respectively, representing a time-since-beetle (TSB) chronosequence from undisturbed (7 sites) to 36-years post-outbreak (Table 1; Appendix A). Tree-ring dating of downed logs bearing beetle galleries confirmed the timing of beetle attack in the 25- to 35-years post-beetle sites, which was evidenced by a pulse of tree mortality within a narrow time window of 1–4 years (Appendix B). Three sites that were initially selected to represent the 35-year post-beetle class (based on historical aerial surveys) were, in fact, attacked in the early 1980s and were reclassified as such, resulting in a slightly unbalanced chronosequence (Table 1).

At time of sampling, live basal area of beetle-killed stands did not differ among beetle disturbance classes (mean = 15 m^2/ha), but was ~60% lower, on average, than in undisturbed sites (mean = 35 m^2/ha; $R^2 = 0.54$; $F_{4,30} = 9.16$; $P < 0.0001$; Fig. 2, Table 1; Appendix A). Beetle-killed basal area showed an opposite trend, with significantly lower values in undisturbed stands (mean = 1 m^2/ha) than in post-outbreak stands (mean = 16 m^2/ha; $R^2 = 0.87$; $F_{4,30} = 50.62$; $P < 0.0001$). Tree-ring reconstruction of stand structure, however, indicated that pre-outbreak basal area of all sites was similar, averaging 31 m^2/ha ($P > 0.1$; Fig. 3A; Appendix C). Outbreak severity (percentage of basal area killed relative to reconstructed pre-outbreak basal area) did not differ among beetle-killed stands, where it ranged from 36% to 82%, but was significantly lower in undisturbed sites (mean = 3%; $R^2 = 0.87$; $F_{4,30} = 52.05$; $P < 0.0001$; Fig. 3B; Appendix C). Stand age (time since a stand-replacing fire) at the time of beetle outbreak did not significantly vary with TSB within each chronosequence, but the sites sampled in 1981 were 63 years

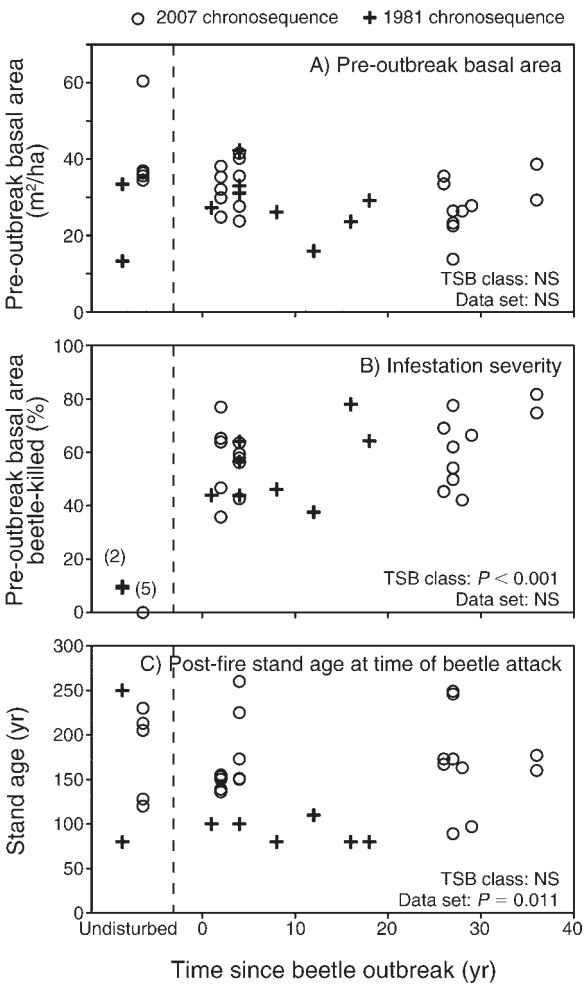


FIG. 3. (A) Reconstructed pre-outbreak basal area, (B) outbreak severity, and (C) postfire stand age at time of beetle outbreak in the chronosequence sites sampled in 2007 ($n = 25$) and 1981 ($n = 10$). Data points to the left of the dashed line (time of outbreak) represent undisturbed sites and are offset for clarity; values in parentheses indicate the number of superimposed data points (two + symbols and five open circles). P values associated with the effects of time-since-beetle (TSB) class, data set (1981 vs. 2007 data), and their interaction are shown, but the interaction term is only shown when significant.

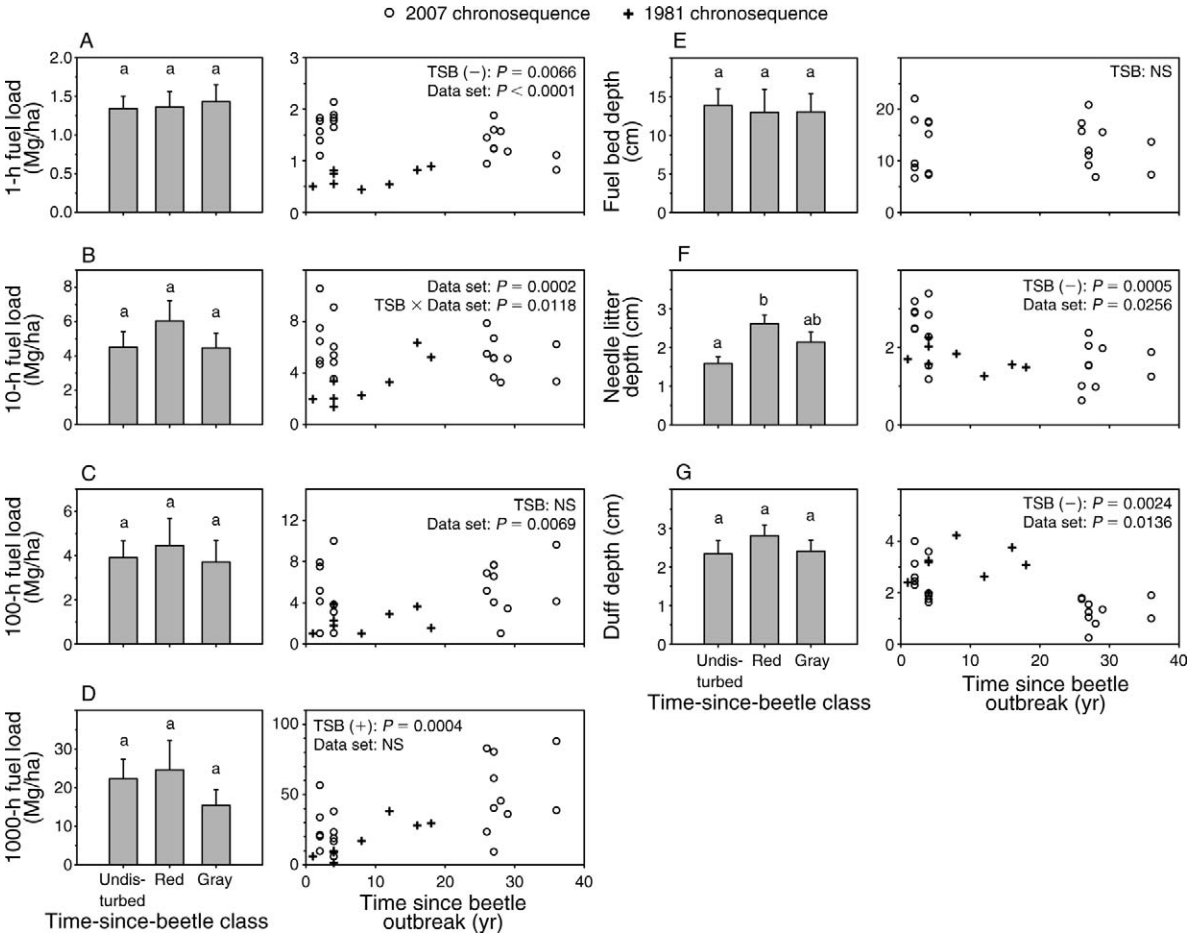


FIG. 4. Fuel load of dead surface fuels in the (A) 1-h, (B) 10-h, (C) 100-h, and (D) 1000-h time lag categories, and depth of (E) fuel bed, (F) needle litter layer, and (G) duff layer in the chronosequence sites ($n = 35$). Left-hand panels show means + SE for the undisturbed, red-stage, and gray-stage stands only. Lowercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 0.05$). Right-hand panels show the relationship between each fuel category and the time since the beetle outbreak (TSB) for beetle-killed sites only. *P* values associated with the effects of time since the beetle outbreak, data set (1981 vs. 2007 data), and their interaction are shown, but the interaction term is only shown when significant. The "(+)" or "(–)" symbols following the TSB effect indicate the sign of the slope when significant ($\alpha = 0.05$). Note that the *y*-axes in the panels have different ranges.

younger, on average, than those sampled in 2007 (171 years; $F_{1,33} = 12.8$; $P = 0.011$; $n = 35$; Fig. 3C, Table 1).

Fuel characteristics

Dead surface fuels.—In the first five years following bark beetle outbreak (i.e., red and gray stages), there was no significant change in the load of any of the dead surface fuel categories (1-h to 1000-h time lag fuels) compared to the undisturbed stands (Fig. 4A–D). Needle litter depth in the red stands (mean = 2.6 cm) was 60% thicker than in the undisturbed stands and had intermediate values in the gray stands (Fig. 4F). Fuel bed depth and duff depth did not vary between the undisturbed, red stage, and gray stage (Fig. 4E, G). Fuel loads of the generally younger stands sampled in 1981 were ~60% lower than those of the 2007 data for the 1-h, 10-h, and 1000-h fuel categories (Appendix D).

Over the entire post-outbreak chronosequence, excluding the undisturbed stands, the 1-h fuels decreased from ~1.5 Mg/ha in the red and gray stages to ~1 Mg/ha at 35 years post-outbreak (Fig. 4A). The 10-h fuels increased from year 1 to year 18 in the 1981 data but decreased in the 2007 chronosequence (Fig. 4B). The 100-h fuels and fuel bed depth showed no trend with time since a beetle outbreak. During the same period, coarse fuel loads (1000-h, diameter > 7.62 cm) tripled, from ~20 Mg/ha in the red stage to ~60 Mg/ha by 35 years after outbreak (Fig. 4D), and both litter and duff depth declined by 45–50% between 2 and 35 years post-beetle (Fig. 4F, G). Surface fuel loads in the 1-h and 100-h categories were ~55% lower, and litter layer depth was 23% lower in the younger stands of the 1981 data set than in the 2007 data set, but the opposite was true for

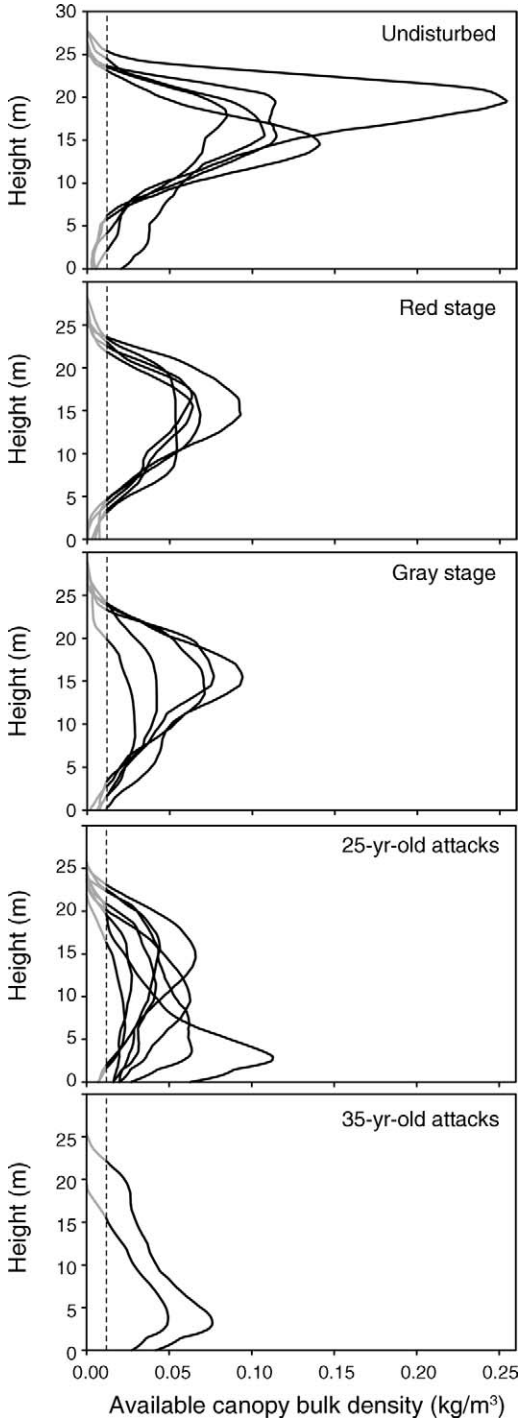


FIG. 5. Vertical profiles of available canopy bulk density in the 2007 chronosequence sites (solid lines; $n = 25$). The vertical dashed line represents the 0.011 kg/m^3 density threshold above which fire can propagate and that determines the effective canopy base height.

the duff layer, which was about 25% deeper in the 1981 chronosequence.

Canopy fuels and live understory fuels.—Vertical profiles of available canopy bulk density, which were constructed for each stand in the 2007 chronosequence, showed important changes in maximum bulk density (i.e., effective bulk density), total fuel load (i.e., available canopy fuel load), and vertical distribution (effective canopy base height) through the post-beetle sequence of stands (Fig. 5). Canopy base height (mean = 3.1 m) and sapling density (mean = 467 stems/ha) did not change in the first few years following the outbreak, but canopy bulk density and canopy fuel load decreased by 50% from the undisturbed to the red and gray stages (Figs. 5 and 6). Canopy moisture content dropped from 100% in the undisturbed stands to 63% in the red-stage sites and was 78% in the gray stands. Live herbaceous fuels doubled in the first few post-outbreak years, from 0.8 Mg/ha to about 1.6 Mg/ha, and live woody fuel load was significantly higher in red-stage stands (mean = 1.2 Mg/ha) than in the undisturbed stands (mean = 0.2 Mg/ha), with gray-stage stands having intermediate values (Fig. 6F, G).

In the longer term, canopy base height decreased substantially from ~3 m in the red stage to 0 m at 35 years post-outbreak whereas sapling density showed the opposite trend, with a 10-fold increase from about 400 to more than 4000 stems/ha (Figs. 5, 6A, B). Canopy bulk density, canopy fuel load, and live woody fuel load did not change between 2 and 35 years post-beetle (Fig. 6D, E, G), but remained below the values in the undisturbed stands. During this period, live herbaceous fuels continued to increase (Fig. 6F) and canopy moisture content returned to pre-outbreak values (Fig. 6C).

We tested whether surface and canopy fuels were influenced by aspect, slope, and elevation, using linear models that also included TSB class. After backward selection to remove nonsignificant variables ($\alpha = 0.05$), we found that none of the fuel components could be explained by the topographic variables (results not shown).

Microclimate

Temperature differed little between air and the litter–duff interface at the undisturbed sites, whereas in red and gray sites, the litter and duff layers were about 2°C cooler than air (Fig. 7). In contrast, the litter–duff interface was 2.5°C warmer than air in sites that were infested 25 years ago. When only mid-afternoon temperatures were considered, the overall pattern remained but temperature differences were amplified in the old attacks, where litter and duff were more than 10°C warmer than air (Fig. 7B).

Fire behavior

Simulation results for the "very dry" fuel moisture scenario suggested that, in the short term, undisturbed, red, and gray stands were unlikely to torch, with torching index values (wind speed needed to initiate torching) well above 100 km/h (Fig. 8). In the long term (2–36 years post-outbreak), torching index was reduced

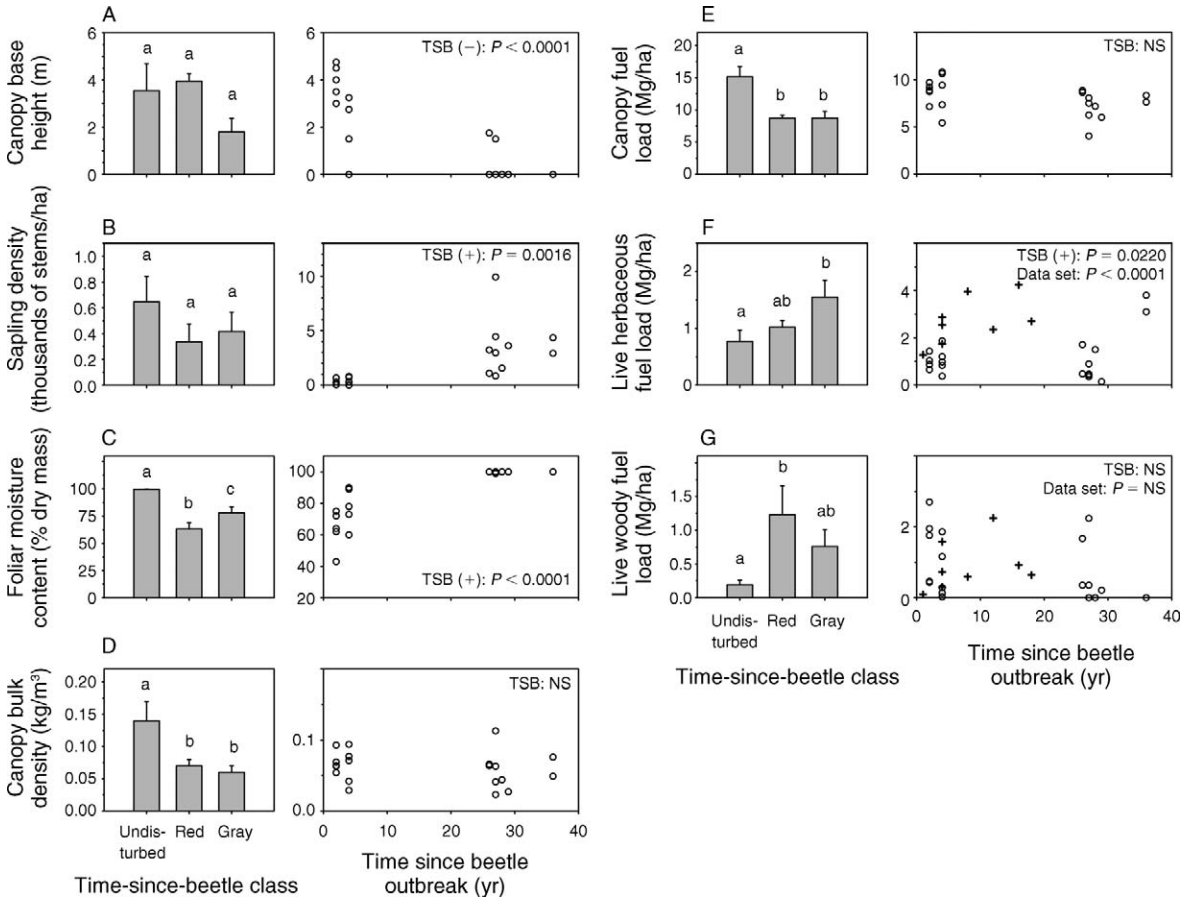


FIG. 6. (A) Effective canopy base height, (B) density of saplings (0 cm < dbh < 7.5 cm), (C) canopy foliar moisture content, (D) effective canopy bulk density, (E) available canopy fuel load, (F) live herbaceous fuel load, and (G) live woody fuel load in the 2007 chronosequence sites ($n = 25$); data from the 1981 chronosequence ($n = 10$ sites) are shown in panels (F) and (G) only, as only surface fuels (not canopy fuels) were sampled in 1981. Left-hand panels show means + SE for the undisturbed, red-stage, and gray-stage stands only. Lowercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 0.05$). Right-hand panels show the relationship between each canopy characteristic and time since beetle outbreak for beetle-killed sites only. *P* values associated with the time-since-beetle (TSB) effect are shown. The "(+)" or "(–)" symbols following TSB effect indicate the sign of the slope when significant ($\alpha = 0.05$). Note that the *y*-axes in the left-hand and right-hand panels have different ranges.

to zero at 35 years post-beetle, indicating that in these stands, passive crown fires may be initiated even without wind. Crowning index (the wind speed needed to sustain an active crown fire) was higher in gray-stage sites (71 km/h) than in undisturbed sites (39 km/h), with intermediate values in the red-stage sites (61 km/h), suggesting that the immediate effect of MPB outbreak was to greatly reduce the probability of active crown fire, because wind speeds above 60 km/h are rarely observed (Rothermel 1991*b*). In subsequent decades, crowning index did not change, with an average value of 71 km/h (Fig. 8B).

In the "very dry" fuel moisture scenario, simulated fire behavior was qualitatively different among the TSB classes, but these differences were sometimes overridden by the effect of wind speed. At wind speeds below 40 km/h, the undisturbed, red and gray stages, and 25-year post-beetle stands were all predicted to have surface fires, whereas for the 35-year post-beetle stands, passive crown fires were predicted (Fig. 9A). At these wind speeds, simulated fire rate of spread and fire line intensity were low (<0.25 km/h and <1000 kW/m, respectively) in all TSB classes, and heat per unit area was not different among classes, with an average value of 7000 kJ/m^2.

For wind speeds between ~40 and 60 km/h, the overall effect of bark beetle outbreak was to reduce the predicted probability of crown fire in the short term compared to the undisturbed stands (Fig. 9). Striking differences in simulated fire behavior were observed between the undisturbed and the red- and gray-stage sites, which were, respectively, predicted to have conditional vs. surface fire, crown fraction burned of 0.58 vs. 0.06 (–90%), head fire rate of spread of 0.89 vs. 0.13 km/h (–85%), heat per unit area of 22 300 vs. 7300 kJ/m^2 (–67%), and fire line intensity of 8300 vs. 600

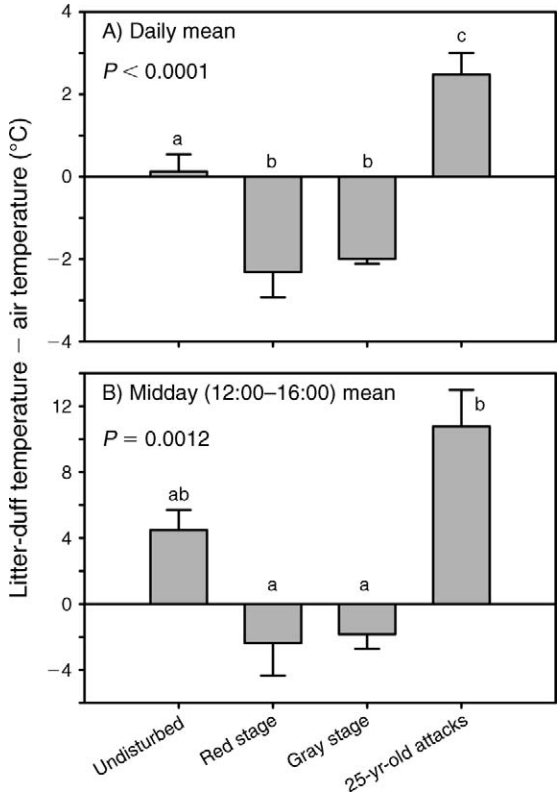


FIG. 7. (A) Daily mean and (B) mid-afternoon temperature difference between the litter–duff interface and air during the 2008 growing season (common period: 20 June–3 August) in the 2007 chronosequence sites. Histogram bars indicate the mean of three (undisturbed and gray stage), four (red stage), or six (25-yr-old attack) sites, and error bars represent SE. Lowercase letters above each bar indicate ANOVA results testing differences in means among classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 0.05$).

kW/m (–93%) at 40 km/h (Fig. 9). The 25- and 35-year post-beetle stands were predicted to have passive crown fires and had values of crown fraction burned, rate of spread, heat per unit area, and fire line intensity that were intermediate between the undisturbed and the red and gray classes. Consequently, for all fire behavior metrics, the predicted long-term trend from undisturbed to 35-year post-outbreak stands suggested a sharp decline in fire activity in the red and sometimes gray stages, followed by a gradual return toward pre-outbreak values.

At very high wind speeds (>60 km/h), most predicted differences among TSB classes disappeared, with all classes having either conditional (undisturbed, red, and gray stands) or active (25- and 35-year-old attacks) crown fires, and having a similar crown fraction burned and head fire rate of spread. Simulated heat per unit area and fire line intensity showed a trend similar to that observed between 40 and 60 km/h, with a decline in the red and gray stands followed by a return toward pre-outbreak values.

Simulation results for the "dry" and "extreme drought" summer scenarios were qualitatively similar to those of the "very dry" scenario (Appendix E). In general, fire activity was greater in the severe drought conditions (lower torching and crowning indices, greater overall probability of conditional and active crown fires, and so on) and lower in the dry summer scenario, but the trends among TSB classes were consistent among the different scenarios. Compared with the intermediate scenario (very dry), the dry and extreme drought scenarios had relatively fewer significant relationships between TSB and predicted fire behavior variables (Fig. 9; Appendix E), suggesting less influence of bark beetle outbreak effects under these more extreme conditions. A notable effect of fuel moisture conditions was to shift the window of wind speed values where simulated fire behavior was affected by bark beetle outbreaks, from 40–75 km/h in the dry, to 40–60 km/h in the very dry, to 25–50 km/h in the extreme drought scenario (Appendix E).

When the fire behavior model was run in a surface fire-only mode for the "very dry" scenario, there was no significant difference between TSB classes or data sets for predicted head fire rate of spread, heat per unit area, and fire line intensity at any of the four simulated wind speeds (Appendix D).

DISCUSSION

Bark beetles and fire as linked disturbances

The results of this study indicate that mountain pine beetle (MPB) and fire are linked disturbances in Greater Yellowstone, and that contrary to conventional wisdom, the interaction was a *negative* feedback in which the probability of active crown fire appeared to be reduced. Over the short term (1–2 years post-outbreak), we had hypothesized that MPB outbreak would increase the probability of active crown fire because dead foliage is still in the canopy and is very dry (Figs. 1 and 10). Estimated canopy moisture content was indeed reduced to ~63% of its pre-outbreak value, but neither torching nor crowning was predicted to increase, probably because canopy moisture in fire behavior models has a relatively small effect compared to other variables. The primary driver of crowning is canopy bulk density (Van Wagner 1977), and post-outbreak reduction of canopy fuels is the most likely mechanism of reduced probability of active crown fire in both red and gray-stage sites. Our field data revealed a 50% reduction in canopy bulk density in these stands compared to undisturbed stands, and simulation modeling predicted a reduced probability of active crown fire. Dead needle fall is already occurring in the red-needle stage, consistent with our field observations of mortality occurring over a number of years. Although individual trees are clearly in the green, red, and gray stage, whole stands cannot be classified as neatly in these stages and usually have a mixture of green, red, and gray trees in different proportions. Contrary to canopy bulk density, canopy

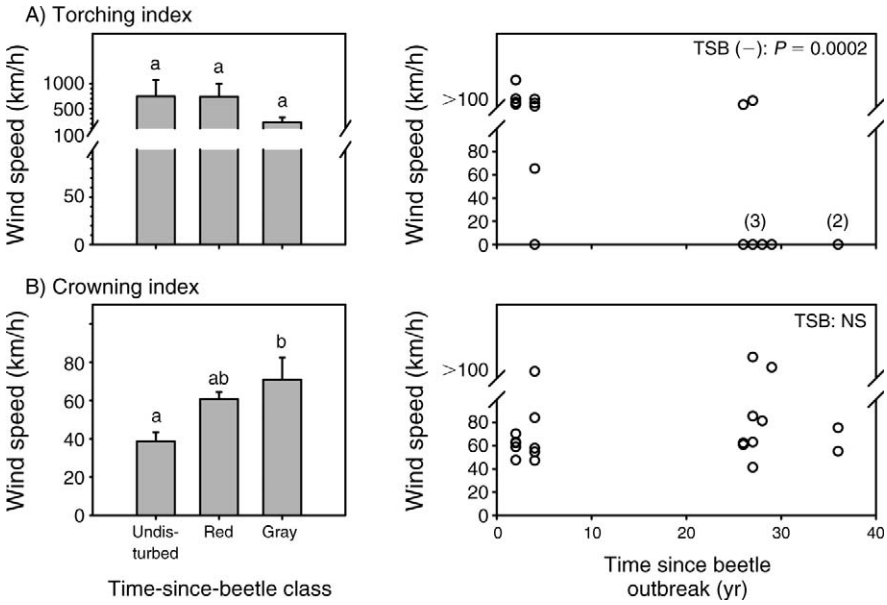


FIG. 8. (A) Torching and (B) crowning index values in the chronosequence sites ($n = 25$) under the "very dry" fuel moisture scenario. Left-hand panels show means + SE for the undisturbed, red-stage, and gray-stage stands only. Lowercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 0.05$). Right-hand panels show the relationship between each index and time since beetle outbreak for beetle-killed sites only. P values associated with the time-since-beetle (TSB) effect are shown. The "(–)" symbol following TSB effect indicates the sign of the slope when significant ($\alpha = 0.05$). In right-hand panel (A), values in parentheses are the number of superimposed data points. Note that the y-axes in the left- and right-hand panels have different ranges.

base height did not change in the short term because of the lagged response of understory tree growth. Consequently, predicted probability of torching also did not differ between the undisturbed, red, and gray-stage stands because torching is directly, although not exclusively, related to canopy base height.

Contrary to our hypothesis (Figs. 1 and 10) and to the findings of other studies (Page and Jenkins 2007*a*, Jenkins et al. 2008), but consistent with Klutsch et al. (2009), we did not observe a short-term increase in dead surface fine fuels or fuel bed depth in the gray-stage stands (3–5 years post-outbreak). Dead surface fuel loads were highly variable among stands of the same TSB class and throughout the chronosequence, even though all stands were similar in age and pre-outbreak conditions, and sustained a comparable disturbance severity. This variability is typically observed in the field and suggests that our chronosequence adequately captured the natural heterogeneity in stands of the same TSB class. Despite this variability, we detected strong trends in crown fire behavior, which suggests that our overall conclusions are robust. Live understory fuel loads, particularly herbaceous fuels, and needle litter depth increased in the short term as hypothesized. However, predicted surface fire intensity and rate of spread (for simulations run in surface fire-only mode) did not differ between TSB classes, suggesting that these changes in live understory fuels were inconsequential for surface fire behavior. Significantly deeper needle litter found in the red stands could produce somewhat different fire behavior in real forests, but this increase in needle litter did not affect our results because this variable does not contribute to surface fire spread in fire behavior models (Rothermel 1972, Scott and Reinhardt 2001). Our hypothesis of predicted increased surface fire intensity in the gray stage was thus not supported (Fig. 10). However probability of active crown fire was predicted to decrease in gray-stage stands, as hypothesized, because canopy bulk density was still low.

Predicted fire behavior in the decades that followed the outbreak (25–35 years post-outbreak) was qualitatively different than at the early stages of the outbreak. As hypothesized (Figs. 1 and 10), passive crown fires were predicted to be the norm in the 25- and 35-year post-outbreak stands because post-disturbance release of understory saplings provided ladder fuels that greatly reduced canopy base height. However, canopy bulk density was still low; thus model simulations did not predict crowning; only passive crown fires were predicted. Because of the lower mass and density of canopy fuels in the old stands, predicted fire intensity and energy released (heat per unit area) were lower than in undisturbed stands.

In light of these results, we revise our hypothesized trends in potential fire behavior (Fig. 10) as follows. Following MPB outbreak, (1) probability of active crown fire is reduced in the short-term and for up to 35 years after outbreak; (2) probability of passive crown fire does not change in the short term but greatly

PLATE 1. Extensive outbreaks of the mountain pine beetle have affected lodgepole pine stands across the Greater Yellowstone Ecosystem. Conspicuous signs of mountain pine beetle attack are pitch tubes, i.e., accumulation of tree resin at the entrance of beetle boring holes (left inset), and J-shaped vertical galleries and pupation chambers under the bark, which can still be observed on downed logs several decades after the outbreak (right inset). Photo credits: M. Simard and J. M. Griffin.

increases in the decades following the outbreak; and (3) probability of surface fire remains unaffected.

Effects of bark beetle outbreaks on microclimate

In addition to their direct effect on forest fuels, beetle outbreaks modify the microclimate of affected stands by opening the canopy, which may indirectly affect fire behavior. Compared to undisturbed stands, the litter–duff interface in the red- and gray-stage stands was much cooler than air, a difference likely caused by the insulating effect of the thick needle litter layer from dead needle fall. In contrast, the litter–duff interface in stands 25–35 yrs post-outbreak was warmer than air, likely as a consequence of two related mechanisms. First, because beetle-killed trees in these stands have fallen to the ground, solar radiation may be higher than in the red or gray stages, although we did not measure this variable. Second, the shallower litter and duff layers in these stands provide less insulation. The warmer temperatures in these stands may lead to reduced moisture content in surface fuels. The extent to which these modifications to stand and surface fuel microclimate affect fire behavior is not clear because we purposefully did not use the temperature data as inputs in our simulations, to be able to focus specifically on the effects of stand structure on fire behavior. However, we speculate that moister surface fuels in the red- and gray-stage stands may reduce surface fire intensity and rate of spread, and that drier fuels in the old attacks would have the opposite effect. This would contribute to reduced probability of surface fire in the red and gray stands and higher probability of torching and passive crown fires in the old stands.

Relationship to other studies

Our results are generally in line with those of the few other prospective studies on the effects of bark beetle outbreaks on potential fire behavior, which have found reduced probability of crowning in all post-outbreak stands and increased probability of torching in older post-outbreak stands of lodgepole pine, Douglas-fir, and Engelmann spruce (Page and Jenkins 2007*a*, *b*, Jenkins et al. 2008, Derose and Long 2009). Contrary to our findings, some of these studies also found a consistent increase in surface fine fuels in the red and gray stages of beetle outbreak, and associated this change with a potential for increased surface fire intensity and rate of spread (Page and Jenkins 2007*a*, *b*, Jenkins et al. 2008). It is impossible to determine whether this increase in surface fire intensity would have resulted in a change in fire type because the probabilities of torching and crowning were not examined in these studies.

Our prospective fire modeling results also agree with some retrospective studies in spruce–fir forests of

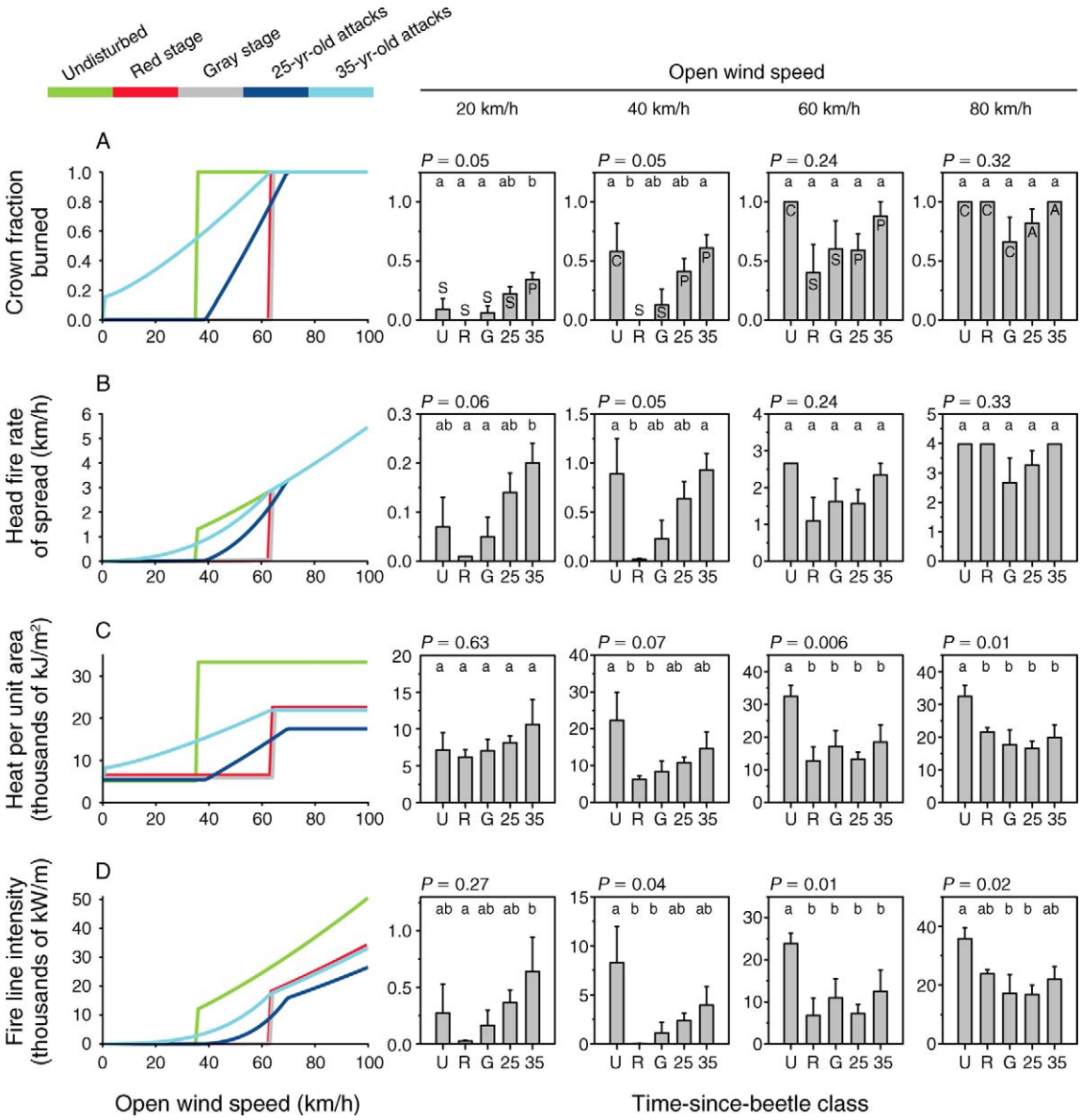


FIG. 9. Fire behavior simulation results for the five time-since-beetle (TSB) classes in the chronosequence sites under the "very dry" fuel moisture scenario. Left-hand panels show change in fire behavior metrics with open wind speed for each TSB class (lines). Each line represents the result of one simulation using the average fuel loads for that class. The right-hand panels show means + SE of each fire behavior metric for each TSB class at 20, 40, 60, and 80 km/h wind speeds. Each bar represents the average of five simulations (one per site) per TSB class (U, undisturbed; R, red stage; G, gray stage; 25 and 35, 25-yr-old and 35-yr-old attacks). Lowercase letters above each bar indicate ANOVA results testing differences in means among the TSB classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 0.05$). P values associated with the ANOVA are shown. For "crown fraction burned" (A), uppercase letters within or just above each bar indicate predicted fire type from simulation results in the left-hand panel (S, surface fire; P, passive crown fire; A, active crown fire; C, conditional crown fire). Note that the y-axes in the different panels have different ranges.

Colorado (Bebi et al. 2003, Kulakowski and Veblen 2007) and in conifer forests of California (Bond et al. 2009), which generally do not support the hypothesis of increased probability of stand-replacing crown fire following bark beetle outbreak. Similarly, in lodgepole pine forests, Kulakowski and Veblen (2007) did not find higher occurrence or severity of fire in 5-year post-beetle stands. At first glance, our results may appear to disagree with those of Bigler et al. (2005), who found a slightly elevated probability of high-severity burns 60 years after spruce beetle outbreak in spruce–fir forests, and Lynch et al. (2006), who found that the 1988 fires in Yellowstone National Park were slightly more likely to occur in lodgepole pine forests that were disturbed by

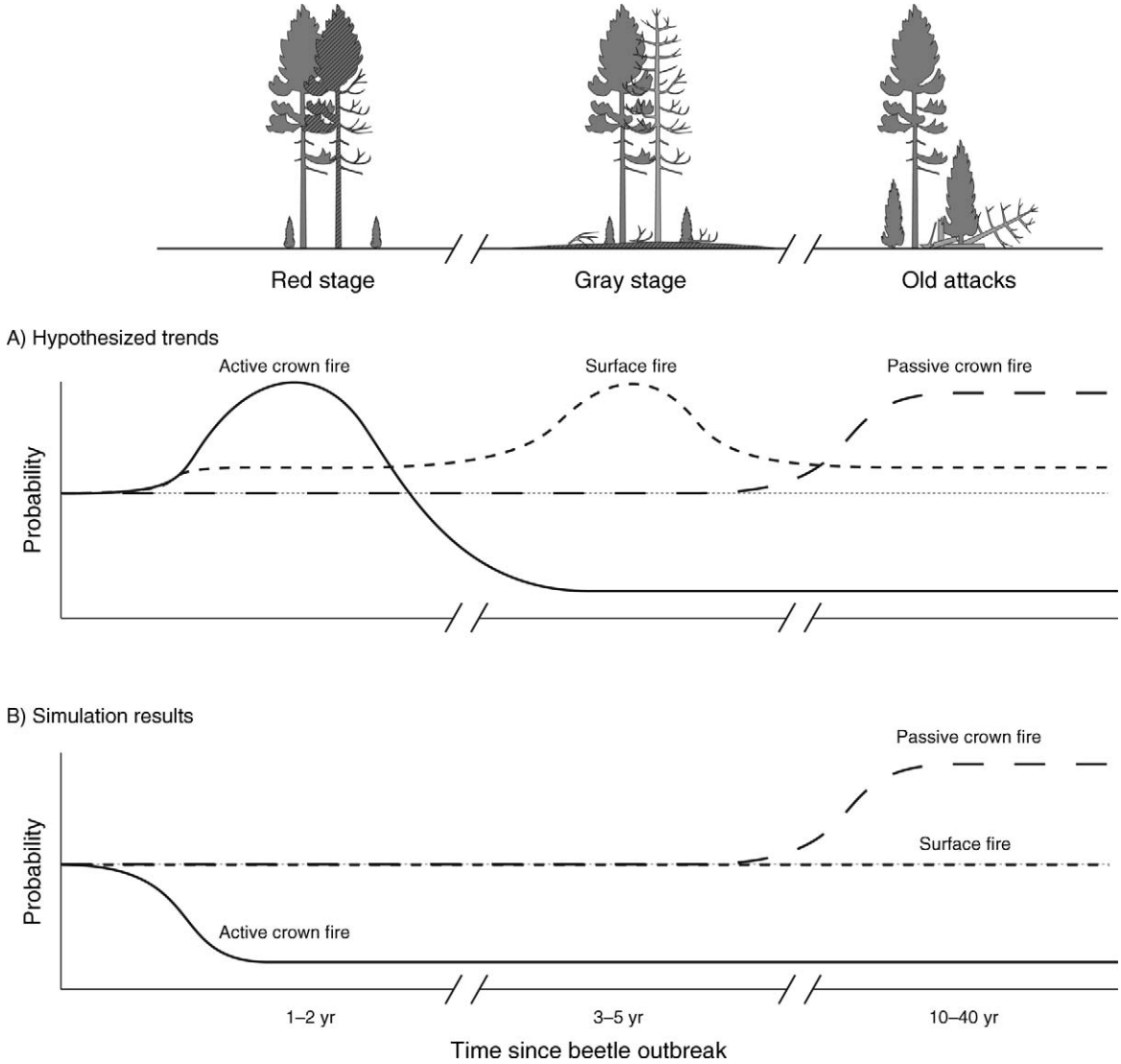


FIG. 10. (A) Hypothesized and (B) modeled net relative change in probability of different fire types relative to pre-outbreak levels (fine dotted line). In the red stage, the tree on the right is "red" and the tree on the left is green (live). In the gray stage, needles of the "red" tree have fallen to the ground.

the MPB in the 1970s (about 15 years post-beetle) but not in the 1980s (about 7 years post-beetle). However, these seemingly contradictory results may agree with our modeling results when time since a beetle outbreak and fire behavior is both considered. In Bigler et al. (2005) and Lynch et al. (2006), elevated probability of fire occurrence was observed at post-beetle periods (60 and 15 years, respectively) characterized, according to our simulations, by higher probability of torching and passive crown fire. Furthermore, Lynch et al. (2006) found no effect of beetle outbreak on fire incidence in 7-year post-outbreak stands, in agreement with our simulation results (Fig. 10B). On the other hand, Turner et al. (1999) found that 7 to 15 years following MPB outbreak, probability of severe fire increased with severe MPB damage and in late-successional stands. However, because beetle damage and successional stage are intercorrelated and were analyzed independently, it is not possible to untangle the respective effects of each. Given the paucity and mixed results of studies in lodgepole pine forests, there is a need for further bark beetle–fire interaction research in this forest type, which represents one of the most dynamic crown fire-dominated ecosystems in North America.

Assumptions, limitations, and uncertainties

Both retrospective and prospective approaches have their advantages and shortcomings. Retrospective analysis of past fires describes actual fire events but does not allow control of weather or of most prefire conditions, and the fire events represent only one realization of multiple possible outcomes. Furthermore, retrospective

analysis of fire events generally does not allow the discrimination of active and passive crown fires. Fire behavior modeling parameterized with field data has the advantages of allowing control of weather conditions and incorporating the mechanisms that link beetle-caused changes in forest structure with fire behavior. However, predictions are influenced by the quality of input data and by the accuracy of the models themselves (Cruz and Alexander 2010). In this study, we validated our chronosequence in multiple ways to ensure that it adequately represented the time sequence that each beetle-killed stand would follow. A central (but often unverified) assumption in chronosequence studies is that stands only differ by time since disturbance, and therefore should have similar pre-disturbance conditions and disturbance severity (Johnson and Miyanishi 2008). Contrary to previous bark beetle prospective studies, we were able to determine the timing of beetle attack and postfire stand age accurately, and to reconstruct pre-outbreak conditions using dendrochronology. This analysis confirmed that stands in different TSB classes had similar pre-outbreak basal area, sustained a similar outbreak severity, and within each chronosequence had the same postfire age at time of beetle outbreak (Fig. 3; Appendices B and C). In addition, our chronosequence was replicated in space (many replicates per TSB class) and time (two independent sampling campaigns: 1981 and 2007), which to our knowledge has never been done in post-disturbance chronosequence studies. Although the stands in the 1981 data set were younger (postfire age at time of beetle outbreak) and consequently had lower fuel loads than those sampled in 2007, both series generally displayed consistent trends with time since a beetle outbreak. These multiple lines of evidence suggest that the chronosequence and the results derived from it are robust.

An important assumption in current fire behavior models is that all foliage and half of the fine (1-h) canopy fuels are consumed during a crown fire (Reinhardt and Crookston 2003). Although this may be a reasonable assumption for live trees, these values may underestimate canopy consumption in dead trees, which would, in turn, underestimate heat per unit area and fire line intensity in the red- and gray-stage stands. However, our own calculations indicated that predictions of fire indices (torching and crowning index) and fire type were fairly robust to these assumptions, and that the trends observed here did not change even when assuming that all 1-h and 10-h fuels are available for consumption (Appendix F).

Another uncertainty about bark beetle effects on fire behavior is how soil heating is affected by large-diameter downed wood in old beetle kills. It is often thought that the abundance of these fallen snags may increase soil heating by smoldering, therefore increasing potential damages to soil biota. However, very little is known about the effects of large fuels on the duration of post-frontal combustion, and current models do not consider either the load or moisture content of 1000-h fuels to calculate soil heating when duff is present (Reinhardt et al. 1997). Field measurements of soil heating in several different crown fires suggest that excessive soil heating (>60°C) may be uncommon in subalpine and boreal ecosystems (J. Reardon, *personal communication*). In these forests, the mineral soil may be insulated from heat by the unburned duff layer and sometimes by the ash created by the fire itself and, consequently, only a few centimeters at the surface of the mineral horizon may have substantial heating. Additionally, coarse fuel loads in old post-outbreak stands are high but cover a relatively small surface area (<10% cover in our plots), so even if substantial heating occurs, it may have a relatively small impact at the stand scale. Clearly, this area of research needs more attention.

When does bark beetle-caused mortality matter for fire behavior?

In this study, the effect of bark beetle outbreaks on predicted fire behavior was constrained by wind speed and fuel moisture conditions. Under low wind speed conditions and when fuels were not very dry, most stands were predicted to have surface fires, whereas at very high wind speeds and when fuels were extremely dry, all stand types eventually achieved crowning. This suggests that, at the stand scale, beetle outbreaks may influence fire behavior only under certain intermediate weather conditions. This scenario is somewhat analogous to the situation that occurred during the 1988 fires in Yellowstone National Park, when forest type influenced the spread of early-season crown fires when fire weather was moderate to severe, but had little effect during the late-summer fires that burned under extremely dry and windy conditions (Renkin and Despain 1992, Turner et al. 1994). So when does stand structure in general, and bark beetle-caused tree mortality in particular, really matter? The relative importance of fuels and weather in explaining fire activity has been debated for some time, but evidence in coniferous subalpine forests points toward climatic control of wildfire area burned at broad scales and control of fire behavior by weather at finer scales (Bessie and Johnson 1995, Schoennagel et al. 2004, Littell et al. 2009). Our study supports this idea, with its finding that at the stand scale, variability in wind speed and fuel moisture had a greater effect on fire behavior than beetle-caused changes in stand structure. Fire behavior models based on Rothermel's (1991*a*) equations, including the one that was used in this study, can only predict fire behavior of wind-driven fires at the stand scale, and not of the more intense plume-dominated fires, during which forest structure attributes appear to have even less influence on fire behavior. Consequently, predictions from these models represent only a portion of the whole range of fire behavior observed in nature. Future research on bark beetle–fire interactions should concentrate on the

actual probability within a given fire year that the structure of beetle-killed stands has an influence on fire behavior, and on the potential consequences of these interactions on wildfire area burned.

This study has shown that a linked disturbance interaction likely exists between MPB outbreaks and wildfire in lodgepole pine forests of the Greater Yellowstone Ecosystem. The direction of the interaction is opposite to what is widely presumed by the public, in that our study predicts a reduction in most measures of fire intensity for up to 35 years after a beetle outbreak, including a reduced probability of active crown fire. Our results also underscore the fact that weather conditions during a burn may have a greater influence than fuel characteristics on fire behavior and effects. This study combined a replicated and validated chronosequence, which provided an empirical characterization of changes in surface and canopy fuels during 35 years after MPB outbreak, with simulations of potential fire behavior under a range of fire weather conditions. Our overall conclusion was that the linkage of prior MPB disturbance to future fire disturbance generally results in a dampening, rather than an amplification, of fire behavior and intensity. Explicit consideration of time since disturbance (e.g., TSB), environmental context (e.g., weather conditions), and underpinning mechanisms (e.g., fire behavior) is essential to understand and predict linked disturbances.

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APPENDIX A

Description of the stands used for the chronosequence study and photographs of representative stands (*Ecological Archives* M081-001-A1).

APPENDIX B

Supplemental information on the methodology used to date mountain pine beetle outbreaks and stand age in the 2007 chronosequence (*Ecological Archives* M081-001-A2).

APPENDIX C

Supplemental information on tree-ring reconstruction of pre-outbreak basal area and outbreak severity (*Ecological Archives* M081-001-A3).

APPENDIX D

ANOVA tables for time-since-beetle class analyses (*Ecological Archives* M081-001-A4).

APPENDIX E

Fire behavior simulation results for two alternative fuel moisture scenarios (*Ecological Archives* M081-001-A5).

APPENDIX F

Fire behavior simulation results for four scenarios of dead canopy fuel consumption (*Ecological Archives* M081-001-A6).