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Spatial and temporal fuels changes in whitebark pine (*Pinus albicaulis*) from mountain pine beetle (*Dendroctonus ponderosae*)

Curtis A. Gray [a,b,*], Chelsea Toone [a], Michael J. Jenkins [a], Sarah E. Null [b], Larissa L. Yocom [a]

[a] Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, UT 84322, United States
[b] Department of Watershed Sciences, Utah State University, 5230 Old Main Hill, Logan, UT 84322, United States

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ABSTRACT

Mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) causes extensive tree mortality in whitebark pine (*Pinus albicaulis* Engelm) forests. Previous studies conducted in lodgepole pine (*Pinus contorta* Douglas), Douglas-fir (*Pseudotsuga menziesii* (mirb.) Franco), and Engelmann spruce (*Picea engelmanni* Parry ex. Engelm) have shown that litter, duff, and 1-h (<0.64 cm) and 10-h (0.64–2.54 cm) time lag fuels are altered significantly from MPB outbreaks, while coarse woody fuels are affected over a longer time frame. MPB activity in conifer stands also alters foliar fuel moisture content over the course of the bark beetle rotation. This study evaluated changes to fine surface fuels and foliar fuel moisture in and under whitebark pine trees infested by MPB at two sites in Montana and Wyoming, USA. Fuel loads and foliar moisture were measured for crown condition classes of green trees (healthy), red trees (within two years since initial MPB attack with at least 50% of needles remaining), and gray trees (more than two years since attack with approximately 15% to 45% needles remaining). Tree locations and condition class were mapped using 2011, 2013, and 2015 NAIP imagery, and spatial point patterns were identified. Duff depths were significantly shallower beneath green trees (10.7–11.9 mm) than red (16.7–17.7 mm) and gray (13.9–16.1 mm) trees. Foliar fuel moisture content was altered dramatically across crown condition classes. Red needled trees had the lowest fuel moisture content, which was less than 18%. Point pattern hot spot analysis revealed increased (hot-spots) fuel hazard in trees 2–3 years post MPB attack, and decreased fuel hazard (cold-spots) in trees more than 3 years after MPB attack because foliage fell from trees and left larger diameter aerial fuels which were less likely to ignite. MPB-attacked trees were often clustered, and thus fuels hazard was not uniform across the landscape following MPB attack.

1. Introduction

Disturbances are regular events in forested ecosystems and they partially determine the physical structure of ecosystems at multiple scales. Interactions among multiple disturbances are of particular interest, where one disturbance alters the likelihood or characteristics of subsequent disturbances (Buma, 2015). For example, bark beetle mortality in conifer forests may increase wildfire hazard immediately following attack through altered fuel characteristics, diminish fire risk, or leave it unchanged. Conversely, fire can increase the risk of insect attack due to decreased tree resistance (Davis et al., 2012) and can amplify beetle-caused tree mortality (McCullough et al., 1998; Thomas and Agee, 1986). Disturbance interactions from bark beetles and fire partly regulate forest dynamics (Jenkins et al., 1998; Veblen et al., 1994), although spatial and temporal fire risk patterns from changing quantity and moisture of surface and canopy fuels following bark beetle outbreaks have yet to be examined.

Mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) is a dominant forest disturbance agent in western North America, impacting millions of hectares of coniferous forest in recent decades (Raffa et al., 2008). MPB is native to western North America and attacks most pine species (Gibson et al., 2009). At endemic population levels, beetles attack older, large-diameter, and weakened trees (Gibson et al., 2009), aiding nutrient recycling and creating canopy openings that allow regeneration (Jenkins, 2011). However, increasing air temperatures have accelerated MPB life cycles (Bentz et al., 2010; Logan and Bentz, 1999), and in susceptible forests, have been a major factor in MPB outbreaks (Bentz et al., 2010). Prolonged periods of drought, increased temperatures, or other abiotic or biotic stressors compromise a tree's ability to repel attacking beetles and produce chemical defenses (Gray

* Corresponding author.
E-mail address: curtis.gray@usu.edu (C.A. Gray).

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et al., 2019; Jewett et al., 2011).

MPB outbreaks quickly and dramatically change pine forest structure and composition (Jenkins et al., 2012, 2008). Bark beetle outbreaks are patchy in nature, with tree mortality likely to occur over several years as beetles move through a pine population over space and time. Bark beetle disturbance patterns are correlated with previous tree mortality (Kautz et al., 2011), windstorm damage (Stadelmann et al., 2014), stand density (Byers, 1984; Smith et al., 2005), and log pile storage areas (Rossi et al., 2009). Spatial patterns of bark beetle infestations have been analyzed using a range of statistical methods, for example second-order statistics such as Ripley's K-function to examine correlation of points over a range of spatial scales (Colombari et al., 2013; Kautz et al., 2013, 2011) and environmental covariates to explain spatial distribution (Baddeley and Turner, 2005). Most ecological modeling of MPB has involved simulation of bark beetle attacks. For example, Fahse and Heurich (2011) used a spatially-explicit simulation model to understand the spatial and temporal aspects of beetle outbreaks at a stand scale and found that poor data quality typically limits sophisticated quantitative spatial analyses. Time series of aerial photographs have often required mapping MBP infestations manually, with large errors in representing small groups of infested trees (Fahse and Heurich, 2011). Investigators have also used the Wildland-Urban Interface Fire Dynamics Simulator (WFDS) to investigate the influence of tree spatial arrangement of MPB-caused tree mortality on simulated fire hazard (Hoffman et al., 2012). There have been efforts to identify tree spatial patterns such as openings, single trees, and clumps of trees with interlocking crowns in fire-frequent conifer forests (Larson and Churchill, 2012). Others have investigated tree spatial patterns using a point modeling approach to quantitatively study the effects of land cover, topography, roads, ownership, and population density on the clustering of fire occurrence (Yang et al., 2007). Finally, Dickson et al. (2006) used point patterns to map landscape factors with fires and found that large seasonal fire events exhibit non-random patterns, and that patterns may affect the regional fire regime more extensively than previously thought.

Fire hazard through space and time is affected when MPB outbreaks alter quantity and moisture content of forest fuels on a landscape scale (Bigler and Veblen, 2011). MPB-caused tree mortality increases fine surface fuels (i.e. litter, duff, 1-h (<0.64 cm) and 10-h (0.64–2.54 cm) fuels) during beetle outbreaks in lodgepole pine (*Pinus contorta* Douglas) stands for up to 20 years (Jenkins et al., 2013, 2008; Klutsch et al., 2011; Page and Jenkins, 2007; Simard et al., 2011). Fine fuels are important for surface fire ignition and spread (Baker, 2009). Crown condition also changes as fuel availability and fire hazard vary through time during a beetle attack. MPB-killed trees remain green until late in the year of attack, or more commonly the following spring when needles fade to yellow, then red. The gray stage occurs when most needles have fallen and the tree begins to lose its twigs and branches (Jenkins et al., 2013, 2012; Page et al., 2012). Surface fuel moisture content (FMC) and canopy fuel moisture are also affected by bark beetle attacks. Generally, red needles have the lowest FMC, although FMC varies with environmental conditions and season (Jenkins et al., 2008; Keyes, 2006; Page et al., 2012). In healthy trees, foliage FMC is low in early spring, increases in late spring, and then decreases again throughout the fire season. FMC of bark beetle-altered foliage decreases quickly and may raise the probability of crown fire initiation and spread (Agee et al., 2002; Jenkins et al., 2012, 2008; Page et al., 2012). Once red needles fall from infested trees, the probability for crown fire decreases, although surface fire risk remains (Simard et al., 2011).

Whitebark pine (WBP; *Pinus albicaulis* Engelm) is a member of the five-needled *Pinus* species in the subgenus *Strobus* and is a keystone species at high elevations (Kegley et al., 2011; Tomback and Achuff, 2010). Important disturbances in WBP communities include both MPB and fire. WBP is most abundant in the Rocky Mountains of Montana, Idaho and Wyoming, though it is present from the coastal ranges of British Columbia to the Sierra Nevada Mountains of California (Tomback and Achuff, 2010). WBP grows in harsh environments on poorly developed soils as a climax species and often takes on a krummholtz form above treeline (Logan et al., 2009). It occurs as a seral species in mixed-species stands (Arno and Hoff, 1989), growing alongside Engelmann spruce (*Picea engelmanni* Parry ex. Engelm) and subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall). WBP provides important ecosystem services such as soil stability, watershed protection, treeline community development, and seeds provide critical food resources for other species. In 2011, the US Fish and Wildlife Service listed WBP (Listing Priority Number (LPN) of 2) under the Endangered Species Act due to threats from MPB and white pine blister rust (*Cronartium ribicola*), and alteration of the fire regime associated with extensive tree mortality (Keane et al., 2011; Kegley et al., 2011; Tomback and Achuff, 2010).

Fires in high-elevation WBP forests are usually ignited by lightning and result in low intensity surface fires that clear the understory. Short snow-free periods and cold temperatures often exclude fire for extended periods (Arno, 2000). However, in high elevation pines sufficient fuels periodically accumulate to carry fire from lower elevations (Gray and Jenkins, 2017). In denser WBP forests, passive crown fires create openings for regeneration and allow new growth into the canopy (Morgan et al., 1994; Veblen et al., 1994). Low-intensity fires are most common on dry sites with less fuels between trees (Morgan et al., 1994), whereas stand replacing fires may occur where WBP grows alongside Engelmann spruce and subalpine fir (Campbell et al., 2011). Mean fire return intervals range between 14 and 400+ years (Campbell et al., 2011). Time since MPB outbreak is one key factor determining fire risk after a bark beetle disturbance (Hicke et al., 2012; Jenkins et al., 2008), although spatial changes to fuels in MPB-killed WBP forests have only recently received attention (Jenkins, 2011; Millar and Delany, 2019; Stalling et al., 2017).

This study combined field data, remote sensing, and spatial point pattern analysis to characterize surface and aerial fuels of WBP trees infested by MPB at two sites in Montana and Wyoming, USA. We measured surface fuels and FMC at green-needle, red-needle, and gray-tree crown condition classes, then used point pattern analysis to quantify fire hazard following MPB outbreaks through space and time. We are the first to demonstrate how WPB fuel hotspots vary at stand and landscape spatial scales. Our research questions were: 1) How does surface fuel loading under WBP trees vary by bark beetle crown condition class? 2) How does foliar FMC of WBP trees vary by bark beetle crown condition class? 3) How does fire hazard vary across a WBP landscape over space and time in response to changing fuel conditions?

2. Methods

2.1. Field measurements

Sites dominated by WBP and affected by MPB were selected using US Forest Service Aerial Detection Survey maps and GIS layers (USDA Forest Service, 2010) followed by field reconnaissance. Two sites were chosen (Fig. 1A) which had a mixture of green (G), green infested (GI), red-needled (R), and gray (GR) trees. The Deadline Ridge site, west of LaBarge, WY on the Bridger-Teton National Forest, lies at elevations between 2740 and 3050 m. This site is characterized by dry, rocky soils and supports an overstory of WBP, subalpine fir and Engelmann spruce. The Branham Lakes, MT site is in the Beaverhead-Deerlodge National Forest at elevations between 2440 and 2740 m. Branham Lakes are within a large glacial cirque characterized by dry, rocky soils, with a mixture of WBP, subalpine fir and Engelmann spruce (Fig. 1D).

In 2011, 156 study plots were installed at the Deadline Ridge site (Fig. 1B) and 141 plots were installed at the Branham Lakes site (Fig. 1C). In each site, plot centers were located along N-S and E-W transects approximately 100 m apart (Fig. 1B and C). At each plot, three single-stemmed WBP trees >15.2 cm in diameter at breast height (DBH) growing nearest to plot center were selected for measurement; one in each of three crown condition classes (G, R, GR) (Fig. S1-1). G trees that were selected had no visible signs of insect infestation, blister rust, or

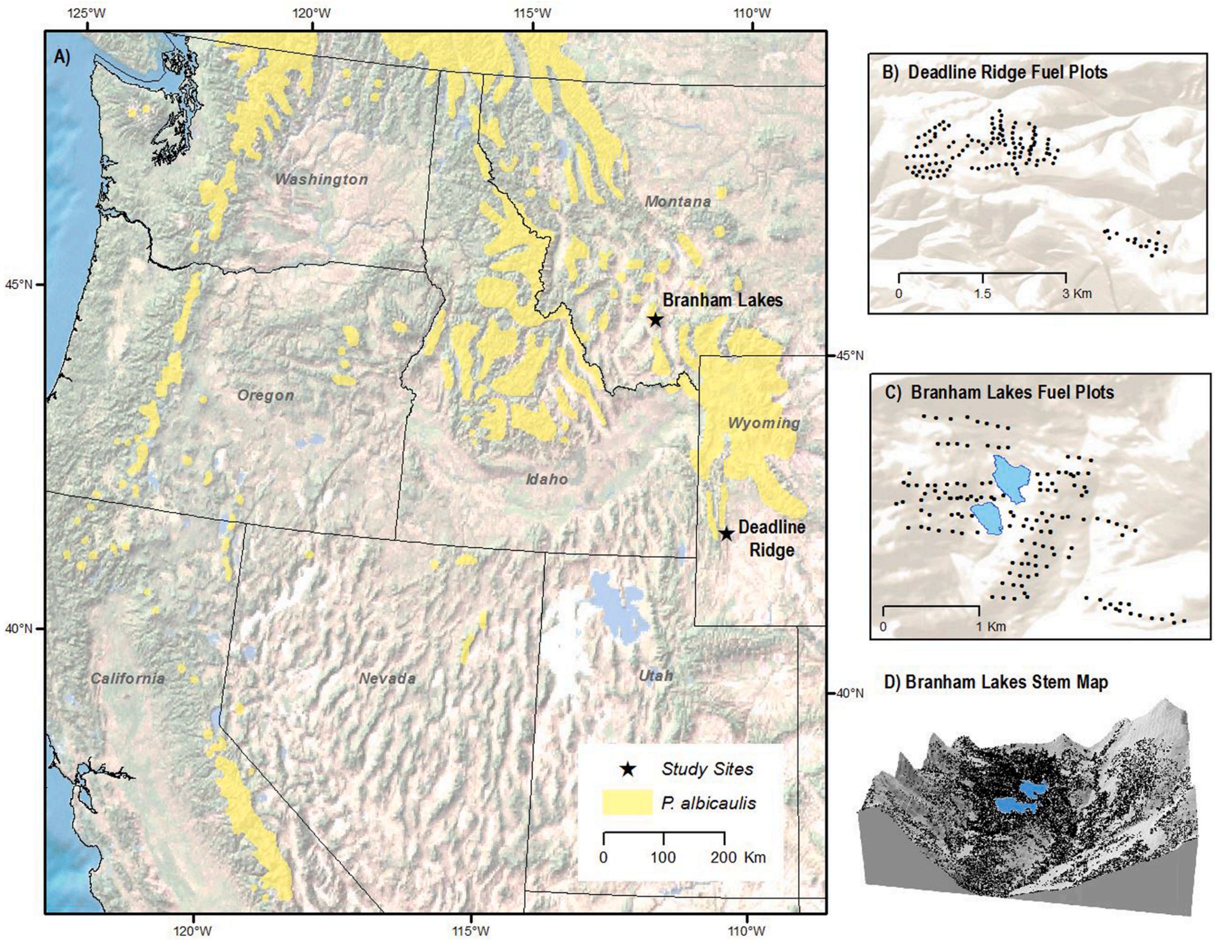

Fig. 1. A) *P. albicaulis* distribution within the U.S. is shown in yellow. Fuel plot locations for B) Deadline Ridge, WY, and C) Branham Lakes, MT; black dots are plot center. D) Stem map and terrain at Branham Lakes, black dots represent trees. Elevation ranges from 2500 to 3160 m. (Vertical exaggeration = 2x's). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

any other health issue. Trees with signs of MPB attack (e.g. exit holes, galleries) were chosen for R and GR trees. Measurements for each sample tree included DBH, height, and height to base of live crown.

Surface fuels were measured at the Deadline Ridge site in 2011 and at the Branham Lakes site in 2012. Litter and duff depths were measured at 4 points below the drip line (cardinal points at crown width) under each sample tree (Fig. S1-2) to capture fuels contributed primarily by each sample tree, although we acknowledge some fuels could have been contributed from neighboring trees. On the south side of each tree, 1-h and 10-h time lag fuels were inventoried along a 2 m transect following Brown (1974). While larger fuel classes are typically measured on longer transects, the standard Brown's transect protocols call for fine fuel measurements on a short (2 m) segment of the transect. A 1 m^2 vegetation sub-plot, located on the north end of each tree's crown width (Fig. S1-2), was used to visually estimate percent cover. Average height of live and dead shrubs and forbs was measured with a meter stick. These data were converted to biomass (kg m^{-2}) using calculations from Lutes et al. (2006).

To obtain estimates of litter bulk density, litter was collected from a 30 × 30 cm quadrat in the northwest corner of the vegetation subplot on every 5th fuel plot, and then it was oven-dried at 105 °C for 24 h and weighed. Litter bulk density (kg m^{-3}) was computed as the oven dry mass of litter (kg) divided by the product of the litter layer depth (mm) and sample area (m^2) (Van Wagtendonk et al., 1998).

Foliar FMC was measured in 2012 at the Deadline Ridge site. Four plots were selected, each including one G, GI, yellow (Y), and R tree (n = 16). Y and GI trees were added to this portion of the study to quantify FMC throughout the stages of MPB attack. Collections were made weekly from June 21 through Sept 27, between 0900 and 1400 h with temperature ranging from 7 to 22 °C, and relative humidity ranging from 16% to 70% (Mean: RH = 30%; Temperature = 17 °C). Data from two weeks in July are absent due to a road closure for the Fontenelle Fire. Needles were separated and weighed in the field, then later oven dried at 105 °C for 24 h. FMC was calculated by expressing the water content as a percentage of oven dry weight.

2.2. Field data analysis

Mean values for litter and duff depth (mm), fine down woody fuel loads (1-h and 10-h fuels; kg m^{-2}), litter bulk density (kg m^{-3}), and live and dead biomass of shrubs and forbs (kg m^{-2}) were calculated for G, R, and GR sample trees for both study areas. A one-way ANOVA test was used on the pooled data to determine if differences existed between the two study areas. This test indicated that there were significant differences in litter depth ($p < 0.0001$) and duff depth ($p < 0.0002$) between the study areas. Therefore, data for the Deadline Ridge and Branham Lakes study areas were analyzed separately. Analysis of covariance (ANCOVA) was used to assess mean fuel differences between MPB crown condition classes at each site using the GLM procedure in SAS, version 9.3 (SAS Institute Inc., 2012). The covariates of DBH, tree height, and crown width were selected to control for the influence of tree size on surface fuel accumulation based on analysis of the linear relationship of surface fuels with the tree measurements. If significant differences among crown condition classes were found, a post-hoc Tukey test was performed to compare pairs of means. Transformations were applied when necessary to meet the assumptions of normality and homogeneity. Mean FMC was also calculated from samples collected from G, GI, Y and R WBP trees from four different plots at Deadline Ridge.

2.3. Landscape-scale tree crown delineation

To map beetle-killed trees, digital orthophotos (1 m pixel spatial resolution) of the Branham Lakes study area were obtained from the National Agriculture Imagery Program (NAIP) (US Department of Agriculture, 2018) for 2011, 2013, and 2015. Individual tree crowns were identified in a two-step process. First, using the red, green, and blue spectral bands from the 2011 NAIP digital orthophoto, we used a mean shift image segmentation protocol (Comaniciu and Meer, 2002) modified by Basu et al. (2015), to group pixels in close proximity and with similar spectral characteristics into segments. Using ArcGIS v10.6.1, the level of importance given to the spectral differences (h_r) was set relatively high at 15 (values range from 1.0 to 20.0), to distinguish all tree crowns which have similar spectral characteristics. Spatial detail (h_s), which is the importance given to the proximity between features, was set to 18 (1–20), appropriate in this case because features of interest are small and clustered together. A minimum segment size of 9 pixels was chosen to represent individual tree crowns. Second, to delineate conifer tree crowns from other segments, an unsupervised classification using the Iso-Cluster and Maximum Likelihood Classification function in ArcGIS v10.6.1, was performed on the 2011 image (Jensen and Lulla, 1987). Two classes were manually identified as either conifer or other land cover. The areas identified as conifer were then used as a mask and these pixels were classified again using unsupervised classification to differentiate live (green) trees from dead (red) trees. The centroid of each segment was used as the location of the tree stem for each point classified as conifer and all non-conifer points were eliminated from analysis (Fig. 1D and Fig. S2-1). This classification technique was repeated on the 2013 and 2015 images to determine the year a tree first exhibited red needles. Accuracy of the point density and locations was assessed by manually photo-interpreting the tree crown location at 10 random 7.3 m radius plots (Table S2-1).

2.4. Point pattern analysis

Each mapped tree was assigned a hazard rating for each year (2011, 2013, and 2015) (Fig. 2). Trees that were classified as alive were given a *Medium* hazard rating. A *High* hazard rating was given to trees that were classified as red (newly dead) in an image for that year. This is because passive or active crown fire (depending on canopy bulk density) is predicted when foliar moisture falls below approximately 50% (Wagner, 1977), and recently killed trees (red and yellow) consistently had canopy fuel moisture under that threshold (see results). These trees were then classified with a *Low* hazard rating two years later when the needles fell from tree crowns to the ground. We assumed that in this stage foliage had fallen from the tree, resulting in a loss of all canopy needle biomass and a reduction in the likelihood of crown fire spread. To quantify the fire hazard of these categorical classes at different trees we present fuel hazard as a function of fine surface fuels and fuel moisture content (FMC).

Hot spot analysis is a type of point pattern analysis (Kalinic et al., 2018) used to identify clustering of spatial phenomena. Spatial phenomena are depicted as points on a map and refer to locations of events

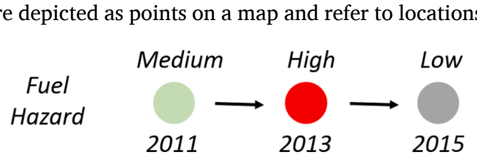

Fig. 2. Example of one tree that was alive in 2011 (hazard rating Medium), was first detected as dead in 2013 (hazard rating *High*) and was subsequently assigned hazard rating *Low* in 2015.

or objects, in this case green, red, and gray trees. A hot spot is defined as an area that has higher concentration of points compared to the expected number given a random distribution (Chakravorty, 1995). In this study we use the Getis-Ord G_i* local statistic (Getis and Ord, 2010) for cluster analysis because, as a local indicator of spatial association (Anselin, 1995), it is generated by a robust approach that allows for testing a given level of statistical significance while identifying hot spots and cold spots (Nelson and Boots, 2008). Other spatial statistical methods like Local Moran's I can assess clustering, however the Getis-Ord G_i* statistic has the advantage of being able to distinguish hot spots/cold spots of clustered high and low values. Hot spot analysis was performed on tree crown locations and fuel hazard. We used the Getis-Ord G_i* statistic (Getis and Ord, 2010) at $\alpha = 0.10$, 0.05, and 0.01 significance levels with a neighborhood search threshold of 50 m using the 'inverse distance' spatial relationship to map fire hazard hot spots/cold spots. We chose 50 m as a starting value for neighborhood distance because it represents average distance of fire brands in wildfires (Storey et al., 2020). Tuning neighborhood distance in the model can change the number of trees that are calculated as a hotspot and thus the size of clusters; however, tuning neighborhood distance does not change the general location of hot and cold spots.

3. Results

3.1. Surface fine fuels

MPB activity significantly increased litter and duff depths at both Deadline Ridge and Branham Lakes, as shown in the ANCOVA analysis comparing fine surface fuels between G, R, and GR crown condition classes (Fig. 3). R trees had the highest litter (20.6 and 17.7 mm at Deadline Ridge and Branham Lakes respectively) and duff (16.7 and 17.7 mm) depths, GR trees had intermediate litter (18.2 and 14.8 mm) and duff (13.9 and 16.1 mm) depths, and G trees had the smallest litter (13.4 and 9.8 mm) and duff (10.7 and 11.9 mm) depths. There were significant differences in mean litter and duff depths between trees in different crown condition classes for both sites (Tukey test $p < 0.001$; Fig. 3).

After accounting for the effects of tree size, 1-h and 10-h fuels were not significantly different among beetle crown condition classes at Deadline Ridge. DBH and crown size were more influential on the amount of 1-h and 10-h fuels than beetle crown condition class for the Deadline Ridge study site (Table 1). 1-h fuels for the Branham Lakes study site were significantly different among beetle crown condition classes. 10-h fuels at the Branham Lakes study site were not significantly altered by beetle crown condition class but were more influenced by crown size and the interaction of crown size and beetle condition class (Table 1).

Statistical comparisons revealed no significant differences in live and dead shrub and forb biomass by bark beetle crown condition classes in either site. Similarly, litter bulk density was not significantly altered by bark beetle crown condition class during either sampling year (Supplemental Section 4).

3.2. Foliar fuel moisture content

Foliar FMC varied by bark beetle crown condition class (Fig. 4), with R and Y FMC substantially lower than G FMC, and GI FMC falling significantly below G FMC in late summer. The FMC of green needles averaged 84% at the end of June with a peak of 116% during the growing season. GI needles were sampled at the end of July after the MPB flight period and sample tree attack. GI FMC did not significantly differ from G FMC during the first part of the sampling season but became significantly lower in the latter half of the sampling season. Y foliage FMC was 54% at the first sampling date but was under 20% for most of the summer. R foliage remained consistent throughout the sampling period, ranging from 6% to 16%.

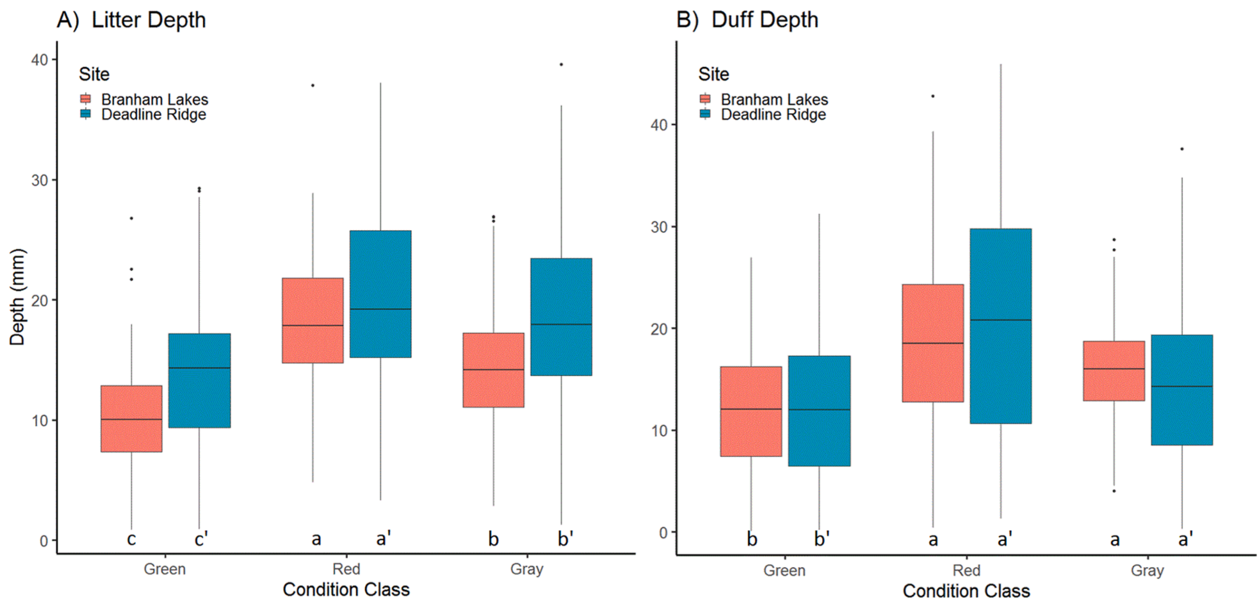

Fig. 3. Litter and duff depths (mm) for green (G), red (R), and gray (GR) trees. Different letters below boxplot indicate significant differences, α = 0.05; ' indicates Deadline ridge analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
1-hr (kg m^{-2}) and 10-hr (kg m^{-2}) down woody fuels by bark beetle condition class using ANCOVA. Different letters next to mean values indicate significant differences, α = 0.05.

Site	Fuel type and beetle condition	N	Mean	Standard Error	df	variable*	F	P
	1-hr				*1-hr*			
Deadline Ridge	Green	138	0.010b	0.0059	2	TC	0.15	0.8609
	Red	131	0.010b	0.0018	1	DBH	33.6	<0.0001
	Gray	141	0.013a	0.0021	1	CR	8.81	0.0032
	10-hr				*10-hr*			
	Green	138	0.19b	0.0291	2	TC	2.61	0.0745
	Red	131	0.20b	0.02901	1	DBH	34.41	<0.0001
	Gray	141	0.27a	0.04402	1	CR	13.79	0.0002
	1-hr				*1-hr*			
Branham Lakes	Green	141	0.04b	0.0107	2	TC	25.02	<0.0001
	Red	130	0.06a	0.0133				
	Gray	135	0.07a	0.0356				
	10-hr				*10-hr*			
	Green	141	0.17b	0.0632	2	TC	4.35	0.0136
	Red	130	0.23ba	0.0929	1	CR	26.37	<0.0001
	Gray	135	0.24a	0.1289	2	CR*TC	3.9	0.0211

* Variable: TC = beetle crown condition class. DBH = diameter at breast height. CR = crown size

3.3. Point pattern analysis

Tree delineation and the 2011, 2013, and 2015 MPB crown condition class spatial clustering at Branham Lakes are shown in Fig. 5. Increased surface and aerial fuels are expected in the significantly clustered hot spots, while cold spots would exhibit fuel hazards similar or lower than a pre-MPB infested forest, with little canopy fuels in gray trees. *High* fuel hazard hot spots were small and widely scattered in 2011, representing ~5% of the landscape (Table 2, Fig. 5A). None of the forest is mapped as *Low* fuel hazard in 2011 because the MPB attack had just begun. *High* fuel hazard hot spots in 2013 (Fig. 5B) are larger and more widespread, representing 10% of the landscape (Table 2). Cold spots appeared in 2013 (Fig. 5B I3-I4) that did not have any changes in fuel characteristics (e.g. no beetle attack), because the Getis-Ord G_i* statistic calculates hot and cold spots relative to other samples, and in 2013 there were nearby hot spots (Fig. 5B J2-J3). Approximately 7.8% of the study area had a *Low* fuel hazard rating in 2013. By 2015, the red needled trees from the 2013 NAIP image had become gray trees (Fig. 5C), with a much smaller proportion of remaining live WBP trees left to be attacked. Only 2.2% of the landscape was classified as *High* fuel hazard that year, while 11.3% was mapped as *Low* fuel hazard. Note that 86% of the basin did not change fuel hazard during the analysis window due to clusters of spruce and fir trees remaining alive and unaffected by MPB attack.

4. Discussion

4.1. Temporal fuel changes

A predictable change occurs to WBP foliage in western conifer forests as trees progress from the green (G) to gray (GR) stage over the course of a MPB outbreak, resulting in a net transfer of canopy foliage to the forest floor (Klutsch et al., 2009; Page and Jenkins, 2007; Simard et al., 2011). The amount of time for complete needle loss to occur can be from two to four years after MPB colonization in WBP (Jenkins, 2011). Increases in fuels due to MPB outbreaks have also been observed in Engelmann spruce (Jorgensen and Jenkins, 2011; Kulakowski et al., 2003) and Douglas-fir (*Pseudotsuga menziesii* (mirb.) Franco) (Donato et al., 2013). Forest floor needle litter is short-lived because decomposition begins to

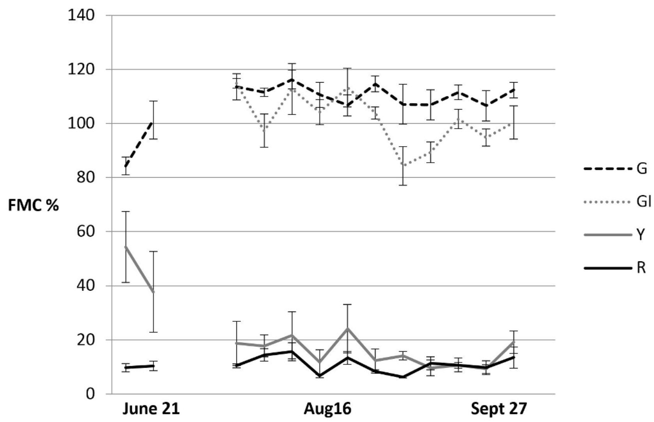

Fig. 4. The seasonal change in foliar moisture content (FMC) of WBP foliage from green (G), green-infested (GI), yellow (Y) and red (R) sample trees at Deadline Ridge, WY. The mean values and associated error bars are shown for each collection date between June 21 and September 27, 2012. No collections were made on weeks 3 and 4 due to road closures for the Fontenelle Fire near LaBarge, WY.

balance accumulation, however this varies in response to moisture and temperature regimes and can be quite prolonged in high elevation WBP which can have very long fire return intervals (Campbell et al. 2011). Later, branches and boles of bark beetle-killed snags fall to the forest floor to decompose over a period of decades (Hicke et al., 2012; Jenkins et al., 2013, 2012, 2008). Most studies report minor to no difference in surface fuel loads between beetle crown condition classes. However, in this study, we found significant differences in litter and duff between G and R/GR trees at both of our sites, and differences in 1-h and 10-h fine woody fuels by crown condition class at both sites. Linking these results with a novel ecological application of point pattern analysis, our research suggests that a predictable fuels shift occurred approximately two years following MPB attack, with increased fuels and higher incidence of *High* fuel hazard hot spots during the red needle phase and a decrease in fuels and fuel hazard across the landscape in subsequent years when trees had transitioned to the GR phase.

Changes in FMC in bark beetle-infested trees have been described in lodgepole pine (Jolly et al., 2012; Page et al., 2012) and Engelmann spruce (Page et al., 2014). In this study, we described similar changes to foliage in MPB-infested WBP trees. In all studies, the sequence of foliar FMC is similar. At the onset of spring sap flow, conifer foliar FMC increases rapidly to maximum levels in G trees. G trees are attacked in the summer and by late summer GI foliage has significantly lower foliar FMC than G trees (Fig. 4). The foliar FMC of Y and R needles measured at the beginning of the growing season is significantly lower than either G or GI needles. R needles have FMC similar to fuel moisture of dead surface litter, driven by diurnal temperature and relative humidity conditions (Page et al., 2014). It is the influence of low FMC in R needles that contributes to the high flammability hazard of bark beetle infested forests in the R stage as described by Jenkins et al. (2013, 2012) and observed by fire managers in fires that have burned in bark beetle-affected fuels (Church et al., 2011; Stiger and Infanger, 2011).

Campbell et al. (2011) described the fire regime in WBP forests as having a range of intensities from low intensity surface fires to high intensity stand replacing fires, burning at intervals between 14 and 400+ years. Larson et al. (2009) found that fire activity in high elevation, pure WBP forests was related to biophysical site characteristics and disturbance, and the fire regime was characterized by low intensity fire. Our Deadline Ridge study area was similar to the Larson et al. (2009) study area, with low tree density and discontinuous fuel that would inhibit the likelihood of fire spread between adjacent trees. However, in the Branham Lakes study area, trees were more dense and intercrown distance was shorter, creating the potential for crown fire and spread during the red phase. The red phase is a short period considering the centuries needed for WBP forest development. However, bark beetle affected fuels may create conditions for high intensity surface fires with capability for crown fires across a wide range of fire weather conditions.

In addition to the increased risk of crown fire during the red phase, there is also the possibility that surface fire effects on soil and subsurface processes could be more severe due to the transfer of crown fuels to the forest floor. With increased duff and litter loads under MPB-killed trees, heating of the soil could lead to the loss of mycorrhizal fungi (Trusty and Cripps, 2011), altered soil structure (Huffman et al., 2001), or other secondary effects in the years following a wildfire. Increased surface fuels were highest during the red phase in our study, although litter and duff were still elevated in the gray phase compared to the green phase. This elevated risk of surface heating due to increased surface fuels would decline over time as the fine fuels decomposed.

4.2. *Spatial fuel changes*

Often fuels studies are assumed to be one dimensional; however, we examined changes in fuels through time (the course of a MPB attack) and across space in the watershed. Our approach to assess fuel hazard hot spots spatially is valuable because fuels that are contiguous pose a much greater hazard than fuels spread intermittently across landscapes or watersheds. It has become increasingly clear that spatial patterns in fuels influence fire behavior within forest stands, whether from MPB or otherwise. Our results suggest that changes in fuels caused by MPB mortality are variable over both time and space, which means fire behavior within a stand varies depending on the timing and location of fires and the point of ignition. Abundant spatial environmental data, including the remotely sensed data used for this study, provide new tools to understand increased fuel hazards in space and time, and to better manage fuels and fires.

This was the first time we know of that Getis G_i* hot spot analysis was used to examine fuels through space and time. The Getis G_i* evaluates every point for higher fuels hazard in relationship to its neighborhood, so a point that represents a live tree can still have a high Getis G_i* value (hot spot) if its neighbors have *High* fuel hazard ratings. The interpretation of the Z-score is straightforward: a large positive value suggests a cluster of increased fuel hazard (hot spot) and a large negative value indicates a cluster of low or decreasing fuel hazard (cold spot). This is a reasonable model for fuels dynamics on the landscape. A large patch of dead trees with low foliage moisture increases the likelihood of a crown fire moving through the stand, even if a few live trees remain. Other measures of spatial dependence, like Moran's *I*, indicate whether clustering exists in an area, yet provide no information on where clusters are located.

4.3. *Interactions among disturbances*

Complex assemblages of conifer species, bark beetle-altered fuels condition classes, and the activity of other biotic and abiotic disturbance agents over complex terrain complicate fire regimes, especially over long temporal and large spatial scales. Disturbance agents alter the landscape-scale fuel complex and may affect fire spread, intensity and severity within and beyond the disturbed landscape. The potential for crown fire in high-elevation, WBP forests is greatest in mixed, transitional forests at lower elevations where WBP is a minor seral species in stands composed of lodgepole pine, Douglas-fir and/or true firs (*Abies* spp.) and Engelmann spruce. Hazardous fuel conditions in pure and mixed WBP stands can result from; 1) the suppression and exclusion of fire; 2) recent MPB outbreaks; 3) bark beetle outbreaks triggered by drought in other species such as Douglas-fir and Engelmann spruce; 4) vertical fuel ladders resulting from cyclic western spruce budworm (*Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) outbreaks affecting true firs and Douglas-fir; and 5) other agents of disturbance including dwarf mistletoes (*Arceuthobium* spp), root pathogens and rust

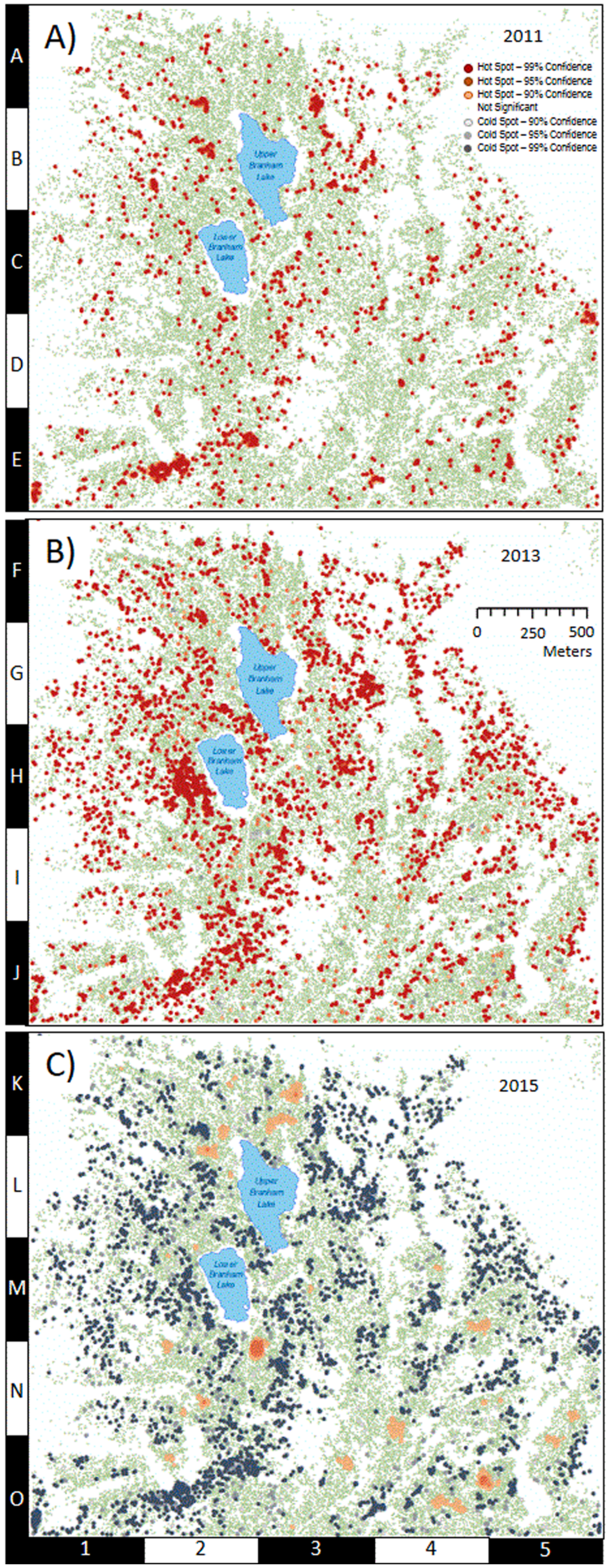

Fig. 5. Tree crown locations of canopy dominant trees in Branham Lakes Basin, MT. Years since death was based on image classification of 2011, 2013 and 2015 NAIP imagery. Hot spot analysis showing high Getis-Ord G_i*scores for (A) 2011 (B) 2013 and (C) 2015. Each point represents a tree, with green points representing green healthy trees. Clustered hot spots (warm hues) indicate increased fine surface fuels and lower crown fuel moisture due to dead trees from recent mountain pine beetle (MPB) infestation, while cold spots (gray hues) exhibit fuel hazards lower than a pre-MPB infested forest due to less foliage on gray trees that have lost their needles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Getis-Ord G_i* values for hot spot analysis of fuels, Branham Lakes Basin, MT. Values for each year are the number of trees per G_i* bin (N = 47,971).

	G_i*	Confidence Interval	2011	%	2013	%	2015	%
Increased Fuel Hazard	> 2.57	99%	1,609	3.4	3,224	6.7	0	0.0
	1.96 – 2.56	95%	399	0.8	957	2.0	105	0.2
	1.65 – 1.95	90%	379	0.8	680	1.4	964	2.0
Not Significant	-1.64 – 1.64	N.S.	45,584	95.0	39,346	82.0	41,447	86.4
Decreased Fuel Hazard	-1.65 – -1.95	90%	0	0.0	2,830	5.9	625	1.3
	-1.96 – -2.56	95%	0	0.0	925	1.9	1,028	2.1
	< -2.57	99%	0	0.0	9	0.0	3,802	7.9

fungi that are increasingly common in overmature conifer forests characteristic of the fire suppression era. The net result is a variably flammable, disturbance-altered complex of surface, ladder, and canopy fuels that may extend up in elevation to stands where high-elevation five-needle pines are a major seral or climax species.

Better understanding changing spatial and temporal configuration of fuels and fire, as well as interactions among forest disturbance, is needed to improve holistic watershed management (Stone et al., 2010). The loss of mature trees due to MPB outbreak reduces ecosystem carbon storage; however, this is balanced by surviving trees and new seedling's ability to grow more quickly from reduced competition and carbon pools in snags and coarse woody debris (Hansen, 2014). Following MPB outbreaks, forests could switch from carbon sinks to carbon sources but typically recover within 5–20 years (Hansen, 2014). Bark-beetles and tree mortality also affect snowpack depth and can lead to earlier snowmelt (Teich et al., 2016). Forests, fuels, and fires affect the accumulation and transport of water, nutrients, sediment, and thermal energy, and thus can drive ecosystem health (Luce et al., 2012). Forest disturbances, paired with climate change, have the potential to reduce late summer streamflow throughout western North America (Ficklin et al., 2018). Watershed management is already inextricably linked to cyclical and spatially non-uniform drought cycles (Null and Viers, 2013; Null et al., 2012; Dzara et al. 2019). We provided another layer of cyclical and spatially non-uniform fuels and fire risk information, derived from publicly-available data, to enable forest managers and firefighters to best manage western forests.

4.4. Study limitations

While image segmentation successfully delineated trees for this study (Supplemental Table S2-1), accuracy could be improved with finer resolution data or forest structure information from LiDAR (Hu et al., 2014). Additionally, longer photo time series would help inform the start, end, and rates of the MPB epidemic. NAIP imagery is only available every 2 years rather than on an annual time scale. We were unable to assess MPB activity in 2017 because the ground was too snowy, and we were unable to assess MPB activity in 2009 or prior because endemic levels of MPB were undetectable. In this study fuel hazard was designated based on fine surface fuel amounts and arrangement (aerial or surface) and fuel moisture content (FMC). However, many other factors affect fuel hazard including topography, stand age, and species composition. In addition, differences in tree chemistry of individual trees can affect flammability (Page et al., 2012). Recent studies of chemical compounds in high elevation five needle pines have shown proportions of compounds emitted from pine foliage changed consistently with elevation (Gray et al., 2019), revealing that environment can have consistent and predictive influence on tree chemistry. MPB attacks exacerbate this effect, with five needle pine species emitting distinctive ratios of compounds in response to attack (some of which increase flammability) (Runyon et al., 2020).

5. Conclusions

This study showed that litter, duff, and fine surface fuels increased beneath MPB-affected WBP. Hot spot analysis demonstrated that fuel hazard was spatially widespread across the landscape at the height of the MPB outbreak, but not uniform across the landscape. High hazard clusters were evident in several locations (Fig. 5B; H2, J2-J3). Fuel hazard hot spots increased and shifted across the landscape over time, then fire hazard hot spots were reduced approximately two to four years following MPB outbreak (Fig. 5C; O2-O3). MPB-affected stands can provide a suitable environment for WBP regeneration if seed sources are available (Larson and Kipfmueller, 2010), but a large-scale reduction in seed-producing trees, the impact of blister rust on seedlings and saplings, and the uncertain effects of climate change place the future of WBP forests in western North America in peril. Active management and restoration, including planting WBP seedlings or planting rust-resistant trees in MPB-affected stands, may be needed to maintain WBP populations. Other management activities that increase overall stand health and vigor, such as thinning dense forests, can increase resistance and resiliency to bark beetles (Filip et al., 2007; Jenkins et al., 2012, 2008). Prescribed fire or managed wildfire can also be an effective tool to increase the health of WBP forests. Our research provides a method to identify large high fire severity patches so that they can be avoided.

CRediT authorship contribution statement

Curtis A. Gray: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. **Chelsea Toone:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. **Michael J. Jenkins:** Conceptualization, Methodology, Resources, Supervision, Project administration, Funding acquisition. **Sarah E. Null:** Writing - original draft, Writing - review & editing, Validation. **Larissa L. Yocom:** Writing - original draft, Writing - review & editing, Validation, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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