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Influence of Mountain Pine Beetle on Fuels, Foliar Fuel Moisture Content, and Litter and Volatile Terpenes in Whitebark Pine

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INFLUENCE OF MOUNTAIN PINE BEETLE ON FUELS, FOLIAR FUEL MOISTURE CONTENT,

AND LITTER AND VOLATILE TERPENES IN WHITEBARK PINE

by

Chelsea Toone

A thesis submitted in partial fulfillment
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ABSTRACT

Influence of Mountain Pine Beetle on Fuels, Foliar Fuel Moisture Content, and Litter and

Volatile Terpenes in Whitebark Pine

by

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Utah State University, 2013

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Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has caused extensive

tree mortality in whitebark pine (*Pinus albicaulis* Engelm) forests. Previous studies

conducted in lodgepole pine (*Pinus contorta* Douglas), Douglas-fir (*Pseudosuga menziesii*

(mirb.) Franco), and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) stands

have shown that litter, duff, and one hour (< 0.64 cm diameter) and ten hour (0.64 cm

to 2.54 cm diameter) time lag fuels are altered most significantly compared to hundred

hour and thousand hour fuels during a bark beetle outbreak. Bark beetle activity in

conifer stands has also been shown to alter foliar fuel moisture content and chemistry

over the course of the bark beetle rotation.

The objective of this study was to evaluate changes to fine surface fuels, foliar

fuel moisture, chemistry and litter chemistry in and under whitebark pine trees infested

by mountain pine beetle. Fuels were measured beneath green (healthy) trees compared

to red (two years since initial MPB attack with 50% or greater needles remaining) and

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gray (greater than two years since attack with between 15% and 45% needles remaining) trees. Foliar moisture content was measured in four mountain pine beetle crown condition classes: green-uninfested, green-infested (current year's attack), yellow (last year's attack), and red. Total terpene content was analyzed in whitebark pine needle litter and volatile terpenes were collected and analyzed from green, green-infested, yellow, and red trees.

Significant differences were found in litter depths under green, red, and gray trees. Duff depths were significantly less beneath green trees than red and gray trees. One hour and ten hour fuels were more influenced by diameter and crown size than beetle crown condition classes. Foliar fuel moisture content dramatically decreased from green-infested to the red beetle crown condition class. No differences were detected in shrub and forb biomass between green, red, and gray trees. Green-infested trees had significantly lower foliar fuel moisture than green trees and by late in the season showed fuel moisture levels similar to red trees, which had the lowest fuel moisture content. Total terpene analysis of needle litter identified 16 compounds. Total terpene content in red needle emissions are greater than either infested or yellow needles. Litter beneath red trees contained large amounts of terpenes, including some compounds known to increase foliage flammability. Moreover, yellow and green-infested foliage tended to emit greater amounts of volatile terpenes, which has been shown to promote increased flammability in lodgepole pine.

(63 pages)

PUBLIC ABSTRACT

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Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has caused extensive

tree mortality in whitebark pine (*Pinus albicaulis* Engelm) forests. Previous studies

conducted in various conifer forests have shown that fine surface fuels are significantly

altered during a bark beetle outbreak. Bark beetle activity in conifer stands has also

been shown to alter foliar fuel moisture content and chemistry over the course of the

bark beetle rotation.

The objective of this study was to evaluate changes to fine surface fuels, foliar

fuel moisture and chemistry and litter chemistry in and under whitebark pine trees

infested by mountain pine beetle. Fuels were measured beneath green (healthy) trees

compared to red (two years since initial MPB attack with 50% or greater needles

remaining) and gray (greater than two years since attack with between 15% and 45%

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beetle crown condition classes: green-uninfested, green-infested (current year's attack),

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INTRODUCTION AND LITERATURE REVIEW

In every forest there is a natural accumulation of litter and twigs due to trees growing old or branches being shaded out. Accumulation of fuels is further affected by natural disturbances such as wildfire, disease, drought, and insects that commonly cause mortality in coniferous forest ecosystems (Filip et al., 2006). Extensive tree mortality associated with disturbance can change forest composition and structure (Filip et al., 2006) and increase the amount and composition of surface fuels. The current mountain pine beetle (*Dendroctonus ponderosae* Hopkins, MPB) outbreaks in western North America have altered the quality and quantity of forest fuels on a landscape scale which may affect fire hazard in fire-prone ecosystems (Bigler and Veblen, 2011). Additional studies are needed to characterize the impact of MPB activity on wildland fuels in whitebark pine (*Pinus albicaulis* Engelm, WBP) forests.

MPB has caused extensive tree mortality in lodgepole pine (*Pinus contorta* Douglas) and high-elevation five needle pine forests in the Intermountain West. Recent studies have shown that MPB-caused tree mortality significantly alters the quantity of fine surface fuels i.e. litter, duff, one hour (<0.64cm diameter) twigs and ten hour (0.64 cm to 2.54cm diameter) twigs during beetle outbreaks in lodgepole pine stands (Page and Jenkins, 2007a; Jenkins et al., 2008, 2014; Klutsch et al., 2011; Simard et al., 2011). These fine fuels are extremely important to surface fire ignition and spread (Baker, 2009). Changes in fuels due to bark beetle outbreaks have also been studied in Engelmann spruce (*Picea engelmanni* Parry ex. Engelm) (Kulakowski et al., 2003; Jorgenson and Jenkins, 2011) and Douglas-fir (*Pseudotsuga menziesii* (mirb.) Franco)

(Donato et al., 2013). The changes to fuels in MPB-killed WBP forests have only recently received attention (Jenkins, 2011) and further investigation is warranted. The objectives of this study were to quantify the changes to fine surface fuels and vegetation directly beneath MPB-affected WBP and to quantify foliar fuel moisture content, and terpene changes to the crowns of MPB-affected WBP.

Whitebark pine

WBP is a member of the five-needled stone-pine group and is considered to be a keystone species on important high-elevation sites (Kegley et al., 2011; Tomback and Achuff, 2010). It is the most northerly and broadly distributed of the white pines in North America. It is distributed from the coastal ranges and Cascades of British Columbia, to the Sierra Nevada Mountains of California, and is abundant in the Rocky Mountains of Montana, Idaho and Wyoming (Tomback and Achuff, 2010). WBP grows in harsh environments on weakly developed soils as a climax species and often takes on a krummholtz form above timberline (Logan et al., 2010). It also occurs as a seral species in mixed-species stands (Arno and Hoff, 1990) growing alongside Engelmann spruce and subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) at lower elevations. WBP is a slow-growing, long-lived species with individual trees commonly over 400 years old and some surviving more than 1,000 years (Perkins and Swetnam, 1996; Keane, 2011). WPB is intermediate in shade tolerance and in the absence of fire may be succeeded by shade tolerant species due to lack of fire (Arno and Hoff, 1989; Keane, 2011).

Because WBP typically occurs at high elevation sites that are difficult to access, it is removed from "common human interaction" and is not valued as a timber species (Gibson et al., 2008; Logan et al., 2009). However, it provides important watershed protection values and the wingless seeds provide critical food resources for many wildlife species. WBP stands serve to regulate high-elevation ecosystems by providing shade and shelter from wind which prolongs snowmelt and affects winter and spring snowfall distribution. Most rivers in the western U.S. are regulated by accumulation of winter and spring snowmelt, and reduction in WBP canopy may affect peak runoff (Logan et al., 2010).

WBP cones remain closed at maturity, and seed removal and dispersal is accomplished primarily by the Clark's nutcracker (*Nucifraga columbiana*) or American red squirrel (*Tamiasciurus hudsonicus*) (Tomback, 1982; Tomback, 2001; Lorenz et al., 2008). A Clark's nutcracker can hold up to 100 seeds in its sublingual pouch and may carry seeds a distance of 10 km before burying them in caches (about 15 seeds/cache)(Keane, 2011). Nutcrackers recall their caches by using pattern recognition (Keane, 2011). Recently burned and open areas are favored for caching because of the rich landscape patterns created by the disturbance. WBP regenerates well in these areas due to lack of competition and exposed soil. The American red squirrel collects WBP cones in summer and fall and caches them in middens (Mattson et al., 2001). Clusters of multi-trees commonly result from the multiple seeds that may germinate in each cache (Campbell and Antos, 2000).

WBP is under consideration for listing as a threatened and endangered species due to threats from white pine blister rust (*Cronartium ribicola*) and MPB, successional replacement by shade tolerant species, and alteration of the fire regime associated with extensive tree mortality (Tomback and Achuff, 2010; Keane, 2011; Kegley et al., 2011). In 2011 the US Fish and Wildlife Service determined that WBP warranted listing under the Endangered Species Act (ESA). WBP was added to the list of species eligible for protection under ESA and its status will be reviewed annually (USFWS, 2011).

White pine blister rust is caused by the non-native fungus *Cronartium ribicola* (*Uredinales: Cronartiaceae*), that was introduced around 1910 from Europe (Maloy, 2001). The disease causes dieback in branches, reproductive failure, and tree mortality (Maloy, 2001). Acting alone, white pine blister rust usually takes more than a decade to kill a tree (Kendall and Keane, 2001). Kegley et al. (2011) found that as elevation increases the level of blister rust infection decreases suggesting increased survival for WBP at higher elevations. Kegley et al. (2011) also found more than half of the 2400 WBP trees examined in their study were infected with blister rust, but only 10% had infections severe enough to impact cone production. Blister rust-weakened trees have been shown to be more susceptible to MPB attack (Kegley et al., 2011). Other stressors such as extreme weather conditions in high elevation environments can also predispose WBP to MPB attack (Hessburg et al., 1994; Campbell et al., 2004).

MPB outbreaks have the greatest ability to change composition and structure of pine forests in the shortest period of time (Jenkins et al., 2008; Jenkins et al., 2012). MPB-caused WBP tree mortality during the most recent outbreak has resulted in

extensive tree mortality in Greater Yellowstone Ecosystem WBP stands (Macfarlane et al., 2013).

WBP decline influences many aspects of its ecosystem. A significant impact is the effect on grizzly bears (*Ursus arctos*) that obtain significant amount of their fat requirements from WBP seeds (Mattson et al., 2001). Grizzly bears in the Greater Yellowstone Ecosystem commonly seek out red squirrel middens to feed on the highly nutritious and fatty seeds that are advantageous for overwintering (Mattson et al., 2001). However, due to decline of WBP forests seed caches are not as plentiful, forcing bears to find alternative food sources including garbage or gut piles left behind by hunters increasing human/bear interactions (Mattson et al., 2001).

Clark's nutcrackers and American red squirrels are also affected by WBP forest decline and may leave areas where tree mortality is high to find alternative food sources, reducing regeneration potential. Loss of WBP also reduces thermal cover at high elevations and may negatively impact elk-calf survival during calving season (Logan et al., 2010).

Mountain pine beetle

MPB is native to western North America and infests all pine species within its range (Gibson et al., 2009). During severe outbreaks, adult MPB may attack spruce (*Picea* spp.) but brood development is rarely successful (Furniss and Carolin, 1980). At endemic population levels the beetle infests older, large-diameter, and weakened trees

(Gibson et al., 2009), aiding in nutrient recycling and creating canopy openings that allows for regeneration (Jenkins, 2011).

MPB broods feed and develop within the phloem of host trees. After mating, female beetles lay eggs along the sides of vertical egg galleries. Upon hatching, larvae feed on the phloem tissue creating tunnels perpendicular to the main egg gallery. This feeding activity girdles the tree by disrupting the flow of essential nutrients from crown to roots (Kramer and Kozlowski, 1979). Water transport to the tree crown is also disrupted by blue-staining fungi introduced by bark beetles as they feed on the sapwood of host trees (Parmeter et al., 1989; Bleiker et al., 2009). Results of phloem girdling by bark beetle larvae and development of blue-staining fungi results in tree death within a year of MPB attack (Bentz et al., 2010; Six and Wingfield, 2011; Hubbard et al., 2013).

Seasonal temperatures largely determine which larval instar will overwinter; however, the fourth instar is the most typical overwintering stage. The manufacture of cryoprotectants enables overwintering larvae to withstand cold temperatures during winter months (Bentz and Mullins, 1999). Sambaraju et al. (2012) found that cold snaps resulting in temperatures of -20°C for four consecutive days resulted in sufficient beetle mortality to decrease the probability of outbreak. One hundred percent beetle mortality was found to occur at -40°C (Regniere and Bentz, 2007). Without protection of insulating snow, unusually cold spring or fall temperatures may kill developing beetle brood (Sambaraju et al., 2012). The timing of cold snaps appears to be just as important to beetle survival and continued development as actual temperature (Jewett et al., 2011; Sambaraju et al., 2012). Cold snaps in October through November had greater

impacts on beetle populations than cold snaps in the spring (Sambaraju et al., 2012).

The following spring, larvae construct pupal chambers at the end of their feeding

galleries, and after a few more weeks, emerge as adults. MPB generally produces one

generation per year. However, life cycles may require two years to complete at higher

elevations where temperatures are cooler. Summer temperatures in high latitude or

high altitude environments are usually not warm enough to support a one-year life cycle

(Logan et al., 2010). For example in the 1970's climatic factors limited the geographic

distribution of MPB to a range smaller than that occupied by available hosts (Amman,

1973; Safranyik, 1978). This is still true today but MPB continues to increase its

distribution. Increases in temperature accelerate MPB life cycles (Logan and Bentz,

1999; Bentz et al., 2010). One-year populations were recorded by Bentz et al. (2010) at

higher elevation sites in the Greater Yellowstone area. Accelerated rates of

development may become increasingly common with global warming and contribute to

greater potential for outbreaks. Such findings may also serve as indicators of climate

change (Logan and Bentz, 1999).

Bark beetles evolved mass attack behaviors to overcome host tree defenses

(Franceschi et al., 2005). Healthy trees possess both pre-formed (constitutive) and

induced defense mechanisms for protection against insect attack. Trees translocate

resins to attack sites that effectively "pitch out" beetles. It takes multiple successful

attacks to kill a healthy tree (Franceschi et al., 2005).

Prolonged periods of drought, or stress induced by other abiotic or biotic factors,

compromises a tree's ability to pitch out attacking beetles and produce defensive

chemicals (Jewett et al., 2011; Gaylord et al., 2013). Therefore, silvicultural management activities that increase overall stand health and vigor, such as thinning dense forests, can increase resistance and resiliency to bark beetle infestation (Filip et al., 2006; Jenkins et al., 2008, 2012). Reducing stand density decreases competition for water and nutrients and provides trees a greater ability to produce sufficient amounts of pitch. Thinning can also increase exposure to sunlight and raises bole temperatures potentially resulting in conditions unfavorable to developing broods (Bartos and Amman, 1989).

MPB outbreaks in WBP can occur in stands having large quantities and high densities of susceptible host species, and under conditions that result in high risk such as favorable weather and tree stress (Jenkins, 2011). In the Intermountain West, MPB populations in high elevation-pine ecosystems increased dramatically during the last decade (Gibson et al., 2008). By 2008, MPB had caused mortality on 405,000 hectares of high-elevation pines (Gibson et al., 2008). Although warming temperatures have been a major factor in the development of outbreaks (Bentz et al., 2010), epidemics would not have developed in the absence of susceptible stand conditions. Landscape scale fire suppression and reduction in timber harvesting in pine stands over the past century have created conditions suitable for bark beetle population growth and spread in lower elevation conifer forests.

Large MPB outbreaks are not unprecedented in WBP and outbreaks have been recorded at least three times in the twentieth century (Logan et al., 2010), and as long ago as the last glacial retreat (Brunelle et al., 2008). Persistent snags from an outbreak

that developed in southern Canada and expanded to northern Wyoming between 1909

and 1940 (Ciesla and Furniss, 1975; Arno and Hoff, 1989) suggest that outbreak lasted 8-

12 years (Perkins and Swetnam, 1996). However, the current North American mountain

pine beetle outbreaks in lodgepole pine and high elevation pines forests are some of the

largest in terms of geographic scale in recorded history (Regniere and Bentz, 2007;

Gibson et al., 2008; Bentz et al., 2010). An important difference in the current outbreak

in WBP forests is the impact of white pine blister rust on WBP regeneration in MPB-

affected stands (Kegley et al., 2011). Blister rust has advanced to such a high level and

caused such a decline in cone production that the very survival of WBP is threatened

throughout its range (Schwandt, 2006).

Whitebark pine restoration

Keane (2011) suggested the best way to restore WBP is to retrieve seeds from

existing WBP and then replant WBP seedlings (Hoff et al., 2001). Prescribed burning has

also been suggested as a way to restore WBP but it requires a delicate balance: "cool"

enough to not kill mature WBP; but "hot" enough to remove competing, shade-tolerant

species (Keane, 2011). Another option is to let wildland fires burn in high-elevation

forests as much as can be allowed (Keane, 2011). However, as blister rust continues to

spread, more aggressive and innovative management practices will be needed to

restore and maintain WBP (Keane, 2011; Kegley et al., 2011).

WBP survives and regenerates well after wildland fire, more so than associated

shade-tolerant species (Arno and Hoff, 1990). Keane (2011) observed after prescribed

burning that Clark's nutcrackers were caching in burned areas, but significant

regeneration had not yet been noted. Keane (2011) was successful in burning to create

conditions that would be favorable for WBP regeneration. Unfortunately blister rust

infecting surrounding mature trees has reduced cone production, forcing nutcrackers to

reclaim more cached seeds (Keane, 2011).

Fire and fuels in bark beetle-affected forests

Jenkins (2011) described the phases of MPB outbreak in WBP forests. The

endemic stage is found in a relatively healthy stand with enough large host species to

support an outbreak, but mortality is restricted to a few older weakened or stressed

trees. Stands enter the epidemic phase when drought or some other short term stress

occurs, allowing MPB populations to increase over a period of 5 - 10 years in otherwise

healthy, thick-phloemed trees. Post-epidemic phase occurs after 80% or more of host

trees have been killed during epidemic phase. The post-epidemic phase lasts decades to

centuries until stand conditions are again suitable to support an outbreak.

Fires in high-elevation WBP forests are highly variable over space and time

(Campbell et al., 2011). Fires are usually ignited by lightning and result in low intensity

surface fires that clear the understory, and create openings for regeneration and allow

new growth into the canopy in denser WBP forests (White et al., 1984; Veblen et al.,

1994; Morgan et al., 1994). Low-intensity fires are most common on dry sites where

there are less fuels between trees (Morgan et al., 1994). In contrast, stand replacing

fires may be common in some areas where WBP grows alongside Engelmann spruce and

subalpine fir (Campbell et al., 2011). Mean fire return intervals range between 13 to

400+ years (Campbell et al., 2011). Fire is important to high-elevation ecosystems

(Morgan and Bunting, 1990; Morgan et al., 1994; Murray et al., 2000). WBP is better

adapted to regenerate and survive than the shade-tolerant species that grow alongside

WBP (Arno and Hoff, 1990).

      Jenkins et al. (2008, 2012, 2014) and Hicke et al. (2012) discussed changes to

surface and canopy fuels in bark beetle-infested stands of Engelmann spruce, Douglas-

fir, and lodgepole pine. The alteration of canopy fuels by bark beetles varies with time

since attack and the bark beetle/host system. For example, MPB-killed trees remain

green until late in the year of attack, or more commonly the following spring when

needles fade to yellow. By late summer or early fall the needles turn red and needles

begin to fall. The gray stage occurs when all needles have fallen and the tree begins to

lose its twigs and branches, generally after 2-3 years in lodgepole pine forests. The

needles of Engelmann spruce turn yellow and fall within the year after spruce beetle (*D.

rufipennis* Kirby) attack (Page et al., 2014).

      Bark beetle outbreaks increase fine surface fuels compared to non-beetle

infested stands in Douglas-fir, Engelmann spruce, and lodgepole pine forests (Page and

Jenkins, 2007a,b; Jenkins et al. 2008; Klutsch et al., 2009; Jorgenson and Jenkins, 2011;

Donato et al., 2013). Needle and branch shed by dead trees add small diameter woody

fuel to the surface fuel load of MPB-affected lodgepole pine forests (Jenkins et al., 2008;

Jenkins, 2011).

Changes to surface fuel moisture content (FMC), temperature and mid-flame windspeed resulting from decreased canopy sheltering may alter ignition probability and surface fire behavior in lodgepole pine stands (Brown, 1975; Page and Jenkins, 2007a; Klutsch et al., 2009; Jenkins et al., 2012, 2014). MPB colonization of lodgepole pine causes a rapid decline in foliar FMC and foliar chemistry of needles and twigs (Jolly et al., 2012; Page et al., 2012). Generally red needles have the lowest FMC, but can vary with environmental conditions and season (Agee et al., 2002; Keyes, 2006; Jenkins et al., 2008; Page et al., 2012). In healthy trees, foliage typically has low FMC in early spring that increases to high FMC in late spring and then decreases throughout the season. FMC of bark beetle-altered foliage decreases quickly and may have important influences on crown fire initiation and spread (Agee et al., 2002; Jenkins et al., 2008, 2012; Jolly et al., 2012; Page et al., 2012). Once red needles fall from infested trees, the probability for crown fire decreases, due to lack of aerial fuel continuity (Simard et al., 2011). However, Page and Jenkins (2007a) showed that later in the post-epidemic stage, chances for crown fire again increase as snags fall and coarse woody surface fuel accumulates in the presence of lower crown base heights on advanced regeneration.

It is important to note that weather plays a major role in fire behavior. A conifer forest experiencing extreme fire weather has a greater potential for high intensity and severe fires under many different fuel conditions (Kulakowski and Jarvis, 2011). Kulakowski and Jarvis (2011) suggested that drought is a more important factor on fire behavior than MPB outbreaks in lodgepole pine stands in Colorado and Wyoming. Kulkowski et al. (2003) showed that spruce beetle outbreaks in Englemann spruce and

subalpine fir stands do little to increase fire risk due to the cool, moist conditions prevalent at high elevation sites.

Objectives

The objective for this study was to characterize the surface and aerial fuels in WBP trees following attack by MPB. This was done by 1) measuring foliar FMC in WBP crowns of varying crown condition (i.e., green, green-infested, yellow and red) 2) measuring litter and duff depths, one hour and ten hour timelag fuels, and shrub and forb biomass under MPB-attacked WBP 3) by measuring total terpene compounds in red needle surface litter beneath MPB-attacked WBP, and 4) measuring foliar total terpene compounds in trees of different MPB crown conditions.

METHODS

Study area

Data were collected in MPB-affected WBP stands from two study areas selected using USDA Forest Service Aerial Detection Survey maps and GIS followed by field reconnaissance. WBP stands were selected in each study area that provided a mixture of green (G), green- infested (GI), red-needled (R), and gray (GR) trees.

In 2011, surface fuels data and red surface litter terpene samples were collected from a study area located on Deadline Ridge west of LaBarge, Wyoming on the Bridger-Teton National Forest at elevations between 2743 and 3048 meters (Table 1). This study area was characterized by dry, rocky soils and supported an overstory of WBP, subalpine fir and Engelmann spruce. Sampling was done on 156 plots in two adjacent stands with average slope steepness between 0 and 25%. Foliar FMC was also measured at this study area in 2012 (Table 1).

In 2012, surface fuels data and aerial terpene crown emissions were collected at Branham Lakes, east of Sheridan Montana in the Tobacco Root Range of the Beaverhead-Deerlodge National Forest at elevations between 2438 and 2743 meters (Table 1). This study area was within a large glacial cirque characterized by dry, rocky soils, and having a mixture of WBP, subalpine fir and Engelmann spruce. Sampling was conducted throughout the glacial basin on 141 plots between 0 and 50% slope steepness.

Table 1. Plots, variables measured, and crown condition classes (green=G, green-infested=GI, yellow=Y, red=R, and gray=GR) between Deadline Ridge and Branham Lakes study areas.

Study area	Plot type	Crown condition	Variables measured
Deadline Ridge	Fuels	G, R, GR	litter and duff depths
		G, R, GR	1 and 10 hour fuels
		G, R, GR	shrub and forb biomass
		G, R, GR	litter bulk density
		R	surface litter terpenes
	Foliar fuel moisture (2012)	G, GI, Y, R	foliar fuel moisture content
Branham Lakes	Fuels	G, R, GR	litter and duff depths
		G, R, GR	1 and 10 hour fuels
		G, R, GR	shrub and forb biomass
		G, R, GR	litter bulk density
	Foliar volatile terpene	G, GI, Y, R	foliar volatile terpenes

Data collection

<u>Fuels plots</u>

WBP stands commonly have greater space between trees than in other conifer stands due to extreme environment and dry rocky soils at high elevations (Figure 1). This inspired the sampling method for measuring surface fuels used in this study.
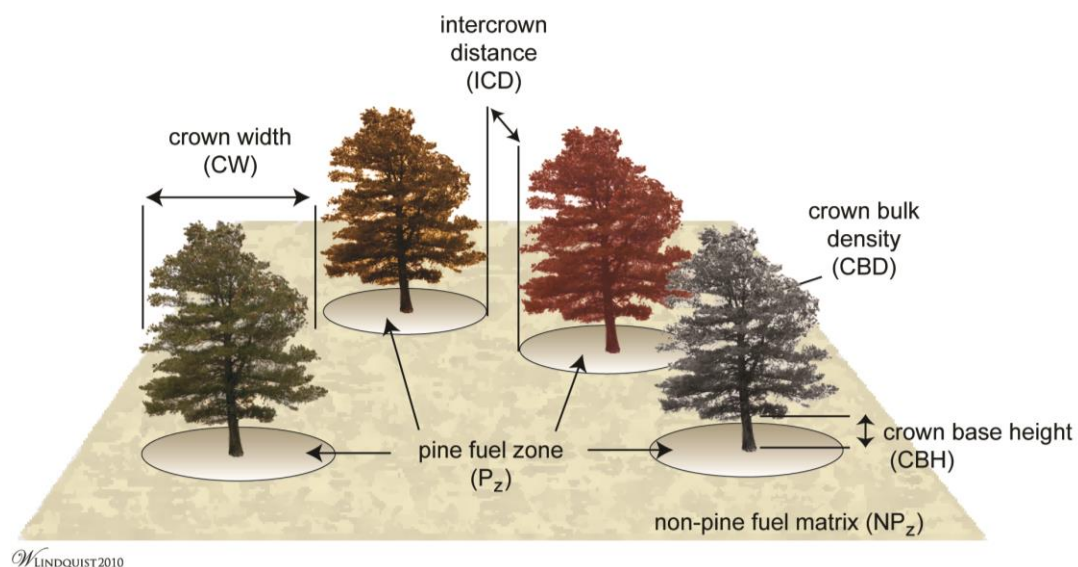
Fig. 1. Bark beetle-affected surface and canopy fuel matrix and the important variables affecting crown fire initiation and spread during the course of the bark beetle rotation.

Data collection began in the summer as soon as study areas were accessible (July for 2011 and June for 2012). In 2011, northwest/southeast running transect lines were placed within stands as determined from pre-selected GPS points. Plots for 2011 were selected by establishing points spaced five-chains apart along each transect. In 2012 east/west running transect lines (generally along contour lines) were established in suitable stands approximately 100 meters apart. Plots were again spaced five-chains apart along each transect. The GPS coordinates, aspect and elevation were recorded for each plot. One single- stemmed WBP greater than 15.2 cm in diameter at breast height (DBH) growing nearest to plot center for each crown condition class (G, R, GR) was selected for measurement (Fig. 2). Surface fuels were measured beneath G, R, and GR trees because most crown fuels won't transfer to the ground surface until the R stage.

G trees that were selected had no visible signs of blister rust or any other notable disease or insect infestation. In some cases only multi-stemmed trees could be found and measured. If no suitable sample tree in each condition class could be found within 60 meters from plot center, that condition class was not sampled.
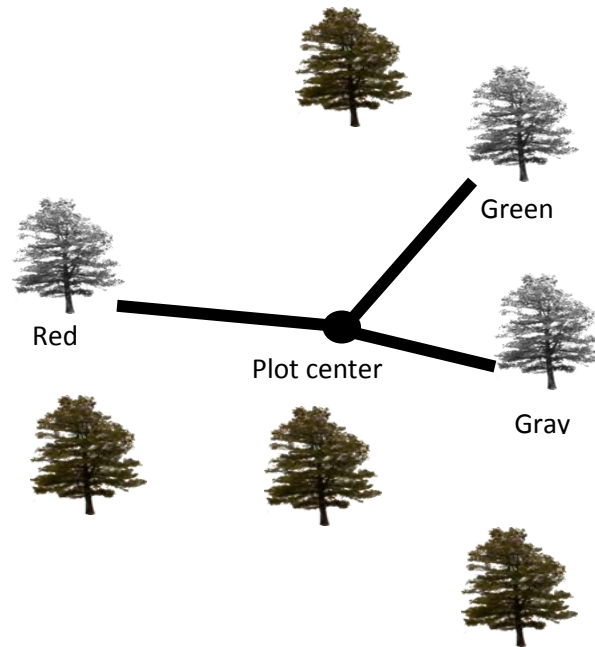
Fig. 2. The nearest green, red, and gray sample tree to plot center was measured for Deadline Ridge and Branham Lakes study areas.

Specific measurements for each sample tree included the following; DBH, height, and height to base of live crown. Under the drip line (crown width) of each sample tree, litter and duff depths were measured along two transect lines – one running north to south, and the other east to west. The length of each sampling transect was equivalent to the entire width of the tree crown with the tree's base located at the center. Along each transect, a metal pallet was hammered into the duff/soil interface halfway between the tree base and the drip line on either side of the tree. An ocular

measurement of litter and duff depths was made to the nearest millimeter using a clear plastic ruler.

On the south side of the tree, one hour and ten hour woody time lag fuels were inventoried along a 2 meter transect running north and south following procedures described by Brown (1975). The slope of this transect was measured from the south side of each sample tree.

Vegetation sub-plots

A one meter square vegetation plot was located on the north end of the north/south transect. In this plot the percent and average height of live/dead shrubs and forbs were measured. Live shrub and forb percentages from vegetation sub plots were converted to biomass (kg/m^2) using calculations from Lutes et al. (2006).

Litter bulk density

Bulk density is the way needles are packed in space. Most conifers have a bulk density value assigned to them as determined in previous research to use in fuel loading calculations. However, there is not a common bulk density value assigned to WBP.

To determine bulk density, litter was collected from a 30 cm X 30 cm square in the northwest corner of the vegetation subplot on every 5th fuels plot in 2011 and 2012. The litter sample was placed in a bag and taken back to the lab where it was placed in an oven at 105° C for 24 hours and then weighed to the nearest gram. 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 fuel moisture content

Foliar FMC was measured in 2012 at the Deadline Ridge study area separate from fuels plots. Four plots were selected along a road. Each plot included G, GI, yellow (Y), and R sample trees that were 50 to 70 meters from the road. Sample trees within plots were no farther than 50 meters from each other. G, GI, Y, and R sample trees were selected to measure because of previous studies showing differences in FMC between these different crown condition classes (Jenkins et al., 2008). Overall Deadline Ridge did not have very many Y trees in 2012, therefore, plots were selected by driving the road and finding the nearest Y tree in four different locations. Y and GI trees were included in this portion of the study because it has been shown in previous studies that there is a decline in foliar FMC between the GI and the Y crown stages (Jenkins et al., 2008). Collections were made every week from June 21 through Sept 27. Two collections in July were not made due to a road closure for the Fontenelle Fire.

A hand pruner was used to collect a sample of foliage from three random locations in the lower to mid-crown on each sample tree. The needles of each sample were separated from twigs and then weighed in the field to determine wet weight in grams. Needles were bagged and taken back to the lab at Utah State University where they were oven dried at 105° C for 24 hours. After drying, needle samples were weighed again to determine oven dry weight. FMC was calculated as the percentage of oven dry weight. Relative humidity and temperature were calculated using a sling psychrometer and recorded at plots 1 and 4.

<u>Foliar volatile terpene collection and analysis</u>

Page et al., (2012) found that volatile terpene chemistry is altered by MPB activity and can affect flammability of lodgepole pine foliage, which inspired this portion of the study. In 2012 volatile terpenes were collected and analyzed from four plots of WBP foliage from G, GI, Y and R trees at the Branham Lakes study area separate from the fuels plots.

Volatiles were collected four times from mid-July through mid-September (approximately 20 days apart between collection dates) using portable volatile collection systems comprised of automated vacuum pumps enclosed in a waterproof case (Volatile Assay Systems, Rensselaer, NY). Four trees of similar size (greater than 15.2 cm in diameter) and with no visible signs of blister rust were chosen in each condition class. For each tree, approximately 70 cm of the apical part of a lower branch was enclosed in a clear Teflon® bag (50 cm wide x 75 cm deep; American Durafilm Co., Holliston, MA) and air was pulled out through a side port (0.5 liters min^{-1}) through volatile traps containing 30 mg of the adsorbent HayeSep-Q® (Restek, Bellefonte, PA). Volatile emissions were collected for 30 minutes from each tree between 1100 and 1500 hours. Once collections were completed, the enclosed portion of branch and foliage was clipped and placed into a plastic bag for transport back to the laboratory to obtain fresh weight.

The volatile collection traps were transported to the Rocky Mountain Research Station laboratory in Bozeman, MT for analysis of volatile emissions. Volatiles were eluded from traps with 200 μl of dichloromethane; 1,000 ng of *n*-nonyl-acetate was

added as an internal standard. Samples were analyzed using an Agilent 7890A gas chromatograph (GC) coupled with a 5975C mass spectrometer and separated on a HP-1ms (30 m x 0.25 i.d, 0.25 μm film thickness) column; helium was used as the carrier gas. The GC oven was maintained at 35°C for 3 min and then increased by 5°C per min to 125°C, then 25°C per min to 250°C. Quantifications were made relative to internal standards using ChemStation software (Agilent Technologies, Wilmington, DE), and identifications of compounds confirmed by comparing retention times and mass spectra to commercial standards. We lacked internal standards for identification of some compounds which are labeled as unknown terpenes 1 through 6.

<u>Red litter terpene extraction and analysis</u>

During the 2011 field season, approximately 5 g of litter was collected from four cardinal directions beneath every 10th R sample tree in the fuels plots at the Deadline Ridge study area. These collections were placed in an envelope and sent to the Rocky Mountain Research Station in Bozeman MT to extract and analyze within-litter terpenes. Extractions followed the procedures used by Ormeño et al. (2009) with some modifications. Approximately five grams of each litter sample was ground to a fine powder in liquid nitrogen using a mortar and pestle. Approximately 0.1 g of powdered litter was transferred into 2 ml FastPrep tubes (MP Biomedical, Solon, Ohio) and 1.5 ml of cyclohexane was added and sonicated at room temperature for 20 minutes. Tubes were then centrifuged at 13,000 g for one minute and 200 μl of cyclohexane (top layer) was transferred to a gas chromatograph (GC) vial for analysis. Terpenes were measured

as described for volatiles except the GC oven was ramped to 275°C. Total terpene

concentrations are reported on a fresh weight basis.

Data analysis

Mean litter and duff depths in millimeters, mean fine down woody fuel loads in

kg/m^2 (one hour and ten hour fuels), mean bulk density in kg/m^3, and mean live biomass

of shrubs and forbs in kg/m^2 were calculated from sample data collected beneath G, R,

and GR WBP sample trees within fuels plots for both study areas.

A one-way ANOVA test run with pooled data determined that differences existed

between the two study areas. Therefore, data were analyzed separately.

Analysis of covariance was used to assess mean fuel differences between MPB

crown condition classes for all sampled fuels in fuels plots at the Deadline Ridge and

Branham Lakes study areas 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 beneath crown surface fuel accumulation based

on analysis of the linear relationship of each measured surface fuel parameter with the

tree measurements. If significant differences among crown condition classes were found

a post hoc test (Tukey test) was used to compare pairs of means while controlling the

experiment-wise error rate. Transformations were applied when necessary to meet the

assumptions of normality and homogeneity.

There were 49 multi-stemmed trees in the fuels plots at Deadline Ridge and 4 on

the fuels plots at Branham lakes. These were removed due to the variability of crown

size because of the multi-stems and because of the influence of the multi-stems on the surface litter.

Mean FMC was also calculated and graphed from samples collected from G, GI, Y and R WBP sample trees from four different plots at Deadline Ridge study area.

Mean R surface litter total terpene compounds were calculated from collections made under R sample WBP trees in fuels plots at the Deadline Ridge study area.

All measurements of volatile emissions are reported as nanograms per hour (ng hr^{-1}). Volatile data were square-root transformed to meet variance assumptions and analyzed using ANOVA; individual means were compared with Tukey's honestly significantly different means separation test.

RESULTS

Surface fine fuels

Analysis of the pooled data 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.

The results of the ANCOVA analysis comparing fine surface fuels between G, R, and GR MPB crown condition classes revealed that MPB activity significantly altered litter and duff at the Deadline Ridge (Table 2) and Branham Lakes (Table 3) study areas. R and GR trees had the highest litter and duff depths for both study sites. G trees had the least litter and duff depths for both study sites. The Tukey test showed significant differences in mean litter depths between all MPB crown condition classes for both sites. The Tukey test showed significant differences in mean duff depths between GR and G, GR and R, and G and R MPB crown condition classes for both sites.

Table 2. ANCOVA results testing for differences in litter and duff depths (mm) among green, red, and gray crown conditions at Deadline Ridge study area. Different letters next to means indicate significant differences, α = 0.05.

Fuel type and beetle condition	N	Mean	Standard Error	df	F	P
Litter				2	49.99	<.0001
Green	138	13.36c	0.5715			
Red	131	20.61a	0.6714			
Gray	141	18.21b	0.5789			
Duff				2	24.16	<.0001
Green	138	10.69b	0.7489			
Red	131	16.66a	1.3796			
Gray	141	13.91a	0.8035			

Table 3. ANCOVA results testing for differences in litter and duff depths (mm) for green, red, and gray crown conditions at the Branham Lakes study area. Different letters next to means indicate significant differences, α = 0.05.

Fuel type and beetle condition	N	Mean	Standard Error	df	F	P
Litter				2	81.22	<.0001
Green	141	9.79c	0.3771			
Red	130	17.70a	0.53134			
Gray	135	14.79b	0.4279			
Duff				2	22.55	<.0001
Green	141	11.90b	0.5998			
Red	130	17.65a	0.8133			
Gray	135	16.13a	0.3854			

After accounting for the effects of tree size on one hour and ten hour fuels, the effect of MPB crown condition class was not significant at Deadline Ridge. DBH and crown size were more influential on the amount of one hour and ten hour fuels than MPB crown condition class for Deadline Ridge study site (Table 4). One hour fuels for the Branham Lakes study site were significantly altered by MPB crown condition class. Ten hour fuels at the Branham Lakes study site were not significantly altered by MPB

crown condition class but were more influenced by crown size and the relationship of

crown size and MPB crown condition class (Table 5).

Table 4. ANCOVA results for analysis of one hour (1-hr)(kg/m^2) and ten hour (10-hr)(kg/m^2) down woody fuels by bark beetle condition class at the Deadline Ridge study area. Different letters next to means indicate significant differences, α = 0.05.

Fuel type and beetle condition	N	Mean	Standard Error		df	variable*	F	P
1-hr					*1-hr*			
Green	138	0.010b	0.0059		2	TC	0.15	0.8609
Red	131	0.010b	0.0018		1	DBH	33.6	<.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	<.0001
Gray	141	0.27a	0.04402		1	CR	13.79	0.0002

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

Table 5. ANCOVA results for analysis of one hour (1-hr)(kg/m^2) and ten hour (10-hr)(kg/m^2) down woody fuels by bark beetle condition class at the Branham Lakes study area. Different letters next to means indicate significant differences, α = 0.05.

Fuel type and beetle condition	N	Mean	Standard Error		df	variable*	F	P
1-hr					*1-hr*			
Green	141	0.04b	0.0107		2	TC	25.02	<.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	<.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

Statistical comparisons revealed no significant alterations due to the amount of live and dead shrubs and forbs in the MPB crown condition classes in Deadline Ridge (Table 6) and Branham Lakes (Table 7).

Table 6. Mean comparison of shrub and forb fuel loading at the Deadline Ridge study area. Different letters next to mean indicate significant differences, α=0.05

Fuel type and beetle condition	N	Mean	Standard Error	df	F	P
Shrubs (kg/m^2)						
Green	138	0.03a	0.01	2	0.51	0.5985
Red	131	0.04a	0.01			
Gray	141	0.02a	0.01			
Forbs (kg/m^2)						
Green	138	0.06a	0.01	2	0.81	0.4434
Red	131	0.07a	0.01			
Gray	141	0.08a	0.01			

Table 7. Mean comparison of shrub and forb fuel loading at the Branham Lakes study area. Different letters next to mean indicate significant differences, α= 0.05

Fuel type and beetle condition	N	Mean	Standard Error	df	F	P
Shrubs (kg/m^2)						
Green	141	0.05a	0.01	2	1.54	0.2149
Red	130	0.04a	0.01			
Gray	135	0.05a	0.01			
Forbs (kg/m^2)						
Green	141	0.02a	0.003	2	0.16	0.8527
Red	130	0.02a	0.002			
Gray	135	0.02a	0.002			

Litter bulk density

Transformed litter bulk density means for Deadline Ridge and Branham Lakes

study areas are shown in Figure 3a and b, respectively. Litter bulk density was not

significantly altered by MPB crown condition class during either sampling year. Table 8

shows the pre-transformed means and standard error of litter bulk density for both

study areas.

Table 8. Mean (± standard error) litter bulk density (kg/m^3) for green (G), red (R), and
gray (GR) sample trees at the Deadline Ridge and Branham Lakes study area.

Study area	G	R	GR
Deadline Ridge	17.24 ± 2.8	18.81 ± 1.5	18.67 ± 2.1
Branham Lakes	8.65 ± 2.5	8.72 ± 1.2	7.57 ± 1.2

Fig. 3a. Distribution of square root transformed bulk density values from litter samples collected in 2011 from the Deadline Ridge study area. The boxplots indicate the mean (♦), the median, the 25th and 75th percentiles for the lower and upper portions of the box, respectively, the maximum and minimum values within 1.5 times the interquartile range, and any outliers for the beetle crown condition classes of green, red and gray. Differences between the mean values for each crown condition class were not significant, *P*-value = 0.6007, F = 0.51.
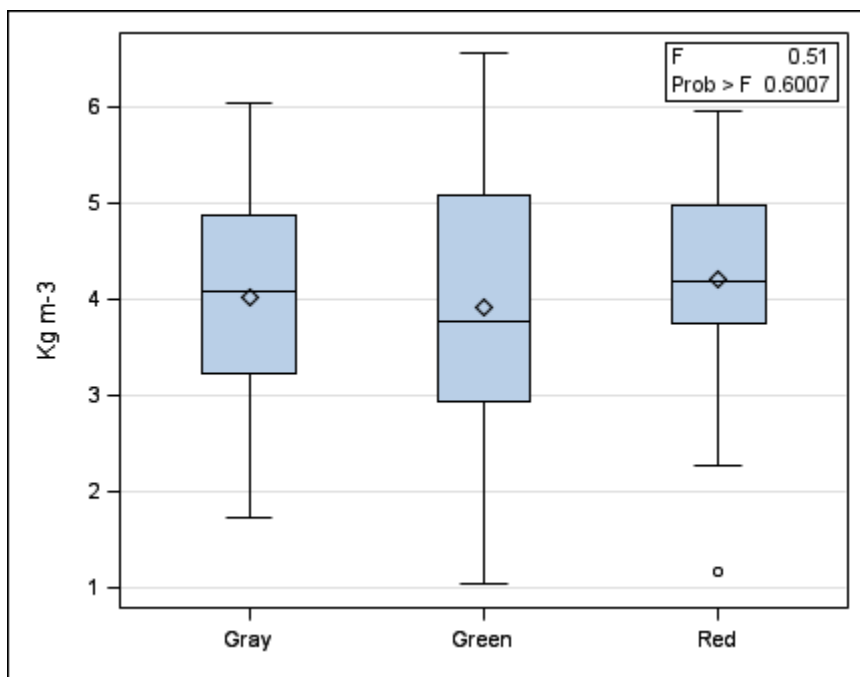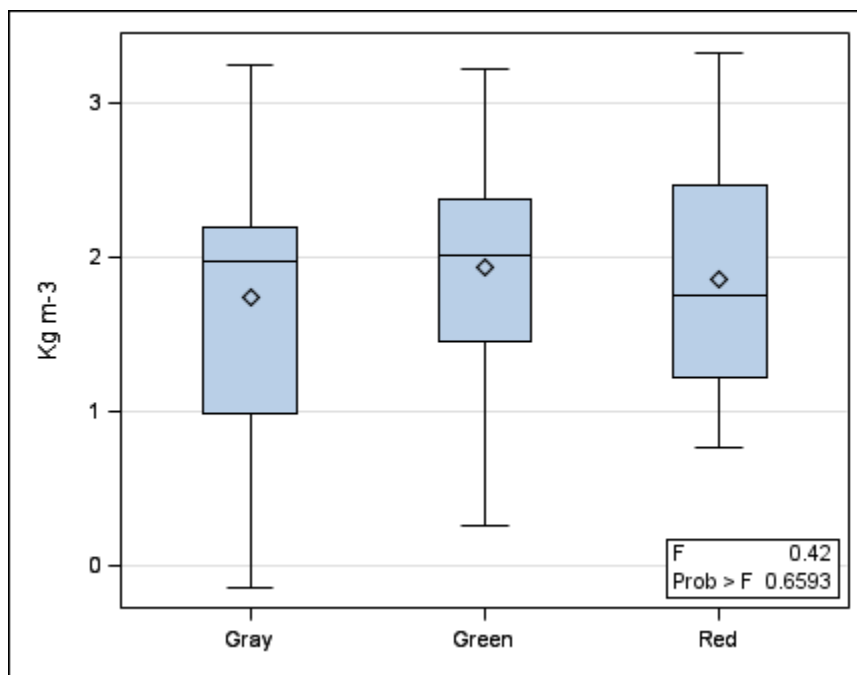
Fig. 3b. Distribution of log transformed bulk density values from litter samples collected in 2012 from the Branham Lakes study area. The box plots indicate the mean ($\diamond$), the median, the 25th and 75th percentiles for the lower and upper portions of the box, respectively, the maximum and minimum values within 1.5 times the interquartile range, and any outliers for the beetle crown condition classes of green, red and gray. Differences between the mean values for each crown condition class were not significant, *p*- value = 0.6593, F = 0.42.

Foliar fuel moisture content

All collections for 2012 were made between 0900 and 1400 hours when the

temperature was between 7 and 22° C, and relative humidity was between 16 and 70%.

The highest relative humidity value was 70% during the last collection at the end of

September. The average relative humidity was 30% and the average temperature was

17° C during the sampling season.

Figure 4 shows the results of foliar FMC for G, GI, Y and R trees sampled in 2012.

The FMC of G needles ranged between 84% at the end of June and increased to 116% by

the end of September. GI needles were sampled after the MPB flight period and sample

tree attack. The earliest GI trees were sampled at the end of July when the FMC was

115%. FMC of GI trees did not significantly differ from FMC of G trees 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 when Y and R foliage

samples varied similarly to one another. R foliage remained consistent throughout

sampling ranging between 6% and 16%.
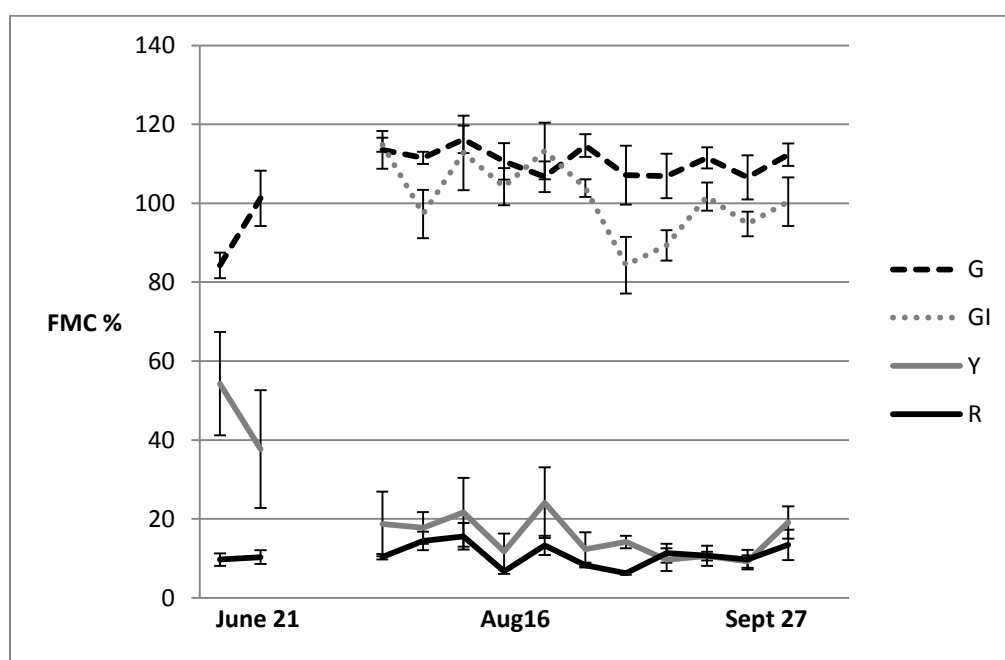
Fig. 4. The seasonal change in foliar moisture content of WBP foliage from green (G),
green-infested (GI), yellow (Y) and red (R) sample trees at Deadline Ridge, Wyoming.
The mean values and associated error bars are shown for each collection dates between
June 21 and September 27, 2012. No collections were made on weeks 3 and 4 due to
road closures for the Fontenelle Fire near LaBarge, Wyoming.

Foliar volatile terpene

Thirty-two terpene volatile compounds were collected from WBP foliage across G, GI, Y, and R condition classes. Nineteen of the compounds were identified; unidentified compounds were numbered "unknown monoterpene 1", "unknown sesquiterpene 2", etc. The most abundant compounds were monoterpenes and include α-pinene, β-pinene, camphene, β-myrcene, 3-carene, β-phellendrene, D-limonene, p-cymene, and terpinolene. Total volatiles were not different among MPB crown condition classes on 17 July and 23 August; however, Y foliage emitted significantly more terpenes on 03 August, and Y and GI foliage emitted more terpenes on 14 September (Figure 5). On 03 August, Y foliage released significantly more of some individual compounds (α-pinene, β-pinene, unknown monoterpene 3, α-phellendrene, β-phellendrene, α-terpinene, p-cymene) than G, GI or R foliage. On 14 September, Y and GI foliage emitted more β-pinene, β-myrcene, α-phellendrene, α-terpinene, p-cymene, β-phellendrene, and (E)-β-ocimene than G or R foliage.
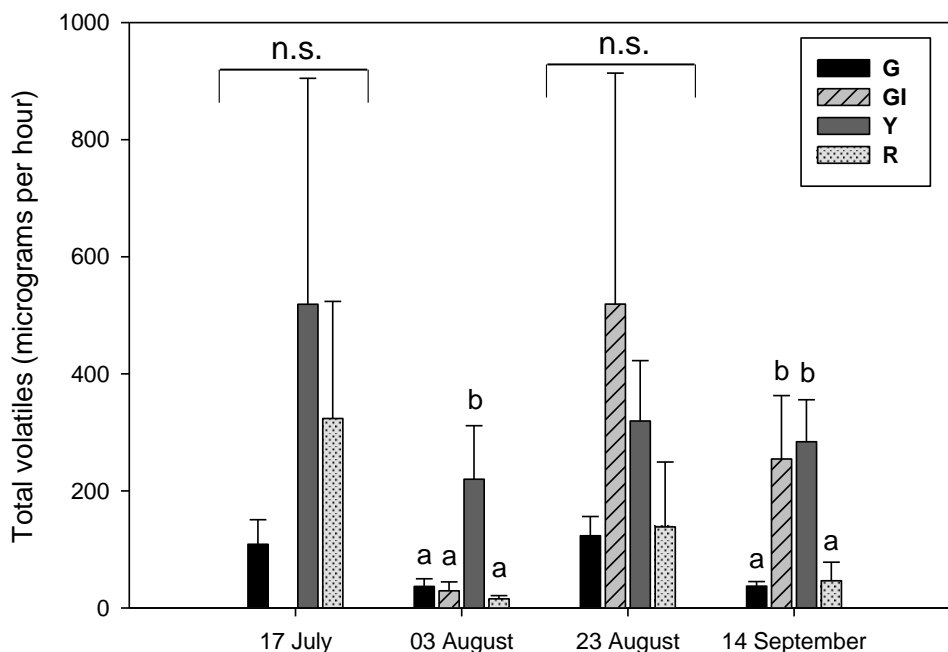
Fig. 5. Mean total volatiles (micrograms per hour ± SEM; n = 4) emitted by foliage of WBP trees of different mountain pine beetle crown condition classes (G, green uninfested; GI, green- infested; Y, yellow; R, red) in July, August and September of 2012 at the Branham Lakes study area. Different letters indicate significance differences among treatments (P <0.05); n.s. = no significance

Litter terpene analysis

More than 100 terpene compounds were found to occur in surface litter collected beneath red-stage WBP trees. Most of the compounds could not be confidently identified due to lack of authentic standards; unidentified compounds were numbered "unknown 1," "unknown 2," etc. Thirty compounds accounted for greater than 90% of total terpenes; these included α-pinene, β-pinene, and 3-carene. This WBP litter contained an average of 5,486 µg per g of terpenoids across all sampling dates.

There was a trend for increased terpene content in litter later in the year (Figure 6), but this was not significant (P-value = 0.1198, F = 2.49).
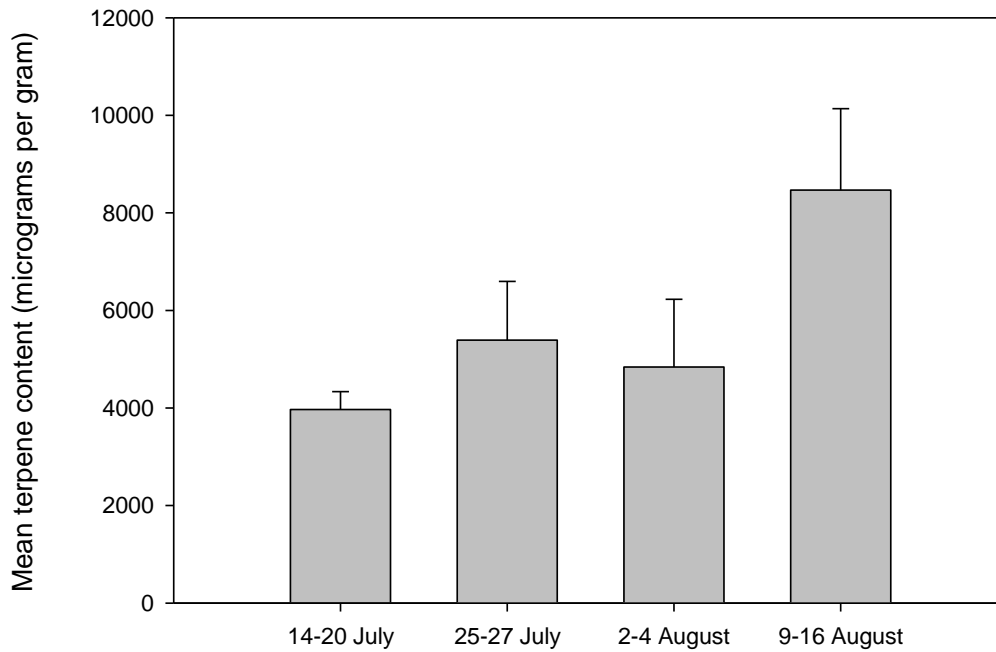
Fig. 6. Mean terpene content (micrograms per gram fresh weight ± SEM; n = 3) of litter collected beneath red WBP trees in July and August 2011 at the Deadline Ridge study area. Differences among dates are not significantly different, P-value = 0.1198, F = 2.49.

DISCUSSION

A predictable change occurs to WBP foliage in western conifer forests as trees progress from the G to GR stage over the course of a bark beetle rotation (Jenkins, 2011). Phloem feeding by bark beetles coupled with blue stain development decreases nutrients and moisture to needles, resulting in needle death and net transfer of canopy foliage to the forest floor. The amount of time for needle shed to occur can be as short as one year after beetle colonization in Engelmann spruce (Page et al., 2014), to two to four years in lodgepole pine (Page and Jenkins, 2007a) to four or more years in whitebark pine as described by Jenkins (2011). The transition of needles from crown to forest floor results in significant increases in litter in Engelmann spruce (Jorgensen and Jenkins, 2011) and lodgepole pine (Page and Jenkins, 2007a; Klutsch et al., 2009; Simard et al., 2011). In this study we found significant increases in WBP needle litter under the crowns of individual MPB-attacked R and GR trees compared to G trees. R needles are retained in tree crowns in WBP for longer periods of time than other species studied so that the significant pulse of needle litter to the forest floor may last for several years. The duration of a significant increase in litter is short once R needles have fallen and decomposition begins to balance accumulation.

A number of review studies have provided generalizations concerning the accumulation of fine and coarse woody fuel during the prolonged post-epidemic phase of the bark beetle rotation (Jenkins et al., 2008, 2012, 2014; Hicke et al., 2012). Ultimately the bark beetle-killed snag will lose its small and large branches and fall to

the forest floor to decompose and return its biomass to the system over a period of decades. The prolonged and variable period of woody fuel accumulation and decomposition, and the snap shot nature of research studies makes determination of significant differences in woody fuel loads difficult. Most studies referenced above report minor to no significant differences in fine or coarse woody fuel loads between MPB crown condition classes at the time of measurement. In this study we also found minor significant differences in one and ten hour fine woody fuels under R and GR trees when compared to G trees. Although significant, differences are small and will be of short duration similar to litter fall.

Important changes to understory vegetation occur during the post-epidemic phase. The response of shrubs, forbs and advance conifer regeneration is largely determined by site, soil moisture and habitat type characteristics. Both shrubs and forbs were found to increase significantly in mesic, high-elevation, post-epidemic Engelmann spruce stands in Utah (Jorgensen and Jenkins, 2011). Significant differences in forb response were found in post-epidemic stands in Douglas-fir in Wyoming (Donato et al., 2013) and lodgepole pine in Colorado (Klutsch et al., 2009). Page and Jenkins (2007a) found significant increases in advance fir regeneration in post-epidemic lodgepole pine stands in Utah. The WBP stands sampled in the present study grow at high elevations and on thin rocky soils that do not support a large shrub or forb component. No differences were found in shrub or forb response in data collected under GR WBP sample trees.

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 sample 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 GI foliar FMC follows a similar pattern to G trees until later in the season when GI foliage has significantly lower foliar FMC than G trees (Fig. 4). Important changes occur to GI WBP foliar FMC over the winter as blue stain fungal development advances and moisture flow from the roots to crown is compromised (Jenkins, 2011). The foliar FMC of Y needles measured at the beginning of the growing season is reduced from values determined at the end of the previous season and is significantly lower than either G or GI needles. We believe this reflects the continuing development of blue stain in the sapwood beyond the end of the growing season and perhaps into and through the winter. Early in the growing season Y needles have significantly higher FMC compared to R needles. R needles in trees have low FMC and are similar in FMC to dead surface litter. Changes in FMC of R needles occur in response to diurnal changes in temperature and relative humidity (Page et al., 2014). It is largely the influence of lowered FMC in Y and R needles that contributes to the high degree of flammability of bark beetle infested forests in the R stage as described by Jenkins et al. (2012, 2014) and observed by fire managers in conifer fires burning in bark beetle-affected fuels (Church et al., 2011; Stiger and Infanger, 2011).

An increasingly detailed analysis is emerging on changes in foliar chemistry and the influence of the changes on flammability in a number of bark beetle-affected conifer species including lodgepole pine (Jolly et al., 2012; Page et al., 2012) and Engelmann spruce (Page et al., 2014). In this study we evaluated changes to terpenes in foliage on MPB-attacked WBP trees. A complex array of terpenes is described which change in abundance over the course of the bark beetle rotation. The five most abundant terpenes have been studied in detail in relation to bark beetle pheromone production and its influence on bark beetle population dynamics. Page et al. (2012) described the influence of terpenes on flammability and found that α-pinene and β-pinene, positively increased the rate of mass loss in needles in laboratory flammability tests. These two compounds were among the most common in WBP needles sampled in this study. Volatile terpene amounts in Y foliage were higher than those described by Page et al. (2012) who emphasized, however, that FMC is the overriding factor determining changes in flammability in bark beetle-affected fuels. In this study we also analyzed the total terpene content of R needle litter and found a large variety of many, mostly unidentified, compounds not found in volatiles analyzed as emitted by needles on trees. Total terpene content in WBP litter sampled in this study was much higher than values reported by Page et al. (2012) in lodgepole pine litter. We suggest that many terpenes are contained in living parenchyma cells and vacuoles in living needle tissues and that once needles die cytolysis results in a flood of terpenes into R needles attached to trees and in litter. The very low FMC of R needles combined with the presence of flammable terpenes likely contributes to the extreme fire behavior observed during the R stage in

MPB-affected pine forests.   It is also feasible that R litter could exhibit a higher probability of ignition, greater rates of spread, surface fire intensity and crown fire potential than might otherwise be expected. From this study we know that R litter retains terpenes throughout the fire season, but we do not know how long terpenes remain in other MPB crown condition classes. Ormeño et al. (2009) found increased terpene concentration and flammability in the litter of Mediterranean *Pinu*s spp. studied. Mutch (1970) speculated that natural selection might favor increased flammability in certain fire regimes.

High intensity, stand-replacing crown fires superimposed over a low intensity surface fire regime characterize many high elevation western North American conifer forests. Campbell et al. (2011) considered the fire regime in WBP forests as a range of intensities from low intensity surface fires to high intensity stand replacing fires of intervals between 14 and 400+ years. Larson et al. (2009) studied fire regimes in WBP at three different mountain tops in Montana and found that the differences in fire activity are likely a result of biophysical site characteristics and disturbance. The type of fire and return interval will be determined by topography, stand composition and structure and connectivity of WBP stands to other forest cover types (Morgan and Bunting, 1990; Murray et al., 2000; Kitchen, 2012). The present study was conducted in pure high elevation WBP forests characterized by a low intensity fire regime. Jenkins (2011) characterized the WBP fuel zone under individual tree crowns as distinct from the fuel intermix (Fig. 1). In stands similar to the Deadline Ridge study area tree density is low and the discontinuous nature of the fuel intermix decreases the likelihood of fire spread

between adjacent trees. Therefore, alteration of surface fuels would have little impact

other than to create conditions increasing the probability of ignition in areas where R

needles or litter are present. Decreases in canopy sheltering of wind and solar radiation

will result in higher midflame windspeeds and temperatures and lower surface FMC as

described by Page and Jenkins (2007a). The presence of red needle litter during the

period of increasing bark beetle-caused tree mortality may increase the probability of

ignition and spread of the low intensity surface fires. Even so the surface fuel condition

described will be a relatively short period of one to several years until needles have

fallen and litter decomposes to duff. In the Branham Lakes study area tree density is

higher and intercrown distance is decreased creating the potential for crown fire and

spread during the red phase. This is also a short period of time when considered over

the centuries of a WBP forest development. Real-time fire weather characterized by

low relative humidity, high wind speeds, and low fuel moisture across live and dead fuel

classes will dominate fire behavior regardless of fuel bed characteristics (Bessie and

Johnson, 1995). However, bark beetle-affected fuels may create conditions capable of

producing high-intensity surface fires with the ability to transition to crown fires across

a wider range of fire weather conditions. This is particularly true at higher elevations

where narrow fire weather conditions exist due to a shorter snow free period, higher

relative humidities, and lower temperatures.

The infinite array and complex assemblages of conifer species, bark beetle-

altered fuels condition classes, and the activity of other biotic and abiotic disturbance

agents over complex terrain and large spatial and long temporal landscape scales also

complicates potential fire regime alterations. Disturbance agents alter the landscape-scale fuel complex and may affect actual fire spread, intensity and severity within and beyond the affected 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 lodgepole pine, Douglas-fir and/or true firs (*Abies* spp.) and Engelmann spruce. Kitchen (2012) described a much different fire regime in low elevation transitional forests and woodlands compared to high elevation bristlecone pine forests in the Great Basin. We consider the situation to be similar in WBP forests where disturbance corridors provide pathways for disturbance agents, including stand replacing fires. Disturbance corridors may create hazardous fuel pathways resulting from; 1) the suppression and exclusion of fire; 2) recent MPB outbreaks that developed in pine types at lower elevations and spread up into pure five-needle pine stands; 3) bark beetle outbreaks triggered by drought in the numerous susceptible stands of 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 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 (Fig. 7).

Fig. 7. Forests altered by agents of disturbance such as bark beetles, dwarf mistletoes, root pathogens and rust fungi create disturbance corridors and pathways for fire spread to high-elevation whitebark pine forests (Wyoming Range photo by M. Jenkins).

WBP is in decline due to MPB, blister rust, and succession of other species. Larson and Kipfmueller (2010) looked at patterns of regeneration and their relationship to biophysical site characteristics and found that there was a positive relationship of regeneration with elevation and canopy tree mortality and a negative relationship was found with moisture availability, temperature and succession. Larson and Kipfmueller (2010) indicated that if there were sufficient seed sources MPB outbreaks can create an ideal environment for WBP regeneration. However, 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 at peril the future of WBP forests in western North

America.

     Active restoration and management needs to continue to help save WBP.

Planting rust resistant trees in MPB affected stands, prescribed burning, and thinning

out shade-tolerant species are all possible management tools to help in WBP

restoration.

CONCLUSION

In summary this study indicates that litter depths increase beneath MPB affected WBP. One hour and ten hour fuels increase beneath R and GR trees compared to G. However this pulse of fine fuels will last for a relatively short duration and is more influenced by tree size than MPB crown condition. Foliar FMC decreased dramatically from the G MPB condition class to the R MPB condition class. The most flammable foliar volatile terpenes found by Page et al. (2012) in lodgepole pine stands were also found to be among some of the most prevalent terpenes in MPB affected WBP in this study. Terpenes in R surface litter remain in the needles throughout the fire season. All of these factors may have an impact on WBP fire regimes by increasing flammability during the time R needles remain in the trees and as long as the R surface litter remains.

Again, the future of these high elevation forests is uncertain due to blister rust, MPB, and climate change. MPB affected stands can provide a suitable environment for regeneration (Larson and Kipfmueller, 2010) therefore, planting WBP seedlings needs to happen in these areas. Fire can also be an effective tool to increase the health of WBP forests. Active restoration efforts need to be carried out to ensure the survival of WBP.

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