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Douglas-Fir Beetle Mediated Changes to Fuel Complexes, Foliar Moisture Content and Terpenes in Interior Douglas-Fir Forests of the Central Rocky Mountains

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DOUGLAS-FIR BEETLE MEDIATED CHANGES TO FUEL COMPLEXES, FOLIAR MOISTURE CONTENT, AND TERPENES IN INTERIOR DOUGLAS-FIR FORESTS OF THE CENTRAL ROCKY MOUNTAINS

by

Andrew D. Giunta

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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Approved:

Mike Jenkins Major Professor	Ted Evans Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Douglas-fir Beetle Mediated Changes to Fuel Complexes, Foliar Moisture Content and Terpenes in Interior Douglas-fir Forests of the Central Rocky Mountains

by

Andrew D. Giunta, Master of Science

Utah State University, 2016

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Recent bark beetle outbreaks have caused extensive tree mortality in conifer forests across western North America, which has altered forest fuels. These changes have raised concerns about forest health and wildfire risk. Studies focused on interactions between bark beetles, forests fuels, and changes in fire behavior have been primarily led in upper elevation forests characterized by high-severity fire regimes, principally in lodgepole pine (*Pinus contorta* Douglas ex Loudon) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) forests. Few studies to date have addressed bark beetle fuel interactions in lower to middle montane forests characterized by a mixed-severity fire regime, with available research focused strictly on assessing fuel load conditions or stand structural changes. The goal of this research was to quantify and characterize surface and canopy fuel changes in middle montane interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.)) forests infested by Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), while also measuring physical and chemical changes to foliage in terms of moisture content and terpenes, which are known to play important roles in foliage flammability.

Our results revealed few changes in surface fuels following Douglas-fir beetle infestations aside from a significant increase in litter depth and loading in red stage sample plots. Substantial changes to canopy fuels were detected in the red stage of an outbreak with a significant reduction in foliar moisture content measured as tree crowns faded from a healthy green phase to red. During this period, volatile emissions and within-needle concentrations of terpenes increased, including some terpenes previously associated with increased foliage flammability in other tree species. Furthermore, aerial fuel parameters that estimate the likelihood of crown fire initiation, including canopy bulk density and canopy base height, showed a substantial reduction in gray stage sample plots. Based on our findings we judge the influence of Douglas-fir beetle activity on altering fuels is most pronounced in the aerial fuels complex. Our results suggest bark beetle affected interior Douglas-fir stands with a high percentage of trees in yellow and red crown phases could have could have an increased threshold for crown fire initiation based on higher levels of flammable monoterpenes and lower foliar moisture content.

(174 pages)

PUBLIC ABSTRACT

Douglas-fir Beetle Mediated Changes to Fuel Complexes, Foliar Moisture Content and Terpenes in Interior Douglas-fir Forests of the Central Rocky Mountains

Andrew D. Giunta

Bark beetle outbreaks have affected millions of hectares of forests across western North America and are a major concern for forest managers. Aside from causing extensive tree mortality, other associated changes include alterations to forest structure in terms of modifications of surface and aerial fuels, which have led to concerns about overall forest health and wildfire risk. The majority of research into the interactions between bark beetles, fuels, and wildfire, has focused on upper elevation forests primarily in lodgepole pine and Engelmann spruce. Little research has been led in lower to middle montane forests which typically are more structurally and compositionally diverse, and often more fuel limited, which could have strong impacts on fire in these types of forests infested by bark beetles. Additionally, the few studies to have addressed this issue, strictly confined their research to characterizing changes to fuel loads or stand structural conditions. The purpose of this research was to quantify changes to surface and canopy fuels in middle montane interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) forests infested by Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), while also measuring physical and chemical changes to foliage in terms of moisture content and terpenes which has yet to be reported in current literature.

Study results indicated the most substantive changes were found in canopy fuels where significant reductions in foliar moisture were measured as tree foliage transitioned

from green (non-infested) phase to red (2-3 year post infested) phase. During this period emissions and concentrations of terpenes associated with elevating foliage flammability increased and peaked in trees exhibiting a yellow or red crown. This could have important implications for raising the threshold for crown fire initiation in conjunction with suitable fire weather conditions. Following the red crown phase, trees shed their needles leading to significant reductions in canopy bulk density (measure of the amount of fuel in the canopy of a stand), and a decreased canopy base height (average height of canopy fuel above the forest floor across a stand), which would likely lead to a reduction in crown fire potential.

Overall, this study contributes to the growing body of literature in assessing bark beetle fuel interactions by providing evidence of physical and chemical changes to tree foliage following infestations by Douglas-fir beetle. Furthermore, the inherent variable structure, composition, and mixed-severity fire regime characteristic of interior Douglas-fir forests presents a challenge for creating a blanket description of how these forests will react in terms of fuel changes following bark beetle infestations. Additional fuel studies concentrated in interior Douglas-fir stands in other geographic locales throughout the central Rocky Mountains will help further expand knowledge in regards to bark beetle induced modifications to fuels throughout the lower to middle montane zone.

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CHAPTER 1

INTRODUCTION

Problem Statement and Research Objective

Bark beetles (Curculionidae: Scolytinae) in the genus *Dendroctonus* are important biotic disturbance agents in North American conifer forests (Paine et al., 1997; Meddens et al., 2012). Bark beetle outbreaks cause extensive tree mortality and change forest structure, composition, and function (Raffa et al., 2008). In particular, bark beetle outbreaks have been linked to changes in the arrangement and loading of forest fuels (Hicke et al., 2012). Stand dynamics and population dynamics of bark beetles are often highly interrelated (Coulson, 1979; Goheen and Hansen, 1993; Jenkins et al., 2012). Over the past two decades, forests in the western United States have been affected by the largest outbreaks of bark beetles in at least a century, impacting over 28 million hectares, which has raised concern about future forest health and wildfire risk (Black et al., 2013; USFS, 2013). As a result, the effects of bark beetles on fuels and related altered fire behavior, have been a focal point for many forest and fire researchers (e.g. Page and Jenkins, 2007a, 2007b; DeRose and Long, 2009; Diskin et al., 2011; Jorgensen and Jenkins, 2011; Collins et al., 2012; Schoennagel et al., 2012). Although these studies have begun to address bark beetle, fuels, and fire interactions, research has been primarily led in forest types that experience infrequent high-severity stand replacing fire regimes (e.g. lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests infested by mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) forests infested by spruce beetle (*Dendroctonus rufipennis* Kirby) (Donato et al., 2013). Few studies however, have assessed bark beetle impacts on fuel complexes in drier, lower elevation montane forest types characterized as having a mixed-severity fire regime (Jenkins et al., 2008). Lack of research on bark beetle effects on forest structure and physical and chemical changes to tree foliage in lower mountain zone forests in the central Rocky Mountains, provides an opportunity to better understand these interactions and response of this forest type to insect disturbance.

The objective of this research was to quantify and describe how select forest fuel characteristics in the surface and aerial fuel complexes associated with surface and crown fire potential, are influenced by bark beetle infestations. For these studies, we used interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) and Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) as a representative mid montane forest-bark beetle system found commonly throughout the central Rocky Mountains.

Research Questions

A comprehensive literature review is represented in chapter two on the general topic of forest health issues associated with interior Douglas-fir forests. Included in this review are the topics of interior Douglas-fir, Douglas-fir beetle, fuels, and fire which are the focal points for this thesis project. The remaining chapters (three and four), are directed at answering the following research questions which represent the main body of work for this project:

1. How do select ground, surface, and aerial fuel loads vary between green, red, and gray stage interior Douglas-fir plots infested by Douglas-fir beetle? (Chapter 3)

2. Are there differences in foliar moisture content between the four crown classes, green, green-infested, yellow, and red, associated with Douglas-fir beetle infestations in interior Douglas-fir? (Chapter 3)
3. How do Douglas-fir beetles affect volatile terpene emission rates in infested interior Douglas-fir trees? (Chapter 4)
4. Do differences in within-needle terpene concentrations exist between green, green-infested, yellow, and red foliage associated with successful Douglas-fir beetle infestation in interior Douglas-fir trees? (Chapter 4)

Hypotheses

1. Reduction in canopy cover following tree mortality in gray stage plots should lead to increases in light and water resources which would lead to increases in herbaceous cover compared to green and red stage plots. Following needle release from infested trees, red stage plots should have deeper litter and duff layers compared to green plots. In addition, trees killed by Douglas-fir beetle will eventual fall and should lead to increased 1000 hr. fuel loads in gray stage plots.
2. Foliage from green and green-infested trees should have higher foliar moisture content values due to the active transpiration process in living trees. Foliage from yellow and red tree crowns are predicted to have lower foliar moisture content values due to needle desiccation and loss of moisture retention in needles as a result of tree mortality.
3. 4. Yellow and red crown foliage should have elevated terpene emissions and within-needle terpene concentrations as terpenoid storage vesicles break down

following foliage desiccation and mortality, as well as with the loss of water mass which should be expressed as an increase in terpene concentrations within-needles.

Chapter five comprises a summary of the preceding four chapters and includes a conclusion for the entire thesis project. The format of this thesis is organized based on a multiple manuscript format, with each chapter, aside from Chapter 1 and Chapter 5, structured as a separate research paper. Based on this, the formats follow the style and guidelines set-forth by the journal selected for publication for chapters 2, 3, 4, and are organized for the respective journal for which the work is targeted.

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CHAPTER 2

DISTURBANCE AGENTS AND THEIR ASSOCIATED EFFECTS ON FOREST HEALTH OF INTERIOR DOUGLAS-FIR FORESTS IN THE CENTRAL ROCKY MOUNTAINS

Abstract

Interior Douglas-fir forests are a prevalent forest type that occurs within the middle montane zone in the central Rocky Mountains. Disturbance history including the interactions between fire, windthrow, avalanches, insect outbreaks, and pathogens, drive forest community development in these forests. Past management actions including fire exclusion and suppression, has led to an expansion of this forest type and created dense stand conditions which are now reaching maturity. These forests are subject to severe damage from an array of forest health issues including Douglas-fir beetle infestations, western spruce budworm outbreaks, root disease, and increased incidences and severity of dwarf mistletoe. The cumulative effects of these disturbances can have serious consequences for forest fuel conditions which influence fire behavior, while also affecting wildlife habitat, watersheds, as well as the loss of interior Douglas-fir which is an important timber species that has strong economic value. Although this species covers a broad geographic range, few studies have described or quantified the interactive effects of disturbance agents on influencing forest conditions in the lower to middle montane zone. The variable nature of interior Douglas-fir montane forests presents unique challenges for forest managers in their approach to devise ecologically appropriate and economically feasible strategies for managing the health and sustainability of these forests. In this paper we synthesize recent literature and describe the role and mechanisms

in which disturbance processes including insect outbreaks, pathogens, fire, and other abiotic events affect forest structure and development in interior montane forests with an emphasis placed on interior Douglas-fir forests. Linkages between compound disturbances and subsequent forest health issues are addressed, as well as potential consequences associated with forest health concerns. Furthermore, we identify current knowledge gaps where further research is required to better understand the mechanisms in which disturbances and current forest health issues in this forest type are connected.

Introduction

Disturbances are natural phenomena that exert a strong influence over forest development expressed across variable temporal and spatial scales of magnitude (Oliver, 1981; White and Pickett, 1985). Over the past century land management strategies including fire suppression and exclusion policies, and grazing pressure, have greatly altered forest stand conditions across the west including mid-montane interior Douglas-fir forests (Parsons et al., 1979; Savage and Swetnam, 1990; Westerling et al., 2006). The consequences of these actions have led to increased tree densities, unnatural fuel accumulations, and the spread of fire-intolerant species within previously fire adapted forests that historically had short-interval, low-severity surface fire regimes (Allen et al., 2002; Fulé et al., 1997; Lentile et al., 2005). In the absence of frequent surface fires, shade-tolerant white-fir (*Abies concolor* Lindl.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Mirb. Franco) have established and expanded in previous open, park like stands where they have formed dense thickets effectively lowering canopy base heights, increasing ladder fuels, and elevating the hazard for high-severity crown fires (Baker, 1992; Baker et al., 2007; Covington and Moore, 1994; Schoennagel et al., 2004).

Furthermore, the expansion of interior Douglas-fir also creates additional forest health issues including western spruce budworm (WSBW) (*Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae) and Douglas-fir beetle (DFB) (*Dendroctonus pseudotsugae* Hopkins Curculionidae: Scolytinae) outbreaks in forests that once had limited Douglas-fir overstory. Logging activities including widespread clear cutting operations during the 19th and early 20th century throughout the Rockies, have also created forest areas in similar size and age which are now suitable bark beetle habitat (Bentz, 2005). As a consequence, over the past two decades, forests in the western United States have been affected by the largest outbreaks of bark beetles in at least a century, impacting over 28 million hectares, which has raised concerns about forest health and wildfire risk (Black et al., 2013; Jenkins et al., 2008; Jenkins et al., 2012; USFS, 2013).

The role of natural and anthropogenic disturbances in relation to forest health has been well studied, in particular since the implementation of the Forest Ecosystems and Atmospheric Research Act of 1988 (Kolb et al., 1995). The degradation of forest conditions can have a profound negative effect on wildlife habitat, timber production, water quality, recreation, grazing, and biodiversity (Coulson and Stephen, 2006; in Fettig et al., 2007).

Overall assessments of forest health in interior Douglas-fir forests have been often confined to specific disturbance factors, e.g. the effect of fire on DFB outbreaks (Amman, 1991; Cunningham et al., 2005; Kimmey and Furniss, 1943), or the consequences of dwarf mistletoe (*Arceuthobium* spp.) on Douglas-fir growth rates (Filip et al., 1993l; Mathiasen et al., 1990). In the central Rockies, the synergistic effects of compound disturbances exert a strong control over forest developmental trajectories (Bebi et al., 2003; Bigler et al., 2005; Kulakowski and Veblen, 2002). From a management perspective, it is important to understand how multiple disturbances potentially interact to affect ecosystem patterns and processes including susceptibility to subsequent disturbances (Kulakowski et al., 2012). The complexity of the interactions between multiple disturbance agents in middle montane interior Douglas-fir forests and their subsequent effects in terms of forest health has not readily been quantified or qualified in this often overlooked forest type.

From previous published literature, we construct a synthesis of the roles of major natural disturbance agents and how their interactions influence community structure, development, and health of middle montane interior Douglas-fir forests within the central Rocky Mountains. We will first discuss the role of fire on influencing forest conditions followed by discussions of Douglas-fir beetle (DFB) and WSBW and their interacting roles in regulating vegetative dynamics. The impacts of dwarf mistletoe and root disease will be highlighted in regards to their effect on predisposing interior Douglas-fir forests to subsequent disturbances. Throughout this paper we will describe potential forest health issues associated with each disturbance factor and identify current knowledge gaps in addressing these problems. Finally, management implications in relation to disturbances and forest health concerns highlighted in this paper, are discussed where applicable. Overall, this paper is meant to offer land managers a readily available source of information for guiding management decisions regarding current and future disturbance hazards to interior Douglas-fir forests in the central Rocky Mountains.

Characterization of Interior Douglas-fir Forests

Montane interior Douglas-fir are one of the dominant forest types within the central Rocky Mountains which sustains a rich diversity in composition and structure primarily determined by biogeoclimatic, genetic, and disturbance factors (Meidinger and Pojar, 1991). These forest systems form complex community assemblages in part attributed to the broad environmental amplitude of the dominant overstory species Douglas-fir, which is one of the most widely distributed conifers in western North American forests (Arno, 1979; Levin, 2005; Silen, 1978; Simard, 2009), (Fig. 2.1). This species is highly adapted to a range of site conditions that extend across xeric to mesic gradients where it is able to establish in soil conditions which range from dry nutrient poor to wet nutrient rich substrate (Donato et al., 2013; Simard, 2009). The geographic extent of the interior variety of Douglas-fir extends from north-central British Columbia (55^{o} N) to central Mexico (19^{o} N) and is well established across an elevation range between 580 to 3500 m (Fowells, 1965; Wright et al., 1971). Throughout its range, climate, soil, and elevation influence the locations where this species will occur (van Hooser et al., 1991). At the southern latitudinal limits of its range, moisture is the largest factor that influences its establishment, where it is restricted to north slopes at high elevations which constitute predominantly mesic sites (Peet, 2000). For example, in the Santa Catalina mountains of Arizona, Douglas-fir is the dominate conifer species on peaks above 2450 m (Niering and Lowe, 1984). As one moves north in latitude, the life zones for Douglas-fir shifts down slope in elevation with temperature the main limiting factor for growth (Hermann and Lavender, 1990; Windell et al., 1986). Microclimate conditions predominated by temperature and moisture regulate its distribution across slope aspect. Douglas-fir is well suited for cool moist sites which typically occur on northerly aspects where dense stands can develop. However, other conifer species including white fir, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) which are more shade-tolerant, are stronger competitors for available moisture and will replace Douglas-fir as canopies close over time in absence of disturbance (Franklin et al., 2002; Kilgore, 1981). On relatively warmer, drier sites (lower elevations, southerly aspects); soil moisture and precipitation typically are low with high evapotranspiration rates. These environmental constraints limit the establishment of more water limited conifer species. In these locations, Douglas-fir becomes the climax overstory forest species, even in the absence of disturbance. At these sites, tree density is often low because seedling establishment is limited to microsites where an adequate supply of water exists, which can result in scattered distributions of trees across the landscape (Harlow et al., 1979; Hermann et al., 1965). Across the front range of Colorado, Douglas-fir dominates north slopes between 1650-2700 m, while its establishment on open south facing slopes is restricted to higher elevations up to 2800 m where temperatures are cooler and soil moistures are higher (Peet, 2000). It was observed by Tesch (1981) in Montana, interior Douglas-fir on mesic north slopes formed dense even-aged stands, while neighboring south facing slopes led to a slow recruitment of seedling germination, resulting in uneven stand development with lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) growing alongside Douglas-fir in an open canopy stand.

Beyond latitudinal and elevation influences, the high degree of compositional heterogeneity within interior Douglas-fir stands is also attributed to its landscape position as a transitional forest environment. Often these forest communities are situated between two distinct life zones consisting of low elevation open woodland environments, and upper montane forest zones (Griesbauer, 2008; Peet, 2000). These “transitional areas between life zones, called ecotones, are characterized by a gradation of physical factors, which results in a mixture of flora and fauna from the two adjacent ecosystems" (Windell et al., 1986 p. 20).

In the central Rocky Mountains, interior Douglas-fir is largely distributed within the mid-elevation montane zone which ranges between 900 and 1500 m (Bailey, 1980). At the margin between the montane and subalpine zones, Douglas-fir intermixes with spruce-fir forests dominated by subalpine fir and Engelmann spruce, high elevation pine forests comprised of lodgepole pine, limber pine (*Pinus flexilis* James), and Great Basin bristlecone pine (*Pinus longaeva* Bailey) (Eyre, 1980; Habeck and Mutch, 1973). At the lower end of its elevation range, Douglas-fir is often dispersed throughout the upper elevation limits of ponderosa pine (*Pinus ponderosa* Laws.), white fir, and woodlands comprised of piñon pine (*Pinus edulis* Engelm.), juniper (*Juniperus* sp.), bigtooth maple (*Acer grandidentatum* Nutt.), and Gambel oak (*Quercus gambelii* Nutt) (Harlow et al., 1979). The diversity of this forest type also extends to its association with understory composition depending on location. In Utah alone, 14 distinct Douglas-fir habitat types are characterized, seven for northern Utah and seven for southern Utah. These include Douglas-fir/ ninebark (*Physocarpus malvaceus*), Douglas-fir/ mountain snowberry (*Symphoricarpos oreophilus* A. Gray), and Douglas-fir/ greenleaf manzanita (*Arctostaphylos patula* Greene) (Mauk and Henderson, 1984; Youngblood and Mauk, 1985). Other common associated understory species include, mountain mahogany (*Cercocarpus montanus* Raf.), chokecherry *(Prunus virginiana* L.), big sagebrush *(Artemisia tridentata* Nutt.*),* serviceberry *(Amelanchier* sp. Medik.*)* and currant (*Ribes* spp.) (Alexander, 1985; Eyre, 1980).

From a commercial stand point, Interior Douglas-fir forests are an important resource for the forest products industry where it is used for a number of applications from lumber and plywood, to house logs and fuel wood. It is also an important resource to local economies centered on logging (Keegan, 1990; Van Hooser et al., 1991).

Interior Douglas-fir forest communities also provide critical wildlife habitat for a variety of bird species. These include Ruby Crowned Kinglets (*Regulus calendula*), Evening Grosbeaks (*Coccothraustes vespertinus*), Western Flycatchers (*Empidonax occidentalis*), and Northern Goshawks (*Accipiter gentilis*), which require late successional stage stands with mature trees 20-75 cm in diameter, and dense canopy cover of 40-89%, to provide adequate nesting cavities (Lanner, 1984; Lileholm et al., 1993).

Disturbances and Associated Forest Health Issues Affecting Interior Douglas-fir Forests

Over the past century, interior Douglas-fir forests have been greatly changed (Gruell, 1983), with insect and disease problems stemming from management actions "which have upset the biological balance that existed in the natural forests" (Byler and Zimmer-Gorve, 1990 p.104). Fire and forest insects are two of the most critical disturbance agents in these forest ecosystems affecting species composition, nutrient cycling, stand structure, as well as other ecological processes (McCullough et al., 1998). With mean global temperatures expected to rise 2.6°C to 4.0°C over the twenty-first century (Collins and Knutti, 2013), the occurrence and expansion of insect outbreaks and severity and incidences of fires is expected to rise (Bentz et al., 2010; Kirilenko and Sedjo, 2007; McKenzie et al., 2004; Raffa et al., 2008; Woods et al., 2010). Situated within the middle montane zone, any significant perturbation within interior Douglas-fir forests may serve as conduit or disturbance corridor for the movement of fire, insects, or invasive species into upper montane forest environments. The loss, decline, or degradation of this forest system can have serious implications for timber, wildlife habitat, stand composition, hydrological impacts, fire regime alterations, as well as a reduction in biodiversity (Meddens et al., 2012).

Fire Disturbance

Wildfires are one of the most important abiotic disturbance agents strongly influencing vegetative patterns across North America (Hicke et al., 2012; Jenkins et al., 2012; McKenzie et al., 2004). Fire effects over a landscape are measured using a multitude of parameters including, frequency, intensity, severity, spatial and temporal extent of a burn (Brown, 2000; Kilgore, 1987; Morgan et al., 2001; Pyne et al., 1996). Collectively these measures constitute the basis for describing an environments' fire regime (Halofsky et al., 2011). One common method for classifying a fire regime is through a severity index which qualitatively describes how fire intensity affects an ecosystem, and is often related to the amount of biomass lost above and below ground (Keeley, 2009). High-severity fire regimes are characterized as those where fire transitions from surface fuels into the crowns of trees and consumes a majority of overstory vegetation (Agee, 1990; Agee, 1993). In contrast, low-severity fire regimes are classified as those where fires of frequent return intervals of (4-30 years) burn on the ground surface at low-severity and low intensity consuming dead branches, twigs, needles, cones, grasses, herbaceous vegetation, and where little to no mortality of live standing vegetation occurs (Graham et al., 1999; Odion et al., 2014).

Interior Douglas-fir forests throughout the central Rocky Mountains are characterized by a mixed-severity fire regime (Donato et al., 2013; Schoennagel et al., 2004). Under this classification, forest stands experience natural fires across severity levels that range from low, to medium, to high (Simard, 2009), and with variable fire return intervals that span 30-100 years (Arno et al., 2000). This regime is typical of middle montane forest ecosystems which tend to receive intermediate levels of precipitation compared to upper elevation spruce-fir forests and lower elevation ponderosa pine forests. These conditions favor the establishment of less drought and fire intolerant species (e.g. Douglas-fir, white-fir, and grand fir (*Abies grandis* Dougl. Lindl.) which grow more densely compared to shade-intolerant pines contributing to higher fuel loads than those found in lower montane forests (Brown et al., 2004; McKenzie et al., 2014). The mixed-severity fire regime is one of the most complex fire regimes in the western U.S., particularly in regard to the influence of fire on forest dynamics (Chappel and Agee, 1996; Lentile et al., 2005). The complexity of this regime is driven in part by the presence of both frequent low-severity surface fires and infrequent high-severity stand replacing fires that create mosaic patches of forest structure varying in age and tree density (Agee, 2005; Arno et al., 2000; Baker et al., 2007; Taylor and Skinner, 1998). The disparity in fire severities are related to site influences including, topography, aspect, and fuel continuity (Lertzman et al., 1997 in Everett et al., 2000). This will create unique fuel complexes in each stand controlled by associated factors including, microsite temperature, precipitation, fuel moisture, stand densities, and the presence or absence of ladder fuels (Brown, 1983; Turner and Romme, 1994). Variable fire intensities within the mixed-severity regime drive a forest composition that is comprised of seral fire dependent tree species and components of late successional trees that are multistoried and uneven-aged (Agee, 1998; Arno et al., 2000). Across a landscape scale, even-age forest structures are most common where stand replacing fires are prevalent and interspersed between these even-age patches, are uneven-aged stands where frequent surface fires are dominant (Brown et al., 1999; Kauffmann et al., 2000).

Historically, infrequent high-severity fire events in these forests were restricted to dense even-age stands typical of moist, cool sites which experienced previous stand replacing fires. Episodic droughts coupled with dense canopy cover composed of trees with close intercrown distances and large fuel accumulations create environments conducive to extreme fire weather conditions which favor the initiation and spread of crown fires. This can lead to consumption of most of the vertical and horizontal, live and dead components of the fuel strata resulting in stand-replacement (Hardy, 2005). Often interior Douglas-fir stands occupy steep slopes (>30^o) which are also critical slope angles which support the initiation of avalanche releases (Luckman, 1977). This type of disturbance agent can perpetuate future high-severity fire events by providing a mechanism for creating a rapid buildup of fuels through uprooting and snapping mature trees which get deposited throughout an avalanche run out zone (Butler and Malanson, 1990 in Walsh et al., 1994).

Low-severity fires were common in stands that experienced frequent surface fires that periodically burned understory grasses, brush, litter, seedling and saplings that have thin bark and low crown to ground ratios, but had little effect on large mature overstory trees with thick bark (Agee, 1994; Brown et al., 2004; Turner and Krannitz, 2001). In these stand types, interior Douglas-fir is often intermixed with ponderosa pine which sheds long needles that are non-compacted on the fuel bed surface and become highly susceptible to fire ignitions. The lack of dense fuels coupled with low fuel moistures and low relative humidity during the fire season, increase the susceptibility to frequent surface fires which occurred on the order of every 7-20 years in lower montane zone forests throughout the Rocky Mountains (Houston, 1973; Arno, 1976). Frequent low to moderate intensity surface fires create open park-like stands with light fuel loadings (Meisser et al., 2013; Steele et al., 1986). Overstory trees often experience minimal mortality levels where mature Douglas-fir have adapted thick bark that protects the inner cambium from heat energy (Fowler and Sieg, 2004; Habeck and Mutch, 1973; Minore, 1979). The survival of overstory Douglas-fir helps to maintain mixed-age class structures as successive understory Douglas-fir seedlings and saplings become recruited into sub-canopy and canopy layers in the absence of fire.

Human activities during Euro-American settlement in the western U.S. have greatly altered fire regimes in the mixed-conifer montane forests. Throughout the past century, increased grazing pressure from large scale livestock operations has reduced fine fuel loads which previously carried low intensity surface fires (Faulk, 1970; Sackett et al., 1996). Federal fire suppression and exclusion policies dating back to early 20th century have reshaped the landscape leading to extended fire-free intervals in montane forests allowing understory conifers to develop in formerly open stands (Baker et al., 2007; Covington et al., 1994; Dana and Fairfax, 1980; Gruell et al., 1982). In a fire reconstruction study in southwestern Montana it was reported the increase in tree establishment of Douglas-fir in grassland-sage communities starting in the mid 1880's, coincided with the prevention of surface fires (Heyerdahl et al., 2006). The dense buildup of understory conifers leads to an increase in fuel loads. This provides a mechanism for the transition of surface fire into the canopy through the buildup of ladder fuels, which can increase the potential for crowning and the occurrence of high-severity, stand replacing fires (Hansen, 2014; Iverson et al., 2002). Changes in forest conditions can have a great impact on interior Douglas-fir stands, where the prevalence of high-severity fires may become more commonplace in these forests which previously experienced historic low-severity fire regimes (Covington and Moore, 1994; Daniels, 2004). Along the Colorado Front Range for example, Veblen et al. (2000) found that the contemporary ponderosa pine / Douglas-fir forest structure and landscape had been shaped by high-severity fire events that occurred as a result not only of prolonged drought coupled with extreme fire weather conditions, but also high fuel loads.

Climate change predictions call for a mean change in temperature of 2.6^{o}C to 4.8^{o}C over the 21st century (Collins and Knutti, 2013). Expected increases in fire activity will follow based on more variable precipitation patterns and increases in drought periods and or warming trends (Littell et al., 2009; Marlon et al., 2009; Westerling et al., 2006). More frequent high-severity fire events can lead to substantial increases in the loss of old fire tolerant trees which is a concern (Perry et al., 2011). Old remnant mature trees serve as biological legacies acting as important seed sources for repopulating the next generation of interior Douglas-fir and other species in a stand (Keeton and Franklin, 2005).

The direct effect of fire leads to either instantaneous tree mortality during initial fire passage, or delayed mortality resulting from severe injury through damage to foliage, cambium, fine roots, and conductive tissues whose physiological processes are important for growth and development (Stephens and Finney, 2002; Wyant et al., 1986). In the canopy layer, two types of crown damage determine the likelihood of fire-induced tree mortality. These include crown scorch where the foliage is killed by hot gases rising from flames, and crown consumption where foliage and occasionally small twigs directly support combustion (Van Wagner, 1973). Crown scorch is a principal cause of fire-related tree mortality (Sucoff and Allison, 1968; Van Wagner, 1963; Wagener, 1961).

Two important parameters for predicting post-fire tree mortality associated with crown scorch include crown scorch volume and crown scorch height. Crown scorch volume is measured as the percent of the crown that is scorched (Chambers et al., 1986; Methven, 1971; Peterson, 1985), while crown scorch height refers to the height at which the heat from a fire is lethal to living foliage (Van Wagner, 1973). Scorch height is dependent upon fireline intensity, wind speed, and air temperature. The physiological effects of crown scorch can lead to a decrease in carbohydrate production further weakening a trees response to stress and lowering its resistance to insects, drought, and other disturbances (Peterson and Arbaugh, 1986).

The physical attributes of an individual tree can greatly influence whether or not a tree survives a fire. Tree size is widely recognized as a factor in resistance to fire damage. As height increases, a greater proportion of the foliage is likely to be above the height of lethal scorching from a passing surface fire (Ryan et al., 1988). In Colorado, Wyant et al. (1986) found large diameter ponderosa pines and Douglas-firs had proportionally less crown and or stem damage in comparison to smaller fire-killed trees following prescribed fires. Bevins (1980) also found surviving Douglas-firs following a prescribed surface fire in west-central Montana tended to be tall (>15.0 m), large diameter (> 20.0 cm) trees, with lower crown scorch heights (< 3 m), and a lower percentage of live foliage scorch compared to dead trees.

Heat induced damage to tree boles can also affect a tree’s likelihood of survival after a wildfire (Peterson and Arbaugh, 1989). Bole charring that result in cambial death is dependent upon both the amount of heat received by a tree and the insulating capacity of the bark (Ryan and Reinhardt, 1988). Older, large diameter trees tend to have thicker bark with a greater capacity for absorbing heat thus providing greater resistance to injury

(Costa et al., 1991; Peterson and Arbaugh, 1989). Mature Douglas-fir is often comprised of a high percentage of cork in their bark which can aid in the thermal diffusion of heat (Ryan and Reinhardt, 1988). Douglas-fir stands with a greater proportion of large diameter trees are likely to survive low intensity fires. However, these trees can be more susceptible to DFB infestations which seek larger diameter weakened and stressed trees (Furniss, 2014). Ryan et al. (1988) found that bole damage, expressed as the number of quadrants that contained dead cambium, was more important for predicting Douglas-fir mortality than either scorch height or the percentage of crown volume scorched. The location on a tree which receives direct flame contact can alter the probability for survival. Bole damage that occurs a few meters in height above the surface of the ground is thought to be more critical to tree survival than damage to the base of the tree (Miller and Keen, 1960). As a consequence, low intensity surface fires with low flame lengths result in less tree mortality when compared to fires that burn through heavy loads of thousand hour fuels. In the event bole scorch does not produce a fatal response through cambial injury, partial basal girdling, and root damage may lead to moisture stress and reduced resistance to insects and disease (Chambers et al., 1986; Geiszler et al., 1984).

Sustained smoldering combustion of litter, duff, or down woody material within the surface and ground fuels layers can lead to root injury and mortality. Soil temperature, soil moisture, root spatial distribution, heat residence time and fuel loading, greatly influences the degree of root damage during a burn (Hungerford et al., 1991; Stephens and Finney, 2002). Temperatures as low as 48-60°C have been attributed to cause root desiccation or death (Egan, 2011; Neary et al., 1999). It was found by Swezy and Agee (1991), prescribed surface fires set in ponderosa pine stands in Oregon led to lethal temperatures (> 60° C) that penetrated down 5 cm in depth which is also where the greatest concentration of fine root mass (1-2 cm diameter) occurred. Other studies have also concluded both low and high severity burns reduce overall fine root mass (Hart et al., 2005; Stendell et al., 1999). The loss of root biomass can have great implications for decreased capacity in essential nutrient and water uptake, and can increase stress and susceptibility of affected stands to future insect and pathogen outbreaks (Gordon and Jackson, 2000; Reubens et al., 2007). The functional role of anchoring soils to prevent erosion and runoff would also be impacted by the reduction in root systems (De Baets et al., 2006; Gyssels et al., 2005).

The cumulative effects of more prolific fire events can elevate the hazard and predispose fire affected stands to future biotic disturbances including insect outbreaks and disease (Dale et al., 2001; Fowler and Sieg, 2004; McCullough et al., 1998). As an example, recently fire killed Douglas-fir often serve as hosts for *Cryptoporus volvatus*, a fungus that causes a white sapwood which can rapidly spread to non-fire injured trees (Parker et al., 2006). Non-lethal fire effects also modify forest conditions by creating mosaics of standing, fire-weakened and injured trees that also often succumb to insect attack and disease (Ryan and Reinhardt, 1988).

Douglas-fir beetle biology and ecology

The developmental patterns in montane interior Douglas-fir forests are not regulated by fire alone. Bark beetles are also a major disturbance agent that has a large ecological role in reshaping forest structure by attacking old, large diameter, weakened trees essentially removing them from the overstory, and promoting the recruitment of the next generation of trees in a stand (Raffa et al., 2008). Bark beetles and their hosts have coevolved over the past 200 million years (Raffa and Berryman, 1987).

Within interior Douglas-fir forests in the middle montane zone of the central Rocky Mountains, the most prevalent bark beetle species is the DFB which utilizes Douglas-fir exclusively (McGregor et al., 1984; Negrón et al., 2001; Rudinsky, 1966; Schmitz and Gibson, 1996). Density-independent factors that influence the population dynamics of this insect include the availability and suitability of breeding sites (Ross and Daterman, 1997). Freshly felled or downed trees > 20 cm diameter provides adequate brood source material containing phloem and other essential nutrients for development (Furniss, 1965; Lejeune et al., 1961). These resources typically lack or experience reduced effective defense mechanisms including decreased or cessation of resin production, a key compound containing mono and sesquiterpenes that entrap or elevate toxins to levels fatal to beetles (Franceschi et al., 2005; Lewisohn et al., 1991; Woodward, 1992; Oven and Torelli, 1994). In one example, Wood (1962), working with the bark beetle species, California five-spined engraver (*Ips confusus* Lee, Coleoptera: Scolytinae), and found this insect became established the quickest in cut logs where pitch tubes (a defensive mechanism), pressure dropped to zero or near zero (Smith, 1972b). In past studies, trees with low oleoresin pressure have been associated with increased susceptibility to bark beetle attacks (Cates and Alexendar, 1982; Vité, 1961). Consequently, eruptions of DFB are often related to disturbances including, windthrow, root disease, or avalanches that produce an abundance of downed trees with impaired defenses (Fredericks and Jenkins, 1988; Goheen and Hansen, 1993), or trees physiologically weakened by drought (Mattson and Haack, 1987), fire (Cunningham et al., 2005), snow damage (McGregor et al., 1974), defoliation, and/or disease (McMullen and Atkins, 1962, Wright et al., 1984). DFB overcome the defenses of live host trees through the use of mass attack strategies. Female beetles typically initiate attacks on potential host trees (Hardwood and Rudinsky, 1966). If the host tree is suitable for brood production, they produce pheromones that attract other females and males to the tree (Anderson, 2012; Lejeune et al., 1961). Primary DFB aggregation pheromones include, frontalin (1, 5-dimethyl-6, 8-dioxabicyclooctane) (Kinzer et al., 1971; Gries et al., 1988; Lindgren, 1992) *trans*-verbenol (Rudinsky et al. 1972), seudenol (3-methylcyclohex-2-en-1-ol), and MCOL (1-methylcyclohex-2-en-1-ol) (Libby et al., 1983; Madden et al., 1988; Pitman and Vité, 1970). A male beetle pairs with an individual female, mate and the process of brood production begins. Once a host tree is completely occupied by DFB, colonizers release the anti-aggregation pheromone MCH (3-methyl-2-cycolohexen-l-one) to cause late arriving beetles to focus attacks on nearby non-infested host trees.

Insect-induced tree mortality influences the development, senescence, and rebirth of stands which in turn affects energy flows and nutrient cycles (Samman and Logan, 2000). *Dendroctonus* species (Coleoptera: Curculionidae, Scolytinae) are particularly capable of reshaping stand structure, composition, and function (Jenkins et al., 1998; Jenkins et al., 2008, 2012, Kashian et al., 2011), with stand dynamics and population dynamics of bark beetles often highly interrelated (Coulson, 1979). Coulson (1979 p. 433) stated, “tree age, diameter, and phloem thickness are all correlated and in turn are related to beetle survival, i.e. the large-diameter trees, with thick phloem accommodate large beetle populations and have high survival rates. In stands with mixed diameter classes the percentage of trees killed during outbreaks is related to tree diameter, with the greatest number of trees being killed in the diameter class representing the highest basal area. Epidemics continue until large-diameter trees in the stands are depleted”.

Dissimilar to lodgepole pine or spruce/fir forests which form dense uniform even-age forests which are products of stand replacing fire history, the intrinsic characteristics of interior Douglas-fir forests limit the availability for DFB to cause landscape scale Douglas-fir mortality. Throughout the central Rocky Mountains, Interior Douglas-fir stands often occur in mixed species stands or in small groups surrounded by non-host trees at the edge of their upper and lower elevation limits. In these types of stands, suitable DFB hosts are typically distributed unevenly throughout a forest (Atkins, 1966). Where Douglas-fir are the uniform dominant overstory component, past logging and fire history often create mosaics in which Douglas-fir oscillates in age and density (Furniss, 2014). Consequently, the varied age and size classes do not necessarily meet conditions that warrant epidemic outbreaks, and mortality centers become confined to small groups of trees (Jenkins et al., 2008). A stand hazard rating system developed by Weatherby and Thier (1993) suggest the highest potential for tree mortality due to a DFB outbreaks occur in stands with basal areas greater than 250 ft^2/ ac., that have a proportion of Douglas-fir that is greater than 50%, with an average stand age above 120 years, and an average diameter at breast height > 50.0 cm.

Under the right conditions (e.g. drought coupled with a supply of fresh down material from windthrow events, avalanches etc.), these subsequent disturbances can facilitate the development of endemic into epidemic population levels which may overcome host resistance and initiate attacks that overwhelm standing live trees creating localized stand scale (hectare) outbreaks (Fig. 2.2).

Epidemic level infestations serve a role similar to a stand replacing fire, leading to widespread tree mortality, and promote forest succession (Hicke et al., 2012; Pelz and Smith, 2012; Wood, 1982). Old, large diameter weakened trees are prone to attack and are essentially removed from the canopy while creating microhabitats suitable for the recruitment of the next cohort of trees (Christiansen et al., 1987). Another consequence from tree death is the release of important resources (sunlight, water, and nutrients) that can be utilized by surviving trees (Veblen et al., 1991). Species composition may also shift leading to increases in the ratios of light-loving to shade-loving species that may persist for more than 60 years (Raffa et al., 2008). Additional consequences stemming from bark beetle outbreaks include changes to nutrient cycling and carbon sequestration processes (Hansen, 2014), as well as changes to the timing of seed releases affecting future forest regeneration (Teste et al., 2011a,b).

Douglas-fir beetle mediated fuel complex changes

Only recently has the interactive effects between bark beetles and fuel complexes have been studied thoroughly. Much of the recent research in this realm has been predominantly conducted in forest systems that experience infrequent high-severity fire regimes, (e.g. lodgepole pine forests infested by mountain pine beetles (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytinae), and Engelmann spruce forests infested by spruce beetles (*Dendroctonus rufipennis* Kirby (Coleoptera: Scolytinae) (DeRose and Long, 2009; Jorgensen and Jenkins, 2011; Collins et al., 2012). Jenkins et al. (2008, 2012), provides an extensive review of fuel complex changes during typical bark beetle rotations. In contrast to these forest types, it has been hypothesized lower and middle montane forests will respond much differently to bark beetle outbreaks based on drier, more open conditions with lower biomass and lower tree-crown base heights (Parker et al., 2006; Hicke et al., 2012 in Donato et al., 2013).

Fuel complex changes induced by DFB are complicated based on the spatial dynamics of an attack which often results in a patchwork outbreak pattern within a stand. Figure 2.3 shows select fuel characteristic changes associated with a Douglas-fir beetle rotation. Donato et al. (2013) inventoried changes to surface and aerial fuels in interior Douglas-fir forests across four different DFB outbreak stages including, green (undisturbed), red (1-3 yr.) post-infestation, gray (4-14 yr.) post-infestation, and silver (25-30 yr.) post infestation, across a range of Douglas-fir habitats in the Greater Yellowstone Ecosystem (GYE). The results from his study indicated that significant reductions in available canopy fuel load and canopy bulk density occurred with increasing time since outbreak, while significant changes to surface fuels were few aside from an increase in 1000 h fuels during the silver stage (Donato et al., 2013). In a similar study conducted in northern Utah, Giunta et al. (in review) found in the surface fuels layer, a significant (P=0.02) increase in litter depth (cm) and litter loading (kg m^{-3}) occurred during the epidemic phase of an outbreak as the pulse of needle loss occurs during this period yet did not extend into the post-epidemic phase. Following the loss of overstory canopy, an increase in herbaceous biomass followed in the post-epidemic phase as increased levels of light was able to infiltrate to the forest floor. In an additional study, McMillin and Allen (2000) found DFB induced changes to interior Douglas-fir stands resulted in a reduction in basal area of 40-70%, a mean diameter at breast height reduction of 8-40%, and a three-fold increase in forbs, grasses and herbaceous plants in infested stands.

Alterations to aerial fuels have been attributed to a series of physiological changes directly resulting from the colonization of host trees by beetles and the introduction of the associated blue-stain fungi principally the species, *Ceratostomella pseudotsugae* Rumbold (= *Ophiostoma pseudotsugae* (Rumbold) von arx, von Arx, 1952). Once a tree has been inoculated with blue-stain fungi, it is considered “green infested” while the crown is still green in color (Wulder et al., 2006). Evidence of successful host colonization is determined by the presence of pitch streams, entrance / emergence holes, egg galleries, and frass accumulations near the base of trees (Edmonds and Eglitis, 1989; Kegley, 2011; Schmitz and Gibson, 1996). Blue-stain fungi penetrate sapwood and phloem tissues adjacent to larval galleries contributing to the disruption of water transport between root systems and foliage (Hubbard et al., 2013; Lewinshon et al., 1994; Rane and Tattar, 1987). During this stage, active photosynthesis ceases as the movement of water from the roots to the foliage is blocked. As needle desiccation progresses, foliage fades from green to yellow where the combined destruction of xylem and phloem tissues effectively leaves host trees girdled leading to tree death (Hubbard et al., 2013). By the second year post infestation, most of the foliage fades to red (Amman, 1982). It is during the red needle stage where the probability of torching and crowning can increase where canopy foliar moisture declines to its lowest moisture content levels, yet dead needles are still retained in the canopy (Simard et al., 2011.) Three years after initial infestation most trees will have lost all their needles (Wulder et al., 2006). A reduction in canopy fuels allows more sunlight to reach the forest floor, and other resources including nutrients and water become available for regenerating understory species.

Giunta et al. (in review) measured foliar moisture content in infested Douglas-fir trees across all four crown condition classes (green, green-infested, yellow, and red) as associated with DFB outbreaks. Their findings showed yellow and red crown condition classes had a significantly (P<0.0001) lower foliar moisture content based on percent of oven dry weight, compared to green and green-infested foliage.

Douglas-fir beetle interactions with other disturbances and effects on forest health

Prior insect disturbances in a stand can serve as initial stressors to tree vigor which subsequently diminishes tree defenses increasing the likelihood of successful DFB host colonization. In 2011, DFB caused tree mortality in southern Idaho, Nevada, and Utah more than doubled. This increase was partly attributed to induced stress on mature Douglas-fir caused by several years of defoliation by WSBW (Man, 2011). Lessard and Schmid (1990) found that trees in Colorado infested by DFB had reduced growth attributed to prior infestation by WSBW (Negrón, 1998). During the past 50 years singular, overlapping, and repeated outbreaks of WSBW and DFB have greatly altered the structure and composition of montane forests along the Colorado Front Range (Hadley and Veblen, 1993). Negrón (1998) mentioned "In the Colorado Front Range, it seems that the primary disturbance agent, although not the only one, that triggers DFB outbreaks is WSBW defoliation". In Logan Canyon, Utah, Fredericks and Jenkins (1988) found that fire-damaged trees subsequently defoliated by WSBW provided additional host material that supported a DFB outbreak.

The Douglas-fir tussock moth (DFTM) (*Orgyia pseudotsugata* McDunnough Lepidoptera: Lymantriidae) is another important defoliator that feeds on Douglas-fir in all age classes (Beckwith, 1978). Its feeding activity can induce significant growth reduction, top-kill, and decrease plant vigor predisposing hosts to subsequent DFB infestations (McGregor et al., 1984). Wright et al. (1984) found total DFB attacks and emergence of females and offspring peaked one to two years following a DFTM infestation. Others have found inverse relations between percent defoliation and DFB attack densities which have been found to increase from 3 per ft^2 during initial infestation to 11 per ft^2 three years post infestation as tree resistance to DFB infestation is reduced with increased levels of defoliation (Berryman and Wright, 1978). DFB productivity expressed as the ratio of emergent offspring to parents that produced them has been found to be greatest the year following peak defoliation by DFTM (Wickman, 1978).

Pathogens serve as an additional mechanism for modifying stands in favor of DFB infestations. Bark beetles and pathogens have co-evolved for millennia as integral components in conifer forests (Goheen and Hanson, 1993). Some of the most important pathogens affecting trees which support bark beetle infestations are root rot diseases. In the Rocky Mountains, *Armillaria* spp. is the most important and widespread (RMR 2010). This fungus spreads through soil layers via rhizomorphs from infected sites grafting onto non-infected hosts. It penetrates root tissues via mechanical pressure and enzyme action, killing phloem and cambium layers (Williams, 1989). Once established, it induces decay within the root collar and eventually trees become susceptible to windthrow or topple over on their own from weakened root systems (RMR, 2010; Hansen and Goheen 2000). Root disease outbreaks also affect non-infested trees by creating forest gap openings where healthy trees along gap margins can be exposed to high winds (Goheen and Hansen 1993). Significant wind events in root disease patches can lead to substantial amounts of suitable fresh felled host material for DFB exploitation.

Following non-stand replacing fire events, impacts from a wildfire can predispose stands to subsequent bark beetle disturbances. Trees impacted by crown scorch, bole charring, and root damage associated with fire, become attractive targets for DFB. For example, Furniss (1965) reported 70 percent of fire-injured Douglas-fir was infested by DFB following a fire in southern Idaho. Proportion of attacks increased with cambium injury but declined in the heavy injury class where it is likely phloem and other essential resources were damaged beyond utilization by beetles. Other studies have found DFB mass attack trees where crown scorch is greater than 50%, and inner cambium damage ranged between 25-50% of the entire bole (Hood and Bentz, 2007; Flowers and Kanaskie, 2007; Rasmussen et al., 1996). It has also been discovered infestation patterns following fire events progress from recently killed trees, to fire damaged trees, to healthy live trees over time as suitable phloem resources became scarcer in successively damaged classes (Cunningham et al., 2005; Ryan and Amman, 1994). It should be noted, not all fire-injured trees are susceptible to DFB attacks. Trees that are completely defoliated by crown fires that also result in the complete burning or severe scorching of the inner bark, especially in thin-barked trees, will no longer be suitable for bark beetle infestations (Amman, 1991; Amman and Ryan, 1991).

Western spruce budworm and interior Douglas-fir forests

Insect defoliators have an important influence on the condition of interior Douglas-fir forests. Some of the most important impacts of insect defoliation are tree mortality, growth loss, rotation delays, and increased susceptibility to secondary insects and disease (Kulman, 1971). The WSBW is considered one of the most widespread and destructive defoliators in western coniferous forests, particularly where Douglas-firs and true firs dominate stand composition (Brookes et al., 1987; Fellin and Dewey, 1982; Swetnam and Lynch, 1993). Depending on environmental and biological conditions, the timing of WSBW outbreaks is highly variable and episodic in nature where the periodicity can range from 13 to 35 years (Myers, 1988; Ryerson et al., 2003). The life history requirements for WSBW are highly interdependent upon forest stand structure and conditions. These insects have a one year life cycle where adults emerge in late spring to early July to mate. Adults are photopositive who orient themselves towards light sources often near the crowns of host trees where females deposit eggs on the underside of conifer needles (Fellin and Dewey, 1982). Newly formed first instars spin a protective hibernaculae in sheltered locations on host trees after which they molt into second instars without feeding and overwinter in their hibernaculae (Brookes et al., 1987; Chen et al., 2001; Nealis and Régnièr, 2009). The following spring after emergence, second instars descend through the canopy via silk threads in search of host resources to feed upon and complete their life cycle through four additional instar periods and pupation (Fellin and Dewey, 1982).

This insect preferentially feeds on current years' growth where larvae penetrate swelling buds that have the highest food quality and offer the best protection from predators (Fredricks and Jenkins, 1988; Murdock et al., 2013). Bud phenology, specifically bud development and the timing of budburst, can greatly influence WSBW population dynamics. Trees that exhibit delayed budburst have been related to a reduction in WSBW success as new bud formation occurs after larvae emerge from hibernation and initiate feeding (Cates et al., 1983). Douglas-fir forests with a large proportion of trees with a genetic makeup that promotes delayed budburst timing will likely have a greater resistance to WSBW infestations. Site location can also affect biological processes that influence WSBW population dynamics. Sites with warm soils and warmer temperatures have been linked to earlier budburst timing (Wulf and Cates, 1987). Sites situated along south and west aspects that lead to earlier bud development and coincide with the period of larvae feeding after winter emergence, could help explain the greater success rate of WSBW on drier sites.

Influence of western spruce budworm on forest structure

Multi-age stands with multi-level forest canopies dominated by host trees provide optimal WSBW habitat as second instar larvae are dependent upon a successful canopy descent to reach host resources (Carlson et al., 1983). The tiered structure of a multi-level stand increases the foliar area for larvae to land on facilitating the vertical dispersal of larvae from canopy to sub-canopy trees, seedlings, and saplings (Hadley and Veblen, 1993). Weather factors including wind and stand composition, exert a large control over the success rate of locating a suitable host.

The multi-age, multi-tiered canopy layer is largely a product of mixed-severity fires (O’Hara and Nagel, 2006). The greatest impact of WSBW is on sub-canopy and understory layers where larvae feed on host regeneration within the understory. Conifer seedlings have relatively few needles and buds, and new growth can become deformed or killed by only a few larvae (Fellin and Dewey, 1982). Future regeneration within a stand is further impeded by WSBW feeding on developing cones and seeds (Dewey, 1970). Frank and Jenkins (1987) found that there were a higher percentage of larvae feeding on seed cones as opposed to pollen cones. This could affect future regeneration where Douglas-fir are known to have infrequent cone crops every 2-7 years at low elevations (Owens, 1976), and 1 in 11 years at higher elevations (Lowry, 1966). Consecutive years of WSBW feeding on overstory host trees can lead to decreased stem growth, top killing, and in some cases tree mortality (Fellin and Dewey, 1982). Using tree-ring reconstructions, Swetnam and Lynch (1989) found overstory trees in Devil’s Gulch located in the southern Rockies experienced 60% mortality from WSBW feeding. In another tree-ring study conducted in Canada near Pemberton, B.C., Alfaro et al. (1982) found that 39.3% of total trees per hectare died within three years after a WSBW outbreak. Often, the absence and more importantly release patterns of growth rings in mature Douglas-fir and other host species coincide with WSBW outbreaks (Swetnam et al., 1985; Swetnam and Lynch, 1989). Reduced radial growth reduction can lead to an overall decrease in a stands' basal area which could have implications for meeting timber harvest projections if merchantable stands become infested. Hadley and Veblen (1993) used dendrochronological analysis to reconstruct past WSBW and DFB infestations throughout the Colorado Front Range. It was determined budworm outbreaks were responsible for high levels of mortality of seedlings, saplings, and small diameter trees. Most sampled stands displayed host growth reduction characteristics evidenced by reduced tree ring widths during budworm outbreaks. It was found older, less vigorous stands with suppressed Douglas-fir trees were most susceptible to WSBW infestations. Stands with fewer host trees had lower levels of mortality over various size classes (Hadley and Veblen, 1993).

Western spruce budworm and fire

Past management practices of fire exclusion have led to an increase in the frequency, duration, or intensity of outbreaks attributed to human-caused changes in forest stand structure and composition (Anderson et al., 1987; Carlson et al., 1983; Fellin et al., 1983). Many open-canopy stands that were once maintained by frequent surface fires have succeeded to densely stocked, closed canopy stands composed of shade-tolerant species of an uneven age, creating forests that are more continuous across the landscape than during pre-settlement times (Gruell, 1983; Swetnam and Lynch, 1989). Collectively these conditions have favored WSBW increasing both the frequency and duration of outbreaks following decreased forest fire frequency in western states (Anderson et al., 1987).

Beyond the ecological and economic impact of WSBW, its outbreak patterns, population dynamics, responses to climatic variability, and effects on fire occurrence and behavior are not fully understood (Gavin et al., 2013). Most insect outbreaks and fire interactions focus on species that result in high levels of tree mortality such as bark beetles. The impacts of WSBW on fuel loads and fire behavior however, are likely different from bark beetle species (Gavin et al., 2013). Bark beetle infestations do not directly decrease crown volume, but rather contributes to a reduction in canopy bulk density by resulting in desiccation of needles that eventually drop one to two years after an attack. WSBW directly alters aerial fuels by consuming fresh needles. The resulting net reduction in canopy bulk density decreases the likelihood of torching and crown fire initiation and spread. After following a WSBW outbreak in Washington, Hummel and Agee (2003) measured decreases in canopy closure and a reduction in the density of small diameter (< 20 cm) trees over an eight year period. Incorporating these inputs from stand data, they used the fire behavior model BEHAVE (Burgan and Rothermel, 1984), to simulate fire spread in their study site. Crown characteristics that contributed to crown fire initiation (e.g. canopy base height and canopy bulk density) remained stable and did not indicate any significant increase in crown or torch potential. In a similar study, Gavin et al. (2013) used the Wildland-Urban Interface Fire Dynamic Simulator (WFDS) which has a greater ability to model fine scale fuel changes. They found defoliation consistently reduced both the vertical and horizontal spread of crown fire across a range of surface fire intensities. They also discovered that a row of defoliated trees released substantially less heat than a row of non-defoliated trees due to the lack of fuel which decreases flame intensities. It has been speculated changes to surface fuel loads as a result of the effects of WSBW may increase fuel loading and elevate the risk in fire severity and or occurrence (Hummel and Agee, 2003; McCullough et al., 1998). Hummel and Agee (2003) found coarse woody debris loads increased by 50% following a WSBW outbreak in central Washington. When plot data was input into fire modeling software, surface fire models predicted surface fire flame lengths would increase significantly because coarse woody debris levels were significantly higher. This increase in fuels contributes directly to a predicted increase in surface fire flame lengths (Hummel and Agee, 2003).

Dwarf mistletoe and interior Douglas-fir forests

Dwarf mistletoes (*Arceuthobium* spp.) are one of the most important, widespread disease agents in North American conifer forests, and are found throughout montane forest ecosystems (Hawksworth and Wiens, 1996; Hoffman, 2010; Watson, 2001). These plants form obligate hemparsitic relationships with host plants extracting vital water and minerals through a haustorium from their hosts (Pate, 1995; Shaw et al., 2004). This process depletes essential photosynthetic reserves used for growth and maintenance by host trees (Hoffman, 2010). Although dwarf mistletoes are capable of complete photosynthesis, upwards of 60% of their carbohydrates are extracted from their hosts (Lamont, 1983). Degenerative induced effects on host plants include, stem and height growth reductions, top kill, and reduced reproductive output and forest productivity (Geils and Mathiasen, 1990; Tinnin et al., 1982). In particular, Douglas-fir dwarf mistletoe (*Arceuthobium douglassii* Engelm.) is one of the most damaging species that parasitizes Douglas-fir (Hawksworth and Wiens, 1996; Sala et al., 2001). Douglas-fir dwarf mistletoe is host specific and slow spreading, making stand composition, tree size, and structure important for its persistence in a forest community (Smith, 1972a). Spread rates of Douglas-fir dwarf mistletoe are often accelerated in multi-storied Douglas-fir stands where understory trees receive abundant seed rain from infected overstory trees. The presence of non-host species can slow the spread of the disease agent. Stands with open canopies are often more susceptible because dense stands create shading conditions which retard Douglas-fir dwarf mistletoe growth while also intercepting seeds from infected trees (Hadfield et al., 2000).

The role of fire and mistletoe is important to note. Episodic natural fires helped keep mistletoe populations from aggressive expansion through the removal of infected trees and killing potential host carriers in the understory (Parker et al., 2006). Through the advent of past fire suppression policies, Douglas-fir regeneration has been able to expand throughout the central Rocky Mountains. This has led to an increase in the number of susceptible hosts in stands while simultaneously limiting infection removal processes (Hadfield et al., 2000). Stand density increases have not only raised fuel accumulations, but has also increased the spread of Douglas-fir mistletoe. The growth form of mistletoe creates clumps of closely spaced small branches that trap fallen needles. This creates vertically oriented fine fuels that enhance stand flammability. Furthermore, this broom like growth termed ‘witches broom’, typically occurs in the lower portion of tree crowns which tend to self-prune less often than non-infected hosts. Koonce and Roth (1985) reported 73% greater aerial fuels (live and dead witches’ brooms) in dwarf mistletoe-infested stands compared to non-infested stands. This leads to the development of vertical ladder fuels which provide a mechanism for surface fire to transition into crowns increasing wildfire risk in Douglas-fir stands (Dickman and Cook, 1989; Hoffman, 2010; Parker et al., 2006).

The interaction of Douglas-fir dwarf mistletoe with other disturbances within a stand could lead to poor stand health conditions. Seedlings and saplings, especially those with main stem infections, readily succumb to this parasite (Hadfield et al., 2000). The combined presence of Douglas-fir dwarf mistletoe and WSBW in a stand could have substantial effects on regeneration. The physiological reduction of fitness as a result of dwarf mistletoe infections can lead to elevated susceptibility to DFB infestations affecting overstory layers and creating unnatural fuel accumulations elevating future wildfire risk (Hagle et al., 2003).

Future Research Needs

The complex and heterogeneous nature of interior Douglas-fir montane zone forests creates difficulties in assigning a blanket classification in terms of forest health conditions. Each individual forest will have unique challenges in quantifying the extent of impairment, based on past disturbance and land use history. A multi-prong approach will be necessary to maintain ecosystem functions, biodiversity, while reducing catastrophic fire risk in these forests. Before attempts are made to categorize a holistic approach to restoring the health of these ecosystems, much research is still needed to understand how multiple disturbance agents actually affect these forest communities.

Since the early 20th century, “forest structure, fuel characteristics, and fire regimes of the mixed conifer forests in the western United States have been dramatically altered” (Graham et al., 2004; Stephens and Collins, 2004 in Stephens and Moghaddas, 2005 p.22). One of the most pressing issues is understanding the historic role and extent of fire in these ecosystems. As previously described, these forests are defined by a mixed-severity fire regime which is considered one of the least understood of all fire regime types (Halofsky et al., 2011). Further complicating matters is many historic frequent surface fire adapted forests in the interior montane zone have experienced an increase in the density of shade-tolerant species which have created large accumulations of live and dead fuels attributed in part to past fire exclusion policies. This has led to shifts in the fire regime to one which has more high-severity behavior (Perry et al., 2011). It has been acknowledged the occurrence of, “high-severity crown fires are not outside the historical range of variability, although their size and frequency may be increasing” (Schoennagel et al., 2004, p. 673). To better understand these changes, inferences and information from past fire regimes must first be accounted for (Heyerdahl et al., 2012). In addressing this issue, additional fire reconstruction studies and evidence of past fire events should be collected to gain insight into past natural fire regimes in interior zone montane forests across different geographic locales. Detailed documentation of fire behavior and record collections from current and future fires that occur in montane mixed-conifer / interior Douglas-fir, will aid fire and forest managers in assessing suppression strategies and forest health conditions for future fires in this forest type.

Restoration of historic fire regimes has been proposed as a tool to improve declining forest health conditions across the west (Allen et al., 1998; 2002, Arno, 2000; Caprio and Graber, 2000). In the Rocky Mountains, it has been estimated fires will need to burn three to seven times more than at the current rate to reset the natural balance (Keene et al., 2002). Current conditions of overstocked interior montane zone forests warrant caution when planning to implement fire prescriptions. Although thinning and fire restoration treatments may seem appropriate in densely stocked interior Douglas-fir stands that now occupy historic open canopy forests, too little is known about how these forests will take to low-severity prescriptions. Studies on fire effects on soils, plants, microbial propagules, wildlife habitat, and watersheds in overgrown interior montane zone forests should be undertaken before large scale fire restoration activities are implemented. Furthermore, the dense accumulation of snags and logs over time, have come to provide key habitat functions which should be taken into account by resource managers when developing plans to recondition these forests (Wisdom et al., 2000).

As stand composition and structure has shifted, so too has changes to fuel complexes. Although a few studies have started to address the influence of DFB on fuel complex alterations, the inherent variability of interior Douglas-fir stands which range across xeric to mesic gradients and between lower montane and subalpine zones collectively influence forest fuel conditions as well. Further research on the effects of DFB in geographic locales occupied by interior Douglas-fir that have not yet been studied, will help contribute to a better understanding of how these insects affect fuel complexes in lower interior montane forest environments in regards to future fire potential. Defoliators including WSBW and DFTM are suspected to reduce overall canopy fuels while subsequently removing seedlings and saplings in the understory which are typically incorporated into a ladder fuel matrix. In intuitively this would reduce the risk of high-severity crown fires. More field studies and research into this hypothesis is needed to provide fire managers with quantitatively supported knowledge on how defoliated stands might react during a fire event. Furthermore, the effects of compound overlapping disturbances which affect both overstory and understory canopies (e.g. DFB and WSBW outbreaks) need to be studied to discern how these two disturbance agents affect stand structure, biodiversity, and wildlife habitat at the local stand scale (hectare).

The elevation band in which interior Douglas-fir forests are situated, between lower and upper montane zones serve as conduits for perpetuating disturbance into upper elevation forests. For example, red stage DFB infested stands may elevate the risk of crown fire which could then be carried into subalpine environments under extreme fire weather conditions (Jenkins *personal communication*). The interactions between disturbances in different forest types across montane zones have received almost no study. Research in this realm could provide key information as climate change in terms of precipitation and temperature at local, regional, and global scales are expected to influence the occurrence, timing, frequency, extent, and duration of future disturbances (Baker, 1995; Turner et al., 1998). New advances in the use of Landsat time series data coupled with Forest Service Inventory Analysis data (Schroeder et al., 2014), could provide a useful tool for monitoring changes to these forests while locating future at risk areas which could help land managers prioritize areas to allocate resources for intervention.

Conclusion

Interior Douglas-fir forests are the principal forest type in the interior montane zone. These forests are important and unique ecosystems that are highly diverse both structurally and compositionally based on their adaptability to a variety of site conditions and a great latitudinal range covered by Douglas-fir. Natural disturbance processes including fire, insect outbreaks, and pathogens, will continue to have an important role in shaping these forest communities (Fig. 2.4).

In particular, the mixed-severity fire regime will continue to exert a large influence over future developmental dynamics including stand composition and structural arrangements as fire in historic low-severity fire environments become more severe. Consequences of past forest management policies which has promoted the advancement of more insect and pathogen outbreaks, and in turn modifying the susceptibility to future disturbance events (e.g. windthrow, landslides, avalanches), will continue to affect the overall health of these forests.

The diversified nature of interior Douglas-fir forest communities discourages a “one size fits all” approach to manage these environments. The disturbance regime history and present site conditions collectively have a strong influence in the direction, structure, and composition of interior Douglas-fir forests into the future. Depending on implied management actions (e.g. hazardous fuels reduction objectives, wildlife habitat improvement, watershed protection, or insect outbreak eradication programs), a diversified approach in administering these forests will be necessary to meet management objectives while improving the health of these forest environments into the future.

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Fig. 2.1. Geographical distribution of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) outlined in light green, and interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) outlined in light blue. Digital representation of "Atlas of United States Trees" Elbert L. Little Jr. Map produced by U.S. Geological Survey (USGS).

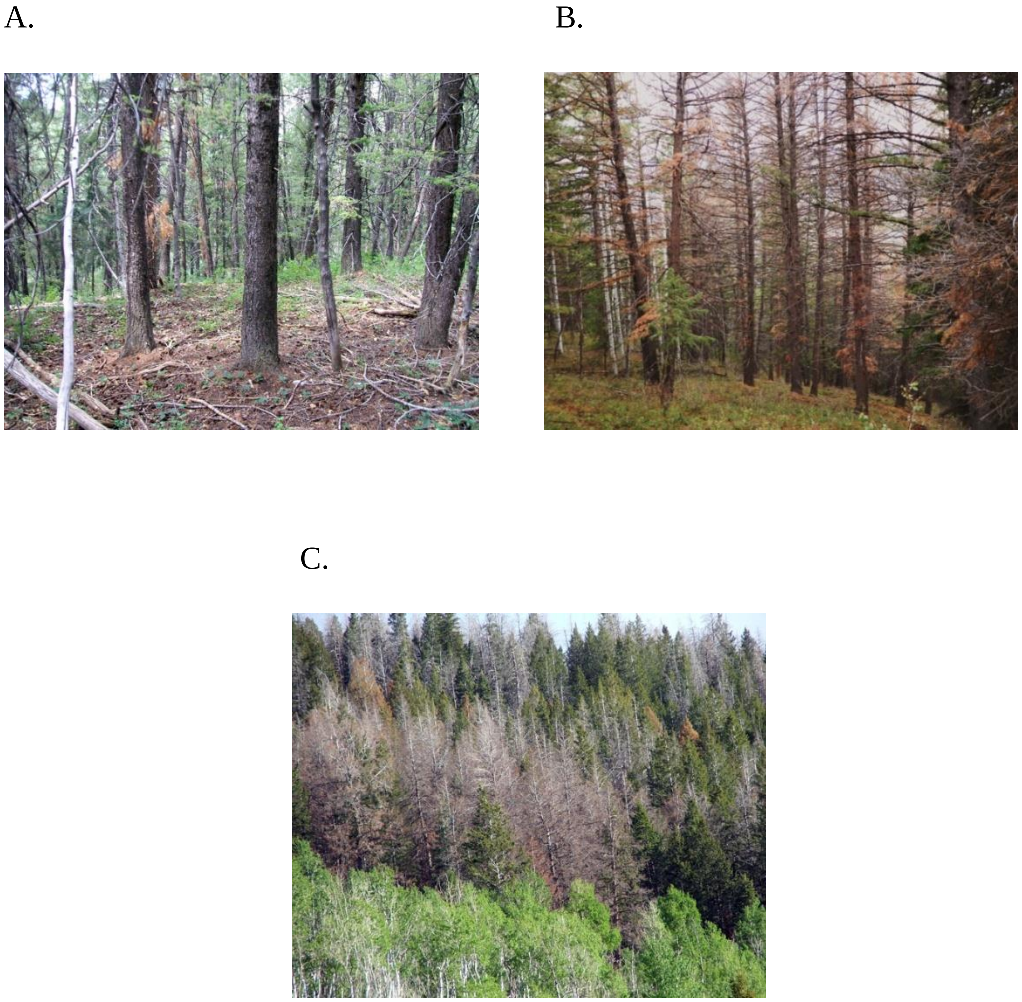

Fig. 2.2. Interior Douglas-fir stand conditions following Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins, Coleoptera: Scolytinae) infestations. (a) green (G), (b) red (R), and (c) gray (GY) stages. Photos by (a) Mike Jenkins, (b) Andrew Giunta, (c) Mike Jenkins.

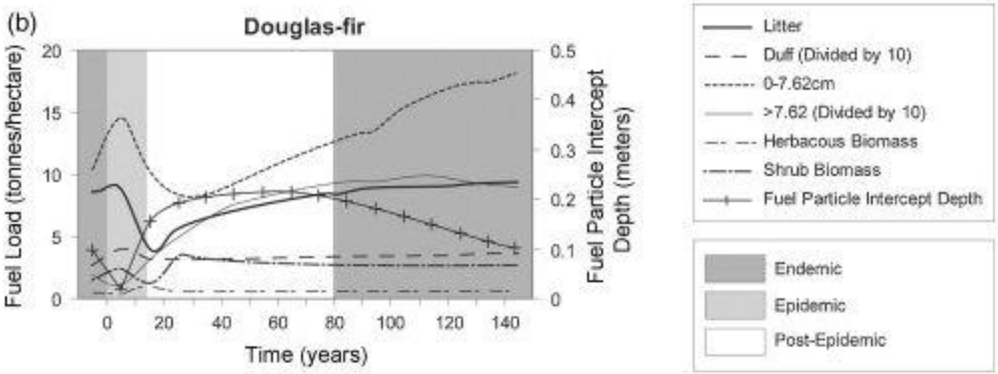

Fig. 2.3. Select fuel characteristic changes in interior Douglas-fir forests over the course of a Douglas-fir beetle rotation. Figures and data from Jenkins et al. 2008.

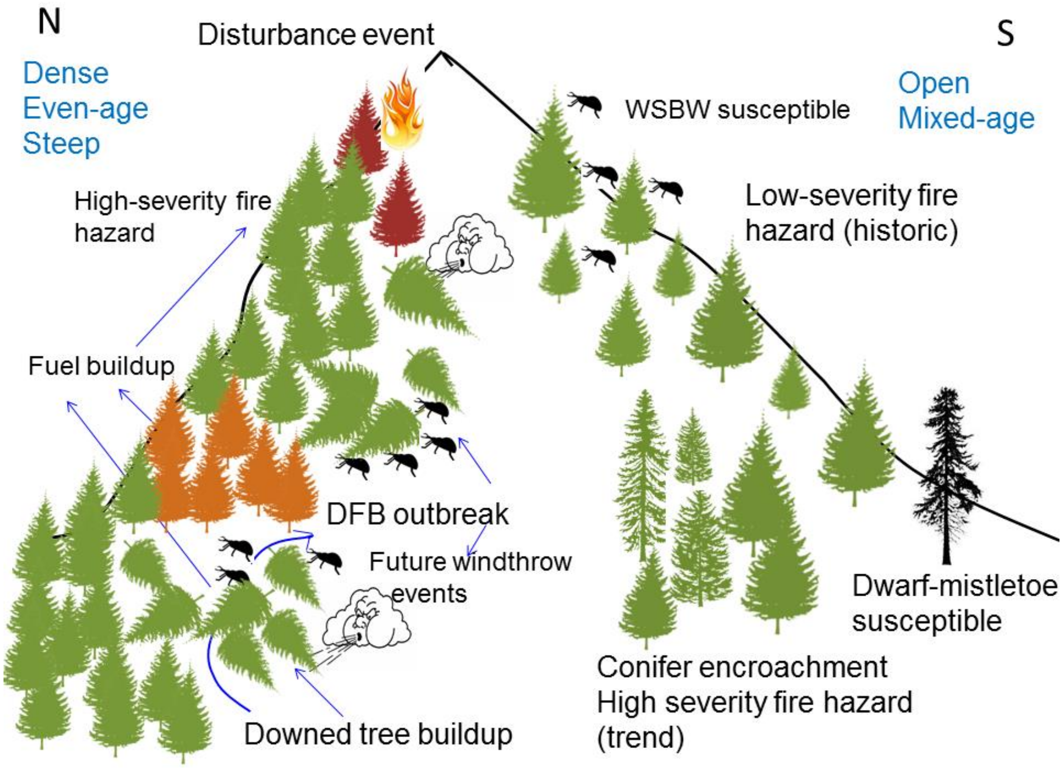

Fig. 2.4. Conceptual schematic of interacting biotic and abiotic disturbance agents and associated forest health issues in interior Douglas-fir forests. On north facing slopes, dense stands are more susceptible to DFB outbreaks which can lead to accumulations of dead and down fuels. This can further escalate future crown fire hazard where these stands are characterized as having a high-severity fire regime. Furthermore, steep north facing slopes > 30˚ are prime slope angles for avalanche releases, which can create a buildup of freshly felled trees increasing DFB outbreak susceptibility. Also, the loss of overstory trees can lead to increased 20 ft. wind speeds making stands more susceptible to windthrow events which provides additional down material for promoting future DFB outbreaks. Douglas-fir stands on south and west facing slopes often have an open canopy composed of mixed-age classes that promote a diverse canopy structure that increases the susceptibility of WSBW outbreaks. On south and west slopes, fire suppression policies implemented during the early 20th century has led to an increase in shade-tolerant conifer encroachment due to decreased incidences of low-severity fire events and lengthening of the fire return interval. This has led to higher host density of Douglas-fir which has increased susceptibility to WSBW, Douglas-fir dwarf mistletoe, and elevated fire hazard from low to high severity due to increased fuel loads. Illustration credit A. Giunta.

CHAPTER 3

DOUGLAS-FIR BEETLE MEDIATED CHANGES TO FUELS AND FOLIAR MOISTURE IN CENTRAL ROCKY MOUNTAIN DOUGLAS-FIR FORESTS

Abstract

Relationships between bark beetle-caused tree mortality and subsequent changes to fuels complexes and fire behavior have been extensively studied over the past decade, principally in upper elevation forests that experience high-severity fire regimes. However, relatively few studies have assessed bark beetle impacts on fuels in middle to lower elevation montane forests. We evaluated changes to ground, surface, and aerial fuels in green, red, and gray stage plots in Douglas-fir (*Pseudotsuga menziesii var. glauca* (Mirb.) Franco) forests following Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae, Scolytinae), infestations. We also examined foliar moisture changes in green, green-infested, yellow, and red tree crowns as a means to indirectly assess crown fire potential. Results from our study revealed slight changes to surface fuels between different outbreak stages, with mean litter depth significantly higher in recently-attacked red stage plots. In aerial fuels, a reduction in canopy bulk density between green and gray plots was detected. Mean seasonal foliar moisture content was significantly higher in green crowns when compared to yellow and red tree crowns. The cumulative effect of Douglas-fir beetle infestations within our study area was minor alterations to surface fuels and significant changes to aerial fuels in terms of both moisture content and loading.

Introduction

Large scale bark beetle outbreaks of multiple species across western North America has led to landscape scale tree mortality covering millions of hectares (Bentz et al. 2010). Forest composition, structure and associated changes to fuel complexes caused by tree mortality, have raised forest health and wildfire hazard concerns for forest and fire managers (Jenkins et al. 2008, 2012, 2014, Black et al. 2013, Harvey et al. 2013). A large growing body of research has evolved focused primarily on lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) and ponderosa pine (*Pinus ponderosa* Lawson) forests infested by mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae)) (Page and Jenkins 2007, Kashian et al. 2011, Hansen et al. 2015), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) forests infested by spruce beetle (*Dendroctonus rufipennis* Kirby) (DeRose and Long 2009, Jorgensen and Jenkins 2011). Although these studies have contributed to a better understanding of the interconnection between bark beetles, fuels, and wildfire, few studies have addressed the impacts of *Dendroctonus* species on fuel complexes in drier, lower to middle elevation montane forest systems that have a characteristic mixed-severity fire regime (Jenkins et al. 2008, Donato et al. 2013). It has been hypothesized that lower montane forests will respond much differently to bark beetle outbreaks based on drier, more open conditions with lower biomass and lower tree-crown base heights (Parker et al. 2006, Hicke et al. 2012, Donato et al. 2013), raising the importance of conducting additional research in these forest systems to better understand future outbreak consequences in terms of changing fuel and fire dynamics.

A common forest cover type in the middle montane zone in the central Rocky Mountains is interior Douglas-fir (*Pseudotsuga menziesii var. glauca* (Mirb). Franco).

These forests are subject to periodic infestations by Douglas-fir beetle (DFB) (*Dendroctonus pseudotsugae* Hopkins) that utilize Douglas-fir exclusively (McGregor et al. 1984, Schmitz and Gibson 1996, Negrón et al. 2001). The nature of DFB outbreaks is dependent upon many factors including stand structure, stand composition, and past disturbance history. Generally, a less aggressive bark beetle species, DFB often persists at an endemic level where beetle populations are low and where breeding is confined to fallen trees or host trees weakened by root rot, drought, lightning, defoliation, and disease (Lejeune et al. 1961, McMullen and Atkins 1962, Powers et al. 1999). Subsequent disturbances including wildfire, avalanches, logging, and windthrow, produce an abundance of freshly felled brood material which supports increased brood production (Christiansen et al. 1987, Cunningham et al. 2005). Following these events, large DFB populations can build to epidemic levels where they are capable of mass attacking healthy live Douglas-fir hosts in high densities (Wright et al. 1984, Fredericks and Jenkins 1988, Negrón 1998). In most cases, DFB-induced tree mortality is patchy, where individual stands do not suffer catastrophic levels of tree death (Negrón et al. 2001). When DFB population numbers are high, adjacent stands can be susceptible, and large outbreaks are possible. Although rare, previous large scale outbreaks have occurred in California in 1966, and in Idaho between 1970 and 1973 causing the loss of millions of board feet of timber (Wright et al. 1984, Schmitz and Gibson 1996).

Previous research into the relationship between DFB and fire has focused on post-fire stand susceptibility to future infestations (Furniss 1965, Amman and Ryan 1991, Cunningham et al. 2005, Hood and Bentz 2007). Few studies to date have addressed the effects of DFB-induced tree mortality on fuel complex changes in interior Douglas-fir forests. Donato et al. (2013) found DFB associated changes in fuel complexes mirrored background variations in stand structure, with a reduction in canopy bulk density (CBD, kg m^{-3}) to be most significant. The Donato et al. (2013) study is representative of Douglas-fir forests in the Greater Yellowstone Ecosystem however, the geographical range of Douglas-fir is extensive, and it is one of the most widely distributed conifers in North America (Silen 1978). Fuel response to insect disturbances including DFB outbreaks are likely to differ across the wide range of stand and sites inherent in Douglas-fir forests (Donato et al. 2013). Studying DFB outbreak influences on fuels in additional different Douglas-fir habitat types within the central Rocky Mountain region will contribute to the knowledge gaps in understanding the dynamics of DFB influences on fuels and fire dynamics.

Once trees are infested by bark beetles, they undergo physiological alterations including changes in foliar moisture content (FMC) (Jolly et al. 2012, Page et al. 2012). Crown FMC alterations occur during the initial phase of an infestation as bark beetle-vectored blue-stain fungi (*Ophiostoma* spp.) penetrate water conducting xylem tissue in the sapwood and block water transport from the soil to the canopy leading to foliage desiccation (Ballard et al. 1984, Lewinsohn et al. 1994, Paine et al. 1997). Combined with larval feeding in the phloem, can lead to rapid tree mortality (Rane and Tattar 1987, Hubbard et al. 2013).

In assessing the potential for crown fire initiation, FMC is often considered an important metric (Van Wagner 1977). Previous studies have shown FMC declines by over 100% from green to red crown phases in other bark beetle infested conifer species (Jolly et al. 2012, Page et al. 2012, 2014a). We hypothesize similar changes should occur within interior Douglas-fir, and to our knowledge no studies have yet quantified FMC change between green, green-infested, yellow, and red crown phases associated with

DFB infestations. This work will further contribute to a better understanding of the physiological changes that affect crown fire potential in DFB infested interior Douglas-fir trees.

The objective of this study was to quantify and compare changes in the characteristics of ground, surface, and aerial fuels following DFB infestations in forests representing three outbreak stages; endemic (green), epidemic (red), and post-epidemic (gray). Additionally, because of the possible importance of FMC on crown fire potential we also tracked changes in FMC among four crown phases (green, green-infested, yellow, and red) associated with DFB attacks. Based on previous research we hypothesize that the greatest changes in affected fuel complexes would occur in the aerial fuels layer where CBD was expected to decrease between red and gray stage sample plots as this is the period where foliage loss is greatest following needle release. Following the loss of canopy fuel, an increase in herbaceous biomass was expected as light, water, and nutrients become more readily available. Furthermore, FMC of attacked trees (yellow and red tree crowns) was expected to be lower compared to green and green-infested trees where uptake of water for photosynthesis is still ongoing.

Methods

Site Selection and Study Areas

During the summers of 2007 and 2008 a detailed inventory of ground, surface, and aerial fuels was conducted. Twelve separate study sites located on the Ashley and Uinta-Wasatch-Cache National Forests in north-central and northeastern Utah were used in the study (Figure 3.1). Forest community type for all sites was predominantly interior

Douglas-fir with a minor component of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and/or white fir (*Abies concolor* Lindl.) on certain subplots (Appendix B).

Initial site selection for fuel complex inventories was accomplished using Forest Health Monitoring Aerial Detection Survey maps (ADS), with input from local Forest Service personnel. Map polygons showing DFB infestations in northern Utah within 10 years of the onset of the study, were identified as potential study sites. Ground reconnaissance and visual site inspections for DFB presence were conducted to determine if three treatment levels, i.e. green (control), red, and gray stage conditions existed at each proposed site within close-proximity (< 5 km) to each other. Green stage sample plots were classified as those that were non-infested or where less than 5 Douglas-fir trees ha^{-1} were infested (Jenkins et al. 2008). Red stage sample plots consisted of those that had increasing DFB populations where observable signs, including, the presence of frass accumulations, foliage fading, and emergence holes were found in > 50% of the trees in the immediate area of sampling. Gray stage sample plots were classified as those with greater than 50% DFB-induced tree mortality of overstory trees in the immediate vicinity of sampling, and based on presence of past DFB larval galleries and absence of canopy foliage in dead trees. Also, there could be no observable signs of any new infestations in surrounding trees within five years prior to sampling (Jenkins et al. 2008). Sample plots representing the three infestation stages (green, red, and gray) were chosen at each site based on the ecological premise of “space for time” substitution principals outlined by Pickett et al. (1989), which was employed in similar bark beetle-fuel treatment studies (Page and Jenkins 2007, Jorgensen and Jenkins 2011). To reduce potential confounding factors associated with the geographical distance between study sites, individual sites as well as the three sample plots within each site were selected based on similar site characteristics including, age, density (trees per hectare), basal area (Table 3.1), and aspect, elevation, slope, and habitat type (Appendix A). In addition, sites with evidence of other disturbance factors, including fire, avalanches, non-DFB insect infestations, and presence of root disease were excluded.

FMC samples were collected once per week from 24 Douglas-fir trees for 15 weeks during the summer of 2014 in a Douglas-fir stand located on the Caribou-Targhee National Forest infested by DFB beginning in 2011 (USDA Forest Service, ADS). The sampling time period represented a typical western U.S. fire season (June-September). The site was located on a southwest aspect, with a mean slope percentage of 30% and an elevation range between 2239 and 2271 m above mean sea level. Overstory vegetation consisted of an open mixed-aged stand dominated by interior Douglas-fir (100% overstory composition), surrounded by Engelmann-spruce / subalpine-fir mixed with lodgepole pine on the north and east aspects. Stand characteristics included a mean basal area of 41.3 m^2 ha^{-1}, density of 399 stems ha^{-1}, a dbh range of 18.8 to 59.4 cm, and mean tree height of 17.9 m.

Study Design – Fuels Complex

Ground, surface, and aerial fuels were inventoried using a cluster sample design scheme to account for the heterogeneity and the variable attack patterns associated with DFB outbreaks (Dodds et al. 2006a, Dodds et al. 2006b, Negrón et al. 2014). At each site, one sample plot per outbreak stage (green, red, gray), was established and this design was replicated at a total of 12 separate sites. Each sample plot consisted of four individual subplots arranged in a square pattern around one central subplot for a total of five subplots sampled per outbreak stage per site (Figure 3.2). Each central subplot was randomly established within the observed center of mortality for each sample plot, and the distance between the centers of each outer subplot was 43.2 m and the distance from each outer subplot center to the central subplots' center was 30.5 m.

Abiotic site conditions including geographic location, slope, aspect, elevation, and habitat type using classifications based on Mauk and Henderson (1984), were recorded at this point. Stand age was determined by counting annual rings from increment cores taken at dbh from one representative live Douglas-fir 'in' tree from each subplot. The averages from all five subplot tree ages were used to determine age for the sample plot. Percent mortality of Douglas-fir trees per subplot was calculated by dividing the number of DFB infested Douglas-fir per subplot by the total number of Douglas-fir trees on the subplot, multiplied by 100 and expressed as a percent.

Surface Fuel Complex Measurements

Each subplot contained four line transects used for measuring fine and coarse woody dead and down debris. Transects were established at azimuths of 45^0, 115^0, 225^0, and 315^0 from subplot center, and were 19.8 m in length. For the central subplot, transects were established at azimuths of 90^0, 180^0, 270^0, and 360^0 from the central subplot center and measured 19.8 m in length.

Ground and surface fuels including litter / duff depth and fuel height intercepts were measured at intervals of 10.7 and 19.8 m along each transect (Brown 1974). Litter and duff depths were measured separately as duff bulk density is typically twice the amount of litter densities (Chojnacky et al. 2009). Fuel height at each location was measured using an imaginary plane oriented perpendicular to the main transect, and included the distance from the bottom of the litter layer to the top of the highest dead fuel particle measuring less than 7.6 cm in diameter (Page and Jenkins 2007). The average particle height was used to calculate the average fuel bed bulk depth based on taking 63.8% of the average particle height (Albini and Brown 1978). Duff and litter loading was calculated by multiplying the average duff and litter depth along each transect by the respective bulk density factor for each (duff = 8.0 kg m^{-3}; litter = 5.0 kg m^{-3}), based on bulk densities provided for Douglas-fir in Brown (1981), and Brown et al. (1982).

Dead and down surface fuels were collected along each of the four (19.8 m) transects based on the planar intercept technique developed by Brown (1974). All down woody debris consisting of 0 to 0.6 cm (1 h) and 0.6 to 2.5 cm (10 h) diameter fuels were tallied between the 1.5 to 3.4 m mark and the number of 2.5 to 7.6 cm (100 h) diameter fuels were tallied between the 1.5 to 6.1 m marks along the length of each transect. Fuels greater than 7.6 cm in diameter (1000 h) were tallied from the 1.5 m to 19.8 m mark, with the diameters of each fuel particle measured and assigned a decay class on a scale of 1 to 5. A rank of one consisted of down woody debris that was sound with all bark intact to five which was coarse woody debris that was completely rotten (Maser et al. 1979, Sollins 1982, Waddell 2002). A distance of 1.5 m from plot center extending outwards along each transect was left unmeasured due to possible fuel displacement during plot set-up. All surface and ground fuel loading calculations for each size class (e.g.1 h, 10 h, 100 h, 1000 h, and litter and duff) were determined using equations developed by Brown (1974).

Shrub and herbaceous data were collected in 1 m^2 microplots at the 10.7 m and 19.8 m intervals along each transect. Percent cover of live and dead shrubs, and percent cover of live and dead herbaceous vegetation along with average height of both shrub and herbaceous vegetation were recorded. Percent cover estimates were separated into classes based on 10% intervals and based on cumulative species present within each microplot. Live and dead shrub / herbaceous biomass bulk densities were calculated based on the product of the average height, percent cover, and bulk density, using the bulk density factors of 0.8 kg m^{-3} for herbaceous and 1.8 kg m^{-3} for shrubs adopted from Caratti (2004).

Tree regeneration stem counts and stem heights were measured and recorded by species within a 1.5 m fixed area plot inside each subplot center for a total of five regeneration plots per green, red, gray stage per site. Regeneration was stratified based on 0.3 m height class increments up to 3.0 m (Brown et al. 1982).

Aerial Fuel Complex Measurements

Aerial fuels and mortality assessments were collected from each subplot center using a variable radius 20 basal area factor wedge prism. Tree species, dbh, dominance status (dominant, co-dominant, intermediate, suppressed), and condition (‘live green’, and ‘dead’) were recorded for each ‘in’ tree within the variable radius plot. Live green trees were those that had green needles with little to no indication of any biotic or abiotic damage. Dead trees were classified as those killed by DFB. An ocular estimate of the percent of needles (to the nearest 25%) remaining in the crown of each tree was also recorded. Pre-disturbance condition comparison for estimated needle loss was based on using the presence of dead branches still retained in the crown to roughly estimate total un-compacted crown likely present when a tree was still alive and green.

One randomly selected live Douglas-fir ‘in’ tree per subplot, had its height, crown base height, and crown width measured in the field to be used as a representative of crown conditions for each subplot following similar procedure used by Jorgensen and

Jenkins (2011). From this data, tree height, crown ratio (cr), and crown base height for all sample trees were estimated using equations provided by Keyser and Dixon (2008) for use in the Forest Vegetation Simulator (FVS) software program using the Utah variant. These equations use height-diameter relationships developed through a logistic function, and for height, $HT = 4.5 + \exp((B1 + B2)/(dbh + 1.0))$, where B1=4.5879, B2= -8.9277, and crown ratio, $CR = -1/(1 + \exp(X + N(0, 0.6957))$. Crown base height (cbh) was estimated by multiplying the crown ratio percent by tree height to obtain a crown length which was then subtracted from the total tree height.

Data collected from the field were used to compute estimates of CBD, canopy base height (CBH), and available canopy fuel load (ACFL), which are important canopy fuel characteristics related to crown fire initiation and spread (Van Wagner 1977, Alexander 1988, Scott and Reinhardt 2001, Scott 2006, Reinhardt et al. 2006). For this study, CBD was calculated based on the estimated dry weight of foliage per unit area divided by canopy length (Keane et al. 2005), which was initially derived using the Canopy Fuel Stratum Characteristics Calculator developed by Cruz et al. (2003). This method uses species specific regression equations linked with stand level data including basal area (m^2 ha^{-1}), mean stand height (m), and stem density (trees ha^{-1}) to calculate CBD based on crown foliage biomass divided by the mean length of the canopy fuel stratum (Cruz et al. 2003). One disadvantage of using Cruz et al. (2003) method is that it does not incorporate partial foliage loss in individual trees that naturally occurs as successfully attacked trees shed their needles.

To gain an additional representation of aerial fuels in each outbreak stage sample plots including the amount of foliage loss, a second approach involving hand calculations of CBD was employed and compared to the Cruz et al. (2003) method. Hand calculations of CBD were based on the crown weight equations developed for western conifer tree species by Brown (1978). Crown weights for each ‘in’ tree were calculated using species, dbh, and crown dominance with the appropriate equation. Crown weights were then corrected by the percent of needles remaining for each ‘in’ tree to obtain an accurate estimate of foliage loading, which was divided by average crown length to obtain an estimate of CBD per plot. It has been noted that forest stands do not typically have a uniform distribution of canopy fuels which is the underlying assumption when calculating CBD using a foliage load over canopy length approach (Scott and Reinhardt 2001). To account for this, a third computation of CBD was generated using the Fire and Fuels Extension (FFE) in FVS (Reinhardt and Crookston 2003). This method is based on using the maximum value of the 4 m running average weight of crown fuel to derive CBD and incorporates both foliage and fine branch wood (0-0.6 cm in diameter) (Rebain et al. 2010). Calculations of mean CBH were derived by entering stand characteristics (tree height, dbh, species) into the FFE-FVS program which uses a minimum CBD threshold of 0.011 kg m^{-3} to compute CBH values. ACFL was also calculated using Canopy Fuels Stratum Characteristics calculator developed by Cruz et al. (2003).

Foliar Moisture Content Sampling

FMC measurements were collected weekly from early June to late September during the summer of 2014. Collections were made in the four crown phases associated with bark beetle infestations, including, non-infested (green, G), current years infestation (green-infested, GI), previous year infestation (yellow, Y), and two years post-infestation (red, R) (Amman 1982, Wulder et al. 2006, Jenkins et al. 2008) following methods developed by Page et al. (2012, 2014a). A total of 24 trees were included in the study, six in each of the four crown condition phases. Initially only 18 trees (six G, six Y, and six R) were sampled in early June before the DFB flight period, i.e. green-infested trees were not available. To ensure that GI trees would be present based on the difficulty with locating newly infested trees, six healthy trees situated near the previous years' attack were baited using one Pherotech DFB lure comprised of 0.3 g of frontalin, 121 g of ethanol, and 0.2 g of seudenol applied 1.8 m above ground on the north aspect of each tree bole. Sample trees included in the study were selected based on similar height, dbh, dominance status (co-dominant) and located on similar aspects, slope, and elevation within the study area. The mean dbh of selected trees were, G (46.0 cm), GI (39.6 cm), Y (49.3 cm), R (47.8 cm), and mean heights were, G (18.1 m), GI (15.4 m), Y (17.3 m), and R (21.8 m). Sampling took place between the hours of 1000 and 1800. Prior to the start of each sampling period, temperature and relative humidity were measured using a sling psychrometer.

Three subsamples of approximately 20 to 40 g of foliage were collected from three separate randomly selected branches from the lower one-third of each tree crown. Needles were removed from the branches and separated into current year's needle growth and old needles (determined by color, texture, and location of previous year's terminal bud). The fresh wet weight of each needle sample was measured using an AWS SC-2kg digital scale before being labeled, placed in plastic bags, and transported back to the lab. All branches less than 0.6 cm diameter leftover from needle removal were combined from the three subsamples per tree, weighed, and returned to the lab (Page et al. 2012). Needles and branch samples were placed in a forced-air drying oven set to 60^0 for 24 hours, then re-weighed to obtain a dry weight. Foliar moisture content was expressed as the percent of oven-dry weight (Jolly and Hadlow 2011). Due to damage to some of the current year's needle samples during the drying process, only old needle samples were analyzed.

Data Analysis- Fuel Complexes

Data were analyzed using a randomized complete block design with site as a blocking factor and three treatment levels based on outbreak severity (green, red, and gray). It should be noted, treatment levels were not truly randomized, but constrained to each block based on outbreak dynamics per site. Response variables included forest structure data (basal area, tree density, quadratic mean diameter) and surface and canopy fuel parameters (1 to 1000 h timelag classes, herbaceous, shrub, CBD, CBH, and ACFL load). Each response variable was averaged over each of the five subplots contained within each sample plot to produce an average per sample plot per site, i.e. for each outbreak stage. Sample plot means per outbreak stage were then combined for all twelve sites to determine if significant differences existed for each fuel complex variable between each outbreak stage. All data were analyzed using the software program SAS (version 9.4). Analysis of age, total basal area, Douglas-fir basal area, total stem density, and quadratic mean diameter per sample plot for each site were run, to determine if significant differences in background sample plot stand characteristics existed between outbreak stages (Table 1). One-way ANOVA using the Proc Glimmix procedure was utilized to compare the sample means between green, red, gray stages for each fuel variable of interest. All tests of significance were performed at an α level of 0.05. When required, log transformations were used to meet linear mixed model assumptions for normality and equal variances. Standard errors of the estimates were reported as necessary.

Data Analysis- Foliar Moisture Content

For FMC data, the three subsamples of old foliage from each sample tree in each crown phase, were averaged to obtain an overall mean for each tree for each sampling period. A total of 15 sampling periods were completed and used for foliar moisture comparisons. Repeated-measures analysis of variance using the Proc Glimmix procedure was used to identify any significant differences in mean foliar moisture response between crown condition phases and across time with crown condition phase and sampling date set as fixed effects. To account for the appropriate covariance structure, the models that minimized Akaike's information criterion were selected, which included, autoregressive with random effect (AR1+RE) structure and compound symmetry (heterogeneous) structure. Cube root transformations were employed to meet assumptions of normality and homogeneity of variance. Tests of significant differences between crown condition phases were carried out using a post-hoc means comparison approach with the experimental-wise error rate controlled using the Tukey-Kramer method.

Results

Fuels Complex- Stand Characteristics

Utilizing study sites with similar characteristics can reduce the influence of confounding factors associated with stand conditions when evaluating the impact of bark beetle effects on fuel complexes across different outbreak time periods. Background site characteristics including age, total basal area, Douglas-fir basal area, total stem density, and average quadratic mean diameter (cm) were not significantly different between green, red, and gray sample plots (Table 3.1).

Following successful DFB infestations, significant changes in the quantity of Douglas-fir based on basal area and tree density were discovered. The percentage of Douglas-fir mortality induced by DFB increased significantly ($P<0.0001$) from green (5%) to gray (55%) plots. Consequently, a significant difference in dead Douglas-fir tree density was found between green and gray stage plots. Green stage plots had the lowest mean number of dead Douglas-fir and the highest number of live Douglas-fir, while gray stage plots had the highest mean number of dead Douglas-fir trees and the lowest numbers of live Douglas-fir (Table 3.1). Live Douglas-fir basal area was also greatest ($P=0.0001$) in green plots, followed by red and gray stage plots.

Fuel Complex- Ground and Surface Fuels

DFB-induced alterations to ground and surface fuels were found to be minor across each infestation stage (Table 3.2). In the surface fuels layer, a significant increase in litter loading and depth was detected between green and red stage sample plots, but not between the green and gray plots. Understory response resulted in a significant increase in live herbaceous biomass between green and gray sample plots (Figure 3.3). Tree regeneration including mean number of stems per plot and mean regeneration height failed to show any statistically significant differences between outbreak conditions (Table 3.3). Species composition per outbreak stage is provided in Table 3.4. A detailed analysis and comparison of ground and surface fuels for each outbreak stage is provided in Table 3.2.

Fuel Complex- Aerial Fuels

Statistical analysis of the aerial fuel components within the fuels complex revealed significant changes between green, red, and gray sample plots. Stand level mean CBH was significantly lower in gray plots compared to green plots (Table 3.5). Estimates of CBD were significantly higher in green plots compared to gray plots based on the Brown (1974), Cruz et al. (2003) and FFE methods. The mean amount of ACFL was 43% greater in green plots compared to gray plots.

Foliar Moisture Content

Considerable variability in mean FMC was discovered between all crown condition phases over the course of the study (Figure 3.4). Green and GI crowns recorded their lowest FMC, 78% and 70% respectively, during the month of June, which was associated with the spring dip (Philpot and Mutch 1971, Jolly et al. 2014a). Moisture content in needles of G crowns had a sharp decline (13%) between sample periods (June 25 and July 7), before steadily increasing to 104% by early August and then declining through late August. Foliage from GI crowns exhibited a similar trend. Significant differences (P<0.0001) in mean FMC were detected between G and GI crowns for all sample periods except for June 18 (P=0.40), September 20 (P=0.70), and September 28 (P=0.90).

The FMC of Y foliage was significantly lower (P<0.0001) when compared to G and GI crowns throughout the entire sampling period. Yellow crowns reached a low FMC of 3% on July 22 and a high of 19% at the end of September. Trees with R crowns had the overall lowest mean FMC when averaged across all sampling periods. There was a significant difference (P<0.0001) in mean FMC between the R and Y crown classes for six out of 15 sampling periods (Table 3.6). Overall, when averaged across all sample periods, there was a significant difference (P<0.0001) in FMC among all crown phases.

Mean moisture content of small diameter (<0.6 cm) twigs was significantly different (P <0.0001) between crown phases when averaged across all sample periods (Table 3.7). Twigs from G and GI crowns were not significantly different (P=0.58), but were significantly different (P <0.0001) from Y and R crowns. Twigs from Y crowns reached a low moisture content of 9% on July 15, while twig moisture content from R crowns reached a minimum of 7% on July 22 (Figure 3.5). June 10th and September 20th were the only sample periods were Y and R twig moisture were significantly different (P=0.01).

Discussion

Stand Characteristics

Stand characteristics including basal area, overstory host density, and dbh are primary factors that influence stand susceptibility to bark beetle outbreaks (Fettig et al. 2007). Stand structure modifications attributed to DFB infestations in green, red, and gray interior Douglas-fir outbreak stages at our study sites, were consistent with results from similar DFB studies reported by Furniss (1979), Negrón et al. (1999), and McMillin and Allen (2003). These changes included reductions in live Douglas-fir basal area and reductions in the number of live Douglas-fir stems following DFB infestations. Overall stand characteristics attributed to DFB susceptibility are provided in the Appendix A. This pattern of an increase in dead host trees following bark beetle infestation is not surprising where similar findings have been reported for more well studied upper-elevation lodgepole pine (Klutsch et al. 2009, Peltz and Smith 2012), and lower montane ponderosa pine forests (Negrón et al. 2009, Hoffman et al. 2012). In limited cases under red stage conditions, DFB outbreaks may result in nearly one hundred percent mortality of suitable host trees (Furniss and Carolin 1977), however, this level of mortality was not observed at our study sites, where red stage sample plots reached a maximum mean percent mortality of 62%.

Ground and Surface Fuels

The results from our study indicated DFB infestations resulted in only minor changes to ground and surface fuels at our study sites. The loading of dead and down woody debris for all timelag classes (1 to1000 h) varied little between outbreak stages. Similar findings were reported by Donato et al. (2013), aside from their detection of a significant increase in sound 1000-h fuel loads in stands (25-30 yr) post infestation. The gray stage plots sampled for our study were five to ten years post-outbreak with the majority of trees classified as standing dead. A possible discrepancy between our results and their findings could be a result of differential snag fall rates between study areas and time since outbreak when coarse wood material was sampled. The structural and compositional complexity of interior Douglas-fir forests are regulated by wide variations in disturbances and their adaptability to a wide range of site conditions (Daubenmire and Daubenmire 1968, Pfister et al. 1977, Simard 2009). These circumstances likely have a stronger influence over dead and down fuel loads as opposed to direct alterations initiated by DFB. These results are in contrast to findings in higher elevation, mesic forest ecosystems including lodgepole pine and Engelmann spruce, where significant increases in dead and down woody fuels, and shrub and herbaceous fuel loading levels have been detected over time from initial onset of a bark beetle infestation (Romme et al. 1986, Page and Jenkins 2007, Schoennagel et al. 2012).

One component of the surface fuels layer that was significantly altered following DFB infestations was the litter layer. Litter depths were 79% higher in red stage sample plots compared to green plots, and 48% higher compared to gray plots. Also, the amount of litter loading was significantly higher in red stage sample plots to green sample plots. Shifts in litter loading could be attributed to the loss of foliage following the inoculation of host sapwood with blue-stain fungi transported via burrowing bark beetles, which leads to the disruption of water transportation processes between root systems and foliage (Rane and Tattar 1987). Without an adequate supply of moisture, active photosynthesis ceases and needle desiccation occurs creating a buildup of dead canopy foliage that is released as a pulse of litter to the forest floor during the red stage (Jenkins et al. 2012, Donato et al. 2013).

Increases in the litter component of a fuels complex is important because these fine fuels are highly flammable and are often completely consumed during the passage of an active flaming front, and contribute to surface fire spread (Kauffman and Martin 1989). This effect will only persist where weather conditions are conducive for fire ignition and spread. Although a part of the ground fuels layer, initial decomposition from increased litter deposition had little effect on changes to duff layers because they typically build up slowly over many years (Baker 2009). In other dry montane forests, Hoffman et al. (2012) also found no significant change in duff levels between non-mortality and mortality plots seven years post-outbreak following bark beetle infestations in ponderosa pine. It should be noted, ponderosa pine forests are typically drier compared to middle montane interior Douglas-fir forests, where decomposition rates that contribute to duff layering would likely be lower.

The structure of the understory was also impacted by DFB infestations. Significant increases in the amount of live herbaceous biomass were measured in gray stage sample plots. These findings support similar results by McMillin and Allen (2000) who found a three-fold increase in the abundance of herbaceous plants in infested Douglas-fir plots compared to non-infested plots. Donato et al. (2013) also measured a significant 50% (0.5 Mg ha^{-1}) increase of herbaceous biomass, but this effect was not detected until the silver stage (25-30 years post-outbreak). The increase in understory herbaceous and shrub biomass has also been observed in lodgepole pine (Page and Jenkins 2007), ponderosa pine (McCambridge et al. 1982), and spruce forests following bark beetle outbreaks (Veblen et al. 1991, Jorgensen and Jenkins 2011).

A reduction in canopy cover from the loss of overstory trees decreases the amount of solar radiation and precipitation intercepted by the canopy leading to, “increased sunlight and water available in the soil surface” (Edburg et al. 2012 p.420) and results in releases of nutrients into a stand (Veblen et al. 1991). With these resources becoming more available, we expected to see an increase in the density of regeneration (number of seedlings / saplings < 3 m in height) in gray stage plots. No significant differences were found for this fuel component when compared between the three outbreak stages. Harvey et al. (2013) found variable rates of regeneration of Douglas-fir following DFB infestations, though it should be noted their work was also based on compound disturbances of bark beetle outbreaks and fire, where fire burn severity can exert a strong control over vegetation reestablishment (Johnstone and Chapin III 2006, Baker et al. 2007). Ultimately the amount of mature cone producing trees killed by bark beetles will influence the rates of tree regeneration where Douglas-fir lack a serotinous cone stock and the level of regeneration is in part dependent upon the survivorship of annual cone crops where, “seeds are shed annually during autumn and winter” (Larson and Franklin 2005, p. 32).

Aerial Fuels

The importance in characterizing canopy fuels in a stand is to help determine the likelihood of crown fire initiation and spread (Reinhardt et al. 2006, Clark et al. 2010). Three main metrics, CBD defined as mass of available canopy fuel per unit volume, CBH defined as the lowest height above the ground at which there is sufficient canopy fuel to propagate fire vertically through the canopy, and available canopy fuel load ACFL which accounts for the potential energy release from canopy fuels, are important in assessing crown fire potential (Call and Albini 1997, Scott and Reinhardt 2001, Ruiz-González and Álvarez-González 2011).

Based on limited direct sampling of tree metrics (tree height, crown ratio, and crown base height), we had to rely on using estimates for these measurements derived from height diameter logistic equations developed in FVS using the Utah variant. We acknowledge the use of estimates could lead to error rates that are likely underestimated. Future studies with field collected tree measures would greatly improve predicting CBD, CBH, and ACFL changes between DFB infested forests across different outbreak time periods and would help verify the accuracy of our estimates.

Changes to canopy fuels between green, red, and gray stage sample plots were detected at our study sites following DFB infestations. One of the most prominent changes to canopy structure over the course of a bark beetle outbreak is a reduction and loss of crown foliage in infested trees (Jenkins et al. 2008). Both the Cruz et al. (2003) and Brown (1978) methods for assessing CBD revealed significant reductions in CBD between green and gray stage plots. Although not directly compared to the other methods because of its incorporation of 1-h fuels into its calculation, the FFE-FVS approach also showed a significant reduction in CBD between green and gray sample plots, which supports previous findings (e.g. Page and Jenkins 2007, Jorgenson and Jenkins 2011, Donato et al. 2013), that bark beetle outbreaks do cause reductions in canopy foliage leading to decreases in CBD and ACFL estimates. In green stage plots, the higher percentage of basal area represented by live overstory Douglas-fir contributed to significantly higher CBD and ACFL measures. ACFL was found to be 40% higher in green plots compared to gray plots. The substantial reduction over time in CBD and ACFL was related to the fact that the gray stage five to ten years post outbreak had the highest levels of overstory mortality where these trees are devoid of needles, twigs, and small branches comprising small diameter (<0.6 cm) fuels. It would be expected that crown fire hazard would diminish in gray stage plots due to the loss of potential combustible material in the canopy layer.

The lack of any significant change in the amount of regeneration between outbreak stages indicates DFB had little effect on altering the distribution of ladder fuels at our study sites which are important for serving as a conduit for fire movement from surface to the canopy layers (Menning and Stephens 2007). Any change in torching potential is unexpected until the recruitment of the next generation of seedlings and saplings moves from the surface to canopy level which can take many years following episodic cone crops of Douglas-fir which can range from 1-11 years depending on elevation (Owens 1976).

The findings from this study are similar to those observed by Donato et al. (2013) for CBD and ACFL in Douglas-fir, and also in lodgepole pine, Engelmann spruce, and ponderosa pine following mountain pine beetle and spruce beetle infestations, where CBD, ACFL, and CBH decreases as stand conditions progress from recently infested to five years or more post-infestation (Page and Jenkins 2007, DeRose and Long 2009, Jorgenson and Jenkins 2011, Schoennagel et al. 2012, Hansen et al. 2015).

Foliar Moisture Content

Over the course of an outbreak, DFB infested stands typically contain pockets of infested trees interspersed between patches of un-infested trees. This creates a heterogeneous mix of live and dead crowns composed of live (G, GI needles) and dead (Y, R needles) FMC levels where live fuel moisture is driven by physiological changes within a tree due to soil water relations, evapotranspiration, and foliage desiccation, while dead FMC is driven by diffusion of water between the fuel and surrounding atmosphere, (Jolly et al. 2014b). Both are important factors influencing crown fire initiation and spread in stands susceptible to crown fire activity (Van Wagner 1977, Alexander 2010).

In recent studies both Page et al. (2012, 2014a) and Jolly et al. (2012, 2014a) attributed shortened time to ignition and overall increased flammability in Y and R lodgepole pine and spruce needles following bark beetle infestations with decreased FMC. Flammability tests on Douglas-fir needles from four crown phases associated with DFB outbreaks would help further strengthen the assumption that decreased FMC in Y and R Douglas-fir needles would lead to increased flammability based on quantifiable output. Many current fire behavior models that predict crown fire potential, including, BehavePlus, NEXUS, and FARSITE, are based on models developed by Rothermel

(1972) and Van Wagner (1977). These empirical driven models do not incorporate variability in FMC and stand crown condition heterogeneity following bark beetle outbreaks (Jenkins et al. 2012, Moran et al. 2012, Alexander and Cruz 2013). More recently, the development of physics-based models including, FIRETEC and the Wildland-Urban Interface Fire Dynamics Simulator (WFDS) used to predict wildfire behavior (Hoffman et al. 2015a, 2015b), are capable of operating in three-dimensional space and can theoretically handle the complex crown and canopy fuel conditions found in bark beetle-affected forests. Future use of these models may contribute to a better understanding of the importance of changing FMC on crown fire potential as better, more detailed models of crown fire initiation and spread become refined (Page et al. 2014b).

To our knowledge no previous work has documented seasonal changes in FMC caused by DFB related tree morality. Donato et al. (2013, p.14) acknowledged, “foliar moisture would be reduced for some trees before any needles drop, a 1 to 2 year window that has not yet been reported quantitatively”. Our study is the first to quantify changes in FMC in interior Douglas-fir across the four crown phases (G, GI, Y, and R) associated with bark beetle outbreaks. Although we ultimately were only able to track changes in old needles, future studies where both current year’s growth and old needle FMC values from G, and GI trees are measured will contribute to the lack of knowledge about FMC changes in DFB infested trees. Our results showed trees in the Y and R crown phases had significantly lower FMC values, compared to G and GI trees. These phases occur over the course of 1 to 2 years following initial DFB attack where a lack of adequate moisture leads to reduced photosynthesis and needle desiccation. Foliage fades from G to Y and eventually R by the second year post attack (Amman 1982). It is during the R phase where the probability of torching and crowning may be increased because FMC is reduced but dead needles are still retained in the canopy (Page et al. 2014b).

By the end of the sampling period (late September), GI trees had an average moisture content loss of 9% compared to G trees, while an average moisture reduction of 114% occurred between GI and Y trees. The bulk of moisture loss between GI and Y phase trees is assumed to occur between the fall and spring following the period of infestation, although to validate this hypothesis, further work though field sampling and analysis is necessary. The moisture content of fine branches (<0.6 cm) in diameter followed the same trend as foliage, where G twigs retained higher moisture content levels compared to twigs from R crowns which had the lowest FMC values. The results from this study support previous research in lodgepole pine and Engelmann spruce where G foliage was found to have the highest FMC values with a significant reduction in moisture content as trees receded from GI to R crown phases (Page et al. 2012, Jolly et al. 2012, Page et al. 2014a). It should be noted that extrapolation of this data should be limited to the vicinity of this study area, and additional foliar moisture studies in multiple DFB infested stands where new and old foliage classes are measured will provide additional insight into the nature of FMC changes across different DFB infested crown phases.

Conclusion

The objective of this study was to quantify aerial and surface fuel changes between green, red, and gray stages of a DFB outbreak in interior Douglas-fir. Detailed fuel assessments were conducted at 12 separate study sites to determine the impact DFB has on modifying interior Douglas-fir fuel complexes. We found that over the course of an outbreak, the amount of live basal area composed of overstory Douglas-fir is reduced while the number of Douglas-fir snags associated with DFB infestation increases, reaching a high in gray stage plots. Although no significant changes in the amount of coarse woody fuels between each stage were detected, other fuel components were significantly altered. After initial infestation, the moisture content of tree crowns declines following the disruption of xylem transport systems (Rice et al. 2007). By the second year post-infestation, foliage moisture content levels reached their lowest point possibly elevating the crown fire hazard during this period. Following tree mortality, a release of fine fuels, especially needles, are transferred from the aerial to surface fuels layer resulting in a significant build-up of needle litter on the forest floor. With a newly opened canopy, an increase in herbaceous biomass follows into the gray stage. During this time, important stand characteristics including CBD and ACFL, which are important metrics for assessing crown fire initiation and spread, are reduced, which could potentially decrease active crown fire potential. A buildup of 1000 h sound and rotten fuels is expected over time as snag fall rates increase which will contribute to future surface fuel loads.

The results from this study supplement both, previous research which looked at the role of bark beetles in modifying fuel complexes in middle montane forest ecosystems (Donato et al. 2013), and recent studies that measured the post-outbreak response of fuel complexes to fire (Stevens-Rumann et al. 2015). Furthermore, it was the first attempt to quantify FMC changes throughout different crown condition phases in interior Douglas-fir, in association with DFB infestations. Ultimately, the inherent variability of interior Douglas-fir stands which range across xeric to mesic gradients and between lower montane and subalpine zones, and past disturbance history, collectively influence forest fuel conditions. Therefore, our findings are based on site-specific variation in fuel complexes and crown conditions encountered at our study sites, which may limit the generality of assessing DFB impacts in non-related interior DFB forest systems. Further research on the effects of DFB in other interior Douglas-fir habitat types will help contribute to a better understanding of how these insects affect fuel complexes in lower to mid-montane forest environments.

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Table 3.1. Average sample plot characteristics for the 12 study sites for each stage on the Uinta-Wasatch-Cache and Ashley National Forests. Comparisons of characteristics between outbreak stages were calculated using Tukey-Kramer least squares means adjustment for multiple comparisons.

Stand Characteristic	Outbreak Condition	Mean	S.E.	df	F	P	Comparison†	df	t-value	P
Age (yr)	G	113.8^{a}	9.10	22	0.25	0.79	G vs. R		-	-
	R	113.4^{a}	9.70				G vs. GY		-	-
	GY	120.4^{a}	11.4				R vs. GY		-	-
Total BA (m^{2} ha^{-1})	G	31.09^{a}	2.84	22	0.20	0.82	G vs. R		-	-
	R	32.07^{a}	2.36				G vs. GY		-	-
	GY	30.15^{a}	2.21				R vs. GY		-	-
DF Live BA (m^{2} ha^{-1})	G	18.35^{a}	2.88	22	11.5	0.0004	G vs. R	2	4.2	0.001
	R	7.73^{b}	1.01				G vs. GY		4.1	0.001
	GY	8.11^{b}	1.31				R vs. GY		-	-
DF Dead (m^{2} ha^{-1})	G	4.06^{a}	1.27	22	16.0	<.0001	G vs. R	2	2.2	0.04
	R	9.03^{b}	2.17				G vs. GY		4.4	<.001
	GY	17.07^{b}	2.08				R vs. GY		9.1	<.001
Total Trees ha^{-1}	G	491.80	67.6	22	0.40	0.68	G vs. R		-	-
	R	459.91	51.0				G vs. GY		-	-
	GY	425.96	38.4				R vs. GY		-	-
Live DF Trees ha^{-1}	G	309.21	56.4	22	3.41	0.05	G vs. R		-	-
	R	196.63	28.9				G vs. GY		-	-
	GY	170.59	47.8				R vs. GY		-	-
Dead DF Trees ha^{-1}	G	37.86^{a}		22	15.4	0.01	G vs. R	2	-	-
	R	74.13^{b}	17.1				G vs. GY		-5.5	<.001
	GY	146.03	16.9				R vs. GY		-3.6	.041
QMD (cm)	G	31.79^{a}	1.99	22	0.51	0.61	G vs. R		-	-
	R	32.73^{a}	1.86				G vs. GY		-	-
	GY	33.87^{a}	1.90				R vs. GY		-	-
Percent DF	G	5.37^{a}	2.72	22	24.6	<.0001	G vs. R	2	-6.5	<.001
	R	61.50^{b}	5.19				G vs. GY		-5.5	<.001
	GY	55.20^{b}	4.50				R vs. GY		-	-

* G = Green, R = Red, GY = Gray, QMD = Quadratic mean diameter; DF = Douglas-fir; BA = Basal area
Superscript letters indicate test of significance based on Tukey-Kramer pairwise comparisons using one way ANOVA tests. Different lowercase letters indicate statistically significant differences at the α =0.05 level

†Pairwise comparisons based on least squares means adjustments for multiple comparisons

Table 3.2. Mean coarse woody debris loads for select ground and surface fuel characteristics for each outbreak stage. Comparisons for each fuel characteristic between stages were calculated using Tukey-Kramer least squares means adjustment for multiple comparisons between each outbreak stage.

Fuel Type	Outbreak condition*	Mean	SE	df	F	P	Comparison†	df	t-value	P
1-hr	G	0.29^{a}	0.04				G vs. R		-	-
(kg m^{-2})	R	0.29^{a}	0.03	22	0.12	0.88	G vs. GY		-	-
	GY	0.30^{a}	0.05				R vs. GY		-	-
10-hr	G	0.87^{a}	0.18				G vs. R		-	-
(kg m^{-2})	R	0.79^{a}	0.14	22	0.28	0.76	G vs. GY		-	-
	GY	0.84^{a}	0.13				R vs. GY		-	-
100-hr	G	1.14^{a}	0.31				G vs. R		-	-
(kg m^{-2})	R	1.36^{a}	0.34	22	0.21	0.81	G vs. GY		-	-
	GY	1.40^{a}	0.34				R vs. GY		-	-
1000-hr-sound	G	1.90^{a}	0.64				G vs. R			
(kg m^{-2})	R	1.11^{a}	0.68	22	1.14	0.34	G vs. GY		-	-
	GY	1.85^{a}	0.95				R vs. GY		-	-
1000-hr-rotten	G	2.82^{a}	0.73				G vs. R		-	-
(kg m^{-2})	R	1.83^{a}	0.60	22	0.16	0.86	G vs. GY		-	-
	GY	2.29^{a}	0.67				R vs. GY		-	-
Litter	G	0.17^{a}	0.03				G vs. R		-3.00	0.02
(kg m^{-2})	R	0.29^{b}	0.04	22	4.57	0.02	G vs. GY	22	-	-
	GY	0.22^{ab}	0.05				R vs.GY		-	-
Litter Depth	G	1.19^{a}	0.20				G vs. R		-2.66	0.04
(cm)	R	1.92^{b}	0.26	22	4.48	0.02	G vs. GY	22	-	-
	GY	1.44^{a}	0.29				R vs. GY		2.51	0.05
Duff	G	0.65^{a}	0.12				G vs. R		-	-
(kg m^{-2})	R	0.75^{a}	0.10	22	0.93	0.41	G vs. GY		-	-
	GY	0.78^{a}	0.10				R vs. GY		-	-
Duff Depth	G	2.58^{a}	0.44				G vs. R		-	-
(cm)	R	2.87^{a}	0.38	22	0.93	0.41	G vs. GY		-	-
	GY	2.96^{a}	0.39				R vs. GY		-	-

*G = Green, R = Red, GY = Gray

Superscript letters indicate test of significance based on Tukey-Kramer pairwise comparisons using one way ANOVA tests. Different lowercase letters indicate statistically significant differences at the α=0.05 level.

†Pairwise comparisons based on least squares means adjustments for multiple comparisons

Table 3.3. Live tree regeneration characteristics for the three outbreak stages G, R, GY

Fuel type	Outbreak condition*	Mean	SE	df	F	P	Comparison†	df	t-value	P
‡ Stems / Plot	G	4.18^a	2.26				G vs. R		-	-
	R	2.58^a	1.05	22	2.04	0.15	G vs. GY		-	-
	GY	3.10^a	1.50				R vs. GY		-	-
Regeneration Height (m)	G	0.25^a	0.10				G vs. R		-	-
	R	0.29^a	0.17	22	0.03	0.27	G vs. GY		-	-
	GY	0.23^a	0.11				R vs. GY		-	-

*G = Green, R = Red, GY = Gray

‡Stem refers to live woody vegetation represented in the overstory and is < 3 m in height

Superscript letters indicate test of significance based on Tukey-Kramer pairwise comparisons using one way ANOVA tests. Different lowercase letters indicate statistically significant differences at the α=0.05 level

†Pairwise comparisons based on least squares means adjustments for multiple comparisons

Table 3.4. Mean number of stems / plot and height (m) of live tree regeneration by species averaged across all sites for green, red, and gray outbreak stages. Species abbreviations are, PSME: *Pseudotsuga menziesii*, ABLA: *Abies lasiocarpa*, ABCO: *Abies concolor*, POTR: *Populus tremuloides*.

Outbreak Condition*	Species	Stems / plot (mean)‡	Avg. Height (m)
G	PSME	11.00	0.25
	ABLA	6.17	0.38
	ABCO	2.25	0.10
R	PSME	6.17	0.35
	ABLA	4.92	0.12
	ABCO	0.75	0.02
GY	PSME	7.83	0.20
	ABLA	3.00	0.08
	ABCO	4.83	0.12

*G = Green, R = Red, GY = Gray

‡Stem refers to live woody vegetation represented in the overstory and is < 3 m in height

Table 3.5. Aerial fuels characteristics for each outbreak stage. Three calculation methods were employed to derive aerial fuel estimates. These methods included hand calculations (Hand) based on Brown (1974) allometric equations, Fire and Fuels Extension in the Forest Vegetation Simulator (FVS), and through the Cruz et al. (2003) equations (Cruz) which incorporate mean stand height (m), mean stand basal area (m^2 ha^{-1}), and mean stand density (trees ha^{-1}) based on cover type. Comparisons for each fuel characteristic between outbreak stages were calculated using Tukey-Kramer least squares means adjustment for multiple comparisons.

Fuel Type	Outbreak Condition*	Mean	SE	df	F	P	Comparison†	df	t-value	P
CBH FVS	G	4.71^{a}	0.59				G vs. R		2.62	0.03
(m)	R	3.88^{b}	0.63	22	9.50	0.0001	G vs. GY	22	4.33	<.0001
	GY	3.32^{b}	0.91				R vs. GY		-	-
CBD Hand	G	0.11^{a}	0.02				G vs. R		-	-
(kg m^{-3})	R	0.07^{ab}	0.01	22	4.43	0.02	G vs. GY	22	-	-
	GY	0.07^{b}	0.02				R vs. GY		2.80	0.02
CBD FVS	G	0.08^{a}	0.02				G vs. R		-	-
(kg m^{-3})	R	0.06^{ab}	0.02	22	4.51	0.02	G vs. GY	22	3.00	0.02
	GY	0.03^{b}	0.01				R vs. GY		-	-
CBD-Cruz	G	0.13^{a}	0.02				G vs. R		-	-
(kg m^{-3})	R	0.09^{b}	0.01	22	4.89	0.02	G vs. GY	22	3.12	0.01
	GY	0.07^{b}	0.01				R vs. GY		-	-
ACFL Cruz	G	0.82^{a}	0.12				G vs. R		-	-
(kg m^{-2})	R	0.60^{ab}	0.06	22	6.67	0.0054	G vs. GY	22	3.65	0.0039
	GY	0.40^{b}	0.04				R vs. GY		-	-

*G= Green, R = Red, GY = Gray

CBH = Canopy Base Height, CBD = Canopy Bulk Density, ACFL = Available Canopy Fuel Load

Superscript letters indicate test of significance based on Tukey-Kramer pairwise comparisons using one way ANOVA tests. Different lowercase letters indicate statistically significant differences at the α=0.05 level.

†Pairwise comparisons based on least squares means adjustments for multiple comparisons

Table 3.6. Mean and (+ / -) standard error percentage of oven-dried foliar moisture content between yellow and red crown condition classes across all sampling periods (June-September 2014).

	Yellow		Red	
Date	Mean	S.E.	Mean	S.E.
10-Jun	6.98^{a}	1.05	3.52^{b}	0.36
18-Jun	9.18^{a}	0.78	6.36^{a}	0.23
25-Jun	7.24^{a}	0.75	4.93^{b}	0.17
30-Jun	5.93^{a}	0.53	5.31^{a}	0.25
7-Jul	4.66^{a}	0.50	4.69^{a}	0.30
15-Jul	3.82^{a}	0.40	3.48^{a}	0.16
22-Jul	3.37^{a}	0.36	3.53^{a}	0.27
29-Jul	7.53^{a}	0.55	6.15^{b}	0.40
7-Aug	9.91^{a}	0.73	9.74^{a}	0.25
13-Aug	9.86^{a}	0.29	8.91^{a}	0.70
30-Aug	11.50^{a}	0.69	8.02^{b}	0.46
8-Sep	7.21^{a}	0.47	8.69^{b}	0.44
13-Sep	11.50^{a}	0.69	8.02^{b}	0.46
20-Sep	8.10^{a}	0.37	8.58^{a}	0.21
28-Sep	19.01^{a}	0.68	17.43^{a}	0.74

Means with a different letter in each row represent sampling periods where foliar moisture content is significantly different between each crown condition class at (α=0.05).

Table 3.7. Mean and (+ / -) standard error percentage of oven-dried foliar moisture content and fuel particles <0.64 cm diameter, averaged across all sampling periods (June-September) for each crown condition class.

	G	I	Y	R
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Foliage (%)	94.95^a ± 2.43	86.0^b ± 2.60	7.89^c ± 0.59	6.70^d ± .36
Twig <0.64 cm (%)	88.24^a ± 2.27	87.36^a ± 2.60	13.75^b ± 0.89	10.08^c ± .66

Means followed by a different letter in each row represent significant differences in foliar moisture content between crown condition classes at (α=0.05).

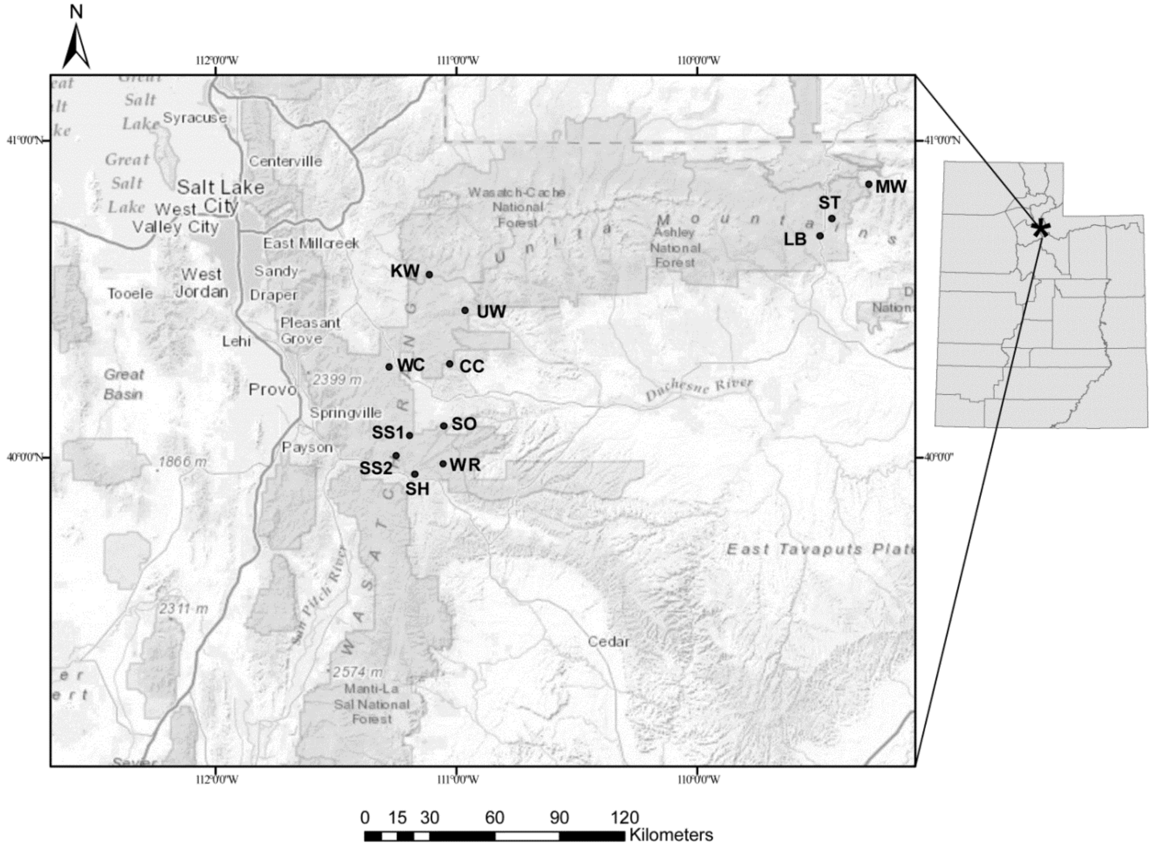

Figure 3.1. Map of the twelve study sites on the Ashley and Uinta-Wasatch-Cache National Forests in north-central and northeastern Utah. Each site consisted of one green, one red, and one gray outbreak stage sample plot denoted by the dark circles. Site abbreviations defined as, CC: Currant Creek, KW: Kamas Woodland, LB: Little Brush, MW: Matt Warner Reservoir, SH: Scofield Highway, SO: Strawberry Reservoir, SS1: Soldier Summit 1, SS2: Soldier Summit 2, ST: Steinaker Reservoir, UW: Uinta-Wasatch, WC: Wasatch-Cache, WR: White River.

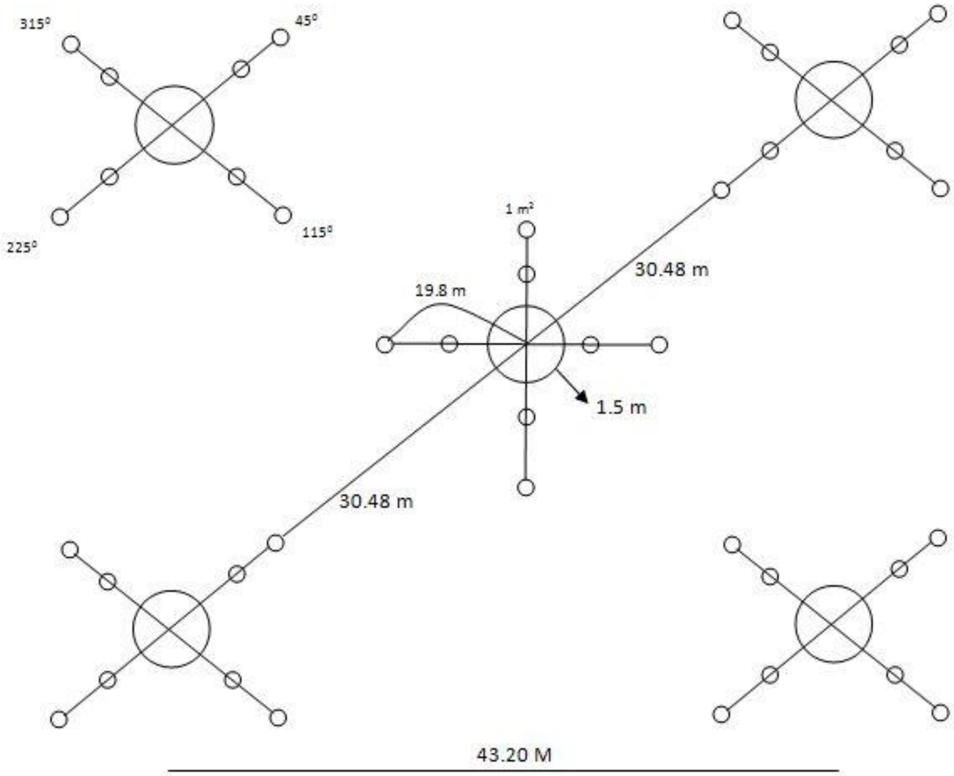

Figure 3.2. Fuels complex sampling layout for each outbreak stage. Each sampling cluster contained four subplots arranged in a square pattern with a fifth subplot established in the center of the square pattern. For the four corner subplots, four 19.8 m long transects were laid out at azimuths of 45^0, 115^0, 225^0, and 315^0 from each subplot center. Transects on the central subplot were established at azimuths of 90^0, 180^0, 270^0, and 360^0 from subplot center and each measured 19.8m. Subplots along each transect measured 1 m^2. Total distance between each outside subplot is 43.2 m, and the distance between each outer subplot center to the central subplot center is 30.5 m.

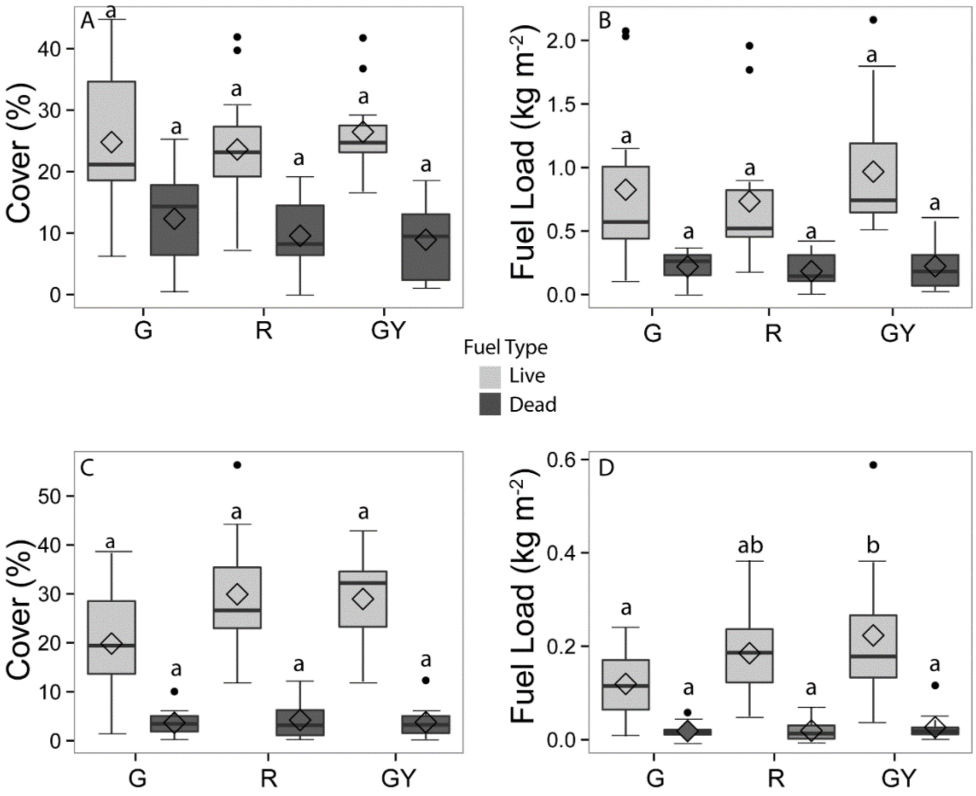

Figure 3.3. Live and dead shrub and herbaceous fuel loading for each outbreak stage; green (G), red (R), and gray (GY) averaged across all 12 study sites with associated standerd error bars. Graph A is percent cover of shrubs; graph B is shrub fuel loading; graph C is percent cover herbaceous; graph D is herbaceous fuel loading. Different lower case letters indicate significant differences at (α =0.05) level.

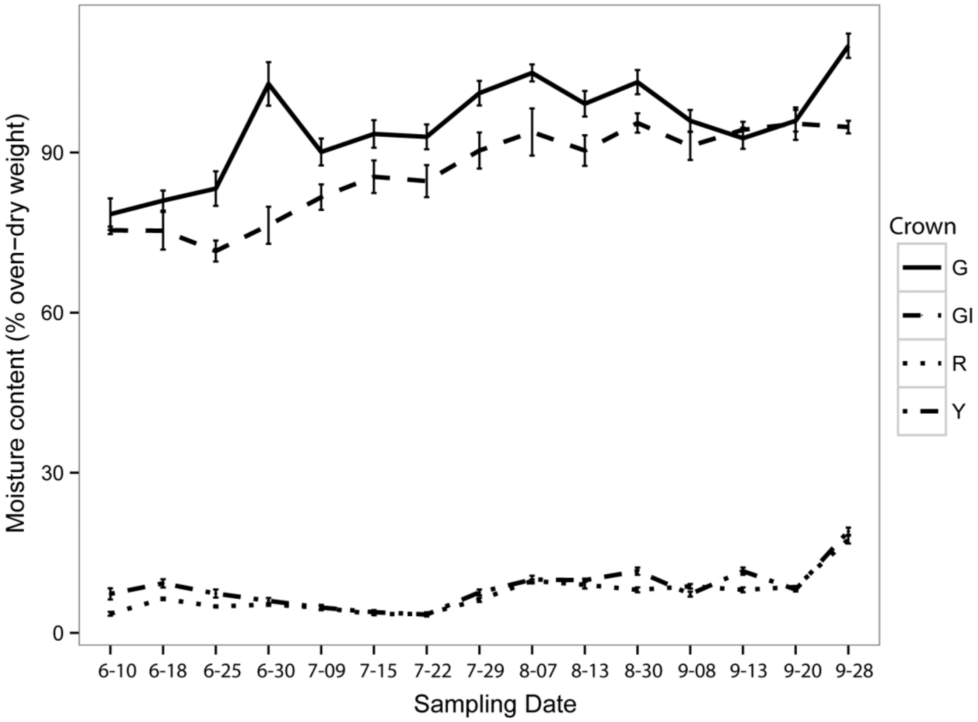

Figure 3.4. Mean foliar moisture content for green (G), green-infested (GI) yellow (Y), and red foliage (R) for all sampling periods (June-September), with associated standard error bars.

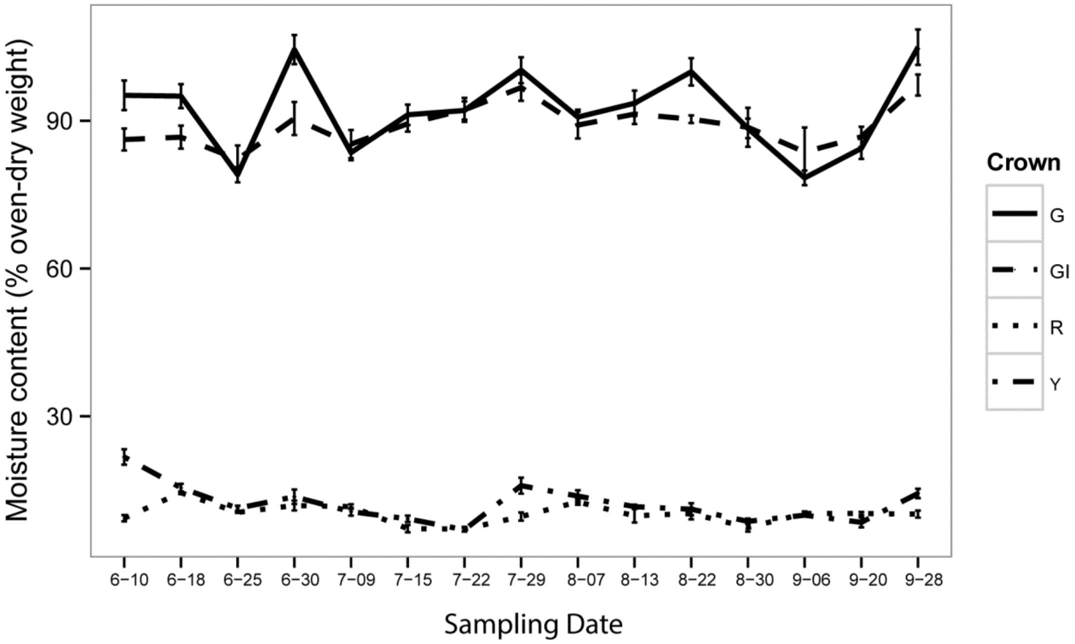

Figure 3.5. Mean moisture content of small diameter (<0.6 cm) woody aerial fuels from green (G), green-infested (GI), yellow (Y), and red (R) tree crowns across all sampling periods (June-September) with associated standard error bars.

CHAPTER 4

VOLATILE AND WITHIN-NEEDLE TERPENE RESPONSE OF INTERIOR DOUGLAS-FIR TREES TO ATTACK BY DOUGLAS-FIR BEETLES (COLEOPTERA: CURCULIONIDAE)

Abstract

Bark beetle activity alters foliar chemistry causing foliage of infested trees to transition from green to green-infested, to yellow, to red crown phases following tree decline and death. Previous studies of *Dendroctonus* attacked lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) have found elevated emissions of monoterpenes and increased flammability in yellow and red foliage. Terpene response of interior Douglas-fir (*Pseudotsuga menziesii var. glauca* Mirb. Franco) to attack by Douglas-fir beetles *(Dendroctonus pseudotsugae* Hopkins) has not been studied. We collected volatile emissions and within-needle terpene concentrations from six trees in each crown phase during a typical fire season. The effects of each crown phase on total and individual terpene responses were evaluated using a repeated measure analysis of variance and through regression analyses. Terpene emissions correlated with increased flammability in other conifer species were highest in yellow and red crowns. Mean total within needle-terpene concentrations were also highest in red crowns. Our results suggest interior Douglas-fir stands with a higher percentage of tree crowns in the red phase are likely to support alterations to crown fire behavior based on the presence of higher levels of flammable terpenes when needles are still retained in the canopy.

Introduction

Recent bark beetle outbreaks have affected millions of hectares of coniferous forest across western North America (Black et al. 2013, Bentz et al. 2010). Beyond causing widespread tree mortality, bark beetle activity changes forest structure, composition, function, and fuel complexes (Romme et al. 1986, Parker et al. 2006, Fettig et al. 2007, Page and Jenkins 2007, Jenkins et al. 2008, 2012, Raffa et al. 2008). Recently, a number of studies have focused on bark beetle induced modifications to forest fuels and their relation to potential altered fire behavior (DeRose and Long 2009, Jorgensen and Jenkins 2011, Simard et al. 2011, Collins et al. 2012). In particular, concern has been focused on changes to the aerial fuels complex which is the fuel strata underlying stand replacing crown fires and erratic fire behavior that pose potential safety risks to firefighters (Cruz et al. 2003; Jenkins et al. 2012). Recent studies have quantified changes to canopy fuels such as reductions in the amount of aerial fuels including canopy bulk density, available live canopy fuel load, and decreases in canopy base heights (Page and Jenkins 2007, Jorgensen and Jenkins 2011, Simard et al. 2011, Schoennagel et al. 2012), which are important parameters for calculating the likelihood of crown fire behavior (Call and Albini 1997, Scott and Reinhardt 2001).

More recently, studies have begun to investigate physical and chemical changes to needles of beetle-killed trees while the foliage is still in tree crowns. During an infestation, beetles vector a complex of blue-stain fungi into the subcortical tissues of an infested tree (Paine et al. 1997). Fungal hyphae penetrate xylem tissue in the sapwood blocking water transport from the soil to the canopy contributing to tree mortality (Ballard et al. 1984, Lewinsohn et al. 1994, Hubbard et al. 2013). Over the course of this period, foliar moisture declines as photosynthesis ceases and needle desiccation sets in

(Parmeter et al. 1989) and crowns of infested trees transition through four phases: non-infested (green, G), current year's infestation (green-infested, GI), previous year's infestation (yellow, Y), and two years post infestation (red, R) (Amman 1982, Wulder et al. 2006, Jenkins et al. 2008). Researchers conducting studies in lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) infested by mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae)), determined the main factor for increased flammability in attacked trees was the decline in moisture content as trees progressed from G to R phase (Jolly et al. 2012, Page et al. 2012). In general, foliar moisture content is considered an important parameter for influencing whether or not crown fire initiation will occur (Van Wagner 1977). Although foliar moisture has a strong impact on the likelihood of a beetle infested stand experiencing elevated crown fire hazard, chemical changes in bark beetle altered foliage has also been shown to play a role in altering fire behavior (Jolly et al. 2012, Page et al. 2012).

Chemical changes are primarily related to essential plant compounds (e.g., cellulose, hemicellulose, lignin, and extractives which include terpenes (Philpot and Mutch 1971, Page et al. 2012). In particular, plant terpenes can alter fire behavior based on their high heat values, low flash points, and Low Flammability Limits (Nuñez-Regueira et al. 2005, Ormeño et al. 2009). Owens et al. (1998), found concentrations of the monoterpenes bornyl acetate and limonene in Ashe juniper (*Juniperus ashei* Buchholz) had a significant effect on the amount of plant material burned. In a separate study, Ormeño et al. (2009) found among six Mediterranean plant species, those with higher terpene concentrations in their needles had higher flammability, sustainability, ignitability, and combustibility rates. Volatile terpenes have also been shown to shorten time to ignition and lower the temperature at ignition in beetle-attacked lodgepole pine

(Page et al. 2012). Furthermore, the lack of uniform crown conditions associated with bark beetle outbreaks could affect volatile terpene emission rates which have yet to be studied outside of upper elevation lodgepole pine and Engelmann spruce forests (Hicke et al. 2012).

Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.)) Franco dominated forests are common at the low to mid montane zone growing between 900 to 1500 m above mean sea level throughout the central and northern Rocky Mountains (Bailey 1980, Meidinger and Pojar 1991). These forests exhibit diverse structure and composition attributed to their biogeoclimatic adaptability and past disturbances including fire and insect infestations. Interior Douglas-fir forests have a characteristic mixed-severity fire regime defined by fires that are variable in burn severity, frequency and are the most complex and least understood of all fire regimes (Schoennagel et al. 2004, Lentile et al. 2005). At the landscape scale, even-age forest structures are most common where stand replacing fires are prevalent and interspersed between these even-age patches, are uneven-aged stands where frequent surface fires are dominant on a historical return order of 7-20 years (Arno 1976, Brown et al. 1999, Kauffmann et al. 2000). Aside from fire, the Douglas-fir beetle (DFB) is a major disturbance factor for Douglas-fir (Rudinsky 1966, McGregor et al. 1984, Schmitz and Gibson 1996, Negrón et al. 2001). Outbreaks are often limited to the stand scale leading to patchy distributions of tree mortality, although under certain epidemic conditions the loss of the majority of suitable hosts in a stand can occur (Negrón et al. 2001). Recent work by Donato et al. (2013) and Giunta et al. (in review) quantified DFB induced changes to fuels complexes including reductions in canopy bulk density, decreases in canopy base height, and declines in foliar moisture content as tree crowns transition from G to R phase.

Here, we examine changes in foliage chemistry, both volatile emission rates and within-needle terpene concentrations, of DFB-attacked Douglas-fir trees as needles change from G (healthy, non-infested) to GI (green-infested, year 1), to Y (yellow, year 2), and to R (red, year 3). We hypothesized that Y and R crowns will have greater terpene emissions compared to G and GI crowns, while we expect GI crowns to contain higher within-needle terpene concentrations compared to G crowns due to the production of terpene-based defensive compounds during the period of initial infestation. No study to date has quantified changes in foliar chemistry of interior Douglas-fir infested by DFB. This information is needed to fill gaps in our understanding of changes that occur to forest fuels in drier, lower montane forests following bark beetle infestations (Donato et al. 2013).

Materials and Methods

Study Site and Stand Characteristics.

Study site selection was made using Forest Health Monitoring Aerial Detection Survey maps (ADS), with input from USDA Forest Service personal. Map polygons showing recent (< 2 year old) DFB outbreaks greater than 10 ha in size on U.S. National Forest lands throughout northern Utah and southern Idaho were identified as potential study locations. Ground reconnaissance and visual site inspections were conducted to verify the presence of DFB activity with all four crown classes (G, GI, Y, and R) represented. The site chosen for this study was located in the northern portion of the Bear River Range in southeastern Idaho on the Caribou-Targhee National Forest (42°42’9” N, 111°10’36” W). Elevation of the approximately 10 ha study site was 2250 m plus/minus

25 m above mean sea level with a mean slope of 30% located on a southwest aspect. Overstory vegetation consisted of an open, mixed-aged stand of interior Douglas-fir (100% overstory composition), surrounded by Engelmann spruce / subalpine fir (*Abies lasiocarpa* Hook. Nutt.) intermixed with lodgepole pine on north and east aspects. Understory vegetation was mostly grasses and chokecherry (*Prunus virginiana* Nutt. Torr.). Climate conditions for this area are characterized by a thirty year mean maximum July temperature of 25^0C and January mean low temperature of -12^0C, with total annual precipitation normals of 864 mm (PRISM). Stand characteristics include mean basal area of 41.3 m^2 ha^{-1}, density of 399 stems ha^{-1}, a dbh range of 18.8 cm to 59.4 cm, and mean tree height of 17.9 m. The current DFB outbreak has been ongoing for the past four years (USDA Forest Service ADS).

Experimental Design.

Four crown condition classes associated with DFB outbreaks were included in this study as assessed at the start of sampling on June 12 (Fig. 4.1). Green (G) trees were assessed as those that were healthy, non-infested, and had live, green foliage. GI trees were assessed as those with current year’s attack based on the presence of fresh pitch streams, entrance holes, frass accumulations around the base of the tree, and the presence of DFB actively infesting hosts. Yellow trees were classified as those that were successfully infested the previous year based on presence of DFB galleries, emergence holes, and foliage that had transitioned to a yellow coloration. Red trees were those killed by DFB evidenced by characteristic DFB galleries, frass accumulations, exit holes, and with red crown foliage.

Six trees per crown class were selected that had similar heights, diameter at breast height, and showed no signs of secondary disturbance (e.g. herbivory, root disease, drought stress, frost damage, and or fire damage). To obtain infested (GI) trees, six healthy trees were each baited using one Pherotech DFB lure comprised of 0.3 g of frontalin, 121.0 g of ethanol, and 0.2 g of seudenol (Ross and Daterman 1997). The DFB lure was attached 1.8 m above the surface of the forest floor on the north aspect of each GI tree bole for one week during the DFB flight period before trees became infested. The mean dbh (± SE) of selected trees were: G 46.0 ± 4 cm, GI 39.6 ± 3 cm, Y 49.3 ± 2 cm, R 47.8 ± 4 cm, and mean heights (± SE) were, G 18.1 ± 1.2 m, GI 15.4 ± 1.8 m, Y 17.3 ± 0.3 m and R 21.8 ± 1.1 m. Volatile terpene emissions and within needle-terpene concentrations were measured every two weeks between early June and early October (nine sampling periods total) which coincides with a typical fire season in southern Idaho. All sampling took place between 1000 and 1800 local Mountain Standard Time (MST). Prior to the start of each sampling period, temperature and relative humidity were measured using a sling psychrometer (Fig. 4.2).

Field Sampling Methods

Volatile emissions were collected from one randomly selected branch (approximately 50 cm long) less than 1.5 m above the forest floor. This selected branch on each sample tree was used for all subsequent sampling periods to minimize any confounding factors associated with branch condition, aspect, and location. Branches were enclosed in a clear Teflon bag (50 cm x 75 cm; American Durafilm Co., Holliston, Massachusetts) and volatiles collected by pulling air out using a portable vacuum pump (SKC AirLite Sampler Model 110-100) through a volatile trap containing 30 mg of the adsorbent material HayeSep-Q (Restek, Belefonte, Pennsylvania). Air was sampled at a rate of 0.5 L minute^{-1} for 30 minutes. Following the conclusion of the last sampling period (October 4), branches were clipped and needles removed and weighed.

Laboratory Analyses

Analysis of terpene compounds and emission rates were quantified based on procedures following Runyon et al. (2008) and Page et al. (2012). Volatiles were eluted from traps using 200 µL of dichloromethane and 1000 ng of *n*-nonyl-acetate was added as an internal standard. An Agilent 7890A gas chromatograph (GC) coupled with a 5975C mass spectrometer were used to analyze samples, with helium as the carrier gas. Internal temperature of the GC oven was set at 35°C for three minutes before being raised to 5°C min^{-1} and up to 125° C, followed by an increase of 25°C min^{-1} up to 250° C. Quantification of volatile compounds were determined through comparison to the internal standard using ChemStation software (Agilent Technologies). Volatile emission rates are reported on a fresh weight basis (ng h^{-1} g^{-1}). Compound identification was performed by measuring and comparing mass spectra and retention rates with commercial standards, when available.

For within-needle terpene concentration measurements, 15-20 g of foliage from the lower third of each tree crown were clipped in the field, labeled, placed in plastic bags, and stored in a freezer at -80 ^{0C} until processed. Terpenes were extracted from foliage following Page et al. (2014). Five grams of needles were randomly pulled from the 15-20 g collected and ground into fine powder in liquid nitrogen (N_2O) using a mortar and pestle. Approximately 0.1 g of powdered needles was transferred in separate vials with each containing 1.5 ml of cyclohexane, and then sonicated at room temperature (~

21^0 C) for 20 minutes. Vials 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. The process for identifying compounds based on peak retention times and quantification of within-needle terpene concentrations followed procedures described above for the volatile analyses. Within-needle terpene concentrations were reported on a μg^{-1} per fresh needle weight (g) basis.

Statistical Analyses

Eight compounds were chosen for statistical analyses based on rank abundance and established role in affecting foliage flammability (Owens et al. 1998, Ormeño et al. 2009, Page et al. 2012). The terpene compounds included for analyses were, α-pinene, β-pinene, β-myrcene, camphene, E-β-ocimene, *P*-cymene, D-limonene, and tricyclene. Data were analyzed using a repeated-measures analysis of variance (ANOVA) using the Proc Glimmix procedure in SAS (version 9.4, SAS Institute, Inc. 2014) to identify significant differences in terpene emission rates and within-needle terpene concentrations between crown condition classes and across time. Crown condition class and sampling date were set as fixed effects. Measures from six sample trees per crown class were averaged together to produce one sample mean representing each crown class per sampling period. To account for the appropriate covariance structure, the models that minimized Akaike's information criterion were selected, which included autoregressive with random effect (AR1+RE) structure and compound symmetry (heterogeneous) structure. Log and square root transformations were employed to meet assumptions of normality and homogeneity of variance. Tests of significant differences between crown condition classes were carried out using a post-hoc means comparison approach with the experimental-wise error rate controlled using the Tukey-Kramer method, and performed at $\alpha = 0.05$ level.

Pearson's correlation coefficients (r) were used to identify linear relationships between ambient air temperature and volatile emission rates, as well as any linear relationships between within-needle concentrations and volatile emission rates. A simple linear regression model, $Y_i = \beta_0 + \beta_1 X_1 + \varepsilon_i$ where Y = response variable (volatile emission rate), $_i$ = observation number (tree sampled), β_0 = intercept, β_1 = slope of X_1, where X_1 = temperature, ε_i = error term for subject $_i$, was performed to see if there were any significant relationships between temperature (^{0}C) and volatile emission rates per crown class for individual terpene compounds when averaged across all sample periods. The model $Y_i = \beta_0 + \beta_1 X_1 + \varepsilon_i$ where Y = response variable (volatile emission rate), $_i$ = observation number (tree sampled), β_0 = intercept, β_1 = slope of X_1, X_1 = needle concentration, ε_i = error term for subject $_i$, was performed to see if there were any significant relationships between within-needle concentrations and volatile emission rates. The R statistical software package was used for regression analyses.

Results

We identified 46 volatile compounds emitted by Douglas-fir trees, the majority of which were monoterpenoids (38 compounds) (Table 4.1). These 46 compounds were produced by all trees throughout the study period (June-October) regardless of crown class. Volatile emissions varied greatly among crown classes and among sampling periods for total amounts (Fig. 4.3) and individual compounds (Fig. 4.4). Total volatile emissions among crown classes were marginally non-significant ($P = 0.05$) when averaged across all sampling periods (Table 4.2); trees in the Y crown phase emitted the most total volatiles, 40% more on average than G trees. Emissions of individual volatile compounds were greater in Y and R foliage than G and GI foliage when averaged across all sample periods (Fig. 4.5). The volatile compound D-limonene (t = -2.95; df= 3, 20; *P* = 0.04) was emitted in greater amounts by R compared to G trees. Emissions of camphene (t = -2.98; df = 3, 20; *P* =0.03) were higher in R compared to G trees, R compared to I trees (t = -1.24, df = 3, 20; *P*=0.003) and Y compared to R trees (t = 0.94; df = 3, 20; *P* = 0.03), while emissions of *P*-cymene were higher in Y compared to G trees (t = -1.03; df = 3, 20; *P* = 0.04). Tricyclene emissions peaked in GI foliage (100 ng h^{-1} g^{-1} fresh weight), following the DFB flight period (June 12). From early July to early October, Y foliage produced significantly (F = 3.08; df = 3, 20; P= <0.0001) greater emissions of tricyclene compared to G, GI, and R crowns. When averaged across all sample periods, tricyclene emissions were higher in R compared to G trees (t = -2.96; df = 3, 20; *P* = 0.04) and in R compared to I trees (t = -1.15; df = 3, 20; *P* = 0.006).

Relationships between temperature and volatile emission rates as well as the effect of terpene concentrations on volatile emission rates were found to be weak among crown classes for total and individual compounds from sampled trees at our study site. The only significant relationships detected were for the effect of temperature on volatile emission rates of camphene in R trees (t = 2.29; df = 2, 46; *P* = 0.02) and *P*-cymene in R trees (t = 2.00; df = 2, 46; *P* = 0.05) (Fig. 4.6), as well as the relationship between within-needle concentrations and volatile emission rates for camphene (P = 0.007).

Within-needle Terpene Concentrations

Results from within-needle terpene concentrations generally mirrored those found with volatile emissions. A total of 85 compounds, including the 48 found in volatile emissions, were found to occur within needles, the majority of which were monoterpenoids (45 compounds) and sesquiterpenoids (36 compounds). Seven compounds, α-pinene, β-pinene, *p*-cymene, β-myrcene, camphene, D-limonene, and tricyclene were selected for additional analyses based on their abundance and known effects on foliage flammability. Mean total within-needle terpene concentrations averaged across all sample periods were significantly higher in R compared to G foliage (t = -9.87; df = 3, 20; P = <0.0001), GI foliage (t = -10.39; df = 3, 20; P = <0.0001), and Y foliage (t = 3.85; df = 3, 20; P = <0.005); Y foliage also contained more terpenes than G (t = -6.01; df = 3, 20; P = <0.0001) and GI foliage (t = -6.54; df = 3, 20; P = <0.0001) (Fig. 4.7). Over the course of the season, total within-needle terpene concentrations varied considerably both within crown classes and between crown classes (Table 4.2). GI foliage had significantly (t = 130.88; df = 3, 20; P = <0.0001) higher concentrations of total terpenes following the DFB flight period (6/12), compared to subsequent sampling periods (6/28 and 7/14), before decreasing throughout August and reaching the highest levels in late September and early October (Table 4.2). Mean total within-needle terpene concentrations in R foliage varied considerably over the course of the study dropping to its lowest levels on June 28 and reaching peak levels on July 30 (Table 4.2). An overall 40% increase in concentration of mean total within-needle terpenes in Y foliage was measured between early June and early October.

Measures of within-needle concentrations of individual terpene compounds also varied greatly between crown classes (Fig 4.8). Concentrations of tricyclene were significantly higher in R compared to G foliage (*t* = -12.21; df = 3, 20; *P* = <0.0001), GI foliage (*t* = -12.13; df = 3, 20; *P* = <0.0001), and Y foliage (*t* = 4.01; df = 3, 20; *P* = 0.0007). Similar results were found for α-pinene whose concentrations were found to be significantly higher (*t* = -10.55; df = 3, 20; *P* = <.0001) in R than G (*t* = -10.97; df = 3, 20; *P* = <.0001), GI (*t* = 3.51; df = 3, 20; *P* = .001), and Y foliage (*t* =3.51; df =3, 20; *P* = 0.01). Y foliage also contained more terpenoids than G foliage (*t* = -7.05; df = 3, 20; P = <0.0001). There was a 65% increase in the mean amount of D-limonene in Y than G foliage when averaged across all sample periods (Fig. 4.8). Y foliage had the highest concentrations of camphene, D-limonene, tricyclene, and *p*-cymene compared to all other crown classes.

Discussion

Douglas-fir trees attacked and killed by DFBs undergo large chemical changes as foliage transitions from green (G) to green-infested (GI) to yellow (Y), and finally to red (R). Total and individual volatile emission rates changed greatly both within and between crown classes over the course of the sampling period (from June-October). Mean total volatile emission rates tended to be higher in Y and R crowns than G crowns when averaged across all sample periods. The associated increase in volatile emissions in post-infested trees (e.g. Y and R crowns) were attributed to passive diffusion of monoterpene releases following foliage desiccation and occurs after the breakdown of terpene storage vesicles within needles.

Ambient air temperature has been shown in previous studies to have a strong influence over plant volatile emission rates, with some estimates indicating a two to three fold increase in monoterpene emissions for every 10^0C increase in temperature (Schuh et al. 1997, Constable et al. 2001, Gouinguene´ and Turlings 2002, Niinemets et al. 2004). In one study, Tingey et al. (1980) found air temperature increases from 20 to 46^{0}C led to an exponential increase in volatile emission rates in slash pine (*Pinus elliottii* Engelm.). At our study site, temperatures fluctuated throughout the study period with a steady increase through June to a peak max mean high temperature of 23^{0}C on July 14 before declining to a peak low mean temperature of 7^{0}C on October 2. Peak mean total volatile emissions in G, GI, Y, and R crowns were (1695, 5881, 28112, 17835) ng $h^{-1}g^{-1}$ respectively, which occurred on sample period July 14 and coincided with the warmest sampling day. After computing a simple linear regression analysis of the effect of temperature on the response for individual terpene emission rates, significant relationships were detected for the compounds *p*-cymene and camphene in R crowns. This could have implications for decreasing time to ignition for R foliage, which is further susceptible to elevated flammability based on it typically has the lowest foliar moisture content (Jolly et al. 2012, Page et al. 2012). We expected to find a similar trend for total and each individual terpene compounds for R foliage, yet surprisingly this was not the result. The mechanisms underlying the effect of temperature on volatile terpene emission rates is still not fully understood (Kesselmeier and Staudt 1999, Penuelas and Llusia 2001). Individual plants of the same species often have different emission rates under the same temperatures (Flyckt 1979, Yokouchi and Ambe 1984 in Lerdau et al. 1995). Other important factors include the amount of irradiance (Langenheim 1994, Bertin et al. 1997), water availability (Penuelas and Llusia 2001), and presence of a phytophagous attack (e.g. GI trees) (Miller et al. 2005), which all have been found to influence VOC emission rates.

The DFB-induced changes to Douglas-fir trees reported here have potentially important consequences for increasing the threshold in which torching and crowning might occur during a wildfire because several affected compounds have previously been associated with increased flammability of foliage in other conifer species (Owens et al. 1998, Page et al. 2012). For example, in mountain pine beetle attacked lodgepole pine, the monoterpene tricyclene was related to a shortened time to ignition (Page et al. 2012) and this compound increased in Douglas-fir trees attacked by DFB. Moreover, total volatile terpene emissions and emission of nine individual monoterpenes were positively correlated with a key measure of burning rate (maximum rate of mass loss) (Page et al. 2012). We found that 4 of these compounds α-pinene and *p*-cymene in Y and R trees, as well as camphene and tricyclene in R trees increased in DFB-attacked trees (Table 4.1, Fig.4.5). From field collections, α-pinene, camphene, β-pinene, β-myrcene, and tricyclene were the most notable based on rank abundance. There was an overall 50% increase in camphene emission rates from R crowns compared to G crowns when averaged across all sample periods. Emission rates of camphene, D-limonene, *p*-cymene, and tricyclene, were also higher in Y and R crowns compared to G and GI crowns. These results suggest Douglas-fir stands infested by DFB with a high percentage of trees with Y and R crowns could potentially be at risk for increased crown fire initiation and spread based on higher emissions of increased flammable terpenes compared to stands comprised predominantly of G healthy trees. It should be noted, foliar moisture content along with canopy bulk density, canopy base height, and presence / absence of ladder fuels are considered the most critical factors which determine crown fire initiation and spread (Van Wagner 1977, Call and Albini 1997, Scott and Reinhardt 2001, Alexander 2010). Still, evidence of increased flammable terpenes in a stand could serve as a factor in influencing and raising crown fire hazard in conjunction with fire weather conditions conducive to supporting crown fire runs.

Within-needle total terpene concentrations followed a similar pattern as with volatile emissions. We found for a number of compounds, (α-pinene, β-myrcene, camphene, D-limonene, *p*-cymene, and tricyclene) that concentrations were higher within Y and R foliage compared to G and GI foliage. This is related to observations of foliar moisture content (FMC) reported by (Giunta et al. in review), who found Y and R foliage had lower FMC values compared to G and GI foliage (Appendix C). As the overall mass within needles declines with the loss of water between the G and R crown phase, it is translated into an increase in terpenes which then occupy the majority of the needle mass.

Concentrations of individual terpenes camphene and tricyclene averaged across all sample periods were greatest in Y and R crown classes, while concentrations of β-myrcene averaged across all sample periods were found to be greatest in foliage of R crowns. Elevated concentrations of the flammable terpenes (α-pinene, camphene, tricyclene, β-myrcene, D-limonene) in R foliage could influence surface fire spread during periods where foliar moisture content values are low, which typically coincides with needle release and deposition on the forest floor following the R stage of an outbreak (Wulder et al. 2006, Edburg et al. 2012).

Measuring within-needle terpene concentrations is important because terpene concentration levels in plant tissue can affect volatile terpene emissions (Lerdau 1991, Tingey et al. 1991, Lerdau et al. 1995). In evaluating the response of volatile emission rates based on within-needle terpene concentrations, we found the concentration of camphene in R needles had a positive correlation with volatile emission rates emitted from R needles. A similar positive relationship was also discovered in R foliage for the compounds α-phellendrene and bornyl-acetate, yet their relationship to elevating the flammability of forest fuels is unknown. These results suggest as foliage desiccation sets in following an infestation, concentrations of individual monoterpenes that have built up within needles are released through passive diffusion of volatiles from needles to the atmosphere and consequently leads to higher emission rates in the post-infested crown classes Y and R.

Through this study we identified the complex of terpene compounds that are present in interior Douglas-fir foliage following a DFB infestation. We were able to demonstrate that as crown foliage fades from the G to R phase during an outbreak, the rate of volatile organic compounds (terpenes) and the amount of within-needle terpenes both collectively and for individual compounds increases. Our results suggest Douglas fir stands with a higher percentage of trees with Y and R crowns are likely to support increased crown fire initiation and spread based on the presence of higher levels of flammable monoterpenes while foliage is still retained in the canopy 1-3 years post outbreak. Overall this study contributes to the growing literature in understanding the role of monoterpenes in not only their relation to fire and fuels, but in the larger context of terpene roles in forest environments which is a research topic that has only started to be explored (Byers et al. 2000).

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Table 4.1. Volatile emission rates (ng hr^{-1} g^{-1}) per compound averaged across sample periods (June-October). MT = unidentified monoterpene, ST= unidentified sesquiterpene.

	Green (G)		Infested (GI)		Yellow (Y)		Red (R)		
Compound	Mean	SE	Mean	SE	Mean	SE	Mean	SE	P-value
α-Pinene	**322.3^{a}**	**165.8**	**813.9^{a}**	**482.2**	**1485.4^{b}**	**702.2**	**1097.7^{b}**	**580.3**	**0.030**
3-Carene	**64.1^{a}**	**38.2**	**371.9^{ab}**	**255.0**	**1652.1^{b}**	**818.5**	**834.0^{b}**	**541.8**	**0.001**
D-Limonene	**113.2^{a}**	**56.6**	**280.4^{ab}**	**201.6**	**696.0^{b}**	**364.8**	**599.6^{b}**	**334.5**	**0.030**
Camphene	**147.8^{a}**	**67.6**	**161.9^{a}**	**84.9**	**127.7^{a}**	**46.3**	**304.9^{b}**	**109.7**	**0.003**
β-Pinene	75.8^{a}	39.3	139.6^{a}	85.8	210.1^{a}	96.7	189.3^{a}	102.6	0.097
sabinene	**113.2^{a}**	**56.6**	**280.4^{ab}**	**201.6**	**696.0^{b}**	**364.8**	**599.6^{b}**	**334.5**	**0.021**
β-Myrcene	36.8^{a}	18.7	109.5^{a}	75.6	110.0^{a}	40.8	109.2^{a}	52.2	0.094
α-Terpinene	**0.2^{a}**	**0.1**	**0.9^{a}**	**0.3**	**44.2^{a}**	**39.6**	**182.4^{b}**	**180.2**	**<.000**
Terpinolene	**4.8^{a}**	**2.1**	**24.1^{a}**	**19.2**	**124.1^{b}**	**72.2**	**55.1^{a}**	**39.1**	**0.014**
Bornyl acetate	**36.0^{ab}**	**19.7**	**41.9^{a}**	**25.0**	**27.7^{a}**	**13.7**	**73.4^{b}**	**32.8**	**0.024**
β-phellandrene	24.5^{a}	12.0	44.0^{a}	23.4	41.3^{a}	17.9	34.4^{a}	11.8	0.275
Linalool	12.2^{a}	10.0	64.8^{a}	46.1	0.8^{a}	0.3	0.4^{a}	0.2	0.068
Tricyclene	**30.5^{a}**	**14.0**	**32.9^{a}**	**17.2**	**34.4^{a}**	**13.6**	**62.5^{b}**	**23.9**	**0.007**
Verbenone	0.4^{a}	0.1	1.3^{a}	0.8	1.2^{a}	0.8	1.0^{a}	0.5	0.420
E- β -Ocimene	1.3^{a}	0.7	2.7^{a}	2.3	3.7^{a}	2.0	15.5^{a}	12.1	0.103
santene	2.2^{a}	1.0	9.3^{a}	6.1	2.2^{a}	0.6	3.3^{a}	1.4	0.804
***p*-cymene**	**2.0^{a}**	**1.1**	**7.4^{b}**	**4.3**	**21.6^{b}**	**10.7**	**21.2^{b}**	**11.4**	**0.002**
MT1	**0.8^{a}**	**0.2**	**2.7^{ab}**	**1.6**	**13.0^{c}**	**7.0**	**7.5^{b}**	**4.4**	**0.007**
benzenoid 1	**0.5^{a}**	**0.2**	**1.8^{ab}**	**1.1**	**14.6^{bc}**	**9.3**	**6.3^{c}**	**4.1**	**0.003**
α-Phellendrene	**0.4^{a}**	**0.1**	**0.9^{b}**	**0.5**	**1.4^{b}**	**0.6**	**1.3^{b}**	**0.67**	**0.009**
β-Phellendrene	24.3^{a}	12.0	44.0^{a}	23.4	41.3^{a}	17.9	34.4^{a}	11.8	0.275
z- β -Ocimene	**0.7^{a}**	**0.2**	**1.9^{bc}**	**0.9**	**20.1^{b}**	**12.1**	**11.0^{c}**	**7.3**	**0.006**
Gamma-terpinene	**0.9^{a}**	**0.4**	**4.4^{ab}**	**3.3**	**27.6^{bc}**	**17.5**	**12.1^{c}**	**9.1**	**0.011**
MT3	0.2^{a}	0.1	1.1^{a}	0.7	2.7^{a}	1.9	1.3^{a}	0.7	0.161
a,p-dimethylstyrene	1.1^{a}	0.4	4.8^{a}	3.2	4.0^{a}	2.1	3.5^{a}	1.6	0.233
MT4	**0.2^{a}**	**0.0**	**0.7^{ab}**	**0.4**	**2.3^{b}**	**1.3**	**1.1^{b}**	**0.6**	**0.038**
MT5	**1.1^{a}**	**0.3**	**2.6^{ab}**	**1.3**	**3.9^{c}**	**1.5**	**3.9^{bc}**	**1.5**	**0.009**
Camphor	3.0^{a}	1.1	6.7^{a}	3.6	7.9^{a}	3.5	6.3^{a}	2.8	0.273
MT6	**0.3^{a}**	**0.1**	**1.3^{ab}**	**0.9**	**3.5^{b}**	**2.2**	**2.3^{b}**	**1.5**	**0.007**
MT7	0.5^{a}	0.2	1.6^{ab}	1.2	7.5^{ab}	4.6	5.0^{b}	3.3	0.044
MT8	**0.5^{a}**	**0.1**	**1.3^{ab}**	**0.8**	**1.6^{b}**	**0.7**	**1.8^{b}**	**0.8**	**0.028**
Borneol	1.7^{a}	1.0	6.2^{a}	4.3	1.0^{a}	0.4	1.1^{a}	0.6	0.339
***P*-cymen-8-ol**	**0.9^{a}**	**0.5**	**3.0^{ab}**	**2.0**	**6.6^{ab}**	**3.8**	**5.8^{b}**	**3.6**	**0.030**
cis-Carveol	**0.1^{a}**	**0.1**	**1.7^{ab}**	**1.4**	**2.8^{b}**	**1.6**	**2.3^{b}**	**1.5**	**0.052**
meSA	0.4^{a}	0.1	1.4^{a}	0.9	1.0^{a}	0.5	1.2^{a}	0.6	0.248
α-Terpineol	0.2^{a}	0.3	1.5^{a}	2.7	0.05^{a}	0.07	0.2^{a}	0.2	0.438
Thyml-methyl ether	**1.3^{a}**	**0.5**	**3.3^{ab}**	**1.6**	**6.3^{ab}**	**3.4**	**5.6^{b}**	**2.9**	**0.052**

MT9	0.4^{a}	0.4	9.3^{a}	19.6	0.7^{a}	0.9	1.8^{a}	3.5	0.653
MT10	**0.2^{a}**	**0.1**	**1.8^{ab}**	**1.1**	**4.2^{b}**	**2.2**	**2.9^{b}**	**1.8**	**0.010**
ST1	0.2^{a}	0.0	0.7^{a}	0.4	0.9^{a}	0.5	0.7^{a}	0.4	0.099
ST2	0.02^{a}	0.01^{a}	0.01	0.01^{a}	0.03	0.02	0.08^{a}	0.06	0.105
ST3	0.3^{a}	0.2	0.1^{a}	0.06	0.2^{a}	0.1	0.1^{a}	0.05	0.590
ST4	0.3^{a}	0.1	0.8^{a}	0.5	1.5^{a}	1.0	1.5^{a}	0.8	0.096
ST5	**0.5^{a}**	**0.2**	**0.9^{ab}**	**0.5**	**1.7^{b}**	**0.8**	**2.1^{bc}**	**0.9**	**0.003**
α-Farnesene	2.9^{a}	1.9	5.4^{a}	4.5	5.03	4.7^{a}	0.6	0.2^{a}	0.187
MT2	**0.4^{a}**	**0.08**	**0.9^{a}**	**0.3**	**6.99^{b}**	**3.1**	**4.3^{b}**	**2.2**	**<.0001**
Total Volatiles	910.7^{a}	430.2	2223.3^{ab}	1329.5	4997.9^{b}	2415.4	3819.4^{b}	2104.5	0.0509

Superscript letters indicate test of significance based on Tukey-Kramer pairwise comparisons. Different lowercase letters indicate statistically significant differences at the α = 0.05 level

Table 4.2. Mean total volatile terpene emission rates (ng per hr per g fresh weight) and within-needle terpene concentrations (µg per g fresh weight) with standard errors for each sample period for each crown condition class (*n* = 6).

Date	Green (G)		Infested (GI)		Yellow (Y)		Red (R)	
	Volatiles (ng/hr^{-1} g^{-1})	Within-needle (µg g^{-1})	Volatiles (ng/hr^{-1} g^{-1})	Within-needle (µg g^{-1})	Volatiles (ng/hr^{-1} g^{-1})	Within-needle (µg g^{-1})	Volatiles (ng/hr^{-1} g^{-1})	Within-needle (µg g^{-1})
*6/12	870 ± 417^{a}	3781 ± 382^{a}	4472 ± 2759^{a}	6452 ± 650^{bc}	1998 ± 1008^{a}	9514 ± 966^{b}	2615 ± 1739^{a}	17197 ± 1906^{c}
6/28	1515 ± 737^{a}	5565 ± 858^{a}	1472 ± 834^{a}	4635 ± 524^{a}	4458 ± 2343^{a}	6984 ± 1423^{a}	2048 ± 724^{a}	14191 ± 1717^{b}
7/14	1695 ± 797^{a}	6287± 689^{a}	5881 ± 3685^{a}	4390 ± 503^{a}	28112 ± 14285^{a}	12613 ± 595^{b}	17835± 7415^{a}	18699 ± 933^{c}
7/30	571 ± 226^{a}	8052 ± 637^{a}	2480 ± 1094^{ab}	7486 ± 783^{a}	4466 ± 2402^{ab}	12698 ± 2079^{b}	1257 ± 440^{b}	19005 ± 1745^{c}
8/7	284 ± 59^{a}	2000 ± 329^{a}	462 ± 189^{a}	2831 ± 497^{a}	536 ± 221^{a}	8738 ± 974^{b}	725± 214^{a}	15690 ± 1919^{c}
8/31	557 ± 251^{ab}	7250 ± 832^{a}	229 ± 68^{a}	2885 ± 481^{b}	1590± 432^{b}	12785 ± 1009^{c}	736 ± 214^{ab}	15337 ± 742^{c}
9/16	842 ± 268^{a}	7695 ± 1184^{a}	724 ± 243^{a}	8309 ± 521^{a}	611 ± 281^{a}	14911 ± 1045^{b}	1066 ± 547^{a}	17283 ± 1988^{b}
10/2	948 ± 684^{a}	8948 ± 697^{a}	2124 ± 1782^{a}	9778 ± 1112^{a}	1086 ± 163^{a}	13313± 887^{b}	882 ± 157^{a}	18798 ± 1087^{c}
Total	893± 434^{a}	6197±701^{a}	2231±1332^{ab}	5846±634^{a}	4607±2464^{b}	11444±1122^{b}	3610±926^{b}	17025±1505^{c}

Different lower case letters indicate significant differences within a sampling date between crown classes ($\alpha = 0.05$).
*DFB flight period

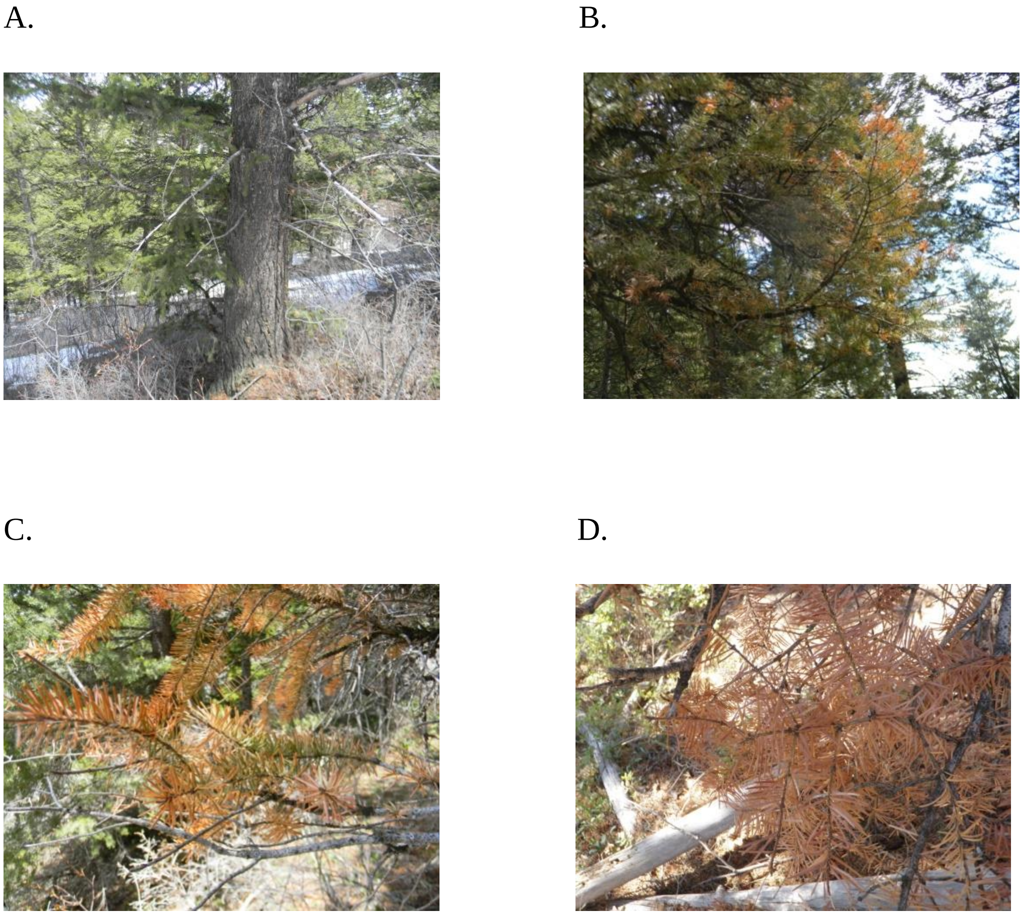

Fig. 4.1. Four crown condition classes (A) green, (B) green-infested, (C) yellow, and (D) red, associated with Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins infestations in interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests.

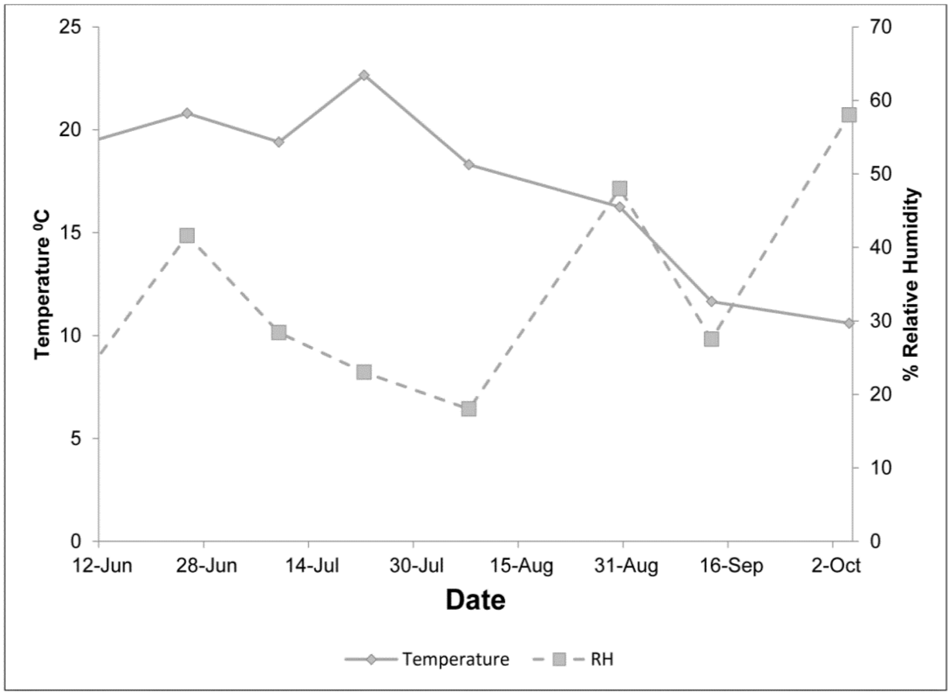

Fig. 4.2. Mean air temperature (^{0}C) and percent of relative humidity during the hours of 1000-1800 at the study site for each sampling period (June to October 2014).

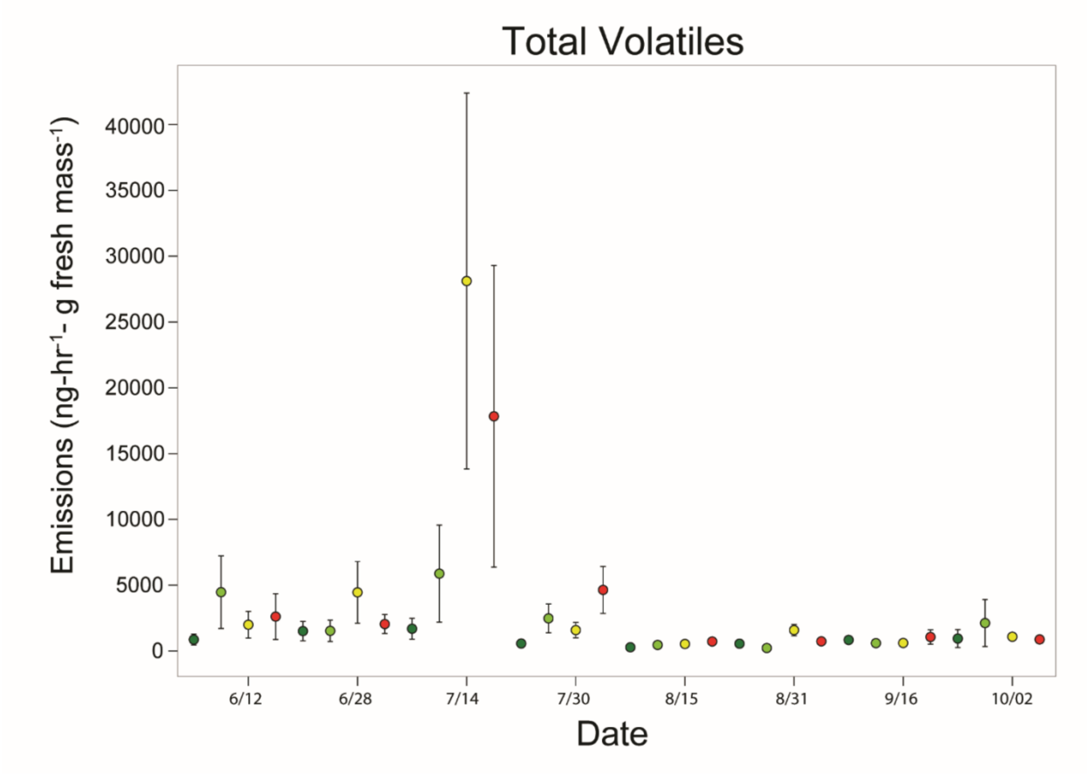

Fig. 4.3. Mean emission rates with associated standard error bars for total volatile emissions per sampling period for each crown class, G, GI, Y, R, (n=6).

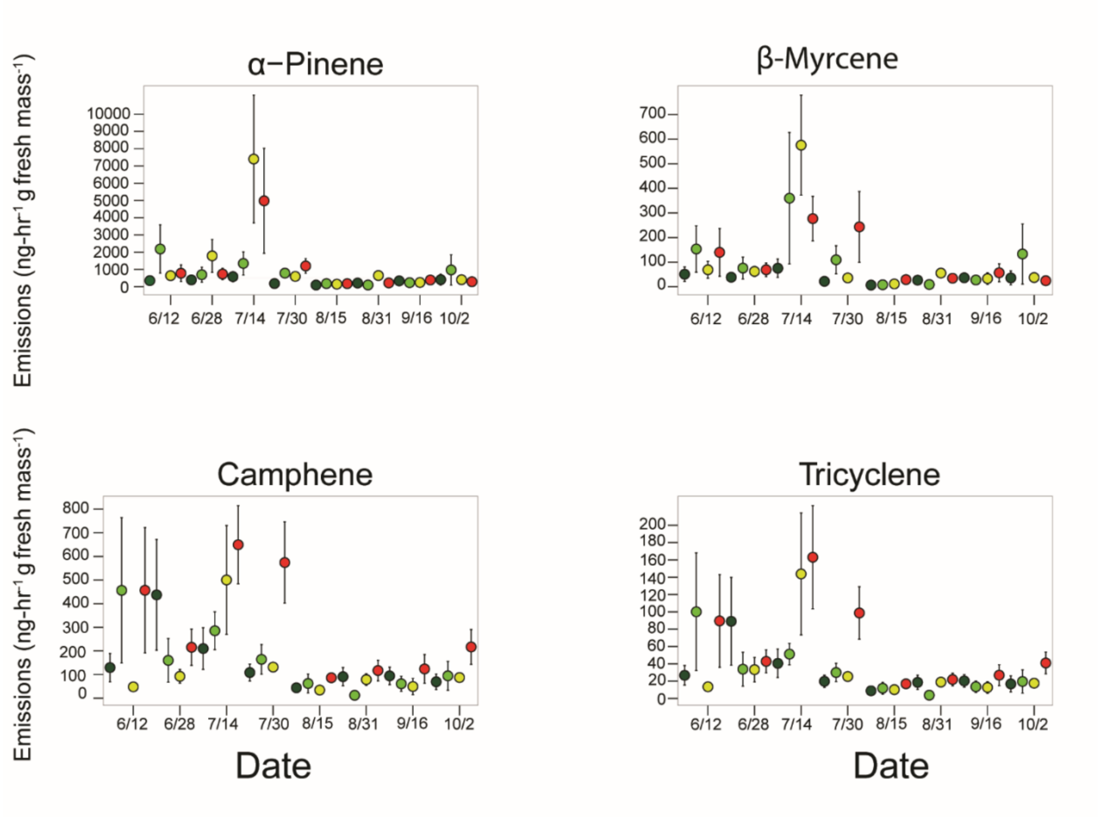

Fig. 4.4. Continued, on pg. 145.

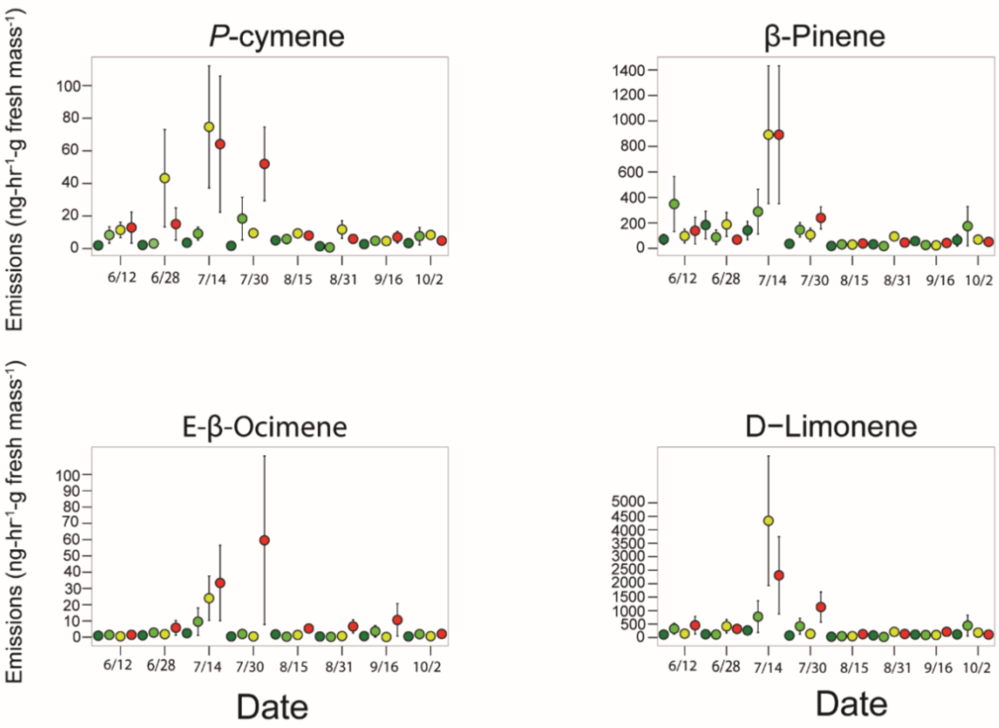

Fig. 4.4. Mean volatile emission rates with associated standard error bars for α-pinene, β-myrcene, camphene, tricyclene, *p-c*ymene, e-β-ocimene, β-pinene, and D-limonene per sampling period for each crown class G, GI, Y, R (n=6). Note different scales.

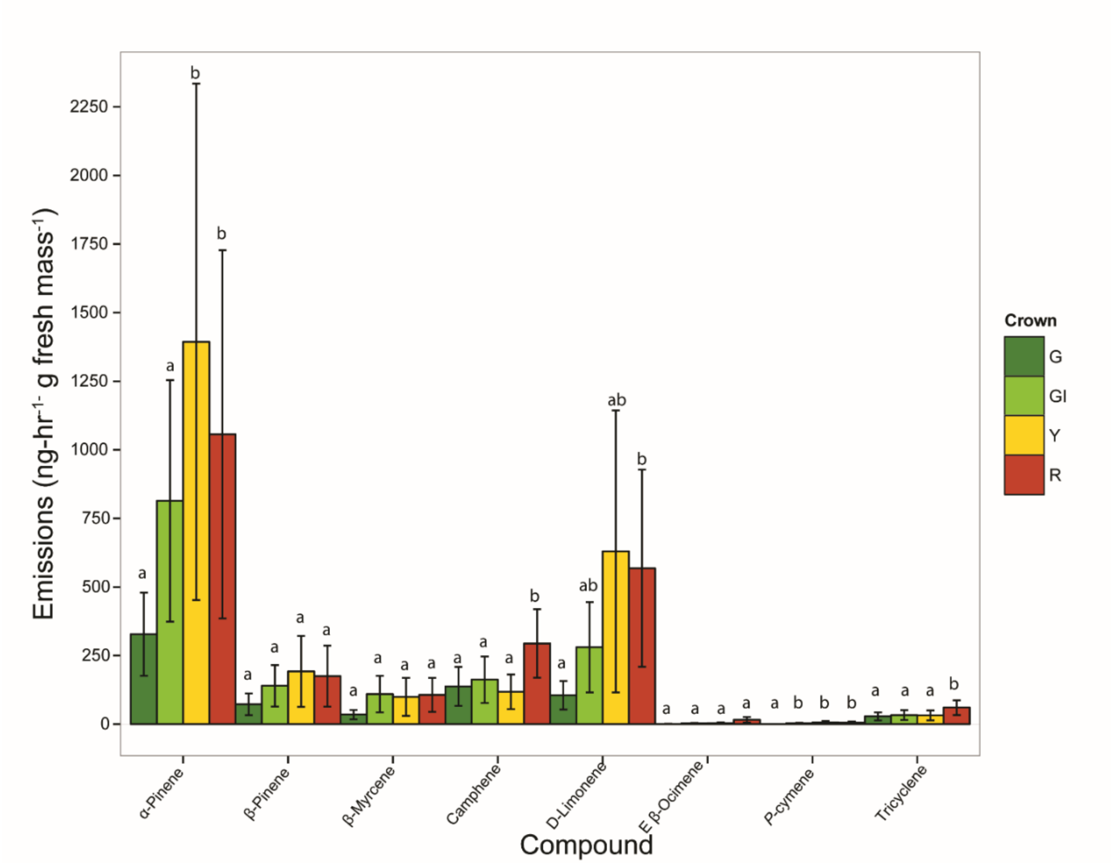

Fig. 4.5. Mean emission rates (ng hr^{-1} g^{-1}) of select individual volatile compounds with associated standard error bars per crown class averaged over all sampling periods. Note: Different lower case letters indicate significant differences between crown classes (α = 0.05).

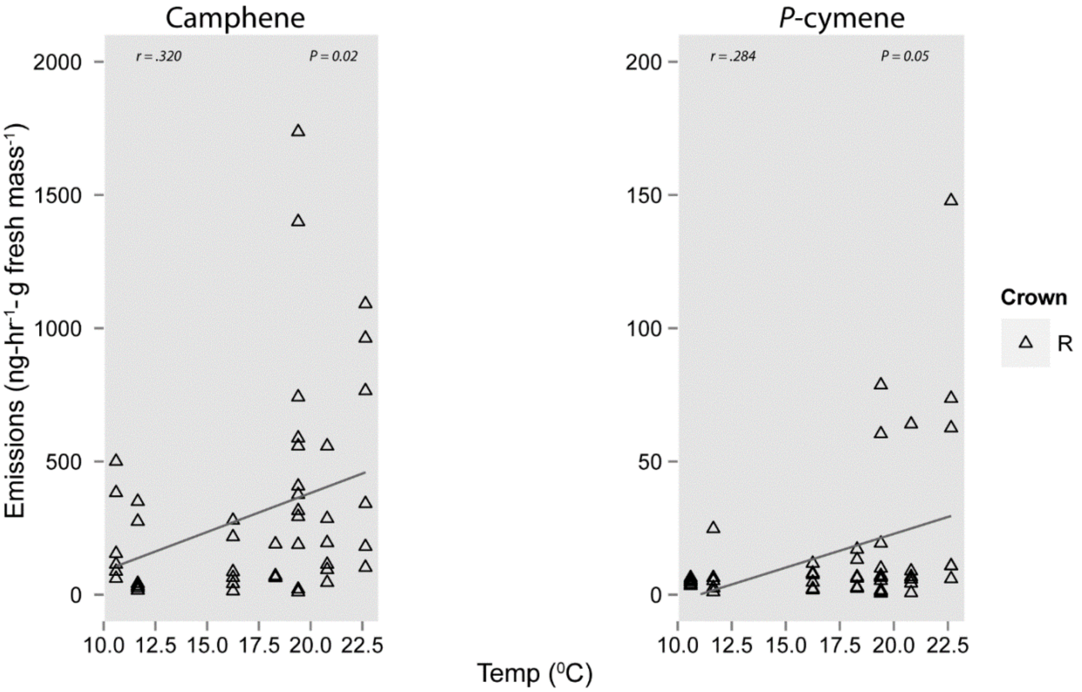

Fig. 4.6. Simple linear regression line for mean temperature (^{0}C) versus mean volatile emissions (ng g^{-1} hr^{-1}) measured over all sampling periods in red crowns for the compounds camphene and *P*-cymene. Pearson's correlation coefficients (*r*) and associated *P* values are reported for each compound, (n=6).

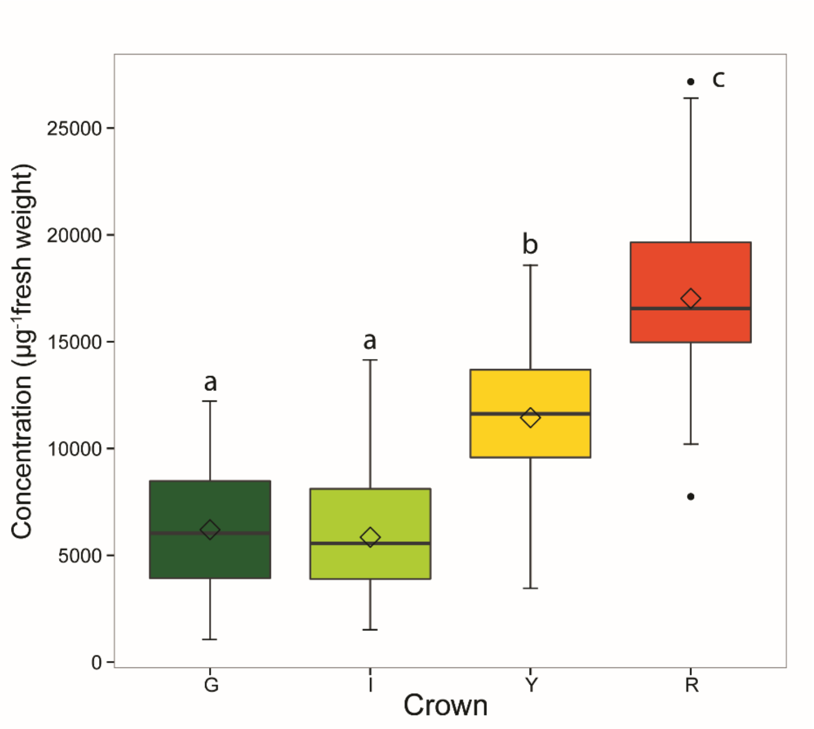

Fig. 4.7. Box and whisker plots of mean total within-needle terpene concentrations (μg^{-1} fresh weight) measured over all sampling periods. The median, 25th percentile, and 75th percentiles are denoted by the center line and box edges, the 10th and 90th percentiles by the whiskers. The mean is denoted by the diamond symbol and filled circles represent outliers. Note: Different lower case letters indicate significant differences between crown classes (α = 0.05).

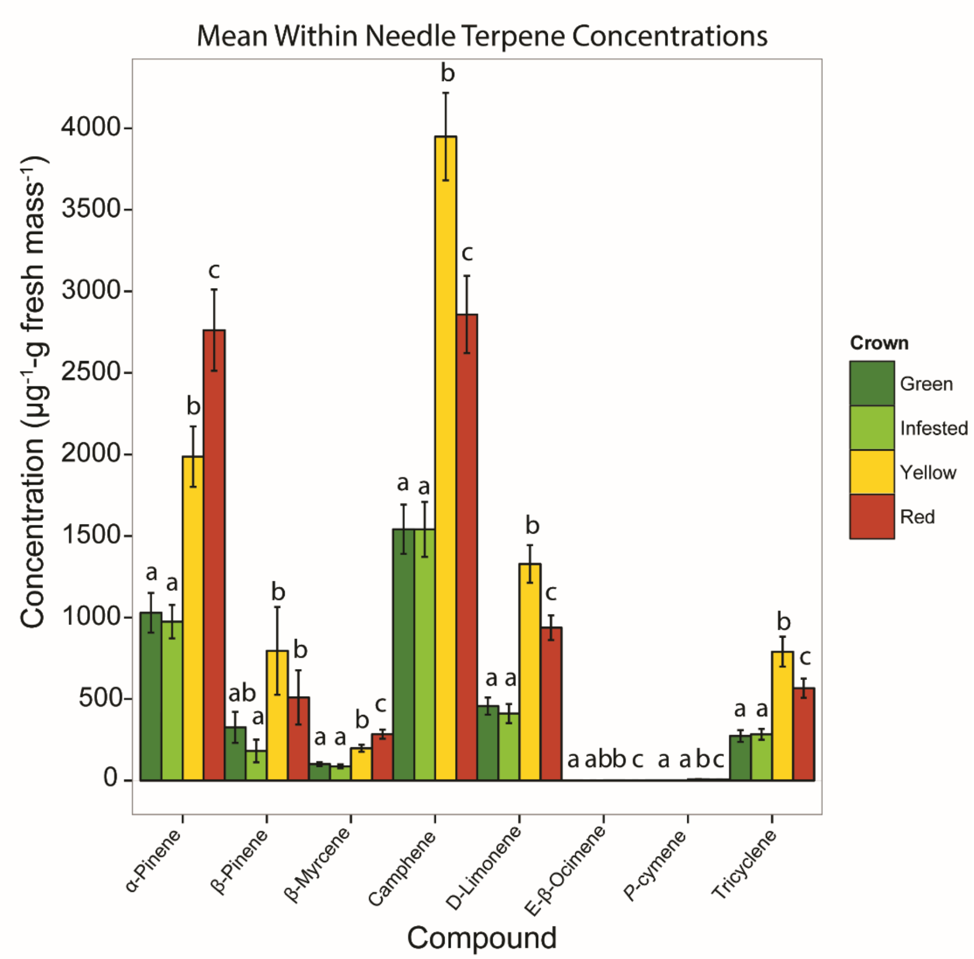

Fig. 4.8. Mean individual within-needle terpene concentrations (μg^{-1} fresh weight) with associated standard error bars per crown class measured over all sampling periods. Note: Different lower case letters indicate significant differences between crown classes (α = 0.05).

CHAPTER 5

SUMMARY AND CONCLUSIONS

Introduction

The term forest health encompasses a broad description of issues which collectively affect the composition and functioning of forest ecosystems. It ranges from nuances of its meaning depending on if one is referring to forest health defined as the state of a forest system meeting management objectives, e.g. a tract of timber reaching merchantable volume quotas, to an ecosystem perspective expressed as one where pests, pollution, and other disturbances do not adversely reduce primary productivity, biodiversity, or substantially increase nutrient loss (Haskell et al., 1992; Kolb et al., 1994). Perturbations within forest ecosystems are prime factors linked to affecting the health of forests. Attempts to express forest health issues in middle montane forests throughout the Rocky Mountains have been restricted to independent abiotic or biotic disturbance agents including, mixed-severity fire (Arno et al., 2000; Schoennagel et al., 2004), Douglas-fir beetle (DFB) (Furniss, 2014b), and western spruce budworm (Ryerson et al. 2003). With few studies addressing compound interactions between two disturbance agents e.g. DFB and fire (Cunningham et al., 2005; Hood and Bentz, 2007), or DFB and western spruce budworm outbreaks (Fredericks and Jenkins, 1988; Hadley and Veblen, 1993). To my knowledge no attempt has been made to synthesize information regarding a broad spectrum of disturbance agents and their collective effects on forest health as a whole in middle montane forest systems. It is important for forest managers to understand how multiple disturbance agents will affect ecosystem processes, functions, and susceptibility to future disturbances (Turner 2010; see Chpt. 2, 2015).

Interior Douglas-fir Forest Health

Chapter two of this thesis provides an in-depth synthesis of recent literature in regards to forest health of middle montane zone forests with a focus on interior Douglas-fir forests of the central Rocky Mountains. It begins with an overview of Douglas-fir forests in general with discussions about climate, aspect, elevation, and geographic setting which collectively influence the diverse and complex structural and compositional nature of these forests. The remaining portions of this chapter review compound disturbance interactions between a number of different notable agents (fire, DFB, western spruce budworm), as well as important yet often overlooked agents including root disease, windthrow, and dwarf mistletoe. Within this chapter key knowledge gaps regarding our understanding of forest health issues in these forests are addressed. Most importantly, the intent of this publication is to provide land managers with a reference for guiding management decisions regarding current and future disturbance risks to interior Douglas-fir forests in the central Rocky Mountains.

Douglas-fir beetle Effects on Fuels

The remainder of this thesis is focused on the interactions between Douglas-fir beetles, fuels and fire in interior Douglas-fir forests of the central Rocky Mountains. In chapter three, detailed results of the effects of DFB infestations on fuels among green, red, and gray stage plots within infested stands are presented. Changes in foliar moisture content among four crown classes (G, GI, Y, R) associated with DFB infestations were also evaluated. In the surface fuels complex, only slight alterations to forest fuels were detected. The most notable changes occurred with the increase in litter depth and loading in red stage plots following needle release from the canopy to the forest surface. Following five years post initial infestation, termed “gray stage”, an increase in herbaceous biomass was detected with the loss of overstory canopy cover which typically blocks sunlight transmission to the forest floor which is necessary for herbaceous plant growth. Significant changes to aerial fuels were found among outbreak stages with reductions in canopy bulk density and decreased canopy base height most apparent in gray stage plots. This is intuitive where the majority of canopy mass is comprised of foliage, and needle loss rates peak 3-5 years post-infestation, leaving standing dead trees with limited crown fuel, which would likely decrease crown fire risk in stands in this stage. In terms of physical changes to tree foliage, a significant decrease in foliar moisture was detected between green healthy unattacked trees and trees with red crowns (2-3 years post-infestation). The largest reduction occurred between green-infested (current year infested) and yellow crowns (1 year post-infested). It is believed the bulk of moisture loss occurs between the fall and spring following an infestation. Due to logistics in starting the study in early June, we were unable to capture this trend. Additional studies tracking moisture over the winter months as foliage transitions to the yellow phase will be necessary for this observation to be properly documented. The results from this portion of the study are related to similar findings in lodgepole pine and Engelmann spruce (Page et al., 2012; Page et al., 2014). With the lowest foliar moisture detected in red crowns, the implications for these results are that trees in the red crown phase would likely increase the onset of crowning for a period of one to three years until the majority of needle loss occurs.

Douglas-fir beetle Effects on Foliage Chemistry

In addition to the physical changes to foliage as a result of bark beetle infestations, other notable changes in terms of foliage chemistry have been observed in previous studies. Chapter four presents the results from investigating the effect of DFB infestations on volatile and within-needle terpenes among green, green-infested, yellow, and red crowns. This was the first study to identify a number of different terpene compounds associated with interior Douglas-fir that have not been previously cited in literature. Some of the more prominent findings were related to the terpenes D-limonene, camphene, and *P*-cymene which have been correlated with increasing foliage flammability in other conifer species (e.g. lodgepole pine). Trees in the red crown phase produced significantly higher emissions and had higher concentrations of these compounds in their needles compared to non-infested green trees. This could have important implications for raising the threshold for crown fire initiation in conjunction with low fuel moisture and adequate fire weather conditions that support the onset of crowning.

Volatile emissions of α-pinene were also found to be higher in yellow and red crowns compared to green and green-infested crowns. In addition to its correlation to increased flammability, α-pinene also acts as a synergist for the aggregation pheromone frontalin, which is used by DFB to mass infest trees (Heikkenen and Hrutfioid, 1965; Rudinsky, 1966; Furniss, 2014a). With the patchy nature of DFB infestations, stands with large populations of trees with yellow and red crowns surrounded by green non-infested viable hosts could further prolong an outbreak by supplementing chemical signals towards host-seeking beetles and communicating that potential green hosts are in the area, increasing the chances for successful colonization based on increased emissions of α-pinene from yellow and red trees. Furthermore, Furniss (2014a) found α-pinene constitute in bole resin interacts with pioneer beetles release of frontalin to initiate mass attacks on trees. The question remains, do emissions of α-pinene in its volatile form, have the same host attraction effect in the presence of frontalin which is a volatile pheromone? Further studies in lab and field settings are required to pursue this hypothesis. A potential project could be to manipulate volatile emission rates of α-pinene in a lab setting with live female beetles to measure the rates of frontalin production to see if it increases in the presence of increased volatile emissions of α-pinene. Overall, this was the first study to show the release of α-pinene from foliage increases as crowns fade from G to R following DFB infestations.

Conclusion

Collectively the work within this thesis constitutes findings related to bark beetles and fuel interactions. It serves as both a guide for forest managers to help identify forest health concerns associated with interior Douglas-fir forests, while also contributing to the knowledge gaps in understanding bark beetle fuel relationships in middle montane forest ecosystems. The diverse nature and complexity of interior Douglas-fir forests warrants additional studies across different geographic locales and at different temporal scales to contribute to further understanding of the insect and fuel interactions in this often overlooked forest ecosystem.

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APPENDICES

Appendix A. Site characteristics for the 36 sample plots included in the study. Site abbreviations defined as, CC: Currant Creek, KW: Kamas Woodland, LB: Little Brush, MW: Matt Warner Reservoir, SH: Scofield Highway, SO: Strawberry Reservoir, SS1: Soldier Summit 1, SS2: Soldier Summit 2, ST: Steinaker Reservoir, UW: Uinta-Wasatch, WC: Wasatch-Cache, WR: White River. Stand conditions defined as G: Green, R: Red, GY: Gray. Habitat abbreviations defined as, ABCO: *Abies concolor,* ABLA: *Abies lasiocarpa*, BERE: *Berberis repens*, CACA: *Calamagrostis canadensis*, CARU: *Calamagrostis rubescens,* OSCH: *Osmorhiza chilensis*, PHMA: *Physocarpus malvaceous,* PSME: *Pseudotsuga menziesii*.

Site	Elevation (m)	Slope (degrees)	Aspect	Habitat type
CC-G	2323	23.75	N	PSME/PHMA
CC-R	2483	24.70	N	PSME/PHMA
CC-GY	2426	22.78	N	PSME/PHMA
KW-G	2545	12.41	E	ABLA/PHMA
KW-R	2510	22.78	N	ABLA/CARU
KW-GY	2473	11.31	N	ABLA/PHMA
LB-G	2509	11.86	N	PSME/BERE
LB-R	2514	14.57	N	PSME/OSCH
LB-GY	2509	20.30	N	PSME/BERE
MW-G	2068	11.86	N	PSME/CARU
MW-R	2230	10.76	NE	PSME/CARU
MW-GY	2056	14.57	N	PSME/CARU
SH-G	2538	17.75	N	ABLA/BERE
SH-R	2594	11.30	N	ABLA/PHMA
SH-GY	2449	15.11	N	ABLA/PHMA
SO-G	2515	12.95	N	ABLA/PHMA
SO-R	2658	17.60	N	ABLA/CACA
SO-GY	2613	15.11	N	ABLA/CACA
SS1-G	2489	15.64	N	ABCO/PHMA
SS1-R	2409	17.22	N	PSME/CARU
SS1-GY	2409	12.41	N	ABLA/PHMA
SS2-G	2385	23.27	N	PSME/CARU
SS2-R	2409	14.00	N	PSME/CARU
SS2-GY	2412	15.64	N	ABCO/OSCH
ST-G	2791	15.64	E	PSME/CARU
ST-R	2597	15.11	NW	PSME/CARU
ST-GY	2630	10.76	W	PSME/CARU
UN-G	*	13.50	*	ABLA/BERE
UN-R	*	15.11	*	ABLA/BERE
UN-GY	*	12.95	*	ABLA/BERE
WC-G	*	14.57	*	ABLA/BERE
WC-R	*	14.10	*	ABLA/BERE

WC-GY	*	15.11	*	ABLA/PHMA
WR-G	2408	19.30	N	ABCO/BERE
WR-R	2408	4.57	N	ABCO/OSCH
WR-GY	2538	15.11	NE	ABCO/BERE

* Denotes missing data

Appendix B. Sample plot characteristics for each outbreak stage G: Green, R: Red, and GY: Gray, for all 12 sites included in the study.

Site	Total BA (m^2ha^{-1})	Total DF BA (m^2ha^{-1})	Live DF BA (m^2ha^{-1})	Dead DF BA (m^2ha^{-1})	AF BA (m^2ha^{-1})	WF BA (m^2ha^{-1})	Avg. QMD (cm)	TPH
CC-G	24.11	21.81	21.81	0.00	1.84	0.00	27.11	389.10
KW-G	22.96	18.37	4.59	13.78	2.76	0.00	46.99	89.21
LB-G	36.74	28.47	26.63	1.84	0.00	0.00	26.31	692.00
MW-G	32.14	32.14	25.72	6.43	0.00	0.00	23.74	721.31
SH-G	29.39	20.20	19.29	0.92	4.59	2.76	26.68	591.53
SO-G	23.88	15.61	9.18	6.43	6.43	0.00	34.97	339.68
SS1-G	12.86	12.86	12.86	0.00	0.00	9.18	38.91	278.86
SS2-G	30.31	21.12	11.02	10.10	0.00	0.00	27.91	242.84
ST-G	33.98	33.98	31.23	2.76	0.00	0.00	32.44	529.76
UN-G	43.16	18.37	17.45	0.92	14.69	1.84	25.35	900.57
WC-G	50.51	35.82	34.90	0.92	0.00	11.94	36.07	662.15
WR-G	33.06	10.10	5.51	4.59	2.76	17.45	35.00	464.51
CC-R	24.80	12.86	12.86	0.00	0.92	0.00	22.56	662.25
KW-R	27.55	13.78	4.59	9.18	0.92	4.59	38.21	250.66
LB-R	37.65	31.23	10.10	21.12	0.00	0.00	39.22	364.14
MW-R	29.39	11.94	8.27	3.67	0.00	0.00	38.04	262.37
SH-R	21.12	15.61	8.27	7.35	2.76	1.84	25.82	466.27
SO-R	40.41	8.27	5.51	2.76	8.27	0.00	25.61	827.55
SS1-R	23.88	11.94	8.27	3.67	3.67	0.92	31.18	504.02
SS2-R	35.82	20.20	12.86	7.35	0.00	0.00	32.13	291.79
ST-R	40.41	22.04	5.51	16.53	0.00	0.00	30.19	518.24
UN-R	22.96	16.53	0.92	15.61	1.84	0.00	32.12	401.15
WC-R	45.92	30.31	10.10	20.20	0.92	11.94	32.93	622.53
WR-R	34.90	6.43	5.51	0.92	0.00	2.76	44.81	347.88
CC-GY	23.88	23.88	17.45	6.43	0.00	0.00	23.72	716.01
KW-GY	49.59	42.25	11.02	31.23	0.92	5.51	40.83	383.89
LB-GY	30.31	30.31	12.86	17.45	0.00	0.00	30.69	458.07
MW-GY	21.12	19.29	8.27	11.02	0.00	0.00	31.77	330.63
SH-GY	22.96	19.29	10.10	9.18	0.92	0.92	23.77	598.10
SO-GY	24.80	22.04	6.43	15.61	2.76	0.00	30.25	426.64
SS1-GY	25.72	22.04	6.43	15.61	1.84	10.10	37.08	503.51
SS2-GY	32.14	20.20	6.43	13.78	0.00	2.76	36.32	334.00
ST-GY	33.98	33.98	10.10	23.88	0.00	0.00	45.79	221.56
UN-GY	33.98	17.45	3.67	13.78	10.10	9.18	34.13	404.83
WC-GY	33.98	25.72	0.92	24.80	0.92	3.67	32.53	419.66
WR-GY	29.39	25.72	3.67	22.04	0.92	2.76	39.75	314.60

* TPH = Trees ha^{-1}; BA = Basal area; DF = Douglas-fir; AF = Subalpine fir, WF = White fir
dbh = diameter at breast height

Appendix C. Mean foliar moisture content for green (G), green-infested (GI) yellow (Y), and red foliage (R) for all sampling periods (June-September), with associated standard error bars.