TREES DIE, FORESTS LIVE:
QUANTIFYING THE IMPACTS OF INSECT DISTURBANCES
IN THE INTERMOUNTAIN WEST

A Dissertation

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AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Kendra G. Schotzko, submitted for the degree of Doctorate of Philosophy with a Major in Entomology and titled "Trees Die, Forests Live: Quantifying the Impacts of Insect Disturbances in the Intermountain West," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

Disturbance is often a critical aspect of forest ecosystems, and those caused by insects and disease can have a variety of effects on ecosystems. We used ground surveys to assess disturbances impacting forests within the Intermountain West. Target habitats were high elevation whitebark pine (*Pinus albicaulis* Engelmann) forests impacted by recent mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks and riparian subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt.) forests that were potentially infested with balsam woolly adelgid (*Adelges piceae* Ratzeburg). With regard to whitebark pine forests, the percentage of whitebark pine killed by mountain pine beetle varied widely. Overall, whitebark pine killed by mountain pine beetle had larger diameters than surviving whitebark pine. The diameter of whitebark pine killed by mountain pine beetle that were part of a tree-clump, however, were smaller than killed whitebark pine occurring as single-trunk trees, suggesting that host growth form impacts host selection by mountain pine beetle. Within these stands, subalpine fir regeneration was more dominant at lower elevations, and whitebark pine was dominant within the regeneration at higher elevations. Our surveys of riparian fir stands documented balsam woolly adelgid throughout Idaho. Infestations on subalpine and grand fir stems were positively correlated with gouting. Thinning and fading of crowns, however, were not correlated with stem infestations. Heavy stem infestations were negatively correlated with elevation for both subalpine and grand fir, which may indicate the importance of habitat or climatic factors in the expansion of balsam woolly adelgid populations.

ACKNOWLEDGEMENTS

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CHAPTER 1: INTRODUCTION

All landscapes are dynamic. The concept of succession helps to describe the sequence of biotic assemblages that occupy a given area over time, and is often specified to be a directional change (Barbour et al., 1998). Primary succession describes the process of organisms (typically lichens, algae, fungi, and plants) colonizing a substrate previously devoid of life. Secondary succession occurs as the result of changes within, or to, a habitat already supporting a community of organisms. Two general types of change drive successional processes: autogenic changes, which are caused by the organisms themselves, and allogenic changes, which are initiated by external forces in the environment (Barbour et al., 1998). Many allogenic changes are broadly referred to as disturbances.

DISTURBANCE

Periodic disturbances contribute to landscape diversity by progressive exposure of new land (e.g. land exposed by a retreating glacier) or by re-initiating successional processes in different areas at different times (e.g. wildfires, biotic agents, etc.) (Barbour et al., 1998). Periodic wildfire not only initiates succession and facilitates the persistence of landscape mosaic diversity, but can also recycle nutrients, create habitat features critical to wildlife species, promote propagation of many plant species, and either perpetuate the dominance of an overstory community or initiate its replacement (Waring and Running, 2007; Wuerthner, 2006). Biotic agents, such as insects and disease, can have diverse effects on ecosystems depending on the species involved, the mechanism of disturbance, and the context in which they occur.

Defoliators are insects that consume the leaves of plants and when they become abundant, they can cause dramatic impacts within forests. For example, the western spruce budworm (*Choristoneura occidentalis* Freeman) is an important defoliator in western North America (Furniss and Carolin, 1977), and principally feeds on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and true firs (*Abies* spp.) (Fellin and Dewey, 1982; Harvey, 1985). Feeding by this and similar species often occurs in stands with reduced growth efficiency, suppressed trees in the understory, and trees with below average growth efficiency in the overstory. These trees are also frequently the most likely to suffer mortality as a result of defoliation (Brookes et al., 1987; Coyea and Margolis, 1994). Such mortality of suppressed or less vigorous trees reduces their density and essentially thins the stand, reducing resource competition for the surviving trees (particularly within the understory) (Waring and Running, 2007). Additionally, the physical breakdown of foliage and deposition of frass (excrement from insect larvae) can accelerate nutrient cycling by concentrating and redistributing nutrients within affected stands (Waring and Running, 2007).

Bark beetles represent another example of insects that act as important disturbance agents within forests. In contrast to defoliators, tree mortality caused by bark beetles usually results in reduced tree density (thinning) in the overstory of the stand. Bark beetles within the subfamily Scolytinae (Coleoptera: Curculionidae) are considered the most influential group of insects in conifer forests, and include the genera *Dendroctonus*, *Ips*, and *Scolytus* (Doane et al., 1936; Furniss and Carolin, 1977; Triplehorn and Johnson, 2005; Wood, 1982). Among the bark beetles of western North America, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is the most destructive (Furniss and Carolin, 1977). Adults are cylindrical, black to dark brown and range in size from 4.0-7.5 mm in length (Furniss and

Carolin, 1977). The most visible stage of the mountain pine beetle lifecycle is the dispersal phase, during which adult mountain pine beetle emerge from natal pine hosts and seek new hosts (living trees in the genus *Pinus*) using olfactory, visual, and tactile cues (Phillips and Croteau, 1999). Aggregation pheromones produced by pioneering mountain pine beetle initiate mass attack of a host, which increases the likelihood of attack success by communicating to other dispersing mountain pine beetle when an acceptable host is located (Phillips and Croteau, 1999).

Mountain pine beetle populations can expand dramatically (referred to as outbreaks or epidemics) and result in forests being thinned of over-mature and/or less vigorous trees. In some forests, thinning by mountain pine beetle can reduce competition among remaining trees, increasing their vigor due to increased access to light, water, and nutrients (Waring and Running, 2007). In other stands, widespread mortality of pine species may release or facilitate the establishment of non-pine conifers such as fir and spruce, and contribute to succession toward shade-tolerant conifers (Arno, 1986).

Human activities within forests have created additional forms of disturbance, as well as changed the characteristics of natural disturbances. Numerous animals, plants, pathogens, insects, and other invertebrates have been introduced into North America (largely from Europe and Asia) in the past half century (Niemelä and Mattson, 1996 and references therein), of which many have become invasive.

White pine blister rust (*Cronartium ribicola* J.C. Fischer in Rabenhorst) (Pucciniales: Cronartiaceae) is an Asian pathogenic fungus introduced to North America in the early 1920s. First documented in southeastern British Columbia in 1921, it rapidly spread through the Pacific coastal mountains, the inland Oregon Cascades, northern Idaho, Montana, the

greater Yellowstone area, western Wyoming, and southeastern Idaho (Putnam, 1931 *in* Geils et al., 2010; Brown, 1970 *in* Geils et al., 2010). Successful infection of host material by white pine blister rust requires cool temperatures and high humidity (Schwandt et al., 2010), conditions common to the Pacific Northwest and parts of the Intermountain West. White pine blister rust has a complex life cycle with both telial and aecial hosts. Telial hosts of white pine blister rust include members of the genera *Ribes* (Grossulariaceae), and *Pedicularis* and *Castilleja* (Orobanchaceae). Within these hosts white pine blister rust produces both urediniospores that can re-infect other telial hosts and basidiospores that can infect aecial hosts. All species within the *Strobi*, *Balfourianae*, and *Cembrae* subsections of *Pinus* can be aecial hosts for white pine blister rust (Geils et al., 2010 and references therein). Within aecial hosts, white pine blister rust produces aeciospores that infect telial hosts.

White pine blister rust enters aecial hosts by penetrating the stomata of needles, and infection progresses by fungal growth through the intercellular spaces of shoots, inner bark, and outer xylem (Geils et al., 2010 and references therein). Young aecial hosts are rapidly killed by white pine blister rust (Geils et al., 2010), such that mortality of understory pine hosts often occurs before mortality of mature overstory host trees. The fate of older hosts is more variable and if an infection occurs high in the canopy a host may survive for many years. Host death will still occur, however, if the infection reaches the lower bole (Slipp, 1953 *in* Geils et al., 2010). Kean and Arno (1993) estimate that white pine blister rust can kill mature trees within two to three decades after initial infection. A substantial portion of the cone crops may be eliminated before host death, however, because the initial infection may occur on cone bearing branches high in the canopy. Thus, before mature trees are removed

from the landscape, their ability to contribute to regeneration in that area is often reduced or eliminated.

The balsam woolly adelgid (*Adelges piceae* Ratzeburg) (Hemiptera: Adelgidae) is a minute insect introduced to the east coast of North America in the early 1900s from Europe, and was present on the west coast of North America as early as 1928 (Mitchell and Buffam, 2001). Adelgids associated with firs typically have complex life histories involving both sexual and parthenogenetic reproduction alternating between two genera of hosts, *Abies* spp. and *Picea* spp. (Hain, 1988). For balsam woolly adelgid in North America, only parthenogenetically reproducing wingless females are known (Mitchell and Buffam, 2001) and balsam woolly adelgid has lost the ability to produce migrant forms and utilize multiple host genera (Hain, 1988). Consequently, this insect only feeds on eastern and western species of North American true firs (*Abies* spp.) (Mitchell and Buffam, 2001).

Balsam woolly adelgid dispersal is passive and may be facilitated by wind or animals (Hain, 1988). Motile nymphs locate a suitable feeding site on a host (usually 24-48 hours after hatching) and begin feeding by inserting their stylets (mouthparts) into the bark. After feeding commences, they transform into a flat wax-covered sessile form (without molting) (Hain, 1988). At this point the insect is permanently attached at that location. Balsam woolly adelgid feeding results in swelling at the nodes and internodes of branches throughout the crown of host trees, which in turn leads to reduced growth, crown deformity, and possible mortality within 10-20 years (Mitchell and Buffam, 2001; Spiegel et al., 2013). When infestations are concentrated on the main stem, growth can be reduced by more than 50%, and severe infestations can kill mature trees within three years (Spiegel et al., 2013).

White pine blister rust and balsam woolly adelgid are two examples of invasive organisms causing disruption of and disturbance to western forests. Unlike natural disturbance, invasive organisms are often met with little, no, or misguided defensive response(s) by the host tree. Thus, these invaders often proliferate within ecosystems unperturbed by factors regulating native disturbance agents (e.g. competition and predation). In the cases of white pine blister rust and balsam woolly adelgid, their impacts may lead to reduced growth and productivity of mature overstory trees and deformity or death of understory regeneration. Unlike defoliation or stand thinning by native bark beetles, the effects of non-native invasive organisms on long term stand succession are largely unknown. Probable consequences of these disturbances, however, may include: extirpation of susceptible host species or genera (either locally or regionally), or changes in tree species or genera composition within affected forests.

Human activities have also impacted natural and native disturbances. Land management records show a dramatic decline in the acreage of forested land burned since the early 1900s, largely due to organized fire suppression (Arno, 1986). Fire suppression typically favors species that are shade-tolerant, such as subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Englem.) (Keane and Arno, 1993; Logan and Powell, 2001), and reduces the competitiveness of many shade-intolerant pine species (Waring and Six, 2005). In this manner fire suppression has reduced the opportunities for some species to successfully regenerate (Keane and Arno, 1993) and altered natural landscape patterns.

ASSESSMENT

Documenting the occurrence, extent, and impacts of disturbance is key to understanding its relationship to landscapes. In turn, such documentation can also illuminate how best to manage and utilize these landscapes to maintain ecosystem services, support wildlife diversity, and support economic interests from recreation to industry. Disturbances large enough to impact more than a handful of trees can be detected through aerial detection surveys (ADS) or sketch mapping, which involves an observer identifying forest damage from an aircraft and manually recording the area and event on a map (Johnson and Ross, 2008).

Considered qualitative in nature, ADS data is primarily collected in order to locate areas where insects or disease are causing tree stress or, more often, tree mortality (Johnson and Ross, 2008). Dead or dying trees are typically drawn on a map as either a point or polygon, while noting the tree species, damage agent, and approximate location and area affected. As such, ADS is a valuable tool for detection of new disturbances and general monitoring of tree mortality (Johnson and Ross, 2008). These surveys do not typically include documentation of total stand conditions during and after disturbances, and mortality estimates are not always framed within the context of the abundance or species composition of surviving trees.

Unlike ADS, air photo interpretation (digital image classification) is a quantitative method of describing forest disturbances (Johnson and Ross, 2008). As such, this method is better suited to accurately monitor the progression of disturbances caused by insects and disease. Air photo interpretation typically documents the distribution and abundance of dead or dying trees within a target landscape. While less area is usually assessed by air photos than

ADS due to cost differences, the data is typically more precise. Like ADS, air photos, however, are not well suited to quantifying total stand conditions and describing the abundance or species composition of surviving trees or regeneration.

When more precise data is required, ground surveys of target areas provide higher resolution data than can be obtained by ADS or aerial photos. For understanding long term impacts of widespread disturbance events, data produced through the Forest Inventory and Analysis (FIA) research program can be useful. FIA collects data on a broad suite of vegetative and landscape characteristics on permanent study plots located throughout the United States (Smith, 2002). These plots are re-measured every 5-10 years (depending on the state in which they are located), and are randomly and widely spaced across the landscape (Smith, 2002).

FIA data is well suited to document the species composition, stand density and structure, as well as approximate mortality within stands. These plots are, however, of limited use for identifying uncommon or subtle disturbance agents. FIA plots are also not ideal for quantifying disturbances that were either localized or did not occur uniformly over a wide area, or capturing disturbance effects that occurred rapidly or over a brief period of time.

These disturbances are best assessed by ground surveys designed to examine specific disturbed areas. Ground surveys depend upon the aforementioned detection and monitoring tools to establish their need, location, and extent, but can provide much more detailed information. Ground surveys can be conducted using relatively standardized methods to enhance their applicability, but also modified on a case by case basis to address specific questions or challenges of different areas and disturbances.

The ground surveys (Figure 1.1) described in this dissertation (Chapters Two, Three, and Four) sought to assess aspects of two different disturbances affecting forests within the Intermountain West, and in doing so, to quantify the following parameters within the target habitat types:

- Cumulative mortality and patterns of mortality,

- Abundance and condition of trees that survived the disturbance,

- Changes in species composition and abundance, and to

- Estimate future forest conditions by assessing the abundance, health and composition of tree regeneration.

Target habitats were high elevation whitebark pine (*Pinus albicaulis* Engelmann) forests impacted by recent mountain pine beetle outbreaks and riparian subalpine fir forests that were potentially infested with balsam woolly adelgid. Whitebark pine is a five-needle stone pine (Owens et al., 2008) typical of many high elevation forests in western North America. As a group, high elevation five-needle pines are among the oldest documented living organisms (Logan and Powell, 2001). Slow growing and often occurring in areas with limited access, whitebark pine is of little commercial value. The value of whitebark pine is instead associated with its stabilization of steep slopes, watershed protection and snow pack retention, aesthetics, and important relationships with wildlife (Arno and Hoff, 1989; Gibson et al., 2008; Logan and Powell, 2001; Waring and Six, 2005 and references therein).

Like whitebark pine, subalpine fir is not usually considered a primary timber species, but is valued as an important buffer species for riparian areas and valuable wildlife habitat. Subalpine fir is very susceptible to balsam woolly adelgid (Spiegel et al., 2013), and the most severe infestations often occur in mesic low elevation areas (Mitchell and Buffam, 2001),

suggesting riparian habitats of the Intermountain West may be some of the most severely impacted by balsam woolly adelgid. Balsam woolly adelgid infestations have removed subalpine fir from entire meadows and other areas where subalpine fir is colonizing habitats opened up by disturbances (Mitchell and Buffam, 2001). Similar patterns may be highly problematic in areas where subalpine fir may succeed whitebark pine after mountain pine beetle infestations have reduced the latter from the landscape.

Balsam woolly adelgid has limited cold tolerance, but increased damage in high elevation subalpine fir forests has been observed following a 3-4 year period of above average temperatures (Mitchell and Buffam, 2001). The higher temperatures appear to have increased heat accumulation enough to allow more balsam woolly adelgids to reach the first instar prior to winter, allowing the population to expand. Physiological changes of the subalpine fir may also have led to greater susceptibility to balsam woolly adelgid attack (Mitchell and Buffam, 2001). Sustained increases in temperatures associated with climate change may allow balsam woolly adelgid populations to expand their range into new habitats and possibly sustain populations in high elevation subalpine fir (Mitchell and Buffam, 2001; Spiegel et al., 2013). This pressure, in addition to the insect and disease pressures impacting whitebark pine, could lead to substantial changes in high elevation ecosystems.
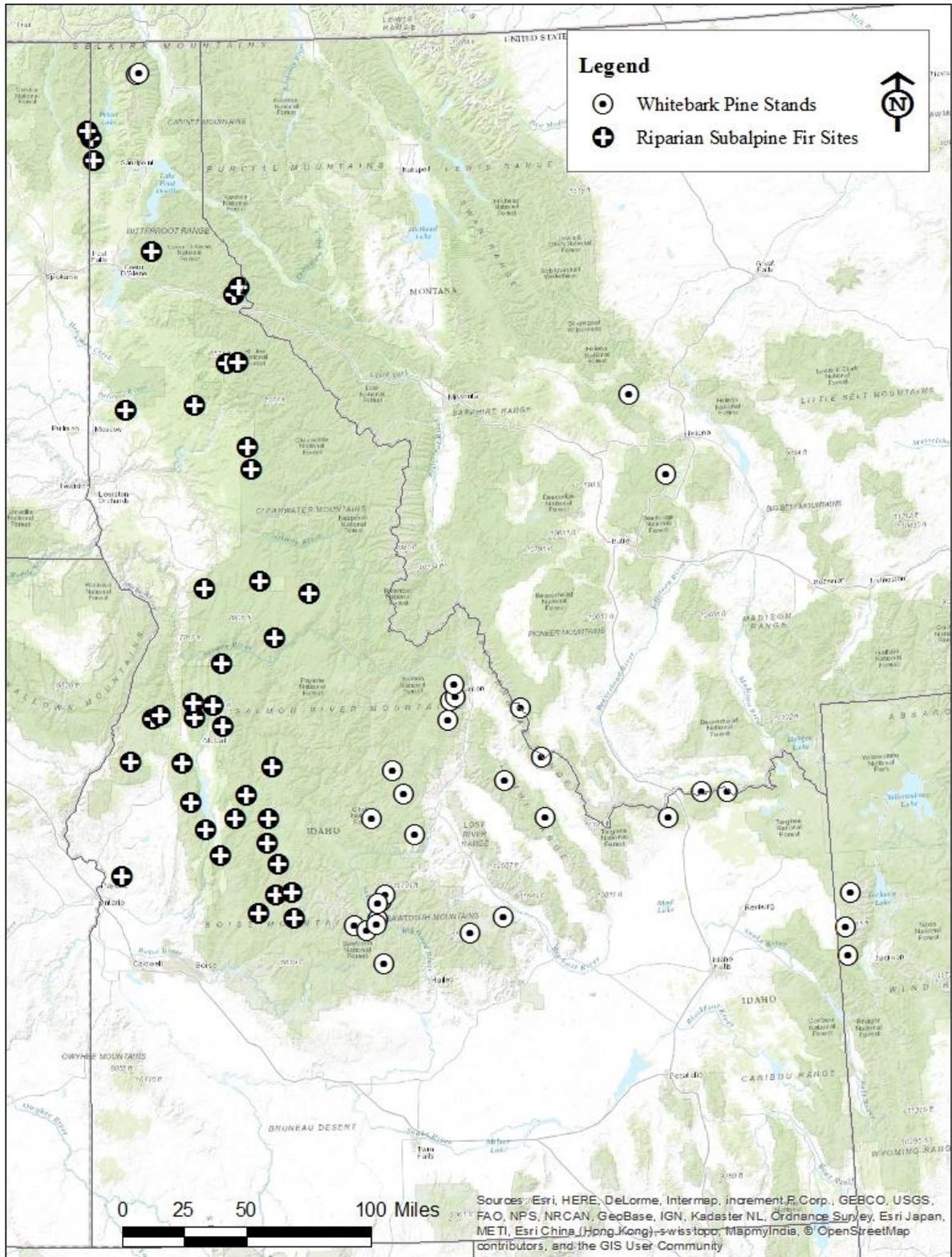
Figure 1.1. Whitebark pine stands (dot within circle) and subalpine fir (cross within circle) assessed by ground surveys.

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CHAPTER 2: WHITEBARK PINE STAND CONDITIONS AFTER MOUNTAIN PINE BEETLE INFESTATION

ABSTRACT

Pinus albicaulis Engelmann (whitebark pine) is a keystone species within many high elevation forest stands of the Intermountain West. Recent outbreaks of *Dendroctonus ponderosae* Hopkins (mountain pine beetle) have caused high mortality within many of these stands. The remote and rugged locations of these stands, as well as their relatively limited extent, often make these areas difficult to monitor and assess. Our objectives were to quantify and describe the severity of mountain pine beetle impacts on whitebark pine within high elevation forests. Thirty-two stands were assessed in 2012 and 2013 in central Idaho and adjacent areas in Wyoming and Montana where recent mountain pine beetle outbreaks occurred. The percentage of whitebark pine killed by mountain pine beetle ranged from five to 88%, averaging 47%. Whitebark pine killed by mountain pine beetle had significantly larger diameters than surviving whitebark pine. More whitebark pine that were part of tree clumps, however, were killed by mountain pine beetle than single-trunk whitebark pine; and the percentage of whitebark pine occurring in tree clumps was significantly greater at higher elevations.

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelmann) is an important species found in many high elevation forests in western North America (Logan and Powell, 2001). Whitebark pine is currently threatened throughout much of its natural range due to a combination of recent outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera:

Curculionidae), an introduced pathogenic fungus known as white pine blister rust (*Cronartium ribicola,* J.C. Fischer in Rabenhorst) (Pucciniales: Cronartiaceae), and forest succession (Gibson et al., 2008; Keane et al., 2002).

Mountain pine beetle is an important landscape level ecological force (Logan and Powell, 2001; Wood, 1982) and is widely known in western North America for its eruptive population dynamics (Bentz et al., 2011 and references therein). Mountain pine beetle is a member of the Scolytinae subfamily, which are considered the most destructive group of insects in conifer forests, and include the genera *Dendroctonus*, *Ips*, and *Scolytus* (Doane et al., 1936; Furniss and Carolin, 1977; Triplehorn and Johnson, 2005; Wood, 1982). Mountain pine beetle kill host trees by cutting off water and nutrient flow within the tree. This is done by their tunneling and feeding within the thin phloem layer (nutrient transport tissue), and by the pathogenic fungi they bring with them growing through the phloem and xylem layers (water transport tissue) (Phillips and Croteau, 1999).

Despite the harsh climate of high elevation habitats (Arno and Hoff, 1989; Logan and Powell, 2001) there appears to be a long association between mountain pine beetle and whitebark pine (Pureswaran, 2003). In the early 1900s explosive mountain pine beetle populations were recorded in the western United States (Gibson et al., 2008). During this time, high elevation whitebark pine in central Idaho experienced substantial mortality as a result of the outbreak (Perkins and Swetnam, 1996). More recently, the highest recorded mortality of high-elevation five-needle pines occurred as a result of mountain pine beetle epidemics between 1999 and 2009 (Gibson et al., 2008; Kegley et al., 2010).

Although mountain pine beetle outbreaks have occurred historically in whitebark pine, the additional impacts of white pine blister rust have exacerbated the landscape level

impacts of mountain pine beetle caused mortality (Schwandt, 2006). White pine blister rust is a non-native pathogenic fungus able to infect and kill five-needle pines, including whitebark pine. Mortality of five-needle pines from white pine blister rust infection is most rapid for small understory pine hosts (Geils et al., 2010), but large overstory hosts often experience reduced cone production for years before dying as a result of infection (Keane and Arno, 1993).

Whitebark pine is a stone pine in the subgenus *Strobus* (Owens et al., 2008) and is among the oldest documented living organisms (Logan and Powell, 2001). Slow growing and often occurring in areas with limited access, whitebark pine is of little commercial value. The value of whitebark pine is instead associated with its stabilization of steep slopes, watershed protection and snow pack retention, aesthetics, and its important relationships with wildlife (Arno and Hoff, 1989; Gibson et al., 2008; Logan and Powell, 2001; Waring and Six, 2005 and references therein). For example, whitebark pine is considered an important food resource for Clark's nutcracker (*Nucifraga columbiana* Wilson), squirrels (*Tamiasciurus* spp.), and bears (*Ursus* spp.) (Arno and Hoff, 1989; Hutchins and Lanner, 1982; Logan and Powell, 2001). While some cones may naturally fall to the ground and decay to release their seeds, ripening cones are frequently broken apart by seed predators (Arno and Hoff, 1989). Clark's nutcracker forages on whitebark pine seeds, and facilitates short and long distance seed dispersal of whitebark pine (Arno and Hoff, 1989; Hutchins and Lanner, 1982; Logan and Powell, 2001).

The remote and rugged locations of many whitebark pine stands, as well as their relatively limited extent, can make these areas difficult to monitor. Aerial detection surveys are used to document tree mortality, but coverage is not always complete or consistent, and

surveys only record current mortality, so cumulative mortality is not always known if areas are not flown annually. These surveys also fail to provide information on the abundance or condition of tree regeneration in the understory after a disturbance. Forest Inventory and Analysis crews collect a much finer resolution of data for forests throughout the United States, but only a small subset of areas are measured during any given year which limits the total amount of data available to assess the effects of specific forest disturbance events.

Kegley et al. (2010) helped address this information gap by documenting some of the impacts of mountain pine beetle outbreaks on whitebark pine in 42 stands throughout Idaho, Montana, and Wyoming. This project has expanded beyond those original 42 stands by incorporating additional areas within those states and increasing the resolution of data collected. The main objective was to quantify and describe the severity of mountain pine beetle impacts on whitebark pine within high elevation stands.

METHODS

Data Collection

Areas in central Idaho and adjacent areas in Wyoming and Montana where recent mountain pine beetle outbreaks occurred (approximately 1999-2009) were identified from past aerial detection surveys, local specialists, and other surveys. Within these areas, stands with a whitebark pine component (whitebark pine equal or exceeding approximately 25% of the stand) were sampled using modified FINDITS protocols (Forest Insect and Disease Tally) (Bentz, 2000; Kegley et al., 2010) with variable radius plots (up to ten) for mature overstory trees (diameter at breast height (DBH) greater than 12cm). Plots were two or more chains apart (minimum of 40.23m) along one of two transect bearings. The same number of chains were used between all plots within a stand. Bearings were determined at or before the first

plot. Bearing selection was based on the shape of the area in which the whitebark pine occurred, and with the intention of staying within the whitebark pine area, characterizing as much of that area as possible, and minimizing changes in slope, aspect, and elevation. For all plots a 2.5m prism was used to determine which trees were measured. Data recorded for variable radius plots included elevation, tree species, DBH (measured at a height of 1.4m above ground surface), condition, occurrence within a clump (multiple stems sharing a base), and mountain pine beetle impacts (as in Kegley et al., 2010).

Data Analysis

For each stand, tree composition was assessed by calculating the percent of the stand that each tree species represented. Within the whitebark pine component of each stand, the percent represented by each of the four condensed condition codes (defined below) were also calculated. Density was assessed by calculating the basal area of each measured tree ($0.0000785375*DBH^2$), and summed within a plot. Total plot density was then averaged across a stand.

Growth form was recorded for each stem as a binary characteristic. Following the terminology of Carsey and Tomback (1994), whitebark pine were classified as either single-trunk trees or tree clumps. We chose to use this terminology because multi-trunk trees (multiple trunks of one genet) and tree clusters (multiple trunks of two or more genets) are indistinguishable without genetic analysis (Schuster and Mitton, 1991). For our purposes, if a tree had multiple trunks (stems) originating below DBH it was considered a tree clump; otherwise the tree was considered a single-trunk tree. In this way, growth form was later averaged across each stand. Site characteristics such as elevation were measured at each plot and averaged by stand for analysis.

For ease of analysis at the stand level, whitebark pine FINDIT condition codes were condensed to represent four general conditions: live (FINDITS codes zero and five), recent mountain pine beetle caused mortality (FINDITS codes two, three, and four), old mountain pine beetle caused mortality (snags with J-shaped mountain pine beetle galleries) (Perkins and Swetnam, 1996) (FINDITS modified code 30 (Kegley et al., 2010)), and unknown cause of mortality (FINDITS codes one, eight, and nine) (Perkins and Swetnam, 1996). To describe individual tree mortality during the most recent mountain pine beetle epidemic, FINDITS codes were adjusted such that codes zero, five, and six corresponded to live trees, codes two, three, and four described trees recently killed by mountain pine beetle, and codes one, eight, nine, and thirty were excluded from analysis. As such, tree mortality caused by mountain pine beetle was regarded as a binary variable. For both rounds of FINDITS code adjustment, code seven trees (older mountain pine beetle strip attack) were assessed on a tree by tree basis relative to the other condition codes and comments pertaining to the tree.

Thirty-two stands were assessed in 2012 and 2013 within five national forests and one national recreation area (Table 2.1). Of these areas, the minimum mean stand elevation was 2,057m, the maximum was 3,033m, and the overall mean elevation of evaluated stands was 2,711m. The number of variable radius plots within stands ranged between four and 10, averaging 7 to 8 plots/stand. Overstory tree species observed on plots in addition to whitebark pine included lodgepole pine (*Pinus contorta* Douglas ex Loudon), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Englem.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The percentage of whitebark pine killed by mountain pine beetle ranged from five to 88%, averaging 47%.

Table 2.1. Number and land jurisdiction of whitebark pine stands assessed in 2012 and 2013.

National Forest or Recreation Area & State	Stands Assessed
Caribou-Targhee National Forest, ID	4
Caribou-Targhee National Forest, WY (Jedediah Smith Wilderness)	2
Helena National Forest, MT	2
Idaho Panhandle National Forest, ID (Kaniksu National Forest)	2
Salmon-Challis National Forest, ID	13
Sawtooth National Forest, ID	1
Sawtooth National Recreation Area, ID	8

Generalized linear mixed models and Pearson chi-square tests were used for analysis as appropriate for comparisons (SAS Enterprise Guide Version 6.100 Copyright 2013 by SAS Institute Inc.). No data transformations were performed, but binomial distributions were specified where relevant to the data. For analysis of individual tree mortality, stand was considered a random effect. Significance was determined relative to an alpha (α) value of 0.05.

RESULTS

Diameter at breast height of mature whitebark pine within measured stands ranged from 13cm to 171cm. At the stand level, average whitebark pine DBH had a more moderate range of 23cm to 65cm. The diameter of mature whitebark pine was significantly related to whether or not it was killed by mountain pine beetle, such that smaller diameter trees were more likely to have survived the mountain pine beetle infestation than larger diameter trees ($F(1,1378) = 70.71$, $p < 0.0001$).

The clumped growth form of whitebark pine was observed in all stands. The frequency of clumped whitebark pine among stands ranged from a minimum of 24% of the measured whitebark pine stems being part of a tree clump, to a maximum of 96%, and an

overall mean of 62% of the measured whitebark pine stems being part of a tree clump. The percent of whitebark pine occurring in tree clumps was significantly greater at higher elevations ($F(1,30) = 10.80$, $p = 0.0026$) (Figure 2.1), and whitebark pine growing in tree clumps had significantly smaller diameters than whitebark pine growing as single-trunk trees ($F(1,1365) = 23.67$, $p < 0.0001$).
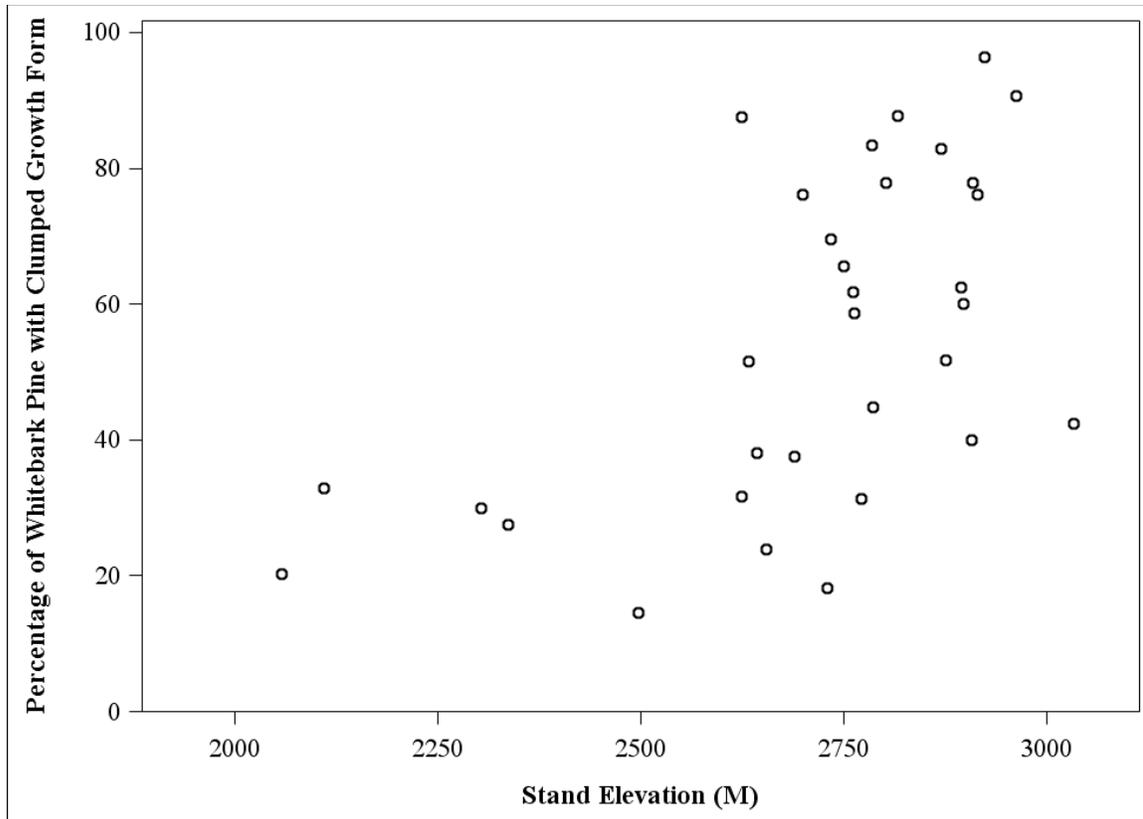
Figure 2.1. Distribution of the average percentages of whitebark pine that were part of a tree clump within stands across the mean elevation (meters) of stands.

The diameters of surviving whitebark pine (those not killed by mountain pine beetle) were not significantly different between trees that were part of a tree clump and single-truck trees ($F(1,420) = 0.74$, $p = 0.3901$) (Figure 2.2). That whitebark pine killed by mountain pine beetle had significantly larger diameters than surviving whitebark pine held true regardless of if the tree was growing as part of a tree clump ($F(1,876) = 28.70$, $p < 0.0001$) or as a single-

trunk ($F(1,456) = 40.29,\ p < 0.0001$) (Figure 2.2). The diameter of trees killed by mountain pine beetle that were part of a tree-clump, however, were significantly smaller than the diameter of single-trunk whitebark pine killed by mountain pine beetle ($F(1,912)=40.74$, $p<0.0001$) (Figure 2.2).
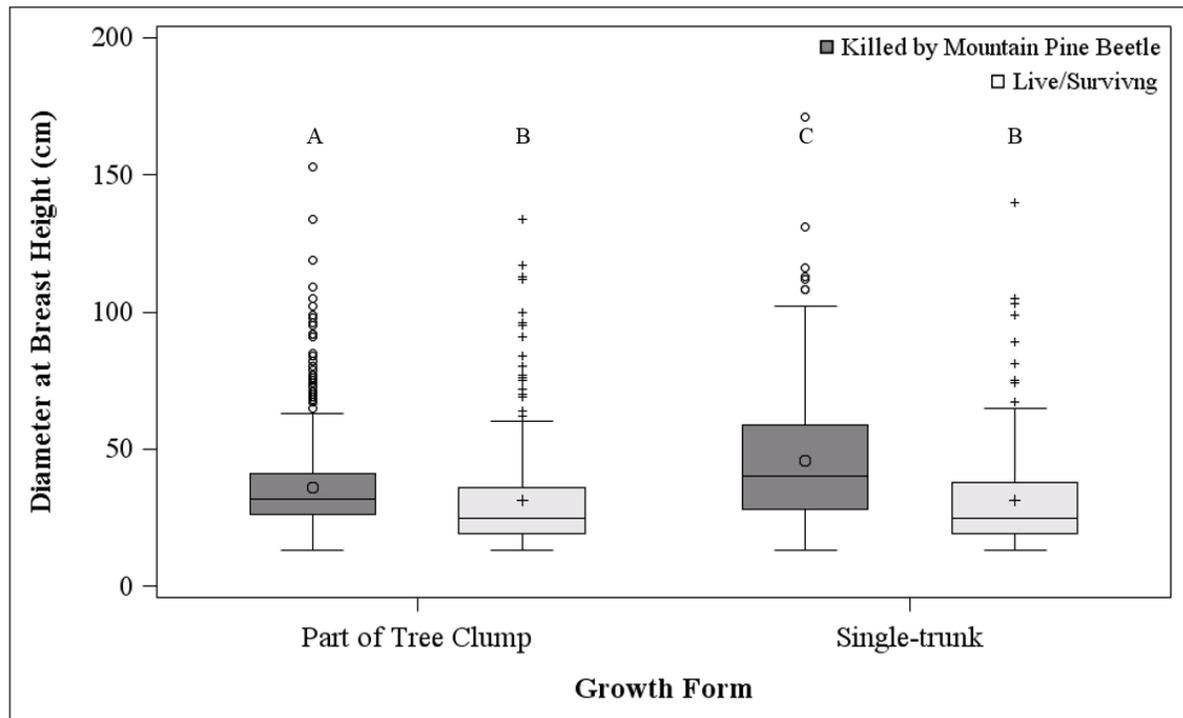
Figure 2.2. Distribution of diameters among whitebark pine that were either part of a tree clump or single-trunk trees, relative to whether or not they were killed by mountain pine beetle (excluding snags). Different letters indicate groups that were significantly different.

The percentages of whitebark pine that were part of a tree clump or single-trunk trees, and that were either killed by mountain pine beetle or live/surviving, were not equally distributed (χ^2 1,$N = 1398) = 7.9616, p = 0.0048$) (Table 2.2). The odds of a whitebark pine being killed by mountain pine beetle were 1.4 times greater if the tree was part of a tree clump than if it were single-stemmed.

Table 2.2. Frequency and percentages of whitebark pine occurring as part of a tree clump and as single-trunk trees relative to condition (killed by mountain pine beetle or live/surviving).

		Whitebark Pine Growth Form	
		Part of Tree Clump	**Single-trunk**
Whitebark Pine Condition	**Killed by Mountain Pine Beetle**	638 (Frequency)	307 (Frequency)
		45.64% of Total	21.96% of Total
		67.51% of Row	32.49% of Row
		70.19% of Column	62.78% of Column
	Live/Surviving	271 (Frequency)	182 (Frequency)
		19.38% of Total	13.02% of Total
		59.82% of Row	40.18% of Row
		29.81% of Column	37.22% of Column

At the stand level, the percent of whitebark pine killed by mountain pine beetle was not significantly related to the mean elevation of the stand, the density of whitebark pine within the stand (basal area), the percentage of the whitebark pine occurring in clumps, or the average diameter of whitebark pine within the stand. The percent of whitebark pine killed by mountain pine beetle was, however, significantly and negatively related to the percent of whitebark pine snags within the stand. This relationship remained significant for both snags bearing mountain pine beetle scars ($F(1,30) = 9.36$, $p = 0.0046$) (presumably from the outbreak occurring in the 1920's and 1930's), and trees without clear signs of a mortality agent (unknown mortality) ($F(1,30) = 6.21$, $p=0.0184$). Additionally, live whitebark pine had significantly smaller diameters than both whitebark pine recently killed by mountain pine beetle and old mountain pine beetle caused mortality ($F(3,1791) = 22.30$, $p < 0.001$). Whitebark pine recently killed by mountain pine beetle also had significantly smaller diameters than old mountain pine beetle caused mortality ($F(3,1791) = 22.30$, $p < 0.05$).

DISCUSSION

Our finding that larger diameter whitebark pine were more likely to have been killed by mountain pine beetle than smaller diameter trees is consistent with a large body of research relating host tree diameter to likelihood of attack by mountain pine beetle (Amman and Baker, 1972; Cole and Amman, 1969; Perkins and Roberts, 2003; Shanahan et al., 2016). This relationship held true regardless of tree growth form, such that larger stems were killed by mountain pine beetle more often than smaller stems for both single-trunk trees and tree clumps. Selection of larger host trees may benefit mountain pine beetle as these trees generally produce more brood, both in terms of beetles per unit area of bark and per tree (based on the greater surface area of bark) (Cole and Amman, 1969; Reid, 1963).

Interestingly, the tree diameter of single-trunk whitebark pine killed by mountain pine beetle was significantly greater than the DBH of clumped whitebark pine killed by mountain pine beetle. At the same time, the DBH of remaining live trees were not significantly different between single-trunk trees and clumped whitebark pine. Mountain pine beetle also killed more trees that were part of tree clumps than they did single-trunk whitebark pine. Therefore, the influence of diameter on mountain pine beetle host selection appears to be different for single-trunk trees and tree clumps. This finding is in agreement with earlier studies that have identified similar patterns for whitebark pine (Perkins and Roberts, 2003) and limber pines (Donnegan and Rebertus, 1999).

Mechanisms of mountain pine beetle host selection are not fully understood, but it is probable that visual (Shepherd, 1966) and olfactory (Moeck and Simmons, 1991) cues are used to select hosts, as well as random landing and assessment of close range host characteristics (gustatory, etc.) (Raffa and Berryman, 1982). Our results suggest that

mountain pine beetle attacked smaller diameter trees if they were part of a tree clump. The mechanism(s) behind this finding is not known, but we hypothesize that it may be the result of at least one of two scenarios. First, tree clumps may appear to have a larger silhouette (due to the adjoining stems) than single-trunk trees, and are thus perceived by mountain pine beetle as similar to a single, large-diameter tree. In other words, the stems within the tree clumps may have seemed larger to the mountain pine beetle than they actually were.

Second, the proximity of stems within a clump may have meant that if one stem within a tree clump was attacked by mountain pine beetle, the other stems within that tree clump were more likely to be attacked. The localized increase in stem density represented by tree clumps may have made individual stems within a clump more susceptible to mountain pine beetle selection and attack than the more widely spaced single-trunk trees (Mitchell and Preisler, 1991). Once one stem within a tree clump was attacked, mountain pine beetle may have been more likely to attack the adjoining stems due to spillover associated with aggregation pheromones produced by beetles within the initially attacked stem. Alternatively, one stem within a clump being colonized by mountain pine beetle may have increased the likelihood of the other stems within that clump being attacked due to the very close proximity of the stems to one another (relative to the distance between stems of separate trees) which would have offered a very short dispersal distance for new adult beetles emerging from the initially attacked stem (Perkins and Roberts, 2003).

Even when stems within a tree clump arise from different seeds (and are thus distinct individuals) they are more likely to be more closely related to their clump-mates than other single stemmed trees or other tree clumps (Furnier et al., 1987; Schuster and Mitton, 1991). This relatedness of stems may have served to further increase the likelihood of all stems

within a tree clump being attacked by mountain pine beetle once any stem within the tree clump was attacked.

Additional research is necessary to elucidate the mechanisms behind the relationships between host tree diameter, growth form, and mountain pine beetle attack. Such information could be provided by annual assessment of whitebark pine stands infested with mountain pine beetle, where the status of individual stems (single-trunk tree or part of tree clump) could be tracked relative to mountain pine beetle activity.

Without genetic analysis, we can only speculate as to the cause of the growth form variability we observed in whitebark pine. Proximate causes of whitebark pine tree clumps may include the caching behavior of Clark's nutcracker (Carsey and Tomback, 1994; Tomback, 1982), predisposition for early branching inherent to whitebark pine, and/or damage or stress resulting in a release from apical dominance (Schuster and Mitton, 1991). We suspect that the ultimate cause of the tree clumps we observed may, at least in part, be related to factors correlated with elevation. We found the percentage of whitebark pine occurring in tree clumps was positively correlated with higher elevations. Arno and Hoff (1989) also observed variability in the growth form of whitebark pine, and attributed it to environmental factors. When occurring at high elevation or near the tree line, Arno and Hoff (1989) noted that whitebark pine grew in krummholz and appeared more shrub-like. In New Zealand's temperate montane forests, multi-stemmed trees also increased in frequency with increasing elevation (Bellingham and Sparrow, 2009). When access to light is not limited by competing trees, multi-trunk trees may be better competitors for soil resources, and have greater resource 'sinks' (Chamberlin and Aarssen, 2017 and references therein).

Similarly, we can only speculate on the relationship between diameter and growth form, but it may, at least in part, be related to how the data were collected. Carsey and Tomback (1994) found that for limber pine (*Pinus flexilis* James) the clumped growth form regularly resulted from germination of multiple seeds clustered together (presumably in forgotten animal caches) and from branching of single seeds (genets) after germination. In our study, it may be that large diameter, multi-top trees began their lives as a clump of multiple stems, with the closely related stems fusing over time as the tree grew (Schuster and Mitton, 1991). Alternatively, it may be that stem-to-stem competition results in the individual stems within a clump growing more slowly relative to single stemmed trees.

At the stand level, few variables were significantly related to the percentage of the whitebark pine recently killed by mountain pine beetle. There was no significant relationship between the percentage of whitebark pine killed by mountain pine beetle in a stand and stand elevation or dominance of the clumped growth form in a stand. This lack of significance is counterintuitive given the positive association between elevation and the occurrence of clumped whitebark pine, and the increased likelihood of mountain pine beetle attacking clumped whitebark pine compared to single stemmed whitebark pine. There were also no significant relationships between the percentage of whitebark pine killed by mountain pine beetle and the density of whitebark pine in a stand, or the average diameter of whitebark pine within a stand. However, live whitebark pine did have significantly smaller diameters than both whitebark pine recently killed by mountain pine beetle and old mountain pine beetle caused mortality. Additionally, recently killed whitebark pine had significantly smaller diameters than old mountain pine beetle-caused mortality.

These findings are in agreement with earlier studies of the mountain pine beetle outbreak that affected whitebark pine stands between 1909-1940s, which peaked in 1930 (Perkins and Swetnam, 1996). These studies found that small diameter trees were killed less frequently than larger diameter trees, and suggested that during the 1930s outbreak, mountain pine beetle preferred larger diameter whitebark pine hosts (Perkins and Roberts, 2003; Perkins and Swetnam, 1996). It is possible, if not probable, that the old mountain pine beetle caused mortality we observed is from the 1930s outbreak, and thus our observations corroborate those of earlier studies. Thus, it may be that the patterns we observed relate to historical outbreaks of mountain pine beetle in these whitebark pine stands and the cumulative effects of mountain pine beetle host selection behavior on whitebark pine stand structures.

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CHAPTER 3: REGENERATION PATTERNS WITHIN WHITEBARK PINE STANDS AFTER MOUNTAIN PINE BEETLE INFESTATION

ABSTRACT

Whitebark pine (*Pinus albicaulis* Engelm.) is a keystone species of high elevation ecosystems throughout western North America. Whitebark pine is experiencing high mortality throughout much of its range due to a combination of recent insect outbreaks, an introduced pathogenic fungus, and forest succession (Gibson et al., 2008; Keane et al., 2002) (Gibson et al., 2008; Keane et al., 2002). Our objective was to quantify the abundance, health, and species composition of tree regeneration within high elevation forests, and to look for possible patterns of association between regeneration in the understory and the condition and composition of trees in the overstory. On average, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) regeneration was more abundant than any other species. Whitebark pine was the second most abundant species, followed by lodgepole pine (*Pinus contorta* Douglas ex Loudon). There was a strong association between mature subalpine fir in the overstory and subalpine fir regeneration, both in terms of density and percent of the stand composed of subalpine fir. The percentages of whitebark pine and subalpine fir regeneration were inversely associated relative to elevation, such that subalpine fir regeneration was more dominant at lower elevations, and whitebark pine was more dominant within the regeneration at higher elevations.

INTRODUCTION

Pinus albicaulis Engelmann, commonly known as whitebark pine, is a five-needle stone pine in the subgenus *Strobus* (Owens et al., 2008) typical of many high elevation forests in western North America. High elevation five-needle pines are among the oldest

documented living organisms (Logan and Powell, 2001). Slow growing and often occurring in areas with limited access, whitebark pine is of little commercial value. The value of whitebark pine is instead associated with its stabilization of steep slopes, watershed protection and snow pack retention, aesthetics, and its important relationships with wildlife (Arno and Hoff, 1989; Gibson et al., 2008; Logan and Powell, 2001; Waring and Six, 2005 and references therein). As such, whitebark pine is considered a keystone species of high elevation ecosystems throughout western North America.

Between approximately 1999 and 2009 mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae)) epidemics occurred throughout the Intermountain West, including within forest stands at high elevations (Gibson et al., 2008; Kegley et al., 2010). As a result, whitebark pine experienced elevated mortality levels throughout much of its natural range. Impacts of mountain pine beetle in these areas have been exacerbated by mortality and reduced cone production caused by white pine blister rust (*Cronartium ribicola* J.C. Fischer in Rabenhorst (Pucciniales: Cronartiaceae), a non-native pathogenic fungus), and competition resulting from forest succession (Gibson et al., 2008; Keane et al., 2002). Although mountain pine beetle outbreaks have historically occurred in whitebark pine, the additional impacts of white pine blister rust have complicated and intensified the landscape level impacts of mountain pine beetle-caused mortality (Schwandt, 2006).

The remote and rugged locations of these stands, as well as their relatively limited extent, often make them difficult to monitor. Aerial detection surveys are used to document tree mortality, but coverage is not always complete or consistent, and surveys only record current mortality, so cumulative mortality is not always known if areas are not flown

annually (Kegley et al., 2010). These surveys also fail to provide information on the abundance or condition of tree regeneration in the understory after a disturbance. Forest Inventory and Analysis crews collect a much finer resolution of data for forests throughout the United States, but only a small subset of areas are measured during any given year on a set schedule, which limits the total volume of data available to assess the effects of specific forest disturbance events.

Kegley et al. (2010) helped address this information gap by documenting some of the impacts of mountain pine beetle outbreaks on whitebark pine in 42 stands throughout Idaho, Montana, and Wyoming. Kegley et al. (2010) also assessed tree regeneration within these stands using 1/300th acre subplots, but found this plot size too small to consistently quantify the condition of whitebark pine regeneration. Given this limitation, Kegley et al. (2010) assessed the condition of whitebark pine regeneration of most stands using off-plot tallies. They found that the regeneration of 69% of measured stands was dominated by subalpine fir. Additionally, between zero and 81% of whitebark pine regeneration was infected with white pine blister rust. This project has expanded beyond those original 42 stands by incorporating additional areas. Our objective was to quantify the abundance, health, and species composition of tree regeneration by using larger plots to capture more of the understory, and to look for possible patterns of association between regeneration and the condition and composition of trees in the overstory.

METHODS

Data Collection

Areas in Idaho and adjacent areas in Wyoming and Montana where recent mountain pine beetle outbreaks occurred (approximately 1999-2009) were identified from past aerial

detection surveys, local specialists, and other surveys. Within these areas, stands with a whitebark pine component (at or exceeding approximately 25% of the stand) were sampled using two different types of plots. Mature trees (DBH greater than 12cm) were sampled using modified FINDITS protocols (Bentz, 2000) with variable radius plots (up to ten). A 2.5m prism was used to determine which trees were measured. Data recorded for variable radius plots included elevation, tree species, diameter, condition, and mountain pine beetle impacts (as in Kegley et al., 2010).

Variable radius plots were two or more chains apart (minimum of 40.23m) along one of two transect bearings. The same number of chains were used between all plots on a site. Bearings used to move between plots were determined at or before the first plot. Bearing selection was based on the shape of the area in which the whitebark pine occurred, and with the intention of staying within the whitebark pine area, characterizing as much of that area as possible, and minimizing changes in slope, aspect, and elevation.

Regeneration was quantified along the distance (straight line transect) between variable radius plots. These rectangular plots were 36.1m long and 2m wide, with an area of 72.2m^2. Within these plots, regeneration of all tree species was recorded. Regeneration was defined as trees with a diameter at breast height (1.37m) less than 12cm, and broken into three size classes: seedling (height less than 15.2cm), intermediate (height greater than 15.2cm, but less than 1.37m), and sapling (height greater than 1.37m). For whitebark pine regeneration, trees were also assessed for visible white pine blister rust infections.

Thirty-two stands were assessed in 2012 and 2013 in the Caribou-Targhee National Forest (Idaho and Wyoming), Helena National Forest (Montana), Kaniksu National Forest (Idaho Panhandle National Forests, Idaho), Salmon-Challis National Forest (Idaho),

Sawtooth National Forest (Idaho), and the Sawtooth National Recreation Area (Idaho).

Stands ranged from 2,057-3,033m, with an average elevation of 2,711m. The number of

variable radius plots within stands ranged between four and 10, averaging 7 to 8 plots/stand.

Overstory tree species observed on plots in addition to whitebark pine included lodgepole

pine (*Pinus contorta* Douglas ex Loudon), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.),

Engelmann spruce (*Picea engelmannii* Parry ex Englem.), and Douglas-fir (*Pseudotsuga*

menziesii (Mirb.) Franco).

Data Analysis

For each stand, tree composition was assessed by calculating the percentage of the

stand represented by each recorded tree species. Within the whitebark pine component of

each stand, the percent represented by each of the four condensed condition codes (see

below) were also calculated. Density was assessed by calculating the basal area of each

measured tree ($0.0000785375*DBH^2$), and summed within a plot. Total plot density was then

averaged across a stand. Clumping (as defined in Chapter Two) was recorded for each stem

as a binary variable (present or not present), and averaged across each stand. Site

characteristics such as elevation were measured at each plot and averaged by stand for

analysis.

For ease of analysis at the stand level, whitebark pine FINDITS condition codes

(Bentz, 2000) were condensed to represent four general conditions: live (FINDITS codes

zero and five), recent mountain pine beetle caused mortality (FINDITS codes two, three, and

four), old mountain pine beetle caused mortality (snags) (FINDITS modified code 30

(Kegley et al., 2010)), and unknown cause of mortality (FINDITS codes one, eight, and

nine). FINDITS code seven trees (older mountain pine beetle strip attack) were assessed on a tree-by-tree bases relative to the other condition codes and comments pertaining to the tree.

Regeneration within stands were averaged across plots for the species and size classes represented to derive composition percentages. Species that were unidentifiable or infrequently observed (contributing less than five percent to total species composition of a stand) were grouped into a single category called minor species (MS). Minor species included Douglas-fir, Engelmann spruce, aspen (*Populus* spp.), and juniper (*Juniperus* spp.). Due to sites having different numbers of plots within them, regeneration abundance was standardized by dividing the number of trees of each species and size class by the number of plots occurring within that site. ANOVA was used for comparisons among size classes of regeneration (SAS Enterprise Guide Version 6.100 Copyright 2013 by SAS Institute Inc.). Pearson correlations analyses were used for comparisons among variables and attributes (SAS Enterprise Guide Version 6.100 Copyright 2013 by SAS Institute Inc.). Significance was determined relative to an alpha (α) value of 0.05.

RESULTS

The density of size classes (seedling, intermediate, and sapling) of whitebark pine regeneration were not significantly different ($F(2, 93) = 0.95$, $p = 0.3892$), however, intermediate sized trees tended to be the most common. A similar pattern was observed for lodgepole pine regeneration ($F(2, 93) = 1.26$, $p = 0.2884$). The abundance of minor species size classes (Douglas-fir, Engelmann spruce, juniper, aspen, and unidentifiable regeneration) followed a similar pattern, and differences were not significant ($F(2, 93) = 2.71$, $p = 0.0716$). For subalpine fir, intermediate sized trees were significantly more common than both seedlings and saplings ($F(2, 92) = 4.50$, $p = 0.0137$).

The percentage of regeneration made up by whitebark pine was negatively correlated (r(n=30) = -0.61310, p = 0.0002) with the percentage of the overstory that was made up of non-pine species (such as subalpine fir, Engelmann spruce, and Douglas-fir). There was a weak negative correlation between the average density of whitebark pine regeneration (trees/hectare) and the basal area of stands (r(n=30) = -0.33489, p = 0.0610). There were no significant correlations between any size class of whitebark pine regeneration and any condition class of mature whitebark pine. The percentage of lodgepole pine in the regeneration was positively correlated with the percent of lodgepole pine in the overstory (r(n=30) = 0.75416, p < 0.0001). Similarly, the average density of lodgepole pine regeneration (trees/hectare) was positively correlated with the basal area of live mature lodgepole pines (r(n=30) = 0.82379, p < 0.0001) and the basal area of mature lodgepole pine (r(n=30) = 0.57220, p = 0.0006).

There was a positive correlation between the percentage of the overstory that was composed of mature subalpine fir and the percentage of subalpine fir regeneration (r(n=30) = 0.60212, p = 0.0003), specifically seedling (r(n=30) = 0.36346, p = 0.0409) and intermediate (r(n=30) = 0.49873, p = 0.0037) sized trees. Additionally, the average density of subalpine fir regeneration was positively correlated with the basal area of live mature subalpine fir (r(n=30) = 0.38329, p = 0.0304). On average, subalpine fir regeneration was more abundant per hectare than whitebark pine, lodgepole pine, or minor species; whitebark pine regeneration was more abundant than either lodgepole pine or minor species regeneration (F(3, 379) = 22.60, p < 0.0001). The average density of lodgepole pine or minor species regeneration were not significantly different from one another.

There was no apparent association between the density of whitebark pine, lodgepole pine, or minor species of regeneration and elevation. The density of subalpine fir regeneration was negatively correlated with elevation (r(n=30) = -0.40674, p = 0.0209), as was the total density of regeneration (r(n=30) = -0.37612, p = 0.0339). A similar pattern was observed between the basal area of mature tree species and elevation, such that there was no apparent association between the basal area of whitebark pine, lodgepole pine, or minor species and elevation, but the basal area of subalpine fir was negatively correlated with elevation (r(n=30) = -0.49733, p = 0.0038).

For regeneration, elevation was positively correlated with the percentage of whitebark pine present (r(n=30) = 0.49492, p = 0.0040), and negatively correlated with the percentage of subalpine fir (r(n=30) = -0.46603, p = 0.0072) in the regeneration (Figure 3.1). Elevation was also positively correlated with the percentage of mature whitebark pine (r(n=30) = 0.51284, p = 0.0027), and negatively correlated with the percentage of mature subalpine fir (r(n=30) = -0.52939, p = 0.0018) in the overstory.
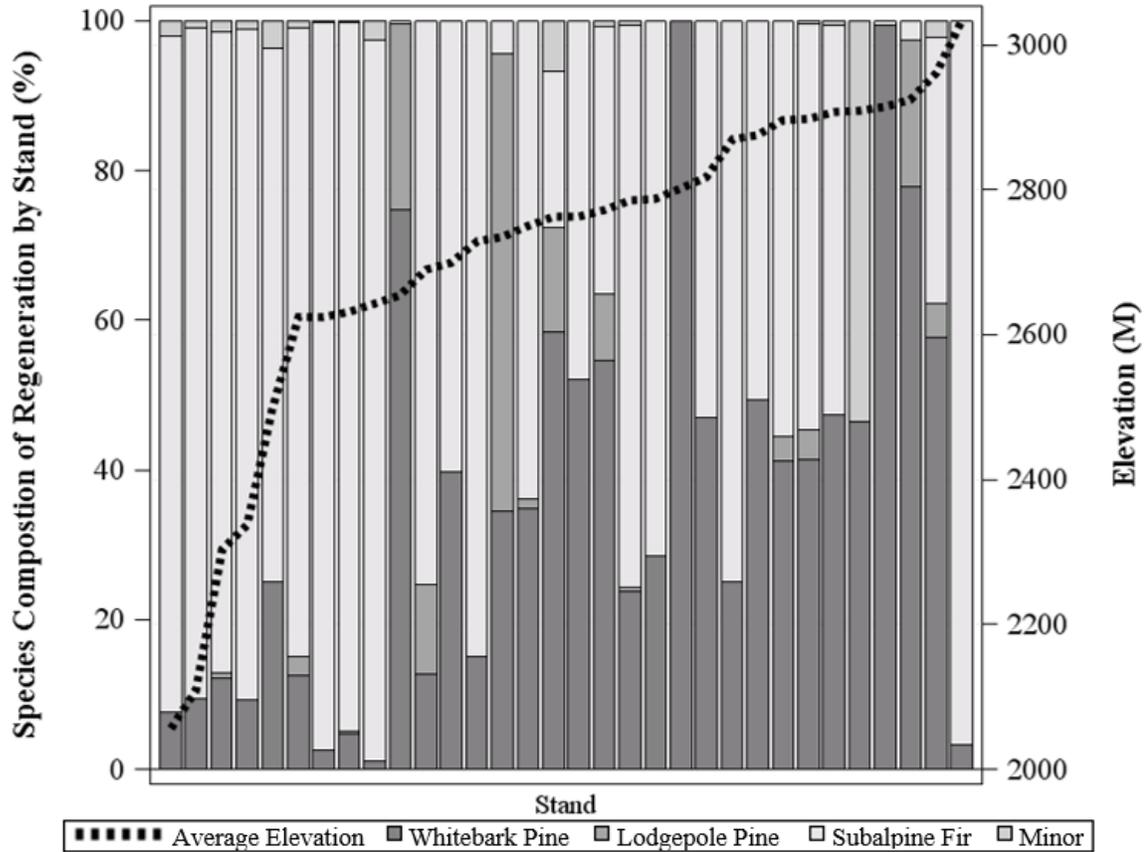
Figure 3.1. Species composition of regeneration measured within stands (each species shown as percent of total regeneration for respective stands), relative to average elevation of each stand.

The percentage of mature whitebark pine with visible white pine blister rust infections was positively correlated with the percentage of whitebark pine regeneration that had visible blister rust infections (r(n=30) = 0.53194, p = 0.0062). Elevation was negatively correlated with both the percentage of mature whitebark pine (r(n=30) = -0.46678, p = 0.0081) and the percentage of whitebark pine regeneration (r(n=30) = -0.80325, p < 0.0001) with visible white pine blister rust infections (Figure 3.2).
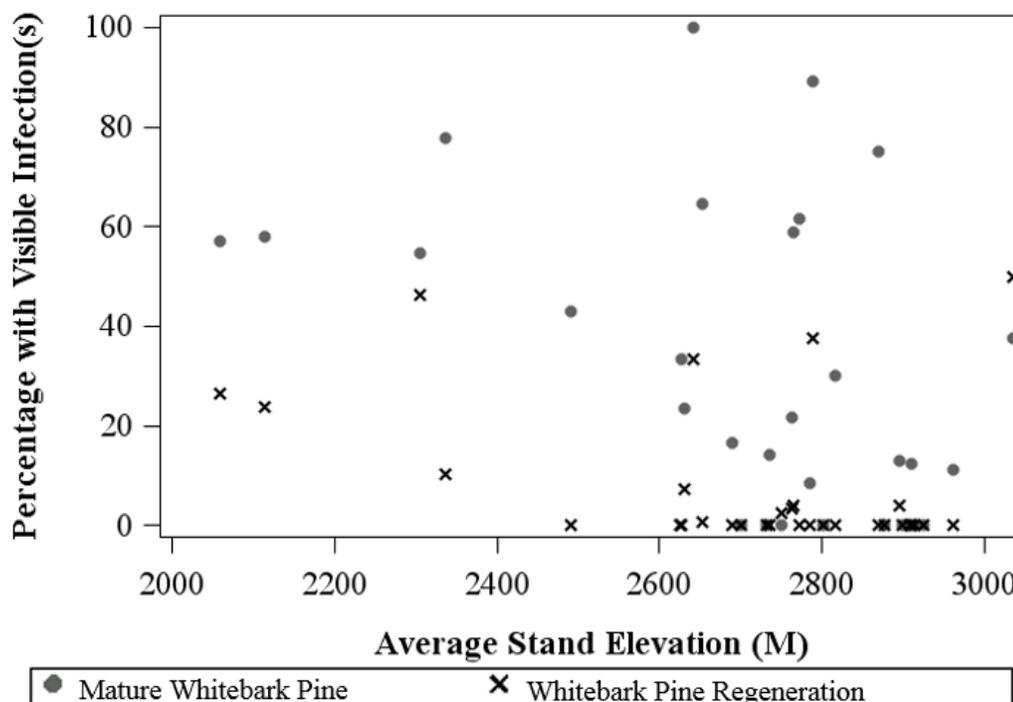
Figure 3.2. Percentage of mature whitebark pine and percentage of whitebark pine regeneration that had visible blister rust infections relative to the average elevation of the stand in which they occurred.

DISCUSSION

Among whitebark pine and lodgepole pine, respectively, the density of size classes (seedling, intermediate, and sapling) were not significantly different, but intermediate sized trees tended to be the most common. The abundance of minor species size classes (Douglas-fir, Engelmann spruce, juniper, aspen, and unidentifiable regeneration) followed a similar pattern. For subalpine fir, intermediate sized trees were significantly more common than seedlings and saplings. It may be that the recent disturbances in the overstory of these stands temporarily increased the number of seeds or seedling success, which might explain the relative abundance of intermediate sized regeneration (Parker, 1988). Alternatively, the abundance of intermediate sized trees may have increased the competition faced by establishing seedlings, reduced their success, and thus also their abundance. Otherwise, this

finding may simply reflect the influence of temporally variable climatic patterns on cone crop production of mature subalpine fir (Parker, 1988; Woodward et al., 1994).

Whitebark pine is typically considered a shade-intolerant species (Parker, 1988). Within the context of the stands we measured, our results suggest that whitebark pine regeneration is more likely to be successful in relatively open stands dominated by mature whitebark pine. This conclusion is supported by our observation that the percentage of the regeneration that was whitebark pine was negatively correlated with the percentage of the overstory that was made up of non-pine species, and that the average density of whitebark pine regeneration (trees/hectare) was negatively associated with stand basal area. Higher basal area of mature whitebark pine, however, was not correlated with whitebark pine regeneration. Thus, the whitebark pine overstory component of these stands may not always directly contribute to understory whitebark pine regeneration. This would be supported by studies that demonstrate the importance of long distance bird-mediated seed dispersal for whitebark pine regeneration (Tomback, 2001, 1982). There are likely many other factors that influence the success of whitebark pine regeneration, such as soil characteristics and recent climate trends. Thus our conclusions regarding patterns of whitebark pine regeneration are generalizations of an undoubtedly complex process.

On the other hand, there was a strong association between mature lodgepole pine in the overstory and lodgepole pine regeneration. The total density of lodgepole regeneration was positively correlated with mature lodgepole pine basal area. Similarly, the percentage of lodgepole pine in the regeneration was positively correlated with the percentage of lodgepole pine in the overstory. Unlike whitebark pine, lodgepole pine is not well known for having bird-mediated long distance seed dispersal. Therefore the positive association between

mature and understory lodgepole pine is consistent with the life history and biology of this species.

There was a strong and consistent association between mature subalpine fir in the overstory and subalpine fir regeneration, both in terms of density and percentage of the stand composed of subalpine fir. On average, subalpine fir regeneration was more abundant per hectare than any other species. Whitebark pine was the second most abundant species, followed by lodgepole pine and other minor species. In stands where it occurs, the numerical dominance of subalpine fir likely represents an important source of resource competition for other trees species, including whitebark pine. This pattern was also observed by Kegley et al. (2010), who found subalpine fir to be the most abundant species of regeneration in over half of the whitebark pine stands they assessed.

While there was no apparent association between the density of whitebark pine, lodgepole pine, or minor species of regeneration and elevation, the density of subalpine fir regeneration was negatively correlated with elevation, as was the total density of regeneration. A similar pattern was observed between the basal area of mature tree species and elevation, such that there was no apparent association between the basal area of whitebark pine, lodgepole pine, or minor species and elevation, but the basal area of subalpine fir was negatively correlated with elevation. The basal area of mature subalpine fir and the density of subalpine fir regeneration were both greater at lower elevations.

Elevation was positively correlated with the percentage of mature whitebark pine, and negatively correlated with the percentage of mature subalpine fir in the overstory, such that a greater percent of stands at higher elevations were made up of whitebark pine, and at lower elevations there was a greater percent of subalpine fir present within mature stands. The

percentages of whitebark pine and subalpine fir regeneration were inversely associated relative to elevation, such that subalpine fir was more dominant within the regeneration at lower elevations, and whitebark pine was more dominant within the regeneration at higher elevations.

Thus patterns were detected among the different percentages of regeneration species relative to elevation, but not always between the density of species and elevation. This finding may indicate that for less common species, such as lodgepole pine and minor species, their occurrence was too sporadic or infrequent for patterns to become apparent. For whitebark pine, it appears that while the density of regeneration does not change with elevation, the relative dominance of that regeneration within the understory community does change with elevation. This may indicate that whitebark pine regeneration experiences less competition from other species at higher elevations. Furthermore, elevation was negatively correlated with both the percentage of mature whitebark pine and the percentage of whitebark pine regeneration with visible white pine blister rust infections. Thus higher elevation habitats may be less susceptible to white pine blister rust infection, possibly because of more arid conditions or other factors associated with air (and thus spore) movement. These higher elevation sites, however, may be less productive than their lower elevation counterparts. Additional studies investigating growth rates and survival of whitebark pine regeneration in relation to competitive pressure and environmental factors (such as those associated with elevational gradients) could help fill this information gap.

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CHAPTER 4: CONDITION OF RIPARIAN SUBALPINE FIR IN IDAHO RELATIVE TO BALSAM WOOLLY ADELGID INFESTATION

ABSTRACT

Balsam woolly adelgid (*Adelges piceae* Ratz.) is a European species of tree-infesting hemipteran invasive in North America on true fir (*Abies* spp.). Subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) exhibits little resistance to this insect and has been severely impacted in many areas of Oregon, Washington, and Idaho. We documented balsam woolly adelgid infestations in riparian fir forests of Idaho. Balsam woolly adelgid stem infestations were positively correlated with gouting in mature crowns of both subalpine fir and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.). Heavy balsam woolly adelgid stem infestations were negatively correlated with elevation for both subalpine fir and grand fir. Similar to what was observed in mature fir trees, the percentage of host regeneration with balsam woolly adelgid stem infestation was positively correlated with the percent of host regeneration with gouting for both subalpine fir and grand fir. The percentage of subalpine fir regeneration with balsam woolly adelgid stem infestation was also positively associated with the percentage of infested mature subalpine fir and the percentage of the site made up of true fir species. Among true fir regeneration, balsam woolly adelgid stem infestations of subalpine fir and grand fir were positively correlated with one another. Further work is needed to fully describe the chronology of impacts balsam woolly adelgid has on different host species under different growing conditions in western North America.

INTRODUCTION

The balsam woolly adelgid (*Adelges piceae* Ratz.) (Hemiptera: Adelgidae) is a European species of tree-infesting hemipteran (Balch 1952). Balsam woolly adelgid was first

documented on species of true fir (*Abies* spp.) in North America around 1900 in the northeastern United States and southeastern Canada (Balch, 1952; Kotinsky, 1916). Records of balsam woolly adelgid on fir in the western coastal forests of the United States and Canada followed in 1928 (Mitchell and Buffam 2001). Since its introduction, balsam woolly adelgid has steadily spread inland and become an influential mortality agent of true firs in North America (Mitchell and Buffam, 2001 and references therein).

Members of the subfamily Adelginae, to which the balsam woolly adelgid belongs, typically have a two-year, two-host life cycle (Mitchell and Buffam, 2001). Spruce (*Picea*) species serve as the primary host and harbor the sexually reproducing stage, while true firs are the secondary host and the feeding substrate for the parthenogenetic subcycle of wingless females (Mitchell and Buffam, 2001). In North America (and much of Europe), balsam woolly adelgid populations are made up exclusively of parthenogenetic wingless females, and thus only occur on species of true firs. Dispersal between host trees is passive, and only eggs and the immature crawler (motile nymph) stage are able to disperse among hosts by wind or animal transport. Balsam woolly adelgid populations can expand rapidly (females produce 50 to 250 eggs each, and multiple generations per year may occur) where host trees are available (Balch, 1952; Hain, 1988; Ragenovich and Mitchell, 2006; Tunnock and Rudinsky, 1959).

Balsam woolly adelgid feeds by inserting long stylets into the intercellular spaces within the cortex (and sometimes phloem) of host trees (Balch 1952). As the adelgid feeds, it probes within the tree tissue, but does not fully extract the stylet after the initial insertion (Balch 1952). Salivary secretions are also injected into the host tissue, forming a "sheath" around the stylet (Balch 1952). These secretions are hypothesized to be disruptive or toxic to

the host, and result in abnormal cell growth leading to gouting of buds and nodes on branches, and formation of rotholz (red wood or premature heartwood) within the main stem (Balch 1952; Hain 1988). In the case of gouting, branch elongation and needle retention and production are reduced (Livingston, 2000). The formation of rotholz in the xylem tissue leads to reduced water transport, and consequently reduced photosynthesis and respiration (Hain, 1988 and refences therein). These effects of balsam woolly adelgid infestation can lead to reduced growth, deformity, and tree death (Hain, 1988; Mitchell and Buffam, 2001; Spiegel et al., 2013).

All species of true firs native to North America are potential hosts for balsam woolly adelgid. Susceptibility of these hosts depends on species, location, and host condition and/or site productivity (Mitchell and Buffam, 2001). Subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) exhibits little resistance to balsam woolly adelgid and is considered one of the most susceptible host species. Subalpine fir has been severely impacted by balsam woolly adelgid infestations in many lower elevation areas in Oregon and Washington (experiencing up to 52% mortality (Spiegel et al., 2013)), and up to 90% mortality of true firs in some parts of Idaho (Livingston, 2000). Balsam woolly adelgid infestations were first discovered in Idaho in 1983 (Livingston and Pederson, 2010), and have been predicted to encompass most of the range of subalpine fir in Idaho (Livingston, 2000).

While not typically considered an economically important species, subalpine fir is an important habitat component in high elevation forests and sensitive riparian zones. The intrusion of balsam woolly adelgid into these ecosystems could reduce the abundance of subalpine fir and change the structure of these ecosystems. Reduction of subalpine fir in high elevation and riparian forests may have negative consequences for the ecological services

provided by these sensitive habitats, which could be followed by cascading effects throughout adjoining landscapes.

Aerial detection survey (ADS) is widely used for monitoring the presence, extent, and severity of numerous insect and disease agents within forested landscapes. Although forest mortality caused by balsam woolly adelgid has been recorded by ADS for much of Idaho since the late 1990s, it is estimated that millions of acres of Idaho forests host balsam wooly adelgid populations at levels undetectable from the air (Livingston, 2000). Moist, poorly drained sites represent high quality habitats for subalpine fir, and have been associated with larger populations of balsam woolly adelgid than dry well-drained sites (Hain, 1988). In Washington and Oregon, such areas were also associated with the most damaging balsam woolly adelgid population (Mitchell and Buffam, 2001).

The impact and extent of balsam woolly adelgid-caused mortality in riparian areas of Idaho, however, are not well understood. Our overall goal was to address this information gap by documenting balsam woolly adelgid infestations in riparian fir forests of Idaho. We used ground surveys to quantify balsam woolly adelgid and associated symptoms of infestation on mature trees in the overstories of these stands. We also assessed the abundance, species composition, and condition of understory tree regeneration within these riparian areas.

METHODS

Data Collection

Stands affected by balsam woolly adelgid were identified using recent ground and aerial survey data, and by consulting with local experts. A riparian subalpine fir site was defined as an area within 100m of surface water (stream, lake, river, etc.) where subalpine fir

occurred in the overstory of the stand. No more than three sites were placed along any given waterway.

At each site, three plots were established to measure mature trees in the overstory. Prior to entering Plot 1, six subalpine fir were identified and used within a randomization process to initiate exact plot location. These six trees were temporarily numbered and a roll of a six-sided die determined which tree was used to determine plot center. For the tree whose number was rolled, we measured 15m from that tree towards the waterway. This 15m served as the plot diameter, and 7.5 meters from the tree toward the waterway was plot center. Thus the area of each plot was 176.71m^2, or 0.017671 hectares. Where possible, Plots 2 and 3 were placed on either side of Plot 1. Plots were located at least 25m apart. Distance between neighboring plots was straight, but may have pivoted from plot-to-plot to follow the contours of the waterway.

Only trees with a diameter at breast height (DBH) of 5cm or greater were classified as mature. For every mature tree within a plot, species, DBH, and foliage condition (Table 4.1) were recorded. For true firs, balsam woolly adelgid stem infestations, gouting, and crown thinning were also recorded (Table 4.1). Relative to stem infestations, balsam woolly adelgid branch infestations were uncommon, and thus only recorded secondarily as observations where they were seen. Tree mortality was derived from foliage condition and thinning ratings (N and 3, respectively).

Four regeneration plots were measured at each site. The 25m between plot centers was delineated with a measuring tape, and the number of regeneration trees within one meter of the tape was recorded. Thus the area of regeneration plots was 50m^2 (25m x 2m). Trees were considered to represent regeneration if their DBH was less than 5cm, and their

height greater than 15cm. For true fir regeneration, the presence or absence of balsam

woolly adelgid and gouting were also noted.

Table 4.1. Characteristics of tree condition assessed for mature true fir trees.

Conditions Assessed	Code	Description
Balsam Wooly Adelgid Stem Infestation Level	0	No adelgids observed
	L	Light/low infestation: Fewer than 50 visible on tree bole.
	H	Heavy/high infestation: Greater than 50 visible on bole.
Crown & Limbs: Foliage Condition	G	Green: Foliage is predominantly live and green.
	Y	Yellow: Foliage is yellowing/fading.
	R	Red: Foliage is dead, red or brown in color.
	N	None: No foliage present.
Crown & Limbs: Thinning	0	Crown is full, no thinning evident.
	1	Light. Some thinning present, a minority of branches thinning.
	2	Severe. Thinning present throughout entire crown.
	3	Complete. No foliage present.
Crown & Limbs: Gout	P	Present: Gouting observed.
	A	Absent: No gouting observed.
	X	Unable to assess presence or absence of gouting.

In total, 40 sites were sampled between 2014 and 2015. The distribution of the sites

was: within the Kaniksu National Forest (2 sites), on lands managed by the Kalispell Tribe

(1), the Coeur d'Alene National Forest (2), the St. Joe National Forest (2), private land (1),

the University of Idaho Experimental Forest (2), the Nez Perce – Clearwater National Forest

(7), the Payette National Forest (10), and the Boise National Forest (13). Average site

elevation was 1,528m, and ranged from 714m in the Kaniksu National Forest to 2,005m in

the Boise National Forest. Over half of the sites (26 of 40 sites) were located above 1,500m.

Subalpine fir occurred on all sites, and was often mixed with a combination of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), lodgepole pine (*Pinus contorta* Douglas ex Loudon), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), mixed softwood species (such as hemlock (*Tsuga* spp.), cedar (*Thuja* spp.), western white pine (*Pinus monticola* Douglas ex D. Don), and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson)), and mixed hardwood species (including alder (*Alnus* spp.), maple (*Acer* spp.), mountain ash (*Sorbus* spp.), cottonwood and aspen (*Populus* spp.), and unknown hardwoods).

Most sites were dominated by true firs (subalpine and grand fir). Across all sites, true fir species composed an average of 67% of mature trees, and ranged from 34 to 97%. Subalpine fir made up between 15 and 97% of all mature measured trees (averaging 58%). Grand fir was present on just over half of measured sites (21), and averaged between zero and 55% of mature measured trees (averaging 15% of mature measured trees in sites where it occurred, and 8% overall). Fir regeneration was present at all sites. Subalpine fir regeneration was observed on all but two sites, and where it occurred ranged from one to 100% of the measured regeneration within sites, averaging 56% overall. Grand fir regeneration was present on 16 sites, and ranged from two to 94% of the measured regeneration where it occurred, averaging 21% where it occurred and 8% overall.

Data Analysis

For each site, composition of mature trees and regeneration were assessed by calculating the percent of the site that each recorded tree species represented. Density of mature tree species within sites were generated by calculating the basal area (BA) of individual trees ($0.0000785375 * DBH^2$), summing across the plots in which they occurred

and averaging those values across sites. Regeneration density was averaged across plots (trees/50m^2). Site characteristics, such as elevation, were measured at each plot and averaged by stand for analysis. The balsam woolly adelgid stem infestation metric for mature trees was analyzed based upon the degree of infestation (trees were characterized as not infested, lightly infested, or heavily infested) and for regeneration trees as simply presence or absence. Pearson correlations and chi-square tests were used for comparisons (SAS Enterprise Guide Version 6.100 Copyright 2013 by SAS Institute Inc.), and significance was determined relative to an alpha (α) value of 0.05.

RESULTS

On all but one of the 40 sites, balsam woolly adelgid stem infestation(s) were observed. For stands where balsam woolly adelgid was observed, the percentage of subalpine fir with light stem infestations ranged from seven to 90% (averaging 50%), and the percentage with heavy stem infestations varied from zero to 93% (averaging 30%). Of the 21 sites with grand fir, grand fir was infested with balsam woolly adelgid on 17 sites. The percentage of grand fir with light stem infestations ranged from zero to 100% (averaging 63%), and the percentage with heavy stem infestations varied from zero to 50% (averaging 10%).

The percent of mature trees with balsam woolly adelgid stem infestations were positively correlated with the percent of trees with visible gouting for both subalpine fir (r(n=40) = 0.68907, $p < 0.0001$) and grand fir (r(n=19) = 0.54912, $p = 0.0149$). Furthermore, the percentage of trees with or without stem infestations and with or without gouting were unevenly distributed for subalpine fir (χ^2 1,N =1076) = 202.4283, $p < 0.0001$) and grand fir (χ^2 1,N = 128) = 13.6680, $p = 0.0002$) (Table 4.2). Specifically, the odds of a subalpine fir

tree with an infested stem having gouting was 12.71 times greater than the odds of no

gouting being observed on that tree. Similarly, the odds of a grand fir with an infested stem

having gouting were 11.23 times greater than the odds of an infested grand fir not having

gouting.

Table 4.2. Percentages of mature subalpine fir and grand fir with or without balsam woolly adelgid stem infestations and with or without gouting observed in the crown.

	Balsam Woolly Adelgid Stem Infestation	No Balsam Woolly Adelgid Stem Infestation
Gout Observed on Branch(es)	49.81% (Subalpine Fir) 53.91 % (Grand Fir)	2.79% (Subalpine Fir) 1.56% (Grand Fir)
No Gout Observed	27.70% (Subalpine Fir) 33.59% (Grand Fir)	19.70% (Subalpine Fir) 10.94% (Grand Fir)

Thinning within the crowns of site trees was common. The percentage of mature

subalpine fir with any degree of crown thinning ranged from 27 to 100% (71% average). And

for mature grand fir the percentage with any degree of crown thinning ranged from zero to

100%, and averaged 49%.

Compared to crown thinning, the percentage of mature fir with any degree of crown

fading (yellowing or red foliage) was less common. Fading of subalpine fir ranged from zero

to 24% (4% average), and for grand fir ranged from zero to 33% (2% average). We detected

no significant correlations between the percent of mature subalpine fir with any level of

balsam woolly adelgid stem infestation and the percentage of mature subalpine fir with any

degree of thinning (light or severe) or foliage fading (yellowing or red foliage) of the crown

($p > 0.05$). The percentages of grand fir with either absent, light, or heavy balsam woolly

adelgid stem infestations were also not correlated with any degree of thinning foliage or

fading ($p > 0.05$).

The percentage of subalpine fir and grand fir (respectively) with observed gouting was also not correlated with foliage condition (green, yellow, or red). Gouting in the crowns of mature subalpine fir was, however, associated with severe thinning (r(n=40) = 0.34421, p = 0.0296), such that as the percentage of mature subalpine fir with gouting increased so did the percentage of mature subalpine fir with severe thinning. Similarly, as the percentage of mature grand fir with either light (r(n=19) = 0.55484, p = 0.0137) or severe (r(n=19) = 0.55240, p = 0.0142) thinning increased so did the percentage of mature grand fir with observed gouting.

Heavy stem infestations were negatively correlated with elevation for both subalpine fir (r(n=40) = -0.46068, p = 0.0028) and grand fir (r(n=21) = -0.66598, p = 0.0010), but absolute stem infestation (present or absent) was only weakly related to elevation for subalpine fir (r(n=40) = -0.30817, p = 0.0530). There was no association between elevation and presence or absence of balsam woolly adelgid stem infestations on grand fir. However, most of the sites with grand fir occurred below 1,800m (19 of 21 sites), and over half (12 sites) were below 1,600m.

The percentage of trees within a site with gouting was not correlated with elevation for either host species. Nor were the percentages of balsam woolly adelgid stem infestations or gouting on mature subalpine fir correlated with the percentage of subalpine fir or total hosts within sites, mean subalpine fir BA of sites, mean host species BA of sties, mean BA of all species within sites, or mean diameter of subalpine fir. Similarly, the percentage of mature grand fir with balsam woolly adelgid stem infestations or gouting was not correlated with the percentage of grand fir or total host species within sites, mean grand fir BA, or mean host species BA. The percent of grand fir with gouting, however, was correlated with mean BA of

all species (r(n=19) = -0.56400, p = 0.0119) within sites, as well as mean diameter of grand fir (r(n=19) = 0.50928, p = 0.0259) within sites. Therefore, more gouting was observed on grand fir in stands with lower mean BA (all species within the site) and within sites where grand fir diameters were larger.

Measures of tree mortality for mature subalpine and grand fir (assessed by complete thinning/foliage absence) were essentially redundant, and thus, very strongly correlated ($p < 0.0001$). Neither of these measures, however, were correlated with either balsam woolly adelgid stem infestations (at any observable level) or evidence of gouting ($p > 0.05$). Tree mortality was also not correlated with elevation for subalpine or grand fir ($p > 0.05$).

The percentage of host regeneration with balsam woolly adelgid stem infestation was positively correlated with the percent of host regeneration with gouting for both subalpine fir (r(n=38) = 0.80323, $p < 0.0001$) and grand fir (r(n=16) = 0.53542, $p = 0.0326$). The percentage of subalpine fir regeneration with balsam wooly adelgids observed on the stem was also positively associated with the percentage of infested mature subalpine fir (r(n=38) = 0.54439, $p = 0.0004$) (Figure 4.1) (particularly mature subalpine fir with Heavy BWA stem infestations observed (r(38) = 0.57270, $p = 0.0002$)) and the percentage of the site made up of true fir species (r(n=38) = 0.41717, $p = 0.0092$). For grand fir, the percentage of regeneration with balsam wooly adelgids observed on the stem was not significantly related to percentage of infested mature grand fir (Figure 4.1) or the percentage of the site made up of true fir species. Among true fir regeneration, balsam woolly adelgid stem infestations of subalpine fir and grand fir were positively correlated (r(n=14) = 0.56287, $p = 0.0361$).

Figure 4.1. Percentage of fir regeneration with balsam wooly adelgid observed on the stem relative to the percentage of infested mature fir.

DISCUSSION

Thinning and fading of crowns are easily observed symptoms that can indicate a tree is under stress and can be observed without close inspection of a tree. Therefore, there has been interest in using these symptoms to increase the speed and efficiency of documenting balsam woolly adelgid infestations in the Intermountain West (Cook et al., 2010). Our results, however, suggest that these symptoms should be used with caution until further research investigates the mechanisms behind the expression of these symptoms.

In general, thinning or fading in the crowns of true firs, as in other conifers, indicates stress but is not always indicative of the cause of that stress. Thinning and fading within true fir crowns are documented symptoms of balsam woolly adelgid (Ragenovich and Mitchell, 2006), but are also symptoms of disease, water stress, and/or other insects (Hagle et al., 2003; Rocky Mountain Region, 2010). It is also unknown how the duration and severity of balsam

woolly adelgid stem infestations relate to tree stress (and subsequent crown thinning and fading). Our results suggest that such symptoms of infestation may not be consistently expressed by fir infested with balsam woolly adelgid. This inconsistency may arise from variation either in terms of time (duration of infestation prior to observation of foliage) or space (landscape or habitat level variation). For mature true firs measured within our sites (subalpine fir and grand fir), we detected no significant correlations between any level of balsam woolly adelgid stem infestation and foliage condition (fading or thinning) of the crown. This does not eliminate the potential for localized areas of balsam woolly adelgid infested fir to be observed with consistent thinning or fading in the crown for discrete periods of time. The lack of a significant correlation also does not dispute the finding that crown fading may be a symptom of balsam woolly adelgid infestation within the context of hyperspectral analysis (Cook et al., 2010).

Unlike crown thinning and fading, balsam woolly adelgid stem infestations were positively correlated with the presence of gouting in mature crowns of both subalpine fir and grand fir. This finding is contrary to some previous work (Ragenovich and Mitchell, 2006; Spiegel et al., 2013). It may be that the presence of branch gouting in areas where branch infestations were not commonly observed indicates that this type of infestation is supported only intermittently, or that this symptom can arise independent of balsam woolly adelgid feeding on branches. It should be noted that only gouting of branch tips within the crown were considered in this study, and we did not incorporate swellings or (apparent) tumors into this metric. We are unaware of literature documenting that gouting of branch tips and swellings/tumors on the main stem arise from the same process or agent.

Among the characteristics we assessed, gouting in the crowns of mature subalpine and grand firs was not correlated with foliage condition, but for subalpine fir gouting was correlated with severe thinning, as well as light and severe thinning of grand fir. These patterns of symptom co-occurrence fit within the known consequences of gouting on crown condition of true firs (Spiegel et al., 2013). Gouting most immediately effects meristematic tissue within the buds of branch tips, and it may be that these impacts also effect the retention of needles near gouts. Alternatively, it may be that gouting was simply more readily observed in crowns with less foliage to interfere with observations. Further research into the effects of gout induction and foliage retention is clearly warranted.

Balsam woolly adelgid is not considered to be a cold tolerant insect (Greenbank, 1970) and may be susceptible to the harsh climates typical of high elevation forests where early fall or late spring cold snaps may be common (Hain, 1988). Reminiscent of the findings of Page (1975), we found that heavy stem infestations were negatively correlated with elevation for both subalpine fir and grand fir, but absolute stem infestation (present or absent) was only weakly related to elevation for subalpine fir and there was no association between elevation and presence or absence of balsam woolly adelgid stem infestations on grand fir. Our study areas may not have covered the elevational range necessary to fully elucidate patterns of balsam woolly adelgid occurrence relative to elevation. Alternatively, our results may have been influenced by fluctuations of the balsam woolly adelgid populations, which may be more dramatic or less predictable in less hospitable environments. Our findings are also limited by the infrequency of grand fir on our sites relative to subalpine fir.

Our observation that the mature subalpine fir and grand fir mortality was not correlated with visual stem infestations or gouting may not preclude these trees having been

impacted (or killed) by balsam woolly adelgid. Given that initial infestation of stands may have occurred as long as 10-35+ years ago, and that the majority of balsam woolly adelgid caused fir mortality likely occurred soon after initial infestation (Livingston, 2000; Livingston and Pederson, 2010; Ragenovich and Mitchell, 2006; Spiegel et al., 2013), it may be that the evidence of balsam woolly adelgid we were looking for had not been consistently preserved across the sites. Alternatively, it may be that because all but one of our sites was infested with balsam woolly adelgid, our data essentially had no non-infested baseline with which to compare mortality within infested stands. Furthermore, it is possible that current infestation levels observed (absent, low, or high) did not reflect past infestation levels of now-dead trees, as balsam woolly adelgid population densities are known to fluctuate (Ragenovich and Mitchell, 2006).

Our interpretations are limited because we did not collect data on other possible causes of fir mortality such as bark beetles and diseases. How long signs of bark beetles and disease would have persisted on fir in these moist habitats is unclear, and their observation would still not have precluded balsam woolly adelgid playing a role in predisposing hosts to, or acting in concert with, other mortality agents. Future studies aiming to quantify balsam woolly adelgid related fir mortality in the Intermountain West would probably benefit from identifying other, more well preserved signs or symptoms of infestation (such as rotholz formation (Hain, 1988)). Alternatively, it may be that the only reliable method to quantify fir mortality resulting from or relating to balsam woolly adelgid infestation is to monitor stands repeatedly from the time of initial infestation. Although unlikely, there is also the possibility that in the Intermountain West, balsam woolly adelgid is not responsible for or related to the fir mortality we observed.

In agreement with our observations of mature fir, the presence of balsam woolly adelgid stem infestations and gouting on regeneration were correlated for both subalpine fir and grand fir. For subalpine fir, balsam woolly adelgid stem infestations and gouting were positively correlated between regeneration and mature trees. Sites more dominated by true fir species were also positively correlated with balsam woolly adelgid stem infestations and gouting on subalpine fir regeneration. These results suggest that balsam woolly adelgid infestation of mature subalpine fir may be reflected in subalpine fir regeneration. The specific relationships between overstory and understory infestation are not clearly understood, but likely relate to overstory stand structure and microclimate (temperature, wind, and sunlight perceived by the adelgids) (Hain, 1988) as well as the size of understory regeneration (Ragenovich and Mitchell, 2006; Spiegel et al., 2013). Wind dispersal by balsam woolly adelgid may result in some individuals landing on both overstory and understory trees, depending upon wind speed and the canopy height from which the individual disperses. Similar patterns were not observed for mature grand fir and grand fir regeneration, but the relative infrequency of grand fir within our sites may have limited our detection of possible associations. Furthermore, the positive correlation among balsam woolly adelgid stem infestations on subalpine fir and grand fir regeneration suggest that they may experience similar balsam woolly adelgid pressure regardless of the relative abundance of these species in the overstory community.

Our findings highlight both variability and patterns associated with balsam woolly adelgid infestation of true fir stands. That balsam woolly adelgid populations can rapidly expand under favorable conditions or contract when conditions change may, at least in part, explain disparities between our observations and those of others. Further work is also needed

to fully describe the chronology of impacts balsam woolly adelgid has on different host species under different growing conditions in western North America. This could be accomplished by initiating new, or expanding current, monitoring efforts to sequentially sample of both balsam woolly adelgid populations, host responses, and stand conditions. This type of work could help explain the variation observed among and within studies addressing the effects and impacts of balsam woolly adelgid on true firs, and may also shed light on possible future range expansion and impacts of this invasive species.

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CHAPTER 5: SYNTHESIS

Disturbance is often a critical aspect of forest ecosystem change, and disturbances caused by insects and disease can have a variety of effects on these ecosystems depending on the species involved, the mechanism of disturbance, and the context in which they occur. In many western forests, native bark beetles within the genera *Dendroctonus*, such as *D. ponderosae* Hopkins (Coleoptera: Curculionidae), are important disturbance agents (Furniss and Carolin, 1977; Phillips and Croteau, 1999). Mountain pine beetle populations can grow dramatically and result in forests being thinned of mature or over-mature pine trees, which can facilitate the establishment of other non-host conifers such as fir and spruce, and contribute to succession toward shade-tolerant conifers (Arno, 1986).

Anthropogenic impacts within forests have also created new forms of disturbance, as well as changed the characteristics of natural disturbances. Numerous organisms have been introduced into North America (Niemelä and Mattson, 1996 and references therein), of which many have become invasive with dramatic consequences. White pine blister rust (*Cronartium ribicola* J.C. Fischer in Rabenhorst) (Pucciniales: Cronartiaceae) and balsam woolly adelgid (*Adelges piceae* Ratzeburg) (Hemiptera: Adelgidae) are two examples of invasive organisms causing disturbance within western forests. In both cases, all sizes and ages of host tree species can be impacted, but the severity and consequences of these impacts vary.

Documenting the occurrence, extent, and impacts of disturbances such as mountain pine beetle, white pine blister rust, and balsam woolly adelgid is key to understanding their relationship to landscapes. In turn, such documentation can also inform how best to manage these landscapes to preserve ecosystem services, sustain wildlife diversity, and support

economic interests. Observations and documentation can be conducted at many scales, from landscape level aerial surveys to targeted ground surveys designed to examine specific disturbed areas.

The ground surveys described in this dissertation (Chapters Two, Three, and Four) sought to assess aspects of different disturbances affecting forests within the Intermountain West. Target habitats were high elevation whitebark pine (*Pinus albicaulis* Engelmann) forests impacted by recent mountain pine beetle outbreaks (as well as white pine blister rust) and riparian subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt.) forests that were potentially infested with balsam woolly adelgid.

With regard to whitebark pine forests, our objective was to quantify and describe the severity of mountain pine beetle impacts on mature whitebark pine within the overstory of high elevation forests. We found that the percentage of whitebark pine killed by mountain pine beetle varied widely (ranging from five to 88%), but individual whitebark pine killed by mountain pine beetle had significantly larger diameters than surviving whitebark pine. Interestingly, the diameter of trees killed by mountain pine beetle that were part of a tree-clump were significantly smaller than the diameter of mountain pine beetle-killed whitebark pine occurring as single-trunk trees, which may suggest that host growth form impacts host selection by mountain pine beetle.

In addition to describing mountain pine beetle impacts on mature whitebark pine, we also assessed tree regeneration within these forests and investigated possible patterns of association between regeneration in the understory and the condition and composition of trees in the overstory. On average, subalpine fir regeneration was more abundant than any other species in the stands we measured, followed by whitebark pine. We found that

subalpine fir was more dominant within the regeneration at lower elevations, and whitebark pine was more dominant within the regeneration at higher elevations. Our results suggest that within mature whitebark pine stands, whitebark pine regeneration is most successful in relatively open, higher elevation stands, with few (or no) non-pine overstory trees. Long term success of such whitebark pine regeneration in these areas, however, will also likely be impacted by the prevalence of white pine blister rust. Despite no pine-to-pine transmission of white pine blister rust, infections were positively correlated among understory and overstory whitebark pine.

For both mature trees and regeneration, balsam woolly adelgid infestation of riparian subalpine and grand fir were found throughout Idaho. Infestations on subalpine and grand fir stems were positively correlated with gouting (swelling of branch nodes and tips), suggesting that this symptom is likely a reliable indicator of balsam woolly adelgid infestation. Thinning and fading of crowns, however, can result from many stress-inducing factors and were not correlated with balsam woolly adelgid stem infestations. Heavy balsam woolly adelgid stem infestations were negatively correlated with elevation for both subalpine fir and grand fir, which may indicate the importance of habitat or climatic factors in the expansion of balsam woolly adelgid populations.

Both whitebark pine and subalpine fir are valued as ecologically important species. Whitebark pine growing at high elevation helps stabilize slopes, maintain snow pack, and provides food to animals and cherished vistas to recreationalists. At lower elevations, subalpine fir is valued for its role in buffering waterways and providing wildlife habitat, but at higher elevations it is sometimes viewed negatively and interpreted as a source of

competition for whitebark pine. Both species, however, can help maintain many of the ecosystem services provided by high elevation forests.

Given the periodic and ongoing insect and disease pressures negatively impacting high elevation whitebark pine, greater attention to insect and disease pressures that could impact other high elevation species (such as subalpine fir) are warranted. The potential for sustained increases in temperatures associated with climate change may to allow balsam woolly adelgid to expand into new habitats and possibly sustain populations in high elevation fir (Mitchell and Buffam, 2001; Spiegel et al., 2013). This possibility heightens the need for continued monitoring, assessment, and research of all species within high elevation forests. Such efforts would begin to fill knowledge gaps regarding not only how disturbances impact individual tree species, but also how high elevation landscapes as a whole are affected by and respond to insect and disease driven disturbance in terms of composition, structure, density, and function. Information within the framework of long term community level response and change would aid management decisions focused on maintaining the many critical services provided by these high elevation forests.

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