Forest Ecology and Management 427 (2018) 200–207

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Mountain pine beetle attack faster growing lodgepole pine at low elevations in western Montana, USA

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ARTICLE INFO

Keywords:
Mountain pine beetle
Lodgepole pine
Basal area increment
Montana
Climate
Disturbance

ABSTRACT

Global change has impacted forests through altered disturbance regimes. In the western US, climate change has resulted in extensive and severe mountain pine beetle outbreaks. These outbreaks have the potential to impact forest function through the selection of certain phenotypes. We investigated the potential for bark beetle-induced selection by way of measuring growth and climate response in mountain pine beetle-killed and surviving lodgepole pine in the Northern Rockies. We had three objectives: (1) investigate differences in growth between beetle-killed and surviving lodgepole pine prior to a recent outbreak, (2) compare the climate-growth relationships for beetle-killed and surviving lodgepole pine and how those relationships explain observed growth differences and predict mortality risk, and (3) investigate growth differences and growth-climate relationships across north- and south-facing aspects and over an elevation range representing local climate gradients. Significantly higher growth rates were observed in beetle-killed trees at low-elevation sites, but not at mid or high elevations. While aspect influenced overall growth, it did not have a significant influence on the difference in growth between beetle-killed and surviving trees. Growth showed significant relationships with several climate variables (i.e., previous-year August temperatures, October temperatures, annual precipitation, and summertime climatic water deficit), with slight differences in those relationships between beetle-killed and surviving trees. Mixed effects models demonstrated that higher growth rates and age increased the probability of mortality during the outbreak at all elevations, and also that climatic water deficit and previous-year August maximum temperatures were related to the magnitude of growth differences between beetle-killed and surviving trees. Overall, mountain pine beetles tended to attack large, fast-growing, lodgepole trees, especially at lower elevations where trees may be more susceptible to seasonal water stress.

1. Introduction

Forests are globally important due to the ecosystem services they provide (Trumbore et al., 2015). Recently, widespread mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks have occurred in the western United States and Canada, resulting in mass mortality across large areas of forest (Meddens et al., 2012). These outbreaks are driven in part by changes in regional climate, where temperatures have increased and precipitation patterns have shifted (IPCC, 2014). Warmer and drier conditions stress host trees and provide a longer period of temperatures suitable to beetles (Dale et al., 2001; Raffa et al., 2008; Bentz et al., 2010). Thus, beetles are both more capable of reproducing rapidly and can more easily overwhelm tree defenses (Mitton and Ferrenberg, 2012). As water stress is predicted to increase in many ecosystems in the western US (Seager et al., 2007; IPCC, 2014), the need to more fully understand the relationship between host trees, bark beetles, and climate is significant. Specifically, it is important to understand how host trees interact with climate and to determine the impact of those interactions on host tree susceptibility to beetle attack.

Mountain pine beetles are a native, ‘irruptive,’ insect in western North America. Beetles attack trees by burrowing through the tree’s bark and into the phloem. Successful attacks occur when sufficient numbers of beetles are recruited to attack the tree via the release of pheromones by the initial attackers (Raffa, 1988). These mass attacks succeed by overwhelming tree defenses, and result in mortality of the host tree. Beetles also introduce blue-stain fungus to trees during attacks, which helps to kill trees by blocking the xylem with fungal spores. Tree defenses include producing resins to physically expel beetles and producing defensive compounds, processes that require a substantial investment of resources (Raffa and Berryman, 1983). Trees become more susceptible to successful attack when climate conditions are stressful because their resources are already limited (Waring and Pitman, 1983). Additionally, climate conditions that are stressful to host trees are typically beneficial to the beetles, with warmer

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https://doi.org/10.1016/j.foreco.2018.05.048
Received 8 January 2018; Received in revised form 18 May 2018; Accepted 20 May 2018

temperatures allowing some species to grow and mature faster (Bentz et al., 2010). While mountain pine beetles attack several species, their most common host is lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Raffa, 1988).

Numerous climatological variables have been linked to bark beetle outbreaks, including vapor pressure deficit (VPD) (Littell et al., 2010; Hart et al., 2014), climatic water deficit (CWD) (Millar et al., 2012), high previous-year summer and fall temperatures (Berg et al., 2006; Chapman et al., 2012), and multi-decadal oscillations such as the Atlantic Decadal Oscillation (Hart et al., 2014). Similar climate variables have been found to limit the growth of lodgepole pine (Chhin et al., 2008; Lo et al., 2010), reinforcing the link between climate and host tree resource limitation. All of these climate conditions decrease the availability of water to the host tree, inhibiting both its ability to grow and its ability to produce resin with which to pitch out attacking beetles (Kane and Kolb, 2010).

Mountain pine beetle outbreaks have the potential to influence the characteristics of host stands through beetle preference for certain host tree characteristics, as well as through differential success of beetle attacks based on tree traits. Resistance to mountain pine beetles may vary among stands and individuals due to environmental or genetic variation (Raffa and Berryman, 1983; Alberto et al., 2013), such that in the right outbreak conditions, trees with lower resistance may be killed more readily than trees with naturally higher resistance (Ferrenberg et al., 2014). During severe outbreaks, it is therefore possible that the phenotypic traits of host stands may shift due to extensive mortality within one resistance group (de la Mata et al., 2017).

The results of previous studies on selection for certain phenotypes, both in lodgepole pine and other pine species, are highly variable. High levels of mortality in ponderosa pine were found to primarily affect slower-growing individuals, leading towards selection for faster-growing trees (Knapp et al., 2013). Similarly, Millar et al. (2012) found evidence for selection towards faster-growing whitebark pine in the eastern Sierra Nevada, CA due to higher mortality among slower-growing individuals from mountain pine beetle. However, a separate study on ponderosa pine found that a greater number of individuals from fast-growing families were killed during an intense bark beetle outbreak, resulting in selection towards slower growth in the population (de la Mata et al., 2017). Results from a study in British Columbia, Canada on lodgepole pine also found that faster-growing families within populations were more susceptible to mountain pine beetle attack (Yanchuk et al., 2008). In an Aleppo pine (*Pinus halepensis* Mill.) plantation in Spain, high bark beetle mortality was observed in both fast- and slow-growing individuals. However, individuals that were more responsive to annual climate variations were less likely to have been killed (Sanguesa-Barreda et al., 2015). The ages of the stands in these studies differed substantially, with the Knapp et al. (2013) and Millar et al. (2012) studies focusing on relatively old (> 150 years) stands, and the de la Mata et al. (2017), Yanchuk et al. (2008), and Sanguesa-Barreda et al. (2015) studies focusing on a younger (< 50 years) stands. These studies suggest high variability in the impacts of bark beetles on pine stands, potentially due to variations in local climate, host species, stand age, and topographic variables. Studies have consistently found that water deficit plays a role in regulating annual tree growth and pine susceptibility to attack, and that climate-related growth differences may exist between trees that succumbed to pine beetles and trees that survived outbreaks. Further research is therefore necessary to illuminate the relationship between climate (e.g., water deficit) impacts on growth and how that relationship translates into mountain pine beetle susceptibility.

Differences in growth between beetle-killed and surviving trees may suggest a difference in the allocation of resources (Ruel and Whitham, 2002; Bigler and Veblen, 2009). Trees may differ in the amount of carbon allocated towards growth versus defensive compounds (Herms and Mattson, 1992), or carbon compounds used for growth and maintenance when drought limits photosynthetic activity. Trees that are affected more by drought may also have a higher chance of successful beetle attack (Hanks et al., 1999). If an outbreak occurs with sufficient severity, this could push the local host tree population towards having lower growth, but higher defenses. However, this has not been demonstrated consistently (Lahr and Krokene, 2013; Hood and Sala, 2015), suggesting that differences in growth may instead be explained by environmental context. Trees growing in more or less favorable environments may naturally react differently to climate stress, resulting in differential mortality during bark beetle outbreaks. While the trees may appear phenotypically different when examining growth and growth-climate responses, they may not have any natural differences in allocation strategies. In this scenario, trees with higher growth might also have greater natural resistance to pine beetles (Mitchell et al., 1983) due to greater access to resources (Christiansen et al., 1987).

For this study, we had three objectives: (1) investigate differences in growth between beetle-killed and surviving lodgepole pine prior to a recent outbreak, (2) determine and compare the climate-growth relationships for beetle-killed and surviving lodgepole pine and how those relationships explain observed growth differences and predict mortality risk, and (3) investigate growth differences and growth-climate relationships across north- and south-facing aspects and over an elevation range representing a local gradient in climate stress.

2. Methods

2.1. Study area

Our study sites occur within the Boulder Mountains of the Beaverhead-Deerlodge National Forest (Fig. 1), where elevation ranges from ~1400 m to ~3100 m. The area experienced a severe mountain pine beetle outbreak in the mid-2000s. Primary tree species in the area are lodgepole pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt), and whitebark pine (*Pinus albicaulis* Engelm.). Douglas-fir and lodgepole pine are dominant species at low to mid elevations, and whitebark pine, subalpine fir, and lodgepole pine are dominant species at higher elevations. According to the nearest climate station, located ~34 km away in Boulder, MT, January was the coldest month between 1949 and 2015, with an average temperature of −12.4 °C. July was the warmest month with an average temperature of 28.2 °C [http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?mt1008]. Within this period, annual precipitation averaged 279 mm, with most precipitation falling in June. The actual study site temperature and precipitation are likely slightly colder and wetter, as Boulder, MT is located just outside the forested area at a lower elevation (1521 m).

2.2. Plot selection and design

Twelve plots were selected for the study from the Thunderbolt Creek and Boulder River drainages. The plots span both north and south aspects, and three elevational bands across a 600 m gradient. Potential plot locations were selected based on apparent lodgepole pine dominance, significant mortality due to mountain pine beetle, and stand access (Montana Natural Heritage Program, 2017; USDA Forest Service, 2000–2014). Actual plots were selected upon visiting the sites, with selection determined by (1) dominance of lodgepole pine in the canopy, (2) substantial mountain pine beetle-caused mortality in the stand (> 40%), and (3) survival of at least 10 trees in the plot and immediate vicinity. In order to capture more of the variability in stand dynamics, two plots were chosen within each aspect-elevation combination (e.g., south – low #1 = SL1, south – mid #2 = SM2, etc.). Plots were required to be a minimum of 100 m from one another so as to limit spatial autocorrelation.

Ten beetle-killed trees were selected within a 10 m radius circular plot, and two increment cores were taken at 1.37 m height on opposite sides of the tree, perpendicular to the slope. Beetle-killed trees were randomly