



Mountain pine beetle host selection behavior confirms high resistance in Great Basin bristlecone pine



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ABSTRACT

Over the last two decades, mountain pine beetle (*Dendroctonus ponderosae*) populations reached epidemic levels across much of western North America, including high elevations where cool temperatures previously limited mountain pine beetle persistence. Many high-elevation pine species are susceptible hosts and experienced high levels of mortality in recent outbreaks, but co-occurring Great Basin bristlecone pines (*Pinus longaeva*) were not attacked. Using no-choice attack box experiments, we compared Great Basin bristlecone pine resistance to mountain pine beetle with that of limber pine (*P. flexilis*), a well-documented mountain pine beetle host. We confined sets of mountain pine beetles onto 36 pairs of living Great Basin bristlecone and limber pines and recorded beetle status after 48 h. To test the role of induced defenses in Great Basin bristlecone pine resistance, we then repeated the tests on 20 paired sections of Great Basin bristlecone and limber pines that had been recently cut, thereby removing their capacity for induced defensive reactions to an attack. In tests on cut trees, we also investigated the potential for population-level differences in mountain pine beetle host selection behavior by testing beetles from two separate geographic regions. Beetles placed on Great Basin bristlecone pine rarely initiated attacks relative to those placed on limber pine in both studies, regardless of the beetle population source. Our results indicate that Great Basin bristlecone pine has a high level of resistance to mountain pine beetle due at least in part to stimuli that repel pioneering attackers from initiating attacks, even when induced defenses are compromised.

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1. Introduction

Sustainable forest management in the face of climate change requires predictions of how shifting natural disturbance regimes will impact forest environments (Dale et al., 2001). Bark beetles (Coleoptera: Curculionidae, Scolytinae), particularly ‘aggressive’ species that can attack and kill living trees, are important natural disturbance agents in western North American forests (Hicke et al., 2015). Due to the strong relationship between thermal conditions and bark beetle population success (Safranyik and Carroll, 2006; Powell and Bentz, 2009), climate-induced changes in native bark beetle outbreaks are a major concern for land managers. Warmer than average temperatures have the potential to improve winter survival, speed lifecycle completion, and allow for range expansion into areas where outbreaks were previously limited by cold (Bentz et al., 2010; Sambaraju et al., 2012; Weed et al.,

2015). In addition to favorable climate conditions, access to host resources is required for bark beetle outbreaks. Host trees that are unable to resist attacks can be killed and used for bark beetle reproduction and proliferation, but sufficiently resistant trees represent resources that are inaccessible for bark beetle use (Lieutier, 2002). Understanding these important relationships, particularly along expanding latitudinal and elevational range margins, is vital to evaluating stand susceptibility, predicting outbreak development, and planning for forest conservation.

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae), a native bark beetle that infests most species of pine (*Pinus*) throughout western North America, recently experienced population irruptions that resulted in large-scale outbreaks across its range (Raffa et al., 2008; USDA Forest Service, 2015). In addition to killing millions of acres of lower-elevation lodgepole pine (*Pinus contorta* Douglas), a primary host species, mountain pine beetle caused substantial mortality among high-elevation pines. Although outbreaks at high elevations are not unprecedented (Perkins and Swetnam, 1996), their extent

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has previously been limited by cool temperatures (Amman, 1973; Gibson et al., 2008; Bentz et al., 2011). Therefore, high-elevation pines are hypothesized to be especially susceptible to attacks due to insufficiently coevolved resistance mechanisms (Raffa et al., 2013). Keystone high-elevation species such as whitebark (*P. albicaulis* Engelm.) and limber (*P. flexilis* James) pines have experienced high levels of mountain pine beetle-caused mortality over the past several decades (Macfarlane et al., 2013; Cleaver et al., 2015), but susceptibility has not been shown for all high-elevation pine species. Successful mountain pine beetle attacks on Great Basin bristlecone pine (*P. longaeva* Bailey), an extremely long-lived species found at high elevations in Utah, Nevada and California, have not been documented, despite evidence of extensive mountain pine beetle activity occurring in limber pines within the same stands (Bentz et al., 2016b). With the expectation that climate conditions will continue to support mountain pine beetle success at high elevations throughout this century (Bentz et al., 2016a; Buotte et al., 2016), a better understanding of Great Basin bristlecone pine's apparent resistance to mountain pine beetle is needed for insight into managing these ecosystems.

Tree resistance to the mountain pine beetle involves complex interactions between the insect and the potential host. Mountain pine beetle adults emerge from their natal host trees in mid-summer to locate and colonize new hosts for reproduction. Synchronous emergence and dispersal are critical for mountain pine beetle success because high numbers of “mass attacking” beetles are required to deplete the defensive resources of new hosts. In successful attacks, adult beetles bore through the bark of new host trees, mate, and females deposit eggs along vertical galleries in the phloem. After egg hatch, larvae feed and develop in the phloem over the next ~ one to three seasons (Bentz et al., 2014), typically killing the host tree, before completing their life cycles and emerging through the bark as adults (Safranyik and Carroll, 2006). Due to this selective pressure, host trees have evolved defense systems to resist bark beetle use. These systems generally involve a combination of pre-formed constitutive defenses and attack-activated induced defenses that reduce insect colonization success and/or prevent brood development and survival. Constitutive defenses may include either mechanical mechanisms such as physically obstructive compounds built into the bark, or chemical mechanisms such as toxic phloem compounds (Franceschi et al., 2005). Important induced defenses for tree resistance to the mountain pine beetle include toxic resin flow that impedes or kills attacking beetles and hypersensitive phloem reactions that entrap beetles in lesions impregnated with inhibitory compounds (Lieutier, 2002). Relative to limber pine, a well-documented susceptible mountain pine beetle host species, Great Basin bristlecone pine has high concentrations of constitutive chemical phloem compounds (Bentz et al., 2016b) that are associated with tree defense (Raffa, 2014). Information about induced defenses in Great Basin bristlecone pine is lacking. Moreover, the direct impact of Great Basin bristlecone pine defense traits on mountain pine beetle attacks is unknown.

Mountain pine beetles contend with tree defenses through flexible host selection behavior that enhances their chance of successfully colonizing a favorable host (Raffa et al., 2016). Female beetles are the pioneering attackers and therefore play a central role in selecting susceptible hosts and avoiding resistant or otherwise unsuitable trees. Research has shown that mountain pine beetle females use a combination of visual cues and random landings to locate potential hosts (Hynum and Berryman, 1980; Wood, 1982), but tree volatiles also play an important role in host attraction (Moeck and Simmons, 1991). After landing on a potential host, a female decides whether or not to attack based on several factors including short-range olfactory and gustatory cues (Raffa and Berryman, 1982). If the host tree is accepted, the female will pro-

ceed to initiate gallery construction in the phloem, emitting aggregation pheromones that can instigate a mass-attack by attracting other adult mountain pine beetles (Safranyik and Carroll, 2006). Appropriate female host selection decisions are critical because accepting unsuitable trees results in reduced survival and reproduction, but prolonged host searching increases exposure to predators, expends energy, and can lead to high intraspecific competition with earlier attackers. Due to these challenges, host acceptance decision-making is not only driven by an assessment of the potential host tree, it is also mediated by individual beetle and population conditions that influence the likelihood or degree of reproductive success (Boone et al., 2011; Chubaty et al., 2014; Burke and Carroll, 2017). Host selection behavioral traits have been shown to have a heritable component in other bark beetle species (Wallin et al., 2002), which may result in varying behavior between populations. Variation in host selection behavior between geographically-separated populations of the same species has been documented in other insect species (Keeler and Chew, 2008), and in some cases insects have the capacity to locally adapt to highly defended host species (Zovi et al., 2008). Understanding mountain pine beetle host selection choices and how they can vary with population is important for understanding the potential for local adaptation to host defenses and for predicting future host tree vulnerability to attack.

Ultimately, pioneering female mountain pine beetles incorporate both internal and external stimuli to choose a host that provides the greatest likelihood of maximizing their reproductive success. Host acceptance therefore would suggest that a tree is both susceptible to successful mountain pine beetle colonization and can support brood development and survival. Host rejection implies that a tree is either highly resistant, poor quality (i.e., thin or low-nutrient phloem), or incompatible with the biological needs of the insect and unlikely to support the goal of reproductive success. The lack of mountain pine beetle attacks observed on Great Basin bristlecone pine (Bentz et al., 2016b) suggests that it falls into one of the latter categories compared to limber pine in mixed stands. However, Great Basin bristlecone pine susceptibility to attack has not been tested when there are no alternative host species present. Additionally, Great Basin bristlecone pine foliage volatiles have been shown to be unattractive to mountain pine beetle (Gray et al., 2015), but it is unknown if the same repellent qualities are present in short-range stimuli from the bole, where mountain pine beetles land to initiate attacks. Furthermore, the roles of constitutive and induced tree defenses and the importance of mountain pine beetle population trait variation in Great Basin bristlecone pine resistance remain unclear.

The goal of our study was to test and characterize Great Basin bristlecone pine resistance to mountain pine beetle by evaluating mountain pine beetle host selection behavior. We used no-choice attack box tests (Netherer et al., 2015) to compare the host selection responses of pioneering female mountain pine beetles placed on Great Basin bristlecone pine boles with the responses of those placed on co-occurring limber pine boles, a susceptible host species. Specifically, we asked (1) whether female mountain pine beetles have a low preference for Great Basin bristlecone pine relative to limber pine when exposed to the tree boles, (2) whether host tree capacity for induced defensive responses influences host selection behavior, and (3) whether mountain pine beetle populations from different geographic locations exhibit different host selection responses to Great Basin bristlecone and limber pines. We hypothesized that mountain pine beetle females would demonstrate aversive host selection behavior toward Great Basin bristlecone pine relative to limber pine, and that tree capacity for induced defense would play an important role in mountain pine beetle host selection decisions on both tree species. We also pre-

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