

DOES WILDFIRE INCREASE THE RISK OF MOUNTAIN PINE BEETLES OUTBREAKS IN LODGEPOLE PINE FORESTS OF THE GREATER YELLOWSTONE ECOSYSTEM?

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♦ ABSTRACT

We examined whether wildfire injury increased lodgepole pine, *Pinus contorta*, susceptibility to mountain pine beetle, *Dendroctonus ponderosae*, how it affects beetle reproduction, whether this interaction differs between endemic and epidemic populations, and how wildfire influences tree defense physiology. Wildfire predisposed trees to mountain pine beetle attack. In particular, fire-injured trees had a lower ability in synthesized monoterpenes in response to simulated attacks than did non-injured trees. However, beetles responded in a non-linear fashion; moderately-injured trees were most preferred. This interaction was influenced by beetle population size. Healthy and fire-injured trees were attacked when populations were high, but no healthy trees and no severely-injured trees were killed when populations were low. Beetle brood production per female was also curvilinear being highest in moderately-injured trees. This reflected a trade-off between high intraspecific competition arising from the large number of beetles needed to overcome defenses in healthy trees, and high interspecific competition and low substrate quality in severely injured trees.

These results suggest that fire-injured trees can provide a resource for mountain pine beetles during the extended periods when populations are not high enough to overcome defenses of vigorous trees. But the likelihood that populations could transition from endemic to epidemic levels due to increased tree susceptibility from wildfire is constrained by the opposing factors of lower nutritional quality and more competition load in severely-injured trees, and the relatively low incidence of moderately-injured trees. Wildfire may cause some reproductive

increases in populations that are already in outbreak mode.

♦ INTRODUCTION

Conifer forests in western North America are strongly affected by wildfire and bark beetle outbreaks (Romme and Knight 1981, Veblen et al. 1994). These disturbance agents can have interacting effects, but they are not well understood. For example, wildfire injury to trees can sometimes lead to increased rates of attack by bark beetles, but this varies with beetle and tree species, and environmental conditions, (Rasmussen et al. 1996, Ryan and Amman, 1996, Wallin et al. 2003, Hood and Bentz 2007, Six and Skov 2009).

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is of major concern throughout the western United States and Canada. It has recently caused extensive mortality throughout all of western North America (Hicke and Jenkins 2008, Hicke et al. 2006, Kurz et al. 2008, Safranyik et al. 2010). The primary host of the mountain pine beetle is lodgepole pine.

Mountain pine beetle adults emerge from their brood trees, fly, and select new host trees based on chemical cues. They enter the bark, mate, oviposit, and the larvae feed in the phloem. The resulting destruction of transport tissues kills the tree. Trees can defend against attack by employing constitutive and induced defenses, including rapid accumulation of toxic monoterpenes (Zulak and Bohlmann 2010). Bark beetle aggregation attract more beetles, and these mass attacks can overwhelm tree defenses (Raffa and Berryman 1983).

Physiological stress can weaken tree defenses (Wallin and Raffa 2001, Jones et al. 2004, Kolb et al. 2007).

The question of whether burn injury increases susceptibility to mountain pine beetles has important policy implications, with regard to both formulating responses to wildfire and prescribing controlled burns. The population dynamics of tree-killing bark beetles are characterized by lengthy endemic periods, during which beetles occur at very low densities and attack only a few severely stressed trees, followed by large-scale outbreak (Boone et al. 2011). We do not know whether wildfires cause beetle populations to cross the critical threshold between these phases (Raffa et al. 2008).

✦ METHODS

We sampled 16 lodgepole pine sites conducted in the Greater Yellowstone Ecosystem. Eight experienced wildfire, and eight were unburned. Four of the burned sites were within areas where mountain pine beetle was in outbreak, and four were in nonoutbreak areas. There were a total of 2056 trees. We measured attack, brood production and competitors within subsampled trees, and in pheromone-baited flight traps.

During 2010-2012, we mapped the spatial extent and intensity of bark beetle infestation (both new activity and older infestations) and the proximity of damage to fires. We partnered with the USGS and NPS to acquire SPOT 10m and 5m satellite imagery over most of the Greater Yellowstone Ecosystem. These images are currently being processed for two sets of analyses: 1) mapping of bark beetle damage with respect to fire locations and 2) mapping of forest vertical structure associated with long-term disturbance history and forest regeneration. The remote sensing efforts were linked to field data collected in 2010-2011.

We evaluated the defense chemistry of lodgepole pines that were uninjured or injured by wildfire. We analyzed monoterpenes by gas liquid chromatography. These measurements include both constitutive chemistry and induced chemistry in response to simulated attack.

✦ RESULTS

Responses of Mountain Pine Beetle to Wildfire

Wildfire injury strongly influenced mountain pine beetle attack on lodgepole (Powell et

al. 2012). Moderately injured trees experienced the highest rates of attack. Brood production per females was also highest on moderately injured trees. Attack densities were highest on uninjured trees, which generated high intraspecific competition and lower brood production per attack. Interspecific competition was highest on severely injured trees. The major competitors were *Ips*, *Monochamus*, and *Pityogenes*. Populations of predators, buprestids, and turpentine beetles were low (Powell et al. 2012).

Background populations had a strong effect on mountain pine beetle attack dynamics (Powell et al. 2012). When mountain pine beetle was already in outbreak mode, uninjured trees were attacked. We did not see this at low populations.

Spatial Extent and Intensity of Bark Beetle Infestation Relative to Proximity and Extent of Wildfires.

Field data included plot-based samples of mortality, red trees, newly infested trees and unattacked trees. Because accessibility to large numbers of plots in remote areas was not feasible, we additionally developed a new method in which we used infrared and visible camera with telephoto lenses to take pictures of distant slopes. Using GPS locations, bearings and camera tilt, we precisely located the photos using Google Earth to place the actual camera shot locations on SPOT images. From 47 sets of photos, we co-located 97 positions.

Lodgepole Pine Defense Chemistry

Total concentrations of volatiles (including thirteen monoterpene hydrocarbons four allylic monoterpene alcohols, one ester and one phenyl propanoid) within constitutive phloem tissue did not vary with fire injury (Powell and Raffa 2011). But the concentrations of induced volatiles decreased by nearly half with wildfire injury. These results illustrate the importance of actively induced biochemical responses in tree defense against mountain pine beetle.

Fire injury also influenced the proportions of some volatiles in both constitutive and induced phloem tissue (Powell and Raffa 2011). Some of these alterations may relate to the behavioral mechanisms by which bark beetles detect weakened trees and communicate during mass attacks.

✦ MANAGEMENT IMPLICATIONS

The results of our study have implications to mountain pine beetle population dynamics, disturbance interactions, and natural resource management. Fire-injured trees appear to serve as a reservoir for bark beetles during their extended nonoutbreak population phase, when they cannot overcome the defenses of vigorous trees (Wallin et al. 2003, Powell et al. 2012).

The likelihood that population increases in fire-injured trees could trigger outbreaks, however, is reduced by increased competition and reduced substrate quality in severely-injured trees, and the lack of moderately-injured trees at the stand level (Powell et al. 2012). If an increase in population density following wildfire were to be accompanied by additional predisposing factors such as warm temperatures or drought, however, their combined effects would be more likely to favor transition to outbreaks. Wildfire could also potentially increase total beetle reproduction in stands already experiencing outbreaks.

✦ CURRENT WORK

Beginning in 2009, we have been comparing the defense chemistry and physiology of whitebark versus lodgepole pines, mountain pine beetle's relative preference for each species in the field and laboratory assays, and how predators and competitors respond to mountain pine beetles in each environment. Results to date indicate that both coevolutionary history and spatial context affect these relationships. Continuing work is extending these studies to the landscape scale, to improve our ability to incorporate chemical ecology, host selection behavior, and forest structure into management strategies.

✦ ACKNOWLEDGEMENTS

In addition to support from the UW-NPS Research Station, this project has received funding from the National Science Foundation, McIntire Stennis, and the University of Wisconsin College of Agricultural and Life Sciences. Megan Fork, Katherine Molter, Christopher Foelker, Melissa Greulich, Christopher Pennings, Andrew Long, Hillary Thompson, Jake Griffin, and Martin Simard provided valuable assistance in the field. Nicholas Keuler at the Univ. Wisconsin Statistical Consulting Lab and Jun Zhu at the Univ. Wisconsin Dept. of

Entomology provided statistical advice, Steven Krauth at the Univ. Wisconsin, Entomology Dept. and Donald Bright at Colorado State Univ., Dept. of Bioagricultural Sciences & Pest Management provided help with insect identification, and William Romme (Colorado State Univ.), Daniel Tinker (Univ. Wyoming), and Monica Turner (Univ. Wisconsin) assisted with field site selection.

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