

A HINT LEFT BY MOUNTAIN PINE BEETLE ON ANATOMICAL DEFENSES OF LODGEPOLE PINE TREES: LARGER RESIN DUCTS ENHANCE TREE RESISTANCE

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Mountain pine beetle (MPB) [*Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae)] populations have increased in Alberta since they have crossed the Rocky Mountains and colonized pine forests in western Alberta in 2006. Millions of mature lodgepole pine (*Pinus contorta* var. *latifolia*) trees have been killed, leaving only a low number of residual overstory mature lodgepole pine trees and non-host tree species, such as spruce and *Populus*, remaining in beetle-killed stands (Taylor et al. 2006, Dhar et al. 2016). The reason behind the survival of residual trees remains unknown. The change in nutrient cycling, underground soil communities, forest structure, and other factors in post-MPB stands can certainly affect the health condition of residual pine trees and potentially change their suitability to other insects and tree pathogens (McIntosh and Macdonald 2013b, Cigan et al. 2015, Karst et al. 2015, Pec et al. 2015). Considering the low pine recruitment and regeneration in MPB-affected stands (Astrup et al. 2008, McIntosh and Macdonald 2013a), the residual overstory pine trees might be the only seed source for the future pine regeneration in Alberta. Thus, studies on the future health conditions of residual pine trees in these disturbed landscapes are urgently needed. While concentration of chemical compounds in tree phloem can vary between resistant and susceptible lodgepole pine trees (Erbilgin et al. 2017), anatomical defense represents tree defense capacities over a longer time. Here we analyzed patterns in anatomical defenses and tree increment growth to understand (1) how residual trees survived the MPB outbreak, (2) whether the outbreak altered growth/defense relationships, and (3) identify relationships with current health conditions of residual trees.

We selected 31 sites in post-MPB stands in western Alberta, Canada. At most of the selected sites we established 2 plots (n = 61 plots in total). In plots, we sampled the wood from 140 beetle-killed trees using wedges and 210 residual trees using increment cores at breast height (1.4 m). Samples were collected in 2016. All trees had a diameter at breast height (DBH) over 15 cm and had a crown class of intermediate, codominant, or dominant. We confirmed MPB-killed tree by the presence of MPB attack signs such as beetle entrance holes (pitch tubes) and extensive beetle galleries under bark. The sampled residual trees were classified into three groups based on tree health conditions and included 76 healthy, 62 declining due to biotic agents other than MPB, and 72 trees that survived MPB with signs of attack but appeared vigorous.

We measured ring width (mm yr⁻¹) from bark to pith on all samples by using WinDendro™ (Regent Instruments 2008). A master chronology was developed based on the ring width series of cores from healthy residual trees. The strength of cross-dating was confirmed by COFECHA (Grissino-Mayer 2001). This master chronology was used to justify any missing or false rings on cores before any calendar year was assigned to each ring. The year of death for beetle-killed trees was adjusted by visual cross-dating due to the low number of years sampled on wedges. Since most sites experienced beetle mortality at multiple years, the start of an outbreak was considered as the year of the earliest death caused by MPB that occurred in a site.

A sampling area of 0.9 mm for cores and wedges was used to count and measure resin ducts. The resin duct characteristics that were measured

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from the sampling area included annual resin duct production (no. year⁻¹) and individual resin duct area (mm² year⁻¹), which were determined by ImageJ (version 1.50i, National Institutes of Health, USA). Two standardized variables of resin duct characteristics were also calculated on each core or wedge: resin duct density (no. mm⁻² year⁻¹) and relative resin duct area (percent year⁻¹).

There were no differences on mean growth rate between beetle-killed and residual trees within the first 10-year preceding outbreak. However, beetle-killed trees produced 127–131 percent more xylem axial resin ducts than residual trees, while the size of individual duct in residual trees was 18–27 percent larger than those in MPB-killed trees. A logistic model was built to predict the survival probability of lodgepole pine trees during the MPB outbreak based on the resin duct production and resin duct size within 10 years before the MPB outbreak. The survival probability increased with larger resin ducts, but less numbers of resin ducts. Meanwhile, trees that survived attack responded to MPB outbreaks in the stand with a lower mean growth rate in the first 3- and 5-year following outbreak, and higher mean resin duct production for up to 10 years after outbreak, while healthy trees only showed increased resin duct production in the total growth period after the MPB outbreak. Furthermore, we found that healthy trees had larger individual resin ducts than declining trees in the recent 20 years (1996 to 2015), while survived trees also had larger resin ducts than declining trees most of the time from 1996 to 2015.

Our results indicated that anatomical defenses were critical components of lodgepole pine survival during beetle attacks as well as they might continue to play major roles in tree defense to bark beetles in post-outbreak stands. Thus, pine anatomical defenses appear to be important traits for understanding tree resistance to bark beetles, supporting earlier studies (Kane and Kolb 2010, Hood and Sala 2015). Although it is not clear

whether resin duct size is heritable, but if so, we expect that the next generation of lodgepole pine forests in western Alberta would be resistant to future bark beetle attacks. Using the logistic model generated in the current study, the survival probability of pine trees during MPB attacks could be calculated by determining resin duct production and resin duct size. Thus, keeping, and not harvesting, these residual trees should be the highest priority for land managers to assure the future sustainability of lodgepole pine forests in western North America.

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