



# Whitebark pine (*Pinus albicaulis*) growth and defense in response to mountain pine beetle outbreaks

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## Introduction

Whitebark pine (WBP; *Pinus albicaulis*) is a critical keystone forest species of U.S. Northern Rocky Mountain subalpine ecosystems (Tomback et al. 2001). There is growing concern that WBP may be largely extirpated from its current habitat over the next century due to cumulative impacts of climate change, insect-related mortality, changing fire regimes, increased competition from shade-tolerant species, and the invasive exotic pathogen white pine blister rust (*Cronartium ribicola*). While insects, fire, disease, and drought have contributed to recent mortality of WBP, these processes are also thought to play an important role in the long-term establishment and persistence of Northern Rocky Mountain WBP forests. Historical records detailing patterns and characteristics of disturbance that promote or inhibit WBP establishment and persistence are poorly lacking, highlighting a critical research need.

Within conifers, resin-based defenses (direct expulsion of beetles from tree phloem/cambium via resin flow through ducts) have long been recognized as the primary mechanism by which trees respond to attack by bark beetles and pathogens. Resin ducts are permanent anatomical features within the secondary xylem and have been shown to correspond with resin flow, such that greater total area of resin ducts facilitates increased production, storage, and mobilization of oleoresin to sites of wounding. As resin ducts are produced regularly (typically every year to every few years), they can be measured, along with tree rings, to assess how trees allocate resources between growth and defense over time. Several researchers have linked physical properties of resin ducts to survivorship during periods of increased beetle activity (see Kichas et al. 2020 for key references).

In this study, we evaluated whether

diameter growth and resin duct characteristics differed between residual live trees (hereafter “live trees”) and trees that died (hereafter “dead trees”) during recent disturbance episodes (e.g., mountain pine beetle outbreaks, drought, fire). Understanding resin defense systems is of particular importance as these structures represent the primary defense mechanism of WBP to biotic disturbance. Evaluating relationships between resin duct structures, oleoresin production, and disturbance can provide valuable insight into overall defensibility of these trees to stressors that are projected to increasingly impact this important species.

## Methods

Data for this study were collected across two high-elevation WBP sites on the Flathead Indian Reservation as part of a larger fire history reconstruction for the Confederated Salish and Kootenai Tribes (Kichas et al. 2020). Both areas were

affected by numerous large-scale bark beetle outbreaks, occurring in the 1930s, 1960s–1980s and most recently 2002–2009 (Harley et al. 2019, Jenne and Egan 2019). The majority of WBP mortality was due to cumulative impacts from mountain pine beetle and white pine blister rust, which was introduced to this region of the Northern Rocky Mountains circa 1950 (Geils et al. 2010). Of the 701 sampled WBP trees, 82% were dead, with the majority of dead trees (76%) showing evidence of beetle activity (J-shaped galleries along the tree stem and / or presence of blue-stain fungi (*Grosmannia clavigera*), which is introduced to WBP trees by bark beetles during colonization.

To assess the influence of disturbance on growth and defense characteristics, live trees and corresponding dead trees (hereafter “pairs”) were identified from the larger suite of demography data. Suitable pairs were identified based on distance (< 20 m apart) and size (< 3 cm difference diameter) to control for potential microsite differences. Overall, we identified 144 trees (72 live and 72 dead). A more detailed description of the methods and analyses used can be found in Kichas et al. (2020).

## Results

Whitebark pine trees that died grew 22% faster than living trees, primarily during the period of 1911–1975 (Figure 1a). In the 20-years preceding mortality, growth in whitebark that died declined by 26% relative to live trees, especially post-1975. Dead WBP also produced 20% more resin ducts compared to live trees (Figure 1b). This relationship declined (by 10%) in the 20-years preceding mortality, with the greatest difference occurring from 1990–2000. However, despite producing more resin ducts on average, the ducts were smaller for dead WBP (56% smaller on average) compared to live trees (Figure 1c). Similar to growth, duct size showed an

increasing trend post-1975, where duct size in live trees continued to increase relative to dead trees.

Resin duct area was also greater in live trees (48% increase; Figure 1d) and duct area showed a similar post-1975 trend, with increasing duct area in live WBP relative to dead trees. In contrast, resin duct density was greater in dead trees (18% greater; Figure 1e) and post-1975, duct density continued to increase in dead WBP throughout the remainder of the

record. Relative duct area (% of annual ring occupied by resin ducts) was significantly greater in live WBP (57% increase; Figure 1f). Unlike the other metrics, there was no clear temporal trend for relative duct area.

The two most significant metrics influencing tree survivorship were resin duct size, and relative duct area. WBP trees that are able to produce larger resin ducts (> 0.001 mm<sup>2</sup>) with greater overall duct area (> 10% annual ring) had a

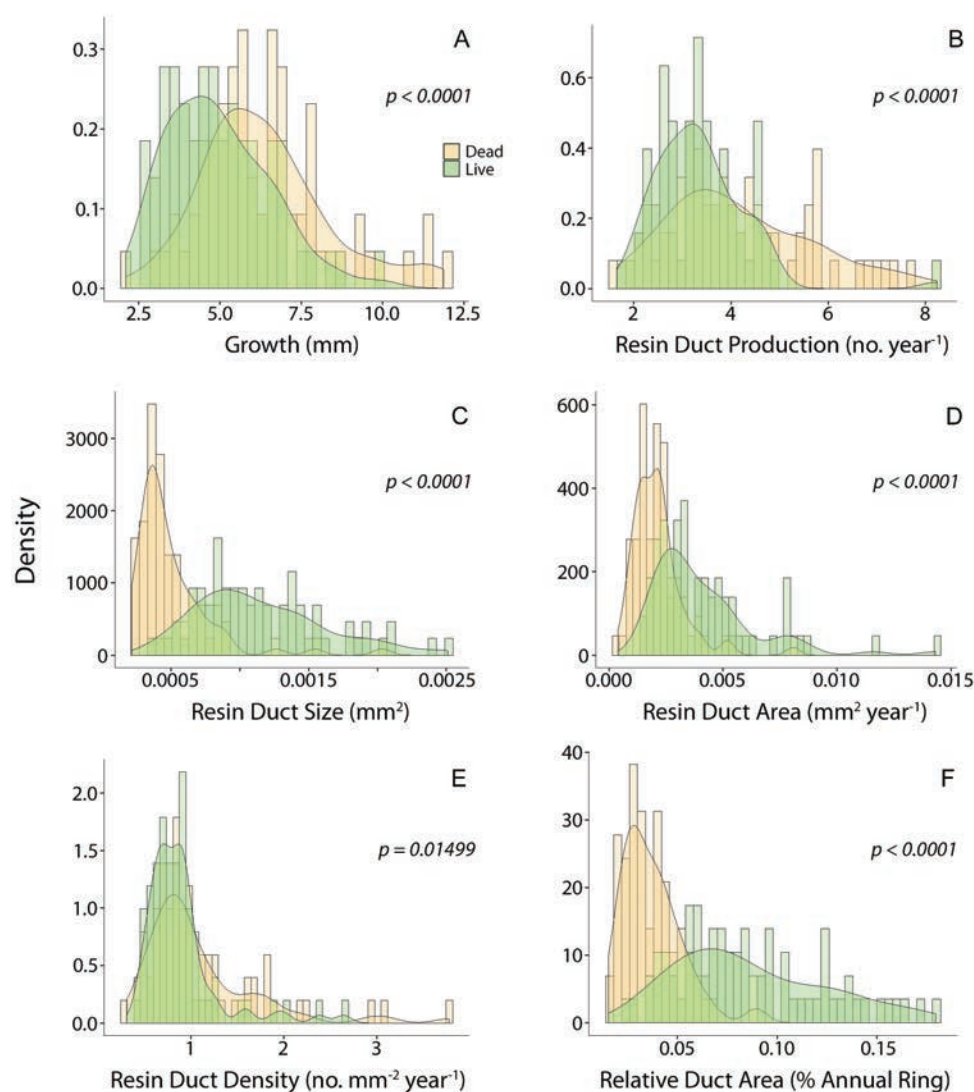


Figure 1. Kernel density plots for growth and defense metrics across pairs of live and dead WBP. These plots visualize the distribution of samples (depicted as vertical bars) over each continuous variable with a smoothing kernel (smooth lines with shading) applied to assist in visualization of the distributions.



significantly greater chance of survival (~80%; Figure 2).

## Discussion

Whitebark pine trees that produced larger resin ducts were far more likely to survive disturbance events at each of our study sites. The presence of larger resin ducts and greater duct area in live trees could be associated with an increased capacity to mobilize oleoresin in response to attack or infection and may be a factor in the ability of live trees to endure numerous disturbance events over time. Although dead trees produced more resin ducts on average the ducts were smaller, which might have been insufficient in area to produce, store, and mobilize adequate amounts of oleoresin in response to wounding by bark beetles and blister rust infection. This reduced resin flow in dead trees could be linked to lowered defense and higher mortality despite increased density of ducts, particularly in the years leading up to death.

Importantly, our results suggest that WBP trees that invest a relatively greater amount of resources into the production of constitutive resin-based defenses have a higher probability of surviving disturbance events, which parallels previous research on other conifers (Kichas et al. 2020). Whitebark pine trees appear to exhibit different strategies in the allocation of resources toward growth and defense depending on their biophysical setting and climate and disturbance history. Live trees that persisted through 20th century disturbance events produced larger resin ducts with a greater overall annual duct area relative to growth. In contrast, those trees that died invested more into growth, at the expense of defense. Both strategies involve tradeoffs that can confer fitness benefits under different circumstances. For example, during relatively long disturbance-free intervals (decades to

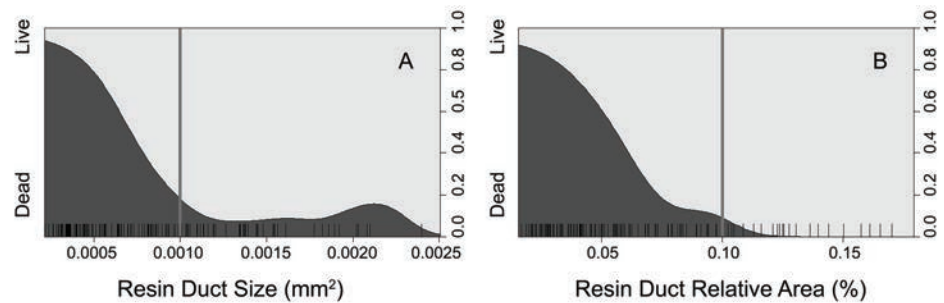


Figure 2. Conditional density plots describing the probability of mortality in relation to principle resin duct metrics (A) resin duct size [mm<sup>2</sup>] and (B) relative resin duct area [% annual ring]. Light shading reflects live trees while dark shading reflects dead trees. Vertical

centuries) WBP trees that invest more resources into growth may thrive. As defensive features are energetically expensive to produce and maintain, the presence of these characteristics suggests there is strong selective pressure from disturbances to invest in these defenses. Our results lend insight into resin duct characteristics that may be beneficial to increasing WBP survivorship and highlight how variable physiological traits confer advantages under different circumstances.

## References

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