WHITEBARK PINE GROWTH AND DEFENSE IN RESPONSE TO MOUNTAIN PINE BEETLE OUTBREAKS

NORTHERN ROCKIES FIRE SCIENCE NETWORK

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Whitebark pine (WBP; *Pinus albicaulis*) is a critical keystone species of U.S. Northern Rocky Mountain subalpine ecosystems. There is growing concern that WBP may be eliminated 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 disturbance events are also thought to play an important role in the long-term establishment and persistence of WBP forests. Historical records detailing patterns and characteristics of disturbance that promote or inhibit WBP establishment and persistence are lacking.

Within conifers, resin-based defenses (i.e., 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. Greater total resin duct area facilitates increased production, storage, and mobilization of resin 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 tree survival during periods of increased bark beetle activity (see Kichas et al. 2020 for key references).

In this study, we evaluated whether diameter growth and resin duct characteristics differed between live trees and dead trees during recent disturbance events (e.g., mountain pine beetle outbreaks, drought, fire). Evaluating relationships between resin duct structures, resin production, and disturbance can provide valuable insight into how these trees will respond to stressors that are projected to increasingly impact whitebark pine.

Methods

Data for this study were collected across two high–elevation (>1900 m or >6,200 ft above sea level) WBP sites on the Flathead Indian Reservation, Montana, 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 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 and/or presence of blue–stain fungi (*Grosmannia clavigera*) usually carried by bark beetles.

To assess the influence of disturbance on growth and defense characteristics, "pairs" of live trees and corresponding dead trees were identified based on distance (<20 m apart) and size (<3 cm difference in diameter) to control for potential microsite differences. Overall, we identified 144 trees (72 live and 72 dead).

Key Management Findings

- **Maintaining genetic variability and the traits associated with this variability may be critical for the long-term persistence of whitebark pine.**
- **Live trees that survived 20th century disturbance events produced larger resin ducts with a greater overall annual duct area relative to growth. In contrast, trees that died invested more into growth.**
- **Management prescriptions should consider climate-disturbance feedbacks and interactions that forests will experience in the future.**
- **Management actions that may help maintain genetic variability include:**
    1) **Allow for natural whitebark regeneration after disturbance.**
    2) **Limit post-disturbance impacts (e.g. post-fire treatments that undermine natural regeneration).**
    3) **Avoid prescriptions that preselect for specific traits that may be advantageous under certain conditions yet detrimental under unforeseen future conditions.**

Results

Of the WBP pairs, trees that eventually died grew 22% faster over their lifespan than living trees during the same time period (Figure 1a), primarily between the years 1911–1975 (for more information on trends over time, see Kichas et al. 2020). In the 20-years preceding mortality, growth in WBP that died declined by 26% relative to live trees, especially post-1975. Dead WBP also produced 20% more resin ducts compared to live trees over their lifespan (Figure 1b), with the greatest difference occurring between 1990-2000. However, despite producing more resin ducts, the ducts were smaller in diameter 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.

Total 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 trend over time 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^2) with greater overall duct area (>10% annual ring) had a significantly greater chance of survival (~80%; Figure 2).

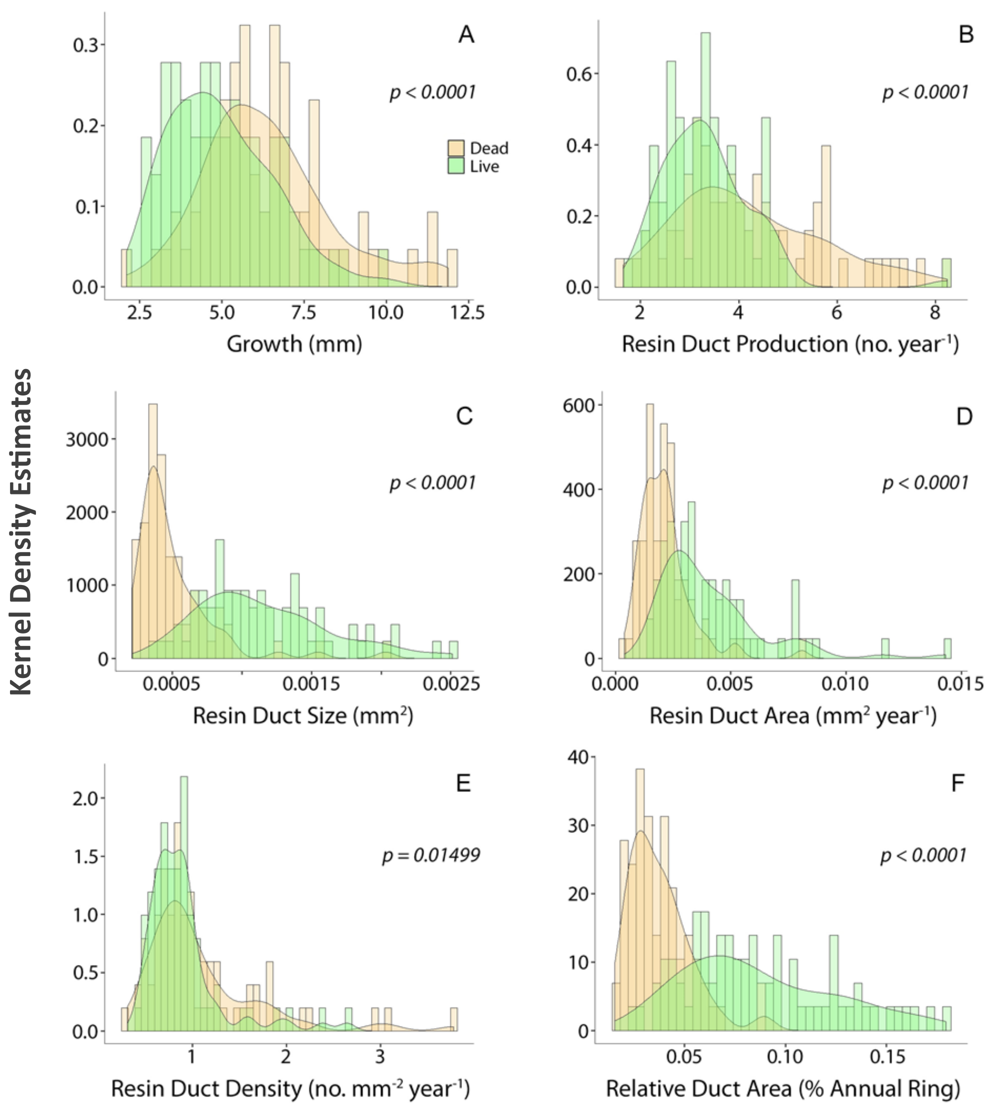

Figure 1. Tree growth and resin duct metrics across pairs of live (shown in green) and dead (shown in tan) WBP. These kernel density plots show the distribution of samples (vertical bars) over each continuous variable with a smoothing kernel (smooth lines with shading) applied to assist in visualization of the distributions.

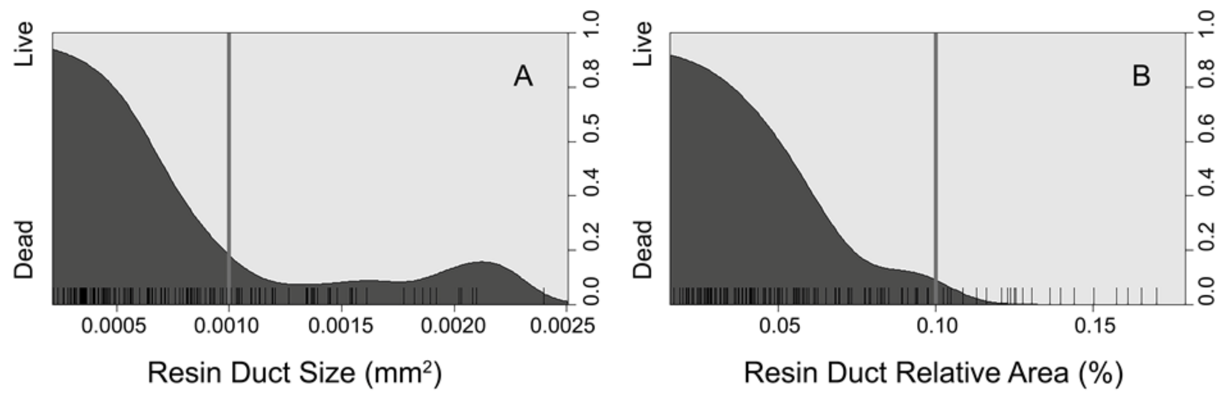

Figure 2. Plots showing the probability of mortality in relation to resin duct metrics (A) resin duct size [mm^2] and (B) relative resin duct area [% of annual ring]. Light shading reflects live trees while dark shading reflects dead trees. Short vertical black bars along the x–axis represent the distribution of samples, while the tall gray bar in each graph represents a potential threshold.

Management Implications

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 resin in response to attack or infection and may be a factor in the ability of live trees to endure multiple disturbance events over time. Although dead trees produced more resin ducts on average the ducts were smaller, and may have been insufficient to produce, store, and mobilize adequate amounts of resin in response to wounding by bark beetles and blister rust infection. This reduced resin flow in trees that died could be linked to lowered defense and higher mortality despite increased density of ducts, particularly in the years leading up to death.

Whitebark pine trees appear to use different strategies in the allocation of resources toward growth and defense depending on their location 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. Both strategies involve tradeoffs under different circumstances. For example, if the time between disturbance events is relatively long (decades to centuries), WBP trees that invest more resources into growth may thrive. Defense mechanisms require energy to produce and maintain, so the presence of these characteristics suggests there is strong selective pressure from disturbances to invest in these defenses.

This study provides insight into how resin duct characteristics are related to WBP survivorship, and highlight how different physiological traits are advantageous under different circumstances. **Whitebark pine forests are likely to experience complex biophysical and biological stressors in the future, so management actions that support genetic variability and the traits associated with this variability will be important for supporting the long-term persistence of whitebark pine.**

References

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