

Commentary

Tree physiology and bark beetles

Irruptive bark beetles usually co-occur with their co-evolved tree hosts at very low (endemic) population densities. However, recent droughts and higher temperatures have promoted widespread tree mortality with consequences for forest carbon, fire and ecosystem services (Kurz *et al.*, 2008; Raffa *et al.*, 2008; Jenkins *et al.*, 2012). In this issue of *New Phytologist*, Netherer *et al.* (pp. 1128–1141) experimentally explore the direct link between tree symptoms of drought and spruce bark beetle attack success rate. The study combined precipitation removal with a novel method for assessing bark beetle attacks. Lower soil moisture promoted lower tree water potentials, relatively lower tree resin flow, and a higher proportion of successful bark beetle attacks. Although attack rates were low, their results also suggest that host attractiveness to beetles decreased at the highest level of water stress. The Netherer *et al.* paper highlights the complex nature of interactions of trees with bark beetles. For example, the bark beetles show variability in the propensity to attack trees that may or may not be tied to environmental and tree cues. Factors related to the intrinsic beetle biology, combined with changes in tree physiology, highlight the difficulty of unraveling these interactions. In this commentary, we briefly review this complexity and offer suggestions for making further progress on this important problem particularly from the point of view of tree physiology.

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Endemic and epidemic phases of bark beetles

Irruptive bark beetles are endemic in most forests that they attack. During endemic stages, beetle populations are low and can only overcome defenses in less abundant, stressed trees (Boone *et al.*, 2011), such as lightning struck, diseased, or light-suppressed trees. The low size or vigor of these hosts limits brood production and subsequent increases of beetle populations (Boone *et al.*, 2011; Bleiker *et al.*, 2014), helping perpetuate the endemic stage. Bark beetles must kill their tree hosts for successful reproduction, a process driven by pheromone-mediated cooperative behavior to mass attack trees and exhaust their defenses. In a mass attack, pioneer beetles assess appropriate hosts (health and species) likely

using a combination of visual and chemical cues, including volatiles (Campbell & Borden, 2006). A few pioneer beetles first attack, and, if successful, use monoterpenes in host resins to produce aggregating pheromones that elicit the mass attack. Resin production and toxicity are critical physical and chemical barriers that pioneer beetles must overcome to prevent entrapment, death, and failure to produce pheromones.

Eruption to outbreak stages is poorly understood, but occurs when a number of positive and negative feedbacks operating from tree- to landscape-scales align to allow beetle populations to increase (Raffa *et al.*, 2008; Bleiker *et al.*, 2014). Multiple factors appear to determine the transition from endemic to outbreak stages. These include host availability, defenses and nutritional quality; beetle behavior and development; presence of beetle predators, symbionts and other microorganisms; stand structure and landscape features. Past outbreaks have been linked to regional drought and warm winters (Bentz *et al.*, 2009). However, suitable climatic events do not always trigger outbreaks, and outbreaks can continue even when weather conditions ameliorate.

The positive feedbacks involved for a rapid and sustained population increase are difficult to identify, but the availability of host trees may be key. As beetle population density increases, beetle preference switches to larger, healthier trees because of improved food quality, even though these trees are better defended (Boone *et al.*, 2011). If the availability of stressed hosts limits beetle populations in the endemic stage, drought-induced increases of stressed hosts may be sufficient to increase beetle populations. The rate and magnitude that these high-quality (but defense-impaired) hosts become available, coupled with timing of regional weather conditions favoring beetles, may start an outbreak. Another factor promoting epidemics may be an increasing tolerance to monoterpenes as beetle population size increases (Wallin & Raffa, 2004), suggesting that when populations begin increasing, ensuing generations can tolerate and overwhelm trees with higher defenses. This finding may also explain how outbreaks continue when drought subsides, and why tree defenses do not regulate beetle populations during outbreaks.

Linking tree physiology to defense

Drought, warming, fire and wind-throw have negative effects on tree physiology and defense and can increase the number of hosts suitable to beetles (Gaylord *et al.*, 2013). At the whole-tree scale, drought and warming can decrease photosynthesis and growth, decrease respiration, alter stored carbohydrates, and increase partitioning of photosynthesis to belowground (McDowell, 2011). Drought can decrease resin flow (Netherer *et al.*), change monoterpene production, composition and volatile emissions, and increase beetle attraction (Raffa, 2014). Drought can also reduce phloem thickness (reducing beetle reproductive success), increase

phloem viscosity and sugar concentration, and reduce the effectiveness of tree defenses against the fungi introduced with beetle attack (Croise & Lieutier, 1993).

Linking the better-studied components (growth and photosynthesis), with the poorly studied components (carbohydrate storage, resin production, volatile emissions) will help identify physiological mechanisms that control these components. For example, drought may reduce carbon availability for resin production (McDowell, 2011), but drought could also lower connectivity in the resin canal network, impair resin exudation by reducing turgor pressure exerted on resin canals, limit flow through increased viscosity, reduce carbohydrate availability through impairment of phloem transport or storage availability, and reduce induced defenses. Understanding the links between tree physiology and tree defense under the endemic and transition-to-epidemic phases will enable a better understanding and predictability of bark beetle epidemics.

A way forward

Understanding tree resistance, attractiveness, and defense for bark beetles is a complex problem where interactions play a substantial role. We believe that such a complex system is best approached using an integrative approach. Such an approach would include concurrent measurements of all the relevant components of the system, including carbon and water status, and resin and volatile production and composition of the tree hosts, the intensity of drought, and bark beetle population density and developmental stage (Fig. 1). The Netherer *et al.* study has many of these components and serves to stimulate future studies. However, additional complementary measurements would allow a more mechanistic interpretation of results. For example, measurements of photosynthesis, carbohydrate pools, and phloem flow would have enabled a better understanding of the link between resin

production and tree carbon and water status. Similarly, measurements of volatile flux and composition would have allowed better interpretation of the patterns in beetle attack. Combining these measurements with tree growth and phloem thickness measurements and local beetle population status and activity would provide further information about tree attractiveness to beetles. The novel beetle 'attack box' method outlined in the Netherer *et al.* study represents a real advance, because the trees and beetles themselves provide an integrated answer. However, for future application such methodology should be optimized for box size and number of beetles. Finally, simple metrics such as growth efficiency (Waring & Pitman, 1985) may be used to rank experimental trees by their likely susceptibility to bark beetle attack and reduce experimental variability.

Another method for reducing the enormous variability of field experiments would be to examine the links between tree physiology, defense and attractiveness using small trees in a controlled glasshouse environment, where individual components can be separately modified. Assessing some components of tree physiology is simple (leaf water potential, relative water content (RWC), osmotic potential), but linking these with carbohydrate storage, tree carbon economy, and resin and volatile production and composition is very difficult. Because this system is so complex, experiments in a controlled environment are likely the best way to make the concurrent measurements necessary to disentangle the mechanisms between tree physiology and defense. While attractiveness to bark beetles might be measured, trees in a glasshouse would be too small to be attacked. However, such controlled experiments could answer questions that could then be tested in the field, such as: What are the best metrics to identify a stressed tree that is attractive to beetles, particularly the pioneer beetles? How does drought change tree attractiveness to beetles, and how is this linked with the tree's carbon, water, and nutrient metabolism? How long do drought effects on tree physiology persist after the end of

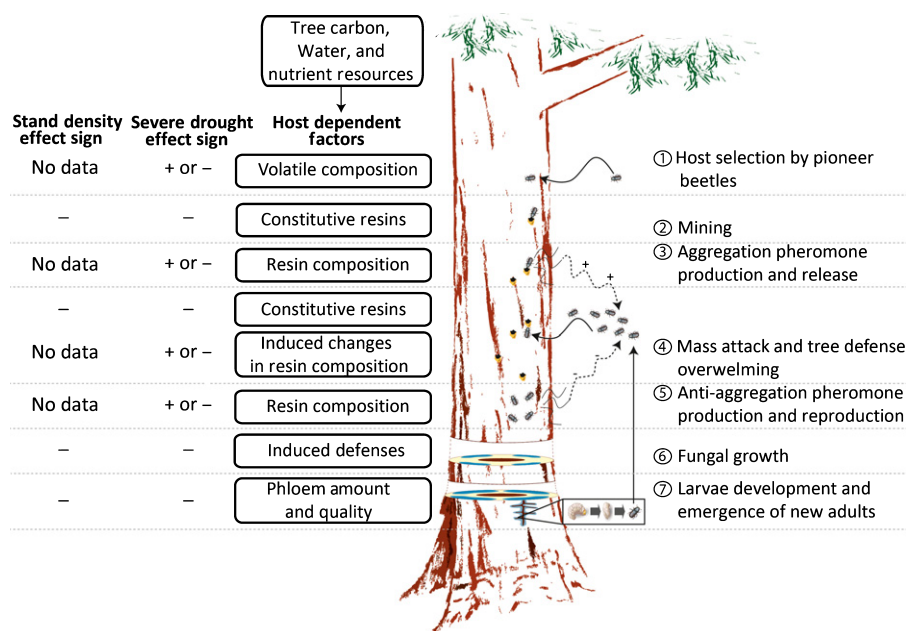


Fig. 1 Effects of severe drought and stand density on tree host factors influencing and interacting with bark beetle life cycle stages. The + and - for stand density and severe drought show the potential correlations of tree host factors with the component that interacts with the bark beetles.

drought? Field and controlled environment experiments that focus on the tree physiology and bark beetle interactions during the endemic stage or the transition from the endemic to outbreak stages will likely prove the most useful for predicting future outbreaks.

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