

Forest management treatments, tree resistance, and bark beetle resource utilization in ponderosa pine forests of northern Arizona

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Abstract

We show experimentally that forest restoration treatments that used thinning to reduce ponderosa pine density near Flagstaff, Arizona decreased the percentage of trees with successful bark beetle attacks induced by beetle community response to a *Dendroctonus brevicomis* pheromone. Underlying mechanisms for the beneficial effect of restoration treatments on tree resistance to bark beetles included stimulation of resin defenses. Resin flow after phloem wounding was greater in full and partial restoration treatments than the control in the first and second year after treatment. Five bark beetle species, *Ips pini*, *D. brevicomis*, *D. valens*, *D. adjunctus*, and *D. frontalis*, colonized and produced brood in the trees. There was a negative correlation between resin volume and number of brood that emerged from the bole. Niche breadth of the bark beetle species over bole positions was widest for *I. pini* and narrowest for *D. brevicomis*.

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1. Introduction

Thinning densely stocked stands of suppressed trees followed by prescribed fire is commonly used as a restoration treatment in forest ecosystems that are adapted to frequent, low-intensity fire (e.g., Covington et al., 1997; Moore et al., 2004). Restoration treatments that use thinning and prescribed burning have been shown to stimulate resource uptake and growth of ponderosa pine (*Pinus ponderosa*) in the Southwest U.S. (Schubert, 1974; Kolb et al., 1998; Zausen et al., 2005; McDowell et al., 2006). Such treatments have been reported to increase production of carbon-based defenses against bark beetles, such as resin, in some (Kolb et al., 1998; Feeney et al., 1998; McDowell et al., 2007), but not all (Zausen et al., 2005) studies. However, few studies have explored the effects of restoration treatments on bark beetle colonization, impacts of

increased resin volume on brood production of beetles, and within-tree resource utilization.

Ponderosa pine forests support complex communities of bark beetles (Coleoptera: Curculionidae, Scolytinae) (D.L. Wood, 1982; Gaylord et al., 2006). Bark beetle success is influenced by dynamic interactions with host trees and local populations of conspecifics (Lanier and Wood, 1975; Lanier et al., 1980). The effects of these interactions on bark beetle success likely shifts with changes in host defenses and density of local beetle populations. For example, at endemic population levels, beetles primarily attack less vigorous trees (Wallin and Raffa, 2005). However, beetles will attempt to colonize vigorous trees as conspecifics and other biotic agents deplete less vigorous trees (Berryman, 1982). Bark beetles emit pheromones to attract mates and coordinate mass attacks that can overcome defenses, such as resin (Rudinsky, 1962; Borden, 1982; S.L. Wood, 1982).

Bark beetle aggregation pheromones attract conspecifics, mates, and inter-specifics (Gaylord et al., 2006). Multiple species of bark beetles may respond to these pheromones and live and breed within the phloem tissue of the same tree species and even the same tree (Paine et al., 1981; Smith et al., 1990). Intra- and inter-specific competition for food and space frequently limits

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bark beetle reproductive success (Borden et al., 1993). However, the costs of competition may be offset by the benefit of entry by a large number of beetles within a short time frame that can exhaust host defenses (D.L. Wood, 1982; Raffa and Berryman, 1983; Robins and Reid, 1997; Raffa, 2001). In addition, inter-specific competition can be lessened by varied resource utilization patterns, or niche differentiation among beetles, within a single host tree (Birch, 1978; Paine et al., 1981; Wagner et al., 1985; Haack et al., 1987; Amezaga and Rodriguez, 1998; Ayres et al., 2001).

The occurrence and importance of synchronized attacks by bark beetles in overcoming host defenses in southwestern ponderosa pine forests are poorly understood. In these forests *Dendroctonus adjunctus* and *D. valens* often occur from the base of the tree to 0.5 m in height. *D. brevicomis* and *D. frontalis* are found in mixed assemblages from the base to 2.0 m or more in height tree (Breece et al., 2008). *Ips pini* are generally found above 2.0 m in height (Breece et al., 2008), or where bark is thin (Kolb et al., 2006). Beetle success in killing a vigorous host by a synchronized attack could offset costs of inter-specific competition. Alternatively, niche overlap of two or more species may prevent an individual species from ever dominating utilization of the resource and reaching outbreak levels.

Restoration treatments that consisted of tree thinning and prescribed burning of logging slash increased water uptake, photosynthesis, and radial growth of ponderosa pine at our study site in northern Arizona (Skov et al., 2004, 2005). Our study addresses the influence of these restoration treatments on ponderosa pine resistance to bark beetles for the first and second post-treatment years. We measured tree resistance to bark beetles as resin volume after phloem wounding, number of successful attacks, and by the relationship between resin flow and beetle brood production. Because bark beetle populations were at endemic levels during the study, we collected attack data with and without the use of pheromone lures placed on trees. A secondary goal was to describe resource utilization and niche partitioning within the tree for the bark beetle community that included five beetle species at our study site.

2. Materials and methods

2.1. Study site

The study site was the Fort Valley Experimental Forest located approximately 10 km NW of Flagstaff, AZ (35°15'58"N lat. and 111°42'13"W long.; or zone 48, 500,000 m east, 3,873,043 m north; elevation 2200 m). Annual precipitation averages 570 mm with about half occurring as winter snow and half as late-summer rain (Western Regional Climatic Center: <http://www.wrcc.dri.edu/index.html>). Soils are derived from basalt and are classified as a fine montmorillonitic complex of frigid Typic Argiborolls and Mollic Eutroboralfs (Miller et al., 1999). The frost-free season in the region of the study sites averaged 94 days (Schubert, 1974). Tree composition at the site was dominated by ponderosa pine, which was 99.8% of all trees (Skov et al., 2005).

The restoration treatments (described in detail in Skov et al., 2005) occurred between December 1998 and September 1999 and used tree thinning to experimentally establish four levels of

tree density. All thinning treatments were followed by prescribed burning of logging slash in 1999 or 2000. We included three levels of tree density in this study and each level was replicated twice spatially by a 17 ha plot.

The three treatments used in our study were full restoration, partial restoration, and control. No old trees (estimated age > 150 years, diameter at breast height (dbh) > 54 cm, having yellow bark) were cut in the thinned treatments. All younger trees were cut, except for trees that were retained when nearby there was evidence (stumps, stump holes, snags, down logs) of dead trees (following Covington et al., 1997 and described in detail in Skov et al., 2005). The full and partial restoration treatments differed only in the number of trees that were retained to replace old, dead trees. The full restoration treatment replaced each pre-settlement tree with an average of 1.5 trees \geq 40 cm dbh, or three trees < 40 cm when larger trees were not available. The full restoration treatment reduced average basal area by 58% (38–16 m² ha⁻¹) and average tree density by 85% (966–142 trees ha⁻¹). The partial restoration treatment used replacement levels of three larger or six smaller trees for each evidence of an old tree, and reduced average basal area by 35% (34–22) and average tree density by 77% (1055–245 trees ha⁻¹) (Skov et al., 2005). Basal area of the unthinned, control treatment averaged 38 m² ha⁻¹ and tree density averaged 1201 trees ha⁻¹ (Skov et al., 2005).

2.2. Tree resin defense response to restoration treatments

Tree resin flow after phloem wounding and prior to colonization by subcortical insects was used as a measure of resistance against bark beetles. We sampled 12 trees per treatment and per replication, totaling 72 trees, during pre- (June) and post- (August) monsoon seasons in years 2000 and 2001. Each sampled tree had a diameter 1.4 m from the base of the tree between 23 and 29 cm. Resin flow was measured using methods of Lorio (1993). The outer bark was removed with a drawknife, and the remaining bark and phloem were punctured with a 2.5-cm-diameter arch punch, avoiding injury to xylem. Aluminum troughs were pinned to the bark below the wound and resin was channeled into a graduated tube (Lorio, 1993; Kolb et al., 1998; Wallin and Raffa, 2001). After 24-h, the vials were removed and total volume was measured to the nearest 0.1 ml.

We compared resin flow among treatments in each year with a fixed-effects ANOVA model using ANOVA and SAS JMP software (SAS, 1996) that included thinning treatment, season (June and September), and their interaction as factors. Variances were homogeneous among treatments and dates as indicated by Levene's test (Sokal and Roalf, 1995). Mean comparisons among treatments and months with a year were performed with Fisher's protected LSD at $p = 0.05$.

2.3. Bark beetle colonization and resource utilization

We visually assessed the bole of the 72 trees that were sampled for resin flow, plus an additional 72 similar-size trees (12 per treatment per replication), for the presence of bark beetles in 2000 and 2001. During beetle flight, the entire length

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