Abstract

In the presence of herbivores, plants must allocate a portion of their accumulated carbon toward defense to survive. For example, trees susceptible to bark beetle attack are primarily reliant on resin production for protection. Tree mortality may be reflected by individual differences in the ability of plants to produce defensive structures and compounds. We compared the radial growth rates, resin duct production, density, and size between living and dead ponderosa pine trees in northern Arizona using standard dendrochronological techniques. As a result, we found four main findings: 1) living ponderosa pines had 33% more resin ducts than dead pines ($t = 2.97, P < 0.003$); 2) resin duct size was 13% larger in living than in dead pines ($t = 3.00, P = 0.003$); 3) both resin duct density and size were predictive of mortality (Wald's $Z = 1.9, P < 0.05$); and 4) resin duct production was positively correlated with growth rate. Our results suggest dendrochronology can quantify defense structure production and predict tree mortality in ponderosa pine forests in northern Arizona.

Introduction

Plants, in the presence of herbivores, must differentially allocate carbon between growth and defense (Loomis 1932, Herms and Mattson 1992). For trees susceptible to bark beetle attack (Fig. 1), insufficient appropriation of carbon to defense may result in mortality. Previous studies have quantified defense through resin production; however, these measures have been varied in their ability to predict tree mortality. Few studies have tried to use a retrospective approach to quantify resin duct production to predict tree mortality. As a result, we compared resin duct properties between living and dead ponderosa pine trees in northern Arizona to ask the following questions:

1. Can resin duct production, density, and size predict mortality in ponderosa pine?
2. Is growth rate related to resin duct production and does it support the growth differentiation balance hypothesis?

Methods

• All data was collected on the Coconino National Forest in northern Arizona.
• Three to five live and dead tree pairs (Fig. 1) were sampled at four previously established plots ranging in tree mortality between 14 and 62% (Negron et al. 2009).
• Tree pairs consisted of one living and dead tree within 15 m distance and within 2 cm dbh from one another (n = 28 pairs).
• Tree dbh ranged from 13 to 40 cm.
• One 12 mm increment core was taken from each tree at dbh and all cores were cross-dated using standard dendrochronological techniques (Stokes and Smiley 1968).
• For each core, ring width (mm), resin duct density ($n$ mm$^{-2}$), and resin duct production ($n$ mm$^{-3}$) measures were made for 10 yrs preceding death of the dead pine. Additionally, resin duct width (mm) measures were made for all resin ducts present in the 10 yrs preceding death.

Results

• Living ponderosa pines had 33% greater resin duct density in the 10 yrs growth preceding death of the dead pine ($t = 2.97, P < 0.004$; Fig. 2 & 3).
• Living ponderosa pines also had 13% wider resin ducts compared to dead pines ($t = 3.00, P < 0.003$; Fig. 2 & 3).
• Mean ring width was positively correlated with mean resin duct production over a 10 year period for both living ($r^2 = 0.725, P < 0.0001$) and dead ($r^2 = 0.556, P < 0.0001$) pine trees (Fig. 4a), while both living and dead mean ring width were negatively correlated to mean resin duct production (Fig. 4b).
• Ponderosa pine survivorship, based on logistic regression, was significantly predicted by both resin duct density (Wald's $Z = 1.90, P = 0.057$) and width (Wald's $Z = 1.99, P < 0.05$), with 68.0% of the observations correctly classified.

Conclusions

• Standard dendrochronology techniques can be used to retrospectively quantify and characterize defense properties in ponderosa pine trees.
• Both resin duct density and size differed between living and dead ponderosa pines and were significantly predictive of mortality. However, basal area index and ring width did not differ by tree status.
• Mortality prediction may aid restoration efforts, reduce loss in wood production, and improve predictive mortality models to better anticipate the impacts of climate change.
• A positive correlation between growth rate and resin duct production supports the growth differentiation balance hypothesis (GDBH; Loomis 1932, Herms and Mattson 1992) at low resource availability (i.e., soil moisture). However, a negative correlation between growth rate and resin duct density would support the GDBH at high resource availability.
• Our results suggest that individual ponderosa pines may differ genetically in resin duct density and size, which may subsequently ward off bark beetle attack through increased storage and delivery of resin during extreme drought. While the differences in resin duct widths were subtle, Poiseuille’s law states that increases in diameter may confer increases in flow by as much as a power of four.

Acknowledgements

This project is funded by a fellowship through the Science Foundation of Arizona. Plot location and present mortality data was graciously provided by Joel McMullin and Joe Negron. Helpful comments and suggestions were made by Tom Whitham. Additional thanks go to fellow members of the forest ecology group at NAU for editorial suggestions and comments.

Literature Cited