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Bark beetles and dwarf mistletoe interact to alter downed woody material, canopy structure, and stand characteristics in northern Colorado ponderosa pine

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ABSTRACT

Due to the recent outbreaks of bark beetles in western U.S.A., research has focused on the effects of tree mortality on forest conditions, such as fuel complexes and stand structure. However, most studies have addressed outbreak populations of bark beetles only and there is a lack of information on the effect of multiple endemic, low level populations of biotic disturbance agents that could influence forest dynamics, fuel heterogeneity, and species composition. Downed woody material, fuel parameters and stand characteristics were assessed in areas of ponderosa pine (*Pinus ponderosa*) infested with southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*), and in areas with endemic populations of mountain pine beetle (*Dendroctonus ponderosae*) and *Ips* spp. (Coleoptera: Curculionidae, Scolytinae) in northern Colorado. Both endemic bark beetles and dwarf mistletoe were associated with more dense stands than uninfested plots and resulted in reducing basal area of live trees. The amount of downed woody material was positively related to time since tree mortality and basal area of bark beetle-attacked trees. There was an increase of up to 10% for fine and coarse downed woody material for every increase of 1 m^2 ha^{-1} basal area of mortality from mountain pine beetle that was 4–15 years after death. The average intensity of dwarf mistletoe infections on live trees was positively related to amount of 10-h downed woody material and negatively associated with percent live ponderosa pine crown. Fuel bed and canopy characteristics were dependent on the presence of both dwarf mistletoe and mountain pine beetle-caused mortality. Together these endemic biotic disturbances have an effect on downed woody material biomass accumulation, fuel arrangements, stand densities and species composition.

1. Introduction

Recent studies have identified significant effects of bark beetle outbreaks on downed woody material and stand conditions (Kulakowski et al., 2003; Billings et al., 2004; Schulz, 2003; Lynch et al., 2006; Page and Jenkins, 2007a; Klutsch et al., 2009). However there is little information on the effect of endemic disturbances. Biotic disturbance agents at low population levels are characterized as endemic and tend to be restricted to a small number of trees scattered in the landscape. Information on the effects of multiple endemic disturbances is even more limited. This is despite the presence of multiple endemic biotic disturbances that occur throughout most forests. Due to the importance of low-level populations of biotic disturbances and their interactions, we examined the impact of three endemic disturbances on stand characteristics and downed woody material in ponderosa pine (*Pinus ponderosa* Laws.) forests in the Colorado Front Range.

There is increased interest in managing and understanding the factors that contribute to downed woody material in forests (Woodall et al., 2013). Downed woody material and other fuel complexes such as vegetation are part of the determination of fire hazard. Authors working in ponderosa pine forests (Alexander and Hawksworth, 1976; Lundquist, 2007; Hoffman et al., 2007; Stanton, 2009) and subalpine forests (McCullough et al., 1998; Kulakowski et al., 2003; Lynch et al., 2006; Page and Jenkins, 2007a,b; Jenkins et al., 2008; Klutsch et al., 2011) have identified relationships between fire hazard and bark beetle outbreaks and pathogens. Along with contributing to increased fire hazard, downed woody material plays a crucial role in providing habitat for wildlife and invertebrates, giving structure to the forest floor for retention of sediments and stream characteristics, and contributing to nutrient cycling and nitrogen fixation (Harmon et al., 1986; Vanderwel et al., 2006).

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Large disturbances, such as bark beetle epidemics, can lead to shifts in species composition and increased structural diversity post-infestation forests (Collins et al., 2011; Kayes and Tinker, 2012). Multiple disturbances can also alter forest composition, which can have consequences for forest successional trajectories and susceptibility to future disturbances (Kulakowski et al., 2013). However, it is not known if the impact of mortality of a limited number of widely dispersed trees due to endemic biotic disturbances has the same consequence for stand characteristics and species composition as epidemic disturbances.

Endemic populations of two bark beetles species and one pathogen were studied to identify changes in downed woody material and stand characteristics in ponderosa pine. At epidemic population levels, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Curculionidae, Scolytinae) infestations can cause extensive mortality in susceptible pine forests. However, tree susceptibility is not static and is dependent on beetle population size along with tree size and stand conditions. Populations of endemic mountain pine beetle are maintained on a low number of weak and low vigor trees, such as trees with root disease or damaged from lightning (Furniss and Carolin, 1977; Schmid and Amman, 1992; Schmid and Mata, 1996; Negrón and Popp, 2004). These trees are generally greater than 15–20 cm diameter at breast height (dbh, at height of 1.37 m) (Negrón and Popp, 2004; Smith et al., 2011). Stand conditions that contribute to the susceptibility of a ponderosa pine to infestation by eruptive populations of mountain pine beetle include: high stand stocking >17.1 $m^2\ ha^{-1}$ basal area, high stand density index (SDI), and high quadratic mean diameter (Negrón and Popp, 2004). Species of *Ips* (Coleoptera: Curculionidae, Scolytinae), such as *I. pini* (Say) and *I. knausi* Swaine, that infest ponderosa pine in the Rocky Mountains are secondary bark beetles that usually infest small diameter stressed trees, and generally cause limited mortality in ponderosa pine of northern Colorado (Furniss and Carolin, 1977).

Along with endemic populations of bark beetles, we examined the effect of the pathogen dwarf mistletoe on ponderosa pine forests. Dwarf mistletoes are obligate parasitic plants that infest conifer species in the Pinaceae family (Hawksworth and Wiens, 1996). In Colorado, southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum* [Engelm.] Hawksworth and Weins) infects ponderosa pine causing abnormal shoot growth, reduced radial growth, persistence of infested branches, and reduced tree vigor eventually leading to tree mortality. Dwarf mistletoe infestations can increase the amount of downed woody material on the forest floor and provide fire ladders that together can move surface fires into the crown by an increase in the amount and flammability of branches and foliage (witches' brooms) near the ground as compared to uninfested stands (Koonce and Roth, 1985; Hoffman et al., 2007; Stanton, 2009).

There may also be interactions between these disturbance agents that can result in changes in downed woody material and stand characteristics. Although the extent of dwarf mistletoe-induced susceptibility to bark beetle attack is unclear, studies have documented a predisposition of dwarf mistletoe infected trees to infestation by *Ips* spp. (Negrón and Wilson, 2003; Kenaley et al., 2006; Beam, 2009) and an association between dwarf mistletoe and mountain pine beetle (Johnson et al., 1976; McCambridge et al., 1982b; Smith et al., 2011). The compound effect of these two disturbance types (bark beetles and pathogen) that infest the same host species may lead to greater shifts to non-host species along with increases in downed woody material.

This study examined dynamics of downed woody material, canopy and fuel bed characteristics, along with stand structure during endemic bark beetle populations and dwarf mistletoe infestation in ponderosa pine in northern Colorado. The objectives were to: (1) identify changes in stand characteristics created by bark beetles or dwarf mistletoe or both; (2) quantify downed woody material and determine whether the biomass is a function of the amount of tree mortality, time since bark beetle-caused mortality, and dwarf mistletoe intensity; and (3) examine the effect of interactions between endemic bark beetle-caused mortality and dwarf mistletoe infestation on fuel bed and canopy fuel characteristics.

2. Materials and methods

2.1. Study site and plot selection

The study was conducted in the Canyon Lakes Ranger District, Arapaho-Roosevelt National Forest along the eastern slopes of the Front Range in the Rocky Mountains of northern Colorado (40°37′N, 105°28′W). The study area comprises approximately 2500 km^2 and ranges in elevation from 2060 to 2730 m. Populations of mountain pine beetle in northern Colorado have ranged from epidemic episodes (McCambridge et al., 1982b; Schmid and Mata, 1996) to endemic levels in ponderosa pine (Harris, 2005; USDA and CSFS, 1996–2006 Aerial Detection Surveys http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/). Our study area contained endemic populations of mountain pine beetle and *Ips* spp. The number of killed trees was small (∼2–20/patch), not substantially increasing over time, and reflected infestations from varying years, which suggested low-level chronic beetle populations. Southwestern dwarf mistletoe had a moderate occurrence where 19–27% of surveyed plots had infected trees in northern Colorado, which is the northern limit of southwestern dwarf mistletoe distribution (Merrill et al., 1987; Beam, 2009).

In 2005 and 2006, stand and fuel conditions were measured in 150 fixed radius plots (0.04 ha) within the ponderosa pine forest type. Plots were established to represent four disturbance types: uninfested (38 plots), those infested with only dwarf mistletoe (17 plots), only bark beetles (37 plots) and both disturbances together (58 plots). Areas with biotic disturbances were located using aerial survey maps for mountain pine beetle (USDA and CSFS, 1996–2006 Aerial Detection Surveys http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/) and local knowledge of dwarf mistletoe infestation areas (Merrill et al., 1987; Beam, 2009). When infested trees were encountered within a stand, plot center was determined by choosing a random distance and direction from an approximate disturbance center, while ensuring that plots were a minimum of 100 m apart. Plots with uninfested trees were established within 500 m of infested plots.

2.2. Sampling methods

Site characteristics recorded in each plot included percent slope, aspect (degrees), and elevation (m). For all live and dead trees with a measurable diameter at breast height (1.37 m, dbh), we recorded tree species, tree height (m), dbh, live crown length as a percentage of tree height, and height to bottom of live crown. Average quadratic mean diameter, height, density (trees/ha), basal area ($m^2\ ha^{-1}$), and stand density index (SDI) were calculated for ponderosa pine and for all tree species combined. Thirty year (1971–2000) average annual maximum and minimum temperatures were assigned to all plots from PRISM 800 m resolution (PRISM Group at Oregon State University, 2006).

The dwarf mistletoe infection intensity on a tree was assessed on all living ponderosa pine using the Hawksworth dwarf mistletoe rating with a scale of zero to six (Hawksworth, 1977). Plot average dwarf mistletoe rating for a plot was calculated by averaging the dwarf mistletoe rating of all susceptible trees (i.e., both uninfested and infested ponderosa pine trees). To estimate time since tree mortality, tree degradation status was assessed for all dead trees