Radial growth response and vegetative sprouting of aspen following release from competition due to insect-induced conifer mortality

Mario Bretfeld [a,*], James P. Doerner [b], Scott B. Franklin [a]

[a] School of Biological Sciences, University of Northern Colorado, Greeley, CO 80639, United States
[b] Department of Geography and GIS, University of Northern Colorado, Greeley, CO 80639, United States

ABSTRACT

Eruptive bark beetle outbreaks such as the recent mountain pine beetle epidemic in western North America often result in substantial changes to species composition, abiotic factors, and a highly altered fuel complex. Little is known about the implications of these outbreaks to non-host species, such as aspen (*Populus tremuloides* Michx.), which may be beneficiaries due to release from competition. We investigated radial growth response in aspen following mountain pine beetle-induced conifer mortality in north-central Colorado through dendrochronological analysis using the percent growth change method based on 5-year and 10-year running medians, and we quantified regeneration responses in these areas compared to areas where beetle activity was largely absent. We hypothesized that growth in mature aspen would increase, expressed through wider annual growth rings, while vegetative regeneration (i.e. resprouting from the parent root system) would not increase in forests affected by bark beetles.

Results showed a clear radial growth release in mixed aspen-conifer stands that were subject to extensive conifer mortality but not in forests that remained largely unaffected by beetles. Comparison of extent of suckering showed no significant differences, supporting our hypotheses and suggesting that additional resources due to release from competition were allocated towards radial growth rather than initiation of sucker growth, potentially indicating a trade-off between maintenance of existing stems and regeneration. Results from this study provide the first account of radial release detection in aspen following beetle-induced conifer mortality and help predict aspen persistence and future stand composition in these forests. Additional research, with a higher sample size and more time between sampling and bark beetle disturbance is highly recommended to confirm our findings and optimize release detection methods in aspen.

1. Introduction

Bark beetles are an important disturbance agent in North American forests. Eruptive bark beetle outbreaks often result in substantial changes to species composition and a highly altered fuels complex (Lynch et al., 2007; Jenkins et al., 2008; Collins et al., 2012; Jenkins et al., 2012). Tree species that are not directly affected by these outbreaks (i.e. non-host species) may be beneficiaries of beetle-induced conifer mortality, including quaking aspen (*Populus tremuloides*), a species of high ecological importance in the Intermountain West due to elevated productivity and taxonomic diversity in aspen-dominated habitats (Chong et al., 2001; Stam et al., 2008). Although little is known about the immediate implications of beetle-induced conifer mortality on aspen (Pelz and Smith, 2013), two possible responses benefitting the species include (a) elevated growth of individuals that were established prior to disturbance (growth response) and (b) increased rate of suckering (i.e. clonal or vegetative reproduction), the main regeneration strategy of aspen in its southern distribution (regeneration response). This study aims to detect and measure these responses in aspen of the subalpine forests of north-central Colorado.

Mortality of pine trees from bark beetle epidemics increases light to the forest floor and decreases competition; factors that favor both aspen growth and regeneration (Amacher et al., 2001; Shepperd et al., 2006). While the extent of aspen regeneration was included in several studies assessing forest trajectories following bark beetle epidemics (see below), no studies were found that specifically addressed changes in growth of mature aspen in

* Corresponding author at: Smithsonian Tropical Research Institute, Roosvelt Ave., Balboa, Ancón, Panamá, Panama. Tel.: +507 (676) 17331.
E-mail addresses: m.bretfeld@gmail.com (M. Bretfeld), james.doerner@unco.edu (J.P. Doerner), scott.franklin@unco.edu (S.B. Franklin).

beetle-affected areas. Characteristic of a pioneer species, aspen is a weak competitor and very intolerant to shade (Perala, 1990). Therefore, aspen are generally replaced by more shade-tolerant species that regenerate under the aspen overstory as part of typical succession (Peet, 1981; Bartos, 2000; Lieffers et al., 2002; Frey et al., 2004). Mortality of succeeding species temporarily resets this transition, effectively prolonging the lifespan of aspen that would otherwise gradually give way to coniferous species. Such a release from competition should be detectable by wider annual growth rings in the years following the beetle outbreak (i.e. competitor mortality). To assess a possible growth response, we investigated radial growth in aspen by means of dendrochronological analysis.

Dendrochronology and dendroecology are excellent tools to reconstruct past disturbance events (Fritts and Swetnam, 1989). The presence of releases, i.e. abrupt increases in radial growth, are indicative of past disturbance events and can be interpreted at a high spatial and temporal resolution (Frelich, 2002). Although dendrochronological research on aspen is rare due to the difficulty of core preparation and ring identification, and the short life span of aspen compared to other species, tree ring data were successfully used in some Canadian studies to reconstruct western tent caterpillar outbreaks in aspen by comparison of host and non-host chronologies (Cooke and Roland, 2007; Huang et al., 2008) or by identification of pale rings (Hogg et al., 2002).

Besides detecting a possible growth release in pre-disturbance established aspen, initiation of suckering is an area of great interest as aspen are believed to have been declining in the western United States for several decades (Packard, 1942; Krebill, 1972). In addition, the recent loss of overstory trees dubbed "Sudden Aspen Decline" suggests drought as the initial driver of aspen decline (Worrall et al., 2008, 2013; Rehfeldt et al., 2009; Anderegg et al., 2012, 2013). Although not mutually exclusive, growth of existing stems and suckering are controlled by opposing ends of the same regulatory mechanism. New aspen suckers (or ramets) develop from meristems on lateral roots of the parent root system (Schier et al., 1985). In addition to genetics, time of disturbance, pre-disturbance stand conditions, and nutrient and water supply, phytohormones such as auxin play a crucial role in sucker development of aspen (Schier et al., 1985; Frey et al., 2003). Auxin is synthesized in the apical buds and transported to the roots, inhibiting lateral growth on both stem and roots. Loss of overstory stems due to disturbances, such as fire or herbivory, halts the supply of auxin and promotes pulses of regeneration from the surviving parent root system (Romme et al., 1995; Jones et al., 2005). However, after selective disturbances such as bark beetle outbreaks, apical dominance from remaining mature ramets is maintained and may lead to allocation of additional resources towards existing ramets rather than initiation of new sucker growth. Furthermore, increased litter accumulation 5–10 years after bark beetle disturbance (Klutsch et al., 2009, 2011; Collins et al., 2011, 2012; Hicke et al., 2012) may potentially limit sprouting from the parent root system as thicker layers of organic matter have been shown to inhibit suckering (Lavertu et al., 1994; Fraser et al., 2004).

To evaluate a possible regeneration response, we quantified and compared the extent of suckering in areas showing heavy beetle-induced conifer mortality to areas with little beetle activity. Increased aspen suckering has been shown in several studies, although results were not conclusive. A modeling approach based on data spanning 13 western states by Shaw (2004) suggested that mountain pine beetle outbreaks may result in pure aspen stands. Collins et al. (2012) also predict an increase in aspen density in stands affected by mountain pine beetle in north-central Colorado, especially when followed by salvage logging. A moderate increase in relative abundance was found in Rocky Mountain National Park, Colorado, compared to pre-outbreak conditions (Diskin et al., 2011). Contrarily, Klutsch et al. (2009) found no

differences in seedling/sapling densities of aspen between infested and uninfested plots.

To the knowledge of the authors, the present study is the first account to directly assess and contrast growth and regeneration response in aspen following beetle-induced conifer mortality. We hypothesized that (a) pre-disturbance ramets show increased radial growth following disturbance in areas affected by bark beetles, and that (b) suckering from the parent root system does not significantly increase due to allocation of resources towards radial growth.

2. Materials and methods

2.1. Sampling area

Sampling sites were located near the Fraser Experimental Forest, in the Sulphur Ranger district of the Arapaho-Roosevelt National Forest in Grand County, Colorado. All plots were located in the subalpine elevation zone; elevation ranged from 2757 to 3052 m, mean aspect and slope angle were 188.2° and 18.7°, respectively (Table 1).

Dominant overstory species were subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and aspen (*P. tremuloides*). The most common understory shrubs included *Vaccinium myrtillus, Juniperus communis*, and *Shepherdia canadensis*.

First signs of bark beetle activity were reported in 2003 and by 2006 most of the forests in the sampled area exhibited widespread tree mortality (Hubbard et al., 2013). While data from aerial surveys provided dates for tree mortality at relatively high spatial resolution, ranging between 2003 and 2007 (USDA Forest Service; Table 2), these data "only provide rough estimates of location, intensity and the resulting trend information for agents detectable from the air" (excerpt from the survey data disclaimer).

2.2. Sampling procedure

Plots were chosen based on presence of aspen and ratio of live/dead conifers in the overstory, excluding areas with evidence of other recent disturbances (e.g. wind throw, fire) and avoiding sites in valley bottoms or near bodies of water to minimize confounding factors from different local hydrology. Two types of plots were sampled for comparison: mixed aspen-conifer forests affected by bark beetles (>50% conifers, of those >75% dead) and healthy, mixed aspen-conifer forests (>50% conifers, of those <25% dead). Seven mixed-healthy and eight beetle-killed plots were sampled (Table 2). In addition, two aspen-dominated stands (<10% conifers) were sampled for comparison but not analyzed in depth given the low sample size. Due to the extent of the recent bark beetle outbreak, coniferous components in mixed-healthy were generally comprised of subalpine fir and Engelmann spruce rather than lodgepole pine, since no areas were found with adequate proportions of healthy (alive and without signs of beetle effects) lodgepole pines. In each plot, two 50 m tapes were laid out in cardinal

Table 1
Sampling depth, averages and standard deviations of aspen diameters at breast height, and comparison of averages of abiotic factors per treatment.

Type	Sampling depth			Abiotics			Diameter (cm)	
	Plots	Trees	Cores	Elev. (m)	Aspect (°)	Slope (°)	Average	STDev
Beetle	8	39	76	2891	188.1	23.6	17.4	5.0
Mixed	7	33	62	2811	185.0	11.9	31.9	7.9
Aspen	2	10	19	2817	191.5	20.5	34.4	7.1