Forest Ecology and Management 353 (2015) 240–259

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Aspen mortality in the Colorado and southern Wyoming Rocky Mountains: Extent, severity, and causal factors

M.M. Dudley [a,*], K.S. Burns [b], W.R. Jacobi [a]

[a] Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, USA
[b] USDA Forest Service, Forest Health Protection, Lakewood Service Center, Golden, CO 80401, USA

ARTICLE INFO

Article history:
Received 5 February 2015
Received in revised form 31 May 2015
Accepted 1 June 2015
Available online 10 June 2015

Keywords:
Aspen
Forest health
Dieback
Cytospora
Regeneration

ABSTRACT

Aspen mortality and overstory dieback have occurred at unusually high levels throughout Colorado and western North America over the past fifteen years. Findings from southwestern Colorado indicated dieback and mortality was clearly related to climate stress, coupled with disease and insect attack. To determine whether similar amounts and causes of mortality were occurring in other mountainous regions of Colorado and southern Wyoming, we determined the health status of aspen on five national forests during 2009–2010. We established 500 random characterization plots in aspen-dominated stands on four of the five national forests and 97 detailed measurement plots, with half in 'damaged' and half in 'healthy' aspen stands (as defined by USDA Forest Service aerial detection surveys). Overstory aspen was healthy overall, in spite of nearly ubiquitous presence of disease among plots (99%) and high incidence of insect damage (50–75%); in detailed plots standing adult dead aspen percentages ranged from 20% to 33% among the five national forests. Adult aspen in damaged stands occurred at lower densities, and had thinner crowns (41% dead crown, compared to 16% in healthy stands). Damaged stands also had more standing dead adult trees (37%) than in healthy stands (16%). The proportion of live sapling stems and density of saplings did not differ between healthy and damaged stands. Incidence of select mortality agents, including wood-boring insects (*Agrilus liragus* and *Saperda calcarata*) (40% in damaged, 18% in healthy), aspen bark beetles (*Procryphalus mucronatus* and *Trypophloeus populi*) (31% in damaged, 12% in healthy) and Cytospora canker (caused by fungi in the genus *Cytospora*) (40% in damaged, 18% in healthy) was considerably greater among damaged stands. Aspen bark beetles were more common on south-facing sites than east or west-facing sites (27%, 17%, and 15%, respectively); Cytospora canker was less common on sites above 2800 m (23%) than on lower-elevation sites (28–34%). Prevalence of wood borers, aspen bark beetles and Cytospora canker were all significantly and negatively correlated with latitude among at least two of three aspen size classes. Attempts to model various measures of health of adult aspen (i.e. crown dieback and stem mortality) using site and climatic variables were largely unsuccessful. Since no differences were detected in density of regeneration between damaged or healthy stands, we conclude that most stands will persist upon the landscape for the foreseeable future. Further, we note that although observed densities of regeneration in damaged stands are not as great as levels observed following complete stand removal, suckering does occur, and stems are measurably healthier than regeneration in healthy stands.

1. Introduction

In Colorado and southern Wyoming, quaking aspen (*Populus tremuloides*) covers nearly 1.5 million hectares, and is one of the few hardwood tree species that occurs in the mountains. Aspen is an important early successional tree species throughout the conifer forests of the Rocky Mountains, but in many areas of Colorado and southern Wyoming, aspen forms stable and self-sustaining stands (Barnes, 1966; Mueggler, 1985; Long and Mock, 2012). Like many species in the Salicaceae family, aspen regenerate from root suckers that form a similar-aged cohort after a disturbance kills all or some of the overstory trees (Sandberg, 1951; Mueggler, 1985). Stand establishment occurs through the production of a cohort of regeneration after a major disturbance event, either by seed or through sprouting from existing roots (Mueggler, 1985). Aspen produces high numbers of suckers

* Corresponding author.
E-mail addresses: meg.dudley@rams.colostate.edu (M.M. Dudley), ksburns@fs.fed.us (K.S. Burns), william.jacobi@colostate.edu (W.R. Jacobi).

http://dx.doi.org/10.1016/j.foreco.2015.06.002
0378-1127/

following stand-replacing fire or other disturbances (Scheier and Campbell, 1978; Perala, 1995; Romme et al., 1995); sucker density is typically highest following a complete removal of the overstory, but regeneration still occurs in lower amounts as gaps in the canopy are produced (Shepperd, 1993; Shepperd and Smith, 1993; Shepperd et al., 2001). Widespread mortality of aspen across western North America has raised questions as to whether aspen will continue to occupy its current range in the face of a warming and drying climate (Rehfeldt et al., 2009). Several factors are thought to act synergistically to increase the occurrence of aspen dieback and mortality. These include drought conditions, site factors (such as stand aspect and elevation), and variable levels of clone susceptibility to disease and damage agents (Anderegg et al., 2014; Anderegg et al., 2013a, 2013b; Marchetti et al., 2011; Worrall et al., 2010, 2008; Bartos, 2008; Hogg et al., 2008; Fairweather et al., 2008). Biological agents that may affect survival of trees include Cytospora canker (caused by *Cytospora* spp.), the root disease fungus *Ganoderma applanatum*, the poplar borer (*Saperda calcarata*), the bronze poplar borer (*Agrilus liragus*), and two aspen bark beetle species (*Trypophloeus populi* and *Procryphalus mucronatus*) (Worrall et al., 2008; Worrall and Fairweather, 2009; Marchetti et al., 2011). These agents are generally considered to be of secondary importance to tree health, as compared with more aggressive (i.e. primary) damage agents, such as sooty bark (*Encoelia pruinosa*) and Cryptosphaeria (*Cryptosphaeria ligniota*) cankers, as well as forest tent caterpillar (*Malacosoma disstria*), which can attack apparently healthy trees. Stands which are experiencing drought stress often experience increased mortality from secondary disease and damage agents (Worrall et al., 2008, 2010; Marchetti et al., 2011).

Widespread aspen mortality and dieback has been documented across western North America over the past half century (Scheier, 1975; Scheier and Campbell, 1980; Bartos, 2008; Hogg et al., 2008; Worrall et al., 2008; Fairweather et al., 2008). Forest health researchers have documented stand mortality in southern Utah, Idaho, western Wyoming (Bartos, 2008; Guyon and Hoffman, 2011), Arizona (Fairweather et al., 2008; Zegler et al., 2012), Oregon and Washington (Flowers and Kohler, 2011) and the aspen parklands of Alberta and Saskatchewan (Hogg et al., 2008). Rapid overstory mortality was observed in southwestern Colorado beginning in 2004 by Worrall et al. (2008) who used the term 'sudden aspen decline' (SAD), to describe the rapid mortality. SAD is characterized by a rapid rate of branch death, coupled with adult stem mortality and variable regeneration density (Worrall et al., 2008, 2010).

Background overstory mortality rates in aspen stands are normally high during early periods of stand establishment; initial sucker density is so high that massive density-dependent mortality (i.e. natural thinning) occurs and gradually slows as the stand matures (Shepperd, 1993; Mueggler, 1985; Brandt et al., 2003; Vankat, 2011). Determining baseline mortality rates is key to identifying abnormal amounts of stem mortality. Annual mortality rates for mature overstory aspen are not easily available except from repeat measures such as the USDA Forest Service (USFS) Forest Inventory and Analysis (FIA) National Program plots. According to FIA data, the estimated proportion of standing dead stems >5 cm diameter are 32%, 20% and 21% for the Medicine Bow–Routt, Pike–San Isabel, and White River National Forests (FIA Datamart, www.apps.fs.fed.us/fiadb-downloads/datamart.html). If it is estimated that aspen remain standing for up to five years after death (as reported by Hogg et al., 2002), these standing dead amounts translate into 6.4%, 4.0% and 4.2% mortality per year. These estimates include shade-induced mortality of pole-sized (DBH < 12 cm) stems, and are thus likely higher than mortality estimates of adult (overstory) stems. Other stand mortality data come from monitoring plot studies in WY, MT, ID, USA and AB, MB, and SK, Canada. Results indicate ranges of yearly mortality rates of overstory trees from 2% to 4% in the US to 7% in Canada (Blodgett et al., 2009; Hart and Hart, 2011; Brandt et al., 2003; Steed and Kearns, 2010).

The USFS conducts annual aerial detection surveys (ADS) to map forest disease and insect activity (USDA and CSFS, aerial detection surveys http://www.fs.fed.us/r2/resources/fhm/aerial-survey). In response to the massive mortality noted in southwestern Colorado (and to reports of mortality in other areas of the state), aerial surveys by USFS in Colorado and Wyoming focused more specifically on aspen beginning in 2005. Aspen dieback and mortality was first included in the survey in 2008 as a separate damage category from other common damage agents in aspen, such as tent caterpillar defoliation. The ADS revealed considerable overstory mortality in areas outside of southwestern Colorado, but there was no information available on exact amounts and possible causes of stand-wide mortality (Appendix Fig. A.1).

Based on the occurrence of dieback in other nearby aspen ecosystems and the importance of aspen to the forests of Colorado and southern Wyoming, we formulated two main project objectives. These were: (1) To determine the current health status of aspen stands on five national forests in Colorado and southern Wyoming; (2) to identify the causes of increased rates of adult (DBH $\geqslant$ 12 cm) tree mortality and dieback in damaged stands. These forests were selected because roughly half occur on the east side and west on the side of the Continental Divide; areas east of the divide receive about a third less precipitation than west-side forests (Appendix Table A.6) (Daly et al., 2002). Thus, we could place plots in aspen stands located in areas of contrasting temperature, moisture, and other site conditions to assess the impact of recent regional drought episodes and estimate potential future changes in temperature and precipitation on aspen health.

We assessed the health status of aspen stands throughout Colorado and southern Wyoming through two separate surveys to answer the following specific questions:

1. Is the proportion of aspen dieback uniform among random stand characterization plots in sampled forests and tree diameter classes, stand density, or stand structure?
2. Is the level of dieback and mortality related to any observed site or stand characteristics?
3. Do measures of aspen health and levels of regeneration relate to site, stand characteristics or climatic variables?
4. Does the incidence of insects and diseases on aspen trees relate to the mortality noted and to any predisposing site, stand or climatic factors?

2. Methods

2.1. Study areas

Five study areas or national forests were assessed. Three national forests largely east of the Continental Divide (Fig. 1; Appendix Fig. A.1) were the Pike National Forest (Pike's Peak, South Platte, and South Park Ranger Districts) with 45,600 ha (487 km^2) of aspen stands, San Isabel National Forest (Salida and San Carlos Ranger Districts) with 77,800 ha (779 km^2) and the Medicine Bow National Forest (Brush Creek/Hayden, Laramie and Douglas Ranger Districts) with 25,900 ha (389 km^2) of aspen (Table 1). The two forests located on the west side of the Continental Divide included the White River National Forest (Blanco, Aspen–Sopris and Rifle Ranger Districts) with 136,500 ha (2264 km^2) of aspen stands, and the Routt National Forest (Yampa and Hahn's Peak Ranger Districts) with 113,100 ha (985 km^2) (Table 1). The particular ranger districts within each forest were selected for sampling because they contained the