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ASPEN CROWN DIEBACK AND MORTALITY ON THE WILLIAMS RANGER DISTRICT, KAIBAB NATIONAL FOREST, ARIZONA

Thomas J. Zegler

A Thesis

Submitted in Partial Fulfillment

Of the Requirements for the Degree of

Master of Science

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ABSTRACT

ASPEN CROWN DIEBACK AND MORTALITY ON THE WILLIAMS RANGER DISTRICT, KAIBAB NATIONAL FOREST, ARIZONA

Thomas J. Zegler

Crown dieback and mortality of quaking or trembling aspen (*Populus tremuloides*) were extensive within pine-oak and mixed conifer forest types of the Williams Ranger District, Kaibab National Forest in northern Arizona. I collected data from 48 aspen sites to determine if predisposing site and stand factors and contributing damaging agents were associated with aspen crown dieback and mortality. Overstory aspen mortality averaged 50% by stems per hectare and 44% by basal area. Based upon univariate relationships, elevation was the most significant site factor related to both overstory aspen crown dieback ($R^2 = 0.15$, $P = 0.0069$) and overstory aspen mortality ($R^2 = 0.24$, $P = 0.0004$). The most significant stand factor related to crown dieback was live aspen density ($R^2 = 0.18$, $P = 0.0029$), while percent conifer ($R^2 = 0.45$, $P < 0.0001$) was the most significant stand factor related to mortality. Canker diseases, wood-boring insects, and animal damages were common in the overstory size class. The significant damaging agents in relation to both overstory crown dieback and mortality were canker diseases ($R^2 = 0.13$, $P = 0.0123$; $R^2 = 0.18$, $P = 0.0028$, respectively) and wood-boring insects ($R^2 = 0.24$, $P = 0.0005$; $R^2 = 0.56$, $P < 0.0001$, respectively). Sapling and tall sucker aspen mortality were high (> 80 and 70%, respectively), while short sucker mortality was low (16%). Many sites did not have live aspen regeneration, therefore, sample sizes were low, and relationships were often inconclusive or weak. Animal

damages and canker diseases were common in the sapling and tall sucker size classes. Only animal damages were common in the short sucker size class. Among damaging agents and regeneration size classes, the only significant univariate relationship found was between animal damages and short sucker aspen mortality ($R^2 = 0.15$, $P = 0.0198$). Based on a negative exponential diameter distribution, there was lack of aspen recruitment in saplings and small diameter overstory stems. If high mortality and low recruitment continues, aspen stands will be replaced by conifer after larger, and presumably older, overstory aspen stems die. The multivariate relationships of overstory aspen crown dieback, overstory aspen mortality, and short sucker aspen mortality among site, stand, and damaging agent factors were explored using step-wise multiple regression. The significant multivariate associations with overstory aspen crown dieback were elevation ($F_{1,44} = 16.38$, $P = 0.0002$) and incidence of canker diseases ($F_{1,44} = 15.02$, $P = 0.0004$). The significant factors explaining the variation in overstory aspen mortality were forest type ($F_{1,43} = 5.92$, $P = 0.0192$), overstory percent conifer ($F_{1,43} = 8.24$, $P = 0.0063$), and incidence of canker diseases ($F_{1,43} = 33.05$, $P < 0.0001$), and wood-boring insects ($F_{1,43} = 33.29$, $P < 0.0001$). The significant factors explaining the variation in short sucker aspen mortality were slope ($F_{1,31} = 4.90$, $P = 0.0344$), short sucker percent conifer ($F_{1,31} = 5.00$, $P = 0.0327$), and incidence of animal damages ($F_{1,31} = 6.85$, $P = 0.0136$). According to previous research, ungulate herbivores contribute to aspen decline in northern Arizona by causing damage to aspen regeneration. Ungulate damages were common in all size classes (between 49 and 66%), but significant relationships were limited to short sucker aspen mortality. No data were collected from within ungulate

exclosures in this study. Controlled experiments inside and outside of ungulate exclosures are needed to determine the impact of ungulates.

KEYWORDS: *Populus tremuloides*, aspen decline, conifer encroachment, canker disease, wood-boring insect, ungulate herbivore

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PREFACE

My thesis contains a short introduction (Chapter 1) and one manuscript chapter (Chapter 2). Chapter 2 is written in manuscript format so that it may be submitted for publication in a scientific journal. Please excuse any redundancy due to the manuscript format.

CHAPTER 1: Introduction

Many forests in western North America experienced increased crown dieback and mortality of quaking or trembling aspen (*Populus tremuloides*) over the past 15 years. The scientific community generally considers this loss of aspen trees and stands as a "decline". This decline is categorized into two types: "aspen decline" and "sudden aspen decline" (SAD). Aspen decline is typically regarded as a long-term process that is driven mostly by forest succession and chronic browsing of aspen regeneration by ungulates (Bartos and Campbell, 1998; Ripple and Larson, 2000; Kulakowski et al., 2004; Di Orio et al., 2005). SAD occurs rapidly and is characterized as a landscape-scale event (Worrall et al., 2008). When crown dieback and mortality of aspen are caused by many interacting factors, a useful way to organize and conceptualize these factors is within the framework of a decline disease (Frey et. al, 2004). A decline disease includes a complex interaction of predisposing, inciting, and contributing factors.

Since 2000, the northern and eastern regions of Arizona have experienced thousands of acres of aspen crown dieback and mortality (Fairweather et al., 2008) It is widely believed that both long-term (e.g., site and stand conditions) and short-term factors (e.g., a suite of disease, insect, and animal damaging agents) interact to cause aspen decline. My study was conducted on the Williams Ranger District, Kaibab National Forest in northern Arizona. During the summers of 2009 and 2010, I collected data corresponding to the predisposing and contributing factors of aspen decline outlined in previous research.

Chapter 2 presents these data and addresses the following objectives: i) determine the current structure, composition, and aspen crown dieback and mortality levels of aspen

stands; and ii) examine the relationships between and among aspen overstory crown dieback and mortality and regeneration density and mortality to predisposing site and stand factors and contributing damaging agents. Chapter 2 provides descriptive information about site, stand, and damaging agent conditions within a randomized set of 48 aspen stands. Simple linear regression was used to explore factors associated with overstory aspen crown dieback and mortality and regeneration aspen density and mortality. Multiple linear regression models developed for overstory aspen crown dieback and mortality and regeneration mortality provided information about the relative importance of site, stand, and damaging agent factors.

CHAPTER 2: Aspen crown dieback and mortality on the Williams Ranger District, Kaibab National Forest, Arizona

Introduction

Crown dieback and mortality of quaking or trembling aspen (*Populus tremuloides*) have rapidly increased over the past 15 years in parts of western North America (Fairweather et al., 2008; Hogg et al., 2008; Worrall et al., 2008). In many western landscapes, aspen is the principal upland deciduous tree species. Therefore, aspen trees and stands are biologically and economically important because they provide critical, disproportionally high, amounts of plant and animal habitat and human aesthetic enjoyment (Romme et al., 2001; McCool, 2001). White et al. (1998) noted that in the western United States, aspen are second only to riparian areas in terms of biodiversity. Therefore, the loss of aspen is a loss of biodiversity and landscape diversity and has negative impacts on local economies.

The terminology associated with the loss of aspen trees and stands over time is vague and controversial. Forest scientists generally use the terms "aspen decline", "aspen dieback", and "aspen die-off" synonymously to describe a reduction in aspen forest type on a broad range of spatial scales, but driven mostly by long-term successional processes under altered disturbance regimes (Bartos and Campbell, 1998; Kulakowski et al., 2004; Di Orio et al., 2005). However, the term "sudden aspen decline" (SAD) was coined for the rapid and synchronous crown dieback and morality of aspen on a landscape-scale (Worrall et al., 2008). There is a general consensus that both aspen decline and SAD are occurring in at least some portions of aspen's wide geographic distribution (Guyon, 2006; Fairweather et al., 2008; Hogg et al., 2008; Worrall et al., 2008).

It can be difficult to determine what type of decline is affecting any given deteriorating aspen stand because no single set of site, stand, and damaging agent conditions can be applied to aspen forests in general (Kashian et al., 2007). However, long-term and sudden declines share common symptoms, of which crown dieback and mortality are two of the most apparent, and therefore, commonly reported (Hogg et al., 2008). Whether one observes a slower aspen decline that is driven in part by forest succession (but not caused by succession alone) or observes a more rapid aspen decline like SAD, a useful way to understand aspen crown dieback and mortality is within the conceptual framework of a decline disease (Frey et al., 2004). A tree decline disease occurs when abiotic and biotic factors interact to cause widespread tree mortality. As described by Manion (1991) and Manion and LaChance (1992), a decline disease includes a complex of three types of factors: predisposing, inciting, and contributing. Predisposing factors are long-term, slowly changing factors (e.g., site and stand conditions). Inciting factors are short-term factors that cause acute stress (e.g., drought). Contributing factors are mostly biological agents (e.g., fungi and insects) that kill trees that have been weakened by predisposing and inciting factors. Trees affected by any one type of factor may recover quickly; it is the interacting effect of many factors that cause a decline disease. Therefore, it is impractical to use this concept to deduce specific causal relationships (Ostry et al., 2011). Despite this limitation, previous researchers and forest scientists identified the predisposing, inciting, and contributing factors of aspen decline.

Predisposing factors of aspen decline include long-term climate change (Hogg et al., 2002), plant succession (Mueggler, 1985; Rogers, 2002), and site and stand characteristics (Frey et al., 2004). In the context of aspen decline, the more explicit term

“conifer encroachment” is commonly used in place of “plant succession” (e.g., Stam et al., 2008). Conifer encroachment, especially in regions with short historical fire cycles is believed to be an effect of fire suppression in western North America (Hessl and Graumlich, 2002; Margolis et al., 2007). Other predisposing site factors include low elevation and southerly aspects, while stand factors include stand age, large stem size, and low stand density (Rogers, 2002; Fairweather et al., 2008; Worrall et al., 2008). Severe drought and high temperatures during the growing season (Hogg et al., 2008; Rehfeldt et al., 2009) and defoliation by insects or late frost (Frey et al., 2004; Fairweather et al., 2008) are important inciting factors. Ungulate browsing, wood-boring insects, and canker diseases are examples of key contributing damaging agent factors (Baker et al., 1997; Binkley, 2008; St. Clair et al., 2010).

Arizona occupies some of the most southerly and dry aspen habitat in the United States (Burns and Honkala, 1990) and the northern and eastern regions of the state have experienced aspen crown dieback and mortality over thousands of hectares (Fairweather et al., 2008). Aerial detection surveys conducted between 2006 and 2008 by the Forest Health Protection (FHP), Arizona Zone Office, USDA Forest Service support these observations. Aspen damage in Arizona was as detected on an increasing number of hectares from 2006 – 2008: ~ 27,100 in 2006, ~ 40,300 in 2007, and ~ 49,800 in 2008 (USDA Forest Service, 2007, 2008, and 2009). Of the aspen damage detected in 2008, 53% occurred on the Kaibab National Forest (USDA Forest Service, 2009). However, aerial detection surveys are a coarse-scale, rapid assessment tool, so the severity of crown dieback and mortality at the local site-level is unknown, and the specific biotic and abiotic factors (damaging agents) responsible for aspen damage are speculative.

Attempts to gather more detailed information on the severity of aspen crown dieback and mortality and damaging agents in Arizona have been initiated. On the Coconino National Forest in northern Arizona, Fairweather et al. (2008) reported an overall cumulative mortality level of 55% between 2000 and 2007, with 95% mortality in low-elevation xeric sites (< 2,300 m) and 61% mortality in mid-elevation sites (2,300 - 2,600 m). Their study noted an accelerated rate of decline following a severe frost event in June 1999, and severe drought in 2002. Damaging agents contributing to the mortality of already stressed aspen were canker diseases and wood-boring and defoliating insects. Wild ungulate browsing was common and severely limited aspen sucker height. On the Apache-Sitgreaves National Forest in eastern Arizona, overall cumulative mortality was 46% between 2001 and 2006 (M. Fairweather, USFS FHP, May 2011, personal communication).

I collected data from a set of randomized, permanent aspen sites located on the Williams Ranger District of the Kaibab National Forest in northern Arizona. Specific objectives of the study were to determine:

i) the current structure, composition, and crown dieback and mortality levels of aspen stands.
ii) the relationships between and among overstory aspen crown dieback and mortality and a) predisposing site factors); b) predisposing stand factors; and c) contributing damaging agents.
iii) the relationships between and among current aspen regeneration density and mortality and a) predisposing site factors); b) predisposing stand factors; and c) contributing damaging agents.

Methods

Study Area

My study area was the Williams Ranger District of the Kaibab National Forest in northern Arizona (Fig. 1). Aspen stands in the study area are distributed over ~ 382,400 ha. According to an inventory conducted by Williams Ranger District personnel in 2005, aspen forest type occupies < 1% of that area (~ 970 ha in ~ 330 stands). The majority of stands are discontinuous and small (0.1 – 25 ha) and occur at lower elevations (< 2,400 m). Larger stands are also present and tend to occur on north slopes at higher elevations (> 2,400 m) on Bill Williams, Kendrick, and Sitgreaves Mountains. Aspen stands are intermingled with ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambelii*) at lower elevations, and southwestern white pine (*Pinus strobiformis*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and white fir (*Abies concolor* var. *concolor*) at higher elevations.

The Williams Ranger District is grazed and browsed by domestic cattle and sheep (Family: *Bovidae*) and wild deer and elk (Family: *Cervidae*). Domestic ungulate use is managed by a permit system, and there are contract specifications on location, number of animals, and duration of use. Wild ungulate use is unregulated. Therefore, the study area is grazed year-round, except when deer and elk move to lower elevations to escape deep snow.

Site Selection

I used stratified random sampling with proportional allocation to select a subset of aspen sites across the Williams Ranger District. Using ArcGIS, a 30 m digital elevation model, and an ESRI shapefile (.shp) of the distribution of aspen forest type (provided by

Williams Ranger District personnel), I stratified the ~ 330 mapped aspen stands by elevation, slope, and aspect. Based upon the mid-point of the range of elevations and slopes within the distribution of aspen forest type, I classified elevation by low (≤ 2,400 m) and high (> 2,400 m) and slope by low (≤ 28%) and high (> 28%). Aspect was classified into flat, north, east, south, and west. These classes were combined to create 20 strata, each representing a unique combination of topographic classes. I then selected a random sample of 201 potential sampling points (site centers) based upon the proportion of each stratum to the total population (ArcGIS, Sampling tool). Therefore: i) common strata received more potential random sampling points; and ii) a range of stands were selected for sampling versus the selection of aspen stands with only the best or worst site conditions.

Of the 201 selected sampling points, 48 sites were sampled and 153 sites were rejected for the following reasons: i) < 10 standing live or dead aspen stems (n = 66); ii) < 200 m from a previously installed site (n = 36); iii) > 4 hour hike (n = 24); iv) within a fire restricted area (n = 15); v) within an ungulate exclosure (n = 10); or vi) high human impact (n = 2). All live conifer and dead aspen were recently cut at one of the high human impact sites and the other was adjacent to a road, several homes, and a trailhead parking lot.

Tree Sampling and Measurement

Plot design

I used a nested plot design adapted from Brown et al. (2006) to collect detailed site, stand, and damaging agent data at each site (Fig. 2). At each site to be sampled, I established four 8 m radius overstory plots (~ 0.02 ha; 201.1 m^2) at cardinal directions 20

m from the site center. Within each of the 8 m subplots, one 4 m radius nested regeneration plot (~ 0.005 ha; 50.3 m^2) was installed. The site was the sampling unit; all data from the 8 and 4 m plots were combined and converted to a per-hectare basis (Brown et al., 2006).

Site center

Site center was permanently marked with rebar, tagged, and the Universal Transverse Mercator location was recorded with a global positioning system. Elevation, percent slope, and aspect were recorded at site center.

Overstory plots

Stems ≥ 10.1 cm in diameter measured at 1.37 m above ground (diameter at breast height, DBH) were defined as "overstory". Overstory size class stems with their centerline inside the 8 m plot were considered "in". I marked stems with numbered tags at DBH on the uphill side, starting north and moving clockwise. Tree species, condition class, DBH, height, crown dieback, and damaging agent variables were collected for overstory size class stems.

Condition class categories for all tree species were live and standing dead. Stems with any amount of green foliage or live cambial tissue were considered "live" even though death may have been imminent.

Percent crown dieback was estimated only for live aspen. Crown dieback was defined as the number of dead branches in the tree crown located above crown base divided by the total number of branches in the tree crown located above crown base. Crown dieback classes were light (0-33%), moderate (34-66%), and heavy (67-100%).

These classes were suggested by FHP scientists in the field (J. Guyon, USFS FHP, May 2009, personal communication).

Incidence of disease, insect, and abiotic, and animal damages (Ostry et. al, 1989) were collected for all live and dead aspen with bark present. Damaging agents were identified in the field by signs and symptoms. Recently dead stems were included because the signals of many damaging agents cited in previous research to be "important" are detectable even with minimal bark (Ostry at al., 1989). A maximum of three present and harmful damaging agents per stem were recorded (Steed and Kearns, 2010). Damaging agents were collected individually and then pooled into disease, insect, and abiotic and animal damage groups to create site averages (Appendix A). Of the animal damages caused by ungulates, "barking and rubbing" is only known to occur from wild members of the cervidae family (Debyle, 1985), which is limited to deer and elk in northern Arizona.

Regeneration plots

I divided live and dead regeneration into three size classes and defined each as "sapling" (≥ 5.1 but < 10.1 cm DBH), "tall sucker" (≥ 1.37 m tall but < 5.1 cm DBH), and "short sucker" (< 1.37 m tall). The short sucker size class was determined by height alone because the height of aspen suckers, rather than the age or diameter, is a better indicator of the likelihood of aspen recruitment into the canopy (Baker, 1997; Kashian et al., 2007).

Tree species, DBH, condition class, crown dieback, and damaging agent variables were collected for sapling size class stems. Crown dieback was not analyzed because aspen saplings were usually live and vigorous or they were dead.

Tree species, condition class, and damaging agents were collected for tall and short sucker size class stems. The incidence of a maximum of three present and harming individual damaging agents were tallied for aspen in each class, and then pooled into groups to create site averages. Of the animal damages caused by ungulates, "browsing" and "trampling" is known to occur from members of both the cervidae and bovidae families. Therefore, I was not able to distinguish between the browsing and trampling damages of domestic and wild ungulate herbivores.

Data Analyses

Table 1 provides a set of predisposing and contributing factors suggested by previous research to be associated with aspen decline disease (both as part of forest succession and SAD), and the corresponding variables I analyzed in this study. Data from the four overstory plots were used to calculate mean aspen DBH, mean aspen height, total and aspen live stems ha^{-1} (TPH), total and aspen live basal area (BA; always reported as m^2 ha^{-1}), percent conifer by TPH and BA among living stems, percent aspen crown dieback > 33%, and percent aspen mortality by TPH and BA. All data from the four regeneration plots were converted to a per-hectare basis. Raw aspect was transformed into a continuous scaled variable with a 0 – 2 range (set to maximum for northeast slopes) following the equations in Beers et al. (1966) so that I could calculate heat load. Heat load is a unit-less index with a 0.03 – 1.11 scale, and was calculated from slope, aspect, and latitude following the methods outlined in McCune and Keon (Equation 3, 2002). JMP 8.0.2 (SAS Institute, 2009) was used for all analyses and significance for all tests was set at $\alpha = 0.05$.

ANOVA (two-tailed t-test) was used to test differences between continuous variables in two forest type groups: pine-oak and mixed conifer. The Wilcoxon rank-sum test was used when normality assumptions were not met. Tukey's honestly significant difference (HSD) was used for multiple comparisons of means among overstory, sapling, tall sucker, and short sucker aspen mortality. Paired, two-tailed student's t-tests were used to compare live versus dead aspen DBH and live versus dead aspen TPH.

Simple linear regression was used to determine the univariate relationships between: i) response versus explanatory variables; ii) response versus response variables; and iii) explanatory versus explanatory variables. Overstory response variables were percent aspen crown dieback > 33% and percent aspen mortality by BA. Moderate crown dieback was chosen as the dieback threshold for analysis because > 33%: i) is a commonly accepted threshold of serious dieback used by forest health experts in the field (J. Guyon, USFS FHP, May 2009, personal communication) and is supported with my data; and ii) indicates substantial stress to a hardwood species due to reduced photosynthetic potential (Steinman, 2000). The explanatory variables were site, stand, and damaging agent factors. For the ordinal variable "forest type", indicator (dummy) variables were used: pine-oak type = 0 and mixed conifer type = 1. Explanatory variables that had a mathematical dependency with the response variable were not analyzed (e.g., percent aspen mortality by BA versus live aspen BA). Analyses for overstory aspen crown dieback were run with n = 47 sites because one site had no live overstory aspen stems, and therefore, a null value for percent aspen crown dieback. All 48 sites were used for overstory aspen mortality analyses.

Regeneration response variables were live aspen TPH and percent aspen mortality by TPH, while the explanatory variables were site, stand, and damaging agent factors. Regeneration (especially sapling and tall sucker) analyses were problematic because of small sample size, many zero and 100% values, potential outliers, and possible non-linear relationships. Sample size was: n = 48 (with 36 zero values) for sapling live aspen TPH analyses; n = 32 (with 20 100% values) for sapling aspen mortality analyses; n = 47 (with 38 zero values and one potential outlier) for tall sucker live aspen TPH analyses; n = 23 (with 14 100% values) for tall sucker mortality analyses; n = 47 (with five zero values and one potential outlier) for short sucker live aspen TPH analyses; and n = 43 (with zero 100% values) for short sucker mortality analyses. To remove zero and 100% values from sapling and tall sucker analyses, I limited the sample sizes of respective tests to the sites where live aspen saplings and tall suckers occurred. Outliers were identified through a combination of visual inspection of residual by predicted and outlier box plots and violation of threshold values ($D_i > 4/n$) for Cook's distance. One outlier for each tall and short sucker live aspen TPH analyses was excluded. Finally, analyses of log-transformed regeneration response and explanatory variables were examined to clarify possible non-linear relationships.

Multiple linear regression was used to develop preliminary and final models for overstory aspen crown dieback, overstory aspen mortality, and short sucker aspen mortality. No multivariate models were produced for aspen saplings or tall suckers because small sample sizes in these classes prevented multivariate analyses. Overstory percent aspen crown dieback > 33%, overstory percent aspen mortality by BA, and log-transformed short sucker percent aspen mortality by TPH were the response variables,

while raw site, stand, and damaging agent factors were the explanatory variables. Log-transformed short sucker mortality was used because the relationships in this size class did not appear to be linear. Sample size was: n = 47 for overstory aspen crown dieback analyses; n = 48 for overstory aspen mortality analyses; and n = 35 for short sucker aspen mortality. Sample size was lower for short sucker mortality because five sites had no live or dead short sucker aspen (5 null percentage values) and 8 sites had 0% aspen mortality (8 null log-transformed values). Candidate explanatory variables for the preliminary models were chosen from the most significant univariate variables. Candidate explanatory variables for the final models were tested using stepwise-forward multiple regression in various combinations using a probability of 0.05 to both enter and leave the model (Draper and Smith, 1998). Final multiple regression models were tested for homoscedasticity, normality, and variance inflation. Homoscedasticity of errors was validated by visual inspection of the predicted versus residual plot and a constant variance test. Normality of errors was validated by visual inspection of a normal quantile plot and a Shapiro-Wilk test. Calculations of the variance inflation factor showed no evidence of multicollinearity among explanatory variables in each final model.

Results

Predisposing Site and Stand Factors

I sampled 48 aspen sites from a range of elevations, slopes, aspects, and forest types across the study area in the summers of 2009 and 2010 (Table 2). Site elevations ranged from 2,094 m (on knolls southeast of Bill Williams Mountain) to 2,888 m (near the top of Kendrick Mountain) (Table 2). Slopes averaged 25% and ranged from 3 – 59%. Aspen sites occurred on all aspects, but the majority of sites (59%) were on

northerly aspects (38% of sites fell between 315° and 359° and 21% were between 0° and 45°). The average heat load was 0.91, and 69% of sites were in the hotter and drier upper 20th percentile of the heat load scale. With increasing elevation, percent slope increased (R^2 = 0.23, P = 0.0004), heat load decreased (R^2 = 0.13, P = 0.0126), and aspect was non-significant (R^2 = 0.0006, P = 0.8713). By forest type, 15 of the 48 sites were in pine-oak and 33 sites were in mixed conifer. In the mixed conifer forest type, elevation (P < 0.0001) and slope (P = 0.0002) were greater, while heat load was lower (P = 0.0315) than in pine-oak type. Aspect was non-significant between pine-oak and mixed conifer (P = 0.9308).

Overstory stems and univariate relationships

Aspen stems in the overstory size class occurred on all 48 sites, and 47 sites (98%) had an overstory live aspen component (Table 2). DBH of overstory live and dead aspen stems averaged 20.3 cm and ranged in size from 12.0 to 39.3 cm. Across all sites, mean live aspen DBH (21.7 cm) was greater than dead aspen DBH (18.2 cm) (P < 0.0001). Mean BA of live aspen ranged from 0 – 52 m^2 ha^{-1}, with a mean of 11.7 m^2 ha^{-1}. Live aspen TPH ranged from 0 – 1156, with a mean of 271. Percent conifer in the overstory size class (overstory percent conifer) averaged 67% by BA and 59% by TPH, with a range of 0 – 100%. However, only one site each had 0 or 100% conifer; the remaining 46 sites were a mixture of aspen and other tree species. Overstory aspen stems with light, moderate, and heavy recent crown dieback averaged 52%, 28%, and 19%, respectively. Aspen mortality averaged 44% by BA and 50% by TPH.

Between pairs of response variables and site and stand factors, overstory percent aspen crown dieback relationships were negative with elevation and overstory live aspen

TPH and positive with overstory percent conifer by TPH (Table 3). Overstory percent aspen mortality relationships were negative with elevation and positive with overstory percent conifer by BA and TPH. Although the relationship was weak, there was more mortality in pine-oak than mixed conifer type (Table 3).

Between the two response variables, overstory percent aspen crown dieback had a positive relationship with overstory percent aspen mortality ($R^2 = 0.28$, $P < 0.0001$).

Between pairs of site and overstory stand factors, with increasing elevation, overstory aspen height ($R^2 = 0.37$, $P < 0.0001$), overstory total live BA ($R^2 = 0.43$, $P < 0.0001$) and overstory live aspen BA ($R^2 = 0.52$, $P < 0.0001$) increased, while overstory percent conifer by BA decreased ($R^2 = 0.28$, $P <0.0001$). In general, these relationships show that higher elevation sites are more favorable to overstory aspen. In the mixed conifer forest type, overstory aspen height, overstory live total BA, and overstory live aspen BA were also higher ($R^2 = 0.35$, $P < 0.0001$; $R^2 = 0.25$, $P = 0.0003$; and $R^2 = 0.20$, $P = 0.0016$, respectively). There was no difference between overstory percent conifer by BA in pine-oak and mixed conifer type ($R^2 = 0.07$, $P = 0.0794$).

Saplings and univariate relationships

Aspen stems in the sapling size class occurred on 32 sites (67%), only 12 sites (25%) had a sapling live aspen component, and 8 sites (17%) had no live stems of any species. Sapling live aspen TPH ranged from 0 – 298, with a mean of 25. Of the 40 sites with live stems of any species, percent conifer in the sapling size class (sapling percent conifer) by TPH was 85%. Sapling percent aspen mortality for the 32 sites with aspen was 82% by TPH.

Between pairs of response variables and site and stand factors, raw and log-transformed sapling live aspen TPH had no significant relationships with raw or log-transformed site or stand factors. Limiting the sample and analysis to sites where live aspen saplings occurred (n = 12) also produced no significant results. Sapling percent aspen mortality by TPH had a positive relationship with sapling percent conifer by TPH (Table 4). Log transformations of the response and explanatory variables support this raw result. No other relationships with site and stand factors (including overstory factors) were significant. Limiting the sample and analysis to sites where live aspen saplings occurred showed that sapling percent aspen mortality by TPH had a weak negative relationship with slope.

I found no significant relationships between site and sapling stand factors.

Tall suckers and univariate relationships

Aspen stems in the tall sucker size class occurred on 24 sites (50%), only 10 sites (21%) had a tall sucker live aspen component, and 10 sites (21%) had no live stems of any species. Tall sucker live aspen TPH ranged from 0 – 3,332, with a mean of 145. Of the 38 sites with live stems of any species, percent conifer in the tall sucker size class (tall sucker percent conifer) by TPH was 89%. Tall sucker aspen mortality for the 24 sites with aspen was 72% by TPH.

Between pairs of response variables and site and stand factors, tall sucker live aspen TPH had a positive relationship with slope (Table 4). Log transformations of the response and explanatory variables produced no significant results. No other significant relationships with site and stand factors were found. Limiting the sample and analysis to sites where live aspen tall suckers occurred (n = 10) produced no significant results. Tall

sucker percent aspen mortality by TPH relationships were negative with elevation and slope and positive with heat load. The mixed conifer forest type tended to have less tall sucker aspen mortality (Table 4). Log transformations of the response and explanatory variables support these raw results. No other relationships with site and stand factors were significant. The above relationships are also significant when the sample was limited to sites where live aspen tall suckers occurred.

Between pairs of site and tall sucker stand factors, tall sucker percent conifer by TPH has positive relationships with sapling percent conifer by TPH ($R^2 = 0.38$, $P < 0.0001$) and overstory percent conifer by TPH ($R^2 = 0.24$, $P = 0.0023$).

Short suckers and univariate relationships

Aspen stems in the short sucker size class occurred on 43 sites (90%), all of these sites had a short sucker live aspen component, and all 48 sites had ≥ 1 live stem of any species. Short sucker live aspen TPH ranged from 0 – 17,109, with a mean of 2,550. Percent conifer in the short sucker size class (short sucker percent conifer) for the 48 sites was 52% by TPH. Short sucker aspen mortality for the 43 sites with aspen was 16% by TPH. This level of aspen mortality is significantly lower than aspen mortality in other size classes ($P < 0.0001$ for all pair-wise comparisons). However, short sucker aspen stems fall over and decay quickly, therefore, my ability to detect dead stems in this class was limited.

Between pairs of response variables and site and stand factors, short sucker live aspen TPH had negative relationships with overstory percent aspen mortality by TPH and overstory percent conifer by TPH (Table 4). Log transformations of the response and explanatory variables support these raw results. No other significant relationships with

site and stand factors were found. No significant relationships were found between raw short sucker percent aspen mortality and raw site and stand factors. However, log-transformed percent short sucker aspen mortality had a negative relationship with raw slope and positive relationship with raw short sucker percent conifer by TPH (Table 4).

I found no significant relationships between site and short sucker stand factors.

Size Distributions

The TPH of live aspen trees by size class across all sites are shown in Fig. 3. The best-fit, negative exponential, null model was generated from the TPH of live aspen stems 15.1 cm DBH through > 40.1 cm DBH and estimated for the sapling and 0.1 – 15.0 cm size classes. The diameter distribution of healthy, self-replacing aspen stands were shown by Shepperd et al. (2001) to have the characteristic reverse-J distribution for uneven-aged stands, where smaller, younger size classes are more abundant than larger, older size classes (Oliver and Larson, 1996). Based upon the best-fit, or expected line, there was a lack of live aspen stems in the tall sucker, sapling, and smallest overstory (10.1 -15.0 cm DBH) size classes. Fig. 4 includes both live and dead aspen TPH. There were significantly more dead aspen stems than live aspen stems in the sapling and smallest overstory size classes ($P < 0.0001$ for both). While total stems suggests that recruitment levels may be sufficient, Fig. 4 shows many dead aspen stems within these size classes. Fig. 5 further separates live and dead aspen stems into pine-oak and mixed conifer forest types. Mortality trends by size class are also shown, and are similar in that dead aspen stems were was significantly greater than live aspen stems in the sapling and smallest overstory size class for both forest types ($P < 0.05$ for all). Furthermore, there were more dead tall sucker aspen stems than live tall sucker aspen stems in pine-oak type

(P = 0.0039), which was not true for aspen tall suckers in mixed conifer type. Compared to the pine-oak type, mixed conifer had, in general, greater number of large overstory stems. There was no difference in short sucker live aspen stems between pine-oak and mixed conifer (P = 0.1853).

Contributing Damaging Agents

Specific damaging agents were collected on individual aspen stems. Across all sites I assessed 1,805 overstory stems, 115 sapling stems, 220 tall sucker stems, and 2,984 short sucker stems for aspen damaging agents. However, damaging agents were analyzed by site averages per damaging agent group. Fig. 6 provides a summary of the site averages of grouped damaging agent by size class. In general, canker diseases, wood-boring insects, and animal damages were the most common damaging agent groups in overstory and sapling aspen, while animal damages was the most common agent group in tall and short sucker aspen. Specific widespread and common damaging agents were Cytospora canker (*Valsa sordida*), sooty-bark canker (*Encoelia pruinosa*), bronze poplar borer (*Agrilus liragus*), flathead poplar borer (*Dicerca tenebrica*), and ungulate damages from domestic cattle and sheep and wild deer and elk.

Overstory stems and univariate relationships

The top three aspen damaging agent groups in the overstory size class were wood-boring insects (68%), canker diseases (53%), and animal damages (51%). The top wood-boring insect was bronze poplar borer (24%), the top canker was Cytospora (27%), and the top animal damage was ungulate barking and rubbing (49%).

Between pairs of response variables and damaging agent groups, overstory percent aspen crown dieback had positive relationships with canker diseases and wood-

boring insects and no relationship with animal damages (Table 3). Overstory percent aspen mortality by BA had positive relationships with canker diseases and wood-boring insects and no relationship with animal damages (Table 3).

Between pairs of top damaging agent groups, an unexpected negative relationship between canker diseases and animal damages was observed ($R^2 = 0.14$, $P = 0.0084$). I expected a positive relationship because stem wounds provide infection courts for canker diseases (Hinds, 1985; Hart and Hart, 2001). There was no relationship between canker diseases and wood-boring insects ($R^2 = 0.0006$, $P = 0.8663$) and wood-boring insects and animal damages ($R^2 = 0.02$, $P = 0.3087$).

Between pairs of top damaging agent groups and site and stand factors, there were more canker diseases in mixed conifer than pine-oak type ($R^2 = 0.12$, $P = 0.0178$). Mesic sites should have more canker activity because canker diseases, in general, require moist conditions to complete their life cycle (Johnson et al., 1995). Wood-boring insects had a positive relationship with overstory percent conifer by BA ($R^2 = 0.33$, $P < 0.0001$) and overstory live aspen BA ($R^2 = 0.36$, $P < 0.0001$). Wood-boring insects had negative relationships with elevation ($R^2 = 0.37$, $P < 0.0001$) and forest type ($R^2 = 0.16$, $P = 0.0050$). In general, more xeric sites should have greater wood-boring insect activity because wood-boring insects tend to invade drought-stressed trees (Ives and Wong, 1988). Animal damages had a negative relationship with slope ($R^2 = 0.12$, $P = 0.0182$).

Saplings and univariate relationships

The top three aspen damaging agent groups in the sapling size class were canker diseases (74%), animal damages (66%), and wood-boring insects (53%). The top canker

was Cytospora (66%), the top animal damage was ungulate barking and rubbing (66%), and the top wood-boring insect was bronze poplar borer (30%).

Between pairs of response variables and top damaging agent groups, sapling live aspen TPH had a slight negative relationship with canker diseases (Table 4) and no relationship with wood-boring insects ($R^2 = 0.007$, $P = 0.6709$) or animal damages ($R^2 = 0.05$, $P = 0.2630$). Log transformations support these results. Limiting the sample and analysis to sites where live aspen saplings occurred ($n = 12$) produced no significant results. Sapling aspen mortality by TPH had a slight positive relationship with canker diseases (Table 4) and no relationship with wood-boring insects ($R^2 = 0.12$, $P = 0.0762$) or animal damages ($R^2 = 0.07$, $P = 0.1889$). Log transformations support these results. However, limiting the sample and analysis to sites where live aspen saplings occurred produced a significant positive relationship with wood-boring insects.

No significant relationships were found between top damaging agent groups within the sapling size class. However, between sapling top damaging agent groups and corresponding overstory top damaging agent groups, sapling wood-boring insects had a positive relationship with overstory wood-boring insects ($R^2 = 0.42$, $P = 0.0001$). No other significant relationships were found.

Between pairs of sapling top damaging agent groups and site and stand factors, canker diseases had no significant relationships with site and stand factors. Wood-boring insects had a negative relationship with elevation ($R^2 = 0.34$, $P = 0.0009$) and there were less wood-boring insects in the mixed conifer type. Animal damages had no significant relationships with site and stand factors.

Tall suckers and univariate relationships

The tall sucker size class had two top aspen damaging agent groups; animal damages (68%) and canker diseases (30%). The top animal damage was ungulate barking and rubbing (51%) and the top canker was Cytospora (28%).

Between pairs of response variables and top damaging agent groups, tall sucker live aspen TPH had no relationship with canker diseases ($R^2 = 0.10$, $P = 0.1389$) or animal damages ($R^2 = 0.15$, $P = 0.0602$). Log transformations and limiting the sample and analysis to sites where live aspen tall suckers occurred ($n = 10$) also produced no significant results. Tall sucker aspen mortality by TPH had a positive relationship with canker diseases (Table 4) and no relationship with animal damages ($R^2 = 0.11$, $P = 0.1198$). Log transformations and limiting the sample and analysis to sites where live aspen tall suckers occurred supported these results.

No significant relationships were found between tall sucker top damaging agent groups, or between tall sucker top damaging agent groups and corresponding overstory and sapling top damaging agent groups.

Between pairs of tall sucker top damaging agent groups and site and stand factors, canker diseases had a negative relationship with elevation ($R^2 = 0.39$, $P = 0.0010$) and slope ($R^2 = 0.48$, $P = 0.0002$) and a positive relationship with heat load ($R^2 = 0.23$, $P = 0.0178$). No aspen tall sucker stem above 2,400 m had a canker, and therefore, mixed conifer had less canker diseases than pine-oak ($R^2 = 0.27$, $P = 0.0092$). These results are contrary to earlier results in larger size classes. Animal damages had a positive relationship with tall sucker percent conifer by TPH ($R^2 = 0.29$, $P = 0.0149$). No other significant relationships were found.

Short suckers and univariate relationships

The short sucker size class had only one top aspen damaging agent group; animal damages (58%). The top animal damage was ungulate browsing (58%).

Between pairs of response variables and the top damaging agent group, short sucker live aspen TPH had no relationship with animal damages ($R^2 = 0.01$, $P = 0.5214$). Log transformations supported this result. The lack of a relationship may be explained by the observation that levels of animal browsing were high no matter how many live short suckers were present. Short sucker aspen mortality by TPH did not have a significant relationship with animal damages (raw data; $R^2 = 0.09$, $P = 0.0525$), however, the relationship was significantly positive when the y-axis was log-transformed (Table 4).

No significant relationships were found between short sucker animal damages and overstory, sapling, and tall sucker animal damages, or between short sucker animal damages and site and stand factors.

Multivariate Models

The preliminary model for overstory percent aspen crown dieback (Table 5) accounted for 34% of the variation based upon an adjusted R^2 ($F_{4,42} = 6.81$, $P = 0.0003$). The standard error of regression was 21.55. The explanatory variables selected were elevation ($F_{1,42} = 4.24$), live aspen TPH ($F_{1,42} = 0.17$), percent incidence of grouped canker diseases ($F_{1,42} = 8.72$), and percent incidence of grouped wood-boring insects ($F_{1,42} = 1.81$). In the preliminary model, overstory aspen crown dieback decreased with increasing elevation, increased with incidence of canker diseases, and had no significant relationship with live aspen TPH and incidence of wood-boring insects (Table 5).

The final model for overstory percent aspen crown dieback (Table 5) accounted for 34% of the variation based on adjusted R^2 ($F_{2,44} = 12.76$, $P < 0.0001$). The standard error of regression was 21.51. The explanatory variables selected were elevation ($F_{1,44} = 16.38$) and percent incidence of grouped canker diseases ($F_{1,44} = 15.02$). In the final model, overstory aspen crown dieback decreased with increasing elevation and increased with higher incidence of canker diseases (Table 5). Ranking these factors based upon F-values (Draper and Smith, 1998) shows that the predisposing site factor explains slightly more variation in overstory aspen crown dieback than the contributing damaging agent.

The preliminary model for overstory percent aspen mortality by BA (Table 5) accounted for 77% of the variation based upon an adjusted R^2 ($F_{5,42} = 32.27$, $P < 0.0001$). The standard error of regression was 13.22. The explanatory variables selected were elevation ($F_{1,42} = 0.07$), forest type ($F_{1,42} = 3.72$), overstory percent conifer by TPH ($F_{1,42} = 5.33$), percent incidence of grouped canker diseases ($F_{1,42} = 26.16$), and percent incidence of grouped wood-boring insects ($F_{1,42} = 24.14$). In the preliminary model, overstory aspen mortality increased with increasing overstory percent conifer by TPH and higher incidence of canker diseases and wood-boring insects and had no significant relationship with elevation and forest type (Table 5).

The final model for overstory percent aspen mortality by BA (Table 5) accounted for 78% of the variation based on adjusted R^2 ($F_{4,43} = 41.47$, $P < 0.0001$). The standard error of regression was 13.05. The explanatory variables selected were forest type ($F_{1,43} = 5.92$), overstory percent conifer by BA ($F_{1,43} = 8.24$), percent incidence of grouped canker diseases ($F_{1,43} = 33.05$), and percent incidence of grouped wood-boring insects ($F_{1,43} = 33.29$). In the final model, overstory aspen mortality decreased from pine-oak to mixed

conifer, increased with increasing overstory percent conifer by BA, and increased with higher incidences of canker diseases and wood-boring insects (Table 5). Ranking these factors based upon F-values shows that contributing damaging agents explain far more variation in overstory aspen mortality than predisposing factors.

The preliminary and final models (both were the same) for short sucker percent aspen mortality by TPH (Table 5) accounted for 34% of the variation based on adjusted R^2 ($F_{3,31} = 6.80$, $P = 0.0012$). The standard error of regression was 0.77. The explanatory variables selected were slope ($F_{1,31} = 4.90$), short sucker percent conifer by TPH ($F_{1,31} = 5.00$), and percent incidence of grouped short sucker animal damages ($F_{1,31} = 6.85$). In the final model, short sucker aspen mortality decreased with increasing slope and increased with increasing short sucker percent conifer by TPH and higher incidence of short sucker animal damages (Table 5). Ranking these factors based upon F-values shows that the contributing damaging agent explains the most variation of the three variables, but that predisposing factors combined explain more variation in short sucker aspen mortality than the contributing damaging agent.

Discussion

Crown dieback and mortality of aspen stems are two of the most commonly measured and important indicators of aspen health (Hogg et al., 2008). My results document extensive aspen crown dieback and mortality in pine-oak and mixed conifer forests of the Williams Ranger District, Kaibab National Forest. My study was observational, and therefore, was not designed to test for mechanisms or causal relationships. Instead, I found that predisposing site and stand factors, and contributing damaging agents were significantly related to aspen crown dieback and mortality.

Therefore, many combined factors contributed to the generally poor condition of aspen I observed across the study area. These findings are consistent with the conceptual framework of a decline disease. The most important predisposing and contributing factors depended on the aspen size class, and, in general, the strongest relationships were with aspen mortality.

Overstory

Stand factors and damaging agents were more strongly related to overstory aspen crown dieback and mortality than site factors. The most significant site factor related to both aspen crown dieback and mortality was elevation, which spanned 800 m and is related to moisture availability (Pearson, 1920). Both crown dieback and mortality decreased as elevation increased. Other site factors such as aspect, slope, and heat load were not strongly related to aspen crown dieback or mortality because they did not represent a wide range of conditions (e.g., most sites were on north-facing slopes). Since the aspen stands occurred on relatively similar sites, stand factors and damaging agents were more important for describing dieback and mortality.

Of the stand factors, only percent conifer and forest type were significantly related to overstory aspen mortality. In general, as conifer density in the aspen stands increases, so does aspen mortality. The gradual replacement of aspen by confers is a well-documented successional process (Baker, 1925; Jones, 1974, Bartos, 2001; and others). Aspen mortality was higher in the pine-oak than mixed conifer forest type. Because there was no difference in percent conifer between forest types, this difference is likely explained by the higher elevations and more favorable moisture conditions of the mixed conifer forest type. Conifer density and forest type had a weak and no relationship,

respectively, with crown dieback. In general, most stand factors were not related to aspen crown dieback.

Damaging agents, specifically canker diseases and wood-boring insects, were the most important single factors in describing overstory aspen crown dieback and mortality. Of the cankers, only two were widespread and common: Cytospora and sooty-bark. Sooty-bark is widely considered to be the most aggressive and primary killer of aspen in western North America, as it can kill an otherwise healthy mature aspen stem in just a few years (Juzwik et al., 1978; Hinds, 1985). The other canker diseases and all of the wood-boring insects are considered secondary because they require declines in host condition before their attacks can be successful (Frey at al., 2004). Nevertheless, these agents are considered secondary for the timing of their attack (after something else weakens the host), and not for lack of importance as killers of aspen (Hart and Hart, 2001). Despite a high level of animal wounding, aspen crown dieback and mortality had no relationship with animal damages. Baker et al. (1997) also observed no relationship with animal damage and overstory aspen mortality.

Not all damaging agent findings were congruent with previous research. The poplar borer (*Saperda calcarata*) is a cerambycid (round-headed) wood-boring insect that is often cited as a major contributor to aspen mortality (St. Clair et al., 2010; Steed and Kearns, 2010). Although it was found to contribute to SAD on the adjacent Coconino National Forest (Fairweather et al., 2008), it was rare (only 1% of overstory aspen stems across all sites) and did not contribute to aspen damage on the Williams Ranger District. In the summers of 2009 and 2010, outbreaks of defoliating insects commonly associated with aspen defoliation and dieback were not observed; defoliating insects as a group were

found only 6% of overstory aspen stems across all sites. The most notably absent species was the western tent caterpillar (*Malacosoma californicum*), which had known outbreaks in 2004, 2005, and 2007 on the Coconino National Forest (Fairweather et al., 2008) but was found on only 2% of overstory aspen stems across all sites.

The crown dieback levels I observed were high but not unprecedented. For my study, live aspen with at least moderate crown dieback (> 33%) was 48% compared to: i) 22% in healthy stands and 34% in damaged stands with at least 40% crown dieback in northwestern Alberta, Canada (Hogg et al., 2002); ii) 18% with at least 33% crown dieback in the northern Rocky Mountains (Steed and Kearns, 2010); iii) 20% with "substantial" crown dieback in southwestern Colorado (Worrall et al., 2008); and iv) 60% in damaged stands with at least 40% crown dieback in the Coconino National Forest in northern Arizona (M. Fairweather, USFS FHP, May 2011, personal communication).

The aspen mortality levels I observed were generally higher than those reported in other studies. Overstory percent aspen mortality by TPH for my study was 50% compared to: i) 17% in healthy stands and 33% in stressed stands northwestern Alberta, Canada (Hogg et al., 2002); ii) 7% in the northern Rocky Mountains (Steed and Kearns, 2010); iii) ~ 26% in damaged stands across the Intermountain West (St Clair et al., 2010); iv) 32% overall and 45% in damaged stands in southwestern Colorado (Worrall et al., 2008); and v) ~ 50% cumulative between 2000-2007 in damaged stands in northern Arizona (M. Fairweather, USFS FHP, May 2011, personal communication). A recent survey conducted by Williams Ranger District employees in my study area reported 54% mortality in mature aspen stems. Therefore, while my aspen mortality values are higher than values reported in many studies, they are not unprecedented.

Regeneration

Many of my sites did not have live aspen regeneration, therefore, the sample sizes were small, and relationships with live aspen regeneration TPH were often inconclusive or weak. The strongest relationship was that short sucker live aspen TPH decreased with overstory percent aspen mortality. This relationship is intriguing because vigorous vegetative regeneration (the most common way aspen regenerates) is promoted by a deteriorating aspen overstory through a well-documented hormonal process (Schier et al., 1985; Bartos, 2001). One explanation for this result involves the association of root mortality with overstory mortality. It is possible that the aspen stands in my study have extensive root mortality as well. The positive association of root mortality with overstory aspen damage was demonstrated by Worrall et al. (2010), but was beyond the scope of this study.

Mortality of aspen regeneration varied with size class. Sapling and tall sucker aspen mortality were high (greater than 80 and 70%, respectively), while short sucker aspen mortality was low (16%). Sapling aspen mortality was greatest with a greater percentage of conifer saplings. Tall sucker aspen mortality increased with decreasing slope and elevation, increasing heat load, and location within pine-oak type. Short sucker aspen mortality increased with decreasing slope and increasing percentage of conifer seedlings. Canker diseases and animal damages were common in the sapling and tall sucker size classes. The only common short sucker damaging agent was ungulate browsing. I found that higher levels of canker diseases (almost exclusively Cytospora) increased sapling and tall sucker aspen mortality. Cytospora canker is a common, well-documented mortality agent of aspen regeneration throughout western North America

(Hinds, 1985; Guyon et al., 1996). While animal damages did not appear to relate to sapling or tall sucker aspen mortality, these size classes had small sample sizes and high levels of animal damages regardless of mortality levels. Short sucker mortality, however, increased with ungulate browsing. The interactions among ungulates (especially elk) and aspen regeneration in northern Arizona is as well-studied as it is controversial. Previous research has shown that heavy, persistent ungulate browsing can prevent successful regeneration of aspen (Rolf, 2001; Bailey and Whitham, 2002; Fairweather et al., 2008). Examination of aspen regeneration inside and outside of exclosures is required quantify the amount of browsing damage and mortality attributable to domestic and wild ungulates.

Size Distributions

In general, the size-density relationship of self-replacing aspen follows a negative exponential (reverse-J) shaped curve, a common feature of uneven-aged tree species (Oliver and Larson, 1996; Shepperd et al., 2001). Steed and Kearns (2010) found the condition of aspen in Montana and northern Idaho to be generally healthy, with low levels of crown dieback and mortality, sufficient aspen regeneration, and a reverse-J size distribution. I fitted a null model to live aspen stems > 15.1 cm DBH. Based upon this model, there appears to be a lack of recruitment in tall sucker, sapling, and overstory stems between 10.1 and 15.0 cm. This observation becomes less certain when dead stems are taken into account. Why do aspen in the sapling and smallest overstory size classes die before they can recruit to the larger size classes? In both the sapling and the overstory size classes, aspen mortality increases with increasing conifer density. The smallest (and likely youngest) overstory aspen stems are the first to succumb to overtopping by conifer

(Shepperd et al., 2001). Additionally, small circumference aspen stems are at a greater risk to girdling by cankers and flathead, cambial-feeding borers than larger stems. Because of this, secondary agents of mature aspen stems (e.g., Cytospora) can cause substantial mortality of regeneration stems (Jacobi and Shepperd, 1991).

Diseases, Insects, and Drought

Many interacting factors contribute to aspen crown dieback and mortality on the Williams Ranger District. While I could not assign a single cause, signs and symptoms of canker and wood-boring insect activity were pervasive on dead and crown damaged aspen. Based upon my univariate and multivariate relationships, I have little doubt that contributing damaging agents finally killed most standing dead aspen. However, I concluded, as did Fairweather et al. (2008), that cankers and insects likely played a secondary role in observed aspen crown dieback and mortality. If this is true, what stressor weakened aspen to the point where they could no longer resist attacks from secondary damaging agents? Canker and insect activity were likely mediated by long-term drought conditions in the study area (Fairweather et al., 2007; Ganey and Vojta, 2011). Although I did not measure drought (an inciting factor) directly, the Southwest has experienced a regional drought since 1996, with particularly dry conditions from 1996 to 2007 and severe drought in 2000 and 2002 (Breshears et al., 2005; Ganey and Vojta, 2011). These hot, dry conditions stressed aspen (and other tree species), rendering vigorous aspen stems susceptible to insects and disease (Hogg et al., 2008; Rehfeldt et al., 2009; Worrall et al., 2010).

Conclusions and Management Implications

Aspen Decline and Sudden Aspen Decline

Aspen decline describes the reduction in aspen type on a broad range of spatial scales, but driven mostly by long-term successional processes under altered disturbance regimes and often amplified by heavy ungulate browsing (Ripple and Larsen, 2000). Sudden aspen decline (SAD) describes the rapid deterioration of aspen on a landscape-scale, often accompanied by root mortality and insufficient regeneration to replace overstory losses (Worrall et al. 2008). My observational study was not designed to test *a priori* assumptions about what kind of aspen decline, sudden or not, occurred on the Williams Ranger District. While the extensive crown dieback and mortality exhibited by aspen in the study area is comparable to SAD elsewhere, long-term successional processes have a significant role in the current health of aspen forests on the Williams Ranger District. Therefore, I cannot assign my observations into a single type of decline. This does not mean that aspen in the study area do not suffer from some type of decline. For example, the lack of live aspen stems in the sapling and 10.1 -15.0 cm overstory size classes is alarming. If high mortality and low recruitment continues, aspen stands will be replaced by conifer after larger, and presumably older, overstory aspen stems die.

Risk Factors

A recent document (O'Brien et al., 2010) published by the Utah Forest Restoration Working Group (UFRWG) summarized a set of aspen risk factors based upon the findings of Mueggler (1989) and Bartos and Campbell (1998). The risk factors relevant to the aspen stands on the Williams Ranger District are: i) conifer understory and overstory cover are greater than 25%; and ii) dominant aspen trees are greater than 100

years old. The majority of stands I sampled fit these criteria. I encourage the District to implement proposed aspen restoration actions (2011), especially the thinning of conifer in high-risk aspen sites. Additionally, the thinning of small (sapling-sized) conifer may reduce the high mortality levels of aspen stems between 5.1 and 15.1 cm DBH.

The UFRWG emphasizes that very low or nonexistent aspen regeneration is nearly always a cause for further investigation. Four risk scenarios are proposed: i) overstory aspen with regeneration, but depleted recruitment; ii) overstory aspen, but little regeneration; iii) dying mature aspen with regeneration, but depleted recruitment; and iv) dying mature aspen, but little regeneration. The first tends to describe the mixed conifer type aspen stands, while the third tends to describe the pine-oak type aspen stands on the Williams Ranger District, Kaibab National Forest. "Depleted recruitment" refers to when an aspen stand is not recruiting suckers into the overstory, and therefore, is not self-replacing. This problem appears to occur across all sites (Figs. 3 and 4). Aspen stands are considered to be not self-replacing if aspen stems > 2 m but < canopy height (approximately my tall sucker and sapling size classes) and aspen < 2 m tall (approximately my short sucker size class) each have < 1,250 live TPH (Bartos and Campbell, 1998; Kurzel et al., 2007; Rogers et al., 2010). Live short sucker TPH was below this level at 48% of my sites (five sites had zero live aspen short suckers). Live sapling and tall sucker combined TPH was below this level at 96% of my sites (30 sites had zero live aspen saplings and tall suckers). The lack of sapling and tall sucker stems is a genuine problem, and will likely require restorative management to mitigate.

Ungulates and Exclosures

The browsing of aspen suckers by ungulates is an important management consideration for the Williams Ranger District. While I did not study ungulate browsing directly, previous research shows that ungulate browsing has a significant impact on the success of aspen regeneration (Rolf, 2001; Bailey and Whitham, 2002; Fairweather et al., 2008). This is precisely why forest managers erect ungulate exclosures. This observational study did not include data from sites within ungulate exclosures. A controlled experiment that examines aspen overstory and regeneration inside and outside of exclosures is required to explore specific relationships between aspen and ungulates. In addition, further studies are required to disentangle the impacts of cattle, sheep, deer, and elk. Needed are: i) exclosures that separate domestic and wild ungulate damage; and; ii) wildlife cameras that explicitly separate the kind of wild ungulate.

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Table 1. List of predisposing, inciting, and contributing factors associated with crown dieback and mortality of aspen (adapted from Frey at al., 2004) and variables analyzed. All variables were analyzed at the site spatial scale.

Factor	Scale of Measurement	Variable(s) Analyzed
Predisposing		
Climate	--	Not measured in this study
Ecosite	Continuous	Elevation, slope, aspect, and heat load[a]
Successional processes	Continuous	Percent conifer by BA[b] and TPH[c]
Stand structure	Continuous	DBH[d] (cm), height (m), BA, and TPH
Stand composition[e]	Ordinal	Forest type (0-1)[f]
Age	--	Not measured in this study
Clonal aspects	--	Not measured in this study
Inciting		
Drought	--	Not measured in this study
Contributing		
Diseases	Continuous	Incidence of diseases (%)
Insect borers	Continuous	Incidence of wood-boring insects (%)
Insect defoliators[g]	Continuous	Incidence of defoliating insects (%)
Abiotic damages[g]	Continuous	Incidence of abiotic damages (%)
Animal damages[g]	Continuous	Incidence of animal damages (%)

[a] Heat load was calculated as outlined in McCune and Keon (2002)

[b] BA = basal area (m^2 ha^{-1})

[c] TPH = stems ha^{-1}

[d] DBH = diameter measured at 1.37 m above ground

[e] Not specifically addressed by Frey et al. (2004)

[f] 0 = pine-oak, 1= mixed conifer

[g] Considered inciting factors by Frey et al. (2004). For this study these variables were measured at a discrete time at a site versus landscape spatial scale

Table 2. Site and stand factors of 48 study sites on the Williams Ranger District, Kaibab National Forest, Arizona.

Factor	Mean	Standard Deviation	Range
Site			
Elevation (m)	2438	217	2094 - 2888
Slope (%)	25	15	3 - 59
Aspect[a]	1.3	0.6	0.03 - 2.0
Heat load[b]	0.91	0.10	0.66 - 1.06
Overstory structure			
Total aspen DBH[c] (cm)	20.3	5.6	12.0 - 39.3
Total aspen height (m)	15.1	4.1	4.8 - 24.6
Live total BA[d]	31.8	15.8	5.1 - 76.5
Live aspen BA	11.7	13.2	0.0 - 51.9
Live total TPH[e]	638	348	162 - 1766
Live aspen TPH	271	265	0 - 1156
Percent conifer by BA	67	26	0 - 100
Percent conifer by TPH	59	26	0 - 100
Percent aspen crown dieback > 33%	48	26	10 - 100
Percent aspen mortality by BA	44	28	1 - 100
Percent aspen mortality by TPH	50	25	5 - 100
Sites with live aspen (%)	98	--	--
Sapling structure			
Live total BA	0.9	0.9	0.0 - 4.4
Live aspen BA	0.1	0.3	0.0 - 1.2
Live total TPH	217	209	0 - 1044
Live aspen TPH	25	56	0 - 298
Percent conifer by TPH	85	30	0 - 100
Percent aspen mortality by TPH	82	29	0 - 100
Sites with live aspen (%)	25	--	--
Tall sucker structure			
Live total TPH	793	1018	0 - 3332
Live aspen TPH	145	529	0 - 3332
Percent conifer by TPH	89	28	0 - 100
Percent aspen mortality by TPH	72	41	0 - 100
Sites with live aspen (%)	21	--	--
Short sucker structure			
Live total TPH	5324	4608	99 - 19596
Live aspen TPH	2550	3280	0 - 17109
Percent conifer by TPH	52	35	0 - 100
Percent aspen mortality by TPH	16	19	0 - 88
Sites with live aspen (%)	90	--	--

[a] Beers et al. (1966); 0 - 2 scale (0 = 225°, 1 = 315° or 135°, 2 = 45°)

[b] McCune and Keon (2002); unitless index with 0.03 - 1.11 scale

[c] DBH = diameter measured at 1.37 m above ground; includes live and dead

[d] BA = basal area (m^2 ha^{-1})

[e] TPH = stems ha^{-1}

Table 3. Univariate relationships between overstory response and explanatory factors. Factors with an asterisk were significant at $\alpha = 0.05$. The "sign" of a significant relationship was positive (+) or negative (-) or neutral (O). Neutral indicates an insignificant P-value.

Factor	Sign	R^2	P-value
Percent aspen crown dieback > 33%			
Site			
Elevation (m)	-	0.15	0.0069 *
Slope (%)	O	0.03	0.2120
Aspect[a]	O	<0.01	0.6981
Heat load[b]	O	<0.01	0.6491
Stand			
Overstory aspen DBH[c] (cm)	O	<0.01	0.9771
Overstory aspen height (m)	O	0.01	0.5387
Forest type [0-1][d]	O	0.04	0.1764
Overstory live aspen BA[e]	O	0.06	0.0993
Overstory live aspen TPH[f]	-	0.18	0.0029 *
Overstory percent conifer by BA	O	0.05	0.1193
Overstory percent conifer by TPH	+	0.15	0.0075 *
Damaging agent groups			
Canker diseases (%)	+	0.13	0.0123 *
Wood-boring insects (%)	+	0.24	0.0005 *
Animal damages (%)	O	0.03	0.2295
Percent aspen mortality by BA			
Site			
Elevation (m)	-	0.24	0.0004 *
Slope (%)	O	0.04	0.1761
Aspect	O	0.01	0.4734
Heat load	O	0.05	0.1194
Stand			
Overstory aspen DBH (cm)	O	0.02	0.3458
Overstory aspen height (m)	O	0.03	0.2462
Forest type [0-1]	-	0.10	0.0275 *
Overstory percent conifer by BA	+	0.43	<0.0001 *
Overstory percent conifer by TPH	+	0.45	<0.0001 *
Damaging agent groups			
Canker diseases (%)	+	0.18	0.0028 *
Wood-boring insects (%)	+	0.56	<0.0001 *
Animal damages (%)	O	0.05	0.1186

[a] Beers et al. (1966); 0 - 2 scale (0 = 225°, 1 = 315° or 135°, 2 = 45°)
[b] McCune and Keon (2002); unitless index with 0.03 - 1.11 scale
[c] DBH = diameter measured at 1.37 m above ground; includes live and dead
[d] 0 = pine-oak, 1 = mixed conifer
[e] BA = basal area (m^2 ha^{-1})
[f] TPH = stems ha^{-1}

Table 4. Univariate relationships between regeneration response and explanatory factors. All factors reported in this table were significant at $\alpha = 0.05$. There were too many size classes to include non-significant relationships. The "sign" of a significant relationship was positive (+) or negative (-).

Factor	Sign	R^2	P-value
Sapling live aspen TPH[a]			
Sapling canker diseases (%)	-	0.15	0.0397 *
Sapling percent aspen mortality by TPH			
Sapling percent conifer by TPH	+	0.20	0.0187 *
Sapling canker diseases (%)	+	0.16	0.0341 *
Tall sucker live aspen TPH			
Slope (%)	+	0.13	0.0139 *
Tall sucker percent aspen mortality by TPH			
Elevation (m)	-	0.22	0.0201 *
Slope (%)	-	0.60	<0.0001 *
Heat load[b]	+	0.21	0.0238 *
Forest type (0-1)[c]	-	0.17	0.0441 *
Tall sucker canker diseases (%)	+	0.27	0.0091 *
Short sucker live aspen TPH			
Overstory percent aspen mortality by TPH	-	0.20	0.0017 *
Overstory percent conifer by TPH	-	0.10	0.0350 *
Short sucker percent aspen mortality by TPH[d]			
Slope (%)	-	0.16	0.0182 *
Short sucker percent conifer by TPH	+	0.02	0.0167 *
Short sucker animal damages (%)	+	0.15	0.0198 *

[a] TPH = stems ha^{-1}

[b] McCune and Keon 2002: unitless index with 0.03 - 1.11 scale

[c] 0 = pine-oak, 1 = mixed conifer

[d] Log (y)

Table 5. Preliminary and final multiple regression models. Factors with an asterisk were significant at $\alpha = 0.05$.

Factor	Parameter Estimate	Standard Error	t-ratio	P-value
Overstory percent aspen crown dieback				
Preliminary model				
Elevation (m)	-0.05	0.02	-2.06	0.0458 *
Overstory live aspen TPH[a]	0.01	0.02	0.41	0.6814
Overstory canker diseases (%)	0.38	0.13	2.95	0.0051 *
Overstory wood-boring insects (%)	0.17	0.12	1.35	0.1855
Final model				
Elevation (m)	-0.06	0.02	-4.05	0.0002 *
Overstory canker diseases (%)	0.41	0.11	3.87	0.0004 *
Overstory percent aspen mortality by BA[b]				
Preliminary model				
Elevation (m)	0.01	0.02	-0.26	0.7925
Forest type [0-1][c]	-13.41	6.95	-1.93	0.0605
Overstory percent conifer by TPH	0.26	0.11	2.31	0.0260 *
Overstory canker diseases (%)	0.37	0.07	5.12	<0.0001 *
Overstory wood-boring insects (%)	0.33	0.07	4.91	<0.0001 *
Final model				
Forest type [0-1]	-11.74	4.82	-2.43	0.0192 *
Overstory percent conifer by BA	0.26	0.09	2.87	0.0063 *
Overstory canker diseases (%)	0.39	0.07	5.75	<0.0001 *
Overstory wood-boring insects (%)	0.35	0.06	5.77	<0.0001 *
Short sucker percent aspen mortality by TPH[d]				
Preliminary and final model				
Slope (%)	-0.02	0.01	-2.21	0.0344 *
Short sucker percent conifer by TPH	0.01	0.00	2.24	0.0327 *
Short sucker animal damages (%)	0.02	0.01	2.62	0.0136 *

[a] TPH = stems per ha^{-1}

[b] BA = basal area (m^2 ha^{-1})

[c] 0 = pine-oak, 1 = mixed conifer

[d] Log (y)

Fig. 1. Locations of aspen study sites on the Williams Ranger District, Kaibab National Forest, Arizona.

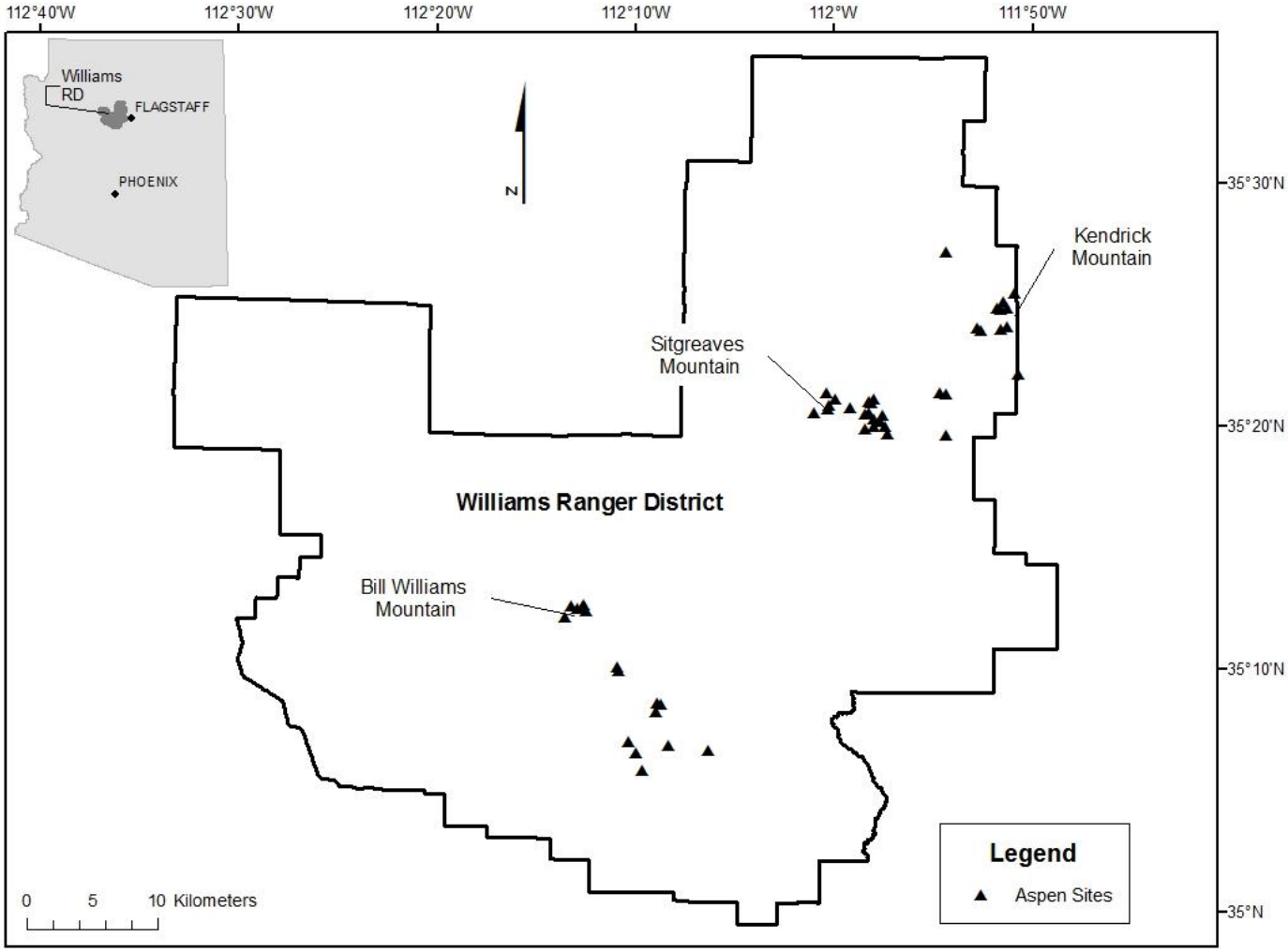


Fig. 2. Illustration of plot design. Site factors (elevation, slope, aspect) were collected at site center. Stand factors and damaging agents data were collected in the overstory and regeneration plots.

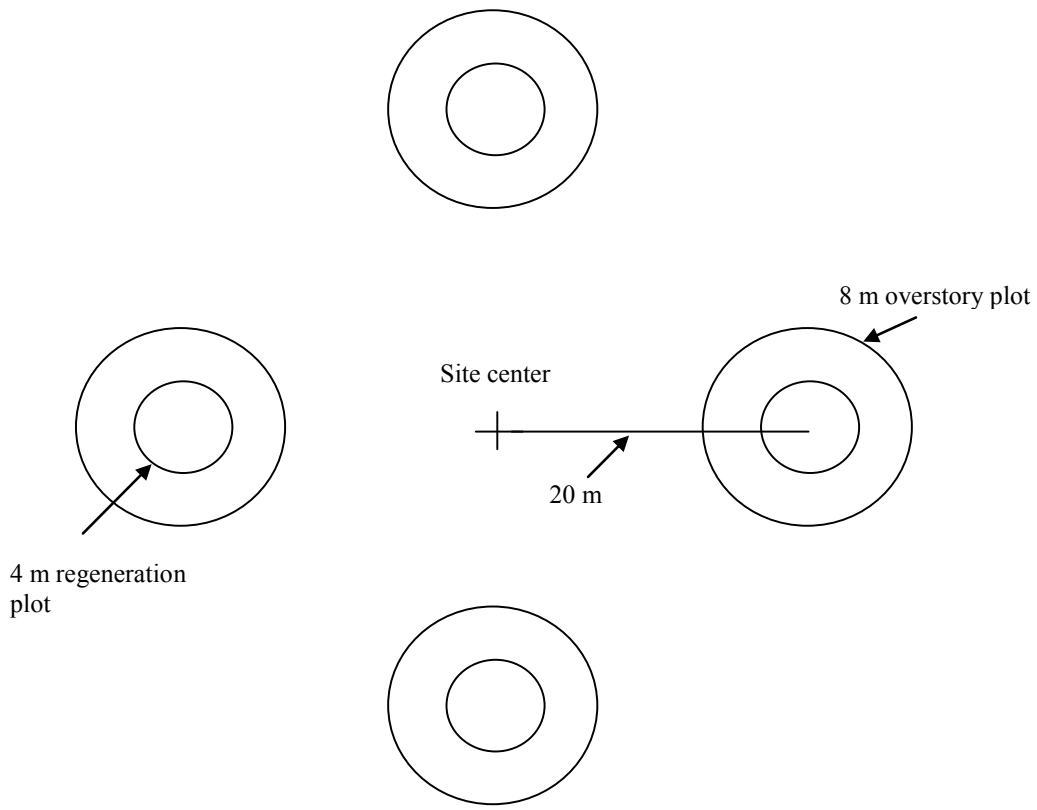


Fig. 3. Size-density distribution of live aspen stems from 48 sites on the Williams Ranger District, Kaibab National Forest, Arizona. Expected line is a single, two parameter, negative exponential relationship.

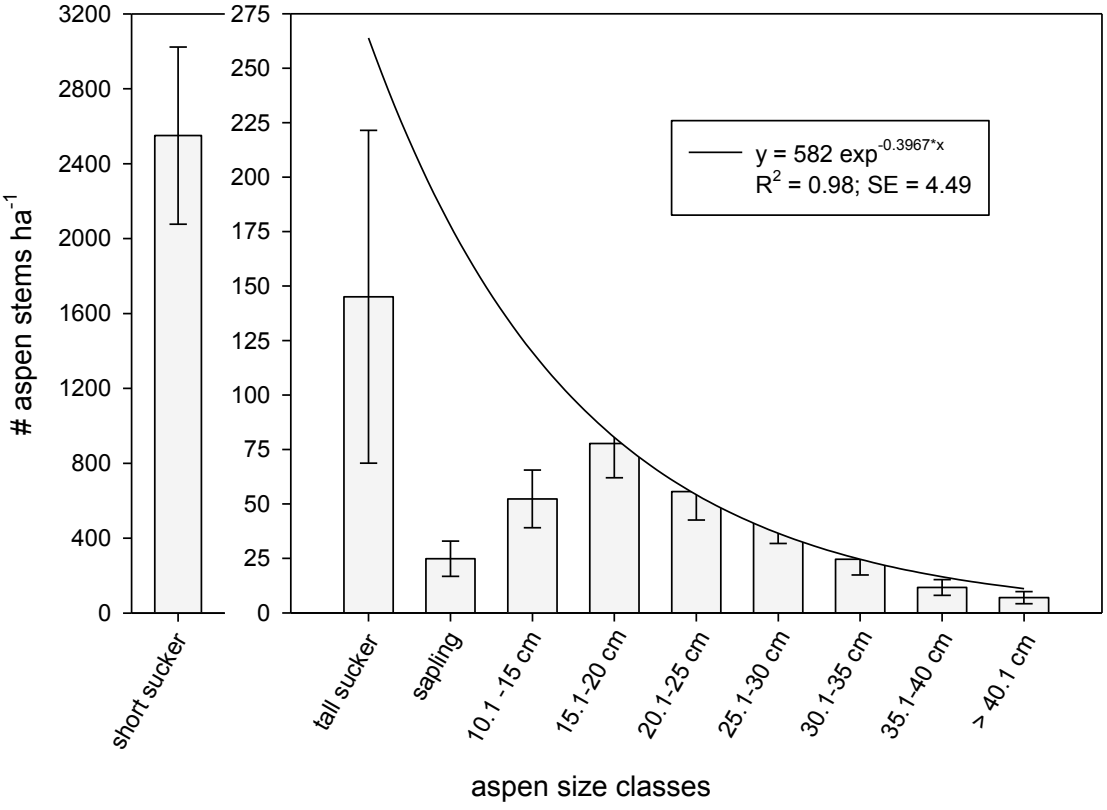


Fig. 4. Size-density distribution of live and dead aspen stems from 48 sites on the Williams Ranger District, Kaibab National Forest, Arizona. Expected line is a single, two parameter, negative exponential relationship.

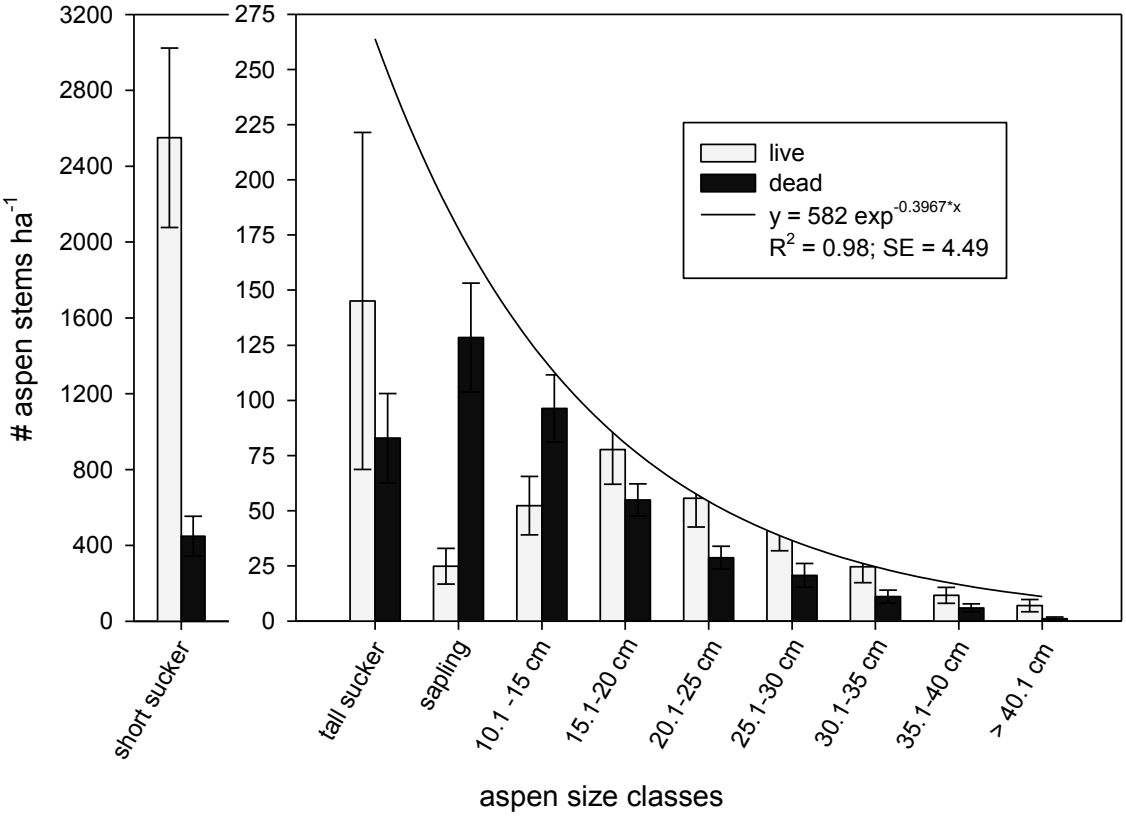


Fig. 5. Size-density distribution of live and dead aspen stems on the Williams Ranger District, Kaibab National Forest, Arizona by forest type: a) pine-oak type (n = 15) and b) mixed conifer type (n = 33).

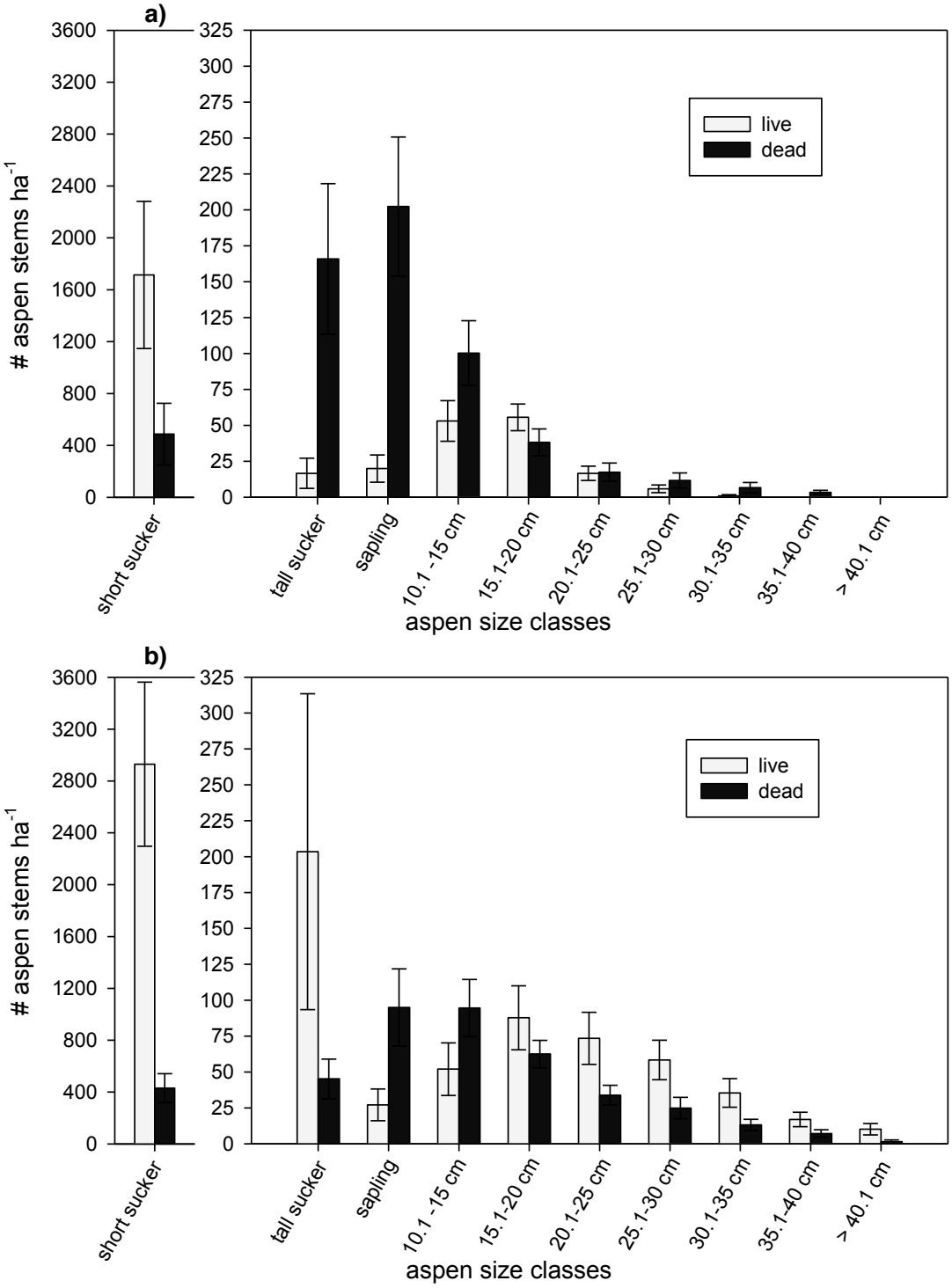
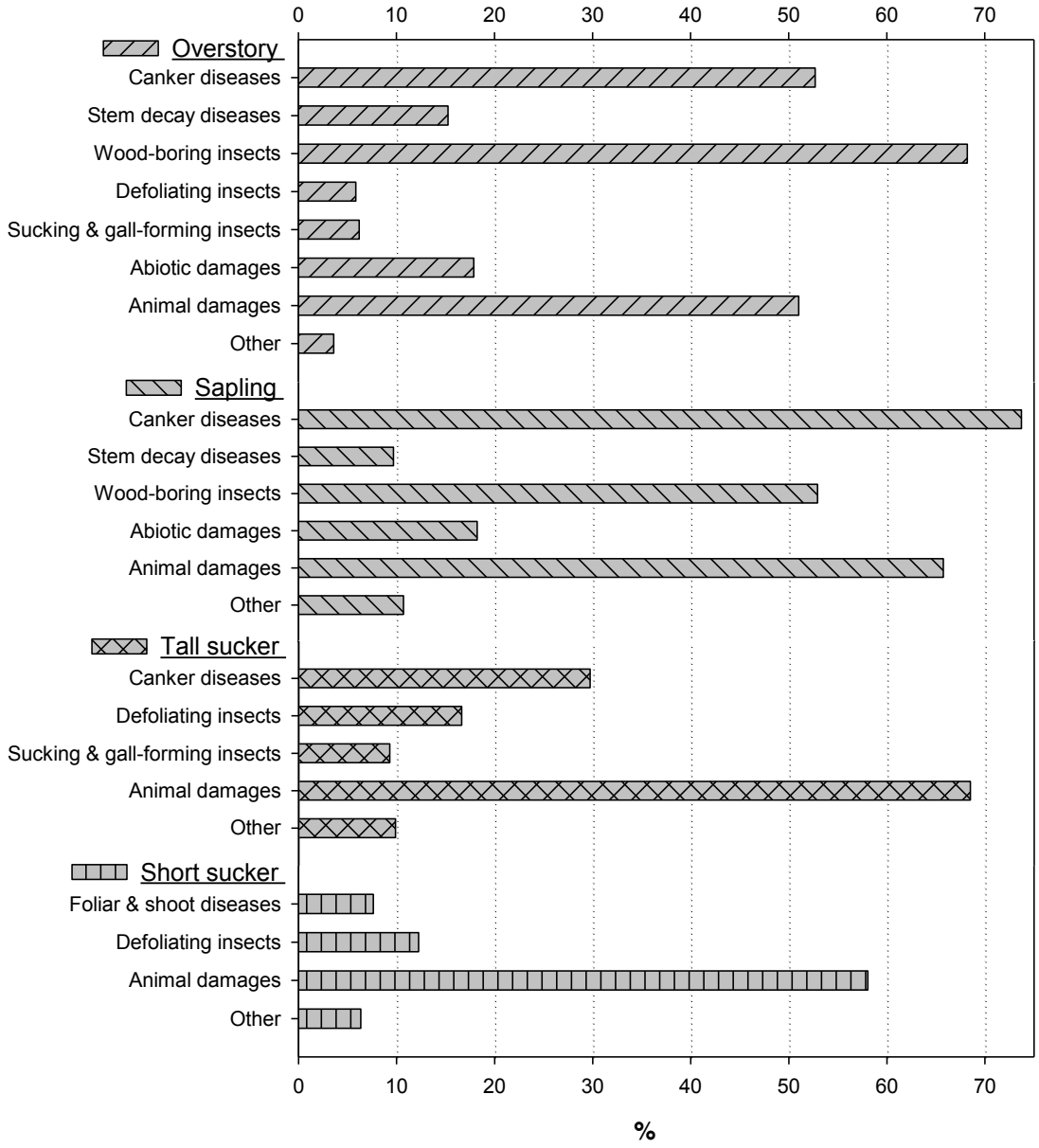


Fig 6. Aspen damaging agent group percentages by size class averaged across 48 sites on the Williams Ranger District, Kaibab National Forest, Arizona. Percentages by size class do not add up to 100 because a maximum of three damaging agents per stem were recorded.



APPENDICES

Appendix A. List of 45 (not including generic) aspen damaging agents by groups on the Williams Ranger District, Kaibab National Forest. The list excludes 18 aspen damaging agents that were looked for but not observed in the study area.

Group	Common name	Scientific name
Diseases		
Foliar and shoot		
	Generic[a]	--
	Ink spot	*Ciborinia whetzelii*
	Shoot blight	*Venturia tremulae*
Canker		
	Generic	--
	Sooty-bark	*Encoelia pruinosa*
	Black	*Ceratocystis fimbriata*
	Cytospora	*Valsa sordida*
	Snake	*Cryptosphaeria populina*
	Nectria	*Nectria galligena*
Root and butt		
	Generic	--
	Artist's conk	*Ganoderma applanatum*
	Armillaria	*Armillaria spp*.
	Aspen velvet foot	*Flammulina populicola*
Stem decay		
	Generic	--
	White trunk rot	*Phellinus tremulae*
	Inky cap	*Coprinus atramentarius*
	Peniophora	*Peniophora polygonia*
Rough-bark		
	Rough-bark	*Macrophoma tumefaciens*
	Corky-bark	*Diplodia tumefaciens*
Insects		
Wood-boring		
	Generic roundhead	Family: *Cerambycidae*
	Generic flathead	Family: *Buprestidae*
	Poplar borer	*Saperda calcarata*
	Poplar branch borer	*Oberea schaumii*
	Bronze poplar borer	*Agrilus liragus*
	Ambrosia beetle	*Trypodendron retusum*
	Aspen bark beetle	*Trypophloeus populi*
	Flathead poplar borer	*Dicerca tenebrica*

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Defoliating		
	Generic	--
	Western tent caterpillar	*Malacosoma californicum*
	Large aspen tortrix	*Choristoneura conflictana*
	Aspen leaf tier	*Pseudosciaphila duplex*
	Aspen two-leaf tier	*Enargia decolor*
	Aspen leafroller	*Pseudexentera oregonana*
Sucking and gall-forming		
	Oystershell scale	*Lepidosaphes ulmi*
	Eriophyid gall mite	Family: *Eriophyidae*
	Poplar gall saperda	*Saperda moesta*
	Twig gall fly	*Hexomyza schineri*
	Cecidomyiid gall midge	Family: *Cecidomyiidae*
	Poplar leaf aphids	*Chaitophorus populicola* & others
	Leaf-curl galls	*Aculus lobulifera* & *Mordvilkoja vagabunda*
Physical damages		
Abiotic		
	Fire	--
	Frost crack	--
	Mechanical damage	--
	Broken top	--
	Windthrow	--
	Sunscald	--
Animal		
	Bear clawing	*Ursus americanus*
	Ungulate barking and rubbing	Family: *Cervidae*
	Ungulate trampling	Family: *Bovidae* & *Cervidae*
	Ungulate browsing	Family: *Bovidae* & *Cervidae*
	Wildlife Hole	Class: *Aves*
	Sapsucker pecking	*Sphyrapicus spp.*

[a] Generic was used when damage could only be identified to the agent group. Some groups did not require this category.