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Populus tremuloides mortality near the southwestern edge of its range

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ABSTRACT

Mortality and crown dieback of quaking aspen (*Populus tremuloides*) were extensive on the Williams Ranger District, Kaibab National Forest in northern Arizona. We collected data from a random sample of 48 aspen sites to determine the relationship of predisposing site and stand factors and contributing agents to ramet mortality. Mortality of overstory (⩾10.1 cm DBH) aspen stems averaged 50% (44% by basal area). Pine–oak type aspen stands suffered greater basal area mortality (57%) than stands in mixed conifer type (38%). An average of 48% of live overstory aspen stems had >33% crown dieback, and mortality significantly increased with increasing crown dieback. Based upon univariate relationships, elevation was the most significant site factor and relative conifer basal area was the most significant stand factor related to overstory mortality. Canker diseases and wood-boring insects were significantly related to overstory mortality. Sapling (⩾5.1–10.1 cm DBH) and tall regeneration (<5.1 cm DBH) aspen mortality were high (>80% and 70%, respectively), while short regeneration (<1.37 m tall) mortality was low (16%). Many sites did not have live aspen sapling or tall regeneration stems; therefore, relationships were often inconclusive or weak. Based on a null size–density model, there was a lack of tall regeneration, sapling, and 10.1–15 cm DBH overstory aspen recruitment. Multiple regression was used to explore multivariate relationships among aspen mortality and site, stand, and damaging agent factors. Forest type, relative conifer basal area, and incidence of canker diseases and wood-boring insects were significantly associated with overstory mortality. Slope, relative conifer density, and incidence of animal damages were significantly associated with short regeneration mortality. Ungulate damages to aspen stems were common across all size classes, but significant relationships were limited to short regeneration mortality. The Southwest is forecasted to transition to a more arid climate, and aspen in pine–oak sites are already experiencing a population crash. If high mortality and low recruitment continues, conifer will replace aspen stands after overstory aspen stems die.

1. Introduction

Mortality of quaking aspen (*Populus tremuloides*) has 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 and is biologically and economically important because it provides disproportionally high amounts of critical plant and animal habitat and esthetics (White et al., 1998; Romme et al., 2001; McCool, 2001). Therefore, the loss of aspen is a loss of biodiversity and landscape diversity and has the potential to negatively impact local economies.

As a concept, the loss of aspen trees and stands over time suffers from loose usage of terminology. Forest scientists use the term "aspen decline" to describe reduction in aspen forest type on a broad range of temporal and spatial scales, driven mostly by successional processes under altered disturbance regimes (Bartos and Campbell, 1998; Kulakowski et al., 2004; Di Orio et al., 2005). Worrall et al. (2008) coined the term "sudden aspen decline" (SAD) to distinguish the rapid and synchronous mortality of aspen on a landscape-scale in Colorado from the slower successional processes described by Bartos and Campbell (1998) and others. Similar discrete episodes of heavy aspen mortality have been reported in parts of Arizona, Utah, and the prairie provinces of Canada (Gitlin et al., 2006; Guyon, 2006; Fairweather et al., 2008; Hogg et al., 2008).

The conceptual framework of a decline disease is a useful way to categorize the causes of large-scale episodes of abrupt aspen mortality (Frey et al., 2004). Forest pathologists define a tree decline disease as rapid mortality of a tree species due to a complex of predisposing, inciting, and contributing factors (Manion, 1991; Manion and LaChance, 1992). 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., episodic drought). Contributing factors are mostly biological agents (e.g., fungi and insects) that kill trees already weakened by predisposing and inciting factors (Worrall et al., 2008). Trees affected by any one

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type of factor do not suffer from a decline disease; a decline disease is characterized by the interacting effect of many factors. This is why the decline disease concept is not an appropriate frame for long-term, successional aspen decline. In the case of aspen decline disease (abrupt, heavy aspen mortality consistent with a tree decline disease), previous workers across western North America have already identified many of the probable predisposing, inciting, and contributing factors (see Frey et al., 2004; Kashian et al., 2007; Fairweather et al., 2008; Hogg et al., 2008; Worrall et al., 2008, 2010; Rehfeldt et al., 2009; St. Clair et al., 2010; Marchetti et al., 2011).

Arizona and northern Mexico contain the southwestern edge of contiguous aspen habitat in North America (Burns and Honkala, 1990), and, as a result, aspen stands at this edge often grow on warmer and drier sites than stands in the more northerly parts of its geographical range. The northern and central regions of Arizona have experienced recent aspen crown dieback, defoliation, and mortality over thousands of hectares (Gitlin et al., 2006; Fairweather et al., 2008). The extent of aspen dieback and/or defoliation in Arizona detected by Forest Health Protection (FHP) aerial survey increased from ~27,100 ha in 2006 to ~49,800 ha in 2008 (USDA Forest Service, 2007, 2008, and 2009). Of the dieback and/or defoliation detected in 2008, 53% occurred on the Kaibab National Forest.

Fine-scale (site-level) aspen mortality information has been gathered in parts of Arizona. Gitlin et al. (2006) examined local and regional patterns of drought-associated mortality near Flagstaff, AZ and found that average mortality of aspen by site varied from 7–24%, with an average of 18% at lower elevation sites and 9% at higher elevation sites. On the Coconino National Forest in northern Arizona, Fairweather et al. (2008) reported a cumulative mortality level of 55% between 2000 and 2007, with 95% mortality in low-elevation xeric sites (<2300 m), 61% mortality in mid-elevation sites (2300–2600 m), and 16% mortality in high-elevation mesic sites (>2300 m). On the Apache-Sitgreaves National Forest in eastern Arizona, cumulative mortality was 46% between 2001 and 2006 (M. Fairweather, USFS FHP, May 2011, unpublished observation). All studies noted an accelerated rate of mortality following a frost event in June 1999 and severe drought and high temperatures during the growing season in 2002. Additionally, canker diseases and wood-boring and defoliating insects contributed to the mortality of already stressed aspen (Fairweather et al., 2008), while wild ungulate browsing severely limited aspen sucker height growth (Bailey and Whitham, 2002; Fairweather et al., 2008). Although some site-level information about aspen mortality has been collected in Arizona, the relationships among aspen mortality to specific biotic and abiotic factors (damaging agents) at the southwestern fringe of contiguous aspen habitat are still largely speculative. Furthermore, site-level information for the Kaibab National Forest (west of both the Coconino and Apache-Sitgreaves National Forests) is practically unknown.

To investigate the extent and characteristics of aspen mortality on a landscape located near the southwestern edge of its contiguous range, we quantified the current condition of aspen stands on the south zone of the Kaibab National Forest. Our objectives were to: (i) determine the current structure, composition, and mortality and crown dieback levels of aspen stands; and (ii) examine how predisposing site and stand factors and contributing agents relate to aspen mortality.

2. Methods

2.1. Study area

The study area was the Williams Ranger District of the Kaibab National Forest in northern Arizona (Fig. 1), located near the cities of Williams and Flagstaff. Aspen stands are distributed over ~382,400 ha, but occupy only <1% of that area (~970 ha in ~330 loosely defined stands). The majority of stands are discontinuous and small (0.1–25 ha) and occur at lower elevations (<2400 m). Larger stands tend to occur on north-facing slopes at higher elevations (>2400 m) on Bill Williams, Kendrick, and Sitgreaves Mountains. Aspen stands are intermingled with Gambel oak (*Quercus gambelii*) and ponderosa pine (*Pinus ponderosa*) at lower elevations, and white pine (*Pinus strobiformis* or *Pinus flexilis* var. *reflexa*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), white fir (*Abies concolor* var. *concolor*), and corkbark fir (*Abies lasiocarpa* var. *arizonica*) at higher elevations. Pure aspen stands are rare, and the Kaibab National Forest has not formally defined aspen-dominated forest types (e.g., aspen forests in parts of Colorado, Utah, and Wyoming). Therefore, the two dominant forest types that contain aspen are low-elevation pine–oak and high-elevation mixed conifer.

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

2.2. Site selection

We used stratified random sampling proportional to aspen's distribution to select a subset of aspen sites across the Williams Ranger District. Based upon a digital elevation model and a map of the distribution of aspen stands (provided by Williams Ranger District personnel), we stratified aspen stands by two elevation (⩽2400 m; >2400 m), two slope (⩽28%; >28%), and five aspect (flat, north, east, south, and west) classes. These classes were then combined into 20 unique strata and we 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, common strata received more potential sampling points but a diverse range of stands were selected for sampling.

Of the 201 potential sampling points, we sampled 48 sites and rejected 153 sites 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 h hike ($n = 24$); (iv) within a fire closed area ($n = 15$); (v) within an ungulate exclosure ($n = 10$); or (vi) high human impact ($n = 2$). We decided to sample areas open to ungulate browsers because an analysis of exclosed versus unexclosed sites was beyond the scope of this study.

2.3. Plot design and data collection

We used a nested plot design adapted from Brown et al. (2006) to collect detailed site, stand, and damaging agent data. At each site to be sampled, we established four 8 m radius overstory plots (~0.02 ha) 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) 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 was permanently marked with rebar, tagged, and geo-referenced with a global positioning system. Elevation, percent slope, aspect, and forest type were recorded at site center. Sites were assigned as pine–oak if aspen were present with only Gambel oak and/or ponderosa pine, and as mixed conifer if aspen were present with only two or more conifer species.

Stems ⩾10.1 cm in diameter measured at 1.37 m above ground (diameter at breast height, DBH) were defined as "overstory". Tree species, condition class, DBH, crown dieback, and damaging agent

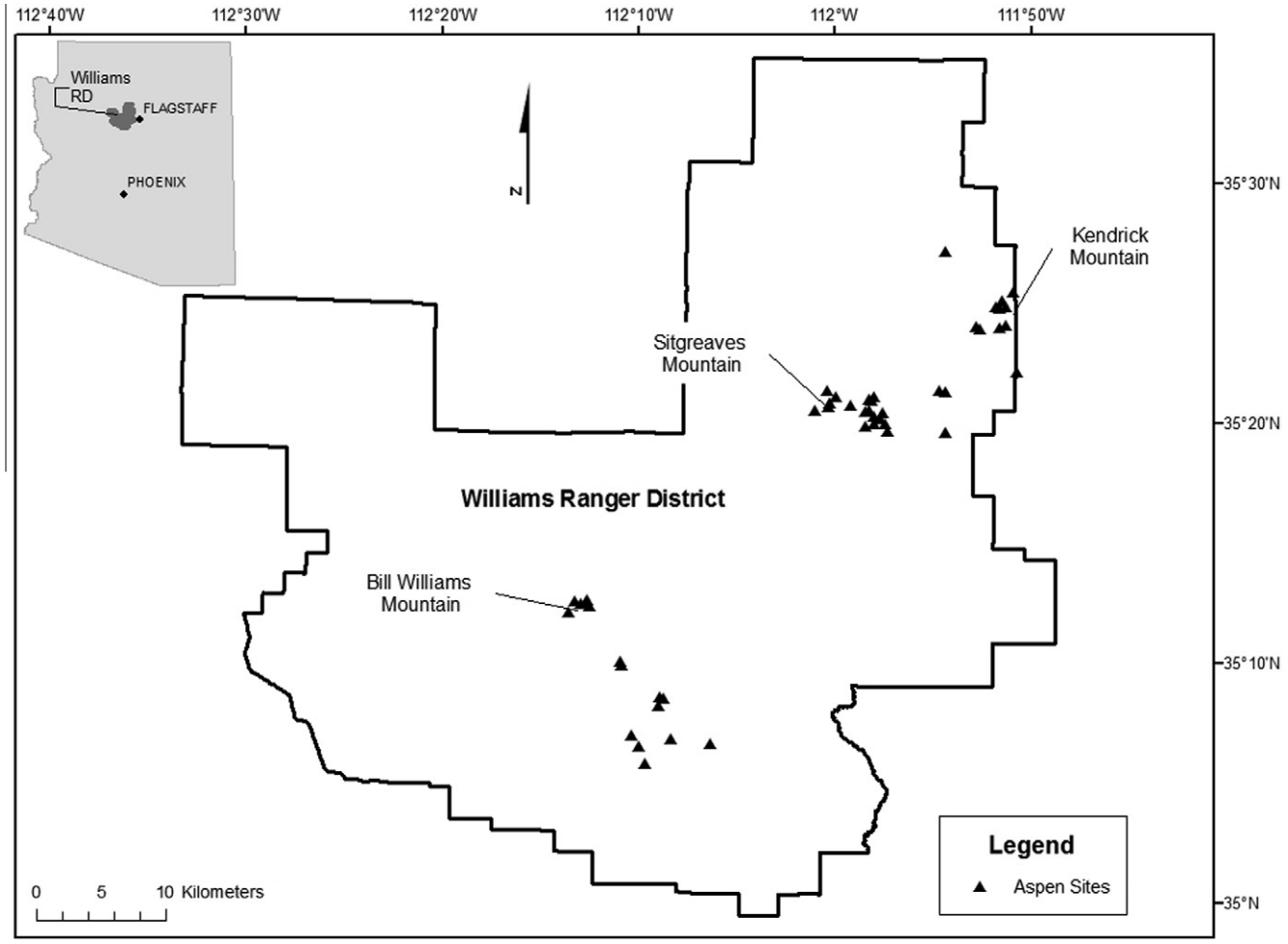

Fig. 1. Locations of aspen study sites on the Williams Ranger District, Kaibab National Forest, Arizona.

variables were collected for overstory 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 "live" even though death may have been imminent. Percent crown dieback was estimated only for live aspen. We estimated based upon the percentage of dead branches in the tree crown in three classes: light (0–33%), moderate (34–66%), and heavy (67–100%). 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 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 et al., 1989). A maximum of three present and harmful damaging agents per stem were recorded (Steed and Kearns, 2010). When more than three damaging agents were apparent, preference was given to agents with the greatest severity of impact. Damaging agents were collected individually and then pooled into disease, insect, and abiotic and animal damage groups (Appendix A) to create site averages. Of the animal damages caused by ungulates, "barking and rubbing" is only known to occur from members of the cervidae family (Debyle, 1985), which here include Rocky Mountain elk and white-tailed and mule deer.

We divided regeneration stems into three size classes and defined each as "sapling" ($\geqslant$5.1–10.1 cm DBH), "tall regeneration" (<5.1 cm DBH), and "short regeneration" (<1.37 m tall). The short regeneration 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 recruitment into the canopy (Baker et al., 1997). Tree species, condition class, and damaging agent variables were collected for sapling, tall regeneration, and short regeneration stems. For tall and short regeneration 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. We were not able to distinguish between the "browsing" and "trampling" damages of domestic versus wild ungulates.

2.4. Data analysis

We selected a set of predisposing and contributing factors suggested by previous research to be associated with aspen decline disease (Frey et al., 2004; Table 1). Data from the four plots per site were used to calculate mean aspen DBH, total tree and aspen only live density, total tree and aspen only live basal area (BA), relative conifer density and/or BA among living stems, grouped damaging agent percentages, and percent aspen stem and/or BA mortality. 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). This was necessary to calculate "heat load" following the methods outlined in McCune and Keon (Equation 3, 2002). Heat load is an index of temperature based on steepness of slope, aspect about a northeast-southwest line, and latitude. JMP 8.0.2 (SAS Institute, 2009) was used for all analyses and significance for all tests was set at $\alpha = 0.05$.

Table 1
List of predisposing, inciting, and contributing factors associated with abrupt mortality of aspen (adapted from Frey et al., 2004) and variables analyzed. All variables were measured at a discrete time and 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	Relative conifer density[b] and BA[c] (%)
Stand structure	Continuous	DBH[d] (cm), height (m), density, and BA
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
Frost events	–	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] Calculated; McCune and Keon (2002).
[b] Density = stems ha^{-1}.
[c] BA = basal area (m^2 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).

Two-tailed *t*-tests were used to test differences between continuous variables in the pine–oak and mixed conifer forest types. The Wilcoxon rank-sum test was used when normality assumptions were not met. Tukey's honestly significant difference was used for multiple comparisons of means among overstory, sapling, tall regeneration, and short regeneration aspen mortality. Paired, two-tailed t-tests were used to compare live versus dead aspen DBH and density.

Simple linear regression was used to determine the univariate relationships between variables (Zegler, 2011). Relationships among explanatory variables were used to check for collinearity. Percent aspen BA mortality was the overstory response variable and percent aspen stem mortality was the response variable for regeneration classes. The explanatory variables for overstory and regeneration tests were site, stand, and damaging agent factors (Appendices A and B). For the ordinal variable "forest type", indicator (dummy) variables were used: pine–oak type = 0 and mixed conifer type = 1. All 48 sites were used for overstory mortality analyses. Regeneration mortality analyses were problematic because of small sample sizes, many 100% mortality values, and possible nonlinear relationships. Sample size was: $n = 32$ (with 20 100% values) for sapling analyses; $n = 24$ (with 14 100% values) for tall regeneration analyses; and $n = 43$ (with zero 100% values) for short regeneration analyses. Additional tests with sample sizes limited to the sites where live sapling ($n = 12$) and tall regeneration ($n = 10$) aspen stems occurred were run to remove 100% mortality values from sapling and tall regeneration analyses. For short regeneration, percent aspen stem mortality was log-transformed to meet assumptions of linearity.

We used stepwise-forward multiple linear regression analyses to explore multivariate relationships of overstory and short regeneration mortality as a function of site, stand, and contributing factors. The stepwise regression technique allowed us to screen a large number of potentially useful explanatory variables to isolate those few that contribute most to the explanation of aspen mortality; it is the first step to more complex multivariate techniques. No models were produced for sapling or tall regeneration stems due to small sample sizes. Sample size was $n = 35$ for short regeneration mortality because five sites had no live or dead short regeneration aspen stems (5 null percentage values) and 8 sites had 0% mortality (8 null log-transformed values). Candidate explanatory variables were tested in various combinations using a probability of 0.05 to both enter and leave the model (Draper and Smith, 1998). Selected variables were ranked by how much variation each explained based upon *F*-values (Draper and Smith, 1998). 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 model. No outliers were identified from visual inspection of residuals by predicted values and outlier box plots.

3. Results

3.1. Predisposing Site and Stand Factors

During the summers of 2009 and 2010, 48 sites were sampled from a range of elevations, slopes, and aspects (Zegler, 2011; Appendix B). Site elevations ranged from 2094 to 2888 m. Percent slope ranged from 3 to 59, with a mean of 25. Aspen sites occurred on all aspects, but the majority of sites (59%) were on northerly aspects (between 315° 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 (0.03–1.11). Results of regression among explanatory site factors showed that with increasing elevation, slope increased ($R^2 = 0.23$, $P = 0.0004$), heat load decreased ($R^2 = 0.13$, $P = 0.01$), and aspect was not significant ($P = 0.87$). Of 48 sites, 15 were in were in pine–oak and 33 were in mixed conifer. In the mixed conifer forest type, slope ($P = 0.0002$) was greater and heat load was lower ($P = 0.03$) than in pine–oak type. Most sites (63%) were within livestock grazing allotments.

3.1.1. Overstory and univariate relationships

Of the 48 sites, 47 had live aspen stems in the overstory class. Mean live aspen DBH (21.7 cm) was greater than dead aspen DBH (18.2 cm) ($P < 0.0001$). Mean aspen BA ranged from 0 to 52 m^2 ha^{-1}, with a median of 5.3 m^2 ha^{-1}. Relative conifer BA for this size class was 67%. Aspen stem mortality averaged 50%, with 59% in pine–oak and 45% in mixed conifer. Aspen BA mortality averaged 44%, with 57% in pine–oak and 38% in mixed conifer. Aspen stems with light, moderate, and heavy recent crown dieback averaged 52%, 28%, and 20%, respectively (48% had at least moderate crown dieback), and there was a positive relationship between BA mortality and crown dieback ($R^2 = 0.28$, $P < 0.0001$). Aspen mortality decreased with elevation and increased with relative conifer BA. There was significantly more mortality in pine–oak than mixed conifer type (Table 2), but there was no difference between relative conifer BA in pine–oak and mixed conifer type ($P = 0.09$).

3.1.2. Regeneration and univariate relationships

Of the 48 sites, 40 had stems in the sapling class, 32 had aspen saplings, and only 12 had live aspen saplings. Density of aspen saplings ranged from 0 to 298 stems ha^{-1}, with a median of 0 stems ha^{-1}. Relative conifer density for this size class was 85%. Sapling aspen stem mortality was 82%. Aspen mortality increased with relative conifer density (Table 2) and had no relationship with total

Table 2
Significant ($\alpha = 0.05$) univariate relationships between aspen mortality and explanatory factors.

Factor	Sign[a]	R^2	*P*-value
Overstory BA[b] mortality (%)			
Elevation (m)	–	0.24	0.0004*
Forest type [0–1][c]	–	0.10	0.0275*
Overstory relative conifer density[d] (%)	+	0.45	<0.0001*
Overstory relative conifer BA (%)	+	0.43	<0.0001*
Overstory canker diseases (%)	+	0.18	0.0028*
Overstory wood-boring insects (%)	+	0.56	<0.0001*
Sapling stem mortality (%)			
Slope (%)[e]	–	0.35	0.0422*
Sapling relative conifer density (%)	+	0.20	0.0187*
Sapling canker diseases (%)	+	0.16	0.0341*
Sapling wood-boring insects (%)[e]	+	0.35	0.0423*
Tall regen stem mortality (%)			
Elevation (m)	–	0.22	0.0201*
Elevation (m)[e]	–	0.57	0.0115*
Slope (%)	–	0.60	<0.0001*
Slope (%)[e]	–	0.56	0.0127*
Heat load[f]	+	0.21	0.0238*
Forest type (0–1)	–	0.17	0.0441*
Forest type (0–1)[e]	–	0.81	0.0004*
Tall regen total live density	–	0.58	<0.0001*
Tall regen canker diseases (%)	+	0.27	0.0091*
Tall regen canker diseases (%)[e]	+	0.62	0.0068*
Log (short regen stem mortality) (%)			
Slope (%)	–	0.16	0.0182*
Short regen relative conifer density (%)	+	0.16	0.0167*
Short regen animal damages (%)	+	0.15	0.0198*

[a] Sign indicates a positive (+) or negative (–) relationship.
[b] BA = basal area (m^2 ha^{-1}).
[c] 0 = pine–oak, 1 = mixed conifer.
[d] Density = stems ha^{-1}.
[e] Sample size limited to sites where live aspen stems occurred.
[f] McCune and Keon (2002); unitless index with 0.03–1.11 scale.

live density ($P = 0.06$). Limiting the sample and analysis to sites with live aspen saplings produced a slight negative relationship with slope (Table 2).

Of the 48 sites, 38 had stems in the tall regeneration class, 24 had tall regeneration aspen stems, and only 10 had live tall regeneration aspen stems. Density of tall regeneration aspen ranged from 0 to 3332 stems ha^{-1}, with a with a median of 0 stems ha^{-1}. Relative conifer density for this size class was 89%. Tall regeneration aspen stem mortality was 72%. Aspen mortality decreased with elevation, slope, and total live density, and increased with heat load. The mixed conifer forest type tended to have less aspen mortality (Table 2). Except for heat load and total live density, the above relationships were also significant when the sample was limited to sites with live tall regeneration aspen stems (Table 2).

Of the 48 sites, all had stems in the short regeneration class and 43 had short regeneration aspen stems. Of these 43 sites, all had a live aspen component. Density of short regeneration aspen ranged from 0 to 17,109 stems ha^{-1}, with a median of 1517 stems ha^{-1}. Relative conifer density for this this size class was 52%. Short regeneration aspen stem mortality was 16%. This level of mortality was significantly lower than aspen mortality in other size classes ($P < 0.0001$ for all pair-wise comparisons). Aspen mortality decreased with slope, increased with relative conifer density (Table 2), and had no relationship with total live density ($P = 0.59$).

3.2. Size distributions

We produced a size–density distribution of live and dead aspen trees by size class across all sites (Fig. 2). The best-fit, negative exponential, null model was generated from the density of live aspen stems ⩾ 15.1 cm DBH. Based upon the best-fit or expected line, there was a lack of live aspen stems in the tall regeneration, sapling, and smallest overstory (10.1–15 cm DBH) size classes. There were significantly more dead than live aspen in the sapling and smallest overstory size classes ($P < 0.0001$ for both). Separate distributions of live and dead aspen were also determined for pine–oak and mixed conifer forest types (Fig. 3). Consistent with overall trends, there were significantly more dead than live aspen in the sapling and smallest overstory size classes for both forest types ($P < 0.05$ for all). However, unlike the overall and mixed conifer distributions, pine–oak sites had more dead than live tall regeneration aspen ($P = 0.004$). There was no significant difference in the density of short regeneration aspen stems between pine–oak and mixed conifer ($P = 0.19$).

3.3. Contributing damaging agents

We collected data for 45 aspen damaging agents on individual aspen stems (Appendix A). We assessed 1805 overstory stems, 115 sapling stems, 220 tall regeneration stems, and 2984 short regeneration stems for damaging agents, and analyzed damaging agents by site averages per damaging agent group. Fig. 4 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 for overstory and sapling aspen, while animal damages was the most common agent group for tall and short regeneration aspen. Cytospora canker (*Valsa sordida*), sooty-bark canker (*Encoelia pruinosa*), bronze poplar borer (*Agrilus liragus*), flathead poplar borer (*Dicerca tenebrica*), and ungulate damages were widespread and common. We observed high amounts of ungulate damages across all sites regardless of site location inside or outside of livestock grazing allotments (data not shown).

3.3.1. Overstory and univariate relationships

The top three damaging agent groups in the overstory class were wood-boring insects (68%), canker diseases (53%), and animal damages (51%) (Fig. 4). 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%). Aspen mortality increased with canker diseases and wood-boring insects (Table 2) and had no relationship with animal damages ($P = 0.12$).

3.3.2. Regeneration and univariate relationships

The top three damaging agent groups in the sapling class were canker diseases (74%), animal damages (66%), and wood-boring insects (53%) (Fig. 4). 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%). Aspen mortality had a slight positive relationship with canker diseases (Table 2) and no relationship with wood-boring insects ($P = 0.08$) or animal damages ($P = 0.19$). Limiting the sample and analysis to sites with live aspen saplings produced a slight positive relationship with wood-boring insects (Table 2).

The tall regeneration class had two common damaging agent groups; animal damages (68%) and canker diseases (30%) (Fig. 4). The top animal damage was ungulate barking and rubbing (51%) and the top canker was Cytospora (28%). Aspen mortality increased with canker diseases (Table 2) and had no relationship with animal damages ($P = 0.12$). The relationship with canker diseases was also positive and significant when the sample was limited to sites with live tall regeneration aspen stems (Table 2).

Animal damages (58%) was the only common short regeneration class damaging agent group (Fig. 4). The top animal damage was ungulate browsing (58%). Aspen mortality increased with animal damages (Table 2).

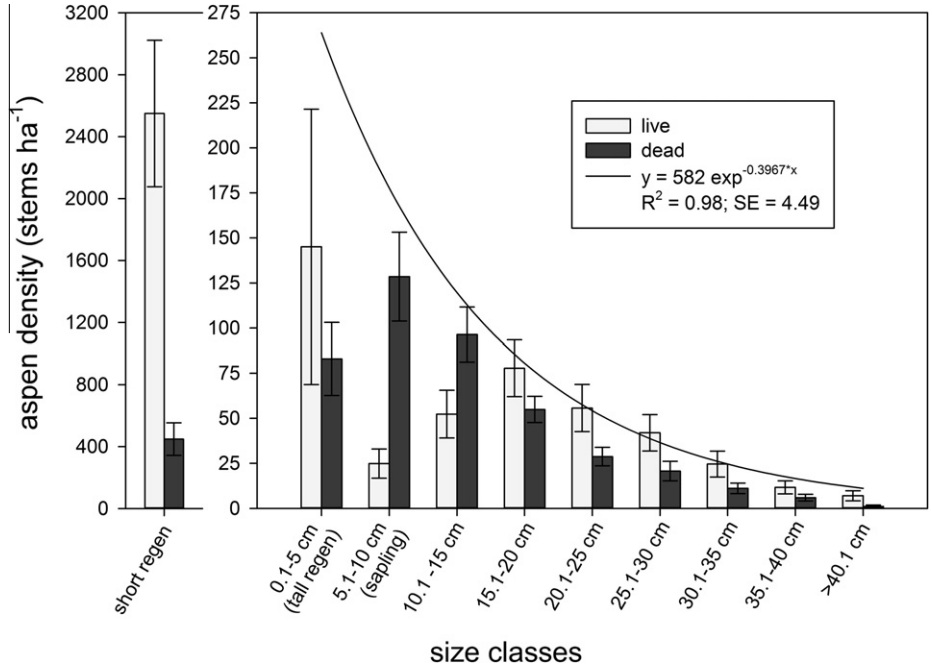

Fig. 2. Size–density distribution of live and dead aspen stems from 48 sites on the Williams Ranger District, Kaibab National Forest, Arizona. Expected line is a single, two parameter, negative exponential relationship. Error bars are ± standard error.

3.4. Multiple regression models

We examined multiple regression models for aspen mortality. The model for overstory mortality (Table 3) accounted for 78% of the variation based on adjusted R^2 ($F_{4,43} = 41.47$, $P < 0.0001$). Mortality decreased from pine–oak to mixed conifer ($F_{1,43} = 5.92$) and increased with increasing relative conifer BA ($F_{1,43} = 8.24$) and higher incidences of canker diseases ($F_{1,43} = 33.05$) and wood-boring insects ($F_{1,43} = 33.29$) (Table 3). The contributing damaging agents explained far more variation in mortality than predisposing factors.

The model for short regeneration mortality (Table 3) accounted for 34% of the variation based on adjusted R^2 ($F_{3,31} = 6.80$, $P = 0.001$). Mortality decreased with increasing slope ($F_{1,31} = 4.90$) and increased with increasing relative conifer density ($F_{1,31} = 5.00$) and higher incidence of animal damages ($F_{1,31} = 6.85$) (Table 3). The contributing damaging agent explained the most variation of the three variables, but the predisposing factors combined explained more variation mortality than the contributing damaging agent.

4. Discussion

Our results document extensive aspen crown dieback and mortality in the pine–oak and mixed conifer forests of the Williams Ranger District, Kaibab National Forest. Predisposing site and stand factors, and contributing damaging agents were significantly related to aspen mortality, and contributed to the generally poor condition of aspen 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, aspen mortality related most strongly to relative conifer density or BA and damaging agents.

4.1. Overstory

The only significant site factor related to overstory aspen mortality was elevation (inverse relationship), which spanned 800 m and is related to moisture availability (Pearson, 1920; Gitlin et al., 2006; McDowell et al., 2011; Vankat, 2011). Other site factors such as aspect, slope, and heat load were not strongly related to 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 mortality.

Of the stand factors, only relative conifer BA and forest type were significantly related to overstory aspen mortality. As relative conifer BA increased, so did aspen mortality. The gradual replacement of aspen by confers is a well-documented successional process (Baker, 1925; Mueggler, 1985; Jones, 1974; Rogers, 2002; Strand et al., 2009; and others). Aspen mortality was higher in the pine–oak than mixed conifer forest type. Because there was no difference in relative conifer BA between forest types, this difference is likely explained by the higher elevations and more favorable moisture conditions of the mixed conifer forest type. Though it was beyond the scope of this study, an analysis of how aspen mortality relates to climate variables is the next logical step, and we plan to explore the relationships between aspen annual ring growth and climate (especially drought) (see Hanna and Kulakowski, 2012).

Damaging agents, specifically canker diseases and wood-boring insects, were the most important group of factors that explained overstory aspen mortality. Of the cankers, only two were widespread and common: Cytospora and sooty-bark. Sooty-bark is widely considered 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). While Cytospora canker and all of the wood-boring insects are important killers of aspen, they are secondary agents that attack after something else weakens host condition (Hart and Hart, 2001; Frey et al., 2004). Despite a high level of animal wounding and the possible infection courts they provide (Hinds, 1985), overstory mortality did not have positive relationships with animal damages. This conflicts with a study conducted in northwestern Wyoming (Hart and Hart, 2001), but agrees with as study conducted in Rocky Mountain National Park (Baker et al., 1997).

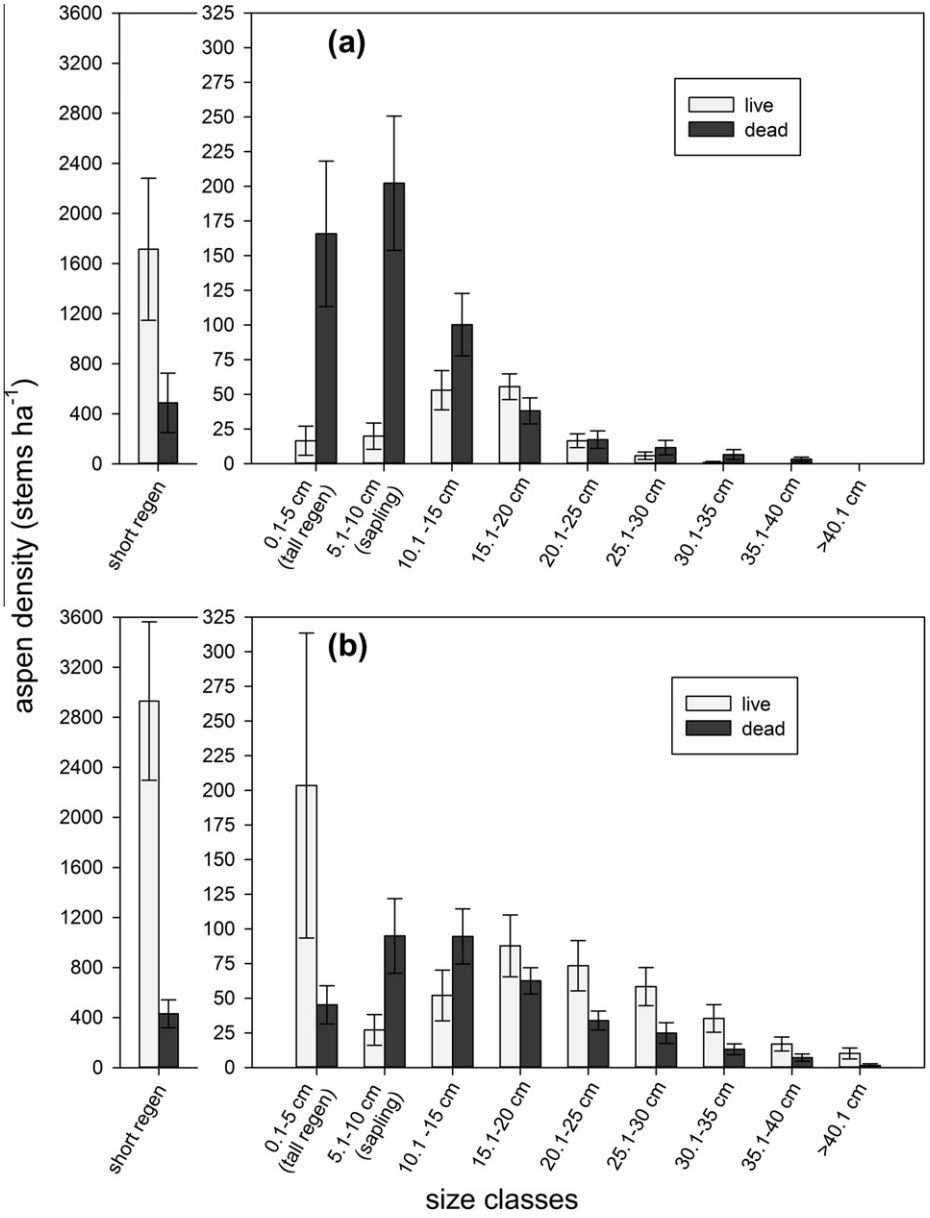

Fig. 3. Size–density distribution of live and dead aspen stems on the Williams Ranger District, Kaibab National Forest, Arizona by forest type: (a) pine–oak type (n = 15) and b) mixed conifer type (n = 33). Error bars are ± standard error.

The overstory aspen mortality levels we observed were generally higher than those reported in other studies. This is remarkable because our sample of sites was random. We found 50% aspen stem mortality across all sites compared to: (i) ~7% in the northern Rocky Mountains (Steed and Kearns, 2010); (ii) ~26% in damaged stands across the Intermountain West (St. Clair et al., 2010); (iii) ~7% in healthy stands and ~45% in damaged stands in southwestern Colorado (Worrall et al., 2010); (iv) ~15% near Flagstaff, Arizona (Gitlin et al., 2006); and (v) ~50% cumulative between 2000 and 2007 in damaged stands in northern Arizona (M. Fairweather, USFS FHP, May 2011, unpublished observation).

4.2. Regeneration

In addition to high levels of overstory mortality, many of our sites did not have aspen sapling or tall regeneration stems, and a few sites had no aspen regeneration at all. This is intriguing because death of the aspen overstory promotes vigorous vegetative regeneration through a well-documented hormonal process (Shier et al., 1985; Bartos, 2001). Our best explanations for missing size classes (cohorts) include: (i) the positive association of root mortality with overstory mortality (Worrall et al., 2010). It is possible that the aspen stands in our study suffered extensive root mortality; (ii) the timing of the study compared to the death of the overstory. With the high amounts of browse observed on short regeneration aspen stems, the evidence may have been consumed; and (iii) past mortality events that affected these size classes (e.g., droughts or episodes of intense browsing similar to those detected by Binkley et al. (2006) on the North Kaibab).

Mortality of aspen regeneration varied with size class. Sapling and tall regeneration aspen mortality were high (greater than 80% and 70%, respectively), while short regeneration aspen mortality was low (16%). However, our ability to detect short regeneration mortality was limited because tiny dead stems do not persist upright for as long as larger size classes and ungulates

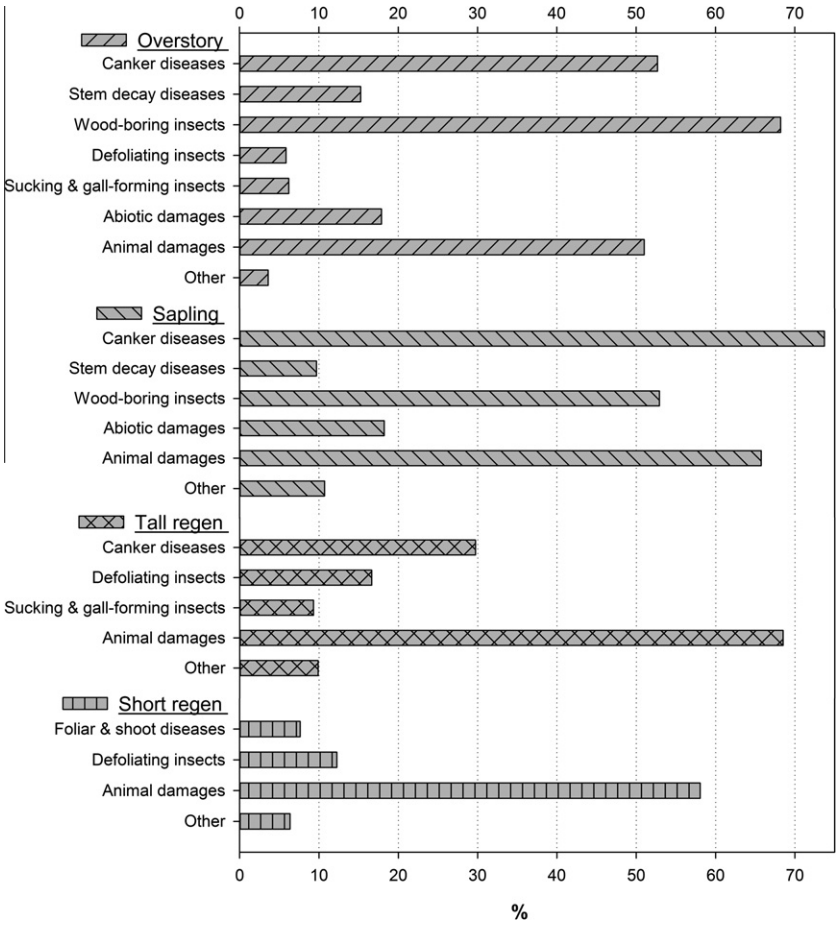

Fig. 4. Aspen damaging agent group percentages by size class averaged across 48 sites on the Williams Ranger District, Kaibab National Forest, Arizona. Percentages by size class do not add up to 100 because a maximum of three damaging agents per stem were recorded.

Table 3
Multiple regression models for aspen mortality. All factors were significant at $\alpha = 0.05$.

Factor	Parameter estimate	Standard error	*t*-ratio	*P*-value
Overstory BA[a] mortality (%)[b]				
Forest type [0–1][c]	−11.74	4.82	−2.43	0.0192*
Overstory relative conifer 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*
Log (short regen stem mortality) (%)[d]				
Slope (%)	−0.02	0.01	−2.21	0.0344*
Short regen relative conifer density[e] (%)	0.01	<0.01	2.24	0.0327*
Short regen animal damages (%)	0.02	0.01	2.62	0.0136*

[a] BA = basal area (m^2 ha^{-1}).
[b] $n = 48$; $R^2 = 78\%$ ($F_{4,43} = 41.47$, $P < 0.0001$).
[c] 0= pine–oak, 1 = mixed conifer.
[d] $n = 35$; $R^2 = 34\%$ ($F_{3,31} = 6.80$, $P = 0.0012$).
[e] Density = stems ha^{-1}.

browse away the evidence of the mortality they cause. Sapling aspen mortality was greatest where relative conifer density was highest. Tall regeneration aspen mortality decreased with increasing slope, elevation, and total live density, and increased with heat load and location within the pine–oak type. Short regeneration aspen mortality increased with decreasing slope and increasing relative conifer density. Overall, regeneration mortality was not density-dependent. Canker diseases and animal damages were common in the sapling and tall regeneration size classes. The only common short regeneration damaging agent was ungulate browsing. We found that higher levels of canker diseases (almost exclusively Cytospora) increased sapling and tall regeneration aspen mortality. Cytospora is a common, well-documented mortality agent of aspen regeneration throughout western North America, and the severity and extent of Cytospora canker increases with drought stress (Hinds, 1985; Guyon et al., 1996). While animal damages did not appear to relate to sapling or tall regeneration aspen mortality, these size classes had small sample sizes and high levels of animal damages regardless of mortality levels. Short regeneration mortality, however, increased with ungulate brows-

ing. Abundant previous research has shown that heavy, persistent ungulate browsing can prevent successful regeneration of aspen (Rolf, 2001; Bailey and Whitham, 2002; Binkley et al., 2006; Fairweather et al., 2008). We observed high browsing pressure across the entire study area.

While most sites were within livestock grazing allotments, the steep terrain of many sites likely deterred cattle and sheep from accessing aspen regeneration. Slopes $\geqslant 40\%$ are thought to deter cattle and sheep (J. Stevens, USFS, January 2012, personal communication). Out of the 48 sites, we estimated that 61% were not grazed by cattle and sheep (38% outside allotments; 23% inside but too steep).

4.3. Size distributions

Shepperd et al. (2001) showed the size–density relationship of healthy, self-regenerating aspen stands to follow a negative exponential (reverse-J) shaped curve, where smaller, younger size classes are more abundant than larger, older size classes. Steed and Kearns (2010) found the condition of aspen in Montana and northern Idaho to be generally healthy, with low levels of mortality and crown dieback, sufficient aspen regeneration, and a reverse-J size–density distribution. Except for missing or dead intermediate size classes, the distribution of all 48 sites (Fig. 2) appears to follow a reverse-J. Based upon a null model that we calculated from the data (versus forced on our data), there was a lack of recruitment in tall regeneration, sapling, and smallest overstory stems, suggesting that aspen will not be able to replace current and future overstory losses. However, these classes had many dead stems. Given that mortality was not density-dependent, why did aspen in the sapling and smallest overstory size classes die before recruiting to the larger size classes? In both the sapling and overstory classes, aspen mortality increased with increasing relative 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 stems are easier for cankers and cambial-feeding flathead borers to girdle than larger stems. Because of this, secondary agents of normally resistant mature aspen stems (e.g., Cytospora) are available to kill regeneration stems (Jacobi and Shepperd, 1991). This holds especially true if some other inciting factor (e.g., drought and high temperatures) allows for the successful attack of contributing, secondary agents.

4.4. Diseases, insects, and inciting factors

Many interacting factors contributed to aspen mortality on the Williams Ranger District. The interaction of factors in a decline disease scenario makes it impractical to deduce single cause (Ostry et al., 2011), especially because these interactions are complex and poorly understood (Gitlin et al., 2006). However, signs and symptoms of canker and wood-boring insect activity were pervasive on dead and crown damaged aspen. Based upon our univariate relationships and multiple regression models, we have little doubt that contributing damaging agents ultimately killed most of the currently standing dead aspen stems. However, we concluded, as did Fairweather et al. (2008) in Arizona and Marchetti et al. (2011) in Colorado, that cankers and insects played a secondary role in observed aspen mortality and were likely facilitated by long-term climate trends and short-term extreme weather events, such as severe drought and frost events (USDA, 2000; Williams et al., 2010; Ganey and Vojta, 2011). 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 extremely hot and dry conditions rendered aspen susceptible to the attacks of cankers and insects (Hogg et al., 2008; Marchetti et al., 2011).

5. Conclusions

Quaking aspen populations in the Southwest, as elsewhere in the western United States, are experiencing recent and rapid crown dieback and mortality. We initiated this study to quantify the crown dieback and mortality of aspen and to explore relationships between mortality and site and stand characteristics and contributing biotic agents. We found that half of the aspen overstory recently died, and of the remaining living stems, roughly half suffer from considerable recent crown dieback. We can expect many of these living but crown damaged stems to succumb to mortality in the near future. As with other studies that have observed significant tree mortality in southwestern forests at this elevation (Gitlin et al., 2006; Ganey and Vojta, 2011), we may be observing signs of long-term climate trends and short-term extreme weather events. The Southwest is forecasted to transition to a more arid climate (Seager et al., 2007; Seager and Vecchi, 2010). Under climate change, the aspen stands we see in decline today may not just be a temporary phase but a shift in this species' distribution (Gitlin et al., 2006; Rehfeldt et al., 2009), as the aspen in our low-elevation pine–oak sites are experiencing a population crash as described by Breshears et al. (2008). Since our study area is located near the southwestern edge of aspen's contiguous geographical range, it will likely experience some of the greatest drought-related impacts.

Long-term aspen decline is not primarily a mortality issue, nor is it a decline disease; it is a reduction in aspen type, 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, and often accompanied by root mortality and insufficient regeneration to replace overstory losses (Worrall et al., 2008). While the extensive mortality and crown dieback exhibited by aspen in the study area is comparable to a rapid decline of aspen elsewhere, successional processes also play a significant role in the current health of aspen forests on the Williams Ranger District. Aspen in our study area suffer from extensive mortality relating to predisposing and contributing factors of a decline disease, and, in addition, an important inciting factor: frequent intense drought.

The lack of live small-diameter aspen stems across the study area epitomizes aspen's poor current condition, and, in the absence of intensive management, likely forecasts a grim future. The authors of a recent summary document about aspen restoration (O'Brien et al., 2010) assert that self-replacing (self-regenerating) aspen stands require two regeneration size classes each to maintain live densities of at least 1250 stems ha^{-1} (Bartos and Campbell, 1998; Kurzel et al., 2007; Rogers et al., 2010). The combined live density for aspen sapling and tall regeneration stems (roughly one of their classes) was below this level at 96% of our sites, while the density of live short regeneration stems (roughly their other class) was below this level 48% of our sites. If current trends in depleted recruitment continue, conifer will come to dominate aspen stands after mature overstory aspen stems die.

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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	*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*
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* and others
	Leaf-curl galls	*Aculus lobulifera* and *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* and *Cervidae*
	Ungulate browsing	Family: *Bovidae* and *Cervidae*
	Wildlife Hole	Class: *Aves*
	Sapsucker pecking	*Sphyrapicus spp.*

[a] Generic was used when damage could only be identified to the agent group.

Appendix B

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	0–2
Heat load[b]	0.91	0.10	0.66–1.06
Overstory structure			
Live total density[c]	638	348	162–1766
Live aspen density	271	265	0–1156
Live total BA[d]	31.8	15.8	5.1–76.5
Live aspen BA	11.7	13.2	0.0–51.9
Relative conifer density (%)	59	26	0–100
Relative conifer density BA (%)	67	26	0–100
Aspen stem mortality (%)	50	25	5–100
Aspen BA mortality (%)	44	28	1–100
Aspen crown dieback >33% (%)	48	26	10–100
Sites with live aspen (%)	98	–	–
Sapling structure			
Live total density	217	209	0–1044
Live aspen density	25	56	0–298
Relative conifer density (%)	85	30	0–100
Aspen stem mortality (%)	82	29	0–100
Sites with live aspen (%)	25	–	–
Tall sucker structure			
Live total density	793	1018	0–3332
Live aspen density	145	529	0–3332
Relative conifer density (%)	89	28	0–100
Aspen stem mortality (%)	72	41	0–100
Sites with live aspen (%)	21	–	–
Short sucker structure			
Live total density	5324	4608	99–19596
Live aspen density	2550	3280	0–17109
Relative conifer density (%)	52	35	0–100
Aspen stem mortality (%)	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] Density = stems ha^{-1}.
[d] BA = basal area (m^2 ha^{-1}).

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