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POPULATION ECOLOGY - ORIGINAL RESEARCH

Slow lifelong growth predisposes *Populus tremuloides* trees to mortality

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Abstract Widespread dieback of aspen forests, sometimes called sudden aspen decline, has been observed throughout much of western North America, with the highest mortality rates in the southwestern United States. Recent aspen mortality has been linked to drought stress and elevated temperatures characteristic of conditions expected under climate change, but the role of individual aspen tree growth patterns in contributing to recent tree mortality is less well known. We used tree-ring data to investigate the relationship between an individual aspen tree's lifetime growth patterns and mortality. Surviving aspen trees had consistently higher average growth rates for at least 100 years than dead trees. Contrary to observations from late successional species, slow initial growth rates were not associated with a longer lifespan in aspen. Aspen trees that died had slower lifetime growth and slower growth at various stages of their lives than those that survived. Differences in average diameter growth between live and dead trees were significant ($\alpha = 0.05$) across all time periods tested. Our best logistical model of aspen mortality indicates that younger aspen trees with lower recent growth rates and higher frequencies of abrupt growth declines had an increased risk of mortality. Our findings highlight the need for species-specific mortality functions in forest succession models. Size-dependent mortality functions suitable for late successional species may not be appropriate for species with different life history strategies. For some early successional species, like aspen, slow growth at various stages of the tree's life is associated with increased mortality risk.

Keywords Quaking aspen · *Populus tremuloides* · Tree mortality · Growth pattern · Decline · Dendroecology

Introduction

A growing body of evidence shows that forest dieback and tree mortality rates have increased in recent decades, both globally and in the western United States (Allen et al. 2010; Anderegg et al. 2012). This increase in tree mortality has been linked to drought conditions, which are expected to become more frequent and severe with climate change (Breshears et al. 2008; Gitlin et al. 2006; van Mantgem et al. 2009). Rapid and widespread tree mortality, driven by changing climate conditions, has the potential to alter forest structure and composition with implications for ecosystem services and ecological functions (Anderegg et al. 2012; van Mantgem et al. 2009). High mortality rates could result in rapid contraction of some species' distributions (Rehfeldt et al. 2006, 2009). Understanding the processes of tree mortality is critical to predicting and managing forest change under future climate conditions (van Mantgem et al. 2009).

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Although the processes leading to individual tree mortality play an important role in predicting future forest dieback, mechanisms of tree death remain poorly understood (Bigler and Bugman 2004b; Keane et al. 2001). Tree growth at different times during a tree's lifespan has been linked to mortality (Bigler and Bugman 2004b; Bigler and Veblen 2009; Das et al. 2007; Pedersen 1998). However, many models of forest dynamics, including gap models, treat mortality as a function of slow growth, age or size without consideration of how variable growth at different stages of a tree's life may contribute to the probability of mortality (Keane et al. 2001; Manusch et al. 2012). Decreased growth in the 5–50 years preceding tree death has been correlated with increased risk of mortality across many different tree species, including several conifer species, oaks, and aspen (e.g., Bigler and Bugman 2003; Das et al. 2007; Kane 2012; Ogle et al. 2000; Pedersen 1998). Fast growth in the first 50 years of a tree's life has been associated with a shorter lifespan (Bigler and Veblen 2009; Black and Colbert 2008). Consistently slow lifetime growth rates are associated with increased longevity, especially in long-lived shade-tolerant species (Loehle 1988).

Between species, a trade-off between growth rates and longevity has been well-documented (Bigler and Bugman 2004a; Bigler and Veblen 2009; Black and Colbert 2008; Loehle 1988). Late successional species invest more in defensive compounds and structural support (i.e., higher wood density) and reach sexual maturity at a later age, but grow more slowly than fast-growing pioneer species (Loehle 1988). A similar trend has been observed within species, where slower-growing individuals are often the oldest trees and trees that initially grow fast frequently die at younger ages (Bigler and Veblen 2009; Black and Colbert 2008). Much of the work linking intraspecific tree growth patterns to the probability of mortality has focused on late successional, shade-tolerant conifers (e.g., Bigler and Bugman 2004a; Bigler and Veblen 2009; Das et al. 2007). But, some studies have also shown support for an inverse relationship between growth rate and longevity in shade-intolerant, pioneer species, such as ponderosa pine (*Pinus ponderosa*) and bigtooth aspen (*Populus grandidentata*) (e.g., Black and Colbert 2008; Johnson and Abrams 2009).

Aspen (*Populus tremuloides*) provide a good opportunity to investigate the broad applicability of the relationships between tree growth rates and mortality because they offer another example of a shade-intolerant, pioneer species. Additionally, aspen serve as a good example of the need to better understand tree mortality because aspen forests are currently experiencing extensive forest dieback (Worrall et al. 2013). Rapid and severe canopy dieback and mortality in aspen forests, termed sudden aspen decline (SAD), has been observed across much of North America, including southwestern Canada, the Great Lakes, throughout much of the Rocky Mountains, and in the southwestern US (Fairweather et al. 2008; Frey et al. 2004; Huang and Anderegg 2012; Worrall et al. 2008, 2010; Zegler et al. 2012).

Aspen overstory tree mortality is particularly high in northern Arizona, which is near the southwestern limit of the species' contiguous range in North America. In the San Francisco Peaks in northern Arizona, aspen stands sustained cumulative mortality levels of 55 % from 2000 to 2007 (Fairweather et al. 2008). Based on stand conditions sampled between 2009 and 2010 on the Kaibab National Forest, Zegler et al. (2012) reported the highest overstory aspen mortality for the western US (50 % by tree density; 44 % by basal area). Aspen sustained the highest overstory (45 %) mortality rates of four tree species studied in mixed conifer forests that were sampled in 2008 in this region (Kane 2012). Sixty-two percent of the measured aspen mortality in these stands occurred between 1996 and 2008 (Kane 2012). Following a period of severe drought, aspen sustained relative overstory mortality rates (dead trees as a proportion of live trees) of 85 % between 2002 and 2007 in northern Arizona (Ganey and Votja 2011). As other authors have suggested, these high mortality rates may represent early indications of aspen's response to climate warming near the southern edge of its distribution (Ganey and Votja 2011; Gitlin et al. 2006).

Factors related to site and stand conditions, as well as the prevalence of insect attacks and tree diseases have been linked to SAD. Spatial settings with higher moisture stress, such as lower elevations, flatter slope angles, and southern and western facing slopes are associated with SAD (Huang and Anderegg 2012; Worrall et al. 2008, 2010). Forest type and conifer basal area interact with drought and late-spring frosts to contribute toward aspen mortality (Fairweather et al. 2008; Zegler et al. 2012). For example, aspen overstory mortality in northern Arizona was higher in lower elevation ponderosa pine-Gambel oak (*Pinus ponderosa* and *Quercus gambelii*) dominated forests (57 % of aspen basal area) than in nearby mixed conifer forests (38 % by basal area; Zegler et al. 2012). In the same study, the most important factors explaining aspen overstory mortality were contributing factors, especially wood-boring insects and canker diseases (Zegler et al. 2012).

Although the links between site and stand factors, climate, insects, diseases and recent aspen mortality have been investigated, the contribution of individual aspen growth patterns to recent tree mortality has received relatively little attention. In the two studies to examine the impact of previous growth on aspen mortality, multiple years of reduced growth and abrupt growth decreases were associated with mortality (Hanna and Kulakowski 2012; Kane 2012). However, both of these studies focused on a single forest type, either pure aspen stands (Hanna and Kulakowski 2012) or mixed-conifer forests (Kane 2012). To our knowledge, this is the first study to examine the links between aspen mortality and growth across a range of forest types over the elevational gradient of aspen's distribution and at multiple different stages of a tree's lifespan.

In this study, we use tree-ring data to examine the relationship between growth patterns at different stages of an aspen tree's life and individual tree mortality. We compare growth patterns between trees that died and those that survived across the tree's entire lifespan, at the beginning of life, and in the years preceding death. Specifically, our objectives were to determine whether trees that died and those that survived exhibited different growth patterns (1) across their entire lifespan, (2) within the initial 50 years of growth, and (3) in the 5–100 years prior to death. Finally, we built models of tree mortality using growth pattern variables at these different periods within a tree's life to explore the utility of tree growth variables in predicting aspen tree mortality.

Materials and methods

Study area

The study area was the 248,234 hectare Williams Ranger District of the Kaibab National Forest, in northern Arizona in the United States. Aspen occupies <1 % of the study area and occurs primarily as small and patchy stands, with larger stands (approximately 30–40 ha) at higher elevations (>2,400 m) on Bill Williams Mountain, Kendrick Peak, and Sitgreaves Mountain (Zegler et al. 2012). At the lowest elevations, aspen stands are often surrounded or mixed with ponderosa pine and Gambel oak. At middle elevations and north-facing slopes, aspen co-occur with Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), southwestern white pine (*Pinus strobiformis*), and ponderosa pine. In addition to Douglas-fir and southwestern white pine, the highest elevation aspen stands are also mixed with white fir (*Abies concolor*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*).

Elevations within the study area range from 1,435 to 3,175 m, and aspen stands are found between 1,900 and 3,125 m. Precipitation in the study area is bimodal with peaks during the summer monsoon (July–September) and winter (January–March). Climate summaries from the Williams, Arizona weather station 1897–2012 show that total precipitation averages 549 mm annually, 199 mm during the monsoon and 161 mm during the winter (WRCC 2012). June is the driest month, with an average of 12 mm precipitation. The coldest month is typically January and the warmest month is July, with average minimum and maximum temperatures of −6.9 °C and 28.7 °C, respectively.

Sampling design

Zegler et al. (2012) previously sampled 48 aspen stands within our study area. We randomly selected a subset of their stands, stratified by three forest types, described below. We chose to sample by forest type because differences in species composition reflect differences in slope, soils, stand history, or other factors not accounted for by elevation alone. Within each forest type, we randomly selected a subset of their sites that had never been exclosed and had at least five live overstory aspen and nine dead overstory aspen from which to take increment cores. We classified sites as ponderosa pine forest (*Pinus ponderosa*, abbreviated as PIPO using the first two letters of the species and genus name) if aspen were present with ponderosa pine as the only conifer species present. If ponderosa pine and Douglas-fir were present in the absence of white fir or subalpine fir, sites were classified as ponderosa pine and Douglas-fir forest (*Pinus ponderosa/Pseudotsuga menziessii*, abbreviated as PIPO/PSME). When white fir or subalpine fir was present with Douglas-fir, sites were classified as Douglas-fir and white fir forest (*Pseudotsuga menziesii/Abies concolor*, abbreviated as PSME/ABCO). PIPO forests were at the lowest elevations, followed by PIPO/PSME and PSME/ABCO forests, but there were overlaps in elevation ranges (Table 1). We randomly selected 5 sites each within PIPO/PSME and PSME/ABCO forests, but only 4 sites within the PIPO forest had enough living overstory aspen to meet our criteria, giving us a total of 14 sites. We accepted fewer samples from live trees to include sites from the PIPO forest, where mortality was so high that only four of the sites with sufficient dead trees had five or more living overstory aspen.

Table 1 Site characteristics for aspen sites sampled in three forest types

Characteristic	Forest type		
	PIPO	PIPO/PSME	PSME/ABCO
Number of sites	2	5	5
Elevation range (m)	2,158–2,2207	2,446–2,716	2,547–2,888
Slope range (%)	4–7	10–43	18–54
Aspects	N, W	Flat, E, W	Flat, N, W
Total BA (m^2 ha^{-1})	24.5 (13.7)	29.6 (3.1)	58.6 (5.1)
Conifer BA	20.0 (12.8)	16.2 (3.3)	25.0 (3.7)
Aspen BA	4.5 (0.9)	13.4 (3.3)	33.6 (5.0)

PIPO Ponderosa pine dominated forest; *PIPO/PSME* ponderosa pine/Douglas-fir dominated forest; *PSME/ABCO* Douglas-fir/white fir dominated forest) in northern Arizona

BA basal area, values reported are mean (standard error); 4 sites were originally sampled in the PIPO forest type, but only 2 sites had live trees with at least 50 years growth and could be used in statistical analyses

Plot design and overstory sampling methods are described in detail in Zegler et al. (2012). Briefly, Zegler et al. (2012) sampled overstory trees on four 8-m radius (~0.02 ha) plots at each site. Overstory trees were defined as those trees ≥10 cm in diameter at 1.37 m above the ground (diameter at breast height, DBH). Trees were permanently marked with metal tags and tree species, DBH, and condition class were recorded. We reclassified the condition classes measured by Zegler et al. (2012) into two classes: live and dead. Trees that we classified as dead fell into the following categories, as classified by Zegler et al. (2012): (1) loose-bark snag, (2) clean-bark snag, (3) snag broken above breast height (BH), (4) snag broken below BH, and (5) dead and down.

Tree-ring analysis

Increment cores were collected from all live aspen trees ≥20 cm DBH and a 10 % random sample of smaller aspen (>5 cm DBH), to sample a minimum of five live aspen cores per site. The majority of live tree cores were collected during initial site visits by Zegler et al. (2012), in 2009 and 2010, although we collected a few supplemental cores in 2012 to bring the sample size up to our minimum of five live aspen cores per site. We revisited the sites in 2012 and collected increment cores from any standing dead aspen or aspen logs that were not too rotten to sample (approximately 10.5 % of snags/logs attempted), for a minimum of 9 and up to a maximum of 15 dead aspen cores per site. We used data collected by Zegler et al. (2012) to ensure that all sampled dead aspen had been dead when the site was initially sampled, in 2009 or 2010. Whenever possible, we took cores at 40 cm above the ground, but occasionally sampled at BH when cores taken from the lower sampling height were too rotten; we recorded the height at which cores were sampled. If a selected tree was too rotten, we sampled the closest aspen tree of similar size (DBH). We attempted to reach pith whenever possible. Because our goal was to investigate relationships between growth and mortality, it was most important to us to have intact outer rings, so we accepted cores that did not reach the pith due to rot, but had at least 50 years of growth preceding the outer ring. When cores were on a slope, we collected cores perpendicular to the slope of the plot to avoid compression wood.

Increment cores were prepared and crossdated using standard dendrochronology techniques (Stokes and Smiley 1968), as described below. All cores were mounted and sanded with progressively finer grit sandpaper, finishing with ANSI 400-grit (20.6–23.6 μm) and then hand-polished using 40, 30, and finally 15 μm sanding film until rings were clearly visible under a microscope. All cores from live trees were visually crossdated, ring widths were measured for a maximum of ten samples for live aspen from each site, and we verified our crossdating using the COFECHA software program (Holmes 1983). Once we had developed a reliable chronology for live aspen trees from each site, we visually crossdated the dead aspen trees. We also measured ring widths for a maximum of ten dead aspen samples at each site and assessed our crossdating against the live samples using COFECHA.

For those trees that either had pith or came within an estimated 20 rings of the pith, we estimated age as the number of rings from pith to the outermost ring. We estimated the number of missing rings using a pith locator based on the curvature of the inner rings (Applequist 1958). Because aspen can elongate to at least 1 m in height in their first growing season (Romme et al. 1995), we did not adjust age for coring height. All ages presented in this study are age at coring height.

We converted ring width measurements to inside-bark basal area increments (BAI) to remove any age-related growth trends, using the dplR package in R (Bunn 2008). As has been frequently shown in studies of tree mortality, BAI is considered a better measure of overall tree growth than ring width because it reliably reduces the trend of declining growth as trees age (Bigler and Bugman 2003, 2004a, b; Biondi and Qeadan 2008). Since conversion from ring-widths to BAI assumes that ring widths decline with age, we examined plots of both raw ring widths and BAI against tree ages for those trees with at least 50 years growth and whose age we could estimate within 20 rings of pith (Table 2). We found that, within a given age class, mean ring width did decline with age and that converting to BAI reduced this age related growth trend; therefore, we concluded that converting ring widths to BAI represented the most appropriate measure of overall tree growth (Appendix S1 in Online Resources).

Comparing lifetime and initial growth

Our first goal was to determine whether lifetime growth patterns differed between trees that ultimately died (henceforth, dead trees) and those that survived (live trees). Secondly, we were interested in testing whether dead trees had higher initial growth rates than live trees. To characterize average lifetime growth of each tree, we calculated mean BAI from the pith to the last annual ring. For comparisons of early growth rates, we summarized average BAI during the first 50 years of each tree's life. We decided to use the first 50 years to represent early growth because previous authors have linked fast growth during this early stage of a tree's life to reduced longevity (Bigler and Veblen 2009; Black and Colbert 2008). To meet assumptions of normality in statistical tests and to reduce the weight of very high BAI values, we transformed our average BAI measurement

Table 2 Sample sizes of aspen increment cores used in growth analyses

Status	Total sampled	Crossdated	Measured	50 years growth, with pith[a]	50 years growth[b]	Aged[c]	100 years growth[d]
Live	267	261	125	35	112	99	67
Dead	166	165	132	44	108	87	56

[a] Trees with at least 50 years of growth and which actually had pith (not estimated) were used to calculate and test differences between live and dead trees' average basal area increment across trees' entire lifespan and the first 50 years of growth

[b] Trees with at least 50 years of growth prior to death (or sample date) were used to calculate and test differences in growth characteristics (average basal area increment and proportion of abrupt declines) between live and dead trees at the end of life

[c] Only those trees with at least 50 years of growth and which had pith (or were within an estimated 20 years of pith) and could be accurately aged were used to develop logistic regression models predicting the probability of aspen survival

[d] Trees with at least 100 years of growth prior to death (or sample date) were used to test long-term differences in growth characteristics between live and dead trees

over each time period (bai_Lifetime, bai_first50) using the natural logarithm (*ln*bai_Lifetime, *ln*bai_first50) (Bigler and Bugman 2003). Since an accurate measure of the initial 50 years of growth requires that all of the first years of growth are present, we restricted this analysis to those trees that actually had pith (not estimated) and at least 50 years of growth (Table 1). Two sites from the lowest elevation forest type (PIPO) had no live trees with 50 years of growth and had to be excluded from all statistical analyses.

We tested for differences in average lifetime growth and average initial growth of live and dead aspen trees using multivariate analysis of variance (MANOVA) (SAS Proc GLM; SAS Institute 2011). Dependent variables were each tree's average lifetime growth (lnbai_Lifetime) and average growth over the first 50 years of life (lnbai_first50). We considered the effects of status (live or dead), forest type (PIPO, PSME/PIPO, and PSME/ABCO), and the interaction between status and forest type.

We used a MANOVA model in order to test multiple dependent variables while controlling for multicollinearity and the overall alpha level. Normality and homoscedasity assumptions were tested graphically prior to fitting the final MANOVA models, which were reduced to only significant factors ($\alpha = 0.05$) in the final model. When overall MANOVA models were significant, we tested for significant differences for each growth interval using separate ANOVAs.

Testing growth differences at the end of life

To compare how growth differed between live and dead trees later in life, we calculated average BAI over seven time-periods of 5, 10, 20, 30, 40, 50, and 100 years prior to death (dead trees). Following the example of Bigler and Bugman (2003), we used the last annual growth ring as the last year in live trees. We also analyzed the data using the mean year of death (2002) as the last ring for live trees, but since the results show the same trends we do not report them here.

In addition to average growth, we also calculated the frequency of abrupt declines, which has been an important predictor of tree mortality in previous studies of growth characteristics preceding tree death (Das et al. 2007; Pedersen 1998). The frequency of abrupt declines was calculated by summing the number of times that BAI declined by more than 50 % from 1 year to the next over each time period (Das et al. 2007; Pedersen 1998). We converted the number of abrupt declines over a given time period to the proportion of years in each time period with an abrupt growth decline (abrupt_last5, abrupt_last10….abrupt_last50), to meet assumptions of normality.

Again, we used multivariate analysis of variance (MANOVA) to test for differences between growth characteristics of live and dead aspen trees and among forest types (SAS Proc GLM; SAS Institute 2011). Dependent variables were the vectors of growth characteristics for each time period preceding death or sampling date (e.g., lnbai_last5, lnbai_last10, lnbai_last20, lnbai_last30, lnbai_last40, lnbai_last50) and factors were status (live or dead), forest type (PIPO, PSME/PIPO, and PSME/ABCO) and the interaction between status and forest type. Separate MANOVA models were fit for the two different growth characteristics (average BAI and abrupt declines).

For this analysis, we did not require trees to have pith, since we were interested in growth rates at the end of life. However, we used only cores with at least 50 years of growth in our analyses. Since we did not need pith, we had a larger sample size than in our analysis of lifetime and initial growth (Table 2) and we averaged the growth characteristics for each individual tree by status and site. Thus, site represented the unit of analysis for this MANOVA ($n = 24$; $n = 12$ site averages for live trees; $n = 12$ site averages for dead trees). As before, we used separate ANOVAs to test for significant differences in each time period when overall MANOVA models were significant.

Using a smaller subset of cores, we also tested differences in growth characteristics between live and dead trees with at least 100 years of growth prior to death. However, since the sample size for trees with at least 100 years of growth was small compared to those with 50 years of growth, we analyzed the 100-year growth differences separately from the other time-periods of growth (see below). None of the trees from sites in the PIPO forests had at least 100-years of growth, so PIPO forests were not included in the analysis of 100-year growth differences. Nine sites had some live and dead trees with at least 100 years of growth.

We tested longer-term (100-year) differences in growth characteristics (average BAI and abrupt declines) between live and dead trees, by forest type, using ANOVA techniques (R Statistical Package; R Development Core Team 2012). Because fewer trees overall ($n = 123$ trees; 67 live, 56 dead) and fewer trees per site had at least 100 years of growth to test, we used individual trees, rather than sites, as the unit of analysis for the ANOVAs and ran the tests separately from the MANOVAs described above. If the ANOVA test for differences in each growth characteristic was significant, we tested pairwise differences between forest types using *t* tests.

Modeling aspen mortality

We applied logistic regression techniques to model the probability of aspen survival, where a probability of one indicated the tree was alive. Independent predictor variables included each of the growth characteristic variables for each time period, live conifer BA (as a proxy for competition with conifer), forest type (PIPO, PIPO/PSME, and PSME/ABCO), tree age and tree DBH at the time of death or at the sampling date for live trees. We randomly split the data into model development ($n = 99$; 53 live, 46 dead) and validation ($n = 87$; 46 live, 41 dead) datasets.

Because we included tree age and DBH in our models, we tested overall differences in these variables between live and dead trees, by forest type, using ANOVA techniques (R Statistical Package; R Development Core Team 2012). We followed significant ANOVAs with pairwise *t* tests for differences among live and dead trees by forest type.

We used Akaike's Information Criterion, adjusted for small sample size ($\mathrm{AIC_c}$), to select both the best univariate growth characteristic models and the most parsimonious combined model (Burnham and Anderson 1998). Our model selection followed methods described by Das et al. (2007). We selected the best two variables for each growth characteristic category (e.g., lnbai_last5, lnbai_last10…., lnbai_Lifetime), as well as any variables within two AIC units ($\Delta\mathrm{AIC_c}$) of the best variable or those with Akaike weights (w_i) of 0.10 or greater. We considered growth characteristics for time periods up to 50 years prior to death or sampling and also included average growth (BAI) over each tree's entire lifetime (lnbai_Lifetime). However, we did not use growth characteristics for the 100-year time period, because restricting the analysis to only trees with at least 100 years of growth would have reduced our sample size by nearly half. Next, we developed models with all the selected variables and any of the additional independent predictor variables (conifer BA, forest type, tree age, tree DBH). Candidate models were restricted such that no model could have more than one growth characteristic category (e.g., no more than one abrupt decline variable). We used the R package glmulti (Calcagno and de Mazancourt 2010) to perform automated model selection using $\mathrm{AIC_c}$ and package AICcmodavg (Mazerolle 2012) to generate tables of $\mathrm{AIC_c}$, $\Delta\mathrm{AIC_c}$ and w_i. Multicollinearity in the independent variables was assessed by calculating variance inflation factors (VIFs) and models were excluded if VIFs exceeded 10 (Neter et al. 1996). We report the area under the receiver operating characteristic (ROC) curve for each model as a fit criterion for model comparison (calculated using ROCR package in R; Sing et al. 2012). The ROC statistic is a measure of the ability of the model to accurately discriminate between classes with values below 0.5 suggesting no discrimination, 0.7–0.8 suggesting acceptable discrimination, and 0.8–0.9 suggesting excellent discrimination (Hosmer and Lemeshow 2000).

To validate our best model, we applied it to the validation dataset and classified trees as dead when the predicted probability fell beneath a specific threshold, which was selected as follows. We determined an "optimal" threshold by plotting the specificity (proportion of correctly classified live trees in the model development dataset) and the sensitivity (proportion of correctly classified dead trees in the model development dataset) curves and selecting the point at which they intersect as the threshold (Hosmer and Lemeshow 2000). Finally, the percent of correctly classified live and dead trees in the validation dataset and the kappa coefficient (κ), a measure of how well the classification performs as compared to random assignment, were calculated for the best model (R package caret; Kuhn 2013).

Results

Aspen overstory mortality was higher in the two lower elevations forest types, PIPO and PIPO/PSME forests than in the higher, more mesic PSME/ABCO forests (see Appendix S2 in Online Resources). Although live conifer basal area did not differ among forest types, live aspen basal area was highest in the PSME/ABCO forests (Appendix S2).

The majority of the dead trees we sampled died in recent decades. Our earliest recorded death date was 1963 and the most recent death date was in 2008. Across all of our sites, the mean death date was 2001, but the modal year of death was 2004. Ninety percent of the sampled snags died since 1991 (between 1991 and 2008), while 63 % died since the

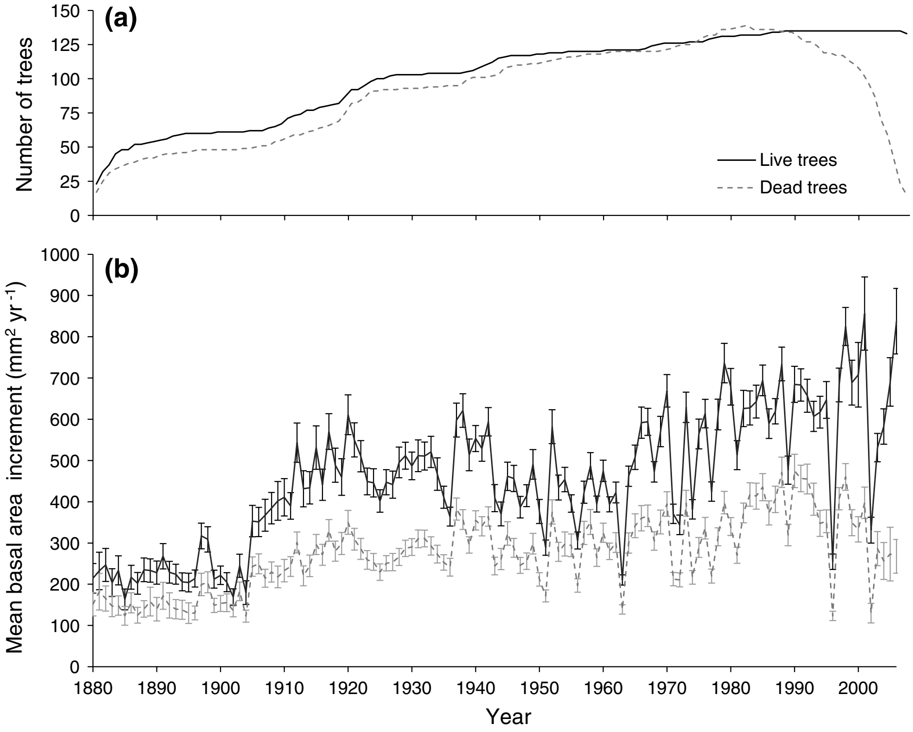

Fig. 1 Time series plots from 1879 to 2006 of live and dead aspen (*Populus tremuloides*) trees for **a** number of measured trees and **b** mean basal area increment (BAI; $x \pm$ SE). We had a total of 135 measured dead trees and 141 measured live trees. For clarity, only the time frame (1879–2006) where we had measurements for at least 10 % of measured live and dead trees (14 trees in each category) is shown

severely dry year of 2002. A major pulse of aspen mortality began around 2000 and continued through 2008.

We sampled a total of 267 live and 166 dead aspen trees, of which we were able to crossdate 261 (98 %) and 165 (99 %), respectively (Table 2). Live and dead aspen trees exhibited large and persistent differences in BAI (Fig. 1). Differences were apparent over approximately 130 years (since 1879). A large increase in mean BAI is apparent in both live and dead trees starting in 1905 (Fig. 1). Although beyond the scope of this study, this rise may be due to the persistent drought conditions of the preceding decade. The Palmer Drought Severity Index—an index of moisture availability where negative values represent drier than average conditions—was negative in every year from 1895 to 1904 and switched to positive in 1905 (Cook et al. 2004).

Lifetime and initial growth differences

Live trees had higher average growth rates across their lifetime and in the first 50 years of growth than dead trees (Fig. 2a, c; MANOVA Wilk's $\lambda_{(2,72)} = 0.67$, $P < 0.0001$). The univariate ANOVAs showed that live trees had higher average growth rates than dead trees for both lifetime growth ($F_{\text{status}} = 18.46$, $P < 0.0001$) and initial growth ($F_{\text{status}} = 4.45$, $P = 0.04$).

The effect of forest type was also significant, with the highest average growth rates in PIPO/PSME forests (Fig. 2; MANOVA Wilk's $\lambda_{(4,144)} = 0.72$, $P < 0.0001$). PIPO/PSME forests also had higher growth rates than the other two forest types in univariate tests for both lifetime growth ($F_{\text{forest type}} = 8.56$, $P = 0.0003$) and initial growth ($F_{\text{forest type}} = 3.88$, $P = 0.02$).

Differences between live and dead trees varied by forest type, with a significant multivariate effect of the interaction between status and forest type (Fig. 2; MANOVA Wilk's $\lambda_{(4,144)} = 0.85$, $P < 0.02$). However, these differences were significant in univariate tests for lifetime average growth rate ($F_{\text{status} \times \text{forest type}} = 0.73$, $P = 0.05$), but not for initial growth ($F_{\text{status} \times \text{forest type}} = 0.95$, $P = 0.39$). The univariate tests revealed that live trees had higher lifetime growth rates than dead trees in both PIPO/PSME (Fig. 2b; $P < 0.004$) and PSME/ABCO (Fig. 2b; $P < 0.0001$) forests when comparison were made within forest types. But, within PIPO forests live and dead trees' lifetime growth rates were the same (Fig. 2b; $P = 1.0$).

Growth differences at the end of life

Later in life, average BAI showed larger and more consistent differences between live and dead aspen trees across time periods than the proportion of abrupt declines (Fig. 3). Live trees in PIPO forests had much higher average BAI in recent years (most recent 5–10 years) than either of the other two forest types, but converged toward average BAI in PIPO/PSME forests over longer time periods.

Live trees had higher average BAI across all time periods than dead trees. Forest type and the interaction between status (live/dead) and forest type were nonsignificant, so

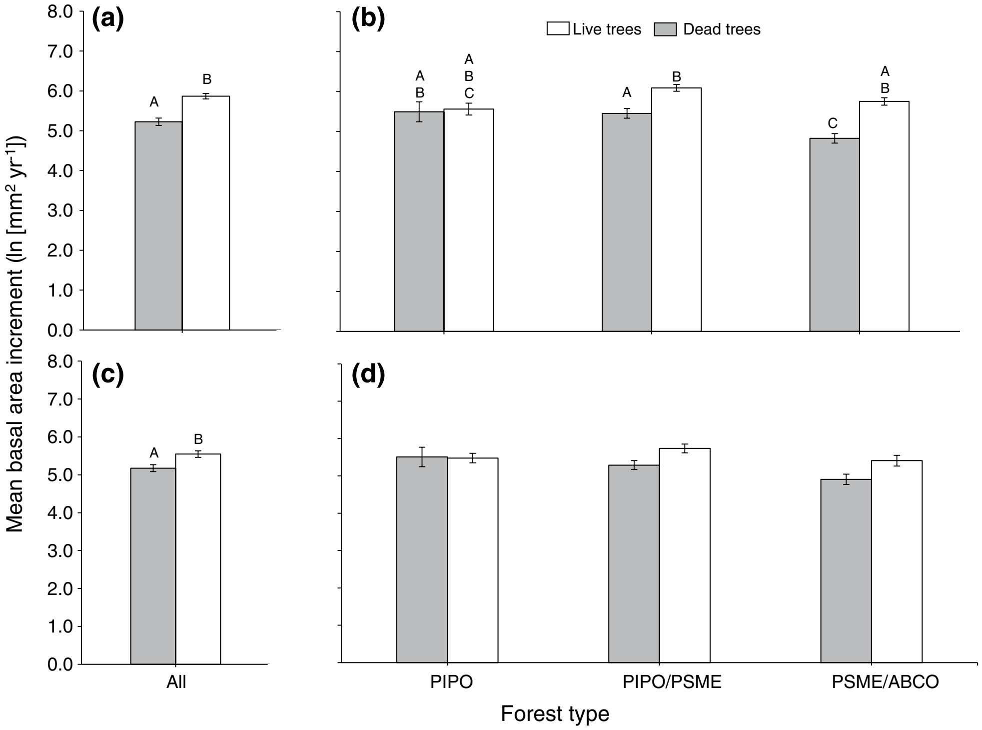

Fig. 2 Differences between live and dead trees in **a** lifetime mean BAI over all forest types, **b** lifetime mean BAI for three forest types, **c** initial (first 50 years) mean BAI over forest types and **d** initial mean BAI for three types. *Bars* Mean ± SE. Mean BAI is shown on a natural logarithmic scale. *Bars* that share a capital letter are not significantly different ($\alpha = 0.05$) from one another. *Letters* denoting significant differences are not shown in *panel* (**d**) because the interaction between forest type and status (live/dead) was not significant for initial growth ($F_{\text{status} \times \text{forest type}} = 0.95$, $P = 0.39$)

they were removed from the MANOVA model. However, differences between live and dead trees' average BAI for each time period were significant (MANOVA; Table 3). Univariate analyses for each time period indicated that live trees' average BAI was higher than that of dead trees across all time periods (Table 3).

There was no difference in the proportion of abrupt declines across tree status (MANOVA Wilk's $\lambda_{(6,13)} = 0.45$, $P = 0.07$), forest type (Wilk's $\lambda_{(12,26)} = 0.48$, $P = 0.49$), or their interaction (Wilk's $\lambda_{(12,26)} = 0.31$, $P = 0.12$). Because none of the factors in the overall MANOVA for abrupt declines were significant, no further multivariate or univariate analyses for each time period were examined.

Dead trees exhibited slower average growth than live tree over long time frames. Dead trees had lower average BAI (by 201.2 mm^2 year^{-1}) than live trees over the 100 years preceding death (ANOVA $F_{(2,\ 120)} = 24.9$, $P < 0.0001$). The effect of forest type was significant ($P = 0.0001$). However, with $\alpha = 0.025$ to control the Type I error rate of conducting two *t* tests, differences between live and dead trees were not significant in PIPO/PSME forests ($P = 0.05$) and significant in PSME/ABCO forests ($P < 0.0001$). In PSME/ABCO forests, the average BAI of dead trees was 182.0 mm^2 year^{-1} lower than that of live trees over the previous 100 years. Differences between live and dead trees in the proportion of abrupt declines during the preceding 100 years were not significant (ANOVA $F_{(2,\ 120)} = 0.54$, $P = 0.58$).

Predicting aspen mortality

Trees that died were generally younger and smaller than those that survived. The average age of dead trees was lower (by 19.5 years) than live trees (*df* = 3, 175; $F = 93.65$; $P < 0.0001$) and the average DBH of live trees was larger (by 8.9 cm) than that of dead trees (*df* = 3,175; $F = 37.2$; $P < 0.0001$). For both age and DBH, the effect of forest type in the overall ANOVAs was significant ($P < 0.0001$ for age; $P = 0.0002$ for DBH), as was the effect of status (live/dead; $P < 0.0001$ for age and DBH). Differences between live and dead trees' ages were driven by the PSME/ABCO forest type, and differences in tree DBH were significant for the PIPO/PSME and PSME/ABCO forest types (see Appendix S3 in Online Resource 1).

The best univariate model of aspen mortality for the average BAI category was average BAI over the past 40 years (lnbai40). Lifetime BAI and BAI over the most recent 10 years had $\Delta\text{AIC}_c > 2$ and $w_i < 0.10$ and were not used to construct multiple variable models. All of the remaining average BAI variables were considered in our multiple variable models. For abrupt declines, the best model was the 5 year time period (abrupt5), followed by the 30 year (abrupt30), 50 year (abrupt50) and 40 year (abrupt40) time periods, which all had $w_i > 0.10$ and were included for consideration in our multiple variable models.

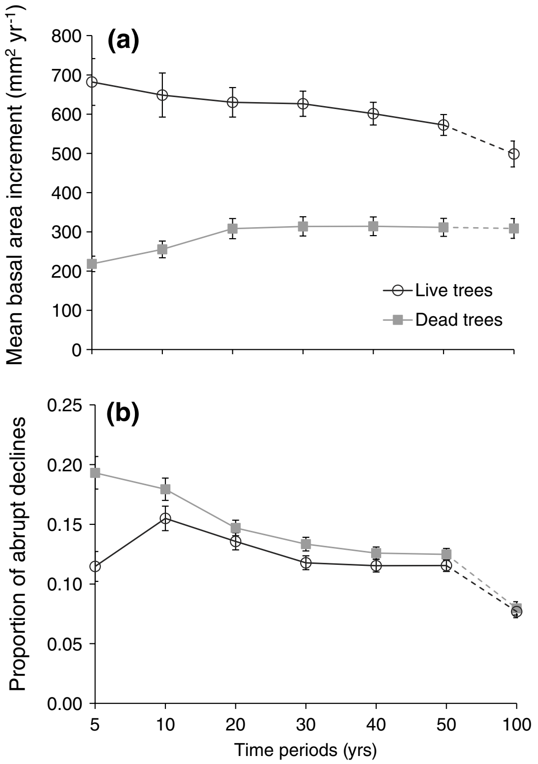

Fig. 3 Temporal trends of live and dead aspen trees, **a** basal area increment ($x \pm$ SE) and **b** proportion of abrupt declines in growth over the 100 years preceding death (dead trees) or sampling (live trees). For the 5–50 year time periods, average values are shown for trees with at least 50 years of growth preceding death (or sample date for live trees; $n = 112$ live trees and $n = 108$ dead trees). *Dashed lines* indicate that a smaller subset of trees were used to calculate average values for this time period because fewer trees had 100 years of growth ($n = 67$ live trees, $n = 56$ dead trees)

Growth patterns in the most recent 5 years were strong predictors of aspen mortality. Five models fell within two AIC$_c$ units of the best model (Table 4). All five of these models included average BAI over the most recent 5 years. In addition, the variables abrupt decline over the most recent 5 years, tree age, and tree DBH were each included in three out of the five best models. Forest type was included in two of the best models. The area under the ROC curve ranged from 0.88 to 0.90 for the best five models, suggesting excellent discrimination among live and dead trees. Multicollinearity was not apparent in any of the best models (VIF < 3.0).

The selected model included average BAI and abrupt declines over the most recent 5 years, as well as age (Table 5). When applied to the validation dataset, this model had an overall accuracy of 77 % and $\kappa = 0.54$. The model correctly classified 85 % (35/41) of dead trees and 70 % (32/46) of live trees at a threshold level of 0.59.

Discussion

The relationship between tree growth and mortality is used widely to predict risk of tree mortality. A large number of studies have reported a decline in growth rates in the years preceding the death of an individual tree (Bigler and Bugman 2004b; Das et al. 2007; Ogle et al. 2000; Pedersen 1998). Another commonly reported relationship is the trade-off between high growth rates at the beginning of a tree's life and reduced longevity (Bigler and Bugman 2004a; Bigler and Veblen 2009; Black and Colbert 2008). We present here an analysis of the relationship between an individual aspen tree's lifetime growth patterns and mortality.

Differences in average growth between live and dead aspen were apparent over both long and short time periods,

Table 3 Results of multivariate analysis of variance (MANOVA) test for differences in average growth rates (natural log of basal area increment) between live and dead trees across different time periods in 12 sites ($n = 12$ site averages for dead trees, $n = 12$ site averages for live trees; $df = 23$)

	Overall MANOVA	Univariate ANOVAs					
		5 years	10 years	20 years	30 years	40 years	50 years
SS type III[a]		6.58	4.21	3.28	3.05	2.73	2.38
Wilk's λ	0.334						
F	5.66	17.83	11.59	8.41	9.69	9.7	9.68
p	0.002	0.0004	0.0025	0.0083	0.0051	0.0051	0.0051

Only trees with at least 50 years of growth prior to death (sample date in live trees) were included. Because the MANOVA test was significant at $\alpha = 0.05$, results of univariate ANOVAs for status (live/dead) (Type III sums-of-squares, status: live/dead) for each time period are also shown

[a] Type III sums-of-squares for the model (status: live/dead)

Table 4 Logistic regression results for the five best performing models of aspen mortality based on growth characteristics for a given time period

Model	*df*	AIC_c^a	ΔAIC_c^b	w_i^c	Area under ROC curve[d]
lnbai5 + abrupt5 + age	88	85.87	0.00	0.47	0.89
lnbai5 + age	89	86.94	0.07	0.09	0.88
lnbai5 + abrupt5 + age + DBH	87	87.27	0.35	0.07	0.90
ForType + lnbai5 + abrupt5 + DBH	87	87.38	0.52	0.07	0.90
ForType + lnbai5 + DBH	88	87.69	0.89	0.06	0.89

Variables in models: *lnbai* mean natural log transformed basal area increment, *abrupt* proportion of years with abrupt declines, tree *age* (years), *DBH* diameter at breast height (cm), *ForType* forest type

Models were developed using a subset of the data ($n = 99$; $n = 53$ live and $n = 46$ dead) by combining variables from the best single variable models, with the restriction that no more than one variable from each growth characteristic category (mean BAI and abrupt declines) could be included in a model

[a] Akaike's information criterion; corrected for finite sample size

[b] ΔAIC_c = Difference in AIC relative to the best model

[c] w_i = AIC weights, which represent the probability that the given model is the best model

[d] Area under the ROC curve, a fit criterion where 0.5 indicates no discrimination, 0.7–0.8 indicates moderate discrimination, and >0.8 represents excellent discrimination (Hosmer and Lemeshow 2000; Das et al. 2007)

Table 5 Estimates of model coefficients for the best performing logistic regression model of the probability of aspen mortality (1 = live; 0 = dead)

	Estimate	SE	Pr (>|z|)	G^2	*df* [a]	*P*
(Intercept)	−13.21	2.93	<0.0001	49.736	3	<0.0001
ln_bai5	1.80	0.40	<0.0001			
Abrupt_prop5	−3.17	1.78	0.0744			
Age	0.03	0.01	0.0007			

Reported results include the difference in deviance between the best model and a model including only the intercept term (G^2), degrees of freedom (*df*) and *P* value for a Pearson χ^2 test for how well the model fits the data relative to a model including only the intercept

[a] Degrees of freedom (*df*) for the Pearson χ^2 test are calculated as the difference between the *df* for a model with only the intercept (*df* = 91) and the *df* for the best model (*df* = 88)

extending across entire tree life spans and sometimes as far back as 100 years prior to death. Across all stages of a tree's life, live aspen trees had higher growth rates than trees that ultimately died. For the years leading up to tree death, our results support previous work in other tree species linking reduced growth in the years prior to death to an increased probability of mortality (Bigler and Bugman 2004b; Das et al. 2007; Ogle et al. 2000; Pedersen 1998). However, our findings that live trees had higher lifetime and initial average growth rates than dead trees contradict previous work suggesting a trade-off between growth rates and longevity (e.g., Bigler and Bugman 2004a; Black and Colbert 2008; Johnson and Abrams 2009).

For shade-tolerant conifers, rapid average growth during the first 50 years of the tree's life reduced tree longevity, possibly as a result of trade-offs between growth and defense (Bigler and Veblen 2009). Our results suggest the opposite trend for aspen, with slow growth over long time frames leading to increased mortality. Even when comparing the first 50 years of growth, trees that died had slower growth rates than those which survived. For fast-growing, shade-intolerant species like aspen, investment in rapid growth may provide a stronger advantage than investment in defense (Bigler and Bugman 2003).

A major limitation of many forest succession models is the lack of species-specific, empirically derived relationships between growth and tree mortality (Bigler and Bugman 2004b; Keane et al. 2001). Although models that use size-dependent mortality functions may be able to produce the negative relationship between tree growth rate and longevity observed for many tree species (Manusch et al. 2012), our results indicate the need for implementation of different mortality functions for trees with different life history strategies. For some pioneer species, like aspen, slow growth at various stages in the tree's lifecycle is linked to a higher probability of mortality.

Although aspen tree mortality differed by forest type (Appendix S2), variation in growth rates was related more strongly to whether trees had died or survived than to differences among forest types. Only lifetime average growth rates differed by forest type, early growth rates and growth rates in all the time periods prior to death were similar across forest types. These results are consistent with previous work in other tree species suggesting that reduced growth in the years preceding death is a reliable predictor of mortality (e.g., Bigler and Bugman 2004b; Das et al. 2007; Ogle et al. 2000; Pedersen 1998), but our results showed a much longer growth difference than has been reported previously. Longer-term differences in growth between live and dead trees, extending 20–25 years prior to death, have been documented in Norway spruce (*Picea abies*), white fir, and oak-hickory forests (Bigler and Bugman 2004a; Das et al. 2007; Pedersen 1998). Similar to our study, Kane (2012) found growth differences between live and dead aspen up to 50 years prior to death. Our record of tree measurements extended further back in time than any previous study of aspen growth and mortality and documented persistent differences in average growth for 50–100 years prior to the present, as well as over the entire lifespan of the trees.

Predicting tree mortality

Short-term growth characteristics are also associated with aspen mortality. Aspen mortality was correlated with lower average growth and higher variability in growth (frequency of abrupt declines) in the most recent 5 years, as well as with younger age. Our results indicate that trees with lower recent (past 5 years) growth were more likely to die. Similar to our findings, the most recent 5 years of growth was an important predictor of aspen mortality in models for three of ten sites in Colorado (Hanna and Kulakowski 2012) and was an important predictor in three of the four best models of aspen mortality in northern Arizona mixed-conifer forests (Kane 2012). Our model's success rate at classifying live and dead aspen trees (77 % overall accuracy) is similar to those of Hanna and Kulakowski (2012; 72 % overall accuracy) and Kane (2012; live trees: 75–77 %; dead trees: 76–84 %).

Trees that had died experienced more abrupt growth declines than surviving trees, as indicated by the inclusion of the frequency of abrupt declines in the past 5 years as an important predictor in our best model of aspen mortality. Multiple drought events in a short period of time, such as the 2000 and 2002 drought events, may stress trees that are already growing slowly to the point that they cannot recover, causing death. Abrupt growth declines have been found to improve predictions of tree mortality models in previous work (Das et al. 2007; Pedersen 1998). In mixed-conifer aspen forests, the frequency of abrupt declines over the most recent 20 years was an important predictor of aspen mortality (Kane 2012).

Dead trees were younger than live trees, a result consistent with findings from Colorado (Hanna and Kulakowski 2012). However, differences in age between live and dead trees in our study area were associated primarily with PSME/ABCO forests and not the other two forest types. Although age was not a significant predictor of aspen mortality in overall aspen models in Colorado, it was an important predictor at four out of the ten sites studied (Hanna and Kulakowski 2012). Age differences between live and dead trees could be a sampling artifact resulting from decay that prevented us from adequately sampling the age range of dead trees. Dead trees were more likely to be rotten in the center, so our data could be biased toward trees that were smaller and younger when they died. Although we were able to crossdate some very old trees (oldest live tree: 231 years, oldest dead tree: 199 years), we may not have a complete sample of the age range of trees that died.

We found that dead trees were smaller than live trees for the two higher elevation forest types (PIPO/PSME and PSME/ABCO). Aspen DBH was an important predictor of aspen mortality in three out of ten sites in Colorado, but not in overall aspen mortality models (Hanna and Kulakowski 2012). Although our results show some parallels with those of Hanna and Kulakowski (2012), it is worth noting that other studies of aspen mortality have not found a relationship between aspen mortality and either tree size or age (Worrall et al. 2008). The larger size of live trees could be a result of their higher growth rates, on average, or that they had more years of continued growth than the trees which had died (Hanna and Kulakowski 2012).

Since we found no significant differences in conifer basal area between forest types (see Appendix S2), there may not have been enough variability in conifer basal area for it to be an important predictor of aspen mortality in our sites. Across sites, conifer basal area ranged from 1 to 34 m^2 ha^{-1}, with an average basal area of 10 m^2 ha^{-1} (standard deviation = 10 m^2 ha^{-1}). But, average conifer basal area by forest type ranged from 13 to 25 m^2 ha^{-1}, with an average basal area of 18 m^2 ha^{-1} (standard deviation = 10 m^2 ha^{-1}).

Conclusions and management implications

Growth patterns of individual trees are strong predictors of whether an individual tree will survive. Forest managers who wish to predict aspen mortality for a stand would need at least some rough estimate of growth rates, such as an estimate of BAI over the past 5–10 years calculated from an increment core in the field, to apply our models. Managers could find other important variables such as tree size, age, or forest type in forest inventory data. However, average BAI or the frequency of abrupt declines were included in all of our best models, emphasizing the importance of measuring these variables to accurately predict aspen mortality.

Two different trajectories of aspen decline may be occurring within our study area. Long-term aspen decline, driven largely by successional processes, competition, and fire exclusion (Romme et al. 1995) could account for most of the aspen mortality in the higher elevation PSME/ABCO forests. In these forests, trees that died exhibited slower long-term growth and were smaller and younger than trees that survived, suggesting that mortality could be driven by intraspecific competition and shading. The high rates of overstory mortality in the lower elevation forest types and strong associations between recent (5-year) growth characteristics and death suggest that SAD may be most important here. Zegler et al. (2012) also suggested that overstory aspen mortality was consistent with both long-term gradual decline and SAD.

Since our study area lies near the southern edge of aspen's distribution in North America, recent aspen tree mortality and reductions in aspen growth, especially in the lower elevation forest types, may be indicative of aspen's response to future climate change. Most instances of recent aspen dieback in North America occurred in areas projected to be outside of aspen's distribution under future climate scenarios (Rehfeldt et al. 2009; Worrall et al. 2013). As climate change progresses and moisture availability decreases in the Southwest, climatically suitable aspen habitat is projected to decrease at the southern edge of its distribution (Worrall et al. 2013).

Climate change may slow average growth rates in the future. Trees with higher average growth rates were better able to recover from pronounced periods of growth reduction. So, the identification of trees with higher average growth rates and management strategies aimed at maintaining these individuals may offer a means of mitigating the potential effects of future climate change on aspen forests in the Southwest. Testing different management strategies will be important to maintaining aspen forests in the face of future drying trends. One possibility might be to experimentally reduce tree density in different combinations of the conifers and some of the smallest, slowest-growing aspen trees in aspen stands in an attempt to promote increased growth of the remaining trees.

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