

Full length article

Effects and etiology of sudden aspen decline in southwestern Colorado, USA

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ABSTRACT

Sudden aspen decline (SAD), affecting *Populus tremuloides*, was first observed in Colorado in 2004. By 2008 it affected at least 220,000 ha, an estimated 17% of the aspen cover type in the state. In southwestern Colorado, we examined site and stand features in paired healthy and damaged plots to assess the effects of SAD on aspen and to identify factors associated with decline. Root mortality increased significantly with recent crown loss. Consequently, density of regeneration did not increase as the overstory deteriorated, and regeneration that originated since 2002 decreased significantly in stands with moderate to severe SAD. However, mortality of regeneration did not increase with that of the overstory. Remeasurement of a subset of plots after 1–2 yrs showed significant increases in severity. Contrary to expectations, overstory age and diameter were not related to SAD severity as measured by recent crown loss or mortality. Severity of SAD was inversely, but weakly, related to basal area, stem slenderness, and site index, and positively related to upper slope positions. This is consistent with moisture stress as an underlying factor. To test the role of climate as an inciting factor for SAD, a landscape-scale climate model was used to compare moisture status of declining and healthy aspen at the height of the warm drought in water year 2002. Polygons identified as damaged aspen in the 2008 aerial survey had greater moisture deficits than healthy aspen in the 2002 water year. SAD has led to loss of aspen cover in some stands, and is occurring in areas where early loss of aspen due to climate change has been predicted. Further warm, dry growing seasons will likely lead to recurrence of SAD.

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1. Introduction

Rapidly increasing branch dieback and mortality of trembling aspen (*Populus tremuloides*) was first noted in southwestern Colorado in 2004 (Worrall et al., 2008). By 2006 it was observed by aerial survey on 56,091 ha of Colorado. Because the disease appears to be a decline in the strict sense, has appeared suddenly and progressed rapidly, and to distinguish it from what has been widely termed “aspen decline,” we named it “sudden aspen decline” (SAD). SAD is characterized by rapid, synchronous branch dieback, crown thinning and mortality of aspen stems on a landscape scale, without the involvement of aggressive, primary pathogens and insects. Preliminary evidence suggested that affected stands may fail to produce suckers in response to the crown loss and mortality (Worrall et al., 2008). Similar damage to aspen apparently began several years earlier in Arizona (Fairweather et al., 2008) and southern Utah (Ohms, 2003; Bartos, 2008). Branch dieback, growth loss and mortality of aspen in the aspen parkland and southern boreal forest of

Alberta and Saskatchewan increased following a severe drought in 2001–2002 (Hogg et al., 2008).

Etiology of decline diseases is often complex and can be considered in three categories (Manion, 1991; Manion and LaChance, 1992). Predisposing factors are long-term, static or slowly changing factors such as site or stand conditions. Inciting factors are short-term physiological or biological factors that cause acute stress. Trees affected by inciting factors alone may recover quickly, but recovery is much slower if the damage is exacerbated by predisposing factors. Finally, contributing factors, or proximate causes, kill trees that have been debilitated by predisposing and inciting factors. We proposed a decline disease model for SAD as follows (Worrall et al., 2008). Predisposing factors included low elevations, south/southwestern aspects, physiological maturity, and low stand density. Inciting factors were acute drought with high temperatures during the growing season. Contributing factors were insects and pathogens that tend to invade and kill stressed trees, as opposed to those capable of attacking otherwise healthy, vigorous stems. In previous work, we provided direct evidence for several predisposing factors and reported putative contributing agents commonly found in affected stands, including *Cytospora* canker (usually caused by *Valsa sordida*), aspen bark beetles (espe-

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cially *Trypophloeus populi*), poplar borer (*Saperda calcarata*), and bronze poplar borer (*Agrilus liragus*). Here, we provide additional evidence for predisposing and inciting factors and better characterize the impacts on aspen stands.

Our objectives were to: (a) determine the effects of SAD on aspen stands, their regeneration, and their roots; (b) better characterize the etiology of SAD by identifying associated fine-scale site and stand factors; and (c) test the hypothesis that SAD was incited by a severe, hot drought.

2. Methods

Our primary approach was intensive sampling of neighboring healthy and damaged plots, measuring a broad range of variables that could be related to occurrence of SAD. Because the distribution and landscape factors were already identified (Worrall et al., 2008), this paired design was chosen to eliminate confounding variables, such as those frequently observed with changes in elevation, making plots as similar as possible except in fine-scale site and stand factors that might be related to SAD. In addition, to test the drought hypothesis, we used a landscape-scale climate model that incorporated aerial survey, vegetation maps, and historic weather data to calculate moisture deficits in healthy and declining aspen across the landscape.

2.1. Aerial survey

Aerial surveys were conducted as described previously (Worrall et al., 2008). In 2008, criteria for recording aspen dieback and mortality were made more uniform and SAD was recorded in three categories: low, dieback or thin crowns with no mortality; moderate, with mortality $\leq 50\%$; and high, with mortality $> 50\%$. For estimation of the proportion of cover type affected, area of the cover type for Colorado (1,314,257 ha) was obtained from USDA Forest Service, Forest Inventory and Analysis, and that of the ranger districts that we sampled (359,201 ha) was obtained from each national forest.

2.2. Plot sampling

The field study was conducted in 2007 and 2008 on four national forests in southwestern Colorado: Gunnison, Grand Mesa, Uncompahgre, and the Mancos-Dolores Ranger District of the San Juan. Using the aerial survey from 2006 (for 2007 sampling) and 2006/2007 (for 2008 sampling), damaged sample points were randomly selected within polygons identified as aspen decline and within 1.0 km of a road. Healthy sample points were then selected as near as possible to each damaged point, but at least 200 m away. In preliminary reconnaissance of polygons identified with aspen decline in aerial survey, it appeared that 25% recent crown loss of a stand was the approximate minimum threshold for detection and recording in aerial survey. Therefore, we established that as the dividing line between damaged and healthy plots in our study.

At each point, a preliminary prism plot and crown loss estimate was done to verify that the plot met sampling criteria: (a) no evidence of damage by fire; (b) minimum aspen basal area of $2 \text{ m}^2 \text{ ha}^{-1}$; (c) aspen was the leading species in basal area; and (d) for healthy plots, $\leq 25\%$ recent crown loss, and for damaged plots, $> 25\%$ recent crown loss. When points did not meet criteria, we evaluated the nearest 30-m grid point that appeared to be satisfactory. At each accepted point, we recorded the actual location with a global positioning system and slope position.

We identified the three shrub species and three herb species with the greatest cover and recorded the average height and percent cover of each. Regeneration ($> 0.3 \text{ m}$ tall but $< 12 \text{ cm}$ DBH) of tree species was measured in a 100 m^2 circular plot centered at

the point. Each tallied stem was recorded by species, live or dead, and size class (small: 0.3–1.4 m tall; medium: $> 0\text{--}3 \text{ cm}$ DBH; large: $\geq 3\text{--}12 \text{ cm}$ DBH). In a subsample of 62 plots, we aged three stems of each regeneration size class if available.

Trees $\geq 12 \text{ cm}$ DBH were recorded in variable-radius (prism) plots. We used 1, 2, or 3-BAF metric prisms, attempting to include 10–19 stems in the plot. For each included stem, we recorded species, DBH and, for aspen, recent crown loss.

Recent crown loss of aspen was estimated as the percent of foliage that was apparently lost, either due to branch and twig dieback or crown thinning. Old, dead branches, defined as those without fine twigs or with $< 50\%$ of bark intact, were not considered as part of the crown for this estimate. Dead trees with no recently dead branches were recorded as old snags and were not included in crown loss estimates; dead trees with any recently dead branches were recorded as 100% crown loss. Plot crown loss was determined by averaging that of live and recently dead aspen in the plot. Based on measurements of crown dimensions vs. DBH and the properties of prism sampling, we found that averaging crown data from a variable-radius plot provides a good estimate of the status of the overall canopy (data not shown).

Four dominant or codominant aspen stems were systematically selected for increment coring and height measurements. Those with stem decay were avoided. Where suitable trees were not in the plot, neighboring trees were selected. Heights were measured with a digital laser rangefinder/hypsometer. Cores were mounted in blocks with the vessels vertical and sanded progressively to 600-grit sandpaper before counting rings under a stereo-zoom microscope (Asherin and Mata, 2001). Difficult cores were stained with phloroglucinol before aging (Patterson, 1959). Site index was calculated for each tree using the formula of Edminster et al. (1985), with a base age of 80 yr, and averaged to obtain a plot value. Slenderness coefficient was calculated as the ratio of height to DBH (Wang et al., 1998).

Aspen roots $\geq 4 \text{ mm}$ diameter were measured with a root trench (Shepperd et al., 2001) adjacent to the plot center. Trenches were 3 m long and 20 cm deep. The diameter and condition (live or dead) of each intercepted aspen root were recorded. Live roots were identified by their light tan inner bark; dead roots have dark brown inner bark. By modifying van Wagner's (1968) formula for volume of wood in fuel transects, we calculated the root length per unit area of soil surface (R , m/m^2) as:

$$R = \frac{(\pi^2 / (8L)) \sum d^2}{(\pi/n) \sum (d^2/4)} = \frac{\pi n}{2L}$$

where d is root diameter (m), n is the number of roots encountered, and L is the transect length (m).

Soil conditions were assessed with a standard soil pit (Schoeneberger et al., 2002). We recorded the depth, color, texture, mottling, and proportion and size class of coarse fragments of each soil horizon. From these data, we classified the soil to subgroup and texture class (Soil Survey Staff, 2006), and calculated water-holding capacity.

In 2009, we revisited 31 healthy plots and 35 damaged plots to determine progression of SAD. We remeasured recent crown loss for each tree and determined a new plot average of recent crown loss.

2.3. Climate moisture index

To test the hypothesis that the warm drought was an inciting factor for SAD, we compared moisture availability between declining and healthy aspen in the four national forests of the study area. We used polygons of aspen decline from the 2008 aerial survey. A healthy aspen layer was generated by clipping out the decline poly-

gons from an aspen cover-type layer (Worrall et al., 2008). As an index of moisture availability, we used the climate moisture index (CMI) approach of Hogg (1997). CMI is precipitation minus potential evapotranspiration, expressed in mm water, and is an index of moisture surplus or deficit. Annual CMI was determined as the sum of monthly values. Using ArcGIS 9.3, monthly PRISM climate data on a 4-km grid (Daly et al., 2009), and elevation from a digital elevation model with 30-m resolution, we calculated CMI on a 60-m grid for the 2002 water year (October 2001–September 2002), the driest and hottest year of the drought (Pielke et al., 2005). After confirming that it gave the same results as the more complex Penman–Monteith formula, we used the simplified formula of Hogg (1997) incorporating a corrected calculation of vapor pressure deficit (E.H. Hogg, personal communication) to calculate monthly CMI for each point:

$$\text{CMI} = P - (93Dc e^{A/9300})$$

where

- P is the monthly precipitation (mm);
- $D = 0.5(e_{T_{\max}}^* + e_{T_{\min}}^*) - e_{T_{\text{dew}}}^*$ (vapor pressure deficit in kPa), where
 - $e_{T_{\max}}^* = 0.61078e^{(17.269T_{\max}/(237.3+T_{\max}))}$ (saturation vapor pressure at T_{\max});
 - $e_{T_{\min}}^* = 0.61078e^{(17.269T_{\min}/(237.3+T_{\min}))}$ (saturation vapor pressure at T_{\min});
 - $e_{T_{\text{dew}}}^* = 0.61078e^{(17.269T_{\text{dew}}/(237.3+T_{\text{dew}}))}$ (saturation vapor pressure at T_{dew});
 - T_{\max} and T_{\min} are mean monthly maximum and minimum temperatures ($^{\circ}\text{C}$);
 - T_{dew} is mean monthly dew point, estimated as $T_{\min} - 2.5$ ($^{\circ}\text{C}$).
- c is a cold-temperature reduction factor based on $T_{\text{mean}} = 0.5(T_{\max} + T_{\min})$. When:
 - $T_{\text{mean}} \geq 10$ $^{\circ}\text{C}$, $c = 1$;
 - 10 $^{\circ}\text{C} > T_{\text{mean}} > -5$ $^{\circ}\text{C}$, c is reduced linearly from 1 to 0;
 - $T_{\text{mean}} \leq -5$ $^{\circ}\text{C}$, $c = 0$;
- e is the base of the natural logarithm;
- A is elevation in meters.

For each national forest, we then calculated the mean CMI of all the grid points that fell in aspen decline polygons and those that fell in healthy polygons.

2.4. Statistical analyses

Generally, our analyses were designed to detect differences in healthy vs. damaged plot pairs or trends of variables with recent crown loss. Statistix 9.0 (Anonymous, 2008) was used unless noted otherwise. Paired, two-tailed t -tests were used for comparing one continuous variable in healthy vs. damaged plots. When more than two groups were being compared, ANOVA with post hoc Tukey's HSD or LSD all pairwise comparison tests were used to test differences in the means of the groups. Linear regression was used to compare trends in two continuous variables, most often using recent crown loss as the dependent variable. For all tests, $\alpha = 0.05$.

To classify plots into vegetation types, we conducted ordinations using TWINSpan (Hill and Šmilauer, 2005). In the ordinations, presence/absence of plant species was used to separate plots; tree species were given twice the weight of shrubs and herbs. Three divisions were used to produce eight vegetation types.

Multivariate analyses were conducted with stepwise linear regression and best subset regression. Recent crown loss was the dependent variable; site and stand characteristics were the independent variables. For categorical variables, indicator (dummy) variables were used. Candidate independent variables were first

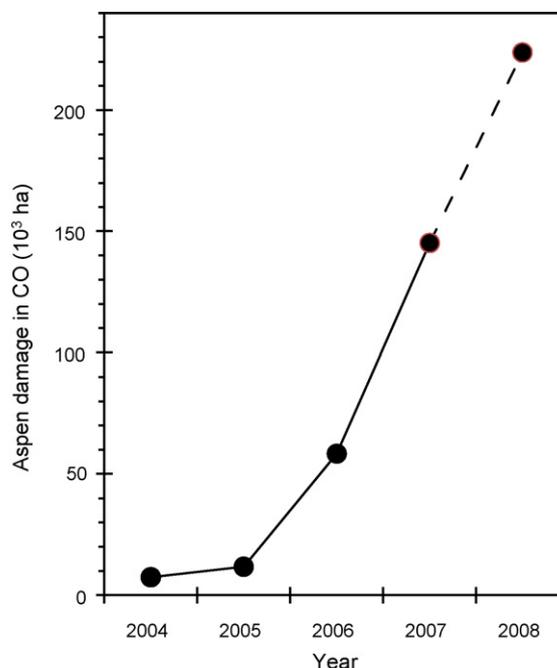


Fig. 1. Area of aspen damage recorded by aerial survey in Colorado, 2004–2008. A dashed line is used between 2007 and 2008 because the aerial survey methods changed in 2008 and trends including that year may be less reliable.

tested with stepwise linear regression in various combinations using both forward selection and backward elimination with an entrance and exit P -value of 0.05. Because there were inconsistent results from the stepwise linear regression, variables that were significant in any analysis were then used together in best subset regression. The best models were chosen based on three factors: (a) $C_p < \text{number of variables} + 1$; (b) $\text{AIC}_c - \text{Min AIC}_c$ between 0 and 2, showing good support for the model; and (c) an adjusted R^2 closest to 1 (Anonymous, 2008).

Because climate moisture index and aspen condition were obtained for the entire study area, the means and standard deviations are population parameters rather than sample statistics. Therefore, hypothesis testing was not conducted.

We completed 162 plots (81 pairs) over the two years of sampling. Two anomalous damaged plots that did not fit the pattern of SAD were removed from analyses. One was a riparian site that was flooded with standing water at the time of sampling and no soil pit could be dug. The stand had 91% crown loss, 63% recent mortality, was relatively old (overstory ages ranged from 161 to 174 yrs), sooty-bark canker (a primary pathogen not associated with SAD) contributed substantially to mortality, and live aspen regeneration was $31,400 \text{ ha}^{-1}$, far exceeding any other plot. The other had severe insect defoliation that caused most of the recent crown loss (total recent crown loss 36%) and no dead roots. These are agents that attack vigorous trees, rather than secondary, stress-related agents that typically function as contributing factors. Normal SAD agents (Worrall et al., 2008) were nearly absent. In one additional plot, no cores could be reliably aged, so data involving age are based on 159 plots.

3. Results

3.1. Effects of SAD on aspen

3.1.1. Area, crown loss, and change

Area of aspen damage recorded in aerial survey increased steadily each year from 2005 through 2008 (Fig. 1). In 2008,

when SAD was recorded in three levels of severity, Colorado had 243 ha of low, 121,001 ha of moderate, and 97,934 ha of severe, for a total of 219,178 ha of SAD. This is equivalent to 17% of the aspen cover type. The 4600 additional hectares for 2008 in Fig. 1 were affected by defoliating insects and other damage agents. In the ranger districts where we established plots, SAD was recorded on 68,047 ha in 2008, or 19% of the aspen cover type.

The mean recent crown loss of healthy plots was 10.9% (SE 0.4) and that of damaged plots was 53.9% (SE 1.4). Total mortality (including old snags) in the two kinds of plots was 7.3% (SE 0.7) and 45.3% (SE 1.6), respectively. A histogram of crown loss showed an approximately normal distribution among healthy plots, centered at the mean (data not shown). If the threshold between healthy and damaged plots had been set too high, we would expect a mean crown loss at the low end of the healthy plots, with a tail on the right where damaged plots were included. A slight tail in the distribution suggests that some of the “healthy” plots may have been in the early stages of decline but had not crossed the threshold.

This was confirmed by remeasurements of plots. In 2009, we remeasured recent crown loss in a subsample of 31 healthy and 35 damaged plots. Recent crown loss increased significantly in both healthy and damaged plots (Fig. 2). In healthy plots, recent crown loss increased from 10.6% in 2007 to 16.0% and from 11.2% in 2008 to 14.2% (Fig. 2). Two healthy plots crossed the 25% threshold for being considered damaged. In 2007, they had 20 and 24% recent crown loss, but in 2009 they had 43 and 35%, respectively. In damaged plots, recent crown loss increased from 50.6% in 2007 to 59.4% and 53.0% in 2008 to 60.8%. In damaged plots, when only trees that were alive in the first measurement were included, the increases are much greater. Almost all trees with >70% crown loss in the first measurement were dead in 2009.

3.1.2. Roots and regeneration

Root condition was strongly connected with condition of the overstory. Compared to healthy plots, damaged plots had significantly lower mean length of live roots and greater length of dead roots (Fig. 3A). A regression of recent crown loss on root mortality showed a highly significant relationship, with root mortality explaining about 29% of the variation in crown loss (Fig. 3B).

Density of live aspen regeneration did not differ significantly between healthy and damaged plots (Table 1). However, the Gunnison National Forest showed a tendency for higher regeneration on damaged plots than on healthy plots ($P=0.054$). Similarly, live aspen regeneration did not increase with recent crown loss. With all regeneration size classes grouped together, the trend was flat with a mean of 2968 stems ha^{-1} ($P=0.71$, $R^2 < 0.001$). There was also no response of regeneration to recent overstory mortality alone ($P=0.48$, $R^2 = 0.003$).

None of the three size classes of aspen regeneration showed any significant trend with crown loss (Fig. 4). There was some evi-

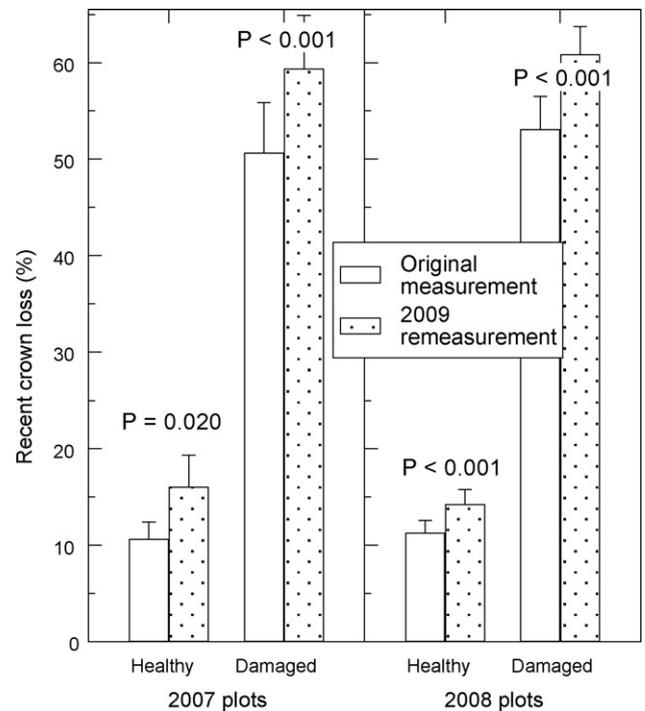


Fig. 2. Recent crown loss (with standard error) in a subsample of plots that were remeasured in 2009. Original measurements were in 2007 and in 2008, and means for healthy and damaged plots are reported separately. For 2007 plots, bars are the means of 13 healthy and 16 damaged plots; for 2008, 18 healthy and 19 damaged plots. Values with each pair of bars are P-values from paired, two-tailed t-tests comparing original and 2009 measurements. Trees that were recently dead in the first measurement are included.

dence of moderately higher density of small regeneration in plots with 25–35% crown loss. When only damaged plots are considered, regeneration tended to decrease with increasing crown loss (Fig. 4). This relationship was weak, but significant for small and medium regeneration.

SAD did not significantly affect mortality of regeneration. For all size classes of regeneration, mortality in damaged plots was slightly, but not significantly, higher than that in healthy plots (Fig. 5). Comparisons among size classes were not tested because the residence time of dead standing stems probably varies greatly among the classes. However, it appears that in healthy plots, mortality of regeneration is higher than that in the overstory, while in damaged plots, mortality of regeneration is lower than in the overstory.

Mean ages of small, medium and large regeneration were 3.5 yrs (SE 0.2, $n = 172$), 7.7 yrs (SE 0.4, $n = 144$), and 27 yrs (SE 0.9, $n = 136$), respectively. The small class contained some relatively old stems (up to 11 yrs) whose height had been kept low by repeated browsing. The percentages of stems older than 6 yrs in the small, medium and large classes, respectively, were 8.7, 50, and 100%.

Table 1

Mean density (stems ha^{-1}) of live aspen regeneration (30 cm tall to 12 cm DBH) in healthy and damaged plots, by forest. P-Values indicate results of paired, two-tailed t-tests between healthy and damaged plots.

National forest	Healthy plots ($\leq 25\%$ crown loss)	Damaged plots ($> 25\%$ crown loss)	P	n
Grand Mesa	3467	3519	0.973	42
Gunnison	1712	3729	0.054	34
San Juan ^a	2904	3527	0.251	52
Uncompahgre	2507	1860	0.471	30
Mean of all plots	2722	3252	0.310	158

^a On the San Juan National Forest, only the western portion (Mancos-Dolores Ranger District) was included.

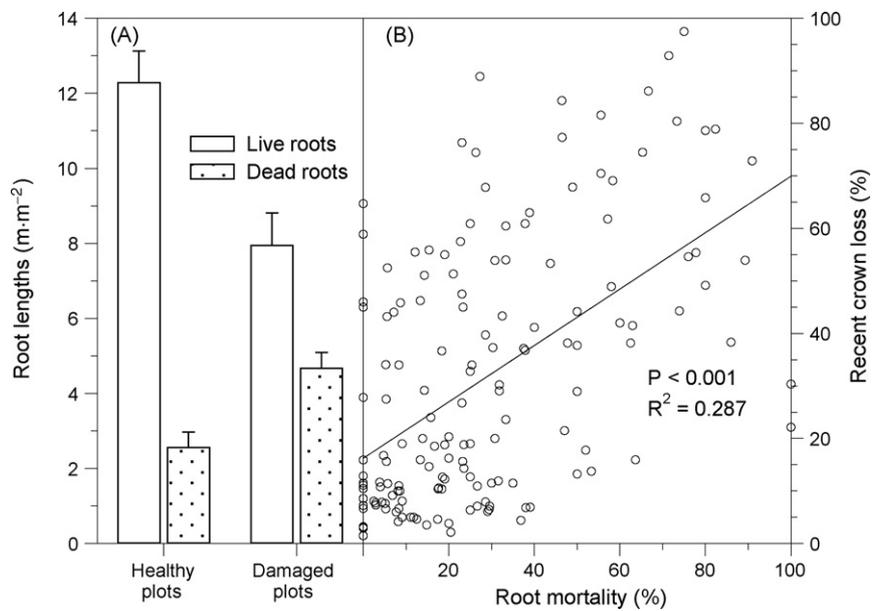


Fig. 3. (A) Mean length, with standard error, of live and dead aspen roots in healthy and damaged plots. Length of live roots is significantly less and that of dead roots significantly greater in damaged than in healthy plots (both $P < 0.001$; $n = 81$ healthy and 79 damaged plots). (B) Relationship between recent crown loss and root mortality (based on root lengths; $n = 156$ plots).

3.2. Stand, site, and climatic factors

3.2.1. Stand factors

The mean basal area (all live and dead standing stems) of healthy plots ($34.5 \text{ m}^2 \text{ ha}^{-1}$) was significantly greater than that of damaged plots ($28.7 \text{ m}^2 \text{ ha}^{-1}$; $P = 0.014$ from paired t -test, $n = 158$ plots). A regression showed that recent crown loss decreased significantly as basal area increased, but basal area explained only a small part of the variation in crown loss ($P = 0.009$, $R^2 = 0.042$). Crown loss and mortality also decreased with increasing stem density, but those relationships were not significant (not shown). Basal area of conifers in the plots was unrelated to recent crown loss ($P = 0.76$, $R^2 < 0.001$). Most plots had no conifers in the overstory, violating the assumption of normality, but examination of the remaining plots also showed no relationship.

Age of the overstory was unrelated to severity of crown loss. Age of dominant and codominant stems ranged from 23 to 219 yrs, with a mean of 99.5 yrs. Plot means ranged from 41 to 174 yrs. Recent crown loss on plots did not vary significantly with mean age (Fig. 6A). The same was true when using the oldest stem in the plot to represent age, and also when using individual stems rather than plots as variates (not shown). Age also was not significantly different between healthy and damaged plots when compared using a paired, two-tailed t -test ($P = 0.316$). Mean age did increase significantly with elevation ($P < 0.001$, $R^2 = 0.232$). Plot elevations ranged from 2355 to 3320 m.

Mean DBH of aspen ≥ 12 cm DBH in the plot was also unrelated to recent crown loss ($P = 0.50$, $R^2 = 0.003$). Similarly, the within-plot ratio of DBH of recently dead and dying stems (25–100% crown loss) to that of healthy stems was unrelated to plot crown loss (not shown).

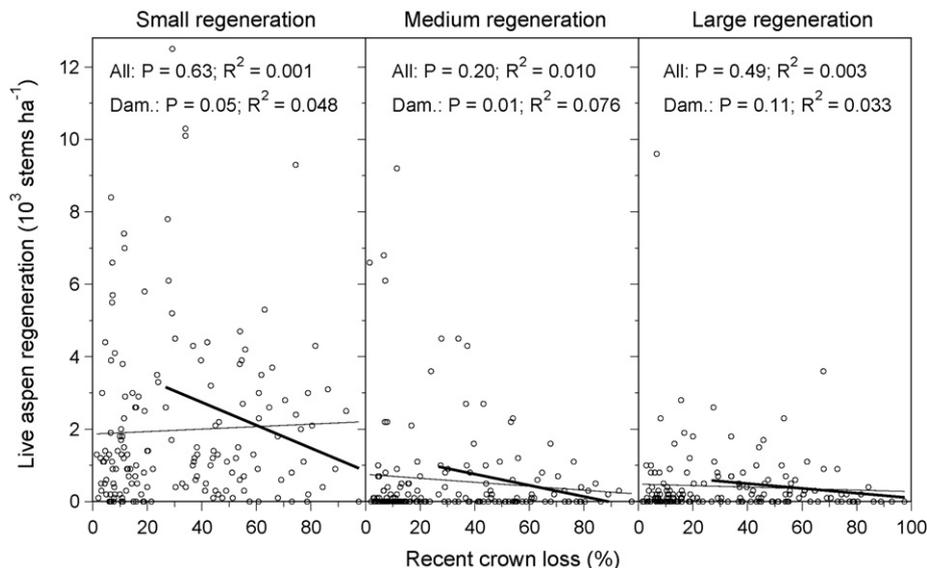


Fig. 4. Density of live aspen regeneration in three size classes vs. recent crown loss. Regression lines and associated statistics are shown for all plots (thin lines, $n = 160$) and for damaged plots only (bold lines; recent crown loss $> 25\%$; $n = 79$). Class sizes are: small, 30 cm to 1.4 m tall; medium, 0–3 cm DBH; large, 3–12 cm DBH.

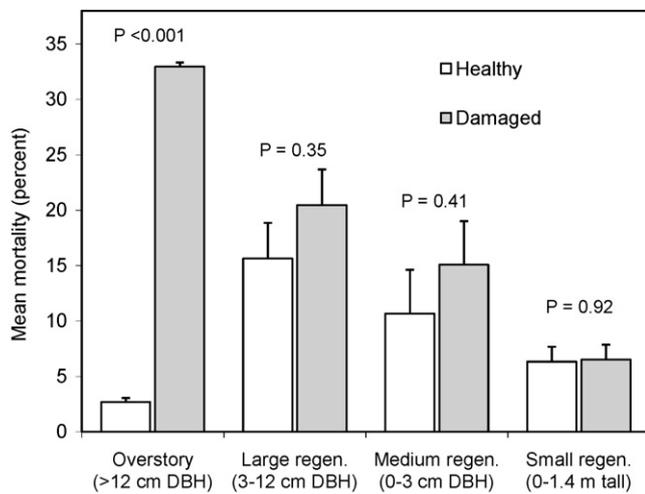


Fig. 5. Recent mortality (mean of plot values with standard error) in the overstory vs. mortality in three size classes of regeneration, in healthy and damaged plots. Healthy and damaged plots were compared within each size class by a paired, two-tailed *t*-test. For each pair of bars, $n = 159, 104, 87,$ and 144 plots, respectively.

However, plots with high variance in DBH tended to be less affected by SAD than plots with uniform DBH. A regression of recent crown loss on plots on the standard deviation of aspen DBH was negative and significant, though it accounted for a small amount of the variation in crown loss ($P = 0.016, R^2 = 0.036$). Thus, as variation in DBH within plots increased, recent crown loss tended to decrease.

Slenderness coefficient (ratio of height to diameter) was significantly, negatively related to recent crown loss (Fig. 6B). Height alone was also highly significant and negative ($P < 0.001, R^2 = 0.089$). The relationship between site index and recent crown loss was similar (Fig. 6C), indicating that plots with low site index tended to have high crown loss. However, slenderness coefficient explained somewhat more variation in recent crown loss (higher R^2). Slenderness was closely related to site index ($P < 0.001, R^2 = 0.44$).

Ordination of vegetation resulted in eight vegetation types. Tukey's all pairwise comparisons test found no significant differences among them in recent crown loss. However, the following type was a significant indicator variable in multivariate analysis (see Section 3.2.3).

The highest crown losses (mean 46%) were in a vegetation type characterized by *Juniperus communis*, *Arctostaphylos uva-ursi*, and *Festuca thurberi* in the first ordination; and *Symphoricarpos rotundifolius*, *Achillea lanulosa*, and *Pinus ponderosa* in the second ordination. Mean annual precipitation was low in this type and it occurred at intermediate elevations, ranging from 2636 to 3045 m. It was represented by 13 plots.

The lowest crown losses (mean 21%) were in a vegetation type that was in the same class as above in the first ordination, but characterized by *Rosa woodsii* and *Mahonia repens* in the second ordination, and *Picea engelmannii* and *Carex* spp. in the third ordination. Mean annual precipitation was intermediate, but it occurred at the highest elevations of all subtypes, ranging from 3005 to 3320 m. It was represented by 8 plots.

Shrub height and cover increased with recent crown loss, although the relationships were weak (height $P = 0.016, R^2 = 0.036$; cover $P = 0.031, R^2 = 0.029$).

3.2.2. Site factors

We tested many soil variables, including some estimated directly in the soil pits and others derived from soil pit data. None were significantly related to recent crown loss. These include soil classification at the great group and subgroup level, percentage of coarse fragments, water-holding capacity of the soil profile to various depths, depth of organic horizon, depth of a mollic horizon, mollic classification (nonmollic, mollic, or pachic-mollic) and percentage of clay. There was a trend suggesting that soil moisture regimes had an effect, with aquic (moist) regimes having lower recent crown loss and ustic (dry) regimes having higher recent crown loss. However, we did not have enough information to confidently classify all soil pits by moisture regime.

Recent crown loss showed a clear, consistent relationship with slope position (Fig. 7). There was a gradient of crown loss along the sequence of slope positions from a maximum at summit positions to a minimum at toeslope positions. Slope position reflects local, fine-scale topography, not elevation patterns.

3.2.3. Multivariate analyses

The results from the final best subset regression were adjusted $R^2 = 0.378, C_p = 1.4,$ and $AIC_c - \text{Min } AIC_c = 0$. The included variables were stem slenderness, shrub cover, root mortality, live root length, and the indicator variables for summit slope position and the dry vegetation type with the highest crown loss, as described above.

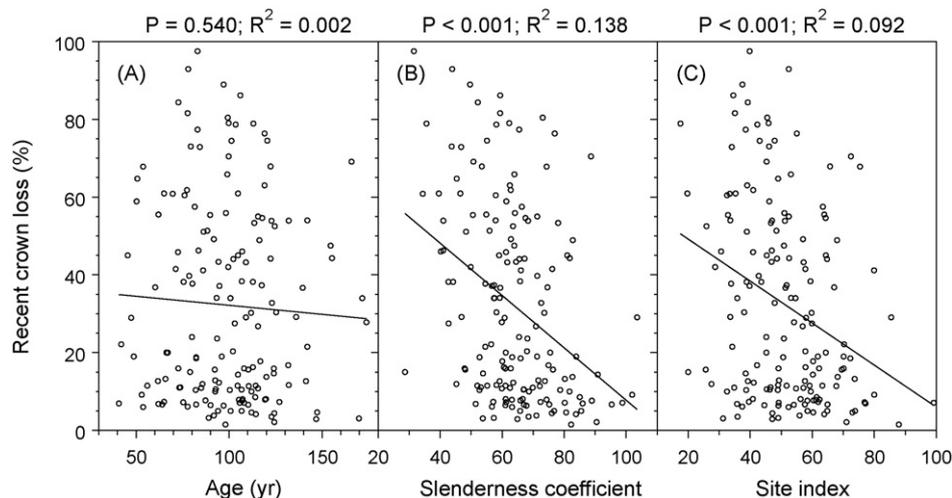


Fig. 6. Regression of recent crown loss on (A) age, (B) slenderness coefficient and (C) site index. Each point represents a plot; $n = 159$ plots. The three variables on the x-axes are the means for dominant and codominant trees from which increment cores were taken and heights measured; recent crown loss is the mean value for all aspen stems ≥ 12 cm DBH, except old snags, in the variable-radius plot. Site index is based on age of 80 yrs.

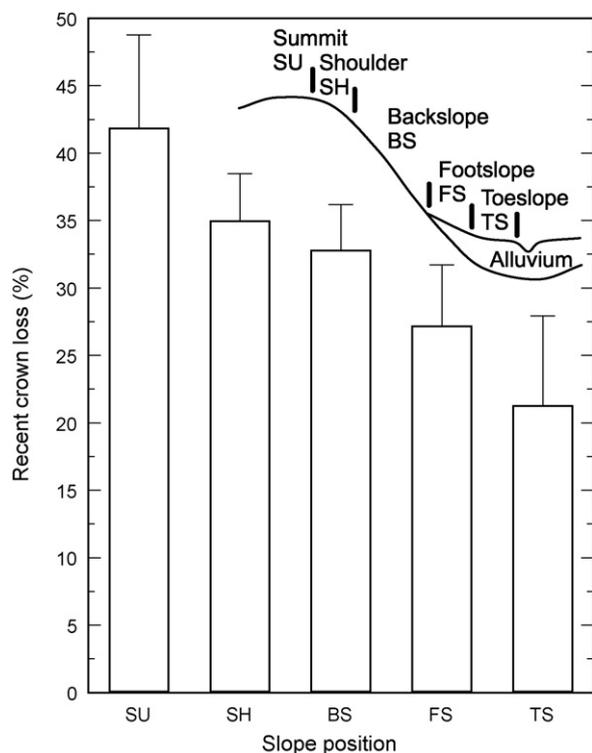


Fig. 7. Recent crown loss (with standard error) in relation to slope position. The drawing is a key to the slope positions. At $\alpha = 0.05$, Fisher's LSD showed a significant difference in crown loss between summits vs. toeslopes, but Tukey's HSD showed no significant differences. Bars represent the means of 14, 51, 53, 30 and 14 plots from left to right, respectively.

Table 2

Mean climate moisture index (and standard deviations) for water year 2002 on four national forests in aspen that was healthy vs. damaged in 2008.

National forest	Climate moisture index (cm water)		
	Healthy	Moderate damage	High damage
Grand Mesa	-14.2 (13.3)	-17.0 (15.0)	-15.7 (16.8)
Gunnison	-29.7 (15.4)	-30.1 (15.0)	-33.7 (16.0)
San Juan ^a	-36.4 (13.5)	-43.9 (7.4)	-45.0 (10.4)
Uncompahgre	-33.1 (12.8)	-37.1 (10.8)	-41.0 (11.0)

^a On the San Juan National Forest, only the western portion (Mancos-Dolores Ranger District) was included.

The root variables noted above contributed consistently to significant models, but these are considered part of the symptoms of SAD rather than as true independent variables that might reveal why some stands are declining and others healthy.

3.2.4. Climate moisture index of 2002 and subsequent decline

Mean CMI values for the 2002 water year were negative in all cases, meaning an overall water deficit in aspen forests (Table 2). On all national forests, aspen that later showed decline had lower CMI values (greater moisture deficits) than aspen that remained healthy. The San Juan National Forest had the lowest CMI values for both healthy and declining aspen and the greatest differences between healthy and declining stands. On all forests except the Grand Mesa, areas recorded in aerial survey with high damage had greater moisture deficit than areas with moderate damage.

4. Discussion

In the field survey, the damaged plots were a random sample from areas identified by aerial survey (constrained by road

proximity). However, the healthy plots were not a random sample of healthy aspen, and therefore data from healthy plots do not represent all healthy cover type. Also, because plots and the CMI analysis were restricted to southwestern Colorado, the results may not apply to SAD in other areas.

4.1. Effects of SAD on aspen

4.1.1. Area, crown loss, and change

The aerial survey showed a large, consistent, annual increase in area affected by SAD beginning in 2005. Several caveats must be considered in interpreting these data. First, this was a new type of damage, and awareness and focus of aerial surveyors increased beginning in 2005. Therefore, the damage is underrepresented in the first few years. Second, in every year, portions of the aspen cover type were not surveyed, so the data here are underestimates. Third, the criteria for mapping this aspen damage were made more uniform in 2008, so trends including 2008 are less reliable than usual trend information from aerial survey.

Indeed, most foresters and forest health workers in southwestern Colorado did not observe large new areas affected by SAD on the ground in 2008 and 2009 as they had in previous years. This suggests that the area affected is approaching a maximum. If SAD was incited chiefly by the severe, warm drought earlier in the decade, as the evidence indicates (Worrall et al., 2008; Rehfeldt et al., 2009), and precipitation and temperatures remain at moderate levels, the progress of SAD should eventually stop as stressed trees succumb and the associated disease and insect epidemics run their course. In retrospect, SAD will then be perceived as a large, synchronized, region-wide pulse of mortality over a period of 5–10 yrs. On the other hand, if summer temperatures and the frequency of drought increase, as predicted (Core Writing Team et al., 2008), SAD will likely recur.

Although area affected may be approaching a maximum, our remeasurements of a subsample of plots, as well as data from another study (Smith and Shepperd, personal communication), indicate that crown loss continues in affected stands. Stems that had 30–80% crown loss in the original measurement showed the largest increases on remeasurement. Individual healthy trees generally did not change much, and trees near death simply did not have far to go. This increase in damage represents the continued loss in vigor and death of affected stands, aided by the biotic contributing factors.

Our study area had 19% of the aspen cover type affected by SAD, comparable to 17% statewide. However, the figure for our area includes only national forest land. Lower-elevation land with aspen outside the national forests likely had a higher percentage (Worrall et al., 2008). In calculating the percentages, we used the area of aspen cover type as the basis. However, it is possible that a small portion of the decline recorded in aerial survey was outside the cover type, where aspen was a minority component. This means that, like the area of decline, the area of the sampled forest could be a slight underestimate.

4.1.2. Roots and regeneration

There was a significant, positive relationship between root mortality and recent crown loss. However, it is not clear which comes first and drives the other, or whether they occur simultaneously. There was a dense spread of plots with elevated root mortality up to about 40%, but with healthy canopies (Fig. 3B). Elsewhere in the root mortality–crown loss space, plots were more uniformly distributed, the two measures increasing broadly together. This pattern suggests that root mortality initially precedes substantial canopy loss, but at later stages of decline, the two factors increase together. Indeed, the decline concept of Manion (1991) suggests that root mortality generally precedes crown symptoms. Once root

mortality begins to affect the canopy, a downward spiral of positive feedbacks between the above- and belowground portions is likely as the physiological system deteriorates.

The increase in root mortality with overstory deterioration is relevant to the lack of regeneration response. Several studies have shown that suckering ability of live, excised roots does not differ significantly between healthy and deteriorating clones (Schier, 1975; Schier and Campbell, 1980; Ohms, 2003); nor is there a relationship between carbohydrate or other storage reserves and number of suckers initiated (Frey et al., 2003). Instead, suckering is related to the amount of live roots in the soil (Shepperd et al., 2001). Thus, the lack of regeneration response in deteriorating plots is due to lower live root lengths in damaged plots and an increase in root mortality with canopy deterioration. Subsequent growth of suckers is strongly correlated with carbohydrate reserves (Frey et al., 2003), and roots under stressed, dying stems likely are depleted in such reserves.

There are two approaches to evaluating and interpreting the regeneration data for damaged plots. The first is to compare it to regeneration in relatively healthy, intact stands to see if there is increased suckering in response to overstory deterioration. The answer is unequivocally negative. The lack of increased regeneration in plots with increased levels of crown loss and mortality indicates that suckering has not increased with deterioration of the overstory. These results, from 160 plots widely scattered across southwest Colorado, were nearly identical to those based on only two nearby sites earlier (Worrall et al., 2008). With catastrophic disturbance, such as fire or cutting, regeneration density in southwestern Colorado increases from a background level in intact stands of about 2500 stems ha^{-1} to 70,000 or more stems ha^{-1} in 1 yr (Crouch, 1983), far above the levels observed in our plots. The somewhat elevated density of small regeneration in plots with 25–35% crown loss may indicate that some stands with minor damage from SAD begin to sucker, but stands with higher levels of damage do not. When only damaged plots are considered, the significant decrease in small and medium regeneration with increasing crown loss confirms the general failure of regeneration response.

The second approach is to compare regeneration densities in damaged plots to densities cited in the literature as being minimally adequate to replace a stand. The literature on this point is mostly speculative and often based on even-aged stands and density at a certain size or age. For example, DeByle (1985) stated that 1000 stems ha^{-1} are needed when they reach a height of 4 m. This corresponds with our large size class of regeneration, which averaged about 400 stems ha^{-1} . Sampson (1919) recommended at least 6200 stems ha^{-1} at 3 yr or 1 m tall. This size corresponds with our small size class, which averaged about 2100 stems ha^{-1} . Mueggler (1989) stated that mature, undisturbed stands would likely experience regeneration problems if they contained less than 1235 suckers ha^{-1} (suckers were defined as stems less than 1.4 m tall). However, this would require most suckers to survive to maturity (our healthy plots had a mean aspen density of 777 stems ha^{-1} , including live and dead stems ≥ 12 cm DBH), which may be unrealistic, or substantially more suckers to be produced as the overstory deteriorates, which our stands showed no signs of doing. Bartos and Campbell (1998) used the same density of regeneration (1235 stems ha^{-1}) as a risk factor for aspen-dominated landscapes, but applied it to stems 1.5–4.6 m tall. This size range includes our medium and large classes, which together had an average of 900 stems ha^{-1} in our study. Kurzel et al. (2007) considered stands to be self-replacing if they had either ≥ 2500 stems ha^{-1} of small regeneration (<1.5 m tall) or ≥ 100 stems ha^{-1} of a size class from 1.5 m tall to 20 cm DBH. By these criteria, 21% of our plots would be considered non-self-replacing. In summary, depending on the guidelines, many to most of the stands we studied may

have inadequate regeneration to replace the deteriorating overstory. But because of variations in attrition, it is difficult to predict the adequacy of any absolute density of regeneration. For example, the 1988 fires in Yellowstone National Park resulted in a mean of 38,000 suckers ha^{-1} in spring of 1990, but recruitment of large stems was not expected because of heavy elk browsing (Romme et al., 1995). Another problem with this approach is defining what replacement means; based on management objectives this could be anything from a fully stocked stand to one stem of the clone surviving to maturity.

What are the implications of low regeneration to establishment of a new stand? Frey et al. (2003) point out that, because juvenile stands within a range of stem densities often converge to a common density, it is often assumed that initial sucker density is not critical for stand establishment. However, high initial densities maintain more of the clonal root system, limit competing vegetation, provide more uniform distribution, and have higher rates of growth than low initial densities (Frey et al., 2003). High initial densities also provide insurance against attrition due primarily to browsing, but occasionally to insects and pathogens. Thus, in the presence of high browse pressure, diseases, insects, or interspecific competition, low levels of suckering may result in shrub fields with scattered aspen, or complete loss of aspen from a site.

Mortality of regeneration was not affected by SAD as was that of the overstory. Although mortality of large and medium regeneration was slightly elevated in damaged plots, mortality in none of the size classes differed significantly between healthy and damaged plots. Thus, roots were not responding to overstory loss with additional suckers, but the suckers that were present were relatively healthy.

Similarly, young, regenerating patches of aspen appear to be healthy. We did not sample regenerating stands dominated by stems <12 cm DBH, but it has been widely observed by silviculturists and others that aspen regenerating after patch cuts in the last 30 yrs is consistently healthy, even when surrounded by dead and dying residual overstories (C. McKenzie and M. Krabath, personal communication). Consistent with a decline disease, juvenile aspen, whether in a regenerating stand or in the understory of a SAD stand, appear to be much less affected by SAD than the overstories > 12 cm DBH.

We aged regeneration primarily to estimate the proportion of each size class that arose after 2002, the worst and presumably most damaging year of the drought. None of the large size class, about half of the medium, and 90% of the small size class originated after 2002. Thus, some suckering continued in many plots after the worst of the drought, but numbers of suckers have not increased following crown loss and mortality. This is consistent with the ephemeral nature of young aspen suckers: most do not survive (Jones, 1974). Although some suckers arose after the drought, most of even the small suckers probably arose before the recent overstory mortality, which began around 2004 and continued during the study.

4.2. Etiology of SAD

4.2.1. Predisposing factors

Based on our hypothesis that moisture stress due to warm drought was an inciting factor, we predicted that SAD would be associated with low site index, poor soils, exposed sites, dry vegetation types, open stands, and old, large stems.

Several site and stand factors were consistent with the hypothesis. Low site index was associated with SAD, as predicted. Thus, SAD tended to occur on sites that have supported relatively poor growth of aspen in the history of the current stand, suggesting that site factors may be predisposing.

The clear trend of increasing severity of SAD with upper slope position follows the prediction that drought-associated dieback would occur on exposed, xeric sites (Frey et al., 2004). Compared to lower slope positions, upper slope positions generally have lower soil moisture availability and are more exposed to the drying effects of sun, higher temperatures, and wind. Although the trend was consistent, differences were significant only at the extremes of summits vs. toeslopes. Similarly, the significance of the dry vegetation type with the highest crown loss in the multivariate analysis suggests a role of moisture stress and site conditions.

Greater shrub growth and low basal area were associated with crown loss, consistent with open stand conditions associated with SAD (Worrall et al., 2008). Open stands are more exposed to drying conditions from sunlight and wind. Low basal area could be an effect of SAD, but low basal area often follows low site index (Jones et al., 1985), suggesting that it is more likely connected with a cause. Recent crown loss was also negatively, though weakly, correlated with tree slenderness. Drought-associated aspen decline was hypothesized to increase with tree slenderness (Frey et al., 2004), based on the rationale that taller trees would have more difficulty with hydraulic conductivity and greater penetration of stands by the drying effects of sun and wind. However, at least in our study area, slenderness and site index were tightly correlated: good sites produce tall, slender stems; both factors are negatively related to SAD.

Several factors did not correlate with SAD as expected. Even at low elevations, healthy aspen is often found near damaged aspen, all presumably with similar climates. In cases where elevation, aspect, slope position, site index, and basal area do not account for the difference, we expected that plots might be differentiated by overstory age, diameter, or soil characteristics.

The lack of relationships of aspen age and size to SAD (considering only stems ≥ 12 cm DBH) was somewhat unexpected. It has been widely speculated that SAD is partly an expression of the old age of many aspen stands. However there were no differences in age between healthy and damaged plots. Physiological maturity is one factor that leads to declines according to the decline concept of Manion (1991). This is consistent with the fact that understory trees (<12 cm DBH) and recent clear cuts did not experience mortality to the same degree as the overstory. Among overstories, however, ranging from 41 to 174 yrs in mean age, there were no relationships of age to crown loss or mortality.

The increase in age with elevation actually contradicts the hypothesis that SAD is an expression of old age, because SAD is more prevalent at low elevations. We observed healthy aspen over 200 yrs old at high-elevation mesic sites.

Similarly, DBH of stems ≥ 12 cm DBH was unrelated to SAD. Although our early data from two sites in southwestern Colorado suggested that the within-stand ratio of DBH of dying trees to healthy trees increased with increasing levels of mortality (Worrall et al., 2008), this larger study did not confirm that. However, we did find that plots with large variation in DBH tended to be healthier. We found no relationship between conifer density and crown loss, suggesting that succession is not a driving force in SAD.

Another factor may be responsible for local variation in occurrence of SAD in some cases. Ohms (2003) suggested genotypic variation may play an important role in determining susceptibility to climatic conditions. Observations suggest that occurrence of SAD does seem to vary with apparent clonal boundaries (M. Krabath, personal communication). If this is the case, identifying, conserving, and promoting expansion of clones with tolerance to such conditions may be important in building resilience to extreme climatic conditions in the future.

4.2.2. Climate and SAD

In each national forest, aspen that showed decline in 2008 had experienced a greater mean moisture deficit than healthy aspen during the extremely warm, dry conditions of 2002. The area with the most severe moisture deficit was the area where decline was first noticed in southwestern Colorado and where, as of 2006, decline was most severe (Worrall et al., 2008). The effects of heat and drought, which together contribute to moisture deficit, are more pronounced on exposed, upper slope positions, southern aspects, low elevations, open stands, and poor sites, all of which are associated with occurrence of SAD. Greater moisture deficit in areas of high damage than in areas of moderate damage on all forests except the Grand Mesa is also consistent with the relationship between CMI and SAD. Earlier, we showed that the Grand Mesa also had an anomalous relationship between elevation and occurrence of SAD, with a peak of SAD occurring at high elevation (Worrall et al., 2008). This was related to the droughty soils in the unique landslide bench near the upper rim of this large landform. Precipitation and thus CMI tend to increase with elevation, which may explain why the pattern was reversed here.

The drought of 2002 was not unique in terms of precipitation, but the high temperatures that accompanied it made it an extreme drought in terms of vegetation impacts (Pielke et al., 2005). For this reason, it has been characterized as a global-change-type drought (Breshears et al., 2005). Beginning in fall of 1999, weather was already so warm and dry that 2000 was the most severe wildfire season recorded to date in the western USA, but September 2001 to August 2002 was more extreme. It was the driest such period on record for just over half of representative stations scattered through Colorado, with stations in some months receiving less than 10% of average precipitation. In the 2002 water year, most stations had precipitation 1–3 standard deviations below average. Temperatures in forested areas of the state during this period were below average in March, but otherwise ranged up to 3.5 °C above average, with many record high temperatures. The wildfire season started 5–6 weeks before normal; Colorado had the largest fire and the most acres burned in the state's records (http://www.nifc.gov/fire_info/fire_stats.htm), River flows in the state were the lowest or near the lowest on record, with an estimated 436-yr return interval, and tree rings were the narrowest in 150 yrs or more (Pielke et al., 2005). Breshears et al. (2005) compared the drought to the previous severe, subcontinental drought of the 1950s and found that this one was slightly wetter but considerably warmer, especially during summers.

The moisture-related predisposing factors reported here and elsewhere (Worrall et al., 2008), together with the CMI results, suggest that the warm drought of 2002 was a primary inciting factor for SAD. Recent work (Rehfeldt et al., 2009) has provided strong additional evidence, as well as showing that SAD is consistent with losses of aspen predicted based on climate change: (a) 2002 had the most extremely unfavorable climate based on indices of climate favorability for aspen; (b) sites where SAD is occurring are at the fringe of aspen's realized climate niche; (c) the lower elevation of climate suitable for aspen in the southern Rocky Mountains is expected to rise 250 m by 2030 and 750 m by 2090; and (d) predictions based on aspen's climate profile and climate change scenarios suggest that 76% of sites with SAD in 2006 will be outside aspen's climate profile by 2060. We repeated the latter analysis for Colorado and southern Wyoming using SAD mapped from 2003 to 2009 and Rehfeldt et al.'s model data. We found that 82% of SAD occurred where all models agree that the climate will be unsuitable for aspen by 2060 (unpublished). The corresponding figure for the San Juan National Forest was 92%. Thus, although a particular weather event at a particular place and time cannot be definitively connected to a very large-scale, long-term phenomenon like global

climate change, this drought had characteristics of weather events anticipated under climate change, and had impacts consistent with those predicted from climate change.

Although extremely warm, dry conditions are involved, some alternative hypotheses on the mechanism of decline cannot be ruled out. For example, low snow accumulation during winter and/or early snowmelt may lead to freezing damage to roots, as has been documented in Alaska yellow-cedar decline (Hennon et al., 2006). Indeed, site and stand factors that would predispose to drought are also consistent with a root-freezing hypothesis. Physiological experiments and field measurements may be needed to distinguish among these and other potential mechanisms of decline.

5. Conclusion

SAD was first noted in 2004, but has rapidly increased in area, affecting over 17% of the aspen cover type in Colorado and 19% in our study area. However, observations in southwestern Colorado suggest that spread of SAD may now have slowed or stopped. Within affected areas, mortality and crown loss have resulted in loss of about half the canopy on average, with crowns continuing to deteriorate and die. The damage, especially at low elevations, is severe and unprecedented in our experience, but most of the cover type in Colorado is still relatively healthy. Even in declining stands, complete mortality is still uncommon.

The evidence implicates an extremely warm drought as the major inciting factor in this episode of SAD. Predisposing factors documented here and elsewhere (Worrall et al., 2008) point to moisture stress as an underlying factor. Our CMI analysis and the modeling of Rehfeldt et al. (2009) provide more direct evidence that the warm drought of 2002 was a primary inciting factor.

In light of the low levels of regeneration, increased root mortality, and increased shrub cover and height in damaged plots, we conclude that some severely affected stands are likely to convert to other vegetation types, especially where herbivory is intense. On the other hand, most affected areas had some aspen regeneration, and, unlike mature overstories, mortality of regeneration was not affected by SAD.

In stands with very low levels of regeneration and high levels of crown loss and mortality (correlated with high root mortality), silvicultural manipulations may be unsuccessful in maintaining significant aspen cover on the site. Instead, management efforts may be better directed toward stands with intermediate levels of crown loss and/or higher levels of pre-existing regeneration, indicating that roots are still abundant and vigorous enough to respond to disturbance. Where regeneration is marginal to deficient and herbivory is significant, reduction of herbivore pressure will aid in recovery and increase the likelihood of aspen cover in the future. In the long run, resilience of aspen-dominated landscapes to acute, warm droughts in the future will be enhanced by increasing the proportion of regenerating stands (<12 cm DBH).

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