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***Populus tremuloides* stands continue to deteriorate after
drought-incited sudden aspen decline**

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Abstract: Reports of forest damage have increased with the frequency of climatic extremes, but longer-term impacts of such events on population dynamics of forest trees are generally unknown. Incited by the turn-of-the-century drought, sudden aspen decline (SAD) damaged 535,000 ha of *Populus tremuloides* in the Southern Rockies ecoregion of western North America. Although spread of the disease stopped about 2009, most affected stands continued to deteriorate. Remeasurement of plots in southwestern Colorado showed that, since the peak of the epidemic, live basal area in sick plots decreased an additional 28% to only 38% of that in healthy plots. Sick plots had much more recent damage than healthy plots: almost three times as much recently dead basal area, over twice the density of recently dead trees, and almost four times as much recent crown loss. The important contributing agents in SAD were still active in sick stands in 2013. Density of small regeneration showed opposite trends, increasing in healthy plots and decreasing in sick plots. Timely regeneration treatments may be needed in some such stands to facilitate recovery. In addition to acute damage from climatic extremes, long-term decline diseases like SAD will likely be a common signature of forest damage from climate change.

Keywords: decline disease; climate change; regeneration; recent crown loss.

34 **Introduction**

35 Partly as a result of recent climatic extremes, reports of tree mortality are increasing around the
36 world (Allen et al. 2010). These include subtle increases in rates of “background” mortality (van
37 Mantgem et al. 2009) as well as spectacular, large-scale episodes of mortality (Michaelian et al.
38 2011).

39 Climatic extremes impact tree species in complex ways, interacting with various other abiotic
40 and biotic factors. The concept of decline diseases is useful in understanding the processes
41 involved in large-scale mortality events because it helps to organize and attribute roles to the
42 various causal factors, highlighting the complexity rather than a simplified focus on a single
43 cause. Often, etiology is organized into predisposing, inciting, and contributing factors (Manion
44 1991; Manion and LaChance 1992). Predisposing factors are long-term, static or slowly
45 changing factors such as site and stand conditions or chronic damage from insects and
46 pathogens. Inciting factors are short-term abiotic or biotic agents that cause acute stress at a
47 point in time, such as climatic extremes or severe defoliation events. Trees affected by inciting
48 factors alone may recover quickly, but recovery is much slower if the damage is exacerbated by
49 predisposing factors. Finally, contributing factors, or proximate causes, kill trees that were
50 debilitated by predisposing and inciting factors. Contributing factors are typically a suite of
51 secondary insects and pathogens.

52 Sudden aspen decline (SAD) is a decline disease of trembling aspen (*Populus tremuloides*) that
53 is incited by severe, warm drought (Rehfeldt et al. 2009; Worrall et al. 2013). Predisposing
54 factors include site conditions that render stands vulnerable to drought damage, such as low
55 elevation, southern to western aspects, relatively flat slopes, and upper slope positions (i.e.,

summits vs. toeslopes) (Worrall et al. 2010). Contributing factors include a variety of interchangeable, secondary insects and pathogens that kill stressed trees. Subsequent high populations of these agents may allow them to kill relatively healthy trees (Marchetti et al. 2011). Symptoms of SAD are rapid, synchronous branch dieback, crown thinning, and mortality of overstory trees on a landscape scale, without the involvement of primary pathogens and insects.

In 2002, a multi-year drought that stretched from western Mexico to the Canadian Prairies reached its peak with the most severe drought conditions on record in many areas. Often called the turn-of-the-century drought, by some measures it was the most severe in western North America in over 800 years (Schwalm et al. 2012). In Colorado, SAD was first noticed in 2004 (Worrall et al. 2008). The largest area recorded by aerial survey was in 2008, and by 2010 it had practically ceased to affect new areas. Over 2000-2010, SAD was recorded on about 535,000 ha in the Southern Rockies ecoregion and 492,000 ha in Colorado. Similar, roughly contemporaneous declines were noted in aspen across North America (Worrall et al. 2013).

In 2007-2008, affected stands in southwestern Colorado had an average 54% recent crown loss and 45% of the standing aspen stems were dead (Worrall et al. 2010). Compared to healthy stands, the proportion of roots that were dead nearly tripled in affected stands, and regeneration did not increase in response to overstory damage. This led to management concerns over the future of aspen in affected landscapes.

There are many reasons to maintain aspen where possible. It is a keystone species in western North America, important to diversity of wood-decay fungi (Gilbertson 1980), plants (Kuhn et al. 2011; Mueggler 1985), birds (Flack 1976; Turchi et al. 1995), and mammals large and small

(Oaten and Larsen 2008). Aspen modifies hydrological properties (LaMalfa and Ryel 2008) and microclimate in ways that improve stream flow and foster luxuriant growth of varying herb and shrub layers, providing forage for wildlife and livestock. Aspen wood is useful for paneling, oriented strandboard, pulp, and excelsior. The scenic beauty of aspen is a major contributor to the tourism economy in many areas.

To guide management responses to such an episode, we need to understand: (a) causal factors; (b) impact of the episodes on subsequent population dynamics, and; (c) future climate trends and their long-term impacts on the species' local climatic niche. Our focus in this paper is (b). Do forests impacted by drought-incited declines recover naturally, or can such climatic extremes initiate long-term deterioration? Such knowledge also can help us anticipate the impacts of severe droughts that are expected to be more common in the future due to climate change. However, since the peak of the epidemic, the subsequent fate of affected stands has been largely unknown. While limited remeasurement of a small subset of plots a year or two after the first measurement indicated continuing deterioration (Worrall et al. 2010), some observers have suggested that affected stands have largely recovered and that the impact of the disease was difficult to discern several years after the epidemic. Thus, our objectives were to compare current overstory and regeneration conditions in healthy and damaged stands with conditions immediately at the peak of the epidemic, and thereby infer trends in overstory mortality and regeneration.

Methods

During the peak of the SAD epidemic in 2007/2008, 162 plots were established throughout much of southwestern Colorado (Fig. 1) (Worrall et al. 2010). All plots were required to have live

100 aspen basal area $\geq 2 \text{ m}^2 \text{ ha}^{-1}$ with aspen as the leading species in basal area. Half were in sick
101 aspen stands randomly selected from polygons identified as SAD in aerial survey; for plot
102 establishment they were required to have $> 25\%$ recent crown loss. Each was paired with a
103 randomly selected, neighboring, healthy ($\leq 25\%$ recent crown loss) aspen plot. Plot centers were
104 marked with wood stakes and GPS coordinates were recorded.

105 To remeasure plots in 2013, we navigated to the GPS coordinates. If we found the stake with the
106 tip still embedded in the soil, we used that point as plot center and the plot was noted as precisely
107 relocated. Otherwise, we used the plot center indicated by the GPS coordinates and noted the
108 plot as imprecisely relocated. Such plots were checked to see if they met the original criteria.
109 For the 11 plots that did not, systematic rules were followed to establish a replacement plot in the
110 immediate area without bias. All plot centers were marked with steel rods.

111 As before (Worrall et al. 2010), overstory trees ($\geq 12 \text{ cm DBH}$) were sampled with a variable-
112 radius plot, choosing a basal-area factor (1, 2, or $3 \text{ m}^2 \text{ ha}^{-1}$) to target 10-20 trees for sampling.
113 Recent crown loss (RCL) was estimated as the percent of foliage that was apparently lost, either
114 due to recent branch and twig dieback or crown thinning. Old dead branches without fine twigs
115 or with $< 50\%$ of bark intact were not considered part of the crown and were ignored. Dead
116 standing trees were considered recently dead (i.e., 100% RCL) if they had any recently dead
117 branches; otherwise they were considered snags and not included in the average RCL.

118 Regeneration was sampled in 0.01-ha plots (radius 5.642 m), and evidence of browsing of
119 regeneration was recorded. Regeneration was sampled in three size classes: small (30 to 137 cm
120 tall), medium (0.1 to 2.9 cm DBH), and large (3.0 to 11.9 cm DBH). Only small regeneration
121 responded to the factors studied here, so data on medium and large regeneration are not

presented. Small aspen regeneration is referred to here as “suckers”, although some may have been seedlings.

Also as before, we recorded presence of damaging insects and pathogens on live and recently dead aspen. These included aspen bark beetles (dominated by *Trypophloeus populi*, but *Procryphalus mucronatus* could not be consistently distinguished in the field), bronze poplar borer (*Agrilus liragus*), Cytospora canker (caused by several species, but usually attributed to *Valsa sordida*), poplar borer (*Saperda calcarata*), white trunk rot (caused by *Phellinus tremulae*), and sooty-bark canker (caused by *Encoelia pruinosa*).

Stable aspen stands are those that tend to regenerate to aspen over long periods of time, often in the absence of disturbance, while seral stands undergo gradual succession to conifers (Rogers et al. 2014). We used two criteria to classify stands as stable (P.C. Rogers, personal communication, 2014): < 10% live basal area in conifers, and < 100 conifer seedlings or saplings (< 12 cm DBH) per hectare.

Statistical analysis

Two sick plots were removed in the first analysis because they were outliers in various respects (Worrall et al. 2010), and were removed this time also. One was frequently flooded, old, with a nearly dead overstory (not related to SAD) and heavy regeneration. The other had severe insect defoliation causing heavy crown loss and had no dead roots. In addition, a healthy plot that had been harvested in the interim was removed because the study was not designed to study harvesting as a factor. Although it barely met the criteria for sampling, regeneration was much higher than any other plot as a result of the harvest (58,400 stems ha⁻¹).

To account for the pairing of two measurements, for each plot and variable we subtracted 2007/08 values from 2013 values. Thus, the variates we worked with were the change between years. As the yearly measurements were consistent with log normal distributions, pairing them produced normally distributed change variables.

Statistical procedures are described in Venables and Ripley (2002) and in the documentation of R (R Core Team 2014), which was used to conduct the analyses. Each change variable was analyzed by fitting a multiple linear regression model using plot type (healthy vs. sick), precise relocation (yes or no), nine other covariates representing site and stand factors (elevation minus mean elevation, stand structure [single-story, two-story, multi-story, and mosaic], slope, slope position, aspect encoded by quadrant as north, east, south, or west, upland vs. riparian, conifer relative basal area, stable vs. seral, and browse) as main effects, and terms representing the interaction between plot type and the remaining covariates. This saturated model contained 21 parameters, most of which were not statistically significant. To remove the nonsignificant terms a termwise deletion procedure was applied using the Akaike information criterion (AIC) to remove the least significant term at each step to produce a reduced model. Any remaining interaction terms were assessed termwise using nested ANOVA and removed if not statistically significant ($\alpha=0.05$). After the nonsignificant interaction terms were removed, each main term not involved in a remaining interaction term was tested with an F-test and removed if not significant to produce the final model for the change variable. The only variables significantly influenced by precise relocation were live basal area (main effect, $p<0.001$) and live density (interaction with plot type, $p=0.022$). Therefore, we analyzed these change variables using only precisely relocated plots (77 of 159 plots).

To compare healthy and sick plots within years (not using the difference variables), we used Wilcoxon rank sum tests (= Mann-Whitney test). For frequencies of biotic agents and other tests of frequencies, equality of proportions was tested using a chi-squared test for equal distribution.

Results

Overstory

Change between measurements. In healthy plots, overstories experienced little change. Most variables did not change significantly (Figs. 2 and 3; density data are not shown as they largely mirror basal area), including basal area of live trees ($p=0.132$, $t=1.522$, $df=73$, multiple regression on significant covariants), of recently dead trees ($p=0.53$), and of snags ($p=0.09$), and recent crown loss ($p=0.96$). The only exceptions were an overall increase in density of snags regardless of plot type (46 stems ha^{-1} ; $p=0.002$) and, after correcting for the effects of relative basal area of conifers and seral status, an increase in density of recently dead trees (71 stems ha^{-1} ; $p=0.006$).

Sick plots, on the other hand, experienced greater change. Some measures of current damage decreased since the first measurement, at the peak of the SAD epidemic. These include basal area of recently dead trees and recent crown loss (both $p<0.001$). However, other change variables showed continuing losses. Density of recently dead trees decreased but the change was marginally significant at the 95% level ($p=0.052$), live basal area decreased 28% ($p=0.008$), and snag basal area increased ($p<0.001$).

Although density of live trees decreased 25% in sick plots and 7% in healthy plots, the overall change was explained by elevation and stand structure and was not significant after removing the

effects of those variables ($t=-0.724$, $p=0.471$). Change in live density was not influenced by plot type ($F=1.0154$, $p=0.317$).

Healthy vs. sick plots. In both measurements, sick plots had significantly less live density and basal area than healthy plots (all $p<0.001$). By 2013 the live basal area in sick plots dropped to only 38% of that in healthy plots. Levels of recent damage in sick plots still far exceeded those in healthy plots. In 2013, sick plots had significantly higher basal area of recently dead trees, density of recently dead trees, and recent crown loss than healthy plots (all $p<0.001$).

Insects and biotic diseases. All biotic agents that were significantly more frequent in sick plots than in healthy plots in 2007/08 (Marchetti et al. 2011) remained so in 2013 (Table 1). Between the measurements there were significant increases or decreases of some agents, but the magnitudes of these changes were small compared to the differences between plot types, especially for the contributing agents. The most notable example of such change was bronze poplar borer, which nearly doubled in healthy plots and decreased by a quarter in sick plots.

Regeneration

Density of aspen suckers increased in healthy plots, but decreased in sick plots. In linear models with change of sucker density as a response variable, and various site and stand factors as independent variables, only plot type was important ($p=0.002$). In healthy plots, suckers increased significantly ($p=0.014$) with a mean increase of 670 stems ha^{-1} . In contrast, sick plots lost an average of 500 stems ha^{-1} over the course of the study, although that change was not significant in the stepwise analysis ($p=0.066$). Because the stepwise analysis determined that only plot type was important, we investigated the change in sick plots further with the Wilcoxon test, which indicated that the change in sick plots was significant ($p=0.003$). In 2013, of 79 sick

plots, 11 had no suckers (14% of plots; 95% confidence interval = 7-24%). Thirty-six plots had ≤ 300 stems ha^{-1} (46% of plots, 95% confidence interval = 34-57%).

Density plots (Fig. 4) show a qualitative shift in sucker density among healthy plots. The plateau that formed in 2013 at about 4500 stems ha^{-1} suggests that a sizable subset of healthy plots changed their mode, moving from near 0 stems ha^{-1} to the range 3000-6000. Further examination showed that 13 healthy plots with <2000 stems ha^{-1} in 2007/08 had >3000 in 2013. These tended to be the healthiest of plots: compared to other healthy plots they had little or no recent dead, snag density went down instead of up, recent crown loss decreased greatly, and live basal area was high. Among sick plots, there was an opposite but less distinct shift to lower sucker density, with the population becoming more concentrated near 0 stems ha^{-1} .

Site and stand factors

Seral type (stable or seral) had no influence on SAD occurrence. Using a criterion of $<10\%$ basal area in conifers, 70% of our plots were in stable stands. For analysis we used the additional criterion of <100 conifer seedlings or saplings per hectare, resulting in 64% stable. There was no relationship between plot type (healthy/sick) and seral type (chi-squared test for equality of proportions, $p=1$).

However, stable stands had lower sucker density than seral stands. Because sucker density was substantially non-normal, we conducted a Wilcoxon test and found that 2013 sucker density was systematically lower in stable plots (median=800 stems ha^{-1}) than in seral plots (1850 stems ha^{-1} , $p=0.001$).

Browsing had no apparent relation to SAD occurrence. Browsing of regeneration was noted in 20% of plots and noted as heavy in 7% of plots. The proportion of plots browsed did not differ significantly between healthy and sick plots (chi-squared test for equality of proportions, $p=0.5$).

In the multiple regression analyses of the nine change variables, site and stand factors were generally insignificant. However, change in live basal area was significantly influenced by both plot type and stand structure ($p<0.001$ and $p=0.009$, respectively). In this case, live basal area did not change significantly in two-story and multi-story stands, but single-story stands lost an average of $5.1 \text{ m}^2 \text{ ha}^{-1}$ in live basal area after removing the effect of plot type. There was no significant interaction between plot type and stand structure.

Change in live density over time was significantly influenced by elevation ($p=0.015$) and stand structure ($p=0.027$). Elevation had a positive effect of one additional stem per hectare for every four meters increase in elevation. Consistent with the effect of stand structure on live basal area, single-story stands had about 163 fewer stems ha^{-1} than did two- and multi-story stands after removing the effect of elevation.

Discussion

Because the SAD epidemic peaked in 2008 and was virtually over by 2009, a decrease in recent damage was expected for sick plots. Also, due to older damage, fewer trees were available in sick plots to show damage. Indeed, some measures of recent damage decreased in sick plots, including basal area of recently dead trees and to a lesser extent recent crown loss.

However, sick plots lost 28% of their live basal area since the first measurement. Moreover, they continued to experience much higher levels of recent deterioration than healthy plots. Even in 2013, sick plots still had almost three times as much recently dead basal area and over twice

the density of recently dead trees compared to healthy plots. Recent crown loss was almost four times higher in sick than in healthy plots. These measures of recent damage are estimated to have occurred over the previous 2-3 years. This indicates that current damage in sick plots, although not as severe as it was during the peak of the SAD episode, is still substantial. The significant decrease in live basal area and increase in snag basal area in sick plots are evidence of the cumulative impact of the ongoing damage. Considering that sick plots have well below half the live density and basal area of healthy plots, but are losing stems, basal area and canopy 2-4 times faster, such stands are clearly continuing to deteriorate.

Healthy plots were stable and significantly increased in suckering (small regeneration), especially among the healthiest plots. However, change in sucker density over time was significantly different between healthy and sick plots. While sucker density increased significantly in healthy plots, it trended in the opposite direction in sick plots, even as the overstory continued to deteriorate.

Why have SAD-affected stands continued to deteriorate, long after drought conditions abated? There may be several reasons. First, several of the secondary agents that were heavily involved in SAD are capable of attacking and killing otherwise healthy trees when their populations are high (Marchetti et al. 2011). Most important in this regard are the aspen bark beetle, bronze poplar borer, and *Cytospora* canker. The large populations that grew through 2008 thus continued to kill trees for some time after the inciting agent, drought, was no longer directly involved. This conclusion is supported by the fact that these agents remained significantly more frequent in sick plots than in healthy plots, often at three times the frequency.

Second, heavy root mortality experienced during the SAD epidemic (Worrall et al. 2010) means fewer roots to produce suckers and less water and nutrient absorption. Thus, stress on surviving trees may be prolonged.

A third important factor is the positive feedback of overstory deterioration. Once aspen stands begin to open up substantially, the forest floor is exposed to sun and wind, and the rest of the stand can deteriorate rapidly (Fralish 1975; Walters et al. 1982). Indeed, microclimate measurements in stands affected by SAD showed higher air and soil temperatures and lower soil moisture than in healthier stands, suggesting stress and increased susceptibility to secondary insects and pathogens for residual trees (Korb et al. 2014). Such deterioration is complete within 3-6 years in some regions, but can be more protracted in the Rocky Mountains (Frey et al. 2004).

Aspen stands not obviously impacted by SAD in a portion of our study area experienced significant decreases in both density (stems > 1.37 m tall) and basal area over a longer sampling interval (Coop et al. 2014). The authors concluded that this may represent the expected dynamics of stand maturation, but also subtle influences of drought. A similar decrease in live density was observed in our healthy plots along with increased density of recently dead trees, but this was balanced with increased regeneration.

When we classified stands by conifer presence as stable or seral, several unexpected results were found. One might hypothesize that seral stands are more likely to suffer from SAD, and indeed conifer presence was associated with SAD in another area (Zegler et al. 2012). However, relative conifer basal area was inversely related to elevation in that system, so the effect of elevation may have been confounded with conifer presence. Our plots had a weak but opposite pattern of conifer presence vs. elevation. Our data showed that the proportion of sick plots was

equal among stable vs. seral plots. Similarly, one might expect stable stands to regenerate better than seral stands, but quite the opposite was true. Stable stands had much lower 2013 sucker density, although the proportion of SAD-affected stands was the same as in seral stands. Further study is needed to better understand differences in regeneration potential between stable and seral stands.

This study was not designed to assess the role of ungulate browsing in regeneration following SAD. Browsing was not a significant factor influencing the change in regeneration between measurements, and the proportion of browsed plots did not differ between healthy and sick plots. However, some browsing may have gone undetected, especially when small suckers were completely consumed. In many areas, browsing can be a major influence on aspen regeneration (e.g., Binkley et al. 2006; Ohms 2003; Ziegler et al. 2012).

Climate change will have substantial, negative impacts on aspen in much of its current range (Rehfeldt et al. 2009; Worrall et al. 2013). A recent study concluded that, by the 2030's, moisture conditions during the turn-of-the-century drought "... will become the new norm in western North America. Towards the latter half of the twenty-first century the precipitation regime associated with the turn of the century drought will represent an outlier of extreme wetness" (Schwalm et al. 2012, pp. 552-553). It has also been suggested that there may be indirect, positive impacts of climate change due to increased disturbance creating regeneration opportunities for aspen (Kulakowski et al. 2013; Worrall et al. 2013). These are not contrary views. Indeed, assuming climate is at least minimally suitable for aspen (which is unlikely to remain true throughout the current distribution of aspen), disturbance is the key to (a) aspen recovery where it is deteriorating following SAD, as reported here; (b) increasing drought resilience; and (c) preparing seedbeds for aspen in newly suitable areas. Where disturbances

occur naturally, they will counter the negative effects of climate change on aspen to some extent. Where they do not, forest management can create those opportunities for aspen.

Management implications

On average, the overstories in affected stands are continuing to deteriorate and regeneration is decreasing. Especially where ungulate browsing of suckers is common, the current trajectory would suggest that such stands are unlikely to recover as the aspen stands that they were. Without intervention, substantial areas of aspen forest may be lost.

Two studies indicate that aspen stands affected by SAD can be regenerated effectively, if treatment is done before about 50% of the stand is lost. Both studies involved cutting, but fire would probably be as effective. In southwestern Utah, coppice harvest was conducted in stands with varying levels of mortality (Ohms 2003). In stands with 10-50% mortality, post-harvest regeneration ranged from about 10,000 to 100,000 stems ha^{-1} , but above 50% mortality it dropped to near 0. Similarly, the regeneration response of SAD-affected stands was tested in the Terror Creek watershed of southwestern Colorado (Shepperd et al. 2015). Mean sucker density in uncut stands was higher in their study area (3865 stems ha^{-1}) than in our survey (2069 stems ha^{-1}). Regeneration response was excellent, ranging from about 14,000 stems ha^{-1} in treatments that had >60% pretreatment basal area dead or declining, to 55,000 stems ha^{-1} in stands that had 0-20% dead or declining basal area. Sucker density was strongly associated with SAD severity and pre-harvest live basal area.

These studies show that management intervention is likely to have good outcomes if not delayed too long. Our results indicate that such management may be needed to facilitate recovery in many aspen stands affected by SAD.

In addition, the fact that most basal area was lost in single-story stands suggests that creating multi-story stands, where feasible, may improve resilience. This is consistent with greater resilience of young stands < 40 yr old (Worrall et al. 2013).

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Table 1. Percentage of live and recently dead aspen stems with insects and biotic diseases. The first three were the most important contributing agents in SAD (Marchetti et al. 2011).

Insect or disease	Plot type	Percent of stems		2007 vs. 2013 ^a
		2007	2013	
Aspen bark beetle	Healthy	4.3	5.4	p = 0.264
	Sick	30.5	25.8	p = 0.051
	Healthy vs. sick ^a	p < 0.001		
Bronze poplar borer	Healthy	6.2	11.5	p < 0.001
	Sick	41.6	31.4	p < 0.001
	Healthy vs. sick	p < 0.001		
Cytospora canker	Healthy	12.6	13.2	p = 0.753
	Sick	46.0	34.1	p < 0.001
	Healthy vs. sick	p < 0.001		
Poplar borer	Healthy	10.5	17.1	p < 0.001
	Sick	21.8	29.0	p = 0.002
	Healthy vs. sick	p < 0.001		
White trunk rot	Healthy	19.2	20.8	p = 0.395
	Sick	21.8	18.3	p = 0.101
	Healthy vs. sick	p = 0.256		
Sooty-bark canker	Healthy	0.5	1.8	p = 0.008
	Sick	5.5	3.7	p = 0.124
	Healthy vs. sick	p = 0.028		

^a Equality of proportions infested was assessed with a chi-squared test for equal distribution.

Proportions were based on 1186 and 1021 trees inspected in healthy and sick plots in 2007/08, and 1016 and 601 trees in 2013, respectively.

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Figures

Figure 1. Locations of plot pairs (healthy and sick) in southwestern Colorado.

Figure 2. Basal area of live, recently dead and long-dead (snag) standing trees in healthy and sick plots in 2007/08 and 2013. The lower and upper box edges are the first and third quartile (containing the middle 50% of values), the bold horizontal line is the second quartile (median), the whiskers extend to the farthest points within 1.5 times the range of the box, the dots are outliers, and the solid diamond is the mean. To show detail in the lower end of the scale, two healthy plots with outliers of live basal area are not shown: 90 and 102 m² ha⁻¹ in 2007 and 93 m² ha⁻¹ each in 2013.

Figure 3. Recent crown loss in healthy and sick plots as measured in 2007/08 and 2013. Symbolology is as described for Fig. 2. Recent crown loss is based on twig and branch condition and is estimated to have occurred within the preceding 2-3 years.

Figure 4. Estimated frequency distribution of sucker density among healthy and sick aspen stands in 2007/08 vs. 2013, based on repeated measurement of 159 plots. Likelihood is a smoothed representation of a histogram; its value is proportional to the likelihood of the corresponding sucker density in the sampled population.