Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA

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Abstract

Concentrated patches of recent trembling aspen (*Populus tremuloides*) mortality covered 56,091 ha of Colorado forests in 2006. Mortality has progressed rapidly. Area affected increased 58% between 2005 and 2006 on the Mancos-Dolores Ranger District, San Juan National Forest, where it equaled nearly 10% of the aspen cover type. In four stands that were measured twice, incidence of mortality increased from 7–9% in 2002/2003 to 31–60% in 2006. Mortality generally decreased with increasing elevation over the primary elevation range of aspen and occurred on less steep slopes than healthy aspen. Slope-weighted mean aspects of aspen cover type were northern at low elevations and generally southern at high elevations. Relative frequency of mortality was generally highest on southern to western aspects. In 31 stands measured in detail, mortality ranged from 0 to 100% (mean 32%) and was negatively correlated with stand density ($P = 0.033$). Size of trees affected was strongly correlated with amount of current mortality ($P < 0.001$), and current mortality was skewed toward larger diameter classes. Density of regeneration was in a low range typical of undisturbed stands and did not increase with overstory mortality.

Agents that typically kill mature trees in aspen stands were unimportant in this mortality. Instead, a group of interchangeable, usually secondary agents was most commonly associated with mortality, including Cytospora canker (usually caused by *Valsa sordida*), aspen bark beetles (*Trypophloeus populi* and *Procryphalus mucronatus*), poplar borer (*Saperda calcarata*), and bronze poplar borer (*Agrilus liragus*). The rapidity of mortality, mortality agents involved, and probably other causal factors distinguish this phenomenon from the long-term loss of aspen cover usually attributed to successional processes operating in an altered disturbance regime (and often exacerbated by ungulate browsing). Our data are consistent with a hypothesis that (a) predisposing factors include stand maturation, low density, southern aspects and low elevations; (b) a major inciting factor was the recent, acute drought accompanied by high temperatures, and; (c) contributing factors and proximate agents of mortality are the common biotic agents observed. On sites with poor regeneration and weak root systems, clones may die, resulting in the long-term loss of aspen forest cover.
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1. Introduction

Rapid mortality of trembling aspen (*Populus tremuloides*) has been reported from multiple locales in southwestern Colorado by varied observers since 2004. The suddenness and synchronicity of the phenomenon are striking in the context of stand-level mortality processes that are typically observed in

aspen. Adding to the concern, regeneration appears to be sparse in many stands with heavy overstory mortality.

Studies of unusual aspen mortality in the past have revealed varied patterns and have been attributed to a number of causes. During the 1970s, widespread deterioration of aspen in the Great Lakes region was primarily attributed to high mean annual temperature (Shields and Bockheim, 1981). Stands with open canopy often deteriorated rapidly because they had increased exposure of the forest floor to sun and wind and increased moisture loss (Fralish, 1975). Most stands had established in the early 20th century due to widespread cutting and fire, so many stands were mature and thus susceptible to such damage. Clonal

differences were also implicated in susceptibility (Shields and Bockheim, 1981). Deterioration was interpreted by some as part of a successional process, returning composition to shade-tolerant, presettlement species (Fralish, 1975).

Also in the early 1970s, widespread deterioration of aspen was noted in the inland west, particularly in Utah and western Wyoming (Krebill, 1972; Loope and Gruell, 1972; Schier, 1975). Causes were considered to be fire exclusion, which allowed maturation of aspen stands established at the time of settlement, along with increased susceptibility to diseases and insects that accompanies maturation. However, concern encompassed not only mortality of ramets, but poor suckering. Suckering beneath deteriorating overstories was a fraction of that in healthy stands and was often insufficient to replace the mortality. Deteriorating aspen clones were often replaced by conifers or meadows. Heavy browsing by elk hastened the transition in some areas (Loope and Gruell, 1972; Ripple and Larsen, 2000). Root systems regressed in deteriorating stands, surviving primarily near the residual live stems (Schier, 1975). In southern Utah, deteriorating aspen stands had lower root densities than adjoining healthy stands (Shepperd et al., 2001), and suckering was suppressed by apical dominance of residual stems over the smaller root systems (Schier, 1975; Schier and Campbell, 1980). As in the Great Lakes region, observations suggested that genotype was an important factor determining which clones deteriorated. This ongoing deterioration of aspen stands and decrease in area of the cover type, due to vegetation succession under altered disturbance regimes and often exacerbated by ungulate browsing, has been termed ''aspen decline'' (e.g., Ripple and Larsen, 2000; Kulakowski et al., 2004; Kaye et al., 2005).

More recently, similar dieback, growth loss and mortality of aspen began in the 1980s or early 1990s in the prairie provinces of Canada, especially the aspen parkland and southern boreal forest of Alberta and Saskatchewan (Brandt et al., 2003; Frey et al., 2004; Hogg et al., 2005). Mortality is associated with dual stresses of drought and insect defoliation followed by secondary wood-boring insects and diseases. Continuing degradation of those aspen forests is anticipated under a warmer and drier climate. Unusually high rates of aspen mortality have also been observed recently in northern Arizona (M.L. Fairweather, personal communication) and in southern Utah and Montana (W.D. Shepperd, unpublished observations).

Our purpose in this report is to describe recent aspen mortality in southwestern Colorado, assess related landscape-scale and stand-level characteristics, and to develop a hypothesis as to the cause.

The southern Rocky Mountains of Colorado rise from arid, treeless deserts and plains at 1500–1700 m to peaks as high as 4400 m. Due to orographic and adiabatic processes, precipitation generally increases and mean temperature decreases as elevation increases. Most tree species have a broad band of elevation where these and related conditions are suitable for growth. Aspen occurs generally in the range 2100–3300 m in southwestern Colorado. Annual precipitation in the aspen forests ranges from approximately 38 to 110 cm, depending on elevation and local weather patterns. Because a species' lower

elevation range may be determined by moisture limitation, periods of drought and warm temperature may have their greatest impact at low elevations. Moisture availability and tree distribution also vary with aspect, because intense solar radiation on southern and southwestern aspects greatly increases temperature and evapotranspiration.

2. Materials and methods

2.1. Aerial survey

Aerial survey, also known as aerial sketch-mapping, is a remote sensing technique of observing forest damage events from an aircraft and documenting them manually onto a base map. Aerial surveys were conducted over most forested areas of Colorado in high-winged aircraft flying between 150 and 600 m above ground. Aerial observers delineated declining aspen polygons onto computer touch screens incorporating a moving map display, which is referenced to the aircraft's location using global positioning system data. Base maps included United States Geological Survey (USGS) 1:100,000 scale topographic series digital raster graphs and USGS digital orthographic quarter quadrangles. The 2006 aerial survey of Colorado was conducted from 10 July through 26 September. The southwestern part of the state, where our analysis was focussed, was surveyed mostly in September, but the Gunnison National Forest was surveyed in late July.

The aerial signature of ''aspen decline'' ranges from a general lack of foliage representing groups of dead trees to areas with considerable dieback of tree branches. Because observers look for generally foliage-free aspen stands, it is fairly easy to discern this signature from other aspen stressors such as insect defoliation or frost damage, where foliage is often thin yet still present.

2.2. Analysis of geographic data

Within the boundaries of four national forests of southwestern Colorado, we generated a healthy aspen layer by clipping an aspen cover type layer with the damage polygons from the aerial survey. We used these layers to calculate the percentage of the cover type affected on these national forests and to compare Digital Elevation Model (DEM) and other data between healthy and damaged aspen. Aspen cover type is defined as forest in which aspen is the leading species in crown cover (*Picea engelmannii* and *Abies bifolia* are lumped together for this calculation).

Elevation, slope and aspect were calculated using DEM data with resolution of 3 arc-seconds (approximately 72 m × 92 m). A 30 m × 30 m grid of points was created, associated with data of the DEM cell in which they occurred, and the points that fell within polygons of interest were used as variates for analysis and frequency distributions. Slope was calculated as a simple mean and standard error of percent slope. Cover-type elevation was represented as means with frequency diagrams to indicate the distribution around the mean. Proportion of cover type affected was calculated in the same elevation classes. Aspect

was represented as relative frequency in polar histograms; mean aspect was calculated as the angular mean ($\bar{\theta}$) using circular statistics (Zar, 1984). Because aspect has greater importance on steeper slopes, the angular mean was weighted by slope (w) (Levine, 2002):

$$\bar{\theta} = \arctan\!\left(\frac{\sum_{i=0}^{i=n} w_i \sin \theta_i}{\sum_{i=0}^{i=n} w_i \cos \theta_i} \right)$$

If $\Sigma w \cos \theta < 0$, $180°$ was added to the result; if $\Sigma w \sin \theta < 0$ and $\Sigma w \cos \theta \geq 0$, $360°$ was added to the result.

A measure of concentration around the mean aspect, r, was calculated from the mean, unweighted sine and cosine as follows (Zar, 1984):

$$r = \left[\left(\frac{\sum \sin \theta}{n} \right)^2 + \left(\frac{\sum \cos \theta}{n} \right)^2 \right]^{1/2}$$

r ranges from 0 (complete dispersion) to 1 (all variates have the same angle). Because the geographic data represent a complete population and not a sample, significance tests were not conducted.

2.3. Stand data

Reconnaissance based on aerial survey and ground observation was conducted on the Mancos-Dolores Ranger District, San Juan National Forest in 2006. Two areas with $\geq 20\%$ loss of canopy were identified for further study. In these areas, 31 stands ranging from 3 to 19 ha were delineated. A systematic grid was used to locate three to nine sample points in each stand, with one point per two hectares and a minimum of three points per stand. At each point, a 0.0081 ha plot was established. Species, diameter at 1.37 m (DBH), height, and condition were recorded for all standing trees ≥ 12.7 cm DBH. Condition was recorded as live and ''healthy'' (full crowns with little or no dieback), dying (substantial dieback and/or foliage loss), recent dead (intact bark and fine branches), and old dead (deteriorated bark and missing fine branches). For some analyses, dying and recent dead were grouped as ''current mortality''. A regeneration plot 0.0040 ha was placed at the same point, and live aspen were tallied as regeneration, if ≥ 30.5 cm tall but < 12.7 cm DBH.

2.4. Field observations

Reports of affected aspen stands from aerial survey observations, forest managers, and from sightings made in the field by forest health workers provided information on distribution of the phenomenon. Formal site visits were made to 15 locales in five of the six forest districts in the immediate study area of southwestern Colorado where the symptoms of foliage loss, branch dieback and stem mortality had been reported. These field sites were distributed throughout the study area over the range of geographic distribution and general stand conditions of aspen. Information recorded included slope, aspect, topography, and evidence of defoliating insects, foliage pathogens, cankers, bark beetles, stem decays, wood-boring

insects, and root pathogens. Specific stand factors were noted and, where appropriate, samples of observed agents were taken to facilitate accurate identification.

3. Results

3.1. Aerial survey and geographic analysis

Across Colorado, 56,091 ha were recorded with ''aspen decline'' in the 2006 aerial survey (Fig. 1). This causal agent category is based on concentrated patches of recent mortality not immediately attributable to a known cause. ''Other'' damage in Fig. 1 represents a wide variety of causes, but in 2006, 99% of it was defoliation by western tent caterpillar, *Malacosoma californicum*, giving a total damaged aspen area of 58,374 ha for the state.

Before 2006, aerial surveyors generally prioritized conifer issues and bark beetle outbreaks over aspen damage. Therefore, the area of ''aspen decline'' for prior years may be underestimated. However, there clearly has been a large increase in aspen mortality observed in aerial survey since 2004. The 2006 data represented a sharp increase in a trend first begun in 2005; before then total aspen damage was under 10,000 ha.

Aspen mortality in Colorado was most common west of the Continental Divide (where most of the aspen is located), particularly in the northwest and southwest portions of the mountains (Fig. 2).

On the four national forests of southwestern Colorado that we analyzed in detail, the most severe damage was on the Mancos-Dolores Ranger District of the San Juan National Forest, where nearly 10% of the aspen cover type was affected (Table 1; Fig. 3). Damage on other districts ranged from 0.6 to 4.5% of the cover type. Cover-type data are not uniformly
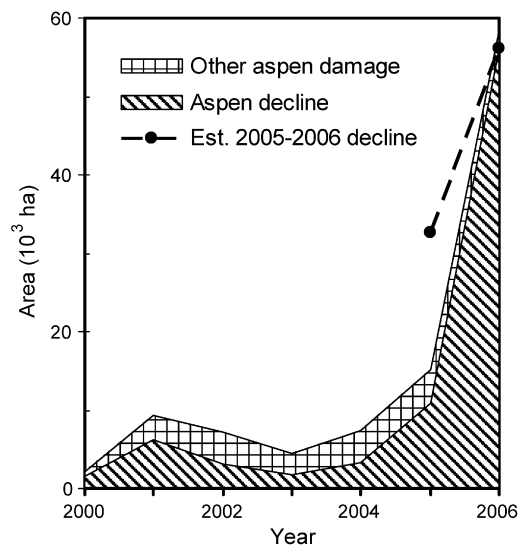

Fig. 1. Area of aspen damage recorded on lands of all ownerships by aerial survey in Colorado, 2000–2006. Aspen was not a priority in most surveys before 2006 and may be under represented. An estimate of 2005 Colorado ''aspen decline'' was made by applying the 58% increase from 2005 to 2006 documented on the Mancos-Dolores Ranger District to the statewide 2006 value (dashed line).
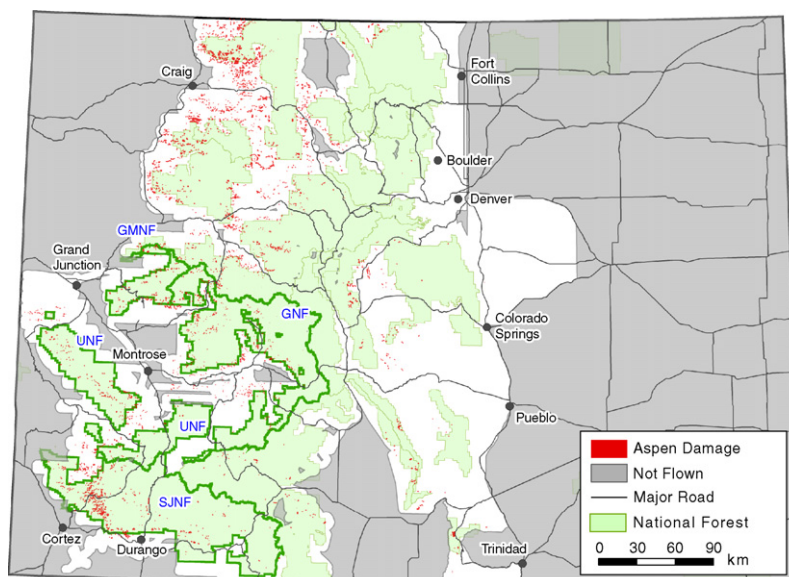
Fig. 2. Map of aspen damage (including all causes) in Colorado as determined by aerial survey in 2006. National forests that were analyzed in detail are outlined in bold green lines (GMNF = Grand Mesa, GNF = Gunnison, UNF = Uncompahgre, SJNF = San Juan). The damage polygons were slightly expanded to enhance visibility at this large scale. Intensity of damage in shaded areas is variable and not all trees in shaded areas are dead. Many of the most destructive diseases are not represented on this map because these agents are not detectable from aerial surveys.

available outside forest boundaries, but observations suggest that damage on these generally lower-elevation lands may be more severe than on the national forests.

Because substantial damage observed on the Mancos-Dolores Ranger District in 2004 had raised concern, the 2005 aerial survey in that area specifically prioritized aspen. "Aspen decline" was recorded on 3298 ha of the Mancos-Dolores District (6.8% of the cover type) in 2005. The 2006 data for that District (Table 1) thus represent a 58% increase in affected area over 1 year.

On three of the four intensively studied forests, "decline" occurred primarily at lower elevations. Over the elevations where most aspen occurred, the proportion of the cover type affected decreased as elevation increased, and the mean elevation of mortality was lower than that of aspen in general (Fig. 4). On the Grand Mesa National Forest, however, there was no difference in mean elevation and there was significant mortality at 2900–3200 m, where it was relatively low on other forests.

Mean slope of cells in "decline" aspen was less than that of healthy aspen in all of three major elevation bands, especially on the San Juan National Forest (Table 2). Again, the difference was slight on the Grand Mesa National Forest.

Healthy aspen was generally most frequent on northern to northwestern aspects at low elevations, shifting to southern

Table 1

Results of 2006 aerial survey for concentrated patches of recent aspen mortality[a] on four national forests of southwestern Colorado

Forest	Ranger district	Aspen cover type (ha)[b]	Mortality	
			Area (ha)[a,b]	Percentage of cover type
Grand Mesa	Grand Valley	41,167	1842	4.47
	Total	41,167	1842	4.47
Gunnison	Gunnison	82,511	466	0.56
	Paonia	82,488	1541	1.87
	Total	164,999	2007	1.22
Uncompahgre	Grand Valley	22,424	399	1.78
	Norwood	29,490	654	2.22
	Ouray	48,233	824	1.71
	Total	100,147	1877	1.87
San Juan	Mancos-Dolores	52,887	5204	9.84
	Columbine	43,806	1374	3.14
	Pagosa	25,242	272	1.08
	Total	121,935	6850	5.62

[a] Areas coded during aerial survey as 'aspen decline', indicating concentrated patches of recent mortality not directly attributable to other causes.
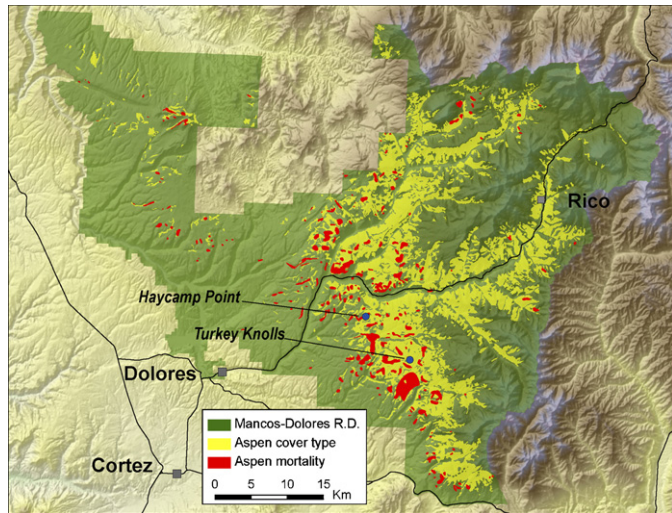[b] Data for national forest lands only.

Fig. 3. Concentrated patches of recent aspen mortality detected by aerial sketch-mapping, distribution of aspen cover type, and locations of stand sampling on the Mancos-Dolores Ranger District, San Juan National Forest.

Table 2
Mean slope and standard error of grid cells with healthy aspen vs. dead aspen on four national forests of southwestern Colorado

Forest[a]	Slope (%)					
	Healthy			Mortality		
	Mean	S.E.	n[b]	Mean	S.E.	n[b]
San Juan						
2100–2499 m	26	0.76	10,679	18	2.12	956
2500–2899 m	26	0.25	106,711	15	0.59	8354
2900–3300 m	32	0.37	62,140	27	2.73	991
Uncompahgre						
2100–2499 m	24	0.93	6,504	18	4.07	219
2500–2899 m	17	0.18	96,733	15	1.01	2348
2900–3300 m	26	0.47	31,229	19	4.97	125
Grand Mesa						
2100–2499 m	18	1.43	1,300	15	4.21	108
2500–2899 m	20	0.29	40,113	19	1.35	1753
2900–3300 m	18	0.45	15,313	17	1.81	918
Gunnison						
2100–2499 m	24	0.51	20,628	21	2.09	836
2500–2899 m	22	0.20	105,196	20	1.42	1716
2900–3300 m	26	0.25	103,782	18	2.71	453

[a] Only national forest land is represented.
[b] Number of cells in the Digital Elevation Model layer represented in the statistics.

aspects at high elevations (Fig. 5). This elevation trend was strong (reversal of slope-weighted mean aspect and high *r*-values) on all forests except the Uncompahgre, where healthy aspen was fairly uniformly distributed among aspects at high elevations. Compared to healthy aspen, mortality at low and middle elevations was more frequent on southern to western aspects, and mean aspect of mortality was more southerly than that of healthy aspen. This pattern was clear on all forests except the Gunnison National Forest, where generally equal proportions of aspen were killed on all aspects. At upper elevations, healthy aspen and mortality both had southern aspects, except on the Uncompahgre National Forest.
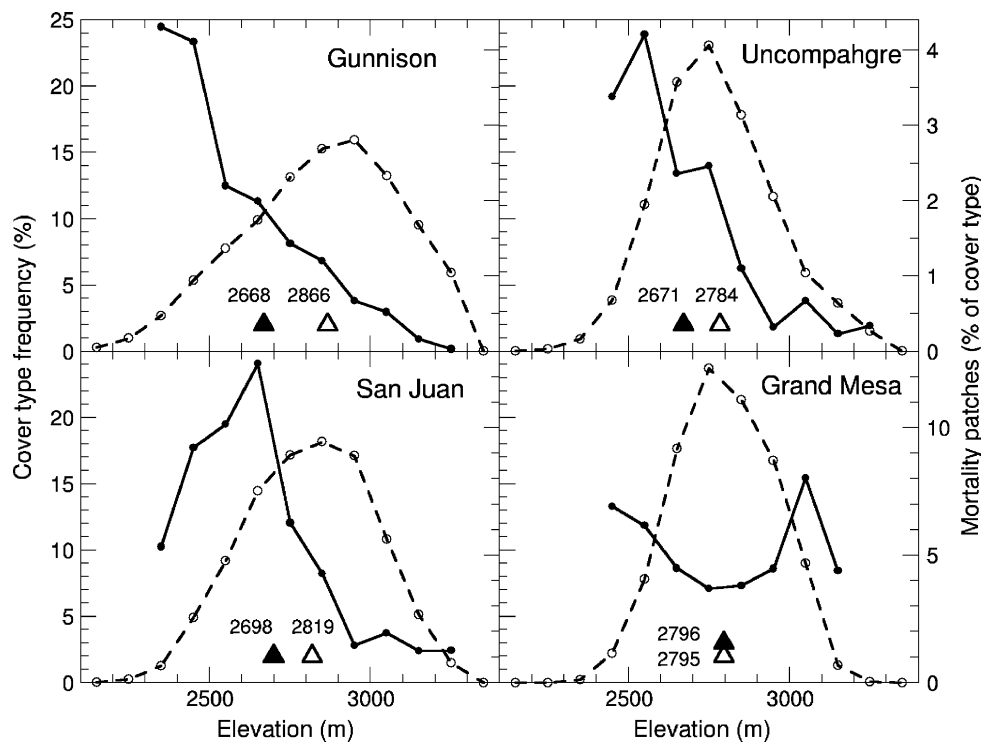

Fig. 4. Elevation distributions of the aspen cover type (relative frequency of live plus dead; dashed lines) and percentage of the cover type in concentrated patches of recent mortality (solid lines) on four national forests of southwestern Colorado. Data are in 100 m elevation classes plotted at the middle elevation of each class. Mortality is not calculated at elevations where <1% of the cover type occurs. Triangles indicate mean elevations of live (hollow) and dead (solid) aspen and are annotated with the values.
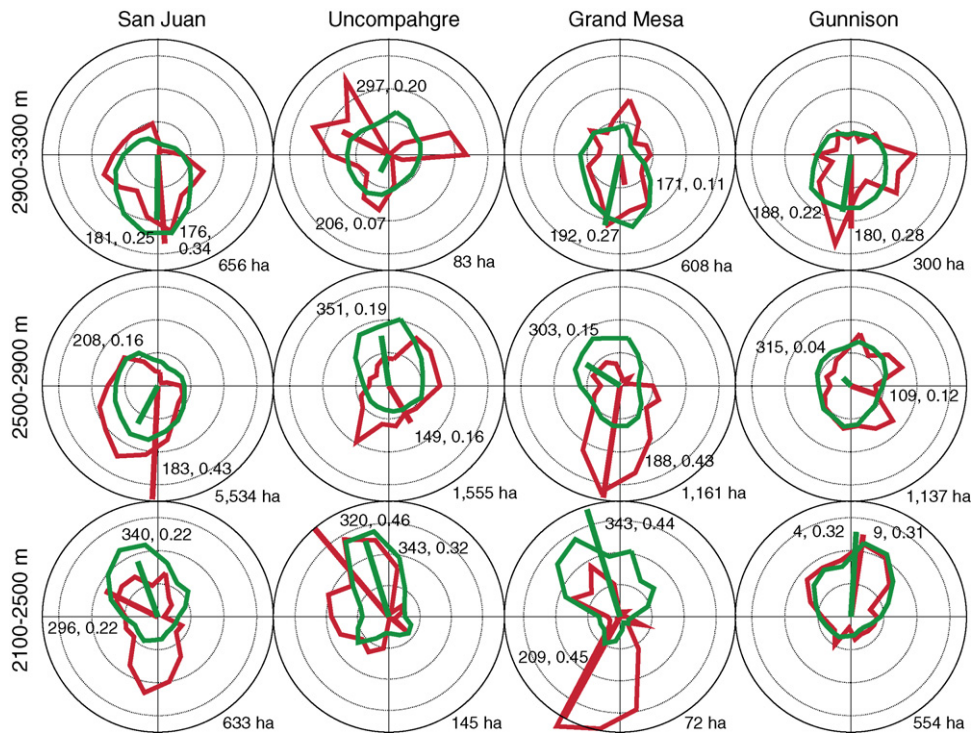
Fig. 5. Aspect (slope orientation) of healthy aspen (green) and mortality (red) in three elevation bands on four national forests. Graphs are arranged like a compass dial with north up and east to the right. Polygon vertices represent relative frequency of aspect in 18, 20-degree classes. Radial lines indicate the corresponding slope-weighted angular mean of aspect and its *r*-value (a measure of concentration around the mean); these values are annotated near the lines (mean aspect, *r*). Concentric, dotted circles represent 0.05 units of relative frequency and 0.125 units of *r*. The value at the lower right of each graph is the approximate area of mortality represented in the graph.

3.2. Stand data

In the 31 stands that were measured on the ground, mortality ranged from 0 to 100% of standing aspen stems with a mean of 32%. Overall, 19.9% of the 603 remaining live aspen stems were dying (substantial branch dieback and/or foliage loss). No
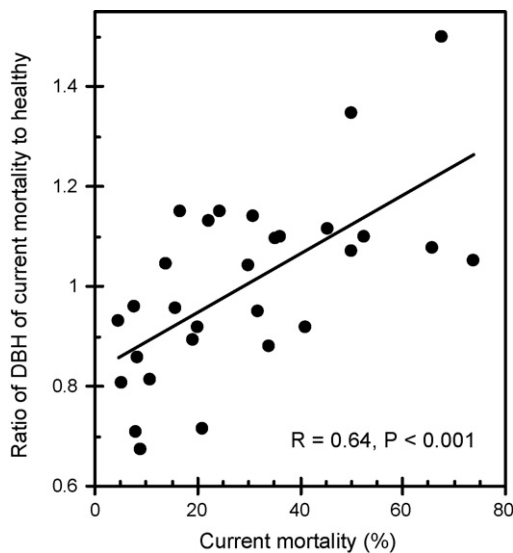
significant difference ($P = 0.22$) in mean DBH was found between live, healthy stems (23.4 cm, $n = 480$) vs. current mortality (recent dead and dying stems; 24.1 cm, $n = 245$). However, diameter distributions showed that current mortality was skewed to larger size classes (i.e., among stems >30 cm DBH, relative frequency of current mortality was greater than that of healthy stems; data not shown). Among stands, there was a highly significant correlation ($R = 0.64$, $P < 0.001$, $n = 29$ stands) between proportion of current mortality and the size ratio of current mortality to healthy stems (Fig. 6), indicating that relatively larger stems were affected with increasing mortality.

Data from 2002/2003 are available for four of the stands. In 2002/2003, these four stands all had less than 10% mortality (Table 3). In 3–4 years, the increase in proportion of mortality for the four stands ranged from 288 to 567%.

Mortality did not appear to be density-dependent (Fig. 7). The relationship between mortality and stem density (live and

Fig. 6. Increasing relative size of current aspen mortality (recent dead and dying stems ≥12.7 cm DBH) with proportion of current mortality in the stand. The ordinate is the number of recent dead and dying stems as a percentage of all standing stems in each stand. N = 29 stands.

Table 3
Comparison of mortality in 2002/2003 vs. 2006 for four stands in the Turkey Knolls area, Mancos-Dolores Ranger District, San Juan National Forest

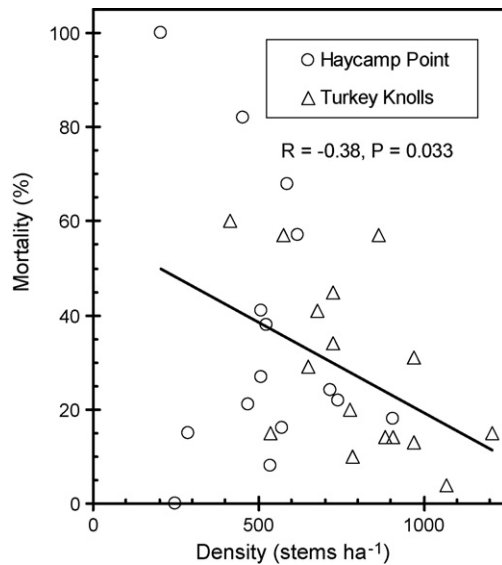| Unit	2002/2003	2006	
	Mortality (%)	Mortality (%)	Density (stems ha^{-1})
6	8	31	971
7	9	41	680
8	7	34	724
13	9	60	413

Fig. 7. Relationship of mortality to total stem density (live plus dead stems ≥12.7 cm DBH) in 31 stands in two areas of the Mancos-Dolores Ranger District, San Juan National Forest in 2006. Stands were composed largely or purely of aspen; data include only aspen.

dead) was negative rather than positive as expected for density-dependent mortality ($R = -0.38$, $P = 0.033$).

Regeneration ranged from 370 to 5850 stems ha^{-1} except for one anomalous stand with 100% overstory mortality that had 14,908 stems ha^{-1} of regeneration (Fig. 8). The anomalous stand had only old mortality and thus apparently died before the current episode. Aside from the anomalous stand, density of regeneration was unrelated to amount of overstory mortality and the mean density of regeneration was 2217 stems ha^{-1}.

3.3. Field observations

The state of deterioration of the dead trees confirmed the observations of local silviculturists, who indicated that mortality occurred quickly, over a span of 3 years or less. Mortality agents that generally kill otherwise healthy aspen in
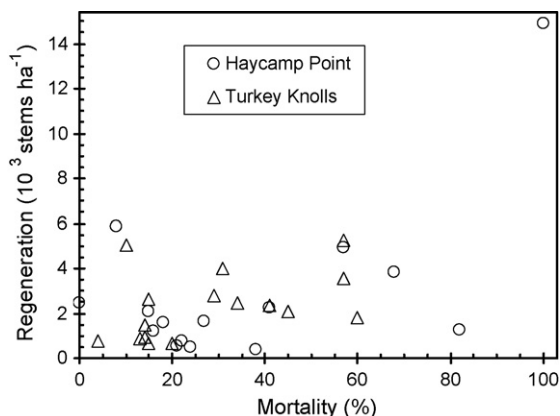

Fig. 8. Standing mortality of trees ≥12.7 cm DBH vs. regeneration density in stands in two areas of the Mancos-Dolores Ranger District, San Juan National Forest in 2006. Stands were composed largely or purely of aspen; data include only aspen.

mature stands were present, but their incidence was no higher and often lower than typically found in mature stands. These included sooty-bark canker caused by *Encoelia pruinosa* (the primary cause of mortality of mature aspen in Colorado; Hinds, 1985) and white mottled root rot caused by *Ganoderma applanatum*.

Instead, five other agents were found in various combinations on most dying and dead stems. Two wood borers that were typically present, individually or together, were the poplar borer (*Saperda calcarata*) and the bronze poplar borer (*Agrilus liragus*). Cytospora canker, usually caused by *Valsa sordida*, was often present and sometimes appeared to play a major role in mortality.

Two small bark beetles that were previously unimportant in Colorado, *Procryphalus mucronatus* and *Trypophloeus populi*, were abundant in many dying and recently dead stems examined, often in association with Cytospora canker. Galleries were also found frequently in live bark on otherwise healthy trees. The first indication of their presence was an entrance hole, about 0.8–1.0 mm in diameter, surrounded by an area of lightly brown-stained bark about 2–4 cm in diameter, surrounded in turn by live bark. Beneath the stained area was a tightly convoluted gallery system. Although galleries did not extend down to the cambium, in later stages the necrosis associated with the gallery did extend deeper, resulting in often dense patches of dead cambium. Exit of the young adults resulted in a fine shot-hole appearance of the bark surface above the gallery.

4. Discussion

The 58% increase in area of recent aspen mortality on the Mancos-Dolores District from 2005 to 2006 and the three- to five-fold increase in incidence of mortality over 3–4 years confirm field observations suggesting that most of the observed mortality occurred rapidly and recently. Such rapid increases in area and incidence of mortality apparently have not been documented in reports of previous episodes of deteriorating aspen.

The 58% increase in affected area is subject to some error inherent in aerial sketch-mapping. Although the spatial extent of the 2005 and 2006 aerial surveys were the same and data collection methods were standardized, different sketch-mapping teams, with possible subjective differences in mapping technique, performed the survey in each of those years. The magnitude of differences nonetheless indicates a major increase in area of aspen mortality.

Aspen regeneration was low in the stands we studied, regardless of the level of overstory deterioration. Uncut, intact aspen stands typically have about 2500 suckers ha^{-1} in southwestern Colorado (Crouch, 1983). Clearcutting results in 76,600 suckers ha^{-1} after 1 year. Partial cutting of aspen in the same area also stimulates suckering: removal of a mean of 58% of stems >15 cm DBH in one study resulted in 34,909 suckers ha^{-1} within a few years, while uncut control stands had only about 3294 (Walters et al., 1982). Two-thirds of our stands had sucker densities below that typical for intact,

undisturbed stands and the mean was also below that level, indicating that there has been little to no regeneration in response to the overstory mortality. Only one of our 31 stands showed substantial suckering approaching the level expected after disturbance, but overstory mortality in that stand (100%) was all classified as old mortality and apparently predated the current episode.

Because of attrition of suckers through herbivory, diseases and other causes, high levels of suckering are important to maintenance of aspen on the site. Poor regeneration of aspen has been associated with conifer succession or conversion to shrubs and grasses (Schier et al., 1985; Shepperd et al., 2001). Aspen cover may be lost on some sites if most of the overstory is dead, root systems are in poor condition, and little regeneration is present. Preliminary root sampling in several stands of the Mancos-Dolores District suggested that roots in some stands may be moribund (W.D. Shepperd, unpublished observation). Additional sampling of roots is needed to determine if root mortality is associated with rapid overstory mortality.

Large populations of ungulates heavily browse suckers in some areas and injure the bark of saplings and larger trees during winter feeding. Although the ungulates are not involved in mortality of most mature trees, heavy browsing on suckers is an additional concern in stands with limited regeneration.

Proportion of the cover type affected decreased as elevation increased on three of four forests analyzed in detail, especially over the range where most aspen occurred. Observations indicate that mortality is high at lower elevations outside the national forests, where the analysis was not conducted. This pattern suggests the possibility of stress due to drought and/or high temperatures during the growing season.

The exceptions to the elevation pattern are likely due to edaphic factors that vary with elevation. For instance, anomalously high mortality occurred near the upper end of aspen distribution on the Grand Mesa. The Grand Mesa is capped with volcanic flow basalt. Glaciation removed sedimentary material and, in some areas, broke up the surface basalt, followed by rockslides and slumping that resulted in a coarsely fragmented landslide bench surrounding the basalt cap of the Grand Mesa proper (Yeend, 1969). It is this landslide bench that supports most of the high-elevation aspen with anomalous mortality, and its soils are particularly prone to drought. A similar feature may occur in the western San Juan Mountains at 2500–2700 m, where mortality was greater than at lower elevations.

The reason for the general occurrence of mortality on less steep slopes than healthy aspen is not clear. One hypothesis is that flat benches and bottom slopes are abundantly supplied with moisture during normal years, so rooting is shallow and clones are thus more susceptible to drought stress on such sites.

The predominance of aspen on northern aspects at low elevations and southern aspects at high elevations is consistent with studies from other areas (Reed, 1971; Jones et al., 1985b). At lower elevations, northern slopes have moderate temperature and moisture conditions that favor aspen, but at higher elevations, the competitive advantage of conifers in cool, wet conditions may make succession to conifers more likely (Johnston and Huckaby, 2001). The relatively high mortality on southern to western aspects at low and middle elevations is consistent with stress due to drought and/or high temperatures during the growing season. In the middle elevations of the San Juan National Forest, where the greatest amount of mortality occurred, mortality was greatest on southwestern slopes, but the slope-weighted mean aspect of mortality was almost due south and had a high r-value. This suggests that southern aspects with mortality had particularly steep slopes. In the upper elevations, mortality was still on predominantly southern aspects on three of the four forests, but here it simply followed the overall aspect distribution of aspen.

Several relationships suggested that large trees were more vulnerable than small trees. The size distribution of current mortality was skewed to large stems compared to the distribution of healthy stems. More importantly, there was a strong relationship between incidence and relative size of current mortality. Because extensive fires in the late 19th century resulted in aspen regeneration in the area (Kulakowski et al., 2004), consistent with average stand ages of about 120 years (Shepperd, 1990), many stands have large, physiologically mature stems that are potentially predisposed to abiotic and biotic stress. However, many stands older than 120 years in Colorado have not been affected, so additional factors are clearly involved. These trends are consistent with the recent deterioration of aspen in the aspen parklands and southern boreal forest of the Canadian prairie provinces, where stand maturity and tree size were also associated with high levels of dieback and mortality (Brandt et al., 2003).

Mortality is typically density-dependent during the aggrading phase of aspen stand development, with a positive relationship between initial density and mortality (Shepperd, 1993; Johnstone et al., 2004). The relationship between density and mortality in our stands was not strong, but was significant and negative. Similar trends were observed during aspen deterioration in Wisconsin (Fralish, 1975) and in the prairie provinces of Canada (Brandt et al., 2003). Such a trend is consistent with the frequent occurrence of *S. calcarata*, *Phellinus tremulae*, and *Armillaria* root disease in stands of low density (Jones et al., 1985a; Brandt et al., 2003).

Mortality was associated with a suite of biotic agents that often appeared in different combinations. None are typically primary killers of vigorous aspen, but tend to succeed in trees that are previously stressed by other biotic or abiotic agents. Cytospora canker begins in bark that is injured or weakened by various causes, and its spread is generally limited in vigorous trees (Hinds, 1985; Guyon, 1996; Sinclair and Lyon, 2005; Shepperd et al., 2006). Both of the wood-boring beetles commonly associated with mortality are known to seek out hosts that are already weakened by some other factor (Jones et al., 1985a; Shepperd et al., 2006). However, all of the agents noted were at least occasionally observed attacking live trees with full crowns. The agents that typically kill otherwise vigorous aspen in Colorado were infrequent and clearly not involved in most of the mortality we observed.

Because galleries of the aspen bark beetles were often abundant in live bark on otherwise healthy trees, these closely

related beetles may also play a major role in mortality. The only study of the natural history of these beetles found that their life habits were similar. Both species seek out damaged and unhealthy hosts, with *P. mucronatus* apparently preferring trees that are in later stages of decline (Petty, 1977). The two species of beetles are difficult to differentiate in the field due to their small size, but can be distinguished with the use of a microscope (Wood, 1982). Further investigations are needed to elucidate the role that each species is playing in the current mortality.

4.1. Etiology

The mortality reported here appears to be distinct from the successional process often referred to as ''aspen decline'' (see Section 1). First, the recent mortality in southwestern Colorado had a sudden onset and was very rapid, while the deterioration termed ''decline'' is continuous and more gradual, consistent with succession. Second, the mortality agents appear to be different. In typical mortality of mature aspen, other agents generally are primary. In the current episode, the usually secondary agents appear to be primary invaders.

Several lines of evidence suggest that climate/site factors are involved. Aspen's drought tolerance rating is 1.77, between very intolerant (1) and intolerant (2) (Niinemets and Valladares, 2006). Drought and/or high temperatures were linked to aspen deterioration in the Great Lakes region (Shields and Bockheim, 1981) and other declines of aspen (Frey et al., 2004). In our results, proportion of cover type affected was greatest at low elevations and on southern to western aspects, where conditions are dry and warm. On the Grand Mesa, anomalous high-elevation mortality was associated with drought-prone soils. Also, mortality tended to be associated with open stands, where such conditions would have a greater impact. Acute drought with warm growing seasons in southwestern Colorado (and other parts of the west) from 2000 to 2005 (Breshears et al., 2005; Pielke et al., 2005) was associated with disease and insect epidemics in other species, including an immense and historically unprecedented outbreak of *Ips confusus* in *Pinus edulis*, Davisomycella needle cast in *P. ponderosa*, and *Dendroctonus* species in *P. ponderosa*, *P. contorta*, *Pseudotsuga menziesii*, and *Picea engelmannii* (Worrall and Sullivan, 2002; Breshears et al., 2005; Shaw et al., 2005; Anonymous, 2006). Drought was recently associated with mortality of aspen and other species in Arizona and, as in our study, aspen mortality was inversely related to elevation (Gitlin et al., 2006; M.L. Fairweather, personal communication). In 2005, a particularly dry, hot spring and early summer resulted in widespread scorch symptoms on aspen in parts of Colorado (Anonymous, 2006; unpublished observations). In the following year, several periods beginning as early as November 2005 and ending with June 2006 were the second driest such periods on record for the state (U.S. National Climatic Data Center, http://www.ncdc.noaa.gov/oa/climate/research/2006/jun/st005dv00pcp200606.html). During such events, stomatal conductance and photosynthesis are greatly reduced (Wan et al., 1999; Hogg et al., 2000). Tree mortality may occur years after an inciting drought (Bigler et al., 2006).

Other potential causal factors include viruses. The poplar potyvirus and poplar mosaic virus can infect aspen (Martin et al., 1982; Cooper, 1993; Sinclair and Lyon, 2005). However, we have not observed characteristic symptoms in the current syndrome.

The concept of decline disease may help in organizing the role of potential causal factors. Although the term ''decline'' has been applied to aspen with various meanings, it has been widely used for a long time in a more specific sense. In this sense, decline refers to gradual deterioration of vigor of many individual trees in a population, often leading to widespread mortality, and may be caused by chronic stress from one or more factors (Sinclair and Lyon, 2005). A widely used concept of decline disease in trees involves three types of factors (Manion, 1991; Manion and LaChance, 1992). Such a decline disease leads to gradual, general loss of vigor and eventual death of large numbers of trees, affects primarily the most physiologically mature component of a population, and is associated with low reserves of storage carbohydrates and degeneration of feeder roots and mycorrhizae before onset of symptoms in the aboveground portion of the tree. Predisposing factors are long-term, slowly changing factors, such as age, site and stand factors, and long-term climate changes. Inciting factors are short-term physiological or biological factors that cause acute stress, including drought, insect defoliation, frost, and air pollution. With these factors alone, trees may recover quickly, but recovery is much slower if the population is affected by predisposing factors. Finally, contributing factors kill trees that have been debilitated by predisposing and inciting factors. Contributing factors are mostly biological agents, including canker fungi, wood-boring insects, and bark beetles.

The application of the decline concept to aspen was recently reviewed. Frey et al. (2004) used the term ''dieback'' for aspen deterioration, but discussed it in terms of Manion's (1991) concept of decline. Predisposing factors included long-term climate, succession, and site and stand characteristics. Severe drought was noted as a particularly important inciting factor. Common contributing factors included wood-boring insects and several diseases. Guyon (2006) emphasized the clonal nature of aspen, suggesting that the fate of the population of clones was the major issue, and that high incidence of ramet mortality should not be considered a decline if the clone successfully produced new ramets. He concluded that the decline concept can be useful in some cases but was not needed when a single factor or two can explain the deterioration.

Several factors identified or suggested by our results are consistent with a decline disease and with literature on other episodes of aspen deterioration. We suggest this decline scenario as a hypothesis consistent with our results. Likely inciting factors are the acute drought with high temperatures during the growing season. Predisposing site factors include low elevations and south/southwestern aspects, where those conditions would be most pronounced. Predisposing stand factors include large stem size (physiological maturity) and low stand density, which would increase susceptibility to those conditions. The biotic agents reported here are the proximate causes of mortality, functioning in the role of contributing factors of a decline disease.

5. Conclusion

Rapidly increasing mortality, synchronized on a landscape-scale, occurred in southwestern Colorado over the last several years. The proximate cause was a group of interchangeable, usually secondary, biotic agents. There has been little regeneration response in sampled areas and roots in some stands may be moribund, suggesting that clones as well as stems may be dying. Relative to healthy aspen, recent mortality occurred at lower elevations and on flatter slopes, affected larger tree sizes, was associated with stands of low density, and tended to occur on southern and western aspects at lower and middle elevations. These results suggest that a decline disease resulting from inciting, predisposing, and contributing factors may be responsible. Investigation is needed to further assess the role of the factors identified here and to identify additional factors.

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