



Landscape assessment of a stable aspen community in southern Utah, USA

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ABSTRACT

Recent reports of rapid die-off of aspen (*Populus tremuloides*), coupled with vigorous debate over long-term reduction of aspen cover in western North America, has prompted considerable research given the importance of this forest type for economic and non-economic interests. Despite this interest, indicators of aspen conditions are poorly understood, and there is a lack of systematic monitoring of stable aspen landscapes. Stable aspen are defined here as being predominantly aspen overstorey (>80% basal area) with little or no conifer regeneration. We examined a putative stable aspen landscape in southern Utah and addressed (1) stand structure and (2) indicators of decline. We sampled 83 aspen-dominated stands within a 275 km² landscape using established forest health monitoring protocols. Eighty-four percent of sample stands on Cedar Mountain exhibited stable aspen characteristics. Principal findings include: (1) a relatively uniform age of adults within the study area; (2) approximately 10% crown dieback on half of the plots sampled; (3) roughly 50% of the study plots had greater than 50% of the trees with damage to the bole; (4) about 25% of the adult basal area was dead; and (5) over half the plots had few sub-canopy individuals and/or limited regeneration. Physiographic variables including elevation, slope, and aspect were generally not strong indicators of aspen condition, typically explaining less than 15% of the variation in basal area, mortality, dieback, or damage. Healthy stands were rarely observed in the most drought prone locations, though the inverse was not necessarily true; healthy and unhealthy stands were found in more mesic settings. Principal components analysis identified two clusters of plots that differed considerably in regeneration; however, no other variables differed between these groupings. We suggest exogenous factors such as land-use history or altered disturbance regimes and endogenous factors such as soils and geology influence aspen condition on this landscape. Further research is necessary to test these hypotheses.

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1. Introduction

Quaking aspen (*Populus tremuloides*) is well known for its broad tolerance of physical settings throughout North America. As with many widespread species, aspen also exists in a diversity of types from high basal area forests in montane western North America to a component of deciduous forest in the East. Much of the focus of traditional aspen ecology and forest management has been directed at seral stands; those subject to succession toward dominance by a variety of shade-tolerant western conifers (e.g., DeByle and Winokur, 1985 and citations therein). In the western U.S., recent literature has often highlighted differences between “seral” and “stable” aspen communities and their alleged declines, persistence, or increases (Rogers, 2002; Di Orio et al., 2005; Bartos

and Campbell, 1998; Manier and Laven, 2002; Kulakowski et al., 2004). Earlier works have estimated that roughly a third, or less, of aspen stands demonstrated stable attributes in a variety of Rocky Mountain locales (Mueggler, 1989; Rogers, 2002; Kashian et al., 2007; Zier and Baker, 2006; Strand et al., 2009); though it is probable that these characteristics, and thus cover by type, vary across the region (Mueggler, 1985). Still, there is agreement that, overall, stable types comprise a minority of western U.S. aspen stands (Mueggler, 1985; Shepperd et al., 2006). While most attention has been focused on conifer encroachment (or not) during the 20th century, there is a paucity of information regarding the status of stable aspen forests.

The subject of the current study is a detailed investigation of a putative stable aspen landscape. We define stable aspen as being predominantly aspen overstorey (>80% basal area) with little or no conifer regeneration. Mueggler's (1985, 1988) work chronicles the common occurrence of stable aspen types and the largest of these communities in the U.S. apparently reside within the Colorado Plateau region (Kurzel et al., 2007; Mueggler, 1988). While the

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long-term (200–1000 years) stability of these forests remains in question, a fairly clear demarcation can be made between short-term (<200 years) stability and seral stands based on the presence of conifers. Contemporary research has favored the term “persistent” to characterize aspen stands with little or no conifer encroachment (Barnett and Stohlgren, 2001; Kashian et al., 2007; Kulakowski et al., 2004; Rogers et al., 2007), but focuses less effort on questions of longer term or larger scale stability. Mueggler (1988), however, allows for potentially longer successional periods toward conifer dominance where aspen were presently stable in defining “community types” (community types pointedly suggest a temporary, or unknown, period of dominance or “climax;” contrast with “habitat type”).

Several studies published in the past two decades suggest long-term decline and loss of aspen communities in western North America since settlement by Euro-Americans (e.g., Bartos and Campbell, 1998; Di Orio et al., 2005; Strand et al., 2009) while a more recent publication indicates rapid local losses (Worrall et al., 2008). Thus, reports of “sudden aspen decline” (SAD) appear distinct from the long-term process of conifer encroachment. Qualitative claims of declining aspen stands on Cedar Mountain, in southern Utah, USA have arisen over the previous decade (Dr. James Bowns, Southern Utah University, Personal communication), although no formal studies have been conducted to quantify alleged losses. Furthermore, Cedar Mountain appears to represent a predominantly stable aspen system; hence an examination of conditions here addresses the dearth of information on stable aspen communities while also addressing local concerns of SAD.

This work details a landscape assessment of aspen on Cedar Mountain Plateau, near Cedar City, Utah. Previous efforts on Cedar Mountain evaluated a select area of the landscape for aspen and rangeland health (Ohms, 2003; Bowns and Bagley, 1986; Tshireletso, 2008). We believe a missing element locally and regionally has been a systematic landscape assessment of stable aspen communities. We define “systematic” as having two basic elements: (1) a pre-determined equal-area, non-biased, sample of the aspen population for a given landscape and; (2) a clear and widely accepted definition of the minimum sample unit – often called the “stand” – in terms of specific area. These caveats facilitate defensible statements regarding condition and status of a landscape or region as a whole.

The objectives of this study were to describe the characteristics of a reputed stable aspen community and to assess the status of a purportedly declining population. This was accomplished by examining the level of “purity” of aspen (i.e., proportion of stands considered stable) on Cedar Mountain as a whole, as well as assessments of stand structure, tree damage and mortality, and aspen regeneration on the landscape. Findings from this research will have implications for stable aspen communities throughout the Colorado Plateau and functionally similar aspen forests in western North America.

2. Materials and methods

2.1. Study area

Cedar Mountain, located southeast of Cedar City, Utah (Fig. 1), is a high-elevation plateau (1800–3200 m) characteristic of those found within the Nevada-Utah Mountains Semi-desert province (Bailey, 1995) and Utah High Plateaus and Mountains section (McNab and Avers, 1994). These physiographic provinces fall within the greater Colorado Plateau region, which is characterized by high-elevation massifs and desert canyons within four western states: Utah, Colorado, Arizona, and New Mexico. The aspen component on the Cedar Mountain is largely located above 2500 m elevation. The total area of the mesa top, the effective suitable

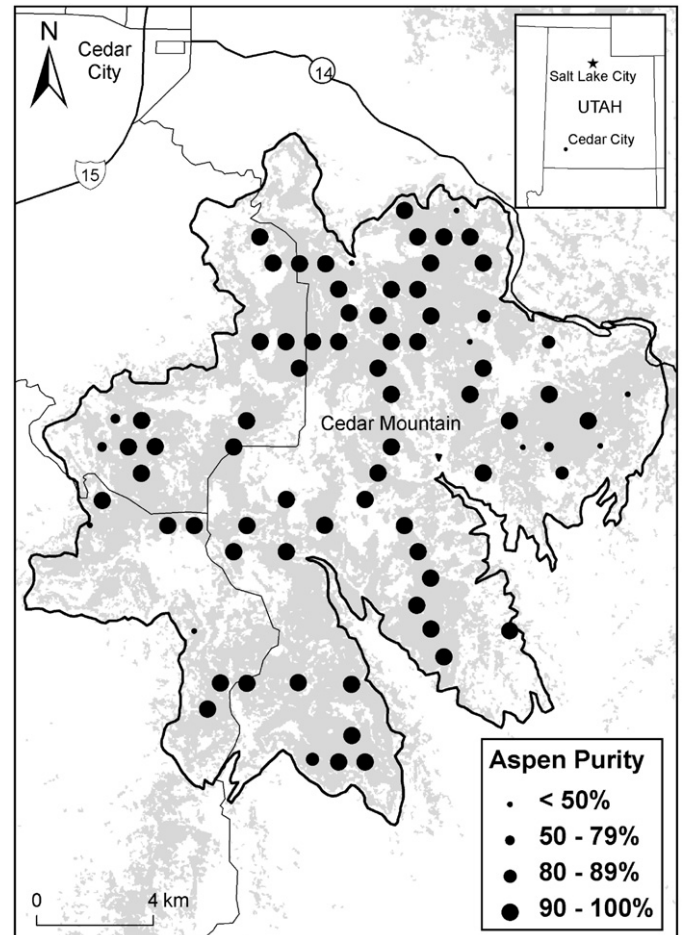


Fig. 1. Map of study site by live basal area of aspen. Cedar Mountain study site located in southwest Utah. The study site is largely delineated by the 2500-m elevation contour. Shaded area indicates aspen extent in the region. Map symbols represent the location of each of 83 sample plots and are scaled by percent of total live basal area as aspen.

growing area for aspen, is roughly 275 km². Precipitation within this montane zone averages 835 mm annually and daily temperature means range from January at –6 °C to July at 13 °C (NRCS, 2007). Soil types vary generally from mollisols to alfisols (McNab and Avers, 1994). Vegetation on Cedar Mountain consists of four primary communities: aspen and aspen–conifer, riparian and upland shrubs, montane grassland, and a small amount of conifer forests. Past work has strongly suggested that long-term sheep (*Ovis* sp.) grazing since Euro-American settlement has transformed understory communities in both aspen and meadow types from forb to graminoid dominated (Bowns and Bagley, 1986). Within aspen communities, the aspen type is more prevalent than aspen–conifer, though a landscape assessment of proportions has not previously been conducted.

2.2. Field methods

We first established potential sample locations using a 900-m hexagonal grid placed over the Cedar Mountain plateau. Sample locations of one hectare extent, hereafter called “plots,” were selected from these candidates using three criteria: (1) they fell in aspen or aspen–conifer vegetation types as classified in the Southwest Regional GAP analysis (Lowry et al., 2007); (2) they were at least 2500 m elevation; and (3) they did not fall outside a subjective NE geographic limit (specifically, <UTM X-coordinate 336,000 and Y-coordinate 4,170,000) where elevation poorly

delineates the study area. This selection procedure resulted in 134 potential plots, of which we randomly sub-sampled 90 sites. Following initial grid selection, we checked all potential plots on 1:6000 aerial photographs to confirm the presence of aspen and, if necessary, made minor position adjustments to ensure that plots were surrounded by a minimum of 90 m of aspen forest in all directions. Seven of the 90 plots were eliminated due to inaccessible terrain, misclassification, or access denial by landowner resulting in a final sample of 83 plots. The resulting map defines our sample population and plot locations in relation to area landmarks (Fig. 1).

Field sampling took place during July and August 2008. At each plot we surveyed plot- and tree-level attributes using techniques developed by the U.S. Forest Service (USDA Forest Service, 2007). At the plot-level, we estimated overall conditions by assessing amounts and types of vegetation cover, physiographic setting, number of distinct stand layers, recent disturbance, including domestic and wild animal impacts, and stand age. Select trees in the overstorey of good health were cored at breast height to determine stand age. Specifically, if rotten cores were encountered, then alternative trees were selected with discernable rings. Aspen tree rings are sometimes difficult to accurately read. Potential sources of error (Campbell, 1981) in aging aspen were addressed in the field by (1) re-boring trees when the pith was not encountered, (2) moistening cores before counting with saliva or water, (3) viewing faint tree ring cores using direct sun as backlighting (this highlights a translucent spring wood and increases contrast with the darker late-season wood), and (4) inspecting cores with a hand lens to discern narrow rings. To address the issue of age up to core height, one sucker in each stand with a total height near 1.3 m was cut at ground level and rings were counted to determine site specific age needed to reach breast height. A detailed survey of tree conditions was conducted by sub-sampling the 1 ha plot with four fixed-area “subplots” (7.32 m radius) measuring mature trees and each containing a smaller “microplot” (2.01 m radius, at center of subplot) for sampling tree regeneration (USDA Forest Service, 2007). For each mature tree (diameter at breast height [dbh] \geq 12.7 cm) data were collected on tree dbh, total tree height, canopy position, damage severity and type, and tree status (live/dead). Damage types consisted of common bole symptoms, such as cankers, conks, open wounds, insect damage, breakage, and resinosis; field crews were not equipped to identify specific canks and cankers. On microplots, a count was made of aspen suckers by height classes (Class 1: 0.3–1.3 m height; Class 2: $>$ 1.3 m height, but $<$ 2.5 cm dbh) and browsing damage classes, including both terminal and lateral branch/bud damage for the current year ($<$ 20%, 20–80%, and $>$ 80% leaf/bud browsed). A browsing class was assigned for a given microplot by determining which class was most common among all suckers examined. We also measured dbh, height, canopy position, and damage on “saplings” (dbh \geq 2.5 cm and $<$ 12.7 cm) on microplots.

2.3. Analytical methods

All data were checked and edited for errors after completing the field survey. Sampling values for all variables were compiled at the plot-level for further analysis. Derived variables include, on a per hectare basis, stand age; number of suckers; basal area of aspen, standing dead trees, and conifers; mean percent dieback; mean percent damaged trees; and percent aspen cover. Stand age was estimated by adding the mean stand breast height age with the site specific age of a sucker 1.3 m tall. To discriminate between stable and seral stands, a maximum of 20% conifer overstorey was our prime determinant (Smith and Smith, 2005). Those plots with less than 20% conifer basal area were considered stable aspen.

We approached analysis of stand structure, health, and reproduction with a three step procedure that incorporated: (1) identifying study plots with shared characteristics through principal components analysis; (2) a model selection procedure to identify combinations of landscape position variables that best explain the first three principal component axes; and (3) statistical tests to examine differences in measured variables among identified clusters. All analyses were conducted with SAS (2005).

Principal component analyses included the following variables: live basal area of mature aspen, stem density of mature aspen, overstorey height, live basal area of aspen saplings (2.5–12.7 cm dbh), stem density of aspen saplings, density of suckers in class 1 ($<$ 1.3 m in height), density of suckers in class 2 ($>$ 1.3 m in height, but $<$ 2.5 cm dbh), percent of total aspen basal area that was dead, percent of mature trees exhibiting damage, percent overstorey dieback, percent crown cover ($>$ 2 m height), and live basal area of conifers.

The resulting first three principal component axes were used as response variables in a model selection procedure to determine the fraction of variation in stand structure, health, and reproduction that are explained with position on the landscape and age of the stand. Landscape position variables including elevation, slope, and aspect were derived from a 10-m digital elevation model (DEM) and averaged over the 1-ha study plot (ca. 100 points from each plot). Aspect was transformed into a moisture index ranging from 0 (southwest aspect) to 1 (northeast aspect) to eliminate inaccuracies from averaging aspect values that straddle 0 degrees (Roberts and Cooper, 1989). All possible combinations of predictive variables were tested for each response variable and the model with the highest adjusted r^2 – which down weights models with many variables with little explanatory power – was selected (Quinn and Keough, 2002). Residuals were examined for violation of normality and equality of variance assumptions.

Study plots associated with primary principal component groupings were statistically analyzed with t -tests to determine if they differed in slope, aspect, elevation, live basal area of mature (overstorey) aspen, dead basal area of mature aspen, percent dead basal area of mature aspen, stem density of mature aspen, overstorey height, basal area of sapling (mid-storey) aspen, stem density of saplings, density of suckers in classes one and two, percent damage, percent overstorey dieback, age, and basal area of mature conifers. Tests for equality of variance among the two groups were performed; when variances were equal, a pooled-variance t -test was used; where variances were not equal, the Satterthwaite approximation was used (Sokal and Rohlf, 1995). A contingency table analysis (Fisher’s Exact test) was used to determine if there was an association between principal component groupings and intensity of browsing due to the categorical nature of this variable. All differences were considered significant at $p < 0.05$.

3. Results

3.1. Cedar Mountain and the region

The ecological setting of our study site is similar to that of aspen in southern Utah as determined by land cover classification from Southwest Regional GAP analysis (Lowry et al., 2007) and 10-m DEM. Mean elevation of aspen pixels on the Cedar Mountain study site was 2710 m; for the region, mean elevation was 2720 m. Variation about the mean was somewhat higher in the region than on the study site (169 vs. 107 s.d.). Identical slopes of 22.6% were observed on the study site and the region; these means also had similar variation. Finally, mean site moisture index values obtained from a transformation of aspect were 0.534 for Cedar Mountain and 0.540 for the region. Although standard deviation in the

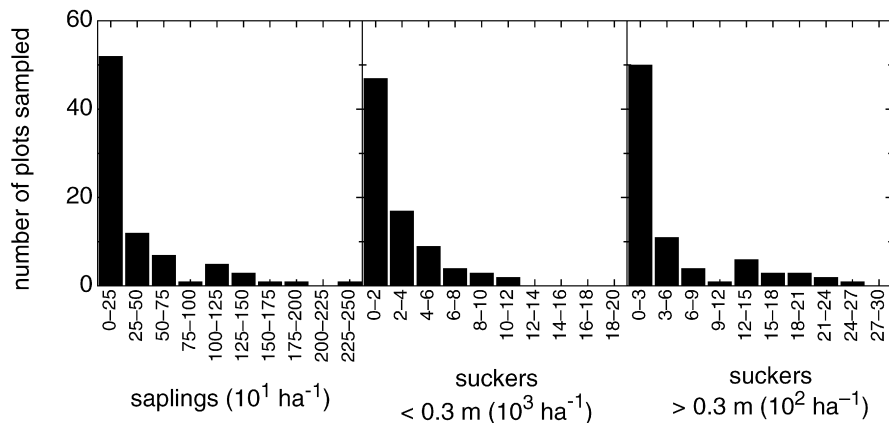


Fig. 2. Aspen regeneration on Cedar Mountain. Histograms indicating the distribution of saplings and suckers of two size classes among sample plots on Cedar Mountain. In each case, greater than 50% of the plots were categorized into the smallest bin.

moisture index was high (0.340) for both the study site and region, ca. 30% of the study plots had moisture index values between 0.9 and 1.0 indicating some preference for north-facing aspects by aspen communities.

According to GAP data, aspen were the dominate vegetation type, accounting for ca. 63% of the 27,200 ha study area. The vast majority of these sites were classified as aspen (stable); aspen-conifer (seral) communities accounted for only 2% of the landscape. Conifer communities, mostly spruce-fir, occupied ca. 5.5% of the landscape; 1% of the landscape is classified as ponderosa pine (*Pinus ponderosa*). Sagebrush shrublands (*Artemisia* spp.) and Gambel oak woodlands (*Quercus gambelii*) occupied nearly 20% of the landscape while grasslands were less common, occupying ca. 6%.

3.2. Characteristics of aspen stands on Cedar Mountain

Of the 83 plots sampled, 59 (71%) had 100% of mature BA in aspen; an additional 11 (13%) plots were greater than 80% aspen (Fig. 1). One plot had no mature trees and only aspen regeneration. Thus, based on our sample, the aspen community in our study area is comprised of 84% stable stands. Of the remaining 16% – logically, the seral community – mean aspen composition of the BA was 39%. Sub-alpine fir (*Abies lasiocarpa*) and Douglas-fir (*Pseudotsuga menziesii*) were the next most common tree species found. Other species detected in the study plots include white fir (*Abies concolor*), Utah juniper (*Juniperus osteosperma*), Engelmann spruce (*Picea engelmannii*), limber pine (*Pinus flexilis*), and Gambel oak.

Stand ages are based on average age of the overstorey component (ramets). Age of ramets does not reflect genet age; genets may survive for multiple generations. Mean age of mature trees on Cedar Mountain is 87 (± 23 s.d.) years, indicating that 68% of the canopy was produced between 1898 and 1944. Stand ages ranged from 22 years old (start 1986) to 131 years old (start 1877).

Mean live BA was 20.7 (± 13.8 s.d.) $m^2 ha^{-1}$ indicating considerable variation on the landscape. One plot contained no mature individuals, while another plot had a BA of nearly 59 $m^2 ha^{-1}$. Similarly, overstorey tree density was quite variable, ranging from 0 to 967 individuals ha^{-1} with a mean of 315 (± 201 s.d.) individuals ha^{-1} . Forest overstoreys are generally discontinuous on Cedar Mountain; cover averaged 31.5% (± 16.2 s.d.). Mature trees are not particularly tall, averaging 17.4 m (± 2.7 s.d.).

Regeneration throughout the study area is quite limited; several plots had no individuals in the understorey (Fig. 2). Those stands with only an overstorey layer represent 18% of our plots. The number of distinct layers at the stand-level amounted to 70% of plots having two or fewer layers, including overstorey, in the

stand. Only a single plot displayed four distinct layers. The number of trees in the sub-canopy (saplings) ranged from 0 to 238 ha^{-1} , but averaged only 32 (± 50 s.d.). Greater than 50% of the plots had no sub-canopy trees. Suckers between 0.3 and 1.3 m in height were absent from 20 of the sample plots while larger suckers, greater than 1.3 m in height, but less than 2.5 cm dbh were absent from 41 of the plots. Mean sucker density in class one was 2760 (± 3700 s.d.) ha^{-1} , ranging as high as 26,400; density in sucker class two was 600 (± 1220 s.d.) ha^{-1} , ranging as high as 9040.

On average, 26.1% (± 23.8 s.d.) of the BA per plot was in standing dead trees; percent dead BA ranged from 0 to 94.0% (Fig. 3). Mean plot-level crown dieback for mature aspen was 12.1% (± 11.0 s.d.) and ranged as high as 48.1%. A portion of trees at each plot typically showed significant damage to the bole (i.e., >20% stem circumference affected by cankers, conks, open wounds and/or stems broken, cracked, or otherwise affected by damage agents); mean damage at the plot-level for live overstorey aspen was 38.4% (± 26.5 s.d.) and ranged from 0 to 100%. At the tree-level, of 2908 live mature aspen sampled, 2204 trees (76%) showed no signs of damage. Among damaged trees, cankers and conks on tree boles were the most common symptoms recorded.

3.3. Principal component analyses

The first three principal component axes explained 55% of the total variation in the dataset (28, 15, and 12% for axes 1 through 3,

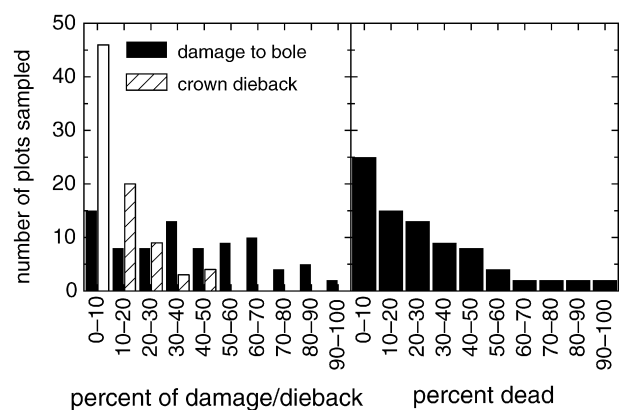


Fig. 3. Damage, dieback, and mortality on Cedar Mountain. Histograms indicating the distribution of damage, dieback, and dead basal area among sample plots on Cedar Mountain. Data suggest crown dieback to be limited, damage to be widespread, and percent of aspen basal area that is dead to be moderate. Greater than 50% of the sample plots had less than 20% dead aspen basal area.

Table 1

Eigenvectors for the first three principle component axes accounting for 28, 15, and 12% of the total variation in the input data set.

Variable	PC1	PC2	PC3
Live basal area of canopy aspen	-0.463	0.151	0.191
Canopy height	-0.229	-0.131	-0.099
Density of canopy aspen individuals	-0.415	0.227	0.166
Live basal area of sub-canopy aspen	0.180	0.568	-0.344
Density of sub-canopy aspen individuals	0.238	0.559	-0.192
Density of individuals in sucker class 1	-0.064	0.383	0.201
Density of individuals in sucker class 2	0.167	0.248	0.344
Percent dead of canopy aspen basal area	0.389	-0.198	-0.215
Percent of individuals with damage	0.202	0.004	0.579
Percent canopy dieback	0.343	0.008	0.302
Percent canopy cover	-0.342	0.086	-0.263
Live basal area of conifers	0.112	-0.134	-0.266

respectively). Eigenvectors suggest the first axis largely describes the condition of the stand with high loadings for BA and stem density of adults, canopy cover, canopy dieback, and percent of total adult BA that was dead (Table 1). The sign (+ or -) of the loadings indicates a contrast between positive and negative aspects of stand condition. The second axis is heavily weighted with variables that describe regeneration (BA and stem density of saplings, and suckers in class two). The third principal component axis is more difficult to interpret with many variables receiving moderate loadings; the highest loading was in percent of trees damaged at the study plots. Principal component analysis identified two distinct groups separating along axis 2 when plotted vs. axis 1 and axis 3; no other clear groupings existed in the first three axes (Fig. 4).

Model selection suggests landscape position and stand age explain only a small proportion of the variation in stand structure, health, and reproduction (Table 2). For the first principal component axis, the top model selected contained elevation, slope, and aspect; these variables explained 15% of the total variation on this axis. In examining the sign (+ or -) of the parameter estimate and the sign of variable loadings on the first axis, there is a slight trend for stands in the best condition – high BA and stem density, low canopy dieback and percent dead BA (Table 2) – to be located in the high-elevation regions of the study site where slopes are shallow and aspect would be expected to have little influence. For the second principal component axis, no model was found with a statistically significant explanation based on landscape position; age was the best predictor, but it was also not significant. For the third principal component axis, elevation was the only statistically

Table 2

Regression of landscape variables and age on the first three principle component axes. Model selection was accomplished in a least-squares framework using the maximum adjusted r^2 of all possible candidate models. Symbols adjacent to parameters indicate parameter estimates that were positive (+), or negative (-) for interpretation of parameter relationships with eigenvectors.

Axis	Parameter	P	Adj- r^2
PC1 (28%)	Elevation (-)	0.002	0.149
	Slope (-)	0.017	
	Aspect (-)	0.081	
PC2 (15%)	Age (-)	0.002	0.009
		0.201	
PC3 (12%)		0.201	0.062
	Elevation (+)	0.016	
		25	

significant predictor, but its ecological significance is doubtful as it only explains 6% of the variation.

The groupings identified on principal component axis two largely correspond to sites with substantial regeneration and sites with considerably fewer saplings and suckers. Considerable difference was observed in BA of saplings ($0.042 \text{ m}^2 [\pm 0.085 \text{ m s.d.}] \text{ ha}^{-1}$ vs. $0.36 \text{ m}^2 [\pm 0.22 \text{ m s.d.}] \text{ ha}^{-1}$), stem density of saplings ($11.3 [\pm 19.6 \text{ s.d.}]$ vs. $108 [\pm 56.8 \text{ s.d.}]$), suckers in class one ($1966 [\pm 2450 \text{ s.d.}]$ vs. $5640 [\pm 5980 \text{ s.d.}]$), and suckers in class two ($337 [\pm 602 \text{ s.d.}]$ vs. $1550 [\pm 2,150 \text{ s.d.}]$). These differences were statistically significant and these groupings differed only marginally in two other variables; canopy height (Table 3) and browsing damage class ($p = 0.052$). Canopy height values, which were measured on only two trees per plot and estimated for the rest, were similar enough (ca. 2 m) to cast doubt on the ecological significance of this difference. Browsing damage, however, appeared to be a possible indicator of regeneration. Of the 17 plots in the 'regeneration' category, only one was classified as having intense browsing and ca. 65% of those plots had minimal browsing; all but one of the plots categorized as having intense browsing were in the non-regenerating group. Twenty plots (42%) in the non-reproductive group, however, were classified as having minimal browsing.

4. Discussion

A vigorous discussion has ensued regarding the condition of aspen forests throughout western North America. Most of that debate has focused on the 'decline' of seral aspen communities (e.g., Strand et al., 2009), though Kurzel et al. (2007) rightly point out that stable aspen stands have garnered much less attention and

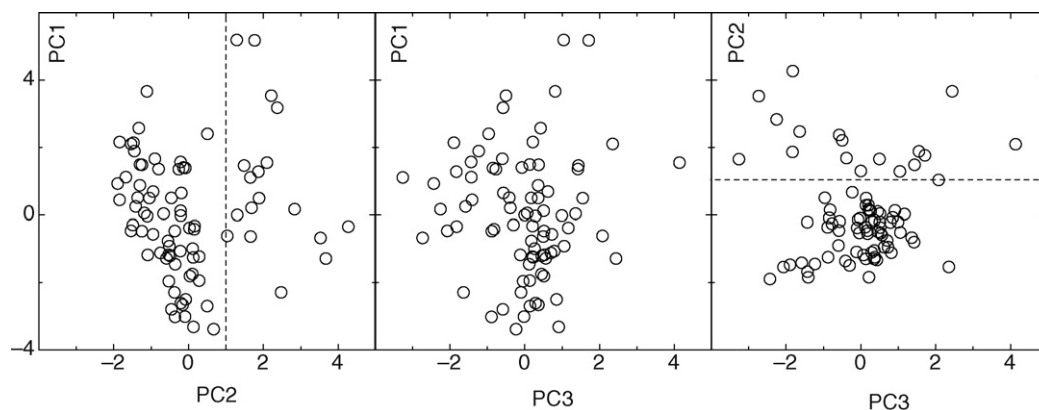


Fig. 4. Principal component analysis scatterplots. Scatterplots of the first three principal component axes accounting for 55% of the total variation in the dataset. Separation of sample points into distinct groups is evident on axis two with a break (dotted line) between the groups at ca. 1. Plots that fall into the group with principal component scores less than 1 largely lack reproduction while those in the group with principal component scores greater than 1 has sub-canopy individuals and suckers present in much greater numbers.

Table 3

T-tests examining differences in measured variables among groupings identified from the second principle component axis. Tests were performed with standard pooled variance procedure when equality of variances was satisfied, or the Satterthwaite procedure when variances were not equal. Only the appropriate statistic is reported.

Variable	DF	t	P
Slope	81	0.56	0.579
Aspect	81	0.10	0.919
Elevation	81	0.97	0.334
Age	77	1.48	0.142
Live basal area of canopy aspen	81	0.21	0.836
Canopy height	80	2.02	0.045
Density of canopy aspen individuals	81	0.22	0.824
Live basal area of sub-canopy aspen	18.4	5.91	<0.001
Density of sub-canopy aspen individuals	18.1	7.14	<0.001
Density of individuals in sucker class 1	18.6	2.55	0.020
Density of individuals in sucker class 2	17.7	2.36	0.030
Percent dead of canopy aspen basal area	80	0.06	0.954
Percent of individuals with damage	80	1.09	0.277
Percent canopy dieback	20.8	1.34	0.195
Percent canopy cover	81	0.30	0.766
Live basal area of conifers	44.6	0.78	0.440

often are not in a state of “decline.” We set out to assess conditions on a large, putatively stable, aspen landscape in southern Utah, USA. The context for this study revolves around a purported “rapid mortality” or “sudden aspen decline” (SAD) in the region (Worrall et al., 2008). A regional aspen consortium (Dr. Wayne Shepperd, Personal communication; Western Aspen Alliance: www.western-aspen-alliance.org) have defined this sudden decline as having two basic elements: (1) rapid (1–3 years) die-off of mature overstorey; and (2) absence of, or limited (i.e., non-sustainable), regeneration. Interpretation of results here will look at aspen predominance and physical conditions in a regional context, assess overstorey structure and health, and examine regeneration status and trends.

4.1. Landscape and regional context

Our study is limited to inference on stable aspen landscapes in the Colorado Plateau region. We quantify aspen stability in a two-step process. First, of the landscape classified as aspen or aspen-conifer using Southwest Regional GAP, 95% of Cedar Mountain and 79% of the region is considered aspen. Second, stand assessments at our 83 study plots indicate that 84% of the landscape is stable aspen ($\geq 80\%$ of total live BA aspen). Few studies have directly quantified aspen stability on large landscapes with systematic methods (but see Smith and Smith, 2005). Many however, consider a healthy aspen stand in the western US to have very few non-aspen trees in the canopy (Mueggler, 1989; Campbell and Bartos, 2001). The stability of our landscape arises from our study design and choice of study area; we sought to quantify condition of a stable aspen landscape, and chose a high-elevation plateau where that criterion would be met.

Landscape position and stand age played little role in describing variation in measured variables among study plots. The variation in the first principal component, which largely summarizes stocking and condition, was partly (ca. 15%) explained by landscape position suggesting best condition at higher elevation on moderate slopes. The relationship with landscape position is not surprising as it suggests aspen performs best on sites with lower abiotic stress (i.e., less evapotranspiration based on our assessment of site moisture index), a finding consistent with aspen being largely intolerant of water stress (Niinemets and Valladares, 2006). The predictive power of this relationship, however, is weak; higher elevation plots typically have stands in good condition, but the opposite is not true at lower elevations where variation among aspen plots is greater.

Landscape position, and its influence on moisture stress, is considered a pre-disposing factor in aspen stand decline (Shields and Bockheim, 1981; Frey et al., 2004) and moisture stress is implicated in aspen decline through western North America (Hogg et al., 2008; Worrall et al., 2008). Findings however, are not broadly consistent; Schier and Campbell (1980) report little influence of landscape position on stand health, and Worrall et al. (2008) found higher mortality on moderate slopes than steep slopes. In most cases, fine-scale processes such as soil texture, soil depth, or subsurface topography play a greater role in moisture delivery to aspen individuals at the stand or watershed scale. In the current study, a narrow range of variation in elevation and slope likely contributes to the lack of explanatory power. Landscape position is likely a better predictor of aspen presence at larger spatial scales (Sexton et al., 2006). However, stand-level die-offs within the study area suggest factors that have not been fully identified may be responsible for condition. We hypothesize these may include unidentified diseases, aspen bark beetles (*Trypophloeus populi*; Petty, 1977), changes in community structure (more woody species biomass) with significant biomass reductions and/or species changes in the understory, and differences in late summer water availability to stands due to stand-scale differences in ecohydrology (LaMalfa and Ryel, 2008). Ecologists and foresters need to explore additional variables to predict aspen condition at local and regional scales.

4.2. Stand structure and health

The dominant stand structure of stable aspen communities is characterized by multiple stand layers and either continuous low-level or gap/phase type regeneration (Mueggler, 1989; Mueggler, 1985; Kashian et al., 2007; Kurzel et al., 2007). Generally, stable aspen forests are not subject to stand replacing events, such as crown fires, mass insect attacks, or large-scale blowdowns (Kurzel et al., 2007). Discussions with a local expert (Dr. James Bowns, Personal communication), as well as field observations on Cedar Mountain, reveal no indication of fire for many decades (i.e., no fire scarred stumps or charcoal present in the litter). With this model in mind, we evaluate the health of the entire aspen community on Cedar Mountain. We found that most stands displayed only one or two distinct layers where we would expect to see multi-layered stands, and one in five stands had only the overstorey layer. Lack of sapling presence suggests low recruitment.

Stands ages on Cedar Mountain are within the range of aging aspen communities throughout the Rocky Mountain region (Mueggler, 1989; Rogers, 2002). Age is commonly implicated in aspen decline; stand deterioration may accelerate as ramets approach 120 years (Mueggler, 1989). Though stand ages averaged 87 years here, this variable did not explain the variation we found in our primary clusters describing conditions on Cedar Mountain. Nonetheless, the possibility remains of age-related accelerated decline on Cedar Mountain in the next one to two decades. This type of decline in mature trees may be exacerbated with the onset of significant drought in the region (Worrall et al., 2008).

Levels of damage to mature aspen stems in our study area appear to be lower than those of other regional studies with comparable methods (Rogers, 2002; Keyes et al., 2001). However, aspen diebacks in mature crowns were at slightly higher rates than those found in hardwoods as a whole in a state-level assessment of tree crowns for Utah (Keyes et al., 2001). We found less than 5% of sampled plots exhibited severe dieback (90–100% dead); however, 19% of surveyed stands exhibited mean dieback of $>20\%$. Dieback, however, could not be consistently correlated with tree damage levels, stand mortality, or low regeneration. Thus, widespread exhibition of ‘sudden aspen decline’ characteristics (Worrall et al., 2008) were not present in our Cedar Mountain dataset.

Judging from stable or recently encroached stands in northern Utah (Rogers and Ryel, 2008), mean Cedar Mountain aspen basal area seems comparable ($\sim 20 \text{ m}^2/\text{ha}$). However, Kashian et al. (2007) found that their “low elevation self-replacing aspen” averaged $27.6 \text{ m}^2/\text{ha}$ basal area. We suspect, given the geographic distance between our study area and that of Kashian et al. in Colorado’s northern Front Range, that we are not only dealing with a 500 m elevation difference, but possibly very different aspen functional types (Shepperd et al., 2006). In all of these works, we must caution, variance in basal area is somewhat high indicating probable differences in site characteristics even within landscapes.

Although we examined a stable aspen landscape, stem density appears relatively low at our study site ($315 \text{ stems ha}^{-1}$, based on a 2.5 cm DBH minimum). Stem density in the celebrated ‘Pando’ clone (DeWoody et al., 2008) in central Utah (Fishlake National Forest) is estimated at $1175 \text{ stems ha}^{-1}$ (Kemperman and Barnes, 1976); nearby Shepperd et al. (2001) estimated stem density in excess of $1500 \text{ stems ha}^{-1}$ (based on a 10 cm DBH minimum). Substantial variation in stem density among stands is expected since overstorey tree density in aspen is influenced by interacting processes that promote regeneration (i.e., apical dominance, disturbance history) and mortality (Mueggler, 1985). Basal area is a better indicator of stocking, but not necessarily of stand condition or decline since site physical conditions and stand genetics can also influence basal area (Schier and Campbell, 1980). In summary, aspen on Cedar Mountain have basal area generally comparable to other stable aspen sites, but with lower stems per hectare, indicating a landscape where many stands consist of relatively sparse and large overstorey trees as compared to other locales.

4.3. Aspen regeneration

Where catastrophic disturbance does not appear to play a strong role (i.e., stable aspen stands in the Rocky Mountains), stand replacement via continuous suckering and/or forest gap-scale recruitment appears to prevail (Mueggler, 1985; Kashian et al., 2007; Kurzel et al., 2007). Thus, we closely scrutinized sucker and sapling layers within our dataset in order to verify (or not) a pattern of regular recruitment. The Cedar Mountain study area provides evidence of reproductive impairment by two measures: a visual count of distinct stand layers and a supporting sapling inventory that indicate a missing mid-storey layer in many stands (at decadal scales) and a quantitative assessment of limited recent suckering at most plots examined (i.e., annual scale). Since visual counts only show qualitative expressions at the landscape scale, we focused our analysis on quantitative regeneration tallies. We observe separation of plots along principal component axis two into a group that largely lacks reproduction and another, smaller group, with considerable reproduction. Plots within these groupings, however, do not differ in structure, age, landscape position, or health (stem/crown damage and tree mortality); nor are they clustered on the landscape. We conclude that regular recruitment is largely absent from a major portion of the landscape.

We took a multidimensional approach to quantifying aspen reproduction by including sucker density in two size classes, sub-canopy individual density, and basal area of sub-canopy individuals. In doing so, we could assess reproduction, which can vary from a continuous to episodic process (Kurzel et al., 2007). For example, only considering sucker density may miss a sub-canopy layer that more accurately represents a true recruitment layer (Strand et al., 2009). Here, we observe all our reproductive variables to be significantly greater in the ‘reproductive’ plots compared to the ‘non-reproductive’ plots. Determining if this reproduction is sufficient to regenerate the canopy following mortality is difficult. Clearly, the sub-canopy density of individuals

in both reproductive and non-reproductive categories is considerably below the density of canopy individuals; canopy regeneration will not be possible without a substantial fraction of the suckers recruiting into larger size classes. Sucker density, however, may be satisfactory, especially in the ‘reproductive’ plots. Mueggler (1989) considers sucker density between ca. 1300 and 2500 ha^{-1} to be adequate; by this criterion, combining our sucker classes appears sufficient to regenerate stands. In contrast, Schier and Campbell (1980) found their deteriorating clones had a mean sucker density of nearly 3700 ha^{-1} .

Categorizing stands into adequate or inadequate reproductive status is complicated by: (1) the episodic nature of reproduction; (2) lack of a standard distinction between suckers and adults in the literature; and (3) multiple modes of reproduction in aspen. Reproduction in seral aspen is often driven by disturbance typically resulting in even-aged cohorts on the landscape (Mueggler, 1985; Rogers, 2002). However, stable aspen are characterized by gap-level perturbations and continuous, long-term regeneration (Mueggler, 1985; Kashian et al., 2007; Kurzel et al., 2007). Without site specific information to inform regeneration mechanisms and numbers of recruits, it is difficult to predict sustainable regeneration levels with exactitude based on landscape studies. Here, we use a size cutoff of 2.5 cm DBH for separating suckers from the recruitment class (“saplings”), but values from 2 to 10 cm are common (see Schier and Campbell, 1980; Shepperd et al., 2001). This range of variation can produce tremendous differences of individuals on a ha^{-1} basis given the rapid thinning expected following vigorous suckering (Shepperd, 1993). Finally, the long-held assumption that aspen do not reproduce sexually in western North America except under very unusual circumstances (Mitton and Grant, 1996; Romme et al., 1997) is not supported by recent molecular evidence (Mock et al., 2008). If sexual reproduction is more common, reproductive episodes may be triggered by factors other than canopy disturbance.

Regardless of adequacy of regeneration, we observed plots to exist in ‘reproductive’ and ‘non-reproductive’ modes on Cedar Mountain and our data do not provide a clear explanation for this dichotomy. Recent literature widely attributes lack of sustainable recruitment to the exogenous factor of both wild and domestic ungulate browsing (Kay and Bartos, 2000; Kaye et al., 2005). Browsing, however, was not a *definitive* cause of reproductive failure on Cedar Mountain. While 95% of reproductive plots experienced minimal to moderate browsing, 63% of the non-reproductive plots fell into the same browsing categories. Our sample period may have missed late-season browsing, which would have increased what already appears to be a prevalent impact. Moreover, attribution of reproductive failure to browsing is complicated by the many plots that had no suckers; browsing could not be assessed on those plots and they were eliminated from our analysis. It is possible that browsing has eliminated reproduction from those plots, but we could not observe it. Therefore, browsing effects remain a viable explanation on Cedar Mountain as nearly the entire study area is under private control and has been, and continues to be, used by sheep from mid-summer to fall. Similarly, wild ungulates likely contribute further to the overall browse of aspen regeneration, but separating wild from domestic browsing effects was not possible using the current landscape methodology.

We cannot, however, dismiss the possibility of endogenous differences among study plots since considerable genetic variation can exist in aspen landscapes (Mock et al., 2008; DeWoody et al., 2008) and does exist on Cedar Mountain (K. Mock, Unpublished data). Previously, clones were demonstrated to differ in suckering volume (Schier, 1974) and mechanistic traits at the ramet level (e.g., initial stem growth, number of leaves, and water use; Kanaga et al., 2008). Ongoing investigations at this

large-scale study site are planned to further scrutinize both genetic and browsing issues.

5. Conclusions and implications

We examined a large aspen-dominated landscape using the general metric of 'sudden aspen decline' (Worrall et al., 2008). This phenomenon is characterized by rapid die-off of mature overstorey in aspen coupled with an absence, or unsustainable level, of regeneration. While few stands measured here on the Colorado Plateau in Utah have experienced stand-wide mortality, a majority of these stable aspen forests appear to have limited regeneration. Thus, while not meeting the criteria of a 'sudden aspen decline' on the landscape, there is cause for concern where much of an aging cohort does not appear to possess enough recruits to regenerate the stand. Further, our initial assessment of stand structure and aspen health indicates generally good conditions, with the exception of an apparent lack of the vertical diversity expected in stable aspen stands (Mueggler, 1985; Kashian et al., 2007; Kurzel et al., 2007). Though long-term wild and domestic ungulate grazing is anecdotally implicated in this lack of regeneration, we were unable to present conclusive evidence to support that hypothesis with the current dataset.

In a regional context, this systematic survey of a stable aspen landscape may be placed alongside other studies documenting long-term change in stable and seral type mosaics on the Colorado Plateau and adjacent regions (Rogers, 2002; Kulakowski et al., 2004; Smith and Smith, 2005; Kashian et al., 2007). While we did not expressly examine temporal change – our focus was on the current outlook of the landscape – there are implications of historic and current practices dramatically affecting stable aspen types as they do in more commonly studied seral forests. It should be clear from this and other works (Kashian et al., 2007; Zier and Baker, 2006), though, that all aspen forests are not the same and, thus, should not be managed as one type. We selectively chose a study site thought to be comprised predominately of stable aspen. This functional type is characterized by a lack of large disturbance and a need for continuous regeneration. Where that pattern is impaired by human actions, future stable aspen types may be at risk of landscape- or regional-scale mortality.

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References

Bailey, R.G., 1995. Descriptions of the Ecoregions of the United States, Washington, DC. U.S. Department of Agriculture, Forest Service, Washington Office.

Barnett, D.T., Stohlgren, T.J., 2001. Persistence of aspen regeneration near the National Elk Refuge and Gros Ventre Valley elk feedgrounds of Wyoming. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Eds.), Sustaining Aspen in Western Landscapes: Symposium Proceedings. Grand Junction, Colorado, USA, 13–15 June 2000. RMRS-P-18, 27–37. Rocky Mountain Research Station, USDA, Forest Service.

Bartos, D.L., Campbell Jr., R.B., 1998. Decline of quaking aspen in the Interior West—examples from Utah. *Rangelands* 20 (1), 17–24.

Bowns, J.E., Bagley, C.F., 1986. Vegetation responses to long-term sheep grazing on mountain ranges. *Journal of Range Management* 39 (5), 431–434.

Campbell Jr., R.B., 1981. Field and Laboratory Methods for Age Determination of Quaking Aspen. INT-RN-314. Intermountain Forest and Range Experiment Station, USDA, Forest Service, Ogden, Utah.

Campbell Jr., R.B., Bartos, D.L., 2001. Aspen ecosystems: objectives for sustaining biodiversity. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Eds.), Sustaining Aspen in Western Landscapes: Symposium Proceedings., Grand Junction, Colorado, USA, 3–15 June 2000. RMRS-P-18, 299–307. Rocky Mountain Research Station, USDA, Forest Service.

DeByle, N.V., Winokur, R.P., 1985. Aspen: Ecology and Management in the Western United States. RM-GTR-119. 283, Fort Collins, CO, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

DeWoody, J., Rowe, C.A., Hipkins, V.D., Mock, K.E., 2008. "Pando" lives: molecular genetic evidence of a giant aspen clone in central Utah. *Western North American Naturalist* 68 (4), 493–497.

Di Orto, A.P., Callas, R., Schaefer, R.J., 2005. Forty-eight year decline and fragmentation of aspen (*Populus tremuloides*) in the South Warner Mountains of California. *Forest Ecology and Management* 206 (1–3), 307–313.

Frey, B.R., Loeffers, V.J., Hogg, E.H., Landhäusser, S.M., 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Canadian Journal of Forest Research* 34, 1379–1390.

Hogg, E.H., Brandt, J.P., Michaelin, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of Canadian aspen forests. *Canadian Journal of Forest Research* 38, 1373–1384.

Kanaga, M.K., Ryel, R.J., Mock, K.E., Phrender, M.E., 2008. Quantitative-genetic variation in morphological and physiological traits within a quaking aspen (*Populus tremuloides*) population. *Canadian Journal of Forest Research* 38, 1690–1694.

Kashian, D.M., Romme, W.H., Regan, C.M., 2007. Reconciling divergent interpretations of the quaking aspen decline on the northern Colorado Front Range. *Ecological Applications* 17 (5), 1296–1311.

Kay, C.E., Bartos, D.L., 2000. Ungulate herbivory on Utah aspen: assessment of long-term exclosures. *Journal of Range Management* 53 (2), 145–153.

Kaye, M.W., Binkley, D., Stohlgren, T.J., 2005. Effects of conifers and elk browsing on quaking aspen forests in the central Rocky Mountains, USA. *Ecological Applications* 15, 1284–1295.

Kemperman, J.A., Barnes, B.V., 1976. Clone size in American aspens. *Canadian Journal of Botany* 54 (22), 2603–2607.

Keyes, C., Rogers, P., LaMadeleine, L., Atkins, D., 2001. Utah Forest Health Report: A Baseline Assessment 1999/2001. State of Utah, Department of Natural Resources, Division of Forestry, Fire and State Lands, Salt Lake City, UT.

Kulakowski, D., Veblen, T.T., Drinkwater, S., 2004. The persistence of quaking aspen (*Populus tremuloides*) in the Grand Mesa area, Colorado. *Ecological Applications* 14 (5), 1603–1614.

Kurzel, B.P., Veblen, T.T., Kulakowski, D., 2007. A typology of stand structure and dynamics of Quaking aspen in northwestern Colorado. *Forest Ecology and Management* 252, 176–190.

LaMalfa, E.M., Ryel, R.J., 2008. Differential snowpack accumulation and water dynamics in aspen and conifer communities: implications for water yield and ecosystem function. *Ecosystems* 11 (4), 569–581.

Lowry, J.H. Jr., Ramsey, R.D., Thomas, K.A., Schrupp, D.L., Kepner, W.G., Sajwaj, T., Kirby, J., Waller, E., Schrader, S., Falzarano, S., Langs Stoner, L., Manis, G., Wallace, C., Schulz, K., Comer, P., Pohs, K., Rieth, W., Velasquez, C., Wolk, B., Boykin, K.G., O'Brien, L., Prior-Magee, J., Bradford, D., Thompson, B., 2007. Land cover classification and mapping. (Chapter 2) In: J.S. Prior-Magee, et al. (Eds.) Southwest Regional Gap Analysis Final Report. U.S. Geological Survey, Gap Analysis Program, Moscow, ID (<http://fws-nmcfwru.nmsu.edu/swregap/report/SWReGAP%20Final%20Report.pdf>).

Manier, D.J., Laven, R.D., 2002. Changes in landscape patterns associated with the persistence of aspen (*Populus tremuloides* Michx.) on the western slope of the Rocky Mountains, Colorado. *Forest Ecology and Management* 167, 263–284.

McNab, H.W., Avers, P.E., 1994. Ecological Subregions of the United States: Section Descriptions. USDA, Forest Service, Washington, DC.

Mitton, J.B., Grant, M.C., 1996. Genetic variation and the natural history of quaking aspen. *Bioscience* 46 (1), 25–31.

Mock, K.E., Rowe, C.A., Hooten, M.B., Dewoody, J., Hipkins, V.D., 2008. Clonal dynamics in western North American aspen (*Populus tremuloides*). *Molecular Ecology* 17, 4827–4844.

Mueggler, W.F., 1985. Vegetation associations. In: DeByle, N.V., Winokur, R.P. (Eds.), Aspen: Ecology and Management in the United States. RM-GTR-119. Rocky Mountain Forest and Range Experiment Station, USDA, Forest Service, CO, Fort Collins, pp. 45–55.

Mueggler, W.F., 1988. Aspen Community Types of the Intermountain Region. GTR-INT-250. Intermountain Research Station, USDA, Forest Service, Ogden, UT.

Mueggler, W.F., 1989. Age distribution and reproduction of Intermountain aspen stands. *Western Journal of Applied Forestry* 4 (2), 41–45.

Ninemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76, 521–547.

NRCS, 2007. Natural Resources Conservation Service, SNOTEL precipitation data for Webster Flat and Kolob (1980–2007). Utah. 2 March 2009.

Ohms, S.R., 2003. Restoration of aspen in different stages of mortality in southern Utah. Logan, UT, College of Natural Resources, Utah State University [Thesis].

Petty, J.L., 1977. Bionomics of two aspen bark beetles *Trypophloeus populi* and *Procryphalus mucronatus* Coleoptera Scolytidae. *Great Basin Naturalist* 37 (1), 105–127.

- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- Roberts, D.W., Cooper, S.V., 1989. Concepts and techniques of vegetation mapping. In: Ferguson, D., Morgan, P., Johnson, F.D. (Eds.), *Land Classification based on Vegetation: Applications for Resource Management*. INT-257, 90–96. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Rogers, P., 2002. Using Forest Health Monitoring to assess aspen forest cover change in the southern Rockies ecoregion. *Forest Ecology and Management* 155 (1–3), 223–236.
- Rogers, P.C., Shepperd, W.D., Bartos, D.L., 2007. Aspen in the Sierra Nevada: regional conservation of a continental species. *Natural Areas Journal* 27 (2), 183–193.
- Rogers, P.C., Ryel, R.J., 2008. Lichen community change in response to succession in aspen forests of the Rocky Mountains, USA. *Forest Ecology and Management* 256, 1760–1770.
- Romme, W.H., Turner, M.G., Gardner, R.H., Hargrove, W.W., Tuskan, G.A., Despain, D.G., Renkin, R.A., 1997. A rare episode of sexual reproduction in aspen (*Populus tremuloides* Michx.) following the 1988 Yellowstone fires. *Natural Areas Journal* 17 (1), 17–25.
- SAS, 2005. SAS Institute. Cary, NC, USA, SAS Institute Inc., 2005.
- Schier, G.A., 1974. Vegetative propagation of Aspen: clonal variation in suckering from root cuttings and in rooting of sucker cuttings. *Canadian Journal of Forest Research* 4 (4), 565–567.
- Schier, G.A., Campbell, R.B., 1980. Variation Among Healthy and Deteriorating Aspen Clones. RP-INT-264. Intermountain Forest and Range Experiment Station, USDA, Forest Service, Ogden, Utah.
- Sexton, J.O., Ramsey, R.D., Bartos, D.L., 2006. Habitone analysis of quaking aspen in the Utah Book Cliffs: effects of site water demand and conifer cover. *Ecological Modeling* 198, 301–311.
- Shepperd, W.D., 1993. Initial Growth, Development, and Clonal Dynamics of Regenerated Aspen in the Rocky Mountains. RM-RP-312. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Shepperd, W., Rogers, P.C., Burton, D., Bartos, D., 2006. Ecology, Biodiversity, Management, and Restoration of Aspen in the Sierra Nevada, RMRS-GTR-178. Rocky Mountain Research Station, USDA, Forest Service, Fort Collins, CO.
- Shepperd, W.D., Bartos, D.L., Mata, S.A., 2001. Above- and below-ground effects of aspen clonal regeneration and succession to conifers. *Canadian Journal of Forest Research* 31 (5), 739–745.
- Shields Jr., W.J., Bockheim, J.G., 1981. Deterioration of (over-mature) trembling aspen clones in the Great Lakes region. *Canadian Journal of Forest Research* 11 (3), 530–537.
- Smith, A.E., Smith, F.W., 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA. *Forest Ecology and Management* 213, 338–348.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*. W.H. Freeman and Company, New York.
- Strand, E.K., Vierling, L.A., Bunting, S.C., Gessler, P.E., 2009. Quantifying successional rates in western aspen woodlands: current conditions, future predictions. *Forest Ecology and Management* 257, 1705–1715.
- Tshireletso, K., 2008. Simulated browsing impacts on aspen suckers' density, growth, and nutritional responses. Logan, Utah, Utah State University [Dissertation].
- USDA Forest Service, 2007. Field methods instructions for Phase 2 (Forest Inventory) and Phase 3 (Forest Health) of the National Forest Inventory and Analysis program.
- Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *Forest Ecology and Management* 255, 686–696.
- Zier, J.L., Baker, W.L., 2006. A century of vegetation change in the San Juan Mountains, Colorado: an analysis using repeat photography. *Forest Ecology and Management* 228, 251–262.