## RESEARCH ARTICLE

# Quaking Aspen in the Residential-Wildland Interface: Elk Herbivory Hinders Forest Conservation

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ABSTRACT: Quaking aspen (Populus tremuloides) forests are experiencing numerous impediments across North America. In the West, recent drought, fire suppression, insects, diseases, climate trends, inappropriate management, and ungulate herbivory are impacting these high biodiversity forests. Additionally, ecological tension zones are sometimes created at residential-wildland interfaces with divergent management directives. For example, private conservation reserves bordering public land may be degraded from browsing where game species find refuge from hunting and plentiful forage. We examined putative herbivore impacts to nearly pure aspen forests at Wolf Creek Ranch (WCR), a sparsely developed residential landscape in northern Utah. Forty-three one-hectare monitoring plots were established to measure forest attributes including site characteristics, tree and vegetation condition, and herbivore use. Additionally, we tested the ability of a plot-level visual rating system to characterize objective field measures. Results suggest elk (Cervus elaphus) herbivory is currently having a strong effect on aspen in the study area, reducing many locations to nearly single-layer aspen forests dominated by aging canopy trees. Regeneration (<2 m tall stems) is experiencing moderate to high browse impacts, and recruitment (2-6 m stems) is below replacement levels on approximately half of WCR's aspen forests. The visual rating system accurately reflected significant trends in forest cover, canopy height, plot aspect, regeneration, recruitment, and tree mortality. Ordination of plot and forest data indicated a strong negative relationship between elk presence and recruitment success. We make recommendations for addressing difficult herbivore-aspen interactions where publicly managed wildlife present barriers to conservation within residential forest reserves.

Index terms: browse, forest health, monitoring, recruitment, Rocky Mountains

#### **INTRODUCTION**

Quaking aspen (*Populus tremuloides* Michx.) communities are often considered biodiversity "oases" surrounded by dominant conifer or meadow types in western settings (Mueggler 1985; Griffis-Kyle and Beier 2003; Kuhn et al. 2011; Gonzalez et al. 2013). Previous work has shown that aspen forests disproportionately support high levels of diversity compared to their landscape coverage (Kuhn et al. 2011). While aspen forests are highly valued for their flora and fauna, in some locales herbivores are having great impacts on the ability of these systems to maintain this high diversity (Martin and Maron 2012).

Browsing ungulates-both wild and domestic-in many western states are inhibiting recruitment as they consume juvenile aspen (DeByle 1985; Zeigenfuss et al. 2008; DeRose and Long 2010; Rogers et al. 2010; Bork et al. 2013). This phenomenon seems particularly acute where wild ungulate populations are thought to be above historical population levels (e.g., Bailey et al. 2007; Stritar et al. 2010) or where predation is minimal or hunting is prohibited (Beschta and Ripple 2009). Moose (Alces alces L.), elk (Cervus elaphus L.), mule deer (Odocoileus hemionus Raf.), and smaller mammals may severely damage mature trees by debarking portions

of boles via chewing or when (for larger ungulates) rubbing their antlers to remove velvet during rutting (Hinds and Krebill 1975; DeByle 1985; Johnston and Naiman 1990). Physical penetration of aspen bark may lead to further infections by a range of lethal pathogens (Walters et al. 1982).

Similar to wild herbivores, domestic ungulates will browse aspen sprouts, particularly where preferred forage is depleted (DeByle 1985; Jones et al. 2005; Rogers et al. 2010). The long-term effects of repeated heavy browsing of regeneration include reduction of vertical stand structure in stable aspen and elimination of aspen understory in seral systems (Kuhn et al. 2011). In both cases, dying mature trees may lose the physiological reserves required to continue producing aspen suckers, resulting in complete forest loss as a maturing overstory eventually dies.

There are at least two distinct western aspen functional types: seral and stable (Harniss and Harper 1982; Rogers et al. 2014). Seral aspen, over a period of decades to centuries, compete with one to several conifer species for forest dominance. Forest disturbance favors quick reproduction and early dominance by aspen. Following removal of mature trees via natural or human mechanisms, seral aspen have a competitive advantage by producing thousands of root sprouts (DeByle 1983; Shepperd et al. 2006). Stable aspen-also called "pure" or "persistent" aspen-forests are essentially single-species forests with little or no competition from western conifers (Harniss and Harper 1982; Shepperd 1990). These forests contrast with seral aspen communities: stable aspen rely on gap-phase dynamics and structural diversity, whereas seral aspen display complex interactions with conifers, are dependent on stand-replacing events, and the mass sprouting often results in an even-aged aspen component (Rogers et al. 2014). Traditional aspen management has favored stand-replacing methods appropriate for seral aspen but inappropriate for stable communities. Fire events have historically played an important role, along with favorable climatic conditions, in aspen's long-term persistence on landscapes (Kulakowski et al. 2004; Rogers et al. 2007, 2011). Conversely, lack of disturbance facilitated by cool, moist, climate patterns favors conifer domination of shade-intolerant aspen (Rogers et al. 2011).

In areas with moderate ungulate herbivory, wildfire (and other disturbance) initiates sprouting opportunities for successful aspen recruitment. Further, future climate warming is expected to result in larger, more frequent forest fires, as well as interacting effects of multiple disturbances (e.g., fire, wind throw, insect mortality). Recent research suggests that multiple and frequent overlapping disturbances in western forests will favor aspen forest development if herbivory is limited (Kulakowski et al. 2013). Better understanding of the interactions of disturbance scale, intensity, and ungulate consumption patterns would help managers make decisions that increase aspen resilience under future climate scenarios. In stable aspen forests, stand-replacing disturbances are uncommon (Shinneman et al. 2013; Rogers et al. 2014). For this aspen type, structural diversity facilitated by continuous regeneration and recruitment of young aspen stems is a key indicator of forest resilience (Rogers et al. 2010; Rogers and Mittanck 2014).

Increasingly, "exurban" or residentialwildland home development is driving population growth in the Mountain West

(Riebsame and Robb 1997; Theobald and Romme 2007). Many second home buyers invest in properties adjacent to national forests or other public lands because they wish to be surrounded by scenic, quiet, and biodiverse landscapes. Residentialwildland properties are also seen as savvy investments, given that adjacent lands will not be sold and future owners will be assured of a similar aesthetic, therefore preserving or increasing property value. Many owners are unaware of the dynamic nature of, and potential threats to, residential development where forest fires, insects and disease, landslides, and even large ungulate herbivory may drastically alter forest communities (Theobald and Romme 2007).

We undertook an assessment of aspen forest conditions at Wolf Creek Ranch (WCR), Utah. WCR is a sparsely developed residential landscape with home sites dispersed amongst stable aspen, mixed-conifer forests, sagebrush meadows, and riparian areas. Preliminary surveys indicated that most of the forests are stable aspen and a lack of aspen recruitment may be related to herbivore use. Our landscape-level aspen monitoring at WCR had three prime goals: (1) produce an objective assessment of aspen forest conditions at the landscape level; (2) determine causal factors of problems, if detected, in WCR aspen forests; and (3) make recommendations for sustainable management of these natural systems. Findings from this effort are expected to help reserve managers meet the challenges of maintaining aspen forests that are surrounded by natural areas with competing agency directives. This case study combines unique elements of residential-wildland landscapes, stable aspen communities, and ungulate impacts. All of these factors are increasingly relevant to researchers and managers faced with competing uses and expanding wildland development in the western United States.

# METHODS

# Study Area

Wolf Creek Ranch is located in northeastern Utah near the intersection of the Wasatch and Uinta Mountains (Figure 1). The WCR property covers 5382 ha, with an estimated 2333 ha (~43%) of this area dominated by aspen forests. The study area consists of an aspen-conifer topped plateau that descends north to the Provo River and south to the Heber Valley. Thirty separate soil types can be found on WCR, most of which are loams, in a variety of terrains. Surface soils overlay primarily Keetley volcanic tuffs. Overall, the soils of the study area resemble those typically found in forested landscapes in this region. WCR ranges from 1950 to over 2750-m elevation, however most of the aspen on the property can be found between 1950 and 2443 m. The closest rain gauge (SNOTEL #330) recorded an average annual precipitation of 694 mm between 1987 and 2012. Most precipitation occurs as winter snow, with midsummer being the driest period.

Given the considerable elevation gradient from the top of WCR to the lower portion of the ranch, aspen display marked variation in phenology and morphology, and in community composition (Abraham 2013). In general, at dry sites and at lower elevations, aspen and conifer forests on WCR are among areas of mountain big sagebrush (Artemisia tridentata ssp. vaseyana Rydb.) or bigtooth maple (Acer grandidentatum Nutt.) and Gambel oak (Quercus gambelii Nutt.) woodlands. Forested uplands at WCR are dominated by stable aspen communities, with some conifer (mainly Douglas-fir (Pseudotsuga menziesii Franco), subalpine fir (Abies lasiocarpa Nutt.), and white fir (Abies concolor Lindl. ex Hildebr.) cover on steeper north and east facing slopes.

Primary large herbivores on WCR include deer, elk, and domestic sheep (*Ovis* spp.). Moose are found in the area, but in very low numbers. Domestic livestock, unlike wild herbivores, tend to browse aspen only late in the season after herbaceous plants have senesced (Beck and Peek 2005). WCR allows 3000 sheep to graze on the property each year for two weeks in early June and for another six to seven weeks in October and November. Sheepherders have been instructed to keep sheep out of aspen stands, though this is sometimes difficult to achieve. Based on anecdotal sightings

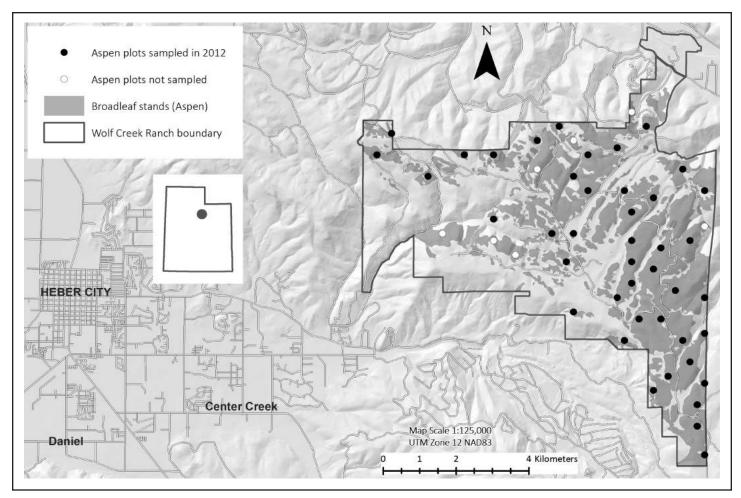


Figure 1. Wolf Creek Ranch, Utah, study area and sample plot locations (black dots). Some plots were not sampled because they were dominated by forest cover other than aspen (white dots). Sampling was conducted 15 June–30 July, 2012.

and preliminary vegetation surveys, elk populations are thought to be moderate to high for this habitat (see Methods section below). Deer numbers, while declining statewide in recent decades, are not well known in the context of WCR. Hunting of wild ungulates is allowed on adjacent public lands. In 2013 (after data collection for this study), a small number of guided elk hunting permits were issued.

#### **Study Design and Field Methods**

Using GIS, we overlaid a 500-m grid on the WCR landscape and selected 50 sample points at random from those sites intersecting a pre-existing digital aspen cover layer. A 1-ha monitoring plot was placed at each point. Seven plots were eliminated because they had less than 50% aspen canopy cover based on ground truthing, resulting in 43 sample locations. At each plot, we measured forest structure, tree composition, regeneration and recruitment, landscape elements, browse level, and herbivore use. Additionally, we noted plot-level conditions using a subjective rating system specifically designed for aspen forest assessment. Field crews were trained to accurately describe stand type (stable or seral), number of vertical aspen layers, percent aspen canopy cover, and recent disturbance.

Field data were collected during June and July of 2012 by "citizen scientists" who were trained and quality checked by the study's principal authors. Some basic forest measurements, for example, tree diameters and heights, were converted to estimates or classifications to accommodate nonexpert data collection in a consistent manner. A more thoroughly trained field technician was present on all field plots to ensure

quality and standardization. All field measurements were performed within two  $2 \times$ 30 m belt transects oriented perpendicular to each other, at cardinal directions, to capture terrain variations. Within transects we counted all aspen regeneration (number of stems <2 m height), recruitment (stems  $\geq 2$  m and  $\leq 6$  m height), and mature canopy trees (trees >6 m height). For each aspen regeneration stem, we examined leaders and lateral branches for browsed buds and twigs to determine percent browse. Personnel were trained to observe the difference between browse and other forms of stem necrosis initiated by pathogens. Mature trees (those  $\geq$ 7.6 cm dbh), both live and dead, were counted in three diameter classes: 7.6–15.2 cm, >15.2–25.4 cm, and >25.4 cm. Midpoints of each of these diameter classes were used to calculate basal area per ha. Estimates of average canopy height were taken for the tallest layer of trees using a Biltmore stick. Also along transects, field crews counted distinct ungulate fecal piles (Bunnefeld et al. 2006). Individual piles were distinguished as having at least three pellets per defecation. Fecal counts were separated by species for mule deer, elk, and domestic sheep. Where fecal piles could not be positively identified, they were not counted. Mean values of calculated variables were assumed to represent the surrounding 1 ha and total counts were expanded from the fixed area of transects (120 m<sup>2</sup>) to 1 ha values (× 83.33).

To characterize environmental conditions at the plot level, a number of descriptive variables were recorded. Aspen stand types may be typed either seral or stable. If conifers were present (>10% cover) or actively reproducing within an aspendominant plot, it was considered seral. Stable aspen forests were those having few, if any, conifers present and were at least 40 years postdisturbance. Intact stable aspen types commonly display a complex vertical stand structure (Kurzel et al. 2007; Rogers et al. 2010, 2014). Field crews were trained to distinguish vertical aspen layers by looking horizontally through the forest from plot center and counting clearly distinguishable aspen layers (i.e., understory, young recruitment, intermediate height, and canopy-level trees). The presence of small numbers of regeneration or recruitment did not a priori constitute an easily distinguishable "layer." Where layers could not be determined due to continuous vertical stand structure, field crews were instructed to record the maximum value (four layers). A mean aspen canopy cover was derived from 14 visual estimates (without instruments) located equidistantly along transects. Averaging these values across the plot gave a gross estimate of aspen canopy coverage. Recent forest disturbances include damage to trees, vegetation, or the forest floor that significantly affect the condition of the sample plot (e.g., >50% of area or trees affected). Types of disturbances include such things as recent fires, heavy grazing or browsing, insect or disease infestations, other animal damage, or weather damage such as frost or heat scald.

A visual estimation of plot conditions

was developed in a previous study as a time-saving method of forest assessment (Rogers and Mittanck 2014). Written guidelines for visually assessing tree damage and mortality, aspen layers, and overall browse impact were used to arrive at overall rankings of "Poor," "Moderate," or "Good" aspen forest conditions. The Moderate category encompasses a much greater range of conditions, whereas Poor and Good groups are defined by proportional extremes making these rankings more difficult to achieve. It is important to note that plot-level visual assessments are always made prior to objective data collection to avoid potential circularity in categorical analysis (i.e., ratings could not be used to verify objective measures if they were influenced by data collection). Field crews were trained and checked for consistency in distinguishing these broad categorical distinctions.

Additional environmental variables, such as location, elevation, aspect, and slope, were determined for each plot using digital databases post hoc. We took average readings (100 points) from digital maps of the 1-ha area surrounding the plot center. Plot aspect (the downhill compass direction of a sloped sample site) was transformed from a 360° scale to a moisture index (0-1) from dry (southwest) to wet (northeast), respectively (Roberts and Cooper 1989).

Residents contracted with the Utah Division of Wildlife Resources to conduct a helicopter survey of WCR elk populations in the fall of 2012 (after leaf-off). This information was combined with a landowner road survey (17.7-km circuit), taken throughout the summer and fall, and modeled based on "sight-ability" from specific points along the circuit. Surveys were not conducted during winter as elk move to lower elevations during this time due to heavy snowpack.

## **Data Analysis**

Thresholds for regeneration, recruitment, and browse intensity taken from the literature (Mueggler 1989; Jones et al. 2005; O'Brien et al. 2010; Rogers and Mittanck 2014) were compared with our results to gauge plot- and landscape-level aspen status at WCR. Next, we wanted to test whether visual cues, if corroborated by objective measures, could provide a reliable assessment of general aspen conditions across the 1-ha sample area. We tested the visual condition rating system for its ability to detect categorical differences in field measures using the nonparametric Kruskal-Wallace test. Output from this test is shown as Wilcoxon scores (SAS<sup>®</sup> v 9.3; Zar 1999). All plot variables were then evaluated using non-metric multidimensional scaling (NMS) using PC-ORD (McCune and Mefford 2006), an ordination procedure used to extract ecological patterns from the most important indicators of vegetative conditions (McCune et al. 2002). We ran the NMS with and without location data (elevation, GPS coordinates) to find the best results. The ordination was initiated with a random start number upon 250 runs of the actual data set using Sørensen distance measure. A Monte Carlo test was then run on the lowest stress solution using 250 randomized runs to evaluate the probability of results being greater than chance occurrence. All analyses in this study were considered significant when P  $\leq$  0.05. Significant results were mapped to look for geographic patterns across WCR's aspen landscape.

# RESULTS

The WRC aspen landscape is dominated by stable aspen communities with only two of our 43 plots (<5%) being seral types. Using regeneration standards provided by O'Brien et al. (2010; (Mueggler 1989; Campbell and Bartos 2001; Kurzel et al. 2007; Rogers et al. 2010 cited within)), 46% of plots sampled at WCR are not self-replacing (<1250 stems ha<sup>-1</sup>) and an additional 19% are marginally self-replacing (1250–2500 stems ha<sup>-1</sup>). We compared browse levels on regeneration at WCR to a 20% sustainable browse threshold provided by Jones et al. (2005). By this standard, 72% of aspen plots did not meet the threshold for sustainability. Fifty-one percent of sample locations did not have the minimum 1250 recruitment stems ha<sup>-1</sup> recommended by O'Brien et al. (2010) to be self-replacing. A more rigorous measure of recruitment threshold is geared to specific site conditions by calculating the

number of recruitment stems as a percentage of the live aspen overstory trees—100% equals overstory replacement—using a site-specific approach (Rogers and Mittanck 2014). Using this metric, 41% of our plots had less than 100% of canopy tree recruitment (Figure 2). Exactly half of our WCR aspen sample locations had greater than 20% mortality. We recorded no significant stand-level disturbances within the study area. Survey-wide animal pellet counts were as follows: sheep – zero, deer – eight, and elk – 96. Field crews did see sheep dung near sample locations, but it was never tallied on transects.

Wilcoxon scores for the Kruskal-Wallace test are displayed in Figure 3 for those field measures with significant differences. Aspen canopy cover (Figure 3A;  $\chi^2 = 9.69$ , P = 0.004), canopy height (Figure 3B;  $\chi^2 =$ 8.26, P = 0.009), plot aspect (Figure 3C;  $\chi^2$ = 5.50, P = 0.056; slightly above threshold), aspen regeneration (Figure 3D;  $\chi^2 = 10.02$ , P = 0.003), recruitment as a percentage of trees ha<sup>-1</sup> (Figure 3E;  $\chi^2 = 10.21$ , P =0.003), and aspen recruitment ha<sup>-1</sup> (not shown, redundant to previous measure;  $\chi^2 = 11.26$ , P = 0.001) were all positively correlated with visual plot condition. For aspect this means that south and southwest aspects, overall drier locations, correlate with poorer plot conditions. Mature tree mortality was negatively correlated with plot condition (Figure 3F;  $\chi^2 = 5.67$ , P = 0.048).

Figure 4 shows results of NMS ordination with the WCR aspen data set used to indicate important indicators of plot and landscape conditions. The NMS produced a two-dimensional solution with a final stress of 12.50 (instability < 0.000; Axis 1  $r^2 = 0.69$ ; Axis 2  $r^2 = 0.20$ ; orthogonality = 99.2%). Monte Carlo test results show that the two-axis solution using real data was significant (P = 0.004). The results displayed in Figure 4 show statistical relationships in "plot space" between sample points, with an overlay of condition ratings by plot, and a display of vectors with Pearson's r values greater than 0.5 or less than -0.5. In total, the degree of stability, Monte Carlo results, and variability explained by this analysis indicate a highly significant NMS result (McCune et al. 2002). Vectors show both strength and direction of significant forest attributes. All indicator relationships to the primary axes are shown in Table 1. Axis 1 represents a strong negative correlation between successful recruitment and elk presence. Axis 2 represents a general measure of forest vitality as represented by total live trees, cover, and regeneration. There is overlap in these two prime axis themes in the form of positive responses of cover and regeneration to both ordination axes (Table 1). These general relationships are also depicted in the plot condition rating; plots in good condition correspond to positive points on the prime axes and poorly rated plots fall predominantly in the negative portions of

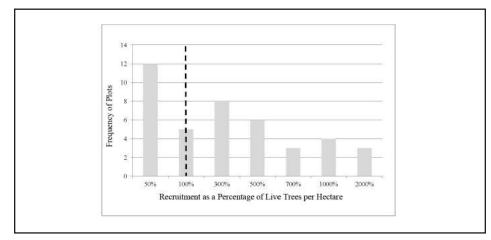


Figure 2. Histogram of aspen recruitment as a percentage of live mature trees per ha<sup>-1</sup>. Dotted line represents the threshold, or 1:1 ratio or 100% of recruitment to mature trees, required for self-replacement of the forest over time (Rogers and Mittanck 2014). Sampling at Wolf Creek Ranch, Utah, was conducted 15 June to 30 July 2012.

the joint plot (Figure 4).

Combined helicopter and ground surveys of elk presence resulted in an estimate of 425 seasonally resident animals. When divided by the total area of WCR, we estimate a population density of 7.8 elk/ km<sup>2</sup>.

#### DISCUSSION

#### Aspen Conditions Implicate Elk Herbivory

There is cause for concern regarding the sustainability of the aspen forests at WCR. Nearly half of our sample locations showed low recruitment and poor regeneration (Figures 2, 4, 5). According to the guidelines of previously published work (Jones et al. 2005), nearly three quarters of the WCR survey locations contained browse levels deemed unsustainable over time. Overall, aspen canopy cover, regeneration, and recruitment clearly were lower, and mortality was higher, as plot condition decreased (Figure 3). There was an inverse relationship between elk presence and aspen recruitment: where there is more elk scat there is less recruitment (Figure 4). When we plotted these data spatially (Figure 5), we found a concentration of poor regeneration (Figure 5A), poor recruitment (Figure 5B), and visually poor plot conditions (Figure 5D) near the center-east portion of the study area where there was generally high elk presence as indicated by scat (Figure 5C). We can only speculate, without further study, that these locations provided prime habitat for seasonal (summer/fall) elk use: moderate terrain, ample moisture/forage, and low levels of hunter threat, which may occur near WCR boundaries. We note, however, that many locations within the WCR aspen landscape appeared to show moderate to good conditions. Overall, the condition of these ecosystems is not as severe as locations in Utah where climates appear to be dryer, browsing is heavier, and recovery times are slower (i.e., Rogers and Mittanck 2014).

Previous work suggests that aspen may be successfully recruited where elk densities are  $\leq 1$  animal/ km<sup>2</sup> (Durham and Marlow 2010; Runyon et al. 2014). Where WCR

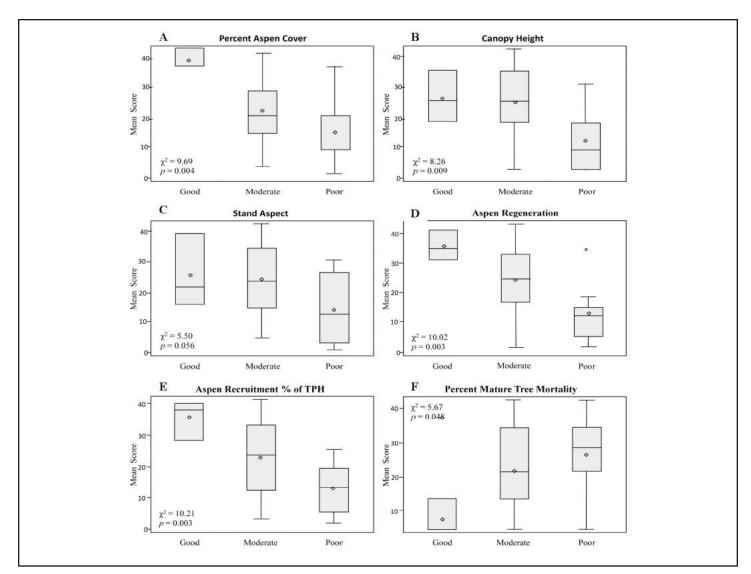


Figure 3. Box plots based on results of Kruskal-Wallace nonparametric tests for differences between plot condition groups (Good, Moderate, Poor) for: (A) percent aspen canopy cover, (B) canopy height, (C) stand (plot) aspect, (D) aspen regeneration ha<sup>-1</sup>, (E) recruitment as a percent of overstory stems, and (F) mortality trees as a percent of live overstory tree count. Output from Kruskal-Wallace test (SAS®) is shown in Wilcoxon mean scores on the Y-axis. Whiskers show minimum and maximum values, boxes represent 25–75% data ranges, horizontal lines within boxes are medians, and diamond symbols are means. Results are considered significant where a Monte Carlo simulated Chi-square test using 10,000 runs produced an estimated *P* value of <0.05. Sampling at Wolf Creek Ranch, Utah, was conducted 15 June to 30 July 2012.

populations are nearing eight elk/ km<sup>2</sup> this is an additional indicator of potential aspen habitat impacts and corroborates shortfalls in aspen recruitment in this landscape.

Recruitment is both a measure of structural diversity—particularly important to avian diversity—and longer-term browse patterns. One-time measures of low or absent recruitment strongly suggest a temporal pattern, particularly in stable aspen types where recruitment should be continuous (Kurzel et al. 2007; Rogers et al. 2010); lack of recruitment in stems typically 5–40 years of age demonstrates sustained preclusion of growth (DeByle 1985; Zeigenfuss et al. 2008). Previous work shows that decadal fluctuations in ungulate populations are correlated with survival of young aspen suckers through recruitment and into mature stages (Larsen and Ripple 2003). Using O'Brien et al. (2010) as a generalized guideline for WCR, we found that 51% of our locations did not meet the minimum recruitment standard (1250 stems ha<sup>-1</sup>) to be considered self-replacing. A more sensitive approach determines recruitment success based on the number of aspen present in the canopy at each site (Rogers and Mittanck 2014).

The logic behind this measure is that environmental conditions control the number of trees that can grow at each location and that recruitment should at least be equal to the number of mature trees (i.e., 1:1 ratio). Taking this approach, WCR aspen overall fared slightly better with 41% of locations having less than 100% of canopy tree recruitment (Figure 2). It should be stressed that both criteria—amounting to 41%–51% of the landscape falling short of recruitment thresholds—are based on *minimum* stems needed to replace existing overstory, which is a very conservative metric for a predominantly stable landscape

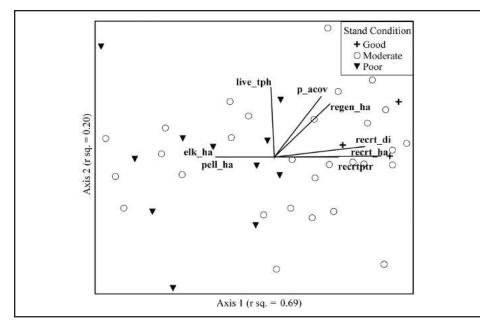


Figure 4. Non-metric multidimensional scaling (NMS) joint plot depicting an ordination of all final WCR aspen indicator variables. Symbols represent plot condition ratings of individual survey plots in data space. Vectors show only indicators with Pearson's *r* values greater than 0.5 (Table 1). Vectors describe indicator direction and strength (length of line). Amount of the total data set explained is shown as  $r^2$  values along each axis. Generally, Axis 1 is defined by recruitment (+) and elk presence (-). Axis 2 corresponds most directly to live trees ha<sup>-1</sup>. From left to right, indicators are: pell\_ha = total pellets (all species) ha<sup>-1</sup>; elk\_ha = elk pellets ha<sup>-1</sup>; live\_tph = live mature aspen trees ha<sup>-1</sup>; p\_acov = percent aspen cover; regen\_ha = aspen regeneration ha<sup>-1</sup>; recrt\_di = recruitment defined by diameter; recrt\_ha = recruitment (by height) ha<sup>-1</sup>; recrtptr = recruitment (by height) as a percent of live aspen trees ha<sup>-1</sup>. Sampling at Wolf Creek Ranch, Utah, was conducted 15 June to 30 July 2012.

Table 1: Pearson's coefficients (r) between environmental variables and primary ordination axes. The strongest response variables are in bold type where r > 0.5 or < -0.5. TPH = trees ha<sup>-1</sup>. Sampling at Wolf Creek Ranch, Utah, was conducted 15 June to 30 July 2012.

	Pearson's r	
	Axis 1	Axis 2
% Aspen Cover	0.584	0.553
Canopy Height	0.051	0.474
Aspect	0.392	0.167
Slope	-0.01	-0.241
Regeneration ha <sup>-1</sup>	0.632	0.508
Percent Browse	-0.118	0.034
Recruitment (Height) ha <sup>-1</sup>	0.835	-0.041
Aspen TPH	-0.113	0.706
Recruitment % of Aspen TPH	0.643	-0.128
Mortality % of Aspen TPH	-0.026	-0.432
Recruitment (DBH) ha <sup>-1</sup>	0.78	0.149
Basal Area	0.019	0.229
Elk Pellets ha <sup>-1</sup>	-0.617	0.099
Deer Pellets ha <sup>-1</sup>	0.112	0.118
Total Pellets ha <sup>-1</sup>	-0.574	0.113

presumed to function based on continuous recruitment with an overall uneven age structure (Mueggler 1985; Kurzel et al. 2007; Rogers et al. 2014).

Mortality is a common indicator of plot "health" in all types of forests (Keyes et al. 2001). Half of our WCR aspen sample locations had greater than 20% mortality. While this is not an unusually high number for aspen, combined with a moderate to high level of browse, this may be an indication of forests beginning to degrade in both mature and juvenile age classes simultaneously (i.e., from "above" and "below"). As overstory trees die and are not replaced by new recruits, a general decrease in root resources may lead to declining regeneration capacity (Frey et al. 2003; Anderegg et al. 2012). With this type of progression we expect to see conversions of understory communities away from herbaceous cover and toward shrub dominance (Bartos 2001).

Separation of plot condition classifications (Good, Moderate, Poor) in ordination space reinforces actual differences as measured with all the other objective plot variables combined (Figure 4). Use of the visual classification could only take place after we had first established some objective basis to the visual rating system (Figure 3). This categorical variable is not part of the ordination analysis per se; it is used as an overlay in total plot and dataset space (Figure 4). In light of this, "Poor" condition plots fall almost exclusively on the left, signifying our objectively impacted plots. Several plots, however, also appear to have a relatively high number of trees ha<sup>-1</sup>, but low recruitment and frequent elk visitation, signaling a potentially robust recovery should browsing decrease. The majority of stands, at least from a visual rating standpoint, are spread across the data landscape (as we might expect) in the very broad "Moderate" category.

In terms of indicator strength and direction, the most notable trend is the inverse relationship between recruitment and elk pellets ha<sup>-1</sup> (axis 1). While our between group tests described a trend that was not statistically significant, the more rigorous

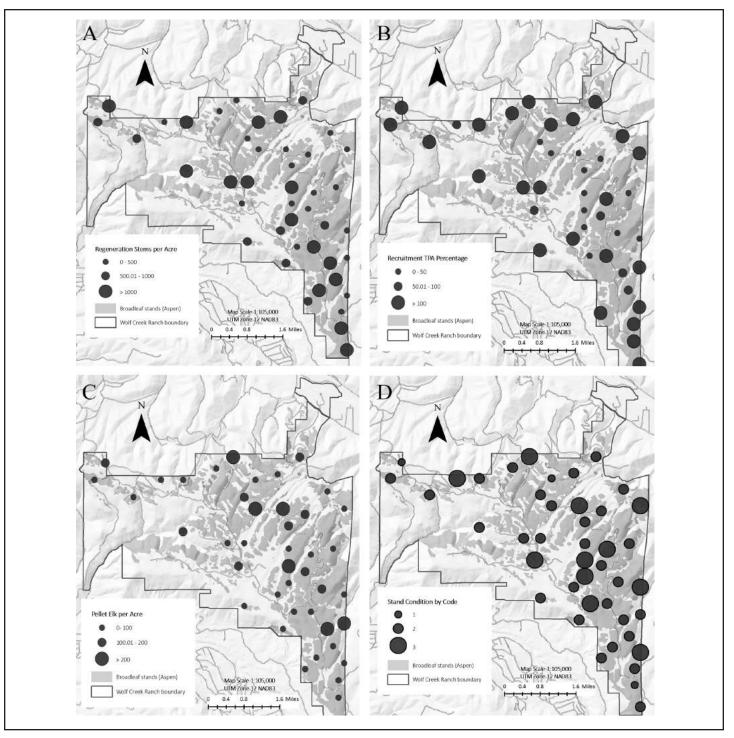


Figure 5. Maps of Wolf Creek Ranch monitoring plot locations by key indicators: (A) Regeneration stems ha<sup>-1</sup>, (B) Recruitment as percent of live mature trees ha<sup>-1</sup>, (C) Elk pellets ha<sup>-1</sup>, (D) Plot (stand) condition rating (see Methods). Sampling was conducted 15 June to 30 July 2012.

NMS ordination revealed a clear negative correlation between elk pellets and aspen regeneration and recruitment (Table 1). Axis 2, representing significantly less of the explanatory power of the NMS, describes fecundity of aspen, overall, on the landscape. The NMS analysis indicates other important relationships even where Pearson's r values do not meet the 0.05 threshold (Table 1). For example, aspen plot aspect (a moisture-related index) relates positively to recruitment (and other measures of aspen growth) and negatively to elk presence. It may be that elk favor drier aspects, their browse impacts are more evident in these areas, or that their scat was simply easier to detect with less plant cover found in such locations. Overall plot canopy height corresponds closely to mature aspen trees ha<sup>-1</sup>, but negatively to standing dead trees (mortality) ha<sup>-1</sup> (axis 2). Interestingly, we did not see a strong relationship between elk presence and slope, which fluctuated little (mean = 10%, SD 5%). This phenomenon has been documented elsewhere (Rogers and Mittanck 2014).

We acknowledge that our pellet count method of documenting ungulate use has some weaknesses. The first weakness, by design, is also a strength: we attempted to take animal visit measures at the same scale as forest mensuration data. While we believe this has the benefit of comparing all data at the same spatial metric, there is inherent variability in annual visitation by herbivores that may confound these findings. Secondly, collection of data by citizen scientists may add error, particularly where elk scat may be confused with sheep droppings, or dense vegetation may have obstructed visual counts. Still, corroboration with an independent elk density count, and the fact that WCR is managing sheep to avoid aspen, in terms of browse and recruitment levels (e.g., Durham and Marlow 2010; Runyon et al. 2014), diminishes these potential shortcomings.

Concentrated and long-term use by either wild or domestic ungulates can strain aspen system resilience to various disturbance and climatic factors (Fortin et al. 2005; Jones et al. 2005; Beschta and Ripple 2009; Rogers and Mittanck 2014). At WCR we detected little sheep dung, and only a few more deer pellets, so these factors were considered insignificant. Consistent with other studies comparing multiple large ungulates (Bork et al. 2013; Rogers and Mittanck 2014), elk appear to be the dominant browser in this system, with no natural predators to limit either their numbers or time spent at particular aspen locales. Consequently, elk appear to be exerting a strong negative influence on current aspen regeneration and recruitment. Thus, some groves may degrade severely at WCR as mature trees die from a combination of common diseases, insect infestations, and complexes of diseases and insects brought on by old age. On a positive note, elk are not impacting the landscape uniformly (Figure 5). These patterns of vegetation use and herbivore presence can be used to inform effective restoration.

There are a number of options for addressing aspen communities suffering from excessive herbivory. Options for restoration may address symptoms, causes, or both simultaneously. Our "toolbox" for addressing poor recruitment includes partial cutting, root ripping, burning, or a combination of these prescriptions, whose selection must be influenced by local conditions and social context (Shepperd et al. 2006). For example, in a residential setting such as WCR, aversion to widespread tree felling (or other activities causing visual impact) is common among property owners. We caution that clearfelling or burning are inappropriate in stable stands that rarely experience stand-replacing disturbances (Rogers et al. 2014). Burning is also difficult to implement in pure aspen stands (Shinneman et al. 2013). Limited silvicultural practices, barring extreme drought, will result in abundant regeneration. A more difficult challenge lies in confronting the base cause of herbivory, which can threaten the success of any regenerative practices.

Addressing the underlying cause of recruitment failure seems to be more difficult than stimulating sprouting; however, addressing underlying causes is critical. A recent review of aspen-ungulate issues in the West recommends that no active management be undertaken until ungulate browsing is evaluated and addressed (Seager et al. 2013). Contemporary hunters and recreationists demand high numbers of big game species, including elk, complicating reductions in the numbers of wild ungulates that browse aspen. Reintroduction of large predators, such as brown bears (Ursus arctos horribilis L.) or gray wolves (Canis lupus L.), that historically limited elk numbers, is politically difficult at this time. In the absence of predators, increased hunting, sterilization, or translocation of overabundant elk may provide options for recovery. Published findings suggest a minimum of 30% reduction in elk numbers (Seager et al. 2013) and/or no more than 20% annual browse of aspen sprouts (Jones et al. 2005) can provide initial guideposts toward sustainable management. In addi-

tion to culling of elk populations, WCR has begun to issue limited guided elk tags to discourage the "safe refuge" effect of large private landholdings. Though residents were initially opposed to any elk culling near home sites, it was felt that active hunting would help to keep elk alert and moving to avoid continued sedentary browse patterns. An alternative to wildlife culling is fertility manipulation via contraception; either temporary or permanent control agents may be employed (Bradford and Hobbs 2008). A final consideration is habitat manipulation to lure herbivores away from impacted vegetation (Augustine and Jordan 1998). There may be limited application of these techniques, however, where elk, deer, and sheep commonly use forests for shade and cover and aspen is the dominant forest type available at WCR to provide it. Any herbivore management scheme (most likely a combination of multiple approaches) is contingent upon consistent follow-up monitoring to verify expected outcomes. Previous and current work reinforces the critical nature of monitoring recruitment and animal presence (at a minimum) in aspen ecosystems where ungulate browsing is affecting resilience (Bork et al. 2013; Seager et al. 2013; Rogers and Mittanck 2014).

Lack of aspen recruitment presents additional concerns within residential-wildland settings. In the case of WCR, many residents visit only seasonally and reside in more developed regions of the country for much of the year. They often come to the Mountain West for aesthetic reasons and do not wish to see highly manipulated environments. Additionally, laypeople from urban settings, who may not have faced issues of resource depletion first-hand, will often view "no action" as the best means of preserving both aesthetics and property investment. Unlike surrounding state and federal lands, privately owned conservation reserves frequently do not have resource specialists or resident experts on hand. Thus, natural disturbances that originate on public land often spill over to residential properties that may be ill-equipped to address them. Management tools such as prescribed fire, hunting or trapping to cull wildlife, or large-scale tree felling may either be dangerous or visually unpleasant to nearby property owners. Without additional education or hired resource expertise, solutions to complex issues such as aspen-herbivore management may be avoided altogether. This, in turn, leads to further complications in locales such as WCR where legal conservation agreements govern long-term biodiversity and sustainability mandates.

In the case of WCR, we have recommended solutions using a combination of approaches focusing on symptoms and causes: ecologically appropriate protection of highly impacted stands in conjunction with active initiation of new aspen stems, with curtailment of herbivore numbers. Similar recommendations would likely be warranted at other locations where aspen forest conditions are in poor to moderate condition primarily because of ungulate herbivory. Aspen treatments should initially be limited and carefully monitored for financial, ecological, and conservation reasons. Fencing of regeneration in targeted stands should be used as long as elk numbers remain high, although there is potential for elk impacts to simply be relocated and concentrated outside fenced areas. Additional research is needed to understand why elk intensively use some areas and lightly browse others. Stimulation of additional regeneration in protected stands should be considered experimental or used when monitoring indicates that a stand will not be capable of regenerating itself at levels that lead to stand-replacing recruitment.

# CONCLUSIONS

Systematic monitoring of aspen communities within the study area found broad patterns of concern, particularly in limited structural diversity and its effects on greater ecosystem functions. However, in some places aspen forests appear to be healthy, warranting little action. On nearly half of the 43 plots in our aspen landscape, results suggest that recruitment of new aspen stems was insufficient for stand replacement. We documented high levels of browsing on young aspen and statistically significant relationships between several forest indicators and elk use of the area, suggesting that low levels of aspen recruitment correspond with heavy elk browsing. Since recruitment stems take several years, or even decades, to grow, low occurrence of aspen in the subcanopy strongly implies a sustained level of herbivory (Larsen and Ripple 2003; Zeigenfuss et al. 2008). Low detection rates of sheep and deer signify that these animals have little effect on aspen recruitment on these privately owned lands. Aspen mortality in mature trees at WCR is reflected in general thinning of canopy cover and possible drying out of understory vegetation where shrub cover is replacing formerly lush grass and herb cover. Loss of these key ecosystem components will have cascading impacts on system biodiversity. Overall, aspen forest health appears to be declining due to impacts of unrestrained elk herbivory.

Stewards of residential natural areas have many choices regarding maintenance of ecological, economic, and aesthetic values of their properties. However, in general, choices and available expertise may be more limited than those employed in public land-only situations. The aspen forests at WCR provide a biodiversity legacy for future generations; aspen cover amounts to nearly half (43%) of the total WCR land. The condition of a large proportion of this resource is currently on a nonsustainable trajectory given the level of elk browsing. We examined management options for correcting, or at least improving, this situation. Ultimately, however, vested decision-makers here, as elsewhere, will need to prioritize the importance of healthy aspen forests and resources to enact monitoring and stewardship decisions. Participation by residents in the monitoring efforts is a positive initial development. Use of WCR residents as citizen scientists in this effort will ensure future "ownership" in aspen stewardship efforts, as well as a knowledge base in monitoring methods and experiences that can be passed on to newcomers. A complementary approach may be to engage all stakeholders in "envisioning" a variety of forest futures from deteriorating aspen to improved forest resilience. Full benefits of an aspen legacy should be spelled out, alongside other concerns and priorities, to illicit informed decision-making for these valuable natural landscapes.

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## LITERATURE CITED

- Abraham, P.J. 2013. Wolf Creek Ranch Forest Stewardship Plan. Utah Division of Forestry, Fire and State Lands. Heber City, UT.
- Anderegg, W.L., L.D.L. Anderegg, C. Sherman, and D.S. Karp. 2012. Effects of widespread drought-induced aspen mortality on understory plants. Conservation Biology 26:1082-1090.
- Augustine, D.J., and P.A. Jordan. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. The Journal of Wildlife Management 62:1076-1085.
- Bailey, J.K., J.A. Schweitzer, B.J. Rehill, D.J. Irschick, T.G. Whitham, and R.L. Lindroth. 2007. Rapid shifts in the chemical composition of aspen forests: an introduced herbivore as an agent of natural selection. Biological Invasions 9:715-722.
- Bartos, D.L. 2001. Landscape dynamics of aspen and conifer forests. Pp. 5–14 *in* W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, eds., Sustaining

Aspen in Western Landscapes: Symposium Proceedings, 13–15 June, 2000, Grand Junction, CO. RMRS-P-18, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

- Beck, J.L., and J.M. Peek. 2005. Diet composition, forage selection, and potential forage competition among elk, deer, and livestock on aspen-sagebrush summer range. Rangeland Ecology and Management 58:135-147.
- Beschta, R.L., and W.J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401-2414.
- Bork, E.W., C.N. Carlyle, J.F. Cahill, R.E. Haddow, and R.J. Hudson. 2013. Disentangling herbivore impacts on *Populus tremuloides*: a comparison of native ungulates and cattle in Canada's Aspen Parkland. Oecologia 173:895-904.
- Bradford, J.B., and N.T. Hobbs. 2008. Regulating overabundant ungulate populations: an example for elk in Rocky Mountain National Park, Colorado. Journal of Environmental Management 86:520-528.
- Bunnefeld, N., J.D.C. Linnell, J. Odden, M.A.J. van Duijn, and R. Anderson. 2006. Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. Journal of Zoology 270:31-39.
- Campbell, R.B., and D.L. Bartos. 2001. Aspen ecosystems: objectives for sustaining biodiversity. Pp. 299–307 *in* Sustaining Aspen in Western Landscapes: Symposium Proceedings, 13–15 June, 2000, Grand Junction, CO. Proceedings RMRS-P-18, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- DeByle, N.V. 1983. The role of fire in aspen ecology. P. 326 in Proceedings—Symposium and Workshop on Wilderness Fire. GTR-INT-182, US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Missoula, MT.
- DeByle, N.V. 1985. Animal impacts. Pp. 115–123 in N.V. DeByle and R.P. Winoker, eds., Aspen: Ecology and Management in the Western United States. GTR-RM-119, US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- DeRose, R.J., and J.N. Long. 2010. Regeneration response and seedling bank dynamics on a *Dendroctonus rufipennis*-killed *Picea engelmannii* landscape. Journal of Vegetation Science 21:377-387.
- Durham, D.A., and C.B. Marlow. 2010. Aspen response to prescribed fire under managed

cattle grazing and low elk densities in southwest Montana. Northwest Science 84:141-150.

- Frey, B.R., V.J. Lieffers, S.M. Landhäusser, P.G. Comeau, and K.J. Greenway. 2003. An analysis of sucker regeneration of trembling aspen. Canadian Journal of Forest Research 33:1169-1179.
- Fortin, D., H.L. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, and J.S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320-1330.
- Gonzalez, N., S.J. DeBano, C. Kimoto, R.V. Taylor, C. Tubbesing, and C. Strohm. 2013. Native bees associated with isolated stands in Pacific Northwest bunchgrass prairie. Natural Areas Journal 33:374-383.
- Griffis-Kyle, K.L., and P. Beier. 2003. Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests. Biological Conservation 110:375-385.
- Harniss, R.O., and K.T. Harper. 1982. Tree dynamics in seral and stable aspen stands of central Utah. INT-RP-297, US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Hinds, T.E., and R.G. Krebill. 1975. Wounds and canker diseases on Western Aspen [*Populus tremuloides*]. Forest Pest Leaflet 152, US Department of Agriculture, Forest Service, Washington, DC.
- Johnston, C.A., and R.J. Naiman. 1990. Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Research 20:1036-1043.
- Jones, B.E., D. Burton, and K.W. Tate. 2005. Effectiveness monitoring of aspen regeneration on managed rangelands. R5-EM-TP-004, US Department of Agriculture, Forest Service, Pacific Southwest Region, Vallejo, CA.
- Keyes, C., P. Rogers, L. LaMadeleine, and D. Atkins. 2001. Utah Forest Health Report: A Baseline Assessment 1999/2000. State of Utah, Department of Natural Resources, Division of Forestry, Fire and State Lands, Salt Lake City, UT.
- Kuhn, T.J., H.D. Safford, B.E. Jones, and K.W. Tate. 2011. Aspen (*Populus tremuloides*) stands and their contribution to plant diversity in a semiarid coniferous landscape. Plant Ecology 212:1451-1463.
- Kulakowski, D., C. Matthews, D. Jarvis, and T.T. Veblen. 2013. Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). Journal of Vegetation Science 24:168-176.
- Kulakowski, D., T. Veblen, and S. Drinkwater. 2004. The persistence of quaking aspen

(*Populus tremuloides*) in the Grand Mesa area, Colorado. Ecological Applications 14:1603-1614.

- Kurzel, B.P., T.T. Veblen, and D. Kulakowski. 2007. A typology of stand structure and dynamics of Quaking aspen in northwestern Colorado. Forest Ecology and Management 252:176-190.
- Larsen, E.J., and W.J. Ripple. 2003. Aspen age structure in the northern Yellowstone ecosystem: USA. Forest Ecology and Management 179:469-482.
- Martin, T.E., and J.L. Maron. 2012. Climate impacts on bird and plant communities from altered animal-plant interactions. Nature Climate Change 2:195-200.
- McCune, B., J.B. Grace, and D.L. Urban. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, OR.
- McCune, B., and M.J. Mefford. 2006. PC-ORD: multivariate analysis of ecological data. MjM Software, Gleneden Beach, OR.
- Mueggler, W.F. 1985. Vegetation associations. Pp. 45–55 in N.V. DeByle and R.P. Winoker, eds., Aspen: Ecology and Management in the Western United States. GTR-RM-119, US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Mueggler, W.F. 1989. Age distribution and reproduction of Intermountain aspen stands. Western Journal of Applied Forestry 4:41-45.
- O'Brien, M., P.C. Rogers, K. Mueller, R. MacWhorter, A. Rowley, B. Hopkins, B. Christensen, and P. Dremann. 2010. Guidelines for aspen restoration on the National Forests in Utah. Western Aspen Alliance, Utah State University, Logan, UT.
- Riebsame, W., and J. Robb, eds. 1997. Atlas of the New West: Portrait of a Changing Region. Norton & Company, New York.

- Roberts, D.W., and S.V. Cooper. 1989. Concepts and techniques of vegetation mapping. Pp. 90–96 *in* D. Ferguson, P. Morgan, and F.D. Johnson, eds., Land Classification Based on Vegetation: Applications for Resource Management. GTR-INT-257, US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Rogers, P.C., D.L. Bartos, and R.J. Ryel. 2011. Historical patterns in lichen communities of montane quaking aspen forests. Pp. 33–64 *in* J.A. Daniels, ed., Advances in Environmental Research, Vol. 15. Nova Science Publishers, Hauppauge, NY.
- Rogers, P.C., S.M. Landhäusser, B.D. Pinno, and R.J. Ryel. 2014. A functional framework for improved management of western North American aspen (*Populus tremuloides* Michx.). Forest Science 60:345-359.
- Rogers, P.C., A.J. Leffler, and R.J. Ryel. 2010. Landscape assessment of a stable aspen community in southern Utah, USA. Forest Ecology and Management 259:487-495.
- Rogers, P.C., and C.M. Mittanck. 2014. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. Journal of Vegetation Science 25: 457-469.
- Rogers, P.C., W.D. Shepperd, and D.L. Bartos. 2007. Aspen in the Sierra Nevada: regional conservation of a continental species. Natural Areas Journal 27:183-193.
- Runyon, M.J., D.B. Tyers, B.F. Sowell, and C.N. Gower. 2014. Aspen restoration using beaver on the northern Yellowstone winter range under reduced ungulate herbivory. Restoration Ecology 22:555-561. doi: 10.1111/rec.12105.
- Seager, S.T., C. Eisenberg, and S.B. St Clair. 2013. Patterns and consequences of ungulate herbivory on aspen in western North America. Forest Ecology and Management

299:81-90.

- Shepperd, W.D. 1990. A classification of quaking aspen in the central Rocky Mountains based on growth and stand characteristics. Western Journal of Applied Forestry 5:69-75.
- Shepperd, W.D., P.C. Rogers, D. Burton, and D. Bartos. 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. RMRS-GTR-178, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Shinneman, D.J., W.L. Baker, P.C. Rogers, and D. Kulakowski. 2013. Fire regimes of quaking aspen in the Mountain West. Forest Ecology and Management 299:22-34.
- Stritar, M.L., J.A. Schweitzer, S.C. Hart, and J.K. Bailey. 2010. Introduced ungulate herbivore alters soil processes after fire. Biological Invasions 12:313-324.
- Theobald, D.M., and W.H. Romme. 2007. Expansion of the US wildland–urban interface. Landscape and Urban Planning 83:340-354.
- Walters, J.W., T.E. Hinds, D.W. Johnson, and J. Beatty. 1982. Effects of partial cutting on diseases, mortality, and regeneration of Rocky Mountain aspen stands. RM-RP-240, US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Zar, J.H., ed. 1999. Biostatistical Analysis. 4th ed. Prentice-Hall, Upper Saddle River, NJ.
- Zeigenfuss, L.C., D. Binkley, G.A. Tuskan, W.H. Romme, T. Yin, S. DiFazio, and F.J. Singer. 2008. Aspen ecology in Rocky Mountain National Park: age distribution, genetics, and the effects of elk herbivory. Open File Report 2008-1337, US Department of Interior, Geological Survey, Reston, VA.