Learning from spatial variability: Aspen persistence
in the Centennial Valley, Montana

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Abstract

Quaking aspen (Populus tremuloides) is commonly believed to be declining throughout western North America. A literature review of recent local-scale aspen studies, however, indicates that regional-scale spatial variability in aspen dynamics is greater than previously recognized and there are areas of successful aspen regeneration and recruitment. This study examines 20th century aspen recruitment and regeneration patterns along a 15 km long lower forest–grassland ecotone in the Centennial Valley, Montana to determine if the Centennial Valley ecotone aspen stands support the observation that there are areas of successful recruitment and regeneration and provide another example of such areas. A total of 525 adult aspen stems were cored and 8924 aspen suckers were counted and mapped in 106 rectangular plots randomly distributed along the ecotone. Aspen-age distribution was constructed at a decadal time scale to examine 20th century recruitment patterns. Sucker density was examined to evaluate aspen regeneration. The tree-age distribution patterns indicated successful aspen recruitment during the 20th century, while the sucker density assessment suggested successful regeneration. The Centennial Valley ecotone aspen stands appear to support the observation that aspen recruitment and regeneration are spatially variable and there are areas of aspen persistence. Learning about the underlying factors that enable successful aspen regeneration and recruitment in such areas can help management and restoration activities at other locales. Recognizing the regional-scale spatial variability in aspen dynamics can inform regional-level policy and management.

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1. Introduction

Much concern has been expressed both in scientific and public media that quaking aspen (Populus tremuloides) cover is declining in western North America (Bartos and Mueggler, 1981; Bartos, 2001). Many western states and counties now have local task forces dedicated to this issue. Restoration activities such as controlled burning and logging are encouraged to address the concern (Kilpatrick and Abendroth, 2001; Zier and Baker, 2006). However, recent studies suggest persistent or increasing aspen stands at some locations and much lesser degree of aspen decline than previously estimated (Barnett and Stohlgren, 2001; Manier and Laven, 2002; Kaye et al., 2003; Kulakowski et al., 2004; Brown et al., 2006; Zier and Baker, 2006). This might indicate that regional-scale spatial variability in aspen dynamics is greater than previously recognized. Little is known about regional-scale aspen dynamics (Kaye et al., 2003) and greater understanding is needed to guide regional policy and management decisions (Brown et al., 2006). Learning about the spatial variability can contribute to the current understanding of regional-scale aspen dynamics.

Aspen is the most widely distributed deciduous tree in North America (Bartos, 2001). Approximately 33% of the aspen communities in the west are considered to be climax (Mueggler, 1989), while many are thought to be fire-dependent (DeByle and Winokur, 1985). Aspen can reproduce both by seed or root suckering (DeByle and Winokur, 1985). However, aspen establishment from seed is considered rare (Turner et al., 2003; Romme et al., 2005) and most stems are believed to establish from root suckers within pre-existing aspen clones (Bartos, 2001). A clone can cover up to 90 ha (Bartos, 2001), and live for thousands of years through repeated suckering, which generally requires a disturbance event (Bartos, 2001), such as fire (Bartos and Mueggler, 1981; Kay and Bartos, 2000). In the absence of fire, apical dominance prevents suckering and aspen is replaced
by grasses, forbs, shrubs, or conifers (DeByle and Winokur, 1985). When suckering is successful, wild ungulate browsing can reduce sucker density and decrease regeneration (Kay and Bartos, 2000). In the western US national parks where elk density is especially high, recruitment of large aspen stems into the canopy is thought to be low or absent even when regeneration is successful (Romme et al., 1995; Ripple and Larsen, 2000; Hessl and Graumlich, 2002). Browsing by domestic livestock is also known to reduce aspen regeneration and recruitment (Weatherill and Keith, 1969; Smith et al., 1972; Rumble et al., 1996; Kay and Bartos, 2000). Other proposed factors of aspen decline include conifer encroachment and climate fluctuations (Kaye et al., 2003; Brown et al., 2006).

While the concern that aspen is declining in the west is largely based on 20th century tree-ring data, Kulakowski et al. (2004) argue that the 20th century trend alone might not represent the entire range of variability in aspen dynamics. They suggest that a single snapshot in time can underestimate the full range of temporal variability in aspen dynamics and lead to inappropriate management activities. Similarly, landscape-scale studies have revealed greater spatial variability in aspen dynamics. Suzuki et al. (1999) and Kaye et al. (2003) indicate that at landscape scales aspen decline is not apparent in the Rocky Mountain National Park and aspen regeneration is common in this national park of Colorado. Kulakowski et al. (2004) indicate persistent aspen stands, even without fire disturbance, and increasing aspen cover rather than decreasing aspen cover in the Grand Mesa area of Colorado. Brown et al. (2006) indicate much lower levels of aspen decline than previously suggested in the Greater Yellowstone Ecosystem in Montana, Idaho, and Wyoming, while Rogers (2002) indicates evidence of aspen decline at other locations in Idaho, Wyoming, and Colorado. Knight (2001) summarizes many Intermountain aspen communities as declining, whereas Mueggler (1989) suggests that many aspen stands (approximately 33%) are persistent even though some are declining.

A literature review of recent local-scale aspen studies in the western US demonstrates a similar spatial variability at a regional scale with a full range of aspen dynamics including aspen decline, persistence of aspen stands, and increase in aspen cover (Fig. 1) (Table 1). Recognizing the spatial variability informs regional-scale extrapolation of aspen patterns, which is often based on local-scale studies. Regional policy and management decisions based on such extrapolated information, in turn, have important implications for local-scale management and task force activities. This review also illustrates much higher clusters of aspen studies in the national parks where elk densities are substantially higher compared to the rest of the region. This pattern might suggest that aspen stands outside of the national parks are under-represented in the current literature. Furthermore, this review identifies locations of successful aspen regeneration, recruitment, and persistent or increasing aspen cover. Learning about underlying factors that enable successful aspen regeneration, recruitment, and persistence at such locations can provide key information for management activities at other locations in the region.

This study deals with one potential location of aspen persistence at a lower forest–grassland ecotone. As another local-scale study, this study examines 20th century aspen recruitment and regeneration along a lower forest–grassland ecotone in the Centennial Valley, Montana, where Douglas-fir (Pseudotsuga menziesii) expansion and livestock browsing, two proposed factors in aspen decline, have been previously documented in a larger study (Sankey et al., 2006). The primary question of interest is: are aspen stands along this ecotone declining as in other areas of the Rocky Mountain region or could this ecotone be an area of successful aspen recruitment and regeneration?

2. Methods

2.1. Study site

A single, 15 km long lower forest–grassland ecotone was studied in the Centennial Valley in southwestern Montana in the summer of 2003 (Fig. 1). The Centennial Valley runs east–west at approximately 2100 m elevation and experiences extreme continental climate with cold winters and hot, dry summers. Annual precipitation in the valley is 442 mm. The lower forest–grassland ecotone is on the northerly aspect (260° through north to 40°) and relatively gentle slopes (5–20°) of the Centennial Mountain Range on the south side of the valley. Soil profile
descriptions at 100 locations along the ecotone indicated that the current forest–grassland boundary is found mostly on grassland soils, Mollisols (Sankey, 2005). The thickness of mollic epipedon decreases towards the full canopy forest (Sankey, 2005).

The ecotone runs through the Red Rock Lakes Wildlife Refuge and three adjacent areas of private land. The vegetation community type along the ecotone is Aspen-Douglas-fir/Pinegrass (POTR-PSME/CARU c.t.) (Mueggler, 1988). Understory vegetation is structurally simple with 64% graminoids, 35% forbs, and 1% shrubs (Mueggler, 1988). Common graminoids include Agropyron cristatum, Calamagrostis rubescens, Elymus glaucus and Carex geyeri. Common forbs are Fragaria vesca, Geranium viscosissimum, Thalictrum fendleri, and Osmorhiza chilensis. Rosa woodsii and Berberis repens are common shrubs (Mueggler, 1988). Fire was suppressed historically in the valley. There has been no fire in the valley since European settlement or over the last 130 years except the Winslow fire that burned in the late summer of 2003 after the field work for this study was completed. The Winslow fire burned approximately 8000 ha of potential aspen habitat in August, 2003 (Korb, 2006) and included the western boundary of this study site. Historic fire frequency, prior to European settlement, at forest–grassland ecotones in southwestern Montana was 25–50 years (Lesica and Cooper, 1998). Elk population in the valley has increased substantially over the last several decades, but elk density is lower compared to that in the adjacent Yellowstone National Park about 45 km east of the Centennial Valley (Brannon, personal communication, 2005). The current estimates of elk density in the Centennial Valley are 1.92 elk/km² in the year-long range excluding areas of non-use and 1.36 elk/km² in the year-long range including areas of non-use (Brannon, personal communication, 2007). Elk hunting is permitted in the Red Rock Lakes Wildlife Refuge and the adjacent private lands along the ecotone and hunter density is 1.43 hunters/km² in the year-long elk range excluding areas of non-use (Brannon, personal communication, 2007). The valley has been grazed by domestic livestock since the mid-1800 s. Early homesteaders used this area for year-around grazing. This area has been primarily used as summer pasture for cattle over the last 50–80 years (Sankey et al., 2006). Due to the different land ownership present, the entire length of the ecotone in this

Table 1
Summary of recent local-scale studies on aspen recruitment and regeneration patterns

<table>
<thead>
<tr>
<th>#</th>
<th>Author, year</th>
<th>Type of evidence</th>
<th>Study area extent</th>
<th>Sample size</th>
<th>Documented aspen trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Romme et al., 1995</td>
<td>Tree rings</td>
<td>Not estimated</td>
<td>78 trees from 15 stands</td>
<td>Lack of recruitment since 1900</td>
</tr>
<tr>
<td>2</td>
<td>Baker et al., 1997</td>
<td>Tree rings and stem density</td>
<td>Not estimated</td>
<td>114 trees from 33 stands</td>
<td>Decline and no successful regeneration</td>
</tr>
<tr>
<td>3</td>
<td>Kay and Bartos, 2000</td>
<td>Stem density</td>
<td>Not estimated</td>
<td>8 exclosures</td>
<td>No successful regeneration outside exclosures</td>
</tr>
<tr>
<td>4</td>
<td>Ripple and Larsen, 2000</td>
<td>Tree rings</td>
<td>1000 km²</td>
<td>98 trees from 92 stands</td>
<td>Almost no recruitment since 1920</td>
</tr>
<tr>
<td>5</td>
<td>Barnett and Stohljen, 2001</td>
<td>Stem density</td>
<td>1090 km²</td>
<td>68 stands</td>
<td>Successful regeneration and recruitment</td>
</tr>
<tr>
<td>6</td>
<td>Hessl and Graumlich, 2002</td>
<td>Tree rings</td>
<td>Not estimated</td>
<td>774 trees from 30 stands</td>
<td>Successful recruitment, but at low frequencies</td>
</tr>
<tr>
<td>7</td>
<td>Manier and Laven, 2002</td>
<td>Repeat photography</td>
<td>3000 km²</td>
<td>24 photosets</td>
<td>Increasing cover</td>
</tr>
<tr>
<td>8</td>
<td>Elliott and Baker, 2004</td>
<td>Repeat photography</td>
<td>31080 km²</td>
<td>3 photosets, 343 stems from 9 stands</td>
<td>Increasing density, successful regeneration, and encroachment into grassland and conifer</td>
</tr>
<tr>
<td>9</td>
<td>Moore and Huffman, 2004</td>
<td>Tree rings and stem density</td>
<td>Not estimated</td>
<td>1810 stems (live and dead)</td>
<td>Increasing cover and encroachment into meadows</td>
</tr>
<tr>
<td>10</td>
<td>Di Orio et al., 2005</td>
<td>Repeat aerial photography</td>
<td>647 km²</td>
<td>126 photosets</td>
<td>Cover decline</td>
</tr>
<tr>
<td>11</td>
<td>Smith and Smith, 2005</td>
<td>Stem density and tree rings</td>
<td>3440 km²</td>
<td>168 trees from 53 stands</td>
<td>Decreasing dominance, but pure stands are persistent</td>
</tr>
<tr>
<td>12</td>
<td>Zier and Baker, 2006</td>
<td>Repeat photography</td>
<td>Not estimated</td>
<td>146 photosets</td>
<td>Increasing cover and successful regeneration</td>
</tr>
</tbody>
</table>

See Fig. 1 for their approximate geographic locations and the regional-scale distribution of aspen trends. The numeric labels in this table correspond to the number coding in Fig. 1.

The ecotone runs through the Red Rock Lakes Wildlife Refuge and three adjacent areas of private land. The vegetation community type along the ecotone is Aspen-Douglas-fir/Pinegrass (POTR-PSME/CARU c.t.) (Mueggler, 1988). Understory vegetation is structurally simple with 64% graminoids, 35% forbs, and 1% shrubs (Mueggler, 1988). Common graminoids include Agropyron cristatum, Calamagrostis rubescens, Elymus glaucus and Carex geyeri. Common forbs are Fragaria vesca, Geranium viscosissimum, Thalictrum fendleri, and Osmorhiza chilensis. Rosa woodsii and Berberis repens are common shrubs (Mueggler, 1988). Fire was suppressed historically in the valley. There has been no fire in the valley since European settlement or over the last 130 years except the Winslow fire that burned in the late summer of 2003 after the field work for this study was completed. The Winslow fire burned approximately 8000 ha of potential aspen

Table 2
Sample sizes and estimates of aspen recruitment and regeneration during the 20th century at the five contiguous sites along the lower forest–grassland ecotone in the Centennial Valley

<table>
<thead>
<tr>
<th>Sites</th>
<th>Number of aspen stems cored</th>
<th>Percent of aspen stems established during the 20th century</th>
<th>Sucker density/ha (SE)</th>
<th>Livestock grazing pressure (AUM/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>95</td>
<td>78</td>
<td>3.529 (1.013)</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>151</td>
<td>85</td>
<td>2.654 (943)</td>
<td>0.11</td>
</tr>
<tr>
<td>3</td>
<td>82</td>
<td>90</td>
<td>4.283 (1.238)</td>
<td>0.17</td>
</tr>
<tr>
<td>4</td>
<td>92</td>
<td>75</td>
<td>9.842 (3.553)</td>
<td>0.79</td>
</tr>
<tr>
<td>5</td>
<td>105</td>
<td>93</td>
<td>11.306 (4.927)</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Recruitment is indicated by the percent of aspen stems established during the 20th century, while regeneration is indicated by sucker density/ha.
study was divided into five contiguous sites and each site comprised 2–4 km sections (40–80 ha) of the ecotone (two sections of the Red Rock Lakes Wildlife Refuge and three adjacent private lands). The five sites were carefully selected to minimize differences in physiographic and climatic variables. However, the different land ownerships represent different management objectives (e.g., wildlife habitat on the wildlife refuge vs. livestock grazing on the private lands) and grazing regimes (Sankey et al., 2006). All, but one site, are grazed by cattle and average cattle grazing pressure of the last 35–40 years varies among sites between 0.00 and 1.00 Animal Unit Months per hectare (AUM/ha) (Table 2).

2.2. Field methods and tree-age estimate

A total of 106 rectangular plots were randomly located along the ecotone with 20–25 plots at each site (25–150 m apart depending on the length of ecotone at each site) with their long axis perpendicular to the ecotone. All plots were 10 m wide with varied lengths of 20–366 m depending on the width of the ecotone, although most plots were 80–100 m long. The width of the ecotone was determined by the definition of ecotone used in this study: a transition zone between 80% adult tree canopy cover in the forest and 100% herbaceous cover in the grassland. The forest end of each plot was positioned at 80% tree canopy cover, which was ocularly estimated, to represent full canopy forest and included mature trees that appeared to be at least 60 years old. Each plot extended from the full canopy forest into the adjacent grassland. The grassland end was positioned at 100% herbaceous cover and included the farthest out aspen sucker. All alive, standing adult aspen stems were mapped within the plots and cored at 30 cm above ground with an increment borer to estimate age (Table 2). The core samples were processed and dated using standard dendrochronological methods (Stokes and Smiley, 1968; Asharim and Mata, 2001). When core samples missed the pith, a geometric approach was used to estimate the number of missing rings to the pith (Duncan, 1989). A maximum of 20 missing years were added. Core samples missing >20 years were not aged and eliminated from the analysis. Approximately equal portions of the core samples were eliminated for all sites.

All stems ≤8 cm in diameter at coring height (30 cm above ground) were classified as suckers. Aspen regeneration in the Rocky Mountains from seed has been rare (Barnett and Stohlgren, 2001; Turner et al., 2003). Seedlings and suckers were not distinguished in this study and all juvenile stems herein are referred to as suckers. Suckers were not cored because of their size, although they included many pole-sized stems. The range of sucker age was estimated using an age distribution of 30 suckers, which were destructively sampled for cross-section discs at the root collar. The same sucker samples were also used to build a regression model of height and age relationship to adjust for coring height. This regression model produced a low coefficient of determination (0.02) and a large p-value (0.46). No additional rings were, therefore, added to the ring count of adult aspen samples. DeByle and Winokur (1985) indicate that aspen stems reach 1.5 m in 2–5 years, but some can reach 1.5 m height in the first year. Romme et al. (1995) indicate that unsuppressed and unbrowsed suckers can grow up to 1 m a year making it unnecessary to adjust ages for coring height. All aspen suckers observed in this study showed rapid early growth. Suppressed radial growth and lateral stem dominance due to heavy browsing was not observed at any of the sites, although scarring was observed on some adult tree trunks.

The entire area of each rectangular plot along the ecotone was divided into multiple neighboring quadrats 5 m × 5 m in size. This allowed two adjacent quadrats within the 10 m width of each plot, but the number of quadrats along the total length of the plots varied up to 73, depending on the length of plot. On average, each plot had a total of 40 quadrats. All live suckers were counted and mapped in all 5 m × 5 m quadrats within each plot. Additional field data included measurements of topographic aspect and slope at the plot level and a description of the landform and landscape position of each plot location (i.e., concave topography, alluvial fan, etc.).

Prior to all statistical analysis, a spatial autocorrelation test was performed and no patterns were observed in the variogram. Firstly, average sucker density per hectare was calculated based on the sucker count from each plot (n = 106) and compared among the five contiguous sites using a one-way analysis of variance (ANOVA) test with Tukey’s multiple comparisons (all pair-wise) to determine if aspen regeneration varied along the ecotone due to potential site differences. The sites were the predictor variable and the calculated sucker density per hectare was the response variable. Secondly, a multiple regression model was constructed to examine the effects of topographic variables on sucker density. Topographic slope (in percent) and aspect (cos transformed) were the predictor variables with an interaction term and the observed sucker density within each plot was the response variable (n = 106). Thirdly, an ANOVA model was constructed with Tukey’s multiple comparisons to examine the effects of landforms and landscape positions of the plot locations on sucker density (n = 106). The observed landforms and landscape positions of the plots were divided into three groups: (1) swales with concave slope shape down slope and across slope, (2) earthflows with hummocky terrain, and (3) alluvial fans with linear slope shape in the down-slope and across-slope dimensions. The three types of landforms were the predictor variables and the observed sucker density within each plot was the response variable.

3. Results

A total of 525 adult aspen stems were cored and 331 aspen samples were successfully dated (Table 2). A tree-age distribution was constructed at a decadal scale to examine 20th century aspen recruitment (Fig. 2). Eighty-one percent of all aspen stems dated were established during the 20th century. From 75 to 95 percent of the adult aspen stems at the five individual sites were new trees that established during the 20th century (Table 2). Almost 200 aspen core samples were eliminated due to rotten wood.

A total of 8925 suckers were counted and mapped in the 5 m × 5 m quadrats of all plots. The sucker-age estimate
indicated that sucker age ranged between 1 and 10 years. The calculated sucker density varied between 2654 and 11,306 stems/ha (Table 2). The ANOVA test of the calculated sucker density indicated that there were no statistically significant differences in sucker density/ha (p values >0.05) among the five sites along the ecotone. The multiple regression model of topographic variables and the observed sucker density per plot produced a low coefficient of correlation ($R^2 = 0.008$) with $p$ values of 0.19, 0.45, and 0.32 for aspect, slope, and the interaction term, respectively. The ANOVA model of landforms and landscape positions did not indicate statistically significant differences in the observed sucker density per plot among the three groups ($p$-value of 0.15). The difference in sucker density was largest between alluvial fan plot locations ($\mu = 55$ suckers/plot) and earthflow plot locations ($\mu = 170$ suckers/plot). The mean sucker density per plot was 85 for concave plot locations. This might be due to the subjective sampling of suckers. All stems $\leq 8$ cm in diameter at coring height (30 cm above ground) were not cored and were classified as suckers because of their size. Suckers thus included many pole-sized stems observed in the field. During the destructive sampling of suckers, however, all suckers were pulled out of the ground with a part of their roots so that the cross-section discs could be sampled at the root collar rather than above ground. Well established larger stems were avoided because they were difficult to pull out of the ground. This subjective sampling excluded pole-sized stems, which were likely the older suckers that established in the decade of 1980.

The calculated sucker densities per hectare along the ecotone included a wide range (Table 2), but they were all above the required number of suckers of 2500/ha for successful regeneration in mature stands (Baker et al., 1997). Kay and Bartos (2000) considered aspen regeneration “successful” at their study site, when sucker density was 4474/ha, a greater density than the estimate used by Baker et al. (1997). Some of the sucker density estimated in this study was also similar to or above the density used by Kay and Bartos (2000). Furthermore, the estimated range of sucker densities in this study (2654–11,306/ha) is much higher than the threshold used in Kulakowski et al. (2004) to determine whether aspen stands were persistent or not. Kulakowski et al. (2004) classified aspen stands as persistent, when $\geq 100$ aspen saplings/ha were found. In their stem size classification, saplings corresponded with stems $\leq 3$ cm in diameter at breast height (dbh), but $\geq 30$ cm in height, a much smaller size class than suckers in this study defined as stems $\leq 8$ cm in diameter at 30 cm above ground. It is very likely that many of the stems classified as suckers in this study would be the same size as the sapling class in Kulakowski et al. (2004) study, because many stems were at least $\geq 30$ cm in height, if not $\geq 3$ cm in diameter at dbh or $> 8$ cm in diameter at 30 cm. Only 1–4 percent of the observed suckers in this study would need to be $\geq 30$ cm in height to meet Kulakowski et al.’s criteria and the Centennial Valley ecotone aspen would be classified as persistent. The ecotone sucker density, though highly variable throughout the study site, indicates successful aspen regeneration in the Centennial Valley, despite the absence of fire in the last 130 years. This is consistent with Kulakowski et al. (2004) study that documented aspen persistence without fire disturbance. Taken together, our studies might suggest that aspen persistence is possible at some locations even without fire, although fire stimulates suckering (Bartos and Muegger, 1981; Kay and Bartos, 2000).

Non statistically significant differences were found in sucker density along the ecotone due to potential differences among sites. This result was possibly due to the high level of variation in sucker density at each site (Table 2). This pattern of no significant difference was not expected because the five sites along the ecotone were different in terms of management objectives and livestock grazing pressure (Sankey et al., 2006) and previous studies of sucker density indicated negative effects of livestock grazing pressure on sucker density (Rumble et al., 1996; Kay and Bartos, 2000). Furthermore, the analyses of topographic variables did not explain the observed variation.
in sucker density. This might be due to the relatively homogenous topography of the Centennial Valley ecotone. The topographic slope, aspect, and landforms vary little throughout the observed length of the ecotone.

4.2. Spatial variability in aspen dynamics

Contrary to many other aspen studies in the western US, the results of this study indicate successful aspen recruitment and regeneration during the 20th century in the Centennial Valley. This might suggest that the Centennial Valley aspen stands indeed support a hypothesis of greater spatial variability in aspen dynamics at a regional scale. The successful recruitment and regeneration in this study might be observed due to several reasons. Consistent with this study, previous aspen studies indicated successful aspen regeneration and recruitment along ecotones (Manier and Laven, 2002; Moore and Huffman, 2004; Elliott and Baker, 2004; Zier and Baker, 2006). Ecotonal aspen might have different stand dynamics, while aspen stands up the hill might be susceptible to conifer replacement during succession. Trees along ecotones create a more mesic environment by providing shade and increased snow accumulation (Zier and Baker, 2006). They can also provide protection from winter winds (Zier and Baker, 2006). Aspen might persist by successfully establishing at the grassland end of ecotones where conifers are not present. Even when conifers increase and push down the hill into aspen stands, Zier and Baker (2006) indicate that ecotonal aspen might be able to persist by expanding into the adjacent grassland or shrubland.

The topographic position of the Centennial Valley ecotone might contribute to the successful aspen recruitment. The ecotone is at similar or slightly higher elevation as the valley, approximately 2100 m. This is within the most dominant range of elevations of 1830–2290 m for aspen distribution (Turner et al., 2003). The predominantly northerly aspect and gentle slopes along this ecotone are also favorable variables for aspen persistence because soil moisture can be better captured and stored on such aspects and slopes (Turner et al., 2003). The Centennial Valley ecotone aspen stands were also found largely on soils with a thick mollic surface horizon (30 cm on average). Johnston (2001) previously documented successful aspen regeneration on sites with a thick mollic surface horizon (32 cm on average), but inadequate regeneration on sites with a thin mollic horizon (18 cm on average). Another reason for the observed successful recruitment in the Centennial Valley might be the lower elk density compared to those in the nearby national parks and national forests, where many aspen decline studies have been conducted (Romme et al., 1995; Ripple and Larsen, 2000; Hessl and Graumlich, 2002). These studies have largely focused on the northern range of the Yellowstone National Park and the Jackson Hole Valley, which support the first and second highest elk densities in the world, respectively (Brown et al., 2006). Brown et al. (2006) indicate that these areas are not representative of even the Greater Yellowstone Ecosystem and the regional-scale herbivory effects on aspen dynamics are unknown. It is probably not surprising if aspen stands outside these areas of high elk density are more persistent. Moreover, landscape-scale studies by Suzuki et al. (1999) and Kaye et al. (2003) in Colorado indicate greater spatial variability in aspen dynamics regardless of elk density and even challenge the common belief that elk impact aspen.

Among many other potential reasons for the successful recruitment and regeneration is sampling strategy. Previous studies that showed aspen decline commonly used limited number of tree samples (Ripple and Larsen, 2000; Romme et al., 1995). However, similar to this study, Hessl and Graumlich (2002) were able to identify periods of successful aspen regeneration in Wyoming during the 20th century by using a large number of tree samples. Some of the previous studies also sampled only the dominant canopy trees of the stand or a subsample of trees in each size class. However, Hessl and Graumlich (2002) indicate that biased sampling of only the dominant canopy trees would not fully represent age distribution, but would underestimate the temporal variability in the age structure. This study sampled all adult stems in the plots and eliminated subjective selection of stems. Lastly, some of the previous studies sampled only a few representative stands, instead of many different stands, from their study areas (Ripple and Larsen, 2000; Romme et al., 1995). Kaye et al. (2003) argue that conclusions from many local-scale aspen decline studies are limited because they covered a small spatial extent and sampled few subjectively chosen stands within their study areas. This study had well distributed and randomly located plots to include numerous stands and to accurately represent the aspen spatial variability throughout the entire ecotone. Barnett and Stohlgren (2001) also hypothesize that previous aspen decline studies had subjective plot location (i.e., stand selection) within their study sites and spatially-restricted study sites that greatly underestimated aspen regeneration at the landscape scale. They suggest that randomly chosen sampling locations within study sites yield much higher rates of aspen regeneration than previously documented. These factors have important implications for management decisions and task force activities, especially when extrapolating information to a regional scale. Barnett and Stohlgren (2001) caution that many of the previous studies might have been not able to tell the “whole story” by underestimating temporal and spatial variability. To accurately represent local-scale spatial variability, greater numbers of trees and stands at random locations should be sampled within study sites. A greater spatial extent with a large number of samples from randomly chosen trees and stands well-distributed across the landscape might be required to capture the spatial variability in aspen dynamics at the regional scale.

5. Conclusion

Many studies have demonstrated that quaking aspen is declining throughout the Rocky Mountain region. However, a literature review indicates greater spatial variability in aspen dynamics at a regional scale and suggests that there are areas of successful aspen recruitment and regeneration. The results of this study indicate that the Centennial Valley lower ecotone is one of such areas of successful aspen recruitment and regeneration and supports the hypothesis of greater spatial
variability in regional-scale aspen dynamics. Recognizing the spatial variability in aspen recruitment and regeneration at the regional scale has important implications for management activities and policy decisions.

References