2001

Persistence of aspen regeneration near the National Elk Refuge and Gros Ventre Valley elk feedgrounds of Wyoming

D.T. Barnett

T.J. Stohlgren

Recommended Citation

Barnett, DT and Stohlgren, TJ. 2001. Persistence of aspen regeneration near the National Elk Refuge and Gros Ventre Valley Elk feedgrounds of Wyoming. WD Shepperd et al (compilers). Sustaining Aspen in Western Landscapes: Symposium Proceedings. Proceedings RMRS-P-18. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, CO.

Persistence of Aspen Regeneration Near the National Elk Refuge and Gros Ventre Valley Elk Feedgrounds of Wyoming

David T. Barnett[1] **and Thomas J. Stohlgren**[1,2]

***Abstract**—We investigated aspen (*Populus tremuloides*) regeneration in the Gros Ventre River Valley, the National Elk Refuge, and a small part of Grand Teton National Park, Wyoming, to see if elk (*Cervus elaphus*) browsing was as damaging as previously thought. We conducted a landscape-scale survey to assess aspen regeneration across gradients of wintering elk concentrations using 68 randomly selected aspen stands in the 1,090 km^2 study area. Forty-four percent of the stands sampled supported regeneration of saplings (stems greater than 2 m in height but less than 10 cm in diameter). There were no significant differences of regeneration across elk winter range classification ($p = 0.25$) or distance from feedgrounds ($p = 0.96$). Our results suggest that some regeneration persists across the landscape at a variety of elk densities.*

Aspen (*Populus tremuloides* Michx.) contributes uniquely to the ecology of the Rocky Mountains. Many studies estimate that aspen occupy 0.5–2% of the landscape (Baker 1925; Krebill 1972), yet it supports floral (Stohlgren et al. 1997), butterfly (Simonson 1998), and bird (DeByle 1985a) species otherwise rare on the landscape. Native ungulates such as elk (*Cervus elaphus*) and moose (*Alces alces*) seek aspen and understory species as a favored food source. Aspen is also an economic asset by providing forage for livestock (DeByle 1985b) and aesthetic and recreational value (Johnson et al. 1985).

A great deal of work has documented aspen decline throughout the Rocky Mountains (Krebill 1972; Loope and Gruell 1973; Schier 1975; Olmsted 1979; Weinstein 1979; Bartos et al. 1991; Baker et al. 1997l; Kay 1997; White et al. 1998). As decadent stems expire, few new stems successfully regenerate to reach tree-size. Elk browsing on juvenile stems (Krebill 1972; Olmsted 1979; Baker et al. 1997), fire suppression that eliminates an important disturbance regime (Gruell and Loope 1974; Kay 1997), or a suite of factors including elk, fire, and climate change (Romme et al. 1995) seem to be responsible for this apparent decline in successful regeneration. The more extreme positions (Krebill 1972; Kay 1997; White et al. 1998) question the long-term persistence of aspen (Olmsted 1979; Baker et al. 1997) in specific landscapes.

Conflicting investigations and a variety of regeneration conditions create uncertainty about aspen decline. Romme et al. (1995) indicated that aspen may not be in immediate danger of extirpation in Yellowstone National Park, Wyoming. In Rocky Mountain National Park, Colorado, Suzuki et al. (1999) expanded the scale and extent of previous studies and recorded vigorous regional aspen replacement except in localized areas that were highlighted in previous studies (Olmsted 1997; Hess 1993; Baker et al. 1997). Both national parks have a history of fire suppression (White et al. 1998), large ungulate herds (Smith and Robbins 1994; Hess 1993), and extensive aspen research. The regions of Yellowstone National Park and Rocky Mountain National Park are ecologically different from each other and from the study site addressed in this paper. But similar trends in aspen population dynamics have been reported across the Rocky Mountain region, so comparison is useful.

[1]Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.
[2]Midcontinent Ecological Science Center, U.S. Geological Survey, Fort Collins, CO.

Intense ungulate browsing and a century of fire suppression may jeopardize the condition of aspen in the Southern Greater Yellowstone Ecosystem. Many studies recognize stand deterioration and regeneration suppression (Krebill 1972; Bartos et al. 1991; Gruell and Loope 1974; Weinstein 1979; Romme et al. 1995). The success of fire in stimulating stand-replacing regeneration seems to depend on ungulate browsing pressure (Gruell and Loope 1974; Romme et al. 1995). Fire stimulates a flush of stem regeneration, but often not in quantities that can escape elk browsing pressure (Bartos et al. 1991; Romme et al. 1995). Not even the large Yellowstone fires of 1988 enabled extensive aspen regeneration in highly productive burned areas or in unburned stands with less aspen and less vegetative forage that might make these stands less attractive to elk (Romme et al. 1995). At the scale measured, these aspen were unable to regenerate enough to counteract the effects of elk browsing; few stems survived to tree size (>2 m). Several other studies attribute lack of regeneration to ungulate pressure (Krebill 1972; Weinstein 1979). If elk are significantly browsing new growth, regeneration suppression should be most severe where elk densities are most concentrated.

Given previous findings, we formulated a simple hypothesis. A spatially considerate, highly replicated, landscape-scale survey of aspen regeneration would demonstrate that less regeneration occurs in areas of high elk use.

Study Site

Aspen stands were sampled in and around the Gros Ventre River Valley of the Bridger-Teton National Forest, the National Elk Refuge, and the southeast part of Grand Teton National Park, Wyoming (figure 1). The study site covers an area of 1,090 km^2. Elevations range from 1,890 m on the National Elk Refuge to just under 3,000 m at the upper reaches of aspen in the Gros Ventre River Valley. The average annual precipitation at Moran, WY, is about 57 cm, and the monthly mean temperatures vary from –11 °C in the winter months to 14.7 °C in July (Smith and Robbins 1994). The region serves as winter range for elk of the Jackson elk herd. The National Elk Refuge was established in 1912 to protect winter habitat and separate elk from livestock to prevent disease transmission (Smith and Robbins 1994). The National Elk Refuge and the southeastern part of Grand Teton National Park are characterized by rolling hills of grassland, riparian, and mixed conifer vegetation types. The Gros Ventre is more extreme topographically, with a narrow river valley of grassland in the bottomlands and mixed conifer and aspen at higher elevations.

We selected the area because of its long history of aspen investigation (Krebill 1972; Bartos et al. 1991) and because a part of the area functions as important elk winter range for the Jackson elk herd (Smith and Robbins 1994). Several factors make this winter range ideal for testing aspen regeneration theories across a gradient of elk densities. The Wyoming Department of Game and Fish (the agency responsible for management of elk in the Bridger Teton National Forest) and the United States Fish and Wildlife Service at the National Elk Refuge supply elk with supplemental feed during the winter months of the year at specified feedgrounds (Smith and Robbins 1994). Feeding at these locations generates high concentrations of elk during the months elk occupy the winter range. Observations (Smith and Robbins 1994) and aerial survey data indicate elk concentrations decrease as distance from feedground increases. The State of Wyoming Game and Fish winter range classification provides another indicator of elk distribution. They define two types of elk winter range according

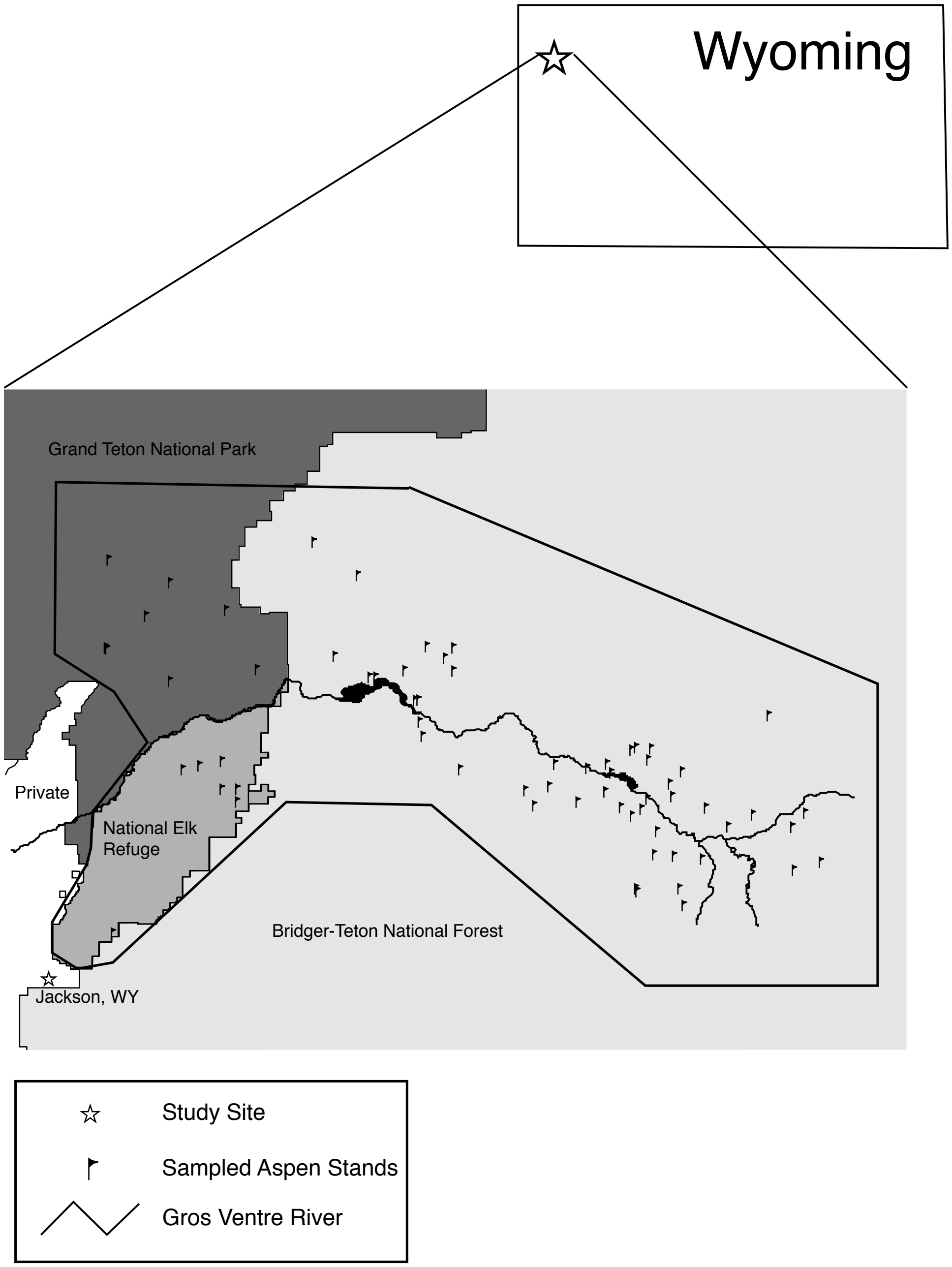

Figure 1—Regional location of study site within the state of Wyoming. The inset displays the study area and location of sampled aspen stands in the Bridger-Teton National Forest, Grand Teton National Park, and the National Elk Refuge.

to elk use: (1) Crucial Winter Range is "range or components of habitat that play a determining factor in a population's ability to meet and sustain population management objectives." (2) Winter Range represents "winter habitat substantially utilized by a population or portion of a population" (Strickland 1985).

Methods

We designed our methods to quickly quantify aspen at landscape scales and measure patchy regeneration within a stand. Stands were selected by randomly generating point locations in the study area. At each location we sampled the closest aspen stand to the north (NNW-NNE). If we did not encounter a stand within 500 m, we returned to the point and tried east, south, and west directions in turn. If no stands were located, we chose another random point to sample. We located and sampled 68 stands in the summer of 1998. At each sample point we recorded the slope in degrees, aspect measured by compass, elevation, stand area, location (Universal Trans Meter coordinate), dominant species in the surrounding canopy, dominant understory species, and evidence of disturbance.

For the purposes of this paper, successful regeneration was defined by saplings, those stems >2 m tall but <10 cm d.b.h. Suckers were stems <2 m in height; the term stem is used in reference to all aspen stems growing in a stand. We based the definition of successful regeneration on studies by Baker et al. (1997) who used stems greater than 2.5 m and 6 cm d.b.h., while Krebill (1972) used 15 cm d.b.h. to isolate pole-like stems indicative of new regeneration.

Once located, a stand was stratified according to patches of saplings (or lack thereof) within the stand, and a 5 x 5 m plot was randomly placed in each stratum (figure 2). Strata were defined as homogeneous patches of regeneration or regions of a stand that had no regeneration. For suckers (<2 m tall), we recorded the number of stems, number of dead stems, and percent of branches browsed. For stems over 2 m in height (>2 m tall), the number of stems, diameter at breast height (d.b.h.), number of dead stems, visual estimates of percent of bark browsed, and percent of branches browsed were recorded. Other stratum characteristics noted included percents of canopy cover, plant cover (combined herbaceous and shrub), rock, litter, soil, woody material, and stratum area (m^2) as measured by tape or calibrated human paces.

Variables measured in all strata within a stand were pooled by a weighted-area average to calculate total regeneration per hectare. The randomly located

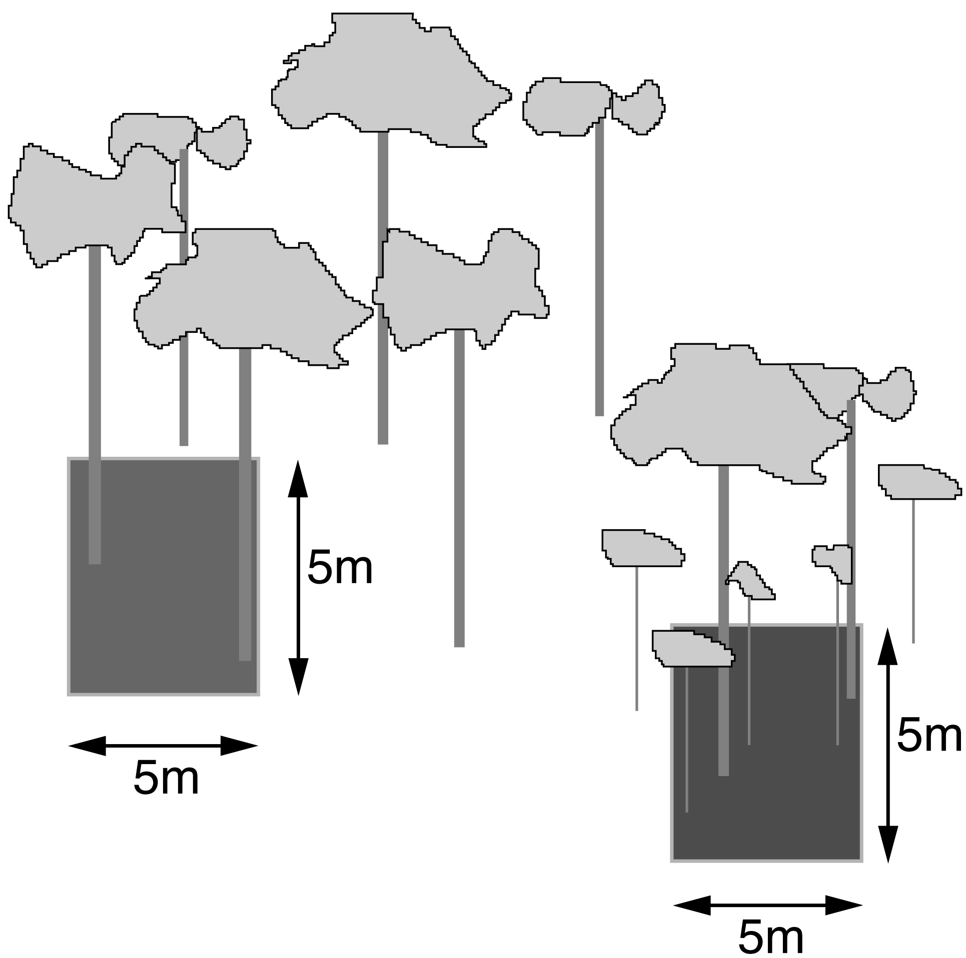

Figure 2—Aspen stands were stratified by patches of regeneration. One 5 x 5 m plot was randomly placed in each stratum to quantify aspen regeneration.

stands were classified in three ways. We used the Wyoming Department of Game and Fish elk winter range classifications of Crucial Winter Range and Winter Range and used a Nonwinter Range classification (stands that fell outside these two ranges) (figure 3). We also used categorical distances from state and federal feedgrounds classed at <1.5 km, 1.5–3 km, and >3 km. These distance classes were chosen to represent potentially different areas of elk use as reflected by field observation from land managers and telemetry data (S. Kilpatrick 1998, personal communication, Wyoming Department of Game and Fish, Jackson, WY). Both classifications were assumed to be indicators of elk density on the winter range.

Statistical Analyses

A one-way analysis of variance (ANOVA) of the sapling per hectare values was used to determine differences between mean sapling stem density for both the winter range classifications and the categorical distances from feedgrounds. A log transformation of the number of saplings was performed to meet ANOVA assumptions of normality. One-way ANOVAs with the same classes were used to evaluate differences in density of suckers (<2 m tall; density of suckers was square-root transformed for distance and classification ANOVAs to meet ANOVA assumptions of normality), percent browse on suckers (<2 m), percent browse on branches of saplings (square-root transformation for distance and classification), percent stem browse on saplings, and percent bark browse on stems <10 cm. When the ANOVA indicated significant differences between means, individual comparisons were made by controlling mean experiment wise error rate with the REGWQ method (SAS Institute 1996). ANOVA statistical manipulations were carried out in SAS (SAS Institute 1996).

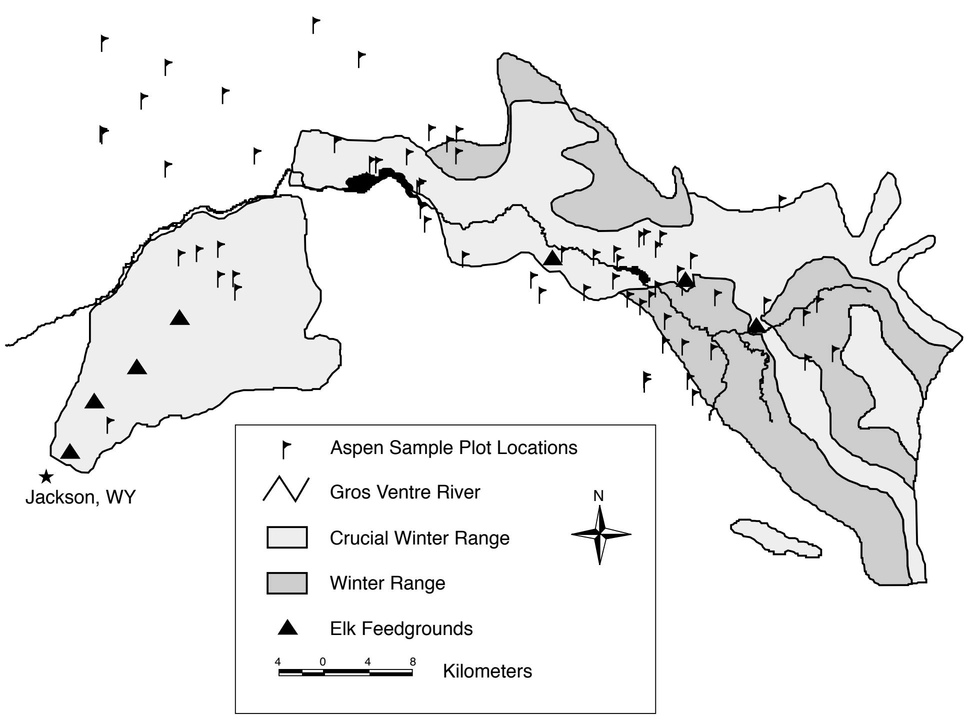

Figure 3—Location of aspen regeneration sample plots and State of Wyoming Game and Fish Elk Winter Range classifications in the study area.

Results

We sampled 68 aspen stands in and around the Gros Ventre River Valley and southeastern part of Grand Teton National Park. Thirty of the 68 stands sampled, 44%, demonstrated some evidence of successful aspen regeneration (saplings) in the stand. Sapling values ranged from zero to 2,900 stems per ha (table 1).

Elk Winter Range Classification

There was no significant difference (p = 0.25) between the number of saplings in the three winter range classifications (table 2). However, the amount of bark browsing on saplings was higher (2% ± 0.7) in the Crucial Winter Range as compared to the Nonwinter Range and Winter Range (0.2% ± 0.1). The Winter Range had significantly more suckers than the Crucial Winter Range and Nonwinter Range (p = 0.01; table 2).

Distance From Elk Winter Feedground

There were no significant differences in the number of saplings or any of the other variables analyzed at increasing distance classes from elk winter feedgrounds (table 3). The percent browse on suckers (<2 m tall) was nearly significant

Table 1—Summary statistics for aspen stands sampled by winter range class and distance to feeding grounds in the southern Greater Yellowstone Ecosystem.

Stand characteristic	Crucial winter range	Winter range	Non-winter range	<1.5 km from feeding grounds	1.5–3 km from feeding grounds	>3 km from feeding grounds
Number of stands sampled	26	15	27	8	18	42
Percent stands w/saplings (regeneration stems/ha)	50	53	33	37	44	43
Minimum stand saplings (regeneration stems/ha)	0	0	0	0	0	0
Maximum stand saplings (regeneration stems/ha)	2,900	1,400	1,200	900	2,900	1,700

Table 2—Comparison of aspen stands in Wyoming Department of Game and Fish elk winter range classifications in the southern Greater Yellowstone Ecosystem. Mean and standard errors (SE in parentheses) are presented. Significantly different means in a row have different subscripts.

Stand characteristic	Crucial winter range	Winter range	Nonwinter range
Saplings (regeneration stems/ha)	370 (137)	227 (105)	188 (72)
Percent bark browse on saplings (regeneration stems)	2.0a (0.7)	1.0 (0.6)	0.2b (0.1)
Percent stem browse on saplings (regeneration stems)	22 (7)	21 (9)	7 (2)
Percent bark browse on mature stems	42 (8)	20 (6)	40 (7)
Suckers (stems <2 m tall/ha)	1433a (330)	2975b (583)	1127a (533)
Percent browse on suckers (stems <2 m tall)	47 (7)	61 (5)	39 (6)

Table 3—Comparison of aspen stands in <1.5 km, 1.5-3 km, and >3 km from elk feeding grounds in the southern Greater Yellowstone Ecosystem. Mean and standard errors (SE in parentheses) are presented.

Stand characteristic	<1.5 km from feeding ground	1.5-3 km from feeding ground	>3 km from feeding ground
Saplings (regeneration stems/ha)	243 (140)	332 (183)	222 (70)
Percent bark browse on saplings (regeneration stems)	1.0 (1.0)	2.0 (1.0)	1.0 (0.3)
Percent stem browse on saplings (regeneration stems)	21 (12)	17 (7)	15 (4)
Percent bark browse on mature stems	39 (15)	47 (8)	31 (5)
Suckers (stems <2 m tall/ha)	1552 (805)	2138 (535)	1463 (379)
Percent browse on suckers (stems <2 m tall)	51 (12)	60 (7)	40 (4)

($p = 0.07$), indicating that browsing 1.5–3 km from the feedgrounds might be greater than the areas closer or farther away.

Discussion

We expected to find no aspen regeneration in this high elk density study area. That 56% of the aspen stands sampled on the landscape showed no sign of aspen regeneration might indicate that aspen is doing poorly under present conditions. Current regeneration rates may not be sufficient to replace all aspen stands on the landscape. However, in 44% of the stands, we did find some regeneration scattered throughout the landscape (table 1).

The Pattern

The absence of significant differences in aspen regeneration at various elk densities (tables 1 and 2) refutes our primary hypothesis that we would find less successful regeneration at higher elk densities. Given the number of stands without sapling regeneration, these results suggest a certain evenness or spatial ubiquity of elk browsing on the landscape at the scale we sampled. There is neither indication of less regeneration in the heart of the elk winter range, nor more in areas presumed to be less frequented by elk.

There were more suckers (stems <2 m tall) in the Winter Range than Crucial Winter Range and Nonwinter Range. This result may be irrelevant as the majority of these stems were browsed, but some were just new stems. The difference may suggest that elk tend to feed more on supplemental feed in the Crucial Winter Range and browse more aspen in the Winter Range. We did see an indication that the bark of sapling (>2 m, <10 cm d.b.h.) stems may be browsed more heavily in the Crucial Winter Range. However, this result may be inconsequential given the low browsing percentages as compared to mature stems, and that these stems often grow in dense cohorts that can make elk bark browsing difficult (Gruell and Loope 1974). Furthermore, this trend was not reflected in the number of these sapling stems, which ultimately contributes to maintenance of mature aspen canopy cover. The resulting pattern is one of no saplings in just over one-half of the aspen stands with some saplings in under one-half of the aspen stands scattered throughout the landscape.

Why the Pattern Is Different

Our results of widely scattered aspen saplings do not concur with the findings of many other investigations in the area. Given the variability of heterogeneous landscapes, extrapolation to unsampled areas must be presented tentatively. Additionally, any study that disagrees with such an abundance of literature from the same region should proceed with caution and critical logic. We offer three possible hypotheses that may explain why many studies predict a near complete demise of aspen while our data suggest its persistence. The hypotheses are presented in the order of least to most likely:

Hypothesis 1: The sample size may inadequately represent the entire landscape

This study had a small sample size relative to the larger, unsampled-heterogeneous landscape, and some might suggest that a larger sample size is needed to adequately represent the extensive landscape and adequately confirm the suggestion that aspen will persist on the landscape. While theoretically possible, a retro-analysis of our data through the use of Monte Carlo simulations suggests that about 30 randomly selected plots would have yielded approximately the same results as our 68 plots (figure 4). The upward trend of the simulation suggests that a larger sample size would likely detect even more regeneration. The initial findings also agree with casual field observations, where sporadic aspen regeneration was often seen while hiking to and from the random plot locations.

Hypothesis 2: Successful regeneration has increased since the earlier studies in the 1960s and 1970s

Many studies that predicted the demise of aspen through regeneration suppression were conducted 30 or 40 years ago (Beetle 1968; Krebill 1972), and the regeneration situation in the region covered by this study may have changed. General climate warming (VEMAP 1995) or favorable microclimates may have stimulated more successful aspen regeneration. However, climate effects are difficult to evaluate at landscape scales due to the lack of spatially extensive, long-term data on microsite variation and interactions with temporal and spatial variation of local browsing pressure. A series of large, long-term, randomly located plots and perhaps wide belt transects that span large environmental gradients (e.g., Stohlgren et al. 1999b) are needed to fully evaluate this

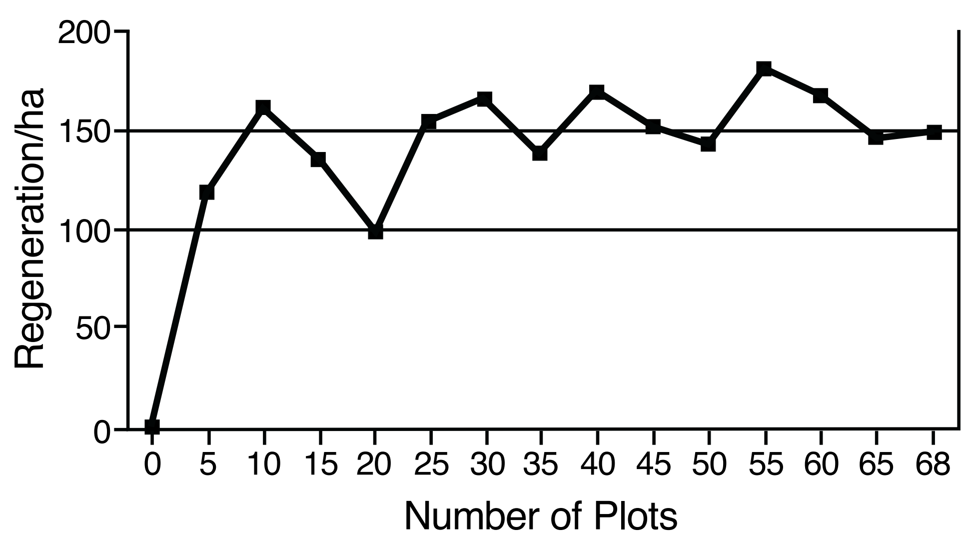

Figure 4—Monte-Carlo simulations predict that approximately 30 aspen stands may have been sufficient to capture significant aspen regeneration. See Methods section for details.

hypothesis. It should be noted that revisiting the few, subjectively selected stands measured in the original studies can't be used reliably as the foundation for an unbiased time series, nor can they isolate the interaction of climate and browsing pressure at plot to landscape-scales.

Hypothesis 3: Patches of successful regeneration were simply missed in previous studies

The previous investigations may have missed aspen regeneration due to small plot sizes and subjective plot location. This hypothesis has been tested indirectly in Rocky Mountain National Park, Colorado, where Suzuki et al. (1999) and Stohlgren et al. (1999a) showed that spatially restricting study sites can greatly underestimate aspen regeneration in the broader landscape. As in the present study, sampling objective, randomly selected plot locations yields far more aspen regeneration than previously realized.

We see this third hypothesis as the most likely answer to the question of aspen regeneration on this landscape. Landscapes are inherently variable in space (Stohlgren et al. 1999b). Subjective sampling, and/or small sample sizes common in many studies (Beetle 1968; Krebill 1972; Gruell and Loope 1974; Weinstein 1979), could have missed patchy but successful aspen regeneration, and therefore support the common conclusion of a threatened aspen population.

The results of our relatively large number of randomly located stands across the landscape might suggest that aspen persists in a patchy mosaic. It is important to note that regeneration of some stems does not guarantee stand replacement. Our weighted average regeneration densities for a stand do not satisfy stocking requirements (Gruell and Loope 1974) aimed to maintain aspen dominance across the whole stand. The regeneration stem densities that we report highlight the fact that much of the regeneration encountered was patchy even within a stand.

Persistence might be defined as the continued presence of a species in a specific area for a specific time (Donalson and Nisbet 1999; Fagan 1999). Most species are rare, few are dominant, and the strategy for rare species is to survive, reproduce, and persist in the presence of dominant species and many environmental stresses. The presence of patchy stem regeneration may be evidence of temporary persistence. Long-term stand persistence and extirpation remain fertile areas of research (Margot Kaye, Colorado State University, unpublished data). Scientists, resource managers, or society may have reasons to protect individual stands or restore aspen to 4% forest cover or 4,000 regenerating stems per hectare, but these human-imposed quotas for local areas may be unrelated to aspen persistence at larger spatial scales or over long time periods.

Historical photographs and tree-ring data (Gruell and Loope 1974; Baker et al. 1997; Romme et al. 1995) indicate a flux of regeneration occurred in the region during the years of 1850–1900. Given the age of many of the even-aged stands, this burst of regeneration resulted in the aspen cover we see today. With aspen decline, it is a likely possibility that these aerial cover percentages may not be sustained. The pockets of aspen persistence observed in this study may represent important sources or refuges of aspen and other obligate species in periods between conditions suitable to abundant regeneration. Disturbance to an apical meristem reduces auxin levels in the roots and permits suckering or development of new stems (Schier et al. 1985). Disturbances such as fire, clearcutting, or avalanches frequently encourage flushes of regeneration that could represent an opportunity for aspen to increase aerial cover if conditions were suitable (Romme 1995). Additionally, even under significant browsing pressure, root systems may be maintained indefinitely through the presence of small-shrub aspen or young shoots (Despain 1990). The 200-year life cycle of an aspen stem (Krebill 1972) and much longer life cycles of large clones make investigations of historical fluctuations and trends difficult. Since only one incidence of episodic regeneration has been documented, the applicability of this notion over longer time frames still needs to be tested.

Conclusion

Our work indicates that aspen is regenerating in patches throughout the winter range in the Gros Ventre River Valley, the National Elk Refuge, and the southeastern portion of Grand Teton National Park. Consideration of aspen on large yet detailed scales is essential as aspen regenerate and may persist on these scales. Many previous assessments of the condition and trend of aspen are not wrong, but their lack of appreciation for temporal and particularly spatial variability may prevent them from telling the whole story. Most studies, even those that do recognize patches of regeneration (Gruell and Loope 1974; Baker et al. 1997), tend to focus on the grave implications of aspen deterioration. We see the spatially intricate patches of successful regeneration as potential for future aspen success and continued persistence in elk winter range landscapes.

Acknowledgments

We would like to thank Jim Ozemberger of the U.S. Forest Service, Bruce Smith of the U.S. Fish and Wildlife Service at the National Elk Refuge, Bob Schiler of Grand Teton National Park, and Steve Kilpatrick and Diane Abendroth of the Wyoming Department of Game and Fish for their insight and logistical support. Bob Waltermire of the USGS, Geneva Chong of the USGS, Margot Kaye of Colorado State University, and Michelle Lee of the Natural Resource Ecology Laboratory provided valuable help and comments on the manuscript. William Romme of Fort Lewis College and two reviewers provided valuable comments on an early draft. Funding was provided by the U.S. Geological Survey. To all we are grateful.

References

Baker, F. S. 1925. Aspen in the central Rocky Mountain region. Bulletin No. 1291, U.S.Department of Agriculture, Washington, DC.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effects of elk on aspen in the winter range of Rocky Mountain National Park. Ecography 20: 155–165.

Bartos, D. L., W. F. Mueggler, and R. J. Campbell. 1991. Regeneration by suckering on burned sites in western Wyoming. USDA Forest Service Research Paper INT-448, Ogden, UT, 10 p.

Beetle, A. A. 1968. Range survey in Teton County, Wyoming. Part 3. Trends in vegetation. Wyoming Agriculture Experiment Station Resource Journal 26. 16 p.

DeByle, N. V. 1985a. Wildlife. In: Aspen: Ecology and Management in the Western United States. USDA Forest Service General Technical Report RM-119, Fort Collins, CO: 135–152.

DeByle, N. V. 1985b. Management for esthetics and recreation, forage, water, and wildlife. In: Aspen: Ecology and Management in the Western United States. USDA Forest Service General Technical Report RM-119, Fort Collins, CO: 223–232.

Despain, D. G. 1990. Yellowstone vegetation: Consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, CO.

Donalson, D. D. and R. M. Nisbet. 1999. Population dynamics and spatial scale: effects of system size on population persistence. Ecology 80: 2492–2507.

Fagan, W. F. 1999. Weak influences of initial conditions on metapopulation persistence times. Ecological Applications 9: 1430–1438.

Gruell, G. E. and L. L. Loope. 1974. Relationships among aspen, fire, and ungulate browsing in Jackson Hole, Wyoming. National Park Service, U. S. Department of the Interior, Moose, WY. 33 p.

Hess, K., Jr. 1993. Rocky times in Rocky Mountain National Park: an unnatural history. University of Colorado Press, Niwot, CO.

Johnson, C. W., T. C. Brown, and M. L. Timmons. 1985. Esthetics and landscaping. In: Aspen: Ecology and Management in the Western United States. USDA Forest Service General Technical Report RM-119, Fort Collins, CO: 185–188.

Kay, C. E. 1997. Is aspen doomed? Journal of Forestry 95: 4–11.

Krebill, R. G. 1972. Mortality of aspen on the Gros Ventre winter range. USDA Forest Service Research Paper INT-129, Ogden, UT. 16 p.

Loope, L. L. and G. E. Gruell. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quaternary Research 3: 425–443.

Olmsted, C. E. 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain National Park. In: North American Elk: Ecology, Behavior, and Management. Edited by, Boyce, M. S. and Hayden-Wing, L. D. University of Wyoming, Laramie, WY: 89–97.

Olmsted, C. E. 1997. Twenty years of change in Rocky Mountain National Park elk winter range aspen. University of Northern Colorado, Greeley, CO. 45 p.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76: 2097–2106.

SAS Institute, I. 1996. SAS Campus Drive, Cary, NC.

Schier, G. A. 1975. Deterioration of aspen clones in the middle Rocky Mountains. USDA Forest Service Research Report INT-170, Ogden, UT. 14 p.

Schier, G. A., J. R. Jones, and R. P. Winokur. 1985. Vegetative regeneration. In: Aspen: Ecology and Management in the Western United States. USDA Forest Service General Technical Report RM-119, Fort Collins, CO: 71–76.

Simonson, S. 1998. Rapid assessment of butterfly diversity: a method for landscape evaluation. Thesis, Colorado State University, Fort Collins. 50 p.

Smith, B. L. and R. L. Robbins, 1994. Migrations and management of the Jackson elk herd. U.S. Department of the Interior, National Biological Service, Washington, DC. 61 p.

Stohlgren, T. J., G. W. Chong, M. A. Kalkhan, and L. D. Schell, 1997. Multi-scale sampling of plant diversity: effects of minimum mapping unit size. Ecological Applications 7: 1064–1074.

Stohlgren, T. J., M. Kaye, C. Villa, Y. Otsuki, A. D. McCrumb, and B. Pfister. 1999a. Using new video mapping technology in landscape-scale ecological studies. Bio Science.

Stohlgren, T. J., L. D. Schell, and B. Van Heuvel. 1999b. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9(1): 45–64.

Strickland, D. 1985. Standardized definitions for seasonal wildlife ranges. State of Wyoming Game and Fish Department, Cheyenne, WY. 2 p.

Suzuki, K., H. Suzuki, D. Binkley, and T. J. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: differences at local and landscape scales. Landscape Ecology 14: 231–237.

VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biochemistry models in a continental scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochemical Cycles 40: 407–437.

Weinstein, J. 1979. The condition and trend of aspen along the Pacific Creek trail in Grand Teton National Park. In: North American Elk: Ecology, Behavior, and Management. Edited by, Boyce, M. S. and Hayden-Wing, L. D. University of Wyoming, Laramie, WY: 79–82.

White, C. A., C. E. Olmsted, and C. K. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain National Parks of North America. Wildlife Society Bulletin 26(3): 449–462.