# A LANDSCAPE APPROACH TO ASPEN RESTORATION: UNDERSTANDING THE ROLE OF BIOPHYSICAL SETTING IN ASPEN COMMUNITY DYNAMICS



# KATHRYN BROWN + ANDREW J. HANSEN + ROBERT E. KEANE + LISA GRAUMLICH MONTANA STATE UNIVERSITY + BOZEMAN

Considerable debate surrounds the persistence of quaking aspen (Populus tremuloides) communities in western North America. Loss of aspen cover has been documented in several studies in various Rocky Mountain ecosystems (Loope and Gruell 1973; Romme et al. 1995; Renkin and Despain 1996; Wirth et al. 1996; Baker et al. 1997; Kay 1997; Bartos and Campbell 1998; White et al. 1998; Gallant et al. 2003). Explanations for loss of aspen include conifer encroachment, fire exclusion, herbivory, and climatic fluctuations (Loope and Gruell 1973; Mueggler 1985; Bartos et al. 1994; Romme et al. 1995; Kay 1997; White et al. 1998). However, many studies documenting aspen decline have been geographically limited or based on a small sample of subjectively chosen stands (Barnett and Stohlgren 2001; Hessl 2002; Kaye et al. 2003).

Our understanding of aspen dynamics across regional scales is poorly developed (Kaye et al. 2003). In fact, recent landscape-scale studies of aspen dynamics in Colorado reveal increasing or stable aspen populations (Suzuki et al. 1999; Manier and Laven 2002; Kaye et al. 2003; Kulakowski et al. In Press). Less is known about the pattern of aspen dynamics at landscape scales in the areas surrounding Yellowstone and Grand Teton National Parks. Although several small-scale studies suggest aspen decline in Yellowstone and Grand Teton National Parks and surrounding areas, a regional assessment of aspen change is needed to fully understand aspen dynamics in the Greater Yellowstone Ecosystem (GYE).

Currently, no regional estimates of aspen distribution or abundance exist across the entire GYE. Also, understanding the role environmental gradients play in defining the niche of aspen presence is a necessary first-step in developing a large-scale perspective on aspen dynamics. If aspen are disappearing in some locations but stable or even increasing in other areas, which landscape settings permit the persistence and regeneration of aspen and what are the characteristics of those sites? We expect environmental gradients to interact with levels of herbivory, occurrence of fire, or shading from conifer in defining aspens' realized niche.

The aim of this study was to document the influence of biophysical gradients on aspen population dynamics, to serve as baseline knowledge for understanding the effects of fire, conifer encroachment, and herbivory on aspen. Key questions were: (1) how much aspen is in the GYE and what are the environmental factors defining the biophysical niche of aspen presence? (2) how has aspen's distribution and abundance changed over the past 50 years? (3) is change in aspen cover occurring in particular biophysical settings? and (4) how might biophysical controls on aspen presence and growth explain loss?

#### ✦ METHODS

#### Study Area

The study was conducted across the Greater Yellowstone Ecosystem (GYE) in Montana, Idaho, and Wyoming, as defined by (Hansen et al. 2002; Fig. The GYE encompasses strong gradients in 1). topography, climate, and soils. Soil types and climate vary with elevation in the region. Nutrientpoor rhyolite and andesite soils dominate higher elevations while valley bottoms contain nutrient-rich glacial outwash and alluvial soils (Hansen et al. 2000). Aspen is generally found in small patches in mesic sites such as toeslopes or topographic concavities (Despain 1990; Hansen et al. 2000; National Academies of Science 2002). Aspen often occurs at the ecotone between shrub steppes and low elevation coniferous forests (Marston and Anderson 1991; Gallant et al. 2003).



Figure 1. The Greater Yellowstone Ecosystem (GYE) was the study area. Aspen is rare in the GYE, occupying only 1.4% of the land area. The shaded area represents the Custer and Shoshone National Forests, which did not have data on aspen distribution.

#### Study Design

Since no regional assessment of aspen distribution existed for the GYE, we began by mapping aspen distribution from vegetation maps collected from the national forests and national parks within the GYE. We then used classification and regression tree analysis (CART) to explore aspen's biophysical niche within the GYE. To investigate change in aspen cover over time, we distributed aerial photography transects across the GYE and measured percent aspen cover between 1956 and 2001. Analysis of variance (ANOVA) was used to investigate which biophysical settings characterized areas of aspen loss versus areas where aspen were stable or even increasing in aerial cover. Finally, we sampled aspen plots across the GYE and measured aspen growth as above-ground primary productivity (ANPP) using radial growth rates from increment cores and stand biomass estimates. We used multiple linear regression to examine variability in aspen ANPP relative to biophysical variables.

## ✦ RESULTS

#### Aspen Distribution and Abundance

Aspen is rare in the GYE, occupying only 1.4% of the mapped land area (Fig. 1). Additionally, aspen is much more prevalent south of Yellowstone National Park (3.7% of land area) than in the northern region (0.2% of the land area).

Our CART model characterized the biophysical niche of aspen as warm, wet, and with high radiation availability, snowfall, potential evapotranspiration, and temperature (Fig. 2). Growing season short-wave radiation explained the largest proportion of the deviance in class membership. The higher values (> 69.9 W $\cdot$  m<sup>-2</sup>) of growing season short-wave radiation are primarily in the southern portion of the GYE (Whitlock and Bartlein 1993; Brown 2003). Our model validation yielded an overall accuracy of 80% for the CART With a producer's accuracy for aspen model. presence of 92%, the model performed well at classifying aspen presence. The user's accuracy for aspen presence was lower, only 74% of the observations that the model classified as aspen presence really were aspen presence; the model overpredicted the occurrence of aspen. The model predicted aspen absence (producer's accuracy = 68%) with lower accuracies, probably as a result of the over-prediction of aspen presence; however, most of

the observations that it classified as aspen absence really were aspen absence (user's accuracy = 90%).



Figure 2. Results of a classification and regression tree (CART) analysis for the entire GYE to examine aspen presence relative to biophysical setting. GS refers to growing season. If the rule at the top of a branch is true, then follow the left branch; if false, follow the right branch. N indicates the number of observations classified in a terminal node; P indicates the probability that the classification is correct.

#### Change In Aspen Cover

We measured 242 plots from the aerial photographs to examine changes in the aerial cover Our landscape-scale analysis showed of aspen. lower rates of decline, overall, than more local-scale studies have reported. Between 1956 and 2001, the median change in aspen cover was a 10% decline. However, the percent change ranged from a decrease of 80% to a gain of 70% over the past 50 years. The majority of our plots (59%, N = 143) were classified as stable, with between -10% and +10% change in aspen cover over the past 50 years. However, some areas did experience decline, 34% (N = 83) of our plots lost 20% or greater aspen cover over the past fifty years. A small number (7%, N = 16) gained aspen cover. Most plots showed no change in conifer cover (83%), few lost conifer cover (3%), and some gained conifer cover (14%).

Biophysical variables had some ability to discriminate between plots which gained aspen cover and those that lost or did not change in aspen cover. Biophysical variables which exhibited a significant difference ( $\alpha = 0.05$ ) between aspen change classes were annual growing degree-days, annual shortwave radiation, growing season shortwave radiation, annual potential evapotranspiration, growing season potential evapotranspiration, annual precipitation, growing season precipitation, annual snowfall, growing season actual evapotranspiration, and annual soil water potential. Most of these variables showed a significant difference between gain and no change classes and/or between gain and loss class using Tukey-Kramer confidence intervals with  $\alpha = 0.05$ . Only annual precipitation, growing season actual evapotranspiration, and annual snowfall showed a significant difference between no change and loss classes.

#### Biophysical Correlates of Aspen Growth

We sampled 107 field sites and measured aspen increment from cores from 613 aspen to determine aspen productivity. Mean aspen increment across all cores collected was 1.03 mm/year (standard error = 0.02, min. =0.023, max. =3.055). The mean ANPP across the 107 sites was 6191 kg  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup> (standard error =607, min. =57, max. =31,025).

Our regression model explained 37% of the variation in aspen ANPP (p < 0.0001) using annual growing season precipitation, annual minimum temperature, the interaction between precipitation and temperature, percent clay, and conifer biomass, while controlling for aspen stem density (Table 2). This regression model for aspen ANPP across our field sites predicts high ANPP to be associated with warmer, wetter areas with lower conifer biomass and high levels of clay in the soil (Table 2).

Table 2. Results of regression relating aspen annual net primary productivity (ANPP) to biophysical variables. Model shown is the best overall model as selected using AIC<sub>c</sub>. The coefficients and associated statistics shown are for variables standardized around mean = 0 and standard deviation = 1. The variables were scaled in order to make the coefficient of each variable indicative of its influence in the regression equation.

equation.							
Response	Variable	Parameter r estimate	Standard d error	t Value	$\Pr >  t $	95% Confidence Limits	
Aspen ANPP	Intercept	4536	564	8.04	<0.001	3452	5620
(all sites)	gPpt	378	580	0.65	0.516	-737	1494
	Tmin	1829	566	3.22	< 0.001	741	2917
	gPpt*Tmin	2255	588	3.83	< 0.001	1125	3385
	Clay	1902	501	3.80	< 0.001	939	2865
	Conifbio	-970	481	-2.01	0.046	-1895	-45

# + DISCUSSION

Aspen is rare in the GYE, representing only 1.4% of the land area. Although we found areas of local decline, with 34% of our plots showing aspen loss, the majority of aspen plots (59%) were stable over the past 50 years. Our results suggest that, at landscape-scales, aspen decline is less prevalent than smaller-scale studies have reported.

Although aspen is the most widely distributed tree species in North America (Jones 1985), it has a very narrow realized niche within the GYE. Our CART model predicted aspen occurrence in areas with high light availability, warm temperature, and relatively high moisture (Fig. 2). Our model predicts aspen to occur in locations where it is currently absent (user's accuracy = 74%), suggesting that aspen occupies only a portion of the areas which might be suitable for its growth.

In the GYE, aspen has a very narrow biophysical niche and we found that maximum aspen growth is at the edges of its biophysical niche. Most aspen in the GYE occupy high light environments, with growing season short-wave radiation above 65.8  $W \cdot m^{-2}$  (Fig. 2) and are primarily in the southern GYE where radiation is generally higher (Whitlock and Bartlein 1993). It is possible that the increased abundance of aspen in the southern GYE and areas with high radiation values is linked to more frequent fire in these areas.

Aspen occur in relatively warm areas (Fig. 1) and aspen growth is positively correlated with warm temperatures (Table 2). However, the highest ANPP was found at the upper limit of aspen's distribution along temperature gradients where aspen is less abundant. Finally, aspen ANPP was positively correlated with growing season precipitation (Table 2). Sites with the highest ANPP were those with much higher precipitation than where most aspen are present.

Aspen's narrow and suboptimal realized niche in the GYE likely contributes to aspen decline. Since aspen growth is not maximized in much of its limited distribution in the GYE, aspen growing in suboptimal conditions may be more susceptible to the effects of disease, herbivory, competition, and fire exclusion. Our ANPP analysis indicates that most aspen in the GYE grow in suboptimal biophysical conditions, these aspen may be especially vulnerable to the effects of herbivory. Indeed, the biophysical characteristics of areas with the highest aspen abundance corresponded with areas with slower growth rates and higher rates of loss. In poor growth conditions, plants may be less able to tolerate herbivory as a result of lower growth rates and decreased production of defensive secondary metabolites (Augustine and McNaughton 1998). Since most aspen in the GYE occupy biophysical settings less favorable to their growth, these aspen are probably more resource-limited than aspen in more favorable settings and may be less able to compete with conifers. Finally, the majority of aspen, which occupy less favorable settings, may be less likely to sucker following fire and fewer suckers may be likely to survive to maturity. Since most aspen in the GYE occupy biophysical settings in which growth is not optimal, aspen decline in this region may result from multiple stresses acting on a species existing near the edge of its biophysical tolerance.

#### Management Recommendations

Land managers interested in aspen restoration efforts should consider attempting to establish aspen in locations favorable to their distribution but which are currently unoccupied by mature aspen stands. Such efforts could be guided by the biophysical limits that our models establish for the current distribution of aspen within the GYE. Aspen plantings could be attempted in areas with high light-availability, moderate snowfall, and warm temperatures. Prescribed fire or fuels-reduction logging would likely be necessary prior to any planting attempts to remove competing vegetation.

To the extent land managers can prioritize areas for aspen restoration efforts, it would be useful to experiment with such tools as prescribed fire or ungulate exclosures across a variety of biophysical gradients (e.g. differing elevation, light exposures, temperature and moisture regimes) and monitor aspens' response. Such an adaptive management strategy may help shed light on interactions between herbivory, fire exclusion, competition and aspen response.

#### ACKNOWLEDGEMENTS

We would like to thank Roy Renkin at Yellowstone National Park for invaluable advice regarding aspen ecology and assistance with initial study design and access to aerial photography at Yellowstone National Park. Don Despain also provided valuable advice on aspen ecology in the Greater Yellowstone Ecosystem. We thank Tim Kaminski for providing vehicles, housing, and logistical support. For their long hours and assistance with fieldwork and data collection, we thank Casey Sensesqua, Chris Brown, and Steve Wilcox.

Funding for this research was provided by the University of Wyoming-National Park Service Research Station, Fire Sciences Laboratory of the Rocky Mountain Research Station, U.S. Forest Service, and Yellowstone National Park Cooperative Ecosystems Study Unit.

## ✦ REFERENCES

- Augustine D. J., and McNaughton S. J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62 (4):1165-1183.
- Baker W. L., Munroe J. A., and Hessl A. E. 1997. The effects of elk on aspen in the winter range of Rocky Mountain National Park. Ecography 20 (2):155-165.
- Barnett D. T., and Stohlgren T. J. 2001. Aspen persistence near the National Elk Refuge and Gros Ventre elk feedgrounds of Wyoming, USA. Landscape Ecology 16:569-580.
- Bartos D. L., Brown J. K., and Booth G. D. 1994. Twelve years biomass response in aspen communities following fire. Journal of Rangeland Management 47 (1):25-28.
- Bartos D. L., and Campbell R. B., Jr. 1998. Decline of quaking aspen in the interior Westexamples from Utah. Rangelands 20 (1):17-21.
- Brown K. 2003. Understanding the role of biophysical setting in aspen persistence. Thesis. Montana State University, Bozeman.
- Despain D. 1990. Yellowstone vegetation. Consequences of environment and history in a natural setting. Roberts Rhinehart, Boulder, CO, USA.
- Gallant A. L., Hansen A. J., Councilman J. S., Monte D. K., and Betz D. W. 2003. Vegetation dynamics under fire exclusion and logging in a Rocky Mountain watershed: 1856-1996. Ecological Applications 13 (2):385-403.

- Hansen A. J., Rasker R., Maxwell B., Rotella J. J., Johnson J., Wright Parmenter A., Langner U., Cohen W., Lawrence R., and Kraska M. P. V. 2002. Ecological causes and consequences of demographic change in the New West. Bioscience 52 (2):151-168.
- Hansen A. J., Rotella J. J., Kraska M. P. V., and Brown D. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecology 14:505-522.
- Hessl A. E. 2002. Aspen, elk, and fire: the effects of human institutions on ecosystem processes. Bioscience 52 (11):1011-1021.
- Jones J. R. 1985. Distribution. Pages 9-10 in DeByle N. V. and Winokur R. P., editors. Aspen: ecology and management in the western United States. U. S. Department of Agriculture, Forest Service, GTR RM-119, Fort Collins, Co.
- Kay C. E. 1997. Is aspen doomed? Journal of Forestry 95 (May):4-11.
- Kaye M. W., Stohlgren T. J., and Binkley D. 2003. Aspen structure and variability in Rocky Mountain National Park, Colorado, USA. Landscape Ecology 18:591-603.
- Kulakowski D., Veblen T. T., and Drinkwater S. In Press. The persistence of quaking aspen (Populus tremuloides) in the Grand Mesa Area, Colorado. Ecological Applications.
- Loope L. L., and Gruell G. E. 1973. The ecological role of fire in the Jackson Hole Area, Northwestern Wyoming. Quaternary Research 3:425-443.
- Manier D. J., and Laven R. D. 2002. Changes in landscape pattern associated with the persistence of aspen (*Populus tremuloides* Michx.) on the western slope of the Rocky Mountains, Colorado. Forest Ecology and Management 167:263-284.
- Marston R. A., and Anderson J. E. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5 (3):338-346.

- Mueggler W. F. 1985. Vegetation Associations. Pages 45-55 in DeByle N. V. and Winokur R. P., editors. Aspen: ecology and management in the western United States. U. S. Department of Agriculture, Forest Service, GTR RM-119, Fort Collins, Co.
- National Academies of Science. 2002. Ecological dynamics on Yellowstone's Northern Range. Committe on Ungulate Management in Yellowstone National Park, Board of Environmental Studies and Toxicology, Division of Earth and Life Sciences, National Research Council, National Academy Press, Washington, D. C., U. S. A.
- Renkin R., and Despain D. 1996. Preburn root biomass/basal area influences on the response of aspen to fire and herbivory. Pages 95-103 *in* Greenlee J. M., editor. The ecological implication of fire in Greater Yellowstone, Proceedings of the Second Biennial Conference on the Greater Yellowstone Ecosystem. International Association of Wildland Fire, Fairfield, WA, U. S. A.
- Romme W. H., Turner M. G., Wallace L. L., and Walker J. S. 1995. Aspen, elk, and fire in Northern Yellowstone National Park. Ecology 76 (7):2097-3010.

- Suzuki K., Suzuki H., Binkley D., and Stohlgren T. J. 1999. Aspen regeneration in the Colorado Front Range: differences at local and landscape scales. Landscape Ecology 14:231-237.
- White C. A., Olmsted C. E., and Kay C. E. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin 26 (3):449-462.
- Whitlock C., and Bartlein P. J. 1993. Spatial variation of Holocene climatic change in the Yellowstone region. Quaternary Research 39:231-238.
- Wirth T., Maus P., Powell J., and Lachowski H. 1996. Monitoring aspen decline using remote sensing and GIS: Gravelly Mountain Landscape, southwestern Montana. Prepared for the Remote Steering Committee, U.S. Department of Agriculture, Forest Service, Salt Lake City, UT, U. S. A.