MONTANA STATE UNIVERSITY

Understanding the role of biophysical setting in aspen persistence
by Kathryn Brown

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University
© Copyright by Kathryn Brown (2003)

Abstract:
Aspen communities are critically important for maintaining biodiversity, soil -quality, firebreaks, scenic beauty and nutrient cycling. However, widespread decline of aspen has been documented in much of the western United States. This loss of aspen has been attributed to fire exclusion, ungulate herbivory and climatic change. The role of biophysical factors in controlling aspen dynamics is poorly understood. In this study I quantify the relationship between aspen distribution, performance and landscape change with biophysical variables such as climate, topography, and soils. Specifically, I analyzed how aspen distribution, aboveground net primary productivity, and change in aspen cover over the past 50 years vary with respect to environmental gradients. I used classification and regression tree analysis to relate aspen distribution to biophysical variables. I collected aspen increment cores to calculate aspen aboveground net primary productivity. I interpreted aerial photographs over the past 50 years to determine landscape change in aspen cover. I used Akaike's Information Criterion to select multiple regression models relating aspen primary productivity and landscape change to biophysical variables. My findings show strong biophysical control over aspen distribution. I was able to explain 37% of the variation in aspen primary productivity across the Greater Yellowstone Ecosystem using biophysical variables. Additionally, I documented a 34% reduction in aspen cover between 1955 and 2001. I was able to explain between 13% and 43% of the variation in aspen change using biophysical setting. My models of aspen distribution predict aspen presence in more areas than it currently occupies. I propose that aspen distribution in the Greater Yellowstone Ecosystem is restricted such that it does not currently occupy the full range of its abiotic tolerances. Aspens' range may have been constricted by limited seedling recruitment since the last glaciation, past and present fire regimes, competition with conifer, and ungulate herbivory. Aspen in this region appears to be restricted to a small proportion of its abiotic niche such that primary productivity is not optimized in current locations. As a result, aspen in this region may be susceptible to factors such as fire exclusion, competition, and herbivory.

UNDERSTANDING THE ROLE OF BIOPHYSICAL SETTING IN ASPEN PERSISTENCE

by

Kathryn Brown

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 2003

N378
B8138

APPROVAL

of a thesis submitted by

Kathryn Brown

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Dr. Andrew Hansen Andrew J Hansen 11-24-03
(Signature) Date

Approved for the Department of Ecology

Dr. Scott Creel Scott Creel 11/24/03
(Signature) Date

Approved for the College of Graduate Studies

Dr. Bruce McLeod Bruce R. McLeod 11-25-03
(Signature) Date

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library.

If I have indicated my intention to copyright this thesis by including a copyright notice page, copying is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for permission for extended quotation from or reproduction of this thesis in whole or in parts may be granted only by the copyright holder.

Signature Kathy Bar

Date 11/24/03

ACKNOWLEDGMENTS

I would like to thank my graduate advisor, Andrew Hansen, and committee members, Robert Keane and Lisa Graumlich for their invaluable advice and assistance with all aspects of this study. Andrew Hansen provided guidance with study design and concepts. Additionally, Robert Keane developed and implemented the WXFIRE model which was vital to our modeling efforts and Lisa Graumlich provided her expertise and the equipment necessary for tree-ring analyses. Roy Renkin of Yellowstone National Park and Don Despain of USGS-BRD provided helpful advice on aspen ecology. Tim Kaminski of the Bridger-Teton National Forest provided logistical support in the form of housing, vehicles, and salaries for field assistants. For their long hours and assistance with fieldwork and data collection, I thank Casey Sensesqua, Chris Brown, and Steve Wilcox. I also thank Steve Wilcox for the many hours he spent interpreting aerial photographs to collect landscape change data.

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

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES - CONTINUED

ABSTRACT

Aspen communities are critically important for maintaining biodiversity, soil quality, firebreaks, scenic beauty and nutrient cycling. However, widespread decline of aspen has been documented in much of the western United States. This loss of aspen has been attributed to fire exclusion, ungulate herbivory and climatic change. The role of biophysical factors in controlling aspen dynamics is poorly understood. In this study I quantify the relationship between aspen distribution, performance and landscape change with biophysical variables such as climate, topography, and soils. Specifically, I analyzed how aspen distribution, aboveground net primary productivity, and change in aspen cover over the past 50 years vary with respect to environmental gradients. I used classification and regression tree analysis to relate aspen distribution to biophysical variables. I collected aspen increment cores to calculate aspen aboveground net primary productivity. I interpreted aerial photographs over the past 50 years to determine landscape change in aspen cover. I used Akaike's Information Criterion to select multiple regression models relating aspen primary productivity and landscape change to biophysical variables. My findings show strong biophysical control over aspen distribution. I was able to explain 37% of the variation in aspen primary productivity across the Greater Yellowstone Ecosystem using biophysical variables. Additionally, I documented a 34% reduction in aspen cover between 1955 and 2001. I was able to explain between 13% and 43% of the variation in aspen change using biophysical setting. My models of aspen distribution predict aspen presence in more areas than it currently occupies. I propose that aspen distribution in the Greater Yellowstone Ecosystem is restricted such that it does not currently occupy the full range of its abiotic tolerances. Aspens' range may have been constricted by limited seedling recruitment since the last glaciation, past and present fire regimes, competition with conifer, and ungulate herbivory. Aspen in this region appears to be restricted to a small proportion of its abiotic niche such that primary productivity is not optimized in current locations. As a result, aspen in this region may be susceptible to factors such as fire exclusion, competition, and herbivory.

INTRODUCTION

Climatic change and biodiversity loss have stimulated renewed interest in the relationship between plant communities and population dynamics and environmental gradients. Knowledge of species' responses to their abiotic and biotic environment is integral to understanding species distribution, land cover changes, and ecosystem management. Numerous studies have related vegetation distributions and change to biophysical gradients (Austin 1987, Stephenson 1990, Franklin 1995, Stephenson 1998, Austin 2002, Oksansen and Minchin 2002, McKenzie et al. 2003). The extensive decline of aspen (*Populus tremuloides* Michx.) and its relative importance in Rocky Mountain ecosystems have generated concern for the persistence of this species. Understanding aspen's relationship with its biophysical environment will be vital to management of the species. The goal of this study was to quantify the influence of environmental gradients on aspen persistence.

Widespread loss of aspen in the western United States has been well documented. Aspen stands are declining in the landscape, becoming invaded by conifer, and failing to recruit young stems into the overstory (Kay 1997, Bartos and Campbell 1998, White et al. 1998). Wirth et al. (1996) estimated a 45% decline in pure aspen and mixed aspen/conifer acreage between 1947 and 1992 in the Gravelly Mountains of southwestern Montana. In the Centennial Mountains of Idaho, aspen declined by 75% since the mid-1800s (Gallant et al. 2003). An estimated loss of 4,000 ha of aspen coverage in Yellowstone National Park since the late 1800s has accompanied minimal regeneration since 1900 (Romme et al. 1995, Renkin and Despain 1996). Most aspen stands in Banff, Yoho, Kootenay, Yellowstone, and Rocky Mountain national parks fail to recruit overstory trees (White et al. 1998).

Although aspen represents a minor component of western forests (Baker 1925, Despain 1990), it is critically important to Rocky Mountain ecosystems. Aspen communities are "hotspots" of avian biodiversity (Hansen and Rotella 2002) and sustain rare plant and butterfly species (Barnett and Stohlgren 2001). Additionally, aspen stands have high primary productivity (Hansen et al. 2000) which contributes to the role of aspen communities in forage production for native ungulates and domestic livestock (Bartos and Campbell 1998). Aspen contribute significantly to nutrient cycling through the addition and decomposition of leaves (Jones and DeByle 1985c, Cryer and Murray 1992, Bartos and Amacher 1998) and loss of aspen may lead to decreases in soil organic matter, increases in soil pH, and decreases in soil nutrients (Bartos and Amacher 1998). Also, aspen forests often function as fire breaks because fuels are generally scarce and moist relative to adjacent conifer forests, crown fires in coniferous forests often drop to the ground upon entering aspen forest (Jones and DeByle 1985b).

Succession, fire exclusion, herbivory, and climatic change are the most widely advanced explanations for loss of aspen. Aspen are shade-intolerant and are often overtopped and replaced by conifer (Mueggler 1985). In addition, successful germination of aspen seedlings in the arid west is rare (Kay 1993) and suckering is inhibited through hormonal control by mature aspen stems (Schier et al. 1985). Fire exclusion has removed a process important to aspen regeneration; fire stimulates vegetative reproduction through mortality of both mature aspen and fire-sensitive conifer (Jones and DeByle 1985b, Bartos et al. 1994), increased light availability, and increased soil temperatures (Brown and DeByle 1987, Hungerford 1988). Seedling recruitment may also occur when favorable conditions, such as increased light availability, bare mineral soil, and high soil moisture content, follow fire (Kay 1993, Romme et al. 1995, Stevens et al. 1999). Heavy browsing by ungulates, especially elk (*Cervus elaphus*), may counteract the effects of fire and prevent successful recruitment of tree-sized stems (Kay 1993, Bartos et al. 1994, Romme et al. 1995, Baker et al. 1997, White et al. 1998, National Academies of Science 2002); however, in some cases downed woody debris following fire may protect aspen suckers permitting recruitment (Ripple and Larsen 2001). In the winter range of the Jackson Hole elk herd, Hessl and Graumlich (2002) found that periods of aspen regeneration coincided with low to moderate elk population size and that aspen regeneration seldom occurred when elk populations were high. Finally, the longevity and clonal nature of aspen (Barnes 1966) that allow it to persist through climatic fluctuations, have led some authors to suggest that aspen is maladapted to current climatic conditions and that this may be a factor in the observed decline (Romme et al. 1995).

Although aspen decline is widely documented and several hypotheses have been advanced as potential explanations, aspen has persisted and even successfully regenerated in some areas. Aspen response to fire is highly variable and aspen has also been shown to persist in the presence of elk browsing pressure. Some aspen stands also appear to be stable and resistant to conifer encroachment even in areas with fire suppression policies. Repeat photography shows that on the western slope of the Colorado Rocky Mountains the total cover and relative patch size of aspen has increased over the past 80-100 years (Manier and Laven 2002). Aspen increased in cover and patch size in burned and unburned landscapes (Manier and Laven 2002). Although Baker et al. (1997) found almost no aspen regeneration in the Estes Valley of Rocky Mountain National Park, when Suzuki et al. (1999) expanded the study area they found frequent aspen regeneration across the Front Range of Colorado except in areas of locally high elk use. In the National Elk Refuge near Jackson, Wyoming, Barnett and Stohlgren (2001) found no significant difference in aspen regeneration across elk winter range classifications (crucial winter range, winter range, and non-winter range) or elk densities. Thus, exceptions to the documented decline of aspen exist.

This begs the question: which landscape settings permit the persistence and regeneration of aspen and what are the characteristics of those sites? Very little is known about the influence of site characteristics on changes in aspen communities. However, several studies describe the environments in which aspen in the west is typically found. Aspen most often occupy mesic sites with moderate climates. These sites are often topographic concavities that concentrate moisture (Jones and DeByle 1985c, Burke et al. 1989, Hansen et al. 2000) and have a long growing season and moderate summer and winter temperatures (Jones and DeByle 1985a, Hansen et al. 2000). Because climatic conditions vary with elevation, aspen occurs at lower elevations as latitude increases (Jones 1985, Bartos and Amacher 1998). In fact, in Colorado, radial growth rate decreased with increasing elevation (Mitton and Grant 1980). Aspen also has relatively high soil moisture and nutrient demands; thus, the soils that support aspen communities are often fine-textured with a high silt/clay content (Jones and DeByle 1985c) and contain a thick, nutrient-rich A horizon (Cryer and Murray 1992, Bartos and Amacher 1998).

Environmental variables are likely to strongly mediate the ability of aspen to respond to fire, tolerate herbivory, and compete with conifer. I expect abiotic gradients to interact with levels of herbivory, occurrence of fire, or shading from conifer resulting in differing aspen response to these stressors at different locations along the gradient. Tolerance to herbivory, either through compensatory growth or production of defensive compounds, is influenced by environmental conditions (Augustine and McNaughton 1998). Additionally, in the absence of appropriate growth conditions for plants, competitive relationships between plant species may favor those species less palatable to herbivores (Augustine and McNaughton 1998). In grassland ecosystems, the influence of climate and soil variables on aboveground net primary production (ANPP) differed in accordance with differing fire regimes and levels of herbivory (Knapp et al. 1998). I suggest that biophysical gradients should influence aspen growth and may interact with fire, conifer encroachment or herbivory to affect aspen persistence.

I propose that biophysical setting directly affects aspen dynamics and mediates the effects of fire, competition, and herbivory on aspen productivity and decline (Fig. 1). Gradients in such variables as growing season length, light availability, precipitation, and nutrient availability act directly on aspen distribution by defining the limits of its environmental niche space and probably by differentially affecting aspen growth at different locations along a given gradient (Fig. 1).

However, these same gradients likely indirectly affect aspen performance, in terms of growth or persistence on a site, by influencing the direct affects of additional factors such as fire exclusion, competition, and herbivory (Fig. 1, Table 1). I suggest that aspen which occupy more favorable biophysical settings (e.g. moderate temperature, long growing season, high light availability) are likely to have faster growth rates and/or possibly higher allocation of carbon to defensive secondary metabolites. As a result, aspen in favorable biophysical settings may be more able to tolerate high levels of herbivory either through compensatory growth or the production of defensive compounds. Additionally, aspen in these more favorable setting may be more likely to sucker following fire and more suckers may be likely to survive to maturity. Finally, aspen in biophysical settings more favorable to their growth are probably less resource-limited than aspen in harsher settings and may be able to better compete with conifers, thus maintaining dominance at a site over longer periods of time. Also, because fire and competition with conifer closely interact (Fig. 1), if aspen in more favorable settings respond more favorably to fire they are more likely to recruit overstory trees and maintain dominance on a site and therefore less likely to be overtopped by conifer. Moreover, favorable biophysical settings that produce many suckers following fire may also have high growth rates permitting many suckers to escape herbivory. These interactions of biophysical setting, fire, herbivory, and competition and their influences on aspen would suggest that management actions aimed at restoring aspen focus on areas where aspen are more likely to quickly resprout after fire, tolerate herbivory, and resist conifer encroachment.

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. I quantified the effect of topography, climate, soils and biotic interactions on the distribution, growth rate, and decline of aspen. I tested the following three hypotheses: (1) Aspen distribution in the

Greater Yellowstone Ecosystem is limited by biophysical setting such that it is present in a subset of the available combinations of gradients in climatic, topographic, or soil variables, (2) within this distribution, aspen aboveground primary productivity (ANPP) varies with respect to biophysical gradients, and (3) because different biophysical settings likely confer different abilities of aspen to compete with other vegetation, rates of change in the aerial cover of aspen vary in relation to biophysical gradients.

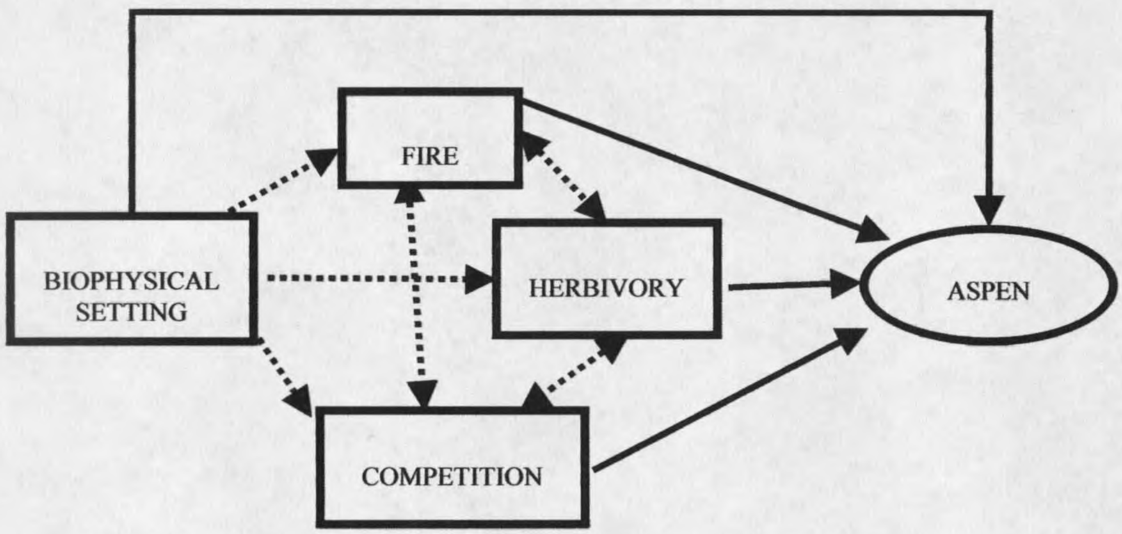

Figure 1. In my conceptual model of influences on aspen, biophysical setting directly affects aspen and also mediates the affects of herbivory, fire, and competition on aspen. Solid lines represent direct effects while dashed lines represent interactions or indirect effects.

This study is unique in attempting to quantify aspens' distribution, performance, and change over time to biophysical gradients across a large landscape. Aspen decline has been documented in several smaller-scale studies within the Greater Yellowstone Ecosystem (GYE) (Loope and Gruell 1973, Renkin and Despain 1996, Wirth et al. 1996, Hessl and Graumlich 2002, National Academies of Science 2002, Gallant et al. 2003) as well as aspens' response to fire (Loope and Gruell 1973, Jones and DeByle 1985b, Brown and DeByle 1987, Kay 1993, Bartos et al. 1994, Romme et al. 1995, Renkin and Despain 1996, Gallant et al. 2003) and herbivory (DeByle 1985, Romme et al. 1995, Baker et al. 1997, Kay 1997, White et al. 1998, Hessl and Graumlich 2002, National Academies of Science 2002). Loss of aspen has generated concern in the region, however this is the first study to look at ecosystem-wide changes in aspen cover and the first to examine distribution, productivity, and change in aspen at the level of the GYE. The GYE encompasses strong gradients in climate, topography, and soils making it uniquely suited to my study of aspen in the context of biophysical gradients.

Table 1. Biophysical setting, fire, competition, and herbivory are proposed as factors influencing aspen dynamics. This table summarizes the likely affects of each of these factors on aspen presence, growth, or canopy cover. I specifically test the influence of biophysical setting and competition (with conifer) on aspen presence, growth rates, and change in aerial cover.

Aspen attributes		Biophysical	Fire	Competition	Herbivory
Seedlings/suckers					
	Presence	Yes	Yes - seedling establishment, sucker regeneration	Yes	Yes - kills
	Growth	Yes	Yes	Yes	Yes - suppresses elongation, aspen as shrub growth form
Adults					
	Presence	Yes	Yes	Yes	Seldom
	Growth	Yes		Yes	No
	Canopy cover	Yes, via interaction with competition	Yes, via interaction with competiton	Yes	No

METHODS

To examine aspen dynamics in the context of biophysical setting, I related three different response variables: aspen distribution, aspen performance, and change in aerial coverage in the GYE to topographic, soils, and climatic explanatory variables. To understand existing patterns of aspen occurrence, I first mapped aspen distribution in the GYE and related that distribution to potential biophysical explanatory variables. Within aspen's distribution, I measured aspen ANPP to examine variability in aspen performance relative to the suite of explanatory variables. Finally, I measured landcover change (change in aerial cover) for aspen between the 1950's and 2001 to examine any relationship between percent change and the explanatory variables.

Study Area

The study was conducted across the Greater Yellowstone Ecosystem (GYE) in Montana, Idaho, and Wyoming, as defined by Hansen et al. (2000) (Fig. 2). The GYE comprises 7.3 million ha of public and private lands. Public lands include two national parks, seven national forests, national wildlife refuges, and Bureau of Land Management and state lands. (Greater Yellowstone Coordinating Committee 1987). Public lands are primarily in high and middle elevations, while private lands are generally located in valley bottoms and the plains surrounding public lands.

The GYE encompasses strong gradients in topography, climate, and soils. Soil types and climate vary with elevation in the region. Nutrient-poor rhyolite and andesite soils dominate higher elevations while valley bottoms contain nutrient-rich glacial outwash and alluvial soils (Hansen et al. 2000). Temperatures and growing season length generally decrease with increasing elevation (Despain 1990) while precipitation generally increases (Marston and Anderson 1991). The majority of the precipitation falls as snow (Hansen et al. 2000). Mean annual precipitation is 65 cm but ranges from 19-208 cm. Lower elevations (< 2000 m) receive an annual average of 25 cm of precipitation and higher elevations receive an annual average of 75 cm, most of which falls as snow. Mean annual average temperature is 2.17°C and ranges from -6.00°C to 8.00°C. Lower elevations average 5.12°C while higher elevations average 0.64°C, annually. Mean annual growing degree-days is 2013 °C-day and ranges from 498 °C-day to 3634 °C-day. Lower elevations average 2753 °C-day while higher elevations average 1630°C (Thornton et al. 1997).

Eight species of ungulates are found in the GYE: mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mountain goat (*Oreamos americanus*), and elk (Greater Yellowstone Coordinating Committee 1987, Singer 1991). Elk are the primary herbivores that feed on aspen and are widely distributed through the GYE. Eight elk herds summer in Yellowstone National Park and seven of those herds migrate to lower elevation wintering or feeding areas surrounding the park (Greater Yellowstone Coordinating Committee 1987, Singer 1991); the Northern Yellowstone herd winters on Yellowstone National Park's northern range (Greater Yellowstone Coordinating Committee 1987). The combined elk population estimate for all eight herds in 1988 was 47,880 of which 21,000 were members of the Northern Yellowstone herd (Singer 1991).