

UNDERSTANDING THE ROLE OF BIOPHYSICAL SETTING IN ASPEN
PERSISTENCE

by

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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, Oksanen 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, Hessel 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.

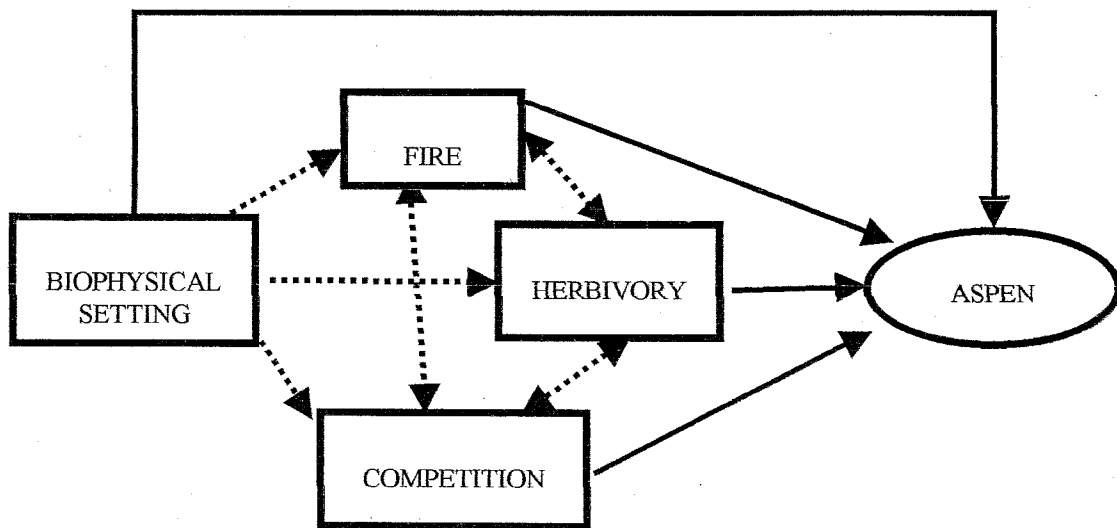


Figure 1. In my conceptual model of influences on aspen, biophysical setting directly affects aspen and also mediates the affects of herbivory, fire, and competition on aspen. Solid lines represent direct effects while dashed lines represent interactions or indirect effects.

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 competition	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).

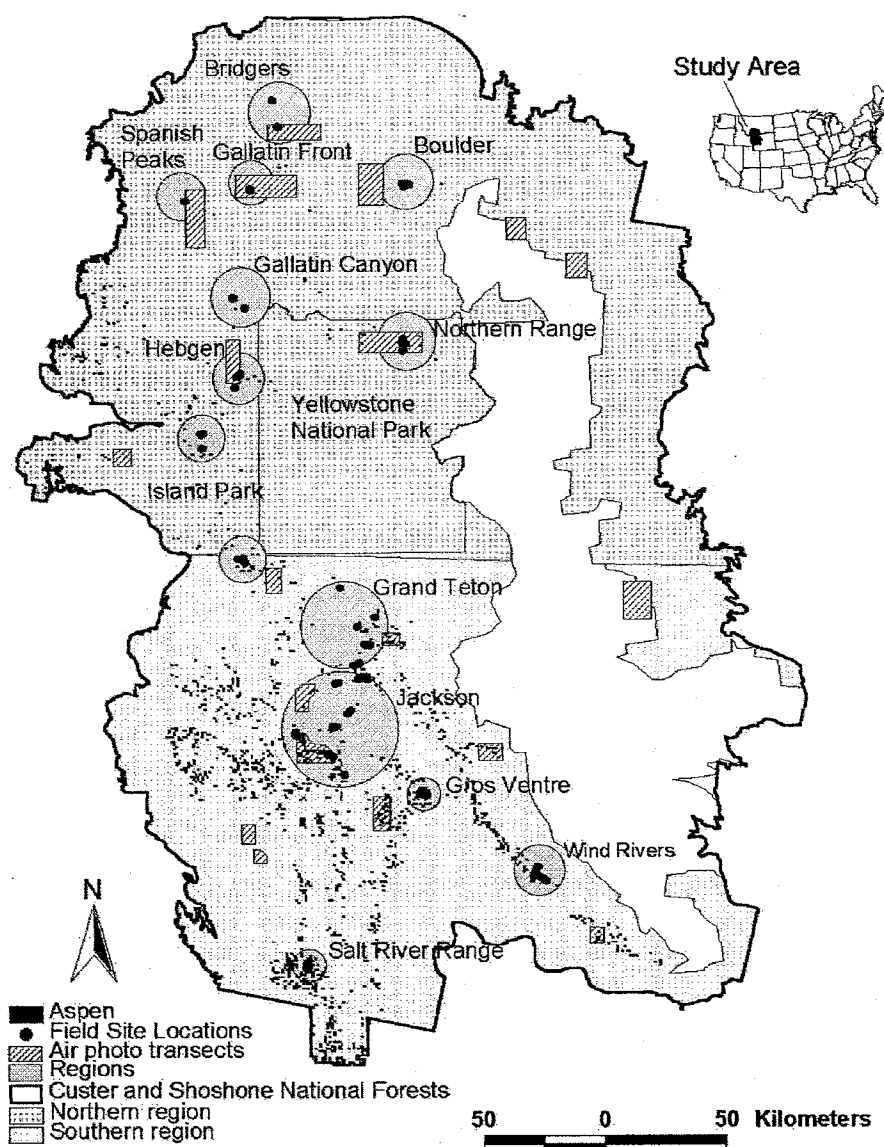


Figure 2. The Greater Yellowstone Ecosystem (GYE) was the study area. Aspen distribution was examined for the (GYE) as a whole and also within the northern and southern subregions shown here. Aspen annual net primary productivity (ANPP) was sampled as a measure of aspen performance at field site locations throughout the GYE. Field sites were clustered into regions (Bridgers, Boulder, etc.) for exploratory analysis of patterns in aspen performance across the study area. Aerial change in aspen cover from 1956-2001 was examined along the photo transects depicted here; these transects were randomly placed within regions of deciduous landcover.

Vegetation in the region closely follows climatic patterns (Marston and Anderson 1991). Low and dry elevations consist of shrub steppes often dominated by big sagebrush (*Artemisia tridentata*) or grasslands (Marston and Anderson 1991). As moisture increases, forests of Rocky mountain juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), or Douglas-fir (*Pseudotsuga menziesii*) occur. Upland elevations and rhyolitic soils generally support extensive lodgepole pine (*Pinus contorta*) forests (Marston and Anderson 1991, Hansen et al. 2000). Cottonwoods (*Populus angustifolia*, *P. balsamifera*, and *P. trichocarpa*) and willows (*Salix* spp.) dominate riparian communities. High elevation conifer forests consist of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) (Despain 1990, Marston and Anderson 1991). 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).

Generation of Biophysical Explanatory Variables

I used a 30-m resolution digital elevation model (DEM) from the United States Geological Survey (USGS) as my measure of elevation and used ArcView GIS (ESRI 1992) to derive aspect, and slope (Table 2). Climatic and soils explanatory variables were derived using the WXFIRE computer model, a computer program that produces spatially-explicit biophysical data layers at any chosen resolution (Keane et al. In press).

Climate and soil variables were summarized both annually and over the growing season, defined as April 1 - September 30.

Table 2. Biophysical variables used as potential explanatory variables in analyses of aspen distribution, performance, and landscape change. Each of the variables generated by WXFIRE was summarized both annually and over the growing season (April 1 - September 30, designated with a 'g' prefix in later tables).

Variable	Abbreviation	Units	Source
Elevation	Elev	m	USGS DEM
Aspect*	Aspct	degrees	USGS DEM
Slope	Slope	degrees	USGS DEM
Daily maximum temperature	Tmax	°C	WXFIRE
Daily minimum temperature	Tmin	°C	WXFIRE
Daily average temperature	Tave	°C	WXFIRE
Daily average daytime temperature	Tday	°C	WXFIRE
Daily average nighttime temperature	Tnight	°C	WXFIRE
Growing degree-days above 0.0°C	Dday	°C	WXFIRE
Precipitation	Ppt	cm	WXFIRE
Potential evapotranspiration	PET	cm	WXFIRE
Actual evapotranspiration	AET	cm	WXFIRE
Average daily snowfall	Snowfall	cm/day	WXFIRE
Vapor pressure deficit	Vpd	Pa	WXFIRE
Total daily solar radiation	Srad_t	W/m ²	WXFIRE
Shortwave radiation	Srad_fg	W/m ²	WXFIRE
Photosynthetically active radiation	Par	W/m ²	WXFIRE
Soil water potential	Psi	MPa	WXFIRE
Soil water lost to runoff	Outflow	cm/day	WXFIRE
Soil water transpired by canopy	Trans	cm/day	WXFIRE
Growing season water stress	Gsws	MPa	WXFIRE
Parent Material	Parmat	categorical	USGS ICBMP
Soil depth	Sdepth	cm	STATSGO
Percent sand in soil	Sand	%	STATSGO
Percent silt in soil	Silt	%	STATSGO
Percent clay in soil	Clay	%	STATSGO

*transformed aspect following the methods of Beers et al. (1966).

As a brief summary of WXFIRE, the model uses daily weather data from the 1-km DAYMET climate model (Thornton et al. 1997) to rescale climate data to the chosen

site level (30-m for this study) and generate additional biophysical variables (Table 2) (Keane et al. In press). Topographic and soils parameters are required inputs to WXFIRE. Topographic parameters required are elevation (m), aspect (degrees), and slope (percent), which I derived from the DEM. The soils parameters required - soil depth, percent sand, silt, and clay - were derived from the State Soil Geographic database (STATSGO). Five variables from the DAYMET database are used by WXFIRE for calculation of biophysical variables: daily minimum temperature ($^{\circ}\text{C}$), daily maximum temperature ($^{\circ}\text{C}$), total daily precipitation (cm), vapor pressure deficit (Pa), and solar radiation (kW/m^2). Vapor pressure deficit is assumed to be constant over 1-km and is not scaled down to the site level. However, the other four variables are rescaled to the site level.

Temperature and precipitation data from DAYMET are scaled from 1-km to 30-m using dynamic lapse rates to account for changes in topography (Keane et al. In press). The difference between the site's elevation and the elevation of the DAYMET pixel containing the site (the reference pixel) is calculated and multiplied by a lapse rate to calculate the change in temperature or precipitation needed to scale down the DAYMET data. To calculate the lapse rate, the weather data for the 8 DAYMET pixels surrounding the reference pixel are obtained. Then, the difference in temperature (or precipitation) between the DAYMET reference pixel and the 8 surrounding pixels is calculated, along with the difference in elevation, and the lapse rate is the ratio of difference in temperature (precipitation) and difference in elevation. These 8 lapse rates are averaged to get the daily lapse rate for the reference pixel. These lapse rates are then used to calculate temperature or precipitation for the site over the appropriate time period.

Solar radiation data from DAYMET are adjusted to the site level based on atmospheric transmissivity (Keane et al. In press) and scaled to the site level by accounting for slope and aspect using solar declination and altitude angle for a 1400 time of day. WXFIRE calculate different forms of solar radiation (Table 2) using the scaled down solar radiation (Keane et al. In press).

The scaled down temperature variables are used to derive daily nighttime, daytime and soil temperature (Keane et al. In press). Growing degree-days are calculated as sum of the difference between daily daytime temperature and 2.0°C (Keane et al. In press). Soil variables (Table 2) are calculated based on equations using percent sand, silt, and clay (Keane et al. In press). Potential and actual evapotranspiration (PET and AET, respectively) are calculated by WXFIRE using the Penman equation (Keane et al. In press).

Aspen Distribution

I used existing GIS vegetation data, which were verified through aerial photograph interpretation, to map the distribution of aspen in the GYE. Vegetation maps were obtained from Gallatin National Forest, Beaverhead National Forest, Yellowstone National Park, Bridger-Teton National Forest, Teton National Park, and the Targhee-Caribou National Forest (Appendix A). Thus, analysis of aspen distribution was restricted to these portions of the study area.

Using aerial photographs, I verified the accuracy of the agency maps along transects. I placed transects to sample across elevation, major aspect, and parent material types. Along these transects, I obtained aerial photographs from the national forests and

national parks and mapped all visible aspen on each aerial photograph. Within the transects, I then compared my classification of aspen with the classification in the agency maps by conducting an accuracy assessment as described below.

I used the entire mapped population of aspen in my analysis of aspen distribution by generating a point at the center of each 1-km grid cell containing aspen ($N_{\text{presence total}} = 1440$). Since aspen is much more prevalent in the southern GYE ($N_{\text{presence north}} = 147$, $N_{\text{presence south}} = 1293$), I defined northern and southern subregions such that the southern boundary of Yellowstone National Park divided the two regions (Fig. 2). I then generated random samples of aspen absence stratified by geographic region (north vs. south) to enable us to conduct the analysis at different spatial scales ($N_{\text{absence total}} = 1438$, $N_{\text{absence north}} = 717$, $N_{\text{absence south}} = 721$). My total sample size for presence and absence observations was 2878. I randomly selected 1/3 of the total observations ($N_{\text{validation}} = 950$, $N_{\text{presence}} = 475$, $N_{\text{absence}} = 475$) and reserved them for validation. The remaining observations ($N_{\text{model}} = 1928$, $N_{\text{presence}} = 965$, $N_{\text{absence}} = 963$) were used to build a classification trees with class membership defined as aspen presence or aspen absence at the three different spatial scales: the entire GYE, the northern GYE, and the southern GYE.

I used classification and regression tree (CART) analysis (TREE package, Ihaka and Gentleman 1996, R Development Core Team 2003) to relate biophysical variables (Table 2) to aspen distribution. CART recursively partitions data into subsets based on the single best predictor variable (Breiman et al. 1984) and is useful in discovering relationships in predictors that may be hierarchical, nonlinear, or nonadditive in their interactions (Breiman et al. 1984, Franklin 1995, Iverson and Prasad 1998). The final

CART models were generated after pruning the full tree to that tree which maximized the deviance explained while minimizing the misclassification error rate from cross-validation.

The rules from the CART model were used to predict the class membership (aspen presence or aspen absence) of each observation in the validation dataset. I calculated errors of omission (producer's accuracy), errors of commission (user's accuracy), and overall model accuracy. Producer's accuracy measures the probability that an observation was correctly classified and was calculated as the number of correctly classified observations divided by the number of reference observations collected for that class (Jensen 1996). User's accuracy measures the probability that a classified observation actually represents that category and was calculated as the number of correctly classified observations divided by the total number of observations classified in that category (Jensen 1996). Overall accuracy was calculated as the total number of correctly classified observations in both categories divided by the total number of observations in the validation dataset.

Aspen Performance

To evaluate aspen performance relative to biophysical setting, I sampled aspen growth rates, stand structure, and species composition in 108 aspen sites stratified by elevation, aspect, and parent material in the summers of 2001 and 2002. I calculated ANPP as an index of aspen performance and investigated the relationship of aspen ANPP to biophysical setting using multiple regression.

I generated random points within my map of aspen distribution that were stratified by elevation, aspect, and parent material and proportional to the occurrence of these strata within aspen's distribution in the GYE. These random points represented potential field sites. I sampled as many field sites over the course of two 3-month field seasons as possible. Sites were widely distributed through the GYE (Fig. 2) and located using a global positioning system (GPS). I used a nested-plot sampling design similar to that described in Hansen et al. (2000). At each site, I established four 8-m radius subplots located 20-m from site center at each of the cardinal directions (north, south, east, and west) (Fig. 3). I collected data on tree and shrub density and size distributions to enable us to later estimate tree and shrub biomass as potential explanatory variables. Within the 8-m radius plots (Fig. 3), I tallied tree density by species and size class. Tree size class was defined by diameter at breast height (dbh, in cm) and divided into 8 categories: 2-10, >10-20, >20-30, >30-40, >40-60, >60-90, >90-120, and >120 cm. For aspen at each 8-m radius plot, one tree of each size class represented in each subplot was cored using a 1.27 cm diameter increment borer (Fig. 3). The actual dbh and height (in m, determined by triangulation using a clinometer) of each cored tree were measured. Within each 8-m radius plot, I established a 2-m radius plot at the center of the larger plot (Fig. 3). In the 2-m radius plots, I tallied shrub density by species and basal diameter class (in cm) in 7 categories: 0.5-1, >1-2, >2-3, >3-4, >4-6, >6-10, and >10 cm. Finally, I established a 0.25-m² plot 5-m due north from the center of each 8-m radius plot (Fig. 3). Within this square plot, I measured herbaceous biomass (a potential explanatory variable) by clipping all nonwoody plants at ground level and these samples were dried and weighed at the laboratory. I collected soil samples, so that soil characteristics could be included in later

analyses, using a 2.54 cm diameter soil sampling probe within the 0.25-m² plot. Soil samples were brought to the laboratory and weighed (wet weight) in grams, then dried at 24°C in an oven for 24 hours and reweighed (dry weight). Soil samples were then submitted to the Soil Analysis Testing Lab at Montana State University to be analyzed for nitrate and ammonium content. I calculated tree and shrub densities (expressed as numbers/ha) and soil moisture (expressed as a percent of wet weight). Sites were considered independent units of analysis for this study, so I averaged the data across the four subplots within each site.

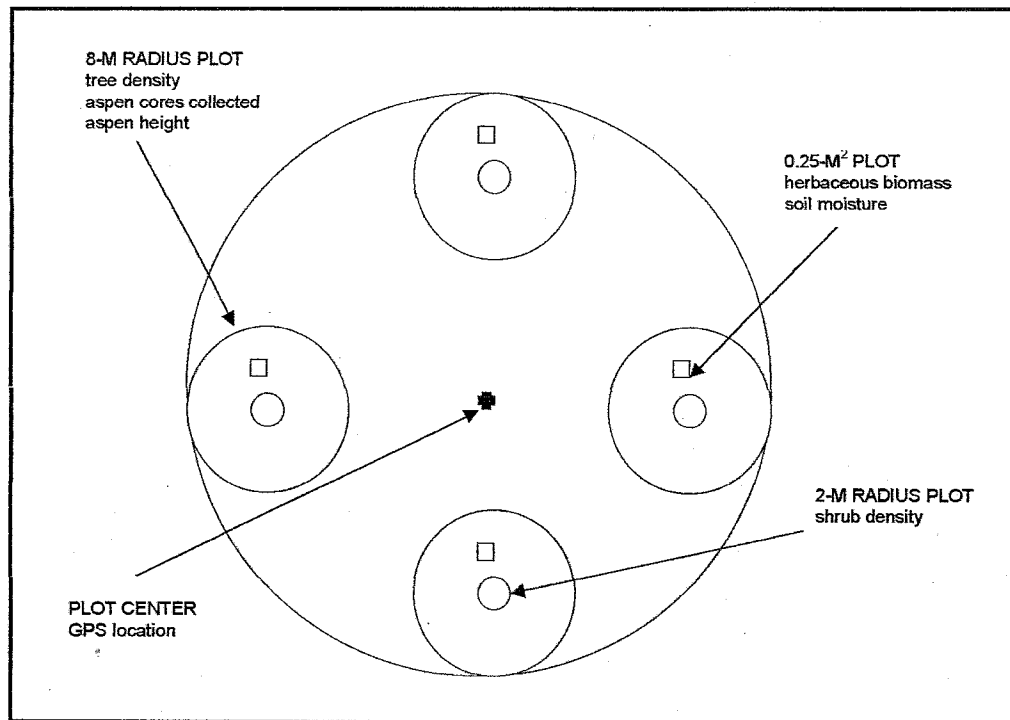


Figure 3. A nested-plot design was used to sample aspen ANPP and vegetation characteristics. Aspen ANPP was used as an indication of aspen performance. ANPP was calculated from aspen growth rates which were measured from increment cores taken at field sites. Tree and shrub species and size class were also measured to characterize vegetation at a site.

Average annual radial growth of aspen was used in my calculation of ANPP. I measured average annual radial growth (termed increment) of 613 aspen trees from the cores. Cores were mounted and sanded until annual rings were clearly visible. The most recent 20 years of growth were determined by identifying annual rings using a dissecting microscope and counting back from the bark end to the 21st annual ring. I determined 20-year radial increment by measuring the length (mm) from the outside edge of the most recent summerwood ring to the outside edge of the twenty-first summerwood ring. On trees less than 20 years old, I used either 5- or 10-year increment. The measured radial increment was divided by the appropriate number of years to calculate average annual increment for each tree. Those cores with extensive heart-rot were not used in the analysis, although this represented a small fraction of trees sampled (2.4%).

Our calculation of ANPP followed the methods of Hansen et al. (2000). I estimated aboveground biomass of aspen using BIOPAK software (Means et al. 1994), which calculates the biomass of plant components based on allometric equations derived from field studies. To estimate ANPP, I first estimated aboveground biomass of aspen from current dbh and estimated height. Following the methods of Hansen et al. (2000), I fit a negative exponential function to measured dbh and height data for aspen (N=615 trees) and used this relationship to estimate aspen height at the median of each dbh class. The median dbh and estimated height were used to estimate aspen biomass using BIOPAK. I then estimated tree dbh one year ago for each size class based on diameter increment (radial increment $\times 2$) and used previous dbh to estimate aspen biomass one year ago. ANPP of aspen was calculated as the difference between current and previous

biomass multiplied by the density of aspen trees in the size class per site. ANPP was expressed as $\text{kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$.

I also estimated aboveground biomass of other species of trees and shrubs using BIOPAK so that I could use these measures as potential predictors of aspen ANPP in my analyses. As much as possible, I used equations derived from data from the Rocky Mountains. Some of the species in my study area were not included in BIOPAK so I used substitutions (Appendix B). To calculate aboveground biomass of shrubs, I needed the basal diameter class of the shrub while for trees I needed dbh and height. I calculated total aboveground biomass estimates from the median of the basal diameter class for shrubs. For trees, I used functions derived from a previous study in the GYE (Hansen et al. 2000) to estimate height at the median of each dbh-class for all tree species and used the median dbh and estimated height to estimate tree biomass by species. Estimates of tree and shrub biomass were multiplied by the densities of each species at each site to estimate tree and shrub biomass by species for a given site, expressed as $\text{kg} \cdot \text{ha}^{-1}$. Tree and shrub biomass by species were then summed at each site to estimate total tree and shrub biomass per site.

To understand the distribution of aspen ANPP across the study area, I conducted exploratory analyses prior to model building. I divided my study sites into geographic regions (Fig. 2) so that I could look at broad-scale patterns in ANPP. I examined boxplots of ANPP by region and by plots within region to examine variability both between and among regions. I tested for differences in ANPP between the different regions using one-way analysis of variance and Tukey-Kramer confidence intervals. (PROC ANOVA, SAS Institute 2001).

I used multiple linear regression to examine the relationships between aspen ANPP and the explanatory variables (Table 2). I graphically examined the univariate relationships between ANPP and each of the potential explanatory variables to determine the nature of the relationships (i.e. linear, quadratic). I separated the potential explanatory variables into categories of temperature, moisture, radiation, soils, competition (biomass of other vegetation), and topographic variables. I examined quadratic terms in the models for predictors in the temperature, moisture, radiation, and soils categories since several studies suggest that species may show a unimodal response to environmental gradients (McKenzie et al. 2003). Quadratic terms were only used if they had a negative coefficient because a positive coefficient produces a concave-up response, which is not biologically meaningful and does not represent the unimodal response. When it was appropriate to use a quadratic term, I centered the variable around its mean and squared the centered variable such that the simple linear regression equation takes the form:

$$Y_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2$$

where $x_i = X_i - X_{\text{bar}}$,

X_i is the original variable and X_{bar} is the mean of the original variable, in order to reduce collinearity between the variable and the variable squared (Neter et al. 1996).

The density of aspen stems at a site contributes to overall ANPP at that site. The relationship between aspen ANPP and stem density is multiplicative such that, all else being equal, greater aspen density should experience greater ANPP. Therefore, I controlled for the effect of aspen density upon overall site ANPP using an offset variable (PROC GENMOD, SAS Institute 2001). An offset variable is incorporated into the

regression model as a covariate with a fixed regression coefficient. Regression coefficients are usually unknown parameters which are estimated by the procedure but I fixed the coefficient of aspen density at one. This allowed the actual aspen stem density at each site to be controlled for in the model.

I used Akaike's Information Criterion adjusted for small sample-size (AIC_c) to select the single best predictor of ANPP within each category (Burnham and Anderson 1998, Stafford and Strickland 2003). A difference of 2 in AIC_c units was used to choose the most parsimonious models in each category (Burnham and Anderson 1998). Finally, I combined variables from the selected models in each category and also permitted interaction terms between the moisture and temperature categories. I used AIC_c to select the most parsimonious models containing combinations of those variables selected from each category.

Since aspen is more abundant in the southern portion of the GYE, I wanted to see if different biophysical variables influenced aspen ANPP at different scales of analysis. Therefore, I divided my field sites into northern and southern regions defined in the same manner as described for the aspen distribution analysis. I then built regression models, as described above, for all my sites and then separately for just the northern sites and for just the southern sites.

Landscape Change

Changes in the aerial cover of aspen and conifer were examined using a time-sequence of aerial photography, from 1955 to 2001. I sampled landscape change across the GYE and stratified my sampling by elevation and aspect and restricted my sampling

to regions containing deciduous landcover in order to sample aspen sites. I used USGS landcover data, from 1992, to identify regions of deciduous and coniferous landcover. I chose the USGS landcover data rather than the agency vegetation maps used previously in order to extend my sampling area across the GYE and because I desired one consistent classification of both deciduous and coniferous vegetation across the GYE. Although the USGS data were less accurate and therefore unsuited to my previous analyses, I used this data here because I was able to verify the accuracy at each point during aerial photograph interpretation.

I placed twenty transects to cross elevation and major aspect in areas of deciduous landcover (Fig. 2). I obtained 1:15,840 scale aerial photographs from an early time period (1955-1963) and a current time period (1992-2001) along each transect from the Aerial Photography Field Office in Salt Lake City, Utah. For one transect, in the northern range of Yellowstone National Park, I used 1969 photographs for the early period because these were the earliest available photographs. I then generated random 0.81 ha plots, stratified by elevation, aspect and land cover (deciduous versus coniferous) within each transect for sampling of change in aerial cover.

I measured change in aerial cover in 242 plots by interpreting the percentage of aspen and conifer cover in each 0.81 ha plot for each time period. The point-intercept method was used to determine the percent aspen and conifer cover in each plot. A grid of 10 points was overlain on top of the 0.81 ha plot and points that intercepted aspen or conifer were recorded as the appropriate cover type at 10-percent increments. The number of points of each cover type was summed to generate percentage of aspen and conifer cover in each plot. Each plot was interpreted for both the early and current time

period. Evidence of logging (e.g. clear-cuts, roads), fire (e.g. snags, blackened trees, young even-aged stands), or disease was recorded and assigned to the time period in which it was apparent. To avoid the confounding effects of disturbance, those plots that showed signs of disturbance were removed from analysis. Percent change in aspen and conifer cover was calculated by subtracting the current percent cover from the early percent cover.

I divided the plots into three classes of change: loss (a 10% or greater decline in aspen cover), no change (between 10% decline and 10% gain in aspen cover), and gain (a 10% or greater gain in aspen cover). I used one-way analysis of variance (PROC ANOVA, SAS Institute 2001) to examine differences between stands exhibiting loss, no change, or gain in aspen cover relative to the biophysical explanatory variables. Multiple linear regression (PROC REG, SAS Institute 2001) was used to examine the relationship between the various explanatory variables (Table 2) and the percent change in aspen cover. I used the same methods described in the aspen performance section with the exception that the competition variable used was the percent change in conifer cover.

Since competition with conifer is widely believed to influence loss of aspen, I also examined the relative contribution of biophysical setting and competition by building separate regression models for loss plots with conifer present and loss plots with conifer absent. I followed the same methods to select these models as described above.

RESULTS

Aspen Distribution

I conducted an accuracy assessment of the agency map of aspen distribution. The overall accuracy of the aspen map was 78%. Of those points I identified as aspen the map correctly classified 54% (producer's accuracy). However, of all points classified as aspen 88% actually were aspen (user's accuracy). The producer's accuracy for aspen absence was 94%, meaning most of the time the map correctly classified aspen absence. User's accuracy for aspen absence was 74% which reflects the percentage of points classified by the map as aspen absence which were actually aspen absence.

To examine the relationship of aspen distribution to biophysical setting, I conducted CART analysis of aspen presence and absence at three spatial scales: the entire GYE, the northern GYE, and the southern GYE (Fig. 1). Each CART model was pruned to the minimum number of terminal nodes which explained the maximum deviance in aspen presence or absence classes, using cross-validation (Ihaka and Gentleman 1996, R Development Core Team 2003).

The CART model for the entire GYE was pruned to eight terminal nodes (Fig. 4). The model predicts aspen to occur in warm, wet locations based on radiation, snowfall, potential evapotranspiration, and temperature (Fig. 5). Growing season shortwave radiation explained the largest proportion of the deviance in class membership (Fig. 4). The first split of the CART model, separates high ($> 68.9 \text{ W/m}^2$) and lower values for growing season shortwave radiation (Fig. 4). These higher values of growing season shortwave radiation are primarily in the southern portion of the GYE, and the CART

model for the southern GYE (Fig. 6) reflects this in its similarity to the right portion of the CART for the model for the entire GYE. Even in the northern GYE, aspen is associated with higher values of radiation (Figs. 4, 7).

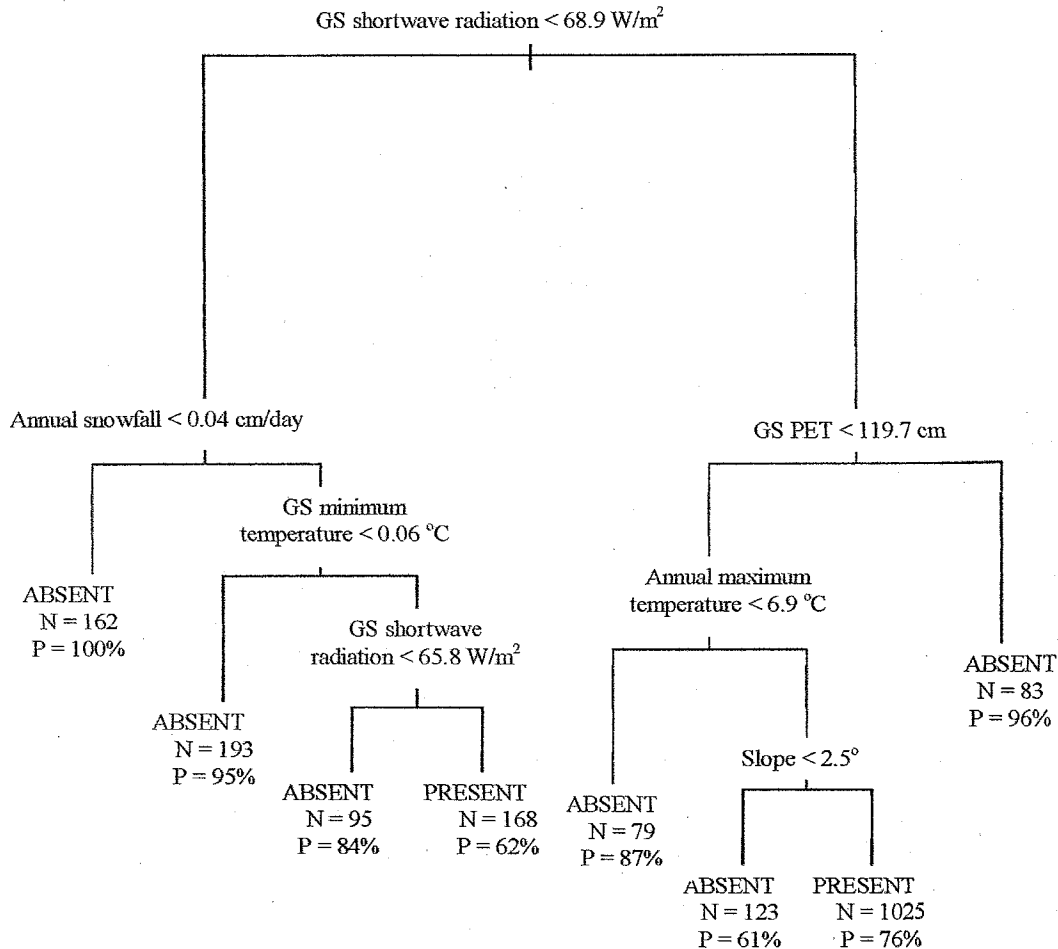


Figure 4. Results of a classification and regression tree (CART) analysis for the entire GYE to examine aspen distribution relative to biophysical setting. GS refers to growing season. Overall accuracy of the model was 80%. The length of the branches is proportional to the amount of deviance explained, thus growing-season shortwave radiation explains the largest proportion of the deviance in the data. This CART model with 8 terminal nodes explained the greatest proportion of the deviance in aspen presence or absence. 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.

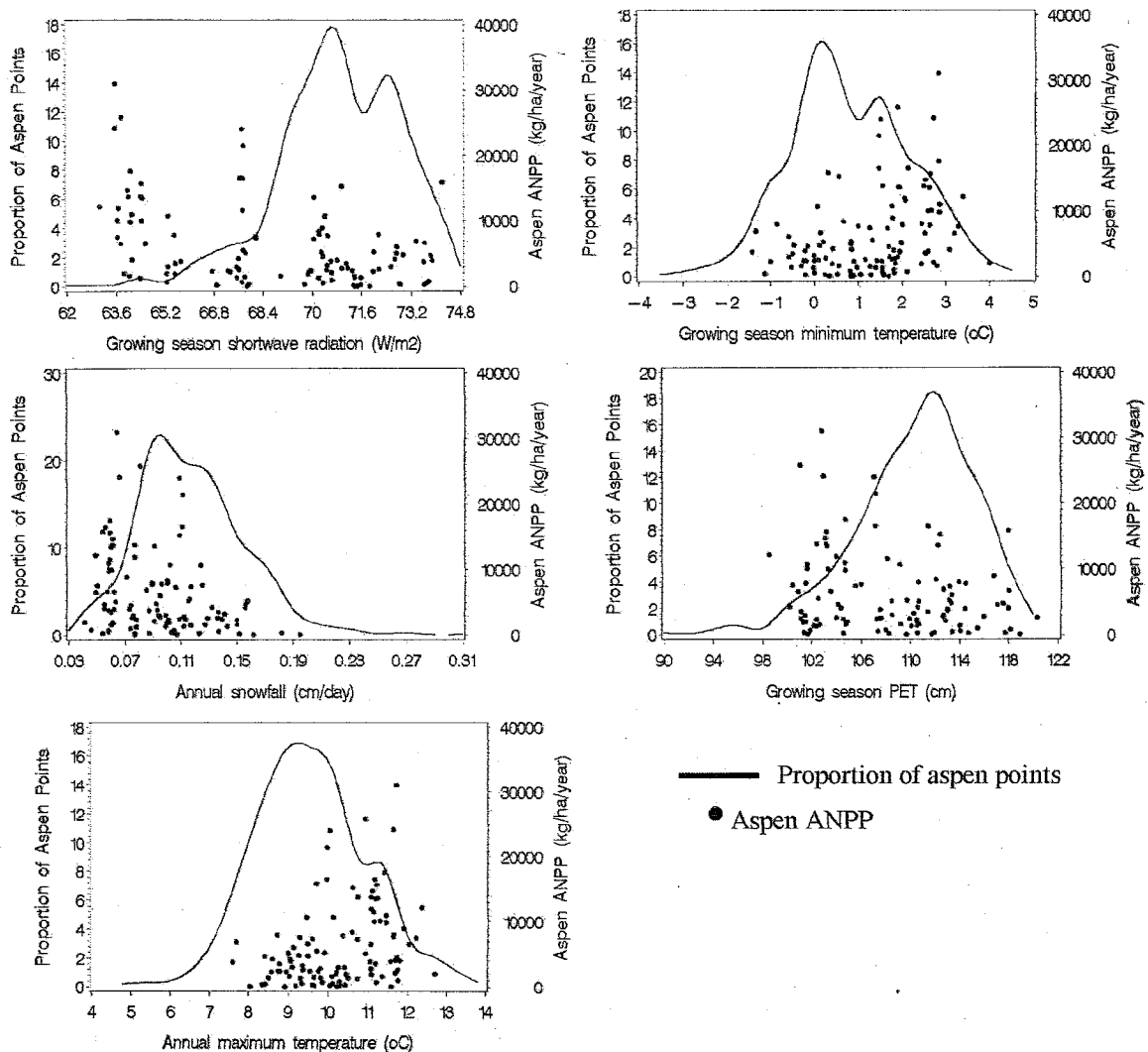


Figure 5. Results of the CART model for the GYE show growing season shortwave radiation, growing season minimum temperature, annual snowfall, growing season PET, and annual maximum temperature to be the best predictors of aspen presence. These graphs show the distribution of aspen relative to each of these variables (left axis) with aspen ANPP (right axis) overlain on the same gradient. Although most aspen occurs at higher radiation and PET values, highest ANPP occurs at lower levels for these variables. Conversely, higher temperatures at the tail of aspens' distribution have the highest aspen ANPP values.

Our model validation yielded an overall accuracy of 80% for the CART model for the entire GYE, using a validation dataset. With a producer's accuracy for aspen

presence of 92%, the model performed well at classifying aspen presence - 92% of the aspen presence observations were correctly classified as aspen presence. The user's accuracy for aspen presence was lower (74%) meaning that only 74% of the observation that the model classified as aspen presence really were aspen presence; in other words, the model over-predicted the occurrence of aspen. The model less accurately predicted aspen absence (producer's accuracy = 68%), 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).

The main split on growing season shortwave radiation for the model of the entire GYE (Fig. 4) seems to have effectively split the GYE into the northern and southern subregions. The left half of the split which continues splitting on annual snowfall, growing season minimum temperature, and growing season shortwave radiation (Fig. 4) is very similar to the CART developed for the northern GYE, with the only difference that growing season solar radiation flux is substituted for growing season shortwave radiation (Fig. 7). Similarly, the CART for the southern GYE (Fig. 6) is nearly identical to the right half of the CART for the entire GYE (Fig. 4), with the only difference that the importance of annual maximum temperature and growing season PET are reversed between the two models. The CART for the northern GYE yielded an overall accuracy of 81%. For aspen presence it had a producer's accuracy of 72% and user's accuracy of 45%, it less accurately predicts aspen presence than the model for the entire GYE but is also less likely to over-predict the occurrence of aspen. For aspen absence the northern CART model had a producer's accuracy of 83% and user's accuracy of 94%. The CART for the southern GYE yielded an overall accuracy of 78%. It correctly classified

most aspen presence observations (producer's accuracy = 94%) but often over-predicted aspen presence (user's accuracy = 77%). For aspen absence it had a producer's accuracy of 49% and a user's accuracy of 83%.

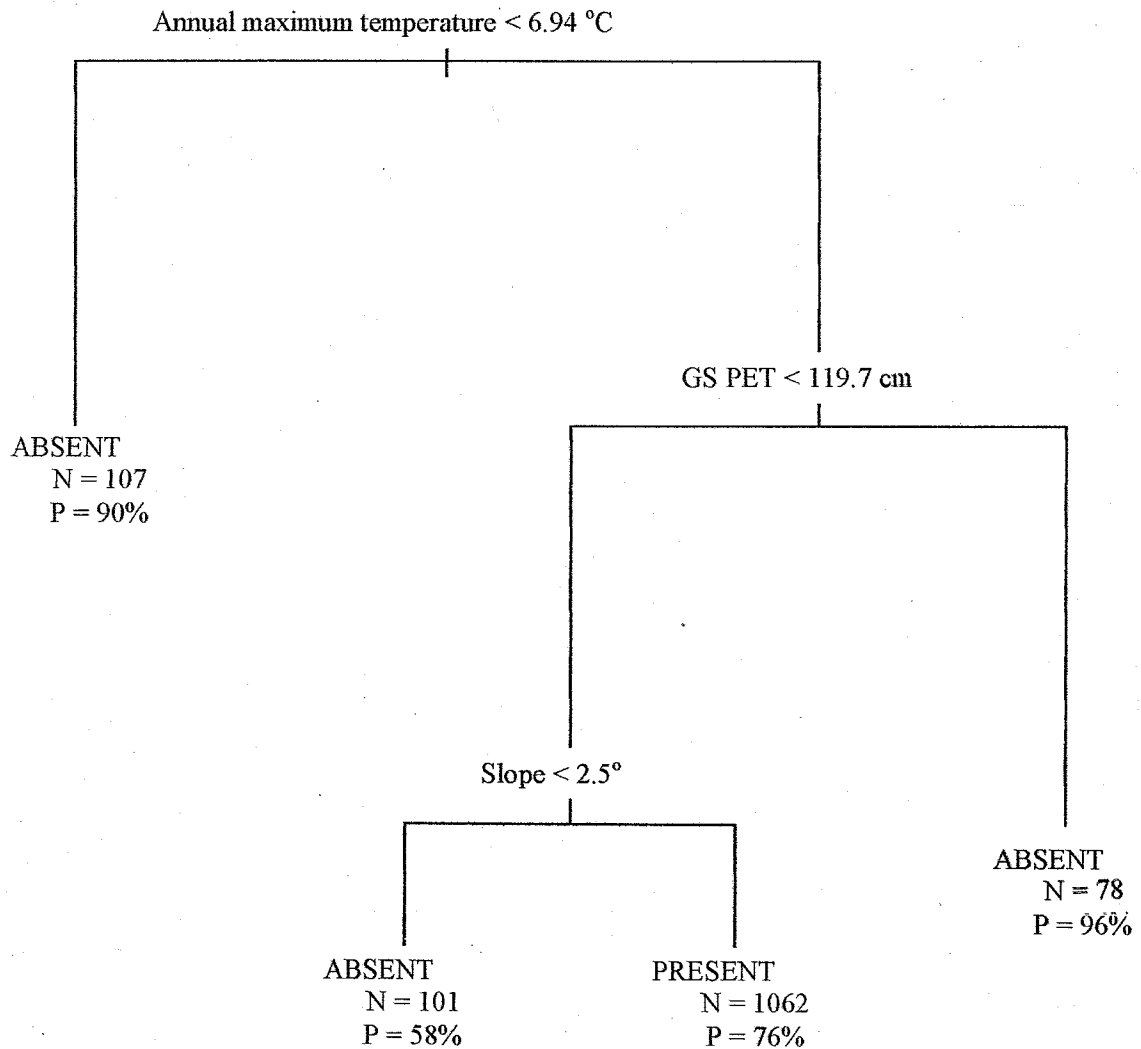


Figure 6. Results of a classification and regression tree (CART) analysis for the southern GYE to examine aspen distribution relative to biophysical setting. This CART model had an overall accuracy of 78%. If the rule at the top of a branch is true, then follow the left branch; if false, follow the right branch. N indicates the number of observations classified in a terminal node; P indicates the probability that the classification is correct.

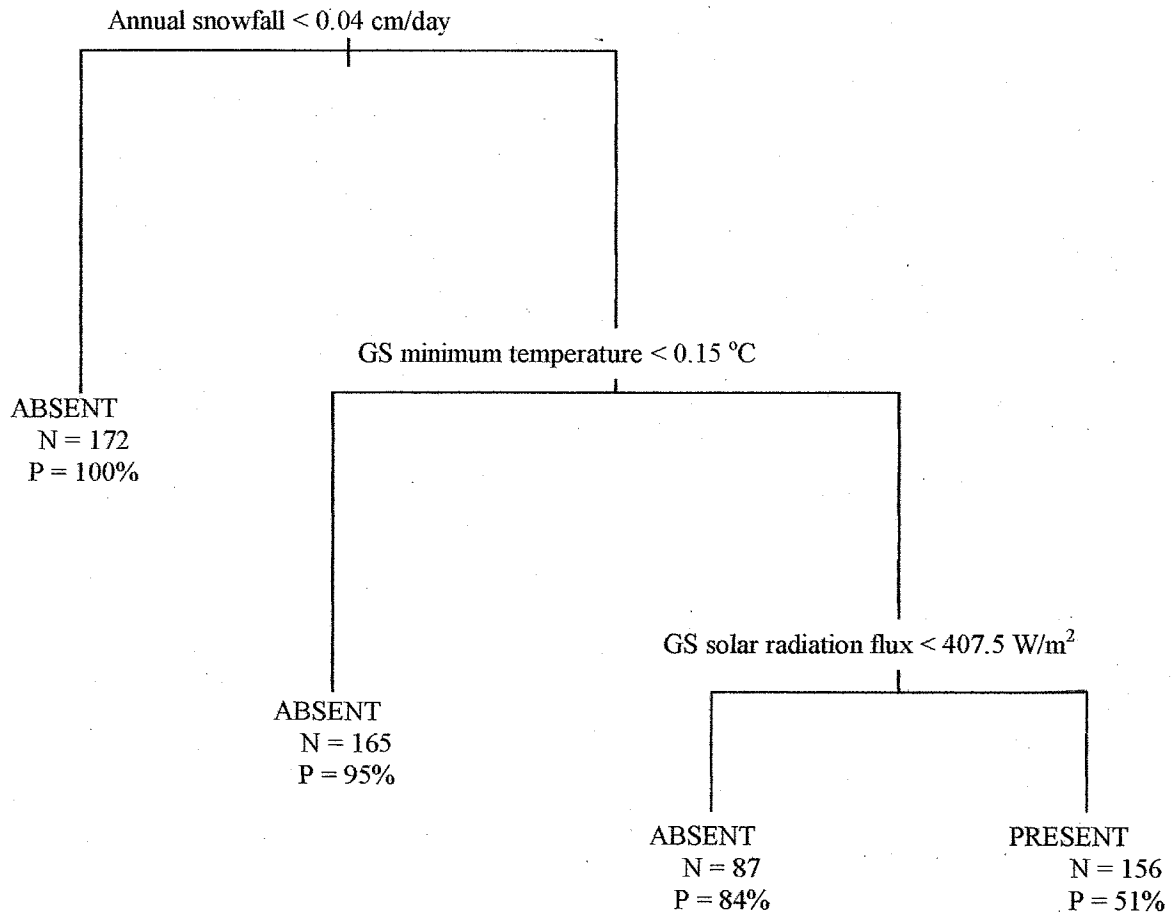


Figure 7. Results of a classification and regression tree (CART) analysis for the northern GYE to examine aspen distribution relative to biophysical setting. This CART model had an overall accuracy of 81%. If the rule at the top of a branch is true, then follow the left branch; if false, follow the right branch. N indicates the number of observations classified in a terminal node; P indicates the probability that the classification is correct.

Aspen Performance

I sampled 108 field sites and collected increment cores from 628 aspen trees, 613 of which did not have heart-rot and were used for analysis. One field site yielded no

readable cores (all the cored trees had extensive heart-rot), reducing the sample size for analysis to 107 sites. The largest size class of aspen represented on my field sites was class 4 trees (40-60 cm dbh). 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/ha/year (standard error =607, min.=57, max.=31,025).

To understand patterns of aspen performance across the GYE, I examined boxplots of aspen increment and ANPP by geographic regions (as shown in Fig. 2). These regions represented areas where biophysical setting was similar within sites, with respect to elevation, precipitation, and soils, but differed between regions. Thus, for this exploratory analysis, region served as a rough proxy for biophysical gradients. My hypothesis was that aspen performance varies across gradients in climate, topography, and soils. If this hypothesis were true, I would expect to see significant variation in aspen growth rates and primary productivity among samples from different locations along the biophysical gradient. A one-way analysis of variance test (ANOVA) indicated that aspen ANPP varied significantly among regions ($p < 0.001$). Tukey-Kramer confidence intervals showed that ANPP in the Gallatin Front stands was significantly higher than any of the other regions. Additionally, ANPP was significantly higher in the Boulder region than in the Jackson region. (Fig. 8).

I used AIC_c (Burnham and Anderson 1998) to identify the single predictor variables within each of five classes (moisture, temperature, radiation, soils, topography, and biotic) that best explained the variation in aspen ANPP for all the sites. The variables selected were growing season precipitation, annual minimum temperature, percent clay in the soil, annual average daily solar radiation flux, elevation, and conifer

biomass (Table 3). Although I selected the variables within each category with the lowest AIC_c for the category, often several variables were comparably well supported as evidenced by the AIC_c weights (Table 3). AIC_c weights represent the relative support for a model given the data and the competing models (Burnham and Anderson 1998). For example, growing season precipitation has 26% support as the "best" moisture model but snowfall is also well supported with 23% support. The radiation variables as a group generally had the highest explanatory power, followed by temperature variables, topographic variables, soils variables, and lastly the biotic variables (Table 3).

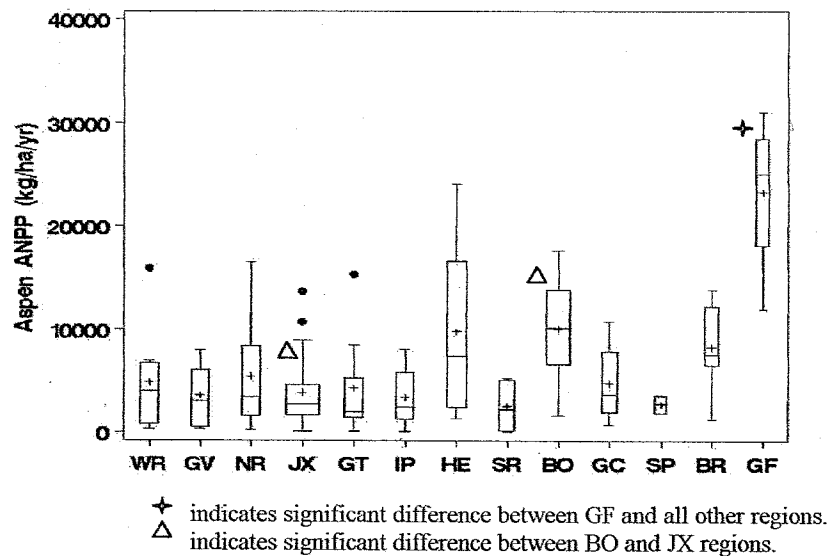


Figure 8. Boxplots of aspen annual net primary productivity (ANPP) between regions which differ in biophysical setting. Regions are sorted from low (WR) to high (GF) values of annual minimum temperature and growing season precipitation, since their interaction was the strongest predictor of aspen ANPP in the regression model. Labels along the x-axis are the names of the transects: WR=Wind Rivers, GV=Gros Ventre, JX=Jackson, GT=Grand Teton, IP=Island Park, NR=Northern Range, SR=Salt River Range, HE=Hebgen, BO=Boulder, GF=Gallatin Front, SP=Spanish Peaks, GC=Gallatin Canyon, BR=Bridgers. Central lines represent the mean and whiskers are drawn to the lowest and highest values within 1.5 units of the interquartile range (IQR), extreme observations are represented by dots. Using ANOVA, ANPP varied significantly ($p < 0.001$) between regions.

I did not allow variables with a Pearson correlation greater than 0.80 to be included in the same model, this arbitrary cut-off was used in an attempt to reduce multicollinearity in the models. Annual minimum temperature and annual average daily solar radiation flux were highly correlated as were annual minimum temperature and elevation. I then built models with all combinations of these variables (subject to the above constraint) and I also allowed an interaction term between moisture and temperature (growing season precipitation * annual minimum temperature) to be considered if both growing season precipitation and annual minimum temperature were in a model; from these competing models, I selected the final overall model using AIC_c (Table 3).

The selected model explained 37% of the variation in aspen ANPP across all my sites ($p < 0.0001$) 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 4). The interaction between growing season precipitation and annual minimum temperature was proportionally the strongest predictor of ANPP, as shown by its scaled coefficient, and was positively correlated with ANPP (Table 4). Aspen ANPP was the highest in areas with warmer temperature and intermediate growing season precipitation (Fig 9). The percent of clay in the soil was positively related to ANPP and the next strongest predictor of ANPP (Table 3). In the univariate setting, aspen ANPP closely tracks the distribution of aspen relative to percent clay in the soil, except for a few sites with 17% clay in the soil which had much higher ANPP (Fig. 10). The percent of clay in the soil was followed by annual minimum temperature which was positively correlated with aspen ANPP

(Table 4). The highest aspen ANPP was associated with warmer temperatures at the upper limit of aspen's distribution, but ANPP was variable at intermediate temperatures (Fig. 10). The coefficient for growing season precipitation was not significant at $\alpha = 0.05$, however it is necessary in the regression model because of the significant interaction term and was positively correlated with aspen ANPP. ANPP was variable across aspen's distribution relative to growing season precipitation (Fig. 10). If competition influences aspen growth rates (Table 1), I would expect conifer biomass to be negatively correlated with aspen ANPP which is what I found (Fig. 10), although conifer biomass was more weakly correlated with ANPP than were the biophysical predictors (Table 3). This regression model for aspen ANPP across all of my field sites in the GYE predicts high ANPP to be associated with warm, wet areas with lower conifer biomass and high levels of clay in the soil.

The variables selected for building models in the northern GYE sites were annual vapor pressure deficit, growing season maximum temperature, ammonium concentration in the soil, annual solar radiation flux, slope, and conifer biomass (Table 5). The radiation variables, as a group, had the strongest explanatory power and were negatively correlated with aspen ANPP in the northern sites (Table 5). All of the top moisture variables related to vapor pressure deficit (Table 5) and temperature variables were all positively correlated with aspen ANPP (Table 5). I had strong support for the ammonium as the best soils variable and it was positively correlated with ANPP (Table 5). Biotic variables in my northern sites, including conifer biomass, were not significant in the univariate setting and had very low explanatory power (Table 5). Vapor pressure deficit and growing season maximum temperature were highly correlated and were not

allowed in the same model; for this reason, I did not include models with a temperature*moisture interaction term in the suite of competing models for the northern sites.

Table 3. AIC_c values were used to select the best model of aspen ANPP from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Moisture	gPpt	+	1	2156.25	0.00	0.26	0.12*
	Snowfall	--	1	2156.49	0.24	0.23	0.12*
	Vpd Vpd ²	+, --	2	2157.44	1.20	0.15	0.13*
Temperature	Tmin	+	1	2149.35	0.00	0.23	0.17*
	Tnight	+	1	2149.66	0.31	0.20	0.16*
	Tave	+	1	2150.17	0.82	0.15	0.16*
	Tsoil	+	1	2150.33	0.99	0.14	
Soils	Clay	+	1	2160.21	0.00	0.29	0.09*
	NH ₄ ⁺	+	1	2161.01	0.80	0.20	0.08*
	Outflow	--	1	2161.82	1.61	0.13	0.07*
	gOutflow	--	1	2161.82	1.61	0.13	0.07*
Radiation	Srad	--	1	2156.25	0.00	0.28	0.21*
	gSrad	--	1	2156.49	0.24	0.25	0.21*
	Srad_fg	--	2	2157.44	1.20	0.16	0.21*
Topography	Elev	--	1	2152.07	0.00	0.99	0.15*
Biotic	Conifbio	--	1	2166.80	0.00	0.38	0.03
	Herbbio	+	1	2166.96	0.16	0.35	0.02
	Shrbio	+	1	2167.50	0.70	0.27	0.02
Overall Model gPpt Tmin gPpt*Tmin Clay Conifbio			5	2130.37	0.00	0.71	0.37*

* indicates the model is significant at $p < 0.05$

Table 4. Results of regressions relating aspen ANPP to biophysical variables. Models shown are the best overall model as selected using AIC_c. 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.

Response	Variable	Parameter estimate	Standard error	t Value	Pr > t	95% Confidence Limits	
Aspen ANPP (all sites)	Intercept	4536	564	8.04	<0.001	3452	5620
	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
Aspen ANPP (northern sites)	Intercept	8115	787	10.32	<0.001	6606	9623
	NH ₄ ⁺	2758	802	3.44	<0.001	1221	4996
	Srad	-2564	803	-3.19	<0.001	4104	1025
	Slope	-1875	808	-2.32	0.025	-3425	-325
Aspen ANPP (southern sites)	Intercept	3522	397	8.88	<0.001	2753	4291
	Herbbio	1442	401	3.60	<0.001	665	2220
	Gsws	-956	401	-2.39	0.021	-1734	-179

The selected model of aspen ANPP for my northern sites explained 45% of the variation in ANPP ($p < 0.001$) using ammonium concentration of the soil, annual solar radiation flux, and slope (Table 4). The strongest predictor of aspen ANPP in the northern sites was ammonium concentration in the soil which was positively correlated with ANPP (Table 4). At low values of soil ammonium, aspen ANPP in the northern region was variable but ANPP sharply increased at 60 mg/kg of ammonium in the soil (Fig. 11). Inversely correlated with ANPP, annual solar radiation flux was the next strongest predictor of aspen ANPP in the north and slope was also negatively correlated with ANPP (Table 4). The lower limit of aspen's distribution relative to annual solar

radiation flux in the northern GYE was associated with the highest levels of aspen ANPP (Fig. 11). However, ANPP was variable between 296 and 320 W/m² radiation but lower at values greater than 320 W/m² (Fig. 11). In the univariate setting, aspen ANPP in the northern GYE closely tracked aspen distribution relative to slope angle, with the highest ANPP at low to intermediate slope angles (Fig. 11). The sign of the relationship between each of the selected variables and ANPP was the same for both the northern sites alone and for all the sites together (Tables 3, 5).

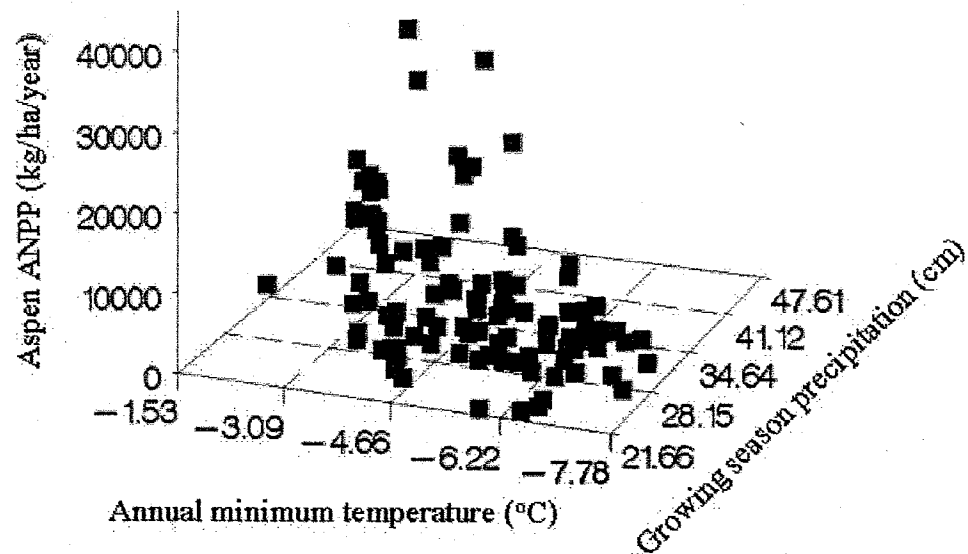


Figure 9. The interaction between annual minimum temperature and growing season precipitation was the strongest predictor of aspen ANPP across all sites. The highest aspen ANPP was found at warmer temperatures and intermediate values of growing season precipitation.

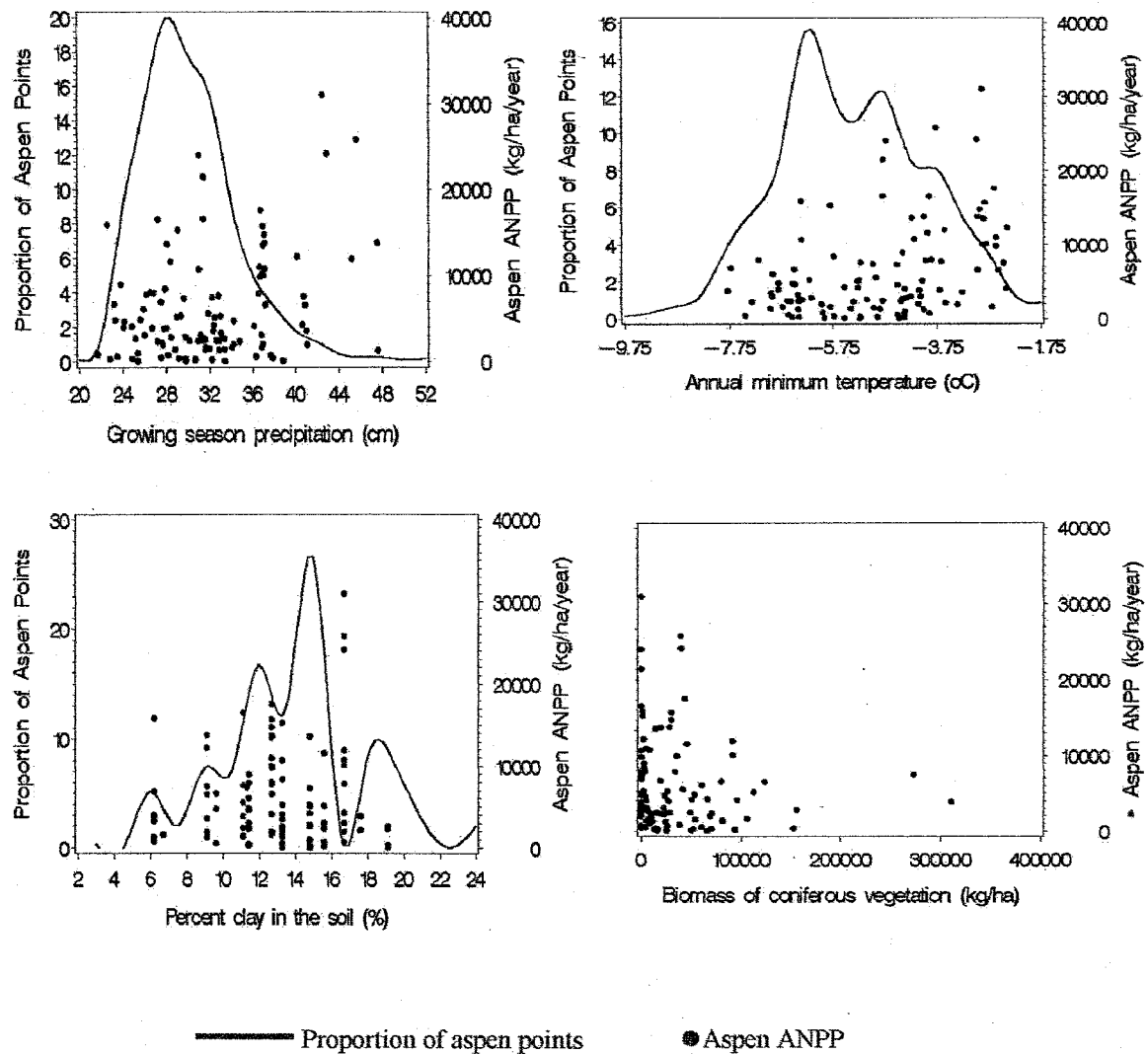


Figure 10. Univariate relationships of the variables used in the best regression model of aspen ANPP and biophysical setting. The distribution of aspen relative to the selected variables is shown by the solid line and the right vertical axis. The dots show aspen ANPP (left vertical axis) relative to the selected variables and the dashed line represents the univariate regression for aspen ANPP.

Table 5. AIC_c values were used to select the best model of aspen ANPP in northern GYE sites from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Moisture	Vpd	+	1	1045.39	0.00	0.27	0.19*
	gVpd	+	1	1045.64	0.24	0.24	0.18*
	Vpd Vpd ²	+, --	2	1045.65	0.25	0.24	0.22*
	gVpd gVpd ²	+, --	2	1046.32	0.92	0.17	0.21*
Temperature	gTmax	+	1	1048.41	0.00	0.11	0.13*
	gTday	+	1	1048.77	0.37	0.09	0.13*
	gDday	+	1	1048.80	0.39	0.09	0.13*
	Tmax	+	1	1048.81	0.40	0.09	0.13*
	gTsoil	+	1	1049.05	0.64	0.08	0.12*
	Dday	+	1	1049.12	0.71	0.08	0.12*
	Tday	+	1	1049.16	0.75	0.07	0.11*
	gTave	+	1	1049.18	0.78	0.07	0.12*
	gTnight	+	1	1049.50	1.10	0.06	0.11*
	Tave	+	1	1049.51	1.10	0.06	0.11*
	Tsoil	+	1	1049.51	1.11	0.06	0.11*
	Tnight	+	1	1049.72	1.32	0.06	0.11*
	Tmin	+	1	1050.38	1.97	0.04	0.09*
Soils	NH ₄ ⁺	+	1	1043.71	0.00	0.83	0.22*
Radiation	Srad	--	1	1044.94	0.00	0.27	0.20*
	Par	--	1	1044.94	0.00	0.27	0.20*
	Srad_t	--	1	1045.44	0.50	0.21	0.19*
Topography	Slope	--	1	1047.61	0.00	0.58	0.15*
	Elev	--	1	1048.37	0.76	0.40	0.14*
Biotic	Conifbio	--	1	1052.72	0.00	0.52	0.05
	Herbbio	--	1	1053.96	1.24	0.28	0.03
	Shrbio	+	1	1054.66	1.94	0.20	0.01
Overall Model	NH ₄ ⁺ Srad Slope		3	1031.69	0.00	0.22	0.45*
	Vpd NH ₄ ⁺ Srad Slope		4	1031.76	0.07	0.21	0.47*
	Vpd NH ₄ ⁺ Srad		3	1033.20	1.51	0.10	0.43*
	gTmax NH ₄ ⁺ Srad Slope		4	1033.48	1.79	0.09	0.45*

*indicates the model is significant at $p < 0.05$.

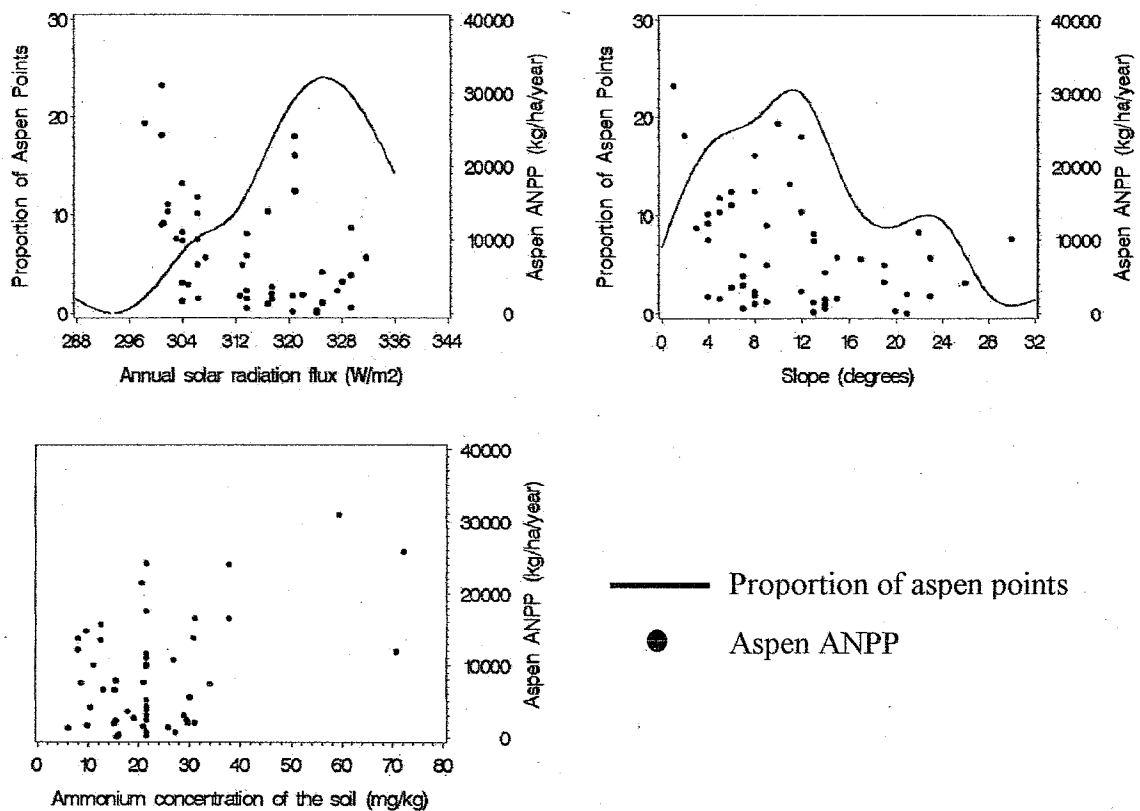


Figure 11. Univariate relationships of the variables used in the best regression model for aspen ANPP of northern sites and biophysical setting. The distribution of aspen relative to the selected variables is shown by the solid line and the right vertical axis. The dots show aspen ANPP (left vertical axis) relative to the selected variables and the dashed line represents the univariate regression for aspen ANPP.

The variables selected for building models in the southern GYE sites were growing season actual evapotranspiration, annual maximum temperature, growing season water stress, annual shortwave radiation, aspect, and the biomass of herbaceous vegetation (Table 6). The category with the strongest explanatory power for aspen ANPP was the biotic category with strong support for herbaceous biomass compared to

other biotic variable (Table 6). Herbaceous biomass was positively correlated with ANPP of southern aspen sites (Table 6). Soils variables and moisture variables were the next strongest predictors of ANPP, but variables within these categories were comparable in explanatory power, as evidenced by their AIC_c weights (Table 6). Radiation and temperature variables had low explanatory power and within these categories no single variable was strongly supported over the other variables (Table 6). Similar to the results for the sites as a whole and the northern sites, aspen ANPP was positively correlated with all the temperature variables and negatively correlated with radiation (Table 6).

Table 6. AIC_c values were used to select the best model of aspen ANPP in southern GYE sites from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Moisture	gAET	--	1	1070.57	0.00	0.12	0.10*
	AET	--	1	1071.06	0.49	0.10	0.09
	gPpt	--	1	1071.23	0.66	0.09	0.08
	gSnowfall	--	1	1071.49	0.92	0.08	0.07
	Snowfall	--	1	1071.70	1.13	0.07	0.07
	Vpd	+	1	1071.93	1.35	0.06	0.06
	gVpd	+	1	1072.00	1.43	0.06	0.06
	gRh	--	1	1072.12	1.55	0.06	0.06
	Ppt	--	1	1072.31	1.74	0.05	0.07
	gPET	+	1	1072.53	1.96	0.05	0.05
Temperature	Tmax	+	1	1071.92	0.00	0.09	0.06
	gTmax	+	1	1072.06	0.14	0.09	0.06
	gDday	+	1	1072.24	0.32	0.08	0.05
	gTday	+	1	1072.24	0.33	0.08	0.05
	Tday	+	1	1072.25	0.33	0.08	0.05
	Dday	+	1	1072.26	0.34	0.08	0.05
	gTsoil	+	1	1072.42	0.51	0.07	0.05
	gTave	+	1	1072.44	0.52	0.07	0.05
	Tave	+	1	1072.55	0.64	0.07	0.05

Table 6 -- continued

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
	gTnight	+	1	1072.60	0.68	0.07	0.05
	Tsoil	+	1	1072.63	0.71	0.07	0.05
	Tnight	+	1	1072.73	0.81	0.06	0.05
	gTmin	+	1	1073.03	1.11	0.05	0.04
	Tmin	+	1	1073.15	1.23	0.05	0.04
Soils	Gsws	--	1	1069.67	0.00	0.12	0.10*
	gGsws	--	1	1069.67	0.00	0.12	0.10*
	gPsi	--	1	1069.99	0.32	0.10	0.10
	gTrans	--	1	1070.25	0.58	0.09	0.10
	Psi	--	1	1070.32	0.65	0.08	0.10
	Trans	--	1	1070.58	0.91	0.07	0.10
	gSwf	--	1	1070.96	1.29	0.06	0.09
	gVmc	--	1	1071.23	1.56	0.05	0.08
	Gsws Gsws2	--, --	2	1071.58	1.91	0.04	0.11
	gGsws gGsws2	--, --	2	1071.58	1.91	0.04	0.11
	NO ₃ ⁻	--	1	1071.65	1.98	0.04	0.08
Radiation	Srad_fg	--	1	1073.42	0.00	0.13	0.04
	Srad	--	1	1073.45	0.02	0.13	0.04
	Par	--	1	1073.45	0.02	0.13	0.04
	SradtW	--	1	1073.51	0.09	0.13	0.04
	gSrad_fg	--	1	1073.63	0.21	0.12	0.04
	gSradtW	+	1	1073.66	0.24	0.12	0.04
	gSrad	--	1	1073.67	0.25	0.12	0.04
	gPar	--	1	1073.67	0.25	0.12	0.04
Topography	Aspct	+	1	1070.81	0.00	0.60	0.04
	Elev	--	1	1072.50	1.69	0.26	0.05
Biotic	Herbbio	+	1	1063.14	0.00	0.98	0.23*
Overall Model	Gsws Herbbio		2	1059.58	0.00	0.20	0.30*
	gAET Tmax Tmax*gAET Herbbio		4	1060.05	0.47	0.15	0.35
	gAET Herbbio		2	1061.16	1.59	0.09	0.29*
	Tmax Gsws Herbbio		3	1061.21	1.63	0.09	0.31
	Gsws Srad_fg Herbbio		3	1061.53	1.96	0.07	0.31

*indicates the model is significant at $p < 0.05$.

The selected model for aspen ANPP for my southern sites explained 30% of the variation in ANPP ($p < 0.001$) using just herbaceous biomass and growing season water stress (Table 4). Herbaceous biomass was the stronger predictor of ANPP and was positively correlated with ANPP (Table 4). The highest aspen ANPP was associated with between 400 and 800 kg/ha of herbaceous biomass and ANPP was more variable at lower levels of herbaceous biomass (Fig. 12). Growing season water stress was inversely related to aspen ANPP (Table 4) with the highest ANPP between -260 MPa and -100 MPa where aspen presence is low (Fig. 12).

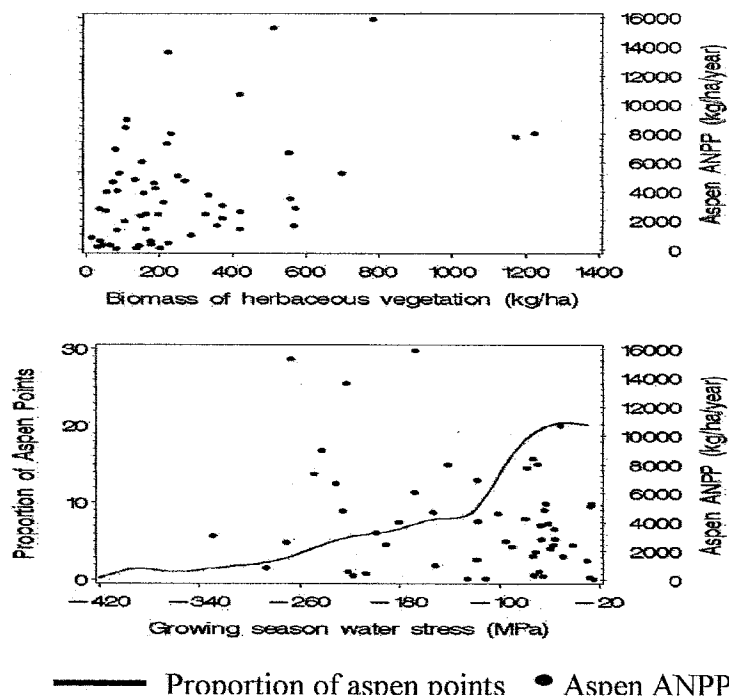


Figure 12. Univariate relationships of the variables used in the best regression model for of aspen ANPP of southern sites and biophysical setting. The distribution of aspen relative to the selected variables is shown by the solid line and the right vertical axis. The dots show aspen ANPP (left vertical axis) relative to the selected variables and the dashed line represents the univariate regression for aspen ANPP.

Landscape Change

I interpreted 242 landcover change plots to examine changes in the aerial cover of aspen. Fifty-nine percent of the aspen stands ($N = 143$) did not change in aerial cover between 1956 and 2001, 34% lost aspen cover ($N = 83$), and 6% gained aspen cover ($N = 16$) (see Methods for definitions of no change, loss and gain classes of aspen cover). Historic change in aspen cover ranged from a decrease of 80% between the early and late time period to a gain of 70% aspen cover in the same time period. The distribution of change in aspen cover was skewed towards a decrease in aspen cover (Fig. 13) with a median of a 10% decline. Most plots showed no change in conifer cover (83%), few lost conifer cover (3%), and some gained conifer cover (14%).

I used one-way analysis of variance (ANOVA) to examine differences between stands exhibiting loss, no change, or gain in aspen cover relative to the biophysical explanatory variables. Biophysical variables which exhibited a significant difference $\alpha = 0.05$ between aspen change classes were annual growing degree-days ($p = 0.01$), annual shortwave radiation ($p < 0.001$), growing season shortwave radiation ($p < 0.001$), annual potential evapotranspiration ($p = 0.001$), growing season potential evapotranspiration ($p < 0.001$), annual precipitation ($p < 0.001$), growing season precipitation ($p = 0.001$), annual snowfall ($p < 0.001$), growing season actual evapotranspiration ($p = 0.03$), and annual soil water potential ($p = 0.04$). Most of these variable showed a significant difference between gain and no change classes and/or between gain and loss class using Tukey-Kramer confidence intervals with $\alpha = 0.05$ (Table 7). Only annual precipitation, growing season actual evapotranspiration, and

annual snowfall showed a significant difference between no change and loss classes (Table 7).

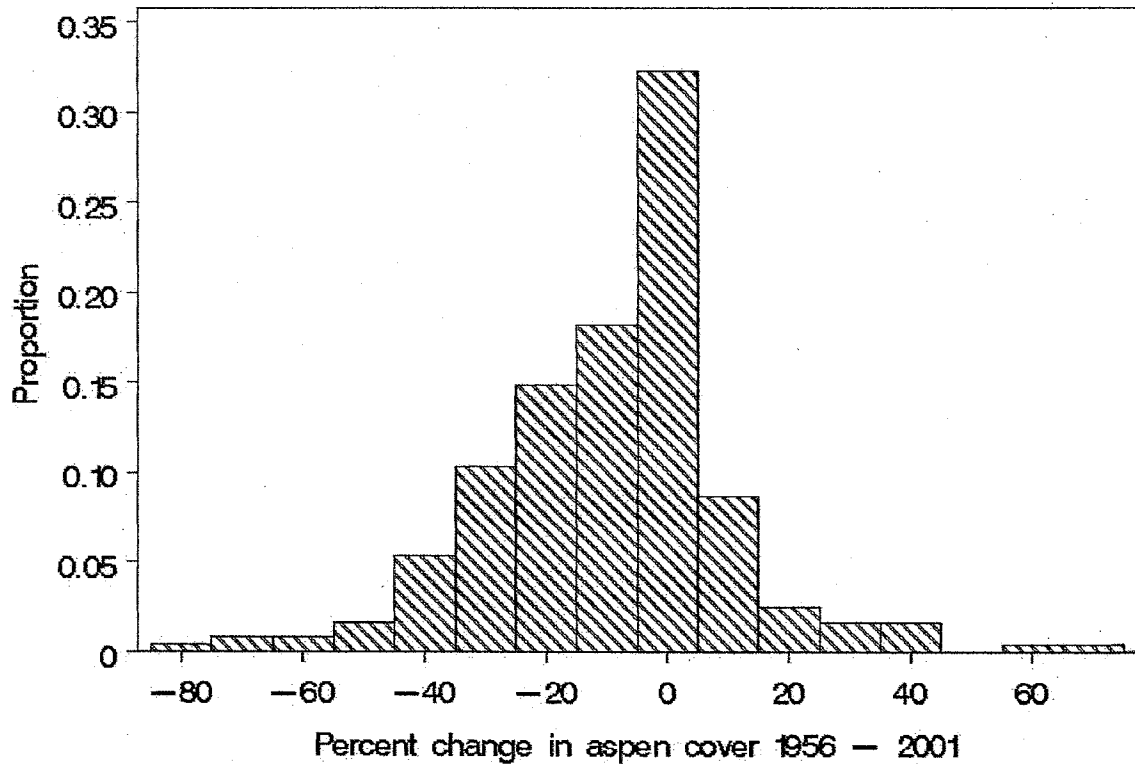


Figure 13. Histogram of change in aspen cover between 1956 and 2001. Tick marks on the x-axis refer to the mid-point of the histogram bin. Change in aspen cover is negatively skewed, showing an overall decline in aspen cover.

Places which gained in aspen cover had higher growing season precipitation and soil water potential than those that lost or did not change in aspen cover (Table 7). In addition places that gained aspen cover had lower values for annual and growing season PET, several measures of radiation, annual snowfall, and annual and growing season soil

water lost to runoff than areas that lost or did not change in aspen cover (Table 7).

Places that gained aspen cover also had lower values of annual precipitation and growing season soil water transpired by the canopy than places that lost aspen cover (Table 7).

Significant differences between areas which lost and those that did not change in aspen cover were related to annual precipitation, growing season AET, annual snowfall, growing season soil water lost to runoff, and growing season soil water transpired by the canopy; for all of these variables, areas that lost aspen cover had higher values of the variable than those areas that did not change in aspen cover (Table 7).

Table 7. Tukey-Kramer means comparison confidence intervals are shown for those biophysical variables which ANOVA showed to differ significantly between classes of aspen change, see Table 2 for abbreviations. The class which had higher values for the biophysical variable is listed for each class comparison, blanks indicate a nonsignificant confidence interval.

Variable	F	P > F	Significant Confidence Intervals (alpha = 0.05)		
			no change - gain	loss - gain	no change - loss
Ppt	9.01	< 0.001		loss	loss
gPpt	6.72	0.001	gain	gain	
PET	6.43	0.002	no change	no change	
gPET	7.39	< 0.001	no change	loss	
Dday	4.50	0.010		gain	
PAR	9.26	< 0.001	no change	loss	
gPAR	10.84	< 0.001	no change	loss	
Srad_fg	9.16	< 0.001	no change	loss	
gSrad_fg	9.94	< 0.001	no change	loss	
Srad	9.64	< 0.001	no change	loss	
gSrad	11.32	< 0.001	no change	loss	
gAET	3.56	0.030			loss
Psi	3.19	0.040		gain	
Snowfall	11.93	< 0.001	no change	loss	loss
Outflow	6.74	< 0.001	no change	loss	
gOutflow	7.19	< 0.001	no change	loss	loss
gTrans	4.84	0.008		loss	loss

I built multiple regression models relating percent change in aspen cover to the biophysical explanatory variables in the same manner as for aspen ANPP. To represent competition in this case, however, I used the percent change in conifer cover. To determine if the relationships differed between plots that gained or lost in conifer cover, I first built a regression model for the full dataset and additionally built regression models for the loss and no change plots together and separately for the plots that gained aspen cover.

For the full dataset, none of the variables selected in each of the categories exhibited a unimodal relationship with aspen change, thus quadratic terms were not used for these variables. The selected variables were annual snowfall, annual daytime temperature, growing season soil runoff, growing season total daily solar radiation, and elevation (Table 8). Annual daytime temperature and elevation had a Pearson correlation greater than 0.80 and were not included together in a model. The moisture-temperature interaction term annual snowfall*annual daytime temperature was added to the appropriate models; from the competing models, the final overall model was selected using AIC_c (Table 8). The selected model for the full dataset explained 18% of the variation in aspen change ($p < 0.0001$) using annual snowfall and percent change in conifer cover (Table 9). Snowfall was negatively correlated with change in aspen cover (Table 9). Increase in conifer cover was also negatively correlated with change in aspen cover (Table 9).

Table 8. AIC_c values were used to select the best model of percent aspen change between 1956 and 2001 (for all plots sampled) from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC Weights	R ²
Moisture	Snowfall	--	1	1437.14	0.00	0.96	0.09*
Temperature	Tday	+	1	1444.91	0.00	0.15	0.06*
	Tave	+	1	1444.97	0.05	0.15	0.06*
	Tnight	+	1	1445.10	0.19	0.14	0.06*
	Tsoil	+	1	1445.17	0.26	0.13	0.05*
	Tmax	+	1	1445.22	0.31	0.13	0.05*
	Tmin	+	1	1445.65	0.74	0.11	0.05*
	Dday	+	1	1446.46	1.55	0.07	0.05*
Soils	gOutflow	--	1	1441.42	0.00	0.58	0.07*
	Outflow	--	1	1442.16	0.74	0.40	0.07*
Radiation	gSrad_t	--	1	1445.51	0.00	0.26	0.05*
	gPar	--	1	1446.24	0.74	0.18	0.05*
	gSrad	--	1	1446.25	0.74	0.18	0.05*
	gSrad_fg	--	1	1447.46	1.95	0.10	0.05*
Topography	Elev	--	1	1451.23	0.00	0.89	0.03*
	Slope	--	1	1456.81	5.59	0.05	0.01
Overall Model	Snowfall Conchg		2	1414.06	0.00	0.14	0.18*
	Snowfall gOutflow Conchg		3	1415.15	1.09	0.08	0.18
	Snowfall gSrad_t Conchg		3	1415.34	1.27	0.07	0.18
	gOutflow gSrad_t Conchg		3	1415.40	1.34	0.07	0.18
	Snowfall Elev Conchg		3	1415.87	1.81	0.06	0.18
	Snowfall Tday Conchg		3	1416.01	1.95	0.05	0.18
	Snowfall gSrad_t Elev Conchg		4	1416.06	2.00	0.05	0.18

*indicates model the model is significant at $p < 0.05$.

Table 9. Results of regressions relating percent change in aspen cover to biophysical variables. Models shown are the best overall model as selected using AICc. 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.

Response	Variable	Parameter estimate	Standard error	t Value	Pr > t	95% Confidence Limits	
% Aspen change (full dataset)	Intercept	-9.22	1.18	-7.80	<0.001	-11.54	-6.89
	Snowfall	-4.93	1.19	-4.11	<0.001	-7.29	-2.57
	Conchg	-6.13	1.19	-5.11	<0.001	-8.49	-3.77
% Aspen change (loss/no change plots)	Intercept	-12.21	1.04	-11.63	<0.001	-14.28	-10.14
	Ppt	-3.37	1.05	-3.19	0.002	-5.45	-1.29
	Conchg	-4.82	1.06	-4.56	<0.001	-6.89	-2.74
% Aspen change (gain plots)	Intercept	44.08	4.65	9.47	<0.001	34.02	54.13
	$^{\circ}\text{gSrad}$	0.89	0.34	2.65	0.020	0.16	1.62
	$^{\circ}\text{gSrad}^2$	-0.03	0.01	-3.11	0.008	-0.05	-0.01
% Aspen change (loss plots/conifer present)	Intercept	-29.68	1.53	-19.46	<0.001	-32.73	-26.63
	Conchg	-2.70	1.43	-1.75	0.085	-5.76	0.38
% Aspen change (loss plots/conifer absent)	Intercept	-31.30	3.23	-9.69	<0.001	-38.09	-24.51
	Soildepth	0.17	0.08	2.13	0.047	0.00	0.33

$^{\circ}$ indicates the variable is centered around its mean, rather than around mean = 0, standard deviation = 1, see Methods section.

Using just areas that lost or did not change in aspen cover, again none of the variables selected in each of the categories exhibited a unimodal relationship with aspen change, and quadratic terms were not used for these variables. The selected variables were annual precipitation, annual maximum temperature, growing season soil runoff, growing season total daily solar radiation, and elevation (Table 10). Annual maximum temperature and elevation had a Pearson correlation greater than 0.80 and were not

included together in a model. The moisture-temperature interaction term annual precipitation*annual maximum temperature was added to the appropriate models. The selected model (Table 10) for loss and no change areas explained 13% of the variation in aspen change ($p < 0.0001$) using annual precipitation and percent change in conifer cover (Table 9). Aspen change was negatively correlated with both annual precipitation and change in conifer cover (Table 9).

Table 10. AIC_c values were used to select the best model of percent aspen change between 1956 and 2001 (for only plots that lost or did not change in aspen cover) from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC Weights	R ²
Moisture	Ppt	--	1	1270.19	0.00	0.70	0.05*
Temperature	Tmax	+	1	1274.33	0.00	0.14	0.03*
	Tday	+	1	1274.65	0.32	0.12	0.03*
	Tave	+	1	1275.01	0.68	0.10	0.03*
	Tsoil	+	1	1275.14	0.81	0.10	0.03*
	Dday	+	1	1275.15	0.82	0.09	0.03*
	Tnight	+	1	1275.25	0.92	0.09	0.03*
	Tmin	+	1	1275.92	1.60	0.06	0.03*
Soils	gOutflow	--	1	1272.23	0.00	0.43	0.04*
	Outflow	--	1	1272.67	0.44	0.34	0.04*
Radiation	gSrad_t	--	1	1279.39	0.00	0.16	0.01
	gPar	--	1	1279.64	0.24	0.14	0.01
	gSrad	--	1	1279.64	0.25	0.14	0.01
	gSrad_fg	--	1	1279.99	0.59	0.12	0.01
	Srad_t	--	1	1280.10	0.70	0.11	0.01
	Par	--	1	1280.24	0.85	0.11	0.01
	Srad	--	1	1280.24	0.85	0.11	0.01
	Srad_fg	--	1	1280.35	0.96	0.10	0.01
Topography	Elev	--	1	1451.23	0.00	0.89	0.03*

Table 10 -- continued

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC Weights	R ²
Overall Model	Ppt Conchg		2	1252.05	0.00	0.15	0.13*
	Ppt Tmax Conchg		3	1252.53	0.48	0.12	0.14
	Ppt gOutflow Conchg		3	1253.27	1.22	0.08	0.13
	Ppt Elev Conchg		3	1253.60	1.55	0.07	0.13
	Ppt gSrad_t Conchg		3	1253.77	1.72	0.07	0.13
	gOutflow Conchg		2	1254.04	1.99	0.06	0.12*

* indicates the model is significant at $p < 0.05$.

When considering only areas that gained in aspen cover, the variable selected in the radiation category exhibited a unimodal relationship with aspen change and was represented with a quadratic term (Table 11). This variable was growing season daily solar radiation flux and it was centered to reduce collinearity (see Methods). The other variables selected were not quadratic and they were growing season vapor pressure deficit, growing season maximum temperature, percent silt in the soil, and elevation (Table 11). Growing season daily solar radiation flux had a Pearson correlation greater than 0.80 with both growing season maximum temperature and with elevation and these variables were not included in the same model. Also, growing season maximum temperature and elevation had a Pearson correlation greater than 0.80 and were not included together in a model. The moisture-temperature interaction term growing season vapor pressure deficit*growing season minimum temperature was added to the appropriate models. The selected model for areas that gained aspen (Table 11) included only the quadratic form of growing season radiation flux and explained 43% of the variation in aspen change ($p = 0.027$) (Table 9).

Table 11. AIC_c values were used to select the best model of percent aspen change between 1956 and 2001 (for only plots that gained in aspen cover) from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Moisture	gVpd	+	1	87.67	0.00	0.24	0.23
	Vpd	+	1	88.40	0.72	0.17	0.19
	gSnowfall	--	1	89.52	1.85	0.10	0.13
	Ppt	+	1	89.66	1.98	0.09	0.12
Temperature	gTmax	+	1	90.15	0.00	0.09	0.10
	gTday	+	1	90.33	0.18	0.08	0.09
	gDday	+	1	90.38	0.24	0.08	0.08
	gTsoil	+	1	90.42	0.27	0.08	0.08
	gTave	+	1	90.47	0.32	0.08	0.08
	gTnight	+	1	90.55	0.40	0.08	0.07
	gTmin	+	1	90.76	0.62	0.07	0.06
	Dday	+	1	90.81	0.67	0.07	0.06
	Tmax	+	1	90.82	0.68	0.07	0.06
	Tday	+	1	90.88	0.74	0.06	0.05
	Tave	+	1	90.92	0.78	0.06	0.05
	Tsoil	+	1	90.93	0.78	0.06	0.05
	Tnight	+	1	90.95	0.81	0.06	0.05
Soils	Silt	+	1	87.36	0.00	0.19	0.24*
	Sand	--	1	87.99	0.63	0.14	0.21
	gVmc	+	1	88.21	0.85	0.12	0.20
	gSwf	+	1	89.01	1.65	0.08	0.16
	Vmc	+	1	89.04	1.68	0.08	0.16
Radiation	gSrad gSrad ²	--, --	2	85.51	0.00	0.17	0.43*
	gpar gpar ²	--, --	2	85.51	0.01	0.17	0.43*
	gSrad_t gSrad_t ²	--, --	2	85.53	0.02	0.16	0.43*
	gSrad_fg gSrad_fg ²	--, --	2	85.84	0.34	0.14	0.41*
	Srad_fg srad_fg ²	--, --	2	86.22	0.72	0.12	0.40*
	Srad_t Srad_t ²	--, --	2	87.21	1.70	0.07	0.36*
Topography	Elev	--	1	90.73	0.00	0.34	0.06
	Slope	--	1	91.14	0.41	0.27	0.04
	Taspect	+	1	91.22	0.50	0.26	0.03

Table 11 -- continued.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Topography	Elev Elev ²	--, --	2	92.66	1.93	0.13	0.10
Overall Model	gSrad gSrad ² *		2	85.51	0.00	0.18	0.43*
	Silt gSrad gSrad ²		3	86.55	1.04	0.11	0.49
	Silt		1	87.36	1.85	0.07	0.24*
	gVpd Conchg		2	87.46	1.95	0.07	0.35

* indicates the model is significant at $p < 0.05$.

To understand the relative role of competition with conifer in aspen decline, I also built separate regression models for plots which lost aspen cover in the presence of conifer and those which lost aspen cover but where conifer were absent. For loss plot without conifer present, soils variables were the strongest predictors of change in aspen cover (Table 12). Among the soil variables, the depth of the soil was the most strongly supported variable, deeper soils were associated with a lower percentage of aspen loss (Table 12). The topographic and moisture categories were the next strongest predictors of aspen change and the selected variables were slope and annual relative humidity (Table 12). Increasing slope angles and relative humidity were both associated with increasing loss of aspen (Table 12). Neither radiation nor temperature variables had a strong relationship to aspen change (Table 12). The selected model of aspen change for loss plots without conifer present explained 20% of the variation in aspen change ($p = 0.047$) using just soil depth (Table 9).

Biophysical variables had very low explanatory power for aspen change in loss plots with conifer present (Table 13). None of the categories of predictor variables explained more than 2% of the change in aspen cover in these plots (Table 13). The

selected model for these plots explained only 5% of the variation in aspen change ($p = 0.085$), using the percent change in conifer cover (Table 9).

Table 12. AIC_c values were used to select the best model of percent aspen change for plots which lost aspen cover in the absence of conifer between 1956 and 2001. Models were selected from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	AIC_c	Delta AIC_c	AIC_c Weights	R^2
Moisture	Rh	--	111.75	0.00	0.11	0.11
	gRh	--	112.04	0.29	0.10	0.10
	gPpt gPpt ²	+, --	112.11	0.36	0.09	0.20
	gPpt	--	112.13	0.38	0.09	0.10
	AET	+	112.63	0.88	0.07	0.08
	gAET	+	112.85	1.10	0.07	0.06
	gSnowfall	--	113.14	1.39	0.06	0.05
	PET	+	113.40	1.65	0.05	0.04
	gPET	+	113.51	1.76	0.05	0.03
	gVpd	+	113.52	1.77	0.05	0.03
	Vpd	+	113.52	1.77	0.05	0.03
Temperature	gTmax	+	113.82	0.00	0.08	0.02
	Tmax	+	113.87	0.06	0.08	0.02
	gTmin	--	114.04	0.23	0.07	0.01
	Tmin	--	114.05	0.23	0.07	0.01
	gDday	+	114.07	0.25	0.07	0.01
	gTday	+	114.07	0.25	0.07	0.01
	Dday	+	114.07	0.26	0.07	0.01
	Tday	+	114.10	0.29	0.07	0.00
	gTsoil	+	114.17	0.35	0.07	0.00
	gTave	+	114.17	0.36	0.07	0.00
	Tnight	--	114.18	0.36	0.07	0.00
	Tave	+	114.18	0.36	0.07	0.00
	gTnight	--	114.18	0.37	0.07	0.00
	Tsoil	+	114.18	0.37	0.07	0.00
Soils	Soildepth	+	109.69	0.00	0.18	0.20*
	gPsi	+	110.65	0.96	0.11	0.16
	Gsws	+	110.85	1.16	0.10	0.15
	gGsws	+	110.85	1.16	0.10	0.15
	Psi	+	110.90	1.22	0.10	0.15

Table 12 --continued.

Category	Model	Slope	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Soils	Soildepth Soildepth ²	+, --	111.48	1.79	0.07	0.23
Radiation	gSrad_fg	+	113.95	0.00	0.13	0.01
	gPar	+	113.97	0.03	0.13	0.01
	gSrad	+	113.97	0.03	0.13	0.01
	Srad_fg	+	113.99	0.05	0.13	0.01
	gSrad_t	+	114.01	0.06	0.13	0.01
	Srad_t	+	114.08	0.13	0.12	0.01
	Srad	+	114.09	0.14	0.12	0.00
	Par	+	114.09	0.14	0.12	0.00
Topography	Slope	--	110.97	0.00	0.63	0.15
	Taspect	--	112.89	1.93	0.24	0.06
Overall Model	Soildepth		109.69	0.00	0.14	0.20*
	Rh Slope		110.27	0.58	0.10	0.27
	Soildepth Slope		110.66	0.97	0.08	0.26
	Slope		110.97	1.28	0.07	0.15

*indicates the model is significant at $p < 0.05$.

Table 13. AIC_c values were used to select the best model of percent aspen change for plots which lost aspen cover in the presence of conifer between 1956 and 2001. Models were selected from each predictor category and from the overall models combining these variables (see Table 2 for abbreviations). The selected model is listed first in each category and models within 2 AIC_c units of the selected model are shown.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Moisture	PET	+	1	320.62	0.00	0.10	0.01
	gPET	+	1	320.73	0.12	0.10	0.01
	Vpd	+	1	320.85	0.24	0.09	0.01
	gVpd		1	320.91	0.30	0.09	0.01
	Ppt	--	1	320.92	0.31	0.09	0.01
	Snowfall	--	1	321.10	0.49	0.08	0.00
	gPpt	--	1	321.19	0.57	0.08	0.00
	gSnowfall	--	1	321.27	0.65	0.08	0.00
	AET	+	1	321.30	0.69	0.07	0.00
	gRh	+	1	321.34	0.72	0.07	0.00
	gAET	+	1	321.34	0.73	0.07	0.00

Table 13 -- continued.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Moisture	Rh	+	1	321.34	0.73	0.07	0.00
Temperature	gTsoil	+	1	320.94	0.00	0.05	0.01
Temperature	Tmax	+	1	320.95	0.01	0.05	0.01
	Tsoil	+	1	320.97	0.03	0.05	0.01
	Tday	+	1	320.97	0.03	0.05	0.01
	gTday	+	1	320.99	0.04	0.05	0.01
	gTave	+	1	320.99	0.05	0.05	0.01
	gDday	+	1	320.99	0.05	0.05	0.01
	gTnight	+	1	320.99	0.05	0.05	0.01
	Tave	+	1	320.99	0.05	0.05	0.01
	gTmax	+	1	321.00	0.06	0.05	0.01
	Tnight	+	1	321.01	0.07	0.05	0.01
	Dday	+	1	321.02	0.08	0.05	0.01
	gTmin	+	1	321.03	0.09	0.05	0.01
	Tmin	+	1	321.07	0.12	0.05	0.00
	Tmax Tmax ²	+, --	2	322.48	1.54	0.02	0.02
	Tday Tday ²	+, --	2	322.68	1.74	0.02	0.01
	Dday Dday ²	+, --	2	322.81	1.87	0.02	0.01
	Tsoil Tsoil ²	+, --	2	322.81	1.87	0.02	0.01
	Tave Tave ²	+, --	2	322.87	1.93	0.02	0.01
Soils	Sand	--	1	320.35	0.00	0.08	0.02
	Silt	+	1	320.40	0.05	0.07	0.02
	Outflow	--	1	320.44	0.09	0.07	0.01
	gOutflow	--	1	320.44	0.10	0.07	0.01
	Clay	+	1	320.56	0.21	0.07	0.01
	gVmc	+	1	320.81	0.46	0.06	0.01
	Vmc	+	1	320.86	0.51	0.06	0.01
	Soildepth	+	1	320.93	0.58	0.06	0.01
	gSwf	+	1	320.96	0.61	0.06	0.01
	Swf	+	1	320.98	0.63	0.06	0.01
	gPsi	+	1	321.25	0.91	0.05	0.00
	Trans	+	1	321.30	0.95	0.05	0.00
	Psi	+	1	321.31	0.96	0.05	0.00
	Gsws	+	1	321.33	0.98	0.05	0.00
	gGsws	+	1	321.33	0.98	0.05	0.00
	gTrans	+	1	321.33	0.98	0.05	0.00
	Outflow Outflow ²	--, --	2	322.12	1.78	0.03	0.02
	gOutflow	--	2	322.24	1.89	0.03	0.02

Table 13 -- continued.

Category	Model	Slope	K	AIC _c	Delta AIC _c	AIC _c Weights	R ²
Radiation	gSrad_t	+	1	320.61	0.00	0.13	0.01
Radiation	gSrad_fg	+	1	320.64	0.03	0.13	0.01
	gSrad	+	1	320.65	0.04	0.13	0.01
	gPar	+	1	320.65	0.04	0.13	0.01
	Srad_fg	+	1	320.68	0.07	0.13	0.01
	Srad_t	+	1	320.72	0.11	0.12	0.01
	Srad	+	1	320.75	0.14	0.12	0.01
	Par	+	1	320.75	0.14	0.12	0.01
Topography	Slope	--	1	320.71	0.00	0.32	0.01
	Elev	--	1	321.30	0.59	0.24	0.00
	Aspct	--	1	321.32	0.61	0.24	0.00
	Slope Slope ²	--, --	2	322.70	1.99	0.12	0.01
Overall Model	Conchg	--	1	318.27	0.00	0.10	0.05*
	Sand Conchg		2	319.31	1.03	0.06	0.06
	gSrad_t Conchg		2	319.74	1.47	0.05	0.06
	Slope Conchg		2	319.75	1.47	0.05	0.06
	PET Conchg		2	319.81	1.54	0.04	0.06
	gTsoil Conchg		2	320.04	1.76	0.04	0.05

*indicates the model is significant at $p < 0.10$.

DISCUSSION

Aspen Distribution

Gradients in environmental variables are recognized to shape species' distributions (Austin 1987, Stephenson 1990, Franklin 1995, Stephenson 1998, Austin 2002, McKenzie et al. 2003). I hypothesized that biophysical variables would limit the distribution of aspen in the GYE. Aspen is rare in the GYE, representing only 1.4% of the study area (Fig. 2). The majority of aspen occurs in the southern GYE, with 90% of mapped aspen stands occurring south of Yellowstone National Park. My results indicate a strong relationship between biophysical gradients and aspen distribution, such that aspen is restricted to a narrow subset of the available biophysical settings in the GYE (Figs. 4, 6, 7).

The CART models I developed predict aspen occurrence in high-light, warmer, moister environments. Shortwave radiation during the growing season is generally higher in the southern GYE. The CART model for the entire GYE uses growing season shortwave radiation for the initial split (Fig. 4) which appears to effectively split the GYE into the northern and southern regions. The right side of the CART for the entire GYE is identical to the CART for the southern GYE (Figs. 4, 6). The left side of the CART for the entire GYE is similar to the CART for the northern GYE, with growing season solar radiation flux substituted for growing season shortwave radiation at the last split (Figs. 4, 7). Thus, my results indicate growing season shortwave radiation to be the primary abiotic explanation for the increased prevalence of aspen in the south (Fig. 4). The remaining variables used in the CART models characterize aspen's abiotic niche as

warmer (gT_{min} and T_{max}) and possibly wetter (Snowfall, which may replenish soil moisture) than areas where aspen are absent.

In the northern GYE, where values of growing season shortwave radiation are generally lower, aspen occurs in moister areas with warm temperatures and higher values of radiation. In the southern GYE, where radiation is generally higher, the primary biophysical variable accounting for aspen distribution is growing season potential evapotranspiration (PET). Maps of growing season PET for the data show that only a few points in valley bottoms had PET values greater than 119 cm. PET seems to have separated aspen from the non-forest boundary.

Austin (2002) defined three types of gradients used in modeling plant-environment relationships. Indirect gradients have no physiological effect on plant growth and their correlation with species distributions is attributed to location-specific correlation with such variables as temperature or precipitation. Resource gradients include variables, such as light or nutrients, which are consumed by plants. Direct gradients are those variables which exert a direct physiological influence on plant growth but which are not consumed by plants. Models based on direct and resource gradients are more widely applicable than more location-specific models based on indirect gradients (Franklin 1995, Austin 2002). The CART models I built are based on both resource and direct gradients. The temperature variables and snowfall represent direct gradients associated with aspen presence. Aspen are found in generally warmer and moister environments than areas from which aspen are absent. Potential evapotranspiration integrates radiation, temperature, and air humidity to represent the evaporative demand experienced by plants and represents a resource gradient relating to

water availability for plants. Radiation, the most important variable in my CART model, is a resource gradient which can be limiting to aspen growth.

Aspen is considered to be highly shade-intolerant relative to many North American tree species (Jones 1985, Mueggler 1985, Despain 1990, National Academies of Science 2002). Aspens' occurrence in areas with high radiation is probably related to its high light requirements which in turn influence aspen growth rates. Aspen growth and carbon assimilation have been shown to be positively correlated with high light levels (Jones 1985, McDonald et al. 1999, Hogg et al. 2000, Hogg et al. 2002). Aspens' low ratio of photosynthesis to respiration under low light intensity explains its shade-intolerance, resulting in lower carbon allocation for growth under low light conditions (Jones 1985). However, temperature interacts with light availability to influence aspen distribution and growth; at lower light levels in warmer environments aspen stem growth is reduced but a similar reduction in growth is less pronounced in cooler environments (Jones 1985). At high light availability, the ratio of aspen photosynthesis to respiration is not limiting and temperature has less influence; however, at low light levels the strongest reduction in aspen growth was with warmer temperature regimes (Jones 1985). My results indicate that aspen in the northern GYE occupy a lower light regime than southern aspen; in addition aspen in the northern GYE are restricted to warmer locations and may suffer lower growth rates due to the interaction of low light and warm temperatures.

My results indicate that aspen distribution in the GYE is correlated with high light availability and warmer temperature, possibly indicating that aspen distribution in the region is limited by energetic requirements of photosynthesis and carbon allocation. The higher radiation regime of the southern GYE may be more conducive to aspen

photosynthesis than the northern GYE with its lower radiation regime. Since with cooler temperatures the negative growth effects of low light availability are less pronounced, aspens' occurrence in high light availability--warm temperature locations in my models supports the idea that aspen distribution in the GYE may be limited by aspens' photosynthetic requirements. Because the southern GYE is generally higher in growing season shortwave radiation than the northern GYE, this would suggest that the prevalence of aspen in the southern GYE relative to the northern GYE is related to increased photosynthetic capacity in the southern portion of the ecosystem.

Aspen Performance

Within aspens' narrow distribution in the GYE, biophysical variables explained 37% of the variation in aspen ANPP across all field sites, 45% of the variation in ANPP in the northern GYE, and 30% of the variation in ANPP in the southern GYE, while controlling for aspen stem density. I expected productivity of aspen stands, as measured by aspen ANPP, to vary relative to biophysical gradients. Exploratory analyses of the geographic distribution of ANPP revealed some broad-scale variation, mainly between the highly productive Gallatin Front region and all other regions (Fig. 8). The Gallatin Front is a low-elevation area with a relatively mild climate at the lower forest boundary. I sampled four aspen stands in the area, all of which were densely stocked with small-diameter trees, as well as larger trees. Some of the high ANPP of this region is probably due to the high densities of young aspen, however, I controlled for the effects of aspen density in my regression analyses. My regression results showed the highest aspen ANPP at warm annual minimum temperatures and intermediate to high growing season

precipitation (Table 4, Fig. 9) and the Gallatin Front had the highest values of both annual minimum temperature and growing season precipitation for any of the regions (Fig. 8). The high ANPP of this region also appears to be linked to favorable growing conditions. The Boulder region which had significantly higher ANPP than the Jackson region also had some of the higher levels of annual minimum temperature and growing season precipitation (Fig. 8).

Within the regions, sites varied greatly in aspen ANPP and I was able to explain 37% of the variation across all sites using biophysical variables. Growing season precipitation, annual minimum temperature, and the interaction between the two were positively correlated with aspen ANPP (Table 4). For both temperature and precipitation, the highest ANPP occurred at the upper limit of aspens' distribution with respect to the variable, although ANPP was variable at lower values of these variables (Fig. 10). The percent of clay in the soil was also positively correlated with aspen ANPP (Table 4), although ANPP varied widely at different values of percent clay (Fig. 10). As I expected, competition with conifer appears to negatively influence aspen ANPP (Table 4).

Annual minimum temperature represents a direct gradient and the higher productivity of aspen at warmer temperatures is probably linked to earlier onset of growth in the spring. Spring temperature determine when aspen growth begins and thus the length of the growing season (Jones and DeByle 1985a). It appears that little to no growth of aspen occurs below 4°C (39°F), maximum growth rate occurs around 22°C (77°F), and the upper limit beyond which no growth occurs is 36°C (97°F) (Jones et al. 1985). Although I used annual minimum temperature in my regression model and its

range of values is below this critical limit, aspen ANPP was positively correlated with all temperature variables and growing season average temperature fell well within the range of aspen growth (mean = 9.80°C, minimum = 6.89°C, maximum = 12.18°C).

Aspen has high evapotranspirative demands (Jones and DeByle 1985a, Jones et al. 1985) and its growth in the GYE is probably limited by water availability. The higher ANPP of aspen in areas with greater growing season precipitation is likely a consequence of balancing evapotranspirative demands with the warmer temperatures at which aspen also grows best. Aspen growth in Alberta has been positively correlated with a climate moisture index incorporating precipitation and potential evapotranspiration as well as with growing degree-days (Hogg et al. 2002).

Since aspen distribution varies from north to south in the GYE, I also looked at aspen ANPP separately for the northern and southern regions of the GYE. When I built regression models of aspen ANPP in the northern GYE, I was able to explain 45% of the variation in ANPP. I found a strong positive relationship between aspen ANPP and ammonium concentration in the soil. In the Upper Midwest aspen growth has been correlated with available nitrogen and in many aspen stands in the western United States legumes are significant components of the understory, contributing to higher soil ammonium concentration (Jones and DeByle 1985c). In the northern sites, annual solar radiation flux was inversely related to aspen ANPP (Table 4) with the highest ANPP at the lower limit of aspen's distribution relative to solar radiation flux in the north (Fig. 11). Slope was also negatively related to ANPP (Table 4) although variable across intermediate slope angles (Fig. 11).

Why would high aspen ANPP be inversely related to radiation in the northern GYE? Several authors report opposite relationships and my distribution results indicate a positive correlation between radiation and aspen presence. Aspen growth rates have been shown to increase with increasing light availability, presumably due to increased photosynthetic efficiency at higher light levels (Jones 1985, McDonald et al. 1999, Hogg et al. 2000, Hogg et al. 2002).

One possible explanation for the disparity between these two results is that radiation is a limiting resource for which aspen and conifers compete. Areas conducive to high aspen growth rates may also be areas where conifers (e.g. Douglas fir) experience high growth rates and competition may have shifted aspens' distribution away from areas more favorable to its growth (Fig. 14). Competitive interactions between species with similar environmental niches may exclude one species from an area where climate-based models would predict it to be present (McKenzie et al. 2003). An optimal distribution for aspen growth (ANPP) may include lower values along these gradients but competition may have excluded aspen from these more favorable sites (Fig. 14).

When I built regression models for aspen ANPP in the southern GYE, I was able to explain 30% of the variation in aspen ANPP. High ANPP in the southern GYE was associated with high levels of herbaceous biomass and low growing season water stress. Aspen stands are often associated with higher levels of herbaceous cover than adjacent conifer forests (Jones and DeByle 1985c). Herbaceous cover can improve soil water holding capacity, nutrient levels, and soil permeability through decomposition (Jones and DeByle 1985c). The high transpiration demands (Jones and DeByle 1985a, Jones et al.

1985) of aspen account for the negative relationship between growing season water stress and aspen ANPP.

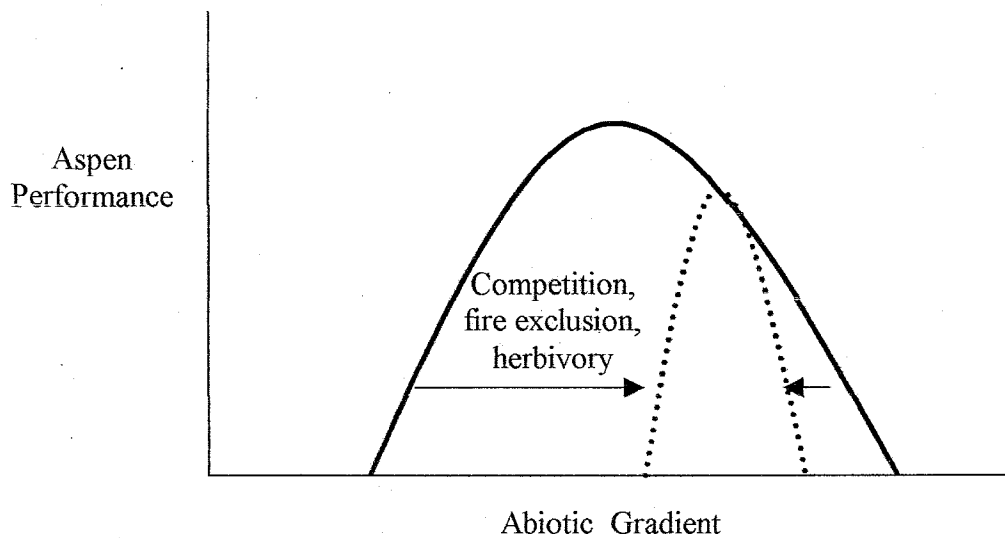


Figure 14. Aspen distribution in the GYE may not reflect the distribution which would be optimal for aspen performance. The disparity between my distribution results and result for aspen aboveground primary productivity (ANPP) may reflect the shifting and/or narrowing of aspen distribution by factors such as competition, fire exclusion, or herbivory such that aspen does occupy the portion of an abiotic gradient which would be optimal for growth. The solid line represents the hypothesized optimal distribution for growth of aspen along an abiotic gradient and the dashed line indicates the idea that the observed distribution and growth of aspen have been narrowed and shifted from the optima.

Forest productivity has generally been shown to vary with respect to elevation, precipitation, temperature, and soil moisture (Whittaker 1966, Whittaker and Niering 1975, Running and Coughlan 1988, Hansen et al. 2000). ANPP of various tree species has been shown to be positively correlated with moisture indices in the Great Smoky Mountains (Whittaker 1966) in North Carolina and negatively correlated with elevation in cooler regions, such as the Great Smoky Mountains and the GYE (Whittaker 1966,

Hansen et al. 2000). However, tree ANPP is positively correlated with elevation in desert regions such as the Santa Catalina Mountains in Arizona (Whittaker and Niering 1975). In the few studies of aspen growth rates, aspen has also responded to environmental gradients (Mitton and Grant 1980, Jelinski 1993, McDonald et al. 1999, Hogg et al. 2000, Hogg et al. 2002, Gustafson et al. 2003). Mean annual increment growth in aspen decreases with increasing elevation (Mitton and Grant 1980, Jelinski 1993). In the Upper Great Lakes region, growing season precipitation, June moisture deficit (precipitation - PET), growing degree-days, and soil drainage were positively correlated with aspen volume increment growth (Gustafson et al. 2003). Relative growth rate, carbon assimilation rates, and mean annual increment of aspen all have been shown to increase with higher light availability (Jones 1985, Jelinski 1993, McDonald et al. 1999, Hogg et al. 2000, Hogg et al. 2002).

Biophysical setting probably does not act alone in explaining variation in aspen productivity. I measured biophysical variables and competition but unmeasured factors may have also influenced aspen ANPP. Genetic variation is one possible explanation for differences in growth rate, higher rates of increment growth have been associated with high levels of heterozygosity (Mitton and Grant 1980, Jelinski 1993). Gender of the clone is another possible, unmeasured, source of variation. Female aspen have been shown to have higher increment growth than male aspen (Jelinski 1993). Also, I did not measure herbivory which may account for some of the variation that was not explained by biophysical setting.

I hypothesized that aspen ANPP varied with biophysical gradients in the GYE. Although I was able to explain 30 - 45% of the variability in aspen ANPP across the

study area, other factors in my conceptual model (Fig. 1) probably account for much of the remaining variation. Several authors suggest that extremely high populations of elk severely limit aspen growth and regeneration in the GYE (DeByle 1985, Romme et al. 1995, Kay 1997, White et al. 1998, Hessler and Graumlich 2002, National Academies of Science 2002) and maybe the effect of herbivory is much stronger than that of biophysical gradients. Others have proposed that fire exclusion and the resulting increase in conifer cover are primarily responsible for deteriorating aspen stands (Loope and Gruell 1973, Jones and DeByle 1985b, Bartos et al. 1994, Bartos and Amacher 1998, Bartos and Campbell 1998, Gallant et al. 2003); lack of stimulation by fire or shading by conifer may overshadow any influences of biophysical gradients on aspen productivity. The National Academies of Science (2002) argue that on Yellowstone's northern range, although fire exclusion and environmental variables likely interact to influence aspen regeneration, elk herbivory is primarily responsible for aspen condition in the area. However, my explanation of 30 - 45% of the variation in aspen ANPP indicates that environmental variables may act in concert with other factors in influencing aspen productivity.

Landscape Change

The results of my analysis of landscape change support the hypothesis of widespread aspen decline. I documented a 34% decline in aspen cover among sample plots which were widely distributed across the GYE. Although the majority of sampled plots exhibited little or no change in aspen cover over the past 50 years, these locations may be susceptible to future decline. The results of my ANOVA indicated little

difference in locations of aspen loss versus locations with no change in aspen cover with respect to biophysical variables (Table 7). The small number of plots that gained in aspen cover, however, differed significantly from both loss and no change plots with respect to several biophysical variables (Table 7).

Areas that gained aspen cover were characterized as generally moister during the growing season and warmer than areas which lost aspen cover. Areas which gained aspen cover had higher precipitation, soil water potential, and growing degree-days (Table 7) and lower values of growing season PET, radiation, and soil water runoff than areas which lost aspen cover. Both annual precipitation and snowfall were lower in areas which gained aspen than areas that lost aspen, possibly indicating that a milder winter environment is more favorable to aspen persistence.

Areas of aspen loss were generally drier during the growing season than those that did not change in aspen cover. Plots which lost aspen had higher values of growing season actual evapotranspiration (AET), growing season PET, soil water runoff, and soil water transpired by the canopy than areas that did not change in aspen cover. Snowfall and annual precipitation were higher for plots which lost aspen than plots which gained or did not change, possibly indicating that a harsher winter environment in combination with a drier growing season environment is detrimental to aspen persistence.

I was able to explain 18% of the variation in aspen change for all of the plots. Aspen succession to conifer is responsible for loss of aspen in many areas (Loope and Gruell 1973, Jones and DeByle 1985b, Mueggler 1985, Bartos and Amacher 1998, Bartos and Campbell 1998, Hessler and Graumlich 2002, Gallant et al. 2003). In support of conifer encroachment influencing the loss of aspen, change in conifer cover from 1956-

2001 was negatively correlated with change in aspen cover. The results of my ANOVA indicated that loss of aspen occurred in areas with high snowfall and high annual precipitation. My regression results support this finding, showing a negative correlation between snowfall and aspen change for the full dataset. I also found a negative correlation between annual precipitation and aspen change for plots that lost or did not change in aspen cover. Conifer change alone explained 12% of the variation in the full dataset. I explained 13% of the variation in aspen change in those plots which lost or did not change in aspen cover and conifer change alone explained 9% of the variation for these locations. Several of the plots (62) that lost aspen cover experienced no change in conifer cover during the past 50 years, for half of these plots this is explained by the lack of conifer in either time period. However, half of these plots had between 10% and 70% conifer cover and experienced no change in conifer cover but a loss of aspen cover.

Although conifer encroachment seems to be linked to aspen decline in some places, these results indicate that aspen loss can occur even in the absence of conifer encroachment. My ANOVA results indicate that areas susceptible to loss may be those with dry growing season and harsh winter climates. To understand the relative influence of competition and biophysical setting on aspen loss, I modeled aspen loss separately for areas of conifer presence and areas of conifer absence. In the absence of conifer, greater levels of aspen loss were associated with shallower soils (Table 9), explaining 20% of the variation in aspen change in these areas. As expected, in the presence of conifer an increase in conifer was associated with greater loss of aspen (Table 9); however, conifer change only explained 5% of the variation in aspen change and no biophysical variables explained more than 2% of the change in aspen cover (Table 13).

Using only growing season solar radiation flux, I explained 43% of the variation in areas which gained aspen cover. Most of the plots which gained in aspen cover had solar radiation values below 400 W/m^2 . Two plots which only gained 20% aspen cover had the highest solar radiation values of the gain points, between 440 and 450 W/m^2 .

I hypothesized that rates of change in aerial cover of aspen would vary with biophysical setting as a result of differing competitive abilities of aspen along environmental gradients. As aspen stands are replaced by conifer, soils exhibit a decrease in organic matter accumulation, reduction in mollic horizon thickness, and slight increase in soil pH and slight decrease in soil exchangeable potassium (Cryer and Murray 1992, Bartos and Amacher 1998), but these are results of aspen conversion to conifer and it is unclear if soil properties influenced the conversion. Gallant et al. (2003) documented aspen decline and concomitant conifer increase in "moist Douglas-fir forest", described as cool, moist habitats between 1900 and 2400 meters. In a study encompassing Colorado, Wyoming, and Utah, the strongest correlates of aspen decline were the presence of other species (primarily lodgepole, spruces and firs, and Douglas-fir) and whether other species were regenerating, but environmental conditions were not characterized (Rogers 2002). I found some correlation between aspen loss and increases in conifer, but I also found aspen decline in areas with no change in conifer cover. Biophysical variables had even less ability to predict aspen change than did change in conifer cover (Table 4). This suggests that other factors may be responsible for the observed decline in aspen cover (Fig. 1). Disease or insect outbreaks may account for some loss of aspen in the absence of conifer invasion. In Alberta, Canada, aspen crown dieback and aspen growth rate were negatively correlated with outbreaks of forest tent

caterpillar (*Malacosoma disstria* Hbn.) and the consequent defoliation led to secondary damage from wood-boring insects and *Armillaria* root rot (Hogg et al. 2002). Reduced regeneration as a result of fire exclusion (Loope and Gruell 1973, Jones and DeByle 1985b, Bartos et al. 1994, Bartos and Amacher 1998, Bartos and Campbell 1998, Gallant et al. 2003) and high levels of ungulate herbivory (DeByle 1985, Romme et al. 1995, Kay 1997, White et al. 1998, Hessel and Graumlich 2002, National Academies of Science 2002) may account for low or no recruitment of aspen stems into the overstory, resulting in a decrease in aerial aspen cover over time.

Comparisons with My Conceptual Model

Aspen occupy a small proportion of the GYE, representing only 1.4% of the land area, and are much more prevalent south of Yellowstone National Park than in the northern region. I was able to explain aspen presence at the scale of the entire ecosystem and within the northern and southern portions with high accuracy. These results support my first hypothesis that aspen occupies a subset of the available biophysical settings in the GYE. I was also able to explain between 30% and 45% of the variation in aspen ANPP with biophysical variables, supporting the hypothesis that aspen productivity varies with biophysical setting but indicating other factors (e.g. fire, herbivory, competition) probably interact to influence aspen growth. Finally, I found that areas that lost and gained in aspen cover over the past 50 years were significantly different in biophysical setting. Areas which gained aspen cover were generally moister during the growing season and had lower snowfall than areas which lost aspen. Additionally, I was able to explain 43% of the variation in aspen change for areas that gained aspen.

Biophysical setting and competition explain some of the variation in aspen change for areas which lost or did not change in aspen cover; however, other factors are likely to influence loss of aspen cover.

I proposed a conceptual model in which biophysical setting directly influenced aspen distribution, productivity, or decline through aspens' differential response to different regimes of such variables as moisture, temperature, or nutrients (Fig. 1). I also suggested that biophysical setting might influence the effects of recognized influences on aspen dynamics, namely fire exclusion, competition, and herbivory (Fig. 1). I tested hypotheses suggesting that aspen response to biophysical gradients would be apparent in its distribution, productivity, and change in aerial cover at differing points along these gradients. My results support my first hypothesis, that aspen distribution varies with biophysical setting. My results also lend support to my remaining two hypothesis, that aspen ANPP and change in aerial cover vary with biophysical setting but suggest that other factors may also have an influence (Fig. 1, Table 1). Biophysical setting explained 37% of the variation in aspen ANPP across all my sites, the remaining variation may be related to herbivory, competition, fire, or genetic variation in growth rates. I explained 43% of the variation in aspen change for areas which gained aspen and found significant differences between areas that gained, lost, or did not change in aspen based on biophysical variables related to moisture and radiation.

Despite the narrow distribution predicted by my CART models, these models still predict aspen to occur in locations where it is currently absent. Thus, my results suggest that there are more sites favorable to aspen presence than are currently occupied by aspen (Fig. 11). In the Upper Great Lakes regions, Gustafson et al. (2003) found that aspen did

not occupy the most favorable biophysical sites for its growth. If aspen in the GYE is constrained to a small portion of its abiotic niche, aspen performance may not be optimized in current locations (Fig. 11). If this were the case, aspen ANPP may be similar within this narrow distribution and both performance and change in aspen cover could be more susceptible to additional factors (e.g. herbivory, fire exclusion). Perhaps, in the GYE, factors such as herbivory, fire exclusion, or competition are more important in determining aspen productivity and decline than is biophysical setting. There are several possible explanations for the further constriction of aspens' distribution apparent on the ground (Fig. 11) with implications for productivity and decline of aspen, these include climatic changes, past and current fire regimes and competition, and herbivory.

Extant aspen stands may be a relic of the past, maladapted to current climatic conditions. Aspen seedling establishment in western North America is rare due to unsuitable climate conditions and it is widely believed that establishment of aspen stands in the region has not occurred since the last glaciation 10,000 years ago (Jelinski and Cheliak 1992, Mitton and Grant 1996). The longevity of aspen as a clonal plant (Barnes 1966) and lack of recent sexual reproduction suggest that existing stands may not be adapted to current climatic conditions (Stevens et al. 1999). Jelinski and Cheliak (1992) documented genetic diversity in aspen populations in Waterton Lakes National Park, arguing for occasional seedling establishment since the last glaciation. However, aspen seedlings that established in Yellowstone National Park following the 1988 fires were genetically similar and probably had genetically similar parents (Stevens et al. 1999). This indicates that existing aspen stands in Yellowstone, or at least those that produced seed following the fire, may be close genetic relatives. No data are available on genetic

variation of aspen for the GYE as a whole. However, if aspen stands throughout the GYE are genetically similar and adapted to previous climatic conditions, growth rates of aspen may no longer be adapted to current distributions and aspen may be more susceptible to competition and herbivory. This suggests the possibility of a genetic basis for aspen decline (Stevens et al. 1999).

Prior to European settlement and the effective exclusion of fire in Rocky Mountain ecosystems, fire shaped vegetation distributions in the GYE (Loope and Gruell 1973, Hessler and Graumlich 2002, Gallant et al. 2003). I have shown that aspens' distribution correlates with biophysical setting, however the current distribution of aspen has probably been narrowed (relative to the full range of its tolerances) as a result of past fire regimes. Aspen seedling establishment in the GYE is rare, however fire may provide favorable conditions and an opportunity for seedling recruitment (Kay 1993, Romme et al. 1995, Stevens et al. 1999). Historic establishment of aspen genets is likely to have occurred in burned areas, restricting aspen distribution to areas which had burned. The persistence of established aspen clones into current times is probably also dependent on fire regimes because aspen require fire for regeneration and recruitment (Loope and Gruell 1973, Jones and DeByle 1985b, Brown and DeByle 1987, Hungerford 1988, Bartos et al. 1994, Romme et al. 1995). Fire in the Douglas-fir zone, where much of the aspen in the region occurs (Gallant et al. 2003), was frequent through the late 1800's but has been effectively excluded in this zone since (Littell 2002). Because the lifespan of mature aspen stems is only ~ 200 years (Loope and Gruell 1973), fire frequencies of < 200 years are likely necessary to maintain aspen on a site. Indeed, fire exclusion during the past century has contributed to aspens' succession to conifer and decreased aspen

abundance (Loope and Gruell 1973, Jones and DeByle 1985b, Mueggler 1985, Despain 1990, Bartos et al. 1994, Bartos and Campbell 1998, Gallant et al. 2003).

The results of my distribution analysis indicate both that aspen is restricted to a narrow subset of biophysical settings in the GYE and that its distribution may be further restricted such that it does not occupy all sites which are favorable to its growth (Fig. 11). Ungulate herbivory has frequently been shown to suppress aspen regeneration (DeByle 1985, Romme et al. 1995, Baker et al. 1997, Kay 1997, White et al. 1998, Hessler and Graumlich 2002). However, some studies have documented successful aspen regeneration despite browsing pressure (Suzuki et al. 1999, Barnett and Stohlgren 2001). I suggested that aspen response to herbivory may be mediated by environmental variables (Fig. 1). I explained 37 - 45% of the variation in aspen ANPP with biophysical variables and some of remaining variation may be related to an interaction between biophysical setting and herbivory. If only a small portion of the areas in which aspen occur are favorable to growth, as indicated from my ANPP analysis, ungulate herbivory may be operating on aspen that are currently at the edge of their abiotic tolerances. In poor growth conditions, plants may be less able to tolerate herbivory and high levels of herbivory are likely to shift competitive relationships to favor the less palatable species (Augustine and McNaughton 1998).

In summary, my results indicate that aspen distribution does vary with biophysical setting. Biophysical variables were able to explain some of the variation in aspen performance (ANPP) or change over time. It is likely that competition, herbivory, or fire exclusion and interactions between these factors and biophysical variable account for much of the remaining variation. Although biophysical setting may directly influence

aspen distribution, the distribution of aspen may be narrowed by additional factors (Fig. 1) such that aspen does not occupy the full range of its abiotic tolerances. Fire exclusion, herbivory, or competition may be operating on aspen that occupy areas at the edge of their abiotic tolerance. Thus, within a possibly narrowed distribution, these additional influences on aspen may act in concert with environmental gradients in determining aspen ANPP and changes in aerial cover.

Scope and Limitations

Our understanding of biophysical influences on aspen is limited by my ability to infer causation. I identified biophysical variables which show varying degrees of correlation with aspen distribution, growth, and decline, however, these variables may simply be correlated with other factors influencing aspen. For example, I identified radiation as positively correlated with aspen distribution, but radiation and southerly aspects are also likely correlated with the distribution of fire on the landscape. Additionally, the extrapolation of these results to areas outside the GYE should be undertaken with caution. In areas with different fire regimes, species assemblages, or ranges of climatic conditions than the GYE, the influences on aspen may differ.

Our results are influenced by the accuracy of my data layers including the maps of aspen distribution, my biophysical predictor variables, biomass estimates, and aerial photograph interpretation. The maps of aspen distribution that I used were reasonably accurate, however I know from my accuracy assessment that these maps carried 32% error. Any errors in the map of aspen distribution could influence my analysis of aspen distribution and also of aspen ANPP because I selected field sites from this map. I used

the best widely-available data on vegetation distribution to map aspen distribution, restricting data sources to those which used aerial photography or stand exams rather than satellite imagery (Appendix A). Additionally, errors in each data layer used as predictive variables could influence my final results. Since I was working with such a large study area and large datasets, it was logistically impossible to collect site-level information on my predictor variables, such as temperatures, precipitation, elevation, etc. Therefore, I relied on digitally available information for my predictor variables. Sources of error in my predictor variables include: the Digital Elevation Model used for topographic variables and as input into the WXFIRE model, the STATSGO soils data used as input into the WXFIRE model, DAYMET data which are rescaled by WXFIRE, and the fact that all this potential error could propagate to affect the results of the WXFIRE model. The accuracy of the DAYMET data is limited by the spatial locations of the weather stations from which data are extrapolated. Weather stations are generally sparse in the western United States and in mountainous terrain. However, cross-validation results of the DAYMET data in the northwestern U.S. showed mean absolute errors of only 0.7°C and 1.2°C for annual average maximum and minimum temperature, respectively (Thornton et al. 1997). Cross-validation of precipitation data showed mean absolute errors of 13.4 cm for annual total precipitation (Thornton et al. 1997). Additionally, the DAYMET data are calculated from weather data from 1980-1997 so the time-frame is relatively short and does not capture such climatic events as the extreme drought of the 1930's.

Our estimates of aspen ANPP and the biomass of other vegetation rely on the assumption that equations used in BIOPAK can adequately estimate biomass for the

species I encountered. Equations in BIOPAK are derived from field studies and I felt represented a reasonable method of estimating biomass (Means et al. 1994). Estimates of aspen and conifer change over time assume accurate detection of aspen and conifer cover in aerial photographs. Fortunately, aspen are easily distinguishable from conifer based on color, texture, and growth form and I am reasonably confident in my estimates of relative aspen and conifer cover.

The scale of the variables used in my analysis could potentially have been limiting. Although the WXFIRE model allowed us to simulate biophysical variables at reasonably fine resolution, gradients operating at finer scales may have shown stronger correlation with aspen ANPP or land cover change. For my distribution and change analyses, it is likely that 30-m climate data were adequate to represent site condition for an aspen stand. Growth rates may be influenced by finer-scale changes in soil characteristics such as percent sand, silt, or clay or variables pertaining to soil moisture. For example, microclimates resulting from shading or fine-scale change in nutrient availability may more directly influence aspen ANPP than the broader-scale biophysical variables used here.

Finally, biophysical setting likely interacts with other factors which were beyond the scope of this study to measure. Levels of herbivory, disease, insect outbreaks, genetic variation within and among clones, and past and current fire regimes are a few examples of possible influences on aspen which could interact with biophysical setting to influence aspen.

Research Needs

I started with a conceptual model in which biophysical setting directly influences aspen growth or persistence and indirectly influences aspen's response to stressors such as fire exclusion, competition and herbivory (Fig. 1). My data support my first hypothesis, that aspen distribution is limited to specific combinations of biophysical variables. I explained some of the variation in aspen ANPP and change in aerial cover, however future research should focus on quantifying the interacting affects of biophysical setting and competition, fire, and herbivory to better understand the role each of these influences play in aspen dynamics. Further research into the controls on aspen dynamics needs to consider the interactions of biophysical setting, herbivory, competition, and fire exclusion. My research highlights the need for detailed, spatially explicit studies of aspen growth relative to abiotic gradients, such as light, temperature, nutrients, and moisture. Additionally, because the distribution of aspen on natural landscapes is likely an artifact of additional factors such as past fire regimes, establishment history, or competition, understanding of the biophysical controls on aspen requires specific description of aspens' abiotic niche. I propose that experimental studies, both laboratory and field-based, are needed to fully explore the control of biophysical setting on aspen dynamics. It will be vital to our understanding of aspen dynamics to consider aspens' response to herbivory, fire exclusion, competition, and climatic change in the context of such studies. Examples of such studies include:

1. Experimental research could determine the limits of aspens' abiotic niche. For example, growing aspen in controlled laboratory conditions under a factorial design and

manipulating such biophysical variables as: air and soil temperature, soil substrate, soil nitrogen and potassium concentrations, soil moisture, and radiation intensity and compare relative growth rates. Additionally, planting aspen saplings of similar genetic stock across gradients in these same variables would be valuable in establishing how field and laboratory results differ.

2. Field-based experiments would help determine the interaction between aspen growth rate, carbon allocation, and herbivory. Either planting sapling or locating suckering stands along different biophysical gradients and simulating herbivory and establishing no-herbivory controls (exclosures) would allow for the monitoring of relative growth rate and secondary metabolite production in relation to the interacting effects of biophysical setting and herbivory.

3. Prescribed fire treatments spanning environmental gradients could be used to establish the interaction of fire and biophysical setting and post-fire response. Treatments could include a factorial design of controls, fire, simulated herbivory, and plantings of competing species.

Although I found strong biophysical control over aspen distribution, future studies integrating biophysical controls with additional factors such as fire regimes or herbivory will be important in understanding aspen dynamics. This study represents one of the first attempts to quantify the affects of biophysical setting on aspen distribution, productivity, and decline at a landscape scale; however, experimental studies aimed at determining the specific abiotic tolerances of aspen in combination with stressors such as herbivory are needed to fully understand aspen dynamics.

Management Implications

Several authors have documented aspen decline at small scales in the western United States (Loope and Gruell 1973, Renkin and Despain 1996, Wirth et al. 1996, Baker et al. 1997, Bartos and Campbell 1998, Hessler and Graumlich 2002, Gallant et al. 2003). However, some evidence suggests that aspen stands in some areas may be able to persist (Suzuki et al. 1999, Barnett and Stohlgren 2001, Manier and Laven 2002, Rogers 2002). This is the first study to document change in aspen cover over time across the entire Greater Yellowstone Ecosystem. My data indicate that aspen decline is occurring in the GYE, with 34% of sampled aspen plots losing at least 20% of their aerial cover since 1955.

Our data indicate that aspen distribution in the GYE is restricted to a narrow range of biophysical conditions and I suggest that aspen may be excluded from sites more favorable to its growth. Similarly, Gustafson et al. (2003) found that aspen occupied only 6.7% of the sites predicted to have highest growth potential for aspen in national forests of the Upper Great Lakes Region.

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. In many cases, aspen may persist as shrubs in the understory after being overtopped by conifer (Loope and Gruell 1973). These shrub-aspen stands may benefit from management actions such as prescribed fire or partial logging, possibly under fuels reduction plans. Restoration efforts, however, should be prioritized such that areas demonstrated to be well within the abiotic tolerances of aspen

receive first priority. The results of my distribution models could help guide such efforts; for example, restoration efforts in the southern GYE should focus on areas with a high shortwave radiation but restoration in the northern GYE may be more successful if focused in areas with moderate snowfall and high growing season temperatures.

Additionally, land managers could consider attempting to establish new aspen stands in areas currently unoccupied by aspen. Again, such efforts could be guided by the abiotic limits that my 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.

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APPENDICES

APPENDIX A

GIS Vegetation Data Used to Derive Maps of Aspen Distribution

Appendix A. GIS vegetation data used to derive maps of aspen distribution; NF refers to a national forest, NP refers to a national park.

Agency	Publication Year	Source Data	Verification
Beaverhead-Deerlodge NF	2000	1:24,000 source maps	None
Bridger-Teton NF	1988	1:15,840 aerial photographs	None
Gallatin NF	1996	1:15,840 aerial photographs	None
Grand Teton NP	1992	1:16,000 aerial photographs	selected sites ground-verified. field use indicated 80% accuracy
Targhee-Caribou NF	1991	1:24,000 aerial photographs; stand exam data; Landsat satellite imagery where stand data unavailable. All aspen locations were from stand exams.	Field verified
Yellowstone NP	1990	pre-1988 aerial photographs and classified satellite image used to identify burned areas and update the map	None

APPENDIX B

Species Substitutions Used for Species Not Modeled in BIOPAK

Appendix B. Species substitutions used for species not modeled in BIOPAK.

	Species	Species substitution used
Shrubs	<i>Alnus incana</i>	<i>Alnus sinuata</i>
	<i>Betula occidentalis</i>	
	<i>Arctostaphylos uva-ursi</i>	<i>Berberus repens</i>
	<i>Paxisima myrsynites</i>	
	<i>Chrysothamnus nauseosus</i>	<i>Artemisia tridentata</i>
	<i>Gutierrezia sarothrae</i>	
	<i>Craetagus douglassi</i>	<i>Amelanchier alnifolia</i>
	<i>Pentaphylloides floribunda</i>	<i>Physicarpus malvaceus</i>
	<i>Ribes cereum</i>	<i>Ribes spp.</i>
	<i>Ribes lacustre</i>	
	<i>Ribes viscosissimum</i>	
Trees	<i>Pinus flexilis</i>	<i>Pinus albicaulis</i>
	<i>Juniperus osteosperma</i>	<i>Juniperus occidentalis</i>
	<i>Juniperus scolulorum</i>	