

Research Article

Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem

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Abstract

Loss of aspen (*Populus tremuloides*) has generated concern for aspen persistence across much of the western United States. However, most studies of aspen change have been at local scales and our understanding of aspen dynamics at broader scales is limited. At local scales, aspen loss has been attributed to fire exclusion, ungulate herbivory, and climate change. Understanding the links between biophysical setting and aspen presence, growth, and dynamics is necessary to develop a large-scale perspective on aspen dynamics. Specific objectives of this research were to (1) map aspen distribution and abundance across the Greater Yellowstone Ecosystem (GYE), (2) measure aspen change in the GYE over the past 50 years (3) determine if aspen loss occurs in particular biophysical settings and (4) investigate the links between biophysical setting and aspen presence, growth, and change in canopy cover. We found that aspen is rare in the GYE, occupying 1.4% of the region. We found an average of 10% aspen loss overall, much lower than that suggested by smaller-scale studies. Aspen loss corresponded with biophysical settings with the lowest aspen growth rates, where aspen was most abundant. The highest aspen growth rates were at the margins of its current distribution, so most aspen occur in biophysical settings less favorable to their growth.

Introduction

Considerable debate surrounds the persistence of quaking aspen (*Populus tremuloides*) communities in western North America. Although aspen is the most widely distributed tree species in North America (Jones 1985), loss of aspen cover has been documented in various Rocky Mountain ecosystems (Loope and Gruell 1973; White et al. 1998). Proposed explanations for loss of aspen include conifer encroachment, fire exclusion, herbivory, and climatic fluctuations (Loope and Gruell 1973;

Bartos et al. 1994; Romme et al. 1995; Kay 1997; White et al. 1998). However, many studies documenting aspen decline have been geographically limited or based on a small sample of subjectively chosen stands (Kaye et al. 2003). Our understanding of aspen dynamics across regional scales is poorly developed (Kaye et al. 2003), leading to controversy over the cause and extent of aspen decline.

Recent landscape-scale studies of aspen dynamics in Colorado reveal increasing or stable aspen populations (Suzuki et al. 1999; Manier and Laven

2002; Kaye et al. 2003; Kulakowski et al. 2004). In and around Rocky Mountain National Park, aspen decline is not apparent at landscape scales (Suzuki et al. 1999; Manier and Laven 2002; Kaye et al. 2003). Based on repeat photography, aspen cover increased over the past 80–100 years in both burned and unburned forests of the western slope of the Rocky Mountains in Colorado (Manier and Laven 2002). In the Grand Mesa area of Colorado, Kulakowski et al. (2004) found no evidence of aspen decline since 1898, but rather an increase in aspen cover even in comparison with the landscape prior to widespread burning. Persistent or increasing aspen stands were more common at lower elevations, but many aspen stands were self-replacing even in the absence of fire. Additionally, Suzuki et al. (1999) found frequent aspen regeneration in Rocky Mountain National Park, except in areas of locally high elk (*Cervus elaphus*) use. On one Rocky Mountain National Park landscape, there was little evidence of aspen decline despite widespread evidence of browsing by elk (Kaye et al. 2003).

Less is known about the pattern of aspen dynamics at landscape scales in the areas surrounding Yellowstone and Grand Teton National Parks. Most studies in the GYE have primarily focused on the Jackson Hole valley in northwestern Wyoming and the northern range of Yellowstone National Park (Loope and Gruell 1973; Bartos et al. 1994; Romme et al. 1995; Hessler and Graumlich 2002). Studies limited to these portions of the GYE have predominantly shown loss of aspen cover and limited aspen recruitment (Kaye 1993; Romme et al. 1995; Ripple and Larsen 2001; Hessler and Graumlich 2002). In the Gros Ventre River Valley north of Jackson, Wyoming, in contrast, aspen regeneration was evident, even in areas with high elk densities (Barnett and Stohlgren 2001).

Only three larger-scale studies of aspen dynamics in the region have been published, and these are at the scale of small watersheds. In a watershed in the Centennial Mountains of Idaho, aspen declined by 75% since the mid-1800s (Gallant et al. 2003). Wirth et al. (1996) estimated a 45% decline in pure aspen and mixed aspen/conifer forests between 1947 and 1992 in the Gravelly Mountains of southwestern Montana. In elk winter range of Yellowstone National Park and adjacent basins of the Gallatin and Shoshone

National Forest, aspen canopy cover declined by approximately 22.7–38.6% between the 1950's and the 1990's (Larsen 2001).

A regional assessment of aspen change is needed to fully understand aspen dynamics in the Greater Yellowstone Ecosystem (GYE). These local to small watershed-scale studies suggest that aspen is declining in the GYE and propose fire exclusion, advancing succession, and herbivory as potential causes. However, little is known at the regional scale about fluctuations in aspen populations, the factors influencing changes in aspen cover, or even the factors shaping aspen's current distribution.

Environmental gradients are likely to provide an important context for understanding aspen dynamics at this regional scale. Gradients in light, temperature, and precipitation are known to generally affect plant species distributions, growth rates, and defenses according to a species' physiological tolerances (Bryant et al. 1983; Austin et al. 1990). We expect the distribution and growth rates of aspen in the GYE to similarly be related to environmental conditions. Additionally, aspen growing at their optimal value along environmental gradients are more likely to be stable or increasing in cover.

The aim of this study was to document the influence of biophysical gradients on aspen population dynamics. Key questions were: (1) what is the aerial extent of aspen in the GYE and what are the environmental factors defining the biophysical niche of aspen presence? (2) how has aspen's distribution and abundance changed over the past 50 years? (3) is change in aspen cover occurring in particular biophysical settings? and (4) how might biophysical controls on aspen presence and growth explain changes in aspen cover?

Methods

Study area

The study was conducted across the Greater Yellowstone Ecosystem (GYE) in Montana, Idaho, and Wyoming, as defined by Hansen et al. (2002) (Figure 1; 108°45' to 112°30', 42°15' to 46°15'). The GYE encompasses strong gradients in topography, climate, and soils. Soil types and climate vary with elevation in the region with nutrient-poor rhyolite and andesite soils dominating higher elevations

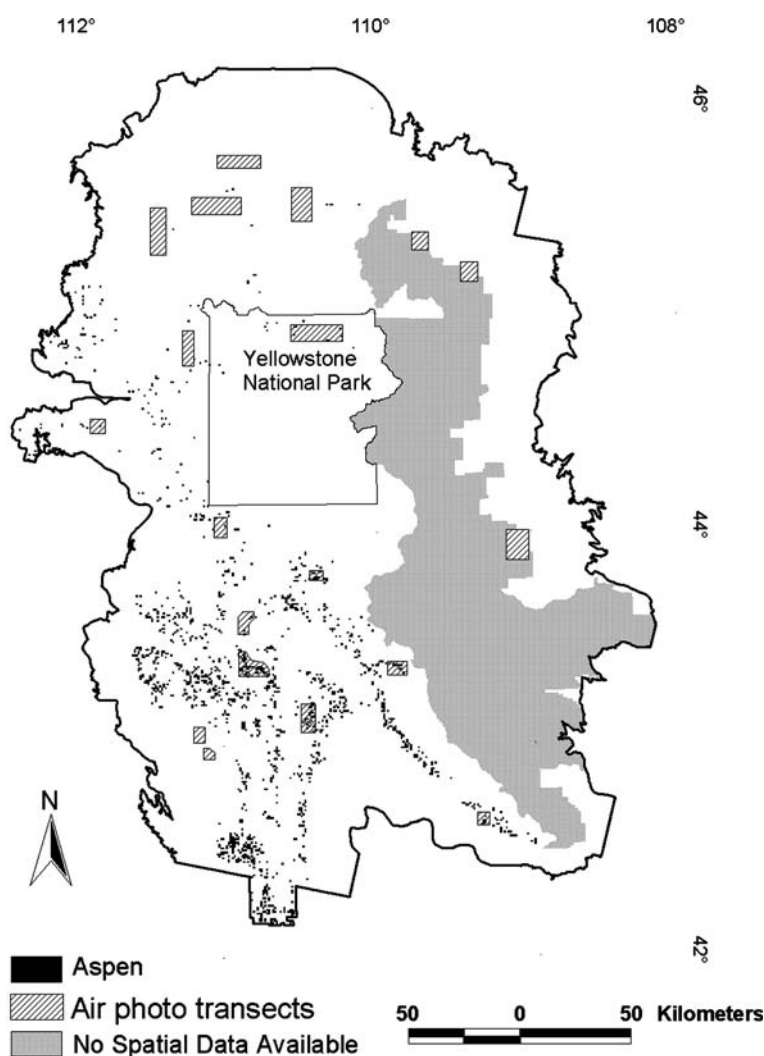


Figure 1. The Greater Yellowstone Ecosystem (GYE) was the study area. Aspen occupy only 1.4% of the land area. We measured change in aspen canopy cover, between 1956 and 2001, along the aerial photo transects shown. The shaded area represents the Custer and Shoshone National Forests, which lacked digital data on aspen distribution and were not included in our aspen presence or growth analyses.

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). Mean annual precipitation is 65 cm but ranges from 19 to 208 cm, with the majority of the precipitation falling as snow. Lower elevations (< 2000 m) receive an annual average of 25 cm of precipitation and higher elevations receive an annual average of 75 cm, most as snow. Mean annual average temperature is 2.8 °C and ranges

from -6.0 to 8.0 °C. Lower elevations average 5.1 °C while higher elevations average 0.6 °C, annually. Mean annual growing degree-days is 2013 °C-day and ranges from 498 to 3634 °C-day. Lower elevations average 2753 °C-day while higher elevations average 1630 °C-day (Thornton et al. 1997).

Vegetation in the region closely follows climatic patterns. 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. Higher 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 toe slopes or topographic concavities (Despain 1990; Hansen et al. 2000). Aspen often occurs at the ecotone between shrub steppes and low elevation coniferous forests (Marston and Anderson 1991; Gallant et al. 2003).

Fire regimes are variable across the region with respect to elevation. Higher elevation forests of lodgepole pine historically experienced severe, infrequent fires with 100–250 year return intervals, with subalpine fir, Englemann spruce, or whitebark pine replacing lodgepole pine 80–120 years post fire (Bowerman et al. 1997; Romme 1982). At middle elevations above the valley bottom, where sagebrush, juniper, limber pine or dry Douglas-fir communities are currently found, fire return intervals ranged from 20 to 40 years (Barrett 1994; Bowerman et al. 1997; Littell 2002). The lower forest boundary, dominated by Douglas-fir, was characterized by mixed severity, more frequent fires (20–50 year return intervals) prior to 1860 (Barret 1994; Bowermann et al. 1997; Littell 2002). Few fires

burned in these lower elevation forests following the advent of fire suppression, until the large fires of 1988 (Barrret 1994; Littell 2002). Grasslands in the valley bottoms were maintained by frequent (10–20 year return interval), low severity fires (Fischer and Clayton 1983; Barrett 1994). Much of the aspen in the GYE is found in low to mid-elevation forests and at the lower forest boundary, in the understory of Douglas-fir forests or in small patches surrounded by sagebrush steppe (Despain 1990; Marston and Anderson 1991). In lower elevation forests, Douglas-fir may overtop aspen and dominate a site after about 60-years post fire (Barrett 1994; Bowerman et al. 1997).

Study design

We investigated the influence of biophysical gradients on aspen population dynamics by relating aspen presence, change over time, and growth rates to gradients in climate, topography and soils (Table 1). First, aspen distribution was mapped from GIS vegetation maps collected from the national forests and national parks within the GYE. We then used classification and regression tree analysis (CART) to explore aspen's biophysical niche within the GYE. To investigate change in aspen cover over time, we used aerial photography transects across the GYE and measured percent aspen cover between 1956 and 2001. Analysis of variance (ANOVA) was used to investigate the biophysical settings that experience aspen loss vs. areas where aspen were stable or even increasing in aerial cover. Finally, we sampled aspen plots

Table 1. Separate analysis methods were used to examine aspen presence, change, and growth rates with respect to environmental variables.

Response variable	Methods used	Reasoning
Presence (binary - presence/absence)	CART	• Binary response (presence vs. absence), suitable for classification tree • Suitable for nonlinear, nonnormal relationships • Useful in discovering hierarchical or nonadditive relationships • Exploratory technique
Change (% aspen change)	ANOVA	• Used to determine which environmental variables differed significantly between aspen change classes (loss, stable, and gain)
Growth (ANPP)	Univariate plots	• Graphical exploration allowed comparison of aspen growth rates vs. distribution along environmental gradients
	Regression	• Determine the strength of correlation and direction of the relationships between environmental variables and aspen growth rates

across the GYE and measured aspen growth as above-ground primary productivity (ANPP) using radial growth rates from increment cores and stand biomass estimates. We used multiple linear regression to examine variability in aspen ANPP relative to biophysical variables.

Generating biophysical explanatory variables

Topographic, soil, and climatic variables were evaluated as predictors of aspen presence, change, and growth rates. Topographic variables were elevation, aspect, and slope computed from a 30-m resolution digital elevation model (DEM) from the

USGS National Elevation Dataset (Table 2; see <http://edcnts12.cr.usgs.gov/ned>). Soil parent material was from the major lithology dataset of the USGS Interior Columbia River Basin Ecosystem Management Project (Table 2; see <http://www.icbemp.gov>). We used the WX-FIRE computer model (Keane and Holsinger, 2006) to rescale existing climate data and to generate new soil and climatic variables (Table 2). WX-FIRE is a computer program that produces spatially-explicit biophysical data layers at any chosen resolution. Climate and soil variables were summarized both annually and over the growing season, defined as April 1–September 30. The model uses daily weather data from the 1-km DAYMET climate

Table 2. Biophysical variables used as potential explanatory variables in analyses of aspen distribution, growth, and change in canopy cover. Each of the variables generated by WX-FIRE was summarized both annually and over the growing season (April 1–September 30, designated with a 'g' prefix in later tables/figures). Additional data sources were the United States Geographic Survey (USGS) digital elevation model (DEM), USGS Interior Columbia River Ecosystem Management Project (ICBEMP), and State Soil Geographic database (STATSGO).

Variable	Abbreviation	Units	Source
Elevation	Elev	m	USGS DEM
Aspect	Aspct	degrees	USGS DEM
Slope	Slope	degrees	USGS DEM
Daily maximum temperature	Tmax	°C	WX-FIRE
Daily minimum temperature	Tmin	°C	WX-FIRE
Daily average temperature	Tave	°C	WX-FIRE
Daily average daytime temperature	Tday	°C	WX-FIRE
Daily average nighttime temperature	Tnight	°C	WX-FIRE
Growing degree–days above 0.0 °C	Dday	°C	WX-FIRE
Precipitation	Ppt	cm	WX-FIRE
Potential evapotranspiration	PET	cm	WX-FIRE
Actual evapotranspiration	AET	cm	WX-FIRE
Average daily snowfall	Snowfall	cm day ⁻¹	WX-FIRE
Vapor pressure deficit	Vpd	Pa	WX-FIRE
Total daily solar radiation	Srad_t	W m ⁻²	WX-FIRE
Shortwave radiation	Srad_fg	W m ⁻²	WX-FIRE
Photosynthetically active radiation	Par	W m ⁻²	WX-FIRE
Soil water potential	Psi	MPa	WX-FIRE
Soil water lost to runoff	Outflow	cm day ⁻¹	WX-FIRE
Soil water transpired by canopy	Trans	cm day ⁻¹	WX-FIRE
Growing season water stress	Gsws	MPa	WX-FIRE
Parent material	Parmat	Categorical	USGS ICBEMP
Soil depth	Sdepth	cm	STATSGO
Percent sand in soil	Sand	%	STATSGO
Percent silt in soil	Silt	%	STATSGO
Percent clay in soil	Clay	%	STATSGO
NO ₃ ⁻ in soil*	NO ₃ ⁻	mg ha ⁻¹	Field sampled
NH ₄ ⁺ in soil*	NH ₄ ⁺	mg ha ⁻¹	Field sampled
Conifer biomass*	Conifbio	kg ha ⁻¹	Field sampled
Shrub biomass*	Shrbio	kg ha ⁻¹	Field sampled
Herbaceous biomass*	Herbbio	kg ha ⁻¹	Field sampled

*Variables were measured from field data and only used in analysis of aspen ANPP.

modeled database (Thornton et al. 1997) to rescale weather data to the chosen site level (30-m for this study) and generate additional biophysical variables (Table 2; Keane and Holsinger, 2006). Topographic parameters required by WX-FIRE are elevation, aspect, and slope, which we derived from the DEM. The required soil parameters of soil depth, percent sand, silt, and clay were derived from the State Soil Geographic database (STATSGO; National Resource Conservation Service 1994), after resampling to 30-m resolution based on topographic parameters. Five daily variables from the DAYMET database are used by WX-FIRE for calculation of biophysical variables: minimum temperature ($^{\circ}\text{C}$), maximum temperature ($^{\circ}\text{C}$), precipitation (cm), vapor pressure deficit (Pa), and solar radiation (kW m^{-2}). Vapor pressure deficit is assumed to be constant over 1-km because humidity is a characteristic of the air mass and is only slightly correlated to topography. Therefore, vapor pressure deficit is usually the same across a wide region depending on the frontal systems and is the only variable not scaled down to the site level. Temperature and precipitation data from DAYMET are scaled from 1-km to 30-m using dynamic lapse rates based on elevation and the weather data from the eight 1-km DAYMET pixels surrounding the reference DAYMET pixel (Keane and Holsinger, 2006). Solar radiation data from DAYMET are adjusted to the site level based on atmospheric transmissivity and scaled to the site level by accounting for leaf interception, slope, and aspect using solar declination and altitude angle for the time 1400 h (Keane and Holsinger, 2006).

Aspen distribution and the biophysical niche of aspen presence

We mapped the distribution of aspen in the GYE using existing spatial vegetation data in a Geographical Information Systems (GIS), which we verified by comparing aerial photography along linear transects to the compiled aspen map and performing an accuracy assessment. The overall accuracy of the compiled map was 78% (see Brown 2003 for details). Vegetation GIS maps were obtained from Gallatin National Forest, Beaverhead National Forest, Yellowstone National Park, Bridger-Teton National Forest, Grand Teton National Park, and the Targhee-

Caribou National Forest, thereby restricting the analysis of aspen distribution to these portions of the study area (Figure 1).

We used classification and regression tree (CART) analysis (TREE package in R; Ihaka and Gentleman 1996) to relate biophysical variables (Table 2) to aspen presence or absence. CART recursively partitions data into subsets based on the single best predictor variable and is useful in discovering relationships in predictors that may be hierarchical, nonlinear, or nonadditive in their interactions (Breiman et al. 1984). The entire mapped population of aspen (Figure 1) was used to determine the biophysical niche of aspen presence. To minimize computing time, particularly for running WX-FIRE, we aggregated our mapped aspen to 1-km cells and generated a point at the center of each grid cell containing aspen. The sample size was 1440 cells of aspen presence and 1438 cells of aspen absence. One third of these cells were randomly selected and reserved for validation while the remaining observations were used to build a classification tree with class membership defined as aspen presence or absence. Initial CART models can be more complex than necessary (i.e., over-fitted models), so simplification techniques may be needed to achieve the most parsimonious fit (Breiman et al. 1984). Thus, our final CART model was generated after selecting that tree which maximized the deviance explained while minimizing the misclassification error rate from cross-validation (prune tree function in R; Ihaka and Gentleman 1996). The rules from the CART model were used to predict the class membership (aspen presence or absence) of each observation in the validation dataset. We calculated overall accuracy, producer's accuracy and user's accuracy using standard error matrix techniques (Jensen 1996). Producer's accuracy measures the probability that an observation was correctly classified. It is associated with errors of omission, error resulting when a pixel is omitted from its correct class, 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. It measures errors of commission, error which results when a pixel is committed to an incorrect class, and was calculated as the number of correctly

classified observations divided by the total number of observations classified in that category (Jensen 1996).

Change in aspen cover and biophysical correlates

Change in aspen cover over time was quantified using a time-sequence of aerial photography, from 1956 to 2001. Twenty transects were distributed across the study area with the constraint that they intersect deciduous forest across the range of elevations and aspects where it occurred and be widely spaced geographically. Because no map of aspen existed for the entire GYE (our compiled map lacked the Custer and Shoshone National Forests), we used the deciduous cover type from the 1992 USGS National Land Cover Dataset (see <http://landcover.usgs.gov/natl/landcover.asp>). We obtained 1:15,840 scale aerial photographs from an early time period (1956–1963) and a current time period (1992–2001) along each transect from the Aerial Photography Field Office in Salt Lake City, Utah. We then generated random 0.81 ha plots, stratified by elevation and aspect within each transect for sampling of change in aerial cover. The aerial photographs were inspected to identify and include a subset of plots of deciduous vegetation that were aspen.

We measured change in aerial cover by interpreting the percentage of aspen and conifer cover in each 0.81 ha plot for each time period. Our predictor data were at 30-m resolution, so we chose 0.81 ha plots to correspond to a 3×3 pixel window as the finest resolution at which we could accurately measure canopy cover from the aerial photographs. Using the point-intercept method (Parmenter et al. 2003), we overlaid a 10-dot grid over each plot and points that intercepted aspen or conifer were identified to the appropriate cover type at 10-percent increments. For example, if one point intercepted aspen and three points intercepted conifer, the plot would be assigned 10% aspen and 30% conifer canopy cover. We chose to measure in 10% increments because this was the highest precision we could accurately measure on 1:15,840 scale photographs. Our choice in the scale of our photographs was limited by availability, especially of older photographs. Although other deciduous species (e.g., *Salix* spp., *Betula* spp., other *Populus* spp.) were sometimes present, we

only recorded the percent cover of aspen and conifer, since aspen dynamics were the focus of interest and succession to conifer is one potential mechanism for decline in aspen cover. Change in aspen cover was calculated by subtracting the aspen cover in the current time period from the aspen cover in the early time period; conifer change was calculated in the same manner, using the measured conifer cover from each time period. To avoid false precision in our data, we grouped our 10% increment data into change classes for analysis. Our three classes of aspen change were: loss (greater than 10% decline in aspen cover), stable (between 10% decline and 10% gain in aspen cover), and gain (greater than 10% gain in aspen cover). We used one-way analysis of variance (PROC ANOVA, SAS Institute 2001) to examine differences between stands which lost, remained stable, or gained aspen cover relative to the biophysical explanatory variables (Table 2).

Quantifying the biophysical relations of aspen growth

To understand how biophysical setting might influence aspen growth, we sampled aspen radial growth rates across 107 sites. We calculated aboveground net primary productivity (ANPP) as our measure of aspen growth rate and investigated the relationship of aspen ANPP to biophysical variables using multiple regression. We also collected data on stand structure and species composition in each site so we could determine the influence of competing vegetation on aspen growth.

Field sites were selected from our map of aspen distribution and stratified by elevation, aspect, and parent material and placed proportional to the occurrence of these strata within aspen's distribution in the GYE. Sites were constrained to be within 1.5 km of trails or roads to allow efficient sampling. Sites were widely distributed through the GYE and located using a global positioning system (GPS). Our sampling design was similar to that described by Hansen et al. (2000). At each site, we established four 8-m radius subplots located 20-m from site center at each of the cardinal directions (Figure 2). Tree density and size distributions were recorded within the 8-m radius plots and shrub density and size distributions were

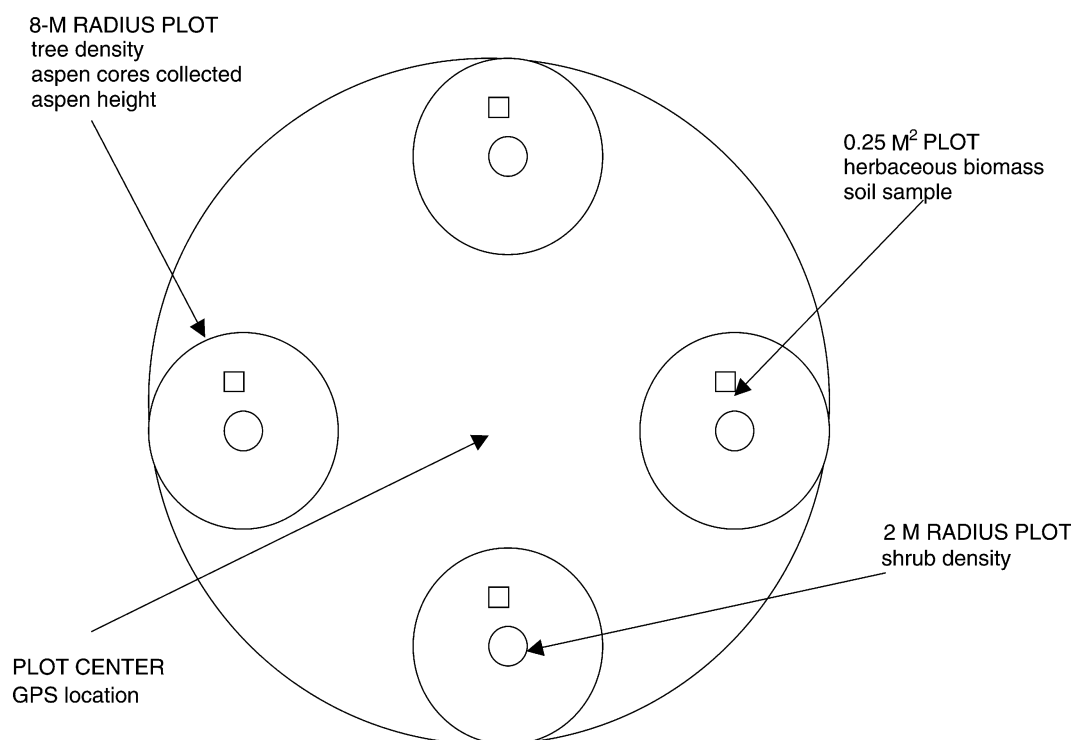


Figure 2. A nested plot design shown here was used to collect field data, including aspen cores to measure aspen above-ground net primary productivity (ANPP), tree and shrub densities by size classes, herbaceous biomass, and a soil sample.

recorded in 2-m radius plots centered within the 8-m radius plots (Figure 2; Table 3). We then used BIOPAK software (Means et al. 1994), which calculates the biomass of plant components based on allometric equations derived from field studies, to calculate tree and shrub biomass as potential explanatory variables. We also collected herbaceous biomass, on 0.25-m² plots, as a potential explanatory variable (Figure 2; Table 3).

Soil samples were collected using a 2.54 cm diameter soil sampling probe within the 0.25-m² plot (Figure 2; Table 3), then weighed, dried at 24 °C for 24 h and reweighed, to calculate soil moisture as a percent of wet weight. Soil samples were then submitted to the Soil Testing Lab at Montana State University to be analyzed for nitrate and ammonium content, which were also used as potential explanatory variables in analyses of aspen ANPP.

We cored aspen trees at each site so that average annual radial growth could be measured and used in calculating aspen ANPP. For aspen at each 8-m radius plot, we measured the diameter at breast height (DBH) and height of one tree from each size

class represented in each subplot and cored the tree at breast height (1.37 m) using a 1.27 cm diameter increment borer (Table 3). We measured average annual increment from the mounted and sanded cores (Table 3). Those cores with extensive heart-rot (only 2.4% of trees sampled) were excluded from the analysis.

Our calculation of ANPP followed the methods of Hansen et al. (2000). We estimated aboveground biomass of aspen using BIOPAK software (Means et al. 1994). To estimate ANPP, we first calculated aboveground biomass of aspen from current DBH and height–diameter relationships. We fit a negative exponential function to the field measured DBH and height data for aspen and then 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. We 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

Table 3. Variables measured at each aspen ANPP field site. Data collected at each field site were used to characterize vegetation and soils at each site and to calculate aspen growth rate (ANPP) for each field site.

Attribute	Description and collection method
Location	Global positioning system location
Tree density	Density of stems (≥ 2 cm dbh) by species by dbh classes within 4 8-m radius plots placed 20 m from point center. Dbh classes are (cm): 2–10, > 10–20, > 20–30, > 30–40, > 40–60, > 60–90, > 90–120, > 120
Radial growth	Twenty-year radial increment determined by measuring the length (mm) from the outside edge of the most recent latewood band to the outside edge of the 21st annual ring. On trees less than 20 years old, we used either 5- or 10-year increment. Cores were mounted and sanded until annual rings were clearly visible. The most recent 20 years of growth were measured by identifying annual rings using a dissecting microscope and counting back from the bark end to the 21st annual ring. The measured radial increment was divided by the appropriate number of years to calculate average annual increment for each tree
Tree DBH	Diameter at breast height (cm) was measured for trees tallied for radial growth
Tree height	Height of tree (m) determined by triangulation for trees where radial growth was measured (using clinometer)
Shrub density	Density of shrubs (≤ 0.5 cm bd) by species by basal diameter class (0.5–1, >1–2, >2–3, >3–4, >4–6, >6–10, >10 cm) within 4 2-m radius plots placed 20 m from point center at the 4 cardinal directions
Herbaceous biomass	All nonwoody plants were clipped at ground level in 0.25-m^2 plots located 5-m due north of the center of each 8-m radius plot. Samples were dried and weighed (g)
Soil sample	Within each of the 0.25-m^2 , a soil sampling probe was used to collect 1-inch (2.54 cm) diameter soil samples. Samples were dried and weighed (g), to calculate soil moisture. Samples were analyzed for nitrate and ammonium content

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

We used multiple linear regression to examine the relationships between aspen ANPP and the explanatory variables (Table 2). The potential explanatory variables were separated into categories of temperature, moisture, radiation, soils, competition (tree, shrub, and herbaceous biomass estimates), and topographic variables. We centered the predictor variables around a mean of zero and standard deviation of one, since this scales variable coefficients in the regression model such that larger values indicate stronger relationships with the response (Neter et al. 1996). Akaike's Information Criterion adjusted for small sample-size (AIC_c) was used to select the single best predictor of aspen change within each category (Burnham and Anderson 1998). A difference of two in AIC_c units was used to choose the most parsimonious models in each category (Burnham and Anderson 1998). Finally, we combined variables from the selected models in each category and also permitted interaction terms between the moisture and temperature categories. However, we did not allow variables with a Pearson correlation greater than 0.80 to be included in the same model, to help reduce multicollinearity in the models.

We used AIC_c to select the most parsimonious models containing combinations of those variables

selected from each category. We examined quadratic terms in the models for predictors in each category since tree species often show a unimodal response to environmental gradients (Austin et al. 1990). Finally, we needed to account for the influence of aspen stem density on ANPP. 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, sites with greater aspen density should experience greater ANPP. Therefore, we 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 that are estimated by the procedure, but we fixed the coefficient of aspen density at one, which allowed the actual aspen stem density at each site to be controlled for in the model.

Results

Aspen distribution and abundance

We found that aspen is rare in the GYE, occupying only 1.4% of the mapped land area (Figure 1). Additionally, aspen is much more prevalent south

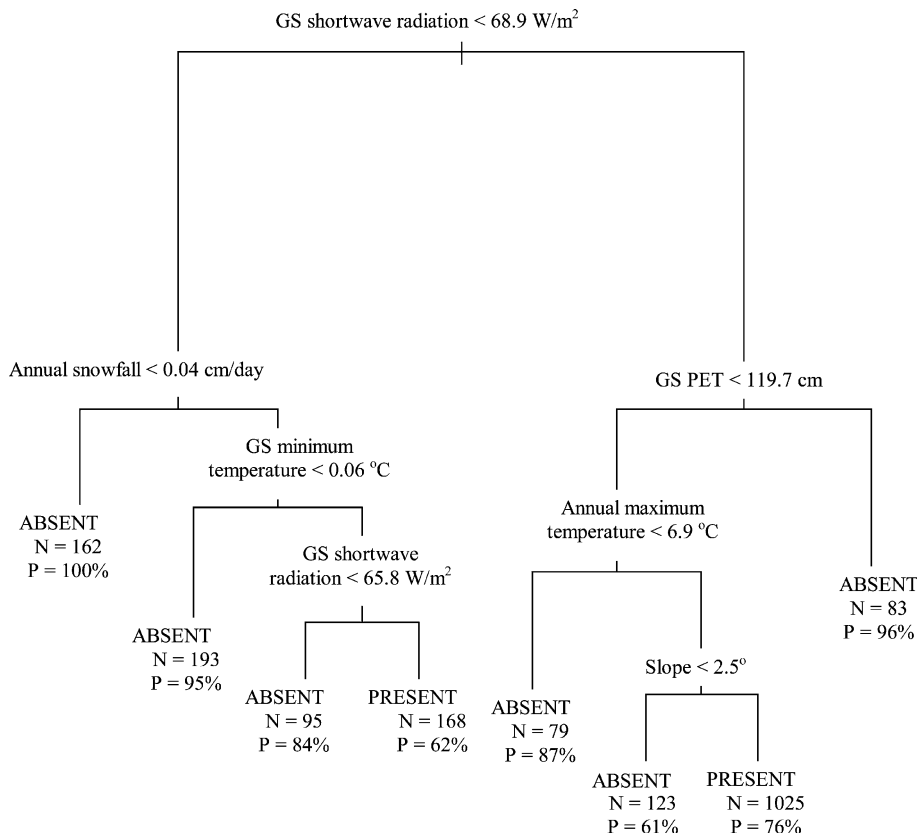


Figure 3. Results of a classification and regression tree (CART) analysis for the GYE to examine aspen presence relative to biophysical setting. GS refers to growing season. The length of the branches is proportional to the amount of deviance explained, thus growing-season short-wave radiation explains the largest proportion of the deviance in the data. 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.

of Yellowstone National Park (3.7% of land area) than in the northern region (0.2% of the land area). Aspen was found from 1559 to 2921 m in elevation, across the GYE, with a mean elevation of 2300 m and annual precipitation averaging 70.6 cm but ranging from 33.8 to 153.4 cm. Average annual temperature across aspen's distribution was 2.1 °C and ranged from −2.2 to 6.1 °C. Aspen occurred more often on shale, glacial till, and sandstone parent materials than expected and was less common than expected on calc-alkaline, alluvium, volcanic, and granitic parent materials, based on the abundance of parent material classes in the GYE ($\chi^2 = 788.3$, $df = 18$, $p < 0.001$).

Our CART model characterized the biophysical niche of aspen as warm, mesic, and with high radiation, snowfall, potential evapotranspiration,

and temperature (Figure 3). Growing season short-wave radiation explained the largest proportion of the deviance in class membership (Figure 3). The higher values ($>68.9 \text{ W m}^{-2}$) of growing season short-wave radiation are primarily in the southern portion of the GYE (Whitlock and Bartlein 1993). Where radiation was above the threshold, aspen was present where growing season PET was below 119.7 cm, annual maximum temperature was above 6.9 °C, and slope was greater than 2.5°. Where solar radiation was below the threshold, aspen was present under higher annual snowfall, higher growing season minimum temperature, and higher growing season radiation (Figure 3).

The CART model had a misclassification error rate of 21%, as reported by R (Ihaka and Gentleman 1996). Using the observations ($n = 950$) reserved from building the CART model, our

model validation yielded an overall accuracy of 80% for the CART model. With a producer's accuracy for aspen presence of 92%, the model performed well at classifying aspen presence. The user's accuracy for aspen presence was lower (74%), indicating that the model sometimes predicted aspen to occur where it was actually absent.

Change in aspen cover

We measured 242 plots from the aerial photographs to examine changes in the aerial cover of aspen. This regional-scale analysis showed much lower rates of decline than other local-scale studies have reported. Between 1956 and 2001, aspen cover declined an average of 10%, ranging from a decrease of 80% to a gain of 70%.

The majority of our plots (59%, $n = 143$) were classified as stable, with between -10% and $+10\%$ change in aspen cover over the past 50 years. Some areas did experience decline, where 34% ($n = 83$) of our plots lost 20% or greater aspen cover over the past 50 years. A small number (7%, $n = 16$)

gained aspen cover. Most plots showed no change in conifer cover (83%), few lost conifer cover (3%), and some gained conifer cover (14%). Biophysical variables differed significantly ($\alpha = 0.05$) along the gradient from plots which gained, remained stable, or lost aspen cover (Table 4). Loss plots had less summer precipitation than gain plots and more winter precipitation and snowfall than either gain plots or stable plots. Annual growing degree-days were lower for loss plots. Several measures of light were higher in areas losing aspen cover. Finally, loss plots were higher in potential and actual evapotranspiration, transpiration of ground water, and runoff. Thus, loss plots were in locations of more winter precipitation, which likely leads to more water in deep soil layers, more runoff, and more evapotranspiration. They were also cooler but had high light levels.

Biophysical correlates of aspen growth

We sampled 107 field sites and collected increment cores from 613 aspen trees to determine aspen

Table 4. ANOVA analysis showed significant differences between aspen change classes along environmental gradients (see Table 2 for variable abbreviations). Declining aspen plots had drier summers and wetter winters, cooler temperatures, more light, and more water loss. Only variables with significant differences ($\alpha = 0.05$) between change classes are shown, F -statistics and probability values are for the overall ANOVA for each variable.

Variable		F	$p > F$	Characteristics of aspen change classes			Conclusions
				Gain	Stable	Loss	
Precipitation	Ppt	9.01	< 0.001	Drier ^a	Intermediate ^a	Wetter	Loss plots have less summer precipitation and more winter precipitation and snowfall
	gPpt	6.72	0.001	Wetter ^a	Drier	Drier	
	Snowfall	11.93	< 0.001	Lowest snowfall ^a	More snowfall ^a	Most snowfall	
Temperature	Dday	4.50	0.010	Warmer ^a	Cooler	Cooler	Loss plots have a shorter growing season and are cooler
Light	PAR	9.26	< 0.001	Less light ^a	More light ^b	More light	Loss plots have higher light
	gPAR	10.84	< 0.001	Less light ^a	More light ^b	More light	
	Srad_fg	9.16	< 0.001	Less light ^a	More light ^b	More light	
	gSrad_fg	9.94	< 0.001	Less light ^a	More light ^b	More light	
	Srad	9.64	< 0.001	Less light ^a	More light ^b	More light	
	gSrad	11.32	< 0.001	Less light ^a	More light ^b	More light	
Water flow	gPET	7.39	< 0.001	Lower ^a	Higher ^b	Higher	Loss plots are more arid and higher in evapotranspiration and runoff
	gAET	3.56	0.030	Lower	Lower ^a	Higher	
	Psi	3.19	0.040	Higher ^a	More runoff ^b	Lower	
	Outflow	6.74	< 0.001	Lowest runoff ^a	More runoff ^b	More runoff	
	gOutflow	7.19	< 0.001	Lowest runoff ^a	More runoff ^b	Most runoff	
	gTrans	4.84	0.008	Low transpiration ^a	Intermediate	Most transpiration	

^a Indicates a significant difference ($\alpha = 0.05$) in Tukey-Kramer confidence intervals between gain or stable plots and loss plots.

^b Indicates a significant difference between stable and gain plots.

productivity. Mean aspen increment was $1.03 \text{ mm year}^{-1}$ (standard error = 0.02, min = 0.023, max = 3.055). The mean ANPP across the 107 sites was $6191 \text{ kg ha}^{-1} \text{ year}^{-1}$ (standard error = 607, min = 57, max = 31,025). We graphed aspen distribution and ANPP with respect to the variables selected by our CART model of aspen presence (Figure 4) to determine if aspen growth was maximized within its biophysical niche. The highest values of aspen ANPP often did not correspond with the areas of highest aspen presence (Figure 4). The majority of aspen in the GYE occurs at radiation values between 66.4 and 73.2 W m^{-2} , but the highest ANPP values were in the lower tail of aspen's distribution, below 65.2 W m^{-2} (Figure 4). The majority of aspen occur in areas with annual potential evapotranspiration (PET) values between approximately 106 and 114 cm, but the highest ANPP values were at the lower tail of aspen's distribution (Figure 4). Aspen ANPP more closely corresponds with aspen presence along gradients of temperature and snowfall, however, the highest values of ANPP were still at the edges of aspen's distribution (Figure 4).

We also built a multiple regression model and compared the relationships between ANPP and biophysical variables. The variables selected by AIC_c in each predictor category were growing season precipitation, annual minimum temperature, percent clay in the soil, annual average daily solar radiation flux, elevation, and conifer biomass. Annual minimum temperature and annual average daily solar radiation flux were highly correlated (>0.80 correlation), as were annual minimum temperature and elevation; these correlated variables were not included together in the candidate models.

The selected model explained 37% of the variation in aspen ANPP ($F = 12.07$, $df = 101$, $p < 0.0001$) 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 5). 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 5). Aspen ANPP was the highest in areas with warmer temperature and higher ($>36 \text{ cm}$) growing season precipitation (Table 5). Conifer

biomass was negatively correlated with aspen ANPP, likely due to competitive influences on aspen growth rates (Figure 4, Table 5). This regression model for aspen ANPP across our field sites predicts high ANPP to be associated with warmer, wetter areas with lower conifer biomass and high levels of clay in the soil.

The biophysical niche of aspen presence was characterized by warm temperatures, high summer precipitation, and high light availability (Figure 3). Aspen ANPP is also highest at warm temperatures and high precipitation (Table 5), but aspen growth is not maximum within the biophysical niche of aspen presence. Although the peak of aspen distribution lies between 24 and 36 cm of growing season precipitation, the highest ANPP was found where precipitation exceeded 36 cm and where little aspen occurred (Figure 4). Aspen ANPP was more variable across aspen's distribution with respect to annual minimum temperature, but was still maximum at the upper tail of the distribution at temperatures above -3.75°C (Figure 4). Finally, 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 that had much higher ANPP (Figure 4).

Discussion

Biophysical niche of aspen presence and growth

Our results suggest that aspen occupies a much constricted realized niche relative to biophysically favorable settings in the GYE. In fact, applying our CART model to map predicted aspen distribution, aspen presence is predicted in 41.5% (3,276,602 ha) of the study area, whereas actual aspen presence is restricted to 1.4% (130 ha) of the study area (Figure 5). Additionally, aspen growth rate was lower in locations where it was most abundant, with the highest growth rates occurring at the edges of aspen's realized niche (Table 6). Aspen distribution was primarily limited by temperature, precipitation, and radiation. However, maximum growth rates were found at higher values of temperature and precipitation and lower values of radiation than where most aspen occur.

The realized niche of a species may be constricted from its fundamental niche by competi-

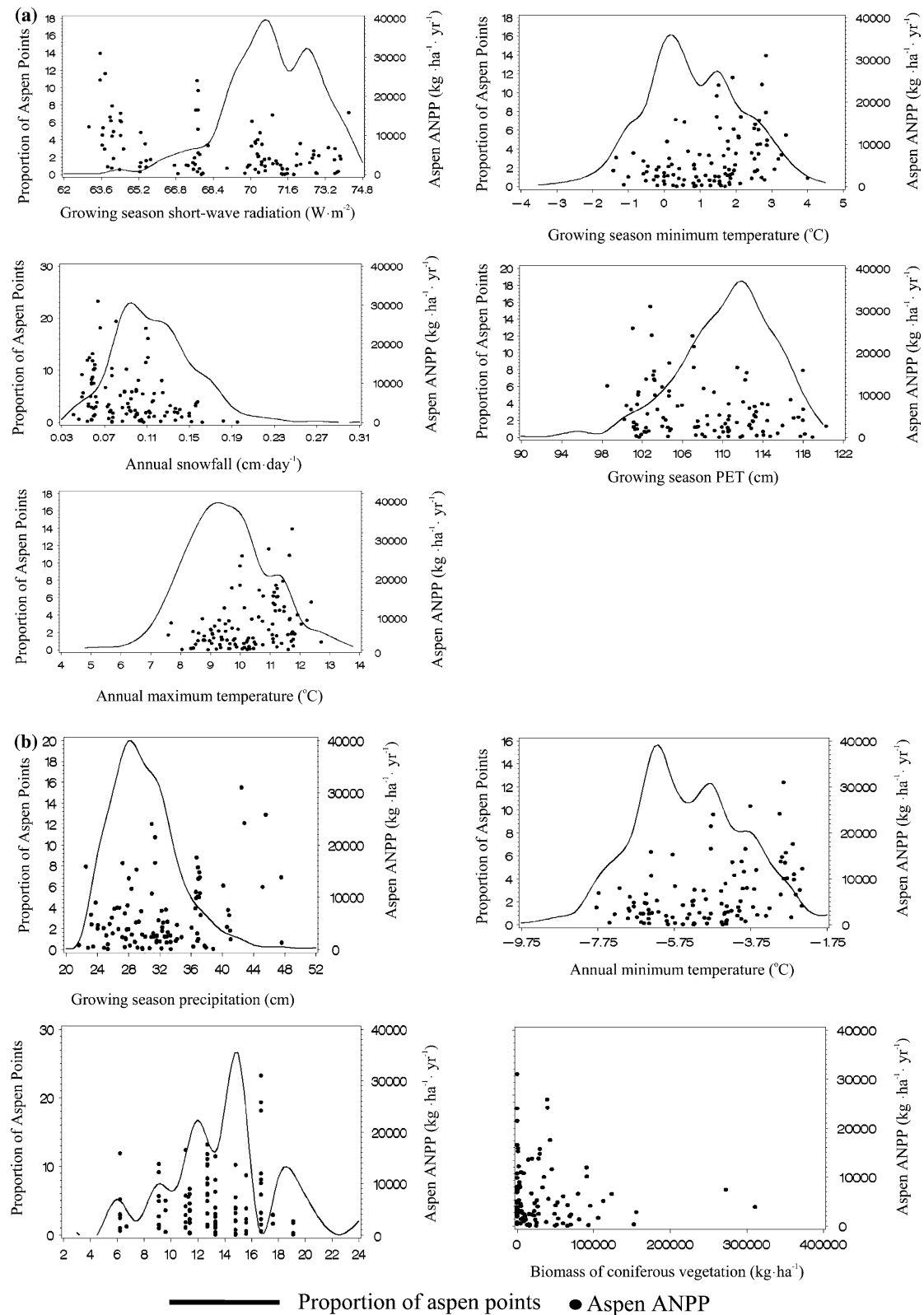


Figure 4. Graphs of aspen distribution and ANPP relative to the biophysical variables (a) selected through CART analysis as the best predictors of aspen presence and (b) the variables used in the selected regression model for aspen ANPP. These graphs show the distribution of aspen relative to each of these variables, shown as a smoothed histogram (left axis). Aspen ANPP (right axis) is shown as points overlain on the same gradient, except in the case of conifer biomass which was only available as a predictor of ANPP and not aspen presence.

Table 5. Results of regression relating aspen annual net primary productivity (ANPP) to biophysical variables. Model shown is the best overall model as selected using AIC_c. The coefficients and associated statistics shown are for variables standardized around mean = 0 and SD = 1. The variables were scaled in order to make the coefficient of each variable indicative of its influence in the regression equation. The 95% confidence limits show the lower confidence limit (LL) and upper confidence limit (UL) for each parameter estimate. See Table 1 for variable definitions.

Response	Variable	Parameter estimate	Standard error	t-Value	Pr > t	95% Confidence limits	
						LL	UL
Aspen ANPP	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

tion, dispersal capabilities or other biotic interactions such that a species may be excluded from areas where climate-based models predict it to be present (Austin et al. 1990). Along the eastern slope of the Colorado Rocky Mountains, for example, lodgepole pine limits aspen to the margins of its habitat along elevation and moisture gradients (Peet 1978). The reduced growth of aspen in much of its distribution might indicate a similar exclusion of aspen from the most biophysically favorable locations.

Aspen change in particular biophysical settings

Our regional assessment of aspen change revealed lower levels of aspen decline than might be expected from the published literature, with an average loss of 10% canopy cover overall. Localized aspen decline has been well documented in several studies in the Jackson Hole valley and the northern range of Yellowstone National Park and the adjacent forests (Loope and Gruell 1973; Bartos et al. 1994; Romme et al. 1995; Kay 1997; Hessl and Graumlich 2002). Wirth et al. (1996) estimated a 45% decline in pure aspen and mixed aspen/conifer forests 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). Approximately 4000 ha of aspen canopy coverage has been lost in Yellowstone National Park since the late 1800s (Despain 1990; Renkin and Despain 1996). Between 1958 and 1995, Larsen (2001) reported aspen

loss from 22.7 to 38.6%, as a proportion of 1958 canopy cover, in the elk winter range in and around Yellowstone National Park. With a median decline of only 10%, our results suggest a generally lower incidence of aspen loss across the entire GYE, but with more spatial variability indicating local areas of high aspen loss or even aspen gain.

Our small sample size of plots which gained aspen cover ($n = 16$) requires caution in interpreting the results, however, some general trends merit further investigation. Areas that gained aspen cover were characterized as generally moister during the growing season and warmer than areas which lost aspen cover (Table 4). Both annual precipitation and snowfall were lower in areas which gained aspen than areas that lost aspen (Table 4), possibly indicating that a milder winter environment is more favorable to aspen persistence. Areas of aspen loss were characterized as drier during the growing season, but with harsher winters than plots which gained aspen cover. These results suggest that a harsher winter environment in combination with a drier growing season environment and higher light levels may be detrimental to aspen persistence. These are the characteristics of sites that are expected to favor forest over grasslands and conifers over deciduous trees (Neilson et al. 1992).

Scope and limitations

Across large ecosystems, the impact of elk browsing on aspen dynamics is unclear. The lack of

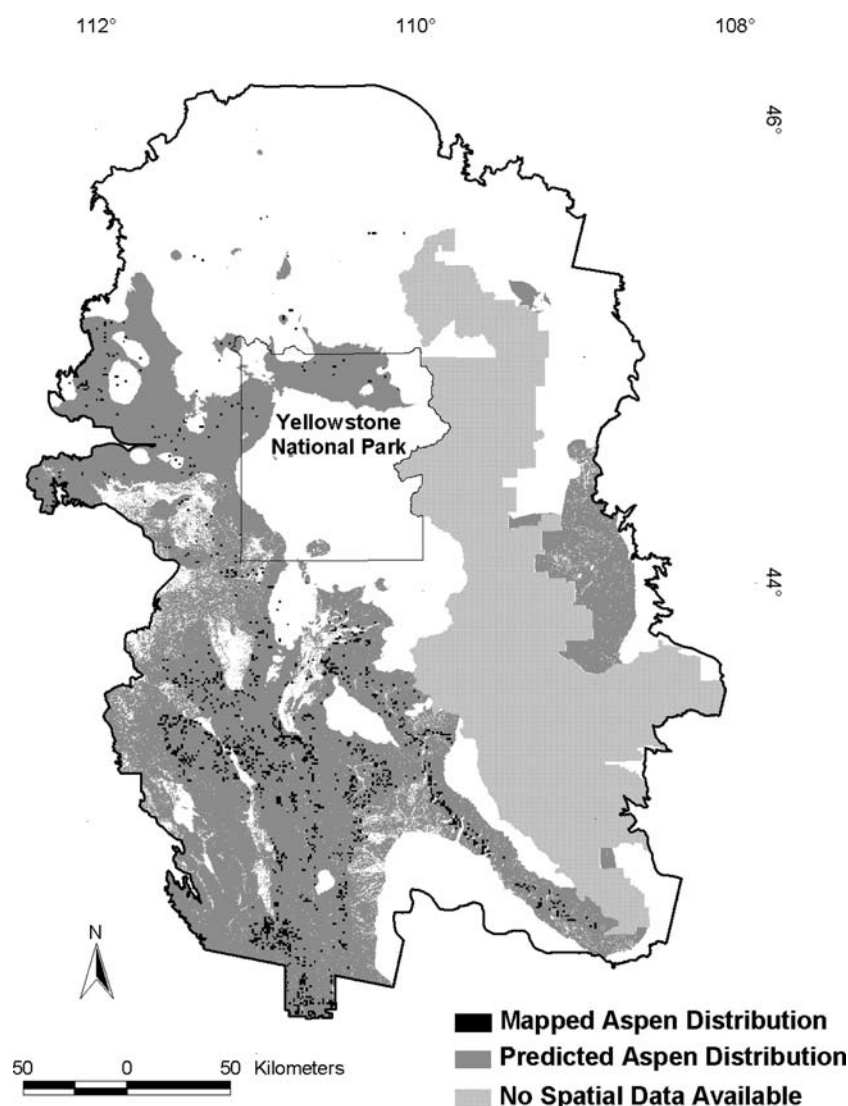


Figure 5. The predicted distribution of aspen, based on biophysical variables, is much greater than aspen's actual, current distribution in the GYE. Aspen is predicted to occupy 41.5% of the study area, whereas its current distribution is just 1.4% of the study area.

consistent spatial data on elk distributions across the entire GYE prevented us from addressing herbivory in this study. In both Yellowstone National Park and Rocky Mountain National Park, studies focused on areas with high elk densities have frequently linked herbivory with aspen decline. However, larger-scale studies in Colorado have refuted both the degree of decline and the influence of elk browsing (Suzuki et al. 1999; Kaye et al. 2003). Many previous studies in the GYE have centered around the Jackson Hole area or the northern elk winter range of Yellowstone National

Park (Kay 1993; Romme et al. 1995; Ripple and Larsen 2001; Hessel and Graumlich 2002), where the highest elk densities are found (Boyce 1989; Toman et al. 1997). In fact, Yellowstone's northern elk herd is the largest in the world, seconded only by the Jackson herd (Boyce 1989), suggesting that aspen dynamics in these areas may not be representative of the GYE as a whole. Although these smaller-scale studies indicate that elk likely influence aspen recruitment at local scales, the regional impact of herbivory across the GYE is largely unknown.

Table 6. Biophysical settings with the highest aspen presence generally had lower growth rates (ANPP) and were associated with loss of canopy cover. In biophysical settings where aspen presence was low, at the edges of its distribution, ANPP was higher and some areas exhibited gains in canopy cover.

Category	Variable	Presence	Growth	Conclusions on gradient from gain to loss	Overall conclusions
Precipitation	Ppt				
	gPpt	Highest at lower half of gPpt gradient	Fastest at upper half of gPpt gradient	Loss plots have less summer precipitation and more winter precipitation and snowfall	Presence is highest at medium snowfall and lower summer precipitation. Growth is fastest with lower snow and high summer precipitation. Loss plots are where growth is slowest
Temperature	Snowfall	Highest at mid to upper range of snowfall	Fastest at lowest levels of snowfall		
	Tmax	Highest at middle values	Fastest at upper values	Loss plots have a shorter growing season and are cooler	Presence is highest at moderate temperatures. Growth is faster at higher temperatures and loss is in cooler places
Light	Tmin	Highest at middle values	Fastest at upper values		
	gTmin	Highest at middle values	Fastest at higher values		
	gSrad_fg	More presence at higher light	Growth slowest at higher light	Loss plots have more light	Most present at high light but slow growth here and more loss of cover
	PAR				
Water flow	gPAR				
	Srad_fg				
	Srad				
	gSrad				
	gPET				
	PET	Highest at middle to upper levels	Fastest at lower levels of gPET	Loss plots are more arid and higher in evapotranspiration and runoff	Presence is highest in middle to higher levels of evapotranspiration, but growth is faster in less arid atmospheres. Loss is associated with higher evapotranspiration and runoff
	gAET				
	Psi				
	Outflow				
	gOutflow				
	gTrans				

We were unable to address the influence of fire history on aspen presence, due to the lack of spatially-explicit data on fire regimes across the entire GYE. However, past fire regimes may have contributed to the current distribution of aspen in the GYE. Fire maintains aspen stands by stimulating regeneration and limiting competition with conifer species (Loope and Gruell 1973; Jones and DeByle 1985). Conversely, some recent studies document aspen regeneration in the absence of fire (Manier and Laven 2002; Kulakowski et al. 2004), complicating our understanding of the effects of fire on aspen at large scales. Most aspen in the GYE grow in low to mid-elevation forests dominated by Douglas-fir, where fire return intervals ranged from 20 to 50 years (Barrett 1994; Bowermann et al. 1997; Littell 2002). In these areas, rapid increase in conifer cover over the past 100 years has been attributed to fire exclusion (Powell 2004). Since higher elevation lodgepole forests, like those found in much of Yellowstone National Park, experienced much longer fire return intervals of 100–250 years (Bowerman et al. 1997; Romme 1982), the effects of fire exclusion are not yet as apparent (Powell 2004). As spatial fire regime data become available, linking fire history and biophysical gradients will enhance our understanding of aspen changes at regional scales.

Since we were working with such a large study area and large datasets, it was logistically impossible to collect site-level information on our predictor variables. However, we used the best widely available digital data on vegetation, soils, climate and topography. Although DAYMET and WX-FIRE data are limited by the spatial distribution of the weather stations from which data are extrapolated, validation results show good accuracy (Thornton et al. 1997; Keane and Holsinger, 2006).

Conclusions

We found much lower levels of aspen decline than previous studies would suggest. This result supports recent landscape-scale work in Colorado showing that aspen stands were stable or even increasing (Suzuki et al. 1999; Manier and Laven 2002; Kaye et al. 2003; Kulakowski et al. 2004). Additionally, we found the highest growth rates at the edges of aspen's distribution in the GYE, which

were also the biophysical settings most likely to be gaining in aspen cover (Table 6). The biophysical settings where most aspen were found were also those with lower growth rates and more likely to be associated with loss of aspen cover (Table 6). In the GYE, aspen has a very narrow biophysical niche and maximum aspen growth is at the edges of that niche. As a result, most aspen occupy biophysical settings where aspen growth is not optimal, which are also areas where aspen are declining (Table 6).

Although aspen decline appears less widespread than expected at the scale of the GYE, our results lead to new questions. Why do most aspen occur in biophysical settings where aspen growth is reduced? Are aspen growing in these suboptimal conditions vulnerable to proposed mechanisms of aspen decline, such as fire exclusion or herbivory? How do fire, herbivory, and biophysical gradients interact to influence aspen dynamics at regional scales? Research into these questions, at regional scales, is needed to fully understand aspen dynamics across entire ecosystems. Finally, our results are specific to aspen dynamics within the GYE. Large-scale studies in multiple geographic areas are needed to determine the relative influence of biophysical setting, fire, competition, and herbivory on aspen dynamics.

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