Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem

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Abstract

Landscapes are often heterogeneous in abiotic factors such as topography, climate, and soil, yet little is known about how these factors may influence the spatial distribution of primary productivity. We report estimates of aboveground net primary productivity (ANPP) in 90 sample stands stratified by cover type and elevation class, and use the results to predict ANPP across a portion of the Greater Yellowstone Ecosystem. Tree ANPP was estimated by sampling tree density by species and diameter classes and estimating average annual diameter increment by tree coring. Biomass for current tree diameter and past tree diameter were calculated by species and diameter class for each stand using the dimension analysis software BIOPAK. Shrub ANPP was estimated by calculating current biomass from basal area using BIOPAK and dividing by the assumed average life span of the shrubs. Clipping at the end of the growing season was used to estimate herb ANPP. Differences in ANPP among cover types and elevation classes were examined with analysis of variance. Multiple regression was used to examine relationships between ANPP, and soil parent material, topography, and cover type. The best regression model was used to predict ANPP across the study area.

We found ANPP was highest in cottonwood, Douglas-fir, and aspen stands, intermediate in various seral stages of lodgepole pine, and lowest in grassland and sagebrush cover types. Parent material explained significant variation in ANPP in mature and old-growth lodgepole pine stands, with rhyolite ash/loess being the most productive parent material type. ANPP decreased with increasing elevation in most cover types, possibly because low temperatures limit plant growth at higher elevations in the study area. ANPP was not related to elevation in mature and old-growth lodgepole pine stands, due to relatively rapid growth of subalpine fir at higher elevations.

A regression model based on cover type and elevation explained 89% of the variation in ANPP among the sample stands. This model was used to generate a spatially continuous surface of predicted ANPP across the study area. The frequency distribution of predicted ANPP was skewed towards lower levels of ANPP, and only 6.3% of the study area had a predicted ANPP level exceeding 4500 kg/ha/yr. Patches high in predicted ANPP were primarily at lower elevations, outside of Yellowstone National Park, and near the national forest/private lands boundary. These patterns of ANPP may influence fire behavior, vertebrate population dynamics, and other ecological processes. The results reinforce the need for coordinated management across ownership boundaries in the Greater Yellowstone Ecosystem.

Introduction

Net primary productivity (NPP) is an important process in ecosystems that influences nutrient cycling, food web structure, disturbance regimes, species abundances, community structure, and other ecosystem functions (Whittaker 1975; Perry 1994). While a great deal has been learned about NPP levels and controlling factors within and between ecosystems (e.g., Bormann et al. 1970; Crow 1978; Graumlich et al. 1989), relatively few studies have quantified spatial variation in NPP across landscapes. Knowledge of spatial patterns in NPP may enrich our understanding of the role of NPP in driving ecosystem and landscape function.

NPP is a product of complex interactions among abiotic factors, green plants, and other members of the biotic community. To the extent that driving factors of NPP such as soil, climate, disturbance, and herbivory vary across a landscape, we can expect NPP to vary. Elevation, for example, often represents complex gradients in climate, soils, and topography (Whittaker 1975). Several authors have found that NPP varied across elevation gradients in association with temperature, precipitation, vapor pressure deficit, topographic position, and fire history (Whittaker and Niering 1975; Law and Waring 1994; Singh et al. 1994; Keane et al. 1996; Raich et al. 1997). Similarly, local and regional spatial patterns in NPP have been correlated with climatic, topographic, soil, and land use factors (Burke et al. 1991; Knapp et al. 1993; White and Running 1994; Turner et al. 1997; Burke et al. 1997).

The spatial patterning of NPP across a landscape may have particularly strong consequences for ecological processes and organisms whose dynamics depend upon flows over a landscape. The spread of fire, for example, is a function of ignition, weather conditions, and fuel distribution (Turner and Romme 1993). In landscapes where NPP creates abundant fuels that are well connected, fire size may be relatively large and burning events in phase across the landscape (Baker 1992). Similarly, the population dynamics of some organisms may depend upon the spatial patterning of NPP. If patches high in NPP confer high resource availability to individuals in a population, then organism survival and reproduction may be especially high in these patches and allow them to serve as population source areas (Pulliam 1988; Pulliam and Danielson 1991). Such source areas may be critical for maintaining regional populations.

The Northern Rocky Mountains in the United States are characterized by high levels of spatial variability in topography, climate, and soils. We speculate that these abiotic factors cause NPP to vary considerably over the landscape, but in ways predictable based on knowledge of the controlling factors. We have estimated spatial patterns of aboveground NPP (ANPP) in a portion of the Greater Yellowstone Ecosystem as part of a study to understand controls on species population dynamics and community diversity. In this paper, we report estimates of mean and variance in ANPP across cover types and elevation classes, analyze relationships between predictor variables (soil, topography, and cover type) and ANPP, and extrapolate levels of ANPP across the study area. The spatial patterns of ANPP are then analyzed by elevation and ownership class.

Methods

Study area

The 9500 km^2 study area includes the upper Gallatin, Madison, and Henry's Fork watersheds in Montana, Idaho, and Wyoming, USA (Figure 1). These rivers originate on a plateau in Yellowstone National Park (YNP), pass through the Gallatin and Targhee National Forests, and flow into privately-owned agricultural floodplains in the lowlands. Climate severity increases with elevation in the study area. Mean annual temperature and growing-degree days vary from 5.8 °C and 2787 days below 1500 m to 0.26 °C and 1356 days above 2400 m. Much of the precipitation falls as snow. Average snowmelt date is May 1 at 1500 m and July 1 at 2400 m.

Parent rock of the study area includes Paleozoic and Mesozoic limestones, sandstones, and shales (Rodman et al. 1996). Volcanic activity in the Eocene buried the region in thick deposits of andesite lava. Quaternary age rhyolite flows and rhyolitic ash deposits are common in YNP. Currently, rhyolite and rhyolite-ash soils cover the southern portion of the study area on the Yellowstone Plateau and in the Targhee National Forest. At lower elevations in the Targhee National Forest, this ash is overlain by loess deposits originating in the Snake River Plains (Bowerman et al. 1997). Andesite-based soils are abundant in the northern portion of the study area, especially in the mountains of the Gallatin National Forest (Davis and Shovic 1996). Sandstones and shales also occur in the Gallatin National Forest and are exposed in landslide areas. Glacial outwash and alluvium soils occur in floodplains.

Vegetation of the study area is a mosaic of forests, shrublands, and grasslands. Upland rhyolite soils support lodgepole pine (*Pinus contorta*) forests between 2000 and 2600 m (Despain 1990). Douglas-fir (*Pseudotsuga menziesii*) is common up to 2300 m on andesite soils and in warmer microclimates. Above these elevations on both soil types, subalpine fir(*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) dominate. Sagebrush shrublands occur on dry, fine-textured soils from low to mid elevations. Grasslands exist on fine-textured soils from valley bottoms up to mid slopes.

Figure 1. Map of the Greater Yellowstone Ecosystem with the Study area denoted by the hatched pattern.

Aspen (*Populus tremuloides*) is distributed in relatively small patches, primarily on moist toeslopes or on fractured rocks. Larger floodplains are dominated by black cottonwood (*Populus trichocarpa*) and narrowleaf cottonwood (*P. angustifolia*).

Both fire and logging are common disturbances in the study area. The Yellowstone fires of 1988 burned sections of lodgepole pine and grassland in the southern portion of the study area. The Targhee National Forest conducted an extensive logging program in 1960s and 1970s. Approximately 54% of the Targhee lands within the study area were clearcut under a staggered-setting design. Much of the Gallatin National Forest has checkerboard landscape ownership, with private individuals owning alternate sections. Varying amounts of the private and Forest Service lands within the Gallatin National Forest boundaries have been logged.

Lowland valleys in the study area are mostly under private ownership. Agriculture, range, rural residential development, and urban are common land use types in these private lands.

Study design

Field data were collected in 90 samples that were stratified by cover type, seral stage, and elevation class (Table 1). Cover types included aspen, cottonwood, Douglas-fir, grassland, lodgepole pine, and sagebrush. These compose the major cover types of the study area below the alpine zone. Three seral stages of lodgepole pine were studied: seedling/sapling stands created by the 1988 fires (lodgepole pine-burned), seedling/sapling created by clearcutting between 1970 and 1990 (lodgepole pine-clearcut), and mature and old-growth (lodgepole pine-MOG). The number of replicates varied by cover type and elevation class as determined by their distribution over the landscape and by the experimental design of our biodiversity study. Sample locations were widely spaced to maximize the range of topographic, climatic, and soil settings. However, samples were constrained to be within 1.5 km of a road to allow access.

Within each replicate we estimated biomass and growth rate for the herbaceous plants, shrubs, and trees. These measurements were made at six points within each sample location. The six points were spaced ≥ 200 m apart and all points were placed >125 m from the outer perimeter of the vegetation unit of interest. The scheme used to sample vegetation at each point is depicted in Figure 2 and the variables
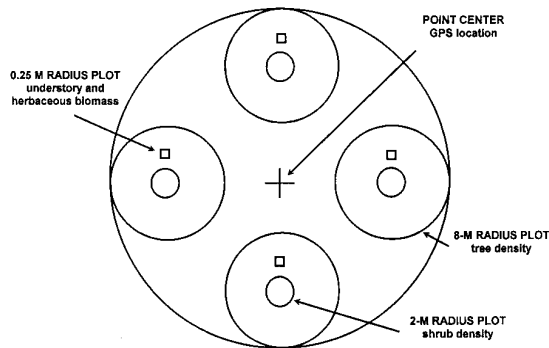

Figure 2. Scheme for sampling vegetation at each of the six sampling points within study stands. See Table 2 for a description of the variables measured in this study.

measured are described in Table 2. Shrubs and trees were sampled in each stand either in 1995 or 1996. Herbaceous plants were sampled in all stands in 1997.

Aboveground net primary production

Trees

Our approach was to first derive average annual diameter increment and tree density per tree size class and species for each stand. Tree diameter at breast height (dbh) one year earlier was estimated for each tree size/species class based on average annual diameter increment. Aboveground biomass was then calculated for previous dbh and current dbh using the biomass software package BIOPAK (Means et al. 1994). ANPP was calculated as the difference between previous and current biomass multiplied times the density of trees in this size class.

Diameter increment data were collected for the dominant tree species in each cover type. Data for the 5-, 10-, and 20-year diameter increments were divided by 5, 10, or 20, respectively, to derive average annual increment for each tree sampled. Mean and variance in average annual increment were then estimated per size/species class for each stand. The current dbh of trees was assumed to be the midrange of the dbh class (the dbh of the >90 cm dbh class was assumed to be 100 cm). Tree dbh from one year ago was estimated by subtracting two mean annual increments from current dbh.

Aboveground biomass for current dbh and previous dbh was estimated using BIOPAK (Means et al. 1994). This program calculates the biomass of plant components based on allometric equations derived from field studies. The calibration data are primarily

Table 1. Number of stands sampled in each stratum of cover type and elevation. MOG refers to the mature and old-growth seral stage.

Cover Type	Dominant species	Elevation class (m)		
		<2200	2200–2400	>2400
Aspen	Quaking Aspen (*Populus tremuloides*)	6		
Cottonwood	Black Cottonwood (*Populus trichocarpa*)			
	Narrowleaf Cottonwood (*P. angustifolia*)	6		
Douglas-fir	Douglas Fir (*Pseudotsuga menziesii*)	6		
Grassland	Idaho fescue (*Festuca idahoensis*)			
	bearded wheatgrass (*Agropyron caninum*)			
	Bluebunch wheatgrass (*A. spicatum*)	6	5	
Lodgepole pine-burned	Lodgepole pine (*Pinus contorta*)		7	7
Lodgepole pine-clearcut	Lodgepole pine (*Pinus contorta*)			
	Engelmann spruce (*Picea engelmannii*)			
	Limber pine (*Pinus flexilis*)			
	Subalpine fir(*Abies lasiocarpa*)			
	Whitebark pine (*Pinus albicaulis*)	8	7	7
Lodgepole pine-MOG	Lodgepole pine (*Pinus contorta*)			
	Engelmann spruce (*Picea engelmannii*)			
	Limber pine (*Pinus flexilis*)			
	Subalpine fir(*Abies lasiocarpa*)			
	Whitebark pine (*Pinus albicaulis*)	7	7	7
Sagebrush	Big sagebrush (*Artemisia tridentata*)			
	Idaho fescue (*Festuca idahoensis*)			
	Rocky Mountain Juniper (*Juniperous scopulorum*)	4		

Table 2. Vegetation variables measured at each stand.

Attribute	Description and collection method
Location	Global Positioning System location
Three 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.
Radial growth	20-year diameter increment determined by measuring length (mm) from outside edge of most recent summerwood to outside edge of twenty-first summerwood ring on a core extracted from breast height. Either 5-year or 10-year diameter increment was recorded for younger trees. Cores were measured in the field when annual rings were readily visible. If rings were not distinguishable, the core was sanded in the laboratory and rings counted with a dissecting scope. Measurements were regularly distributed among the six sample points where possible. For less common species and size classes, samples were taken for any trees within the stand that met the sample criteria.
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.
Shrub density	Density of shrubs (>=0.5 cm dbh) by species by basal diameter classes (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 centers at the 4 cardinal directions.
Herbaceous biomass	All nonwoody plants were clipped at ground level in the 0.25 m² plots located 5 m N of each 8-m radius plot. Clipping was done just after the peak of the growing season in 1997. Samples were dried and weighed (g).

from studies in the Pacific Northwest and the Northern Rockies. Whenever available, we selected BIOPAK equations derived from data from the Rocky Mountains. Some of the common species in our study area were not included in BIOPAK. Thus, we used equations for red alder (*Alnus rubra*) to calculate biomass for thinleaved alder (*Alnus incana*), whitebark pine for limber pine (*Pinus flexilis*), and black cottonwood for narrowleaf cottonwood.

Most biomass equations for trees in BIOPAK are based on tree dbh. However, height is also a parameter in some equations for trees. Thus, we needed to derive height estimates for the midrange dbh of each dbh class for trees from the estimated dbh for one year earlier. We did this by first quantifying the relationship between measured dbh and measured height for eight tree species using a negative exponential function. Sample sizes ranged from 75–235 for seven of the species, sample size for common chokecherry (*Prunus virginiana*) was 27. These functions accounted for 92–95% of the variation in the calibration data, depending upon species. The functions were then used to estimate the heights for trees in the mid-range of each dbh class and for estimated dbh for trees one year earlier.

Current biomass and biomass one year ago were then calculated for each dbh size class and species class per stand using BIOPAK. Two biomass variables were generated: foliage biomass and aboveground-wood biomass. These were summed to represent total aboveground biomass. Annual change in aboveground biomass per species/size class was estimated by subtracting the biomass estimates from the previous year from those from the current year. The estimates were multiplied times the tree density in each size/species class for each stand to derive ANPP for each class and summed across classes.

Diameter increment data were not collected for some of the tree species that were subordinate in a cover type. We substituted biomass estimates for species that were sampled for similar species that were not sampled as follows: thinleaved alder estimates were used for mountain alder (*Alnus viridis*), rocky mountain maple (*Acer glabrum*), water birch (*Betula occidentalis*), and willow; quaking aspen estimates were used for red dogwood (*Cornus stolonifera*), black hawthorn (*Crataegus douglasii*), and Russian olive (*Elaeagnus angustifolia*); and lodgepole pine estimates were used for Utah juniper (*Juniperous osteosperma*) and rocky mountain juniper (*J. scopulorum*). These species comprised a small percentage of

total biomass, so any errors in ANPP associated with these substitutions were relatively small.

ANPP estimates were aggregated into conifer and deciduous classes. ANPP of foliage for deciduous trees was assumed to be the total biomass of foliage for the current year. For conifers, current foliage biomass was divided by five, the assumed average life span in years of conifer needles. Total annual tree ANPP was calculated by summing annual foliage NPP and annual aboveground NPP for wood.

Shrubs

Included in the shrub class were shrubs of all sizes and tree seedlings (dbh <2 cm). As was the case for trees, foliage and aboveground wood biomass was estimated by species for the midrange of the basal diameter class (the midrange of the >10-cm class was assigned to be 10.5 cm).

Substitute equations were used as follows for shrub species not included in BIOPAK: Douglas-fir was used for subalpine fir, Englemann spruce, whitebark pine, lodgepole pine and limber pine; common juniper was used for Utah juniper and Rocky Mountain juniper; Sitka alder (*Alnus sinuata*) was used for thinleaved alder and water birch; service berry (*Amelanchier alnifolia*) was used for black hawthorn, Russian olive, black cottonwood, narrowleaf cottonwood, and quaking aspen; cascade hollygrape (*Berberis nervosa*) was used for creeping hollygrape (*Berberis repens*); *Ribes* spp. was used for golden current (*R. aureum*), swamp gooseberry (*R. lacustre*), and sticky current (*R. viscosissimum*); common snowberry (*Symphoricarpos albus*) was used for buckbrush (*S. occidentalis*), and blue huckleberry (*Vaccinium globulare*) was used for oval-leaved huckleberry(*V. ovalifolium*).

The time over which shrubs accumulated biomass was not well known. We divided aboveground biomass of deciduous shrubs and wood biomass of coniferous shrubs ≥2 cm dbh by eight, under the assumption that eight years was the average age of these shrubs. This assumption was based on limited sampling of annual rings in deciduous shrubs. Foliage of conifers ≥ 2 cm was divided by five. Coniferous shrubs <2 cm (primarily tree seedlings) were divided by three years. All sagebrush plants were tallied as shrubs, even though many stems were ≥2 cm dbh. As many of these stems were relatively large and sagebrush is slow-growing, we assumed the average age of these shrubs was 16 years.

Herbaceous vegetation

The dry weight of herbaceous material clipped at the end of the growing season in 1997 was assumed to represent ANPP of herbaceous plants. ANPP of herbs, shrubs, and trees was summed to estimate total ANPP.

Assumptions

Resources did not allow us to measure all factors relevant to estimating ANPP. Hence, we made the following assumptions:

1. Losses of ANPP to mortality or herbivory represented a relatively small proportion of total ANPP in our study area.
2. The average times over which shrubs and conifer leaves accumulated biomass were as stated above.
3. The results were not biased by using a biomass equation for a species that is modeled in BIOPAK for a species tallied in the study area but not modeled in BIOPAK.

Statistical analyses

We considered stands as independent units of analysis in this study. Hence, we averaged the data across the six sample points within each stand. Stem density was expressed as number/ha, biomass as kg/ha, and ANPP as kg/ha/yr.

Differences in average annual increment among cover types and among elevation classes were examined with analysis of variance and multiple range tests (Fisher's LSD, SAS 1991). Differences in ANPP among cover and elevation classes were assessed with two-way analysis of variance. The distribution of the data and variance of the residuals were assessed following Sabin and Stafford (1990). The residuals did not deviate substantially from being normally distributed with constant variance. Thus, no data transformations were used.

Multiple regression was used to assess the relationship between ANPP and various abiotic and biotic factors. Predictor variables included cover type, elevation, aspect, slope, specific catchment area, parent-material class, mean snow-melt date. Cover types over most of the study area were derived from classification of a 1991 Landsat Thematic Mapper image using the methods of Ma and Redmond (1995). A validation exercise using independent data from aerial photographs revealed an overall classification accuracy of 75%. Cover type accuracies were: Aspen – 65%, Douglas-fir – 74%, Grassland/Sagebrush – 60%, Lodgepole pine-Burned – 97%, Lodgepole pine-Seedling/sapling

– 71%, Lodgepole pine-MOG – 87% (Hansen et al. in prep.).

The Landsat scene used did not include a small area in the northern portion of the study area. Thus, we supplemented this vegetation map with data from the Gallatin National Forest and the USDA Natural Resource and Conservation Service (NRCS). Both agencies mapped vegetation based on aerial photograph interpretation. Photos used by the Gallatin National Forest were from 1981 and those used by the NRCS were from the mid- to late-1980s. Accuracy assessments were not done on either of these data sets.

Elevation, slope, and aspect data where derived from USGS 100-m digital elevation models. Specific catchment area for each stand replicate was calculated by applying the ARC/INFO 'WATERSHED' function (ESRI 1982–1997) to flow directions derived from the 3-arc second digital elevation model (U.S. Geological Survey 1993).

Soils were grouped into six classes that integrated consideration of parent material, soil type, and soil texture (Table 3). These classes were developed in consultation with soil scientists from the Gallatin and Targhee National Forest and the NRCS. The global positioning system location of the six sample points in each stand were overlaid on soil survey maps (Rodman et al. 1996; Davis and Shovic 1997; Bowerman et al. 1997) and each stand was placed into one of the seven parent-material classes.

The extent of correlation among the predictor variables was assessed and closely correlated variables were omitted. Next, several biologically-meaningful candidate models were analyzed and compared. Models with the highest Akaike Information Criterion (AIC) values (Akaike 1973; Burnham and Anderson 1992) were considered 'best' models in accounting for variation in ANPP and evaluated for model fit and coefficient of determination.

The best regression equation was used to predict ANPP in each cell across the study area using the 30-m cover type data layer and the 100-m elevation data layer. Predicted ANPP was mapped in four classes over the study area to provide a visual representation of the distribution of this variable. Spatial attributes of each class were quantified with the landscape metrics package FRAGSTATS (McGarrigal and Marks 1994). A 100-m edge width was used to calculate core area. These analyses were stratified by ownership and elevation classes. Standard error of each predicted value of ANPP was quantified using the CLM option with Proc Reg in SAS (1991). Standard error was then divided by

Table 3. Parent material classes used in this study.

Class name	Parent material	Texture
Hard crystalline	Glacially derived or weathered granitic rock	Medium to coarse
Shale/sandstone	Glacially derived or weathered shales and sandstones	Fine to medium
Outwash and dry alluvium	Deep outwash deposits of multiple parent materials	Medium to coarse
Wet alluvium	Continuously or seasonally inundated alluvial deposits	Medium
Rhyolite	Glacially derived or weathered rhyolite	Medium to coarse
Rhyolite ash/loess	Glacially derived or weathered rhyolite with volcanic ash and loess	Fine to medium

predicted ANPP to estimate coefficient of variation in the prediction. These estimates of coefficient of variation were mapped over the study area to represent the spatial distribution of confidence in the regression predictions. Statistical results were considered significant at the P<0.05 level.

Results

ANPP across samples

ANPP was significantly related to cover type and elevation class (df = 8,84, F = 10.64, P < 0.0001), with cover type accounting for 76% of the explained variation. Among the cover types in the lowest elevation class, cottonwood, Douglas-fir, and aspen had the highest ANPP, exceeding 4400 kg/ha/yr (Table 4). These cover types were significantly higher in ANPP than lodgepole pine-clearcut and grassland, which had ANPP values of less than 2600 kg/ha/yr (df=33, LSD=1795, P=0.05). Lodgepole pine-MOG was intermediate in ANPP, not differing significantly from aspen or lodgepole pine-clearcut.

The relationship of ANPP and elevation differed among cover types. Within cover types, mean ANPP was generally greatest in the lowest elevation class (Table 4). This difference was significant, however, only for lodgepole pine-burn (df = 1,12, F = 5.61, P < 0.035). Mean ANPP in lodgepole pine-MOG was similar in the highest and lowest elevation classes (Table 4).

Within lodgepole pine cover types, ANPP did not differ significantly among several stages in either low or medium elevation classes. At the highest elevation class, MOG was higher than clearcut or burn (df = 2, 18, F = 18.45, P < 0.0001).

The proportion of ANPP comprised by herbs, shrubs, and trees varied among cover types (Table 4).

Herbaceous vegetation dominated ANPP in grassland, while trees comprised the majority of ANPP in Douglas-fir and lodgepole pine-MOG. Herbs and small conifer trees were well represented in lodgepole pine-clearcut and lodgepole pine-burn. Sagebrush and herbs made up all of the ANPP in the sagebrush cover type. ANPP was most evenly distributed among herbs, shrubs and trees in aspen and cottonwood.

Tree diameter increment

Under our methods, tree ANPP was a function of average annual tree diameter increment and tree density by dbh class. Within closed-canopy stands in the lowest elevation class, cottonwood trees had significantly higher average annual tree diameter increment (termed increment) than other species across all dbh classes (Table 5). Douglas-fir was generally lower in increment than aspen and the conifer species in lodgepole pine-MOG, though the strength of this difference varied with dbh class.

Within lodgepole pine-MOG, increment was significantly higher for lodgepole pine in the lowest elevation class relative to the other two elevation classes. However, this was not the case for subalpine fir, limber pine, whitebark pine, or Englemann spruce. Subalpine fir had significantly higher increment than lodgepole pine in the highest elevation class. However, increment did not differ significantly between these two species in the lowest elevation class.

Lodgepole pine saplings grew very fast in the lodgepole pine-clearcut cover type. Mean increment for this species in the lowest elevation class of lodgepole pine-clearcut was nearly twice that for cottonwood. Increment was significantly higher in seedling/sapling lodgepole stands created by clearcutting than in those resulting from fire. Across elevation classes within these open-canopy stands, increment was significantly higher in lower elevation classes

Table 4. Mean and standard deviation (in parentheses) of ANPP across cover types and elevation classes. Cover type abbreviations are: AS-aspen, LP-BU-lodgepole pine-burned, CW-cottonwood, DF-Douglas-fir, HE-grassland, LP-CC-lodgepole pine-clearcut, LP-MOG-lodgepole pine-mature and old growth, SA-sagebrush. Elevation classes are: $1 = < 2200$ m, $2 = 2200$–2400 m, $3 => 2400$ m.

Cover type	Elev. class	ANPP (kg/ha/yr)			
		Herbs	Shrubs	Trees	Total
AS	1	1219	1375	1820	4413
		(143)	(478)	(244)	(572)
LP-BU	3	181	470	69	720
		(30)	(136)	(62)	(184)
LP-BU	2	228	2359	19	2606
		(32)	(781)	(12)	(774)
CW	1	756	2397	2355	5508
		(153)	(682)	(360)	(848)
DF	1	245	1494	3488	5228
		(64)	(537)	(924)	(923)
HE	2	1456	118	0	1574
		(352)	(70)		(373)
HE	1	2002	74	0	2077
		(212)	(64)		(234)
LP-CC	3	329	172	927	1428
		(65.7)	(48)	(415)	(367)
LP-CC	2	668	237	627	1532
		(39)	(43)	(209)	(229)
LP-CC	1	1009	513	1036	2558
		(95)	(122)	(731)	(698)
LP-MOG	3	165	827	2101	3093
		(55)	(122)	(167)	(270)
LP-MOG	2	236	531	1422	2188
		(107)	(129)	(319)	(450)
LP-MOG	1	331	517	2117	2964
		(122)	(81)	(201)	(248)
SA	3	911	979	0	1890
		(174)	(330)		(397)

for lodgepole pine in lodgepole pine-clearcut (all dbh classes) and in lodgepole pine-burn for dbh class 3. However, means did not differ with elevation class for subalpine fir in lodgepole pine-clearcut or for lodgepole pine dbh classes 1 and 2 in lodgepole pine-burn.

Tree and shrub density

The high ANPP of cottonwood and aspen was largely a product of relatively high tree increment (see above), and high tree and shrub densities. Douglas-fir was relatively high in ANPP in spite of moderate to low increment, due to the high density of larger trees and high shrub densities. Among the open-canopy lodgepole-pine cover types, ANPP was not higher in clearcuts than in burns despite increment being higher in clearcuts. This is largely due to the high density

of tree seedlings (basal diameter classes 1 and 2) in the burns. Among all three lodgepole pine cover types tree density was generally higher and shrub density lower at higher elevations. The greater tree density at higher elevations probably reflects higher tree species richness there. Subalpine fir, Englemann spruce, and whitebark pine were abundant in the highest elevation class but present at very low densities at the lowest elevation class.

Predictors of ANPP

None of the potential predictor variables were found to be highly correlated, and all were considered in the analyses. Among the potential predictor variables, aspect and specific catchment area were found not to be significantly related to ANPP (Table 6). Cover

Table 5. Results of statistical comparisons of average annual increment. Elevation classes 1–3 are low, medium, and high, respectively. Cover type and elevation class abbreviations are defined in Table 4.

Comparison	DBH class	N	F-value	Pr.>F	R^2	Multiple Range Test
LP-BU vs LP-C	1	113	151	0.0001.	0.57	LP-CC[a] LP-BU[b]
Elev. Classes 2-3, PINCON	2	108	123	0.0001	0.53	LP-CC[a]LP-BU[b]
LP-BU across	1	37		NS		Elev. 1[a] Elev. 2[a]
Elev. Classes 2-3,	2	41		NS		Elev. 1[a] Elev. 2[a]
PINCON	3	41	14	0.0006	0.26	Elev. 1[a] Elev.2[b]
LP-CC across	1	116	8.6	0.0003	0.13	Elev. 1[a] Elev. 2[a] Elev. 3[b]
Elev. Classes 1-3, PINCON	2	108	5.3	0.006	0.09	Elev. 1[a] Elev.2[a] Elev. 3[b]
LP-CC across Elev.	1	52		NS		Elev. 1[a] Elev. 2[a] Elev. 3[a]
Classes 2-3, ABILAS	2	52		NS		Elev. 1[a] Elev. 2[a] Elev.3[a]
AS, CW, DF, LP-MOG	1	193	15.8	0.0001	0.20	CW[a] AS[b] LP-MOG [bc] DF[c]
in Elev. Class 1,	2	185	10.8	0.0001	0.15	CW[a] AS[b] LP-MOG [b] DF[b]
Dominant Species in	3	172	20.7	0.0001	0.27	CW[a] AS[b] LP-MOG [bc] DF[c]
Each Cover Type	4	151	20.1	0.0001	0.29	CW[a] LP-MOG[b] AS[c] DF[c]
	5	96	5.1	0.008	0.10	CW[a] DF[b] AS[b]
	6	65	28.0	0.0001	0.31	CW[a] DF[b]
	7	30		NS		CW[a] DF[a]
LP-MOG by Elev.	1	141	7.6	0.0008	0.10	Elev. 1[a] Elev. 2[b] Elev.3[b]
Classes 1-3, PINCON	2	185	10.8	0.0001	0.15	Elev. 1[a] Elev. 2[b] Elev. 3[b]
	3	172	20.7	0.0001	0.27	Elev. 1[a] Elev. 2[b] Elev. 3[b]
	4	104	31.3	0.0001	0.38	Elev. 1[a] Elev. 2[b] Elev. 3[b]
	5	39		NS		Elev. 2[a] Elev. 3[a]
LP-MOG by Elev.	1	77		NS		Elev.1[a] Elev. 2[b] Elev. 3[b]
Classes 1-3, ABILAS	2	70		NS		Elev. 1[a] Elev. 2[a] Elev.3[a]
	3	44		NS		Elev. 1[a] Elev. 2[a] Elev.3[a]
	4	44		NS		Elev. 1[a] Elev. 2[a] Elev.3[a]
	5	22		NS		Elev. 1[a] Elev. 2[a] Elev.3[a]
LP-MOG, PINCON:	1	78		NS		ABILAS[a] PINCON[a]
Elev. Class 1 vs	2	83		NS		ABILAS[a] PINCON[a]
ABILAS Elev. Class 3	3	76		NS		ABILAS[a] PINCON[a]
	4	64	9.95	0.003	0.13	ABILAS[a] PINCON[b]
LP-MOG, PINCON vs	1	83		NS		ABILAS[a] PINCON[a]
ABILAS, Elev. Class 3	2	88	14.4	0.0003	0.14	ABILAS[a] PINCON[b]
	3	81	5.5	0.02	0.06	ABILAS[a] PINCON[b]
	4	77	6.6	0.01	0.08	ABILAS[a] PINCON[b]
	5	41	12.2	0.001	0.23	ABILAS[a]PINCON[b]

Lodgepole Pine-Burn

ANPP (Thousands of kg/ha/yr)

Soil Type

Lodgepole Pine-Clearcut

ANPP (Thousands of kg/ha/yr)
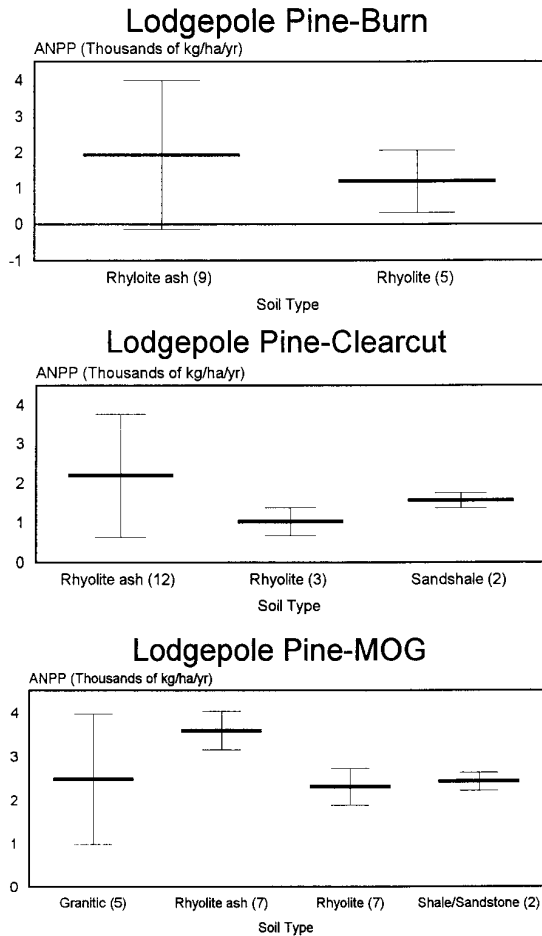

Soil Type

Lodgepole Pine-MOG

ANPP (Thousands of kg/ha/yr)

Soil Type

Figure 3. Mean (± one standard deviation) of ANPP across parent material types for the three lodgepole-pine cover types.

Area (thousands of ha)

Predicted ANPP (kg/ha/yr)

Figure 4. Frequency distribution of predicted ANPP (kg/ha/yr) across the study area. Column labels are mid ranges.

and not significantly different from, rhyolite ash/loess and rhyolite.

Spatial distribution of ANPP

We used the best model (Table 6) to predict ANPP for each 30-m cell across the study area. The distribution of predicted ANPP approximated a leptokurtic normal distribution with a high number of values in the range of 2400–3000 kg/ha/yr and a skew towards higher levels of ANPP (Figure 4). Predicted ANPP levels were relatively low over most of the study area, with 84.0% of the classified area having predicted ANPP below 3000 kg/ha/yr (Figure 5). Only 6.3% of the classified area had predicted ANPP above 4500 kg/ha/yr. These areas of higher predicted ANPP occurred primarily in cottonwood, aspen, and Douglas-fir cover types. The highest predicted ANPP class had a relatively small mean patch size, substantially lower core area (100-m edge width), and larger mean nearest neighbor distance than the other predicted ANPP classes (Table 10). This highest predicted ANPP class was concentrated at lower elevations, with 91.2% of this class occurring below 2000 m elevation. The majority of this highest class was on private lands (51.7%), and the majority of the high ANPP patches on public lands were near the boundary with private lands (Figure 5).

The coefficients of variation of predicted ANPP were below 0.25 over most of the study area, including most of the aspen, cottonwood, and Douglas-fir cells that were highest in predicted ANPP (Figure 6). Coefficient of variation was very high (>1.0) only in grassland cells.

type, elevation and parent-material class each individually explained significant variation in ANPP. The best model, based on cover type and the interaction between cover type and elevation, explained 89% of the variation in estimated ANPP.

The significant relationship between parent material and ANPP was partially due to higher growth rates of vegetation on rhyolite ash/loess among the lodgepole-pine cover types. Mean ANPP on rhyolite ash/loess was greater than that on rhyolite or shale/sandstone in lodgepole pine-burned and lodgepole pine-clearcut, but these differences were not statistically significant (Figure 3). In lodgepole pine-MOG, ANPP was significantly higher on rhyolite ash/loess than on rhyolite (df=3,17, F =5.87, P<.004). Granitic was intermediate in ANPP between,

Table 6. Results of regression analysis for ANPP across all samples. Data are sample size (N), F-value, coefficient of determination (R^2), P-value, and Akaike Information Criteria (AIC).

Model	N	F-Value	R^2	P.>F	AIC
Aspect	90	1.17	0.01	0.28	
Specific catchment area	89	0.86	0.01	0.37	
Parent material	90	2.87	0.22	0.007	1394
Elevation	90	27.78	0.24	0.0001	1360
Cover type	90	11.28	0.48	0.0001	1351
Cover type, elevation*cover type	90	34.5	0.89	0.0001	1324
Cover type, elevation*cover type, parent material	90	24.2	0.89	0.0001	1330

Table 7. Spatial measures of the distribution of the 4 classes of predicted ANPP across the study area.

Landscape Metric	Predicted ANPP class (kg/ha/yr)			
	0–1500	1500–3000	3000–4500	>4500
Percent of study area	12.0	72.0	9.7	6.3
Number of patches	10757	5206	5269	2981
Mean patch size (ha)	9.5	118.2	15.7	18.1
Patch size coefficient of variation (%)	1751.7	6616.1	1952.5	1231.3
Total core area (ha)	36131.0	401730.0	34649.0	22066.0
Mean nearest neighbor distance (m)	201.6	142.5	177.8	243.0
Nearest neighbor coefficient of variation (%)	100.4	121.6	132.2	138.7

Discussion

The vegetation of the Northern Rocky Mountains is striking in its heterogeneity of cover types. Coniferous forests, shrublands, grasslands, and deciduous forests are interspersed across the landscape, often reflecting fine-scale variation in topography, soils, climate, and disturbance (Veblen 1998). While there has been substantial effort to describe species composition, successional trajectories, and vegetation structure of these cover types (Daubenmire 1952; Romme 1982; Bradley et al. 1992), relatively little is known about patterns of primary productivity across these cover types.

Our results indicate that ANPP in the study area varies substantially across cover types, elevation classes, and parent material types. Cottonwood and Douglas-fir cover types had ANPP levels more than 75% higher than lodgepole pine-MOG and 160% higher than grassland and sagebrush cover types. Aspen was also relatively high in ANPP and did not differ significantly from that in cottonwood and Douglas-fir. We speculate that soils and climate explain much of the variation among cover types. Cottonwood occurred only in major floodplains at lower elevations on wet alluvial soils. The high soil-nutrient content, soil-water availability, and relatively long growing season in this setting likely allowed for high plant-growth rates. Douglas-fir and aspen occurred on several parent material types. However, both of these cover types were low to moderate in elevation, had relatively long growing seasons, often grew on toeslopes with moderate soil moisture, and had accumulated moderate to high levels of soil organic matter. Grassland and sagebrush typically occurred where soil moisture was limiting due to low precipitation or high evapotranspiration. Lodgepole pine grew on more nutrient poor soils in relatively cold microhabitats.

Within cover types, the results suggested relationships between ANPP and elevation. ANPP was significantly higher at lower elevations for lodgepole pine-burned. Also, elevation was included as a pre-
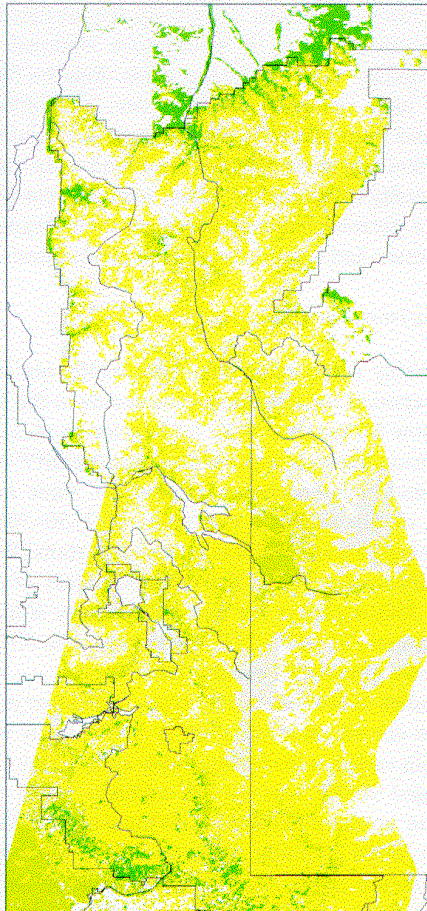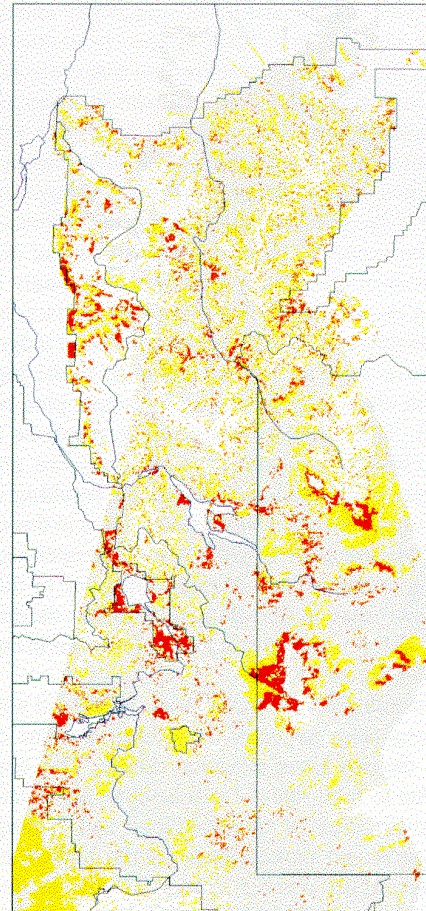
Actual Net Primary Productivity (kg/ha/yr)

- 0-1500
- 1500-3000
- 3000-4500
- >4500

Figure 5. Predicted distribution of ANPP over the study area based on cover type and elevation.

Coefficient of Variation

- 0 - 0.25
- 0.25 - 0.50
- 0.50 - 1.00
- > 1.00

Figure 6. Coefficient of variation in predicted ANPP across the study area.

dictor variable in the best model for predicting ANPP. The relationships between ANPP and elevation were not due to biases in soil type, as soil types were relatively random across elevation classes. Rather, we suspect that climate underlies the relationship between ANPP and elevation in most cover types. Although precipitation increases with elevation in the study area, temperature and length of growing season likely most limit plant growth at higher elevations in the study area.

Evaluating the relative effects of elevation and climate in the study area is problematic because elevation and average climate are closely related. For a related study, we predicted several climatic variables for the years 1995–1997 for each of the study stands based on data from meterological stations. Temperature, precipitation and snowmelt date averaged over these three years were highly correlated with elevation. While it is likely that ANPP within an elevation zone varies with climate on an annual basis, the close correlation between climate and elevation on the 5–20 year time scale used to estimate ANPP in this study precluded separation of the relative effects of climate and elevation.

The lack of relationship between ANPP and elevation in Lodgepole Pine-MOG appears to be due to differences in tree species composition across elevations. While lodgepole pine was dominant at lower elevations, subalpine fir and lodgepole pine were equally abundant at higher elevations, with subalpine fir best represented in the understory and mid-canopy. Growth rates of lodgepole pine did decrease with elevation as would be expected. However, average annual diameter increment for subalpine fir was suprisingly large where it occurred at higher elevations. In fact, increment for subalpine fir was larger than that of lodgepole pine above 2400 m, and subalpine fir in the highest elevation class grew as fast as lodgepole pine below 2200 m. The relatively fast-growing subalpine fir at higher elevations balanced the relatively fast growth of lodgepole pine at lower elevations, resulting in no relationship between ANPP and elevation in this cover type. Under the higher light levels of the open-canopy seral stages burned and clearcut, subalpine fir did not grow faster than lodgepole pine at higher elevations. Hence, ANPP was higher at lower elevations in burned and clearcut cover types.

Controlling for elevation class, ANPP did not differ among seral stages of the Lodgepole Pine cover type in the two lower elevation classes. This appears to be due to high rates of regeneration and relatively fast growth rates of tree seedlings and saplings in the clearcut and burned sites. In the highest elevation class, ANPP was higher in MOG than in clearcut or burned, presumably because of the relatively fast growth of subalpine fir in lower canopy layers of MOG.

The relationship between parent material and ANPP cannot be adequately assessed in this study for some cover types due to inadequate samples. Some cover types occurred only on one parent material class (e.g., cottonwood was only found on wet alluvium), which confounds the effects of cover type and parent material on ANPP. Other cover types such as aspen and Douglas-fir occurred across several parent material classes, but we had only one or two replicates on each parent material class. The results did suggest that rhyolite ash/loess was associated with higher ANPP than rhyolite among lodgepole pine cover types. Rhyolite ash/loess has finer texture, higher nutrient content, and higher water holding capacity than rhyolite (Bowerman et al. 1998).

Predicted ANPP was relatively low over most of the study area. Patches with values >4500 kg/ha/yr occurred primarily in deciduous and Douglas-fir habi-

tats at lower elevations. Relatively few of these high ANPP patches were in Yellowstone National Park. The majority were on private lands. Patches high in ANPP were relatively small in size, had little core area, and were relatively distant from one another. To the extent that these patches are found to be high in biodiversity or ecological value, management will be made a greater challenge based on their fragmented distribution and location on or near private lands.

Comparisons with other studies

Reasonably comparable data from within our region were reported for lodgepole-pine stands in the Medicine Bow Mountains, WY., by Pearson et al. (1987). Dimension analysis was used to estimate NPP of living trees (including below-ground) for three mature stands of fire origin at elevations of 2750–3050 m. Assuming 25% of NPP was allocated to roots (Waring and Schlesinger 1985), the reported values of 2800, 2200, 2800 kg/ha/yr for tree NPP is very similar to our estimates of 1421–2117 kg/ha/yr for tree ANPP in lodgepole pine-MOG stands (Table 4).

Studies of our other cover types from other regions suggest considerable variation in ANPP, likely resulting from variation in climate and/or soils. Crow (1978) estimated ANPP was 10 430 kg/ha/yr in an aspen stand in northern Wisconsin. Whittaker and Niering (1975) found a similar figure of 10 512 kg/ha/yr for aspen in the Santa Catalina Mountains of Arizona. These values are more than double the estimate for aspen in our study. ANPP of Douglas-fir varied from 13 100 kg/ha/yr in moist forests of western Oregon (Law and Waring 1994) to 8400 in the Santa Catalina Mountains of Arizona (Whittaker and Niering 1975) to 5227 kg/ha/yr in our study area. Juniper/sagebrush and sagebrush communities in the high desert of eastern Oregon varied in ANPP from 530–1550 kg/ha/yr (Law and Waring 1994), somewhat lower than our estimate of 1890 kg/ha/yr in sagebrush stands in the study area.

The relationship between primary productivity and elevation also varies among ecosystems. ANPP was found to increase with elevation in the Santa Catalina Mountains, Arizona, in association with increased soil moisture (Whittaker and Niering 1975). Temperature limitations resulted in ANPP decreasing with elevation on the west slopes of the northern Rocky Mountains in Montana (White and Running 1994) and on Mauna Loa in Hawaii (Raich et al. 1997). ANPP did not vary with elevation below 2700 m the Himalayan foothills of northern India, likely because neither tem-

perature nor moisture was limiting in this zone (Singh et al. 1994). These studies suggest that interactions between the distribution of abiotic factors and vegetation tolerances largely underlay the relationships between primary productivity and elevation.

We speculate that temperature and length of growing season are the primary limiting factors for most of the cover types in the study area, resulting in higher ANPP in lower elevations due to higher temperatures there. However, this effect may be reduced somewhat at lower elevations due to reduced precipitation. Lodgepole-pine stands at lower elevations, for example, likely undergo moisture stress in late summer in some years due to low rainfall and soils with lower water holding capacity (T. Bowerman, personal communication).

In lodgepole pine-MOG, ANPP did not vary with elevation, likely due to the presence of subalpine fir at higher elevations. This species grew much faster than lodgepole pine at higher elevations, and subalpine fir at high elevations had equal growth rates to lodgepole pine at low elevations. Raich et al. (1997) also found that the relationship between elevation and growth rates varied among plant species. It is not clear how subalpine fir was able to perform so well under the short growing seasons found at higher elevations in the study area.

Studies that have quantified NPP across landscapes remain few. Working in prairie systems, Knapp et al. (1993), Turner et al. (1997), and Burke et al. (1997) all found high levels of spatial heterogeneity in NPP associated with variation in climate, soils, and disturbance history. White and Running (1994) and Keane et al. (1996) used computer models to simulate NPP across the McDonald Watershed in northwestern Montana. They found that carbon production ranged from about 2000 to 20000 kg/ha/yr across the watershed. Productivity was highest at lower elevations on southeast facing slopes, probably due to higher temperature and radiation loads in this landscape setting. The frequency distribution of primary productivity was highest towards low to moderate levels in the McDonald Watershed studies, but not as much as found in our study area. The colder temperatures on the east side of the Rockies may inhibit NPP at higher elevations relatively more than on the west side of the Rockies.

Assumptions and limitations

These results should be interpreted within the constraints of various assumptions and limitations of the methods. Some fraction of ANPP is lost each year to plant mortality and to herbivory. In sampling herbaceous biomass, we avoided areas that showed indication of herbivory. However, we did not otherwise measure or account for mortality and herbivory. We were also unable to find published estimates of these processes from the Northern Rocky Mountains. We made the assumption that these processes accounted for a relatively small proportion of total ANPP in our study area. If subsequent studies find this not to be true, our ANPP estimates should be modified accordingly.

The ages of shrubs in this region are also poorly know. Moreover, these ages are likely to vary considerably among cover types and seral stages. Lodgepole pine seedlings likely grow relatively fast, while sagebrush and deciduous shrubs like *Vaccinium* under dense canopies grow very slowly. Limited sampling of the annual rings of the more abundant deciduous shrubs in aspen and cottonwood cover types (e.g., *Alnus incana, Prunus virginiana*) suggested that an average age of 8 years was a reasonable assumption for deciduous shrubs. Our assumption of 3 years for conifer shrubs is based on the fact that conifer tree seedlings comprised the great majority of stems in these groups. These seedlings grow relatively rapidly in the lodgepole pine cover types where they were primarily found. Sagebrush growth rates are likely to vary by species and location (C. Waumboldt, personal communication). Again, our ANPP estimates should be revised if subsequent studies find that these assumptions about shrub age are unreasonable.

A third assumption we made in estimating ANPP was that biomass equations can be applied among species of similar lifeform. This is commonly done in dimension analysis of biomass (Means et al. 1994) and is reasonable to the extent that the species in question do have similar diameter/biomass relationships. Fortunately, biomass equations were available for all of our major species, so any bias due to substitutions in this study should be small.

Another limitation of this and many studies that extrapolate information across space involves error propagation. Error in each data layer used in an extrapolation may be additive, resulting in large amounts of error in the final map (Walsh et al. 1994). Typically, some or all of this error is not quantified. Three sources of potential error in our extrapolation of ANPP are those associated with: the cover type layer, estimates of elevation from the Digital Elevation Model,

and the regression equation used to relate ANPP to cover type and elevation.

Validation of predicted ANPP against independent field data would be the best way to quantify the accuracy of predicted ANPP. Such data were not available, however. We quantified error for the cover type map and for predicted ANPP. Furthermore, we assumed that error in the DEMs were relatively small. However, we cannot quantify the interaction of error in the cover type maps with that associated with the regressions used to predict ANPP. Total error is likely be least in the three lodgepole-pine cover types due to relatively high classification success of these cover types and relatively low coefficients of variation in predicted ANPP. Error is also likely low in cottonwood because this cover type was mapped from aerial photographs with likely high accuracy and because of the relatively low coefficient of variation of predicted ANPP for this cover type. Similarily, aspen and Douglas-fir habitats are likely intermediate in total error. In contrast, total error is likely to be relatively high in grassland and sage, based on poor cover-type classification accuracy and high coefficient of variation in predicted ANPP. In the case of grasslands, ANPP likely varies considerably with annual climate. The year we measured grassland ANPP, 1997, was relatively wet and our estimates may be higher than for years of average precipitation. Thus, the results for grassland and sage should be used with caution.

Implications

The higher levels of NPP at lower elevations in the study area likely exerted influence on fire regimes in preEuropean settlement times. Fire history studies on the Yellowstone Plateau in Yellowstone National Park have suggested a fire-return interval in high-elevation lodgepole pine forests of 250 to 300 years during the late Holocene (Romme 1982). The combination of relatively high NPP and relatively low summer precipitation at lower elevations in our study area leads us to speculate that natural fire was more frequent and less severe at low elevations compared to high elevations in the study area. This prediction is consistent with Barrett (1994), who found fire-return intervals of 50–75 years in moderate-elevation Douglas-fir forests in the Northern Range of Yellowstone National Park. Given that the lower elevations in the study area are generally windward of the Yellowstone Plateau, we speculate that the frequent fire in the Henry's Fork, Madison, and Gallatin Watershed lowlands acted as

ignition sources for the area that is now Yellowstone National Park. Logging, road building and fire suppression have likely reduced fire ignition and spread at these lower elevations and reduced the incidence of fire in Yellowstone National Park. If true, then the fire regime in the park is not functioning as it did in preEuropean settlement times, calling into question the 'natural regulation' fire-management policy (Boyce 1991) currently in place in Yellowstone National Park. Restoration of forests in these lowland areas and/or prescribed fire may be necessary to allow a fire regime in Yellowstone National Park that is more typical of preEuropean settlement times.

These lowland areas that are high in NPP may also be important habitats for many plant and animal species in the Greater Yellowstone Ecosystem. The abundance of individual species and species richness is often positively associated with NPP (Rosensweig 1994; Huston 1994). This high NPP in conjunction with more equitable climate likely explain the strong seasonal migration of some ungulate species between the Yellowstone National Park and surrounding lowlands (Keiter and Boyce 1991). The importance of these productive lowland habitats for other species is less known. Initial results from our studies of biodiversity indicate that bird abundance and species richness are particularly high in cottonwood, aspen and low-elevation conifer forests (Hansen et al. 1999). Relative both to fire and biodiversity, the high levels of NPP and equitable climate at lower elevations in the study area suggest that coordinated management is needed among the multiple agency jurisdictions and private lands in this area to maintain ecological processes and native species.

Acknowledgements

References

Akaike, H. 1973. Information theory an extension of the maximum likelihood principle. *In* Int. Symp. Inf. Theory, second ed. pp. 267–281 Editetd by Petran B.N. and Csaki, F. Adakemial iadi, Budapest, Hungary.

Baker, W. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecol. 7(3):181–94.

Barrett, S.W. 1994. Fire regimes of andesitic mountain terrain in northeastern Yellowstone National Park, WY. Int. J. Wildland Fire 4(2): 65–76.

Bormann, F.H., Siccama, T.G., Likens, G.E. and Whittaker, R.H. 1970. The Hubbard Brook ecosystem study: composition and dynamics of the tree stratum. Ecol. Monographs 40: 373–388.

Bowerman, T.S., Dorr, J., Leahy, S., Varga, K., Warrick, J. 1997. Targhee National Forest Ecological Unit Inventory. USDA Forest Service, Targhee National Forest, St. Anthony, ID.

Boyce, M.S. 1991. Natural Regulation or the Control of Nature? *In* The greater yellowstone ecosystem. pp. 183–208. Edited by Keiter, R.B., Boyce, M.S. Yale University Press, New Haven, CT.

Bradley, A.F., Fischer, W.C. and Noste, N.V. 1992. Fire ecology of the forest habitat types of eastern Idaho and Western Wyoming. USDA Forest Service, Intermountain Research Station, GTR-INT-290, Ogden, UT.

Burke, I.C., Kittel, T.G.F., Lauenroth, W. K., Snook, P. and Yonker, C.M. 1991. Regional analysis of the central Great Plains: sensitivity to climate variability. Bioscience 41(10): 685–692.

Burke, I.C., Lauenroth W.K. and Parton, W.J. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology 78(5): 1330–1340.

Burnham, K.P. and Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. *In* Wildlife 2001: Populations. pp. 16–30. Edited by McCullough, D.R. and Barrett, B.H. Elsevier Sci. Publ., New York, NY.

Crow, T.R. 1978. Biomass and production in three contiguous forests in northern Wisconsin. Ecology 59: 265–273.

Daubenmire, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monog. 22: 301–330.

Davis, C.E., and Shovic, H.F. 1996. Soil Survey of the Gallatin National Forest, Montana. USDA Forest Service, Gallatin National Forest, Bozeman, MT.

Despain, D. 1990. Yellowstone Vegetation. Roberts Rinehart Publishers, Boulder, CO.

ESRI. 1982-1997. ARC/INFO on-line documentation. Environmental Systems Research Institute, Inc. Redlands, California.

Graumlich, L.J., Brubaker, L.B. and Grier, C.C. 1989. Long-term trends in forest net primary productivity: Cascade Mountains, Washington. Ecology 70: 405–410.

Hansen, A.J., Rotella, J.R. and Kraska, M.L. 1999. Dynamic habitat and population analysis: A filtering approach to resolve the biodiversity manager's dilemma. Ecol. Appl. 9(4): 1459–1476.

Huston, M.A. 1994. Biological Diversity. Cambridge University Press, Cambridge.

Keane, R.E. Ryan K.C. and Running, S.W. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. Tree Physiology 16: 319–331.

Keiter, R.B. and Boyce, M.S. ed. 1991. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press, New Haven, CT

Knapp, A.K., Fahnestock, J.T., Hamburg, S. P., Statland, L. B., Seastedt, T. R. and Schimel, D.S. 1993. Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. Ecology 74: 549–560.

Law, B.E. and Waring, R.H. 1994. Combining remote sensing and climatic data to estimate net primary production across Oregon. Ecol. Appl. 4: 717–728.

Ma, Z. and Redmond, R.L. 1995. Tau Coefficients for Accuracy Assessment of Classification of Remote Sensing Data. Photog. Eng. Remote Sensing 61 : 435–439.

McGarigal, K., and Marks, B.J. 1994. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. Forest Science Department, Oregon State University, Corvallis, OR.

Means, J.E., Hansen, H.A., Koerper, G.J., Alaback, P.B. and Klopsch, M.W. 1994. Software for Computing Plant Biomass–BIOPAK Users Guide. USDA Forest Service, Pacific Northwest Research Station, Gen. Tech. Rep. PNW-GTR-340, Portland, OR.

Pearson, J.A., Knight, D.H. and Fahey, T.J. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. Ecology 68: 1966–1973.

Perry, D.A. 1994. Forest Ecosystems. The Johns Hopkins University Press, Baltimore, MD., USA.

Pulliam, H.R. 1988. Sources, sinks and population regulation. Am. Nat. 132: 652–661.

Pulliam, H.R., and Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137: S50–S66.

Raich, J.W., Russell, A. E. and Vitousek, P.M. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. Ecology 78: 707–721.

Rodman, A., Shovic, H. and Thoma, D. Soils of Yellowstone National Park. 1996. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-NRSR-96-2.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monog. 52(2): 199–221.

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge Universtiy Press, Cambridge.

Sabin, T.E., and Stafford, S.G. 1990. Assessing the Need for transformation of response variables. Special Publication 20, Forest

Research Lab, College of Forestry, Oregon State University, Corvallis, OR.

SAS. 1991. SAS/STAT User's Guide. Release 6.03, SAS Institute Inc., Cary, NC.

Singh, S.P., Adhikari, B.S. and Zobel, D.B. 1994. Biomass, productivity, leaf longevity, and forest structure in the central Himalayan. Ecol. Monog. 64: 401–422.

Turner, C.L., Blair, J.M., Schartz, R.J. and Neel, J.C. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology 78: 1832–1843.

Turner, M.G. and Romme, W.H. 1993. Landscape dynamics in crown fire ecosystems. Landscape Ecol. 9: 59–77.

U.S. Geological Survey. 1993. Data Users Guide 5: Digital Elevation Models. Reston, Virginia.

Veblen, T.T. 1998. RockyMountains. *In* Terrestrial Vegetation of North America. Edited by Barbour, M.G., and Billings, D. Cambridge University Press, Cambridge U.K.

Walsh, S.J., Brown, D.G., Bian, L. and Allen, T.R. 1994. Effects of spatial scale on data certainty: An assessment through data dependency and sensitivity analyses. International symposium on the spatial accuracy of natural resource data bases. Am. Soc. Photog. Remote Sensing, 151–160.

Waring, R.H., and Schlesinger, W.H. 1985. Forest ecosystems: concepts and management. Academic Press, Orlando, FL.

White, J.D. and Running, S.W. 1994. Testing scale dependent assumptions in regional ecosystem simulations. J. Veg. Sci. 5: 687–702.

Whittaker, R.H. 1975. Communities and ecosystems. MacMillan Publishing Co., Inc. New York.

Whittaker, R.H. and Niering, W.A. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. biomass, production, and diversity along the elevation gradient. Ecology 56: 771–790.