

Landscape Patterns of Sapling Density, Leaf Area, and Aboveground Net Primary Production in Postfire Lodgepole Pine Forests, Yellowstone National Park (USA)

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ABSTRACT

Causes and implications of spatial variability in postfire tree density and understory plant cover for patterns of aboveground net primary production (ANPP) and leaf area index (LAI) were examined in ninety 11-year-old lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) stands across the landscape of Yellowstone National Park (YNP), Wyoming, USA. Field studies and aerial photography were used to address three questions: (1) What is the range and spatial pattern of lodgepole pine sapling density across the burned Yellowstone landscape and what factors best explain this variability? (2) How do ANPP and LAI vary across the landscape and is their variation explained by abiotic factors, sapling density, or both? (3) What is the predicted spatial pattern of ANPP and LAI across the burned Yellowstone landscape? Stand density spanned six orders of magnitude, ranging from zero to 535,000 saplings ha⁻¹, and it decreased with increasing elevation and with increasing distance from unburned forest ($r^2 = 0.37$). Postfire densities mapped from 1:30,000 aerial photography revealed that 66% of the burned area had densities less than 5000 saplings ha⁻¹ and approximately 25% had

densities greater than 10,000 saplings ha⁻¹; stand density varied spatially in a fine-grained mosaic. New allometric equations were developed to predict aboveground biomass, ANPP, and LAI of lodgepole pine saplings and the 25 most common herbaceous and shrub species in the burned forests. These allometrics were then used with field data on sapling size, sapling density, and percent cover of graminoid, forb, and shrub species to compute stand-level ANPP and LAI. Total ANPP averaged 2.8 Mg ha⁻¹y⁻¹ but ranged from 0.04 to 15.12 Mg ha⁻¹y⁻¹. Total LAI averaged 0.80 m² m⁻² and ranged from 0.01 to 6.87 m² m⁻². Variation in ANPP and LAI was explained by both sapling density and abiotic factors (elevation and soil class) (ANOVA, $r^2 = 0.80$); abiotic variables explained 51%–54% of this variation. The proportion of total ANPP contributed by herbaceous plants and shrubs declined sharply with increasing sapling density ($r^2 = 0.72$) and increased with elevation ($r^2 = 0.36$). However, total herbaceous productivity was always less than 2.7 Mg ha⁻¹ y⁻¹, and herbaceous productivity did not compensate for tree production when trees were sparse. When extrapolated to the landscape, 68% of the burned landscape was characterized by ANPP values less than 2.0 Mg ha⁻¹y⁻¹, 22% by values ranging from 2 to 4 Mg ha⁻¹y⁻¹, and the remaining 10% by values greater than 4 Mg

Received 19 January 2003; accepted 29 July 2003; published online 30 September 2004.

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$\text{ha}^{-1}\text{y}^{-1}$. The spatial patterns of ANPP and LAI were less heterogeneous than patterns of sapling density but still showed fine-grained variation in rates. For some ecosystem processes, postfire spatial heterogeneity within a successional stage may be similar in magnitude to the temporal variation observed through succession.

INTRODUCTION

Understanding the patterns and causes of spatial heterogeneity in ecosystem function remains at the frontier of ecosystem and landscape ecology (Schimel and others 1997; Turner and Carpenter 1999; Turner and others 2001). The abiotic template is a powerful constraint on ecosystem function (for example, Barnes and others 1998), but spatial processes such as natural disturbance, land use, and the activities of organisms also influence the rates and patterns of ecosystem processes. Although many ecosystem processes are well understood over relatively small spatial extents (for example, Bormann and Likens 1979; Swank and Crossley 1988; Likens and Bormann 1995), a more synthetic understanding of spatial heterogeneity in ecosystem processes remains an important research need. In this study, we examined the implications of a large infrequent disturbance—the 1988 Yellowstone fires—for spatial variability in postfire stand density, aboveground net primary production (ANPP), and leaf area index (LAI).

Temporal variation in net primary productivity (NPP) with successional time has been well studied at the stand level in forest ecosystems (for example, Sprugel 1985; Pearson and others 1987; Gower and others 1996; Ryan and others 1997; Law and others 2001). ANPP, LAI, and biomass accumulation increase with stand development to a maximum before declining (Fahey and Knight 1986; Long and Smith 1992; Ryan and Waring 1992; Gower and others 1996; Ryan and others 1997). Spatial variation in some ecosystem processes has also been described across forested landscapes (for example, Zak and others 1989; Murphy and others 1998; Brown and Schroeder 1999; Hansen and others 2000; Gower and others 2001; Wirth and others 2002). For example, the spatial variation in NPP associated with climatic and edaphic heterogeneity can be as great as the variation with stand age (Gower and others 2001). However, spatial variation in ecosystem process rates within a given successional stage is not well known. Stand-replacing disturbances such as crown fires often affect vast areas and produce extensive even-aged stands,

Key words: disturbance; succession; leaf area index; fire ecology; net primary production; allometric equations; landscape pattern; aerial photography; *Pinus contorta*; Rocky Mountains; ecosystem processes.

but stand structure and function within a disturbed area varies widely. Stand composition and structure can be established quickly following catastrophic disturbance (Johnson and Fryer 1989; Muir 1993; Timoney and others 1997; Turner and others 1997) depending on the prefire state of the ecosystem and characteristics of the disturbance (Turner and others 1998). However, the importance of the postdisturbance mosaic for ecosystem function remains poorly understood (Reed and others 1998; Clark and others 2001).

Forest fire is a well-studied disturbance (for example, Johnson 1992; Johnson and Miyanishi 2001), and the landscape of Yellowstone National Park (YNP) is ideal for studying the effects of a fire-generated landscape mosaic on ecosystem processes. The 1988 Yellowstone fires affected more than 250,000 ha, creating a mosaic of burn severities (Christensen and others 1989; Turner and others 1994) and producing surprising variation in postfire lodgepole pine (*Pinus contorta* var. *latifolia* [Engelm. Ex Wats.] Critchfield) density across the landscape (Anderson and Romme 1991; Turner and others 1997, 1999; Romme and Turner 2004). Such large fires occur at intervals of 100–300 years in this landscape (Romme 1982; Romme and Despain 1989; Millspaugh and others 2000). The relative similarity of substrate and climate across a large, relatively flat area allows the effects of disturbance and postfire succession to be studied without the confounding influences of the steep environmental conditions that characterize many coniferous landscapes. Furthermore, most of YNP is managed as a wilderness area where postfire responses have been little affected by human actions.

Lodgepole pine dominates YNP forests, and postfire stand development in lodgepole pine has been well studied (for example, Moir 1969; Day 1972; Whipple and Dix 1979; Taylor 1980; Romme 1982; Despain 1983, 1990; Veblen 1986; Pearson and others 1987; Johnson and Fryer 1989; Veblen and others 1991). Lodgepole pine is serotinous, producing closed cones that release their seeds when heated, and it often regenerates in dense, even-aged stands (Moir 1969; Whipple and Dix

1979; Lotan and Perry 1983; Johnson 1992). However, stand-level percent serotiny varies across the landscape with elevation and stand age (Muir 1993; Tinker and others 1994; Turner and others 1997; Schoennagel and others 2003), and postfire tree recruitment can be sparse and slow in burned areas of low serotiny (Catellino and others 1979; Peet 1981; Parker and Peet 1984; Veblen 1986; Parker and Parker 1994). Measurements made in permanent plots in YNP revealed that initial post-fire pine seedling densities varied over several orders of magnitude with stand-level percent serotiny, fire severity, patch size, and distance from a severe-surface fire (Turner and others 1997, 1999; Romme and Turner 2004).

Stand function can be strongly related to stand structure, particularly tree density (Moir and Francis 1972; Reed and others 1998). Thus, biomass accumulation can differ among even-aged stands that differ in structure, even on similar sites (Pearson and others 1987; Long and Smith 1990). Trees in low-density stands tend to have larger crowns and more leaf area compared with trees in high-density stands (Long and Smith 1981), but lodgepole pine stands of different density may also have identical leaf area (Moir and Francis 1972; Knight and others 1981). We used field studies and aerial photography to address three questions: (1) What is the range and spatial pattern of lodgepole pine sapling density across the burned Yellowstone landscape and what factors best explain this variability? (2) How do LAI and ANPP vary across the landscape and is their variation explained by abiotic factors, sapling density, or both? In answering this question, we also tested the null hypothesis that total LAI and total ANPP would not differ spatially across the burned landscape but that the relative contributions of herbaceous and tree LAI and ANPP would differ. If leaf area of understory vegetation was inversely proportional to leaf area of trees, then LAI and ANPP could be similar in stands that vary in sapling density. (3) What is the predicted spatial pattern of ANPP and LAI across the burned Yellowstone landscape? If ANPP and LAI vary similarly with stand density, then spatial patterns of stand density, ANPP, and LAI should be similar. However, if ANPP and LAI are unrelated to stand density, then the spatial patterns should be different from that of stand density.

STUDY AREA

Yellowstone National Park encompasses 9000 km² on a high forested plateau in northwest Wyoming. Approximately 80% of the park is dominated by

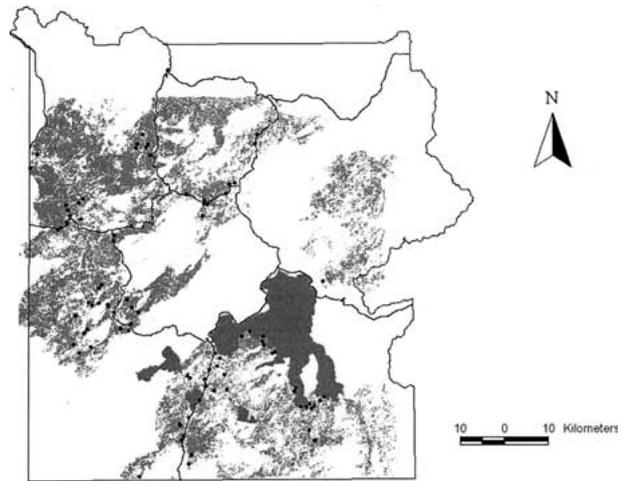


Figure 1. Map of Yellowstone National Park showing the area of the subalpine plateau that was burned by the 1988 fires (shaded) along with major lakes and roads. The distribution of the 90 plots (0.25 ha) sampled for this study are indicated by circles.

lodgepole pine forest, although subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.], Engelmann spruce [*Picea engelmannii* Parry], and whitebark pine [*Pinus albicaulis* Engelm.] may be locally abundant in older stands and at higher elevations (Despain 1990). Our study area was the subalpine forested plateau that covers most of Yellowstone (Figure 1) and encompasses dry, infertile, rhyolitic substrates as well as more mesic and fertile andesitic and former lake-bottom substrates. The climate is generally cool and dry with mean January temperature of -11.4°C , mean July temperature of 10.8°C , and mean annual precipitation of 56.25 cm (Dirks and Martner 1982). The summer of 1988 was the driest on record since 1886, with precipitation in June, July, and August at 20%, 79%, and 10%, respectively, of average (Renkin and Despain 1992). As with large, infrequent crown fires in other systems, the 1988 fires were due largely to synoptic climate patterns and were generally not affected by variation in stand age or structure (Johnson and Wowchuck 1993; Turner and others 1994; Bessie and Johnson 1995; Flannigan and Wotton 2001). The approximately 174,000 ha of stand-replacing burned area on the subalpine plateau comprised our study area (Figure 1).

METHODS

Spatially Extensive Field Sampling

Vegetation was sampled in 0.25-ha plots during the summers of 1999 ($n = 88$) and 2000 ($n = 2$) to measure postfire stand density and to estimate

ANPP and LAI across the range of conditions representative of the burned landscape (Figure 1); the two 2000 plots were added to include more of the highest-density stands. Sampling locations were separated by at least 1 km and were selected in a stratified random design to assure coverage across the geographic extent of the Yellowstone Plateau and its range of elevation and substrate. Because Yellowstone is so remote, access by boat or trail was also considered when selecting plot locations. We tested for spatial autocorrelation in postfire lodgepole pine seedling density by using data in which all pine seedlings were counted in contiguous 1-m² quadrats along seven transects ranging in length from 187 to 3394 m (unpublished data). Interpretation of correlograms and semivariograms revealed that autocorrelation declined over short distances ($r^2 < 0.10$ at lag distances ≤ 120 m, even in high-density stands). Therefore, a 1-km separation was considered adequate to assure independence among samples, although most locations were farther apart.

Sampling locations were stratified based on general substrate: rhyolite, which weathers into dry, infertile soils, or andesite, which produces somewhat more mesic and fertile soils; and expected density of lodgepole pine saplings, based on our prior knowledge and visual inspection of 1:30,000 color infrared aerial photographs obtained in August 1998. Four expected lodgepole pine sapling density classes were developed prior to field sampling and aerial photo classification: less than 5000 stems ha⁻¹; 5000–20,000 stems ha⁻¹; 20,000–50,000 stems ha⁻¹; and more than 50,000 stems ha⁻¹. These classes were used only to assist in locating sampling locations, which were then selected from each combination of substrate and expected sapling density for a total of 88.

The center of each 0.25-ha plot was established randomly and its location recorded using a global positioning system (GPS); slope and aspect were also recorded in the field. A 50-m transect was then extended on a north-south bearing with the midpoint of the transect on the plot center. Two additional 50-m transects were established parallel and 25 m to either side of the central transect; thus, all measurements were made within a 50-m \times 50-m area. The number of lodgepole pine saplings was recorded within a 2-m belt along each transect (100-m² sample area along each transect). Percent cover of understory plants was recorded by species within eight 0.25-m² quadrats positioned at 5-m intervals along the two outer transects, and nine quadrats positioned similarly along the center transect ($n = 25$ quadrats per plot). Basal diameter,

height, and 1998 height growth increment were recorded on a total of 25 randomly chosen lodgepole pine saplings along the three transects.

For each plot, digital maps of fire severity class (crown fire or severe-surface fire), distance to the nearest unburned forest, soil type, and elevation were developed or obtained from existing GIS data layers obtained from the Spatial Analysis Center, YNP (<http://www.nps.gov/yell/gis>). All GIS analyses were performed using Arc/Info (ESRI 1992). Soil categories were aggregated to four classes based on physical characteristics of the soils and their expected effects on vegetation (Rodman and others 1996). Three of the soil categories are Inceptisols: "rhyolite till" occurs on rolling or dissected glaciated uplands and plateaus and comprises glacial till derived from rhyolite; "rhyolite-glacial" occurs on glaciofluvial outwash plains and include glaciofluvial alluvium derived from rhyolite or rhyolitic ash-flow tuff or thermal deposits; "rhyolite-low base saturation" occurs largely on lacustrine plains and glaciated plateaus and again is derived from glacial rubble and till from rhyolite and rhyolitic ash-flow tuff. The fourth category, "andesite," includes Mollisols that occur on glacial trough valley bottoms, alluvial fans, and concave glaciated uplands; it comprises andesites plus alluvial or lacustrine soils and organic deposits. These classes were used subsequently in ANOVA analyses. Based on their relative suitability for plant growth, considering both nutrient status and water-holding capacity, soils were ranked ordinally from the least fertile (rhyolite till = 1) to the more fertile (rhyolite-glacial = 2, rhyolite-low base saturation = 3, and andesite = 4) for testing in regression models (A. Rodman, Soil Scientist, Yellowstone National Park, personal communication).

Stepwise multiple regression was used to relate lodgepole pine density at the 90 plots to the environmental variables, namely elevation (which is negatively correlated with prefire serotiny [Tinker and others 1994; Schoennagel and others 2003]), soil category, fire severity, and distance to unburned forest. Sapling density was transformed using $\log_{10}(\text{density} + 1)$ prior to analysis to normalize the data. Multiple regression was also used to determine whether the morphometry of the saplings (sapling height, basal diameter) and 1998 height increment varied predictably with sampling density, elevation, and soil class. Prior to analysis, basal diameter and 1998 height increment were transformed using $\log_{10}(x + 1)$ and sapling height was square-root transformed to achieve normality.

Table 1. Characteristics of the Four Study Sites Sampled during 1999 in Yellowstone National Park to Develop Allometric Equations for Young Lodgepole Pine Saplings^a

Study Site	Elevation (m)	Lodgepole Pine Sapling Density (Stems ha ⁻¹)	UTM coordinates
Pitchstone	2392	767 (low)	528552 E 4900863 N
Riddle Lake	2437	9000 (moderate)	533166 E 4911764 N
Fern	2374	33,000 (high)	514809 E 4920611 N
Gravel Pit	2074	454,000 (very high)	500984 E 4945028 N

^aAll sites were on rhyolite substrate.

Mapping Lodgepole Pine Sapling Density

Color infrared aerial photographs (1:30,000) of YNP were taken in August 1998 under cloud-free conditions from an altitude of approximately 4.6 km. Photos were timed to enhance the visual differences among conifer saplings, herbaceous vegetation, and bare soil. All photos were taken with 70% endlap and 30% sidelap. Photos ($n = 587$) encompassing the subalpine plateau were scanned at 700 dpi and orthorectified using the software program OrthoMapper[®] (Scarpace and others 2000) using 1994 panchromatic digital ortho-quarter-quadrangles and a 30-m digital elevation model (1:40,000) provided by the YNP Spatial Analysis Center. A minimum of six control points was used in orienting each photo. Multiple orthophotos were joined using the mosaic function in ERDAS Imagine (ERDAS, Inc. 1999). The photos were output from OrthoMapper at 5-m resolution then degraded to 50-m resolution, which corresponds to the scale at which field data were obtained, prior to classification.

Supervised classification of the photo mosaic was completed using the maximum-likelihood algorithm in ERDAS Imagine 7.0 (ERDAS 1999) and assigning cells to one of six sapling density classes: less than 1000 stems ha⁻¹, 1001–5000 stems ha⁻¹, 5001–10,000 stems ha⁻¹, 10,001–15,000 stems ha⁻¹, 15,001–50,000 stems ha⁻¹, and more than 50,000 stems ha⁻¹. The 88 0.25-ha plots sampled in 1999 were used as a training set, and an additional set of 61 independent 0.25-ha plots sampled the same way during 2000 and 2001 was used to test the classification (test data from Litton 2002 and Schoennagel 2002). The overall accuracy, error matrix, and the K_{hat} statistic (Congalton 1991; Lillesand and Kiefer 1994) for the classification were used to assess classification accuracy. Further details on photo classification, including a comparison of alternative classification methods, can be found in Kashian and others (in press) and Kashian (2002). The final map contained the six sapling

density classes mapped at 50-m resolution across the burned areas of Yellowstone's subalpine plateau. Area of each density class was determined, and the spatial pattern of postfire sapling density classes was analyzed using FRAGSTATS (McGarigal and Marks 1995). To characterize spatial pattern of the density classes, we selected metrics that are less sensitive to map extent or the presence of single-cell patches in the interpreted image. These included patch density, area-weighted mean patch size (a geometric mean that minimizes the influence of single-cell patches on the mean), and an index of patch clumpiness. The latter ranges from -1 (maximum disaggregation) to 1 (maximum aggregation), with zero indicating a random distribution. In addition, we computed two metrics of overall landscape structure: Shannon's Evenness Index (range 0–1) and contagion (range 0–100).

Allometric Equations for ANPP and LAI

Existing allometric equations for lodgepole pine (Pearson and others 1987; Comeau and Kimmins 1989; Long and Smith 1990, 1992) were developed for mature stands and thus cannot be applied to young saplings, and there are no existing allometric models for the herbaceous species and shrubs. Therefore, a necessary and major component of our study was the development of new ANPP and LAI allometric equations for the lodgepole pine saplings and the dominant forbs, graminoids, and shrubs found in Yellowstone's burned forests. Allometric relationships were developed by harvesting woody and herbaceous species during July and August 1999 at four sites that represented the range of postfire sapling densities present in the burned areas of the subalpine plateau (Table 1). All four sites were on relatively infertile rhyolite substrates at 2050–2450-m elevation. Postfire pine sapling density and percent cover of ground layer vegetation were measured in 0.25-ha plots as described above for the spatially extensive vegetation plots.

Lodgepole Pine Aboveground Biomass (AB), ANPP, and LAI. Lodgepole pine aboveground biomass (AB) and ANPP were estimated by harvesting the aboveground portions of 30 saplings at each site ($n = 120$): 5 of the smallest saplings, 5 of the tallest saplings, and 20 from the range of intermediate sizes. Because sampling occurred before the summer's growth was completed, we measured the biomass accumulated during the 1998 growing season to assure that the measured annual height and radial growth increment represented an entire growing season. Therefore, all 1999 foliage and stem/branch buds were removed from each sapling and discarded prior to harvesting. The height of the sapling was then measured from the ground to the top of the 1998 stem growth. The 1998 height increment was measured from just below the 1998 branch whorl to the top of the stem. In addition, the diameter at the base of the sapling and the diameter of the stem just below the 1998 branch whorl were measured.

All biomass produced during 1998 (1998 branch whorl, all stem wood above the whorl, and all 1998 foliage and twig wood) was removed and placed in a paper bag. The remaining branches were then removed and placed in another paper bag. With calipers, we measured the basal diameter and top diameter of the stem from the pith through the 1997 annual ring, through the 1998 annual ring, and through the bark. Using these numbers plus the height of the tree, we computed the volume of a cone representing total bole wood growth through 1997, total bole wood growth through 1998, and total bole wood plus bark growth. We estimated the 1998 wood volume increment by subtracting the total 1997 volume from the total 1998 volume. Similarly, we estimated annual bark increment by subtracting the 1998 wood volume from the total wood plus bark volume and dividing by 3 (assuming that the current bark represents the last three years of growth; Reed and others 1999). The stem was then cut into pieces with its needles intact and placed into a third paper bag. Because we did not account for fine litterfall, losses to consumers, and volatile and leached organics, our estimates of lodgepole ANPP are likely underestimates (Clark and others 2001). However, litterfall rates for the young saplings in our study are relatively low (Litton 2002), and herbivory on lodgepole pine is typically minimal (personal observations).

All samples were oven-dried to a constant weight at 70°C, and dry weights of the individual fractions were determined using an electronic balance. All needles were stripped from their branches and

weighed separately. The amount of radial increment in stem wood added in a single year was estimated along with its proportion of total stem wood biomass. This proportion was applied to all pre-1998 branch wood, providing an estimate of the amount of branch wood added in a single year. Total biomass added during 1998 was calculated as the sum of 1998 needle, twig, stem wood, branch wood, and bark biomass.

Allometric methods for determining leaf area for lodgepole pine saplings were developed from 90 saplings (30 each from the Pitchstone, Riddle Lake, and Fern sites; Table 1) using the water displacement method (Chen and others 1997), which is based on the relationship between the buoyant force required to push a sapling shoot or branch into a container of water and the mass or volume of the water displaced by the shoot.

A single branch estimated to be three years of age was removed from each sapling. Using 3-year-old branches assured that there were fully expanded needles from the previous year's growth but that needles had not yet fallen off of the branch (O'Reilly and Owens 1989; Moore 1981). In the laboratory, a plastic vessel (approximately 1 L) was partially filled with water and weighed on an analytical balance. A small amount of dishwashing detergent was added prior to weighing to prevent air bubbles from adhering to the needles that were to be immersed. Each branch was treated as follows: All 1999 growth was removed from the end of the branch because all needles had not yet fully expanded. A mark was made on the stem to delineate the point to which the branch should be immersed into the water. The branch was then immersed into the water, taking care not to touch the sides or the bottom of the vessel. The force (in grams) required to immerse the branch was recorded from the balance.

All needles were then removed from the branch. The bare stem was again immersed into the water up to the point previously marked and the force required to immerse the bare branch was recorded. Needle mass and volume were determined by taking the difference between the forces required to immerse the branch with and without needles. Therefore, if needle volume is known, the surface area may be calculated using the formula:

$$SA = X \sqrt{VnL}, \quad (1)$$

where SA is the total surface area for the group of needles immersed, X is a shape factor representing the shape of the cross-sectional area of the needle (this differs by species), V is the volume of the

needles as determined by the branch immersion, n is the number of needles in the sample, and L is the mean length of the sampled needles. We used a shape factor of 4.10, developed for black pine needles which are hemicylindrical in shape, as are lodgepole pine needles. Results are reported as hemispherical surface area (HSA), which is total surface area divided by 2.

All needles that had been immersed and removed from the branch were counted. Needle length was measured to the nearest 0.1 mm on every third fascicle removed (up to 10) using a caliper, and average needle length was computed. All needles were then placed in a paper bag and dried to a constant weight at 70°C. A relationship between HSA and the dry weight of each sample of needles was then calculated.

Nonlinear regression using untransformed data was used to develop allometric relationships between lodgepole pine sapling morphometry and AB and ANPP, and stepwise linear regression was used to develop an allometric equation for lodgepole pine LAI. Both approaches used preharvest measures of sapling morphometry. We tested for effects of stand density on the allometric equations but there were no significant differences; although tree size varied, the allometry between size and AB, ANPP, and LAI was not affected. Litton (2002) and Litton and others (2003) also found that carbon allocation patterns for coarse root biomass were independent of tree density for lodgepole pine in YNP. Therefore, a single model was developed, aggregating data from all stands. We tested equations based on the following attributes of each sapling: diameter at the base (cm), sapling height (cm), and the 1998 height growth increment (cm). For the nonlinear regression analyses, a power function was used of the form

$$Y = aX^b, \quad (2)$$

where Y is the dependent variable (lodgepole pine AB or ANPP), X is the independent variable (basal diameter, height, 1998 height growth increment), and a and b are equation constants derived through an iterative method (sequential quadratic programming algorithm). We also tested linear regression models using both untransformed and transformed data to examine relationships between lodgepole pine morphometry and AB and ANPP. Evaluation for goodness of fit of all models was conducted by a comparison of P -values, mean square of the error (MSE), sums of squares of the residuals (SSR), and coefficient of determination (r^2) for each model tested. Coefficients of determi-

nation were computed for all linear models using the equation:

$$r^2 = 1 - (\text{SSR} \div \text{Corrected SST}) \quad (3)$$

where SSR is the sum of squares of the residuals and SST is the total sum of squares. These statistical analyses were conducted using SAS (SAS Institute 1996) and SPSS (SPSS Inc. 1999).

Herbaceous and shrub AB, ANPP, and LAI. AB, ANPP, and LAI for herbaceous plants and shrubs were measured by correlating these parameters with percent cover during peak biomass (as estimated visually in the field)—an approach similar to that employed by Gilliam (1990). The peak biomass approach leads to underestimates of ANPP because of some losses to herbivory and detritus prior to harvest, but there is no practical alternative for broad-scale studies that require sampling many stands in remote areas accessible only by foot. Such losses also are probably minor because of the short growing season and lack of evidence for high levels of herbivory in our study areas. We identified 25 common plant species that represented the range of morphological characteristics of herbaceous and shrubby plants encountered in the burned forests (Table 2). For each species, we located populations in the field, then placed a series of 0.25-m² quadrats over the plants in positions that represented samples of increasing percent cover (for example, 1%, 5%, 10%, 25%, and 50%), as estimated visually, and clipped the aboveground plant material of that species within the quadrat. We thus obtained 5–8 samples of biomass and percent cover across the range of percent cover values that we had observed in the field for each species. Samples were returned to the laboratory and oven-dried at 70°C to a constant weight. Dry weights of herbaceous species represented the AB produced during a single year (1999), which we assumed to be equivalent to ANPP for that year. For shrub species, the leaves and stems produced during the current year were removed prior to drying and weighing. The dry weights of all species sampled were regressed against their percent cover (linear regression) to develop predictive relationships between percent cover and AB/ANPP.

Leaf area of herbaceous and shrub species was determined digitally. Subsamples of the leaves and photosynthetic stems of each of the 25 species were scanned on a Hewlett Packard ScanJet 6300C (Hewlett-Packard, Inc., Palo Alto, CA) flatbed scanner at 150-dpi resolution. Scanned images of the leaves and stems were converted in an intermediate step to .TIF images, and leaf area for each

Table 2. The 25 Plant Species that Represent the Range of Morphological Characteristics of the Herbaceous and Shrubby Plants Encountered in the Burned Forests of YNP

Species	Family	Common name	Structural form	Other species of similar form
Graminoids				
<i>Agrostis scabra</i>	Poaceae	Bentgrass	Thin-leaf grass	<i>Danthonia</i> sp.
<i>Calamagrostis canadensis</i>	Poaceae	Reedgrass	Broad-leaf grass	<i>Calamagrostis rubescens</i> , <i>Bromus</i> sp.
<i>Carex geyeri</i>	Cyperaceae	Geyer's sedge	Clump-forming sedge with linear leaves	<i>Carex rossii</i>
<i>Trisetum spicatum</i>	Poaceae	Trisetum	Raceme spike like	<i>Poa nervosa</i>
Forbs				
<i>Achillea millefolium</i>	Asteraceae	Yarrow	Erect, dissected leaves	<i>Chaenactis</i> sp.
<i>Agoseris glauca</i>	Asteraceae	False dandelion	Basal rosette of lanceolate/linear leaves	<i>Agoseris</i> sp.
<i>Anaphalis margaritacea</i>	Asteraceae	Pearly everlasting	Erect; entire leaves	<i>Eriophyllum</i> sp.
<i>Antennaria microphylla</i>	Asteraceae	Pussytoes	Caespitose	<i>Phlox</i> sp., <i>Campanula rotundifolia</i>
<i>Arabis</i> sp.	Brassicaceae	Rock Cress	Erect; clasping stem leaves; basal rosette	<i>Draba</i> sp.
<i>Arnica cordifolia</i>	Asteraceae	Heart-leaf arnica	Leaves heart-shaped, petiolate	<i>Arnica</i> sp.
<i>Aster meritus</i>	Asteraceae	Aster	Leaves lanceolate	<i>Erigeron</i> sp.
<i>Astragalus</i> sp.	Fabaceae	Milkvetch	Pinnate compound leaves; leaflets elliptic	<i>Hedysarum alpinum</i>
<i>Cirsium arvense</i>	Asteraceae	Canada thistle	Leaves spiny, dissected	<i>Cirsium</i> sp.; <i>Carduus</i> sp.
<i>Collinsia parviflora</i>	Scrophulariaceae	Blue-eyed Mary	Very tiny forb; leaves linear	<i>Collomia linearis</i>
<i>Epilobium angustifolium</i>	Onagraceae	Fireweed	Tall, erect, lanceolate leaves	<i>Senecio serra</i>
<i>Fragaria virginiana</i>	Rosaceae	Strawberry	Dentate basal leaves	<i>Thalictrum</i> sp.
<i>Gayophytum diffusum</i>	Onagraceae	Ground smoke	Small, delicate forb; leaves linear	<i>Epilobium paniculatum</i>
<i>Gnaphalium</i> sp.	Asteraceae	Cudweed	Erect; lanceolate leaves	<i>Gnaphalium</i> sp.
<i>Hieracium albiflorum</i>	Asteraceae	Hawkweed	Basal rosette of oblanceolate leaves	<i>Crepis</i> sp.
<i>Lupinus argenteus</i>	Fabaceae	Lupine	Palmately-compound leaves	<i>Lupinus</i> sp.
<i>Solidago</i> sp.	Asteraceae	Goldenrod	Basal and cauline leaves	<i>Senecio</i> sp, <i>Viola</i> sp.
<i>Taraxicum officianale</i>	Asteraceae	Dandelion	Basal leaves strongly dissected	<i>Lactuca serriola</i>
Shrubs				
<i>Vaccinium scoparium</i>	Ericaceae	Dwarf whortleberry	Ovate leaves	<i>Vaccinium</i> sp.

image was calculated to the nearest cm^2 using Scion Image for Windows software (National Institutes of Health, Bethesda, MD, 1999). Samples were then oven-dried to a constant weight at 70°C and a dry weight/leaf area coefficient was developed by dividing the measured leaf area by the dry weight of the scanned material for each percent cover sample. Final leaf area/dry weight coefficients were developed for each species by computing the mean coefficient value for all scanned samples. Biomass could therefore be predicted from nondestructive field estimates of percent cover for each species, and LAI could then be estimated using the appropriate leaf area/dry weight coefficient. Finally, we used the vegetation data obtained to characterize plant community structure in each

stand to estimate stand-level AB, ANPP, and LAI for each of the four study sites.

Estimation of Stand-level ANPP and LAI

The new allometric relationships for tree and herbaceous + shrub ANPP and LAI were used to estimate ANPP and LAI for each of the 90 plots. For tree ANPP, the regression equation was applied to each of the 25 measured trees in each plot, and a mean value for ANPP and leaf area per tree was determined. The mean values were then multiplied by sapling density to predict tree ANPP ($\text{Mg ha}^{-1}\text{y}^{-1}$) and LAI ($\text{m}^2 \text{m}^{-2}$) for each plot. For herbaceous species and shrubs, the allometric relationships based on percent cover were applied to

the percent cover of each species recorded in the 25 quadrats within the plot. In some cases, the same allometric relationship was applied to more than one species with similar growth forms (for example, *Carex rossii* Boott and *Carex geyeri* Boott). Total herb/shrub ANPP and LAI were obtained by summing across all species. Because shrub cover was extremely low in the plots, we refer to the herbaceous plus shrub ANPP and LAI as "herbaceous" through the rest of this article. Total ANPP and LAI for each sampling plot were determined by summing the tree and herbaceous estimates. All values were reported in $\text{Mg ha}^{-1}\text{y}^{-1}$ and $\text{m}^2 \text{m}^{-2}$.

ANOVA was used to explain variability in total ANPP and LAI as a function of lodgepole pine density, elevation, and soil category, with Type III sums of squares interpreted for significance of independent variables. Elevation was categorized into three classes using ordinal variables: (1) 2300 m or lower, (2) 2301–2500 m, and (3) above 2500 m. Models were estimated separately with and without sapling density to determine how much variation in ANPP and LAI could be explained by abiotic variables alone. Significant differences among means were evaluated using Tukey's Studentized range test. Significant interactions among main effects were examined using scatter plots and regression analysis. Prior to analysis, total ANPP was square root transformed, and LAI was transformed using $\log_{10}(\text{LAI} + 1)$ to achieve normal distributions.

The proportion of total ANPP contributed by herbaceous vegetation and trees was determined for each plot and regressed against lodgepole pine sapling density. ANOVA was also used to examine variability in tree and herbaceous ANPP and LAI among the 90 plots as a function of sapling density, elevation class, and soil class. All statistical analyses were performed using SAS (SAS Institute 1996).

Landscape Patterns of ANPP and LAI

To predict spatial patterns of ANPP and LAI within the area burned by the 1988 fires, multiple regression models were developed for total ANPP and LAI using sapling density class and elevation class of the 90 sampled plots. The regression models were then applied to 0.25-ha grid cells within a GIS environment (Arc/Info; ESRI 1992) using the appropriate independent variables for each cell. Values of sapling density for each cell were obtained from the classified aerial photos. The range of predicted ANPP and LAI was divided into 5 classes for map display and analysis. FRAGSTATS (McGarigal and Marks 1995) was used to evaluate the spatial

heterogeneity of ANPP and LAI distributions across the landscape. The same landscape metrics used for the sapling density classes were also used for the ANPP and LAI classes.

To assess accuracy of the extrapolated landscape patterns of ANPP and LAI, the predicted values from the map were compared with independent data collected at 41 locations during the summer of 2000 within the 1988 burn using the same field methods described above (Schoennagel 2002). The UTM of the center of each of the 41 field plots was located on the map of ANPP. Because these plot centers were not centered within the map grid cells (that is, the center of a field plot could occur at the corner of a map cell), accuracy was assessed by examining the cell in which the plot center was located and the four nearest neighbor cells. Thus, we used a window of ± 50 m for locating the plot within the grid. A prediction was scored as correct if at least one of these cells matched the ANPP or LAI class as measured in the field.

RESULTS

Variability and Pattern of Postfire Lodgepole Pine Density

The density of lodgepole pine saplings in the 90 sample plots spanned six orders of magnitude, ranging from 0 to 535,000 stems ha^{-1} (note that all plots had been forested when they burned in 1988). Mean sapling density was 29,381 stems ha^{-1} (SE = 8824), but the median density was only 3100 stems ha^{-1} . Variation in sapling density was explained largely by elevation (partial $r^2 = 0.34$, $F = 43.136$, $P < 0.0001$); distance to unburned forest was significant but explained only 3% more of the variation ($F = 3.922$, $P = 0.0509$). Lodgepole pine sapling density declined significantly with increasing elevation (Figure 2) and increasing distance from unburned forest. Although significant, the overall model explained only 37% of the variation in measured sapling density. Neither fire severity as recorded from 1989 Landsat imagery nor soil type explained variation in sapling density, and local measurements of prefire serotiny could not be made 11 years after the fires.

The 11-year-old lodgepole pine saplings ($n = 2248$ saplings) averaged 81 cm in height with a maximum height of 294 cm. The mean 1998 height increment among trees was 17.2 cm, and mean basal diameter was 2.5 cm with a maximum of 10.7 cm. Among the 25 saplings measured within a plot, the coefficient of variation for morphological characteristics and 1998 height incre-

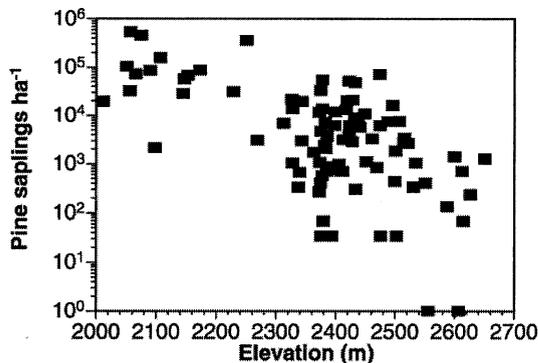


Figure 2. Lodgepole pine sapling density vs. elevation as measured in 90 plots (0.25-ha) in YNP. All stands burned in 1988 and were sampled in 1999 ($n = 88$) or 2000 ($n = 2$).

ment was generally less than 40%. Among the 90 plots, mean sapling height was best explained by a nonlinear model including sapling density, elevation and soil class (regression model, $r^2 = 0.58$, Adj. $r^2 = 0.56$, $P < 0.0001$). The relationship of height with sapling density was quadratic, with greater heights at intermediate sapling densities; mean sapling height also declined with increasing elevation and increasing soil fertility. The mean 1998 height increment was similarly predicted with a quadratic relationship with sapling density and a negative relationship with elevation; soil fertility was not significant (regression model, $r^2 = 0.69$, Adj. $r^2 = 0.67$, $P < 0.0001$). The model for mean basal diameter followed the same trends (regression model, $r^2 = 0.64$, Adj. $r^2 = 0.62$, $P < 0.0001$). Among the 90 plots, mean sapling height, 1998 growth increment, and basal diameter were all positively correlated ($r^2 > 0.80$, $P < 0.0001$).

The sapling density map produced from supervised classification and interpretation of the aerial photos (Figure 3) was 75% accurate using the six sapling density classes (Kashian 2002; Kashian and others in press). Approximately 66% of the area burned by the 1988 fires had postfire stand densities of less than 5000 saplings ha^{-1} (Table 3). However, nearly 25% of the burned area had densities greater than 10,000 saplings ha^{-1} and about 7% of the landscape had densities exceeding 50,000 saplings ha^{-1} . Although there was a general tendency for high-density classes to occur in the west-central portion of the Yellowstone Plateau and low-density classes to occur in the south and south-central region (Figure 3), the spatial analyses revealed a fine-grained mosaic of density class variation across the overall landscape. The burned YNP landscape was dominated by the lower-density

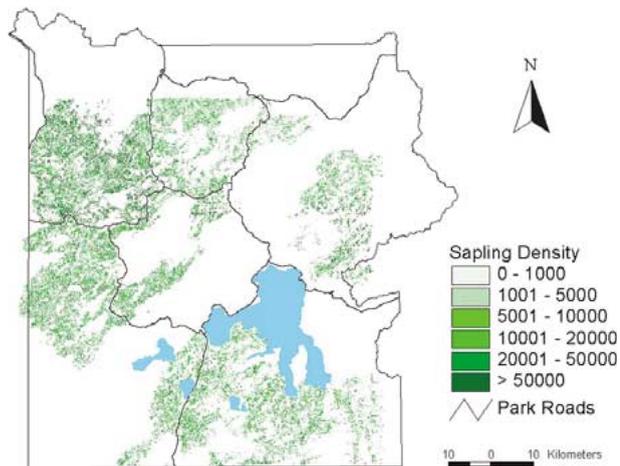


Figure 3. Mapped lodgepole pine sapling density derived from 1988 1:30,000 color IR aerial photographs. Overall map accuracy using six categories of sapling density was 76%.

classes (less than 5000 ha^{-1}), and the area-weighted mean patch sizes reflect the larger patch sizes of these low-density classes (Table 3). Patches of high-density saplings tended to be 2–6 ha in size (Table 3). However, the patch densities for most sapling density classes were surprisingly similar, ranging from 16 to 21 patches/100 ha (Table 2), but the highest-density class had the lowest patch density. The index of clumpiness was generally similar among the sapling density classes (Table 3), suggesting a similar, near-random spatial dispersion of density classes. For the overall landscape, Shannon's Evenness Index was relatively high (0.87), indicating dominance of the landscape by relatively few classes, yet contagion was relatively low (17%), indicating fine-grained dispersion of the density classes. Collectively, the landscape metrics describe a matrix of larger patches of low-density lodgepole pine that is randomly interspersed with smaller patches of higher pine densities.

Allometric Relationships

Lodgepole Pine Aboveground Biomass Allocation. For all 120 harvested saplings, the mean biomass per sapling was 245 g. The majority of AB allocation in the developing saplings was accounted for by foliage. Of the AB, 44.8% (110 g) was in needles, only 19.0% (47 g) was in branches, and 36.2% (89 g) of AB was in stem wood (Table 4). Mean sapling AB decreased with increasing sapling density (Table 4). Notably, mean AB for saplings in the highest-density stand (454,000/ha) was only 10.3 g per sapling, compared with 229–373 g per

Table 3. The Spatial Distribution of Lodgepole Pine Sapling Density Classes in 1999 within the Subalpine Plateaus of Yellowstone National Park burned in 1988^a

Pine sapling density (No. ha ⁻¹)	Proportion of landscape	Patch density (No./100 ha)	Area-weighted mean patch size (ha)	Clumpiness index (unitless)
<1000	0.36	18	179	0.30
1001–5000	0.30	21	51	0.22
5001–10,000	0.10	17	1.6	0.13
10,001–15,000	0.08	16	3.3	0.15
15,001–50,000	0.09	17	1.5	0.12
>50,000	0.07	10	5.9	0.25

^aPine sapling density was mapped from 1:30,000 color infrared aerial photographs (see Methods). Spatial pattern analyses were conducted using FRAGSTATS (McGarigal and Marks 1995) with a raster map of 50-m × 50-m cells.

Table 4. Mean Needle, Branch, Stem, and Total Aboveground Biomass for All 120 Lodgepole Pine Saplings, and for Those from Each Study Site ($n = 30$)^a

SITE	Needle Biomass (g/sapling)		Branch Biomass (g/sapling)		Stem Biomass (g/sapling)		Total Aboveground Biomass (g/sapling)
	Mean (SE) (CV)	% of total	Mean (SE) (CV)	% of total	Mean (SE) (CV)	% of total	Mean (SE) (CV)
All sites ($n = 120$)	109.7 (13.2) (1.3)	44.8	46.5 (8.0) (1.9)	19.0	88.6 (10.2) (1.3)	36.2	244.8 (30.7) (1.4)
Pitchstone ($n = 30$)	163.8 (38.8) (1.3)	43.9	82.0 (28.3) (1.9)	22.0	127.0 (27.1) (1.2)	34.1	372.8 (93.0) (1.4)
Riddle Lake ($n = 30$)	169.8 (23.6) (0.7)	46.3	62.7 (10.4) (0.9)	17.1	134.2 (22.1) (0.9)	36.6	366.7 (55.2) (0.8)
Fern ($n = 30$)	101.9 (12.6) (0.7)	44.4	40.1 (5.2) (0.7)	17.5	87.3 (11.8) (0.7)	38.1	229.3 (27.5) (0.7)
Gravel pit ($n = 30$)	3.1 (0.6) (1.1)	30.1	1.4 (0.3) (1.2)	13.6	5.8 (0.9) (0.9)	56.3	10.3 (1.8) (0.9)

^aThe proportions of each compartment to the total biomass values are also shown. **Bold** values in parentheses represent one standard error; italicized values in parentheses represent the coefficient of variation.

sapling in the three lower-density stands (Table 4). Biomass allocation patterns to stem, branch, and foliage differed only for the highest-density stand but were similar among the other three stand densities (Table 4). In the three lower-density stands, approximately 44%–46% of the biomass was in needles, 17%–22% in branches and twigs, and 34%–38% in stems. In contrast, in the high-density stand, only 30.1% was in needles, 13.6% in branches, and the majority of AB (56.3%) was allocated to stems (Table 4). Total lodgepole pine AB per stand (computed by stand density × mean tree biomass) was 0.28 Mg ha⁻¹ in the lowest-density

stand (767 ha⁻¹), 3.3 Mg ha⁻¹ in the moderate-density stand (9000 ha⁻¹), 7.6 Mg ha⁻¹ in the high-density stand (33,000 ha⁻¹), but dropped to 4.7 Mg ha⁻¹ in the highest-density stand (454,000 ha⁻¹).

Allometric Models for Predicting Lodgepole Pine AB, ANPP, and LAI. Nonlinear regression provided the best models for predicting total lodgepole pine biomass, lodgepole pine biomass allocation by compartment, and lodgepole pine ANPP (r^2 values range from 0.86 to 0.92; $P < 0.005$; Figure 1 and Table 5). Sapling diameter at the base explained more of the variation in lodgepole pine biomass and ANPP than did sapling height and 1998 height

Table 5. Allometric Equations for Predicting Aboveground Net Primary Productivity (ANPP), Total Aboveground Biomass, and Aboveground Biomass by Component (g dry weight) from Outside Bark Basal Diameter (cm), and Leaf Area (mm²) from Foliage Biomass (g dry weight) for 10-year-old *Pinus contorta* var. *latifolia* in Yellowstone National Park, WY

Dependent variable	<i>n</i>	<i>a</i> (SE)	<i>b</i> (SE)	MSE	<i>r</i> ²	<i>F</i> -ratio	<i>P</i>
ANPP	120	9.539 (1.286)	2.577 (0.092)	2610.98	0.89	786.45	<0.005
Total aboveground biomass	120	13.144 (1.762)	2.888 (0.089)	10530.69	0.91	920.13	<0.005
Stem biomass	120	8.604 (1.262)	2.435 (0.101)	1781.48	0.86	625.96	<0.005
Branch biomass	120	0.416 (0.077)	4.183 (0.113)	604.82	0.92	917.47	<0.005
Foliage biomass	120	7.193 (1.021)	2.729 (0.095)	2382.14	0.89	763.53	<0.005
Leaf area	90	4896.3 (184.2)	1288.9 (249.2)	578244.7	0.89	706.4	<0.001

Note: Equations for ANPP and all biomass components are of the form $Y = aX^b$, where *Y* is the dependent variable in g dry weight (for example, ANPP) and *X* is outside bark basal diameter (cm). *a* and *b* are constants in the equation, SE is the asymptotic standard error of the parameter estimate, MSE is the mean square of the error, and *R*² is the coefficient of determination. *F*-ratio and *P*-level of models are also indicated. The equation for leaf area is of the form $Y = aX + b$, where *Y* is the dependent variable in mm², *X* is total needle biomass (g dry weight), *a* is the slope, and *b* is the *y*-intercept. *R*² is the adjusted *r*², calculated from Pearson's correlation coefficient.

growth increment, for both nonlinear and linear regression approaches. Total needle biomass (dry weight) was the best predictor of lodgepole pine leaf area ($r^2 = 0.89$, $P < 0.001$; Table 5).

The equations were relatively insensitive to stand density. Using stand density of the four study sites as a class variable in ANOVA, only 5%–10% of the variability in the residuals for the allometric equations was attributable to stand density. The ANPP allometric equation was the least sensitive to stand density ($r^2 = 0.05$, $P > 0.05$), and the foliage biomass model was most sensitive to stand density ($r^2 = 0.10$, $P < 0.05$).

Allometric Models for Predicting Herbaceous ANPP and LAI. Percent cover of herbaceous plants was strongly correlated with dry weight (AB and ANPP) for the 24 species tested (Table 6). The r^2 values for all regression models ranged from 0.88 to 0.99. The single shrub model, developed using estimates of percent cover of *Vaccinium scoparium*, provided the least robust model with an r^2 value of 0.84. Note that for some herbaceous species, very low field estimates of percent cover (less than 0.5%) required separate models that forced the intercept through the origin (Table 6).

Variability in Stand-Level ANPP and LAI

Total ANPP and LAI. Total ANPP in the 90 plots ranged from 0.04 to 15.12 Mg ha⁻¹y⁻¹ with a mean of 2.80 Mg ha⁻¹y⁻¹. Total LAI ranged from 0.01 to 6.87 m² m⁻² with a mean of 0.80 m² m⁻². Results of ANOVA revealed that 80% of the variation in both ANPP and LAI was explained, with lodgepole pine density being the most important independent variable (Table 7). ANPP and LAI increased with lodgepole pine density ($r^2 = 0.56$ and 0.81, re-

spectively; Figure 4a and b) and declined with increasing elevation (Figure 5a and b). Among soil classes, ANPP was significantly higher on rhyolitic till compared with the other three soil types, which did not differ from one another (Figure 5c). Similarly, LAI was highest on rhyolitic till, lower on the other two rhyolite-derived soils, and lowest on andesite (Figure 5d). There were significant interactions between lodgepole pine density and both elevation and soil type (Table 7). Regression analyses to explore these interactions showed that ANPP was generally high but varied weakly with lodgepole pine density at low elevations ($P = 0.06$, $r^2 = 0.24$) and varied strongly with density at intermediate elevations ($P < 0.0001$, $r^2 = 0.66$). At high elevations, ANPP was generally low and did not vary significantly with pine density ($P = 0.53$). Regression analyses of LAI by elevation class were similar, with weaker relationships at both low and high elevations ($P = 0.03$, $r^2 = 0.30$ and $P = 0.02$, $r^2 = 0.33$, respectively) and strong, positive relationships at intermediate elevations ($P < 0.001$, $r^2 = 0.62$).

Although the relationship between total ANPP and lodgepole pine density across all plots was strong (Figure 4 and Table 7), the relationship varied with tree density. When lodgepole pine density was 1000 or more saplings/ha, there was a strong positive relationship between total ANPP and tree density ($r^2 = 0.70$). However, when lodgepole pine density was less than 1000 saplings/ha, total ANPP was not significantly correlated with tree density. In these sparse stands, total ANPP was generally low (mean of 1.26 Mg ha⁻¹y⁻¹), and most (70%–100%) of the total ANPP was herbaceous. In contrast, there was a strong increase in LAI with lodgepole pine density over the full range

Table 6. Regression Models Developed to Predict ANPP (that is, Aboveground Biomass, in grams) for Graminoids, Forbs, and Shrubs Based on Percent Cover Estimates^a

Species groups	Equation coefficients		r^2	LAI/biomass coefficients
	a	b		
Graminoids				
<i>Agrostis scabra</i>	0.5794	0.0536	0.91	269.1
<i>Calamagrostis canadensis</i>	0.5395	1.0525	0.99	269.1
<i>Carex geyeri</i>	2.235	-7.201	0.96	122.0
	2.0154*	0*	0.94	
<i>Trisetum spicatum</i>	0.8483	0.8356	0.98	269.1
Forbs				
<i>Achillea millefolium</i>	0.4248	0.0583	0.98	130.1
<i>Agoseris glauca</i>	0.1668	6.7305	0.97	29.7
<i>Anaphalis margaritacea</i>	0.7852	0.843	0.98	165.7
<i>Antennaria microphylla</i>	0.6598	-0.9515	0.92	210.9
	0.5941*	0*	0.91	
<i>Antennaria rosea</i>	0.8716	-1.5354	0.99	210.9
	0.8244*	0*	0.99	
<i>Arabis</i> sp.	1.2094	-0.0416	0.88	91.8
	1.2029*	0*	0.88	
<i>Arnica cordifolia</i>	0.4335	-0.6221	0.99	225.2
	0.3828*	0*	0.97	
<i>Aster meritus</i>	0.2649	0.2067	0.95	190.4
<i>Astragalus</i> sp.	0.4165	-0.8961	0.95	181.8
	0.3871*	0*	0.94	
<i>Cirsium arvense</i>	0.7851	-0.1786	0.97	103.6
	0.7682*	0*	0.97	
<i>Collinsia parviflora</i>	0.384	-0.03	0.98	183.4
	0.374*	0*	0.98	
<i>Epilobium angustifolium</i>	0.541	0.3088	0.98	194.4
<i>Fragaria virginiana</i>	0.3598	-0.1136	0.91	189.0
	0.3494*	0*	0.91	
<i>Gayophytum diffusum</i>	0.0835	-0.0267	0.99	120.0
	0.0797*	0*	0.99	
<i>Ghaphalium</i> sp.	1.0547	0.8941	0.98	174.2
<i>Hieracium albiflorum</i>	0.1786	0.1864	0.97	159.6
<i>Lupinus argenteus</i>	0.6144	-1.2602	0.99	190.3
	0.5782*	0*	0.99	
<i>Solidago</i> sp.	0.6618	1.0342	0.98	175.6
<i>Taraxicum officianale</i>	0.3381	0.2055	0.93	233.6
Shrubs				
<i>Vaccinium scoparium</i>	0.7134	0.372	0.84	158.7

^aEquations are all in the form of $Y = aX + b$, where Y is dry weight in grams, a is the slope, and b is the y-intercept. Coefficients denoted with an asterisk are used for percent cover estimates less than 0.5%. LAI/biomass coefficients are used to estimate LAI from dry weights ($LAI = \text{dry weight} \times \text{coefficient}$).

of densities. Even at densities less than 1000 saplings/ha, LAI was still largely explained by variation in lodgepole pine density and the interaction between density and elevation (ANOVA, $r^2 = 0.68$, $P = 0.0001$).

When ANOVA models were run excluding lodgepole pine density from the predictor variables, elevation and soil class explained 54% of the variation in total ANPP (DF = 89, MSE = 2.034, $F = 10.30$, $P < 0.0001$), and elevation alone ex-

plained 51% of the variation in total LAI (DF = 89, MSE = 0.221, $F = 9.30$, $P < 0.0001$). Soil category was no longer significant in the model for LAI.

Components of Total ANPP and LAI. The proportion of total ANPP contributed by herbaceous plants and shrubs declined sharply with increasing lodgepole pine sapling density ($r^2 = 0.72$, $P < 0.0001$; Figure 6) and increased with elevation ($r^2 = 0.36$, $P < 0.0001$). Although the relative contributions of herbaceous vegetation and trees to

Table 7. ANOVA Results Pertaining to the Variation in Stand-Level Total ANPP and LAI in 90 0.25-ha plots located in that portion of Yellowstone National Park that Burned in 1988^a

Predictor variable	DF	Type III MSE	F	P
Total ANPP (model $r^2 = 0.81$, $P < 0.0001$, $df = 89$)				
Pine density	1	4.23	49.18	<0.0001
Elevation class	2	1.37	15.95	<0.0001
Soil category	3	0.57	6.65	0.0005
Pine density \times elevation class	2	1.24	14.49	<0.0001
Pine density \times soil category	4	0.64	7.44	<0.0001
Total LAI (model $r^2 = 0.80$, $P < 0.0001$, $df = 89$)				
Pine density	1	0.620	61.51	<0.0001
Elevation class	2	0.128	12.68	<0.0001
Soil category	3	0.045	4.49	0.0059
Pine density *elevation class	2	0.133	13.22	<0.0001
Pine density *soil category	4	0.053	5.23	0.0009

^aTotal ANPP was square root transformed, and LAI and pine density were log transformed prior to analysis.

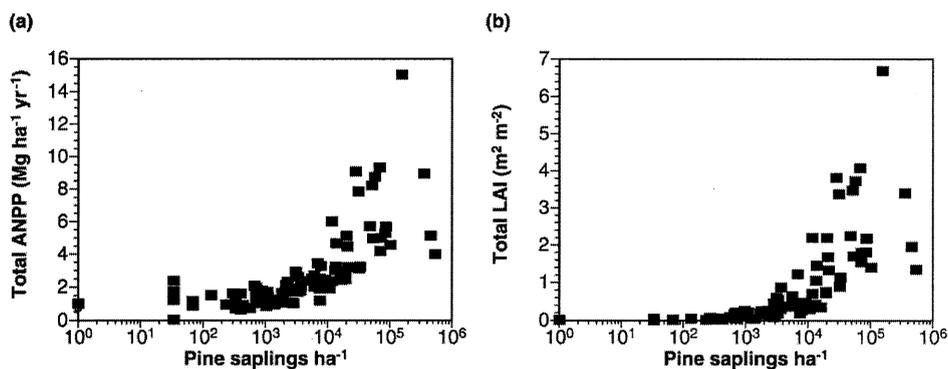


Figure 4. Total ANPP and LAI as a function of lodgepole pine sapling density in ninety 0.25-ha plots sampled in 1999 ($n = 88$) or 2000 ($n = 2$).

total ANPP varied with sapling density, herbaceous productivity did not compensate for tree production when trees were sparse.

Tree ANPP averaged $1.71 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ but ranged widely from 0 to $14.59 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, thus spanning most of the range of total ANPP. Tree ANPP varied with sapling density, elevation, and soil category (Table 8), and most of the variation in tree ANPP was explained by these factors ($r^2 = 0.87$). Lodgepole pine density and the interaction of pine density and elevation class were the most important predictors, and the relationships were similar to those described for total ANPP. Lodgepole pine LAI averaged $0.8 \text{ m}^2 \text{ m}^{-2}$ and varied from 0 to $6.86 \text{ m}^2 \text{ m}^{-2}$. Tree LAI was also strongly correlated with variation in lodgepole pine sapling density and elevation class, and, again, most of the variation was explained by these variables (Table 8).

Herbaceous ANPP averaged $1.09 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and ranged only from 0.02 to $2.72 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in the 90

plots, spanning only 25% of the range of total ANPP. Herbaceous LAI was also low, averaging $0.02 \text{ m}^2 \text{ m}^{-2}$ and ranging from 0.00 to $0.04 \text{ m}^2 \text{ m}^{-2}$. The proportion of total ANPP that was herbaceous declined sharply with increasing pine sapling density (Figure 6a). Results of ANOVA (Table 8) indicated that herbaceous productivity was related to tree ANPP, declining as tree ANPP increased (Figure 6b); however, only 27% of the variation was explained (Table 8). Despite the low r^2 , two qualitatively different regions are apparent in the plot of herbaceous vs tree ANPP (Figure 6b). At relatively high tree ANPP (more than $5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), herbaceous ANPP is less variable and consistently low (less than $1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$); at relatively low tree ANPP (less than $5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) herbaceous ANPP varies widely from 0 to $2.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. Herbaceous LAI also declined with tree ANPP, varied among soil categories (Table 8), and was significantly greater on andesitic compared to the rhyolitic soil

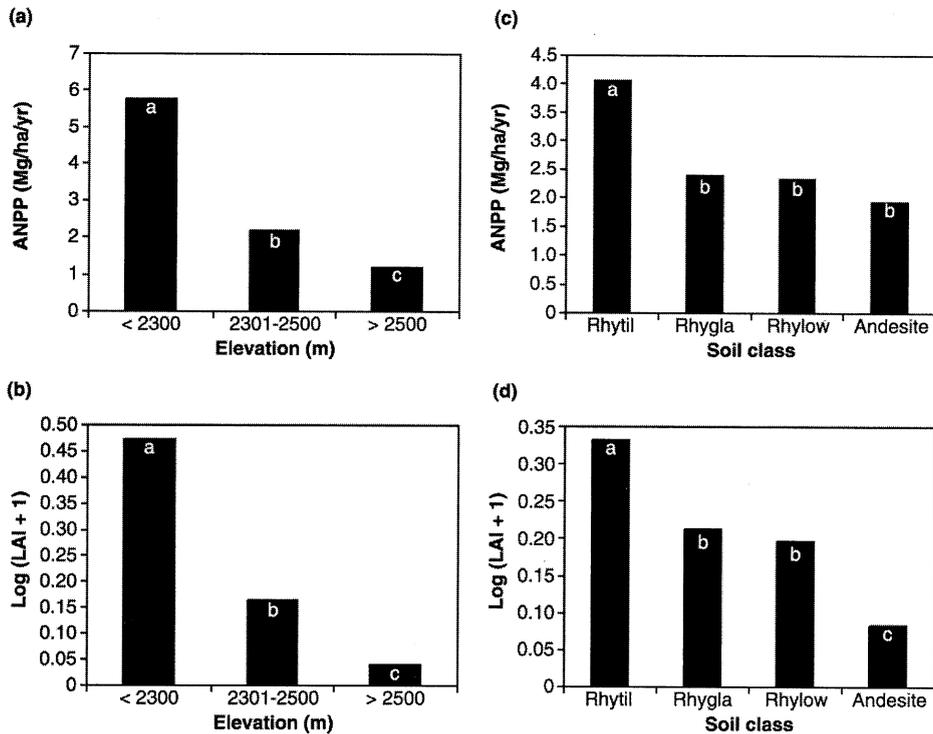


Figure 5. Total ANPP and LAI in ninety 0.25-ha plots sampled in 1999 ($n = 88$) or 2000 ($n = 2$) as a function of elevation (a, b) and soil class (c, d). Means with different letters indicate significant differences (Tukey's Studentized range test).

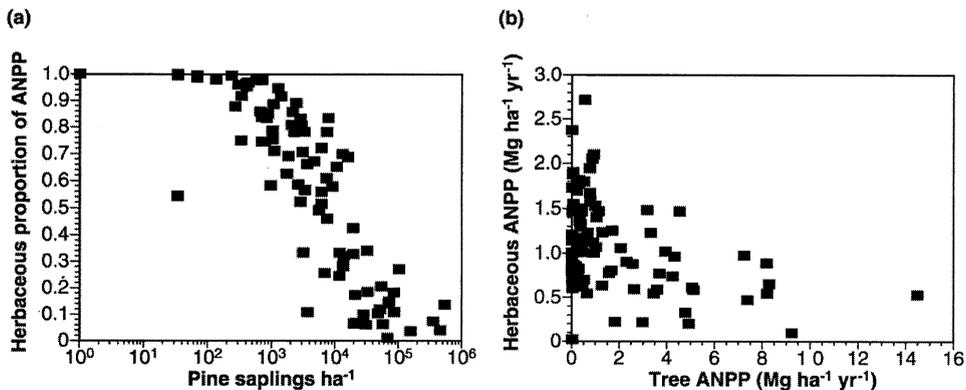


Figure 6. (a) Proportion of total ANPP contributed by herbaceous plants and shrubs as it varies with log density of lodgepole pine saplings ($r^2 = 0.73$). The proportion of total ANPP contributed by the pine saplings is the inverse of this pattern. (b) Herbaceous ANPP plotted as it varies with tree ANPP. Data are from ninety 0.25-ha plots sampled in 1999 ($n = 88$) or 2000 ($n = 2$).

types (Tukey's Studentized range test, $P < 0.05$). Again, explained variance was relatively low ($r^2 = 0.31$).

Landscape Patterns of ANPP and LAI

The allometric models for ANPP and LAI of lodgepole pine saplings and understory species were highly predictive, and lodgepole pine density was a

significant predictor for total ANPP and LAI at the stand level (results above). Because there were significant interactions including lodgepole pine density in the ANOVA models, regression models were estimated separately for densities of 1000 or more ha⁻¹ and less than 1000 ha⁻¹. Predictive power was good for the higher-density stands ($r^2 > 0.69$), and we applied the following ANPP model to stands with sapling densities greater than 1000 ha⁻¹. Sapling

Table 8. ANOVA Results Pertaining to Variation in Tree and Herbaceous ANPP and LAI Considered Separately^a

Predictor variable	DF	Type III MSE	F	P
Tree ANPP (model $r^2 = 0.87$, $P < 0.0001$, $df = 89$)				
Pine density	1	1.644	13.97	0.0004
Elevation class	2	0.974	8.28	<0.0006
Soil category	3	0.264	2.24	0.0903
Pine density * elev class	2	1.351	11.49	<0.0001
Soil category*elevclass	4	0.224	1.90	0.1193
Pine density * soil category	3	0.444	3.77	0.0140
Tree LAI (model $r^2 = 0.85$, $P < 0.0001$, $df = 89$)				
Pine density	1	0.686	12.18	0.0008
Elevation class	2	0.439	7.81	<0.0008
Soil category	3	0.164	2.92	0.0396
Pine density * elev class	2	0.581	10.31	0.0001
Soil category*elev class	4	0.108	1.93	0.1151
Pine density * soil category	3	0.257	4.57	0.0054
Herbaceous ANPP (model $r^2 = 0.27$, $P = 0.0003$, $df = 89$)				
Tree ANPP	1	0.986	4.71	0.0329
Soil category	3	0.345	1.65	0.1848
Tree ANPP * soil cat	3	0.153	0.73	0.5362
Herbaceous LAI (model $r^2 = 0.31$, $P < 0.0001$, $df = 89$)				
Tree ANPP	1	0.00017	4.02	0.0481
Soil category	3	0.00012	2.85	0.0423
Tree ANPP * soil cat	3	0.000027	0.65	0.5880

^a Tree ANPP was square root transformed, and tree LAI and pine density were log transformed prior to analysis. Herbaceous ANPP and LAI were normally distributed and thus not transformed.

density was the only predictor used; when elevation was included in the regression model, the model r^2 increased only by 0.01 with a $P = 0.09$.

$$\begin{aligned} \text{sqrt}[\text{Total ANPP}(\text{Mg ha}^{-1}\text{y}^{-1})] &= 0.177 \\ &+ 0.285(\log_{10}\text{ pine sapling density}). \end{aligned} \quad (4)$$

The predictive models for ANPP in low-density sites was poor; therefore, we applied the mean value of ANPP observed in the low-density plots ($1.25 + 0.2 \text{ Mg ha}^{-1}\text{y}^{-1}$) to cells with lodgepole pine density less than 1000 ha^{-1} . LAI was strongly related to sapling density across the full range of densities; therefore, regression models were used to predict LAI in all cells based on pine sapling density:

$$\begin{aligned} \log[\text{Total LAI}(\text{m}^2\text{m}^{-2})] &= -0.612 \\ &\times (\log_{10}\text{ pine sapling} \\ &\times \text{density} + 1) \times -2.672, \end{aligned}$$

$$\text{Model } r^2 = 0.83. \quad (5)$$

Results of the landscape predictions of ANPP and LAI (Figure 7) produced a heterogeneous mosaic of

ANPP varying from 1.26 to $10.27 \text{ Mg ha}^{-1} \text{ y}^{-1}$ and of LAI ranging from 0.02 to more than $2.0 \text{ m}^2 \text{ m}^{-2}$. When compared with independent field estimates, ANPP class was correctly predicted in 83% of 41 plots, and LAI class was correctly predicted in 80% of the plots.

Approximately 68% of the burned landscape was characterized by total ANPP values less than $2.0 \text{ Mg ha}^{-1}\text{y}^{-1}$, representing the area of the landscape dominated by low-density lodgepole pine. Approximately 22% of the burned landscape had ANPP values ranging from 2 to $4 \text{ Mg ha}^{-1}\text{y}^{-1}$, and the remaining 10% of the landscape had ANPP values greater than $4 \text{ Mg ha}^{-1}\text{y}^{-1}$. Nearly 70% of the landscape had total LAI values of 0.50 or less $\text{m}^2 \text{ m}^{-2}$, and about 15% had values between 0.51 and $1.0 \text{ m}^2 \text{ m}^{-2}$. Only 15% of the burned landscape was characterized by values greater than $1.0 \text{ m}^2 \text{ m}^{-2}$.

The spatial pattern of ANPP across the landscape was less heterogeneous than the spatial pattern of sapling density. The range of variation of ANPP was much less, spanning two orders of magnitude rather than the six orders of magnitude observed in sapling density. The patch densities and sizes of the ANPP classes varied considerably. The low-ANPP class had moderate patch densities and a very high

Table 9. Results from Analysis of the Spatial Patterns of Predicted ANPP and LAI Classes in 1999 within the Area of the Subalpine Plateaus in Yellowstone National Park Burned in 1988^a

	Proportion of landscape	Patch density (No./100 ha)	Area-weighted mean patch size (ha)	Clumpiness index (unitless)
ANPP class (Mg ha⁻¹ y⁻¹)				
<2.0	0.68	8	4280	0.25
2.01–4.0	0.22	15	19	0.25
4.01–6.0	0.08	13	7	0.23
6.01–8.0	0.02	3	2	0.21
>8.0	0.003	0.8	0.5	0.09
LAI class (m² m⁻²)				
0.002–0.50	0.81	4.8	12,107	0.01
0.51–1.0	0.10	14.3	3.5	0.19
1.01–1.50	0.03	6.1	1.3	0.15
1.51–2.0	0.04	5.9	6.6	0.29
>2.0	0.02	4.2	2.4	0.23

^aThe predictions were based on 1999 pine sapling density mapped from 1:30,000 color infrared aerial photographs (Figure 3) and the equations shown in Tables 5 and 6. Spatial pattern analyses were conducted using FRAGSTATS (McGargigal and Marks 1995) with a raster map of 50-m × 50-m cells.

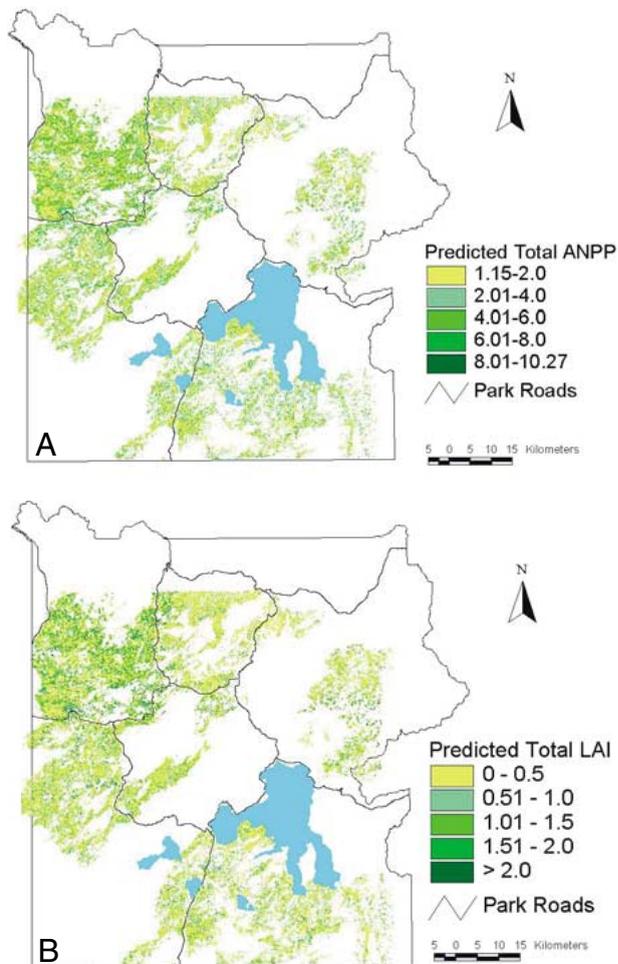


Figure 7. Predicted values of (A) ANPP and (B) LAI for 0.25-ha cells within the burned portion of the subalpine plateau in YNP.

area-weighted mean patch size (Table 9). In contrast, the high-ANPP classes had extremely low patch densities and very small area-weighted mean patch sizes (Table 9). Thus, patches of very high ANPP were small and relatively infrequent across the landscape, although they were still randomly distributed, as indicated by the index of clumpiness (Table 9). Across the burned landscape, Shannon's Evenness Index was lower for ANPP (0.54) than for sapling density (0.87), but contagion was substantially higher for ANPP (51%) compared with sapling density (17%). Nonetheless, despite the increased dominance of large patches of relatively low ANPP, these metrics suggest widespread distribution of smaller patches of high productivity associated with patterns of high tree density across the landscape.

The spatial pattern of LAI across the landscape was qualitatively similar to that of ANPP, but low LAI values were even more dominant, occupying 81% of the burned landscape and having a very large area-weighted mean patch size (Table 9). Patches of the highest LAI value occupied just 2% of the landscape and had a similar distribution to the two highest ANPP classes. LAI patches also had a random spatial distribution.

DISCUSSION

Variability and Pattern of Postfire Lodgepole Pine Density

The postfire variation in lodgepole pine density across the YNP landscape was extremely high,

spanning six orders of magnitude. Although lodgepole pine is well known for its ability to recolonize following fire, this degree of variability in postfire stocking densities was striking. Using the postfire data available for this study 11 years after the fires, we could explain only 37% of the variation in early stand density, leaving most of the variance unexplained. Explanatory power would probably improve if accurate measurements of key variables identified in earlier studies (for example, Anderson and Romme 1992, Turner and others 1997, 1999), namely, prefire serotiny and fire severity, could be obtained across the landscape. The relationship between postfire stand density and local stand serotiny measured directly in the field is strong (Anderson and Romme 1991; Ellis and others 1994; Turner and others 1997, 1999), but serotiny must be recorded within the first several years following fire. Serotiny levels are related to elevation and stand age (Tinker and others 1994; Schoennagel and others 2003), but they cannot be predicted with high confidence across the landscape ($r^2 \sim 0.60$; Schoennagel and others 2003). The influence of elevation on postfire stand density may reflect the general tendency of serotiny to increase at lower elevations. However, understanding the controls on spatial and temporal variation in serotiny in lodgepole pine would likely improve the ability to predict postfire densities of lodgepole pine.

Similarly, local variation in fire severity as measured directly in the field influences postfire stand density (Anderson and Romme 1991; Turner and others 1997, 1999). Lodgepole pine densities are significantly greater in areas of severe-surface fires compared with crown fires, and distance from a severe-surface fire is also significant (Turner and others 1997, 1999). In the current study, however, we relied on fire severity as interpreted from Landsat imagery (Turner and others 1994) because variation in the severity of stand-replacing fires cannot be assessed in the field 11 years after the fire. The apparent absence of a significant influence of fire severity in this study probably reflects the scale and accuracy of the satellite classification rather than a lack of influence. Thus, we suggest that the inability to reconstruct accurately the spatial heterogeneity of important variables limits the ability to explain or predict broad-scale variation in sapling density.

The largest lodgepole pine saplings, as indicated by sapling height and basal diameter, were found at intermediate sapling densities (approximately 10^3 – 10^4 stems ha^{-1}) and at lower elevations. Lower elevations in YNP have substantially longer growing season than higher elevations. For example, at about 2100 m, snow accumulation begins on Octo-

ber 23, reaches its maximum accumulation on April 5, and melts out by May 24 (Despain 1990). In contrast, at about 2700-m elevation, snow accumulation begins on October 5, reaches a maximum on April 25, and melts out by July 3 (Despain 1990). Thus, the lower elevations have a snowpack duration of 213 days compared with 271 days at the higher elevations (Despain 1990). Elevation is also strongly correlated with temperature, particularly during the nonwinter months (Despain 1990), and water may be somewhat limiting at lower elevations. Thus, the effect of elevation on lodgepole pine sapling growth is likely due primarily to differences in climate. Also, although more fertile andesite substrates are more common at higher elevations, any gain from the marginal increase in site fertility may be counteracted by the shorter growing season.

Using aerial photography to describe the patterns of postfire lodgepole pine density produced a map with 75% accuracy using six density classes. Although there was a general decline in pine sapling density with elevation, variation in density also occurred over short distances, producing a fine-grained mosaic of differences in stand structure. Thus, although the 1988 fires created extensive areas of even-aged lodgepole pine, the burned landscape is characterized by complex spatial heterogeneity in stand structure. Such landscape patterns have not previously been described or quantified within extensive even-aged stands.

Landscape pattern analyses are sensitive to the scale of the data and the choice of categories used (Turner and others 2001). Therefore, our quantification of the spatial pattern of stand densities would differ had we selected other density classes or used data at different resolutions. All analyses of categorical raster data share this sensitivity, but the important point is to select categories and scales that are meaningful for a particular study or objective. The categories used in our analysis were selected based on the observed range of variation and our ability to distinguish differences with confidence using the aerial photos. The 0.25-ha scale was selected based on our prior studies and observations of variation in the field. However, numerical comparisons of our results to other locations or future time periods in YNP should be done with care, assuring consistency in the density classes and the 0.25-ha cell size.

Allometric Models

Lodgepole Pine Biomass Allocation. Initial stand density seemed to be important in determining total AB and allocation patterns within trees only

in the highest-density stand (454,000 stems ha^{-1}). Mean total AB per sapling was very similar in the low-, moderate-, and high-density stands (767–33,000 stems ha^{-1}), but substantially lower in the highest-density stand (454,000 stems ha^{-1}). Biomass allocation to needles was also similar in the three lower-density stands but decreased substantially in the highest-density stand.

Allocation patterns for the young saplings in this study were much different from patterns measured in mature stands. In stands ranging from 70 to 240 years of age, Pearson and others (1984) estimated stand-level biomass allocation to needles to be only 5%–13%, which was the smallest proportional allocation of all biomass components. In contrast, the young saplings in our study area allocated most (45%) of their biomass to needles. Interestingly, the lowest proportional allocation to needles found by Pearson and others (1984) was in their lowest-density stand, in contrast to our study where needle biomass was lowest in the highest-density stand (Table 4). However, it should be noted that their lowest-density stand was over 200 years of age, while our stands were approximately 10 years old. Branch biomass allocation was more similar between the two studies [8%–11% for Pearson and others (1984); 17%–22% for this study], but stem allocation was much greater for the older trees [78%–84% for Pearson and others (1984); 34%–38% for this study]. These data suggest not only that differences exist in allocation patterns between young and old stands, but they also suggest the ecological importance of our new allometric models for predicting biomass and allocation in young, developing stands.

The allocation patterns that we measured in 10-year-old lodgepole pine saplings are likely to change over the next few decades. Sapling densities are likely to change as less dense stands experience infilling from seeds produced by nearby unburned trees or by the current cohort as it matures, and dense stands will experience thinning mortality. We observed many 12-year-old saplings producing cones and releasing seeds in stands of different densities in 2001. As competition for light, water, and nutrients changes within stands of varying densities, biomass allocation to aboveground components will likely change. Stems will develop more fully in lower-density stands and lower branches will begin to self-prune in higher-density stands, reducing biomass allocation to foliage and branchwood while increasing allocation to stems.

Two interesting questions emerge regarding the applicability of our models. First, because allometric models that predict biomass allocation for ma-

ture trees do not work for young saplings, it follows that our models will not be applicable for mature trees. The question then becomes: How long will they apply to the developing trees? Resampling and reassessment of the equations are required to determine the temporal range of applicability of these models, or the models could be applied to trees within a chronosequence of ages (for example, 15–50 years old) to determine the age at which the models fail. Second, can these models predict AB, ANPP, and LAI for saplings of other conifers (for example, *Pinus ponderosa*, *Abies lasiocarpa*, *Pinus albicaulis*, *Picea engelmannii*, *Pseudotsuga menziesii*)? Most, if not all, allometric models that predict biomass allocation for mature trees are species-specific. Because of the absence of these kinds of models for younger trees, it is difficult to assess interspecific application without additional field studies.

Allometric Models for Herb and Shrub ANPP and LAI. Percent cover of herbaceous plants, including grasses, forbs, and shrubs, was an excellent predictor of ANPP for those species in our study area. Our equations may be useful as general models for estimating herbaceous and shrubby ANPP for three reasons. First, our approach accounts for the variability in species composition among sites, making the equations more useful for extrapolation to larger areas within similar landscapes and similar species composition. Second, by grouping plant species according to structural characteristics, a single equation may be applied to numerous species, eliminating the need for a specific equation for each species. Furthermore, as new species are encountered in the field, they may be classified according to the structural form they most resemble from our equation list and estimates of ANPP may be obtained. Finally, although there is still uncertainty about the applicability of the lodgepole pine allometric models over time, the regression models for the herbs and shrubs should remain valid because (1) most annual and perennial plants do not vary significantly in growth form and size from year to year; and (2) our models were developed based on relationships between ANPP and percent cover, which should account for seasonal or annual differences in biomass due to climatic variability or periods of drought.

Variability in Stand-Level ANPP and LAI

The levels of ANPP and LAI reported here are within the ranges reported for other Rocky Mountain coniferous ecosystems, but the variation exceeds that reported for similar mature forests. For

example, tree ANPP in similar conifer forests ranges from 1 to 7 Mg ha⁻¹ y⁻¹ (Pearson and others 1984, 1987; Box and others 1989; Fassnacht and Gower 1997; Hansen and others 2000; Binkley et al. 2003), and LAI for similar mature conifer forests ranges from 2 to 14 m² m⁻² (Moir and Francis 1972; Pearson and others 1984, 1987; Mencuccini and Grace 1996; Keane and Weetman 1987; Jack and Long 1991; Binkley and others 1995; Fassnacht and Gower 1997). Average ANPP in the plots we sampled was 2.8 Mg ha⁻¹ y⁻¹, with the trees contributing about 60% and the herbaceous vegetation about 40% to the mean. Average LAI in the plots was 0.80 m² m⁻² due largely to the trees; herbaceous vegetation contributed only about 2.5% to the mean.

Our results suggest important influences on ANPP and LAI of both the abiotic template (particularly elevation, with soil class of less importance) and the postfire biotic community (particularly postfire stand density). Together, these variables explained 80% of the variation in ANPP and LAI, with the abiotic template alone accounting for about 50% and postfire stand density about 30%. Because stand density is known to vary with contingent factors—in particular, prefire serotiny and fire size, severity and pattern—our results suggest that these factors also influence postfire ecosystem function.

The influence of elevation on ANPP and LAI likely reflects climate variation with elevation in YNP, as discussed above for sapling size. The elevation of our study plots ranged from 2011 to 2650 m, which represents a 60-day variation in snowpack duration. Climatic variation likely explains much of the effect of elevation on ANPP and LAI. Soil effects were minimal but probably reflect differences in both nutrients and soil water-holding capacity. Among the soil categories, andesite-derived soils have substantially more organic carbon and total nitrogen than rhyolite-derived soils as well as higher surficial available water; andesitic substrates have a higher incidence of meadows, presumably because of higher mineral nutrition (Despain 1990). However, these are all relatively poor soils. Site index computed for stands ranging in age from 45 to 200 y on the subalpine plateau ranged only between 9 and 20 m (Kashian 2002), suggesting that soil fertility differences in YNP are insufficient to cause stand-level responses in mature trees. Our results suggest that soil differences also had a small effect on the young lodgepole pine stands.

Herbaceous ANPP was always less than 3 Mg ha⁻¹ y⁻¹, but tree ANPP was as high as 14 Mg ha⁻¹

y⁻¹. This suggests that total stand productivity is higher with higher tree density and that lodgepole pine is a better competitor for required resources than the dominant understory species. We had anticipated that differences among soil types would have an important influence on herbaceous ANPP, but soil type was insignificant in the ANOVA model (Table 8). The apparent lack of soil influence on herbaceous production may simply reflect the general similarity among soil types in our study area; all of the soils are derived primarily from relatively infertile volcanic substrates. Limitations on herbaceous production may be due to plant morphology and stature, competition for horizontal space, water or nutrient use efficiency, or the generally cool, short growing seasons and infertile soils that characterize our study area.

Our current study has focused on ANPP, but evidence suggests that the trends reported here are likely to reflect trends in net primary production (NPP). Litton (2002) and Litton and others (2004) quantified both above- and belowground production in a subset of the ninety 11-year-old stands sampled in this study as well as older lodgepole pine stands in YNP. Results demonstrated a remarkably consistent ratio (0.63:0.66) of total belowground carbon allocation (TBCA) to TBCA plus ANPP, despite wide differences in sapling densities and between young and old stands (Litton and others 2004). Therefore, the ANPP values reported here for the YNP landscape should provide a good index to the variation in NPP. The constant ratio should also simplify efforts to quantify the future trajectory of ecosystem development through successional time across the YNP landscape.

Variation in weather between years produces variation in ANPP, although interannual variability in ANPP in natural temperate and boreal ecosystems is generally low when compared to other biomes (Knapp and Smith 2001). Our data were obtained for one year (most sampled in 1999 and measuring 1998 pine productivity and 1999 herbaceous and shrub production; two plots sampled in 2000) with the objective of describing spatial heterogeneity within a given year rather than temporal heterogeneity. However, the absolute values reported here for ANPP and LAI may certainly differ between years that vary in temperature or precipitation.

Landscape Patterns of ANPP and LAI

By combining spatial data with results of our field studies, we predicted the spatial pattern of ANPP

and LAI in the early successional forests of the postfire YNP landscape reasonably well. Our results suggest a dominant background of relatively low ANPP and LAI that is frequently punctuated by small patches of relatively high ANPP. Hansen and others (2000) studied spatial patterns of ANPP in a 9500-km² western area of the Greater Yellowstone Ecosystem that included a mosaic of forest types and successional stages, shrublands and grasslands. Similar to our results, they found a dominant matrix of lower ANPP (approximately 0.6–3 Mg ha⁻¹ y⁻¹) with a distribution skewed to higher values (approaching 9 Mg ha⁻¹ y⁻¹). In their analysis, cover type and elevation explained 89% of the variation in ANPP across the landscape. Our data suggest that spatial variation in ANPP within a single successional stage may be of comparable magnitude to that observed across a landscape of varying cover types and stand ages. Large, infrequent disturbances such as the 1988 fires produce complex spatial mosaics of disturbance severity across the landscape (Foster and others 1998), and our results suggest that they also produce spatial mosaics of ecosystem structure and function. Hansen and others (2000) speculated that areas of high productivity within the Greater Yellowstone Ecosystem may provide important habitats for many plant and animal species; whether the islands of high productivity we have identified within the burn mosaic have implications for the distribution of other species or the rates of other ecosystem processes is not known. The dense stands of young lodgepole pine may also provide important habitat for some of the wildlife in YNP, particularly elk (*Cervus elaphus*), now that wolf (*Canis lupus*) are now well-established throughout the park (Smith and others 2003).

The potential sources of error in the steps leading to the development of the landscape models of ANPP and LAI must be acknowledged. These errors may derive from sampling within the 0.25-ha plots; from the allometric equations themselves, in which a small portion of the variance remains unexplained; in computing the average sapling density and basal diameter on a plot, even though the coefficients of variation (CVs) were less than 40%; and in the map of lodgepole pine densities. These sources should be recognized when these maps are presented.

The spatial variation in ANPP and LAI observed in early successional stands of the same age in YNP also suggests variability that may be of similar magnitude to that observed through successional time, particularly given the range of values reported for multiage stands within the Greater Yel-

lowstone Ecosystem (Hansen and others 2000). Spatially explicit simulations of ANPP and LAI dynamics in Glacier National Park under varying climate-fire scenarios also suggest a similar range of variation in ANPP and LAI through time as we observed across space (Keane and others 1999). Will ecosystem function in YNP converge across the landscape through time, or does the disturbance-created mosaic leave a persistent functional legacy? Variation in stand density will likely be reduced through time as high-density stands self-thin and low-density stands continue to have gradual recruitment (Kashian 2002). In particular, the 25% of the landscape with high sapling densities and high ANPP rates will likely experience greater sapling mortality rates, which should moderate rates of ANPP. However, the initial postfire mosaic is likely to influence the structure and function of the YNP landscape for at least a century. Analyses of basal area increment (BAI) in lodgepole pine stands spanning a range of age classes and densities indicate that BAI varies with density until about 125 years in age (Kashian 2002; Kashian and others in press).

Projections of increased frequency and extent of forest wildfires with scenarios of global climate change (for example, Price and Rind 1994; Flannigan and others 1998; Stocks and others 1998) underscore the importance of understanding the spatial and temporal dynamics and variability of ecosystem processes during postfire succession. For example, the extent of forest wildfires in the boreal and western regions of North America has increased 6- to 9-fold since 1977, and 132 × 10⁶ ha of temperate boreal forest is estimated to have burned between 1977 and 1990 (Auclair and Carter 1993). Projections using a 2 × CO₂ climate suggest that the length of the forest fire season in Canada may increase by as much as 30 days (Flannigan and van Wagner 1991; Wotton and Flannigan 1993). Global ecosystem models commonly represent the landscape as “stable” and “mature,” not accounting for effects of disturbance on species composition, stand age, structure, and function (Gower and others 2001). Shifts in the age class distribution in northern conifer landscapes may have a strong impact on ANPP and overall carbon budgets at the landscape level (Kasischke and others 2000; Gower and others 2001; Chen and others 2002). Our data suggest that spatial variation in tree density of early successional stages may be as important as age-class distribution in predicting carbon dynamics. Because climate-induced changes in forest fire regimes may be more important than the direct effects of climate change in altering forest ecosys-

tems (Graham and others 1990; Weber and Flannigan 1997; Dale and others 2001), it is imperative that the full suite of ecological responses to crown fires be understood more fully. In particular, quantifying carbon dynamics during postfire succession is critical for determining how fire may alter regional and global carbon budgets (Auclair and Carter 1993; Amiro 2001).

The large 1988 Yellowstone fires produced a complex spatial mosaic of burn severity, postfire stand structure, and postfire ecosystem function. Postfire ANPP in 11-year-old lodgepole pine stands ranged from 0.04 to 15.12 Mg ha⁻¹ y⁻¹, spanning much of the range of variation expected through successional time. The greatest uncertainty in predicting landscape patterns of ANPP and LAI in the early successional forests of YNP was not in developing allometric relationships but rather in quantifying the postfire mosaic of tree density, which reflected both the spatial heterogeneity of the abiotic template (elevation, soils) and the contingent effects of the disturbance and the prefire community (fire severity, serotiny). The effects of disturbance-generated landscape patterns on spatial variability in successional communities and ecosystem processes are not generally well known, but the results reported here suggest they may be very important.

ACKNOWLEDGEMENTS

This work could not have been accomplished without the hard work of our 1999 field crew, and we are extremely grateful to them: Heather Arrowwood, Teresa Cohen, Yvonne Corcoran, Jamie Corcoran, Janice Corcoran, Eleanor Erwin, Donna R. Kashian, and Tania Schoennagel. We thank Tania Schoennagel for generously sharing her data on lodgepole pine density so that the goodness of fit of our sapling density map could be evaluated with independent data. Anne Rodman of the GIS Laboratory, Center for Resources, Yellowstone National Park, graciously helped interpret the soils map of YNP for use in our analyses. The University of Wyoming National Park Service Research Center provided valuable logistical support during the field season. Many members of the Yellowstone Ranger Division, particularly Dave Phillips and Kathleen O'Leary of the South Entrance, were extremely helpful during our study. Our ideas benefited from discussions with Mike Ryan and Dennis Knight, and the article was improved by helpful comments from Dennis Knight, Tania Schoennagel, and Erica Smithwick. This research was funded by the Ecology and Ecosystem Studies Programs, National

Science Foundation (Grant No. DEB-9806440) and by a grant from the Andrew W. Mellon Foundation.

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