Variability in Leaf Area and Stemwood Increment Along a 300-year Lodgepole Pine Chronosequence

Daniel M. Kashian,[1]* Monica G. Turner,[2] and William H. Romme[3]

[1]Departments of Zoology and Forest Ecology and Management, University of Wisconsin–Madison, Madison, Wisconsin 53706, USA; [2]Department of Zoology, University of Wisconsin–Madison, Madison, Wisconsin 53706, USA; [3]Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, Colorado 80523, USA

ABSTRACT

Large disturbances such as the 1988 Yellowstone fires produce considerable spatial heterogeneity in ecosystem processes across landscapes, in part by affecting vegetation structure. However, the persistence of this heterogeneity with time since disturbance, and thus the role of large disturbances in shaping the heterogeneity of ecosystem processes over large spatial and temporal scales, remains unclear. Such an inquiry requires that variability as well as mean conditions of forest structure and growth be examined if changes are to be projected for heterogeneous postdisturbance landscapes. We studied a chronosequence of unburned, mature lodgepole pine stands (stand ages ranging from 50 to 300 or more years) to examine the variability in stand density, leaf-area index (LAI), and stem growth [basal area increment (BAI), a surrogate for aboveground net primary productivity (ANPP)] with stand age, the relationships between these factors, and how these factors were related to stand and site characteristics. Variation in LAI and BAI was explained primarily by differences in stand density and age ($r^2 = 0.51$ for both LAI and BAI), and both LAI and BAI were most variable in the youngest age class [coefficient of variation (CV), 38% and 41% for LAI and BAI]. The relationship between LAI or BAI and stand density was significantly weaker ($r^2 < 0.20$) at stand ages characterized by canopy closure (50–175 years), suggesting that stand structure and production are closely linked. Thus, the spatial variability of stand production, which is initially very high following large fires in this landscape, is detectable for over a century before successional changes in forest structure greatly affect the initial postdisturbance landscape pattern of stand production. Given the recent focus on spatial heterogeneity of ecosystem processes across large landscapes, projecting changes in postdisturbance patterns of stand production has very strong significance for ecosystem science.

Key words: basal area increment; convergence; disturbance; fire ecology; forest production; forests; leaf-area index; *Pinus contorta*; Rocky Mountains; stand development; stand production; stand structure; succession; Wyoming; Yellowstone National Park.

INTRODUCTION

Age-related changes in growth and production of forests have been well studied [see Assmann (1970), Gower and others (1996), and Ryan and

others (1997) for review], but a thorough understanding of the spatial heterogeneity of forest productivity has yet to be developed for large spatial and temporal scales. Natural disturbances are important in shaping variability in ecosystem processes across landscapes because they act to renew vegetation, creating a patchwork of younger, vigorous forests characterized by increased productivity (Assmann 1970; Turner and Long 1975; Long and Smith 1992; Ryan and Waring 1992). However, substantial spatial variation may also be found between stands of the same age across landscapes affected by large disturbances (Reed and others 1998; Turner and others 2004). If such variability persists through time on a landscape [see Foster and others (1998)], early patterns of stand structure and function may influence future fire behavior (Baker 1992; Turner and Romme 1994), survival and reproduction of vertebrate organisms (Pulliam 1988; Pulliam and Danielson 1991), and a host of ecological properties and processes, including nutrient cycling, food-web structures, species richness and abundance, and community composition (Whittaker and Nehring 1975; Perry 1994; Schimel and others 1997). The spatial heterogeneity in ecosystem function present following large disturbances is just beginning to be addressed in ecosystem science [see Litton and others (2003) and Turner and others (2004)], but the stability of this variation with successional time is not well understood for forested landscapes.

Age-related changes in productivity of an average forest stand of a given type are well documented, but the factors causing these changes are strongly debated. Stemwood growth (hereafter termed *stand production*), which dominates aboveground net primary productivity (ANPP) in mature forest stands, typically increases to a maximum at a relatively young age (usually at the point of canopy closure) and then gradually decreases with age (Assmann 1970; Ryan and Waring 1992; Gower and others 1996; Ryan and others 1997). Increasing stemwood respiration coincident with decreasing gross primary production, once the standard explanation for this decline, is generally not supported by field evidence [see Gower and others (1996) and Ryan and others (1997)]. Instead, age-related changes in stand production may be explained based on other processes of individual-tree ecophysiology (Kaufmann and Ryan 1986; Ryan and Waring 1992; Binkley and others 2002), whereby processes such as reduced hydraulic conductance or photosynthetic rates, or variation in tree resource use efficiency within stands, may reduce productivity. Alternatively, age-related changes in stand pro-

duction may be explained by population or stand dynamics that influence changes in canopy structure [see Smith and Long (2001)].

Stand structure is an important factor influencing stand production (Long and Smith 1990; Fassnacht and Gower 1997; Kollenberg and O'Hara 1999; Smith and Resh 1999; Smith and Long 2001; Binkley and others 2002). The relationship between stand structure and production has been thoroughly examined for even-aged lodgepole pine forests (Knight and others 1981; Pearson and others 1984; Long and Smith 1988, 1992; Comeau and Kimmins 1989; Ryan and others 1997; Smith and Resh 1999), often in terms of changes in leaf area. Although varying with age, leaf area in lodgepole pine is theoretically a plastic structural trait that varies little with density once leaf area approaches equilibrium (Knight and others 1981; Long and Dean 1986; Long and Smith 1990; Jack and Long 1991). This plasticity occurs because self-thinning redistributes total leaf area among fewer but larger individuals in even-aged conifer forests (Long and Smith 1984; Dean and Long 1986). Because successional changes in stand structure may affect the relationship between leaf area and stemwood growth—or between stand structure and production—critical examination of this relationship over large temporal scales is necessary if changes in the spatial patterns of forest production are to be projected.

The 1988 Yellowstone fires produced a 250,000-ha landscape mosaic of lodgepole pine (*Pinus contorta* var. *latifolia* Englem. ex Wats.) seedling densities ranging from fewer than 50 stems/ha to more than 500,000 stems/ha (Turner and others 2004). The post-1988 landscape was characterized by wide variation in stand leaf area and ANPP in the burned areas, likely linked to stand density (Reed and others 1998; Litton and others 2003; Turner and others 2004). Kashian et al. (2005) suggests that the initial post-1988 variability in stand density will decrease with time and may converge within the next two centuries, thus the variability of stand production across the Yellowstone landscape may also converge if stand structure and production are closely related. Variability in forest productivity across landscapes has been described [for example, see Sala and others (1988), Brown and Schroeder (1999), Hansen and others (2000), and Jenkins and others (2001)], but few studies have examined how long this heterogeneity persists as stands within a landscape mosaic age and develop. In fact, nearly every study of age-related changes in stand production has examined average conditions of stemwood growth, leaf area, and stand density in a typical forest stand to describe age-related changes,

either assuming these factors to be homogeneous or minimizing variance between sampled stands for logistical ease. However, the importance of variability in ecosystem functional characteristics across landscapes, rather than mean conditions, remains at the forefront of ecosystem science (Schimel and others 1997; Clark and others 2001).

Given the wide variability in stand density, leaf area, and productivity on the post-1988 Yellowstone landscape (Reed and others 1998; Litton and others 2003; Turner and others 2004), we examined the relative influence of stand density, stand age, and substrate on leaf area and basal area increment (BAI) in stands unburned by the 1988 fires. By examining both the mean and variance of leaf area and BAI along a chronosequence across the Yellowstone landscape, we suggest future changes that may occur in the current spatial heterogeneity of leaf area and stand production within the areas burned in 1988. We addressed the following questions: (a) How do the mean and variance of leaf area and BAI vary with stand age for lodgepole pine stands in Yellowstone? (b) What is the relationship between leaf area and BAI for these forests, and does this relationship change with stand age? (c) What is the relative importance of stand age, stand density, and site factors for determining leaf area and BAI, and are these relationships consistent over stand age? We expected similar age-related changes in leaf area and BAI as documented for other forests, but that the variance of BAI and leaf area would decrease with increasing stand age. Furthermore, we hypothesized that the relationship between leaf area and BAI would vary with stand structure more than with abiotic conditions, although the relationships would differ with stand age.

Methods

Study Area

Our study was conducted on the high-elevation, forested, subalpine plateaus of Yellowstone National Park (YNP) in northwestern Wyoming. Subalpine fir (*Abies lasiocarpa* Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) occur as codominants on fertile or mesic sites in the park, but we focused on the 80% of the plateaus that are forested by nearly pure stands of lodgepole pine (Despain 1990). The 1988 Yellowstone fires affected about 45% of this area (Turner and others 1994). The climate is cool, with moist springs and dry summers (Martner 1986). Moisture increases with elevation, which ranges in the park from

approximately 1900 to 3000 m, although most of the subalpine plateaus range from about 2100 to 2600 m. Nearly two-thirds of the park includes dry, infertile soils derived from rhyolite, and the remainder includes more mesic and fertile andesites and lacustrine sediments. Soils derived from rhyolitic parent materials typically are coarser and have fewer base cations and lower water-holding capacity than soils derived from andesite or lacustrine sediments; lacustrine sediments typically have the highest silt and clay content, base cations, and water-holding capacity of the three soil types (Despain 1990). Elevation and soil fertility are considered to be the two most important abiotic gradients controlling forest vegetation on the subalpine plateaus (Despain 1990).

As is the case in many Rocky Mountain forest ecosystems, fire has played a dominant role in influencing the flora, fauna, ecological processes, and landscape patterns of YNP (Habeck and Mutch 1973; Loope and Gruell 1973; Wright and Heinselman 1973; Arno 1980; Romme 1982; Romme and Knight 1981, 1982; Knight 1987; Romme and Despain 1989; Despain 1990). Although the extent of the 1988 Yellowstone fires was the largest since the early 1700s, these fires probably represented a major natural disturbance event that occurs at intervals of 100–300 years in this landscape (Romme and Despain 1989). Smaller fires (usually less than 5000 ha) occur more frequently on the Yellowstone landscape during the interval between these large fires (Despain 1990). As a result of this fire regime, Yellowstone currently contains a mosaic of young stands created by the 1988 fires and small fires that have occurred since 1988, as well as stands ranging from 25 to 450 years old.

Study Design

During the summers of 1999–2001, we sampled 48 stands of 5 ha or greater in area and unburned by the 1988 fires in four discrete stand age classes (50–100 years, 125–175 years, 200–250 years, and 300–350 years) on the subalpine plateaus of YNP (Figure 1). We used stand age classes rather than stand age as a continuous variable because the stands do not represent a continuous age gradient on the Yellowstone landscape due to discrete fire events. Due to the relatively flat plateaus and extensive areas of homogeneous soils that dominate the Yellowstone landscape, we could select sites that controlled for differences in slope, aspect, soil type, and elevation, and thereby assign all stands to one of two distinct chronosequences. It is important to note that chronosequences are
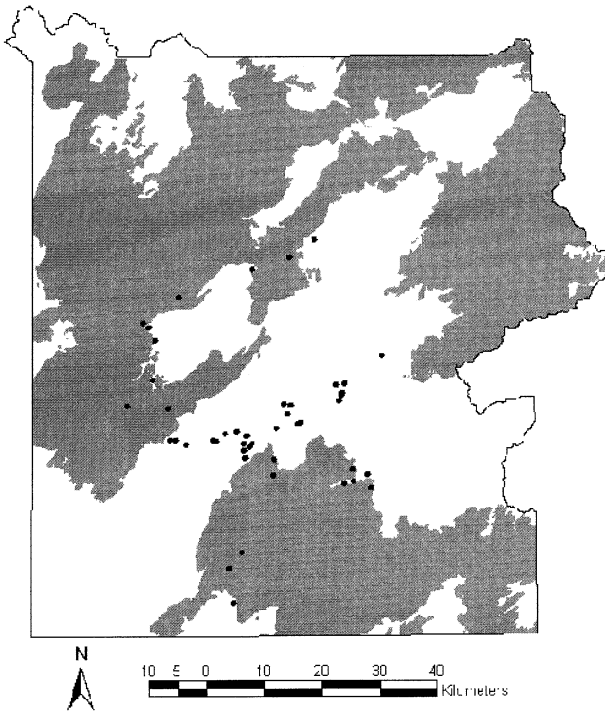
Within each stand, a 10 × 50-m (500 m^2) rectangular plot was established that was representative of stand structure and physiognomy of the 5-ha area. Density for each stand was calculated by counting all live trees 4 cm or greater in diameter at breast height (DBH) within the plot and scaling to trees per hectare. The age of each stand was determined initially from a stand age map (Tinker and others 2004) and verified by using increment cores taken from each plot [see Kashian et al. (2005)]. Within the plot, 50 live trees were randomly selected by identifying the tree nearest to each even-numbered distance along each side of the long axis of the plot (0 m, 2 m, 4 m, and so on), and DBH, total height, height to base of live crown, and crown position (dominant, codominant, intermediate, or overtopped) were recorded. Although trees from all size and height classes were included as part of this 50-tree random sample, trees with broken or noticeably forked crowns or heavy dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Englem.) infestations were avoided; such trees constituted less than 1% of all trees in all plots. Two perpendicular increment cores were collected for each tree at DBH, and the sapwood boundary of each tree was marked directly on the cores in the field at the time of sampling.

Leaf Area

We estimated projected leaf area, expressed as leaf-area index (LAI, m^2/m^2) for each of the 50 trees in each plot by using an allometric equation developed for lodgepole pine by Long and Smith (1988). They sampled stands in southeastern Wyoming in regions receiving precipitation averaging 600 mm/year and ranging from 400 to 900 mm/year; Yellowstone averages 560 mm/year of precipitation, ranging from 500 to 1000 mm/year. In addition to its development in an environment similar to that of YNP, the Long and Smith (1988) allometric was chosen for the large range of stand densities sampled to build the equation. Litton and colleagues (2003) validated several allometric equations developed for lodgepole pine leaf area and noted that models developed in southeastern Wyoming were effective in estimating LAI in Yellowstone. The actual model was

$$\text{projected leaf area} = (0.064 A_S^{1.43} D^{-0.73}) \times 1.24 \tag{1}$$

where A_S is the cross-sectional area of tree sapwood at DBH in centimeters, D is the distance in meters from breast height to the center of the tree crown, and 1.24 is a correction factor for fresh needles

Figure 1. Location of sampling points used to estimate leaf-area index (LAI) and basal area increment (BAI) in Yellowstone National Park. The *shaded area* represents the area burned in 1988.

descriptive rather than experimental tools and do not provide causal data. Short of large-scale manipulations and long-term measurements (more than 300 years) of changes in forest structure and production, our study design is most useful in describing general patterns and correlations rather than proving causal factors.

For each chronosequence, all sampled stands originated following a stand-replacing fire and were located on flat sites (0%–2% slopes) of similar elevation, a minimum of 100 m from roads, were visibly free from other major structure-altering disturbances (for example, severe windthrow, recent non-stand-replacing fires, or past insect infestations), and were composed of at least 85% live lodgepole pine. Within each age class, 8–10 stands representing the range of stand density (as determined from aerial photographs and field reconnaissance) in that class were sampled on rhyolite substrates, and 4–5 stands in all age classes except the oldest (300–350) were sampled on lacustrine sediments (Table 1). The two chronosequences therefore differed only by broad substrate. Due to limited accessibility to many remote regions of the park, stands in each age class were selected randomly from those stands within 2 km of roads or trails.

Table 1. Selected Characteristics of Stands Within the Two Chronosequences Sampled in Yellowstone National Park[a]

Age Class	N	Substrate	Density Range (Stems/ha)	Height Range (m)	Mean Age (Years)	Age Range (Years)	Elevation range(m)
50–100	9	Rhyolite	1180–11,320	5.4–11.2	79.9	45–100	2252–2541
125–175	10	Rhyolite	1020–9540	10.0–18.5	131.7	119–170	2174–2405
200–250	8	Rhyolite	640–1640	13.3–20.4	227.5	205–252	2379–2548
300–350	8	Rhyolite	460–1920	12.3–20.3	324.3	297–359	2374–2568
50–100	5	Lacustrine	1360–3660	12.2–18.4	87.8	69–100	2347–2374
125–175	5	Lacustrine	860–2200	15.6–18.9	131.6	130–140	2359–2387
200–250	4	Lacustrine	840–2120	14.1–19.7	249.3	243–259	2362–2418

[a]*Chronosequences differed only in substrate.*

(Long and Smith 1988). Sapwood cross-sectional area was calculated from the DBH measurements, and the average sapwood measurement of the two cores was extracted at breast height for the 50 trees in each plot. Stand LAI was calculated as the product of the mean of the LAI for the 50 trees sampled in each stand, the density of the stand, and an adjustment factor determined by double sampling (Cochran 1977). Double sampling adjusts plot estimates by using the ratio of the mean stand basal area to the mean sample basal area to ensure that the sample is an accurate representation of the stand (Ryan and Waring 1992).

Basal Area Increment

Basal area increment was chosen to represent stand production in Yellowstone because the remoteness and protected nature of the park precluded us from harvesting trees to measure ANPP or volume increment in many stands. In addition, allometric equations for ANPP, which are much more sensitive to site differences than those for LAI (S. T. Gower and M. G. Ryan personal communication), have not been developed for forests in YNP. BAI was estimated for each of the 50 random trees in each of the 48 mature stands as the average difference between basal area of the current year and the previous year, calculated for the previous 5 years. Radial increment was measured for the last full 5 years of growth to the nearest 0.001 mm using the WinDendro software package (Regent Instruments 2001); ring measurements of the two increment cores were averaged to obtain the radial increment for each tree. Change in inside-bark DBH was then determined by subtracting double the mean ring width of the past 5 years from current inside-bark DBH. Diameter increment (in centimeters) was then converted to basal area

increment (in square meters), averaged for the 50-tree sample, multiplied by stand density, and scaled to square meters per hectare per year (m^2/ha/y). All stand BAI estimates were adjusted using double sampling.

Statistical Analyses

Statistical analyses were performed using the S-plus (MathSoft 1998) statistical package. We first examined the validity of each chronosequence by testing for differences in site factors (slope, aspect, elevation, and geographic location) among age classes by using analysis of variance (ANOVA). We assumed the chronosequences to be valid if site differences were not significantly different among age classes. In addition, we used stepwise multiple linear regression to test for relationships between LAI and BAI and site factors. For these and all statistical procedures, $\alpha = 0.05$, the data structure was examined for normality, and equal variances were tested using Bartlett's test for equal variances and Lillifor's test for normality. Stand density was log-transformed, but otherwise no serious departures from normality or equal variances were noted. Multiple colinearity was absent among the independent variables in the multiple regression.

To examine the variability in stand density, LAI, and BAI along the chronosequence, the mean and coefficient of variation (CV) of these data were plotted for each age class. Mean values of density, LAI, and BAI were compared across age classes using analysis of covariance (ANCOVA) (Zar 1999), with significant predictor variables identified with stepwise regression (see below) included as covariates. ANCOVA was run in SYSTAT (SPSS 1996); and the Fischer Least Significance Difference (LSD) method was used for pairwise multiple comparisons of means. Assumptions of ANCOVA were
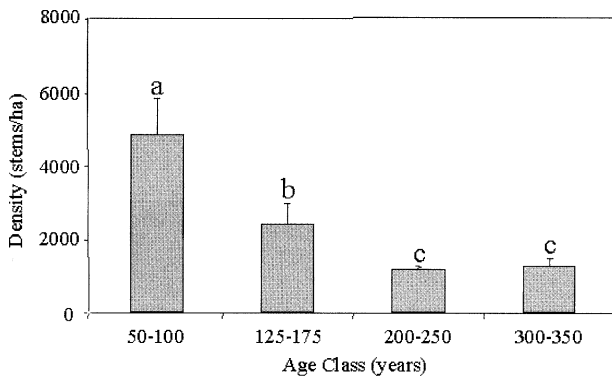
Figure 2. Mean tree density for a chronosequence of lodgepole pine sampled in Yellowstone National Park. Density estimates were made for trees 4 cm or greater in diameter at breast height. *Error bars* represent 1 standard error. *Bars having the same letter* indicate a lack of significant differences at $\alpha = 0.05$.

examined, including homogeneity of regressions among treatments and independence of covariates from treatments, and no serious departures from these assumptions were noted. Within-class variances of each variable were compared among age classes by using an independent-sample t test with variances assumed equal (Zar 1999).

We used linear regression to examine the relationship between LAI and BAI with LAI as the independent variable. These analyses were conducted on the pooled set of stands, but were repeated for each age class separately to examine how the relationship may differ along the chronosequence. All regressions were free of heteroscedasticity. Regression equations for each age class were compared by substituting dummy variables for age class and including the interactions of the dummy variables and density in a regression model to test for pairwise significant differences in the slope and intercept of the regression lines.

Given the apparent initial link between LAI, ANPP, and density in regenerating lodgepole pine stands immediately following wildfires in YNP (Reed and others 1998; Turner and others 2004), we examined the relationship between LAI or BAI and density across all age classes as well as by age class to examine changes in the relationship along the chronosequence. The Fischer LSD method (Zar 1999) was used for pairwise multiple comparisons of age-class means, and the slopes and intercepts of the regression lines were again compared between age classes by using dummy variable techniques. Stepwise multiple linear regression was then used to examine the relative importance of stand age class, stand density, site factors, and the interactions of these terms in explaining the variation in

LAI and BAI across the Yellowstone landscape by using α to enter and remove equal to 0.05. Substrate underlying each stand was determined from Geographic Information System data as the intersection of the sample point with either rhyolitic substrates or lacustrine sediments.

RESULTS

Consistent with our establishment of a chronosequence, differences in site factors were not significant among age classes. In addition, measured site parameters alone did not explain variation in either LAI or BAI ($r^2 = 0.14$), and site parameters were not significant when included in a multiple regression model with stand density and stand age ($P > 0.35$). Substrate was not related to either LAI or BAI across all sites, suggesting that the relative differences in site quality between the two substrate types differentiated in our study are unimportant for mature tree growth in YNP. Thus, all stands ($n = 48$) were considered part of a single chronosequence for analysis.

Variation in Density, LAI, and BAI with Stand Age

Mean stand density exhibited a decline from 4900 stems/ha at the 50- to 100-year age class to 2600 stems/ha at the 125- to 175-year age class, due to self-thinning and the initiation of mature stand structure (Kashian et al. 2005) (Figure 2). Stand density continued to decline beyond the 125- to 175-year age class, but at a slower rate, falling to a mean value of 1200 stems/ha at the 200- to 250-year age class, after which stand density remained constant across the rest of the chronosequence.

Stand-projected LAI declined by 21% from a mean value of 2.3 m^2/m^2 in the 50- to 100-year stands to 1.8 m^2/m^2 at the 125- to 175-year age class, after which LAI remained relatively constant across the rest of the chronosequence (Figure 3). BAI declined significantly by 37% from a mean value of 5.7 $m^2/ha/y$ in the 50- to 100-year age class to 3.6 $m^2/ha/y$ at the 125- to 175-year age class; beyond the 125- to 175-year age class, BAI did not change significantly (Figure 4).

Variation in stand density, LAI, and BAI differed among age classes and decreased with increasing stand age (Figure 5). Although the trend in CV with age class was similar for LAI and BAI, stand density was more variable (higher CV) than LAI and BAI within every age class. For example, density varied by a factor of 10 in the 50- to 100-
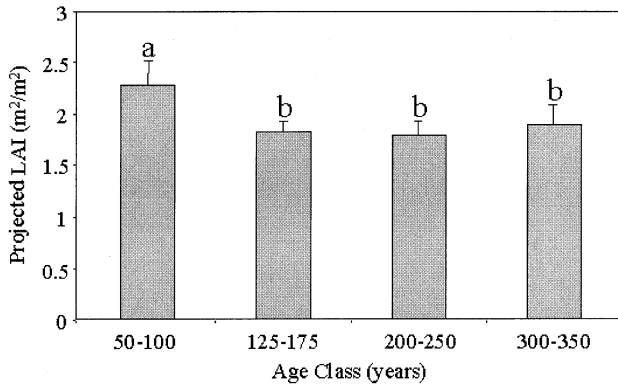
Figure 3. Projected leaf-area index for a chronosequence of lodgepole pine sampled in Yellowstone National Park. *Error bars* represent one standard error. *Bars having the same letter* indicate a lack of significant differences at α = 0.05.
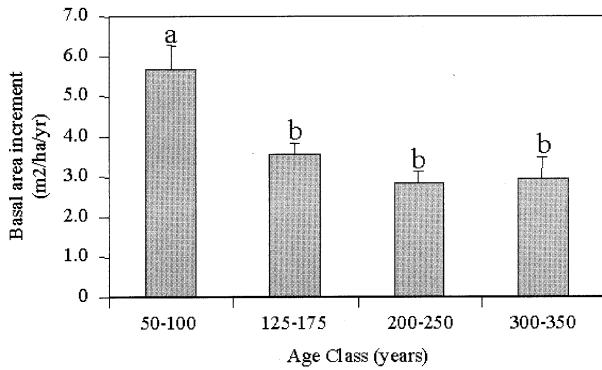

Figure 4. Basal area increment for a chronosequence of lodgepole pine sampled in Yellowstone National Park. *Error bars* represent one standard error. *Bars having the same letter* indicate a lack of significant differences at α = 0.05.

Figure 5. Coefficient of variation for stand density, leaf-area index (LAI), and basal area increment (BAI) by age class for a chronosequence sampled in Yellowstone National Park. *Bars having the same letter* indicate a lack of significantly different variances at α = 0.05.

Figure 6. Linear relationship of basal area increment (BAI) and leaf-area index (LAI) for 48 lodgepole pine stands sampled in Yellowstone National Park aged 45–350 years ($r^2 = 0.62$, $P < 0.001$).

year age class, but LAI and BAI varied only by approximately a factor of 4. Similarly, density varied by a factor of 11 and 4 in the 125- to 175-year and 300- to 350-year age classes, respectively, but only by a factor of 2 for LAI and BAI in both age classes. For density, variance in the 50- to 100-year and 125- to 175-year age classes was significantly higher than in the 200- to 250-year and 300- to 350-year age classes ($P = 0.05$) (Figure 5). For both LAI and BAI, variance in the youngest class was significantly higher than in all other classes ($P <$ 0.05); differences in variance among the oldest three classes were not significant.

LAI was positively and linearly correlated with BAI (Figure 6). When examined by age class, this relationship was fairly strong ($r^2 > 0.60$) across all age classes except the 50- to 100-year age classes
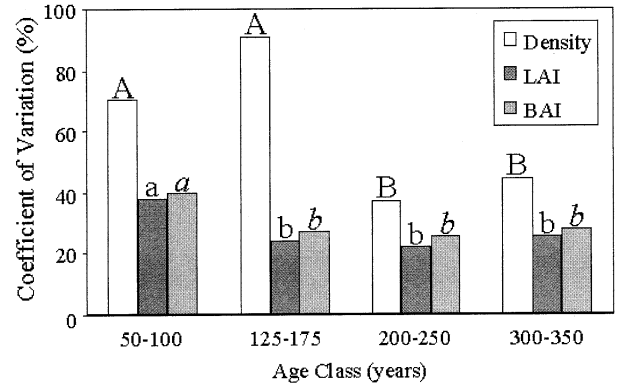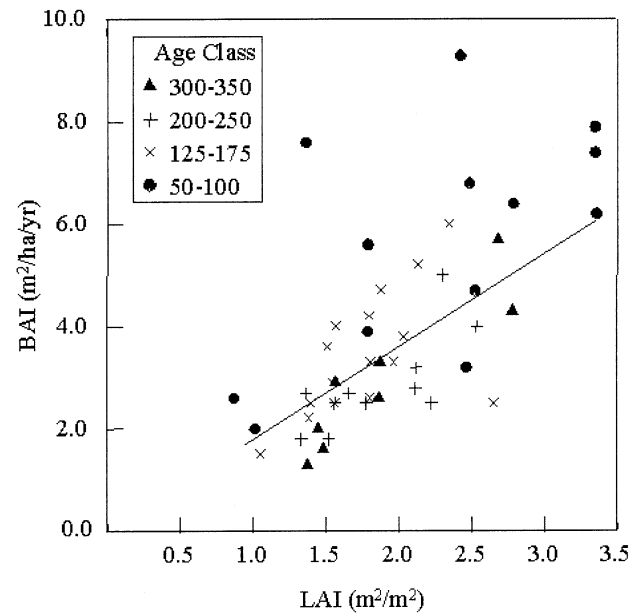
($r^2 = 0.34$) (Table 2). The slope ($P = 0.05$) and intercept ($P = 0.03$) of the regression line for both the 50- to 100-year and 125- to 175-year age classes was significantly different from those of all other regression models (Table 2).

Relationship of Stand Characteristics to LAI and BAI

Stand density and stand age were the most important predictors of LAI ($r^2 = 0.51$) and BAI

Table 2. Statistics for Linear Regression to Predict Basal Area Increment (BAI) Using Leaf-area Index (LAI) for All Stands and by Age Class

Age Class	N	F Ratio	Pr > F	MSE	r^2
Pooled	48	71.813	< 0.001	1.184	0.620
50–100[a]	13	5.655	0.037	3.633	0.340
125–175[a]	15	31.321	< 0.001	0.545	0.707
200–250[b]	12	11.763	0.009	0.147	0.595
300–350[b]	8	58.961	< 0.001	0.236	0.922

Superscript letters represent significance in slope of the regression line; classes having the same superscript letter indicates a lack of significantly different slopes at α = 0.05. MSE, mean standard error; and Pr, predicted.

Table 3. Multiple Regression Results for Models to Predict Leaf-area Index (LAI) or Basal Area Increment (BAI) Using Stand and Site Parameters for All Stands

	Df	Coecient	F Ratio	Pr > F	r^2
LAI					
Model	3		13.128	< 0.0001	0.514
Stand density	1	7.878	6.357	0.015	0.279
Age class^2	1	0.802	3.164	0.052	0.121
Age class	1	−5.241	2.483	0.051	0.114
BAI					
Model	3		15.197	< 0.0001	0.509
Age class^2	1	0.384	9.105	0.004	0.268
Stand density	1	2.244	12.514	0.001	0.139
Age class	1	−3.038	23.972	< 0.0001	0.102

No site parameters were significant in the models. Pr, predicted.

($r^2 = 0.51$) (Table 3). The relative importance of stand density in the multiple regression model suggests that initial postfire differences in density may have an important, persistent influence on LAI and BAI. LAI ($P < 0.001$) and BAI ($P < 0.001$) were both significantly different across all age classes even after correcting for stand-density differences with an analysis of covariance (Table 4). For both LAI and BAI, age class was significant as a quadratic term in the model (Table 3).

Stand density alone was a poor predictor of both LAI ($r^2 = 0.22$) and BAI ($r^2 = 0.22$) (Table 5), suggesting that stand age is also an important factor in explaining variation in LAI and BAI. In particular, the relationship between stand density and LAI or BAI was not consistent across all age classes. Stand density was a fair predictor of LAI at the 200- to 250-year and 300- to 350-year age classes, and similar trends hold for BAI. For both LAI and BAI, however, stand density was a poor predictor at the younger, mature age classes (50–100 and 125–175; $r^2 = 0.11$ and 0.11, respectively, for LAI, and $r^2 = 0.20$ and 0.13 for BAI) (Table 5). For LAI

versus density, the regression lines of the 50- to 100-year and 125- to 175-year age classes were different from the older age classes, having significantly different intercepts ($P = 0.05$), but not from each other. Similarly for BAI versus density, the intercept and slope of the 50- to 100-year age-class regression ($P = 0.04$ and 0.05, respectively) and the intercept of the 125- to 175-year age-class regression ($P = 0.05$) were significantly different from those of the older age classes.

DISCUSSION

Age-related Trends in Mean and Variance of LAI and BAI

LAI and BAI both were most variable in the youngest age class (50–100 years), and mean LAI and BAI remained stable beyond the 125- to 175-year age class. This probably owes to the wider variability in stand structure in younger stands. Young (less than 100 years), vigorously growing stands in YNP range from open-canopied forests with large trees

Table 4. Results of ANCOVA for Leaf-area Index (LAI) and Basal Area Increment (BAI) for All Stands, Including Density as a Covariate

Source	df	Mean Square	F Ratio	Pr > F
LAI (model $r^2 = 0.50$)				
Age class	3	0.223	0.737	0.054
Density	1	2.011	6.629	0.001
Error	43	0.303		
BAI (model $r^2 = 0.52$)				
Age class	3	3.074	1.962	0.034
Density	1	23.862	12.636	0.001
Error	43	1.888		

Pr, predicted.

Table 5. Statistics for Linear Regression Models Predicting Leaf-area Index (LAI) and Basal Area Increment (BAI) by Using Stand Density for All Stands and by Age Class

Age Class	N	F Ratio	Pr > F	MSE	r^2
LAI					
Pooled	48	12.264	< 0.001	0.288	0.223
50–100[a]	13	1.418	0.259	0.710	0.114
125–175[a]	15	1.431	0.255	0.080	0.107
200–250[b]	12	6.819	0.026	0.137	0.405
300–350[b]	8	12.393	0.017	0.112	0.713
BAI					
Pooled	48	71.693	< 0.001	51.545	0.220
50–100[a]	13	6.184	0.035	29.431	0.197
125–175[a]	15	19.982	0.001	0.645	0.128
200–250[b]	12	13.741	0.005	0.448	0.491
300–350[b]	8	6.337	0.046	1.235	0.722

Superscript letters represent significance of slope of the regression line; classes having the same superscript letter indicates a lack of significantly different slopes at α = 0.05. MSE, mean standard error; and Pr, predicted.

(1150 trees/ha; average DBH, 18 cm, and average height, 12 m) to dense forests with smaller trees (11,000 trees/ha; average DBH, 7 cm, and average height, 8 m). However, far less structural variation is found in older forests, which have undergone longer periods of stand dynamics and development, and stand structure converges at about 200 years (Kashian et al. 2005). Wirth and colleagues (2002) also noted that much variability in stem production was explained by stand age across Siberian landscapes dominated by pine forests.

Along the chronosequence, changes in mean LAI and stemwood increment with age were consistent with our initial hypothesis and similar to values reported in other studies of coniferous forest ecosystem production (Assmann 1970; Ryan and Waring 1992; Gower and others 1996; Ryan and others 1997). A decline in mean LAI beyond the 50- to 100-year age class was also consistent with other studies of lodgepole pine in this region (Long

and Smith 1992; Olsson and others 1998; Smith and Resh 1999), although mean LAI in YNP at ages 50–100 years was generally lower in the present study. These differences likely result from our averaging values of LAI for multiple stands ranging in age and density within each age class (Table 1), since most studies examining LAI across a chronosequence calculate these values for a single stand at a given age rather than for many stands within an age class.

The decreasing variation in LAI and BAI that occurs with increasing stand age appears to be related to the simultaneous decrease in variation of stand density through time in Yellowstone. In the centuries following a large fire, initially high variation in stand density decreases due to self-thinning of dense stands and colonization of sparse stands; stand density converges across the landscape within 200 years after fire (Kashian et al. 2005). Our data show that variation in LAI and BAI

also decreases over time and eventually converges, likely in response to these changes in forest structure. Thus, changes in the variability of stand structure (particularly density) drive the variability in stand function (stemwood growth), likely due to the relationship of LAI to stand density.

Although variation in density, LAI, and BAI all decrease across the landscape over time after a large disturbance, LAI and BAI converge sooner than stand density. For example, LAI and BAI are less variable than stand density in the first few decades after fire and converge toward an equilibrium value by the 125- to 175-year age class; stand density is much more initially variable than LAI or BAI, and converges by the 200- to 250-year age class (Figure 5). In addition, stand density exhibits higher variation in every age class than either LAI or BAI. These trends suggest that there is at least some compensation for density in LAI and BAI. Because variation in density, LAI, or BAI is strongly reduced across the landscape as stands develop, the direct influence of large fires on the variability of LAI and BAI may endure for only about 125 years compared with about 200 years for stand density.

Relationship Between LAI and BAI

There was a positive linear relationship between LAI and BAI across all age classes, suggesting a link between stand structural characteristics (LAI) and stand function (BAI) in the lodgepole pine forests of YNP. However, the strength of this relationship varied with stand age. LAI and BAI were more strongly correlated in the oldest stands (200- to 250-year and 300- to 350-year age classes) compared with young, aggrading forests (50- to 100-year age class). The variation of the LAI–BAI relationship among stand age classes was consistent with our original hypotheses and may again be explained by the higher structural variability present in stands aged 50–100 years compared with those aged more than 100 years. Stands having similar LAI may have very different rates of aboveground production based on the distribution of leaf area among fewer large trees in sparse stands or many small trees in denser stands (Long and Smith 1990). Thus, it is not surprising that the relationship between LAI and BAI is weaker in young stands, where higher structural variability subsequently creates high variability in stand production.

The relationship between LAI and BAI suggests that foliage production and redistribution play a critical role in age-related declines in stand production, as suggested by Smith and Long (2001),

and that stand structural characteristics that may correspond or directly affect LAI, including stand density, may also influence stand production. Studies by Long and Smith (1990, 1992) have also shown that LAI is positively correlated to stand volume increment for lodgepole pine in the Rocky Mountains, although they found the relationship to be nonlinear, where mean volume growth increases with mean leaf area at a decreasing rate. Kollenberg and O'Hara (1999) noted a linear but weak ($r^2 = 0.34$) relationship between volume increment and leaf area in multi-aged stands.

A limitation of our approach for estimating LAI was our inability to validate the allometric equations for stands in YNP, as well as our use of these equations for a very wide range of tree sizes across the landscape. The effects of variable tree sizes on leaf-area allometry for coniferous forests are not trivial, and LAI estimates for this study were based on data for lodgepole pine stands sampled in a slightly different geographic region and for a smaller range of tree sizes, where all stands were even aged (Long and Smith 1988). Nevertheless, other studies have used the Long and Smith equation to estimate LAI in slightly different geographic regions and in uneven-aged stands (Kollenberg and O'Hara 1999). Although few studies have examined leaf area by using allometry in stands more than 300 years old (Kashian et al. 2005), we noted that relatively little change in LAI appears to occur beyond 125 years. In addition, the mean and range of our LAI values were well within those reported for young (11–12 years) lodgepole pine stands in YNP and were within the range reported in other studies for lodgepole pine in the northern and central Rocky Mountains (Table 6). In any case, the tremendous variation in tree size, stand age, and stand density present across the Yellowstone landscape demands that our final values of LAI be interpreted cautiously, particularly for the oldest age class.

Because allometric equations for ANPP are more sensitive than those for LAI to differences between sites (S. T. Gower and M. G. Ryan personal communication), we were also limited in our ability to investigate directly the relationship between stand structural characteristics and stand functional characteristics, as well as the variability of ANPP in mature forests across the Yellowstone landscape. Currently, no allometric equations for ANPP have been developed or validated for estimating ANPP for mature forests in Yellowstone. We note that BAI is a useful index of ANPP, because ANPP is generally dominated by stemwood growth in mature lodgepole pine stands (Long and Smith 1984,

Table 6. Comparison of Leaf-area Index (LAI) Calculated for Other Studies of Lodgepole Pine in the Northern and Central Rocky Mountains

Location	Age (Years)	Density (Stems/ha)	Stand-projected LAI (m^2/m^2)	Reference
Interior British Columbia	22	3500–109,000	0.9–5.4[a]	Keane and Weetman 1987
Yellowstone National Park	9	100–62,800	0.002–1.8	Reed and others 1998
Yellowstone National Park	11	0–535,000	0–6.9	Turner and others 2004
Yellowstone National Park	12	425–598,462	0.04–2.2	Litton and others 2003
Yellowstone National Park	45–359	460–11,320	0.87–3.4	This study
Southeastern Wyoming	10–117	528–35,833	1.2–6.5	Long and Smith 1992
Southeastern Wyoming	15–260	12,500–1133	0.9–4.1	Smith and Resh 1999
Southeastern Wyoming	30–200	917–1642	1.5–3.4	Olsson and others 1998
Southeastern Wyoming	75–240	420–14,640	1.8–4.0[a]	Pearson and others 1984
Southeastern Wyoming	100	2217–14,640	2.8–2.9[a]	Knight and others 1981
Northern Colorado	71–77	1600–8600	1.8–5.6[a]	Moir and Francis 1972
Northern Colorado	40–245	1067–4376	3.0–4.9[a]	Ryan and Waring 1992
Northern Utah	67–134	208–6300	2.2–4.9	Jack and Long 1991

[a]*Values reported as total or all-sided LAI were converted to stand-projected LAI here by dividing by 2.5 (Waring 1983).*

1990, 1992; Pearson and others 1984; Kollenberg and O'Hara 1999; Smith and Resh 1999), and that the relationships between LAI and BAI observed in this study suggest that forest stand structure may influence functional characteristics. Thus, our results have important implications for understanding variability in forest ecosystem function across disturbance-prone landscapes. Nevertheless, directly examining such variability in forest productivity represents an important avenue for future research.

Relationship of LAI and BAI to Stand Characteristics

As we hypothesized, stand age and tree density were the two most important factors in explaining variation in both LAI and BAI. The unimportance of substrate to the model was somewhat surprising, given the number of studies that show a positive correlation between leaf area and site quality for lodgepole pine (Moir and Francis 1972; Long and Smith 1990) or other conifers (Wirth and others 2002) and the link between leaf area and nutrient and water availability (Nadelhoffer and others 1985; Gower and others 1992, 1995; Snowdon and Benson 1992; Herbert and Fownes 1995; Fassnacht and Gower 1997). In at least one of these studies (Moir and Francis 1972), leaf area differed only among stands having very different (>30 m) site indices. Although Despain (1990) noted differences in texture, base cations, and water-holding capacity between soils derived from rhyolite or lacustrine sediments, 100-year site indices calculated for

stands aged 45–200 years in our study ranged only from 9 to 20 m (mean, 13 m). These data suggest that site quality differences between the broad substrates considered in this study are not large. Because soil fertility may vary at very fine scales, investigating the relationships between soil fertility and LAI or BAI in Yellowstone, rather than broad substrate type, is an important topic for future research.

Similar to the relationship between LAI and BAI, the relationship of LAI and BAI to tree density varied with stand age. Though weak in young stands aged 50–175 years, the LAI/BAI-density relationships were very strong in stands older than 300 years. Variation in the LAI-density relationship is evident but subtle in the literature, often leading to contrasting conclusions about the relationship. For example, the relationship between LAI and tree density has recently been shown to be very strong for stands aged 11–12 years in YNP (Turner and others 2004; Litton and others 2004). Notably, most studies concluding that LAI is closely related to density [for example, see Keane and Weetman (1987)] were conducted in stands less than 30 years old. However, the majority of studies concluding that LAI is independent of density in lodgepole pine, or that LAI exhibits a plastic response to various types of stand structure (Moir and Francis 1972; Knight and others 1981; Pearson and others 1984; Long and Smith 1990; Jack and Long 1991), similar to our results for stands aged 50–175 years, were conducted in stands aged 50–150 years. This plastic response may be characteristic of closed-canopy stands that maintain a given

LAI regardless of density. Given this reasoning, it would follow that LAI is more strongly correlated to density in the 200- to 250-year age class than in younger stands, but exhibits a weaker relationship than older stands. In Yellowstone, the canopies of stands aged 200–250 years typically are transitional between closed canopies of younger stands and the more open, ''broken'' canopies of stands older than 300 years. Nevertheless, LAI and BAI always exhibited less variation than density in each age class, suggesting at least some plasticity in BAI and LAI for density.

Implications of Landscape Variation in Tree Density, LAI, and BAI After Large Disturbances

Understanding the implications of landscape heterogeneity for ecosystem processes is one of the most important challenges for ecosystem science (Schimel and others 1997; Clark and others 2001). Several recent studies have noted wide variation in ecosystem processes, including LAI and ANPP, related to the spatial heterogeneity in initial postfire pine-seedling density after the 1988 Yellowstone fires (Reed and others 1998; Litton and others 2003; Turner and others 2004). Our results suggest that, as the post-1988 stands age and develop, the landscape pattern of ANPP is also likely to change as variation in stand density and LAI is reduced. However, our data also suggest that postfire variation in lodgepole pine density may influence landscape patterns of stand production for approximately 125 years. Therefore, if BAI is an adequate approximation of ANPP, large, stand-replacing fires in YNP may shape the variability of stand functional characteristics across the landscape for at least a century. Such variation in stand production may also influence other ecosystem processes, such as nutrient cycling.

Although age-related changes in average forest productivity and stand structure are well documented for Rocky Mountain lodgepole pine forests (Knight and others 1981; Pearson and others 1984; Long and Smith 1988, 1992; Comeau and Kimmins 1989; Ryan and others 1997; Smith and Resh 1999), implications of the variability we observed in stand density, relationships between LAI and BAI, and LAI-density relationships within each age class across heterogeneous landscapes have not been considered. Although we have not measured forest ecosystem function directly, our emphasis on variability as well as average values of stand production provides an important step in addressing the links between stand development and ecosystem processes across large spatial and temporal scales. Furthermore, our focus on variability provides a basis for inference about how the variability of forest productivity, which is initially very high after a large disturbance (Reed and others 1998; Litton and others 2002; Turner and others 2004), may change on landscapes over long periods of forest succession and how these trajectories may be related to those of forest structure. Given the recent focus on spatial heterogeneity of ecosystem processes, such information has very strong significance for ecosystem science.

The patterns of LAI, BAI, and stand density noted in our study may not apply to other forest types. The general relationships of leaf area, stemwood growth, and stand density in our study reflect the relatively simple structure of lodgepole pine forests, infertile substrates, low precipitation during the growing season, and short growing season that characterize the subalpine plateaus of Yellowstone. More mesic forest types that contain shade-tolerant species would likely more quickly achieve peak LAI and have more complex relationships due to the greater influence of competition on forest structure. Thus the patterns described in our study might be most applicable to coniferous forest types characterized by stand-replacing fire regimes (Turner and Romme 1994), although caution must be taken before our results are applied to coniferous types such as spruce–fir forests, which include shade-tolerant species.

Although we note the primary influence of stand density and age on the variability of LAI and BAI, factors other than density and time since the disturbance will become increasingly important through successional time. Spatial variation in the abiotic environment (for example, climate, topography, and soil) often creates wide variation in LAI and forest productivity across landscapes, particularly in late-successional forests (Knapp and others 1993; Keane and others 1996; Burke and others 1997; Hansen and others 2000). Additional small fires that occur between large fires in YNP create a mosaic of stand ages across the landscape that will influence the variability of LAI and BAI. Finally, other disturbances that may be unrelated to fire, such as windthrow events and infestations of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), will create additional variation in LAI and BAI across the landscape.

REFERENCES

Arno SF. 1980. Forest fire history in the northern Rockies. J For 78:460–5.

Assmann E. 1970. The principles of forest yield study. Oxford: Pergamon.

Baker WL. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecol 7:181–94.

Binkley D, Stape JL, Ryan MG, Barnard HR, Fownes J. 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5:58–67.

Brown SL, Schroeder PE. 1999. Spatial patterns of aboveground productions and mortality of woody biomass for eastern U.S. forests. Ecol Appl 9:968–80.

Burke IC, Laurenroth WK, Parton WJ. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology 78:1130–340.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JE, Ni J. 2001. Measuring net primary production in forests: concepts and field methods. Ecol Appl 11:356–70.

Cochran WG. 1977. Sampling Techniques. 3rd ed. New York: John Wiley and Sons.

Comeau PG, Kimmins JP. 1989. Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. Can J For Res 19:447–54.

Dean TJ, Long JN. 1986. Variation in sapwood area–leaf area relations within two stands of lodgepole pine. For Sci 32:749–58.

Despain DG. 1990. Yellowstone vegetation Boulder. (CO): Roberts Rinehart.

Fassnacht KS, Gower ST. 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Can J For Res 27:1058–67.

Foster DR, Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large, infrequent disturbances. Ecosystems 1:497–510.

Gower ST, Isebrands JG, Sheriff DW. 1995. Carbon allocation and accumulation in conifers. In: Smith WK, Hinckley TM, editors. Resource physiology of conifers: acquisition, allocation, and utilization. New York: Academic. p 217–54.

Gower ST, McMurtrie RE, Murty D. 1996. Aboveground net primary production decline with stand age: potential causes. Tree 11:378–82.

Gower ST, Vogt KA, Grier CC. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. Ecol Monogr 62:43–65.

Habeck JR, Mutch RW. 1973. Fire-dependent forests in the northern Rockies. Quat Res 3:408–24.

Hansen AJ, Rotella JJ, Kraska MPV, Brown D. 2000. Spatial patterns of primary productivity in the Greater Yellowstone ecosystem. Landscape Ecol 15:505–22.

Herbert DA, Fownes JH. 1995. Phosphorous limitation of forest leaf area and net primary production on a highly weathered soil. Biogeochemistry 29:223–35.

Jack SB, Long JN. 1991. Analysis of stand density effects on canopy structure: a conceptual approach. Trees Struct Funct 5:44–9.

Jenkins JC, Birdsley RA, Pan Y. 2001. Biomass and NPP estimation for the Mid-Atlantic region (USA) using plot-level forest inventory data. Ecol Appl 11:1174–93.

Kashian DM, Turner MG, Romme WH, Lorimer CG. 2005. Variability and convergence in coniferous stand structure with forest development on a fire-dominated subalpine landscape. Ecology. Forthcoming.

Kaufmann MR, Ryan MG. 1992. Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests. Tree Physiol 2:47–59.

Keane RE, Ryan KC, Running SW. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. Tree Physiol 16:316–31.

Keane MG, Weetman GF. 1987. Leaf area-sapwood cross-sectional area relationship in repressed stands of lodgepole pine. Can J For Res 17:205–9.

Knapp AK, Fahenstock JT, Hamburg SP, Statland LB, Seastedt TR, Schimel DS. 1993. Landscape patterns in soil–plant water relations and primary production in tallgrass prairie. Ecology 74:549–60.

Knight DH. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In: Turner MG, editor. Landscape heterogeneity and disturbance. New York: Springer-Verlag. p 59–83.

Knight DH, Fahey TJ, Running SW, Harrison AT, Wallace LL. 1981. Transpiration from 100-yr-old lodgepole pine forests estimated with whole-tree potometers. Ecology 62:717–26.

Kollenberg CL, O'Hara KL. 1999. Leaf area and tree increment dynamics of even-aged and multiaged lodgepole pine stands in Montana. Can J For Res 29:687–95.

Litton CM, Ryan MG, Tinker DB, Knight DH. 2003. Below- and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density. Can J For Res 33:351–63.

Litton CM, Ryan MG, Knight DB. 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. Ecol Appl 14:460–475.

Long JN, Dean TJ. 1986. Sapwood area of *Pinus contorta* stands as a function of mean size and density. Oecologia (Berl) 68:410–2.

Long JN, Smith FW. 1984. Relation between size and density in developing stands: a description and possible mechanism. For Ecol Manage 7:191–206.

Long JN, Smith FW. 1988. Leaf area–sapwood area relations of lodgepole pine as influenced by stand density and site index. Can J For Res 18:247–50.

Long JN, Smith FW. 1990. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests the influence of site quality and stand structure. J Appl Ecol 27:847–56.

Long JN, Smith FW. 1992. Volume increment in *Pinus contorta latifolia:* the influence of stand development and crown dynamics. For Ecol Manage 53:53–64.

Loope LL, Gruell GE. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quat Res 3:425–43.

Martner BE. 1986. Wyoming climate atlas Lincoln: University of Nebraska Press.

MathSoft1998. S-Plus 2000:rofessional release.

Moir WH, Francis R. 1972. Foliage biomass and surface area in three *Pinus contorta* plots in Colorado. For Sci 18:41–5.

Nadelhoffer KJ, Aber JD, Melillo JM. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Tree Physiol 16:187–200.

Olsson U, Binkley D, Smith FW. 1998. Nitrogen supply, nitrogen use, and production in an age sequence of lodgepole pine. For Sci 44:454–7.

Pearson JA, Fahey TJ, Knight DH. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Can J For Res 14:259–65.

Perry DA. 1994. Forest ecosystems Baltimore: Johns Hopkins University Press.

Pulliam HR. 1988. Sources, sinks, and population regulation. Am Nat 132:652–61.

Pulliam HR, Danielson BJ. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am Nat 137:S50–S66.

Reed RA, Finley ME, Romme WH, Turner MG. 1998. Aboveground net primary production and leaf-area index in early postfire vegetation in Yellowstone National Park. Ecosystems 2:88–94.

Regent Instruments. 2001. WinDendro 2001a Quebec: Regent Instruments.

Romme WH. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol Monogr 52:199–221.

Romme WH, Despain DG. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39:695–9.

Romme WH, Knight DH. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62:319–26.

Romme WH, Knight DH. 1982. Landscape diversity: the concept applied to Yellowstone Park. Bioscience 32:664–70.

Ryan MG, Binkley D, Fownes JH. 1997. Age-related decline in forest productivity: pattern and process. Adv Ecol Res 27:213–62.

Ryan MG, Waring RH. 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73:2100–8.

Sala OE, Parton WJ, Joyce LA, Lauenroth WK. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–5.

Schimel DS, participants VEMAP, Braswell BH. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecol Monogr 67:251–71.

Smith FW, Long JN. 2001. Age-related decline in forest growth: an emergent property. For Ecol Manage 144:175–81.

Smith FW, Resh SC. 1999. Age-related changes in production and below-ground carbon allocation in *Pinus contorta* forests. For Sci 45:333–41.

Snowdon P, Benson ML. 1992. Effects of combinations of irrigation and fertilization on the growth of aboveground biomass production of *Pinus radiata*. For Ecol Manage 52:87–116.

SPSS. 1996. SYSTAT 6.0 for Windows Richmond (CA): SPSS.

Tinker DB, Romme WH, Despain DG. 2003. Historic range of variability in landscape structure in subalpine forests of the Greater Yellowstone Area. Land Ecol. 18:427–439.

Turner J, Long JN. 1975. Accumulation of organic matter in a series of Douglas-fir stands. Can J For Res 5:681–90.

Turner MG, Hargrove WH, Gardner RH, Romme WH. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J Vegetat Sci 5:731–42.

Turner MG, Romme WH. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecol 9:59–77.

Turner MG, Tinker DB, Romme WH, Kashian DM, Litton CM. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7:751–775.

Waring RH. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Adv Ecol Res 13:327–54.

Whittaker RH, Nehring WA. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. Ecology 56:771–90.

Wirth C, Schulze E-D, Kusznetova V, Milyukoa I, Hardes G, Siry M, Schulze B, Vygodskaya NN. 2002. Comparing the influence of site quality, stand age, fire and climate on aboveground tree production in Siberian Scots pine forests. Tree Physiol 22:537–52.

Wright HE Jr, Heinselman ML. 1973. Introduction to symposium on the ecological role of fire in natural coniferous forests of western and northern America. Quat Res 3:319–28.

Zar JH. 1999. Biostatistical analyses. 4th ed Upper Saddle River (NJ): Prentice-Hall.