VARIABILITY AND CONVERGENCE IN STAND STRUCTURAL DEVELOPMENT ON A FIRE-DOMINATED SUBALPINE LANDSCAPE

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Abstract. The 1988 Yellowstone fires resulted in a complex mosaic within which post-fire lodgepole pine seedling densities varied by over five orders of magnitude. Investigators have speculated that such postfire mosaics of vegetation structure may persist until the next large disturbance, but the fate of the initial structural variability of postfire communities is currently poorly understood. We studied lodgepole pine (*Pinus contorta* var. *latifolia* Englem. ex Wats.) stands in Yellowstone National Park (Wyoming, USA) unburned by the 1988 fires to determine how variation in stand structure changes with increasing stand age. The coefficient of variation in stand density decreased from 231% in 12-yr-old stands to 91% in stands aged 50–100 yr, and to 37% for stands ages 200–250 yr. Substantial variability in age distributions both within and among age classes suggested that both gradual infilling of initially sparse stands and self-thinning of initially dense stands are important processes affecting variation in stand density. Variation in stand density was explained primarily by stand age ($P < 0.0001$) and by geographic location ($P < 0.01$). Field estimates and reconstructions of stand density trajectories suggest the importance of biotic processes and the contingent effects that produce initial patterns of stand density. Variation in stand density is substantially reduced 125 yr following fire and remains relatively unchanged beyond approximately 200 yr. These results suggest that large, infrequent fires impose a pattern of stand structural variability that may persist for centuries, but stand density likely converges within the fire-free interval in this landscape.

Key words: convergence; fire; forest; landscape; lodgepole pine; self-thinning; stand density, stand dynamics, stand structure; subalpine forests; succession; Yellowstone National Park, Wyoming (USA).

INTRODUCTION

Disturbances such as wildfires create complex patterns of vegetation across forest landscapes. Heterogeneity on forest landscapes may occur as mosaics of patches generated by many events (Romme 1982, Pickett and White 1985, Romme and Despain 1989, Wu and Loucks 1995), but also may be created by single large events that occur infrequently on a given landscape (Turner et al. 1997, Foster et al. 1998). Because initial variation in composition and structure within vegetation of the same successional stage may lead to multiple successional trajectories (e.g., Cattelino et al. 1979, Abrams et al. 1985, Halpern 1988, Fastie 1995), initial vegetation patterns may have important long-term implications for landscape pattern (Turner et al. 1997, Foster et al. 1998, Turner et al. 1998).

In Yellowstone National Park (YNP), large wildfires in 1988 created a complex mosaic of lodgepole pine (*Pinus contorta* var. *latifolia* Englem. ex Wats.) densities ranging from <100 to >500 000 seedlings/ha across the landscape (Anderson and Romme 1991, Ellis et al. 1994, Turner et al. 1997, 2004, Kashian et al. 2004). Investigators have speculated that these relative differences in stand structure will persist until the next set of large fires occur (Anderson and Romme 1991, Ellis et al. 1994, Turner et al. 1997). By affecting spatial patterns of stand structure, this legacy of the 1988 fires could have important implications for ecological processes on the landscape, such as forest productivity (Reed et al. 1998, Litton et al. 2003, Turner et al. 2004, Kashian et al. 2005), carbon dynamics (Pearson et al. 1987, Smith and Resh 1999, Litton et al. 2003, 2004), the production of coarse woody debris (Tinker and Knight 2000), the diversity or behavior of flora and fauna (Taylor 1973, Spies and Turner 1999), and the spread of subsequent disturbances (Van Wagner 1977, Knight 1987).

Lodgepole pine forests are typically associated with stand-replacing fires (Moir 1969, Day 1972, Whipple and Dix 1979, Lotan and Perry 1983, Veblen 1986,

PLATE 1. Two lodgepole pine stands in Yellowstone National Park similar in age (approximately 130 yr) but very different in structure. The sparser stand at left has a density of approximately 1020 trees/ha and very little density-dependent mortality; the dense stand at right has a density of 5400 stems/ha and much evidence of self-thinning. Stem maps for these stands are found in Appendix B. Photo Credits: D. Kashian.

Johnson and Fryer 1989, Veblen et al. 1991) and are characterized by strongly negatively skewed age distributions and density-dependent mortality (self-thinning) (Peet and Christensen 1980, Knowles and Grant 1983, Kenkel 1988, Lotan and Critchfield 1990, Johnson 1992). However, the age structures of lodgepole pine stands may be much more variable across the Rocky Mountains than the traditional dogma suggests (Whipple and Dix 1979, Peet 1981, Despain 1983, Komarkova et al. 1988, Muir 1993, Parker and Parker 1994). Variation in fire severity (Turner et al. 1994) or prefire stand serotiny (Tinker et al. 1994, Schoennagel et al. 2003) may also result in young stands characterized by low initial densities (Anderson and Romme 1991), which require a longer period of development to reach crown closure (Romme 1982, Parker and Peet 1984, Veblen 1986). These stands, with continuous rather than episodic seedling establishment, often exhibit normal age distributions and an increase in stand density with increasing stand age. Multimodal age distributions, which indicate multiple pulses of reproduction, may also develop in very old stands where young cohorts establish in gaps created as the original cohort begins to experience mortality (Whipple and Dix 1979).

Variability in lodgepole pine stand development across a landscape may lead to substantial reduction in the high initial variation in stand structure found after large disturbances. Large fires similar to those in 1988 burned the YNP landscape every 100–300 yr (Romme 1982, Romme and Despain 1989), and probably produced wide variation in pine seedling density similar to that produced in 1988. Currently, however, far less variation in mature stand structure exists in the unburned portions of the landscape compared to post-1988 seedling densities (Romme 1982, Anderson and Romme 1991, Ellis et al. 1994), suggesting that the initial variability in stand structure following these historical fires may decrease as stands develop. Understanding changes in variability may have important im-

plications for understanding underlying causal processes in vegetation and landscape structure (Benedetti-Cecchi 2003), but few studies have examined the long-term significance of variation in initial postdisturbance vegetation structure in forests (but see Odion and Davis 2000 for chaparral systems), and none has examined the persistence of initial variability in a landscape context.

The scale and heterogeneity of the 1988 fires provide a unique opportunity to examine the fate of the initial postfire structural variability of ecological communities resulting from a single disturbance event (Christensen et al. 1989, Knight and Wallace 1989). Using density as a surrogate for stand structure, our general objective was to determine how variation in stand structure changes with increasing stand age, and whether there is evidence for convergence of initially dissimilar stand structures (see Plate 1). We approached this objective by examining the nearly 360 000 ha of the subalpine plateaus of YNP not burned by the 1988 fires. In doing so, we hypothesized that: (1) the variability as well as the mean of stand density decreases with stand age, and the variability of age distributions is highest for stands in younger age classes; (2) past stand development patterns were dominated by self-thinning and a general reduction in stand density; and (3) stand density changes at rates determined by initial stand structure, such that the density of initially dense stands would change more rapidly than sparser stands.

METHODS

Study area

Our study focused on the 80% of the high, forested, subalpine plateaus of YNP in northwestern Wyoming dominated by nearly pure stands of lodgepole pine. Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Englemann spruce (*Picea engelmannii* Parry ex Engelm.) are common in the overstory only on mesic sites and in older stands (Despain 1990). Precipitation increases

with elevation; elevation ranges in the park from ~1900 to 3000 m, although most of the subalpine plateaus range from ~2100 to 2600 m. The area includes relatively little variation in site quality resulting from the relatively gentle topography and the dominance of dry, nutrient-poor soils across the landscape. Nearly two-thirds of the park includes dry, infertile rhyolite substrates, and the remainder includes less dry and slightly less infertile andesite substrates and lacustrine sediments. Stand-replacing fire is a dominant factor shaping the YNP landscape, and large, infrequent fires occur every 100 to 300 yr (Romme and Despain 1989). Small fires (usually <5000 ha) burn during the interval between large fires (Despain 1990), such that YNP includes 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 yr old. Approximately 45% of the subalpine plateaus was burned by the 1988 fires (Turner et al. 1994).

Study design

During the summers of 1999–2001, we sampled 48 stands ≥5 ha that were left unburned by the 1988 fires. We were able to select sites that controlled for differences in slope, aspect, soil type, and elevation; in a separate study, Kashian et al. (2005) found that site parameters did not explain differences in tree growth among the 48 stands. All stands contained ≥85% lodgepole pine, originated following a stand-replacing fire, were located on flat sites (0–2% slopes) of similar elevation, ranged in site index between 9 and 13 m, and were visibly free from other major structure-altering disturbances (e.g., severe windthrow, recent low-severity fires, or past insect infestations) (see Appendix A for descriptions of stands). We used several lines of evidence in selecting our older stands that controlled for potential variability in disturbance history, including the amount and extent of decay of coarse woody debris present on the forest floor, the presence of fire scars, and the presence of tree species other than lodgepole pine.

Sampling was stratified using four discrete stand age classes (50–100, 125–175, 200–250, and 300–350 yr). Stands were classified using ages determined initially from a stand age map (Tinker et al. 2003) and verified using increment cores taken from the dominant trees in the stand. Within each age class, 12–15 stands were sampled that represented the range of stand density (as determined from aerial photographs and field reconnaissance); eight stands were sampled in the oldest age class. Due to limited accessibility to remote regions of the park, stands were selected randomly from those stands within 2 km from roads or trails. All stands were located at least 1 km from each other.

Field methods

Stand characteristics.—Within each stand, a 10 × 50 m (500 m²) rectangular plot was randomly located within the ≥5-ha area chosen for sampling. In each plot, the diameter at breast height (dbh; 1.4 m) of all living and dead trees ≥4 cm dbh and basal diameter of stumps was recorded. ''Stumps'' were identified as a basal portion of a tree that did not extend to breast height, and were measured when dbh ≥4 cm as inferred from basal diameter. All live stems <1.4 m in height or <4 cm dbh were classified as saplings/seedlings, counted, and placed into three height classes (<10, 10–100, and >100 cm) by species. Percent cone serotiny was estimated for each stand by scoring 50 randomly selected live trees in each plot as having either open or closed cones and expressed as percent serotinous trees for the stand (see Tinker et al. 1994).

Age class distributions.—Age class distributions were used to deduce stand history, although great care must be used when inferring stand dynamics and past periods of recruitment (Lorimer 1985, Johnson et al. 1994). In each plot, an increment core was extracted at 30 cm above mineral soil from all live and dead trees ≥4 cm dbh (n = 9522 cores for all plots). Where stand density was <2000 stems/ha (<100 trees within the plot), trees immediately outside the plot were selected at random for core extraction and dbh measurement until a minimum of 100 live trees were sampled.

Point pattern analyses.—Changes in tree spatial patterns may provide evidence that a given stand experienced density-dependent mortality rather than mortality due to other factors such as disease, insect infestations, or low-severity fires. Self-thinning often causes the spatial pattern of trees to move from a clustered toward a random distribution (Daniels 1978, Kenkel 1988, Mast and Veblen 1999, He and Duncan 2000). The relatively slow decomposition of dead stems in YNP permitted the reconstruction of spatial patterns in stands younger than 200 yr to the point in time just prior to the mortality events that produced most of the fallen stems within the plot (sensu Kenkel 1988, He and Duncan 2000). This method was preferable to using dead bole dynamics for dating mortality (Johnson and Greene 1991) because cross-dating a large sample of dead boles in each stand was problematic. In the field, a precise map of stems in each plot was constructed by recording to the nearest 0.1 m the *X*- and *Y*-coordinates of all living trees, standing and fallen dead trees, and stumps ≥4 cm dbh within each plot (see Appendix B for example of stand maps).

Analytical methods

Stand characteristics.—Density for each stand was calculated for all live trees ≥4 cm and scaled to trees per hectare. The mean values of stand density for each age class were compared using one-way analysis of variance (ANOVA) to examine changes along the chronosequence; the Fischer LSD method was used for pairwise multiple comparisons of age class means. The coefficient of variation (CV) of stand density was computed for each age class, and within-class variances of

stand density were compared among classes using independent-sample *t* tests with variances assumed equal. Stepwise multiple linear regression was used to examine the relative importance of stand age class, elevation, geographic location (*X*- and *Y*-coordinates of the Universal Transverse Mercator Grid System), percent serotiny, and the interactions of these terms in explaining the variation in stand density across the Yellowstone landscape using $\alpha = 0.05$ to enter and remove. Substrate type and site index have been shown to have little influence on tree growth in YNP (Kashian et al. 2005) and were not used as predictive variables. In all regression analyses in this study, age class was included as a categorical variable, density was log-transformed, and percent serotiny was arcsine square-root transformed.

Age class distributions.—Increment cores were mounted and sanded per standard techniques (Stokes and Smiley 1968), and annual rings were counted using the WINDENDRO software package (Regent Instruments 2001). Tree ages are reported as ring counts plus an estimate of the number of years required to reach 30 cm (core height). To obtain this estimate, 400 seedlings between 20 and 100 cm tall were harvested from areas burned in 1988 ranging in density from <100 to >100 000 stems/ha, aged at the base, and used to build regression equations describing height/age relationships at varying densities (see Romme 1982, Fastie 1995). Cross-dating of increment cores was problematic due to a general lack of sensitivity of lodgepole pine growth to annual differences in climate in YNP. However, based on ring counts of trees in YNP within burned areas of known fire dates, we estimate dating errors to be ≤5 yr (similar to Romme 1982), which should have only minimal effects on age class distributions for the purposes of this study (see Appendix C for discussion of potential errors in age estimation). Age class distributions were constructed for each stand using 5-yr intervals.

Point pattern analyses.—We used a transformation of Ripley's *K* function, the "L_h" function (Ripley 1977), to quantify the spatial patterns of live and dead stems and stumps in young stands. L_h is estimated at a series of given distances or spatial scales *h* and is expected to be zero for a random distribution of trees. Values of L_h significantly greater than zero indicate clustering (spatial attraction) whereas negative values indicate regularity (spatial repulsion) (Getis and Franklin 1987). We used Monte Carlo simulations to evaluate the significance of the departure of L_h from zero by generating 1000 sets of random coordinates to approximate 95% confidence envelopes ($P < 0.05$). We concluded that self-thinning had occurred when the distribution of live trees + dead trees + stumps was clustered, while the distribution of live trees only was random (sensu He and Duncan 2000).

Dendrochronological analyses.—We used current tree ring widths in stands of differing densities in each age class to predict earlier densities of older stands, thus enabling reconstruction of stand density trajectories. The growth of lodgepole pine, similar to many shade-intolerant conifers, is very sensitive to stand density, and mean dbh reflects the spacing of trees during their growth (Lotan and Critchfield 1990, Oliver and Larsen 1996). Although dendrochronological reconstructions contain several potential sources of error (Romme and Knight 1981, Johnson and Fryer 1989, Norton and Ogden 1990, Johnson et al. 1994, Donnegan and Rebertus 1999), several recent studies have used ring width patterns as indicators of tree density during the establishment period (Fastie 1995, Winter et al. 2002).

Ring widths for trees from each of the 48 stands were measured to the nearest 0.001 mm using WINDENDRO and cross-dated against stand-specific master chronologies developed for each stand using visual cross-dating (Stokes and Smiley 1968). Because many ring series lacked distinctive ring width signatures, master chronologies were developed from only 5–7 trees from each stand. Six to eight additional ring series from each stand were used in developing regression equations relating stand density to 5-yr average annual tree ring width (to minimize effects of autocorrelation between annual rings). We selected a standard age ("model age") at which to model ring width that was within 30 yr of the age of the majority of stands within an age class. Stands in the regression that were up to 30 yr older than the model age were included in the regressions because the majority of seedling establishment in lodgepole pine stands typically occurs within 30 yr following the disturbance (Whipple and Dix 1979, Romme 1982). Stands younger than the model age were included only if they were within 5 yr of the model age; thus stand density was reconstructed in only 39 of the 48 stands.

Once a model was built for ages 70, 125, and 220 yr (representing the 50–100, 125–175, and 200–250 yr age classes, respectively), each model was applied to the corresponding ages of successively older trees, where applicable, to reconstruct density for each stand. To reconstruct density back to the initial establishment period (12 yr), an additional model was built using 25 basal discs collected from 16 12-yr-old (sapling) stands representing the range of sapling density present across areas burned by the 1988 fires. All sapling stands were located on flat sites at similar elevations to those of the mature stands. Thus to reconstruct the density of a 300-yr-old stand, for example, the regression models for model ages 12, 70, 125, and 220 yr were used to back-predict stand density of the stand from the ring widths of the stand at those corresponding ages. For the 5-yr averages corresponding to our model ages, the Palmer Drought Severity Index (PDSI) for the YNP region (Cook et al. 1999) was always within one standard deviation of the mean PDSI for the past three centuries (see Appendix D). As a result, and because
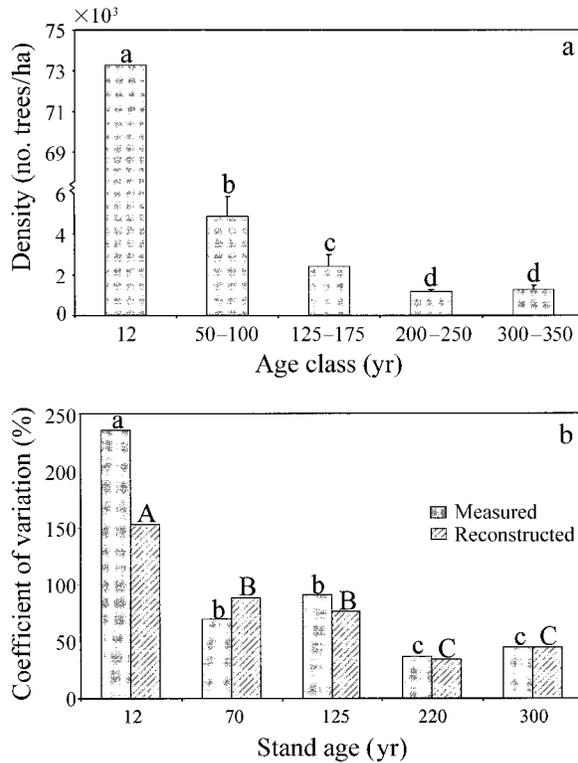
FIG. 1. (a) Stand density (mean + 1 SE) for stands sampled across five age classes in Yellowstone National Park. Data for 12-yr-old stands are from Litton (2002). (b) Age-related changes in the coefficient of variation of stand density. Solid bars represent the coefficient of variation of stand density measured directly in the field; cross-hatched bars represent that reconstructed using tree ring widths (see *Results*). Bars having the same letter and case are not significantly different ($P > 0.05$).

RESULTS

Variation in stand density

Mean stand density steeply declined from 73 347 stems/ha (median = 16 975 stems/ha) in the 12-yr-old age class to 4906 stems/ha at the 50–100 yr age class (Fig. 1a). Mean stand density declined at a much slower rate beyond the 50–100 yr age class, falling 76% to a mean value of 1170 stems/ha at the 200–250 yr age class, after which it did not change appreciably (Fig. 1a). The coefficient of variation of stand density also dropped sharply from 235% in the 12-yr class to 91% at the 50–100 yr age class, did not change significantly between the 50–100 and 125–175 yr age classes, then declined again to 37% at the 200–250 yr age class and was stable thereafter (Fig. 1b). Variance in density in the 12-yr age class was significantly different from variance in all other classes, and the 50–100 and 125–175 yr age classes were different from the 200–250 and 300–350 yr age classes. The extremely high variability in density in the 12-yr-old stands is evident in the mean density calculation of Kashian et al. (2005), who reported a much lower mean density of 22 718 stems/ha using 149 sample points in the area burned in 1988.

Variation in stand density was explained primarily by differences in age and geographic location for all stands (Table 1). Stand age class (partial $R^2 = 0.37$) was the most important variable in the multiple regression model ($R^2 = 0.61$), followed by northing (partial $R^2 = 0.17$) and easting (partial $R^2 = 0.07$), suggesting that the amount of variability of stand density is strongly related to developmental changes in stand structure across the landscape. Percent serotiny ($P = 0.78$), all abiotic factors, and all interaction terms were unimportant in explaining variation in stand density (Table 1).

Variation in age structures

Age distributions showed substantial diversity both within and among stand age classes (see Appendix E for age distributions of stands). Dense stands had strongly peaked age distributions with a pronounced negative skew, indicating the establishment of a large proportion of the trees soon after the stand originated. Stands >300 yr generally had bell-shaped or multi-modal distributions. Sparse stands were often uneven aged and exhibited flat or nonskewed distributions, with a significant amount of tree establishment occur-

most ring series did not show distinct width signatures, we did not adjust our regression models for differences in growth rate due to differences in climate.

Curves were plotted that represented the trajectories of stand density for each stand density reconstruction. Where possible, trajectories for young stands with a significant number of dead stems were validated by reconstructing stand density at the model age using the age and density of dead stems. The age of the cohort of dead stems was approximated by cross-dating 5–10 dead stems of average dbh in each stand. Validation using dead stems was generally possible only for stands in the 125–175 yr age class, where stems had died recently enough that decomposition did not hinder measurement of dbh and/or age. Due to more rapid decomposition of dead seedlings and small saplings, it was not possible to validate the density trajectories of younger stands (≤100 yr) to the previous model age (12 yr); in addition, older stands (>220 yr) generally did not have dead stems sound enough to allow validation.

TABLE 1. Multiple regression results for predicting stand density using stand and site parameters for all stands.

Parameter	df	Coefficient	F	P	r^2
Model	3		22.441	<0.0001	0.605
Age class	1	−0.192	40.794	<0.0001	0.367
Northing	1	<0.001	18.950	0.0004	0.170
Easting	1	>−0.001	7.579	0.009	0.068

Note: No interaction terms were significant in the models.

TABLE 2. Regression equations used to back-predict stand density based on 5-yr average annual tree ring width (measured in millimeters).

Model age	No. plots	Regression equation	R^2	No. predictions
12	16	density = 96402.16 − 40961.47(ring width)	0.81	39
70	10	density = 12772.99 − 8059.58(ring width)	0.84	29
125	13	density = 11191.24 − 17432.90(ring width)	0.73	16
220	10	density = 2598.89 − 4633.56(ring width)	0.70	6

Notes: Each model was used to predict density at that model stand age for all stands older than that age. ''Number of predictions'' indicates the number of times the equation was used to back-predict stand density as shown in Fig. 2.

ring up to 70 yr following the origin of the stand. In a limited number of stands, nearly continuous tree recruitment occurred throughout the life of the stand.

Self-thinning and changes in tree spatial patterns

Overall, many dense to moderately dense stands aged 125–200 yr displayed clustered premortality distributions and random postmortality distributions within a distance of 5 m, suggesting the prevalence of self-thinning (see Appendix F for a description of each stand). We detected clustered premortality spatial patterns in 21 of the 28 (75%) stands currently younger than 175 yr. Very dense stands <100 yr often had clustered distributions for all stems as well as for live trees only, suggesting that self-thinning is ongoing. In contrast, trees in sparse, often uneven-aged stands, as well as in older stands where self-thinning may have already taken place, typically exhibit a random spatial pattern to a distance of 5 m regardless of the inclusion of dead stems into the analysis.

Dendochronological analyses

Stand density explained much of the variation in 5-yr-average annual tree ring widths, with R^2 ranging from 0.70 in older stands to 0.84 in younger stands (Table 2). When these equations were used to reconstruct stand density, variation in stand density showed a sharp decline with increasing stand age (Fig. 2a–d). Stand density decreased over time in 34 of the 39 (87%) stands we reconstructed; stands having very high initial densities tended to exhibit the steepest declines in stand density. For most stands, stand density decreased most quickly between 12 and 70 yr but slowed with increasing stand age, reflecting a reduction in density-dependent competition (Table 3). When stands increased in density with age, stand density increased at the greatest rate early (<70 yr) and late (>220 yr) in stand development (Table 3), likely reflecting periods before canopy closure and after crown breakup. Notably, three of the six stands in the 300–350 yr age class decreased in stand density through the 220-yr model age, followed by an increase in stand density (Fig. 2). When compared with density of stands in the 125–175 yr age class validated using dead stems, reconstructions of stand density using annual ring widths were consistently within 10% of the values obtained by aging dead

boles (Table 4). Ring width-based density reconstruction at age 125 yr for one stand >200 yr also yielded differences near 10% of those obtained with validation.

Comparisons of CV between reconstructed stand densities were nearly identical to those made using field measurements of density across the landscape (Fig. 1b). For the six reconstructed stands >300 yr, CV of density decreased dramatically from ~89% at 12 yr to 47% by year 300, and CV of the 10 reconstructed stands from the 200–250 yr age class decreased from 117% at 12 yr to 39% by year 200. For all stands, CV of reconstructed density decreased significantly from ~150% at the 12-yr model age to 88% at 70 yr. CV of density was not significantly different between 70 and 125 yr, but dropped from 76% at age 125 to 36% at age 220 yr, where it remained stable throughout the remainder of the chronosequence (Fig. 1b).

DISCUSSION

Variability in stand structure

Despite the fact that all stands in our study originated following stand-replacing fires (Romme 1982), stand density was highly variable across the landscape not burned by the 1988 YNP fires, and it was more variable in younger age classes compared to older classes. In particular, the six order of magnitude variation in pine seedling density following the 1988 YNP fires (Anderson and Romme 1991, Ellis et al. 1994, Turner et al. 1997, 2004, Kashian et al. 2004) is striking when compared to the relatively low variation in stands >200 yr old. A decrease in variability is evident both from field measurements of density (Fig. 1) as well as from density reconstructions using tree ring widths (Fig. 2). The drastic reduction of the variance in stand density across our chronosequence and the relative importance of stand age in explaining variation in density present strong evidence that stand density converges over time between large fires.

Age distributions were also diverse within and among age classes. Nearly 88% of stands <250 yr had the classical size and age distributions for lodgepole pine, characterized by steep, negatively skewed, uni-model age distributions with corresponding positively skewed, unimodal size distributions, suggesting pine seedling establishment was episodic immediately after
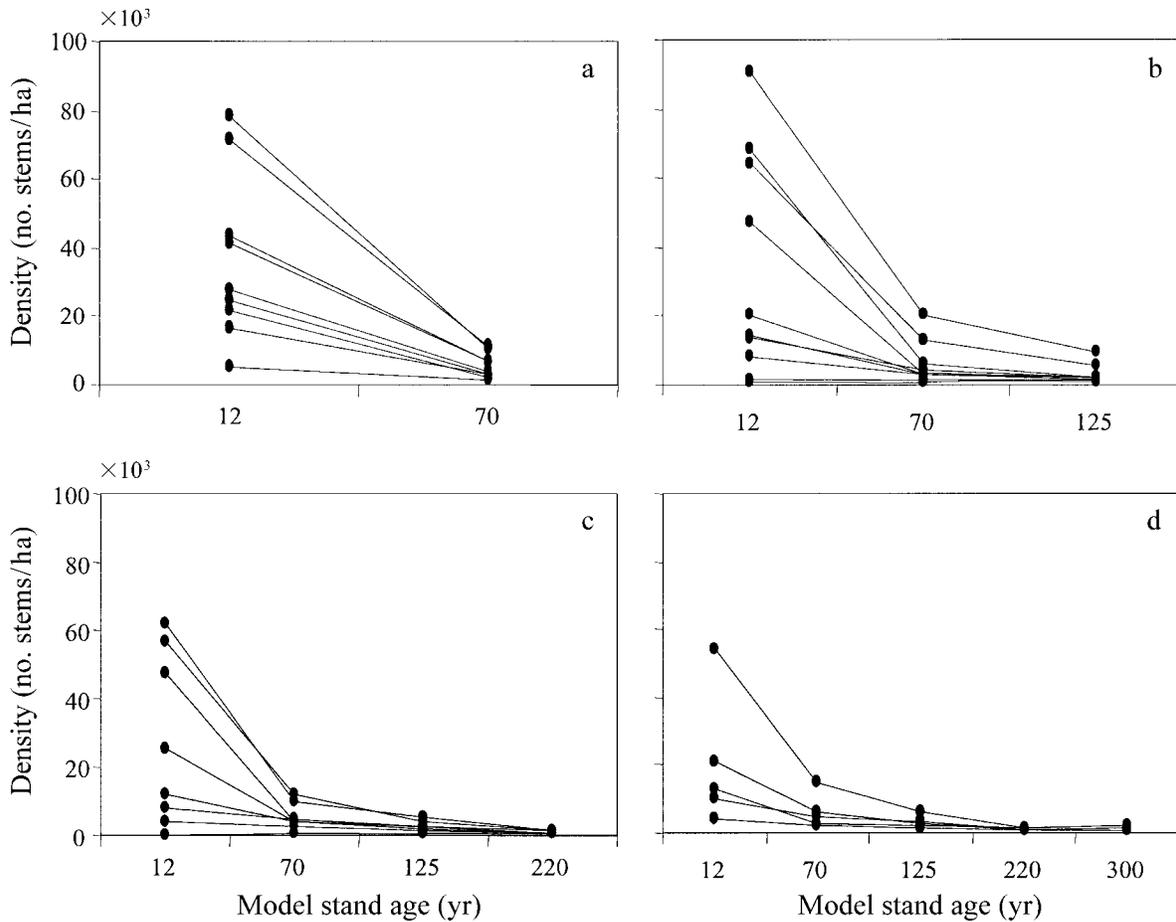
FIG. 2. Trajectories of change in stand density as reconstructed from annual tree ring widths. Each panel represents all reconstructed stands that were younger than the maximum model age: (a) stands not modeled beyond 70 yr; (b) stands not modeled beyond 125 yr, excluding those in (a); (c) stands not modeled beyond 220 yr, excluding those in (a) and (b); (d) stands modeled to 300 yr.

fire. Though initial density may have varied greatly, stands having these distributions likely experienced a reduction in density via self-thinning (as suggested by spatial statistics). However, even in young stands characterized by closed canopies, self-thinning, and apparent initially dense conditions, sporadic establishment of trees may occur for many decades following the disturbance. These age trends contrast with many studies that show that establishment of lodgepole pine occurs primarily in the first few decades after fire (e.g.,

Johnstone et al. 2004; see Appendix C). This extended period of recruitment has been documented by numerous investigators to be the result of variability in initial spatial patterns of trees or fine-scale disturbances that may create small canopy openings. For example, endemic levels of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) may kill a sufficient number of individual trees to create minor canopy gaps, or crown pruning due to physical damage by ice or mechanical abrasion with neighboring trees may be suf-

TABLE 3. Percentage change and mean slopes of reconstructed stand density trajectories using density reconstructions from annual ring width data for 39 stands sampled in Yellowstone National Park, Wyoming, USA.

Trajectory segment (yr)	Mean % decrease	Range of % decrease	Mean − slope	Mean % increase	Range % increase	Mean + slope
12–70	74.2	22.2–94.0	1537.6	23.8	6.4–44.5	11.5
70–125	47.1	9.4–66.3	350.2	13.6	1.8–9.6	9.0
125–220	52.7	23.4–77.1	88.2	2.4	1.1–46.5	5.9
220–300	10.3	2.5–18.8	13.4	29.5	22.1–41.2	18.5

TABLE 4. Comparison of stand density predicted by ring width regressions with density reconstructed from dead stems for six stands in Yellowstone National Park, Wyoming, USA.

| | | Density (no. stems/ha) | | | | | |
| | | | 70 yr | | 120 yr | | Percentage |
Stand	Stand age (yr)	Current	Measured	Predicted	Measured	Predicted	difference
0002	135	3360	5880	5722	...	...	2.7
0006	130	5400	14 240	13 048	...	...	8.4
0018	125	9240	19 740	20 563	...	...	4.0
0110	131	2020	2980	2816	...	...	5.5
0117	143	1500	2580	2819	...	...	8.5
0011	252	1560	...	...	3620	4027	10.1

ficient to create small gaps (Whipple and Dix 1979, Veblen 1986, Kenkel et al. 1997, Long and Smith 1992, Parker and Parker 1994).

Although most stands had classical age structures as described previously, ~13% of stands <250 yr had flatter, broader age class distributions, indicating relatively sparse initial density and continuous rather than episodic establishment following fire. In younger (<175 yr old) stands, uneven-aged structures appeared to be associated with current low stand density, even in stands where canopy closure had already occurred. We also noted the presence of persistent dead lower branches in several stands <175 yr, indicating formerly open initial conditions. Very old stands (>300 yr) were almost exclusively uneven-aged, likely due to the development of multiple cohorts following gradual canopy breakup (Romme 1982). Uneven-aged stand structures have been documented for lodgepole pine (Whipple and Dix 1979, Peet 1981, Pearson et al. 1984, Jakubos and Romme 1993, Muir 1993, Parker and Parker 1994), as well as for the closely related jack pine (*Pinus banksiana* Lamb; Abrams 1984). However, several of these studies included stands that established through meadow invasion or disturbances other than stand-replacing fires, and most examined a relatively narrow range of stand densities.

Given the enormous variability in initial conditions on similar sites, initial conditions present at the onset of seedling establishment appear to be at least as important for mature stand structure and dynamics as differences in site quality (e.g., McCune and Allen 1985, Muir 1993, Parker and Parker 1994). The importance of initial conditions in explaining variation in stand structure suggests the dominant effects of biotic processes (e.g., seed dispersal, competition) and the contingent effects that produce initial patterns of stand density (e.g., variation in patch size, burn severity, and possibly serotiny). We did not compare rates of forest succession or stand dynamics in YNP between sites of differing quality (Romme and Knight 1981, Veblen 1986, Rebertus et al. 1991, Donnegan and Rebertus 1999), but it is unlikely that substrates across the YNP subalpine plateaus vary enough to affect rates of stand development (Kashian et al. 2005). If substrate affects stand dynamics, it likely does so by affecting initial stand conditions, perhaps by promoting increased herbaceous plant cover immediately after fire, which may increase competitive effects on pine seedlings, thereby reducing initial seedling establishment and/or recruitment.

Age distributions were strongly influenced by stand age, and age structures were most variable in the younger age classes. Our results for changes in stand density measured both in the field (Fig. 1a–b) and with stand reconstructions (Fig. 1b) suggest that mean and CV of stand density was significantly reduced by the 125–175 yr age class, decreased again to the 200–250 yr age class, and remained unchanged beyond the 200–250 yr age class. If convergence in stand density is defined as the point at which metrics of variability in stand density no longer exhibit a significant decrease, then we interpret these results as evidence for convergence in stand density by at least 200 yr following fire. Convergence is gradual throughout the fire interval, but generally is fully achieved at this point. Such a pattern explains the relative similarity in stand structure of older stands across the YNP landscape, and suggests that the area burned in 1988 will experience a general reduction in the current heterogeneity of pine seedling densities.

The chronosequence approach utilized here has been criticized as having confounding spatial and temporal trends when inferring stand dynamics (Donnegan and Rebertus 1999), especially because it assumes similar postestablishment histories between stands. In YNP, lack of small-scale disturbances (e.g., low-intensity surface fires, insect infestations) for stands >200 yr old is speculative, and thus the uneven-aged characteristics of many older stands in our study may actually be the result of additional disturbances that followed the stand-replacing fire at the point of stand origin. However, our rigorous selection criteria for older stands, the presence of uneven-aged stands in younger age classes, and uneven-aged characteristics of the original cohort in many older stands suggests that the presence of uneven-aged stands is probably a result of the original stand-replacing fire rather than an artifact of multiple disturbances.

Potential mechanisms reducing variability in stand structure

Reconstructions of stand density and spatial point pattern analyses showed that self-thinning is the most common process characterizing lodgepole pine stand development across the Yellowstone landscape (sensu Peet and Christensen 1980). Stands with initial density >50 000 stems/ha self-thin at rates much higher than those with <20 000 stems/ha, and stands with initial density near 5000 stems/ha will thin at a very slow rate only after they attain canopy closure (see Drew and Flewelling 1977). Thus, the occurrence of self-thinning at differing rates (Fig. 2, Table 3) appears to be the primary mechanism for the reduction of variability in stand structure over time.

The presence of young, uneven-aged stands suggests that continuous seedling establishment following fire is also an important process for many stands on the YNP landscape. Infilling enables initially sparse stands to increase in density with age and thus become more similar to stands declining in density (Fig. 2c–d). Since dispersal distance for lodgepole pine seeds is only about 60 m (Lotan and Perry 1983), and infilling appears to occur more slowly than self-thinning (Table 2), infilling probably occurs over smaller areas of the landscape and has a smaller effect on structural convergence than self-thinning. In addition, pine seedling counts suggest that infilling is important only in stands <100 yr, before canopy closure occurs, and >200 yr old, once canopy gaps begin to form with age-related mortality. Remarkably, half of the stands >300 yr old that we reconstructed showed an increase in density beyond 220 yr, even when self-thinning had occurred prior to 220 yr (Fig. 2d). Given that infilling requires a local seed source and a lack of herbaceous plant competition, stand density of initially sparse stands isolated within the interior of a very large burned area may potentially remain unchanged for centuries. Infilling may also occur within gaps in high-density stands (see Appendix C).

Percent serotiny was unimportant in explaining stand density across the Yellowstone landscape in our study, but was generally low in stands where density was low and highly variable for high-density stands. Our results showing higher stand densities in the north and west portions of YNP, together with studies documenting the highest percent serotiny in younger stands at lower elevation in the northwest region of YNP (Tinker et al. 1994, Schoennagel et al. 2003) further suggest at least some correspondence between high percent serotiny and high stand density at a landscape scale. Notably, extended periods of establishment evident even in dense stands with high percent serotiny suggest that even small proportions of trees with open cones within a stand are sufficient to provide a continuous seed source to postfire stands. These data highlight the rel-ative importance of percent serotiny for lodgepole pine stand development in this system.

Implications for landscape dynamics following large disturbances

The reduction in variability of stand structure has important consequences for landscape dynamics, particularly the structural mosaic and the persistence of landscape heterogeneity. Obviously, convergence of stand structure with increasing stand age implies a reduction of landscape heterogeneity with time since disturbance. Following the 1988 fires in YNP, many investigators suggested that large, infrequent fires in this system act to ''reset'' landscape pattern, creating unique patterns of heterogeneity in seedling density that were thought to persist as differences in structure among mature stands until a similar set of fires occurred centuries later (Anderson and Romme 1991, Ellis et al. 1994, Turner et al. 1997). Our data suggest that these initial patterns may persist for approximately two centuries, indicating that the 1988 fires will indeed leave a long-lasting imprint on variation in forest stand structure. Convergence in stand structure in YNP depends directly on the length of the fire interval, which may vary between 100 and 300 years (Romme and Despain 1989). Our data suggest that large fires occurring more frequently than 200 yr would permit far less stand structural convergence, which would ultimately increase heterogeneity in stand density (and subsequent stand structures) across the landscape.

Examples of the persistence of relative variability in stand structure in YNP are evident in some stands not burned by the 1988 fires. For instance, two 130-yr-old sample stands in this study (stands 0010 and 0031; see Appendix E) were located <50 m apart within the perimeter of the same stand-replacing fire, but had markedly different densities and age structures. Stand 0031 appeared to be self-thinning while stand 0010 showed evidence of infilling (see spatial patterns in Appendix F). Thus, relative initial differences may have persisted for 130 yr, although structural differences between the two stands will likely converge within the next century.

Due to the very long interval between large fires in YNP, we assumed that a series of smaller, more frequent stand-replacing fires would produce similar variability in postfire seedling density (and thus similar variability in mature stand structure) as the large, infrequent fires that occurred in YNP in 1988. However, the range of our reconstructed stand densities was narrower than that of post-1988 densities, suggesting either a narrower range of stand densities following smaller fires or that our sample did not capture stands once initially very dense or very sparse. Extremely high- or low-density stands may preclude their convergence with other stand structures within the 300-yr fire-free interval.

Large fires are notable for the heterogeneity they create within their perimeters. Based on age-related

changes in stand density, age structures, and reconstructions of stand density, we conclude that long fire intervals associated with large disturbances in this system allow the imprint of large disturbances to persist for at least two centuries after fire in this landscape. During this period, however, stand-level processes substantially reduce the among-stand variation in stem density, and multiple self-thinning trajectories and significant infilling of initially sparse stands appear to be the primary mechanisms reducing the initial variability in stand density.

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APPENDIX A

A table showing the structural characteristics of stands sampled in four age classes is available in ESA's Electronic Data Archive: *Ecological Archives* E086-033-A1.

APPENDIX B

A figure showing stem maps for two selected stands of similar age (130 yr) but contrasting density is available in ESA's Electronic Data Archive: *Ecological Archives* E086-033-A2.

APPENDIX C

A discussion of potential error sources in age estimation, a figure showing stand maps of two stands within 10×50 m plots, a table showing canopy characteristics for five selected young dense stands, and associated literature cited are available in ESA's Electronic Data Archive: *Ecological Archives* E086-033-A3.

APPENDIX D

A table showing mean values of the Palmer Drought Severity Index for the Yellowstone region for each of the 5-yr periods over which ring widths were regressed against stand density is available in ESA's Electronic Data Archive: *Ecological Archives* E086-033-A4.

APPENDIX E

A figure showing age class distributions for stands sampled in Yellowstone National Park is available in ESA's Electronic Data Archive: *Ecological Archives* E086-033-A5.

APPENDIX F

A table showing results of transformed Ripley's K(*L*-hat) analyses for tree spatial pattern before and after mortality for stands sampled across four age classes in Yellowstone National Park is available in ESA's Electronic Data Archive: *Ecological Archives* E086-033-A6.