

THE INFLUENCE OF FIRE INTERVAL AND SEROTINY ON POSTFIRE LODGEPOLE PINE DENSITY IN YELLOWSTONE NATIONAL PARK

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Abstract. The time interval between stand-replacing fires can influence patterns of initial postfire succession if the abundance of postfire propagules varies with prefire stand age. We examined the effect of fire interval on initial postfire lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) density in Yellowstone National Park (YNP) following the 1988 fires. We asked whether postfire propagule abundance, measured as prefire percent serotiny, varied with fire interval and could explain patterns in postfire succession. The response of lodgepole pine density to variation in fire interval was explained by spatial and temporal variation in prefire serotiny. At low elevations, postfire lodgepole pine recruitment correlated strongly with prefire percent serotiny, which varied nonlinearly with prefire stand age. As a result, postfire lodgepole pine densities varied nonlinearly with fire interval. In contrast, at high elevations serotiny was low, varied little with stand age and did not influence postfire lodgepole pine densities, although, fire interval was still a significant predictor of postfire densities. At high elevations, fire interval varied nonlinearly with postfire lodgepole densities, presumably due to the temporal variation in propagule abundance from open cones in adjacent unburned stands. Temporal variation in stand-level serotiny at low elevations was best explained by age of individual trees. Logistic regression indicated that trees expected to be serotinous had a low probability of exhibiting serotiny at a young age, with increasing probability as trees matured up to 140 yr. This increase in serotiny with tree age likely accounts for the initial increase in stand-level percent serotiny with stand age at low elevations. The spatial variation in serotiny was correlated with variation in historical fire regimes. Fire interval models derived from lower elevations in YNP indicate that fire occurred historically at 135–185-yr intervals, whereas at higher elevations fires occurred at 280–310-yr intervals. The spatial patterns of serotiny appear to have been influenced by variability in historical fire regimes across the Yellowstone landscape, which has conditioned contemporary successional responses to disturbance.

Key words: climate change; disturbance; fire ecology; fire interval; landscape ecology; multiple successional pathways; *Pinus contorta* var. *latifolia*; postfire succession; serotiny; Yellowstone National Park.

INTRODUCTION

Fire regimes vary spatially across heterogeneous landscapes and temporally as climate and fuel conditions change. In Yellowstone National Park, mean fire intervals (the time between two fire events at a particular location) on the subalpine plateaus have varied from 70 to 400 yr throughout the Holocene in close association with regional climate variation (Whitlock 1993, Millspaugh et al. 2000). Strong correlations between fire interval and regional climate have been well documented in many crown-fire dominated systems (Cwynar 1987, Clark 1988, 1990, Johnson et al. 1990, Johnson and Wowchuk 1993). Changes in fire interval may influence successional patterns, yet the direct effects of varying fire intervals on postfire vegetation have not been well studied in stand-replacing fire systems.

The abundance and arrangement of postdisturbance propagules (viable seeds) influence postfire community composition and structure (Turner et al. 1998). Life history traits such as the timing of seed production or the time interval required between successful vegetative reproduction events, will influence how variation in fire interval affects propagule abundance and postfire recruitment. In Yellowstone, the abundance of postfire propagules is closely tied to serotiny (Tinker et al. 1994, Turner et al. 1997, 1999). Serotiny is the long-term storage of seeds within mature closed cones which, when heated by fire, open to release seeds onto newly exposed mineral soil. Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) predominantly exhibit either open or closed cones (Koch 1996), and we refer to trees with the ability to produce closed cones during their lifetime as serotinous trees. The proportion of lodgepole pine trees bearing serotinous cones within a stand varies considerably within Yellowstone National Park (Tinker et al. 1994) and throughout the Rocky Mountain region (Critchfield 1957, Muir and Lotan

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1985, Koch 1996). Observations also suggest that stand-level proportions of serotiny vary with age of the stand (Mason 1915, Crossley 1956, Lotan 1975). Because viable seeds from multiple years accrue in the canopy of serotinous trees, the density of postfire seedlings may be linked to the age of stands as they burn (the fire interval).

Prefire percent serotiny, the percentage of serotinous trees in a stand, has been shown to be a strong predictor of postfire lodgepole pine densities in Yellowstone National Park (Tinker et al. 1994, Turner et al. 1997, 1999), but how stand-level percent serotiny may vary with time is not well understood. Fire interval relative to levels of serotiny may determine the rate and density of postfire tree recruitment. If fire occurs in stands when serotiny is low, postfire recruitment may be sparse, as seeds will be consumed rather than released by fire. If the same site were subject to fire when levels of serotiny are high, postfire recruitment may be very dense. Thus, temporal variation in propagule abundance could be important for predicting successional responses to altered fire regimes in coniferous forests. If global climate change causes fire intervals to shift beyond certain temporal thresholds, nonlinear vegetation responses may produce unexpected patterns of succession (Turner et al. 1998).

We studied the effect of fire interval on initial post-fire succession in Yellowstone following the 1988 fires and addressed four questions: (1) Is fire interval significant in explaining variation in postfire lodgepole pine density given similar environmental conditions and across broad environmental gradients? (2) How does stand-level serotiny vary with stand age? (3) What mechanisms can explain temporal variation in stand-level serotiny? (4) Does variation in historical fire regimes across the landscape explain spatial variation in serotiny across the park?

STUDY AREA

Yellowstone encompasses 9000 km² primarily in the northwest corner of Wyoming. Approximately 80% of the park is covered with coniferous forests dominated by lodgepole pine (Despain 1990). Our study focused on the subalpine forested plateaus that comprise most of the park and support predominantly similar vegetation throughout. These subalpine plateaus encompass dry, infertile habitats on rhyolite substrates and more mesic, fertile habitats that occur on andesite substrates or laucustrine deposits. The climate is generally cool with relatively moist springs and dry summers (Martner 1986). The two most important environmental gradients controlling vegetation on the plateau relate to elevation and geological substrate (Despain 1990), with moisture generally increasing with elevation and soil fertility lower on rhyolite than on andesite and detrital substrates.

The 1988 Yellowstone fires affected ~45% of the park, burning >200 000 ha of forest on the subalpine

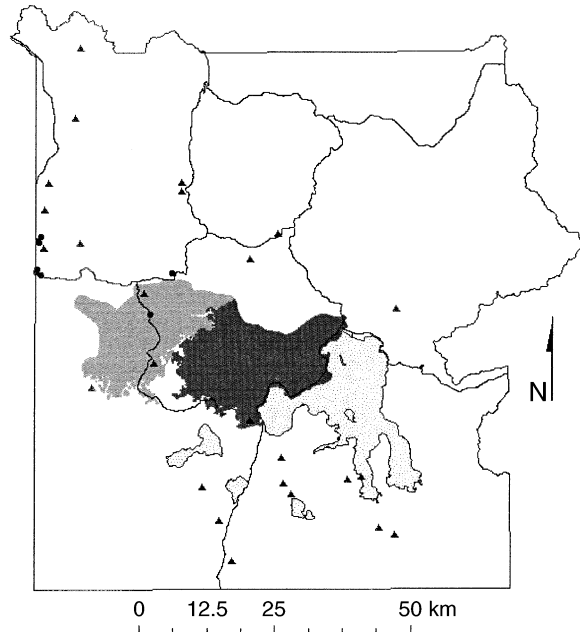


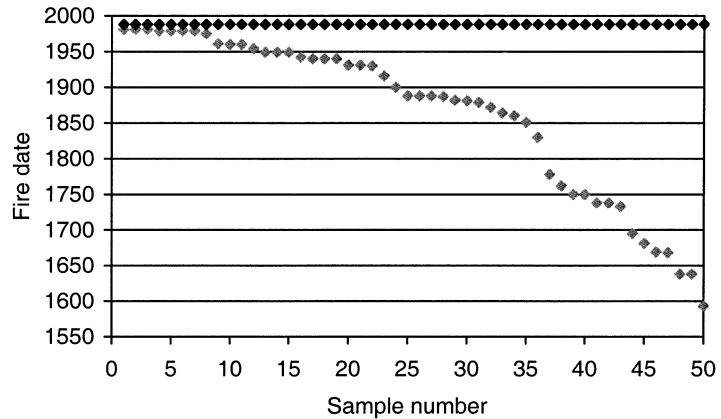
FIG. 1. Map of sampling locations and delineation of data sets analyzed. Triangles represent 25 locations where response to fire interval ($n = 50$) and prefire percent serotiny at the stand-level were sampled ($n = 50$). Circles represent 10 sites sampled to determine how serotiny varies with tree age. Two sites not represented on the map are in high-serotiny areas of Grand Teton National Park. Gray areas represent the high-elevation (dark) and low-elevation (light) regions of the time-since-fire map analyzed to determine historical influence of mean fire intervals on spatial pattern of serotiny. Stippled areas represent lakes. Lines mark all roads and the Yellowstone National Park boundary.

plateaus (Christensen et al. 1989, Turner et al. 1994). Fires of this scale have occurred in Yellowstone in the past, most recently in the early 1700s (Romme 1982, Romme and Despain 1989). Smaller fires have also occurred; for example, within the last century, 4000–7000 ha burned yearly in 1910, 1931, 1940, and 1981. Although the mean fire interval for the subalpine plateaus is estimated to be ~300–350 yr (Romme 1982), ~32 000 ha of forest on the subalpine plateaus burned twice within the last 100 yr, with some stands experiencing as little as 7 yr between stand-replacing fires. Under extreme climate conditions such as 1988, fires can burn stands of any age with some stands burning at short intervals.

METHODS

We took a hierarchical approach to address the four questions above, employing independent data sets at three different scales. At the stand level, we addressed (1) fire interval effects on postfire recruitment and (2) variation in percent serotiny with stand age by sampling 25 locations (Fig. 1). We employed two additional data sets to investigate factors that may govern the spatio-temporal patterns in serotiny influencing successional

FIG. 2. Summary of all fire intervals sampled in 2000, with the most recent fire occurring in 1988 represented by the black symbols, and the previous fire occurring at some time within the previous 400 yr represented by the gray symbols. The time between these successive fires defines the fire interval at the sites we sampled.



responses to fire interval observed at the stand level. At the tree level, we intensively sampled 10 sites to determine (3) if tree-level mechanisms can explain temporal variation in serotiny with stand age in areas where high levels of serotiny are expected (Fig. 1). At a landscape level, we examined a broad-scale fire history map to determine (4) if historical fire regimes have exerted landscape-scale constraints on the spatial patterns of serotiny observed at the stand level (Fig. 1).

Stand-level effects of fire interval on postfire sapling density

During the summer of 2000, we sampled 50 paired plots of 12-yr-old stands at 25 locations (Fig. 1) that all burned in 1988 but varied in previous fire interval (time between the last two fire events within a stand) from 7 to 395 yr (Fig. 2). Short fire-interval (<100 yr) and long fire-interval (>100 yr) plots were paired in

the field to control for environmental variation that might confound the influence of fire interval on lodgepole pine densities, for a total of 50 plots sampled. Short fire intervals ranged from 7 to 107 yr, whereas long fire intervals ranged from 100 to 395 yr. There is a small overlap in range of the two fire-interval groups, yet short fire intervals were always shorter than the long intervals at a location.

Short fire intervals were located by overlaying a map of historical fires during the 1900s compiled from park records with a map of 1988 fire extent and severity in a geographical information system (GIS). From historical park-wide aerial photos (1:40 000–1:60 000), we transferred the perimeters of the historic fires and the 1988 fires onto topographic maps (1:24 000). This allowed detailed delineation of patches created by the short fire intervals, in which we randomly located a plot. Adjacent to each short fire interval we sampled a topographically similar patch that also burned in 1988, but had not burned previously for >100 yr (Fig. 3), in which we randomly located a long fire interval plot. Each of the paired plots was <1000 m apart, with the majority ($n = 16$) <420 m apart. We cored several of the largest trees in each 0.5-ha plot to confirm the length of the fire interval. We recorded postfire tree sapling densities by species in four parallel 2×50 m belt transects spaced 25 m apart. Sapling density was determined by averaging counts on the four 100-m² transects in each plot and scaling to stems per hectare.

The paired plots permitted analysis of fire intervals almost 400 yr long while minimizing effects of environmental heterogeneity. Only stand-replacing fires were considered, and elevation, aspect, slope, distance to unburned edge, and soil fertility were similar for each pair of short and long fire-interval plots (Table 1). To reduce edge effects and to ensure that sampling occurred within known fire perimeters, all plots were at least 75 m from unburned forest. Lodgepole pine exhibit relatively short dispersal distances, with highest seed deposition occurring within 40 m leeward of mature trees (Perry and Lotan 1977, Greene and Johnson 1989). Sampling points were overlaid with a soil sub-

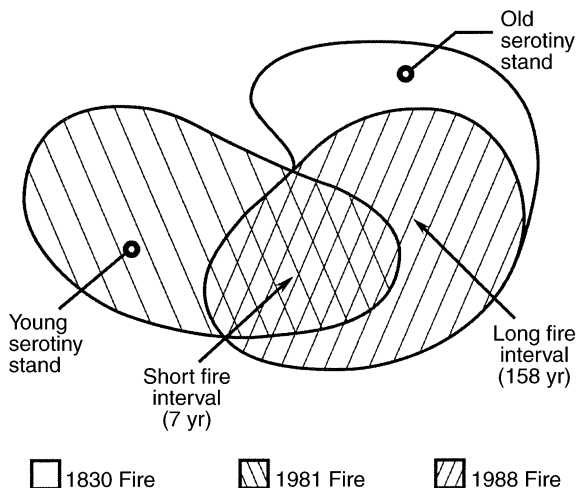


FIG. 3. A schematic depiction of the sampling design with example dates. All sampling in the fire interval plots and serotiny stands occurred in 2000. In this example, the short fire interval is 7 yr, whereas the long fire interval is 158 yr. The serotiny stands did not burn in 1988 and serve as estimates of percent serotiny present when the adjacent fire-interval stands burned in 1988.

TABLE 1. Summary of mean values of environmental variables for short and long fire-interval plots, significance of paired *t* tests for each variable ($n = 25$), and the range of the variable across all plots ($n = 50$).

Variable	Short fire interval	Long fire interval	<i>P</i>	Variable range
Fire interval (yr)	38	211	<0.0001	7–395
Elevation (m)	2377	2378	0.433	2011–2618
Aspect (degrees)	132	118	0.083	30–296
Slope (%)	4.5	4.4	0.407	0–32
Distance to unburned edge (m)	130	171	0.212	75–850
Soil fertility (categorical)	0.28	0.28	...	0–1
Serotiny (%)	4.9	14.0	0.015	0–87

strate map in a GIS to categorize soil fertility at each site as either infertile rhyolite (0) or more fertile andesite/detrital substrates (1). In addition, distance to the closest unburned forest edge was calculated from the center of each plot in a GIS.

A series of statistical analyses were used to test the influence of fire interval on postfire sapling densities (SAS Institute 1990). Due to the predominance of lodgepole pine, all statistical analyses used lodgepole pine density (number of stems per hectare) as the dependent variable representing postfire stand succession. Lodgepole pine density was log transformed prior to analysis to reduce heteroscedasticity of residual variance. A paired *t* test was used to evaluate whether lodgepole pine densities differed between the paired short and long fire-interval plots ($n = 25$). This result was compared to an unpaired *t* test of the same data to assess site-level vs. broad-scale influences on lodgepole pine densities. Last, multiple regression models were constructed for all plots in an unpaired design ($n = 50$) to evaluate the relative influence of fire interval and other environmental variables on lodgepole pine densities. We subsequently constructed regression models to explain variation in lodgepole pine density for low- and high-elevation regions of the park. In regression analyses, fire interval was included as a continuous variable. We included elevation, aspect, slope, soil fertility, distance to 1988 unburned edge, stand-level percent serotiny (see next section), and interactions among these terms as independent variables, using $P < 0.05$ as the cut-off for significance of individual variables in the model.

Stand-level variation in percent serotiny

To evaluate how postfire propagule abundance may change with fire interval, we examined how stand-level percent serotiny varied with stand age at 25 locations (Fig. 1). Adjacent to each of the paired fire-interval plots, we sampled stands within the perimeter of the historical fire but which did not burn in 1988 (Fig. 3) to provide an estimate of prefire percent serotiny as each of the fire interval plots burned in 1988. Although serotinous and open cones show distinct morphology and angle of attachment (Koch 1996, Tinker et al. 1994), prefire serotiny cannot be measured directly in

burned plots after ~5 yr following fire due to cone deterioration (D. B. Tinker, *personal communication*). Tinker et al. (1994) found that the coefficient of variation for percent serotiny in stands of similar age was low at scales <1 km, so spatial variation in serotiny at these scales should not confound our results.

To estimate stand-level percent serotiny, we scored 20 canopy trees within each of three 10 m radius circles spaced 10 m apart for the presence of serotinous cones following methods of Tinker et al. (1994). Individuals of *Pinus contorta* var. *latifolia* exhibit either open or closed cones predominantly (Koch 1996). The number of serotinous trees observed per plot was divided by the total number of trees sampled (60) to calculate percent serotiny for the stand.

We analyzed how percent serotiny varies with stand age under similar environmental conditions and across a broad environmental gradient, using a number of statistical tests. The dependent variable percent serotiny was transformed prior to analysis using the function arcsine(square root(x)) to reduce heteroscedasticity of residual variance. We first tested for differences in stand-level percent serotiny between paired young (<119 yr) and old serotiny stands (>112 yr) using paired *t* tests. (Note that each serotiny stand is 12 yr older than the associated fire intervals sampled, because the serotiny stands did not burn in 1988 and all sampling was conducted in 2000). We then used multiple regression ($n = 50$ plots) to examine the relative influence of stand age (as a categorical variable), and other environmental variables (elevation, slope, aspect, slope, soil fertility) on stand-level percent serotiny. Next we compared separate singular regression models to evaluate how serotiny varied with stand age (as a continuous dependent variable) for low- and high-elevation regions of the park.

Tree-level mechanism controlling change in serotiny with stand age

We evaluated the hypothesis that temporal changes in stand-level percent serotiny results from age-dependent variation in cone morphology. We sampled trees in a stratified random sampling scheme in areas of known high serotiny within stands initiated after stand-replacing fires of known age and location (Fig. 1). We

TABLE 2. Descriptive statistics for elevation and stand age within the selected low- and high-elevation regions of the time-since-fire map spanning the central plateau of Yellowstone National Park.

Statistic	Elevation (m)		Stand age (yr)	
	Low-elevation region	High-elevation region	Low-elevation region	High-elevation region
Mean	2334	2491	192	276
Standard deviation	96	73	90	87
Range	2114–2507	2284–2625	36–355	75–457

selected trees that were the largest and presumably the oldest in the stand. These conditions confer a high likelihood that sampled trees would be serotinous, thereby reducing the possibility of type II errors (not rejecting the null hypothesis when in fact it is false). Although some of the oldest trees in the stand may not have been the biggest, it is expected that the biggest trees represent many of the oldest trees in monospecific stands of lodgepole pine, a species that does not grow quickly in shade to reach the canopy.

We sampled 10 stands that originated between 12 and 140 yr ago from stand-replacing fires. In each stand, we sampled the largest tree within a 10×25 m subplot centered at each 10-m point along each of four 120-m transects spaced 25 m apart, for a total of 48 trees sampled per stand. We took increment cores from each tree to estimate age and scored each tree as either serotinous or open coned. Lodgepole pine can produce cones by 10 years of age (Koch 1996). We cored trees on an angle to intersect the pith at ground-level, rather than coring perpendicular to the ground at a set distance above the root-shoot interface, which preserves relative tree-ring widths but requires missing tree rings below that height (Gutsell and Johnson 2002). Core samples were dried, mounted, and sanded according to standard procedures (McBride 1983), and rings were counted to estimate tree age. For samples that did not intersect the pith directly, we employed methods by (Kipfmüller and Baker 1998) for estimating the number of rings to the pith. Age corrections made to core samples that missed the pith resulted in an average of seven rings added to 34% of the samples.

We used logistic regression to test if tree age was a significant predictor of the occurrence of serotiny in individual trees. Trees without cones or only immature cones present were excluded from the analysis, resulting in a final sample size of 419 trees.

Landscape-level influence of historical fire regimes on the spatial pattern of serotiny

To explore potential landscape-scale constraints on the spatial pattern of serotiny, we asked whether serotiny, which varies inversely with elevation (Tinker et al. 1994), was correlated with variation in historical fire regimes. Fire intervals shorter than the lifespan of lodgepole pine should promote serotiny, whereas fire intervals greater than the lodgepole pine lifespan

should select for open cones. We used a large time-since-fire map compiled by Romme and Despain in 1985, which covers 130 000 ha of the central plateau within the park (Romme and Despain 1989; Tinker et al., *in press*). We estimated historical fire interval probabilities for low- and high-elevation regions of the map (Fig. 1; mean elevations were ~ 2330 m and ~ 2500 m, respectively) to assess if spatial variation in selective pressure by historical fire regimes might explain the observed spatial patterns of serotiny.

Field methods for developing the time-since-fire map, conducted by Romme and Despain (1989), record the occurrence of the most recent fire in each unit of the landscape following standard procedures (Heinselman 1973, Johnson and Gutsell 1994). Stands of similar age were initially delineated as polygons from color aerial photos (1:30 000). To establish the origin date for each stand and to verify homogeneity of stand age within the polygon, increment cores of the largest trees were taken throughout the delineated stand. Cores were obtained at 20 cm above the base of tree and an estimate of age at coring height was added to the ring count for each core, based on the age of saplings growing at a similar rate at the height of 20 cm (see Romme 1982 for details). Available living fire-scarred trees were sectioned with a bow saw to corroborate stand origin dates. In the lab, samples were sanded and rings were counted to age the trees and date the fire scars. Estimates of error in age dating are ± 2 yr for the last 100 yr, ± 3 yr between 100 and 200 yr, and ± 5 yr for ages >200 yr (Romme 1982). This procedure was followed for contiguous forest polygons, resulting in a map that displays the age and size of forested stands throughout the study area.

We spatially partitioned this large time-since-fire map into two regions of different elevation (Fig. 1, Table 2) to compare their respective fire regimes. To define the two regions, we overlaid the perimeter of the time-since-fire map onto a 30-m USGS digital elevation map for the park to visually separate it into two nonoverlapping, contiguous regions of lower and higher elevation of relatively similar size. We then derived elevation estimates for each cell within the two regions and tested for significant difference in elevation between the regions. Next, we derived fire interval probability distributions for these regions from the

TABLE 3. Summary of multiple regression analysis accounting for broad-scale variance in postfire lodgepole pine densities across all sampled stands ($n = 50$).

Factor	df	Coefficient	<i>F</i>	<i>P</i>	r^2
Model	5		12.98	<0.0001	0.596
Soil fertility	1	-0.748	18.04	0.0001	0.235
Percent serotiny	1	0.017	9.93	0.0029	0.129
Fire interval	1	0.008	7.33	0.0096	0.096
(Fire interval) ²	1	-0.00002	6.02	0.0182	0.079
Slope	1	-0.023	4.36	0.0426	0.057

Note: The term (Fire interval)² indicates a quadratic, nonlinear relationship with lodgepole density.

time-since-fire data according to the following methods (Johnson and Gutsell 1994).

Time-since-fire maps provide the size and age of forested stands established after fire, permitting development of survivorship distributions, $A(t)$, which give the cumulative proportion of the landscape surviving without fire longer than time t , and represent the probability that a stand will survive to time t :

$$A(t) = \exp[-t/b]^c. \quad (1)$$

The parameter b is the stand age exceeded 36.8% of the time and correlates with mean fire intervals experienced within the region historically. The shape parameter, c , when >1 , defines a Weibull fire frequency model where the hazard of burning increases with age. For each of the elevation regions, we estimated these two parameters by statistically fitting the $A(t)$ model to the cumulative survivorship data for each region (R statistical package, NLS procedure; Becker et al. 1988). We constructed 95% confidence intervals for the parameters b and c (R; ellipse procedure) to determine if the fire regimes were significantly different between the high- and low-elevation regions.

The cumulative survivorship distribution, $A(t)$, is related to a cumulative mortality distribution, $F(t)$, as $F(t) = 1 - A(t)$, which represents the probability of fire burning a stand before time t . A fire interval probability distribution is represented by the density mortality distribution, $f(t)$, which is the probability of fire occurring on the landscape at the interval t to Δt :

$$f(t) = ([ct^{c-1}]/b^c \exp[-t/b]^c). \quad (2)$$

Applying the 95% confidence intervals of the parameters b and c , we estimated the expected range of historical mean fire intervals for the two regions of the time-since-fire map from the density mortality distributions, in order to characterize broad-scale spatial variation in selective pressure promoting serotiny.

RESULTS

Effects of fire interval on postfire lodgepole pine densities

Postfire lodgepole pine recruitment varied significantly with previous fire interval. We found significantly higher lodgepole pine densities following long

fire intervals compared to the short fire intervals (paired t test; $df = 24$, $t = -3.843$, $P = 0.001$). When the data were unpaired, the strength of the difference between short and long interval treatments was attenuated, although significant (t test, $df = 48$, $t = -1.950$, $P = 0.057$), suggesting that broader scale factors may promote correlation among paired sites at a location.

Broad-scale variance in postfire lodgepole pine densities was best explained by soil fertility, percent serotiny, fire interval and slope ($r^2 = 0.596$) (Table 3). Fire interval was significant as a quadratic term in the model, suggesting a more complex, nonlinear response to fire interval not detected by the paired t tests. Differences in lodgepole pine density reflect the greatest variation in initial postfire succession in Yellowstone, with lodgepole pine dominating all of the 12-yr-old fire interval sites we sampled ($n = 50$). Twenty-six percent of the sites recorded other tree species present, but these comprised a mean of $<1\%$ of the total sapling density at each of those sites.

Variation in stand-level percent serotiny

Percent serotiny was significantly lower in younger stands (4%) compared to older stands (14%) given similar environmental conditions (paired t test, $df = 24$, $P = 0.013$). At a broad scale, using multiple regression of all sites in an unpaired analysis, variance in serotiny was best explained by stand age (as a categorical variable), elevation, and the interaction of age and elevation ($r^2 = 0.593$), indicating that serotiny varies both spatially and temporally. The age \times elevation interaction reveals that at high-elevation sites (>2400 m), stand age has little influence on percent serotiny, which generally is low. However, at low-elevation sites (<2400 m) serotiny was lower in stands <100 yr old but significantly higher in stands >100 yr old (Fig. 4). Therefore, stand age primarily influences serotiny levels at lower elevation in the park. Considering stand age as a continuous variable at low elevation, regression analysis shows that serotiny varies quadratically with stand age across a 7–325 yr range ($r^2 = 0.448$). At high elevation, in contrast, serotiny does not vary significantly with stand age as a linear or quadratic term ($r^2 = 0.081$, Fig. 5).

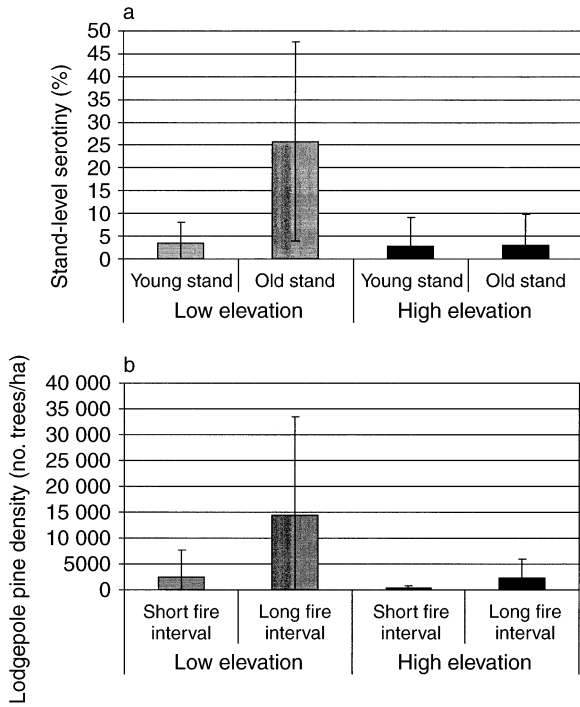


FIG. 4. (a) Graph of the significant interaction between stand age and elevation influencing variation in percent serotiny. (b) The relationship is similar for fire interval and lodgepole pine density, but is not significant in the regression model for log(lodgepole pine) density. Young stands are <100 yr old, and low elevation is <2400 m. Error bars represent ±1 SD.

Based on this elevation contrast, we compared regression equations explaining lodgepole pine densities separately for high and low elevations. At low elevation, lodgepole pine density varies positively with serotiny and negatively with soil fertility and slope ($r^2 = 0.498$). Serotiny varies nonlinearly with stand age, apparently promoting the nonlinear relationship between lodgepole pine density and fire interval at low elevations (Fig. 6a). At high elevations, density varied inversely with soil fertility and nonlinearly with fire interval ($r^2 = 0.546$, Fig. 6b), but serotiny was not a significant variable in this regression. Therefore, post-fire propagule abundance appears to vary nonlinearly with fire interval; at low elevations propagule abundance is strongly correlated with prefire serotiny, whereas at high elevations, it is not. We made no direct measures of propagule abundance from open cones, however, these results suggest that the abundance of seed from open cones in adjacent unburned stands may vary nonlinearly with prefire stand age (fire interval), as distance to unburned edge did not covary with continuous fire interval ($P = 0.723$, $r^2 = 0.003$). Overall, the mean and variance in lodgepole pine densities is lower in high-elevation, low-serotiny stands, compared to low-elevation, high-serotiny stands (25–13 700 trees/ha and 115–56 025 trees/ha, respectively). As a

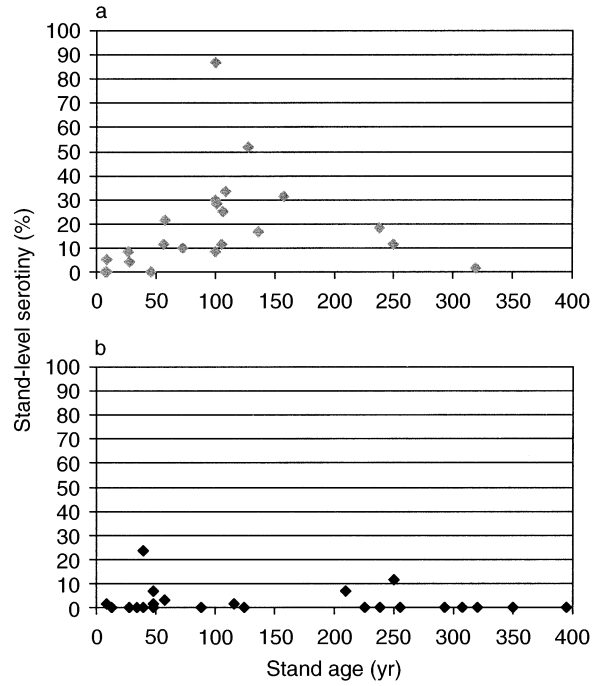


FIG. 5. Scatter plots representing variation in prefire percent serotiny with stand age for (a) low-elevation (<2400 m) and (b) high-elevation (>2400 m) sites sampled.

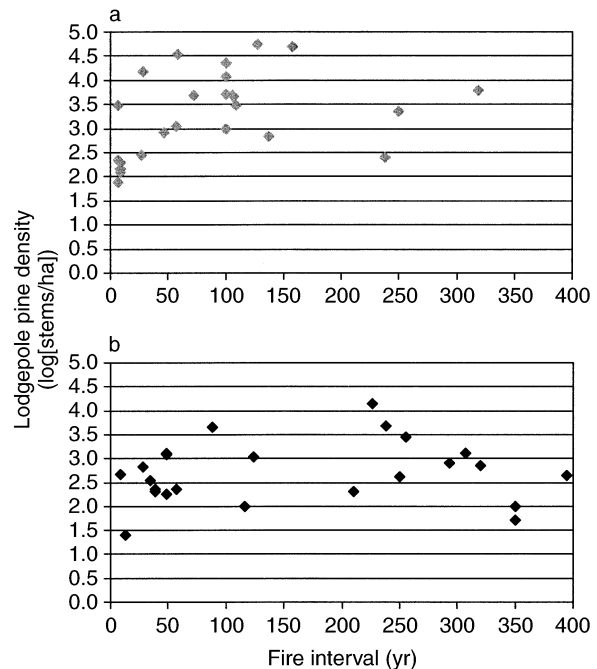


FIG. 6. Scatter plots representing variation in postfire lodgepole pine density with fire interval for (a) low-elevation (<2400 m) and (b) high-elevation (>2400 m) sites sampled. Note that the dependent variable is log transformed, so subtle changes in the slope of the line represent orders of magnitude difference in lodgepole pine density as fire interval varies.

TABLE 4. Summary of logistic regression model explaining the probability that a sampled tree would be serotinous as a function of the age of the tree ($n = 419$).

Parameter	df	Coefficient	Chi-square	<i>P</i>
Intercept	1	-2.3482	80.87	<0.001
Tree age	1	0.0227	47.92	<0.001

Note: Percent concordance = 72.5.

consequence, although fire interval is still significant outside areas of high serotiny, its impact on the magnitude of variation in postfire succession is much less.

Changes in serotiny with tree age

In sampling individual lodgepole pine trees with a high likelihood of being serotinous, tree age was a strong predictor of the probability that an individual tree would be serotinous up to 140 yr, the maximum age we sampled (logistic regression; $\chi^2 = 47.92$, $P < 0.001$). With each yearly increase in tree age, there was an expected increase of 2.3% in the probability that an individual tree would be serotinous (Table 4), indicating the rate at which stand-level serotiny may change through time.

Spatial variation in fire intervals with elevation

The two distinct contiguous regions representing low- and high-elevation portions of the central plateau time-since-fire map covered 22 817 ha and 33 070 ha, respectively. Although there was overlap in elevation ranges across the two regions (Table 2), mean elevation was significantly different (*t* test; $t = -14.25$, $P < 0.001$).

We detected significantly different historical fire regimes for the high- and low-elevation regions of the study area with no overlap in 95% confidence intervals of the fire frequency parameters between regions (Fig. 7, Table 5). The 95% confidence interval for parameter *b*, which corresponds to the stand age exceeded 36.8% of the time for the specified region, was 193–213 for the low-elevation region and 316–333 for the high-elevation region. The 95% confidence interval for the shape parameter *c* was 1.97–2.62 for the low-elevation region and 3.07–3.93 for the high-elevation region. Together these parameters indicate that a stand surviving to a certain age has a higher probability of burning in the low-elevation region compared to the high-elevation region. Based on the confidence intervals for these parameters, 135–185-yr fire intervals were most likely in the low-elevation region, while 280–310-yr fire intervals were most probable the high-elevation region.

DISCUSSION

The influence of fire interval on postfire recruitment

The time interval between stand-replacing fires in subalpine lodgepole pine forests in Yellowstone National Park influences patterns of initial postfire succession. Previous work suggests similar trends in post-

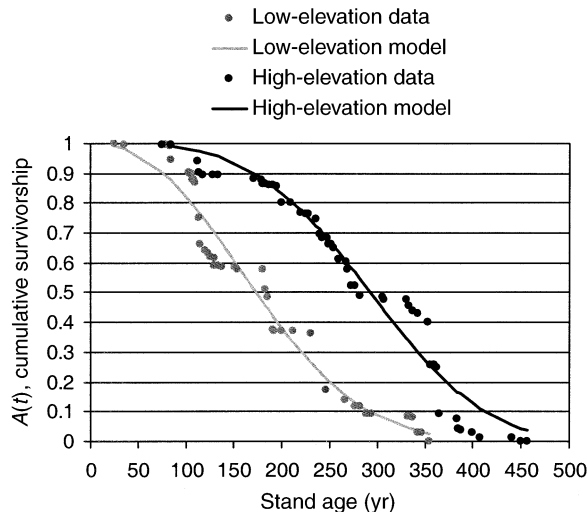


FIG. 7. Comparison of the cumulative survivorship distributions for the low- and high-elevation regions of the time-since-fire map, which represent the probability of a stand going without fire for a period longer than time *t*. Lines represent the best fit of the survivorship model, $A(t)$, to the data (the proportion of the total area occupied by each stand age); 95% confidence intervals for parameters defining the two models are reported in Table 5.

fire lodgepole pine densities in response to fire interval. For example, early reports in Idaho by Leiberg (1899) indicate that little reforestation occurred in lodgepole pine stands that burned at short intervals. Additional observations show that severe reburns at 30–50-yr intervals in subalpine sites often produce only scattered lodgepole pine or persistent shrubland (Smith and Fischer 1997). However, few studies have offered a possible explanation for such relatively low levels of post-fire recruitment of lodgepole pine.

Our results suggest that temporal changes in postfire propagule abundance, characterized by variation in pre-fire serotiny with stand age, may account for the high variation in lodgepole pine recruitment observed following fires of different intervals. At lower elevations

TABLE 5. Confidence intervals of parameters defining the cumulative survivorship distributions, $A(t)$, for the low- and high-elevation regions of the time-since-fire map, where *b* is the stand age exceeded 36.8% of the time and *c* is the shape parameter that reflects an increasing hazard of burning with stand age.

Map region	95% CI of fire frequency parameters		Expected mean fire interval
	<i>b</i>	<i>c</i>	
Low elevation	193–213	1.97–2.62	135–185
High elevation	316–333	3.07–3.93	280–310

Notes: Mean fire intervals are defined by the mortality density distribution, $f(t)$, based on the confidence intervals of parameters *b* and *c*. See Methods: Landscape-level influence of historical fire regimes on the spatial pattern of serotiny for details.

(<2400 m) where the mean and variation in serotiny is generally higher, fires occurring at short intervals (<100 yr) result in lower postfire recruitment of lodgepole pine, while longer fire intervals (>100 yr) result in very high recruitment of lodgepole pine. Examination of postfire responses to continuous fire intervals at lower elevations indicate highest postfire recruitment following fires of intermediate (70–200 yr) intervals. Highest levels of prefire serotiny are also found within this age range, suggesting a peak in propagule abundance in stands of intermediate age contributes to high postfire densities when stands of this age burn.

In areas of high elevation where mean serotiny is low (<4%), fire interval is also significant in explaining patterns of lodgepole pine recruitment, with highest densities following fire intervals 100–250 yr old, and lower densities following shorter and longer intervals. At these low-serotiny sites, propagule abundance appears to be governed by open-cone seed sources and seems to vary nonlinearly with age of adjacent unburned stands, rather than prefire serotiny, although we did not directly measure propagule abundance associated with open cones. Previous studies have shown that young stands (<100 yr) carry fewer open cones relative to more mature stands (100–250 yr old; Koch 1996), while older stands (>250 yr old) have fewer lodgepole pine in the canopy overall (Peet 1981, Romme and Despain 1989). Hence, when portions of very young or very old stands burn, the adjacent unburned portion of the stand contributes significantly fewer lodgepole pine seeds to the burned patch relative to stands burned at intermediate intervals. The overall mean and variance in lodgepole pine densities in low-serotiny sites, however, is much lower compared to high-serotiny sites. As a result, the relative influence of fire interval varies across the park, with greater consequence in areas of higher serotiny.

Temporal variation in serotiny

Results from logistic regression analysis indicated that trees expected to be serotinous had a very low probability of exhibiting serotiny at a young age, with increasing probability over the age span considered in this study (12–140 yr old). These results support previous observations that serotinous individuals of lodgepole pine produce open cones early in life and closed cones later in life (Crossley 1956, Armit 1964, Lotan 1975, Critchfield 1980, Koch 1996). This transition has been estimated to occur between 15–60 yr of age, but little statistical evidence has supported this hypothesized change in cone morphology, nor have the ecological ramifications been investigated.

An increase in the occurrence of serotinous cones with tree age likely accounts for the observed increases in stand-level percent serotiny with stand age. However, long-term monitoring would be the best means of detecting when and if there is a threshold age at which this occurs, and whether the timing may be environ-

mentally influenced. Additional dendrochronological work which detects uneven-aged rather than even-aged cohorts of mature serotinous lodgepole pines within stands of high serotiny would provide further evidence that serotinous trees maintain a window of open cone production early in life that would contribute to multiple-aged cohorts of older serotinous trees.

Lotan and Perry (1983) suggest that a temporal switch from open to closed cones in lodgepole pine may be an adaptation that permits serotinous individuals to further colonize poorly stocked areas during early postfire succession. If individuals produced closed cones throughout their lifetime, they could only colonize new sites in response to a severe fire event. So early open-cone production would be advantageous where fire intervals or severities were highly variable. Producing open cones early on following fire would coincide with conditions of reduced light competition necessary for successful lodgepole pine establishment and permit ongoing tree establishment. Dendrochronological studies indicate that lodgepole pine may continue to establish 10–30 yr following fire (Johnson and Fryer 1989, Muir 1993). Our data suggest a mechanism for this temporal variation in establishment, where propagules come from within the stand rather than only through dispersal from neighboring stands. In dense stands, however, early open cones would not confer advantage where the cost of cone production would be high relative to opportunities for successful establishment. Therefore, simply delaying closed-cone production would be more cost-effective in dense stands. However, if fire intervals vary considerably over evolutionary time, as they have throughout the last 17 000 yr across the Yellowstone plateaus (Millspaugh et al. 2000), stand-level serotiny and postfire densities would also vary significantly. Hence, although it may be costly to produce open cones early in life in dense stands where competition is high, maintaining a window of open cone production confers evolutionary flexibility in a dynamic landscape.

Influence of disturbance on spatial patterns of serotiny

Stand-level percent serotiny and fire interval both vary with elevation in Yellowstone National Park, suggesting that spatial variation in fire history has exerted selective pressure on lodgepole pine cone morphology throughout the park. At the stand level, percent serotiny is inversely correlated with elevation, with highest serotiny occurring primarily below 2400 m. Previous studies indicate a similar inverse relationship between serotiny and elevation (Crossley 1956, Critchfield 1957, Lotan 1968, Illingworth 1970, Tinker et al. 1994). However, Lotan (1975) and Muir and Lotan (1985) found that serotiny showed little response to elevation in Montana, and the reverse relationship was suggested for northwestern Washington (Lotan 1975).

The estimates of mean fire interval derived from historical survivorship data from the Central plateau in Yellowstone indicate that fire regimes were significantly different in high- and low-elevation regions within the park. Fire interval models derived for the lower elevation region estimate the highest probability of fire occurring at 135–185-yr intervals, whereas the high-elevation regions models estimated the highest probability of fire occurring at 280–310 year intervals. Elevation in YNP is strongly correlated with summer temperatures and precipitation, with warmer, drier sites at lower elevations that would promote shorter fire intervals (Dirks and Martner 1982).

Our fire interval estimates are consistent with previous studies in the Yellowstone region. Based on fire history and postfire stand age in a 6400-ha study area at high elevation (2450–2650 m), Romme (1982) estimated mean fire intervals between 300 and 350 yr. In contrast, Barrett (1993) estimated a mean fire return interval of ~150 yr for a 3500-ha study area dominated by lodgepole pine at lower elevation sites (1830–2410 m) just north of Yellowstone National Park. A significant positive relationship between elevation and fire interval in the northern Rocky Mountain and interior West also corroborate this trend (Agee 1991, Barton 1994, Kushla and Ripple 1997, Veblen et al. 2000, Brown et al. 2001, Heyerdahl et al. 2001).

In understanding how broad-scale variation in fire regimes can exert selective pressure on patterns of serotiny, it is important to consider the average fire interval relative to the typical lifespan of the lodgepole pine in subalpine stands. In areas of low elevation where fire intervals are shorter and more probable within the lifetime of the tree, serotinous individuals would be preferentially selected. Given lethal fires occurring repeatedly during serotinous cone production, levels of serotiny within a stand would increase. With a fairly low probability of fire occurring at very short intervals during their lifetime, say <70 yr, the open-cone trait in young serotinous individuals would rarely be selected against.

At high elevations, the probability that lodgepole pine trees die before fires recur at 300-yr intervals is high, so open cones are advantageous. Numerous studies suggest that 300-yr-old stands have a smaller proportion of shade-intolerant lodgepole pine than earlier in the stands' history, as lodgepole are lost from older stands when overtopped by shade-tolerant *Abies lasiocarpa* Hooker Nuttall and *Picea engelmannii* Parry (Romme and Despain 1989). Hansen et al. (2000) demonstrate that the relative growth rates of *Picea engelmannii* were much higher compared to lodgepole pine at high elevations >2400 m in Yellowstone National Park. Mortality of lodgepole pine from the initial fire cohort increases as stands mature and relative growth rates decline (Johnson and Fryer 1989). In Colorado, Peet (1981) showed that the density and basal area of lodgepole pine decline with stand age; relative impor-

tance of lodgepole pine (the mean of relative density and relative basal area) was 55 in 125–175-yr-old stands, yet only 13 in 250–350-yr-old stands. As these studies indicate, higher lodgepole pine mortality is expected during a 300-yr fire interval, compared to fire intervals half as long. Thus, individuals with open cones have an adaptive advantage at high elevations where a cooler, wetter climate promotes longer fire intervals, during which the probability of dying before fire is higher compared to shorter fire interval regimes at lower elevations

Givnish (1981) argued that historical fire frequency, rather than gene flow, should determine local levels of serotiny in pitch pine (*Pinus rigida* Miller) while Gauthier et al. (1996) correlated serotiny in jack pine (*Pinus banksiana* Lamb.) with history of lethal fires. Models further suggest that fitness of a serotinous individual is maximized at intermediate fire intervals relative to the lifetime of the species and that high variance in fire intervals favors open cone phenotypes. (Enright et al. 1998, Lamont and Enright 2000). Indeed, Muir and Lotan (1985) detected no correlation between serotiny in lodgepole pine and a proxy for fire frequency in a study conducted in the highly dissected Bitterroot Mountains. Such environments may experience greater heterogeneity in fire spread and occurrence compared to the gently rolling topography that characterizes the Yellowstone plateaus. In Yellowstone, fire regimes may be more influenced by broad-scale factors such as elevation correlated with climate, rather than fine-scale changes in aspect and slope in highly dissected drainages. A meta-analysis of pine species throughout North America, Europe, and Asia indicates that serotiny is high among species growing in environments where stand-replacing fires predictably occur during the expected lifetime of those species (Keeley and Zedler 1998).

CONCLUSIONS

The time interval between stand-replacing fires can significantly influence patterns of initial postfire succession if the abundance of propagules varies with stand age. In subalpine forests of Yellowstone National Park, the abundance of lodgepole pine propagules in the canopy seed bank is a function of the percent of serotinous trees. Percent serotiny varies nonlinearly with stand age at lower elevations, but tends to be uniformly low regardless of stand age at higher elevations. At higher elevations, postfire lodgepole pine density does not vary with serotiny, but varies nonlinearly with the age of stands burned (fire interval). The spatial patterns of serotiny appear to have been influenced by variability in historical fire regimes across the Yellowstone landscape, and these patterns in turn have conditioned recent responses to disturbance. Although researchers have speculated on patterns of variation in serotiny, this study is the first mechanistic explanation at the landscape scale.

Understanding the influence of variation in disturbance interval is difficult in systems characterized by large, severe and infrequent disturbances such as crown fires. Historical events are hard to reconstruct in stand-replacing fire systems, and few opportunities exist to compare variation in disturbance history, while holding the time since last disturbance constant. As a result, the successional consequences of disturbance legacies can remain invisible. Understanding the ecological ramifications of temporal variation in disturbance regimes, however, is central to concepts such as the historical range of variability and in considering potential responses to global climate change. We have taken advantage of the "natural experiment" of the 1988 Yellowstone fires, the great variability in stand age and serotiny that existed in Yellowstone's lodgepole pine forests at the time of the fires, and the availability of previous work on fire history to address fundamental questions about the influence of variable fire intervals on postfire ecological responses.

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