Landscape-scale heterogeneity in lodgepole pine serotiny

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A 1992 study of serotiny in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in Yellowstone National Park asked four questions: (*i*) are there morphological characteristics that can be used to estimate prefire proportion of serotinous trees in forests that burned in 1988?; (*ii*) at what spatial scale does percent serotinous trees vary across the landscape?; (*iii*) which environmental factors are correlated with serotiny?; and (*iv*) what is the relationship between prefire serotiny and postfire lodgepole pine seedling density? We first sampled cone characteristics in serotinous and nonserotinous trees along four 2950-m transects in unburned forests, and examined burned trees nearby. Results indicated that asymmetrical cones and an acute angle of cone attachment to the branch were reliable indicators of serotiny even in burned trees. We then sampled nine patches of lodgepole pine forest that had burned in 1988, and varied in size from 1–3600 ha. We sampled serotiny at varying intervals along two perpendicular transects that crossed in the center of each patch. At each sample point, the 12 nearest canopy lodgepole pines were classified as serotinous or nonserotinous. We concluded that the percentage of serotinous trees is most variable at intermediate scales of 1–10 km, and is relatively homogeneous at both fine scales (<1 km) and at very broad scales (tens of kilometers). Percent serotiny was generally more variable and greater at low to middle elevations. Prefire density of serotinous trees was a more important predictor of postfire seedling density than aspect, slope, or soil type. These findings have important implications for landscape-level patterns in postfire regeneration of lodgepole pine.

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Une étude de 1992 portant sur l'expression du caractère sérotineux du pin de Murray (*Pinus contorta* var. *latifolia*) dans le parc national de Yellowstone a soulevé quatre interrogations : (*i*) existe-t-il des caractéristiques morphologiques pouvant être utilisées pour estimer la proportion des arbres sérotineux avant incendie dans les forêts ayant brûlé en 1988; (*ii*) à quelle échelle spatiale la proportion des arbres sérotineux varie-t-elle à travers le territoire; (*iii*) quels facteurs environnementaux sont-ils corrélés avec l'expression du caractère sérotineux des pins; (*iv*) quelle est la relation entre la nature sérotineuse avant incendie et la densité des semis de pins de Murray après feu? Nous avons d'abord mesuré les caractéristiques morphologiques des cônes d'arbres sérotineux et non sérotineux le long de quatre transects de 2950 m dans des forêts non brûlées et nous avons examiné des arbres brûlés situés à proximité. Les résultats ont indiqué que la forme asymétrique des cônes et un angle aigu d'insertion des cônes à la branche constituaient des indicateurs faibles du caractère sérotineux, même chez les arbres brûlés. Nous avons ensuite échantillonné 9 secteurs de la forêt de pin de Murray qui ont brûlé en 1988, dont la superficie variait entre 1 et 3600 ha. Nous avons déterminé le caractère sérotineux à des intervalles variables le long de deux transects perpendiculaires placés au centre de chacun des secteurs. Les 12 tiges de pin de Murray les plus rapprochées de chaque point d'échantillonnage ont été classées comme sérotineuses ou non sérotineuses. Nous en avons conclu que la variation de la proportion d'arbres sérotineux est la plus forte à l'échelle intermédiaire de 1 à 10 km. Celle-ci est relativement homogène, autant à petite échelle (<1 km) qu'à très grande échelle (dizaines de kilomètres). La proportion d'arbres sérotineux était généralement plus variable et plus forte aux altitudes basses à moyennes. D'une manière générale, la densité d'arbres sérotineux avant incendie s'avérait un meilleur prédicteur de la densité de la régénération naturelle de pin de Murray après feu que l'exposition, la pente ou le type de sol. Ces découvertes sous-entendent l'existence de patrons de régénération du pin de Murray après incendie à l'échelle du territoire.

Introduction

The forests of the Yellowstone plateau in northwestern Wyoming are dominated by lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex S. Wats.), which forms large mosaics of even-aged stands (Romme 1982). An interesting characteristic of lodgepole pine is its production of serotinous cones, which do not open upon maturity, but remain closed until subjected to high temperatures. Any particular stand may include a mix of serotinous trees and trees having cones that do open at maturity. Many studies have examined the biology of serotiny, its relationship to disturbances such as fire, and its role in natural regeneration of burned forests (Clements 1910; Critchfield 1957; Lotan 1970, 1975; Pfister 1975; Muir and Lotan 1985*a*, 1985*b*). However, little information is available regarding the variability in serotiny either within stands or across an extensive landscape.

Serotinous, or closed, cones remain sealed until exposed to temperatures of 45–60°C (Clements 1910; Crossley 1956; Beaufait 1960; Perry and Lotan 1977; Knapp and Anderson

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1979), such as a fire would create. These temperatures are necessary to break the resinous bonds that hold the cone scales closed. In the absence of fire, temperatures sufficient to break the resinous bonds do not occur naturally in the crowns of lodgepole pine. Recent work has shown that both fire intensity and rate of spread are important in controlling the opening of serotinous cones (Johnson and Gutsell 1993). Both open and serotinous cones of lodgepole pine fully mature in two growing seasons. Serotinous cones attain a characteristic light-gray color after 10–15 years of weathering (Lotan 1970).

Despite extensive research, a definitive genetic model explaining the maintenance of polymorphism in *P. contorta* does not exist. Perry and Lotan (1979) reported that Teich (1970) and Sittman and Tyson (1971) provided evidence that serotiny may be genetically controlled by two allelomorphs segregating at a single locus. However, Muir and Lotan (1985*a*) deny any tight genetic linkage, based on the lack of covariance between serotiny and other life-history characteristics.

The relative abundance of serotinous versus open-coned trees in a stand appears to be controlled primarily by the nature of the most recent disturbance (Perry and Lotan 1979; Muir and Lotan 1985*b*). In western Montana, Muir and Lotan (1985*b*) found that stands originating after a severe burn produced trees with a high percentage of closed cones, whereas stands that originated after a disturbance other than fire generally produced a large percentage of open-coned trees. Other factors, such as topography and elevation, also may influence the proportion of serotinous trees in a stand (Crossley 1956; Lotan 1975; cited in Muir and Lotan 1985*b*). However, Muir and Lotan (1985*b*) found no significant statistical relationship between percent serotiny and any single environmental variable, other than the nature of the most recent disturbance. Lotan (1975) studied the distribution of serotinous cone-bearing trees in the greater Yellowstone area and found the percentage of serotinous trees extremely variable, ranging from 0 to 72%, but on the average quite low. Ellis et al. (1994) found similar variability in serotiny (0–48%) among stands in Yellowstone Park, but observed that the proportion of trees bearing serotinous cones was greatest at low- and mid-elevation sites (1900–2300m).

Research on postfire regeneration following the 1988 Yellowstone fires has indicated that the density and distribution of serotinous trees may be a critical factor determining the reestablishment of lodgepole pine (Ellis et al. 1994). Consequently, we designed this study as a component of our broad investigation of differential responses of plants having different modes of reproduction to variation in fire size and severity. Because our study sites were in areas that burned in 1988, we first had to develop a method for distinguishing serotinous and open cones in burned trees, a challenging task because serotinous cones are opened and often damaged by fire. Therefore, we addressed four questions: (*i*) are there specific morphological characteristics of serotinous cones which can be used to estimate prefire proportion of serotinous trees in burned stands; (*ii*) at what spatial scales does percent serotiny vary across the landscape in Yellowstone National Park; (*iii*) with what environmental variables is percent serotiny correlated; and (*iv*) what is the relationship between prefire serotiny and postfire seedling density in burned stands of Yellowstone National Park?

Methods

Study area

Yellowstone National Park covers some 9000 km^2 in the northwest corner of Wyoming and adjacent Idaho and Montana. See Despain (1990) for general descriptions of environment and vegetation in Yellowstone. Approximately 80% of the park is covered with coniferous forests dominated by lodgepole pine, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelm.) are abundant in some locations (Despain 1990). The climate is generally cool and dry. At West Yellowstone, mean January temperature is −11.4°C and mean July temperature is 10.8°C; mean annual precipitation is 56.25 cm with relatively moist springs and dry summers (Dirks and Martner 1982).

Question 1: cone morphology

To identify the most reliable morphological characteristics for distinguishing serotinous and nonserotinous trees it was necessary to sample in unburned forests. The sampling process was designed so that results could also be used to address question 2 (spatial scale of variation in percent serotiny). We used information in Ellis et al. (1994) to select two sampling sites in unburned forest, one with relatively high proportions of serotinous trees (Firehole Cascades site) and one with relatively low proportions (Dunraven Pass site) (Table 1, Fig. 1). Two parallel, east–west transects, 2950 m long and 1 km apart, were laid out using hip chains and sighting compasses at each site. Sample points were distributed along each transect as follows: 10 sample points at 50-m intervals; five sample points at 100-m intervals; five sample points at 200-m intervals; and two final sample points at 500-m intervals. Each sample point was a circular area of approximately 50 m^2, which was divided into four quadrants by laying out a rope perpendicular to the transect bearing. The five closest canopy lodgepole pine trees in each quadrant were examined with binoculars, for a total of 20 trees per sample point, and the following data were recorded for each tree: diameter at breast height (DBH), an estimate of maximum limb diameter at which serotinous cones were attached, predominantly acute or right angle of cone attachment on the limbs (cones with an angle greater or less than 90° were classified as acute), cone symmetry, cone color, open- or closed-cone morphology, and an overall rating of the tree as serotinous or nonserotinous. The last five characters were considered as binary, i.e., present or absent. Trees that contained any closed, mature cones were considered serotinous. If no closed, mature cones were observed, the tree was classified as nonserotinous. (In fact, nearly all trees either had no closed cones or ⩾10% closed cones, so this distinction was usually clear.) In addition, the closest sample tree in each quadrant was cored using an increment borer, and the cores were subsequently mounted, sanded, and aged.

Analysis of variance (ANOVA) was performed to determine which morphological characteristics were most strongly related to the classification of a tree as serotinous or nonserotinous. The dependent variable was tree type (serotinous or nonserotinous) and the independent variables were cone symmetry, angle of attachment, color, tree age, and presence or absence of closed cones on branches larger than 2 cm in diameter at the point of attachment (these are older branches, from which nonserotinous cones presumably would have dropped). The analysis showed that cone symmetry and angle of attachment were the best predictors of serotinous versus nonserotinous trees (see Results), and subsequent observations revealed that these characteristics could be detected reliably even in severely burned trees. Therefore, we were able to address questions 2–4, which required sampling prefire serotiny in burned forests.

Questions 2–4: spatial scale, environmental correlates, and seedling density

We had previously established three sampling sites in areas that burned in 1988 (Table 1, Fig. 1). The sites were selected

TABLE 1. Sampling site characteristics in unburned and burned lodgepole pine forests in Yellowstone National Park

Site	Spatial scale (m)	Elevation (m)	Substrate
Unburned			
Firehole Cascades	1975	2100	Rhyolite
Dunraven Pass	1975	2560	Rhyolite
Burned			
Cougar Creek			
Small Patch	159	2180	Rhyolite
Moderate Patch	1100	2240	Rhyolite
Large Patch	2504	2120	Rhyolite
Fern Cascades			
Small Patch	370	2360	Rhyolite
Moderate Patch	582	2480	Rhyolite
Large Patch	2330	2360	Rhyolite
Yellowstone Lake			
Small Patch	190	2360	Andesite
Moderate Patch	1396	2420	Andesite
Large Patch	4302	2545	Andesite
Forest Lake area	3200	2210	Rhyolite

NOTE: Spatial scale is the approximate diameter of a circle enclosing the sampling area.

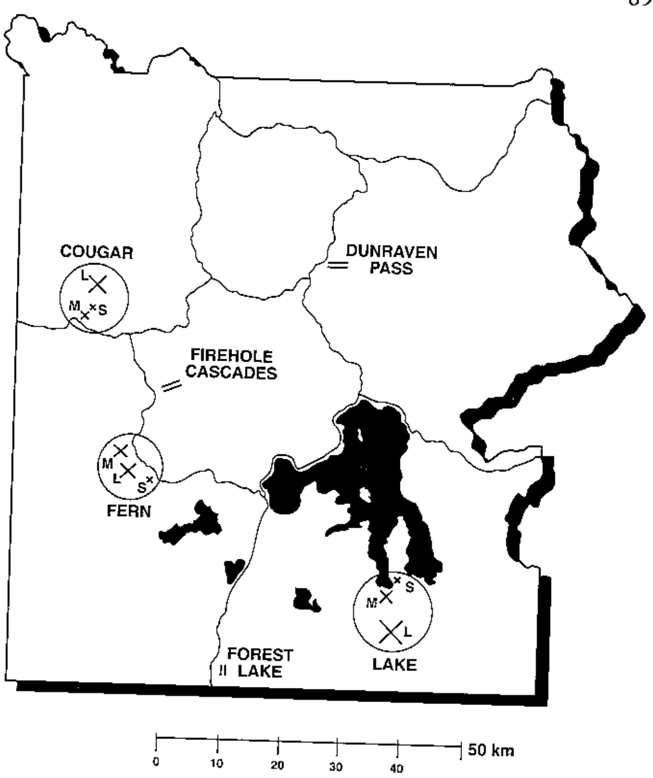

FIG. 1. Map of study areas in Yellowstone National Park. X's indicate the location of the nine sampled patches in burned forest; parallel lines indicate the location of other study sites: the two pilot study sites in unburned forests (Firehole Cascades and Dunraven Pass), and a mosaic of burned and unburned forest (Forest Lake site). Cougar refers to the Cougar Creek site, Fern to the Fern Cascades site, and Lake to the Yellowstone Lake site; S,M, and L refer to the small, moderate, and large patches, respectively, within each site (Table 1).

in part for their variable burn severity patterns, but general environmental conditions (e.g., elevation and substrate) were fairly homogeneous within each site. Each site consisted of three burned patches: small, moderate, and large. Two perpendicular transects extended through each patch, one running northwest–southeast and the other southwest–northeast. Sampling points were located at variable intervals (10–100 m) along these transects to represent a range of distances from the edge of the surrounding unburned forest. The number of sampling points ranged from 34–43 in the small patches to 86–101 in the large patches. Points were permanently marked, and a variety of measures of plant cover and density were made each year from 1990–1993 within a 50-m^2 plot centered on the point.

The proportion of serotinous trees at each point was estimated as follows. We established a circular sampling area with a radius of 10 m and divided it into four quadrants. The three nearest cone-bearing lodgepole pine trees were then located in each quadrant and, using binoculars, each tree was rated as serotinous (closed coned) or nonserotinous (open coned) based on the morphological characteristics identified from the unburned forests (see Results). If there were not three suitable trees within 10 m in one or more quadrants, additional trees in the next quadrant(s) were rated to obtain a total of 12 sample trees in the immediate vicinity of the sample point. Occasionally there were not 12 trees within 10 m of the point, resulting in a smaller sample size. It was assumed that the trees within a 10 m radius represented the potential seed source for the 50-m^2 area sampled at that point.

To detect the spatial scale(s) of variation in percent serotiny, the percentage data were normalized by the arcsine transformation, and the coefficient of variation in percent serotiny was plotted against the area of the study site. Area was expressed as the approximate diameter of a circle enclosing the sampled area. In addition to the nine patches distributed in the three sites described above, and the two sites in unburned forests (question 1), we sampled serotiny in this same manner in a site near Forest Lake (Fig. 1) to increase our geographic coverage of Yellowstone Park. In addition to plotting coefficient of variation for individual study sites, the study areas were aggregated into nested, successively larger geographic regions to observe variation at a range of spatial scales from small (radius ca 100 m) to large (tens of kilometers). For example, we aggregated all of the sample points from the three Cougar Creek patches into a single Cougar Creek site, and then aggregated the points from the Cougar Creek site with those from the Firehole Cascades site (Fig. 1). The approximate diameter of each aggregated site was determined by measuring its dimensions on the map. Each aggregated site included two or more sampling areas plus the unsampled area(s) between them. The largest area used in this analysis included all of our study areas, and encompassed almost two thirds of Yellowstone Park (Fig. 1). We then examined the plot of coefficient of variation as a function of spatial extent, and looked for regions where variation increased, decreased, or remained constant (cf. Krummel et al. 1987).

To explore the relationships between percent serotiny and environmental variables, ANOVA was performed using percent serotiny at each sample point as the dependent variable, and site, aspect, burn severity, successional stage, and slope (Table 2) as independent variables. We had elevation data for all of our sites and patches, but not for individual sample points, so we examined separately the relationship between elevation and serotiny by plotting mean percent serotiny of each study site against elevation. Study sites included the nine patches plus the two pilot sampling areas and the two areas near Forest Lake (Fig. 1). To determine the relative importance of percent serotiny and other environmental parameters as predictors of lodgepole pine seedling density in burned forests, we performed another ANOVA in which the dependent variable was the density of lodgepole pine seedlings that had established since the 1988 fires, and the independent variables were the density of serotinous trees at each sample point, slope, aspect, and site (Table 2).

TABLE 2. Environmental parameters tested as independent variables in ANOVA (Tables 3,4)

Variable	Description
Site	Cougar Creek, Fern Cascades, or Yellowstone Lake (Fig.1, Table 1)
Burn class	
0	Unburned; no fire effects
1	Low-intensity surface fire; some of the organic litter layer consumed, little mortality in canopy or ground layer
2	High-intensity surface fire; most of the organic litter layer consumed, nearly all of the canopy killed but not consumed
3	Crown fire; all of the organic litter layer consumed, all trees killed and their leaves consumed by the fire
Slope class	Flat or gentle slope, moderate slope, or steep slope
Aspect class	Mesic (N, NW, NE), xeric (S, SW, SE), or intermediate (E, W)
Successional stage[a]	
LP0	Recently burned forest, dominated by herbaceous vegetation, age ca 0–40 years post fire
LP1	Dense forest of small- to moderate-sized, even-aged lodgepole pine, little understory, age ca. 40–150 years
LP2	Even-aged forest of mature, full-sized lodgepole pine, little understory, age ca. 150–250 years
LP3	All-aged forest with well-developed understory, age >250 years
Density of serotinous trees[b]	Number of serotinous trees recorded within 10m of the sample point (range 0–12; see Methods)

[a] From Despain 1990.

[b] This variable was used instead of percent serotinous trees, because some sites were dominated by tree species other than lodgepole pine (i.e., spruce or fir); if such a point contained only one lodgepole and it was serotinous, then serotiny would be 100% but the potential seed would nevertheless be small.

TABLE 3. Results from ANOVA of cone characteristics observed on unburned trees

Independent variable	df	F	MSE	P
Cone symmetry	1	220.92	18.389	0.0001
Cone angle	1	43.17	3.593	0.0001
Cone color	1	7.04	0.586	0.0084
Tree age	1	0.67	0.055	0.4143
2-cm branch diameter	1	0.02	0.002	0.8841

NOTE: The dependent variable was tree type (serotinous vs. nonserotinous); the independent variables were cone symmetry (symmetrical or asymmetrical), cone angle of attachment (acute or right angle), cone color (gray or brown), tree age, and presence or absence of closed cones on branches larger than 2 cm in diameter at the point of cone attachment ($r^2 = 0.81$).

Results

Question 1: Serotinous cone morphology

Strongly asymmetrical cone shape and an acute angle of cone attachment to the branch were found to be the most powerful indicators of the serotinous trait ($P < 0.0001$; $r^2 = 0.81$ for the entire model, Table 3). These two characteristics usually occurred together, but not always. A light-gray, weathered color on closed, mature cones was statistically significant, but was unreliable in the burned stands. Tree age, DBH, and branch diameter at the point of oldest cone attachment were not significant factors ($P > 0.05$, Table 1).

Question 2: Spatial scale of variation in serotiny

The coefficient of variation in percent serotinous trees (arcsine square root transformed) was consistently low in two regions: sampling areas with diameter less than ca 1 km and areas with diameter greater than ca 10 km (Fig. 2). In the intermediate range, i.e., diameters ca 1–10 km, the coefficient of variation was variable, ranging from very low to very high (Fig. 2).

Question 3: Environmental factors correlated with percent serotiny

A variable called "site" (i.e., Cougar Creek, Fern Cascades, or Yellowstone Lake; Fig. 1), which reflects broad-scale gradients in substrate and elevation (Table 1), when entered in the ANOVA was the most important predictor of prefire percent serotinous trees ($P < 0.0001$; $r^2 = 0.71$ for the entire model, Table 4). Percent serotinous trees was highest at the Cougar Creek site (65% ± 2; mean ± SE), low at the Fern site (6 ± 1%), and very low at the Lake site (2 ± 1%). Aspect class was also significant although its explanatory power was only a fraction of that of site, as indicated by its low mean-square value (Table 4). A Tukey test showed that percent serotiny was higher in xeric and intermediate aspect classes (mean percent serotiny = 32%) than in mesic aspect classes (mean percent serotiny = 20%). Burn severity class, successional stage, and slope class were not significant.

Elevation and percent serotiny were strongly correlated, with an exponential decline in serotiny as elevation increased (Fig. 3). There also appeared to be a threshold around 2300 m; lower elevations (e.g., the Cougar Creek site) were characterized by greater variability but generally high percentage of serotiny, whereas at upper elevations (e.g., the Yellowstone Lake site) serotiny was consistently low (Fig. 3).

Question 4: Environmental variables correlated with lodgepole seedling density

The density of lodgepole pine seedlings that established after the 1988 fires was significantly correlated with the density of serotinous trees in the 50-m^2 sample area ($P < 0.0001$; $r^2 = 0.24$ for the entire model). None of the other variables tested (site, slope class, aspect class; Table 5) were significant.

Discussion

The classification of individual trees as serotinous or nonserotinous within burned stands varied in difficulty according to the burn severity of a particular stand. Those stands that were only slightly or moderately burned contained many serotinous trees that still possessed closed cones, and thus were easily distinguishable as serotinous or nonserotinous. Trees within severely burned stands, while somewhat more difficult to classify because most of the closed cones had opened, were nonetheless recognizable as to tree type since

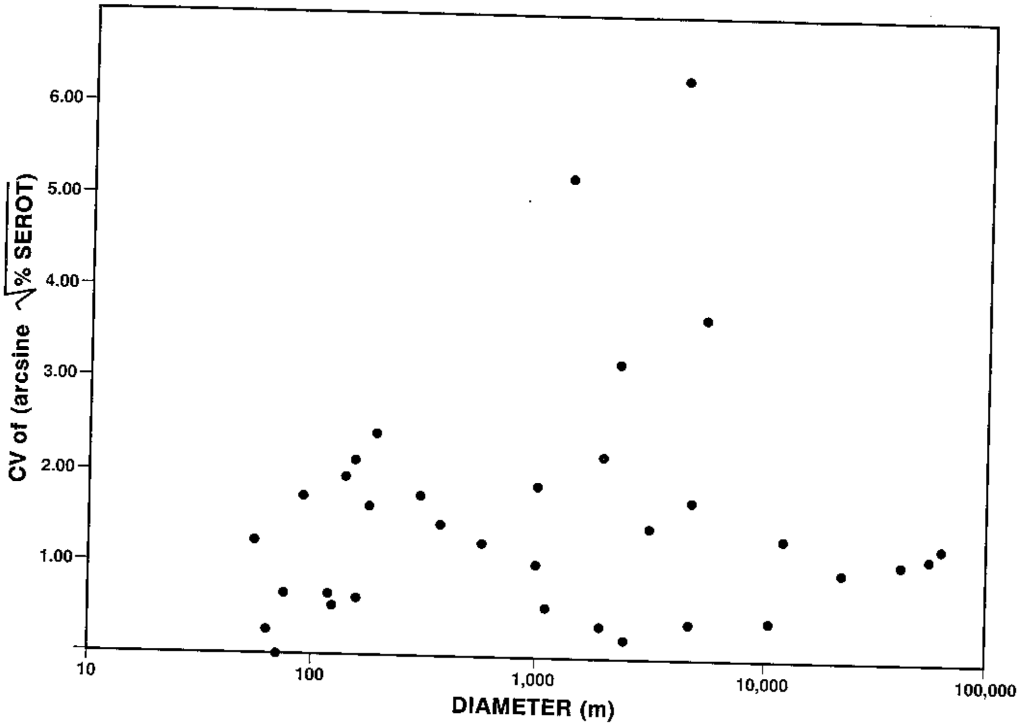

FIG. 2. Coefficient of variation in percent serotinous trees, plotted as a function of spatial scale of sampling (i.e., approximate diameter of a circle enclosing the study area).

TABLE 4. Results from ANOVA of environmental predictors of percent serotiny

Source	df	Sum of squares	Mean square	*F*	*P* >*F*
Model	11	365 657.049	33 241.549	99.14	0.0001
Error	436	146 185.472	335.287		
Corrected total	447	511 842.521			
Site	2	161 012.158	80 506.079	240.11	0.0001
Burn class	3	645.926	215.308	0.64	0.5882
Slope class	1	0.025	0.025	0.00	0.9930
Aspect class	2	5 170.838	2 585.419	7.71	0.0005
Successional stage	3	642.752	214.250	0.64	0.5902

R^2 = 0.714 394 CV = 73.460 Root MSE = 18.310 Mean percent serotiny = 24.926

NOTE: The dependent variable was percent serotinous trees; the independent variables were site, aspect class, burn severity class, successional stage, and slope class (Table 2). Type III sums of squares were calculated for the independent variables.

the remnants of serotinous cones had maintained their asymmetrical shape and acute angle of attachment to the branch.

The occurrence of serotinous cones in lodgepole pine forests of the Yellowstone Plateau appears to be homogeneous or heterogeneous depending on the spatial scale at which it is measured. Small areas, with diameter <1 km, and very large areas, >10 km, exhibited low variability in percent serotiny. However, areas of intermediate size, 1–10 km, varied considerably in percent serotiny, indicating that serotiny is more heterogeneous at intermediate scales than at fine or broad scales. The smaller sampling areas (<1 km), where percent serotiny is relatively homogeneous, roughly coincide with the modal size distribution of individual patches created by prehistoric, stand-replacing fires on the Yellowstone Plateau (D. Despain and W.H. Romme 1991, and unpublished). This suggests that individual patches within the landscape mosaic of fire-generated stands have relatively homogeneous proportions of serotinous trees. (Our subjective observations as we walked the long transects through the forest also were consistent with this idea.) The high variation in percent serotiny at the intermediate scale (ca 1–10 km) probably results from the sample encompassing a mosaic of stands of different successional stages, each stand having a different level of serotiny because of its unique disturbance history (Muir and Lotan 1985*b*). In addition, there is considerable heterogeneity in environmental variables such as elevation and substrate at this scale. The decrease in variation in percent serotiny at the very broadest scales (>10 km) is more difficult to explain. It may be simply the result of greatly increased sample size.

Site (i.e., Cougar Creek, Fern Cascades, or Yellowstone Lake) was clearly the most powerful predictor of the percentage of serotinous trees within a 50-m^2 sampling point, and aspect class was the only local abiotic characteristic that helped explain the occurrence of serotiny. This suggests that certain environmental characteristics provide optimum conditions for expression of the serotinous trait. Low-elevation sites on rhyolite substrates, with south-, east-, or west-facing

TABLE 5. Results from ANOVA of lodgepole pine seedling density

Source	df	Sum of squares	Mean square	F	$P > F$
Model	6	84 965.978	14 160.996	23.98	0.0001
Error	447	263 975.332	590.548		
Corrected total	453	348 941.311			
Density of serotinous trees	1	32 233.133	32 233.133	54.58	0.0001
Site	2	140.854	70.427	0.12	0.8876
Slope class	1	13.619	13.619	0.02	0.8794
Aspect class	2	872.646	436.323	0.74	0.4782
$R^2 = 0.243\ 496$	CV = 293.3072	Root MSE = 24.301	Mean density = 8.285		

NOTE: The dependent variable was the density of lodgepole pine seedlings (seedlings/m^2) that established since the 1988 fires; the independent variables were density of serotinous trees within the 50-m^2 sample area, site, slope class, and aspect class (Table 2). Type III sums of squares were calculated for the independent variables.

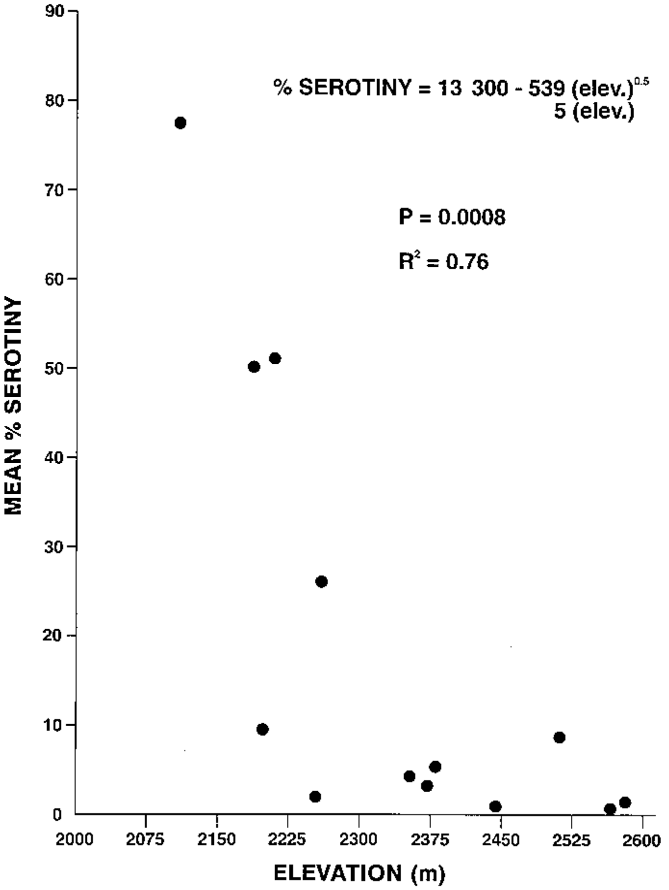

FIG. 3. Mean percent serotinous trees as a function of site elevation.

aspects, are most likely to have a high proportion of serotinous trees in Yellowstone National Park. We also found a strong correlation between percent serotiny and elevation (Fig. 3), in contrast to the findings of Muir and Lotan (1985*b*) in western Montana. In Yellowstone, we found that low- and mid-elevation sites exhibited more variability and generally higher percent serotiny than high elevation sites, which had uniformly low serotiny. Muir and Lotan found no correlation between elevation and serotiny. It should be noted, however, that all of their study sites were located at elevations below 2300 m, which is within the elevational range where we found the greatest variability. In contrast, our high elevation sites, where we found low serotiny, were between 2300–2600 m.

Our results confirmed the conclusions of Ellis et al. (1994) that percent serotiny in the prefire forest is an important predictor of postfire lodgepole pine seedling density. Seedling density was far higher in places that contained a large number of serotinous trees as a seed source than in otherwise similar places lacking serotinous trees. Seedling density in burned stands ranged from 3–4 seedlings/ha where percent serotiny was near zero (Yellowstone Lake site), to >200 seedlings/m2 in stands with 50–75% serotinous trees (Cougar Creek site). Our analyses of the entire long-term data set (1990–1993) from the nine burned patches are still in progress, but they too suggest that local density of serotinous trees (i.e., within several meters) is far more important for postfire seedling establishment than distance from the unburned edge or any other variables that we measured.

The spatial distribution of serotinous trees and the corresponding lodgepole seedling density have important implications for the long-term structure of stands which establish following fires (Anderson and Romme 1991). Our results suggest that intense fires in stands containing a high percentage of serotinous trees leads to dense, "doghair" stands. In contrast, fires in stands having low levels of serotinous trees result in sparsely distributed lodgepole pine seedlings. Seedling density within the first few years following a fire may dictate stand structure for the life of the stand, i.e., until the next stand-replacing fire (Anderson and Romme 1991; C.D. von Dohlen, M. Ellis, J.E. Anderson, and W.H. Romme, submitted). Stand structure in turn influences numerous ecological processes, such as wildlife habitat, nutrient cycling, understory plant species composition, and landscape hydrology.

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