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Source: *Ecological Monographs*, Vol. 67, No. 4 (Nov., 1997), pp. 411-433
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/2963464
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Ecological Monographs, 67(4), 1997, pp. 411–433
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EFFECTS OF FIRE SIZE AND PATTERN ON EARLY SUCCESSION IN YELLOWSTONE NATIONAL PARK

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Abstract. The Yellowstone fires of 1988 affected >250 000 ha, creating a mosaic of burn severities across the landscape and providing an ideal opportunity to study effects of fire size and pattern on postfire succession. We asked whether vegetation responses differed between small and large burned patches within the fire-created mosaic in Yellowstone National Park (YNP) and evaluated the influence of spatial patterning on the postfire vegetation. Living vegetation in a small (1 ha), moderate (70–200 ha), and large (500–3600 ha) burned patch at each of three geographic locations was sampled annually from 1990 to 1993. Burn severity and patch size had significant effects on most biotic responses. Severely burned areas had higher cover and density of lodgepole pine seedlings, greater abundance of opportunistic species, and lower richness of vascular plant species than less severely burned areas. Larger burned patches had higher cover of tree seedlings and shrubs, greater densities of lodgepole pine seedlings and opportunistic species, and lower species richness than smaller patches. Herbaceous species present before the fires responded individually to burn severity and patch size; some were more abundant in large patches or severely burned areas, while others were more abundant in small patches or lightly burned areas. To date, dispersal into the burned areas from the surrounding unburned forest has not been an important mechanism for reestablishment of forest species. Most plant cover in burned areas consisted of resprouting survivors during the first 3 yr after the fires. A pulse of seedling establishment in 1991 suggested that local dispersal from these survivors was a dominant mechanism for reestablishment of forest herbs. Succession across much of YNP appeared to be moving toward plant communities similar to those that burned in 1988, primarily because extensive biotic residuals persisted even within very large burned areas. However, forest reestablishment remained questionable in areas of old (>400 yr) forests with low prefire serotiny. Despite significant effects of burn severity and patch size, the most important explanatory variable for most biotic responses was geographic location, particularly as related to broad-scale patterns of serotiny in *Pinus contorta*. We conclude that the effects of fire size and pattern were important and some may be persistent, but that these landscape-scale effects occurred within an overriding context of broader scale gradients.

Key words: disturbance; fire ecology; landscape ecology; patch size; Pinus contorta; *secondary succession; spatial heterogeneity; spatial pattern; Wyoming; Yellowstone National Park.*

INTRODUCTION

A key challenge in ecological research involves determining the influence of spatial patterns on ecological processes (Levin 1992, Kareiva 1994). Spatial pattern has demonstrable effects on habitat use and foraging dynamics (Pearson 1993, Turner et al. 1994*a*), populations (Kareiva 1990, Hanski 1993), nutrient movements (Peterjohn and Correll 1984), and the spread of disturbance (Turner 1987), but few studies have evaluated the relative importance of spatial pattern compared to other controlling variables. Because broad-scale disturbances are heterogeneous in their effects across the landscape, such events provide ideal opportunities for investigating the importance of spatial pattern on succession. Investigations into mechanisms of plant succession following fire and other disturbances often have emphasized the importance of autecology and life history attributes of individual plants and species in determining vegetation dynamics (e.g., Connell and Slatyer 1977, Noble and Slatyer 1980, Peet and Christensen 1980, Pickett et al. 1987, Halpern 1988, 1989, Peterson and Pickett 1995). These studies also demonstrated that species responses may vary with the kind, severity, and spatial and temporal context of disturbance (also see Pickett 1976, Finegan 1984). Patch size, heterogeneity, and distance from undisturbed sites may differentially influence species having particular combinations of life history attributes (Den-

Manuscript received 13 November 1995; revised 10 October 1996; accepted 4 November 1996; final version received 9 December 1996.

slow 1980*a*, *b*, Hartshorn 1980, Miller 1982, Malanson 1984, Green 1989) and may result in multiple pathways for succession (Fastie 1995). In addition, disturbance effects on natural communities are influenced by environmental conditions controlled by landscape position (Foster 1988*a*, *b*, Callaway and Davis 1993, Boose et al. 1994), although this depends on the disturbance (Frelich and Lorimer 1991). Including spatial considerations in explaining post-disturbance succession may extend the power of approaches that incorporate life history factors and environmental variation.

We studied the effects of fire size and pattern on vegetation dynamics following the 1988 fires in Yellowstone National Park (YNP), Wyoming, USA. Fires in 1988 affected $> 25 \times 10^4$ ha in YNP and surrounding lands as a consequence of unusually prolonged drought and high winds (Renkin and Despain 1992, Bessie and Johnson 1995). Such large fires are a major but infrequent disturbance in this landscape, occurring at 100- to 300-yr intervals (Romme 1982, Romme and Despain 1989). As a result of variations in wind, topography, vegetation, and time of burning (Rowe and Scotter 1973, Wright and Heinselman 1973, Van Wagner 1983), the 1988 fires produced a strikingly heterogeneous mosaic of burn severities (effects of fire on the ecosystem) and islands of unburned vegetation across the landscape (Christensen et al. 1989, Turner et al. 1994*b*). The spatial extent and heterogeneity of the 1988 fires provided an ideal opportunity to study effects of fire size and pattern on postfire succession. In this paper, we ask whether vegetation responses differ between small and large burned patches within the fire-created mosaic in YNP and evaluate the importance of spatial patterning on the postfire vegetation.

Four classes of burn severity that were easily discriminated in the field through 1991 were used to characterize heterogeneity of the 1988 fires: unburned (no sign of fire effects), light-surface burns (canopy trees generally survived and retained green needles, stems often were scorched, and soil organic layer remained largely intact); and severe-surface burns and crown fires (extensive tree mortality, soil organic layer completely consumed). Canopy needles were consumed in crown fires but not in severe-surface fires, where a litter layer of dead needles developed rapidly. Spatial analysis of a map of burn severity derived from a 1989 Landsat Thematic Mapper image indicated a highly patchy burn mosaic. Approximately 75% of the area in crown fire was within 200 m of unburned or lightly burned areas that are potential sources of plant propagules (Turner et al. 1994*b*). Even large patches of crown fire contained areas of light- and severe-surface burn.

Natural disturbances are unplanned, and it is usually not possible to study their effects with a well-balanced design. However, events such as the Yellowstone fires provide much-needed empirical data about disturbance effects over very large regions (Glenn-Lewin and van der Maarel 1992) and therefore alternative study designs for assessing effects of such events are necessary. Wiens and Parker (1995) have identified two main problems in studying unplanned events: (1) affected sites are not randomly located and, because they must be defined post facto, "reference" areas are not true controls; and (2) pseudoreplication is a problem because the only true level of independent replication is the disturbance event itself. In practice, effective strategies can be used to deal with non-independence among samples, and post facto study designs that document both initial effects and subsequent recovery (e.g., the interaction between impact level and time), which is our approach in YNP, may actually be more useful than before-after comparisons (Wiens and Parker 1995). Level $\times$ time designs require methods consistent between sampling periods, but the potential severity of errors due to pseudoreplication can be minimized by use of repeated-measures analysis, which we have employed (Wiens and Parker 1995). Although we had some information on prefire forest stand structure across the landscape (see *Methods: Study area*), site-specific data on the herbaceous community would have been immensely valuable in interpreting postfire community response (e.g., see Dayton et al. 1992). We submit that, interpreted appropriately, comparison of postfire vegetation dynamics among burned patches is a valid path of inquiry for studying effects of disturbance size and pattern.

Hypotheses

We present our initial hypotheses concerning individual species and community responses to fire severity, fire size, and distance to unburned forest by grouping similar response variables together (Table 1). We then synthesize the full set of response variables in the Discussion to address how burn size and pattern influence postfire successional dynamics.

We distinguished two categories of plants: (1) forest species, which were important in prefire communities; and (2) opportunistic species, which were absent or only incidental before the fire. Forest species were further classified by their mode of reproduction as: (1) vegetative, in which plants sprouted from surviving belowground structures, and (2) sexual, in which seedling establishment occurred. The major seed sources immediately following fire are the canopy and dispersal from unburned areas, as the number of viable seeds in boreal and high elevation forest soils tends to be extremely low (Johnson 1975, Whipple 1978, Archibold 1989).

Conifer trees in YNP reproduce only by seed. Lodgepole pine (*Pinus contorta* var. *latifolia*) has serotinous cones, regenerates well following crown fire, and requires exposed mineral soil for seed germination and seedling establishment; we therefore expected seedling density to be greatest in areas severely burned by crown fires (Table 1). We also expected that seed might dis-

TABLE 1. Summary of hypotheses about the effects of fire size and pattern on biotic response variables that were tested in this study of early postfire succession in Yellowstone National Park.

Response variable	Independent variable		
	Burn severity	Patch size	Distance to unburned forest
Biotic cover	Decreasing with increasing burn severity	Greater in smaller patches	No effect
Lodgepole pine seedling density and cover	Increasing with increasing burn severity	Greater in smaller patches	Decreasing with increasing distance
Sprouts of forest herbs and shrubs	Decreasing with increasing burn severity	No effect	No effect
Seedlings of forest herbs and shrubs	Greatest in severe-surface burns, lower in light-surface burns and crown fires	Greater in smaller patches	Decreasing with increasing distance
Opportunistic species	Increasing with increasing burn severity	Greater in larger patches	No effect
Species richness	Greatest in severe-surface burns, lower in light-surface burns, and lowest in crown fires	No effect	Decreasing with increasing distance

perse into burned areas from open-cone trees in unburned forest and thus hypothesized that seedling density would be negatively related to the distance from unburned forest.

Most herbs and shrubs can reproduce both vegetatively and sexually (Lyon and Stickney 1976, Stickney 1986), so we distinguished between sprouts and seedlings in our analyses. Forest species used to test for fire effects on sprouts (Table 1) included three forbs, one shrub, and two sedges. *Epilobium angustifolium* (fireweed), and *Arnica cordifolia* (heartleaf arnica) are perennial forbs with light, wind-dispersed seeds. Although *Epilobium angustifolium* is recognized as a fire-adapted species, it is common in unburned forests in YNP as an inconspicuous herb that blooms infrequently. *Lupinus argenteus* (lupine) is a perennial forb with relatively large, heavy seeds. *Vaccinium scoparium* (grouse whortleberry) is the dominant shrub in the unburned forest. *Carex geyeri* (elk sedge) and *Carex rossii* (Ross's sedge) are common graminoids in unburned lodgepole pine forest (Despain 1990).

Forest species used to test for fire effects on seedlings (Table 1) included *Lupinus argenteus, Epilobium angustifolium,* and *Carex* spp. (*C. geyeri* and *C. rossii*). Seedlings of *Arnica cordifolia* and *Vaccinium scoparium* were never observed during the study, and *A. cordifolia* seeds were not successfully germinated even in a greenhouse setting (Romme et al. 1995). Seedlings of *C. geyeri* and *C. rossii* could not be differentiated.

Hypotheses about opportunistic species (Table 1) were tested using four species. *Cirsium arvense* (Canada thistle) is an exotic species that frequently occurred along horse trails, foot trails, and roadways. The thistle invaded several areas burned from 1972 to 1988 and reproduces vegetatively once established. However, it was not present throughout most of the burned area before the fires of 1988, so we expected it to invade burned patches through seed dispersal. *Gayophytum diffusum* (ground smoke) and *Collinsia parviflora* (blue-eyed Mary) are native annuals that may be present in unburned forests but are never abundant or conspicuous, and we hypothesized that these species might respond rapidly to the newly created open habitat. *Lactuca serriola* (prickly lettuce) is an exotic biennial that, like the annuals, was not conspicuous in unburned forest.

STUDY AREA

Yellowstone National Park encompasses 9000 km^2 on a high forested plateau in northwest Wyoming. Approximately 80% of the park is dominated by lodgepole pine forest, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelm.) may be locally abundant (Despain 1990). Our study area was the subalpine forested plateau that covers most of Yellowstone (Fig. 1) and encompasses dry, infertile rhyolite substrates as well as more mesic and fertile andesite and lake-bottom substrates. The climate is generally cool and dry with mean January temperature of −11.4°C, mean July temperature of 10.8°C, and mean annual precipitation of 56.25 cm (Dirks and Martner 1982). The summer of 1988 was the driest on record since 1886, with precipitation in June, July, and August at 20%, 79%, and 10%, respectively, of average (National Park Service, YNP).

METHODS

Field sampling

In order to establish three replicates of three patch sizes that differed in size by an order of magnitude, we selected a small (1 ha), moderate (70–200 ha), and large (500–3600 ha) patch of crown fire at each of three geographic locations (Table 2) across the subalpine plateau (Fig. 1). Regions of lesser burn severity were con-

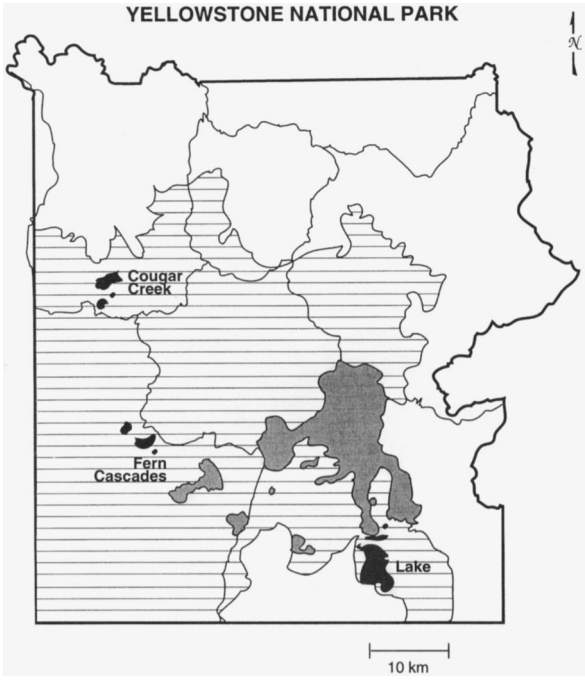

FIG. 1. Map of Yellowstone National Park showing the locations of the three study locations (Cougar Creek, Fern Cascades, and Yellowstone Lake). A small (1–2 ha), moderate (80–200 ha), and large (480–3698 ha) patch of crown fire was studied at each location. The hatched area depicts the Yellowstone Plateau, the gray shading illustrates major lakes, solid black areas show the nine burned patches used in this study, and irregular solid lines indicate Park roads.

tained within and around each patch. Selection was subjectively based on patch size and accessibility based on digital satellite imagery. Availability of accessible large crown-fire patches was limited, and the large patch at Yellowstone Lake was substantially larger than at the other two locations (Table 2).

In July 1990, four permanent transects were established in each of the nine patches, extending from the center to the edge of the patch along subcardinal directions (NE, NW, SW, and SE). Transects varied in length (Table 2) depending on patch size and shape. The edge of the patch was defined by unburned forest, a light-surface burn, a topographic barrier, or an unforested area. Sampling on each transect began 20 m from the center point of the patch and continued at fixed intervals (100 m in moderate patches and the large patches at Fern Cascades and Cougar Creek, 200 m in the large patch at Yellowstone Lake, and 20 m in the small patches) as long as the transect continued through areas affected by crown fire. At transitions between burn severity classes (e.g., between crown fire and a severe-surface burn), sampling points were located on the edge and at three 20-m intervals on either side of the edge. Subsequent sampling points were again located at the fixed intervals until the next edge was encountered. Sampling points were marked in the field with wooden stakes, flagging, and rock cairns and were sampled during July and August of 1990, 1991, 1992, and 1993.

A 50-m^2 circular plot was centered on each sampling point, and slope, aspect, and burn severity were recorded in 1990. The proportion of prefire serotinous lodgepole pine trees was recorded within a 50-m radius of the sampling point in 1992 following methods in Tinker et al. (1994). For vegetation measurements, an 8-m line was centered on the sampling point and extended perpendicular to the main axis of the transect. Percent cover data were recorded within eight 0.25-m^2 plots spaced at 1-m intervals along this line. At each point in a 25-point 0.5 × 0.5 m point-intercept frame (cf. Floyd and Anderson 1982, 1987), the underlying plant species or cover type (exposed mineral soil, unburned litter, charred litter, pebble, cobble, or boulder) was recorded. Percent cover was determined by aggregating the data from the eight 0.25-m^2 plots. Species richness was measured by recording all species within an area extending 1 m along the 8-m line. Nomenclature follows Dorn (1992).

Individuals of *Epilobium angustifolium, Lupinus argenteus, Arnica cordifolia, Carex geyeri, Carex rossii, Pinus contorta,* and *Vaccinium scoparium* were censused within each of the eight 0.25-m^2 plots with perennials classified as seedlings of the year or sprouts based on morphological characters (M. G. Turner et al., *unpublished data*). *Pinus contorta* seedlings were counted by age (in years) to estimate recruitment through time.

Opportunistic species (*Cirsium arvense, Collinsia parviflora, Gayophytum diffusum,* and *Lactuca serriola*), which frequently were sparse at individual sampling points, were sampled along 1 m wide belt transects between sampling points. Belt transects were established to record the total number of individuals observed ≤0.5 m from the transect line.

The similarity in species richness between years at each sampling point was computed by

$$S = 2C/(A + B + 2C)$$

where S = the similarity in species richness between two samples (here, between years), A = the number of species unique to sample 1, B = the number of species unique to sample 2, and C = the number of species that shared in both samples (Pielou 1974:311).

Statistical analyses were performed by using SAS (SAS Institute 1992). An arcsine transform was applied to percent cover data and the similarity index values prior to analysis to eliminate bias in the variance and mean (Zar 1984). A square-root transform was applied to counts of sprouts and seedlings of forest species, including *P. contorta,* and the belt transect data prior to analysis. Data were subject to repeated-measures analysis of variance (ANOVA) because measurements were obtained annually from the same sampling points. Independent variables included geographic location, patch size, burn severity, slope, aspect, distance to the

TABLE 2. General description of the three geographic locations where small, moderate, and large patches of crown fire were sampled in Yellowstone National Park (YNP) from 1990 to 1993.

Attribute	Cougar Creek	Fern Cascades	Yellowstone Lake
Location in YNP	Westcentral YNP near lower forest ecotone	Southwestern YNP near Old Faithful, extensive forest	Southeastern YNP, forest interspersed with occasional meadows
Patch sizes (ha) and no. sampling points			
Large	500 (84 points)	480 (103 points)	3698 (59 points)
Moderate	91 (46 points)	200 (82 points)	74 (67 points)
Small	1 (34 points)	1 (37 points)	1 (40 points)
Elevation range (m)	2150–2300	2270–2500	2400–2700
Geologic substrate (Keefer 1972)	Rhyolite and tuff (moderately infertile Quaternary volcanics)	Rhyolite (infertile Quaternary volcanics)	Lake sediments and andesite (moderately fertile Eocene volcanics)
General vegetation of unburned areas	*Pinus contorta* dominated early and late seral stages; occasional *Pseudotsuga menziesii*; *Ceanothus velutinus*, *Carex rossii*, and *Calamagrostis rubescens* dominated ground layer	*Pinus contorta* dominated early and late seral stages; occasional *Abies lasiocarpa*; *Vaccinium scoparium*, *Carex geyeri*, and *Lupinus argenteus* dominated ground layer	*Pinus contorta* dominated early seral stages; *Abies lasiocarpa* and *Picea engelmannii* dominated late stages; *Vaccinium scoparium*, *Carex geyeri*, and *Arnica cordifolia* dominated ground layer
Relative density (%) of lodgepole pine in prefire stands	Mean = 91 SD = 22 Range = 12–100	Mean = 100 SD = 0	Mean = 63 SD = 35 Range = 0–100
Predominant prefire stand age (from Romme and Despain 1989 and *unpublished data*)	≈130-yr-old even-aged stands that originated after fires in the 1860s	≈290-yr-old even-aged stands that originated after fires in early 1700s	≈250-yr-old even-aged stands that originated after fires in mid 1700s in small and moderate patches; >400-yr-old uneven-aged stands in large patch
Prefire tree density (all species; stems/ha)	Mean = 610 SD = 424 Range = 32–1846	Mean = 470 SD = 212 Range = 96–891	Mean = 470 SD = 182 Range = 64–796
Mean prefire percent serotinous trees (Tinker et al. 1994)	65.0	5.4	1.9

nearest unburned or lightly burned forest (i.e., live forest), distance to the nearest severe-surface burn, and appropriate interaction terms. Distance to nearest live forest was included because of the potential for seeds to disperse into the areas of stand-replacing burn. Distance to the nearest severe-surface burn was included because our initial field observations in 1989 and 1990 suggested that these areas could be sources for lodgepole pine seeds, as cones were heated but not consumed. The repeated-measures ANOVAs were done by using the repeated-measures procedure in SAS to test for between-sampling-point effects and by running an ANOVA in which all effects and interactions were fully nested in time to determine the explanatory power (r^2) of the overall model. Means were separated in the fully nested model by using Tukey's studentized range test ($P < 0.05$). To examine the expansion of *Epilobium angustifolium* and *Lupinus argenteus* across the landscape, the proportion of sampling points with sprouts and seedlings of these species was examined through time.

RESULTS

Our sampling design involved three replicates of the three patch sizes across the subalpine plateau, but analyses of the data revealed a surprisingly strong effect of geographic location in explaining variability in postfire vegetation. Thus, our results report not only the effects of the fire-related variables but also the influence of geographic location and its interaction with other main effects.

Biotic cover

Total biotic cover increased through time and varied in a complex way with location, patch size, burn severity, and interactions among these variables (Table 3). Most variability in total biotic cover was explained by geographic location, with Cougar Creek and Yellowstone Lake having much greater cover than Fern Cascades (Fig. 2). Patch size was next in importance (Table 3), with small patches having greater cover than moderate or large patches (Fig. 3). Biotic cover also decreased as burn severity increased (Fig. 4). By 1993, however, severe-surface burns and light-surface burns had the same percent cover (Fig. 4), although the values varied with location (60–65% at Cougar Creek and Yellowstone Lake and ~40% at Fern Cascades). Total cover increased two to four times in crown fires and severe-surface burns between 1990 and 1993 but did

TABLE 3. Summary of tests for between-sample-points effects on postfire biotic cover from repeated-measures ANOVA. Entries indicate the F and P values for significant effects, and trends for main effects. The two most important effects per column (as indicated by the two greatest F values) are highlighted in boldface type.

Effect	Forbs	Graminoids	Trees	Shrubs	Total cover
Location† (df = 2)	**F = 112.71** P = 0.0001 L > F, C	**F = 43.69** P = 0.0001 C > F, L	**F = 130.28** P = 0.0001 C > F > L	F = 9.02 P = 0.0001 C > F, L	**F = 85.81** P = 0.0001 C, L > F
Patch size‡ (df = 2)	**F = 28.68** P = 0.0001 S > M > L	**F = 17.76** P = 0.0001 S > M, L	NS	F = 8.32 P = 0.0003 L > M, S	**F = 35.86** P = 0.0001 S > M, L
Burn severity‖ (df = 3)	NS	F = 16.18 P = 0.0001 2, 1 > 3	**F = 6.75** P = 0.0002 3, 2 > 1	**F = 18.97** P = 0.0001 1 > 2, 3	F = 24.17 P = 0.0001 2, 1 > 3
Slope (df = 1)	NS	NS	NS	NS	NS
Aspect (df = 2)	NS	NS	NS	NS	NS
Distance to unburned forest (df = 1)	NS	F = 3.88 P = 0.0495 Decreasing with increasing distance	NS	F = 7.39 P = 0.0068 Decreasing with increasing distance	NS
Distance to severe-surface burn (df = 1)	NS	NS	NS	NS	NS
Location × patch size (df = 4)	F = 19.09 P = 0.0001	F = 3.88 P = 0.0041	F = 5.35 P = 0.0003	F = 5.22 P = 0.0004	F = 10.85 P = 0.0001
Location × burn severity (df = 4)	F = 2.53 P = 0.0398	F = 6.22 P = 0.0001	F = 7.24 P = 0.0001	**F = 10.04** P = 0.0001	F = 2.92 P = 0.0210
Patch size × burn severity (df = 4)	F = 3.94 P = 0.0037	F = 9.21 P = 0.0001	NS	F = 9.01 P = 0.0001	F = 5.80 P = 0.0001
Location × patch size × burn severity (df = 6)	NS	NS	NS	NS	NS

Notes: Error df = 497. NS indicates that an effect was not significant. Changes through time were significant for all response variables except shrub cover.

† Abbreviations for locations are: C = Cougar Creek, F = Fern Cascades, and L = Yellowstone Lake.

‡ Abbreviations for patch sizes are: L = large, M = moderate, and S = small.

‖ Abbreviations for burn severities are: 1 = light-surface burn, 2 = severe-surface burn, and 3 = crown fire.

not change significantly in light-surface burns. Nonetheless, average biotic cover in crown-fire areas in 1993 was less than that of light-surface burns in 1990.

Percent cover of forbs was largely explained by geographic location and patch size (Table 3). Forb cover was greatest at Yellowstone Lake (Fig. 2). Patch size was next in importance, with forb cover greatest in small patches and lowest in large patches (Fig. 3). Forb cover at Fern Cascades and Yellowstone Lake increased through time, but forb cover did not change significantly at Cougar Creek through time. Burn severity had no effect.

Variation in graminoid cover was also explained primarily by location differences and patch size (Table 3). Graminoid cover was greatest at Cougar Creek and lower at the other locations (Fig. 2). Among patch sizes, graminoid cover was greatest in small patches (Fig. 3). Among burn severity classes, graminoid cover was significantly greater in the surface burns than in crown fires. In areas of light-surface burn, graminoid cover was similar among locations, ranging from ~15 to 20%. Graminoid cover also was negatively correlated with distance from unburned forest (Spearman r_S = −0.31, P = 0.0001).

Most variability in percent cover of tree seedlings (primarily lodgepole pine) was due to differences among study locations (Table 3), with burn severity also contributing. Tree cover was greatest at Cougar Creek (Fig. 2), reaching ~10% by 1993. Fern Cascades had <1% cover of tree seedlings in 1993, and Yellowstone Lake had <0.1% tree seedling cover. Tree seedling cover was greatest in crown-fire and severe-surface burns (Fig. 4). Patch size did not have a significant effect on tree seedling cover, although there was an interaction of patch size and location. At Cougar Creek, where tree seedling cover was highest among locations, cover was substantially greater in the large patch compared to the moderate and small patches. At both Fern Cascades and Yellowstone Lake, however, tree seedling cover was greater in the smaller patches-but it was still extremely low.

Shrub cover was uniformly low in the burned areas and varied primarily with burn severity and the interaction between location and burn severity (Table 3). Shrub cover did not change during the period of study and was greatest in areas of light-surface burn and lowest in crown fires (Fig. 4). Patch size was next in importance, with large patches having more shrub cover than moderate or small patches. Among locations, shrub cover was greater at Cougar Creek than at Fern

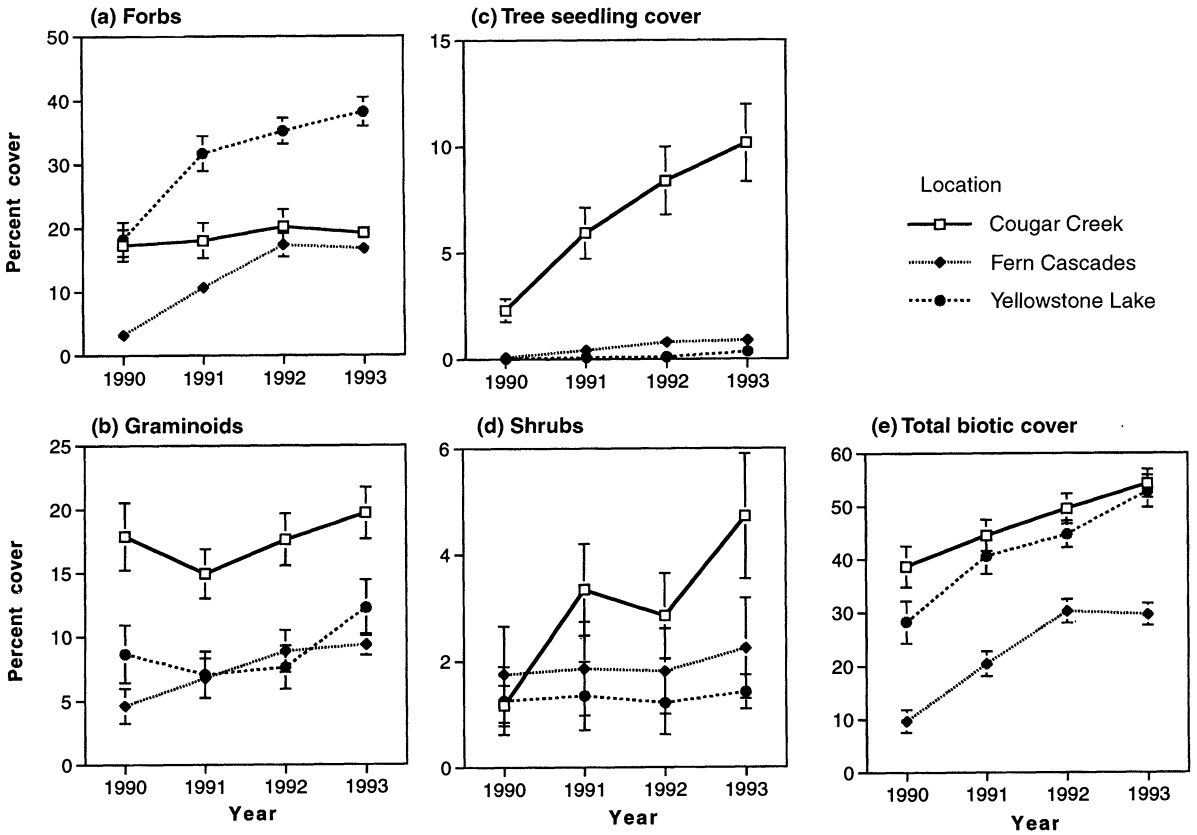

FIG. 2. Percent cover by year at each of the three study locations (Cougar Creek, Fern Cascades, and Yellowstone Lake) in Yellowstone National Park. Data show means ± 2 SE.

Cascades or Yellowstone Lake. Shrub cover was also negatively correlated with distance to the unburned forest edge (Spearman $r_S = -0.15$, $P = 0.0001$).

Lodgepole pine reestablishment

Density of postfire *P. contorta* seedlings did not change between 1990 and 1993, but density of first-year seedlings declined (Fig. 5). Among locations, Cougar Creek had the greatest mean seedling density (11.1 seedlings/m^2), Fern Cascades was lower by two orders of magnitude (0.23 seedlings/m^2), and the Yellowstone Lake location had the lowest density (0.06 seedlings/m^2). The number of prefire serotinous trees within 50 m of the sampling point was the most important variable explaining lodgepole pine seedling density (Table 4), with a positive correlation observed (Table 5). Correlation analysis also revealed interesting variation among locations. Seedling density was positively correlated with number of prefire serotinous individuals at Cougar Creek (Table 5), which had the highest mean serotiny level (65%) among the geographic locations, but the correlation was not significant at Fern Cascades or Yellowstone Lake (Table 5), where mean serotiny and numbers of seedlings were much lower.

Mean seedling density was greatest in severe-surface burns (14 seedlings/m^2) and least in the crown fires and light-surface burns (5 seedlings/m^2). During the four years of the study, seedlings were present at 51–59% of sampling points in light-surface burns, 61–73% in severe-surface burns, and only 34–36% of sampling points in crown fires. Lodgepole pine seedlings always occurred more often than expected in the surface burns, and less often than expected in crown-fire burns ($P < 0.05$ for chi-square analyses for each year). Seedling density was also negatively correlated with distance to the nearest severe-surface burn (Table 5), indicating a potentially important edge effect between burn severity classes.

Patch size was significant but less important (Table 4), and its effect varied among locations. Overall mean seedling density declined with increasing patch size (means of 8.1, 6.8, and 3.9 seedlings/m^2 for large, moderate, and small patches, respectively). At Cougar Creek, seedling density was lower in the small patch than in the moderate or large patch. At Fern Cascades and Yellowstone Lake, however, lodgepole pine seedling density was greater in the small patches than in the large or moderate patches.

Mean density of lodgepole seedlings by annual age class each year indicated that seedling recruitment occurred primarily in 1989 and 1990. Density of first-

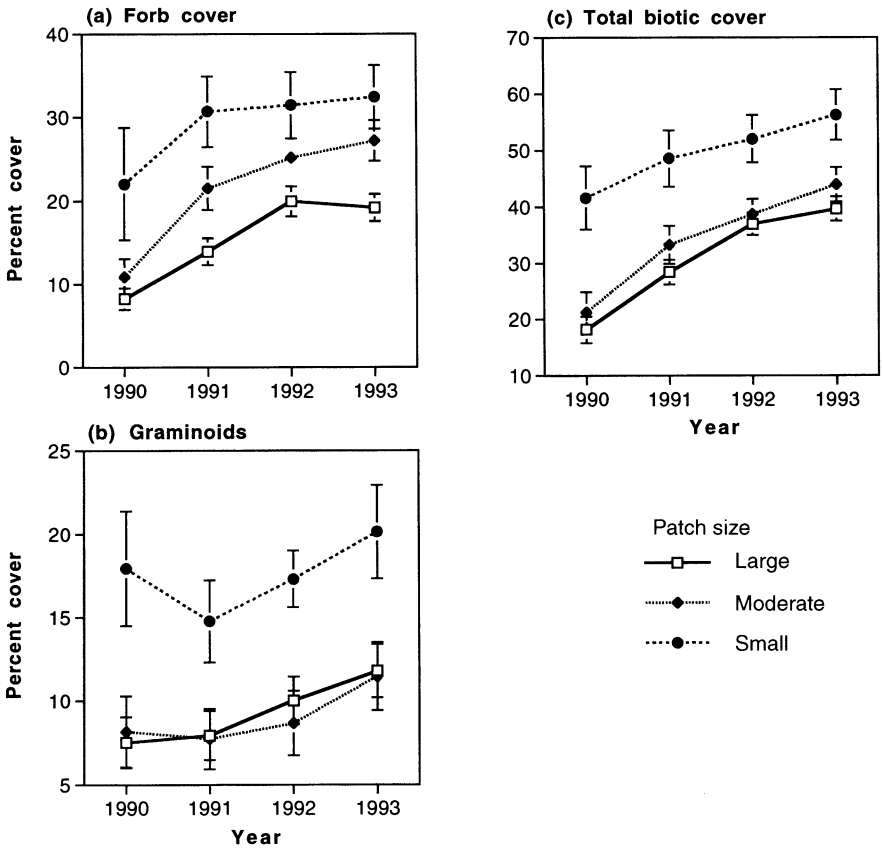

FIG. 3. Percent cover by year for small, moderate, and large burned patches for forb, graminoid, and total biotic cover after the extensive 1988 fires. Data show means ± 2 SE.

year seedlings declined annually from 1.4 seedlings/m^2 in 1990 to 0.01 seedlings/m^2 in 1993 (Fig. 5). As with total seedling density, most variation in first-year seedling density was explained by the number of prefire serotinous individuals, but change through time was significant (Table 4). Examination of the percentage of sampling points containing lodgepole seedlings each year also supported a peak of establishment during the first and second years after the fire. The percentage of sampling points that contained lodgepole pine seedlings was 43% in 1990, 48% in 1991, 46% in 1992, and 45% in 1993, with the same sites generally having seedlings present or absent each year (i.e., new establishment was negligible after 1990).

Reestablishment of forest species

Density of sprouts of forest species.—

1. *Epilobium angustifolium.*—Sprout density across all sampling points increased annually from an average of 4.8 sprouts/m^2 in 1990 to 23.4 sprouts/m^2 in 1993. The ANOVA model fully nested in time for *E. angustifolium* explained 57% of the variance in sprout density (Table 6). Most of the variability in *E. angustifolium* sprout density was explained by differences in location, patch size, and their interactions (Table 6). Sprout density was greatest at the Yellowstone Lake location (Fig. 6). Among patch sizes, sprout density was generally greater in the small and moderate patches compared to the large patches (Fig. 7). Sprout density also varied with burn severity, with densities being greater in the severe-surface burns and crown fires (18.6 and 15.0 sprouts/m^2, respectively) than in light-surface burns (12.2 sprouts/m^2).

2. *Lupinus argenteus.*—The ANOVA model for *L. argenteus* explained only 15% of the variance in sprout density, and most of the variability was due to location and patch size (Table 6). There was no significant difference in sprout density through time. Among locations, *L. argenteus* was most abundant at Yellowstone Lake and Fern Cascades and least abundant at Cougar Creek (Fig. 6). No consistent effect of patch size was observed (Fig. 7). Although burn severity did not explain density of *L. argenteus* sprouts, it did relate to its presence at a sampling point. Chi-square analysis for each year indicated that sprouts of *L. argenteus* were always present more than expected in light-surface burns, as expected in severe-surface burns, and less than expected in crown-fire burns (all χ^2 tests significant at $P < 0.05$).

3. *Arnica cordifolia.*—Density of *A. cordifolia* sprouts increased through time and was explained primarily by differences in location and patch size (Table

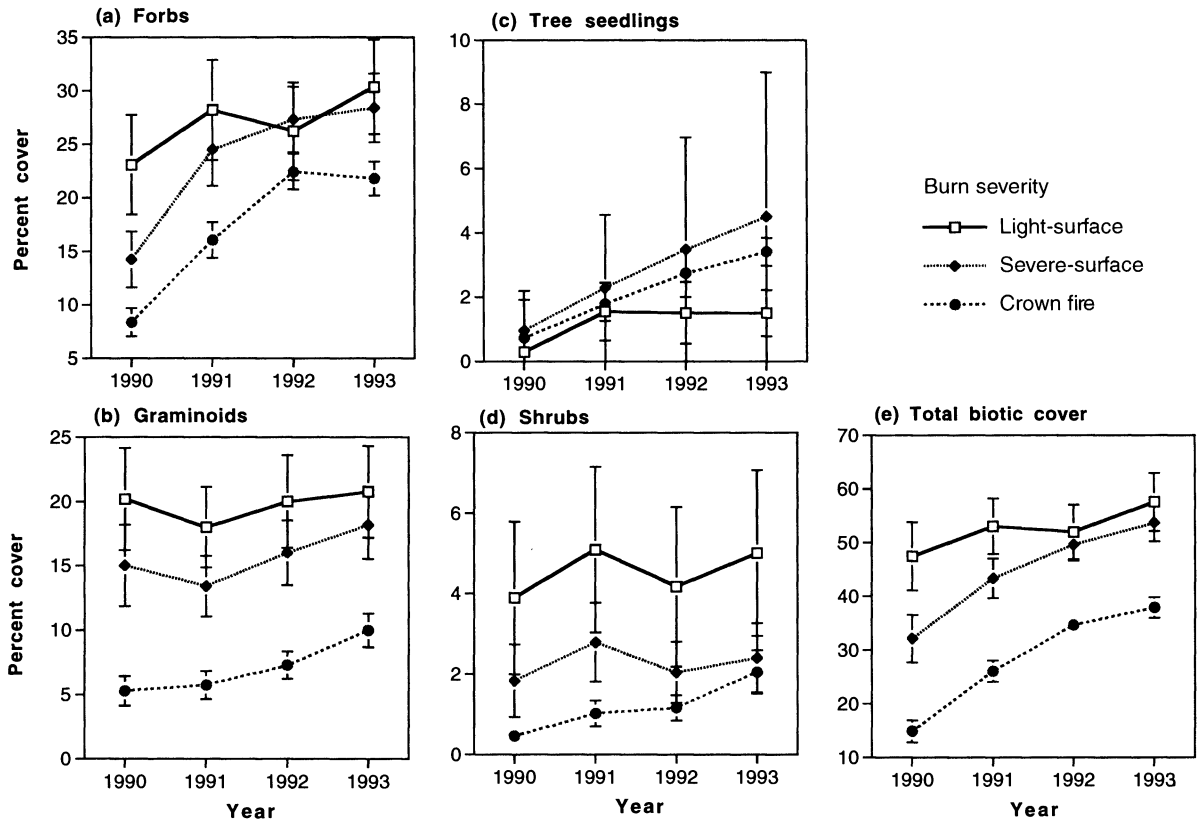

FIG. 4. Percent cover by year for the three burn severity classes. Data show means ± 2 SE.

6). Among locations, *A. cordifolia* sprouts were much more abundant at the Yellowstone Lake location than either of the other locations (Fig. 6). Sprouts were also much more abundant in small patches compared to large or moderate patches (Fig. 7).

4. *Vaccinium scoparium.*—Sprout density of *V. scoparium* was explained primarily by burn severity and location (Table 6). Sprout density clearly declined with increasing burn severity, varying over an order of magnitude (Fig. 8). Among locations, density was highest at the Yellowstone Lake location and lowest at Cougar Creek (Fig. 6). Among patch sizes, density was greatest in small patches and least in the large patches (Fig. 7).

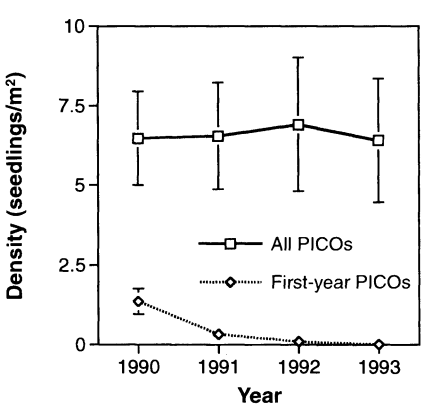

FIG. 5. Mean density of *Pinus contorta* (PICO) seedlings across all sampling points by year. "All PICOs" refers to all seedlings that germinated following the 1988 fires. The first-year PICOs are those seedlings that germinated during the indicated year. Data show means ± 2 SE.

5. *Carex rossii.*—Sprout density of *C. rossii* did not change significantly through time. Variation in the density of *C. rossii* sprouts was explained primarily by location, patch size, and distance from the nearest unburned forest and severe-surface burn (Table 6). Cougar Creek had the greatest sprout density, Fern Cascades was intermediate and Yellowstone Lake the lowest (Fig. 6). *C. rossii* sprouts were most abundant in large patches and lower in the moderate and small patches (Fig. 7). Sprout density was greater in the more severe burns and increased with distance from the nearest unburned forest and severe-surface burn.

6. *Carex geyeri.*—Density of sprouts of *C. geyeri* varied primarily in response to location and patch size with burn severity also an important main effect (Table 6). In contrast to *C. rossii, C. geyeri* was most abundant at the Yellowstone Lake and Fern Cascades locations and least abundant at Cougar Creek (Fig. 6). *C. geyeri* sprouts were more abundant in small patches than in moderate or large patches (Fig. 7), and more abundant in light-surface burns (5.5 sprouts/m^2) than in severe-surface burns (3.1 sprouts/m^2) or crown fires (0.54

TABLE 4. Summary of significant between-sample-points effects on postfire density of lodgepole pine (*Pinus contorta*, PICO) seedlings from repeated-measures ANOVA. Trends are indicated for main effects.

Effect	All postfire PICO seedlings			First-year PICO seedlings		
	F	*P*	Trend	*F*	*P*	Trend
Location† (df = 2)	15.80	0.0001	C > F > L		NS	M > L, S
Patch size‡ (df = 2)	3.70	0.0255	L > M > S	12.53	0.0001	2, 1 > 3
Burn severity‖ (df = 3)	12.42	0.0001	2 > 3, 1	12.98	0.0001	
Distance to severe-surface burn (df = 1)	5.07	0.0249	negative		NS	
Number of serotinous individuals surrounding the sampling point (df = 1)	69.12	0.0001	positive	45.40	0.0001	
Location × patch size (df = 4)	10.22	0.0002		19.77	0.0001	
Location × burn severity (df = 4)	16.21	0.0001		7.63	0.0001	
Patch size × burn severity (df = 4)		NS		5.27	0.0004	
Location × patch size × burn severity (df = 6)	2.96	0.0078		5.51	0.0001	

Notes: Error df = 388. For all postfire seedlings, overall model $r^2 = 0.64$, and change through time was not significant; for first-year seedlings, overall model $r^2 = 0.51$, and change through time was significant.

† Abbreviations for locations are: C = Cougar Creek, F = Fern Cascades, and L = Yellowstone Lake.

‡ Abbreviations for patch sizes are: L = large, M = moderate, and S = small.

‖ Abbreviations for burn severities are: 1 = light-surface burn, 2 = severe-surface burn, and 3 = crown fire.

sprouts/m^2). Sprouts also were most abundant on southerly aspects.

Density of seedlings of forest species.—

1. *Epilobium angustifolium.*—Variation in seedling density of *E. angustifolium* was explained primarily by location and the interaction of location and patch size (Table 7). Seedlings were most abundant at the Yellowstone Lake location (6.8 seedlings/m^2) and least abundant at Fern Cascades and Cougar Creek (~1.4 seedlings/m^2). Among patches, seedling density was greater in the small and moderate patches compared to the large patches. Seedling density did not vary with burn severity, and the presence of sprouts of *E. angustifolium* during 1990 or 1991 did not explain variation in seedling density (Table 7).

2. *Lupinus argenteus.*—Variation in *L. argenteus* seedling density was explained almost exclusively by the presence of sprouts at the sampling point in 1990 or 1991 (Table 7). Seedling densities were much higher when sprouts were present than when they were absent (Fig. 9). Other effects that were significant, but not nearly as important, included location (with Fern Cascades having more seedlings than the other two locations) and patch size (greater density in large and moderate patches than in small).

3. *Carex spp.*—Only 6% of the variance in density of *Carex* seedlings was explained in the statistical model ($r^2 = 0.06$, df = 44/2240, MSE = 0.42, $F = 3.29$, $P = 0.0001$). Most of the variation was explained by the presence of *Carex* sprouts at the sampling point in 1990 and 1991. Differences among locations, years, and the interaction between location and year were the only other significant variables. Burn severity and patch size had no effect.

Presence/absence of Epilobium *and* Lupinus.—In addition to analyzing the density of sprouts and seedlings, we also examined simply the presence of sprouts and seedlings of *E. angustifolium* and *L. argenteus* through time and as a function of burn severity. Although the proportion of sampling points at which each species was present increased during the sampling period, *E. angustifolium* was much more ubiquitous. By 1993, *E. angustifolium* sprouts were present at nearly 90% of the sampling points in crown fires but *L. argenteus* sprouts were present at only ~20% (Fig. 10). However, the proportion of sampling points with seedlings present peaked in 1991 for both species and was quite low by 1993 (Fig. 10). Indeed, we observed very few seedlings of any species in 1993.

Opportunistic species

Between 19 and 46% of the variance in density of opportunistic species was explained by main effects of

TABLE 5. Spearman rank-order correlation coefficients (*r*) between square root of mean seedling density of *Pinus contorta* during 1990–1993 and (a) the numbers of prefire serotinous individuals within a 50-m radius of the sampling point and (b) distance to the nearest surface burn (m) at each sampling point. Significant correlations are highlighted in boldface type.

Variable	Statistic	All locations	Cougar	Fern	Lake
a) Number serotinous individuals	r_S	**0.56**	**0.45**	0.05	0.10
	P	0.0001	0.0001	0.4890	0.3203
	n	454	156	208	90
b) Distance to severe-surface burn	r_S	**−0.23**	**−0.23**	**−0.50**	**−0.39**
	P	0.0001	0.0001	0.0001	0.0001
	n	594	169	230	195

TABLE 6. Summary of tests for between-sample-points effects on postfire density of sprouts of forest species from repeated-measures ANOVA. Entries indicate the F and P values for significant effects, and trends for main effects. The two most important effects per column are shown in boldface type.

Effect	*Epilobium angustifolium*	*Lupinus argenteus*	*Arnica cordifolia*	*Vaccinium scoparium*	*Carex rossii*	*Carex geyeri*
Overall r^2 for ANOVA fully nested in time	0.57	0.15	0.32	0.23	0.23	0.44
Location† (df = 2)	**F = 52.42** P = 0.0001 L > F, C	**F = 7.85** P = 0.0004 L, F > C	**F = 57.27** P = 0.0001 L > C > F	**F = 16.99** P = 0.0001 F, L > C	**F = 12.32** P = 0.0001 C > F > L	**F = 99.41** P = 0.0001 L, F > C
Patch size‡ (df = 2)	F = 3.50 P = 0.0311 S, M > L	**F = 5.15** P = 0.0061 L, S > M	**F = 9.91** P = 0.0001 S > L > M	F = 8.52 P = 0.0002 S > M > L	F = 9.44 P = 0.0001 L > M, S	**F = 80.18** P = 0.0001 S > M, L
Burn severity‖ (df = 2)	F = 10.02 P = 0.0001 3, 2 > 1	NS	F = 4.73 P = 0.0092 1, 2 > 3	**F = 18.60** P = 0.0001 1 > 2 > 3	F = 3.23 P = 0.0402 2, 3 > 1	F = 52.66 P = 0.0001 1 > 2 > 3
Aspect (df = 2)	NS	NS	NS	NS	NS	F = 4.06 P = 0.0178 Greatest on southerly
Distance to unburned forest (df = 1)	NS	NS	NS	NS	F = 9.04 P = 0.0028 Increases with distance	NS
Distance to severe-surface burn (df = 1)	NS	NS	NS	NS	**F = 10.35** P = 0.0014 Increases with distance	NS
Location × patch size (df = 4)	**F = 21.19** P = 0.0001	NS	NS	F = 5.16 P = 0.004	F = 4.61 P = 0.0012	F = 24.34 P = 0.0001
Location × burn severity (df = 4)	NS	NS	NS	F = 5.85 P = 0.0001	F = 2.89 P = 0.0218	F = 17.10 P = 0.0001
Patch size × burn severity (df = 4)	F = 6.72 P = 0.0001	F = 4.67 P = 0.0010	NS	F = 10.06 P = 0.0001	F = 3.98 P = 0.0034	F = 16.07 P = 0.0001
Location × patch size × burn severity (df = 7)	F = 2.49 P = 0.0161	F = 2.64 P = 0.0108	F = 3.42 P = 0.0014	NS	F = 2.51 P = 0.0153	F = 2.20 P = 0.330

Notes: Error df = 499. NS indicates that an effect was not significant. Changes through time were significant for all response variables except *Lupinus argenteus* and *Carex rossii*.

† Abbreviations for locations are: C = Cougar Creek, F = Fern Cascades, and L = Yellowstone Lake.

‡ Abbreviations for patch sizes are: L = large, M = moderate, and S = small.

‖ Abbreviations for burn severities are: 1 = light-surface burn, 2 = severe-surface burn, and 3 = crown fire.

location, patch size, burn severity, and year, as well as interaction effects (Table 8). Three of the four opportunistic species increased in abundance through time (Table 8), some reaching densities approaching 50 × 10^3 stems/ha. Density of three of the four opportunistic species varied among locations. The two native annuals, *Gayophytum diffusum* and *Collinsia parviflora,* were most abundant at the Cougar Creek location, less at Fern Cascades, and least abundant at the Yellowstone Lake location. Of the exotic perennials, *Cirsium arvense* was most abundant at the Yellowstone Lake location, reaching mean densities of ~1100 stems/ha, whereas *Lactuca serriola* did not differ in density among locations (Table 8).

Patch size influenced the density of the native annuals but not the exotic perennials (Table 8). *G. diffusum* and *C. parviflora* were more abundant in the large and moderate patches compared to the small patches (Fig. 11a, b). Burn severity was important for three of the four opportunistic species, and the direction of the effect was the same: density was greatest with the more severe crown-fire burns (Table 8). *C. arvense* was increasing through time in all burn severities, although density was lowest in the light-surface burns and greater in the stand-replacing burns (Fig. 11c). Density of *L. serriola* was negligible in the light-surface burns and peaked in the stand-replacing burns in 1991 (Fig. 11d). *G. diffusum* was most abundant in crown-fire burns, and *C. parviflora* showed no response to burn severity.

For the two native annuals, there was a significant interaction between burn severity and location. *G. diffusum* was always more abundant in the more severe burns, but was decreasing through time at Cougar Creek and Fern Cascades between 1991–1993 and increasing at Yellowstone Lake. *C. parviflora* was most abundant in the crown-fire and severe-surface burns at Cougar Creek and Fern Cascades, but at Yellowstone

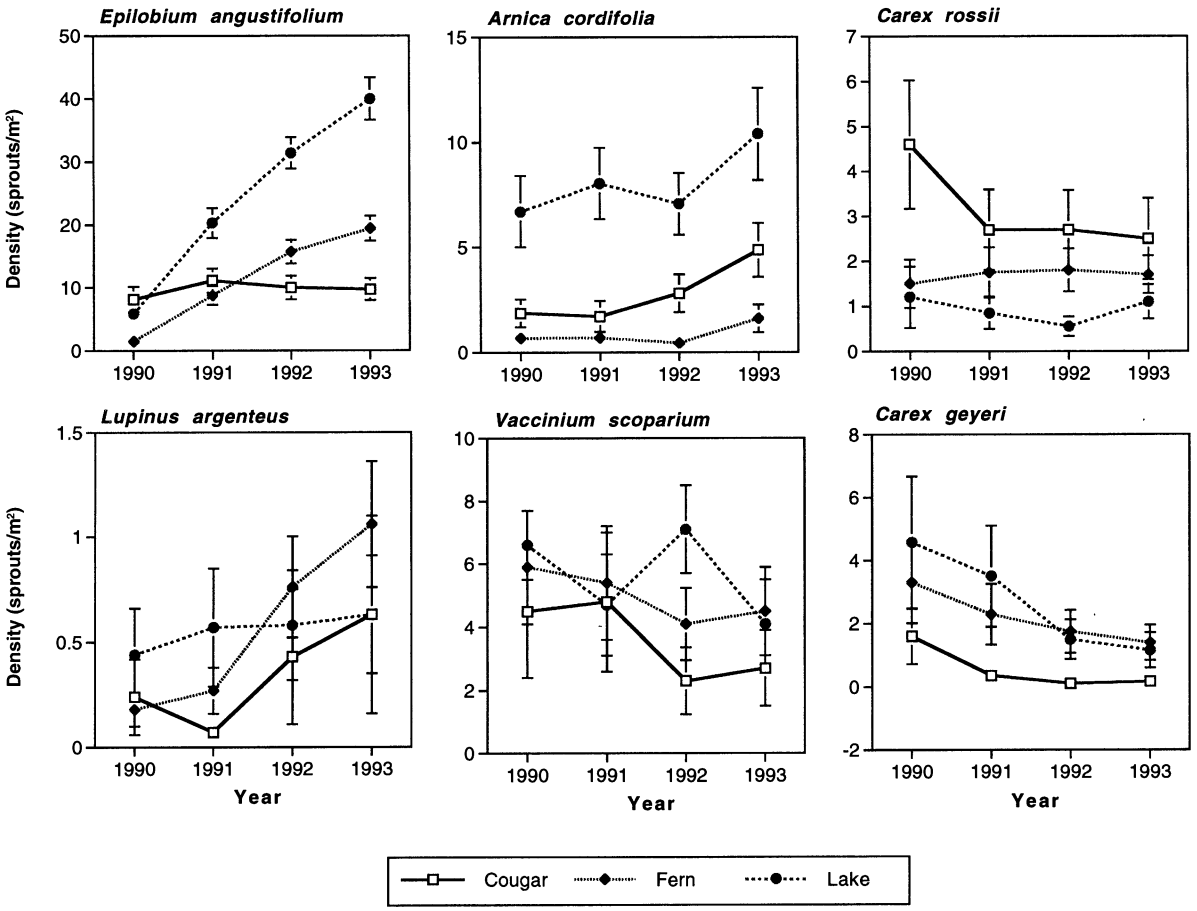

FIG. 6. Annual density of sprouts of five forest species by study location. Data show means ± 2 SE.

Lake was notably more abundant in severe-surface burns than in crown fires. In addition, neither species ever occurred in light-surface burns at Yellowstone Lake.

Species richness

Species richness from 1991 through 1993 varied primarily by year, location, and patch size (Table 9). Overall richness increased through time, averaging 7.3 species per 8-m² plot across all sampling points in 1991 and 11.8 species per plot in 1993. Among the three study locations, species richness was lowest at Fern Cascades and similar at Cougar Creek and Yellowstone Lake (Fig. 12a). Among patch sizes, small patches contained the greatest number of species, followed by large and then moderate patches (Fig. 12c). Species richness was also influenced by burn severity (Table 9), with greater richness observed in the less severe burns (Fig. 12b). Burn severity also contributed to significant interaction effects with location and patch size, however (Table 9). At Cougar Creek, species richness was similar across all burn severities (10.4–11.4 species). At the Yellowstone Lake location, however, species richness decreased with increasing burn severity (average of 15.9, 12.6, and 10.1 species for the light-surface, severe-surface, and crown fires, respectively). At Fern Cascades, species richness was similar in the surface burns (9.4 and 8.3 species for light- and severe-surface burns) and lower in areas of crown fire (6.3 species). The interaction effect between burn severity and patch size reflected a decline in species richness with increasing burn severity in the moderate patches (11.9, 8.8, and 6.4 species for the light-surface, severe-surface, and crown fires, respectively). Species richness was not influenced by slope, aspect, distance to the nearest unburned forest, or distance to the nearest severe-surface burn (Table 9).

We observed a high degree of similarity between years at each sample point (i.e., similarity between 1991 and 1992 and between 1992 and 1993), averaging between 0.837 and 0.915 (Table 10). This high similarity suggests that most species present at a point persisted between years. Some of the variance in between-year similarity was explained by differences in location (ANOVA for similarity index results for 1991 vs. 1992: $r^2 = 0.15$, df = 25/515, MSE = 0.122, $F = 3.64$, $P = 0.0001$; ANOVA for similarity index results for 1992 vs. 1993: $r^2 = 0.20$, df = 25/551, MSE = 0.157, $F =$

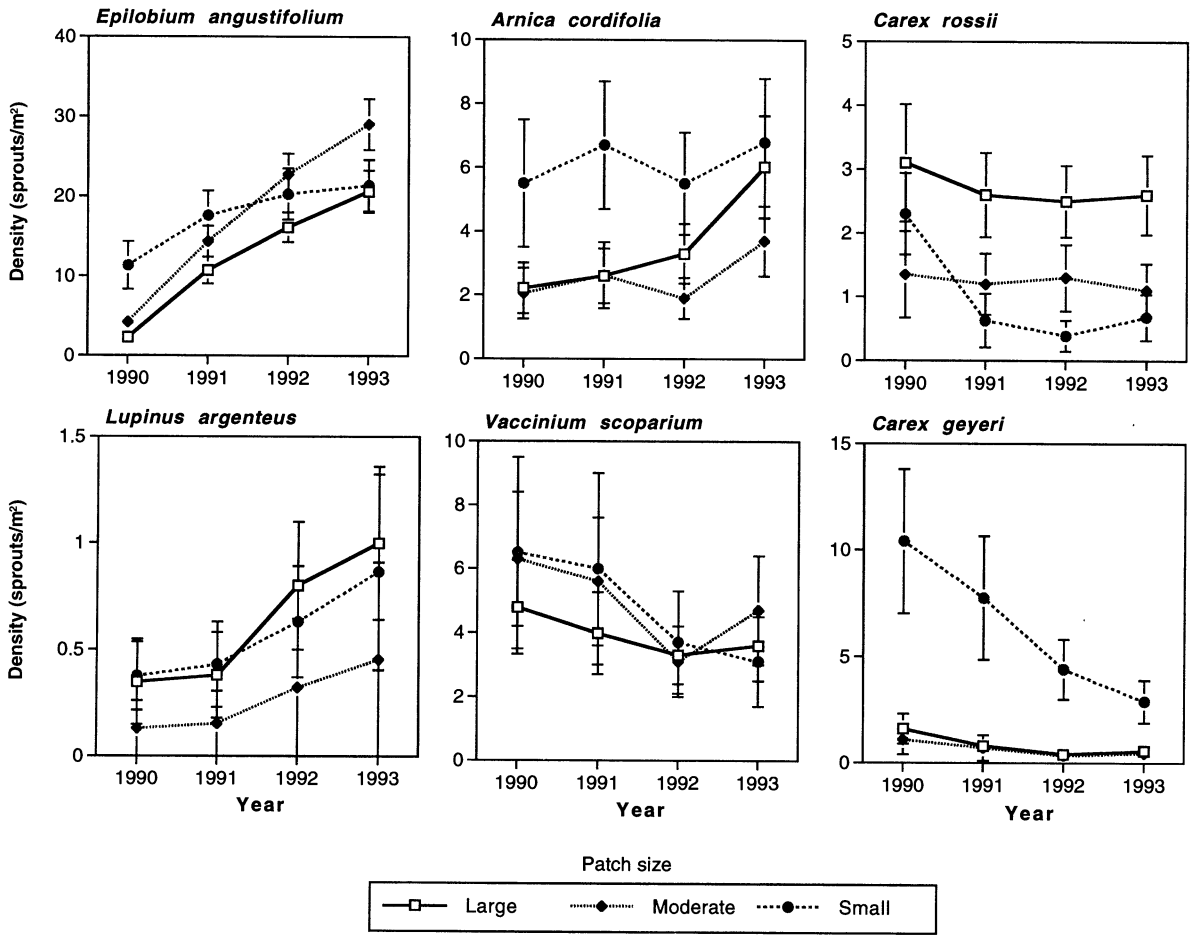

FIG. 7. Annual density of sprouts of five forest species by patch size. Data show means ± 2 SE.

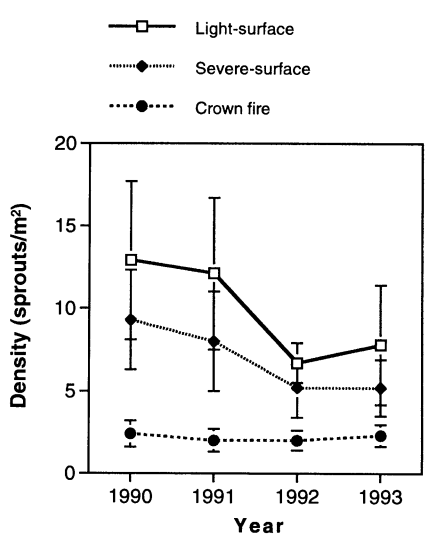

FIG. 8. Mean annual density of *Vaccinium scoparium* sprouts by burn severity. Data show means ± 2 SE.

5.61, $P = 0.0001$). The Cougar Creek and Fern Cascades locations had higher between-year similarities than did the Yellowstone Lake location (Table 10), indicating more community-level change at Yellowstone Lake. The Cougar Creek location also had the narrowest range of similarity values, with a minimum value of 0.61 compared to 0.40 for the other two locations (Table 10). Between-year similarity was not influenced by burn severity or by patch size, suggesting that the rates of change in species composition were affected primarily by broad-scale environmental gradients captured by differences among locations.

DISCUSSION

We organize our discussion by first addressing the results for particular biotic response variables, focusing especially on the differential traits among species that may explain observed responses. We then synthesize our findings to address the general question of how fire size and pattern influence early secondary succession.

Trends in biotic response variables

Biotic cover.—Biotic cover generally responded as we hypothesized (Table 1), but more complex patterns

TABLE 7. Summary of tests for between-sample-points effects on postfire density of first-year seedlings of forest species from repeated-measures ANOVA. Entries indicate the F and P values for significant effects, and trends for main effects. The two most important effects are highlighted in boldface type.

Effect	*Epilobium angustifolium*	*Lupinus argenteus*
Overall r^2 for ANOVA fully nested in time	0.41	0.24
Location† (df = 2)	**F = 46.58** P = 0.0001 L > F, C	F = 3.99 P = 0.0190 F > C, L
Patch size‡ (df = 2)	F = 4.08 P = 0.0174 S > M > L	**F = 4.03** P = 0.0183 L, M > S
Burn severity‖ (df = 2)	NS	NS
Presence of sprouts in 1990 or 1991 of this species (df = 1)	NS	**F = 26.33** P = 0.0001 Greater when sprouts present
Slope (df = 1)	NS	NS
Aspect (df = 2)	NS	NS
Distance to unburned forest (df = 1)	NS	NS
Distance to severe-surface burn (df = 1)	NS	NS
Location × patch size (df = 4)	**F = 5.56** P = 0.0002	NS
Location × burn severity (df = 4)	F = 4.24 P = 0.0022	NS
Patch size × burn severity (df = 4)	F = 3.90 P = 0.0040	NS
Location × patch size × burn severity (df = 7)	F = 2.17 P = 0.0359	NS

Notes: Error df = 498. NS indicates that an effect was not significant. Changes through time were significant for both species.

† Abbreviations for locations are: C = Cougar Creek, F = Fern Cascades, and L = Yellowstone Lake.

‡ Abbreviations for patch sizes are: L = large, M = moderate, and S = small.

‖ Abbreviations for burn severities are: 1 = light-surface burn, 2 = severe-surface burn, and 3 = crown fire.

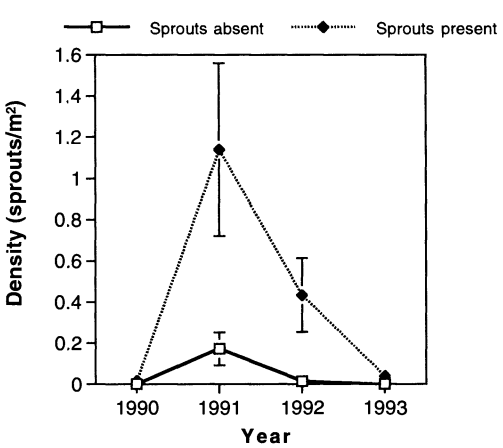

FIG. 9. Seedling density of *Lupinus argenteus* on sampling points that did or did not contain sprouts of *L. argenteus* during 1990 or 1991. Data show means ± 2 SE.

emerged. Local differences in plant community composition were important in interpreting cover patterns. For example, the Yellowstone Lake and Cougar Creek locations had comparable total biotic cover, but for different reasons. Forbs contributed substantially to total cover at Yellowstone Lake, but tree seedling cover was extremely low. In contrast, tree seedling cover dominated at Cougar Creek, but forb cover was relatively low.

The effect of patch size on biotic cover was as hypothesized for total, forb, graminoid, and shrub cover (Table 1), with more cover observed in small than in large patches. Surprisingly, tree seedling cover exhibited the opposite trend. We suspect that increased light availability in large patches plus potentially less competition from herbaceous flora may help explain this result. The 1-ha patches were more shaded by the surrounding forest and had more herbaceous cover, which together may limit tree seedling growth. Although we did not measure the size of lodgepole seedlings through

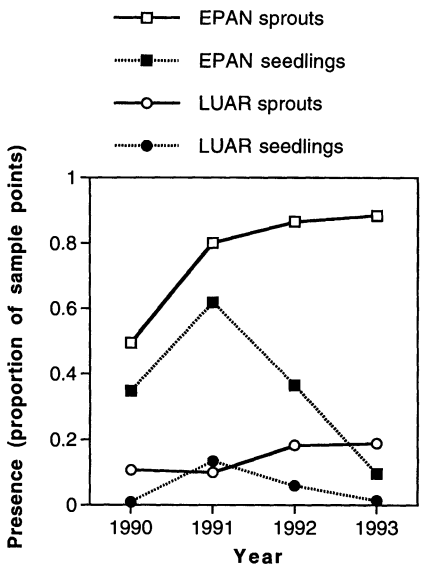

FIG. 10. Proportion of sampling points for crown-fire burn severity on which postfire seedlings and sprouts and seedlings of *Epilobium angustifolium* (EPAN) and *Lupinus argenteus* (LUAR) were present in each year following extensive forest fire in Yellowstone National Park in 1988.

time, individual plants may grow more rapidly in open areas (J. E. Anderson, *personal communication*).

The strong effect of burn severity on shrub cover and lack of any significant changes through time probably reflect the slow-growing habit of *Vaccinium scoparium*, the dominant shrub. We never observed a *Vaccinium scoparium* seedling in either burned or unburned forests in Yellowstone, although we observed berries with viable seeds on plants in unburned forests (Romme et al. 1995); this response is not unusual for *Vaccinium* spp. or ericaceous shrubs in general (Matlack et al. 1993, Motzkin et al. 1996). All postfire shrub regeneration to date appeared to be vegetative. Hence, shrubs grew only in areas in which they occurred prior to the fire, and cover was strongly influenced by local fire severity. Rhizomes of mature *Vaccinium scoparium* are in the litter and upper soil layers, where they are especially vulnerable to fire damage.

Lodgepole pine reestablishment.—In contrast to our expectation (Table 1), lodgepole pine seedling density was greatest in areas of severe-surface burn rather than in crown fires, although tree seedling cover did not differ between these two severities of stand-replacing burn. Lodgepole pine seedlings germinate best in full sunlight and exposed mineral soil, and the more open-grown seedlings in the crown fires may have grown more rapidly than the more crowded seedlings in the severe-surface burns. However, spatial variation in seedling density as a function of burn severity in stand-replacing fires has only recently been reported (Anderson and Romme 1991). Fire intensities and spread rates in severe-surface burns may have been optimal for the opening of serotinous cones and release of seed, but fire conditions in severe crown fires may have resulted in cone ignition or substantially reduced seed

TABLE 8. Summary of analysis of variance results for density of opportunistic species and trends in between-subject effects.

	Native annuals		Exotic perennials	
	Gayophytum diffusum	*Collinsia parviflora*	*Cirsium arvense*	*Lactuca serriola*
a) Full model ANOVA nested in time				
r^2	0.46	0.39	0.30	0.19
df	130/1963	130/1963	130/1963	130/1963
MSE	223.46	95.23	21.85	4.70
F	12.73	9.74	6.61	3.45
P	0.0001	0.0001	0.0001	0.0001
b) Between-subject effects from repeated-measures ANOVA				
Year	increasing	increasing	increasing	NS
Location†	C > F > L	C > F, L	L > F, C	NS
Patch‡	L > M, S	L > M, S	NS	NS
Burn severity‖	3 > 2, 1	NS	3 > 2 > 1	3 > 2 > 1
Slope	NS	NS	NS	NS
Dist. to light-surface	NS	positive	NS	NS
Dist. to severe-surface	NS	NS	NS	positive
Aspect	NS	NS	NS	NS
Location × patch	NS	***	NS	NS
Location × burn	***	***	NS	NS
Patch × burn	NS	NS	NS	NS
Location × patch × burn	NS	NS	NS	NS

*** $P < 0.0001$; NS = not significant.

† Abbreviations for locations are: C = Cougar Creek, F = Fern Cascades, and L = Yellowstone Lake.

‡ Abbreviations for patch sizes are: L = large, M = moderate, and S = small.

‖ Abbreviations for burn severities are: 1 = light-surface burn, 2 = severe-surface burn, and 3 = crown fire.

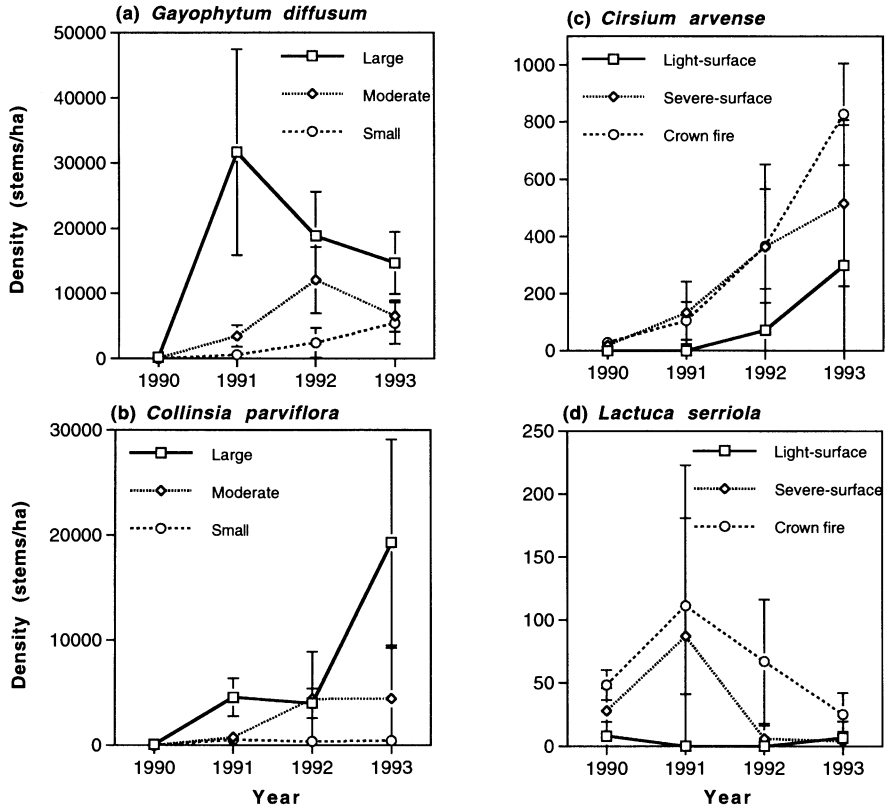

FIG. 11. Effects of patch size and burn severity on density of opportunistic species: two native annuals, *Gayophytum diffusum* and *Collinsia parviflora,* influenced by patch size; and two exotic species, *Cirsium arvense* and *Lactuca serriola,* influenced by burn severity. Data show means ± 2 SE.

viability (Johnson and Gutsell 1993). Rather than unburned forest, it was these severe-surface burns that served as the major seed source for stand regeneration in crown fires, as illustrated by the negative correlation of seedling density and distance to severe-surface burn. Some seeds also survived in most crown fires, especially where serotiny was high, as pine seedlings were found in areas even >200 m from the nearest severe-surface burn.

Lodgepole pine seedling density did not change between 1990 and 1993. Within-stand variability in ages for lodgepole pine stands that regenerate following stand-replacing fires is generally low (Horton 1953, Tande 1979, Muir 1993). In areas of high serotiny, lodgepole pine recruitment may continue through the first decade following fire, as ~10–15 yr of cones may be available to supply seeds (Johnson and Fryer 1989). The duration of time over which present spatial variation in lodgepole pine seedling density will persist across the YNP landscape is not known. The density

TABLE 9. Summary of repeated-measures analysis of variance for species richness in burned forests of the Yellowstone Plateau as measured from 1991 to 1993.

Effect	df	MSE	*F*	*P*
Location	2	1640.2	72.14	0.0001
Patch size	2	1090.2	47.95	0.0001
Burn severity	3	186.6	8.21	0.0001
Slope	1	1.9	0.09	0.7672
Distance to unburned forest	1	0.6	0.03	0.8688
Distance to severe-surface burn	2	44.3	1.95	0.1632
Aspect	2	20.1	0.88	0.4139
Location × patch size	4	73.9	3.25	0.0119
Location × burn severity	4	216.9	9.54	0.0001
Patch size × burn severity	4	146.4	6.44	0.0001
Location × patch size × burn severity	7	76.1	3.35	0.0017
Error	544	22.7		

Note: Overall $r^2 = 0.60$ for ANOVA fully nested in time.

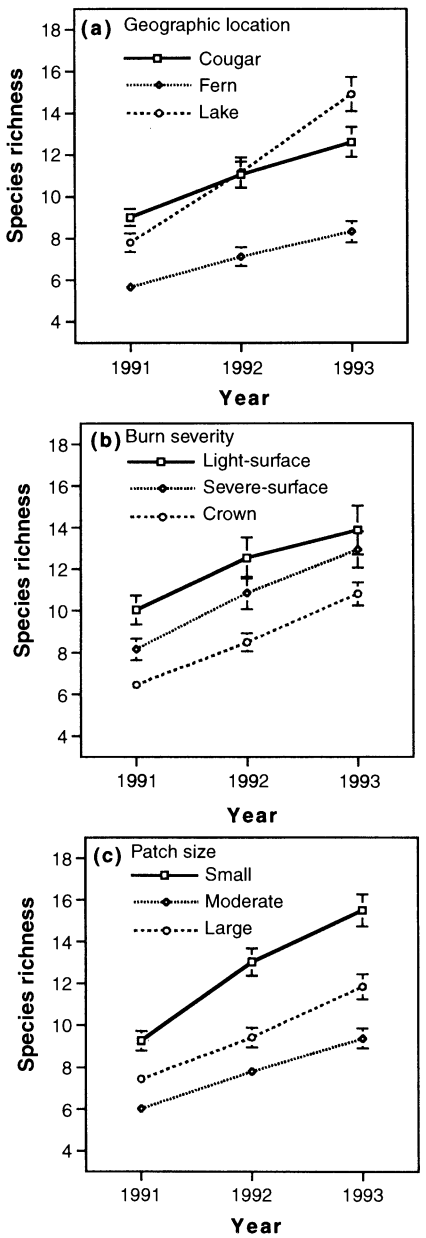

FIG. 12. Annual species richness in burned forests of the Yellowstone Plateau: (a) by location, (b) by burn severity, and (c) by patch size. Data show means ± 2 SE.

of older lodgepole stands varied substantially across the YNP landscape, and these variations in tree density within stands of similar age may have resulted, at least in part, from the spatial heterogeneity of burn severities in past fires.

Lodgepole seedling density was positively related to the number of prefire serotinous trees surrounding the sampling point (see also Tinker et al. 1994). Any particular stand of lodgepole pine may contain a mixture of serotinous trees and trees having cones that open at maturity. The percentage of serotinous trees is extremely variable in Greater Yellowstone, ranging from 0 to

TABLE 10. Values of similarity index comparing species richness at individual sampling points between years for the three study locations.

Statistic	Cougar Creek	Fern Cascades	Yellowstone Lake
a) Similarity index for 1991 vs. 1992			
Mean	0.884	0.867	0.810
N	156	214	188
SD	0.088	0.116	0.121
Minimum	0.615	0.400	0.400
Maximum	1.000	1.000	1.000
b) Similarity index for 1992 vs. 1993			
Mean	0.915	0.903	0.837
N	168	226	200
SD	0.080	0.087	0.111
Minimum	0.667	0.500	0.400
Maximum	1.000	1.000	1.000

72% and being greatest at low-to-mid elevation (1900–2300 m) sites (Lotan 1975, Ellis et al. 1994). The three locations we studied varied from a mean of 2% serotinous trees at Yellowstone Lake to 65% at Cougar Creek (Table 2). Tinker et al. (1994) found scale-dependent variation in the occurrence of serotinous cones in YNP, with low variability in percent serotiny observed across short distances (<1 km) and large distances (>10 km) and high variability over intermediate distances (1–10 km). The strong differences in lodgepole seedling density among our three geographic locations reflected broad-scale patterns of variability in serotiny levels.

Reestablishment of forest species.—Forest species responded individualistically to the 1988 fires. Some species (e.g., *Lupinus argenteus, Vaccinium scoparium,* and *Carex geyeri*) demonstrated a negative relationship between sprout density and fire severity. Other species, (e.g., *Epilobium angustifolium* and *Arnica cordifolia*), achieved greater sprout densities in more severe burns. Differences in depth distribution of rhizomes in the soils may be most important for survival and subsequent resprouting of individuals and species (Granstrom and Schimmel 1993).

Epilobium angustifolium plants readily survive fire and produce great quantities of easily dispersed seeds that germinate quickly in open sites. Dormant buds at depths of 2–8 cm sprout during the first or second subsequent growing season. Seed dispersal may extend over hundreds of kilometers (Archibold 1980, Solbreck and Andersson 1986), and seeds germinate promptly in suitable growing conditions (Granstrom 1987, Romme et al. 1995). *E. angustifolium* flowered profusely in YNP in 1990 and appeared to reach its peak in 1991 when it formed thick patches of waist-high, flowering stems in many areas. Subsequently, its stature decreased, flowering declined, and density of seedlings was reduced.

Lupinus argenteus appears relatively poorly adapted to fire, having heavy seeds with limited dispersal capabilities (Wood and del Moral 1988) that require scar-

ification to ensure rapid germination (Oberbauer and Miller 1982, Romme et al. 1995). Following the fires, *L. argenteus* plants sprouted in many areas of YNP and were subsequently surrounded by seedlings. On sites where adults were killed or were absent before the fires, however, *Lupinus* was rare or absent by the end of our study.

Local dispersal from reproductive plants that survived the fire appeared to be the dominant mechanism for seedling establishment of forest herbs. Although long-distance dispersal is not typically required for initial colonization in small disturbed patches (e.g., <0.5 ha; Holt et al. 1995), we were surprised by the relative unimportance of long-distance dispersal for forest species in the larger patches. However, seedling densities varied considerably among the three geographic locations, suggesting that seed sources may vary substantially across the Yellowstone Plateau—likely due to prefire species distributions. When combined with our anecdotal observations of the spatial distribution of other forest species (e.g., *Hieracium albiflorum, Calamagrostis canadensis, Calamagrostis rubescens*), postfire vegetation patterns suggested that seed dispersal into the burned areas from the surrounding unburned forest was not an important mechanism for the reestablishment of forest species.

Opportunistic species.—The two native annuals showed a response to patch size, being more abundant in the large than in the small patches, but the exotic perennials did not. The exotics, however, showed a response to burn severity; both were more abundant in the more severely burned areas, and Canada thistle was still increasing in density when our study ended in 1993. We hypothesized no relationship between distance to nearest unburned or light-surface burned area and density of opportunistic species, and this hypothesis was rejected for only one species, *Collinsia parviflora,* which increased with distance. This species may have been better able to establish in the centers of the larger patches where competition from other herbaceous species was reduced.

The annual species (*Gayophytum diffusum* and *Collinsia parviflora*) may go through a relatively quick "boom and bust" cycle. Our field observations suggest their abundance may have begun to decline in 1993 when the plants were much smaller and less robust than at their peak in 1991 (M. G. Turner and W. H. Romme, *personal observation*). The exotic Canada thistle, however, showed no sign of decline in 1993 and may have been able to expand its range following the fires.

Species richness.—The number of species per 8-m^2 plot increased significantly during the first 5 yr of postfire succession at all locations. However, there were differences in richness among locations, patch sizes, and burn severity classes. The Yellowstone Lake location had the lowest mean index of similarity from year to year, indicating more rapid addition of new species (or turnover of previous species) in the plant communities in this area. The highest mean similarity index was seen at Cougar Creek, indicating a slow rate of change in plant community composition. The Cougar location also had the greatest lodgepole pine seedling densities, suggesting that dense tree seedlings may have inhibited development of the herbaceous community. However, more experimental studies clearly are needed to establish the mechanisms controlling rate of compositional change.

Richness on a per unit area basis decreased as patch size increased. We originally hypothesized that this would be the case because of reduced seed dispersal from the unburned forest into larger openings. However, in light of our finding that distance from unburned edge was rarely an important variable in predicting densities of sprouts and seedlings, we suggest that the lower species richness observed in larger burned patches may have been a result of relatively more severe abiotic conditions (higher light intensity, evapotranspiration, and diurnal temperature variation) in these environments.

Richness was generally lowest in crown-fire areas, as we hypothesized, but was inconsistent with respect to the other burn classes. At no location did we see highest richness in severe-surface burns, as originally hypothesized. At Cougar Creek and Fern Cascades, there was no significant difference in richness between severe-surface and light-surface burns, whereas at Yellowstone Lake richness was greater in the less severely burned areas. It is possible that the Yellowstone Lake location showed clearer patterns of response to burn severity in part because richness was higher and composition was changing more rapidly there than at either of the other two locations.

Significance of the fire-created pattern for postfire succession

Burn severity and patch size had significant effects on nearly every biotic response variable we measured, suggesting an important influence of the fire-created mosaic on postfire succession. In general, the effects of burn severity in Yellowstone (Table 11) conformed to effects observed elsewhere in the Rocky Mountains (e.g., Habeck and Mutch 1973, Lyon and Stickney 1976, Viereck 1983, Ryan and Noste 1985). The most enduring legacy of the mosaic of burn severities may be spatial variability in lodgepole pine density across the landscape. Areas of severe-surface burn may develop persistent high-density stands of lodgepole pine that grade into areas of lower density. In the shorter term, areas of crown fire provided the best sites for opportunistic species to colonize, although we do not yet know how long they will persist. Our results suggested that the natural variability in fire severity across the landscape is an important source of heterogeneity for the plant community (Table 11).

Patch size influenced early postfire succession in YNP (Table 12), even when no effect was hypothesized

TABLE 11. Synthesis of the effects of fire severity on biotic response variables during early postfire succession in Yellowstone National Park, Wyoming.

Attribute	Crown fire	Low intensity surface fire
Biotic cover	Higher cover of tree seedlings (especially *Pinus contorta*); lower cover of herbs	Higher cover of shrubs and herbs (forbs and graminoids); lower cover of tree seedlings
Density of *Pinus contorta* seedlings	Lower density of seedlings, although the seedlings were generally larger	Higher density of seedlings, but seedlings generally smaller
Density of forest understory species	Higher sprout densities of some forest species (e.g., *Epilobium angustifolia*); lower densities of many others	Higher sprout densities in many forest species (e.g., *Vaccinium scoparium, Lupinus argenteus, Carex geyerii*)
Opportunistic species	Greater densities of opportunists (e.g., *Gayophytum diffusum, Cirsium arvense, Lactuca serriola*)	Lower densities, with the two native annuals (*G. diffusum* and *C. parviflora*) not occurring at all in light-surface burns
Plant species richness	Lower richness of vascular plants	Higher richness of vascular plants

(e.g., for sprout density and species richness). Large patches had greater densities of lodgepole pine seedlings, higher densities of two native annuals considered opportunistic species, lower species richness, and lower cover of herbs. The effect of patch size may be due, in part, to differential fire intensities that generated large and small patches. Previous spatial analyses indicated that the proportion of burned area in crown fire increased with increasing area burned during a day (Turner et al. 1994*b*). Thus, the crown fires that generated our large patches may have burned with greater intensity than the spotty fires that created the small patches of crown fire. Greater fire intensities would lead to reduced survival of the prefire plant community and offer more potential area for colonization by opportunists. Compared with large patches, small patches are likely to provide cooler, moister growing conditions with more shade and wind protection, all of which may enhance plant survival and growth. Snow ablation (i.e., loss by melting or evaporation) in forest openings in southwest Alberta, Canada, also increases with the size of the opening, indicating warmer temperatures and more rapid drying in larger patches (Berry and Rothwell 1992). Thus, patch size effects may also be due, in part, to microclimate conditions.

Despite the statistically and biologically significant effects of fire severity and patch size, geographic location was often the most important independent variable in the statistical analyses, reflecting substantial differences in the plant community among the three study locations (Table 13). Thus, the best predictor of postfire vegetation in YNP may be the prefire vegetation as influenced by stand history and abiotic gradients. Although we were aware of the ranges of elevation, substrate, and forest ages across the three locations at the outset of this study (Table 2), the wide variability in the mean proportion of serotinous lodgepole pines across the landscape was a surprise. Our sites spanned this range of variability, and mean serotiny was strongly related to location. We conclude that the effects of fire size and heterogeneity were important and that at least some will be long lasting, but these landscape-scale effects of fire occurred within an overriding context of gradients, especially in serotiny, on a broader scale.

Succession across much of YNP appeared in 1993

TABLE 12. Synthesis of the effects of patch size on biotic response variables during early postfire succession in Yellowstone National Park, Wyoming.

Attribute	Large patches	Small patches
Biotic cover	Higher cover of woody plants (tree seedlings and shrubs); lower cover of herbs	Higher cover of herbaceous plants (forbs and graminoids); lower cover of trees and shrubs
Density of *Pinus contorta* seedlings	Greater density	Lower density
Density of forest understory species	Higher sprout densities of some forest species (e.g., *Carex rossii*); lower densities of many others	Higher sprout densities of many forest species (e.g., *Vaccinium scoparium, Epilobium angustifolium, Arnica cordifolia,* and *Carex geyerii*)
Opportunistic species	Higher densities of the two native annuals, no effect on the two exotic species	Lower density of the native annuals, some delay in colonizing small patches
Plant species richness	Lower richness of vascular plant species	Higher richness of vascular plant species

TABLE 13. Synthesis of differences among the three study locations (see Table 2) in early postfire succession in Yellowstone National Park, Wyoming.

Attribute	Cougar Creek	Fern Cascades	Yellowstone Lake
Biotic cover	Highest cover of tree seedlings (especially *Pinus contorta*), shrubs (especially *Ceanothus velutinus*), and graminoids (especially *Carex rossii* and *Calamagrostis rubescens*)	Lowest total biotic cover	Highest cover of forbs (especially *Arnica cordifolia* and *Epilobium angustifolium*)
Density of *Pinus contorta* seedlings	Highest	Intermediate	Very low
Density of forest understory species	Higher densities of sprouts of some forest species (e.g., *Carex rossii*); lower densities of others	Higher densities of sprouts of many forest species (e.g., *Vaccinium scoparium, Lupinus argenteus,* and *Carex geyerii*)	Higher densities of sprouts of many forest species (e.g., *Vaccinium scoparium, Epilobium angustifolium, Lupinus argenteus,* and *Arnica cordifolia*)
Opportunistic species	Higher densities of native annuals *Gayophytum diffusum* and *Collinsia parviflora*	Moderate densities of native annuals *Gayophytum diffusum* and *Collinsia parviflora*	Lowest density of native annuals *Gayophytum diffusum* and *Collinsia parviflora*; highest density of exotic *Cirsium arvense*
Plant species richness	High	Low	High

to be moving toward plant communities very similar to those that burned in 1988. For example, dense "dog-hair" thickets of lodgepole pine occurred at Cougar Creek in 1988, and extensive patches of lodgepole pine seedlings >50 stems/m^2 were present in 1993. Prefire stands were more open at Fern Cascades, and pine seedlings in 1993 were substantially less dense (<1 stem/m^2) than at Cougar Creek. Moreover, except for some extremely fire-sensitive, late-successional species like *Linnaea borealis* (Eriksson 1992), all plant species present in unburned forests appeared to occur in nearby burned areas (although densities differed).

Forest reestablishment appeared questionable, however, at our Yellowstone Lake location. In 1993, 5 yr postfire, we found <10 tree seedlings/ha (pine, spruce, and fir combined). Seed viability is <5 yr in lodgepole pine, 3 yr in Engelmann spruce, and only 1 yr in subalpine fir (Archibold 1989, Johnson and Fryer 1989), suggesting that the opportunity for immediate postfire tree seedling establishment had been missed. Different successional trajectories may be initiated within similar abiotic environments because of local variation in disturbance intensity or availability of plant propagules (Glenn-Lewin and van der Maarel 1992, Fastie 1995, Baker and Walford 1995); the paucity of tree seedlings at the Yellowstone Lake location may be due to effects of very severe fire on propagule availability. Reforestation of this area where the local sources for tree seeds were apparently destroyed by the fire will depend on seed dispersal from sources outside the burned area, but much of the 3700-ha large patch is well beyond the effective dispersal distance of conifer seeds (Archibold 1989, Johnson and Fryer 1989). Furthermore, conifer seeds that gradually disperse into the area may be unable to establish because of competition from the well-developed herbaceous community (Lotan and Perry 1983, Coates et al. 1991, Lieffers et al. 1993). Thus, although only from the earliest stages of postfire succession in YNP, our data suggest that pathways of succession potentially leading to nonforest communities were initiated following the 1988 fires.

Concluding remarks

The answer to our question of whether vegetation responses differed between small and large burned patches is not a simple yes or no. Based on our data for early postfire succession, most of the burned forests in YNP appeared to be reestablishing community compositions similar to the prefire vegetation, primarily because extensive biotic residuals persisted even within very large burned areas. Thus, large fires presently are not a threat to plant communities in YNP. Nonetheless, fire size, fire severity, and the spatial heterogeneity of burn severities across the landscape significantly influenced postfire succession. The legacy of variable lodgepole pine density across the landscape and potential conversion from forest to nonforest vegetation in some areas may be detectable for decades to centuries. Further study of these longer term dynamics is clearly needed. Predictability of successional trajectories has received relatively little study (Peet 1992, Wood and del Moral 1993), and it remains challenging to identify the factors controlling vegetation dynamics at multiple spatial scales.

Large fires will likely occur again in YNP, and many other areas in western and northern North America are

covered by vast expanses of coniferous forest subject to infrequent, large, severe fires (Heinselman 1973, Hemstrom and Franklin 1982, Turner and Romme 1994). Understanding the effects of large fires assumes added significance when potential implications of global climate change are considered. Variation in area burned in the Yellowstone region is related to the increased aridity observed there since 1895 (Balling et al. 1992*a, b*). Fire frequency may increase in YNP if the future climate becomes warmer and drier (Romme and Turner 1991, Gardner et al. 1996). Since the late 1970s, there has been a marked increase in the annual extent of wildfires in Canada and the western United States (Van Wagner 1988, Flannigan and Van Wagner 1991 Auclair and Carter 1993), although whether this reflects a global warming trend cannot yet be discerned. Continued research on succession following the 1988 Yellowstone fires should enhance our ability to project future landscape condition under altered fire regimes and provide valuable insight into the patterns and processes expected in other landscapes affected by large infrequent disturbances.

Acknowledgments

We are extremely grateful to the following people who assisted with the field work: Laura Bohland, Teresa Cary, Yvonne Corcoran, Christine Eckhardt, Jeremy Gardner, Nathan Gardner, Sandi Gardner, Dorothy Goigel, Priscilla Golley, John Goodlaxson, Katherine Gould, Gregory Haines, Terri Hargrove, Leonard Hordijk, Sim Huang, Thomas Knight, Susan Lindahl, Stephen Nold, Cyndi Persichetty O'Hara, Michael O'Hara, Anita Parker, Mitzi Pearson, Scott Pearson, Howard Romme, Janelle Stith, Michael Turner, Dan Tinker, Tim Twining, Joe Van Landschoot, and Michi Vojta. The University of Wyoming-National Park Service Research Center provided excellent logistical support, and we especially thank Mark Boyce, Glen Plumb and Hank Harlow for their assistance. The staff of Yellowstone National Park shared their complete GIS data bases and provided much-appreciated logistical assistance. We are especially grateful to South District Ranger Gerry Mernon for assistance with our trips to the South Arm of Yellowstone Lake. John Beauchamp from ORNL provided guidance on the statistical analyses, and Sidey Timmons helped with the GIS work required for study site selection. Our ideas benefited from discussions with Park Biologist Don Despain. The manuscript was improved by thoughtful suggestions from Virginia H. Dale and Scott M. Pearson and insightful reviews from David R. Foster and three anonymous reviewers. This research was supported by funding from the National Science Foundation (BSR-9016281 and BSR-9018381), National Geographic Society (Grant No. 4284-90), and the Ecological Research Division, Office of Health and Environmental Research, U.S. Department of Energy, under contract no. DE-AC05-84OR21400 with Martin Marietta Energy Systems.

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