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Prefire Heterogeneity, Fire Severity, and Early Postfire Plant Reestablishment in Subalpine Forests of Yellowstone National Park, Wyoming

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Abstract

The 1988 fires in Yellowstone National Park provided an opportunity to study effects of a large infrequent disturbance on a natural community. This study addressed two questions: (1) How does prefire heterogeneity of the landscape affect postfire patterns of fire severity? and (2) How do postfire patterns of burn severity influence plant reestablishment? At three sites, 100 sampling points were distributed regularly in a 1-km x 1-km grid and sampled annually from 1989 to 1992. Information was recorded on fire severity (damage to trees, depth of ash and soil charring, and percent mineral soil exposed); pre-fire forest structure (forest successional stage; tree density; tree species; tree size; and evidence of pre-fire disturbance by mountain pine beetle [*Dendroctonus ponderosae* Hopk.] or mistletoe [*Arceuthobium americanum* Nutt. ex Engelm.]); postfire percent cover of graminoids, forbs, and low shrubs; number of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) seedlings; and general topographic characteristics (slope and aspect). Fire severity was influenced by successional stage, with older stands more likely to be in the more severe burn class, and by tree diameter, with tree damage diminishing with tree size. Prefire bark beetle and mistletoe damage also influenced fire severity; severe prefire damage increased the likelihood of crown fire, but intermediate prefire damage reduced the likelihood of crown fire. Fire severity was not influenced by slope, aspect, or tree density. Postfire percent vegetative cover and density of lodgepole pine seedlings varied with burn severity. In lightly burned areas, percent cover returned to unburned levels by 1991. In severely burned areas, total percent cover was about half that of unburned areas by 1992, and shrub cover remained reduced. Recruitment of lodgepole pine seedlings was greatest during the second postfire year and in severe-surface burns rather than in crown fires. Continued monitoring of vegetation dynamics in Yellowstone's burned forests will contribute to our understanding of successional processes following a disturbance that was exceptional in its size and severity.

Keywords:

fire severity
heterogeneity
disturbance
landscape ecology
Yellowstone National Park
Rocky Mountains
Pinus contorta
Dendroctonus ponderosae
Arceuthobium americanum.

Introduction

The 1988 fires in Yellowstone National Park (YNP), USA, were the largest observed since the Park was established in 1872, affecting approximately 45% (~400,000 ha) of the Park (Despain et al. 1989). These fires also sparked public discussion about how large-scale fire should be managed in national parks (Schullery 1989, Knight 1991), and many people feared that the fires were a serious threat to the long-term ecological integrity of the Park (e.g., Bonnicksen 1990). Historical analyses indicate that fires of this magnitude have occurred previously in YNP (Romme and Despain 1989), but questions remained about possible synergistic effects of events prior to 1988 and about postfire recovery within the expansive burned area. An extensive mountain pine beetle [*Dendroctonus ponderosae* Hopk.] outbreak affected YNP from 1969 through the mid 1980s and killed thousands of trees across the Park (Despain 1990). The fuels resulting from beetle infestation may increase the risk of severe, high-intensity fire (e.g., Knight 1987, Schmid and Amman 1992). Mistletoe [*Arceuthobium americanum* Nutt. ex Engelm.]) infestation in conifer trees creates highly flammable 'witches brooms' that may enhance the spread of fire from surface fuels into the canopy (Alexander and Hawksworth 1975, Tinnin 1984, Wicker and Leaphart 1976, Zimmerman and Laven 1984). In this paper, we examine how fire severity was influenced by environmental heterogeneity that existed before the fire, and how the vegetation responded to the variable fire severity resulting from the 1988 burn.

Wildfire is a recurrent phenomenon in the northern Rocky Mountains, having profound influences on the fauna, flora and ecological processes (Habeck and Mutch 1973; Houston 1973; Loope and Gruell 1973; Taylor 1973; Wright and Heinselman 1973; Wright 1974; Arno 1980; Romme and Knight 1981, 1982; Romme 1982; Knight 1987, 1994; Romme and Despain 1989; Despain 1990). Typically, very few fires account for most of the total area burned during a long time period (e.g., one to two centuries; Johnson and Fryer 1987, Romme and Despain 1989, Johnson 1992). These large infrequent fires create the vegetation mosaic that dominates the landscape until the next extensive fire.

A striking feature of the 1988 Yellowstone fires was the resulting mosaic of variable fire severity within burned areas (Christensen et al. 1989, Turner et al. 1994). Burned landscapes generally contain areas affected by low- and high-intensity fire (Van Wagner 1983) because of variations in wind, topography, vegetation type, moisture, natural fuel breaks, and the time of day of the fire (Rowe and Scotter 1973, Wright and Heinselman 1973, Van Wagner 1983, Brown et al. 1985, Peterson and Ryan 1986, Ryan et al. 1988). The variable fire intensities (a function of maximum fire temperature and flame length) result in a heterogeneous pattern of burn severities (i.e., the effects of fire on the ecosystem [Ryan and Noste 1985]) and islands of unburned vegetation. The influence of burn severity on plant reestablishment following fire in the northern Rocky Mountains has been documented (e.g., Habeck and Mutch 1973, Lyon and Stickney 1976, Viereck 1983, Ryan and Noste 1985), but few studies have dealt explictly with the variation of fire effects over a large area (Knight and Wallace 1989, Turner and Romme 1994).

In this paper, we address two general questions. First, how does pre-fire heterogeneity of the landscape affect fire severity? Pre-fire heterogeneity in our study includes spatial variability in abiotic factors (e.g., slope and aspect) and biotic factors (e.g., prefire tree size and density, successional stage, and effects of prior mountain pine beetle or mistletoe infestations). Second, how do the postfire patterns of burn severities influence plant reestablishment? We focus on percent cover of ground-layer vegetation and the density of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), the dominant tree species in Yellowstone.

Study Area

Yellowstone National Park encompasses 9000 km^2 in the northwest corner of Wyoming and is primarily a high, forested plateau. 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.) may be locally abundant (Despain 1990). Our study was conducted on the subalpine forested plateau that covers most of Yellowstone and supports similar vegetation throughout (Figure 1). The climate is generally cool and dry; on the plateau, mean January temperature is -11.4° C and mean July temperature is 10.8° C (Dirks and Martner 1982). Mean annual precipitation is 56.25 cm with relatively moist springs and dry summers (Dirks and Martner 1982). However, the summer of 1988 was the driest on record in YNP; precipitation in June, July and August was 20%, 79%, and 10%, respectively, of the 100-yr average (National Park Service 1988 Weather Station Data, Yellowstone National Park).

We selected three 1-km x 1-km study sites (Figure 1) on the subalpine plateau in which a mosaic of fire severity was observed aerially (by MGT and WHR during helicopter flight in October 1988) and from the ground. Criteria for site selection included the presence of crown fire and unburned forest within each

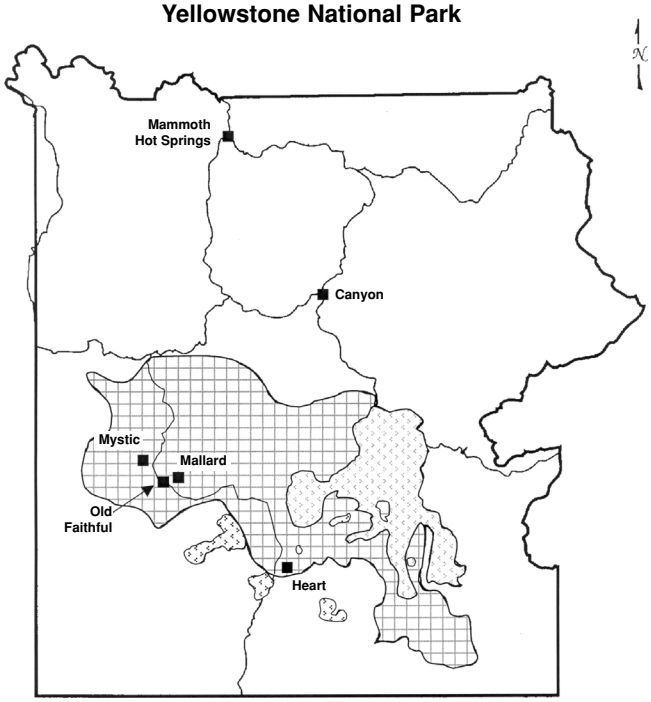

Figure 1. Map of Yellowstone National Park showing the locations of the three 1-km x 1-km study grids (Mystic, Mallard and Heart). The cross-hatched area depicts the area of the Yellowstone Plateau for which fire history is known (Romme and Despain 1989), the partial shading illustrates major lakes, and the lines indicate Park roads.

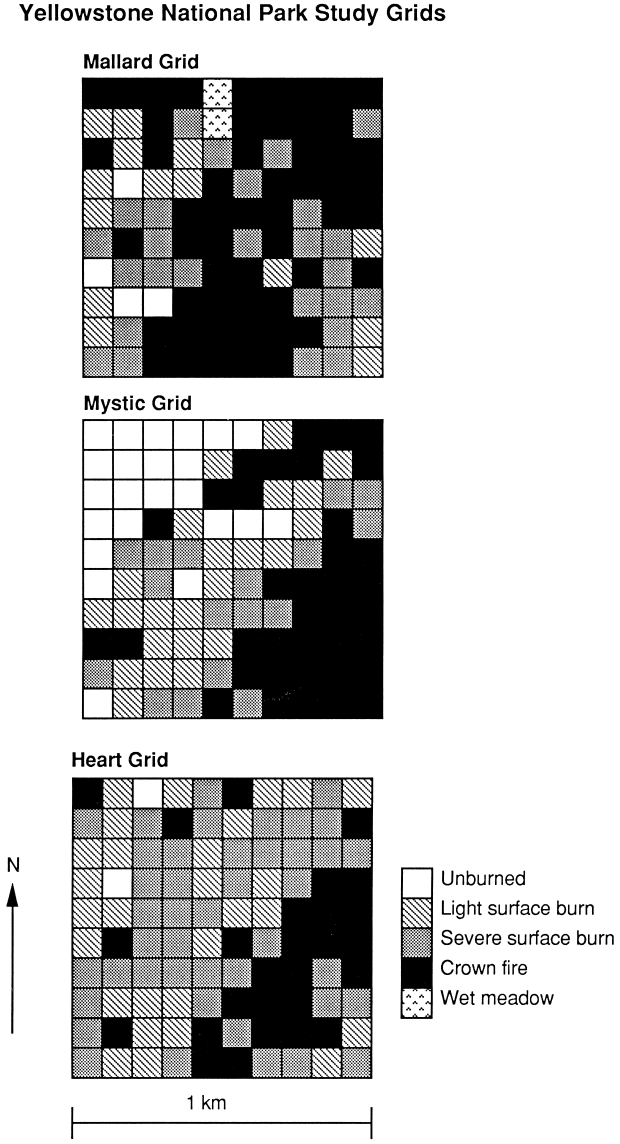

Figure 2. Heterogeneity of burn severities in three 1-km by 1-km grids as measured during 1989. Each grid represents 100 sampling points. The burn severity classes are described in Table 1.

1-km^2 area, similarity in substrate (glacial till composed primarily of rhyolite) and elevation (2300-2400 m), and accessibility (within 5 km of a road). The two most important environmental features controlling vegetation on the plateau are related to elevation and geological substrate (Despain 1990), with moisture generally increasing with elevation and soil fertility lower on rhyolite than on andesite substrate. Our study sites represent the dry and infertile end of the major gradients in YNP. The Mallard and Heart sites were embedded within a larger burn mosaic, whereas the Mystic grid was located at the edge of a large burn, capturing the transition between unburned forest and crown fire (Figure 2). The prior mountain pine beetle outbreak in YNP (Despain 1990) affected our study sites between 1971 and 1983.

Methods

Initial field sampling was conducted during July 1989. A 100-m interval grid was established at each study site (yielding 100 sampling points in each 1-km^2 grid) by locating the initial corner point at random. Each grid was oriented toward true north, and the corners of each grid were permanently marked with rebar and located by triangulation.

The 1989 field sampling used the following procedures. We established a 50-m^2 circular area centered on each sampling point within each grid. Within this circular plot, we recorded slope, aspect, prefire successional stage of the stand (Table 1), burn severity (Table 1), and number of trees (live + dead) taller than breast height (1.5 m) by species. Trees that were dead prior to the 1988 fires were deeply charred in many places on the stem, were almost completely lacking bark, and had

Table 1. Classes of burn severity and successional stage used in this study. Successional stage classes were developed from sampling a chronosequence of stands that originated following fires at various times in the last 400 yrs (from Despain 1990).

Class	Description
Burn severity classes	
0 Unburned	No sign of fire effects.
1 Light surface burn	Low-intensity surface fire in which canopy trees retain green needles and generally did not die, although stems may be scorched; soil organic layer still largely intact, though burned in small patches.
2 Severe surface burn	High-intensity surface fire with extensive canopy tree mortality, but needles on canopy trees are not consumed by fire; pre-fire soil organic layer largely consumed, but soil covered by dead leaves fallen from the canopy after the fire.
3 Crown fire	Needles of canopy trees completely consumed by fire; soil organic layer almost entirely consumed, and soil is bare with no litter.
Successional stages with approximate ages	
LP0 (0-40 yrs)	Recently burned lodgepole pine stands in the grass to seedling/sapling stage before canopy closure; trees usually < 2 m in height.
LP1 (40-150 yrs)	Closed canopy of even-aged, often dense lodgepole pine; young pole stage.
LP2 (150-300 yrs)	Closed canopy dominated by lodgepole pine; overstory still largely intact; understory may contain small conifers, but is generally open and park like.
LP3 (>300 yrs)	Canopy quite irregular, predominantly of old lodgepole pine but containing some Engelman spruce, subalpine fir and whitebark pine in the pole-sized class; understory usually dense.

few or no small branches and twigs (< 2 cm diameter). Trees that were alive prior to having burned in 1988 had no deep charring, generally retained their bark, and usually had at least some small twigs and branches. We also recorded visual estimates of prefire mountain pine beetle and mistletoe damage within the stand by category: none (0%); light (1 - 10% of susceptible trees affected); moderate (10 - 50%); and severe (> 50%). Living trees infested with mistletoe were recognized by the presence of the parasite in the bark. Dead trees that had been infested were recognized from the abnormal growth patterns, i.e., witches brooms and swollen branches, that result from mistletoe infestation (Alexander and Hawksworth 1975). Trees killed by bark beetles were identified from gallery etchings in the wood and/or by pitch tubes on the bark (Furniss and Carolin 1977). Because of slow decomposition rates, trees killed by beetles as long as 20 yr earlier were still readily recognizable.

The circular plot was then subdivided into four quadrants (northeast, northwest, southwest, and southeast). Tree species, diameter at breast height (dbh), and damage level burn severity as indicated by tree damage (Table 1) were recorded for the two trees nearest to the center of each quadrant. Occasionally there was one or no trees within a quadrant, in which case fewer than two trees were sampled. Percent cover of graminoids, forbs, shrubs, litter, and exposed mineral soil were estimated visually within a 1-m^2 plot in each of the four quadrants, and the number of lodgepole pine seedlings and the dominant species by cover recorded. The depth of ash and depth to which the soil was charred were measured by excavating a small hole in the center of each 1-m^2 plot. Ash was recognizable by both color and texture, and charred soil was distinguishable by color. Because we were interested in the broad-scale patterns of heterogeneity rather than microsite differences, data collected at each sampling point (i.e., within the four quadrats) were aggregated to provide a single value for each variable at each 50-m^2 circular plot.

The three grids were resampled during the summers of 1990, 1991, and 1992. The four corners of each grid were permanently marked in 1989, but the individual sampling points within the grid were not. Slope, aspect, prefire successional stage of the stand, and burn severity were recorded in 1990, 1991 and 1992 at each sampling point as described above for the 1989 sampling. Measurements of tree density, tree size, bark beetle damage, and mistletoe infestation were not repeated. Ground-layer vegetation was resampled, but a point-intercept method was used in place of the visual estimate of percent cover to assure consistency among individuals. At each sampling point, an 8-m line was extended perpendicular to the main north-south transect such that the center of the 8-m line coincided with the

sampling point. Percent cover data were recorded within eight 0.25-m^2 point-intercept frames spaced at 1-m intervals along this line. We used a 0.5-m x 0.5-m point-intercept frame containing a total of 25 points (a modification of the method used by Floyd and Anderson [1982, 1987]). The plant species or cover type (exposed mineral soil, unburned litter, charred litter, pebble, cobble, or boulder) that occurred below each intercept point was recorded. Percent cover for each sampling point was determined by aggregating the data from the eight 0.25-m^2 plots.

Statistical analyses were performed using SAS (SAS Institute 1990). Chi-square analysis was used to test for relationships between fire severity and topographic position (slope, aspect), successional stage, and pre-fire mountain pine beetle and mistletoe infestation. Analysis of variance was used to test for relationships between fire severity and prefire tree density and size. Repeated measures analyses of variance was conducted on percent cover and pine seedling data to evaluate the effects of burn severity on postfire plant reestablishment. Independent variables included grid; burn severity; slope; aspect; and distances to the nearest green forest (unburned or light-surface burn) and to the nearest severe-surface burn, which were calculated within a geographical information system based on Landsat Thematic Mapper imagery from August 1989 (Turner et al. 1994). Percent cover estimates were arc-sine-square root transformed prior to analysis to eliminate the bias in the variance and mean that is inherent in data recorded as percentages (Zar 1984). Lodgepole pine seedling density data were square-root transormed prior to analysis. Differences in the means due to significant main effects in the ANOVA were determined by using Tukey's studentized test. Finally, Chi-square analysis was used to examine the relationship between burn severity and the presence/absence of lodgepole pine seedlings.

Results

All four burn severity classes (Table 1) were present in each of our three 1-km^2 grids (Figure 2). The Mallard grid had the greatest amount of crown fire burn (54%), and the Mystic grid had the greatest amount of unburned forest (23%). Across all sites, approximately 70% of the sampling points were located in severe surface or crown fire burns, both of which experienced canopy tree mortality.

We documented 99 species of vascular plants within the sample grids. All but seven are native species. The non-native species were already widespread in the Park at generally low densities before the fires in 1988. The species in the burned areas are all found throughout burned and unburned areas of the Yellowstone Plateau, although several are far less common in unburned areas, viz, *Dracocephalum parviflorum, Gayophytum diffusum*, *Gnaphalium palustre, Gnaphalium viscosum*, and *Populus tremuloides*. In addition to vascular plants, mosses and liverworts (especially in mesic and wet areas) and lichens (especially in dry and mesic areas) were present in all grids.

Most of the plants present in 1989 and 1990 were vegetative sprouts from surviving rhizomes or root stocks or adult forms whose above-ground structures had survived the fire. We observed seedlings of the annual species, *Collinsia parviflora* Lindl., *Gayophytum diffusum* T. & G. and *Gnaphalium palustre* Nutt., and of the perennial species *Epilobium angustifolium*, *Gnaphalium viscosum* Kunth, *Hieraracium albiflorum* Hook., *Lupinus argenteus*, *Pinus contorta*, *Populus tremuloides* Michx., and *Carex* spp. (*C. geyeri* Boott or *C. rossii* Boott or both). Resprouting perennial plants bore few flowers in 1989, but flowered abundantly in 1990, resulting in an increase in the numbers of seedlings in the burned areas in 1991 (Turner et al. 1997a). The annual species, *Gayophytum diffusum*, was rare in 1989 and common after 1990.

Pre-fire Patterns and Fire Severity

Chi-square analyses revealed no significant effects of slope or aspect on fire severity, but there was an effect of successional stage (Table 2). Sampling points located in the oldest successional class (LP3) were in crown fire more than expected, whereas LP2 stands experienced surface fires more than expected. Analysis of variance demonstrated no significant relationship ($P = 0.32$) between pre-fire tree density and burn severity classes (Table 3). The size (dbh) of lodgepole pine trees, however, was associated with burn severity (Table 4). ANOVA revealed that sampling points having trees of greater dbh were associated with lower burn severity classes ($df = 13$, $F = 12.05$, $r^2 = 0.11$, $P = 0.0001$).

Tree size also affected susceptibility to fire damage, with larger trees generally having less fire damage ($P = 0.001$). We also examined how tree size varied with fire damage within the burn severity classes. In light and severe surface burns, larger trees (15.4 to 20.1 cm dbh) were more likely to sustain less damage (alive with a green canopy, but with evidence of scorching), and smaller trees (6.6 to 12 cm dbh) were more likely to sustain more damage (Tukey's Studentized Test, $P < 0.05$). In crown fires, there was no relationship between tree size and damage to individual trees. Thus, where the fire burned less intensely, large trees had less damage but variability in tree size did not influence damage to individual trees when the fire was more intense.

Prefire extent of mountain pine beetle and mistletoe damage influenced fire severity. Sampling points with

Table 2. Observed and expected frequency of sampling points by burn severity and successional stage and pre-fire infestation by mountain pine beetle and mistletoe. Values in boldface indicate > 5% deviation between expected and observed values. Data were obtained in 1989.

	Burn severity								
	Unburned		Light surface		Severe surface		Crown fire		Row totals
Successional stage	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	
LP0	0	0.1	1	0.2	0	0.3	0	0.4	1
LP1	0	0.2	1	0.4	1	0.6	0	0.8	2
LP2	**14**	**2.4**	6	5.2	**1**	**6.9**	**3**	**9.5**	24
LP3	**13**	**26.4**	54	57.2	**82**	**75.6**	**114**	**103.8**	263
Open	1	0.2	0	0.4	1	0.6	0	0.8	2
Wet meadow	2	0.7	3	1.5	1	2.0	1	2.8	7
Column totals	30		65		86		118		299
	$\chi^2 = 89.72$, df = 15, P = 0.0001								
Mountain pine beetle infestation severity	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	
None (0%)	10	12.8	27	27.8	42	37.2	49	50.1	128
Light (1-10%)	8	6.0	**23**	**13.0**	19	17.5	**10**	**23.5**	60
Moderate (11-50%)	**12**	**3.8**	10	8.3	13	11.1	**3**	**14.9**	38
Severe (>50%)	**0**	**7.3**	**5**	**15.9**	**13**	**21.2**	**55**	**28.6**	73
Column totals	30		65		87		117		299
	$\chi^2 = 87.60$, df = 9, P = 0.0001								
Mistletoe infestation severity	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	
None (0%)	**18**	**7.4**	**23**	**16.1**	**21**	**21.5**	**12**	**29.0**	74
Light (1-10%)	6	5.6	14	12.2	16	16.3	20	21.9	56
Moderate (11-50%)	**6**	**15.6**	**28**	**33.7**	47	45.1	**74**	**60.7**	155
Severe (>50%)	0	1.4	0	3.0	3	4.1	11	5.5	14
Column totals	30		65		87		117		299
	$\chi^2 = 48.59$, df = 9, P = 0.0001								

Table 3. Pre-fire tree density by species and burn severity by sampling point for the three 1-km x 1-km grids established in 1989 in Yellowstone National Park. Data are mean (standard deviation) numbers of trees per 50-m^2 sampling area.

		Mean number of trees per 50-m^2 sampling area				
Burn Severity	n	Pinus contorta	Abies lasiocarpa	Pinus Engelmanii	Pinus albicaulis	Total trees
Unburned	30	7.46 (8.91)	0.8 (2.66)	0.06 (0.36)	0.13 (0.51)	8.46 (9.41)
Light surface	64	8.29 (10.37)	1.98 (5.00)	0.65 (1.91)	0.62 (1.36)	11.56 (11.57)
Severe surface	87	8.10 (7.62)	1.77 (4.07)	0.26 (0.83)	0.54 (1.60)	10.67 (8.70)
Crown fire	117	7.84 (7.96)	0.33 (1.81)	0.17 (0.91)	0.09 (0.49)	8.44 (8.32)

Table 4. Diameter at breast height (dbh) by species and burn severity for the three 1-km x 1-km grids established in 1989 in Yellowstone National Park. Data are number of trees sampled (n), mean dbh in cm, and standard deviation (s.d.) in cm.

	dbh (cm) by species											
	Pinus contorta			*Abies lasiocarpa*			*Picea engelmannii*			*Pinus albicaulis*		
Burn Severity	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.
Unburned	123	13.73	11.29	10	5.75	5.47	1	2.50	0	0	-	-
Light surface	240	12.20	10.17	47	8.78	8.45	23	19.52	16.26	15	5.39	3.62
Severe surface	375	11.46	9.15	67	9.71	7.99	18	13.02	12.64	16	5.23	4.73
Crown fire	519	11.19	8.41	15	7.46	3.64	18	20.34	18.1	4	5.18	2.39

Table 5. Analyses of variance results for depth of ash (mm) and depth to which soil was charred (mm) as measured in 1989.

Variable	Source	df	Sum of squares	F	P	Differences among means[1] ($\alpha = 0.05$)
Depth of ash	Grid	2	120.12	7.37	0.0008	Mallard 11.6[a] Mystic 8.1[b] Heart 8.1[b]
	Burn severity	3	29.11	1.19	0.3137	ns
	Grid x burn	6	32.84	0.67	0.6728	
Depth of charred soil	Grid	2	95.97	1.28	0.2804	ns
	Burn severity	3	3165.21	28.08	0.0001	(3) 13.6[a] (2) 9.0[b] (1) 5.8[c] (0) 0.5[d]
	Grid x burn	6	160.37	0.71	0.6407	

[1]Calculated using Tukey's Studentized Test; means followed by the same letter do not differ.

light and moderate levels of bark beetle damage were more likely to be unburned or lightly burned and less likely to have been affected by crown fire (Table 2). However, severe bark beetle damage showed the opposite relationship (Table 2), with crown fire being more likely. Thus, light and moderate levels of beetle damage may reduce the probability of crown fire, but severe levels may increase the probability of crown fire. Effects of mistletoe infestation were similar (Table 2). Sampling points having no or light mistletoe infestation were unburned or lightly burned more often than expected, and crown fires occurred less often than expected. However, points with moderate and severe levels of mistletoe infestation were unburned or lightly burned less than expected, and crown fires occurred more often than expected (Table 2). Thus, the probability of crown fire appeared to increase as the severity of mistletoe infestation increased.

Effects of Burn Severity

Soil charring and ash

Depth to which soil was charred differed among burn severity classes (Table 5). Mean depth of charred soil in 1989 was greatest (13.6 mm) at sampling points that experienced crown fires and declined with decreasing burn severity (9.0 and 5.8 cm in severe-surface and light-surface burns, respectively). Depth of ash in 1989 did not differ with burn severity (Table 5), probably because the ash is easily transported by wind and water. By 1990, no visible ash layer remained at nearly all burned areas.

Percent cover

Total biotic cover increased through time and varied considerably with burn severity (Figure 3, Table 6). Lightly burned areas recovered most rapidly, achieving vegetative cover similar to unburned areas by 1991 (Figure 3). Areas affected by severe surface fire showed a continuous increase in percent cover, and by 1992, total cover was the same in unburned and both surface-burn classes. Crown fire sampling points had the lowest total cover in 1989, but cover increased rapidly through 1991, slowing in 1992. By 1992, crown fire sampling points had ~25% biotic cover, compared to ~40% within the other classes (Figure 3). The independent variables we measured explained 47% of the variability in total biotic cover, with year and burn severity being the most important. However, there were significant differences among sites, with total cover being greater at the Mallard and Mystic grids than at the Heart grid. In addition, biotic cover tended to be greater at points closer to unburned or lightly burned forest.

The components of total cover also varied with burn severity and through time (Figure 4 and Table 6). Percent cover of forbs, grasses and shrubs did not differ between unburned and light-surface burned points by 1991. In more severely burned areas, percent cover of shrubs was low, but forb cover was greater than in unburned or light surface burned points by 1991 (Figure 4).

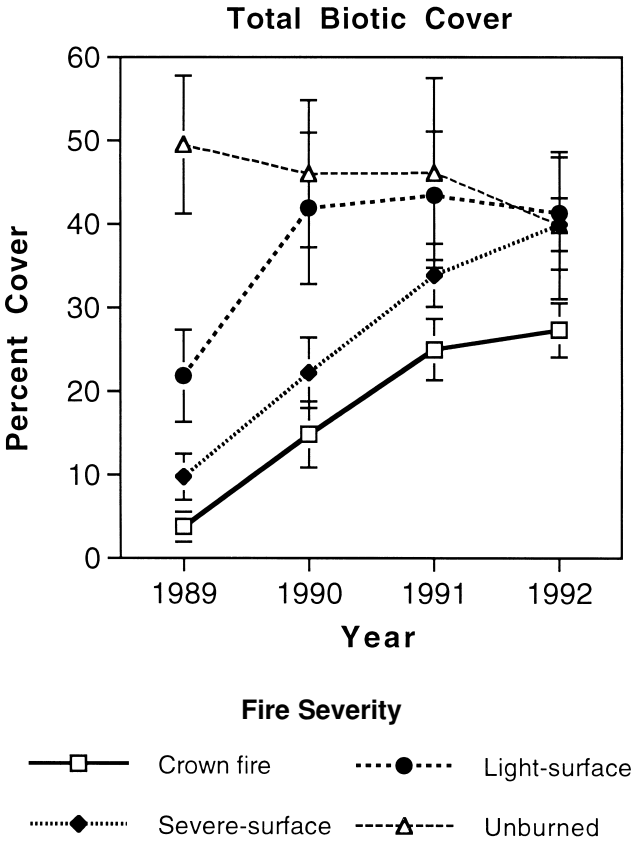

Figure 3. Mean total percent biotic cover between 1989 and 1992 within each of four burn severity classes. Error bars indicate ± 2 standard errors.

Most of the variability in forb and graminoid cover was explained by differences among grids, changes through time, and burn severity (Table 6). Forb cover increased continually through time; however, graminoid cover increased from 1989 to 1990 but did not change significantly from 1990 to 1992. Shrubs, primarily *Vaccinium scoparium*, recovered most slowly and showed strong differences among burn severity classes. There were no significant differences in shrub cover through time, but burn severity and grid explained much of the variance (Table 6). Shrub cover declined dramatically with burn severity. Variability in percent cover of exposed mineral soil was explained primarily by burn severity, and it declined with time (Table 6).

Lodgepole Pine Reestablishment

There was a large increase (Figure 5a) in mean abundance of lodgepole pine seedlings between 1989 and 1990 (Tukey's studentized range test, $P < 0.05$). Mean seedling densities from 1990 to 1992 showed a downward trend but did not differ significantly. In 1992, there were an average of 0.80 seedlings/m^2 across the three grids. The mean prefire density of adult lodgepole pine trees (Table 3) was approximately 0.15 trees/m^2, suggesting that postfire seedling density was substantially greater than prefire tree densities.

Lodgepole pine seedling density varied with burn severity (Figure 5a). Sampling points affected by crown fires had the lowest seedling density (0.19/m^2) in 1989, and no additional recruitment was observed in subsequent years at crown fire points. Sampling points affected by severe surface burns began with low seedling densities but experienced substantial recruitment in 1990, with densities approaching 1.0/m^2. Light surface burn points had the greatest initial seedling densities but did not differ from severe surface burn points by 1992 (Figure 5a). Across all grids, the percent of sampling points containing lodgepole seedlings increased dramatically between 1989 and 1990, then declined gradually (Figure 5b). However, only 25% of the crown fire sampling points contained seedlings in 1989, and this percentage declined with time; i.e., crown fire points received seeds in 1989 but not subsequently (Figure 5b). Chi-square analyses on presence and absence of lodgepole seedlings indicated differences among burn severity classes in all four years ($df = 3$, all $P < 0.0001$). During all years, seedlings were present more often than expected on light and severe surface burn points and less than expected on crown-fire points. In 1992, sampling points in crown fire located > 100 m from the edge of a surface fire frequently contained no lodgepole pine seedlings.

Discussion

Pre-fire patterns and fire severity

The results reported here revealed subtle interactions between burn severity and the pre-fire landscape—especially pre-fire levels of damage due to mistletoe and mountain pine beetle infestation. Although topography can influence fire frequency (Loope and Gruell 1973, Romme and Knight 1981), we found no effect of slope and aspect on fire severity within the grids. This may be because the three grids burned during a severe drought, when fuel moisture was extremely low across the entire landscape (Renkin and Despain 1992), and differences in moisture content among different slope and aspect classes were probably minimal. Heterogeneous fuel characteristics did affect fire severity, even under the drought conditions of 1988. Flammability and probability of crown fire increase with stand age in Yellowstone's conifer forests as large

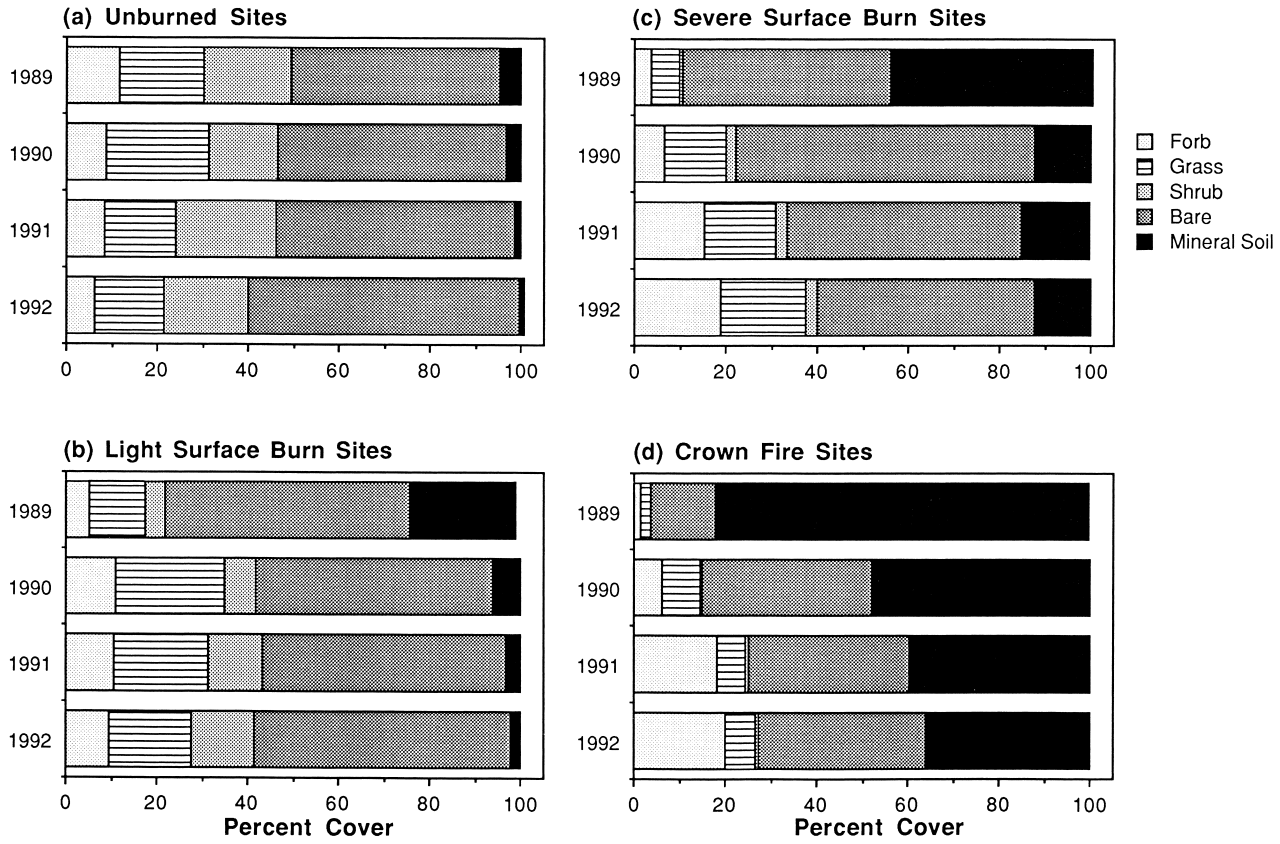

Figure 4. Mean percent cover of forbs, graminoids, shrubs, bare ground with litter, and exposed mineral soil within each of four burn severity classes.

dead woody fuels accumulate and a flammable conifer understory develops (Despain and Sellers 1977, Romme 1982, Romme and Despain 1989, Despain 1990). Probability of crown fire was also positively related to prior levels of mistletoe infestation.

The differential effects of light and moderate versus severe bark beetle damage on fire severity were surprising. Conventional wisdom holds that bark beetle outbreaks increase dead woody fuels and thus increase fire risk (Knight 1987, Schmid and Amman 1992). However, light to moderate outbreaks may reduce the continuity of live canopy fuels, replacing contiguous canopy with patchy canopy that is interspersed with dead tree boles. The dead trees may be more flammable for 2 to 3 yr, while their dead leaves are retained, but after the leaves fall, total crown fuel mass decreases and the remaining fuels are predominantly in large size classes that do not ignite readily. Thus, the probability of crown fire a few years after a light or moderate beetle outbreak may be reduced (Romme et al. 1986a). In contrast, severe beetle outbreaks kill most of the canopy and stimulate understory growth by creating gaps (Romme et al. 1986b). These gaps result in the addition of a large quantity of near continuous ground fuels, increasing continuity between ground and canopy fuels. More favorable burning conditions and an increased probability of crown fire may therefore follow a severe beetle outbreak. Time since the infestation does influence fire hazard (Schmid and Amman 1992), and the our results for an infestation that occurred 5 to 17 years before fire might not hold for shorter or longer intervals.

The differential susceptibility of individual lodgepole pine trees to fire damage as a function of tree diameter suggested that larger trees were generally less susceptible to fire damage than smaller trees. Fire-caused mortality of western conifers decreases with increasing bark thickness, and bark thickness increases with stem diameter (Ryan and Reinhardt 1988), suggesting that fire-induced mortality within a given species would decrease with stem diameter. This size advantage was observed only in areas of light or severe surface burns, however, suggesting that larger trees may have an enhanced likelihood of survival only when fires are less intense.

So, how does pre-fire heterogeneity of the landscape affect fire severity? Our data suggested no influence of spatial variability in abiotic factors (slope and aspect)

Table 6. Analyses of variance results for percent cover of ground layer vegetation.

Variable	Source	df	Sum of squares	F	P	Differences among means[1] ($\alpha = 0.05$)
Total biotic cover	Year	3	2.24	13.81	0.0001	1992^a 1991^a > 1990^b > 1989^c
($r^2 = 0.47$)	Grid (year)	8	2.88	6.65	0.0001	$Mallard^a$ $Mystic^a$ > $Heart^b$
	Burn severity (year)	12	9.73	14.99	0.0001	0^a > 1^b > 2^c > 3^d
	Slope (year)	8	1.47	3.39	0.0008	
	Aspect (year)	8	0.37	0.85	0.5599	
	Dist surface (year)[2]	4	0.20	0.92	0.4504	
	Dist_green (year)[3]	4	0.70	3.24	0.019	
	Grid x burn (year)	20	2.71	2.51	0.0003	
Forbs	Year	3	1.14	15.22	0.0001	1992^a > 1991^b > 1990^c > 1989^d
($r^2 = 0.47$)	Grid (year)	8	3.41	17.11	0.0001	$Mallard^a$ > $Mystic^b$ > $Heart^c$
	Burn severity (year)	12	2.26	7.58	0.0001	2^a $0a^b$ $3b^c$ 1^c
	Slope (year)	8	0.45	2.28	0.0200	
	Aspect (year)	8	0.21	1.04	0.4026	
	Dist_surface[2] (year)	4	0.08	0.77	0.5456	
	Dist_green[3] (year)	4	0.19	1.93	0.1032	
	Grid x burn (year)	20	0.99	2.00	0.0055	
Graminoids	Year	3	0.79	6.00	0.0001	1992^a 1991^a 1990^a > 1989^b
($r^2 = 0.33$)	Grid (year)	8	1.62	4.64	0.0001	$Heart^a$ $Mallard^a$ > $Mystic^b$
	Burn severity (year)	12	4.97	9.46	0.0001	0^a 1^a > 2^b > 3^c
	Slope (year)	8	1.19	3.42	0.0200	
	Aspect (year)	8	0.40	1.14	0.4026	
	Dist_surface[2] (year)	4	0.17	0.96	0.5456	
	Dist_green[3] (year)	4	0.49	2.82	0.1032	
	Grid x burn (year)	20	2.93	3.35	0.0055	
Shrubs	Year	3	0.07	1.16	0.3250	ns
($r^2 = 0.41$)	Grid (year)	8	2.28	13.93	0.0001	$Mystic^a$ > $Heart^b$ > $Mallard^c$
	Burn severity (year)	12	3.41	13.88	0.0001	0^a > 1^b > 2^c > 3^c
	Slope (year)	8	0.15	0.92	0.4976	
	Aspect (year)	8	0.43	2.62	0.0077	
	Dist_surface[2] (year)	4	0.04	0.49	0.7396	
	Dist_green[3] (year)	4	0.12	1.48	0.2065	
	Grid x burn (year)	20	1.59	3.90	0.0001	
Exposed mineral	Year	3	5.14	31.99	0.0001	1989^a > 1990^b 1991^b > 1992^c
soil ($r^2 = 0.68$)	Grid (year)	8	0.95	2.22	0.0238	$Mallard^a$ > $Mystic^b$ > $Heart^c$
	Burn severity (year)	12	29.32	45.57	0.0001	3^a > 2^b > 1^c > 0^d
	Slope (year)	8	1.06	2.46	0.0120	
	Aspect (year)	8	0.18	0.43	0.9050	
	Dist_surface[2] (year)	4	0.20	0.95	0.4324	
	Dist_green[3] (year)	4	0.73	3.39	0.0091	
	Grid x burn (year)	20	2.22	2.08	0.0036	

[1]Calculated using Tukey's Studentized Test; for simplicity, only the classes are shown here, and classes with the same superscript represented means that do not differ significantly.
[2]Dist_surface refers to the distance from the sampling point to the nearest area of severe-surface burn (see Table 1).
[3]Dist_green refers to the distance from the sampling point to the nearest area of unburned forest or light-surface burn, in which the canopy trees were not killed (see Table 1).

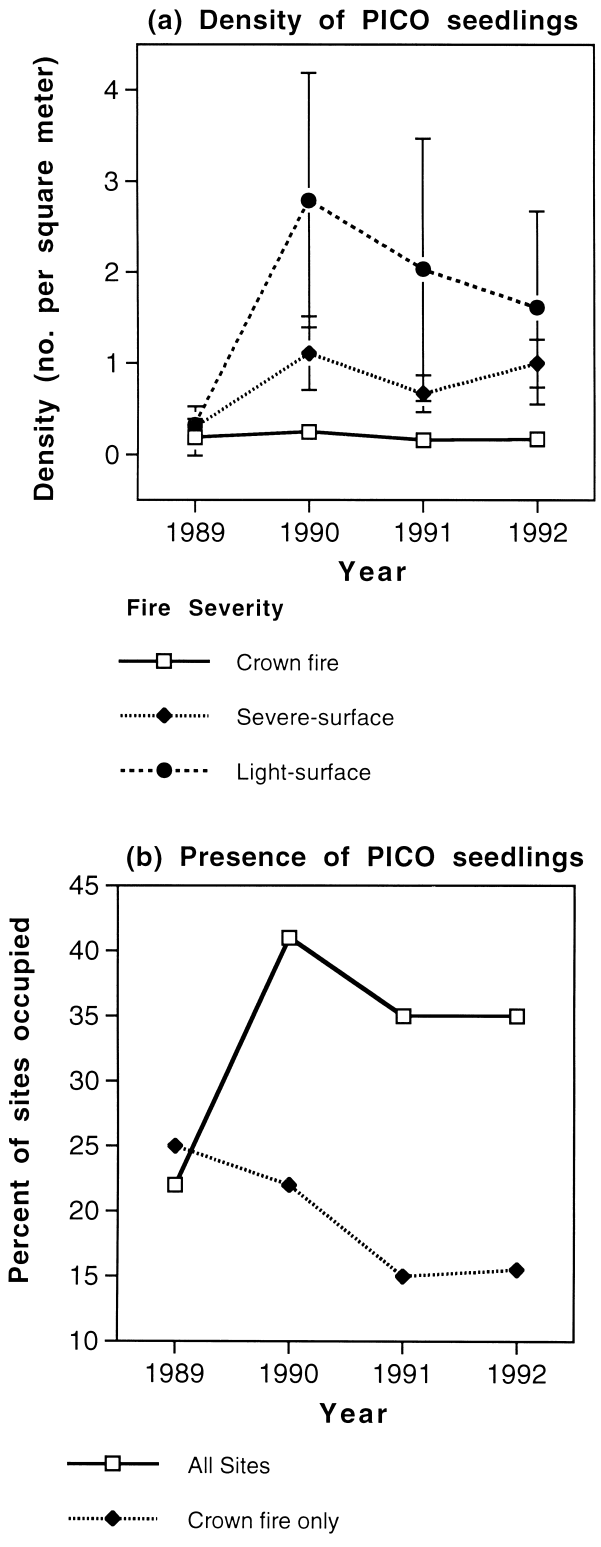

Figure 5. (a) Mean density of lodgepole pine seedlings in burned forest by year and burn severity. Error bars indicate ± 2 standard errors. (b) Frequency (expressed as percent) of sampling points on which lodgepole pine seedlings were present between 1989 and 1992.

on burn severity, but our data identified effects of variation in successional stage and prefire disturbance by mountain pine beetles and mistletoe. Severe, high-intensity fire was more likely to occur in stands of advanced successional stage and in stands which experienced high-intensity prior infestations by mountain pine beetles and mistletoe. Thus, although weather conditions were the primary determinant of the extent of the 1988 Yellowstone fires, the spatial heterogeneity of burn severities was also influenced by pre-fire heterogeneity within the landscape. Pre-fire heterogeneity is likely to be of even greater importance under burning conditions less severe than those that occurred in 1988 (Turner and Romme 1994).

Effects of burn severity on plant reestablishment

Post-fire plant reestablishment in YNP was rapid, with substantial increases in plant cover during the first four years following the fires. Areas affected by surface fires reached total aboveground plant cover comparable to unburned areas by 1992; areas affected by crown fire remained lower but were continuing to increase. Most postfire colonization in Yellowstone appeared to occur from within the burned areas (i.e., not from off-site invaders) (Turner et al. 1997a). Even in areas affected by crown fires, the mean depth to which soil was charred was < 14 mm, suggesting a high potential of survival for roots and rhizomes below this depth. The similarity in floristic composition of burned and unburned areas is consistent with the findings of Lyon and Stickney (1976) and Anderson and Romme (1991) in similar burned areas, and supports Egler's (1954) concept of initial floristic composition in post-fire succession.

Adult lodgepole pine trees do not survive fire except where fire intensity is low, and post-fire regeneration of this species depends entirely on seedling establishment. The seed bank for lodgepole pine is in the canopy of the burned forest. Despite the winged seed, long-distance transport of seeds apparently is far less important than the availability of local, on-site seed sources for reforestation (Clements 1910, Lotan 1976). Lodgepole pine has a classic fire adaptation in the form of serotinous cones, which remain closed at maturity but open in response to high temperatures such as those produced in a high-intensity fire (Knapp and Anderson 1980). Trees may retain closed cones for 40 years or longer, and the canopy thus may contain millions of seed per hectare (Lotan and Jensen 1970). Seed stored in serotinous cones may remain viable for up to 50-75 years (Clements 1910), and seedlings thrive in the high-light environment of a recently burned forest.

The higher abundances of lodgepole pine seedlings observed in low- and high-intensity surface fires were

likely attributable to the presence of cones in the canopy along with abundant exposed mineral soil, implying the presence of both a seed source and suitable germination sites. Fire severity influences the survival of the seeds in the canopy seed bank (Knapp and Anderson 1979, Johnson and Gutsell 1993, Sirois 1993, Despain et al. 1996). In the crown fire areas, although the mineral soil provides suitable germination sites, seed viability was likely reduced by the fire. Seeds must disperse into the severely burned areas, and the silvicultural literature indicates that effective stocking distances for lodgepole pine are generally < 100 m (Fowells 1965, Archibold 1989), and more sophisticated physical models of seed dispersal in lodgepole pine and other conifers predict a rapid decrease in seed density with increasing distance from seed source (e.g., Johnson and Fryer 1989; Greene and Johnson 1989, 1996). This suggests that if the local seed source is eliminated, tree reestablishment will be sparse and slow in large patches of crown fire. The same pattern of greater lodgepole pine seedling densities in less severely burned areas and lower densities in crown fire areas was observed elsewhere in YNP (Anderson and Romme 1991, Ellis et al. 1994, Turner et al. 1997a) where prefire serotiny and postfire seedling densities were much higher than in our study grids.

Recruitment of lodgepole pine seedlings occurred almost exclusively during 1989 and 1990. We observed no significant change in lodgepole seedling densities from 1990 to 1992, although we would expect self-thinning to decrease densities through successional time. Similarly, the frequency of points containing lodgepole seedlings increased in 1990, primarily due to recruitment in severe surface burns, then declined. The frequency of crown-fire sampling points containing lodgepole seedlings decreased through time, suggesting that germination occurred the first year after the fire, and little new colonization occurred subsequently. Variation in both the presence and density of pine seedlings with burn severity suggests that a mosaic of differing postfire stand densities may result. That is, it may be stand structure rather than tree species composition that will be influenced in the long term by fire severity. Continued measurement of sapling and tree survival will be required to test this hypothesis.

Density of lodgepole pine seedlings in the three grids we sampled exceeded prefire stand density by five-fold, on average, suggesting adequate stand regeneration. However, the densities of lodgepole seedlings reported here are representative of only part of the Yellowstone plateau. The percentage of lodgepole pine trees that exhibit serotiny varies considerably at the scale of km (Tinker et al. 1994). Mean percent serotiny across the Yellowstone plateau ranges from nearly 0% to about 65%, and there is corresponding variability in the density of postfire lodgepole seedlings. In areas of high serotiny, lodgepole seedling densities average 21 m^{-2}, whereas in areas of low serotiny, seedling densities may be as low as 1 or 2 ha^{-1} (Tinker et al. 1994, Turner et al. 1997a). The three grids we describe represent intermediate levels of serotiny of approximately 6 to 10% (Tinker et al. 1994, Turner et al. 1997a). Wide variation in tree seedling density across the subalpine plateau will have important implications for the successional trajectory at any given location (Turner et al. 1997a).

How does the pattern of postfire burn severities influence plant reestablishment? Burn severity contributes to postfire variation in the relative abundances of forbs, graminoids and shrubs. Areas of stand-replacing fire (severe surface burns and crown fires) had greater forb cover and lower graminoid and shrub cover than unburned areas or light-surface burns. We anticipate that these differences among burn severity classes will become less pronounced through time as the forest canopy closes, though the degree to which spatial variation in early succession following large, infrequent disturbances will eventually converge on similar endpoints or lead to divergent communities is not yet known (e.g., Christensen and Peet 1984, Leps 1991). However, it is the effect of variation in fire severity on postfire lodgepole pine tree density that may be most pronounced. Across the even-aged stands initiated by the 1988 fires, the spatial pattern of severe-surface burns may have resulted in patches of dense pine trees that will persist within the burned landscape for decades to come.

Ecologists have relatively few long-term studies of disturbances that are large, severe, and infrequent (Turner et al. 1997b). Initial spatial patterns of disturbance may persist to produce long-lasting changes in vegetation composition, and developing detailed, long-term case studies to further our understanding of vegetation recovery from large infrequent disturbances is crucial (Zobel and Antos 1997). The potential for climate-induced changes in fire frequency and extent in the northern Rocky Mountains (Romme and Turner 1991, Flannigan and Van Wagner 1991, Bartlein et al. 1997) also underscores the importance of understanding effects of extreme events like the 1988 Yellowstone fires. Continued monitoring of vegetation dynamics in Yellowstone's burned forests will contribute to our general understanding of successional processes following a disturbance that was exceptional in its size and severity.

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