Chapter 14 Ten Years After the 1988 Yellowstone Fires: Is Restoration Needed?

William H. Romme and Monica G. Turner

Coniferous forests in many parts of western North America have been substantially altered by human activities in the past 150 years and are now at risk of abnormally severe disturbance, impaired ecosystem function, and loss of biodiversity. For example, ponderosa pine forests in many locations today are characterized by unusually high densities of small-diameter trees, a paucity of large trees and snags, severely suppressed herbaceous plants, and excessive quantities of well-connected live and dead fuels. These changes are the result primarily of fire exclusion, excessive livestock grazing, and unsustainable logging activities conducted in the past. Efforts are now under way to restore missing ecological structure, processes, and species in these degraded ecosystems via mechanical thinning, prescribed fire, or a combination of thinning and fire (for example, Covington and Moore 1994, Hardy and Arno 1996, Fule and others 1997, Lynch and others 2000, Allen and others 2002, Friederici 2003).

In the wake of the past several devastating fire years, the public and policymakers have called for accelerated efforts to reduce the risk of uncontrollable wildfires in western coniferous forests by means of log-

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ging, prescribed fire, and other restoration techniques. However, it is critical that restoration efforts focus on ecosystems where structure and processes really have been altered by human activities. Although ponderosa pine forests appropriately have received much attention, some other types of coniferous forest in western North America have not been much altered from their natural range of structure, composition, and ecological function. Mechanical thinning, prescribed burning, and other attempts to "restore" these systems would be misguided at best and potentially destructive at worst (Cole and Landres 1996, Cole 2000).

The fires of 1988 were the largest fires in recorded history in the Yellowstone region. The size and severity of the 1988 fires led many people at the time to conclude that the park had been "destroyed" and that the National Park Service had been remiss in not actively intervening to prevent such fires prior to 1988—for example, by conducting programs of mechanical thinning or manager-ignited prescribed burning. Our objective in this chapter is to evaluate these assertions—in other words, to test the proposition that the 1988 Yellowstone fires were an abnormal event, and that they severely damaged park ecosystems. Based on an examination of Yellowstone's fire history during the past several centuries (Chapters 2, 3), plus the postfire responses that we have measured since 1988, we argue that Yellowstone's coniferous forest ecosystems were not degraded or altered significantly in any abnormal ways, either by the 1988 fires or by pre-1988 management activities. We further suggest that many other high-elevation wilderness areas in western North America are similar, in other words, they remain within their range of natural variation (Landres and others 1999) and do not require active intervention to restore natural conditions.

It is important to note that we restrict our analysis to the high-elevation forested plateaus and mountains that cover approximately 80 percent of Yellowstone National Park plus extensive contiguous areas outside the park boundaries (which we refer to as the Yellowstone Plateau). We do not deal with lower-elevation ecosystems in Yellowstone's northern winter ungulate range, where climate, vegetation, and ecological history are very different from the high-elevation systems upon which we focus. Nor do we challenge the interpretations of ecological change and need for restoration in ponderosa pine and some other low-elevation forest types in western North America. On the contrary, we emphasize that assessments of ecosystem "health" must explicitly consider the ecological characteristics and histories of different forest types, and that management goals and methods must be tailored to unique local conditions (Dahms and Geils 1997).

As a framework for our assessment, we pose a set of general criteria by which

Table 14.1. Criteria for evaluating the need for active restoration

1. Is the current disturbance regime within the historical or natural range of variability?
2. Are current stand structure and landscape structure within the historical or natural range of variability?
3. Are any species or communities extinct or threatened with extinction because of alterations in the disturbance regime?
4. Have recent disturbances been accompanied by normal return of community structure and composition?
5. Have recent disturbances been accompanied by normal return of ecosystem function, for example, energy flow and material cycling?
6. Have recent disturbances been associated with any novel or unexpected effects that are regarded as undesirable?

we can evaluate the need for active intervention to restore degraded ecological conditions (Table 14.1). These criteria may also be useful in other ecosystems to determine whether restoration efforts are needed. Harig and Bain (1998), Moore and others (1999), and others have utilized similar approaches in both aquatic and terrestrial ecosystems.

IS THE CURRENT DISTURBANCE REGIME WITHIN THE RANGE OF NATURAL VARIATION?

Fire is the most important natural disturbance in high-elevation forested landscapes of Yellowstone National Park (Despain 1990). Most lightning-caused fires are small (< 1 ha) and produce little ecological change (Renkin and Despain 1992). However, infrequent large, severe fires create and maintain a mosaic of patches of different stand ages and stages of postfire recovery. This mosaic produces a landscape pattern that is very striking when viewed from the air and that probably influences a variety of ecological characteristics and processes (Romme and Knight 1982, Knight and Wallace 1989, Foster and others 1998). Tree-ring evidence shows that a fire regime dominated by infrequent but large, severe fires has shaped the high-elevation Yellowstone landscape for at least the past three centuries (Romme and Despain 1989). Charcoal and other remains in lake sediments further reveal that infrequent large fires occurred for many centuries prior to the earliest fires documented in tree rings (Millspaugh and others 2000, Chapters 2, 3).

The occurrence of large fires is controlled primarily by regional weather patterns, though fuel conditions also are important under certain weather condi-

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tions (Renkin and Despain 1992, Turner and Romme 1994). Large fires occur only in years with prolonged summer droughts, especially when accompanied by many windy days (Johnson and Wowchuk 1993). The year 1988 was such a time: summer precipitation in Yellowstone Park was 20 percent of normal in June, 79 percent in July, and 10 percent in August. Overall, 1988 was the driest year on record in the park (Christensen and others 1989). In addition to drought, winds exceeding 40 mph were recorded day after day (Rothermel 1991). This distinctive fire regime, which characterizes the high-elevation landscapes of Yellowstone Park, is similar to the fire regimes of boreal forests and other high-elevation or very moist temperate coniferous forest ecosystems (for example, Johnson 1992, Hemstrom and Franklin 1982).

Was Yellowstone's fire history significantly different during the time of park management than during the preceding period without substantial Euro-American influence (Chapter 3)? The period of park management extends from the late nineteenth century through the twentieth century. Although Yellowstone was designated a National Park in 1872, it received little or no fire protection until the U.S. Army assumed management responsibilities in 1886 (Schullery 1997). We regard the century prior to the army's arrival as a reference period characterized by "natural" ecological conditions—at least with respect to fire. This period, from the late eighteenth through late nineteenth century, is a suitable reference period for evaluating the current fire regime because we have reasonably detailed fire history information, and environmental conditions, notably climate, were generally similar (but see Pickett and Parker 1994 for important caveats about this approach).

This is not an easy question to answer. In many southwestern ponderosa pine forests, researchers have applied rigorous statistical models to high-resolution fire history data obtained from tree rings, and have demonstrated that twentieth-century fire intervals have been significantly longer than fire intervals of the eighteenth and nineteenth centuries (for example, Grissino-Mayer 1999, Fule and others 1997). However, for two reasons a rigorous statistical analysis of this kind is problematical in systems—like Yellowstone—characterized by very long fire intervals. First, fire intervals at the scale of individual stands are on the order of decades or centuries even under natural conditions. Therefore even though we have a reasonably detailed 350-year fire history record based on tree rings (Romme and Despain 1989), this record contains too few fire intervals to permit a robust statistical analysis of central tendencies and variance. Second, if we attempt to solve the first problem by extending the fire history record farther back in time based on fire events recorded in lake bottom sediments, we lose

Table 14.2. Occurrence of large fires, by decade since the 1790s, within the 130,000-ha study area in central Yellowstone National Park where Romme and Despain (1989) reconstructed fire history

Decade	Did a Large Fire (>400 ha) Occur in One or More Years?
Period of park management	
1980s	Yes (in 1981 and 1988)
1970s	No
1960s	No
1950s	No
1940s	Yes (in 1940 and 1949)
1930s	Yes (in 1931)
1920s	No
1910s	Yes (in 1910 and 1919)
1900s	No
1890s	No
Premanagement period	
1880s	Yes
1870s	Yes
1860s	Yes
1850s	Yes
1840s	Yes
1830s	No
1820s	No
1810s	Yes
1800s	Yes
1790s	Yes

Note: Large fires are defined as those that burned >400 ha within the study area. Individual fire years are listed for the twentieth century, but precise years are uncertain for earlier fires (see text). The period from the 1890s through the 1980s is regarded as the period of park management; the previous century from the 1790s through the 1880s is the premanagement reference period.

temporal resolution and also encounter significant changes in fire frequency associated with century-scale, regional climatic variation (Millspaugh and others 2000, Chapters 2, 3).

Given these constraints on statistical analysis of Yellowstone's fire history, we made a conservative, semiquantitative assessment based on the frequency of decades in which large fires occurred during the period of park management compared with the preceding reference period (Table 14.2). The focus was on large fires rather than all fires because a few large fires generally account for most

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of the area burned in any century (Johnson 1992), and our fire history reconstructions based on tree rings were focused on detecting large fire events rather than all past ignitions. We chose 400 ha as a minimum fire size for this analysis, because nearly all early fires of this extent would be readily detectable in the landscape mosaic, even if portions had been reburned by later fires. The analysis was restricted to Romme and Despain's (1989) 130,000-ha study area in central Yellowstone National Park, for this is the only portion of the Yellowstone Plateau where we have detailed information on fire occurrence and fire size in the period before written records were kept. (See Houston 1973 and Barrett 1994 and Chapters 2 and 3 for fire history data from other physiographic regions of the park.) Although Romme and Despain (1989 and unpublished data) detected fires as long ago as the 1400s, our analysis here deals only with fires since 1780 because some of the area burned in earlier fires was reburned by later fires, thus obscuring the actual extent of those earlier fires. We identified decades in which large fires occurred rather than individual fire years, because this reflects the resolution of our pre-1900 fire history data: fire scars are uncommon in Yellowstone's subalpine forests, so Romme and Despain (1989) mapped the spatial extent of pre-1900 fires primarily on the basis of the current age structure of dominant trees, tying those age structure data to precise fire-scar dates wherever available. Where we have only the age of the dominant canopy trees, we can determine actual fire dates to within about a decade but cannot distinguish between two or more separate fires within a single year or fires that burned within a few years of each other.

Large fires (greater than 400 ha within the boundaries of the study area) occurred in four of the ten decades between 1890 and 1989 and in eight of the decades from 1790 through 1889 (Table 14.2). The longest intervals without any large fires were three decades in the late twentieth century (1950s–1970s), two decades at the turn of the twentieth century (1890s–1900s), and two decades in the early nineteenth century (1820s–1830s). The three-decade period without large fires in the twentieth century coincides with a period of consistently effective fire suppression in Yellowstone Park. This period began after World War II, when dramatic improvements were made in fire detection and firefighting technologies, and ended in the 1970s when the park implemented a natural fire management program (Schullery 1989). However, the lack of large fires from 1890 through 1909 probably was more a result of wet summer weather conditions than active fire suppression, since the technology for detecting and suppressing fire was not well developed at that time (Schullery 1989, 1997). The relatively fire-free period in the 1820s–1830s was undoubtedly attributable mainly to re-

gional climatic conditions of the time. A paucity of large fires has been documented for this same time period in the American Southwest (Swetnam and Betancourt 1998)—further supporting the idea of regional climate as a primary control on the occurrence of large fires in western North America.

From this analysis we see that the frequency of decades with large fires during the century of park management was about half the frequency during the previous, premanagement century. Especially in the 1950s–1970s, effective fire control undoubtedly prevented some fires that would have been relatively large in the absence of suppression, even if the impact of fire suppression earlier in the century is equivocal. But do those "missing" fires from the 1950s–1970s really make much difference in the long-term history of this landscape? We think not. The 1988 fires probably encompassed some of the areas that would have burned in the 1950s–1970s without suppression. And although burning some of those areas a few decades earlier, rather than all in 1988, might have led to somewhat greater heterogeneity in successional stages and stand structures across the burned landscape, the post-1988 landscape is remarkably heterogeneous (see below). Moreover, large fires (greater than 400 ha) also have occurred in the park in the 1990s and in 2000 and 2001. Finally, although the 1988 fires were seemingly unprecedented in sheer size—they were more extensive than the fires in any other year of the preceding two centuries—the tree-ring data reveal very large fires in the early 1700s that may have been comparable to the 1988 fires (Romme and Despain 1989). We really cannot trace the exact extent of those early-1700s fires because an unknown number of the trees they scarred and of the forests that originated in their aftermath were destroyed by later fires.

We conclude, therefore, that Yellowstone's high-elevation fire regime remains within or nearly within its range of natural variation, and that twentieth-century fire suppression has produced no seriously adverse ecological changes. Thus no attempt at restoration of the fire regime is needed. In fact, it is hard to imagine how we even could "manage" Yellowstone's natural fire regime, controlled as it is mainly by regional climatic patterns rather than local ignitions or fuel conditions. However, we caution that anticipated global climate changes could lead to significant shifts in the disturbance regimes of Yellowstone and many other areas during the new century (Street 1989, Overpeck and others 1990, Balling and others 1992, Flannigan and Van Wagner 1991, Gardner and others 1996, Chapter 2). The question of whether Yellowstone's disturbance regime remains within its range of natural variation should be addressed again in a few decades.

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ARE STAND AND LANDSCAPE STRUCTURE WITHIN THE RANGE OF NATURAL VARIABILITY?

Recent studies in southwestern ponderosa pine forests have shown that tree densities and size class distributions in many stands are far outside the range of natural variability in stand structure because of past grazing, logging, and fire exclusion (for example, Fule and others 1997, Friederici 2003). Although we lack detailed data on past stand structures in Yellowstone's subalpine forests, we have observed nothing here that would suggest abnormal conditions in the twentieth century. For example, photographs taken in the late nineteenth century depict lodgepole pine stands that generally resemble the stands one sees today (Meagher and Houston 1998). A central concern in southwestern ponderosa pine forests is excessive tree density in current stands (for example, Covington and Moore 1994). Many stands in Yellowstone are very dense and have tremendous fuel loads, but these are normal conditions in forests that naturally persist for very long times without major disturbance. We also know that such stand conditions are not unique to the twentieth century. Early European explorers in Yellowstone described similar conditions more than a century ago. For example, after traveling from the Lower to the Upper Geyser Basin in 1875, General W. E. Strong wrote, "We had to pick our way over fallen timber and through dense thickets of pine. . . . We emerged from this labyrinth of down timber." (Strong 1968:72–73). Therefore at the scale of individual subalpine forest stands, current stand structure in Yellowstone apparently is within the range of natural variability.

But what can be said about landscape-scale patterns? Did fire suppression in the twentieth century permit an abnormal area of older forest to develop before the fires of 1988? Is the area of recently burned forest now excessive? We address these questions by examining the mosaic of forest successional stages that existed at various times during the past three hundred years within a 130,000-ha study area in central Yellowstone Park (fig. 2 in Romme and Despain 1989). This historical reconstruction indicates substantial natural variation in proportions of early, middle, and late stages in forest succession. Yellowstone's subalpine landscape is a nonequilibrium system with high variance in landscape structure (Turner and others 1993); no single equilibrium point can serve as a reference condition. Instead, studies of ecological history can help us identify a range of natural variability in landscape structure, and that range can then serve as the reference condition for evaluating current conditions (Pickett and Parker 1994, Cole and Landres 1996, Swetnam and others 1999).

In the mid-1980s, the area occupied by old forests was as high as it had been

at any time during the previous three hundred years (Romme and Despain 1989). However, this pattern cannot be explained entirely or even primarily by twentieth-century fire suppression. A gradual increase in area of old forests began in the late 1800s, long before there was effective fire suppression on Yellowstone's remote high plateaus, because of natural successional processes occurring after very extensive fires that had burned in the early 1700s.

The extent of old forests has been substantially reduced since the 1988 fires, and the area covered by young forests has greatly increased. However, the current proportions of successional stages are similar to the proportions that existed in the mid-1700s, following the extensive fires of the early 1700s (Romme and Despain 1989). Specific locations of old versus young forest patches obviously differ, but the overall landscape mosaic of the year 2000 probably was very similar to the mosaic that existed in 1750. Therefore we conclude that current and recent landscape structures in Yellowstone's subalpine zone are within the range of natural variation for this system.

This interpretation could change during the next century if global climate change leads to increased fire activity, as is predicted by some climate models (Overpeck and others 1990, Chapters 2, 13). Shorter fire intervals and larger fire sizes would produce a landscape dominated by younger forests; old forests might become rare compared to their extent during the past two hundred years (Gardner and others 1996).

ARE ANY SPECIES OR COMMUNITIES EXTINCT OR THREATENED WITH EXTINCTION BECAUSE OF ALTERATIONS IN THE DISTURBANCE REGIME?

Altered disturbance regimes or novel disturbances to ecosystems may lead to local extinctions of species or substantially altered community structure. For example, many marine ecosystems have lost numerous species and are now functionally different than in the past, because of overfishing, pollution, climatic changes, and other factors (Dayton and others 1998). Some southwestern forests may have lost obligate cavity nesting birds because of fire exclusion combined with overharvest of large trees and snags (Balda 1975). Do any of Yellowstone's plant or animal species appear threatened because of changes in fire frequency or severity?

The answer to this question is no—at least for the immediate future and with regard to fire. With the reintroduction of the wolf in 1995, Yellowstone now has its complete complement of pre-Columbian species. There is no evidence that

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the 1988 fires, or the fire suppression that occurred prior to 1988, impaired long-term viability of any population of native species in Yellowstone either through direct mortality or indirect habitat effects (Singer and others 1989). The extent of suitable habitat may be reduced for some obligate old-growth forest species—for example, pine marten *(Martes americana),* but mature or old-growth forests still form large patches encompassing thousands of hectares. The extent of habitat for species that thrive mainly in recently burned forests—for example, Bicknell's geranium *(Geranium bicknellii),* dragonhead *(Dracocephalum parviflorum),* and three-toed woodpeckers *(Picoides arcticus* and *P. tridactylus)*—has increased since 1988, and many of these species became locally abundant during the first three years after the fires (Turner and others 1997 and personal observations). The robust response of these previously rare species to the 1988 fires indicates that they can persist for many decades without large fires, and all of the expected successional stages and habitat types are still well represented on the Yellowstone Plateau. We conclude, therefore, that neither the large fires in 1988 nor the preceding fire suppression has threatened any native species or communities in the park. Indeed, Yellowstone's subalpine landscape demonstrates remarkable ecological integrity (see also Dayton and others 1998).

Despite this optimistic assessment of community response to fire, we must note the potential for other kinds of disturbances to threaten long-term ecological integrity of the Yellowstone subalpine system. Blister rust *(Cronartium ribicola),* an alien fungus disease from Eurasia, has decimated whitebark pine forests in Montana and Idaho (Tomback and others 2001). Although blister rust has not yet caused extensive mortality in whitebark pine in and around Yellowstone Park, the disease is present and could become more serious in the future. Loss of whitebark pine, or even a significant decline in its population, could have cascading effects on the ecosystem. For example, grizzly bears depend heavily on whitebark pine nuts during some portions of the year (Tomback and others 2001). Whitebark pine also may be threatened over longer time frames by global climate change (Bartlein and others 1997, Chapter 2).

HAVE RECENT DISTURBANCES BEEN ACCOMPANIED BY NORMAL RETURN OF COMMUNITY STRUCTURE AND COMPOSITION?

The 1988 Yellowstone fires were not only very large, but also strikingly heterogeneous in burn severity (Turner and others 1994). Even the largest expanses of

severely burned forest contained patches of less severely burned or even unburned forest, and were surrounded by a zone of lower severity. In 1990 we initiated a long-term study of the effects of fire size and severity on early postfire succession, a study that is still ongoing (Turner and others 2003b). We reported our findings as of 1993 in Turner and others (1997), and we report here the trends through 1996.

This research was designed to address two general questions that are directly relevant to the question being addressed in this chapter: (1) What is the relative importance of burned patch size, fire severity, prefire vegetation, and local abiotic conditions (climate and soils) in predicting plant community composition and structure during the first few years after fire? (2) Do initial differences persist for many years, or do community structure and composition converge among sites having different fire size, severity, prefire vegetation, and abiotic conditions?

Methods

In our initial appraisal of the heterogeneity of fire effects in 1989 (Turner and others 2000), we recognized three classes of fire severity that could be readily identified and mapped either in the field or remotely (Table 14.3). We subsequently mapped all patches of crown fire in Yellowstone Park from satellite imagery and then selected three patches in each of three geographic locations within the burned portions of the Yellowstone Plateau (fig. 1 in Turner and others 1997). The three geographic locations encompass a range of elevation and substrate conditions representative of Yellowstone's subalpine plateaus (Table 14.4). In general, the Cougar Creek area is at low elevation on relatively infertile substrates; the Fern Cascades area is at higher elevation on very infertile substrates, and the Yellowstone Lake area is at the highest elevation on relatively fertile substrates. See Turner and others (1997) for additional details.

In each patch, we established four transects radiating from the center in subcardinal directions. Along each transect we placed permanent sampling points at variable distances. Points were generally 100 m apart in large tracts of uniform fire severity but were more closely spaced (5–20 m) in areas of transition between fire severity classes (for example, from crown fire to severe surface fire). Each sampling point was a 50-m^2 circular plot, the center of which was permanently marked with a stake or rock cairn and located with GPS. Within the 50-m^2 plot, we measured percent cover of plants and abiotic components in eight 0.25-m^2 point intercept frames (Floyd and Anderson 1987), and we listed all vascular plant species present within a 10 m × 1 m quadrat. We also determined the pro-

Table 14.3. Classification of fire sever

Crown Fire	Seve
Canopy needles consumed	Canopy not c
Canopy trees killed	Canopy
Organic litter on the forest floor completely consumed	Organic floor scorch from
Aboveground portions of all shrubs and herbs killed	Abovegr most killed
Stand-replacing	Stand-re

Table 14.4. Description of the three geo sampling was conducted from 1990 thr

Attribute	Cougar C
Patch sizes and sampling points	
Large patch	500 ha (84 p
Moderate patch	91 ha (46 po
Small patch	1 ha (34 poi
Elevation range	2150–2300
Geologic substrate	Infertile rhy and tuff
Prefire vegetation	Dense, ca. 130-yr-ol *Pinus con* forests, w *Ceanothu velutinus*, *Calamagr rubescens*, *Carex ross*

Note: See Turner and others 1997 for addition

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Table 14.3. Classification of fire severity

Crown Fire	Severe Surface Fire	Light Surface Fire
Canopy needles consumed	Canopy needles killed but not consumed	Canopy needles unharmed
Canopy trees killed	Canopy trees killed	Canopy trees not killed
Organic litter on the forest floor completely consumed	Organic litter on the forest floor mostly consumed; scorched needles added from the canopy	Organic litter on the forest floor consumed only in patches; mostly intact
Aboveground portions of all shrubs and herbs killed	Aboveground portions of most shrubs and herbs killed	Aboveground portions of shrubs and herbs killed only in patches
Stand-replacing	Stand-replacing	Not stand-replacing

Table 14.4. Description of the three geographic locations and burned patches where sampling was conducted from 1990 through 1996 in Yellowstone National Park

Attribute	Cougar Creek	Fern Cascades	Yellowstone Lake
Patch sizes and sampling points			
Large patch	500 ha (84 points)	480 ha (103 points)	3698 ha (59 points)
Moderate patch	91 ha (46 points)	200 ha (83 points)	74 ha (67 points)
Small patch	1 ha (34 points)	1 ha (37 points)	1 ha (40 points)
Elevation range	2150–2300 m	2270–2500 m	2400–2700 m
Geologic substrate	Infertile rhyolite and tuff	Infertile rhyolite	Moderately fertile andesite and lake sediments
Prefire vegetation	Dense, ca. 130-yr-old *Pinus contorta* forests, with *Ceanothus velutinus, Calamagrostis rubescens,* and *Carex rossii*	Ca. 290-yr-old *Pinus contorta* forests, with *Vaccinium scoparium, Lupinus argenteus,* and *Carex geyeri*	Ca. 250–400+-yr-old forests of *Pinus contorta* and *Picea engelmannii,* with *Vaccinium scoparium, Arnica cordifolia,* and *Carex geyeri*

Note: See Turner and others 1997 for additional details.

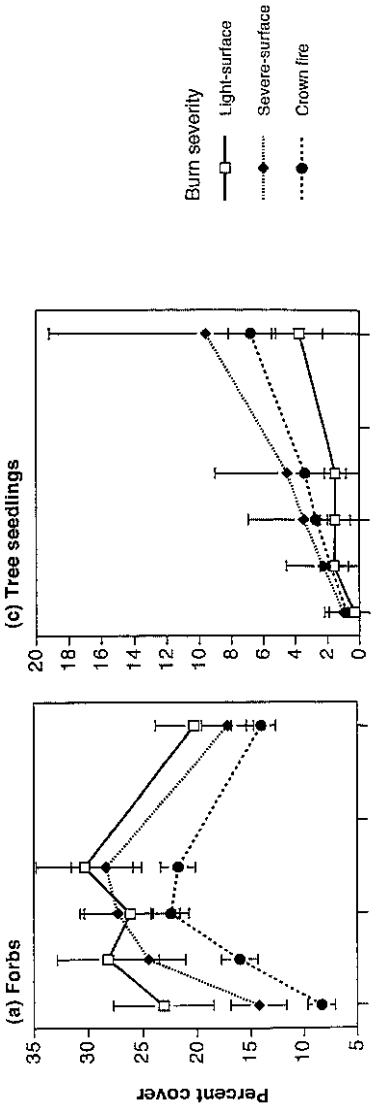
portion of serotinous versus open cone–bearing lodgepole pine trees that had been present at the time of the fire, using methods developed by Tinker and others (1994). See Turner and others (1997) and Chapter 4 for additional sampling details.

Results

Total plant cover was significantly different among *fire severity* classes (Table 14.3) in 1990, with mean values of 14 percent in crown fire sites, 32 percent in severe surface burns, and 47 percent in light surface fires (Fig. 14.1e). Total cover increased from 1990 to 1993 in all severity classes. We then saw an apparent decrease in cover, especially of herbs, from 1993 to 1996 (Fig. 14.1), which could reflect the onset of resource depletion, competition, or other processes. However, we believe that this seeming decline is actually an artifact of the cool, late spring in 1996 that slowed the phenological development of plants throughout our study area. Continued sampling over the next decade(s) will reveal whether the drop in plant cover from 1993 to 1996 is a phenological anomaly or a genuine trend (cf. Turner and others 2003b). What we believe to be the more significant pattern in 1996 is a convergence in total plant cover among all three burn severity classes: the large differences that were so conspicuous immediately after the fires had essentially disappeared within eight years. Trends in percent cover of forbs and graminoids (Fig. 14.1a,b) were generally similar to those for total biotic cover. In contrast, initial differences in tree cover appeared to become more pronounced over time, although confidence intervals generally overlapped (Fig. 14.1c). Shrub cover remained highest in light surface burns throughout the first eight years after fire (Fig. 14.1d).

Patterns in total plant cover related to *patch size* were similar to those of burn severity. Small patches initially had twice the cover of moderate and large patches (approximately 40 percent versus 20 percent), but by 1996 the differences had become smaller and cover appeared to be converging among patch sizes (Fig. 14.2c) (cf. Turner and others 2003b). Patterns for forb and graminoid cover (Fig. 14.2 a,b) largely mirrored the pattern for total biotic cover. However, some closely related species exhibited striking individualistic responses; for example, the highest cover of *Carex geyeri* was seen in small patches, while *Carex rossii* was most abundant in large patches (data not shown).

Differences in total plant cover among *geographic locations* were apparent throughout the period of measurement. The lowest total cover values (Fig. 14.3e) were measured in the Fern Cascades area, which has the most infertile soils. Total percent cover was similar in the Lake and Cougar Creek areas through 1993,



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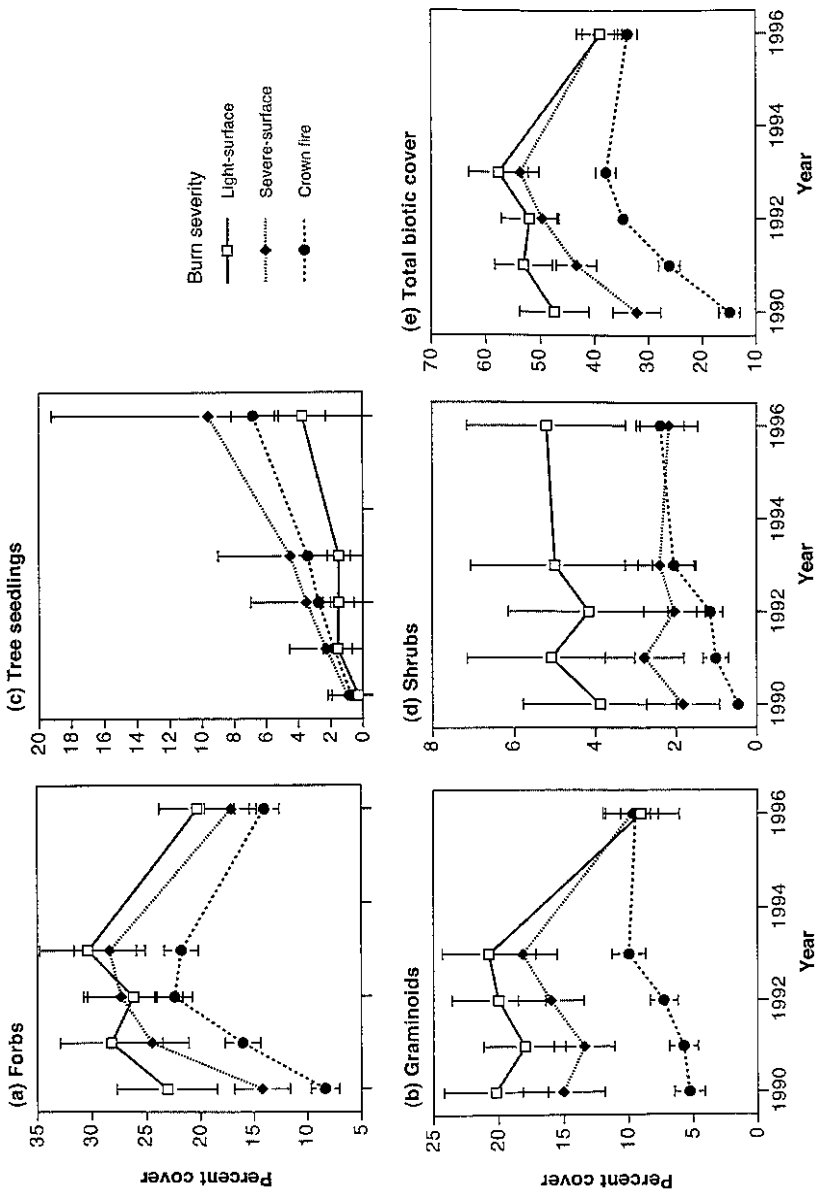
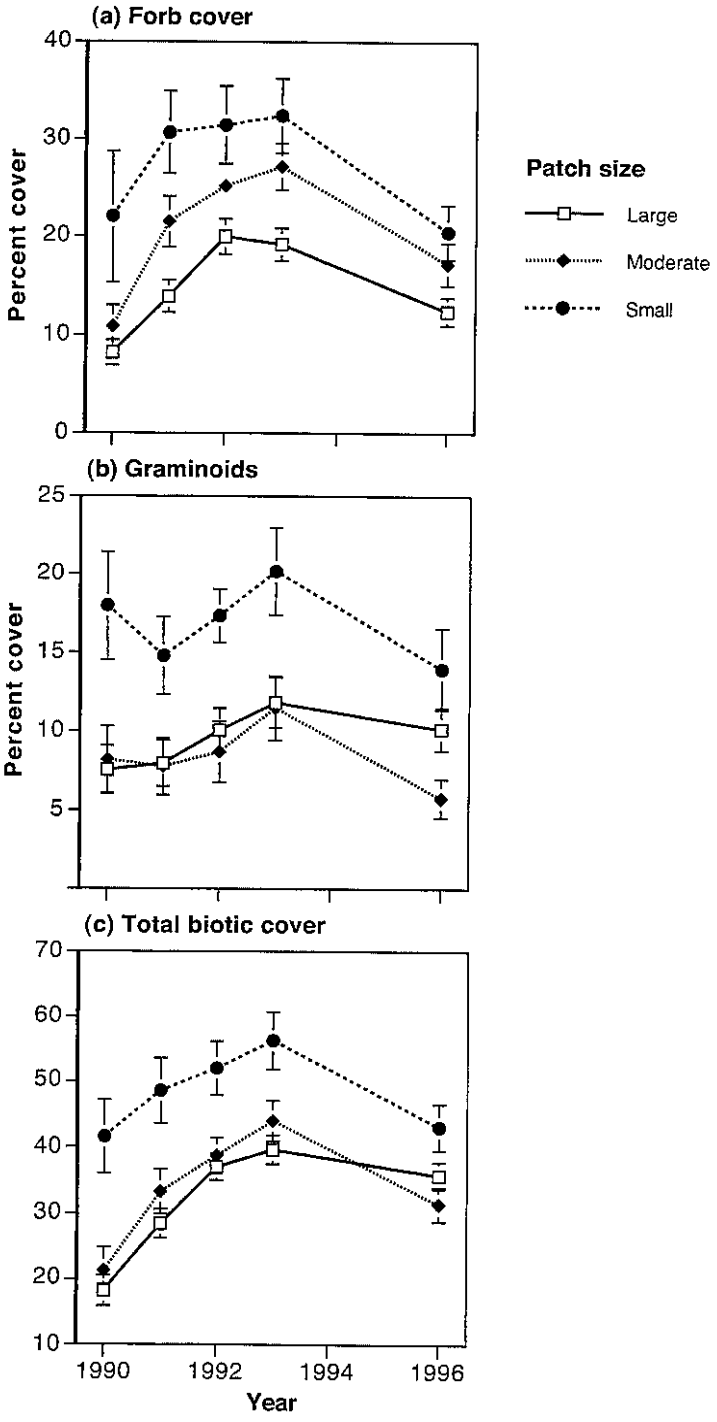


Figure 14.1. Percent cover of forbs, graminoids (grasses and sedges), tree seedlings, shrubs, and all plants combined (total biotic cover) in relation to burn severity in Yellowstone National Park, Wyoming.



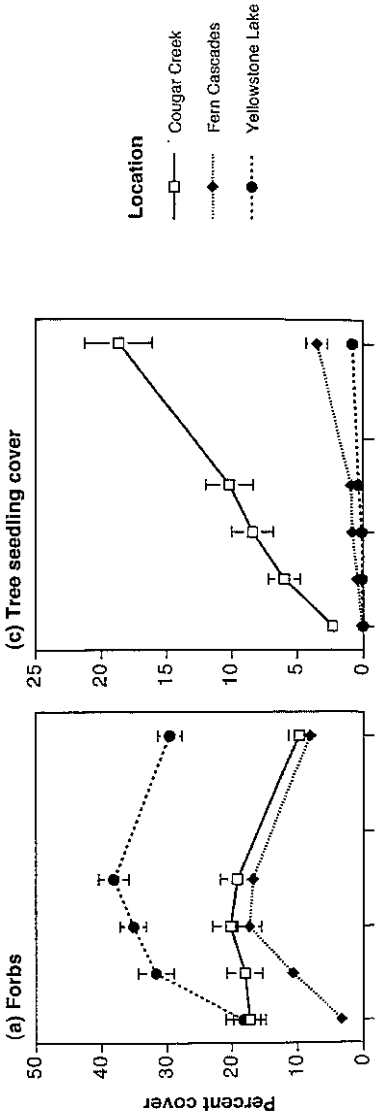


Figure 14.2. Percent cover of forbs, graminoids (grasses and sedges), and all plants combined (total biotic cover) in relation to size of burned patch in Yellowstone National Park, Wyoming.

and sedges), and all plants
d patch in Yellowstone National

Figure 14.3. Percent cover of forbs, graminoids (grasses and sedges), tree seedlings, shrubs, and all plants combined (total biotic cover), in three geographic locations in Yellowstone National Park, Wyoming.

but in 1996 cover at Cougar Creek was dropping toward the level of Fern Cascades, while cover in the Lake area remained high. It appears that total plant cover is now converging toward similar, relatively low levels in the two areas (Fern and Cougar) underlain by infertile rhyolite substrates (cf. Turner and others 2003b). However, the Lake area, with its fertile andesites and lake bottom sediments, is diverging from the other two areas and developing relatively higher total plant cover (Figure 14.3e). Another striking pattern is the development of very different relative proportions of forbs, graminoids, shrubs, and trees among the three geographic locations (Fig. 14.3a–d). The Yellowstone Lake area has been dominated by forbs and graminoids, while the Cougar Creek site initially had high cover of graminoids but by 1996 was dominated by tree seedlings. Shrubs have constituted a relatively small proportion of cover in all locations in all years.

The density of *opportunistic species* (defined as species that require open habitats and are rare in unburned forests) generally was highest in large patches (Fig. 14.4) and in areas of more severe fire (Fig. 14.5). The density of most opportunistic species peaked three to five years after the fires and then decreased substantially. However, some opportunistic species increased again on some sites in 1996 (for example, *Gayophytum diffusum* and *Cirsium arvense,* Figs. 14.4, 14.5). There were no striking differences among geographic locations in the density of opportunistic species (data not shown).

Species richness (the number of vascular plant species in a 10-m^2 plot) was initially similar in all three locations but had diverged greatly by 1996, with means of 17 species/plot in the Lake area but only 9 and 11 in Fern Cascades and Cougar Creek, respectively (Fig. 14.6a). The greater richness of the Lake area probably reflects the higher precipitation and more fertile substrates in this part of Yellowstone Park. Differences in richness related to burn severity were initially slight, and remained slight through 1996 (Fig. 14.6b). With respect to patch size, richness was highest in small patches and lowest in moderate patches, and these patterns persisted through 1996 (Fig. 14.6c).

Perhaps the most striking of all the patterns we observed were those related to *lodgepole pine seedling density.* Most seedlings became established in 1989 and 1990, and these initial spatial patterns in seedling density then persisted throughout the period of measurement. We refer to these plants as "seedlings" even though by 1996 most were eight to nine years old and up to a meter tall. The highest pine seedling densities were seen in severe surface burns, with lower densities in crown fire and light surface fire areas (Fig. 14.7b). This probably was because crown fires killed much of the seed supply in the canopy (Johnson and

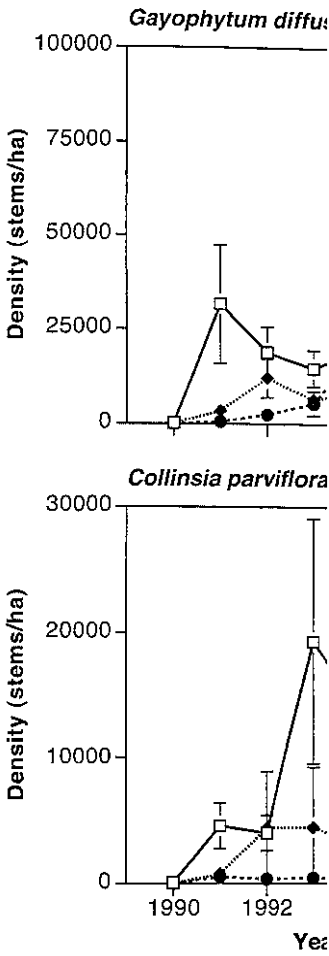


Figure 14.4. Density of two species of oppo
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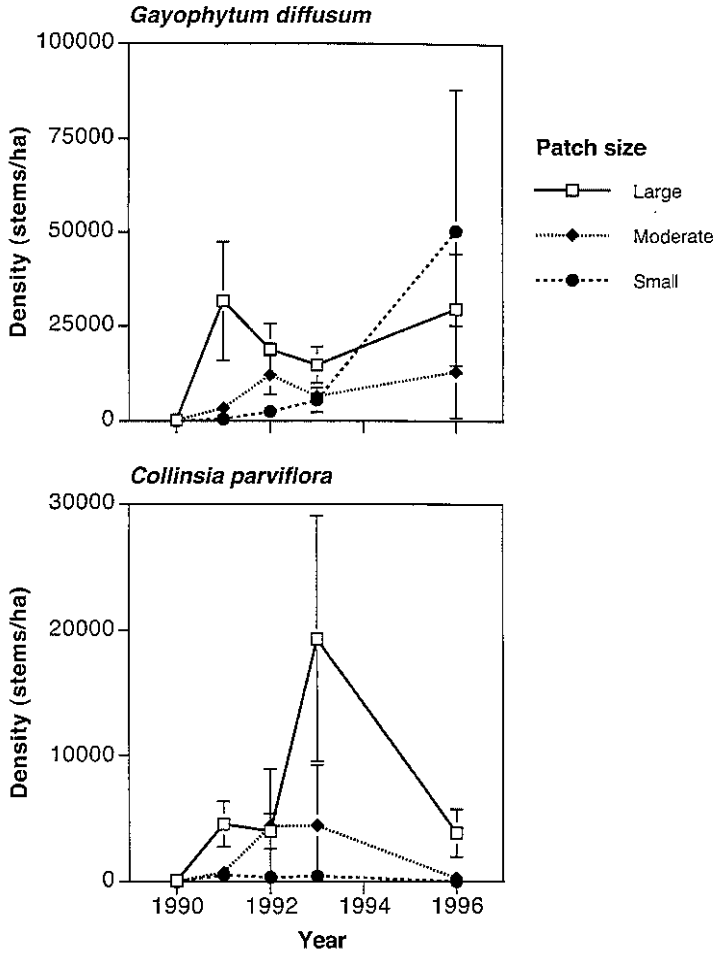

Figure 14.4. Density of two species of opportunistic plants (species that thrive in disturbed areas and are rare in unburned forests) in relation to size of burned patch in Yellowstone National Park, Wyoming. Both species are native annuals.

Gutsell 1993), while light surface fires produced little bare mineral soil for seedling establishment. In contrast, severe surface fires consumed most of the litter on the forest floor and killed the adult trees but did not consume cones and needles in the canopy. Seedling density in crown fire patches also decreased significantly with distance from the nearest patch of severe surface fire (data not shown). Patch size also influenced pine seedling density, with highest densities in large patches and lowest densities in small patches (Fig. 14.7c) (see also Chapter 4).

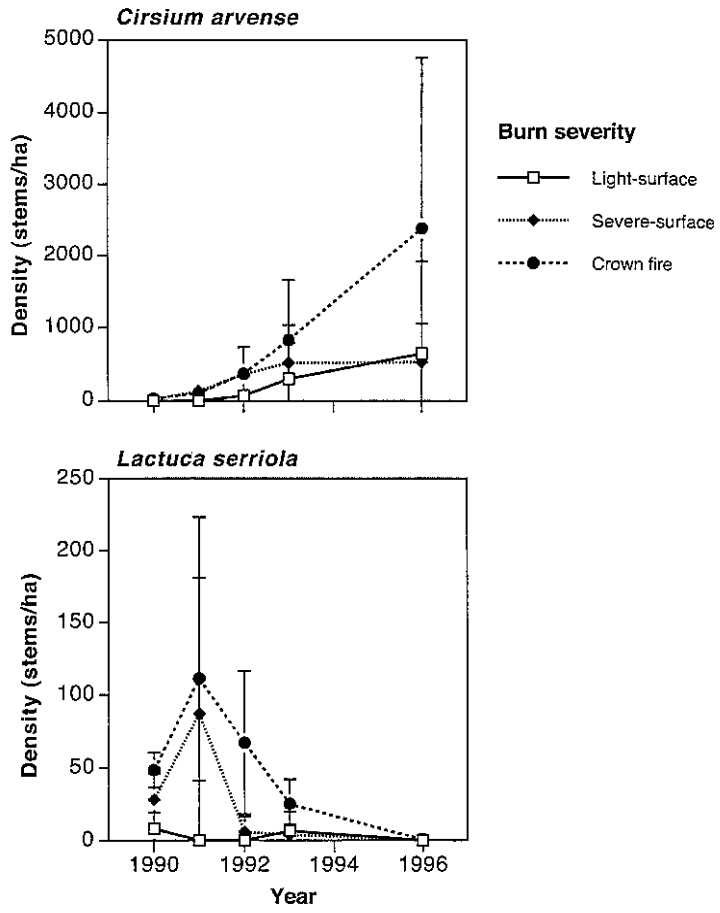

Figure 14.5. Density of two species of opportunistic plants (species that thrive in disturbed areas and are rare in unburned forests) in relation to burn severity in Yellowstone National Park, Wyoming. Both species are nonnative invaders from Eurasia.

By far the greatest differences in lodgepole pine seedling density were seen among geographic locations. Density in the Cougar Creek area was two orders of magnitude greater than in the Fern Cascades or Lake area (Fig. 14.7a). The extremely high densities in the Cougar area were the result of very high levels of cone serotiny in the forests that burned in 1988. Indeed, percent cone serotiny in the prefire forest was the best predictor of postfire pine seedling density. At Cougar, 65 percent of the trees were serotinous, compared with only 5 percent in the Fern Cascades area and 2 percent in the Lake area (Tinker and others 1994, Chapter 4). Correspondingly, mean pine seedling density in 1996 was 43,000

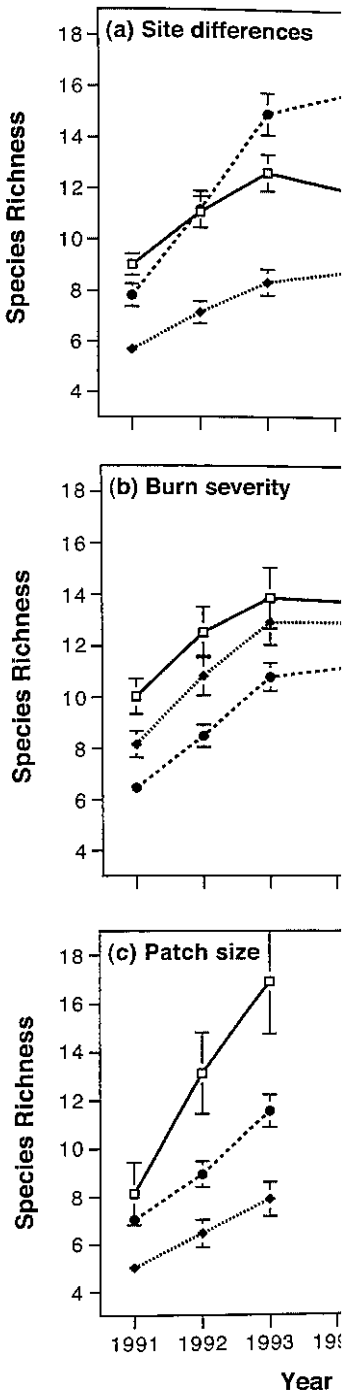

Figure 14.6. Species richness (number of
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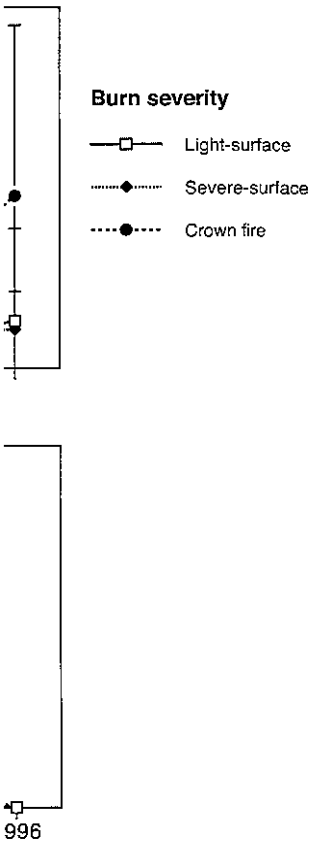

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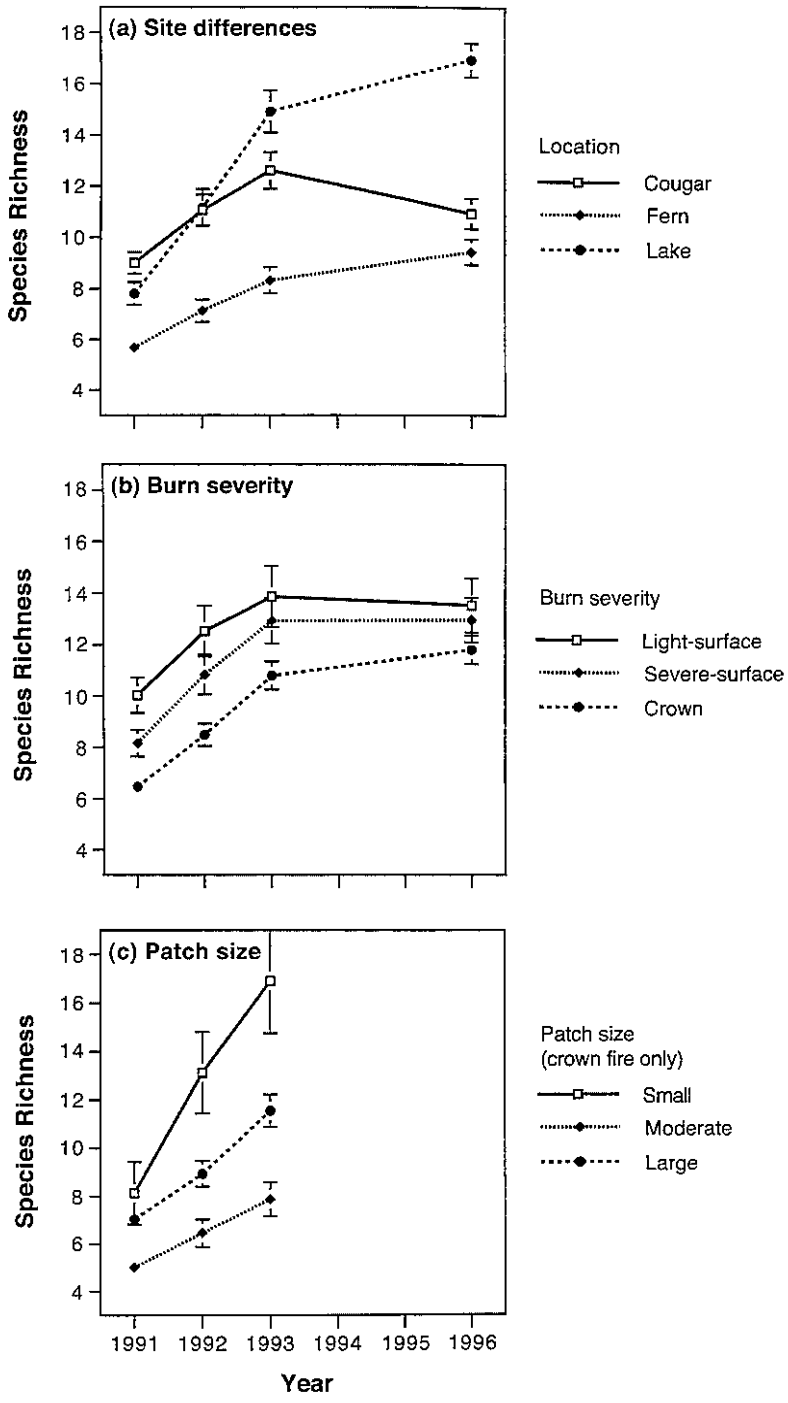

Figure 14.6. Species richness (number of vascular plant species within a 10-m^2 plot) in relation to geographic location (site differences), burn severity, and size of burned patch, in Yellowstone National Park, Wyoming.

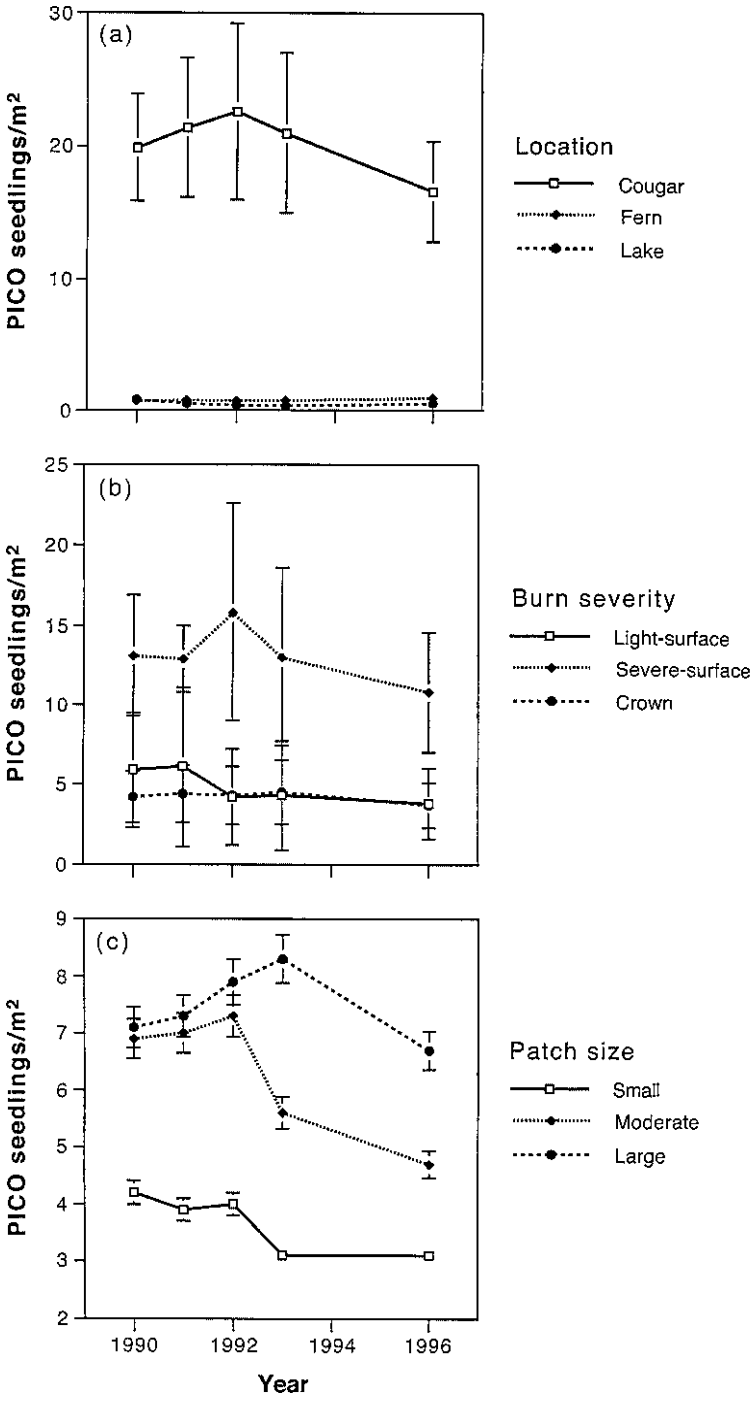

Figure 14.7. Lodgepole pine (PICO) seedling density in relation to geographic location, burn severity, and size of burned patch, in Yellowstone National Park, Wyoming.

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Discussion

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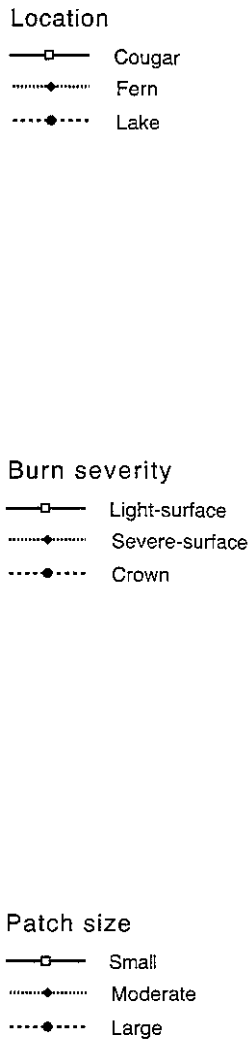

relation to geographic location, National Park, Wyoming.

stems/ha in the large Cougar patch, but only 4,700 and 14 stems/ha in the large patches at Fern Cascades and Lake, respectively.

Discussion

Differences among the three geographic locations became increasingly prominent during the first eight years of postfire succession, reflecting the powerful influence of abiotic gradients in soils and climate on plant community structure and composition. In 1996, total biotic cover and plant species richness were highest on the more fertile substrates of the high-elevation Yellowstone Lake region, and lowest on the infertile substrates of the lower-elevation Fern and Cougar regions. Plant cover was largely herbaceous in the Yellowstone Lake region but consisted mostly of trees and shrubs in the Cougar Creek region. These results suggest a general pattern of initial similarity in community structure and composition, followed within a decade by divergence along abiotic gradients of microclimate and soils conditions.

In contrast, among burn severity classes we observed a general pattern of large initial differences in total plant cover and richness followed by convergence within the first decade. Total plant cover and richness were still significantly higher in 1996 in less severely burned areas, and densities of some opportunistic species were significantly higher in more severely burned areas—but the magnitude of differences had become relatively small. The important exception to this general pattern of convergence was seen in lodgepole pine seedling densities. Differences among burn severity classes, patch sizes, and geographic locations became established early on, and have persisted with little change. Where the burned forest contained a high proportion of serotinous trees, postfire pine seedling density is orders of magnitude greater than in places where few or no trees were serotinous (Chapter 4). For any given level of prefire serotiny, areas of severe surface fire support approximately 2.5 times as many seedlings per hectare as adjacent areas of crown fire or light surface fire, and pine seedling density within crown fire areas decreases with distance from an area of severe surface fire.

The patterns in lodgepole pine seedling density that became established within the first two years after the fires—patterns related to prefire serotiny, fire severity, and patch size—apparently will determine the course of stand development for many decades to come. Although we continue to detect a few new pine seedlings each year, total seedling densities in any given location were not significantly different among the years 1991, 1992, 1993, and 1996. Moreover, we have observed very few dead or dying pine seedlings—even in extremely dense stands (> 100,000 seedlings/ha) (Chapter 4). Self-thinning in dense stands will

Table 14.5. Comparison of three areas (large patches described in Table 14.4) illustrating alternative initial pathways of succession following the 1988 Yellowstone fires

Geographic Location	Initial Successional Pathway	Pine Seedling Density (Mean Stems ha^{-1})	Mean Cover of Trees + Shrubs	Mean Cover of Forbs + Graminoids	Mean # Vascular Plant Species in 10-m^2 Plots
Cougar Creek	High-density lodgepole pine	43,000	32%	7%	10
Fern Cascades	Low-density lodgepole pine	4,700	6%	19%	10
Yellowstone Lake	Nonforest	14	2%	40%	16

Note: All three areas were forested at the time of the fires. Data are from 1996 in areas of crown fire (areas of light or severe surface fire excluded).

surely occur eventually, but no significant thinning had yet begun as of 2003 (Turner and others 2003b). Thus at least three major successional trajectories now can be identified in the forested areas burned by the 1988 fire (Table 14.5). These alternative trajectories, distinguished mainly by huge differences in lodgepole pine seedling density, create a tremendous heterogeneity of stand structure throughout the areas burned in 1988. The functional implications of these alternative trajectories (for example, for productivity and nutrient cycling) are a major focus of our ongoing research, and our findings to date are presented later in this chapter (see Chapter 11, as well).

Returning to the central question of this chapter, whether restoration is needed after the 1988 fires, we find that postfire community development varies enormously across the Yellowstone Plateau—but nowhere do we find evidence of abnormal or dysfunctional response to the 1988 fires. On the contrary, the documented patterns in plant cover, richness, and pine density generally can be explained by variation in climate, soils, fire size, fire severity, and prefire serotiny. Observations by Romme and Despain (1989 and unpublished data), as well as more recent studies (Kashian 2002) suggest that earlier large fires were followed by similar variability in development of community structure.

An especially significant aspect of postfire community development on Yellowstone's subalpine plateaus is the relative scarcity of alien weeds. Invasive alien plant species have dramatically altered postfire succession in many other areas,

and are considered to be one of the r
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HAVE RECENT DISTURBANCES BEEN ACCOMPANIED BY NORMAL RETURN OF ECOSYSTEM FUNCTION?

Major disturbances may disrupt pro
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ANPP and LAI

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Mean Cover of Trees + Shrubs	Mean Cover of Forbs + Graminoids	Mean # Vascular Plant Species in 10-m^2 Plots
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6%	19%	10
2%	40%	16

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and are considered to be one of the major threats to the ecological integrity of natural areas (for example, Mooney and Drake 1986, Drake and others 1989, Cole and Landres 1996, D'Antonio 2000). We have detected several alien species in our study areas (for example, *Cirsium arvense, Filago arvense, Lactuca serriola*), but generally these species are patchily distributed (especially along maintained trails) and one finds only native species throughout extensive areas of the Yellowstone Plateau.

HAVE RECENT DISTURBANCES BEEN ACCOMPANIED BY NORMAL RETURN OF ECOSYSTEM FUNCTION?

Major disturbances may disrupt processes of energy flow and nutrient cycling (Chapter 5, 8). For example, numerous studies have reported increased nutrient loss and runoff following fire or clear-cutting (Vitousek and others 1979, Vitousek and Melillo 1979, Vitousek and Matson 1985, Binkley and others 1992b, Parsons and others 1994, Jewett and others 1995, Likens and Bormann 1995). To evaluate the extent of "damage" to the Yellowstone ecosystem caused by the 1988 fires, we report on studies initiated in 1996 to determine the effects of the fires and subsequent heterogeneity in postfire succession, on three key parameters of ecosystem function. These parameters include aboveground net primary productivity (ANPP), leaf area index (LAI), and rate of nitrogen mineralization. ANPP is important because it reflects total energy flow through the ecosystem and forms the base of the food web. LAI is highly correlated with rates of photosynthesis and transpiration, which in turn are related to rates of nutrient uptake (Knight and others 1985). Nitrogen is a limiting nutrient in many boreal ecosystems (Fahey and others 1985, Fahey and Knight 1986, Binkley and others 1995, Chapter 5). Our research on ecosystem function after fire is ongoing. We report here our results through 1998, and relate these preliminary findings to the question of whether ecosystem processes were abnormally altered by the 1988 fires.

ANPP and LAI

In 1997, nine years after the 1988 fires, we measured ANPP and LAI of lodgepole pine seedlings and ANPP of herbaceous plants. Measurements were made at four sites representing a wide range of lodgepole pine seedling densities (100–62,800 stems/ha) and two different soil fertility classes (relatively fertile and infertile). Standard techniques of dimension analysis were used to measure ANPP and LAI; see Reed and others (1999) for details.

Table 14.6. Aboveground net primary production and leaf-area index in four postfire stands, nine years after the 1988 Yellowstone fires

	Study Site			
	Infertile Nonforest	Fertile Nonforest	Low-Density Pine Forest	High-Density Pine Forest
Lodgepole pine density (stems/ha)	100	1,000	20,100	62,800
Elevation (m)	2750	2560	2560	2070
Substrate	infertile rhyolite	relatively fertile andesite	infertile rhyolite	infertile rhyolite
Mean seedling height in 1997 (m)	0.62	0.44	0.42	0.89
Tree ANPP (mg/ha/yr)	0.0021	0.0164	0.1431	3.8134
Herbaceous ANPP (mg/ha/yr)	0.2434	0.7374	0.7121	0.1998
Total ANPP (mg/ha/yr)	0.2455	0.7537	0.8552	4.0133
Tree LAI (m2/m2)	0.002	0.012	0.138	1.822

Source: Reed and others 1999.
Note: "Nonforest" sites were forested at the time of the 1988 fires, but tree density after the fires is extremely low.

Tree ANPP and LAI generally increased as pine density increased, as would be expected (Table 14.6). Interestingly, total ANPP (trees plus herbs) was comparable in the low-density pine stand and the nonforest stand on a fertile substrate, because of the high herbaceous ANPP in the latter stand (Table 14.6). The highest ANPP and LAI were seen in the high-density pine stand, in part because of the dense trees, but possibly also because of a longer growing season at this lower elevation site.

What do these findings tell us about damage and recovery from the 1988 Yellowstone fires? We have detected considerable variability in ANPP and LAI across the landscape a decade after the fires. However, this variability can be explained primarily by differences in abiotic conditions (local substrate and climate) and in lodgepole pine seedling density (which is a function of fire size, severity, and prefire serotiny, as described in the previous section). We find no evidence of inadequate recovery from the fires. Rather, recovery of ecosystem function appears remarkably rapid. After only nine years, ANPP and LAI in the high-density pine stand was close to or within the range of values measured in mature coniferous forests elsewhere (Chapter 4).

NITROGEN DYNAMICS

Fire has a profound effect on nitrog
trogen is lost directly to the atmosph
and substantial loss of N may follow
over N cycling. Nitrogen is a useful
reasons: N limits primary productiv
nitrate-N in soil water and streamw
bances that lead to N leaching (Born
1979, Parsons and others 1994, Chap
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ers 1973, Helvey and others 1976, T
Gosz and White 1986, Covington an
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term declines in N uptake by vascu
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The consequences for nitrogen a
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Study Site		
st	Low-Density Pine Forest	High-Density Pine Forest
	20,100	62,800
	2560	2070
ite	infertile rhyolite	infertile rhyolite
	0.42	0.89
	0.1431	3.8134
	0.7121	0.1998
	0.8552	4.0133
	0.138	1.822

the 1988 fires, but tree density after the

s pine density increased, as would
ANPP (trees plus herbs) was com-
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of a longer growing season at this

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ole variability in ANPP and LAI
lowever, this variability can be ex-
onditions (local substrate and cli-
y (which is a function of fire size,
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nine years, ANPP and LAI in the
n the range of values measured in

mature coniferous forests elsewhere in North America (Reed and others 1999, Chapter 4).

NITROGEN DYNAMICS

Fire has a profound effect on nitrogen (N) cycling in forested ecosystems. Nitrogen is lost directly to the atmosphere through combustion of organic matter, and substantial loss of N may follow because of the disruption of biotic controls over N cycling. Nitrogen is a useful indicator of ecosystem function for several reasons: N limits primary productivity (Reich and others 1997); the presence of nitrate-N in soil water and streamwater can be used as an indicator of disturbances that lead to N leaching (Bormann and Likens 1979, Vitousek and Melillo 1979, Parsons and others 1994, Chapter 8); and relative rates of nitrogen mineralization are fairly easily estimated. Nitrate in western coniferous forests is present in very low concentrations except after major disturbances (Brown and others 1973, Helvey and others 1976, Tiedemann and others 1978, Binkley 1984a, Gosz and White 1986, Covington and others 1991, Covington and Sackett 1992, Parsons and others 1994, Jurgensen and others 1997). Disturbances lead to short-term declines in N uptake by vascular plants and increased nitrification by soil microbes, thereby enhancing nitrate production. Therefore, nitrate levels can be used as indicators of whether or not ecosystem development since the 1988 fires has produced a sufficient amount of biomass (especially sufficient root biomass to fill root gaps; Parsons and others 1994) to immobilize the ammonium-N made available through mineralization after disturbance.

The consequences for nitrogen availability resulting from the spatial variation in burn severity and successional pathways are not known. Within different successional pathways (Table 14.5), how long will it be before rates of nitrate production no longer differ from intact forest? Within a stand, N availability could simply be related to leaf area development and ANPP, regardless of composition. However, N availability might be strongly influenced by the relative amount of herbaceous and coniferous leaf area, in which case the variability in successional pathways across the landscape may have important effects. Nitrogen mineralization rates were higher in Canadian boreal forest stands with deciduous species than in conifer stands (Pare and others 1993), and large differences in net N mineralization rates have been associated with successional changes from poplar to white spruce in an Alaskan chronosequence (Van Cleve and others 1993). We measured N mineralization in 1997–1998 to determine (1) whether nitrogen availability ten years after the 1988 fires was similar to that ob-

served in similar mature stands, and (2) whether nitrogen availability in the post-1988 stands varied with plant community structure, particularly the density of lodgepole pine seedlings. In addition, we sampled streamwater at the end of snowmelt during the summer of 1997 to determine whether there was any evidence of elevated nitrate concentrations in areas burned during the 1988 fires.

Methods

Nitrogen availability was determined for two incubation periods. First, we conducted three sequential monthlong incubations during the 1997 growing season at two sites burned in 1988 and differing in postfire pine seedling density. Second, we conducted yearlong incubations at six sites, including three sites burned in 1988 but having different postfire pine seedling densities, one site that burned in 1996 (the Pelican fire), and two mature lodgepole pine stands, one located near the Pelican burn with similar topographic and soils conditions, and the other located near the areas burned in 1988 (Table 14.7).

In situ incubations of ion exchange resin (IER) (Binkley and Matson 1983, Binkley 1984b, Hart and Binkley 1985, Binkley and others 1986, Binkley and Hart 1989, Binkley and others 1992a, Giblin and others 1994) were used to determine rates of net nitrification and net nitrogen mineralization in our study areas. IER is useful for examining spatially extensive patterns of nitrogen availability, particularly in remote locations that cannot be visited frequently (Binkley and Hart 1989, Hart and Firestone 1989, Giblin and others 1994). The resin bag method does not provide absolute estimates of N availability, but rather it provides an index of relative availability (Hart and Firestone 1989, Binkley and Hart 1989, Binkley and others 1992a,b, Giblin and others 1994).

Incubations used unsieved soil (20 cm depth) in open 5-cm diameter PVC tubes with resin bags at the bottom (resin cores, after DiStefano and Gholz 1986, Strader and others 1989, Binkley and others 1992a,b) at each site (n = 10 resin cores per site). The resin cores were open to water flow, thereby allowing the products of mineralization to leach from the soil column into the resin bags. Resin bags contained 20 g of mixed bed exchange resin (J. T. Baker #4631) in commercial nylon stocking material. Resin bags were saturated with 2 M KCl for 24 hr before use to reduce interference with colorimetric analyses. Initial soil samples were obtained adjacent to each resin core. At the end of each incubation, soil cores were removed and 20-g subsamples of soil were extracted in 100 ml 2 M KCL; the resin bags were refrigerated, washed with deionized water prior to extraction to remove soil particles, and then extracted with 100 ml of 2 M KCl. Extracts were analyzed for nitrate and ammonium using standard colori-

Table 14.7. Study sites where soil nitrogen availability was measured in 1997

Site	Fire History	Substrate	Vegetation
Pelican burn	Burned in 1996	Relatively fertile lake sediments	Burned forest was an old stand of spruce and fir (>300 yr old). . . . In 1997 the soil was covered by charred litter, with 5–10% cover of resprouting herbs.
Mallard Lake Trail	Burned in 1988	Infertile hot springs deposits	Burned forest was an old stand of spruce, fir, and pine (300 yr old). . . . In 1997 the vegetation was nonforest (ca. 100 pine seedlings/ha) dominated by relatively sparse herbs; sparse litter.

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Mallard Lake Trail	Burned in 1988	Infertile hot springs deposits	Burned forest was an old stand of spruce, fir, and pine (300 yr old). . . . In 1997 the vegetation was nonforest (ca. 100 pine seedlings/ha) dominated by relatively sparse herbs; sparse litter.
Pitchstone Plateau nonforest	Burned in 1988	Infertile rhyolite	Burned forest was an old stand of spruce, fir, and pine (300 yr old). . . . In 1997 the vegetation was nonforest (ca. 100 pine seedlings/ha) dominated by relatively sparse herbs; sparse litter.
Pitchstone Plateau low-density pine	Burned in 1988	Infertile rhyolite	Burned forest was an old pine stand (300 yr old). . . . In 1997 the vegetation was low-density pine forest (20,100 stems/ha) with sparse herbaceous cover; sparse litter.
Mount Haynes	Burned in 1988	Infertile rhyolite/ tuff	Burned forest was a mature pine stand (130 yr old). . . . In 1997 the vegetation was high-density pine forest (62,800 stems/ha) with sparse herbaceous cover; moderate litter layer.
Divide Trail	Unburned	Infertile rhyolite	Old forest of pine, spruce, and fir (>300 yr old) with well-developed herbaceous stratum; deep litter layer.
Pelican unburned	Unburned	Fertile lake sediments	Mid-successional pine forest (ca. 150 yr old) with ca. 1,000 stems/ha, ca. 25% herbaceous cover, and 1–5 cm deep litter layer with almost no bare ground.

metric autoanalyzer methods (Alpchem Corp. 1990, 1991) at the Wisconsin Soil and Plant Analysis Laboratory in Madison. Soil moisture content was determined for the pre- and postincubation soils. Net N mineralization was calculated as the postincubation quantity of ammonium and nitrate in both the soil and resin bags minus the quantities in the preincubation soil.

Streamwater was sampled July 14–15, 1997, near the end of the snowmelt period, in first-order ephemeral streams with little or no riparian vegetation. The snowpack was high during the previous winter, and thus snowmelt was late that year. Replicate samples of streamwater were collected from nine streams at six sites. Two of the streams were from watersheds that burned in 1988, and these were compared to two reference streams in unburned forest (Table 14.8). Two other streams were from the area burned in 1996, and these were compared with one nearby reference stream in an unburned area.

Results

The summer 1997 monthlong soil incubations indicated that net nitrogen mineralization in the nonforest stand was nearly double that at the high-density pine stand ($P < 0.05$) (Table 14.9). Nitrogen mineralization rate was highest during the middle interval when precipitation was unusually high. Nitrogen mineralization rates during the first interval were relatively low, possibly because of greater immobilization of N early in the season and/or the unusually cold temperatures that occurred during June. While these studies need to be repeated at more sites to determine their generality, the results suggest that nitrogen mineralization may decline with increasing ANPP and/or tree LAI, and that mineralization rates are influenced by ambient moisture and temperature conditions.

The yearlong incubation data revealed that 1997–1998 nitrate production was low at all sites except for the 1996 Pelican burn (Fig. 14.8). Among the three sites burned in 1988, mean annual nitrate production ranged only from 0.066 to 0.624 mg NO_3-N/kg soil, constituting from 1.6 to 19 percent of the total nitrogen available. The site with the lowest pine seedling density had the highest mean NO_3-N production, but the amount was still low. There was no significant difference in nitrate production between the three 1988 burn sites and the two mature lodgepole pine sites. Among all sites, nitrate production was highest in the 1996 Pelican burn (4 mg NO_3-N/kg soil), and nitrate constituted 94 percent of the total nitrogen availability.

Ammonification was highly variable across sites. The old-growth lodgepole pine stand had significantly higher mean annual NH_4-N (12.4 mg NH_4-N/kg

Table 14.8. Study sites where streamwater nitrate was measured in 1997

Site	Fire History	Substrate and Elevation	Sampling Site(s)	Vegetation
Pelican burn	Burned in 1996	Fertile lake sediments and infertile rhyolite	Two tiny streams plus the stream below their confluence	Burned forest consisted of mature lodgepole pine stands (ca. 200 yr old) plus old spruce-fir stands (>300 yr old) on a steep slope. . . . In 1997 there was a sparse cover of resprouting herbs in most burned areas, plus a narrow band (1 m) of dense grasses and sedges along the stream.
Pitchstone Plateau Trail	Burned in 1988	Infertile rhyolite	Two ephemeral	Burned forest was an old stand of spruce, fir, and pine (300 yr old) on gentle topography. . . . In 1997 the vegetation was nonforest (ca. 100 pine seedlings/ha)

1990, 1991) at the Wisconsin Soil
Soil moisture content was deter-
Net N mineralization was calcu-
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incubation soil.
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Pitchstone Plateau Trail	Burned in 1988	Infertile rhyolite	Two ephemeral streams	Burned forest was an old stand of spruce, fir, and pine (300 yr old) on gentle topography. . . . In 1997 the vegetation was nonforest (ca. 100 pine seedlings/ha) dominated by relatively sparse herbs; sparse litter.
Lewis River Gorge	Burned in 1988	Infertile rhyolite	One ephemeral stream	Burned forest was an old stand of spruce, fir, and pine (300 yr old) on a moderate slope. . . . In 1997 the vegetation was low-density pine forest (ca. 500 seedlings/ha) dominated by relatively sparse resprouting herbs; sparse litter.
Elephant-back Mountain	Unburned	Infertile rhyolite	Two tiny streams	Mature lodgepole pine forest (ca. 200 yr old) on a steep slope. . . . Moderately dense herbaceous cover and litter; dense growth of grasses and sedges along the streams.
Spring Creek Picnic Area	Unburned	Infertile rhyolite	Three points along a tiny stream	Old lodgepole pine forest (>300 yr) on a steep slope. . . . Moderately dense herbaceous cover and litter.
Divide Roadside	Unburned	Infertile rhyolite	Ephemeral stream	Old lodgepole pine forest (>300 yr) on gently rolling topography. . . . Moderately sparse herbaceous cover except for dense grasses along stream channel.

Table 14.9. Mean net nitrogen mineralization (mg N/kg soil/day) during three intervals of the 1997 growing season at two sites burned in 1988 but with different postfire densities of lodgepole pine saplings

	Early (May 18–July 9)			Mid (July 9–30)			Late (July 30–Sept 20)		
Location	NO_3-N	NH_4-N	Total N	NO_3-N	NH_4-N	Total N	NO_3-N	NH_4-N	Total N
High-density pine	0.001 (0.00006)	0.0078 (0.002)	0.009 (0.002)	0.0018 (0.0004)	0.0265 (0.01)	0.0259 (0.009)	−0.001 (0.0001)	0.0047 (0.0017)	0.0039 (0.002)
Non-forest	0.0031 (0.0012)	0.0148 (0.005)	0.019 (0.006)	0.0044 (0.001)	0.0479 (0.011)	0.0479 (0.010)	0.0018 (0.0007)	0.0479 (0.011)	0.0107 (0.003)

Note: The high-density pine site is Mount Haynes and the nonforest site is the Mallard Lake Trail (Table 14.7). Standard error is indicated in parentheses ($n = 15$).

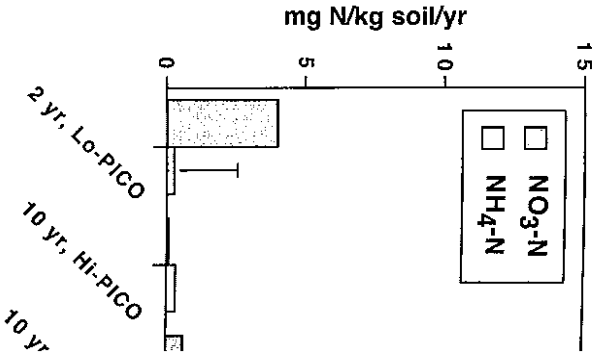

Figure 14.8. Production of nitrate and a
Yellowstone National Park, Wyoming. T
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more than a century, and their ages were
composition. The 120-year-old stand ap
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is from the classification in Table 14.5.

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Pelican burn and the post-1988 hi
mg NH_4-N/kg soil, respectively).
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Streamwater nitrate concentratio

melt revealed very low streamwat
across all nine first-order ephemer
tween burned and unburned wate
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low values indicate that nitrate con
flowing out of the 1996 Pelican b
(Chapter 8).

Non-forest	0.0031 (0.0012)	0.0148 (0.005)	0.019 (0.006)	0.0044 (0.001)	0.0479 (0.011)	0.0479 (0.010)	0.0018 (0.0007)	0.0479 (0.011)	0.0107 (0.003)

Note: The high-density pine site is Mount Haynes and the nonforest site is the Mallard Lake Trail (Table 14.7). Standard error is indicated in parentheses ($n = 15$).

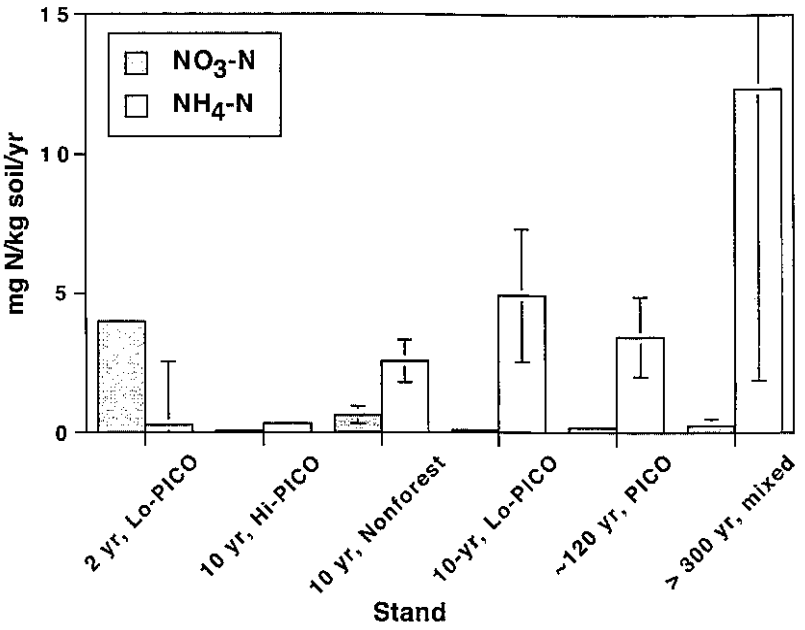

Figure 14.8. Production of nitrate and ammonium nitrate by soil processes in forests of Yellowstone National Park, Wyoming. The 2- and 10-year-old stands were developing after crown fires in 1996 and 1988, respectively. The 120 and > 300 stands had not burned in more than a century, and their ages were estimated from tree size, density, and species composition. The 120-year-old stand appears to represent a forest that is still accumulating biomass, whereas the > 350-year-old stand appears to be in a steady-state condition. The density of lodgepole pine seedlings in the burned stands (Lo-PICO, Hi-PICO, nonforest) is from the classification in Table 14.5.

soil), and the lowest rates of ammonium production were observed in the 1996 Pelican burn and the post-1988 high-density pine seedling sites (0.26 and 0.32 mg NH_4-N/kg soil, respectively). (See Chapter 5 for comparisons of nitrogen in burned and unburned grasslands.)

Streamwater nitrate concentrations, 1997—Samples taken at the end of snowmelt revealed very low streamwater nitrate concentrations (0.04–0.12 mg/L) across all nine first-order ephemeral streams, with no consistent differences between burned and unburned watersheds or among burned watersheds differing in vegetation structure and composition (data not shown). These consistently low values indicate that nitrate concentrations were not elevated even in streams flowing out of the 1996 Pelican burn, as was found by Minshall and others (Chapter 8).

ASSESSMENT: IS ECOSYSTEM FUNCTION RECOVERING NORMALLY?

Our studies to date indicate that ecosystem processes related to ANPP, LAI, and nitrogen dynamics are recovering very rapidly throughout the areas burned in 1988. ANPP and LAI are highly correlated with tree seedling density, and where seedlings are sparse, ANPP and LAI are still relatively low. However, in stands having moderate to high seedling density, by nine years after the fires ANPP and LAI were approaching or already within the range of values observed in mature coniferous forests (Reed and others 1999). Although nitrification was likely elevated immediately following the 1988 fires (as indicated by the data from the 1996 Pelican burn), our data indicate that nitrification rates ten years following the fires were indistinguishable from rates in mature lodgepole pine forests.

We found no evidence of extensive nitrogen loss in streamwater, even in the Pelican burn one year after fire, probably because of rapid uptake and incorporation into plant biomass of this limiting nutrient. Other studies in Yellowstone and in boreal forests (McColl and Grigal 1975, Wright 1976, Albin 1979, Minshall and others 1989) have found similar low nutrient concentrations in streams flowing out of burned watersheds. Franke (2000:94–95) has summarized the studies on lake, stream, and groundwater nutrient concentrations that were conducted during the first few years after the 1988 fires. Results were mixed and inconsistent. Several studies found little or no changes in water chemistry in response to the fires, even in heavily burned watersheds. Other studies detected changes in water chemistry after 1988 but suggested that the changes were due to other factors (for example, drought) rather than direct effects of fire. Two studies reported that nitrate concentrations were 3–33 times as high in streams flowing out of burned watersheds as in unburned watersheds. We conclude from these mixed results that nutrient dynamics related to fire probably vary in relation to watershed characteristics, fire size and severity, postfire weather conditions such as localized storms (Chapter 3, 8), and postfire vegetation responses. More research is needed to clarify these relationships; but the evidence to date suggests that nutrient loss associated with the 1988 fires was localized and of relatively small magnitude overall.

In sum, the 1988 Yellowstone fires appear to have had relatively small and transient effects on ecosystem processes related to energy flow, leaf area, and nutrient dynamics. We see no evidence that the fires "damaged" the system in any important way, nor do we see any need for restoration of ecosystem processes. Interestingly, however, our studies have documented substantial spatial variation in ANPP, LAI, and N minerali
postfire density of lodgepole pine s
derstanding the implications of lar
namics for ecosystem processes is an
and others 1997, Turner and Carper
search is to characterize this variabili
tion at both stand and landscape sc

HAVE RECENT DISTURBANCES BEEN ASSOCIATED WITH ANY NOVEL OR UNEXPECTED EFFECTS?

Most of the areas that burned in 19
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reestablishment of sagebrush or herb
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usually reproduces exclusively by v
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pears to support this prediction.

Extensive surveys across the suba
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north-central part of the park. Mor
more aspen seedlings than less severe
burned patches had higher densiti
1997, Turner and others 2003a,b). Se
no aspen before 1988, suggesting a p
ulations on the Yellowstone Platea

tion in ANPP, LAI, and N mineralization, in relation to the very wide range in postfire density of lodgepole pine seedlings across the burned landscape. Understanding the implications of landscape heterogeneity and disturbance dynamics for ecosystem processes is an important challenge for ecologists (Schimel and others 1997, Turner and Carpenter 1999). A major focus of our ongoing research is to characterize this variability and its consequences for ecosystem function at both stand and landscape scales.

HAVE RECENT DISTURBANCES BEEN ASSOCIATED WITH ANY NOVEL OR UNEXPECTED EFFECTS?

Most of the areas that burned in 1988 appear to be on a successional trajectory returning to vegetation structure and composition very similar to what existed before the fires—for example, where dense mature pine stands burned, we generally see dense stands of pine seedlings today; where open stands burned, we see sparse stands of seedlings; and where sagebrush or meadows burned, we see reestablishment of sagebrush or herbaceous species. However, there was one big surprise after 1988. Quaking aspen *(Populus tremuloides),* which in this region usually reproduces exclusively by vegetative root sprouting, established seedlings throughout much of the burned subalpine forest area (Kay 1993, Romme and others 1997). Turner and others (1998) predicted that novel successional pathways are most probable following disturbances of large spatial extent and high intensity, because such disturbances leave fewer biological legacies and are more slowly filled by propagules migrating from undisturbed areas. The rare episode of sexual reproduction in aspen following the 1988 Yellowstone fires appears to support this prediction.

Extensive surveys across the subalpine plateaus of Yellowstone Park in 1993 and 1996 revealed that aspen seedlings were found only in burned areas, and that they were patchily distributed with densities of 1 to more than 300 stems/ha (Romme and others 1997, Turner and others 2003a). Seedlings were most abundant in the west-central portions of Yellowstone Park, and least abundant in the north-central part of the park. More severely burned sites generally supported more aspen seedlings than less severely burned sites, and small or moderate-sized burned patches had higher densities than large patches (Romme and others 1997, Turner and others 2003a,b). Seedlings were found in many places that had no aspen before 1988, suggesting a possible range expansion. The seedling populations on the Yellowstone Plateau exhibited greater genetic diversity than

adult aspen clones in Yellowstone's northern winter ungulate range (Tuskan and others 1996), but there were no strong genetic patterns among seedling populations that could be explained by differences in elevation, substrate, or geographic location (Stevens and others 1999). The genetic studies indicated that initial seedling establishment patterns were largely random with respect to genetic makeup, and that strong selection pressures have not yet shaped these new aspen populations. However, such selection is likely to occur in the near future.

Continuing surveys indicate that the aspen seedlings are persisting throughout most of the areas where they originally occurred, but densities are decreasing in many places (Romme and Turner, in preparation). Mortality appears largely due to intense ungulate herbivory, but many seedlings are failing to thrive even in exclosures—suggesting that local climate or soils may be unsuitable for aspen in many places (Romme and Turner, in preparation). Most of the seedlings will likely perish over the next few decades, leaving no lasting ecological legacy. However, at least a few new aspen genets are likely to survive and produce new aspen clones. These individuals will inject new genetic diversity into the regional aspen population, and will change the local ecology of sites where aspen was absent before 1988. Especially at lower elevations and in places where seedlings are protected from elk browsing by piles of fallen fire-killed tree boles, many aspen seedlings now exhibit heights greater than 1 m and a robust growth form that bodes well for their long-term survival. Here we see another surprise—the abundant coarse woody debris created by the fires (Tinker and Knight 2000, Chapter 12) may enhance long-term aspen persistence and genetic diversity (Ripple and Larsen 2000). Had the National Park Service "salvaged" the great numbers of dead trees in the aftermath of the fires (fortunately the service had neither the ability nor the will to accomplish this), the establishment of new aspen genets might have been greatly reduced.

Tuskan and others (1996) suggest that episodes of new aspen genet establishment may typically exhibit just such a pattern of initially high seedling densities, followed by extensive mortality but survival of a few individuals that are best adapted to local conditions and which go on to produce clonal structures (Eriksson 1993). Additional seedling establishment events of this kind in the future may be crucial to long-term survival of aspen in the Yellowstone region if climate change in the next century shifts the elevational zones of tolerance for plant species (Romme and Turner 1991, Bartlein and others 1997) and if continued browsing pressure combined with drought and other stresses causes local extirpation of some old aspen clones (Romme and others 2001).

The widespread establishment of aspen seedlings after the 1988 fires was unexpected, but consistent with curren
others 1998). Although postfire suc
because of this unexpected consequ
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In summary, we posed six general
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There are at least three reasons w
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sprout from roots and rhizomes, an
or three years after the fire (for exam
Lupinus argenteus [see Chapter 5 for
nus], Calamagrostis canadensis). Oth
soil (for example, *Dracocephalum p*
velutinus) or in the canopy (for exam
ment of plant biomass probably al

expected, but consistent with current ecological theory (for example, Turner and others 1998). Although postfire succession will be different in some local areas because of this unexpected consequence of fire size and severity, we do not regard aspen seedling establishment to be any kind of threat to the integrity of the Yellowstone ecosystem. On the contrary, the addition of new, genetically novel individuals to the regional aspen population may enhance the resilience of this keystone plant species to ecological changes expected in the next century.

In summary, we posed six general questions to guide assessments of the need for active intervention to restore damaged ecosystem elements or processes (Table 14.1). Within this framework, we evaluated the effects of the 1988 Yellowstone fires and of pre-1988 fire suppression. Our conclusion is that the Yellowstone subalpine ecosystem is still within or nearly within its range of natural variability with respect to (1) disturbance regime, (2) community composition and structure at both stand and landscape scales, and (3) ecosystem function as measured by aboveground net primary productivity, leaf area index, and nitrogen dynamics. The 1988 fires produced quantifiable and spatially heterogeneous effects on ecosystem composition, structure, and function, but none of these effects appears to be either abnormal or a threat to long-term ecological integrity. The Yellowstone subalpine landscape requires no active intervention or restoration. On the contrary, it provides an outstanding example of a naturally functioning system. Yellowstone's high-elevation forests provide a valuable benchmark for comparison of other subalpine forest systems in western North America that have been altered by such activities as timber harvest and extensive road building (for example, Knight and others 2000).

There are at least three reasons why the large and severe fires of 1988 did not cause serious or long-lasting damages to the organisms or ecological processes of the Yellowstone subalpine landscape. First, this area's disturbance history is characterized by similar infrequent but large, severe fires. This disturbance history leads to the second reason why fire damage was so slight: past disturbances have selected for biological characteristics that enable the organisms to withstand large, severe fires (Chapters 4, 5, 15). Many herbs and shrubs are able to resprout from roots and rhizomes, and then to produce prolific seeds within two or three years after the fire (for example, *Epilobium angustifolium, Carex geyeri, Lupinus argenteus* [see Chapter 5 for more detail on the ecological roles of *Lupinus], Calamagrostis canadensis*). Others have long-persistent seed banks in the soil (for example, *Dracocephalum parviflorum, Geranium bicknellii, Ceanothus velutinus*) or in the canopy (for example, *Pinus contorta*). The rapid reestablishment of plant biomass probably also involves rapid uptake of nutrients and

therefore minimal nutrient loss from the system. The third reason why the system was so resilient to the 1988 fires is that there were very few sources of alien plant species capable of invading the burned areas and preempting the space from the native species. We urge the managers of Yellowstone Park to continue an aggressive program of controlling alien weeds so that future large fires do not result in an explosion of nonnative species and potentially very different consequences from those that we measured after 1988.

Many systems can withstand a single disturbance, even if it is large and intense, if the organisms are adapted to that kind of disturbance (Paine and others 1998). However, where multiple disturbances occur within the time frame required for recovery, the system may be pushed into a new state (also see Turner and others 1993). The wilderness landscapes of Yellowstone National Park apparently were not significantly altered either by the 1988 fires or by pre-1988 fire suppression. However, serious future changes could occur if fire frequency increases due to global climate change (Chapters 2, 13), or if the system becomes further stressed by drought or invasion of alien species. Indeed, other Rocky Mountain subalpine ecosystems have been substantially altered by twentieth-century changes in disturbance regimes and by invasion of alien plant species. In national forests near Yellowstone Park, for example, intensive clear-cutting and road building during the past fifty years have dramatically altered landscape patterns (for example, Tinker and others 1998, Baker and Knight 2000). Some of these intensively logged areas also burned in 1988. The combination of intensive logging, road building, and severe fire may constitute the kind of compounded, interacting disturbances that can push an ecosystem into a qualitatively different state (Paine and others 1998). Many subalpine landscapes throughout the Rocky Mountains, where intensive timber harvest and road-building have been conducted, may be at risk of serious degradation if large fires occur in the near future. As a baseline reference for natural ecological structure and processes, the value of Yellowstone's largely untrammeled subalpine system will only increase as we proceed through the next century.

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