

Surprises and lessons from the 1988 Yellowstone fires

Monica G Turner¹, William H Romme², and Daniel B Tinker³

The size and severity of the fires in Yellowstone National Park in 1988 surprised ecologists and managers alike. Much has been learned about the causes and consequences of crown fires from studies of the Yellowstone fires, and some results were surprising. Plant cover in burned areas was restored rapidly by native species, making post-fire rehabilitation generally unnecessary and possibly even counterproductive. While 20th-century fire suppression has affected systems like Yellowstone far less than other ecosystems, managing forests, people, and property in wildfire areas is an ongoing challenge. Insights gained and lessons learned from the Yellowstone fires may be applied elsewhere and can help inform fire policy.

Front Ecol Environ 2003; 1(7): 351–358

Understanding forest fire dynamics is becoming increasingly important as scientists, policy makers, and the public grapple with wildfires every year. Wildfires burn as much as 3.5 million ha annually in the US (NIFC 2003), and fire seasons during the past two decades have been among the most severe and costly on record in western North America. The causes and consequences of these fires remain the subject of considerable discussion. Some experts argue that decades of fire suppression, resulting in extensive and unnatural buildup of fuels, are to blame, while others suggest that variation in climate, particularly the occurrence of persistent and severe drought, is largely responsible.

Each view is correct with respect to some fire events and some ecosystems, but natural fire regimes and human impacts on those regimes are complex and variable from place to place. Furthermore, the interaction between climate change and fire may potentially be as important as the direct effects of global warming on forests (Dale *et al.* 2001). Thus, as policy makers and managers develop and implement measures to reduce future wildfire damage, it is

critical that we incorporate our best understanding of the inherent variability in forest fire dynamics, as well as the importance of natural disturbance in ecological systems. In this article we synthesize the results from 14 years of studying vegetation and ecosystem processes following the 1988 fires in Yellowstone National Park (YNP), WY, highlighting key ecological surprises and lessons learned about the role of fire.

In order to understand the 1988 Yellowstone fires, it is necessary to consider the broader context of fire regimes. Natural forest fire regimes vary widely, yet this complexity is often overlooked and underappreciated. The distinction between natural understory fire regimes and stand-replacing fire regimes is particularly important (Brown 2000). Understory fires burn at relatively low intensity and are typically characterized by short return intervals (from years to several decades). These fires burn along the ground, consuming woody fuels and understory vegetation, reducing tree regeneration, and maintaining an open forest structure. Historically, understory fire regimes dominated the once extensive long-leaf pine (*Pinus australis*) forests of the southeastern coastal plain, the open ponderosa pine (*Pinus ponderosa*) forests of the southern Rocky Mountains, and the ecotone between the forest and the prairie biomes. Because these low-intensity fires can be readily suppressed, many areas of the US that had been characterized historically by an understory fire regime experienced increased fuel buildup and connectivity during the 20th century, raising the risk of high-intensity, stand-replacing fires. In these areas, past fire suppression is a major factor contributing to the increased occurrence and severity of wildfire (Covington and Moore 1994; Allen *et al.* 2002).

Recent wildfire mitigation programs at national and state levels have focused on forests formerly dominated by understory fire regimes. Unfortunately, some of these programs have failed to take into account that fire plays a very different role in many other forest types. Northern and subalpine conifer forests are typically characterized by

In a nutshell:

- Many northern conifer forests such as those in Yellowstone National Park are characterized by natural stand-replacing fires that are infrequent but severe
- Climate is the primary driver of stand-replacing fire regimes, while variation in fuels is less important
- Disturbances of this type and magnitude may influence plant population structure, genetics, and evolution
- Spatial heterogeneity resulting from this type of fire is the rule, not the exception
- Fires and fire regimes are not all the same, and a “one size fits all” approach to wildfire management is likely to be misguided

¹Department of Zoology, University of Wisconsin, Madison, WI 53706; ²Department of Forest Sciences, Colorado State University, Fort Collins, CO 80523; ³Department of Botany, University of Wyoming, Laramie, WY 82070

infrequent, high-severity fires that kill most of the canopy, either via intense surface fire or flames spread through the crowns of the trees. Fire return intervals are long, ranging from about 60 years in jack pine (*Pinus banksiana*) to several centuries in some spruce–fir (*Picea*, *Abies* spp) communities. Stand-replacing fire regimes dominate the extensive boreal forests of North America, Europe, and Asia, as well as the forests of the northern Rocky Mountains, including YNP (Turner and Romme 1994). Climatic conditions, particularly severe regional drought, set the stage for occasional years of extensive conflagrations, and these few large fires account for most of the cumulative area burned over a long period of time (Johnson 1992; Johnson and Wowchuck 1993; Bessie and Johnson 1995; Flannigan and Wotton 2001). Under such extreme fire-weather conditions, variation in fuel structure is often of little importance, and fire suppression appears to have had little influence on recent fire behavior during these big fire years.

A stand-replacing fire regime characterizes the extensive subalpine forests of YNP. Thus, the lessons and surprises gleaned from intensive study of the 1988 fires can help us interpret the effects of recent and future fires in other ecosystems with a similar natural fire regime. Our Yellowstone findings are probably not very applicable to those ecosystems which have understory fire regimes, but this limitation underscores the fundamental point that we must deal with spatial variability in fire regimes.

■ The fiery summer of 1988

Established in 1872 as the world's first national park, Yellowstone is famous for its unique thermal features, natural beauty, and abundance and variety of wildlife. Encompassing 9000 km² in the northwest corner of Wyoming, YNP is primarily a high, forested plateau. Approximately 80% of the park is covered with coniferous forests dominated by lodgepole pine (*Pinus contorta* var *latifolia*). Our focus here is on this forested subalpine plateau and not the lower elevation ecosystems. Tree-ring evidence (Romme 1982; Romme and Despain 1989) and studies of pollen and charcoal accumulation over millennia (Millsbaugh *et al.* 2000) have clearly shown that YNP has experienced large-scale fire throughout the Holocene Epoch (the most recent 10 000 years). Fire return intervals have varied between 100 and 500 years.

Fire suppression was instituted in Yellowstone in 1886, but was not consistently effective prior to about 1945 (Schullery 1989). In response to a growing recognition of the ecological importance of fire, a natural fire program was initiated in 1972, in which lightning-caused fires in remote areas were allowed to burn without interference under proscribed conditions. Of over 200 such fires observed in the park between 1972 and 1988, 83% went out by themselves before burning more than 0.5 ha, and in 1981, the largest fire year prior to 1988, a total of 3300 ha was burned in 28 natural fires (Renkin and Despain 1992).

During the summer of 1988, severe fires burned in YNP under conditions of extreme drought and high winds (Christensen *et al.* 1989; Renkin and Despain 1992). This surprised both managers and researchers, and focused worldwide attention on wildfire. It was reported in the media that the nation's "crown jewel" was being destroyed by wildfires and would never recover (Smith 1996). The fires were indeed large, the most extensive since the park was established, and ultimately affected over 250 000 ha in the Greater Yellowstone Region. However, post-fire research has clearly demonstrated that the park's important features were not "destroyed".

Analyses of the 1988 fires strongly suggest that climate, rather than fuels, was primarily responsible for the extent of the fires (Romme and Turner in press). In June and July, the fires responded in similar fashion to what had been observed between 1972 and 1987 (Renkin and Despain 1992), and during these months, 19 555 ha were burned in subalpine portions of YNP. Full fire suppression efforts began in late July. As severe weather conditions persisted and intensified, fire activity increased. Between August 20 and September 15, another 157 726 ha was added to the area within the burn perimeter. These later fires spread rapidly through all forest successional stages and were influenced primarily by wind speed and direction. Even large natural firebreaks, such as the Grand Canyon of the Yellowstone, did not impede the spread of these late-season fires. Burning embers were carried 1 to 2 miles ahead of the main fire front, initiating new spot fires. Despite full suppression efforts, the fires ultimately stopped only with the arrival of the mid-September snowfall. Thus, it was weather that largely controlled the 1988 fires; landscape heterogeneity had minimal influence, and historic fire suppression probably had little effect.

■ Fires do not homogenize the landscape

The public, and even some ecologists, feared that the 1988 fires had produced a desolate area of uniform devastation, but this was not the case. Instead, one of the most striking features of the 1988 fires was the post-fire heterogeneity of the burned landscape (Christensen *et al.* 1989). The fires created a spatially complex mosaic of unburned and burned patches, encompassing a wide range of burn severities (Figure 1). Understanding the effect of fire on landscape heterogeneity is important because the kinds, amounts, and spatial distribution of burned and unburned areas may influence the reestablishment of plant species on burned sites. A map of post-fire burn severity derived from Landsat Thematic Mapper imagery was used to quantify the isolation of burned areas and the relationship between heterogeneity and fire size (Turner *et al.* 1994). The majority of severely burned areas were within 50–200 m of unburned or lightly burned areas, suggesting that few burned sites were very distant from potential sources of off-site propagules. Spatial heterogeneity was the rule, not the exception, and a synthesis across differ-

ent disturbance types suggests that this characterizes many large, infrequent disturbances (Foster *et al.* 1998).

■ Post-fire vegetation

Plant cover and composition

The forests that burned in 1988 have since been repopulated by extensive stands of lodgepole pine and a wide variety of native herbaceous plants and shrubs. We have sampled the post-fire vegetation in nine patches – a small (1 ha), moderate (70–200 ha), and large (500–3600 ha) burned patch at each of three geographic locations – annually from 1990 to 1993 and again in 1996 and 2000. Post-fire plant reestablishment in most areas of YNP was rapid, with substantial increases in plant cover during the 4 years following the fires (Turner *et al.* 1997, 1999). We were surprised to find that most post-fire colonization occurred from plant parts that survived within the burned areas and then produced seed rather than by dispersal from unburned sites (Turner *et al.* 1997). Perennial herbs, graminoids (grasses and grasslike plants), and shrubs resprouted in 1989 and flowered profusely the following year, and widespread, abundant seedling establishment occurred in 1991 (Figure 2). The mean depth to which soil was charred was <14 mm, even in areas affected by severe surface and crown fires (Turner *et al.* 1999), suggesting that deeper roots and rhizomes had a high chance of survival. Therefore, although the fires were very large and severe, many plants survived and quickly refilled the burned forests. This rapid response of native species may also have provided a natural defense against invasion by exotic species that, surprisingly, did not increase in extent or abundance after the fires.

Our analyses of the vegetation data revealed substantial effects of fire severity and patch size on early post-fire plant cover and species richness (Turner *et al.* 1997, 1999;



Figure 1. The 1988 fires created a complex mosaic of burned and unburned patches. Areas of crown fire (black) or severe surface fire (brown) were stand replacing.

Romme and Turner in press). Some of these effects are now diminishing, but small patches still have greater forb, graminoid, and total cover compared to large patches, and more severely burned sites still have lower cover of forbs, graminoids, and shrubs compared to less severely burned sites (Figure 3). However, the effects of environmental variation on species richness and community composition are becoming more pronounced (Figure 3), and post-fire communities are similar in composition to nearby forests that did not burn. The influence of the abiotic template on vegetation is, therefore, becoming more evident as succession proceeds.

Lodgepole pine

Lodgepole pine reestablished well following the 1988 fires. Adult lodgepoles do not survive fire, except where fire intensity is low, and post-fire regeneration depends entirely on seedling establishment which often generates dense, even-aged stands (Johnson and Fryer 1989). Lodgepole pine is serotinous, meaning that trees may produce cones that remain closed at maturity and only open in response to high temperatures (Figure 4). Trees may retain closed cones for 40 years or longer, and the canopy



Figure 2. (left) Profuse flowering of herbaceous species was observed during 1990 and 1991 following the 1988 fires. By 1993, plants were well established, but flowering was conspicuously reduced. (right) Many perennial plants survived the fires and resprouted from surviving roots and rhizomes, as shown here for *Lupinus argenteus*. Surviving plants were a source for the establishment of new seedlings.

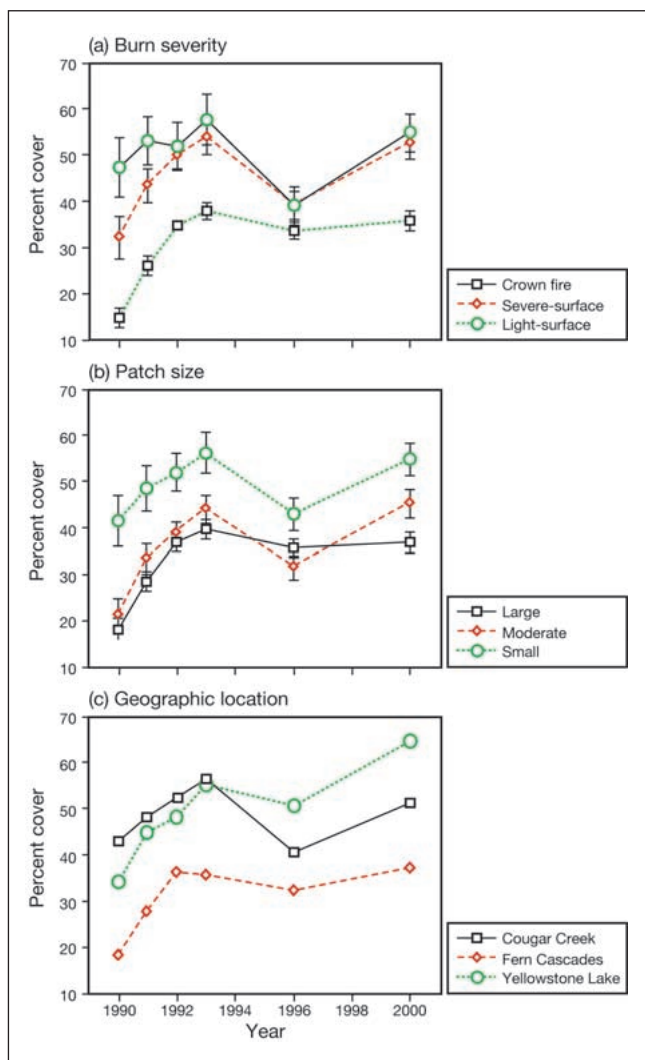


Figure 3. Percent total biotic cover as measured in over 700 permanent plots established in 1990 by burn severity, patch size, and location. Sampling occurred in patches of stand-replacing fire that were small (1 ha), moderate (70–200 ha) and large (>500 ha) in size (methods described in Turner *et al.* 1997). Error bars are 2 SE.

may therefore contain millions of seeds per ha (Clements 1910; Lotan and Jensen 1970). Seed stored in serotinous cones can remain viable for 50–75 years (Clements 1910), and the seedlings thrive in the high-light environment of a recently burned forest.

We found significant influences of fire severity, patch size, and geographic location on post-fire pine seedling densities (Figure 5). Large patches had more pine seedlings than smaller patches, and areas with severe surface burns had more seedlings than areas with crown fires or less severe burns (Figure 5). In areas with severe surface burns, temperatures were probably sufficiently high to break the resin seal on the serotinous cones, but not so high as to reduce viability of the seed; thus, local variation in burn severity (Turner *et al.* 1994) resulted in fine-scale variation in post-fire pine density. However, we did not expect such large variation in pine seedling density



Figure 4. (top) Some lodgepole pine trees produce serotinous cones, such as those shown here. (bottom) In areas of YNP where pre-fire serotiny was high, post-fire recruitment of lodgepole pine seedlings was extremely high.

between the three geographic locations of our study patches. We discovered that our three “replicate” locations had unexpectedly captured a strong and previously undescribed gradient in pre-fire serotiny (Table 1).

Although lodgepole pine is a serotinous species, not all trees produce this type of cone. The spatial and temporal controls on expression of serotiny are not well understood. Measurements of serotiny in unburned lodgepole pine forests in YNP revealed that it is affected by both elevation and stand age (Tinker *et al.* 1994; Schoennagel 2002; Schoennagel *et al.* in press). At high elevations (>2300 m), where estimated fire return interval is ~300 years, serotiny is low. However, at low elevations (<2300 m), where estimated fire return interval is ~180 years, serotiny is low in young stands but high in stands >70 years old (Schoennagel 2002; Schoennagel *et al.* in press). These patterns are consistent with our observations of geographic variation in both serotiny and post-fire pine recruitment in our study patches.

After observing the variation in post-fire pine density in our nine study patches, we were curious about the spatial heterogeneity in pine density across the broader landscape. Using a combination of aerial photography and extensive field studies, we found post-fire pine densities ranging from 0 to 535 000 stems/ha (Turner *et al.* in press). Collectively, our analyses described a matrix of larger patches of low-density lodgepole pine randomly interspersed with smaller patches of high-density pine. The six orders of magnitude

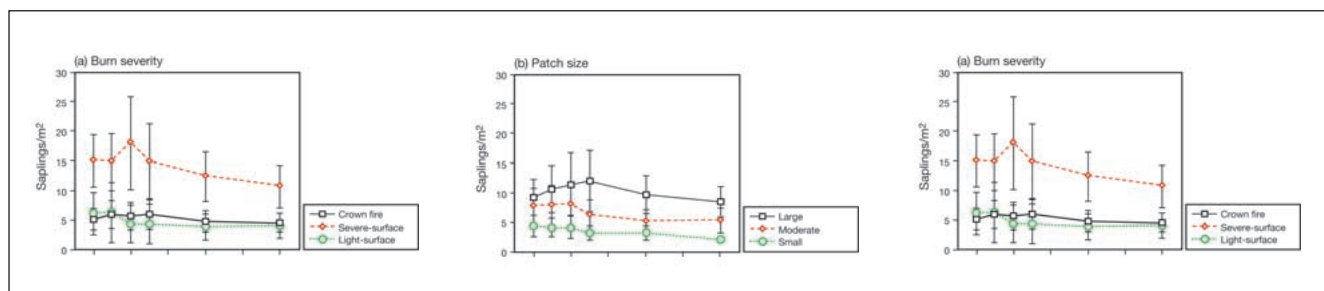


Figure 5. Post-fire density of lodgepole pine as measured in over 700 permanent plots established in 1990 by burn severity, patch size, and geographic location. Sampling occurred in patches of stand-replacing fire that were small (1 ha), moderate (70–200 ha) and large (> 500 ha) in size (methods described in Turner *et al.* 1997). Error bars are 2 SE.

variation in post-fire lodgepole pine density was astounding, and also generated considerable spatial variation in aboveground (Reed *et al.* 1999, Turner *et al.* in press) and belowground (Litton 2002; Litton *et al.* 2003a, b) net primary production. For example, post-fire annual net primary productivity in 11-year-old lodgepole pine stands ranged from 0.04–15.12 mg/ha/yr, spanning much of the range of variation expected through successional time (Turner *et al.* in press). Our results suggest that the factors influencing post-fire stand density – namely, pre-fire serotiny and fire size, severity, and pattern – also influence post-fire ecosystem function.

How long is this post-fire spatial variation likely to persist on the landscape? Variation in stand density will probably be reduced through time as high-density stands self-thin and low-density stands continue to have gradual recruitment (Kashian 2002). However, the initial post-fire mosaic will probably influence the structure and function of the YNP landscape for at least a century. Analyses of basal area increment in lodgepole pine stands spanning a range of age classes and densities indicate that this measurement varies with density until the trees are about 125 years old (Kashian 2002). Clearly, the fire-generated patterns in forest structure have left a legacy that will persist for many decades in the YNP landscape.

Aspen

The post-fire dynamics of aspen (*Populus tremuloides*) in YNP provided yet another ecological surprise. As graduate students, we had absorbed the conventional wisdom that the aspen clones in the northern Rocky Mountains (Figure 6) have persisted since the Pleistocene Epoch and do not reproduce by seed. Therefore, although we anticipated root sprouting of burned aspen clones where they were present before the fires (Romme *et al.* 1995), we did not expect aspen on the plateau. During our 1989 field season, we encountered small seedlings in the burned lodgepole pine forests that we could not identify definitively. In 1990, these seedlings were becoming woody,

and they keyed out to aspen. Indeed, seedling aspen established successfully throughout the burned pine forests and well beyond the pre-fire range of aspen.

We have documented seedling aspen occurring as far as 15 km from the nearest known aspen clone, and most are well over 5 km away (Romme *et al.* 1997; Turner *et al.* 2003). If the statistical models of post-fire aspen seedling occurrence as measured along infrequently used foot trails (Turner *et al.* 2003) are extrapolated spatially to the landscape, we can see areas of YNP in which aspen seedlings have a higher likelihood of occurrence (Figure 7). Genetic analyses of seedling aspen populations found greater variation than that observed among pre-fire clones (Tuskan *et al.* 1996), and most variation occurred within rather than among aspen seedling populations (Stevens *et al.* 1999). Even geographically distant seedling populations shared nearly 90% of the same markers (Stevens *et al.* 1999). Within plots, the amount of genetic variation decreased slightly with increasing percentage of vegetative cover and mean size of the aspen seedlings, suggesting that competition between aspen and other plants might already be eliminating some genotypes.

Aspen is well known as the preferred forage for elk, and the role of ungulate browsing on the dynamics of aspen throughout the Rocky Mountains has been the subject of some controversy (NRC 2002). Nearly all the aspen seedlings that we have observed in the burned pine forests have been browsed and average 30 cm in height (Turner unpublished; Figure 6, top). However, recent studies suggest a potentially complex interaction between fire, post-

Table 1. Mean pre-fire stand serotiny (measured by percentage of lodgepole pine trees bearing serotinous cones) and 1993 post-fire lodgepole pine seedling density for three geographic locations in Yellowstone National Park where we have studied post-fire succession in small, moderate, and large patches (Turner *et al.* 1997)

Location	Pre-fire stand serotiny (percentage of lodgepole pine)	1993 post-fire lodgepole pine seedling density (stems/ha)
Cougar Creek	65%	211 000
Fern Cascades	10%	2300
Yellowstone Lake	<1%	600



Figure 6. (top) Seedling aspen established throughout the burned conifer forests of the subalpine plateau in 1989. However, most aspen seedlings remain short (~30 cm height) and have been browsed, as shown in this 1999 photo. (bottom) However, some aspen seedlings have grown to ~2 m in lower elevation locations, where trees killed by the 1988 fires have now fallen and formed natural protection from browsing.

fire coarse woody debris, and aspen recruitment. Many of the conifers that were killed in the 1988 fires have now fallen to the ground, creating in some areas a thicket of fallen trees that is difficult to traverse, even for elk. Ripple and Larson (2001) observed tall aspen ramets (individual members of a clone) in areas where the plants were protected from browsing by natural piles of fallen trees. Therefore, although most aspen seedlings remain small and are browsed, post-fire coarse woody debris may be creating “safe zones” for aspen, in which new clones appear to be establishing (Figure 6, bottom). We suggest that recruitment of new aspen genets in this region is episodic, is usually associated with large severe fires like those in

1988, and contributes considerably to population genetic structure and diversity. Numerous perennial herbs of the forest floor also appear to persist primarily via asexual sprouting during fire-free intervals, but to recruit new genetic individuals after fire (Romme *et al.* 1993).

Coarse woody debris

The 1988 fires in Yellowstone killed millions of lodgepole pines, creating an estimated 25 million metric tons of standing and downed dead wood, known as coarse woody debris (CWD) (Tinker and Knight unpublished). This wood is one of the most important legacies of the pre-fire forest. CWD in the form of snags, logs, and stumps may cover as much as 24% of the forest floor immediately following an intense fire, and this percentage increases to almost 60% by 50 years after the fire, as the snags fall (Tinker and Knight 2001), modifying the forest floor environment. The decaying logs, roots, and stumps are also a primary source of organic matter inputs to Yellowstone’s generally infertile forest soils, which may help maintain higher levels of productivity. Surprisingly, very little of the CWD that was present on the forest floor at the time of the fires was consumed during 1988. A small proportion (about 8%) was consumed and an equal amount was converted to charcoal (Tinker and Knight 2000). This persistent and important pool of organic material will affect forest floor and soil structure and function for decades after stand-replacing fires.

■ Lessons from the fires

The 1988 Yellowstone fires produced spatially complex patterns of succession in what is often considered a relatively simple system dominated by lodgepole pine. The post-fire spatial variability in forest structure in turn influences – perhaps even dominates – ecosystem function across the landscape, and its imprint will probably persist for at least a century. Long-term study is essential for understanding natural disturbance dynamics, particularly when events are both large and infrequent (Turner *et al.* 1998, 2003). The 1988 fires continue to offer irreplaceable opportunities to address basic questions in ecology and to study natural ecosystem structure, function, and dynamics.

The significance of the 1988 Yellowstone fires extends far beyond the park. Large fires will probably occur again in YNP and in many other areas of western and northern North America, where extensive coniferous forests are characterized by large, infrequent blazes. Many of these areas are prized for their aesthetic beauty and environmental amenities, and are experiencing extensive rural development (Hansen *et al.* 2002; Romme *et al.* in press). This combination may inadvertently set the stage for increasing future conflicts between competing values, similar to those which have developed in flood- or storm-prone regions. Neither complete fire exclusion nor conversion of the natural stand-replacing fire regime to an

understory fire regime appears feasible, either operationally or ecologically (Romme *et al.* in press). Although local thinning to create defensible space around individual homes may be practical, fire management in ecosystems with stand-replacing fire regimes must accept and incorporate large, severe, infrequent fires throughout much of the landscape (Romme *et al.* in press).

What lessons learned from the 1988 fires may be relevant elsewhere? First, distinctions must be clearly drawn between natural stand-replacing fire regimes such as YNP and other areas where past fire suppression has shifted the fire regime from understory to stand-replacing. Interventions such as low-intensity prescribed burning or mechanical thinning to restore natural fire dynamics are not appropriate for crown-fire systems. Second, large stand-replacing fires are an important source of landscape heterogeneity. Even though such fires create patches of even forest age across the landscape, unburned patches are interspersed throughout, and there is tremendous spatial variation in both forest structure and function within the burned area.

Third, natural processes restored plant cover and composition in the burned area quite rapidly, with no deleterious consequences observed (Romme and Turner in press). Thus, active post-fire rehabilitation is probably not needed, and may even be counterproductive. For example, exotic plant species introduced deliberately to expedite revegetation may retard forest recovery. The CWD created by the 1988 fires played an unexpected role in the establishment of new aspen clones – a role that never would have been recognized had the park quickly salvaged the fire-killed trees. Finally, episodic large-scale disturbances may play a key role in the population structure, genetics, and evolution of long-lived clonal plant species such as aspen and many forest floor herbs. Continuing research on the effects of the 1988 Yellowstone fires will lead to additional insights and new surprises about the dynamics of systems characterized by stand-replacing fire regimes.

■ Acknowledgements

We thank our summer field crews and others who worked with us in Yellowstone. The University of Wyoming National Park Service Research Center provided logistical

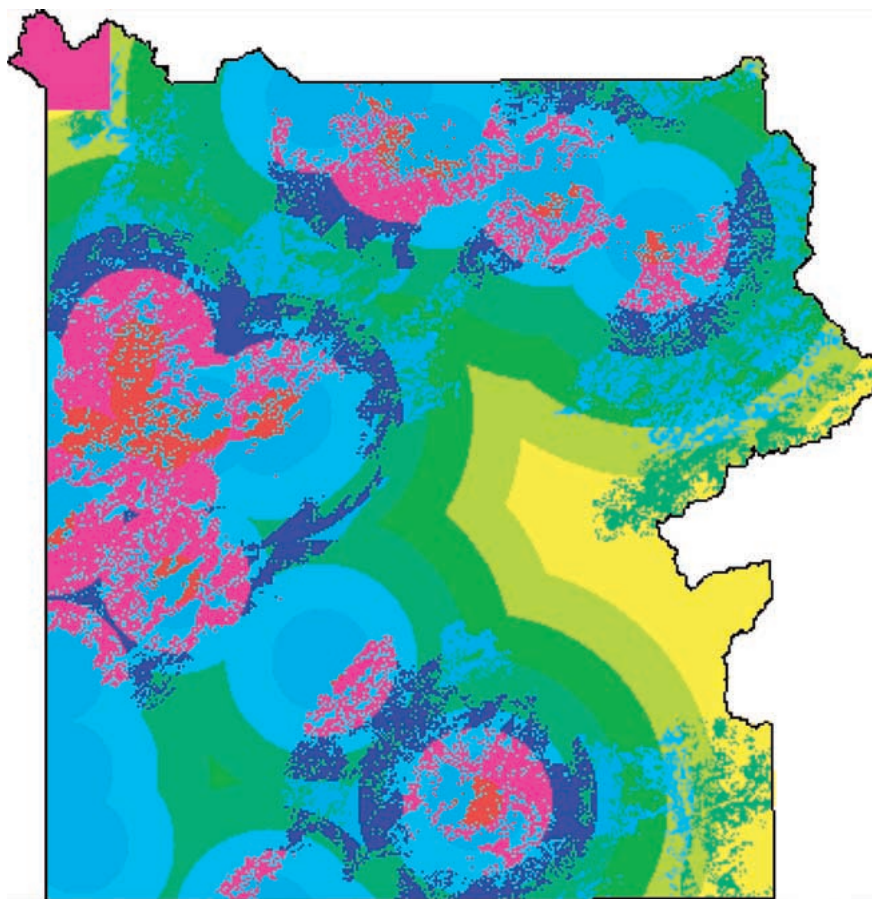


Figure 7. Map of the probability of aspen seedling presence across the Yellowstone landscape, extrapolated within a GIS using results of a logistic regression analyses of aspen seedling occurrence as measured in 1996 along lightly used trails (see Turner *et al.* 2003). Mature aspen stands were located at the center of the concentric circles. The scattered, irregular patches identify areas of burned forest. Highest probabilities of finding aspen seedlings are indicated by reds, intermediate probabilities by blues, and lowest probabilities by light greens and yellows.

support for our fieldwork, and the staff of Yellowstone National Park shared their expertise and offered additional logistical support. Our research has been supported by grants from the Ecology and Ecosystem Studies Programs, National Science Foundation; the US Department of Energy; the USDA National Research Initiative Competitive Grants Program, Forest/Range/Crop/Aquatic Ecosystems Program; the National Geographic Society; and the Andrew W Mellon Foundation.

■ References

- Allen CD, Savage M, Falk DA, *et al.* 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol Appl* 12: 1418–33.
- Bessie WC and Johnson EA. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76: 747–62.
- Brown JK. 2000. Introduction and fire regimes. In: Brown JK and Smith JK (Eds). *Wildland fire in ecosystems: effects of fire on flora*. USDA Forest Service General Technical Report RMRS-GTR-42 Vol 2 (http://www.fs.fed.us/rm/pubs/rmrs_gtr42_2.html).
- Christensen NL, Agee JK, Brussard PF, *et al.* 1989. Interpreting the Yellowstone fires of 1988. *BioScience* 39: 678–85.

- Clements FE. 1910. The life history of lodgepole burn forests. USDA Forest Service Bulletin 79.
- Covington WW and Moore MM. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J Forest* **92**: 39–47.
- Dale VH, Joyce LA, McNulty S, *et al.* 2001. Climate change and forest disturbances. *BioScience* **51**: 723–34.
- Flannigan MD and Wotton BM. 2001. Climate, weather and area burned. In: Johnson EA and Miyanishi K (Eds). *Forest fires*. New York: Academic Press. p 351–73.
- Foster DR, Knight DH, and Franklin JF. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1**: 497–510.
- Hansen AJ, Rasker R, Maxwell B, *et al.* 2002. Ecological causes and consequences of demographic change in the New West. *BioScience* **52**: 151–62.
- Johnson EA. 1992. Fire and vegetation dynamics. New York: Cambridge University Press.
- Johnson EA and Fryer GI. 1989. Population dynamics in lodgepole pine–Engelmann spruce forests. *Ecology* **70**: 1335–45.
- Johnson EA and Wowchuck DR. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationship to mid-tropospheric anomalies. *Can J Forest Res* **23**: 1213–22.
- Kashian DM. 2002. Landscape variability and convergence in forest structure and function following large fires in Yellowstone National Park. (PhD Dissertation). Madison, WI: University of Wisconsin.
- Litton CM. 2002. Above- and belowground carbon allocation in post-fire lodgepole pine forests: effects of tree density and stand age. (PhD Dissertation). Laramie, WY: University of Wyoming.
- Litton CM, Ryan MG, Tinker DB, and Knight DH. 2003a. Below- and aboveground biomass in young post-fire lodgepole pine forests of contrasting tree density. *Can J Forest Res* **33**: 351–63.
- Litton CM, Ryan MG, Knight DH, and Stahl PD. 2003b. Soil-surface CO₂ efflux and microbial biomass in relation to tree density thirteen years after a stand replacing fire in a lodgepole pine ecosystem. *Glob Change Biol* **9**: 680–96.
- Lotan JE and Jensen CE. 1970. Estimating seed stored in serotinous cones of lodgepole pine. USDA Forest Service Research Paper INT-83.
- Millspaugh SH, Whitlock C, and Bartlein PJ. 2000. Variations in fire frequency and climate over the past 17 000 years in central Yellowstone National Park. *Geology* **28**: 211–14.
- NIFC (National Interagency Fire Center). Fire statistics. www.nifc.gov/stats/index.html. Viewed 07/22/03.
- NRC (National Research Council). 2002. Ecological dynamics on Yellowstone's northern range. Washington, DC: National Academy Press.
- Reed RA, Finley ME, Romme WH, and Turner MG. 1999. Aboveground net primary production and leaf area index in initial post-fire vegetation communities in Yellowstone National Park. *Ecosystems* **2**: 88–94.
- Renkin RA and Despain DG. 1992. Fuel moisture, forest type and lightning-caused fire in Yellowstone National Park. *Can J For Res* **22**: 37–45.
- Ripple WJ and Larsen EJ. 2001. The role of post-fire coarse woody debris in aspen regeneration. *West J Appl For* **16**: 61–64.
- Romme WH. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecol Monogr* **52**: 199–221.
- Romme WH and Despain DG. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* **39**: 695–99.
- Romme WH, Bohland L, Persichetty C, and Caruso T. 1995. Germination ecology of some common forest herbs in Yellowstone National Park, Wyoming, USA. *Arctic Alpine Res* **27**: 407–12.
- Romme WH, Turner MG, Gardner RH, *et al.* 1997. A rare episode of sexual reproduction in aspen (*Populus tremuloides*) following the 1988 Yellowstone fires. *Nat Areas J* **17**: 17–25.
- Romme WH, Turner MG, Wallace LL, and Walker J. 1995. Aspen, elk and fire in northern Yellowstone National Park. *Ecology* **76**: 2097–06.
- Romme WH and Turner MG. Ten years after the 1988 Yellowstone fires: is restoration needed? In: Wallace LL (Ed). *After the fires: the ecology of change in Yellowstone National Park*. New Haven, CT: Yale University Press. In press.
- Romme WH, Turner MG, Tinker DB, and Knight DH. Emulating natural forest disturbances in the wildland–urban interface of the Greater Yellowstone Ecosystem. In: Perera AH, Buse LJ, and Weber MG (Eds). *Emulating natural forest landscape disturbances: concepts and applications*. New York: Columbia University Press. In press.
- Schoennagel T. 2002. The effects of fire interval and climate on successional patterns in Yellowstone National Park. (PhD Dissertation). Madison, WI: University of Wisconsin.
- Schoennagel T, Turner MG, and Romme WH. Influence of fire interval and serotiny on post-fire lodgepole pine (*Pinus contorta* var *latifolia* Engelm) density in Yellowstone National Park (USA). *Ecology*. In press.
- Schullery P. 1989. The fires and fire policy. *BioScience* **39**: 686–94.
- Smith C. 1996. Media coverage of fire ecology in Yellowstone after 1988. In: Greelee J (Ed). *The ecological implications of fire in Greater Yellowstone: proceedings of the second biennial conference on the Greater Yellowstone Ecosystem*. Fairfield, WA: International Association of Wildland Fire. p 25–34.
- Stevens MT, Turner MG, Tuskan GA, *et al.* 1999. Genetic variation in post-fire aspen seedlings in Yellowstone National Park. *Mol Ecol* **8**: 1769–80.
- Tinker DB, Romme WH, Hargrove WW, *et al.* 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Can J For Res* **24**: 897–903.
- Tinker DB and Knight DH. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems* **3**: 472–83.
- Tinker DB and Knight DH. 2001. Temporal and spatial dynamics of coarse woody debris in harvested and unharvested lodgepole pine forests. *Ecol Model* **141**: 125–49.
- Turner MG, Baker WL, Peterson CJ, and Peet RK. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* **1**: 511–23.
- Turner MG, Collins S, Lugo A, *et al.* 2003. Long-term ecological research on disturbance and ecological response. *BioScience* **53**: 46–56.
- Turner MG, Hargrove WW, Gardner RH, and Romme WH. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *J Veg Sci* **5**: 731–42.
- Turner MG and Romme WH. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecol* **9**: 59–77.
- Turner MG, Romme WH, and Gardner RH. 1999. Prefire heterogeneity, fire severity and plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *Int J Wildland Fire* **9**: 21–36.
- Turner MG, Romme WH, Gardner RH, and Hargrove WW. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr* **67**: 411–33.
- Turner MG, Romme WH, Reed RA, and Tuskan GA. 2003. Postfire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecol*. **18**: 127–40.
- Turner MG, Romme WH, Tinker DB, and Kashian DM. Landscape patterns of sapling density, leaf area, and aboveground net primary production in post-fire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems*. In press.
- Tuskan GA, Francis KE, Russ SL, *et al.* 1996. RAPDs demonstrates genetic diversity within and among aspen populations in Yellowstone National Park, USA. *Can J For Res* **26**: 2088–98.