A manifest destiny

While fires are part of Yellowstone's natural landscape, many people found it only natural to respond to televised scenes of it burning with offers to plant trees and donate seedlings of more "fire-resistant" species. "We will have growing in Western states a piece of New Jersey," Governor Thomas Kean announced on September 17, 1988, as he held a bundle of seedlings at a statehouse ceremony, "to help restore green to the blackened acres of Yellowstone National Park."

Without casting aspersions on the generosity of the Garden State, it must be said that Yellowstone is no place for a piece of New Jersey. It had its own seeds to sow. Yet as late as 1994, a sixth grade teacher in Fayetteville, Arkansas, was writing *Country Living* magazine to thank them for their continuing sponsorship of a reforestation fund. "My students wanted to put conservation into practice, so they voted to raise money to replant trees in Yellowstone National Park." Actually, the 118,290 seedlings that had been planted in the magazine's campaign to "speed the recovery of acreage destroyed by the Greater Yellowstone Fires of '88" had gone into the adjacent Gallatin National Forest.

Letting Nature Decide

However well-intentioned, such contributions to the park were unnecessary and misinformed. In a national forest where future timber harvests are at stake, intervention may be appropriate after a fire to direct the replanting. In the Gallatin, Shoshone, and Targhee national forests, some of the burned acreage was planted with seedlings, and helicopters dropped tons of grass seeds on steep slopes and along waterways to reduce erosion. But Yellowstone after the fires was no more in need of replanting than is a park that is thawing out at the end of the winter.

The self-seeding forest, October 1998.

Many plant species sprout within weeks after a fire, responding to increased levels of minerals and sunlight, and it is part of Yellowstone's mission to let this transformation proceed without human interference. A hillside of charred trees that has spilled down toward the road after a windstorm may evoke reactions of, "What a mess!" But the park's maintenance crews only remove trees that pose a hazard to visitors' safety, not to their aesthetic sensibilities. The jumble of fallen trees is otherwise left as arranged by nature, to provide the habitat needed by a variety of birds, insects, and small mammals, and as the trees decay, to nourish the soil for the next generation of seedlings.

In Yellowstone, "rehabilitation" was required only for fire-damaged buildings and places where fire suppression efforts had altered the landscape. For the rest of the park, when and where and how the landscape would respond was left to be determined by ecological processes.

Variation as the Constant

On the whole, the research in Yellowstone since the 1988 fires has shown that an ecosystem can be highly variable from place to place and from one year to the next. Lodgepole pine was quick to sprout in many areas in widely varying densities, but not everywhere. Some grasses and flowers, such as fireweed (*Epilobium angustifolium*) and dragon's head (*Dracocephalum parviflora)*, thrived only in the first years after the fires, while others such as pinegrass (*Calamagrostis rubescens*) and showy aster (*Aster conspicuus*), have slowly but steadily increased. Sometimes wildlife appeared to prefer foraging in burned patches, other times they favored unburned areas. Erosion was accelerated in some places, but the amount of soil loss and sediment deposits in streams varied greatly, and in most cases was within the normal range of variation observed before the fires. Just as climate was the main factor affecting the timing and extent of the fires, it has also been a primary factor in determining how the ecosystem has responded in the years since the fires.

Within a few years, Yellowstone's grasslands had largely returned to their pre-fire appearance, and sagebrush areas may be next, in another 20 to 30 years. But the burned forests are still in the early stage of a succession process that may unfold for more than a century, with lodgepole pine seedlings and saplings well-established in many areas, and the first seedlings of Engelmann spruce, subalpine fir and Douglas-fir beginning to emerge. Visitors can still see the stunning sight of acre after acre of charred and singed trees, and hillsides of green pocked with dark scars. As the root systems of the standing dead trees decay and lose their grip on the soil, the trees are gradually falling down, often with the help of a strong wind, but many will remain upright for another decade or more. Remnants of the larger fire-killed trees will still be decomposing on the forest floor 100 years from now, but they will no longer be visible to the untrained eye.

Aside from climate, the key factors in post-fire revegetation are soil moisture and nutrients, and the plant community that was present before the fire. Fertile soils with good water-holding capacity that had a dense, diverse vegetation before the fire were likely to respond quickly with a variety of species and nearly complete plant cover following the fire. Poor, dry soils that had less vegetation before the fire showed a slower response. A secondary factor is elevation, with lower elevations generally responding more quickly.

The key factors in revegetation.

Pollen analysis of pond sediments has shown that the basic vegetation patterns present in the park have been relatively stable for thousands of years. However, these patterns had begun undergoing gradual shifts because of fires and long-term climate changes long before 1988. Because the oldest coniferous trees in the park are more than 500 years old, evaluation of possible climatic effects on vegetation goes back to the Little Ice Age, the coldest part of which occurred in Yellowstone from roughly 1650 to 1890. Tree rings dating from 1751 suggest that the winters of the 1860s and those from about 1885 to 1900 were unusually cold, and the heaviest winter precipitation since the mid-18th century occurred from about 1877 to 1890.[1]

Whether as a result of human alterations to the atmosphere and/or natural fluctuations in the length of the solar cycle or other factors, much of the northern hemisphere has reported a warming trend since the beginning of the 20th century. Average temperatures in Mammoth Hot Springs have risen more than 1°C and, despite an increase in summer precipitation, overall precipitation has declined because of drier winters.[2]

In *Yellowstone and the Biology of Time* (1998), Mary Meagher and Doug Houston compared photographs taken since the 19th century to document changes in the landscape. The vast tracks of lodgepole pine-dominated forests that characterize the central and southern parts of the park, most of which lie between 2,300 m and 2,600 m, had changed little in appearance or extent during the century before the 1988 fires. However, as has been common throughout the northern and central Rocky Mountain region, historic photographs of Yellowstone indicate that conifers at many high-elevation locations have been expanding into adjacent meadows since the mid-1880s. Meagher and Houston believe the major cause of this tree invasion may be a long-term regional trend toward warmer and wetter growing seasons.

Although the relatively short period of effective fire suppression probably had very little effect on most of the Yellowstone landscape, where fires had historically occurred at intervals of 200 years or more, it did contribute to the more dramatic vegetation shifts that took place in the lower portions of the park, where fires had previously occurred at intervals of 20 to 25 years. Much of the northern range, where firefighting efforts could have a bigger impact, has not burned in more than 100 years, despite the fires of 1988. In these areas, landscape diversity has decreased as lodgepole pine and Douglas-fir forests expanded into grassy meadows and drier bunchgrass steppes; Engelmann spruce and subalpine fir increased to a much lesser extent, mainly along streams.[3]

The northern range is an area of 540 square miles that crosses the park's north boundary and is used by many elk, bison, antelope and deer, especially in winter, when because of its lower elevation the snowfall is lighter and the forage more accessible than elsewhere in the park. Some people believe that the presence of a large elk population on the northern range since culling stopped in 1968 has resulted in "over-grazing" and contributed to the decline in aspen and willow.

Pseudotsuga menziesii
Douglas-fir

The Trees That Grow in Yellowstone

Elevation in the park ranges from about 1,800 meters along the Yellowstone River in the north to more than 3,000 meters on the high peaks of the east and northwest. Different vegetation patterns appear within the park based on differences in climate, which varies according to elevation, with mountainous sites being generally cooler and wetter than valley sites. On a broader scale, the central and southern areas of the park tend to have dry summers/wet winters, while the north has wet summers/dry winters.

About 80% of the park is covered with conifer forests dominated by lodgepole pine; subalpine fir and Engelmann spruce are the next most abundant trees. The areas at lower elevations in the north support sagebrush grasslands, with Douglas-fir forests in damper locations and aspen in small groves along forest-grassland boundaries, flood plains, and stream banks. At lower elevations in the Gardner and Lamar valleys, Rocky Mountain juniper and limber pine grow along streams, as do narrow-leaved poplar and water birch. On the cooler subalpine plateaus, extensive lodgepole pine forests are broken by occasional meadows and sagebrush grasslands. The highest ridges may have forests of spruce, fir, and whitebark pine, with subalpine meadows and boulder fields on the more exposed sites. (Based on Meagher and Houston, 1998)

But Meagher and Houston believe that the most striking change in forests below about 2,400 m prior to 1988 was the reduction in area and density of aspen. Sites once occupied by aspen on floodplains, wet swales, and springs on south slopes had become sagebrush grassland or non-native timothy grass meadow, which not only dominated the understory but may have displaced native forbs. Meagher and Houston noted that photos taken outside the park's north, east, and south boundaries show similar increases in forested area and shifts in species composition: aspen declined and conifers increased.

The extent of diversity found in a landscape is the result of two overlapping vegetation patterns: the limits on species distribution set by factors such as elevation and soil moisture, and the patterns of disturbance that occur within the plant communities along those gradients.[4] Instead of advancing as a solid wall of flames that consumes everything in its path, fire sends out probes along the lines of least resistance in the landscape, as determined by fuel load and topography, and it can leap large distances in a single bound. As a result, fire generally increases the heterogeneity of the landscape by fragmenting blocks of older forest with burned patches that will grow new forests. During the preceding century Yellowstone had experienced only relatively small fires, so by 1988 the landscape included a patchwork of successional stages, but also many large, homogenous expanses of mature lodgepole pine.[5]

The fires of 1988 placed a new mosaic of different burn severities atop the patchwork that was already there, while leaving unburned areas across the park in sizes ranging from inches to miles. This jigsaw-puzzle pattern of young, middle-aged, and old forest provides a variety of habitats that can support a variety of animal species. However, the 1988 fires occasionally became so large and powered by wind that they were largely impervious to the effects of local vegetation and topography. Some burned areas therefore became *less* heterogeneous than the previous mosaic had been. That is, where the fire effects were patchy in 1988, they increased the landscape's diversity, but where large areas were intensely burned, the landscape may appear more uniform than it was before the fires.[6]

Researchers have found, though, that even in forests dominated by a single tree species, differences in burn severity and the availability of seeds can result in large-scale patterns of varying tree density and size that may persist until the next stand-reducing fire. In a 1990 study of burned sites, the lodgepole pine density was 4 to 24 times higher in the moderate burns, but the seedlings grew faster and accumulated more biomass per unit of height in the severe burns.[7] A decade after the fires, some areas that had previously been characterized by conifer forest now had pine stands ranging in density from 10,000 to nearly 100,000 saplings per hectare, while other areas were now non-forested or only marginally forested, with fewer than 1,000 saplings per hectare.[8]

Because few species other than Engelmann spruce and subalpine fir can survive on the dark floor of a mature lodgepole forest, the opening of the forest canopy by fire is generally expected to increase the

Landscape diversity.

Lodgepole pine saplings on the Mirror Plateau that sprouted after the 1935 Wrong Creek fire; photograph taken in 1973.

diversity of both the plants growing there and of the animals that can use these plants for food or habitat. In the 1960s, Dale Taylor, a biologist later affiliated with Everglades National Park, censused the plant, bird, and small mammal species at six lodgepole pine sites in Yellowstone that had burned at various times up to 300 years before.[9] Species diversity in all three categories increased with age at the three youngest sites, which still had open canopies: from a total of 55 species at the 7-year site to 112 species at the 25-year site. Biodiversity had declined at the three oldest sites, all of which had a closed canopy: 39 species at the 57-year site and 38 species at both the 111- and 330-year site.

Species diversity.

Although the patchiness of fire is generally assumed to increase the variety of habitats, the overall effect of the 1988 fires on biodiversity is difficult to assess. Insofar as they did not entirely eliminate any habitat type or create one that was not already present in Yellowstone, the fires were unlikely to cause the disappearance of a species or make it possible for a new species to survive in the park. By changing the mix of habitats available for plant and animals species, however, fires may increase or reduce their relative abundance and distribution, at least over the short term.

For example, a decade after the fires, it appears that aspen may have at least temporarily extended their range in Yellowstone (see page 58). But compared to the age of a stand of lodgepole pine, which may endure for centuries, we are still looking at relatively short-term responses to the fires of 1988. Shiny-leaf ceanothus, which was infrequently seen in the park before the fires, sprouted from seeds waiting in the soil and began a shrub layer that may be around for many decades before it is crowded out by growing Douglas-fir trees. Bicknell's geranium also responded to the heated soil by sprouting, but as a biennial it lasted only a few years before retreating to the cover of soil until the next fire.

In any event, although biological diversity is important, it is not the only worthwhile conservation goal, and efforts to maintain maximum species diversity are not always compatible with Yellowstone's primary goal, which is to maintain the park's ecological processes. If biodiversity were the sole criteria, Yellowstone would not be particularly valuable; except for the microorganisms that thrive in its hot springs and some plants that depend on geothermal heat, the park's cold winters and relatively infertile soils do not support flora or fauna that are significantly different from those found elsewhere in the Rocky Mountains.
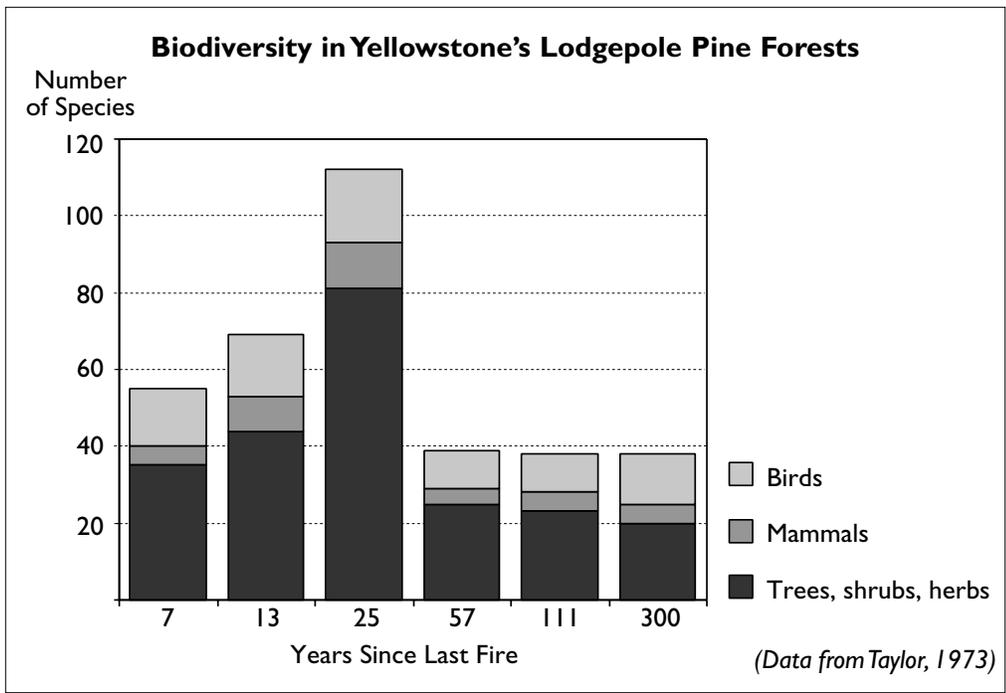
Soils

Providing a reservoir for plant nutrients and moisture, soils play a major role in determining which plant species can grow where. Soil develops as the underlying mineral material (clay, silt, sand, gravel, glacial till, or bedrock) is mixed with dead organic material and living organisms. The two major soil types in Yellowstone, andesitic and rhyolitic, are derived from bedrock that was deposited during two major volcanic events. Andesitic soil, which contains more clay, can hold more plant nutrients and moisture than rhyolitic. The extensive forests of the Yellowstone plateau developed on acidic, infertile soils that originated in the rhyolite lava flows of the Yellowstone caldera, while the drier climate and more productive soils of the Lamar and Yellowstone river valleys, derived largely from andesitic volcanic rock, fostered grasslands with sagebrush. Such differences may explain why a meadow may retain the same shape over time despite fire and other disturbances.[10]

Some soils in Yellowstone supported very little vegetation before the fires and have continued have very little since then. Areas that appear barren and highly erosive did not necessarily become that way because of fire. Crown fires generally have little impact on the soil; it is the slow-moving surface fires that smolder in the forest duff and rotten logs that affect revegetation and erosion. When the soil is burned deeply and long enough, seeds and other reproductive plant material may be killed, and the soil's ability to repel water may be altered. Although some soils are inherently "hydrophobic," this trait may increase when

Ceanothus velutinus
Shiny-leaf ceanothus

Biodiversity in Yellowstone's Lodgepole Pine Forests

Number of Species

Legend:
- Birds
- Mammals
- Trees, shrubs, herbs

X-axis (Years Since Last Fire): 7, 13, 25, 57, 111, 300

(Data from Taylor, 1973)

organic compounds are heated so intensely that vapors condense on the soil, forming a coat that inhibits percolation of water and increases runoff.

Sampling at hundreds of burned areas after the 1988 fires found that in small patches totaling less than 0.1% of the burned area in the park, the soil became hot enough (1,200°F) to kill nearly all the seeds, roots, bulbs, and rhizomes that would otherwise regenerate after a fire.[11] But even these patches were still capable of propagating seeds that may disperse from surrounding areas. The increased hydrophobicity was not expected to significantly affect erosion except in part of the Shoshone National Forest that experienced especially intense burning. (See page 88 for more information about erosion-caused soil loss.)

Scorched earth.

When water filters through the ash of a burned area, it leaches the nutrients from the burned plants back into the soil, where they become available for new plant growth. By analyzing the chemical components of wood ash collected in 1988 before any precipitation had fallen on it, Donald Runnels and Mary Siders of the University of Colorado were able to determine that the ash had lower concentrations of nutrients a year later, and was continuing to release nutrients during "wetting episodes."[12] Different nutrients were released at different rates, resulting in a continually changing soil chemistry.

Soil nutrients after fire.

But the nutrients may filter through the soil if the fire has killed the plant roots that would otherwise intercept them. To test a sampling method that simulates the action of roots in taking up nutrients, scientists from Montana State University compared burned and unburned sites at two locations representative of large areas of the park.[13] They analyzed soil from depths of up to 30 cm using both the standard lab tests, which provide a snapshot of conditions at specific times (in October 1988 and after 30 months), and their *in situ* "resin capsule accumulation" method, which monitored nutrient changes throughout the study period. The resin capsule analysis showed that ammonium and nitrates at the burned Virginia Cascades sites declined during the first 20 months post-fire, then began increasing after 30 months. The Mount Washburn soil, in which ammonium and nitrate levels were naturally much higher, showed little change post-fire. This suggested that when plant roots at the Virginia Cascades burned sites were absent to take it up, nitrogen was being leached to lower depths; as plants grew back, it was retained in the nutrient cycle.

Forests

Although a forest fire may destroy what many regard as useful wood or attractive scenery, it does not destroy the forest itself. In areas burned by crown fires in 1988 (about 41% of the total burned area and 15% of the park), the forest canopy and most of the litter and duff on the forest floor were consumed. These patches were surrounded by halos of singed trees with brown needles, where the fire was not sufficiently intense for complete combustion. Some of these trees died later on because too many of the needles were singed, because too much of the living cambium layer was burned, or because they become more vulnerable to insect infestation, but many survived with only fire scars.

Post-fire survival.

The survival of conifers after a fire depends on the type and degree of fire injury, tree vigor, and post-fire conditions—the influence of insects, disease, and weather. If there is no trunk or root injury and less than 70% of the crown was scorched, trees of normal vigor are more likely to live than die.[14] Mortality resulting from excessive crown injury generally occurs during the first two post-fire growing seasons, while death resulting from trunk and root injury often does not occur until later. And even trees that are killed may leave left behind seeds that will shape the forest's future.

Although also an abrupt change, the harvesting of trees for timber has a very different impact from fire on forest structure. Fire removes mostly leaves and branches; it may char the circumference of trees, but most of the tree boles remain to cast some shade and provide habitat for animals. Burning also consumes much of the forest floor, exposing the soil and facilitating the growth of seedlings. Tree harvesting, in contrast, removes the entire bole and leaves the branches and foliage in the forest. Erosion and nutrient loss may be greater after an intense fire than after tree harvesting, but the charred wood left by a fire eventually becomes incorporated into the soil.[15]

Return of the lodgepole pine.

Nearly all of the burned forests in the park have restocked themselves with seedlings, and nearly all appear to be regenerating plant communities similar to those that were present when the fires of 1988 arrived, primarily because sources of plant reproduction persisted even within very large burned areas.[16] Many of the forests that burned in 1988 were mature lodgepole stands, and this species is now recolonizing most of the burned areas. But although the 1988 fires did not result in vast meadows where forests once stood, lodgepole pine

Yellowstone's forests: past, present and future.

grow slowly in Yellowstone's current climate, and 30 years after the post-fire seedlings have taken root, many may still be less than 10 feet tall. In 50 years, they may form thick stands, 200 to 300 trees to an acre, competing for light, water, and nutrients. And eventually, if there is no other large-scale disturbance or climate change, their crowns will grow together, forming a canopy that shuts off light to the forest floor.

Although regarded as pests in forests used for timber, bark beetles are plant-eating animals with an ecological role that is no more inherently malicious than that of elk or bison. Yet certain insects can be just as deadly to a stand of trees as fire and have a similar canopy-opening effect. And like fire, the bark beetle is heavily influenced by climate, is characterized by large fluctuations in abundance over time, and has an interdependent relationship with the objects of its consumption: bark beetles both affect and are affected by conditions such as forest composition and rates of succession.

Some beetle species have periodically reached epidemic levels in Yellowstone, killing a large portion of trees across vast areas and then diminishing until additional cohorts of susceptible trees mature and conditions again favor an outbreak. Although the mountain pine beetle, Douglas-fir beetle and spruce budworm (*Dendroctonus* spp.) can kill healthy trees, other beetles such as the pine engraver (*Ips* spp.) are typically attracted to weak or already dead trees and may have less impact on tree mortality.

Conspicuous consumers.

Lodgepole pine is most susceptible to infestation by mountain pine beetles (*Dendroctonus ponderosae*) when extensive stands of trees reach at least eight inches in diameter. The last major outbreak in greater Yellowstone began in the Targhee National Forest in the late 1950s and had reached the southwest corner of Yellowstone National Park by 1966. The beetles spread into through an extensive portion of the park's higher elevations, infesting more than 965,000 acres in greater Yellowstone by 1982.[17]

Based on sampling in study plots set up near Bechler Meadows in the southwest corner of the park in 1965, two U.S. Forest Service entomologists estimated that mountain pine beetle infestation had reduced the number of lodgepole pine trees larger than five inches in diameter from 211 to 156 per acre, with mortality peaking in 1969 and subsiding by 1972.[18] In 1990, these researchers, Douglas Parker and Lawrence Stipe, found that more than half of the trees killed from 1966–72 were still standing and, despite widespread crown fire in this area in 1988, the growth of surviving trees had increased the number of live lodgepole pine to 184 per acre.

Canopy fires usually burn or severely scorch the inner bark on which insects feed, reducing the likelihood of widespread infestation, but the crown and bole injuries caused by a surface fire increase the trees' susceptibility to attack. Trees that have escaped fire injury may be exposed to the spread of insect attacks from nearby injured trees. However, assessing the extent of fire damage is often difficult, making it equally difficult to determine the extent to which insects are the agents of death rather than opportunists attacking already mortally injured trees.[19]

Gene Amman and Kevin Ryan of the U.S. Forest Service, who surveyed thousands of trees in unburned and surface burned areas of Yellowstone National Park and Rockefeller Memorial Parkway after the 1988 fires, observed that most trees that had received severe crown scorch or severe bole injury had died within three years; few of the remaining trees had more than half of their crown damaged by fire, and many had no crown injury at all.[20] The mortality of trees after the fires was most often due to fire injury, but insect infestations were a significant factor even for trees with minor crown and bole injury; the level of infestation increased with the percent of the tree's basal circumference killed by fire. Even

Dendroctonus ponderosae
Mountain pine beetle
(larger than actual size)

unburned areas had relatively high levels of infestation, suggesting that insect populations increased in fire-damaged trees and then spread to undamaged ones.

For example, of the more than 1,000 Douglas-fir trees sampled in 1991, 32% were dead by 1992, including almost one third of those that had appeared alive after the fires. Of this delayed mortality, Ryan and Amman attributed 19% to fire injury and 13% to insect infestation, mostly by the Douglas-fir beetle (*Dendroctonus pseudotsugae*). Infestation rates ranged from 16% of the uninjured trees to 80% of the trees in which more than 80% of the basal circumference had been girdled by fire.

Lodgepole pine infestations.

Of the nearly 5,000 lodgepole pine sampled in 1991, half were dead by 1992; 31% because of fire injury and 18% because of insects. The foliage on many of these trees did not fade until they became infested by pine engravers (*Ips pini*) or twig beetles (*Pityophthorus* and *Pityogenes* spp.) three or four years after the fires, and the infestation of uninjured trees increased from 2% in 1991 to 7% in 1992. Infestation rates ranged from 22% of the uninjured trees to 67% of the trees in the 81-100% basal injury class. The pine engraver accounted for most of the infestation; twig beetles and wood borers were also present, but mountain pine beetles were found in less than 1% of the lodgepole pine.

The mountain pine beetle has been a significant cause of lodgepole pine mortality in the West, but populations were low in greater Yellowstone prior to the fires and remained low afterward; these beetles seldom breed in trees injured or killed by fires in numbers sufficient to increase their population. Ryan and Amman were uncertain whether some beetle species would continue to spread to unburned forests, but "historic evidence from other fires suggests major epidemics are unlikely in the absence of additional stress from drought or other sources."

According to the 1997 report on ground and aerial surveys conducted across most of Montana by the U.S. Forest Service in conjunction with the Montana Department of Natural Resources and Conservation, "Bark beetle populations have been again in a general decline except for ongoing outbreaks of mountain pine beetle mortality to lodgepole pine in extreme western Montana."[21] Many groups of insect-killed Engelmann spruce and Douglas-fir were observed in the northeast corner of the Yellowstone National Park that were "remnants of those which built up following the fires in 1988 and the ensuing several years of drier than normal weather. They are gradually returning to endemic levels."

Which came first, the beetle or the fire?

Although the increased vulnerability of fire-damaged forests to beetle infestation is well documented, the reverse is more debatable: are beetle-damaged forests more susceptible to fire? Some scientists such as Parker and Stipe contend that by providing a ready fuel source, the abundance of beetle-killed trees in Yellowstone made the remaining forest in these areas more likely to burn. But Don Despain points out that although the southwest corner of the park has been under nearly continuous beetle attack for more than 50 years, "the vegetation has still not been converted to another timber type, and large fires are no more frequent there than in other parts of the park."[22] Fires as rapacious as those of 1988 showed no apparent preference for beetle-killed trees. Despain has suggested that this may be because beetles actually reduce the fuels suitable for crown fires. Flammability may increase during the first year or two of infestation, but with dead pine needles and twigs falling off and leaving less fuel in the canopy, crown fires that entered areas with many beetle-killed trees in 1988 typically turned into surface fires.

From this perspective, although the presence of fire-damaged trees may encourage the growth of bark beetle populations, infestations appear to be driven more by drought than by fire. Despain notes that both of the major outbreaks that occurred in Yellowstone in the 20th century began during droughts and ended during wet periods.

Ips pini
Pine engraver

A slender tree used by Indians to make lodges and tepees, the lodgepole pine is a sun-loving species, and the only conifer capable of producing fire-resistant seeds. Lodgepole pine's ability to provide an abundant seed source that scatters over the ground within days after a fire gives it an advantage over conifers whose seeds are more easily destroyed by fire and must be brought into a burned area from other another site by wind or animals.

Before fires swept through about a third of the park, it was said that about 80% of Yellowstone was covered with forests dominated by lodgepole pine, and that's still true. Although they may not be most park visitors' idea of forests, thick with tall living trees, nearly all burned lodgepole pine areas are still considered forest habitat, containing primarily forest species. As expected, lodgepole pine seedlings were among the most abundant pioneer species on many burned plateaus during the first years after the fires.

But the density of lodgepole pine seedlings that sprouted in burned areas after the 1988 fires varied greatly, depending on factors such as elevation, fire severity, the abundance of serotinous cones, and seedbed characteristics. Lodgepole pine seeds seldom disperse more than 60 meters from the parent tree.[23] Because the major seed bank for lodgepole pine is in the canopy, seed survival after the fires was greater in areas of surface burn than of crown fire, which may cause cone ignition or substantially reduce seed viability even in serotinous cones. Analysis of video footage showed that tree crowns were most often completely burned in 15 to 20 seconds, while the maximum opening of serotinous cones (37% to 64%) occurs after the cones have been exposed to flames for 10 to 20 seconds.[24] The initial germination rate for non-serotinous cones is higher, but their survival rate decreases about 1.5% for each second in the flames.

In August 1989, Jay Anderson of Idaho State University and Bill Romme of Fort Lewis College in Colorado inventoried plants at 14 plots in the northern part of the park that had been subjected to a moderate burn or a severe crown fire the previous year. Before burning, all of the sites had supported mature, nearly monospecific lodgepole pine stands. After the fire, the density of new pine seedlings was consistently higher in the moderately burned plots, but all sites had mostly the same plant species as before the fire.[25] Of the individual plants found in the first post-fire season, nearly one third were lodgepole pine

Seed survival in the fires.

Some Like It Hot

Lodgepole pine begin producing cones with seeds when they are 5 to 20 years old, depending on the stand density. Between age 20 and 50, some trees start to produce a serotinous cone whose scales are sealed by a resin. The waxy resin will soften enough for the cone to release its seeds only if it is exposed to a temperature of at least 113°F—something that happens in Yellowstone only during a fire.

The proportion of trees in a lodgepole pine stand that bear serotinous cones has been found to range from zero to nearly half, with serotiny more common in even-aged stands and at elevations below 2300 m. This could be because the ratio of serotinous to non-serotinous cones is related to fire frequency, which is generally greater at lower elevations. Many lodgepole pine seeds may be killed by the fire or consumed by birds, squirrels and other animals, but the survivors can sprout from a soil newly rich with minerals and open to sunlight—ideal conditions for the growth of lodgepole pine seedlings, sometimes hundreds of thousands of them per acre. As they grow taller and compete for light and water, only the strongest trees survive. After 200 years, perhaps a few hundred lodgepole pines remain per acre, some with serotinous cones of protected seeds, saving them for a fiery day.

whose seeds had been stored in the canopy; the rest were plants that had survived the fire and grown back. Only about 1.5% of the individual plants and one species (*Dracocephalum parviflora)* grew from seeds that had been stored in the soil. This biennial species flowered only during the first few years after the fire; its seeds will survive in the soil until the next stand-replacing fire occurs. Dispersal of seeds from adjacent areas accounted for less than 1% the plants present.

Variation by type of burn.

Using paired transects at 12 sites in the park that had supported mature, nearly monospecific stands before the fires, Romme and Anderson worked with two other biologists from Idaho State University to compare the effects of surface burn and crown fire on seedling density.[26] They found that by 1990, seedling density increased exponentially with stand serotiny, ranging from 80 seedlings per hectare in a high-elevation stand with no serotinous cones to 1.9 million seedlings per hectare in a low-elevation stand in which nearly half the trees were serotinous. Seedling densities were also consistently higher and the seedlings grew faster in moderately burned as cmpared to severely burned sites. Even after six years there was no evidence that seedling mortality was density dependent.

This research team found that even most of the "remote" crown fire transects (at least 100m from the nearest possible seed source) in their study area had enough seedlings by 1990 to replace the pre-fire stand. But their analysis of aerial photos taken of the entire park in 1998 suggested that while 10% of the area that had burned in 1988 supported very high-density stands of 10-year-old lodgepole pine trees (more than 50,000 stems per hectare), 10% had very low-density stands (fewer than 100 stems per hectare), and density within the remaining burned area was somewhere between those extremes.[27]

John Burger, an entomologist now teaching at the University of New Hampshire, has been a frequent Yellowstone visitor since he began his graduate work in the 1960s, and has been returning annually since 1992 to monitor reforestation as a matter of personal interest. He has been surprised at the enormous variation in the rate of lodgepole pine growth between different sites and between adjacent trees in the same site. In a site near the Mount Holmes trail, the post-fire saplings averaged 205 cm in height by July 2000, but the tallest was 340 cm. South of Norris Junction—"This must be the *ideal* site for lodgepole saplings"—some saplings were more than 400 cm, and the tallest was 444 cm (about 14.5 feet).[28]

Where the forest isn't returning.

Lodgepole seedling, August 1989.

However, reforestation appears uncertain in some areas. After sampling 15 burned sites in the park in 1991 and 1996, Ralph Nyland of the SUNY College of Environmental Science and Forestry noted that the five sites that before the fires had had even-aged lodgepole pine stands (and presumably higher rates of serotiny), now had the highest seedling densities and should have "sufficient trees for a closed-canopy forest to eventually develop."[29] But at the other sites, which had not regenerated well, stand density would increase only when the scattered cohort of initial regeneration begins producing viable seeds, about 10 to 20 years post-fire. And by then these sites may have developed an herbaceous plant community in which lodgepole pine seedlings would compete poorly and may be unable to survive.

Monica Turner, then an ecologist at Oak Ridge National Laboratory in Tennessee, was part of a research group that studied a 3,700-acre area of 400-year-old forest near Yellowstone Lake in which only 1.9% of the pre-fire trees were serotinous.[30] Five years after a crown fire in 1988, it still had fewer than 10 seedlings per hectare. Lodgepole pine seeds are viable for less than five years, suggesting that the opportunity for immediate post-fire tree seedling establishment from local sources at this site had been missed. Although the few seedlings present may be producing seeds by now, replacement of the forest would require seeds from outside the burned area, much of which is beyond the likely dispersal distance of conifer seeds. Based on this data "from the earliest stages of post-fire succession," Turner found that at this site "pathways of succession potentially leading to nonforest communities were initiated following the 1988 fires."

The whitebark pine has kept its distance from most of the human species, having little commercial value and generally growing on high steep slopes. But it has a significant role in the Yellowstone ecosystem, where it helps stabilize soil and rocks on rough terrain, retains snow, and provides an important food. Its large nutritious seeds are eaten by birds, by squirrels that bury the cones, and by grizzly bears, which raid the squirrels' cone middens.

The whitebark pine typically grows above 2,400 m with other conifers, but it can establish nearly pure stands in cold, dry, windswept ridges that are unsuitable for other trees. Its habitat depends on both where it can compete successfully with other vegetation, and where the Clark's nutcracker prefers to cache its seeds. For whitebark pine cones do not release their wingless seeds automatically; the Clark's nutcracker has a near monopoly on their dispersal, using its long bill to extract the seeds and store them under several centimeters of soil in late summer and fall. Carrying dozens of seeds in its throat pouch at a time, the nutcracker may travel miles to find suitable sites for thousands of caches that contain up to 15 seeds. It can later relocate these caches to feed itself and its young until the next year, but nearly half the seeds may remain unretrieved and some will germinate, often after a delay of one or more years, producing clusters of seedlings and multi-trunked trees.[31]

Planted by nutcrackers.

These buried seeds with their delayed germination and the hardiness of the seedlings on exposed sites can give the whitebark pine an initial advantage in large burned areas over conifers that depend on the wind to disperse their seeds.[32] In the absence of fire in more temperate sites, whitebark pines are likely to be shaded out by subalpine fir and Englemann spruce, which are more shade-tolerant and less fire-resistant. However, although whitebark pine frequently survives fire, this slow-growing and long-lived tree is typically more than a century old before it begins producing cones. Consequently, the young trees may die before reproducing if the interval between fires is too short or if they are overtaken by faster-growing conifers.

In much of the northern Rocky Mountains, whitebark pine has been in decline because of a fungal disease known as blister rust. Unlike the bark beetle that causes periodic epidemics in trees (see page 53), whitebark pine blister rust (*Cronartium ribicola*) is not native to the region. Since arriving from Europe around 1910, it has spread to most whitebark pine stands in the moister parts of its range, reaching an estimated mortality rate of 44% of the trees in the Tetons, but only about 7% in Yellowstone's drier climate.[33] Katherine Kendall, a U.S. Geological Survey biologist at Glacier National Park, believes that "the most likely prognosis for whitebark pine in sites already heavily infected with rust is that they will continue to die until most trees are gone," and that to enable the species to continue at a landscape scale, fires must be allowed to burn in the ecosystems they occupy.[34]

Plagued by blister rust.

However, a study of whitebark pine stands in greater Yellowstone did not provide evidence of more prolific regeneration in burned areas. To compare moist and dry whitebark pine sites of different burn intensities, in 1990 Diana Tomback of the University of Colorado set up 275 study plots on Mt. Washburn in the park and on Henderson Mountain, northeast of the park in Gallatin National Forest.[35] Prior to the fires, both areas had mature whitebark pine communities dominated by subalpine fir and Engelmann spruce; the Henderson study area also included unburned sites. Although whitebark pine seedlings had appeared on all sites by 1991, by 1995 there was no significant difference in regeneration density or seedling survival between the burned and unburned sites on Henderson Mountain.

Pinus albicaulis

One of the few deciduous trees found in Yellowstone, aspen can support an abundance of bird life and provide a highly preferred food for elk and beaver. Elk eat the tips of aspen sprouts and the smooth white bark of mature trees, which the tree replaces with a thick black bark. Nearly all large aspen stems in the park have such bark extending up as high as an elk can reach.

On the decline in the Rockies.

Most of Yellowstone's aspen are located in the lower elevations of the northern portion of the park. Until after the 1988 fires, which led to a dispersal and sprouting of aspen seeds, the species was almost entirely absent from the high plateaus that dominate the rest of the park. Instead of reproducing through seeds, Rocky Mountain aspen usually reproduce asexually, with suckers sprouting on the horizontally growing root system, referred to as a "clone." Because the suckers already have a root system to draw water and nutrients from the soils, they can grow quickly into new stems. For the last century, Yellowstone's clones have continued to produce root sprouts, but rarely large stems. Aspen now occupy only about 2% of the northern range, compared to about 6% during the late 1800s.[36] This decline, which has occurred in aspen stands throughout the Rocky Mountains, has been attributed to fire suppression, high elk densitites, a shift to a drier climate, and the resulting greater competition from conifers.

Most of Yellowstone's surviving aspen stands appear to have been established between 1870 and 1890, a period characterized by an unusual combination of a relatively wet climate and low numbers of elk, beaver and moose because trapping, hunting, and wolves were still having a significant impact on the northern range. Infrequent fires and moist conditions may have permitted more rapid growth of sprouts beyond browsing height, and deeper winter snow that made it difficult for ungulates to reach the sprouts; many of the stands are located in depressions and drainages where windblown snow tends to accumulate.

Based on the age distribution of 15 aspen stands on the northern range, Bill Romme concluded that regeneration of large stems was episodic even before the park was established in 1872, and that the right combination of aspen-favorable conditions has not recurred.[37] A moist decade in the 1910s coincided with numerous elk, numerous beaver, and no fires. Reductions in the elk population carried out in the 1950s and 1960s to maintain what was believed to be an appropriate herd size of 5,000 to 7,000, occurred during dry periods when fire suppression was relatively effective on the northern range. A study of 14 aspen stands in the 1960s by park biologist Bill Barmore found that more than 25 "elk use" days per acre resulted in consumption of all aspen sprouts; even at that relatively low elk density, aspen suckers could not grow beyond browsing height.[38] There are also areas in Jackson Hole where ungulate browsing has been light, yet few or no tree-sized stems have developed since the last extensive fires in the late 1800s.

Although aspen as a species is in no immediate danger of disappearing from the park, the canopy of mature stems in many stands has been gradually thinning and disappearing as a result of various diseases and other natural

Populus tremuloides

causes, with little or no aspen understory to replace it. When a dominant stem becomes injured, it stops producing the auxins that otherwise inhibit root sprouting. In this way, even if all the large stems die, the root system can persist, perhaps indefinitely, nourished by small sprouts referred to as "shrub aspen."[39]

According to Roy Renkin and Don Despain's calculations, shrub aspen retain a root biomass of about one ton per hectare and grow about 4 cm in height each summer.[40] They found this shrub condition to be prevalent in aspen across the northern range, as well as in other ecosystems with different elk densities. "Shrub aspen may represent senile yet persistent remnants that germinated and proliferated under more optimal climatic and environmental conditions."

To examine historic browse levels, Renkin and Despain sampled recently fallen aspen trees from each of five clones more than 80 years old across the elevational gradient of the northern range. In 49 of the 50 aspen sampled, previous browsing was evident on the main stem about 33 cm above ground, indicating that current aspen utilization levels are similar to those of a century ago as well as those that occurred during elk herd reductions. Whatever the mechanism was that allowed aspen to grow beyond the browse influence then is not exerting the same influence today.

Meagher and Houston's comparison of historical photographs suggests that even in the late 19th century, when aspen were more abundant on the northern range, they nearly always appeared as dense clumps of short trees, probably the result of fire.[41] Only one out of 22 photographs of aspen taken prior to 1901 shows a stand of mature trees, while 38 of 42 photographs dating from 1901 to 1944 have stands dominated by medium to tall aspen—a maturation that occurred in the presence of high elk densities. Some stands show successful vegetative reproduction, at least on their margins, into the 1920s.

Also using historical photographs, Charles Kay and Frederic Wagner of Utah State University located 81 sites on the northern range that had aspen dating back to 1871, and concluded that one third of the clones had completely died out, without any correlation to slope, aspect, elevation, distance from surface water, or surrounding vegetation.[42] In sites where aspen had survived, they occupied an average of 20% of the area that had historically been covered by clones, and many stands that once contained thousands of trees survived only as small numbers of suckers. Aspen had maintained its presence at some locations for up to 60 years with stems that had never reached a meter in height because of repeated browsing; most stems were less than four years old, and the oldest was 15 years.

Kay also participated in a study that used historical research and photographs to evaluate aspen change over time at Yellowstone and five other Rocky Mountain national parks in the United States and Canada where most stands are in decline.[43] In photos taken before 1910, most aspen stands at all parks were shrub-like in young age classes, with no sign of browsing and abundant evidence of frequent fire, such as burned snags and new forest regeneration, and the few mature aspen stands showed no sign of elk stripping. This study concluded that burning accelerates clone deterioration, and that the combination of fire and elk browsing had hindered aspen regeneration except in northern Jasper National Park, where elk densities appear to have been reduced by wolves in the 1970s.

Shrub aspen in foreground near Tower Junction.

Aspen under fire.

Aspen trees have thin bark and low tolerance for fire, but their insulated root network can survive and sprout suckers. Some optimal fire intensity may be required to maximize this suckering response: a fire of sufficient intensity is needed to disrupt the transport of auxins from the crown to the roots, so that the suckers will sprout, but if the fire is too intense, it will kill the roots from which the suckers arise.[44]

Analysis of aerial photographs has shown that about one-third of the northern range aspen burned in the 1988 fires. They sprouted abundantly during the first two years after the fires, but all sprouts that projected above the winter snow were heavily browsed. To compare the aspen response to fire with and without ungulate browsing, Renkin and Despain identified 18 sites (clones) on the northern range and selected one for a controlled burn in October 1986, and two in October 1987.[45] Two more sites were added to the study after they burned in the 1988 fires. The resulting data suggested that a pre-burn basal area of about 25 square meters per hectare or a root biomass of 20 tons per hectare is required for optimal aspen stocking and growth after fire; aspen stands with the lowest above-ground biomass before the fires produced the lowest amounts of sucker biomass afterward. At the lower growth rates, it would take more than 25 years of protection from browsing for most aspen buds on the main stem to achieve a level at which they could escape herbivory.

The age class structure of aspen at unprotected sites shows that herbivory alone does not always result in accelerated sucker mortality or in the elimination of aspen. One study comparing fenced and unfenced plots found that elk browsing influenced both sucker heights and age-class distribution, but had no effect on sucker density or mortality five to seven years post-burn. When suckers are browsed, the plant's resources are used to produce new suckers instead of growth in height. Renkin and Despain believe that this response allows for the long-term persistence of aspen in a shrub form despite frequent browsing and "represents a viable strategy to remain a component of the landscape."[46]

Another research project led by Bill Romme compared aspen sprout density and browsing intensity in 6 burned and 12 unburned aspen stands.[47] In 1990, the highest density of sprouts was found in the burned stands, but by the fall of 1991 they were approaching the density of the unburned stands. There were no significant differences among the sites in the percent of sprouts browsed by ungulates; the percent was very high (mean 45-75%) both years, and the sprouts were generally short (mean height 21-35 cm).

Based on their observations during the first five years after the fires, Renkin and Despain also concluded that although some aspen clones demonstrated prolific sprouting, most of the burned aspen will not regenerate a forest overstory. "Simply burning aspen does not ensure adequate densities and growth rates to overcome herbivory."[48] Five to seven years post-fire, the shrub aspen appeared to be very similar to their pre-burn condition.

Although Kay and Wagner came to similar conclusions about the lack of improvement in Yellowstone aspen following the 1988 fires, they were convinced that the aspen decline was due to elk browsing.[49] On 22 plots they had measured before the fires, burning stimulated abundant aspen suckering but not growth in height, stem density, or clonal spread. On "tree-

Counting aspen seedlings, August 1989.

type" aspen that were killed by the fire, the suckers grew significantly taller and were produced at significantly greater densities than on shrub-aspen, a result that Kay and Wagner believed was "probably related to clonal vigor," because "tree-type aspen is in better condition than shrub-aspen."

> "The only known way for shrub-aspen to grow back into the types of aspen communities that existed on Yellowstone's northern range ca. 1870 to 1890 is if all ungulate browsing were excluded for 100 years or longer."
>
> — Kay and Wagner, 1996

Kay and Wagner found that the shrub-aspen on their burned plots were about as tall in 1992 as they had been before the fires, and long-term aspen sucker height on the northern range appeared to be primarily a function of snow depth, which limits elk browsing. Shrub aspen located along streams or in other areas with supplemental moisture "could not grow into trees even after they were burned, suggesting that climatic effects are unimportant." Kay has also pointed out that if climate were a significant factor, the condition of aspen in exclosures would be the same as outside.[50] He believes that the current dieback of aspen clones in Yellowstone and other Rocky Mountain parks is due to a combination of higher elk densities and a decrease in fire occurrence.

Sexual reproduction in aspen is very unusual, especially in the present climate of the northern Rockies. The tiny seeds may be dispersed over long distances by the wind in May and June, but seed production varies greatly from year to year and the seeds contain so little food that they remain viable for only a few weeks after their release. They must find bare mineral soil where they can put down roots quickly, consistent moisture to grow leaves to make food, and no other plants with which they must compete for sunlight for several years—a combination of conditions rarely found in Yellowstone. Its original groves of aspen may have become established at the end of the last Ice Age, when glaciers were melting and the land was wet and bare of plants.[51]

The unusual sex life of aspen.

Yet thousands of seedlings appeared in different burned vegetation types in 1989, including sites located several kilometers from and at higher elevations than the nearest aspen clones. Bill Romme believes this could be due to the unusual coincidence in 1989 of prolific seed production, extensive burned areas providing bare soil and reduced plant competition, and moist weather in spring and summer.[52] In subsequent years, not all of these conditions were present, and little or no aspen seedling establishment occurred. Spring and early summer were wet in 1992 and 1993, but plant cover had increased substantially in burned forests by that time. Romme found that aspen seedlings were very patchily distributed throughout the park in 1993, but the greatest concentrations (6 to 340 plants per hectare) were located in burned forests along the Madison and Firehole rivers, east of mature aspen stands growing outside the park's west boundary. Their genetic diversity is greater than that of mature clones sampled on the northern range, with which they have little genetic similarity.

Renkin and Despain noticed that the establishment sites of aspen seedlings usually had deep ash deposits with abundant moss, suggesting that the fires had enhanced soil moisture-holding capacity and retention in these places.[53] They also found about 30 aspen saplings in each of two forest areas that had apparently germinated during the first few years after fires in 1979. Although browsed many times, they had attained heights of 30 to 45 cm.

Research exclosure around aspen seedlings, July 1992.

Survival of the fittest aspen.

In the fall of 1989, Renkin and Despain set up transects in and outside an elk exclosure. They estimated that the initial seedling densities ranged from 500 per hectare to more than 1,000 per square meter. Although browsing caused a significant decline and density generally decreased, all sites still supported aspen seedlings in 1993 and seedling height had increased. Root sprouting was observed in the second growing season on seedlings where the stem had been destroyed by browsing. The relative density of aspen and lodgepole pine seedlings that germinated in 1989 remained about the same, but where lodgepole pine were present, the aspen were two to four times taller than the lodgepole pine.

To document patterns in aspen seedling distribution and abundance, another project involving Bill Romme and Marcia Turner set up belt transects and elk exclosures on portions of Yellowstone's subalpine plateau that had been burned by crown fire.[54] The most important variable in predicting seedling density was geographic location, followed by fire severity and the size of the burned patch. Seedlings were more abundant in more severely burned areas, and in small and moderate-sized rather than large burned patches. In the late summer of 1991, the researchers mapped the 559 pioneer aspen stems found in eight plots that had been established in an area of crown fire adjacent to a wet meadow at Fern Cascades. Increases in density and height were documented in 1991–92 despite frequent browsing by voles, mice, elk, and moose. Recruitment of new stems greatly exceeded mortality from the summer of 1992 through the summer of 1993. As of 1996, the aspen stems were still elongating slowly (a few centimeters a year) and increasing in density in some places despite browsing on at least half of the stems each year.

"We cannot know whether the newly established aspen seedlings will persist for the next 100 or more years. Our data do show, however, that the seedlings have survived the first eight years, that they are elongating slightly and increasing in density in at least some places, and that they are establishing new clonal population structures. It is possible that all of the new genets will perish in some future drought year or during a period of higher browsing pressure."

— Romme et al., 1997

Where no aspen has gone before: submerged seedlings at Swan Lake Flats, 1993.

In addition to stimulating aspen suckers, providing bare ground for aspen seedlings, and enhancing soil moisture, fires may assist aspen growth by toppling conifers that protect aspen from ungulate browsing. That was the hypothesis of two researchers from Oregon State University, William Ripple and Eric Larsen, who measured aspen in and around 28 "jackstraw piles" at least 0.8 m in height on the northern range.[55] They found that during their 1998 sampling period, suckers protected by fallen conifer barriers were, on average, twice as tall as adjacent unprotected suckers.

The debate continues on the relative importance of fire, browsing, climate, competition with other plants, and adverse site conditions as factors limiting aspen growth. But the consensus among researchers seems to be that if for any reason the post-fire seedlings do not grow substantially taller, they are likely to be eliminated from Yellowstone's high plateaus when the post-fire lodgepole pine outgrow them or the climate becomes adverse. In most of the burned forests that now have aspen seedlings, canopy closure could begin to occur in about 40 years and any small aspen plants would likely die from shading.

In the low elevation burned areas of the northern range, elk browsing and trampling are likely to keep seedlings at reduced heights, comparable to trends observed with aspen suckering. However, based on the evidence shown in their paired transects on the northern range, Renkin and Despain proposed that the post-fire aspen seedlings that had established in an elevational zone between 1800 and 2300 m, "particularly within cold-air drainage microsites," had "demonstrated the greatest potential to achieve sexual maturity."[56]

Other Vegetation

Like Yellowstone's trees, most other types of vegetation in the park were not killed by the fires; the portion above ground may have been burned off, but the roots were left to regenerate. The regrowth of Yellowstone's plant communities began as soon as the fire was gone and moisture was available, which in some sites was a matter of days. In dry soils, the seeds and other reproductive tissues had to wait until moisture was replenished the following spring, when yellow arnica, pink fireweed, mountain hollyhock, and blue lupine flowered in burned areas. New seedlings grew even in the few areas where the soil had burned intensely enough to become sterilized. Plant growth was unusually lush in the first years after the fires because of the mineral nutrients in the ash and increased sunlight on the forest floor. Moss an inch or more thick became established in burned soils, and may have been a factor in moisture retention, promoting revegetation and slowing erosion. In some areas such as Blacktail Plateau, such moss was still evident a decade later.

Even in large patches of burned forest, most herbaceous plants came from resprouting survivors and the seeds they provided rather then from dispersed seed from surrounding unburned areas. Monica Turner concluded that differences in depth distribution of rhizomes and seed banks in the soil may therefore be the most important factor in determining post-fire resprouting of individual plants and species.[57]

After sampling nine patches of burned forest in three park locations in the summers of 1990–93, Turner's research team found that the response of herbaceous species that had been present before the fires also varied according to burn severity and patch size. Some species (lupine, grouse wortleberry, and elk sedge) showed a negative relationship between sprout density and fire severity, while others (fireweed and heartleaf arnica) achieved greater densities in more severe burns. Lupine appeared relatively poorly adapted to fire, having heavy seeds with limited dispersal capabilities that require scarification to ensure rapid germination. It sprouted in many areas of the park after the fires, but by 1993 lupine was rare or absent in Turner's study sites if it had been absent before the fires or killed by them.

The aptly named fireweed, in contrast, survives fire in the form of rhizomes (underground horizontal stems) that can live beneath the forest floor for years, awaiting a sunlit opening in which to sprout and produce quantities of seeds that may disperse over hundreds of kilometers and quickly germinate in other open sites. Fireweed spread profusely in the first summer after the fires and appeared to peak in 1991, when in many areas it grew in thick patches of waist-high flowers. Then as competition with other growing plants increased, fireweed declined.

As a way to assess the productivity in four previously forested sites, in July 1997 Turner's research team measured the cumulative new biomass for that year (referred to as "above-ground net primary production" or ANPP) of the lodgepole pine and herbaceous components.[58] All four of the one-hectare sites had been "fully stocked with trees" before the 1988 fires, but they now represented four different types of early post-fire succession as measured in terms of lodgepole pine sapling density: an "infertile non-forest" (fewer than 100 stems per hectare); a "fertile non-forest" (1,000 stems per hectare); a low-density forest (20,100 stems per hectare); and a high-density forest (62,800 stems per hectare). As expected, the tree ANPP generally reflected sapling density, but the herbaceous ANPP was comparable in the infertile non-forest and the more intensely competitive environment of the high-density pine stands. Herbaceous ANPP was also comparable in the fertile non-forest and the low-density pine stand, suggesting that during the early stages of succession, areas dominated by herbaceous vegetation can be as productive as areas returning as forest.

Arnica cordifolia
Heartleaf arnica, 1991.

Benjamin Tracy, a doctoral student at Syracuse University working under Sam McNaughton, found that herbaceous plants growing in burned forest in the Grant Village area produced almost three times more biomass then those in nearby unburned forest.[59] But this striking disparity, evident even five years after the fires, was mainly due to one grass species, blue wild-rye (*Elymus glaucus*) that grew in the newly sunlit forest understory. He found no difference in biomass when comparing burned and unburned meadows in the same area.

Grasslands and Meadows

Most of Yellowstone continues to be considered "forested," even though some of the post-fire forests are comprised mostly of seedlings and saplings. About 6% of the park is still sagebrush grasslands, found primarily on the northern range, which has a warmer, drier climate than the rest of the park, and 7% is higher elevation meadows.[60] Although they accounted for an even smaller portion of the total area that burned in 1988, these grasslands and meadows were important to assess for fire effects because they are an essential source of forage for elk, bison and other large herbivores.

Although damper areas are primarily vegetated by bearded wheatgrass, sedges, and introduced species such as Kentucky bluegrass, the low-elevation grasslands are often dominated by big sagebrush (*Artemisia tridentata*), one of four species of sagebrush that are present in the park, appearing with an understory of native bunchgrasses and forbs. Sagebrush is especially important in parts of the northern range that remain relatively free of snow, where it provides forage for mule deer and pronghorn as well as elk throughout the winter. Sagebrush communities also provide security and thermal cover for ungulates and other animals. Big sagebrush is not tolerant of fire, as the volatile oils in its leaves cause it to burn intensely. Unable to resprout from the root crown as do many other shrubs, sagebrush is greatly reduced after a fire, and the reduction concentrates animal browsing on the surviving or newly reestablishing plants. Any sagebrush that survives the fire produces abundant seeds that germinate readily, but sprouting grasses and forbs dominate in burned areas until the new sagebrush seedlings become established and grow to maturity, which may take up to 30 years.[61]

Many studies have shown that by removing plant litter, fires can increase the productivity of grasslands and alter the foraging behavior of large grazers like elk and bison.[62] In the absence of both fire and significant grazing activity, the accumulation of litter may reduce plant productivity by insulating the soil from sunlight and precipitation, and slowing the decomposition of organic material that provides nutrients needed by the plants. But as with other aspects of post-fire ecological response in Yellowstone, researchers found that "recovery" means different things on different grassland sites.

Using a combination of visual estimations and clipping samples, Evelyn Merrill and Ronald Marrs of the University of Wyoming measured the biomass at 61 burned and unburned sites in grassland habitats during two-week periods for three summers starting in 1989. Vegetation was classified as "green graminoids, green forbs, and standing dead herbaceous material."[63] Although the green forb biomass was significantly higher on burned sites in 1990, they found no significant differences in total green biomass between the unburned sites and those of different burn intensities, and the total herbaceous biomass at all sites was within the range of variation that Merrill had documented for the same area in 1987.

During the 1993 growing season, Ben Tracy compared four sagebrush grassland areas near Hellroaring Creek with different fire histories: one area had burned in 1988, one in 1992 (a deliberately set experimental burn of about 500 hectares), one in both 1988 and 1992, and one not at all in recent history.[64] He found that grasses and sedges produced more above-ground biomass on the burned sites than on the unburned sites. Tracy suggested that the rate at which primary production in sagebrush grasslands recovers from fire may be affected by the patchiness of burned sagebrush, ungulate inputs (nutrients in urine and

Artemisia tridentata
Big sagebrush

feces that stimulate more production on burned than unburned soils), and the fire-induced sprouting of lupine, which is unpalatable to elk and may deter them from using burned areas. (See "Elk and Bison," page 70.)

Where moisture conditions were favorable, the regrowth of grasses after the fires frequently brought significant increases in plant vigor and standing crop, especially for perennial bunchgrasses. However, Meagher and Houston found that although species composition roughly mirrored pre-burn conditions, in some burned subalpine meadows and herblands that have relatively short growing seasons and cool temperatures, the standing crop was lower than in unburned areas two to four years post-fire.[65] Sampling biomass in 1992 and 1993, Tracy found no significant difference in biomass between burned and unburned meadows in the Grant Village area that are interspersed with conifer forest.[66]

Speaking of Wide Open Spaces

Botanists use a variety of terms to describe Yellowstone's northern range: sagebrush grassland, sagebrush steppe, shrub steppe, or bunchgrass steppe—all of which refer to similar plant communities. Sagebrush (*Artemesia*) is the fragrant, grayish-green shrub that is commonly one or two feet tall (though it may reach five feet); its tiny yellow flowers do not appear until August or September. "Bunchgrass" refers to a number of grasses (family Gramineae) that grow in tight clumps and regenerate each year from deep roots.

But as you head up into higher, moister areas of the park, the distinctions get more complicated. "Meadow" generally refers to an area that may have many of the same species as a sagebrush grassland, but is usually smaller in extent and, because of factors such as soil and precipitation, produces more plant biomass. Compared to a "sedge bog," which usually has water at the surface or may even float on a lake, a "sedge meadow" is drier, with water below the surface during a large part of the growing season, and therefore contains different plant species. (Unlike grasses, which usually have a round stem, sedges belong to a plant family with stems that are triangular in cross-section.)

"Subalpine meadow" refers to an elevation zone just below the timberline, while "montane meadow" is a more general term encompassing any relatively high-elevation meadows. "Herblands" are also areas that contain non-woody plants that die back at the end of the growing season, but they are dominated by taller broad-leafed plants instead of grasses and sedges. Although it may have the same plant species, a "forest park" generally refers to an opening in a forested area that is smaller than an herbland.

Bull elk near Lava Creek, November 1990.

Willows

The distribution of willow in the park is largely defined by elevation and precipitation. Although many individual willow plants may be found scattered along stream banks at lower elevations, nearly all of the park's willow communities are located in areas that are above 7,000 feet or receive more than 20 inches of precipitation a year.[67]

Long they may wane.

Willow have persisted in deep-snow areas of the park such as the upper Yellowstone River delta, and colonized active floodplains and some localized wet sites. But evidence from pollen pond sediments[68] and photographic comparisons suggests that they have declined about 60% during the last century at both high and low elevations throughout the park, and been replaced by coniferous forest, sedge meadows, and other herbaceous vegetation. Declines were especially pronounced during the prolonged drought of the 1930s and on ungulate ranges where they have been heavily browsed. As with aspen, similar changes can be seen in photographs taken outside the park, and the decline in willow has been attributed to elk herbivory, beaver declines, a warmer and drier climate, and fire suppression.[69]

After the 1988 fires.

Willow are highly palatable to elk, and are browsed on by Yellowstone's far smaller moose population. Frank Singer, now with the U.S. Geological Survey at Colorado State University, found that about half of the willow stands on the northern range were "browsing suppressed," being only half as tall as "unsuppressed" willows, which averaged 80 cm in height.[70] And because they produce fewer of the compounds that serve as defense mechanisms (through offensive odor or taste, or by disrupting herbivore digestion), suppressed willow become even more vulnerable to browsing. Meagher and Houston have noted that some changes were to be expected with the first appearance of wintering moose on the northern range early in the 20th century; willow communities in Jackson Hole underwent similar changes when colonized by moose.[71]

It has also been suggested that the park's previous policy of fire suppression increased the abundance of conifers and big sagebrush on the northern range at the expense of willow.[72] Fire has been known to increase willow production, vigor, and recruitment by stimulating sprouting and eliminating other vegetation that reduces soil moisture. Prescribed burns are considered an appropriate tool for land managers to use in promoting willow production. Although the riparian areas where most of Yellowstone's willows grow are generally too wet to burn and the fires of 1988 often skipped over them, even where they did not, evidence of better days ahead for Yellowstone's willow are hard to come by.

In connection with his study of moose on the northern range (see page 76), in the spring of 1988 Dan Tyers of the U.S. Forest Service set up 265 plots to monitor eight willow communities.[73] Of the 46 plots that burned that summer, 18 had willow reestablished by 1997. However, in 1992 a mudflow from a burned hillside buried all 35 plots on a site that had partially burned in 1988, and no willow had reestablished there by 1997. The reduction in willow available for browsing because of the fires and drought stress increased the browsing pressure on the surviving stands, which may have further increased their mortality. On plots where willow were still present at the end of his study period, Tyers determined that the average number of twigs produced per plot declined in 1989 and slowly returned to pre-fire levels within about seven years, but overall, more willow had died from one cause or another than were reestablished, and fewer twigs were available for browsing.

Comparing willows at burned and unburned sites on the northern range sites and at Blacktail Creek, Jack Norland of North Dakota State University observed "no positive stature response" after the fires of 1988.[74] Willow protein and digestibility, leaf size, and shoot length increased dramatically, but the effect of burning on willow production varied considerably, with more above-ground biomass in some places and less at others. The difference may have been due to fire intensity, for Norland observed that willow recovery was minimal at other northern range sites where the soil had been extensively heated in 1988.

Enticing to elk and moose.

At the Blacktail Deer Creek site, where the organic matter had been somewhat moist or was not as deep, the shoots from burned willows were signficantly longer, the leaf surface areas about twice as large, and shoot weights were more than twice those of unburned willows. Yet apparently because of the higher protein levels and generally higher digestibility of willow at burned sites, ungulate herbivory increased so much that by three years post-fire, all of the willows at burned sites were shorter than those at unburned sites.

To assist the long-term study of elk impacts on willow, the National Park Service constructed several exclosures around willow on the northern range in 1957 and 1962. Based on data collected in and outside the exclosures in August 1988, Steve Chadde and Charles Kay found no indications that burning would cause resprouting willows to "grow so fast or become so chemically defended that they could grow beyond the reach of elk and reform tall-willow communities."[75]

When protected from elk.

Frank Singer also found that even after protection from ungulates for more than 30 years, previously suppressed willows produced far less above-ground growth than tall-willow communities and showed no community expansion.[76] But he believed that the suppressed willows were located on sites with inherently lower growth potential In a subsequent study with several other USGS scientists, he compared willow communities in Yellowstone and Rocky Mountain national parks, which have had similar elk densities (11-16 elk/km^2), rates of herbivory (26% to 28% of the willows' annual growth), beaver declines since the 1930s, and a long-term trend toward warmer, drier weather on elk winter ranges.[77] They found that annual growth was 250% greater and that the willow shoots were 100% heavier and 41% longer in Rocky Mountain National Park than in Yellowstone. To assess the impact of browsing, willows in both parks that had been protected by an exclosure for at least 30 years were clipped from 1993 through 1995. During this period, the Rocky Mountain willows maintained their rate of annual growth, but the Yellowstone willows did not. Singer believes that the Rocky Mountain willows compensated better for elk herbivory and mechanical clipping because of better growing conditions for elk, i.e., more precipitation, more beaver dams in drainages, and probably higher water tables near streams.

Singer concluded that although high elk density was a major factor, and perhaps the most important factor, ungulate herbivory alone does not explain willow declines on the northern range. He speculated that in addition to the drier climate, the relatively larger beaver decline in Yellowstone may have exceeded a threshold value needed for willow persistence and recruitment. Active beaver ponds enhance conditions for willow growth by raising water tables, flooding willow stands, and increasing the input of nitrogen and phosphorous into the system, and abandoned beaver ponds can provide excellent establishment sites for willow. Common on the northern range until at least the 1920s, beaver are rare there today. Their decline has been also been attributed to climate change and to reduction in habitat and food sources because of elk browsing.

Regardless of the elk population, Singer believes that some willow and aspen declines were to be expected in Yellowstone and Rocky Mountain national parks because of the long-term trend toward aridity, and if this trend hastened beaver declines, then the effect of aridity on willows and aspen would have been exacerbated.

Moose in Willow Park, 1986.

Early in the 20th century, when less was understood about the potential impact of introducing non-native species, hay meadows were cultivated in the Lamar Valley and along Slough Creek for park horses. Some willows were removed, and non-native grasses such as common timothy (*Phleum pratense*), smooth brome (*Bromus inermis*) and crested wheatgrass (*Agropyron cristatum*) were seeded. Common timothy, which can be dispersed by the presence of even minimal wildlife, is now found widely throughout the park on sites where it mixes with and can eventually displace the native alpine timothy (*Phleum alpinum*). Such misguided introductions of non-native species have been augmented by the growing number of uninvited invaders such as cheatgrass (*Bromus tectorum*) and spotted knapweed (*Centaurea maculosa*).

Although the presence of non-native plants in the park had been limited primarily to areas adjacent to roads, park structures, and other human activities, the 1988 fires created corridors into backcountry areas which they might quickly invade. Firefighting activities also scarified the soil, which could increase its receptivity to alien plants, especially if off-road vehicle use inadvertently transported the seeds of species such as leafy spurge and spotted knapweed, which are a problem in many parts of greater Yellowstone. Non-native plants have continued to increase their presence in the park's landscape since 1988, but with the possible exception of Canada thistle (*Cirsium arvense*), there has been little evidence that either the fires or the corridors created by fire lines have made much difference.

Although often seen along park roads and trails, the Canada thistle had not yet invaded most of the area that burned in 1988. But it soon appeared in places that had been used for fire suppression activities and was expected to spread to newly burned patches through seed dispersal. When their study ended in 1993, Monica Turner's group found that Canada thistle was still increasing in all nine sites of varying burn severities.[78] The density of Canada thistle and prickly lettuce (*Lactuca serriola*), an exotic biennial that had not been conspicuous in unburned forest, was greatest in severely burned areas. But prickly lettuce had a negligible presence in light surface burns and peaked in the stand-replacing burns in 1991. Over the short-term, Turner concluded that areas of crown fire provided the best colonization sites for opportunistic species (both native and exotic species that were absent or only incidental before the fires), "but we do not yet know how long they will persist."

Phleum pratense
Common timothy
(non-native)

Phleum alpinum
Alpine timothy
(native)

Cirsium arvense
Canada thistle
(non-native)