A Rare Episode of Sexual Reproduction in Aspen (*Populus tremuloides* Michx.) Following the 1988 Yellowstone Fires

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ABSTRACT: A widely held tenet of Rocky Mountain ecology is that trembling aspen (*Populus tremuloides* Michx.) reproduces almost exclusively by vegetative root sprouting. However, a rare episode of sexual reproduction in aspen occurred following the extensive Yellowstone fires in Wyoming (USA) in 1988. Great numbers of aspen seedlings became established in burned areas in 1989, apparently because of the unusual combination of high seed production, favorable weather conditions, and suitable substrate conditions that existed that year. The new aspen genets are elongating and are developing lateral root systems with numerous sprouts. Genetic diversity of seedling populations on the Yellowstone Plateau is greater than the diversity of mature clones that were sampled in northern Yellowstone National Park. Aspen has become established in many portions of the park where it was absent before the 1988 fires. Thus, we appear to be witnessing an unusual ecological event in which a widespread, ecologically important species has very rapidly expanded its geographic range and genetic variability in response to a large-scale natural disturbance.

Index terms: Populus tremuloides, *Yellowstone National Park, large-scale fires, clonal plants, genetic diversity*

INTRODUCTION

Yellowstone National Park (YNP) is one of the premier natural areas in North America and the world. In 1988 the largest fires in over a century burned more than 250,000 ha in and around YNP (Christensen et al. 1989). At the time there was concern that the natural values of the park were being destroyed, but postfire studies indicate that the Yellowstone ecosystem is resilient and that most of the burned areas are now following expected successional pathways with no major impairment of ecological function or integrity (e.g., Anderson and Romme 1991; Turner et al., in press). Nevertheless, there have been several surprises following the Yellowstone fires. One of the most interesting surprises was the widespread establishment throughout the burned area of seedlings of trembling aspen (*Populus tremuloides* Michx.)—a species formerly thought to reproduce almost exclusively by vegetative sprouting in the Rocky Mountain region (Jelinski and Cheliak 1992). There are now new aspen genets in extensive portions of YNP where there were no aspen before the fires. This unexpected event illustrates the dynamic character of natural ecosystems. It also demonstrates the opportunities that natural areas afford for improving our understanding of fundamental ecological phenomena, such as the genetic consequences of rare sexual reproduction in long-lived clonal plant species (Eriksson 1992) and the ecological consequences of rapid range extension by a major tree species. This unanticipated expansion of aspen populations following the large-scale Yellowstone fires also may be indicative of some of the kinds of additional surprises awaiting us in a world of unusually rapid and intensive global change. In this paper we document the rare event of sexual reproduction in aspen that has occurred in YNP, consider the unusual combination of conditions that allowed it to occur, describe the initial effects on genetic diversity of aspen populations, and speculate on broader ecological implications for the Yellowstone ecosystem.

Trembling aspen is the most widely distributed native North American tree species (Fowells 1985) and an important component of landscapes of the western United States and Canada. Throughout the Rocky Mountains, trembling aspen is a clonal species in which many genetically identical stems arise from a common root system (Barnes 1966). Although aspen can regenerate by two methods, by seeds or through suckering, it is widely believed that establishment of aspen by seed has been extremely rare in the Rocky Mountains since the last glaciation, because climatic conditions have not been suitable for widespread germination and seedling

establishment (Pearson 1914, Baker 1925, Moss 1938, Einspahr and Winton 1976, McDonough 1979). The seedlings require a high light environment plus consistent moisture conditions during the first several years, and thus cannot survive most summers in the Intermountain West under current climate (McDonough 1979). Studies of genetic heterozygosity in aspen clones in Waterton Lakes National Park, Alberta, however, suggest that seedling recruitment must have occurred—even if very rarely—during the past 10,000 years (Jelinski and Cheliak 1992).

The few instances of successful seedling recruitment reported in the literature (see Kay 1993 for a summary of previous reports) suggest that there may be brief "windows of opportunity" characterized by favorable moisture conditions, an absence of competition, the availability of suitable substrates (e.g., burned sites), or a combination of these conditions (Jelinski and Cheliak 1992). In the mid-1980s, Kay (1993) found aspen seedlings in a 400-ha area in Grand Teton National Park that had burned in 1985. However, the most extensive episode of Rocky Mountain aspen seedling establishment documented to date occurred in 1989, when several investigators reported abundant aspen seedlings throughout burned areas of the Greater Yellowstone area (the mountainous region including and surrounding YNP), including sites located several kilometers from the nearest mature aspen clones (e.g., Kay 1993). The 1988 Yellowstone fires affected approximately 45% (400,000 ha) of YNP and adjacent wildland areas (Despain et al. 1989), most of which are dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.). Fires of this scale have occurred in YNP in the past, most recently in the early 1700s (Romme and Despain 1989), and they have had profound effects on the flora and fauna (Christensen et al. 1989, Knight and Wallace 1989, Despain 1991, Turner and Romme 1994, Turner et al. 1994). Although aspen occupied only approximately 1% of YNP prior to the 1988 fires, occurring almost exclusively on the low-elevation sagebrush-grasslands in northern YNP, aspen is ecologically significant because it is the only deciduous forest type present (Despain 1991). Aspen forests support high numbers and diversity of breeding birds and other animals (DeByle 1985) and are visually striking in the fall when the foliage turns yellow in color. Tree-sized aspen generally have not been regenerating in YNP since the late 1800s, although clones have continued to produce root sprouts (Romme et al. 1995), and there has been much recent controversy about the suggested decline in vigor and abundance of aspen in Yellowstone (Despain et al. 1986, Kay 1990, Despain 1991, Wagner and Kay 1993).

We excavated numerous aspen seedlings in 1989 and again in 1991, using fingers and a hand trowel to avoid breaking the roots. Seedlings were readily distinguished from vegetative root sprouts. In 1989 the seedlings had distinct cotyledons, vertical primary roots, and a fibrous lateral root system. By 1991, the seedlings still had the primary root but also many lateral roots that were giving rise to new stems via suckering. The morphology of the Yellowstone aspen seedlings was similar to that described for nursery grown seedlings in Michigan (Day 1944; see Kay 1993 for photographs of seedlings). In 1996, eight years after the fires, these new aspen genets were still present or abundant in many burned areas, suggesting that a seedling recruitment event is now in progress.

Kay (1993) reported new seedling establishment during three successive years following the 1985 fire in Grand Teton National Park. However, we believe that all or nearly all of the aspen seedlings that established after the 1988 Yellowstone fires did so in the first year. All of the genets that we excavated in 1991 had ramets that had originated in 1990 and 1991, as determined from bud scale scars, but these were attached to older ramets and root systems that appeared to have originated in 1989. In the field studies described below, we frequently observed ramets that had originated later than 1989, but they were always in close proximity to older stems. Thus, even though our excavations were not exhaustive, we believe that all or nearly all of the aspen seedling establishment occurred in 1989, the first year after the fires, and that little or no new seedling establishment occurred in subsequent years.

The rarity of aspen seedlings in nature apparently results primarily from very low tolerance for desiccation or for plant-to-plant competition. Seed production varies greatly from year to year, and seeds remain viable only for a few weeks after their release in late spring (Moss 1938). The tiny seeds may be dispersed over great distances by the wind. Seeds require continuously moist soil and cool temperatures for germination and seedling establishment, and seedlings die or are suppressed if buried under soil or litter (Moss 1938, McDonough 1979). Late spring snows may enhance germination and survival by maintaining cool, moist conditions (McDonough 1979). We hypothesized that aspen seedlings became established in Yellowstone in 1989 because of the coincidence in that year of prolific seed production, extensive burned areas providing bare soil conditions with little plant competition, and a cool, moist spring and early summer.

METHODS

To evaluate the hypothesis that aspen seedlings were able to become established in the Yellowstone region in 1989 because of the unusual coincidence of favorable seed production, weather, and substrate conditions, we compiled a table of relevant conditions in each year from 1989 (when establishment clearly occurred) through 1993 (when apparently no new seedling establishment took place). Aspen seed production is known to be highly variable from year to year, but seed production data are not available in the Yellowstone region, so we could not evaluate the importance of this component of the hypothesis. Monthly weather data for the Yellowstone National Park climatic station (located at Mammoth Hot Springs) for the period 1989–1993 were obtained from the Western Regional Climate Center's WCLIM system; these records were compared with long-term (1887–1977) mean temperature and precipitation values for that station (Diaz 1979). General suitability of substrate for establishment of competition-intolerant seedlings within burned areas

was inferred by examining total biotic cover recorded in permanent plots that were sampled annually from 1989 to 1993 on the Yellowstone Plateau in a separate study (Turner et al., unpubl. data).

To document broad spatial patterns in distribution and abundance, we tallied aspen seedlings within long belt transects extending through nine patches burned by crown fire and along eight trails located in different portions of the Yellowstone Plateau that cover most of southern, central, and western YNP (Figure 1). The patches were sampled as part of a more general study of plant reestablishment in relation to fire size and severity (Turner et al., in press). Three geographic locations were identified along a gradient of elevation and geologic substrate in YNP, and within each location large (900–3600 ha), moderate (ca. 100 ha), and small (1 ha) patches burned by crown fire were selected from satellite imagery. Patches were located on the ground, and perpendicular transects were established from the center of the patch to the unburned forest edge in four directions (NE,NW,SW,SE). Permanent sampling points were placed at variable intervals along the transects, with close spacing (10 m) near the unburned edge or near transitions between areas of differential fire severity (Table 1) within the patch, and wide spacing (100 m) in large expanses of uniformly burned forest. We tallied aspen seedlings within 0.5 m on either side of the transect between sequential sampling points in 1990, 1991, 1992, and 1993. Aspen densities (stems/ha) within the belt transects were computed and transformed by taking the square root. The transformed data were then subjected to repeated measures analysis of variance (SAS Institute 1992).

We initiated trailside surveys in 1993 to increase the geographic extent of our sampling. We walked distances of 6–18 km along seven trails, 55%–95% of the distance being within burned forests, and counted aspen seedlings within 2 m on either side of the trail. We estimated distances along the trails from topographic maps. From these data we estimated average aspen density along the trail and local density within individual intervals. Five of the trails were located outside the pre-1988 range of aspen, and two lay just inside the range of aspen; all were in areas dominated by lodgepole pine at the time of the fires (Figure 1). We also sampled along an eighth trail that lay entirely within unburned forest outside the pre-1988 range of aspen but in close proximity to other sampled trails through burned forests, to verify the apparent restriction of aspen seedlings to burned areas. We recognize that trails do not represent an unbiased sampling of a landscape. However, it was not feasible to conduct this kind of extensive sampling in dense forests off of the trails, and in this region of generally undulating topography we believe the bias introduced by trail location and disturbance was relatively minor.

To evaluate survival, mortality, recruitment, and growth of ramets within the newly established aspen genets, we established eight 4-m by 10-m permanent plots in the large patch at Fern Cascades (Figure 1) and mapped all aspen stems in late summer of 1991. The plots were located in a flat area of crown fire adjacent to a wet meadow, a site where aspen was not present before the 1988 fires. For each aspen stem in the plots, we recorded location (x,y coordinates), age (based on bud scale scars), height, and whether browsed or unbrowsed. We resampled the plots in early and late summer of 1992 and 1993, and recorded the same information for every stem still present. We also recorded new stems and stems that had died since the last census.

Because aspen is a favored browse species for many mammals, and browsing may be an important cause of mortality among the aspen seedlings (e.g., Kay 1993), we estimated the abundance of browsing animals within the vicinity of our permanent plots. Using the Schnabel mark-recapture method (Krebs 1989), we captured, marked, and released small mammals over a 5-day period in September 1991. Other potential browsers observed but not quantified in the area included elk (*Cervus elaphus*), moose (*Alces alces*), and snowshoe hare (*Lepus americanus*).

For a preliminary assessment of genetic diversity in Yellowstone aspen populations, we collected small disks from newly emerged leaves in 10 adult aspen stands distributed across northern YNP and in two populations of seedlings that established in 1989 in burned forests on the Yellowstone Plateau outside the pre-fire range of aspen (Figure 1). Each mature stand was at least 0.5 ha in extent and was at least 100 m from any other aspen stand. We established a transect through the long axis of the stand, divided it into 20 equal segments (40 segments in the seedling stands), and collected a leaf disk from one randomly selected stem near the middle of each segment. The samples were returned to the lab under dry ice and subjected to genetic analysis based on randomly amplified polymorphic DNA (RADP) procedures (Williams et al. 1990, Nei and Li 1985; cf. Gilbert et al. 1990), utilizing four 10-mer primers and resulting in 64 polymorphic markers (see Tuskan et al., in press, for details of the genetic analysis).

Table 1. Fire severity classes in subalpine forests of Yellowstone National Park.

0 = unburned

1 = low intensity surface fire (little mortality in canopy and ground layer, patchy consumption of forest floor organic layer)

2 = high intensity surface fire (trees killed but leaves not consumed, aerial portions of ground layer plants burned off but little below-ground mortality, most of forest floor organic layer consumed)

3 = crown fire (trees killed and leaves and small twigs consumed, aerial portions of ground layer plants burned off and moderate mortality of below-ground structures, forest floor organic layer entirely consumed)

RESULTS

The summary of weather and substrate conditions (Table 2) indicates that 1989

was indeed a favorable year for aspen seedling establishment. Precipitation in May was well above normal, and June–August precipitation was about normal. Average monthly temperatures were about normal throughout the season, except in July when they were above normal. Total plant cover in burned coniferous forests was generally very low in this first year after the fires. However, in each of the subsequent years, when little or no aspen seedling establishment occurred, at least some of the measured conditions were noticeably different from 1989. For example, May precipitation also was high in 1990 and 1991, but these two years had relatively dry summers. Spring and early summer were wet in 1992 and 1993, but plant cover had increased substantially in burned forests by this time.

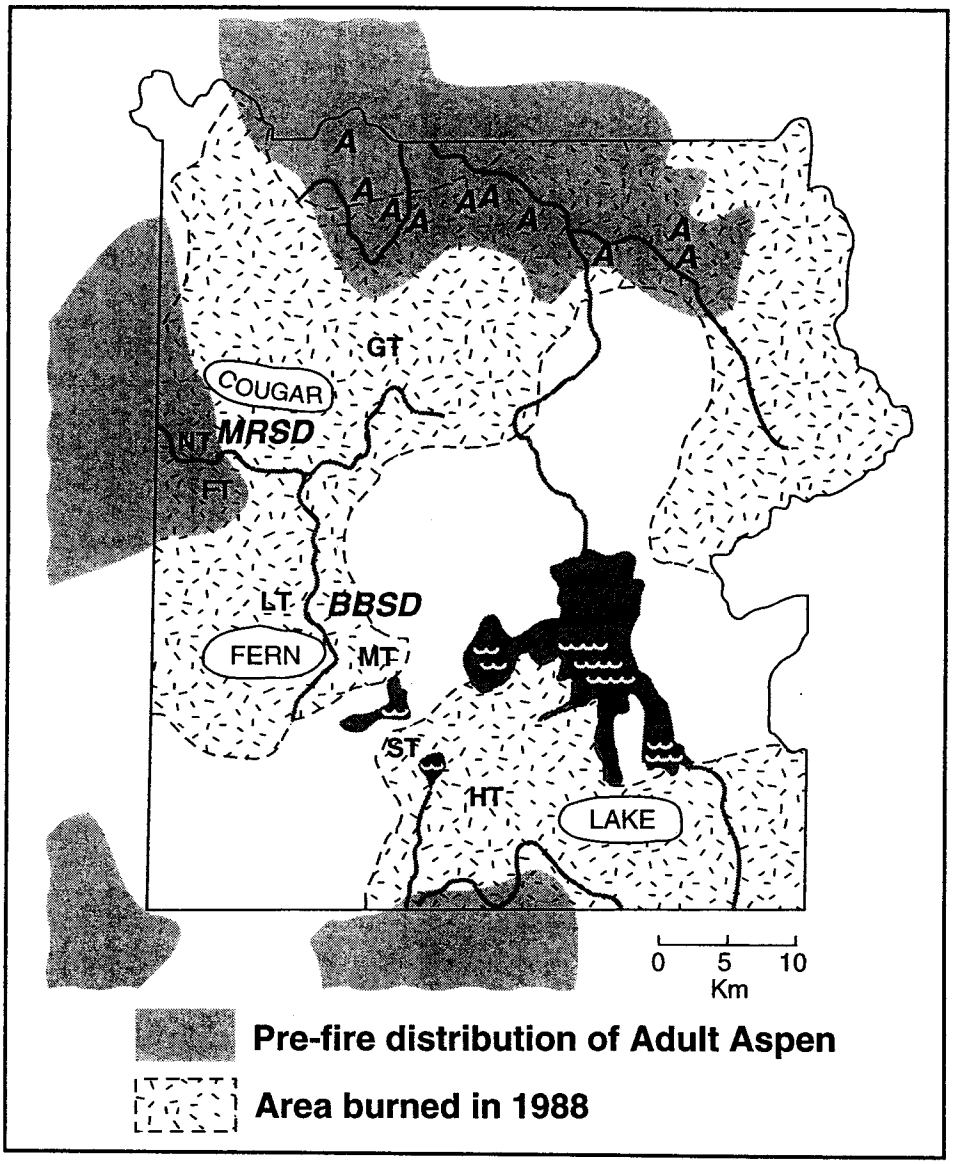

Figure 1. Yellowstone National Park in northwestern Wyoming, USA. "Cougar," "Fern," and "Lake" refer to three geographic locations, each of which contained a sampled large, moderate, and small patch of crown fire. The Cougar Creek area is on infertile rhyolite and tuff substrates at lower elevations (ca. 2,100 m), and the Fern Cascades area is on infertile rhyolite at higher elevations (ca. 2,300 m); the Yellowstone Lake area is on fertile andesite at the highest elevations (ca. 2,500 m). Trails that were surveyed for aspen seedling density: GT = Grizzly Lake Trail, NT = Gneiss Creek Trail, FT = Old Fountain Trail, LT = Little Firehole Trail, MT = Mallard Creek Trail, ST = Shoshone Lake Trail, HT = Heart Lake Trail. Grant's Pass Trail through unburned forest (not shown) is located just east of the Fern Cascades area. Locations where genetics samples were collected: A = adult aspen clones; BBSD = Biscuit Basin seedling population; MRSD = Madison River Bridge seedling population. The permanent plots (see text) were located in the Fern Cascades large patch. The area burned in 1988 is depicted as maximum fire perimeter and contains many large and small unburned patches within the broad outlines shown (Despain et al. 1989).

We examined aspen distribution and abundance both at a broad geographic scale (the entire park) and at a meso-scale (the nine patches ranging from 1 to 3,600 ha). The broad geographic distribution of aspen seedlings in 1993 was based on the transects through the six large and moderate-sized patches and along the eight trails (the three small patches were deleted for this analysis because of their small extent). The plants were most abundant in the west central portion of YNP (Figure 1), where average densities were 6–340 plants ha^{-1} (Table 3). They were also present, but less abundant, in the south-central, southeastern, and northern portions of the Yellowstone Plateau, where average densities were 1–40 stems ha^{-1} (Table 3). Aspen seedling density did not appear to be related to obvious differences in elevation, topography, substrate, or distance to nearest known seed source. However, the greatest concentrations of aspen seedlings were in portions of YNP located to the east of mature aspen stands growing just outside the park's western boundary, suggesting that seed dispersal by predominantly westerly winds accounts for most of the spatial pattern in seedling abundance. Our sampling also revealed that aspen seedlings are almost entirely restricted to burned forests: along several kilometers of trail through unburned forest we observed no aspen seedlings, either within or outside of their pre-fire range of distribution. We also found that the seedlings were very patchily distributed in all areas. Within 100-m segments of the kilometers-long transects and trails, local density ranged from 0 to 10 times the average density along the transect or trail as a whole.

At the meso-scale of our nine sample patches, analysis of variance (Table 4) revealed that the most important variable predicting aspen density was geographic

Table 2. Summary of weather conditions, substrate conditions, and abundance of aspen seedling establishment in Yellowstone National Park, 1989–1993. Total monthly precipitation and mean monthly temperature data for the recent period are from The Western Regional Climate Center's WCLIM system; "normal" climate data (mean monthly values, 1887–1977) are from Diaz (1979). Substrate conditions are reported as mean total % biotic cover (all plant species combined) in permanent plots located within patches of crown fire on the Yellowstone Plateau; the number in brackets is the ratio of total biotic cover in crown fire patches to total biotic cover in unburned forests (even in unburned forests total cover varied annually and never exceeded 40%–50%).

Factor	1989	1990	1991	1992	1993
Precipitation (cm [% normal])					
May	7.6 [161]	6.6 [139]	9.3 [197]	4.4 [94]	6.5 [138]
June	5.3 [105]	4.4 [87]	1.3 [26]	10.6 [210]	9.0 [178]
July	3.1 [99]	0.9 [30]	2.0 [65]	4.6 [145]	5.9 [186]
August	3.6 [112]	2.5 [79]	0.7 [21]	1.1 [33]	3.1 [96]
Temperature (°C [% normal])					
May	8.2 [103]	7.1 [90]	7.6 [95]	11.2 [141]	10.1 [127]
June	13.1 [105]	13.4 [108]	13.7 [110]	13.9 [112]	11.7 [94]
July	19.9 [118]	17.9 [106]	18.5 [110]	14.4 [86]	12.6 [75]
August	15.9 [100]	17.8 [111]	18.9 [118]	16.2 [102]	14.3 [90]
Total Biotic Cover (%) in Crown Fire Patches [ratio burned/unburned]					
	3 [0.02]	14 [0.30]	25 [0.53]	28 [0.70]	— —
Aspen Seedling Establishment					
	abundant, widespread	little or none	apparently none	apparently none	apparently none

location (i.e., the F statistic was highest for this variable), with highest densities in the Fern Cascades area and lowest densities in the Yellowstone Lake area. This pattern is consistent with the broad geographic trends described above. The next most important independent variables were fire severity and patch size. Seedlings were more abundant in the more severely burned areas than in less severely burned areas, and were absent in unburned areas (Table 4). Aspen stems also were more abundant in small and moderate-sized crown fire patches than in large patches (Table 4). Aspect and the interaction between geographic location and year also were significant ($P<0.05$), but their sums of squares were small compared to geographic location, patch size, and burn severity, and hence these variables contributed little to explaining overall patterns of abundance (data not shown). The variables year, slope, successional stage of the forest at the time of the fire, and the interactions burn-x-year and patch-x-year were all nonsignificant ($P> 0.05$) (data not shown).

The eight permanent plots that were established to document survival, mortality, recruitment, and growth contained a total of

Table 3. Aspen seedling densities (stems ha^{-1}) in different geographic locations of Yellowstone National Park in 1993 (Figure 1). All aspen ramets were counted as "stems," even though some ramets shared a common root system (i.e., comprised a single genetic individual that originated from seed in 1989). Known seed sources are adult clones of aspen; closer sources may exist for some populations, but they are undocumented. "Small" local seed sources consist of localized patches (<0.1 ha) of shrub aspen growing on rocky slopes, which probably could not produce enough seed in a single year to stock all of the surrounding area at the densities observed.

Area	Mean Stems/ha	Length of Trail (km)	Percent Burned	Distance and Direction to Known Seed Source(s)
Western and West Central Regions				
Old Fountain Trail	340	6	76	Local adult clones
Mallard Creek Trail	310	11	83	5–10 km W (small); 25 km NW, 45 km SW
Little Firehole Trail	130	6	55	Local (small); 15 km NW, 45 km SW
Gneiss Creek Trail	30	6	84	Local adult clones
Fern Cascades Patches	26	N/A	95	5-10 km W (small); 25 km NW, 45 km SW
Cougar Creek Patches	6	N/A	95	0.5–2.0 km W
Grant's Pass Trail	0	5	0	5–10 km W (small); 25 km NW, 45 km SW
South Central, Southeastern, and Northern Regions				
Shoshone Lake Trail	40	10	89	20 km S, 35–40 km NW, 40 km SW
Heart Lake Trail	10	11	90	20 km S, 40–45 km SW, 40–50 km NW
Yellowstone Lake Patches	1	N/A	95	Local (small), 20–30 km SW
Grizzly Lake Trail	1	9	95	8–15 km N, 25 km W

559 aspen stems in late summer of 1991 (Table 5). Average height was approximately 0.5 m. Over the next winter, 38 of the stems died (6.8% mortality) yet 28 new stems were present in early summer of 1992, for a net loss of 1.8%. Recruitment of new stems greatly exceeded mortality during the summer of 1992 and during the following winter and summer. Thus, after 2 years the number of stems displayed a net increase of 15% (Table 5). All or nearly all of this increase was due to root sprouting from the genets that became established in 1989, as apparently no new seedling establishment occurred during the 1991–1993 period.

We compared height of 482 stems during late summer 1991 and early summer 1992 to determine net change in height (growth and/or loss of height due to browsing or injury) during the season of fall, winter, and spring. The data were negatively skewed, with a minimum of -61 cm (a heavily browsed individual), a maximum of +43 cm, and a median of 0 cm (i.e., no net increase or decrease). Similarly, for the growing season between early summer 1992 and late summer 1992, the data were again negatively skewed with a minimum of -40 cm, a maximum of +33 cm, and a median of +5 cm (n = 478). In 1996, most of the post-1988 aspen stems in the permanent plots, and throughout the rest of our study areas, were 0.2–0.5 m in height.

The increases in ramet density and height that we documented in 1991–1992 occurred in spite of relatively high densities of potential browsing animals. We estimated numbers of voles (*Microtus* sp.) and mice (*Peromyscus maniculatus*) inhabiting the general vicinity (ca. 1 ha) of the permanent plots to be 21–33 and 30–34, respectively, in September of 1991. We also observed elk and moose in the general area on numerous occasions in summer and fall of 1991. About half of the aspen stems in the plots (and throughout our study areas) had browsed tips, but nearly all of these had lateral buds that had assumed apical dominance and were elongating upwards.

The genetic analysis of 10 adult stands in northern YNP revealed very low genetic diversity within stands and moderately low diversity among stands (Table 6). These data suggest that most individual adult aspen stands are clonally derived, though no stand contained a single genotype. Some stands contained as few as 2 genotypes and one stand contained 10. Within seedling populations, some of the band sharing values were lower than those detected among all adult stands (Table 6), suggesting that individual seedling populations contain more genetic variability than all of the sampled mature stands combined. However, there were individual seedling pairs that shared 99% of the bands, and the seedling populations as a whole shared 71% of the markers found in the mature stands. A preliminary cluster analysis of the genetic diversity matrix (Tuskan et al., in press) indicated that the mature stands in northern YNP form a discrete cohort separate from the seedling populations on the Yellowstone Plateau, and that the two geographically separated seedling populations each formed a similar cohort.

Table 4. Patterns in abundance of aspen seedlings in nine patches of crown fire in Yellowstone National Park, in relation to environmental variables. Numbers are mean density (stems ha^{-1}); means followed by the same letter do not differ significantly. Degrees of freedom (df), *F* statistic, and *P* for each variable are from analysis of variance. All aspen ramets were counted as "stems," even though some ramets shared a common root system (i.e., comprised a single genetic individual that originated from seed in 1989). See Table 1 for definition of fire severity classes.

Geographic Location:

Fern	Cougar	Lake
25.61 (a)	5.48 (b)	0.07 (c) (df = 2, $F = 87.44$, $P = 0.0001$)

Fire Severity:

Class 2	Class 3	Class 1	Class 0
7.11 (a)	6.36 (a,b)	0.55 (b,c)	0.00 (c) (df = 3, $F = 13.31$, $P = 0.0001$)

Patch Size:

Small	Moderate	Large
8.55 (a)	7.41 (a)	2.57 (b) (df = 2, $F = 10.61$, $P = 0.0001$)

Table 5. Aspen stem dynamics over 2 years in eight 4-m x10-m permanent plots (total area 320 m^2) in a burned forest in Yellowstone National Park (Figure 1). Fall censuses were made in mid- to late August, near the end of the growing season, and spring censuses were made in late June or early July, soon after buds began to expand.

Census Date	Number of Stems	Interval	Mortality	Recruitment	Net Change
Fall 91	559	—	—	—	
Spring 92	549	Fall 91–Spring 92	-38 (6.8%)	+28 (5.0%)	-1.8%
Fall 92	594	Spring 92–Fall 92	-10 (1.8%)	+55 (10.0%)	+8.2%
Spring 93	614	Fall 92–Spring 93	-33 (5.6%)	+53 (8.9%)	+3.3%
Fall 93	644	Spring 93–Fall 93	-12 (2.0%)	+42 (6.8%)	+4.9%

DISCUSSION

We have documented an unexpected episode of aspen seedling establishment following the 1988 Yellowstone fires. Our

permanent plot study indicates that the new aspen genets that became established in 1989 are persisting, despite browsing on at least half of the stems each year; that the number of ramets is slowly increasing by 5%–10% per year; and that the stems are elongating very slowly (a few centimeters per year). Additional permanent plot and exclosure studies are needed to assess population dynamics and growth trends across a range of environmental conditions in YNP.

The suggested hypothesis to explain why aspen seedling establishment occurred in 1989, namely an unusual coincidence of favorable weather and substrate conditions, cannot be tested unequivocally with an after-the-fact study of this kind (Weins and Parker 1995). However, the summary of weather and substrate conditions from 1989 to 1993 (Table 2) does support the hypothesis. In 1989, all of the presumed limiting conditions were favorable for aspen seedlings, and seedling establishment was abundant. In subsequent years, there was summer drought, high cover of potentially competing vegetation, or a combination of these factors, and seedling establishment was low or absent. Low seed production also could have been important in some years, but this was not measured.

We documented strong spatial patterns in the distribution and abundance of aspen seedlings in YNP. Seedlings were absent or rare in unburned areas, but were found throughout most of the burned forests of the park, where they varied in local density over several orders of magnitude. Highest densities generally were observed in the west central portions of YNP and on more severely burned sites. Environmental variables such as elevation, topography, soil type, and pre-fire vegetation type did not appear to be good predictors of seedling density, although further studies are needed to better evaluate these relationships. Most of the pre-1988 aspen stands within YNP were located in the northern portion of the park, but the low genetic similarity that we found between these northern mature stands and the seedling populations on the Yellowstone Plateau to the south indicates that these northern clones are not the seed sources for most of the seedlings in central and southern YNP. The major seed sources may lie just west of YNP; additional genetic studies are needed to test this hypothesis.

Comparison of genetic diversity within seedling populations and among mature clones that we sampled in northern YNP suggests that overall genetic diversity of aspen within YNP may have increased as a result of recruitment of new genotypes into the population. Our genetic sampling was limited, however, and additional studies (including analysis of the stands west of the park) are needed before we can understand all of the implications of the 1989 seedling recruitment event for aspen population structure and dynamics. The apparently low genetic diversity within and among mature aspen stands in northern YNP is difficult to explain at present, but at least two potential explanations exist: (1) natural selection may be operating to eliminate original genotypes from a sexually reproduced stand, or (2) somatic mutations may be arising over time to maintain genetic diversity within an otherwise monoclonal stand (Tuskan et al., in press).

What are the overall, long-term implications of these new aspen seedlings for the Greater Yellowstone area? 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 8 years, that they are elongating slightly and increasing in density in at least some places despite moderately heavy browsing pressure, 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 (although the low mortality in 1991–1992, when small mammals were abundant, argues against this latter prognosis). Experimental studies (e.g., exclusion of browsers and competitors) are needed to determine whether the present low stature of the plants is caused by continual browsing, by competition with other plants, or by adverse site conditions (soils or microclimate). If the aspen do not grow substantially taller, for whatever reason, then they may be eliminated by light deficiency when the postfire lodgepole pine seedlings eventu-

Table 6. Estimates of band sharing among aspen populations in Yellowstone National Park; estimates were derived from randomly amplified polymorphic DNA (RAPD) markers using polymerase chain reaction techniques. Ten polymorphic markers from four 10-mer primers were used in the calculation of Nei and Li's (1985) band sharing index. See Figure 1 for locations of sampled populations. "Distance" refers to maximum spatial separation of individuals being compared within mature or seedling populations (top three comparisons), or to distance between mature and seedling populations (bottom two comparisons).

Population Comparison	Distance	Band Sharing Index [a]		
		Mean	Minimum	Maximum
Among mature clones in northern YNP	40 km	0.673	0.400	0.889
Among seedlings at Biscuit Basin (BBSD)	<100 m	0.600	0.222	1.000
Among seedlings at Madison River Bridge (MRSD)	<100 m	0.784	0.364	1.000
Between mature clones and BBSD seedlings	50 km	0.645	0.182	0.889
Between mature clones and MRSD seedlings	30 km	0.785	0.200	1.000

[a] Nei and Li's band sharing index can range from 0.0 to 1.0, with 0.0 indicating that no bands are shared, 1.0 indicating that all bands are shared, and values in between indicating the percentage of shared bands.

ally overtop them and form a closed canopy. Pine seedlings are present in nearly all of the burned pine forests that now have aspen seedlings, at densities comparable to the densities of the pre-fire stands (Anderson and Romme 1991, Kay 1993), and canopy closure is expected to occur in about 40 years (Romme and Despain 1989).

If the aspen seedlings do persist, however, then the implications for the Greater Yellowstone area are substantial. Many of the aspen seedling populations are located outside of the pre-1988 range of aspen, so we may be witnessing an unusually rapid range extension in a species that will persist for a very long time through vegetative reproduction even if another opportunity for sexual reproduction does not occur soon (Eriksson 1992). Expansion of aspen into areas that formerly were occupied exclusively by conifers could alter successional trajectories in ways that cannot yet be predicted: our understanding of successional patterns that followed the last very extensive Yellowstone fires (in the 1700s; see Romme 1982, Romme and Despain 1989, Despain 1991) may not provide an adequate base for predicting the long-term successions that will occur after the 1988 fires.

Finally, understanding the response of plant populations to broad-scale disturbances and the ability of species to adapt to changing climatic conditions is crucial for predicting potential ecological effects of global climate change. For clonal plant species such as aspen, either vegetative or seed production may be effective for local reestablishment, but only seed production is effective for long-distance dispersal (Eriksson 1992). Seed dispersal and seedling establishment are key components of a species' ability to persist regionally with climate change. Numerous scientists have hypothesized that climate-induced alterations in disturbance regimes (e.g., fire frequency and extent) may be proximal causes of ecological responses to climate change (Graham et al. 1990). In YNP, the frequency and extent of fires is likely to increase if the climate becomes warmer and drier, and both the upper and lower elevational limits for species may change (Romme and Turner 1991). The recruitment of aspen seedlings within a large natural area following the 1988 fires offers an unusual opportunity to examine the interaction between disturbance and vegetation at the landscape scale and to assess the ability of a population to potentially increase its range within a landscape.

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William Romme, Monica Turner, Robert Gardner, and William Hargrove are interested in the effects of large-scale disturbances on landscape structure and function, and have been investigating the effects of fire size and severity on biotic responses to the Yellowstone fires of 1988. Gerald Tuskan is interested in the application of modern recombinant DNA techniques to questions of genetic structure and dynamics of populations. Don Despain and Roy Renkin have a long interest in the influence of natural fire on vegetation patterns in Yellowstone National Park.

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