Charles E. Kay, Institute of Political Economy, Utah State University, Logan, Utah 84322

Aspen Seedlings in Recently Burned Areas of Grand Teton and Yellowstone National Parks

Abstract

Although aspen (*Populus tremuloides*) produces viable seeds most years, seedling establishment has seldom been reported in the western United States. This paper documents the natural establishment of large numbers of aspen seedlings on recently burned areas in Grand Teton and Yellowstone National Parks. Though a few aspen seedlings were widely scattered throughout the 1985 Beaver Creek burn in Grand Teton National Park, the greatest concentrations occurred at the bottom of kettles or other topographic depressions where densities ranged from 925 to 2,708/ha in 1989. In Yellowstone National Park, aspen seedlings were widely distributed over the area burned by the 1988 wildfires on the northern range but the greatest concentrations occurred in riparian zones that had been burned down to bare mineral soil. In those locations aspen seedling densities as high as 11.5×10^6/ha were recorded and averaged 142,645/ha on permanent plots established in 1989. On permanent plots in the Beaver Creek Burn, the average aspen seedling density increased by 16% from 1989 to 1991 while on permanent plots in Yellowstone Park, aspen seedling densities declined 78% during the same interval. While an abundance of naturally occurring aspen seedlings has not been reported before, evidence suggests that these seedlings may not lead to the growth of mature trees or the development of aspen clones.

Introduction

Throughout the Intermountain West, reproduction of aspen (*Populus tremuloides*) depends almost entirely on the production of adventitious shoots or suckers which arise from lateral roots near the soil surface (Schier *et al.* 1985). Establishment from seed has only occasionally been reported (McDonough 1985). Seedling scarcity is attributed to short-lived seed and demanding seed-bed requirements (Faust 1936, Pauley 1963, Pauley *et al.* 1963, Shier 1981, Jones *et al.* 1985). To grow from seed successfully, aspen seedlings require a combination of bare mineral soil (no competing vegetation), plus high moisture content in surface soils throughout germination and the first growing season. These conditions are frequently met in northern Canada, Alaska, and eastern North America where aspen commonly grow from seed. In the western U.S., however, infrequent rainfalls usually are followed by dry periods which kill any newly germinated seedlings (McDonough 1979, 1985).

Baker (1918, 1925) searched diligently in Utah, southern Idaho, and western Wyoming for 6 years, but failed to find any aspen seedlings even in burned or logged areas. In 25 years of observations, Beetle (1974:9) did not find a single aspen seedling in the Jackson Hole area of western Wyoming. Ellison (1943), though, found one seedling growing near a lake margin on Utah's Aquarius Plateau, while Larson (1944) reported several hundred aspen established from seed on the shoreline of Strawberry Reservoir in central Utah. Barnes (1966:442) observed "numerous aspen seedlings in northern Idaho, predominantly on recently burned sites" but provided no other information. Every and Wiens (1971:141) found five aspen seedlings at unspecified locations in Utah.

Williams and Johnston (1984) documented aspen seedling establishment on spoil from a phosphate mine in southeastern Idaho. Mosts seedlings were concentrated around small seeps, though others were found on all parts of the spoil banks. Seedling densities ranged from 20,000 to 100,000/ha. At the end of four growing seasons, 73% of those seedlings were still alive and had attained heights ranging from 16 to 81 cm. Moss (1938:541) and Every and Wiens (1971:146) suggested that periodic aspen seedling establishment may occur in unusually wet years, though they had no evidence to support their contention.

I have found numerous aspen seedlings in northwest Wyoming and southern Montana on recently burned areas within Grand Teton National Park and on Yellowstone National Park's northern range. Unlike other observations which have usually been associated with some type of human disturbance, these seedlings became established under natural conditions following wildfires.

Study Areas

The two study sites reported in this paper lie within the Greater Yellowstone Ecosystem (Clark and Zaunbrecker 1987). Anderson (1958) and Boyce (1989) provide a general description of the climate and vegetation in Jackson Hole while Dirks (1979), Dirks and Martner (1982), and the National Park Service (1986:12-16) provide more detailed information for Grand Teton National Park. Houston (1982) and Despain (1990) provide a description of the climate, physiography, and vegetation of Yellowstone's northern range.

During late August 1985, the Beaver Creek fire burned approximately 416 ha of mostly coniferous forest in Grand Teton National Park (Sections 10, 11, 14 and 15; T43N, R116W). Fire intensity was sufficient to kill nearly all trees within the burn's perimeter and to exfoliate 8 to 10 cm of stone from granite boulders. The Beaver Creek burn covers the terminal moraine of the glacier that once flowed out of Avalanche Canyon. Much of the area is covered by kettles and kames, and elevation ranged from 2,050 to 2,100 m. Prior to the fire, lodgepole pine (*Pinus contorta*) was the most abundant conifer but stands of Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) were common. Small areas of dry grasslands, riparian zones, and occasional aspen clones were also burned. The Beaver Creek burn is grazed by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) during late spring, summer, and fall as deep snow precludes ungulate use during winter.

During the summer of 1988, approximately 550,000 ha burned in the Greater Yellowstone Ecosystem including a large portion of Yellowstone Park. Approximately 34% of the park's northern range burned, including 8% of dry grasslands, as well as several wet meadows (Singer and Schullery 1989). Elevation ranged from 1,700 m to 2,100 m. Unlike the Beaver Creek burn which is grazed by ungulates during the growing season, Yellowstone's northern range is used by elk and other ungulates primarily during winter, though some summer use does occur (Kay 1990).

Methods

Grand Teton National Park

During the summer of 1988, I found what appeared to be numerous aspen seedlings in the Beaver Creek burn. Several were carefully excavated, photographed, and later verified as aspen seedlings. All had numerous fibrous roots which originated from a central tap root. None were connected to any other aspen via lateral roots as would be the case if they were suckers originating from an aspen clone (Schier 1981). Additional seedlings were excavated during 1989 and deposited in the Intermountain Herbarium, Utah State University, Logan, Utah. The nearest likely sources of aspen seed ranged from 200 m to 800 m.

I searched the entire Beaver Creek Burn for aspen seedlings in 1989 and placed eight permanent 4 x 30 m belt transects in areas that contained the greatest concentrations of seedlings. The ends of the transects were marked with single steel stakes and a 30 m tape was stretched between those points. A distance of 2 m was measured out to the right and left of the transect centerline. The transect centerline was then divided into 3 m segments. This produced a series of 2 x 3 m counting plots to the right and left of the centerline for a total of 20 counting plots per transect. The number of aspen and lodgepole pine seedlings was recorded on each 2 x 3 m counting plot and summed over the entire length of each transect. The height and any evidence of recent ungulate browsing were recorded for each aspen seedling, and for the tallest lodgepole pine seedling on each of the 20 counting plots per transect.

Percent canopy-coverage of grasses, forbs, shrubs (including aspen seedlings), lodgepole pine seedlings, and bare ground was visually estimated on 0.2 x 0.5 m (0.1 m^2) microplots placed adjacent to each belt transect's centerline at 2 m intervals. At each interval, microplots were placed to the right and left of the centerline, except that the transect's beginning and end points were not utilized. Thus, 28 estimates of ground cover were obtained for each 30 m belt transect. All plots were remeasured in August 1991. Aspen seedlings were aged by counting bud scale scars.

The Beaver Creek burn is located approximately 6 km north of park headquarters at Moose, Wyoming where a weather station has been maintained since 1936. That station is about 90 m lower than the burn and may be a little drier (Dirks and Martner 1982). Other weather stations in the valley, such as Jackson or Moran, are even farther removed from the burn and have noticeably different climates (Dirks and Martner 1982). Weather data from 1936 to 1976 were taken from Dirks and Martner (1982) while more recent records were obtained from *Climatological Data: Wyoming* (National Oceanic and Atmospheric Administration 1977-1991).

The mean heights of aspen and lodgepole pine seedlings in 1991 were compared using Student's t test (Sokal and Rohlf 1981). The other data do not lend themselves to comparative statistical analysis (Hurlbert 1984) or the comparative tests were not germane to this study.

Yellowstone National Park

I searched the northern range for aspen seedlings during August and September, 1989 and then established three 2 x 30 m permanent belt transects in a 100 x 300 m area of Yancy's Hole (Universal Transverse Mercator grid coordinates 4975000N 545300E) where aspen seedlings were abundant. The ends of the transects were marked with single steel stakes and a 30 m tape was stretched between those points. A distance of 1 m was measured out to the right and left of the transect centerline. The transect centerline was then divided into 3 m segments. This provided a series of 1 x 3 m counting plots to the right and left of the centerline for a total of 20 counting plots per transect. The number of aspen seedlings was recorded on each 1 x 3 m counting plot and summed over the entire length of each transect. The height and any evidence of recent or past ungulate browsing was recorded for the tallest aspen seedling on each of the 20 counting plots per transect. Transect centerlines were used to measure canopy-coverage of other species via line intercept (Hanley 1978). In a burned-out 30 x 30 m sedge depression near Range Exclosure 25 (Universal Transverse Mercator grid coordinates 4975800N 545700E), aspen seedlings were so abundant that I recorded their numbers in 1 x 1 m plots. A likely source of aspen seed is situated within 100 m of the Range Exclosure 25 site and within 400 m of the Yancy's Hole site. Several seedlings were excavated and deposited with the Intermountain Herbarium.

Results

New aspen seedlings have only a slight resemblance to the adult form. New seedling leaves are nearly lanceolate instead of the familiar orbicular to broadly ovate shape of normal adult aspen leaves (Figure 1). During the first growing season, seedling leaf petioles are not obviously vertically flattened as they are in the adult form and there is no lateral branching. By the second and third growing seasons, though, seedlings produce lateral branches and normal adult aspen leaves. All plants more than 1-year old identified as aspen seedlings in this study had already produced adult form aspen leaves. All plants identified as new aspen seedlings in 1989 produced adult form aspen leaves by 1991. These plants are clearly aspen seedlings, not another species of *Populus*.

Grand Teton National Park

Although a few aspen seedlings were widely scattered throughout the Beaver Creek burn, the greatest concentrations occurred at the bottom of kettles or other topographic depressions where densities ranged from 950 to 2,700/ha in 1989 (Table 1). The mean height of all aspen seedlings four years after the fire (1989) was 39 cm; but height is not a true measure of their growth because 85% had already been browsed at least once by ungulates. In 1991, the mean height of the aspen seedlings was 41 cm. This was partly due to the relatively high rate of recent browsing, 43%, and new short-statured seedlings which lowered the average height of the sampled population. Greatest aspen seedling height growth between 1989 and 1991 was observed on belt transects with the lowest incidence of ungulate browsing and where no new seedlings were present (Table 1).

Even though lodgepole pine was abundant throughout the Beaver Creek area prior to the fire, most lodgepole pine seedlings were restricted to the same sites occupied by aspen seedlings. Fire-killed lodgepole pine were present on all transects, and lodgepole pine seedlings averaged 65,379/ha in 1989 but they had decreased to 55,319/ha by 1991 (Table 1). None of the lodgepole pine seedlings showed any evidence of ungulate browsing (Table 1). Mean height of lodgepole pine seedlings was 42 cm in 1989 and they had grown to an average height of 116 cm by 1991 (Table 1).

Vegetation recovery throughout the burn has been slow and probably reflects the intensity of the fire. Four summers after the burn (1989), grasses, forbs, and shrubs had a combined average canopy-coverage of only 28% on the measured transects while 60% of the area was still bare (Table 2). The combined canopy-coverage of grasses, forbs and shrubs had increased to 53% by 1991. Most of that increase was in the forb component (Table 2). Fireweed (*Epilobium angustifolium*), while present, was not particularly abundant. Mountain hollyhock (*Iliamna rivularis*) and most regenerating shrubs were heavily grazed by elk and mule deer which probably limited those species' canopy-coverages. Lodgepole pine seedlings averaged

Figure 1. Closeup of unbrowsed 3-month old aspen seedlings collected in 1989 from Yancy's Hole on Yellowstone National Park's northern range. Note the root structure where numerous fibrous roots originate from a central tap root and the absence of any suckering lateral roots. Meter stick for scale.

TABLE 1. Density, height, and ungulate use of aspen and lodgepole pine seedlings on the Beaver Creek burn, Grand Teton National Park.

		Aspen Seedlings			Lodgepole Pine		
Belt Transect	Year	Number per ha	Percent Browsed*	Mean Height (SEM) (cm)	Number per ha	Percent Browsed*	Mean Height (SEM) (cm)
BCB-1	1989	1,500	89	38 (3)	27,332	0	41 (1)
	1991	1,250	80	41 (3)	22,991	0	114 (4)
BCB-2	1989	1,750	95	41 (3)	24,666	0	46 (2)
	1991	1,416	41	50 (4)	21,825	0	117 (4)
BCB-3	1989	1,083	92	41 (5)	6,750	0	42 (3)
	1991	916	91	42 (6)	6,414	0	120 (6)
BCB-4	1989	1,000	67	49 (6)	19,999	0	39 (3)
	1991	3,165	11	21 (3)	17,493	0	111 (5)
BCB-5	1989	952	100	36 (4)	28,810	0	51 (2)
	1991	1,428	58	27 (6)	25,466	0	142 (4)
BCB-6	1989	1,833	86	36 (3)	96,996	0	43 (2)
	1991	1,583	11	61 (4)	89,464	0	136 (3)
BCB-7	1989	1,500	89	29 (3)	114,412	0	42 (2)
	1991	1,916	26	36 (5)	101,876	0	106 (3)
BCB-8	1989	2,708	62	38 (3)	204,069	0	33 (1)
	1991	2,603	24	50 (4)	157,020	0	81 (3)
Mean	1989	1,541	85	39 (2)	65,379	0	42 (2)
	1991	1,785	43	41 (5)**	55,319	0	116 (7)**

*Percentage of total seedlings with evidence of summer ungulate browsing the same year that they were measured.
**$t = 8.71$, $p < .01$.

TABLE 2. Percent ground cover on aspen seedling transects in the Beaver Creek burn, Grand Teton National Park.

			Percent Canopy-Coverage			
Aspen Seedling Transect	Year	Percent Bare Ground	Grass	Forbs	Shrubs	Lodgepole Pine
BCB-1	1989	63	11	20	2	4
	1991	29	6	38	2	25
BCB-2	1989	57	22	15	1	5
	1991	17	26	30	3	24
BCB-3	1989	58	13	23	4	2
	1991	20	40	24	4	12
BCB-4	1989	44	28	16	9	3
	1991	12	38	24	9	17
BCB-5	1989	78	2	10	0	10
	1991	28	6	26	2	38
BCB-6	1989	64	4	10	1	22
	1991	7	1	42	1	49
BCB-7	1989	75	1	9	0	16
	1991	6	4	49	1	40
BCB-8	1989	41	23	5	3	28
	1991	1	18	28	2	51
Mean	1989	60	13	13	2	11
	1991	15	17	33	3	32

11% canopy-coverage in 1989 and 32% in 1991. By 1991, the proportion of exposed mineral soil/rock had decreased to 15%.

Grand Teton Park and much of the Intermountain West experienced a drought from 1986 through 1988. Precipitation at Moose was only 63 to 71% of the 50-year average of 617 mm. June, July, and August were particularly dry with precipitation only 16% to 70% of the 50-year means, except for July 1987 when precipitation was 2.5 times above average. Precipitation during June, July, and August 1989 was above average and for the year was nearly normal. But in 1990, precipitation again was only 72% of average. During the 1990 and 1991 growing seasons, precipitation was below average in four of the six months. The amount and timing of rainfall certainly were not within the range commonly thought necessary for aspen seed germination and seedling survival, except perhaps for July 1987 (McDonough 1979, 1985). Daily temperatures during the June-August growing seasons were usually within the range reported for aspen seed germination and seedling growth (McDonough 1979) except that frosts occurred at least 50 times from 1986 to 1991.

Despite the fact that elk and mule deer had browsed a high proportion of the terminal leaders on aspen seedlings (Table 1), I was able to age a random sample of 222 aspen seedlings in 1989 by counting the bud scars on lateral branches and the lower, unbrowsed main stems. Some aspen seedlings became established and survived each year after the fire; 23% began growth in 1986, 60% in 1987, 14% in 1988, and 4% in 1989. The greatest proportion of seedlings began growth in 1987 when July temperatures and precipitation were most favorable. New aspen seedlings were also observed on three of the permanent belt transects in 1991 (BCB-4, 5, and 7; Table 1).

In all years, kettle bottoms and other topographic depressions apparently held the additional soil moisture needed for aspen seedling establishment. Several kettles in the burn contained standing water year-long while others held water during spring.

Yellowstone National Park

The 1988 fires occurred during an extended drought and under extreme burning conditions (Davis and Mutch 1989; Romme and Despain 1989a, 1989b; Schullery 1989a, 1989b). This permitted the fires to burn normally wet riparian zones including seeps and lake margins (Knight and Wallace 1989). Many of those areas had thick sedge (*Carex* spp.) mats and accumulations of organic matter that "were burned down to mineral soil, killing rhizomes and root systems" (Knight and Wallace 1989:704). At the time of aspen seed release during spring 1989, these areas of bare mineral soil and ash held abundant moisture (Figure 2).

Aspen on the northern range produced a prolific seed crop during spring 1989 and temperatures and precipitation were also favorable for aspen seed germination and seedling growth. This combination of factors produced an abundance of aspen seedlings during the summer of 1989. On belt transects in a burned-out sedge meadow in Yancy's Hole, aspen seedlings averaged 142,695/ha (Table 3, Figures 2 and 3). The fire had killed the sedges and the newly established competing vegetation had an average canopy-coverage of only 12% (Table 3). In another burned-out sedge depression near Range Exclosure 25, the average density of aspen seedlings on five 1 m^2 plots was 1,152/m^2 (sd = 410) or over 11.5 x 10^6/ha. By 1991, the mean density of aspen seedlings on the Yancy's Hole belt transects had declined to 31,654/ha while the canopy-coverage of other plants increased to 69% (Table 3). From 1989 to 1991, average height of the aspen seedlings declined from 58 cm to 47 cm. By 1991, all aspen seedlings showed signs of repeated ungulate browsing (Table 3) which probably accounts for the height loss, as new aspen seedlings were not observed in 1991. None of the aspen seedlings showed any evidence of summer ungulate browsing in 1989 or 1991. The incidence of browsing recorded in 1991 apparently occurred during the winters of 1989-90 and 1990-91.

During the summer of 1989, I also observed widely scattered aspen seedlings in burned coniferous forests and even within established aspen stands killed by fire. The tallest observed seedling measured 78 cm and had 24 leaves. Areas with the most abundant seedlings usually had ash deposits 1-5 cm thick on top of mineral soil, suggesting that the ash may have promoted aspen seed germination and survival. This factor apparently has not been previously investigated in studies of aspen seed germination and survival (McDonough 1979, 1985).

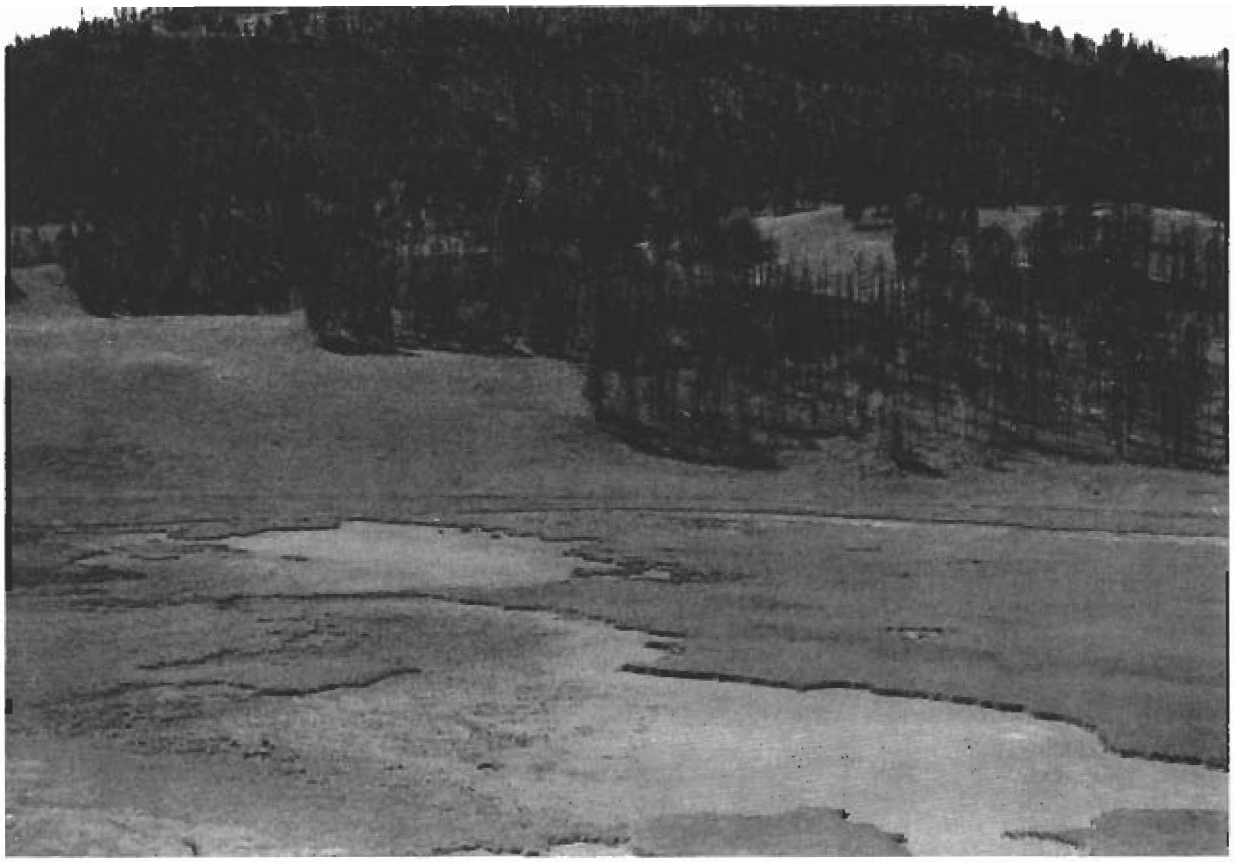

Figure 2. Burned-out sedge meadow in Yancy's Hole near Tower Junction on Yellowstone National Park's northern range in 1989. Prior to the 1988 fires, this area was a continuous sedge meadow with no openings. The burned-out areas were covered with standing water until mid-June 1989. The aspen seedling belt transects are located in the lower-left center.

TABLE 3. Aspen seedling parameters and vegetation ground cover in Yancy's Hole, Yellowstone National Park.

Belt Transect	Year	Number of Aspen Seedlings per ha	Mean Height (SEM) (cm)*	Percent Browsed**	Percent Canopy-Coverage of Other Vegetation
AS-1	1989	177,202	62 (3)	–	12
	1991	32,154	50 (4)	100	65
AS-2	1989	141,362	60 (4)	–	7
	1991	46,148	57 (5)	100	68
AS-3	1989	109,522	53 (7)	–	18
	1991	16,660	34 (3)	100	75
Mean	1989	142,695	58 (3)	–	12
	1991	31,654	47 (7)	100	69

*Mean height of 20 tallest seedlings per belt transect; see text.

**Percent of seedlings that showed evidence of past browsing. This site is grazed during winter and none of the aspen seedlings showed any evidence of summer browsing when they were measured in 1989 or 1991; see text.

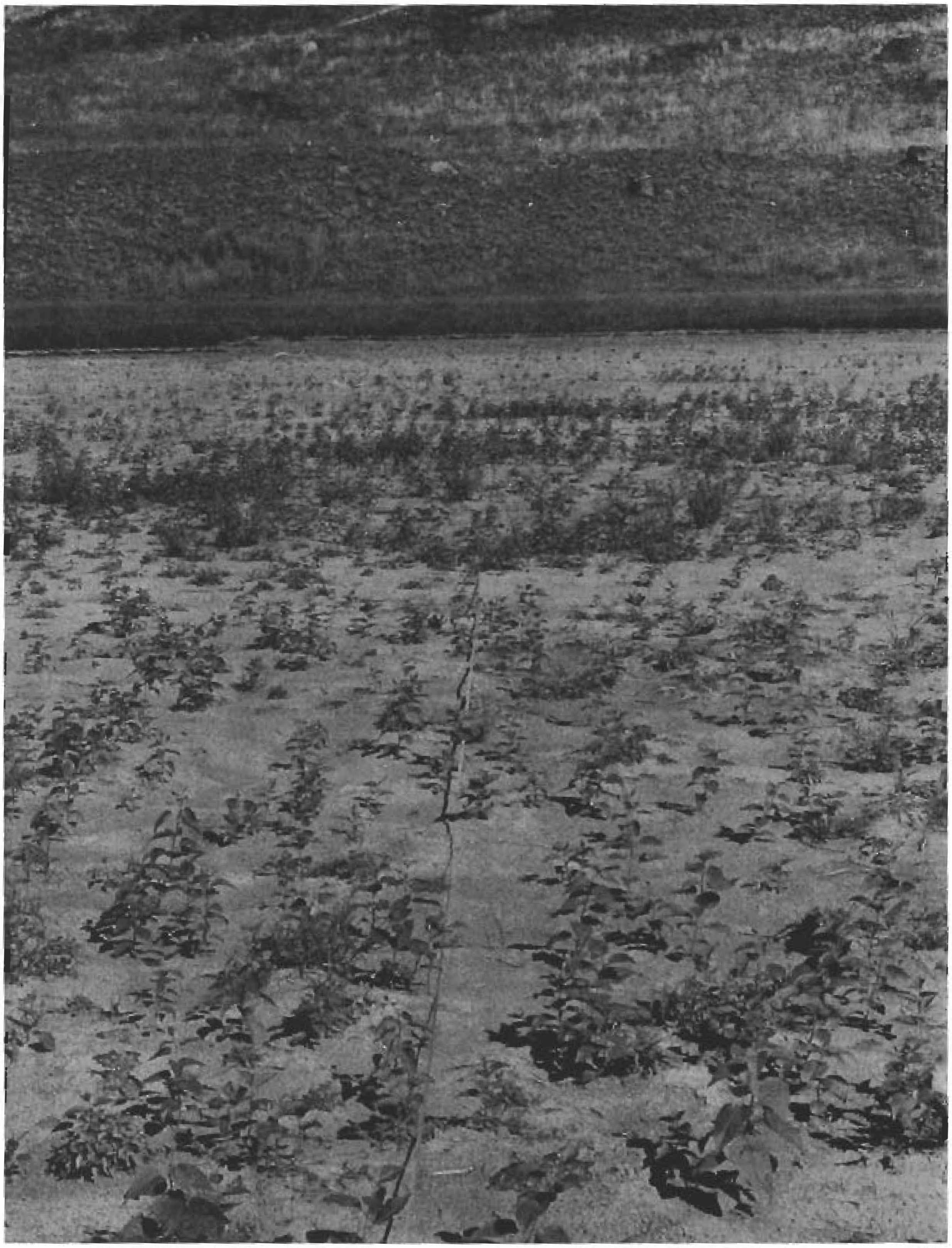

Figure 3. Newly grown aspen seedlings on a permanent belt transect in Yancy's Hole, Yellowstone National Park. Nearly all the plants in this 1989 photograph are aspen seedlings. Aspen seedling density on this transect was 141,362/ha and other species had a canopy-coverage of 7%.

Discussion

Most seedlings and certainly their greatest concentrations were associated with seeps, springs, topographic depressions, or other microsites with abundant soil moisture, conditions that have been established experimentally for aspen seed germination and seedling development (McDonough 1979, 1985). Zasada *et al.* (1983) reported that in interior Alaska aspen seedling establishment and survival was positively correlated with burning intensity. Aspen seedling survival occurred almost exclusively on severely burned surfaces. All of the aspen seedlings observed in Grand Teton and Yellowstone National Parks were associated with bare mineral soil, ash, and an absence of competing vegetation following wildfires. So it appears that high intensity fires may be required for aspen seedling establishment in the West.

Fire has often been used to regenerate established aspen stands because fire-killed trees produce abundant root suckers (Schier 1981, Schier *et al.* 1985). In the upper Gros Ventre drainage of Jackson Hole, aspen sucker densities ranged from 24,000 to 36,000/ha 2 years after the 200 ha Breakneck Ridge aspen burn (Bartos and Mueggler 1981). On other burns in Jackson Hole, aspen sucker densities ranged from 10,000 to 150,000/ha (Bartos *et al.* 1991). One year after the fires on Yellowstone's northern range, burned aspen stands produced sucker densities of 1,000 to 200,000/ha (Kay unpub. data). So, the densities of aspen seedlings on the Beaver Creek burn are much lower than sucker densities which normally occur after established aspen stands are burned. On the other hand, aspen seedling densities on Yellowstone's burned-out sedge meadows were up to 50 times greater than highest aspen sucker densities recorded after the 1988 fires.

Despite an abundance of naturally occurring aspen seedlings in these areas, several lines of evidence suggest that they likely will not lead to the development of mature trees or aspen clones. First, many of the burned-out sedge meadows and other topographic depressions in Yellowstone that contain the highest densities of aspen seedlings are subject to spring flooding. During years of abundant precipitation, these areas may hold water for most of the summer (Brichta 1987, Chadde *et al.* 1988). Since aspen do not tolerate standing water, these seedlings will die if they are flooded for any length of time. This probably explains the reduction of aspen seedlings that occurred on the belt transects in Yancy's Hole, though ungulate browsing and self-thinning may also have been factors.

Second, both study areas have large populations of elk and other ungulates for which aspen is a preferred food. Large numbers of elk now summer in Grand Teton National Park (Boyce 1989) and most of the aspen seedlings in the Beaver Creek burn have been browsed at least once. Elk appear capable of preventing aspen seedling height growth and their development into trees. Elk have prevented height growth of aspen suckers which sprouted in fire-killed aspen stands throughout Jackson Hole (Bartos and Mueggler 1981, Kay 1990).

In Yellowstone, 15,000 to 25,000 elk winter on the northern range (Houston 1982, Lemke and Singer 1989, Singer and Schullery 1989). Unprotected aspen in the park have not been able to regenerate vegetatively for the last 80 or more years because of repeated browsing (Kay 1990). With the level of ungulate use that exists in Yellowstone, it is questionable whether any of the aspen seedlings will grow into mature trees, let alone establish new clones.

Third, in Grand Teton's Beaver Creek burn, the areas with the greatest concentrations of aspen seedlings also have much higher densities of lodgepole pine seedlings (Table 1). Between 1989 and 1991, lodgepole pine seedlings increased in height by an average of 176% while aspen seedlings grew only 5%. By 1991, lodgepole pine seedlings were also significantly taller than aspen seedlings and, unlike aspen seedlings, had not been browsed by ungulates (Table 1). Lodgepole will probably outgrow the aspen seedlings and dominate those sites.

Fourth, during an extensive survey of established aspen stands in and adjacent to Grand Teton and Yellowstone Parks, I observed very few aspen clones growing on sites similar to those occupied by the aspen seedlings described herein (Kay 1985, 1990, and unpub. data). For example, only twice were fire-killed aspen observed in or adjacent to kettles or other topographic depressions in the Beaver Creek burn, and those were single trees. Most of the established stands in this burn are on south-to-east-facing hillsides.

On Yellowstone's northern range, few aspen stands are established along lake margins, in sedge meadows, or topographic depression where aspen seedlings are now most abundant (Kay 1985, 1990; Chadde *et al.* 1988). A few aspen grow near seeps or springs, but that is relatively uncommon. Most established aspen stands are not associated with high water tables, which is not surprising since, as noted previously, aspen seldom survive on saturated soils. This creates a paradox since the sites most favorable to seed germination and seedling growth may not be favorable for the establishment of mature aspen trees or clones. In interior Alaska, Krasny *et al.* (1988) reported that aspen seedlings readily established on river bars but that they seldom grew into mature trees due to repeated spring flooding.

Most aspen clones in the West are larger than those found in other areas of North America (Kemperman and Barnes 1976). Randomly selected clones that I measured on Yellowstone's northern range (n = 268) averaged 0.5 ha, while the largest covered 6.8 ha (Kay 1990). A single aspen clone in southern Utah occupied 43.3 ha, though larger clones probably exist (Kemperman and Barnes 1976). Due to the large size of these clones and the heretofore lack of observed sexual reproduction, it has been postulated that western aspen clones may be 8 to 10,000 or more years old (Jones and DeByle 1985:35). The abundance of large numbers of aspen seedlings in Grand Teton and Yellowstone National Park, though, suggests that catastrophic fires may be important in the establishment of aspen from seed and that establishment of aspen clones in the West may not be as rare as commonly believed.

I would caution, however, that seedling occurrence, in and of itself, may not be sufficient to establish aspen clones under present conditions. Since Yellowstone Park was established in 1872, repeat photographs (n = 81) show that the area occupied by aspen has declined by approximately 95% and that at least one-third of the clones have totally disappeared due to repeated browsing by elk and other native ungulates, not climatic factors (Kay 1990). Only inside ungulate-proof exclosures have established aspen clones expanded in size (Kay 1990), as would be required if aspen clones established from seed.

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