

Quaking Aspen Reproduce From Seed After Wildfire in the Mountains of Southeastern Arizona

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Abstract—Quaking aspen regenerated from seed after a stand replacement wildfire in the Chiricahua Mountains of southeastern Arizona. The wildfire had created gaps in the canopy so that aspen were able to establish from seed. Seedlings were found at a mean density of 0.17 m^{-2} , 30 m or more from the nearest potential seed trees. Six clumps of aspen seedlings contained 18–186 trees, occupying areas of 145–500 square meters at densities of $0.09\text{--}0.27\text{ m}^{-2}$. White-tailed deer (*Odocoileus virginianus*) browsed 14.3% of the seedlings. Occasional sexual reproduction of aspen may be a general trait of the species throughout the western portion of its range in North America.

Introduction

In the Mountain West, quaking aspen trees (*Populus tremuloides*) commonly reproduce by asexual root suckering. After fire or other disturbance that kills overstory stems, suckers sprout from surviving root systems. Reproduction after fire from seed has been reported, but apparently this is exceptional (Kay 1993; Renkin et al. 1994). Aspen seeds require consistently moist soil to germinate and survive, a condition that is rarely met in the climates of the mountains of Western North America. Presumably this is the reason that aspen seedlings are seldom observed in the West. This paper is a preliminary report on a population of aspen established from seed after a wildfire in southeastern Arizona during 1994.

Study Area

The Chiricahua Mountains are located in southeastern Arizona, near the borders of New Mexico and the Republic of Mexico. The range is approximately 65 km long and 32 km wide, with a maximum elevation of 2,975 m. The upper reaches of the range are dominated by a series of ridges and peaks in excess of 2700 m. Common trees at elevations above 2,400 m are Arizona pine (*Pinus ponderosa* var. *arizonica*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), southwestern white pine (*Pinus strobiformis*), and quaking aspen. The primary study area was located at elevations of 2,700 to 2,900 m, immediately north of the Chiricahua Wilderness, within the Coronado National Forest of Cochise County, Arizona. It fell between two meadows named Long Park and Flys Park (Universal Transverse Mercator grid coordinates 3528500N 662100E). Slope in the sampling area varied from 0 to 8%, with an easterly aspect.

Rattlesnake Fire

In June and July of 1994, a fire ignited by lightning burned 11,000 ha of forested land in the Chiricahua Mountains. This fire was the first large fire that had burned through these mountains in about 100 years (Skelecki et al. 1996; Swetnam et al. 1990). The fire burned at various intensities across almost all of

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the upper elevation forests including all areas with aspen. Stands of aspen occurred in scattered clumps through the predominantly coniferous forest in relatively mesic locations above approximately 2,400 m. We estimate that aspen covered less than 10% of the area burned by the fire. The wildfire continued for 3 weeks under burning conditions that were quite variable, propelled by erratic winds, steep terrain, and through various fuel types. It was finally extinguished by the arrival of monsoon rains. Within the fire perimeter the fire burned almost all forested areas; however, the fire intensity was quite variable over the landscape. In some watersheds all trees were killed and the soil structure was destroyed by heat so intense that boulders shattered. At the opposite extreme, some places had light ground fires that burned only the smallest downed fuels. The aboveground parts of most aspen were killed but some canopy aspen, particularly in the more mesic areas, were only lightly scorched at the base. In places many of these large aspen survived, although often the bottom of the tree was partly killed on the side from which the fire approached.

Climate

Maximum precipitation occurs in the monsoonal months of July and August. Nearly one-half of the annual precipitation falls within this period, which is during the growing season for aspen (figure 1). The months of May and June, when aspen seeds are produced and dispersed, are much drier. In some years this period has no precipitation at all. Since aspen seeds require soil that is consistently moist in order to germinate and survive (McDonough 1985), in many years soil moisture conditions would not permit aspen seedlings to become established, even if other physical conditions were optimal. In the Mountain West the lack of soil moisture near the surface during late spring and early summer, even for a very short period, has been presumed to prevent the establishment and survival of aspen seedlings.

Sampling Methods

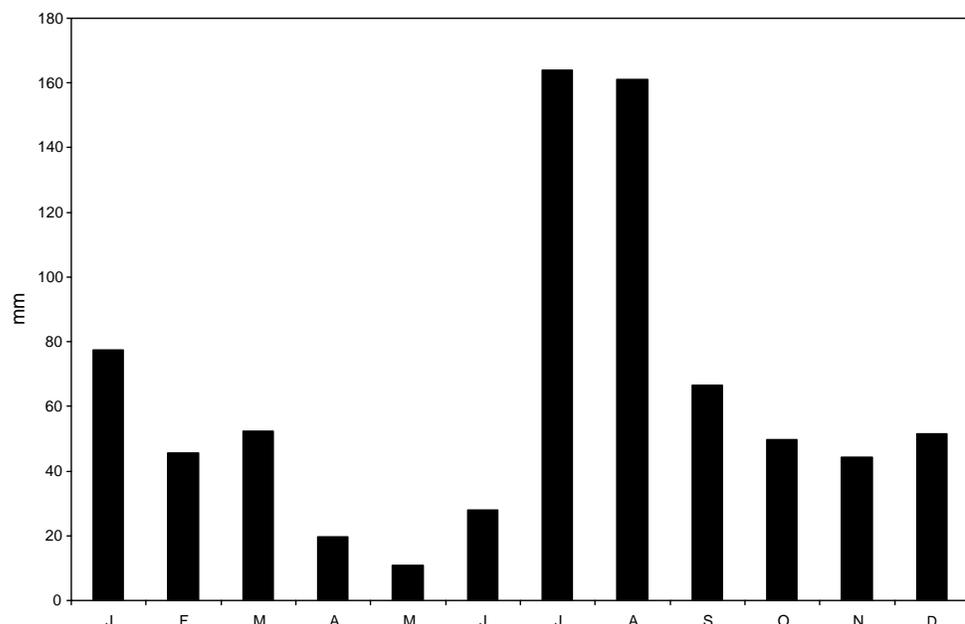


Figure 1—Mean monthly precipitation at Rustler Park, Chiricahua Mountains, Arizona.

In the summer of 1998 a belt transect was established on a gently sloping plateau where most trees had been killed by the 1994 fire. A second belt, perpendicular to the first, was added in 1999. The belts were 4 m wide, with lengths of 225 and 300 m. In 1998 the composition of the prefire forest was measured at points 15 m apart along the center of the 4 x 225 m belt using the point quarter method (Cottam and Curtis 1956). All trees killed by the fire were still standing, and both living and dead stems were included in the tree sample. The cover and species composition of the understory vegetation was measured around the same points using circular plots with a 1-meter radius. In the summer of 1998, tree seedlings of all species within the belt were counted. The height and diameter of each aspen seedling were measured. Seedling measurements were repeated in the summer of 1999 along both belts; all aspen were tagged and mapped; and evidence of browsing on individual aspen was noted.

In the summer of 1998, 11 small aspen, ranging in stem height from 9 to 65 cm, were excavated. The entire root systems were exposed, and the lengths and diameters of all major roots were measured, along with the height and basal diameter of the tallest stem. In 1999, 16 additional aspen were excavated and measured. Plants to be excavated were randomly chosen from the area defined by a 225 x 300 m rectangle that enclosed the perpendicular belt transects, excluding seedlings that fell within the belts. Cross-sections were cut from just above the base of an additional 16 randomly chosen small aspen in the same area. The cross-sections were examined under magnification for growth rings.

Results and Discussion

Forest Composition

Prior to the fire the forest in the study area was comprised of half Arizona pine, mean d.b.h. 27 cm (SD = 12.2), and half Douglas-fir, mean d.b.h. 31 cm (SD = 15.5). Tree density was 700 per hectare. Twenty-six percent of the sampled Arizona pines survived the fire; all of these were growing in an area where the fire did not crown. All Douglas-fir within the study area were killed. The largest diameter tree sampled was a Douglas-fir snag with a d.b.h. of 96 cm. This was the only tree measured that showed a conspicuous scar from fires long before 1994. The estimated height of canopy trees was 16–18 m. Canopy cover from snags in areas where all trees were killed was 53%, and overstory cover was 71% in places with living Arizona pines. Mean understory cover in 1999 was 50%, comprised of a mixture of 45 species of annuals and short-lived perennials from 20 plant families. Asteraceae, with 11 species, was best represented both in terms of number of species and total cover.

Excavated Seedlings

The 11 aspen excavated in 1998, and 16 aspen excavated in 1999, had a mean of 3.3 major roots, with a range of 1–14 (table 1). A major root was defined as one originating from the base of the union between stems and roots, and having a diameter similar to that of the corresponding stem. These roots had a mean diameter of 4.2 mm, as compared to a mean stem diameter of 4.6 mm. Mean root length, measured from the base of the plant to the point where the root divided into two or more secondary roots, was 24 cm as compared to a mean stem height of 26 cm. There was great variation in the length, number, and paths followed by the roots. Some extended to depths greater than 20 cm while others grew

Table 1—Mean characteristics of excavated aspen seedlings (standard deviations in parentheses).

	1998	1999	1998 + 1999
Stem height (cm)	22 (21)	27 (29)	26 (26)
No. stems	2.1 (2.0)	1.7 (1.4)	1.8 (1.6)
Stem diameter (mm)	4.1 (2.7)	4.8 (3.4)	4.6 (3.1)
No. roots	3.1 (2.9)	3.4 (3.2)	3.3 (3.1)
Root diameter (mm)	3.5 (1.5)	4.5 (2.8)	4.2 (2.4)
Root length (cm)	28 (28)	22 (21)	24 (24)
N	11	16	27

laterally only a few cm beneath the surface. Roots grew around and between rocks and other barriers, and some followed very circuitous paths, changing direction several times both horizontally and vertically. Between 1998 and 1999 the seedling population showed development in all variables measured except root length; mean height and diameter of stems increased, and roots became slightly more numerous (table 1). The excavations provided evidence that the small aspen being sampled were in fact seedlings that had originated after the fire and not suckers that had arisen from mature roots. All of the excavated plants had spreading root systems, and neither sinker roots nor feeder roots were observed. For comparison, several suckers approximately the same size as the seedlings were excavated from nearby aspen clones. In every case the feeder root from which the sucker had grown was readily located, and a sinker root provided a direct and obvious connection between the sucker and the feeder. In one case the feeder root had died, but it was still present and the sinker had a markedly different morphology than the roots of the seedlings. No evidence was found in the study area of aspen root systems that predated the 1994 fire. There were no aspen snags or living aspen larger than seedlings within the study area. No evidence of aspen was found close enough to have produced roots to extend inside the study area.

Cross-sections collected from the 16 aspen in 1998, the fourth growing season after the fire, had from one to three growth rings, with a mean of 1.9 (SD = 0.7). Precipitation records from a weather station approximately 4 km from the study site showed that May and June, the critical months for germination and survival of aspen seedlings, were very dry in 1995, the first full growing season after the fire (figure 2). In 1996 there was ample precipitation in June, and in 1997 there was substantial rain in May. There may have been no seedlings with four growth rings because none germinated and survived until 1996, the second year after the fire, when precipitation was adequate. These rainfall and ring patterns support the hypothesis that aspen seeds can germinate in fire areas in the years following fire, provided that moisture is consistently available to them during the first few months of the growing season. Laboratory and field studies have shown that aspen seeds retain viability for only a few months, and after germination even the slightest drying kills them (McDonough 1985). We did not notice aspen seedlings anywhere in the study area or larger fire area before 1997.

Seedling Dispersion

The dispersion pattern of the aspen seedlings along the belts in 1999 was examined using two-term local quadrat variance and paired quadrat variance, dividing up the transects into 4 x 4 m blocks (Krebs 1999). These analyses failed to show a clumped distribution, probably because the scale of sampling was not appropriate to the scale of aspen clumps. A map of the 358 aspen seedlings was

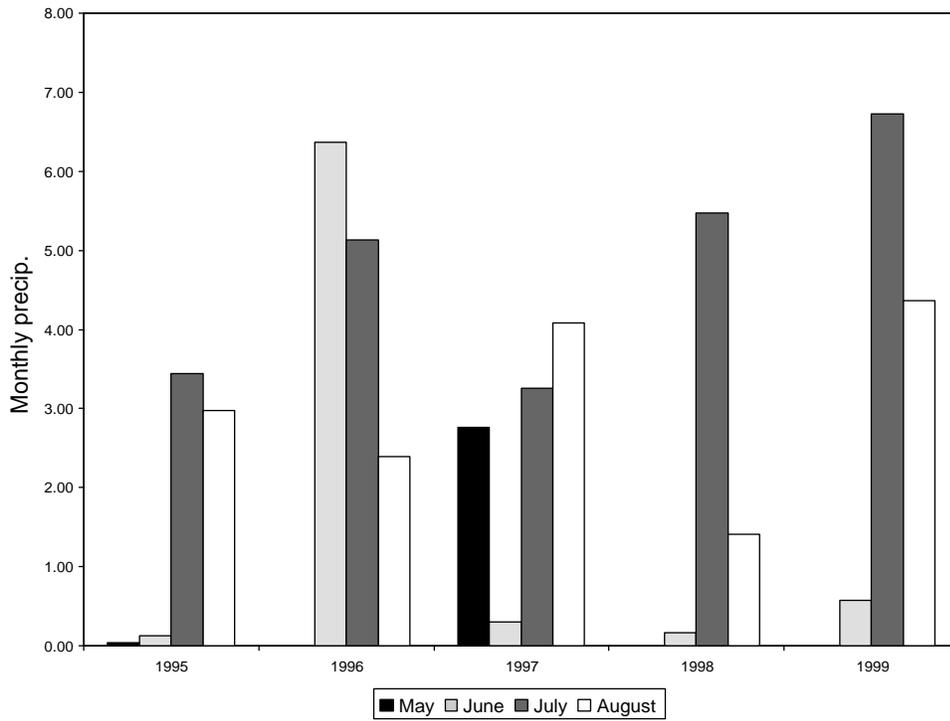


Figure 2—May-August precipitation 1995–1999, Chiricahua Mountains, Arizona.

made from the 1999 data using the GIS software of Arcview. Seedling clumps were identified from this map using a GIS grid interpolation algorithm that divided the belts into an array of 1 x 1 m squares; a circle with a 3.5 m radius was then drawn around the center of each square containing aspen (figure 3). If other aspen were found within that circle, then all trees inside the circle were identified as being members of a clump. The process was then repeated by drawing additional circles around the centers of squares in which aspen had already been encountered. With each iteration more trees might be added to the

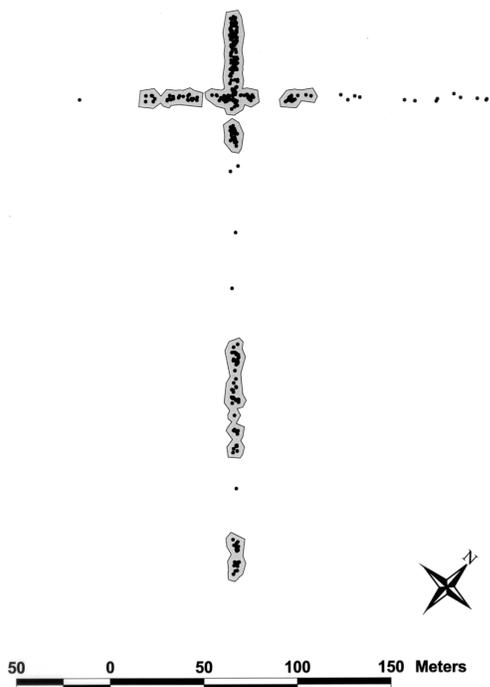


Figure 3—Six aspen seedling clumps. Each dot represents an individual seedling.

clump, and the process was repeated as long as successive circles generated from squares already included continued to capture additional aspen. This analysis identified 16 clumps. Ten of these had fewer than five aspen and these small clumps were excluded from further analysis. Perimeters drawn around the remaining six clumps were defined by a series of overlapping arcs with radii of 3.5 m originating from the center of squares that had captured one or more aspen. These perimeters were confined to within the boundary of the sampling belts. Six clumps of aspen seedlings contained between 18 and 186 trees, occupying areas of 145–500 square meters at densities of 0.09–0.27 per square meter (table 2). Linear regression analysis among the clumps showed no significant relationship between clump density and mean stem elongation (SEL) or between clump density and mean height.

The two clumps with the highest densities of aspen seedlings were at the northwestern end of the sampling belts, 30–75 m from the nearest living canopy aspen that could have been a source of seeds (figure 3). Aspen seeds are dispersed by the wind (McDonough 1985). The prevailing winds in late spring when seeds would be dispersed are from the west and northwest, placing these dense clumps immediately downwind from the nearest potential seed trees. Between aspen clumps there are gaps of as much as 50 m containing few or no aspen seedlings (figure 3). It is probable that wind deposited aspen seed on the ground in a more uniform pattern than that of the seedlings. Aspen clumps probably arose in places where soil moisture and perhaps other variables were most favorable for germination of aspen seed and survival of aspen seedlings.

Herbivory

There is no evidence that herbivory was significant in the observed patterns of aspen regeneration. Only 14.3% of the aspen seedlings on the permanent plots showed evidence of having been browsed in 1999. Between 1998 and 1999 the mean height of seedlings almost doubled, from 0.49 to 0.85 m, and overall seedling density decreased only slightly, from 0.14 to 0.12 m⁻². However, the decrease from 2.1 to 1.7 in the mean number of stems of the excavated seedlings between 1998 and 1999 may have been due to stems killed by deer browsing (table 1). In other parts of North America heavy browsing by cattle, elk (*Cervus elaphus*), or deer (*Odocoileus* spp.) sometimes retards or prevents the regeneration of aspen, even in dense stands of suckers (Romme et al. 1995; Suzuki et al. 1999; Kay and Bartos 2000). Cattle were not present in the study area, and elk have been absent from the Chiricahua Mountains for at least 100 years, if they were ever present at all. The only ungulate now present is white-tailed deer (*Odocoileus virginianus*). Deer have been observed near the study area browsing on aspen. But within the study area these animals were seldom observed, and their scats were rare. In 1999 and 2000, direct observa-

Table 2—Characteristics of six clumps of aspen seedlings. Sel = elongation of uppermost stem during 1999.

Area	Den	N	Mean ht	Mean sel
m ²	m ⁻²		m	cm
698	0.27	186	0.63	19.4
500	0.10	52	0.42	16.8
284	0.09	25	0.81	34.4
199	0.11	22	0.18	8.3
147	0.12	18	0.50	16.7
145	0.21	30	0.63	27.6

tions of deer foraging near the study area among abundant aspen suckers showed they spent over half their feeding time eating items other than aspen, even though aspen was the most abundant species of plant. There were no rabbits (*Sylvilagus* spp.) present.

Conclusion

Fires that last for weeks, across variable topography and variable burning conditions, can produce a very heterogeneous burn pattern. Forest patches where all trees are killed by crown fires and the mineral soil laid bare are interspersed with patches that burn as a ground fire, while other places may be missed by fire altogether. This is the fire pattern that occurred in Yellowstone in 1988 and in the upper reaches of the Chiricahua Mountains in 1994. Aspen were produced from seed in both places. Both of these fire episodes were natural in the sense that they were ignited by lightning and were ultimately extinguished by precipitation, with very uneven burning conditions in between. However, the fire in the Chiricahuas was also an artifact of management because the interval between fires was prolonged by a century of active fire suppression (Skelecki et al. 1994). Fires of this nature are becoming increasingly frequent in many other places in the West. Undesirable as these intense and often uncontrollable fires may be in terms of other public objectives, they open up the canopy so that aspen might be established in new places from seed. Fires of lesser intensity or at closer intervals can rejuvenate aspen clones by suckering; however, to the degree that less intense fires fail to create patches where canopy conifers have been killed and bare soil exposed, it is less probable that aspen will subsequently extend their local range by seeding.

It may be that throughout the western portion of aspen range, occasional sexual reproduction is a more general trait than has been recognized. Seedlings that survive in nature may have been rarely observed due to the exacting and unlikely conditions of fire pattern and subsequent precipitation that are prerequisites for the successful germination and survival of aspen seed. Reproduction from seed as documented by this study, and after the 1988 Yellowstone Fire (Kay 1993; Renkin et al. 1994; Romme et al. 1997), may be important for the long-term survival of aspen populations in the forests of the West. Aspen reproduction from seed, although infrequent, could be important as a source of genetic diversity and as a way of establishing clones on sites previously unoccupied by aspen. Over the long run, sexual reproduction of aspen may be necessary for this species to continue to adapt to the variable environment of the Mountain West, where frequent changes in precipitation and fire regimes have affected the character of forests for thousands of years (Bonnicksen 2000). The aspen stands in the Chiricahua Mountains are growing near the southern edge of the natural range of aspen. Such marginal stands of aspen may be relatively close to the limits of physical tolerance for growth and survival. If this is the case in the Chiricahua Mountains, then the genetic and spatial flexibility conferred by reproduction from seed could be especially important for the long-term survival of these particular populations.

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