

Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA

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Abstract: Trembling aspen (*Populus tremuloides* Michx.) regeneration dynamics including sprout production, growth, and clone size were measured to determine the effects of fire on small aspen clone persistence following a mixed-severity wildfire in the Black Hills, South Dakota. Four years postfire, 10 small, isolated aspen clones per low and high fire severity classes were compared with 10 unburned clones. Regardless of severity, fire did not cause an increase in the area occupied by individual aspen clones. Clones affected by high severity fire had the greatest suckering response producing an average of 31 930 sprouts-ha⁻¹; more than double the sprout density in unburned clones and 67% greater than the sprout density in clones affected by low severity fire. Sprout growth in high severity clones was 135% and 60% greater than sprout growth in unburned and low severity clones. The succession of these clones to more shade-tolerant ponderosa pine was delayed in clones affected by high severity fire as high severity fire caused significant pine mortality within and surrounding the clone, whereas, without further disturbance, pine encroachment and dominance will likely continue in clones affected by low severity fire.

Résumé : La dynamique de régénération du peuplier faux-tremble (*Populus tremuloides* Michx.), incluant la production de drageons, la croissance et la taille des clones, a été mesurée pour déterminer les effets du feu sur la persistance de petits clones de peuplier à la suite d'un feu dont l'intensité était variable dans les Black Hills du Dakota du Sud. Quatre ans après le feu, 10 petits clones isolés de peuplier pour chacune des classes de sévérité, soit faible soit élevée, ont été comparés à 10 clones non brûlés. Peu importe son intensité, le feu n'a pas causé d'augmentation de la superficie occupée par chacun des clones de peuplier. Les clones affectés par le feu de forte intensité ont produit le plus fort drageonnement avec 31 930-ha⁻¹, ce qui correspond à plus du double de la densité de drageons dans les clones non brûlés et à 67 % de plus que la densité observée dans les clones affectés par le feu de faible intensité. La croissance des drageons des clones affectés par le feu de forte intensité était respectivement 135 et 60 % plus élevée que celle des clones non brûlés et affectés par le feu de faible intensité. La succession de ces clones vers le pin ponderosa, une espèce plus tolérante à l'ombre, a été retardée dans les clones affectés par le feu de forte intensité qui a causé une mortalité importante du pin à l'intérieur et à la périphérie des clones. Toutefois, si aucune autre perturbation ne survient, l'envahissement et la dominance du pin devraient se poursuivre dans les clones affectés par le feu de faible intensité.

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Introduction

Trembling aspen (*Populus tremuloides* Michx.) in the Black Hills is rare on the landscape, occupying ~4% of the forested land base. Individual aspen clones are small with nearly one-third of all clones <0.5 ha and are interspersed among extensive ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) forests and open grasslands (Severson and Thilenius 1976). Suitable aspen sites are restricted to elevations between ~1200 and 2100 m and are limited primarily to northerly exposures (Hoffman and Alexander 1987; Shepperd and Battaglia 2002). Much of the aspen in the Black Hills is

classified as seral to ponderosa pine and white spruce (*Picea glauca* (Moench) Voss) and dependent upon fire and the subsequent removal of the surrounding conifer forest to persist and expand (Kranz and Linder 1973; Hoffman and Alexander 1987). For over a century, fire suppression, increased herbivory from wildlife and livestock, and the conversion of aspen stands to conifer stands for increased timber production have altered the distribution and abundance of aspen in the Black Hills (Kranz and Linder 1973). In this study, we examined clonal response to fire within a large, mixed-severity fire in ponderosa pine dominated forests in the Black Hills.

The decrease of aspen abundance and vigor across the western landscape has been attributed to 20th century land use management practices, in particular fire suppression, which alter the regeneration dynamics of aspen (Bartos 2001; Kaye et al. 2003). Aspen is a disturbance-dependent species (Bartos 2001) that regenerates vigorously from vegetative root suckering following stand-replacing disturbance, which historically was fire (Jones and DeByle 1985; Brown and DeByle 1987). This clonal reproductive strategy allows aspen to recolonize and dominate disturbed sites in advance of slower growing conifer species (Mueggler 1988); however, aspen is a short-lived tree, living less than 200 years (Kaye et al. 2003),

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and without further disturbance often succeeds to more shade-tolerant conifer species.

Current stand conditions in many aspen communities throughout the West are an indication of the succession of aspen-dominated sites to conifers at local scales. For example, decreased aspen vigor and increased conifer basal area and height have given Englemann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) a competitive edge over aspen in central Utah (Shepperd et al. 2001) which, without disturbance, may lead to the elimination of aspen at the stand level. In mixed aspen–conifer stands on the Uncompahgre Plateau in Colorado, aspen basal area decreased by 20% in 20 years, coupled with increases in conifer basal area and successful conifer regeneration (Smith and Smith 2005). Alternatively, Kulakowski et al. (2004) suggest that the increased conifer component within aspen communities is within the historic range of variability for the species, and aspen populations are simply returning to conditions prevalent before the widespread stand-replacing fires of the late 1800s. Mueggler (1985) identifies stable aspen communities that produce stable or climax communities. These stable clones are not at risk of being lost on the landscape (Romme et al. 2001; Manier and Laven 2002); however, they represent only one-third of all aspen stands in the West (Mueggler 1989). The remaining aspen communities are seral and without management risk succeeding to less diverse conifer-dominated stands.

Fire is frequently used as a management tool to regenerate declining aspen clones and remove competing conifers (Bartos and Campbell 1994); however, the fire-induced benefits of increased sprouting and stem recruitment are often offset by high rates of herbivory from native and domestic ungulates. Numerous studies document aspen regeneration failure following fire (e.g., Bartos et al. 1994; Romme et al. 1995) in the presence of high herbivore pressure. Aspen forests provide valuable habitat for deer (*Odocoileus virginianus* and *Odocoileus hemionus*) and elk (*Cervus elaphus*) and are a source of highly palatable browse (Kranz and Linder 1973; DeByle 1985). Domestic cattle have been introduced into forested ecosystems, and wildlife populations, in particular elk, have increased leading to greater utilization of aspen than historically occurred.

In late August 2000, the Jasper fire burned ~34 000 ha of the Black Hills National Forest, creating a mosaic of low, moderate, and high severity fire effects (Jasper Fire Rapid Assessment Team 2000). Much is known about the regeneration dynamics of aspen in relation to fire; however, how fire impacts the expansion and persistence of small aspen clones is not well studied. In this study, we measured the clonal response of small, isolated aspen clones 4 years after the Jasper fire to determine if fire, in the presence of high herbivore populations, rejuvenates and maintains aspen clones in the Black Hills. Specifically, we compared the regeneration response of individual aspen clones to different fire severities — unburned, low, and high — and we assessed the growth response of the regenerating sprouts 4 years postfire. We analyzed the effect fire had on clone size to determine if clones expand or maintain their original size following fire. We discuss the role of fire to maintain aspen clones in the ponderosa pine dominated landscape of the Black Hills.

Methods

Study area

This study was conducted within, and adjacent to, the Jasper wildfire on the Black Hills National Forest, South Dakota, USA (latitudes between 43°42'N and 43°56'N and longitudes between 103°46'W and 104°1'W). The Jasper fire burned ~34 000 ha of ponderosa pine dominated forest leaving a mosaic of mixed-severity fire effects (Lentile 2004). The Black Hills is an isolated dome-shaped mountain range surrounded by the Northern Great Plains in southwest South Dakota and northeast Wyoming and forms the easternmost extent of the Rocky Mountains (Froiland 1990). Elevations within the fire perimeter range from ~1500 to 2100 m. Annual precipitation averages from 45 to 48 cm with up to 75% of the annual precipitation falling from April to September, and the mean daily minimum and maximum temperatures are -3.3 and 13.2 °C (Shepperd and Battaglia 2002; Lentile 2004).

Study sites

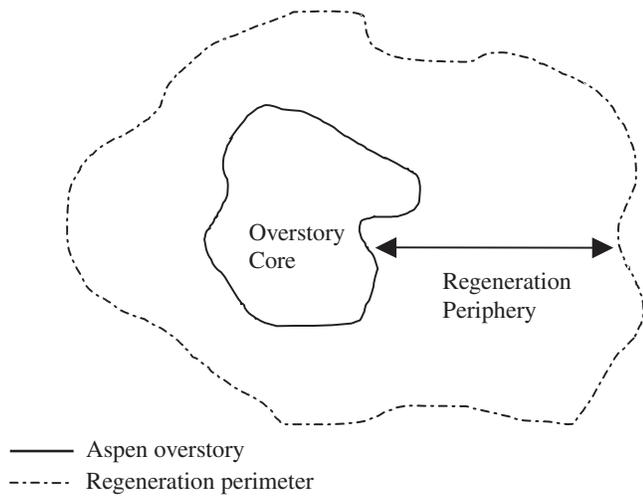
We measured aspen suckering 4 years following fire in unburned and burned, small (<0.25 ha), isolated aspen clones. Potential study sites were identified in an extensive field survey of aspen within and immediately north of the Jasper fire perimeter. Areas likely to contain aspen clones were identified from 1 : 24 000 color aerial photographs taken in 1998 and from forest inventory information. Clones were categorized by fire severity — unburned, low severity, or high severity — based on visual inspection in a field survey. Aspen clones appearing to contain aspen overstory mortality between 25% and 75% were classified as low fire severity, and clones appearing to contain >75% aspen mortality were classified as high fire severity. We located 96 discrete aspen clones: 40 unburned, 27 low fire severity affected clones, and 28 high fire severity affected clones.

We randomly selected 30 clones for measurement from the 96 potential study sites, 10 unburned and 10 from each fire severity class. If a selected aspen clone did not fulfill the criteria for fire severity assigned during the field survey, the clone was discarded as a study site. We also eliminated any selected clones where physical barriers, such as sheer rock walls, roads, or steep ravines could potentially limit aspen root growth and impede clonal expansion. If a selected clone was eliminated from measurement, another clone was randomly selected from the list of potential study sites.

Data collection

For each clone, we identified the area occupied by the mature prefire aspen overstory and the area of regeneration beyond the overstory by flagging the perimeters of the outermost aspen overstory trees (overstory core) and outermost sprouts (regeneration periphery) at 5 m intervals (Fig. 1). The overstory core contained mature (>2.5 cm diameter at breast height (DBH)) aspen and (or) ponderosa pine as well as aspen and (or) pine regeneration. The regeneration periphery contained only mature pine stems (>2.5 cm DBH) and aspen and (or) pine regeneration. Using the flags as a guide, the perimeters of the overstory core and regeneration periphery were then mapped with the Garmin® global positioning system (GPS) GPSmap 76 tracking function in conjunction with

Fig. 1. Diagram of the overstory core and regeneration periphery within an individual aspen clone.



a CSI Wireless, Inc. MBX-3 2-channel automatic real-time differential global positioning system (DGPS) beacon receiver. Three active tracks per overstory core and regeneration periphery perimeter were taken and converted to polygons. ArcView 9.0 GIS[®] was used to calculate the area (ha) of each overstory core and regeneration periphery polygon. We compared repeated measurements of the overstory core and regeneration periphery to evaluate the effectiveness and precision of the differentially corrected GPS data. The average coefficient of variation for repeated measures of the overstory core and regeneration periphery area was 6.3%. In addition to the clone area, we estimated the maximum distance (m) sprouts extend from the edge of the aspen overstory at eight locations (0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°) per clone.

We measured regeneration response of aspen following the Jasper fire, within the overstory core and regeneration periphery of each clone. Six 0.001-hectare regeneration plots were established in each clone. Plots were randomly located at bearings of 0°, 120°, and 240° azimuth, one within the overstory core and one within the regeneration periphery. We measured species, live or dead status, height to the nearest 5 cm of each aspen sucker or pine seedling, and recorded signs of herbivore damage. For this study, a sprout or seedling is defined as an individual stem <2.5 cm DBH.

We measured overstory structure in both the overstory core and regeneration periphery. Species, live or dead status, DBH (cm), and height (m) for each tree >2.5 cm DBH was measured on a 0.01 ha plot placed at the center of the overstory core of each clone. The overstory of the regeneration periphery area was measured using a variable radius plot with a basal area factor of 2.3 m²·ha⁻¹ at each of the regeneration periphery plot centers. Species, live or dead status, and DBH were recorded for each tree >2.5 cm DBH.

Statistical analysis

Sprout and pine seedling density as well as height data were analyzed as a nested experiment with two levels of canopy position (overstory core and regeneration periphery) nested within three levels of fire severity (unburned, low,

Table 1. Prefire overstory core area (SE), postfire regeneration periphery area (SE), and total clone area (SE) for unburned, low, and high fire severity aspen clones within the Jasper fire perimeter in the Black Hills National Forest, South Dakota.

Fire severity	Overstory core (ha)	Regeneration periphery (ha)	Total clone area (ha)
Unburned	0.028 (0.004)	0.089 (0.005)	0.117 (0.007)
Low	0.027 (0.003)	0.092 (0.005)	0.119 (0.007)
High	0.028 (0.004)	0.104 (0.009)	0.132 (0.012)
<i>P > F</i>	0.96	0.20	0.43

and high) ($\alpha = 0.05$). Sprout density was square root transformed to comply with assumptions of normality. Average height of the dominant unbrowsed sprouts from the overstory core and regeneration periphery from each unburned, low, and high fire severity clone was analyzed. Clone area was analyzed as a one-way ANOVA to test for the effects of fire severity on clone size ($\alpha = 0.05$). When significant *F*-tests occurred, means were tested using LSD multiple comparison of means ($\alpha = 0.05$). All analyses were performed in SAS version 9.1 (SAS Institute Inc. 2004).

Results

The aspen clones we sampled were small and averaged 0.123 ha in total area. The size of the overstory core of unburned, low, and high severity clones did not significantly differ and averaged 0.028 ha (Table 1). The size of the regeneration periphery did not differ among fire severities, averaging 0.095 ha, which was 343% larger than the overstory core. Prefire, the overstory core of unburned and burned aspen clones was dense in overstory aspen stems, with densities between 1181 and ~1761 ha⁻¹ (Table 2). Clones of all fire severities were experiencing pine invasion within the overstory core before the Jasper fire with the presence of overstory pine from 70 to 350 stems·ha⁻¹.

Fire had a significant impact on the postfire overstory structure of the small, isolated aspen clones that differed by fire severity. Twenty-eight and ~99% of the mature aspen stems >2.5 cm DBH in the overstory core of low and high fire severity clones were killed by fire, respectively (Table 2). Four years postfire, pine mortality of trees >2.5 cm DBH in the overstory core did not differ between unburned and low severity clones; however, 57% of overstory pines were killed in high severity fire. Similarly, pine density within the regeneration periphery was reduced following high severity fire (Table 2).

Fire severity had a significant influence on postfire aspen regeneration within burned aspen clones (Table 3). Aspen regeneration was prolific even in the absence of fire. Sprout density in unburned clones averaged 15 655 sprouts·ha⁻¹, and varied between ~2700 and 43 700 sprouts·ha⁻¹. Four years postfire, live sprout density in burned clones was high, averaging 25 501 sprouts·ha⁻¹. Increased fire severity resulted in greater suckering among burned clones than in unburned clones. In high fire severity clones, sprout density averaged 31 930 sprouts·ha⁻¹, whereas sprout density in low severity clones averaged only 19 071 sprouts·ha⁻¹. Sprout density

Table 2. Prefire tree density (SE), live tree basal area (BA) (SE), and mortality (dead trees as a percentage of total basal area) (SE) for aspen and ponderosa pine (>2.5 cm DBH) present within the overstory core and pine present within the regeneration periphery of unburned, low, and high fire severity aspen clones within the Jasper fire perimeter in the Black Hills National Forest, South Dakota.

Fire severity	Overstory core						Regeneration periphery		
	Aspen			Ponderosa pine			Ponderosa pine		
	Density (stems·ha ⁻¹)	BA (m ² ·ha ⁻¹)	Mortality (%)	Density (stems·ha ⁻¹)	BA (m ² ·ha ⁻¹)	Mortality (%)	Density (stems·ha ⁻¹)	BA (m ² ·ha ⁻¹)	Mortality (%)
Unburned	1181 (137)	24.8 (4.2)	6.8a (2.2)	70 (42)	0.5 (0.2)	0.0a (0.0)	44a (5)	6.7 (2.4)	7.6a (4.9)
Low	1761 (279)	26.2 (3.4)	27.8b (6.8)	350 (122)	4.6 (2.0)	3.0a (2.4)	76ab (18)	6.0 (1.1)	3.9a (2.3)
High	1331 (202)	18.0 (3.0)	98.8c (1.1)	190 (59)	2.7 (1.0)	57.4b (15.8)	99b (16)	6.0 (1.1)	43.6b (15.7)
<i>P</i> > <i>F</i>	0.16	0.24	<0.01	0.07	0.10	<0.01	0.02	0.95	0.01

Note: Means followed by the same letter are not significantly different ($\alpha = 0.05$).

Table 3. Aspen sprout density (SE), height of the dominant unbrowsed sprouts (SE), and ponderosa pine seedling density related to fire severity for unburned, low, and high fire severity aspen clones within the Jasper fire perimeter in the Black Hills National Forest, South Dakota.

Fire severity	Aspen sprout density (sprouts·ha ⁻¹)	Aspen sprout height (cm)	Pine seedling density (seedlings·ha ⁻¹)
Unburned	15 655a (3889)	24.6a (2.3)	1440a (549)
Low	19 071a (3053)	39.3b (3.7)	1055a (346)
High	31 930b (4565)	57.7c (4.6)	151b (96)
<i>P</i> > <i>F</i>	<0.01	<0.01	<0.01

Note: Ponderosa pine seedlings originated before 2000 and are fire survivors, not postfire germinants. Means followed by the same letters are not significantly different ($\alpha = 0.05$).

throughout clones affected by high severity fire was 104% greater than the sprout density in unburned clones ($p < 0.01$) and was 67% greater than in low fire severity clones ($p = 0.04$). In contrast, sprout density in clones affected by low severity fire did not differ from that in unburned clones. There was no difference in sprout density between the overstory core and regeneration periphery within fire severities. Herbivory was widespread throughout all clones with 58% of all live sprouts sampled showing evidence of current or past browse.

The maximum sprout distance from the edge of the overstory core averaged 10.3 m across all fire severities and did not differ among unburned, low, and high fire severities. The average height of the dominant overstory aspen stems was 11.5 m and did not differ among fire severities. There was no relation between the average maximum sprout distance and the average height of overstory aspen stems. This, however, may be due to the limited variation in height of our sampled clones.

Height of the dominant unbrowsed sprouts increased with increased fire severity (Table 3). The dominant unbrowsed sprouts in unburned clones averaged 25 cm in height, while the dominant unbrowsed sprouts in burned clones were significantly taller 4 years postfire. These sprouts in clones affected by low and high severity fire were 60% ($p < 0.01$) and 135% ($p < 0.01$) taller than the dominant unbrowsed sprouts in unburned clones. There was no difference in sprout height between the overstory core and regeneration periphery within fire severities.

High severity fire substantially reduced amount of prefire established ponderosa pine regeneration present within aspen clones (Table 3). No postfire pine regeneration was found

in the core or regeneration periphery of burned clones. Pine seedling density averaged 1440 seedlings·ha⁻¹ in unburned clones, however was highly variable ranging between ~0 and 7500 seedlings·ha⁻¹ (Table 3). In low severity clones, seedling density did not differ from that in unburned clones. However, in high severity clones, seedling density was 90% lower than in unburned clones ($p < 0.01$) and 86% lower than the seedling density in low severity clones ($p = 0.03$).

Discussion

The aspen clones we sampled in the Black Hills were mature, small (~0.1 ha) clones consisting of a dense aspen overstory. Prior to the Jasper fire, aspen suckering was occurring beneath the overstory and within a ~10 m fringe. However, there was no recruitment of these sprouts into the overstory within the overstory core or regeneration periphery. In addition, most clones were showing evidence of conifer invasion, as ponderosa pine regeneration was often dense, and pine encroachment of the aspen overstory was occurring. Environmental conditions (i.e., open growing conditions) and species characteristics (i.e., vegetative growth) favor the rapid growth and development of aspen over ponderosa pine for the first 120 years following stand reinitiating disturbance (Shepperd and Jones 1985; Mueggler 1989). However, with canopy closure, opportunities for continued aspen recruitment are limited, and more shade-tolerant conifers gain a competitive edge over aspen. Without disturbance, these small, isolated clones would likely experience an increase in ponderosa pine presence and ponderosa pine dominance while experiencing a decrease in aspen dominance (Shepperd et al. 2001; Smith and Smith 2005).

Unlike regeneration and sprout growth, fire did not have an immediate effect on the size of individual aspen clones (Table 1). By mapping the perimeter of the outermost sprouts in an aspen clone, we essentially outlined the boundary of the lateral root system responsible for sprout production (Shepperd and Smith 1993). Therefore, sprout production should not be expected to be stimulated beyond the clonal root system boundary in response to fire, regardless of severity. On average, the regeneration periphery was 343% greater than the overstory core and represents a potentially significant increase in overstory core size if regenerating aspen sprouts are recruited into the overstory within both the overstory core and regeneration periphery.

Sprout production was stimulated above levels observed in unburned clones only in clones affected by high severity fire (Table 3). In clones affected by high severity fire, sprout density was more than double that in unburned clones and was 67% greater than in low severity clones. Fraser et al. (2004) found following a stand replacing, high severity fire in western Canada, sprout production was more than 70% greater than in aspen stands affected by low severity fire. Similarly, following a large crown fire in Arizona, Bailey and Whitham (2002) observed a high severity fire resulting in 100% aspen mortality caused up to a ~300% increase in sprout production over that observed in stands with only ~50% aspen mortality. The differential suckering response between low and high fire severities is largely due to differences in postfire aspen mortality associated with increased fire severity (Table 2). Suckering is stimulated by aspen overstory mortality and increases in soil temperature from increased light penetration and from disturbances such as fire (Maini and Horton 1966; Schier et al. 1985).

The paradigm that fire is a vital process regulating the regeneration, perpetuation, and expansion of many aspen clones throughout the interior western United States (Jones and DeByle 1985) is true for small, isolated aspen clones in the Black Hills as well. Fire does not cause an immediate increase in the area occupied by small, isolated aspen clones; however, depending upon fire severity, it does alter the successional direction, structure, and growing conditions in and around the clone. Small aspen clones affected by high severity fire are most likely to persist on the Black Hills landscape. The combination of the removal of the aspen overstory, increased sprout production, and the significant reduction of competing pine in and around the clone create conditions conducive to future growth and expansion of aspen. These clones are likely to experience pine invasion in the future; however, high severity fire was effective at maintaining aspen dominance for another generation and allows for the future expansion of the overstory core area by an average 343%. Low severity fire was ineffective at decreasing competition from overstory aspen and pine, which will likely lead to the further suppression and eventual death of developing sprouts. Excluding any future stand-replacing disturbance, therefore, low severity clones are likely to continue the current successional pathway and succeed to ponderosa pine.

However, throughout the West, land use practices leading to increased herbivory have had a significant impact on the development and recruitment of aspen (Bartos et al. 1994; Romme et al. 1995). Herbivory in the small aspen component within the Jasper fire was high and amounted to 58% of

all live sprouts sampled. Four years postfire, aspen clones were sufficiently stocked relative to sprout density; however, the high rate of herbivory may, in the long term, inhibit the reestablishment of these small aspen clones. Solutions to herbivory are necessary for the maintenance of these small clones, and may include the construction of aspen enclosures that exclude elk and livestock from regenerating clones until aspen have reached at least 2 m in height (Shepperd 1996).

Aspen is a highly valued component of the Black Hills as it provides pockets of diversity in an otherwise homogenous landscape. Therefore, maintaining and expanding the presence of aspen is often a management objective, and fire is increasingly becoming the preferred tool to carry out this objective. Logistical problems arise when prescribing a high severity fire in aspen, however. It is difficult under acceptable weather conditions to get fire of any intensity to burn through an entire clone (Jones and DeByle 1985). Unlike conifer species, aspen is not flammable, and the understories of clones do not readily carry fire. Combinations of mechanical pretreatment followed by moderate to high intensity prescribed fire can then be used to remove the aspen overstory and stimulate suckering (Shepperd 2001). Regardless of how prescriptions are carried out, data from this study indicate that successful regeneration of small aspen clones in the Black Hills will require high severity fire, removal of invading pine within and surrounding the clone, and steps to control herbivory at the time of treatment. These steps will create conditions favorable to the long-term development and maintenance of small aspen clones in the Black Hills.

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