Seed production, seed rain, and the seedbank of fringed sagebrush

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Abstract

Increases in fringed sagebrush (Artemisia frigida Willd.) following disturbance on Northern Mixed Prairie are due to enhanced growth of established plants and seedling recruitment. The roles of seed production and the soil seedbank in population dynamics of fringed sagebrush following disturbance are, however, unknown. Furthermore, seed rain has not been documented for this species. The objectives of this study were to determine: 1) the effect of disturbances in the sward on seed production; 2) relationships between the soil seedbank and current seed production; and 3) seed rain over time for fringed sagebrush. Disturbances of clipping, litter removal, tillage, and a combination of clipping and litter removal were imposed on a sandy range site in central Saskatchewan. Following disturbance seed production plant⁻¹ either increased or was unchanged compared to the undisturbed control. Greater seed production resulted from increased production of seeds head⁻¹, heads inflorescence⁻¹ and inflorescences plant⁻¹. The timing of seed rain varied considerably among individual plants. Five temporal patterns of seed rain were identified for individual fringed sagebrush plants: 1) 5.2% of the plants began and completed dispersing seeds within 6 to 8 weeks of flowering; 2) 20.8% began dispersing within 6 to 8 weeks of flowering and completed dispersal before snow was received in autumn; 3) 37.7% began dispersing seeds within 6 to 8 weeks of flowering and continued over the winter; 4) 29.9% delayed dispersal of seeds more than 8 weeks after flowering and continued over the winter; and 5) 6.5% began and completed seed dispersal during the winter. The number of fringed sagebrush seeds in the soil was correlated with seed production only when many seeds were produced (r=0.76), indicating that annual seed production is of limited importance for maintaining a seedbank. A persistent seedbank is important in maintaining fringed sagebrush populations when seed production is limited. Diverse rates and times of seed rain along with a persistent seedbank may enable fringed sagebrush to occupy safe sites that develop in time.

Key Words: Artemisia frigida Willd., disturbance, Northern Mixed Prairie, population dynamics, seed dispersal, seed ecology

Fringed sagebrush (Artemisia frigida Willd.) is the most common dicotyledonous species in the Northern Mixed Prairie (Coupland 1950). This suffrutescence perennial produces many small seeds that begin shedding in the fall (Dayton 1940, Wilson 1982), and most seedlings emerge in the spring (Bai and Romo 1996). Individual fringed sagebrush plants can produce up to 190,000 seeds (Wilson 1982). Germination of fringed sagebrush is enhanced by light (Bai and Romo 1994, Bai et al. 1995), and thus this species may form a persistent seedbank in the soil (Thompson and Grime 1979). Seed densities of fringed sagebrush ranged 75 to 183 seeds m⁻² in soil from Mixed Prairie in Alberta (Johnston et al. 1969).

The increase in fringed sagebrush on disturbed sites of Northern Mixed Prairie results from more vigorous growth of established plants and increased recruitment of seedlings (Bai and Romo 1996). The roles of seed production and the soil seedbank in population dynamics of fringed sagebrush are, however, unknown. The objectives of this research were to determine: 1) the effect of disturbances in the sward on seed production of fringed sagebrush; 2) relationships between the soil seedbank and current seed production of fringed sagebrush; and 3) seed rain over time.

Methods

Study Site

Research was conducted over a 3-year period from 1990–1992 at the University of Saskatchewan, Biddulph Natural Area, 25 km south of Saskatoon, Canada (51°58'N, 107°45'W, 505 m). The site is characteristic of the sandhills complex (Coupland 1950, Hulett et al. 1966) of the Northern Mixed Prairie with orthic regosolic soils (Ellis et al. 1968). The area had been protected from livestock grazing for about 40 years, and the ecological condition of this sandy range site was excellent. Needle-and-thread (Stipa comata Trin. & Rupr.) and blue grama (Bouteloua gracilis (HBK.) Lag.) were dominant grasses; fringed sagebrush was the most common dicotyledonous species (Hulett et al. 1966, Pylypec 1989). Annual precipitation at Dundurn, 15 km southeast...
of the study site, averages 380 mm of which 43% is received in May, June, and July. Annual temperatures average 2.4°C with January the coldest month averaging -17.9°C and July the warmest, averaging 18.8°C (Environment Canada 1993).

Temperature and precipitation were recorded at the study sites. In the first growing season following disturbance at site 1 (year 1) monthly temperatures averaged 11°C in May, 17°C in June, 18°C in July, and 18°C in August; precipitation totalled 64, 112, 138, and 38 mm in May, June, July, and August, respectively. Mean monthly temperatures in the second growing season after disturbance at site 1 were 12, 16, 19, and 21°C and precipitation totalled 50, 155, 31, and 15 mm for the same months, respectively.

Temperature the first growing season after disturbance at site 2, year 1, averaged 12, 16, 19, and 21°C in May, June, July, and August, respectively; total precipitation was 70 mm in May, 175 in June, 51 in July, and 35 in August. In the second year at site 2 after treatment mean temperatures were respectively 10, 15, 16, and 15°C in May, June, July, and August and precipitation for the same months totaled 52, 20, 108, and 49 mm.

Experimental Design and Treatments

Experimental units consisted of 30 fringed sagebrush plants of about the same size at each of the 2 sites. The sites were about 150 m apart. Plots 2 X 2 m in size were established around a central plant, and were subjected to 1 of 5 treatments in late April 1990 at site 1 and mid-April 1991 at site 2. Measurements were taken at both sites the year of treatment and the year after. Experimental design was a randomized-complete-block with 6 replicates. The 5 treatments were: 1) clipping of all species except fringed sagebrush at ground level and removing all clipped material; 2) removing the plant litter from the plot with a rake; 3) tilling the soil to a 10-cm depth with a rototiller; 4) clipping as described in treatment 1 plus litter removal as in treatment 2; and 5) an undisturbed control. Treatments were applied only once.

Seed Production

In early September the first and second year after imposing treatments, 10 heads were randomly collected from the plant in each plot and the number of seeds head¹ were counted before seed rain began. At the same time the number of inflorescences plant¹ were counted, and the number of heads inflorescence¹ were determined on 5 randomly selected inflorescences on each plant. Total seed production plant¹ was estimated as the product of the number of seeds head¹, heads inflorescence¹, and inflorescences plant¹.

Seed Rain

Petri dishes 9 cm in diameter were filled with pebbles about 5–10 mm in diameter and used as seed traps. In early September, about 6 weeks after flowering but before seeds were shed from plants, 4 traps were placed on the soil surface 15 cm from the canopy edge in 4 cardinal directions around each experimental plant. The contents of the seed traps were collected at 2-week intervals until snow covered the ground on 14 November 1990, 17 October 1991 and 11 November 1992, and immediately after the snow melted the following March. Inflorescences were examined in March and seed traps were not replaced because no seeds were remaining on the plants. Seeds in the traps were separated from the pebbles using a 0.5-mm sieve. These seeds were put on 1 mm thick germination paper moistened with distilled water and incubated in closed petri dishes at 10°C with a 12-hour photoperiod (395 μmol m⁻² s⁻¹) for 4 weeks. These incubation conditions are optimal for germination of fringed sagebrush seeds (Bai and Romo 1994, Bai et al. 1995). The number of fringed sagebrush seeds that germinated from each seed trap sample was noted, and the data from the 4 traps around each plant were combined. Cumulative seed rain over time was then calculated for each plant.

Soil Seedbank

To prevent seed input into the soil, 2 plastic disks 10 cm in diameter were placed on the soil surface 15 cm from the canopy edge of the central plant in each plot before seed rain began in late August. Soil cores 8 cm in diameter and 10 cm deep were taken from the covered areas and from an adjacent uncovered area the following April. The soil samples were air dried in the laboratory for 2 weeks, sifted through a 0.5-mm sieve and the sifted soil was then placed in 20 X 10 X 5 cm containers. These containers were incubated under natural light for 4 summer months in a greenhouse that did not have controlled temperature. Fringed sagebrush seedlings were counted and removed at 2-day intervals, the soils were stirred, and water was added to keep the soil moist. Using seedling emergence to quantify the soil seedbank tends to underestimate the seedbank if germination requirements are not met (Robert 1981, Baskin and Baskin 1989), but it does provide an estimate of the readily germinable fraction of the seedbank (Gross 1990).

Data Analysis

Except for the data of the seed rain, data were subjected to factorial analysis of variance using site and treatments as main effects within the first and second growing season after treatments were applied (Snedecor and Cochran 1980). In all cases if the interaction of the site and treatment was significant, the means for the sites and treatments were presented and compared. When the interaction was not significant, but the main effects were, the means for the main effects were compared. If neither main effects nor their interactions were significant, the overall mean and the standard error for the mean was calculated and presented. Data of the number of seeds head¹, the number of heads inflorescence¹, and total seed production plant¹ were transformed with X/(X+0.05), where X is the value of the parameter (Snedecor and Cochran 1980). Percent data of cumulative seed rain and germination data from seed traps and the seedbank were transformed with arcsin √p before analysis (Snedecor and Cochran 1980). Seed rain data were analyzed within dates for each site and year with an one-way analysis of variance because the dates and length of time that seed traps were in place were not consistent between sites and years. The number of seeds produced and the number of seeds in the soil were also tested with analysis of variance between years and sites. Means were compared with the least significant difference test (LSD) (Snedecor and Cochran 1980). Correlations were tested (Snedecor and Cochran 1980) between: 1) seed production and the number of seeds caught in traps, and 2) seed production and seedlings emerging from soil samples. Statistical significance for all tests was assumed at P<0.05.
Results

Seed Production

In the first growing season after treatment the number of seeds head was similar (P<0.01) among treatments, averaging 8.0 (SE=1.5). Disturbance favored seed production the second year after disturbance with plants in the treated plots producing 2.5 to 9.5 times more seeds head than those in the control (Table 1). The number of seeds head was 3 times greater (P<0.01) at site 1 than site 2 the first and second growing seasons following disturbance. In the first year the number of seeds head averaged 12 and 4 (SE=0.96) at sites 1 and 2, respectively, and 7 and 2 seeds head (SE=1.5), respectively, the second year.

Following disturbance in the first growing season at sites 1 and 2, the mean number of heads inflorescence was similar among treatments, averaging 84 (SE=6.2, P=0.06). There were 119 heads inflorescence at site 1 and 49 at site 2 (SE=8.8, P<0.01). The number of heads inflorescence among treatments was different between sites the second year as indicated by the interaction of these factors (P=0.01, Table 1). There was no difference in the number of heads inflorescence among treatments at site 2; at site 1 removing litter or tillage increased the number of heads inflorescence that were produced (Table 1). Plants produced the most heads inflorescence where plots were tilled, and plants in the control had the fewest.

Production of inflorescences the first year following disturbance at sites 1 and 2 was affected by treatment and site as indicated by the interaction of these factors (P<0.01). At site 1, tillage increased the number of inflorescences plant, whereas at site 2 there were no differences in inflorescence production among treatments (Table 1). The second year following disturbance, inflorescence production in the tillage treatment was 3.6 to 27 more than for plants (P<0.01) in the remaining treatments (Table 1).

The treatment effect on seed production plant the first year following disturbance was different between sites (P<0.01). At site 1 plants in the tillage treatment produced more seeds plant while at site 2 none of the disturbance treatments had an effect (Table 1). There were no differences in seed production plant among treatments (P=0.26) or between sites (P=0.23) in the second year following disturbance, averaging 9,000 plant (SE=6,100).

Seed Rain

With the exception of the second year following disturbance at site 2, seed rain began in early to mid-September, continued over the winter, and was completed by early spring (Fig. 1). Dispersal began in mid-September and was completed by late October in the second year following treatment at site 2. At site 1, 88 and 79% of the seeds were shed before snow was received in the first and second years after disturbance, respectively. Fifty-two percent of the seeds were dispersed before snow was received at site 2 the first year after treatment, but in the second year all seeds were shed before snow accumulated.

The rate and time of seed rain varied considerably among individual plants and years (Fig. 1). Five temporal patterns of seed rain (n=30 per site and year, total=120) were identified for individual fringed sagebrush plants. Some plants (5.2%) began and completed seed rain within 6 to 8 weeks of flowering. In comparison dispersal in 20.8% of the plants began within 6 to 8 weeks of flowering, but was completed before snow was received in the autumn. Another group (37.7%) began seed rain within 6 to 8 weeks of flowering and continued over the winter, while seed rain in 29.9% was delayed more than 8 weeks after flowering and continued over the winter. Finally, 6.5% of the plants began and completed dispersal during the winter.

Soil Seedbank

One year after the sward was disturbed the number of seeds that germinated in the soils was affected only by site (P<0.01). With seed input, densities averaged 1,436 (SE=373) at site 1 and 3,001 seeds m$^2$ (SE=379) at site 2. Where seed input was prevented, seed densities averaged 222 (SE=39) and 2,666 m$^2$ (SE=309) at sites 1 and 2, respectively.

The number of seeds in the soil was not correlated (P>0.05, n=30) with seed production except for the first year after disturbance at site 1 (r=0.76). The number of seeds produced by fringed sagebrush and collected in the second year following disturbance were (r=0.74 and r=0.99 at sites 1 and 2, respectively).

Discussion and Conclusions

The variable effect of disturbance on seed production between sites indicates that it is not a major factor on seed production by fringed sagebrush, but that other factors, such as climate, exert a

Table 1. The mean number of seeds head, heads inflorescence, inflorescences plant, and seeds plant at sites 1 and 2 for fringed sagebrush in the first or second growing seasons following disturbance.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Year</th>
<th>Site</th>
<th>Clipping (C)</th>
<th>Treatment</th>
<th>Tillage</th>
<th>C+L</th>
<th>Control</th>
<th>LSD$^3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seeds head$^1$</td>
<td></td>
<td>1 &amp; 2</td>
<td>9.5a</td>
<td>2.5a</td>
<td>9a</td>
<td>2.5a</td>
<td>1.0b</td>
<td>1.0</td>
</tr>
<tr>
<td>Heads inflorescence$^1$</td>
<td>2</td>
<td>1</td>
<td>49b</td>
<td>123a</td>
<td>93a</td>
<td>51b</td>
<td>28c</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>8e</td>
<td>2e</td>
<td>15c</td>
<td>2e</td>
<td>2c</td>
<td></td>
</tr>
<tr>
<td>Inflorescences plant$^1$</td>
<td>1</td>
<td>1</td>
<td>38bc</td>
<td>59b</td>
<td>150a</td>
<td>37bc</td>
<td>39bc</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>8bc</td>
<td>8bc</td>
<td>4c</td>
<td>1c</td>
<td>5c</td>
<td></td>
</tr>
<tr>
<td>Inflorescences plant$^1$</td>
<td>2</td>
<td>1 &amp; 2</td>
<td>5b</td>
<td>15b</td>
<td>54a</td>
<td>4b</td>
<td>2b</td>
<td>17</td>
</tr>
<tr>
<td>Seeds plant$^1$</td>
<td></td>
<td>1</td>
<td>73,100b</td>
<td>66,300bc</td>
<td>250,000a</td>
<td>40,800bc</td>
<td>38,700bc</td>
<td>67,000</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td></td>
<td>7,200c</td>
<td>3,200c</td>
<td>700c</td>
<td>200c</td>
<td>4,500c</td>
<td></td>
</tr>
</tbody>
</table>

$^1$Means followed by the same letter within a parameter are not significantly different (P<0.05).

$^2$Least significant difference (P>0.05).
Fig. 1. The mean (n=30), minimum (lower extent of vertical bars), and maximum (upper extent of vertical bars) cumulative seed rain per plant for fringed sagebrush at sites 1 and 2 the first and second growing season after sward disturbance.

Fig. 1. The mean (n=30), minimum (lower extent of vertical bars), and maximum (upper extent of vertical bars) cumulative seed rain per plant for fringed sagebrush at sites 1 and 2 the first and second growing season after sward disturbance.

dominant effect. Disturbing this Northern Mixed Prairie either promoted or had no effect on seed production in fringed sagebrush. Bai and Romo (1996) also reported vegetative growth of fringed sagebrush was unaffected or favored by disturbance. The same plants were studied in both years, thus the highly variable response in seed production in the present study is attributed to climatic conditions because seed production by plants is flexible, and largely reflects environmental stress (Fenner 1985). The highs and lows of seed production also corresponded with years of favorable and limited growth of plants (Bai and Romo 1996), with response to disturbance greatest in wet years. Young et al. (1989) also concluded that year-to-year differences in seed production for big sagebrush (Artemisia tridentata Nutt.) were caused by variation in the physical environment.

Tillage had a greater effect in stimulating seed production than clipping or removing litter. Because soil water and NO3-N were not different among treatments (Bai and Romo 1996) the increase in seed production is attributed to reduced competition from neighboring plants. The different seed numbers head-1 between sites may be due to either genetic or environmental effects, however, they were not possible to separate due to the nature of duplicating the study in time.

A large seedbank masked the correlation between seeds produced and the seedbank size. The positive correlation of germinating seeds in soil with seed production only when many seeds were produced indicates that seeds produced in previous years persisted in the soil and had an overriding effect on the size of the seedbank when seed production was limited. Fringed sagebrush does indeed form a persistent seedbank (Iverson and Walli 1982, Bai and Romo 1994, Bai et al. 1995), and annual seed input to soil is not as important as it is for species with transient seedbanks (O’Connor and Pickett 1992). Therefore, in years with limited seed production, the seedbank is sufficient to maintain populations should established plants perish. Fringed sagebrush seeds in the soil can germinate and seedlings can be recruited any time during the growing season (Bai and Romo 1996).

Species with limited dispersal in space may compensate by dispersing seeds in time (Willson 1993) as observed in fringed sagebrush. The highly variable rates of seed rain among individual plants in fringed sagebrush, along with a persistent seedbank may enable seeds to occupy safe sites as they occur in time. Dispersal of seeds before the onset of the growing season may enable seeds to germinate and seedlings of fringed sagebrush to exploit cool and moist conditions during late spring and early summer, the most favorable period for growth (Bai and Romo 1996). In addition, the role of predation on fringed sagebrush seeds is unknown, but prolonged dispersal may be the result of selection pressures for avoidance of predators (Harper 1977, Willson 1992).

In conclusion fringed sagebrush is characterized by a highly variable response among individuals to disturbance, high seed production, temporally diverse rates of seed rain among individual plants, and a persistent seedbank in the soil. Seeds that do not germinate immediately after dispersal may remain in the seedbed and germinate when conditions become favorable. Whether studying population dynamics, attempting to control fringed sagebrush, or using this perennial in ecological restoration, the
fact that this species forms a large, persistent seedbank and has considerable variation in seed production and dispersal rates among individuals must be recognized.

Literature Cited