Fringed sagebrush response to sward disturbances: Seedling dynamics and plant growth

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Abstract

Fringed sagebrush (Artemisia frigida Willd.), the most common dicotyledonous species in the Northern Mixed Prairie, often increases dramatically following disturbance. It was hypothesized that the increase could be due to release of established plants, increased recruitment of plants, or both. Experiments were conducted on a sandy range site in central Saskatchewan. Tillage, clipping, litter removal, and a combination of clipping+litter removal were compared to an undisturbed control to determine their effects on emergence and survival of fringed sagebrush seedlings and growth of established plants. In no circumstance was seedling emergence or plant growth greater in the undisturbed control than in the disturbed sward. Emergence of fringed sagebrush seedlings increased almost 80-fold the second year after tillage at 1 site, but emergence was not altered relative to the control by clipping, litter removal, or clipping+litter removal. Averaged across treatments, 52 to 98% of the seedlings emerged in May and June, and 47 to 99% of these seedlings survived through the growing season and winter. Plants grew fastest in June when precipitation was highest and temperatures were moderate. Growth of plants was improved 2- to 3-fold by tillage the second year; this stimulation in growth was due to the removal of competition. Activities that reduce or remove vegetation and create bare soil surfaces promote emergence and growth of fringed sagebrush on the Northern Great Plains. Most seedlings of fringed sagebrush emerge in spring and early summer, enabling them to temporally exploit the period for optimal growth. Fringed sagebrush is well adapted to persist in Northern Mixed Prairie in a successional continuum from early to late seral stages.

Key Words: Artemisia frigida Willd., Northern Mixed Prairie, patch dynamics, population dynamics, safe sites, seed reserves, seedling emergence.

Fringed sagebrush (Artemisia frigida Willd.) is the most common dicotyledonous species in the Northern Mixed Prairie (Coupland 1950), and it is naturally distributed in many grass-

lands of the world (Dayton 1937). This perennial half-shrub is one of the first species to establish on abandoned farmland or on roadsides (Shantz 1917, Sarvis 1923, Whitman et al. 1943), and is common in overgrazed grasslands (Sarvis 1941, Coupland 1950). Fringed sagebrush produces many small seeds that germinate over a wide range of temperatures, and it reproduces from rootstocks (Dayton 1937, Wilson 1982).

Increases in fringed sagebrush observed on disturbed Northern Mixed Prairie sites may be due to release of established plants, increased recruitment of seedlings, or both. Changes may occur through disturbance of the soil, alteration of competitive relationships, or modification of the microenvironment. We hypothesized that relative to an undisturbed control, disturbance would improve growth and recruitment of fringed sagebrush. A field study was conducted to investigate influences of 4 disturbances on fringed sagebrush on Northern Mixed Prairie in Saskatchewan. Specific objectives were to determine the effect of tillage, clipping, litter removal, or a combination of clipping+litter removal on the growth of established plants, emergence, and survival of fringed sagebrush seedlings and compare this to an undisturbed control.

Materials and Methods

Study Site

Experiments were conducted at the University of Saskatchewan, Biddulph Natural Area, 25 km south of Saskatoon, (51°58'N, 107°45'W, 505 m). The site is characteristic of the sandhills complex of the northern Mixed Prairie (Coupland 1950) 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. Needleand-thread (Stipa comata Trin. and 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). The ground surface was covered by live or dead clubmoss (Selaginella densa Rydb.), or was bare. Annual precipitation at Dundurn, about 15 km southeast of the study site, averages 380 mm with more than 40% 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).

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Experimental Design and Treatments

Thirty 2 × 2-m plots were established at each of 2 sites with 1 fringed sagebrush plant located in the center of each. Experimental design was a randomized-complete-block with 5 treatments and 6 replicates. Treatments were imposed around the plant in late April 1990 at site 1 and mid-April 1991 at site 2. Treatments were applied only once to each plot. The 5 treatments included: 1) clipping of all species except fringed sagebrush at ground level and removal of all clipped materials; 2) removal of plant litter from the plot with a rake; 3) tillage by rototilling the soil to about a 10-cm depth; 4) clipping as described in treatment 1 plus litter removal as in treatment 2, and; 5) an undisturbed control.

Seedling Emergence

After imposing treatments, a permanent 0.5×0.5 -m observation area was established adjacent to the fringed sagebrush plant in each plot and seedlings were counted and marked with colored wires at weekly intervals from 1 May to 30 August in the year of treatment and the following growing season. Survival of seedlings over the first 2 growing seasons and winters after disturbance was determined. At the time this study was planned the region was experiencing a significant drought, and it was decided to add supplemental water to ensure some seedling emergence in the event of continued low precipitation. A total of 75 mm of supplemental water was supplied in 4 aliquots at site 1 in the first year (1990) and 80 mm at site 2 in the first year (1991) in mid-May, June, July and August.

Seedbeds were characterized by estimating cover of live clubmoss, dead clubmoss and bare soil adjacent to the fringed sagebrush plant with a point frame (Coupland 1950). Estimates were made in each replicate and treatment at both sites in early spring of 1992. The percentage of the 3 surface types within treatments was then calculated.

Plant Growth

Growth of fringed sagebrush was determined by non-destructive sampling. Five stems on the central mature plant in each plot were marked with colored wires after imposing treatments. Length of marked stems and height of plants were measured at weekly intervals from May through August the year of and after treatment.

The relative stem elongation rate (%cm cm⁻¹ day⁻¹) was determined with equation 1.

Relative stem elongation rate=
$$100 \times \frac{d(SL)}{d(t)} \times \frac{1}{SL_0}$$
 (1)

where d(SL) is the change in stem length during that interval; d(t) is the time interval in days, and; SL_0 is the stem length at the beginning of the growing season. Relative height growth rate was calculated with the same equation by substituting the appropriate measurements.

Environmental Conditions

Air temperatures were recorded daily with a Campbell Scientific 21X Micrologger from 1 May to 31 Aug. 1992. Air temperatures during the same period during 1990 to 1992 were obtained from the Vanscoy weather station, about 20 km northwest of the study site. A linear regression equation using data collected at the study site and Vanscoy in 1992 was developed to

estimate the air temperature in 1990 and 1991. Precipitation data for 1990, 1991, and 1992 were also obtained from Vanscoy.

In the first year temperatures averaged 11°C in May, 17°C in June, and 18°C in July and August at site 1, and 12, 16, 19, and 21°C for the same months at site 2. Precipitation plus irrigation totalled 64, 112, 138, and 38 mm in May, June, July, and August, respectively at site 1, and 70, 175, 51, and 35 mm in respective months from May through August at site 2.

Temperatures in the second year averaged 12, 16, 19, and 21°C at site 1, and 10, 15, 16, and 15°C at site 2 in May, June, July and August, respectively. Precipitation in the second year totalled 50, 155, 31, and 15 mm in May, June, July, and August at site 1, and 52, 20, 108, and 49 mm in the same months at site 2.

Soil water in the 0-15 and 0-30-cm depths of each plot was determined gravimetrically weekly from 1 May to 31 August (Reynolds 1970). Soil samples from the upper 0-10-cm depth of the soil profile were collected in July 1992, air dried in the laboratory for 1 week, and matric potentials of soils at -0.03 and -1.5 MPa were determined for 6 replicates with a pressure plate (Richards 1948). Content of soil NO₃-N from the 0-2.5 and 0-10-cm depths of the profile was determined by the Saskatchewan Soil Testing Laboratory in July 1991 and 1992.

Data Analysis

Within the first and second year of study, data were subjected to factorial analysis of variance using sites and sward treatments as main effects. Data of stem elongation and height elongation rates, the total number of emerging seedlings and percentage values for seedling survival, soil water and soil nitrogen were transformed with arcsin √p and subjected to analysis of variance. When treatment effects were significant, means were compared only to the control with Least Significant Difference (LSD) (Snedecor and Cochran 1980). To determine periodicity of seedling emergence, the number of seedlings in all plots was pooled, plotted against time, and related to precipitation, temperature, and soil water. Similarly means of elongation rates in all plots were plotted against time and related to precipitation, temperature and soil water. Statistical significance was assumed at P<0.05.

Results and Discussion

Seedbed Characteristics and Seedling Emergence

Tillage increased the area of bare soil 5- to 10-fold at site 1 and about 3- to 4-fold at site 2 compared to the other treatments (Table 1). Excluding the tilled plots, dead clubmoss covered an average of 38 and 45% of the soil surface at sites 1 and 2, respectively. Cover of live clubmoss averaged 46% at site 1 and 25% at site 2. Soil water in the 0-15-cm depth varied between sites in the first year (12.5% at site 1 vs. 10.8% at site 2, SE=0.3), but there were no differences among sites and treatments in the second year, averaging 8.4% (SE=0.2).

Seedling emergence in the first and second year after treatment was affected by the interaction of site and treatment. In the first year the fewest seedlings emerged from the tillage treatment at site 1 whereas at site 2 response to treatments was similar, averaging 14 seedlings m⁻² (Table 2). In the second year, about 80-fold more seedlings emerged in the tillage treatment compared to the other treatments at site 1. By comparison, seedling emergence was similar among treatments at site 2, averaging about 5 m⁻².

Table 1. Average cover of bare soil, dead clubmoss and live clubmoss within plots at site 1 and site 2 in 1992.

Treatment	Bare soil	Dead clubmoss	Live clubmoss
		Cover (%)	
(Site 1)		, ,	
Clipping (C)	15b ¹	42a	43a
Litter Removal (L)	18b	33a	48a ²
Tillage	100a	0ь	0ь
C+L	10ь	37a	53a
Control	22b	40a	38a
Mean	33	30	37
(Site 2)			
Clipping	32b	48a	20a
Litter Removal	25b	50a	25a
Tillage	100a	0ъ	0ъ
C+L	38ь	37a	25a
Control	28ь	43a	28a
Mean	45	36	20

¹Means with a similar letter within a site and column are not significantly different at 2>0.05.

² Percentage values do not always add to exactly 100% due to rounding error.

Regeneration of many species is successful when gaps are present in resident vegetation (Milthorpe 1961, Miles 1974, Grubb 1976), but seedlings may be predisposed to severe competition with established plants. Disturbances in the present study created openings of different sizes that persisted for varying periods of time. Only tillage, however, directly altered the character of seedbeds for an adequately prolonged period needed for emergence of fringed sagebrush. Tillage eliminated resident vegetation and created a bare soil surface, the most favorable seedbed for germination and emergence of fringed sagebrush (Wilson 1982, Bai and Romo 1995); light requirements for germination (Bai and Romo 1994, Bai et al. 1996) were also likely met. Savchenko (1973) also reported that the population structure of fringed sagebrush was shifted to younger plants following disturbance.

Periodicity of Seedling Emergence

At site 1 in the first year, 86% of the seedlings emerged in May and June 1990, when soil water generally exceeded -0.03 MPa (Fig. 1a). Soil water below -1.5 MPa in early July when air tem-

Table 2. Effects of sward modifications in the first and second years after treatment on emergence of fringed sagebrush seedlings.

Treatment	Year 1	Year 2		
• • • • • • • • • • • • • • • • • • • •	(Seedlings m ⁻²)			
(Site 1)		•		
Clipping (C)	15a¹	0a		
Litter Removal (L)	10a	1a		
Tillage	2b	740b		
C+L	6a	32a		
Control	25a	la		
(Site 2)				
Clipping	6с	7c		
Litter Removal	lc	1c		
Tillage	31c	6c		
C+L	18c	7c		
Control	11c	1c		

¹Means with a similar letter within a site and year are not significantly different from control at P>0.05.

peratures were highest, and only 3% of the seedlings emerged. In August even though soil water remained below -1.5 MPa, 11% of the seedlings emerged, presumably in response to precipitation events in late July. Soil water at site 2 was greater than -0.03 MPa from May through mid-July 1991 and seedling emergence was continuous with 52% emerging in May and June, and 38% emerging in July (Fig. 1b). When soil water decreased below -1.5 MPa in August when air temperatures were highest, seedling emergence declined to less than 3%.

In the second year, 98% of the seedlings emerged in May at site 1 (Fig. 2a). Soil water was lower than -0.03 MPa in late May and seedling emergence was limited in early June. Some seedlings emerged from mid-June to mid-July when soil water exceeded -0.03 MPa; however, no seedlings emerged after mid-July when precipitation was low, temperatures were high and soil water was generally below -1.5 MPa. More than 94% of the seedlings emerged from May to mid-June at site 2 when soil water was greater than -0.03 MPa (Fig. 2b). Except in mid-July when soil water increased to at least -0.03 MPa after several precipitation events, no seedlings emerged from mid-June through August.

Seedling emergence patterns parallel the findings of Bai and Romo (1994) where no well-defined cycles of dormancy were expressed by previously buried seeds of fringed sagebrush. Moisture availability places strong limitations on germination of fringed sagebrush seed (Bai et al. 1995), and this was reflected in emergence with most seedlings emerging in May and June. When the amount of precipitation is low more seedlings emerge if precipitation is concentrated in a few events (Bai and Romo 1995). If soil water and temperatures are within the physiological range for germination of fringed sagebrush seed, seedling emergence can potentially be continuous. Continuous germination and emergence may enable fringed sagebrush to occupy gaps that are created by disturbance at varying times. By comparison continuous emergence may also predispose seedlings to unfavorable environmental conditions such as water limitations or temperature extremes, and seedling mortality may be high.

Seedling Survival

In the first year more seedlings survived over the summer at site 2 (94%) than site 1 (70%) (SE=4.6). Survival over the winter was affected by the interaction of site and treatment and was poorest in the clipping+litter removal treatment at site 2 (Table 3).

Seedling survival in the second summer was the product of interacting effects of treatment and site. At site 1, survival in the

Table 3. Response of seedling survival of fringed sagebrush to several treatments during winter in the first year and summer in the second year of study.

Season		Litter			
and Year	Clipping (C)	removal (L)	Tillage	C+L	Control
			(%)		
(Winter-1)			` ′		
Site 1	100a	100a	100a	100a	98a
Site 2	100a	100a	92a	62b	96a
(Summer-2)	1				
Site 1	$0b^1$	100a	60b	50ъ	100a
Site 2	45b	0 a	90ь	11a	0a

Means followed by the same letter within a row are not significantly different from control (P>0.05).

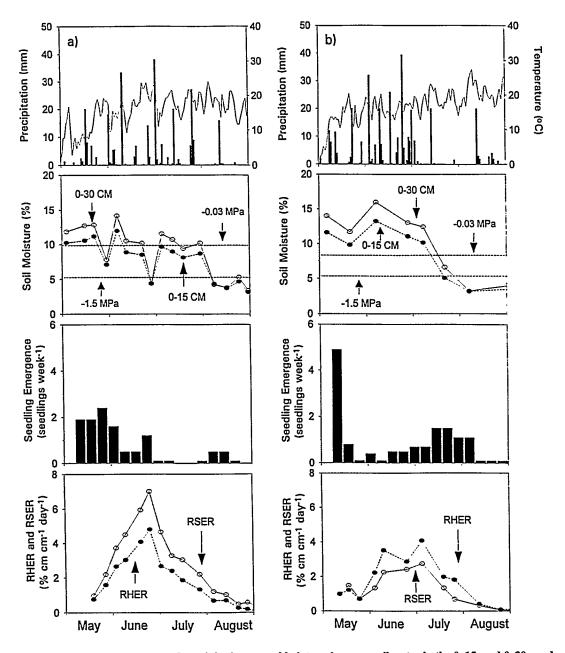


Fig. 1a and 1b. Mean daily air temperature and precipitation at weekly intervals, mean soil water in the 0-15- and 0-30-cm depths, seedling emergence, relative stem elongation rate (RSER) and relative height growth rate (RHER) of fringed sagebrush in the first year at sites 1 and 2. Seedling number and soil water are the average across treatments. Precipitation includes 75 mm of supplemental water at site 1 and 80 mm at site 2.

clipping, tillage and clipping+litter removal treatments was reduced relative to control, but at the second site seedling survival was greatest in the clipping and tillage treatments than in control (Table 3). Survival of seedlings the following winter was higher at site 2 (87%) than the first site (52%) (SE=5.5).

Overall survival of fringed sagebrush seedlings was high compared to silver sagebrush (A. cana ssp. cana Pursh.) in which less than 11% of the seedlings survived (Walton 1984). Even though fringed sagebrush is considered drought tolerant (Coupland 1950, Wilson 1982), desiccation during summer drought appeared to be the major cause of seedling mortality. Many seedlings also perished when ants buried them with soil. Predation, diseases and competition may have also contributed to seedling death (Fenner 1985), but these influences were not isolated.

Plant Growth

In the first year, relative stem elongation rates were similar among treatments, but were more than 2-fold greater at site 1 (2.7 vs. 1.2 %cm cm⁻¹ day⁻¹, SE=0.3) than site 2 despite soil water in the 0-30-cm depth being greater at the second site (7.3% at site 1 vs. 8.5% at site 2, SE=0.2). Changes in height were similar among treatments and sites, averaging 1.75 %cm cm⁻¹ day⁻¹ (SE=0.2). Stem elongation and height growth rates increased from May through June and declined in July and August when soil water was below -1.5 MPa (Fig. 1a and 1b).

In the second year, height growth and stem elongation rates were different between sites and among treatments. Over the year stem elongation rates averaged 1.4 and 0.9 %cm cm⁻¹ day⁻¹ (SE=0.1) at sites 1 and 2, respectively. Stem elongation and

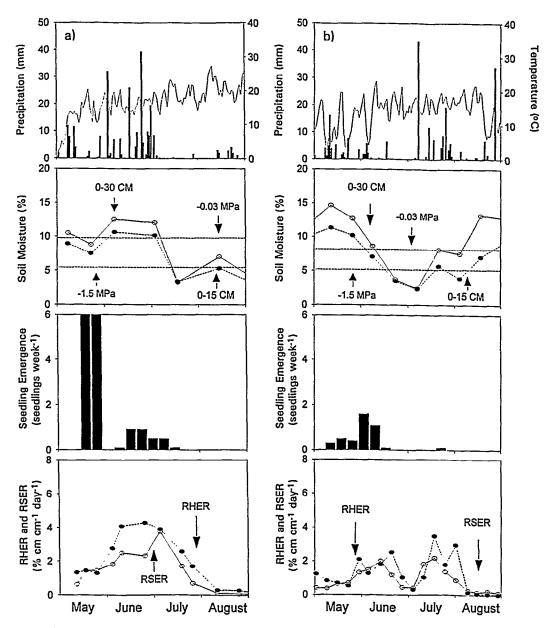


Fig. 2a and b. Mean daily air temperature and precipitation at weekly intervals, mean soil water in the 0-15- and 0-30-cm depths, seedling emergence, relative stem elongation rate (RSER) and relative height growth rate (RHER) of fringed sagebrush in the second year at sites 1 and 2. Seedling number and soil water are the average across treatments. The number of seedlings emerging on the first and second dates in May at site 1 was 74 and 72 m⁻² on each date, respectively.

height growth rates in the tillage treatment were greater relative to the control (Table 4). From mid-June to mid-July stem elongation and height growth rates were greatest at site 1, whereas growth rates peaked in July at site 2 (Fig. 2a, b). Growth of stems and plant height declined the remainder of the summer when soil water was below -1.5 MPa. Over the growing season soil water was similar among treatments and sites, averaging 7.1% (SE=0.2). Concentrations of NO₃-N in the upper 10 cm of the soil were similar among treatments, but greater at site 1 than site 2, averaging 2.5 and 0.6 mg kg⁻¹ (SE=0.08), respectively.

French (1979) concluded that reduced nutrient and water stress enables fringed sagebrush to increase its biomass substantially. In the present study, however, improved growth of fringed sagebrush following tillage is attributed to reduced competition because soil water and NO₃-N were not different among treatments.

Conclusions

Environmental conditions during June and early July are critical in the emergence and growth of fringed sagebrush. Most seedlings of fringed sagebrush emerge in spring and early summer, enabling them to temporally exploit the period for growth when soil water is highest and temperatures are moderate. Menke and Trlica (1981) also reported that growth of fringed sagebrush

Table 4. Response of relative height growth rate (RHGR) and stem elongation rates (RSER) of fringed sagebrush to several treatments at sites 1 and 2 in the second year of study.

		Litter			
Response	Clipping (C)	removal (L)	Tillage	C+L	Control
		(%	cm cm ⁻¹ day	·1) ·	
RHGR	0.9a ¹	0.95a	2.4b	0.8a	0.6a
RSER	1.3a	1.4a	3.0b	1.6a	0.9a

¹ Means followed by the same letter within a row are not significantly different from the control (P>0.05).

was sensitive to variation in precipitation. Furthermore, high precipitation in the previous year may also benefit the growth of fringed sagebrush (Olson et al. 1985).

Under no circumstances was seedling emergence or plant growth greater in the undisturbed control than in the disturbed sward. Emergence and growth of fringed sagebrush were improved by tillage, especially the following year, suggesting that this species is favored by severe disturbance. Generally, clipping, litter removal or the combination of the 2 treatments had no effect on plants. Over the long-term, however, herbage removal may allow fringed sagebrush to increase because production, and presumably vigor of perennial grasses, are reduced by litter removal (Willms et al. 1986).

Reduced competition, the release of established plants, and the recruitment of new individuals contribute to increases in fringed sagebrush following disturbance. Disturbances that reduce or remove vegetation on many spatial scales promote the emergence and growth of fringed sagebrush by bringing seeds to the soil surface or creating bare soil surfaces for seeds that are being dispersed. Seeds that do not reach a favorable position in the seedbed can contribute to a persistent seed bank (Bai and Romo 1994), retaining their viability for prolonged periods. An abundance of robust plants of fringed sagebrush should be viewed as an indication of significant disturbance. Fringed sagebrush has diverse ecological roles, and is well adapted to persist in Northern Mixed Prairie in a successional continuum from early to late seral stages.

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