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SPROUTING AND SEEDLING ESTABLISHMENT IN PLAINS SILVER SAGEBRUSH (*ARTEMISIA CANA* PURSH. SSP. *CANA*)

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ABSTRACT.—The importance and nature of vegetative reproduction was compared with seedling establishment in plains silver sagebrush (*Artemisia cana* Pursh. ssp. *cana*). Sixty-three percent of plants excavated originated from rhizomes. Sites that experienced habitat disturbance did not have a significantly different number of plants originating from vegetative reproduction than did undisturbed sites. Parent rhizomes were significantly older than taproots, which were significantly older than aboveground stems. Rhizome systems were spread 3.3 times that of plant height. Seventy-nine percent of rhizomatous daughter plants were 100 cm or less from parent plants. Up to 52 sprouts were found on one rhizome. Seedling establishment was greatest during wet growing seasons, and vegetative reproduction was greatest during dry years.

Sagebrush (*Artemisia* L.) taxa are among the most important plants on rangelands of the western United States (Beetle 1977). Plains silver sagebrush (*Artemisia cana* Pursh. ssp. *cana*) is a major consideration in the management of rangelands in the northern Great Plains. This is due to the taxon's competitive nature with livestock forages and its importance as a habitat component for several wildlife species. Together with the other two subspecies of silver sagebrush, mountain silver sagebrush (*A. cana* ssp. *viscidula* [Osterhout]) and Bolander silver sagebrush (*A. cana* ssp. *bolanderi* [Gray] Ward), this complex is encountered on millions of hectares in 13 western states and 2 Canadian provinces (Harvey 1981).

The literature (Young and Evans 1972, Bostock and Benton 1979, Went 1979) provides contradictory evidence as to whether seed or vegetative reproduction is more important for survival of plants displaying both habits in arid and semiarid environments. Accordingly, this will have to be determined for each taxon individually. The most pernicious weeds generally grow from underground roots, rhizomes, and buds (Cook 1983); thus, these are important traits to understand in successful rangeland taxa. Paradoxically, vegetative reproduction in sagebrush taxa has not been previously studied in detail despite the importance of these taxa (Beetle 1977, McArthur and Plummer 1978) and their obvious reproductive success (Harvey 1981). Understanding sagebrush reproductive success would provide insight into plant population dynamics throughout western North America (Mott 1979). Our objective was to assess the importance and nature of vegetative reproduction (sprouting) versus seedling establishment in plains silver sagebrush.

STUDY SITES DESCRIPTION

Six study sites were selected in drainages of the Tongue and Yellowstone rivers near Miles City in southeastern Montana. The sites

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were considered typical in climatic and edaphic relationships of plains silver sagebrush habitats in the northern Great Plains (Harvey 1981). Soils at each study site are texturally heterogeneous but are largely a mosaic of loams, with silty clay loams predominant. Three sites (Yellowstone River—frigid Ustic Torrifluvents, Lower Black Springs—mixed [calcareous] frigid Ustic Torrifluvents, and Lower Flood—fine montmorillonitic Borollic Camborthids) had experienced fire or ice scraping and shearing in the preceding five years. No evidence of such disturbance was found at the remaining study locations (Lignite Creek—Camborthid Torrifluvents, Paddy Faye—fine montmorillonitic Borollic Camborthids, and Moon Creek—fine montmorillonitic Borollic Natriargids). All sites have received periodic cattle grazing. The area has an average annual precipitation of 340 mm, with peak precipitation received in May and June.

Methods

Transect Excavations

At each study site a plains silver sagebrush plant 16 to 40 cm in height was located at each 5-m interval along 25-m transects (4). Established plants of this size were selected because rhizomatous connections to parent plants, if present, were still readily apparent. The 20 plants located at each site were excavated to determine whether they had sexual or asexual origins.

Roots were carefully excavated by hand so that fragile rhizome connections remained intact to determine if plants were of independent origin or connected to another plant. Rhizomes were generally found in the top 10 cm of soil, while taproots were excavated to a depth of 1 m or an impenetrable layer. Plants without connecting rhizomes were considered to have originated from seed. Plant height, length of rhizomes, and stem and rhizome diameters were measured on all originally located plants and those plants to which they were directly connected. Root distribution from each excavation was mapped within a grid, and line sketches of each plant were drawn. Samples for age determination (Ferguson 1964) were taken from stem, root, rhizome, and connecting rhizome sections of each excavated plant. Aging of sagebrush was feasible despite the difficulty created by common stem splitting and layering (Ferguson 1964).

To determine whether differences existed in the number of sprouts to seedlings over the six study sites, we conducted a paired Student's t test ($P < .025$). A chi-square analysis ($P < .05$) was performed to learn if fire or ice action on three of the sites was significant in determining the ratio of sprouts to seedlings compared with three undisturbed sites. Analysis of variance (ANOVA) was used for comparison of age and growth means among plant parts. Duncan's multiple range test protected by a prior F-test was used for comparing treatment means.

Isolated Plant Excavations

Two large, well-established plants at the Lower Flood site were the subject of a complete root excavation. Plants were subjectively selected based upon two criteria: (1) the plant had to be relatively isolated from other large plains silver sagebrush plants to minimize major competitive influences, and (2) there had to be an abundance of small plains silver sagebrush plants surrounding the potential parent plant. The two plants selected for excavation were slightly more than 1 m in height. A 5-m area around each of the large plants was excavated so that all roots, including rhizomes of all smaller plants, were exposed. The size of each plant and the root distribution from the excavations were mapped to differentiate seedlings and sprouts. Although we did not analyze the data statistically, our direct observation of the root networks facilitated interpretation of the transect data.

Results

Transect Excavations

Plants arising from rhizomes were more abundant than those that grew from seedlings ($P < .025$) (Table 1). Approximately 63% of the excavated plants were connected by rhizomes to an established plant or rhizome system. Counts of annual rings established that the rhizomatous connections were one to four years old. Usually, a large, established parent plant was the source of rhizomes connecting either single plants or a series of sprouts

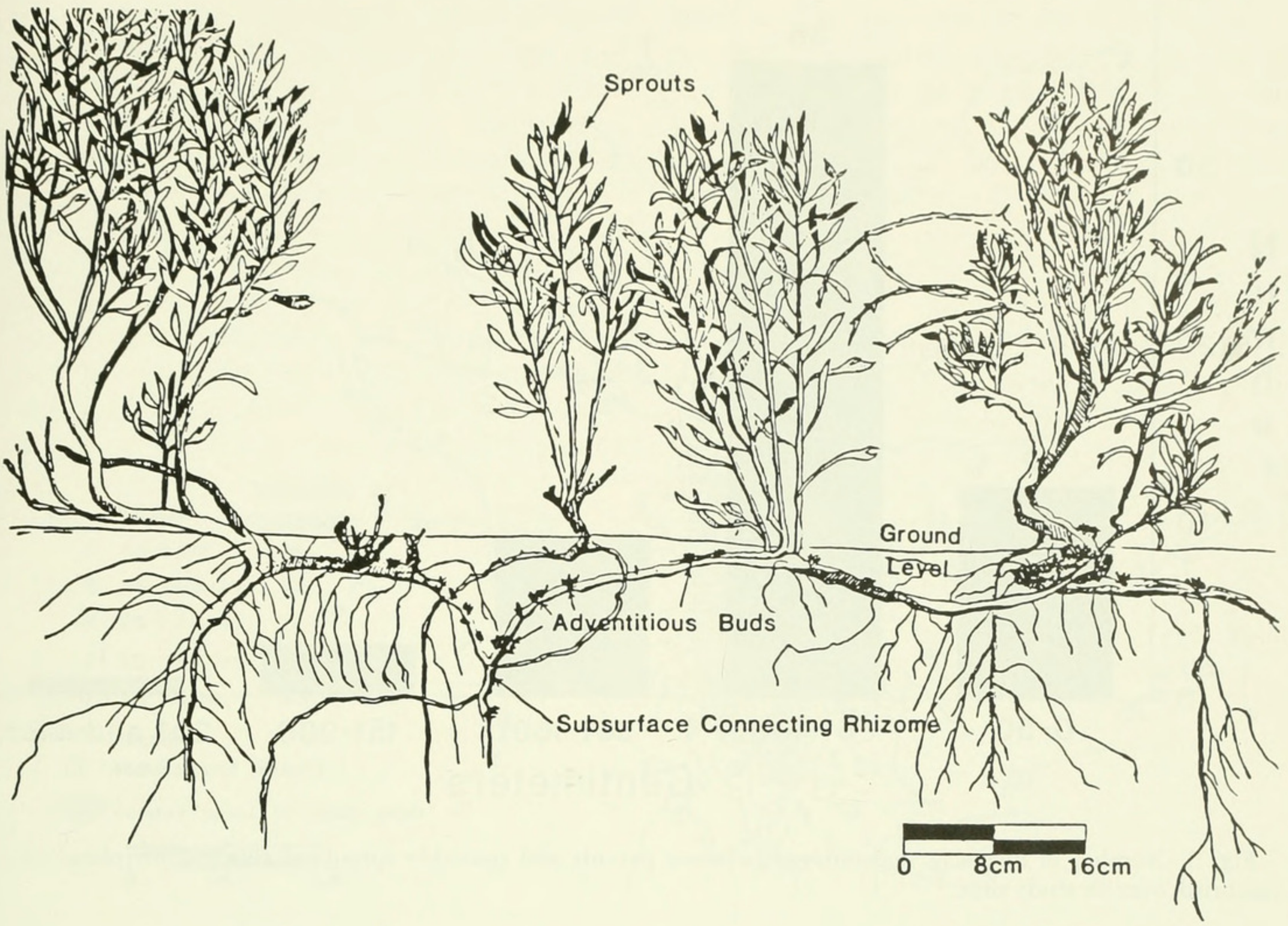

Fig. 1. Graphic example of an excavated sprout connected to a parent plant and other offspring. Original or oldest material is on far right.

TABLE 1. A comparison of the number of rhizomatous to nonrhizomatous plains silver sagebrush plants found at each study site.

	Study site[1]						
	1	2	3	4	5	6	Total
Rhizomatous[2]	13	13	15	7	13	14	75[a3]
Nonrhizomatous	7	7	5	13	7	6	45[b]

[1]Sites are numbered as follows: 1—Yellowstone River, 2—Lower Black Springs, 3—Lower Flood, 4—Lignite Creek, 5—Paddy Faye, 6—Moon Creek.
[2]Plants with rhizome connections (alive or dead) to other plants.
[3]Significant ($P < .025$) differences between rhizomatous and nonrhizomatous plant totals by Student's *t* test are followed by different letters.

(Fig. 1). However, some plants were from a series of sprouts along a rhizome presently terminated with a dead or decadent stump. One site, Lignite Creek, was different in that it had a majority of nonconnected individuals (Table 1). Reduction of available soil moisture due to clay pan soils overlying extensive gravel at Lignite Creek might explain the difference. Plant water use would be less favorable with this condition at the surface, affording an advantage to taprooting plants in reaching deeper, more favorable conditions. The three sites disturbed by fire or ice action were compared with the three undisturbed sites to learn whether the ratio of sprouts to seedlings changed with disturbance. No significant differences ($P < .05$) in numbers of plants arising from rhizomes due to disturbance were found.

Generally, an elaborate subsurface rhizome system was found that was older than aboveground stems. There were significant ($P < .05$) age differences among plant stems, taproots, and parent rhizomes (Table 2) over all six study sites. Aboveground stems were three to five years younger than taproots and associated rhizomes. Parent rhizomes with directly connected sprouts were significantly older than taproots. Taproots and rhizomes without direct connections to a parent plant were not significantly different in age from each other.

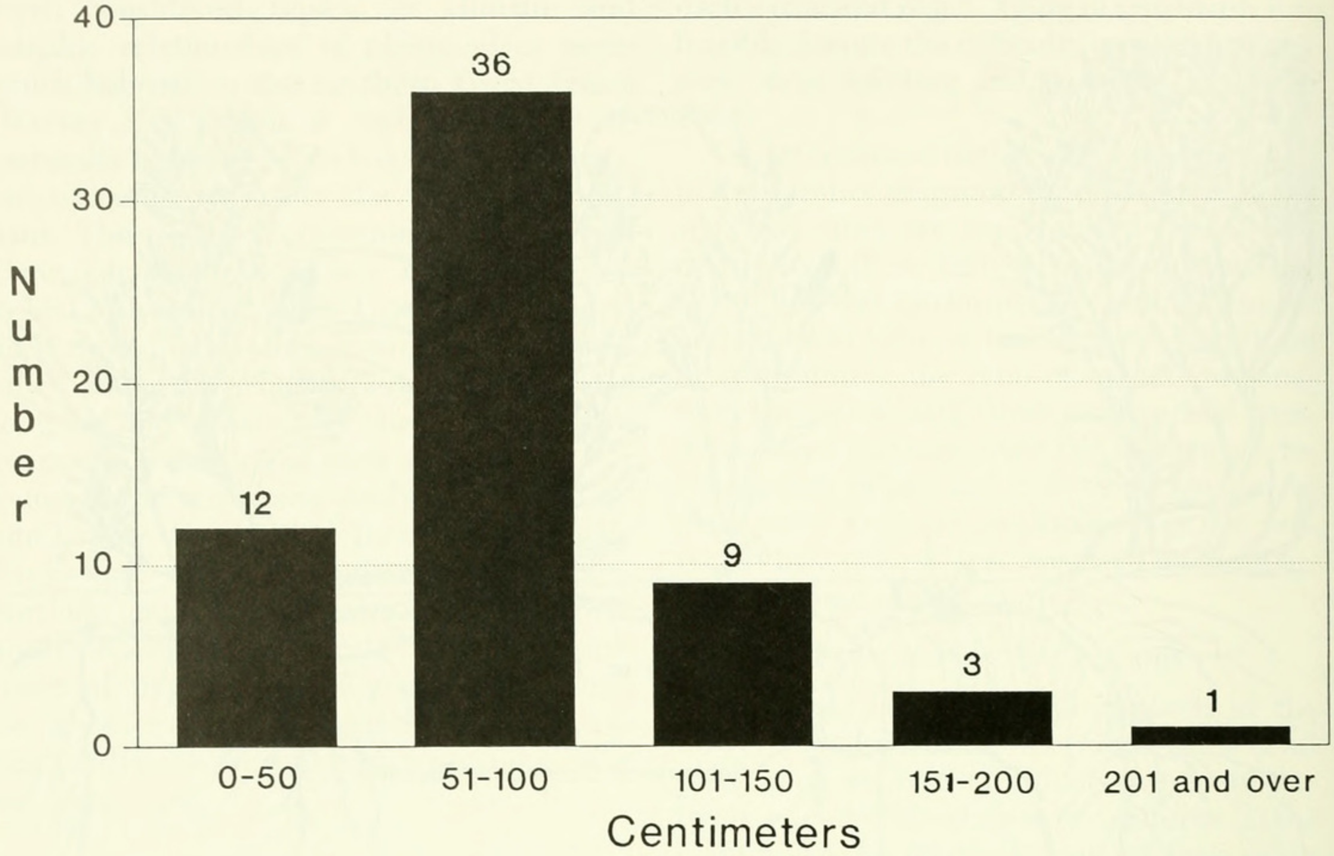

Fig. 2. Number of distances encountered between parents and traceable sprouts of rhizomatous plains silver sagebrush over six study sites.

TABLE 2. Age relationships of above- and belowground parts of plains silver sagebrush plants from the six study sites.

Plant part	Mean age (years)	Standard deviation	Number of samples
Stems	3.4[a1]	2.0	204
Taproots	6.9[b]	3.1	28
Parent rhizome[2]	8.8[c]	3.7	68
Rhizome system[3]	6.0[b]	2.5	128

[1]Significant ($P < .05$) mean differences by Duncan's multiple range test are followed by different letters.
[2]Rhizome originating from a parent plant (or dead stump) to which sprout was directly connected.
[3]Rhizome sections other than in 2 above.

TABLE 3. Growth relationships of above- and belowground parts of rhizomatous plains silver sagebrush plants from the six study areas.

Plant part	Mean (cm)	Range (cm)	Number of samples
Plant (sprout) height	32[a1]	11-59	155
Lateral distance to parent connection[2]	78[b]	14-277	61
Lateral spread of rhizome system[3]	105[c]	11-369	90

[1]Significant ($P < .05$) mean differences by Duncan's multiple range test are followed by different letters.
[2]Lateral distance from parent plant or rhizome to nearest sprout on rhizome system expressed as a mean of all plants with this growth habit.
[3]Total lateral extent of all rhizomes in an excavation expressed as a mean of all plants with rhizome systems.

Rhizome extension was greater than aboveground heights ($P < .05$) (Table 3), even in older plants that had the largest aerial portions. Rhizome length from the selected plant to the parent plant averaged 2.4 times that of plant height. Total lateral spread of the rhizome system averaged 3.3 times that of plant height.

Figure 2 summarizes the number of distances encountered between parent plants and traceable sprouts. The largest proportion (59%) of these connections were from 50 to 100 cm in length, followed by the 0–50-cm distance (20%).

Isolated Plant Excavations

The extensive sprouting nature of plains silver sagebrush was apparent after excavations had been completed in areas surrounding two large, isolated plants. Most roots were part of a shallow, complex underground network of interconnected rhizomes that often included several smaller, nearly independent

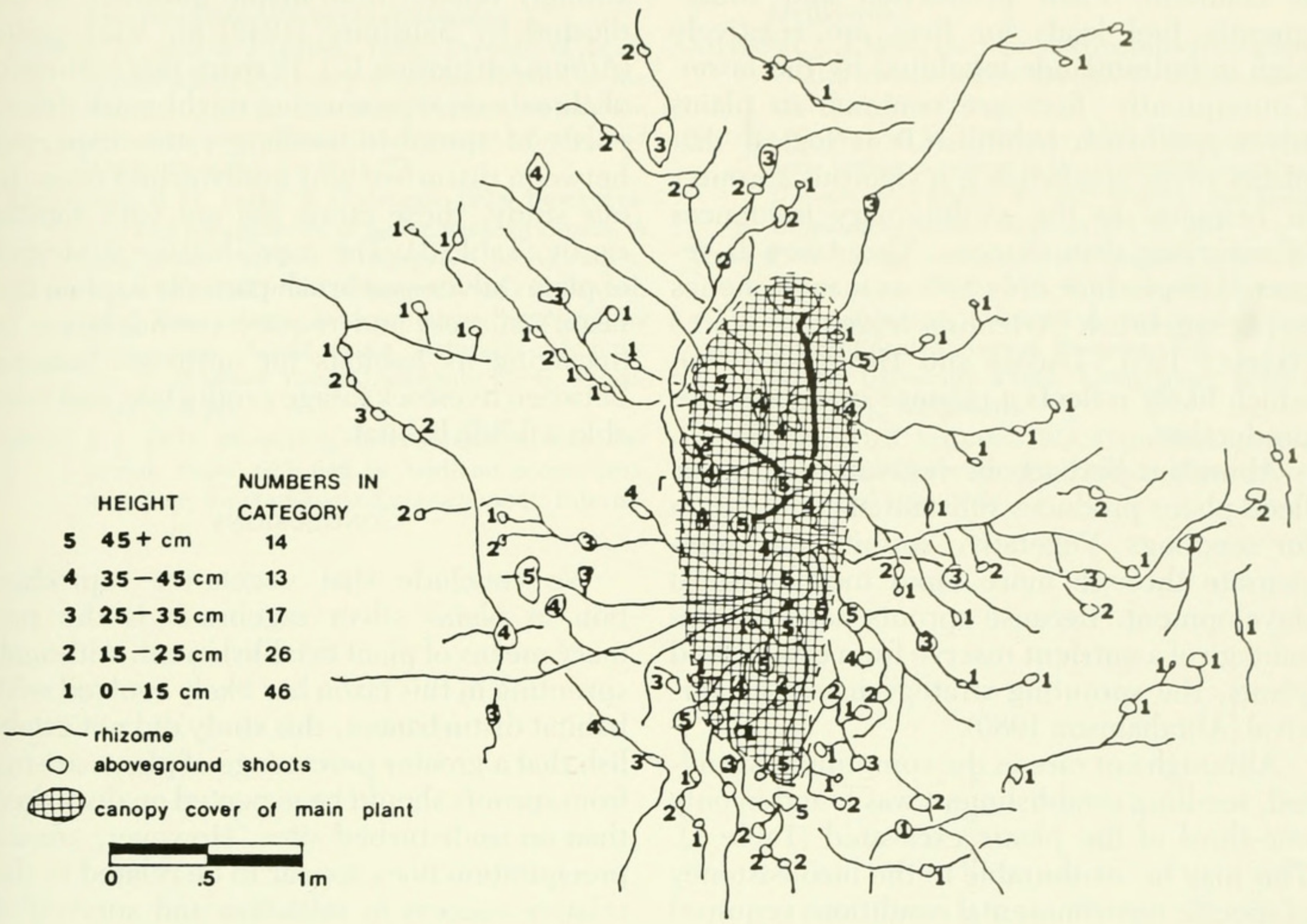

Fig. 3. Diagram of an isolated plant excavation. All aboveground shoots are shown individually and numbered according to height.

systems (Fig. 3). This was most apparent with older, well-established plants from which the network originated (Fig. 3).

Characteristic of the horizontal rhizome expansion were size classes decreasing in concentric circles away from the parent plant. There was considerable variation in rhizome complexity within these individual systems. Excavations established that rhizomes can sprout at least 3 m from the parent plant. Therefore, a large number of progeny may arise asexually from one individual. Individual rhizomes had from 1 to 52 sprouts. No evidence indicated that all individual systems were of the same origin. That is, no common root connections could be traced. However, some might have been connected and later separated after mortality of connective rhizomes.

Discussion

Vegetative reproduction is prevalent in plains silver sagebrush, and the causal agents are of interest and importance to rangeland management. Benefits of vegetative reproduction include (1) an enhanced ability to utilize unevenly distributed resources and (2) an increased competitive ability to occupy adjacent areas (Harper 1977, Cook 1983). In addition, sprouts are better able to resist invasions of seedlings from other species while reducing the probability of extinction. This is accomplished by spreading the risk among many genetically identical individuals (Cook 1983). An evolutionary strategy that employs asexual mechanisms is consistent with the findings of Abrahamson (1980), who reported that increased environmental severity generally shifted emphasis to vegetative reproduction.

Generally, vegetative reproduction is most important where fire, weather phenomena, and other disturbances are common (Bostock and Benton 1979, Went 1979, Abrahamson 1980, Legere and Payette 1981). The sprouting nature of plains silver sagebrush is likely an adaptation to its northern Great Plains habitat. Flooding with associated deposition, along with ice scraping during winter events, is common. Plant production and subsequently fuel loads for fires are relatively high in bottomlands inhabited by the taxon. Consequently, fires are common in plains silver sagebrush habitats. It is logical that plains silver sagebrush is a vigorous sprouter in response to the evolutionary influences of recurring disturbances. This taxon is reported to produce only 18% as many achenes as big sagebrush (*Artemisia tridentata* Nutt.) (Harvey 1981, Tisdale and Hironaka 1981), which likely reflects a reliance on asexual reproduction.

Abundant herbaceous vegetation in mesic flood plains produces substantial competition for seedlings. Vegetative sprouts may compensate through more rapid morphological development. Because sprouts have the advantage of a nutrient reserve from established plants, the sprouting strategy increases survival (Abrahamson 1980).

Although not rare in the communities studied, seedling establishment was found in only one-third of the plants excavated (Table 1). This may be attributable to the inconsistency of specific environmental conditions required for germination and seedling establishment. Environmental factors, especially drought, might best explain differences in ratios of sprouts and seedlings found in 1983. For example, a three-year drought at the study area occurred between 1979 and 1981 when the mean annual precipitation was 23.0 cm and preceded the wet year of 1982 with 41.6 cm of precipitation. The long-term average precipitation is 34.8 cm. This drought coincided with the ages of most plants examined in this study. The relatively moist years preceding (1978 with 44.7 cm) and following (1982 with 41.6 cm) this drought provided the periods of establishment for seedlings at the study sites. However, just as seedlings appear favored during wet years, sprouts were found to have the advantage in establishing during relatively dry periods. The cool, wet growing season of 1982 was followed by a warm, dry (22.3 cm) growing season in 1983. Subsequently, numerous seedlings and few sprouts were produced during 1982, and few seedlings with an abundance of sprouts were produced in 1983. Few seedlings from 1982 survived beyond the dry second season. Therefore, it appears that both the mode and the success of plains silver sagebrush reproduction is strongly related to available moisture as indicated by Salisbury (1942) for wild garlic (*Allium carinatum* L.). Perhaps this influence of climate on reproduction might mask differences of sprout-to-seedling ratios expected between disturbed and undisturbed sites. In our study, these ratios did not vary significantly (Table 1). The reproductive strategies of plains silver sagebrush partially explain the taxon's success and require consideration in managing its habitats for optimum balance between livestock forage production and suitable wildlife habitat.

Conclusions

We conclude that vegetative reproduction in plains silver sagebrush is the primary means of plant establishment. Although sprouting in this taxon has likely evolved with habitat disturbances, this study did not establish that a greater percentage of plants arising from sprouts should be expected on disturbed than on undisturbed sites. However, annual precipitation does appear to be related to the relative success in initiation and survival of seedlings and sprouts. Seedlings apparently require more moisture for both germination and survival than do sprouts.

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