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Seed bank dynamics in a Great Basin salt playa

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Salt playa are common in the Great Basin area with halophytes as the dominant flora. The relationship between the seed bank flora and existing vegetation was studied. The seed bank flora showed a high degree of similarity with that of perennial and annual halophytic vegetation. Both above and below ground components of the community are dominated by halophyte species like *Allenrolfea occidentalis*, *Holosteum umbellatum*, *Salicornia rubra* and *Salicornia utahensis*. Seasonal variation in the seed bank was also studied for the 1995–1996 and 1996–1997 growing seasons. The seeds of *A. occidentalis* persist in the soil of the upper zone in large densities. *Salicornia utahensis* was much higher in the upper zone throughout the study period. Most species demonstrated the persistent nature of the seed banks with their numbers increasing after seed dispersal and decreasing in subsequent months. The variation illustrates the transient nature of the seed bank. We concluded that *A. occidentalis* is more dependent on a large seed bank for maintaining its population than the two annual halophytes. The significance of the seed bank and their variation due to environmental conditions for perennial and annual species of the Great Basin salt playa community is discussed.

Introduction

Allenrolfea occidentalis (S. Wats.) Kuntze (iodine bush) is one of the most salt tolerant stem succulent shrub species occurring in salt marshes and salt playas of western United States and north western Mexico (Jansen & Parfitt, 1977). It grows in the bottom of internally drained basins at the margins of the Great Basin salt playas (Billings, 1945) where the majority of the salt is NaCl with concentrations up to 1027 mM in the soil (Hansen & Weber, 1975). It is often found in association with *Salicornia utahensis, Salicornia rubra, Suaeda maritima*, and *Distichlis spicata* and is a secondary invader to *Salicornia utahensis* in saline soils (Flowers, 1934). Seed production in *Allenrolfea* is abundant even during very dry years (Young *et al.*, 1995), flowering occurs in late July and plants produce seeds in late September. Most of the seeds are disperse onto the saline soil around the parent plant, however wind and water upon which they readily float sometimes causes a long distance seed dispersal. Seeds are borne in utricles that are

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often enclosed by winged, inflated or hairy structures. Most of the appendage structures are lost after the seed has fallen from the plant. Seeds are uniform in size and color with no evidence of polymorphism (Blank *et al.*, 1994).

Salt tolerant species grow in different macroenvironments that range from deserts to high rainfall coastal habitats. Halophytes have evolved a number of seed germination mechanisms for establishment in these saline environments (Ungar, 1991). Salt marsh and salt desert environments often have increasing soil salinity levels during the summer months because greater evaporation during the warm season causes a decrease in soil moisture percentages. Halophytes usually avoid high stress periods as a dormant seed in the soil and germinate under more favorable conditions. Persistent seed banks are usually produced by enforced or induced dormancy and carry seeds over a predictable cold, dry or hyper saline period after which germination occurs. Persistent seed banks serve as a long term seed storage mechanism that allow seeds to remain in the soil over months or years until favorable conditions for germination occur. Because salt marshes and salt desert habitats may be exposed to unpredictable precipitation patterns in many parts of the world, an adaptation to increased salinity levels has evolved at the germination stage of development that permits seeds to remain dormant during these stressfull periods (Jerling, 1984, Zaman & Khan, 1992; Khan, 1993; Ungar & Woodell, 1993; Ungar, 1995; Aziz & Khan, 1996). Vegetation zones of a salt marsh could shift markedly from one year to the next (Badger & Ungar, 1989). Seeds in the seed bank can remain stored in the soil for various lengths of time and than germinate later when the hypersaline conditions are alleviated (Ungar, 1995).

Seed bank studies of the Great Basin desert of the *A. occidentalis* community showed that prolonged leaching of the seedbed soils was required before natural (seeds that are dispersed naturally) or spiked (seeds that remain on inflorescences) seeds would germinate. *Allenrolfea occidentalis* seeds were detected in seed banks were found in the nest of saline harvester ants *Pogonomyrmex salinus* (Young *et al.*, 1995). In the Great Basin desert, plant communities with numerous annuals have seed banks that fluctuate much like those of the hot deserts as a result of the variable productivity of annuals (Young *et al.*, 1981; Young *et al.*, 1995). However some Great Basin communities have seed banks with a much greater proportion of seeds of perennials species than do the hot deserts, and the soil seed densities of these species are less variable than those of annual species (Parmenter & MacMahon, 1983).

Recent studies on saline desert communities have attempted to describe the relationship between existing vegetation with that of the seed bank and their seasonal dynamics (Khan, 1993; Zaman & Khan, 1992; Aziz & Khan, 1996). The crucial and controversial question, whether soil seed banks play an important role in population dynamics of halophytic shrub species in saline deserts, has been difficult to resolve because recruitment from the seed bank appeared to be a rare phenomenon. A few studies have been conducted on the seed bank dynamics of desert communities (Coffin & Lauenroth, 1989; Hegazy, 1990; Zaman & Khan, 1992), inland saline habitats (Ungar & Riehl, 1980; Khan & Ungar, 1986; Khan, 1990), and on coastal halophyte communities (Smith & Kadlec, 1983; Jerling, 1984; Aziz & Khan, 1996).

The seed bank dynamics of Great Basin salt playa communities have not been studied intensively. The aim of the present study was to determine the relationship between seed reserves and vegetation and the seasonal dynamics of seed bank of a salt playa community.

Study site

The site chosen for this study is a salt playa east of Goshen, north-western Utah. It is an area of flat, low lying ground in the bottom of a fairly wide valley that spreads out at the southern end into a vast stretch of flat, salt incrusted plain. The area was a bay of ancient Lake Bonneville that at one time covered most of the area. Today, Utah Lake is approximately 1 mile north of the salt playa considered. The area contains numerous salt marshes and salt playas with nearly pure stands of *Allenrolfea occidentalis*. The site is situated between the Wasatch mountains to the east and the Tintic range on the west (T10 S, R 1 E between 1100 52–32 east and west). Soil type of the area is Jordan loam. The specific conductance in the soil ranges from 5·3 to 29·0 dS m^{-1} and the water table varies from 0·9 to 3 m below the surface. The level of soil salinity is related to the balance between the deposition of salt through evaporation and the dilution effect of precipitation. The precipitation recorded in 1996 was (4·63 cm) and in 1997 (6·25 cm). The precipitation largely occurs in the cold winter months.

Materials and methods

The study was conducted during 1996 and in 1997. Study site was divided into two distinct salinity zones, upper zone low salinity (5·3 dS m^{-1} zone near to the road site) and lower zone high salinity zone (29·0 dS m^{-1} zone received maximum saline water from the Lake). The point centered quarter method (Cottam & Curtis 1956) was used to sample the vegetation over 20 random points and relative frequencies were calculated for each species in the community.

Seed bank data were collected over a period of 2 years from May 1996 to November 1997. To analyse the seed bank 10 random soil samples were collected from each zone (upper and lower) with the help of a soil corer 2·5 cm in diameter and 15 cm in length. The samples were stored in plastic bags for subsequent laboratory analysis. Soil samples were air dried and seeds of each species were sorted manually and counted with the help of a binocular microscope. Seeds that appeared intact and viable were included in the count and identified with the help of a seed identification manual (Martin & Barkley, 1973).

Results

Vegetation

The high and low salinity zones of the salt playa were characterized by an *A. occidentalis* zone (Fig. 1). High areas of the playa were grazed somewhat but had a dense plant cover (13471 ha) of *A. occidentalis* (Table 1). The community was dominated by *A. occidentalis* and other perennial shrubs like *Salicornia rubra*, *Salicornia utahensis* and the grass *Distichlis spicata*. Some dense clumps of a grass *Holosteum umbellatum* were found under the shade of few big *A. occidentalis* plants.

Seed bank

The seed bank studies of the salt playa community showed a close relationship with the vegetation. The seed bank was represented by eight species while the vegetation survey indicated that there were only three dominant species (Table 1). The overall densities for seeds in the lower and higher salinity zones for *A. occidentalis* community was less in 1997 than for 1996 (Fig. 1). The number of *A. occidentalis* seeds after dispersal reaches the maximum density of 86602 seed m^{-2} in October 1996 and declines in November 1996 (Fig. 1). The size of the seed bank was larger in the upper zone and decreased progressively towards the lower zone (Figs 1, 2 & 3). The maximum size of the *A. occidentalis* seed bank in the lower zone was 6011 seeds m^{-2} in July 1996 and 6622 seeds m^{-2} in October 1997 (Fig. 2).

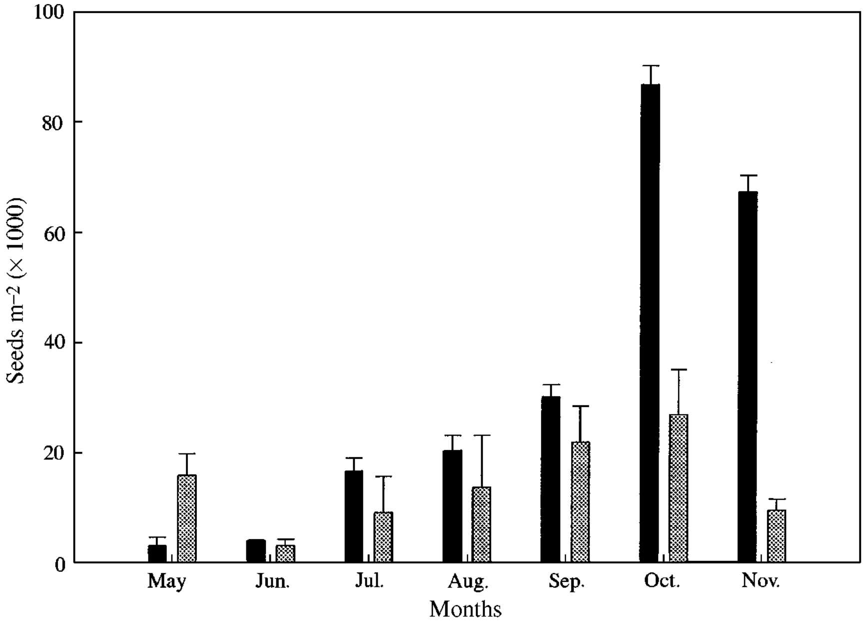

Figure 1. Seasonal distribution of *Allenrolfea occidentalis* seeds in (m^{-2}) in the upper playa zone during the 2 years of study period 1996–1997. 1996 (■); 1997 (▩).

The total density of seeds per square meter in both zones declined in November 1996 through May 1997. The sharpest declines coincided with the fall and spring. The dominant seed bank species at the high salt playa showed a large seed bank flora throughout the growing seasons, but low salinity areas contained fewer seeds in all seasons (Figs 1–3).

The upper marsh had a large increase in seed numbers from 3311 to 105960 seeds m^{-2} of *H. umbellatum* in 1997 that was absent in October and November 1996 (Fig. 3). The total number of seeds varied in each marsh in monthly samples collected during the 1996 and 1997 seasons. The temperature and precipitation changes during this time are shown in Figs 4 & 5. *Allenrolfea occidentalis*, *H. umbellatum* and *S. rubra* were the dominant species of the community throughout the growing seasons for both years (Table 1). Others species in the seed bank flora were *Salicornia utahensis* (509–2457

Table 1. *Species composition of the salt playa community*

Species	Number	Basal area (m^2)	Density (ha^{-1})	RD	RC	RF	IVI
Allenrolfea occidentalis	62	108,953	13,471	78	99	90	89
Salicornia rubra	14	362·1	3042	17	0·2	35	18
Salicornia utahensis	4	851	869	5	0·4	2	9

The columns are represented as follows: RD = relative density; RC = relative cover; RF = relative frequency; IVI = importance value index.

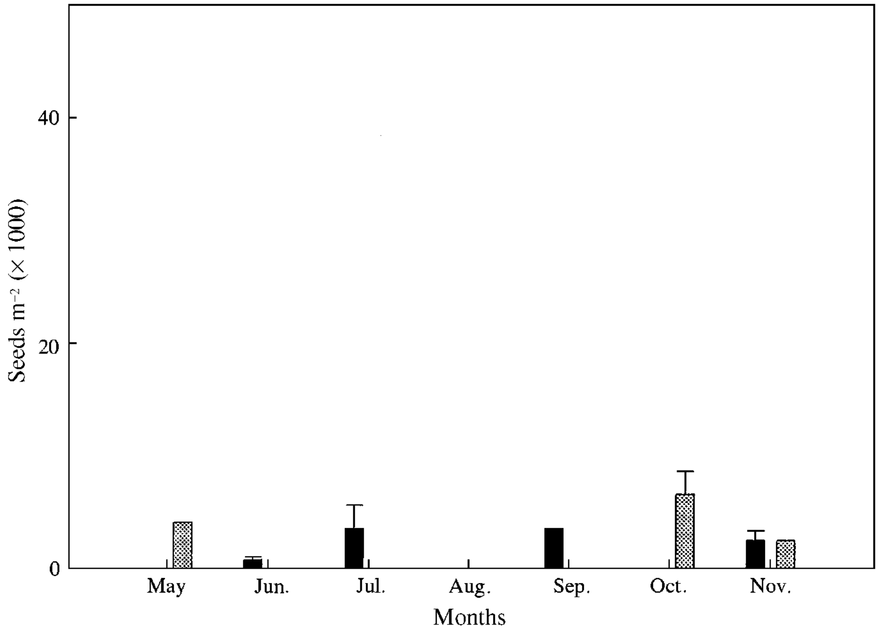

Figure 2. Seasonal distribution of *Allenrolfea occidentalis* seeds (m^{-2}) in the lower playa zone during the 2 years of study period 1996–1997. 1996 (■); 1997 (▩).

seeds m^{-2}), *Suaeda depressa* (509–3057 seeds m^{-2}), *Aster cordifolis* (1019–2547 seeds m^{-2}), *Kochia scoparia* (509 seeds m^{-2}) and *K. americana* (509 seeds m^{-2}).

Discussion

Allenrolfea occidentalis grows in the highly saline regions of an inland salt playa at Goshen, which is situated near the southern end of Utah Lake, south of Goshen Bay, in central Utah. Depressions in the area accumulate sufficient salts to become salt pans or playas. These playas have fine textured, hard surfaces without extensive thick (>1 cm) deposits of crystalline salts (Hubbs & Miller, 1948). Temperatures are generally cool with minimum of 0°C in the winter and maximum about 37°C in the summer (Fig. 4). There are two wet seasons per year, one extending January to May and the other beginning in July or August (Fig. 5). Hansen & Weber (1975) found that temperatures gradually increased from May to July and gradually decreased from August to November (Fig. 4).

Inland salt marshes and salt playas represent a distinct type of habitat where the salinity problem is essentially related to ground-water. The water accumulates in the basin due to the melting of snow. High soil salinity could be the cause of low species diversity in this community. Rainfall may play a prominent role in regulating the establishment of vegetation in saline communities (McMahon & Ungar, 1978).

The *A. occidentalis* community occurs in a dry arid region of Goshen, Utah which is inundated by saline water from saline soils during rainy season. Shrubby halophytes are reported to maintain a seed bank in salt desert communities (Khan, 1993; Zaman & Khan, 1992; Aziz & Khan, 1996). *Allenrolfea occidentalis* was the dominant species in the soil as well as in the vegetation. Eight species were represented in the seed bank but the dominant species consisted of three species. The five additional species in the seed bank, which were rare in abundance, could be found in adjacent areas.

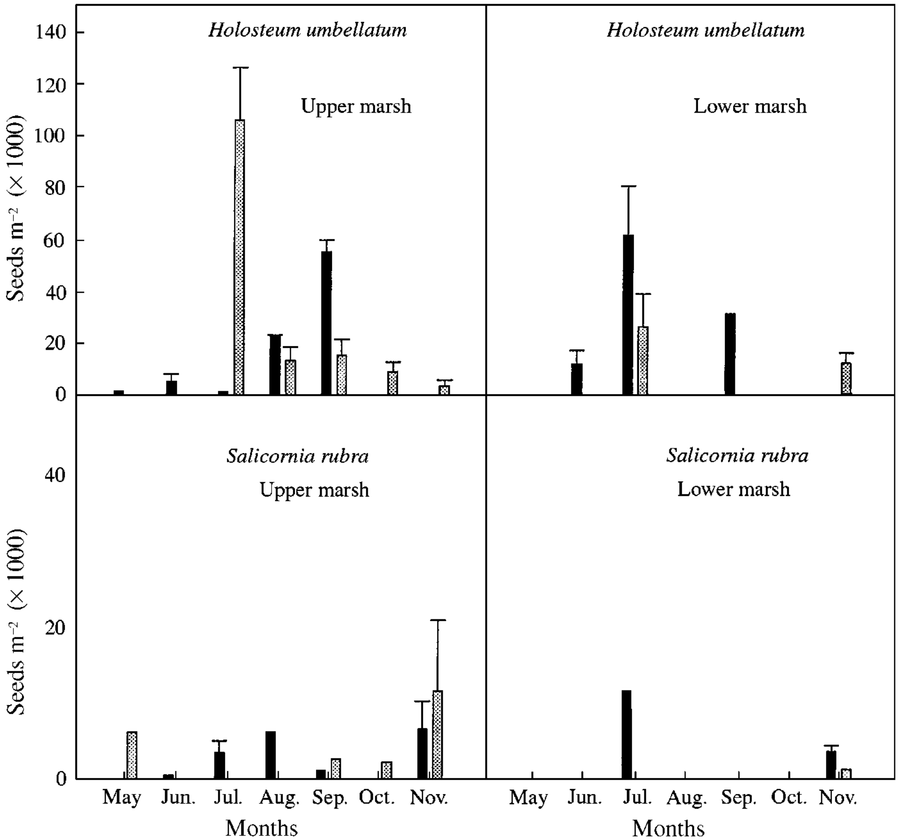

Figure 3. Seasonal distribution of *Holosteum umbelatum* and *Salicornia rubra* seeds (m^{-2}) in the upper and lower playa zones during the 2 years of study period 1996–1997. 1996 (■); 1997 (▩).

Above ground vegetation of our study site is closely represented in the seed bank samples. Our results agree with those of Hopkins & Parker (1984) who suggested that some species in highly saline areas are well represented in the seed bank. Seed bank studies of *A. occidentalis* determined that prolonged leaching of the seedbed soils was required before natural or spiked seeds would germinate (Young *et al.*, 1995). Changes in species composition in zonal halophytic communities related to soil salinity fluctuations have been reported (Ungar, 1995).

The presence of rather low number of seeds of *S. utahensis*, *A. cordifolios*, *K. americana* and *K. scoparia* in upper playa zone of the *A. occidentalis* community, where mature plants do not occur, indicates that their dispersal came through wind and water from adjacent areas. With a change in the salinity gradient, the pattern of plant distribution often changes rapidly because of the availability of new species in the seed bank (Ungar & Riehl, 1980). The longevity of seeds in the soil seed reserve is not known for *A. occidentalis*, but reports of long-term investigations with weed seeds indicate that storage in the soil may be possible for an extended period of time (Harrington, 1972, Kivilan & Bandurski, 1973). Seeds of *A. occidentalis* germinated readily under laboratory conditions and a few of them were able to germinate at 800 mM NaCl at the appropriate temperature regime. Studies of the seeds banks of *A. occidentalis* in the salt deserts of Nevada determined that prolonged leaching of the seedbed soils was required before

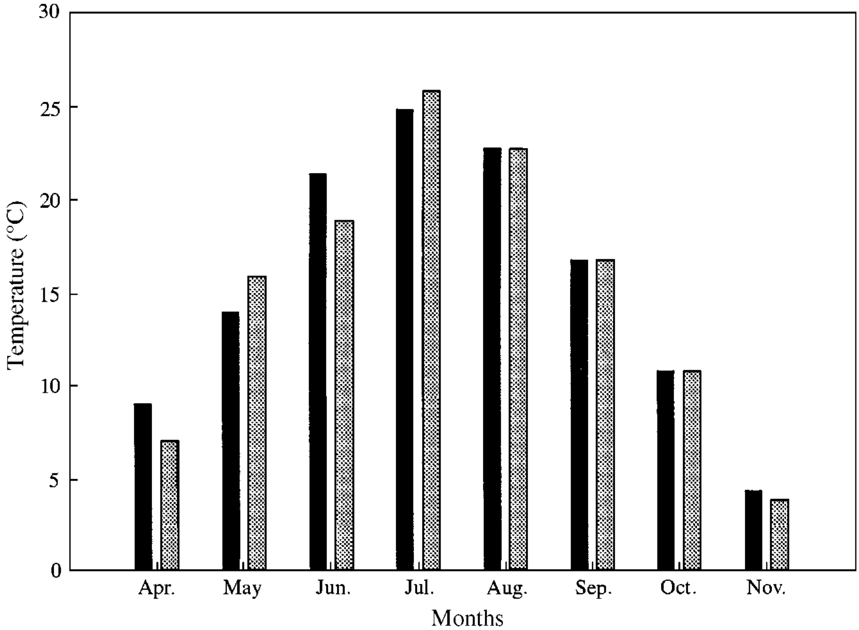

Figure 4. Monthly field temperature (°C) recorded during the years 1996–1997. 1996 (■); 1997 (▩).

natural or spiked seeds would germinate. The unique aspect of this species is that it is the most salt tolerant plant that inhabits arid environments and perhaps the most moisture stress tolerant plant in the world (Young *et al.*, 1995).

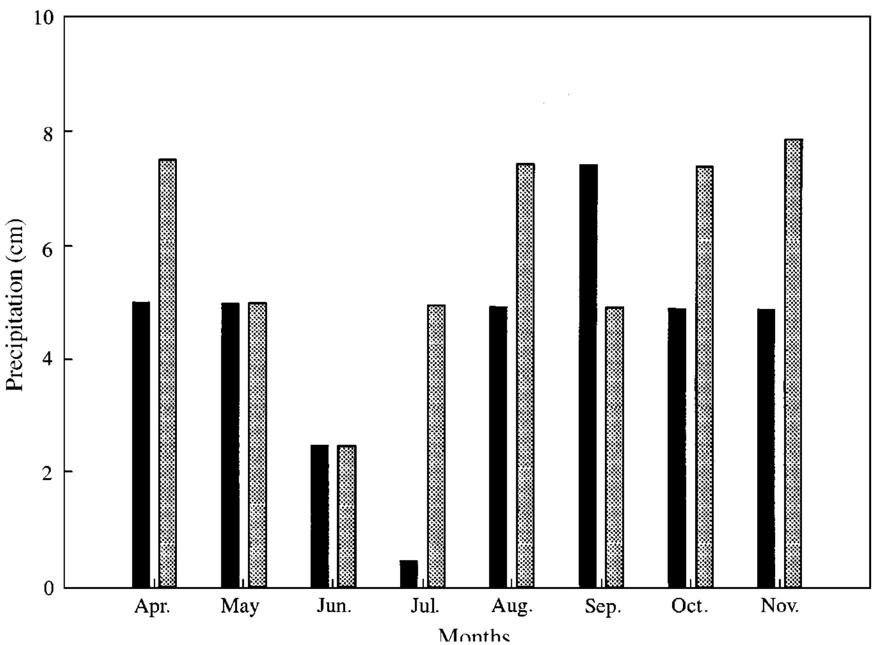

Figure 5. Monthly field precipitation (cm) recorded during the years 1996–1997. 1996 (■); 1997 (▩).

The ability of seeds to remain dormant and stored in the soil under high salinity stress has some survival value for halophytes because it permits a population of seeds to overcome extreme conditions in which mature plants could not survive. Seeds of halophytes remain dormant under highly saline conditions and germinate later when salinity stress is alleviated (Macke & Ungar, 1971; Ungar, 1995).

The upper and lower zone of the *A. occidentalis* community showed a low species diversity that is also reflected in the seed banks. The similarity between seed bank and vegetation was high during the study period in 1996 and in 1997. In hypersaline environments the existing vegetation is strongly represented in the seed bank (Ungar & Riehl, 1980; Philipupillai & Ungar, 1984). Size of the seed bank is highly variable from upper to lower marsh communities (Hopkins & Parker, 1984; Hutchings & Russell, 1989; Jefferies *et al.*, 1981). Several factors may be involved in the small seed bank size in the lower zone of *A. occidentalis*, (1) rapid germination in low stress habitat (Davy & Smith, 1988); (2) mortality of seeds in highly saline or waterlogged conditions (Darwin, 1857; Ungar, 1978); (3) removal of seeds by wind and water (Zaman & Khan, 1992). The data from the lower zone of the *A. occidentalis* community reported here consider the temporal dynamics of the seed bank. The lower zone of the community received maximum saline water from the saline soil during the rainy season in summer (May–August) and from high rains during winter (December–April). The seed bank of *A. occidentalis*, *H. umbellatum* and *S. rubra* showed seasonal and temporal variation during the growing season in both zones. The species which contributed most to the seed bank in 1996 was *A. occidentalis* contributing 11,505–86,602 seeds m^{-2}. *Holosteum umbellatum* was the species that contributed 15,155–105,960 seeds m^{-2} to the seed bank in 1997. A large proportion of their seeds undergo a dormant period during the winter and are added to the seed bank. A combination of factors including high soil salinity, low light intensities associated with seed burial and thermoperiodic conditions could induce or enforce long term dormancy in seeds (Karssen, 1980/1981, 1982). Badger & Ungar (1989) found a persistent seed bank throughout the growing season in an Ohio inland saline marsh.

The significance of seed bank in the soil in determining the establishment of plant populations in hypersaline environments is not clearly understood. Only a limited number of investigations are available concerning the nature of the seed banks in coastal and inland saline habitats. The low species diversity found in the seed bank from a number of investigations on inland salt marshes is probably because the seeds of only a few species of halophytes are adapted to tolerate the high salinity conditions that occur in salt marshes.

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