

FINAL REPORT

As Required by

THE ENDANGERED SPECIES PROGRAM

TEXAS

Grant No. E-1-10

Endangered and Threatened Species Conservation

Project WER20(60): Management of the Puzzle Sunflower (*Helianthus paradoxus*)

Prepared by: O. W. Van Auken



John Herron
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March 13, 2002

FINAL REPORT

STATE: Texas

GRANT NO: E-1-10

PROGRAM TITLE: Endangered and Threatened Species Conservation

PERIOD COVERED: September 1, 1994 - August 31, 1997

PROJECT NUMBER: WER20 (60)

PROJECT TITLE: Management of the Puzzle Sunflower (*Helianthus paradoxus*)

PROJECT OBJECTIVE: To determine the effects of ecological and land-use factors on the growth and reproduction of the puzzle sunflower (*Helianthus paradoxus*).

PROJECT COSTS (Last Segment): \$2,793.21

PREFACE: The attached manuscripts and reprints resulted from this project and are submitted in fulfillment of the Federal Aid Final Report requirement.

List of Enclosed Materials

1. Final Report. Prepared by Dr. O. W. Van Auken, March 13th, 2002.
2. Reprint: Bush, J.K. and O.W. Van Auken. 1997. The Effects of Neighbors and Grazing on the Growth of *Helianthus paradoxus*. Southwestern Naturalist 42(4):416-422.
3. Reprint: Van Auken, O.W., and J.K. Bush. 1998. Spatial Relationships of *Helianthus paradoxus* (Compositae) and Associated Salt Marsh Plants. Southwestern Naturalist 43(3):313-320.
4. Reprint: Van Auken, O.W. 2001. Germination Requirements of Seeds of *Helianthus paradoxus* (Asteraceae). Texas J. Sci. 53(2):157-170.
5. Manuscript: Van Auken, O.W. and S.C. Brown. Composition and Structure of a West Texas Salt Marsh. 36 pp.

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Date: March 13, 2002

APPROVED BY: 

Date: June 27, 2002

Neil E. Carter

Federal Aid Coordinator

FINAL REPORT

SUBMITTED TO:

THE TEXAS PARKS AND WILDLIFE DEPARTMENT

SUBMITTED BY:

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TITLE:

MANAGEMENT OF THE PUZZLE SUNFLOWER

SPECIES STUDIED:

HELIANTHUS PARADOXUS (ASTERACEAE)

THE PUZZLE OR PECOS SUNFLOWER

LOCATION OF THE STUDY AND THE TIME OF STUDY:

PROJECT WAS CARRIED OUT IN TEXAS BETWEEN 1994 AND 1997

THE PROBLEM:

Helianthus paradoxus is a federally threatened rare annual species of Asteraceae with a restricted range. There is little information available concerning its biology or ecology, consequently there is no tenable management strategy available to promote population maintenance and survival.

LITERATURE REVIEW

Helianthus paradoxus is a federally threatened rare annual species of Asteraceae with a restricted range (Bush and Van Auken 1997, McDonald 1999). There is little information available concerning its population densities or inter-annual population changes (Poole 1992, Poole and Diamond 1993, Sivinske 1996, Van Auken and Bush 1998). Helianthus paradoxus is known from two locations in west Texas, near Fort Stockton and Balmorrhea (Pecos County and Reeves County respectively) and four locations in New Mexico (McDonald 1999). Helianthus paradoxus is a recently described species (Heiser 1958, 1965), but it was originally collected in New Mexico in 1851. After the original collection, it was apparently ignored and thought extirpated from New Mexico until recently (Seiler et al. 1981). Helianthus paradoxus is apparently a stabilized hybrid species derived from H. annuus and H. petiolaris (Rieseberg et al. 1990, 1991, Rieseberg 1991, Abbott 1992, Dorado et al. 1992).

Helianthus paradoxus and the parent species are annuals and apparent diploid out-crossers. Helianthus annuus is found across the U. S. usually on heavy clay soils (Correll and Johnston 1979). Helianthus petiolaris is usually encountered on dry, sandy soils in the southwestern United States and H. paradoxus is detected on heavy, saline, waterlogged soils in a few locations in west Texas and New Mexico (Jaco 1980, Rives 1980, Veni 1991, Boghici 1997, McDonald 1999). Both parent species start flowering in late spring or early summer, depending on the location, while H. paradoxus flowers in late fall.

Helianthus paradoxus apparently has both a transient seed bank (seeds germinate the first year after dispersal) and a persistent seed bank (seeds do not germinate until more than one year after dispersal), at least in the soils of the Diamond Y Spring Preserve in west Texas (Cotéff 2000). Newly matured seeds of H. paradoxus are dormant and will not germinate (Van Auken 2001). Seeds require one to three months of after-ripening or dry storage at 4-25°C. With storage at 38°C, seed germination remains low at about 5% even after 10 months of storage. After appropriate storage, H. paradoxus seeds will germinate in 3-7 days when incubated in low light at 25°C. Incubation in the dark at 25°C resulted in low germination. During periods of very low germination (summer), seeds of H. paradoxus could be induced to germinate by scarification (nicking or removing the seed top) and applying 10-50 mg/kg gibberellic acid. Dormancy of H. paradoxus seems to prevent seed germination after dispersal (in winter) when soils are normally wet but killing frosts have a high probability of occurring. In addition, dormancy seems to prevent seed germination in summer when intermittent showers wet the soil surface but surface moisture would not remain high long enough to allow root penetration and seedling establishment.

In western Texas where H. paradoxus could have occurred, wetland habitats associated with rivers, streams and springs have almost completely disappeared because of anthropogenic lowering of the water table (Brune 1981; Poole 1992; Horne and Kahn 1997). One remaining wetland system, a salt

marsh, is associated with the desert springs found along Leon Creek in Pecos County near Fort Stockton, Texas. The species composition, abiotic and biotic gradients present in the wetlands of the Diamond Y Spring Preserve of western Texas have been largely ignored.

Inland salt marshes like those associated with the Diamond Y Spring Preserve are located in continental regions rather than coastal regions (MacNae 1968; Chapman 1974, 1977; Niering and Warren 1980; Haines and Dunn 1985; Odum 1988). They differ from coastal salt marshes because there are no tidal effects, but they are subject to high variation in soil-salt concentrations and time of desiccation, because of high annual variability in precipitation (Borchert 1971; Ungar 1974). Salt concentrations can range from <1% to >25%, composed variously of Na, K, Mg, or Ca cations and Cl, CO₃ or SO₄ anions (Flowers and Evans 1966; Ungar 1970; Burchill and Kenkel 1991).

Community composition and structure as well as the various salt gradients of many of the inland salt marshes of other parts of North America have been reported (Billings 1945; Chapman 1974; Henrickson 1977; Flowers and Evans 1966; Ungar et. al. 1969; Ungar 1970; Burchill and Kenkel 1991). Vegetational zonation, described for marine salt marshes (Chapman 1977; Niering and Warren 1980; Bertness 1991a), with the most salt tolerant species in the lowest part of the marsh, is also present in various inland salt marshes (Chapman 1974; Burchill and Kenkel 1991). This zonation is probably paralleled by one or more environmental gradients (Bertness 1991a; Bertness and Hacker

1994), and may be modified by herbivory and competition (Reinold et. al. 1975; Smith and Odum 1981; Bertness 1991a,b; Furbish and Albano 1994).

Distichlis spicata is one of the dominant species in the salt marsh of the Diamond Y Spring Preserve (Van Auken and Brown 2002). However, it is not a good competitor in coastal marshes (Bertness 1991 b), invading newly exposed areas, but being replaced by community dominants. It seems to increase with differential grazing of associated species that are better competitors in the absence of grazing (Reimond et al. 1975; Smith and Odum 1981; Furbish and Albano 1994). However, in the Diamond Y Spring Preserve salt marsh, it is not clear which species might replace D. spicata. Helianthus paradoxus and Suaeda depressa combined cover was 35% in the D. spicata grassland of the salt marsh and they are both annuals. Thus, they may be short term but not long term replacement species for D. spicata. As annuals, they both may require gaps for establishment (Bush and Van Auken 1997), which may be produced by the grazers. In addition, the removal of the associated species, the competitors, will promote the growth of H. paradoxus. Thus, the presence of large ungulate grazers may have a dual role in this salt marsh community. The grazers may reduce the biomass of other perennial grasses that could compete with or replace D. spicata, but at the same time they create gaps and promote the annual species that are currently present in this community.

The salt marsh found in the Diamond Y Spring Preserve is ecologically important because it is one of few remaining wetland spring communities in

western Texas. In addition, it is the location of one of two Texas populations of the federally threatened sunflower, Helianthus paradoxus (the Pecos or puzzle sunflower, Asteraceae, Correll and Johnston 1979; McDonald 1999). It is also the habitat for two federally listed endangered fish, Cyprinodon bovinus (Leon Springs Pupfish) and Gambusia nobilis (Pecos Gambusia) and three rare snail species (McDonald 1999).

However, there is still little information available concerning the biology and ecology of H. paradoxus or any of the associated species in this marsh system. In addition, the requirements for seedling establishment and growth of this species are still mostly unknown. Plus, the light, water, nutrient requirements, and the necessity of fungal symbionts are also unknown.

OBJECTIVES

There were six objectives of this research project as follows:

1. To determine if the size of the cattle population associated with the H. paradoxus population effected growth and reproduction of the H. paradoxus plants.
2. To determine if the time of the year that the cattle were associated with the H. paradoxus population effected growth and reproduction of the H. paradoxus plants.
3. To determine if the marsh water depth had an effect on the growth and reproduction of the H. paradoxus plants.
4. To determine if the marsh soil water salinity has an effect on the

growth and reproduction of the H. paradoxus plants.

5. To determine if the severity or type of community disturbance has an effect on the growth and reproduction of the H. paradoxus plants.
6. To determine if there are significant differences in density or cover of associated species in areas where H. paradoxus plants are found and does the composition of the community appear to have an effect on the growth and reproduction of the H. paradoxus plants.

METHODS

The methods used in the study were in general as indicated in the proposal.

1. Management of cattle populations. Eight adjacent 0.1-hectare areas were set up and haphazardly situated in the salt marsh in one of the H. paradoxus communities. Once the eight areas were selected, the treatments were randomized, so there were four open cattle access areas and four exclosures. Next, specific disturbance treatments were located in each area (Bush and Van Auken 1997).
2. Management of the time of cattle access to the H. paradoxus habitat.
First, no significant effect of cattle herbivory was detected in the first year of the study (Bush and Van Auken 1997). Second, damage to the target plants was visually estimated during every trip to the salt marsh (approximately two-month intervals). It was noted quickly (year one of the study) that no cattle damage was done to the plants until the

plants started to flower late in the growing season and the damage was not significant (inside or outside of the exclosures, Bush and Van Auken 1997). However, in all future years, the cattle were prevented access to the main population of H. paradoxus at the Diamond Y Spring preserve when the plants started to bud.

3. Management of the marsh water depth. This could not be done as was indicated in the proposal, but the depth to the water table was measured in a series of wells placed in the marsh. A series of 30 wells were dug in the marsh. Five cm outside diameter PVC pipe (one meter long) was placed in each well hole and capped. The depth of the water table was measured seasonally over the course of the project. The plant communities were compared to the depth of the water table.
4. Management of the marsh water salinity. This could not be done as was indicated in the proposal, but the soil surface salinity was measured at 20 positions related to the wells on the south side of the salt marsh. In addition, soil salinity was measured at 10 cm intervals to a depth of 50 cm at these same positions and this was done seasonally.
5. Management of the level of marsh disturbance. This was done as a comparison of the exclosures with the non-exclosure treatments.
6. Management of the marsh plant community composition. This was

done as indicated in the proposal. A series of transects was set up to cross the marsh and at five meter intervals, a 0.1 M quadrat was placed on the surface and the cover of all plants present was estimated (Van Auken and Bush 1998, Van Auken and Brown 2002).

RESULTS AND DISCUSSION

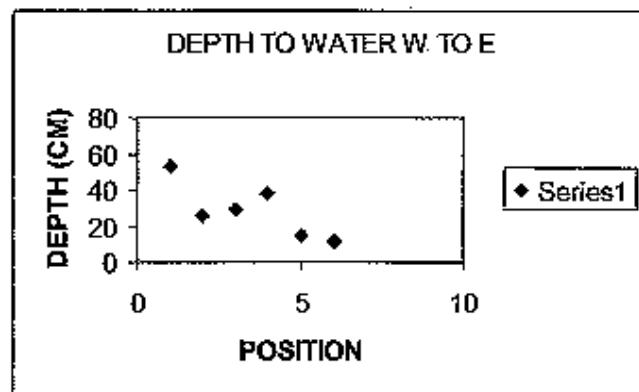
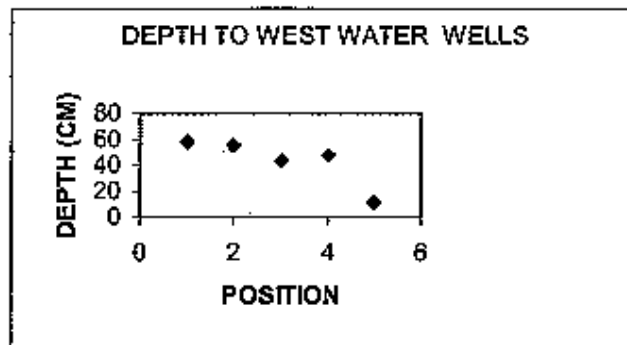
The results of the study and a discussion of the importance and implication of the study will follow. The results will follow the same order as the objectives previously presented.

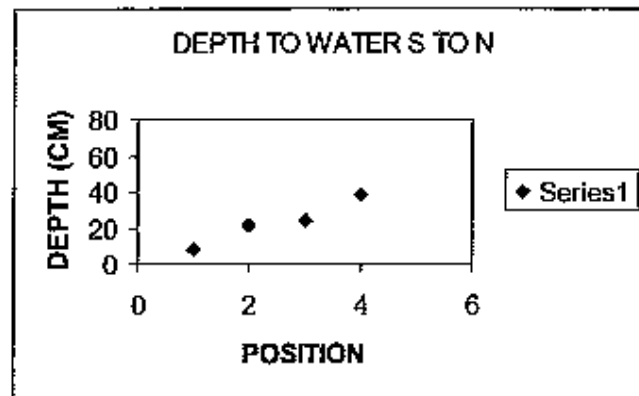
1. Management of cattle populations. The presence of grazers did not have a significant effect on H. paradoxus stem length, but did cause a 32% reduction. The number of flowers (heads) was reduced 22-54% and basal diameter was reduced 3-21% when grazers were present, but the magnitude depended on the neighbors. The presence of grazers caused a reduction in flower, leaf and stem dry mass by 49%, 39% and 25% respectively, but none of the reductions were significant. The presence of neighbors had a greater effect on all of the above parameters. Flower, leaf and stem dry mass increased by 2.38, 2.61, and 2.75 times respectively when neighbors were removed. Thus, grazers reduced all measures of H. paradoxus growth, but none significantly. However, the removal of plant neighbors increased all measures of H. paradoxus growth, but significantly (Bush and Van Auken 1997). A fire treatment was not used because preliminary

results suggested it would not be effective. All of these factors are discussed in more depth in the Bush and Van Auken 1997 publication. Significant effects of cattle grazing on the growth and reproduction of H. paradoxus have been difficult to demonstrate. Damage does occur, but may be limited to dry years and apparently to the H. paradoxus flowering season.

2. Management of the time of cattle access to the H. paradoxus habitat. No significant effect of cattle herbivory was detected in the first year of the study (Bush and Van Auken 1997). However, damage to the target plants was visually estimated during every trip to the salt marsh (approximately two-month intervals during this first year). It was noted quickly (year one of the study) that no cattle damage was done to the plants until the plants started to flower late in the growing season and the damage was not significant (inside or outside of the exclosures, Bush and Van Auken 1997). However, to err in favor of the H. paradoxus plants, and as a precaution, in all future years, the cattle were prevented access to the main population of H. paradoxus plants at the Diamond Y Spring preserve when the plants started to bud.
3. Management of the marsh water depth. Some typical profiles of the depth to the water table at the Diamond Y Spring Preserve may be found below. For the west water wells, position five is in the marsh center, near the drainage, and the water table is approximately 5 cm

from the surface. Position one is upland and the water table is more than 60 cm from the surface. In the second plot, position one is near the center of the drainage and the water table is about 5 cm from the surface and proceeding to the north (away from the drainage) the depth to the water table becomes greater. In the third plot, the depth to the water table decreases generally from west to east.





The above plots are trends demonstrated seasonally and annually.

Interestingly, the water table is almost always near the surface toward the eastern part of the marsh, and the sunflower plants are always smallest here. Secondly, the water is always near the surface in the center of the marsh near the drainage and there are usually no sunflowers here or they are quite small. The cause of these trends could be water content, depth, soil oxygen levels, or some other unidentified factor.

4. Management of the marsh water salinity. This could not be done as was indicated in the proposal, but the soil surface salinity was measured at 20 positions related to the wells on the south side of the salt marsh. In addition, soil salinity was measured at 10 cm intervals to a depth of 50 cm at these same positions and this was done seasonally. Salinity is reported between zero and approximately 40 ppt (parts per thousand). Lowest salinity levels were in the upland areas and highest values were in the *Distichlis spicata*/Helianthus

paradoxus communities. Low values were also associated with the Scirpus olneyi (S. americana) community near the drainage. There was considerable variability in the soil salt levels in these marsh communities (Van Auken and Bush 1998). In addition, H. paradoxus is more sensitive to NaCl compared to Na₂SO₄. Twenty ppt of NaCl caused 100% mortality of H. paradoxus, while 16-24 ppt of Na₂SO₄ reduced growth by about 30% (Mendez 2001). These results suggest that H. paradoxus is probably well adapted to grow in elevated levels of Na₂SO₄.

5. Management of the level of marsh disturbance. This was done as a comparison of the exclosures with the non-exclosure treatments. There were no significant differences between the grazing/disturbance treatment and the non-grazing/non-disturbance treatment. Distichlis spicata is found in many of the areas of this salt marsh system (Van Auken and Bush 1998). It is not a good competitor in coastal marshes and is probably not a good competitor in this inland marsh either (Bertness 1991b). It invades newly exposed areas, but is later replaced by community dominants. It seems to increase with differential grazing of associated species that are better competitors in the absence of grazing (Reimond et al. 1975; Smith and Odum 1981; Furbish and Albano 1994). However, in the Diamond Y Spring Preserve salt marsh, it is not clear which species

might replace D. spicata. Helianthus paradoxus and Suaeda depressa combined cover was 35% in the D. spicata grassland of the salt marsh and they are both annuals. Thus, they may be short term but not long term replacement species for D. spicata. As annuals, they both may require gaps for establishment (Bush and Van Auken 1997), which may be produced by the grazers. Thus, the presence of large ungulate grazers may have a dual role in this salt marsh community. The grazers may reduce the biomass of other perennial grasses that could compete with or replace D. spicata, but at the same time they create gaps and promote the annual species that are currently present in this community. Thus, the large ungulates may be important in this system early to create gaps, but later, consume the flower heads of Helianthus paradoxus possibly reducing their reproductive capacity.

6. Management of the marsh plant community composition. This was done as indicated in the proposal. A series of transects was set up to cross the marsh and at five meter intervals, a 0.1 M quadrat was placed on the surface and the cover of all plants present was estimated (Van Auken and Bush 1998, Van Auken and Brown 2002). The distribution and delineation of the major species found in this marsh community are presented in two publications. Van Auken and Bush (1998) show the distribution and cover of Sporobolus airoides, Distichlis spicata, Scirpus olneyi (ameracana) and Helianthus

paradoxus. Van Auken and Brown (2002) show the distribution and cover of the minor species. Comparisons with other marsh characteristics have not been as illustrative and are not presented.

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GERMINATION REQUIREMENTS OF SEEDS
OF *HELIANTHUS PARADOXUS* (ASTERACEAE)

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Abstract.—This study examined the germination requirements of the seeds of the rare annual *Helianthus paradoxus* (puzzle sunflower), which is known to occur in only two locations in west Texas and a few locations in New Mexico. Flowering and seed (achene) maturation of *H. paradoxus* occurs in late fall (October and November) and seeds are released from the flower head shortly after maturation. Newly matured seeds of *H. paradoxus* are dormant and will not germinate. Seeds require one to three months of after-ripening or dry storage at 4-25°C. With storage at 38°C, seed germination remains low at about 5% even after 10 months of storage. After appropriate storage, *H. paradoxus* seeds will germinate in 3-7 days when incubated in low light at 25°C. Incubation in the dark at 25°C resulted in low germination. During periods of very low germination (summer), seeds of *H. paradoxus* could be induced to germinate by scarification (nicking or removing the seed top) and applying 10-50 mg/kg gibberellic acid. Dormancy of *H. paradoxus* seems to prevent seed germination after dispersal (in winter) when soils are normally wet but killing frosts have a high probability of occurring. In addition, dormancy seems to prevent seed germination in summer when intermittent showers wet the soil surface but, surface moisture would not remain high long enough to allow root penetration and seedling establishment.

In areas with high climatic variability, many annual species have seed dormancy to prevent premature seed germination during periods with rainfall or temperature conditions that are unsatisfactory for seedling growth and survival. Low and uncertain rainfall in central and southwestern Texas as well as winters with killing frosts qualifies these areas as having relatively harsh environmental conditions (Arbinger et al. 1976, Gale Research 1992, National Climatic Data Center 2000). Curiously, some species found in this region produce seeds that display dormancy while seeds of other species are not dormant. *Nassella leucotricha* (Texas winter grass), a perennial Poaceae, produces seeds that are dormant and require 3-6 months at 25-35°C plus scarification before germination of most seeds will occur (Van Auken 1997). Several central Texas winter annual Asteraceae produce seeds that are dormant when produced, while seeds of *Pyrrhopappus multicaulis* (Texas dandelion) another winter annual lack dormancy (Baskin et al. 1992; Elliott 1999). A number of perennial Asteraceae and Rosaceae from central or western Texas, including *Aster ericoides*, *Baccharis neglecta*, *Brickellia dentata*, *Eupatorium havayense*, *Gymnosperma glutinosum* and

paradoxus apparently has both a transient seed bank (seeds germinate the first year after dispersal) and a persistent seed bank (seeds do not germinate until more than one year after dispersal), at least in the soils of the Diamond Y Spring Preserve in west Texas (Cotéff 2000). However, the requirements for seed germination, seedling establishment and growth for this species are unknown. The light, water, nutrient requirements, salt tolerance and the necessity of fungal symbionts are also unknown.

The purpose of this study was to investigate germination requirements of seeds of *H. paradoxus*. The time and temperature requirements for germination or breaking dormancy, the light requirements for breaking dormancy, scarification and the use of various concentrations of gibberellic acid to break dormancy were examined.

MATERIALS AND METHODS

Seeds (achenes) of *Helianthus paradoxus* were collected in October of each year (1995-1998) from plants on the Diamond Y Spring Preserve of the Nature Conservancy of Texas, approximately 13 km north of Fort Stockton, Texas (Pecos County, 31°00.54'N, 102°55.49'W). Prior to use in any experiments, seeds were separated from chafe. Seeds weighed 3.0 ± 0.5 mg (\pm one standard deviation); were almond shaped and black or brown mottled with black, 3.42 ± 0.33 mm long, 1.45 ± 0.22 mm wide and 0.98 ± 0.14 mm thick. All seeds used in all experiments were selected for fullness by inspection and for any insect damage. If they were not full or had insect damage, they were discarded. All seeds were initially stored dry at 25°C in sealed plastic bags for various times prior to experimental use. Seeds were usually used the next spring after they were collected. Aliquots of seeds that were used in the temperature-time study were placed in sealed plastic bags and placed in a refrigerator (4°C), a storage cabinet (25°C) or an incubator (38°C). Temperatures approximated mean minimum winter temperatures (Dec. and Jan.), mean maximum spring and fall temperatures (April and Oct.) and mean maximum summer temperatures (June-Aug.) for the Fort Stockton area (Wallis 1977). Seeds were kept in the dark at these temperatures during the study. At various times (0-13 months), separate bags of seeds were picked randomly and removed from the temperature treatments. Seeds were counted, placed in Petri dishes, moistened with deionized water and then incubated at 25°C for 15 days.

For germination studies, 25 intact, full seeds were placed in a 9 cm

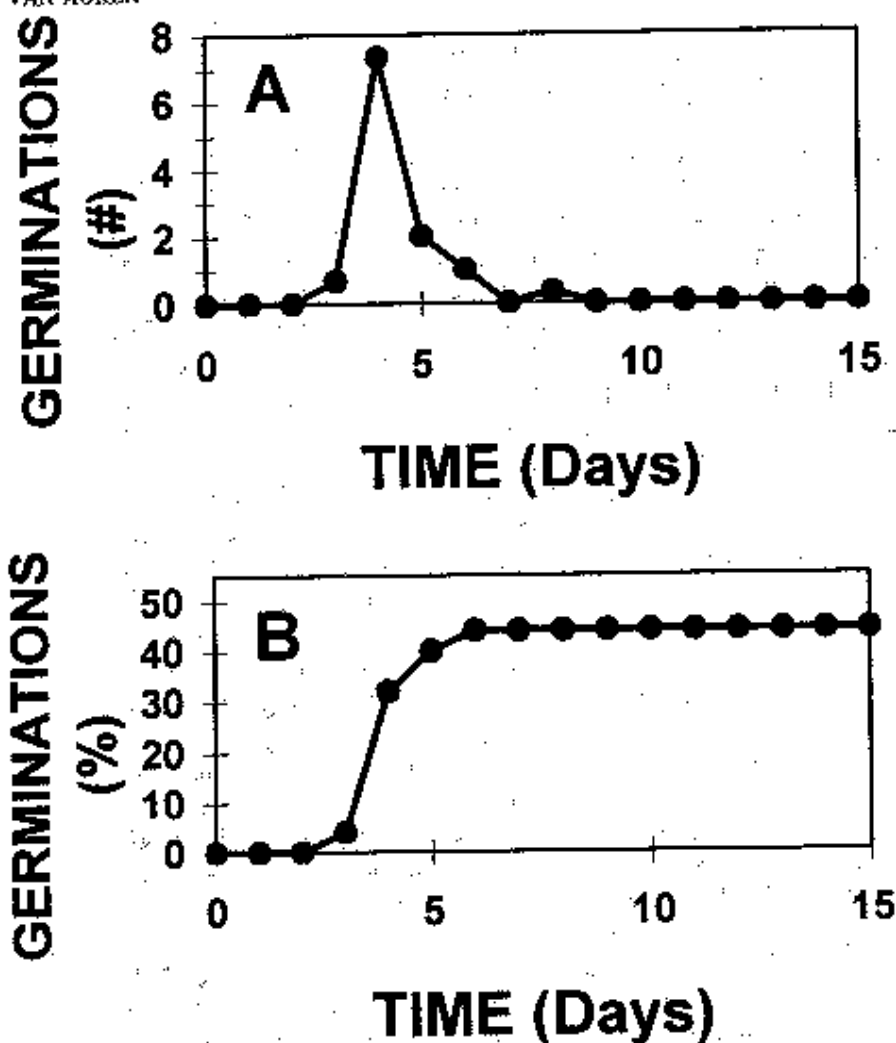


Figure 1. The temporal sequence of *Helianthus paradoxus* seed (achene) germination. Mean number of seed germinations of seed stored dry for 120 days at 25°C is included (a). After 120 days of dry storage, the seeds were checked for intactness, placed on moistened filter paper in Petri dishes and incubated at 25°C in low light for 15 days. Mean cumulative percent germination of *Helianthus paradoxus* seeds stored dry for 120 days at 25°C and then incubated at 25°C in low light is also presented (b). A one-way analysis of variation indicated there was a significant difference in the number of seeds germinating on different days ($F = 54.7$, $P \leq 0.0001$). The minimum significant difference using the Scheffé multiple comparison tests was 1.9 germinations.

$P \leq 0.0001$). There were no germinations until the third day of incubation, with the highest number of seeds germinating on the fourth day of incubation, followed by a decline to zero on day seven. When the mean cumulative percent germination is examined (Fig. 1b), it is clear that

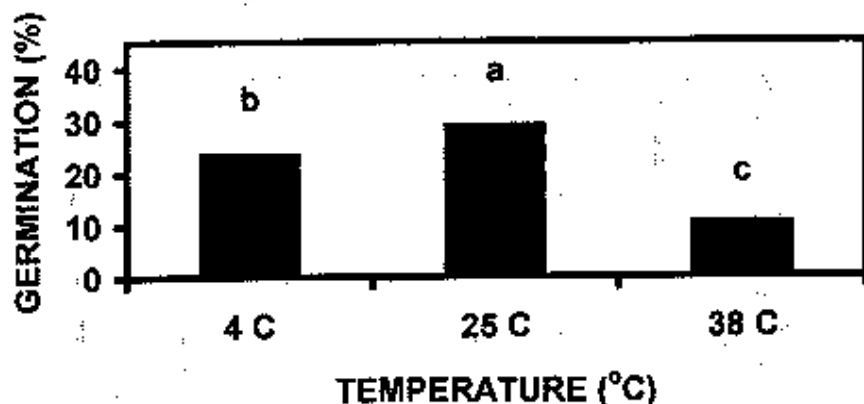


Figure 2. The effect of storage temperature on the mean percent germination of seeds of *Helianthus paradoxus*. This plot presents the effects of storage temperature (main effect) from the temperature-storage time factorial experiment ($F=275.1$, $P\leq 0.0001$). Seeds were stored dry at 4°C, 25°C or 38°C from day zero (Oct. 95) to day 378 (Nov. 96) and the results were pooled over all of the days tested for each temperature. Means with the same letter are not significantly different (Scheffé multiple comparison test, $P<0.05$).

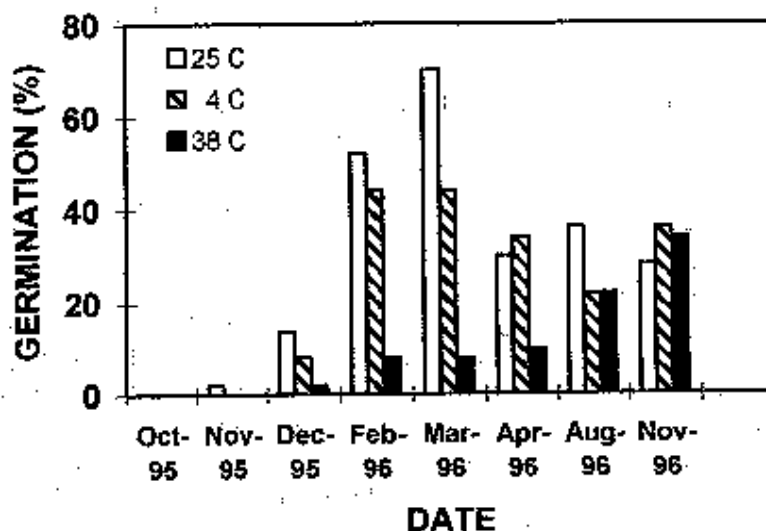


Figure 3. The effect of storage temperature and storage time on the mean percent germination of seeds of *Helianthus paradoxus*. Seeds were stored dry at 4°C, 25°C or 38°C from zero days (Oct. 95) up to 378 days (Nov. 96). At the indicated storage time, seeds were removed from the storage temperature, checked for intactness, moistened on filter paper in Petri dishes and incubated at 25°C in low light for 15 days. The overall two-way ANOVA indicated significant differences ($F=148.1$, $P\leq 0.0001$), and there was a significant temperature effect ($F=275.1$, $P\leq 0.0001$), a significant storage time effect ($F=290.4$, $P\leq 0.0001$), and a significant interaction ($F=58.9$, $P\leq 0.0001$). The minimum significant difference using the Scheffé multiple comparison test was 5.2%.

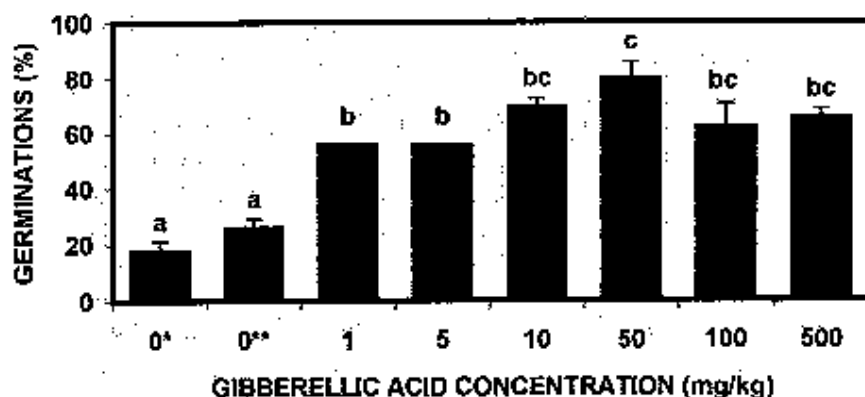


Figure 5. The effect of gibberellic acid concentration (mg/kg) and scarification on the mean percent germination of *Helianthus paradoxus* seeds (achenes). Seeds were collected on October 25, 1998 and stored dry for 681 days at 25°C in low light. On August 16, 2000, the seeds were checked for fullness and insect damage, placed on filter paper in Petri dishes, moistened with deionized water or the appropriate concentration of gibberellic acid and incubated at 25°C in low light for 15 days. The line above each bar is plus one standard deviation. A one-way analysis of variance indicated significant differences among treatment means ($F=54.2$, $P\leq 0.0001$). Means with the same letter at the top of a bar are not significantly different (Scheffé multiple comparison test, $P>0.05$). In the zero* treatment, the seeds were intact and no gibberellic acid was added. In the zero** treatment, the tip of the seed was removed with a sharp razor (scarification) but no gibberellic acid was added. In all other treatments, the tip on the seed was removed.

factors would be physical or mechanical barriers or chemicals present in the plant or seed coat that prevent germination. Endogenous factors that prevent germination are physiological or morphological or a combination of the two (Nikolaeva 1977; Baskin & Baskin 1998). They would include hormone levels that regulate growth, possibly light and temperature requirements, or other factors, all of which must be overcome before germination can be initiated. All of the above factors or conditions usually cause initial or primary dormancy (Harper 1977; Begon et al. 1986; Silvertown 1987). When seeds are induced into dormancy by low light levels or burial in the soil, conditions that would reduce seedling survival, this is called secondary dormancy (Wesson & Wareing 1969; Hazebroek & Metzger 1990).

New, mature seeds (achenes) of *Helianthus paradoxus* will not germinate and thus exhibit primary dormancy (Baskin & Baskin 1985; Begon

The second component of this window of opportunity would relate to the growth pattern of *H. paradoxus* and the other major species in this salt marsh. *Helianthus paradoxus* is a C_3 species and seeds germinate early in the growing season and growth can occur during the early season cool weather, rather than summer. However, the main period of growth seems to be in cooler early fall months, late in the growing season. The two main associated species are C_4 grasses, *Distichlis spicata* (saltgrass) and *Sporobolus airoides* (alkali sacaton), that have their main growth period in summer, the hottest time of year (Gould 1975; Van Auken & Bush 1998). The C_4 grasses are assumed to have a growth advantage over most C_3 species in lower latitudes where temperatures and irradiances are higher (Doliner & Joliffe 1979; Waller & Lewis 1979). Thus, the growth and flowering cycle of *H. paradoxus* would be out of phase with its main associated species and potential competitors. Consequently, these three species seem to temporally partition the environment where they grow on the Diamond Y Spring Preserve of the Nature Conservancy in west Texas. *Helianthus paradoxus* seems to grow best during the early and late part of the growing season while *D. spicata* and *S. airoides* grow best in between, during the hot summer.

The third component of this window of opportunity for seed germination and success for *H. paradoxus* would relate to summer temperatures. Summers are hot and dry in the Fort Stockton area of Pecos County in west Texas. Mean annual July temperature is 35.5°C (National Climatic Data Center 2000). During this study only 10-20% of the *H. paradoxus* seed stored at 38°C would germinate unless treated with gibberellic acid. If the soil surface in the salt marsh at the Diamond Y Spring Preserve were dry, that number would be further reduced. Consequently, the seed dormancy found for *H. paradoxus* seems to be advantageous to this species, maximizing germination at the time of year when environmental conditions are best for successful growth, reproduction and survival, while it is minimized during other times of the year.

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THE EFFECTS OF NEIGHBORS AND GRAZING ON THE GROWTH OF
HELIANTHUS PARADOXUS

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ABSTRACT—*Helianthus paradoxus* (puzzle sunflower) is a rare species of annual sunflower (Compositae) that grows in inland saline marshes in four locations world-wide. One location is the Diamond-Y Springs Preserve, north of Fort Stockton, Texas (31°10'N, 102°45'W) and three locations are in central and southeastern New Mexico. The importance of neighbors (competitors) and the impact of grazing on *H. paradoxus* are unknown. In this experiment, the effects of neighbor removal (clipping and herbiciding) on *Helianthus paradoxus* were evaluated within salt marsh plots that were grazed or ungrazed by large ungulates. Analysis of variance indicated significant effects of neighbors. The presence of grazers did not have a significant effect on plant stem length, but did cause a 32% reduction. The number of flowers (heads) was reduced 22 to 54% and basal diameter was reduced 3 to 21% when grazers were present, but the magnitude was dependent on the neighbors. Overall, with neighbors present, the mean number of flowers was reduced 57% and basal diameter was reduced 39% compared to removal. The presence of grazers caused a reduction in flower, leaf and stem dry mass by 49%, 39% and 25% respectively. Flower, leaf and stem dry mass were all significantly affected by the presence of neighbors and increased 2.38, 2.61 and 2.75 times respectively with neighbor removal. Thus, grazing by large ungulates will reduce various indicators of *Helianthus paradoxus* growth and reproduction, but the presence of neighbors caused the greatest reduction.

The genus *Helianthus* consists of approximately 67 species of annual and perennial herbs made difficult taxonomically by hybridization among its members (Correll and Johnston, 1979). Heiser (1965) divided the genus into four sections based on four distinct phylogenetic lines—1) annual and tap rooted perennials, 2) North American perennials confined to eastern and central North America, with the exception of *H. californicus* and *H. nuttallii*, 3) North American perennials mostly limited to the southwestern United States and northern Mexico, and 4) South American perennials.

Helianthus paradoxus appears to be a relatively new annual species based on distinct morphological characteristics which were first described in 1958 (Heiser, 1958). Subsequently, molecular tests indicated that *H. paradoxus* has combined rDNA (ribosomal) repeat types of the proposed parent species *H. annuus* (common sunflower) and *H. petiolaris* (plains sunflower, Rieseberg et al., 1990, 1991; Rieseberg, 1991). In addition, it has the chloroplast genome of *H. annuus* (Dorado et al., 1992),

which confirms that *H. paradoxus* was derived through hybridization (Rieseberg et al., 1990; Abbott, 1992).

Helianthus paradoxus and the parent species, *H. annuus* and *H. petiolaris*, are annuals belonging to the same section of the genus (*Helianthus*), are obligate out-crossers, and have the same chromosome number ($n = 17$). In spite of these similarities, phenological, morphological, and habitat characteristics are different, making identification relatively easy. *Helianthus annuus* and *H. petiolaris* flower in late spring and summer, while *H. paradoxus* flowers in late fall. Morphologically, *H. paradoxus* is distinguished from the parent species by having smaller heads, nearly glabrous stems, longer and narrower leaves, narrower phyllaries, and fewer ray flowers (Heiser, 1958, 1965, 1981; Heiser et al., 1969; Correll and Johnston, 1979). All three species differ in their habitat preference, with *H. annuus* occurring throughout most of North America on disturbed, heavy soils, that are wet in the spring but dry out by mid-summer. *Helianthus petiolaris* occurs in western North America on sandy soils; and *H.*

TABLE 1.—*P* values from nested analyses of variances of stem length, number of flowers per plant (heads), basal diameter, flower dry mass (heads), leaf dry mass and stem dry mass with grazing (+/- exclosures) as the main effect, with neighbor effects (controls, clipping, and herbicide treatment of competitors) nested in the grazing treatments. *P* values for blocks were all significant, but are not included in the table.

	Stem length	Flowers	Basal diameter	Flower dry mass	Leaf dry mass	Stem dry mass
Grazing	0.7549	0.4676	0.8405	0.1278	0.4872	0.7334
Neighbors	0.0015	0.0008	0.0001	0.0065	0.0001	0.0001

(32%) than the control treatment (Fig. 1a). There were no significant differences in the number of flowers (heads) per plant and basal diameter between grazing treatments, but the neighbor treatment was significant (Table 1). Further analysis of variance indicated that within the grazed treatment, number of flowers and basal diameter were significantly higher when competitors or neighbors were herbicided, compared to the control and clipping treatments, which were not significantly different from one another (Fig. 1b, c). The number of flowers in the grazed herbicide treatment was 2.65 times higher than the controls (Fig. 1b). The number of flowers in the ungrazed herbicide treatment was 2.11 times higher than the controls, but this difference was not significant. There were 22 to 54% fewer flowers in the grazed versus the ungrazed treatment, but again, the difference was not significant. The differences in basal diameter between the ungrazed and grazed plots increased from 0.19 mm to 1.70 mm, with the greatest differences in the clipping treatment (Fig. 1c). In addition, the basal diameter of *H. paradoxus* plants in all of the herbicided plots was 1.58 times greater than the controls.

Analysis of variance of flower dry mass indicated a significant difference between the neighbor treatments (Table 1). Analysis of variance of flower dry mass within the ungrazed treatments showed no significant differences among the competitor treatments, although the *H. paradoxus* plants without neighbors were 2.17 times larger than the control plants. Within the grazed treatments, the plants with neighbors herbicided were significantly larger than those in the controls (Fig. 2a). Plants in the herbicide treatment were 3.01 times larger than the controls. The greatest difference between ungrazed and grazed treatments was a 58% reduction in dry mass in the grazed treatment

when the neighbors were not altered (control), with differences of approximately 50% reduction between the ungrazed and grazed treatments when the neighbors were clipped or removed with herbicide (Fig. 2a).

Analysis of variance of leaf and stem dry mass indicated no significant differences in the grazing treatments, but significant neighbor effects (Table 1). Leaf and stem dry mass in the ungrazed plots, when the competitors were herbicided, was significantly greater than the control by 2.25 and 2.17 times respectively, but was not significantly different from the clipping treatment (Fig. 2b, c). There were also no significant differences between the control and the clipping treatment. Leaf and stem dry mass in the grazed plots, when the competitors were herbicided were 3.35 and 3.86 times greater than the controls respectively. The herbicide treatment was significantly different than the control and the clipping treatment, which were not significantly different from one another (Fig. 2b, c). There was approximately a 50% reduction in leaf and stem dry mass between the grazed and ungrazed plots in the control and clipping treatments (Fig. 2b, c). Leaf dry mass in the grazed, herbicided treatment was reduced approximately 22% compared to the ungrazed, herbicided treatment (Fig. 2b). Stem dry mass was reduced 3.6% compared to the ungrazed, herbicided treatment (Fig. 2c).

DISCUSSION—*Helianthus paradoxus* is a rare species that appears to have a restricted range, but can be locally abundant. However, there is little information available concerning population densities or population fluctuations (Poole, 1992; Van Auken and Bush, In Press). *Helianthus paradoxus* seems to be restricted to inland salt marshes with soil surface salt levels of about ten parts per thousand (Chapman,

1974; Poole, 1992). The salts present where *H. paradoxus* is found are mainly Na, K, Ca, and $MgSO_4$, rather than Cl (Veni, 1991).

Effects of grazing and the presence of neighbors or competitors on the growth and reproductive success of *H. paradoxus* have not been previously reported. However, grazing effects on many other species have been studied. Grazers may affect plants by causing damage to leaves, stems, roots, fruits, seeds or the whole plant (Harper, 1977; Belsky, 1986; Louda et al., 1990). Most damage by herbivores occurs on young, expanding tissues (Coley and Aide, 1991; Aide, 1993). Thus, herbivores may influence the outcome of species interactions by altering a plant's ability to obtain necessary resources or by selectively removing a plant as a competitor (Harper, 1977; Crawley, 1983; Fowler, 1986; Louda et al., 1990). At the population level, damage may cause changes in plant abundance by modifying fecundity, potential regrowth, and also mortality (Harper, 1977; McNaughton, 1983; Sih et al., 1985).

Seedlings of many species do not grow well in the presence of other species, especially grasses, but if the grasses are grazed or clipped to simulate grazing, some plants will grow as if the grasses were not present. This is especially true for woody plants (Glendening and Paulsen, 1955; Van Auken and Bush, 1989, 1990; Bush and Van Auken, 1990). If a herbivore continues to periodically consume a plant or plant parts, plant stature remains small or density will remain low or static, but with the removal of the consumer, plant size and density will increase (Friedel, 1985).

The growth response of two species, if both species are consumed equally or differentially, is not always easily determined (Taylor et al., 1997). Grazing theory would predict that the species grazed most would show the greatest negative effect (Belsky, 1986; Painter and Belsky, 1993). However, considerable controversy exists over the issue of herbivory causing negative effects, no effects, or positive effects on the plant that is eaten (Dyer et al., 1993; McNaughton, 1993; Noy-Meir, 1993; Painter and Belsky, 1993; Van Auken, 1994). Much of this controversy seems to be caused by investigators only measuring the aboveground plant response and then over a relatively short time, and not measuring the total plant response to herbivory. If above- and belowground dry mass

is measured in treatments with and without grazing, the source of the carbon for most of the aboveground regrowth after grazing is the belowground plant mass (Van Auken and Bush, 1989, 1997; Bush and Van Auken, 1995). Therefore, with continual or periodic grazing, root biomass is reduced, reducing the plants ability to acquire belowground resources.

During the current studies with *H. paradoxus*, there were no significant differences between plants within and outside of the exclosures. This experiment was completed during a relatively wet year, and perhaps there was enough forage available for the herbivores. In subsequent years during times of drought, we have observed severe herbivory of *H. paradoxus* and extreme differences in the stem length and number of flowers (unpublished). Therefore, the effects of large grazers of *H. paradoxus* may be dependent on the availability of moisture and its effects on the grazers preferred forage plants.

However, the presence of neighbors caused large reductions in *H. paradoxus* vegetative and reproductive parts. The greatest reductions were seen when comparing ungrazed treatments where the neighbors were removed (largest plants), with the grazed treatment where the neighbors were not manipulated (smallest plants, controls). This certainly suggests that the cattle consume some of the *H. paradoxus* dry mass. It also demonstrates that *H. paradoxus* is reduced by the presence of neighbors and may require vegetation gaps for establishment. This is not unusual for annual species and suggests that large herbivores may play a dual role in the life cycle of *H. paradoxus*. They may be important in reducing neighbor dry mass, which would promote the sunflowers, but they appear to consume *H. paradoxus* biomass which is detrimental to the sunflowers. The direct effect of the grazers on the sunflowers may only occur in certain years, perhaps dry ones, and as such is difficult to detect.

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SPATIAL RELATIONSHIPS OF *HELIANTHUS PARADOXUS* (COMPOSITAE)
AND ASSOCIATED SALT MARSH PLANTS

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ABSTRACT—*Helianthus paradoxus* (the puzzle sunflower, Compositae) is a rare species, only found along Leon Creek in the Diamond Y Springs Preserve, in closely associated areas near Fort Stockton, Texas (31°10'N, 102°45'W), and in several locations in central and eastern New Mexico. In the Diamond Y Springs Preserve, it is found in specific habitats and exhibits high spatial fluctuations in density and cover. It does not occur in *Larrea tridentata* (creosote bush) communities on shallow upland soils or in *Prosopis glandulosa* (honey mesquite) communities on deep upland soils. As one descends slightly in elevation from dry *P. glandulosa* upland communities into the salt marsh, a *Sporobolus airoides* (alkali sacaton) grassland is encountered. The next major community is a *Distichlis spicata* (saltgrass) grassland. *Helianthus paradoxus* usually is found with various cover values ranging from 0 to 70% or at densities from 0 to 23 plants/0.1 m², associated with *D. spicata*. *Helianthus paradoxus* usually is not found in the deepest, saturated soils in the lowest part of the salt marsh associated with the drainage where *Scirpus olneyi* (bulrush) typically is the dominant species.

RESUMEN—*Helianthus paradoxus* (girasol de perplejidad, Compositae) es una especie rara que se encuentra solamente a lo largo del riachuelo Leon Creek en la reserva Diamond Y Springs Preserve, en áreas muy asociadas, próximas a Fort Stockton, Texas (31°10'N, 102°45'O), y en varias localidades del centro y del este de Nuevo México. En la reserva Diamond Y Springs Preserve se encuentra en hábitat específicos que exhiben amplias fluctuaciones espaciales en densidad y cubierta. Esta especie no se encuentra en comunidades *Larrea tridentata* (mata de creosote) de tierras altas y de poca profundidad ni en comunidades *Prosopis glandulosa* (mesquite de miel) de tierras altas y profundas. Al bajar un poco en elevación, donde existen las altas y secas comunidades *P. glandulosa*, uno llega a un pantano salado, donde se encuentra el pastizal de *Sporobolus airoides* (sacate álcali). La siguiente comunidad mayor, es pastizal de *Distichlis spicata* (pasto salado). Usualmente, se encuentra *H. paradoxus* con diferentes valores de cubiertas desde 0 hasta 70% o de densidades del 0 al 23 plantas/0.1 m²; asociada con *D. spicata*. Por el contrario *H. paradoxus* no se encuentra en las tierras más profundas y saturadas en las partes bajas del pantano salado asociadas con el drenaje donde se encuentra *Scirpus olneyi* (junco), la especie típicamente dominante.

Rare species may have one of several distribution patterns. A species can be geographically widespread and locally rare, it can have a restricted range and be locally abundant, or it can be restricted geographically and locally rare (Stebbins, 1942; Drury, 1974, 1980; Fiedler, 1986; Van Auker, 1997). *Helianthus paradoxus* (the puzzle sunflower, Compositae), a rare species, appears to have a restricted range and may be locally abundant, but there is little information available concerning population densities (Poole, 1992; Poole and Diamond, 1993). *Helianthus paradoxus* is known from one location in west Texas near Fort Stockton in Pecos County (31°10'N, 102°45'W). It is re-

ported also from two locations in eastern New Mexico, near Santa Rosa and Roswell (Guadalupe and Chaves counties, respectively) in the Pecos River drainage and one site in central New Mexico near Grants in the Rio San Jose drainage (Valencia and Cibola counties, Sivin-ski, 1996).

Helianthus paradoxus is a recently described species (Heiser, 1958, 1965; Heiser et al., 1969), but was originally collected in New Mexico in 1851. After the original collection, it was ignored apparently and thought extirpated from New Mexico until recently (Seiler et al., 1981). The specimen used in the species description was from the west Texas population.

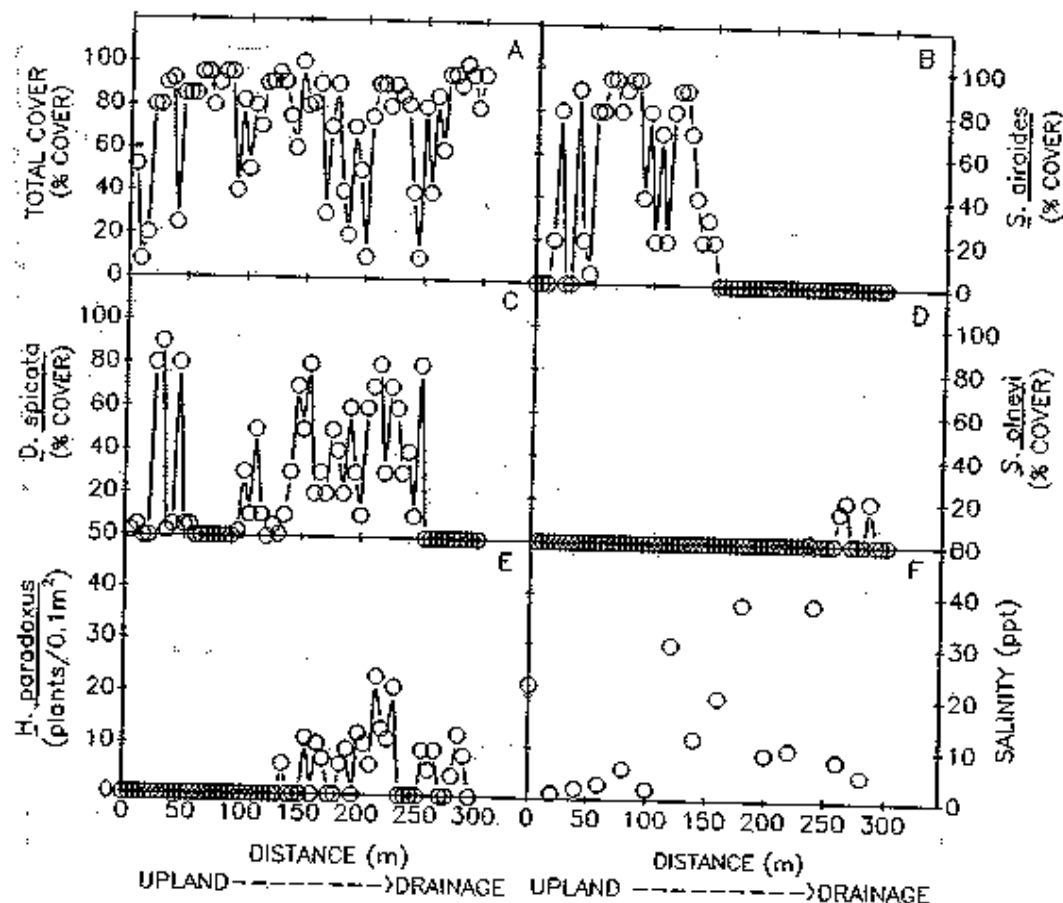


FIG. 1.—Total cover (%) (A), *Sporobolus airoides* cover (%) (B), *Distichlis spicata* cover (%) (C), *Scirpus olneyi* cover (%) (D), *Helianthus paradoxus* density (plants/0.1 m²) (E), and soil salinity (parts per thousand) (F), as a function of distance (m) from the *Prosopis glandulosa* upland vegetation (zero) to the creek edge (drainage). Each plant sampling point was 5 m apart and each soil sample 20 m apart.

white with lowest cover or density to black with highest cover. Plots with as many as 24 cover or density classes were examined, but the best visual presentation was found when only four classes were used. The four classes were 0, 1 to 34, 34 to 67, and 67 to 100% cover for *S. airoides*, *D. spicata*, and *S. olneyi*. Three density classes were used for *H. paradoxus* including 0, 1 to 8, 8 to 15, and 15 to 23 plants/0.1 m².

RESULTS—The single example transect from the upland *Prosopis* savanna to the lowest part of the marsh demonstrated that species generally occurred in specific locations in the salt marsh. Total cover along this transect was approximately 80%, with a few open spaces, as noted by the lower cover values (Fig. 1a). *Sporobolus airoides* (alkali sacaton) was found main-

ly along the first part of the transect, in the area with highest elevation. It was found in the first 150 m in this example transect, with cover values from 0 to almost 100% (Fig. 1b). *Sporobolus airoides* and *D. spicata* (saltgrass) were usually mutually exclusive. *Distichlis spicata*, for the most part, had low cover in the first 150 m of the transect, then increased to 60 to 80% in the next 100 m of the transect (Fig. 1c). *Scirpus olneyi* (bulrush) was always in the drainage, in the lowest part of the marsh (Fig. 1d). It was usually with *Sporobolus texanum* (data not shown) and sometimes with *H. paradoxus*. In this example transect, *H. paradoxus* was located in the mid-part of the transect (Fig. 1e). It was not in the first 130 m of the transect with *S. airoides* and it had a low density along the last part of

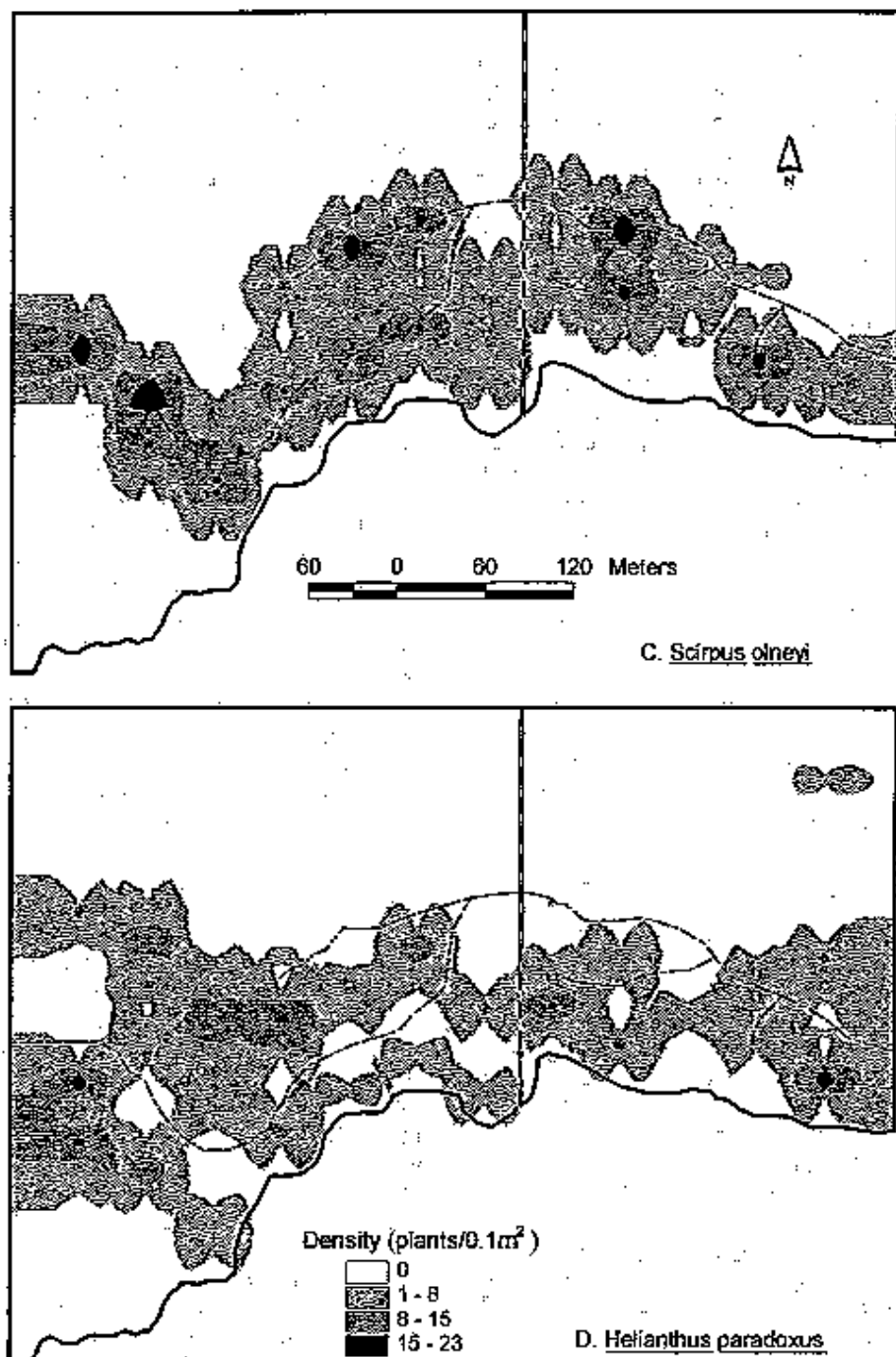


FIG. 2—Continued.

growth as reported for other species (Webb and Mendelsohn, 1996).

Helianthus paradoxus was found with *Distichlis spicata*, but the relationship of the two species was not clear. *Distichlis spicata* is not a good competitor in coastal marshes (Bertness, 1991b), invading newly exposed areas, but being replaced by community dominants. It seems to increase with differential grazing of associated species that are better competitors in the absence of grazing (Reinold et al., 1975; Smith and Odum, 1981; Furbish and Albano, 1994). In addition, *H. paradoxus* may require gaps for establishment (Bush and Van Auken, 1997), which may be produced by the grazers.

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RUNNING HEAD: INLAND SALT MARSH COMMUNITIES

COMPOSITION AND STRUCTURE OF A WEST TEXAS SALT MARSH

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Key words: alkali sacaton, bulrush, Distichlis spicata, Helianthus paradoxus,
inland salt marsh, Pecos sunflower, puzzle sunflower, saltgrass, Scirpus
americana, Sporobolus airoides, west Texas, wetland

ABSTRACT--An inland salt marsh is found along Leon Creek in the Diamond
Y Spring Preserve in Pecos County near Fort Stockton, Texas (31°00.54'N,
102°55.49'W). Chihuahuan Desert communities dominated by Larrea tridentata

(creosote bush) are found on shallow upland soils and other communities dominated by Prosopis glandulosa (honey mesquite) are on deep soils surrounding the salt marsh. Considering the area of the salt marsh sampled, mean plant cover was 80%. Mean species cover (\pm SD) of Distichlis spicata (saltgrass) was highest at $33 \pm 32\%$. It was followed by Sporobolus airoides (alkali sacaton) at $22 \pm 31\%$, Helianthus paradoxus (Pecos or puzzle sunflower) at $12 \pm 26\%$, Suaeda depressa (seepweed) at $7 \pm 14\%$, and Scirpus americana (bulrush) at $3 \pm 11\%$. Limonium limbatum (sea lavender), Sporobolus texanus (Texas sporobolus), and Flaveria chloraefolia (yellow flaveria) cover was 1% each. Seven other species had cover values $< 1\%$ (15 total species found). Helianthus paradoxus mean density in the salt marsh was 35 ± 71 plants/m². As one descends slightly in elevation into the marsh from the dry upland, three plant communities are encountered. From driest to wettest, the sequence is an S. airoides grassland, a D. spicata grassland, and in the drainage an S. americana marsh community. The communities are simple, composed of few species (6 to 11). In limited areas of the wettest, most disturbed parts of the S. americana community, E. chloraefolia, Juncus mexicanus (Mexican rush), Samolus cuneatus (brookweed), Spartina pectinata (prairie cordgrass), Heliotropium curassavicum (alkali heliotrope), Agalinis maritima (salt marsh gerardia) and Eleocharis palustris (spikerush) may be found with cover values of 1-100%. Soil water content, salt levels, oxygen levels, disturbance or herbivory are probably factors controlling the cover and composition of the communities.

Most low elevation desert grasslands throughout southwestern North America, including western Texas, have changed in both composition and structure over the past 150 y (Van Auken, 2000). Native woody species have encroached into the grasslands, increased in density and cover as the native grasses have decreased. Similar changes have occurred in the upland communities in the Diamond Y Spring Preserve in west Texas with Larrea tridentata (creosote bush) and Prosopis glandulosa (honey mesquite) being the major encroaching woody species. In addition to the increases in density of woody plants in the upland communities, wetland habitats associated with rivers, streams and springs throughout this region have almost completely disappeared because of anthropogenic lowering of the water table (Brune, 1981; Poole, 1992; Horne and Kahn, 1997). One remaining wetland system is associated with the desert springs found along Leon Creek in Pecos County near Fort Stockton, Texas.

The species composition, abiotic and biotic gradients present in the wetlands of the salt marsh of the Diamond Y Spring Preserve and other inland salt marshes of western Texas have been largely ignored (but see Henrickson, 1977). However, community composition and structure as well as the various salt gradients of many of the inland salt marshes of other parts of the United States and Canada have been reported (Billings, 1945; Chapman, 1974; Flowers and Evans, 1966; Ungar et. al., 1969; Ungar, 1970; Burchill and Kenkel, 1991). Vegetational zonation described for marine salt marshes (Chapman, 1977;

Niering and Warren, 1980; Bertness, 1991a), with the most salt tolerant species in the lowest part of the marsh, is also present in various inland salt marshes (Chapman, 1974; Burchill and Kenkel, 1991), and is probably paralleled by one or more environmental gradients (Bertness, 1991a; Bertness and Hacker, 1994).

Furthermore, the importance of herbivory and competition in these west Texas marshes has been largely ignored, in spite of their relevance to patterns and species success in other salt marshes (Reinold et. al., 1975; Smith and Odum, 1981; Bertness, 1991a,b; Furbish and Albano, 1994).

Inland salt marshes are located in continental regions rather than coastal regions (MacNae, 1968; Chapman, 1974, 1977; Niering and Warren, 1980; Haines and Dunn, 1985; Odum, 1988). They vary greatly in size and shape as well as the concentration and the kinds of salts present (Flowers and Evans, 1966; Burchill and Kenkel, 1991). Salt concentrations can range from <1 % to >25%, composed variously of Na, K, Mg, or Ca cations and Cl, CO₃ or SO₄ anions (Ungar, 1970; Burchill and Kenkel, 1991). They differ from coastal salt marshes because there are no tidal effects, but they are subject to high variation in soil-salt concentrations and time of desiccation, because of high annual variability in precipitation (Borchert, 1971; Ungar, 1974).

Salt gradients, as well as high spatial variation in soil salt levels in the salt marsh of the Diamond Y Spring Preserve have been reported (Van Auken and Bush, 1998). The soils of the upland Chihuahuan Desert communities dominated by Larrea tridentata or by Prosopis glandulosa have very low levels of

salt. The salts present in the lower elevation soils of the marsh seem to be mainly Na, K, Ca, and MgSO_4 with less Cl (Veni, 1991; Boghici, 1997) and are between zero and 40 ppt (parts per thousand, Van Auken and Bush, 1998).

The spring system and the associated salt marsh communities found in the Diamond Y Spring Preserve are ecologically important because it is one of few remaining wetland spring communities in western Texas. It is the location of one of two Texas populations of the federally threatened sunflower, Helianthus paradoxus (the Pecos or puzzle sunflower, Compositae, Correll and Johnston, 1979; McDonald, 1999). The springs and associated salt marsh and drainages are habitat for two federally listed endangered fish, Cyprinodon bovinus (Leon Springs Pupfish) and Gambusia nobilis (Pecos Gambusia) and three rare snail species (McDonald, 1999).

However, much of the biology and ecology of this spring system and the associated species, including H. paradoxus is anecdotal. The presence of neighbors has been shown to be detrimental to H. paradoxus plants, while large herbivores had mixed effects on its growth (Bush and Van Auken, 1997). The species associated with H. paradoxus are largely unknown and the composition and spatial limits of the plant communities in this salt marsh are also unknown. Helianthus paradoxus seems to be restricted to inland salt marshes with soil surface salt levels of approximately ten parts per thousand (Poole, 1992; Poole and Diamond, 1993; Sivinski, 1996). It is not reported from upland L. tridentata or P. glandulosa communities and is found infrequently in S. airoides grasslands

(Van Auken and Bush, 1998). It is also not usually found with S. americana in the lowest part of the salt marsh. However, there is still little information available concerning population cover or density, or population fluctuations of H. paradoxus or any of the associated species in this marsh system.

Consequently, the first purpose of this study was to determine the plant species present in the salt marsh along Leon Creek in the Diamond Y Spring Preserve. The second purpose was to determine the kinds of plant communities present in the salt marsh and then to delineate them. The third purpose was to determine the cover of the dominant and lesser species found in the salt marsh communities. The fourth purpose was to determine the specific location of the various species in the marsh system and clarify any possible associations.

MATERIALS AND METHODS--For this study, field surveys were carried out in October of 1998 in the Diamond Y Spring Preserve of the Nature Conservancy of Texas. The Preserve, consisting of 607 ha of upland and salt marsh communities, is located approximately 13 km north of Fort Stockton, Texas (Pecos County, 31°00.54'N, 102°55.49'W). The site is located on Leon Creek, which flows from Leon Spring and drains into the Pecos River (Fig. 1). Soils in the Leon Creek drainage are alluvial, gray-black clays of the Balmorhea Association (Jaco, 1980; Rives, 1980). Elevation increases slowly away from the drainage, but the soils change dramatically. Orla association soils are fairly level, somewhat saline, pale-brown loams just upslope from the drainage. Further upland, soils are of the Lozier association and are light brown to gray,

very shallow, gravelly, stony soils on limestone hills.

The species found in the salt marsh were identified according to descriptions found in Correll and Johnston (1979) and nomenclature updates were checked in Hatch et al. (1990). The physical location and distribution of all of the species found including species cover or density and spatial changes in population cover or density were estimated using the quadrat procedure (Van Auken and Bush, 1995). Fourteen linear transects were permanently marked and set up to cross the marsh along Leon Creek (Fig. 1). Transects were 50 m apart and perpendicular to the drainage from the edge of the P. glandulosa savanna on the north to the edge of this same community on the south side of the salt marsh. The most westerly transect was 25 m from the fence delineating the western property line of the Diamond Y Spring Preserve. Transects began five m from a fence on the north edge of the salt marsh. Transects ranged in length from approximately 250 to 480 m, depending on the distance across the marsh, and included 50 to 96 quadrats. Plant cover of all species was visually estimated in 0.1 m quadrats (20 x 50 cm) at 5 m intervals along each transect line (Brower and Zar, 1977). In addition, H. paradoxus density was measured in each quadrat. This was done because very large changes in cover of H. paradoxus occur from early to late in the growing season because it is a broad-leaved annual. To illustrate species distributions, two example transects were used to show the changes in major species cover from the upland to the drainage.

A grid corresponding to transect sample points was created with AutoCAD[®]. Using the Geographic Information System ArcView[®] (version 3.2) and its Spatial Analyst extension, this grid was interpolated into a raster surface plot. Cover and density measurements for each species were averaged over the 12 nearest sample points to create each plot. Contour plots were prepared for each species using cover or density. A gray monochromatic plot was used, with various shades from white with lowest cover or density (zero) to black with the highest values, because of the complexity of the distribution. Plots with as many as 23 cover or density classes were examined, but the best visual presentation was found when only four classes were used. The four classes were 0, 1 to 33, 34 to 66, and 67 to 100% cover for S. airoides, D. spicata, S. americana, Suaeda depressa (seepweed), Limonium limbatum (sea lavender), Sporobolus texanus (Texas sporobolus), and Flaveria chloraefolia (yellow flaveria). Four density classes were used for H. paradoxus including 0, 1 to 20, 21 to 40, and 41 to 60 plants/0.1 m².

A generalized map was prepared consisting of the three major communities found in the salt marsh. The communities were an S. airoides grassland, a D. spicata grassland, and an S. americana bulrush marsh. Community limits for the S. airoides grassland and the D. spicata grassland were established by extrapolation to points on the map where their cover was 40%. Community limits for the S. americana bulrush community were set at 10% cover. Total area of this map and the individual species distribution maps is 18.636 ha.

RESULTS--Sporobolus airoides (alkali sacaton) was found mainly along the

first part of one of the example transects presented (Fig. 2a, northwest corner of the map, Fig. 3). It was not present in the center of the transect and then it occurred again (but less consistently) along the last part of the transect (south side of the marsh, Fig. 2a). In both parts of this transect, it was found along the edge of the salt marsh, in areas with the highest elevation (personal observation), but in this example transect, it was found down to the drainage, which was not typical. It was found in the first 175 m in this example transect, with cover values from 0 to 100% (Fig. 2a). It was not in the center of this transect, and less consistently from the 360 m point to the end of the transect.

Sporobolus airoides and D. spicata (saltgrass) seem to be almost mutually exclusive. Distichlis spicata, for the most part, had low cover in the first 175 m of this transect (north, Fig. 2a), then increased to 30 to 100% in the next 200 m of this transect and was more sporadic in the last part of the transect (south). In this example transect, H. paradoxus (Pecos or puzzle sunflower) was located in the mid-part of the transect (Fig. 2b). It was not in the first 195 m of the transect with S. airoides nor was it in the last 100 m with S. airoides.

Helianthus paradoxus was usually found in the salt marsh mixed with D. spicata (Fig. 2ab). Helianthus paradoxus cover ranged from 0 to as high as 100% in some quadrats and density was 0 to 600 plants/m² (note, density of H. paradoxus is exaggerated in the figure). Helianthus paradoxus was usually not found in the salt marsh mixed with Scirpus americana (bulrush), although it was found growing associated with it along the edge of this community as shown in

the second example transect (Fig. 2c). Scirpus americana was always in the drainage, in the lowest part of the marsh (Fig. 2c). It was usually found with Sporobolus texanus.

Because of the apparent exclusiveness of the main perennial species found in this west Texas salt marsh, we felt that we could delineate specific communities. The three communities and their locations in the Diamond Y Spring Preserve salt marsh as delineated in this 1998 survey are presented in Fig. 3. The S. airoides community was found in the parts of the salt marsh that were slightly higher in elevation (personal observation). These areas were mainly in the northwest part of salt marsh and all along the southern edge of the marsh. The edge of this community was set at 40% cover for S. airoides. In the lowest part of the salt marsh along the drainage of Leon Creek, in soils that are saturated for at least part of the year, we found the S. americana community, which is somewhat disconnected. The edge or limit of this community was set at 10% S. americana cover. Between these two communities at intermediate elevations and apparently intermediate levels of soil water saturation is the D. spicata community, with D. spicata as the dominant perennial species. The edge of this community was set at 40% cover for D. spicata. This community was found extensively in the salt marsh, from one end to the other. Helianthus paradoxus, an annual species is present almost exclusively in this community along with Suaeda depressa, another annual. Both of these species distributions in the salt marsh are presented separately for

simplicity.

Of the 18.636 ha of the salt marsh sampled, the Distichlis grassland community occupied 57.1% of the total area (Table 1). The S. airoides grassland community covered 34.6% of the salt marsh. The S. americana bulrush community was the smallest, covering 8.2% of the salt marsh. Helianthus paradoxus was found in the Distichlis grassland community at a density of more than 5 plants/m² on 4.53 ha or on 20.7% of the area sampled.

There were 15 species of herbaceous plants found in the salt marsh at the Diamond Y Spring Preserve but no woody species were encountered (Table 2). Distichlis spicata had the greatest mean cover averaged over the area of the salt marsh sampled at $33 \pm 32\%$ (\pm SD), followed by S. airoides at $22 \pm 32\%$ cover. Helianthus paradoxus cover was $12 \pm 26\%$ with a density of 35 ± 71 plants/m² over the area of the salt marsh sampled. Twelve other species had cover values of less than 10%. Sporobolus airoides cover was $55 \pm 35\%$ in the Sporobolus grassland. Five other species were found in the S. airoides community, but at much lower cover values (Table 2). Distichlis spicata had the greatest cover in the Distichlis grassland at $50 \pm 31\%$ cover, followed by H. paradoxus at $25 \pm 25\%$ cover and Suaeda depressa at $10 \pm 19\%$ cover. Six other species were found in this community with low cover values. The highest mean density of Helianthus paradoxus was found in the Distichlis grassland community at 63 ± 103 plants/m². Scirpus americana had the greatest cover in the Scirpus community at $34 \pm 31\%$. Distichlis spicata and Sporobolus texanus,

two vegetatively similar grasses, had cover values of $21 \pm 33\%$ and $10 \pm 16\%$ respectively in this community. Eight other species were found in this community, for a total of 11 species, making it the community richest in total species.

Spatial patterns of the five species with overall cover values between one and 12% are best displayed in gray monochromatic contour plots (Fig. 4).

Limonium limbatum was usually found in the parts of the salt marsh with higher elevation, associated with Sporobolus airoides in the Sporobolus grassland. It was found sporadically in the Distichlis grassland, usually in the upper part of this marsh community, decreasing in cover toward the drainage (Fig 4a). This distribution is essentially in the northwestern and southwestern edges of the marsh, somewhat elevated from the drainage and close to the P. glandulosa upland community.

Suaeda depressa was fairly widespread in the Distichlis grassland community, with mean cover values usually in the range of 1-33%. However, Suaeda was also encountered in parts of the higher elevation grasslands, where S. airoides cover was high (Fig. 4b). Suaeda seemed to have 1 to 33% cover in approximately half of the area of the salt marsh sampled with higher cover in the wetter parts of the Distichlis communities. Sporobolus texanus was only present along the drainage associated with standing water in the Scirpus americana community in the wettest part of the marsh. It was never detected with S. airoides in the higher elevation, drier grasslands of the salt marsh (Fig.

4c).

Flaveria chloraefolia was not usually associated with S. airoides, in the higher elevation, drier grasslands of the salt marsh (Fig. 4d). It was only found in the wettest part of the salt marsh, the part of the salt marsh that had soil that seemed to be wet year round (personal observation). It was usually associated with S. texana or S. americana, but sometimes it was mixed with D. spicata and H. paradoxus. It was only encountered in the southeastern corner of the salt marsh.

Helianthus paradoxus was fairly wide spread in the salt marsh, but mostly in the Distichlis grassland community (Fig. 4e). It was usually not in the S. airoides grassland or in the wettest part of the salt marsh with S. americana, thus H. paradoxus was not distributed uniformly across the salt marsh. There are large areas in the Distichlis grassland community without any Helianthus and other parts of this grassland that have high densities. Helianthus paradoxus was detected on more than 20% of the salt marsh sampled, all in the Distichlis grassland community, and 36.6% of this grassland had some H. paradoxus plants.

DISCUSSION—In the past, desert grasslands were found in many areas of western Texas, New Mexico, Arizona and northern Mexico (Sims, 1988; Barbour et al., 1999). Common grasses on sandy and gravelly upland soils were various species of Bouteloua, Sporobolus, and Muhlenbergia including Bouteloua eriopoda (black grama), Sporobolus flexuosus (mesa dropseed),

Muhlenbergia porteri (bush muhly) and others (Schmutz et al., 1991; McClaran, 1995). Common grasses on clay bottomland soils were various species of Aristida, Hilaria, Bouteloua, Scleropogon, and Sporobolus including Hilaria mutica (tobosa), Scleropogon brevifolius (burrograss), Sporobolus airoides and others. Most of these desert grasslands have changed dramatically in composition and structure. Grass cover has declined and woody plant cover and density has increased in most areas (Van Auken, 2000). The driving force for these community changes seems to be chronic, high levels of herbivory by domestic animals leading to the reduction of fine fuel and a concomitant reduction or elimination of grassland fires.

Thus, it is unusual to find not one, but two different, relatively intact grasslands in the Diamond Y Spring area of west Texas. The Sporobolus airoides grassland is on clay soils in the salt marsh (Jaco, 1980; Rives, 1980), but slightly above the drainage at slightly higher elevations (personal observation). As such, the soils are not as wet or water logged throughout the year and the salt levels do not appear to be as high as in the lower parts of the salt marsh. This seems to be the typical habitat for S. airoides (Schmutz et al., 1991). The Distichlis spicata grassland is also on clay soils in the salt marsh, but it is at a slightly lower elevation, just above the drainage. The soils of the Distichlis grassland are wetter throughout the year and seem to be higher in salt levels (Van Auken and Bush, 1998). Distichlis is reported from many coastal and inland salt marshes (Reinold et. al., 1975; Henrickson, 1977; Pinkava, 1977;

Smith and Odum, 1981; Bertness, 1991a,b; Furbish and Albano, 1994).

It is not clear how the grasslands in the salt marsh are maintained as grasslands when the surrounding upland communities have become Larrea tridentata shrublands or Prosopis glandulosa woodlands (Van Auken, 2000; and personal observation). The grassland communities are presently grazed and have been for many years. There is considerable evidence of Prosopis and Tamarix (salt cedar) seedling encroachment into the grassland (personal observation). The relatively high levels of water in the salt marsh soils may allow for continuous growth of the C₄ grasses during the hot summers, reducing potential growth of the woody plant seedlings in spite of the grazing of the grass by large ungulates. The thick grass growth may support high levels of rodents and other browsers that continually feed on the new seedlings of woody plants, keeping them suppressed or removing them. Another possibility would relate to periodic fires. In spite of grazing, considerable light fluffy fuel remains at the end of each growing season. Apparently there is enough fuel to support grassland fires (personal observation). Fire frequency could be high enough to keep parts of the salt marsh free of encroaching woody plants, but the historical record of fire frequency in the salt marsh is unknown. Probably all of these factors are acting together to keep areas of this salt marsh free of woody plants.

The kind of species present, number of species, community types, and salt gradients of many of the inland salt marshes of the United States and

Canada have been reported (Billings, 1945; Chapman, 1974; Flowers and Evans, 1966; Ungar et. al., 1969; Ungar, 1970; Burchill and Kenkel, 1991). The vegetational zonation described for marine salt marshes (Chapman, 1977; Niering and Warren, 1980; Bertness, 1991a) is also present in inland salt marshes (Chapman, 1974; Burchill and Kenkel, 1991), and is probably paralleled by one or more environmental gradients (Bertness, 1991a; Bertness and Hacker, 1994). Zonation does appear in the Diamond Y Spring Preserve salt marsh as one descends from the slightly higher elevation around the edge of the salt marsh into the center (Fig. 3). Sporobolus airoides occurs around the edge of the salt marsh, D. spicata is found in the next zone (lower), and S. americana is in the lowest (center) of the salt marsh. In spite of the above, community composition, and abiotic and biotic gradients in the inland salt marshes of western Texas and northern Mexico have been largely ignored and their composition and structure are unreported. The low-density species present in the Diamond Y Spring Preserve salt marsh are found mainly in one community associated with one of the dominant species. However, overall there are very few species present in this salt marsh system.

The reason for the low number of species reported from the two grassland salt marsh communities is unknown. Some species that are present in the Diamond Y Spring Preserve could have been missed because of low cover, low density, cryptic nature, seasonality or a clumped population distribution. We physically covered the whole marsh area that is presented in the figures and

sampling was uniform. We sampled or measured 955-0.1 m² quadrats or 95.5 m² of the 18.636 ha of the salt marsh community that is presented in the figures. A low number of species has been reported previously for saline habitats in western Texas and northern Mexico (Hendrickson, 1977; Pinkava, 1977). The relatively high levels of Na₂SO₄ in the soil of the Diamond Y Spring Preserve (10 to 40 ppt) and the shallow water table (personal observation) may play a role. These two factors coupled to high cover of S. airoides and high cumulative biomass could prevent entry of other species into the S. airoides grassland. The D. spicata grassland also has few species, but almost twice as many as the S. airoides grassland. The cover of the D. spicata grassland may be higher than the S. airoides grassland (Table 2), but the biomass appears to be lower (personal observation). Distichlis spicata is not a perennial bunchgrass, but a perennial sod forming grass, and it is lower in stature. In addition, more biomass may be removed from this community by large ungulates, but this is undocumented.

Most of the species reported here are not found in the upland Larrea tridentata or Prosopis glandulosa communities. These upland areas have low levels of salt, but are also probably too dry most of the year for the growth of these species. In the lowest part of the salt marsh, the concentration of organic material in the soil, low soil oxygen, or possibly the redox potential of the soil does not seem suitable for growth of some upland species as has been reported for other salt marsh communities (Webb and Mendelssohn, 1996).

The largest number of species (eleven) was found in the Scirpus americana community. This community was only present in the drainage or around the springs, in the wettest part of the salt marsh (Fig. 3). The commonest species associated with S. americana were D. spicata and S. texansus. They were usually encountered around the edge of the S. americana community, but mixed with it. Flaveria chloraefolia had high cover in some of the wettest areas of the salt marsh and it was associated with S. americana, D. spicata and S. texansus. All of the other species found in this community seemed to occur in ungulate created disturbances around a spring or seep in the wettest part of the salt marsh. These species are reported from saline habitats in other parts of western Texas and northern Mexico but not from other non-saline habitats (Hendrickson, 1977; Pinkava, 1977).

Distichlis spicata is not a good competitor in coastal marshes (Bertness, 1991b), invading newly exposed areas, but being replaced by community dominants. It seems to increase with differential grazing of associated species that are better competitors in the absence of grazing (Reimond et al., 1975; Smith and Odum, 1981; Furbish and Albano, 1994). However, in the Diamond Y Spring Preserve salt marsh, it is not clear which species might replace D. spicata. Helianthus paradoxus and Suaeda depressa combined cover was 35% in the D. spicata grassland of the salt marsh and they are both annuals. Thus, they may be short term but not long term replacement species for D. spicata. As annuals, they both may require gaps for establishment (Bush and Van

Auken, 1997), which may be produced by the grazers. Thus, the presence of large ungulate grazers may have a dual role in this salt marsh community. The grazers may reduce the biomass of other perennial grasses that could compete with or replace D. spicata, but at the same time they create gaps and promote the annual species that are currently present in this community.

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Table 1. Community type, community area (ha), percent of the total area of each of the communities identified and the total area sampled in the salt marsh of the Diamond Y Spring Preserve near Fort Stockton, Texas.

Community Type	Community Area	%
<u>Distichlis spicata</u> grassland	10.641	57.1
<u>Sporobolus airoides</u> grassland	6.448	34.6
<u>Scirpus americana</u> bulrush marsh	<u>1.527</u>	<u>8.2</u>
Total area	18.636	99.9

Table 2. Cover (%) \pm one standard deviation for each species found in the area sampled in the salt marsh of the Diamond Y Spring Preserve near Fort Stockton, Texas. In addition, the mean cover \pm one standard deviation of each species found in each of the three communities identified in the salt marsh is presented.

Density (plants/m²) is also presented for H. paradoxus. A zero in a column indicates that species was not found in that community.

Community Types				
Species	Marsh total	<u>Sporobolus</u>	<u>Distichlis</u>	<u>Scirpus</u>
<u>Distichlis spicata</u>	33 ± 32	13 ± 21	50 ± 31	21 ± 33
<u>Sporobolus airoides</u>	22 ± 31	55 ± 35	2 ± 10	0
<u>Suaeda depressa</u>	7 ± 14	3 ± 9	10 ± 19	0
<u>Scirpus americana</u>	3 ± 11	0	1 ± 5	34 ± 31
<u>Limonium limbatum</u>	1 ± 3	2 ± 5	--*	0
<u>Sporobolus texanus</u>	1 ± 6	0	1 ± 6	10 ± 16
<u>Flaveria chloraefolia</u>	1 ± 7	0	1 ± 8	5 ± 20
<u>Juncus mexicanus</u>	--*	0	--*	--*
<u>Spartina pectinata</u>	--*	0	0	--*
<u>Samolus cuneatus</u>	--*	0	0	--*
<u>Sesuvium verrucosum</u>	--*	--*	0	0
<u>Heliotropium curassavicum</u>	--*	0	0	--*
<u>Aqalinis maritima</u>	--*	0	0	--*
<u>Eleocharis palustris</u>	--*	0	0	--*
<u>Helianthus paradoxus</u>	12 ± 26	4 ± 22	25 ± 25	11 ± 26
<u>Helianthus paradoxus</u>	35 ± 71**	6 ± 30**	63 ± 103**	9 ± 23**
Total cover	80	77	90	81

* < 1% cover

**Density, plants/m²

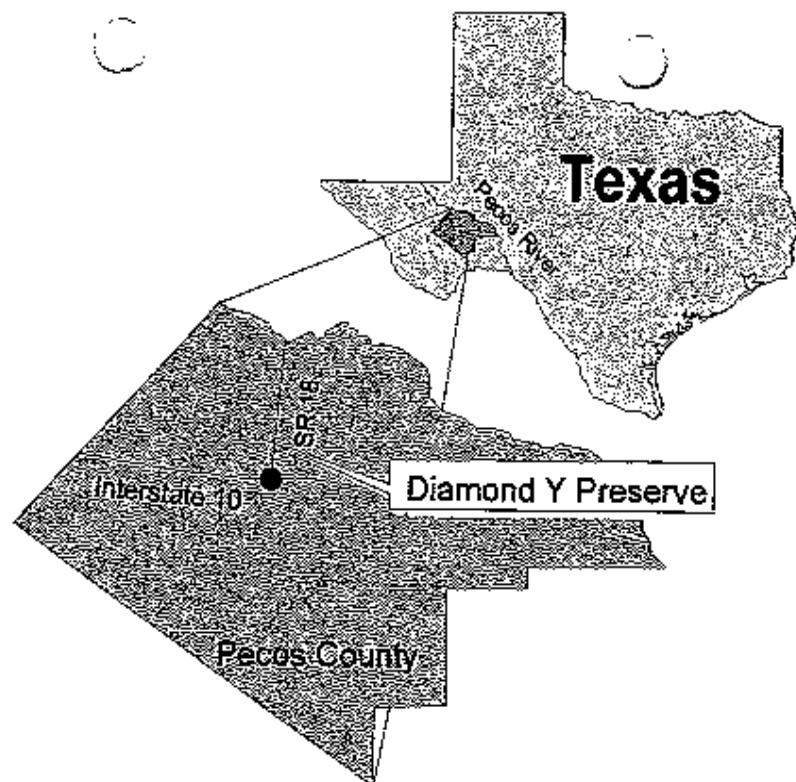
Fig. 1--Map of Texas showing the location of Pecos County and the Diamond Y Spring Preserve study site.

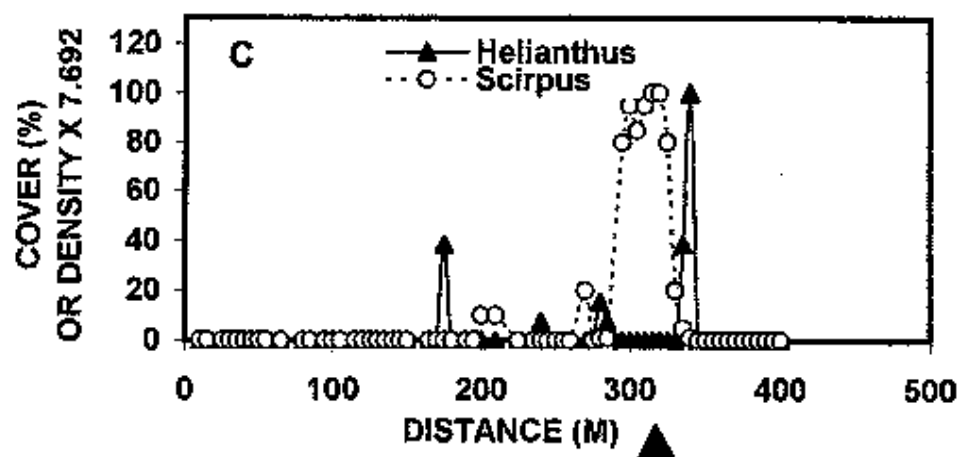
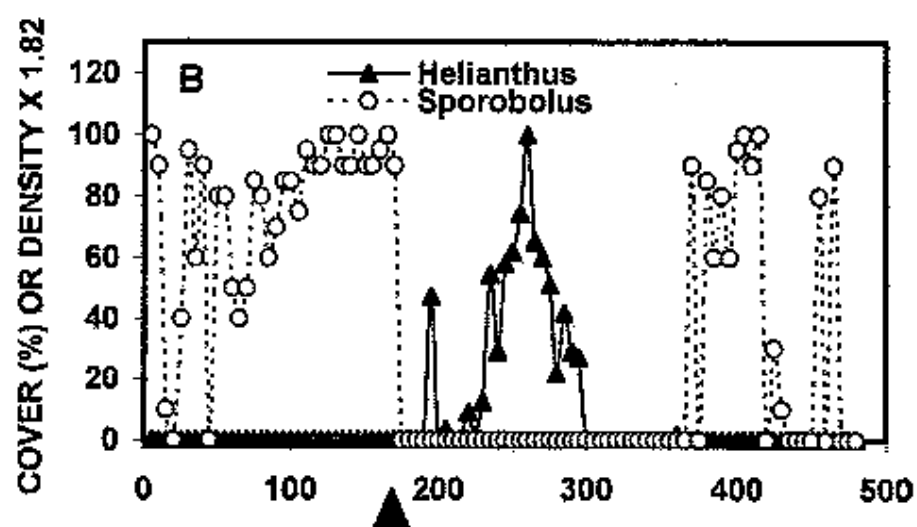
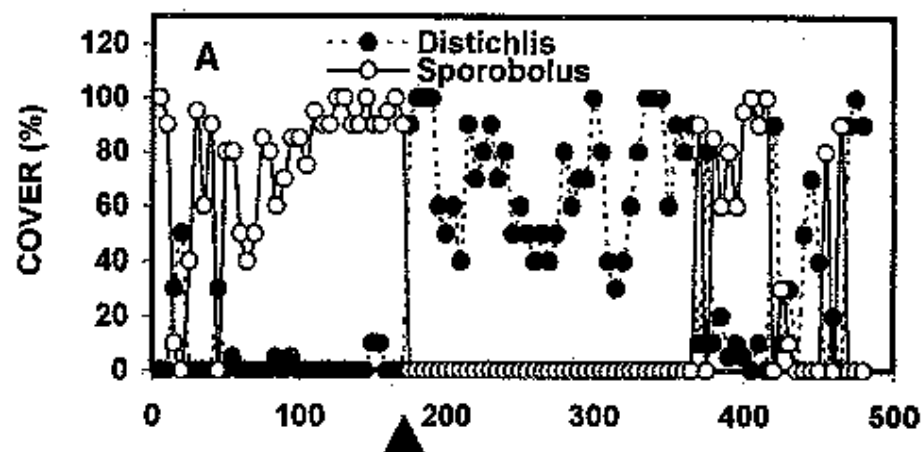
Fig. 2--Sporobolus airoides and Distichlis spicata cover (%) (A), S. airoides cover and Helianthus paradoxus density (plants/0.1 m²) (B), and Scirpus americana cover and H. paradoxus density (C) as a function of distance (m). The figure represents two transects that extend from the Prosopis glandulosa upland vegetation on the north of the salt marsh (zero) to the creek edge (drainage, lowest part of the marsh), and then to the P. glandulosa upland vegetation on the south (500). Each plant sampling point was 5 m from the previous one. Data in A and B are from the transect on the west edge of the marsh, while the data in C are from the transect on the west side of the road (Fig. 3). The black triangle below the x axis indicates the location of Leon Creek.

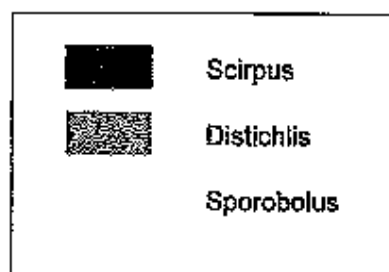
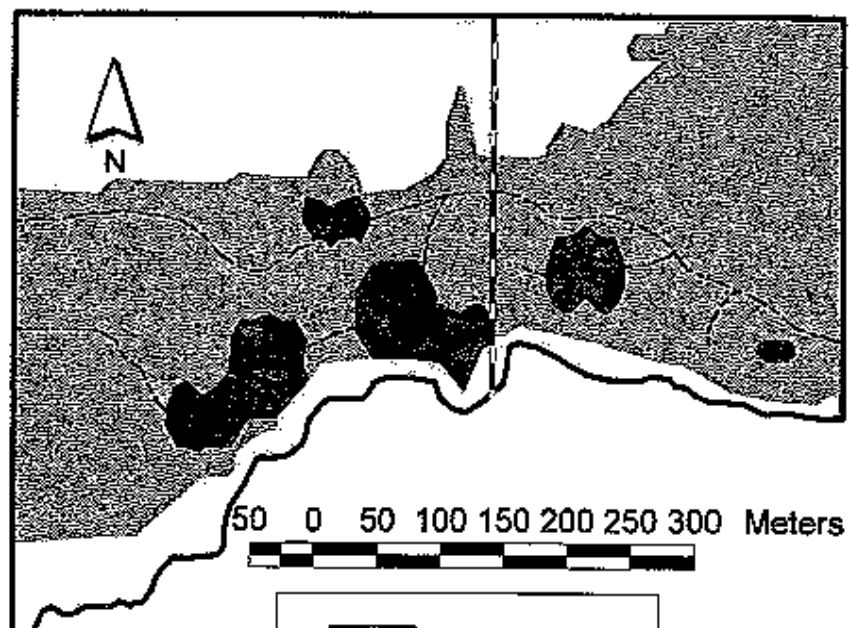
Fig. 3--Generalized Geographic Information System (GIS) map of the three plant communities identified along the Leon Creek drainage in the Diamond Y Spring Preserve near Fort Stockton, Texas. The communities are a Scirpus americana community in the wettest part of the marsh, a Distichlis spicata grassland community and a Sporobolus airoides grassland community in the highest, driest part of the salt marsh. The dashed line is the Leon Creek drainage. The straight line running north-south in each figure is a dirt road that

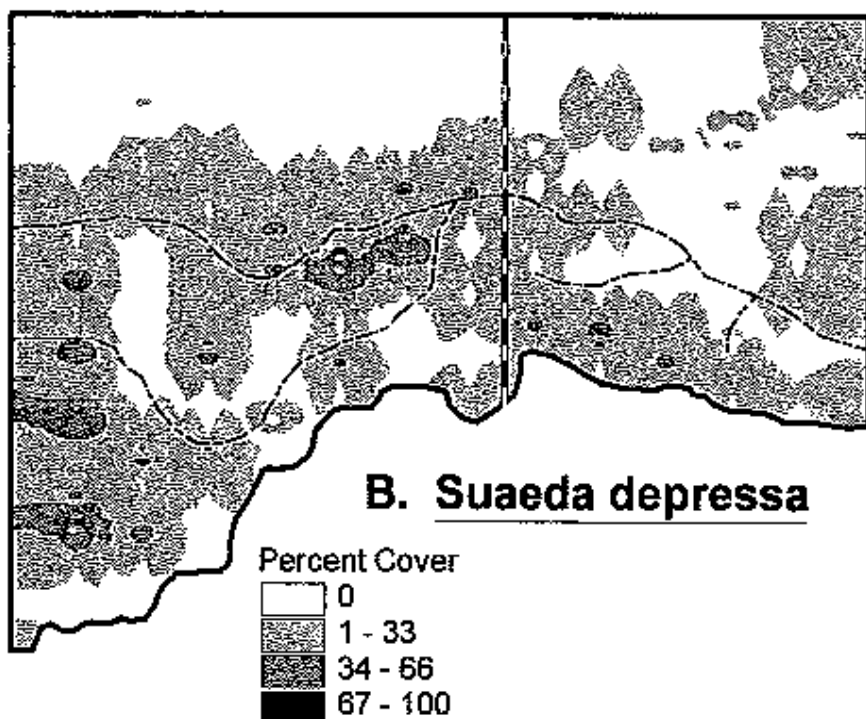
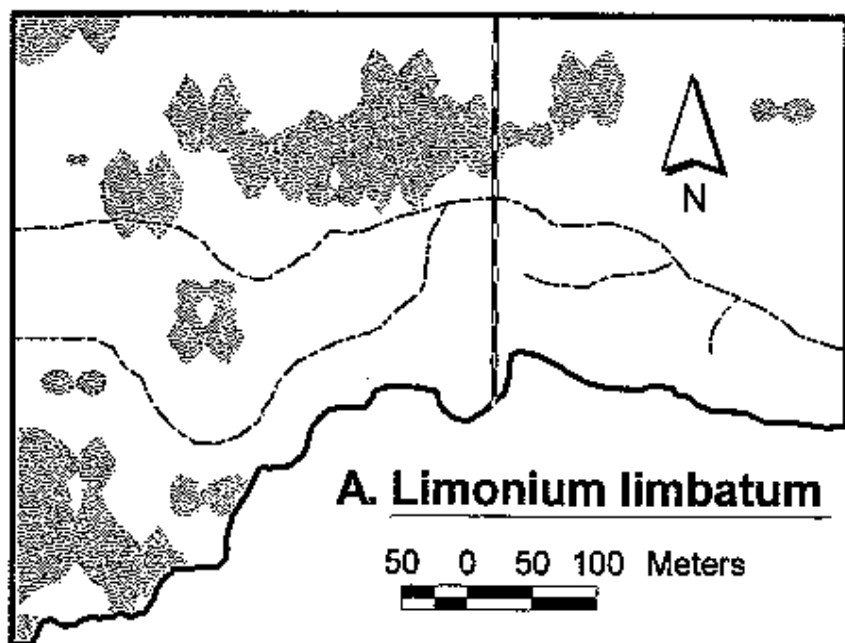
crosses the salt marsh. The boundaries for the S. airoides and the D. spicata community were 40% cover. For the S. americana community, the boundary was 10% cover. Data used to create the map was collected in the fall of 1998.

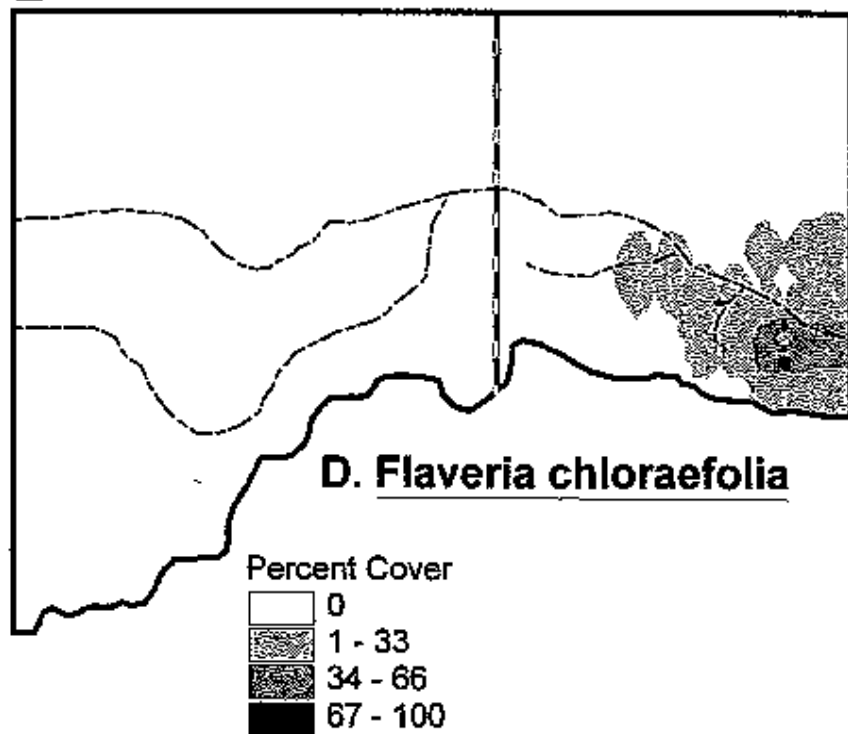
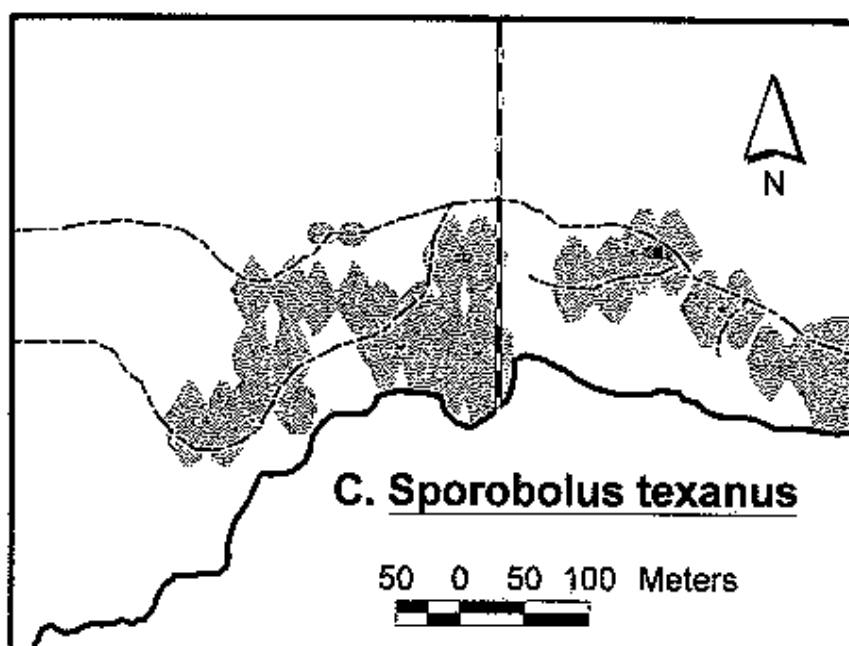
Fig. 4--Geographic Information System (GIS) plot of the salt marsh along the Leon Creek drainage in the Diamond Y Spring Preserve near Fort Stockton, Texas. The figure includes Limonium limbatum (sea lavender) percent cover (A), Suaeda depressa (seepweed) percent cover (B), Sporobolus texanus (Texas sporobolus) percent cover (C), Flaveria chloraefolia (yellow flaveria) percent cover (D) and Helianthus paradoxus (Pecos or puzzle sunflower) density (E). North is to the top of each plot and to the north and south of each plot is the edge of the Prosopis glandulosa woodland. The distance scale is in meters and is the same for each plot. The range of cover values is the same in each plot. The dashed line is the Leon Creek drainage. The straight line running north-south in each figure is a dirt road that crosses the salt marsh.

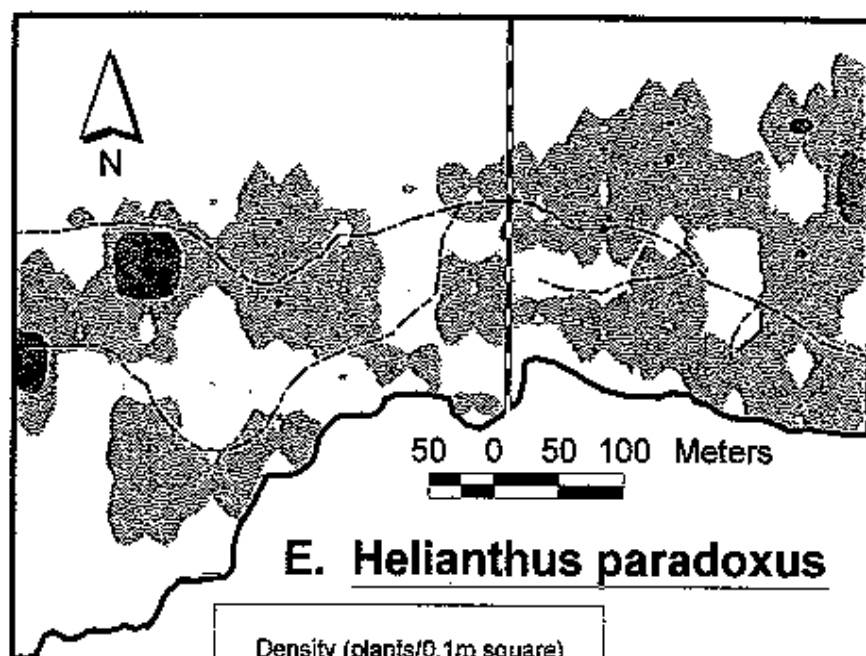













E. Helianthus paradoxus

Density (plants/0.1m square)

	0
	1 - 20
	21 - 40
	41 - 60