

The Importance of Competition in the Isolation and Establishment of *Helianthus Paradoxus* (Asteraceae)

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ABSTRACT: *Helianthus paradoxus* (the Pecos or puzzle sunflower) is a threatened, federally listed annual species that is found in a few locations in west Texas and New Mexico. Two greenhouse experiments were conducted to evaluate the ability of *H. paradoxus* to compete with its progenitors and a with potential ecosystem competitor, *Distichlis spicata* (saltgrass) in simulated salt marsh and non-salt marsh environments. The results were usually dependent on soil salinity. *Helianthus paradoxus* was the better competitor in high saline soil and its progenitor *H. annuus* (common sunflower) was the better competitor in low saline soil. However, *H. paradoxus* was the better competitor in both high and low saline soils when compared to its progenitor *H. petiolaris* (plains sunflower) and to *D. spicata*, an ecosystem competitor. The ability of *H. paradoxus* to tolerate higher saline conditions, and perhaps even restrict the more geographically widespread *H. annuus* in saline soils may have allowed *H. paradoxus* to establish, become genetically isolated and survive as a species in inland salt marshes. Data presented here indicate that while *H. paradoxus* can grow in low saline soil, interference from *H. annuus* in low saline soils could restrict *H. paradoxus* to saline environments within salt marshes. The ability of *H. paradoxus* to out-compete *D. spicata* at high or low salt levels indicates that gaps in *D. spicata* vegetation would not be necessary in the salt marsh to allow the establishment and persistence of *H. paradoxus* in the saline soils of the salt marsh environment.

INTRODUCTION

It has been difficult to demonstrate that interspecific hybridization can be adaptive (Abbott 2003). Interspecific hybridization could produce a significant array of genotypes, including some with reasonable levels of fertility. If hybridization between two related species does occur, to be successful, some of the resulting offspring must survive and be fertile. In addition, the fertile hybrid must be isolated from the parents by a very strong post zygotic barrier. Thus, any subsequent mating between the parents and hybrid would result in few or no fertile offspring. In

addition, if the hybrid individuals were found in a population of either parent, few fertile offspring would be produced because of the low probability of pollen from one hybrid plant reaching another hybrid plant. If the hybrids were adapted to a habitat different from that of either of the parents, the hybrids could be isolated from the parents and avoid any minority type disadvantages and possible negative effects of interspecific competition.

Hybridization between two common sunflowers (*Helianthus annuus* L. and *H. petiolaris* Nutt.) and the molecular genetics of the resulting hybrids between

them have been recently reported (Rieseberg et al. 2003). They were interested in the mechanism that allowed the hybrid species, *H. paradoxus*, to become established and persist in unusual inland sulfate dominated salt marshes. They found that the chromosomal segments that were responsible for specific characteristics or traits in the parent species had at least one segment or trait with an effect in an opposite direction compared to the other segments. These specific traits were related to the parents' inability to survive in extreme habitats such as salt marshes. If the chromosomal segments should be separated during sexual reproduction, then potential recombinations could be created that might be successful in extreme environments. Thus, hybridization could result in recombinants with genes and traits producing extreme phenotypes and plants that could occupy unusual habitats.

Abiotic factors are often considered to be the main factors controlling establishment and patterns of vegetation. Salinity and flooding are often thought to be the key in determining zonation patterns in salt marshes. However, an important role for competition has been hypothesized in determining the limits of a species distribution along these salt marsh salinity gradients (Bertness 1991a, b; Bertness and Ellison 1987; Davy and Smith 1985; Snow and Vince 1984; Ungar 1998). For *H. paradoxus*, a narrowly distributed hybrid endemic, both abiotic factors (specifically soil salinity) and interference or competition between its progenitors may have contributed to its isolation and limited distribution. Its ability to tolerate higher saline soils, and even perhaps restrict the

more geographically widespread *H. annuus* in saline soils may allow it to survive in inland salt marshes where its progenitors are not found. Both *H. annuus* and *H. petiolaris* are found throughout the range of *H. paradoxus*, but not in its the salt marsh habitat.

Helianthus paradoxus is known to be more salt tolerant than *H. annuus* (Mendez 2001; Welch and Rieseberg 2002), but it is unknown if this salt tolerance is enough to promote the differential growth of *H. paradoxus* and *H. annuus* in the same habitats. *Helianthus paradoxus* does produce more biomass when grown with *H. annuus* or *H. petiolaris* at high salt levels, but at low soil salt levels, *H. annuus* produces more biomass (Bush and Van Auken 2004). In addition, it is unknown if *H. paradoxus* could establish and grow in a salt marsh in the presence of common species already established in the marsh such as *Distichlis spicata* (L.) Greene (saltgrass). *Helianthus paradoxus* is found with *D. spicata* in inland salt marshes (Figs. 1 and 2), but gaps could be required for establishment and maintenance (Van Auken and Bush 1998). It has been shown that the presence of neighbors reduces the growth of *H. paradoxus*, while disturbances promote its growth ((Bush and Van Auken 1997; Van Auken and Bush 2004). This certainly suggests that competition from neighbors could play a very important role in the ecology and management of this threatened species.

The purposes of the studies presented here are to examine the competitive abilities of *H. paradoxus* with its progenitors and the competitive abilities of *H. paradoxus* with *D. spicata*, a grass



FIGURE 1—Habitat photograph of the Diamond-Y Spring salt marsh looking to the north. A high-density stand of *Helianthus paradoxus* is on the right and a high-density stand of *Distichlis spicata* is on the left. *Helianthus paradoxus* is not present in the *Distichlis spicata* community, but *Distichlis spicata* is below the sunflowers although it cannot be seen in this photograph.

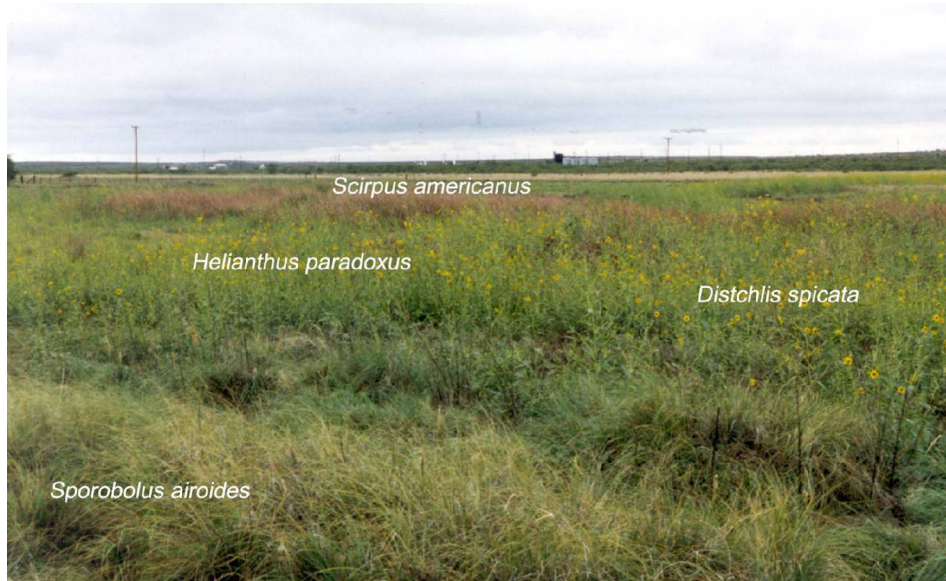


FIGURE 2—Habitat photograph of the Diamond-Y Spring salt marsh looking to the northwest. The foreground with the *Sporobolus airoides* grassland is slightly higher in elevation and slightly drier than the remainder of the salt marsh. *Helianthus paradoxus* and *Distichlis spicata* occur together at slightly lower and wetter parts of the salt marsh. *Scirpus americanus* is usually found in the wettest part of the salt marsh that usually has standing water.

and a potential major environmental competitor.

SPECIES ACCOUNT AND HABITAT

Helianthus paradoxus is estimated to be between 75,000 and 208,000 years

old (Welch and Rieseberg 2002). It is an annual species based on distinct morphological characteristics (Correll and Johnston 1979). It was first described in 1958 and later distinguished as a species (Heiser 1965, 1958). F₁

hybrids between *H. paradoxus* and its progenitors are largely sterile with low pollen stainability and seed set (Heiser 1965, 1958; Heiser et al. 1969). Also, *H. paradoxus* has a stable karyotype and expresses no meiotic abnormalities (Chandler et al. 1986), and has a much larger genome than either of its parent species (Sims and Price 1985). Molecular tests indicated that *H. paradoxus* has combined rDNA repeat types of *H. annuus* and *H. petiolaris*, and has the chloroplast genome of *H. annuus*, confirming that *H. paradoxus* was derived through hybridization (Lexer et al. 2003; Rieseberg et al. 1990; Welch and Rieseberg 2002).

The genus *Helianthus* consist of approximately 67 species of annual and perennial herbs made taxonomically difficult by hybridization among its members (Correll and Johnston 1979). The genus has been divided into four sections based on fairly distinct phylogenetic lines (Heiser 1965). *Helianthus paradoxus* and its parent species *H. annuus* and *H. petiolaris* are annuals belonging to the same section, 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 the spring and summer (depending on location), while *H. paradoxus* flowers in fall, usually 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 (Correll and Johnston 1979; Heiser 1958). All three of these species of *Helianthus* differ in their habitat preference. *Helianthus annuus* occurs throughout North America on disturbed, heavy soils, that are wet in the spring but dry out by midsummer. *Helianthus petiolaris* occurs in western North America on sandy soil. *Helianthus paradoxus* is found in 25 locations in west Texas and New Mexico on brackish, saline, marsh soils (McDonald 1999). *Helianthus paradoxus* has been reported from two west Texas counties and two eastern New Mexico Counties in the Pecos River watershed and two western New Mexico Counties in the Rio Grande watershed (Fig. 3). The largest population of *H. paradoxus* is reported from a salt marsh associated with *Distichlis spicata* (saltgrass) at the Diamond-Y Spring Preserve near Ft.

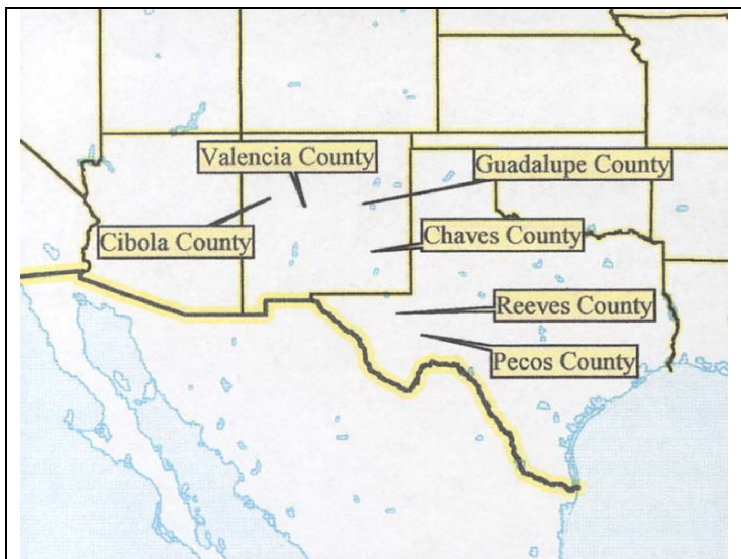


FIGURE 3—Distribution map of *Helianthus paradoxus* in western Texas and New Mexico. The counties where *H. paradoxus* is found are shown. The counties in eastern New Mexico and western Texas are in the Pecos River watershed. The counties in Western New Mexico are in the Rio Grande watershed.

Stockton, Texas (Van Auken and Bush 1998).

MATERIAL AND METHODS

Seeds of *Helianthus paradoxus*, *H. annuus* (common sunflower), and *H. petiolaris* (plains sunflower) were collected from native plants located north of Ft. Stockton, Texas in Pecos County, Texas (31° 0.54' N, 102° 55.49' W), in northwestern Bexar County, Texas (29° 37' N, 98° 36' W) and in central Bernalillo County, New Mexico (35° 5' N 106° 39' W), respectively. Seeds were placed on wet paper toweling in 5 cm deep trays covered with plastic wrap and placed at 4° C for three weeks to break dormancy. Deionized water was added as needed to keep the toweling moist. Clumps of *Distichlis spicata* were collected from the salt marsh at the Diamond-Y Spring Preserve near Fort Stockton, Texas. Clumps were approximately 15 x 15 x 15 cm and were collected by extraction with a shovel. Clumps were placed in large plastic bags for transport to the greenhouse in preparation for the experiment. Clumps were kept in the greenhouse for approximately one week prior to removal of the *D. spicata* rhizomes for placement into the experiment. Clumps were kept in open-top plastic tubs with several centimeters of water at the bottom. Deionized water was added as needed to keep the soil wet. Rhizomes were carefully removed from the soil by washing. Live rhizomes were cut into 3-cm lengths and placed in tap water and then randomly selected for transplanting. Aboveground parts and roots were trimmed to 5-cm lengths prior to transplantation.

Seedlings and saltgrass rhizomes were transplanted into pots containing 1400 g of Patrick series soil described as

clayey-over-sandy, carbonatic-thermic, typic calciustoll, with the A horizon varying in depth from 25 to 41 cm (Taylor et al. 1966). The soil was air dried and sieved (6.4 mm mesh) prior to placement into pots lined with plastic bags (to prevent nutrient, salt and water loss). Soil analysis indicated 5-10 g/kg carbon, 11.6 g/kg calcium, 1.3 g/kg magnesium, 1.0 mg/kg total nitrogen, 12 mg/kg phosphorus, 138 mg/kg potassium, and 196 mg/kg sulfur. Each pot was supplemented with 0.2 g N as NH₄NO₃, 0.15 g P as Na₂PO₄, 0.1 g K as KCl, and 0.04 g S as MgSO₄.

A fiberglass greenhouse was used for plant growth with photosynthetically active photon flux density (PPFD, 400-700 nm) at 37% ± 12% of the outside mean PPFD (1,542 ± 18 μmol/m²/sec ± SD averaged over the experiment). Light level was measured with a LI-COR® LI-188 integrating quantum sensor.

COMPETITION BETWEEN *HELIANTHUS PARADOXUS* AND ITS PROGENITORS

The growth of each species (*H. paradoxus*, *H. annuus* and *H. petiolaris*) grown alone was compared to growth with each of the other species. For each growth parameter evaluated: above ground, below ground and total dry mass or yield, (Van Auken & Bush 1997), a 2 x 2 analyses of variances was used which tested the main effects of soil salinity (two levels) and competition (two levels). The interaction term of the two main effects was also entered into the models. The two levels of salinity were 0 and 5 g/kg. The two levels of competition were growth alone and growth in mixture with one of the other species. There were five replications of each treatment. For example, an analysis

of variance of *H. paradoxus* aboveground dry mass evaluated the effects of soil salinity, and the growth alone with growth with *H. annuus*. A separate analysis of variances of *H. paradoxus* aboveground dry mass evaluated the effects of soil salinity, and the growth with *H. petiolaris*. Because there were three growth parameters analyzed, there were a total of six ANOVA's performed for each species (SAS 1990). This was done because the competition between any species and a second species was independent of the other species. Total density in each pot was four plants, either four individuals of one species for growth in monoculture, or two of each species in mixture. This density was chosen because intraspecific experiments indicate that *H. paradoxus* and *H. annuus* compete at this density (Bush and Van Auken, unpublished data).

Soil was either native Patrick soil or native soil supplemented with creek water collected from the Diamond-Y Spring Preserve north of Ft. Stockton, Texas, one of only twenty-five locations where *H. paradoxus* occurs. Creek water was added to obtain a total soil salinity of 5 g/kg. The chemical composition of the creek water is presented in Table 1 (Veni 1991). Spatial and temporal

TABLE 1. Ions and their concentration found in the Diamond-Y Springs water, which was used to adjust the soil salinity in the experiment (analysis done by (Veni 1991).

Ion	Concentration (mg l ⁻¹)
Ca	500
Mg	300
Na	1250
Cl	1750
SO ₄	2450
HCO ₃	300
K	48
NO ₃	5

differences in total soil salt levels at the Diamond Y Spring Preserve have been reported between 5 and 40 g/kg (Van Auken and Bush 1998), which is mostly Cl and SO₄. Current interest was in slight growth suppression of the test species with soil salts, and changes in their competitive abilities; thus, relatively low soil salt levels were tested.

Ten weeks after initiation of the experiment, after growth had stopped, plant tops were harvested by clipping at the soil surface, separating by species, and determining dry mass by drying at 100° C to a constant mass. Ash-free belowground dry mass (Bohm 1979) was measured by carefully washing the soil from the roots, separating by species, drying to a constant mass at 100° C, weighing, ashing at 650° C for 3 hours, reweighing, and subtracting the inorganic components. The roots were easily separated by species; however, since the inorganic matter was often difficult to remove without losing finer roots, ash-free dry mass was determined for the roots. Mean dry mass or yield per plant was determined by dividing the total mass by the density, and was used to compare growth in mixture and monoculture (Van Auken and Bush 1997). There were five replications of each treatment.

COMPETITION BETWEEN HELIANTHUS PARADOXUS AND DISTICHLIS SPICATA

Total density in each pot in the sunflower-saltgrass competition experiment was six plants, either six individuals of one species for growth in monoculture, or proportions of 4:2, 3:3, or 2:4 of the species in mixture. For the salinity treatment in this experiment, 5 g/Kg NaCl was added to each pot.

Twelve weeks after initiation of the experiment and after growth had stopped, plant tops were harvested by clipping at the soil surface, separating by species, and determining dry mass by drying at 100° C to a constant mass. As previously described, ash-free belowground dry mass (Bohm 1979) was measured. Mean dry mass or yield per plant was determined by dividing the total mass by the density, and was used to compare growth in mixture and monoculture (Van Auken and Bush 1997). There were five replications of each treatment.

As previously described, ANOVA's were performed separately for each species to test the effects of soil salinity and interference on aboveground, belowground, and total dry mass (SAS 1990). Main effects and their interactions were entered into the model.

RESULTS

When *H. paradoxus* aboveground, belowground, or total dry mass was compared with *H. annuus*, ANOVA's indicated that interference (competition, monoculture versus mixture), soil salinity, and their interaction were significant factors ($P \leq 0.05$). *Helianthus paradoxus* aboveground, belowground, and total dry mass was the same, regardless of the soil salinity. However, when grown with *H. annuus* in low soil salt conditions, *H. paradoxus* relative yield or relative total dry mass was 12% compared to monoculture (100%, Table 2). When grown in higher saline soil with *H. annuus*, *H. paradoxus* relative

yield or relative total dry mass was 150% or 50% higher compared to growth in monoculture (Table 2).

When *H. annuus* aboveground, belowground, or total dry mass was compared when grown with *H. paradoxus*, ANOVA's indicated that salinity was a significant factor influencing growth or relative yield. The effects of salinity, however, were dependent on interference or competition, as indicated by a significant interaction between interference and salinity. Interference was not a significant factor by itself. The growth or relative yield of *H. annuus* was essentially the reverse of the growth response of *H. paradoxus* when they were grown together. Growth of *H. annuus* was greater in the lower saline soil than the high saline soil. In low saline soil, *H. annuus* aboveground, belowground, and total dry mass when grown with *H. paradoxus* was higher compared to *H. annuus* growth in monoculture. Relative yield of total dry mass was 136% (Table 2) or 36% higher than relative yield in monoculture. In high saline soil, relative yield of *H. annuus* when grown with *H. paradoxus* was 8%, 3%, and 5% (aboveground, belowground, and total dry mass, respectively) compared to growth in monoculture (100%). Or, for

TABLE 2. Relative yields of *Helianthus paradoxus*, *H. annuus*, and *H. petiolaris* total dry mass when they were grown with each other in low and high saline soil. Relative yield in monoculture was 100% for each species and condition.

Salinity	Species	Competitor		
		<i>H. paradoxus</i>	<i>H. annuus</i>	<i>H. petiolaris</i>
-	<i>H. paradoxus</i>	—	12	100
	<i>H. annuus</i>	136	—	166
	<i>H. petiolaris</i>	80	20	—
+	<i>H. paradoxus</i>	—	150	160
	<i>H. annuus</i>	5	—	110
	<i>H. petiolaris</i>	0	0	—

total dry mass, the relative yield of *H. annuus* when grown with *H. paradoxus* was 5% of growth in monoculture (Table 2). In addition, it should be noted that in low saline soil the dry mass of *H. annuus* in monoculture was 92% higher than *H. paradoxus* in monoculture. In high saline soil, *H. paradoxus* dry mass was 7% higher than *H. annuus* growth in monoculture.

When *H. paradoxus* aboveground and total dry mass was compared with *H. petiolaris*, ANOVA's indicated that interference (competition), salinity, and their interaction were significant factors ($P \leq 0.05$). For belowground dry mass, only salinity was a significant factor. Growth of *H. paradoxus* in low saline soil was the same, regardless of the interference (monoculture or mixture). When grown in high saline soil with *H. petiolaris*, *H. paradoxus* relative yield of total dry mass was 160% or 60% higher compared to growth in monoculture (Table 2). *Helianthus paradoxus* belowground dry mass in the high saline soil was 16% higher when growth in mixture as compared to growth in monoculture (data not presented).

ANOVA's of *H. petiolaris* aboveground, belowground, and total dry mass when grown with *H. paradoxus* indicated that only salinity was a significant factor (data not shown). The interaction plots showed that growth in low saline soil was higher than growth in high saline soil; and as indicated by the ANOVA's, growth in monoculture or mixture with *H. paradoxus* was the same. In the high saline soil, there was 100% mortality of *H. petiolaris*.

ANOVA's of *H. annuus* aboveground and total dry mass when grown with *H. petiolaris* indicated that

interference (competition) and salinity were significant factors ($P \leq 0.05$). For belowground dry mass, salinity and the interaction of salinity and interference were significant factors. Aboveground, belowground, and total dry mass of *H. annuus* in lower saline soil was greater than in higher saline soil. For *H. annuus* when grown with *H. petiolaris* in the low saline soil, relative yield of total dry mass in mixture was 166% or 66% higher than growth in monoculture (Table 2). In high saline soil, relative yield of total dry mass in mixture was 110% or 10% greater than growth in monoculture (Table 2).

The ANOVA's of *H. petiolaris* when grown with *H. annuus* indicated that interference, salinity, and the interaction term were significant ($P \leq 0.05$). Growth of *H. petiolaris* was greater in low saline soil than in high saline soil. In the low saline soil, *H. petiolaris* relative yield of total dry mass when grown with *H. annuus* was 20% when compared with monoculture (Table 2). In the high saline soil, there was 100% mortality of *H. petiolaris*. There were no mortalities of *H. annuus* or *H. paradoxus* in any of the experiments at either level of soil salinity.

When *H. paradoxus* total dry mass was compared with *D. spicata*, ANOVA's indicated that interference (competition, monoculture versus mixture) was significant ($P \leq 0.05$); but, soil salinity and their interaction were not significant factors ($P > 0.05$). When grown in monoculture, *H. paradoxus* and *D. spicata* total dry mass was the same, regardless of the soil salinity. However, when *H. paradoxus* was grown with *D. spicata* in low soil salt conditions, relative yield or relative total dry mass of *H. paradoxus* was 181-

329% compared to monoculture (100%, Table 3), depending on the proportion. The greater the proportion of *H. paradoxus*, the greater the relative yield of *H. paradoxus*. In low salt soil conditions, relative yield of total *D. spicata* dry mass in mixture with *H. paradoxus* was 9-19% compared to monoculture (100%, Table 3), depending on the proportion. The greater the proportion of *H. paradoxus*, the lower the relative yield of *D. spicata*.

When *H. paradoxus* was grown with *D. spicata* in higher saline soil, relative yield of *H. paradoxus* total dry mass was 136-184% or 36-84% higher depending on the proportion, compared to growth in monoculture (100%, Table 3). The greater the proportion of *H. paradoxus*, the greater the relative yield of *H. paradoxus*. In high soil salt conditions, relative yield of *D. spicata* total dry mass grown with *H. paradoxus* was 24-39% compared to monoculture (100%, Table 3), depending on the proportion. The greater the proportion of *H. paradoxus*, the lower the relative yield of *D. spicata*. Growth of *D. spicata* was better in the higher salt treatments, but dry mass was reduced in the presence of *H. paradoxus*.

DISCUSSION

These west Texas and New Mexico salt marshes where *H. paradoxus* is found today (McDonald 1999) were probably very important in the past for the establishment and maintenance of new populations genetically isolated from the parent species (Abbott 2003;

Rieseberg et al. 2003). The hybridization event that led to the populations of *H. paradoxus* in this area apparently occurred between 75,000 and 208,000 years before the present (Welch and Rieseberg 2002). Ecological or spatial isolation in these salt marshes allowed the original population of *H. paradoxus* to escape any minority type disadvantages and avoid interspecific competition with the parent species (Abbott 2003). Thus, the hybrid species was able to establish in ecological isolation as a result of possessing a hybrid genotype adapted to the new habitat, the salt marsh. *Helianthus paradoxus* can produce more biomass and thus out-compete its parental species (*H. annuus* and *H. petiolaris*) in saline soils similar to those found in west Texas and New Mexico salt marshes (Bush and Van Auken 2004), (Table 2).

In addition, *H. paradoxus* grows faster and produces more biomass than *Distichlis spicata* (an environmental competitor) when both species are started together at the same time (Table 3). In greenhouse studies, *H. paradoxus* can out-compete a species found at high densities in these same salt marsh environments (Fig. 1). Furthermore, *H. paradoxus* should be able to establish and out-compete *D. spicata* in the salt marsh environment. In fact, we showed

TABLE 3. Relative yield of *Helianthus paradoxus* and *Distichlis spicata* total dry mass when grown with each other in low and high saline soil. There were three different proportions of *Helianthus paradoxus* to *Distichlis spicata* (4:2, 3:3, 2:4) at a constant density of 6 plants per pot. Relative yield in monoculture was 100% for each species and condition.

Salinity	Species	Competitor					
		<i>Helianthus paradoxus</i> Proportion			<i>Distichlis spicata</i> Proportion		
		4:2	3:3	2:4	4:2	3:3	2:4
-	<i>H. paradoxus</i>	---	---	---	329	219	181
	<i>D. spicata</i>	19	17	9	---	---	---
+	<i>H. paradoxus</i>	---	---	---	184	164	136
	<i>D. spicata</i>	39	32	24	---	---	---

that neighbors including *D. spicata* reduce the growth of *H. paradoxus* in the salt marsh (Bush and Van Auken 1997) and that disturbances promote the growth of *H. paradoxus* (Van Auken and Bush 2004). Others have reported low competitive ability of *D. spicata* in coastal marine environments where it is also found (Bertness 1991a).

Helianthus paradoxus has characteristics like some other halophytes in that it can apparently actively exclude sodium and some other mineral ions (Lexer et al. 2003), it can sequester other ions (Rieseberg et al. 2003) and has increased leaf succulence (Welch and Rieseberg 2002). In addition, *H. paradoxus* is competitively superior to the parent species in slightly saline soils (Bush and Van Auken 2004, Table 2).

Hybrid species, such as *H. paradoxus*, are often shown to be more tolerant of harsh conditions than parental species. Salt tolerance of hybrid species relative to parental species is one way that that hybrid species may escape parental competition, and may determine the sites where hybrids colonize (Abbott 2003). *Helianthus anomalus*, another diploid hybrid of *H. annuus* and *H. petiolaris*, has also been shown to be a mosaic of parental-like and transgressive phenotypes (Schwarzbach et al. 2001). The fitness effects of the transgressive characters, however, are not known. In addition, some hybrids of *H. annuus* and *H. petiolaris* appear to have the genetic ‘architecture’ which allows these individuals to colonize in salt marsh habitats (Lexer et al. 2003). It has been shown that segregating hybrids commonly show traits that are extreme relative to those of their progenitors (Anderson and Stebbins 1954; Lewontin

and Birch 1966; Rieseberg et al. 1999; Rieseberg et al. 2003; Welch and Rieseberg 2002). Specifically, *H. paradoxus* is more tolerant of NaCl than its parental species, and *H. paradoxus* was found to have traits commonly associated with salt tolerance in plants (Welch and Rieseberg 2002). They found that leaf sodium concentrations and leaf succulence were statistically higher in *H. paradoxus* than its progenitors. In addition, *H. paradoxus* is also found to be more tolerant of soil salts, especially sulfate, than *H. annuus* (Mendez 2001). On the other hand, not all hybrids are found to show increased salt tolerance or phenotypic plasticity. Working with native, exotic, and hybrid species of the genus *Carpobrotus* (Aizoaceae) found in coastal plant communities throughout California, Weber and D'Antonio (1999) showed that the parental species and their hybrids were very similar in their ability to adjust to saline environments.

Some endemic species like *H. paradoxus* have morphological traits that enables them to survive in harsh environments. *Solidago shortii* Torr. & Gray, another member of the Asteraceae family, is a narrow endemic found in Kentucky. This species was shown to have morphological traits that enabled it to tolerate drier habitats than its widespread congener, *S. altissima* L. (Walck et al. 1999). While it is evident that there is a strong relationship between endemic plant species and unusual edaphic characteristics (Kruckeberg and Rabinowitz 1985), the relative role of these species response to the abiotic factors and competition in influencing distributions is debated.

In the current study with the endemic hybrid species *H. paradoxus* and its

progenitors *H. annuus* and *H. petiolaris*, the progenitors were better competitors, but only in low saline conditions. Under harsh condition (high saline soils), *H. paradoxus* reduced *H. annuus* growth indicating it has a competitive advantage (Table 2). *Helianthus petiolaris* growth was restricted in both monoculture and mixture, indicating that its lack of growth under high saline conditions results from its intolerance of the abiotic conditions rather than competition.

The role of abiotic conditions in influencing plant distributions and communities has long been recognized, and the distribution of vegetation in marshes as been shown to be dependent on species' varying tolerances to physical factors (Cooper 1982; DeJong 1978; Etherington 1984; Ewing 2000; Mahall and Park 1976a; Mendelsohn et al. 1981; Naidoo et al. 1992; Rand 2000; Schat 1984; Snow and Vince 1984; Valiela et al. 1978; Vilarrubia 2000). While water has often been found to be one of the most critical factors in determining the growth and distribution of species in marshes (El-Ghani 2000; Mahall and Park 1976a, 1976b; Onkware 2000; Rogel et al. 2001; Vilarrubia 2000), differential species tolerance to salinity has also been shown to contribute to broad zonation of coastal vegetation (Oosting and Billings 1942; Rogel et al. 2001; Vilarrubia 2000; Vince and Snow 1984). Data from this study suggests that these three *Helianthus* species do respond differently to salinity; and, that these differences may be important, in part, in determining the out-come of competition between them. The relative competitive ability of these three species in saline conditions similar to those found where *H. paradoxus* occurs is *H. paradoxus* >

H. annuus > *H. petiolaris*. The data indicate that *H. petiolaris* absence from these areas may result from its inability to grow in the higher saline conditions. However, for *H. annuus*, while the soil salinity by itself will not prevent its growth, when grown in competition with *H. paradoxus*, interference interacts with soil salinity to reduce its growth. *Distichlis spicata* does not seem to be able to prevent the establishment and growth of *H. paradoxus* in saline or non-saline soils. Based on greenhouse and limited field studies, *H. paradoxus* should be able to establish in mature stands of *D. spicata* although this has not been conclusively demonstrated.

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