

**COMPETITION BETWEEN *HELIANTHUS PARADOXUS*
(ASTERACEAE) AND *DISTICHLIS SPICATA* (POACEAE)**

O. W. Van Auken¹ and J. K. Bush²

Department of Biology¹, Department of Earth and Environmental
Sciences²

University of Texas at San Antonio

San Antonio, TX 78249, U. S. A.

oscar.vanauken@utsa.edu; janis.bush@utsa.edu

ABSTRACT

Helianthus paradoxus (Asteraceae) is a threatened annual species found in a few inland salt marshes in west Texas and New Mexico. It is a diploid hybrid species, found on saline soils where its progenitors are absent. Intraspecific competition of *H. paradoxus* was examined at various densities to determine the density at which competition occurs. In addition, the effect of soil salinity on the growth and competition between *H. paradoxus* and *Distichlis spicata* (Poaceae), a potential salt marsh competitor, was examined in greenhouse experiments. These experiments were conducted to determine the role of competition in allowing *H. paradoxus* to establish in inland salt marshes. In the intraspecific competition experiment, total dry mass of *H. paradoxus* was approximately 10 g/pot and did not change with densities from 1-16 plants/pot. Dry mass per plant of all factors measured (except flowers, which were not produced in the experiment) decreased significantly as density increased from 1 to 4 or 8 plants/pot and then remained constant to 16 plants/pot. *Distichlis spicata* was a poor competitor at both soil salinities tested and in all of the proportions of the two species tested. Results suggest that *H. paradoxus* could establish in salt marshes in the presence or absence of *D. spicata*. The ability of *H. paradoxus* to out-compete *D. spicata* at high or low salt levels indicates that gaps or disturbances in *D. spicata* vegetation would not be necessary to allow the establishment and persistence of *H. paradoxus* in the salt marsh environment.

KEY WORDS: Asteraceae, Compositae, competition, *Distichlis*, *Helianthus*, inland salt marsh, Poaceae, sunflowers, saltgrass.

INTRODUCTION

The genus *Helianthus* consists 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 (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 October.

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; Correll and Johnston 1979). *Helianthus annuus* occurs throughout North America on disturbed, heavy soils. *Helianthus petiolaris* occurs in western North America on sandy soil. *Helianthus paradoxus* is found in west Texas and New Mexico on brackish, saline, marsh soils (McDonald 1999).

Hybridization between two common sunflowers (*Helianthus annuus* and *H. petiolaris*) resulted in the production of a hybrid species, *H. paradoxus*. *Helianthus paradoxus* is an annual species based on distinct morphological characteristics (Correll and Johnston 1979), that was first described in 1958 (Heiser 1958; Heiser 1965). F₁ hybrids between *H. paradoxus* and its progenitors are largely sterile with low pollen stainability (low viability) and seed set (Heiser 1958; Heiser 1965; 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). *Helianthus paradoxus* has combined rDNA repeat types of *H. annuus* and *H. petiolaris*, and has the chloroplast genome of *H. annuus*, confirming that it arose through hybridization (Rieseberg et al. 1990; Welch and Rieseberg 2002; Lexer et al. 2003).

It has been estimated that the hybridization event that created *H. paradoxus* occurred between 75,000 and 208,000 years ago (Welch and Rieseberg 2002). For interspecific hybridization to be successful, some of the resulting offspring must survive and be fertile (Abbott 2003). In addition, the fertile hybrid must be isolated reproductively. It has been shown that *H. paradoxus* is a very poor competitor when grown with *H. annuus* in conditions similar to the habitat favored by *H. annuus* (Bush and Van Auken 2004; Van Auken and Bush 2004). If hybrids are adapted to a habitat different from that of either of the parents, hybrids could be spatially isolated from the parents and avoid any minority type disadvantages and possible negative effects of interspecific competition from its progenitors. *Helianthus paradoxus* is genetically isolated from its parents, and was able to become established and persist in a habitat different from that of either of its parents. This species is endemic to inland sulfate dominated salt marshes (McDonald 1999). Hybridization resulted in recombinants with genes and traits producing extreme phenotypes and plants that could occupy an extreme habitat compared to the parental species (Rieseberg et al. 2003). Thus, hybridization resulted in genetic recombinants that could occupy an extreme habitat.

It has been shown that *H. paradoxus* is more salt tolerant than *H. annuus* (Mendez 2001; Welch and Rieseberg 2002), and *H. paradoxus* does produce more biomass and is a better competitor when grown with *H. annuus* or *H. petiolaris* at high salt levels (Bush and Van Auken 2004; Van Auken and Bush 2004). Although experiments indicate that *H. paradoxus* can out-compete its progenitors in the extreme salt marsh environment, in order for this hybrid to persist, it must be able to compete with other established habitat competitors in an extreme habitat. *Helianthus paradoxus* has been reported to grow with *Distichlis spicata* (saltgrass) in two west Texas counties (Pecos and Reeves), two eastern New Mexico counties in the Pecos River watershed (Chaves and Guadalupe), and two western New Mexico counties in the Rio Grande watershed (Cibola and Valencia).

The largest population of *H. paradoxus* is reported from a salt marsh at the Diamond-Y Spring Preserve near Ft. Stockton, Texas (McDonald 1999). Within this marsh, there is a gradient of abiotic characteristics and vegetation as one moves from the lowest elevation in the marsh to the

upland. The change in elevation is only 1 m over a distance of between 50 and 150 m, depending on location. However, soil salinity is normally lower and soil water content higher in the drainage of the marsh, with soil salinity increasing and soil water content decreasing as one moves upland (Van Auken and Bush 1998). Immediately adjacent to the drainage in the wettest part of the marsh, *Scirpus americanus* (bulrush) is the dominant species. Moving slightly upland, populations of *H. paradoxus* can be found growing with *D. spicata*, in areas where soil salinity and soil water content are intermediate (Van Auken and Bush 1998). Further upland, the grass *Sporobolus airoides* (alkali sacaton) dominates in some areas. In similar areas, *Prosopis glandulosa* (honey mesquite) is a dominant. Finally in the driest environments, *Larrea tridentata* (creosote bush) a common Chihuahuan Desert species is dominant (Hart 2002).

The abilities of *H. paradoxus* to compete with *D. spicata* are unknown. 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). Thus, competition from neighbors could play a very important role in the establishment, ecology and management of this threatened species. Competition between plants has been studied extensively, and appears to be one of the central forces shaping the structure of plant communities (Grace and Tilman 1990). Moreover, competition is suggested to be one of the driving forces leading to temporal changes in community composition during plant succession (Bazzaz 1990). The interaction between species during succession may be competitive, neutral, or facultative (Connell and Slatyer 1977), but rarely seems to be one type. In addition, the nature of the interaction probably changes as abiotic conditions are altered.

One of the purposes of the studies presented here was to examine the intraspecific competitive abilities of *H. paradoxus* in order to determine appropriate densities to be used in the interspecific competition experiment. Secondly, the interspecific competition ability of *H. paradoxus* and *D. spicata*, a grass and a potential major environmental competitor, were examined under different soil salinity levels. We hypothesized that these two species would be equal competitors with one another, based on their co-dominance within the marsh.

METHODS

Seeds of *H. paradoxus* were collected from native plants located north of Ft. Stockton, Texas in Pecos County (31° 0.54' N, 102° 55.49' W). 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 *D. spicata* (saltgrass) 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 and placed in large plastic bags for transport to the greenhouse in preparation for the experiment. Clumps were kept in open-top plastic tubs with several centimeters of water at the bottom in the greenhouse for approximately one week prior to removal of the *D. spicata* rhizomes. 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 1,400 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). This soil was chosen because it is friable and allows for harvesting of roots. Other experiments have shown that it supports the growth of the species used in this experiment. 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 7.5 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. Because of the low nutrients in the soil, each pot was supplemented with 0.2 g N as NH_4NO_3 , 0.15 g P as Na_2HPO_4 , 0.1 g K as KCl, and 0.04 g S as MgSO_4 .

A fiberglass greenhouse was used for plant growth with photosynthetically active photon flux density (PPFD, 400-700 nm) at $37\% \pm 12\%$ of the outside mean PPFD ($1,542 \pm 18 \mu\text{mol}/\text{m}^2/\text{sec} \pm \text{SD}$

averaged over the experiment). Light level was measured with a LI-COR® LI-188 integrating quantum sensor.

Intraspecific competition—Effects of intraspecific competition were examined for *H. paradoxus* at densities of 1, 2, 4, 8, and 16 plants/pot (van den Bergh 1968). Plants were grown for 88 days after which flower, leaf, stem, aboveground (= flower + stem + leaf dry mass), belowground, and total dry mass were determined 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, drying to a constant mass at 100° C, weighing, ashing at 650° C for 3 h, reweighing, and subtracting the inorganic components. Mean dry mass per plant was determined by dividing the total mass by the density. There were five replications of each treatment.

Analyses of variance (ANOVAs) were completed for each per pot and per plant measure (leaf, stem, aboveground, belowground, and total dry mass) with density (1, 2, 4, 8, and 16) as the main effect. No flowers were produced, therefore no analysis of flower dry mass was conducted. The Scheffé Multiple Comparison Test was used to detect differences between the density treatments (SAS 1990).

Interspecific Competition—Total density in each pot in the *H. paradoxus*-*D. spicata* competition experiment was six plants, either six individuals of one species for growth in monoculture or proportions of *Distichlis:Helianthus* of 4:2, 3:3, or 2:4 for the species in mixture (van den Bergh 1968; Harper 1977). 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. Total mean dry mass per plant was determined by adding the aboveground and belowground dry mass and dividing the total mass by the density. There were five replications of each treatment.

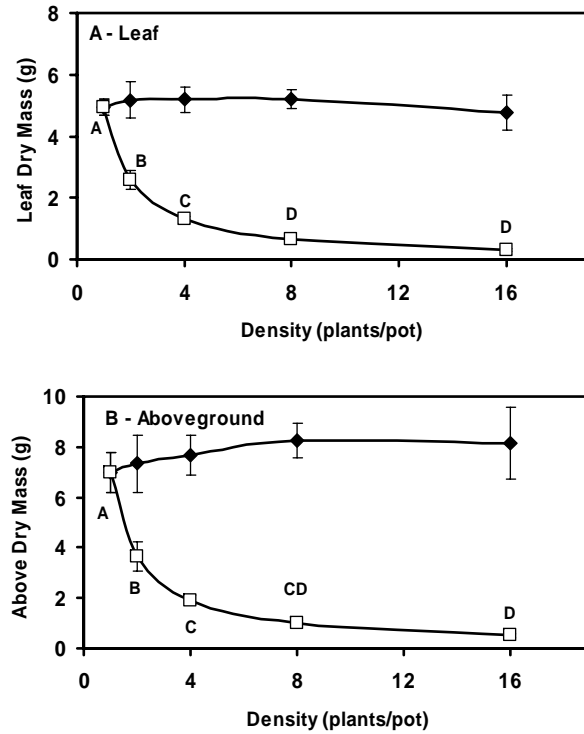


Figure 1—*Helianthus paradoxus* leaf (A) and aboveground dry mass (B) per pot (■) and dry mass per plant (□) as a function of density. There were no significant differences between any of the per pot measurements ($P > 0.05$, Scheffé Multiple Comparison Test). For per plant measures, symbols with the same letter are not significantly different ($P > 0.05$, Scheffé Multiple Comparison Test). Error bars represent one standard deviation.

ANOVA were performed separately for each species to test the effects of soil salinity (with and without NaCl) and proportion (*D. spicata*:*H. paradoxus*, 6:0, 4:2, 3:3, 4:2, and 0:6 plants/pot) on total dry mass per plant (SAS 1990). Main effects and their interactions were entered into the statistical model.

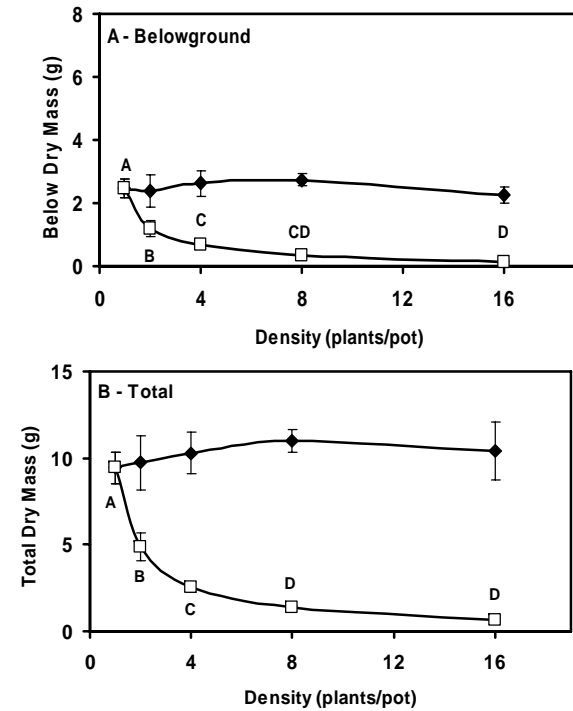


Figure 2—*Helianthus paradoxus* belowground (A) and total dry mass (B) per pot (■) and dry mass per plant (□) as a function of density. There were no significant differences between any of the per pot measurements ($P > 0.05$, Scheffé Multiple Comparison Test). For per plant measures, symbols with the same letter are not significantly different ($P > 0.05$, Scheffé Multiple Comparison Test). Error bars represent one standard deviation.

RESULTS

Intraspecific competition—For the intraspecific competition experiment, no flowers were produced, therefore flower dry mass per plant and per pot were zero for all densities (data not shown). Leaf, aboveground, belowground, and total dry mass per pot remained relatively constant over the range of densities tested and there were no significant differences among the densities (Fig. 1 and Fig. 2; One-way ANOVA; $P > 0.05$, Scheffé Multiple Comparison Test). Leaf dry mass per plant decreased with increasing densities. The leaf dry mass per

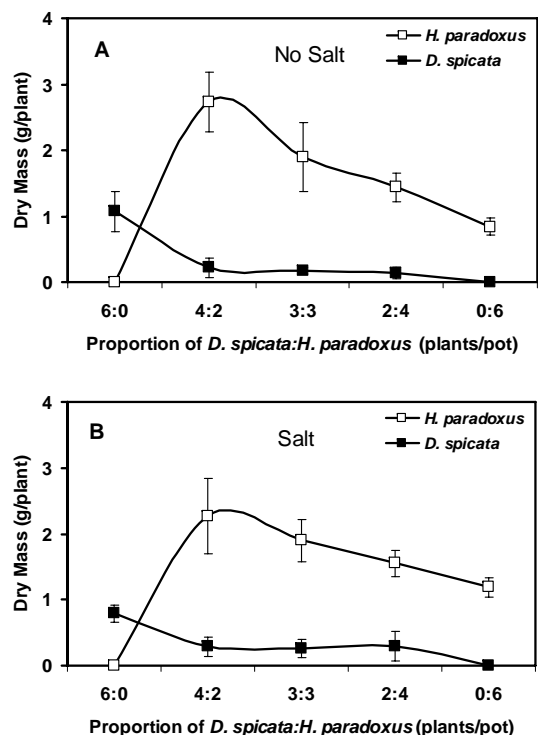


Figure 3—Dry mass (g/plant) of *Distichlis spicata* (■) and *Helianthus paradoxus* (□) without the addition of sodium chloride (A) to the soil and with the addition of sodium chloride to the soil (B). For *D. spicata*, mixture dry masses (proportions of 4:2, 3:3, and 2:4 plants/pot) were significantly lower than dry mass in monoculture (proportion of 6:0); while for *H. paradoxus*, mixture dry masses were significantly greater than dry mass in monoculture (proportion of 0:6 plants/pot).

plant at densities of 1, 2 and 4 plants/pot were significantly different from each other and from all others, while at densities of 8 and 16 plants/pot, leaf dry masses were not significantly different from one another, but were significantly lower than all other densities tested (Fig. 1a; One-way ANOVA; $P \leq 0.05$, Scheffé Multiple Comparison Test).

Source	<i>Helianthus paradoxus</i>			<i>Distichlis spicata</i>	
	df	SS	F	SS	F
Proportion	1	11.3060	87.784**	3.0773	65.944**
Salt	1	0.0003	0.002	0.0002	0.006
Proportion x Salt	1	0.7733	6.005*	0.2337	5.071*
Error	36	4.5078		1.6700	
Total	39	16.5874	31.162**	4.9812	23.673**

Table 1. Effect of proportion, salt treatment, and their interaction on the dry mass per plant of *Helianthus paradoxus* or *Distichlis spicata*. For the ANOVA of each species, there were four levels of proportion, the monoculture treatments (*D. spicata*:*H. paradoxus*; 6:0 or 0:6) and the mixture treatments (4:2, 3:3, and 2:4) and two levels of salt (with and without NaCl). * = $P < 0.05$; ** = $P < 0.0001$

Aboveground dry mass per plant (leaves and stems) and belowground dry mass per plant also decreased with increasing density (Fig. 1b and 2a). Both aboveground (Fig. 1b) and belowground (Fig. 2a) dry mass per plant at densities of 1 and 2 plants/pot were significantly different from all others, while there were no significant differences between aboveground and belowground dry mass per plant at densities of 4 and 8 plants/pot. There were also no significant differences between densities of 8 and 16 plants/pot (Fig. 1b and Fig 2a; Scheffé Multiple Comparison Test).

Total dry mass per plant also decreased with increasing densities. Total dry mass per plant at densities of 1, 2 and 4 plants/pot were significantly different from all others, while at densities of 8 and 16 plants/pot, total dry masses were not significantly different from one another, but were significantly lower than all other densities tested (Fig. 2b; Scheffé Multiple Comparison Test).

Interspecific competition— ANOVA of *D. spicata* dry mass per plant indicated that proportion (*D. spicata*:*H. paradoxus*; 6:0, 4:2, 3:3, and 2:4 plants/pot) was a significant factor in the model, as well as the interaction of proportion and soil salt treatment (Table 1). Soil salt treatment was not a significant factor by itself. Dry mass of *D. spicata* in monoculture (proportion 6:0 plants/pot) was significantly greater than dry mass in all of the mixture treatments (proportions of 4:2, 3:3, 2:4 plants/pot) regardless of salinity treatment, suggesting that interspecific competition from *H. paradoxus* was greater than intraspecific competition (Fig. 3a and b). As indicated by the significant interaction term, however, the changes in dry mass as a function of proportion were dependent on the salinity treatment. In the no salt treatment, there was a greater decrease in dry mass from monoculture (6:0 plants/pot) to the mixture treatments (4:2, 3:3, 2:3 plants/pot)(Fig. 3a) than the decrease from monoculture to mixture in the salt treatment (Fig. 3b).

ANOVA of *H. paradoxus* dry mass per plant indicated that proportion (*D. spicata*:*H. paradoxus*; 4:2, 3:3, 2:4 and 0:6 plants/pot) was a significant factor in the model, as well as the interaction of proportion and soil salt treatment (Table 1). Soil salt treatment was not a significant factor by itself; however, as with *D. spicata* dry mass, the effects of soil salinity on dry mass were dependent on density. Regardless of salt treatment, *H. paradoxus* total dry mass per plant increased with decreasing density of *H. paradoxus*, or with increased density of *D. spicata*, suggesting that intraspecific competition was greater than interspecific competition (Fig. 3a and b). At the higher density of *H. paradoxus* (0:6 proportion), dry mass of *H. paradoxus* was lower in the no salt treatment (Fig. 2a) compared to the salt treatment (Fig. 3b). *Helianthus paradoxus* (4:2 plants/pot) total dry mass was greater in the lowest density of *H. paradoxus*. In addition, *H. paradoxus* dry mass was highest in the no salt treatment (Fig. 3a) compared to the salt treatment (Fig. 3b) at this density.

DISCUSSION

The salt marshes in western Texas and New Mexico where *H. paradoxus* is found today (McDonald 1999) were probably very

important in the past for the establishment and maintenance of new populations of *H. paradoxus* that were genetically isolated from the parent species (Abbott 2003; Rieseberg et al. 2003). 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; Rieseberg et al. 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 and probably exclude its parental species (*H. annuus* and *H. petiolaris*) in saline soils similar to those found in these west Texas and New Mexico salt marshes (Bush and Van Auken 2004).

In order to become isolated from its parents in this environment, not only does *H. paradoxus* have to be able to out-compete its progenitors in this environment, but also out-compete any habitat competitors. Greenhouse experiments presented here show that, *H. paradoxus* produces more biomass and out-competes *Distichlis spicata* (an environmental competitor) when both species are started together (Fig. 3). Field studies showed that neighbors including *D. spicata* reduced the growth of *H. paradoxus* in the salt marsh (Bush and Van Auken 1997) and that disturbances including neighbor-removal promote the growth of *H. paradoxus* (Van Auken and Bush 2004). However, the growth reduction measured in the field was not seen in the greenhouse studies. This apparent anomaly may be due to the size disparity of *D. spicata* in the field at the start of the experiment compared to the relative equal size of the plants in the current greenhouse study. Or, it could be due to a temporal phenomenon. In the field experiment, *H. paradoxus* was planted into an environment with *D. spicata* and other ecosystem competitors already growing. This may put *H. paradoxus* at a disadvantage because it is a C₃ plant while *D. spicata* and the marsh grasses are C₄ plants. Others have reported low competitive ability of *D. spicata* in coastal marine environments where it is also found (Bertness 1991). They suggested that *D. spicata* is an early successional species and is soon replaced by mature community species. Curiously, *H. annuus*, one of the parental species of *H. paradoxus*, seems to be an early successional or gap species where it is found. As an annual, *H. paradoxus* would seem to require gaps, or be a

better competitor compared to *D. spicata*. We report here that it is a better competitor.

Although competition has been suggested as a major force in plant community development (Grime 1979; Tilman 1988; Keddy 1989; Grace and Tilman 1990), it is a hotly and persistently debated issue (Grace 1993; Wilson 1994; Grace 1995). There does not seem to be a question about plants growing together having reduced dry mass. The major issue concerns interference especially as resources change (Harper 1977; Grace 1993; Wilson 1994; Grace 1995). Does one plant cause interference and thus growth reduction of the second, or is differential growth of the two species merely a result of their individual growth potentials under a given set of abiotic conditions? We feel we are measuring the performance of one or both species as they respond to the imposed conditions. *Distichlis spicata* may grow better than *H. paradoxus* at higher salt levels, but this may be both species' response to salt, the abiotic factor, not to interference. However, at lower salt levels such as imposed in this experiment, *H. paradoxus* seems to be able to reduce the growth of *D. spicata* and, therefore, is the better competitor at both salt levels tested.

Helianthus paradoxus, like some other halophytes, can apparently actively exclude sodium and some other mineral ions (Lexer et al. 2003), can sequester other ions (Lexer et al. 2003), and has increased leaf succulence (Welch and Rieseberg 2002). These characteristics may have led to the competitive superiority of *H. paradoxus* in slightly saline soils compared to the parent species (Bush and Van Auken 2004).

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.

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; Welch and Rieseberg 2002; Rieseberg et al. 2003). However, not all hybrids show increased salt tolerance or phenotypic plasticity. Native, exotic, and hybrid species of the genus *Carpobrotus* (Aizoaceae) found in coastal plant communities throughout California, were very similar in their ability to adjust to saline environments (Weber and D'Antonio 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.

The role of abiotic conditions in influencing plant distributions and communities has long been recognized, and the distribution of vegetation in marshes has been shown to be dependent on species' varying tolerances to physical factors (Mahall and Park 1976a; DeJong 1978; Valiela et al. 1978; Mendelsohn et al. 1981; Cooper 1982; Etherington 1984; Schat 1984; Snow and Vince 1984; Naidoo et al. 1992; Ewing 2000; Rand 2000; 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 (Mahall and Park 1976a; Mahall and Park 1976b; El-Ghani 2000; Onkware 2000; Vilarrubia 2000; Rogel et al. 2001), differential species tolerance to salinity has also been shown to contribute to broad zonation of coastal vegetation (Oosting and Billings 1942; Vince and Snow 1984; Vilarrubia 2000; Rogel et al. 2001). However, biotic and abiotic factors seem to interact to cause the distribution of species in these inland salt marshes (Bush 2006a, 2006b). Data from this study suggests that *D. 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*. Once *H. paradoxus* is established in the *D. spicata* community, the grassland community structure probably changes. The changes could include reduced grass

cover, density and biomass and are probably caused by shading by the sunflowers, although this has not been conclusively demonstrated.

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