

RELATIVE COMPETITIVE ABILITY OF *HELIANTHUS PARADOXUS* AND ITS PROGENITORS, *H. ANNUUS* AND *H. PETIOLARIS* (ASTERACEAE), IN VARYING SOIL SALINITIES

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The effect of soil salinity on the growth and competition among *Helianthus paradoxus*, *H. annuus*, and *H. petiolaris* was examined in a greenhouse experiment to determine the role competition might have in leading to the narrow endemism of *H. paradoxus*. *Helianthus paradoxus* (the Pecos sunflower or puzzle sunflower) is a threatened annual species that is federally listed and only found in a few areas in west Texas and New Mexico. It is a diploid hybrid species that occurs in saline soils where its progenitors, *H. annuus* and *H. petiolaris*, are absent. The response of the target species to the competing species was usually dependent on soil salinity. *Helianthus paradoxus* was the better competitor in high-saline soil and *H. annuus* the better competitor in low-saline soil. Aggressivity values in low-saline soil indicated the following competitive hierarchy: *H. annuus* > *H. paradoxus* > *H. petiolaris*. In the higher-saline soils the competitive hierarchy was *H. paradoxus* > *H. annuus* > *H. petiolaris*. The ability of *H. paradoxus* to tolerate higher-saline conditions and perhaps even restrict the more geographically widespread *H. annuus* in saline soils may allow *H. paradoxus* to survive in inland salt marshes. Data presented here indicate that while *H. paradoxus* can grow in low-saline soil, competition from *H. annuus* could restrict it, leading to its narrow endemism within salt marshes.

Introduction

Helianthus paradoxus is a rare, threatened annual sunflower found in inland salt marshes in parts of western Texas and New Mexico (McDonald 1999). Understanding the habitat requirements of this species and the reasons for its limited range has been enigmatic (Bush and Van Auken 1997; Van Auken and Bush 1998). Grazing by large ungulates reduced various indicators of *H. paradoxus* growth and reproduction (Bush and Van Auken 1997). However, the presence of neighbors caused the greatest reduction in its growth and reproduction. Alternatively, disturbances like fire and tilling had positive effects on *H. paradoxus* growth, particularly in ungrazed areas (Van Auken and Bush, in press). *Helianthus paradoxus* is more salt tolerant than its parental species and has several traits that are commonly associated with salt-tolerant plants (Welch and Rieseberg 2002). This does not, however, indicate that *H. paradoxus* can outcompete its progenitors, since competition among the three species has not been evaluated. In addition, the response of *H. paradoxus* to sulfate, which is the major anion in its habitat, has not been appraised.

Physiochemical factors are often considered to be the main factors that control establishment and patterns of vegetation. In salt marshes, salinity and flooding are often thought to be the key in determining zonation patterns; however, competition has been hypothesized to play an important role in

determining the upper limits of a species' distribution along these salinity gradients (Snow and Vince 1984; Davy and Smith 1985; Bertness and Ellison 1987; Bertness 1991a, 1991b) or both the upper and lower limits (Ungar 1998). For *H. paradoxus*, a narrowly distributed hybrid endemic, both abiotic factors (specifically, soil salinity) and competition between its progenitors may contribute to its limited distribution. Its ability to tolerate higher-saline soils and even perhaps to 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 west Texas and New Mexico but not in the salt marshes of this region.

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 1958, 1965). F₁ hybrids between *H. paradoxus* and its progenitors are largely sterile, given low pollen stainability and seed set (Heiser 1958, 1965; Heiser et al. 1969). Also, *H. paradoxus* has a stable karyotype and expresses no meiotic abnormalities (Chandler et al. 1986); it 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 (Rieseberg et al. 1990; Welch and Rieseberg 2002; Lexer et al. 2003).

The genus *Helianthus* consists of ca. 67 species of annual and perennial herbs and is made taxonomically difficult by hybridization among its members (Correll and Johnston

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1979). Heiser (1965) divided the genus into four sections based on four fairly distinct phylogenetic lines. *Helianthus paradoxus* and its parent species *H. annuus* and *H. petiolaris* are annuals belonging to the same section, are obligate outcrossers, 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 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; Correll and Johnston 1979). All three species differ in their habitat preference, with *H. annuus* occurring in disturbed, heavy soils throughout North America that are wet in the spring but dry out by midsummer. *Helianthus petiolaris* occurs on sandy soil in western North America. *Helianthus paradoxus* occurs in brackish, saline marshes in 25 locations in west Texas and New Mexico (McDonald 1999). The largest population of *H. paradoxus* is found in a salt marsh associated with *Distichlis spicata* (salt grass) at the Diamond-Y Spring Preserve near Fort Stockton, Texas (Van Auken and Bush 1998).

The purpose of this study was to determine the role that competition might have had in leading to the narrow endemism of *H. paradoxus*. We evaluated the effects of soil salinity and competition on the growth of *H. paradoxus* and its two parent species, *H. annuus* and *H. petiolaris*. We hypothesized that *H. paradoxus* will be the better competitor in high-saline conditions based on the current distributions of these species. Further, in low-saline conditions, we hypothesized that the two parent species will be the better competitors, which might explain the restriction of *H. paradoxus* to these inland salt marsh areas.

Material and Methods

Seeds of *Helianthus paradoxus* Heiser, *H. annuus* Linnaeus (common sunflower), and *H. petiolaris* Nuttall (plains sunflower) were collected from native plants located north of Fort Stockton, Texas, in Pecos County, Texas (31°00.54'N, 102°55.49'W), in northwestern Bexar County, Texas (29°37'N, 98°36'W), and in central Bernalillo County, New Mexico (35°05'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 3 wk to break dormancy. Deionized water was added as needed to keep the toweling moist. On March 12, 1994, seedlings were transplanted to pots containing 1400 g of a 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) before placement into pots lined with plastic bags (to prevent nutrient, salt, and water loss). Soil analysis indicated 5–10 g kg⁻¹ carbon, 11.6 g kg⁻¹ calcium, 1.3 g kg⁻¹ magnesium, 1.0 mg kg⁻¹ total nitrogen, 12 mg kg⁻¹ phosphorus, 138 mg kg⁻¹ potassium, and 196 mg kg⁻¹ sulfur.

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 (1542 ± 18 μmol m⁻² s⁻¹, ± SD averaged over the experiment). Light level was measured with a Li-Cor LI-188 integrating quantum sensor.

The growth of each species alone was compared to the growth with each of the two other species. For each growth parameter evaluated (aboveground, belowground, and total dry mass per plant), a 2 × 2 ANOVA was used that 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⁻¹. 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 ANOVA of *H. paradoxus* aboveground dry mass evaluated the effects of salinities of 0 and 5 g kg⁻¹ and the growth alone and with *H. annuus*. A separate ANOVA of *H. paradoxus* aboveground dry mass evaluated the effects of soil salinity and the growth with *H. petiolaris*. This was done because the competition between any species and one of the others was independent of the third species. Because three growth parameters were analyzed, six ANOVAs were performed for each species (SAS Institute 1990). There was a total density in each pot of four plants, either four individuals of one species for growth in monoculture or two of each species in mixture; however, dry mass per plant, rather than per pot, was the experimental unit. This density was chosen because intraspecific experiments indicate that *H. paradoxus* or *H. annuus* compete at this density (J. K. Bush and O. W. Van Auken, unpublished data). Intraspecific experiments with *H. petiolaris* have not been conducted.

Soil was either native Patrick soil or native soil supplemented with creek water collected from the Diamond-Y Spring Preserve north of Fort Stockton, Texas, one of only 25 locations where *H. paradoxus* occurs. Creek water was added to obtain a total soil salinity of 5 g kg⁻¹. The chemical composition of the creek water is presented in table 1 (Veni 1991). Charge balance is not indicated because Fe, Al, and possibly other ions are not included. 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.

Ten weeks after initiation of the experiment and after growth had stopped, plant tops were harvested by clipping at

Table 1
Ions and Their Concentration Found in the Diamond-Y Spring Water Used to Adjust the Soil Salinity in the Experiment

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

Source. Analysis by Veni (1991).

the soil surface; they were separated by species, and dry mass was determined by drying at 100°C to a constant mass. Ash-free belowground dry mass (Böhm 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 h, 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 per plant was determined by dividing the total mass by the density.

Aggressivity for each species was also calculated with the following formulae (Harper 1977; Snyder et al. 1994; Walck et al. 1999).

$$\text{Aggressivity of } i = A_i = \frac{RY_i}{p} - \frac{RY_j}{q},$$

$$\text{Aggressivity of } j = A_j = \frac{RY_j}{q} - \frac{RY_i}{p},$$

where $RY_i = Y_{ij}/Y_{ii}$; $RY_j = Y_{ji}/Y_{jj}$; p and q = proportions of species i and j , respectively, in mixture ($p + q$) = 1; Y_{ij} (or Y_{ji}) = total yield of species i (or j) when grown with species j (or i); and Y_{ii} (or Y_{jj}) = mean total yield of species i (or j) in monoculture. The aggressiveness of each species was calculated as the mean depression it caused in the species it was grown with in mixture compared to that species grown in monoculture (Harper 1977). An aggressive species will have higher values of aggressivity than its neighboring species in the pot, while a subordinate species will have smaller (even negative) values than its neighbor.

Results

ANOVAs of *Helianthus paradoxus* aboveground, belowground, and total dry mass when grown with *H. annuus* indicated that competition (monoculture or mixture), soil salinity, and their interaction were significant factors (fig. 1A–1C). The interaction plots show that, when grown in

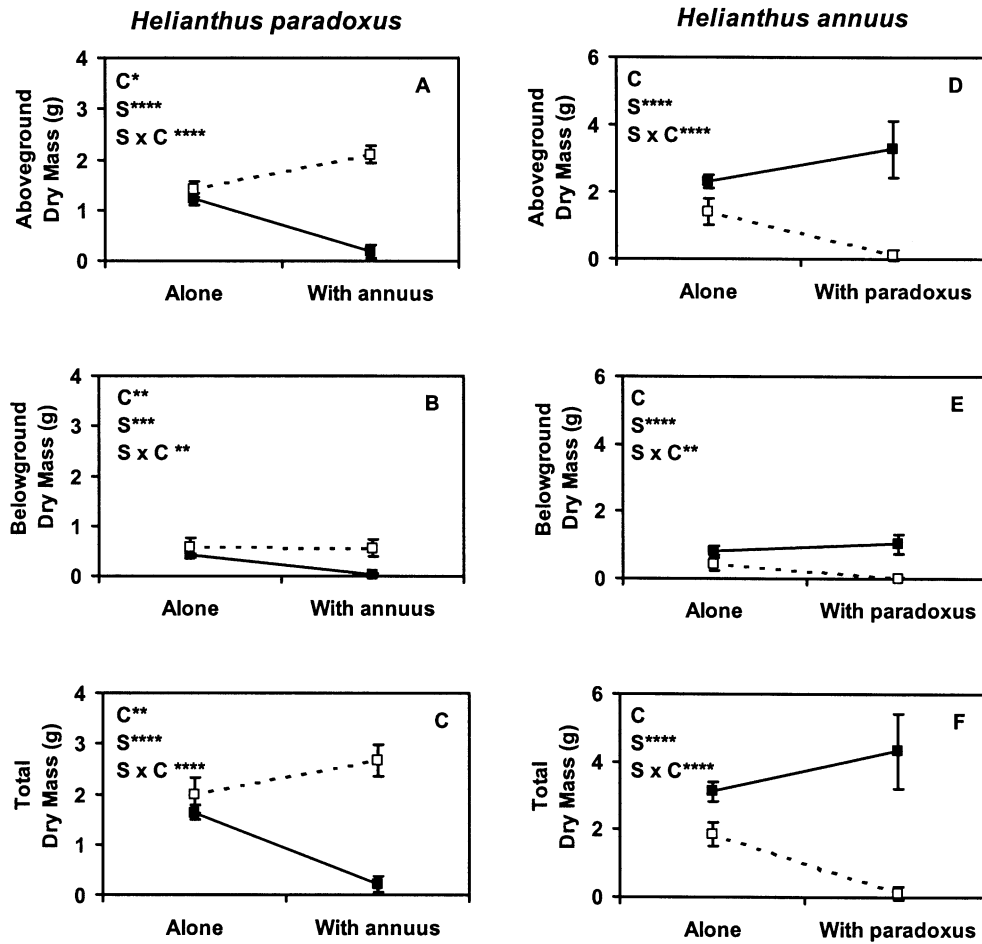


Fig. 1 *Helianthus paradoxus* aboveground (A), belowground (B), and total dry mass (g) per plant grown in monoculture or in competition with *H. annuus* (C). *Helianthus annuus* aboveground (D), belowground (E), and total dry mass (g) per plant grown in monoculture or in competition with *H. paradoxus* (F). Treatments were low-salinity soil (0 g kg⁻¹; solid square) or high-salinity soil (5 g kg⁻¹; open square). Results of ANOVA of main effects (competition, C; salinity, S) and their interaction (S x C) are also presented. One asterisk indicates $P \leq 0.05$, two asterisks indicate $P \leq 0.01$, three asterisks indicate $P \leq 0.001$, and four asterisks indicate $P \leq 0.0001$. Error bars are ± 1 SD.

monoculture (alone), *H. paradoxus* aboveground, belowground, and total dry mass was the same, regardless of the soil salinity (fig. 1A–1C). When grown with *H. annuus* in low-saline conditions, *H. paradoxus* aboveground, belowground, and total dry mass decreased by 85%, 93%, and 87%, respectively, when compared to growth in monoculture (fig. 1A–1C). When grown in higher-saline soil with *H. annuus*, aboveground and total dry mass increased by 49% and 34% when compared with growth in monoculture (fig. 1A, 1C), and belowground dry mass remained the same (fig. 1B).

ANOVAs of *H. annuus* aboveground, belowground, and total dry mass when grown with *H. paradoxus* indicated that salinity was a significant factor influencing growth. The effects of salinity, however, were dependent on competition, as indicated by the significant interaction between competition and salinity (fig. 1D–1F). Competition was not a significant factor by itself. Contrasted with the growth of *H. paradoxus*, *H. annuus* growth was greater in the lower-saline soil than in the high-saline soil. In low-saline soil, *H. annuus* above-

ground, belowground, and total dry mass when grown with *H. paradoxus* was 42%, 25%, and 38% higher when compared to growth in monoculture (fig. 1D–1F). In high-saline soil, dry mass of *H. annuus* when grown with *H. paradoxus* was 92%, 97%, and 94% lower (aboveground, belowground, and total dry mass, respectively), compared to growth in monoculture (fig. 1D–1F). 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.

ANOVAs of *H. paradoxus* aboveground and total dry mass when grown with *H. petiolaris* indicated that competition, salinity, and their interaction were significant factors (fig. 2A, 2C). For belowground dry mass, only salinity was a significant factor (fig. 2B). The interaction plots show that growth of *H. paradoxus* in low-saline soil is the same, regardless of the competition (monoculture or mixture; fig. 2A–2C). In high-saline soil, *H. paradoxus* aboveground and

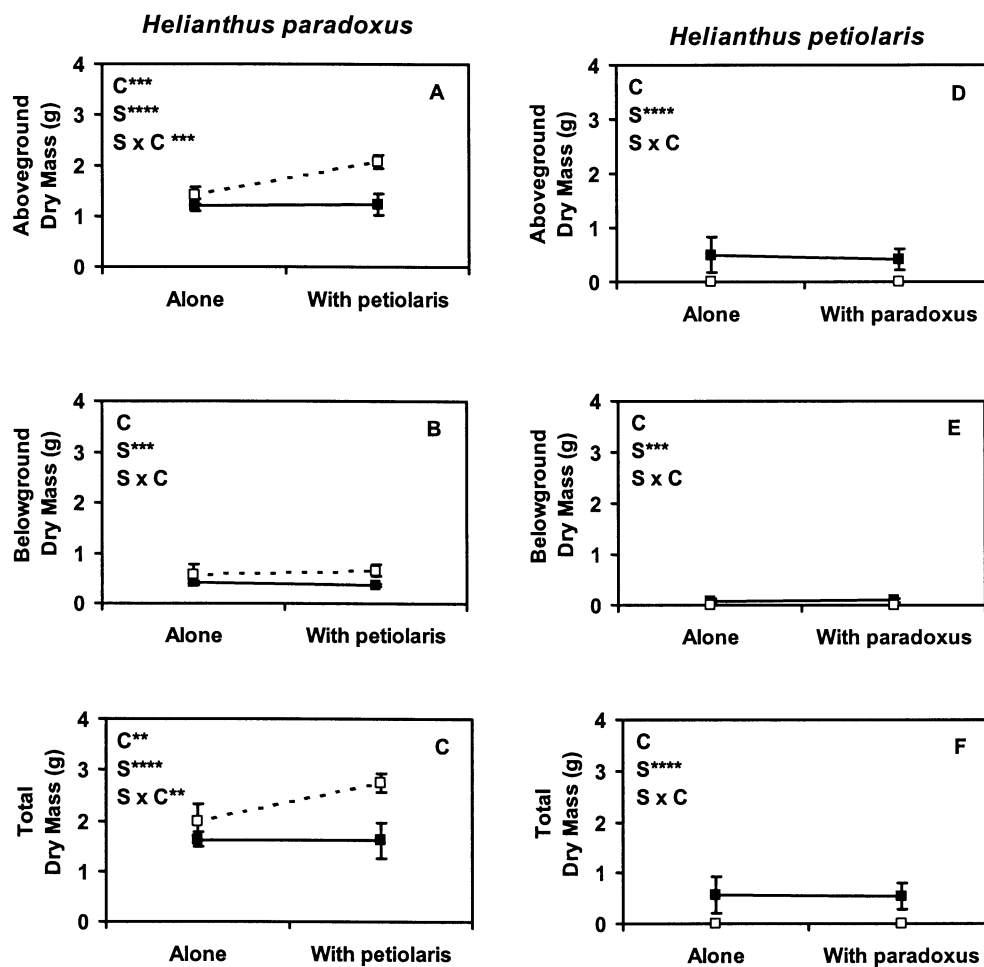


Fig. 2 *Helianthus paradoxus* aboveground (A), belowground (B), and total dry mass (g) per plant grown in monoculture or in competition with *H. petiolaris* (C). *Helianthus petiolaris* aboveground (D), belowground (E), and total dry mass (g) per plant grown in monoculture or in competition with *H. paradoxus* (F). Treatments were low-salinity soil (0 g kg^{-1} ; solid square) or high-salinity soil (5 g kg^{-1} ; open square). Results of ANOVA of main effects (competition, C; salinity, S) and their interaction ($S \times C$) are also presented. One asterisk indicates $P \leq 0.05$, two asterisks indicate $P \leq 0.01$, three asterisks indicate $P \leq 0.001$, and four asterisks indicate $P \leq 0.0001$. Error bars are $\pm 1 \text{ SD}$.

total dry mass in mixture with *H. petiolaris* was 48% and 38% higher than growth in monoculture (fig. 2A, 2C). *Helianthus paradoxus* belowground dry mass in the high-saline soil was 16% higher when grown in mixture as compared to growth in monoculture (fig. 2B).

ANOVAs of *H. petiolaris* aboveground, belowground, and total dry mass when grown with *H. paradoxus* indicated that only salinity was a significant factor (fig. 2D–2F). The interaction plots show that growth in low-saline soil was higher than growth in high-saline soil; and as indicated by the ANOVAs, growth in monoculture or mixture with *H. paradoxus* was the same (fig. 2D–2F). In the high-saline soil, there was 100% mortality of *H. petiolaris*.

ANOVAs of *H. annuus* aboveground and total dry mass when grown with *H. petiolaris* indicated that competition and salinity were significant factors (fig. 3A, 3B). For belowground dry mass, salinity and the interaction of salinity and

competition were significant factors (fig. 3B). The interaction plots indicate that aboveground, belowground, and total dry mass in lower-saline soil were greater than in higher-saline soil (fig. 3A–3C). For *H. annuus* when grown with *H. petiolaris* in the low-saline soil, aboveground, belowground, and total dry mass in mixture were 49%, 72%, and 56% higher, respectively, than growth in monoculture (fig. 3A–3C). In high-saline soil, aboveground and total dry mass in mixture was 30% and 19% greater than growth in monoculture (fig. 3A, 3C). Belowground dry mass was reduced by 12% (fig. 3B).

ANOVAs of *H. petiolaris* when grown with *H. annuus* indicated that competition, salinity, and their interaction term were significant (fig. 3D–3F). Growth was greater in low-saline soil than in high-saline soil (fig. 3D–3F). In the low-saline soil, *H. petiolaris* aboveground and belowground and total dry mass when grown with *H. annuus* were reduced

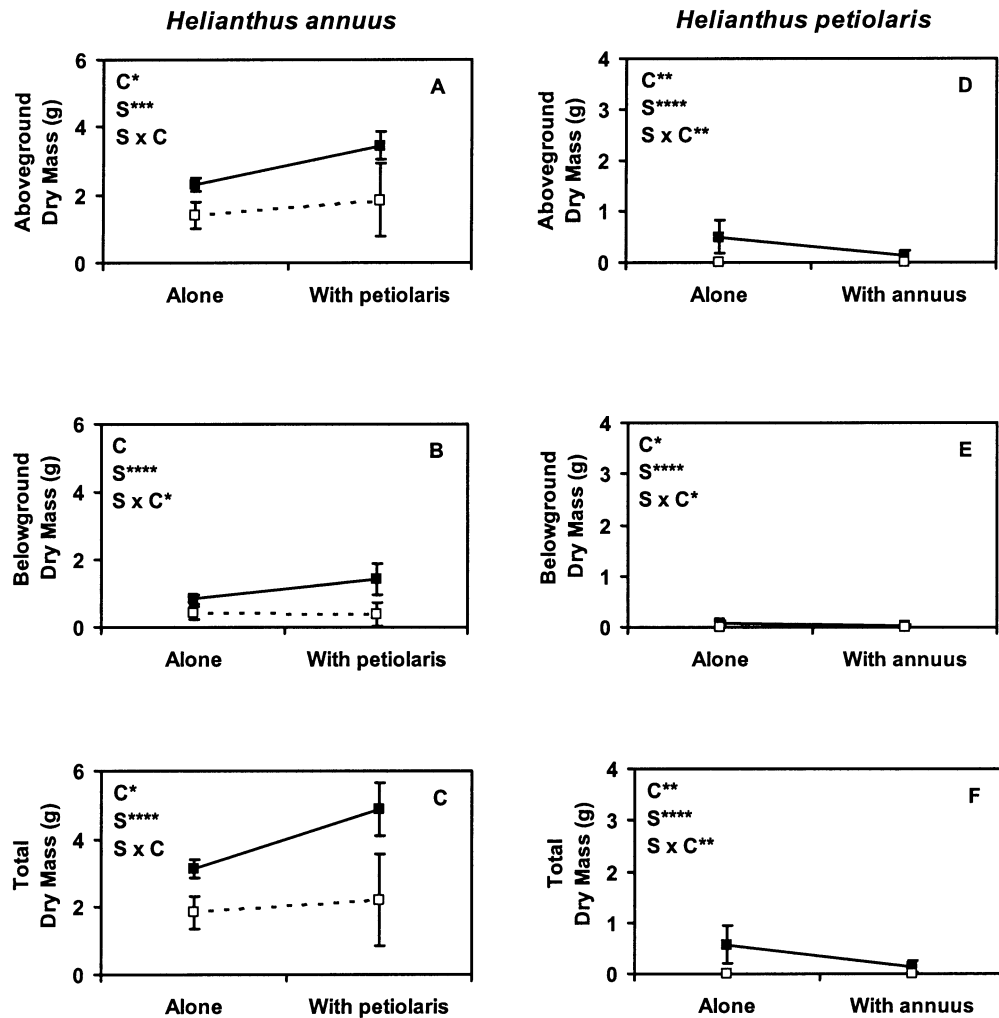


Fig. 3 *Helianthus annuus* aboveground (A), belowground (B), and total dry mass (g) per plant grown in monoculture or in competition with *H. petiolaris* (C). *Helianthus petiolaris* aboveground (D), belowground (E), and total dry mass (g) per plant grown in monoculture or in competition with *H. annuus* (F). Treatments were low-salinity soil (0 g kg^{-1} ; solid square) or high-salinity soil (5 g kg^{-1} ; open square). Results of ANOVA of main effects (competition, C; salinity, S) and their interaction ($S \times C$) are also presented. One asterisk indicates $P \leq 0.05$, two asterisks indicate $P \leq 0.01$, three asterisks indicate $P \leq 0.001$, and four asterisks indicate $P \leq 0.0001$. Error bars are ± 1 SD.

76%, 72%, and 75% when compared with monoculture (fig. 3D–3F). 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.

In the low-saline soil, the mean aggressivity value for *H. annuus* was higher (0.65) than either *H. paradoxus* (−0.13) or *H. petiolaris* (−0.52) (table 2). In the high-saline soil, however, the mean aggressivity value for *H. paradoxus* was highest (0.67), followed by *H. annuus* (−0.02) and *H. petiolaris* (−0.64) (table 2).

Discussion

Competition and salinity are important factors influencing the growth of *Helianthus paradoxus*, as well as the growth of its progenitors *H. annuus* and *H. petiolaris*, as indicated by ANOVAs. However, the species responded differently to the experimental conditions imposed.

Data presented here indicate that while *H. paradoxus* can grow in low-saline soil, competition from one of its progenitors, *H. annuus*, could restrict it in these areas, leading to the narrow endemism within salt marshes (fig. 1). In low-saline soils, the *H. paradoxus* growth rate would be about half that of *H. annuus* (fig. 1). Thus, in low-saline soils, if water were not limiting, *H. annuus* would produce about twice as much biomass as *H. paradoxus*, overgrowing it and probably shading it and further reducing its growth. *Helianthus annuus* can grow in saline soils (especially those dominated by SO_4), but growth is reduced. When grown with *H. paradoxus* in saline soils, data indicate that *H. annuus* growth is reduced further (fig. 1). In salt marshes where *H. paradoxus* is found, *H. annuus* would probably not be able to establish. If it did establish, its growth, flowering, and reproduction would probably be reduced and it would not persist in the marsh.

Spatial and temporal differences in total soil salt levels at the Diamond-Y Spring Preserve have been reported between 5 and 40 g kg^{-1} (Van Auken and Bush 1998), which is mostly SO_4 (table 1). Others have demonstrated considerable growth suppression or mortality of *H. paradoxus* or *H. annuus* at 11 g kg^{-1} NaCl (Welch and Rieseberg 2002); however, few studies have looked at the effects of NaSO_4 or mixed salts from the west Texas and New Mexico marshes on these species. Several studies have shown that a plant's

response to salinity depends on the kind of salts (sulfates or chlorides) that contribute to the salinity (Manchanda et al. 1982; Warne et al. 1990; Mor and Manchanda 1992). In one study, Na_2SO_4 was shown to be less inhibitory than NaCl to *H. paradoxus* and *H. annuus* (Mendez 2001), and Na_2SO_4 is more common in the soils of the *H. paradoxus* habitat. Current interest was in moderate growth suppression of the species from soil salinity, rather than a maximum inhibitory response. Therefore, a total salinity of 5 g kg^{-1} was chosen. We are certain that some accumulation of salts occurred, as reported previously (Rieseberg et al. 2003). However, we did not examine accumulation of salts or uptake of salts in this experiment.

Apparently, these west Texas and New Mexico salt marshes where *H. paradoxus* is found today (McDonald 1999) were very important in the past in the establishment and maintenance of populations of *H. paradoxus*, which were genetically isolated from *H. annuus* and *H. petiolaris* (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 the salt marsh apparently allowed the original population of *H. paradoxus* to avoid potential adverse effects of interspecific competition with a parent species and to escape any minority-type disadvantages (Abbott 2003). Thus the hybrid species was able to establish in ecological isolation as a result of possessing a hybrid genotype adapted to an extreme habitat, the salt marsh. *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 it has increased leaf succulence (Welch and Rieseberg 2002). In addition, *H. paradoxus* is competitively superior to the parent species in slightly saline soils (figs. 1–3).

Salt tolerance and potential phenotypic plasticity of hybrid species relative to parental species is one way that hybrid species may escape parental competition and may determine the sites where hybrids colonize (Abbott 2003). Hybrid species such as *H. paradoxus* are often shown to be more tolerant of harsh conditions. *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 that 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, 2003; Welch and Rieseberg 2002). Specifically, Welch and Rieseberg (2002) showed that *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. They found that leaf sodium concentrations and leaf succulence were statistically higher in *H. paradoxus* than its progenitors. 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

Table 2

Aggressivities of *Helianthus paradoxus*, *H. annuus*, and *H. petiolaris* When Grown with Each Other in Low- and High-Saline Soil

Species	Competitor			Overall mean
	<i>H. paradoxus</i>	<i>H. annuus</i>	<i>H. petiolaris</i>	
Low salinity:				
<i>H. paradoxus</i>	...	−0.63	0.37	−0.13
<i>H. annuus</i>	0.63	...	0.66	0.65
<i>H. petiolaris</i>	−0.37	−0.66	...	−0.52
High salinity:				
<i>H. paradoxus</i>	...	0.64	0.69	0.67
<i>H. annuus</i>	−0.64	...	0.60	−0.02
<i>H. petiolaris</i>	−0.67	−0.60	...	−0.64

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.

Endemic species like *H. paradoxus* also seem to show morphological traits that enable them to survive in harsher conditions. *Solidago shortii*, like *H. paradoxus*, 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, *Solidago altissima* (Walck et al. 1999). While it is evident that there is a strong relationship between endemic plant species and unusual edaphic characteristics (Kruckenberg and Rabinowitz 1985), the relative role of these species' response to the abiotic factors and competition in influencing distributions is debated.

Several studies have investigated the competitive abilities of endemics. Many of these studies tested the competitive abilities of the endemics with grasses and other herbaceous species, which may help in understanding the factors that affect the current or future density or distribution of the endemics. However, competitive studies between endemics and congeners or progenitors, which may better explain the development of endemism, are limited. Gottlieb and Bennett (1983) found that competitive abilities between *Stephanomeria malheurensis*, an Oregon endemic, and *Stephanomeria exigua* ssp. *coronaria*, a geographically widespread progenitor, were equal. They found that *S. malheurensis* neither gained or lost advantage when grown in mixture and, therefore, concluded that sympatry between the newly arisen species and its parent appeared to be dependent on the nature of the environment at the time of its origin. Similarly, a Tennessee cedar glade endemic, *Echinacea tennesseensis*, was found to compete slightly better than one geographically widespread relative, *Echinacea angustifolia*, and almost as well as another, *Echinacea pallida* (Snyder et al. 1994).

The endemic *S. shortii* was a poorer competitor than its widespread congener *S. altissima* (Walck et al. 1999). Similar results were found in our study with the endemic hybrid species *H. paradoxus* and its progenitors *H. annuus* and *H.*

petiolaris, but only in low-saline conditions. Under harsh conditions (high-saline soils), *H. paradoxus* reduced *H. annuus* growth, indicating that it has a competitive advantage (fig. 1). *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 from competition (figs. 2, 3).

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 (Mahall and Park 1976b; DeJong 1978; Valiela et al. 1978; Mendelssohn 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, 1976b; Weigert et al. 1983; 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; Abbott 2003). Data from our study indicate that these three *Helianthus* species do respond differently to salinity and that these differences may be important, in part, in determining the outcome of competition between them. The aggressivity 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*'s absence from these areas may result from its inability to grow in the higher-saline conditions. For *H. annuus*, the soil salinity by itself will not prevent its growth, but when grown in competition with *H. paradoxus*, competition interacts with soil salinity to reduce its growth.

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