

VEGETATION COMPOSITION ALONG SALINITY
GRADIENTS AT THE SALT PLAINS NATIONAL
WILDLIFE REFUGE, ALFALFA COUNTY,
OKLAHOMA

By

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CHAPTER I

INTRODUCTION

Understanding the factors influencing species distribution is a major focus of community ecology. Studies of changes in abundance and distribution of vegetation communities along environmental gradients provide insight into the fundamental factors influencing community composition. In particular, environmental gradients are useful in addressing questions concerning community composition due to their often sharply defined zonal communities. Salt marshes provide a model system for studying plant community patterns (Bertness 1991) because marsh vegetation exhibits conspicuous zonation (Chapman 1960) caused by differences among plant species in salinity tolerance (Hester *et al.* 1996).

In both coastal and inland salt marshes, physiological tolerance to salt and competitive ability drive patterns of vegetation zonation along salinity gradients (Wilson and Keddy 1986; Bertness and Ellison 1987; Crain *et al.* 2004; Pennings *et al.* 2005). At lower salinities, glycophytes typically displace the competitively inferior halophytes. Salt tolerance of halophytes allows their colonization of the most stressful environments where better competitors, typically glycophytes, are unable to survive the extreme conditions. Lack of competitive ability due to a physiological cost of stress tolerance (Herbst 2001) limits the distribution of halophytes into less saline areas (Shumway and

Bertness 1991; Crain *et al.* 2004; Pennings *et al.* 2005). Thus, tolerance of physiologically stressful conditions could be a mechanism to avoid competition (Herbst 2001; Bertness *et al.* 1992).

Soil salt concentrations may drive plant community structure on the salt flats of SPNWR because germination occurs near the surface where salinity is typically highest, effectively selecting for the most halotolerant species (Ungar 1966; Ungar 1968). Selection reduces the total number of successfully germinating halophyte seeds and/or delays germination until more favorable conditions arise (Ungar 1982). Most germination occurs in spring and early summer when salinities are lowest and the probability of establishment is greatest (Ungar 1982; Ungar 1996; Carter and Ungar 2003). Delaying germination until salinities are low increases the probability that the growing plant can germinate and complete its life cycle (Ungar 1982). The ability of halophytic seeds to survive hypersaline conditions distinguishes them from glycophytes (Ungar 1996). In general, older plants are more halotolerant than seedlings because their root systems are capable of reaching below the top few centimeters of salt at the surface to find fresh water (Ahi and Powers 1938; Ungar 1982).

Few studies exist on vegetation community composition along salinity gradients of inland salt marshes. Understanding community composition of inland salt marshes would help determine if inland salt marshes approximate the conditions of salt pollution more nearly than coastal marshes, because inland marshes fluctuate more widely in salinity with a less predictable disturbance regime than coastal marshes. In addition to naturally occurring coastal and inland saline environments, ecosystems are exposed to salinity stress or salt pollution from a number of sources, including drought, agricultural

irrigation in semiarid climates, road deicing (DiTommaso 2004), oil and gas production (Brokaw 2004; Aschenbach 2006), and industrial waste (Piernik 2003). Use of salinized water in landscape and agricultural irrigation has increased the use and desirability of salt tolerant turf grasses (Qian *et al.* 2000; Alshammary *et al.* 2004; Chinnusamy *et al.* 2005).

Ephemeral hypersaline environments, such as the Salt Plains National Wildlife Refuge (SPNWR), provide poor environments for life, supporting only halophytes. A stressful environment requiring high physiological tolerance causes a concurrent reduction in competitive ability, leading to low species diversity. For example, the SPNWR supports seven plant communities, six dominated by a single species with 90% or more basal cover (Ungar 1968).

At SPNWR, *Distichlis spicata* and *Sporobolus airoides* are dominant or co-dominant along the perimeter of the salt flats. *Distichlis spicata* typically borders the salt flats directly, forming a conspicuous ecotone between the salt flats and the vegetated prairie. *Sporobolus airoides* occurs on raised hummocks in the salt flats and along the perimeter of the flats where the ground is slightly elevated. With the exception of *Sesuvium verrucosum* and *Suaeda calceoliformis*, *Distichlis spicata* and *Sporobolus airoides* are the most abundant plant species that occur in the salt flats or along the perimeter, presumably at the highest salt concentrations.

To determine the salt tolerance of *Distichlis spicata* and *Sporobolus airoides*, I measured plant height, number of inflorescences, fresh weight and dry weight of shoots, relative water content, and greenness. Under the assumption that salt stress inhibits plant growth (Chartzoulakis 1994; Henley 2001; Zhu 2001; Alam *et al.* 2002; Netondo *et al.* 2004a) and reduces photosynthetic functions (Bertness *et al.* 1992; Shalhevet 1993;

Netondo *et al.* 2004b), all outcome variables were expected to decrease with increasing salinity.

The purposes of this study were 1) to characterize the vegetation community structure along salinity gradients at the Salt Plains National Wildlife Refuge (SPNWR), Alfalfa County, Oklahoma; 2) to quantify salt tolerance of two dominants at the SPNWR, *Distichlis spicata* and *Sporobolus airoides*, across a salinity gradient in the greenhouse; and 3) to quantify germination ability of *Distichlis spicata* and *Sporobolus airoides* across a salinity gradient in a laboratory experiment.

CHAPTER II

DESCRIPTION OF STUDY SITE

Study Site

The Salt Plains National Wildlife Refuge (SPNWR), Alfalfa County, Oklahoma, was established by Executive Order 5314 in 1930 on 7,875 hectares and expanded in 1941 to 13,112 hectares. Today, SPNWR occupies about 12,949 hectares, with about 4,856 hectares composed of salt flats, 3,642 hectares of a shallow, flood control reservoir, 101 hectares of freshwater ponds, and about 546 hectares of farmland (Williams 1954; USACE 1978; USFWS 1986), providing six major habitat types within the refuge: rangeland, cropland, riparian, shelterbelts, salt flats, and freshwater streams and ponds (USACE 1978). With the exception of 348 hectares of land and water immediately surrounding the dam site under control of the U.S. Army Corps of Engineers, the 12,575 hectares of reservoir and surrounding land act as Salt Plains National Wildlife Refuge, under the jurisdiction of the U.S. Fish and Wildlife Service (USACE 1947). Maximum elevation at SPNWR is 358 m and minimum elevation is 344 m (USGS 2006).

The U.S. Army Corps of Engineers impounded the Salt Fork of the Arkansas River in July 1941, primarily as a means of flood control for the Salt Fork Valley in the Arkansas River Watershed under the Flood Control Act of 1936 (USACE 1947; USACE

1963). The Great Salt Plains Dam is 12.9 km (8 miles) northeast of Jet, Oklahoma and 19.3 km (12 miles) east of Cherokee, Oklahoma, in Sec 11-T26N-R9W, N36°44'40" W98°8'8" (USACE 2006). Since impoundment, the reservoir has steadily filled with sediment supplied by the Salt Fork of the Arkansas (Arkansas-White-Red River Committee 1961). The U.S. Army Corps of Engineers (USACE, 1978) predicted the Great Salt Plains Reservoir to be completely filled with sediment by 2050.

Average annual rainfall in the area of SPNWR is 79.4 cm (NOAA 2000), most of which falls during the 207 day growing season from early April to late October (Ungar 1968). Average annual temperature for nearby Cherokee, Oklahoma is 14.3 °C, with an average annual high temperature of 21.6 °C and an average annual low of 7.1 °C (NOAA 2000). Summer afternoon soil temperatures exceed 50 °C, whereas winter air temperatures drop below 0 °C (Ungar 1968; Caton *et al.* 2004; Major *et al.* 2005; Kirkwood and Henley 2006). Summer afternoon air temperatures are routinely 40 °C, rarely reaching 45 °C.

SPNWR has been described as a saline marsh (Williams 1954), more specifically, salt water-saturated alluvial sand (USACE 1947), resulting from artesian seepage of Permian brine to the surface, causing a thin salt crust on the surface (Jenkins 1949; Williams 1954; Ward 1963). During the Permian Period, a shallow inland sea covered much of western Oklahoma, stretching from what is today west Texas to the Dakotas. Upon evaporation, the sea left a bed of gypsum and salts that now form the bedrock of the region (Johnson 1976), which is overlain between Cherokee and Jet by unconsolidated alluvium (Schoff 1950). Chapman (1960) and Waisel (1972) describe the Great Salt Plains as “hydromorphic saline” because the salinity is derived from a saline

water table near the surface. SPNWR lies within the Western Sand Dune Belts geomorphic province, which consists of “hummocky fields of grass-covered dunes” (Tyrl *et al.* 2002). The Western Sand Dune Belts dissect the central Redbed Plains of Oklahoma, which consist of rolling plains of red Permian shales and sandstones (Tyrl *et al.* 2002).

Salinities at the Great Salt Plains vary both spatially and temporally and can range from near zero to saturated, depending upon precipitation and stream flow, dropping abruptly at the edge of the flats (Richards 1947; Ungar 1968; Caton *et al.* 2004). The Great Salt Plains contribute an average of 1980 tons per day of total dissolved solids (TDS) to the Salt Fork of the Arkansas (Ward 1963; USACE 1981), resulting in an increase in TDS from a mean of 1320 ppm (= 1320 mg/L) above the flats to 6199 mg/L below the flats (USACE 1978).

Study Site Vegetation

Nomenclature follows the USDA Plants Database (USDA, NRCS 2008), except where otherwise noted. The geology of SPNWR promotes the establishment of halophytic vegetation (Chapman 1960). The salt flats *per se* are generally devoid of vegetation (Williams 1954), except near the sandy hummocks on the fringes of the flats. There Penfound (1953) noted *Sporobolus airoides* covering the tops and sides of hummocks, with *Distichlis spicata* (= *D. stricta* var. *spicata*, = *D. spicata* ssp. *stricta*) forming the border between the hummock and the salt flats. *Sesuvium verrucosum* and *Suaeda calceoliformis* (= *S. depressa*, = *S. maritima*) grow sparsely on the flats, in microhabitats provided by driftwood or grass clumps (Jenkins 1949; Grover 1979). *D.*

spicata, *Sesuvium verrucosum*, *Suaeda calceoliformis*, and *Tamarix chinensis* (= *T. pentandra*) occupy the most saline sites at SPNWR and appear to be pioneer species (Penfound 1953; Ungar 1966; Ungar 1968) on the open flats. *Sporobolus airoides* and *Sporobolus texanus* typically border these same areas (Ungar 1966).

Grasslands at SPNWR are predominately tallgrass. *A. hallii* (= *A. gerardii* ssp. *hallii*, = *A. chrysocomus*), *Sorghastrum nutans*, *Sporobolus airoides*, and *Eragrostis* spp. are abundant with *A. hallii* and *Schizachyrium scoparium* (= *A. scoparius*) scattered in the sandier soil found north of Great Salt Plains Reservoir (Williams 1954). The grasslands of Cherokee, OK are a *Stipa-Bouteloua* association, appearing as a mixed grass prairie (Bruner 1931; Ungar 1968) of *Schizachyrium scoparium*, *Bothriochloa laguroides* (= *A. saccharoides* var. *torreyana*, = *B. saccharoides* var. *torreyana*), and *Bouteloua* spp. (Bruner 1931). The sandier areas to the north of the reservoir are dominated by *A. hallii*, *D. spicata*, *Aristida oligantha*, and *Bouteloua rigidiseta* (= *Bouteloua texana* (Hitchcock 1950)) (Bruner 1931).

The Salt Fork floodplain at SPNWR is dominated by *Tamarix chinensis* (Jenkins 1949; Williams 1954; Ungar 1966; Grover 1979). In some cases, *T. chinensis* forms monospecific stands covering the entire floodplain (Williams 1954). By the late 1970s, *T. chinensis* was widespread at the refuge in dense stands around the reservoir and tributaries entering the reservoir (USACE 1978), including North Clay Creek (Glover 1979), Clay Creek, south Clay Creek, and the west branch of the Salt Fork of the Arkansas (USFWS 1980). The gradual sedimentation of the reservoir slowly creates new salt flats to the west of the reservoir, which *T. chinensis* quickly colonizes (Butler 1980). *Salix* spp. and *Melia azedarach* codominate the floodplain (USACE 1978).

CHAPTER III

MATERIALS AND METHODS

Field Observation

To record vegetation community composition and structure at SPNWR, I installed 25 belt transects parallel to the natural salinity gradient at 25 points around the perimeter of the salt flats (Figure 1). For each 50 m transect, quadrats 1-24 were in the salt flats, quadrats 25-34 were in the transition zone between the salt flats and the vegetated prairie, and quadrats 35-50 were in the vegetated prairie. Each belt transect was composed of 50 adjoining 1x1 m quadrats, with each transect measuring 50x1 m total. Transects were grouped in clusters of two to four. To reduce the bias of locating transects along the existing salinity gradient, I located an area along the perimeter of the salt flats with a pronounced salinity gradient and took its coordinates from a global positioning system (G.P.S.). I used those coordinates to choose a number from a random number table corresponding to nearby coordinates. Once the new coordinates were located, I measured 25 m into the salt flats from the vegetation line (corresponding to the conspicuous *Distichlis* sp. ecotone), which presumably occurs perpendicular to the existing salinity gradient, and marked those coordinates as the beginning of the transect with polyvinyl chloride pipe. The first two transects at SPNWR were located using the method just described, then the distance between the two was measured and halved, creating another

transect in between transects one and two, at the same time establishing the distance between transects for the remainder of the study. The direction of each transect was maintained by recording the bearing as reported by G.P.S. and by line of sight using a compass.

Along each transect, I recorded plant species present, visually estimating percent cover of each species within each 1x1 m quadrat. All transects were sampled once during spring (7-21 April 2007), once during early summer (24 May-10 June 2006), and once during fall (November 2007). One voucher specimen was collected for each taxon encountered for deposition in the OSU Herbarium.

To determine the effect of position along the transect, and thus along the salinity gradient, on percent cover of *Distichlis spicata* and *Sporobolus airoides*, I performed linear regressions (PROC REG, SAS Institute). To determine the effect of location along the salinity gradient on plant species richness, I performed linear regression (PROC REG, SAS Institute). Data from the three sampling seasons were analyzed separately.

Growth Experiment

To estimate relative salt tolerances as well as growth and physiological characteristics across a salinity gradient of two common grasses from SPNWR, *Distichlis spicata* and *Sporobolus airoides*, I collected approximately 2 m² sods of each species from established populations at SPNWR in late October 2007 for use in a greenhouse experiment. Sods of both species were separated into similarly sized clumps, washed free of soil, and transplanted into individual 2 L pots in a greenhouse, using 50:50 sand:potting soil mixture. Plants were grown under two 300 watt incandescent bulbs and

two fluorescent bulbs, using a 16:8 hour light:dark period for five months. Plants were watered as needed. After five months, individuals showing no signs of regeneration were discarded.

Following establishment, sixteen individuals of each species were randomly assigned to treatments of 0%, 1%, 2%, 3%, and 4% NaCl, with three replicates for each treatment and species (N=32). A replicate was defined as a tray to which a salinity treatment was applied containing one pot of each species. Each tray received 1.25 L of salt solution every three days for nine weeks. Prior to the addition of salt solution, each pot was flushed with 1 L freshwater to inhibit salt accumulation in the soil. Following assignment to a treatment, all plants were clipped to 15cm above the top of the pot. Experimental design was a split-plot randomized block with two blocks. I used a Minolta SPAD meter to quantify greenness weekly. Culm number (*D. spicata* only), plant height (cm), and number of inflorescences were measured weekly. Following ten weeks of salinity treatment, relative water content (Smart and Bingham 1974; Hansen *et al.* 1975), absolute water content (*sensu* Bertness *et al.* 1992; Ahmaad and Jhon 2005; Liste and Felgentreu 2006), and fresh weight (g) and dry weight (g) of leaves and inflorescences were determined for all pots. Relative water content (RWC) was calculated by determining fresh weight, turgid weight, and dry weight of samples, then by dividing the difference of fresh weight and dry weight by turgid weight. To determine RWC fresh weight, I weighed leaf samples from each plant, consisting of 2 cm of the tips of the three uppermost fully expanded leaves, then I soaked the leaf samples in water for 12 hours before re-weighing (RWC turgid weight), and then I dried the leaf samples in an at 60°C in a drying oven until each sample reached a constant weight (RWC dry weight).

Absolute water content was calculated as the difference between fresh weight and dry weight. Root fresh weight and dry weight were not calculated because it was not possible to completely remove potting medium from the root system.

To determine the effect of salinity treatment, species, salinity treatment-by-species interaction, and block on growth characteristics (difference between initial and final height and number of inflorescences) and physiological characteristics (relative water content, greenness, fresh weight and dry weight of leaves), I performed two fixed effect multivariate analyses of variance (PROC GLM, SAS Institute). For *Distichlis spicata*, I conducted separate fixed effect ANOVAs to determine the effect of salinity treatment and block on culm number and fresh and dry weight of inflorescences. Finally, to determine whether the effect of salinity on plant reproduction and greenness was due to effects on plant height, I conducted ANCOVAs with salinity treatment, species, salinity treatment-by-species interaction, and block as fixed effects and plant height as a covariate (PROC GLM, SAS Institute). To compare the strength of response of the growth and physiological variables to salinity treatment, I standardized all outcomes to a mean of zero and a standard deviation of one (PROC STDIZE, SAS Institute) before performing individual linear regressions followed by t-tests to compare the slopes of the lines of the response variables.

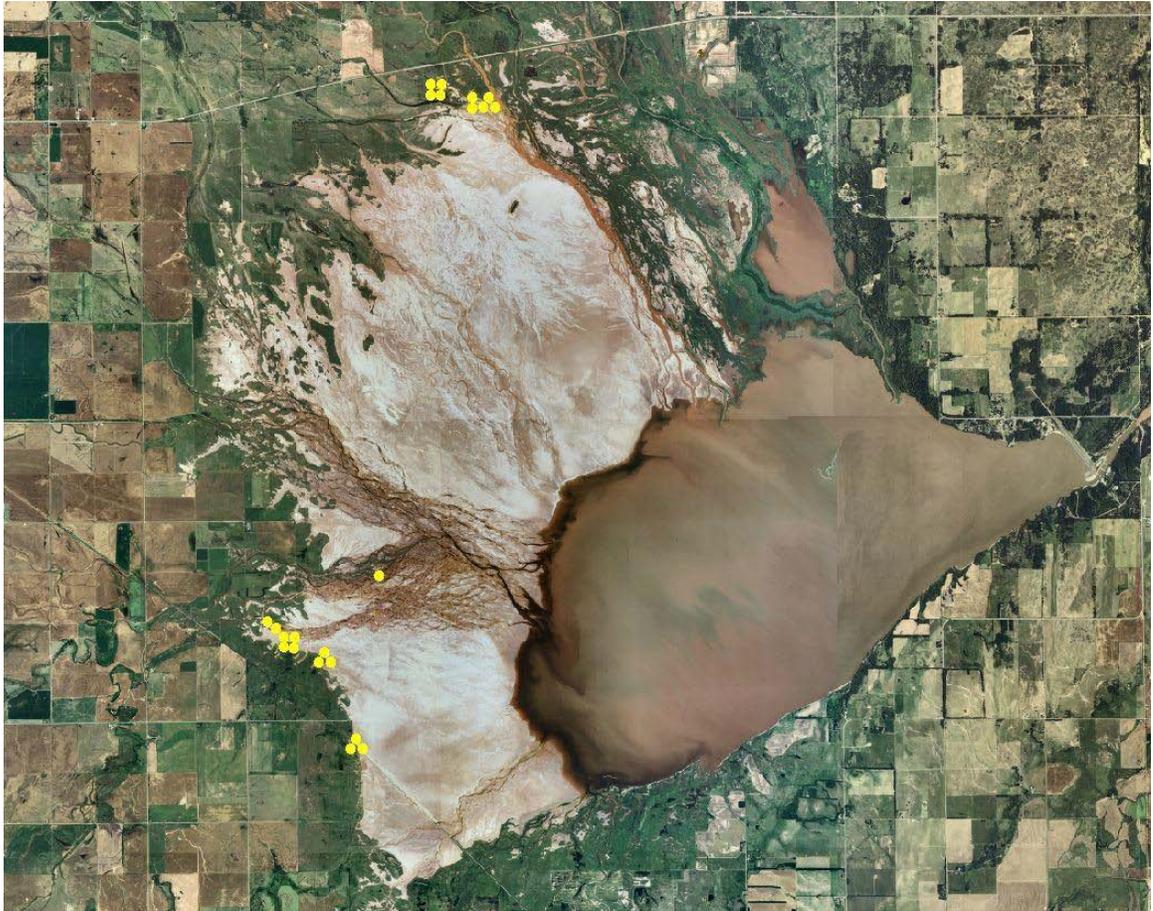
Germination Experiment

To estimate the effect of salinity on germination, seeds of *Distichlis spicata* and *Sporobolus airoides* were collected at SPNWR in November 2007 for use in a growth chamber experiment. Seeds were stored in paper bags on the laboratory shelf at room

temperature until ready for use. *Distichlis spicata* seeds were moist stratified in the dark at 4°C for one month (Shumway and Bertness 1992). Seeds of *S. airoides* were not stratified. Following stratification, 25 seeds of each species were placed in a Petri dish on filter paper. Petri dishes were randomly assigned to treatments of 0%, 1%, 2%, 3%, and 4% NaCl, with three replicates for each treatment and species. Each dish received 5mL of salt solution at the beginning of the experiment and was sealed with Parafilm. Additional solution was added in 1 mL increments as needed to maintain saturation of the filter paper throughout the duration of the experiment. Petri dishes were placed in a Percival growth chamber using a 14:10 hour light:dark period with a corresponding 30:18°C thermoperiod. Experimental design was a randomized block with three blocks. Over a 21 day period, I monitored Petri dishes daily for germination. After a seed was scored as germinated, I removed it from the Petri dish (Ungar 1996; Badger and Ungar 1994). Germination was defined as the radicle reaching a length of 2mm (cited in Khan and Gulzar 2003). Percent germination was calculated for each Petri dish (Okçu *et al.* 2005).

To determine the effect of salinity treatment, species, salinity treatment-by-species interaction, and block on percent germination, I conducted a fixed effect ANOVA (PROC GLM, SAS Institute) as well as linear regression (PROC REG, SAS Institute).

Figure 1. Aerial photograph of the Salt Plains National Wildlife Refuge. Transect locations are represented by dots.



CHAPTER IV

RESULTS

Field Observation

Vegetation composition along salinity gradients at SPNWR varied noticeably (Figures 2-4). Generally, only very small populations or isolated individuals of *Suaeda calceoliformis* and *Sesuvium verrucosum* inhabited the open salt flats. *Distichlis spicata* formed monospecific stands along the edge of the salt flats, in the transition zone between the open salt flats and the vegetated prairie. *Sporobolus airoides* often co-occurred with *D. spicata* along the prairie edge of the transition zone but also formed monospecific stands in some areas. Width of the transition zone depends on the steepness of the change in the elevational gradient between the salt flats and the vegetated prairie. When the elevation change was abrupt, the transition zone was narrow, only 1-2 m wide in some cases. When the elevation change was more gradual, the transition zone was wider, sometimes up to 20 m. Co-occurrence of *Distichlis spicata* and *Sporobolus airoides* most often occurred when the elevation gradient was very steep, increasing 1-2 m in a vertical escarpment. In the spring, *Poa arachnifera* occurred in the transition zone with *D. spicata* and *S. airoides*.

Toward the vegetated prairie from the transition zone, tallgrasses and forbs increased dramatically in abundance, typically displacing *Distichlis spicata* and *Sporobolus airoides*. Common species of the tallgrass prairie, such as *Ambrosia*

psilostachya, *Andropogon hallii*, *A. gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, and *Sorghastrum nutans*, inhabited areas elevated above the open salt flats and transition zone. Other forbs typical of prairie communities also occurred in areas elevated above the salt flat, including *Achillea millefolium*, *Apocynum cannabinum*, *Helianthus annuus*, *H. ciliaris*, *H. petiolaris*, *Liatris* sp., and *Salvia azurea*.

Along the western edge of the salt flats, approximately 200 m south of Clay Creek, a small, dense stand of *Prunus angustifolia* dominated the upland with *Yucca glauca* occasionally present. Several hundred meters south of the *Prunus angustifolia* stand, *Baccharis salicina* formed small clumps of nearly monospecific stands, almost entirely in habitats elevated above the salt flats by approximately 2 m. Tallgrass prairie species, listed above, bordered these clumps of *Prunus angustifolia* and *Baccharis salicina*. Along the northeastern border of the salt flats, in sandier, wetter areas in the floodplain of the Salt Fork of the Arkansas, but at the same approximate distance from the salt flats as *Prunus angustifolia* and *Baccharis salicina*, *Baccharis salicina* was absent. Instead, tallgrass prairie species occurred intermixed with *Juncus torreyi*, *Schoenoplectus americanus*, and *Chamaecrista fasciculata*.

While dominated by native species, the vegetated prairie had notable populations of exotic species, including *Bromus tectorum*, *Commelina communis*, *Medicago sativa*, *Polypogon monspeliensis*, *Salsola tragus*, *Thinopyrum ponticum*, and *Tamarix chinensis*.

Tamarix chinensis was the most abundant exotic species, dominating riparian areas, often forming monotypic stands, but sometimes with a sparse understory of *Distichlis spicata* and *Sporobolus airoides*. *Bromus tectorum* was the second most abundant exotic species, usually forming dense populations within tallgrass communities.

Salsola tragus was more common in the sandier soils on the northern edge of the salt flats, but occasionally occurred elsewhere. *Commelina communis* occurred infrequently along the northern and northeastern edges of the salt flats. *Thinopyrum ponticum* and *Polypogon monspeliensis* occurred only rarely on the northern edge of the salt flats. *Medicago sativa* occasionally occurred along the western edge of the salt flats.

Percent cover of both *Distichlis spicata* (spring, $y=0.232x + 0.033$, $r^2=0.2880$, $P<0.0001$; summer, $y=0.343x + 0.407$, $r^2=0.2059$, $P=0.0009$; fall, $y=0.423x + 0.794$, $r^2=0.2252$, $P=0.0005$) and *Sporobolus airoides* (spring, $y=0.353x - 2.028$, $r^2=0.8289$, $P<0.0001$; summer, $y=0.232x - 0.808$, $r^2=0.7604$, $P<0.0001$; fall, $y=0.313x - 2.099$, $r^2=0.7474$, $P<0.0001$) increased with distance from the salt flats. *D. spicata* showed a pronounced peak in abundance in the transition zone, but *S. airoides* steadily increased with distance from the salt flats (Figures 5-7).

Similarly, species richness increased with distance from the salt flats (spring, $y=0.07626x - 0.598$, $r^2=0.8821$, $P<0.0001$; summer, $y=0.07286x - 0.567$, $r^2=0.8815$, $P<0.0001$; fall, $y=0.07405x - 0.608$, $r^2=0.8867$, $P<0.0001$). Species richness per quadrat ranged from 0 to 6 species m^{-2} . Species richness was ≤ 2 species m^{-2} for the quadrats in barren salt flats (quadrats 1-24), and steadily increased to the maximum of 6 species m^{-2} at the furthest quadrats away from the salt flats (Figure 8).

Figure 2. Mean percent cover + SE in spring 2007 of six common species along a salinity gradient at the Salt Plains National Wildlife Refuge.

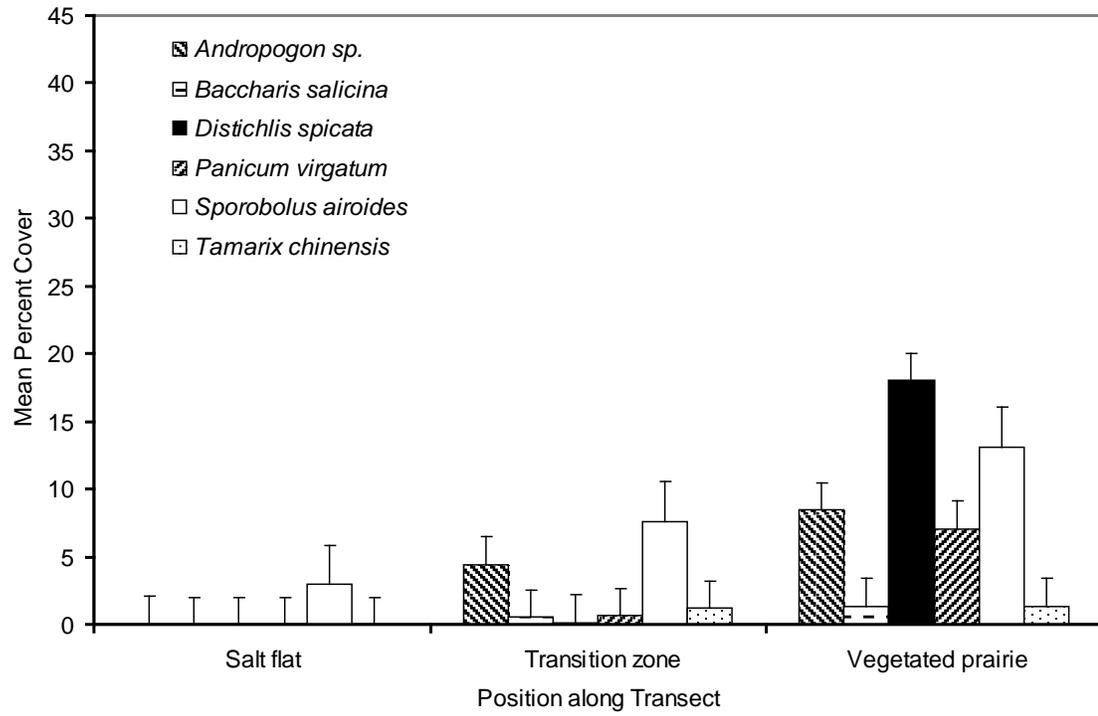


Figure 3. Mean percent cover + SE in summer 2006 of six common species along a salinity gradient at the Salt Plains National Wildlife Refuge.

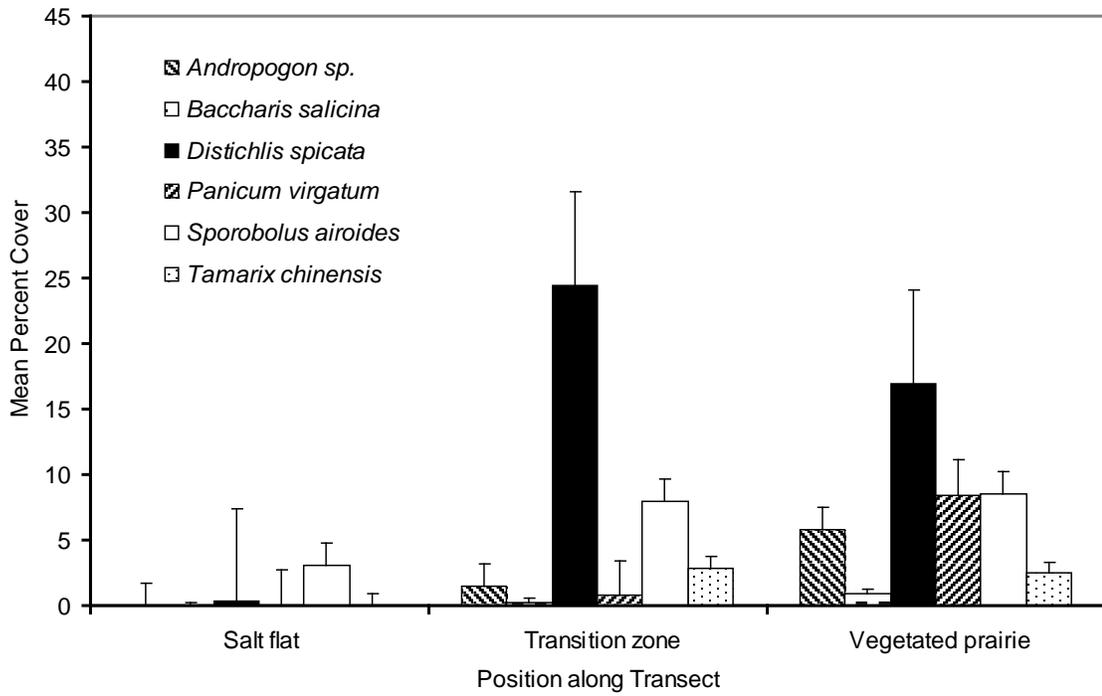


Figure 4. Mean percent cover + SE in fall 2007 of six common species along a salinity gradient at the Salt Plains National Wildlife Refuge.

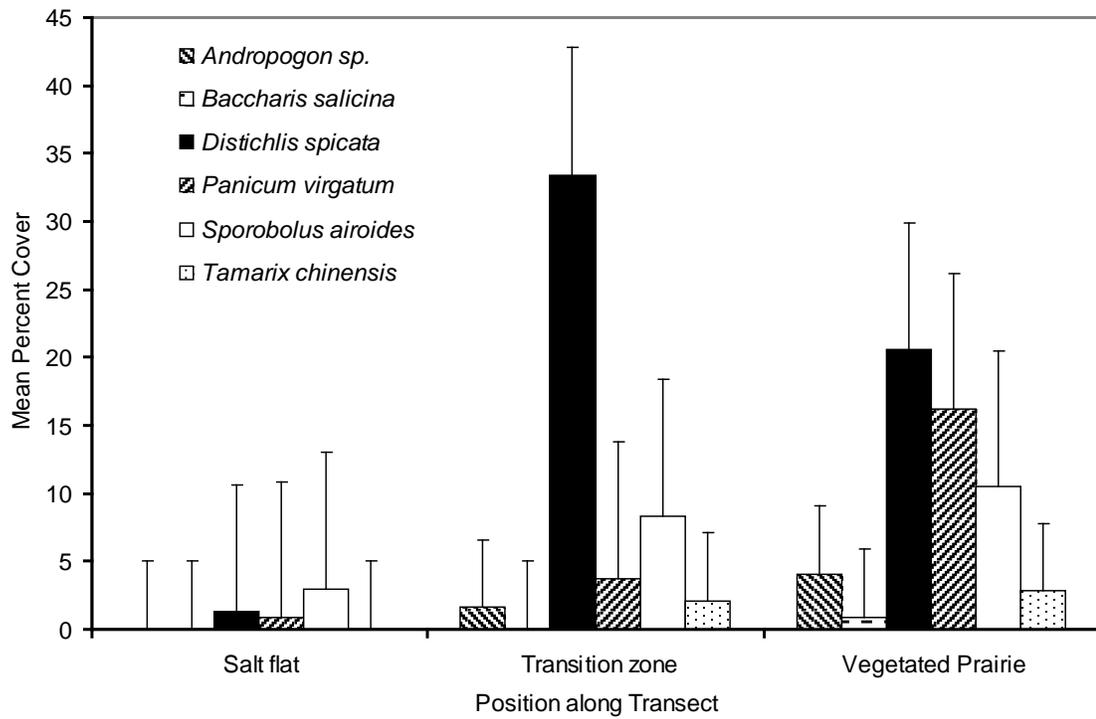


Figure 5. Mean percent cover in spring 2007 for *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient at the Salt Plains National Wildlife Refuge. Transects begin in the salt flats.

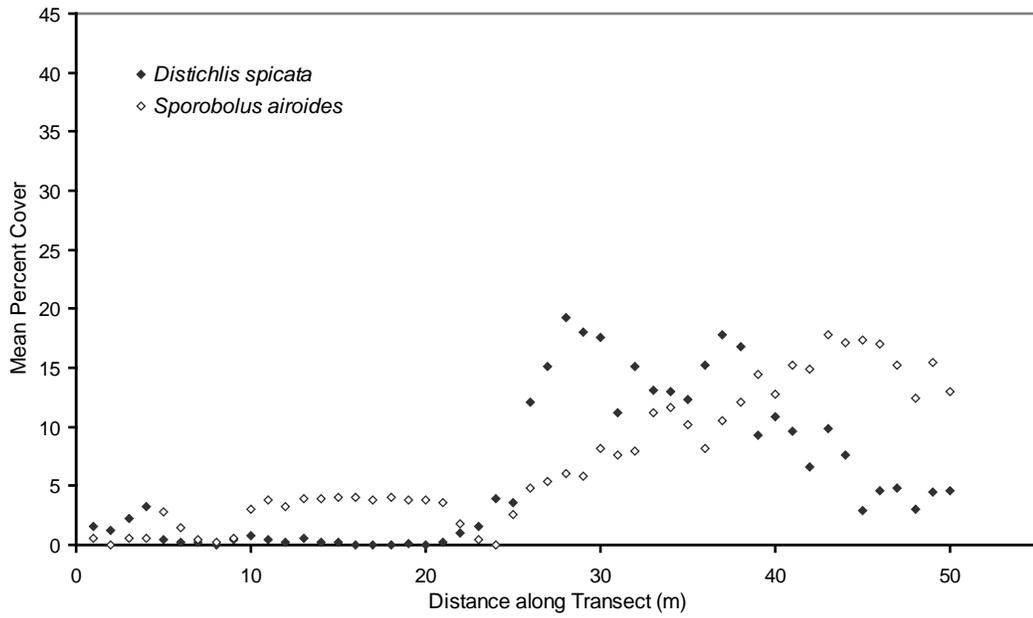


Figure 6. Mean percent cover in summer 2006 for *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient at the Salt Plains National Wildlife Refuge. Transects begin in the salt flats.

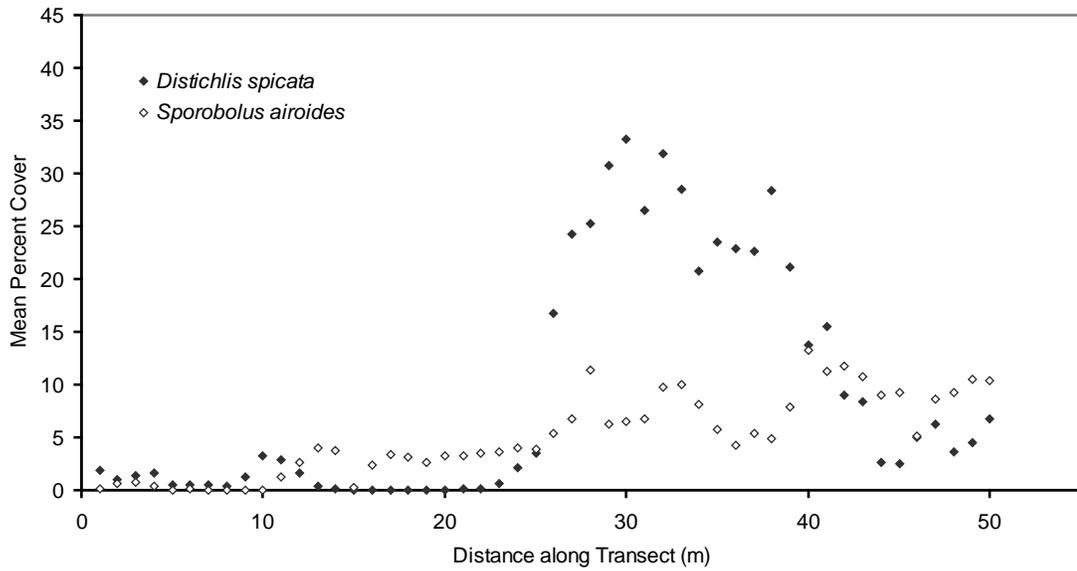


Figure 7. Mean percent cover in fall 2007 for *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient at the Salt Plains National Wildlife Refuge. Transects begin in the salt flats.

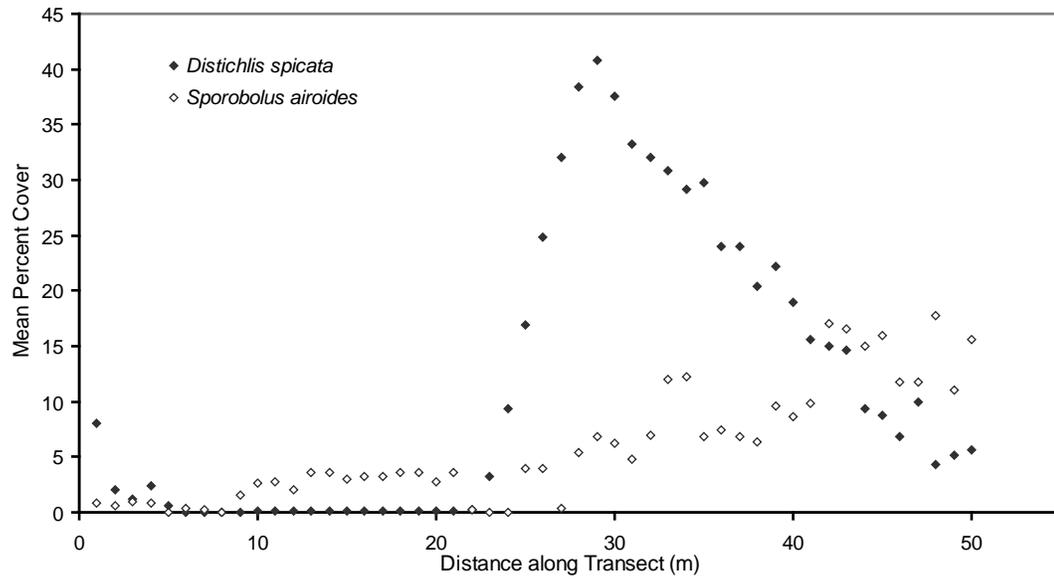
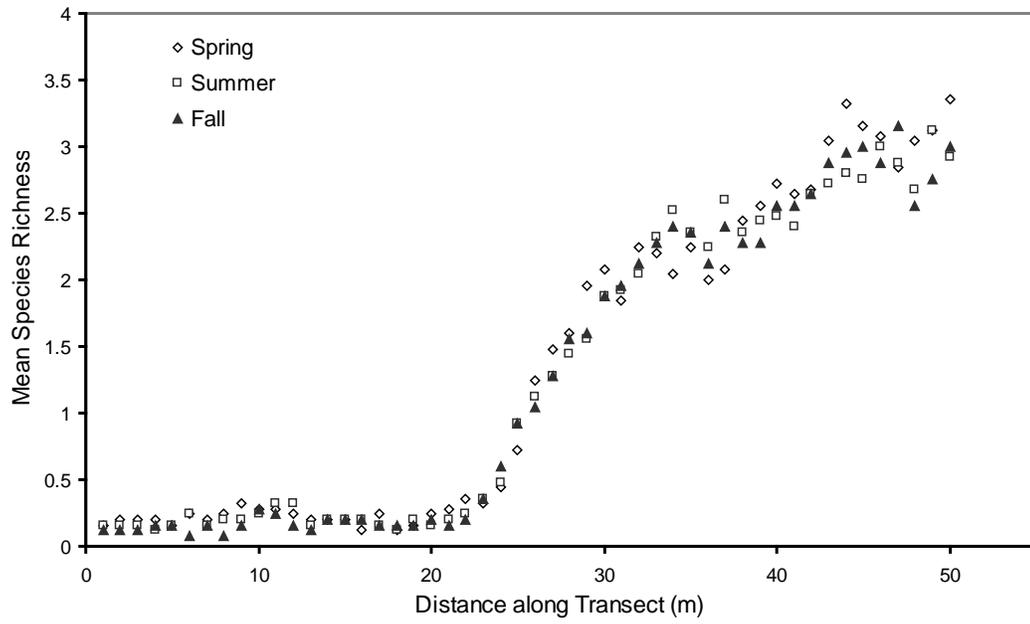


Figure 8. Mean species richness in spring, summer, and fall, averaged across all transects at the Salt Plains National Wildlife Refuge. Transects begin in the salt flats.



Growth Experiment: Treatment effects and species-by-treatment interactions

Salinity treatment significantly affected the response of growth and reproduction traits (MANOVA overall treatment effect: $F_{8,40} = 5.60$; $P < 0.0001$). Salinity treatment significantly affected plant height ($F_{4,21} = 9.55$, $P = 0.0001$, Figure 9). Pooled across species, plants in the 1, 2, 3, and 4% NaCl treatments were 7, 19, 19, and 23% shorter, respectively, than the 0% NaCl treatment (Figure 9). Number of inflorescences was also significantly different between treatments ($F_{4,21} = 4.56$, $P = 0.0083$, Figure 10). Across species, plants in the 1, 2, 3, and 4% NaCl treatments having 37, 7, 57, and 37% as many flowers, respectively, as the 0% NaCl treatment. Species-by-treatment interaction was significant (MANOVA overall species*treatment effect: $F_{8,40} = 3.44$; $P = 0.0042$). Species by treatment interaction was significant for height and number of inflorescences ($P = 0.0172$; $P = 0.0413$, respectively).

Physiological traits were significantly affected by salinity treatment (MANOVA overall treatment effect: $F_{16,56} = 2.44$; $P = 0.0072$). Greenness differed significantly between treatments. Across both species, the 1, 2, 3, and 4% NaCl treatments were 16, 21, 20, and 22% greener than the 0% NaCl treatment, respectively ($F_{4,21} = 2.76$, $P = 0.0546$, Figure 11). However, most of the difference was attributable to *S. airoides*. Relative water content did not differ significantly between treatments ($F_{4,21} = 1.48$, $P = 0.2446$, Figure 12).

Fresh weight of leaves was significantly different between treatments ($F_{4,21} = 5.41$, $P = 0.0037$, Figure 13). Pooled across species, the 1, 2, 3, and 4% NaCl treatments had 29, 30, 50, and 29% of the leaf biomass of the 0% treatment. Dry weight of leaves was significantly different between treatments ($F_{4,21} = 7.30$, $P = 0.0008$, Figure 14). Pooled

across species, the 1, 2, 3, and 4% NaCl treatments, had respectively 33, 32, 54, and 36% as much dry leaf biomass as the 0% NaCl ($F_{4,21}= 7.30$, $P=0.0008$, Figure 14). Species-by-treatment interaction (MANOVA overall species*treatment effect: $F_{16,56}= 1.18$; $P=0.3157$) and block effect (MANOVA overall block effect: $F_{4,18}= 1.57$; $P=0.2246$) were not significant.

Salinity treatment did not significantly affect fresh weight of inflorescences ($P=0.2314$, Figure 15) or dry weight of inflorescences ($P=0.3055$, Figure 16) of either *D. spicata* or *S. airoides* or the number of culms in *D. spicata* ($P=0.2381$, Figure 17).

Growth Experiment: Species differences

The two species, *D. spicata* and *S. airoides*, differed significantly in response of growth variables (difference in initial and final height (cm) and flower number) (MANOVA overall species effect: $F_{2,20}= 395.96$; $P<0.0001$). *S. airoides* was three times taller and had approximately 22 times more inflorescences than *D. spicata* ($F_{1,21}= 773.19$, $P<0.0001$; $F_{1,21}= 180.57$, $P<0.0001$, respectively).

Likewise, the two species differed significantly in the response of the physiological variables (final greenness, relative water content, fresh and dry weight (g) of leaves; MANOVA overall species effect: $F_{4,18}= 27.59$; $P<0.0001$). *S. airoides* was 47% greener, had 8% higher relative water content, 99% heavier fresh weight of leaves, and 98% heavier dry weight of leaves than *D. spicata* ($F_{1,21}=63.34$, $P<0.0001$; $F_{1,21}=1.30$. $P=0.2666$; $F_{1,21}=68.86$, $P<0.0001$; $F_{1,21}=49.10$, $P<0.0001$, respectively).

Figure 9. Mean height \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

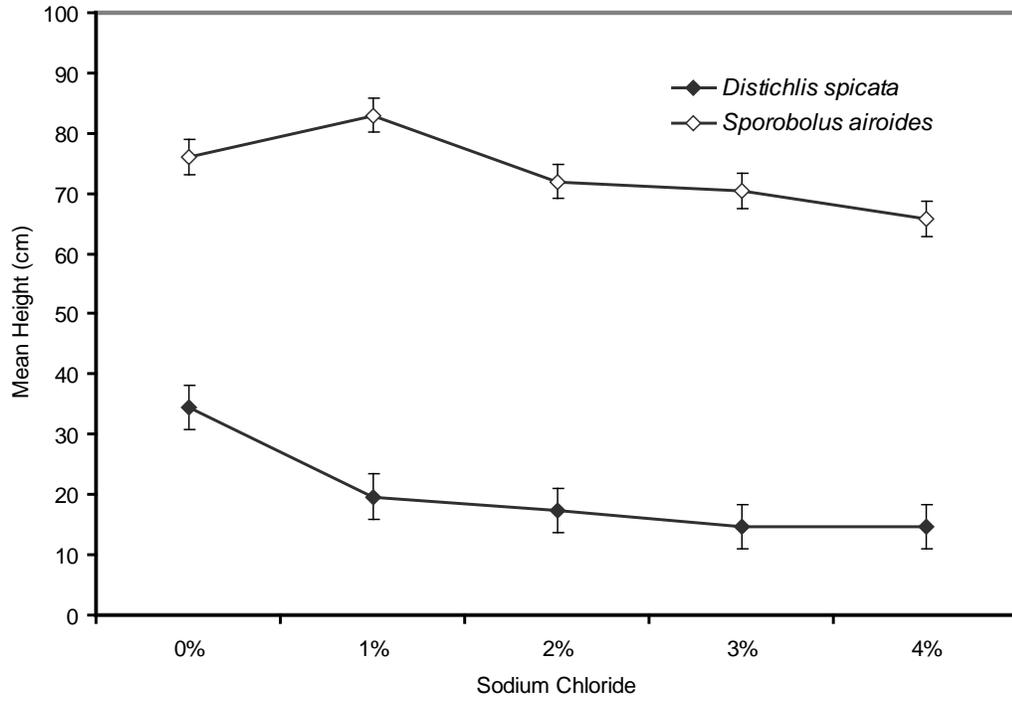


Figure 10. Mean number of new inflorescences \pm SE in *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

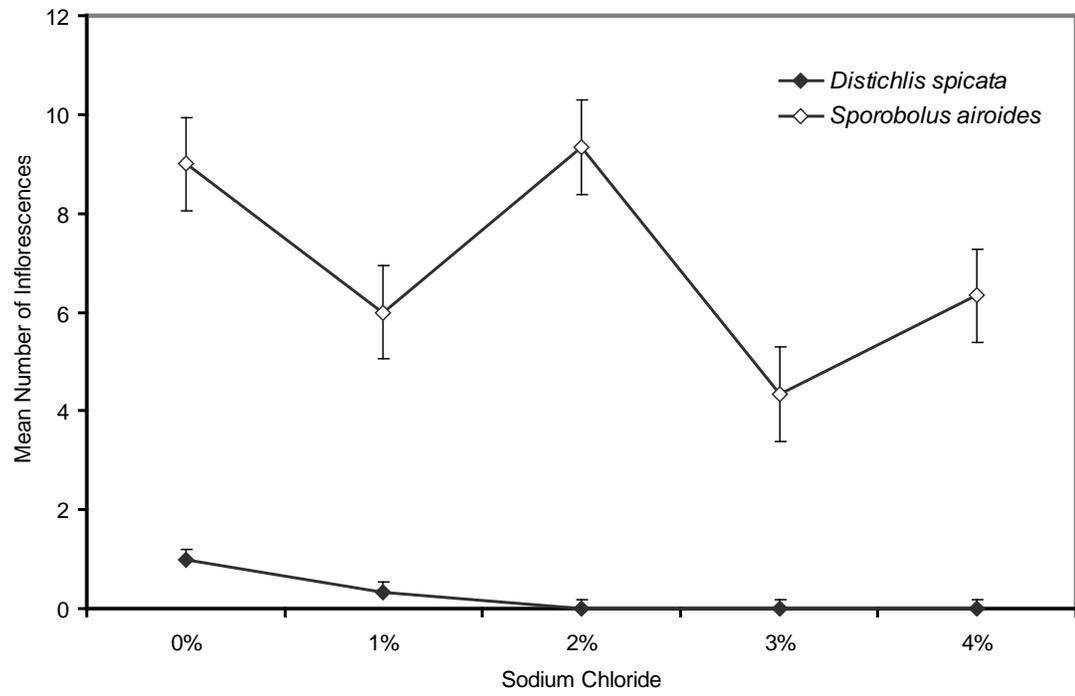


Figure 11. Mean greenness \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

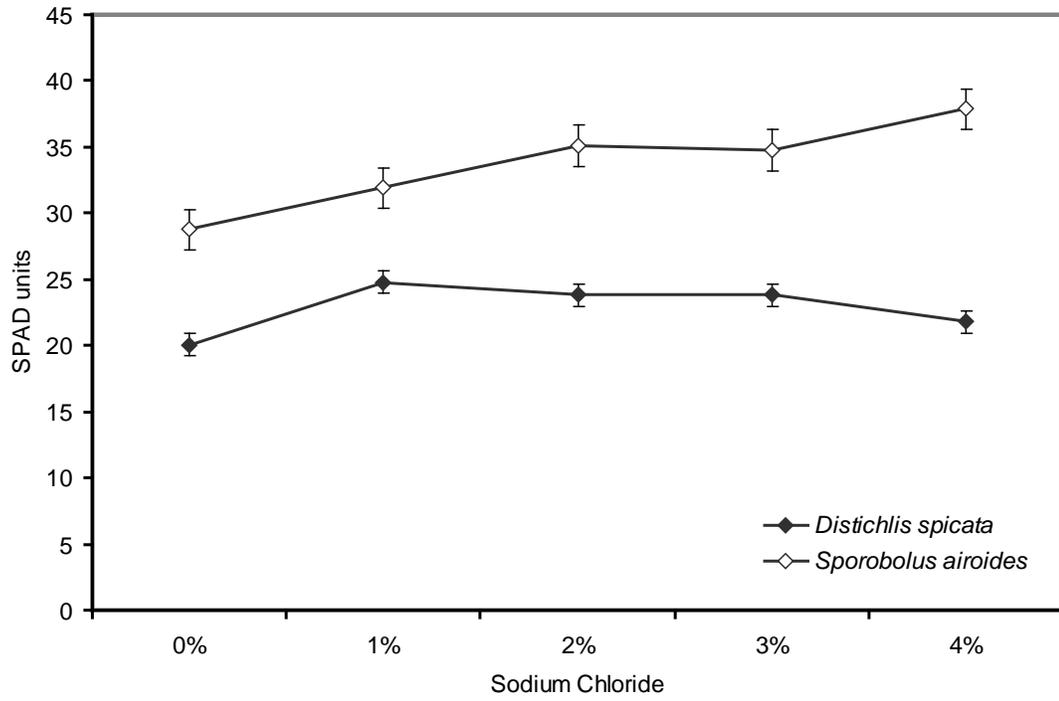


Figure 12. Mean relative water content \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

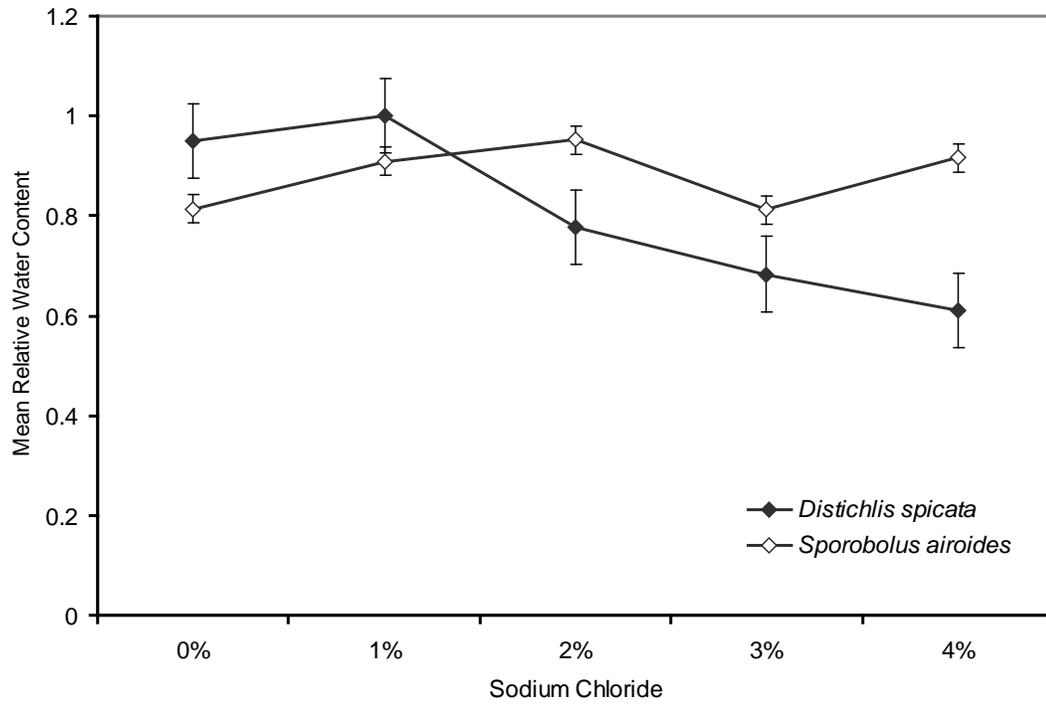


Figure 13. Mean fresh weight of leaves \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

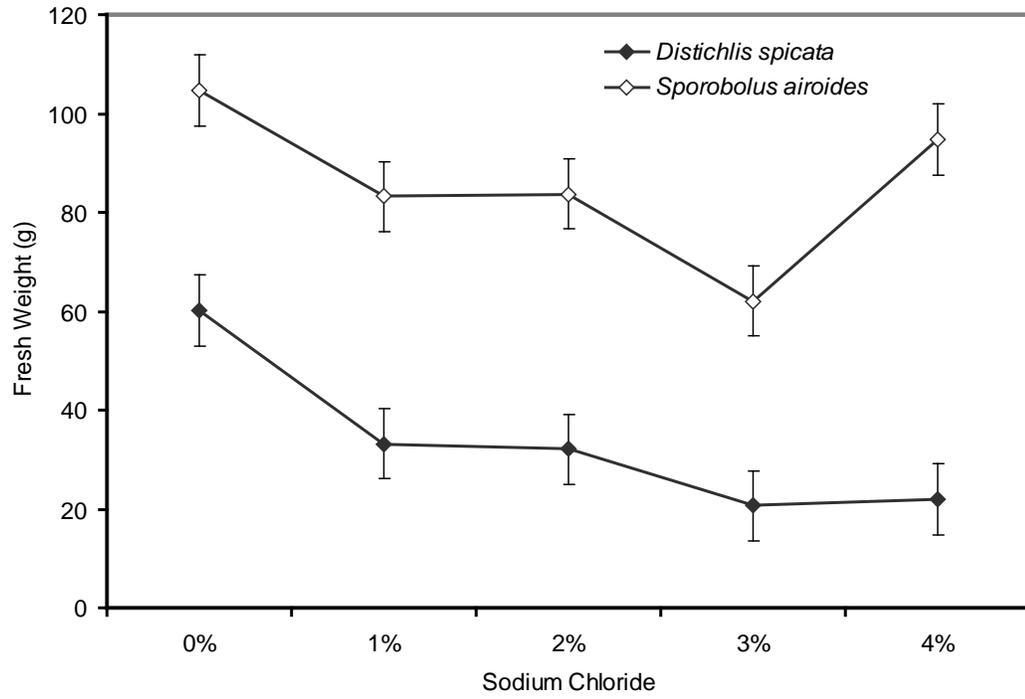


Figure 14. Mean dry weight of leaves \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

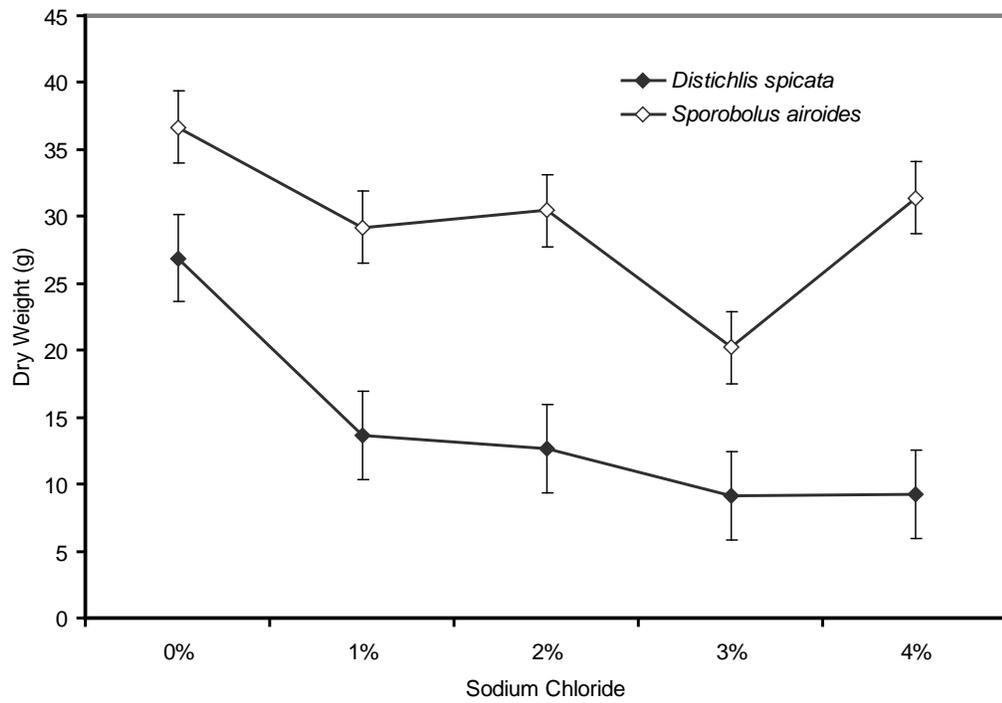


Figure 15. Mean fresh weight of all inflorescences \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

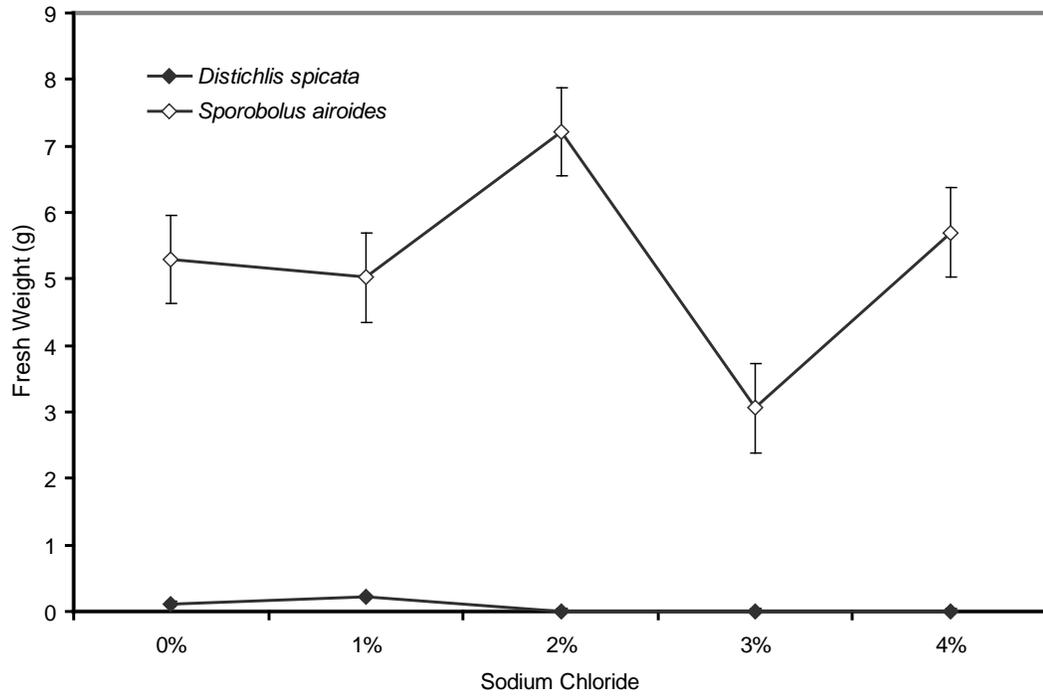


Figure 16. Mean dry weight of inflorescences \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in the greenhouse.

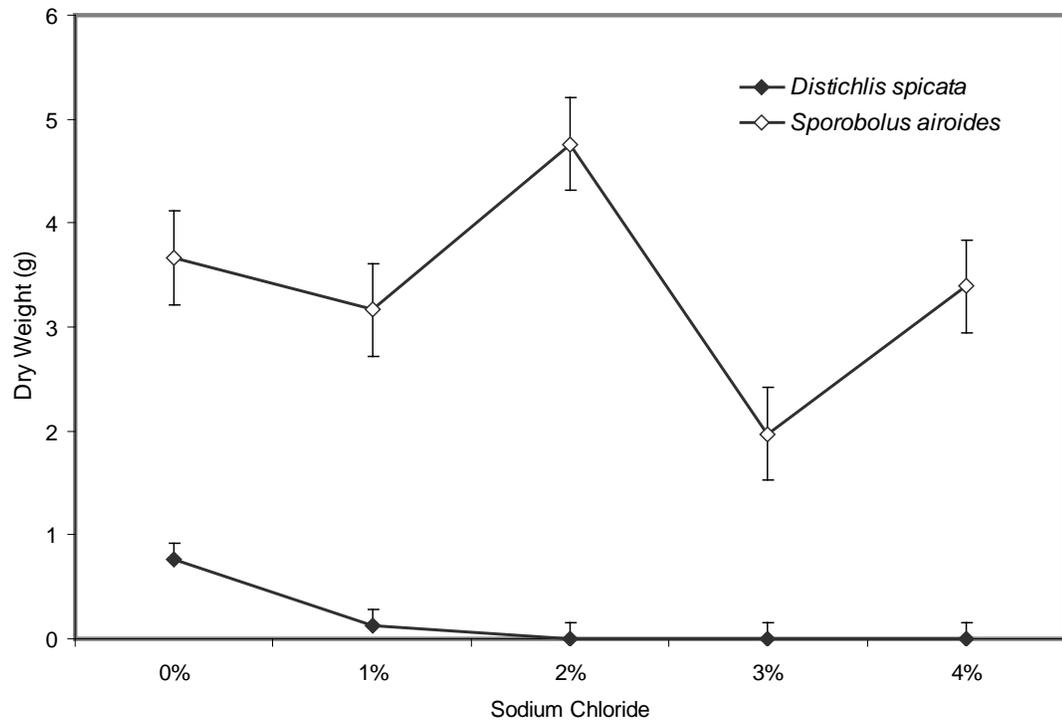
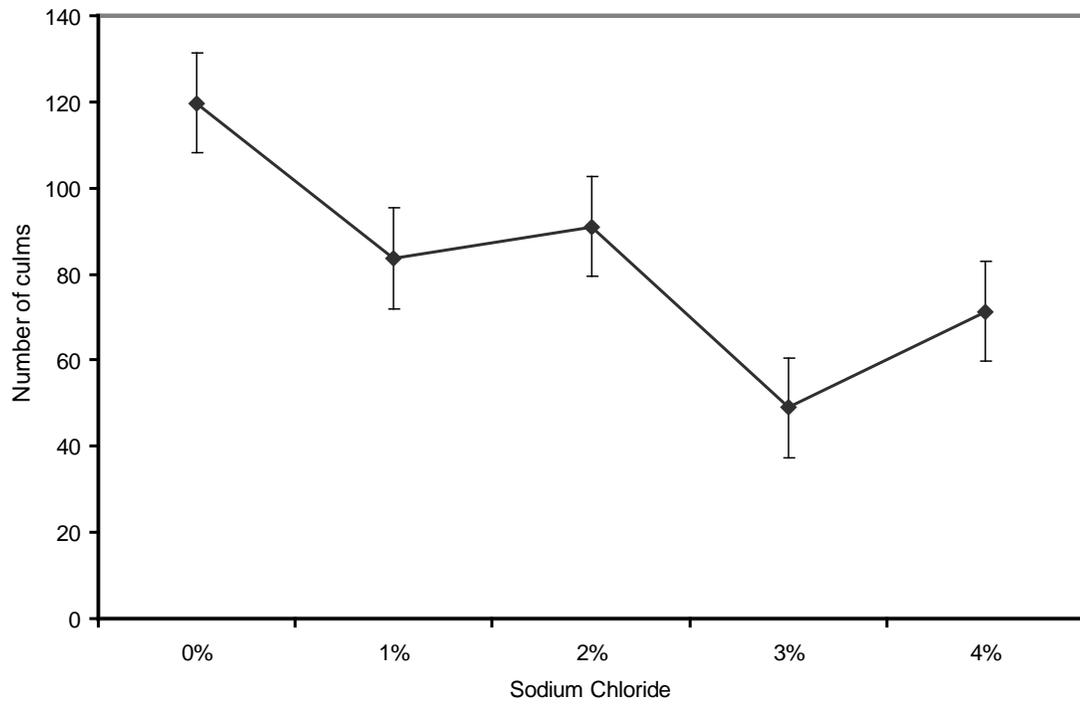


Figure 17. Mean number of culms \pm SE of *Distichlis spicata* along a salinity gradient in the greenhouse.



Germination Experiment

Germination percentage decreased with increasing salinity of irrigation water in both species tested (*Distichlis spicata*, $y=-20.00x + 87.200$, $r^2=0.7408$, $P<0.0001$; *Sporobolus airoides*, $y=-9.07x + 28.267$, $r^2=0.6075$, $P=0.0006$, Figure 18). Species, salinity treatment, and species-by-salinity interaction significantly affected percent germination ($F_{1,18}=57.98$, $P<0.0001$; $F_{4,18}=19.06$, $P<0.0001$; $F_{4,18}=4.80$, $P=0.0082$), whereas block did not ($F_{2,18}=0.27$, $P=0.7641$).

Distichlis spicata germinated in all treatments, whereas *Sporobolus airoides* did not germinate above 2% NaCl. In *S. airoides*, approximately 40% and 5% of all seeds germinated in 0% and 1 % NaCl, respectively. Only one *S. airoides* seed germinated in the 2% NaCl treatment. In *D. spicata*, approximately 75%, 55%, 60%, 25%, and <1% of all seeds germinated in 0%, 1%, 2%, 3%, and 4% NaCl, respectively.

Germination time courses also varied with increasing salinity in both species (*Distichlis spicata*, Figure 19; *Sporobolus airoides*, Figure 20), with seeds in lower salinities germinating more quickly than seeds in higher salinities.

Figure 18. Mean percent germination \pm SE of *Distichlis spicata* and *Sporobolus airoides* along a salinity gradient in a laboratory experiment following 21 days of exposure.

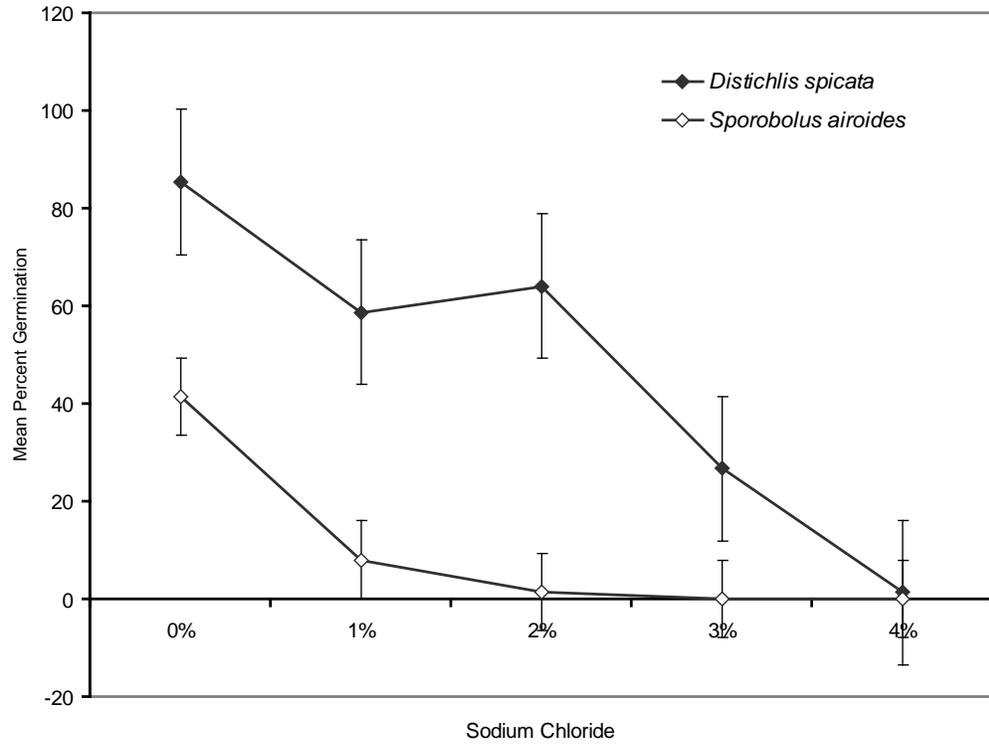


Figure 19. Cumulative percent germination of *Distichlis spicata* along a salinity gradient over 21 days.

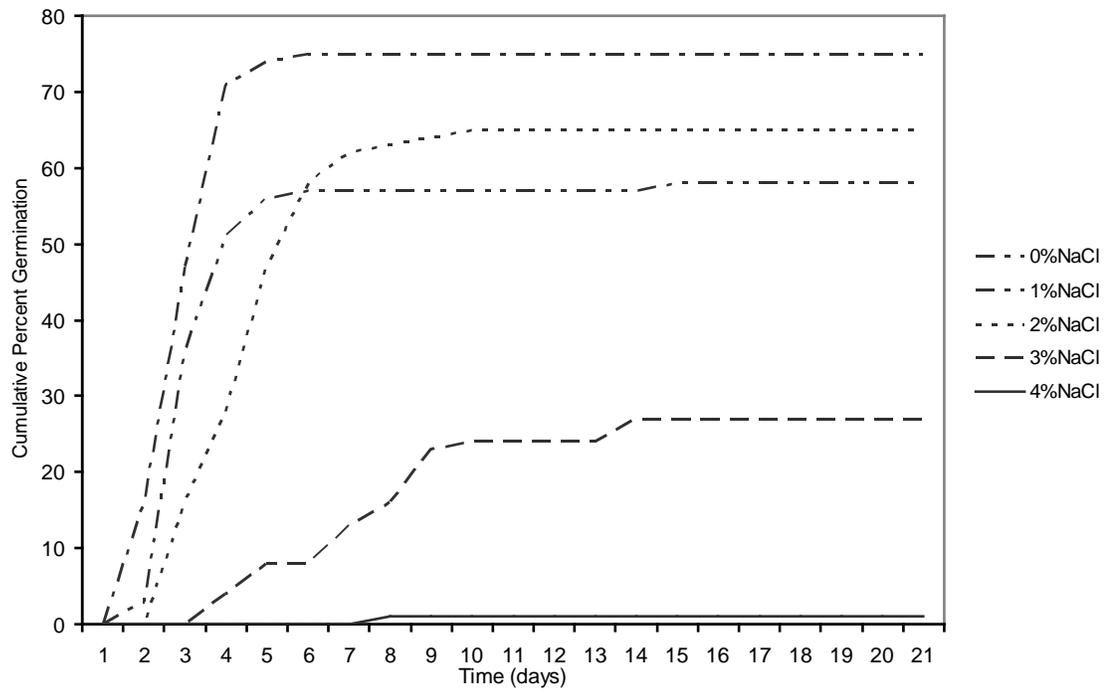
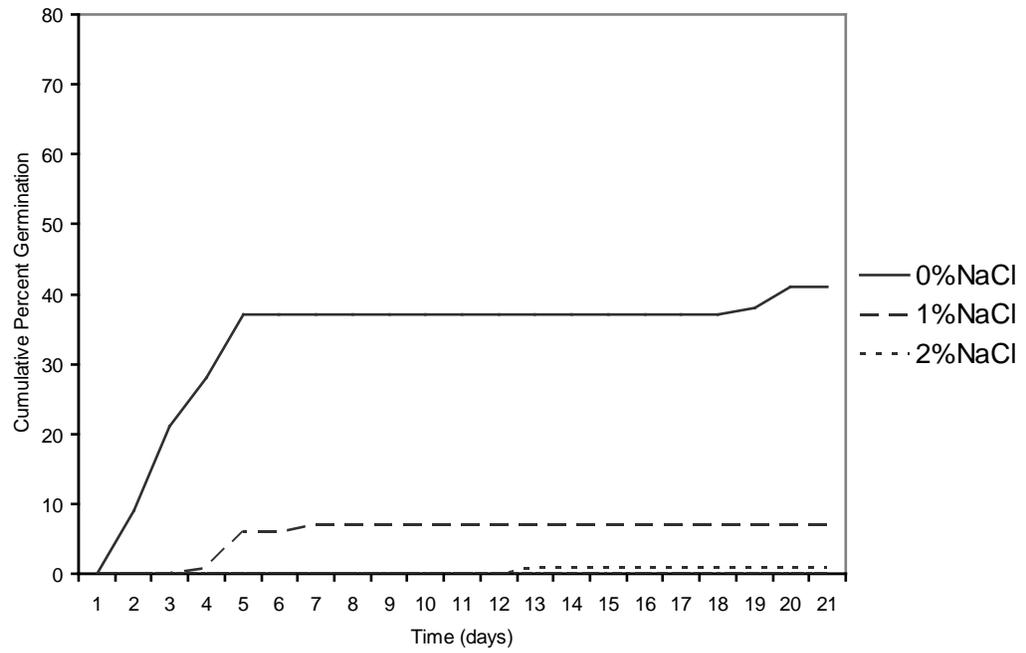


Figure 20. Cumulative percent germination of *Sporobolus airoides* along a salinity gradient over 21 days.



CHAPTER V

DISCUSSION

Overall, species richness increased with increasing distance from the salt flats. Physiological stress tolerance allows the presence of only one or two species in the most stressful environments. As conditions become more moderate, competitive species lacking physiological tolerance mechanisms displace the competitively inferior species capable of stress tolerance.

The greenhouse experiment conducted in this study focused on determining salinity tolerances for *D. spicata* and *S. airoides*, which influence distributional limits toward the salt flats. To understand the factors that influence distributional limits toward the vegetated prairie, the effects of competition should also be investigated in the field or in the greenhouse.

Greenhouse and germination experiments demonstrated that the tolerance limits of two common species along the transition zone, *Distichlis spicata* and *Sporobolus airoides*, were different. Germination was more sensitive than growth to salinity stress. Overall, *Distichlis spicata* was more salt tolerant but less vigorous than *Sporobolus airoides*. I speculate that growth habit and physical size make *Sporobolus airoides* a better competitor than *Distichlis spicata*, helping *S. airoides* compete with less salt tolerant prairie species.

Field Observation

Vegetation community structure exhibits conspicuous zonation along salinity gradients from the salt flats to the vegetated prairie, with species richness increasing with increasing distance from the salt flats. Elevation influences the salinity gradient at in coastal marshes, and presumably at SPNWR, where increased elevation causes a concurrent decrease in salinity (Burchill and Kenkel 1991; Bertness *et al.* 1992; Sánchez *et al.* 1996).

Ability to grow in high salinities leads to the dominance of halophytes, such as *Suaeda calceoliformis*, *Sesuvium verrucosum*, and *Distichlis spicata*, at the highest salinities at SPNWR (≤ 45.2 ppt; Ungar 1966). Occurrences of these same species at much lower salinities (5 ppt; Ungar 1966) suggest they are facultative halophytes limited in lower salinities by inferior competitive ability, herbivory, pathogens, or other unknown factors. *Distichlis spicata* occurred at the SPNWR at salinities above 3‰ but was also found at less than 0.5‰ salinity, indicating a lack of a high salt requirement for growth (Ungar 1966). *D. spicata* survived at 7% NaCl for eight weeks in the greenhouse (Crain *et al.* 2004).

Distichlis spicata and *Sporobolus airoides* were most common in the transition zone between the salt flats and the vegetated prairie, similar to the findings of Penfound (1953) and Ungar (1966). Even though *Distichlis spicata* and *Sporobolus airoides* commonly co-occur, both Jenkins (1949) and Baalman (1965) listed the two species as dominants of distinct zones at SPNWR, with *D. spicata* dominant in the saltiest zone. Accordingly, in this study, *D. spicata* showed a pronounced peak in abundance in the transition zone at the edge of the salt flats. In contrast, *Sporobolus airoides* increased

steadily with distance from the salt flats. *D. spicata* colonizes the transition zone by sending rhizomes into the salt flats where salinity is otherwise too high to allow colonization (Hansen *et al.* 1975; Brewer *et al.* 1998). In certain areas of SPNWR, the sharp peak of *D. spicata* abundance in the transition zone was clear, with *D. spicata* abruptly excluded toward the vegetated prairie by *S. airoides* or other tallgrasses, presumably through shading and coincident reduction in salinity (Baalman 1965; Bertness 1991; Bertness *et al.* 1992).

Beyond the transition zone into the vegetated prairie, glycophytes typical of tallgrass prairie dominated. Along the northern perimeter of the salt flats, *Andropogon gerardii*, *A. hallii*, *Panicum virgatum*, and *Sorghastrum nutans* dominated the vegetated zone of the salinity gradient, as they did in the time of Bruner (1931) and Williams (1954). *Tamarix chinensis* invasion along the floodplains of SPNWR has been well documented (Jenkins 1949; Williams 1954; Ungar 1966; USACE 1978), including along Clay Creek (Grover 1979; USFWS 1980). In Kansas and Oklahoma, *T. chinensis* occurs at salinities (≤ 37.2 ppt) approaching those of *Suaeda calceoliformis* and *Sesuvium verrucosum* (Ungar 1966). In this study, no mature *T. chinensis* occurred at the highest salinities, but *T. chinensis* seedlings did occur at high salinities with *Suaeda*. In the spring, seedlings of *T. chinensis* formed dense beds in floodplains following cessation of flood waters. These seedling beds occurred in flood prone areas, thus recruitment was limited by submergence or scouring in subsequent flood events. Likewise, overall size of established *T. chinensis* was much smaller in flood prone areas than in more protected sites.

Medicago sativa, a commonly cultivated agricultural species, occurred along the western edge of the salt flats. Flood waters likely deposited seeds from cultivated fields directly west of SPNWR along the vegetation line, where salinities are low enough for these species to enter the seed bank and germinate under favorable conditions. The seed banks of inland salt marshes are known to contain seeds of cultivated species (Ungar 1987).

Growth Experiment

Both *Distichlis spicata* and *Sporobolus airoides* responded to increased salinity with decreased height, number of inflorescences, and fresh weight and dry weight of leaves. Salinity-induced reduction of culm height, internode length, and leaf length collectively are known as plant miniaturization (Blits and Gallagher 1991). *S. airoides* was more physically and reproductively vigorous than *D. spicata*. *S. airoides* flowered in all treatments, unlike *D. spicata*, which flowered only in 0% and 1% NaCl. Consistent with the enormous difference in number of inflorescences and height between *D. spicata* and *S. airoides* in the greenhouse, *D. spicata* produces fewer inflorescences on average in the wild, instead relying on its rhizomatous habit to colonize nearby open habitat (Blits and Gallagher 1991). Interestingly, fresh and dry weight of inflorescences was not related to salinity in either *D. spicata* or *S. airoides*.

The large differences in height due to salinity treatment were not surprising, because salt stress inhibits plant growth (Chartzoulakis 1994; Henley 2001; Zhu 2001; Alam et al. 2002; Netondo et al. 2004a), impairs nutrient assimilation (Waisel 1972; Ungar 1996; Chen et al. 2001), and reduces photosynthetic functions (Bertness et al.

1992; Shalhevet 1993; Netondo *et al.* 2004b), possibly through direct damage of photosystem II or by a reduction in chlorophyll content (Netondo *et al.* 2004b; Ahmad and Jhon 2005). Growth under salt stress may be impaired by ion toxicity (Chinnusamy *et al.* 2005), ion imbalance, osmotic stress (Chinnusamy *et al.* 2005), water deficit (Alam *et al.* 2002) or by calcium mediated signal transduction (Chen *et al.* 2001). Ion toxicity occurs when sodium replaces potassium in biochemical reactions and by conformational changes and loss of function as sodium and chloride penetrate hydration shells of proteins (Chinnusamy *et al.* 2005).

Salt stress could also affect plant growth by impairing assimilation of many mineral nutrients. As sodium and chloride content increases, potassium ion content decreases dramatically (Ungar 1996); (Alam *et al.* 2002). With increasing salinity, concentrations of potassium, magnesium, and calcium in leaves and roots decrease (Renault *et al.* 1999; Chen *et al.* 2001; Alam *et al.* 2002; Netondo *et al.* 2004a). Decreased cation concentration with increasing salinity is likely due to direct competition between potassium, calcium, magnesium and sodium at the site of ion uptake in the roots (Alam *et al.* 2002; Netondo *et al.* 2004a).

Surprisingly, greenness increased from 0%NaCl to 4%NaCl, especially in *S. airoides*. The increase in greenness with salinity could reflect the leaves retaining a constant total amount of chlorophyll as the plant decreases in size with increasing salinity. That is, cell division and/or expansion are inhibited more than chlorophyll synthesis.

Leaf relative water content was not significantly different between treatments, but was significantly lower for *Distichlis spicata* than for *Sporobolus airoides*. This could be

due to heavy spider mite infestation of all *D. spicata* individuals included in the study or the different growth habits (*D. spicata* is rhizomatous and *S. airoides* is caespitose) of the two species.

Distichlis spicata and *Sporobolus airoides* are able to survive at high salinities due to traits associated with halotolerance. Ecophysiological traits attributable to organisms living in intermittent high salinity include extreme halotolerance afforded by compatible solutes such as sorbitol, proline, or glycine betaine (Waisel 1972; Ungar 1982; Lambers *et al.* 1998; Chinnusamy *et al.* 2005), compartmentalization of salts into the vacuole (Lambers *et al.* 1998, Chen *et al.* 2001; Chinnusamy *et al.* 2005), and rapid growth when hydrated followed by a dormant phase (Jeffrey 1987; Herbst 2001). Compatible solutes typically increase with increasing salinity to provide osmotic balance, protect membranes and macromolecules, without interfering with biochemical reactions. The osmotic balance provided by compatible solutes enables maintenance of turgor and therefore growth (Ahmad and Jhon 2005), through lowered solute potential afforded by active solute accumulation (Chinnusamy *et al.* 2005). Osmotic adjustment may occur by utilizing available ions, such as sodium, or by synthesizing compatible solutes (Chinnusamy *et al.* 2005), as described above.

Germination Experiment

Percent germination decreased with increasing salinity in both *Distichlis spicata* and *Sporobolus airoides*. In general, halophytic seeds respond to salinity stress with decreased germination (reviewed in Ungar 1982) due to osmotic stress (Ungar 1978). Similar to *Sporobolus airoides* in this study, seeds of *Sporobolus virginicus* failed to

germinate at 2% NaCl (reviewed in Ungar 1982). Similarly, *Sporobolus ioclados* exhibited a negative relationship between germination and salinity (Khan and Gulzar 2003), and germination decreased in *Sporobolus airoides* under moisture stress (Knipe 1971).

In this study, *Distichlis spicata* germinated at much higher percentages than *Sporobolus airoides*, possibly because stratification artificially increased germination percentage in *D. spicata*. However, scarification and moist stratification of *Sporobolus airoides* seeds is unnecessary to achieve germination (Toole 1941). Likely, *D. spicata* is simply more salt tolerant than *S. airoides*.

In the lowest salinities of 0% and 1% NaCl, more than 90% of *Distichlis spicata* seeds germinated. Even though percent germination was high, each individual from which the seed was collected had few inflorescences, indicating low seed production in the field. Instead of high seed production, *D. spicata* relies on its rhizomatous habit for dispersal until favorable conditions arise, at which time, *D. spicata* flowers and seeds from the seed bank germinate (Baalman 1965).

Sporobolus airoides produced high numbers of inflorescences in the field, but germination percentages were low in the laboratory, indicating dormancy or mortality of seeds at high salinities. I am currently monitoring germination of these seeds after transfer to 0% salinity. If a large percentage germinate, it would indicate that exposure to high salinity is not lethal to seeds.

Seeds of annual plants represent the largest portion of the seed bank (Ungar 1987), as perennials such as *Distichlis spicata* and *Sporobolus airoides* either produce non-dormant seeds or produce very few seeds that enter the seed bank. Furthermore, the

seed bank of inland salt marshes may contain species with wide spatiotemporal variation, not accurately representing above-ground vegetation composition (Egan and Ungar 2000).

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APPENDIX 1

Taxa listed below were encountered between May 2006 and March 2008 along salinity gradients at the Salt Plains National Wildlife Refuge, Alfalfa County, Oklahoma. Taxa appear in alphabetical order within family, and those marked with an asterisk (*) are exotic to North America. Nomenclature and exotic status follow USDA PLANTS Database (USDA, NRCS 2008).

AGAVACEAE

Yucca glauca Nutt.

AIZOACEAE

Sesuvium verrucosum Raf.

APOCYNACEAE

Apocynum cannabinum L.

ASTERACEAE

Achillea millefolium L.
Ambrosia psilostachya DC.
Artemisia filifolia Torr.
Artemisia ludoviciana Nutt.
Baccharis salicina Torr. & A. Gray
Helianthus ciliaris DC.
Helianthus petiolaris Nutt.
Helianthus sp. L.
Solidago sp. L.

BRASSICACEAE

Descurainia pinnata (Walter) Britton
Lepidium oblongum Small

CHENOPODIACEAE

Bassia scoparia (L.) A.J. Scott
Chenopodium sp. L.
**Salsola tragus* L.
Suaeda calceoliformis (Hook.) Moq.

COMMELINACEAE

**Commelina communis* L.

CYPERACEAE

Schoenoplectus americanus (Pers.) Volkart ex
Schinz & R. Keller

FABACEAE

Chamaecrista fasciculata (Michx.) Greene
var. *fasciculata*
**Medicago sativa* L.

JUNCACEAE

Juncus torreyi Coville

PLANTAGINACEAE

Plantago sp. L.

POACEAE

Andropogon gerardii Vitman
Andropogon hallii Hack.
Andropogon sp. L.
Bromus arvensis L.
**Bromus tectorum* L.
Calamovilfa gigantea (Nutt.) Scribn. & Merr.
Distichlis spicata (L.) Greene
Echinochloa crus-galli (L.) P. Beauv.
Elymus canadensis L.
Eragrostis spectabilis (Pursh) Steud.
Hordeum pusillum Nutt.
Digitaria cognatum (Schult.) Pilg.
Panicum virgatum L.
Poa arachnifera Torr.
**Polypogon monspeliensis* (L.) Desf.
Schizachyrium scoparium (Michx.) Nash
Sorghastrum nutans (L.) Nash
Sporobolus airoides (Torr.) Torr.
**Thinopyrum ponticum* (Podp.) Z.-W. Liu &
R.-C. Wang

ROSACEAE

Prunus angustifolia Marsh.

SALICACEAE

Salix nigra L.

TAMARICACEAE

**Tamarix chinensis* Lour.

VITA

Chrisdon Brooke Bonner

Candidate for the Degree of

Master of Science

Thesis: VEGETATION COMPOSITION ALONG SALINITY GRADIENTS AT THE SALT PLAINS NATIONAL WILDLIFE REFUGE, ALFALFA COUNTY, OKLAHOMA

Major Field: Botany

Biographical:

Personal Data: Born in Oklahoma City, Oklahoma on 7 October 1980 to Donald Wayne and Christina Bonner. Married to Hunter Wade under the harvest moon in 2004.

Education: Graduated from Duncan High School, Duncan, Oklahoma in 1999. Received the Bachelor of Arts in Biology, Cum Laude, from Western State College of Colorado, Gunnison, Colorado, in 2003. Completed the requirements for the Master of Science in Botany at Oklahoma State University, Stillwater, Oklahoma in December 2008.

Experience: Graduate Research Assistant, Oklahoma State University Department of Botany, 2005-2006. Graduate Technical Laboratory Assistant, Oklahoma State University Department of Botany, 2007. Graduate Teaching Assistant, Oklahoma State University Department of Botany, 2006-present. OSU Botanical Society Vice-President 2006-2007, President 2007-present.

Professional Memberships: Phi Kappa Phi, Oklahoma Native Plant Society

Name: Chrisdon Brooke Bonner

Date of Degree: December, 2008

Institution: Oklahoma State University

Location: Stillwater, Oklahoma

Title of Study: VEGETATION COMPOSITION ALONG SALINITY GRADIENTS AT
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Pages in Study: 54

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Major Field: Botany

Scope and Method of Study:

Understanding the abundance and distribution of communities along environmental gradients provides insight into the understanding of the factors influencing community composition. Environmental gradients are useful in addressing questions concerning community composition due to their often sharply defined zonal communities. Few studies exist on vegetation community composition along salinity gradients of inland salt marshes. In this study, I characterized the vegetation community structure along salinity gradients at the Salt Plains National Wildlife Refuge (SPNWR), Alfalfa County, Oklahoma, quantified the salt tolerance of two dominants at SPNWR, *Distichlis spicata* and *Sporobolus airoides*, in the greenhouse, and quantified the germination ability of *Distichlis spicata* and *Sporobolus airoides* in a laboratory experiment.

Findings and Conclusions:

Species richness and percent cover of both *Distichlis spicata* and *Sporobolus airoides* increased with increasing distance from the salt flats. Greenhouse and germination experiments suggested that germination is more sensitive than growth to salinity stress. Overall, my findings suggest that physiological tolerance to high salinity, specifically ability to germinate at high salinity, limits distribution of vegetation along the margin of the salt flats.

ADVISER'S APPROVAL: William J. Henley
