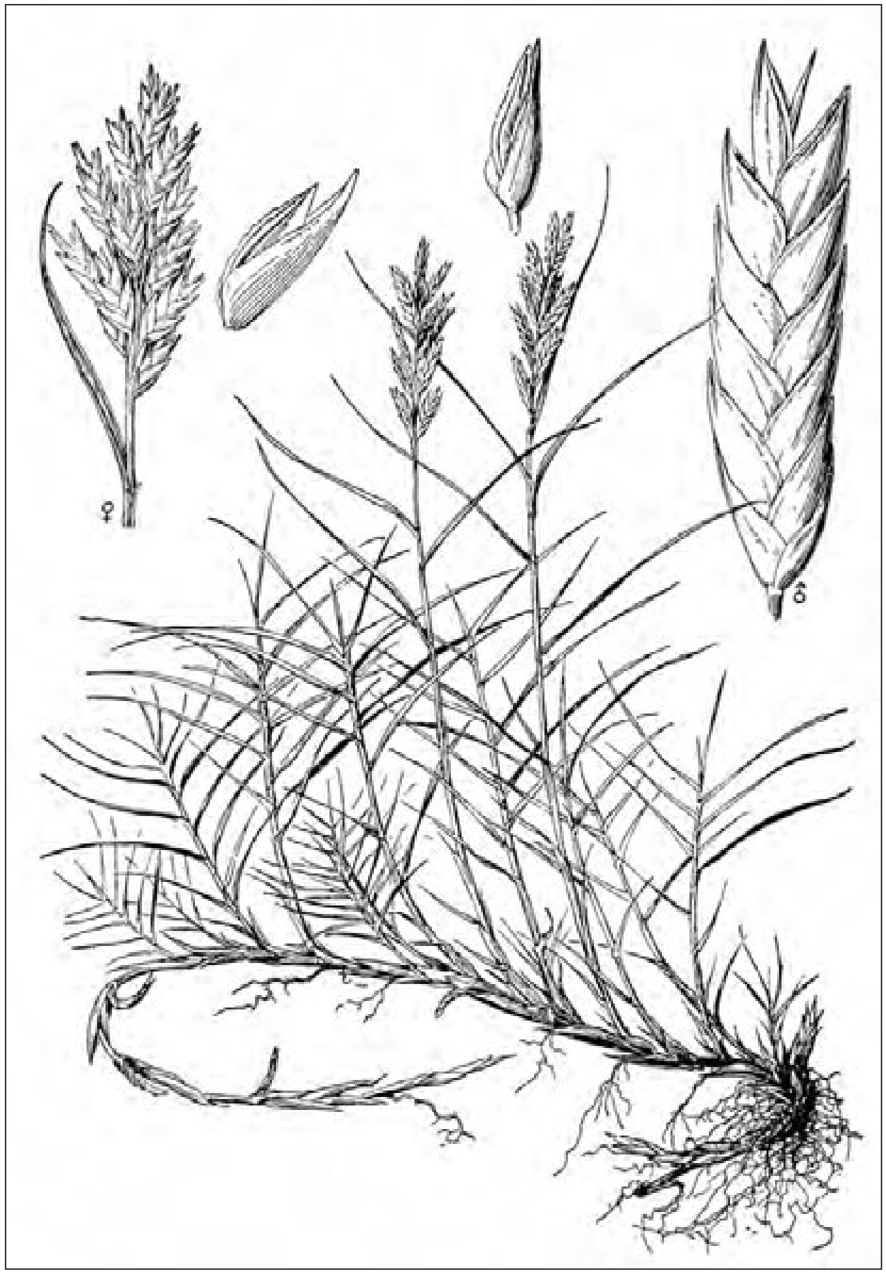
Sex and the Single Saltgrass

Caitlin Coberly
Merlin Ecological LLC, PO Box 763 Lebanon, OR 97355

Saltgrass (*Distichlis spicata*) is widely distributed throughout the United States, from coastal marshes along the eastern seaboard south to Florida, in prairie potholes of the northern Great Plains, in the shrub steppes of the Great Basin, to the shores and estuaries along the Pacific coast (http://plants.usda.gov/). The common name saltgrass may come from the fact that this species "sweats" salt from its leaves, making it very salty on the tongue. Alternately, the name may come from the plant's ability to grow on saline/alkaline soils. A halophile (salt lover), saltgrass grows in environments that many other plants can't tolerate: coastal shores and internally drained basins. In these environments, evaporation concentrates salts to a level at which neither you (nor the neighbor's cow) can drink the water. The amount of salt exuded is related to the concentration of salt in the environment, and is thought to be an adaptation for getting rid of excess salts absorbed from the saline/alkaline soils (Kitzes 2003).

The plant's specific epithet *spicata* (Latin for "arranged in spikes") describes the spike-like inflorescences. The generic name *Distichlis* comes from the Greek *distichos* meaning two-ranked, and refers to another identifying characteristic, the way the leaves are arranged on opposite sides of the stalk (Hitchcock and Chase 1950). When viewed from above, this leaf arrangement appears flat or two-dimensional. Plants are clonal, spreading via rhizomes (underground stems), and it can be difficult to tell whether you are looking at genetically-identical ramets of a clone or a group of genetically distinct individuals.



Line drawing by Agnes Chase of saltgrass, showing both male plant, spikelet and floret and female panicle and floret. Note the two-ranked (distichous) leaves. Reprinted from Hitchcock and Chase (1950).

Generally, saltgrass plants are low growing; the flowering stalks rise above the rest of the plant and may reach a foot in height. The inflorescence is pale straw yellow at maturity, while the leaves remain a dusty green year-round. The salt crystals contribute to the dusty appearance, and may provide an additional benefit for this desert plant as a sun screen.

Behind the somewhat drab appearance lies a fascinating sex story. Saltgrass hedges its bets by reproducing both asexually and sexually. Its asexual reproduction is obvious and straight-forward: rhizomes produce large clonal colonies. Sex (seed production) is a much more complicated affair, one that has multiple implications for the plant and the botanist.

The Boarding School Model?

Saltgrass is dioecious: male and female flowers are produced on separate plants, a condition found among several members of the grass family (*Poaceae*) that ensures that offspring receive genetic material from two sources (Kellogg 2000). Species that reproduce with two parents (by outcrossing) avoid the negative genetic consequences of inbreeding, and may ensure that at least a few offspring survive environmental fluctuations.

Distichous leaf arrangement. Photo by Caitlin Coberly.

Habitat and Gender

The two major habitats for saltgrass in Oregon are the shores and estuaries of the Pacific coast and surrounding alkaline lakes and in playas of the shrub steppe region. In the latter habitat, standing water appears to limit saltgrass on the lower side, while competition with other plants or arid conditions contain it on the uphill side. Female plants are found closer to the water, while male plants form a concentric ring above the female plants, at a slightly higher elevation. In these saline/alkaline playa rings, females are at most only a few yards from the males.

In fact, the playa ecosystem often appears to consist of series of concentric bands of different species outward and upward from the water. One such ringed ecosystem I observed was made of parallel bands, at increasing elevation from the water, of glasswort (*Salicornia rubra*), female saltgrass, male saltgrass, western wheatgrass (*Pascopyrum smithii*), and sagebrush *(Artemisia tridentata*). A similar pattern has been reported in salt marshes on the East coast (Bertness *et al.* 1987) and California (Eppley *et al.* 1998).

From a distance, male and female plants look similar. But if you look closely, you will notice that the males have slightly taller flowering stalks, while the plumper female flowers are clustered either within or barely above the leaves. The females also often appear slightly darker after the seeds have ripened.

Interestingly, like a single-sex boarding school, saltgrass takes gender separation one step farther than most other dioecious taxa. Not only do male and female flowers occur on separate plants, but male and female plants are further segregated by growing in slightly different environments.

Why do the saltgrass sexes grow in different environments? Why should botanists know about it? The gender distribution pattern for saltgrass is of practical interest to plant collectors, who want to collect both male and female ramets for complete specimens. Although seed collectors could work more efficiently by learning to distinguish female from male plants, male and female plants look alike with a quick glance. By knowing where to focus their search for female plants (the lower elevations), collectors can avoid having to look at each plant carefully. Plant propagators may need to control the growth environments in order to prevent favoring one gender over another.

Alkaline playa in the northern Alvord Desert in the Mickey Basin near Mickey Hot Springs showing saltgrass spreading in a linear fashion by rhizomes. Accompanying shrub component is black greasewood. Photo by Stu Garrett.

Is Saltgrass a Sex-changer?

In some plant species, gender is not a set character, but can change in response to environmental conditions. Thus, one question that scientists had is whether environmental conditions determine gender in saltgrass. Factors that affect spatial patterns of dioecious plants include nutrient availability, light, temperature, photoperiod, and hormones (DeSoto *et al.* 2008, Zimmerman 1991, Heslop-Harrison 1957). A good example is jack-in-the-pulpit (*Arisaema triphyllum*), a native understory arum in eastern North America. In this environment, larger plants bear female flowers, while smaller plants produce male flowers. Female-biased populations are found in brighter and richer environments, while male-biased populations are found in shadier, nutrient-poor environments (Vitt *et al.* 2003). In reciprocal transplant studies, males became females and *vice versa* (Lovett-Doust and Cavers 1982), firmly establishing that, in this case, the environment determines gender.

Female saltgrass inflorescence. Photo by Robert L Carr.

Male saltgrass inflorescence. Photo by Robert L Carr.

The connection of females with richer sites is relatively common among sex-changing plant species, perhaps because seeds require more energy to produce than pollen (Heslop-Harrison 1957, Bierzychudek and Eckhart 1988). Plants that become females in rich environments produce the maximum number of seeds, while those that switch to male in relatively poor environments (where seed production would be very limited) still produce large quantities of pollen.

However, and despite the evidence from reciprocal transplant studies in other species, this is not the case in saltgrass. Using DNA markers, Eppley and others (1998) found that gender in saltgrass is genetically determined. Not only were they able to show that saltgrass plants are genetically male or female, but also that there were more female plants in the lower elevations and more males in the higher elevations, thus ruling out that idea that males and females simply did not flower in the reciprocal environments. This still leaves a big question—one which might affect plant propagators. Why are the plants segregated sexually? Eppley and her team decided to test the hypothesis that males and females have different germination and survival rates in response to environmental factors.

Which Environmental Factors Are Critical?

Zonation of different species across environmental gradients is often attributed to differences in germination, survival, or competitive advantage under stress (Freeman *et al.* 1976, Emery *et al.* 2001). Suggesting a similar mechanism for the sexes does not seem so far-fetched; all it would require is a difference in selective advantages for each gender in the alternate environments. The inherently different resource needs for producing pollen and seeds would seem to provide plausible traits upon which natural selection could act.

Is it Salt?

Evaporation of salts near the water line concentrates salts there, and waves lapping against the shore cause minerals to precipitate out at different locations. In California saltmarsh soils where concentrations of phosphates are highest, female saltgrass plants dominate (Eppley 2006).

If salt causes differences in survival and reproduction, then we would expect the frequency of one gender would be higher under high salt conditions. However, Eppley (2001) found that not only do male and female plants survive across a broad range of saline conditions, both genders also germinate across a broad range of salt concentrations. Thus, salinity doesn't segregate males from females.

Is it the Water?

Water is a scarce commodity in desert environments, and playas are surrounded by an obvious gradient of decreasing availability. Water could easily be a critical environmental factor in the "seed is expensive, pollen is cheap" hypothesis. Soil moisture is plentiful for vegetation of the inner rings of the playa, at least during the spring when seeds are developing, but is increasingly scarce with distance from the waterline.

Eppley (2001) did indeed find an affect of water, but not for the reasons one might expect. Nearly twice as many female as male plants survived inundation from a high tide event. Interestingly, this experiment did not show that females at lower, and thus wetter, elevations produced more offspring. Instead, it showed a difference in survival. No factors affecting female survival in the higher elevations has been found—thus leaving us with the mystery as to why female plants are found less frequently at higher elevations in the playa.

Eppley's studies (2006) have identified other factors affecting sex-ratio and spatial segregation. Female plants outcompete male saltgrass plants. Female plants also appear to be preferentially colonized by mycorrhizal fungi, which could increase their competitive advantage over male plants in harsh environments (Eppley *et al.* 2006). Finally, and of some importance to plant propagators wishing to maintain balanced sex ratios or good seed set, Eppley (2001) showed a strong female bias in germinating seedlings (more females germinate than males in the laboratory), suggesting the sex-ratio of seeds may be strongly female biased.

What Mystery Remains?

Research to date has found differences in germination, survival, competitive ability, and mycorrhizal colonization between male and female plants. More females than males germinate under Eppley's experimental conditions. Female plants appear to survive inundation better than male plants. Female plants are competitively dominant over male plants—males, in the presence

Female (left) and male (right) saltgrass plants, showing differences in robustness and stalk length of male and female plants. Photo by Robert L. Carr.

of females, are stunted, whereas the presence of male plants has no effect on the size of female plants. And finally, female plants are preferentially colonized by mycorrhizal fungi, possibly increasing their salt or drought tolerance.

However, the mystery remains as to *why* some saltgrass plants do better in one environment over another; *i.e.*, what mechanism allows female plants to survive inundation that is lethal to male plants? The mystery also remains as to what produces the male-biased populations; is it reduced survival of females under drought conditions, particularly during seed production?

How these known and unknown advantages and disadvantages interact with spatial and temporal environmental conditions has not been fully explored. Saltgrass is a rich subject for studying evolution of plant gender, sex-ratios, sexual segregation, and is possibly relevant for the study of dioecy itself.

Acknowledgements

I am deeply indebted to the many people who have obliged me by discussing grasses and plant mating system evolution. In particular, I would like to thank my editor, Dr. Cindy Roché, Dr. Christina Muirhead (University of California), Dr. Cindy Salo of Sage Science, Dr. Halse of the OSU Herbarium, and Dr. Barbara Wilson of the Carex Working Group. Their ideas and questions have enriched this paper immensely.

References

Bertness MD, Wise C, Ellison AM. 1987. Consumer pressure and seed set in a salt marsh perennial plant community. Oecol. 71:190-200.

Bierzychudek P, Eckhart V. 1998. Spatial segregation of the sexes of dioecious plants. Am. Nat. 132(1):34-43.

DeSoto L, Quintanilla LG, Méndez M. 2008. Environmental sex determination in ferns: effects of nutrient availability and individual density in *Woodwardia radicans*. Ecol. 96(6):1319-1327.

Eppley SM, Stanton ML, Grosberg RK. 1998. Intrapopulation sex ratio variation in the salt grass *Distichlis spicata*. Am. Nat. 152(5):659–670.

Eppley SM. 2001. Gender specific selection during early life history stages in the dioecious grass *Distichlis spicata.* Ecol. 82(7):2022-2031.

Eppley SM. 2006. Females make tough neighbors: sex-specific competitive effects in seedlings of a dioecious grass. Oecol. 146(4):549-554.

Emery NC, Ewanchuk PT, Bertness MD. 2001. Competitors and salt-marsh zonation: stress tolerators may be dominant competitors. Ecol. 82(9):2471-2485.

Freeman DC, Klickoff LG, Harper KT. 1976. Differential resource utilization by the sexes of dioecious plants. Sci. 193:597-599.

Heslop-Harrison J. 1957. The experimental modification of sex expression in flowering plants. Biol. Rev. 32(1): 38–90.

Hitchcock A, Chase A. 1950. Manual of the Grasses of the United States. Washington (DC): US Govt. Printing Office.

Kellogg EA. 2000. The grasses: a case study in macroevolution. Ann. Rev. Ecol. Syst. 31:217-238.

Kitzes J. 2003. http://www.mbari.org/staff/conn/botany/seagrass/justin/index.htm

Lovett-Doust J, Cavers PB. 1982. Sex and gender dynamics in jack-in-the-pulpit, *Arisaema triphyllum* (Araceae). Ecol. 63(3):797-808.

Vitt P, Holsinger KE, Jones CS. 2003. Local differentiation and plasticity in the size and sex expression in jack-in-the-pulpit, *Arisaema triphyllum* (Araceae). Am. J. Bot. 90:1729-1735.

Zimmerman JK. 1991. Ecological correlates of labile sex expression in the orchid *Catasetum viridiflavum*. Ecol. 72(2):597-608.

Caitlin Coberly grew up and lives in western Oregon with her family. She finished a BS in Ecology and Evolution at University of Oregon in 1996. After completing her PhD at Duke University in 2003 on the evolution of flower color, she studied the effect of spatial distribution on competition at the University of Idaho. Caitlin worked in native plant restoration, starting the native seed division of American Grass Seed Producers (AGSP), before moving to Minnesota to take a position as an ecological consultant. She has since returned to Oregon, becoming the principal ecologist for Merlin Ecological, LLC. Merlin Ecological provides consulting services for environmental impacts, as well as wildlife and rare plant surveys. Caitlin recently assisted the USFWS as a technical advisor to the Federal Advisory Committee to the Secretary on Wind and Wildlife. She is currently conducting studies on the migration pathways of bats and analysis of avian night migration patterns.