Contrasting salinity responses of two halophytes

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Despite their salinity, tidal marshes are highly productive. Salt marsh plants are often reported to have rates of productivity exceeding those of many cultivated species. Although little used today, some halophytes have been exploited historically as a food source for humans or domestic animals. Many of these or related species are found in California, such as eelgrass *(Zostera marina)*, salt grass *(Distichlis spicata)*, and cord grass *(Spartina alternifolia)*.

Many of California's marshes are managed to increase production of species desirable as waterfowl forage. One such area, Suisun Marsh in the Sacramento River delta, usually supports 10 percent (in dry years, up to 25 percent) of the duck population of the Central Valley, the main wintering area for the Pacific Flyway. One-third of the ducks' total diet consists of alkali bulrush *(Scirpus paludosus)*, a perennial tuberous sedge. However, in 1978, this species covered only 13.2 percent of the marsh, while up to half the area was covered by two species that are undesirable for waterfowl but more salt-tolerant: pickleweed *(Salicornia virginica)* and salt grass.

Growth and physiological characteristics of alkali bulrush and pickleweed are of agricultural interest because of their strikingly different responses to salinity. Alkali bulrush, like most crop species, lacks special adaptations such as salt glands or succulence found in more tolerant halophytes. It is less salt-tolerant than pickleweed: it is most abundant at field sites where spring salinity is at least 10 dS/m (about 7,000 mg/L) but peak summer salinity does not exceed 70 dS/m (50,000 mg/L), whereas pickleweed is abundant at salinities up to 100 dS/m (70,000 mg/L). Still, alkali bulrush begins spring growth at salinities that many crop species cannot tolerate. It belongs to the class of halophytes that resist salinity by excluding salt from the shoots, and its growth, like that of other such species, is best in fresh water. In contrast, pickleweed is a succulent shrub that absorbs soil ions for osmotic adjustment, and it grows best under saline conditions.

In a University of California study, the two species were grown in the laboratory at salinities ranging from 0 to 45 dS/m (30,000 mg/L). As expected from field data, total growth and rates of growth in the absence of salinity were significantly higher in alkali bulrush than in pickleweed. However, both measures of growth decreased markedly under all salinity treatments in alkali bulrush, while pickleweed growth increased with salinity, up to 30 dS/m (20,000 mg/L).

Lab experiments also showed that reproductive patterns of these species are very different. In alkali bulrush, salinity decreases the number of shoots per plant, thus limiting both vegetative development and (because inflorescences are terminal) seed yield. Inflorescences are also terminal in pickleweed, but since salinity enhances growth in this species, it probably does not suppress seed yield. Both species reproduce vegetatively, forming extensive clones from rhizomes or trailing stems. However, alkali bulrush differs from pickleweed in having tubers, and it increases its proportional allocation of dry weight to these storage organs under the 15 and 30 dS/m (10,000 and 20,000 mg/L) treatments. Tubers, by virtue of their large size relative to seeds, provide important carbohydrate reserves (up to 60 percent of the tuber by weight), permitting rapid resumption of growth in the spring, when salinities are low.

Experiments were conducted to identify possible causes of differences in growth rates under salt stress in these two species. Differences in photosynthetic capacity only partially explain the contrasting growth responses. In the absence of salinity, maximum photosynthetic rates in pickleweed were only about half those in alkali bulrush; however, total growth in pickleweed was much less than half that in alkali bulrush, attributable mostly to the lower leaf area of pickleweed. With salinity, the pattern reversed. Pickleweed maintained its photosynthetic and growth rates, while in alkali bulrush, both rates declined with salinity. Furthermore, in alkali bulrush, growth was more suppressed than were photosynthetic rates: rates of leaf expansion, leaf size, and numbers of leaves per plant were reduced. These observations illustrate the point that the development and maintenance of photosynthetic leaf area may be more significant than photosynthetic capacity at the cellular level for continued growth under stress. Nonetheless, increase in photosynthetic rates under salt stress, a phenomenon noticed in other salt-tolerant species, is presumably beneficial, since it provides increased energy and metabolites.

Other experiments were conducted to determine how salinity affects development of leaf area in alkali bulrush. The fact that leaf expansion rates and size decline with salinity might suggest that insufficient turgor pressure for cell expansion is what limits growth under high

Pickleweed grows well in saline marsh water by absorbing salt ions for osmotic adjustment. Other plants, lacking special salt glands, are less salt tolerant.

salinity. At low salinity, however, leaf expansion rates, turgor pressure, and photosynthetic rates are maintained while growth declines, suggesting that other factors must also limit growth potential. Species like alkali bulrush that exclude mineral salts use a considerable proportion of their photosynthetic products for osmotic adjustment, and this process must certainly compete with growth. Like related species, alkali bulrush may accumulate sugars under stress, and this may explain its desirability for herbivores. In contrast, pickleweed utilizes soil salts rather than photosynthetic products for osmotic adjustment, accounting for much of its stimulated growth under salinity — and its salty taste.

Alkali bulrush and pickleweed thus show that halophytes differing greatly in physiology and in vegetative and reproductive growth patterns can grow in equally saline soils. Rapid growth rates during periods of low soil salinity and greater plant height, combined with vegetative propagation from spreading rhizomes and tubers, probably allow alkali bulrush to compete successfully with the more salt-tolerant pickleweed. Better understanding of the diverse adaptations of halophytes to salinity should aid agriculturists in selecting for increased salt-tolerance in existing cultivated species, and perhaps in the development of new crops.

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Salt tolerance of mesquite

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California's native mesquite grows primarily in areas of shallow ground water where temperatures are rarely below 24°F. Many of these areas have naturally occurring saline surface or subsurface soils — up to 88 dS/m (about 56,300 mg/L) in the saturation extract. Root systems of mesquite, including the native species, *Prosopis glandulosa* var. *torreyana*, are well adapted for growth in areas where the plant must rely primarily on ground water. Another species, *Prosopis tamarugo*, native to the Atacama Desert of Chile, where average annual rainfall is less than ½ inch, relies wholly on groundwater derived from snow and rain in the Andes Mountains.

Over the past several years, mesquite varieties have been considered as sources of biomass for firewood, forage, and energy generation, but these trees are not likely to replace conventional crops where water and soil quality are good. On marginal lands, however, especially where moderately saline groundwater or surface water is available, salt-tolerant woody species may be grown without competing with agronomic crops for resources.

In research to learn the extent of this plant's salinity tolerance, we took soil samples from a field site of native mesquite near the Salton Sea. The surface soil had an electrical conductivity in the saturation extract as high as 20 dS/m (salinity of about 12,800 mg/L). This surface zone, down to 20 or 24 inches, was heavily rooted with fine absorbing roots, even though average annual rainfall on the site is less than 3 inches. The groundwater, at about a 16-foot depth, had an electrical conductivity of 2.8 dS/m (about 1,800 mg/L). Based on soil samples taken in 1-foot increments down to the water table, we found there tended to be a bulge in concentration (up to 12 dS/m — 7,700 mg/L) between 3 and 6 feet above the water table. Fine roots generally occurred within 3 feet of the water table, with electrical conductivities as high as 5 dS/m (3,200 mg/L) in this zone.

To further define mesquite's sensitivity to groundwater salinity, we started seedlings in the greenhouse in 6-foot-tall polyvinyl chloride columns containing sandy loam soil. The bottom 4 inches of soil were kept saturated with one of three simulated groundwaters based on 0.5, 1, or 2 times the field groundwater composition: 1.7, 2.8, or 5.5 dS/m (about 1,000, 1,800, or 3,500 mg/L). Plants were grown for 10 months and then harvested. At harvest, average weights of the 2.8 and 5.5 dS/m plants were 80 and 45 percent, respectively, of the 1.7 dS/m plants' weight. In the most highly salinized zone 12 inches above the water table, electrical conductivity exceeded 29 dS/m (18,500 mg/L) in the high-salt treatments.

Total nitrogen accumulated through symbiotic nitrogen fixation by the tree also decreased with increasing salinity: nitrogen in the 2.8 and 5.5 dS/m treatments was 83 and 44 percent, respectively, of that in the 1.7 dS/m treatment. Active nodules occurred even in the most highly salinized zone.

Mesquite appears able to survive and even flourish in soils more saline than 20 dS/m (12,800 mg/L), if the tree can obtain water from a portion of the root zone with lower salinity. The roots can apparently continue to extract water from soil with salinities greater than 28 dS/m (17,900 mg/L). Further research is required to determine how long salts can accumulate in the subsaturated zone above the water table before growth is seriously decreased or the plant dies. It is apparent, however, that the trees rapidly produce substantial amounts of biomass, using low-quality, saline waters, relying on nitrogen fixation with little or no soil or fertilizer nitrogen.

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Mesquite flourishes in soils of greater than 12,800 mg/L salt, if its roots can obtain water of lower salinity.