Mortality of the Salt Marsh Species *Salicornia europaea* and *Atriplex prostrata* (Chenopodiaceae) in Response to Inundation[1]

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ABSTRACT. **Waterlogging and salinity are considered to be the two major factors affecting growth and plant distribution in salt marshes. But while the effects of salinity are well known, few studies have investigated the impact of the former on plant survival. The purpose of this laboratory experiment was to determine the effects of water level on growth and survival of the halophytes *Salicornia europaea* and *Atriplex prostrata*. Plants were grown in the laboratory at the following levels of inundation: 1) roots and shoots completely submerged (high water), 2) roots completely submerged (medium water), 3) water level at the bottom of the pot (low water). The high water treatment caused 100% mortality in both species within one week. Survival was high for both species when grown in the other treatments, but there was an indication of lower survival (70%) in the medium water treatment for *A. prostrata* than in the low water treatment (90%) after three weeks submersion. There was no significant difference ($P > 0.05$) in biomass production between medium and low water treatments in either species.**

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INTRODUCTION

Flooded soils with reduced aeration are considered to be a major factor affecting plant distribution in salt marshes, but few studies have documented its impact on plant survival (Adam 1990; Ungar 1991). *Salicornia europaea* L. (common glasswort or samphire) and *Atriplex prostrata* Willd. (orache) are halophytes that inhabit inland and coastal salt marshes (Gleason and Cronquist 1991) where they are subjected to seasonal changes in water level due to precipitation in the colder months and dehydration in the summer months. Prolonged periods of flooding in soils can be detrimental to plant growth, because these soils become anoxic except for a thin oxygenated layer near the surface (Ponnamperuma 1984). Anoxic conditions may develop in just hours or up to several days after flooding as water fills the air spaces around soil particles and plant roots and microbial activity consume the remaining oxygen (Ponnamperuma 1984). When this occurs, the resulting anoxic conditions may inhibit plant growth by preventing plants from exporting salt and metabolic wastes such as ethanol and fatty acids from their roots (Van Diggelen 1991). Prolonged periods of saturated soils also induce a specific ion toxicity in halophytes from sulfide accumulated in the soils and promote the uptake of excessive amounts of reduced iron and manganese (Jeffrey 1987). Finally, because of the inhibitory effects mentioned above, waterlogged soils cause an inhibition of photosynthesis and disrupt plant hormonal balance (Van Diggelen 1991).

Salicornia europaea is one of the most salt tolerant plants in general and is capable of growing under highly saline conditions on the lowest part of salt marshes (Ungar 1977). It occurs predominantly in salt marsh soils that are water saturated and often flooded (Ungar 1977). However, *S. europaea* has little aerenchyma (7.1% root volume) tissue present in the roots compared to other species that grow under anoxic soil condition, including *Agropyron pungens* (Pers.) Roem. and Schult., *Aster tripolium* L., and *Oryza sativa* L., which contain 15.9 to 16.5% aerenchyma in their roots (Pearson and Havill 1988). Therefore, *S. europaea* must employ other means for supplying oxygen to its roots. It is possible that oxygen is brought in from the plant shoot. Jeschke and others (1995) determined that high atmospheric pressures from a Scholander pressure chamber were needed to remove sap from *Atriplex hortensis* L. which had little aerenchyma tissue compared to *Leptochloa fusca* (L.) Kunth, where pressure exerted caused the sap to easily pass through aerenchyma tissue in the root. It is therefore likely that *S. europaea* and *A. prostrata* oxygenate their roots via aboveground shoots. An investigation comparing two species, *Salicornia dolichostachya* Moss and *Salicornia ramosissima* J. Woods, demonstrated that anaerobic environments caused a decrease in their relative growth rates (Schat and others 1987), so the supply of oxygen to the roots of *S. europaea* is very important to plant growth and survival.

When *A. prostrata* plants were grown hydroponically, mechanically aerated plants were able to accumulate more Na^+ and Cl^- in their leaves than plants that were not aerated (Karimi and Ungar 1986), so root aeration is important to salt tolerance. Root oxygenation from the aboveground vegetation is likely to be important for halotolerance in *A. prostrata* because its roots do not contain aerenchyma tissue (Egan 1999). Field observations of Atriplex *prostrata*, a less salt tolerant halophyte than *S. europaea*, indicated that it grew in less saline soils in our study area, bordering the zone dominated by *S. europaea* which grew directly in the salt pan in the Rittman salt marsh (Egan and Ungar 2000).

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Field observations at a salt marsh in Rittman, OH, indicated that unseasonably high flooding for up to two weeks appears to have caused high mortality in an area of the marsh dominated by *S. europaea* and *A. prostrata* (Egan 1999). In April 1996 there were approximately 140,000 *S. europaea* and 54,500 *A. prostrata* seedlings per square meter. By mid June 1996 the area was flooded and no plants survived in the plots monitored in April. Because of the high field mortality under complete submersion of these species, we were interested in determining how different levels of submersion affected these halophytes under controlled experimental conditions. The purpose of this laboratory experiment was to determine 1) the effect of water level on growth of these two halophytes and 2) the influence of different levels of submersion on survival of plants.

MATERIALS AND METHODS

Salicornia europaea seedlings were collected from a salt marsh in Rittman, Wayne County, in the northeast corner of the state of Ohio (long. 81°47'39" W; lat. 40°57'30" N) on 14 June 1996 from an area of the marsh with little to no standing water. *Atriplex prostrata* plants were obtained by germinating seeds collected from the same location on 17 November 1995. Medium sized (1.5-2.0 mm diameter, Khan and Ungar 1984) seeds were germinated in an incubator with a 12 hr thermoperiod of 5° C:25° C, and a 12 hr photoperiod of dark:light (20.0 µmol photons $m^{-2}sec^{-1}$, 400-700 nm). Both species were grown in a growth chamber for two months at a 15 hr photoperiod of dark:light (276.3 µmol photons $m^{-2}sec^{-1}$, 400-700 nm) before inundation treatments (Khan and Ungar 1984). At the beginning of the experiment mean height for *S. europaea* was 67.5 mm ± 2.3, *A. prostrata* was 119.5 mm ± 5.0.

Salicornia europaea and *A. prostrata* plants were placed in one of three levels of 1/2 strength Hoagland and Arnon No. 2 nutrient solution (Moore 1960) containing 170 mM NaCl to prevent *S. europaea* from wilting while not overstressing *A. prostrata* (Khan and Ungar 1984; Ungar 1991). Ten 4 L plastic containers (25 cm high × 23.5 cm wide × 14 cm deep) were used for each experiment (n = 10 replicates). Three different treatments were contained within each of the ten blocks by positioning pots at different levels: 1) roots and shoots completely submerged (high water), 2) roots completely submerged (medium water), and 3) water level at the bottom of the pot (low water). The medium and low levels were chosen because *S. europaea* and *A. prostrata* often grow under these conditions and we wanted to determine which condition was most advantageous for plant growth. The high water condition was chosen to replicate the observed flooded field conditions and we wanted to determine how long these species could tolerate complete inundation. *Salicornia europaea* plants were grown in pots containing field soil cores thinned down to avoid damaging the fragile root systems (10 plants per 7.5 cm diameter pot) from 20 June to 10 July 1996. *Atriplex prostrata* plants were transplanted from petri dishes to fine sand (1 plant per 9 cm diameter pot) from 18 July to 12 August 1996 during their peak growing season.

Dissolved oxygen in each of the 4 L receptacles was measured weekly with a Ciba-Corning® oxygen probe (M90 Checkmate Modular Testing System) at low, medium, and high levels of inundation. Mean values for *S. europaea* and *A. prostrata* treatments were 7.19 ± 0.12 S.E. ppm and 8.48 ± 0.35 S.E. ppm O_2, respectively. Data were analyzed using a one-way ANOVA (however, height data for *A. prostrata* failed the assumptions for normality and homoscedasticity and a Wilcoxon-Signed Rank test was used (NCSS 1995)). A Chi-square test was used to determine significant differences in the proportional data of percent survival among treatments (NCSS 1995).

RESULTS

There was 100% mortality of the completely inundated (high water) *S. europaea* and *A. prostrata* plants after one week. Therefore, the statistical tests compared the characteristics of plants from only medium and low water levels. Mean values between medium and low treatments did not differ between any pairs tested for height, number of internodes, number of internodes with branches, and dry mass (Table 1 and 2; $P > 0.05$). There was no significant difference ($P > 0.80$) in dissolved oxygen concentration at any water level.

Survival for *S. europaea* in medium (96% ± 0.24) and

TABLE 1

Effects of submergence of medium and low water treatments on mean (± S.E.) height, internode number, nodes with branches, and dry mass of Salicornia europaea *and* Atriplex prostrata.

	Salicornia europaea		*Atriplex prostrata*	
	Medium	Low	Medium	Low
Height (mm)	148.5 ± 3.8	153.2 ± 4.0	323.0 ± 51.5	285.4 ± 18.1
Internodes (No.)	15.8 ± 0.3	16.1 ± 0.3	9.0 ± 0.7	9.4 ± 0.4
Nodes with Branches (No.)	8.0 ± 0.5	8.3 ± 0.4	6.1 ± 0.6	6.6 ± 0.4
Mass (g)	0.7 ± 0.1	0.8 ± 0.1	0.9 ± 0.2	0.7 ± 0.1

TABLE 2

Results of one-way ANOVA for the effects of submergence in medium and low water treatments on growth parameters of Salicornia europaea *and* Atriplex prostrata.

	Salicornia europaea		*Atriplex prostrata*	
Variable	F-Ratio	Probability	F-Ratio	Probability
Height	0.41	0.524	0.5916*	0.554
Internodes	2.61	0.108	0.39	0.544
Nodes with Branches	0.22	0.637	0.3	0.591
Plant mass	1.79	0.197	0.6	0.450

*Represents Z-score for Wilcoxon-signed rank test.

low (98% ± 1.33) treatments was high throughout the experiment (Table 3). There was relatively high survival for *A. prostrata* in medium (70%) and low (90%) treatments at week three. A Chi-square analysis for both species demonstrated no significant difference ($P > 0.05$) in survival between medium and low treatments, but did demonstrate a significant difference ($P < 0.05$) between the high treatment and both of the other treatments.

DISCUSSION

Our results demonstrate that *S. europaea* and *A. prostrata* grew equally well in soils that were well drained after being saturated (field capacity) or remained saturated (waterlogged). Our results also agree with Farkhunda and others (1994) who determined that there was no difference in *Atriplex amnicola* growth at soil moisture concentrations of 75, 100, and 125%. In contrast, Cooper (1982) demonstrated that waterlogged soils caused a decrease in the biomass for *S. europaea*, but the effect of waterlogging was alleviated by an increase in salinity. Langlois and Ungar (1976) determined that a brief daily tidal immersion stimulated growth in the coastal species *Salicornia stricta* Dumort, but not in the inland species *Salicornia ramosissima* Woods. *Atriplex prostrata* is another species that is not inhibited by tidal inundation (Ungar 1991). The results from our experiment with *S. europaea* and *A. prostrata* demonstrated that there was no difference in biomass production due to low or medium levels of inundation. These results are in contrast to the results in an investigation with *Scirpus maritimus* var. *paludosus* (Lieffers and Shay 1980). When *S. maritimus* was grown with water above or at the soil surface, there was an increase in underground biomass, a greater number of tillers, and decreased seed production. Inundated plants were taller and produced more seeds, but formed fewer tillers and had reduced below ground biomass (Lieffers and Shay 1980). Some halophytic species are able to grow in environments with tidal inundation regimes (Hopkins and Parker 1984). Langlois and Ungar (1976) compared the growth of *Salicornia stricta* from a coastal salt marsh with that of *S. ramosissima* from an inland salt marsh under tidal regimes. They found that *S. stricta* grew best in a tidal inundation regime, and its inland congener grew better when not submerged. This suggests that plant populations growing in inland salt marshes are better adapted to the absence of inundation. Tidal inundation causes submersion of vegetation in the lowest marsh zones for a few hours (Adam 1990), whereas flooding caused the complete submersion of plants in the inland salt marsh at Rittman, OH, for days. The constant submersion of plants without intertidal periods may have been a major factor in the observed plant mortality.

Complete submersion of plants caused 100% mortality in both *S. europaea* and *A. prostrata* within one week. These data are significant in explaining the high mortality in field plants submersed in water. Both species are tolerant of a high water table and must have a mechanism to transfer oxygen from their shoots to roots. Complete submersion of shoots in water for prolonged periods of time prevents oxygen transfer to roots and results in high mortality of some halophyte species (Adam 1990).

This experiment demonstrates that flooding in inland salt marshes can cause high levels of mortality in salt marsh species. In the populations at the inland salt marsh at Rittman, OH, the persistent seed bank was able to produce a new cohort of the above ground vegetation, and these later cohorts of *Salicornia europaea* and *Atriplex prostrata* replenished the seed bank by the end of the growing season. Further research is needed to determine the response of halophytes to submersion at different stages of plant development. This might include performing experiments with plants of different ages, or include another treatment in which only one half of the aboveground vegetation is submersed.

TABLE 3

Percent survival for Salicornia europaea *and* Atriplex prostrata *in low, medium, and high water treatments.*

		Percent Survival	
	Week	*S. europaea*	*A. prostrata**
Low Water	1	98 ± 1.33	90
	2	98 ± 1.33	90
	3	98 ± 1.33	90
Medium Water	1	98 ± 0.20	100
	2	98 ± 0.22	90
	3	96 ± 0.24	70
High Water	1	0	0
	2	0	0
	3	0	0

**A. prostrata* does not have S.E. values because there was only one plant per pot.

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