

## NITROGEN NUTRITION AND SALINITY TOLERANCE OF *DISTICHLIS SPICATA* AND *SPARTINA ALTERNIFLORA*<sup>1</sup>

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**Abstract.** In a greenhouse investigation *Distichlis spicata* (L.) and *Spartina alterniflora* (Loisel.) were grown from seed on freshwater, brackish, and marine sediments. These species were also concurrently grown in sand culture under conditions of nitrogen or phosphorus limitation in order to establish critical tissue concentrations of these elements. These experimentally determined values were used to assess the limiting nutrient status of the plants grown on the sediments.

Growth of both species was nitrogen limited on most sediments, and phosphorus was consumed luxuriously on all sediments. Aboveground biomass was correlated with interstitial water nitrogen concentration of the sediments. Under low nutrient conditions relatively more biomass was allocated to belowground rather than aboveground portions of the plants.

Although the availability of nitrogen ultimately determined biomass accrual, growth rate was affected by the sediment salinity. Analysis of plant tissues and the sediment interstitial water at the end of the investigation revealed selective uptake of potassium and exclusion of sodium. These processes increased the ratio of sodium to potassium in the interstitial waters and also resulted in increased sediment salinities. The effect of salinity stress on plant growth in *Spartina* marshes is discussed in relation to nitrogen limitation.

**Key words:** *Distichlis*; ion selection; nitrogen limitation; plant nutrition; salinity tolerance; salt balance; salt exclusion; salt marsh; sediment nutrients; *Spartina*.

### INTRODUCTION

It is commonly accepted that the productivity of North American salt marshes is limited by the availability of nitrogen (Squiers and Good 1974, Valiela and Teal 1974, Gallagher 1975). Evidence for nitrogen limitation has been based predominantly on the response of the vegetation to nitrogen fertilization (Sullivan and Daiber 1974, Valiela and Teal 1974, Gallagher 1975, Patrick and Delaune 1976). These results may be misleading due to the secondary effects of nitrogen fertilization on other aspects of the salt marsh ecosystem. Additions of nitrogen can increase rates of decomposition, and subsequent mineralization of other nutrients from organic matter (Tusneem and Patrick 1971, Almazan and Boyd 1978), decrease rates of nitrogen fixation (Van Raalte et al. 1974, Hanson 1977), and alter the ionic composition and pH of the interstitial water. It is therefore desirable to evaluate the nitrogen nutrition of salt marsh plants without altering the sediment environment.

Tissue analysis has been widely used for determining limiting nutrients in agricultural crops (reviewed by Bates 1971) and more recently for submersed aquatic plants (Gerloff and Kromholz 1966, Gerloff 1969, 1975) and emergent freshwater macrophytes (Barko and Smart 1979). This technique allows an evaluation of the adequacy of supply of a nutrient by comparing its concentration in the tissue with the minimum required concentration of that particular nu-

trient (critical concentration). Advantages of this technique include the ability to determine limiting nutrients without altering the sediment environment and, with repetitive sampling, to determine when the nutrient becomes limiting. One of the objectives of this study was to determine experimentally the critical concentrations of nitrogen and phosphorus for the salt marsh plants *Distichlis spicata* (L.) and *Spartina alterniflora* (Loisel.). These values were then used to evaluate the limiting nutrient status of plants grown on a variety of sediments.

In addition to limitation by nitrogen, plant growth in salt marshes has also been shown to be inhibited by salinity (Good 1965, Nestler 1977a). Smart and Barko (1978) attributed reductions in growth of several salt marsh species on nutrient-rich, fine-textured sediments to differences in sediment salinity. They also demonstrated the importance of salt exclusion by plant roots and suggested that potassium was selectively absorbed and sodium excluded. The second objective of this investigation was to examine in greater detail these ion exclusion/selection mechanisms.

### MATERIALS AND METHODS

The investigation was conducted between June and November 1977, in the greenhouse facility of the Environmental Laboratory in Vicksburg, Mississippi, USA. This facility is equipped with thermostatically controlled heating and evaporative cooling systems. Temperature and relative humidity were maintained within limits representative of growing seasons in the southeastern United States.

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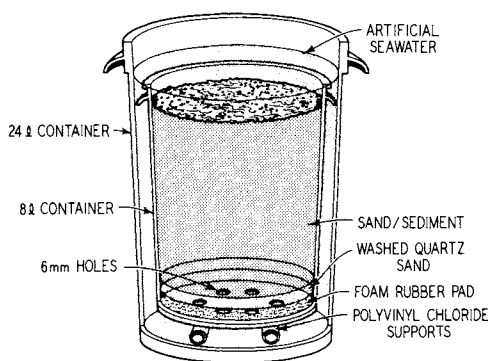


FIG. 1. Plant culture apparatus.

#### Sand culture experiment

The plant culture apparatus used in the investigation consisted of an outer reservoir of nutrient-enriched "tidal" water and an inner container filled with sand to contain the plant roots (Fig. 1). The inner container had a capacity of 8 l, a surface area of 275 cm<sup>2</sup>, and a depth of 30 cm which corresponds to the depth of root penetration reported for a *Spartina* marsh in Massachusetts (Valiela and Teal 1974). Nutrient and water exchange between the inner and outer containers occurred through holes in the bottom of the inner container and also through the sand surface which was permanently submerged.

The nutrient solution was prepared from deionized water and Instant Ocean (Aquarium Systems, Eastlake, Ohio). The solution was diluted to a salinity of 15‰, and ammonium nitrate, potassium phosphate, zinc sulfate, copper sulfate, and iron EDTA were added to equivalent Hoagland concentrations (Hoagland and Arnon 1938). All other essential elements were present in the Instant Ocean mixture. The pH of the solution was adjusted to 6.5 with sulfuric acid.

The inner containers were filled with washed quartz sand, completely immersed in the nutrient solution and planted with pregerminated seeds of *S. alterniflora* or *D. spicata* obtained from Environmental Concern, St. Michaels, Maryland. The containers were then randomly assigned to tables in the greenhouse. Salinity and water levels were monitored on a daily basis and deionized water or Instant Ocean salts were added as necessary to maintain the salinity of the nutrient solution between 14 and 16‰. Nutrient solutions were changed every 10–20 d throughout the study. During the 1st 2 mo we maintained the plants in the complete nutrient solution to ensure rapid initial growth. After this period we began selectively deleting nitrogen or phosphorus from the nutrient solution supplied to a set of containers at each solution change. We thereby subjected plants of both species to nitrogen- or phosphorus-free solutions in order to impose nutrient limitation by each element, respectively. Nu-

trient deletion continued at each solution change until only one set of containers received the complete nutrient solution. This set represented plant growth under nonlimiting conditions. Respective nutrient conditions were maintained throughout subsequent solution changes for the duration of the experiment.

The plants were grown for 148 d, then harvested and separated into aboveground live, aboveground dead, and belowground biomass. All plant materials were rinsed in deionized water prior to drying at 105°C to constant mass in a forced air oven. After drying, aboveground live and belowground biomass were ground in a Wiley mill and digested for analysis of total Kjeldahl nitrogen (TKN) and phosphorus according to methods described in Smart and Barko (1978).

#### Sediment culture experiment

Sediments were collected by dredging at two to three sites at each of five estuarine locations and from a single freshwater site on Lake Michigan. Estuarine locations included Baltimore Harbor (COL, BER, NWB), Corpus Christi Ship Channel (CC1, CC2, CC3), Oakland Harbor (OH1, OH2, OH3), the Duwamish Waterway near Seattle (SE1, SE2, SE3), and Bridgeport Harbor (BRH, JNC). The freshwater sediment was collected from Michigan City Harbor (MC2) and was also used in a similar experiment with the freshwater emergent plant *Cyperus esculentus* (Barko and Smart 1979).

After thorough mixing, sediments were sampled and characterized on the basis of texture, organic matter, and nutrient content. Sediment texture was determined by the hydrometer method (Day 1956). Moisture content was determined gravimetrically. These same samples were subsequently combusted for 4 h at 550° to estimate organic matter content. Total Kjeldahl nitrogen was determined by the method of Bremner (1965). Total phosphorus, sodium, and potassium were determined after nitric acid digestion (Smart and Barko 1978). Sediment samples for interstitial water characterization were taken at the beginning and end of the investigation and were maintained at 4° for several days prior to extraction. Interstitial water was obtained by high-speed centrifugation at 4°, followed immediately by millipore filtration (0.45 μ). This technique minimized exposure of the samples to air and avoided the problem of phosphorus precipitation with iron. Salinity of the interstitial water was estimated with a refractometer. The samples were then acidified with sulfuric acid prior to analysis of NH<sub>4</sub>-N, NO<sub>2</sub> + NO<sub>3</sub>-N, and PO<sub>4</sub>-P (Technicon Autoanalyzer), and Na and K (flame photometry).

Sediments were placed in the culture containers shown in Fig. 1, and were flooded with Instant Ocean diluted with deionized water to a salinity of 15‰. This solution contained only trace quantities of nitrogen and phosphorus and plant growth was thus dependent

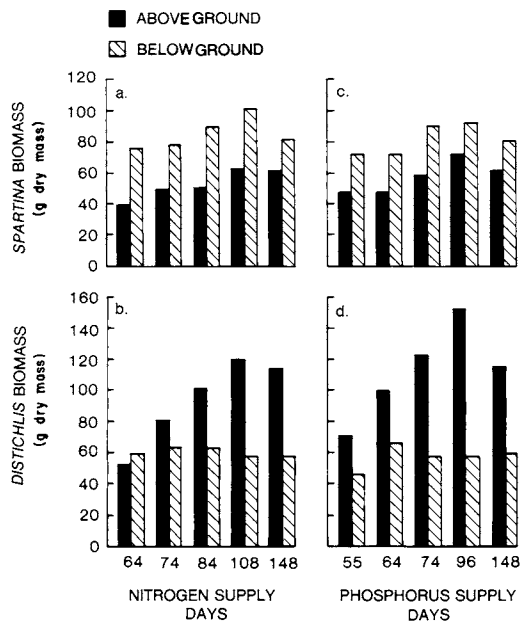


FIG. 2. Relationship between aboveground and belowground biomass accrual and the duration of nitrogen (a, b) or phosphorus (c, d) supply. Plants were initially grown in a complete nutrient solution and nitrogen or phosphorus was deleted from the solution on the days indicated. All plants were harvested after 148 d.

solely on nitrogen and phosphorus derived from the sediments.

Three containers of each sediment were planted with seeds of *D. spicata* and three with *S. alterniflora*. The containers were then randomly assigned to tables in the greenhouse. Salinity and water levels were maintained as in the sand culture experiment. Solutions were replaced every 6 wk for the duration of the investigation (140 d). At this time the plants were harvested and analyzed as described for the sand culture experiment.

## RESULTS AND DISCUSSION

### Sand culture experiment

**Biomass response.**—Removal of either nitrogen or phosphorus early in the experiment resulted in nutrient-limited growth of both *Distichlis* and *Spartina* (Fig. 2). Aboveground biomass accrual was proportional to the supply of nitrogen through day 108 and phosphorus through day 96. Additional supplies of either nutrient did not result in increased growth. Belowground biomass of *Distichlis* was unresponsive to changes in nitrogen or phosphorus while that of *Spartina* was apparently stimulated by later removals of either nutrient. Both of these species therefore exhibited increased belowground to aboveground biomass ratios under nutrient-limiting conditions. These results are similar to those obtained by Gallagher (1975) and also by Valiela et al. (1976) who suggested that *Spar-*

*tina* plants produce only enough roots to process the needed nitrogen. The results of our investigation substantiate this trend for phosphorus as well as nitrogen. The ability to allocate a greater proportion of photosynthate to the production of absorptive and/or storage organs may be of ecological advantage to perennial plants growing in nutrient-poor environments (Barko and Smart 1978, 1979).

**Tissue nutrients.**—Concentrations of tissue nitrogen and phosphorus in the two species were similar for plants grown under similar conditions and are subsequently treated collectively. Concentrations of tissue nitrogen and phosphorus plotted against biomass in Fig. 3 form curves very similar to the idealized relationship (Bates 1971, Epstein 1972). Under nutrient-limiting conditions increases in nutrient availability result in incremental increases in plant growth, thus the tissue concentration of the limiting nutrient remains constant. This critical concentration is exceeded only when the availability of the nutrient exceeds the requirements of the plant. Luxury consumption can occur when the nutrient no longer limits growth. From Fig. 3 the first three nitrogen or phosphorus removal points, indicating nutrient-limited plant growth, were used to establish critical concentrations and 95% confidence limits of  $7.3 \pm 0.7$  g nitrogen/kg and  $0.44 \pm 0.05$  g phosphorus/kg. Tissue phosphorus concentrations of plants grown in the nitrogen removal experiment were indicative of luxury consumption of phosphorus. Likewise plants grown in the phosphorus removal experiment contained luxurious levels of tissue nitrogen.

The mass ratio of critical nitrogen to critical phosphorus is unique in that it gives the relationship between the minimum requirements of these elements. The (N:P) ratio of 16.6 determined for *Distichlis* and *Spartina* in this investigation is considerably higher than the commonly accepted stoichiometric ratio of 7. In an investigation of the nutritional ecology of an emergent freshwater plant, Barko and Smart (1979) determined a critical nitrogen to critical phosphorus ratio of 7.5 (mass basis). The higher ratio determined for *Distichlis* and *Spartina* is thus indicative of a higher requirement for nitrogen relative to phosphorus. This high ratio is of interest due to the recent evidence that some salt marsh plants, primarily within the Chenopodiaceae, may use a number of nitrogen compounds such as proline (Stewart and Lee 1974) or glycinebetaine (Storey and Wyn Jones 1977) for maintaining osmotic balance under saline conditions.

### Sediment culture experiment

**Sediment comparisons.**—On the basis of texture (Table 1) all the sediments would be classified as clay except for BER (sandy clay) and OH3 (sandy clay loam). Organic matter content showed considerable variation among the different sediments and is indicative, in a general sense, of the degree of sediment

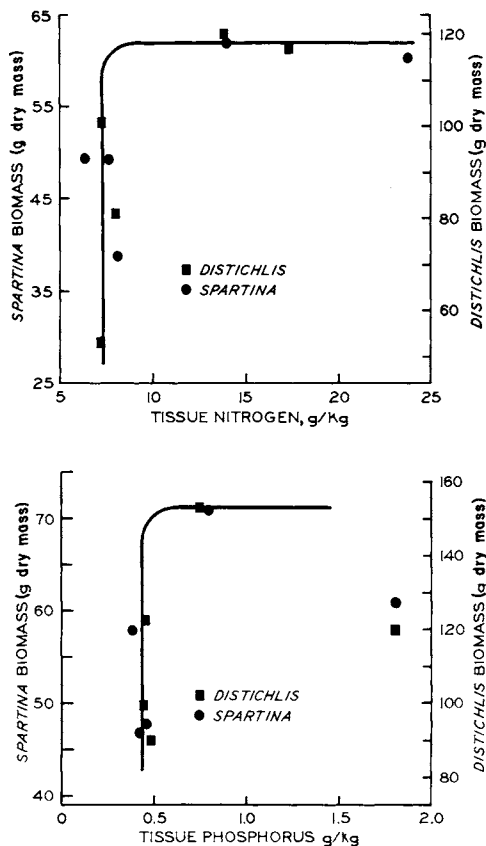


FIG. 3. Relationship between aboveground biomass accrual and tissue concentration of nitrogen and phosphorus.

fertility. Both total Kjeldahl nitrogen and total phosphorus concentration were positively correlated with organic matter content of the sediments.

Sediments were classified as freshwater, brackish, or marine on the basis of interstitial water salinity (Table 2). Due to the highly reduced nature of these sediments, concentrations of  $\text{NO}_2 + \text{NO}_3\text{-N}$  in the interstitial water did not exceed 0.3 mg/l in any of the 15 sediments. Concentrations of  $\text{NH}_4\text{-N}$  (Table 2) generally exceeded the highest values reported for salt marsh sediments in Georgia (Maye 1972) and North Carolina (Mendelssohn 1979a) and for estuarine sediments in southern Louisiana (Ho and Lane 1973). The high  $\text{NH}_4\text{-N}$  concentrations reflect the eutrophic nature of the environments from which they were collected and the lack of exposure of these sediments to rooted plants. Concentrations of interstitial water  $\text{PO}_4\text{-P}$  (Table 2) covered a range of about three orders of magnitude and are similar to values reported for salt marsh sediments in Georgia (Maye 1972).

**Plant growth and nutrition.**—Both *Distichlis* and *Spartina* exhibited a wide range of growth on the different sediments. Aboveground biomass values of both species ranged from 6–108 g dry mass. The similarity of the growth responses of the two species was

TABLE 1. Sediment texture and organic matter. Means are based on three replications.

| Sediment | Texture |         | % organic matter |
|----------|---------|---------|------------------|
|          | % fine* | % sand† |                  |
| MC2      | 72.9    | 27.1    | 14.2             |
| COL      | 78.3    | 21.7    | 10.0             |
| BER      | 54.2    | 45.8    | 26.7             |
| NWB      | 89.6    | 10.4    | 11.9             |
| CC1      | 98.3    | 1.7     | 8.9              |
| CC2      | 100.0   | 0.0     | 9.0              |
| CC3      | 78.7    | 21.3    | 8.3              |
| OH1      | 95.8    | 4.2     | 8.3              |
| OH2      | 87.5    | 12.5    | 8.0              |
| OH3      | 34.6    | 65.4    | 2.8              |
| SE1      | 64.2    | 35.8    | 6.6              |
| SE2      | 62.1    | 37.9    | 6.2              |
| SE3      | 82.5    | 17.5    | 8.5              |
| BRH      | 63.3    | 36.7    | 16.4             |
| JNC      | 82.5    | 17.5    | 11.6             |

\* <0.05 mm.

† >0.05 mm.

remarkable. The aboveground biomass of *Spartina* was highly correlated with that of *Distichlis* ( $r = .97$ ) and the slope was close to unity ( $m = 0.93$ ). Due to this similarity biomass data for the two species will be combined for later discussion.

Concentrations of nitrogen and phosphorus in the aboveground tissues of *Distichlis* and *Spartina* are compared with the respective critical concentrations in Fig. 4. Tissue concentrations of nitrogen in *Spartina* plants grown on the different sediments were within or below the critical concentration range for this element, and indicate probable nitrogen limitation of *Spartina* growth on all 15 sediments. Nitrogen concentrations in *Distichlis* also indicate probable nitro-

TABLE 2. Interstitial water salinity,  $\text{NH}_4\text{-N}$ , and  $\text{PO}_4\text{-P}$  concentrations. Means  $\pm 1$  SE are based on three replications.

| Sediment   | Salinity (g/kg) | $\text{NH}_4\text{-N}$ (mg/l) | $\text{PO}_4\text{-P}$ (mg/l) |
|------------|-----------------|-------------------------------|-------------------------------|
| Freshwater |                 |                               |                               |
| MC2        | 3 $\pm$ 0.0     | 130 $\pm$ 1.3                 | <0.1 $\pm$ 0.0                |
| Brackish   |                 |                               |                               |
| COL        | 10 $\pm$ 0.0    | 59 $\pm$ 0.4                  | 0.6 $\pm$ 0.0                 |
| BER        | 9 $\pm$ 0.2     | 134 $\pm$ 0.3                 | <0.1 $\pm$ 0.0                |
| NWB        | 11 $\pm$ 0.0    | 31 $\pm$ 0.3                  | 1.2 $\pm$ 0.1                 |
| Marine     |                 |                               |                               |
| CC1        | 26 $\pm$ 0.0    | 27 $\pm$ 0.3                  | 4.4 $\pm$ 0.1                 |
| CC2        | 27 $\pm$ 0.2    | 19 $\pm$ 0.1                  | 3.8 $\pm$ 0.3                 |
| CC3        | 27 $\pm$ 0.9    | 55 $\pm$ 0.1                  | 10.9 $\pm$ 0.0                |
| OH1        | 29 $\pm$ 0.2    | 30 $\pm$ 0.2                  | 5.0 $\pm$ 0.1                 |
| OH2        | 31 $\pm$ 0.0    | 25 $\pm$ 0.3                  | 6.1 $\pm$ 0.1                 |
| OH3        | 31 $\pm$ 0.5    | 29 $\pm$ 0.3                  | 10.2 $\pm$ 0.3                |
| SE1        | 29 $\pm$ 0.3    | 23 $\pm$ 0.2                  | 2.0 $\pm$ 0.1                 |
| SE2        | 30 $\pm$ 0.7    | 19 $\pm$ 0.1                  | 3.1 $\pm$ 0.6                 |
| SE3        | 29 $\pm$ 0.2    | 76 $\pm$ 0.9                  | 13.0 $\pm$ 0.2                |
| BRH        | 27 $\pm$ 0.8    | 94 $\pm$ 0.5                  | 17.5 $\pm$ 0.6                |
| JNC        | 27 $\pm$ 0.5    | 43 $\pm$ 0.5                  | 20.4 $\pm$ 0.5                |

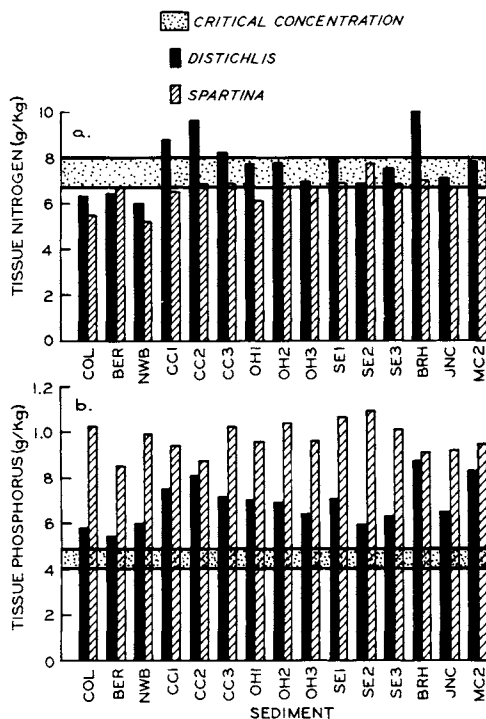


FIG. 4. Comparison of nitrogen and phosphorus in the aboveground tissues of plants grown on sediments with the 95% confidence intervals of critical nitrogen (a) and phosphorus (b). Concentrations within the critical range indicate probable nutrient limitation.

gen limitation on 11 of the 15 sediments. Concentrations of tissue phosphorus in both species, however, exceed the critical concentration range for this element, indicating a lack of phosphorus limitation of plant growth on any of the sediments used in the investigation.

Interstitial water  $\text{NH}_4\text{-N}$  concentrations measured at the end of the study decreased at least two orders of magnitude to values of  $\approx 0.1$  mg N/l. Interstitial water  $\text{PO}_4\text{-P}$  concentrations also decreased on most sediments, but to a lesser extent than those for nitrogen.

Additional evidence for nitrogen limitation is the highly significant relationship between the aboveground growth of both species and the initial concentration of interstitial water  $\text{NH}_4\text{-N}$  in the sediments (Fig. 5). Belowground biomass of both species was also correlated with increased  $\text{NH}_4\text{-N}$  concentration, but the response was not as great as that for aboveground biomass so that belowground to aboveground biomass ratios decreased with increasing interstitial water  $\text{NH}_4\text{-N}$  (Fig. 5).

Valiela et al. (1976) determined belowground productivity for a *Spartina* marsh in Massachusetts and found that it greatly exceeded aboveground productivity. In our investigation belowground production (biomass accrual) of both *Spartina* and *Distichlis* ranged

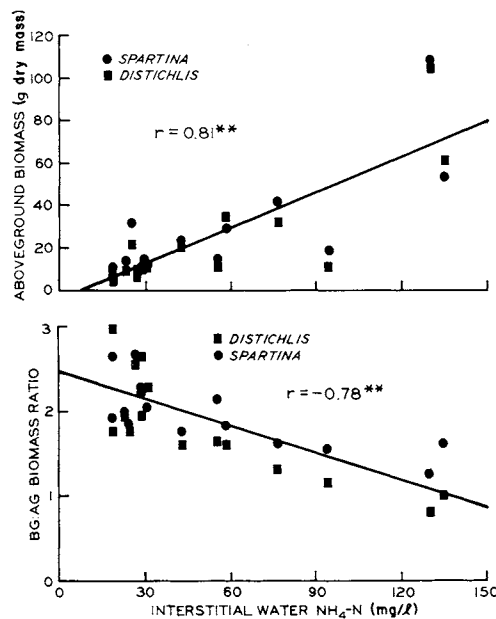


FIG. 5. The relationship between interstitial water  $\text{NH}_4\text{-N}$  and aboveground biomass and the belowground to aboveground (BG:AG) ratio. Asterisks indicate significance at the 99% level.

from one to three times the aboveground production. It appears likely that the belowground productivity of nitrogen-limited high marsh plants may substantially exceed that determined for aboveground portions. However, in the more fertile creek bank areas, belowground productivity is probably comparable to that obtained above ground.

**Salinity tolerance.**—In addition to the currently accepted view of predominant nitrogen limitation of *Spartina* marshes, more recent information has suggested a significant effect of salinity on the productivity and form of *Spartina alterniflora*. Nestler (1977a) presented evidence that *Spartina* growth in a Georgia salt marsh was limited by interstitial water salinity. Smart and Barko (1978) indicated that, under favorable nutrient conditions, increased sediment salinity substantially reduced the growth of salt marsh plants. Results of solution culture studies have also demonstrated reductions in plant growth due to salinity (Goselink 1970, Mooring et al. 1971, Phleger 1971, Mahall and Park 1976, Parrondo et al. 1978). In our investigation initial growth rates of both species were highest on sediments of low salinity, and final biomass accrual was highest on the freshwater sediment (MC2). These observations support the above conclusions regarding the inhibitory effects of salinity on *Spartina* productivity.

The mechanisms of growth inhibition by salinity are poorly understood, particularly in the case of *Spartina* and *Distichlis*. Reductions in growth of halophytes have generally been ascribed to excess ion accumulation rather than direct osmotic effects (Epstein 1969,

TABLE 3. Initial and final salinity (g/kg) of the sediment interstitial water. Means  $\pm$  1 SE are based on *n* observations.

| Sediment   | <i>n</i> | Initial      | Final             |                 |
|------------|----------|--------------|-------------------|-----------------|
|            |          |              | <i>Distichlis</i> | <i>Spartina</i> |
| Freshwater | 3        | 3 $\pm$ 0.0  | 32 $\pm$ 0.2      | 32 $\pm$ 0.9    |
| Brackish   | 9        | 10 $\pm$ 0.3 | 24 $\pm$ 0.8      | 23 $\pm$ 0.5    |
| Marine     | 33       | 28 $\pm$ 0.3 | 24 $\pm$ 0.4      | 23 $\pm$ 0.3    |

Jefferies 1972, Ranwell 1973). A number of physiological strategies for coping with excess salinity have been reviewed by Waisel (1972) and Poljakoff-Mayber and Gale (1975).

**Salt exclusion.**—In the absence of salt exclusion mechanisms, influxes of 15‰ tidal water due to plant uptake and transpiration would be expected to cause the salinity of all sediments to approach 15‰. However, salinities of the freshwater and brackish sediments at the end of the investigation were significantly higher than that of the tidal water (Table 3). Salinity of the marine sediments decreased from initial values but not to the level of salinity in the tidal water. These patterns indicate that substantial quantities of salts were excluded by the roots of both *Distichlis* and *Spartina*. Salt exclusion was apparently proportional to biomass accrual, thus the final salinity attained was highest on the freshwater sediment (MC2). The initially high growth rates of plants grown on the low-salinity sediments may have resulted in rapid and substantial increases in sediment salinity. Growth rates of plants grown on these sediments were severely curtailed during the latter portion of the study, possibly due to the increased salinity.

**Salt-secreting species** such as these were thought to passively accumulate salts from the sediments and secrete them through salt glands or hydathodes (Waisel 1972). The results of this and an earlier investigation (Smart and Barko 1978) suggest, however, that salt exclusion by the roots may be important in regulating the salt content of plants subjected to high salinities. In another salt-secreting species, *Tamarix aphylla*, salt secretion is reduced at NaCl concentrations of 0.4 M (Waisel 1961). This failure of the secretion mechanism occurs concomitantly with a reduction in growth due to salinity and may be due either to inability to take up water under these low osmotic potentials or to impairment of the secretion mechanism itself. Whatever the cause, salt regulation under conditions of high salinity may be more dependent on salt exclusion by the roots than on secretion by shoots.

**Ion selection.**—In addition to salt exclusion, the roots of *Distichlis* and *Spartina* also function effectively in ion selection. Smart and Barko (1978) suggested that potassium, being less toxic than sodium, might be selectively accumulated while sodium was excluded. Analysis of sodium and potassium concen-

TABLE 4. Initial and final ratios of Na:K (mass basis) in the sediment interstitial water. Means  $\pm$  1 SE are based on *n* observations.

| Sediment   | <i>n</i> | Initial      | Final             |                 |
|------------|----------|--------------|-------------------|-----------------|
|            |          |              | <i>Distichlis</i> | <i>Spartina</i> |
| Freshwater | 3        | 4 $\pm$ 0.1  | 204 $\pm$ 29.0    | 115 $\pm$ 3.6   |
| Brackish   | 9        | 23 $\pm$ 0.6 | 46 $\pm$ 6.3      | 52 $\pm$ 3.0    |
| Marine     | 33       | 29 $\pm$ 0.8 | 33 $\pm$ 1.2      | 37 $\pm$ 0.7    |

trations in the interstitial water at the end of the current investigation (Table 4) confirmed this. The Na:K ratio (mass basis) in the artificial seawater used in this investigation was  $\approx$ 26 which is similar to the ratio of these elements in seawater (Riley and Chester 1971). Interstitial water Na:K ratios of the brackish and marine sediments were initially similar to that of seawater. By the end of the investigation, however, selective uptake of potassium by plant roots had resulted in substantial increases in the Na:K ratio of the interstitial water, particularly in those sediments which produced the most biomass.

In spite of the predominance of sodium ions in the interstitial water, plants of both species maintained low concentrations of sodium in the aboveground and belowground tissues (Table 5). As in Smart and Barko (1978) potassium concentrations in the aboveground tissues were elevated in plants exposed to the higher salinity sediment (MC2). Potassium concentrations in the belowground tissues exhibited the opposite trend, and tended to decrease in plants exposed to higher salinities. This reduction in potassium concentrations resulted in elevated Na:K ratios in the belowground tissues of these plants and may indicate an impaired ability to assimilate potassium under salinity stress. It should be noted that imbalances in the Na:K ratio of the interstitial water may be more important in this regard than the actual salinity of the interstitial water. For example, Rains and Epstein (1967) indicated inhibited potassium uptake by the salt-tolerant mangrove *Avicennia marina* under elevated Na:K ratios.

**Nitrogen and salinity as limiting factors.**—In an attempt to relate plant growth to both interstitial water salinity and  $\text{NH}_4\text{-N}$ , we conducted a multiple linear regression analysis using only these two independent variables. While salinity alone was negatively correlated with aboveground biomass accrual ( $r = -.65$ ), the addition of this parameter to the regression did not significantly increase the correlation obtained using only  $\text{NH}_4\text{-N}$  as the independent variable ( $r = .81$ ). A significant negative correlation between interstitial water salinity and  $\text{NH}_4\text{-N}$  suggested a possible negative interaction between these two variables.

A number of other investigators have observed correlations between both nitrogen and salinity and the productivity or standing crop of *Spartina*. Nixon and

TABLE 5. Concentrations of Na and K, and Na:K ratios (mass basis) in aboveground (AG) and belowground (BG) biomass of plants exposed to different salinities.

| Sediment—Species             | Salinity (g/kg) | Biomass | Na(g/kg)   | K(g/kg)    | Na:K        |
|------------------------------|-----------------|---------|------------|------------|-------------|
| Brackish and marine*         |                 |         |            |            |             |
| <i>Distichlis spicata</i>    | 24 (0.5)        | AG      | 13.1 ± 0.4 | 6.6 ± 0.4  | 2.07 ± 0.15 |
|                              |                 | BG      | 3.7 ± 0.2  | 6.6 ± 0.3  | 0.56 ± 0.01 |
| <i>Spartina alterniflora</i> | 23 (0.3)        | AG      | 7.7 ± 0.8  | 5.7 ± 0.3  | 1.46 ± 0.22 |
|                              |                 | BG      | 6.9 ± 0.2  | 11.6 ± 0.5 | 0.60 ± 0.02 |
| Freshwater (MC2)†            |                 |         |            |            |             |
| <i>Distichlis spicata</i>    | 32 (0.2)        | AG      | 12.9 ± 1.2 | 7.5 ± 0.6  | 1.75 ± 0.28 |
|                              |                 | BG      | 3.6 ± 0.1  | 4.9 ± 0.2  | 0.73 ± 0.02 |
| <i>Spartina alterniflora</i> | 32 (0.9)        | AG      | 7.0 ± 0.1  | 6.1 ± 0.2  | 1.16 ± 0.05 |
|                              |                 | BG      | 6.8 ± 0.1  | 6.0 ± 0.1  | 1.15 ± 0.02 |

\* Means ± 1 SE are based on 42 observations.

† Means ± 1 SE are based on three observations.

Oviatt (1973) reported significant correlations between both salinity and  $\text{NH}_4\text{-N}$  and standing crop of *S. alterniflora* in Rhode Island salt marshes. Broome et al. (1975) observed a highly significant negative correlation between soil salinity and yield of nitrogen limited *Spartina* in a North Carolina salt marsh. Valiela et al. (1976) state that nitrogen-limited *Spartina* repeatedly shows greening and increased growth following a substantial rainfall. They did not report interstitial water salinity, but lowered salinities following heavy rains have been documented for *Spartina* marshes in England (Ranwell et al. 1964). These lowered salinities may have been responsible for the increased growth observed by Valiela et al. In a later investigation Valiela et al. (1978) state that 4 yr of nitrogen fertilization in the high marsh had not produced plants equivalent to those occurring along creek banks. They suggest the possibility of a secondary limiting factor such as salinity. Similarly, Mendelssohn (1979a) suggests that some factor in addition to nitrogen may be limiting growth of *Spartina* in a North Carolina salt marsh. He measured higher concentrations of  $\text{NH}_4\text{-N}$  in the interstitial waters of a short *Spartina* marsh than in the more productive creek bank marsh, perhaps indicating an inability of the short *Spartina* to assimilate this nitrogen. Although nitrogen fertilization stimulated plant growth, these plants did not attain the productivity of creek bank *Spartina* (Mendelssohn 1979b).

These recent studies indicate that nitrogen limitation alone may not account for the variation in productivity and form observed in *Spartina* marshes. Plant-induced increases in the salinity and Na:K ratio of the sediment interstitial water may exert a controlling influence on the productivity of short form *Spartina*. The water table in most salt marshes is very near the surface (except along creek banks and at the upper limits of the marsh) and is hydraulically stagnant (Gardner 1973, Nestler 1977b), thus promoting the accumulation of excluded salts. Evidence for this is presented by Nestler (1977a) who observed increased interstitial

water salinity, and decreased plant productivity, with distance from tidal creeks. Increased water fluxes in creek bank sediments may mitigate salinity stress and nitrogen deficiency by flushing excluded salts from the sediments and by providing additional nitrogen supplies. This hypothesis may explain the beneficial effects of tidal energy subsidies on salt marsh plant productivity (Odum and Fanning 1973, Odum 1974, Steever et al. 1976).

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