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doi:10.1016/0304-3770(83)90090-6

## THE SEAGRASS, *ZOSTERA MARINA* L.: PLANT MORPHOLOGY AND BED STRUCTURE IN RELATION TO SEDIMENT AMMONIUM IN IZEMBEK LAGOON, ALASKA

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### ABSTRACT

Short, F.T., 1983. The seagrass, *Zostera marina* L.: plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. *Aquat. Bot.*, 16: 149-161.

The relationship between the morphology of eelgrass, *Zostera marina* L., and ammonium in the sediment interstitial water was examined. The size of eelgrass plants collected from an intertidal terrace showed a consistent relationship with the size of the interstitial ammonium pool. Leaf area, length, and width all showed a linear increase in size towards stations having higher ammonium, while within the stations with the highest ammonium the leaf size was relatively unchanged. The size and extent of the root system in eelgrass varied across the environmental gradient. Eelgrass shoot density and flower abundance were inversely correlated with sediment nitrogen across the eelgrass meadow. Shoot density described a strong logarithmic relation with interstitial ammonium, opposite to the relationships for leaf size. Comparison of these results indicates the importance of sediment nitrogen in determining eelgrass bed structure.

### INTRODUCTION

The striking difference in the morphology of eelgrass, *Zostera marina* L., between areas of different substrate was described early in the study of these marine macrophytes. So obvious was the relationship between plant morphology and sediment environment that Ostenfeld (1908) described two forms, both growing in deep water, as the "narrow-leaved sand *Zostera*" and the "broad-leaved mud *Zostera*". Some time later Philip (1936) described this same phenomenon as the inshore narrow-leaved and the offshore broad-leaved forms of *Zostera marina* occurring in different substrates. Additionally, in his analysis of the chemical factors limiting *Zostera* distribution, Philip

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suggested that "the nitrogen content of the mud" might account for the differences in leaf size.

Numerous other investigations have described different growth forms of *Zostera marina* and related them to variations in one specific environmental factor (temperature, Setchell, 1929; light, Burkholder and Doheny, 1968; wave action and substrate, Harrison and Mann, 1975; sediment texture, Aioi, 1980). However, a fertilization study (Orth, 1977) is the only investigation to expand on the implications of Philip's 1936 suggestion that nutritional factors in the sediment might be important in controlling eelgrass morphology.

The density of shoots within eelgrass beds has been related to water depth and light intensity (Burkholder and Doheny, 1968; Backman and Barilotti, 1976; Jacobs, 1979; Phillips, 1980). Experimental evidence shows a decrease in shoot density resulting from reduced light, from either light attenuation with depth or shading of plants at constant depth (Short et al., 1974; Backman and Barilotti, 1976). Extensive work with agricultural crop plants supports a relationship between shoot density and light intensity; reduced light decreases new shoot (tiller) production (Evans et al., 1964; Milthorpe and Moorby, 1974).

The major environmental factor influencing flower production was initially reported to be temperature (Setchell, 1929). However, this early scheme of temperature control has been criticized as too simple (Phillips, 1974; Riggs and Fraclick, 1975; Harrison and Mann, 1975; Jacobs and Pierson, 1981). Reduced irradiance was shown to decrease flowering in experimental shading studies (Backman and Barilotti, 1976). Flower development in eelgrass has been examined in relation to the environmental factors of light and temperature (De Cock, 1981b, c). The phenology of floral shoot production and flowering has also been described (De Cock, 1980; Phillips, 1980; Jacobs and Pierson, 1981). Observations suggest that the period of abundant flowering coincides with the early summer increase in vegetative biomass (Sand-Jensen, 1975). The actual environmental factor or factors controlling both floral induction and the extent of spathe production are not yet known (Churchill and Riner, 1978; De Cock, 1981a).

The eelgrass sediment environment is an anoxic system composed of many chemical species (e.g.,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ ,  $\text{H}_2\text{S}$ ,  $\text{CH}_4$ ,  $\text{H}^+$ ; C.P. McRoy and M.J. Klug, 1980, unpublished) that could exert an influence on eelgrass morphology. Of these, ammonium ( $\text{NH}_4^+$ ) is the major nitrogen supply to the plants; however, it shows large differences in concentration between eelgrass beds. At some locations where ammonium becomes depleted, it is the nutrient resource limiting eelgrass growth (Short, 1983). Nitrogen is primarily taken up by eelgrass roots, although uptake by eelgrass leaves is also known (Iizumi and Hattori, 1982; Short, 1981). The uptake of nitrogen from anoxic eelgrass sediments is determined by the interstitial ammonium concentrations. The supply of ammonium to the sediments from decomposition, the losses by uptake and diffusion, and the exchange at sediment particle surfaces all

determine the actual amount of available nitrogen. However, the ammonium concentration is a reasonable indicator of nitrogen availability (Short, 1981).

In this study plant nutrition has been examined, and specifically how the availability of sediment nitrogen might influence seagrass morphology, plant density and the extent of flowering during the peak growth season. Observations of sediment conditions are correlated with plant measurements and these relationships are discussed with respect to other environmental factors.

## METHODS

The assessment of the relationship between nitrogen assets and eelgrass morphology was approached using a simple comparison of resource availability and plant characteristics. Measurements of leaf length, width, and area, shoot density, and flowering were made routinely when sampling eelgrass standing stock in the vicinity of Grant Point in Izembek Lagoon, Alaska (Fig. 1). Observations of root structure were obtained from many of the same stations. Stations were selected to provide a variety of eelgrass beds having different standing stocks and different sediment interstitial ammonium concentrations. The numbered station series was a transect established across a shallow meadow and into deep water away from shore (0.2–1.4 m).

Samples used in this analysis were collected during June and July from 1976 through 1978. Leaf material was clipped at the sediment surface within a 1/16 m<sup>2</sup> area and the plant material below the sediment surface was collected with a 16 cm diameter core sampler to a depth of about 30 cm from selected stations at Izembek Lagoon (Fig. 1). The values for leaf length and width were obtained by averaging the maximum leaf size of 10 vegetative shoots. One-sided leaf area was measured on the same shoots using a Lambda LI-3100 area meter. Eelgrass shoots were counted for each sample and individual spathes on the floral shoots were counted separately. Rhizome length measurements were made by determining the total length of horizontal rhizome in each core sample. Root size and root hair development were also examined.

Interstitial ammonium concentrations were determined from replicate core samples collected at each station to a depth of 15 cm, a depth which includes 89% of the root system (C.P. McRoy, 1978, unpublished). These core samples were sectioned into a sediment squeezer (Reeburgh, 1967) and the interstitial water was filtered through a glass fiber filter into a sealed Vacutainer. Ammonium samples were diluted (1:10) and analyzed colorimetrically (Koroleff, 1976). The interstitial ammonium pool was determined by multiplying the ammonium concentration times, the sediment moisture content times, the sediment density for each section and integrating this measured quantity of ammonium to a depth of 15 cm.

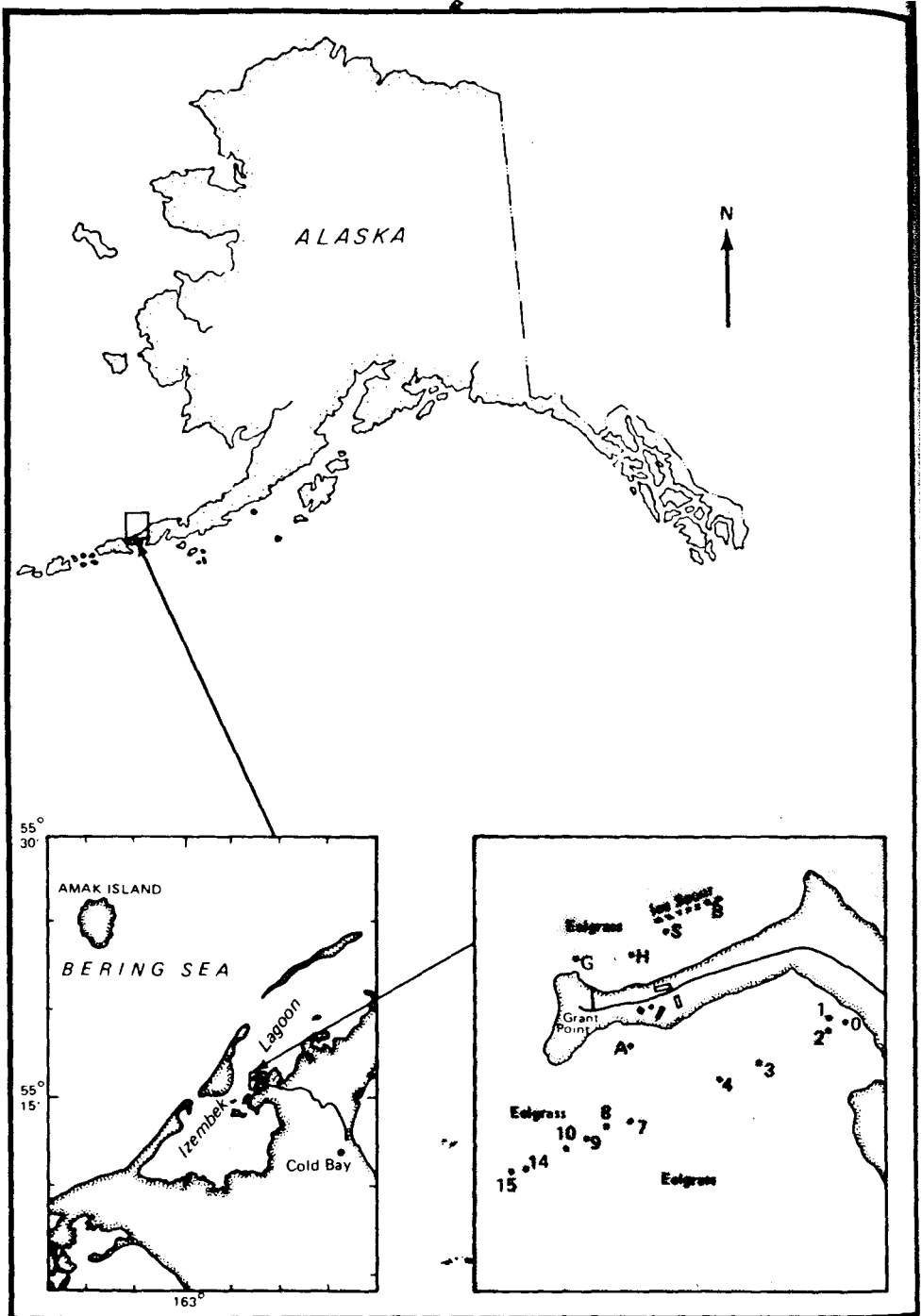


Fig. 1. Map of Alaska showing locations of Izembek Lagoon and Grant Point. The area of continuous eelgrass meadow (shading) and the sampling stations are shown.

## RESULTS

An extensive eelgrass meadow on a gradually sloping intertidal terrace that extended into deep water provided eelgrass shoots varying in size from short narrow-leaved plants growing in sandy sediment to long wide-leaved plants growing in mud (Fig. 2). The stations represent a gradient in sediment conditions from nitrogen-poor sediments at the shallow end to nitrogen-rich sediments at the deep end. The plants across the terrace were exposed at mean low water, while at the deeper end the plants were exposed only at extreme low tides.

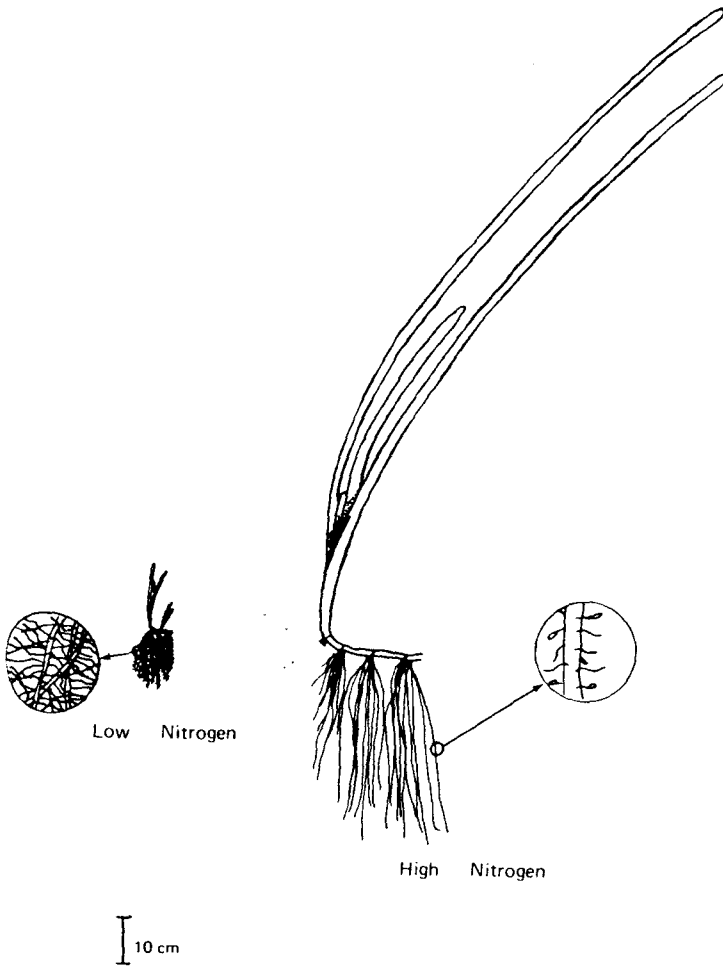


Fig. 2. Schematic diagram of eelgrass shoots in environments of low and high sediment nitrogen. Leaf, rhizome, and root structure are shown in relative proportion with extensive root hairs on the small branching plants and reduced root hairs on the large plants.

### Leaf size

There is a good correlation between the ammonium pool and all leaf measurements (Fig. 3). These data show a linear increase in leaf area, leaf length, and leaf width with an increase in the ammonium pool up to about 25 mmol N m<sup>-2</sup> (low nitrogen region, Table I); above this level (high nitrogen region) leaf size is relatively constant.

The size of eelgrass leaves growing at different nitrogen levels shows a response similar to that found in crop plants: "higher nitrogen supplies lead to larger leaves" (Milthorpe and Moorby, 1974). However, the relationship between nitrogen assets and eelgrass leaf size is complicated by differences in water depth.

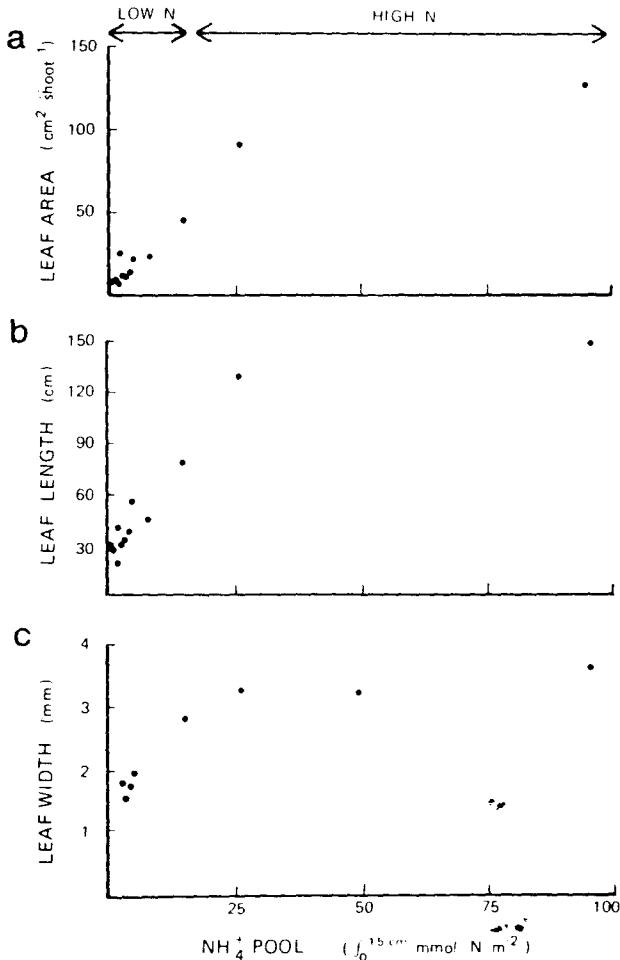


Fig. 3. Relationship between eelgrass leaf size and the sediment interstitial ammonium pool for July 1976–78 (10 replicate shoots): (a) mean leaf area per shoot; (b) length of mature leaves; (c) maximum leaf width.

TABLE I

Statistical linear correlation coefficient for leaf size, and rhizome length in low nitrogen eelgrass beds and for log transformed shoot density and flowering data

Variables	Correlation coefficient
Low nitrogen data (0–25 mmol N m <sup>-2</sup> )	
Leaf area vs. NH <sub>4</sub> <sup>+</sup> pool	0.97*
Leaf length vs. NH <sub>4</sub> <sup>+</sup> pool	0.98*
Leaf width vs. NH <sub>4</sub> <sup>+</sup> pool	0.97*
Rhizome length vs. NH <sub>4</sub> <sup>+</sup> pool	0.77
Log transformed data	
Log (density) vs. log (NH <sub>4</sub> <sup>+</sup> pool)	-0.94*
Log (flowering) vs. log (NH <sub>4</sub> <sup>+</sup> pool)	-0.75

\*Significance at the 99% level.

### Root size

The size of the rhizome and root structure is directly associated with the leaf size for all stations. Eelgrass rhizome length per m<sup>2</sup> of bottom, representing the size of the underground eelgrass system, shows a hyperbolic increase in beds of increasing sediment ammonium (Fig. 4c).

A large variation in root structure (Fig. 2) was observed at Izembek Lagoon. The root structure in the low-nitrogen environment consists of 2 bundles of 10 fine roots extending vertically 10–15 cm into the sediment from each rhizome node. Each root is covered with dense root hairs similar to those described by Smith et al. (1979) providing a large rhizosphere. Eelgrass roots in the nitrogen-rich muds were relatively large, up to 1 mm in diameter, extended deeper into the sediments, and had fewer and shorter root hairs. The development of root hairs, although not quantitatively examined, appeared to be related to the sediment nitrogen pool. Short root hairs were observed on the coarse white roots in the nitrogen-rich soft mud, while in the sandy nitrogen-poor sediment the shorter roots had long rusty-brown root hairs (the color results from the oxidation of iron on the root hair surface).

### Shoot density

Eelgrass shoot density demonstrates a negative logarithmic relationship to the interstitial ammonium pool size for all eelgrass beds sampled (Fig. 4a, Table I). The highest shoot densities, from 3000 to 10000 shoots m<sup>-2</sup>, were found in low nitrogen areas having less than 10 mmol N m<sup>-2</sup>. Sediments of large ammonium pool size, from 10 to 100 mmol N m<sup>-2</sup>, were associated with decreasing shoot density. The sediment ammonium levels represent a



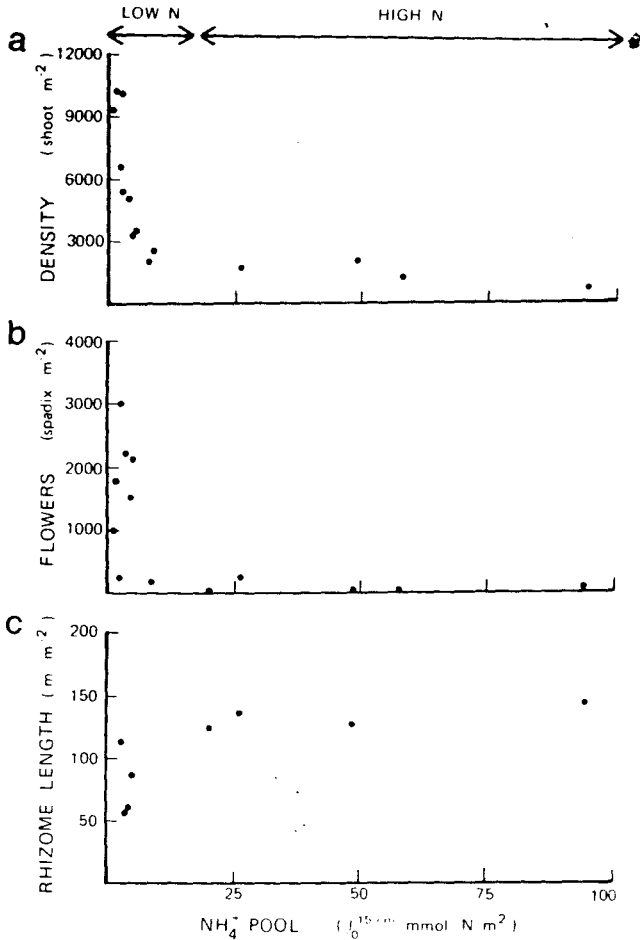


Fig. 4. Relationship between eelgrass and sediment interstitial ammonium pool for June and July 1976–78 (mean of replicate samples): (a) shoot density  $\text{m}^{-2}$ ; (b) flowering spathe density  $\text{m}^{-2}$ ; (c) rhizome length.

gradient along a gradually sloping terrace into deeper water. The shallow region was an area of uniform light level and slight temperature gradient (ca.  $1.5^\circ\text{C}$ ). At the deeper region light decreased steadily and water temperature remained constant.

### *Flowering*

Flowering in eelgrass beds reflects the same pattern as shoot density (Fig. 4b), with the largest number of flowering spathes in the area of very low sediment ammonium. The scarcity of flowers in the nitrogen-rich sediments was evident for all samples collected at Izembek Lagoon.

## DISCUSSION

Environmental variables other than climatic considerations must be addressed in attempts to understand the controls on eelgrass bed structure. Nitrogen availability and utilization are important environmental controls on the size and structure of eelgrass beds. Similar to other environmental assessments, my analysis does not examine the overlapping influence of many environmental factors. However, their effects are reduced by the selection of sampling stations along an environmental gradient.

As in terrestrial plants, the size of eelgrass leaves and shoots is controlled by many factors (light intensity, temperature, and nutrients) rather than one specific variable, although submersion in seawater may alter the effects of these factors. Nonetheless, a useful perspective was developed in the extensive studies of agricultural crops: "The potential for development of a leaf is set primarily by irradiance and temperature but its realization depends on nutrient supply" (Milthorpe and Moorby, 1974).

Eelgrass leaf area per shoot in Izembek Lagoon was generally larger in eelgrass beds having more sediment nitrogen (Fig. 3a). Similar results have been found in several terrestrial plants, e.g., in sugar beets and potatoes (Watson, 1963) and other crop plants (Langer, 1966).

Leaf length and width data depict the same relationship to the sediment ammonium pool found for leaf area (Fig. 3) suggesting a strong nitrogen influence in the shallow eelgrass meadow. This finding is supported by an enrichment experiment in which the addition of nitrogen-containing fertilizer to eelgrass sediments produced a substantial increase in eelgrass leaf length and width (Orth, 1977).

A gradual increase in water depth across the shallow portion of the eelgrass meadow paralleled the gradient in interstitial ammonium, so that the observed increase in leaf length may partly result from the slight depth increase. The same effect was observed across a shallow eelgrass meadow (depth less than 1 m) in Humboldt Bay, California (Keller and Harris, 1966).

The relationship between eelgrass leaf length and sediment ammonium is different in the deeper nitrogen-rich beds. The important environmental factor in deeper beds, apparently dominating the influences of nitrogen, is the attenuation of light. Short et al. (1974) showed experimentally that leaf length in subtidal eelgrass was less when light levels were reduced by shading.

Eelgrass shoot density demonstrates a remarkable inverse correlation with the distribution of ammonium in the sediment interstitial water (Table I). This response of density to sediment nitrogen is the opposite of that for leaf size. Eelgrass flowering reflects a similar inverse relationship to sediment ammonium as that seen for shoot density (Fig. 4b).

The relationship of shoot density and the ammonium pool is such that areas of high ammonium have sparse plants and areas of low ammonium have dense plants (Fig. 4a). Experimental enrichment studies (Orth, 1977) contradict this relationship, showing increased shoot density after fertilization.

This contradiction is not a new phenomenon in plant studies concerning soil mineral concentrations and the addition of fertilizers (Milthorpe and Moorby, 1974). The effect of increasing the nutrient supply on shoot (tiller) density of crop plants was reviewed by Langer (1966). The experimental studies examined in his review, similar to the eelgrass enrichments (Orth, 1977), added fertilizer to growing plants to increase the nitrogen supply, producing an increase in plant density, but in another crop study in which the nitrogen supply was available to the plant before growth started (Yoda et al., 1963 in White and Harper, 1970) the density of plants per  $m^2$  showed an inverse logarithmic relationship to fertility, identical to the type of relationship observed in eelgrass beds (Fig. 4a).

My explanation for this contradiction concerning shoot density for both eelgrass beds and field crops lies in the nature of the nitrogen supply. If the nitrogen supply to the plants is increased by the addition of fertilizer, the plants initially respond by producing new shoots. If the nitrogen supply is initially present in the environment or if long term responses are examined, areas of greater nitrogen supply produce fewer, but larger shoots than low-nitrogen areas.

Production of high shoot density in low-nitrogen environments is advantageous to the plant since an increase in density (and subsequently in number of roots) results in an increase in nitrogen absorption from the environment (Watson, 1963; Chapin et al., 1980). Increased shoot density becomes a disadvantage when plants become large and self shading occurs, decreasing the leaf area. This situation could occur when leaf size increases at higher sediment ammonium levels (Fig. 3) resulting in decreased shoot density. The result of the leaf size and density interaction must then be a trade-off between obtaining the maximum light energy and simultaneously optimizing the nitrogen resource. Within the local variation across an eelgrass meadow, this scheme demonstrates an area of optimum growth where sediment nutrient and light conditions are most favorable. This trade-off between shoot density and leaf size would be changed by the addition of fertilizer; the plant response of increased size and increased density would lead to overcrowding and degradation of the eelgrass bed.

Eelgrass rhizome growth is directly related to the production of leaf material, since for each leaf that is produced a new section of rhizome is laid down in the sediment. As with terrestrial plants (Evans et al., 1964), climatic conditions account for much of the seasonal change observed in rhizome length (Jacobs, 1979; Short, 1980). The spatial differences observed in eelgrass beds under similar climatic conditions result from other environmental factors. The environmental nitrogen supply directly correlates with rhizome length over much of the eelgrass meadow (Table I). The similar graphs for leaf width (Fig. 3c) and rhizome length (Fig. 4c) demonstrate the close relationship between the leaf size and the size of the rhizomes produced.

The functional importance of root structure in eelgrass beds appears to be related to the sediment environment and, most importantly, to the nitrogen

supply. Acquisition of nitrogen from the sediment interstitial water is dependent on two major factors: (1) the concentration of nitrogen in the interstitial water (Short, 1981), and (2) the size of the rhizosphere (i.e., the volume of sediment that is directly accessible to the root and root hairs; Clarkson, 1974). The root system in the low-nitrogen environment is combined with high shoot density and a large rhizosphere volume that extends throughout the sediment where mineralization occurs. Reduced root hair development in high-ammonium conditions could result from either toxic effects on plant tissue (Haynes and Goh, 1978) or the reduced need for a large adsorptive surface area at high concentrations of nitrogen. The size of the root/rhizome system is larger in high-nitrogen areas than in the low-nitrogen environments, as is the entire plant, but its structure is simpler. The reduced root structure and large sparse plants in high-ammonium sediments are replaced by the greater root development and more roots associated with the dense plants of low-ammonium sediments. These observations indicate a change in plant morphology and bed structure necessitated by the plants' requirement for a more effective nitrogen-collecting system in sediments low in ammonium.

## CONCLUSION

Analysis of interstitial ammonium in eelgrass sediments introduces an important environmental factor relating to eelgrass morphology and the structure of eelgrass beds. Leaf and root morphology as well as density of shoots and flowers demonstrate a good correlation with interstitial ammonium concentrations in areas low in nitrogen. In eelgrass beds with nitrogen-rich sediments, the relationship indicates the lack of a dominant influence of sediment nitrogen on plant morphology.

The quantity of nitrogen as interstitial ammonium available in eelgrass sediments was found to be directly related to leaf size and inversely related to shoot density over the range of nitrogen-poor stations. These results indicate that sediment nitrogen plays an important role in the spatial composition of eelgrass meadows.

## ACKNOWLEDGEMENTS

The author thanks Dr. C. Peter McRoy, Dr. Hans Lambers, Dr. Hitoshi Iizumi, and William Dennison for their assistance during this study. William Dennison provided some of the leaf length and leaf area data utilized in this study and made useful comments on this manuscript. Also, thanks to Dr. John Dacy and Catherine Short for comments and suggestions on this manuscript. Funding for this research was provided by C.P. McRoy from the Seagrass Ecosystem Study, National Science Foundation (OCE-74-13457A02 and OCE-77-27050) and by the Institute of Marine Science, University of Alaska. This is Harbor Branch Foundation, Inc. Contribution No. 326.

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