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INTRASPECIFIC VARIATION OF BIOMASS AND NUTRIENT ALLOCATION IN *SCIRPUS AMERICANUS AND SCIRPUS MARITIMUS*

by

Jim Demetrios Karagatzides

B.A., York University, 1983

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ABSTRACT

Population differentiation was investigated in stands of *Scirpus americanus* and *Scirpus maritimus* on a Fraser River intertidal brackish marsh, Vancouver, Canada (49° 11′ N, 123° 10′ W). A reciprocal field transplant experiment was undertaken concurrent with the measurement of environmental factors affecting plant growth (elevation, soil nutrients, salinity, pH, bulk density and sediment texture) to test the hypothesis that plant resource allocation varies with local environmental conditions.

Significant variations in biomass and nutrient content were found at the species' upper and lower elevation limits. *S. americanus* had greater shoot densities and biomass at the upper elevation. In contrast, *S. maritimus* had greatest shoot densities at its lowest elevation but biomass was greater at high elevations. Growth rates per hour daylight were equivalent within species suggesting that the greater exposure time in the high elevations was the primary cause of greater biomass production in the high marsh environments. Secondary environmental factors affecting plant growth included lower salinities in high marsh *S. americanus* and greater soil nitrogen in soils of high marsh *S. maritimus*. The transplant experiment demonstrated that shoot height, density and biomass were determined by the local environment as these characteristics varied with transfer site.

Plant structures in low marsh *S. americanus* and high marsh *S. maritimus* had the highest nutrient concentrations. By mid-summer, biomass production of high marsh *S. americanus* occurred more rapidly than nutrient allocation to shoots, diluting nutrient reserves in aboveground structures. Although this appeared to occur in high marsh *S. maritimus*, the greater nutrient reserves in belowground structures of these plants resulted in the production of more nutritious shoots than in the low marsh. Nutrient accumulations were greatest in the high marsh in both species. The increased accumulation of nitrogen and phosphorus in belowground structures at the end of the growing season suggests that these elements were stored for rapid mobilization to shoots the following year.

I conclude that high and low marsh *S. americanus* and *S. maritimus* represent ecophenes; genetic divergence in response to local environmental conditions has not occurred. The two populations of *S. americanus* and *S. maritimus* sampled represent a generalist genotype with plasticity for these characters.

ACKNOWLEDGEMENTS

I thank my senior supervisor, Dr. Ian Hutchinson for his assistance in developing this study. As well, thanks for your shoestrings Ian, and for letting me swim on my own. My other committee members, Drs. W. G. Bailey and R. U. Kistritz, contributed several useful comments.

Several friends can now verify that *S. americanus* grows in sandy substrates and *S. maritimus* in soft, anoxic muds. They include Susan Sui Ching Chow, Mirjam "Lab Wench" Stadelman, Cletus Liedtke, Cowboy Jelinski, Patch, Wiggs, Big Lenny, S. R. Smythe, Charlie Jinnouchi, John Olyslager, M. L. Reid, M. Q. Dehn and Bob "Courier de Bases" Lalonde.

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The constructive comments of Dennis Jelinski, Michael Dehn, John Reynolds and Mike Pidwirney were appreciated though not always adhered to. I thank the Boys of Sperling Avenue for providing much needed distractions. Jim Bowers provided the program to calculate sunrise and sunset times. His daily "visits" to the lab reminded me that it was lunch time (or was it coffee break?). The secretaries of the Geography Department, especially Rosemarie Bakker, provided an endless supply of paper and plastic bags for field samples. Danny Koz. was instrumental in putting together the figures, although any errors in artistics are my fault.

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PART A

GENERAL INTRODUCTION

CHAPTER I

THEORETICAL BACKGROUND

From Theophrastus to Turesson

Theophrastus of Eresos (*ca.* 370–285 B.C.) was convinced that species were unstable and readily changeable (Radford *et al.* 1974). This was in contrast to the typological concept of his mentor, Plato, who proposed that individuals, including plants, were expressions of the same type. To Plato, the eidos (or type) was real and the observed variation an illusion, the result of imperfect manifestations of the idea implicit in each species (Mayr 1970). The father of modern taxonomy, Carolus Linnaeus (1707–1778), was influenced by Plato's typological species concept and accepted the assumption that species were fixed entities with a finite number existing in the world. Linneaus later realized that species were derived from other species through hybridization (Mayr 1970). Following Linneaus, other taxonomists began to realize that species change and evolve from a common ancestor and species cannot be represented by a single specimen (Radford *et al.* 1974). It was these ideas that Darwin built upon, laying the foundation for the work of Turesson.

Variation in plant populations

Gote Turresson was one of the first botanists to examine variation in plant habit experimentally. He conducted a series of garden transplant experiments whereby he transplanted morphologically different plants of *Hieracium umbellatum* from different habitats to a common environment (Turesson 1922). Some of these morphologically different plants retained their differences after transplanting and he concluded that these plants were genetically different and their morphology was not primarily under environmental control. These genetically different plants were called ecotypes. Alternatively, plants within a species that were genetically similar but morphologically distinct in response to different envrironmental conditions Turesson called ecophenes (Anderson and Treshow 1980). The notion that ecotypes are adapted to their local environment has been developed since that time.

The major pathways leading to variation among plant populations are illustrated in Figure 1. Biotic factors may include such phenomena as competition and predation. Abiotic factors include disturbance and resources available for plant growth. The biotic and abiotic components of the local environment form the selection forces. In general, a species gene pool is moulded by the forces of selection producing a genetic composition that is adapted to the local environment. All individuals sharing the same genetic composition are genotypes. The genotype dictates the proportion of a plant's resources allocated to various structures. The allocation strategy of a genotype has a degree of plasticity because of the trade-offs of resources between structures within the plant.

The pheno-pathway is comprised of the current environment acting on the genotype. Because the composition of the genotype and the physical environment exhibit spatial variation, different allocation strategies are selected for in different environments and hence, morphological variation is observed. The phenotype is the product of the interaction between the genotype and the environment. The genotype can produce one of a range of phenotypes in order to grow and reproduce: the particular phenotype is a specific response to a given environment (Cox and Ford 1987). Thus, phenotypes are tactical solutions within a strategy that is set by a genotype (Harper 1982). All the naturally occuring phenotypes produced within a given habitat by a single genotype are categorized as ecophenes. Turesson's ecotypes are genetically distinct populations within the genotype that are adapted to the local environment. The allocation strategy of the ecotype is under genetic control and not influenced by the environment.

Phenotypic modification can be caused by the activation of latent genes (Claussen and Hiesey 1958). Genes may be latent if they lack complementaries, are suppressed by other genes, or if environmental conditions are not favourable for their expression. Living organisms may possess latent genes that become activated in environments that differ radically from those in which the organism has evolved. Thus, a species that appears to be highly uniform in one environment can become highly variable in another environment that is radically different (Claussen and Hiessey 1958). This variation can occur in the morphology, microanatomy, physiology and ecology of the plant.

Methods to determine if the observed variation is genotypic or phenotypic include field or garden transplant experiments, gel electrophoresis, and plant type-habitat type correllations.

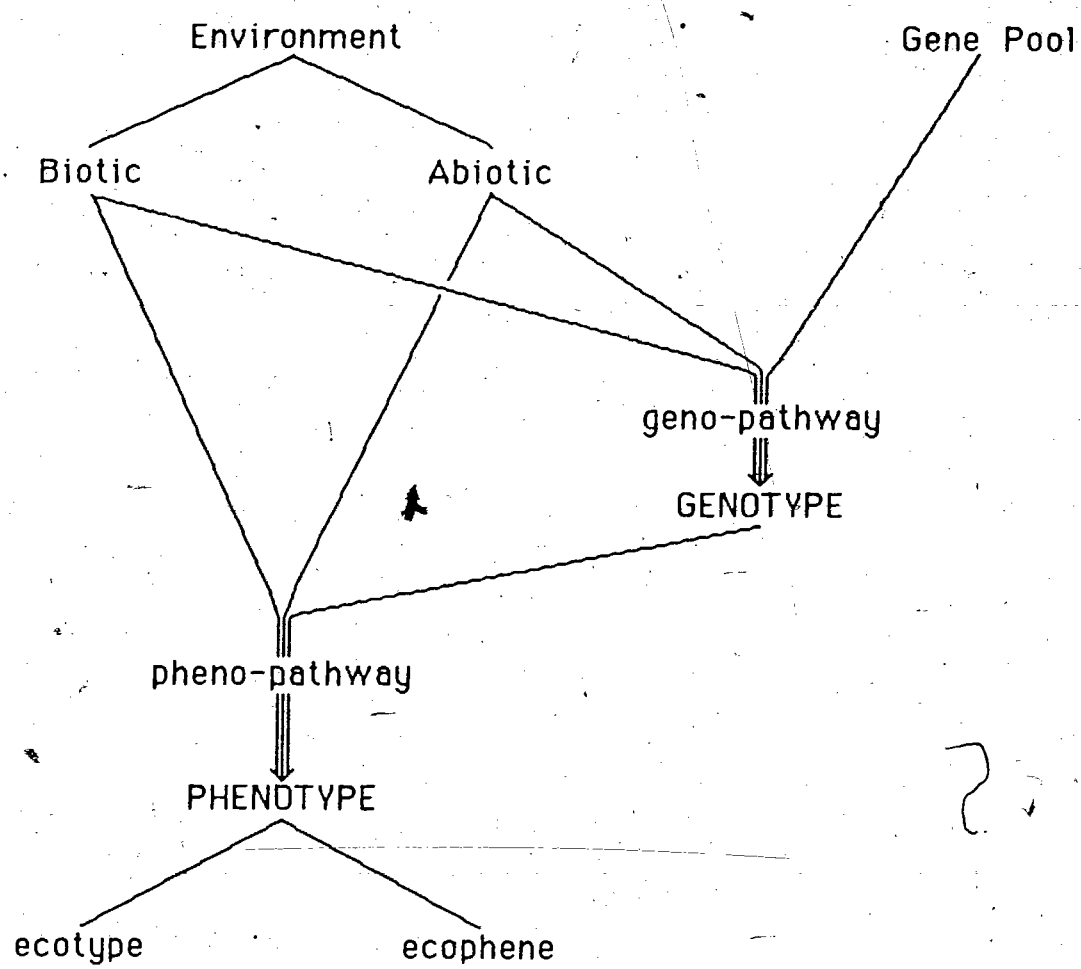

Figure 1. Model illustrating major pathways that cause variation in plant populations.

The garden transplant technique usually eliminates several environmental factors and is not as useful as the field transplant method which may demonstrate that genetic variation is adaptive to local conditions. In addition, environmental variables that appear to affect plant morphology can be correlated with specific characteristics of the plant. Gel electrophoresis can be used to obtain a preliminary estimate of the level of genetic variation in genotypes between and within different populations. Ideally, both reciprocal field transplants and gel electrophoresis should be employed.

This study focused on the abiotic portion of the pheno-pathway to examine intraspecific and interspecific variation in plant populations (Figure 1). Allocation patterns were measured to determine if variation in resource allocation strategy represents different tactics by plants in differing environment. In addition, the geno-pathway was included to determine if allocation patterns were genetically fixed.

Extending the concept of intraspecific variation to nutrient allocation

The majority of studies examining ecotypic variation in morphology have focused on biomass allocation because it is the easiest plant variable to measure. But Turesson's ecotypic concept can and should be extended to nutrient and caloric allocation. These are more important indicators of plant fitness than biomass because they provide a better measure of the investment made by a plant for the construction of various plant structures. For example, caloric data allow one to distinguish among tissues with dissimilar energy contents per gram (Pitelka 1978). It seems likely that the energetic cost of producing such a highly differentiated organ as a flower involves a greater cost than is indexed by the biomass of that organ (McNaughton 1975).

Abrahamson and Caswell (1982) showed that biomass allocation is not a good indicator of allocation of mineral elements in *Verbascum thapsus* and five *Solidago* species. In plants with primarily carbohydrate reserves, however, biomass allocation is related to nutrient or energy allocation. Hickman and Pitelka (1975) found that dry weight indicates energy allocation patterns in populations of *Lupinus nanus, L. variocolor, L. arboreus* and *Polygonum cascadense.* The use of biomass as an indicator of energy or nutrient allocation appears to be species-specific.

Requirements of a test species and study site

A research site to test for intraspecific variation of resource allocation should consist of a strong, simple local resource gradient. Strong gradients produce abrupt changes in vegetation or physical characteristics and simple gradients allow for interpretation of plant-environment interactions with the potential of determining exact causes. The environmental factors that influence plant habit become more evident if they vary in a cyclic, predictable manner. Population differentiation is most likely to occur where growing conditions differ from place to place in a predictable fashion (Davy and Smith 1985). The confounding effect of interspecific competition can be eliminated if large, monospecific stands of a test species are selected. Furthermore, clonal species are desirable because they are long-lived, genetically-uniform and the clone has been exposed to selection pressures for many years.

Genotypic and phenotypic differences within populations growing across ecological gradients should be found at the extremes of the gradient where environmental and hence, selection differences may be greatest. If variation is found at these locations, sampling along the gradient will detect the presence or absence of clinal variation.

Intertidal wetlands: the natural laboratory

Intertidal wetlands present examples of communities developed in response to local ecological gradients. In these environments, allocation strategies may be influenced by nutrient availability and other restraints of the physical environment to plant physiological processes. Specifically, elevation and the tidal regime limit the time available for nutrient uptake and metabolism. As well, the tidal regime may influence soil nutrient content or availability resulting in a heterogeneous environment that varies in a predictable fashion. Therefore, species occupying large elevation gradients in wetlands provide an opportunity to examine population differentiation, describe various investment patterns, and determine any association of these patterns with particular environmental conditions.

In marsh environments along the east and Gulf coasts of North America, two forms of *Spartina alterniflora* have been described: a tall creek bank form and a short high marsh form (de Laune *et al.* 1978, Valiela *et al.* 1978b, Gallagher *et al.* 1980, Reidenbaugh 1983).

This variation in shoot height is now generally regarded as non-genetic on the basis of electrophoretic and reciprocal transplant studies (Shea *et al.* 1975, Valiela *et al.* 1978a). Along the west coast of North America, *Carex lyngbyei* is dominant in intertidal marshes and it too has been reported to have a tall and short growth form (Eilers 1975, Jefferson 1975, Gallagher and Kibby 1981, Dawe and White 1982, 1986). Smythe (1987), however, found that while distinct tall and short growth forms were sometimes visible over distances of several meters, over tens of meters several intermediate shoot heights occurred. The so-called tall and short forms, thus, were the end points of a shoot height continuum. A reciprocal field transplant experiment of 12 *Carex lyngbyei* populations in the Puget Trough indicated that variation in shoot height was primarily ecophenic, although in rare cases, ecotypic variation was detected. Also on the Pacific coast, Seliskar (1985) found that *Deschampsia caespitosa, Distichlis spicata, Grindelia integrifolia, Jaumea glauca* and *Salicornia virginica* all demonstrated morphological and anatomical variations that were not genetically fixed.

Variation in habit can extend to belowground structures. Root to shoot ratios are usually high in plants growing under harsh environmental conditions (Kucera *et al.* 1967, Shaver and Billings 1975, Valiela *et al.* 1976, Smith *et al.* 1979). The high root:shoot ratios appear to be an adaptive response by marsh plants to harsh environmental conditions such as low nitrogen availability, waterlogged soils, anoxic soils, periodic plant inundation, high toxin concentrations, and saline water (Hopkinson and Schubauer 1984). These factors act to decrease the effective uptake of water and nutrients by a unit of root surface. Each unit of aboveground tissue, then, requires a larger amount of root surface than might be the case under more favourable conditions (Shaver and Billings 1975).

Although a number of studies have examined ecotypic variation of biomass for marsh vegetation, few studies (Drifmeyer and Redd 1981, Gallagher *et al.* 1980, Broome *et al.* 1975) have extended Turesson's (1922) ecotypic concept to nutrient allocation. Ewing (1982) presented data on the nutrient content of *Scirpus americanus* shoots collected from high and low marsh environments in the Skagit River marsh (Washington). An analysis of variance on these data indicated that the shoots from the low marsh had significantly higher concentrations of nitrogen, phosphorus and manganese ($P \leq 0.05$), as well as calcium and copper ($P \leq 0.08$). I suggest that nutrient allocation is a characteristic orchestrated by the plant in response to the relative action of environmental factors. Nutrient allocation should

exhibit variation due to habitat as the plant evolves a solution to the local environment.

Kistritz *et al.* (1983) and Hall and Yesaki (unpublished) provide the only data on the nutrient content of marsh vegetation in British Columbia. They examined nutrient movement between total aboveground and belowground compartments in coastal marsh sedges, but did not distinguish allocation to different structures. Seasonal changes in biomass and nutrient allocation should be considered for all plant structures to determine if variation extends beyond characteristics such as shoot height and flowering.

Causes of intraspecific variation in coastal marshes

The physical variables invoked as the causes of morphological variation in shoot height in wetland species include elevation, salinity stress, tidal energy, toxic effects of a reducing environment (sulfide toxicity or anoxia), and soil mineral content, particularly scarcity of available nitrogen or iron. As well, there appear to be interactions between several environmental variables that act to modify plant growth.

Elevation

Elevation relative to critical tidal levels has been used as a surrogate for factors such as tidal exposure and soil redox potential. Surprisingly, studies that accurately determined inundation/exposure times during the growing season and related it to plant size could not be found in the literature. Instead, studies present percent exposure or submergence for an entire year, which is likely not the most sensitive measure for plant growth. The variation observed between tall and short forms in some species may be a simple function of the amount of solar irradiance received during the growing season. Furthermore, submergence not only decreases irradiance received, but also results in sediment loading on shoots which further decreases the surface available for photosynthesis. Submergence decreases the efficiency of roots by impeding gas exchange, although gas transport to roots may occur via the shoot until the shoot is completely submerged (Osmond *et al.* 1987).

Aeration

Mendelssohn and Seneca (1980) determined that the occurrence of the height forms of *S. alterniflora* was directly related to marsh soil drainage and aeration in a salt marsh in North Carolina. They suggested that greater soil drainage and associated higher redox potential near creek banks (the "streamside effect") stimulate growth by oxidizing potential soil toxins, such as sulfide. This, in turn, reduces growth either directly by affecting carbon metabolism or indirectly by inhibiting inorganic nitrogen uptake and/or assimilation. Wiegert *et al.* (1983) found that increasing the subsurface drainage in a stand of intermediate height *S. alterniflora* caused a significant increase in mean shoot height and aboveground production in a two year experiment. Donovan and Gallagher (1985) found that salinity and anaerobic conditions, independently and concurrently, decreased biomass and height of the marsh grass *Sporobulus virginicus.*

Salinity

Adams (1963) and Broome *et al.* (1975) observed that *S. alterniflora* growth was restricted by increased salinity. Nestler (1977) investigated the effect of interstitial salinity as a cause of ecophenic variation in *S. alterniflora.* Nestler found that growth was robust in low saline areas and weak in areas of high interstitial salinity. As well, height of *S. alterniflora* plants was a function of total dissolved salt concentrations of the underlying substrate. De Laune *et al.* (1979) found that soil extractable sodium, magnesium and potassium expressed on a volume basis were directly related to plant yield. No accumulation of salts was observed in the less productive marsh areas.

Soil Minerals

Gallagher and Kibby (1981) suggested that the streamside effect can be simulated by the addition of nitrogen. Valiela *et al.* (1975) found that fertilization with a 10-6-4 (N-P-K) sewage sludge fertilizer increased total peak standing crop of salt marsh vegetation. This fertilization converted low marsh vegetation, consisting mainly of dwarf form *S. alterniflora,* into a sward approaching the biomass and morphology of the tall form. They conclude that the forms of *S. alterniflora* are a response to nitrogen supply.

Broome *et al.* (1983) evaluated the effects of nitrogen and phosphorus fertilizer on the growth and tissue concentration of *S. alterniflora.* There were only slight increases in

growth when either nitrogen or phosphorus were applied alone but when applied together, they acted synergistically to increase plant biomass (Broome *et al.* 1983). Despite the findings of this study, phosphorus is seldom limiting in salt marshes and the turbid estuaries associated with them, because large reserves of phosphorus, much of it as phosphate, are sorbed in clay sediments or peat (Whitney *et al.* 1981).

Some studies imply that the supply of available soil nitrogen does not limit plant growth directly but that nitrogen uptake and assimilation may be inhibited by the environmental conditions in the marsh. For example, Gallagher (1975) found that tall *Spartina alterniflora* did not respond to nitrogen fertilizer. De Laune *et al.* (1983) present data suggesting that the short height form of *Spartina alterniflora* observed in inland areas of Louisiana Gulf Coast marshes is caused by toxic concentrations of sulfide, a result of slightly lower elevation and subsequent lower redox potential than the adjacent productive streamside marsh. They speculated that sulfide may limit growth by preventing nitrogen uptake and root development.

Adams (1963) reported that *S. alterniflora* was restricted to the low marsh where large amounts of iron were available. In an analysis of factors related to standing crop, Nixon and Oviatt (1973) found that low iron availability contributed to reduced standing crop. In Georgia, Gallagher *et al.* (1980) found that mid-summer was a period of slow growth for both the creekbank and high marsh *S. alterniflora*. This coincided with the period of low iron availability and they suggested that iron may be limiting growth in the low marsh in mid-summer.

Objectives

The work presented above demonstrates that the status of the knowledge on the causes of intraspecific variation in biomass of intertidal plant species is scant. Most of this work has focused on the measurement of height differences and total biomass, with limited data available on other measures of plant fitness. Variation in resource allocation has not been examined to a great extent in these environments, yet this represents a more important measure of plant fitness. The objective of this study was to test for population differentiation in two coastal British Columbia sedges. Two species were studied to obtain some measure of between-species variation. I tested for biomass variation in

Scirpus americanus Pers. Syn. and *Scirpus maritimus* L. var. *paludosus* Nels. (nomenclature follows Hitchcock *et al.* 1969) and attempted to extend the ecotype concept to nutrient allocation. If there was intraspecific variation, a secondary objective was to determine if this variation was under genetic control, influenced by local environmental conditions, or both.

These species were selected because they are abundant and show variation in shoot height across an elevation gradient. *S. americanus* is a rhizomatous perennial sedge with sharply triangular culms 0.3 to 1.1 m tall (Mason 1957) (Figure 2). Its inflorescence is a capitate cluster of 1 to 7 spikelets (Mason 1957), essentially sessile in a compact cluster, subtended by a prominent green bract 20 - 150 mm long which appears like a continuation of the stem (Hitchcock *et al.* 1969). *S. maritimus* var. *paludosus* is a stout rhizomatous perennial sedge, 0.2 to 1.5 m tall, reproducing vegetatively and sexually (Figure 2). The rhizomes commonly bear firm tubers but have few secondary rootlets. Culms are sharply triquetrous with several leaves distributed along the stem (Hitchcock *et al.* 1969) and arise from corms found 0.10 - 0.30 m below the marsh surface. The inflorescence is capitate with one to several elongated rays (Mason 1957). Spikes number 3-20 or more, all sessile in a compact terminal cluster, or the principal surpassed by one or more short peduncles each bearing a subsidiary cluster. Scales are reddish brown to pale straw-coloured (Hitchcock *et al.* 1969).

To meet these objectives, monospecific stands of *S. americanus* and *S. maritimus* were sampled along an elevation contour near the upper and lower elevation extremes on the Sea Island foreshore marsh (Figure 3). On the foreshore marshes of Lulu Island, immediately to the south of Sea Island, *S. americanus* forms dense stands along the marsh littoral on well-drained, silty-sand substrates of relatively low moisture content. *S. maritimus* is found on siltier sediments and at higher elevations (Hutchinson 1982). Sea Island was selected because both species are found as large monospecific stands over an elevation gradient of about 0.5 m and the site is accessible during all low tides. Monospecific stands were sampled to eliminate interspecific competition and the task of identifying belowground structures of different species. By sampling relatively dense stands in one environment potential effects of variable stem density were controlled. The elevation extremes were selected because if there is variation, it is expected to occur at the elevation extremes. *S. maritimus* could not be sampled at the upper elevation limit because of the presence of

Figure 2. Diagram of *S. americanus* (left) and *S. maritimus* (right) illustrating inflorescences (i), shoots (s), roots (r), rhizomes (h) and corms (c). Modified from Hitchcock *et al.* (1969) and Mason (1957).

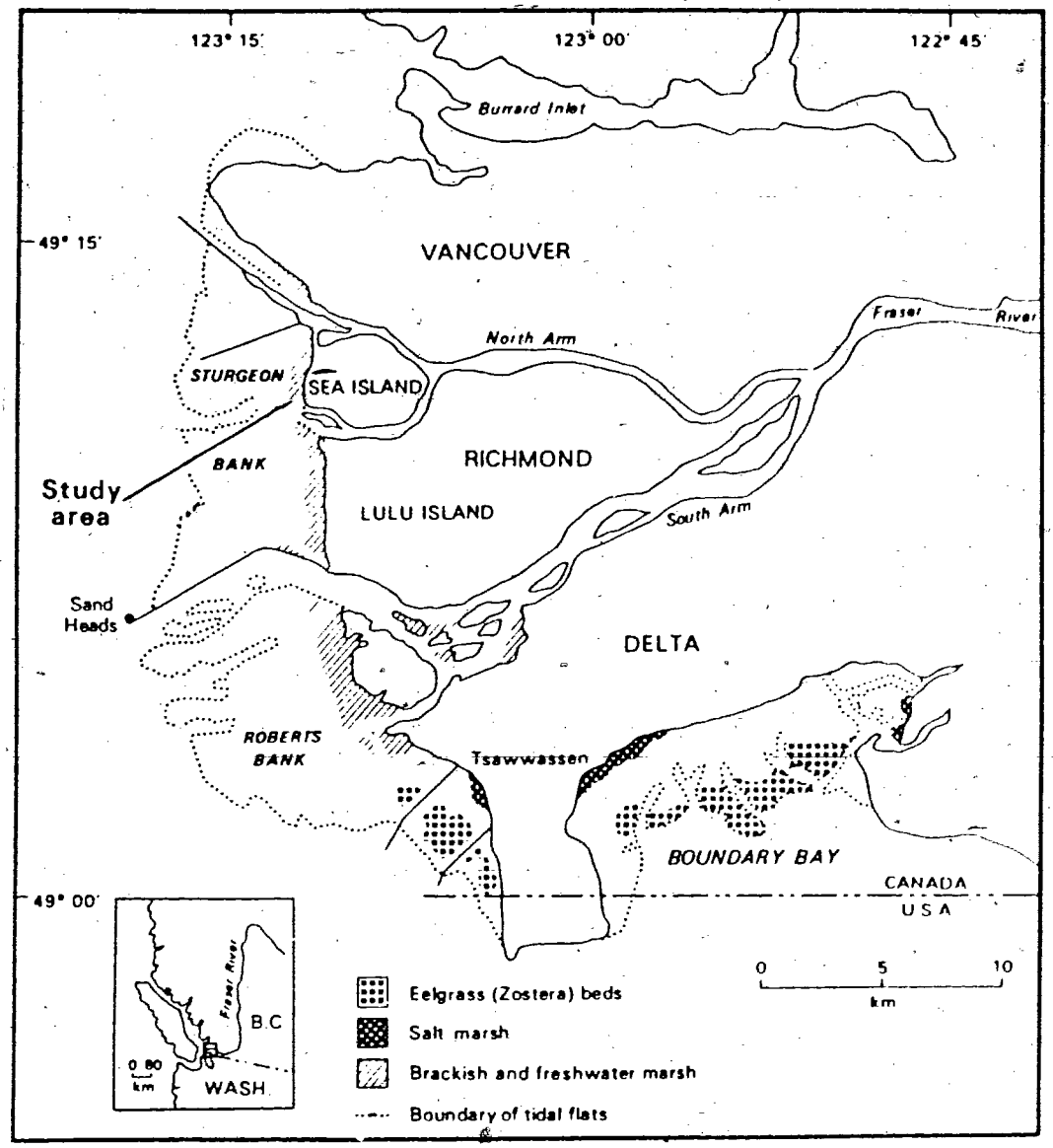

Figure 3. Location of the study site.

other species and was sampled at the mid-point of its elevation range. Therefore, two species were sampled in two environments. *S. americanus* environments are referred to as high and low marsh, while *S. maritimus* are labelled low and middle marsh (Figure 4).

Hypotheses relating resource allocation patterns to the local environment were tested. In this study, the low lying foreshore environment with the longer inundation period was considered to be the stressed environment. Resource allocation to major plant structures were determined for all phases of the annual cycle. Allocation to reproduction was tested for sexual and asexual (vegetative) reproductive organs as separate compartments. From these data, some inferences about resource allocation strategies were elucidated.

The central hypothesis of this study is that biomass and nutrient allocation patterns are a result of the species plastic response to the local environment. Specifically, it is hypothesized that plants in stressed environments put more effort into capturing and defending potentially scarce resources (biomass and nutrients) and thus, adopt conservative strategies. This hypothesis leads to the prediction that nutrient allocation varies as a function of relative availability. Nutrients that are scarce are translocated and stored in belowground structures during senescence of aboveground shoots. It has been hypothesized that nitrogen conservation by *Spartina alterniflora* suggests that primary productivity in salt marshes in eastern North America are nitrogen limited (Hopkinson and Schubauer 1984). I tested this hypothesis for nitrogen in the Sea Island marsh.

A second prediction is that plants in stressed environments will reduce resource allocation to shoots and reduce sexual reproductive effort. Foreshore plants occupy a habitat with a long inundation period and thus, a greater proportion of time available for photosynthesis is devoted to maintenance and growth. This results in a smaller investment towards reproduction. Between species, the proportion of resources allocated to reproduction will be greater in *S. americanus* than in *S. maritimus*. *S. maritimus* occupies more severely reduced soils which stress the plant and therefore require more resources to be channeled towards maintenance and less to reproduction. A consequence of this hypothesis is that within each species, the root:shoot ratio will be highest in the foreshore plants because they occupy the stressed environment.

An alternative hypothesis (H_1) is that allocation patterns are genetically controlled. This hypothesis was tested for biomass allocation using a reciprocal field transplant experiment.

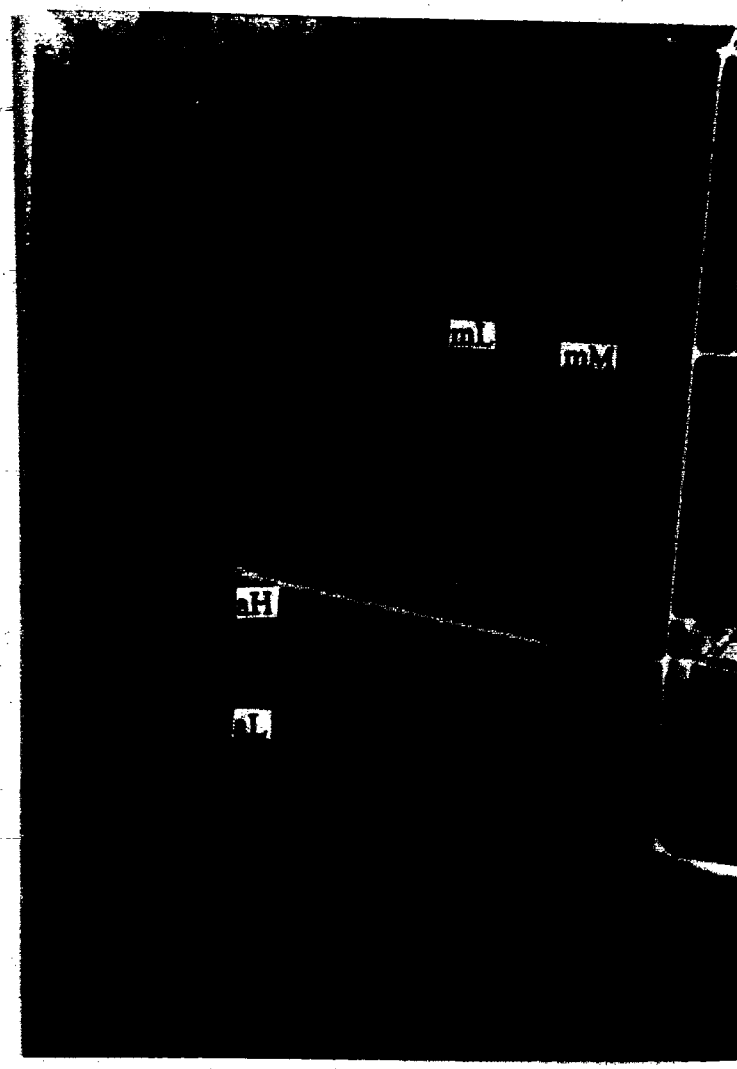

Figure 4. Colour aerial photograph of the study site indicating high and low marsh *S. americanus* (aH, aL) and middle and low marsh *S. maritimus* (mM, mL). Scale 1:12,000.

The concept of variation is the foundation for this study. In Part B, the site, situation and setting are outlined for the study area. Part C deals with the measurement of biomass variation in *S. americanus* and *S. maritimus* and in Part D, the concept of intraspecific variation is extended to nutrient allocation. In Part E, the results of the reciprocal transplant experiment are presented to determine if the variation is genetically fixed. Conclusions about the causes of variation, resource allocation strategies and suggestions for future work are presented in Part F.

PART B

THE PHYSICAL SETTING

CHAPTER I

INTRODUCTION

Description of the Study Site

Physiography

The Fraser River is the largest river reaching the west coast of Canada (Milliman 1980). It breaches the mountainous spine of western British Columbia and discharges into the Strait of Georgia, a semi-enclosed marine basin. Here, it has constructed a delta with a combined intertidal and supratidal area of about 1000 km² during the 10,000 - 11,000 years since the disappearance of the late Pleistocene Cordilleran Ice Sheet. Tidal flats characterize the narrow shelf between the shore face and the edge of the delta front, extending up to 9 km from the landward edge of the delta to the foreslope (Clague *et al.* 1983).

Hydrology

During 60 years of measurement, the mean discharge of the Fraser has been 3500 $m^3 s^{-1}$ at Mission (70 km upstream from the study site). Most of the discharge comes from melting snow and as a result, discharge from late fall through early spring is generally less than 1500 $m^3 s^{-1}$, while during spring freshet (May through mid-July) flow averages more than 4000 $m^3 s^{-1}$ (Milliman 1980). Flow distribution is estimated at 5% to the North Arm, 5% to the Middle Arm (adjacent the study site), 80-85% to the Main (South) Arm, and 5-10% to the small outlets such as Canoe Pass (Hoos and Packman 1974) (Figure 3).

The Fraser River transports between 12 and 30 million tons of sediment annually, 80% of the sediment discharge occuring during freshet. About 40-60 % of freshet suspended load is sand. Suspended matter concentrations within the estuary during all these months are generally less than 50 mg l^{-1} and during high tide often less than 20 mg l^{-1} (Milliman 1980).

The tides in the Fraser River estuary are mixed with a strong diurnal component. There is approximately a 2 week cycle in tidal ranges, and a seasonal cycle. The lowest tide occurs around midnight during the winter months and near midday during the summer. At Point Atkinson (16 km north of the study site), the average tidal range is 3.1 m, but

extremes may be as great as 4.9 m at spring tides and as low as 0.6m at neap tides (Hoos and Packman 1974). During freshet flow in spring and early summer, the Fraser River estuary is essentially fresh; except at Sand Heads and Elbow (Figure 3) during high tide, when a prominent salt wedge develops (Milliman 1980).

Climate

Climatic data (1951–1980) are available for Vancouver International Airport, 1 km from the study site. Mean daily air temperatures are 2.5°C for January, 17.3°C for July, and 9.8°C annual. January precipitation is 130.7 mm rainfall and 257 mm snowfall, compared to 32.0 mm rainfall in July. Mean annual precipitation is 1113 mm (Environment Canada, no date).

Mean monthly temperatures and precipitation for the sampling period are presented in Figure 5. Temperatures during this period were similar to the 30 year normals but precipitation was variable. The total precipitation of 817.4 mm for 1985 was much lower than the long term mean because of the very dry summer. Total precipitation for 1986 was 1219 mm, some 106 mm higher than normal.

Plant Communities

The Sea Island brackish marsh represents about 9% of the 27 km² covered by tidal marshes in the Fraser Estuary (Yamanaka 1975) and is floristically similar to other areas of the Fraser foreshore marsh. The vegetation communities are generally discrete and of low diversity (Figure 4). In the high foreshore marsh, *Typha latifolia* is the dominant species with *Carex lyngbyei*–*Distichlis spicata* dominant in the middle marsh. At lower elevations across the delta front, *S. americanus* and *S. maritimus* are dominant. Small, isolated clones of *S. americanus* are expanding at the seaward edge of the marsh. A survey of historical air photos showed that the *S. americanus* community has expanded some 400m seaward since the installation of the jetty in 1964.

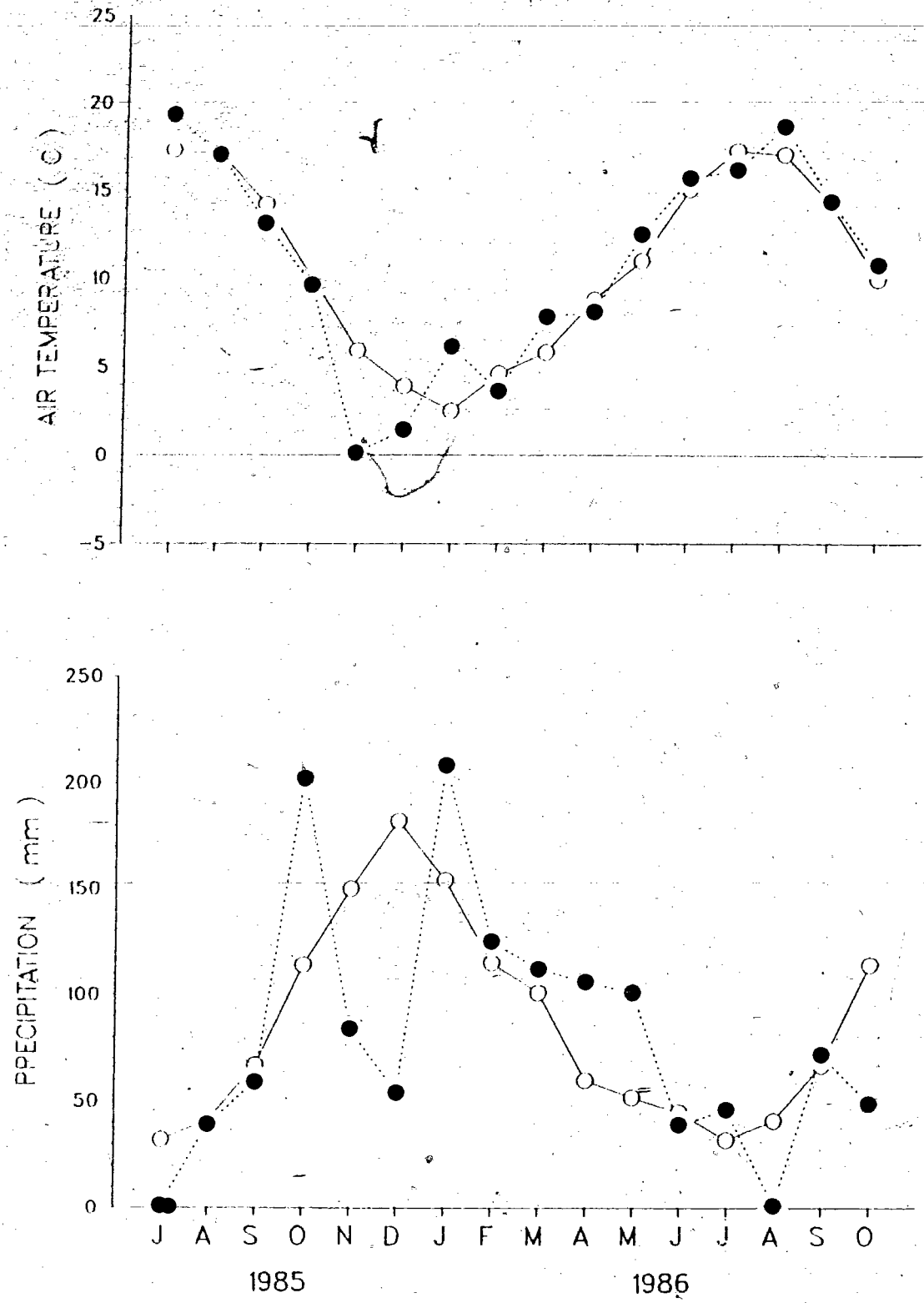

Figure 5. Recorded mean monthly air temperature and precipitation at Sea Island during the sample period, July 1985 to October 1986 (●·····●), and 30 year normal (○——○).

Marsh Environments

The environmental variables that have been shown to be associated with intraspecific variation in other marsh environments were examined at the study sites to assess the degree of similarity between environments. These variables include elevation and thus, exposure time, interstitial salinity, soil chemistry (nitrogen, carbon, pH) and sediment texture and bulk density to estimate drainage conditions.

CHAPTER II

MATERIALS AND METHODS

Sampling frequency was determined by the nature of the variable to be measured. Variables that have large temporal variation, such as interstitial salinity and soil nutrients, were measured at monthly intervals concurrently with vegetation sampling. Soil pH varies with season and was measured quarterly, while site elevation, soil particle size and bulk density were measured at one point in time. While each of these three variables change with time, such change would not occur during this study unless a major flood event occurred.

Elevation

At five points in each environment, marsh surface elevation was measured with a dumpy level and stadial rod divided into 0.01 m increments. Measurements were tied back to a control bench mark on the Sea Island Airport jetty and adjusted to local tide datum (0.00 m geodetic = 2.63 m tide) (Western Canada Hydraulic Laboratories Ltd, no date).

Length of daylight period was calculated for each month of the growing season with a computer program after the method suggested by Sellers (1965). Total monthly exposure hours to daylight was calculated for the mean elevation of each environment using the 1978 tidal cycle with a computer program provided by Hutchinson (unpublished). It was assumed that the differences between the 1978 tidal cycle and those of this study would not result in appreciable differences over a full growing season.

Soil Particle Size Analysis

In July 1986 four soil cores, 0.10 m diameter and 0.40 m in depth, were collected from each site. Each core was divided into 2 equal depths, between 50–100 g of soil removed and air dried for particle size analysis. A 10–20 g subsample of dry soil was passed through a 63 μm sieve to remove the sand portion, percent silt determined by a Micrometrics sedigraph, and the clay portion derived by residual.

Bulk Density

The core method was used to measure bulk density. Five soil samples were collected with a pipe measuring 10 mm diameter and 100 mm depth from each site on October 28, 1986. Samples were oven dried at 105°C for 24 h, weighed (0.01 g) and bulk density calculated as g dry weight mm^{-3} (University of British Columbia Methods Manual 1981).

Soil pH

Soil samples collected in July and October 1985, and February and July 1986, were analysed for pH. Samples were collected to a depth of 0.40 m, between 10 and 20 g of dry soil mixed in a soil:water ratio of 1:2 and pH measured using a Fisher Accumet Model 420 pH/ion meter.

Interstitial Salinity

Interstitial salinity (parts per thousand, ppt) was measured in the field at monthly intervals during the growing season and at bimonthly intervals during winter. Four pits, 0.10 m in diameter and 0.40 m deep, were excavated in each site and water allowed to fill each hole. Salinity of water was determined using a portable Y-S-I Model 33 salinometer within 4 h of low tide.

Soil nutrients

For soil nutrient analysis, four soil cores 0.10 m in diameter and 0.20 m in depth were extracted from each environment at monthly intervals during the growing season (April through October) and bimonthly in winter. To obtain a representative soil sample, each core was divided into eight equal sections from which a 10 g subsample without plant material was removed and air dried. Total C and Total N were analyzed on a Carlo Erba C-H-N Elemental Analyzer on 5-10 mg subsamples. From these data, the soil C:N ratio was used to derive a measure of soil fertility and nitrogen available for plant uptake. Ratios of 20:1 indicate that a large portion of the soil nitrogen is bound in organic matter and not available for plant uptake. Ratios of 10:1 suggest that most of the nitrogen is available for

plant uptake.

Data on soil nutrients are presented on a dry weight basis for comparison to other studies. As well, De Laune *et al.* (1979) determined that soil nutrients expressed on a dry weight basis were not significantly related to growth of *S. alterniflora*. However, several soil nutrients when converted to a soil volume expression (Mg m^{-3}) were positively related to plant growth. Thus, soil nutrient concentrations were converted to a volume expression using the bulk density measurements.

CHAPTER III

RESULTS

Elevation

For *S. americanus*, an elevation difference of 0.57 m was measured between high and low marsh sites, the low marsh being 2.70 m above chart datum and the high marsh 3.27 m (Table 1). Low marsh *S. maritimus* was 2.82 m above chart datum, and the middle marsh 3.48 m, a difference of 0.66 m.

Exposure to daylight for a growing season of April 1 to October 1 was calculated (Table 1). High marsh *S. americanus* had 599 h more exposure than low marsh and middle marsh *S. maritimus* had 751 h more exposure than low marsh. On a monthly basis, high marsh *S. americanus* averaged 100 hr more exposure than low marsh, while middle marsh *S. maritimus* had in excess of 125 hr greater exposure time than low marsh *S. maritimus*.

Bulk Density

All sites had bulk density values less than 1.0 Mg m^{-3} (Table 1). The highest values were in the *S. americanus* environments. Low marsh *S. maritimus* soil had similar bulk density to that of *S. americanus* soil whereas middle marsh *S. maritimus* soil had the lowest density (d = 0.20).

Sediment Texture

There were only small differences in the proportion of sand, silt or clay with depth in the Sea Island substrates (Table 1). High marsh *S. americanus* soils had the largest sand fraction (88%) compared to 1% sand in middle marsh *S. maritimus* soil. Low marsh *S. americanus* soil and low marsh *S. maritimus* soil had intermediate sand contents (72% and 67%, respectively). Middle marsh *S. maritimus* soil was composed of silt (71%) and clay (28%), with a varying admixture of silt and clay at the three other sites.

Table 1. Synopsis of environmental variables measured at Sea Island. Elevation and sediment texture are mean values, bulk density is mean ± 1se and exposure hours are total hours exposed to daylight from April 1 to October 1.

site	elevation m chart	exposure hours April–October	bulk density Mg m^{-3}	sediment texture sand	silt	clay	classification
S. americanus							
low marsh	2.70	1227	0.86(0.03)	72	19	9	loam sand
high marsh	3.27	1826	0.75(0.03)	88	9	3	loam sand
S. maritimus							
low marsh	2.82	1289	0.48(0.03)	67	28	5	sandy clay loam
middle marsh	3.48	2040	0.20(0.01)	1	71	28	clay

Soil pH

Soil pH did not differ with depth and thus seasonal variations are presented for each site as the mean of both depths sampled (Figure 6). Although there were seasonal differences between sites of *S. americanus* and *S. maritimus*, there were no differences between sites within each species. Temporal changes in soil pH were similar for all sites. Soil pH values were greatest in July (pH 7.0 for *S. americanus* and 5.2 for *S. maritimus*). In *S. americanus* soils, pH decreased from October on, reaching a low of 5.5 in February. *S. maritimus* soils had a minimum pH of 4.4 in October, increasing to near summer levels in February.

Interstitial Salinity

For both species, the upper and lower environments had similar seasonal trends in salinity (Figure 7). Salinities were greatest in winter during low river flow and decreased in spring and summer with the Fraser River freshet.

S. americanus environments had the lower salinities because of the close proximity of the Middle Arm of the Fraser River. High marsh *S. americanus* had much lower summer salinity than low marsh during the growing season and approached freshwater levels (1 ppt) in mid-summer. Winter salinities in high and low marsh *S. americanus* were mesohaline.

Winter salinities for low and middle marsh *S. maritimus* were 12 ppt, although the middle marsh had a December maximum of 23 ppt. This December measurement was made during the day shortly after an ebbing tide whereas all other measurements for this month were at night several hours after an ebbing tide. Salinity measurements in these environments were as low as 9 ppt during the growing season but generally remained above 10 ppt. There was no difference in mean monthly interstitial salinity between low and middle marsh *S. maritimus*.

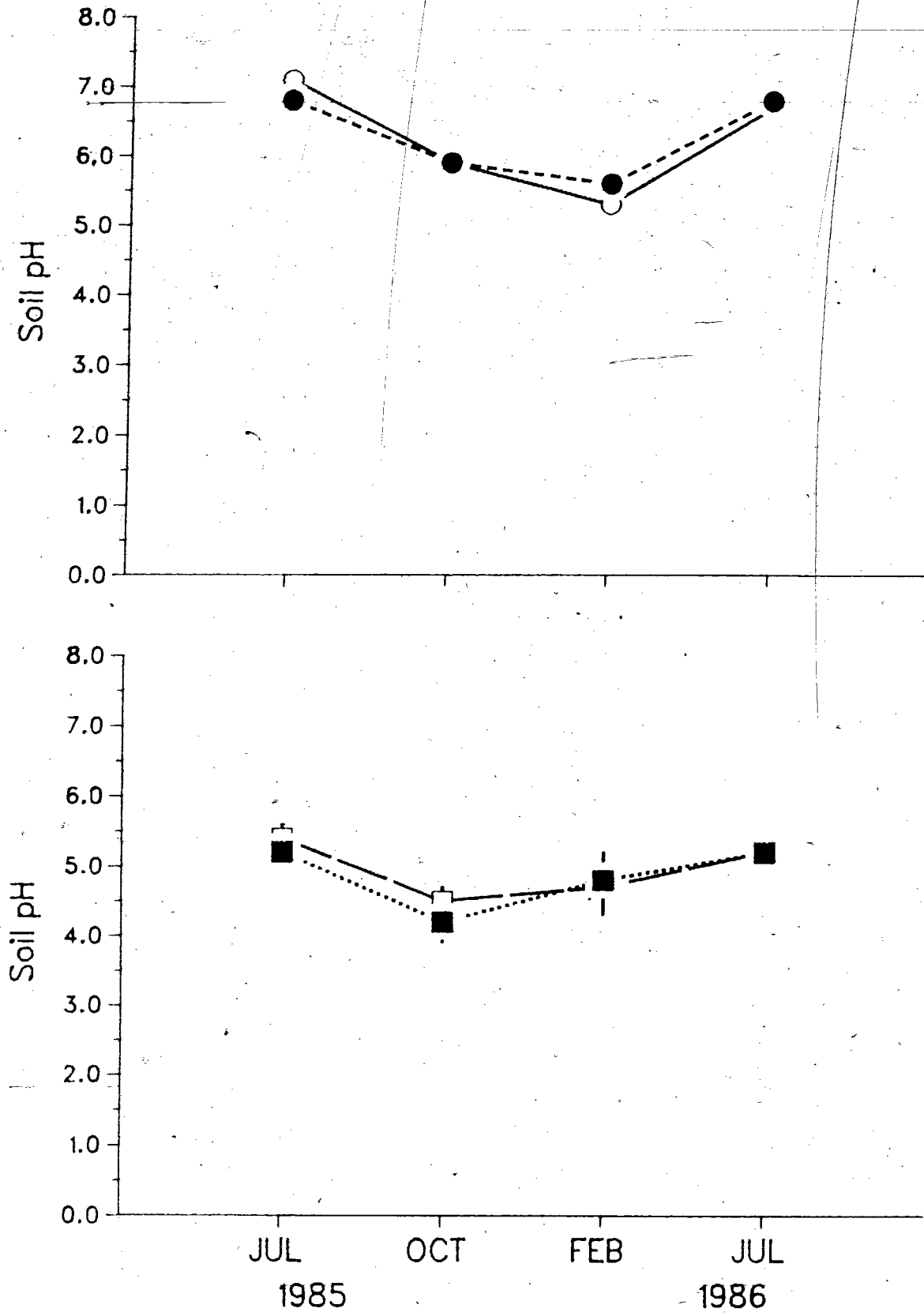

Figure 6. Temporal change in soil pH ($\bar{x}\pm se$) for *S. americanus*, low (●----●) and high marsh (○——○), and for *S. maritimus*, low (■----■) and middle marsh (□— —□).

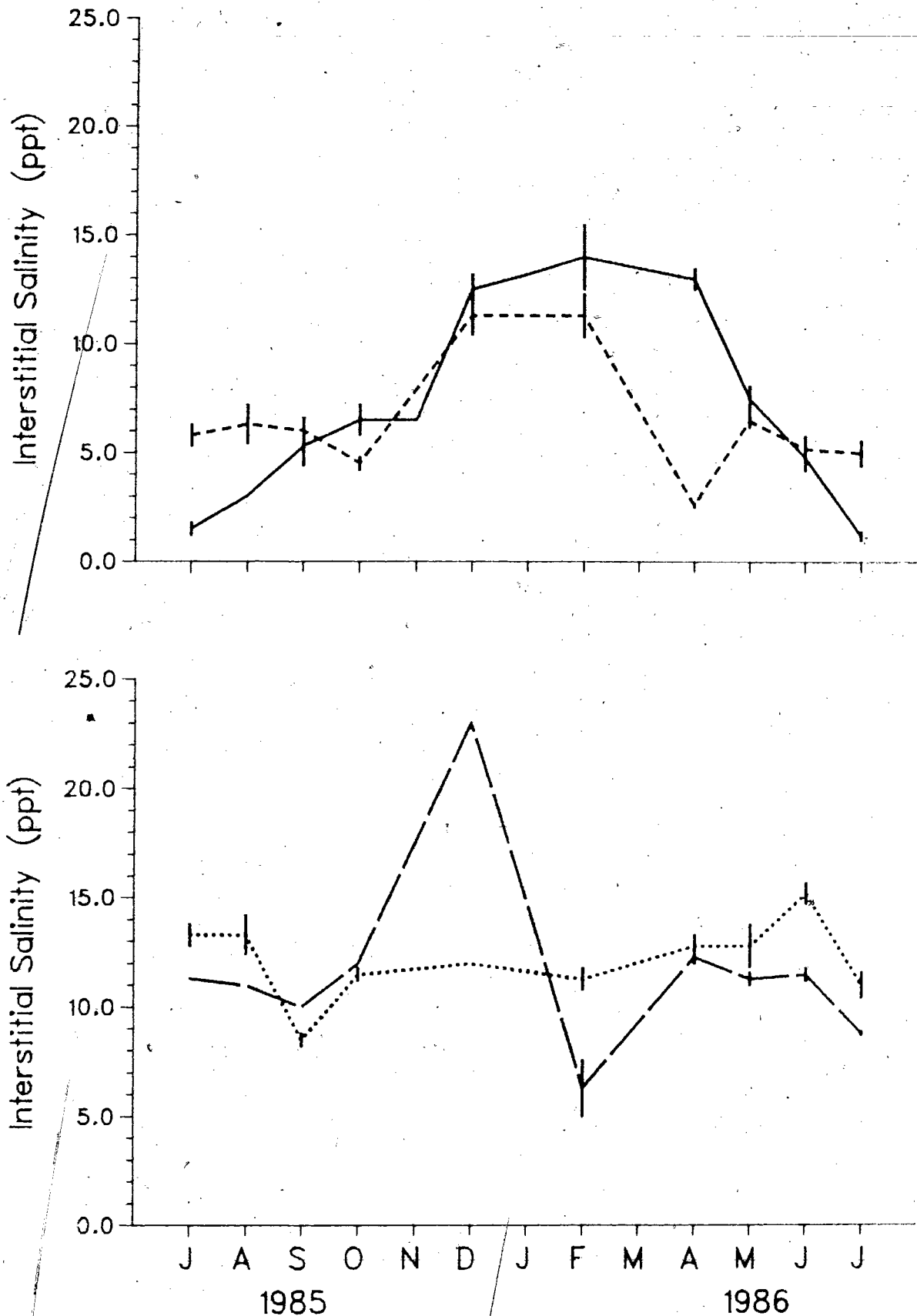

Figure 7. Monthly interstitial salinity ($\bar{x}\pm sc$) for *S. americanus*, low (– – – – – –) and high marsh (————), and for *S. maritimus*, low (----------) and middle marsh (—— —— ——).

Soil Nutrients

The two environments sampled for *S. americanus* had similar total nitrogen concentrations and identical seasonal variations with distinct peaks in winter (Figure 8). Low marsh *S. maritimus* had equivalent summer nitrogen concentrations and these levels remained constant throughout the year (Figure 9). Middle marsh *S. maritimus* soils had an order of magnitude greater nitrogen than the three other sites. The large variability of these measurements masks any possible seasonal variations.

Middle marsh *S. maritimus* had an order of magnitude greater carbon than the other sites and in contrast to soil nitrogen, carbon concentrations were highest during summer in this environment (Figure 9). The three other sites did not have any distinguishable seasonal variations.

Mean annual C:N ratios were ≃10:1 for both *S. americanus* environments (Figure 8) and middle marsh *S. maritimus* compared to 19:1 for middle marsh *S. maritimus* (Figure 9). Seasonal changes in C:N mirror the pattern seen in soil C content. Low *S. maritimus* had very little seasonal change. Monthly values of middle marsh *S. maritimus* ranged between 10:1 and 20:1 with a pronounced increase in May. Low and high *S. americanus* had similar seasonal patterns, the lowest ratios occuring in winter. Ratios during the growing season were approximately 10:1 except in July 1986 when they were much higher.

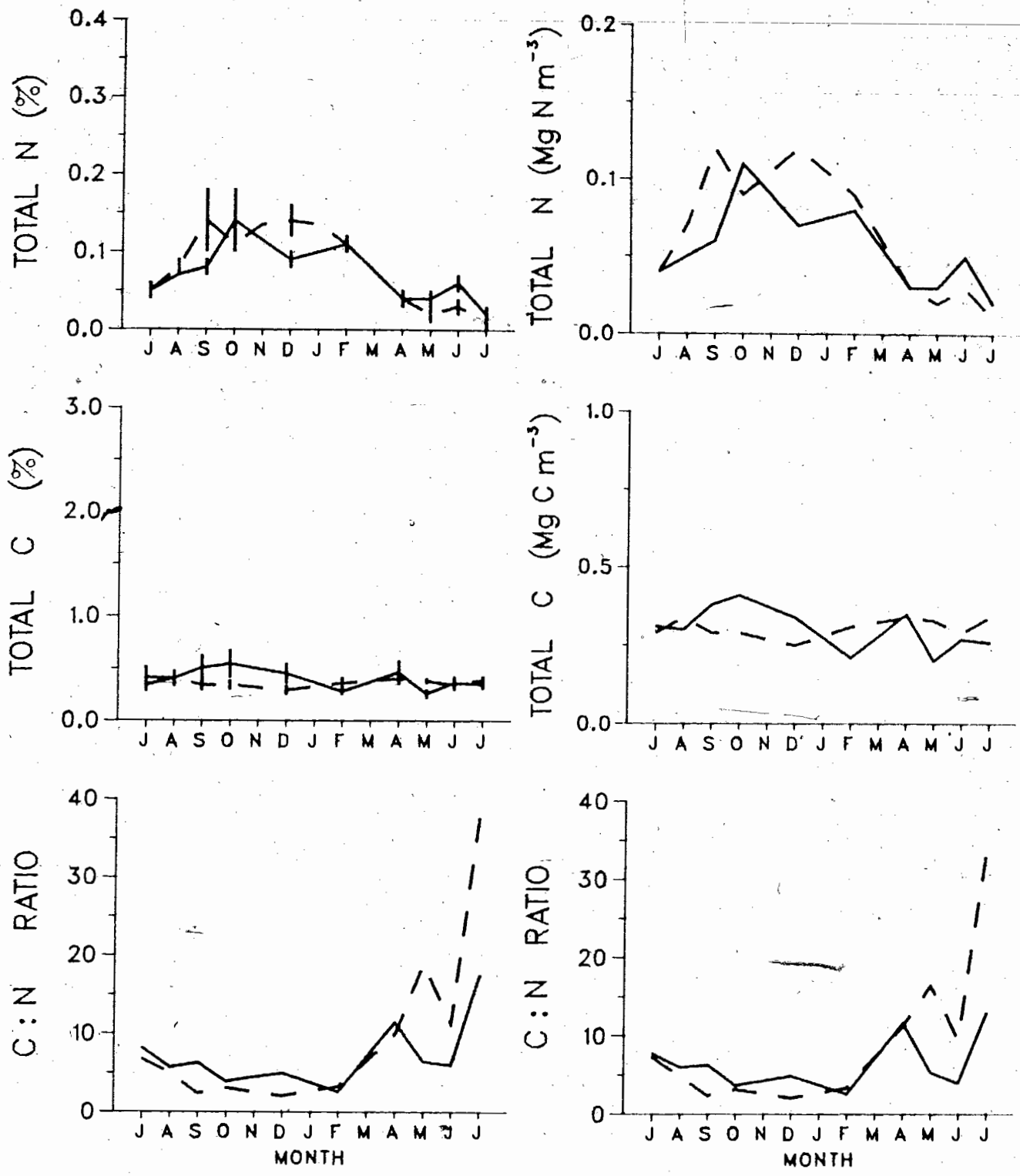

Figure 8. Soil nitrogen, carbon and C:N ratio for high marsh (——— ———) and low marsh (— — — —) *S. americanus* presented as percent dry weight and in Mg m⁻³ ($\bar{x}$±sc).

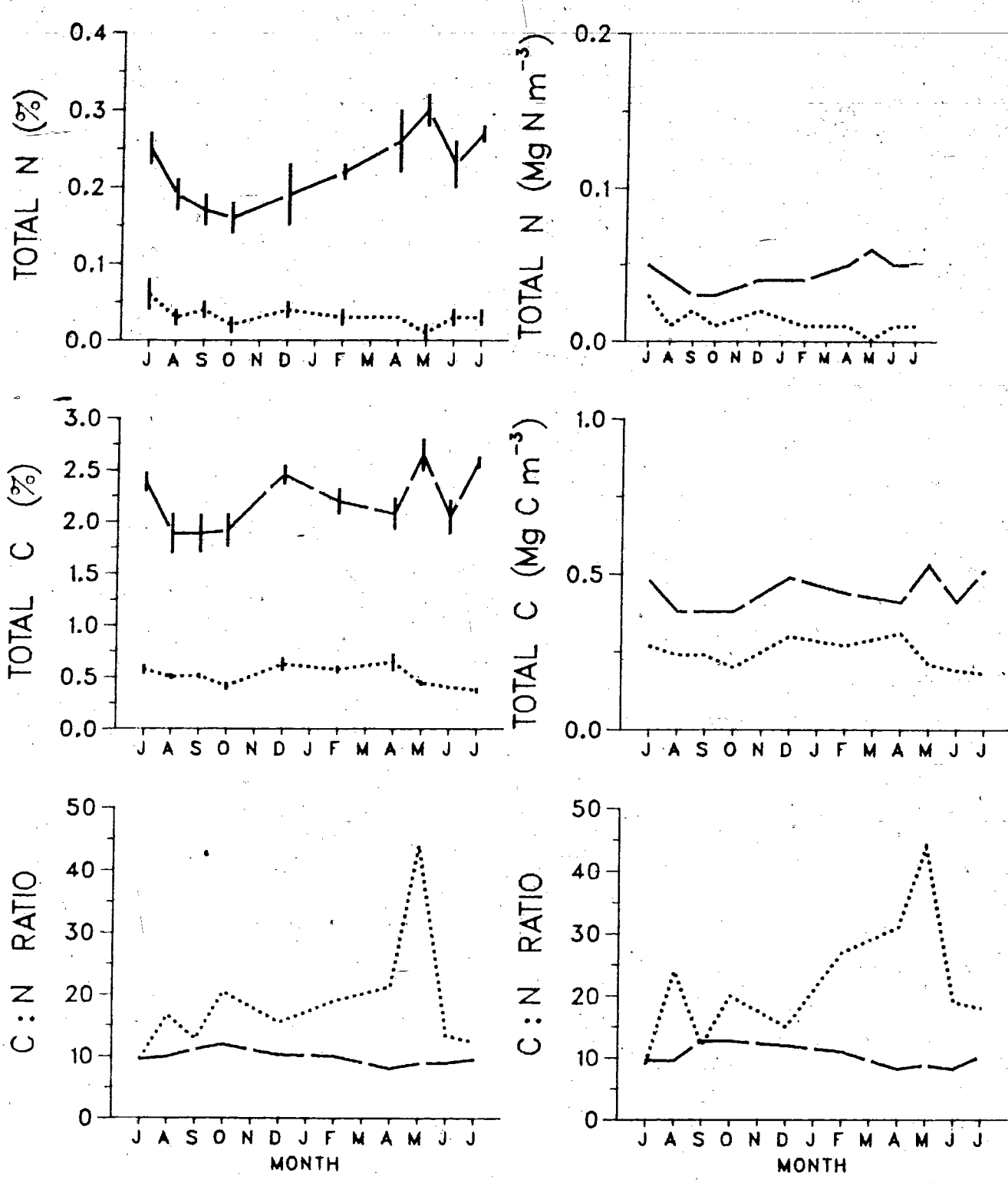

Figure 9. Soil nitrogen, carbon and C:N ratio for middle marsh (—— —— ——) and low marsh (·····) *S. maritimus* presented as percent dry weight and as Mg m^{-3} ($\bar{x}$±se).

CHAPTER IV

DISCUSSION

The elevations of the *S. americanus* populations relative to chart/tide datum at Sea Island are similar to those reported by Hutchinson (1982) for Lulu Island. Thus, the airport jetty does not restrict *S. americanus* to an elevation lower than that found under undisturbed conditions. The upper elevation limit of *S. maritimus* measured by Hutchinson (1982) at Lulu Island was *ca.* 4.15 m which exceeds the elevation of middle marsh *S. maritimus* in this study by 0.65 m. At Sea Island, *S. maritimus* is found above 3.48 m chart, but only as scattered clones amongst *Carex lyngbyei* and *Distichlis spicata*.

The implications of the elevation differences within species environments is that during the growing season, plants at upper elevations have a much longer growing season for photosynthesis and to accumulate biomass. In fall/winter, the longer submergence times in low environments may lead to earlier senescence and subsequent flushing of aboveground material by ebbing tides.

The decline in particle size as marsh elevation increased was a result of lower tidal energy regimes in these environments. The bulk density values in these environments do not correspond to the general values presented by Haussenbuiller (1980) for soils with similar sediment textures, likely as a result of differential origin and a variable organic matter content. However, the trend of greater bulk density in the coarse textured soils of *S. americanus* compared to the *S. maritimus* soils is similar. The high bulk densities of *S. americanus* and low marsh *S. maritimus* soils is a result of the large proportion of sand. Thus, bulk density decreases moving up in elevation on the marsh platform into a low energy tidal environment (Table 1).

The interstitial salinities in these environments can be categorized as mesohaline (5.4 - 18.1 ppt, Cowardin *et al.* 1979). Freshwater discharge of the Fraser River influenced interstitial salinity in *S. americanus* environments. The low salinities of summer were a result of the dilution of tidal water by freshet discharge. Conversely, discharge is lowest in the Fraser River in winter. Hence, the higher salinities measured at this time. The marked decrease in salinity of the low marsh environment one month before the high marsh (Figure 7) may be a function of its close proximity to the river whereby it would receive freshwater

before peak discharge. The high marsh environments would receive freshwater only during peak discharge periods.

The absence of seasonal variation for salinity in *S. maritimus* environments is in large part a result of the airport jetty effectively cutting off these locations from the influence of the Fraser River (Figure 4). In December 1985, middle marsh *S. maritimus* was the only environment sampled during the day and thus, shortly after an ebbing tide. All other environments were sampled at night several hours before or after high tide. The very high interstitial salinities measured in the middle marsh in December cannot be explained (Figure 7).

The nitrogen concentrations measured in soils of *S. americanus* and low marsh *S. maritimus* are an order of magnitude less than the range given by Chalmers (1977, cited by Pomeroy and Wiegert 1981) for nitrogen levels found in coastal marshes. This may be due to the absence of a nitrogen source for these environments. The low summer nitrogen levels may result from the uptake of nitrogen by plants for aboveground growth. Soil nitrogen levels measured in middle marsh *S. maritimus* stands are within the range presented by Chalmers (1977).

The C:N ratio is a useful indicator of the amount of nitrogen available for plant uptake. Generally, ratios >10 occur in soils where most of the nitrogen is bound in organic forms and thus not available for plant uptake. Despite the low concentration of total soil nitrogen measured in these environments, the low C:N ratios suggest that a large portion of this nitrogen is available for plant uptake. Only low marsh *S. maritimus* had C:N ratios consistently near 20:1.

The higher pH measured in the soils of low marsh *S. maritimus* is probably related to the slower decay and removal of organics in this environment compared to *S. americanus* environments and middle marsh *S. maritimus*. This higher organic matter content was reflected in the high C:N ratios measured in this environment.

Most physical characteristics of the two *S. americanus* environments were similar. The exceptions are elevation and therefore tidal regime and salinity. Thus, this study site provided a good opportunity to conduct experiments under field conditions where most variables are controlled. For *S. maritimus* however, edaphic conditions in the middle marsh

were much different than in the low marsh. There is environmental heterogeneity in both *S. americanus* and *S. maritimus* stands suggesting that there may be variation in the plant populations of these environments.

PART C

BIOMASS ALLOCATION

CHAPTER I

INTRODUCTION

Most of the data available on marsh primary production and biomass variation in North America are from the Gulf of Mexico and the east coast of the United States. In comparison, there is a paucity of information for the smaller and more isolated west coast marshes. Despite the fact that >100 "habitats" have been sampled in the Pacific Northwest intertidal marshes, no detailed analysis of biomass allocation has been made, and few studies relate production or standing crop to the environmental regime of the site (Hutchinson 1986).

The objective of this section was to test the hypothesis that plant biomass allocation patterns are a response to the local environment. The environmental variables examined were described in Part B. A second hypothesis tested was that plants in stressed environments should adopt conservative strategies, which includes reduced biomass allocation to shoots and reduced reproductive effort. The stressed environments are those with longer tidal inundation periods. Thus, a gradient of increased allocation to shoots and sexual reproduction should be found with increasing elevation, both within and between species.

CHAPTER II

MATERIALS AND METHODS

Sampling was from July 1985 to October 1986 at monthly intervals during the growing season (April to October) and at bi-monthly intervals during winter. At the beginning of each month four 0.25 m^2 quadrats were located in each environment in relatively dense monospecific stands. All aboveground material was clipped to ground level, the number of live shoots and flowers counted, and the dry weight of live and dead aboveground structures measured separately. *S. maritimus* samples included dead aboveground tissue from the previous years growth and this was distinguished from dead tissue of the current year.

For belowground biomass, a soil core 0.10 m in diameter was extracted from the center of each quadrat with a golf cup cutter. A pilot study of 4 soil cores from each environment indicated that 97% of the belowground biomass for *S. americanus* was within 0.40 m of the surface, whereas belowground biomass of *S. maritimus* extended to a depth of 0.60 m. However, little belowground tissue of *S. maritimus* appeared intact (i.e. live) below 0.20 m. Thus, soil cores collected from *S. maritimus* environments were divided into two sections. Belowground material in the top 0.20 m was separated into roots, rhizomes and corms but roots and rhizomes were pooled in lower sections. Each core was washed over a #45 (0.355 mm) sieve to collect belowground biomass. Some soil cores were soaked in tap water overnight to loosen soil adhering to roots, rhizomes and corms. All plant tissue was dried at 70°C for 72 h.

Live belowground biomass was not distinguished from dead. Visual observation indicated that live and dead belowground structures could be distinguished in some samples. For example, live rhizomes of *S. americanus* were "fleshy" in appearance and solid. Dead rhizomes were black, had a soft exterior texture and occassionally hollow. *S. maritimus* rhizomes were not as large and more difficult to determine as live or dead. Live corms of *S. maritimus* were difficult to crack open and had a solid, white core. Dead corms were very soft, easy to break open and did not have the solid interior core. Roots of both *S. americanus* and *S. maritimus* were difficult to categorize as live or dead, especially fine roots. Based on the difficulty associated with roots and the fact that some rhizomes and corms were in a "grey zone" between live and dead, live belowground biomass was not distinguished from dead using visual observation. No attempt was made with a dye to stain

plant tissue and separate live from dead.

Net annual primary productivity was calculated as the difference between maximum and minimum biomass because it is a simple method to determine production and has been used by others in marsh environments allowing for direct comparisons (e.g. Schubauer and Hopkinson 1984, Ellison *et al.* 1986). Other more complicated but accurate techniques were not employed because of the sampling strategy used in the study. For example, Dickerman *et al.* (1986) compared seven different techniques for calculating net annual aboveground production with varying sampling fequencies on *Typha latifolia*. They concluded that the Allen Curve Method (Allen 1951) was insensitive to sampling frequency, produced consistent results from year to year and relates productivity to important aspects of population dynamics. Because of the requirement for repeated measurements of individual shoots, the Allen curve method could not be used in this study which involved destructive sampling. Similarly, Shew *et al.* (1983) presented a modified Lomnicki method that gave the best prediction of primary production in marsh environments but it requires paired plots which were not established in this study. The Smalley method (Smalley 1959) could be applied to this study if it is assumed that minimal plant material is lost via tidal flushing between sampling periods. Although most of the dead plant tissue remained on the stems of *S. americanus* and *S. maritimus*, there is some uncertainty as to how much plant tissue was removed by tidal flushing precluding the use of this method.

Mean monthly shoot growth rates (g m^{-2} h^{-1} daylight of tidal exposure) were calculated for plants in each environment by dividing the difference in mean monthly biomass by the total number of exposure hours for the month. A negative growth rate value represents the loss of live biomass by tidal export during this time period. Although biomass was not measured in November, observation indicated that there was no live aboveground material at this time. This calculation has two major assumptions. First, that there is no shoot growth at night and second, no shoot growth when shoots are inundated by tidal waters. I found no studies in the literature that presented evidence for growth of *S. americanus* and *S. maritimus* at night. Both species, however, may grow under flooded conditions, especially when only part of the shoot is inundated. However, it is not known to what extent growth is reduced when shoots are inundated. As well, there may be differences in water turbidity between the four environments which would further complicate calculations of growth rates

during tidal inundation. For these reasons, growth rates were calculated only for the time periods that the entire shoot was exposed to daylight.

Reproductive effort, measured as the biomass allocated to reproduction:total biomass (Willson 1983), was calculated for each site for sexual (inflorescences and achenes) and asexual (rhizomes) reproduction separately.

The variation in plant biomass between environments and plant structures were analyzed using a one-way analysis of variance and the Student-Newman-Keul's multiple range test (α = 0.05) (UBC ANOVAR, Greig and Osterlin 1978).

CHAPTER III

RESULTS

S. americanus

By November, all of the current years shoots were removed by tides and currents from the *S. americanus* zone (Figure 10). Roots and rhizomes remained intact below the marsh surface throughout the winter with an equal biomass in each structure (Figure 11). In the low marsh, the belowground structures averaged ≃1000 g m^{-2} compared to ≃ 2000 g m^{-2} in the high marsh. Root growth in spring resulted in a maximum in April of 2623±178 g m^{-2} in the high marsh. In comparison, maximum belowground biomass in the low marsh was only 1040±193 g m^{-2} and occured one month later. The emergence of new shoots in spring brought about concomitant changes in belowground biomass. Shoots emerged in April in both environments but shoot growth was greatest and more rapid in the high marsh. By May, the high marsh contained 1815±83 shoots m^{-2} with a biomass of 11±1 g m^{-2} compared to only 991±50 shoots m^{-2} with a mass of 2±0 g m^{-2} in the low marsh. The differences in aboveground biomass between the two environments is a function of the greater growth rates in the high marsh (compare 0.6 g m^{-2} h^{-1} to 0.2 g m^{-2} h^{-1}) (Figure 12) and the greater exposure time (Table 1).

During the next two months, shoot growth continued as belowground biomass declined. By mid-summer, maximum shoot densities were 3797±213 shoots m^{-2} in the high marsh, with one-half that in the low marsh (1545±46 shoots m^{-2}). At this time, almost 90% of high marsh stems flowered compared to 70% of stems in the low marsh (Figure 10). Peak shoot density coincided with the peak in aboveground live biomass which was measured at 625±48 g m^{-2} in the high marsh and 316±15 g m^{-2} in the low marsh. Shoot growth occurred at the same rate in both the high and low marsh environment during the month of July (1.2 g m^{-2} h^{-1}) (Figure 12).

Belowground biomass was lowest in mid-summer at the time of peak aboveground growth and increased thereafter, peaking in September/October immediately following live shoot removal. Accumulation of dead shoot biomass generally peaked 1-2 months after maximum live shoot biomass and equalled maximum live shoot biomass in the low marsh. The loss of live shoots was different in the two environments. The high marsh had the higher

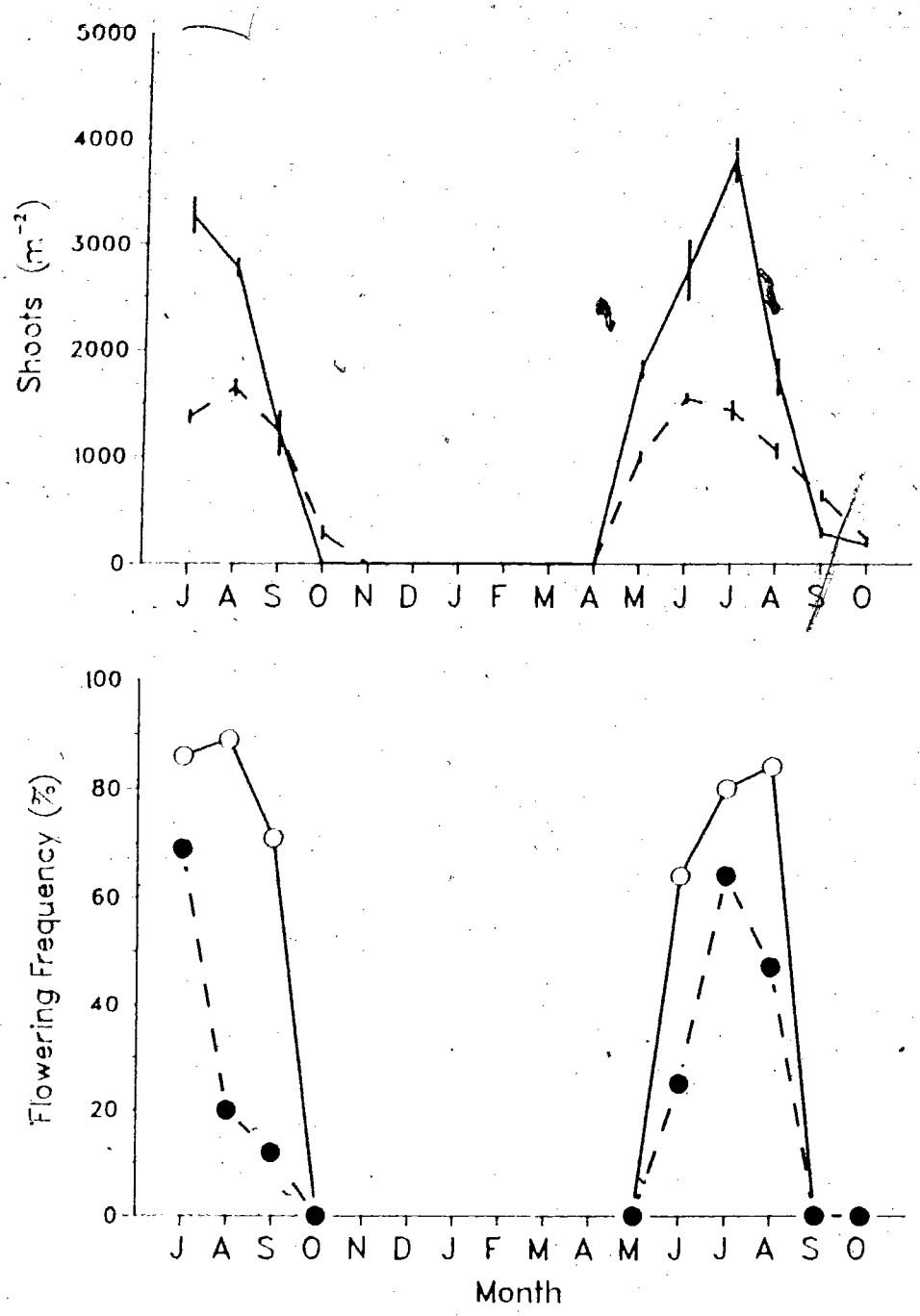

Figure 10. Shoot density ($\bar{x}\pm sc$) and mean flowering frequency of high (———) and low (— —) marsh *S. americanus*.

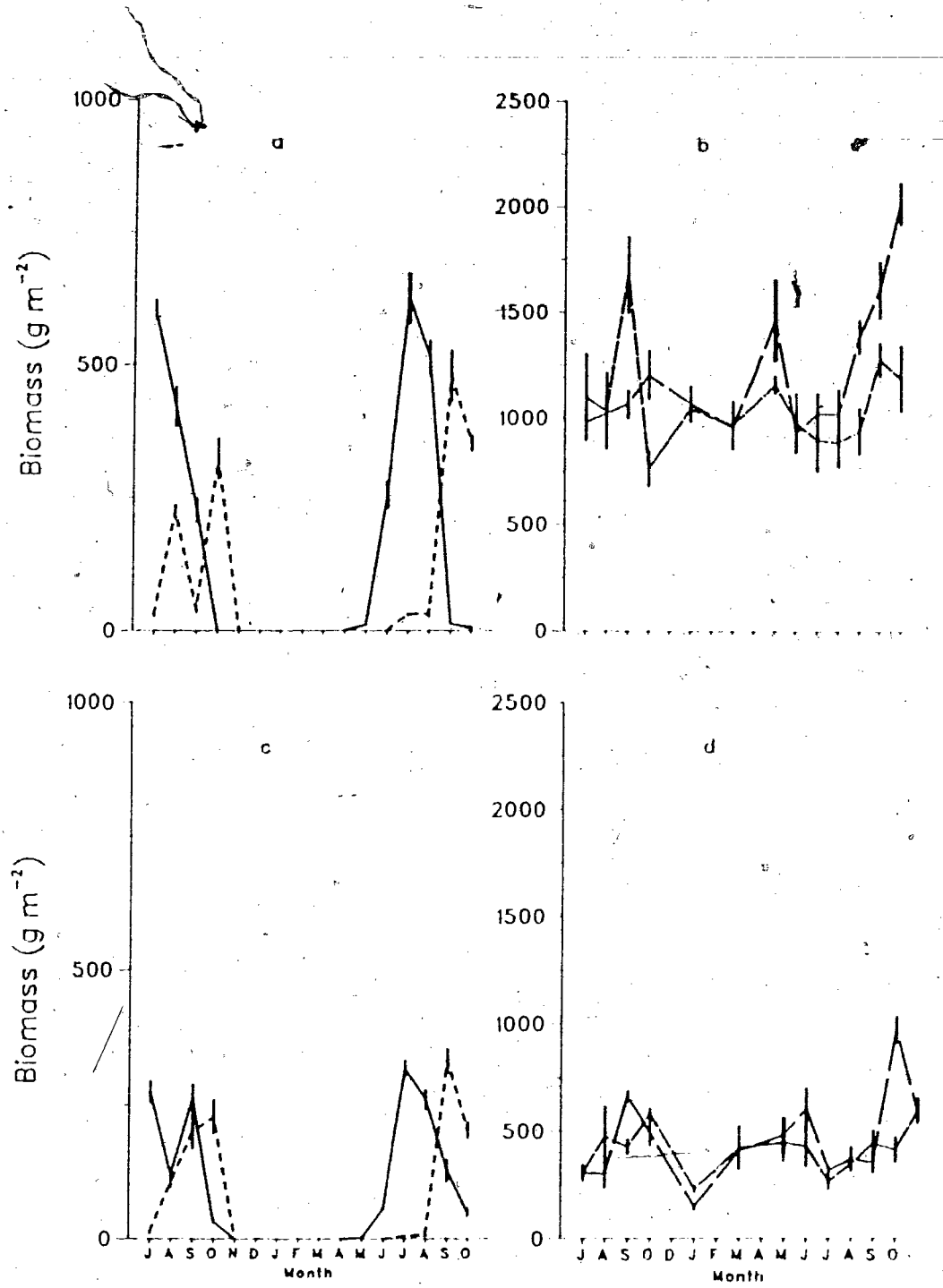

Figure 11. Biomass ($\bar{x}$±se) of photosynthetic shoots (———), dead shoots (- - - - -), roots (— — —) and rhizomes (— · — · —) of high marsh (a,b) and low marsh (c,d) *S. americanus*.

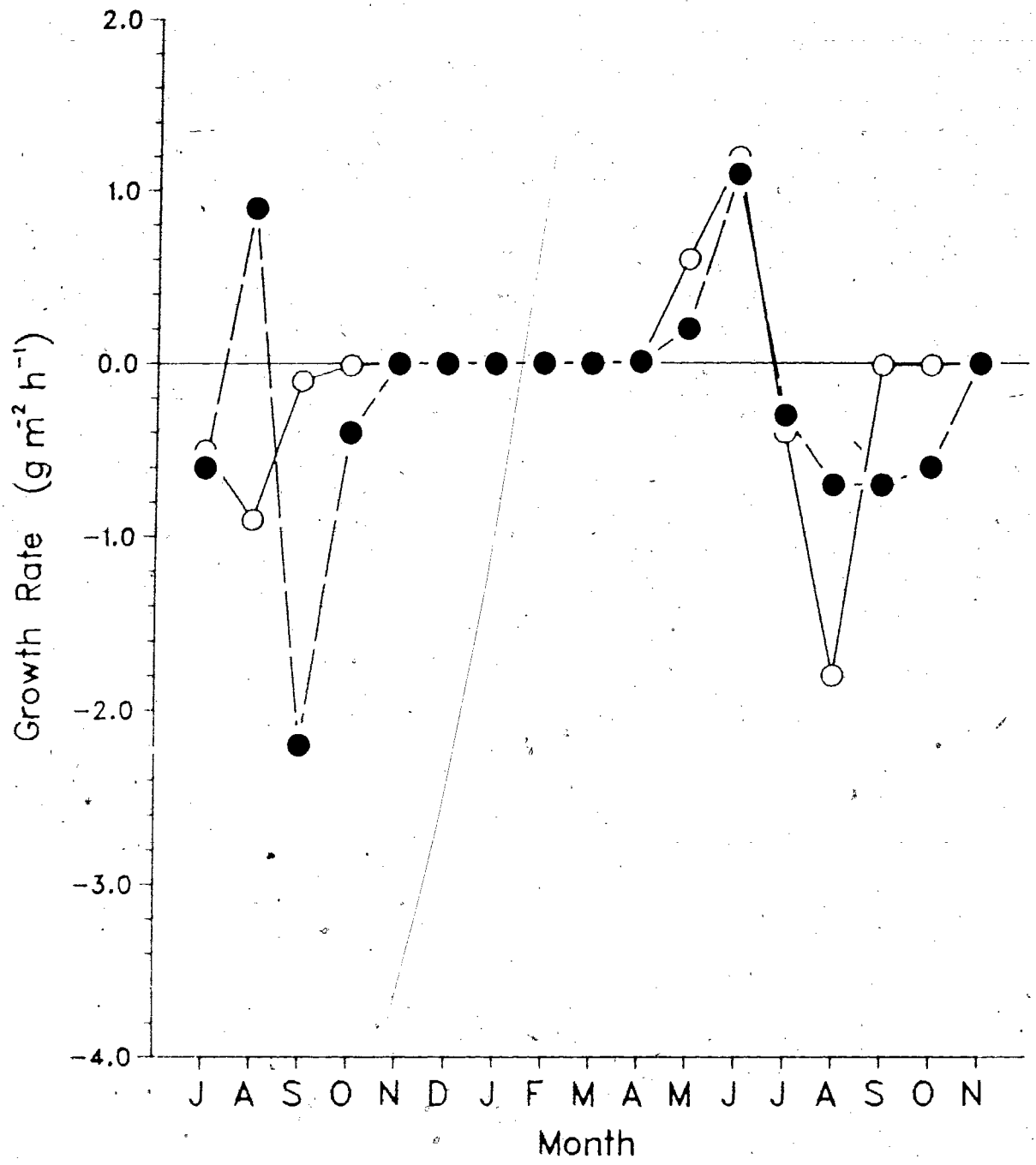

Figure 12. Mean absolute growth rates of low (●—●) and high marsh (○—○) *S. americanus*. Negative values indicate loss of standing crop by tidal removal.

maximum loss rate (−1.8 g m^{-2} h^{-1}), the low marsh with a lower (maximum of −0.7 g m^{-2} h^{-1}) but longer period of shoot loss.

Perhaps the best comparison between environments is to document the relative proportion of total biomass in plant structures through an annual cycle (Figures 13). In high marsh *S. americanus*, root biomass was >50% of total plant weight in winter and during the growing season, with slightly less biomass in rhizomes than roots. Aboveground shoots increased through the growing season peaking at *ca.* 25% of total biomass in July.

Biomass trends in low marsh *S. americanus* were similar to this pattern, with one deviation (Figures 13). At the end of the growing season, there was a sharp increase in the proportion of rhizome biomass. This may be for lateral expansion in the low marsh environment but is misleading because there was only 382±18 g m^{-2} belowground biomass in both roots and rhizomes (Figure 11), the smallest mean monthly belowground biomass value measured during the entire 16 month sampling period. Rhizome proportions decreased in spring and through the entire summer but show a similar trend in fall 1986 as in 1985. Root biomass was less than 50% at all times except spring prior to aboveground shoot production. The pattern of aboveground biomass in the low marsh was similar to the high marsh, although the maximum biomass in July represented 30% of the total biomass compared to 24% in high marsh.

S. maritimus

The pattern for *S. maritimus* was different from that of *S. americanus*. In the *S. maritimus* stands, dead shoots remained standing throughout the winter, especially in the middle marsh (Figures 14a and 14c).

Biomass of current year's dead tissue was equal in both environments although the low marsh was cleared of dead tissue faster than the middle marsh (Figure 14). In the low marsh, dead aboveground biomass declined from 769±79 g m^{-2} in October to 156±10 g m^{-2} in December. In the middle marsh, dead shoot biomass remained near peak levels through December and did not decline to less than 200 g m^{-2} until April. By spring, most of the dead shoots were removed and the new shoots began to emerge concurrently in the low and middle marshes. Whereas *S. americanus* shoot biomass peaked in July and declined

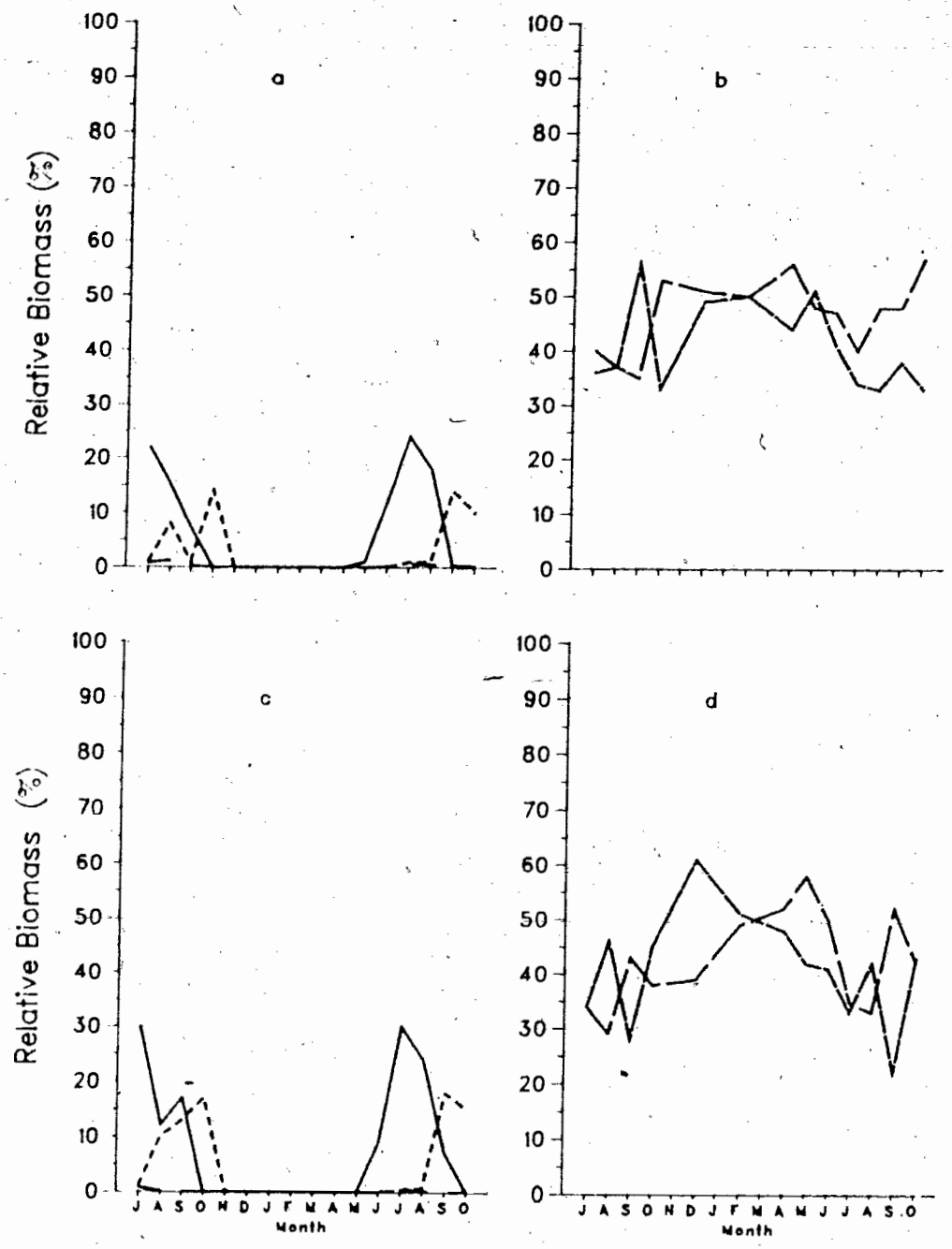

Figure 13. Mean monthly relative biomass of high (a,b) and low (c,d) marsh *S. americanus* for photosynthetic shoots (———), dead shoots (- - - - -), roots (— — —) and rhizomes (— — — —).

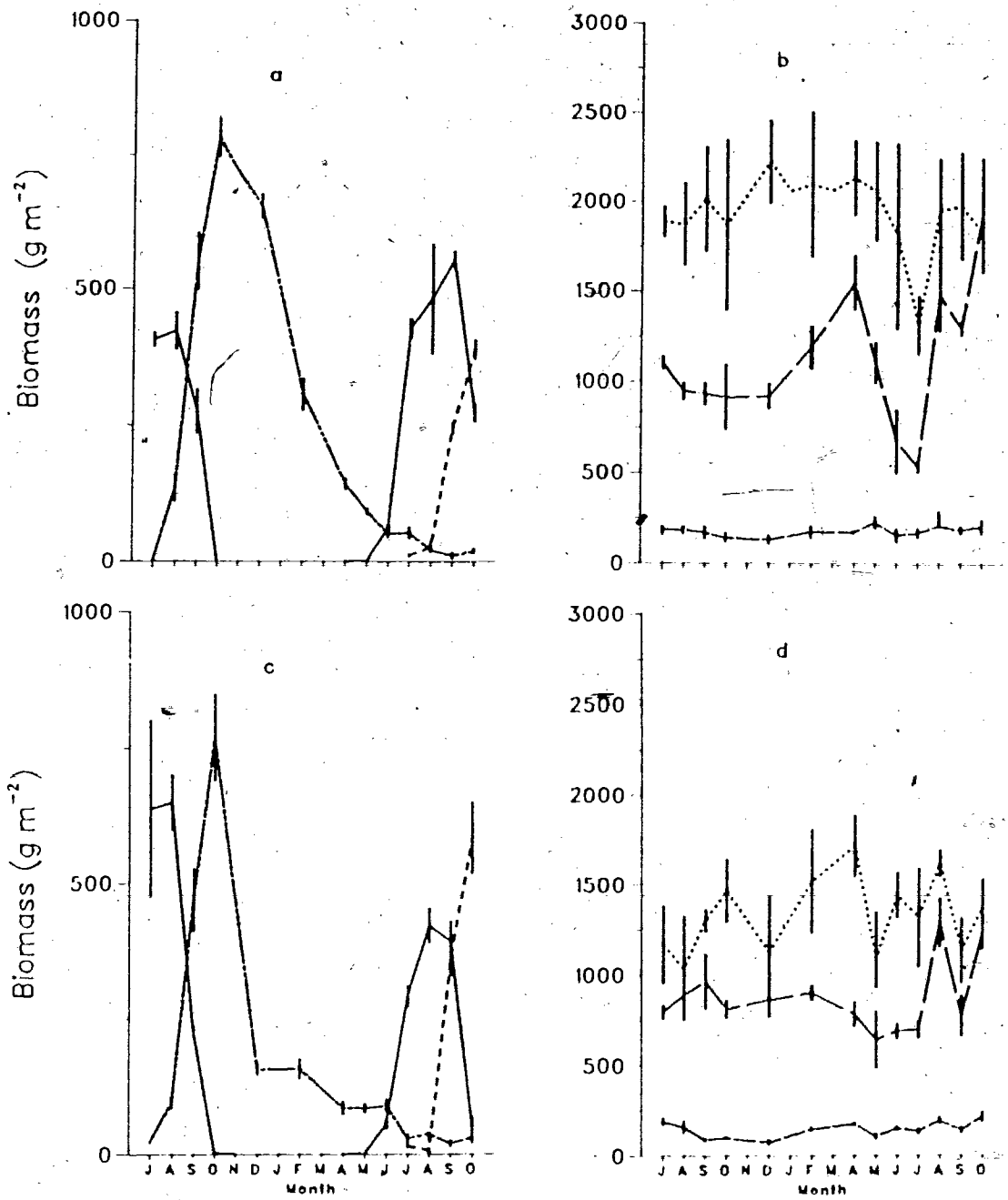

Figure 14. Biomass ($\bar{x}\pm se$) of photosynthetic shoots (———), 1985 dead shoots (— · · · —), 1986 dead shoots (- - - - - -), roots (— — —), rhizomes (— — — —), and corms (· · · · · · ·) of middle marsh (a,b) and low marsh (c,d) *S. maritimus*.

immediately thereafter, maximum shoot densities of 700±23 shoots m^{-2} in the low marsh and 555±18 shoots m^{-2} in the middle marsh occured in July (Figure 15) but shoot biomass peaked in August/September and was not significantly different between environments (420±32 g m^{-2} in the low marsh and 553±17 g m^{-2} in the middle marsh).

The low marsh attained a greater photosynthetic biomass in 1985 but this trend was reversed in 1986. The 1985 maximum standing crop of 649±51 g m^{-2} in the low marsh was not significantly different from the maximum standing crop of 553±17 g m^{-2} measured in the middle marsh in 1986. Maximum growth rates occurred in July in both environments, but the middle marsh shoots had a greater rate (compare 1.3 to 0.9 g m^{-2} h^{-1}) (Figure 16). As live shoot biomass declined in September, dead biomass increased until there were no live shoots by the beginning of November. The rate of loss of live shoots was greatest in the low marsh, where in October 3.2 g m^{-2} h^{-1} were removed compared to 1.4 g m^{-2} h^{-1} in the middle marsh environment.

Whereas 70–90 % of *S. americanus* shoots flowered in the high and low marsh, less than 50% of the *S. maritimus* shoots produced inflorescences (Figure 15). In 1985, low marsh shoots produced more flowers than middle marsh and flowering peaked in July compared to September in the middle marsh. In the middle marsh, 45% of the shoots flowered in September 1985 but in 1986, only 35% of the shoots flowered and it was not until October. In contrast, peak flowering in the low marsh was July for 1985 when 38% of the shoots flowered, yet virtually none of the shoots flowered in 1986.

Biomass of belowground plant structures for *S. maritimus* was significantly greater in the middle marsh (Figures 14). Rhizomes comprised the smallest belowground compartment. Within-site variation in corm biomass masked seasonal trends. Mean annual corm biomass was 1926±62 g m^{-2} in the middle marsh and 1329±59 g m^{-2} in the low marsh. Root biomass exhibited seasonal trends with minimum values in July. Root biomass of middle marsh *S. maritimus* peaked in April (1475±194 g m^{-2}) and at the end of the growing season (1933±316 g m^{-2}). The pattern of root biomass seen in the middle marsh was not as evident in the low marsh. Although there was a distinct peak in low marsh root biomass in fall, there was no apparent sign of a spring growth of roots prior to the growth of aboveground structures. Rather, root biomass peaked in August (1286±135 g m^{-2}) and October (1234±94 g m^{-2}) in the low marsh environment.

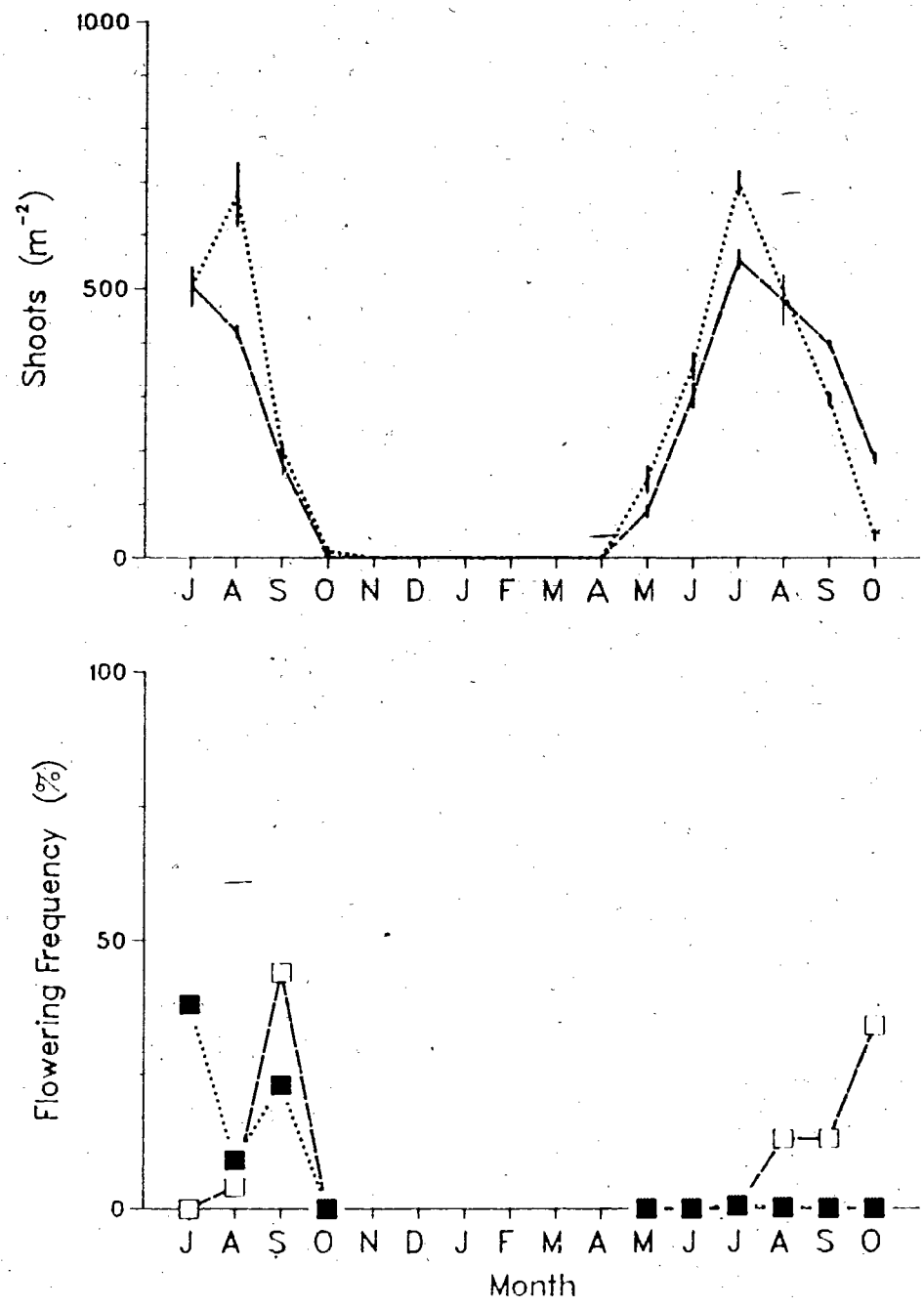

Figure 15. Shoot density ($\bar{x}\pm se$) and mean flowering frequency of middle marsh (——) and low marsh (·····) *S. maritimus*.

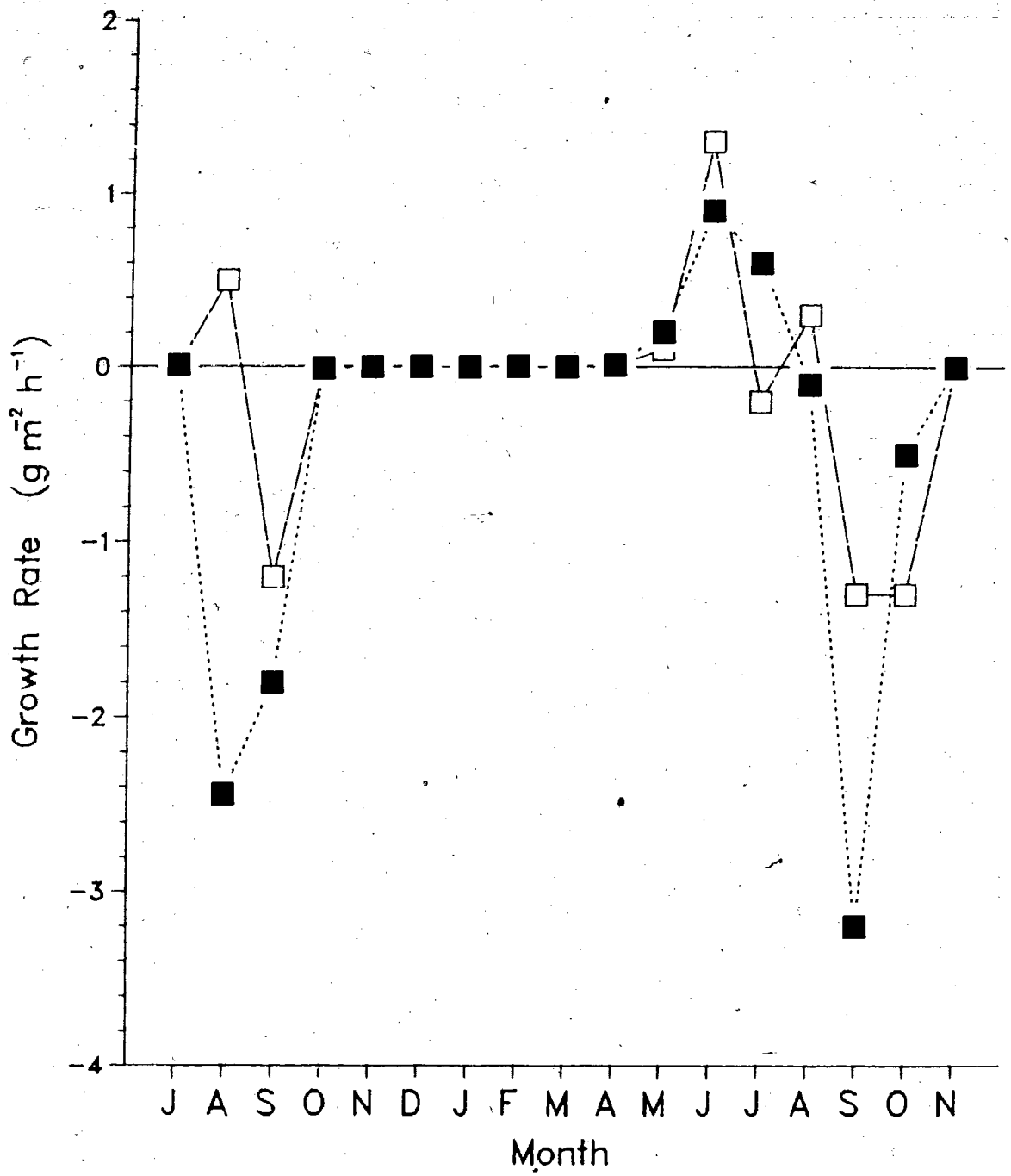

Figure 16. Mean absolute growth rates of low (■····■) and high marsh (□– –□) *S. maritimus*. Negative values indicate loss of standing crop by tidal removal.

Although there were large belowground reserves below 0.20 m (Figure 17), most roots and rhizomes at these depths were fragmented and few live corms were found. These data are presented to show that a large portion of the productivity of *S. maritimus* stands may be found below 0.20 m, although this material seems moribound.

On August 4, 1986, *S. maritimus* was sampled at its highest elevation limit along the Sea Island dyke (Table 2). Although stem densities in this high marsh environment were less than half that of the low and middle marsh, these stems were much larger in size as evidenced by the two-fold increase in total shoot biomass. As well, 26% of the shoots flowered and a large portion of last year's shoot biomass remained on the marsh platform. Examination of the high marsh in October indicated that most of these dead stems from the previous year were washed away. Peak standing crop of 1461±150 g m^{-2} of the high marsh was three times that of low and middle marsh. Similarly, there were large differences in total belowground reserves between the three environments. High marsh plants had much more root biomass but less corm biomass. Rhizome biomass was equal in all three stands.

Aboveground biomass of *S. maritimus* was less than 25% of total biomass (Figure 18). In the middle marsh, photosynthetic tissue comprised only 11% of the total biomass in the summer of 1985 but this increased to 17% in 1986, a reflection of increased shoot biomass in this season. Conversely, low marsh shoots comprised 22% of the total biomass in 1985 and only 14% in 1986. Furthermore, whereas *S. americanus* shoots had a mid-summer peak, *S. maritimus* shoots peaked in July and maintained that peak through September.

Belowground biomass proportions were similar in middle and low marsh *S. maritimus* (Figure 18). Corms made up more than 50% of total biomass during winter and 40-45% during summer. Middle marsh roots peaked in spring, much like *S. americanus* roots, but low marsh roots showed continuous fluctuations. There was less than 5% biomass as rhizomes in both environments.

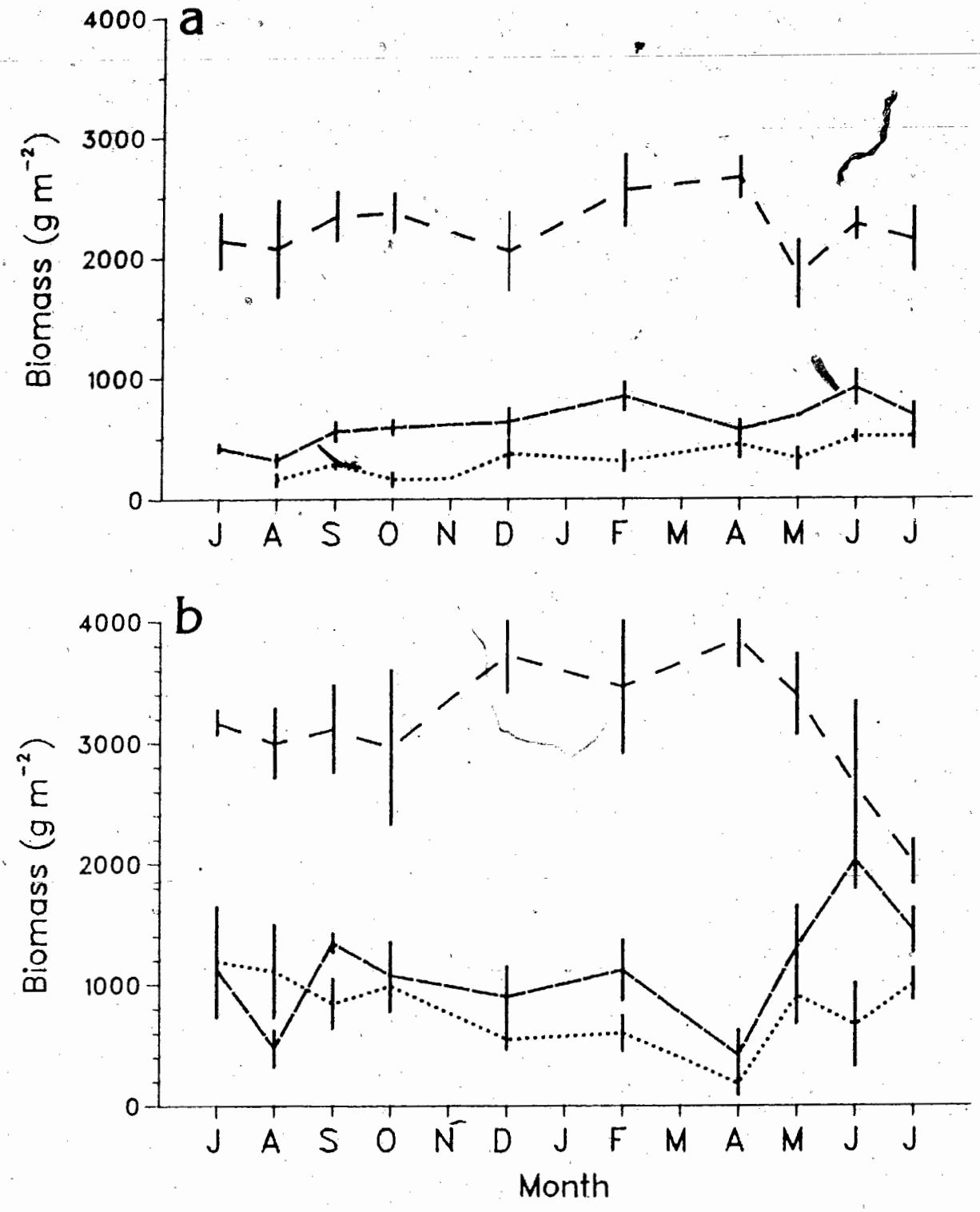

Figure 17. Total belowground biomass ($\bar{x}$±se) of *S. maritimus* low marsh (a) and high marsh (b) for 0 - 0.20 m (— — —), 0.20 - 0.40 m (— — — —) and 0.40 - 0.60 m (----------).

Table 2. Comparison of biomass in high, middle and low marsh *S. maritimus* environments on August 4, 1986 (g m^{-2}, mean ± 1se).

site	stem no.	stem wt.	% flowers	last year dead	current year dead	total above-ground	roots	rhizomes	corms	total below-ground 0–0.2m	Grand Total	Below:Above
low	492 (35)	420 (32)	0	37 (13)	7 (3)	466 (33)	1286 (135)	189 (22)	1615 (75)	3089 (172)	3557 193	6.6
middle	478 (45)	482 (102)	13	21 (5)	25 (8)	535 116)	1475 (194)	204 (18)	1955 (289)	3633 (478)	4168 (446)	6.8
high	217 (36)	973 (146)	26	485 (42)	8 (3)	1461 (150)	4197 (436)	198 (67)	1088 (767)	5488 (528)	6944 (549)	3.8

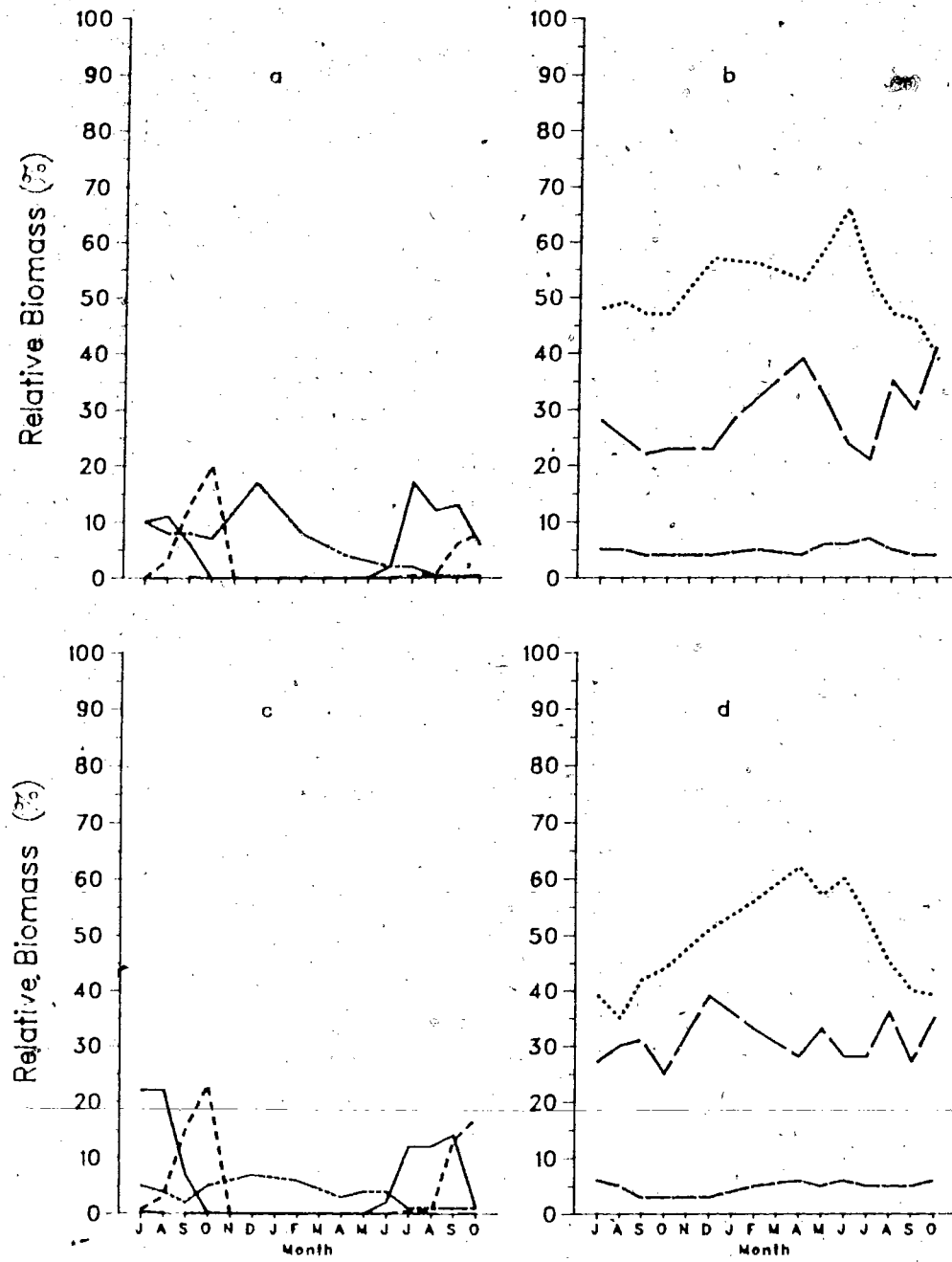

Figure 18. Mean monthly relative biomass of middle (a,b) and low (c,d) marsh *S. maritimus* for photosynthetic shoots (———), current year dead shoots (- - - - -), last year's dead shoots (—- - -—), roots (— — —), rhizomes (———) and corms (·····).

CHAPTER IV
DISCUSSION

Allocation Strategies

It was hypothesized that plants in the stressed, low elevation environments should adopt conservative allocation strategies and invest less into shoot biomass. These predictions were not supported by the findings of this study (Figures 13 and 18). Low marsh *S. americanus* was at the lowest elevation but had the greatest investment into aboveground biomass (31%). At the high end of the elevation gradient, middle marsh *S. maritimus* invested only 17% of the total biomass into aboveground shoots in 1986, and 11% in 1985. Between these end points, low marsh *S. maritimus* invested a maximum of 22% of the total biomass into shoots in 1985 and 12% in 1986. Shoot biomass of high marsh *S. americanus* represented 25% of the total plant biomass in this environment in both sampling seasons. It is unknown what proportion of plant aboveground biomass is lost by tidal export between sampling days. Furthermore, the shoots at low elevations with longer tidal submergence periods are prone to greater losses through leaching. Thus, comparisons between environments should be interpreted with caution.

The proportion of total biomass in aboveground structures of 15–30 % measured in this study is similar to that measured by Kistritz *et al.* (1983) for *Carex lyngbyei*. Similarly, maximum live aboveground biomass of *S. alterniflora* was ≃ 20% of total belowground biomass in Georgia but ≃ 50% of the live belowground biomass (Schubauer and Hopkinson 1984). Ellison *et al.* (1986) measured aboveground and belowground biomass of two height forms of *S. alterniflora* in a Rhode Island marsh. Analysis of their data indicated that peak aboveground biomass of tall form represents ≃65% of total biomass and short form represents 72%.

Reproductive effort (RE) was calculated for sexual and asexual structures (rhizomes). There is some controversy as to whether sexual RE should be calculated for total biomass or just aboveground biomass (Willson 1983). The argument centers on the fact that perennial plants maintain a root and rhizome reserve that should not be included in the measurement of sexual RE. The data for *S. americanus* and *S. maritimus* are presented for both aboveground biomass and total biomass (Table 3). For *S. americanus*, high marsh plants had

Table 3. Mean sexual reproductive effort, measured as percent biomass of live achenes to total biomass and to live aboveground biomass (in brackets) (tr = trace).

Site	1985			1986				
	JUL	AUG	SEP	JUN	JUL	AUG	SEP	OCT
S. americanus								
Low	0.8 (3.0)	0.1 (1.0)	tr (0.5)	0 (0.2)	0.7 (2.0)	0.2 (0.9)	0 (3.0)	0 (0)
High	0.8 (4.0)	1.2 (8.0)	0.3 (4.0)	0.2 (2.0)	0.7 (3.0)	0.6 (3.0)	0 (0)	0 (0)
S. maritimus								
Low	0.3 (1.0)	tr (0.3)	tr (0.4)	0 (0)	tr (tr)	0 (0)	0 (0)	0 (0)
middle	0 (0)	tr (tr)	0.3 (5.0)	0 (0)	0 (0)	0.2 (1.0)	tr (0.7)	0.3 (4.0)

a greater investment in sexual reproduction than low marsh, especially in 1985 when a maximum of 7% of aboveground biomass was inflorescences. This finding supports the hypothesis of greater resource investment to sexual reproduction in the high marsh. Plants in both environments, however, invested ≃1% of their total biomass to sexual reproduction. Clones in both *S. americanus* environments maintained an average of 47% of their total biomass as rhizomes.

It can be argued that allocation to sexual reproduction should include shoot biomass in *S. americanus* because the shoot supports the flower. Based on this assumption, low marsh *S. americanus* allocated 30% of the total biomass to aboveground structures compared to 24% of the total biomass in high marsh plants.

Low marsh *S. maritimus* had <1% aboveground biomass as flowers. The lower investment into flowers measured the second summer may have been a response to environmental stress as this was a very dry summer, which may have increased soil salinities. In the middle marsh, however, over 4% of aboveground biomass was allocated to sexual reproduction in both years. By comparison, high marsh *S. maritimus* had 2% aboveground biomass invested into sexual reproduction for the one time it was sampled (August 1986). This result also supports the hypothesis that allocation to sexual reproduction should be less in *S. maritimus* when compared to *S. americanus*. *S. maritimus* occupies the more severely reduced soils and a greater proportion of the resources should be devoted to maintenance. Clones in both *S. maritimus* environments maintained 40–50% of their total biomass as corms.

Willson (1983) summarized patterns of reproductive allocation and lists many studies that found RE of annual and perennial plants much greater than 10%, with several species having RE of ≃30%. These values greatly exceed those measured in this study. Long-lived clonal perennials are expected to devote more resources to growth than reproduction. RE of vegetative tissue in this study was similar to the range of 40–80% presented by Willson (1983).

Root to shoot ratios are generally presented as the proportion of mean annual live belowground to aboveground biomass. In this study, live and dead belowground biomass was not distinguished and this ratio is presented as the mean annual total belowground:aboveground biomass (Table 4). Since live and dead belowground biomass was not distinguished, the belowground:aboveground trends are valid only if it is assumed that the

Table 4. Total below to aboveground biomass ratios.

Species	Site	Ratio
S. americanus	Low	4.3
	High	6.9
S. maritimus (*)	Low	7.0
	middle	8.4

* total biomass to depth of 0.6 m

proportion of dead to live biomass is similar in all samples. This assumption can be made in *S. americanus* environments where most of the belowground biomass appeared to be live. *S. maritimus* environments, however, contained a large dead belowground biomass compartment. Hence, the higher ratios measured in the *S. maritimus* environments when compared to *S. americanus* (Table 4). As well, the low marsh *S. maritimus* environment appeared to contain a greater proportion of dead belowground biomass than the middle marsh. These differences in belowground biomass negates comparisons between species and indicate that any other comparisons should be made with caution.

The highest ratios were found at the upper elevation limits for each species and in fact, below:above ratios increased consistently with increasing elevation (Table 4). This does not support the hypothesis presented earlier that suggested that root:shoot ratios will be highest in the low elevation stressed environments. Although *S. maritimus* is at higher elevations, the fine sediments in these environments impede drainage leading to low soil redox potentials. In environments with low redox potential, greater root biomass is required to produce a unit of shoot biomass (Shaver and Billings 1975). While this explains the higher root:shoot ratios between species, it does not account for the trends within species. It may be that an environmental factor that was not measured in this study is the cause of this pattern. One such example is hydrogen sulphide which may be found in high concentrations in the high marsh environments.

The root:shoot ratios measured at Sea Island are much higher than values in the literature. This again is a reflection of the large, dead belowground biomass of *S. maritimus* which was included in the calculation. Schubauer and Hopkinson (1984) found root:shoot ratios of 1.7:1 for *Spartina alterniflora* and 2.5 for *Spartina cynosuroides* in Georgia and they cite other studies that measured equivalent ratios. These values were derived from live biomass only which represented 20–25% of the dead belowground biomass compartment. Therefore, their root:shoot ratios would be similar to those measured at Sea Island if total belowground biomass was used in the calculation. Most of the belowground tissue of *S. americanus* appeared to be live. Thus, the ratios of *S. americanus* may be directly compared to *Spartina alterniflora*. In the Pacific Northwest, Kistritz *et al.* (1983) measured total aboveground and belowground biomass of *Carex lyngbyei*. From their data, I calculated a root:shoot ratio of approximately 4:1 for the month of peak biomass (July). This is

similar to the values of *S. americanus* and *S. maritimus*.

Root:shoot ratios vary widely in wetland plants, the differences due to the length of life of underground systems and to differences in soil fertility (Bernard *et al.* 1985). For example, arctic plants typically have higher root:shoot ratios than temperate plants due to low temperature (Barnard *et al.* 1985). Chapin and Chapin (1981) reported values of 0.9–3.2 for *Carex aquatilis* in experimental gardens in Alaska. Grace and Wetzel (1981) noted a greater root growth in low nutrient level *Typha* stands. Similarly, Haines and Dunn (1976) and Valiela *et al.* (1976) observed decreased root production with increased nitrogen availability for *Spartina alterniflora*. The high root:shoot ratio measured for *S. americanus* compared to these other studies is a response to long inundation in *S. americanus* environments which are at the lowest points on the Fraser Delta foreshore marshes. Therefore, in *S. americanus* environments, greater belowground biomass is required to produce a unit of shoot biomass because of the very short exposure time.

Seasonal patterns

S. americanus and *S. maritimus* had a rapid growth of roots and rhizomes in spring, root growth for nutrient uptake and rhizome growth for clone expansion. Belowground biomass was lowest in summer when resources were allocated to shoots and flowers. When aboveground structures senesced, biomass was re–allocated to belowground structures, primarily rhizomes. Rhizomes of *S. alterniflora* function as overwintering storage tissues and also increase in biomass in fall when culm mortality is highest and carbohydrate translocation to storage organs greatest (Lytle and Hull 1980). Seasonality of root biomass is related to availability and demand for plant nutrients. In coastal marshes of Georgia, a large investment in root biomass in winter enabled *S. alterniflora* and *S. cynosuroides* to take advantage of the high NH_4 concentration in the soil in early spring (Schubauer and Hopkinson 1984). Corms serve the role of storage organs in *S. maritimus*; rhizomes are only for clone expansion.

Seasonal fluctuation of biomass of plant structures suggests that there is allocation of resources between aboveground and belowground structures in *S. americanus* and *S. maritimus*. The growth strategy of plants appears to differ in high and low environments. This is evident when biomass allocation to each plant structure is compared between environments as

a relative measure of total biomass. *S. maritimus* had greater year to year variation in photosynthetic biomass than *S. americanus*. However, total aboveground biomass (live and dead) of *S. maritimus* was similar for the 2 years sampled suggesting that this variation may be due to interclone sampling variability as the sampling scheme adopted sampled different clones for each month.

Similar seasonal patterns in aboveground and belowground biomass allocation were observed by Kistritz *et al.* (1983) in *Carex lyngbyei*. Several studies examining *Spartina alterniflora* report maximum belowground biomass in winter (Valiela *et al.* 1976, Smith *et al.* 1979, Schubauer and Hopkinson 1984). Gallagher and Plumley (1979) measured peak belowground standing crop of *S. alterniflora* in fall but Ellison *et al.* (1986) found that peak belowground biomass of *S. alterniflora* was in mid-summer with no secondary peak corresponding with the autumn dieback of aboveground parts.

For *S. americanus*, growth rates during the growing season were similar between environments except during the month of May. During this period, high marsh plants accumulated biomass three times as fast as those in low marsh (compare 0.6 to 0.2 g m^{-2} h^{-1}). This early season difference in growth rate combined with the longer exposure period at higher elevations produced the greater biomass measured in the high marsh. In spring, the warmer soil temperatures of the high marsh enhance shoot growth. In the low marsh, flooding by cold tidal water limits shoot growth to the short exposure time after soils have been warmed.

The cause of the greater biomass measured in low marsh *S. maritimus* in 1985 cannot be explained without knowledge of what happened in early summer. In 1986, the higher growth rate in July in middle marsh *S. maritimus* were offset by the August rates which are higher in the low marsh. Mean growth rates for April 1 to September 1 were 0.3 g m^{-2} h^{-1} in the middle and low marsh. The data indicated that although plants at the higher elevations may have slightly higher growth rates at specific times of the year, the primary factor accounting for biomass differences between environments is total exposure time.

The high rates of tissue loss measured for low marsh *S. maritimus* may be a result of the rapid decline for exposure hours for this environment. Consequently, the longer submergence period leads to rapid plant senescence. Flooding of senescent shoots decreases the integrity of these shoots to withstand flooding. Hence, they are slowly removed from

the marsh platform. The middle marsh has a rapid decline in exposure hours but it remains above 200 hours per month. The result was a slower rate of senescence and longer period of complete removal of dead shoots.

All aboveground production is exported from the *S. americanus* community in late fall/ early winter. The *S. maritimus* shoot biomass is eventually removed from the marsh platform. Belowground production had seasonal peaks and this material must be transported somewhere. It may be allocated aboveground and then lost or lost as belowground biomass, either through grazing, dissolution, or erosion. Valiela *et al.* (1975) reported that the amount of dead *Spartina alterniflora* measured in autumn was substantially less than the maximum amount of live biomass present earlier in the year. They suggested that part of the material is lost by plant respiration, by translocation to belowground parts and by decomposer activity; the remainder must be carried away to deeper waters by tidal flushing. At Sea Island, both high marsh *S. americanus* and middle marsh *S. maritimus* had a similar relationship between live and dead shoot biomass. The low marsh *S. americanus* had dead shoot biomass equivalent to that of live, whereas low marsh *S. maritimus* had much greater dead shoot biomass in late autumn compared to the maximum live shoot biomass recorded. I suggest that a large portion of the primary production of aboveground tissues in *S. maritimus* were lost through several avenues during the season and therefore, not measured as dead material in late autumn.

Since belowground biomass was not separated into live and dead material, growth in one month should be measured the following month either as live or dead matter. The rapid decline in root biomass in the low marsh in December 1985 suggests the removal of this material either as dissolved material or by grubbing snow geese, which overwinter in the Fraser River delta from October/November to April. Burton (1977) found that *S. americanus* and *S. maritimus* comprised 76% of food items identified in gizzards of snow geese (*Anser caerulescens*) grazing on the Fraser Estuary tidal marshes. He estimated that 32% of the total standing crop of *S. americanus* and *S. maritimus* may be removed. Recent observations by Hutchinson (unpublished data) in the low marshes of Sea Island indicate that there is no difference in belowground biomass of *S. americanus* in exclosures compared to areas grubbed by geese. The December 1985 belowground biomass estimate may therefore represent sampling variability.

Standing crop

Shoot densities of both *S. americanus* stands exceeded that of *S. maritimus*. As well, while flowering frequency of *S. americanus* was greater, *S. maritimus* flowers were much larger (Table 5). Aboveground biomass of *S. maritimus* was comparable to that of high marsh *S. americanus*, with low marsh *S. americanus* having the lowest biomass. For *S. maritimus*, shoot density peaked in July, declined therafter as biomass increased. Therefore, competition between shoots for resources results in the development of tall shoots with wide leaf bases that leads to mortality of neighbouring shoots.

Similar to the findings of other studies that have sampled belowground biomass in marsh environments, total belowground biomass exceeded aboveground biomass in both species. A comparison by plant structure indicated that only *S. maritimus* rhizome biomass was less than shoot biomass. These are thin, short rhizomes and thus have low total biomass. Biomass of roots was greater than rhizome biomass and in *S. maritimus*, corm biomass exceeded that of roots. Total belowground biomass of *S. maritimus* exceeded *S. americanus* but *S. americanus* had the greater rhizome biomass.

The peak standing crop of 850 g m^{-2} of *S. americanus* in the Nooksack brackish marsh, Bellingham Bay, Washington, (Disraeli and Fonda 1979) exceeded the maximum of high marsh *S. americanus* at Sea Island (Table 6), but Ewing (1982) recorded a maximum standing crop of *S. americanus* in the Skagit delta marshes equivalent to high marsh *S. americanus* at Sea Island. Moody's (1978) estimate of maximum standing crop of *S. americanus* at Brunswick Point, on the Fraser River delta marsh (397 g m^{-2}) is comparable to low marsh stands at Sea Island. The lowest aboveground standing crop of *S. maritimus* measured at Sea Island was in the middle marsh environment. This value exceeded all other measurements for this species in Pacific coast marshes.

Only Disraeli and Fonda (1979) and Ogwang (1982) provide data on belowground biomass of *S. americanus* and their estimate corresponds to that of the high marsh in this study. No measurements of the belowground production of *S. maritimus* have been made along the Pacific coast.

Carex lyngbyei is the most common and widespread plant in Pacific coast marshes. Aboveground standing crop exceeded 1700 g m^{-2} in a "fresh" environment at Qualicum

Table 5. Mean monthly weight per live achene (mg).

	1985			1986				
	JUL	AUG	SEP	JUN	JUL	AUG	SEP	OCT
S. americanus								
low	7.8	5.2	7.4	0.3	7.8	4.9	0	0
high	8.3	12.8	11.2	3.5	6.4	10.9	0	0
S. maritimus								
low	43.7	26.6	21.3	0	5.0	0	0	0
middle	0	13.9	179.2	0	0	111.5	70.0	190.5
high	–	–	–	–	–	2714	–	–

Table 6. Peak standing crop (g m^{-2}) of monospecific stands of *S. americanus* and *S. maritimus* in Pacific Northwest Wetlands (Source: Hutchinson 1986).

Wetland Community	Peak Standing Crop belowground	aboveground	total	Location	Source
S. americanus	–	622	–	Skagit R., WA	Ewing 1982
	3000	850	3850	Nooksack R., WA	Disraeli and Fonda (1979)
	–	339		Fraser R., BC	Moody 1978
	3440	–	–	Fraser R., BC	Ogwang 1982
low marsh	1093	463	1556	Fraser R., BC	This study
high marsh	2740	673	3413	Fraser R., BC	This study
S. maritimus	–	–		Nehalem R., OR	Eilers 1975
	–	426	–	Skagit R., WA	Ewing 1982
	–	606	–	Fraser R., BC	Hall & Yesaki (no date)
	–	565	–	Fraser R., BC	Moody 1978
high marsh	11,635	1,794	13,429	Fraser R., BC	This study
middle	5,030	1,195	6,225	Fraser R., BC	This study
low	3,195	1,512	4,707	Fraser R., BC	This study

marsh (Kennedy 1982). The range of values for *C. lyngbyei* fall within that measured for *S. americanus* and *S. maritimus* in this study and demonstrate that these two sedges can be as productive as *C. lyngbyei*. Belowground biomass of *C. lyngbyei* is comparable to high marsh *S. americanus* and low and middle marsh *S. maritimus*, but is half that of high marsh *S. maritimus*. Therefore, it appears that *S. maritimus* may represent one of the most productive species in Pacific coast marshes, especially at its upper elevation limits. For comparison, total belowground biomass of *Juncus roemerianus* is between 9–12,000 g m^{-2} in a tidal marsh in Mississippi (de la Cruz and Hackney 1977). Similarly, peak belowground standing crop of *Spartina alterniflora* (6,000 g m^{-2}) and *S. cynosuroides* (8,000 g m^{-2}) (Schubauer and Hopkinson 1984) exceed *S. americanus*.

The difference between maximum and minimum biomass is a crude indication of net annual plant production. Schubauer and Hopkinson (1984) and Ellison *et al.* (1986) have used this method for belowground productivity estimates in wetland environments. Since live and dead belowground biomass was not distinguished in this study, the use of more complicated techniques for calculating production is precluded. For Sea Island, production increased with elevation (Table 6). Low marsh *S. maritimus* had the highest aboveground production, and middle marsh *S. maritimus* the most belowground production. Total production was lowest in low marsh *S. americanus* (1494 g m^{-2}), increasing to 3036 g m^{-2} in middle marsh *S. maritimus*. Only middle marsh *S. maritimus* had total production values that approached those of *Spartina alterniflora*. Generally, the production of the environments sampled in this study were less than 50% of *S. alterniflora*.

Low marsh *S. americanus* plants had only 11% of their total belowground biomass below 0.20 m in depth compared to their high marsh counterparts which had up to 40%. Ellison *et al.* (1985) found decreasing penetration of *Spartina alterniflora* roots and rhizomes into the marsh substrate with increasing tidal height in a Rhode Island marsh. Similarly, Gallagher (1974) found that 69% of belowground biomass of high marsh (negative redox) *Spartina alterniflora* was in the upper 0.15 m of 0.35 m cores compared to only 44% of creek bank (high positive redox). In a greenhouse experiment, Seliskar (1983) concluded that more than 65% of the root and rhizome biomass of *Descahmpsia caespitosa*, *Distichlis spicata*, *Grindelia integrifolia*, and *Salicornia virginica* in the upper 0.10 m of soil was indicative of saturated conditions. Schubauer and Hopkinson (1984) suggest that in northern

latitudes, rhizomes are found at depth to protect them from freezing winter temperatures. Live belowground material is found near the surface where remineralization and supposedly nutrient supply are greatest, but deep enough to avoid damage due to seasonal changes in microclimatology (Schubauer and Hopkinson 1984). High interstitial salinities in *Spartina alterniflora* high marsh compared to the streamside may restrict belowground matter to the top soil layers where rainfall and tidal water keep the salinities lowest. Haines and Dunn (1976) reported reduction of root growth associated with higher salinity in a greenhouse study. A combination of high interstitial salinity, low (negative) redox and microclimate restrict belowground biomass to surface layers of the soil.

Gallagher and Plumley (1979) proposed three types of pattern in macro-organic matter. A Type I pattern has equivalent biomass at all depths, in contrast to a Type III which has most of the belowground biomass near the surface. A Type II pattern has the majority of belowground biomass in the middle layers of the substrate. *S. americanus* appears to belong to the Type III category. In both the high and low environments, the top 0.05 m of soil contains roots, the rhizomes being 0.10–0.20 m below the marsh platform. *S. maritimus* is difficult to categorize because of the large dead, belowground reserve. It does, however, resemble a Type II or III pattern.

Substantial interspecific and intraspecific variation in biomass allocation exists in *S. americanus* and *S. maritimus*. For *S. americanus*, high marsh clones had greater stem densities and biomass. The high shoot densities measured in high marsh *S. americanus* may produce tall shoots through competition for light. In *S. maritimus*, tall plants at higher elevations have broad leaves which shade out neighbouring shoots. Therefore, in these environments, there is a lower shoot density than in the low marsh where shoots are not as tall and hence, not as leafy. Furthermore, the lack of difference in shoot biomass between the low and middle marsh environments of *S. maritimus* may be due to sampling above and below the elevation markers established at the beginning of the sampling period. The first months of sampling were done below the elevation markers in the middle marsh environment and most likely at an elevation similar to that of the low marsh. During the second summer of sampling, most of the middle marsh samples were collected at or above the markers and therefore at a higher elevation than the low marsh. Hence the greater biomass in the middle marsh than in the low marsh. From the calculations involving relative

biomass and growth rates, it appears that these difference were a response to exposure time to sunlight. Reciprocal transplant experiments were undertaken as a further test to determine if this variation is under genetic control (Part E).

PART D
NUTRIENT ALLOCATION

CHAPTER I

INTRODUCTION

The objective of this chapter was to extend the concept of intraspecific variation measured for biomass to nutrient allocation. Nutrient analyses were undertaken because they provide a better measure of the investment made by a plant for the construction of various plant structures. Two groups of nutrients were monitored. The macro-nutrients (N, P, C, H, Ca, Mg, K, Na) are important for plant growth and should be allocated to shoots in large quantity. The micro-nutrients, or trace metals (Al, Fe, Mn, Zn, Cu), are required in small quantities and can be deleterious when present in high concentrations. Seasonal changes in the movement of nutrients between different plant structures were determined on a concentration and an accumulation basis. The proportion of total nutrient pools allocated to different plant structures indicated if plants in a particular environment were conservative with their resources.

Several questions were asked concerning nutrient allocation patterns and strategies. First, which nutrients decrease in live shoots in autumn, concurrent with an increase in belowground structures, suggesting storage? Conversely, nutrients that accumulate in aboveground shoots are subsequently lost by the plant because tidal action removes plant biomass from all four environments. More specifically, is the spendthrift *S. americanus* (complete shoot loss) more likely to relocate nutrients to rhizomes than *S. maritimus*, which maintains dead aboveground material as possible storage reserve? Answers to these questions will indicate if the relative allocation between below and aboveground structures is similar in different environments. Finally, are there consistent trends in the accumulation of selective nutrients in specific plant structures? If so, this may suggest compartmentation of these elements to prevent interference of metabolic processes.

From these questions, the following hypotheses were developed and tested in light of nutrient allocation strategies.

H_1: The hypothesis of conservation of resources.

Plants in stressful environments undertake more extensive and intensive sequestering of nutrients, even though there may be no differences in nutrient availability. Once these nutrients have been sequestered, I hypothesize that plants in stressful environments should be

conservative by storing nutrients. By extension, plants occupying stressed environments should allocate a smaller proportion of their resources to aboveground shoots.

H_2: Nutrients that are scarce (e.g. nitrogen) should be stored in underground structures at the end of the growing season.

In situations where a large effort has been made to acquire nutrients, the plant should store those nutrients for immediate use the following spring and to avoid dependence on external sources to supply those nutrients.

These data provide a measure of plant nutrient conservation or loss and insight into nutrient allocation strategies of plants in different environments. By incorporating the data on spatial and seasonal variation of environmental variables reported in Part B, the cause of any observed variation was determined.

CHAPTER II

METHODS AND MATERIALS

The plant material collected for biomass determination (Part C) constitutes the sample for nutrient measurements. Samples were analyzed for the 13 month period, July 1985 to July 1986. The overlap of July provides some indication of year to year variation of nutrient content. Four samples were collected from each of the four environments at monthly intervals from April to October inclusive, and bimonthly during winter. The plant structures analyzed were photosynthetic tissue, inflorescences, standing dead shoots, roots, rhizomes and corms.

A subsample of plant material was washed to remove all sediment and ground in a Wiley Mill to pass a #80 mesh sieve. For C, H, and N determination, 1-3 mg of tissue was analysed in a Carlo Erba C-H-N Elemental Analyzer. Between 0.200 and 1.000 g of dried tissue was digested in 10 ml of H_2SO_4 at 350C for 2.5 h to extract P, Ca, Mg, Na, K, Al, Fe, Mn, Zn and Cu (Parkinson and Allen 1975). Phosphorus was determined by the molybdenum blue method (Watanabe and Olsen 1965) on a Bausch and Lomb Mini Spectronic 20. A Varian Model 1475 Atomic Absorption Spectrophotometer was used to determine Na and K by flame emission, Ca and Al by atomic absorption spectrophotometry using a nitrous oxide acetylene flame to suppress ionic interference, and Mg, Fe, Mn, Cu and Zn by atomic absorption spectrophotometry using an air acetylene flame. The product of biomass and nutrient concentration was used to derive nutrient accumulation.

All samples were calibrated using 3 reference standards for the calibration curve. Macro-nutrients were measured to 0.01% and micro-nutrients to 1 ppm. Significant differences in nutrient concentration and accumulation between sites and plant structures were revealed by an analysis of variance and Student-Newman-Keul's multiple range test (UBC ANOVAR, Greig and Osterlin 1978) with a 95% confidence level. Concentration data were analyzed after square root arcsin transformation (Sokal and Rolf 1981).

CHAPTER III

RESULTS

For *S. americanus*, nutrient concentrations were higher in all plant structures in the low marsh structures than in the high marsh. For *S. maritimus*, plants in the middle marsh had higher nutrient concentrations than those in the low marsh. However, nutrient accumulation was greater in the higher elevation environments for both species. Because of these consistent trends, the data are graphed to present the nutrient content of different plant structures from one environment on a single graph. Mean annual nutrient concentration of each plant structure is presented in Table 7 for comparison between structures and environments.

Significant seasonal differences in nutrient concentration were detected in virtually all plant structures and all 13 nutrients; only C did not vary with season. The analysis of nutrient stocks showed that there were significant seasonal changes for all elements measured, including C. The seasonal patterns are discussed below by nutrient.

Flowers in *S. maritimus* environments were sparse and little material was available for analysis; they are omitted in the description below. Generally, inflorescences from both the low and middle marsh had nutrient concentrations similar to that of live shoots.

Nitrogen

Shoots in high and low marsh *S. americanus* had maximum N concentrations in June (Figure 19). Maximum N concentrations in flowers were similar to that of shoots. Dead shoots increased in N concentration as the growing season progressed. Rhizomes from both environments had higher N concentrations during winter when there was no aboveground growth; N concentration in rhizomes was lowest in July at the time of peak aboveground biomass.

There was no significant difference in N concentration of *S. maritimus* shoots, but there were differences in the timing of maximum concentration (Figure 19). Middle marsh shoots had peak N concentration in June (3.30% N) compared to May (3.20% N) in the low marsh. Dead photosynthetic tissue from *S. maritimus* environments had a maximum N concentration of about 1.5%. The N concentration of belowground structures in the low

Table 7. Mean annual nutrient concentrations.

Site	%								ppm				
	N	P	C	H	Ca	Mg	K	Na	Al	Fe	Mn	Zn	Cu
S. americanus													
low													
roots	1.08	0.24	36.51	5.10	0.96	0.34	0.37	0.64	4528	23 255	148	75	523
rhizomes	1.55	0.30	36.96	5.74	0.23	0.31	0.84	1.53	2529	12 977	136	38	88
shoots	1.99	0.31	38.40	5.05	0.19	0.33	2.82	2.98	1925	1 601	301	27	45
high													
roots	0.96	0.20	37.19	5.25	0.42	0.36	0.39	0.57	4631	16 257	143	68	444
rhizomes	1.27	0.30	37.63	6.02	0.14	0.28	0.80	1.19	1641	7 039	88	32	65
shoots	1.78	0.34	44.79	5.63	0.16	0.27	2.52	2.60	1510	1 270	221	21	52
S. maritimus													
low													
roots	0.96	0.15	38.3[illegible]	5.19	0.33	0.32	0.22	0.38	6564	21 372	132	69	448
rhizomes	0.96	0.11	37.80	5.17	0.23	0.28	0.25	0.67	4146	10 785	67	52	106
corms	1.00	0.15	40.92	5.68	0.14	0.22	0.33	0.85	2354	7 596	41	50	49
shoots	1.85	0.23	44.63	5.91	0.11	0.29	1.60	3.63	2208	1 257	57	26	18
middle													
roots	1.48	0.29	39.14	5.32	0.40	0.33	0.20	0.41	5913	30 821	118	94	578
rhizomes	1.16	0.12	36.22	5.43	0.22	0.25	0.20	0.73	3357	15 018	62	56	121
corms	1.07	0.21	43.48	5.91	0.16	0.23	0.26	0.95	2143	12 958	50	64	51
shoots	2.19	0.31	42.88	5.91	0.11	0.26	2.04	2.96	2532	734	78	27	48

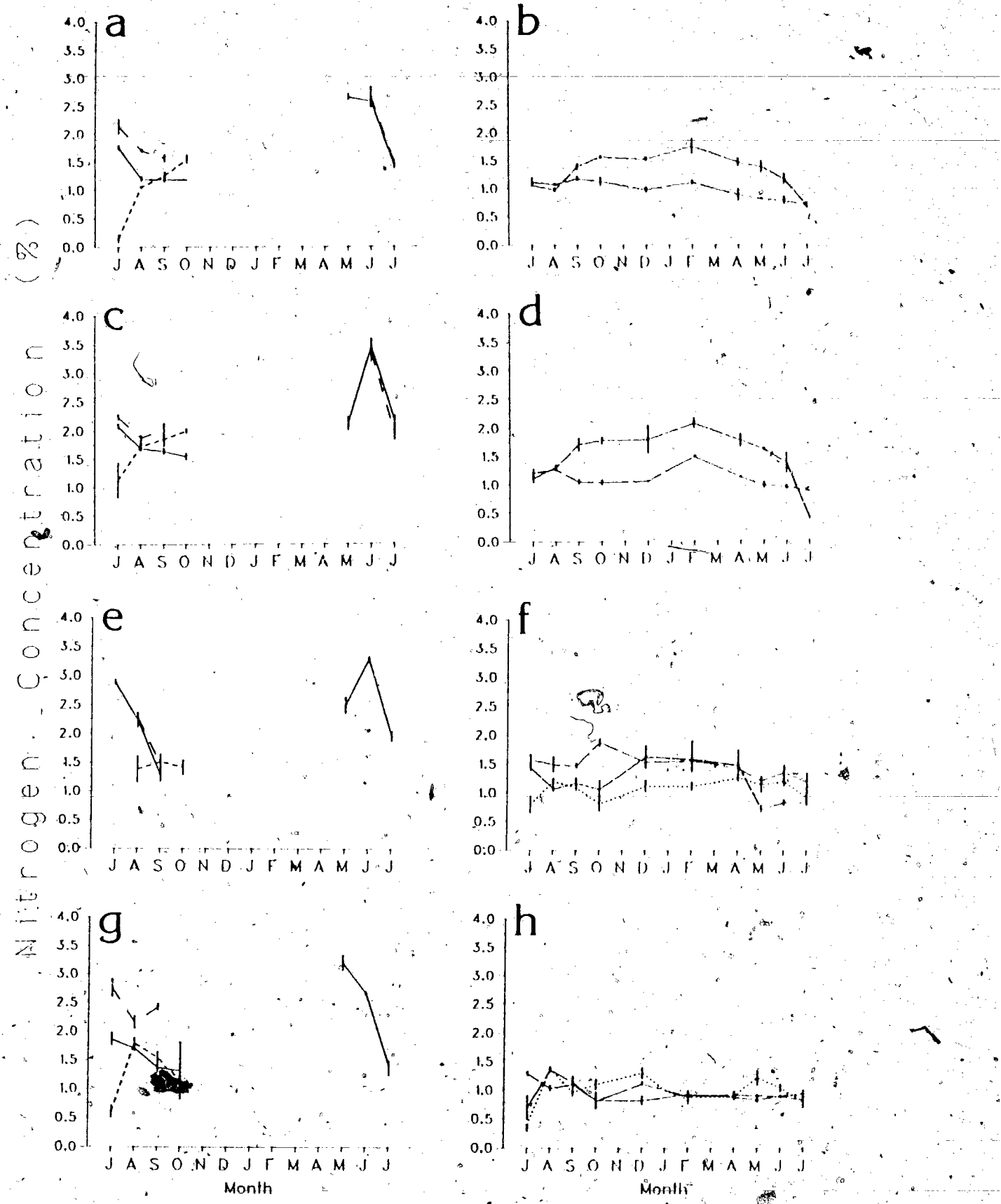

Figure 19. Nitrogen concentrations ($\bar{x} \pm 1se$) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - - -), roots (— — — —), rhizomes (— · — · —) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

marsh was ~ 1% N with no significant seasonal variation. In the middle marsh, roots had the highest mean annual N concentration (1.48% N) but rhizomes showed seasonal variation with winter maximum (1.63% N) and summer minimum (0.73% N). Mean annual concentration of N in corms was 1.07%, the lowest of belowground structures in this environment (Table 7).

Peak N accumulation in photosynthetic tissue was in July for all four environments (Figure 20). Low marsh *S. americanus* showed a second peak in October which coincided with the second biomass peak in this environment (Figure 12). Nitrogen accumulation in dead shoots showed a similar pattern to live shoots, only it lagged behind by a two month interval.

S. americanus rhizomes and *S. maritimus* corms showed clear seasonal changes in N accumulation. Accumulation increased in fall, maintained that level through winter and began to decline in spring with the growth of new shoots. Roots of both species had large fluctuations throughout the year but exhibited a similar seasonal pattern.

Phosphorus

Phosphorus concentrations in *S. americanus* photosynthetic tissues peaked in May (Figure 21) attaining a value of 0.56% P in the low marsh and 0.42% P in the high marsh. As with N, there was no significant difference in P concentration of inflorescences and shoots. Dead shoots had a much lower P concentration than live shoots, although there was a sharp increase in P low marsh *S. americanus* dead shoots in October. Phosphorus concentrations in roots and rhizomes were lowest in summer, a trend most prominent in the low marsh. Rhizomes in both environments had consistently higher P concentrations than roots and had a higher mean annual concentration (Table 7).

Mean P concentrations in middle marsh *S. maritimus* shoots (0.31% P) was significantly greater than in the low marsh (0.23% P) (Table 7). Shoots in middle and low marsh *S. maritimus* environments had maximum P concentrations in June (Figure 21). Inflorescences in the middle marsh had a much lower P concentration than shoots. In the low marsh, the maximum P concentration of 0.48% P in inflorescences was greater than that of shoots, but it declined thereafter to a concentration similar to that of the shoots. Dead shoots from both environments had P concentrations slightly less than that of shoots.

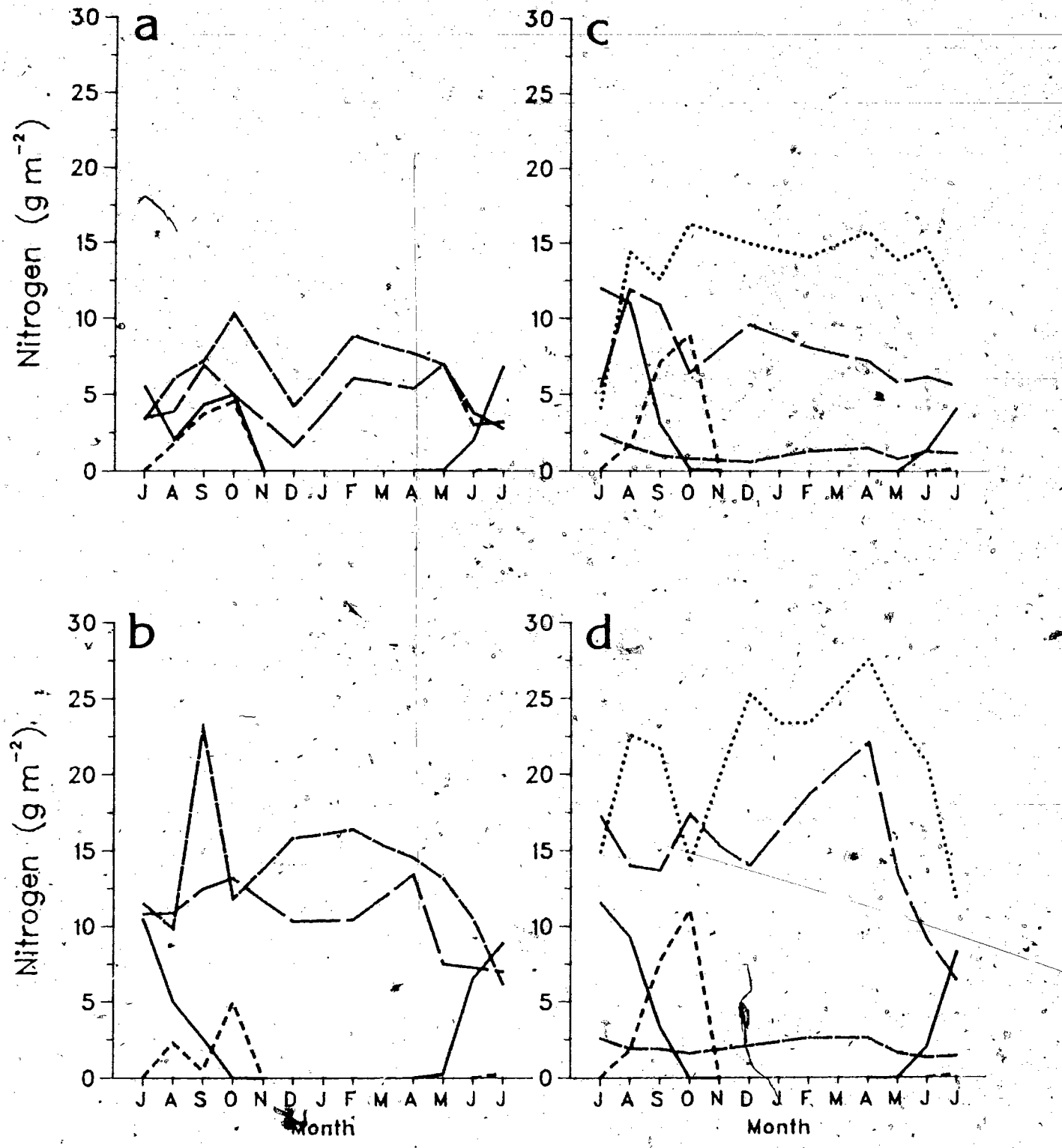

Figure 20. Mean nitrogen accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (—— —— ——) and corms (·····) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

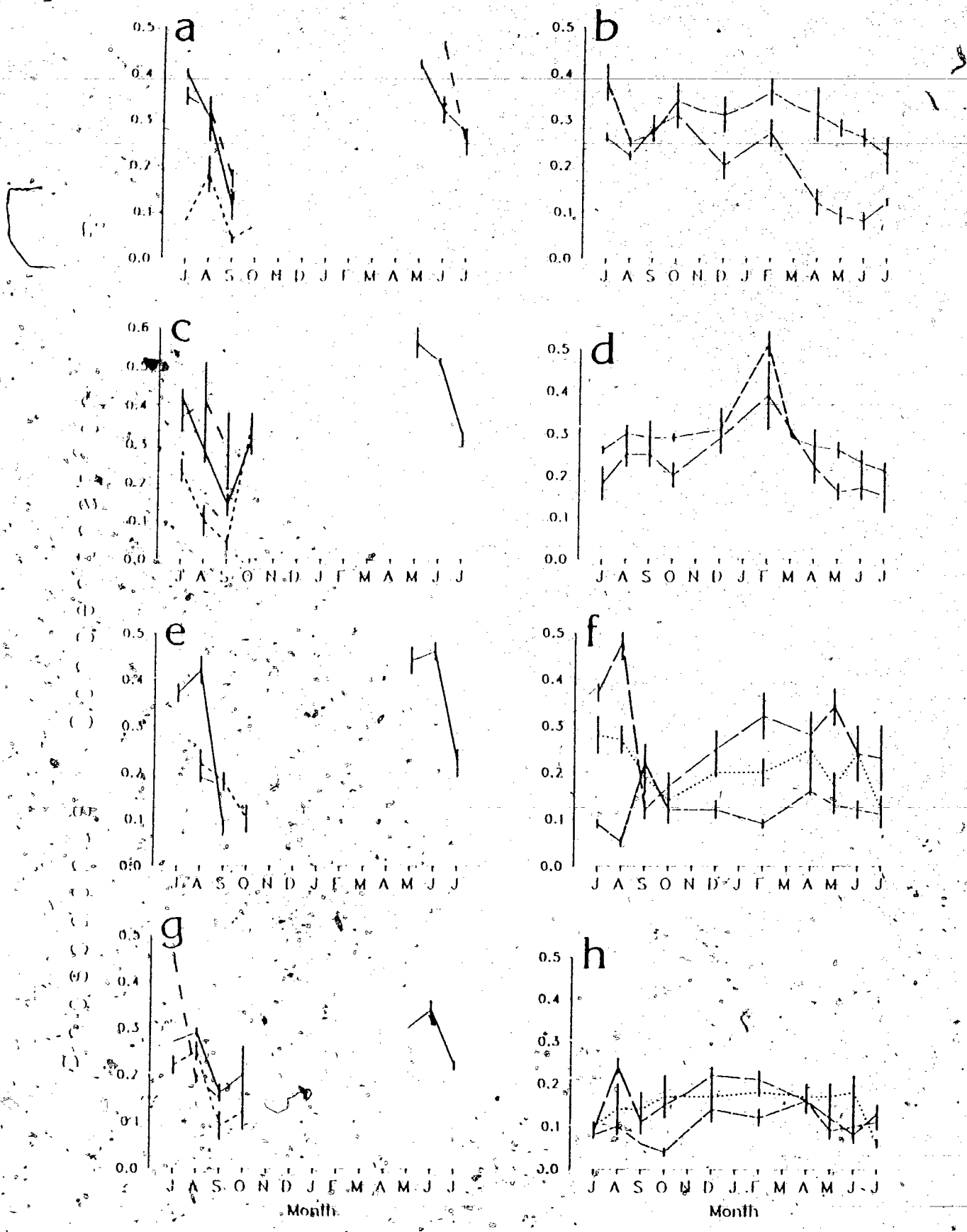

Figure 21. Phosphorus concentrations ($\bar{x} \pm 1sc$) in inflorescences (— . — —), photosynthetic shoots (————), dead shoots (- - - - -), roots (, — — —), rhizomes (— — — —) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

Phosphorus content of belowground structures from *S. maritimus* environments had a greater fluctuation than that of N. Generally, roots had the highest mean annual P concentrations, rhizomes the lowest and corms were intermediate (Table 7). The concentration of P in roots from both environments was highest in winter. There was no significant difference in P concentration over the year in low marsh *S. maritimus* corms.

Seasonal changes in P accumulation in live and dead shoots was similar to that of N (Figure 22). Accumulation peaked in July in live shoots and in October in dead shoots. Accumulation in belowground structures was variable. Although there was no consistent trend in low marsh *S. americanus*, roots and rhizomes of high marsh *S. americanus* showed highest accumulations in winter, declining rapidly in spring similar to the declining P concentrations in these tissues. Roots and corms of *S. maritimus* had large fluctuations between winter maximum and summer minimum levels.

Carbon

Carbon concentration was constant throughout the sampling period in all structures and in all environments (Figure 23). Thus, biomass changes were the cause of accumulation changes between months (Figure 24). Shoots had the highest mean annual C concentrations with equivalent levels measured in *S. maritimus* corms (Table 7). Roots and rhizomes had similar concentrations and lower concentrations than all structures. Middle marsh *S. maritimus* corms and low marsh roots had no significant seasonal variation in C accumulation. Some belowground structures had increased C accumulation in spring and/or fall (Figure 24).

Hydrogen

Live shoots showed the greatest seasonal variation in H concentration with a maximum of about 7.0% in June (Figure 25). Belowground structures had H concentrations between 5–6 %, with little variation throughout the year. Rhizomes from the low marsh *S. americanus* and *S. maritimus* had no significant seasonal variations in H concentration.

Like C, H accumulation was caused by biomass variation. Live shoots had maximum H accumualtion in July and dead shoots in October (Figure 26). Belowground structures from all environments had distinct peaks in fall and spring and these were greatest in *S. maritimus*.

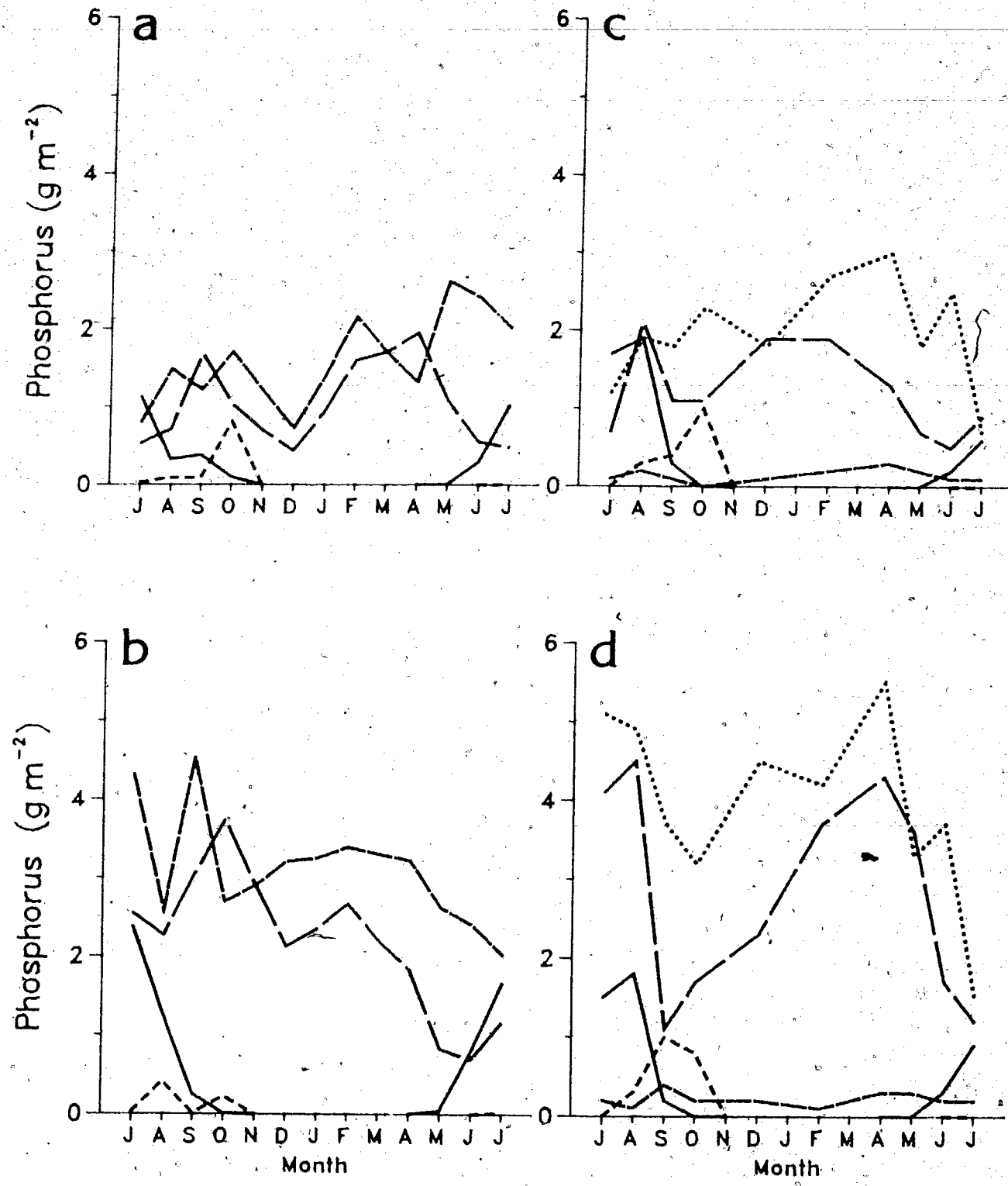

Figure 22. Mean phosphorus accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — —), rhizomes (— · — · —) and corms (·····) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

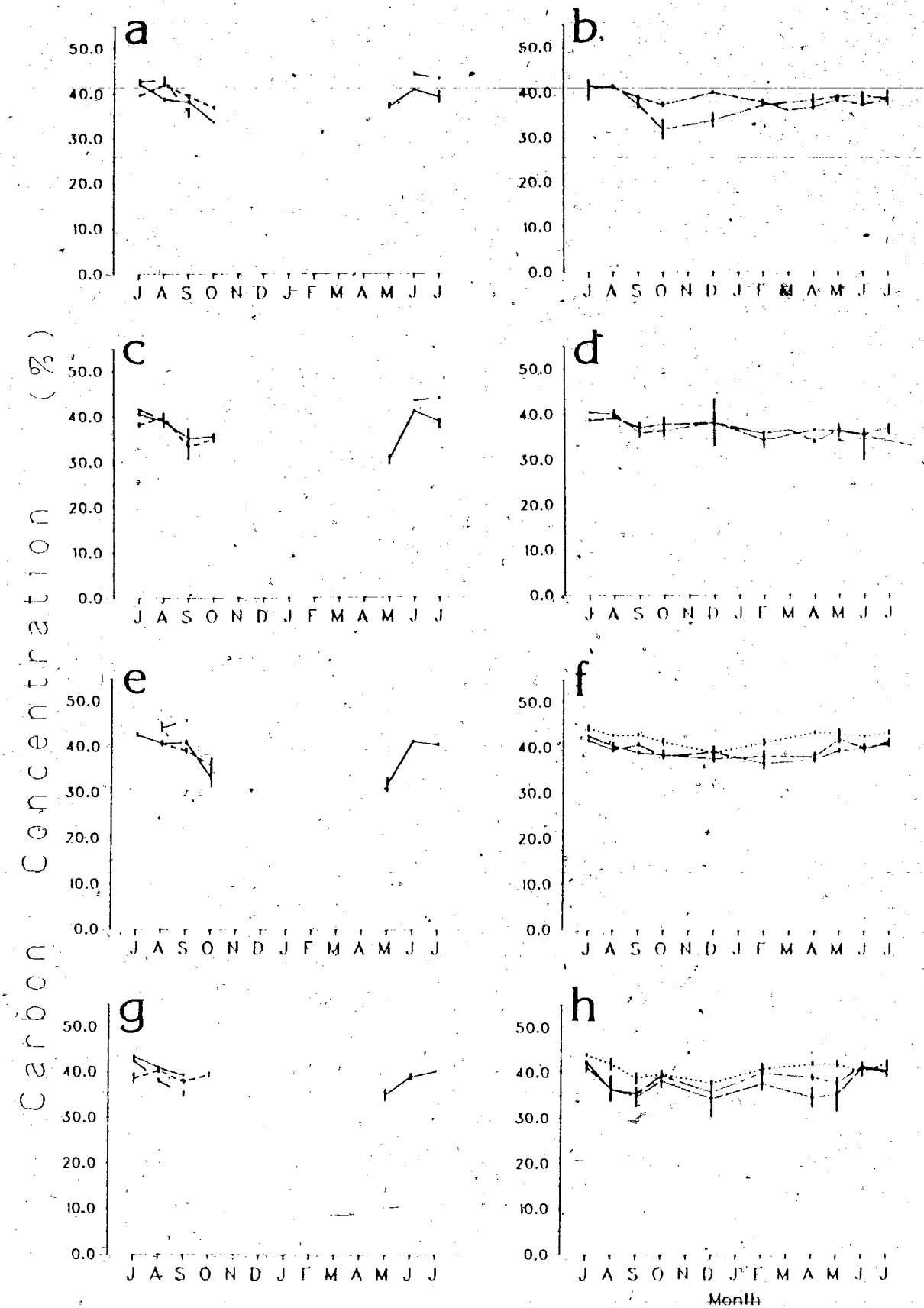

Figure 23. Carbon concentrations ($\bar{x}$ ± 1se) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — — —), rhizomes (— — — —) and corms (.....) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

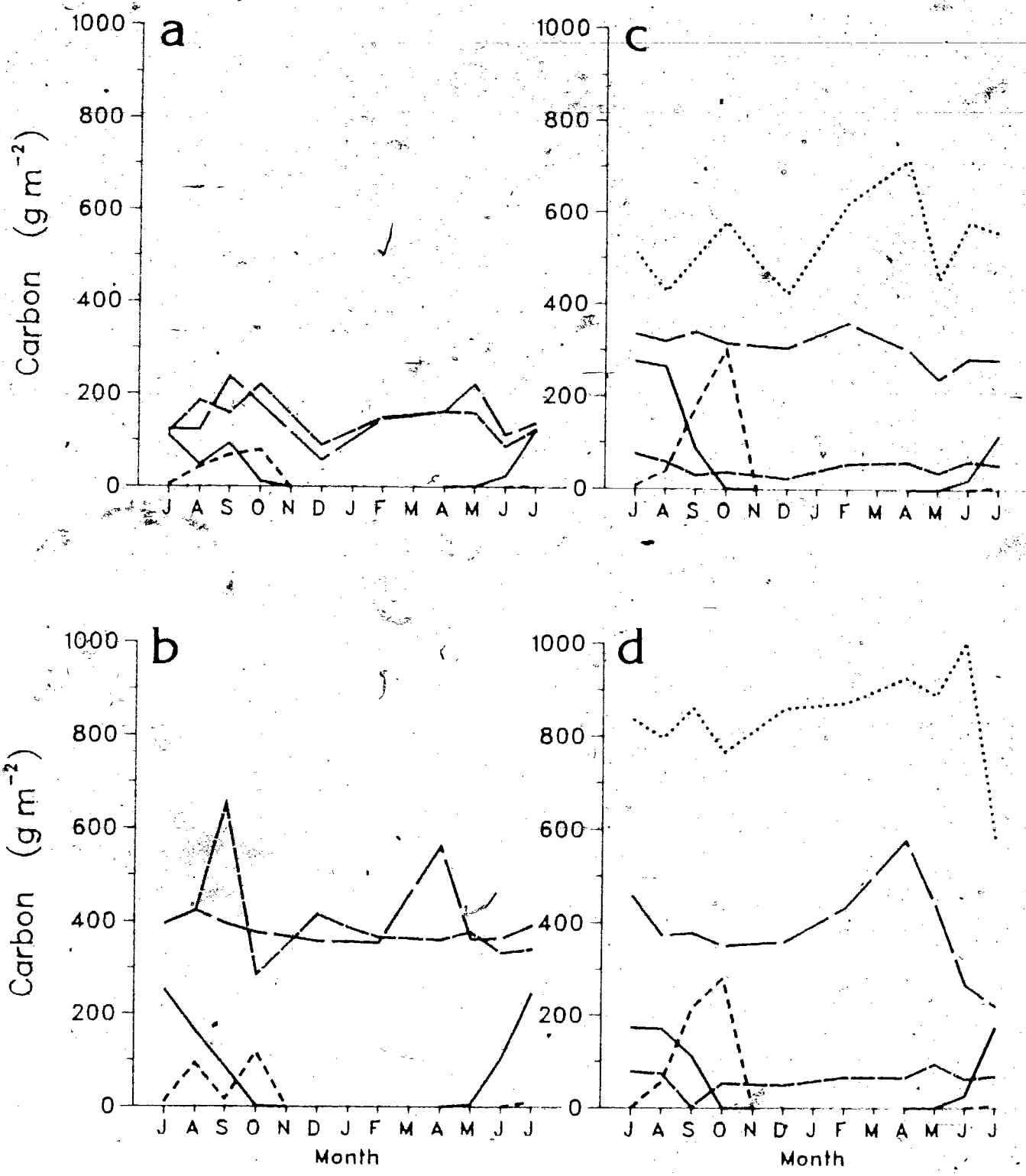

Figure 24. Mean carbon accumulation in photosynthetic shoots (———), dead shoots (- - - - - -), roots (— — —), rhizomes (— · — · —) and corms (·····) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

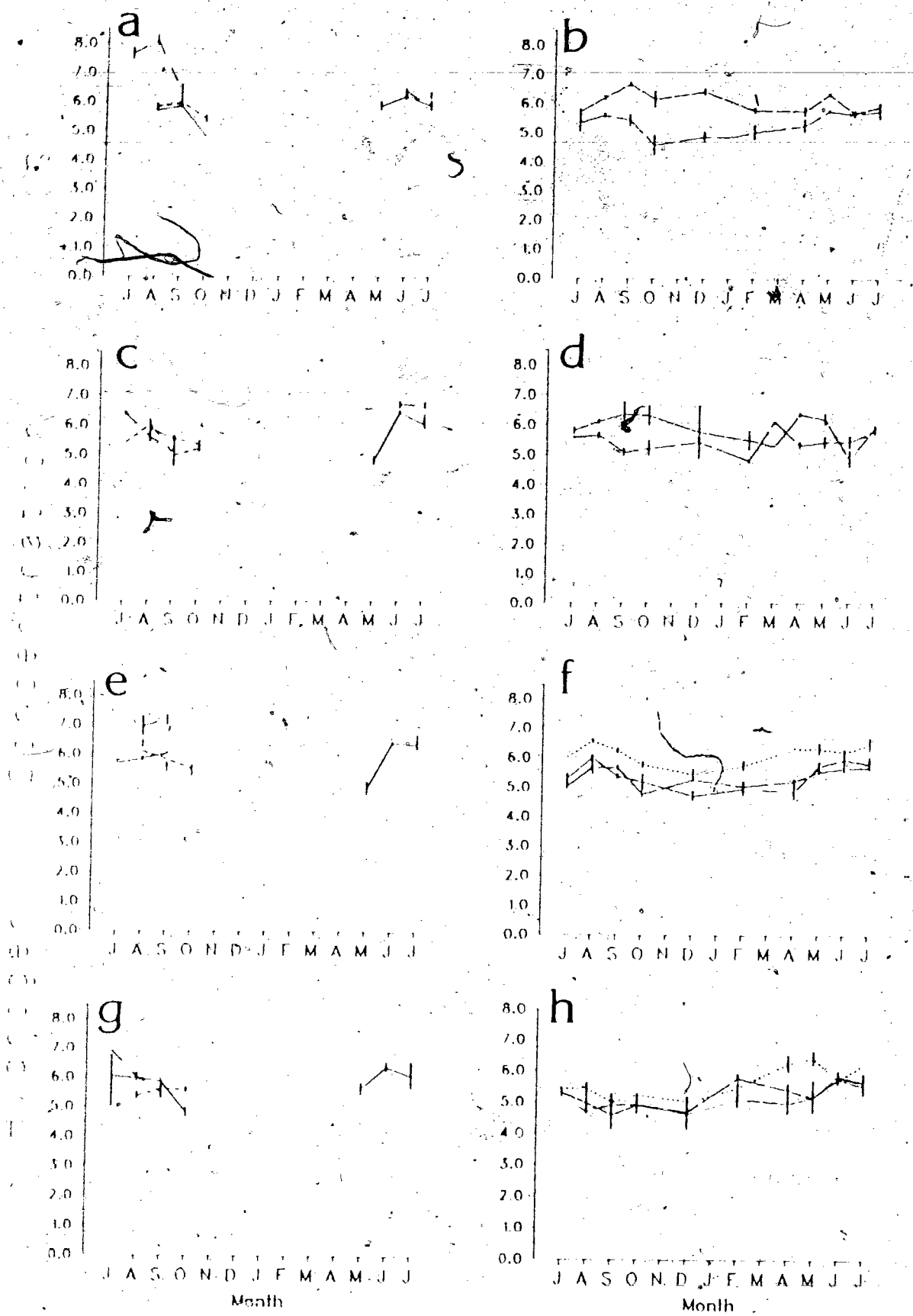

Figure 25. Hydrogen concentrations ($\bar{x} \pm 1sc$) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (------), roots (— — —), rhizomes (————) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

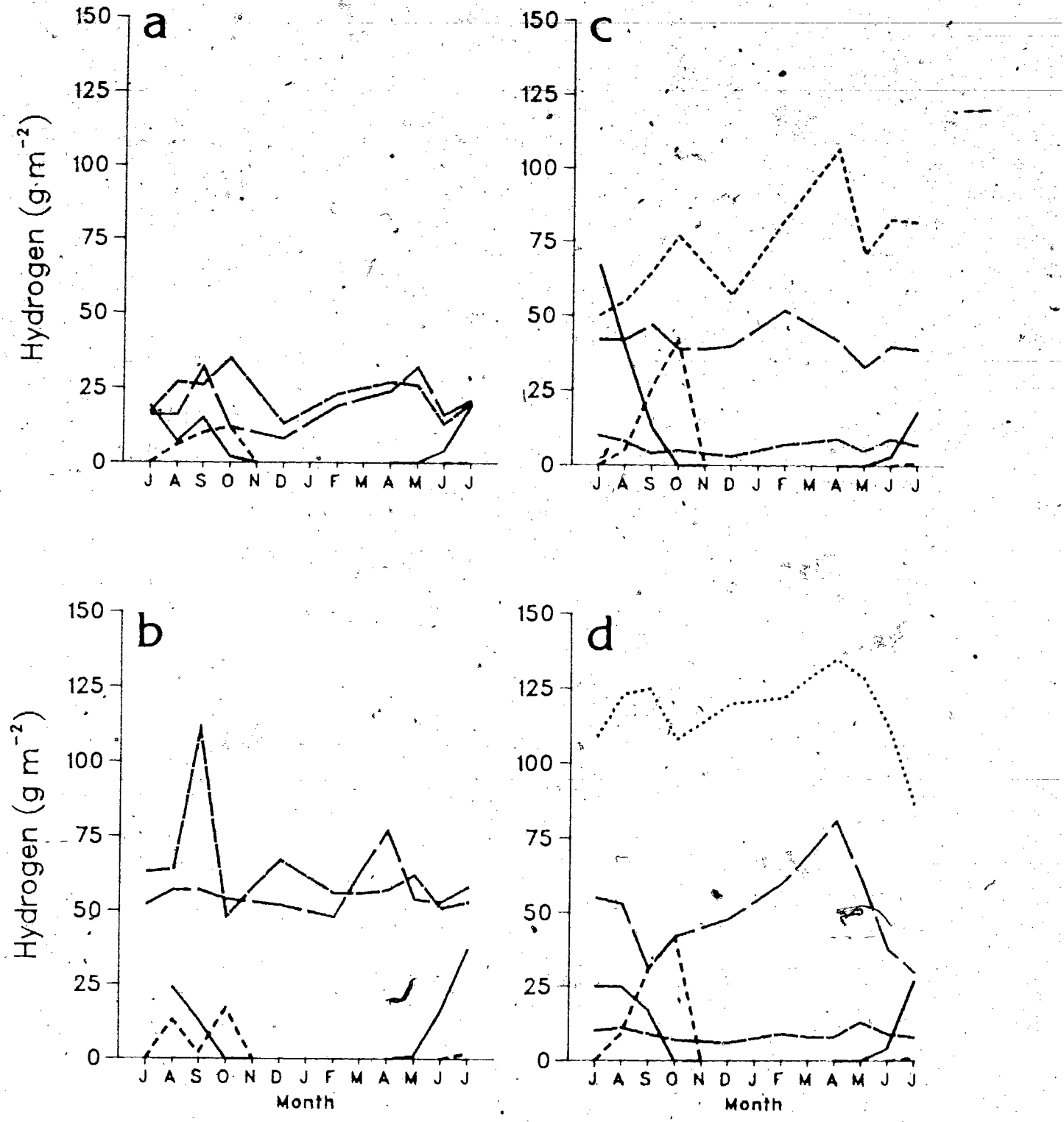

Figure 26. Mean hydrogen accumulation in photosynthetic shoots (———), dead shoots (- - - - - -), roots (—— ——), rhizomes (—— — ——) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

Calcium

In contrast to N and P concentration which decreased as the plants matured, Ca concentration in shoots showed little change throughout the year (Figures 27). Dead shoots had higher Ca concentrations than live shoots in three environments, increasing from mid-summer to fall in *S. americanus* but remaining constant in *S. maritimus*. In low marsh *S. maritimus*, Ca concentration of dead shoots was equivalent to that of live shoots and remained constant throughout the growing season.

Roots in high marsh *S. americanus* had small changes in Ca concentration during the year, but low marsh roots had a marked increase in Ca concentration in December (maximum of 2.08% Ca), declining thereafter to 0.75%. Rhizomes of low *S. americanus* had no significant seasonal variation.

In *S. maritimus*, roots had the highest Ca concentrations at all times with a mid-summer and winter maximums of 0.50% in the low marsh and 0.40% in the middle marsh. Minimum Ca concentrations in roots were measured in fall in both environments. Corms and rhizomes had much lower concentrations (Table 7).

Accumulation of Ca was greater in dead shoots than in live shoots especially in *S. maritimus* environments (Figure 28). Calcium accumulation was greatest in roots in all environments, peaking in October and April in *S. americanus* and August and April in *S. maritimus*. Only rhizomes in low marsh *S. americanus* had a seasonal change in Ca concentration peaking in October concurrent with the sharp increase in Ca concentration.

Magnesium

Magnesium concentrations in shoots were highest at the beginning and end of the growing season in *S. americanus* and low marsh *S. maritimus* (Figure 29). Middle marsh *S. maritimus* shoots had a mean annual Mg concentration of ≈0.26% throughout the growing season, with a maximum of 0.47% in May. Inflorescences and dead shoots had a similar seasonal pattern and had a higher Mg concentration than photosynthetic tissues.

Belowground structures from all environments exhibited small seasonal variation in Mg concentration and generally had an equivalent Mg concentration than aboveground structures. High marsh *S. americanus* roots had no significant seasonal variation but roots in *S. maritimus* had lowest concentrations of Mg in early summer and fall.

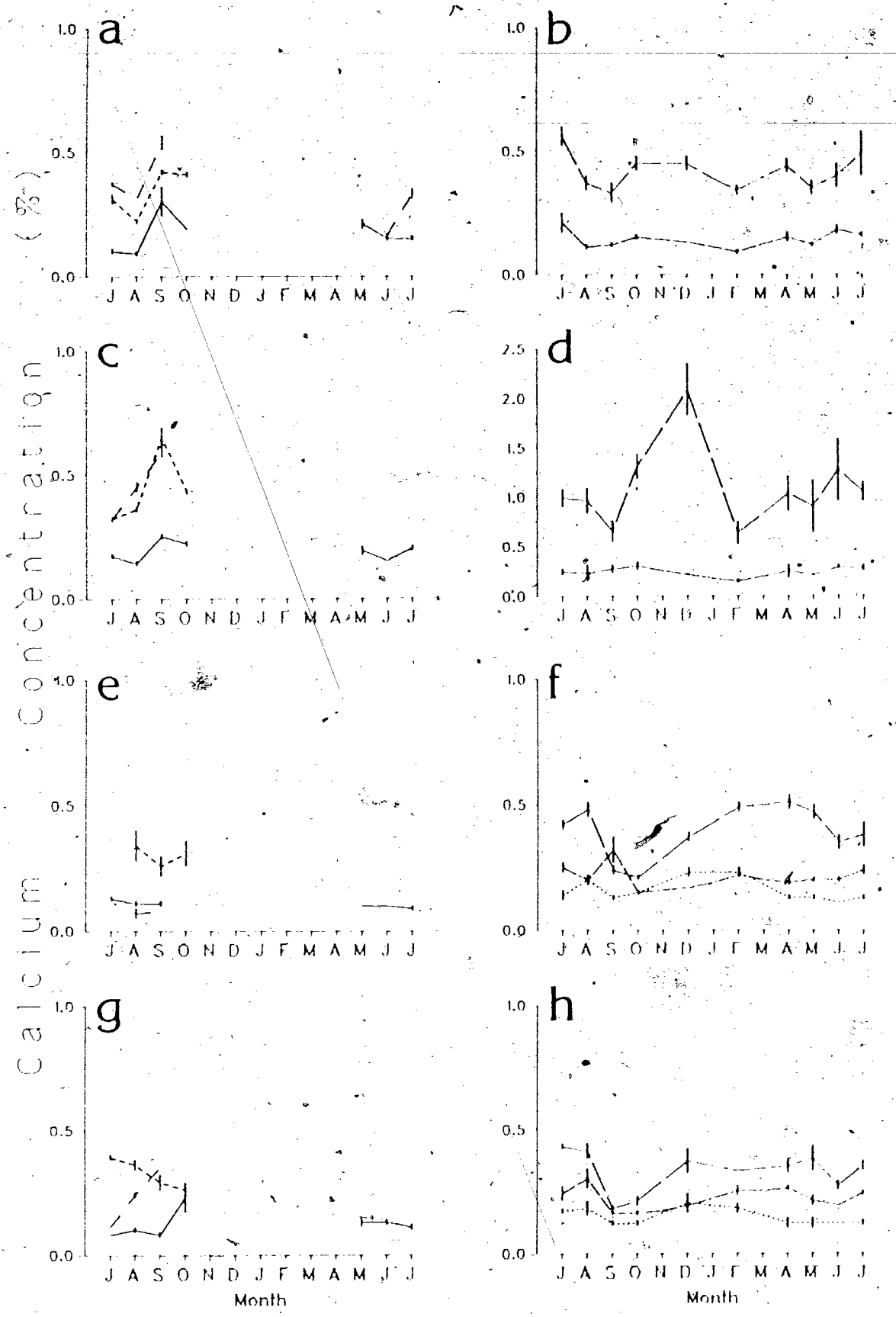

Figure 27. Calcium concentrations ($\bar{x}$ ± 1se) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — — —), rhizomes (— — — —) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

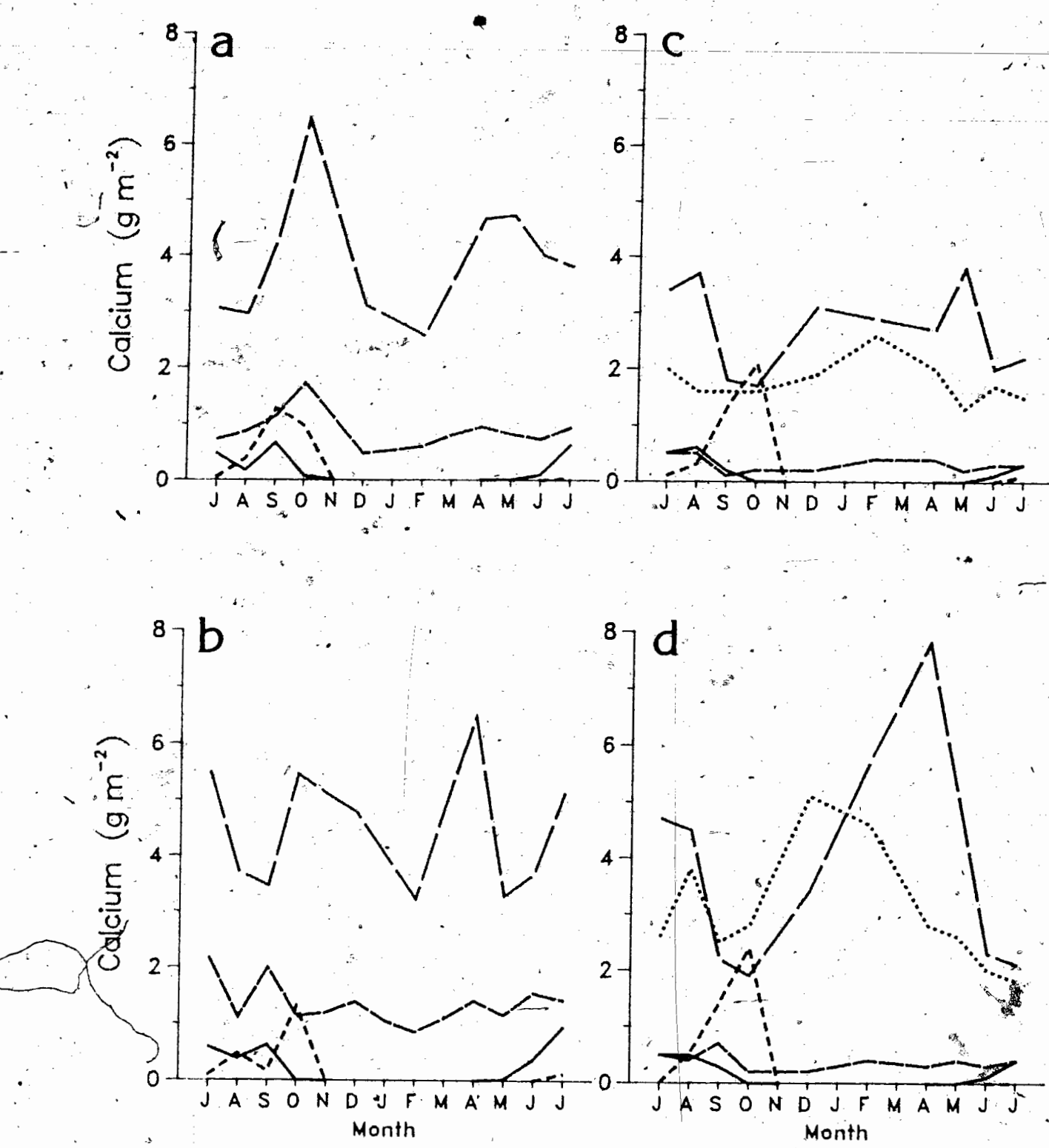

Figure 28. Mean calcium accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — —), rhizomes (— — — —) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

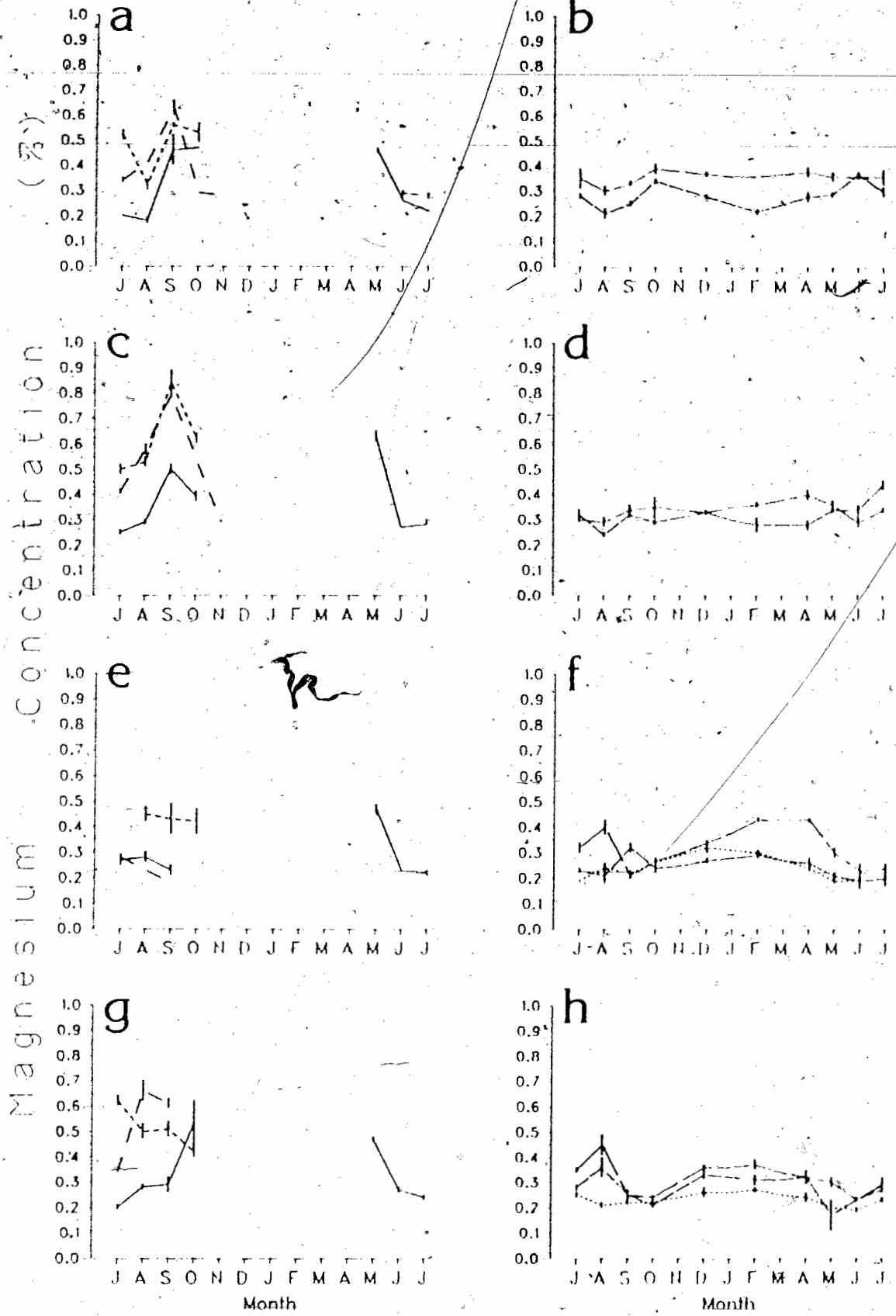

Figure 29. Magnesium concentrations ($\bar{x}$ ± 1se) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (------), roots (———), rhizomes (————) and corms (.....) of low marsh (a, b) and high marsh (c, d) *S. americanus* and, low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

Maximum Mg accumulation in live shoots was in August compared to September/ October for dead shoots (Figure 30). For belowground structures of *S. americanus*, accumulation increased in fall with a rapid decline in early winter. Accumulation increased thereafter, peaking in April/May. In *S. maritimus*, corms had marked seasonal changes in Mg accumulation, particularly in the middle marsh. Accumulation in roots of middle marsh *S. maritimus* was similar to that of corms but the maximum accumulation was attained in April. Rhizomes in low and middle marsh environments had two small peaks in August and April/May. All peaks of Mg accumulation in belowground structures were a result of biomass changes as Mg concentrations in belowground structures were similar throughout the year.

Potassium

Photosynthetic tissues of *S. americanus* and *S. maritimus* (Figure 31) had significantly higher concentrations of K than inflorescences and dead shoots but all aboveground structures had peak K concentration in July. Belowground structures of both species had constant K concentrations throughout the year. *S. americanus* rhizomes in both environments had significantly higher K concentrations than roots. The highest K concentrations in belowground structures of *S. maritimus* were in corms (Table 7).

The greatest K accumulation was in photosynthetic tissues in July in all environments (Figure 32). Dead shoots had a much lower maximum K accumulation in October. There was little seasonal variation in K concentrations of belowground structures and thus the few peaks that occured in accumulation can be attributed to biomass variation.

Sodium

There was no consistent seasonal patterns in Na concentrations between similar structures from different environments. Sodium concentration of high and low marsh *S. americanus* shoots decreased from May to July and then increased from July to October (Figure 33). The Na concentration of inflorescences and dead shoots was significantly less than in photosynthetic tissues. Sodium concentrations of roots and rhizomes of *S. americanus* were also much less than live shoots. Rhizomes had significantly higher concentrations compared to roots and had distinct peaks in July and December in the low marsh.

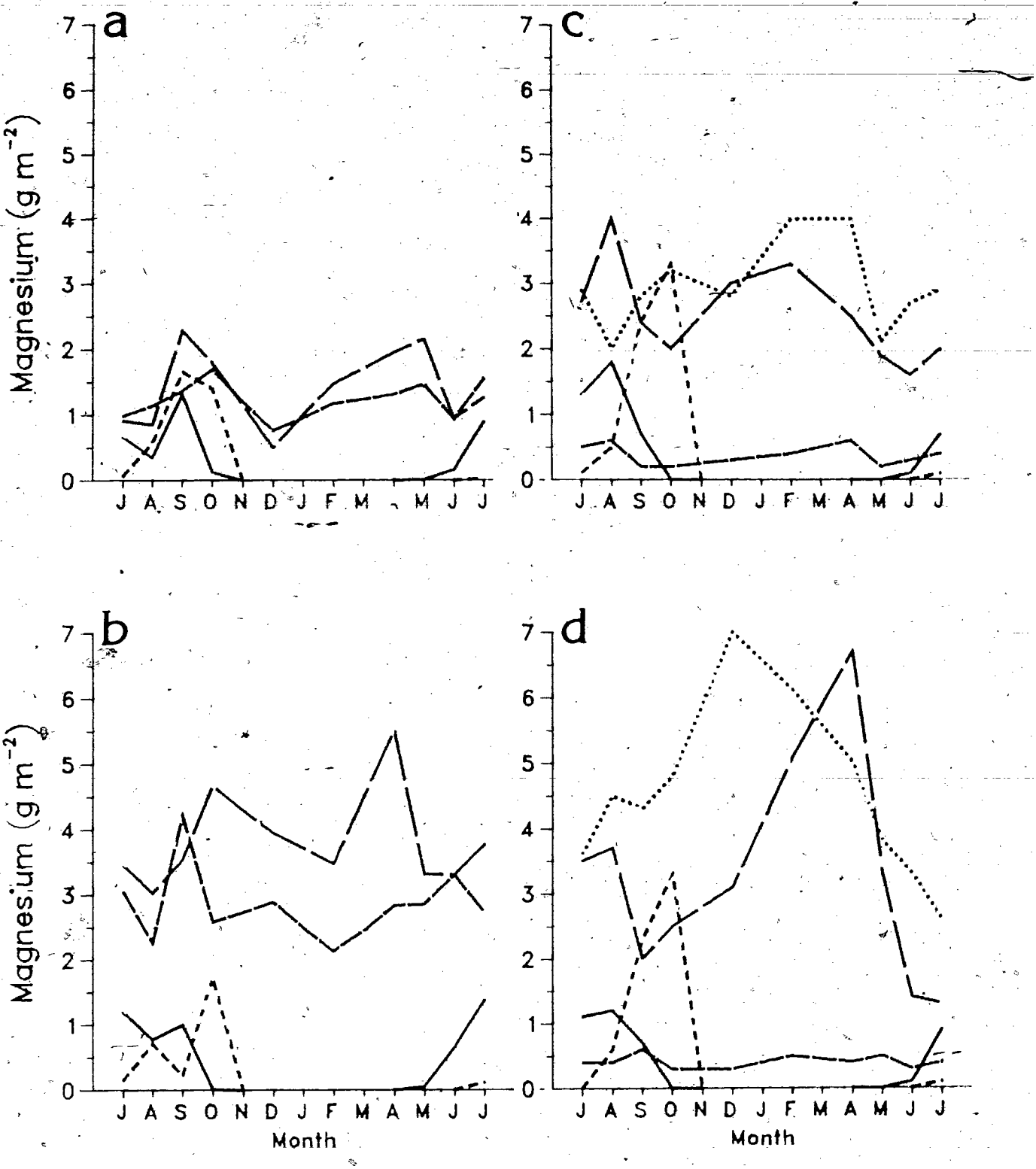

Figure 30. Mean magnesium accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (—— — ——) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

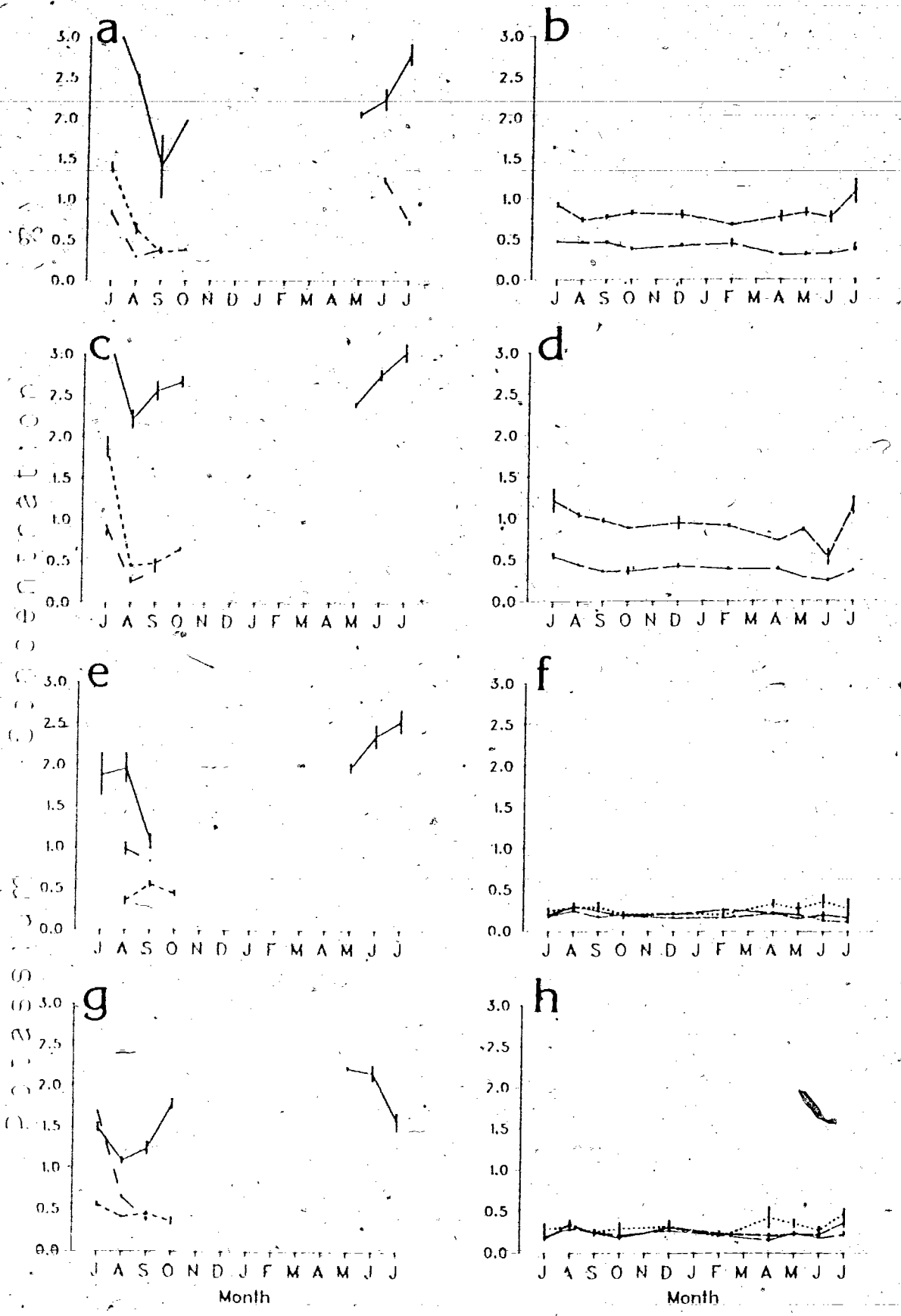

Figure 31. Potassium concentrations ($\bar{x} \pm 1se$) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - -), roots (———), rhizomes (———) and corms (.....) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

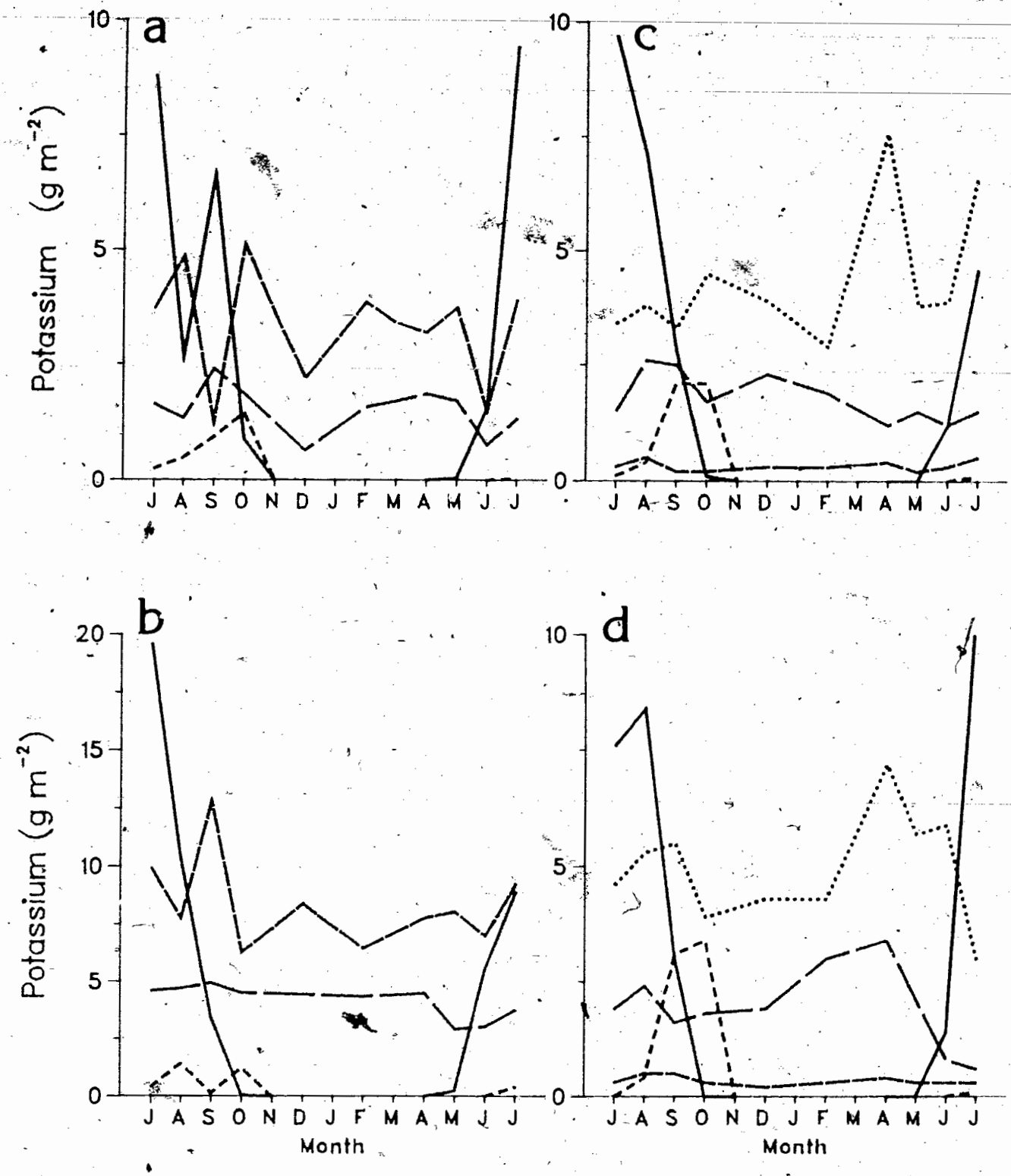

Figure 32. Mean potassium accumulation in photosynthetic shoots (————), dead shoots (- - - - -), roots (—— ——), rhizomes (—— —— ——) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

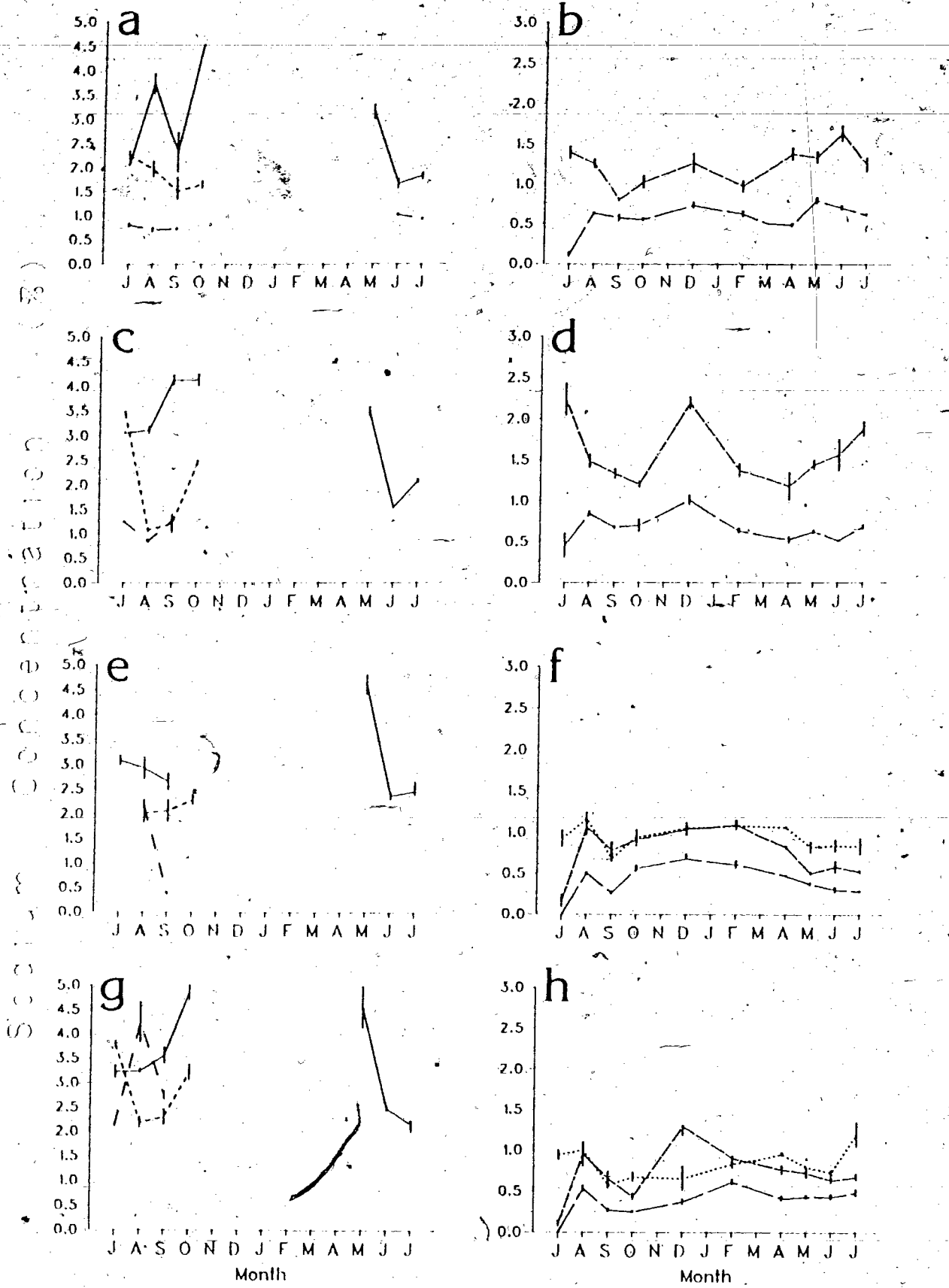

Figure 33. Sodium concentrations ($\bar{x} \pm 1se$) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (———·———), rhizomes (————) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

There was little correspondence in Na concentration of aboveground structures between low and middle marsh *S. maritimus* (Figure 33). Whereas middle marsh shoots had only one peak in May (4.61% Na), low marsh shoots had a peak in May (4.55% Na) and a second peak in October (4.86% Na), similar to *S. americanus* shoots. As well, in the middle marsh, Na concentrations of inflorescences and dead shoots were less than that of shoots. Inflorescences and dead shoots from the low marsh had maximum Na concentrations equal to that of shoots but at other times of the year had lower Na concentrations. Belowground structures of *S. maritimus* had Na concentrations an order of magnitude less than in photosynthetic tissue and generally showed no seasonal pattern. Corms and rhizomes rhizomes had higher mean annual Na concentrations than roots (Table 7).

Similar to K, live shoots of *S. americanus* had the greatest accumulation of Na, the exception being middle marsh *S. maritimus* (Figure 34). In this environment and in low marsh *S. maritimus*, dead shoots had equal or greater Na accumulation. Dead *S. americanus* shoots had much lower accumulation of Na than live shoots. Sodium accumulation in *S. americanus* belowground structures was relatively constant throughout the year. By contrast, corms and roots of middle marsh *S. maritimus* had greatest Na accumulation in winter. In the low marsh, corms had large fluctuations and roots had maximum accumulation in August and February.

Aluminum

Aluminum concentrations were highest in dead shoots and lowest in photosynthetic tissues in all environments (Figure 35). The temporal pattern of Al concentration in aboveground structures of *S. americanus* was similar in low and high marsh environments. Maximum concentrations were measured in September, the structures of low marsh plants having significantly higher levels of Al than high marsh.

S. americanus roots and rhizomes had contrasting seasonal patterns. Roots had significantly higher levels of Al with distinct peaks in August and February. The lowest concentrations of Al in roots in fall coincided with the highest levels measured in rhizomes and in aboveground structures.

Middle marsh *S. maritimus* shoots had the highest concentration of Al in shoots from the four environments (Table 7). The highest mean monthly Al concentration measured was

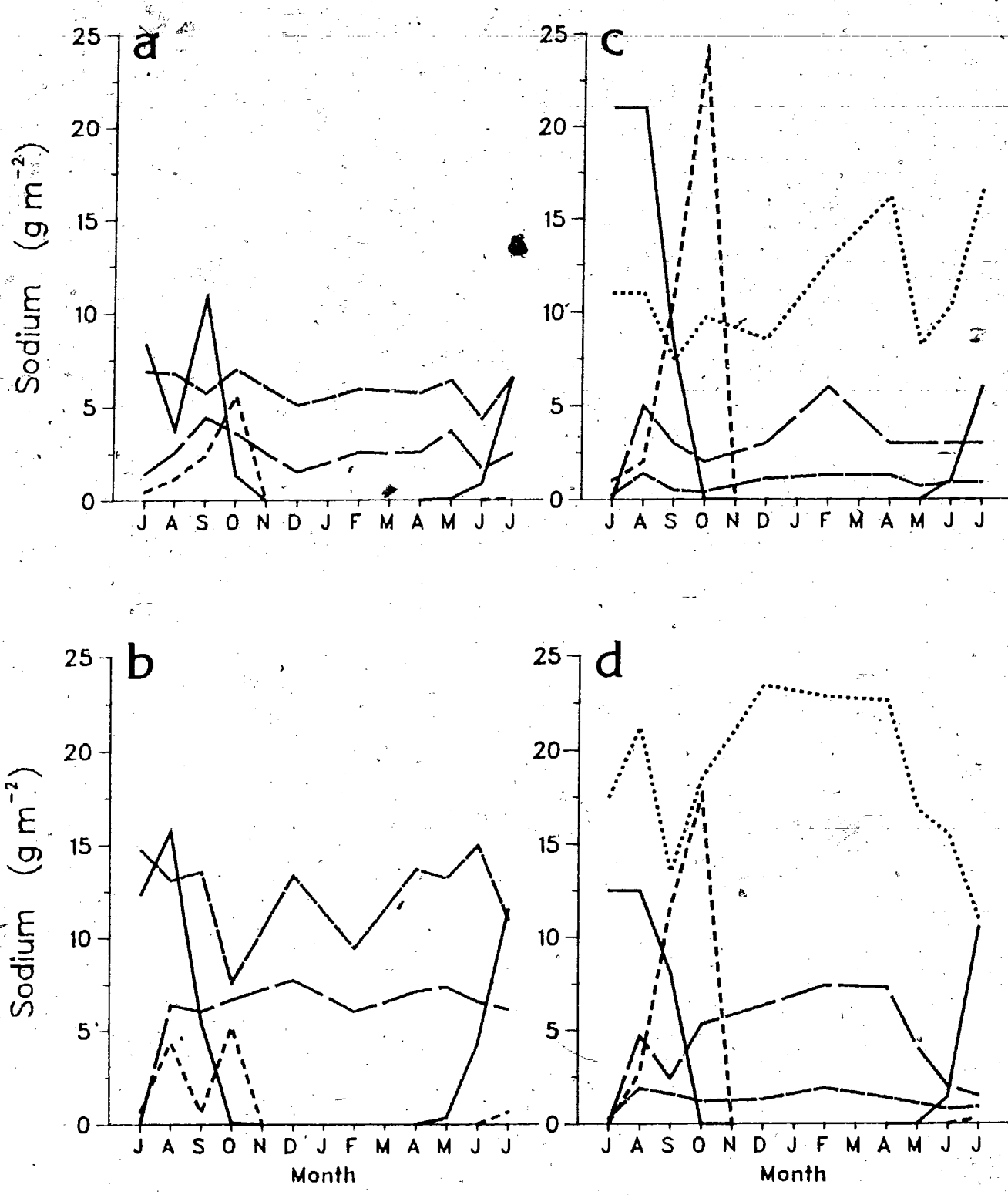

Figure 34. Mean sodium accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — —), rhizomes (— — — —) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

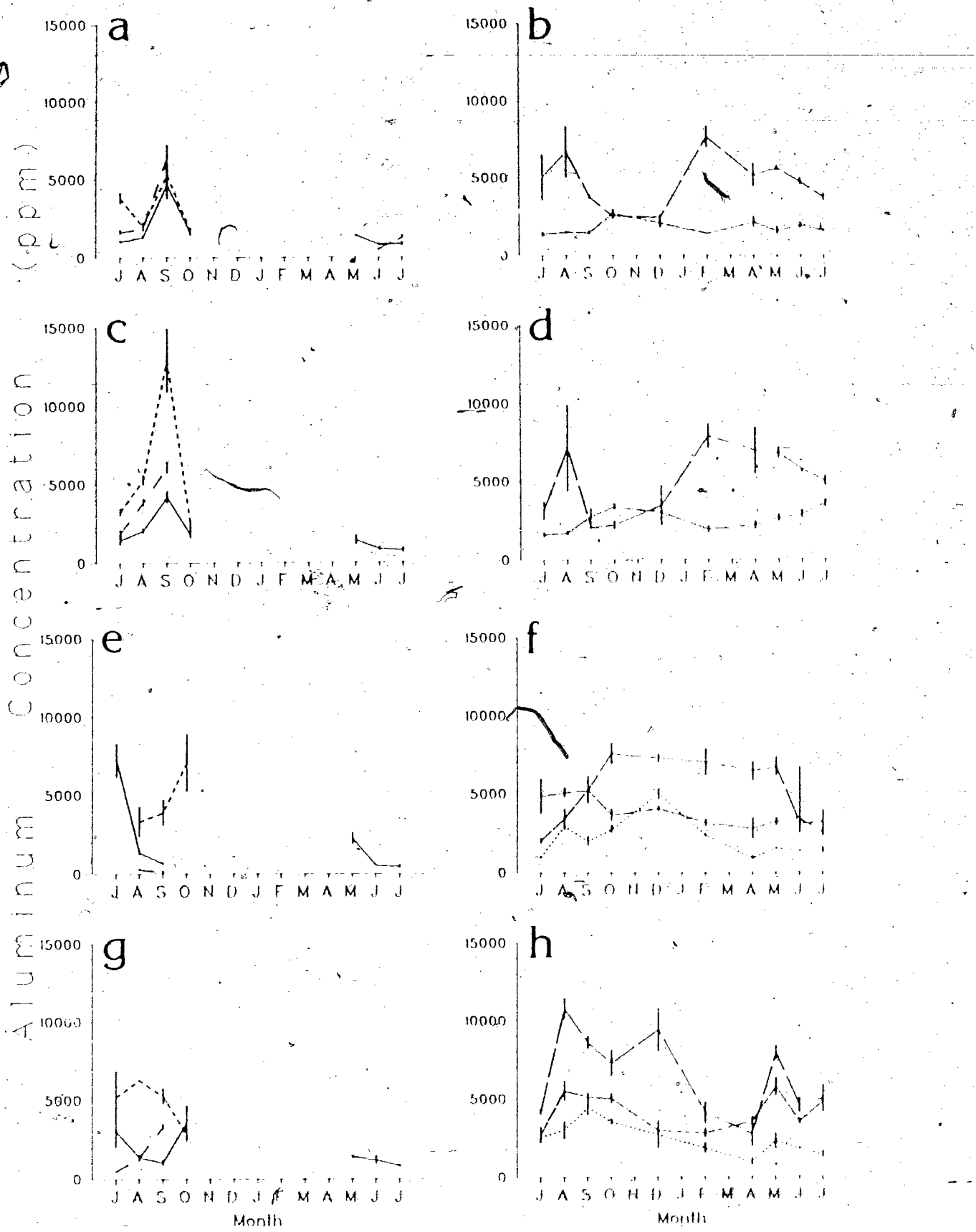

Figure 35. Aluminum concentrations ($\bar{x} \pm 1sc$) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (—·—·—) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

in July 1985, the measurements made the following year being much lower (Figure 35). Dead shoots increased in Al content as the growing season progressed and generally had the highest concentrations. Inflorescences had very low Al concentrations of under 500 ppm. There was no significant seasonal change in Al concentration of live and dead shoots in low marsh *S. maritimus*.

Roots from low and middle marsh *S. maritimus* had the highest concentrations of Al with maximum levels measured in winter (Table 7, Figure 35). Rhizomes in the low marsh and corms in the middle marsh also had winter maximums in Al concentration.

Aluminum accumulation in aboveground structures was greatest in dead shoots but these levels were much less than in belowground compartments (Figure 36). There was no consistent trend in belowground Al accumulation between environments. Low marsh *S. americanus* rhizomes peaked in October compared to late winter for roots in this environment. In high marsh *S. americanus*, rhizomes had no seasonal variation but roots had two marked peaks, one in August and a second in late winter. For *S. maritimus*, corms in both environments had clear peaks but the timing of these peaks was different. Maximum Al accumulation was in September in the low marsh and December in the middle marsh. Roots in low marsh *S. maritimus* had several peaks throughout the year, the highest occuring in August, compared to April in the middle marsh. These patterns of Al accumulation were similar to those of Al cocentration.

Iron

The pattern of Fe concentration in aboveground and belowground structures of *S. americanus* and *S. maritimus* (Figure 37) mirrored that of Al. Highest concentrations were measured at the end of the growing season and in dead shoots.

Iron concentrations were an order of magnitude greater in belowground structures than aboveground and roots had the highest concentrations. Roots and rhizomes of *S. americanus* had lowest levels from October to December. Low *S. maritimus* corms and middle marsh rhizomes did not have significant seasonal variation in Fe concentration. The high variation of *S. maritimus* belowground structures masked any seasonal trends.

Belowground structures had much greater Fe accumulation than aboveground (Figure 38) and maximum levels occured at the time of maximum Fe concentration. *S. americanus* roots

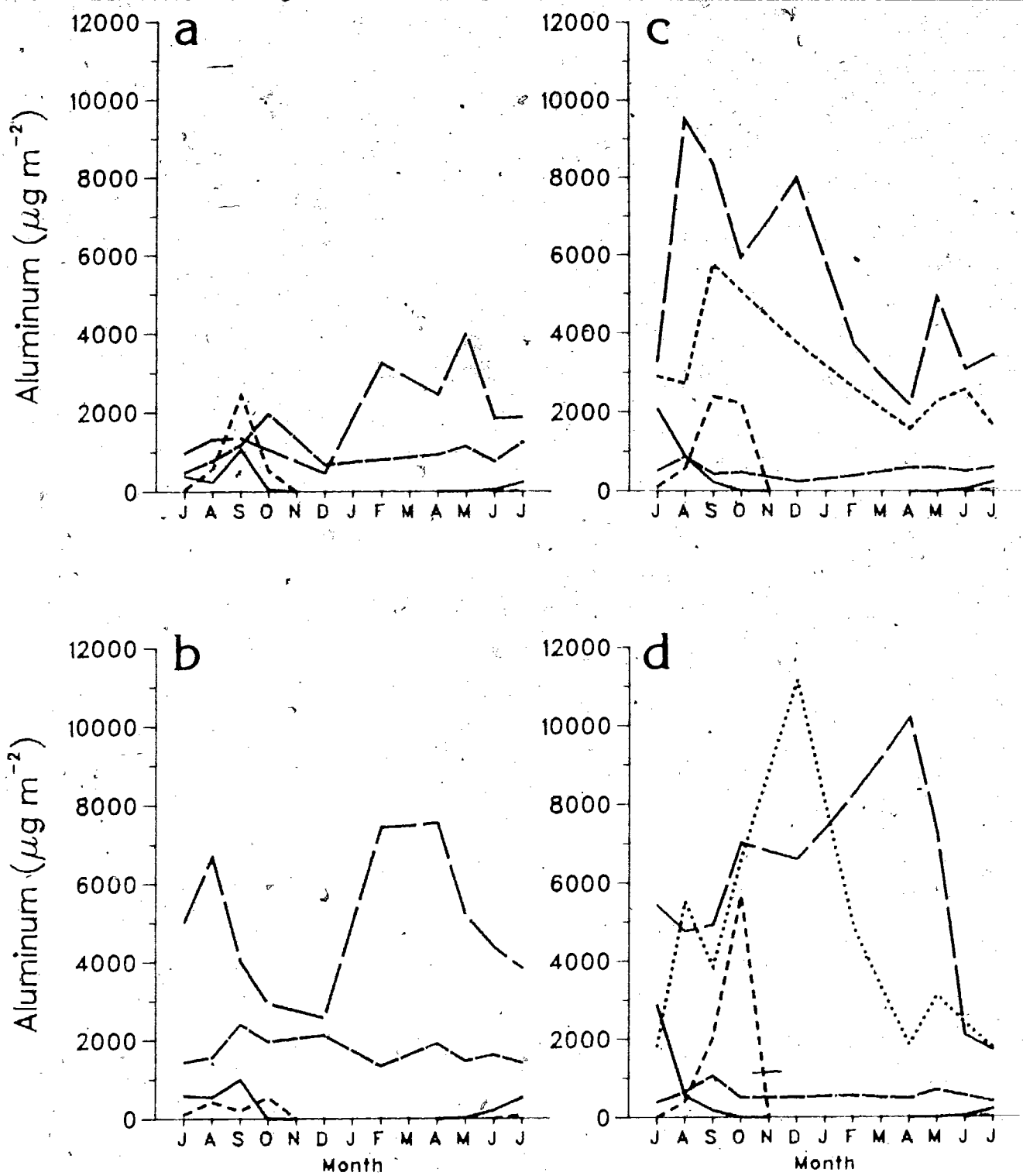

Figure 36. Mean aluminum accumulation in photosynthetic shoots (———), dead shoots (- - - - - -), roots (—— ——), rhizomes (—— —— ——) and corms (·····) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

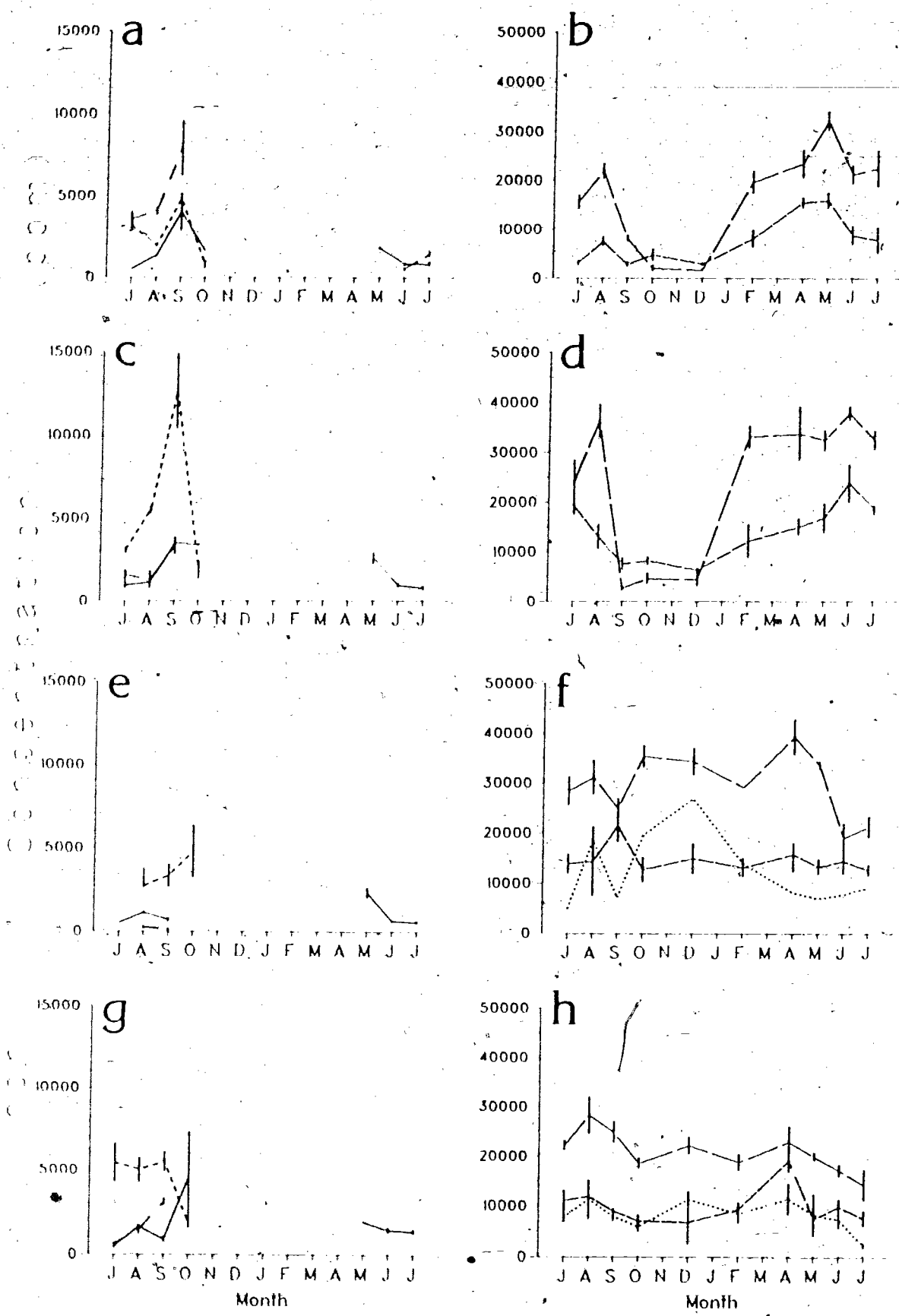

Figure 37. Iron concentrations ($\bar{x}$ ± 1se) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — —), rhizomes (— — — —) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

and rhizomes had greatest accumulation in August and April/May. For *S. maritimus*, accumulation in roots was opposite that of corms. Low marsh roots had greatest values in fall and corms had maximum values in spring. In the middle marsh, Fe accumulation in roots peaked in April and in December in corms. As with Al, Fe accumulation patterns mirrored that of Fe concentrations in these tissues.

Manganese

Manganese concentration of *S. americanus* aboveground structures increased during the growing season (Figure 39). Live and dead shoots had similar levels in both the high and low marsh environments. Inflorescences of the low marsh had the lowest levels. Roots and rhizomes had much lower concentrations than aboveground structures (Table 7).

Manganese concentration of live shoots of middle marsh *S. maritimus* and dead shoots of low marsh *S. maritimus* did not vary with time (Figure 39). Only shoots of low marsh *S. maritimus* showed clear seasonal trends with lowest levels during summer. Highest mean annual Mn concentrations in belowground structues were in roots, greatly exceeding those of rhizomes and corms (Table 7 and Figure 39).

Manganese accumulation patterns were variable between environments (Figure 40). In low marsh *S. americanus*, aboveground tissues had the greatest accumulation of Mn, with live and dead shoots having similar maximum levels and the timing of these maximums. Roots and rhizomes in this environment had maximum Mn accumulations in April.

In high marsh *S. americanus*, roots had the greatest accumulation of Mn, peaking in mid-summer and April. Rhizomes had a similar pattern but with lower accumulation levels. Aboveground accumulation was greatest in live shoots until October when dead shoots had the greatest accumulation.

Patterns of Mn accumulation in aboveground structures of *S. maritimus* were similar for the two environments. Live shoots had the greatest accumulation levels until September/ October when Mn accumulation increased in dead shoots. Belowground, roots had the greatest Mn accumulation. Since concentration of belowground structures was constant throughout the year, the fall and spring peaks in corms and roots was a result of greater biomass of these structures.

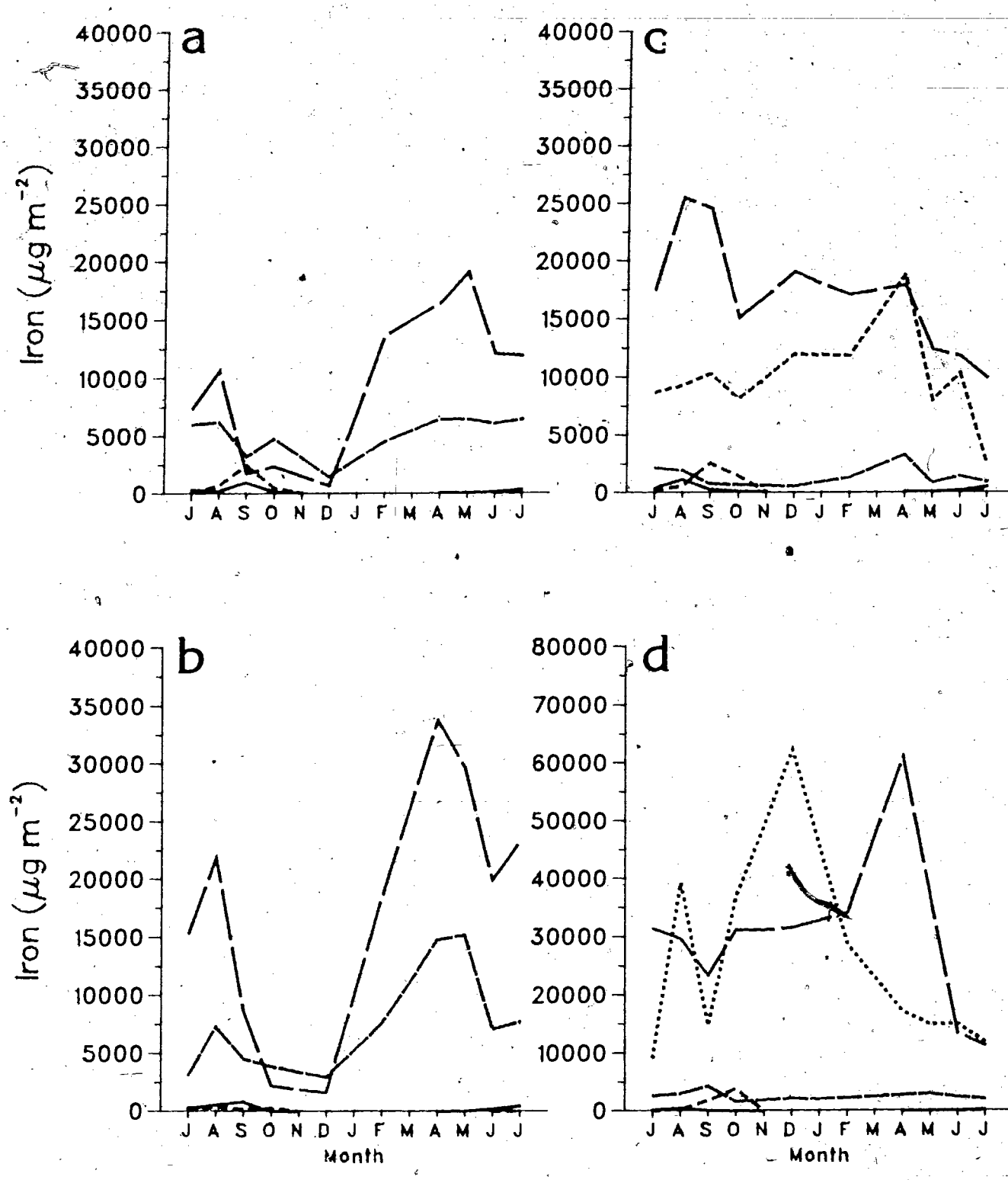

Figure 38. Mean iron accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (—— —— ——) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

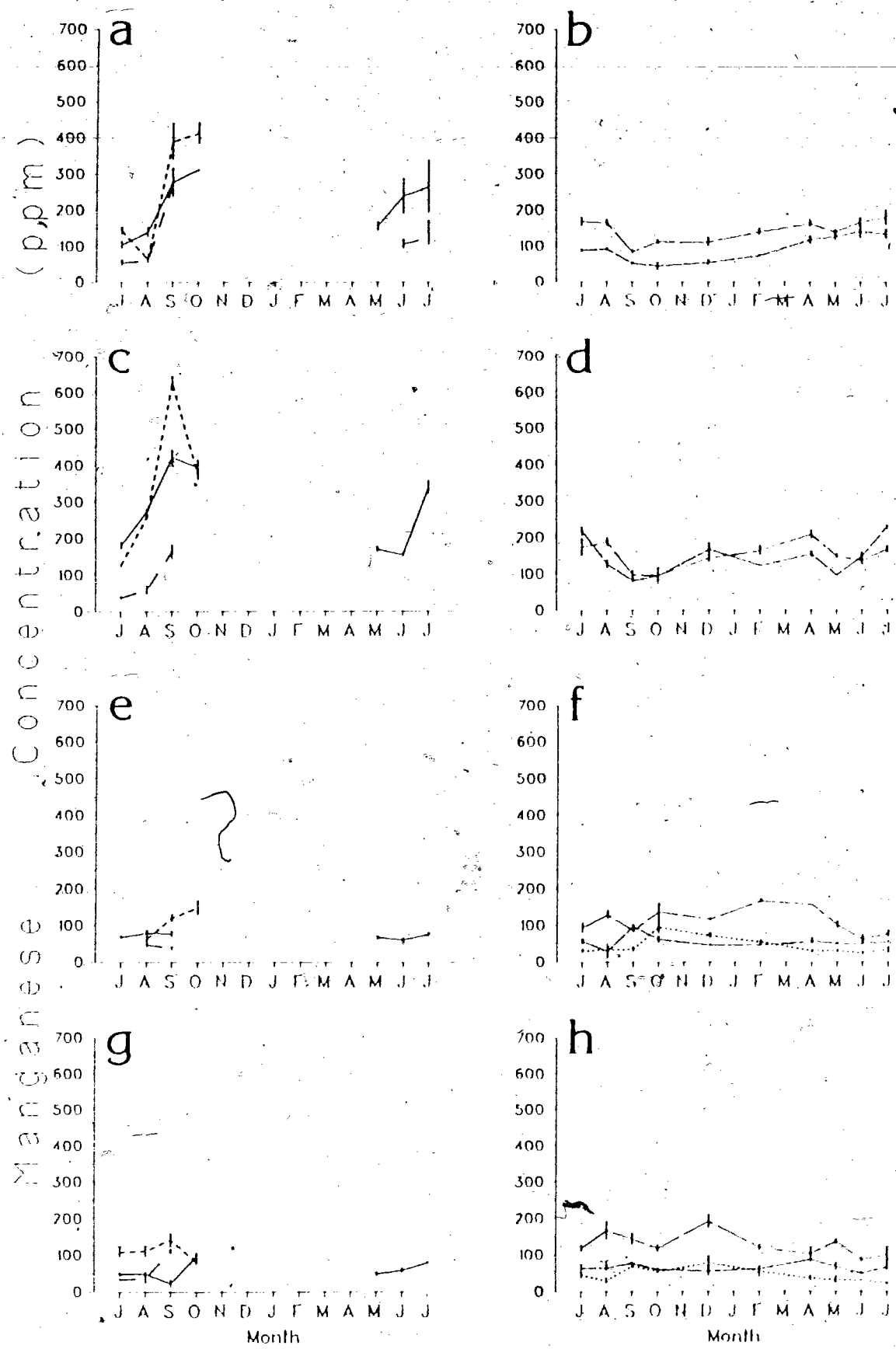

Figure 39. Manganese concentrations ($\bar{x} \pm$ 1se) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (————) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

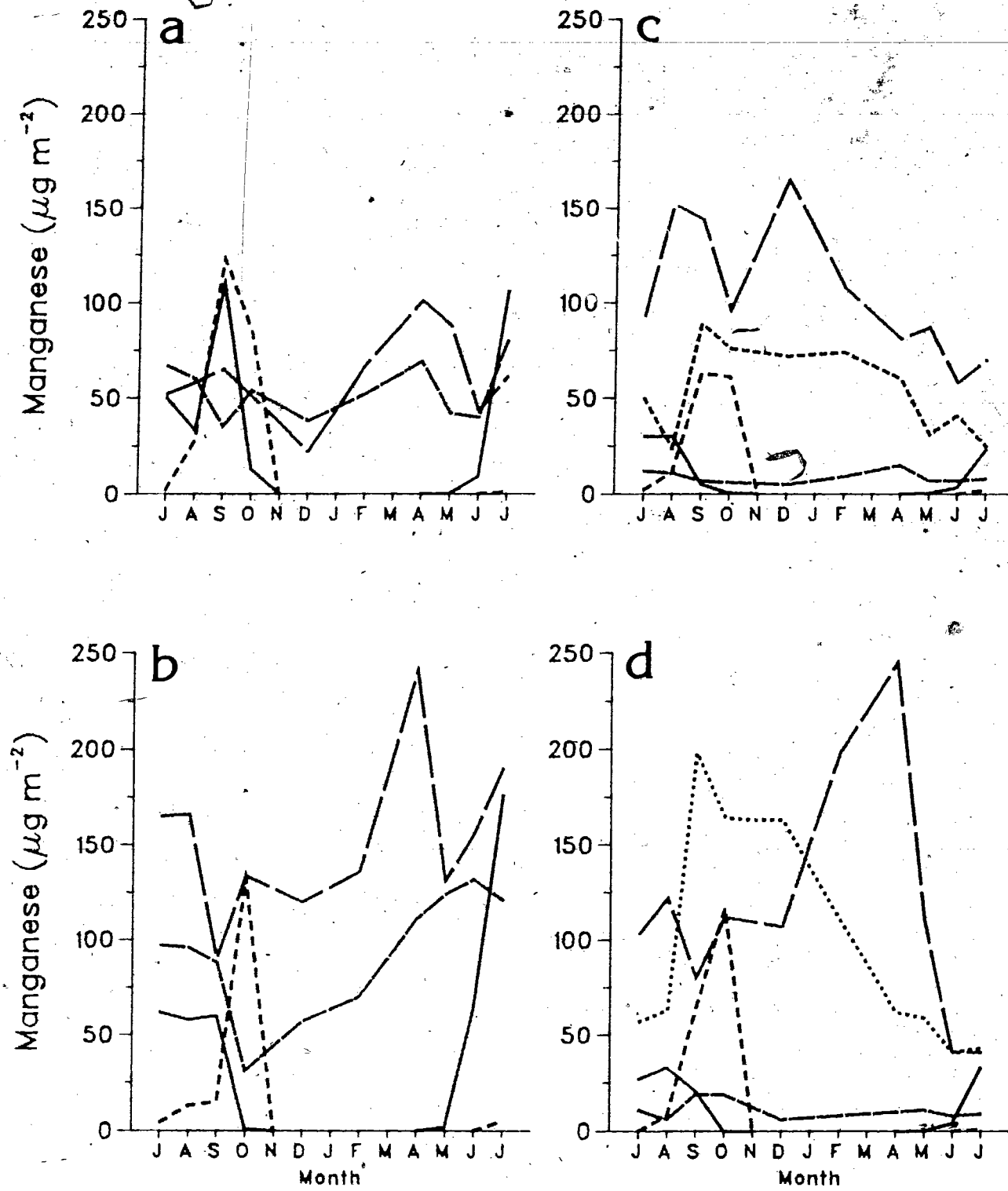

Figure 40. Mean manganese accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (————) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

Zinc

Zinc concentrations in aboveground structures were similar in *S. americanus* and *S. maritimus* (Figure 41). Flowers had the highest concentrations, peaking in autumn, with lowest concentrations measured in photosynthetic tissue. Roots had the highest concentrations of the belowground structures with maximum levels during winter. *S. maritimus* corms had a similar temporal pattern with roots but with lower concentrations. Low marsh *S. maritimus* rhizomes and *S. americanus* rhizomes had no significant seasonal changes in Zn concentration. Middle marsh *S. maritimus* rhizomes had highest levels in September and February.

Zinc accumulation was greatest in belowground plant structures in all environments (Figure 42). Live shoots had greater accumulation of Zn during the growing season when live shoot biomass exceeded dead shoot biomass. *S. americanus* roots had much greater Zn accumulation than rhizome but the timing of peaks was similar in both structures and in both environments. Peaks in late summer and again in early spring coincided with similar peaks in Zn concentration and biomass peaks. For *S. maritimus*, corms generally had the greatest accumulation throughout the year, with highest levels in winter. Maximum Zn accumulation in middle marsh roots was equivalent to that of corms.

Copper

S. americanus and *S. maritimus* aboveground structures had little change in Cu concentration during the growing season and these concentrations were much lower than that measured in belowground structures (Figures 43). *S. americanus* rhizomes and *S. maritimus* corms and rhizomes had Cu levels similar to aboveground structures and did not exhibit seasonal changes. Roots had the highest Cu concentrations with maximum levels in summer. This pattern was not as clear in low marsh *S. maritimus* roots.

Similar to the other trace metals, Cu accumulation was greatest in belowground structures when compared to aboveground structures (Figure 44). As well, roots in all environments had the greatest accumulation, peaking in mid-summer and spring. Furthermore, Cu accumulation in roots in July 1986 was much lower than that measured in July 1985 because of the much higher Cu concentrations measured in July 1985. In contrast to all other metals, Cu accumulation in *S. maritimus* corms was very low.

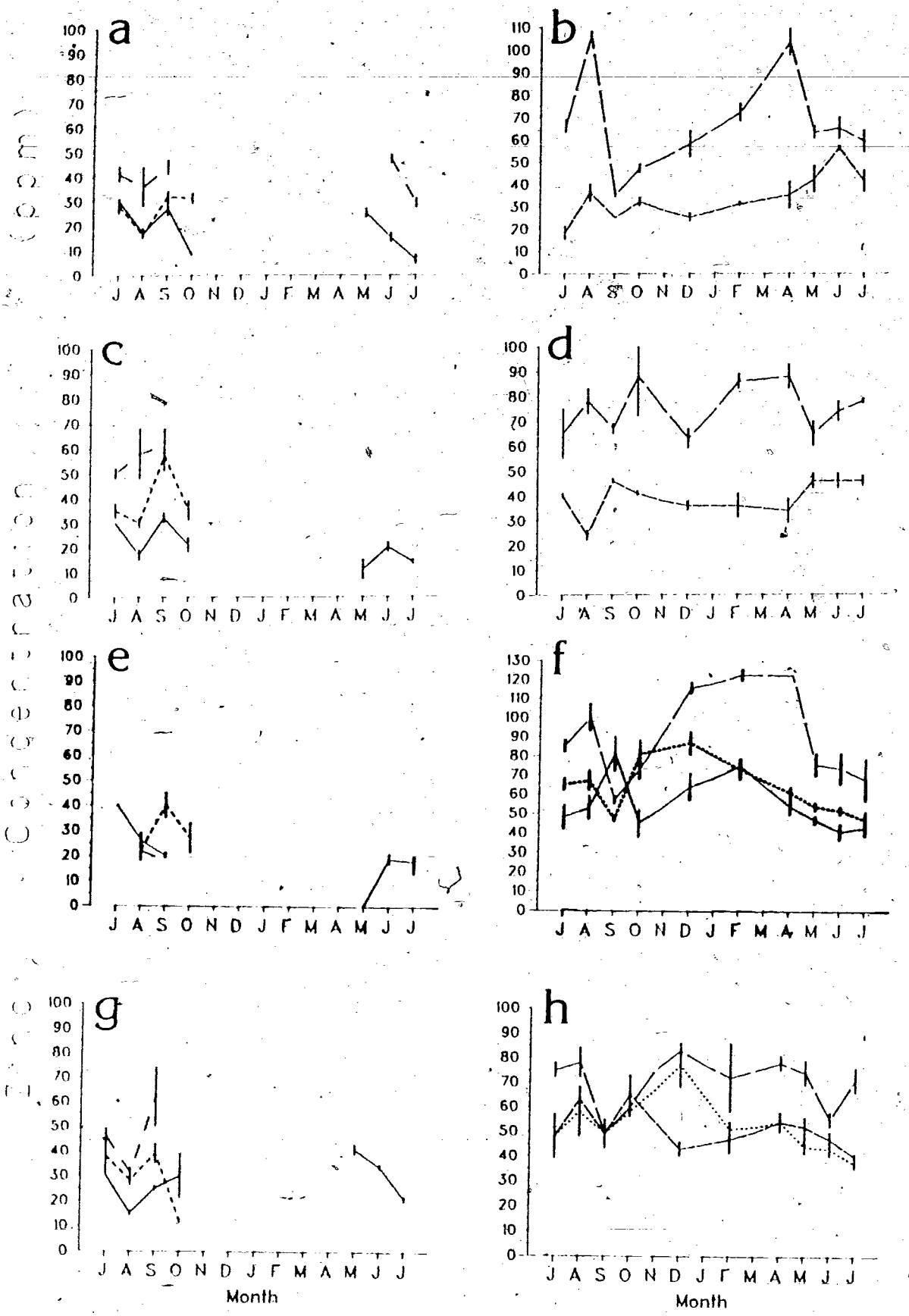

Figure 41. Zinc concentrations ($\bar{x} \pm 1se$) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (————) and corms (.....) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

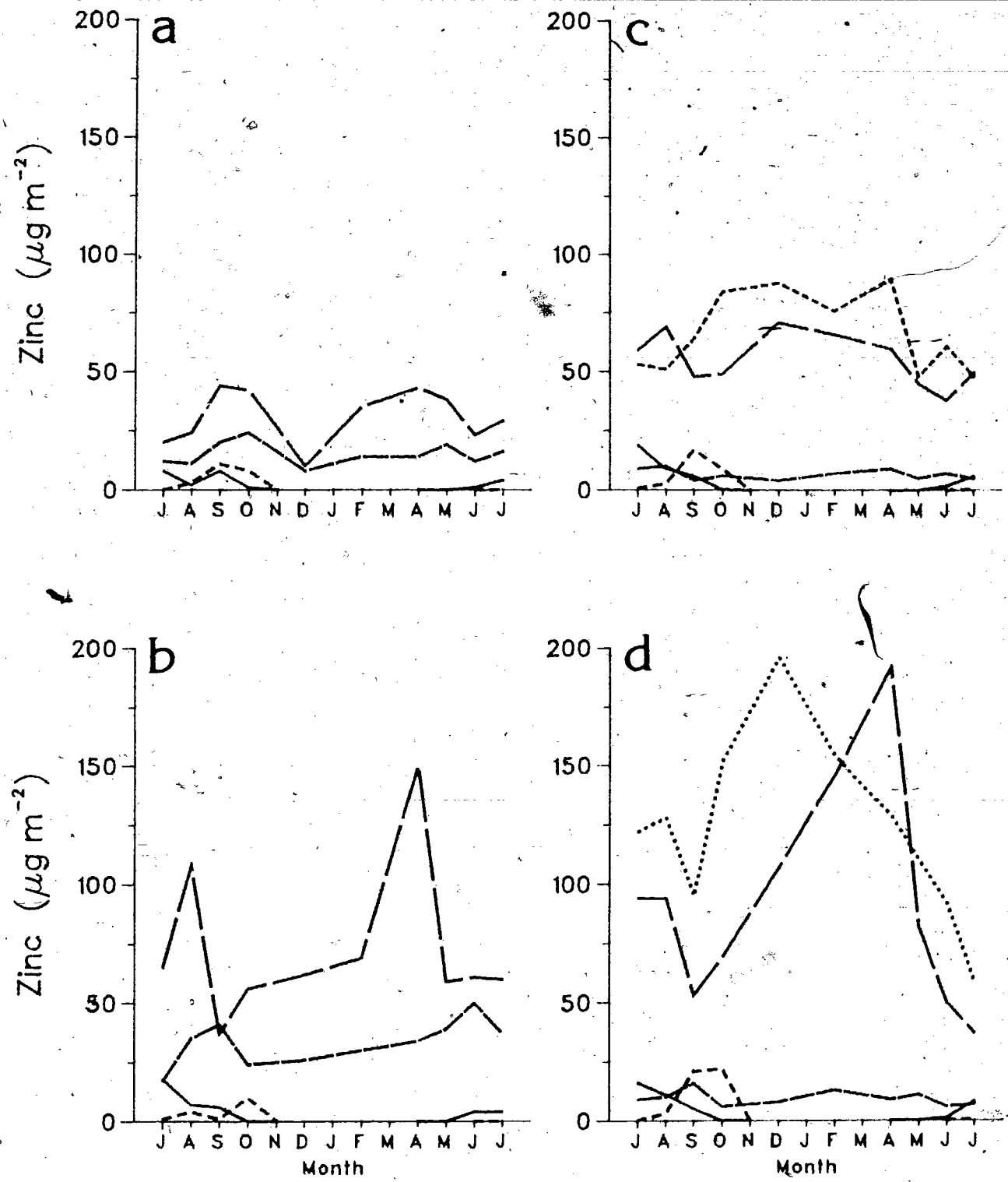

Figure 42. Mean zinc accumulation in photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — — —), rhizomes (————) and corms (.....) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

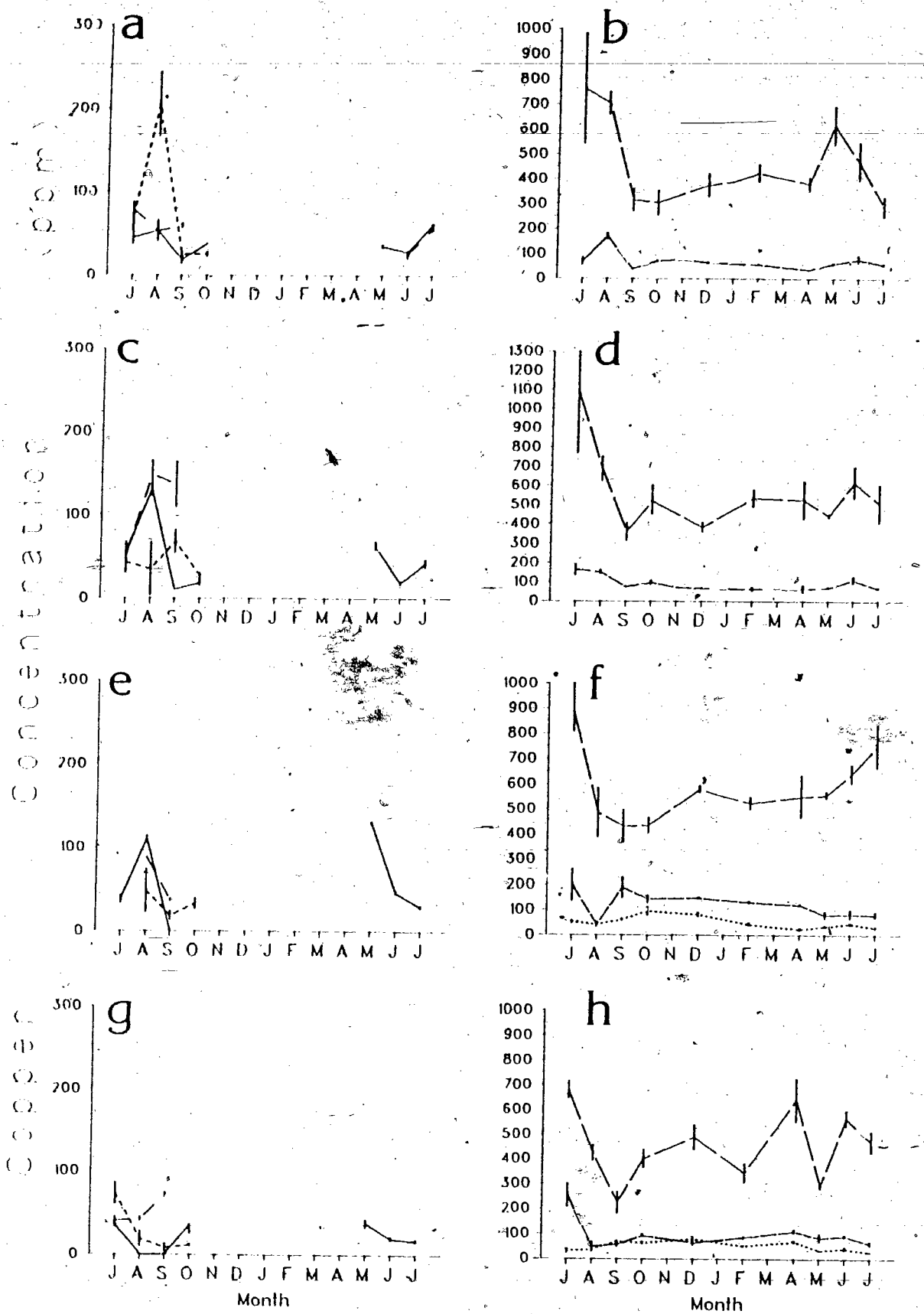

Figure 43. Copper concentrations ($\bar{x}$ ± 1sc) in inflorescences (— — —), photosynthetic shoots (————), dead shoots (- - - - - -), roots (————), rhizomes (————) and corms (·····) of low marsh (a, b) and high marsh (c, d) *S. americanus* and low marsh (e, f) and middle marsh (g, h) *S. maritimus*.

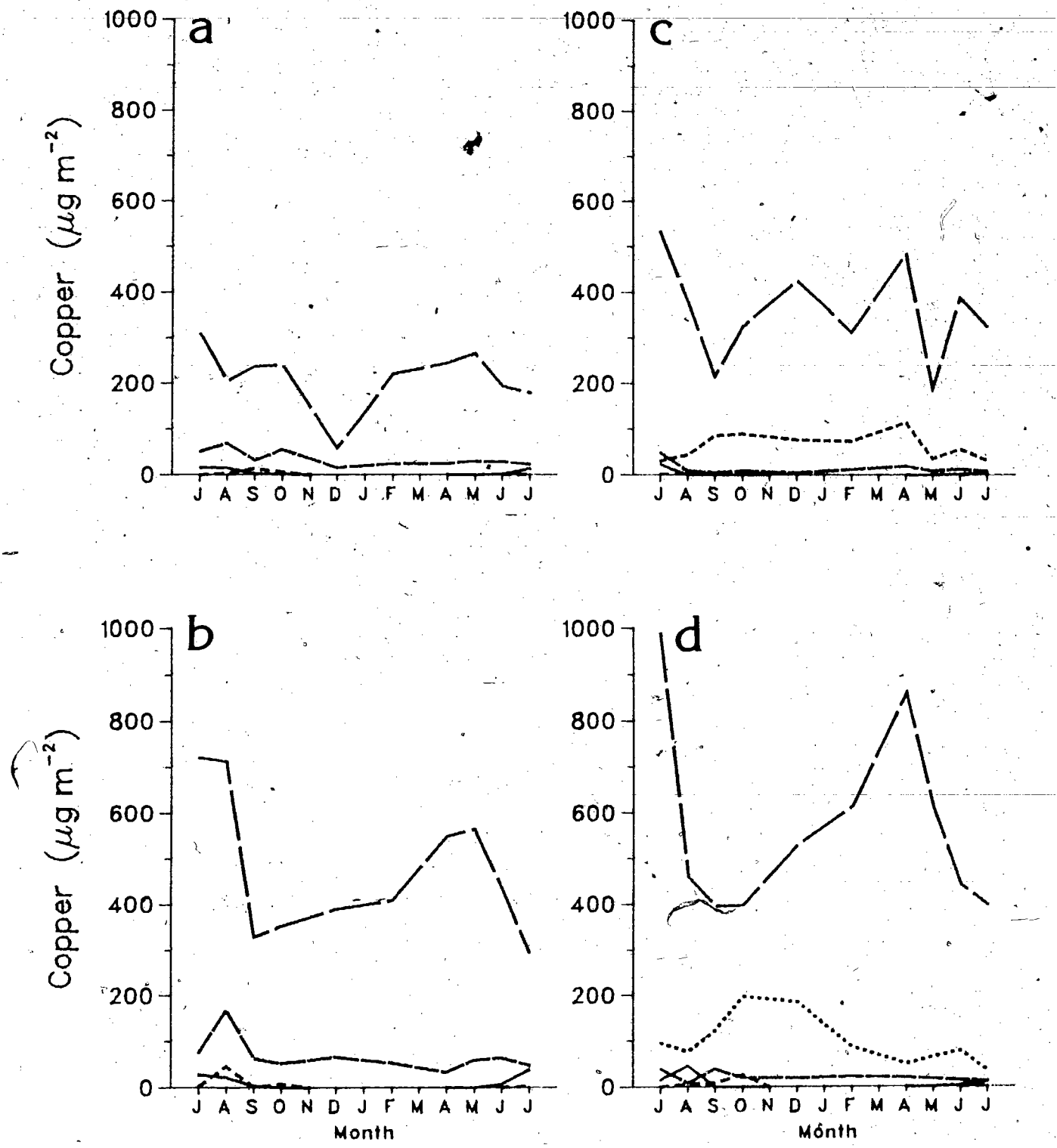

Figure 44. Mean copper accumulation in photosynthetic shoots (———), dead shoots (- - - - - -), roots (—— ——), rhizomes (—— —— ——) and corms (·····) of low marsh (a) and high marsh (b) *S. americanus* and low marsh (c) and middle marsh (d) *S. maritimus*.

At the time of emergence, live shoots had high concentrations of N, P, Mg, Ca, and H, which subsequently declined, suggesting dilution of these nutrients as plants mature. Potassium concentrations in live shoots increased during the first half of the growing season, declining thereafter. Conversely, Na and Fe concentrations were highest in May, declined during the period of rapid shoot growth and increased after peak aboveground biomass was attained. Carbon concentration was constant throughout the growing season, while Al, Mn, Zn and Cu had such large fluctuations that no trend was apparent.

Nutrient concentrations of belowground structures was similar within species but varied between species. In *S. americanus*, maximum N and P occured during winter, whereas *S. maritimus* had winter maximums of Al and Zn concentrations. Plants in all environments had maximum Cu in summer, and belowground tissues of *S. americanus* also had summer maximum of Na concentrations. Elements at minimum concentrations in fall included Ca, Al and Fe in *S. americanus* and Ca and Mg in *S. maritimus*. High marsh *S. americanus* also had lowest Zn concentrations at the end of the summer. Several nutrients showed no seasonal variation in belowground structures: C, H, K, and Mn in *S. americanus* and *S. maritimus*, Mg, in *S. americanus* environments, Zn in high marsh *S. americanus* only, and N, P, Na and Fe in *S. maritimus* environments.

The absence of any seasonal variation in belowground structures of *S. maritimus* was in large part a result of the large dead belowground biomass in these environments which was not separated from the live structures. This may cover any potential variation in nutrient concentration of live structures. Although live and dead belowground structures were not distinguished for *S. americanus*, most of the belowground tissue in these environments appeared to be live. Nitrogen and P were elements that had clear seasonal changes and appear to move between above and belowground structures.

Examination of the nutrient accumulation data indicated that N, P, Mg, Zn and to some extent Al and Mn had opposite trends between aboveground and belowground structures. These elements decreased in senescing live shoots and accumulated in belowground structures. This is an indication of storage of these elements in belowground structures for rapid allocation to shoot growth in spring. The remaining nutrients, C, H, Ca, K, Fe and Cu,

did not have any discernible relationship between aboveground and belowground accumulation levels.

Middle marsh *S. maritimus* had the greatest accumulations of all elements, and low marsh *S. americanus* the lowest. Low marsh *S. maritimus* and high marsh *S. americanus* had intermediate levels. Thus, nutrient accumulation increased with elevation at the Sea Island foreshore marsh.

Nutrient Allocation Proportions

The data on the proportion of nutrients allocated to different plant structures represents the proportion of the total tissue pool for that month in a plant structure. Generally, the values given for shoots represents the maximum value measured over the entire sampling period. This usually was for July, the time of peak nutrient accumulation in shoots.

Low marsh S. americanus

About 50% of the total tissue pool of N, P, Na and K is in photosynthetic tissue during peak summer growth (Figure 45). A small proportion of these elements remain in the dead shoot compartment at the end of summer. In autumn, the proportion in rhizomes shows a marked increase and exceeded the proportion of these elements in roots.

The proportion of C, Mg, Mn and Zn is only ≃25% in live shoots. As live shoots senesce, these elements accumulated in dead shoot tissue suggesting that they were not removed from shoots. Any re-allocation of these four elements in fall appears to be into rhizomes, as roots did not change appreciably in autumn. In spring, however, roots had a greater proportion of these elements compared to rhizomes.

Less than 10% of Ca, Al, Fe and Cu was measured in live shoots, with roots containing 60–70% of these elements. The rapid increase in the proportion of Fe and Al occurred in fall, declining thereafter to proportions similar to roots. Cu had the least seasonal variation as roots had 70–90% of Cu found in plant tissues of low marsh *S. americanus*.

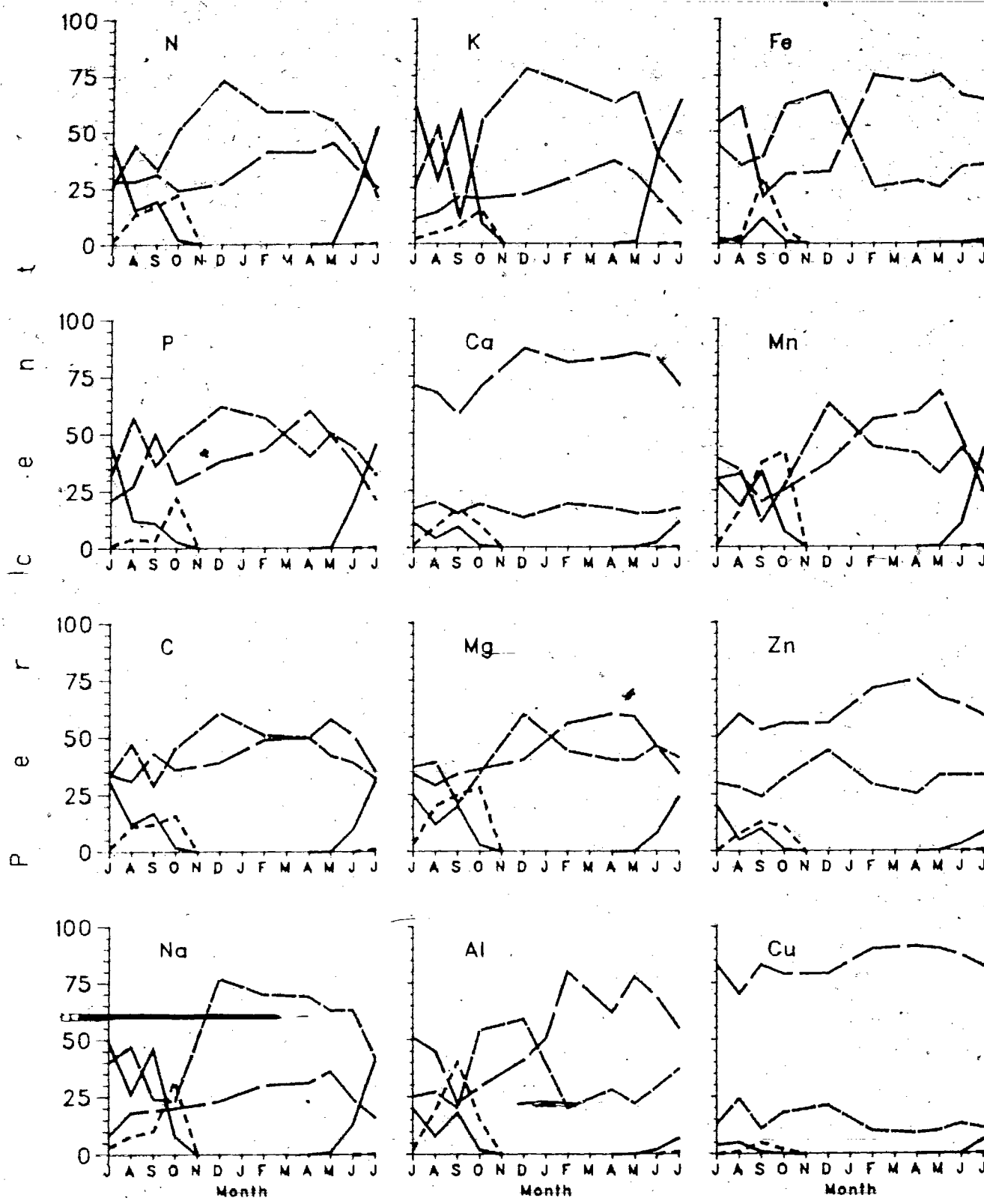

Figure 45. Mean proportion of nutrient accumulations in photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——) and rhizomes (—— — ——) in low marsh *S. americanus*.

High marsh S. americanus

In plant tissues of high marsh *S. americanus*, only Na and K approached 50% in one compartment (Figure 46). As aboveground shoots senesced, Na moved into dead shoot tissue. Over winter, rhizomes continuously had higher proportions of Na and K than roots.

Only 20–25% of other macro-nutrients (N, P, C, Mg) were in live shoots in July, and similar to low marsh *S. americanus*, ≈10% Ca. Roots and rhizomes had equal proportions of C, roots had greater proportions than rhizomes for Ca and Mg and rhizomes had greater proportions of N and P than roots.

Live shoots contained less than 20% of Al, Mn and Zn accumulation and even a smaller proportion of Fe and Cu. Roots contained 75–85% of all Cu, and the majority of Al, Mn and Zn. Only in autumn did rhizomes have a greater proportion of a trace metal and it was Fe.

Low marsh S. maritimus

Live shoots represented the largest compartment for N, P, Na and K in July (Figure 47). As shoots senesced, the proportion of these elements increased in corms except for Na. Na increased in dead shoots in autumn and in corms in early winter when dead shoots were removed from the marsh platform. At all other times of the year, corms were the largest compartment containing 50–75% of N, P, Na and K and roots had 25%.

Live shoots contained only 25% of C and Mg, and less than 10% of Ca. In fact, roots were the structure with the most Ca, the only macro-nutrient with this trend of greatest proportion in a belowground structure.

While shoots had as much as 25% of Al and Mn accumulation, the shoot compartment represented less than 10% of Fe, Zn and Cu accumulation. With the exception of Zn, which was partitioned equally between roots and corms, roots had the greatest proportion of all trace metals. Furthermore, there was very little change in the proportion of Zn in roots and corms over time suggesting little movement of these elements between aboveground and belowground structures.

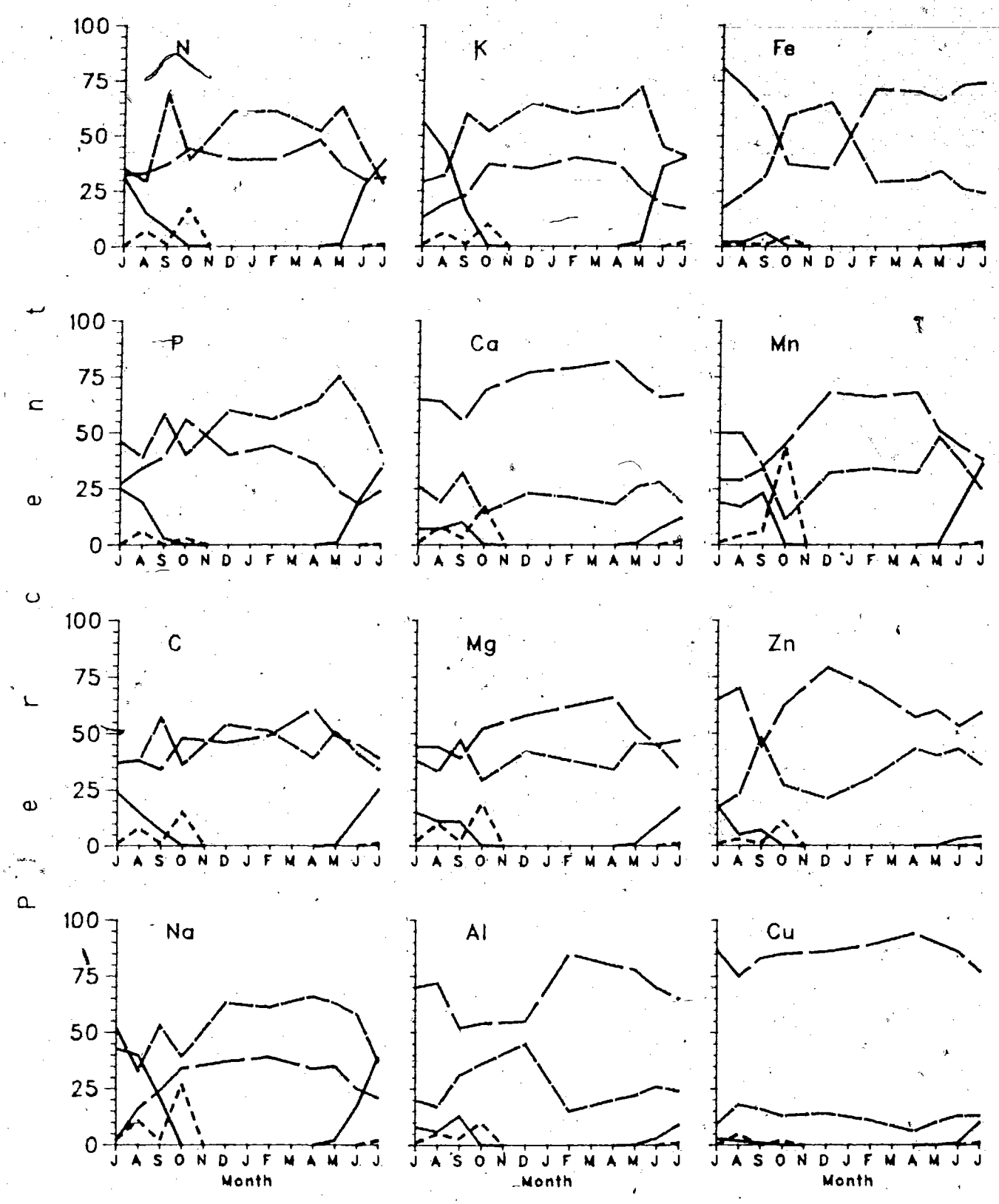

Figure 46. Mean proportion of nutrient accumulations in photosynthetic shoots (———), dead shoots (- - - - - -), roots (— — — —) and rhizomes (———) in high marsh *S. americanus*.

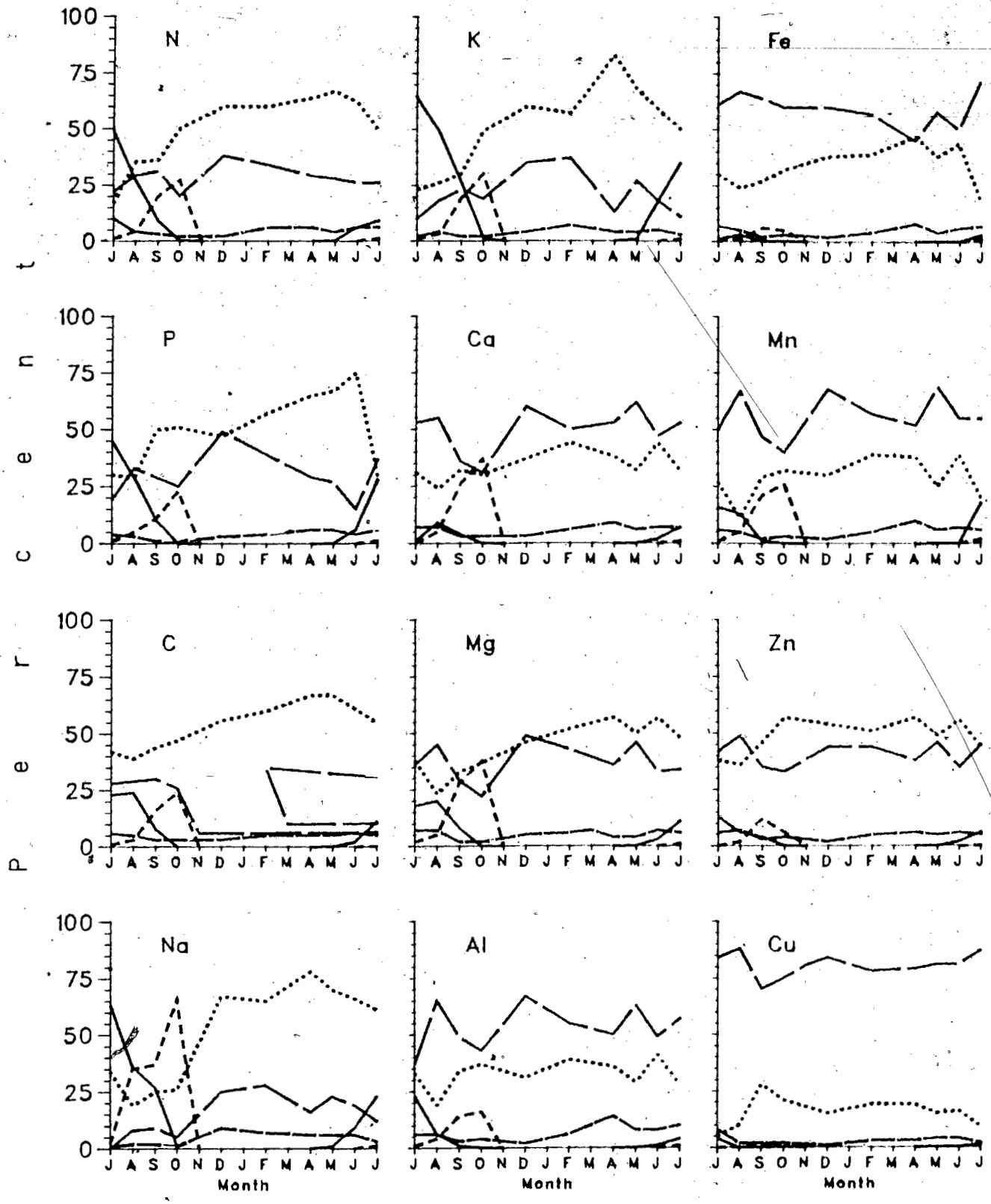

Figure 47. Mean proportion of nutrient accumulations in photosynthetic shoots (————), dead shoots (- - - - - -), roots (—— ——), rhizomes (—— — ——) and corms (.....) in low marsh *S. maritimus*.

Middle marsh S. maritimus

The relative distribution of elements in tissues of middle marsh *S. maritimus* differed from that observed in the low marsh. Only Na and K accumulation approached 50% of the total accumulation in live shoots (Figure 48). Live shoots contained ≃25% of N and P accumulation but only 10% of C, Ca and Mg. Dead shoots mirrored patterns observed for live shoots for N, P, C, Na and K but the proportion of Ca and Mg accumulated in dead shoots exceeded that measured in live shoots. Corms of middle marsh *S. maritimus* contained the bulk of macro-nutrients, especially N, Ca, Mg, Na and K. In spring, roots exceeded corms in Ca accumulation.

Al and Mn accumulation approached 25% in live shoots, but less than 10% of accumulated Fe, Zn and Cu were in live shoots. Similar to the other three sites, the majority of trace metals were in belowground structures. Except in fall, when corms increased in size, roots were the largest compartment, containing in excess of 75% of accumulated Cu. Corms and roots generally had equivalent proportions of other trace metals, except in early spring (April/May) when roots contained the bulk of the trace metals.

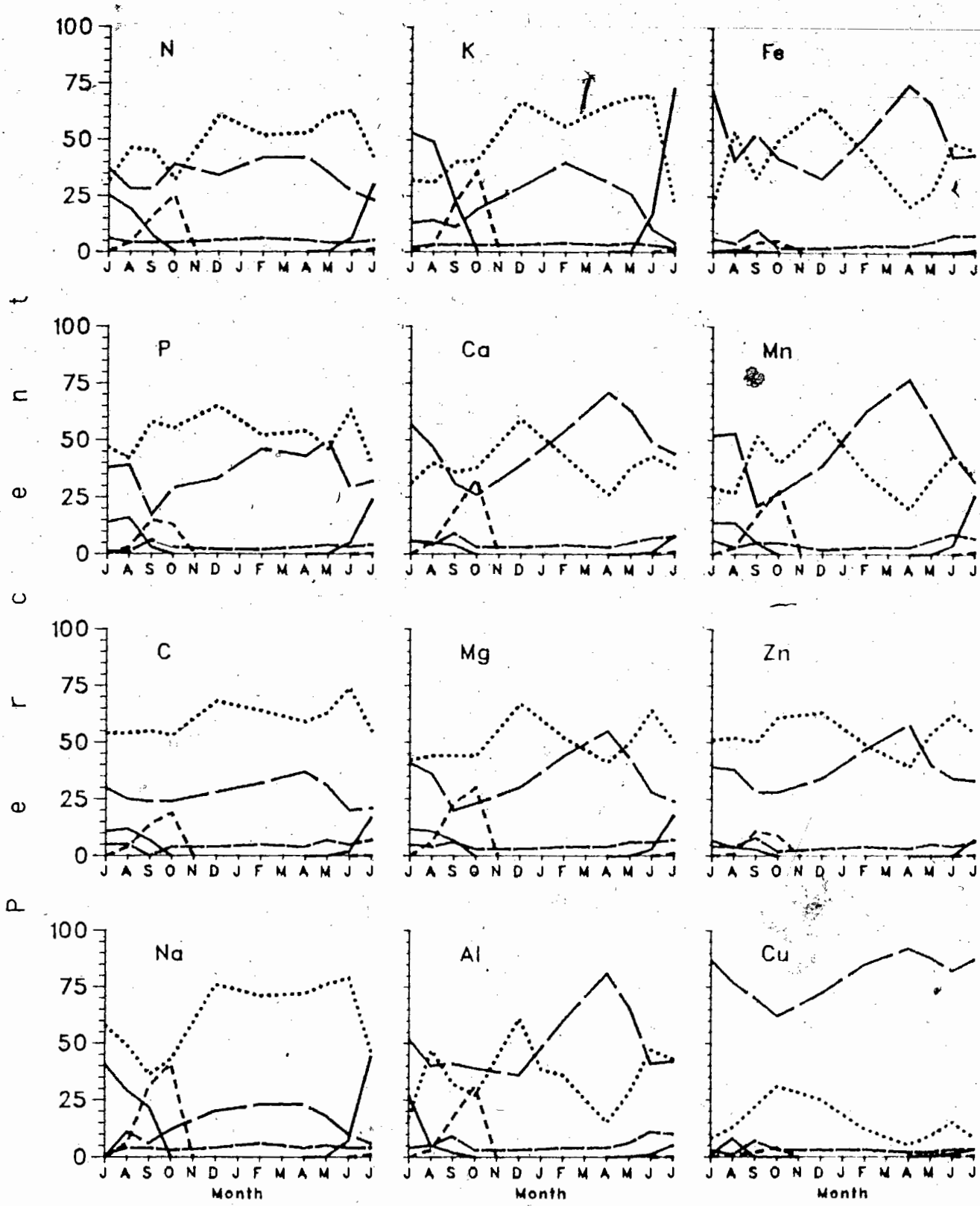

Figure 48. Mean proportion of nutrient accumulations in photosynthetic shoots (————), dead shoots (- - - - - -), roots (— — — —), rhizomes (— — — —) and corms (·····) in middle marsh *S. maritimus*.

CHAPTER IV

DISCUSSION

Low marsh *S. americanus* and *S. maritimus* invested a greater proportion of their total macro-nutrient pool into shoots compared to their counterparts at higher elevations. Comparing the plants in all four environments, middle marsh *S. maritimus*, which is found at the highest point sampled on the Sea Island marsh platform, had the lowest relative investment into shoots. Thus, plants at higher elevations were more "conservative" with their total nutrient pool and invested least in shoot growth. This does not support the hypothesis of conservative allocation strategies at the low elevation environments.

Two explanations are proposed to account for the greater relative investment of nutrients made by plants in low elevations. First, the belowground reserves of plants at the upper elevations may be so large that the exposure time in summer is insufficient for these plants to invest the maximum proportion of their resources to shoot growth. Second, a decrease in the nutrient concentration of shoots concurrent with increased concentrations in belowground structures indicates re-translocation from shoots to belowground structures. It also indicates some loss of nutrients from shoots due to leaching. Kistritz *et al.* (1983) found that large amounts of N and P were leached from shoots of *Carex lyngbyei* during spring and early summer. Loss of minerals through leachates was not measured in this study. *S. americanus* is found at lower elevations than *Carex lyngbyei* in the Fraser River marshes and therefore subjected to longer inundation periods. This may result in greater nutrient losses from shoots of low marsh plants which compensate for this loss by continuously "pumping" nutrients into shoots. As a result, plants in low elevations invest a greater proportion of the total tissue nutrient pool into shoots.

The second hypothesis examined in this part of the thesis is conservation of scarce resources. The movement of N into belowground structures supports the hypothesis of conserving scarce nutrients for re-allocation. Soil nitrogen levels were low in the Sea Island marsh environments necessitating conservation of nitrogen.

While it has been demonstrated that salt marshes have abundant phosphorus supply for plant growth, little is known on the availability of phosphorus in brackish marshes. Hall and Yesaki (unpublished) measured phosphorus concentrations of 0.13% P dry weight (mean

of 3 samples) in a *S. maritimus* stand 1 km north of the Sea Island sampling sites. Phosphorus concentrations in a stand of *Scirpus validus* was 0.10 % P dry weight (mean of 3 samples). These values fall in the range of phosphorus concentrations presented by Allen (1974) for mineral soils (range of 0.02 - 0.2% P). Although soil nitrogen and phosphorus concentrations measured around the Sea Island brackish marsh were low in comparison to other soils, it is not known at what level these elements become limiting for growth in *S. americanus* and *S. maritimus*. Without undertaking experimental studies to determine what concentration these elements become limiting to plant growth (*sensu* Gerloff and Krombholtz 1966), these elements cannot be presented as limiting in the Sea Island marsh.

Similar to N, P concentrations in belowground structures increased during shoot senescence. Lytle and Hull (1980a, 1980b, 1980c) demonstrated that shoot growth in *Spartina alterniflora* was supported in early summer from belowground photosynthate and carbohydrate reserves stored the previous winter. By conserving macro-nutrients that are important for shoot growth, *S. americanus* and *S. maritimus* maintain a nutrient pool to draw upon in spring and perhaps early summer for shoot production. When these shoots become large enough to support themselves, then these nutrients can be allocated to rhizome growth and hence, clonal expansion.

Seasonal storage, like luxury uptake, is essential to the success of perennial species in low-nutrient environments because it buffers the plant from day-to-day dependence on the environment (Chapin 1980). Chapin (1980) found that most species re-translocated half or more of their nitrogen and phosphorus pools to roots, though some studies showed no phosphorus translocation. I suggest that nitrogen and phosphorus were stored in belowground structures because they are important for plant maintenance and growth and to avoid dependence on the environment supplying these elements.

Trace metals were always found in very high proportions in belowground structures of *S. americanus* and *S. maritimus* at Sea Island. Only Mn was measured at high concentrations in aboveground structures. Conversely, Na and to some extent K, accumulate in live and dead aboveground shoots. Both of these patterns may represent compartmentation of elements that are not required in large quantities but cannot be prevented from uptake since they are found in very high concentrations in the local environment. This tactic has been demonstrated for Na in marsh plants (Rozema *et al.* 1985, Osmond *et al.* 1987). The

high levels of trace metals in belowground structures of *S. americanus* and *S. maritimus* may be required to prevent these elements from interfering with plant metabolism and photosynthesis in shoots.

Heathcote *et al.* (1987) demonstrated experimentally that flooding greatly increased the concentration of Fe and Mn in the root system of *Carex flacca*. Flooding also increased the transport of Mn but not Fe to shoots. A comparison of Fe and Mn concentrations of the 4 sites sampled at Sea Island based on a flooding regime are complicated by the different soil textures and bulk densities. Middle marsh *S. maritimus* has the shortest flooding period but has the greatest silt and clay content and hence, the poorest drainage. It was in this environment that the greatest Fe concentrations were measured in all belowground structures. The lowest Fe concentrations were measured in belowground structures of high marsh *S. americanus*, an environment with a relative intermediate flooding period but sandy soils that provide rapid drainage of water. There was no trend in Mn concentrations in shoots or roots at Sea Island that conformed to flooding and drainage regime.

Studies that have examined nutrient content of marsh macrophytes focussed on aboveground and belowground structures as whole compartments. I could not find data in the literature on the nutritional content of individual plant structures. Only live and dead shoots were analyzed separately, as in this study. Flowers are usually very small in marsh plants and thus, the nutrient content of shoots is indicative of the aboveground compartment. Some studies have distinguished between live and dead belowground tissues. Thus, comparisons with other studies are often restricted to these two large compartments. As well, the bulk of the nutrient data available is on N and P concentration and occassionally cations, with few data on trace metals.

The only published data on *S. americanus* was provided by Boyd (1970) for a *S. americanus* stand along the shores of Par Pond near Aiken, South Carolina. The maximum N concentration of 2.72% measured in mid-April was similar to that of high marsh *S. americanus* at Sea Island (2.65% N) but much less than the maximum of 3.45% measured for live shoots in the low marsh environment. As well, Boyd (1970) measured a greater decline in N concentrations as the shoots matured in Par Pond. Minimum nitrogen concentration was 0.83% N at Par Pond compared to 1.54% (low marsh) and 1.18% N (high

marsh) at Sea Island. Similar trends in P was found as with N. Ca concentration at Par Pond was 3–4 times that of Sea Island *S. americanus* live shoots. Maximum K at Par Pond was greater than at Sea Island but shoots in both locations had equivalent K concentrations at other times of the year. Mg concentrations during the growing season were similar between Par Pond and Sea Island, but the spring and fall maximum were greatest at Sea Island. The maximum Na concentrations measured at Par Pond was 0.20% in mid-May, an order of magnitude less than minimum Na concentrations measured at all times for live shoots of *S. americanus* in the intertidal marsh at Sea Island.

Ewing (1982) provided some results on the nutrient content of *S. americanus* shoots from the Skagit marsh. An analysis of variance on his data found that low marsh shoots had significantly higher N, P and Mn concentrations than high marsh shoots ($P < 0.05$). This is in agreement with the results of this study but further comparison of data from this study to Ewing (1982) is difficult because he does not present any information on sampling date.

Although *S. maritimus* has a large biogeographical range and ecological amplitude, only Hall and Yesaki (unpublished manuscript) provide data on the nutritional content of this species. They measured N and P concentrations in live and dead aboveground and belowground tissues at the Musqueam marsh, just 1 km north of Sea Island. Their mean monthly N values ranging from 3.15% in early May to 1.55% in September were similar to the spring/fall measurements of 3.20% and 1.37% N in low marsh *S. maritimus* and 3.30% and 1.26% in the middle marsh at Sea Island. Hall and Yesaki (unpublished manuscript) reported P concentration in live shoots as high as 0.54% in early June which exceeded the highest value fo 0.46% measured for shoots in the middle marsh in this study. Finally, their values of 45% C throughout the growing season were consistently higher than that measured in this study. Comparison of dead aboveground tissue nutrient concentrations between this study with that of Half and Yesaki (unpublished manuscript) found that they measured greater C concentrations but similar N and P concentrations.

Hall and Yesaki (unpublished manuscript) distinguished between live and dead belowground tissue and presented mean N, P and C concentrations of total belowground live tissue for July – September 1980 as 1.60%, 0.21% and 45.8%, respectively. These values are all higher than the corresponding values in this study for the same time of the year (low

marsh: 1.03% N, 0.12 % P, 38.99% C; middle marsh : 1.25% N, 0.23% P, 41.46% C). This is in large part a result of the pooling of live and dead belowground tissues in this study. It may be that dead belowground tissue has very low concentrations of these constituents. Gallagher and Plumley (1979) found that N, P, K and Zn concentrations of *Distichlis spicata* in Delaware all decreased with depth. They attributed this pattern to the greater dead tissue at depth which would have N removed from the dying tissue by bacteria and K leached when the integrity of the membranes is lost as cells senesce. At Sea Island, this would be most prominent in the low marsh which has a very large dead belowground reserve.

Kistritz *et al.* (1983) measured N and P concentrations in *Carex lyngbyei* shoots on Woodward Island marsh, 10 km south of Sea Island. They reported a maximum N concentration of about 2.5% (ash free dry weight) in May, which is less than maximum N concentrations measured for shoots from all four environments in this study. P concentrations of *C. lyngbyei* was similar to high marsh *S. americanus* and low marsh *S. maritimus* but less than low marsh *S. americanus* and middle marsh *S. maritimus*, the 2 environments with the plant tissues containing the highest nutrient concentrations. *C. lyngbyei* seed heads had N and P concentrations similar to seed heads in *S. americanus* and *S. maritimus*.

Kistritz *et al.* (1983) also presented data on N and P accumulation in *C. lyngbyei*. The maximum N accumulation of about 10 g N m^{-2} in *C. lyngbyei* exceeded the N accumulation of low marsh *S. americanus*, but was equivalent to high marsh *S. americanus* and both *S. maritimus* environments. Phosphorus accumulation in *C. lyngbyei* was half that of high marsh *S. americanus* and both *S. maritimus* environments but equivalent to low marsh *S. americanus* P accumulation. Total belowground P accumulation of *C. lyngbyei* was similar to *S. americanus* and *S. maritimus*. *C. lyngbyei* had N accumulation in belowground structures equivalent to low marsh *S. americanus* and *S. maritimus* but much less than high marsh *S. americanus* and middle marsh *S. maritimus*. Kistritz *et al.* (1983) suggested that *C. lyngbyei* is a very important component of the high nutrient value of the Fraser estuary and it appears that *S. americanus* and *S. maritimus* are equally as important.

Gallagher and Kibby (1980) measured the mean annual concentration of several metals in live shoots of *Carex lyngbyei*, *Salicornia virginica*, *Juncus balticus and Potentilla pacifica*. Compared to the Sea Island data, all of these species had lower Cu concentration but greater Zn concentrations. For Fe and Mn, *S. virginica* and *C. lyngbyei* had greater concentrations

than *S. americanus* and *S. maritimus* but lower concentrations were found in *J. balticus* and *P. pacifica*. Dead *J. balticus* had greater metal concentrations than live shoots, a similar pattern to this study.

There is a plethora of data on the nutritional content of *S. alterniflora* and a wide range of values have been presented with no consistent trends. This is in large part a result of the difficulties involved in sampling all plant structures as live and dead, especially belowground, and hence, nutrient movement between plant structures is often difficult to determine. As well, the large ecological amplitude of *S. alterniflora* would result in a large variation in nutrient content. The wide range of nutrient values measured between and within species at Sea Island and the variation in *S. alterniflora* preclude any detailed comparisons. Some general comments on seasonal and spatial variation of nutrient concentration and accumulation are presented below.

Drifmeyer and Redd (1981) measured Mn, Fe, Cu and Zn concentrations in *S. alterniflora* in 6 locations in the York River (Virginia), and in 16 Atlantic coastal marshes. They found significant differences in all elements along a salinity gradient of the York River but no correlation with salinity of river or interstitial water. They also found significant differences in Fe, Cu and Zn between 16 marshes but there was no consistent trend with latitude. As in this study, dead shoots had higher concentrations of metals than live shoots. Other variables, such as soil nitrogen, may be correlated with plant nutrient content.

Compared to the Sea Island sedges, *S. alterniflora* had similar Fe and Zn concentration for both live and dead shoots. Mn concentration of live *S. alterniflora* is equal to *S. maritimus* but much less than *S. americanus*. Only dead shoots in low *S. americanus* had Mn concentrations greater than *S. alterniflora*. The lowest Cu concentrations at Sea Island were measured in low *S. maritimus* and these were equivalent to *S. alterniflora*. Dead shoots of *S. americanus* and *S. maritimus* had Cu concentrations that were much higher than measured in *S. alterniflora*.

Gallagher *et al.* (1980) presented concentration and accumulation data of several nutrients for *Juncus roemerianus* and creekbank and high marsh *S. alterniflora* in Georgia. Their values of maximum N, P and K in early spring were much lower than those of *S. americanus* and *S. maritimus* and did not have as large a seasonal variation as measured in Vancouver. This may be a result of the fact that the year long growing season in Georgia

results in the constant presence of photosynthetic tissue with a low nutrient content as opposed to a deciduous habit that requires a large initial investment for new growth. Concentrations of Ca and Mg were equivalent between this study and the one of Gallagher *et al.* (1980), there was little seasonal change in Ca and Mg concentrations and they were equivalent in the two regions. The pattern of Mn in Georgia of summer minimum and increasing in fall was similar to that of *S. americanus* but *S. americanus* had twice the Mn concentration of *S. alterniflora* and *J. roemerianus*. *S. maritimus* Mn concentrations were lower than those measured in the Georgia marsh plants.

Accumulation patterns and levels were different than concentration. Nitrogen accumulation in photosynthetic tissues of *S. americanus* and *S. maritimus* exceeded the short form *S. alterniflora*. Tall form *S. alterniflora* had N accumulation levels of about 13 g m^{-2} (Gallagher *et al.* 1980) which was equivalent to *S. maritimus* (12 g N m^{-2}), the highest measured at Sea Island. Maximum P accumulation in *S. americanus* and *S. maritimus* was equivalent to short form *S. alterniflora* but only 20% of that measured in *J. roemerianus* and tall form *S. alterniflora*. The Ca accumulation in *S. americanus* and *S. maritimus* of only 1 g m^{-2}, was much less than either height form of *S. alterniflora* (5 and >20 g m^{-2} for shor and tall form, respectively) and of *Juncus* (10 g m^{-2}). For Mg, Gallagher *et al.* (1980) measured maximum accumulation in August of about 1 g m^{-2} for short *S. alterniflora* and *Juncus* but 4–5 g m^{-2} in tall *S. alterniflora*. The maximum Mg accumulation in *S. americanus* and *S. maritimus* was measured in late summer and was intermediate to that of Georgia. The K accumulation levels of 8–10 g m^{-2} measured in low *S. americanus* and both *S. maritimus* environments was slightly less than the maximum of 15 g m^{-2} in tall *S. alterniflora* and *Juncus*. Potassium accumulation in high marsh *S. americanus* (20 g K m^{-2}) exceeded all of these values. Mn accumulation in *Juncus* was three times that of *S. americanus* and *S. maritimus*. Low marsh *S. americanus* had equivalent maximum to tall *S. alterniflora*, with a maximum of 0.1 g Mn m^{-2}. Short form *S. alterniflora* had maximum of 0.05 g Mn m^{-2}, as did high marsh *S. americanus* and middle marsh *S. maritimus*.

Few studies have undertaken nutrient analysis of belowground structures. Those that have are restricted by two flaws; the pooling of different belowground structures or the long interval between analyses. To compensate for such different sampling schemes, comparisons were made on mean annual concentrations of various nutrients.

De la Cruz and Hackney (1977) found no significant differences in N, P and H concentration of total belowground materials with depth in a Mississippi *Juncus roemerianus* marsh. I calculated mean annual concentration for the four depths they sampled (0–0.4 m) of 0.76% N, 0.16% P and 5.75% H. Their N and P values were less than *S. americanus* and *S. maritimus* roots and rhizomes, especially the P levels, while H concentration was within the range of values presented in this study. They found that roots had higher N and P concentrations compared to rhizomes. At Sea Island, rhizomes of *S. americanus* had greater N and P concentrations than roots but roots of *S. maritimus* had greater or equivalent concentrations of N and P to rhizomes and corms.

Gallagher and Plumley (1979) measured the mineral composition of belowground macro–organic matter in a stand of *Distichlis spicata* in Delaware in February, June and November. Peak N concentration was in June (1.25% N) which was within the range of values measured at Sea Island but the P levels measured in *D. spicata* were much less than *S. americanus* and *S. maritimus*. Potassium concentrations of *D. spicata* was similar to roots of *S. americanus* and all belowground structures of *S. maritimus* but was much lower than the K concentrations of *S. americanus* rhizomes. By contrast, *S. americanus* roots had much higher Ca concentrations than *D. spicata*, but all other structures of *S. americanus* and *S. maritimus* had Ca concentrations equivalent to *D. spicata*. Mg concentrations were all similar between *S. americanus*, *S. maritimus* and *D. spicata*. For trace metals, Gallagher and Plumley (1979) reported Mn and Cu concentrations in *D. spicata* that were very low in comparison to *S. americanus* and *S. maritimus*, especially the roots. Zn concentrations were equivalent in all species and belowground structures.

Hopkinson and Schubauer (1984) provide one of the few studies that analyzed live belowground structures separately from dead. They found that the mean annual N concentration of live roots in *S. alterniflora* in Georgia was 0.50±0.04% N compared to 0.43±0.09% N in live rhizomes. Both of these values are less than the N concentrations measured for *S. americanus* and *S. maritimus* at Sea Island. The requirement to produce new shoots quickly in spring in the temperate environment of Sea Island may require a high nutrient reserve to mobilize nutrients to aboveground structures much quicker than would be accomplished if the nutrients had to be taken up from the soil. Also, the soils at Sea Island have very low nitrogen concentrations and it may be necessary for plants to store

nitrogen and not rely on a supply from the local environment. Hopkinson and Schubauer (1984) did not measure dead belowground tissue and thus a comparison cannot be made of the N content of live and dead tissues.

PART E

RECIPROCAL FIELD TRANSPLANT EXPERIMENT

CHAPTER I
INTRODUCTION

Variation in morphology or allocation patterns may reflect modification by the habitat. If there is little habitat modification of morphology or allocation patterns, it indicates that these characters may be genetically controlled. The transplant experiments of Turesson demonstrated genetic variation among plant populations on a scale of kilometers to hundreds of kilometers and he argued, on the basis of functional design, that this variation was adaptive (Waser and Price 1985). Bradshaw (1959) found intraspecific differentiation over much shorter distances (several meters in Britain) and Waser and Price (1985) found fine-scale adaptation (1 m) in Colorado populations of the perennial herb *Delphinium nelsonii*.

The results of Part C demonstrated that there is variation in biomass allocation in *S. americanus* and *S. maritimus* over a distance of 100 m and across an elevation gradient of 0.50 m. High marsh *S. americanus* had greater stem densities and greater above- and belowground biomass. Stem densities in *S. maritimus* were greatest in the low marsh but these shoots were smaller than those in middle marsh and hence, had lower biomass. Is this variation genetically fixed or does it reflect plastic responses to environmental influences? In order to answer this question, shoot density and biomass were measured for *S. americanus* and *S. maritimus* in a reciprocal field transplant experiment. Belowground biomass was also measured to ensure that any apparent differences were not the result of variation in belowground biomass reserves.

CHAPTER II

METHODS AND MATERIALS

Reciprocal plantings between high and low marsh sites (*S. americanus*) and between high, middle and low marsh sites (*S. maritimus*) were set out in the spring of 1986. For *S. maritimus*, the three sites selected included the sites used in the biomass study (low and middle) and the true upper elevation limit. A binomial notation is used to label transplants. The first letter denotes the donor site, and the second letter the site of transplantation. The natural population is denoted by a single letter. L, M, and H represent low, middle and high, respectively. All treatments and controls consisted of 10 cores, 0.10 m in diameter and 0.20 m in depth, planted in 2 x 5 rows with soil from the local environment placed between pots. Cores were placed in plastic pots 0.155 m in diameter, the extra space between the soil core and pot filled with soil without rhizome material. At the base of each pot were four 15 mm x 15 mm holes to allow drainage. For comparison with the local population, the results were converted to g m^{-2}. Since there was room for root and rhizome growth, pot diameter, rather than core diameter was used as a conversion factor.

Soil cores with emerging shoots were taken on March 29 (*S. americanus*) and March 30 (*S. maritimus*) and transplanted to new sites or *in situ* to serve as controls. *S. americanus* was harvested on Aug 2, 1986 and *S. maritimus* the following day providing each species with 126 growing days but variable exposure to sunlight (Table 8). The number of live shoots and flowers were counted, shoot height measured and dry weight of shoots and flowers measured for each pot. Belowground plant tissue was washed, separated into roots, rhizomes and corms and weighed. All plant material was oven dried at 65–75°C for 72 hours. Biomass results are presented as a proportion of rhizome or corm biomass to account for variations in belowground biomass between cores and environments.

Significant differences between treatments were determined by a one-way analysis of variance and Student-Newman-Keul's multiple range test (α = 0.05) (UBC ANOVAR, Greig and Osterlin 1978).

Table 8. Exposure hours of transplant sites.

Site	Total Exposure Hours	% Exposure
S. americanus		
low marsh	916	46
high marsh	1348	68
S. maritimus		
low marsh	976	49
middle marsh	1500	76
high marsh	1590	80

CHAPTER III

RESULTS

Comparison of transplants to local population

Shoot growth of all transplants lagged behind the local populations (Figure 49). Based on this observation, transplants were not harvested until one month after maximum shoot biomass of the natural populations. Furthermore, shoot density and biomass (live aboveground and total belowground) were less for transplants than the local population at harvest (Figures 50, 51).

For *S. americanus*, the transplants had about half the biomass of the local population (Figure 51). An exception was root biomass of low marsh transplants which was equivalent to the biomass of the low marsh population. Similarly, stem number was much less in transplants than the local population, and no shoots in the LL treatment flowered compared to 47% of the natural low marsh residents.

For several plant structures of *S. maritimus*, there was no significant difference between low and middle marsh environments both in transplants and the local population (Figure 52). High marsh had greatest root biomass but least corm biomass and rhizomes were so few that differences between environments were not evident (Figure 53).

Stem numbers of *S. maritimus* in L and M marsh environments were greater than in LL and MM, respectively, but were equivalent between H and HH (Figure 52). Aboveground biomass of the natural population was greater than transplants in all environments. HH and H had the lowest stem densities but greatest biomass and hence, the largest shoots. Again, a similar trend of increasing aboveground biomass with increasing elevation was evident.

Since biomass of all potted plants was significantly less than the local population, this indicates that there was suppression of growth due to excavation and re-planting or that the plants were root bound. There was evidence of roots and rhizomes filling the pots, the rhizomes in some pots growing completely around the perimeter. All comparisons were made to control treatments and it is assumed that plants in all pots received equivalent "transplant shock".

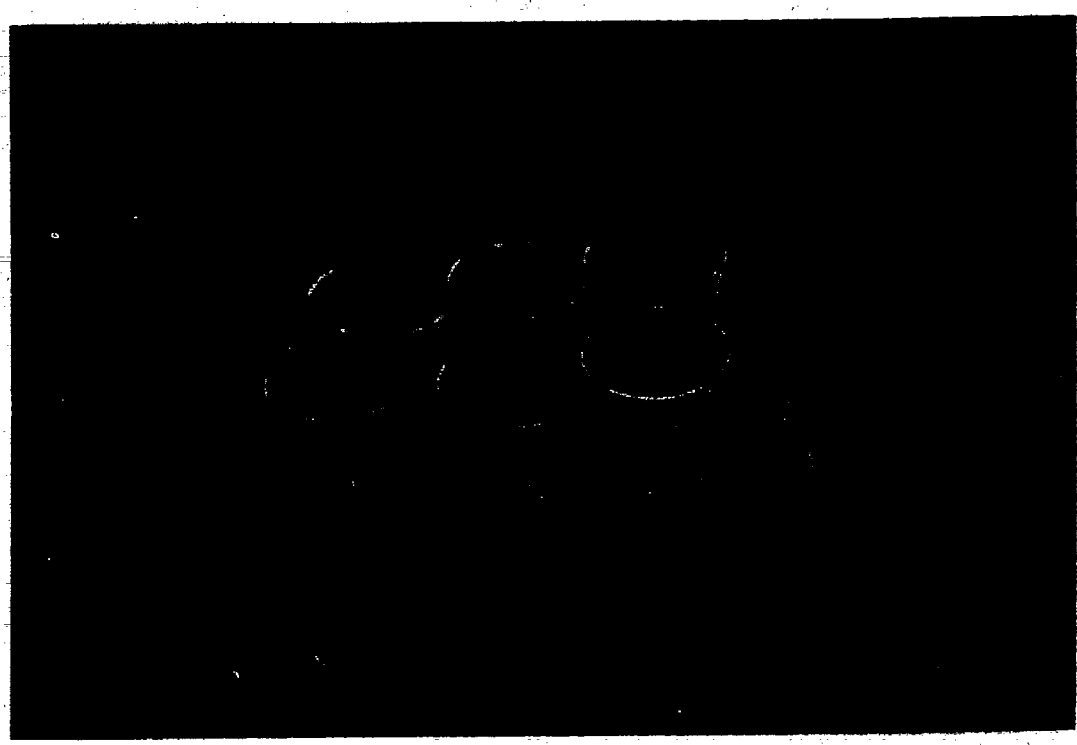

Figure 49. Photograph of low marsh *S. americanus* showing that they lagged behind the natural population in shoot growth (June 3, 1986).

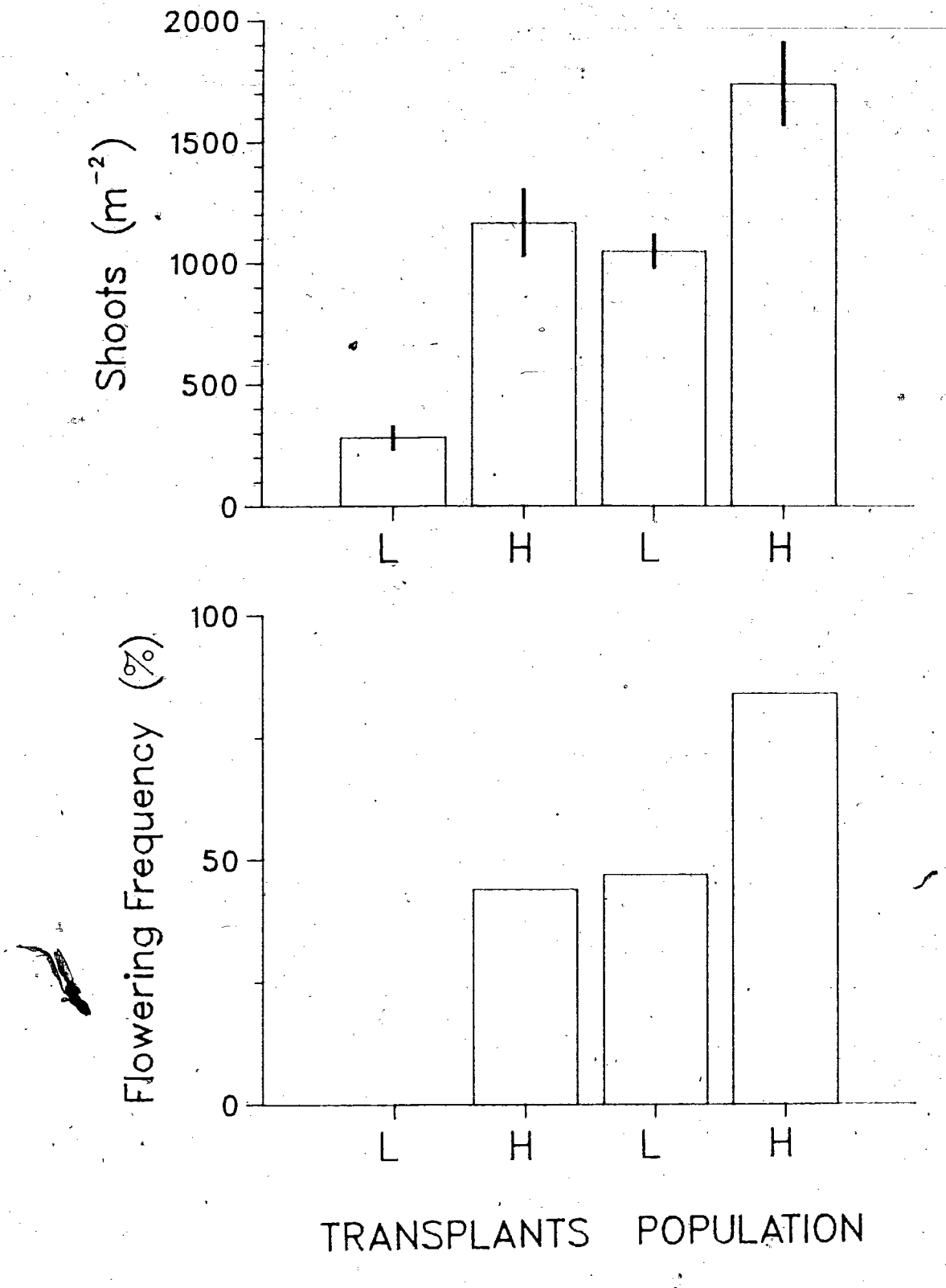

Figure 50. Shoot density ($\bar{x}\pm se$) and mean flowering frequency of *S. americanus* transplants compared to the local population.

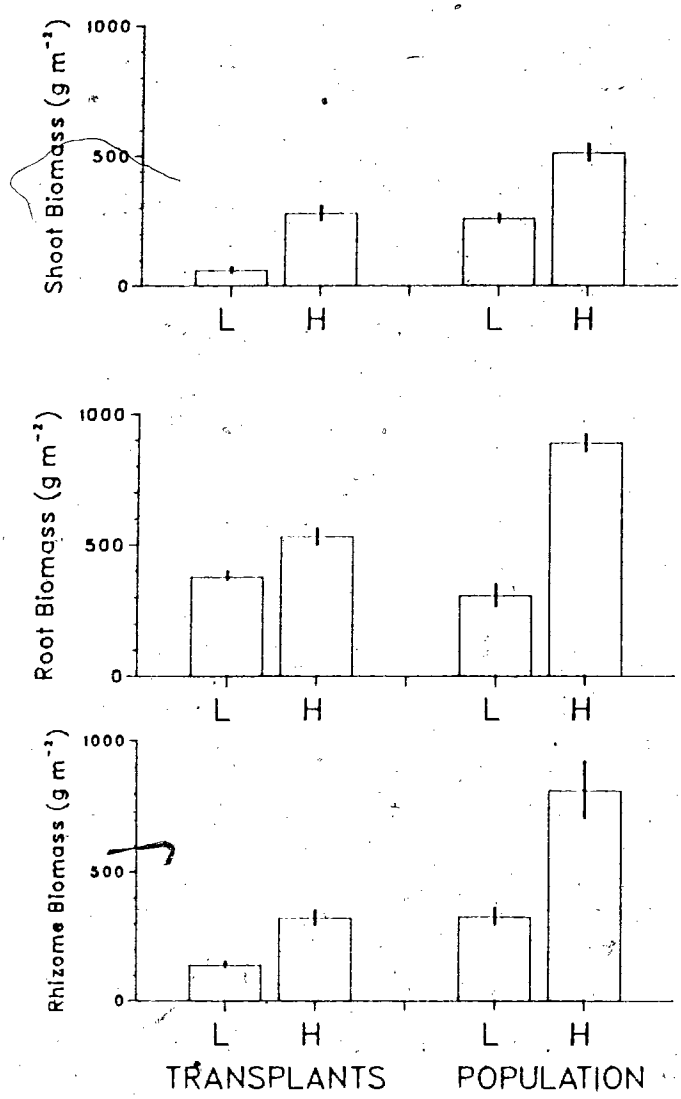

Figure 51. Aboveground and belowground biomass of *S. americanus* transplants compared to the local population ($\bar{x}\pm se$).

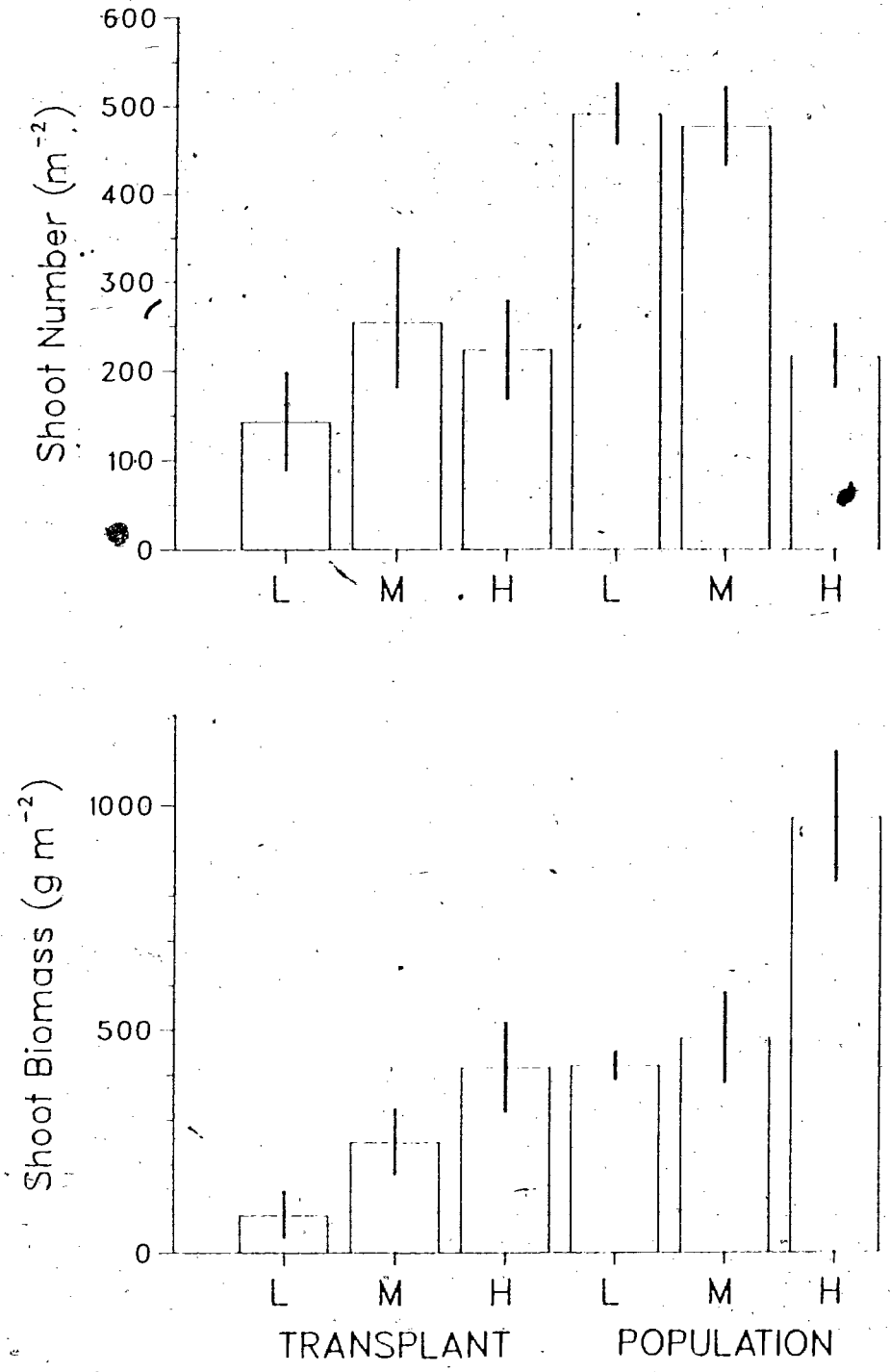

Figure 52. Shoot density and biomass of *S. maritimus* transplants compared to the local population ($\bar{x}\pm se$).

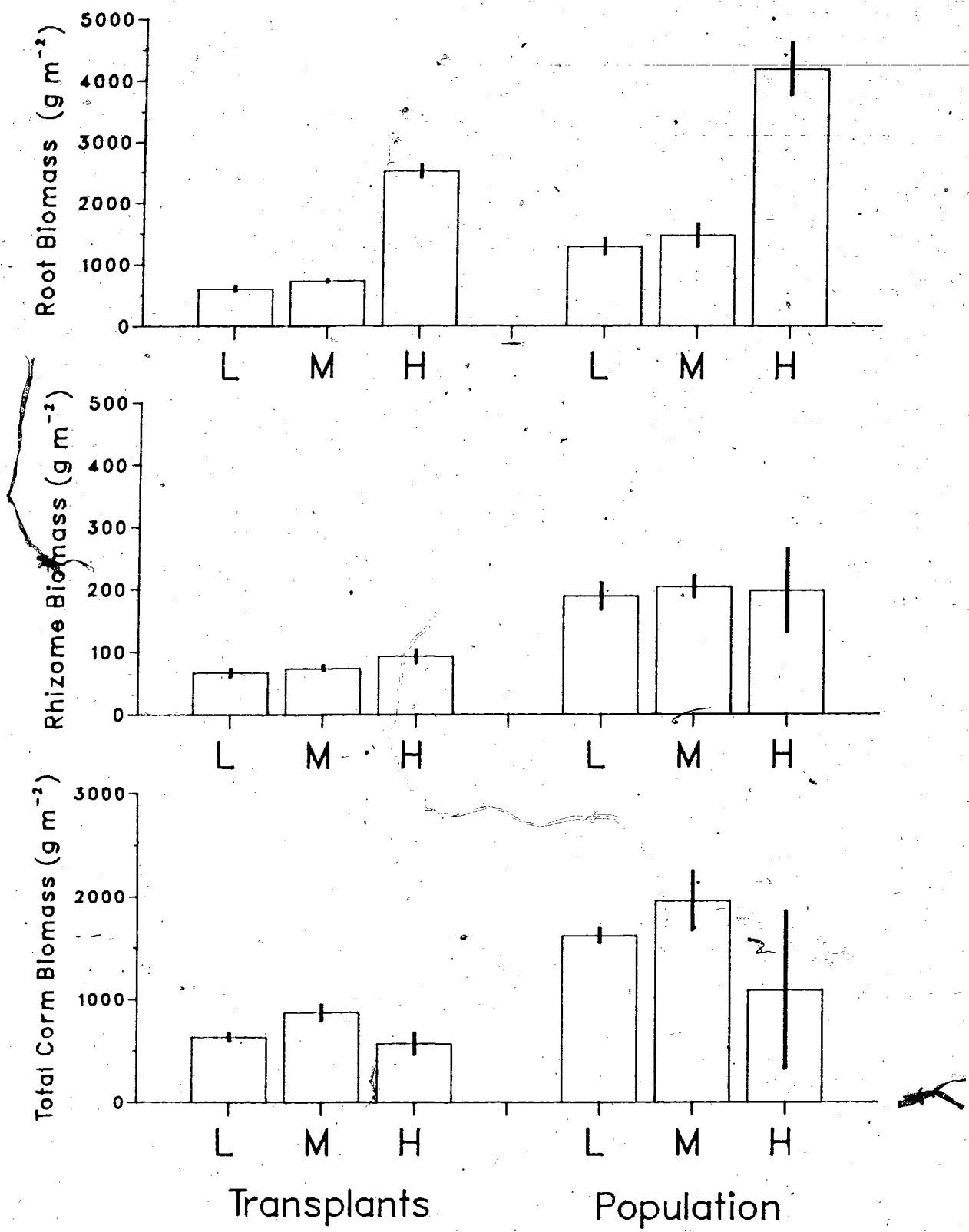

Figure 53. Belowground biomass ($\bar{x}\pm se$) of *S. maritimus* tranplants compared to the local population.

There were significant differences in root and rhizome biomass between the four sets of transplants (Figure 54). LH showed a decrease in root biomass but no significant difference in rhizome biomass. There were significant increases in root and rhizome biomass in HL. Assuming that all cores taken from one environment began the season with the same belowground biomass reserves, an increase in root or rhizome biomass may represent the growth of new tissue in response to locating in a new environment.

There was no significant difference in stem density between LL and LH but stem number of HL was significantly higher than HH and LL (Figure 55a). When the data were converted to stem number per unit weight of rhizome, these differences disappeared (Figure 55b). Stem number of LH was intermediate of LL and HH and the higher mean stem number per gram rhizome of HL was not significantly different from HH. Neither LL or HL flowered but flowering frequency of shoots in the high marsh environments were similar.

There were significant differences in mean stem weight per gram rhizome (Figure 55d). When low marsh plants were moved to the high marsh, more stem biomass was produced per unit rhizome. Conversely, high marsh plants showed a decrease in stem biomass when moved to the low marsh. Both HL and LH represent intermediates to LL and HH. HH rhizomes produced 1 g aboveground for every gram of rhizome compared to 0.4 g in LL (Figure 55d).

Stems produced from LH rhizomes were similar in mass to high marsh controls (Figure 55). The stem weight of HL was significantly less from HH but not LL. Thus, HL put out more shoots but they were smaller.

Height distribution varied greatly between the 4 sets of transplants (Figure 56) as did mean shoot height (Table 9). There was no difference in shoot height between LL and LH whereas HL shoots were shorter than HH. All 4 sets of transplants had similar height frequency distributions (Figure 56).

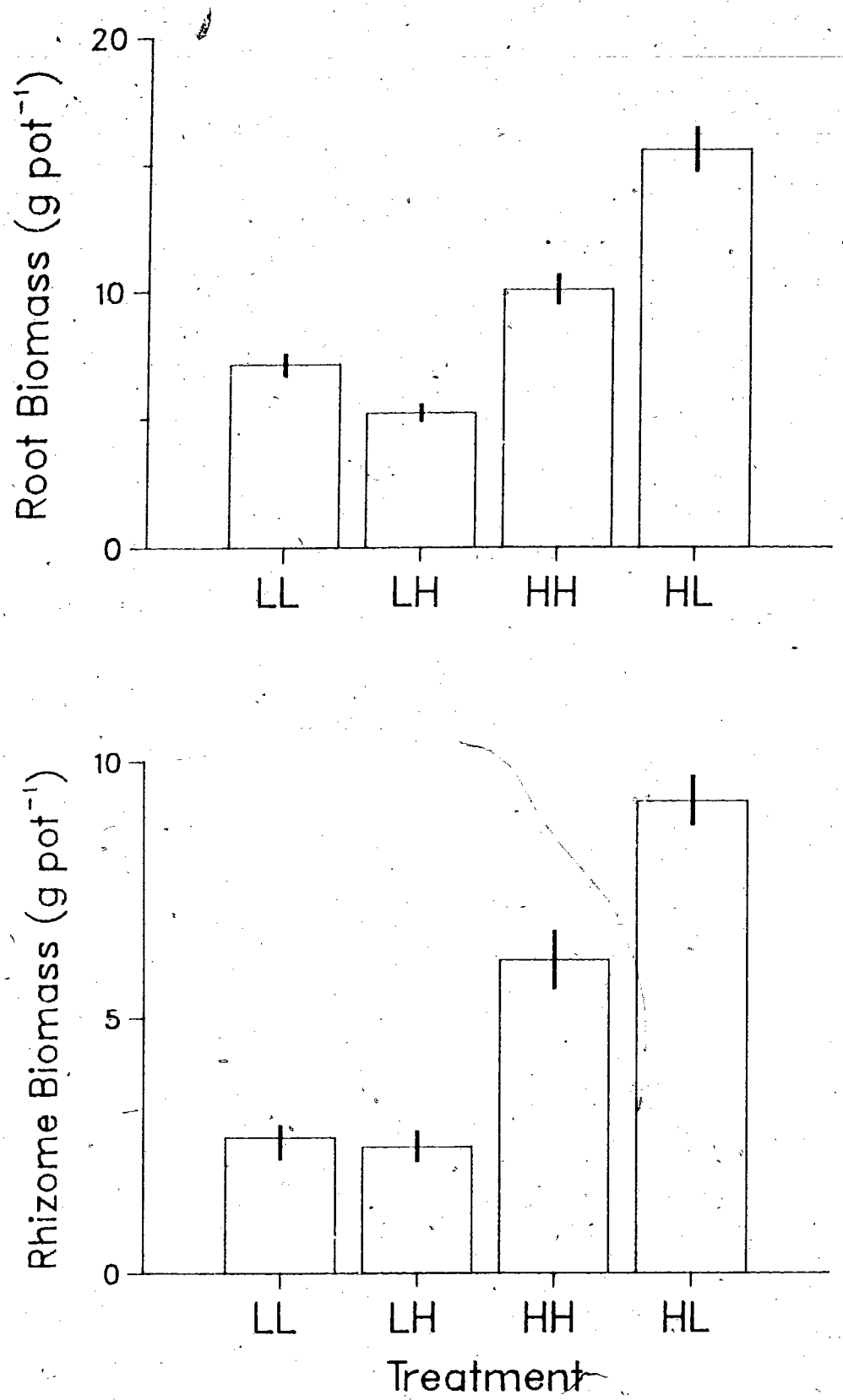

Figure 54. Root and rhizome biomass of *S. americanus* transplants ($\bar{x}\pm se$).

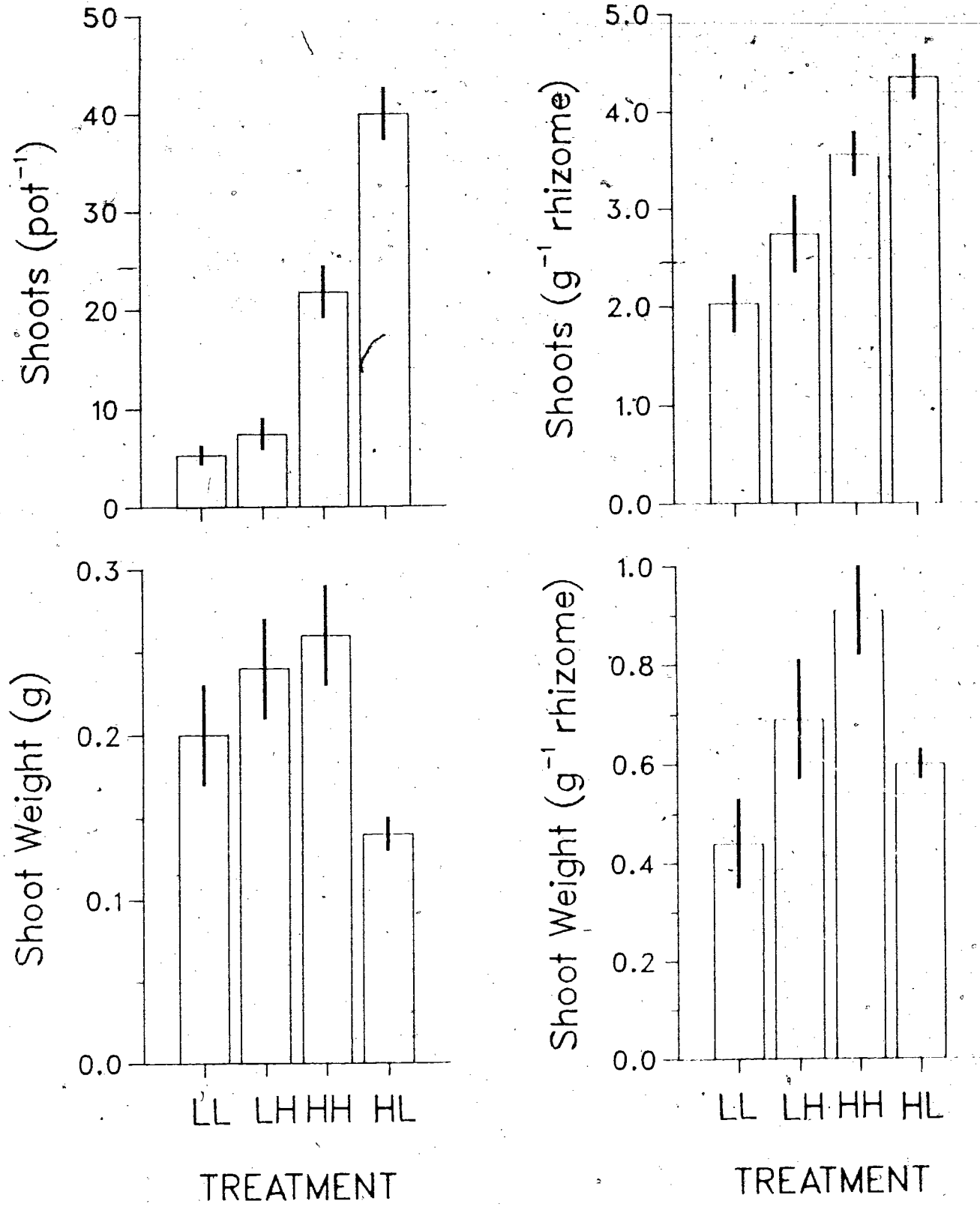

Figure 55. Shoot number and shoot weight of *S. americanus* transplants presented as m^{-2} and standardized on a g^{-2} rhizome basis ($\bar{x}\pm sc$).

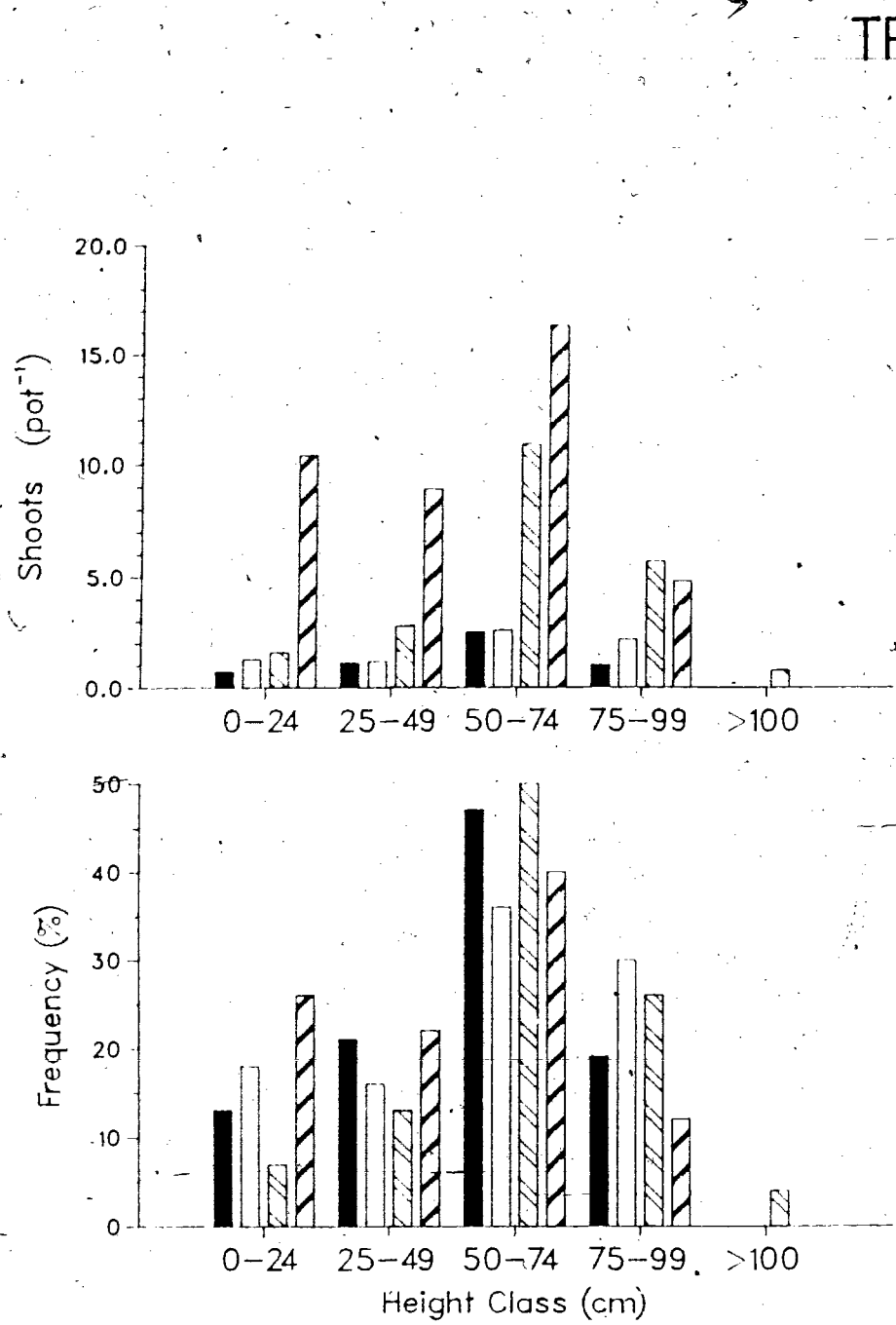

Figure 56. Height distribution of *S. americanus* transplants.

Table 9. Shoot height of transplants (n=total shoots in 10 pots, $\bar{x}$±1se).

Species	Treatment	n	Height (cm)
S. americanus	LL	53	53 (3)
	LH	74	56 (3)
	HH	218	63 (2)
	HL	400	44 (1)
S. maritimus	LL	27	52 (6)
	LM	21	56 (5)
	LH	7	54 (19)
	MM	48	74 (4)
	ML	66	50 (3)
	HH	42	81 (9)
	HL	57	54 (3)

S. maritimus Transplants

High marsh cores had significantly more root biomass than low or middle marsh (Figure 57). There was no significant difference in rhizome biomass between any treatments of *S. maritimus*. Middle and high marsh plants had a greater live corm biomass than those of the low marsh.

There were clear differences in corm number between environments and in the case of the low marsh, within environment. LH had the fewest corms and the lowest corm weight (Figure 58). Cores of the LL and LM treatments had a similar number of corms to HH and HL but were less than half the mass of the HH and HL corms. The middle marsh had the greatest number of corms of the three environments but a similar total biomass to those in the low marsh. Overall, corm number and mean corm weight was not significantly different between treatments from the same native environment. Only LH had corm number significantly different from the other treatments taken in the same native environment (Figure 58). Aboveground measurements of *S. maritimus* transplants were standardized on corm number and weight.

Stem number of low marsh cores decreased when moved to higher elevations (Figure 59). By contrast, stem numbers increased when moved from middle or high marsh environments to low marsh. When shoot number was standardized with corm number, it was evident that no cores produced a 1:1 shoot:corm ratio indicating that not all corms produced a shoot (Figure 59). As well, in no instance was shoot number of a treatment significantly different from its control. HL produced more shoots per corm than LL or ML. As a final comparison, shoot number was presented for a unit weight of live corm (Figure 59). There were no significant differences between any controls and treatments.

There were no significant differences in mean shoot weight between treatments from the low marsh (Figure 60). Shoot weight of ML and HL was significantly less than shoots in their respective native environments. Furthermore, mean shoot weight of ML and HL was not significantly differenct than LL. There were no significant differences in stem weight per unit weight corm (Figure 60).

The height distribution for the *S. maritimus* treatments is presented in Figure 61. The frequency distributions of low marsh cores were similar for all 3 treatments. In the case of

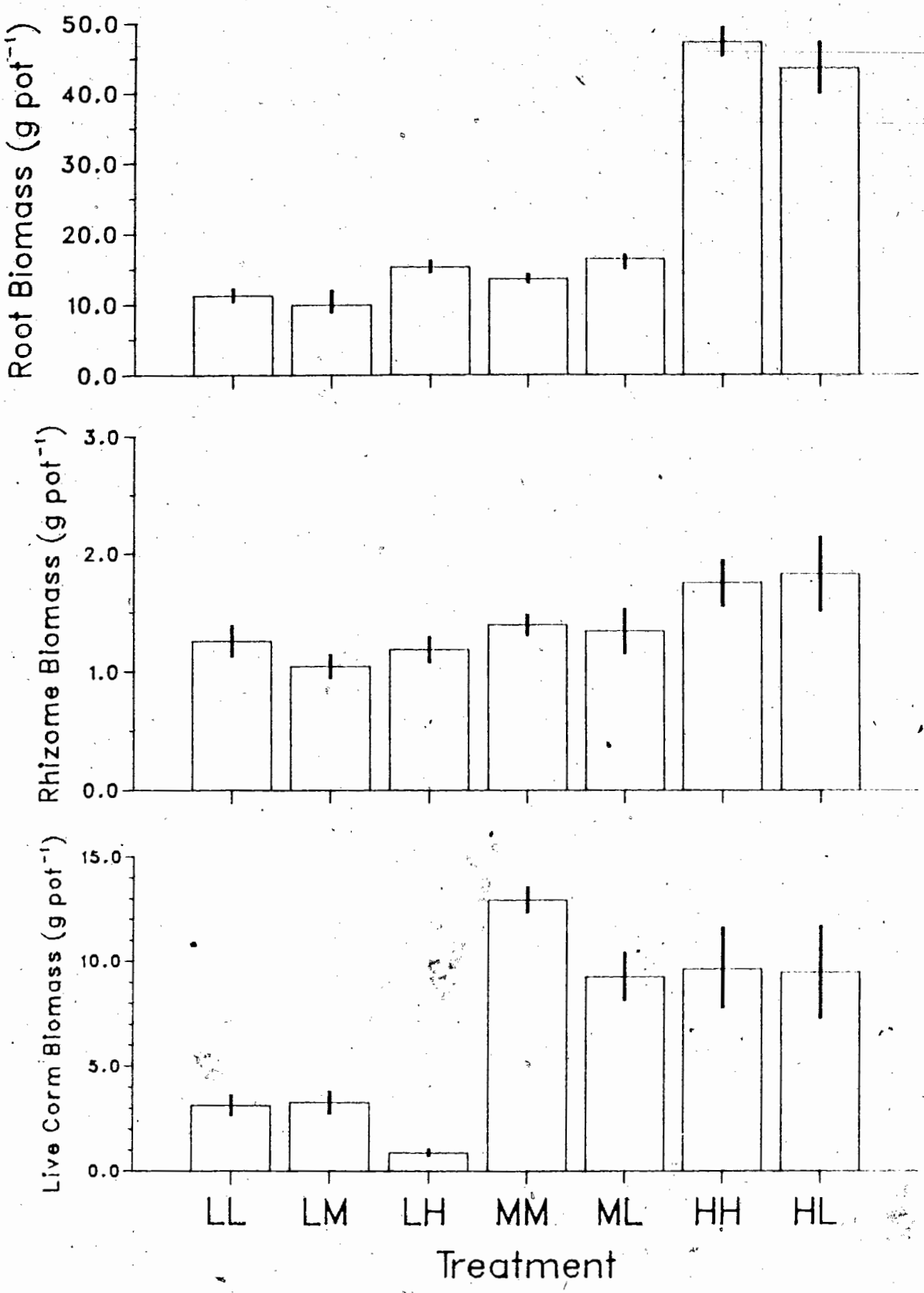

Figure 57. Belowground biomass of *S. maritimus* transplants ($\bar{x}\pm sc$).

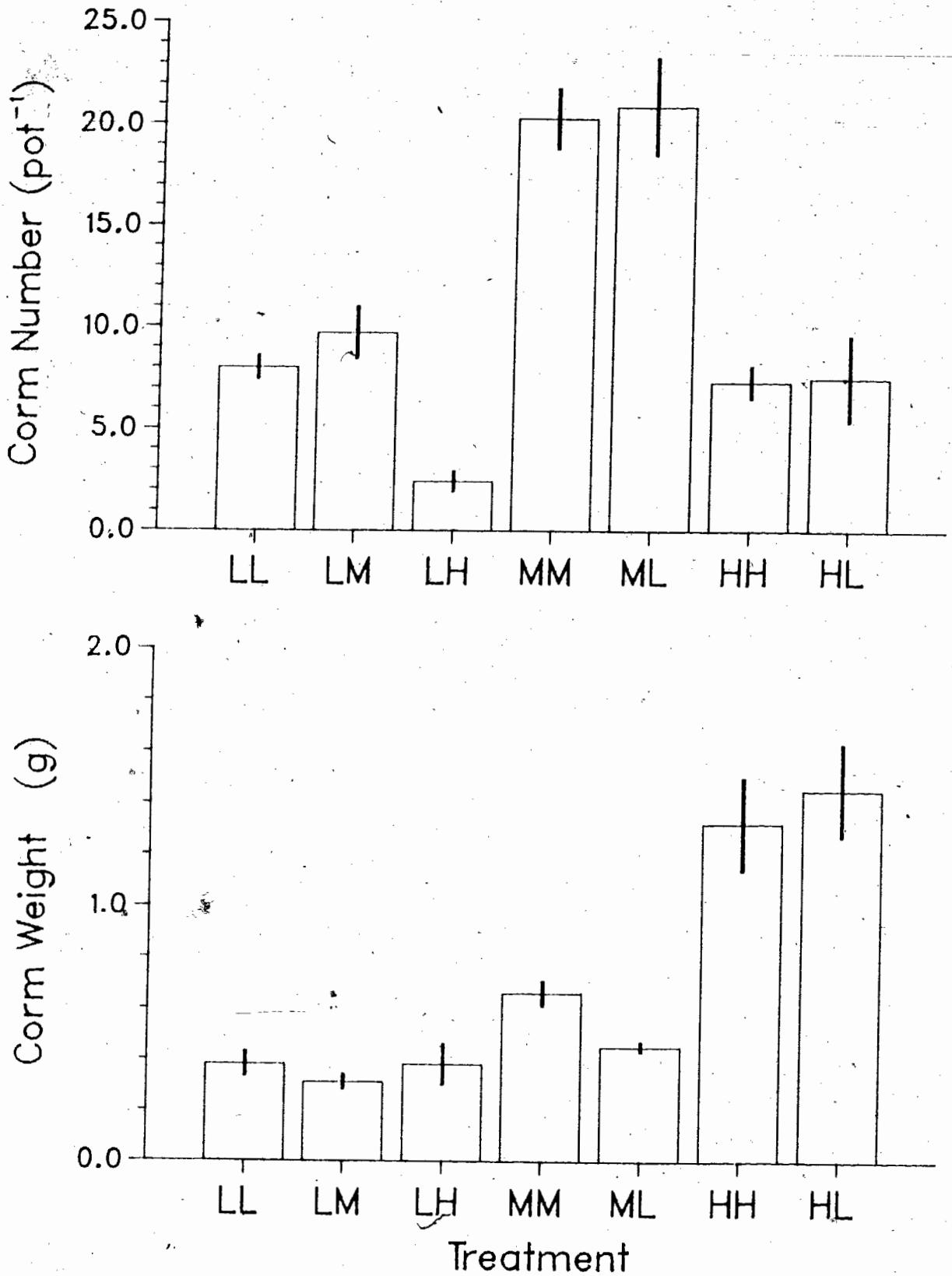

Figure 58. Mean corm number and weight of *S. maritimus* transplants ($\bar{x}$±se).

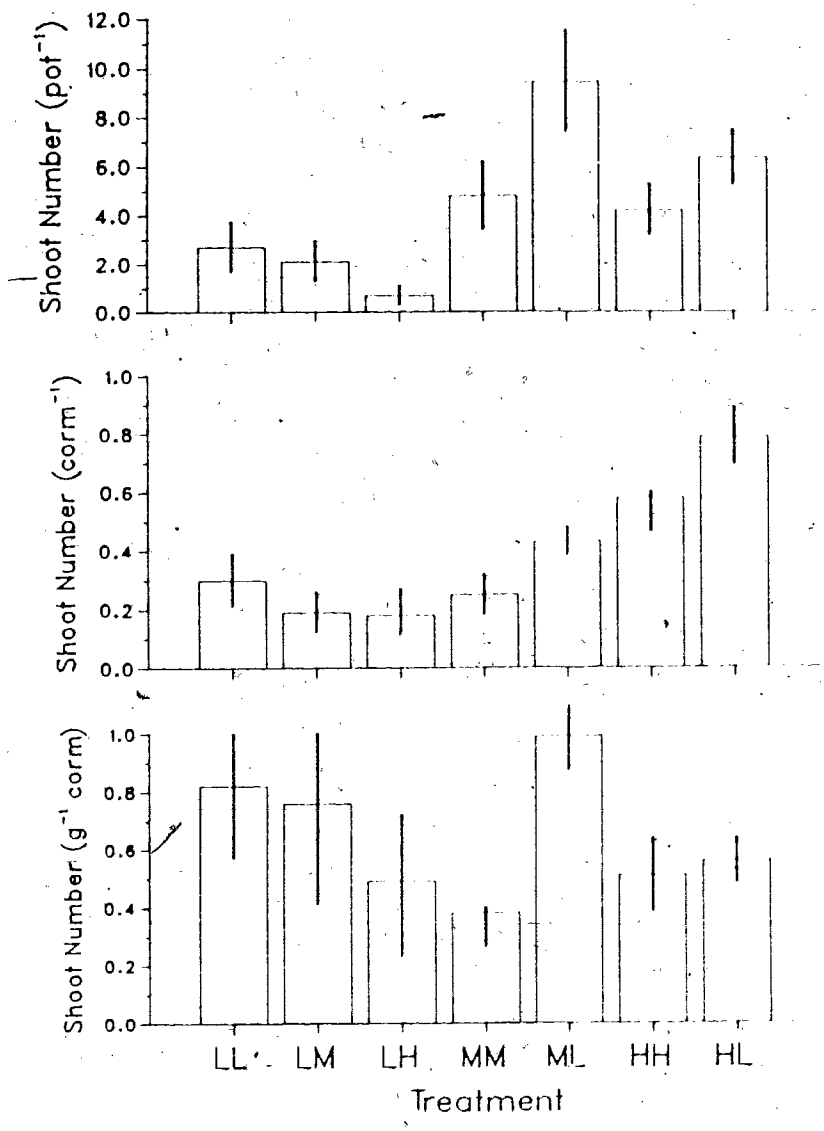

Figure 59. Stem number per pot, per corm and per gram corm of *S. maritimus* transplants ($\bar{x}\pm se$).

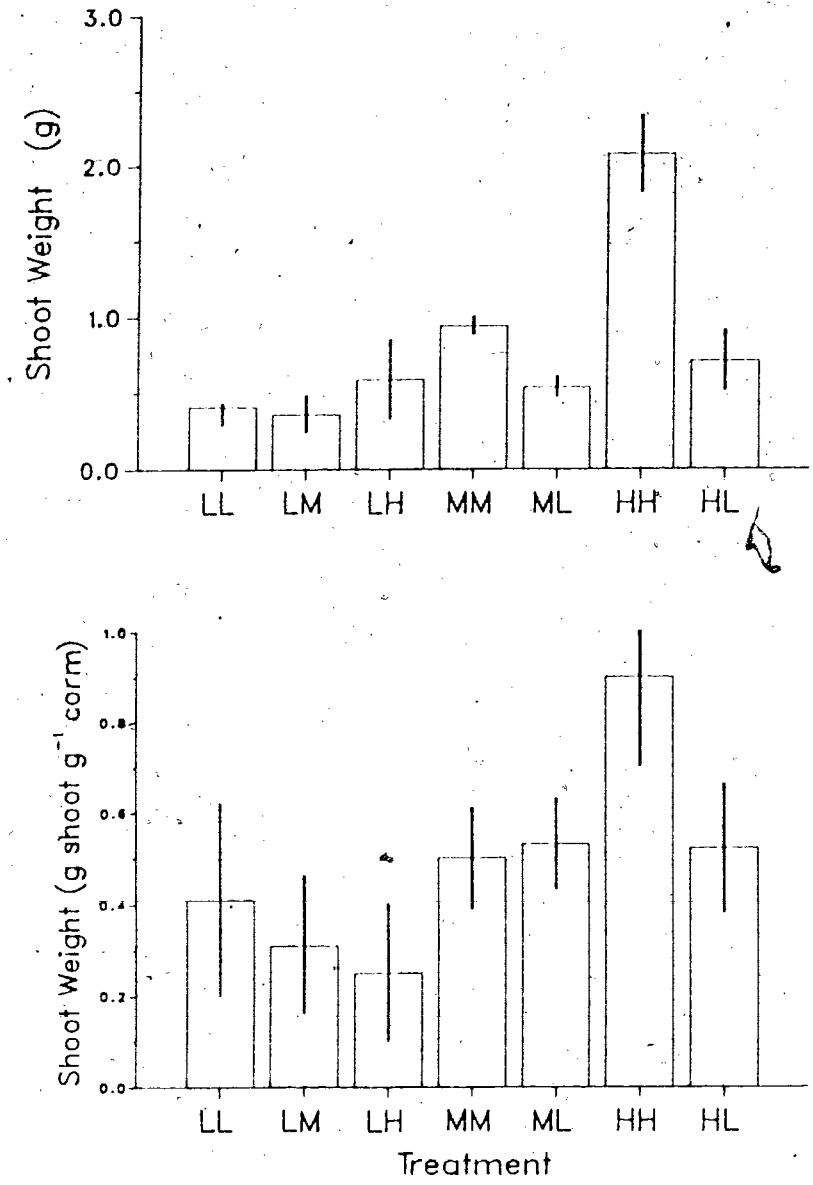

Figure 60. Mean stem weight and stem weight per gram corm in *S. maritimus* transplants ($\bar{x}\pm se$).

the middle and high marsh cores, their height distribution shifted towards the short height classes when moved to the low marsh. These trends are evident when examining mean shoot height (Table 9). Mean shoot height of low marsh cores was equal. ML and HL had similar shoot heights to that of LL and these were much smaller than their controls.

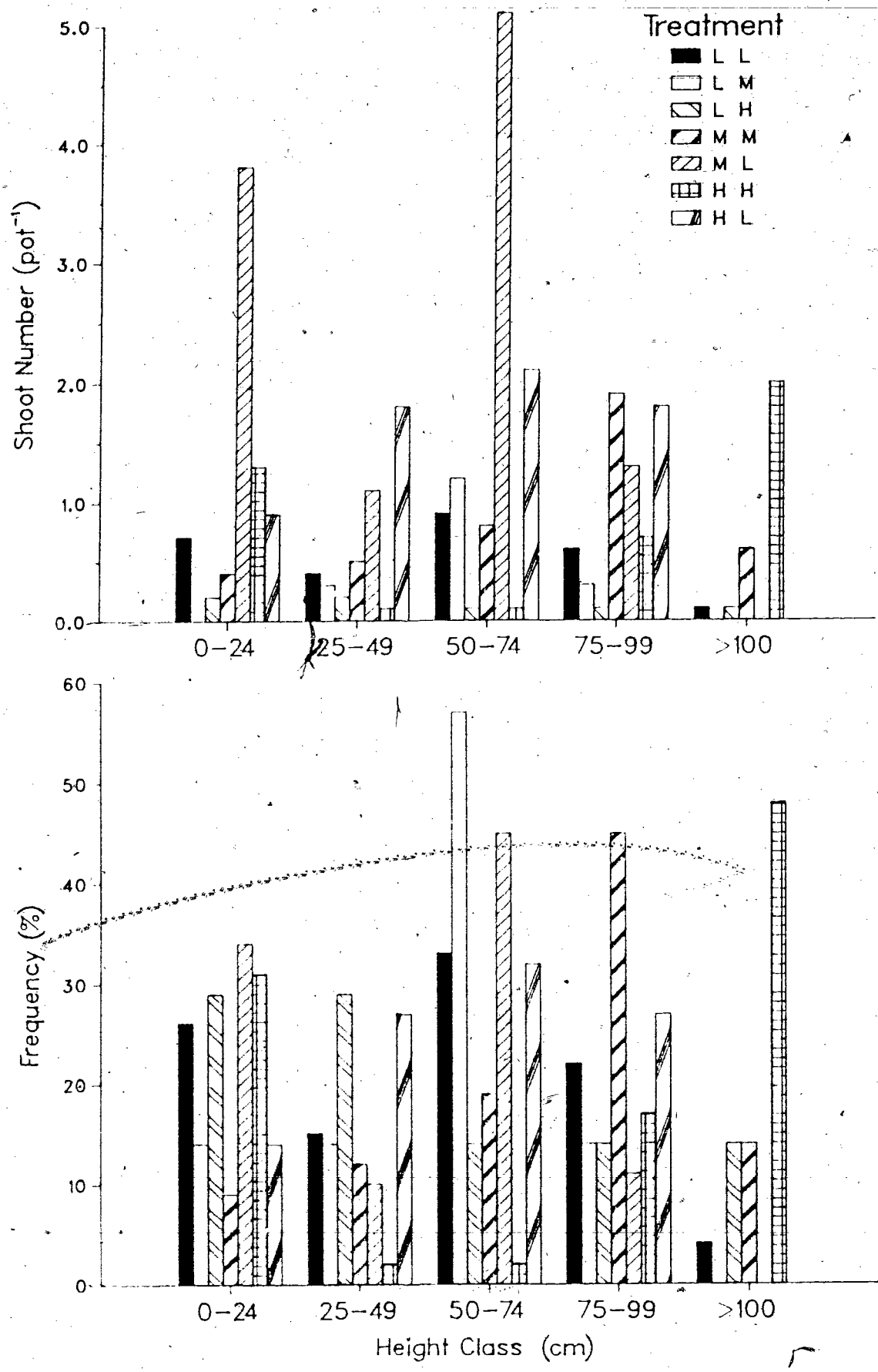

Figure 61. Mean height distribution of *S. maritimus* transplants.

CHAPTER IV

DISCUSSION

The reciprocal transplant experiments suggest that the morphological differences measured for *S. americanus* and *S. maritimus* are not genetically fixed. Plants moved into new environments grew as well as the residents suggesting that there was no local adaptation and that these plants respond plastically to their environment. There can be considerable interelationships between the plasticities of different characters; plasiticity of one character can allow stability of another (Bradshaw 1965). The plasticity of a species must therefore only be considered in terms of the plasticity of individual characters (Bradshaw 1965). In this study, plasticity was measured for shoot height, density, weight and flowering frequency.

The ecophenic variation in *S. americanus* and *S. maritimus* is parallel to results reported by other authors for other marsh species. It is now established that the height forms of *S. alterniflora* are under environmental influence (Shea *et al.* 1975, Valiela *et al.* 1978). Likewise, Seliskar (1985) found that *Deschampsia cespitosa, Distichlis spicata, Grindelia integrifolia, Jaumea carnosa,* and *Salicornia virginica* all demonstrated morphometric plasticity. Smythe (1987) found that only seed germination time was genetically fixed (ecotypic) in populations of *C. lyngbyei* from three Pacific Northwest marshes with different salinity regimes. Characters such as shoot height, shoot number and biomass were ecophenic.

S. americanus cores from the high marsh moved into the low marsh responded with increased root and rhizomes production. Cores moved from the low marsh to the high marsh, showed a decrease in root biomass and no change in rhizome biomass. This conforms with the hypothesis of high root:shoot ratios in harsh environments and may be a response of moving from the stressed low marsh environment (long indundation period), where high root:shoot ratios are required, to the high marsh environment where high root production is not necessary. This interpretation is supported by the transplants using high marsh as donor. This trend of high root:shoot ratios in low elevation environments measured for the transplant experiment contradicts the findings of the field survey (Part C). This pattern assumes that all pots extracted from the same environment contained the same amount of belowground biomass at the start of the field experiment. This assumnption cannot be confirmed and it may be that mean belowground biomass was not equivalent between treatments when these cores were taken. The difference measured at the end of

the experiment therefore, may be an artifact of the original differences.

S. maritimus soil cores (rhizomes and corms) moved from low to high environments showed increased aboveground biomass production. Conversely, plants moved from high to low environments responded with the production of more shoots but they were smaller in height and thus, biomass. This growth pattern is similar to that found in the field survey (Part C). In the high marsh, the maintenance of an erect form is important to prevent shading from neighbouring shoots, particularly in high marsh *S. maritimus* environments, where tall shoots have broad leaves. In the low marsh, low shoot density allows space for many shoots because of greater availability of light during tidal exposure but the long tidal indundation period inhibits shoot elongation.

The results of LL, LM and LH of *S. maritimus* were difficult to interpret as many pots did not produce shoots. This may be due either to the absence of any live corms (Table 10) or the heavy shade produced by the substantial number of tall dead shoots in the high marsh. Almost all of the corms of the high marsh donor sites (HH,HL) were live compared to less than 30% of corms with low marsh donor (LL,LM,LH) (Table 10).

In *S. maritimus* treatments there was no significant difference between the transplants harvested from the low and middle marsh suggesting that the elevation difference between these two sites was insufficient to produce variation. In fact, the variable microtopography in these environments meant that many of the samples from the low and middle marsh were collected at similar elevations.

It should be noted that there were some differences in aboveground values between treatments on the basis of "per pot" measurement. Most of these differences disappeared when aboveground data were presented in terms of weight per unit rhizome (*S. americanus*) or corm weight (*S. maritimus*). This demonstrates the importance of measuring belowground biomass when conducting transplant experiments using a vegetative propagation technique.

The field survey in Part D demonstrated that there were significant differences in the nutritional content of belowground structures from different environments. This was especially pronounced in *S. maritimus* where middle marsh plants had greater belowground nutrient reserves when compared to low marsh plants. In a field transplant experiment conducted in one growing season, these belowground reserves may mask any potential influences of the

Table 10. Proportion of live to dead corm biomass for *S. maritimus* transplants ($\bar{x}\pm sc$). Values represent biomass per pot.

Treatment	Live (g)	Dead (g)	% Live
LL	3.14 (0.49)	8.71 (0.81)	26
LM	3.29 (0.53)	8.46 (0.80)	28
LH	0.89 (0.16)	8.11 (1.32)	10
MM	12.97 (0.61)	1.87 (0.27)	87
ML	9.30 (1.15)	5.22 (1.97)	64
HH	9.67 (1.87)	1.07 (0.47)	90
HL	9.52 (2.21)	0.27 (0.13)	97

environment. The trends observed in this transplant experiment were similar to that measured in the field, suggesting that changes in plant morphollogy were primarily caused by the local environment and not belowground nutrient reserves. It would be useful to analyse the belowground structures of the transplants to determine if there were significant difference in the nutrition of the plants used in the tranplant experiment.

Variation in plant morphollogy may be a response to soil conditions in the pot and not the local environment. For *S. americanus*, the soil characteristics were equivalent between high and low marsh environments, eliminating this concern. Although the nitrogen status of high marsh *S. maritimus* soils is not known, soils from the middle marsh of *S. maritimus* had much higher nitrogen levels when compared to the low marsh (Part B). Thus, plants taken from the middle marsh and moved into the low marsh may be at an advantage because of greater soil nitrogen. It is not known how quickly these soils would transform to a status equivalent to the local environment. Seliskar (year) conducted a reciprocal field transplant experiment in Netarts Bay, Oregon and found that there were differences in the nutrient status of soils from high and low marsh environments. By the end of the summer, however, both native and foreign soils had equivalent nutrient concentrations. The influence of varying belowground nutrient reserves within the plant, differences in soil nutrient status and potential effects of transplant shock can be eliminated by conducting a transplant experiment for more than one growing season.

I conclude that there is ecophenic variation in *S. americanus* and *S. maritimus*. From the data on growth rates of the natural populations, substantial exposure was determined to be the dominant environmental influence (Part C). There should be selection for higher growth rates in the low marsh environment to overcome the longer submergence period. It appears as though plants in all environments have attained maximum growth rates or that growth rate is genetically fixed. It may be, however, that low marsh *S. americanus* and *S. maritimus* have higher growth rates but these rates are reduced to a rate equivalent to their high marsh counterparts by the slightly higher salinities in the low marsh environments. Some preliminary data on growth rates of transplants is presented in Table 11. High marsh donor plants of *S. americanus* had slightly higher growth rates than in the low marsh, but there was no change in growth rate with relocation into a new environment. For *S. maritimus*, only LH did not perform as well as the local plants. This may be a result of

Table 11. Growth rates of transplants ($\bar{x}\pm 1sc$).

Site	Treatment	Growth Rate
S. americanus		mg shoot/g rhizome/h daylight
	LL	0.49 (0.10)
	LH	0.55 (0.10)
	HH	0.67 (0.07)
	HL	0.66 (0.03)
S. maritimus		mg shoot/g corm/h daylight
	LL	0.42 (0.22)
	LM	0.17 (0.07)
	LH	0.18 (0.10)
	MM	0.24 (0.07)
	ML	0.55 (0.11)
	HH	0.57 (0.12)
	HL	0.53 (0.14)

shading from surrounding plants that began growing before the low marsh foreigners began shoot elongation. There are no studies in the literature that suggested exposure time as the primary cause of variation in morphology of marsh plants. Thus, no comparison of growth rates can be made.

PART F

CONCLUSIONS

I conclude that there is population differentiation in *S. americanus* and *S. maritimus* and it is not genetically fixed. The variation measured in shoot height, density and total biomass is ecophenic, primarily under the influence of the local environment. The data on growth rates suggests that exposure time to daylight is the dominant environmental variable influencing plant morphology. Eilers (1975) and Jefferson (1975) determined exposure time for a growing season or monthly interval and related this measure to changes in plant community composition and community location. No studies in the literature have proposed daily exposure time to daylight as the primary cause of variation in growth and morphology of marsh plants, yet it is perhaps the dominant factor in all intertidal environments. Other environmental variables that were deemed important include interstitial salinity in *S. americanus* stands and soil nutrient status in *S. maritimus*. Both high salinity and low soil fertility appear to retard plant growth at the low elevation points of the two species. Thus, the two populations of *S. americanus* and *S. maritimus* sampled at Sea Island represent a generalist genotype with plasticity for these characters.

Variation in nutrient content was also measured for plants at different points of an elevation gradient, but it was not determined if this variation is primarily under genetic or environmental control. It appears, however, to be under environmental control in response to changes in biomass production. In *S. americanus* environments, the factors that resulted in greater biomass production in the high marsh lead to lower nutrient concentrations because of dilution of current stored reserves. In *S. maritimus*, although the middle marsh plants had greater production and therefore dilute nutrient reserves, the greater soil nitrogen levels in the middle marsh environment lead to higher nutrient concentrations in plant structures of this environment. Nutrient accumulations in plant tissues was greatest in high marsh *S. americanus* and middle marsh *S. maritimus*. Nutrient analysis on the plant material from the reciprocal transplant experiment would be a first step in deriving the cause of intraspecific variation in these species.

Exposure time is the driving force in a continuous positive feedback cycle producing greater plant biomass in environments with high exposure times. Plants in high marsh environments with greater exposure time have greater time for photosynthesis and to accumulate aboveground biomass. With greater aboveground biomass accumulated during the year, more resources can be re-allocated belowground at the end of the growing season; this

leads to increased belowground reserves. The following year, plants in the high marsh have greater belowground reserves to allocate to aboveground growth and a longer exposure time to once again accumulate aboveground biomass. After several growing seasons, the high marsh will accumulate much more belowground biomass than the low marsh and hence, greater aboveground biomass.

Plasticity in morphology is not a new phenomenon in plants. Bradshaw (1965) noted that adaptation by plasticity is a widespread and important phenomenon in plants that has been evolved differently in different species. Does the variation measured for *S. americanus* and *S. maritimus* represent various tactics pursued by the same genotype? Differences in the investment of biomass and nutrients to different plant structures both within and between species indicate the employment of different tactics. Plants at the low elevations made greater relative investments of biomass and nutrients into shoots at the time of maximum shoot biomass and nutrient accumulation. This tactic is, in part, a response to tidal inundation. A larger proportion of the nutrient pool is required in shoots to maintain plant physiological processes under stress and, in the *S. maritimus* environments, low soil fertility. There may be a relationship to the minimum amount of photosynthetic tissue required to maintain plant growth with a reduced photoperiod and under more stressed conditions. Furthermore, increased plant leaching and the subsequent loss of dissolved substances at low elevations may result in these plants continuously "pumping" nutrients into shoots. As a result, plants at low elevations invest a greater proportion of nutrients into shoots.

No statistical analyses were undertaken to determine if biomass allocation is a good determinant of nutrient allocation. The trends in biomass allocation of *S. americanus* and *S. maritimus* were similar to that of nutrient allocation; plants in low elevations invested a greater proportion of their biomass and total tissue nutrient pool to shoots. Thus, for *S. americanus* and *S. maritimus*, biomass allocation appears to be a good predictor of nutrient allocation.

Hickman and Pitelka (1975) found that dry weight is related to nutrient or energy allocation in plants with primarily carbohydrate reserves. Lytle and Hull (1980a, 1980b, 1980c) presented evidence that marsh plants such as *Spartina alterniflora* contain carbohydrate reserves in belowground structures. Their studies demonstrated that mature culms of tall *Spartina alterniflora* stands supplied photosynthate for grain production and for carbohydrate

accumulation in rhizomes which may be available for re-growth the following spring (Lytle and Hull 1980a). Until vegetative shoots became energetically independent sometime in June (Lytle and Hull 1980b), carbohydrates in the rhizome supplied carbon for structural development (Lytle and Hull 1980c). Between August and October, the soluble carbohydrate content of rhziome increased sharply in tall stands of *Spartina alterniflora* but did not increase in short-form until mid-October, the time of senescence (Lytle and Hull 1980c). Kistritz *et al.* (1983) suggested a cycle of carbohydrate mobilization between roots, rhizomes and shoots of *Carex lyngbyei* based on the results of other studies which found such a carbohydrate cycle in plants growing in environments with short growing periods, rapid growth rates and overall adverse environmental conditions. These conditions are found in *S. americanus* and *S. maritimus* environments suggesting that these sedges, like *Spartina alterniflora* and perhaps *Carex lyngbyei*, have large carbohydrate reserves. This would support the notion that biomass allocation is equivalent to nutrient allocation.

It is intriguing to speculate on the absence of genetic divergence in *S. americanus* and *S. maritimus*. Two points can be made about the traits examined. First, a small number of traits were studied and thus conclusions can only be drawn about these specific traits. It may be that several traits not studied here are in fact genetically fixed. Secondly, it may be that the traits under examination were not heritable.

There may be abundant gene flow between populations which prevents genetic divergence. Gene flow can be estimated by the amount of sexual reproduction taking place and in the environments of Sea Island, the absence of seedlings suggests low gene flow and rare establishment through sexual reproduction. The low effort measured for sexual reproduction in these species may be another indication of very little gene flow. Long lived plants in intertidal environments that are capable of vegetative reproduction do not require sexual reproduction to maintain the population. This small investment into sexual reproduction, therefore, represents the production of achenes for the possible colonization of new marsh environments and possibly for small additions to the gene pool. It is not known, however, if these species are obligate out-crossers and they may have the capacity to produce achenes without external fertilization. While this would produce seedlings, it would not change the gene pool. Furthermore, the populations sampled may be the product of a common gene pool that has not diverged appreciably in the absence of succesful

establishment of off-spring from sexual reproduction. There may be weak selective forces acting in the Sea Island environment or species may be selected for flexibility of morphology.

I propose the following scenario as an explanation of phenotypic variation in *S. americanus* and *S. maritimus*. Historical aerial photographs of this study site indicate that these clones were not present some 25 years ago, and hence, they are young clones. Sediment accretion builds up the marsh platform and these plants colonize and expand into the new environments leading to more rapid sediment accretion. Plants in the high marsh provide seed or rhizomes for the colonization of the low marsh and once established, prolific vegetative reproduction allows for complete dominance of these newly formed environments. Although *S. maritimus* is not a colonizer of new environments, it is found only in anoxic sediments. The *S. maritimus* environment is homogeneous with only elevation and soil nutrients varying and these increase plant biomass. Thus, there is selection for a genotype that can withstand anoxic conditions and, exposure and soil nitrogen determine the height, biomass and nutrient content of the plants in a particular environment. There has not been ample time for genetic divergence.

A prime area for future study is to determine if variation in nutrient allocation is under environmental or genetic control, or both. Second, it should be determined if any variation is ecoclinal. The traits examined can be expanded to include physiological characteristics (e.g. aerenchymatous tissue) and gel electrophoresis should be undertaken to determine the level of genetic variation.

At the ecosystem level, future studies should center on nutrient pathways between the marsh and estuary. It appears that although a large portion of nitrogen and perhaps other elements in aboveground stems are re-allocated to belowground structures during senescence, all four environments lose nutrients through senescence and tidal export of aboveground shoots and the loss of belowground biomass to grubbing geese. Presently the fate of this material cannot be determined. Some of the plant material may decompose *in situ*, thereby providing nutrients to local plants, or it may be exported to the estuary primarily as dissolved material. This study can be succeeded by a study that elucidates the direction and magnitude of these pathways.

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