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Nitrogen and phosphorus cycling strategies in two tidal freshwater macrophytes, Peltandra virginica and Spartina cynosuroides

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Nitrogen and phosphorus cycling strategies in two tidal freshwater macrophytes, *Peltandra virginica* and *Spartina cynosuroides*

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Nitrogen and Phosphorus Cycling Strategies in Two Tidal Freshwater Macrophytes, Peltandra virginica and Spartina cynosuroides

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Of the Requirements for the Degree of

Doctor of Philosophy

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by

Paul M. Booth, Jr.

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of the requirements for the degree of

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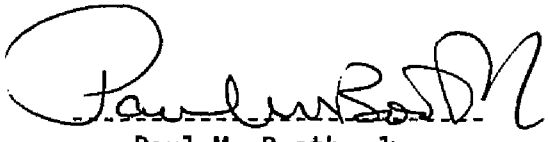

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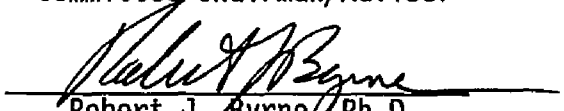

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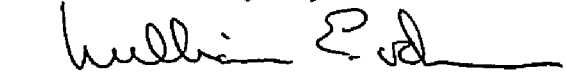

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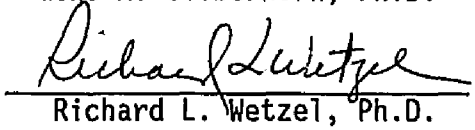

Richard L. Wetzel, Ph.D.

DEDICATION

In memory of my father, General Paul M. Booth and my mother, Isabel B. Booth this study is dedicated to the peaceful coexistence and humane treatment of all God's creatures.

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Abstract

Monotypic stands of the macrophytes Peltandra virginica and Spartina cynosuroides, which shared a common boundary, were studied at Sweethall Marsh, a tidal freshwater marsh located on the Pamunkey River within the Chesapeake Bay estuarine system, Virginia. The primary objective of the study was to evaluate and compare productivity, nitrogen, and phosphorus substrate dynamics in each of the macrophyte species through the development of models which quantitatively assess annual compartmental standing stocks and flows. The secondary objective of the study was to evaluate and compare seasonal patterns of nitrogen and phosphorus use efficiency in the shoots, roots, and rhizomes as well as nitrogen and phosphorus recovery efficiency in the shoots of each macrophyte species. In addition, two hypotheses were studied. The first hypothesis tested was that seasonal nitrogen and phosphorus standing stocks in the shoots, roots, and rhizomes, which reflect uptake and internal cycling patterns, are independent of sediment nitrogen and phosphorus standing stocks, which reflect sediment availability, in each species. The second hypothesis tested was that seasonal nitrogen and phosphorus standing stocks, which reflect uptake and internal cycling patterns, are interdependent, or covary, in the shoots, roots, and rhizomes of each species.

Annual biomass productivity was relatively high in both species. Peltandra shoot productivity, which included relatively high monthly mortality, was characterized by a lag phase in the spring and a rapid growth phase in the summer. Rhizome standing stocks were relatively constant throughout the sampling period. Seasonal patterns of root biomass were apparently asynchronous with those of shoot biomass, increasing from a minimum in July to a peak in January. Spartina shoot productivity, characterized by a spring and summer lag phase and interval periods of rapid growth, reached a peak in September. Seasonal patterns of root and rhizome biomass apparently coincided with shoot productivity, reaching a peak in August and October, respectively. Productivity strategies appear to be adaptive providing each species with certain competitive advantages in terms of resource utilization.

Compartmental models indicate that both Peltandra and Spartina take up, internally cycle, and release to the environment, significant levels of nitrogen and phosphorus. Peltandra appears to conserve higher levels of nitrogen and phoshorus through translocation than Spartina and as such, appears to be more dependent on reallocation and less dependent on de novo root uptake to meet productivity nutrient requirements. Release to the environment is short term in Peltandra in comparison to Spartina due to the fact that shoots fall to the sediment surface and decompose more rapidly. Release of nitrogen and phosphorus through belowground mortality in both Peltandra and Spartina occurs over extended periods of time due to slow decomposition rates. Models suggest that Peltandra and Spartina and their associated sediment compartments are capable of regulating nitrogen and phosphorus fluxes through their uptake and storage capacity.

The relationship between biomass and nitrogen and phosphorus levels was developed through the calculation of use and recovery efficiency indexes. Nitrogen use efficency was significantly higher in the shoots and roots of Spartina compared to Peltandra, while rhizome use efficiency was slightly higher in Peltandra. Phosphorus use efficiency was significantly higher in shoots, roots, and rhizomes of Spartina than in Peltandra. Lower use

efficiency in Peltandra demonstrates a greater demand of nutrient per unit biomass. This demand reflects the increased levels of nitrogen and phosphorus required for photosynthesis and suggests that Peltandra is not limited by nutrient availability. Nitrogen and phosphorus recovery efficiency was higher in Peltandra. Efficiency indexes suggest that although Spartina appears to use nitrogen and phosphorus more efficiently for growth, Peltandra recovers and stores these nutrients more efficiently.

The relationship between tissue and sediment nitrogen and phosphorus was determined through regression analysis. Apparently Peltandra shoot, root, and rhizome tissue nutrient levels are independent of sediment nitrogen and phosphorus availability. Spartina shoot, root, and rhizome nitrogen levels, however, appear dependent on sediment total nitrogen and total phosphorus. the relationship of Peltandra tissue nutrient levels to sediment availabiltiy is explained in terms of the rhizome storage capacity and reallocation of nitrogen and phosphorus to support productivity patterns. Spartina, however, must rely more on de novo root uptake to meet nutrient demands.

Shoot, root, and rhizome nitrogen and phosphorus standing stocks were strongly correlated in both Peltandra and Spartina while sediment standing stocks were not. Nitrogen to phosphorus ratios were higher in the shoots than the roots and rhizomes of both Peltandra and Spartina reflecting the levels of nitrogen required to support photosynthesis. Nitrogen to phosphorus ratios varied over the sampling period, however appeared to converge on an "optimum" ratio. The correlation of nitrogen and phosphorus suggests an interaction between these nutrients although this relationship is unclear. Apparently both Peltandra and Spartina reallocate, as well as require, nitrogen and phosphorus in certain ratios which maximize productivity, uptake, and carbon assimilation.

NITROGEN AND PHOSPHORUS CYCLING STRATEGIES IN TWO TIDAL FRESHWATER MACROPHYTES, *PELTANDRA VIRGINICA* AND *SPARTINA CYNOSUROIDES*

Introduction

Tidal wetlands, an integral component of Atlantic coastal estuarine systems, are generally viewed as transitional zones between open water and terrestial environments. Distributed along a salinity gradient, these vast ecosystems consist of saline wetlands at one extreme, characterized by extensive monotypic stands of Spartina alterniflora and Spartina patens, and freshwater wetlands at the other extreme, characterized by a mixed macrophyte community considered to be among the most diverse and productive in the world (Klopatek, 1975; Whigham et al. 1978). Typical dominant species include Nuphar luteum, Zizania aquatica, Peltandra virginica, Spartina cynosuroides, Carex lacustris, Typha latifolia, Scirpus americanus, and Phragmites communis. This diversity and associated seasonal productivity, afford tidal freshwater macrophyte communities certain structural and functional attributes, among them the ability to act as a biological depository where plant nutrients, especially nitrogen and phosphorus, are cycled (Prentki et al. 1978). As such, tidal freshwater wetlands play an important role in maintaining the ecological balance within estuarine systems.

Tidal freshwater wetlands are defined by the periodic inundation of shallow, freshwater and a water table at, or near, the sediment surface. The resulting saturation produces a substrate of predominantly hydric sediments which are able to support an extensive macrophyte community

through the multi-level biogeochemical cycling of nutrients (Bowden, 1982). The coupling of nutrient cycling within the sediment compartment to macrophyte productivity endows tidal freshwater wetlands with the ability to impact the flow of energy and nutrients within, and out of the system. Indeed, one of the values most often attributed to these wetlands is that of regulating excessive nutrient fluxes. This has led to the popular hypothesis that these wetlands may be modelled as seasonal nutrient sources or sinks, or, in some cases, both (Simpson et al. 1978; Van der Valk et al. 1979; Odum et al. 1984), yet the underlying sediment and community mechanics of these models are poorly understood.

The general estuarine nutrient model for tidal wetlands was developed from work on saline, mesohaline, and brackish wetlands (Axelrad et al. 1976; Haines et al. 1977; Stevenson et al. 1977; deLaune and Patrick, 1980; Nixon, 1980). This model envisions the import of large quantities of dissolved inorganic nitrogen, as ammonium, nitrite, and nitrate, and phosphate, as orthophosphate, to the sediment compartment prior to the growing season as a result of tidal flushing and groundwater inputs (Stevenson et al. 1978; Odum et al. 1984). Within the sediment compartment nitrogen and phosphorus undergo microbial and biological alteration with subsequent uptake by the macrophyte community supporting the seasonal production of above- and belowground biomass. Uptake by the macrophyte community results in temporary storage of significant levels of reduced nitrogen and phosphorus (Klopatek, 1978; Prentki et al., 1978; Nixon, 1980; Patrick and DeLaune, 1980; Gallagher et al. 1980; Hopkinson and Schubauer, 1984). Fall senescence results in the release of significant levels of reduced nitrogen and phosphorus to the environment through decomposition and leaching (Mason

and Bryant, 1975; Dunn, 1976; Odum and Heywood, 1978; Turner, 1978; Hackney and de la Cruz, 1980; Walker, 1984) which may be exported via tidal flushing to adjacent waters (Stevenson et al. 1977; Simpson et al. 1978; Haines et al., 1977) or incorporated into the sediment through sedimentation (Boto and Patrick, 1979; DeLaune et al. 1981) and geochemical processes (Keeney, 1973; Patrick and Reddy, 1976; Rosenfield, 1979; Krom and Berner, 1981; Boatman and Murray, 1982; Bowden, 1982).

The estuarine model, which in recent years has incorporated certain aspects of freshwater data (Klopatek, 1974, 1975; Prentki et al., 1978; Richardson et al., 1978; Whigham and Bayley, 1979; Walker, 1981; Bowden, 1982; Odum et al., 1984), reflects the assumption that tidal freshwater wetlands function in a manner similar to saline and brackish wetlands. There is evidence, however, that the two approaches to nutrient cycling may be different. Bowden (1982), for example, suggested that ammonium uptake by freshwater wetland sediments prior to the growing season is unlikely due to the establishment of concentration gradients which, in effect, inhibit the diffusion of ammonium to the sediments. He demonstrated that these sediments produce sufficient quantities of ammonium through microbial activity to support macrophyte productivity. Klopatek (1975) reported seasonally high levels of available inorganic phosphorus maintained in freshwater sediments suggesting that these wetlands have evolved mechanisms for retaining phosphorus within its boundaries. As these levels were far in excess of those required by the macrophyte community, sediment uptake of large quantities of phosphate seems unlikely. In addition, data from several studies suggest that a large percentage of nitrogen and phosphorus in aboveground shoots, and possibly roots, is translocated to the rhizome

compartment during senescence, rather than lost to the detrital compartment and subsequent decomposition (Klopatek, 1975; Prentki et al., 1978; Van der Linden,1980; Kistritz et al. 1983; Davis and van der Valk, 1983; DeLaune et al., 1986). As such, perennial macrophyte communities may rely on internal cyling to meet much of their nutrient demand rather than depending on de novo root uptake to support seasonal productivity. Thus, the timing of nitrogen and phosphorus uptake, storage, and release by tidal freshwater wetlands may be different than their saline counterparts which, in turn, affects nutrient fluxes and water quality.

Additional data on tidal freshwater wetlands is necessary towards an understanding of their role in nutrient cycling and investigations into this role over the past ten years have provided sufficient baseline data upon which to build future research efforts. The common thread of these research efforts appears to be the dominant role of the freshwater macrophyte community and associated sediment compartments in nutrient cycling as well as most biogeochemical processes (Klopatek and Stearns, 1978). As a result, several basic generalizations regarding tidal freshwater community nutrient dynamics have evolved. It is generally accepted that the macrophyte community acts as a nutrient "pump" regulating the flow of nitrogen and phosphorus from the sediment to the plant, between plant compartments, and to the environment through leaching and death. This pumping mechanism seems to provide certain adaptive advantages by providing an adequate supply of nutrients during characteristic periods of rapid growth, conserving nutrients through translocation and storage, and regulating excessive nutrient fluxes (Howard-Williams, 1985). On the assumption of steady state, de novo root uptake from the sediment compartment is necessary to account

for macrophyte losses through leaching and death. The sediment compartment must therefore be replenished with an available pool of inorganic nutrients either through uptake from the surrounding environment or microbial decomposition of organic matter although the timing mechanisms are unclear.

Although these generalizations may apply to tidal freshwater macrophyte communities as a whole, it is unlikely that, due to the extreme diversity and variations in local environments, all species have adapted identical nutrient strategies. Relatively few individual species, however, have been quantitatively modelled as to annual compartmental nutrient flows. Likewise, little information is available on nutrient efficiency indexes despite the fact that these indexes provide insight into relative productivity and nutrient strategies of tidal freshwater macrophytes. Clearly, modelling annual nitrogen and phosphorus substrate dynamics for individual macrophyte species and their associated sediment compartments are necessary not only to an understanding of the role of macrophytes in nutrient cycling, but in developing the relationship between tissue nutrients and sediment availability as well as the relationship between nitrogen and phosphorus dynamics. This approach to nitrogen and phosphorus dynamics is especially important in areas with extensive tidal freshwater wetlands, like Virginia.

In Virginia, tidal freshwater wetlands are estimated to be one-quarter of the Commonwealth's complement of wetlands, yet little or no data is available as to their role in nutrient cycling (Hershner, 1986). Due to their size, location, and high seasonal macrophyte productivity (Doumlele, 1981), these wetlands have the potential to significantly impact nitrogen and phosphorus cycling within the Chesapeake Bay estuarine system. As a

result, the quantification of nitrogen and phosphorus dynamics within the macrophyte community should clarify the mechanisms by which tidal freshwater wetlands regulate water quality and ecological stability within an estuarine system. It is therefore the purpose of this study to assess annual nitrogen and phosphorus substrate dynamics for two of the dominant macrophyte species in tidal freshwater wetlands, Peltandra virginica and Spartina cynosuroides. The resulting assessment should provide insight as to comparative cycling strategies of individual macrophytes while suggesting best management practices for tidal freshwater wetlands.

Literature Review

Wetland Macrophyte Productivity

The realization that structural and functional attributes of tidal influenced wetlands may be best expressed by measures of macrophyte productivity and that productivity values, in turn, offer a quantitative starting point for further investigation (Klopatek and Stearns, 1978), has resulted in an extensive list of aboveground macrophyte productivity values (Keefe, 1972; Turner, 1976; Whigham et al. 1978; Richardson, 1979; Odum et al. 1984). Estimates of belowground productivity, however, are scarce despite the importance of this component to total annual production (de la Cruz and Hackney, 1977; de la Cruz, 1978; Gallagher and Plumley, 1979; Good et al. 1982). As estimates of annual productivity are essential in the analysis and modelling of energy, carbon, and nutrient flows (Linhurst and Reimold, 1978), accurate assessment of the productivity component becomes increasingly important.

A review of the literature shows that a wide variety of methods have been proposed for estimating macrophyte productivity including those of; peak biomass, consisting of a single harvest; Smalley (1959), which considers changes in live and dead material over an annual growth cycle; Milner and Hughes (1968), which involves the summation of the positive increments in live material over an annual growth cycle; Wiegert and Evans (1964), which calculates an instantaneous rate of disappearence of dead

material from permanent plots; Lomnicki et al.(1968), a modification of the Wiegert and Evans method which estimates productivity by summing mortality and the change in live material from paired plots; Valiela et al. (1975), which estimates productivity from total mortality. These methods have resulted in a wide disparity of production values when applied to a single species (Singh et al. 1975; Linhurst and Reimold, 1978a; White et al. 1978; Shew et al. 1981). As a result, meaningful comparisons of productivity values and nutrient substrate dynamics based on productivity estimates are difficult.

The problem with most of the methods is that they were developed for work in terrestial ecosystems. As such, they do not account for the influence of tidal flushing, decomposition, or other environmental conditions. As these factors directly affect productivity estimates, it essential that a method be selected that is suitable for a particular environment and species. Similarly, there are few standardized methods for obtaining accurate estimates of belowground productivity and for this reason many studies have simply ignored this component (de la Cruz, 1978). Modifications of available methods have been used with some degree of success (Birch and Cooley, 1982), yet the problems associated with accurately estimating productivity remain. A review of the literature should permit an evaluation of the available productivity values within the context of certain environmental parameters and sampling method while providing rationale for future productvity studies.

Aboveground Productivity

Net aerial primary production (NAPP) estimates for wetland macrophytes are highly variable due to differences in sediment and hydrologic regime, geographic location, community type, life history, and biological interaction, yet comparison of productivity estimates must, in theory, consider these as well as all physical, chemical, geological, and biological parameters (de la Cruz, 1978). Similarly, method and sampling interval must be considered since they have been shown to directly affect productivity estimates. For this reason comparison of productivity estimates must be qualitative and a mean value from the literature is often used for comparing recently obtained values (Whigham et al. 1978).

Saline wetlands are generally dominated by relatively monotypic stands of Spartina alterniflora, Spartina patens, Distichilis spicata, and Juncus roemerianus. These species have been shown to be extremely productive over an annual growth cycle, although estimates of aboveground productivity are variable (Keefe, 1972). The variability can usually be attributed to the different degree of stresses faced by saline macrophytes, which include salinity, temperature, and nutrient limitation (Chapin et al., 1987). As with other macrophyte species, there is probably no one best estimate of productivity, but rather values which may be compared on the basis of environmental conditions and sampling method.

NAPP estimates for Spartina alterniflora range from 450 g/m^2 in Delaware (Morgan, 1961; in Walker, 1981) to 3700 g/m^2 for the creekbank tall form in Georgia using the Wiegert and Evans (1964) method (Gallagher et al. 1980). Intermediate annual estimates include 1169 g/m^2 for the tall form in Virginia based on leaf shedding and mortality (Reidenbaugh, 1983), 1089 g/m^2

for the tall form in Mississippi using the Milner and Hughes (1968) method (de la Cruz, 1974), and 2658 g/m^2 in Louisiana using the Wiegert and Evans (1964) method (Hopkinson et al. 1978). The variability in productivity estimates demonstrate the problems associated with a lack of standardized parameters in the estimation of aboveground productivity. For this reason, the most useful estimates of aboveground productivity are often those that compare several methods within the same wetland or compare species productivity in similar wetland types but under a broad latitudinal range.

Linhurst and Reimold (1978a) compared five harvest methods (peak standing crop, Milner and Hughes (1968), Smalley (1959), Valiela et al. (1975), and Wiegert and Evans (1964)) in the estimation of NAPP for Spartina alterniflora on a creekbank in Maine. They reported annual productivity estimates of 431 g/m^2 for both the peak standing crop and the Milner and Hughes method. Higher values of 758 g/m^2 were reported for both the Smalley and the Valiela et al. methods and 1602 g/m^2 using the Wiegert and Evans method. As the latter was considered the only method which incorporated the components necessary for a satisfactory estimate of NAPP, i.e. mortality, this production estimate was considered to be the most accurate. In a similar study, Shew et al. (1981) compared five harvest methods (peak standing crop, Milner and Hughes (1968), Smalley (1959), Wiegert and Evans (1964), and Lomnicki et al., 1968). Results indicated that peak standing crop, Milner and Hughes, and Smalley methods severely underestimated annual production with estimates of 242, 214, and 224 g/m^2, respectively. The methods of Wiegert and Evans and Lomnicki et al., however, were thought to overestimate annual productivity. A modification of the Lomnicki et al.

method provided the best estimate at 454 g/m^2/year. White et al. (1978) reported annual production etimates of 1473, 1527, and 2859 g/m^2 for Spartina alterniflora using peak standing crop, Smalley, and Wiegert and Evans methods, respectively. The authors attributed the disparity in production estimates to the inclusion of mortality in the latter.

NAPP values for Spartina patens, like Spartina alterniflora, have been shown to vary according to location and method used. Walker and Good (1976) reported annual productivity estimates as low as 388 g/m^2 in an upper estuary of New Jersey, while de la Cruz (1974), using the method of Milner and Hughes (1968) estimated annual production at 1922 g/m^2 in Mississippi. Using the Williams and Murdoch (1972) method together with estimates of mortality, Hopkinson et al. (1980) calculated annual production at 4159 g/m^2 in Louisiana with an annual turnover of 4.16. Using the Wiegert and Evans (1964) methods, Hopkinson et al. (1978) reported a maximum literature annual production estimate of 6043 g/m^2 for Spartina patens. The authors concluded that the resulting high turnover rate demonstrated the importances of including interval mortality in the estimate of annual productivity.

Several studies have compared annual productivity for Spartina patens in one location using different methods and at several locations using different methods. In the White et al. (1978) study, annual productivity estimates were 2194, 1342, and 1428 g/m^2 in a Louisiana salt marsh using the methods of peak biomass, Smalley (1959), and Wiegert and Evans (1964), respectively. Linhurst and Reimold (1978b) compared annual production of Spartina patens in Maine, Delaware, and Georgia using several different

methods. In Maine, annual production was estimated at 912, 912, 3523, 2523, and 5833 g/m^2 using the methods of peak biomass, Milner and Hughes (1968), Smalley (1959), Valeila et al. (1975), and Wiegert and Evans (1964), respectively. In Delaware, production estimates were 807, 522, 980, 1241, and 2753g/m^2/year, while in Georgia, values were 946, 705, 1674, 1028, and 3925 g/m^2/year, using the same methods, respectively. As the maximum values in this study represent productivity based on mortality, they are probably the most accurate estimates of annual productivity.

Estimates of annual production for other saline macrophytes are less numerous. Production estimates for Distichlis spicata include 1484 g/m^2year in Mississippi (de la Cruz, 1974) and 1967 g/m^2/year in Louisiana (Hopkinson et al. 1980). Linhurst and Reimold (1978b), in their comparative study reported annual production estimates for Distichlis at 856, 864, 1274, 1191, and 2017 g/m^2 in Delaware and 395, 283, 1258, 988, and 4378 g/m^2 in Georgia using the methods of peak standing crop, Milner and Hughes (1968), Smalley (1959), Valiela et al. (1975), and Wiegert and Evans (1964), respectively. White et al. (1978) reported annual productivity estimates of 1164, 1292, and 1162 g/m^2 in Louisiana using the methods of peak standing crop, Smalley, and Wiegert and Evans, respectively. Annual production estimates for Juncus roemerianus range from 1697 g/m^2 (de la Cruz, 1974) and 2200 g/m^2 (Gallagher et al. 1980). to 3295 g/m^2 (Hopkinson et al. (1980). In their comparative study, White et al. (1978) reported values of 1959, 1740, and 1806 g/m^2/year for Juncus using the methods of peak standing crop, Smalley, and Wiegert and

Evans, respectively. The latter study indicates that mortality contributed little to the annual estimate of primary productvity in Juncus.

Brackish and freshwater tidal wetlands are dominated by an extremely diverse macrophyte community. Dominant species include Spartina cynosuroides, Peltandra virginica, Pontederia cordata, Nuphar advena, Zizania aquatica, Phragmites communis and Typha spp.. Increased interest in brackish and freshwater wetlands in recent years has resulted in an extensive list of macrophyte productivity estimates (Whigham et al. 1978; Richardson, 1979; McCormick and Somes, 1982). Production estimates have been reported to be extremely high often exceeding production of saline macrophytes (Whigham et al. 1978; Odum et al. 1984), classifying tidal freshwater wetlands among the most productive areas in the world (Klopatek, 1975). As with saline macrophytes, available estimates of tidal freshwater macrophyte productivity are variable due to local environmental conditions, and may over- or underestimate productivity depending on sampling method. For example, in a diverse tidal freshwater macrophyte community, the use of peak standing crop will miss not only senesced vegetation but also recruitment following peak biomass, i.e. bimodal peaks (Walker, 1981), and species which dominate at a later time (Whigham et al. 1978). As interval mortality is often significant in tidal freshwater and brackish wetlands, it is essential that this component be included in estimates of annual production. Similarly, decomposition rates which are dependent on morphology, (Dunn, 1978; Turner, 1978; Odum and Heywood, 1978), must also be considered. Compounding the problem is the fact that unlike the relative monotypic macrophyte stands found in saline wetlands, tidal freshwater

macrophyte stands may consist of many species and annual productivity estimates must be evaluated on the mixture present.

Spartina cynosuroides, a dominant species in most brackish and freshwater wetlands, generally occurs in monotypic stands and annual production estimates for this species are variable. Using the Milner and Hughes (1968) method, de la Cruz (1974) reported annual production to be 2190 g/m^2 in Mississippi. Hopkinson et al. (1978), using the Wiegert and Evans (1964) method, estimated productivity to be 1355 g/m^2 in a Louisiana coastal marsh. Flemer et al. (1978), using peak biomass, reported annual productivity to be 951 g/m^2, while McCormick (personal observation, in Whigham et al. 1978) calculated an annual production rate of 3543 g/m^2. Odum and Fanning (1973) combining peak standing crops with dead biomass estimated annual production to be 1175 g/m^2. Schubauer and Hopkinson (1984) estimated annual production at 3080 g/m^2 with an annual turnover rate of 5.35 (annual productivity/mean biomass).

Peltandra virginica also dominates tidal freshwater wetlands and estimates of annual production are extremely variable. Due to growth patterns and morphology, which usually result in periods of rapid growth and extensive shade cover, these species are often found as robust monotypic stands along creekbanks, however may also be found in mixed communities. Good and Good (1975), using peak standing crop, reported annual production for Peltandra between 819 and 1286 g/m^2. Flemer et al. (1978), in a study of two tributaries of the Chesapeake Bay, estimated annual production at 988 g/m^2, not including dead biomass of 132 g/m^2. Doumlele (1981), sampling a

series of transects, estimated that Peltandra virginica accounted for 55%, or 423 g/m^2/year, of total macrophyte production. Whigham and Simpson (1975), using peak standing crop, estimated production at 650 g/m^2/year. In a more recent study, Walker (1981) using multiple harvests through peak standing crop, reported annual production rates of 452 g/m^2 at a site with poorly drained sediments and 637 g/m^2 at a well well drained site. None of the above studies, however, sufficiently account for interval mortality, which has been shown to be extremely high in Peltandra (Pickett,1984; Wohlgemuth, 1989). The Wohglemuth study, which employed permanent quadrats, followed tagged shoots of Peltandra through the growing season and estimated monthly and annual production base on mortality. Turnover was estimated to be approximately 2.24, (annual produtivity/peak biomass) Production values for Pontederia cordata, a species with similar morphology, are relatively scarce with annual estimates of 35 g/m^2 in a Chesapeake Bay mixed community (Doumlele, 1981) and 63 g/m^2 in New Jersey (Jervis, 1969).

Additional species which dominate brackish and freshwater wetlands are also characterized by high annual productivity. Using a sequential harvest, Good and Good (1975) reported annual production in Nuphar advena to reach 605 g/m^{2}in New Jersey while McCormick (1970) estimated production at 1175 g/m^2 in Delaware. Annual productivity estimates for Zizania aquatica range from 330 g/m^2 (Jervis, 1969) to 1600 g/m^2 (Good and Good, 1975) in New Jersey. Phragmites communis annual production is relatively high in comparison to other macrophytes reaching 1792 g/m^2, not including mortality,

(Flemer et al. 1978) and 1074 g/m^2 in New Jersey (Walker and Good, 1976). Annual production estimates for Typha spp. are extreme variability ranging from 894 g/m^2 in New Jersey (Good and Good, 1975) to 1467 g/m^2 in Wisconsin (Klopatek and Stearns, 1978).

Relatively few studies are available which compare methods or location in the estimate of productivity for brackish and freshwater macrophytes. Data that are available point to some of the problems inherent in accurately measuring productivity in these wetlands. Linhurst and Reimold (1978b) reported annual production rates of 920, 965, 1501, 3203, and 1749 g/m^2 for Phragmites communis in Delaware, and 1920, 1866, 2789, 1742, and 6039 g/m^2 for Spartina cynosuroides in Georgia, using the methods of peak biomass, Milner and Hughes (1968), Smalley (1959), Valiela et al (1975), and Wiegert and Evans (1964), respectively. The variability encountered in these methods, demonstrates the need for selecting a suitable sampling method.

Belowground Productivity

Despite the extensive list of aboveground productivity estimates, there are relatively few for the belowground component. This is due, in part, to the lack of reliable sampling techniques and extreme difficulty in obtaining belowground biomass samples (Good et al. 1982). However, as the extensive system of roots and rhizomes in most perennials offer certain adaptations which allow these species to thrive in an otherwise hostile environment, it is important to understand their role in annual productivity and nutrient cycling. The recent recognition of the role of the belowground component to the anchorage, stability, and nutrient uptake of wetland macrophyte species,

has resulted in an increased number of belowground production methods and estimates. More data as well as uniform methods are necessary, however, if belowground productivity, which often exceeds aboveground productivity, is to be understood.

As with aboveground, belowground productivity methods remain variable. The methods that are available are considerd to be less reliable than their aboveground counterparts due to the spatial distribution of belowground biomass (Good et al. 1982). Generally, a type of coring device is used (Good et al. 1982) in both annuals and perennials with relatively small but extensive roots and rhizomes (Gallagher, 1974; Gallagher and Plumley, 1979; Kistritz et al. 1983; Hackney and de la Cruz, 1986). In species with large rhizomes which grow in clumps, complete excavations are often necessary (Good and Good, 1975; de la Cruz, 1978; Walker, 1981). In addition to sampling problems, it is often difficult to separate live from dead material which will, in turn, significantly affect production estimates. For this reason, separation techniques are generally based on color and turgidity (Stroud, 1976) or some type of staining technique (Good et al. 1982). The methods available and appropriate species are reviewed by de la Cruz (1978), who suggests the need for standardized techniques in belowground sampling if meaningful comparisons are to be made.

An excellent review of belowground productivity estimates for both saline and freshwater macrophytes is provided by Good et al. (1982). The majority of belowground productivity estimates available are for saline macrophyte species, the largest number of which are for Spartina alterniflora. Gallagher and Plumley (1979) reported annual productivity in the tall form of Spartina to reach 2100 g/m^2 in Georgia while Valiela et al.

(1976), using enriched fertilization studies, estimated root and rhizome production to reach a peak of 2500 g/m^2 in Massachusettes. Based on a maximum - minimum calculation, Stroud (1976) reported that net annual belowground productivity Spartina in North Carolina ranged from 301 to 325 g/m^2 in the tall form and 309 to 390 g/m^2 in the short form (FWS, 1977). Summing periodic mass changes in live and belowground organic matter (Schubauer and Hopkinson, 1984) estimated root and rhizome productivity in Spartina at 4780 g/m^2/year. This value is relatively high and may be due to the fact that the authors attempted to account for midseason decomposition. Additional species for which annual estimates of belowground productivity are available include Distichlis spicata, 2788 g/m^2 (Good and Frasco, 1979), Juncus roemerianus, 3350 g/m^2 (Gallagher and Plumley, 1979); and Phragmites communis, 3650 g/m^2 (Gallagher and Plumley, 1979; in Good et al. 1982). The extreme variability in these estimates is most likely due to a combination of factors, including latitude and sampling technique, as well as nutrient demands of aboveground biomass, all of which point to the need for a more standardized approach to sampling the belowground component.

Data on belowground productivity in tidal freshwater wetlands is very limited, however there is evidence that in these areas belowground productivity may be more extensive than in saline wetlands. Good and Good (1975), in an extensive study of a tidal freshwater marsh in New Jersey, reported extremely variable estimates of belowground production for the macrophyte comunity. Belowground standing crops ranged from 256 to 890 g/m^2 in Zizania aquatica with annual productivity at 610 g/m^2, 1134 to 1804 g/m^2

in Nuphar advena, a species with a large rhizome component, with annual productivity at 1360 g/m^2, 576 to 1800 g/m^2 in Typha spp. with annual productivity at 1370 g/m^2, and 1169 to 3152 g/m^2 in Peltandra virginica, a species with perhaps the largest belowground component in tidal freshwater wetlands, with annual productivity at 2460 g/m^2 (in Good et al. 1982). Walker (1981), using complete excavation, reported root production for Peltandra virginica to reach 893 g/m^2/year in a poorly drained sediment and 1258 g/m^2/year in a relatively well drained sediment. Estimates for belowground productivity of Spartina cynosuroides include 2200 g/m^2/year (Hackney and de la Cruz, 1986), 3500 g/m^2/year (Gallagher and Plumley, 1979; in Good et al. 1982) and a literature maximum value of 4628 g/m^2/year in a Georgia coastal marsh (Schubauer and Hopkinson, 1984). Additional belowground productivity estimates include 518 g/m^2/year for Zizaniopsis miliacea in a Georgia freshwater wetland (Birch and Cooley, 1982) and 260 g/m^2/year for Carex rostrata in New York (Bernard and Hankinson, 1979).

Belowground:aboveground (R:S) ratios also provide insight into belowground productivity dynamics with higher ratios generally found in species which must acquire limited nutrients from an anaerobic environment (Shaver and Billings, 1975). Whigham and Simpson (1978) established R:S ratios for fifteen tidal freshwater macrophytes using a linear regression model. They found suitable ratios exist, with values ranging from 0.55 for Typha to 8.42 for Peltandra virginica.

The importance of including the belowground component is best demonstrated by the few studies which include both above- and belowground

values in the calculation of total annual productivity. Schubauer and Hopkinson (1984) reported total annual production at 7708 g/m^2 Spartina alterniflora of which 4780 g/m^2 were attributable to the belowground component. As such, belowground productivity accounted for some sixty one percent of the total productivity. In the same study, a total annual production of 7708 g/m^2 was calculated for Spartina cynosuroides, of which 4628 g/m^2 were the result of belowground production, or sixty percent. Of the total annual production of 2048 g/m^2 for Zizaniopsis miliacea, 518 g/m^2, or twenty five percent, were attributable to the belowground component . The effect of belowground production of Peltandra virginica which has a more extensive belowground component is also significant. Walker (1981) reported that of a total annual production of 1345 g/m^2, 893 g/m^2, or sixty one percent, were the result of belowground production in a poorly drained sediment, while in a well drained sediment, of a total annual production of 1895 g/m^2, 637 g/m^2, or fifty percent, were attributable to the belowground component. The belowground component is, then, not only important to annual productivity estimates but to studies which model nutrient substrate dynamics based on estimates of both above- and belowground biomass.

Nitrogen and Phosphorus Dynamics

One of the values most often attributed to wetlands is the regulation of nutrient fluxes through uptake, storage, and release to the environment (Odum et al. 1984). Stevenson et al. (1977) suggested that the ability of wetland systems to cycle nutrients is directly tied to nutrient sources,

tidal flushing, salinity, redox potential, and macrophyte succession. In addition, sediment biogeochemical properties have a marked effect on the ability of wetlands to retain nutrients, especially nitrogen and phosphorus (Patrick and Khalid, 1974; Krom and Berner, 1980; Boatman and Murray, 1982; Bowden, 1982). Nutrient cycling mechanisms involving tidal surface waters, sediments, and macrophyte communities have been studied rather extensively over the past 20 years and there are several excellent reviews available (Kadlec, 1979; Whigham and Bayley, 1979; Nixon, 1980; Odum et al., 1984; Howard-Williams, 1985; Denny, 1987). Despite these efforts, the role of wetlands in the regulation of nutrient fluxes is still unclear. This is due, in part, to the extreme variability in wetland types, location, community structure, and local environmental parameters, each of which affect the seasonal timing and behavior of nutrient fluxes. As a result, general nutrient hypotheses are usually extrapolated from a diverse and largely fragmented data base.

Tidal wetlands are believed to impact nutrient substrate dynamics in many ways. Due to their location, they often intercept agricultural and urban runnoff (van der Valk et al. 1979), tidal inundation, flooding, groundwater (Kadlec, 1979), and seasonal river overflows. Water entering wetland systems in such a manner is assumed to be retained for a sufficient length of time to allow interaction with wetland sediments (Burton, 1981). Phosphorus may be adsorbed on suspended sediments or organic matter (Spangler et al. 1976) followed by deposition, or form insoluble complexes with iron which precipitate onto the sediment surface (Stumm and Morgan, 1970). Nitrogen may be deposited through an interaction with suspended sediments or transformed through microbial processes in the water column

(Keeney, 1973; van der Valk et al. 1979). Following transformations and deposition, nitrogen and phosphorus become available to the root systems of the macrophyte community through sedimentation (Boto and Patrick, 1979) and certain chemical exchange processes (Patrick and Khalid, 1974; Boatman and Murray, 1982). Interaction with the sediments and subsequent uptake by the macrophyte community results in the temporary storage of significant levels of nitrogen and phosphorus within the wetland system. An understanding of the role of the macrophyte commmunity in retaining and cycling nitrogen and phosphorus over an annual cycle is therefore essential to an understanding of the conceptual model for wetland nutrient dynamics.

The majority of the data which supports this conceptual model is the result of work in saline marshes (Axelrad et al. 1976; Haines et al. 1976; Delaune and Patrick, 1980; Nixon, 1980; Nixon, 1981; Hopkinson and Schubauer, 1984). There are, however, an increasing number of studies on the role of freshwater wetlands in the cycling of nitrogen and phosphorus (Klopatek, 1974, 1978; Brinson and Davis, 1976; Simpson et al. 1978; Richardson et al. 1978; Prentki et al., 1978; Walker, 1981; Kistritz et al., 1983). As the majority of these studies deal with plant and sediment mediated nitrogen and phosphorus substrate dynamics, as well as the construction of nutrient models, the following review will be restricted primarily to these components.

Plant Mediated Processes

It has been demonstrated that nitrogen and phosphorus cycling varies within wetland systems due to the structure of the macrophyte community. Monotypic stands in saline wetlands and a diverse community in freshwater

wetlands have been shown to assimilate and release large quanities of these nutrients over an annual cycle (Denny, 1987). As a result, there is a relatively large data base on the role of macrophytes in nutrient cycling. Although nitrogen and phosphorus uptake and storage has been shown to fall within certain ranges for wetland macrophyte species (Boyd, 1978; Kadlec, 1979), distinct seasonal patterns are generally observed (Klopatek, 1975; Mason and Bryant, 1975; Bernard and Solsky, 1976; Gallagher et al. 1980; Walker, 1981). Typically, nitrogen and phosphorus concentrations are highest in aboveground shoots at the beginning of the growing season when standing stocks are lowest (Klopatek, 1975; Walker, 1981; Kistritz et al. 1983; Hopkinson and Scubauer, 1984). Gerloff and Kromholtz (1966) termed the higher concentration of nutrients in excess of tissue demand "luxury" accumulation. Apparently, macrophytes accumulate nitrogen and phosphorus at higher concentrations in early developing shoots and roots which, in turn, are capable of supporting characteristic periods of rapid growth. Concentrations tend to decline to lower or minimum levels as growth proceeds. Hutchinson (1975) in a review of the available literature accepts Gerloff and Kromholtzs' estimate of 1.3% and 0.13% as critical or minimum concentrations of nitrogen and phosphorus, respectively (in Kadlec, 1979). Conversely, rhizome concentrations and standing stocks are both highest prior to shoot production and decrease as seasonal growth increases. This decrease is generally attributed to reallocation which supports above- and belowground productivity. As dieback proceeds in the fall, translocation to belowground rhizomes increases nutrient concentrations and standing stocks which are used to support productivity the following year (Howard-Williams, 1985).

As salt marshes are generally dominated by relatively few species, much of the data on nitrogen and phosphorus cycling in saline macrophytes is limited to a several species. Reimold (1972) reported the pathway by which phosphorus is transferred from the sediment to the plant and to estuarine waters. Reimold noted that Spartina alterniflora serves as a nutrient pump translocating measurable quantities of phosphorus from the sediments to the leaves and then, with tidal inundation, to the marsh. Gallagher et al. (1974) reported peak nitrogen and phosphorus concentrations in Spartina alterniflora shoots at the beginning of the growing season, followed by a steady decrease through the summer. Similar patterns were observed in Juncus roemerianus with peak nitrogen concentrations highest in the late winter and decreasing through the summer, but little change in phosphorus concentrations. Concentration patterns were attributed to early "luxury" accumulation followed by dilution through the growing season. As such, nitrogen and phosphorus standing stocks appeared to be a function of biomass productivity. De la Cruz and Hackney (1977) noted that no significant changes in nitrogen and phosphorus concentrations occured in the belowground biomass of a Juncus roemerianus marsh in Mississippi, suggesting that large amounts of nutrients may become available to the estuary through decomposition. Hopkinson and Schubauer (1984) reported that nitrogen concentration decreased in the shoots and rhizomes of Spartina alterniflora as productivity increased with peak nitrogen standing stocks coinciding with peak biomass.

Several studies have investigated the effects of added nitrogen and phosphorus on the growth of Spartina alterniflora. Buresh et al. (1980) reported a significant increase in aboveground biomass with about half of

the nitrogen in the aboveground attributable to the added ammonium-nitrogen Added phosphorus, however, did not significantly affect plant biomass. In a similar study, Patrick and Delaune (1976) estimated that the percentage of plant nitrogen derived from added inorganic nitrogen ranged from forty-one percent in the summer to thirty-one percent in the fall, while yield was increased fifteen percent. Added phosphorus increased the concentration in aboveground shoots by about twenty percent, however no yield increase was noted. Likewise, Sullivan and Daiber (1974) noted an increase in yield in the nitrogen fertilized area but no effect of phosphorus. The authors suggested that since nitrate is low in anaerobic sediments, that Spartina alterniflora may be adapted to ammonia which is responsible for the growth patterns observed. The data from these studies suggest that available sediment nitrogen may be the limiting nutrient in saline macrophyte growth and photosynthate production.

Closely related to the ability of saline macrophytes to cycle and store nitrogen and phosphorus are the effects of decomposition and leaching. Numerous studies have indicated the importance of decomposition in nutrient cycling and the maintenance of estuarine productivity (Kirby, 1971; Mason and Bryant, 1975; Odum et al. 1973; de la Cruz, 1979). Leaching of live shoots, however, is less understood due to the difficulty in obtaining accurate estimates based on interval tidal flushing. The release of nitrogen and phosphorus to the surrounding environment via these processes impacts the cycling and availability of these nutrients and, as such, is an important aspect of nutrient cycling.

White et al. (1978) reported a 100% decomposition of Spartina alterniflora over a seven month period in Louisana while Kirby and Gosselink

(1976) noted a 90% rate in a nearby area. McKee and Seneca (1982) observed that the taller forms of Spartina, due to increased stem tissue, were more resistant to decay than Juncus roemerianus shoots. Hackney and de la Cruz (1980) reported an annual decomposition rate of 16% in Juncus in the top 20 cm although nitrogen and phosphorus generally increased in the plant tissues over the study period.

Data on leaching rates is relatively scarces. Gallagher et al. (1976) estimated leaching of carbon in leaves of Spartina alterniflora to exceed 6.1 g/m^2/year, most of which was utilized by microbes. Hopkinson and Schubauer (1984) measured the leaching ratio of total dissolved nitrogen to total dissolved carbon in Spartina leaves. The leachate ratios were then multiplied by the seasonal carbon leachate estimated by Gallagher et al. (1976), resulting in an annual nitrogen leaching rate of 0.7 g/m^2.

Tissue nutrient concentrations and standing stocks in freshwater macrophytes are perhaps the most studied nutrient parameters in the literature (Prentki et al. 1978). Boyd (1978) reviewed the available data on the chemical composition of wetland plants and reported with-in site intraspecific variation, between-site intraspecific variation, and interspecific variation. Variations in species like Typha latifolia and Scirpus americanus were such that average compositions were unreliable for use in ecological studies. Klopatek (1974) observed that nitrogen and phosphorus concentrations decreased steadily over the growing season going from approximately 3.0% in May to 0.75% in September in the shoots and 2.25 to 0.75% in the roots and rhizomes of Typha latifolia. Phosphorus concentrations followed a similar pattern in the shoots, decreasing from approximately 0.65 to 0.15% over the growing season, however staying

relatively stable at 0.30% in the roots and rhizomes. Boyd (1969) reported shoot nitrogen tissue concentrations decreased from 2.4 to 0.51% and phosphorus from 0.31 to 0.09% between April and July in Typha latifolia. In the same study, nitrogen concentrations decreased from 2.72 to 0.83% and phosphorus concentrations decreased from 0.30 to 0.13% over the same period in the shoots of Scirpus americanus. Bernard and Solsky (1977) reported that nitrogen concentrations decreased steadily between May and November in both the shoots and new rhizomes of Carex lacustris from 3.0 to 1.0% and 1.75 to 1.00%, respectively. Phosphorus followed a similar pattern decreasing from 0.30 to 0.10% in shoots and 0.35 to 0.20% in new rhizomes over the same period. Bayly and Shibley (1978) reported phosphorus concentrations decreased in Pontederia cordata, from 8.0 to 3.0 mg/g in the shoots and 4.5 to 2.0 mg/g in the stalks betweeen June and September. Similar patterns were observed in the roots and rhizomes with phosphorus decreasing from 6.0 to 2.5 mg/g and 4.2 to 2.4 mg/g, respectively.

Data on nitrogen and phosphorus standing stocks tend to be variable depending on species. Klopatek (1975) noted that shoot nitrogen standing stocks in Scirpus fluviatilis reached a peak of 15.35 g/m^2 while root standing stocks reached a peak of 5.32 g/m^2. In the same study, shoot nitrogen standing stocks in Carex lacustris reached 7.71 g/m^2 while root standing stocks were 1.07 g/m^2. Phosphorus standing stocks were significantly lower reaching a peak of 3.18 g/m^2 in the shoots and 2.00 g/m^2 in the roots of Scirpus and 1.97 g/m^2 in the shoots and 0.24 g/m^2 in the roots of Carex. In a review of several freshwater species, Prentki et al. (1978) reported that nitrogen peak standing stocks varied from 28 (Kvet,

1973) to 43 g/m^2 (Mason and Bryant, 1975) in Phragmites communis, and from 5.3 (Boyd, 1970) to 31 g/m^2 (Prentki et al., 1978) in Typha latifolia. Phosphorus peak standing stocks varied from 2 (Mason and Bryant, 1975) to 5.3 g/m^2 (Dykyjova and Hradecka, 1976) in Phragmites communis and 0.68 (Boyd, 1970) to 3.2 g/m^2 (Prentki et al., 1978) in Typha latifolia. Kistritz et al. (1983) reported a peak nitrogen standing stock of approximately 10.0 g/m^2 in Carex lyngbeyi which coincided with peak aboveground biomass. Belowground nitrogen standing stocks were lowest during peak aboveground biomass but increased steadily to approximately 30 g/m^2 during shoot dieback. Phosphorus aboveground standing stocks followed similar patterns reaching a peak of approximately 1.5 g/m^2 in July, a time at which belowground standing stocks were lowest. Walker (1981) observed that peak aboveground nitrogen standing stocks in Peltandra virginica coincided with peak aboveground standing biomass reaching 10.99 g/m^2 in poorly drained sediments and 10.56 g/m^2 in well drained sediments in June and July, respectively. Seasonal patterns of phosphorus standing stocks were similar reaching peaks of 2.18 and 2.00 g/m^2 in poorly drained and well drained sediments, respectively.

Decomposition and leaching of freshwater macrophyte species have been shown to significantly affect nutrient cycles. Puriveth (1979) studied the decomposition of several freshwater macophytes in Wisconsin, reporting accelerated decay rates in spring and summer. Nitrogen and phosphorus initially declined in the first month but accumulated in the summer due to microrganisms inhabiting the litter. Turner (1978) studied the

decomposition of Spartina cynosuroides and Zizania aquatica and reported that Spartina cynosuroides gained in nitrogen content after an initial period of leaching, while Zizania litter nitrogen declined. After an initial period of leaching, both plants increased in total phosphorus. Odum and Heywood (1978) summarized the data concerning the decomposition of several tidal freshwater plants, including Peltandra virginica, Nuphar luteum, Pontederia cordata, and Zizania aquatica. Rapid rates of decomposition were observed in all species with 70-80% ash free dry weight lost within sixty days. In Peltandra, nitrogen increased from 2.9 to 4-5.5% after 10-20 days, declining to 3.0-3.8% after 50 days. As such, decomposing litter may actually increase nitrogen levels within the marsh.

Fewer studies are available as to leaching rates in freshwater macrophytes. Klopatek (1975) reported that of an annual nitrogen uptake of 17.46 g/m^2 by the shoots of Scirpus fluviatilis, 7.34 g/m^2/year were leached. Leaching of phosphorus was lower at 2.20 g/m^2/year. Kistritz et al. (1983) also reported high levels of leaching in a Carex lyngbyei marsh, estimating nitrogen leaching at 23.9 mg/m^2/day and phosphorus at 7.83 mg/m^2/day. These daily rates are the equivalent of 2.7 g/m^2/year for nitrogen and 0.89 g/m^2/year for phosphorus, or 31% and 66% of the aboveground peak nitrogen and phosphorus standing stocks, respectively. As such leaching is a significant component of nutrient cyling in freshwater macrophytes and should therefore be included in the modelling of nutrient fluxes.

Efficiency Indexes

The relationship between nutrient and biomass standing stocks are generally defined in terms of uptake, use, and recovery efficiency indexes. Uptake efficiency is calculated by dividing tissue nutrient levels by nutrient availability while use efficiency is calculated by dividing tissue biomass by tissue nutrient levels. Recovery efficiency is calculated by dividing the difference in nutrient levels of live and dead tissues by nutrient levels in live tissues (Shaver and Melillo, 1984). Although the majority of available data on efficiency indexes is the result of work in forest ecosystems (Turner, 1977; Vitousek, 1982; Chapin et al., 1987), recent evidence indicates that efficiency indexes also provide insight into relative nutrient cycling strategies in marsh macrophytes (Shaver and Melillo, 1984). It has been suggested that plants from nutrient poor habitats, such as anaerobic sediments, should be able to produce more organic matter per unit of nutrient (Vitousek, 1982) although Chapin (1980) concluded that plants from nutrient-poor habitats are less efficient. Vitousek (1982) pointed out that Chapin's argument was developed for short lived plants. Perennials which withdraw nutrients from senescing leaves use the same unit of nutrient to build several leaves, resulting in increased efficiency indexes.

Vitousek (1982) and Gray and Schlesinger (1983) proposed that as nitrogen or phosphorus availability increased that efficiency indexes would decrease. Pastor (in Shaver and Melillo, 1984) suggested that two possible mechanism regulate these changes in efficiency indexes, 1) changes in nutrient concentrations and 2) changes in biomass allocation. In a study of three marsh macrophytes, Typha, Carex, and Calamagrostis, Shaver and Melillo (1984) demonstrated that indeed all three efficiency indexes increased with

decreased nitrogen and phosphorus availability. Shaver and Melillo suggested that increased efficiency of macrophytes in nutrient limited environments result in a decreased dependency on uptake to meet nutrient demands. The calculation of efficiency indexes, therefore, provide additional information on growth and nutrient cycling strategies in marsh macrophytes.

Sediment Mediated Processes

Nitrogen and phosphorus found in wetland sediments can exist in two phases: dissolved in interstitial waters, or associated with (or in) the solid sediment particles (Kadlec, 1979). The solid phase includes nutrient ions adsorbed on mineral or organic particles, often termed exchangeable, nutrients tied up in organic matter, and nutrients chemically bound in the crystalline lattice of sediment particles (Brannon et al. 1976). Sediment microbial populations constantly transform these nutrients (Howard-Williams, 1985; Krom and Berner, 1981) as do the processes of sedimentation (Delaune et al. 1981), associated cation exchange mechanisms (Kadlec and Tilton, 1979; Rosenfield, 1979; Dolan et al. 1981; Boatman and Murray, 1982), and diffusion and subsequent alteration (Patrick and Khalid (1974). The assumption is often made that the ions dissolved in interstitial water and adsorbed on various particles represent available nutrients while nutrients bound in organic matter are unavailable except through decomposition (Kadlec, 1979). As the phase equilibrium of nutrients continually shift, it is often difficult to accurately assess standing stocks of nitrogen and phosphorus species over intervals of significant length. This problem, coupled to the varibility in methods available for estimating sediment

nutrient levels, has resulted in a wide variety of nutrient values for wetland sediments. As such, comparisons are possible only on a qualitative basis and must consider environmental conditions, sampling methods, and laboratory techniques.

Nitrogen and phosphorus levels in salt marsh sediments limit primary production as well as microbial processes (Haines et al. 1977). Delaune and Patrick (1980) reviewed nitrogen and phosphorus cycling processes in a Gulf Coast salt marsh of the Mississippi River reporting that sedimentation supplied the equivalent of 23 g/m^2/year nitrogen and 2.3 g/m^2/year phosphorus, most of which is in the organic form, to the sediments. They concluded that the marsh was undoubtedly a sink for both nitrogen and phosphorus accumulating these nutrients at the rate of 21 g/m^2/year and 1.7 g/m^2/year, respectively. Perhaps the most significant data from this study was that mineralization of organic nitrogen to ammonium resulted in an input of approximately 40 g/m^2/year, apparently sufficient to support observed macrophyte productvity. As there is little nitrate due to lack of oxygen, ammonium is the primary inorganic form of nitrogen available to macrophytes. Haines et al. (1977) estimated that over 90% of the total measured pools of nitrogen in a salt marsh was sediment nitrogen, which included the labile inorganic pools of ammonium and nitrate. The majority, however, was refractory organic nitrogen and fixed ammonium. The large organic pools showed little seasonal flucuation however, the small exchangeable ammonium and nitrate pools demonstrated marked seasonal flucuations. As the standing pools of inorganic nutrients were generally insufficient to support levels

of macrophyte growth observed, it was concluded that microbial decomposition of organic pools must continually supply the inorganic form of ammonium.

A phase shift in sediment nutrients, in addition to microbial proceses, is controlled by cation exchange processes. As cation exchange processes control nutrient availability to the macrophyte community, they have received increased attention in recent years. Boatman and Murray (1982) modelled the processes and controls of exchangeable ammonium adsorption in marine sediments. They reported that in organically rich sediments a clay-humic complex controls ammonium adsorption while in organically poor sediments the clay mineralogy dictated adsorption. As most estuarine sediments are rich in organic matter, this process, together with mineralization, will control the availability of ammonium for primary production. In a similar study, Rosenfield (1979) measured the differences in dissolved, exchangeable, and fixed ammonium in anoxic sediments from Long Island to Florida. He reported that a dynamic equilibrium existed between these three phases and that exchangeable ammonium increased linearly with increasing levels of dissolved ammonium. Similarly, exchangeable ammonium adsorption, predominantly associated with organic matter, was rapid and reversible. Ammonium adsorption is, therefore, an important process in marine sediments and must be considered when attempting to measure nitrogen availability.

In addition to cation exchange processes, diffusion of inorganic nutrients also regulate sediment nutrient levels. Patrick and Reddy (1976) demonstrated that ammonium in the aerobic surface layer undergoes nitrification creating a concentration gradient which causes ammonium to diffuse upward towards the aerobic layer. Here ammonium also undergoes

nitrification. The nitrate then tends to diffuse downward where it is denitrified to N_2 and N_2O which may be lost to the environment. As nitrification requires oxygen, nitrate is generally unavailable to perennial macrophytes with deep seeded root and rhizome systems, but will support amnnuals with shallow root systems. Patrick and Khalid (1974) reported that anaerobic sediments released more phosphate to sediment solutions low in soluble phosphate and sorbed more phosphate in sediments high in soluble phosphate, indicating that available dissolved phosphate increases in the typically anaerobic sediments found in salt marshes. This increase in anaerobic sediments, however, may create a concentration gradient which causes phosphate to diffuse upward and be released to overlying waters (Pomeroy et al. 1965).

In comparison to salt marsh sediments, relatively little is known regarding the cycling of nitrogen and phosphorus in tidal freshwater marshes. Available data appears highly variable depending on local environmental parameters and sampling method, however certain trends are apparent. The total nitrogen pool is far greater than the inorganic pool with much of this component in the organic form (Kadlec, 1979). Bowden (1984) reported that the majority of nitrogen did exist as organic nitrogen varying from 1.59 to 1.93% on a dry weight basis. Inorganic nitrogen levels were significantly lower but always exceeded the nitrate plus nitrite levels. Klopatek (1975) estimated total nitrogen in the top 15 cm of a tidal freshwater marsh at 1696 g/m^2 in a Scirpus fluviatilis stand. Walker (1981), working in a tidal freshwater marsh, estimated total nitrogen standing stocks in poorly drained sediments at 153 and 185 g/m^2 at the 40-55

and 80-95 cm, respectively, of which, 3.89 and 11.23 g/m^2/year were considered as mineralizable, or available, nitrogen. In well drained sediments total nitrogen pools were 204 and 192 g/m^2 at the 40-55 and 80-90 cm depths of which 11.02 and 5.41 g/m^2/year were considered available. Richardson et al. (1978) reported that total nitrogen reached a peak of 683 g/m^2 in the top 20 cm of northern wetland ecosystems, including, bogs, fens, swamps, and marshes. Only 0.75 g/m^2, however, was considered available.

Total phosphorus standing stocks can be relatively high in freshwater sediments and may include a significant inorganic pool. Bowden (1982) estimated organic phosphorus at approximately 0.30% of dry weight at the surface, decreasing rapidly with depth. Richardson et al. (1978) reported total available phosphorus pools of 24.2 g/m^2 of which 0.45 g/m^2 was available in several northern wetlands. Klopatek (1975) reported a much higher level of available phosphorus reaching 12.1 g/m^2 in the top 15 cm of a freshwater wetland. Klopatek suggested that tidal freshwater marshes may have evolved mechanisms for conserving this often limiting nutrient. Walker (1981), however, reported much lower levels of inorganic phosphorus in a poorly drained sediment, estimating that 0.80 and 1.72 g/m^2/year were available at 40-50 and 80-95 cm, respectively. In well drained sediments, Walker observed a higher level of available phosphorus at 40-55 cm reaching 1.71 g/m^2/year but decreasing to 0.82 g/m^2/year at 80-95 cm. Walkers' lower levels may be attributable to the Bray-2 method which may actually be the best estimate of available phosphorus.

The extreme variability in the reported levels of nitrogen and phosphorus in freshwater sediments points to the need for additional data on wetland sediments. Kadlec (1979), for example, assumes a reasonable approximation of total nitrogen to be 500-1500 g/m^2 on a dry weight basis of which 5-15 g/m^2 is available. Total phosphorus concentrations also may vary widely but are commonly in the 0.01-0.02% range, dependent on extraction and laboratory technique. It appears, then, that little of the available data on wetland sediments may be extrapolated to other wetland systems, but may be compared only on a relative basis.

Sediment - Tissue Relationship

The relationship between sediment and tissue nutrient levels is generally determned through regression or correlation analysis. This approach allows a determination of whether tissue nutrient levels are dependent on sediment availability or if the two paramaters are interdependent. This relationship explains, at least in part, nutrient cycling strategies in marsh macrophytes. Attempts to define this relationship have produced contradictory results. Boyd and Hess (1970) reported a positive correlation between phosphorus water levels and tissue concentrations in Typha. Likewise, Gerloff and Kromholtz (1966), Gossett and Norris (1971), and Klopatek (1978) reported strong correlations between sediment and tissue nutrient concentrations in marsh macrophytes including Typha, Scirpus, and Carex. Klopatek explained the strong relationship between tissue and sediment total nitrogen by the constant proportion of ammonium to total nitrogen in the sediments. The relationship between sediment and tissue phosphorus indicated that indeed the macrophyte

community may control phosphorus fluxes in tidal freshwater marshes. Boyd (1971), Boyd and Vickers (1971), and Walker (1981), however, reported weak or insignificant relationships between sediment and tissue nutrient levels. DeLaune et al. (1979) reported strong correlations between aerial standing crops and sediment nitrogen expressed on a soil volume rather than a dry weight basis in Spartina alterniflora.

Apparently, the relationship between sediment and tissue nutrient levels may be dependent on local environmental conditions and individual species. The relationship should be stronger in annuals which depend on de novo root uptake to supply all nutrient demands and weaker in perennials with a significant rhizome storage component which depend more on rhizome reallocation (Walker, 1981). In addition the strength of the relationship will depend on minerilzation rates and assimilative capacity of the sediments as well as the seasonal timing of root uptake and transport through the plant.

Models

Despite the importance of emergent wetland macrophyte communities and their associated sediment compartments to the cycling of nitrogen and phosphorus, relatively few studies have attempted to incorporate sediment and plant compartment data in the construction of nutrient models. Models of this type are necessary, however, as they provide a quantitative assessment of uptake processes, nutrient conserving mechanisms, and storage capacity of wetland ecosystems. Likewise, models provide information on the processes which limit production and quantification of fluxes to the surrounding environment.

The majority of studies on saline macrophytes have dealt largely with nutrient standing stocks in sediment and aboveground plant parts rather than the integration of these parameters into compartmental flux models (Hopkinson and Schubauer, 1984). In a study of nitrogen dynamics in Spartina alterniflora, Hopkinson and Schubauer (1984) quantitatively estimated compartmental fluxes, uptake, and release to the environment. Annual uptake by the belowground component was estimated at 34.8 g/m^2 of which 33.0 g/m^2 were transfered to aboveground shoots. Of this amount, 14.4 g/m^2/year were lost to the detrital compartment and a relatively low level of 0.7 g/m^2/yr to leaching. Spartina was shown to conserve nitrogen by translocating 17.9 g/m^2/year to the rhizomes at senescence. Root dieback also contributed a significant amount to the sediment compartment of 19.7 g/m^2/yr.

Nutrient models in freshwater wetlands are relatively scarce, yet the diversity of macrophyte species necessitate the quantification of compartmental nutrient fluxes. Richardson et al. (1978), working in a northern wetland ecosystem, estimated an annual nitrogen uptake of 3.0 g/m^2 by the aboveground biomass of leatherleaf and bog birch of which 2.3 g/m^2 were lost to the litter compartment. Phosphorus fluxes were significantly lower with 0.17 g/m^2/year taken up by aboveground biomass of which 0.10 g/m^2/yr were lost to the litter component. Klopatek (1975) reported annual nitrogen uptake by the belowground component of 20.75 g/m^2 of which 17.46 g/m^2 were translocated to aboveground shoots in a Scirpus fluviatilis stand.

Of this uptake, 7.34 and 8.09 g/m^2/year were lost to leachate and detritus, respectively. Scirpus conserved relatively little nitrogen through translocation, reallocating only 2.03 g/m^2/year at senescence. Phosphorus fluxes were lower with an annual uptake by the belowground component of 5.33 g/m^2 of which 3.77 g/m^2 were transfered to aboveground shoots and 2.20 and 1.13 g/m^2 were lost to leaching and detritus, respectively. Conservation of phosphorus was also low with a translocation of 0.44 g/m^2/year at senescence. Walker (1981), in a study of Peltandra virginica, reported an annual transfer of 8.14-9.24 g/m^2 to the rhizomes from the roots in poorly drained sediments of which 10.47 g/m^2 were transfered to aboveground shoots. Of the transfer to the aboveground compartment, 7.84-8.94 g/m^2/year were lost to detritus and a relatively low rate of 2.05-3.15g/m2/yr were translocated at senescence. In well-drained sediments, annual transfer from the roots to the rhizomes was significantly higher at 26.62-26.33 g/m^2 of which 10.11 g/m^2 were transfered to the abveground shoots. A significant loss of nitrogen to detritus and leaching of 10.31-10.56 g/m^2/year was observed together with a low translocation rate of 0.19 g/m^2/year at senescence. Compartmental phosphorus flux levels were significantly lower. At the poorly drained site, annual uptake by the aboveground shoots was estimated at 2.08 g/m^2 of which 1.35-1.70 g/m^2 were lost to detritus and leaching and 0.37-0.72 g/m^2 were translocated to the rhizomes at senescence. At the well drained site, annual uptake by the shoot compartment was

estimated at 1.90 g/m^2 of which 1.80-1.90 g/m^2 were lost to detritus and leaching while 0.09 g/m^2 were translocated to the rhizomes at senescence. The limited availability of nutrient models of this type point to the need for additional studies which incorporate nutrient substrate dynamics into comprehensive compartmental models.

Objectives

The primary objective of the study was to evaluate and compare seasonal productivity, nitrogen, and phosphorus substrate dynamics for Peltandra virginica and Spartina cynosuroides through the development of models which quantitatively assess annual compartmental standing stocks and flows. The secondary objective of the study was to evaluate and compare seasonal patterns of nitrogen and phosphorus use efficiency in the shoots, roots, and rhizomes and recovery efficiency in the shoots of Peltandra virginica and Spartina cynosuroides through the development of efficiency indexes.

Rationale

The dominant role of the emergent macrophyte species, acting as a type of nutrient pump, which regulates the flow of nitrogen and phosphorus in tidal freshwater wetlands, is generally well documented. Certainly, community structure is the result, at least in part, of competition between these species for available resources. As the ability of macrophytes to cycle nutrients is dependant on individual morphology and growth requirements, as well as local sediment biogeochemistry and nutrient availability, individual species have evolved different strategies for uptake and internal cycling of nutrients. To date, however, there are relatively few models which attempt to quantify nutrient pathways for individual species. As such, most general models for freshwater wetlands

remain hypothetical.

A possible explanation for the lack of quantitative nutrient compartmental models is the often difficult and time consuming task of simultaneously measuring all compartments necessary in model construction. For example, estimates of belowground productivity, which are an essential component of nutrient models, are virtually non-existent (Good et al. 1982). Estimates of belowground productivity that are available often do not separate root and rhizome components but rather use composite biomass for nutrient analyses. This practice, however, provides little information on belowground cycling mechanisms which, in fact, may represent the key to understanding nutrient strategies in perennials with extensive rhizome storage compartments. Brinson and Davis (1976), Klopatek (1978), Richardson et al. (1978), Prentki et al. (1978), Walker (1981), and Kistritz et al. (1983) provide the most comprehensive nutrient models for freshwater macrophytes, yet only Walker (1981) separates the root and rhizome compartments when depicting annual flows. As nutrient models represent not only the quantitative aspects of nutrient cycling in tidal freshwater wetlands but also their assimilative capacity and ability to regulate nutrient fluxes, additional studies which quantify compartmental nutrient dynamics for individual macrophyte species are necessary.

There are generally two approaches to the construction of nutrient models for macrophyte communities. The first approach involves the mass balance of all inputs and outputs, which must be directly measured (Whigham and Bayley, 1979). This approach, however, is impractical for several reasons. First, it is virtually impossible to acount for for all inputs to (groundwater, plant dieback, rainfall, tidal flushing, microbial activity)

and outputs (leaching, tidal flushing, groundwater, plant uptake) from the system. Second, since plant uptake is involved, isotope tracer rate measurements are necessary. The use of isotopes results in a large margin of error either in obtaining uniform tracer distribution in sediments and plant tissues or in the extrapolation of short-term uptake to seasonal accumulation (Prentki et al. 1978). The second approach, which will be used in this study, involves monitoring internal compartmental nutrient standing stocks at constant intervals over an annual cycle (Prentki et al. 1978; Whigham and Bayley, 1979). Estimates of annual flows between compartments and to the surrounding environment may then be calculated using changes in these standing stocks. The latter approach provides a more accurate estimate of nutrient flows due to the relative stability of the internal compartments. This approach also provides insight into the uptake, assimilative, and storage capacities of macrophytes and their associated sediment compartments.

Relative macrophyte growth strategies generally involve adaptations to local environments which allow each species to efficiently compete for available nutrient resources. Adaptations may include morphological structures, timing of above- and belowground productivity, and the ability to use and conserve available nutrients. The relationship between biomass production and nutrient standing stocks is generally defined in terms of use and recovery indexes. Use efficiency is generally estimated by dividing biomass by nutrient mass while recovery efficiency is estimated by dividing the difference in nutrient mass in live and dead tissues by nutrient mass in live tissues (Shaver and Melillo, 1984). The efficiency with which a

species uses and recovers nutrients may explain, at least in part, individual nutrient strategies of tidal freshwater macrophytes.

Use and recovery efficiency also have ecosystem level implications. As recovery efficiency decreases, levels of nutrients, especially nitrogen and phosphorus, in litter increases which, in turn, is released through decomposition (Vitousek, 1982). Since high nutrient litter decomposes more rapidly, this may result in significant nutrient pulses to the environment (Melillo et al. 1982). Similarly, if recovery efficiency decreases then nutrient demands for primary productivity must be met through de novo root uptake (Turner, 1977; Gray and Schlesinger, 1983; in Shaver and Melillo, 1984), resulting in greater energy expenditure for nutrient uptake and less available energy for growth and maintenance. This results in a decreased ability to compete with other species for available resources and a decreased role in the community. Coversely, as efficiency increases, there will be less uptake and, therefore, less turnover of nutrients within the system. Shaver and Melillo (1984) suggested that, in fact, more efficient macrophytes should become dominant in sediments characterized by low nutrient availability. Efficiency indexes, then, should provide insight into relative nitrogen and phosphorus cycing strategies in relationship to availability and uptake.

Hypotheses

The first hypothesis studied was that seasonal nitrogen and phosphorus standing stocks, which reflect uptake and internal cycling, in the shoots, roots, and rhizomes of Peltandra virginica and Spartina cynosuroides are independent of sediment nitrogen and phosphorus standing stocks, which reflect availability. The second hypothesis studied was that seasonal nitrogen and phosphorus standing stocks, which reflect uptake and internal cycling, are interdependent, or covary, in the shoots, roots, and rhizomes of Peltandra virginica and Spartina cynosuroides.

Rationale

It has been suggested that macrophyte uptake of nitrogen and phosphorus by aboveground shoots is proportional to the availability of these nutrients in the sediments (Klopatek, 1978). This is unlikely in most tidal freshwater perrenials for several reasons. First, unlike annuals which must depend on de novo root uptake to support seasonal productivity, perennials such as Peltandra virginica and Spartina cynosuroides, which have an extensive rhizome storage compartment, may rely on reallocation of nutrients which have been stored overwinter (Van der Linden, 1980; Kistritz et al. 1983). This type of perrenial often exhibits a phenomenom referred to as "luxury uptake" in which early spring shoot growth is characterized by excessive accumulation of nutrients reallocated from the rhizomes. As such,

the flow of nutrients to aboveground shoots have little relationship to available sediment nutrients. Second, it has been demonstrated that the majority of nitrogen, and in most cases the majority of phosphorus, in wetland sediments is in the organic form which is not available for uptake (Haines et al. 1977; Patrick and DeLaune, 1980; Bowden, 1982). As a result, inorganic nutrient pools, which generally become available through microbial activty and certain geochemical processes, and are subject to high turnover, are relatively low in relationship to shoot accumulation (DeLaune and Patrick, 1980; Bowden, 1982).

In theory, tidal freshwater macrophytes would be at a distinct disadvantage if dependant on uptake from the sediments to support seasonal productivity. Characteristic rapid periods of growth during which macrophytes reach peak standing crop offers certain adaptive advantages yet would require a tremendous expenditure of energy for the active transport of nutrients across the root interface. The energy expenditures are compounded by the fact that macrophytes must overcome hypoxia and other stresses in the uptake of nutrients from the sediment. As a result, most macrophyte species have certain adaptations which allow seasonal aboveground shoot production to proceed despite the low levels of available nutrients often observed in tidal freshwater wetlands. The relationship between available sediment nutrients and aboveground uptake provides insight into whether nutrients are actually limiting in tidal freshwater wetlands. Moreover, the quantification of this relationship should explain how certain macrophytes have adapted to the acquisition of nutrients in a stressful environment. As seasonal macrophyte biomass is considered a significant storage compartment for nitrogen and phosphorus, while the sediment compartment is generally

described in terms of its nutrient assimilative capacity, an understanding of this relationship is essential.

The hypothesized interdependent behavior of nitrogen and phosphorus in the shoot, root, and rhizome compartments of tidal freshwater macrophytes is based on the apparent requirement of nitrogen and phosphorus in certain proportions which eventually approach an "optimum" ratio (Shaver and Melillo, 1984). Shaver and Melillo demonstrated that nitrogen and phosphorus are interdependent in several marsh macrophytes and suggested that there is an interaction between nitrogen and phosphorus. The authors based this suggestion on the fact that tissue nitrogen to phosphorus ratios were correlated with growth solution ratios, although tissue ratios were less extreme, and that the luxury uptake of one nutrient occurred when the other was limiting. If indeed macrophytes do tend towards an "optimum" nitrogen to phosphorus ratio then the seasonal cycling of these nutrients should be interdependent.

Ecologically, uptake and use of nitrogen and phosphorus in certain proportions should provide Peltandra and Spartina with certain advantages in terms of efficient resource utilization. For example, early shoot concentrations of higher nitrogen to phosphorus ratios results in high levels of chloroplast synthesis which allow maximum utilization of sunlight for the production of energy (ATP) and reducing power (NADPH). As shoot biomass increases, nitrogen to phosphorus ratios may decrease as increased phosphorus is reallocated from the rhizomes for use in intermediate compounds and enzymes of the Calvin cycle, cell wall phospholipids, and ATP synthesis, which, in turn, allows maximum carbon fixation to photosynthate. In rhizome tissue, nitrogen and phosphorus standing stocks in certain

proportions allow storage of these nutrients in ratios required for maintenance and structural components, as well as for reallocation to root and shoot biomass. Root nitrogen to phosphorus ratios reflect demand of these nutrients for strucural components (proteins and phospholipids) and energy required for nutrient uptake (ATP), and, as such, should covary in response to demand. Nitrogen and phosphorus may not covary in the sediments due to different uptake and turnover rates, as well as biogeochemical processes which control sediment standing stocks. Development of the nitrogen - phosphorus relationship in the sediments, however, should help define the role of sediments in cycling and storage of these nutrients and the relationship between the macrophyte community and the sediments. The relationship between nitrogen and phosphorus, then, should provide additional insight into individual nutrient cycling strategies of Peltandra and Spartina.

Study Site

Sweethall marsh (37^{o} 34'N 76^{o} 33'W) is one of several extensive tidal freshwater marshes, including Coho, Cousine, Lee, and Eltham, located approximately 19km from the mouth of the Pamunkey River, which together with the Mattaponi River, forms the upper portion of the York River Basin within the Chesapeake Bay estuarine system (Figure 1). The marsh is a peninsular area consisting of over 44 ha of wetlands, 29 ha of wooded swamp, and 30 ha of open streams (Doumlele, 1981) and a border of approximately 7.4 km (Figure 2). Located in a meandering portion of the Pamunkey River which drains an area of approximately 100 km^2, Sweethall Marsh is bounded on three by the Pamunkey River one side by an elevated agricultural area and forested watershed. Sediments, which consist of silty, clay loam and terrace mixed sediments, support an extensive macrophyte community dominated by Peltandra virginica, Spartina cynosuroides, Zizania aquatica, Typha latifolia, Leersia oryzoides, and Scirpus.

Sweethall marsh is flushed twice daily by tidal waters which are relatively turbid due to the large amount of suspended sediments and organic materials. Tidal waters are drained by an array of creeks and channels which extend throughout the marsh. These creeks and channels, in turn, empty into the Pamunkey River. The climate of the area is classified as humid, sub-tropical with an annual temperature of $13.4^{o}C$. Annual

Figure 1. Chesapeake Bay Estuary in Virginia and the location of Sweethall Marsh on the Pamunkey River.

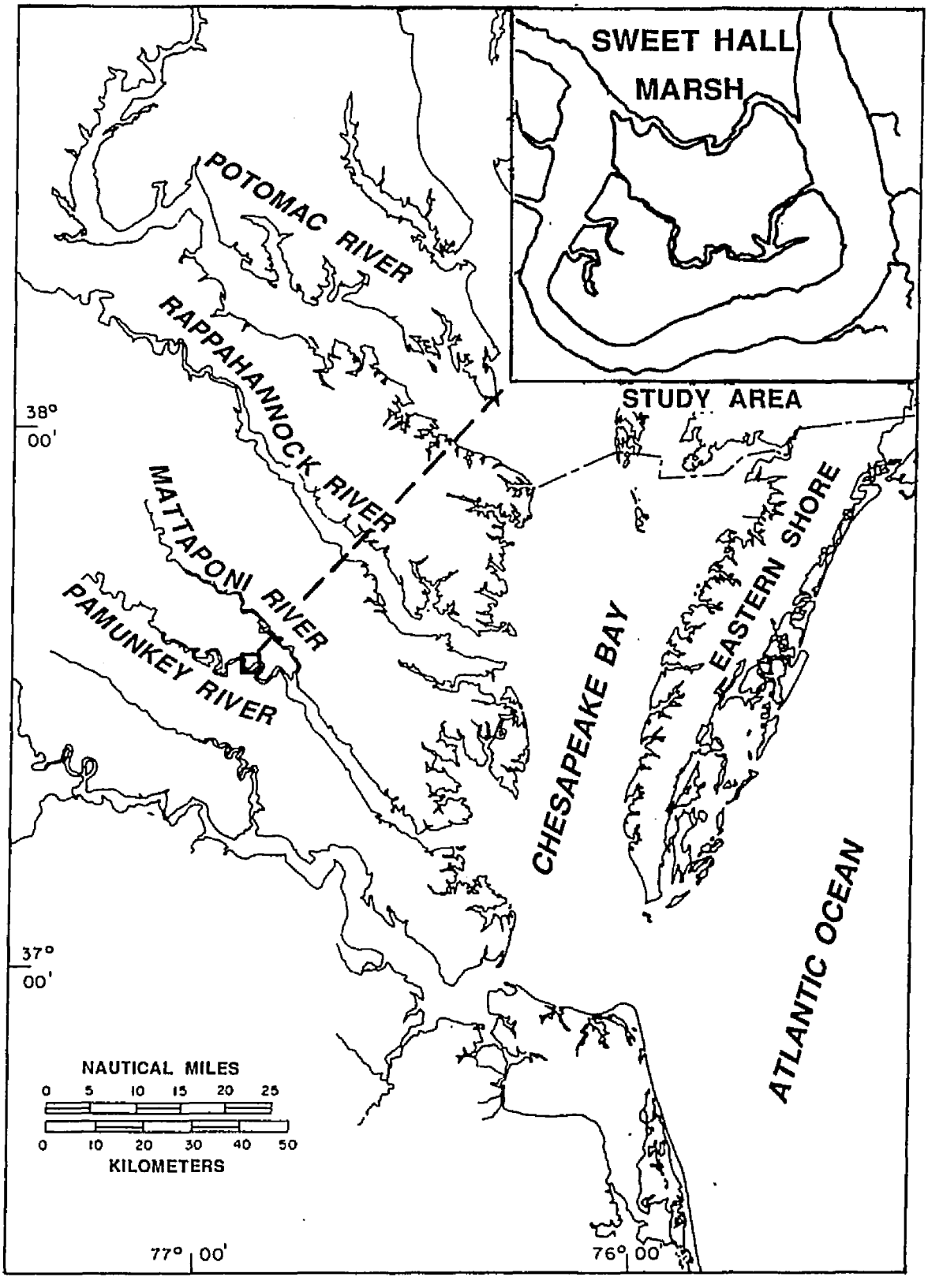
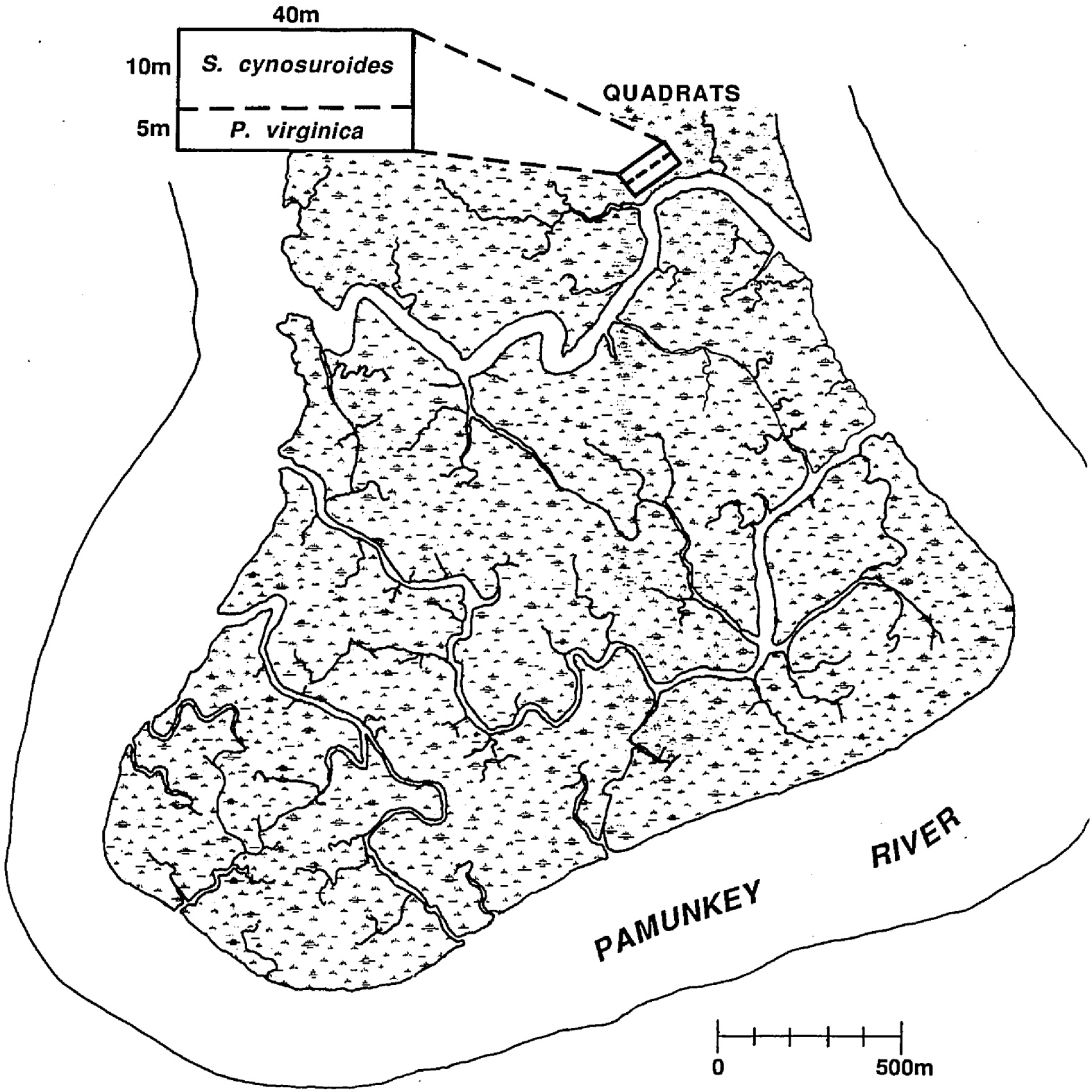

SWEET HALL
MARSH
STUDY AREA
POTOMAC RIVER
RAPPAHANNOCK RIVER
MATTAPONI RIVER
PAMUNKEY RIVER
CHESAPEAKE BAY
EASTERN SHORE
ATLANTIC OCEAN
38° 00'
37° 00'
77° 00'
76° 00'
NAUTICAL MILES
0 5 10 15 20 25
0 10 20 30 40 50
KILOMETERS

Figure 2. Sweethall Marsh study site located apparoximately 19 km from the mouth of the Pamunkey River with the location of the permanent quadrats.


40m
10m
S. cynosuroides
5m
P. virginica
QUADRATS
PAMUNKEY
RIVER
0
500m

precipitation is lowest between September and January, and highest in July and August. Salinity ranges between 0-5 ppt with mean and spring tidal ranges at 82 and 94 cm, respectively. Pollution appears to be minimal.

The study site, which consists of a gently sloping creekbank, dominated by a monotypic stand of Peltandra virginica, and a slightly elevated levee region, dominated by a monotypic stand of Spartina cynosuroides, is located along one of the major channels which extends from the Pamunkey River into the marsh (Figure 2). The site is bounded on three sides by the channel and two smaller creeks, all of which drain the site. The remaining boundary consists of an extensive mixed macrophyte community which extends to the agricultural area. Sediments on the creekbank are relatively well drained while the levee sediments tend to be more waterlogged and are often characterized by low levels of standing water following ebb tide.

Materials and Methods

Experimental Design

Data was collected at monthly intervals from May, 1987 through May, 1988. Sampling dates were January 6, February 15, March 5, April 2, May 3, June 5, July 6, August 6, September 3, October 1, December 16. Prior to sampling, a permanent quadrat (15 x 40 meters) was established at the study site. The permanent quadrat consisted of two smaller quadrats. The first was a 5 x 40 meter creekbank area dominated by a monotypic stand of Peltandra virginica. The second was an adjacent 10 x 40 meter slightly elevated levee area dominated by a monotypic stand of Spartina cynosuroides. As such, the two smaller quadrats shared a common boundary extending 40 meters which, in effect, delineated the creekbank and the slightly elevated levee, as well as the two species. Each of the smaller quadrats was divided into 1 m^2 sub-quadrats. At each monthly sampling interval the sub-quadrats were randomly selected for the collection of aboveground shoots, belowground roots and rhizomes, and sediment cores. If a quadrat had been disturbed or previously sampled, an additional quadrat was randomly selected.

Field Sampling

Aboveground Biomass

Each month five 1 m^2 sub-quadrats were randomly selected in both the

Peltandra and Spartina quadrats for estimating aboveground biomass standing stocks. Within each of these sub-quadrats the center 0.25 m^2 plot was harvested by clipping the shoots approximately 2 cm above the sediment surface. Shoots were stored in plastic bags, returned to the lab, separated into live and dead components, and washed clean of sediments and debris. Shoots were then dried in a circulating air dryer at 75 ^oC for approximately 7 days or until no perceptible change in weight was observed. The five weights were recorded and a mean standing biomass was calculated for each month. Values were then converted to g/m^2.

Belowground Biomass

To estimate Peltandra belowground biomass standing stocks, six 0.50 m^2 quadrats were selected within the Peltandra stand in June 1987 which appeared to support equivalent aboveground biomass standing stocks. Approximately every other month, beginning in July, 1987, belowground biomass, consisting of roots and rhizomes, at one of these quadrats, was sampled by complete excavation of the 0.50 m^2 quadrat to a depth of 1 m. Belowground biomass was stored in plastic bags, returned to the laboratory, and washed clean of sediments and debris using 1 cm^2 mesh sieve. Belowground biomass was then separated into live roots and rhizomes, based on color and turgidity, and dried in a circulating air dryer at 75^oC for approximately 10 days or until no perceptible change in weight was observed. Separate dry weights of both roots and rhizomes were recorded and converted to g/m^2.

Spartina belowground biomass standing stocks were estimated using a modification of the method described by Hackney and de la Cruz (1986). At approximate monthly intervals between June, 1987 and May, 1988, belowground biomass was sampled in each of the sub-quadrats selected for sampling aboveground biomass, using stainless steel core tubes (10 cm in diameter by 50 cm in length). A total of six belowground biomass cores were taken each month. Core tubes were hand driven to a depth of 50 cm within these quadrats, extracted, sealed, and returned to the laboratory. Here the sediment cores were extruded and washed clean of sediments and debris using a 1 cm^2 mesh sieve. Plant tissues were then separated into live roots and rhizomes, based on color and turgidity, and dried in a forced air dryer at 70^{o}C for approximately 7 days or until no perceptible change in weight was observed. Separate dry weights of roots and rhizomes were recorded and a mean monthly standing stock for each calculated. Root and rhizome dry weights were then converted to g/m^2.

Sediment Cores

Each month during the growing season, March to October, and in December, sediments were sampled in both Peltandra and Spartina quadrats. Peltandra sediments were sampled using stainless steel core tubes 7.5 cm in diameter to a depth of 100 cm. Spartina sediments were sampled using stainless steel core tubes 7.5 cm in diameter to a depth of 50 cm. In undisturbed areas adjacent to the quadrats sampled for above- and belowground biomass, core tubes were hand driven to the appropriate depth. Core tubes were extracted, sealed, and returned to the laboratory.

Peltandra sediment cores were extruded and sectioned at 0-10, 10-25, 25-50, 50-75, and 75-100 cm while Spartina sediment cores were extruded and sectioned at 0-10, 10-20, 20-30, 30-40, and 40-50 cm. Wet sediment core sections were placed in sterilized plastic bags and stored at 15^{o}C for bulk density and nutrient analyses (12-24 hr).

Nitrogen and Phosphorus Leaching Experiment

Leaching rates of nitrogen and phosphorus in shoots of Peltandra were estimated in situ using a modification of the method suggested by Gallagher et al. (1976) and chambers modified to accomodate aboveground biomass. In the modification of the Gallagher et al. method, shoots, which included the stalk and leaves, were clipped at the bases and sealed with sterilized latex to prevent guttation. Shoots were rinsed with distilled water and placed in sterilized plastic bags filled with 4.5 liters of filtered estuarine water (45um filter) collected from the adjacent channel. The bags were sealed and placed at the sediment surface for approximately 3 hours. In a concurrent study, leaching was estimated using modified fiberglass chambers 40 cm in length. These chambers were open at one end, which had an approximate 20 cm diameter, and sealed at the other end, which had an opening of approximately 5 cm. The 5 cm opening was placed over growing shoots so that the shoots were enclosed within the chamber and sealed using a split rubber stopper. The chambers were then slowly filled with 4.5 liters of filtered estuarine water and allowed to sit for approximately three hours. At the conclusion of the experiments, the leachate from each experimental bag and each chamber was drained separately into 250 ml brown Nalgene containers. Likewise, clipped shoots from the experimental bags and chambers were placed in

individual sterilized plastic bags and returned to the laboratory. Here shoot biomass was dried at 70°C in a forced air dryer for approximately 48 hours and the weights recorded. Leachate samples were frozen for future nutrient analyses.

Leaching rates of nitrogen and phosphorus in shoots of Spartina were estimated in situ using a modification of the method described by Gallagher et al. (1976) and polyethelyne tubes designed to accomodate aboveground shoots. In the modification of the Gallagher et al. method, detached leaves were rinsed with distilled water, sealed at the base with sterilized latex to prevent guttation, and placed in sterilized plastic bags filled with 3 liters of filtered (45um filter) estuarine water. The bags were sealed and placed at the sediment surface attached to several ring stands for approximately 3 hours. In a conceuurent study, leaching was estimated using polyethylene tubes 4.5 cm in diameter and 125 cm in length. The tubes were placed over several growing shoots so that the shoots extended the length of the tube and sealed at the shoot bases with a split rubber stopper. The tubes were then attached to ring stands, slowly filled with 2 liters of filtered estuarine water, and allowed to stand for approximately three hours. At the conclusion of the experiments, leachate from each of the plastic bags and each of the tubes was drained separately into 250 ml brown Nalgene containers. Likewise, clipped shoots from the tubes and detached leaves from the bags were placed in individual sterilized plastic bags and returned to the laboratory. Here, shoots and leaves were dried at 70°C a forced air dryer for approximately 48 hours and the weights recorded. Leachate samples were frozen for future nutrient analyses.

Laboratory Analyses

Plant Tissue Nitrogen

Monthly nitrogen concentration in the shoots, roots, and rhizomes was determined using random sub-samples of dried plant tissues. Dried samples of whole shoots (including the stalk and leaf), roots, and rhizomes were ground separately in a Wiley Mill through a #40 mesh screen. Five replicates of each tissue type were then analyzed for nitrogen on a Carlo Erbo NA 1500 CNS Autoanalyzer. Monthly shoot, root, and rhizome nitrogen standing stocks were estimated by multiplying monthly biomass standing stocks by tissue concentration.

Plant Tissue Phosphorus

Phosphorus concentrations in the shoots, roots, and rhizomes was determined using the method described by the Soil Testing Laboratory at Virginia Polytechnic Institute and State University. Approximate 1 g sub-samples of dried shoot, root, and rhizome tissues were ashed at 550^{o}C for 6 hours. The ashed samples were placed in plastic Nalgene centrifuge tubes, dissolved with 5 ml concentrated 12 N HCL, and slowly brought to a 50 ml volume with distilled water. The individual samples were then filtered on a Whatman 45um filter and read as orthophosphate on an Orion Autoanalyzer. Monthly shoot, root, and rhizome phosphorus standing stocks were estimated by multiplying monthly biomass standing stocks by monthly tissue concentration.

Leachate Nitrogen

Total leachate nitrogen was determined using the method described by EPA (1979). Leachate sub-samples were subjected to a potassium persulfate digestion in an autoclave at 100^{o}C followed by the addition of 0.3 N HCL and a borate buffer. The samples are then read as nitrate on a Technicon Autoanalyzer.

Leachate Phosphorus

Total leachate phosphorus was determined using the method outlined by EPA (1979). Leachate sub-samples were subjected to an ammonium persulfate digestion in an autoclave at 120^{o}C followed by a pH adjustment with 6 N NaOH and 1 N H_2SO_4. Samples are then read as orthophosphate on an Orion Autoanalyzer.

Sediment Total Nitrogen

Total nitrogen concentration at each depth was determined using dried sub-samples. At each depth a 2 cm^3 plug was extracted and dried at 70^{o}C in a forced air dryer for approximately 24 hours. The plugs were then ground in a Wiley Mill through a #40 mesh screen and analyzed on a Carlo Erbo NA 1500 CNS Autoanalyzer.

Sediment Inorganic Nitrogen

Ammonium and nitrate levels at each depth were determined using fresh sediment sub-samples. Approximate 5 g plugs were obtained from each depth, placed in 50 ml Nalgene centrifuge tubes, and extracted for 1 hour in 40 ml

of 1 N KCL on a reciprocal shaker table. The tubes were then centrifuged at 10000 rpm for 10 minutes and the extractant filtered through a Whatman 45um filter. To remove H_2S gas, the filtrate was adjusted to pH 1 with 12 N HCL and bubbled for approximately 15 minutes with N_2 gas on a Meyer Analytical Evaporator. The filtrate was then adjusted to pH 7 with 12 N NaOH and analyzed for ammonium and nitrate on a Technicon Autoanalyzer. Ammonium was determined as an indophenol dye at 630 nm while nitrate was reduced ti nitrite on a cadmium column and read as a diazode dye at 543 nm.

Sediment Total Phosphorus

Total phosphorus levels at each depth were determined using the method described by Aspila et al. (1976). Approximate 5 g plugs of fresh sediment from each depth were dried at 70^0C in a forced air dryer for 48 hours. The sediments were then ashed at 550^0C for 6 hours and weighed. Ashed samples were then placed in 50 ml Nalgene centrifuge tubes and extracted for 14-18 hr with 1 N HCL on a reciprocal shaker table. The tubes were then centrifuged at 10000 rpm for 10 minutes and the extractant filtered through a Whatman 45 um filter. The filtrate was then diluted 25:1 and read as orthophosphate on an Orion Autoanalyzer.

Sediment Inorganic Phosphorus

Inorganic phosphorus levels at each depth was determined using the method described by the Soil Testing Laboratory at Virginia Polytechnic Institute and State University. Approximate 5 g plugs of fresh sediments were placed in 50 ml Nalgene centrifuge tubes and extracted in a 0.05 N HCL

and 0.025 N H_2SO_4 solution on a reciprocal shaker table for 1 hour. Samples were then centrifuged at 10000 rpm for 10 minutes and the extractant filtered through a Whatman 45um filter. To remove H_2S gas, the filtrate was adjusted to pH 1 with 12 N HCL and bubbled with N_2 gas for approximately 15 minutes on a Meyer Analytical Evaporators. The filtrate was the adjusted to pH 7 with 12 N NaOH and analyzed as a molybdate complex at 880 nm on a Technicon Autoanalyzer.

Sediment Bulk Density

Sediment bulk densities were estimated using modified 5 cm^3 syringes. At each depth a 2 cm^3 wet sediment plug was obtained and weighed. The plugs were then placed in a forced air dryer at 70°C for approximately 48 hours and reweighed. Bulk densities were then determined at each depth for both wet and dry sediment volumes.

Data Analyses

Statistical Analysis

Biomass and nutrient standing stocks are expressed as $\pm$ one standard deviation (S.D.). To determine if biomass and nutrient comparisons met the requirements for the use of linear models, residual analysis was performed on biomass, nitrogen, and phosphorus data. In addition, a Cochran's Test was applied to all data to determine linearity. A log transformation was determined necessary and applied to all biomass, nitrogen, and phosphorus data and tested using a Cochran's and Bartlett Box Test. Arcsine

transformations were applied to all nitrogen and phosphorus concentration analyses. Log and arcsine transformed data for both biomass and nutrient data were analyzed using univariate analysis of variance (ANOVA) where alpha = 0.05. The relationship between sediment organic matter and total nitrogen was determined using correlation analysis. Multiple comparisons were made using a Student Neuman-Keuls (SNK) test and reported as the experimentwise error rate (EWER).

The relationship between sediment and tissue nitrogen and phosphorus was determined using simple and multiple regressions. Coefficients of determination (r^2) were calculated from the regression of monthly shoot, root, and rhizome nitrogen and phosphorus standing stocks, as the dependent variables, against sediment inorganic and total nitrogen and phosphorus levels for all depths, as the independent variables. The relationship between nitrogen and phosphorus was determined using correlation analysis. Correlation coefficients (r) were determined using pairwise comparisons of nitrogen and phosphorus standing stocks in shoots, roots, rhizomes, and sediments.

General Equations

Leaching

Monthly nitrogen and phosphorus leaching rates (LR) for Peltandra and Spartina were estimated using the equation:

$$LR = mg/l \times l \times g^{-1} \times g/m^2 \times hr^{-1} \times hr/mo$$

where mg/l = concentration of nitrogen or phosphorus in leachate, l = liters used in each leaching experiment, g^{-1} = gram dry weight of shoots leached in each experiment, g/m^2 = estimated gram dry weight of monthly shoot biomass standing stock, hr^{-1} = number of hours in each leaching experiment, and hr/mo = computer estimated number of hours the shoots were covered with tidal waters each month.

Sediment Nitrogen and Phosphorus

Monthly sediment inorganic nitrogen and phosphorus as well as total phosphorus standing stocks (NP) at each depth were estimated for Peltandra and Spartina using the equation:

$$NP = mg/l \times l \times g^{-1} \times bd \times sv$$

where mg/l = concentration of nitrogen or phosphorus in extractant, l = liters of extractant, g^{-1} = gram equivalent dry weight of wet weight sediment extracted, bd = dry weight bulk density (g/cm^3), and sv = sediment volume at depth (cm^3).

Monthly sediment total nitrogen standing stocks (TN) at each depth for Peltandra and Spartina were estimated using the equation:

$$TN = np \times bd \times np$$

where np = nitrogen percentage, bd = dry weight bulk density, and sv = sediment volume at depth (cm^3).

Results

Peltandra virginica

Net Annual Productivity

Aboveground Productivity

Seasonal patterns of *Peltandra* shoot biomass standing stocks are shown in Figure 3. Monthly biomass standing stocks were distinctive over the sampling period (ANOVA, F=1.47E+02, DF=8, P<0.0001). Standing stocks increased from a minimum of 9.54 g/m^2 in March to a peak of 969.53 g/m^2 in July. Following peak biomass, a steady decline was observed to a level of 131.00 g/m^2 in October (Table 1). No live biomass was observed in November. Multiple comparisons indicated that peak biomass standing stocks in June and July were significantly different from those in March-May and August-October (SNK:EWER = 0.05).

Monthly shoot mortality was estimated by adjusting the daily mortality rates calculated from a tagging study completed in a nearby monotypic stand of *Peltandra virginica*. Wohglemuth (1988), following the disappearence of tagged shoots over two week intervals within permanently established 0.25 m^2 quadrats, estimated daily shoot mortality rates of *Peltandra* for each monthly interval. To estimate mean monthly mortality (M) in this study the following equation was used:

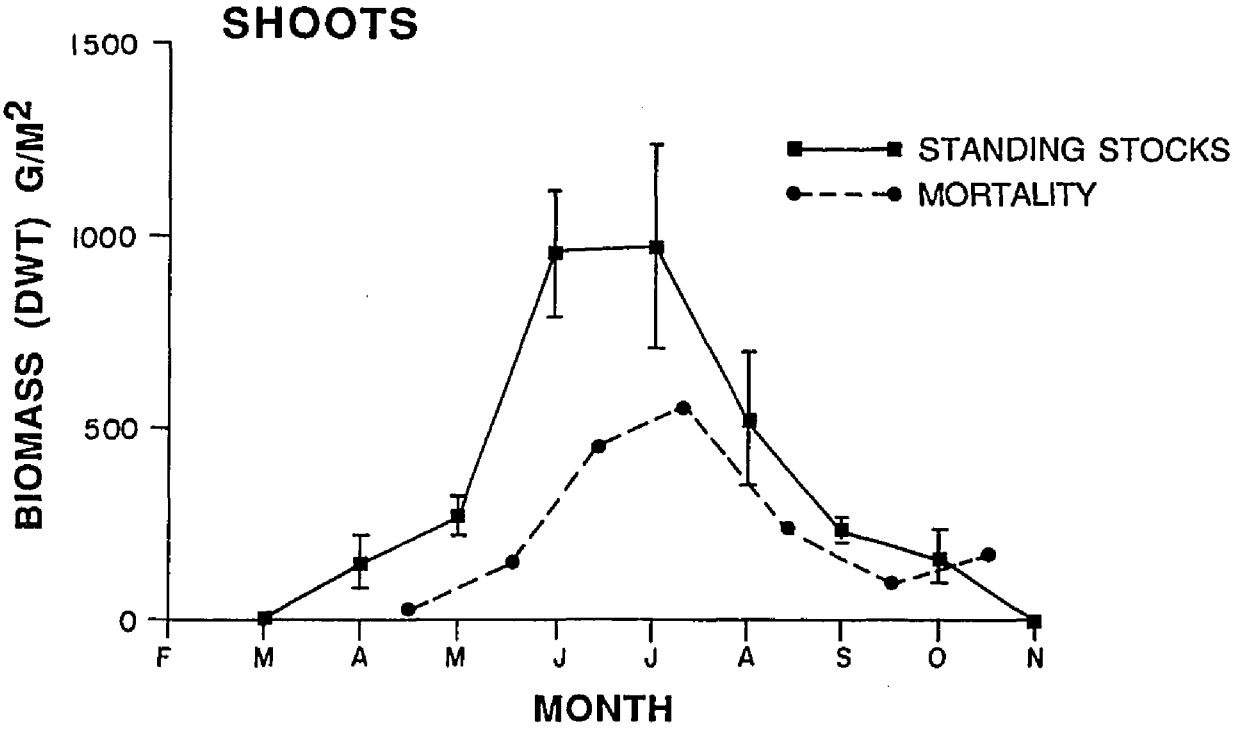
Table 1. Estimated monthly shoot biomass standing stocks ($g/m^2 \pm$ S.D.) and mortality rates (g/m^2/month) for Peltandra virginica expressed as mean dry weights.

Date	Standing Biomass	Mortality
February	-----	
March[a]	9.54 ± 1.99	
		0
April	155.50 ± 65.14	
		2.40
May	272.22 ± 45.47	
		126.80
June[b]	952.23 ± 160.64	
		430.89
July	969.53 ± 260.70	
		554.24
August	524.63 ± 169.00	
		238.41
September	231.46 ± 25.11	
		113.42
October	168.80 ± 61.62	
		168.80
November	-----	

[a]March-May values estimated from 1988 data

[b]June-October values estimated from 1987 data

Figure 3. Seasonal patterns of shoot biomass standing stocks and mortality (g/m^2) of Peltandra virginica expressed as mean dry weights ± S.D..


SHOOTS
BIOMASS (DWT) G/M2
1500
1000
500
0
F
M
A
M
J
J
A
S
O
N
MONTH
STANDING STOCKS
MORTALITY

$M = mdr \times d \times r$

where mdr = appropriate mean daily mortality rates from the tagging study ($g/m^2/day$), d = interval number of days between monthly shoot sampling in this study, and r = ratio of mean monthly shoot biomass in this study to mean monthly biomass in the tagging study. Monthly mortality estimates are shown in Table 1. Mortality between April and June accounted for approximately 8%, while mortality between June and August accounted for approximately 64% of annual mortality. The remaining 28% occurred between September and November.

Monthly shoot primary productivity in Peltandra was estimated by the summation of mean monthly mortality and change in mean monthly shoot biomass. Net annual primary productivity was calculated by summing monthly productivity estimates. Monthly and total annual primary productivity estimates are shown in Table 2. Assuming March 1 to be the beginning of the growing season, the productivity rate between March and May was approximately 4.77 g/day. Between May and July this rate increased to 21.15 g/day and decreased to 1.80 g/day between July and October. As such, productivity between March and May accounted for approximately 17%, while growth between May and July accounted for 77%, of the annual primary productivity. The remaining 6% occurred between August and October at which time a small secondary peak was observed.

Table 2. Estimated monthly and net annual shoot primary productivity for Peltandra virginica expressed as mean dry weights.

Date	Change in Biomass	Mortality	Monthly Productivity
Feb-Mar[a]	9.54	0	9.54
Mar-Apr	146.03	0	146.03
Apr-May	116.65	2.40	119.05
May-June	680.00	126.28	806.28
June-July[b]	17.30	430.89	448.19
July-Aug	-444.90	554.24	109.34
Aug-Sept	-293.15	238.41	-54.74
Sept-Oct	-62.68	113.42	50.74
Oct-Nov	-168.80	168.80	0
			1634.44

Net Annual Primary Productivity = 1634.44 g/m^2

[a] February-June values estimated from 1988 data

[b] June-November values estimated from 1987 data

Belowground Productivity

Seasonal patterns of Peltandra monthly root and rhizome biomass standing stocks are shown in Figure 4. Root biomass increased from a low of 1204 g/m^2 in July to a high of 2772 g/m^2 in December-January. Annual root production was estimated at 1568 g/m^2 using a maximum - minimum calculation. Daily growth rates of 13.81 and 12.31 g/m^2 were observed from July to September and September to January, respectively. Rhizome standing stocks were relatively constant and no annual productivity was detectable. Root and rhizome standing stocks are shown in Table 3.

Total Productivity

Summing shoot and root annual productivity resulted in a total annual productivity of 3202.44 g/m^2 with a net daily productivity of 11.64 g/m^2. A peak belowground:aboveground ratio (B:A = root + rhizome biomass/shoot biomass) was calculated to be 4.12 while the mean B:A ratio was estimated to be 11.45. A peak root:shoot ratio (R:S = root biomass/shoot biomass) was calculated to be 1.24 while the mean R:S ratio was 5.16.

Nitrogen Dynamics

Tissue Nitrogen Concentrations

Seasonal patterns of nitrogen concentrations in the shoot, root, and rhizome compartments of Peltandra are shown in Figure 5. Tissue nitrogen concentrations depended on an interaction effect between compartment and month (ANOVA, F=2.08E+02, DF=8, $P<0.001$). A mean nitrogen concentration of

Table 3. Estimated root and rhizome biomass standing stocks (g/m2) for *Peltandra virginica* expressed as dry weights.

Date	Roots	Rhizomes
Jan[a]	2772	2481
Mar[b]	2520	2673
May	1495	2403
July[c]	1204	2796
Sept	2033	2628
Oct	2672	2500
Dec[a]	2772	2481

[a]Jan-Dec values represent pooled data

[b]Mar-May values estimated from 1988 data

[c]July-Oct values estimated from 1987 data

Figure 4. Seasonal patterns of root and rhizome standing stocks (g/m^2) for Peltandra virginica expressed as dry weights.

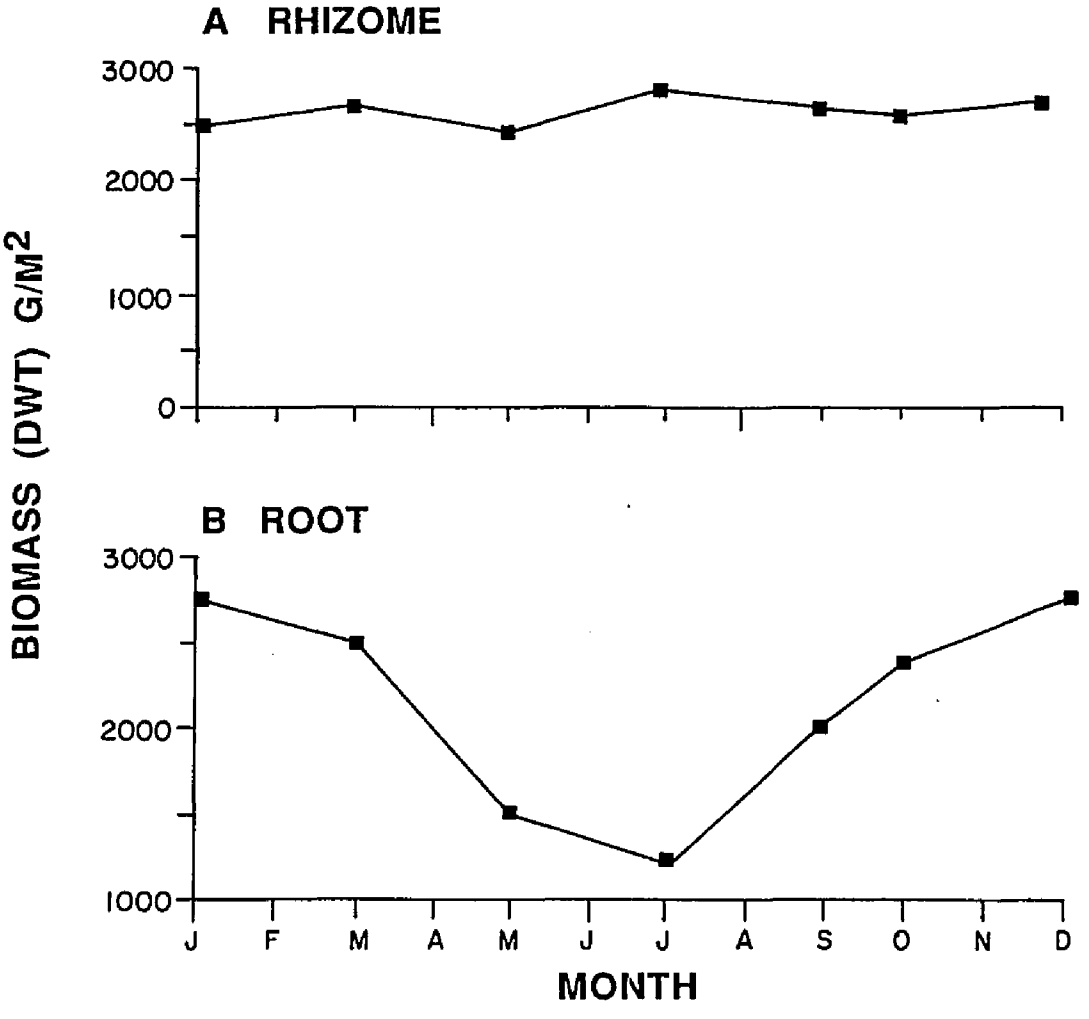

A RHIZOME
3000
2000
1000
0
B ROOT
3000
2000
1000
J F M A M J J A S O N D
MONTH
BIOMASS (DWT) G/M2

Table 4. Mean monthly nitrogen concentrations in the shoots, roots, and rhizomes of Peltandra virginica expressed as % dry weight ± S.D.

Date	Shoots	Roots	Rhizomes
January[a]	-----	1.03 ± 0.06	2.48 ± 0.03
March[b]	3.15 ± 0.08	1.35 ± 0.04	0.97 ± 0.18
April	3.51 ± 0.06	0.91 ± 0.04	1.28 ± 0.03
May	3.77 ± 0.06	0.69 ± 0.02	0.67 ± 0.02
June[c]	2.56 ± 0.28	-----	-----
July	2.57 ± 0.06	1.43 ± 0.03	0.47 ± 0.07
August	1.99 ± 0.19	0.74 ± 0.03	0.16 ± 0.03
September	2.90 ± 0.10	0.91 ± 0.01	0.27 ± 0.02
October	2.73 ± 0.02	0.85 ± 0.02	1.28 ± 0.05
December[a]	-----	1.03 ± 0.04	2.48 ± 0.03
means	2.89	0.99	1.11

[a]Jan-Dec values estimated from pooled data

[b]Mar-May values estimated from 1988 data

[c]June-July values estimated from 1987 data

2.89% in shoots was more than twice that of the mean rhizome concentration of 1.11% and approximately three times the mean root concentration of 0.99% (Table 4).

Peltandra shoot nitrogen concentrations demonstrated significant seasonal patterns over an annual cycle (ANOVA, F=1.50E+02, DF=7, P<0.0001) decreasing from a mean high concentration of 3.77% in May to a mean low of 1.99% in August. Nitrogen concentrations then increased in September to 2.90% Multiple comparisons indicated that nitrogen concentrations in June and July were grouped as distinctive from other months (SNK:EWER = 0.05).

Root nitrogen concentrations exhibited pronounced seasonal patterns (ANOVA, F=3.07E+02, DF=5, P<0.001). A mean high concentration of 1.43% was observed in July at the onset of root growth. Root concentrations then decreased in August and remained relatively constant through December (Table 4). Between March and June, during periods of root dieback, root nitrogen concentrations decreased to a mean low of 0.69%. Rhizome nitrogen concentrations also exhibited pronounced seasonal patterns over an annual cycle (ANOVA, F=3.70E+02, DF=5, P<0.0001) decreasing from a mean high of 2.48% in January to a mean low of 0.16% in August. Rhizome nitrogen concentrations then increased to 1.28% in October.

Tissue Nitrogen Standing Stocks

Peltandra monthly shoot, root, and rhizome compartmental nitrogen standing stocks were estimated by multiplying monthly biomass standing stocks by monthly tissue concentrations. As root and rhizome biomass standing stocks were measured approximately every other month, nitrogen standing stocks for interval months were estimated by multiplying the

Table 5. Mean monthly nitrogen standing stocks (gN/m^2) in the shoots, roots, and rhizomes of *Peltandra virginica* expressed on a dry weight basis ± S.D.

Date	Shoots	Roots	Rhizomes
January[a]	----	28.55 ± 1.55	61.52 ± 1.03
March[b]	00.30 ± 0.05	34.02 ± 1.02	26.16 ± 4.72
April	05.47 ± 1.79	18.27 ± 1.52	32.48 ± 1.01
May	10.23 ± 1.35	10.16 ± 0.15	16.10 ± 0.36
June[c]	24.28 ± 4.05	----	----
July	24.33 ± 5.97	15.27 ± 1.05	14.20 ± 1.83
August	10.44 ± 3.02	10.40 ± 0.30	04.00 ± 0.92
September	06.69 ± 0.60	15.86 ± 1.23	06.08 ± 0.54
October	04.61 ± 1.42	19.18 ± 0.55	30.29 ± 1.04
December[a]	----	28.55 ± 1.55	61.52 ± 1.03
means	10.79	20.02	28.03

[a]Jan-Dec values estimated from pooled data

[b]March-May values estimated from 1988 data

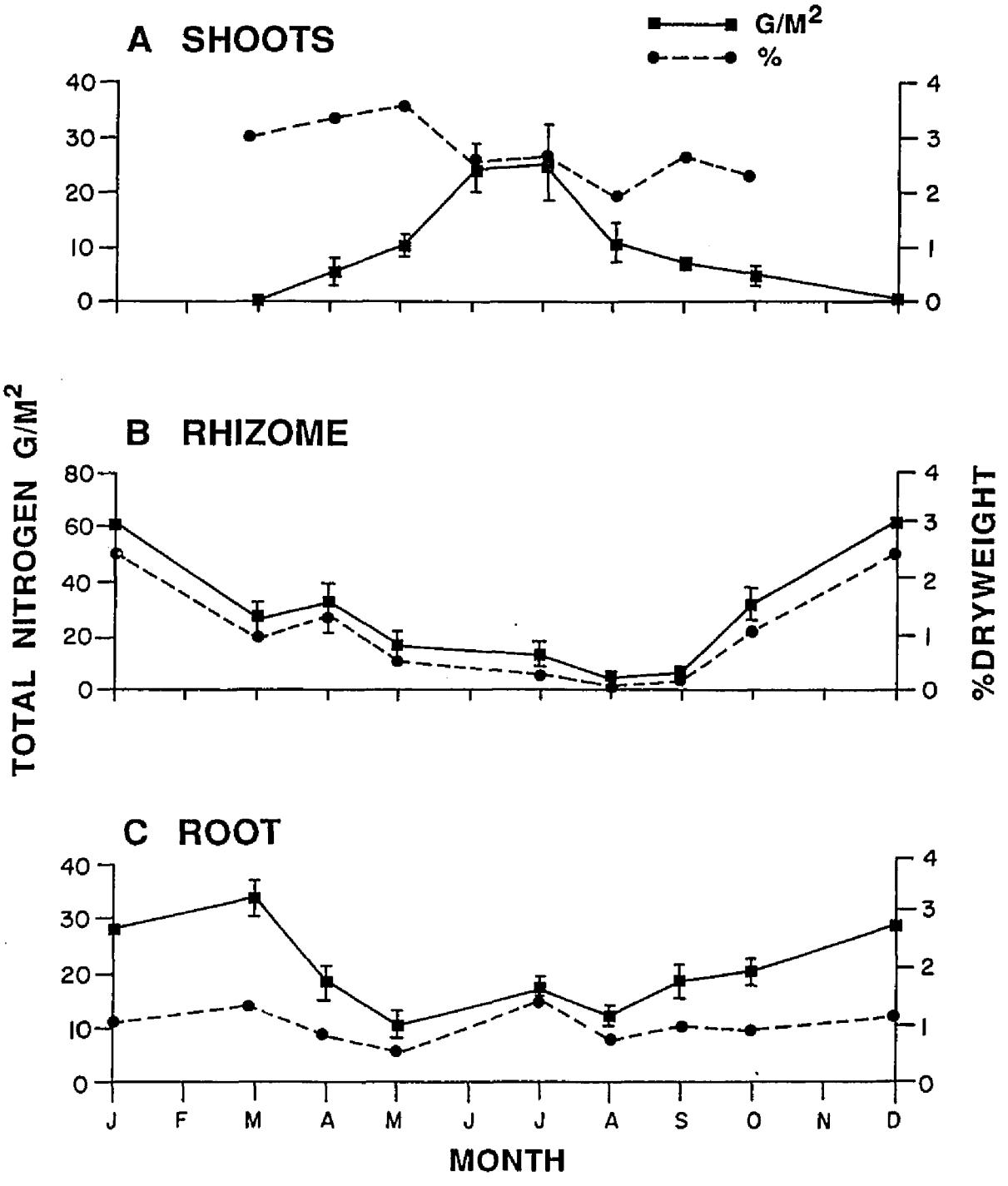
[c]June-Oct values estimated from 1987 data

nitrogen concentration by the estimated mean biomass between the measured months. Seasonal patterns of shoot, root, and rhizome nitrogen standing stocks are shown in Figure 5. Tissue nitrogen standing stocks depended on an interaction effect between compartment and month (ANOVA, F=1.82E+02, DF=8, P<0.001). Mean rhizome nitrogen standing stocks were approximately three times that of the shoots and one and a half times that of the roots (Table 5).

Shoot nitrogen standing stocks varied significantly over an annual cycle (ANOVA, F=6.07E+02, DF=7, P<0.0001), increasing from a low of 0.30 g/m^2 in March to a peak of 24.33 g/m^2 in July (Table 5). Nitrogen standing stocks then stocks decreased steadily to a low of 4.60 g/m^2 in October. Shoot nitrogen standing stocks were strongly correlated with shoot biomass ($r = .98$, $P<.01$). Multiple comparisons indicated that peak nitrogen standing stocks in June and July were significantly different from other months (SNK:EWER = 0.05).

Root nitrogen standing stocks also exhibited pronounced seasonal patterns over the sampling period (ANOVA, F=9.83E+02, DF=5, P<0.0001). A peak standing stock of 34.02 g/m^2 was observed in March followed by a steady decrease to 10.16 g/m^2 in May, a period root dieback. Nitrogen standing stocks then increased to 15.27 g/m^2 at the onset of root growth in July. A relatively steady increase was then observed to a level of 28.55 g/m^2 in December (Table 5). As such, root nitrogen standing stocks were correlated with root biomass ($r = .68$, $P<.10$). Like the roots, rhizome nitrogen standing stocks exhibited pronounced seasonal patterns (ANOVA, F=2.58E+02,

Figure 5. Seasonal patterns of mean monthly nitrogen concentrations (%N) and standing stocks (gN/m^2) in the shoots, roots, and rhizomes of Peltandra virginica expressed on a dry weight basis ± S.D.


A SHOOTS
G/M2
%
40
30
20
10
0
4
3
2
1
0
B RHIZOME
TOTAL NITROGEN G/M2
%DRYWEIGHT
80
60
40
20
0
C ROOT
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

DF=5, P<0.0001). A peak of 61.50 g/m^2 was observed in January followed by a steady decrease to a level of 4.33 g/m^2 in August resulting in a minimum of 57.17 g/m^2 nitrogen available for reallocation. The inverse correlation between rhizome and shoot nitrogen standing stocks, however, was insignificant ($r = -.48$, $P<.20$).

Tissue Nitrogen Leaching

Peltandra monthly leaching rates were estimated using the previously described equation. Summation of monthly leaching rates produced an annual leaching rate of 0.83 g/m^2.

April	0.28 g/m^2
May	0.05 g/m^2
August	0.21 g/m^2
September	0.29 g/m^2
	0.83 g/m^2/year

Tissue Nitrogen Efficiency Indexes

Peltandra use and recovery efficiency indexes are shown in Table 6. Shoot nitrogen use efficiency was generally lower (March - May) during the lag phase of shoot productivity and increased as shoot biomass increased. Peak use efficiency was observed in August during the initial decrease in shoot biomass. Root use efficiency was variable although use efficiency increased with increased biomass. Rhizome use efficiency increased between April and August, a period of maximum shoot productivity, and decreased during periods of shoot senescence and root productivity. Mean use

Table 6. Nitrogen use efficiency in shoots, roots, and rhizomes and nitrogen recovery efficiency in shoots of Peltandra virginica. Monthly use efficiency is estimated by dividing mean monthly tissue biomass by mean monthly tissue nitrogen standing stocks. Monthly recovery efficiency is estimated by dividing the difference in nitrogen of live and dead shoots by nitrogen in live shoots.

Use Efficiency

Date	Shoots	Roots	Rhizomes
January[a]	----	97.09	40.32
March[b]	31.80	74.07	103.12
April	28.42	155.77	78.14
May	26.61	147.15	149.25
June[c]	39.21	----	----
July	39.84	78.84	212.78
August	50.25	155.67	626.32
September	34.59	128.18	370.66
October	36.62	139.31	78.13
December[a]	----	97.09	40.32
means	35.92	119.24	188.78

Recovery Efficiency

Date	Shoots
April-May	0.55
May-June	0.40
June-July	0.40
July-Aug	0.23
Aug-Sept	0.40
Sept-Oct	0.36
Oct-Nov	0.65
mean	0.43

[a]Jan-Dec values estimated from pooled biomass data

[b]March-May values estimated from 1988 data

[c]June-Oct values estimated from 1987 data

efficiency in the rhizomes was approximately five times that of the shoots and one and a half times that of the roots. Recovery efficiency in the shoots decreased between April and August, periods of increased shoot biomass, and increased during periods of shoot senescence.

Sediment Inorganic Nitrogen

Sediment inorganic nitrogen, as ammonium and nitrate, at each depth for Peltandra was estimated using the previously described equation. Each month the standing stocks of both nitrate and ammonium for each depth were summed to represent the total available monthly pools of each of these nutrients to a one meter depth (Tables 7,8). Total monthly nitrate pools increased from a low of 0.001 g/m^2 in March to a high of 0.410 g/m^2 in October. Over the sampling period, monthly nitrate levels varied significantly (ANOVA, F=1.07E+01, DF=7, P<0.0001), however no significant variation was noted with depth (ANOVA, F=3.6E-01, DF=4, P=0.836). Total monthly ammonium pools decreased from a high of 7.53 g/m^2 in April to a low of 1.64 g/m^2 in July. Over the sampling period, monthly ammonium levels were shown to vary significantly (ANOVA, F=3.01, DF=7, P<0.015), however no significant variation was observed with depth (ANOVA, F=8.39E-01, DF=4, P=0.500). Total monthly pools of ammonium and nitrate standing stocks were summed to represent the total monthly available pool of inorganic nitrogen. Seasonal patterns of total monthly available pools of inorganic nitrogen are shown in Figure 6.

Table 7. Mean monthly standing stocks at each sediment layer and total monthly pools of nitrogen as gNO_3/m^2 for Peltandra virginica expressed on a dry weight basis.

	NO_3					
	Sediment Layer					
	0-10cm	10-25cm	25-50cm	50-75cm	75-100cm	Total
Date						
February[a]	0.002	0.002	0.004	0.006	0.003	0.018
March	0.001	---	---	---	---	0.001
April	0.007	0.002	0.004	0.005	0.005	0.023
May	0.005	0.015	0.017	0.020	0.012	0.069
July[b]	0.024	0.004	0.006	0.012	0.011	0.061
August	0.027	0.052	0.128	0.090	0.057	0.381
September	0.023	0.018	0.011	0.037	0.005	0.094
October	0.056	0.071	0.028	0.139	0.116	0.410
					mean	0.132

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

Table 8. Mean monthly standing stocks at each sediment layer and total monthly pools of inorganic nitrogen as gNH_4/m^2 for Peltandra virginica expressed on a dry weight basis.

	NH_4					
	Sediment Layer					
	0-10cm	10-25cm	25-50cm	50-75cm	75-100cm	Total
Date						
February[a]	0.294	0.334	0.545	1.011	0.769	2.953
March	2.142	1.213	0.999	1.948	0.145	6.447
April	1.865	0.733	1.995	1.440	1.500	7.530
May	0.543	0.710	0.857	1.211	0.698	4.019
July[b]	0.987	0.164	0.042	0.250	0.197	1.640
August	0.712	0.484	0.973	1.031	0.666	3.866
September	1.176	0.938	1.334	2.154	1.572	7.174
October	1.986	2.038	0.381	0.139	0.392	4.936
					mean	4.821

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

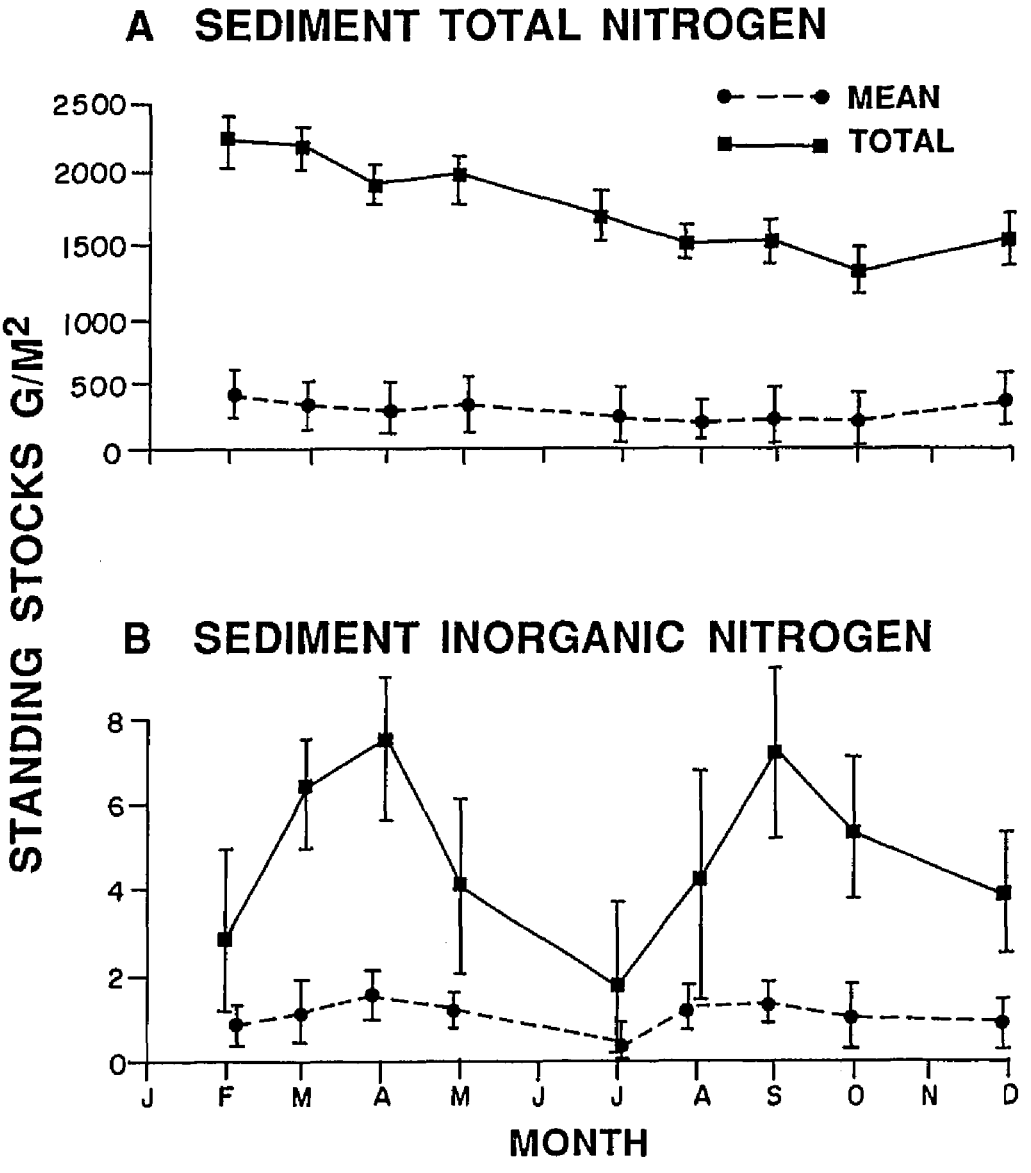
Table 9. Mean monthly standing stocks at each sediment layer and total monthly pools of total nitrogen as gTN/m^2 for Peltandra virginica expressed on dry weight basis.

	Total Nitrogen					
	Sediment Layer					
	0-10cm	10-25cm	25-50cm	50-75cm	75-100cm	Total
Date						
February[a]	250	334	549	627	536	2296
March	186	354	670	575	434	2219
April	214	325	435	442	560	1976
May	212	325	532	480	465	2014
July[b]	225	347	463	427	392	1854
August	191	311	371	348	469	1690
September	127	230	343	627	325	1652
October	115	233	350	426	313	1437
					mean	1892

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

Figure 6. Seasonal patterns of total nitrogen and inorganic nitrogen (NO_3 + NH_4) standing stocks (g/m^2) in the sediments of Peltandra virginica. Monthly standing stocks expressed as the mean and total monthly pools for all depths to one meter on a dry weight basis.


A SEDIMENT TOTAL NITROGEN
MEAN
TOTAL
2500
2000
1500
1000
500
0
STANDING STOCKS G/M2
B SEDIMENT INORGANIC NITROGEN
8
6
4
2
0
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

Sediment Total Nitrogen

Sediment total nitrogen at each depth for Peltandra was estimated using the previously described equation. Monthly total nitrogen standing stocks for each depth were summed to represent the total monthly nitrogen pool to a one meter depth. Total monthly pools of total nitrogen decreased from a high of 2296 g/m^2 in February to a low of 1437 g/m^2 through October (Table 9). Over the sampling period, monthly total nitrogen levels did not vary significantly (ANOVA, F=8.38E-01, DF=7, P=0.56), however significant variation was observed with depth (ANOVA, F=1.77E+01, DF=4, P<0.0001). Seasonal patterns of total monthly nitrogen pools are shown in Figure 6. Statistical analyses indicated that over the sampling period a strong correlation between total nitrogen and organic matter existed for all depths (0-10cm, r = .95, P<.01; 10-25cm, r = .93, P<.01; 25-50cm, r = .97, P<.01; 50-75cm, r = .95, P<.01; 75-100cm, r =.95, P<.01)

Sediment-Tissue Nitrogen Relationship

The relationship between Peltandra sediment and tissue nitrogen standing stocks was developed through simple and multiple regression analysis. Regressions were designed such that monthly shoot, root, and rhizome nitrogen standing stocks, as the dependent variables, were individually regressed against monthly sediment inorganic (NO_3 + NH_4) and total nitrogen standing stocks, as the independent variables, for all depths. Regression analysis indicated that shoot, root, and rhizome nitrogen standing stocks were independent of both sediment inorganic and total nitrogen. Coefficients of determination and levels of significance are shown in Table 10.

Table 10. Coefficients of determination (r^2) with levels of significance (p) for simple and multiple regressions of Peltandra virginica shoot, root, and rhizome nitrogen standing stocks (N) with sediment inorganic (NO_3 + NH_4) and total nitrogen (TN) standing stocks expressed for all depths.

	Sediment (NO_3+ NH_4)	Sediment TN	Sediment (NO_3+ NH_4), TN
Shoot N	r^2 = 0.001 F = 0.002 p = 0.989	r^2 = 0.001 F = 0.007 p = 0.930	NS a = 0.05
Root N	r^2 = 0.001 F = 0.004 p = 0.946	r^2 = 0.002 F = 0.009 p = 0.920	NS a = 0.05
Rhizome N	r^2 = 0.010 F = 0.414 p = 0.523	r^2 = 0.008 F = 0.340 p = 0.562	NS a = 0.05

NS = non significant
a = alpha level

Nitrogen Model

Peltandra compartmental nitrogen standing stocks are estimated from previous sections (Tables 5, 7-9), and include monthly ranges. Annual compartmental fluxes were estimated using productivity, nitrogen concentrations, leaching, and mass balance of certain compartments. Compartmental standing stocks and annual fluxes are shown in Figure 7.

Annual losses to leaching were estimated by the summation of monthly leaching rates resulting in an annual leaching rate of 0.83 g/m^2.

Annual losses to detritus were estimated by the summation of monthly detrital losses. Monthly detrital losses were estimated by multiplying monthly mortality by the nitrogen concentration in dead shoots.

Date	Mortality (g/m^2)	Concentration (%)	Monthly Loss (g/m^2)
April-May	2.40	1.53	0.04
May-June	126.28	1.53	1.93
June-July	430.89	1.53	6.59
July-Aug	554.24	1.53	8.47
August-Sept	238.41	1.73	4.12
Sept-Oct	113.42	1.73	1.96
Oct-Nov	168.80	0.96	1.62

Annual loss to detritus = 24.72 g/m^2

Annual flow from the rhizome to the shoot compartment was estimated by the summation of monthly flows. Monthly flows were estimated by multiplying monthly shoot productivity by nitrogen concentrations in live shoots. Total annual flow into the shoot compartment was estimated by the summation of annual shoot uptake and leaching.

Date	Productivity (g/m^2)	Concentration (%)	Monthly Flow (g/m^2)
Feb-March	9.54	3.15	0.30
March-April	146.03	3.51	5.12
April-May	119.05	3.77	4.48
May-June	806.28	2.56	20.64
June-July	448.19	2.57	11.52
July-Aug	109.34	1.99	2.18
Aug-Sept	-54.74	2.90	-1.58
Sept-Oct	50.74	2.73	1.39

Annual flow from rhizomes 44.05 g/m^2

Leachate + 0.83 g/m^2

Total annual flow to shoots = 44.88 g/m^2

Annual flow from the shoot compartment to the rhizome compartment during senescence was estimated by the difference in total shoot uptake and losses to leaching and detritus (44.88 g/m^2 - (0.83 g/m^2 + 23.89 g/m^2)

Annual flow from shoots to rhizomes = 19.32 g/m^2.

Annual losses due to root mortality, based on the assumption of steady state, were estimated by multiplying annual root mortality by the mean nitrogen concentration in the roots between January and July.

	Mortality (g/m^2)	Concentration (%)	Annual Loss (g/m^2)
Jan-July	1568	0.995	15.60

Annual loss to root mortality = $\underline{15.60\ g/m^2}$

Based on the assumption that the majority of root growth is supported by reallocation from the rhizomes, annual flow from the rhizomes to the roots was estimated by multiplying annual root productivity by mean nitrogen concentration between July and December.

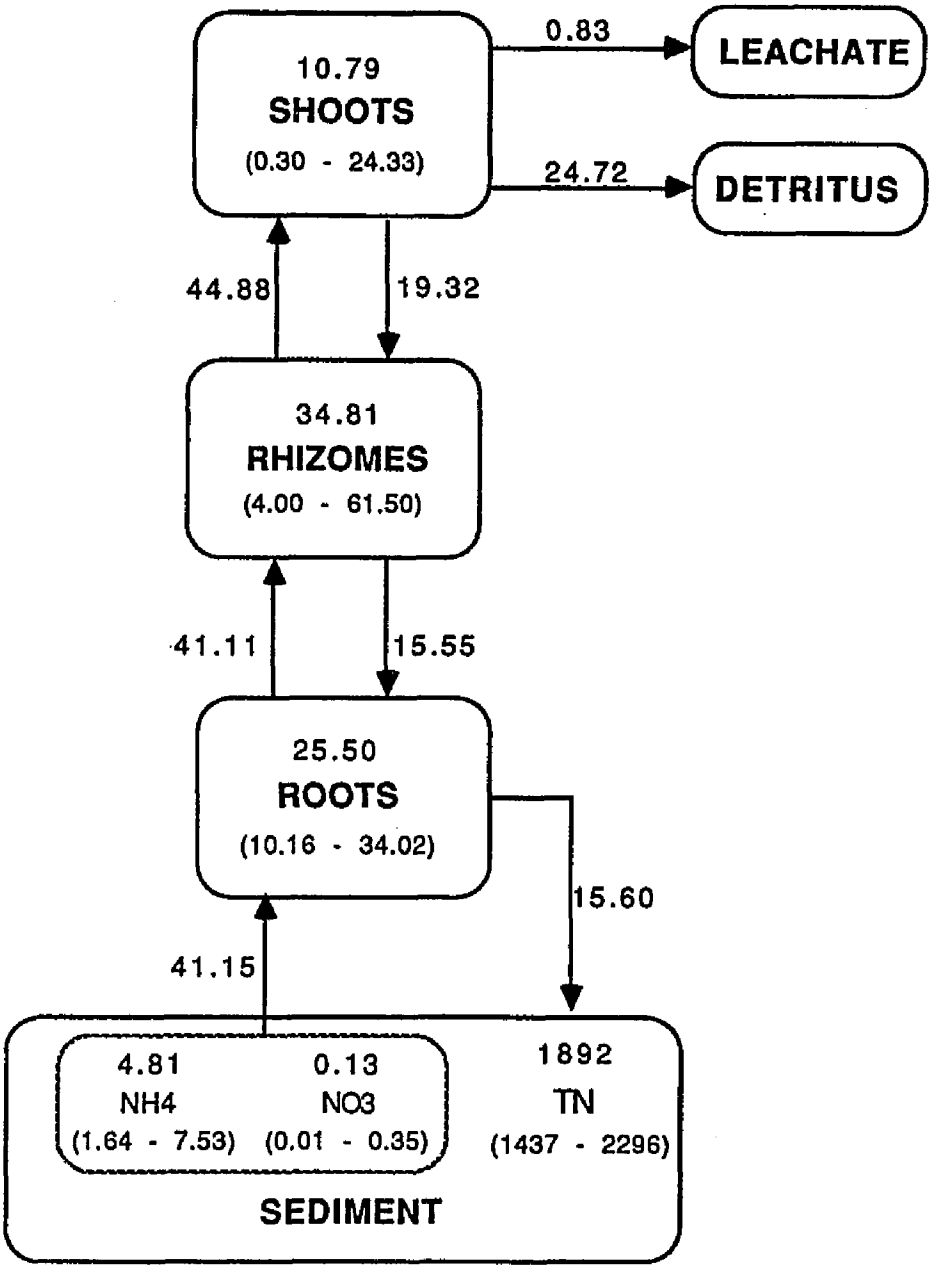
	Productivity (g/m^2)	Concentration (%)	Annual Flow (g/m^2)
July-Dec	1568	0.992	15.55

Annual flow from rhizomes to roots = $\underline{15.55\ g/m^2}$

Annual uptake by the roots from the sediments, based on the assumption of steady state, is equal to the sum of annual losses from the plant i.e. leaching, shoot mortality, and root mortality.

Leaching		Detritus		Root Mortality		Annual root uptake
$0.83\ g/m^2$	+	$24.72\ g/m^2$	+	$15.60\ g/m^2$	=	$\underline{41.15\ g/m^2}$

Figure 7. Nitrogen compartmental model for Peltandra virginica. Compartmental nitrogen standing stocks are expressed as mean gN/m^2 including monthly ranges in parentheses. Sediment nitrogen standing stocks expressed as total monthly pools for all depths. Annual flows are expressed as gN/m^2/year.


10.79
SHOOTS
(0.30 - 24.33)
0.83
LEACHATE
24.72
DETRITUS
44.88
19.32
34.81
RHIZOMES
(4.00 - 61.50)
41.11
15.55
25.50
ROOTS
(10.16 - 34.02)
15.60
41.15
4.81
NH4
(1.64 - 7.53)
0.13
NO3
(0.01 - 0.35)
1892
TN
(1437 - 2296)
SEDIMENT

Annual flow from the roots to the rhizomes was estimated by mass balance of the rhizome compartment.

$$(44.88\ g/m^2 + 15.55\ g/m^2) - 19.32\ g/m^2 = 41.11\ g/m^2.$$

$$\text{Annual flow from roots to rhizomes} = \underline{41.11\ g/m^2}$$

Summary

The quantitative assessment of annual nitrogen flows shows that over an annual cycle Peltandra virginica releases significant levels of nitrogen to the environment. Of the total nitrogen transfer of 44.88 g/m^2 to the shoots, 55%, or 24.72 g/m^2, is transferred to the surrounding environment by shoot mortality while 2%,, or 0.83 g/m^2 is lost through leaching. Root mortality also accounts for a significant loss to the surrounding sediments. Approximately 15.60 g/m^2, or 38%, of the total uptake by the roots of 41.15 g/m^2 is lost to sediments during root dieback.

Peltandra virginica does, however, conserve nitrogen through internal cycling and reallocation. Approximately 43%, or 19.32 g/m^2, of the total uptake by the shoots is conserved through translocation to the rhizome compartment. Of the total transfer of nitrogen to the rhizome compartment by shoot translocation and root uptake, approximately 15.55 g/m^2, or 26%, supports root growth via reallocation. Of the 60.43 gN/m^2 required for shoot and root productivity, approximately 57.17 gN/m^2, or 95% is avaialable for reallocation from the rhizomes. Transfer of 41.11 g/m^2 from the roots

to the rhizomes accounts for approximately 100% of total root uptake of 41.15 g/m^2.

Phosphorus Dynamics

Tissue Phosphorus Concentrations

Seasonal patterns of phosphorus concentrations in the shoot, root, and rhizome compartments of Peltandra are shown in Figure 8. Tissue phosphorus concentrations depended on an interaction effect between compartment and month (ANOVA, F=4.16E+02, DF=8, P<0.001). A mean shoot phosphorus concentration of 0.40% was slightly higher than that of the roots (0.31%) and rhizomes (0.28%) (Table 11).

Peltandra shoot phosphorus concentrations varied significantly over an annual cycle (ANOVA, F=4.30E+02, DF=5, P<0.0001) decreasing from a high mean concentration of 0.65% in April to a low mean of 0.27% in August. Root phosphorus concentrations varied significantly over the sampling period (ANOVA, F=3.17E+01, DF=5, P<0.0001). A peak concentration of 0.41% was observed in March decreasing to a mean of 0.33% between April and August and 0.27% between September and December. Rhizome phosphorus concentrations also varied significantly over an annual cycle (ANOVA, F=1.10E+02 DF=5, P<0.0001) decreasing from a mean high of 0.54% in April to a mean low of 0.12% in August. Concentrations then increased to 0.29% through December.

Tissue Phosphorus Standing Stocks

Peltandra shoot, root, and rhizome phosphorus compartmental standing stocks were estimated by multiplying monthly biomass standing stocks by the

Table 11. Mean monthly phosphorus concentrations in the shoots, roots, and rhizomes of Peltandra virginica expressed as % dry weight ± S.D.

Date	Shoots	Roots	Rhizomes
January[a]	----	0.27 ± 0.02	0.29 ± 0.03
March[b]	0.40 ± 0.02	0.41 ± 0.02	0.19 ± 0.03
April	0.65 ± 0.03	0.32 ± 0.01	0.54 ± 0.01
May	0.55 ± 0.03	0.31 ± 0.02	0.32 ± 0.02
June[c]	0.35 ± 0.02	0.32 ± --	0.34 ± --
July	0.31 ± 0.01	0.36 ± 0.04	0.37 ± 0.01
August	0.27 ± 0.03	0.35 ± 0.01	0.12 ± 0.02
September	0.34 ± 0.03	0.27 ± 0.02	0.16 ± 0.03
October	0.31 ± 0.01	0.27 ± 0.01	0.21 ± 0.01
December[a]	----	0.27 ± 0.02	0.29 ± 0.03
means	0.40	0.36	0.31

[a]Jan-Dec values estimated from pooled data

[b]March-May values estimated from 1988 data

[c]June- Oct values estimated from 1987 data

appropriate mean monthly phosphorus concentration. As root and rhizome biomass standing stocks were measured approximately every other month, phosphorus standing stocks for interval months were estimated by multiplying the estimated mean monthly biomass between the measured months by the monthly tissue concentration. Seasonal patterns of Peltandra shoot, root, and rhizome phosphorus standing stocks are shown in Figure 8. Tissue phosphorus standing stocks depended on an interaction effect between between compartment and month (ANOVA, F=1.85E+02, DF=6, P<0.001). A mean phosphorus standing stock of 6.88 $g/m^2$was equivalent to that of the roots (6.35 g/m^2) but four times that of the shoots (1.45 g/m^2).

Peltandra shoot phosphorus standing stocks varied significantly over an annual growth cycle (ANOVA, F=3.34E+02, DF=7, P<0.0001) increasing from a low mean of 0.04 g/m^2 in March to a high mean of 3.33 g/m^2 in June. Shoot phosphorus standing stocks then decreased to 0.52 g/m^2 in October (Table 12). Shoot phosphorus standing stocks were positively correlated with shoot biomass standing stocks (r = .96, P<.01). Multiple comparisons indicated that phosphorus standing stocks in June and July were significantly different from all other months (SNK:EWER = 0.05).

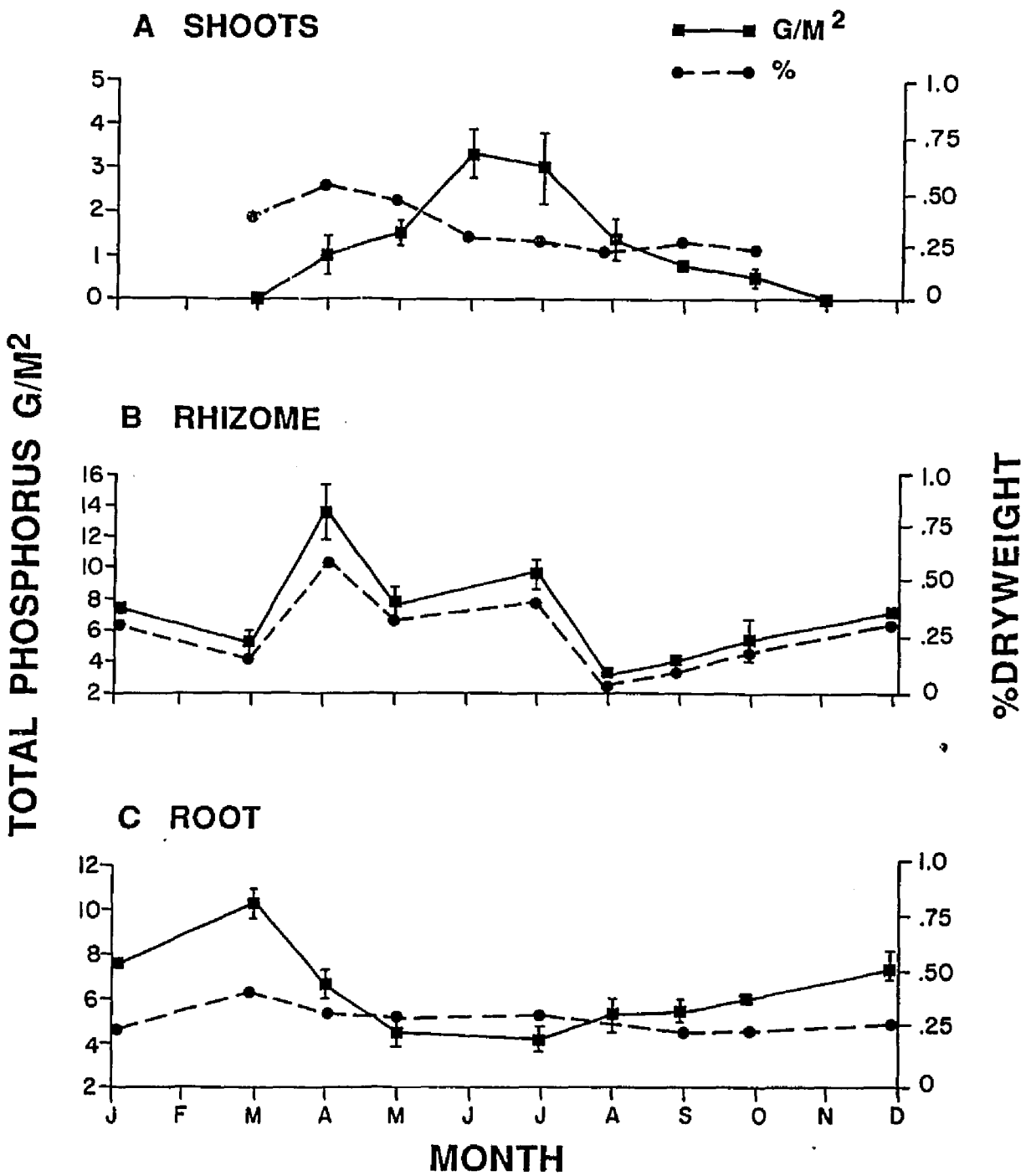
Root phosphorus standing stocks exhibited distinctive seasonal patterns (ANOVA, F=7.97E+02, DF=5, P<0.0001) increasing from a low of 4.33 g/m^2 in July to a high of 10.33 g/m^2 in March. Root phosphorus standing stocks then decreased to the low observed in July. Root phosphorus standing stocks were positively correlated with root biomass standing stocks (r = .79, P<.10). Rhizome phosphorus standing stocks also varied significantly over an annual cycle (ANOVA, F=1.05E+02, DF=5, P<0.0001) decreasing from a mean high of

Table 12. Mean monthly phosphorus standing stocks (gP/m^2) in the shoots, roots, and rhizomes of Peltandra virginica expressed on a dry weight basis ± S.D.

Date	Shoots	Roots	Rhizomes
January[a]	-----	7.48 ± 0.61	7.19 ± 0.83
March[b]	0.04 ± 0.006	10.33 ± 0.52	5.08 ± 0.51
April	1.01 ± 0.33	6.62 ± 0.62	13.71 ± 1.71
May	1.52 ± 0.20	4.49 ± 0.80	7.68 ± 0.81
June[c]	3.33 ± 0.43	-----	-----
July	3.00 ± 0.70	4.33 ± 0.21	10.34 ± 0.63
August	1.42 ± 0.39	4.92 ± 0.41	3.25 ± 0.43
September	0.78 ± 0.07	5.48 ± 0.36	4.24 ± 0.41
October	0.52 ± 0.16	7.21 ± ---	5.38 ± 1.01
December[a]	-----	7.48 ± 0.61	7.19 ± 0.83
means	1.45	6.35	6.88

[a]Jan-Dec values estimated from pooled data
[b]March-May values estimated from 1988 data
[c]June-Oct values estimated from 1987 data

Figure 8. Seasonal patterns of mean monthly phosphorus concentrations (%P) and standing stocks (gP/m^2) in the shoots, roots, and rhizomes of Peltandra virginica expressed on a dry weight basis ± S.D.


A SHOOTS
G/M 2
%
B RHIZOME
C ROOT
TOTAL PHOSPHORUS G/M2
%DRYWEIGHT
MONTH
J F M A M J J A S O N D

13.71 g/m^2 in April to a mean low of 3.25 g/m^2 in August resulting in a minimum of 10.46 g/m^2 phosphorus available for reallocation. Rhizome standing stocks then steadily increased to 7.19 g/m^2 in December.

Tissue Phosphorus Leaching

Using the previously described equation, summation of monthly leaching rates produced an annual leaching rate of 0.12 g/m^2 in Peltandra.

April	0.040 g/m^2
May	0.006 g/m^2
August	0.029 g/m^2
September	0.042 g/m^2
	0.117 g/m^2

Tissue Phosphorus Efficiency Indexes

Peltandra phosphorus use and recovery efficiency indexes are shown in Table 13. Shoot phosphorus use efficiency was generally lower during the early lag phase of shoot development (March-May) and increased during periods of shoot biomass productivity (May-July). Peak shoot use efficiency was observed in August during initial shoot dieback. Root use efficiency was relatively low prior to the onset of root productivity and increased and remained stable during peak shoot biomass. Rhizome use efficiency decreased between March and April at the onset of shoot development and increased significantly through August. Rhizome use efficiency then decreased between September and December during periods of shoot senescence and root productivity. Mean use efficiency in the rhizomes of was slightly higher

Table 13. Phosphorus use and recovery efficiency indexes for Peltandra virginica shoots, roots, and rhizomes. Monthly use efficiency is estimated by dividing tissue biomass by tissue phosphorus standing stocks. Monthly recovery efficiency is estimated by dividing the difference of phosphorus in live and dead tissues by phosphorus in live tissues.

	Use Efficiency		
Date	Shoots	Roots	Rhizomes
January[a]	----	370.58	345.06
March[b]	238.50	243.94	526.18
April	153.96	429.90	185.12
May	179.09	332.96	312.89
June[c]	285.90	----	----
July	323.17	278.06	270.41
August	369.46	329.06	834.46
September	296.74	370.98	619.81
October	324.61	370.59	476.19
December[a]	----	370.58	345.06
means	271.41	340.75	446.26

Recovery Efficiency	
Date	Shoots
April-May	0.69
May-June	0.67
June-July	0.23
July-Aug	0.11
Aug-Sept	0.47
Sept-Oct	0.43
Oct-Nov	0.71
mean	0.47

[a]Jan-Dec values estimated from pooled data

[b]March-May values estimated from 1988 data

[c]June-Oct values estimated from 1987 data

than that of the roots and approximately one and a half times that of the shoots. Peltandra recovery efficiency in the shoots decreased significantly between April and August during periods of peak shoot productivity and senescence. Recovery efficiency then increased through October (Table 13).

Sediment Inorganic Phosphorus

Sediment inorganic phosphorus, as orthophosphate (PO_4), at each depth for Peltandra was estimated using the previously described equation. Each month phosphate standing stocks for all depths were summed to represent the monthly total available phosphate pool to a one meter depth (Table 14). Monthly total phosphate pools increased from a low of 16.87 g/m^2 in August to a high of 78.36 g/m^2 in October. Levels remained relatively constant between February and May averaging 51.57 g/m^2. Over the sampling period, phosphate standing stocks demonstrated no variation with month (ANOVA, F=9.9E-01, DF=7, P=0.44) or with depth (ANOVA, F=1.00, DF=4, P=0.42). Seasonal patterns of total monthly phosphate pools are shown in Figure 9.

Sediment Total Phosphorus

Sediment total phosphorus at each depth was estimated using the previously described equation. Each month total phosphorus standing stocks for all depths were summed to represent the total monthly pool of total phosphorus to a one meter depth (Table 15). Total monthly pools of total phosphorus demonstrated two peaks, 191.86 g/m^2 in February and 179.58 in October. Over the sampling period, total phosphorus standing stocks did not vary monthly (ANOVA, F=1.01, DF=7, P=0.44) or with depth (ANOVA, F=1.36,

Table 14. Mean monthly standing stocks at each sediment layer and total monthly pools of inorganic phosphorus as gPO_4/m^2 for Peltandra virginica expressed on dry weight basis.

	PO_4					
	Sediment Layer					
	0-10cm	10-25cm	25-50cm	50-75cm	75-100cm	Total
Date						
February[a]	10.90	7.21	14.66	9.08	6.80	59.55
March	2.85	11.78	13.96	13.69	19.63	61.91
April	1.76	9.33	12.22	13.02	13.35	49.68
May	3.27	11.95	17.85	9.90	12.28	55.25
July[b]	1.36	2.44	4.97	4.58	4.78	18.13
August	4.69	3.72	0.72	5.98	1.76	16.87
September	7.99	11.72	14.15	----	----	33.86
October	18.25	23.47	12.88	23.76	----	78.36
					mean	46.70

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

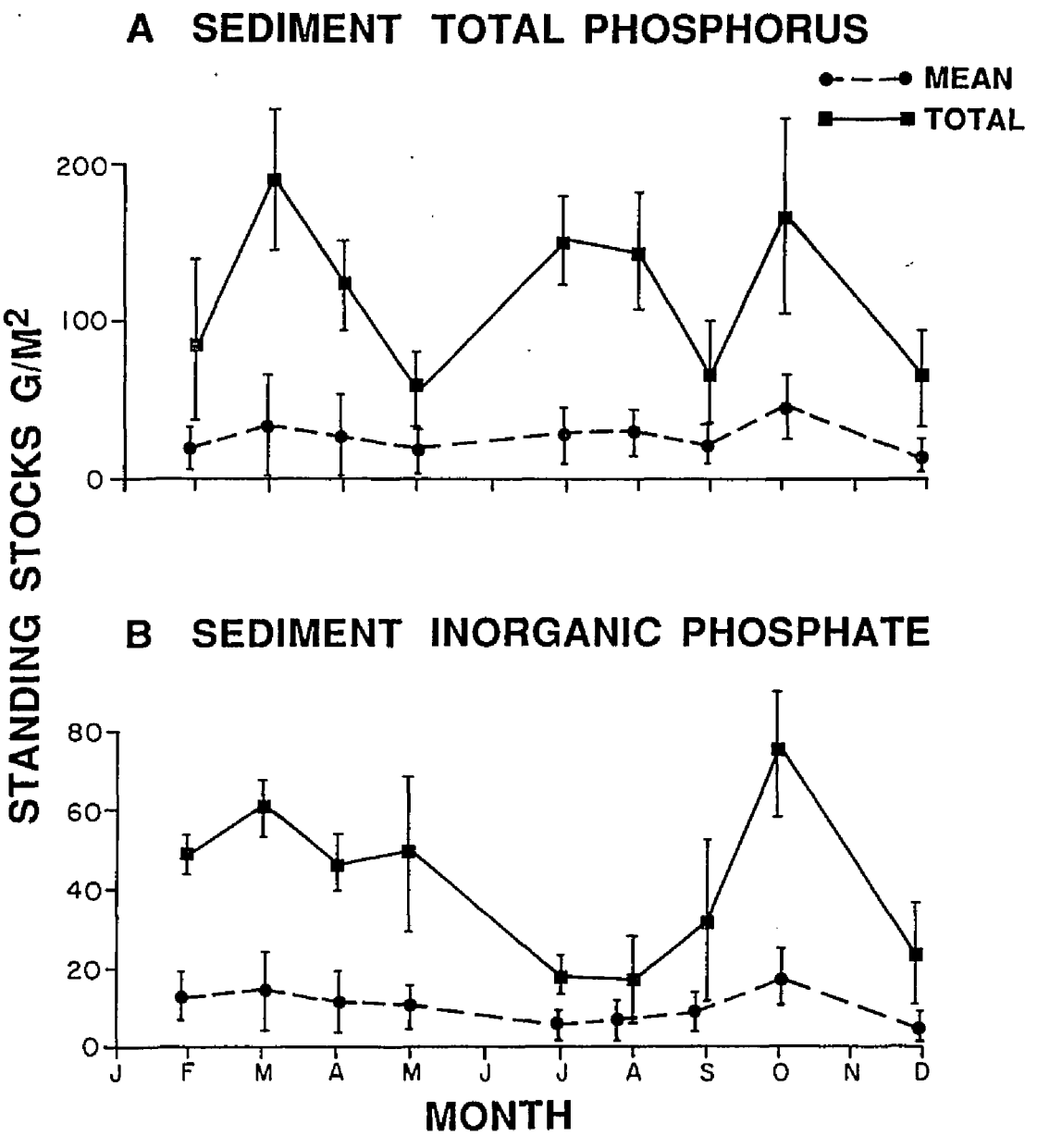
Table 15. Mean monthly standing stocks at each sediment layer and total monthly pools of total phosphorus as gTP/m^2 for Peltandra virginica expressed on a dry weight basis.

	Total Phosphorus					
	Sediment Layer					
	0-10cm	10-25cm	25-50cm	50-75cm	75-100cm	Total
Date						
February[a]	22.98	12.34	13.81	16.58	20.95	86.66
March	26.86	19.92	37.35	38.79	68.94	191.86
April	12.73	12.57	47.22	21.25	25.74	119.51
May	9.84	17.21	27.40	12.85	25.11	92.41
July[b]	26.44	26.68	26.38	38.09	36.47	154.06
August	18.99	32.93	31.20	28.25	33.90	145.27
September	19.54	15.23	16.31	30.25	25.00	106.33
October	25.15	33.15	42.45	42.49	36.34	179.58
					mean	134.46

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

Figure 9. Seasonal paterns of total phosphorus and inorganic phosphorus (PO_4) standing stocks in the sediments of Peltandra virginica. Monthly standing stocks expressed as the mean and total monthly pool for all depths to one meter on a dry weight basis.


A SEDIMENT TOTAL PHOSPHORUS
MEAN
TOTAL
200
100
0
STANDING STOCKS G/M2
B SEDIMENT INORGANIC PHOSPHATE
80
60
40
20
0
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

DF=4, P=0.26). Seasonal patterns of the total monthly pools of total phosphorus are shown in Figure 9.

Sediment-Tissue Phosphorus Relationship

The relationship between sediment and tissue phosphorus standing stocks was developed through simple and multiple regression analysis. Regression analyses were such that monthly phosphorus shoot, root, and rhizome standing stocks, as the dependent variables were individually regressed against sediment inorganic (PO_4) and total phosphorus standing stocks, as the independent variables, for all depths. Regression analysis indicated that shoot, root, and rhizome phosphorus standing stocks were generally independent of sediment inorganic and total phosphorus. A weak relationship, howver, existed between rhizome and inorganic phosphorus standing stocks. Coefficients of determination and levels of significance are shown in Table 16.

Phosphorus Model

Peltandra compartmental phosphorus standing stocks are estimated from previous sections (Tables 12, 14-15) and include monthly ranges. Annual compartmental fluxes are estimated using productivity, concentrations, leaching, and mass balance of certain compartments. Compartmental phosphorus standing stocks and annual fluxes are shown in Figure 10.

Annual losses to leaching were estimated by the summation of monthly leaching rates, resulting in an annual loss of $0.12\ g/m^2$.

Table 16. Coefficients of determination (r^2) with levels of significance (p) for simple and multiple regressions of Peltandra virginica shoot, root, and rhizome phosphorus (P) standing stocks against sediment inorganic (PO_4) and total phosphorus (TP) standing stocks expressed for all depths.

	Sediment PO_4	Sediment TP	Sediment PO_4, TP
Shoot P	r^2 = 0.006 F = 0.214 p = 0.646	r^2 = 0.001 F = 0.423 p = 0.519	NS a = 0.05
Root P	r^2 = 0.010 F = 0.420 p = 0.519	r^2 = 0.003 F = 0.010 p = 0.900	NS a = 0.05
Rhizome P	r^2 = 0.070 F = 3.020 p = 0.090	r^2 = 0.001 F = 0.001 p = 0.990	NS a = 0.05

NS = non significant
a = alpha level

Annual losses to detritus were estimated by the summation of monthly detrital losses. Monthly losses were estimated by multiplying monthly mortality rates by the phosphorus concentrations in dead shoots.

Date	Mortality (g/m^2)	Concentration (%)	Monthly Loss (g/m^2)
April-May	2.40	0.19	0.01
May-June	126.28	0.19	0.23
June-July	430.89	0.24	1.03
July-August	554.24	0.24	1.33
August-Sept	238.41	0.18	0.43
Sept-Oct	113.42	0.18	0.20
Oct-Nov	168.80	0.09	0.15

Annual loss to detritus = 3.38 g/m^2

Annual flow from the rhizome to the shoot compartment was estimated by the summation of monthly flows. Monthly flows were estimated by multiplying monthly shoot productivity by phosphorus concentrations in live shoot tissues. Total annual flow into the shoot compartment was estimated by the summation of annual shoot uptake and leaching.

Date	Productivity (g/m^2)	Concentration (%)	Monthly Flow (g/m^2)
Feb-March	9.54	0.40	0.04
March-April	146.03	0.65	0.95
April-May	119.05	0.55	0.65
May-June	806.28	0.35	2.82
June-July	448.19	0.31	1.39
July-Aug	109.34	0.27	0.30
Aug-Sept	-54.74	0.34	-0.19
Sept-Oct	50.74	0.31	0.16
		Annual flow from rhizomes	6.12
		Leachate	+ 0.12

Total annual flow to shoots = 6.24 g/m^2

Annual flow from the shoot to the rhizome compartment was estimated by the difference in total shoot uptake and losses to leaching and detritus.

$6.24\ g/m^2 - (0.12\ g/m^2 + 3.38\ g/m^2)$

Annual flow from shoots to rhizomes = $\underline{2.74\ g/m^2}$.

Annual losses to root mortality, based on the assumption of steady state, were estimated by multiplying annual root productivity by the mean root phosphorus concentration between January and June.

	Mortality (g/m^2)	Concentration (%)	Annual Loss (g/m^2)
Jan-June	1568	0.33	5.11

Annual loss to root mortality = $\underline{5.11\ g/m^2}$

Monthly flow from the rhizomes to the roots based on the assumption that the majority of root growth is supported by the reallocation from the rhizomes, was estimated by multiplying annual root productivity by the mean phosphorus concentration in root tissues between July and December.

	Productivity (g/m^2)	Concentration (%)	Annual Flow (g/m^2)
July-Dec	1568	0.30	4.76

Annual flow from rhizomes to roots = $\underline{4.76\ g/m^2}$

Annual uptake by the roots from the sediments, based on the assumption of steady state, is equal to the losses from the plant. As such, annual uptake by the roots is equal to the sum of losses to leaching, detritus, and root mortality.

Leaching		Detritus		Root Mortality		Annual Root Uptake
0.12 g/m^2	+	3.38 g/m^2	+	5.11 g/m^2	=	8.61 g/m^2

Annual flow from the roots to the rhizomes was estimated by mass balance of the rhizome compartment. Annual translocation from the shoots to the rhizomes was subtracted from the annual flows from the rhizomes to the shoots and roots (6.24 g/m^2 + 4.76 g/m^2) - 2.74 g/m^2 = 8.26 g/m^2

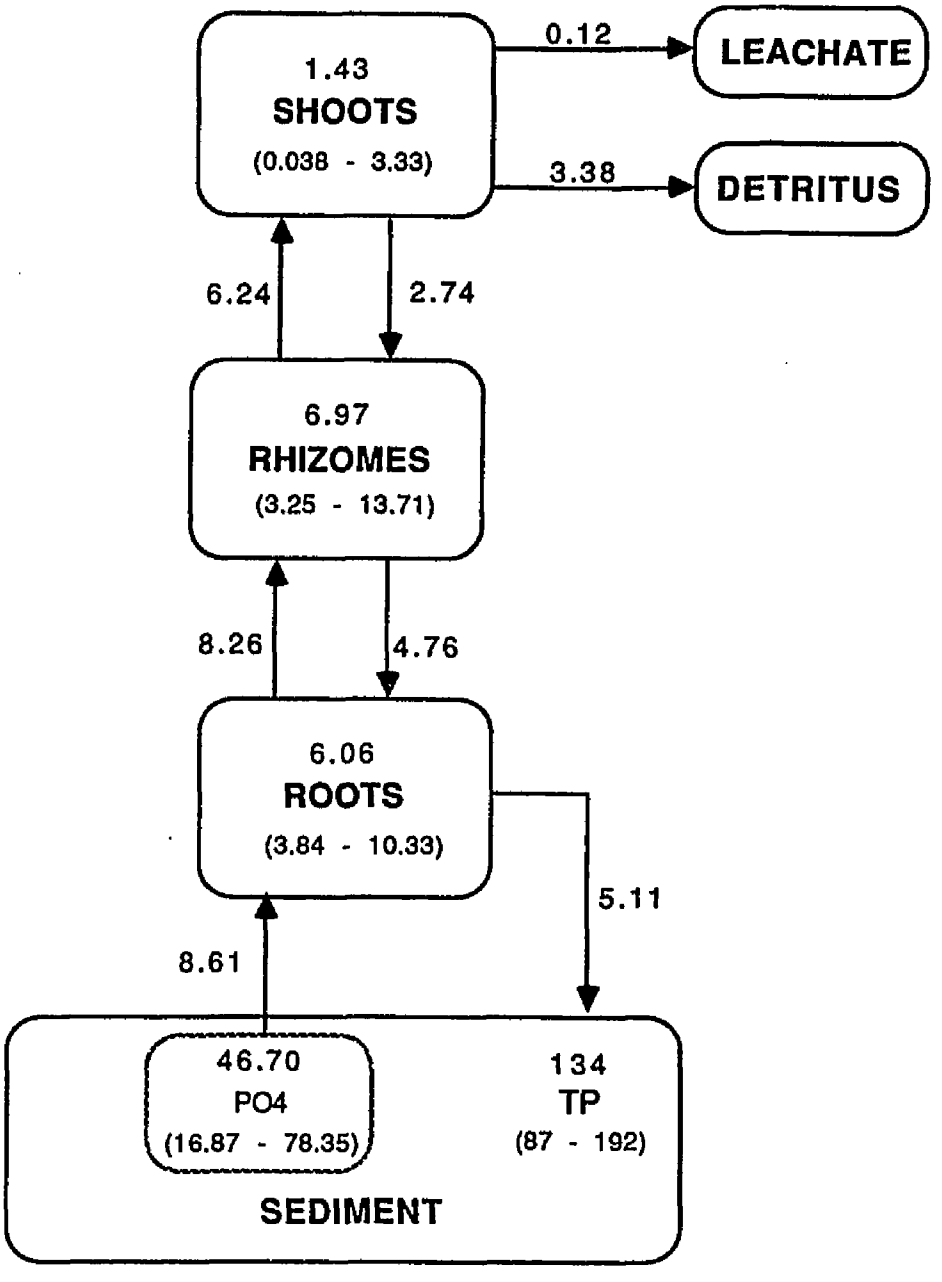
Annual flow from roots to rhizomes = 8.26 g/m^2

Summary

The quantification of annual flows between plant compartments shows the Peltandra virginica cycles significant levels of phosphorus to the environment over an annual cycle. Of the total annual phosphorus transfer to the shoots of 6.24 g/m2, 3.38 g/m^2, or 56%, is lost to the surrounding environment through leaching and death. Root mortality also accounts for a significant loss to surrounding sediments with 5.11 g/m^2, or 59% of the total root uptake of 8.61 g/m^2 lost during dieback.

Peltandra virginica does, however, conserve phosphorus through reallocation and internal cyclng. Approximately 2.74 g/m^2, or 44%, of total shoot uptake is translocated to the rhizomes during dieback. In addition,

Figure 10. Phosphorus compartmental model for Peltandra virginica. Compartmental phosphorus standing stocks are expressed as mean gP/m^2 including monthly ranges in parentheses. Sediment phosphorus standing stocks expressed as the monthly pool for all depths. Annual flows are expressed as gP/m^2/year.


1.43
SHOOTS
(0.038 - 3.33)
0.12
LEACHATE
3.38
DETRITUS
6.24
2.74
6.97
RHIZOMES
(3.25 - 13.71)
8.26
4.76
6.06
ROOTS
(3.84 - 10.33)
5.11
8.61
46.70
PO4
(16.87 - 78.35)
134
TP
(87 - 192)
SEDIMENT

reallocation of 4.76 g/m^2 from the rhizome compartment is used to support root growth which accounts for approximately 43% of the total transfer from the shoots and roots to the rhizomes. Of the annual demand of 11.0 gP/m^2 for shoot and root growth, approximately 10.46 gP/m^2, or 95%, is avaialble for reallocation from the rhizomes. Transfer of 8.26 gP/m^2 to the rhizomes from the roots accounts for approximately 95% of annual root uptake with the remaining 5% apparently conserved by the roots for growth and maintenance.

Nitrogen-Phosphorus Relationship

Correlation analysis indicated that nitrogen and phosphorus cycling and temporary storage, as reflected in the pairwise comparison of monthly standing stocks, are interdependent, or covary, in the shoots, roots, and rhizomes of Peltandra virginica. Sediment inorganic nitrogen (NO_3+ NH_4) and inorganic phosphorus (PO_4), as well as total nitrogen and phosphorus standing stocks, did not covary over the same period. Correlation coefficients and levels of significance are shown in Table 17.

Peltandra nitrogen to phosphorus ratios (N:P) in the shoots, roots, rhizomes, and sediments are shown in Table 18. Shoot N:P ratios were initially high in March at the onset of shoot development and decreased in April. N:P ratios then increased from 5.5 to 8.1 between April and July, periods of increased shoot productivity, followed by a decrease to 7.4 in August. A secondary N:P ratio increase to 7.4 was observed in September, a period of new shoot recruitment. Root N:P decreased from 3.8 in January to 2.3 in May during periods of root dieback. Root N:P ratios then increased in July at the onset of root growth and decreased through October as root

biomass increased. Rhizome N:P ratios were extremely variable, decreasing from 8.5 in January to 1.3 in August, a period of shoot productivity and initial root growth. Rhizome N:P ratios then increased to 8.5% between August and December, a period of shoot senescence and peak root productivity. Sediment inorganic N:P ratios decreased from 0.12 to 0.03 between April and June folowed by an increase to 0.25 in August. As such sediment inorganic N:P ratios decreased during periods of maximum shoot development and increased during periods of root growth. Patterns of sediment total N:P ratios were similar decreasing from 21.8 to 12.0 between May and July followed by an increase to 15.5 in September. Total N:P ratios, then, decreased during periods of apparent decomposition of organic matter.

Table 17. Correlation coefficients (r) with levels of significance (p) for pairwise comparisons of monthly nitrogen (N) and phosphorus (P) standing stocks (g/m^2) in the shoots, roots, rhizomes, and sediments of Peltandra virginica. Sediment comparisons from all depths.

Shoot N:Shoot P	Root N:Root P	Rhizome N:Rhizome P
r = 0.994	r = 0.851	r = 0.625
p = 0.001	p = 0.001	p = 0.001

Sediment TN:Sediment TP	Sediment IN:Sediment IP
r = 0.185	r = -0.067
p = 0.126	p = 0.340

TN = Sediment total nitrogen
TP = Sediment total phosphorus
IN = Sediment total inorganic nitrogen (NO_3+NH_4)
IP = Sediment total inorganic phosphorus (PO_4)

Table 18. Monthly nitrogen to phosphorus ratios (N:P) in the shoots, roots, rhizomes, and sediments of *Peltandra virginica*. Sediment ratios estimated from total monthly pools.

Date	Shoot N:P	Root N:P	Rhizome N:P
January	---	3.8:1	8.5:1
March	7.5:1	3.3:1	5.1:1
April	5.5:1	2.8:1	2.4:1
May	6.7:1	2.3:1	2.1:1
June	7.3:1	---	---
July	8.1:1	3.5:1	1.4:1
August	7.4:1	2.1:1	1.3:1
September	8.6:1	2.9:1	1.4:1
October	8.9:1	2.7:1	5.6:1
December	---	3.8:1	8.5:1
means	7.5:1	3.0:1	4.0:1

Date	Sediment Inorganic N:P	Sediment Total N:P
March	0.11:1	25.0:1
April	0.12:1	10.3:1
May	0.08:1	21.8:1
June	0.03:1	12.0:1
July	0.05:1	12.0:1
August	0.25:1	11.6:1
September	0.21:1	15.5:1
October	0.06:1	8.0:1
means	0.11:1	14.5:1

Spartina cynosuroides

Net Annual Productivity

Aboveground Productivity

Seasonal patterns of Spartina live shoot biomass standing stocks are shown in Figure 11. Monthly shoot biomass standing stocks were distinctive over the sampling period (ANOVA, F=5.15E+01, DF=8, P<0.0001) increasing from a mean low of 1.16 g/m^2 in March to a mean high of 2462.07 g/m^2 in September (Table 19). Following peak biomass, a steady decline was observed to a level of 1145.80 g/m^2 in October. No live biomass was observed in November. Multiple comparisons indicated that June-July were similar and distinctive from all other months (SNK:EWER = 0.05).

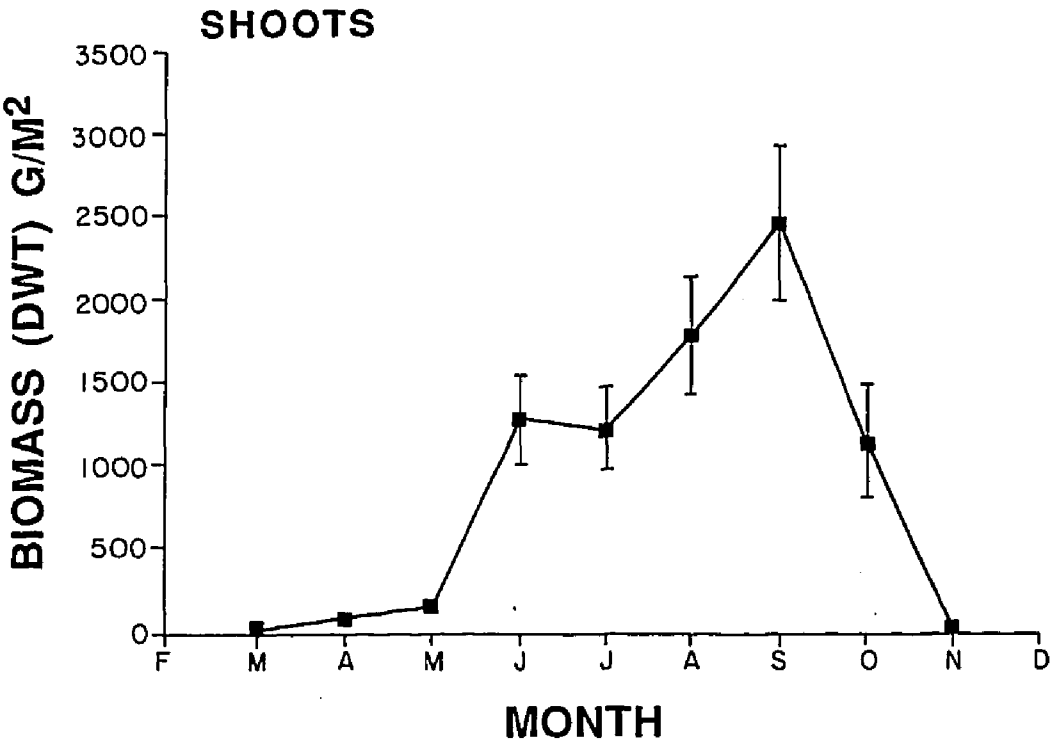
As interval monthly mortality was undetectable, net annual shoot productivity was estimated for Spartina using the method of Milner and Hughes (1968) which sums positive changes in monthly biomass standing stocks. Summing positive changes in monthly shoot biomass, assuming June-July as equal, resulted in a net annual shoot productivity of 2462.84 g/m^2 (Table 19). Shoot productivity was characterized by an initial lag phase, March-May, at which time shoot biomass increased at the rate of 2.38 g/m^2/day. The initial lag phase was followed by a period of rapid shoot growth in which shoot biomass increased at a rate of 17.99 g/m^2/day. A second lag phase was observed between June and July followed by a period of

Table 19. Estimated monthly shoot biomass standing stocks (g/m^2) and net annual productivity (g/m^2/year) for Spartina cynosuroides expressed as mean dry weights ± S.D.

Date	Standing Biomass	Change in Biomass
February	-----	1.16
March[a]	1.16 ± 00.15	82.95
April	82.95 ± 40.05	61.17
May	144.11 ± 38.56	1097.78
June[b]	1272.66 ± 269.81	
	mean=1241.89	
July	1211.12 ± 251.79	533.62
August	1775.41 ± 355.24	686.16
September	2462.07 ± 465.74	---
October	1145.81 ± 33.27	
	Net Annual Productivity =	2462.84 g/m^2

[a]March-May values estimated from 1988 data
[b]June-October values estimated from 1987 data

Figure 11. Seasonal patterns of shoot biomass standing stocks (g/m^2) of Spartina cynosuroides expressed as mean dry weights ± S.D.

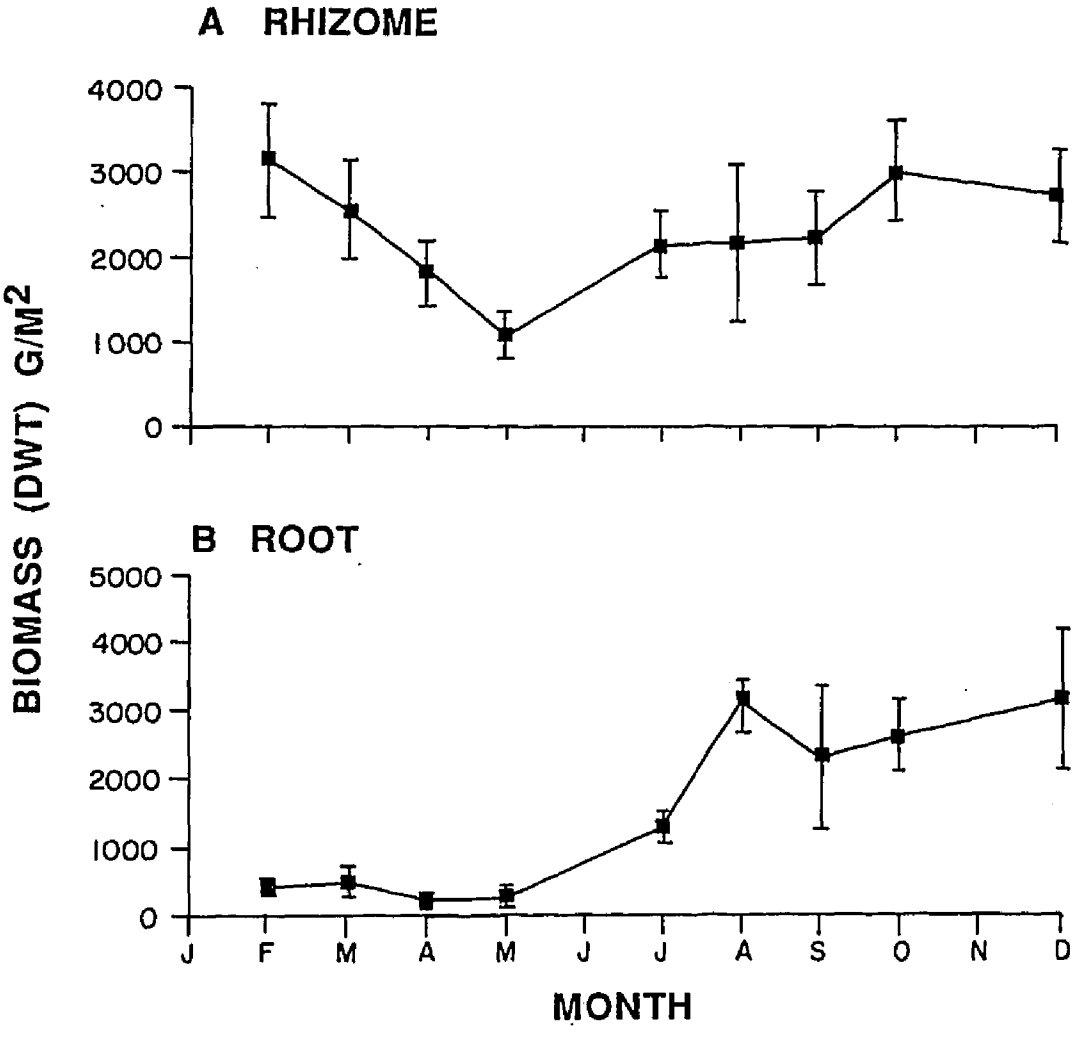

SHOOTS
BIOMASS (DWT) G/M2
3500
3000
2500
2000
1500
1000
500
0
F
M
A
M
J
J
A
S
O
N
D
MONTH

rapid growth in which shoot biomass increased at the rate of 19.99 g/m^2/day between July and September. As such, increase in shoot biomass between March and May accounted for approximately 6%, while increases between May and June, accounted for approximately 45% of net annual shoot productivity. The remaining 49% occured between July and September. Shoot dieback was relatively rapid occurring at a rate of 43.87 g/m^2/day between September and October and 36.93 g/m^2/day between October and November.

Belowground Productivity

Seasonal patterns of Spartina monthly live root and rhizome biomass standing stocks are shown in Figure 12. Rhizome biomass standing stocks varied significantly over an annual cycle (ANOVA, F=5.97, DF=8, P<0.0001) increasing from a mean low of 1075.73 g/m^2 in May to a mean high of 3142.18 g/m^2 in February. Following peak standing stock, rhizome biomass decreased at a steady rate to the May level (Table 20). Multiple comparisons indicated that rhizome biomass in May was distinctive from all other months. Likewise, multiple comparisons indicated that July, August, and September were grouped similar as were October, December, and February (SNK:EWER = 0.05). As such, a mean was calculated for each group. Root biomass standing stocks also demonstrated highly significant seasonal patterns (ANOVA, F=2.39E+01, DF=8, P<0.0001) increasing from a low of 218.65 g/m^2 in April to a peak of 3162.80 g/m^2 in December. Following peak standing stock, root biomass declined rapidly to a level of 462.20 g/m^2 in February (Table 22). Multiple comparisons indicated that February, March, April, and May

Figure 12. Seasonal patterns of root and rhizome biomass standing stocks (g/m^2) of Spartina cynosuroides expressed as mean dry weights ± S.D.


A RHIZOME
4000
3000
2000
1000
0
B ROOT
5000
4000
3000
2000
1000
0
BIOMASS (DWT) G/M2
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

were grouped as similar as were August, September, October, and December (SNK:EWER = 0.05) and a mean root standing stock was calculated for each group.

Net annual productivity of both roots and rhizomes was estimated by summing positive changes in monthly biomass standing stocks (Milner and Hughes, 1968). To estimate rhizome net annual productivity rhizome biomass in May was assumed as the initial standing stock. The positive change in rhizome biomass between May and the mean of July through September was summed with the positive change in rhizome biomass between the mean of July through September and the mean of October through February resulting in a net annual rhizome productivity of 1875.88 g/m^2 (Table 20). Rhizome biomass increased at a rate of 26.04 g/m^2/day between May and July and 15.63 g/m^2/day between September and October. As such, rhizome productivity between May and July accounts for 62%, while productivity between September and October accounts for the remaining 38% of net annual rhizome productivity. Decline in live rhizome biomass from February to May occurred at the relatively stable rate of 22.71 g/m^2/day. To estimate root annual productivity mean root biomass between February and May was assumed to be initial root standing stock. The positive change in root biomass between this mean and root biomass in July was summed with the poitive change in root biomass between July and the mean of August through December. Summation of positive changes resulted in an annual root productivity of 2668.40 g/m^2 (Table 21). Root biomass between May and July increased at a rate of 15.49 g/m^2/day, and between July and August at 14.05 g/m^2/day, accounting for approximately 39% and 61% of net root annual productivity,

Table 20. Estimated monthly rhizome biomass standing stocks (g/m^2) and net annual productivity (g/m^2/year) for Spartina cynosuroides expressed as mean dry weights ± S.D.

Date	Standing Biomass	Change in Biomass
February[a]	3142.18 ± 654.94	
March	2547.80 ± 555.40	
April	1830.26 ± 359.31	
May	1075.73 ± 233.38	
[b]		1172.41[c]
July	2161.00 ± 351.83	
August	2365.21 ± 888.04	
September	2218.23 ± 528.00	
		703.47[d]
October	2994.20 ± 562.47	
December	2718.47 ± 543.39	
	Net Annual Productivity =	1875.88 g/m^2

[a]February-May values estimated from 1988 data

[b]July-December values estimated from 1987 data

[c]Change in biomass represents difference between May and the mean of July-September

[d]Change in biomass represents difference between the mean of July-September and the mean of October-February.

Table 21. Estimated monthly root biomass standing stocks (g/m^2) and net annual productivity (g/m^2/year) for Spartina cynosuroides expressed as mean dry weights ± S.D.

Date	Standing Biomass	Change in Biomass
February[a]	462.20 ± 77.03	
March	520.15 ± 178.90	
April	218.65 ± 74.41	
May	268.79 ± 117.38	
July[b]	1312.00 ± 215.89	944.55[c]
		1723.85[d]
August	3091.46 ± 360.82	
September	2890.49 ± 1030.99	
October	2998.66 ± 475.05	
December	3162.80 ± 1008.37	
	Net Annual Productivity =	2668.40 g/m^2

[a]February-May values estimated from 1988 data

[b]July-December values estimated from 1987 data

[c]Change in biomass represents difference between the mean of February-May and July

[d]Change in biomass represents difference between July and the mean of August-December

respectively. Root dieback was rapid, decreasing at a rate of 43.56 g/m^2/day between December and February.

Total Productivity

Summation of shoot, root, and rhizome annual productivity resulted in a total annual biomass productivity of 7005.96 g/m^2 and a mean daily biomass productvity of 19.19 g/m^2. A mean root to shoot ratio (R:S = peak root biomass/peak shoot biomass) was calculated to be 1.43 while the peak R:S ratio was 1.17. A peak belowground to aboveground ratio (B:A = peak root + rhizome biomass/peak shoot biomass) was calculated to be 3.45 while peak B:A was 2.07.

Nitrogen Dynamics

Tissue Nitrogen Concentrations

Seasonal patterns of nitrogen concentrations of the shoots, roots, and rhizomes of Spartina cynosuroides are shown in Figure 13. Tissue nitrogen concentrations depended on an interaction effect of compartment and month (ANOVA, F=4.30E+01, DF=12, P<0.0001). A mean nitrogen concentration in the shoots of 1.44% was approximately three times the mean root concentration of 0.65% and the mean rhizome concentration of 0.66% (Table 22).

Shoot nitrogen concentrations varied significantly over an annual growth cycle (ANOVA, F=6.06E+01, DF=7, P<0.0001) decreasing from a high mean of 2.02% in March to 1.05% in August. A secondary concentration peak of

Table 22. Mean monthly nitrogen concentrations in the shoots, roots, and rhizomes of Spartina cynosuroides expressed as % dry weight ± S.D.

Date	Shoots	Roots	Rhizomes
February[a]	----	0.54 ± 0.08	1.16 ± 0.20
March	2.02 ± 0.64	0.23 ± 0.13	0.54 ± 0.11
April	2.00 ± 0.05	0.66 ± 0.08	0.94 ± 0.07
May	1.63 ± 0.09	0.95 ± 0.03	0.85 ± 0.03
June[b]	1.43 ± 0.14	----	----
July	1.18 ± 0.01	0.75 ± 0.07	0.45 ± ----
August	1.05 ± 0.12	0.66 ± 0.19	0.33 ± 0.03
September	1.19 ± 0.07	0.78 ± 0.02	0.57 ± 0.02
October	1.00 ± 0.07	0.73 ± 0.04	0.52 ± 0.02
December	----	0.58 ± 0.08	0.57 ± 0.06
means	1.44	0.65	0.66

[a]February-May values estimated from 1988 data

[b]June-October values estimated from 1987 data

1.05% occurred in September at peak shoot biomass followed by a decrease to 1.00% in October.

Root nitrogen concentrations varied seasonally (ANOVA, F=2.71E+01, DF=8, P<0.0001) increasing from a low of 0.23% in March to a high of 0.95% in May. Root nitrogen concentrations then decreased to 0.58% in December. Rhizome nitrogen concentrations also exhibited distinctive seasonal patterns (ANOVA, F=8.22E+01, DF=8, P<0.0001). Rhizome nitrogen concentrations decreased from 1.16% in February to 0.54% in March followed by an increase to 0.54% in March (Table 23). Nitrogen concentrations then decreased to 0.33% in August followed by an increase through February.

Tissue Nitrogen Standing Stocks

Spartina tissue nitrogen standing stocks were estimated by multiplying monthly biomass standing stocks by appropriate tissue nitrogen concentrations. Seasonal patterns of Spartina shoot, root, and rhizome nitrogen standing stocks are shown in Figure 13. Tissue nitrogen standing stocks depended on an interaction effect of compartment month (ANOVA, F=2.94E+01, DF=12, P<0.001). A mean nitrogen standing stock of 15.34 g/m^2 in the rhizomes was slightly higher than that of the roots (11.05 g/m^2) and shoots (12.00 g/m^2) (Table 23).

Spartina shoot nitrogen standing stocks varied significantly over an annual cycle (ANOVA, F=4.97E+01, DF=7, P<0.0001), increasing from a low of 0.02 g/m^2 in March to a peak of 29.36 g/m^2 in September (Table 24). Shoot nitrogen standing stocks covaried with shoot biomass ($r = .91$, $p<0.5$).

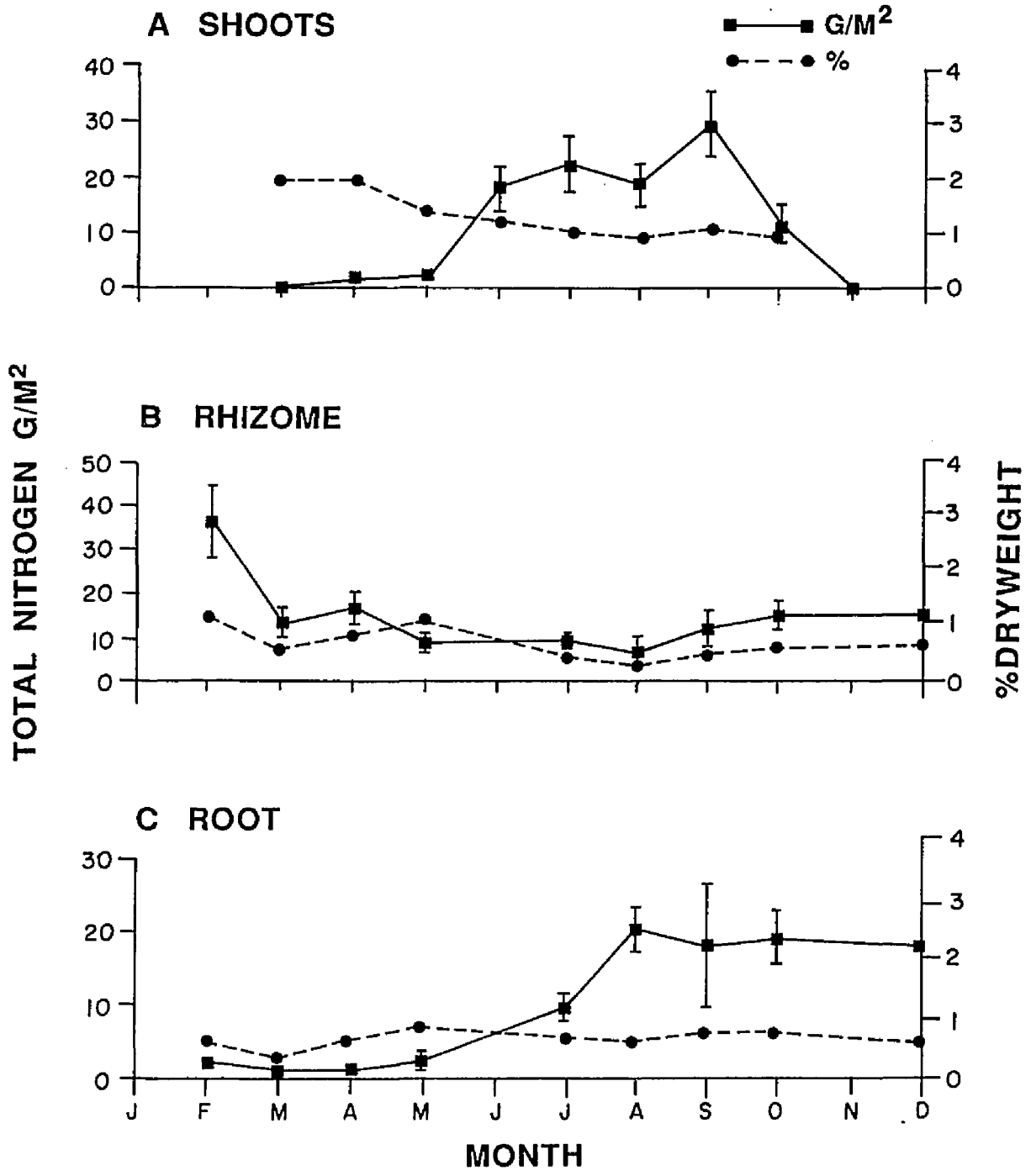
Table 23. Mean monthly nitrogen standing stocks (gN/m^2) in the shoots, roots, and rhizomes of Spartina cynosuroides (gN/m2) expressed on a dry weight basis ± S.D.

Date	Shoots	Roots	Rhizomes
February[a]	----	2.51 ± 0.47	36.64 ± 7.63
March	0.02 ± 0.003	1.21 ± 0.46	13.65 ± 2.97
April	1.66 ± 0.80	1.44 ± 0.49	17.27 ± 3.39
May	2.35 ± 0.63	2.67 ± 1.16	9.10 ± 1.97
June[b]	18.20 ± 3.85	----	----
July	14.28 ± 4.69	9.84 ± 1.61	9.72 ± 1.58
August	18.63 ± 3.72	20.27 ± 2.36	7.83 ± 2.89
September	29.36 ± 5.55	22.58 ± 2.95	12.66 ± 3.01
October	11.56 ± 3.36	20.89 ± 2.99	15.55 ± 2.92
December	----	18.04 ± 5.75	15.66 ± 3.10
means	12.00	11.05	15.34

[a]February-May values estimated from 1988 data

[b]June-October values estimated from 1987 data

Figure 13. Seasonal patterns of mean monthly nitrogen concentrations (%N) and standing stocks (gN/m^2) in the shoots, roots, and rhizomes Spartina cynosuroides expressed on a dry weight basis ± S.D.


A SHOOTS
G/M2
%
40
30
20
10
0
4
3
2
1
0
B RHIZOME
50
40
30
20
10
0
4
3
2
1
0
TOTAL NITROGEN G/M2
%DRYWEIGHT
C ROOT
30
20
10
0
4
3
2
1
0
J
F
M
A
M
J
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MONTH

Multiple comparisons indicated that June and July were grouped as equivalent and that September was distinctive from all other months (SNK:EWER = 0.05).

Root nitrogen standing stocks were distinctive over the sampling period (ANOVA, F=4.71E+01, DF=8, P<0.001), increasing from a low mean of 1.21 g/m^2 in March to a mean high of 22.58 g/m^2 in September (Table 24). Root nitrogen standing stocks covaried with root biomass ($r = .97$, $p<.01$). Multiple comparisons grouped February through May as similar as well as August through December (SNK:EWER = 0.05). Rhizome nitrogen standing stocks also exhibited pronounced seasonal patterns (ANOVA, F=2.41E+01, DF=8, P<0.0001), decreasing from a mean high of 36.64 g/m^2 in February to a mean low of 7.83 g/m^2 in August. Using a maximum - minimum calculation, 28.81 g/m^2 of nitrogen are available for reallocation from the rhizomes. Rhizome nitrogen standing stocks then increased to to the levels observed in February.

Tissue Nitrogen Leaching

Spartina monthly shoot leaching rates were estimated using the previously described equation. Suumation of monthly leaching rates resulted in an annual leaching rate of 0.559 g/m^2.

May	0.185 g/m^2
June	0.374 g/m^2
	0.559 g/m^2/year

Tissue Nitrogen Efficiency Indexes

Table 24. Nitrogen use efficiency in the shoots, roots and rhizomes and nitrogen recovery efficiency in the shoots of Spartina cynosuroides. Monthly use efficiency is estimated by dividing mean monthly tissue biomass by mean monthly nitrogen standing stocks. Monthly recovery efficiency is estimated by dividing the difference in nitrogen in live and dead shoots by nitrogen in the live shoots.

	Use Efficiency		
Date	Shoots	Roots	Rhizomes
February[a]	----	184.14	85.75
March	58.00	429.87	106.93
April	49.96	151.84	105.96
May	61.32	100.67	116.84
June[b]	69.89	----	----
July	53.63	133.33	222.32
August	95.29	152.51	302.07
September	83.09	128.01	175.21
October	99.11	143.54	192.55
December	----	175.32	173.93
means	71.28	194.63	173.50

Recovery Efficiency	
Date	Shoots
Sept-Oct	0.15
Oct-Nov	0.55
mean	0.35

[a]Feb-May values estimated from 1988 data

[b]June-Dec values estimated from 1987 data

Spartina tissue nitrogen use and recovery efficiency indexes are shown in Table 24. Shoot nitrogen use efficiency was lower in April and July, apparent lag phases in shoot productivity, and increased during periods of rapid shoot growth. Peak shoot use efficiency was observed in October, a period of initial shoot dieback. Minimum root nitrogen use efficiency was observed in May at the onset of root productivity and increased through December, a period of peak root biomass, to a peak in March. Root use efficiency then decreased to the observed level in May. Rhizome nitrogen use efficiency increased between March and October, a period of increased shoot biomass followed by a decrease to the observed level in March. As such, rhizome nitrogen use efficiency increased during periods of shoot and root productivity and decreased during shoot senescence and root senescence. Mean use efficiency by the roots was approximatley one and a half times that of the rhizomes and two and a half times that of the shoots. Spartina shoot recovery efficiency was relatively stable between September and November.

Sediment Inorganic Nitrogen

Sediment inorganic nitrogen, as ammonium and nitrate, at each depth for Spartina was estimated using the prevoiusly described equation. Each month the standing stocks for both ammonium and nitrate for each depth were summed to represent the total avaialble monthly pools of each nutrient to a 50 cm depth (Tables 25, 26). Total monthly pools of nitrate increased from a low of 0.002 g/m^2 in March to a high of 0.174 g/m^2 in August. Over tha sampling period, monthly nitrate levels varied significantly (ANOVA, F=7.92E+00, DF=7, P<0.0001), however no variability was noted with depth (ANOVA, F=4.67E-01, DF=4, P=0.75). Multiple comparisons indicated that all monthly

Table 25. Mean monthly standing stocks at each sediment layer and total monthly pools of inorganic nitrogen as gNO_3/m^2 for Spartina cynosuroides expressed on dry weight basis.

	NO_3					
	Sediment Layer					
	0-10cm	10-20cm	20-30cm	30-40cm	40-50cm	Total
Date						
February[a]	0.001	0.001	0.001	----	----	0.003
March	0.000	0.000	0.000	0.000	0.002	0.002
April	0.005	0.004	0.005	0.005	0.005	0.024
May	0.004	0.004	0.007	0.006	0.005	0.026
July[b]	0.013	0.005	0.003	0.003	0.000	0.024
August	0.050	0.031	0.038	0.025	0.032	0.176
September	0.000	0.000	0.000	0.000	0.011	0.011
October	0.055	0.021	0.011	0.013	0.000	0.100
					mean	0.035

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

Table 26. Mean monthly standing stocks at each sediment layer and total monthly pools of inorganic nitrogen as gNH_4/m^2 for for Spartina cynosuroides expressed on a dry weight basis.

	NH_4					
	Sediment Layer					
	0-10cm	10-20cm	20-30cm	30-40cm	40-50cm	Total
Date						
February[a]	0.416	0.210	0.195	0.203	0.198	1.222
March	0.732	0.493	0.430	0.262	0.356	2.273
April	1.950	0.508	0.620	0.460	0.424	3.962
May	0.575	0.290	3.659	0.292	0.302	5.188
July[b]	0.607	0.522	0.084	0.365	0.370	1.948
August	0.564	0.721	0.383	0.239	0.317	2.220
September	0.896	0.528	0.670	0.440	0.360	2.890
October	0.201	0.273	0.135	0.167	0.844	1.620
					mean	2.660

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

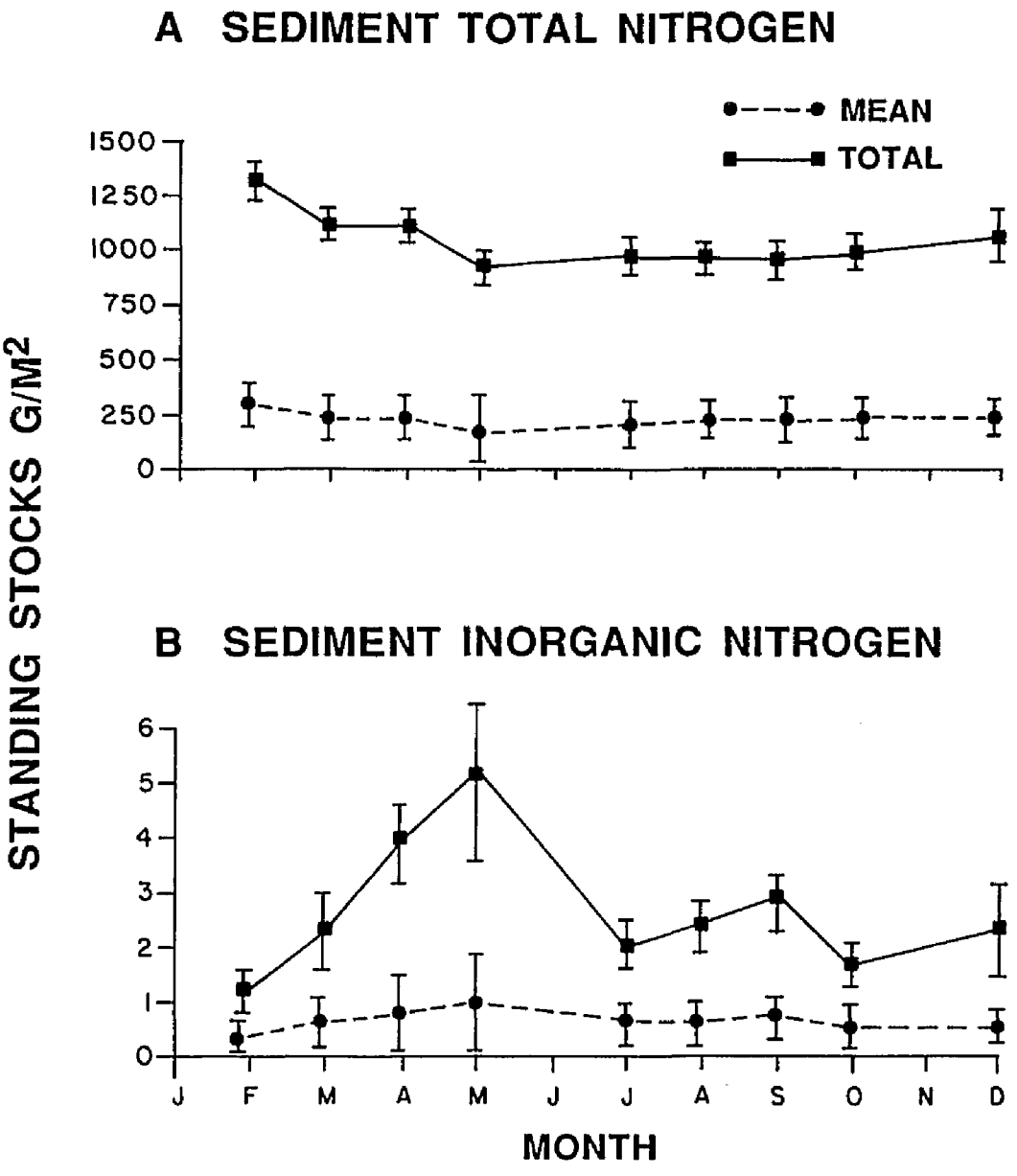
Table 27. Mean monthly standing stocks at each sediment layer and total monthly pools of total nitrogen as gTN/m^2 for Spartina cynosuroides expressed on a dry weight basis.

	Total Nitrogen					
	Sediment Layer					
	0-10cm	10-20cm	20-30cm	30-40cm	40-50cm	Total
Date						
February[a]	262	260	183	325	292	1322
March	216	265	260	180	198	1119
April	230	245	245	201	196	1117
May	220	207	154	162	185	928
July[b]	193	260	182	174	168	977
August	175	160	161	242	235	973
September	152	201	202	194	214	962
October	180	168	205	184	245	981
					mean	1047

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

Figure 14. Seasonal patterns of total and inorganic nitrogen (NO_3+ NH_4) standing stocks in the sediments of Spartina cynosuroides. Monthly standing stocks expressed as the mean and total monthly pools for all depths to 50 cm on a dry weight basis..


A SEDIMENT TOTAL NITROGEN
MEAN
TOTAL
1500
1250
1000
750
500
250
0
STANDING STOCKS G/M2
B SEDIMENT INORGANIC NITROGEN
6
5
4
3
2
1
0
J
F
M
A
M
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MONTH

nitrate levels were different (SNK:EWER = 0.05). Total monthly ammonium levels increased from a low of 1.22 g/m^2 in February to a high of 5.18 g/m^2 in May followed by a decrease to 1.60 g/m^2 in October. Over the sampling period, monthly ammonium standing stocks were not significantly different (ANOVA, F=9.42E-01, DF=7, P=0.48) nor were standing stocks with depth (ANOVA, F=1.02E+00, DF=4, P=0.41). Total monthly pools of ammonium and nitrate standing stocks were summed to represent the total monthly available pool of inorganic nitrogen. Seasonal patterns of total monthly available pools of inorganic nitrogen are shown in Figure 14.

Sediment Total Nitrogen

Sediment total nitrogen at each depth for Spartina was estimated using the previously described equation. Monthly total nitrogen standing stocks for each depth were summed to represent the total monthly nitrogen pool to a 50 cm depth Table 27). Total monthly pools of total nitrogen decreased from a high of 1322 g/m^2 in February to a relatively stable mean level of 964 g/m^2 between May and October. Seasonal patterns of the total monthly pools of total nitrogen are shown in Figure 14. Over the sampling period, total nitrogen levels did not vary monthly (ANOVA, F=1.57E+00, DF=7, P=0.18), however did vary with depth (ANOVA, F=6.99E+00, DF=4, P<0.003). Statistical analysis indicated a strong correlation between total nitrogen and organic matter for all depths (0-10cm, $r = .78$, $p<.05$; 10-20cm, $r = .89$, $p<.01$; 20-30cm, $r = .98$, $p<.01$; 30-40cm, $r = .96$, $p<.01$).

Sediment-Tissue Nitrogen Relationship

Table 28. Coefficients of determination (r^2) with levels of significance (p) for simple and multiple regressions of Spartina cynosuroides shoot, root, and rhizome nitrogen standing stocks (N) with sediment inorganic (NO_3+ NH_4) and total nitrogen standing stocks (TN) expressed for for all depths.

	Sediment (NO_3+ NH_4)	Sediment TN	Sediment (NO_3+ NH_4), TN
Shoot N	r^2 = 0.003	r^2 = 0.287	r^2 = 0.287
	F = 0.118	F = 15.320	F = 15.320
	p = 0.733	p = 0.004	p = 0.004
Root N	r^2 = 0.056	r^2 = 0.186	r^2 = 0.186
	F = 2.280	F = 8.690	F = 8.690
	p = 0.130	p = 0.005	p = 0.005
Rhizome N	r^2 = 0.001	r^2 = 0.150	r^2 = 0.150
	F = 0.029	F = 6.930	F = 6.930
	p = 0.863	p = 0.012	p = 0.012

The relationship between Spartina sediment and tissue nitrogen standing stocks was developed through simple and multiple regression analysis. regressions were designed such that monthly shoot, root, and rhizome nitrogen standing stocks, as the dependent variables, were regressed against monthly sediment inorganic (NO_3 + NH_4) and total nitrogen standing stocks, as the independent variables, for all depths. Regression analysis indicated that shoot, root, and rhizome nitrogen standing stocks were independent of sediment inorganic nitrogen. Shoot, root, and rhizome nitrogen standing stocks were, however, dependent on sediment total nitrogen standing stocks. Coefficients of determination and significance levels of regressions are shown in Table 28.

Nitrogen Model

Spartina compartmental nitrogen standing stocks are estimated from previous sections (Tables 24, 26-28). Annual compartmental nitrogen fluxes are estimated using productivity, nitrogen concentrations, leaching, and mass balance of certain compartments. Compartmental standing stocks and annual fluxes are shown in Figure 15.

Annual losses to leaching were estimated by the summation of monthly leaching rates resulting in an annual leaching rate of 0.56 g/m^2.

Annual losses to detritus were estimated by multiplying yearly shoot mortality, assumed to equal yearly productivity, by the mean nitrogen concentration of dead shoots in September and October.

Date	Mortality (g/m^2)	Concentration (%)	Monthly loss (g/m^2)
Sept-Oct	1316.26	1.14	15.00
Oct-Nov	1145.81.	0.46	5.27
		Annual loss to detritus =	20.27 g/m^2

Annual flow from the rhizome to the shoot compartment was estimated by the summation of monthly flows. Monthly flows were estimated by multiplying monthly productivity rates by nitrogen concentrations in live shoots. Total annual flow into the shoot compartment was estimated by the summation of annual shoot uptake and leaching.

Date	Productivity (g/m^2)	Concentration (%)	Monthly flow to shoots (g/m^2)
Feb-March	1.16	2.02	0.023
March-Apr	82.95	2.00	1.659
Apr-May	61.17	1.63	0.997
May-July	1097.78	1.43	15.698
July-Aug	533.62	1.05	5.603
Aug-Sept	686.16	1.19	8.165
		Annual flow from rhizomes	32.145 g/m^2
		Leaching	+ 0.56 g/m^2
		Total annual flow to shoots =	32.71 g/m^2

Annual flow from the shoot to the rhizome compartment during senescence was estimated by the difference in total shoot uptake and losses to leaching and detritus (32.71 g/m^2 - (0.56 g/m^2 + 20.27 g/m^2)

Annual flow from shoots to rhizomes = 11.88 g/m^2.

Annual losses to root mortality, based on the assumption of steady state, were estimated by multiplying annual root mortality, assumed to equal annual root productivity, by the mean nitrogen concentration in root tissues at the onset of root mortality in December.

Annual Mortality (g/m^2)	Concentration (%)	Annual loss (g/m^2)
2668.40	0.58	15.47

Annual loss to root mortality = 15.47 g/m^2

Annual losses to rhizome mortality, based on the assumption of steady state, were estimated by multiplying annual rhizome mortality, assumed to equal annual rhizome production, by the mean nitrogen concentration in the rhizomes between February and May.

Annual Mortality (g/m^2)	Concentration (%)	Annual Loss (g/m^2)
1875.88	0.87	16.23

Annual loss to rhizome mortality = 16.23 g/m^2

Based on the assumption that the majority of root growth is supported by reallocation from the rhizomes, annual flow from the rhizomes to the roots was estimated by multiplying annual root productvity by the mean nitrogen concentration between May-July and July-Aug.

Date	Productivity (g/m^2)	Concentration (%)	Monthly flow (g/m^2)
May-July	944.45	0.75	7.08
July-Aug	1723.85	0.66	11.37

Annual flow from rhizomes to roots = 18.45 g/m^2

Annual uptake from the sediments by the roots, based on the assumption of steady state, is equal to the annual losses from the the plant i.e leaching and shoot, root, and rhizome mortality.

Leaching + Detritus + Root Mortality + Rhizome Mortality = Annual Root Uptake

$0.56\ g/m^2 + 20.27\ g/m^2 + 15.47\ g/m^2 + 16.32\ g/m^2 = \underline{52.62\ g/m^2}$

Annual flow from the roots to the rhizomes was estimated by mass balance of the rhizome compartment. Annual translocation from the shoots to the rhizomes was subtracted from the sum of the annual losses to rhizome mortality, annual flow from the rhizomes to the roots, and annual flow from the rhizomes to the shoots.

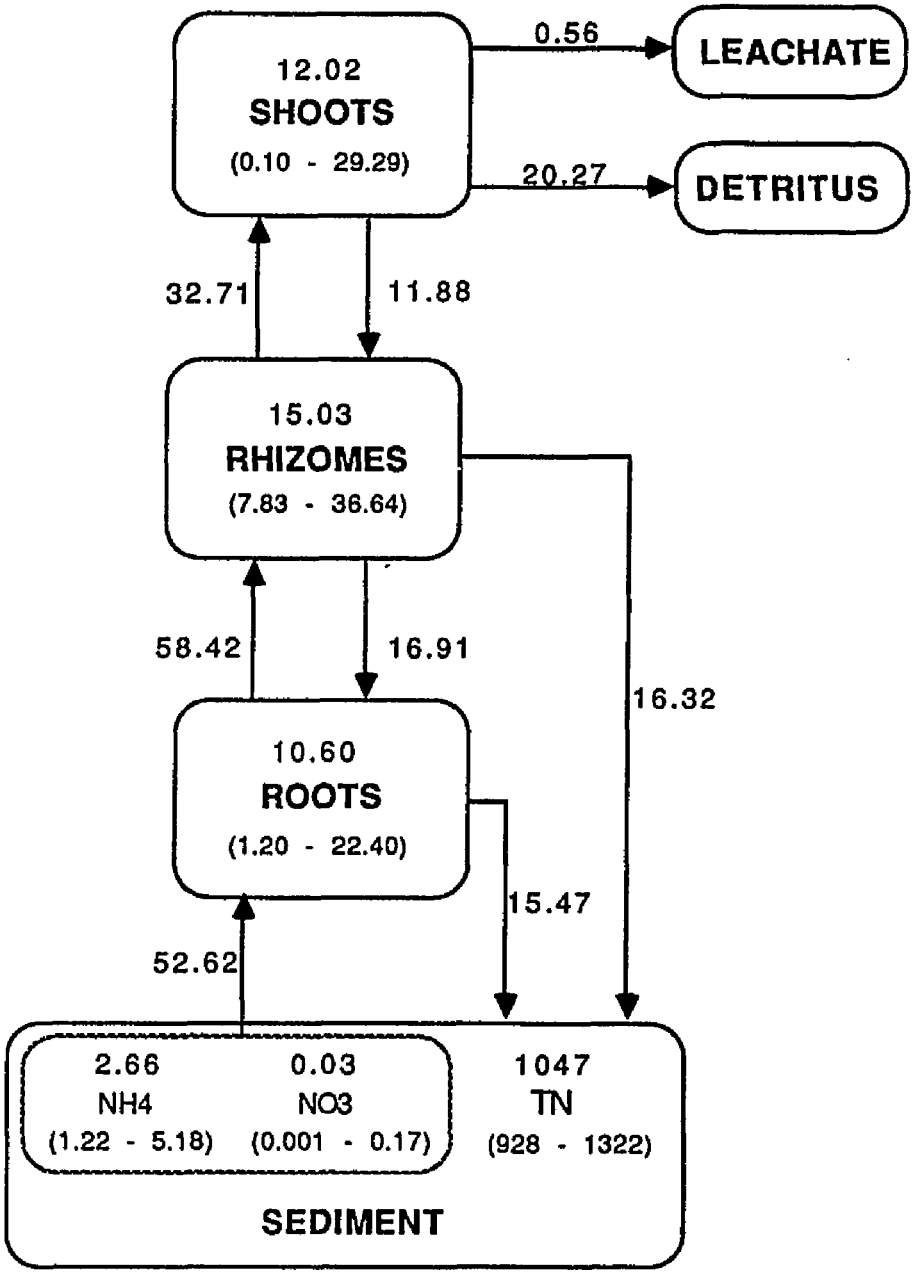
$$(32.71\ g/m^2 + 16.32\ g/m^2 + 18.45\ g/m^2) - 11.88\ g/m^2 = 55.60\ g/m^2$$

Annual flow from rhizomes to roots = $\underline{55.60\ g/m^2}$

Summary

The quantitative assessment of annual compartmental fluxes demonstrates that Spartina cynosuroides releases significant levels of nitrogen to the environment. Of the total nitrogen transfer of 32.71 g/m^2 to the shoots, 20.83 g/m^2, or 63%, is lost to the environment through leaching (2%) and mortality (61%). Root and rhizome mortality also account for significant a significant loss to the surrounding sediments. Approximately 15.47 g/m^2, or 29%, of root uptake is lost through root mortality while 16.32 g/m^2, or 31%, is lost through rhizome mortality.

Figure 15. Nitrogen compartmental model for Spartina cynosuroides. Compartmental nitrogen standing stocks are expressed as mean gN/m^2 including monthly ranges in parentheses. Sediment nitrogen standing stocks expressed as the total monthly pool for all depths. Annual flows are expressed as gN/m^2/year.


12.02
SHOOTS
(0.10 - 29.29)
0.56
LEACHATE
20.27
DETRITUS
32.71
11.88
15.03
RHIZOMES
(7.83 - 36.64)
58.42
16.91
16.32
10.60
ROOTS
(1.20 - 22.40)
15.47
52.62
2.66
NH4
(1.22 - 5.18)
0.03
NO3
(0.001 - 0.17)
1047
TN
(928 - 1322)
SEDIMENT

As such, belowground mortality accounts for 31.82 g/m^2, or 60% of annual root uptake, while the remaining 40% is lost through shoot leaching and mortality.

Spartina cynosuroides also cycles significant levels of nitrogen internally through reallocation. Of the total annual uptake of nitrogen by the shoots, 36% is conserved through translocation to the rhizomes. Of the total reallocation of nitrogen from the roots to the rhizomes of 55.60 g/m^2, 18.45 g/m^2, or 33%, is reallocated to the roots while approximately 10.28 g/m^2, or 18%, is required for rhizome productivity. As shoots require 32.71 g/m^2, or 59%, of the annual reallocation of nitrogen from the roots to the rhizomes, either root or rhizome productivity must be supported, at least in part, by nitrogen translocated at shoot or root senescence. Annual shoot and root productivity require 51.16 g/m^2, of which 28.81 g/m^2, or 56% is available for reallocation from the rhizomes. Transfer from the roots to the rhizomes exceeds root uptake by approximately 5% indicating that roots may conserve nitrogen at senescence through translocation to the rhizomes.

Phosphorus Dynamics

Tissue Phosphorus Concentrations

Seasonal patterns of phosphorus concentrations of the shoots, roots, and rhizomes of Spartina cynosuroides are shown in Figure 16. Tissue phosphorus concentrations depended on an interaction effect between compartment and month (ANOVA, F=2.18E+01, DF=12, P<0.001). A mean

Table 29. Mean monthly phosphorus concentrations in the shoots, roots, and rhizomes of Spartina cynosuroides expressed as % dry weight ± S.D.

Date	Shoots	Roots	Rhizomes
February[a]	----	0.20 ± 0.010	0.12 ± 0.004
March	0.18 ± 0.007	0.21 ± 0.040	0.12 ± 0.006
April	0.33 ± 0.002	0.22 ± 0.020	0.11 ± 0.024
May	0.23 ± 0.002	0.19 ± 0.007	0.12 ± 0.004
June[b]	0.22 ± 0.017	----	----
July	0.19 ± 0.004	0.14 ± 0.023	0.11 ± ----
August	0.12 ± 0.011	0.20 ± 0.012	0.07 ± 0.003
September	0.13 ± 0.018	0.19 ± 0.006	0.08 ± 0.002
October	0.11 ± 0.005	0.17 ± 0.023	0.09 ± 0.002
December	----	0.17 ± 0.007	0.08 ± 0.006
means	0.19	0.19	0.10

[a]February-May values estimated from 1988 data

[b]June-October values estimated from 1987 data

phosphorus concentration in the shoots and roots of 0.19% was approximately twice that of the mean concentration in the rhizomes of 0.10% (Table 30).

Shoot phosphorus concentrations varied significantly over an annual cycle (ANOVA, F=1.43E+02, DF=7, P<0.0001), decreasing from a high mean of 0.33% in April to a mean low of 0.11% in October (Table 29).

Root phosphorus concentrations demonstrated pronounced seasonal patterns (ANOVA, F=4.91E+00, DF=8, P<0.006) decreasing from a high of 0.22% in April to a low of 0.14% in July. Root phosphorus concentrations then increased to 0.20 in August and reained relatively stable through April. Rhizome concentrations also varied significantly over an annual cycle (ANOVA, F=1.24E+01, DF=8, P<0.0001). Rhizome phosphorus concentrations remained relatively stable at a mean of 0.12% between February and July then decreased to 0.07% in August where the concentrations remained relatively stable through December.

Tissue Phosphorus Standing Stocks

Spartina tissue phosphorus standing stocks were estimated by multiplying monthly biomass standing stocks by appropriate monthly phosphorus concentrations. Seasonal patterns of tissue phosphorus standing stocks are shown in Figure 16. Tissue phosphorus standing stocks depended on an interaction effect between compartment and month (ANOVA, F=1.00E+02, DF=12, P<0.001). A mean root phosphorus standing stock of 3.04 g/m^2 was approximately twice that of the shoots (1.57 g/m^2) and one and a half times that of the rhizomes (2.29 g/m^2).

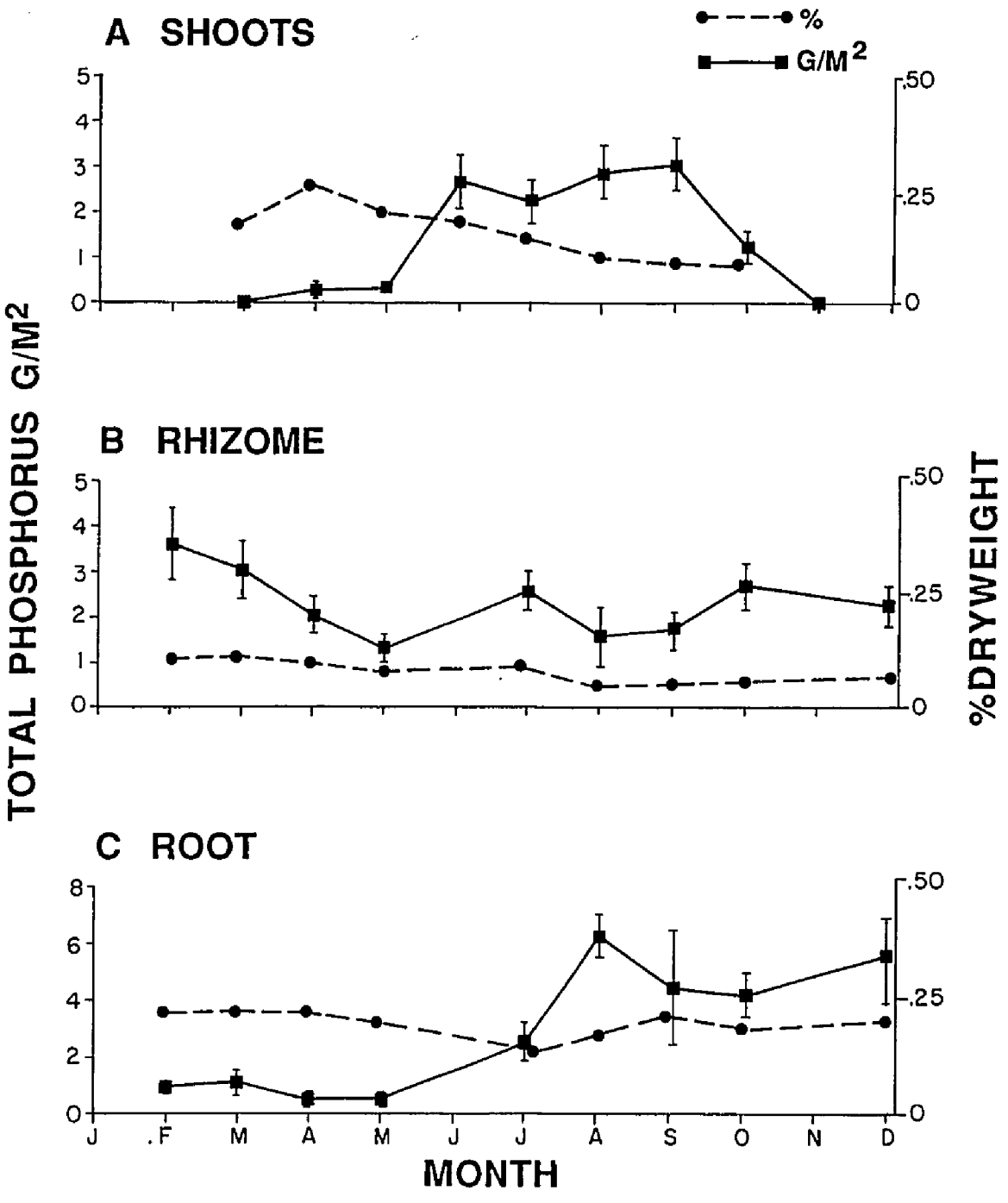
Table 30. Mean monthly phosphorus standing stocks (gP/m^2) in the shoots, roots, and rhizomes of Spartina cynosuroides expressed on a dry weight basis ± S.D.

Date	Shoots	Roots	Rhizomes
February[a]	----	0.92 ± 0.05	3.62 ± 0.12
March	0.002 ± 0.0008	1.09 ± 0.20	2.97 ± 0.14
April	0.267 ± 0.019	0.47 ± 0.03	2.05 ± 0.44
May	0.323 ± 0.020	0.50 ± 0.10	1.31 ± 0.40
June[b]	2.720 ± 0.21	----	----
July	2.214 ± 0.50	1.78 ± 0.30	2.31 ± ---
August	2.180 ± 0.18	6.24 ± 0.35	1.73 ± 0.07
September	3.070 ± 0.42	5.56 ± 0.18	1.73 ± 0.03
October	1.260 ± 0.05	5.07 ± 0.68	2.69 ± 0.05
December	----	5.72 ± 0.22	2.22 ± 0.15
means	1.57	3.04	2.29

[a]February-May values estimated from 1988 data

[b]June-October values estimated from 1987 data

Figure 16. Seasonal patterns of mean monthly phosphorus concentrations (%P) and standing stocks (gP/m^2) in the shoots, roots, and rhizomes of Spartina cynosuroides expressed on a dry weight basis $\pm$ S.D.


A SHOOTS
%
G/M 2
B RHIZOME
C ROOT
TOTAL PHOSPHORUS G/M2
%DRYWEIGHT
MONTH
J
F
M
A
M
J
J
A
S
O
N
D

Shoot phosphorus standing stocks varied significantly over an annual cycle (ANOVA, F=1.11E+02, DF=7, P<0.0001), increasing from a low of 0.002 g/m^2 in March to an initial peak of 2.72 g/m^2 in June and a second peak of 3.07 g/m^2 in September (Table 30). Shoot phosphorus standing stocks were correlated with shoot biomass ($r = .93$, $p<.01$). Multiple comparisons indicated that September and June-July were significantly different than all other groups (SNK:EWER =0.05).

Root phosphorus standing stocks also exhibited pronounced seasonal patterns (ANOVA, F=2.05E+02, DF=8, P<0.0001), increasing from a low of 0.47 g/m^2 in April to a peak of 6.24 g/m^2 in August. Root phosphorus standing stocks were correlated with root biomass ($r = .99$, $P<.01$). Rhizome phosphorus standing stocks varied seasonally (ANOVA, F=4.92E+01, DF=8, P<0.0001) decreasing from a high of 3.62 g/m^2 in February to a low of 1.31 g/m^2 in May. A secondary increase to 2.31 g/m^2 was observed in July followed by a decrease to 1.73 g/m^2 in September. Rhizome standing stocks then increased to the observed level in February. Based on a maximum - minimum calculation, a minimum of 2.89 g/m^2 phosphorus was available for reallocation from the rhizomes.

Tissue Phosphorus Leaching

Spartina monthly leaching rates were estimated using the previously described equation. Summation of monthly leaching rates resulted in an annual leaching rate of 0.07 g/m^2/year.

May 0.022 g/m^2

June 0.045 g/m^2

0.067 g/m^2/year

Tissue Phosphorus Efficiency Indexes

Spartina phosphorus use and recovery efficiency indexes are shown in Table 31. Shoot use efficiency decreased between March and April and remained relatively low through June. Shoot use efficeincy then increased to the observed peak in October. As such, shoot use efficiency increased with increased shoot productivity, reaching a peak in the initial phase of shoot dieback. Root uese efficiency increased between April and May at the onset of root productivity and increased with increased root biomass. root use efficiency then decreasedand remained stable through December. Rhizome use efficiency increased between May and July followed by a decrease in August. Rhizome use efficiency then increased and remained relatively high through February. Rhizome use efficiency, then, reminaed high during periods of shoot and root growth and decreased following shoot and root senescence. Mean phosphorus ues efficiency in the rhizbmes was approximately twice that of the shoots and roots. Shoot phosphorus recovery efficiency decreased between September and November.

Sediment Inorganic Phosphorus

Sediment inorganic phosphorus, as orthophosphate (PO4), at each sediment depth of Spartina was estimated using the previously described equation. Each month the standing stocks of orthophosphate at each depth were summed to represent the total available monthly pools of inorganic

Table 31. Phosphorus use efficiency in the shoots, roots, and rhizomes and recovery efficiency in the shoots of Spartina cynosuroides. Monthly use efficiency is estimated by dividing mean monthly tissue biomass by mean monthly tissue phosphorus standing stocks. Monthly recovery efficiency is estimated by dividing the difference in phosphorus in live and dead shoots by phosphorus in live shoots.

	Use Efficiency		
Date	Shoots	Roots	Rhizomes
February[a]	----	502.39	1415.39
March	580.00	477.20	703.82
April	310.67	465.21	616.24
May	446.16	537.58	524.74
June[b]	467.88	----	----
July	547.02	727.07	1649.61
August	814.40	495.42	1023.89
September	801.97	519.87	1282.21
October	909.37	591.45	1730.75
December	----	552.93	1010.58
means	559.68	541.01	1106.00

Recovery Efficiency	
Date	Shoots
Sept-Oct	0.38
Oct-Nov	0.26
mean	0.32

[a]Feb-May values estimated from 1988 data

[b]June-Dec values estimated from 1987 data

Table 32. Mean monthly standing stocks at each sediment layer and total monthly pools of inorganic phosphorus as gPO_4/m^2 for Spartina cynosuroides expressed on a dry weight basis.

	PO_4					
	Sediment Layer					
	0-10cm	10-20cm	20-30cm	30-40cm	40-50cm	Total
Date						
February[a]	3.65	3.26	4.20	1.00	6.68	18.79
March	11.75	5.30	3.90	6.70	4.44	32.09
April	2.90	3.41	6.30	8.84	5.00	26.45
May	3.50	4.37	4.70	8.20	10.91	31.68
July[b]	11.80	12.00	7.62	8.26	6.75	46.43
August	0.60	1.38	0.38	0.52	0.44	3.32
September	12.70	7.22	12.70	6.88	5.40	44.90
October	13.75	7.91	12.00	14.74	3.79	52.19
					mean	31.98

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

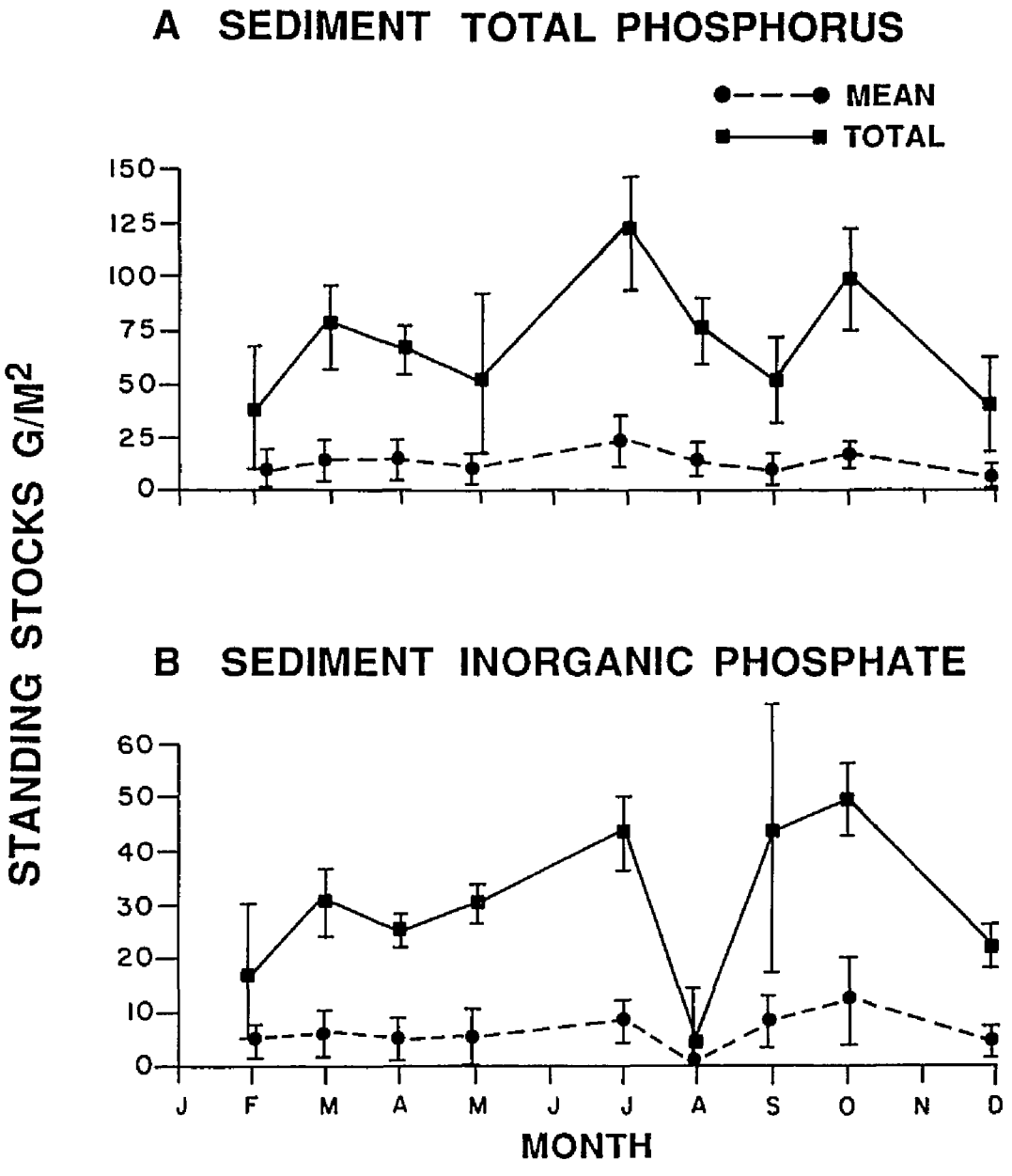
Table 33. Mean monthly standing stocks at each sediment layer and total monthly pools of total phosphorus as gTP/m^2 for Spartina cynosuroides expressed on a dry weight basis.

	Total Phosphorus					
	Sediment Layer					
	0-10cm	10-20cm	20-30cm	30-40cm	40-50 cm	Total
Date						
February[a]	15.14	6.19	5.00	6.40	7.10	39.83
March	21.00	20.00	17.00	9.00	17.00	84.00
April	21.69	17.45	9.02	9.89	11.56	69.61
May	19.21	14.47	3.60	9.29	6.03	52.06
July[b]	28.19	40.69	20.41	24.42	12.44	126.15
August	20.81	17.30	11.24	12.40	15.32	77.07
September	14.77	5.34	17.17	5.22	9.52	52.02
October	22.06	16.56	26.33	19.29	16.89	101.13
					mean	75.23

[a]February-May values estimated from 1988 data

[b]July-October values estimated from 1987 data

Figure 17. Seasonal patterns of total and inorganic phosphorus (PO_4) standing stocks in the sediments of Spartina cynosuroides. Monthly standing stocks expressed as the mean and total monthly pool for all depths to 50 cm on a dry weight basis.


A SEDIMENT TOTAL PHOSPHORUS
MEAN
TOTAL
150
125
100
75
50
25
0
B SEDIMENT INORGANIC PHOSPHATE
60
50
40
30
20
10
0
J F M A M J J A S O N D
MONTH
STANDING STOCKS G/M2

phosphorus to a 50 cm depth. Total monthly pools of PO_4 increased form a minimum of 3.32 g/m^2 in August to a peak standing stock of 52.29 g/m^2 in October (Table 32). Over the sampling period, monthly PO_4 levels varied significantly (ANOVA, F=3.35E+00, DF=7, P<0.008) as did levels with depth (ANOVA, F=2.74E+00, DF=4, P<0.04). Seasonal patterns of total monthly pools of PO_4 are shown in Figure 17.

Sediment Total Phosphorus

Sediment total phosphorus at each depth for Spartina was estimated using the previously described equation. Monthly total phosphorus standing stocks for each depth were summed to represent the total monthly pool of total phosphorus to a depth of 50 cm. Total monthly pools of total phosphorus increased from a low of 52.06 g/m^2 in May to a peak of 126.15 g/m^2 in July. A second peak of 101.13 g/m^2 was observed in October (Table 33). Over the sampling period, total phosphorus standing stocks varied significantly with month (ANOVA, F=3.63E+00, DF=7, P<0.005) but not with depth (ANOVA, F=1.67E+00, DF=4, P=0.18). Correlation analysis indicated no relationship between total phosphorus and organic matter. Seasonal patterns of total monthly pools of total phosphorus are shown in Figure 17.

Sediment-Tissue Phosphorus Relationship

The relationship between Spartina sediment and tissue phosphorus standing stocks was developed through simple and multiple regressions such that monthly shoot, root, and rhizome standing stocks, as the dependent

Table 34. Coefficients of determination (r^2) with levels of significance (p) simple and multiple regressions of Spartina cynosuroides shoot, root, and rhizome phosphorus standing stocks (P) with sediment inorganic (PO_4) and total phosphorus (TP) standing for all depths.

	Sediment (PO_4)	Sediment TP	Sediment PO_4, TP
Shoot P	r^2 = 0.190 F = 0.750 p = 0.390	r^2 = 0.890 F = 3.750 p = 0.060	NS a = 0.05
Root P	r^2 = 0.170 F = 0.680 p = 0.413	r^2 = 0.075 F = 4.990 p = 0.050	NS a = 0.05
Rhizome P	r^2 = 0.030 F = 0.119 p = 0.730	r^2 = 0.010 F = 4.004 p = 0.050	NS a = 0.05

NS = non significant

a = alpha level

variables, were regressed against total monthly pools of inorganic and total phosphorus, as the independent variables. Regression analyses indicated that shoot, root, and rhizome phosphorus levels were independent of sediment inorganic and total phosphorus. Coefficients of determination and levels of significance are shown in Table 34

Phosphorus Model

Spartina compartmental standing stocks are derived from previous sections (Tables 30, 32-33). Annual compartmental fluxes are estimated using productivity, phosphorus concentrations, leaching, and mass balance of certain compartmentss. Compartmental standing stocks and annual fluxes are shown in Figure 18.

Annual losses to leaching were estimated by the summation of monthly leaching losses resulting in an annual leaching rate of 0.07 g/m^2.

Annual losses to detritus were estimated by multiplying yearly shoot mortality, assumed to equal yearly productivity, by the mean phosphorus concentrations of dead shoots in September and October.

Date	Mortality (g/m^2)	Concentration (%)	Monthly loss (g/m^2)
Sept-Oct	1316.26	0.08	1.09
Oct-Nov	1145.81	0.16	1.79
		Annual loss to detritus =	2.88 g/m^2

Annual flow from the rhizome to the shoot compartment was estimated by the summation of monthly flows. Monthly flows were estimated by multiplying monthly shoot productivity by phosphorus concentrations in live shoots. Total annual flow into the shoot compartment was estimated by the summation of annual shoot uptake and leaching.

Date	Productivity (g/m^2)	Concentration (%)	Monthly Flow to Shoots (g/m^2)
Feb-March	1.16	0.18	0.002
March-April	82.95	0.33	0.273
April-May	61.71	0.23	0.140
May-July	1097.78	0.22	2.415
July-Aug	533.62	0.12	0.640
Aug-Sept	686.16	0.13	0.892

Annual flow from rhizomes 4.362 g/m^2

Leaching 0.07 g/m^2

Total annual flow to shoots = 4.43 g/m^2

Annual flow from the shoot to the rhizome compartment during senescence was estimated by the difference in total shoot uptake and losses to leaching and detritus (4.43 g/m^2 - (0.07 g/m^2 + 2.88 g/m^2)

Annual flow from shoots to rhizomes = 1.48 g/m^2.

Annual losses to root mortality, based on the assumption of steady state, were estimated by multiplying annual root mrtality, assumed to equal annual root productivity, by the mean phosphorus concentration in root tissues at the onset of mortality in December.

Annual Mortality (g/m^2)	Concentration (%)	Annual loss (g/m^2)
2668.40	0.17	4.53

Annual loss to root mortality = $\underline{4.53\ g/m^2}$

Annual losses to rhizome mortality, based on the assumption of steady state, were estimated by multiplying annual root mortality, assumed, to equal annual rhizome productivity, by the phosphorus concentration in root tissues between February and May.

Annual Mortality (g/m^2)	Concentration (%)	Annual loss (g/m^2)
1875.88	0.12	2.25

Annual loss to rhizome mortality = $\underline{2.25\ g/m^2}$

Based on the assumption that the majority of root growth is supported by reallocation from the rhizomes, annual flow from the rhizomes to the roots was estimated by multiplying annual root productivity by the the mean phosphorus concentrations between May-July and July-Aug.

Date	Productivity (g/m^2)	Concentration (%)	Monthly flow (g/m^2)
May-July	944.45	0.14	1.32
July-Aug	1723.85	0.20	3.45

Annual flow from rhizomes to roots = $\underline{4.76\ g/m^2}$

Annual root uptake from the sediments, based on the assumption of steady state, is equal to the annual losses from the plant i.e. leaching and shoot, root, and rhizome mortality.

Leaching	Detritus	Root Mortality	Rhizome Mortality	Annual Root Uptake
0.07 g/m^2	+ 2.88 g/m^2	+ 4.53 g/m^2	+ 2.25 g/m^2	= 9.73 g/m^2

Annual flow from the roots to the rhizomes was estimated by mass balance of the rhizome compartment. Annual translocation from the shoots to the rhizomes was subtracted from the sum of annual losses to rhizome mortality, annual flow from the rhizomes to the shoots, and annual flow from the rhizomes to the roots.

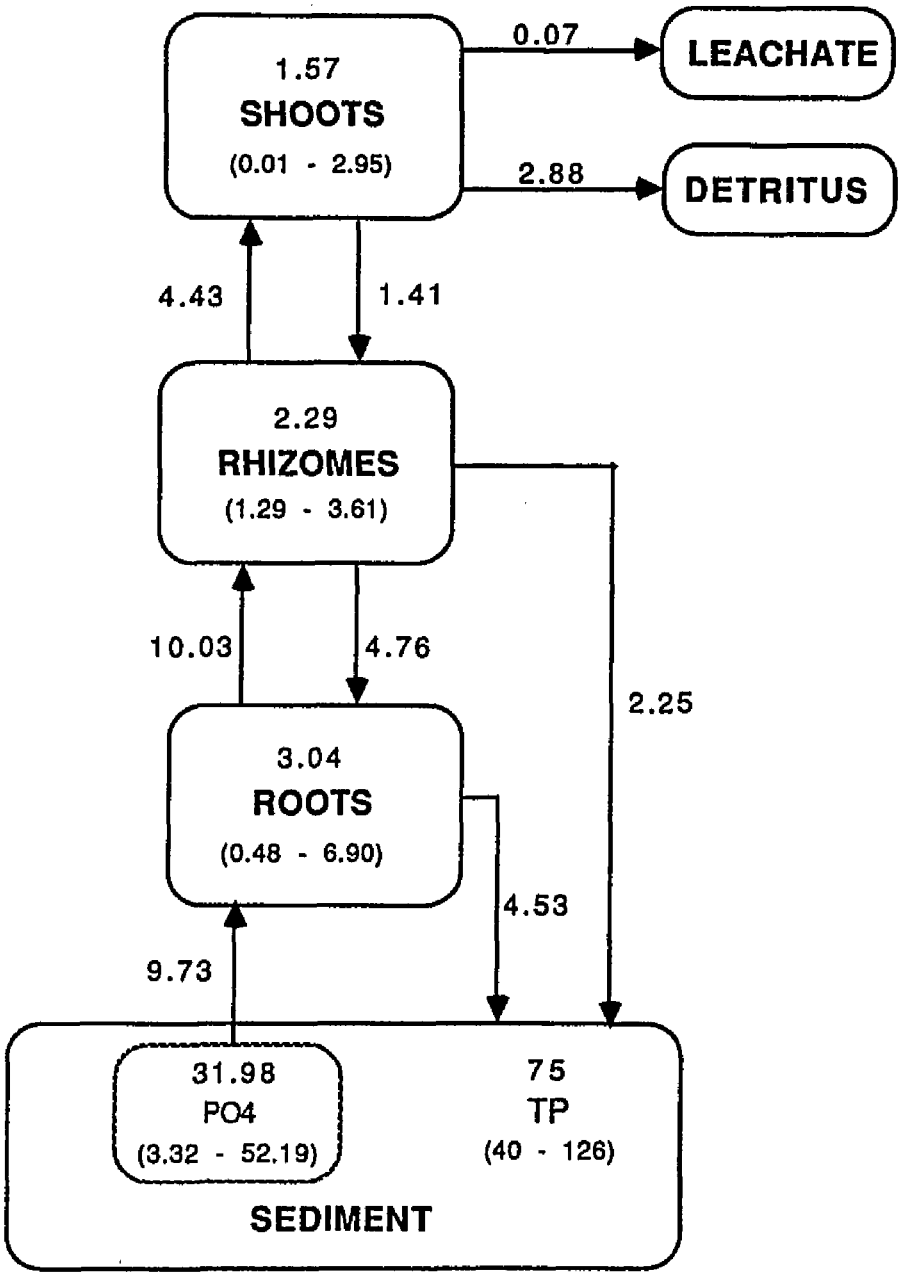
$(4.43\ g/m^2 + 2.25\ g/m^2 + 4.76\ g/m^2) - 1.41\ g/m^2)$

Annual flow from roots to rhizomes 10.03 g/m^2

Summary

The quantitative assessment of annual compartmental fluxes demonstrates that Spartina cynosuroides releases significant levels of phosphorus to the environment over an annual cycle. Of the total phosphorus transfer of 4.43 g/m^2 to the shoots, 2.95 g/m^2, or 67%, is lost to the environment through leaching (2%) and mortality (65%). Root and rhizome mortality also account for significant losses to the surrounding sediments. Approximately 2.25 g/m^2, or 23%, of annual root uptake is lost through rhizome mortality while 4.53 g/m^2, or 47%, is lost through root mortality. As such losses to belowground mortality account for approximately 70% of annual root uptake, while 30% is lost to shoot leaching and mortality.

Figure 18. Phosphorus compartmental model for Spartina cynosuroides. Compartmental phosphorus standing stocks are expressed as mean monthly gP/m^2 including monthly ranges in parentheses. Sediment phosphorus standing stocks expressed as the total monthly pool for all depths. Annual flows are xpressed as $gP/m^2/year$.


1.57
SHOOTS
(0.01 - 2.95)
0.07
LEACHATE
2.88
DETRITUS
4.43
1.41
2.29
RHIZOMES
(1.29 - 3.61)
10.03
4.76
2.25
3.04
ROOTS
(0.48 - 6.90)
4.53
9.73
31.98
PO4
(3.32 - 52.19)
75
TP
(40 - 126)
SEDIMENT

Spartina cynosuroides also cycles and stores significant levels of phosphorus internally through reallocation. Of the annual uptake of 4.43 g/m^2 by the shoots, 1.41 g/m^2, or 32%, is conserved through translocation to the rhizomes. Of the total translocation of phosphorus from the roots to the rhizomes of 10.03 g/m^2, 4.76 g/m^2, or 47%, is reallocated to the roots and 1.65 g/m^2, or 16%, is required for rhizome productivity. As shoots require 4.43 g/m^2, or 44%, of annual transfer of phosphorus from the roots to the rhizomes, either root or rhizome productivity must be supported, at least in part, by phosphorus translocated at shoot or root senescence. Annual root and shoot growth require 9.19 g/m^2, of which a minimum of 2.89 g/m^2 is estimated as available for reallocation from the rhizomes. Transfer from the roots to the rhizomes exceeds annual root uptake by 3% indicating that the roots may conserve phosphorus at senescence through translocation to the rhizomes.

Nitrogen-Phosphorus Relationship

Correlation analysis indicated that nitrogen and phosphorus cycling and temporary storage, as reflected in the pairwise comparison of monthly standing stocks, are interdependent, or covary, in the shoots, roots, and rhizomes of Spartina cynosuroides. Sediment inorganic nitrogen (NO_3+ NH_4) and inorganic phosphorus (PO_4), as well as total nitrogen and phosphorus standing stocks, did not covary over the same period. Correlation coefficients and levels of significance are shown in Table 35.

Spartina nitrogen to phosphorus ratios (N:P) in the shoots, roots, rhizomes, and sediments are shown in Table 36. Shoot N:P ratios were initially high at 10.0 in March at the onset of shoot development, and decreased to 6.2 in April during the initial lag phase of shoot growth. N:P ratios then increased to a secondary peak of 10.2 in July during the second lag phase in shoot growth, and remained relatively high through October. Root N:P ratios increased from 1.1 to 5.5 in July with increaesd root biomass, followed by a decrease to 3.2 in August. Root N:P ratios remained relatively stable through December then decreased to the observed level in March. Rhizome N:P ratios were variable. A sharp decrease from 10.1 to 4.6 was observed between March and April, at the onset of shoot development, followed by an increase to 8.4 in May. Rhizome N:P ratios then decreased to 4.5 through September followed by an increase to the observed level in March. A mean N:P ratio of 8.47 was approximately one and a half times that of the rhizomes two and a half times that of the roots. Sediment inorganic N:P ratios were low and variable decreasing from 0.72 in August to 0.03 in October. Sediment inorganic N:P ratios then increased to 0.16 in June. Sediment total N:P ratios decreased from a peak of 33.2 to a minimum of 7.7 between March and July.

Table 35. Correlation coefficients (r) and levels of significance (p) for pairwise comparisons of monthly nitrogen (N) and phosphorus (P) standing stocks in the shoots, roots, rhizomes, and sediments of Spartina cynosuroides. Sediment comparisons from all depths.

Shoot N:Shoot P	Root N:Root P	Rhizome N:Rhizome P
r = 0.968	r = 0.933	r = 0.800
p = 0.001	p = 0.001	p = 0.001

Sediment TN:Sediment TP	Sediment IN:Sediment IP
r = 0.115	r = 0.107
p = 0.240	p = 0.255

TN = Sediment total nitrogen

TP = Sediment total phosphorus

IN = Sediment inorganic nitrogen (NO_3+ NH_4)

IP = Sediment inorganic phosphorus (PO_4)

Table 36. Monthly nitrogen to phosphorus ratios (N:P) in the shoots, roots, rhizomes, and sediments of Spartina cynosuroides. Sediment ratios estimated from total monthly pools.

Date	Shoots	Roots	Rhizomes
February	----	2.7:1	7.1:1
March	10.0:1	1.1:1	10.1:1
April	6.2:1	3.1:1	4.6:1
May	7.3:1	5.3:1	8.4:1
June	6.7:1	---	---
July	10.2:1	5.5:1	6.9:1
August	8.5:1	3.2:1	4.2:1
September	9.7:1	4.1:1	4.5:1
October	9.2:1	4.1:1	7.4:1
December	----	3.2:1	5.8:1
means	8.5:1	3.6:1	6.5:1

Date	Sediment Inorganic	Sediment Total
March	0.06:1	33.2:1
April	0.07:1	13.3:1
May	0.15:1	16.1:1
June	0.16:1	17.8:1
July	0.04:1	7.7:1
August	0.72:1	12.6:1
September	0.06:1	18.5:1
October	0.03:1	9.7:1
means	0.16:1	16.0:1

Discussion

Peltandra virginica

Net Annual Productivity

Aboveground Productivity

In this study, seasonal patterns of shoot biomass standing stocks were similar to those previously reported for *Peltandra virginica*, increasing from a low of 9.54 g/m^2 in March to a high of 969.53 g/m^2 in July. Wohlgemuth (1988), sampling at two week intervals in a riverside monotypic stand of *Peltandra* at Sweethall Marsh, reported that *Peltandra* shoot biomass increased from a May level of 220.20 g/m^2 to a July peak of 437.48 g/m^2. Doumlele (1981), working in an adjacent area of Sweethall Marsh, reported a peak standing stock of 423.4 g/m^2 in July. Good and Good (1976) reported a June peak standing stock of 1286 g/m^2 for *Peltandra*, the highest literature estimate available. Peak biomass observed in this study is significantly higher than the mean of 686 g/m^2 calculated by Whigham et al. (1978) for *Peltandra virginica* in Middle Atlantic coastal wetlands but approaches the value of 988 g/m^2 observed in two tributaries of the Chesapeake Bay by Flemer et al. (1978).

Estimates of Peltandra shoot productivity have generally been based on the positive changes in monthly biomass through peak standing stocks. These estimates, however, may underestimate shoot productivity as they do not account for interval monthly mortality or new recruitment following peak shoot biomass, both of which may be significant in tidal freshwater macrophytes (Mathews and Westlake, 1969; Whigham et al., 1978). For example, Bernard and Hopkinson (1979) included mortality in their estimates of shoot productivity in Carex rostrata. As a result, annual shoot productivity increased from 540 $g/m^2/yr$, based on the positive changes in monthly shoot biomass, to 1080 $g/m^2/yr$. Pickett (1984), working with several tidal freshwater macrophytes, demonstrated the importance of including shoot mortality and new recruitment in the estimate of annual shoot productivity. Using estimates of interval monthly mortality, Pickett calculated an annual shoot turnover of 2.87 for Peltandra (in Wohlgemuth, 1988). In addition, Pickett reported that shoot recruitment following peak biomass accounted for approximately 35% of annual shoot productivity in Peltandra. In a more recent tagging study, Wohlgemuth (1988), using permanent 0.25 m^2 quadrats, estimated annual shoot productivity at 789.44 g/m^2 for Peltandra based on the summation of monthly mortality rates. Wohlgemuth reported an annual shoot turnover of 2.24 based on the ratio of annual productivity to peak shoot biomass.

Peltandra monthly shoot productivity in this study was estimated by summing changes in shoot biomass and monthly mortality through the growing season. Monthly mortality was calculated by adjusting Wohglemuths' interval daily mortality rates to shoot standing stocks in this study. Summing

monthly shoot productivity estimates resulted in an annual productivity of 1634.44 g/m^2, the highest productivity estimate available for Peltandra, and an annual turnover of 1.68 (annual productivity/peak biomass). The inclusion of mortality and new recruitment following peak biomass, therefore, provide a more realistic estimate of annual of shoot productivity.

In addition to the inclusion of mortality and new recruitment, higher annual shoot productivity of Peltandra in this study may be attributable to the well drained and tidally flushed creekbank sediments which support the Peltandra community. For example, Walker (1981), sampling at two week intervals in well drained sediments, reported that Peltandra shoot biomass increased from a March minimum of 23.6 g/m^2 to a July peak of 637.5 g/m^2 while in poorly drained sediments shoot biomass increased from a March level of 23.8 g/m^2 to a June level of 452.0 g/m^2. Odum et al. (1983) also reported significantly higher annual productivity rates in Zizaniopsis miliacea in a well flushed and tidal influenced area when compared to an impounded area. The authors attributed the disparity to the flushing of dead matter and the recycling of oxygen and nutrients.

Peltandra shoot productivity patterns may be best described in terms of daily growth rates, which in turn provide insight into relative shoot growth strategies. Assuming March 1 to be the beginning of the growing season, shoot productivity increased at the rate of 3.61 g/m^2 between March and May followed by an increase to 20.23 g/m^2 between May and July. Walker (1981), sampling in well drained sediments, reported similar shoot growth patterns in monotypic stands of Peltandra with daily shoot productivity rates

increasing from 6.15 g/m^2 over the first 49 days of the growing season to 22.32 g/m^2 through peak shoot standing stocks in July. Whigham and Simpson (1975) reported that daily growth rates for Peltandra ranged from 6.0 to 13.4 g/m^2 between the end of April and May and 2.6 to 14.1 g/m^2 between May and the end of June (in Walker, 1981). Apparently, seasonal patterns of shoot productivity in Peltandra include an early spring lag phase followed by a period of rapid growth in early summer.

The early lag phase in shoot development, observed in many tidal freshwater macrophytes with extensive belowground storage rhizomes (Whigham et al. 1978, Walker, 1981), provides Peltandra with certain adaptive advantages in a harsh and competitive environment. Initial slow periods of shoot development allow sufficient time for the breakdown of "complex" nitrogen, phosphorus, and energy storage compounds within the rhizomes (Walker, 1981) and reallocation to the shoots. Reallocation from the rhizomes during initial periods of shoot growth allows nitrogen and phosphorus to be concentrated at higher levels then required. This phenomenom is generally referred to as "luxury uptake" (Gerloff and Kromholtz, 1966) and provides Peltandra with an adequate supply of nutrients to support subsequent periods of rapid growth. The rapid growth phase in early summer provides Peltandra with a competitive advantage over other macrophytes. The clustered growth patterns together with broad leaf morphology results in an extensive canopy which effectively blocks light penetration to the sediment surface. In this manner, Peltandra provides leaf surface area with maxixmum sunlight exposure, resulting in maximum photosynthate production, while inhibiting establishment of other

macrophytes within the stand. The secondary period of new shoot recruitment observed in September may represent an attempt by Peltandra to use remaining nutrients and available sunlight in the production and translocation of photosynthate to the rhizomes to support asynchronous root growth and for overwinter storage. As such, shoot growth strategies may represent a type of allelopathy by Peltandra which allows photosynthate production under optimal environmental conditions of sunlight and nutrients (Chapin, 1980) while minimizing competition for limited resources.

Monthly mortality rates, which increase from 8% between April and June to 64% between June and August may also represent a type of growth strategy by Peltandra. Interval monthly turnover of shoots allows Peltandra to shed weak, grazed, or diseased shoots which, in turn, are replaced through new recruitment. In this way, Peltandra maintains a healthy shoot population which, in turn, is capable of supplying an extensive root and rhizome component with sufficient energy through translocation of photosynthate. Monthly turnover and rapid fall dieback also results in the conservation of photosynthate, nitrogen, and phosphorus, through translocation to the rhizomes, which may be recycled to support new shoot recruitment and root productivity. This pattern may keep nutrients in a type of "dynamic equilibrium" which allows maximum efficiency in terms of nutrient utilization, decreased energy expenditure for de novo root uptake, and increased stability within the environment.

Belowground Productivity

Rhizome biomass was relatively constant throughout the sampling period and, as a result, rhizome productivity was undetectable. The inability to

detect changes in rhizome biomass may be attributable to the sampling technique, which may not be sufficiently sensitive to this belowground component, or to the relatively slow turnover rate of rhizomes (Good et al. 1982). Generally, tidal freshwater macrophytes with extensive rhizomes depend on this component for nutrient reallocation and storage, as well as stability, hence the low turnover. Bernard and Solsky (1977) reported an increase in total belowground biomass between June and August for Carex lacustris however rhizome biomass remained constant over the same period. The extensive rhizome component of Peltandra, with a mean monthly standing stock of 2580 g/m^2, apparently functions in a similar manner resulting in increased stability in a flucuating environment. Walker (1981) reported similar, although somewhat higher, rhizome biomass patterns for Peltandra, assuming a constant rhizome standing stock of 3528 g/m^2. An extensive, stable rhizome component characterized by low annual turnover, then, appears essential to the survival and stability of Peltandra. In fact, it has been suggested that the greater allocation to rhizome biomass in comparison to other tidal freshwater macrophytes (Good et al., 1982), enables Peltandra to produce and maintain robust, monotypic stands similar to those observed in this study.

The ability of Peltandra to maintain such an extensive rhizome component in an anoxic environment is somewhat surprising in terms of cost to the plant (Bloome et al., 1985). Braendle and Crawford (1987), working with several marsh macrophytes, however, demonstrated that rhizomes are more tolerant to anoxia than are roots. As the rhizomes act as regenerators of both shoots and roots, they are also more important to the survival of macrophytes than are the roots. Most extensive rhizome systems, like

Peltandra, have well developed aerenchyma tissue that is ventilated by the shoots (Armstrong, 1979), yet despite this unusual capacity for rhizome ventilation, rhizomes have different tolerances to anoxia (Braendle and Crawford (1987). Rhizome tolerance to anoxia may be best explained by the fact that, rhizomes, as perennial organs, must survive in the fall and winter with no oxygen supply. These facts suggest that although Peltandra rhizomes may depend on aerobic respiration during periods of shoot productivity, they appear to depend at least to some degree on anaerobic respiration in the form of ethanol fermentation (Braendle and Crawford, 1987). Peltandra may have evolved mechanisms for switching over from more efficient aerobic respiration during periods of primary productivity, to less efficient anaerobic respiration for maintenance and support of root productivity in the fall. As anearobic respiration requires significant levels of photosynthate per unit ATP production, extended periods in an anaerobic environment increase demand for carbohydrate reserves which must be supplied by translocation from the shoots. The high energetic cost of maintaining an extensive rhizome component, however, is balanced by the stability, shoot and root support, and nitrogen and phosphorus storage capacity provided by Peltandra rhizomes.

Like rhizome biomass estimates, annual root standing stocks and productivity must be interpreted on a relative basis due to the bias incorporated in the single monthly excavation of preselected sites. Peltandra annual root productivity of 1568 g/m^2 in this study was significantly lower than the annual estimate of 2460 g/m^2 reported by Good and Good (1976). Root productivity was, however, similar to the estimated

annual root productivity of 1258 g/m^2 for Peltandra established in well drained sediments reported by Walker (1981). Comparisons are difficult, however, due to the sampling methods used in these studies. Walker (1981), based on the assumption that peak root biomass coincided with peak shoot standing stocks, sampled the belowground component only in June and July. Good and Good (1975) also observed peak belowground standing stocks at the time of peak shoot standing stock but only sampled from June to August. In this study, belowground biomass was sampled throughout the year and this may explain, at least in part, the discrepancies between these studies while providing insight into the relationship between above- and belowground biomass.

In this study, the initial phase of root productivity apparently occurs between July and August, an initial period of shoot dieback. This apparent asynchronous cycle of shoot and root productivity suggests several interesting aspects of growth strategies in Peltandra. As shoot productivity requires expenditure of significant levels of energy and nutrient reserves, it may be ecologically advantageous to support shoot productivity during periods of maximum photosynthetic production while supporting root growth with photosynthate produced at this time and nitrogen and phosphorus translocated during shoot senescence. This pattern of belowground productivity, in the form of a secondary belowground peak, has been observed at the end of the growing season in October and November (Stroud, 1976; White et al., 1978; Smith et al., 1979) reflecting the influence of translocation from aboveground portions (in Good et al., 1982).

As Peltandra root growth occurs in a highly anoxic environment, root cells must have constant supply of oxygen from the shoots to support aerobic

respiration, or shift to anaerobic respiration, i.e. fermentation, for ATP production (apRees et al., 1987). Fermentation, however, is inefficient due to the increased demand of photosynthate per unit of ATP production. As a result, roots dependent on anaerobic respiration require greater energy allocation in the form of photosynthate, which may decrease shoot productivity (Walker, 1981). Roots which are capable of aerobic respiration are more efficient and require oxygen either through diffusion through a well developed aerenchyma tissue (Walker, 1981) or bound in some unknown way to photosynthate (Walker, 1981; apRees et al., 1987). Roots which extend to one meter, like those of Peltandra, have little aerenchymatous tissue, it is assumed that they pay the price energetically in a waterlogged, anaerobic environment (Whigham and Simpson, 1978) by requiring more substrate for fermentation and less shoot to root biomass (Shaver and Billings, 1975). This suggestion is supported by the low shoot to root ratio at peak shoot biomass of 0.80 observed in this study. Further, since most living belowground biomass is located in the top 30 cm, the depth of Peltandra roots suggest a need for roots to extend deeper to meet nutrient uptake requirements (Good et al., 1982). Therefore, Peltandra roots have probably adapted to fermentation which maintains a high root energy status (Mendelssohn and McKee, 1987) and results in sufficient production of ATP required for nitrogen and phosphorus uptake. If indeed fermentation is the major pathway for ATP synthesis in Peltandra roots, then the levels of photosynthate required would be more readily available following peak shoot biomass.

If it is correct that shoot and root productivity in Peltandra is supported primarily through the reallocation of nutrients stored in the

extensive rhizome component, then asynchronous root productivity, which is necessary despite the the cost of energy and nutrients in a limited environment (Bloome et al., 1985), may serve as a resupply mechanism for nutrients lost through leaching and death. In this manner, Peltandra maximizes the use nitrogen and phosphorus in biomass production which, in turn, maximizes photosynthate production required for tissue respiration and growth.

Total Productivity

The contribution of root productivity to total annual productivity in Peltandra is significant. In the current study root productivity accounts for approximately 50% of the total annual biomass productivity of 3202.44 g/m^2. Total annual productivity was significantly higher than the estimate of 1895.5 g/m^2 reported by Walker (1981) and somewhat lower than the annual estimate of 4438 g/m^2 reported for Peltandra by Good and Good (1976). Total annual productivity does, however, approach the level of 3749 g/m^2 reported by Good et al. (1975) (in Whigham et al., 1978). The apparent differences in these studies may be attributable to local environmental conditions, community structure, sampling technique, and inclusion of interval mortality, which demonstrates the need for standardization techniques in estimating total annual productivity (de la Cruz, 1978).

Root to shoot ratios (R:S), as well as belowground to aboveground ratios (B:A), also provide insight into biomass growth strategies of Peltandra. Generally, root to shoot ratios are higher in macrophytes which must compete for nutrients in a limited environment. Shaver and Melillo

(1984) reported higher R:S ratios in several macrophytes when nitrogen was limiting. The higher root to shoot ratios enable the plant to more efficiently compete for uptake of limited nutrients in an anaerobic environment by increasing the surface are of this belowground component (Shaver and Billings, 1975). Lower ratios are expected in shallow rooted perennials because they occur in the portion of the substrate that is not always anaerobic (Whigham and Simpson, 1978) or in perennials with extensive rhizome storage compartments which are capable of supporting a significant proportion of shoot nutrient demands via reallocation. The relatively low peak R:S ratio of 1.24 and mean R:S ratio of 5.16 support the contention that Peltandra supports the majority of shoot growth via rhizome reallocation and as such does not rely on de novo root uptake at this time. A higher peak B:A ratio of 4.12 and mean B:A ratio of 11.45 demonstrate the importance of rhizome biomass to Peltandra and help explain the ability of Peltandra to maintain robust, monotypic stands during periods of low root biomass. The peak B:A ratio observed in this study is significantly lower than the B:A ratio of 8.42 reported for Peltandra, but higher than the range of 0.55 to 3.64 reported for other perennial macrophytes (Whigham and Simpson, 1978).

Nitrogen Dynamics

Tissue Nitrogen Concentrations

Seasonal patterns of nitrogen concentrations in the tissues of Peltandra were similar to those observed by (Walker, 1981), as well as in other tidal freshwater macrophytes (Klopatek, 1975; Boyd, 1978; Richardson

et al., 1978). Shoot nitrogen concentrations reached a peak of 3.77% in May and declined steadily, although maintaining a relatively high concentration, through August. As such, the peak nitrogen concentrations occurred during the lag phase of shoot development and decreased with increased productivity. Boyd (1969, 1970) reported that nitrogen concentrations decreased in the shoots of Typha latifolia and Justicia americana as shoot biomass increased as did Mason and Bryant (1975) in Phragmites communis and Bernard and Solsky (1977) in Carex lacustris. This pattern of nitrogen concentration was also observed by Klopatek (1974, 1975) in several tidal freshwater macrphytes including Scirpus fluvitalis, Typha latifolia, and Carex lacustris. Klopatek referred to the early lag phase of shoot development in which nitrogen concentrations are high as Phase I at which time nitrogen is accumulated until favorable environmental conditions are reached. Walker (1981) observed similar patterns in Peltandra shoots with nitrogen concentrations decreasing from 3.10% in May to 1.66% in July.

This early concentration of nitrogen in apparent excess of required levels has been termed "luxury uptake" by Gerloff and Kromholtz (1966) and may represent an attempt by Peltandra to accumulate levels of nitrogen necessary to support the subsequent rapid growth phase. Hutchinson (1975), in an extensive review of tissue nutrient concentrations, accepts Gerloff and Kromholtz's (1966) estimate of 1.3% as the critical or minimum nitrogen concentration in plant tissue, below which biomass production is limited. Boyd (1969) and Kistritz et al. (1983) suggested that early shoot accumulation of nitrogen in excess of metabolic requirements together with decreased energy allocation for nutrient uptake during periods of rapid growth allow maximum energy input to shoot productivity. Walker (1981)

concluded that the early lag phase in shoot development in Peltandra which is accompanied by higher nitrogen concentrations is the result of reallocation of stored nitrogen from the rhizomes. As stored nitrogen is in the complex form, reallocation requires time for breakdown of these compounds and transport to the developing shoots.

The pattern of shoot nitrogen concentration in Peltandra is best explained in terms of nitrogen metabolic requirements. As the majority of nitrogen (75%) in shoot tissues is incorporated into chloroplasts (Chapin et al., 1987), the early high concentrations between March and May provide Peltandra with a sufficient supply of nitrogen for chlorophyll synthesis which, in turn, provides Peltandra with sufficient levels of photosynthate production. Chlorophyll synthesis, which requires the higher nitrogen concentrations, is apparently high during early periods of shoot development with the pigments subsequently available to meristimatic tissue under optimal environmental conditions (Boyd and Vickers (1971). The decrease in shoot nitrogen concentration between May and July represents a dilution by increasing biomass with the July level apparently the critical nitrogen concentration required by Peltandra. The decrease between July and August is most likely due to translocation to the rhizomes while the secondary increase in shoot nitrogen concentration observed in September coincides with a secondary period of new shoot recruitment observed at this time. As investment of nitrogen into chlorophyll should not exceed levels at which an alternative investment would yield greater returns (Chapin et al., 1987), this secondary increase in shoot nitrogen concentration represents an additional, and apparently necessary, investment of nitrogen into chloroplast and subsequent photosynthate production.

The relatively high shoot nitrogen concentrations maintained throughout the growing season in relation to other macrophyte species (Boyd, 1978; Kadlec, 1979) are probably best explained in terms of shoot morphology. As nitrogen is contained primarily in protoplasmic material in relation to cell wall supporting material, macrophytes like Peltandra with less cell wall supporting tissue would tend to maintain nitrogen at higher concentrations (Boyd, 1978). Morover, due to high levels of dark respiration required for maintenance and growth together with root and rhizome demands in shade intolerant plants, like Peltandra, high nitrogen concentrations are necessary for increased levels of carbon assimilation (Chapin, 1980).

Rhizome nitrogen concentrations followed somewhat similar patterns to those of the shoots decreasing from a high of 2.48% in January to a low of 0.16% in July. As such, rhizome nitrogen concentrations were relatively lower than that of the shoots due to the decreased demand for chlorophyll nitrogen. Based on the critical levels accepted by Hutchinson (1975), Peltandra rhizomes appear capable of storing nitrogen in excess of basic metabolic requirements and demonstrate the importance of this belowground component in the life cycle of Peltandra biomass production. The sharp drop in concentration between January and March and between April and May coincide with periods of shoot development, supporting the contention that the majority of nitrogen which supports shoot productivity is the result of rhizome reallocation rather than de novo root uptake. Apparently, between January and March nitrogen storage compounds are broken down within the rhizomes and reallocated to the shoot bases where they accumulate prior to shoot development. Breakdown and reallocation to both shoots and developing roots continues through August when minimum rhizome concentrations are

reached. The fact that August concentration is well below accepted critical levels of nitrogen required by plant tissues (Gerloff and Kromholtz, 1966; Hutchinson, 1975) demonstrates the ability of Peltandra to maintain an extensive rhizome component at relatively low nitrogen concentrations.

The increase in rhizome concentration between August and December is attributable to the translocation of nitrogen from senescing shoots. In addition, as root biomass increases between July and December, it is assumed that increases in rhizome concentrations during this time is the result of de novo root uptake. De novo root uptake, then, may serve primarily to replenish rhizome concentrations and explain, at least in part, the extremely high concentrations observed through the winter. As such, the rhizomes of Peltandra appear to act as a conserving mechanism through the storage of nitrogen in higher concentrations over the winter. The higher rhizome nitrogen concentrations subsequently allow maximum spring and summer shoot development, which in turn provide the roots and rhizomes with sufficient levels of photosynthate.

Bernard and Solsky (1977) observed similar trends in the rhizomes of Carex lacustris, however Walker (1981) observed less significant patterns in the rhizomes of Peltandra. Walker proposed that younger plants have higher nitrogen concentrations in the rhizomes while older plants may sustain comparable levels of metabolic activity with lower concentrations of rhizome nitrogen, resulting in relatively constant rhizome concentrations. Dykyjova and Hradecka (1976) reported that rhizome nitrogen concentrations in Phragmites decreased in the summer but increased to higher levels in the fall as did Prentki et al. (1978) in rhizomes of Typha latifolia. Similar patterns have also been observed by Davis and van der Valk (1983) who

demonstrated that up to 45% of nitrogen in the shoots of Typha glauca was translocated and stored in the rhizomes. Similarly, van der Linden (1980) reported that Phragmites recycled and stored internally up to 50% of the nitrogen from the shoots.

Root nitrogen concentrations demonstrated no discernible patterns over the sampling periods although concentrations were slightly higher at the onset of root development in July and decreased through October. This pattern may represent a type of luxury accumulation at root bases which supports initial root productivity. Decreased root concentrations between March and May, periods of root dieback, suggest that roots may translocate some levels of nitrogen to the rhizomes although this flux was not measured. Like rhizome nitrogen concentrations, root concentrations drop below accepted critical levels of plant tissues, suggesting that roots require nitrogen at relatively low levels in comparison to shoot tissues. Klopatek (1974, 1975) observed similar patterns of root nitrogen concentrations in several tidal freshwater macrophytes as did Walker (1981) in the roots of Peltandra. It is expected that root nitrogen concentrations would remain relatively stable in comparison to shoot and rhizome concentrations. As roots serve as conduits for nitrogen rather than temporary storage organs like shoots and rhizomes, nitrogen concentrations simply reflect growth patterns and not storage adaptations to a nitrogen limited environment.

Tissue Nitrogen Standing Stocks

While seasonal patterns of tissue nitrogen concentrations provide information on cycling, reallocation, and productivity strategies of Peltandra, tissue nitrogen standing stocks illustrate the quantitative

aspects of nitrogen dynamics. The correlation of nitrogen standing stocks with shoot biomass demonstrate the importance of biomass in regulating shoot nitrogen levels. Despite decreasing shoot nitrogen concentrations between May and July, shoot nitrogen standing stocks increase steadily to the observed peak in July, coinciding with peak shoot biomass. This suggests that increased shoot nitrogen standing stocks are not simply a result of the dilution of the early luxury accumulation of shoot nitrogen but rather the continued reallocation of nitrogen from the rhizomes necessary to support the observed levels of shoot productivity. Peak shoot nitrogen standing stocks occurring at peak shoot biomass suggests that Peltandra invests significant levels of nitrogen in productivity and subsequent photosynthate production under optimal environmental conditions.

Similar patterns of shoot nitrogen standing stocks have been reported for other tidal freshwater macrophytes. Klopatek (1975) reported a shoot nitrogen standing stock of 15.43 g/m^2 in a Scirpus fluviatilis stand and shoot nitrogen standing stocks of approximately 12.0 and 8.0 g/m^2 in Typha latifolia and Carex lacustris, respectively. Richardson et al. (1978) observed shoot nitrogen standing stocks at 6.2 g/m^2 in a leatherleaf and bog birch community while Walker (1981) reported peak shoot nitrogen standing stocks in Peltandra of 10.43 g/m^2 coinciding with peak shoot biomass. Boyd (1971) reported a peak nitrogen standing stock of 44.3 g/m^2 in Justicia americana although Boyd and Vickers (1971) point to the fact that nitrogen standing stocks do not necessarily coincide with peak standing stocks as with Eleocharis quadrangulata.

Shoot nitrogen standing stocks decreased steadily as with decreased shoot biomass. The decrease in monthly nitrogen standing stocks represent an apparent "switching" mechanism in the life cycle of tidal freshwater macrophytes in which nitrogen is translocated to the rhizomes during shoot senescence (Klopatek, 1975). Translocated nitrogen is subsequently available for storage or to support new shoot recruitment and root productivity. This "switching" mechanism is apparently used by Peltandra to support root productivity, which, in this study, is assumed to be asynchronous with shoot productivity. In this manner, then, increased shoot nitrogen standing stocks allow maximum photosynthate production, which in turn supports levels of observed productivity while decreased levels provide an adequate supply of nitrogen to the belowgound component.

As rhizome biomass is assumed to remain relatively constant throughout the year, rhizome nitrogen standing stocks are regulated by changes in nitrogen concentration, i.e. the strong correlation with concentration, rather than changes in biomass. Rhizome nitrogen standing stocks decreased significantly between January and March as complex nitrogen storage compounds are broken down and translocated to developing shoot bases. Walker (1981) reported a significant decrease in Peltandra rhizome nitrogen standing stocks between April and July, from 44.45 to 12.35 g/m^2, the majority of which was assumed to be translocated to the shoots and roots. The increase in April may be the result of de novo root uptake or nitrogen translocated during root senescence, although this flux was not measured. Rhizome nitrogen standing stocks then decreased steadily to the observed minimum in August.

Assuming rhizome biomass standing stocks to be relatively constant throughout the year, the extremely high levels in January demonstrate not only the importance of the concentration factor but also the role of the rhizome component in the storage of nitrogen. In this study, the relatively large decrease between January and May coincides with periods of "luxury" accumulation in the shoots, supporting the hypothesis that the majority of shoot productivity is supported by reallocation from the rhizomes. Similarly, assuming root productivity begins in July, the decrease in nitrogen standing stocks may also be attributed to reallocation to root growth. Using a maximum - minimum calculation, which does not include nitrogen translocated to the rhizomes by monthly shoot mortality, there is apparently sufficient nitrogen stored as "complex" nitrogen in the rhizomes to support the majority of shoot and root productivity, as will be demonstrated in the construction of the Peltandra nitrogen model. Similar rhizome nitrogen patterns have been observed by Kistritz et al. (1983), who concluded that Carex lyngbyei is capable of supporting shoot productivity entirely through rhizome reallocation of nitrogen. As a result, Peltandra need not face the stresses of waterlogged sediments and hydrogen sulfides for an adequate supply of nitrogen during periods of peak shoot development (Smith et al., 1979).

The increase in rhizome nitrogen standing stocks between August and December is assumed to be the result of nitrogen translocation during shoot senescence as well as de novo root uptake between July and January. The increases apparently represent the "switching" mechanism observed by Klopatek (1975) which provide sufficient nitrogen levels to support root productivity and rhizome metabolic requirements. Winter nitrogen standing

stocks represent "luxury" accumulation and are most likely in a "complex" storage form which is not readily available to the rhizomes. Rhizomes, then, act as a central processing unit of Peltandra, regulating compartmental nitrogen fluxes during periods of productivity and serving as a resovoir for nitrogen in the winter.

Root nitrogen standing stocks increased between August and December, coinciding with periods of root productivity. As root nitrogen concentrations remained relatively constant throughout the year, root nitrogen standing stocks are a function of biomass rather than concentration. This indicates that Peltandra roots serve as conduits for nitrogen rather than storage components. Oaks and Hirel (1985) suggested that root synthesis of amino acids, which may not be supplied by storage organs, is significant and therefore may represent a major portion of root standing stocks. Root nitrogen metabolism products are, in turn, used internally or transported through the rhizomes to the shoots. The investment of nitrogen in Peltandra root productivity is high. This may represent a necessary investment that insures an adequate absorption network for nutrient uptake to resupply rhizome nitrogen reallocated to the shoots and roots (Walker, 1981). Walker observed similar patterns in Peltandra roots with peak nitrogen standing stocks occurring at times of peak biomass.

Tissue Nitrogen Leaching

Annual leaching of shoot nitrogen was lower than expected in Peltandra shoots, representing only about 2% of total shoot uptake. The morphology of Peltandra shoots and leaves, which decompose rapidly, should result in relatively high leaching rates but require tidal cover. A computer

generated model, however, indicated that the leaves of Peltandra shoots, assumed to the major component involved in the leaching of nitrogen, were only covered by tidal waters a small percentage of the time during the summer. As such, little or no leaching was detectable during times of peak biomass. The majority of leaching occurred during the lag phase of shoot development in which the leaves were relatively small and supported by shorter stalks. Tukey (1970) suggested that nitrogen leaching rates at this time are greater due to the high levels of inorganic nitrogen in the intercellular spaces of leaves during spring growth or autumn senescence (in Chapin, 1980).

The lower than expected leaching rates have several implications in terms of nitrogen cycling. Leaching may not contribute the high levels of nitrogen to the surrounding waters as previously thought. Instead, the leaching of Peltandra occurs primarily in shoots and leaves which have fallen to the sediment surface and subsequently covered by tidal waters. Live shoots, then, may translocate more nitrogen to the rhizomes at senescence than to the surrounding waters. Klopatek (1975) reported significantly higher annual rates of nitrogen leaching in Scirpus fluviatilis which reached 7.34 g/m^2 or approximately 42% of shoot uptake while Kistritz et al. (1983) estimated annual nitrogen leaching in a Carex lyngbyei marsh at 2.7 g/m^2. These results indicate that some tidal freshwater macrophytes contribute significant levels of nitrogen to the surrounding waters through leaching and therefore have a greater impact on nitrogen cycling through this flux than does Peltandra.

Tissue Nitrogen Efficiency Indexes

The relationship between plant biomass and nitrogen standing stocks is best described in terms of use efficiency, or unit biomass produced per unit nitrogen used where as the relationship between between shoot nitrogen uptake and translocation at senescence is described in terms of recovery efficiency (Shaver and Melillo, 1984). The calculation of nitrogen use and recovery efficiency indexes in the plant tissues, together with tissue nitrogen dynamics, provide a better understanding of nitrogen cycling strategies in Peltandra, as well as other tidal freshwater macrophytes. Pastor (in Shaver and Mellilo, 1984) suggests two possible mechanisms which regulate nitrogen efficiency indexes; 1) changes in nitrogen concentrations in most or all plant tissues and 2) changes in biomass allocation. As a result, slower growing species would tend to have lower use efficiency due to higher nitrogen concentrations than species which are characterized by rapid growth. In Peltandra shoot, root, and rhizome tissues, use efficiency appears directly related to both nitrogen concentration and biomass allocation.

Nitrogen use efficiency in the shoots of Peltandra was significantly lower than in the roots and rhizomes. Bloom et al. (1985) demonstrated that plants use nitrogen most efficiently when nitrogen is limiting to the tissue although leaf potential photosynthatic nitrogen use efficiency increased with increasing nitrogen (in Chapin et al., 1987). The low use efficiency by Peltandra shoots indicates that they are unaffected by the apparently limiting sediment nitrogen levels suggesting that either Peltandra shoot nitrogen levels are independent of sediment nitrogen or that photosynthate demands simply require higher levels of nitrogen. Either of these possible explanations may result in the relatively low use efficiency of Peltandra

shoots in relation to other macrophytes (Shaver and Melillo, 1984). As approximately 75% of shoot nitrogen is linked to investment in chloroplasts and subsequent photosynthate production (Chapin et al., 1987), low nitrogen use efficiency by the shoots may represent a trade-off for required levels of carbon assimilation.

Peltandra shoot nitrogen use efficiencies were generally lower during the lag phase in shoot development and higher during June and July, at times of peak shoot standing stocks indicating that mature shoots use nitrogen more efficiently than the younger shoots. Lower shoot use efficiency is best explained in terms of rhizome reallocation and "luxury" accumulation of nitrogen by young shoots while the higher efficiencies are due to increased shoot biomass in relation to nitrogen. Lower use efficiency is expected when nitrogen is recycled through translocation (Vitousek, 1982) while higher use efficiency occurs when nitrogen availability becomes limited (Shaver and Melillo, 1984), both of which occur during Peltandra monthly shoot mortality and rhizome depletion, respectively. Use efficiency in June and July may therefore represent an "optimum" level of nitrogen assimilation and use by Peltandra shoots. Shaver and Melillo (1984) reported that nitrogen use efficiency decreased in Typha latifolia, Calamagrostis canadensis, and Typha latifolia between sampling intervals however use efficiency increased as nitrogen availability decreased. Mean nitrogen use efficiency was significantly higher in these three species than in Peltandra. This may be due, at least in part, to the use of whole plants by Shave and Melillo in the estimate of use efficiency indexes. The secondary increase in Peltandra shoot use efficiency in August supports Vitousek's (1982) explanation of increased nitrogen use efficiency during times of

shoot translocation while decreased levels of use efficiency in September is explained in terms of new shoot recruitment at this time. Finally, the low mean nitrogen use efficiency of Peltandra shoots conflicts with the suggestion of Shaver and Melillo (1984) that the most efficient plants become dominant. The dominant, monotypic stands of Peltandra observed in this study indicate that macrophytes with extensive rhizome nitrogen storage capacity may not require as efficient use as macrophytes which must rely more on de novo root uptake.

Peltandra rhizome nitrogen use efficiency was highest in August as rhizome nitrogen standing stocks were depleted through reallocation to the shoots and roots. The highest use efficiency apparently represents an optimum or critical level of nitrogen use by rhizomes while the low use efficiency in January demonstrates the importance this belowground component in nitrogen storage. The extensive supply of nitrogen, i.e the low use efficiency in the winter, in the rhizomes may explain the relatively low use efficiencies in the shoots as shoot development is not restricted by nitrogen availability. The higher mean use efficiency in the rhizomes indicate that the rhizome biomass requires extremely low levels of nitrogen in relation to biomass to support basic metabolic requirements when compared to the shoots. As winter rhizome nitrogen is assumed to be "complex" storage compounds, and not used by the rhizomes, actual use efficiency in the rhizomes may be higher in the fall and winter than those calculated. Peltandra rhizomes, however, represent the most efficient users of nitrogen and demonstrate their importance as a major component in nitrogen cycling and storage. Bloom et al. (1985) suggested that storage is directly related to storage costs and chemical conversion to specific storage compounds. In

Peltandra rhizomes the cost of storage may represent a necessary expenditure for the support of productivity at some future time or survival during times of stress. Root use efficiency, as expected, remained relatively constant although at a lower level than the rhizomes. As roots are generally not considered a storage organ but rather as a conduit nutrient uptake, use efficiencies should remain relatively constant.

Recovery efficiency in Peltandra shoots decreased steadily as shoot biomass increased, however mean recovery remained relatively high. Shaver and Melillo (1984) reported that recovery efficiency is directly related to sediment nitrogen availability while Turner (1977) suggested that as recovery efficiency increases shoot growth must depend less on de novo root uptake and more on reallocation. The relatively high recovery efficiency demonstrates that Peltandra conserves nitrogen in a limited environment and therefore depends more on rhizome reallocation to meet shoot and root demands. In this manner, Peltandra conserves energy which must otherwise be expended on root uptake. Lower recovery efficiency during times of peak shoot dieback may be in response to the extremely high levels of shoot nitrogen available for translocation at this time and suggests that Peltandra must adjust translocation levels to shoot biomass. The lower recovery efficiency during times of peak shoot biomass, however, results in significant levels of nitrogen lost to the environment through detrital flux and subsequent decomposition. As Peltandra shoots decompose rapidly (Odum and Heywood, 1978), dieback between July and August results in a significant level of nitrogen released to the sediments and surrounding waters. Nitrogen recovery indexes, then, dictate not only the levels of nitrogen conserved in Peltandra but also the levels of nitrogen which may be be

released to the environment and subsequently incorporated into sediments or flushed into the adjacent waterways.

Sediment Nitrogen

Marsh sediments are generally more fertile than upland sediments and differ primarily due to the anaerobic state throughout the sediment column with the exception of a thin oxidized layer at the sediment surface (Klopatek, 1978). Although Peltandra sediment inorganic nitrogen standing stocks, consisting of ammonium and nitrate, were relatively low throughout the sampling period, ammonium levels were significantly higher than nitrates due to the fact that anaerobic sediments maintain the reduced ions in relationship to their oxidized counterparts (Harter, 1966; in Klopatek, 1978). Seasonal patterns of ammonium standing stocks, which increased between March and August and again in October, are best explained in terms of anaerobic sediment chemistry. Mineralization of organic nitrogen to ammonium, rather than nitrate, occurs due lack of oxygen and ammonium may be incorporated into organic matter or undergo adsorption/desorption (Patrick and Mahapatra, 1968). The release through mineralization is, therefore, considered to be the major source of ammonium to anaerobic sediments (Patrick and DeLaune, 1980; Walker, 1981; Bowden, 1982), explaining higher fall and spring levels. Delaune and Patrick (1980) estimated that approximately 25 g/m^2/year of inorganic nitrogen was supplied through mineralization which was sufficient to support observed levels of macrophyte uptake while Walker (1981) estimated that a 1.17%/day mineralization rate in Peltandra sediments. Macrophyte uptake and incorporation into organic matter eleviates the buildup of sediment ammonium (Klopatek, 1974),

explaining the decreased levels between July and August when Peltandra root biomass increases. In addition, ammonium in the oxidized layer, as a result of oxygen moving through the overlying water column, is nitrified and the resulting ammonium concentration gradient across the aerobic layer causes ammonium in the anaerobic layer to diffuse upward where it also undergoes nitrification (Patrick and Reddy, 1976) resulting in relatively low ammonium standing stocks observed throughout the sampling period. This phenomenom, however, was not observed in this study as the 0-10 cm sediment layer includes approximately 9 cm of anaerobic sediment and, therefore, differences in ammonium and nitrate levels between the aerobic surface and the remaining anaerobic layers could not be detected.

Nitrate produced in the surface aerobic layer subsequently diffuses from the aerobic layer where it is denitrified to nitrogen gas or used as the terminal electron acceptor by bacteria (Patrick and Reddy, 1976). These observations are supported by Vanderborght and Billen (1975) who observed high levels of nitrate at the top several centimeters and decreasing levels in the organic-rich lower anaerobic layers. Nitrate levels in this study are so low, however, that denitrification may be of little consequence (Klopatek, 1978). Alternate pathways of nitrate include uptake by macrophytes where it may diffuse down to, and out of, roots (Ponnamperuma, 1972), entry into groundwater, and incorporation into organic matter (Klopatek, 1974) all of which explain the observed seasonal patterns of nitrate as well as the low nitrate standing stocks at depth.

Maintenance of relatively low inorganic nitrogen standing stocks in the sediments of Peltandra in relation to required uptake levels are best explained in terms of the total nitrogen levels. Total nitrogen levels in

freshwater sediments are generally high throughout the year while the inorganic form remains relatively low. In the current study total nitrogen levels are extremely high throughout the sampling period and are correlated with organic matter. High levels of total nitrogen in tidal freshwater sediments have been previously reported (Klopatek, 1975; Walker, 1981; Bowden, 1982) which are generally correlated with organic matter (Klopatek, 1978; Walker, 1981). A steady decrease, however, is observed throughout the growing season and into the senescent stage and, as a result, Peltandra sediment total nitrogen standing stocks decrease as ammonium levels increase. Boatman and Murray (1982) demonstrated that marsh organic-rich sediments, "a clay-humic complex", may, in fact, control ammonium adsorption and therefore availability. Rosenfield (1979) demonstrated that a "dynamic equilibrium" exists between dissolved, exchangeable and fixed ammonium in marine sediments and of the ammonium produced by the mineralization of organic matter, twice as much is associated with the sediments as is dissolved in the interstitial water.

In Peltandra sediments, therefore, the majority of nitrogen is apparently in the organic form, as indicated by the low levels of inorganic nitrogen, and associated with the sediments. The available inorganic pool may, in fact, be exaggerated due the extraction method used. The extraction method does not allow for discerning between ammonium and nitrate adsorbed to sediments and that in the interstitial water. Rosenfield's work, however, implies that the majority may be associated with the sediments resulting in lower actual standing stocks of readily available inorganic nitrogen. Chapin (1980) suggested that indeed it is sediment properties which control availability and root absorptive capacity. Seasonal patterns

and levels of sediment total and inorganic nitrogen standing stocks are similar to thos observed in other marsh sediments. The mean total pool of total nitrogen of 1892 g/m^2 observed in this study is similar to the level of 1696 g/m^2 observed by Klopatek (1975) in the top 30 cm of Scirpus fluvitalis sediments. Walker (1981) reported mean total nitrogen standing stocks of 192 and 204 g/m^2 at the 40-50 and 80-95 cm depths of Peltandra sediments. Richardson et al. (1978) estimated exchangeable nitrogen (ammonium + nitrate) at 2.17 g/m^2 (in Kadlec, 1979) and total nitrogen standing stocks at 683 g/m^2 in the top 20 cm of leatherleaf and bog birch sediments, both of which were lower than the mean values observed in this study. Haines et al. (1977) reported peak ammonium standing stocks of approximately 0.50 g/m^2 for the top 30 cm of high marsh soils between April and May, similar in pattern, however lower than the April level of 7.53 g/m^2 observed in this study. The higher total pools of sediment inorganic nitrogen observed in this study may also be explained by the fact that sediments were sampled to one meter.

Tissue-Sediment Nitrogen Relationship

The relationship between sediment and tissue nitrogen has been developed for several tidal freshwater macrophytes. Gosset and Norris (1971) demonstrated a positive correlation bewteen the nitrogen concentrations of Eichornia crassipes and the environment, however Boyd and Vickers (1971) were unable to correlate tissue-sediment nitrogen concentrations for Eichornia. Gerloff and Kromholtz (1966) reported that

angiosperm aquatic plants absorb nutrients in relation to environmental concentrations as did Klopatek (1975) who demonstrated strong correlations between sediment nitrogen and nitrogen accumulated in the above- and belowground standing crops of Typha latifolia, Scirpus fluviatalis, and Carex lacustris. Walker (1981) reported weak correlations between sediment total nitrogen and nitrogen in the shoots, roots, and rhizomes of Peltandra at two different sediment layers. Apparently, the relationship between sediment and tissue nitrogen levels is dependant on local sediment nitrogen chemistry as well as on individual species. Annual species are expected to demonstrate a stronger relationship since tissue production is strictly a function of de novo root uptake and dependant on sediment nitrogen availability (Walker, 1981), while perrenials with extensive rhizome storage mechanisms are probably less dependant on sediment availability and rely on reallocation to meet a significant portion of tissue nitrogen requirements.

Klopatek (1978) suggested that riverine marshes have evolved retentive mechanisms to maintain phosphorus within its internal cycle thereby slowing the flux from its boundaries. The same mechanisms may be used by tidal freshwater wetlands to retain nitrogen within the macrophyte community through translocation at senescence, extensive rhizome storage components, and root uptake. As has been previously discussed, the majority of sediment nitrogen is in the organic form and unavailable for uptake (Patrick and Reddy, 1980; Bowden, 1982). Moreover, as will be demonstrated in the construction of a nitrogen model for Peltandra, there appears to be sufficient nitrogen available in the rhizomes to support the majority of shoot and root productivity. As such, it is unlikely that Peltandra tissue nitrogen levels would be dependent on sediment nitrogen, resulting in weak

or insignificant correlations. Finally, it is unlikely that rapid periods of shoot productivity which have been demonstrated in Peltandra could be supported by de novo root uptake based on the energy expenditures required for active root uptake. Therefore, Peltandra shoot and root productivity are supported primarily by reallocated nitrogen from the rhizomes while root uptake is apparently used as a resupply mechanism for the rhizomes. This proposed nitrogen strategy in Peltandra has been supported by Kistritz et al. (1983) who demonstrated that all the nitrogen required for Carex lyngbyei shoot productivity is supplied by rhizome reallocation.

In this study no relationship was demonstrated between shoot, root, and rhizome nitrogen standing stocks and either inorganic or total sediment nitrogen. Peltandra would therefore appear to depend less on sediment nitrogen levels and more on the reallocation of rhizome nitrogen to support biomass productivity. This strategy would enable Peltandra to compete and reach maximum productivity levels in a harsh environment (Broome et al., 1975; Gallagher, 1975); Haines and Dunn, 1976) through its reliance on internal storage rather then sediment availability. This independence on sediment nitrogen levels enable Peltandra to maintain a stable community in a resource limited environment while maximizing production levels. Maximum shoot productivity, in turn, supplies sufficient levels of photosynthate to the roots and rhizomes for growth and maintenance which allows Peltandra to maintain a stable belowground component.

Nitrogen Model

Several methods are available for directly measuring plant compartmental nitrogen fluxes, however these methods produce cumulative

errors when extrapolating from short term uptake to seasonal accumulation (Prentki et al, 1978). As a result, monitoring the changes in seasonal nitrogen standing stocks in macrophytes may provide the best estimation although sampling frequency in species with relatively rapid growth rates such as Peltandra will affect the final calculation of fluxes. Annual compartmental fluxes must be interpreted on a qualitative basis due to the inherent problems with data collection, analysis, and interpretation, however, the quantitative assessment of annual nitrogen compartmental flows provide insight into the nitrogen uptake, assimilation, reallocation, and storage capacity of Peltandra. To date, however, relatively few models of tidal freshwater macrophytes are available which depict annual nitrogen standing stocks as well as compartmental flows although several studies have attempted to quantify annual nitrogen fluxes for domimant macrophyte species (Kloptaek, 1975; Richardson et al., 1978; Walker, 1981; Kistritz et al., 1983; Heckman, 1986).

The nitrogen model for Peltandra illustrates the impact of perennials with an extensive rhizome storage component and high seasonal biomass productivity. The annual shoot uptake of 44.05 g/m^2 is approximately four times the annual shoot uptake of 10.11 g/m^2 reported for Peltandra by Walker (1981) and three times that of 15.9 g/m^2 for Carex reported by Bernard and Solsky (1977). Klopatek (1975) reported an annual shoot uptake of 17.46 g/m^2 in a Scirpus fluviatilis stand. Higher annual shoot uptake by Peltandra in this study is best explained in terms of annual shoot productivity and nitrogen demands, which are apparently higher than in previous studies. Leaching rates of 0.83 g/m^2/year were lower than expected

due to the lack of tidal cover on the creek bank and therefore does not represent a significant release to the environment during periods of shoot productivity. Klopatek (1975) reported much higher leaching rates in Scirpus with approximately 42% of shoot uptake, or 7.34 g/m^2/year lost to the surrounding environment in this manner while Kistritz et al. (1983) reported an annual nitrogen leaching rate of 2.7 g/m^2 for Carex.

The loss of 24.73 g/m^2 to the detrital component represents a significant level of nitrogen released to surface sediments and adjacent tidal waters. This is due to the rapid decomposition rates of Peltandra (Dunn, 1978; Odum and Heywood, 1978). Although it would be of interest to determine what percentage actually is recovered by the sediments during decomposition in relation to that lost to adjacent waters, this measurement is difficult and was not attempted. The levels of sediment total nitrogen which were correlated with organic matter, however, suggests that certain levels of nitrogen from the detrital component may be retained through sedimentation and undergo subsequent mineralization. Recovery of approximately 43%, or 19.32 g/m^2/year, of annual shoot uptake through translocation at senescence demonstrates the importance of nitrogen conservation in what is considered a nitrogen limiting environment. Conservation of nitrogen in this manner provides an adequate supply of nitrogen for new shoot recruitment and root growth and explains, at least in part, the independence of Peltandra on sediment nitrogen availability. High levels of nitrogen conservation through translocation have been observed in other macrophyte species (Gallagher, 1975; Broome et al, 1975; Valiela et al., 1975; Klopatek, 1975; Kistritz et al., 1983). Klopatek

(1975), however, reported low nitrogen recovery. approximately 11% of shoot uptake, through translocation by Scirpus while Walker (1981) observed insignificant levels of nitrogen recovery by Peltandra shoots. Davis and van der Valk (1978) reported an annual recovery through translocation of 9.60 and 2.56 g/m^2 in Scirpus fluviatilis and Typha glauca, respectively.

The belowground component is also involved in significant levels of nitrogen uptake, internal cycling, and release to the environment. As previously discussed, nitrogen stored in the rhizomes during the winter appears sufficently high, based on a maximum - minimum calculation, to support the majority of shoot and root productivity. As such it is hypothesized that the majority of nitrogen required for biomass productivity is reallocated form the rhizomes rather than from de novo root uptake although the level of root biomass standing stocks throughout the year suggest at least some levels of uptake during the growing season. This hypothesis is supported by the weak correlation observed between shoot and sediment nitrogen, the levels of energy which would be required for de novo root uptake during periods of rapid shoot development (Clarkson, 1985), and the low nitrogen use efficiency by Peltandra shoots. As such, the majority of nitrogen reallocated from the roots to the rhizomes, estimated at 41.11 g/m^2/year, is assumed to occur mainly in the fall and winter during periods of root productivity.

Rhizome reallocation to the roots of 15.55 g/m^2 is assumed to be either nitrogen which has been previously stored or nitrogen translocated during monthly shoot mortality. In this manner, Peltandra may most efficiently cycle nitrogen internally and rely less on root uptake. Nitrogen loss to

the sediments, estimated at 15.60 g/m^2 annually, during periods of root dieback represents an overestimation, based on an annual cycle, due to the relatively low decomposition rates of roots and rhizomes in an anaerobic environment (Hackney and de la Cruz, 1980; Good et al., 1982) and the fact that translocation to the rhizomes during root senescence was not estimated. As a result, the majority of nitrogen in decaying roots may remain unavailable for extended periods of time. Walker (1981) reported significantly lower fluxes to the sediments during dieback of Peltandra roots at 8.66 g/m^2 while Klopatek (1975) estimated annual losses to the sediment at 5.08 g/m^2 in a Scirpus fluviatilis stand. Annual root uptake of 41.15 g/m^2 demonstrates the role of Peltandra in removing nitrogen from the sediments and is significantly higher than uptake levels reported for additional macrophytes (Klopatek, 1975; Richardson et al., 1978; Walker, 1982; Kistritz et al., 1983). As ammonium is generally the preferred nitrogen ion (Chapin et al., 1987), Peltandra apparently regulates sediment ammonium levels (Klopatek, 1974). The levels of root uptake also demonstrate the importance of mineralization of organic matter in maintaining sufficient ammonium standing stocks to support observed levels of uptake. The investment in root productivity, although substantial, is therefore necessary to meet nitrogen demands due to the fact that low levels of ammonium and nitrate are quickly depleted at the root interface (Chapin et al., 1987).

Phosphorus Dynamics

Tissue Phosphorus Concentrations

Seasonal patterns of tissue phosphorus concentrations were similar to those observed in Peltandra by Walker (1981) as well as in other tidal freshwater macrophytes (Klopatek, 1974,1975; Brinson and Davis, 1976; Prentki et al., 1978; Bernard and Hankinson, 1979; Kistritz et al. , 1983). Prentki et al. (1978) suggested that critical phosphorus concentrations, usually indicated by minimum seasonal concentration, represent internal concentrations above which plant biomass is no longer limited. Phosphorus concentrations above this level, then, represent "luxury uptake" which are in excess of the plants' needs (Gerloff and Kromholtz, 1966). These limits have not been established for all aquatic plants although Hutchinson (1975) accepts Gerloff and Kromholtz's (1966) estimate of 0.13% as the critical or minimum concentration of phosphorus in plant tissue (in Kadlec, 1979). As such, Peltandra tissue concentrations generally remain above the critical level, with the exception of rhizome concentration in August, and either represent concentrations in excess of tissue requirements or a higher phosphorus demand of Peltandra tissues for carbon assimilation and energy necessary to support observed biomass levels.

In the current study, shoot phosphorus concentrations increased from 0.40% in March to a peak of 0.65% in April followed by a decrease to a low of 0.27% in August. A secondary increase in shoot phosphorus concentration was observed in September, a period of new shoot recruitment. Phosphorus concentrations during the lag phase in shoot development apparently represent accumulation at levels greater than that required by young shoots. As phosphorus is a major constituent of the energy compound ATP, nucleic acids, and cell wall phospholipids, the early accumulation of phosphorus

represents an attempt by Peltandra to concentrate phosphorus at sufficient levels to support the subsequent rapid growth phase between May and July. In this manner, Peltandra shoots have a readily available phoshorus supply for ATP synthesis during the light reactions as well as structural components. Klopatek (1975) observed similar phosphorus concentration patterns in shoots of Scirpus fluviatilis which he considered Phase I, or a lag phase concentration, as did Kistritz et al. (1983) in Carex lyngbyei shoots. Bernard and Hankinson (1979) reported decreasing phosphorus concentrations in aging shoot tissues of Carex rostrata as did Brinson and Davis (1976) in shoot tissues of Nuphar luteum.

It seems that higher concentrations of phosphorus in young, developing shoots of aquatic macrophytes are a common phenomenom and represent an adaption which provides these plants with some type of competitive advantage in terms of growth and stability. The most likely explanation is that higher phosphorus concentrations observed in Peltandra shoots are the result of reallocation from the rhizomes and not from de novo root uptake. Assuming phosphorus is stored as "complex" compounds (Walker, 1981), the lag phase in shoot development allows time for these compounds to be broken down and translocated to the developing shoot bases. The higher concentrations, in turn, support the rapid periods of shoot growth. As such, phosphorus is directed to shoot productivity and allow maximum use of sunlight in the synthesis of ATP and subsequent use of this energy compound in the assimilation of carbon. The increased availability of phosphorus also allows sufficient cell wall synthesis to support growth patterns which inhibit establishment of other species. The secondary increase observed in

September represents an additional, and apparently necessary, investment of phosphorus in carbon assimilation required by the belowground component.

Peltandra rhizome phosphorus concentrations decreased during periods of peak shoot and initial root productivity and increased during periods of shoot senescence and maximum root productivity. The higher rhizome concentrations prior to the onset of shoot development are the result of "complex" phosphorus storage compounds which must be broken down prior to reallocation to the shoots. Rhizome phosphorus concentrations in the winter and spring, then, represent a "luxury" accumulation and therefore are considered as phosphorus compounds which may not actually be used by the rhizomes but rather for the support shoot and root productivity. As such, phosphorus concentrations decrease as shoot and root biomass increase, and are assumed to represent continued reallocation, while minimum phosphorus concentrations demonstrate the relatively low actual phosphorus requirements of rhizomes. The increase in rhizome phosphorus concentrations between August and December represent phosphorus conserved through shoot translocation as well as de novo root uptake while increases between March and April may be the result of phosphorus translocated to the rhizomes during root senescence or additional root uptake. Asynchronous shoot and root growth periods, therefore, may represent the most efficient use of phosphorus by Peltandra tissues by concentrating this nutrient prior to shoot and root development and using shoot translocation and root uptake to resupply rhizome concentrations for the following year.

Walker (1981) reported similar patterns in the rhizomes of Peltandra as did Klopatek (1975) in the roots and rhizomes of Carex lacustris and Scirpus fluviatilis. The higher phosphorus concentrations appear to be common in

perennials with relatively large rhizome storage compartments and demonstrate the importance of this component to the stability of macrophytes. By concentrating phosphorus prior to periods of biomass productivity, perennials, such as Peltandra, rely primarily on reallocated rhizome phosphorus rather then expend significant levels of energy on nutrient absorption during peak shoot productivity and allow more energy to be allocated towards dry matter production (Boyd, 1969; in Kistritz et al., 1983).

Peltandra root phosphorus concentrations remained relatively constant although a slight decrease in concentration was observed between March and June and between July and September. The secondary decrease is assumed to be the result of increased root productivity. This would suggest that roots may concentrate certain levels of phosphorus at developing root bases sufficient to support observed levels of root productivity, which are subsequently diluted with increasing root biomass. Assuming that root phosphorus is derived primarily through rhizome reallocation and that roots are not a storage organ but rather a conduit for phosphorus, phosphorus concentrations should remain relatively constant. Mean phosphorus concentrations demonstrate the relatively equivalent demands of shoot, roots, and rhizomes for phosphorus. Walker (1981) observed similar patterns in Peltandra roots with phosphorus concentrations decreasing between March and July, although Walker assumed root productivity coincided with that of the shoots.

Tissue Phosphorus Standing Stocks

Although seasonal patterns of tissue phosphorus concentrations provide insight into relative phosphorus cycling strategies of Peltandra, tissue phosphorus standing stocks demonstrate the quantitative aspects of phosphorus dynamics. The strong correlation between shoot phosphorus biomass standing stocks illustrates that effect of biomass on phosphorus standing stocks. The relatively small increase in shoot phosphorus standing stocks between April and May may be best explained as a dilution of higher phosphorus concentrations observed during the lag phase in shoot development. The significant increase in shoot phosphorus standing stocks between May and July, however, coincide with decreasing phosphorus concentrations and are the result of increased shoot biomass and continued reallocation from the rhizomes. The increase in phosphorus standing stocks is the result of the increased demand of shoot productivity for energy in the form of ATP as well as cell wall.

Phosphorus is generally stored in the vacuoles as simple storage compounds or converted to phytic acid which, in turn, can transfer phosphorus to ADP during the synthesis of ATP during the light reaction (Bieleski, 1973). Peak shoot phosphorus standing stocks coincide with peak shoot biomass indicating the maximum demand for phosphorus during periods of maximum carbon assimilation. As a result, Peltandra shoots maximize optimum environmental conditions for the production of photosynthate for shoot respiration as well as translocation to belowground components. This allows sufficient photosynthate for belowground cellular respiration, which, as previously discussed, depends on high levels of substrate for anaerobic respiration. Decreased standing stocks between July and August represents a

"switching" mechanism in which phosphorus reserves are reallocated from senescing shoots to the rhizomes (Klopatek, 1975).

Apparently this pattern of shoot phosphorus standing stocks is common in tidal freshwater macrphytes. Walker (1981) observed similar patterns in the shoots of Peltandra with a peak phosphorus standing stock of 2.00 g/m^2 coinciding with peak shoot biomass. Klopatek (1975) observed an identical peak phosphorus standing stock of 3.33 g/m^2 in a Scirpus fluviatilis stand. Brinson and Davis (1976) also observed an increase in phosphorus standing stocks to a peak of 0.197 g/m^2 followed by a decrease during shoot dieback in Nuphar luteum. Boyd (1971) reported shoot phosphorus standing stocks of 2.8 g/m^2 for Justicia americana while Brinson and Davis (1976) reported a much lower level of 0.197 g/m^2 in Nuphar luteum (in Kadlec, 1979). This pattern of shoot phosphorus standing stocks increases related to, and often coincing with periods of peak shoot productivity, followed by a "switching" mechanism in which phosphorus standing stocks decrease as a result of shoot dieback and phosphorus translocation, represent the most efficient use of phosphorus by Peltandra.

As Peltandra rhizome biomass is assumed to remain relatively constant throughout the year, rhizome phosphorus standing stocks are regulated by changes in phosphorus concentrations. Due to the fall translocation of phosphorus from the shoots and root uptake between August and December rhizome standing stocks increased from the minimum observed in August. A peak rhizome phosphorus standing stock, however, was observed in April at the onset of shoot development and is best explained in terms of root uptake or translocation by senescing roots. The high phosphorus standing stocks

observed in April are certainly in excess of rhizome requirements. It is expected, then, that these standing stocks represent either "complex" phosphorus storage compounds which are not actively incorporated into rhizome tissue or simple uptake compounds. Rhizome phosphorus standing stocks decreased significantly between April and August during periods of maximum shoot and initial root productivity. As it has been hypothesized that Peltandra shoot and root productivity are supported primarily from rhizome reallocation rather than de novo root uptake, decreases in rhizome phosphorus standing stocks are considered to be the a result of breakdown and translocation.

As will be demonstrated in the construction of a model depicting annual compartmental fluxes, there are sufficient phosphorus standing stocks, due to conservation of phosphorus through translocation and asynchronous root uptake, to support both shoot and root productivity. The ability of Peltandra to support productivity through reallocation allows maximum investment of phosphorus into carbon assimilation rather than in the ATP required for de novo root uptake. In this manner, Peltandra utilizes energy most efficiently and is able to maintain robust monotypic stands.

This pattern of rhizome phosphorus standing stocks is similar to those reported for other perennial macrophytes. Walker (1981) observed a significant decrease in rhizome phosphorus standing stocks between June and July, coinciding with shoot productivity. Walker attributed this decrease to reallocation to the shoots. Klopatek (1975) also observed this pattern in several tidal freshwater macrophytes as did Brinson and Davis (1976) in Nuphar luteum. Kistritz et al. (1983) reported an inverse relationship between phosphorus standing stocks in the shoots and rhizomes of Carex

lyngbyei as a result of rhizome reallocation for shoot growth and shoot translocation at senescence. This pattern of rhizome phosphorus standing stocks emphasize the importance of the rhizome component in phosphorus cycling which allows the most efficient use of phosphorus in carbon assimilation and root uptake.

As root phosphorus concentrations remain relatively constant, seasonal patterns of root phosphorus standing stocks are the result of seasonal biomass patterns. Root phosphorus standing stocks increased during periods of root productivity and decreased during senescence. This pattern illustrates the role of Peltandra roots as a conduit for phosphorus rather than as a storage component.

Tissue Phosphorus Leaching

Leaching rates of phosphorus from Peltandra shoots was relatively low in comparison to rates observed in other tidal freshwater macrophytes. On the assumption that the majority of phosphorus leached is from the leaves, higher leaching rates were expected due to the morphology of Peltandra leaves, however the lack of tidal cover during times of peak shoot biomass resulted in the observed rates. The majority of leaching, therefore, occurred during the lag phase in shoot development and dieback in the fall when tide levels were sufficiently high to cover shoot biomass, however little or no leaching occurred when the leaves were at their maximum size. The majority of leaching may therefore occur when shoots fall to the sediment surface. As such phosphorus leaching may represent a minor flux from Peltandra shoots to sediments and adjacent waters. Klopatek (1975)

reported significantly higher annual phosphorus leaching rates of 2.20 g/m^2, or 60% of shoot uptake, from the shoots of Scirpus fluviatilis.

Tissue Phosphorus Efficiency Indexes

The relationship between biomass and phosphorus standing stocks is best described in terms of use efficiency while the ability of Peltandra to conserve phosphorus in relation to biomass is best described in terms of recovery efficiency. The calculation of phosphorus use and recovery efficiency indexes help define the role of Peltandra in the cycling of phosphorus. Mean shoot use efficiency was significantly lower than both roots and rhizomes with monthly shoot use efficiency relatively lower during the lag phase in shoot development and increasing during periods of maximum shoot biomass and initial periods of senescence. Low shoot use efficiencies may be best explained in terms of the "luxury" accumulation of phosphorus during the early periods of shoot development. Higher use efficiency at peak biomass represents the optimum level of phosphorus use efficiency by Peltandra shoots when phosphorus concentrations are at a critical level in realtion to biomass.

Shaver and Melillo (1984) suggested that phosphorus use efficiency decreases when phosphorus availability increases. The low use efficiency in Peltandra shoots, in relation to other macrophytes (Shaver and Melillo, 1984) suggests that phosphorus is not limiting to the shoots as a result of rhizome storage and reallocation. The higher use efficiency during at peak shoot biomass may be the result of decreasing levels of available phosphorus in the rhizomes as well as the dilution of the early luxury accumulation of phosphorus by the shoots.

Mean rhizome use efficiency was significantly higher than that of the shoots. As rhizome biomass was assumed relatively constant throughout the sampling period, use efficiency is attributable to the changes in phosphorus concentrations and standing stocks. The relatively low rhizome use efficiency in April are the result of the "luxury" accumulation of stored phosphorus compounds. As shoot productivity increases, complex phosphorus compounds are broken down and reallocated to the developing shoot bases and to the roots. Rhizome use efficiency then increases to an optimum level in August as rhizome phosphorus supplies are depleted. The optimum efficiency in August demonstrates the ability of Peltandra rhizomes to support significant levels of biomass on relatively low standing stocks of phosphorus. Low rhizome use efficiency, on the other hand, is directly related to phosphorus storage and costs (Bloom et al., 1985) and represents a trade-off for a readily available supply of phosphorus. As expected, root use efficiency remained relatively constant throughout the sampling period, reaching an apparent optimum level between September and December.

Recovery efficiency decreased significantly as shoot productivity increased. The minimum recovery efficiency observed during periods of maximum shoot biomass suggests that Peltandra must adjust translocation levels to shoot biomass. By adjusting recovery to the level of shoot biomass, Peltandra rhizomes allow for maximum phosphorus conservation within the assimilative and storage capacity of the rhizomes. Lower recovery efficiency at peak biomass, however, results in significant levels of phosphorus released to the environment through the detrital compartment and subsequent decomposition. Shaver and Melillo (1984) observed similar

recovery patterns in Carex with mean recovery efficiency decreasing between sampling periods.

Sediment Phosphorus

Generally, levels of dissolved inorganic phosphorus in flooded soils and marsh sediments depend on the capacity of the sediments to release phosphate to solutions low in phosphorus and adsorb it from solutions high in phosphorus which, in turn, determines whether orthophosphate in interstitial waters is sufficient to meet plant requirements (Patrick and Khalid, 1974). For this reason, exchangeable phosphorus is considered as the available pool (Carignan and Flett, 1981) with freshwater sediments serving as a phosphorus sink through anion exchange (Klopatek, 1974). Phosphorus anion exchange capacity is, in turn, determined by the chemistry of submerged, anoxic sediments. In submerged sediments there is an increase in solid materials that react with phosphorus with phosphorus movement depependent on ph, redox potential, and iron levels (Klopatek, 1974). Release of phosphorus is therefore due to the capacity of reduced iron hydroxides to sorb and release phosphate, with adsorption to ferric hydroxides resulting in the immobilization rather than precipitation (Patrick and Khalid, 1974). Khalid et al. (1977) demonstrated the importance of phosphate adsorption in estuarine sediments suggesting that this may be the controlling factor. Ponnamperuma (1972), in fact, reported that up to 75% of total sediment phosphorus may be retained as inorganic phosphorus in this manner. The immobilization of phosphorus in this manner explains, at least in part, the high levels of observed phoshorus in freshwater sediments (Klopatek, 1975).

Immobilization and release of phosphorus are controlled by several interacting mechanisms. Submergence changes highly insoluble ferric phosphates to the more soluble form (Ponnamperuma, 1972). Williams et al. (1971) demonstrated that under anaerobic conditions more iron in the Fe^{+2} state is in solution, with phosphate adsorbed onto a iron complex exchanging freely with solution (in Patrick and Khalid, 1974). This due to the reduction of ferric hydroxides to soluble Fe^{+2} which is less efficient at adsorbing phosphate (Emerson, 1976; in Krom and Berner, 1981). Therefore, in anaerobic sediments, such as those of Peltandra, lack of oxygen results in increased levels of dissolved orthophosphate. Phosphate is also released to solution as sediments pass through a redox boundary and iron hydroxides are converted to FeS and FeS_2 (Krom and Berner, 1980), illustrating the role of sulfates, which were observed in Peltandra sediments at lower depths, in regulating phosphate levels. Anaerobic sediment organic matter also control sediment phosphorus levels. Organic rich sediments produce dissolved phosphate which accumulates in pore water and may diffuse out, adsorb onto sediments, or precipitate out in discrete mineral phases (Krom and Berner, 1981). Krom and Berner demonstrated that a large proportion of dissolve phosphate in the top 10 cm, or bioturbation zone, is provided by the release of adsorbed phosphate during reduction of ferric hydroxides while below this zone phosphate is released solely through the decomposition of organic matter. Levels of sediment phosphorus may also be the result of release to overlying waters when water-sediment gradients are sufficient (Patrick and Khalid, 1974) although this flux may be minimal due to the adsorptive capacity of sediments. Conversely, adsorption to clay particles in

overlying waters, followed by deposition on the sediment surface and subsequent sedimentation contribute to higher sediment phosphorus levels (Brock et al., 1983). The ability of anaerobic sediments to maintain phosphorus in pore water and adsorbed onto sediments led Klopatek (1975) to suggest that freshwater wetlands may have evolved retentive mechanisms for retaining this often limiting nutrient. These retentive mechanisms may involve tissue storage as well as sediment chemistry, slowing the flux of phosphorus outwards (Klive-Howard Williams, 1985). This results in apparent "luxury" accumulation of phosphorus which may serve as a buffer to changes in an sediment chemistry.

Inorganic phosphorus in the sediments of Peltandra were relatively high throughout the sampling period suggesting that adsortion is high as well as immobilization with ferric hydroxides, maintaining high levels of available phosphorus. Inorganic levels, reported as the sum total for all sediment layers to one meter, demonstrated a pattern of decrease during periods of increased total phosphorus levels and maximum shoot productivity suggesting that orthophosphate may be incorporated into organic matter or taken up by the roots. Inorganic phosphorus increased as total phosphorus decreasd and following shoot dieback possibly as a result of decomposition of organic matter and detritus. Walker (1981) reported significantly lower levels of Bray P-1 inorganic phosphorus standing stocks in Peltandra sediments while Klopatek (1975) reported similar high levels of inorganic phosphorus in thensediments of Scirpus fluviatilis reaching 12.1 g/m^2 in the top 30 cm.. Total phosphorus levels were also relatively high throughout the sampling period suggesting phosphorus is also retained in freshwater sediments through incorporation into organic matter.

Tissue-Sediment Phosphorus Relationship

Several authors have reported a positive correlation between sediment and plant tissue phosphorus levels (Gerloff and Kromholtz, 1966; Gosset and Norris, 1971; Klopatek, 1978) while others (Boyd and Vickers, 1971; Walker, 1981) have reported weak or insignificant correlations. While it is expected that annuals, which rely on de novo root uptake to supply phosphorus to plant tissues, should demonstrate a strong correlation with sediment phosphorus levels, perennials with extensive rhizome storage capacity are apparently less dependent on sediment phosphorus levels due to reallocation from rhizomes. By relying more on reallocation than de novo root uptake, perennials like Peltandra are less dependant on sediment phosphorus levels and expend less energy on root uptake during periods of peak shoot and root productivity. In this way, Peltandra maximizes photosynthate production while maintaining stability in a harsh environment.

In this study, weak or insignificant correlations were observed between Peltandra tissues and sediment phosphorus. Unlike nitrogen, which appears to be the limiting nutrient in Peltandra sediments, sediment inorganic phosphorus levels are relatively high and appear capable of supporting seasonal patterns of biomass productivity. As significantly high levels of phosphorus are readily available, it seems unlikely that Peltandra tissues are independent of sediment phosphorus levels based on availability but rather on energy demands of shoot biomass. It would seem energetically inefficient for Peltandra to invest significant levels of phosphorus into the ATP levels required for uptake during periods of peak shoot productivity, a time at which phosphorus is required at high levels to support carbon assimilation. As will be demonstrated in the phosphorus

model, Peltandra appears capable of supporting shoot and root productivity through reallocation of stored rhizome phosphorus which may explain the independence of Peltandra tissues on sediment phosphorus levels.

Phosphorus Model

Although the Peltandra phosphorus model must be interpreted on a qualitative basis, the quantitative assessment of annual phosphorus standing stocks and compartmental fluxes provide insight into uptake, assimilation, reallocation, and storage of phosphorus. Despite the information provided by modelling annual compartmental phosphorus fluxes, relatively few models for tidal freshwater macrophytes are available. Models which are available demonstrate impact of the macrophyte community on regulating phosphorus fluxes (Klopatek, 1975; Richardson et al., 1978; Prentki et al., 1978; Walker, 1981; Kistritz et al., 1983; Heckman, 1986).

The annual uptake of 6.24 g/m^2 by Peltandra shoots is approximately three times that reported by Walker (1981) by shoots of Peltandra and three times that of 1.9 g/m^2 by shoots of Carex (Bernard and Solsky, 1977). sediments. Prentki et al. (1983) estimated annual shoot uptake at 3.2 g/m^2 Typha latifolia while Klopatek (1975) reported annual phosphorus uptake at 3.77 g/m^2 in a Scirpus fluviatilis stand. Richardson et al. (1978) estimated aboveground uptake at 1.7 g/m^2/year in leatherleaf and bog birch vegetation. Shoot uptake, then, appears to be species dependant with levels of shoot uptake dependent on productivity and sediment availability. Phosphorus uptake by Peltandra shoots illustrates the role of seasonal shoot productivity in the temporary storage, use in photosynthate production, and

potential availability to leaching and detritus. As previously discussed, shoot phosphorus leaching was relatively insignificant due to the lack of tidal cover during periods of peak shoot biomass and the fact that phosphorus may be incorportaed into compounds not readily leached from the leaves. Klopatek (1975) reported significantly higher annual leaching rates of 2.20 g/m^2 from the shoots of Scirpus fluviatilis as did Kistritz et al. (1983) of 0.89 g/m from shoots of Carex.

Annual phosphorus fluxes to detritus of 3.38 g/m^2 represent a significant flux to the environment. As decomposition rates of Peltandra are rapid (Odum and Heywood, 1978), detrital losses result in seasonal phosphorus pulses to both sediments and adjacent waters. Klopatek (1975) reported lower levels of detrital phosphorus loss at 1.13 g/m^2/year in Scirpus while Walker (1981) estimated losses to detritus in Peltandra as approximately equal to shoot uptake. Conservation of phosphorus through translocation at senescence was relatively high at 44% and supports Klopatek's (1978) contention that wetlands have evolved mechanisms for retaining phosphorus within it's boundaries. Through tranlocation Peltandra replenishes rhizome phosphorus supplies throughout the growing season which may be used to support new shoot recruitment, rhizome metabolic requirements, and asynchronous root growth. In addition, conservation of phosphorus through translocation provides phosphorus for storage and availability for spring productivity. Klopatek (1975) reported significantly lower translocation rates in Scirpus of 0.44 g/m^2, or 11% of annual shoot uptake, while Prentki et al. (1983) estimated translocation from the shoots at 23% of peak shoot standing stock. Kistritz et al. (1983)

estimated translocation at slightly higher rates accounting for approximately 50% of annual shoot uptake.

Annual flux from the roots to the rhizomes approximates annual root uptake and as such demonstrates that the roots serve mainly as a conduit for phosphorus resupply for the rhizomes rather than a storage mechanism. Walker (1981) reported similar annual phosphorus fluxes of 8.03-8.12 g/m^2 in Peltandra. Losses to the environment from root dieback may be overestimated as translocation to the rhizomes at senescence was not estimated. Similarly, as the decomposition of roots is relatively slow (Hackney and de la Cruz, 1980; Good et al., 1982) the losses, based on the assumption of steady state may actually occur over an extended period of time. The transfer of 4.76 g/m^2 from the rhizomes to the roots represents a significant input of phsophorus in root productivity most of which is incorporated into cell walls and ATP required for root uptake. Annual uptake of 8.61 g/m^2 from the sediments represents a significant removal from the sediments most of which is assumed to be translocated to the rhizomes. This assumption is supported by the fcat that uptake by newly developed roots is passed on through older roots to the transpirational stream to the rhizomes or shoots (Bieleski, 1973). Klopatek (1975) reported lower uptake rates by Scirpus at 5.33 g/m^2/year.

Nitrogen-Phosphorus Relationship

Correlation analysis of tissue nitrogen and phosphorus levels of Peltandra indicated a strong standing stock relationship between these nutrients. The significant correlations suggest an interaction between

nitrogen and phosphorus as they are cycled through the shoots, roots, and rhizomes. It would appear that Peltandra biomass requires nitrogen and phosphorus in certain proportions for metabolic and growth processes and therefore reallocation of these nutrients occurs in relative proportions to demand. The best explanation may be that nitrogen and phosphorus are required in certain proportions chloroplast, energy, and cell wall synthesis during individual phases of plant development. Microbial and chemical processes which maintain nitrogen and phosphorus in a dynamic state best explain the weak or insignificant correlation between these nutrients in the sediments.

Shaver and Mellilo (1984) suggested that nitrogen and phosphorus uptake are related in macrophytes with each species having an "optimum" N:P ratio. Shaver and Melillo demonstrated that tissue nitrogen levels increased with increasing nitrogen and phosphorus availability suggesting that there is a limit to the luxury uptake of one element when the other is limiting. In addition, N:P ratios were correlated with available N:P ratios indicating that nitrogen and phosphorus uptake were not independent of each other. The authors suggest that due to this interaction, when nitrogen and phosphorus are available in extreme ratios, uptake results in even more extreme sediment ratios. The tendency of nitrogen and phosphorus to converge on some "optimum" ratio, on the other hand, would result in a plant tissue N:P ratio that was less extreme.

Following a sharp decrease between March and April, shoot N:P ratios increased steadily between April and peak shoot standing stocks in July. This observation suggests that in March nitrogen is initially reallocated from the rhizomes proportionally higher than phosphorus. Higher N:P ratios

in March and between April and July, coincide with decreasing N:P ratios in the rhizomes supporting the observation that nitrogen is being reallocated to the shoots proportionally higher than phosphorus. Conversely, between March and April phosphorus is reallocated proportionally higher than nitrogen. Between April and July, however, nitrogen standing stocks are increasing at a rate greater than phosphorus, resulting in increased N:P ratios. This pattern of N:P ratios suggests that either shoot ratios are converging on an "optimum" ratio at peak biomass (Shaver and Melillo, 1984) or that each phase of shoot development requires nitrogen and phosphorus in certain proportions for maximum photosynthate production.

The increased levels of shoot nitrogen in relationship to phosphorus indicate that shoots require significantly higher levels of nitrogen to meet photosynthetic demands than phosphorus. Rhizome N:P ratios, decreasing from a peak N:P ratio in January, reach an apparent one to one, or "optimum", ratio in July as a result of nitrogen reallocation patterns demonstrating the ability of rhizome to store significant levels of nitrogen in relation to phosphorus in the winter. The decrease in shoot N:P ratios between July and August suggest that nitrogen is translocated from the shoots proportionally higher than phosphorus, explaing the increased rhizome N:P ratios following shoot senescence. Increased rhizome N:P ratios between August and December may also be the result of root uptake of proportionally higher levels of nitrogen at this time. Root N:P ratios decreased between July and August at the onset of root productvity suggesting that, like shoots, roots initially accumulate nitrogen in higher proportions than phosphorus. Root N:P ratios remained relatively constant through the growth period demonstrating the role of root as a conduit rather than a storage

organ. Decreasing root N:P ratios during root dieback sugest that nitrogen may be conserved at a higher rate than phosphorus through translocation although increases in rhizome N:P ratios were not observed at this time. These observations suggest an interaction between nitrogen and phosphorus with internal cycling strategies determining optimum N:P ratios.

Inorganic sediment N:P ratios, as expected, were extremely low supporting the observation that inorganic nitrogen is maintained at low levels within Peltandra sediments and mineralization of organic matter is required to provide sufficient levels required for macrophyte productivity. Decomposition of organic nitrogen in relationship to organic phosphorus is demonstrated in the seasonal patterns of total N:P ratios which decrease during periods of mineralization. There is apparently no "optimum" N:P ratio in the sediments due to the constant seasonal cycling of nitrogen and phosphorus through decomposition and chemical processes.

Spartina cynosuroides

Aboveground Productivity

Seasonal patterns of shoot standing stocks were similar to those previously observed for Spartina cynosuroides, increasing from a low of 1.16 g/m^2 in March to a high of 2462.07 g/m^2 in September. Hopkinson (1984) observed a significantly lower September peak standing stock of 1234 g/m^2 as did Hopkinson et al. (1978) of 808 g/m^2. Peak shoot standing stocks in this study were, however, similar to that of 2190 g/m^2 reported by de la Cruz (1974) and approximates the mean peak standing stock of 2311 g/m^2 for Spartina in tidal wetlands within the Middle Atlantic Coastal Region (Whigham et al., 1978). Apparent discrepancies in these estimates are most likely the result of community structure, location, and sampling technique.

Mortality was not detected in this study, however previous productivity estimates have resulted in a variety of turnover rates for Spartina, including 3.0 (Linhurst and Reimold, 1978), 2.49 (Schubauer and Hopkinson, 1978) and 1.6 (Hopkinson et al., 1978), all estimated by dividing annual productivity by peak biomass. As such, the calculation of annual productivity, estimated from the summation of positive monthly changes (Milner and Hughes, 1968), may represent an underestimate of actual productivity (Mathews and Westlake, 1969; Whigham et al., 1978). Moreover, productivity estimates do not account for respiratory losses or

translocation of organic matter (Brinson et al., 1981). Summation of positive changes in monthly biomass samples, assuming no statistical differences in June and July, resulted in an annual productivity of 2462.84 g/m^2. Annual shoot productivity in this study was lower than the estimate of 3080 g/m^2, based on an annual turnover of 2.49, reported by Schubauer and Hopkinson (1984) but higher than that of 1355 g/m^2, based on an annual turnover rate of 1.6, reported by Hopkinson et al. (1978). Annual shoot productivity in this study is, however, similar to the estimate of de la Cruz (1974), which was based on the Milner and Hughes method. Annual shoot productivity in the present study is significantly higher than the mean value of 1035 g/m^2/year in the Middle Atlantic Coastal Region (Whigham et al., 1978) which may be attributable to the dense, monotypic stands sampled at Sweethall Marsh.

Shoot growth patterns of Spartina cynosuroides are best explained in terms of daily growth rates. Assuming March 1 as the beginning of the growing season, Spartina shoot biomass increased at a rate of 2.38 g/m^2/day between March and May. Daily growth rates then increased to 17.99 g/m^2 between May and June and 17.78 g/m^2 between July and August. Seasonal shoot growth strategies apparently include an initial lag phase between March and May, and a second lag phase between June and July, each followed by a period of rapid shoot development. Birch and Cooley (1982) observed a similar lag phase in Zizaniopsis as did Mason and Bryant (1975) in Phragmites. Similar patterns of shoot productivity were also observed by Linhurst and Reimold

(1978), however Schubauer and Hopkinson (1984) observed no apparent lag phase in shoot productivity of Spartina.

The early lag phase, followed by periods of rapid shoot growth, are generally observed in macrophytes with extensive rhizome storage components. As previously discusssed, the lag phase apparently allows for breakdown of "complex" nitrogen and phosphorus compounds in the rhizomes (Walker, 1981) and reallocation to developing shoot bases in concentrations higher than required to support basic metabolic processes. Uptake of nitrogen and phosphorus in excess of demand during the initial lag phase in shoot productivity provides Spartina with nutrient levels necessary to support the subsequent rapid growth phase. Spartina apparently uses the initial rapid growth phase to reach heights that effectively avoid shading by other macrophytes while providing photosynthate production through increased exposure to sunlight. The second lag phase in shoot productivity may represent the time required for additional accumulation of nitrogen and phosphorus as a result of de novo root uptake while reallocating photosynthate for the support of developing roots and rhizomes. The subsequent period of rapid shoot productivity, which produces shoots often exceeding eight feet, provides leaf surface area with maximum exposure to sunlight and production of photosynthate at levels necessary to support shoot as well as root and rhizome respiration demands. Rapid dieback results in maximum levels of conservation of nitrogen and phosphorus through translocation to the rhizomes. Shoot growth strategies, therefore, help Spartina avoid competition from other macrophytes through maximum levels of productivity while allocating sufficient levels of energy to the roots and rhizomes, which in turn, increase stability within the environment.

Belowground Productivity

In this study, Spartina rhizome standing stocks increased from 1075 g/m^2 in May to 3142.18 g/m^2 in February. Net annual rhizome productivity was estimated by grouping similar monthly rhizome standing stocks, based on multiple comparisons, and then summing positive changes in monthly standing stocks. Using the mean of statistically similar months eliminates some levels of bias incorporated into a maximum - minimum calculation (Hackney and de la Cruz, 1986). This approach resulted in two periods of rhizome productivity which were summed to give an annual rhizome productivity of 1875.88 g/m^2. Schubauer and Hopkinson (1984) reported similar patterns of Spartina rhizome standing stocks increasing from a May level of 750 g/m^2 to a peak of 2750 g/m^2 in February.

Maintaining extensive rhizome standing stocks and supporting annual rhizome productivity under hypoxia requires a significant investment of energy and nutrients by Spartina (Bloom et al., 1985). This investment, however, is necessary for several reasons. First, rhizomes provide Spartina with storage capability and stability. Second, as dead shoots remain attached throughout the winter, annual rhizome productivity provides new sites for developing spring shoots. As previously discussed, rhizomes are more tolerant to hypoxia than roots (Braendle and Crawford, 1987) due to the well developed aerenchyma tissue which is ventilated with oxygen by the shoots (Armstrong, 1979), however rhizomes usually must survive late fall and winter with no oxygen. Spartina rhizomes, however, must depend at least to some degree on anaerobic respiration, despite the fact that they generally extend to a depth of only 25-30 cm and, as such, diffusion of

oxygen through shoots to the rhizomes may provide sufficent levels of oxygen which support some levels of aerobic respiration. Tolerance of Spartina rhizomes to hypoxia in the winter may be explained, at least in part, by the access of the rhizomes to oxygen diffusing through standing dead shoots. A second explanation for rhizome tolerance to anoxia may be that levels of observed shoot productivity are capable of producing sufficient levels of photosynthate to support anaerobic respiration in the form of fermentation. As aerobic respiration requires less photosynthate than fermentation, energetic costs of maintaining an extensive rhizome component through aerobic respiration is energetically more efficient and allows more energy to be allocated to shoot production. Conversely, dependence on fermentation requires a greater energy expenditure by Spartina and may be used only when sufficient oxygen is not available.

Annual root productivity, calculated in a similar manner, was estimated to be 2668.40 g/m^2, increasing from a minimum in May to a peak in August, at which point root standing stocks remained relatively constant through December. Investment of energy and nutrients into this level of root productivity by Spartina is necessary, however, in that it enables Spartina to take advantage of high ammonium levels in the summer (Chambers, 1977; Schubauer and Hopkinson, 1984). Conversely, when sediment nutrient levels are low, increased root surface area provides Spartina with access to nitrogen and phosphorus as these nutrients are depleted near the root interface (Chapin et al., 1987). As will be demonstrated, rhizome nitrogen and phosphorus storage is insufficient to support shoot and root productivity. As a result, Spartina must depend on de novo root uptake of nitrogen and phosphorus to support observed levels of biomass productivity.

Annual root productivity is therefore in a synchronous cycle with shoot and rhizome productivity and apparently necessary to meet biomass nitrogen and phosphorus demands.

Lack of oxygen in the sediments prevents respiratory phosphorylation in and ATP synthesis in roots of Spartina cynosuroides (apRees et al., 1987). As Spartina roots extend to a depth of 50 cm they have little aerenchymous tissue through which oxygen may diffuse and must therefore depend on fermentation for ATP production with toxic ethanol diffusing out the roots (Mendelssohn and McKee, 1987). The levels of photosynthate necessary to support root fermentation may explain the second lag phase in shoot development as photosynthate is reallocated to the roots. Obviously Spartina shoots are capable of photosynthate production necessary to support root productivity which, in turn, provides sufficient levels of nitrogen and phosphorus uptake. Spartina, however, may be capable of some levels aerobic respiration through oxygen diffusion during periods of shoot growth (Breandle and Crawford, 1987). Allocation of energy to root productivity from shoot biomass must, therefore, represent a trade-off for nutrient acquisition in a waterlogged environment.

Summation of root and rhizome productivity resulted in an annual belowground productivity of 4544.28 g/m^2/year with peak belowgrond biomass occurring in late summer and early fall. Peak belowground biomass has also been observed in August for Spartina alterniflora (in Good et al., 1982) as well as in September for Spartina cynosuroides (Gallagher and Plumley, 1979; Hackney and de la Cruz, 1986). Annual belowground productivity in this study was significantly higher than the annual belowground productivity of 2200 g/m^2 (de la Cruz and Hackney, 1977) and 3560 g/m^2(Gallagher and

Plumley, 1979) for Spartina cynosuroides (in Good et al., 1982). Annual belowground productivity, however, approximated that of 4628 g/m^2 estimated for the roots and rhizomes of Spartina cynosuroides in a Georgia coastal marsh using similar sampling techniques (Schubauer and Hopkinson, 1984) . Hackney and de la Cruz (1986) estimated belowground productivity at 2200 g/m^2/year in Spartina cynosuroides increasing from a low of 6000 g/m^2 in April to a high of 8200 g/m^2 in August. As typical belowground productivity estimates range from 1.36 to 2.46 g/m^2 in tidal freshwater marshes (Good and Good, 1975), belowground productivity of Spartina must be considered high. It has been sugested that sediment stresses determine levels of belowground productivity (Shaver and Billings, 1975) which may explain the differences in levels of belowground productivity observed in these studies.

Total Productivity

Total annual productivity, including above- and belowground, of 7005.96 g/m^2 approximates that of 7708 g/m^2 reported by Schuabauer and Hopkinson (1984) indicating the extremely high productivity capability of Spartina. The fact that belowground productivity accounts for approximately 65% of total annual productivity, demonstrates the importance of including this component in annual estimates of productivity.

Root:shoot (R:S) ratios reflect differences in species and habitats with high ratios generally considered adaptive mechanisms to unfavorable soil conditions (Good et al., 1982). Higher R:S ratios are therefore expected in deep rooted perennials which must compete for nutrients under extreme reducing conditions while lower R:S ratios are typical of shallow

rooted perennials which occur in portions of the sediment which are not always anaerobic (Whighmam and Simpson, 1978). In this study, a relatively low peak R:S ratio of 1.17 and a mean R:S ratio of 1.43 are somewhat surprising due the demand for de novo root uptake to support peak shoot productivity. A possible explanation may lie in the efficiency of root uptake by Spartina and the prohibitive energy costs of maintaining a larger root component. Belowground to aboveground ratios (B:A), which include the rhizome component, refect the interaction of the root and rhizome compartments in the support of aboveground productivity. A peak B:A of 2.07 and mean B:A of 3.45, which fall within the range of 0.55 to 3.64 reported as typical for tidal freshwater macrophytes (Whigham and Simpson, 1978), suggests that Spartina invests a significant level of energy in maintaining belowground biomas.

Nitrogen Dynamics

Tissue Nitrogen Concentrations

Spartina shoot nitrogen concentration were relatively low throughout the sampling period and drop below the critical level of 1.3% observed for most plants (Gerloff and Kromholtz, 1966). Lower shoot nitrogen concentrations may best be explained by the relatively low concentrations in reed plants with extensive cell wall supporting material in relation to protoplasm (Boyd, 1978). The low shoot nitrogen concentrations, however, are offset by increased biomass productivity and continued rhizome reallocation which, as will be demonstrated, appear sufficently high to support required levels of carbon assimilation. Shoot nitrogen

concentration decreased from the observed peak in March to a minimum observed in August. As such, peak shoot nitrogen concentrations occurred during the lag phase in shoot development and decreased as shoot biomass increased. This concentration of nitrogen in early developing shoots in excess of tissue requirements has been termed "luxury" uptake by Gerloff and Kromholtz (1966). Since the majority of nitrogen in the early phases of shoot deveopment are presumed to be the result of reallocated nitrogen from winter rhizome storage, the lag phase in shoot development may represent the time required by Spartina rhizomes to break down "complex" nitrogen storage compounds for reallocation to the shoots (Walker, 1981). As approximately 75% of the reallocated nitrogen in plant shoots is allocated to chloroplast development and subsequent photosynthesis (Chapin et al., 1987), the early "luxury" accumulation of nitrogen must represent levels necessary to the support photosynthate production required for rapid periods of shoot development in Spartina. Decreases in shoot nitrogen concentrations are due to shoot elongation and dilution of the nitrogen present (Hopkinson and Schubauer, 1984) as well as translocation to the rhizomes in October. Seasonal patterns of shoot nitrogen concentrations in Spartina cynosuroides were similar to those observed in other aquatic macrophyte species including Spartina alterniflora (Hopkinson and Schubauer, 1984; Patrick and Delaune, 1976); Buresh et al., 1980; Gallagher et al., 1980) and Phragmites communis and Typha augustifolia (Mason and Bryant, 1975) suggesting the early "luxury" accumulation provides most macrophyte species with certain competitive advantages within a tidal environment.

Spartina rhizome nitrogen concentrations followed similar patterns to that of the shoots, decreasing from a high in February to a low in August.

Tha sharp decrease between February and March is best explained as the reallocation of nitrogen to shoot bases while the increase between March and May is most likely the result of de novo root uptake. Between May and August, rhizome concentrations decreased significantly as nitrogen is transferred to both developing shoot and roots. The increased rhizome concentration between August and December is the result of nitrogen translocated to the rhizomes during shoot senescence as well as root uptake at this time. The fact that Spartina rhizome nitrogen concentrations are well below the suggested critical level of 1.3% (Gerloff and Kromholtz, 1966) demonstrate the ability of the rhizomes to support an extensive biomass and store nitrogen at low concentrations. This may be due to an increased dependence on root uptake to supply nitrogen and phosphorus rather than the energy costs of storing these nutrients. Similar patterns were reported in rhizomes of Spartina cynosuroides by Hackney and de la Cruz (1986) and Spartina alterniflora by Hopkinson and Schubauer (1984).

Spartina root nitrogen concentrations increased significantly between March and May during periods of minimum root biomass standing stocks. The early concentrations of nitrogen apparently are the result of rhizome reallocation and may explain part of the significant decrease in rhizome nitrogen concentration between February and March. As such, the nitrogen concentrations prior to root growth may represent a "luxury" accumulation which is required to support the rapid root growth observed between May and August. Root nitrogen concentrations then decreased and remained relatively constant between July and October. Root growth apparently dilutes nitrogen concentrations to a "critical" level required by the roots to maintain metabolic activity. Constant root concentrations during periods of

productvity and nutrient uptake are expected since roots serve mainly as a conduit for nitrogen rather than as a storage component. By investing nitrogen in root productivity, Spartina cynosuroides insures adequate root biomass to meet current nitrogen uptake requirements as well as rhizome storage nitrogen for the following year. Hackney and de la Cruz (1986) also reported relatively stable nitrogen concentrations in the roots of Spartina cynosuroides, although concentrations did increase slightly between August and September, as did Hopkinson and Schubauer (1984) in the roots of Spartina alterniflora.

Tissue Nitrogen Standing Stocks

While seasonal patterns of tissue nitrogen concentrations illustrate Spartina cycling strategies, tissue nitrogen standing stocks provide information on the quantitative aspects nitrogen cycling. Shoot nitrogen standing stocks were correlated with shoot biomass demonstrating the role of biomass in regulating standing stocks. Despite decreasing shoot nitrogen concentrations, shoot nitrogen standing stocks increased between March and June. This suggests that nitrogen standing stocks are not simply the result of the dilution of early luxury accumulation but rather continued reallocation from root uptake. The decrease in shoot nitrogen standing stocks during the second lag phase in shoot development between June and July may be the result of the translocation of nitrogen to the rhizomes or represent to metabolic consumption. Shoot nitrogen standing stocks then increased to a peak in September as nitrogen uptake by the roots is reallocated to the shoots. The energy requirements of biomass production levels observed in this study suggest that although Spartina incorporates

significant levels of nitrogen into cell wall supporting material (Boyd, 1978), chloroplast synthesis, which also requires high levels of nitrogen, must also be significant. Gallagher et al. (1980) and Mason and Bryant (1975) observed similar patterns with peak nitrogen standing stocks coinciding with peak shoot biomass in Spartina alterniflora and Phragmites communis, respectively.

Rhizome nitrogen standing stocks decreased during periods of shoot and initial root productivity and increased during periods of shoot senescence and peak root biomass. The decrease is assumed to be the result of reallocation to shoots and roots while increases are assumed to be the result of translocation and resupply through root uptake. Peak rhizome nitrogen standing stocks represent storage compounds, which based on a mximum - minimum calculation, are insufficient to support levels of observed productivity. As such, Spartina biomass production must depend on significant levels of de novo root uptake. Hopkinson and Schubauer (1984) reported similar patterns of rhizome nitrogen standing stocks in Spartina alterniflora as did Mason and Bryant (1975) in Phragmites communis.

Root nitrogen standing stocks coincided with root bimass standing stocks remaining relatively low between February and May and increasing between May and September. The relatively small increase between May and July is the result of dilution of higher nitrogen concentrations in the root bases. The levels of root nitrogen standing stocks during periods of peak root productivity demonstrate a significant investment of nitrogen by Spartina which is apparently necessary for levels of nutrient uptake required. The relatively stable nitrogen standing stocks through the December demonstrate the role of roots as a conduit for nutrients. The

decrease in nitrogen standing stocks during root dieback are apparently lost to the sediments although no attempt was made to estimate translocation to the rhizomes at this time.

Tissue Nitrogen Leaching

Leaching of nitrogen from the shoots of Spartina cynosuroides was relatively low. Low nitrogen leaching rates are most likely due to the morphology of Spartina shoots in which significant levels of nitrogen are incorporated into cell wall components and therefore not readily leached. In addition, tidal cover was insufficient during periods of peak shoot productivity to effectively cover the leaves. As such, leaching occurred mainly during the lag phase in shoot development when nitrogen is in the intercellular spaces (Tukey, 1970). Leaching of standing dead shoots may occur when tidal levels are high, however this flux was not measured. Hopkinson and Schubauer (1984) reported similar levels of leaching from the shoots of Spartina alterniflora at 0.7 g/m^2/year.

Nitrogen Efficiency Indexes

Nitrogen efficiency indexes provide insight into relative nitrogen cycling strategies in the tissues of Spartina cynosuroides. Although shoot nitrogen use efficiency, which defines the relationship between biomass and nitrogen, remained relatively high throughout the study, a minimum was observed during each of the apparent lag phases in shoot productivity. Minimum values are apparently the result of increased reallocation from the rhizomes, resulting in luxury accumulation, while higher values in August and September, which are assumed to be optimum, reflect increased shoot

biomass in relation to nitrogen levels. Spartina may have evolved more efficient use of nitrogen which results in a decreased level of energy which must be expended on root uptake. As nitrogen use efficiency is hypothesized to increase as nitrogen availability decreases (Vitousek, 1982; Shaver and Melillo, 1984), the increased use efficiency by Spartina requires less investment of energy for root uptake and allows more to be invested in biomass production. The ability to produce significant levels of organic matter per unit of nitrogen, as demonstrated by the low nitrogen concentrations and high biomass productivity of Spartina, result in robust stands in a nitrogen limiting environment. Shaver and Melillo (1984) reported similar levels of nitrogen use efficiency indexes in Carex, Calamagrostis, and Typha.

Rhizome use efficiency was significantly higher than that of the shoots with peak use efficiency occurring during periods of maximum reallocation to the shoots and roots. Rhizome use efficiency was generally lower prior to the onset of shoot development as a result of the significant levels of stored nitrogen compounds. Low use efficiency demonstrates the role of rhizomes in the storage of nitrogen while the higher use efficiency demonstrates the ability of rhizomes to maintain extensive biomass at low nitrogen levels. Use efficiency remained relatively stable during periods of rhizome productivity indicating that nitrogen standing stocks are increasing proportionally as a result of root uptake and shoot translocation. Root use efficiency decreased prior to the onset of root development apparently due to the luxury accumulation of nitrogen at root bases. Use efficiency then remained relatively constant during periods of root growth indicating a proportional allocation of nitrogen to biomass and

the importance of roots as a conduit for nutrient uptake and translocation to the rhizomes. The significantly higher use efficiency in the belowground structures indicates that these components are more capable of supporting biomass at low nitrogen levels than the shoots resulting in increased stability within a limiting environment.

Nitrogen recovery indexes increased between September and November indicating that Spartina concentrates translocation to the rhizomes during a relatively short period of dieback. Shaver and Melillo (1984) reported slightly lower recovery indexes in Carex, Calamagrostis, and Typha with similar increases between harvests in Carex and Calamagrostis. Levels of recovery indicate that Spartina does conserve nitrogen through translocation although levels are probably tied to rhizome storage capacity. Lower recovery through translocation results in significant levels of nitrogen remaining in standing dead shoots which are eventually lost to the environment through decomposition and leaching.

Sediment Nitrogen

Sediment total nitrogen standing stocks remained high throughout the sampling period. Sediment ammonium and nitrate standing stocks, however, remained relatively low, with ammonium levels significantly higher than nitrates. As previously discussed, this is due to the fact that anaerobic sediments maintain reduced ions in relationship to their oxidized counterparts (Harter, 1966; in Klopatek, 1978). Although Spartina inorganic sediment nitrogen levels are relatively low, observed biomass production observed in this study suggest that nitrogen may not actually be limiting. Patrick and DeLaune (1976), experimentally increasing sediment nitrogen,

reported only a 15% increase in biomass but a significant increase in tissue nitrogen in Spartina alterniflora. As a result, photosynthetic capacity may increase with additional nitrogen, however biomass yield may remain constant.

Inorganic nitrogen, mainly as ammonium, increased between February and May as total nitrogen decreased. As ammonium is considered the major source of available nitrogen and monthly standing stocks appear insufficient to support observed levels of productivity, it is assumed that mineralization between February and May produces the observed levels of ammonium. Release through mineralization is therefore considered to be the major source of inorganic nitrogen in anaerobic sediments (Patrick and DeLaune, 1980; Walker, 1981; Bowden, 1982). The decrease in inorganic nitrogen between May and July as well as between September and October coincides with periods of rapid shoot development and is assumed to be the consequence of root uptake by Spartina. Root uptake, in turn, eleviates the buildup of sediment ammonium (Klopatek, 1974). In addition, decreased levels of ammonium may be explained in terms of sediment chemistry. As ammonium in the aerobic surface layer is nitrified a gradient is established which results in ammonium from the anaerobic layer diffusing to the surface (Patrick and Reddy, 1976). Nitrate diffusing from the surface layer is rapidly denitrified (DeLaune and Patrick, 1980) resulting in extremely low levels of nitrate (Vanderbought and Billen (1975), although nitrate reduction to ammonium may conserve nitrogen in the sediments (Bowden, 1982). As a result nitrate is considered a minor source of nitrogen for Spartina cynosuroides as has been demonstrated for Spartina alterniflora (Mendelssohn, 1979). Ammonium which remains in the anaerobic sediment column may be regulated by

the "clay-humic complex" of organic rich sediments, resulting in increased adsorption and decreased availability (Boatman and Murray, 1982). Exchangeable ammonium which is available is therefore dissolved in the interstitial water where levels are maintained by the decomposition of organic matter (Rosenfield, 1979). Spartina sediments, due to poor drainage, were extremely waterlogged. As a result, the majority of available nitrogen is assumed to be dissolved in the interstitial water or adsorbed onto suspended sediments. Klopatek (1975) reported similar patterns of sediment nitrogen with total nitrogen reaching a peak of 1696 g/m^2 in the top 30 cm of a freshwater marsh. Haines et al. (1977) reported peak ammonium standing stocks between April and May, although levels were relatively lower than those observed in this study.

Tissue-Sediment Nitrogen Relationship

As previously discussed, the relationship between tissue and sediment nitrogen levels has been developed for several macrophytes although results heve been conflicting (Gerloff and Kromholtz, 1966; Gosset and Norris, 1971; Boyd and Vickers, 1971; Klopatek, 1975; Walker, 1981). In the present study, shoot, root, and rhizome nitrogen levels were shown to be independent of sediment inorganic nitrogen standing stocks. As will be demonstrated in the nitrogen model, Spartina depends on de novo root uptake to support periods of peak shoot and root productivity. Consequently, a stronger dependence of tissue nitrogen on sediment inorganic nitrogen may be expected. A weak tissue relationship with sediment inorganic nitrogen is most likely due to the seasonal fluctuations of ammonia and nitrate as well as initial periods of reallocation from the rhizomes. A positive

relationship, however, was shown to exist between shoot, root, and rhizome nitrogen and sediment total nitrogen standing stocks. The dependence of tissue nitrogen standing stocks on sediment nitrogen levels are similar to that reported by Klopatek (1975). The relationship may be best explained by the constant proportion of ammonium to total nitrogen, with mineralization of total nitrogen controlling uptake (Klopatek, 1978). If indeed mineralization rates are controlled by aquatic macrophytes then a positive correlation is expected.

Nitrogen Model

The quantification of compartmental fluxes in the shoots of Spartina cynsouroides, which must be interpreted on a qualitative basis, demonstrates the impact of perennials with rhizome storage capacity which, due to levels of biomass productivity, must also depend on de novo root uptake to meet nutrient requirements. The relatively low annual release of nitrogen to leaching is similar to that reported for Spartina alterniflora (Hopkinson and Schubauer, 1984) and is best explained by the lack of tidal cover during periods of peak biomass and shoot morphology. As such, leaching, which has been demonstrated to be extensive in other tidal freshwater macrophytes (Klopatek, 1975; Kistritz et al., 1983), represents a relatively insignificant input to the surrounding environment. The annual nitrogen flux of 20.27 g/m^2 to the detritus compartment does not represent an immediate release to the environment due to the fact that dead shoots remain standing throughout the winter and into the next growing season. The reported flux of nitrogen to the detrital compartment, therefore, is released to the enivironment over extended periods of time as dead shoots

fall to the sediment surface and decompose (Odum and Heywood, 1978; Dunn, 1978; Turner, 1980). Nitrogen uptake of 32.17 g/m^2 by the shoots represents a significant investment in photosynthate production of developing shoots. As rhizome nitrogen storage is insufficient to support this level of uptake it is assumed that early shoot uptake is the result of reallocated nitrogen with the remainder the result of de novo root uptake. Hopkinson and Schubauer (1984) reported similar levels of shoot uptake by Spartina alterniflora at 33.0 g/m^2/year. Translocation of 11.88 g/m^2 of nitrogen to the rhizomes, approximately one third of shoot uptake, represents a significant level of nitrogen conservation. Conservation of nitrogen through translocation in the fall provides storage nitrogen for spring shoot development while decreasing the energy which must be expended for de novo root uptake. Translocation of nitrogen to the rhizomes has also been demonstrated in Spartina alterniflora (Hopkinson and Schubauer, 1984), Typha (Davis and van der Valk, 1983), and Phragmites (Van der Linden, 1980).

Nitrogen uptake of 52.62 g/m^2/year by the roots represents a significant withdrawal from the sediments supporting Klopatek's (1974) contention that macrophytes regulate ammonium levels. As mean monthly sediment inorganic nitrogen standing stocks are relatively low in relation to uptake demand, it is assumed that mineralization of organic nitrogen provides a continuual supply of inorganic nitrogen. Moreover, as rhizome nitrogen standing stocks are insufficient to meet observed biomass nitrogen standing stocks, de novo root uptake during periods of peak biomass productivity is necessary. Nitrogen transfer of 55.60 g/m^2 from the roots to the rhizomes, which exceeds annual root uptake, suggests that nitrogen

may be conserved through translocation during root senescence. Of the nitrogen transfer to the rhizomes from the roots, approximately 9.75 g/m^2/year are required for rhizome productivity, while the remainder is used to support shoot and root productivity. The annual nitrogen reallocation of 18.45 g/m^2 to support root growth, based on the assumption that root productivity is supported through rhizome reallocation, may be overestimated due to the difficulty in determining which percentage of nitrogen is actually reallocated and which percentage is taken up and used directly by the roots (Mendelssohn, 1979). Nitrogen losses to the environment through root and rhizome mortality may also represent overestimates due to relatively slow turnover (Good et al., 1982) and decomposition (Hackney, 1984; Hackney and de la Cruz, 1982).

Phosphorus Dynamics

Tissue Phosphorus Concentrations

The decrease in shoot phosphorus concentrations between April and September suggest that Spartina accumulates phosphorus in excess of requirements during the initial lag phase in shoot development which are then diluted as shoot development proceeds. The early "luxury" accumulation (Gerloff and Kromholtz, 1966) of phosphorus in the shoots of Spartina, assumed to be the result of rhizome reallocation rather than de novo root uptake, during the initial lag phase in shoot development provides a sufficient supply of phosphorus to support the subsequent rapid growth phase. As phosphorus is a major constituent of ATP and cell wall constituents, this nutrient is required for maximum shoot growth and

photosynthate production. The luxury concentrations of shoot phosphorus, then, provide Spartina cynosuroides with required levels of phosphorus for ATP syntheisis during photosynthesis as well building blocks for cell walls, which are significant in reed plants (Boyd, 1978). Consequently, Spartina is capable of supporting periods of rapid shoot development which allow maximum sunlight utilization. The minimum shoot phosphorus concentrations between August and October, during the period of maxiumum shoot biomass, approximates the critical phosphorus concentration of 0.13%, i.e. the concentration above which productivity is not limited, suggested by Gerloff and Kromholtz (1966). Shoot phosphorus concentration during peak biomass must therefore represent the optimum concentrations in shoots in terms of energy and structural requirements. Similar patterns of shoot phosphorus concentrations have been reported for the majority of wetland macrophytes (Boyd, 1978), including Phragmites (Mason and Bryant, 1975), Typha (Prentki et al., 1978) and Spartina alterniflora (Patrick and DeLaune, 1976).

Spartina rhizome phosphorus concentrations remained constant during the initial lag phase and subsequent period of rapid shoot development and decreased during the second period of rapid shoot development and root growth. As it has been hypothesized that the initial lag phase in shoot development is supported by reallocation from the rhizomes, the relatively constant rhizome phosphorus concentrations suggest that rhizome phosphorus is resupplied by root uptake during this period. The decrease in rhizome phosphorus concentration between July and September is the result of continued phosphorus reallocation, in excess of root uptake rates, to the shoots and developing roots. Mason and Bryant (1975), however, reported a steady decrease in rhizome phosphorus concentrations of Phragmites during

periods of shoot development as did Prentki et al. (1978) in the rhizomes of Typha.

Spartina root phosphorus concentrations remained relatively constant throughout the sampling period, although a slight decrease was observed during the initial phase of root growth indicating that root biuomass dilutes phosphorus to a minium or optimal level. The relatively constant root phosphorus concentrations during periods of peak root biomass demonstrate the importance of the roots as a conduit for phosphorus rather than as a storage component. Constant reallocation from the rhizomes explain the relatively constant phosphorus concentrations which are required for ATP synthesis required for active root uptake.

Tissue Phosphorus Standing Stocks

Seasonal patterns of shoot phosphorus standing stocks demonstrate the quantitative aspects of Spartina phosphorus dynamics with the correlation between biomass and phosphorus standing stocks illustrating the impact of productivity on phosphorus concentation. The relatively small increase in shoot phosphorus standing stocks between March and May is best explained as the dilution of the luxury accumulation during the initial lag phse in shoot development. The significant increase in shoot phosphorus standing stocks between May and June is the result of de novo root uptake as rhizome phosphorus standing stocks are resupplied. The decrease in shoot phosphorus standing stocks during the second apparent lag phase in shoot development between June and July may be the result of translocation of phosphorus to support root uptake and growth. Peak shoot phosphorus standing stocks coinciding with peak shoot biomass provide Spartina with sufficient levels

of phosphorus required for photosynthate production occurring at this time. In this manner, Spartina utilizes phosphorus most efficiently for carbon assimilation and root uptake. Similar patterns of shoot phosphorus standing stocks have been observed in Typha latifolia (Prentki et al., 1978) and Phragmites (Mason and Bryant, 1975; Ulehlova et al., 1973; Kvet, 1973). Buresh et al. (1980) and Patrick and Delaune (1976) also observed reported similar patterns of shoot phosphorus standing stocks in the shoots of Spartina alterniflora.

Rhizome phosphorus standing stocks decreased between February and May coinciding with rhizome senescence and shoot productivity during this period. Rhizome phosphorus standing stocks then increased through July followed by a decrease through September. As rhizome phosphorus concentrations remained constant during periods of rhizome senescence, decreased rhizome phosphorus standing stocks are related to biomass dynamics. Uptake by the roots and continued reallocation to the shoots and roots explain rhizome phosphorus patterns between May and September. as previously suggested, rhizomes, which are generally considered as important winter storage organs, apparently do not store significant levels of phosphorus but rather depend on de novo root uptake to meet biomass phosphorus requirements. This may be explained by the extremely high levels of sediment phosphorus available to Spartina and the costs of storage (Bloom et al., 1985). Rhizome phosphorus standing stocks, however, did increase slightly during periods of shoot senescence suggesting that Spartina may conserve and store some phosphorus during the winter. Prentki et al. (1978) reported similar patterns in Typha. As root phosphorus concentrations remained relatively constant throughout the sampling period, seasonal

patterns of root phosphorus standing stocks were dependent on root biomass dynamics. The small increase in root phosphorus standing stocks between May and July, however, is due to the dilution of apparent higher root phosphorus concentyrations prior to the onset of root growth.

Tissue Phosphorus Leaching

The relatively low phosphorus leaching rates from the shoots of Spartina are due to the lack of tidal cover as well as the incorportaion of phosphorus into cell wall constituents which are not readily leached. Consequently, phosphorus input to the environment through leaching is minimal although leaching of standing and fallen dead shoots may contribute additional levels of phosphorus over extended periods of time. Conparison of phosphorus leaching rates of Spartina is difficult due to the lack of leaching data from macrophyte species with similar morphology although Reimold (1972) reported relatively high levels of phosphorus leaching from Spartina alterniflora.

Phosphorus Efficiency Indexes

Phosphorus use efficiency, which defines the relationship between phosphorus standing stocks and biomass, in the shoots of Spartina cynosuroides increased from a low in April to a high during peak shoot shoot biomass standing stocks. The low use efficiency in April is the result of apparent "luxury" accumulation of phosphorus during the initial lag phase in shoot development while increasing use efficiency is due to increasing biomass in relation to phosphorous standing stocks. Assuming that use efficiency increases as availability decreases (Shaver and Melillo, 1984),

the increase in use efficiency as the growing season proceeds may be best explained in terms of decreased rhizome storage of phosphorus as well as the demand for de novo root uptake, which requires significant levels of energy. By using phosphorus more efficiently during periods of peak biomass, Spartina maximizes carbon assimilation while decreasing the energy which would otherwise be expended on root uptake. Maximum use efficiency in October is the result of phosphorus translocated to the rhizomes while biomass remains relatively stable. Shaver and Melillo (1984) reported similar levels of phosphorus use efficiency in Typha and Carex although use efficiency decreased between sampling intervals.

Spartina rhizome use efficiency was significantly higher than that of the shoots and roots. This supports the observation that rhizomes store relatively low levels of phosphorus and must depend on root uptake to meet tissue phosphorus requirements. Rhizome use efficiency remained low during the lag phase in shoot development and the onset of root development and increased significantly during the initial period of rapid shoot growth and root development between May and July. Use efficiency then decreased during periods of assumed root uptake and increased as phosphorus is reallocated to the shoot and roots. The extremely high use efficiency by the rhizomes in the winter illustrates the low storage capacity for phosphorus and the ability to support extremely high biomass standing stocks at low phosphorus standing stocks. Apparently energy requirements of ATP and cell wall structural components in the rhizomes of Spartina are low at this time. Root use efficiency remained relatively constant throughout the year although there was a slight decrease in use efficiency during the initial phase of shoot growth. The relatively constant use of phosphorus by Spartina roots

suggests continued reallocation form the rhizomes or internal cycling of phosphorus by the roots to meet energy demands in relation to biomass production. The relatively low root use efficiency in comparison to the rhizomes may be best explained in terms of the levels of energy required to support root productivity and active root uptake of nutrients.

Recovery efficiency is relatively low indicating the Spartina cynosuroides does not conserve high levels of phosphorus through translocation. As high levels of recovery are often associated with the limitation of a specific nutrient (Denny, 1980), the extremely high sediment phosphorus levels observed may make it unnecessary for Spartina to conserve high levels of phosphorus through translocation. Shaver and Melillo (1984) reported similar phosphorus recovery indexes in Carex and Typha with recovery decreasing between sampling periods, similar to this study.

Sediment Phosphorus

Inorganic phosphorus, expressed as the sum of all depths, in the sediments of Spartina were raelively high throughout the sampling period with the exception of a significant drop between July and August. As such, sediment phosphate levels remained high during the initial lag phase and rapid growth of Spartina shoots and decreased during the second period of rapid shot development. Total phosphorus, expressed as the sum of all depths, followed almost identical seasonal patterns increasing prior to maximum shoot biomass and decreasing during periods of peak shoot productivity.

Seasonal patterns of phosphorus in the sediments of Spartina cynosuroides may be best explained in terms of macrophyte upake and sediment

chemistry. The effects of emergent macrophytes on sediment phosphorus levels has been demonstrated (Klopatek, 1975; Bowden, 1982; DeLaune and Patrick, 1980) with decreased sediment inorganic levels the result of macrophyte uptake. Carignan and Kalff (1979) reported that the available phosphorus for aquatic macrophytes is in the mobile phase which is regulated by the release of phosphate during the reduction of ferric hydroxides in anaerobic soils and adsorption/desorption capacity (Patrick and Khalid, 1974). Carignan and Flett (1981) suggested that phosphorus levels may also be controlled by the vertical migration of phosphorus from relatively deep, anaerobic sediments and accumulation in the upper layers where precipitation may occur. Krom amd Berner (1981) demonstrated that the dissolved phosphate in these upper layers may be provided by the release of phosphates during the reduction of the ferric hydroxides while phosphate levels in the deeper, anaerobic sediments is the result of the decomposition of organic mater. As a result, lack of oxygen results in increased sediment levels of phosphorus. This data suggest that in anaerobic sediments the available pool is in the mobile phase although adsorbed phosphorus, as well as phosphorus incorporated into organic matter (Ponnamperuma, 1972), may eventually become available through desorption and decomposition, respectively. The relatively high levels of inorganic phosphorus observed in the sediments of Spartina, therefore, may be the result of decomposition, immobilization with ferric hydroxides, and adsorption whereas lower levels are the result of root uptake and incorporation into organic matter. Decreased sediment levels, in turn, are renewed through sedimentation (DeLaune et al., 1981), decomposition (Bowden, 1982), and increased binding with ferric hydroxides (Patrick and Khalid, 1974).

The observed levels of sediment phosphorus support Klopatek's (1978) contention that wetlands have evolved mechanisms for conserving phosphorus within its boundaries. The anaerobic state and redox potential of marsh sediments retard the decomposition of organic matter. As a result, sediments high in organic matter are considered phosphorus sinks (Klopatek, 1978) although phosphorus may be released to the overlying water (Patrick and Khalid, 1974). The sediments of Spartina, therefore, appear to act as long term sinks for phosphorus insuring sufficient levels which support both macrophyte and microbial demands. As such, Spartina appears not to be limited in terms of biomass production on phosphorus availability, although the available phosphate pool may be overestimated due to the extraction procedure which assumes both adsorbed and mobile phosphorus as available.

Mason and Bryant (1975) reported similar high levels of interstitial inorganic phosphorus throughout the growing season in Phragmites communis sediments (in Klopatek, 1978). Klopatek (1975) also reported similar levels and seasonal patterns of Bray P-2 available phosphorus in the top 15 cm of a tidal freshwater wetland with levels decreasing between June and July, periods of maximum shoot uptake, and increasing the remainder of the year. DeLaune and Patrick (1980) concluded that a streamside marsh acts as a sink for phosphorus with an annual accumulation rate of 21 g/m^2 and reaching 20 g/m^2 in the top 30 cm of the sediment column.

Tissue-Sediment Phosphorus Relationship

In the present study, regression analysis indicated that shoot, root, and rhizome phosphorus standing stocks were independent of sediment inorganic phosphate levels. This is somewhat surprising due to the levels

of root uptake required to meet annual tissue phosphorus demands. There was, however, a significant level of dependence of shoot phosphorus on sediment total phosphorus. The independence of tissue phosphorus on sediment inorganic phosphorus levels may be the result of the initial reallocation from the rhizomes which supports shoot and root productivity. Moreover, independence of tissue phosphorus standing stocks on sediment levels allows Spartina to use phosphorus most efficiently, i.e. when it is availalble, in the energy required for active root uptake. The dependence of shoot phosphorus standing stocks on sediment total phosphorus is apparently due the levels of orthophosphate associated with organic phosphorus compounds and the minerilization of more resistant phosphorus containing compounds (Klopatek, 1978).

Phosphorus Model

The phosphorus model for Spartina must be interpreted on a qualitative basis, yet quantification of annual compartmental fluxes does provide infromation on relative phosphorus cycing strategies. annual uptake of 4.43 g/m^2 by the shoots demonstrates that Spartina takes up significant levels of phosphorus through rhizome reallocation and root uptake. The relatively low leaching rates are directly attributable to the lack of tidal cover during periods of peak biomass as well as the incorporation of phosphorus into structural components that are not easily leached. The annual flow to the detrital compartment of 2.88 g/m^2 is released to the environment over extended periods of time due to slow decomposition rates and the fact tha Spartina dead shoots remain standing through the winter. The conservation

of phosphorus through translocation to the rhizome compartment of 1.41 g/m^2 may be explained by the inability of Spartina to mobilize phosphorus for translocation or sediment phosphorus levels which make conservation unnecessary.

Annual phosphorus transfer of 10.03 g/m^2 from the roots to the rhizomes is slightly higher than the annual root uptake of 9.73 g/m^2 suggesting that phosphorus may be conserved through translocation by senescing roots. Simarly, annual flow from the roots to the rhizomes suggests that the roots function mainly as a conduit for phosphorus rather than as a storage component with phosphorus passing from new roots to the transpirational stream (Bieleski, 1973). Phosphorus losses to the sediments through root and rhizome mortality are overestimates due to the slow decomposition and turnover of belowground biomass (Hackney and de la Cruz, 1980; Good et al., 1982). As rhizome phosphorus storage is insufficient to meet tissue requirements, phosphorus reallocation of 4.76 g/m^2 from the rhizomes to the roots represents a significant, although necessary, investment by Spartina of energy and structural components into root productivity and subsequent root uptake. Heckman (1986) reported an annual phosphorus uptake of 5.48 g/m^2 in Phragmites with approximately 2.67 g/m^2 reallocated to emergent shoots.

Nitrogen-Phosphorus Relationship

Correlation analysis indicated a strong relationship between tissue nitrogen and phosphorus standing stocks. Significant levels of correlation suggest that nitrogen and phosphorus are not independent in their cycling

through the tissues of Spartina. Further, the correlation of tissue nitrogen and phosphorus suggest an interaction between these nutrients although the mechanisms of interaction are unclear. It would appear, however, that Spartina tissues require nitrogen and phoisphorus in certain proportions through the life cycle of the plant suggesting that reallocation of nitrogen and phosphorus, as well as root uptake, may be in relative proportions to demand. A probable explanation involves the requirements of nitrogen and phosphorus in certain proportions for chloroplast, energy, and cell wall synthesis during individual phases of plant development. Shaver and Melillo (1984) also demonstrated a positive effect of phosphorus on total nitrogen mass in the tissues of Typha, Calamagrostis, and Carex suggesting a nitrogen-phosphorus interaction. Microbial turnover, chemical processes, and plant uptake which maintain nitrogen and phosphorus in a dynamic state best explain the insignificant correlations of nitrogen and phosphorus in the sediments.

Seasonal patterns of nitrogen to phosphorus ratios (N:P) indicate that tissue ratios are variable over an annual cycle with each phase of plant development having a certain N:P ratio. Shaver and Melillo (1984) suggested that nitrogen and phosphorus cycling are related with each plant having an optimum N:P ratio. The tendency of plant tissues to converge on an optimum N:P ratio results in tissue N:P ratios less extreme than N:P ratios in the sediments. Developing shoots appear to accumulate "luxury" levels of nitrogen in relatively higher proportions than phosphorus during early development. This is probably explained by increased nitrogen demand for chloroplast synthesis and subsequent photosynthate by young Spartina shoot in relation to phosphorus. Nitrogen to phosphorus ratios then decrease as

a result of reallocation of phosphorus from de novo root uptake to more optimal ratios during periods of rapid shoot growth. The second increase in N:P ratios during the apparent second lag phase in shoot development is the result of increased nitrogen reallocation from the rhizomes necessary for chloroplast synthesis. N:P ratios then converge on an optimum ratio at peak biomass as phosphorus, which is required for ATP synthesis necessary for carbon assimilation, is now reallocated proportionally higher than nitrogen A slightly lower ratio in October suggests that nitrogen is conserved at higher levels than phosphorus through translocation to the rhizomes.

Rhizome ratios are high prior to the onset of shoot development demonstrating the higher levels of nitrogen storage in relation to phosphorus. Rhizome N:P ratios decrease significantly between March and Aprils supporting the observation that nitrogen is initially reallocated to the shoots at higher proportions than phosphorus. Rhizome ratios then increase between April and May as a result of de novo root uptake and decrease between July and September as nitrogen is reallocated at a faster rate than phosphorus to the shoot and roots. Rhizome ratios then increase in the fall during periods of shoot dieback and root uptake suggesting that root uptake and translocation of nitrogen is greater in relation to phosphorus at this time. Root nitrogen to phosphorus ratios are generally higher prior to the onset of root productivity suggesting the the "luxury" accumulation of nitrogen at developing root bases is greater than phosphorus. The decreasing ratios during periods of root productivity suggest that either nitrogen "luxury" accumulation is simply diluted as phosphorus levels remain constant or that phosphorus is then reallocated from the rhizomes at a greater rate to meet energy demands of root uptake.

Sediment inorganic N:P ratios are extremely low as expected and seasonally variable. The low ratios are best explained in terms of the apparent limiting availability of inorganic nitrogen while the variability is attributable to the constant flux of nitrogen by plant uptake, chemical processes, and microbial conversion. The decrease in N:P ratios between August and October support the premise that the higher rhizome N:P ratios observed at this time are the result of greater nitrogen uptake at this time. Sediment total N:P ratios decreased as a result of mineralization of organic nitrogen to ammonium which explains the increasing inorganic N:P ratios at this time.

Summary and Conclusions

A comparison of productivity and nutrient dynamics indicate that both Peltandra virginica and Spartina cynosuroides take up, internally cycle, and release to the environment significant levels of nitrogen and phosphorus over an annual cycle. Each species, however, approaches productivity and nutrient cycling individually as a result of local environmental conditions, rhizome storage capacity, and biomass nitrogen and phosphorus demands. As such, the seasonal timing of annual nitrogen and phosphorus fluxes through Peltandra and Spartina reflect individual adaptations to a resource limited environment.

Peltandra seaonal patterns of shoot biomass are characterized by a lag phase in the spring and maximum shoot productivity between May and July while increases in root biomass are apparently asynchronous with periods of peak productivity between July and December. Peltandra appears to have adapted to a resource limited environment through a stable rhizome compartment which is apparently capable of storing nitrogen and phosphorus at sufficient levels to support the majority of both root and shoot productivity through reallocation. As a result, Peltandra tissue nitrogen and phosphorus standing stocks are independent of sediment availability. Root productivity is therefore assumed to function primarily in the resupply of nitrogen and phosphorus to the rhizomes. The rhizome storage capacity and independence on sediment uptake results in relatively low nitrogen and

phosphorus use efficiency although recovery through translocation is high. Peltandra impacts sediment nitrogen and phosphorus standing stocks through annual root uptake and releases significant levels of nitrogen and phosphorus to the surrounding environment through monthly mortality and subsequent rapid decomposition. There is apparently an interaction between nitrogen and phosphorus as indicated by the seasonal patterns of N:P ratios and the correlation of tissue nitrogen and phosphorus standing stocks.

Spartina seasonal biomass patterns are somewhat different, with shoot productivity characterized by two lag phases and reaching a peak in September. Root and rhizome productivity are relatively synchronous with respect to shoot biomass. Spartina appears less capable of supporting observed levels of productivity through rhizome storage and reallocation and therefore depends on significant levels of root uptake. As a result, Spartina tissue nitrogen and phosphorus standing stocks are more dependent on sediment availability. Reduced rhizome storage capacity and required levels of root uptake result in higher nitrogen and phosphorus use efficiency in Spartina although recovery through translocation is low. Spartina impacts sediment nitrogen and phosphorus levels through annual uptake however release to the surrounding environment through mortality and subsequent decomposition occurs over extended periods of time. Like Peltandra, there appears to be an interaction between nitrogen and phosphorus as indicated by the seasonal patterns of N:P ratios and the correlation of tissue nitrogen and phosphorus standing stocks.

The data from this study demonstrates that the macrophyte community and associated sediment compartments endow tidal freshwater marshes with certain structural and functional attributes among them the ability to impact

nitrogen and phosphorus fluxes through uptake, assimilation, and storage. As a result, tidal freshwater wetlands function as a natural buffer between terrestial and aquatic ecosystems while regulating nitrogen and phosphorus fluxes within and to the surrounding environment. This nutrient regulatory capacity helps maintain water quality and stability within the Chesapeake Bay estuarine system.

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