ABSTRACT

Cassondra R. Thomas. THE USE OF NETWORK ANALYSIS TO COMPARE THE NITROGEN CYCLE OF THREE SALT MARSH ZONES EXPERIENCING RELATIVE SEA-LEVEL RISE. (Under the direction of Dr. Robert R. Christian) Department of Biology, August 1998.

Network analysis was used to analyze the nitrogen cycles of three salt marshes on the east coast of the U.S.A.; Great Sippewissett in Massachusetts, Upper Phillips Creek in Virginia, and Sapelo Island in Georgia. A general nitrogen cycle model was constructed after a preliminary review of literature on the Great Sippewissett marsh. This model structure was used to construct 9 networks, one for each zone (creekbank, low marsh, and high marsh) within each marsh, largely using data collected from the literature on the 3 marshes.

The networks were analyzed to determine how nitrogen flowed through each zone. The factors used for analysis included how nitrogen import was exported, how imports related to primary productivity, the amount of nitrogen that cycled within the system, and how mature each zone was. These results were then compared between marsh zones to determine if trends existed. The Friedmans test, a nonparametric statistical test, was used to determine the significance of the trends.

When precipitation and Tidal particulate nitrogen (PN) were the imports, export via burial and denitrification significantly increased in importance moving across the marsh from the creekbank to the high marsh. Nitrogen cycling also significantly increased from creekbank to high marsh. The maturity of marsh was measured using the relative ascendency index and a multicriteria analysis with the expectation that maturity would be

highest in the low marsh. Contrary to expectation, it was determined that maturity increased moving across the marsh from the creekbank to the high marsh.

These patterns were used to evaluate how a marsh may respond to increasing relative sea-level rise. Key factors are the slope and sediment supply. If the marsh is able to migrate overland, increasing the high marsh zone, nitrogen cycling will increase on a per unit area basis, and the marsh will display more characteristics of a mature ecosystem. If, however, the marsh stalls because of a steep slope, the amount of cycling will decrease on a per unit area basis, and the marsh will act less mature. If the supply of sediment is great and the marsh progrades toward the sea, the nitrogen cycling and maturity of the marsh may decrease.

THE USE OF NETWORK ANALYSIS TO COMPARE THE NITROGEN CYCLES OF THREE SALT MARSH ZONES EXPERIENCING RELATIVE SEA-LEVEL RISE

A Thesis

Presented to

the Faculty of the Department of Biology

East Carolina University

In Partial Fulfillment

of the Requirements for the Degree

Masters of Science in Biology

by

Cassondra R. Thomas

August, 1998

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TO COMPARE THE NITROGEN CYCLES OF THREE SALT MARSH ZONES
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ACKNOWLEDGMENTS

I would like to thank Dr. Robert Christian, my thesis director, for introducing me to the world of network analysis and looking at the world through a different lens. I would also like to thank him for the time and effort he has put into this creation, and for all the support he has provided. I would also like to thank my committee members, Dr. Mark Brinson, Dr. Joe Luczkovich, and Dr. Iris Anderson for their willingness to indulge me in this process. I would like to thank Tracy Buck for helping out in the field upon occasion and Debbie Daniel for helping out in the lab and running the CHN analyses. I am grateful to The Nature Conservancy for allowing me access to their property in order to conduct my field experiments. I am eternally grateful to Rick and Erica Inge for saving my computer and my data from utter oblivion. I would like to thank my parents, Robert and Virginia Hahn, for their support and encouragement. And finally, I would like to thank my husband, Christopher Woodcock, for going along on this little adventure and for reminding me to go out every once in a while.

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1.0 INTRODUCTION

Nitrogen is a limiting nutrient in salt marsh environments (Day et al., 1989) and influences the productivity of marshes. Furthermore, how much nitrogen flows through the system and in what direction it flows may affect a marsh's ability to respond to stressors related to relative sea-level rise. Network analysis can be used to assess and comparatively analyze how nitrogen flows through marshes, what the important processes are, and what the total system properties are (Wulff et al., 1989; Christian et al., 1996). I apply network analysis to such an assessment and comparison.

1.1 Nitrogen Cycling in Salt Marshes

Major sources of nitrogen to salt marshes include tidal flooding, nitrogen fixation, and precipitation. Groundwater can also be a major contributor depending on the geomorphology (Valiela et al., 1978; Whitney et al., 1981). Nitrogen fixation is the only microbially mediated source (Capone, 1983). The amount of tidal input to an area of marsh is influenced by elevation of marsh, distance from source, and tidal amplitude. Precipitation occurs throughout marshes. Nitrogen can enter marshes in several forms: ammonium (NH_4^+); nitrate (NO_3^-); nitrite (NO_2^-); dissolved organic nitrogen (DON); and particulate nitrogen (PN). The latter 2 are diverse sources that may include various molecules in dissolved form, in organisms, in detritus, and attached to sediment. The species of imported nitrogen will determine initially what flow paths will be taken.

The dominant internal flows within a salt marsh include primary production and mineralization (Whitney et al., 1981). Some flows are more important in different parts of a marsh. For example, mussels tend to live where the marsh is frequently inundated

(Kuenzler, 1961), making filter-feeding more important in low than high marshes. Also whether a flow, such as decay of plant material, is located above- or belowground may affect its relative importance to total cycling.

Nitrogen may leave a marsh in several ways. Hydrologic export is a major avenue of removal. Numerous papers have addressed this “outwelling” (e.g., Teal, 1962; Odum, 1980, 1984), and whether or not it significantly contributes to an estuary’s food web. Another potentially important export is denitrification (Whitney et al., 1981; Anderson et al., 1997b; Valiela and Teal, 1979a). Denitrifying bacteria use NO_3^- to oxidize organic matter with a by-product of nitrogen gas. Burial of nitrogen as organic matter is very important for marsh maintenance against relative sea-level rise (Good et al., 1982).

1.2 Network Analysis

Different processes, such as those mentioned above, interconnect to form nitrogen cycling. It is common to construct a diagram of the different flows and compartments to help describe and analyze the nitrogen cycle (e.g., Anderson et al., 1997b; Baird et al., 1995). Network analysis is a tool that can be used to compare nitrogen cycles of different systems (Christian et al., 1996). It is a group of analyses for evaluation of the structure of a system, the trophic dynamics, cycling, and total system properties such as maturity and stability. The reader is referred to Kay et al (1989) for a detailed description.

1.3 State Change and Sea Level Rise

Salt marshes located on the east coast of the United States can be divided into different zones that reflect different communities and environmental conditions; the creekbank where the tall form of *Spartina alterniflora* grows, the low marsh where the short form of *S. alterniflora* dominates, and the high marsh which is dominated by different plants depending on its geographical location. Some typical plants of the high marsh are *Juncus roemerianus, Distichlis spicata,* and *S. patens*.

Salt marshes respond to increased inundation caused by relative sea-level rise in different ways depending on their slope and the amount of sediment supply (Brinson et al., 1995). The creekbank either may prograde or erode, and the high marsh may either migrate overland or stall. These changes cause specific areas to experience ecosystem state changes from one zone type to another. As zones undergo change in state, the nitrogen cycle may be altered. For example, primary production, a dominant flow within the nitrogen cycle (Whitney et al., 1981), may be altered as each zone experiences state change (Brinson et al., 1995).

1.4 Statement of the Problem

The purpose of this study is to analyze the nitrogen cycle of different salt marsh zones and postulate how rising sea level may affect it. Three well-studied marshes were used for this study, Great Sippewissett marsh in Falmouth, MA, Upper Phillips Creek marsh near Nassawadox, VA, and Sapelo Island marshes in Georgia. Given that the nitrogen cycle may be altered by increasing sea-level rise, it is important to understand how nitrogen flows through the system, and how it influences the marsh's total system properties. Total system properties such as maturity and stability are related to a marsh zone's ability to respond to stressors and disturbances.

2.0 LITERATURE REVIEW

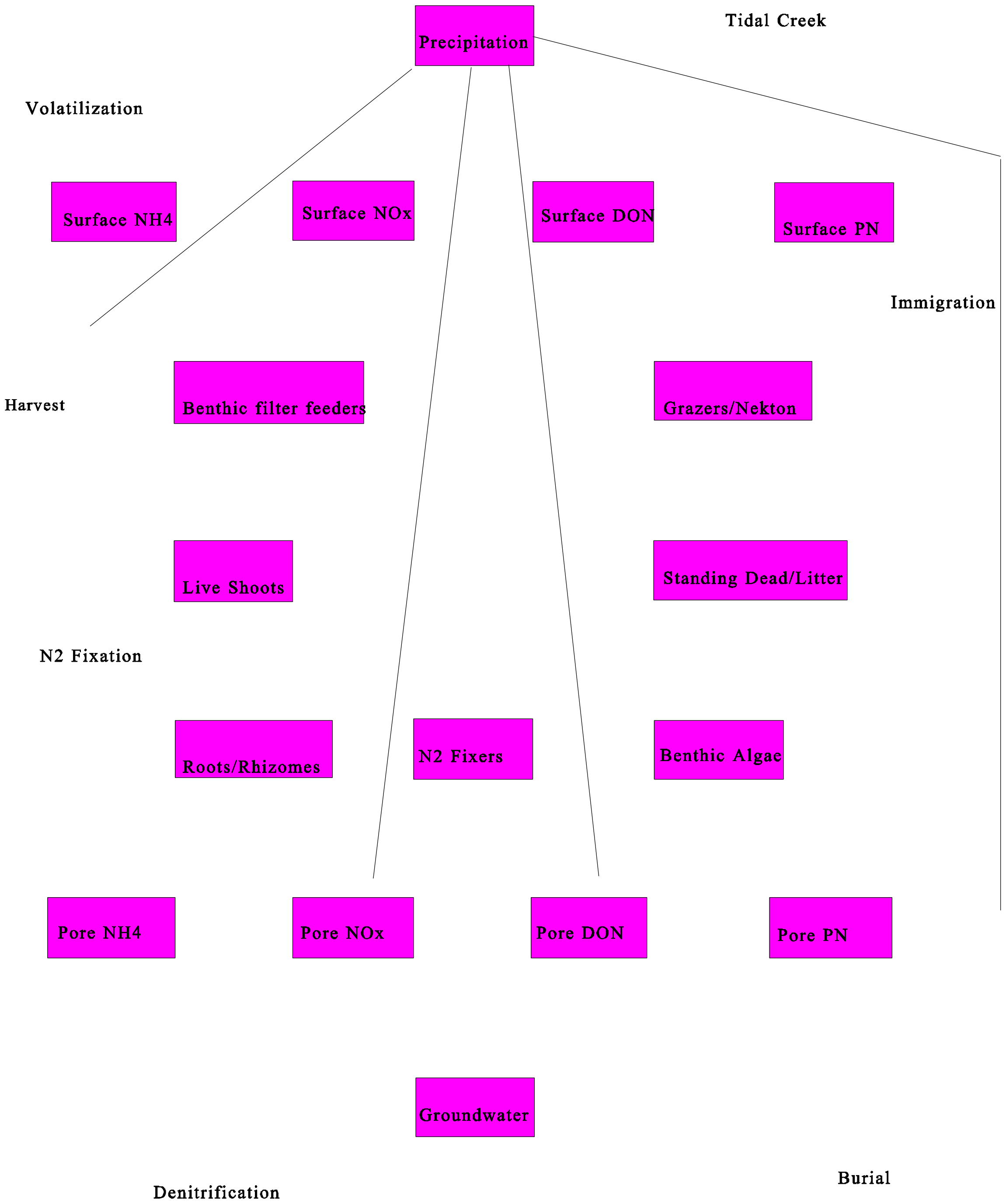
There are a few well-studied marshes along the east coast of the United States, where nutrient cycling was part of the focus. I chose 3 marshes to use for my study; Great Sippewissett in Massachusetts, Upper Phillips Creek in Virginia, and Sapelo Island in Georgia. There are many published studies regarding nitrogen processes in Great Sippewissett and Sapelo Island that span almost 4 decades, 1960s-1990s. I used about 70 articles to create nitrogen cycle models for each marsh. The investigations at Upper Phillips Creek have also produced much data. However, little has been published to date because most experiments were conducted within the last few years. To create models for Upper Phillips Creek, I used the few published articles, the VCR/LTER database (www.vcrlter.virginia.edu), and direct communication with scientists involved in studying the area.

2.1 Nitrogen Cycling in Salt Marshes

Each marsh was divided into 3 zones that represent different flooding regimes and dominant macrophytes. The first zone, Tall, was where the tall form of *S. alterniflora* dominates the plant species, and the area floods during almost every high tide. The second zone, Short, was the low marsh where the short form of *S. alterniflora* dominates, and the area is less frequently flooded by high tides. The third zone, High, was the high marsh where one of several species may dominate including *J. roemerianus, S. patens,* and *D. spicata*. This part of the marsh is rarely flooded by high tides. These zone divisions were used to compare the nitrogen cycle in different areas of marsh. From the literature, I created a generalized nitrogen cycle for salt marshes (Figure 1).

2.1.1 ***Standing Stocks***. Each compartment in Figure 1 represents the standing stock of a potentially important component of the nitrogen cycle in a salt marsh. The compartments that represent the macrophytes include roots/rhizomes, live shoots, and standing dead. The surface water associated with tidal flushing and the sediment pore water were divided into 4 nitrogen species, NH_4^+, NOx, DON, and PN. Surface PN represents bacteria, protists, zooplankton, detritus, and nitrogen attached to sediment particles. Pore PN represents decaying organic matter, microbes and meiofauna, and nitrogen attached to sediment. It also represents material that can be exported as PN arising from standing dead. Nitrogen-fixing bacteria and benthic microalgae were not included in Pore PN but instead given their own compartments in order to better represent their contribution to the nitrogen cycle. The benthic filter feeders are primarily represented by the Atlantic ribbed mussel, *Geukensia demissa* (Finn and Leschine, 1980; Kemp et al., 1990a; Kuenzler, 1961), but theoretically could include all other filter feeders. The Grazer/Nekton compartment is a composite of many common consumers within the marsh system including different species of crabs (e.g., *Uca pugilator*), snails (e.g., *Littorina irrorata*), insects (e.g., *Orchelium fidicinium*), and birds (e.g., *Branta canadensis*) as well as mineralizers found on standing dead and litter. However, data for this compartment were very limited. It theoretically could also include the many species of fish, deer, racoon, and fox, but data were not available in the literature for their contribution to the nitrogen cycle. Furthermore, most of the biological processing of nitrogen is by plants and microbes (Christian and Day, 1989).

Figure 1. Generalized Nitrogen Cycle Model for Salt Marshes



2.1.2 ***Imports.*** The imports into this model include tidal flooding of different nitrogen species, precipitation, groundwater, nitrogen fixation, and immigration by animals. Tidal flooding (Figure 1) is one of the largest sources of nitrogen for the marsh zones. A variety of methods were used to measure the amount of nitrogen within tidal water (Table 1). The differences in estimates may be attributed to methodology and/or other differences.

Table 1. Amount of Tidal Imports of NitrogenUsing Different Methodologies

Marsh	Unit of Import	Duration of study	Methodology	Source
			Flux	
Great Sippewissett	6740-6760 kg PN/yr	7 Years	TSK flow meter/ nutrient analysis	Valiela et al., 1978
Sapelo Island	160 g C/(m2 x yr) (PN)*		simulation modeling	Wiegert, 1986
Sapelo Island	1314 g C/(m2 x yr) (PN)*	1 Year	flume/persulfate oxidation using total carbon analyzer	Chalmers et al., 1985
Great Sippewissett	16300-16346 kg DON/yr	7 Years	TSK flow meter/ Kjeldahl	Valiela et al., 1978
Sapelo Island	2890.8 g C/(m2 x yr) (DON)*	1 Year	flume/persulfate oxidation using total carbon analyzer	Chalmers et al., 1985
Great Sippewissett	2620-2623 kg NH4/yr	7 Years	TSK flow meter/ Technicon autoanalyzer (Solórzano, 1969)	Valiela et al., 1978
Great Sippewissett	540 kg NOx/yr	7 Year	Technicon autoanalyzer (Strickland and Parsons, 1968)	Valiela et al., 1978
			Concentration	
Sapelo Island	14.79 µg PN/l	1.5 Years	micro-Dumas method using nitrogen analyzer	Haines, 1979
Sapelo Island	11.69 µg DON/l	1.5 Years	ultraviolet oxidation (Strickland and Parsons, 1972)	Haines, 1979
			Indophenol blue	

Marsh	Unit of Import	Duration of study	Methodology	Source
Sapelo Island	2.75 µg NH4/l	1.5 Years	method (Koroleff, 1970)	Haines, 1979
Phillips Creek	3.4 µmol NH4/l	5 Years	autoanalyzer (Solórzano, 1969)	VCR/LTER Database
Sapelo Island	1.89 µg NOx/l	1.5 Years	colormetrically (Strickland and Parson, 1972)	Haines, 1979
Phillips Creek	4.25 µmol NOx/l	5 Years	autoanalyzer (Strickland and Parson, 1972)	VCR/LTER Database

*I converted C values into N values using a C:N ratio of 9.5 (Valiela and Teal, 1979b).

Total tidal nitrogen import to the Tall zone ranged from 193.64 g N x m^{-2} x yr^{-1} in Sapelo Island to 80.74 g N x m^{-2} x yr^{-1} in Upper Phillips Creek. The dominant species of nitrogen imported was DON in Great Sippewissett and Sapelo. Tidal DON was not measured in Upper Phillips Creek. In Upper Phillips Creek NOx import exceeded NH_4^+ import.

Nitrogen in precipitation is a very small import compared to tidal flooding. However, it may have a significant influence on primary production (Keene and Galloway, 1997). Similar techniques were used by all scientists to analyze the various nitrogen species found in precipitation. Most followed Strickland and Parsons (1972) and Solórzano (1969) to analyze NOx, DON, and NH_4^+. Total nitrogen import from precipitation ranged from 0.3 g N x m^{-2} x yr^{-1} in Sapelo Island to 0.79 g N x m^{-2} x yr^{-1} in Great Sippewissett.

Groundwater import was a very important source of nitrogen in Great Sippewissett. The other 2 marshes had very little information regarding the contribution of groundwater to the amount of nitrogen imported. The nitrogen content of the groundwater was measured using an autoanalyzer following Strickland and Parsons (1972) and Solórzano (1969) (Valiela et al., 1978). Total nitrogen import ranged from 11.31 to 14.84 g N x m^{-2} x yr^{-1} measured over a 7-year period (Valiela et al., 1978).

Nitrogen fixation is the microbially mediated process by which molecular nitrogen in the atmosphere is reduced by bacteria and cyanobacteria to NH_4^+ (Capone, 1983). The rate of nitrogen fixation is not evenly distributed among zones. For example, Hanson (1977a) found that the activity in the tall *S. alterniflora* marsh was significantly higher than in the short *S. alterniflora* marsh in Georgia. Carpenter et al (1978) found similar patterns among zones in Great Sippewissett during midsummer. They also found that the high marsh had even lower rates.

Nitrogen fixation can be a significant source for a nitrogen-limited ecosystem. In Great Sippewissett Marsh in Massachusetts, it can range from 9-20% of the total nitrogen import (Capone, 1983). It was estimated for this marsh that enough nitrogen was fixed to account for the maximum amount of nitrogen in the aboveground biomass (Van Raalte et al., 1974) and is approximately a third of the needs of primary production (Teal et al., 1979). However, in Phillips Creek marsh, nitrogen fixation is only approximately 5% of primary production (Anderson et al., 1997b). Though acetylene reduction technique (the reduction of acetylene to ethylene as an indicator of the amount of N_2 fixed) was used to determine nitrogen fixation, there were several procedures that differed (Van Raalte et al., 1974, Anderson et al., 1997b).

Literature values are shown in Table 2 for each marsh. There is a wide range of values produced not only within marshes but also between marshes. Some of the between marsh variation may be due to climate as nitrogen fixation rates are higher during warmer temperatures.

Table 2. Nitrogen fixation rates for different marshes

Marsh	Unit of Input ($g\ N \times m^{-2} \times yr^{-1}$)	Duration of Study	Methodology	Source
Great Sippewissett	6.78	7 Years	Acetylene reduction	Valiela and Teal, 1979a
Great Sippewissett	6.43	3 Years	Acetylene reduction	Carpenter et al., 1978
Great Sippewissett	2.67	7 Years	Acetylene reduction	Valiela et al., 1978
Phillips Creek	1	2 Years	Acetylene reduction	Anderson et al., 1997b
Sapelo Island	22.2-52.4	1 Year	Acetylene reduction	Hanson, 1977b
Sapelo Island	6	1 Year	Acetylene reduction	Haines, 1976

Immigration of animals may be very small and is a little-studied pathway of imported nitrogen to salt marshes. Valiela and Teal (1979a) attempted to quantify the amount of nitrogen brought into the marsh by birds. The amount of nitrogen associated with immigration of other animals, including racoons and fishes, was not quantified by Valiela and Teal (1979a).

2.1.3 ***Internal Flows.*** There are many internal flows of the nitrogen cycle. Primary production dominants and contributes to the other flows that dominate the system, such as decay. Primary production may be considered the starting point of most cycles. It is the basis of the food web including the detrital food web as well as the detritus formation/mineralization cycle. The amount of information regarding the cycles varies among marshes and zones. Some processes are very well studied, while others are not.

Accumulation of nitrogen for aboveground primary production is translocated from roots/rhizomes and senescing shoots to live shoots (Figure 1) and varies across marsh zones due to different environmental conditions in each marsh zone (Morris, 1980). In the Tall zone, *S. alterniflora* grows between 1 and 3 m, and aboveground production can range from 700 g x m^{-2} x yr^{-1} in Florida (Kruczynski et al., 1978) to 3700 g x m^{-2} x yr^{-1} in Georgia (Stroud, 1976). In the Short zone the *S. alterniflora* only grows up to 0.8 m, and aboveground production ranges from 130 g x m^{-2} x yr^{-1} in Florida (Kruczynski et al., 1978) to 2895 g x m^{-2} x yr^{-1} in Louisiana (White et al., 1978). The High marsh zone's aboveground production depends on the dominant species. *J. roemerianus* production can range from over 3000 g x m^{-2} x yr^{-1} in Louisiana (Hopkinson et al., 1980) to about 800 g x m^{-2} x yr^{-1} in Virginia (Tolley, 1996) and North Carolina (Christian et al., 1990). *S. patens* can range from 4200 g x m^{-2} x yr^{-1} in Louisiana (Hopkinson et al., 1980) to 600 g x m^{-2} x yr^{-1} in Great Sippewissett (Valiela et al., 1976). *D. spicata* aboveground production can range from 2000 g x m^{-2} x yr^{-1} in Louisiana (Hopkinson et al., 1980) to 600 g x m^{-2} x yr^{-1} in Great Sippewissett (Valiela et al., 1975).

Most aboveground primary production rates are measured in carbon or dry mass using various harvest methods (Table 3). In some cases the Wiegert and Evans (1964) method is applied to estimate production. Production is estimated as the change in live biomass over time plus the change in dead biomass including the disappearance of dead material over time (Wiegert and Evans, 1964). However, Dai and Wiegert (1996) believe that these values may be overestimations of aboveground primary production and physiologically unlikely. They instead propose a canopy model that calculated primary production based on physiology and plant demographics. Using the canopy model, they estimate that primary production in Sapelo Island for tall *S. alterniflora* is 1421 g C x m^{-2} x yr^{-1} and for the short form is 749 g C x m^{-2} x yr^{-1} as compared to 1480 g C x m^{-2} x yr^{-1} for tall (Gallagher and Plumley, 1979) and 540 g C x m^{-2} x yr^{-1} for short (Gallagher et al., 1980) based on Wiegert and Evans (1964) harvest techniques in the same marsh.

Table 3. Aboveground primary production rates

Marsh	Unit of Flow (g dry mass x m^{-2} x yr^{-1})	Duration of Study	Methodology	Source
Great Sippewissett	630	May-November	Harvest (Loss of dead matter=NPP)	Valiela et al., 1975
Great Sippewissett	423.7	May-November	Regression (wt= 0.074 x ht + 15.973)	Valiela et al., 1976
Phillips Creek	442.56-955.7	May-September	Harvest	This study
Phillips Creek	846.9	2 Years	Harvest and Tagging (NPP=Freq of replacement leaves x P/B x biomass)	Tolley, 1996
Sapelo Island	1350-2840	1 Year	Harvest (NPP= biomass x production:biomass) (Gallagher et al., 1980)	Schubauer and Hopkinson, 1984
Sapelo Island	1337-3711	2 Years	Harvest (modified Wiegert and Evans method (1964))	Gallagher et al., 1980

Nitrogen uptake during belowground production from pore water to roots/rhizomes is also a dominant flow of nitrogen (Table 4). Belowground biomass production tends to be higher in the Short zone than the Tall zone. For example, belowground production in Great Sippewissett's creekbank is 3315 g x m^{-2} x yr^{-1} while in the low marsh it is 3500 g x m^{-2} x yr^{-1} (Valiela et al., 1976). The high marsh's primary production depends on the dominant plant species. In Georgia, *J. roemerianus* belowground production was estimated to be 3360 g x m^{-2} x yr^{-1} (Gallagher and Plumley, 1979). *S. patens* ranges from 310 g x m^{-2} x yr^{-1} in Georgia to 3270 g x m^{-2} x yr^{-1} in New Jersey (Good et al., 1982). *D. spicata* ranges from 1070 g x m^{-2} x yr^{-1} in Georgia to 3400 g x m^{-2} x yr^{-1} in Delaware (Good et al., 1982).

Table 4. Belowground primary production rates

Marsh	Unit of Flow (g x m^{-2} x yr^{-1})	Duration of Study	Methodology	Source
Great Sippewissett	3291	7 Years	$^{15}NH_4^+$ Tracer/ Harvest	White and Howes, 1994a
Phillips Creek	676-2143	2 Years	Litter Bag/Harvest	Blum, 1993
Sapelo Island	2100	3 Years	Harvest	Gallagher and Plumley, 1979

Belowground primary production sampling techniques have not been perfected. Usually some sort of harvesting method is employed using corers of various diameters or litter bags (Good et al., 1982; Blum, 1993). Significant sampling error can be introduced throughout the entire process. Cores may become compressed, washing may be incomplete or too rigorous, which can cause a loss of fine root material, and separation criteria of live and dead biomass may vary between investigators (Good et al., 1982).

Physiological factors can also make production estimates difficult. Translocation from aboveground to belowground, death, and aging factors cannot be measured using a harvesting technique (Good et al., 1982).

Translocation is a process, in response to protein breakdown, where aboveground organic nitrogen relocates to belowground biomass (Figure 1) at the end of the growing season for storage over the winter (Larcher, 1995). It can be a significant flow. Hopkinson and Schubauer (1984) determined that potential translocation was approximately 54% of aboveground production in Georgia. However, by comparing the winter increase in belowground nitrogen with the total annual potential translocation (the sum of death and leaching subtracted from aboveground production), they claim that approximately 76% of the potentially translocated nitrogen was not used for winter storage, but instead, was used to support growing-season leaf turnover. White and Howes (1994c) determined that potential translocation, figured in the same manner as Hopkinson and Schubauer (1984), was approximately 38% of aboveground production in Great Sippewissett. They determined that the majority of translocated nitrogen was not used for the following year's growth, but instead, became part of the dead macroorganic matter where it was buried or mineralized. This difference in amount of aboveground nitrogen supplied by translocation from belowground may reflect the longer growing season in Georgia.

Mineralization is the process of transforming organic nitrogen into ammonium (Figure 1), the predominant nitrogen species taken up by salt marsh plants. This process occurs on decaying matter both above- and belowground. Newell et al (1989) found that fungal biomass is the predominant (98%) microbe found on decaying *S. alterniflora* leaves left in the standing position. Nearly all of the dead-leaf nitrogen is incorporated into fungal mass during the initial decay process (Newell et al., 1989). Very little nitrogen is lost to the water column, but instead is translocated to rhizomes, consumed by *Littorina,* or falls to the marsh surface as small particles (Newell et al., 1989).

Belowground mineralization is the result of root and rhizome decay and the turnover of microbial biomass and its exudates (Anderson et al., 1997b). Anderson et al (1997b) could only account for approximately half of the gross mineralization rate with macroorganic matter or aboveground biomass available for decomposition. They propose that the remaining mineralized nitrogen is the result of turnover of nitrogen previously immobilized by bacterial biomass and associated exudates. Table 5 shows various belowground mineralization rates determined with very different methodologies. The litter bag and harvest experiments represent net mineralization, while isotope dilution measures gross mineralization.

The rate of mineralization both above- and belowground is very important in determining the availability of nutrients for plant uptake. If mineralization is inhibited, the dead plant material will accumulate, and eventually the nitrogen will be buried. If mineralization is very rapid there may be very little material available for bioaccretion. In such cases, the system would have to rely on sediment import to accrete at a rate

Table 5. Belowground Mineralization rates

Marsh	Unit of Flow ($g\ N \times m^{-2} \times yr^{-1}$)	Duration of Study	Methodology	Source
Great Sippewissett	14.9-16.3 (net)	7 Years	^{15}N labeled Litter Bag	White and Howes, 1994c
Phillips Creek	84 (gross)	2 Years	$^{15}NH_4^+$ isotope pool dilution	Anderson et al., 1997b
Sapelo Island	70 (net)	Unknown	Unknown	Whitney et al., 1981
Sapelo Island	19.7 (net)	1 Year	Harvest	Hopkinson and Schubauer, 1984

sufficient to maintain marsh elevation relative to sea-level rise.

Leaching from leaves and stems (Figure 1) is a loss of nitrogen for salt marsh plants. In Great Sippewissett, White and Howes (1994c) determined the leaching rate to be 0.4 g N x m^{-2} x yr^{-1} by adding a ^{15}N tracer to the sediment and then exposing the leaves to deionized water. In Sapelo Island, Hopkinson and Schubauer (1984) measured leachate to be 0.7 g N x m^{-2} x yr^{-1} by placing *S. alterniflora* leaves in jars with seawater for 1 hour and then analyzing the water and leaf. Anderson et al (1997b) did not consider leaching in their model which may cause an underestimation of their belowground production estimates (19 g N x m^{-2} x yr^{-1}). However, given the small amount reported by the above authors, Anderson et al's (1997b) belowground production estimate would only be changed by less than 4%.

Filter feeding by mussels can be a major flow in the Tall and Short zones within a salt marsh. The most common mussel is the Atlantic ribbed mussel, *Geukensia demissa* (Jordan and Valiela, 1982). It filters particulates and DON from the water column (Figure 1). It is believed that filter feeding can have a significant effect on the microbial population in the water column, and that it can link the water column with the sediment (Kemp et al., 1990a). Jordan and Valiela (1982) measured the disappearance of suspended particles ranging from 5-15 µm in diameter.in jars filled with seawater, thus ignoring some bacteria (Table 6). Jordan and Valiela (1982) may have underestimated filtration rates because their procedure did not account for a delay in initial filtering and a slowing of filtering when particulates were scarce. Kemp et al (1990a) measured both microbial mass and particulates. They found filtration rates of 1.37 g N x m^{-2} x yr^{-1} were associated with microbial biomass, while particulates removed were as high as 59.6 g N x m^{-2} x yr^{-1}. Kemp et al (1990a) may have overestimated filtration rates because their density of mussels was higher than field density.

Table 6. Filter Feeding Rates of *Geukensia demissa*.

Marsh	Unit of Flow (g N x m^{-2} x yr^{-1})	Duration of Study	Methodology	Source
Great Sippewissett	11.8	2 Years	Disappearance of suspended particles in jars of seawater	Jordan and Valiela, 1982
Sapelo Island	1.37-59.6	1 Month	Water sampling within enclosed pots	Kemp et al., 1990a

Excretion and biodeposition by *G. demissa* (Figure 1) were measured in the same manner as filter feeding by Jordan and Valiela (1982). They found excretion to be approximately 3.24 g N x m^{-2} x yr^{-1}, while biodeposition was 5.9 g N x m^{-2} x yr^{-1}. Other species' feeding, excretion, and biodeposition are not widely studied in the context of nitrogen flow.

Nitrification is an aerobic microbial process performed in 2 steps where NH_4^+ is oxidized first to NO_2^-, and NO_2^- is then further oxidized to NO_3^-. These bacteria use the oxidation of NH_4^+ and NO_2^- to fix CO_2 and obtain energy (Atlas and Bartha, 1993). Nitrification is a critical component of the nitrogen cycle (Figure 1). In the soil, nitrifiers compete with plants for NH_4^+, but at the same time rely on them to create an oxidized rhizosphere around their root system (White and Howes, 1994a; Taylor, 1995). The nitrification process's byproduct, NO_3^-, is a source of terminal electron acceptors for denitrifying bacteria so that they can oxidize organic matter (Atlas and Bartha, 1993). Very few studies have been conducted that compare the rate of nitrification across marsh zones. However, Anderson et al (1997b) found a rate of 4 g N x m^{-2} x yr^{-1} for the Short zone using the $^{15}NO_3^-$ isotope pool dilution. The estimate for Great Sippewissett is 9.8-19.92 g N x m^{-2} x yr^{-1} (Valiela, 1983; Finn and Leschine, 1980). However, direct measurements were not made.

2.1.4 ***Outputs.*** There are 4 main export routes of nitrogen from a salt marsh (Figure 1). They include tidal flushing, burial, denitrification, and loss of animals either through harvest or migration. Tidal flushing is the major source of nitrogen output from a salt marsh. Measurements of tidal output were made in the same way as tidal import in Section 2.1.2. Therefore, wrack export is not considered.

Burial may be an important loss of nitrogen from a salt marsh. Burial helps a marsh maintain its elevation relative to sea-level rise (Good et al., 1982). This may be especially important in high marshes where low-frequency flooding causes peat formation (Good et al., 1982). Table 7 shows the burial rates estimated in a variety of ways.

Assuming a C:N ratio of 38 (Gallagher and Plumley, 1979), Wiegert's estimations equal approximately 0.53-0.68 g N x m^{-2} x yr^{-1}, significantly less than the 3.2-4.6 g N x m^{-2} x yr^{-1} measured by White and Howes (1994c) for Great Sippewissett. Anderson et al's (1997b) estimate agrees well with the rates for Great Sippewissett.

Table 7. Burial Rates

Marsh	Unit of Flow	Duration of Study	Methodology	Source
Great Sippewissett	3.2-4.6 g N x m^{-2} x yr^{-1}	7 Years	^{15}N tracer/Litter Bag	White and Howes, 1994c
Phillips Creek	4.0 g N x m^{-2} x yr^{-1}	2 Years	Accretion=Sea-Level Rise	Anderson et al., 1997b
Sapelo Island	20-26 g C x m^{-2} x yr^{-1}		Simulation Modeling	Wiegert, 1979, 1986

Denitrification is the only microbially mediated export of nitrogen from a salt marsh. It is the process used by facultatively anaerobic bacteria to oxidize organic material using NO_3^- as a terminal electron acceptor. The byproduct is dinitrogen gas which is exported from the marsh system. The creekbank area has the highest rate of denitrification of the three marsh zones in Great Sippewissett (Kaplan et al., 1979). This is believed to be the result of renewed NO_3^- supply by tidal flushing. The high marsh had the lowest rate of denitrification (Kaplan et al., 1979). This can be a significant source of nitrogen loss to the marsh and is not necessarily offset by nitrogen fixation input (Kaplan et al., 1979). However, Anderson et al (1997b) found denitrification to be a fairly small flow (0.6 g N x m^{-2} x yr^{-1}). They considered that their estimate may be an underestimation of the true rate because denitrification may be constrained by nitrification rates due to low concentrations of NO_3^- in Phillips Creek. But, they claim that denitrification is probably not an important loss of nitrogen from the marsh (Anderson et al., 1997b). Taylor (1995) found that denitrification increased when the area is disturbed by wrack in the high marsh of upper Phillips Creek marsh, Va.

Table 8 shows the various methods employed by the authors to measure the rate of denitrification. There is a wide range of rates given. According to Capone (1997), direct measures of N_2 fluxes, such as used by Kaplan et al. (1979) are not sensitive to small increases because of the large N_2 background. Tracer techniques, as used by White and Howes (1994a) and Anderson et al (1997b) offer more direct methods of measurements but can be misled by artificially elevated substrate pools (Capone, 1997). Acetylene block is viewed as a sensitive measure of denitrification except under conditions of low ambient NO_3^-, which is almost always true in salt marshes, or when S^{2-} is present (Capone, 1997). If this is the case, rates are likely to be underestimated (Capone, 1997).

Table 8. Denitrification rate.

Marsh	Unit of Flow	Duration of Study	Methodology	Source
Great Sippewissett	6.85-20.32 g N x m^{-2} x yr^{-1}	1 Year	Bell jar/Gas partition	Kaplan et al., 1979
Great Sippewissett	4.1-5.6 g N x m^{-2} x yr^{-1}	7 Years	Mass balance using $^{15}NH_4^+$	White and Howes, 1994a
Phillips Creek	0.6 g N x m^{-2} x yr^{-1}	2 Years	$^{15}N_2O$ isotope pool dilution	Anderson et al., 1997b
Phillips Creek	0-75.8 µmol x m^{-2} x hr^{-1}	6 months	Acetylene block	Taylor, 1995
Sapelo Island	12 g N x m^{-2} x yr^{-1}	6 months	N_2 Flux	Haines et al., 1977

Harvest of mussels from the marsh for human consumption is a very small export route. Valiela and Teal (1979a) quantified this route for Great Sippewissett. However, their estimate for harvesting was very rough. Many marshes do not have this export route. Emigration by animals is not considered here.

2.2 Maturity/Stability

Maturity can be defined in several ways; the state of age, development, and perfection are some. For my purposes, I adopt the concept of Ulanowicz (1986) which posits that within a mature system, the inputs, outputs, and interactions are organized in such a manner as to pass units of flow efficiently and "most effectively participate in autocatalytic activities" (Ulanowicz, 1997). Autocatalytic activities are positive feedback cycles, where an increase in flow to one part of the cycle will increase the flow of the total cycle. A measurement of this definition of maturity is Ascendency (Ulanowicz, 1986). Stability, on the other hand, is the ability of a system to resist destructive change caused by perturbations. Perturbations may be caused by short term stressors, (e.g., tropical storms), or long term stressors, (e.g., relative sea-level rise). The system's ability to recover or adapt to perturbations as appropriate is its level of stability. A measure of this is Overhead (Ulanowicz, 1986) (Section 2.2.2).

There are theories about what a mature system is (Odum, 1969; Ulanowicz, 1986) and how to measure the level of maturity of a system. Odum (1969) developed a list of criteria for ecological succession from developmental to mature stages based on old field succession, sand dunes, and marine shores. Ulanowicz (1986) developed some measurements of maturity based on information theory and systems analysis. Christensen (1994, 1995) evaluated “goal functions” for ecosystem maturity that can be measured. He analyzed several possible goal functions based on Odum’s list of maturity characteristics. What follows is a summary of an attempt to define and characterize maturity and stability.

2.2.1 ***Succession to Maturity and Stability.*** In 1969, Odum published a seminal paper entitled “The strategy of ecosystem development” in *Science*. In this paper, he attempted to define ecological succession from a developmental standpoint. He believed that succession followed three parameters; “(1) succession was orderly, directional, and predictable, (2) it resulted from modification to the environment by the community within the constraints of physical factors, and (3) the end result was a stable community with maximum biomass and symbiotic functions between organisms” (Odum, 1969). For an ecosystem to undergo succession, there must be a fundamental shift in energy flows toward maintenance. This shift is characterized by a phenomenon called “Maximum Power” by H.T. Odum and Pinkerton (1955). The system that gets the greatest useful energy per unit time is more likely to “survive.” Maximum power is almost always less than maximum efficiency, and usually no more than 50% of ideal reversible efficiency (Odum and Pinkerton, 1955).

Using the above phenomenon as well as field studies of ecosystems, E.P. Odum developed a list of 24 attributes he felt represented successional changes (Table 9). They were divided into six areas; community energetics, community structure, life history, nutrient cycling, selection pressure, and overall homeostasis. Odum proposed that these attributes could help quantify mature stages of ecosystem development and help in testing hypotheses. He felt that the attributes for overall homeostasis were the most likely to be true for all ecosystem types (Odum, 1969). This model has become the basis for new theories and methodologies concerning the maturity and stability of an ecosystem, such as Ulanowicz.

Table 9. Odum's (1969) 24 Attributes of Ecological Succession.

Ecosystem Attributes	Developmental Stages	Mature Stages
Community energetics		
Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1
Gross production/standing crop biomass (P/B ratio)	High	Low
Biomass supported/unit energy flow (B/E ratio)	Low	High
Net community production (yield)	High	Low
Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
Community structure		
Total organic matter	Small	Large
Inorganic nutrients	Extrabiotic	Intrabiotic
Species diversity-variety component	Low	High
Species diversity-equitability component	Low	High
Biochemical diversity	Low	High
Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well-organized
Life History		
Niche specialization	Broad	Narrow
Size of organism	Small	Large
Life cycles	Short, simple	Long, complex
Nutrient cycling		

Ecosystem Attributes	Developmental Stages	Mature Stages
Mineral cycles	Open	Closed
Nutrient exchange rate, between organisms and environment	Rapid	Slow
Role of detritus in nutrient regeneration	Unimportant	Important
Selection Pressure		
Growth form	For rapid growth (r-selection)	For feedback control (K-selection)
Production	Quantity	Quality
Overall homeostasis		
Internal symbiosis	Undeveloped	Developed
Nutrient conservation	Poor	Good
Stability (resistance to external perturbations)	Poor	Good
Entropy	High	Low
Information	Low	High

2.2.2 ***Ascendency and Developmental Capacity.*** Ulanowicz has used information theory to develop indicators of maturity and stability (1986). Based on Odum's hypothesis that ecosystem self-regulation is dependent upon the probable pathways taken by a unit of flow within a system, Ulanowicz used the Shannon-Wiener Index of diversity of flows scaled by the total amount of flow through a system or total system throughput (TST) to determine an ecosystem's Developmental Capacity (Ulanowicz, 1980). This represents the ecosystems upper limit for self-organization.

To determine how much information is contained within a system, the average mutual information (AMI) of flow structure is determined. This is a measure of constraint exerted upon a random unit of flow as it moves from one compartment to another

(Ulanowicz, 1997). In Figure 2, two systems representing different AMIs are shown. The one with an even distribution of flows (A) has a lower AMI than the one with more constrained flows (B). The system with the higher AMI is considered to contain more information. Ulanowicz (1986) scaled the AMI by total system throughput (TST) and called it Ascendency. This represents the portion of Capacity that consists of flows that contain information and thus, are considered organized. It is postulated by Ulanowicz (1986) to represent the maturity of a system. Relative Ascendency is Ascendency divided by Capacity (Ulanowicz, 1986). This measure of maturity can be used to compare different systems or the same system over time (Ulanowicz and Wulff, 1991; Baird and Ulanowicz, 1989).

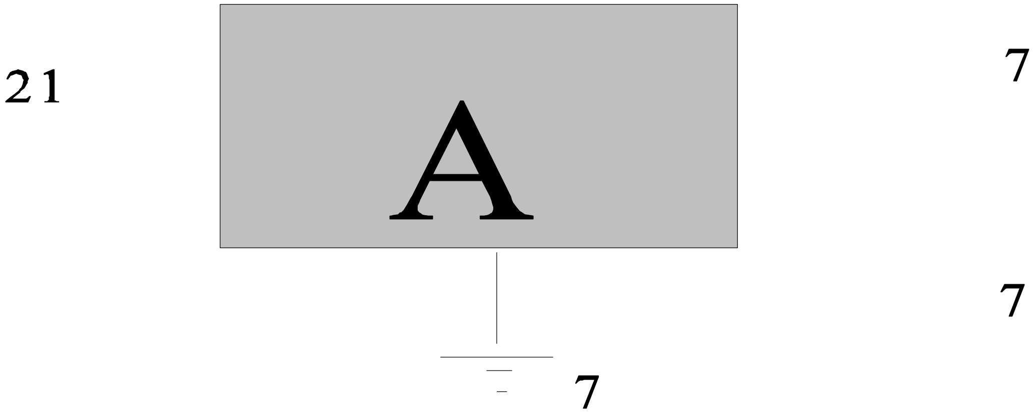
The portion of Capacity not accounted for by Ascendency is called Overhead. This is the part of system complexity that is not organized. Overhead can be divided into 4 parts; uncertainty associated with inputs, uncertainty associated with output, uncertainty associated with dissipations (respirations), and pathway redundancy (Ulanowicz, 1986). Redundancy is believed to be an indicator of stress (Ulanowicz, 1997). For example, a large number of redundant pathways present in a system may represent a system that is adapting to stress.

Ascendency can grow at the expense of overhead. Capacity is limited by a finite source of new inputs and outputs and by the instability of small compartments (Ulanowicz, 1997). With a fixed capacity, as ascendency increases, overhead must necessarily

Figure 2. Systems with Different Average Mutual Information

Box A - The flow is evenly distributed and thus has a low AMI

Box B - The flow is more constrained and thus has a high AMI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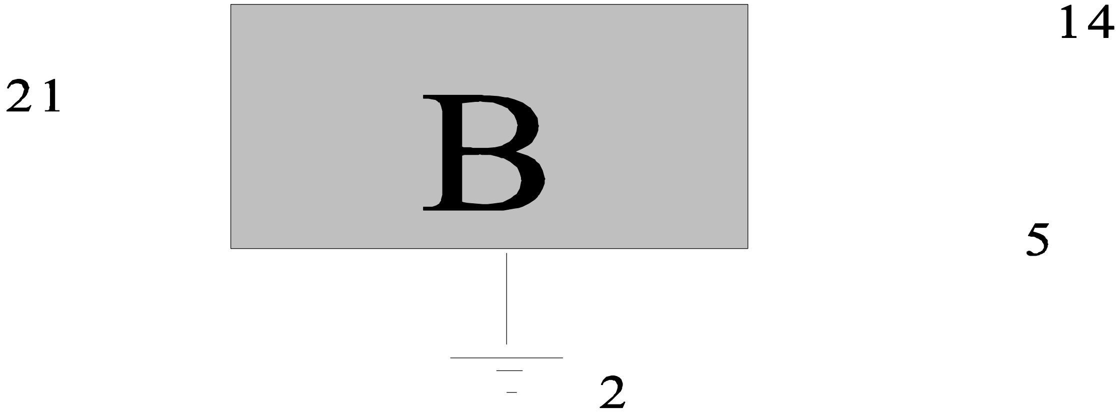
7
7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B
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2

decrease. This could result in decreased redundancy, increased efficiency of imports, increased efficiency of exports, or increased efficiency of dissipations. However, a system can never reach its total capacity. Overhead is needed as a buffer to perturbations (Ulanowicz, 1997). Without it, the system will become brittle, and fall apart with seemingly low levels of stress. Therefore, overhead is believed to be a measure of stability (Ulanowicz, 1997).

Ulanowicz has compared ascendency and capacity as a measure of ecosystem development in relation to Odum's (1969) 24 attributes of successional maturity (Table 9). He believes that 15 attributes are in agreement with ascendency and the remaining 9 are non-inconsistent (Ulanowicz, 1980). Cycling of material is a major contributor to ascendency, as it is a source of organized flow (Ulanowicz, 1980). Several of Odum's (1969) attributes are related to cycling including greater retention of nutrients within the system, increased reliance on detritus, lower P/B ratio, and greater proportions of intrabiotic nutrients (Ulanowicz, 1980). Other attributes that correspond with an increase in ascendency include species and biochemical diversity, specialization, higher information, and internal symbiosis (Ulanowicz, 1980).

2.2.3 ***Empirical Tests of Development Attributes.*** Christensen (1994) has made an attempt to evaluate indicators of maturity and stability in relation to Odum's 24 developmental attributes (Odum, 1969). He referred to these indicators as "goal functions" (1994), and he compared various goal functions, such as ascendency, to Odum's developmental attributes to determine if the indicator is in agreement with Odum.

To do this, he used 41 static models of various aquatic environments from Christensen and Pauly (1993b) (Christensen, 1994). The models were ranked based on 7 "goal functions" of Odum's attributes that could be measured by ECOPATH II, a software package for network analysis. They were biomass/primary production (B/P), biomass/TST, the proportion of flow originating from detritus, flow diversity, production/biomass (P/B), average path length, and residence time. He examined how ascendency, relative ascendency (ascendency/capacity), and exergy (amount of free energy of a system relative to its environment), correlated with these 7 "goal functions" and hence, maturity *sensu* Odum (Christensen, 1994). He found that relative ascendency was the most strongly correlated with maturity *sensu* Odum; however, the correlation was negative (Christensen, 1994). Ascendency and exergy did not correlate with maturity. In an earlier paper, Christensen and Pauly (1993b) evaluated the Finn Cycling Index (FCI) in relation to maturity and found that it might be related to maturity.

In a later paper, Christensen (1995) expanded the goal functions to include total overhead and internal redundancy. He found that total overhead, a measure of system stability, was strongly correlated with maturity. However, internal redundancy, believed by Ulanowicz to be a better indicator of stability than total overhead, did not correlate as well with maturity (Christensen, 1995). He concluded that measures of stability are probably also measures of maturity (Christensen, 1995).

Christensen's (1995) comparison of ascendency to Odum's (1969) maturity attributes may not be adequately reflected in his maturity index. In the 1995 paper, Christensen used 10 of Odum’s 24 attributes to represent maturity. The other attributes were removed from consideration after they were analyzed for cross-correlation. Christensen (1995) was concerned that highly correlated attributes would introduce bias into the analysis if all were used. Of these 10 attributes selected to represent maturity, Ulanowicz (1980) proposed that only 5 result in increased ascendency; P/B ratio, B/E ratio, growth forms, and both variety and equitability species diversity (Table 9). Two of the attributes used by Christensen (1995) are not reflected in the measure of ascendency, the P/R ratio and the average size of organisms (Table 9). The remaining 3 attributes—dominant food chain, nutrient exchange rate, and entropy—are ambiguous as to how they relate to ascendency (Ulanowicz, 1980). Therefore, it may be unwarrented to make comparisons of maturity and ascendency using maturity indicators that are not reflected in the measure of ascendency. Of Odum’s (1969) 24 attributes of maturity, Ulanowicz (1980) believed 15 were reflected in ascendency. Christensen only focused on 5 (1995). Of the 5 attributes Ulanowicz (1980) was unsure how they related to ascendency, Christensen focused on 2 (1995). And of the 4 attributes Ulanowicz (1980) believed were not reflected in ascendency, Christensen focused on 2 (1980). By trying to avoid bias, Christensen may have weakened his index of maturity or at least his ability to compare it to ascendency.

2.3 Network Analysis and Its Use Comparing Nitrogen Cycling

Ulanowicz developed a software program entitled NETWRK that uses network analysis to evaluate a system’s structure including Information Indices such as capacity, ascendency, and overhead. The latest version is NETWRK4.2 (Ulanowicz, 1998). Network analysis is a group of analyses that employ a variety of mathematical techniques to evaluate a system qualitatively and quantitatively. For a more detailed description, the reader is referred to Section 4.5. of this paper, to Kay et al. (1989), and to the documentation for NETWRK 4.2 (Ulanowicz, 1998).

A few investigators have used network analysis to analyze the nitrogen cycle of aquatic systems, especially estuarine (Forès and Christian, 1993; Forès et al., 1994; Baird et al., 1995; Christian et al., 1996; Christian et al., 1997). The 2 main approaches to comparing static networks of systems are to compare the same system at different times (Forès and Christian, 1993; Forès et al., 1994; Baird et al., 1995; Christian et al., 1997), and to make comparisons among systems (Christian et al., 1996). Important aspects of model comparison are that the models have the same units of medium (e.g., g N x m^{-2} x yr^{-1}), and that they have similar topology, flow structure, and degree of aggregation (Baird and Ulanowicz, 1993). This means that the models are similar in the number of compartments, the way compartments are interconnected, and degree of aggregation (DIN vs. NO_2^-, NO_3^-, and NH_4^+). Many indices respond to model structure. For example, the average path length (APL) is highly dependent on the number of compartments. A 4-compartment model may have a very different APL that a 20-compartment model, and comparisons between the models would be ill advised.

In comparing the nitrogen cycle of 5 coastal systems, 2 of which were dominated by rooted macrophytes, Christian et al (1996) determined that the life form and life cycle of primary producer had a significant effect on cycling. Phytoplankton have a much shorter turnover time than rooted macrophytes. This increases the amount of material cycled within the system significantly (Christian et al., 1996).

Christian et al. (1996) also discussed the meaning of cycling in the context of foodweb models versus biogeochemical models. Foodweb models generally focus on carbon flow as a substitute for energy flow. Cycles involve only organic matter. Biogeochemical models focus more on primary production and microbial processes (Christian et al., 1996). Therefore indices that measure cycling such as the Finn Cycling Index (FCI) (the percent of total flow that is involved in cycles) will have different interpretations for the different model types (Christian et al., 1996). Baird and Ulanowicz (1993) found in foodweb models that increased FCI was not an indicator of maturity but of stress. As the system becomes more stressed food chains shorten, causing material to cycle faster. However, in biogeochemical models, the foodweb is only a small part of the total model. Christian et al (1996) found that stress in the form of eutrophication was associated with a lower FCI. Dead organic matter also plays a different role in biogeochemical models than foodweb models. In biogeochemical models dead organic matter can be one of several nonliving compartments, whereas in foodwebs, dead organic matter is the only nonliving compartment.

2.4 Sea-Level Rise

Sea level has been rising since the end of the last glacial maximum approximately 18,000 years ago. There was a rapid rise in eustatic sea level during the early Holocene period, but it slowed around 4,000 years ago to the current rate of approximately 0.11-0.12 cm/year (Orson et al., 1985; Kana et al., 1984). Based on climate models, the rate of sea-level rise is predicted to increase substantially over the next half century. Though there are a number of model predictions based on different assumptions, most predict a global average rise in sea level due to all causes of 0.3-0.6 cm/year (Warrick et al., 1996).

From another perspective, along the east coast of the United States, over the past 8,000 years, relative changes in sea-level ranged from 22 m in Virginia to 18 m in New York, which equals 0.275 cm/yr for Virginia and 0.222 cm/yr for New York (Peltier, 1985). It is believed that the majority of this increase in sea level is due to glacial isostatic adjustment rather than thermal expansion (Davis, 1987). For the time period 1940-1980, the average relative sea-level rise for the east coast of the United States was 0.25±0.017 cm/yr (Davis, 1987).

2.5 Ecosystem State Change

Ecosystem state change is the transformation of one ecosystem class to another (Brinson et al., 1995). Brinson et al (1995) recognized 5 distinct ecosystem classes in salt marsh landscapes; upland or wetland forest, organic high marsh, mineral low marsh, autotrophic benthic system, and heterotrophic benthic system. For a given rate of rising sea level, the rate of state change from one class to another depends on slope, sediment supply, bioaccretion rate, and inundation frequency.

The geomorphic settings of tidal marshes were divided by Brinson et al (1995) into four types depending on slope and sediment supply (Figure 3). The first type of marsh is

Figure 3. Classes of Salt Marshes Responding to Rising Sea Level

(From Brinson et al., 1995)

Box A–Example of a marsh that is expanding as a result of increased inundation in two directions, toward the creekbank due to high sediment supply and overland due to a gentle slope.

Box B–Example of a marsh that is expanding overland due to increased inundation but is eroding at the creekbank due to a low sediment supply.

Box C–Example of a marsh that is stalling at a steep slope and expanding toward the creekbank due to a high sediment supply.

Box D–Example of a marsh that is stalling at a steep slope and eroding at the creekbank due to a low sediment supply.

Sediment Supply

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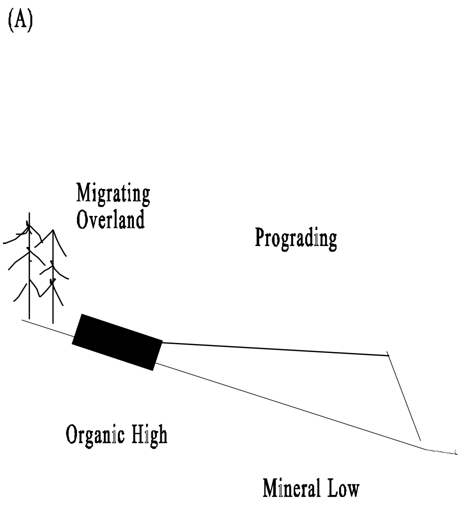
Slope</td><td>


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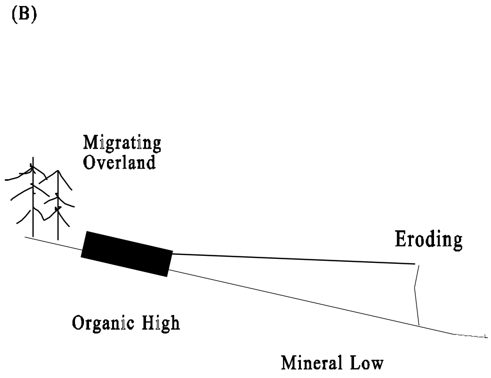

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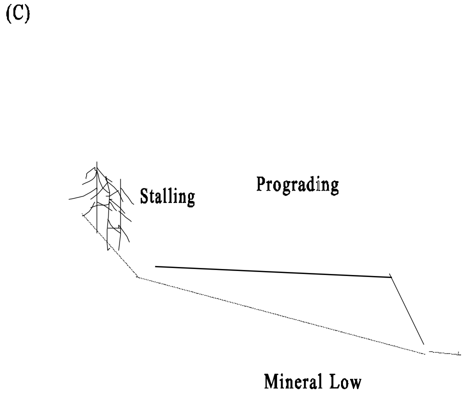
<tr><td>Steep
Slope</td><td>


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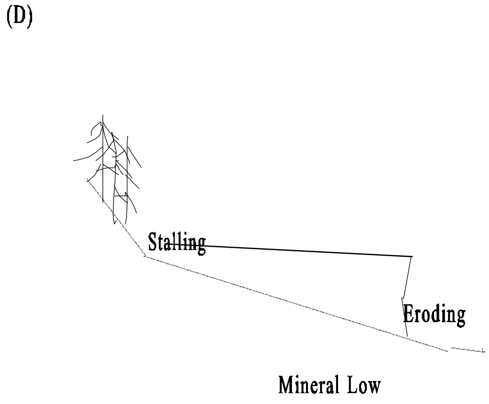

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</table>

From Brinson et al., 1995

an expanding marsh. It has a gentle slope and a high sediment supply. It responds to sea-level rise in two ways. It progrades toward the estuary due to sediment surpluses, and it transgresses overland into the terrestrial forest with rising sea level. This is exemplified by the Barnstable Marsh in Massachusetts and along the Georgia coast (Redfield, 1972; Pomeroy and Wiegert, 1981). The second type of marsh erodes at the creek bank but transgresses toward the terrestrial forest. It is found in areas that have a gentle slope but a low sediment supply. It can be either a maintaining, expanding, or submerging marsh depending on the rate of erosion and overland transgression. This type of marsh can be found in the Mississippi Delta and the Virginia Coast Reserve (VCR) on the eastern shore of Virginia (Brinson et al., 1995). The third type of marsh is another type of expanding marsh. It is found in areas with steep slopes and a high sediment supply. It is unable to transgress overland because of the slope. This is called stalling. Because of the high sediment supply, it is able to prograde toward the estuary (Brinson et al., 1995). The last type of marsh is a submerging marsh. It is eroding at its creekbank and stalling at the forest because of the steep slope. This type of marsh is relatively common at the VCR (Brinson et al., 1995).

2.5.1 ***Maintenance.*** Marshes can maintain their level relative to sea-level rise when there is sufficient sediment and/or peat accumulation. Increased flooding may bring in additional sediments and nutrients to a marsh, which may increase primary production and thus peat accumulation (The Working Group on Sea Level Rise and Wetland Systems, 1997). Major sources of mineral and organic sediment include: sand, silts, and clays from the marine environment or upland erosion; particulate organic material from outside the system; and organic material produced within the system such as roots, rhizomes, and litter from vegetation (Orson et al., 1985).

A negative feedback loop is associated with wetland level maintenance. If marsh elevation is relatively low, it is inundated frequently by tides. This brings in sediment and nutrients, which may enhance plant productivity. With increased plant productivity, there is a greater build-up of organic matter within the sediment from root and rhizome growth as well as litter from the plants. The part of primary production that is not decomposed becomes peat. As the marsh vertically accretes, the tidal water is unable to penetrate the marsh at the same level as before thus reducing the frequency and depth of flooding. This reduces the amount of sediment and nutrients the marsh receives, decreasing primary productivity. This decrease in primary production causes a slowing of the rate of accretion because of decreased peat formation and sedimentation (The Working Group on Sea Level Rise and Wetland Systems, 1997). This feedback mechanism maintains the low marsh relative to sea level. It is when this maintenance feedback loop does not function that marshes expand or submerge.

2.5.2 ***Expansion.*** As can be seen in Figure 3, the marsh may prograde toward the estuary and/or migrate overland (Brinson et al., 1995). Marshes that are able to increase their area by migrating over upland areas begin when upland areas experience infrequent tidal floods caused by extremes such as storms and hurricanes. The salt water infiltrates the soil at a high enough salinity (5-15‰) to result in water stress and possibly sulfide toxicity (Brinson et al., 1995). If soil salinity increases enough, the upland plants will begin to die. The forest soils will be transformed to marsh soils by salinization, deposition of marine sediments, and the accumulation of sulfide by sulfate reduction (Dame et al., 1992). This allows high marsh plants to begin to invade the area. Slope of the land and distance from the tidal creek determine the rate of the conversion from upland to high marsh (Brinson et al., 1995). In areas where the slope is gentle and the creek is close to the forest, salinity and H_2S concentration in forest soils are higher than in areas where the slope is steep and the creek is far from the forest (Hmieleski, 1994).

2.5.3 ***Submergence.*** A marsh can also be converted to open water in response to an increased relative sea-level rise (Brinson et al., 1995). To maintain its elevation relative to sea level, a marsh must accrete either through mineral sediment accumulation or peat accumulation (Orson et al., 1985). When one of these two does not occur at a rate sufficient to maintain its level relative to sea level, the marsh begins to submerge. When tidal flooding increases, headward creek erosion and shoreline erosion can occur under low sediment supply (Brinson et al., 1995). Erosion and wrack deposition can reduce or eliminate vegetation resulting in a mud flat (Brinson et al., 1995). The mud flat may be recolonized by *S. alterniflora* or become subaquatic (Brinson et al., 1995). In either case macrophyte primary production is reduced.

The reduction in plant production also reduces the sediment trapping ability of the marsh. The reduction in primary production results in fewer stems to baffle the incoming waves, and thus less sediment is deposited on the marsh surface. There is also less opportunity for bioaccretion (Orson et al., 1985). This creates a positive feedback loop that further reduces primary production (Orson et al., 1985). As the marsh loses its sediment-trapping ability and primary production, it is subjected to increased flooding and erosion which reduces its sediment trapping ability and primary production. The marsh will eventually become open water (Orson et al., 1985; Brinson et al., 1995).

3.0 GOALS OF RESEARCH/HYPOTHESES

3.1 Research Goals

The three main goals of my research are to compare the nitrogen cycle of three different ecosystem zones within salt marshes, assess how the nitrogen cycle may reflect the zone's maturity and stability, and determine how relative sea-level rise may affect the nitrogen cycle of marshes. One aspect of the nitrogen cycle to be examined is how imports of nitrogen are exported from the system and if there are any patterns across marsh zones associated with the export routes. Another aspect to be examined is how flows within the system relate to primary production and determine if any patterns exist across marsh zones. The third aspect to be examined is how the nitrogen cycle reflects to the marsh zone's maturity and stability. Using the outcome from these examinations, I will postulate how the nitrogen cycle may be affected by rising relative sea-level and how that may affect the maturity and stability of the entire marsh.

3.2 Hypotheses

I have postulated 3 specific relationships within the context of the overall study. My first hypothesis concerns the comparison of the amount of cycling within each marsh zone. I hypothesize that the relative amount of cycling will increase from the creekbank/tall *S. alterniflora* marsh zone to the high marsh as tidal exchanges decrease. The Finn Cycling Index and Average Path Length [(TST-Inputs)/Inputs] are used to determine amount of cycling.

The second hypothesis concerns that relative rate of mineralization. As the import of nitrogen decreases from creekbank to the high marsh resulting in lower TST, I hypothesize that the relative rate of mineralization and its importance to primary production will be highest in the high marsh. The relative mineralization rate will be determined with respect to TST, cycled throughput, and primary production. The mineralization rate's importance to primary production will be determined using the Total Contribution and Total Dependency matrices within Netwrk4 (Section 4.5.2).

The third hypothesis is related to the developmental maturity of each zone. The index used to compare marsh maturity is called relative ascendency and was developed by R.E. Ulanowicz (1986). I hypothesize that relative ascendency (ascendency/capacity) will be highest for the low/short *S. alterniflora* marsh zone because under conditions of rising sea level it is the zone that experiences the least extreme conditions associated with state transition (Brinson et al., 1995).

4.0 METHODS AND MATERIALS

4.1 Research Design

I used network analysis to evaluate the differences in nitrogen cycling between marsh zones. Three well-studied marshes, representing different latitudes, were divided into 3 different zones that represented various flooding regimes and plant communities. The first zone was the creekbank, referred to as "Tall." In all three marshes selected, the creekbank is considered to be flooded by all high tides and is dominated by the tall form of *S. alterniflora*. The second zone was the low marsh, referred to as "Short." This area was considered to be flooded by 50% of all high tides and is dominated by the short form of *S. alterniflora* in all three marshes. The third zone was the high marsh, referred to as "High." This area of the marsh is considered to be flooded by 10% of all high tides and is dominated by plants locally found in high marsh areas. These include *S. patens, D. spicata*, and *J. roemerianus* (Table 4.2.1).

4.2 Site Descriptions

The 3 marshes used to compare nitrogen cycles of different zones were Great Sippewissett Marsh in Massachusetts, Upper Phillips Creek Marsh in Virginia, and Sapelo Island Marshes in Georgia (Table 10 for site descriptions). All are located along the eastern seaboard of the USA.

4.2.1 *Great Sippewissett Marsh*. Great Sippewissett Marsh is located in Falmouth, MA near Woods Hole (41°35'N, 70°38'W) and is approximately 48 ha in size (Finn and Leschine, 1980) (Table 11 for zone characteristics). It is tidally fed by Buzzards

Table 10. Site Descriptions

	Great Sippewissett	Phillips Creek	Sapelo Island
Age	2,000 years (Valiela, 1983)	200 years (Chambers et al., 1992)	15,000 years (Hoyt, 1967)
Geomorphic Setting	Mainland	Mainland	Barrier Island
Tidal Range (mean)	1.6 m (Valiela, et al., 1978)	1.9 m (Anderson et al., 1997b)	2.4 m (Schubauer and Hopkinson, 1984)
Surface Water Salinity	32 ppt (Carpenter, et al., 1978)	9-33 ppt (Hmieleski, 1994)	15-28 ppt (Pomeroy et al., 1972)
Interstitial Salinity	28-38 ppt (Howes, et al., 1986)	9-26 ppt (Anderson et al., 1997b)	35-40 ppt (Nestler, 1977)
Dominant Plants	*S. alterniflora, D. spicata, S. patens*	*S. alterniflora, D. spicata, S. patens, J. roemerianus*	*S. alterniflora, J. roemerianus*
Fresh Water Sources	Groundwater, Precipitation	Precipitation	Precipitation

Bay through a single entrance, Sippewissett Creek (Howes et al., 1986). The marsh is surrounded on three sides by glacial moraine and sand dunes on the fourth side. The marsh is accreting at 1 mm/year in the low and high marsh and as much as 14 mm/year in the creekbank area (Valiela, 1983).

Table 11. Great Sippewissett Marsh Zone Characteristics

	Tall	Short	High
Area (ha)	9.1 (Valiela and Teal, 1979)	12.3 (Valiela and Teal, 1979)	8.9 (Valiela and Teal, 1979)
Dominant Vegetation	*S. alterniflora* (Valiela and Teal, 1979)	*S. alterniflora* (Valiela and Teal, 1979)	*S. patens, D. spicata* (Valiela and Teal, 1979)
Flooding Frequency (% of high tides)	100 (Jordan and Valiela, 1982)	50 (Meany et al., 1976)	10 (extrapolated from Valiela et al., 1985)
Primary Production (g N/m^2/yr)[1]	30	27	29

[1] These numbers were averaged from the following sources: Finn and Leschine (1980); Howes et al. (1985); Teal et al. (1979); Valiela (1983); Valiela and Teal (1979a); Valiela

et al. (1975); Valiela et al. (1976); Valiela et al. (1978); and White and Howes (1994a).

4.2.2 ***Upper Phillips Creek Marsh.*** Upper Phillips Creek Marsh is located near Nassawadox, VA, on the southern end of the Delmarva Peninsula (37°26' 38'' N, 75°52' 05'' W) (Blum, 1993), and is estimated to be over 1.2 ha by topographic survey (Richardson et al., 1995) (Table 12 for zone characteristics). It is part of the Virginia Coast Reserve (VCR) Long-Term Ecological Research Site (LTER) sponsored by the National Science Foundation. The property is owned and managed by the Nature Conservancy. It is tidally fed by Phillips Creek, a tributary of the Red Bank River that feeds into Hog Island Bay. The marsh originated from a Pleistocene sand ridge that was breached by sea level rise within the last 200 years (Chambers et al., 1992). It is surrounded by farm land to the south and pine forests to the north and west (Blum, 1993; Hmieleski, 1994). The marsh grades gradually into the forested areas to the north and more steeply into farmland to the south (Hmieleski, 1994). The marsh has increased in size by 8% in the last 50 years due to the transition from upland areas to high marsh (Kastler, 1993). Sediment is accreting at approximately 2 mm/year in the short *S. alterniflora* marsh (Kastler, 1993), which is considered sufficient to keep pace with the rate of sea-level rise (Davis, 1987; Hayden et al., 1991).

4.2.3 ***Sapelo Island Marshes.*** Sapelo Island Marshes are located on Sapelo Island, GA (31°19''N, 81°18''W) (Schubauer and Hopkinson, 1984) (Table 13 for zone characteristics). The marshes total area is approximately 1140 ha (Kuenzler, 1961). The marshes are fed by the Duplin River, which empties into the Doboy Sound (Imberger et al., 1983). The barrier island was believed to have been formed as the result of beach ridges being intersected by sea level rise, which submerged the area landward of the ridges during the late Holocene forming lagoons and islands (Hoyt, 1967).

Table 12. Upper Phillips Creek Marsh Zone Characteristics

	Tall	Short	High
Area (ha)	0.01 (Richardson et al., 1995)	0.54 (Richardson et al., 1995)	0.65 (Richardson et al., 1995)
Dominant Vegetation	*S. alterniflora*	*S. alterniflora*	*S. patens, Disticlis spicata, J. roemerianus*
Flooding Frequency (% of high tides)	100 (extrapolated from Blum, 1993)	52.4 (extrapolated from Anderson et al., 1997b)	1-10.7 (Hmieleski, 1994)
Primary Production (g $N/m^2/yr$)[1]	21.9	27.3	15.8

[1] These numbers were averaged from the following sources: Anderson et al. (1997b); Blum (1993); Blum and Christian (1997); Tolley (1996); and this study.

Table 13. Sapelo Island Marshes Zone Characteristics

	Tall	Short	High
Area (ha)	91.2 (Kuenzler, 1961, Dai and Wiegert, 1997)	991.8 (Kuenzler, 1961, Dai and Wiegert, 1997)	57 (Kuenzler, 1961, Dai and Wiegert, 1997)
Dominant Vegetation	*S. alterniflora*	*S. alterniflora*	*J. roemerianus, D. spicata*
Flooding Frequency (% of high tides)	92 (Kneib, 1991)	50 (Kuenzler, 1961)	15 (Kuenzler, 1961)
Primary Production (g $N/m^2/yr$)[1]	51.6	38.3	53.5

[1] These numbers were averaged from the following sources: Chalmers (1979); Chalmers et al. (1985); Dai and Weigert (1996); Gallagher and Plumley (1979); Gallagher et al. (1980); Haines (1976); Haines et al. (1977); Hanson (1977b); Hanson (1983); Hopkinson and Schubauer (1984); Kemp et al. (1990b); Schubauer and Hopkinson (1984); Weigert (1979); Weigert (1986); and Whitney et al. (1981).

4.3 Data Collection

4.3.1 ***Literature.*** The majority of data was obtained from literature. Great Sippewissett Marsh and Sapelo Island Marshes were selected specifically because of the extensive literature available regarding the nitrogen processes in these marshes. For Great Sippewissett, 27 articles spanning from 1974 to 1994 were used to obtain data. For Sapelo Island Marshes, I used 42 articles spanning from 1959 to 1997. Much of the data for Upper Phillips Creeks Marsh were also obtained from literature. However, because this marsh has not yet been studied as extensively as the other two marshes, not as many articles have been published. Four articles spanning from 1992 to 1998 were used. Student theses and the VCR/LTER database were also used to obtain data for Phillips Creek Marsh.

4.3.2 ***Field Sampling.*** Samples were taken from Upper Phillips Creek Marsh from May through December 1997 in order to supplement information from the literature.

Aboveground biomass of *S. alterniflora* was collected from two marsh zones (Tall and Short) once in May and once in September. A total of 18 samples were clipped within a 0.0625 m^2 quadrant using hand clippers, stored in plastic trash bags, and transported to the laboratory for processing. The samples separated into live and dead based on the present of green on the stems and leaves. They were then weighed to 0.01-g accuracy on an electronic scale to establish an initial mass, dried to a consistent mass at 85°C in an AC-Lab Equipment convection oven, and then reweighed for calculation of g dry mass x m^{-2}. These samples were then ground in a Wiley mill through a 40-mesh screen. Percent nitrogen was determined using Leeman Labs Control Equipment 440 Elemental Analyzer.

These masses were used to estimate aboveground biomass and primary production. Primary production was considered a very rough estimate because it was the subtraction of May's biomass from September's biomass, thus underestimating production. These numbers, however, were averaged with literature values where they were available for the creation of the networks.

Belowground biomass was estimated in May, September, and December. A 3.5 cm diameter aluminum corer was used to core marsh sediment to a core length of up to 28 cm. The samples were wrapped in aluminum foil for storage and transport. Both macroorganic matter (MOM) (Gallagher, 1974) and bulk densities (Chalmers, 1979) were measured. MOM was determined by cutting the core into two sections 0-10 cm and 10-up to 28 cm. Each section was washed through a 1-mm mesh sieve. After all sediments were visibly washed away, what remained was considered MOM. Some samples were used to determine the ratio of live:dead root matter. Separation was based on color and turgidity (Schubauer and Hopkinson, 1984). The samples were dried to consistent mass at 85°C in an AC-Lab Equipment convection oven and weighed to 0.01-g accuracy on an electronic scale. They were then ground using a Wiley mill through a 40-mesh screen. Percent nitrogen was determined using Leeman Labs Control Equipment 440 Elemental Analyzer. Bulk densities were determined by measuring the volume of the core, weighing to 0.01-g accuracy on an electronic scale, drying to consistent mass at 85°C in an AC-Lab Equipment convection oven, and reweighing the core.

To establish an estimate of the mussel, *G. demissa*, and snail, *L. irrorata*, population, the number of mussels and snails within 0.0625 m^2 quadrats were counted in September by sampling three different areas of the marsh in triplicate to determine populations per m^2.

4.4 Network Construction

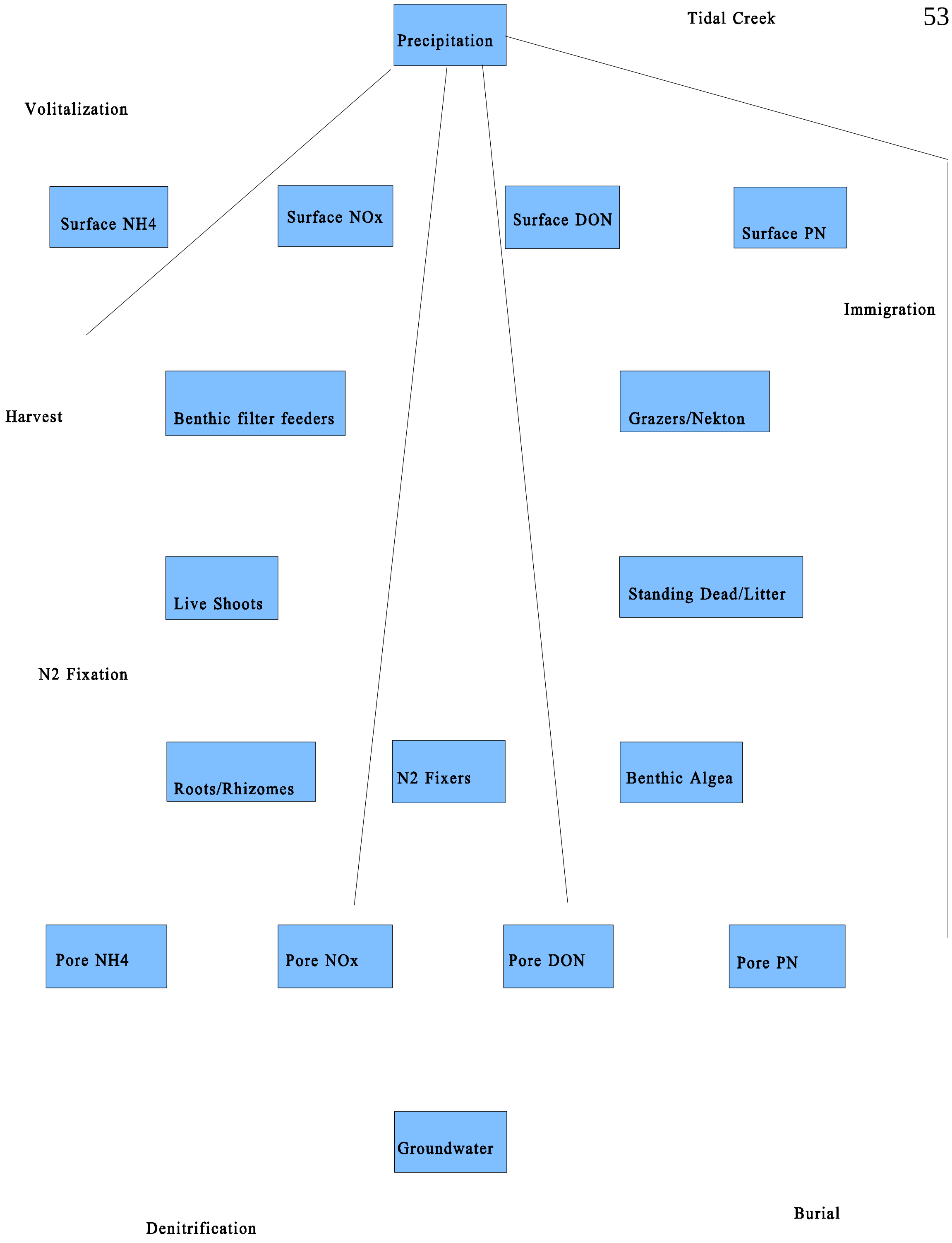
Networks were constructed for each zone of each marsh. The networks were constructed by estimating values for all compartments and flows for the general box and arrow diagram shown in Figure 4. Most of the diagram was created after conducting a literature search for Great Sippewissett Marsh. As more data were collected from Sapelo Island and Upper Phillips Creek, the network was modified to reflect new important data. The diagram reflects the type of data available in literature, and therefore does not contain all possible flows. During network development, I noticed physical exchanges by tides inordinately dominated over those due to biological processes. To allow the networks to better reflect biological activity, tidal flushing was placed outside the system, and the sedimentation/resuspension cycle was made into a net flow.

The type of data used included imports to the marshes such as tidal flow, precipitation, and nitrogen fixation; interactions such as primary production, mineralization, and grazing; and outputs such as tidal flow, denitrification, and burial of peat. Biomasses of each compartment were gathered when available. However, biomasses are not an intricate part of NETWRK4's programing and do not affect network analysis output.

Each compartment represents a potentially important aspect of the nitrogen cycle.

The surface water compartments represent the different species of nitrogen found in surface water (Figure 4). Surface PN includes bacteria, algae, zooplankton, detritus, and

Figure 4. Generalized Nitrogen Cycle Model for Salt Marshes



nitrogen attached to sediment particles. Fungi and bacteria associated with leaf decay are part of the Standing Dead compartment. Benthic filter feeders are predominately represented by *G. demissa*, the Atlantic ribbed mussel, but theoretically represent all filter feeders in the marsh. The Grazer/Nekton compartment is a compilation of many different types of animals. It includes crabs (e.g., *Uca pugilator*), snails (e.g., *Littorina irrorata*), insects (e.g., *Orchelium fidicinium*), and birds (e.g., *Branta canadensis*). However, it could be expanded to fish, racoon, deer, or any other animal present in the marsh. The pore water compartments like the surface water compartments represent the different nitrogen species found in pore water. Pore PN, however, is an aggregation of many things including decaying roots and rhizomes, decaying leaf litter, biodeposition, and nitrogen attached to sediment particles.

4.4.1 ***Assessment of Data Reliability.*** Each data point was assigned a number reflecting its perceived reliability, referred to as the reliability factor (RF). A RF of 4 meant that there was good confidence in the number. For example, a 4 would be assigned to a datum that resulted from a nitrogen fixation experiment where the rate was directly measured over a year or more and there was little to no manipulation needed for it to be standardized to g N m^{-2} x yr^{-1}. A RF of 3 meant that I had good confidence in the original data point but needed to manipulate it into the standard units. For example, this may result from a study directly measuring a carbon flow, and thus requiring a C:N ratio to convert it to nitrogen. A RF of 2 meant that the data point was an estimate or had to be heavily manipulated by conversions or extrapolation of gaps to be in the standard units. This RF assignment would result from a study that had data as a rate per day or month, and/or missing one or more months. Data would have to be scaled up and/or estimated in order to reflect a year's worth of flow. A RF of 1 meant the data point was a very rough estimate. A data point that was not directly measured but was roughly estimated based on other measurements would receive this RF assignment. And, a RF of zero meant I derived it by balancing the inputs and outputs of compartments. Each data point and its RF were averaged with other like data points for the appropriate zone of the appropriate marsh. Thus, a flow or standing stock value for network construction could come from data points from more than one source. The averaged data and RF were then used to construct each network. A data point was not assigned a RF of zero until the networks were being balanced (Section 4.4.2).

The following is an example of the decision making process that occurred during data manipulation. A data point for belowground production in Sapelo Island was given as 2100 g m^{-2} x yr^{-1} (Gallagher and Plumley, 1979). In order to convert this to g N m^{-2} x yr^{-1}, the first bit of information needed was percent nitrogen or carbon. Percent carbon was found to be 38.1 (Gallagher and Plumley, 1979). It was determined that belowground production was 800 g C m^{-2} x yr^{-1}. The next step was to apply a C:N ratio to determine the nitrogen content of the roots and rhizomes. The C:N ratio used was 38 (Gallagher and Plumley, 1979). It could then be determined that the belowground production was 21 g N m^{-2} x yr^{-1}. This conversion was given a RF of 3. C:N ratios, % N, and % C originated from the marsh in question unless no information was available.

4.4.2 ***Balancing.*** Once the initially estimated values for each network were obtained, they were organized into a spreadsheet. Each compartment's surplus or deficit nitrogen flow was determined by adding all inputs to a compartment and subtracting all exports from that compartment. To achieve steady state, each compartment's inputs must equal its outputs. The following rules involving RFs were used as guidelines to help balance each compartment. However, they were not strictly adhered to. If a data point had a RF of 4, it was changed no more than 10% in either direction to help balance the compartment. A RF of 3 was changed no more than 20%, 2 was changed up to 30%, 1 was changed up to 40%, and 0 was changed as needed to balance the compartment. These percentages were arbitrarily chosen to help retain the integrity of the data during the balancing process. These rules were violated when no other option was available to balance the compartment. For example, in the Great Sippewissett Tall network the value for denitrification was assigned a RF of 4 but was changed 50%. This was needed to balance the compartment as no other realistic options were available. Other input and export routes had been manipulated as much as possible to account for the deficit nitrogen flow without becoming unrealistic.

4.5 Network Analysis

Ecosystem Network Analysis was used to evaluate the structure of the 9 networks using a variety of perspectives. The software package used to perform network analysis was NETWRK4 (Ulanowicz, 1987). The package contains several subroutines in FORTRAN for network analysis. I used the subroutine for Structure Analysis, specifically Input Environs Analysis (Section 4.5.1) and matrices of Total Contribution and Total

Dependency (Section 4.5.2). I also used the subroutine for Biogeochemical Cycle Analysis, specifically the Finn Cycling Index (FCI) to determine the amount of recycling in the system (Section 4.5.3). I used the Information Indices, such as Relative Ascendency, Capacity, and Overhead to determine maturity and stability (Section 4.5.4).

4.5.1 ***Input Environs Analysis.*** Input Environs Analysis computes the fraction of flows within the system that results from the exogenous input of one unit of flow into a compartment (Kay et al., 1989). The coefficients in each vector and matrix represent the relative amounts of internal flows and outputs (or probability of flow) resulting from one unit of input (Kay et al., 1989). I used this analysis to determine how inputs to the systems were exported. I compared the distributions of exports between marsh zones and between marshes to evaluate how nitrogen cycling may be different.

4.5.2 ***Total Contribution and Total Dependency Matrices.*** The total contribution matrix evaluates the fraction of a compartment's throughput that contributes to another compartment's throughput both directly and indirectly (Kay et al., 1989). For example, the matrix can determine the fraction of the nitrogen that flows through the benthic filter feeder compartment that will travel directly and indirectly to aboveground production. In this case there is no known direct flow from benthic filter feeders to aboveground production, but a possible indirect flow would be from benthic filter feeders to Pore PN by way of biodeposition (Figure 4). The Pore PN is then mineralized to Pore NH4 and taken up by the plant. For the Great Sippewissett Tall network, this number is 0.0681. This means that 6.81% of the total throughput of the benthic filter feeder compartment will go through the aboveground production compartment.

The total dependency matrix evaluates the fraction of a compartment's total throughput that resided at some point in another compartment (Hannon, 1973). For example, this matrix can determine the fraction of aboveground production's nitrogen throughput that came from benthic filter feeders both directly and indirectly. Again, there is no direct flow, but through the indirect flow, it can be determined what fraction of aboveground production's throughput came from benthic filter feeders. For the Great Sippewissett Tall network, this number is 0.128. This means that 12.8% of aboveground production's throughput came from the benthic filter feeder compartment. The diagonals of both matrices can be used to determine the amount of material that is cycled back to a compartment.

These matrices were used to evaluate how important certain sources of imported nitrogen are to various compartments, such as how important precipitation is to belowground production. This type of analysis can be achieved by making an input a compartment. For example, instead of directing precipitation into the appropriate compartments from outside the system, I created a compartment for precipitation thus internalizing the input flows (Figure 4). It was also used to determine the amount of material cycled through belowground production as an indicator of recycling.

4.5.3 ***Finn Cycling Index and Cycled Throughput.*** Biogeochemical cycle analysis employs graph theory to evaluate the cycles or positive feedback loops within a system (Ulanowicz, 1986). The fraction of material that is involved in the feedback loops compared to the total flow through the system (total system throughput) is called the Finn Cycling Index (FCI) (Finn, 1980). When the FCI is multiplied by the total system throughput (TST), the amount of material cycled, Cycled Throughput (CT) can be determined (Christian, pers. com.). These two indices were used to determine the amount of recycling within each marsh zone.

4.5.4 ***Information Indices.*** Information indices developed by Ulanowicz (1987, 1997) attempt to capture the emergent properties of a system. I focused on ascendency, overhead, redundancy, and internal ascendency to assess how nitrogen cycling may influence system development (Section 2.2.2). Ascendency is the average mutual information (AMI) within a system multiplied by the TST. The AMI is a measure of the amount of constraint on the flow of material (Ulanowicz, 1997). The more possible pathways from a compartment or the more evenly distributed the flows between compartments, the lower the constraint on the flow, and thus the lower the AMI. Ascendency is believed to be an indicator of system maturity (Ulanowicz, 1997). Capacity is TST multiplied by the Shannon Diversity of Individual Flows (Ulanowicz, 1997). The Shannon Diversity of Individual Flows is a way of capturing the indeterminate complexity or entropy of a system. It is the sum of each flow’s potential contribution to system complexity weighted by the frequency each flow occurs (Ulanowicz, 1997). The difference between ascendency and capacity is referred to as overhead. Overhead is the uncertainty associated with inputs, output, dissipations, and internal flows (Ulanowicz, 1997). It is believed to be a measure of stability (Christensen, 1995). Redundancy is the degree of internal flow associated with pathways that have similar functions and/or evenness of flow. The higher the level of redundancy within a system the less benign or more stressed an environment is believed to be (Ulanowicz, 1997). Internal ascendency is a measure of maturity when inputs and outputs are removed from the AMI calculation.

These indices were used to establish a marsh's level of maturity, stability, and level of stress. Relative ascendency was used to compare the maturity of different marsh zones. Overhead was used to compare the stability of the different marsh zones, and Redundancy was used to compare levels of stress.

4.5.5 ***Mineralization.*** Mineralization is an important part of nitrogen cycling within a salt marsh. To determine what fraction mineralization was of total processing of nitrogen, the net mineralization rate of Pore PN and DON to Pore NH_4^+ was divided by TST. To determine if primary production's uptake and/or requirements could be met by mineralization, mineralization was divided by "belowground production" represented by the uptake of NH_4^+ and NOx. "Belowground production" was used because it contained the total flow of nitrogen into the plant which then distributes both above- and belowground. Mineralization was also divided by CT to determine the fraction of CT associated with mineralization.

4.5.6 ***Average Path Length (APL).*** APL is another way of measuring cycling (Finn, 1980). It was originally developed to evaluate foodwebs, and is believed to be a measure of stress as well as cycling. As a system becomes more stressed, the cycles tend to become shorter thus reducing the APL (Kay et al., 1989). It is calculated with the following formula: (TST-Inputs)/Inputs (Kay et al., 1989). It was used to determine cycling and maturity/stability.

4.6 Statistical Analysis

It is assumed that the data are best analyzed using nonparametric statistics, because the underlying data distributions are unknown. The Friedman test was used to determine the significance of various parameters in relation to marsh zone and marsh (Potvin and Roff, 1993). The Friedman test is a nonparametric statistical test that analyzes within-subject effects based on rank. It assumes within each block that errors are mutually independent. Because the models were not true replicates, statistical interactions were not determined. The statistical software used was Systat 7.01 (SPSS, 1997).

Hierarchical Cluster Analysis was used to determine if the marshes clustered by zone or by marsh. Distance metric was Euclidean distance and the single linkage (nearest neighbor) method was used. The indices used for the cluster analysis were FCI, APL, recycling within the belowground primary production compartment, relative ascendency, input overhead, output overhead, redundancy, internal ascendency, and mineralization/primary production. A Pearson correlation matrix was also used on these indices to compare maturity/stability indices and to insure that ranking of marsh zones was not biased by a few indices.

5.0 RESULTS

Overall, the 3 marshes showed consistent patterns among zones in some flows and TST, but not in other flows. For example, TST, tidal imports, and tidal exports decreased moving from Tall to High (Table 14). This was mainly the result of reduced tidal flushing as it was assumed that the Tall zone was inundated by 100% of high tides, Short by 50%, and High by only 10%. The largest internal flows were associated with primary production and mineralization and did not show consistent patterns across marsh zones.

Table 14. Important Network Flows (g N m^{-2} x yr^{-1})

	Great Sippewissett			**Upper Phillips Creek**			**Sapelo Island**		
	Tall	Short	High	Tall	Short	High	Tall	Short	High
Tidal Import	81.1	44.6	8.77	65.8	34.7	8.11	165	87.5	16.3
Precipitation	0.56	0.56	0.56	0.45	0.45	0.45	0.3	0.3	0.3
Groundwater	13.3	13.3	13.3	0.04	0.04	0.04	0.04	0.04	0.04
Nitrogen Fixation	5.03	2.75	5.87	1	1	1	39.8	23.7	4.5
Tidal Export	87.9	45.6	8.83	63.1	30.5	5.6	162	74.5	16.1
Burial	6.13	9.51	11.4	3.6	5.16	3.53	1.44	1.35	1.2
Denitrification	9.58	7.54	8.58	0.6	0.6	0.6	41.6	35.7	3.91
Primary Production	30.2	27	29	21.1	27.7	15.8	51.6	38.3	53.5
Translocation	1.4	1.26	1.26	7	7	7	16.2	14.8	13.3
Detritus Formation	25.3	21.8	24.2	18.4	26.8	14.5	44.4	31.5	46.7
Mineralization	27.2	30.1	30	27.8	31.1	11.7	92.5	79.3	80.9
Nitrification	10	11.9	14.8	3.6	4	3.55	41.5	28.7	3.77
All other flows	114	107	63.4	78.8	72.5	26.1	246	211	162
TST	412	323	220	290	242	98	902	627	403

Not only are there some differences between marsh zones but also between marshes. Sapelo Island marsh had considerably more nitrogen flowing through its system than Upper Phillips Creek marsh. Great Sippewissett was intermediate. Primary production, mineralization, and other microbial processes are also higher in Sapelo Island marsh than the other two marshes.

5.1 How Nitrogen Flows Through Each Marsh Area

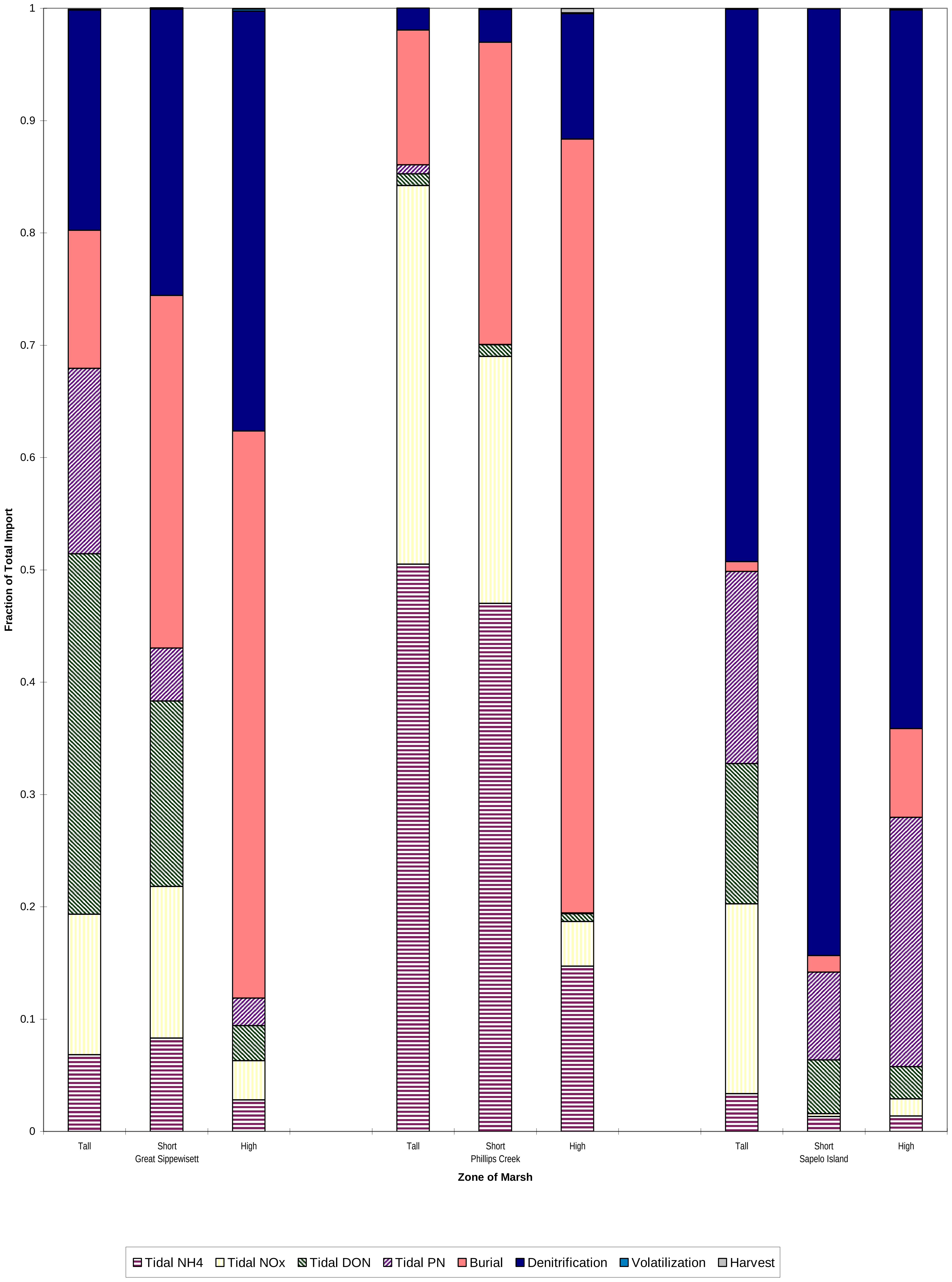
5.1.1 ***Input Environs Analysis.*** I evaluated how imported N from major import routes (Table 14) is exported from each marsh zone. Precipitation and tidal imports of each nitrogen species were considered for analysis. Possible export routes included tidal export of each nitrogen species, denitrification, burial, harvest of mussels, and volatilization.

The following graphs depict the fraction of import that was exported by a particular route in the different marsh zones (Figures 5-9). The output data from Input Environs Analysis were placed in stacked bar graphs. Each bar section represents the fraction of total import that was exported by each potential route. In all cases, harvest and volatilization were very small fractions of export routes and usually are not large enough to see on the bar graphs.

The first import examined was precipitation. In the Tall zone, more than half of the precipitation was exported from the marsh by tide (Figure 5). Tidal export of precipitation steadily decreased in importance moving across the marsh from Tall to High, except for Sapelo Island. Burial became a more important export route moving from the Tall to High marsh zone. Denitrification also generally increased in importance moving across the marsh.

Figure 5. How Precipitation Import Leaves the Marsh

Figure 5. How Precipitation Import Leaves the Marsh



To understand the importance of these patterns, the Friedmans Test was applied. The increase in the importance of burial across marsh zones is a significant pattern. The trends associated with tidal export and denitrification are not significant at the 0.05 level, but there is a distinct pattern (Table 15). Given the limited number of samples (n=9), all 3 marshes must have the same rank order for significance at p=0.05. If one rank pair is reversed, the p-value raised to 0.097. Therefore, in both tidal export in all forms and denitrification, 2 of the marshes showed the same pattern and 1 had a reversal of rank. The reversal was at Sapelo Island between the Short and High zone. This reversal was an artifact of the way the Sapelo Island High marsh model was balanced (Appendix G).

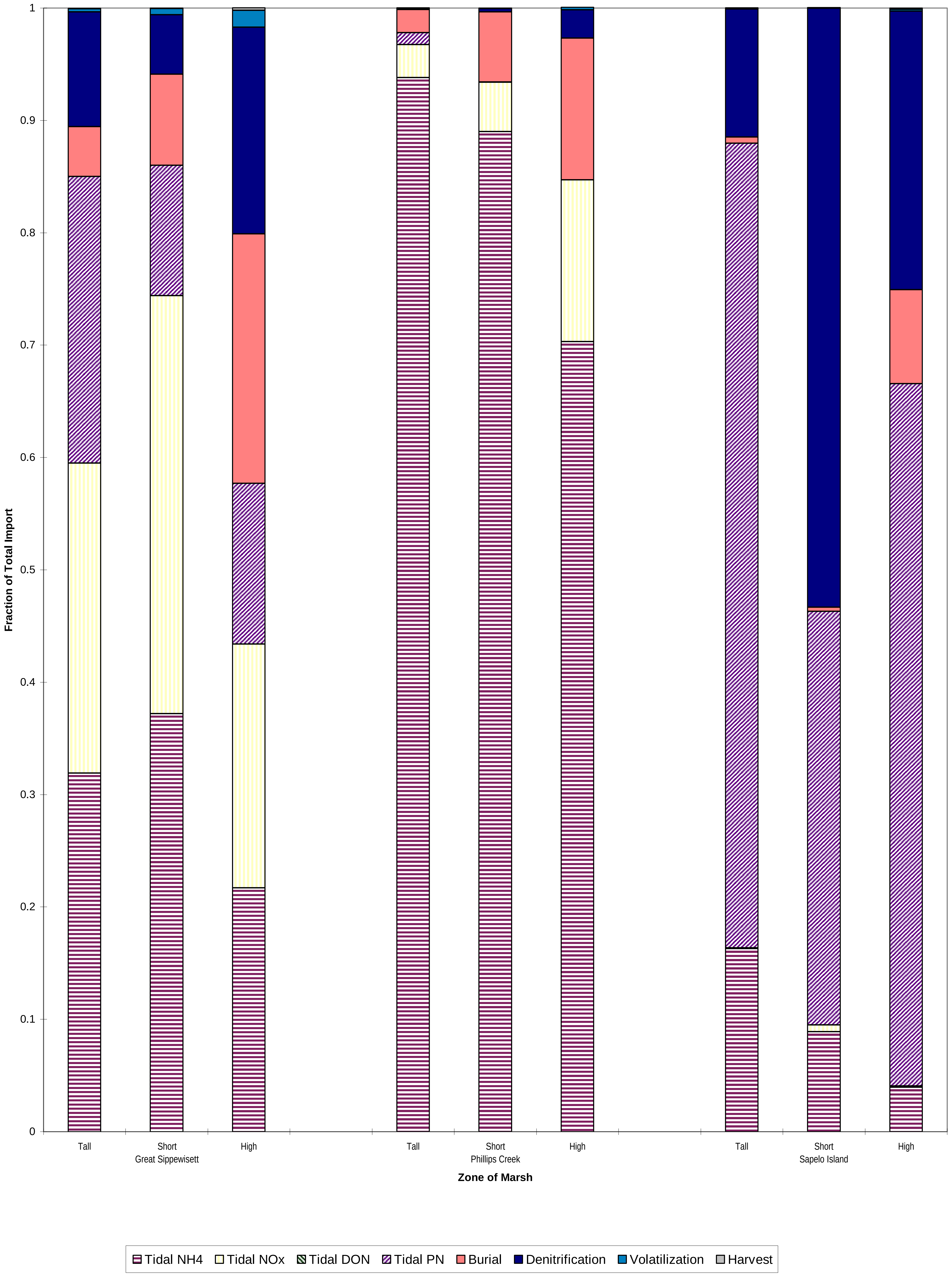
Table 15. Friedmans Test for Significant (μ=0.05) Patterns in Precipitation Export Across Marsh Zones. Numbers are p-values

	Tidal Export	**Burial**	**Denitrification**
p-value	0.097	0.05	0.097

Tidal import of NH_4^+ is a very important source of nitrogen to the marsh. Each marsh processed the NH_4^+ differently as can be seen in the different nitrogen species exported tidally by each marsh, but there were some consistent patterns across marsh zones (Figure 6). The importance of tidal export in each marsh across zones had no significant trend (p=0.264). Burial increased in importance as an export route moving from Tall to High in Great Sippewissett and Upper Phillips Creek. However, this was not a significant trend because of the pattern in Sapelo Island (p= 0.264). Denitrification varied between each marsh zone with no consistent pattern (p=0.368). Therefore, the export of NH_4^+ shows no significant patterns across marsh zones.

Figure 6. How Tidal Import of NH_4^+ is Exported

Figure 6. How Tidal Import of NH4 is Exported



Tidal import of NOx is also an important source of nitrogen to the marsh. The pattern of NOx processing across each marsh differed for each marsh (Figure 7). Tidal flushing showed no significant patterns among marsh zones for all marshes (p=0.264). Burial also shows no significant pattern across marsh zones and is essentially nonexistent as an export route for Tidal NOx in Sapelo Island (p=0.368). Denitrification was a dominant export route in Sapelo, but much less so in the other marshes, and there was no significantly consistent pattern across marsh zones (p=0.264).

Tidal import of DON and its resultant cycling within the marsh is not very well understood. There were very few data regarding DON, so the networks essentially had DON coming in and going out tidally with little transformation (Figure 8). There was no significant trend when the other marshes are included in the statistical analysis (p=0.205). Also at Upper Phillips Creek, burial increased in importance as an export route from Tall to High (Table 16), but again significance testing did not support the trend overall (p=0.205). Denitrification was only a very small export route for all marshes (Table 16) and showed no significant trends (p=0.558).

Import of Tidal PN included bacteria, algae, zooplankton, detritus, and nitrogen attached to sediment particles. Because of this diversity, it was processed within the marsh in many different ways. There were, however, consistent patterns of export routes (Figure 9). Tidal export of all forms decreased significantly in importance across marsh zones from Tall to High (p=0.05). Burial and denitrification increased in importance moving across the marsh from Tall to High. Both trends were significant (p=0.05).

Figure 7. How Tidal Import of NOx is Exported

Figure 7. How Tidal Import of NOx is Exported

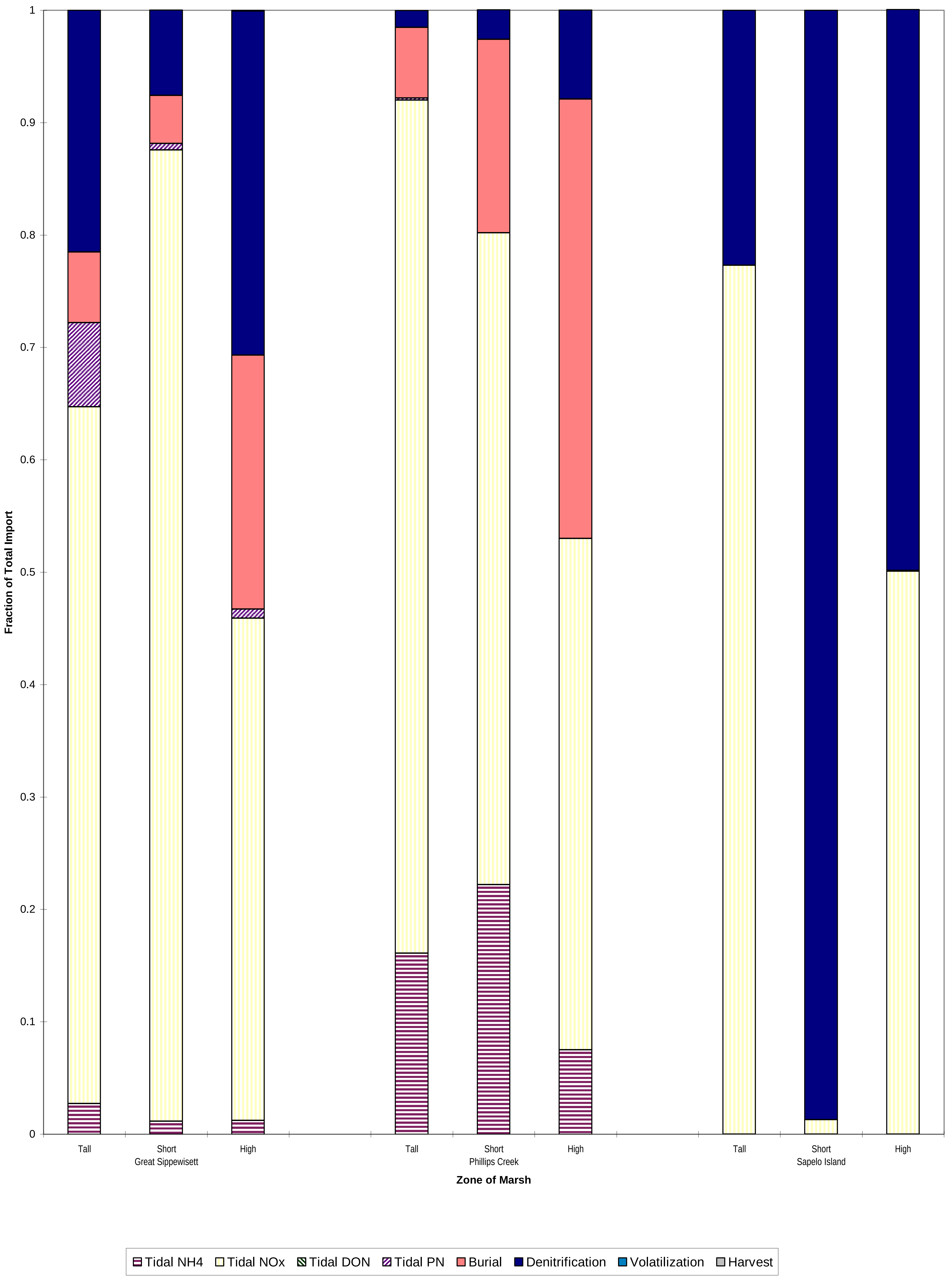


Figure 8. How Tidal Import of DON is Exported

Firgure 8. How Tidal Import of DON is Exported

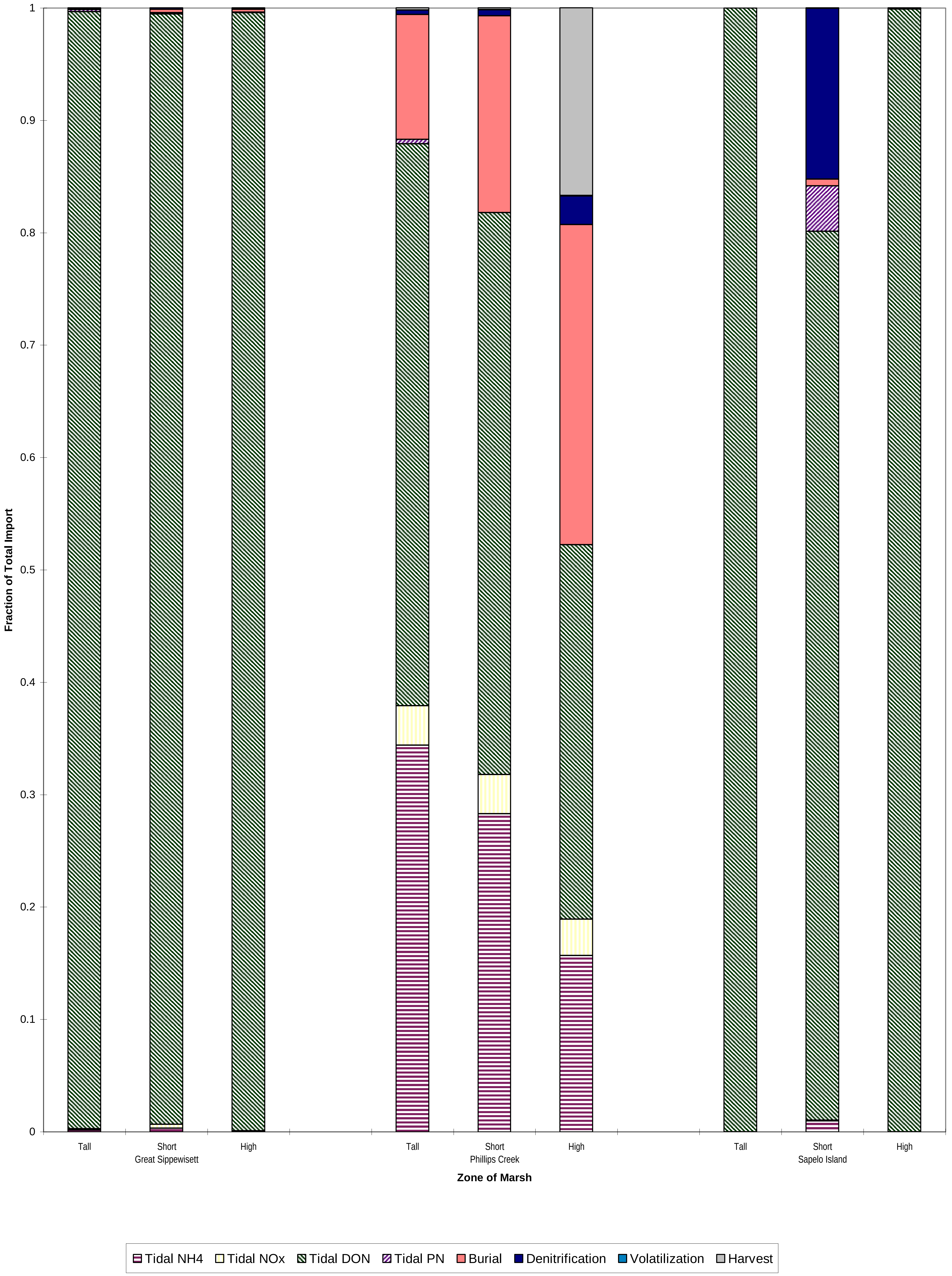


Table 16. Percent of Tidal DON Import that is Exported by Various Routes in Upper Phillips Creek.

	Tall	**Short**	**High**
Tidal Export	88.3	81.8	52.2
Burial	11.1	17.5	28.5
Denitrification	0.4	0.54	2.54

Interestingly, the dominant export trends associated with Tidal PN were all significant, whereas they were not for the other tidal imports.

Groundwater was not considered for analysis because of the very small contribution it makes to Upper Phillips Creek and Sapelo Island marshes. However, it is a large import to the Great Sippewisset Marsh. Like other imports, there is a decrease in the importance of tidal export moving across the marsh from Tall to High (Table 17). There is also an increase in importance in burial and denitrification from Tall to High (Table 17).

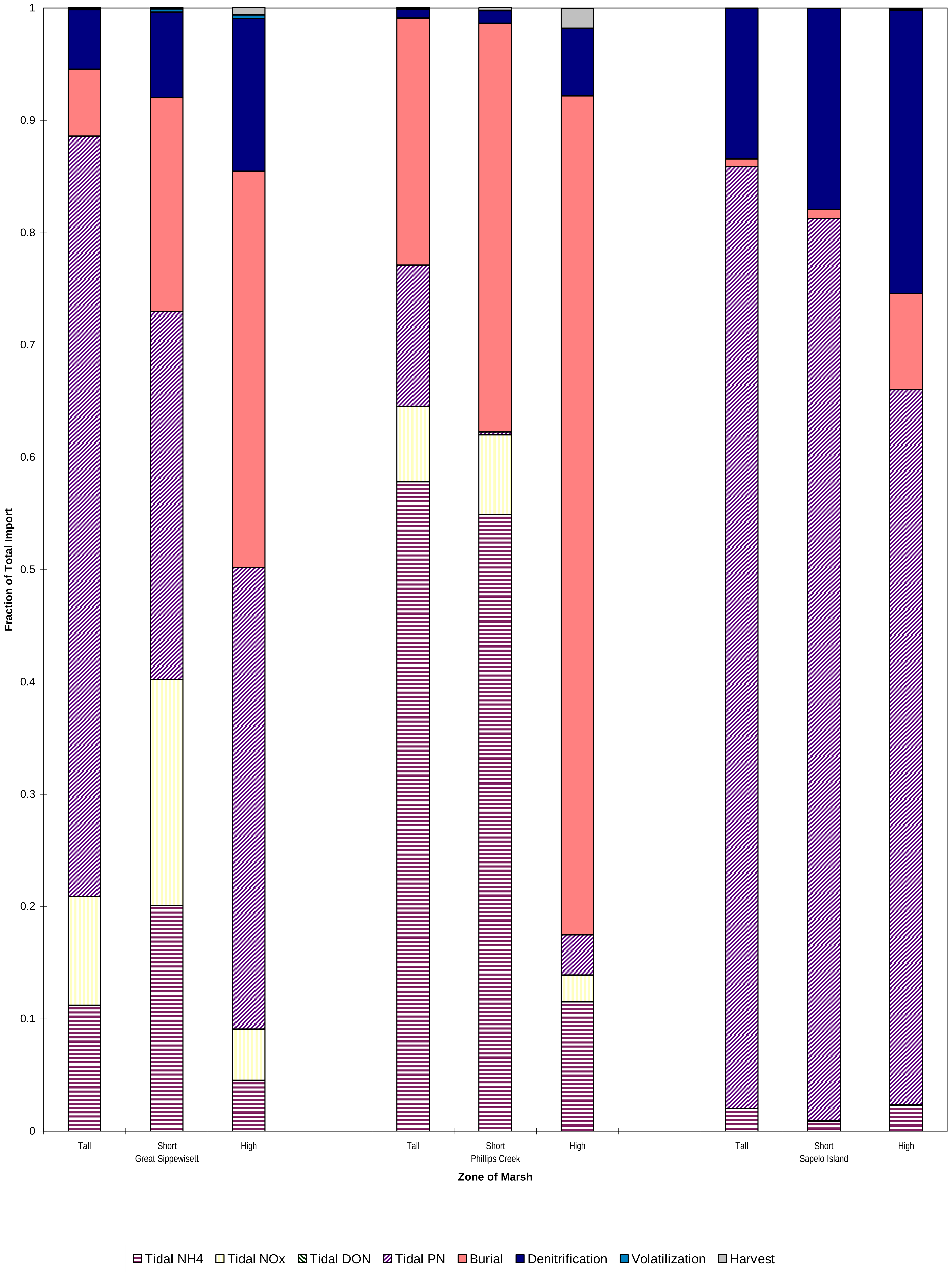
Table 17. Percent of Groundwater Import Exported by Various Routes in Great Sippewissett.

	Tall	Short	High
Tidal Export	42.6	24.2	6.69
Burial	21.1	38.4	50.3
Denitrification	36.2	37.2	42.8

5.1.2 ***Total Contribution of Tide and Precipitation to Primary Production.*** The Total Contribution Matrix was used to determine the fraction of precipitation and tidal inputs that went to primary production, as most major nitrogen flows within marshes revolve

Figure 9. How Tidal Import of PN is Exported

Figure 9. How Tidal Import of PN is Exported

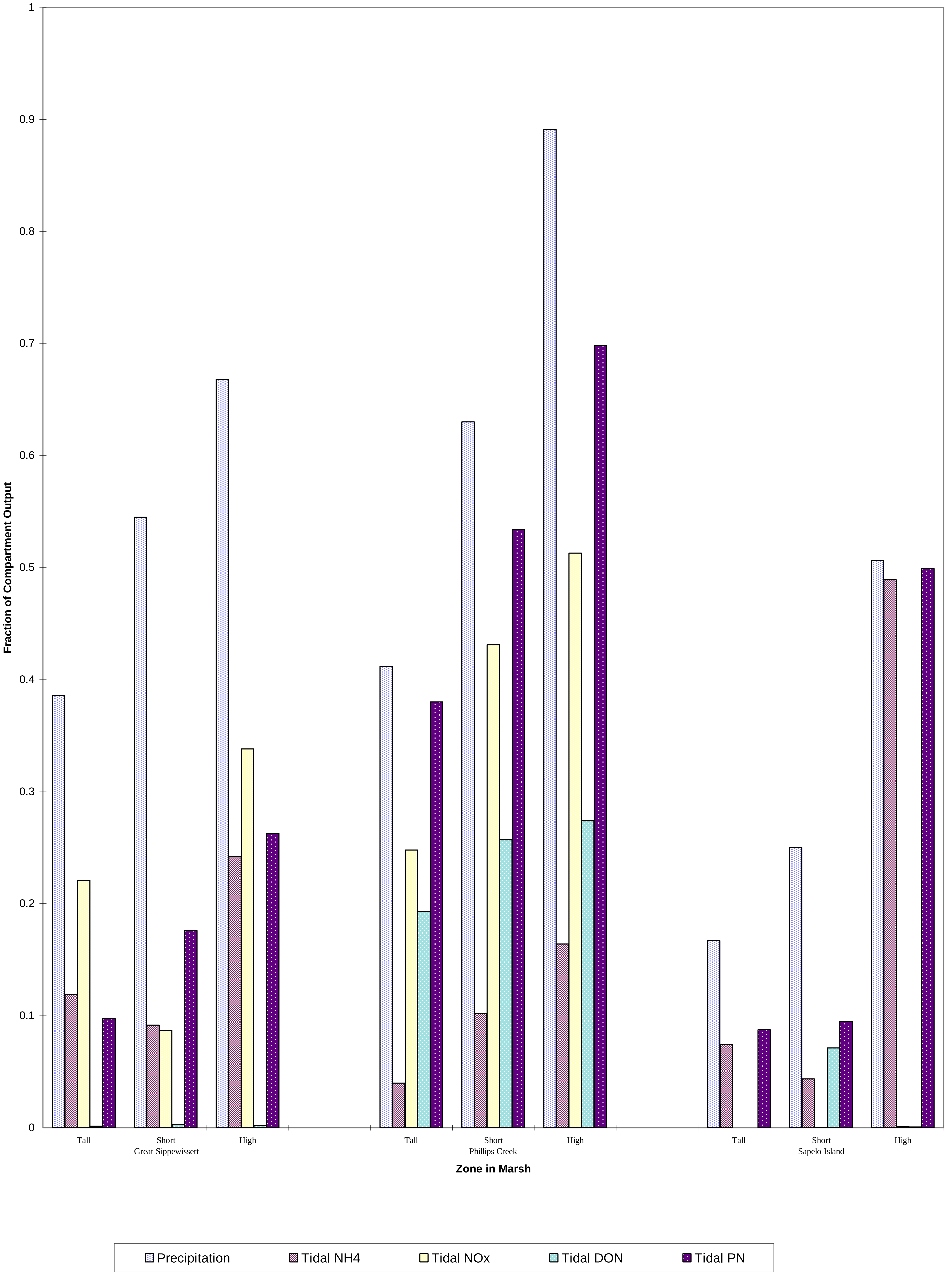


around primary production. Uptake by belowground biomass represented plant primary production, as it reflects production for both below- and aboveground production numbers. In all 3 marshes and in all 3 zones, precipitation had a higher fraction of its throughput go to primary production than each species of nitrogen in tidal import (Figure 10). The fraction increased significantly moving from Tall to High ($p=0.05$). In Upper Phillips Creek High marsh almost 90% of nitrogen from precipitation went to primary production. Tidal contributions also tended to increase from Tall to High (Figure 10). As an exception, the percent of Tidal NH_4^+ throughput contributing to primary production tended to be least in the Short marsh and most in the High marsh at Great Sippewissett and Sapelo Island but not at Upper Phillips Creek. Therefore, there was no significant trend ($p=0.097$). Tidal NOx behaved very differently in each marsh. For Great Sippewissett and Upper Phillips Creek it followed the Tidal NH_4^+ trend, but in Sapelo Island there was no fraction of Tidal NOx that contributed to primary production ($p=0.105$). Tidal DON contributed little if any of its throughput to primary production, except in Phillips Creek. This was a reflection of lack of data as stated above, as I did not ascribe biological activity to this chemical species. In Phillips Creek, tidal DON increased its percent contribution to primary production moving across the marsh from Tall to High, but there were no significant trends when all marshes were considered ($p=0.097$). Tidal PN significantly increased its percent contribution moving across the marshes from Tall to High ($p=0.05$).

In Great Sippewissett, much of the groundwater nitrogen was contributed to

Figure 10. Total Contribution of Input to Primary Production

Figure 10. Total Contribution of Input to Primary Production

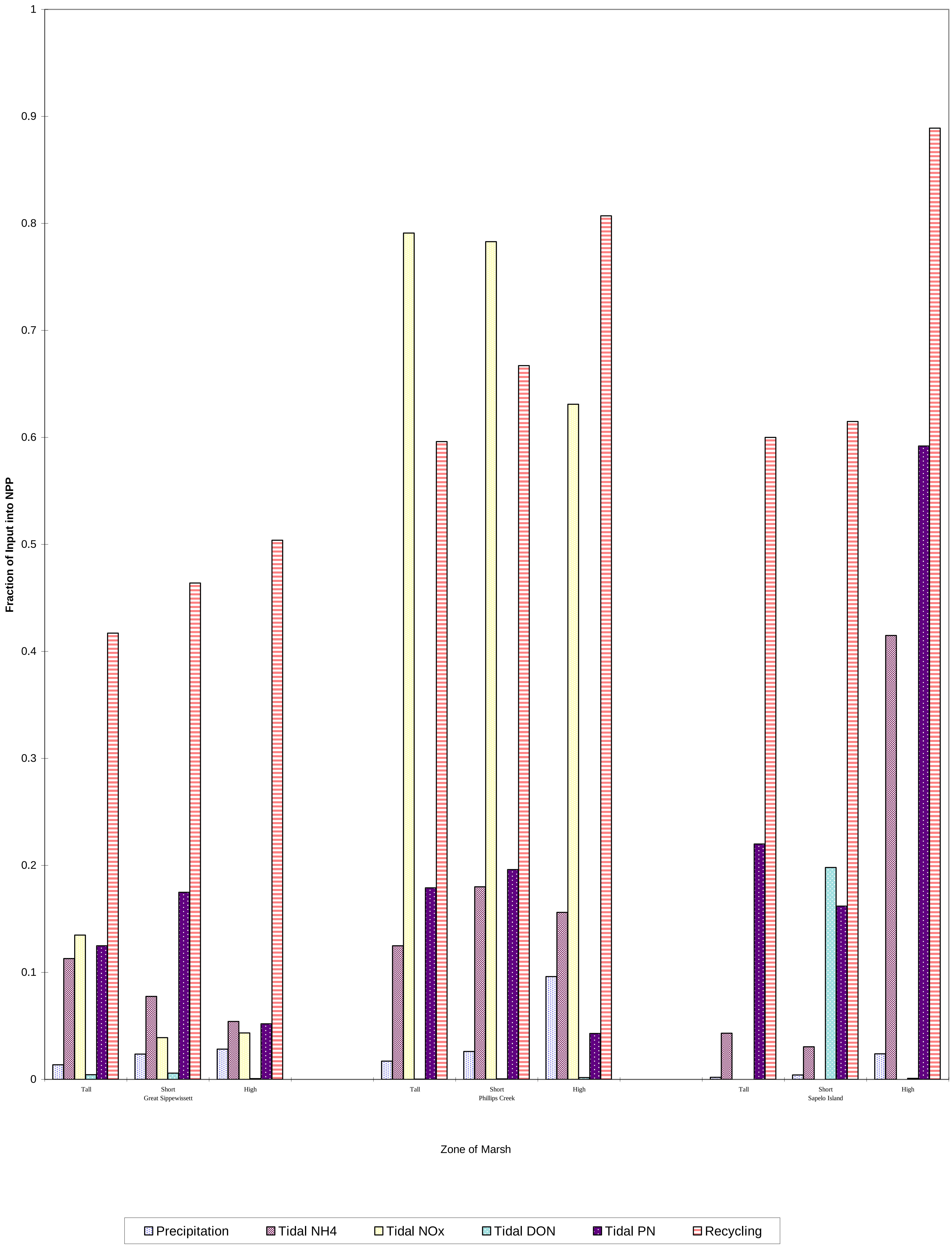


primary production. In the Tall zone, groundwater contributed 68.3% of its throughput to primary production, the Short zone contributed 70.2%, and the High zone contributed 69.4%. No analyses were done on this pattern's significance because of the lack of groundwater flow in the other 2 marshes.

5.1.3 ***Total Dependency of Primary Production on Tide and Precipitation.*** A larger percentage of primary production's throughput originated from tidal import than precipitation in all marsh zones (Figure 11). For example, precipitation only accounted for 0.1-9.5% of primary production's throughput, but Tidal NH_4^+ accounted for 3.1-41.5%. However, precipitation significantly increased in importance moving across the marsh from Tall to High (p=0.05). For example, in Sapelo Island, precipitation was a negligible fraction of primary production's throughput in the Tall zone, but in the High zone it was 2.4%. Tidal imports varied in importance across marsh zones and between marshes. For example, Tidal NH_4^+ decreased in importance to primary production moving across the marsh from Tall to High in Great Sippewissett, increased in Sapelo Island, but was highest in the Short zone at Upper Phillips Creek (p=1.0). Tidal NOx varied greatly in its importance to primary production between marshes and marsh zones. In Great Sippewissett, it was least important in the Short marsh and most important in the Tall marsh. In Phillips Creek, it decreased in importance moving across the marsh from Tall to High. And in Sapelo Island, primary production did not depend on Tidal NOx. Therefore, there was no significant trend across marsh zones (p=0.368). Primary production depended very little on Tidal DON, except in Sapelo Island Short marsh, and

Figure 11. Total Dependency of Primary Production on Rain, Tide, and Recycling

Figure 11. Total Dependency of Primary Production on Rain, Tide, and Recycling



no cross zone patterns were found (p=0.472). Tidal PN played a relatively important role in primary production in all marshes but not in a consistent way (p=0.717). It ranged from 4.3-59.2% of primary production's throughput.

With the exception of Tidal NOx in Upper Phillips Creek, the dependencies were less than 50%. Therefore, recycling through belowground plant biomass was examined as a source of nitrogen for primary production. This was evaluated by the diagonal coefficient for belowground plant biomass within the Total Dependency matrix. In each marsh, recycling associated with primary production significantly increased in importance moving across the marsh for Tall to High (p=0.05), and recycling was a predominant source of flow in each case (Figure 11).

Primary production in Great Sippewissett was also very dependent on groundwater. In the Tall zone, 62.8% of primary production's throughput came from groundwater. In the Short zone, it was 68.1%, and in the High zone, it was 62.6%. Because groundwater was negligible in the other marshes, no comparison of marsh zones was done.

5.2 Nitrogen Cycling

The amount of cycling can be measured in a number of other ways. The Finn Cycling Index (FCI) and Average Path Length (APL) are typically used (Kay et al., 1989). Cycling can also be determined using the diagonals of the Total Dependency Matrix (TDM), as was done above to determine recycling associated with primary production.

Total system cycling as determined by FCI and APL increased moving across the marsh from Tall to High (Table 18). Both FCI and APL significantly increased moving toward the high marsh (p=0.05 for both).

Table 18. Indicators of Cycling within Systems and Compartments (based on Total Dependancy Matrix). Numbers are the fractions of throughput recycled. APL is average number of compartments unit of flow passes through.

	Great Sippewissett			**Phillips Creek**			**Sapelo Island**			**p-value**
	Tall	Short	High	Tall	Short	High	Tall	Short	High	∝=0.05
FCI	0.297	0.365	0.471	0.361	0.5	0.532	0.408	0.415	0.801	0.05
APL	2.98	4.16	6.65	3.31	5.67	9.1	3.40	4.63	18	0.05
Mussels	0.19	0.218	0.068	0.029	0.069	0.000	0.01	0.039	0.524	0.368
Grazers	0.11	0.162	0.11	0.028	0.053	0.049	0.021	0.014	0.298	0.558
Shoots	0.108	0.18	0.229	0.483	0.456	0.712	0.489	0.495	0.788	0.097
Roots	0.417	0.464	0.504	0.596	0.667	0.807	0.600	0.615	0.889	0.05
Benthic algae	0.111	0.196	0.194	0.267	0.275	0.004	0.429	0.496	0.776	0.264
Pore NOx	0.152	0.197	0.257	0.252	0.344	0.400	0.000	0.001	0.002	0.05
Pore PN	0.447	0.509	0.529	0.543	0.65	0.71	0.622	0.65	0.906	0.05
Pore NH4	0.421	0.504	0.533	0.549	0.65	0.71	0.623	0.65	0.906	0.05

Compartmental cycling is the fraction of a compartment's throughput that starts in the compartment, cycles through the system, and returns to the same compartment. It appeared to be significant only when related to primary production. Recycling associated with above- ("shoots") and belowground ("roots") biomass generally increased across the marsh from Tall to High (Table 18). The trend was significant for belowground (p=0.05) but not for aboveground (p=0.097). In Upper Phillips Creek, the Short zone had less recycling than the Tall zone (Table 18). Recycling of the sediment nutrients that primary production depends on also increased moving across the marsh from Tall to High. This trend was significant (p=0.05 for all). The other compartments, such as mussels, grazers, and benthic algae, did not show any significant trends in their patterns of recycling.

5.3 Mineralization

Mineralization was evaluated because of its importance to the nitrogen cycle and primary production. In general, the actual mineralization rates varied little across marsh zones because of a lack of data for different zones (Table 19) (Appendix A-D). To determine the contribution of mineralization rate to each marsh zone in a comparable way, it was divided by three factors, TST, primary production, and cycled throughput (CT).

Table 19. Mineralization Rates for Different Marsh Zones (g N x m^{-2} x yr^{-1})

	Tall	Short	High
Great Sippewissett	14.1 (net)	14.1 (net)	14.1 (net)
Phillips Creek	104 (gross)	104 (gross)	11.6 (gross)
Sapelo Island	70 (gross)	70 (gross)	70 (gross)

5.3.1 ***Mineralization/TST.*** Mineralization was considered as a percentage of TST. In all cases, it was 20 % of TST or less (Figure 12). In both Great Sippewissett and Sapelo Island, the highest percentage was in the High marsh, whereas in Upper Phillips Creek, the highest percentage was in the Short marsh. It was lowest in the Tall zone for each marsh. However, there were no significant trends (p=0.097).

5.3.2 ***Mineralization/Production.*** Mineralization was divided by primary production to

Figure 12. Relative Mineralization

determine if mineralization could provide primary producers with enough nitrogen to meet their need. In most cases, mineralization/production was≥1.0, meaning that mineralization could meet the full demand of primary producers. In Great Sippewissett and Sapelo Island marshes, mineralization/production was highest in the Short marsh (Figure 12). In both Phillips Creek and Sapelo Island mineralization/production was lowest in the High marsh, but in Great Sippewissett it was lowest in the Tall marsh. The trends across zones were not significant (p=0.264).

5.3.3 ***Mineralization/CT.*** Mineralization was divided by CT to determine the percent of CT that resulted from mineralization. In all cases, mineralization was 30 percent or less of CT (Figure 12). In both Phillips Creek and Sapelo Island, the Short marsh showed the greatest amount of mineralization/CT. Great Sippewissett's mineralization/CT was highest in the High marsh. These differences were not significant between marsh zones (p=0.368).

5.4 Maturity/Stability

Maturity and stability were evaluated for each marsh zone using relative ascendency, relative overhead, and relative redundancy. Relative ascendancy is a measure of maturity, relative overhead is a measure of stability, and relative redundancy is a measure of response to stress (Ulanowicz, 1997). Each of these indicators are a fraction of the developmental capacity. Capacity is the Shannon Index of the diversity of flows scaled by TST (Table 20). Capacity decreased from Tall to High, and was highest for Sapelo Island and lowest for Upper Phillips Creek. These indicators were used to determine how nitrogen cycling reflects the system development potential of each marsh zone.

Table 20. System Level Indices of Development (g N x bits x m^{-2} x yr^{-1})

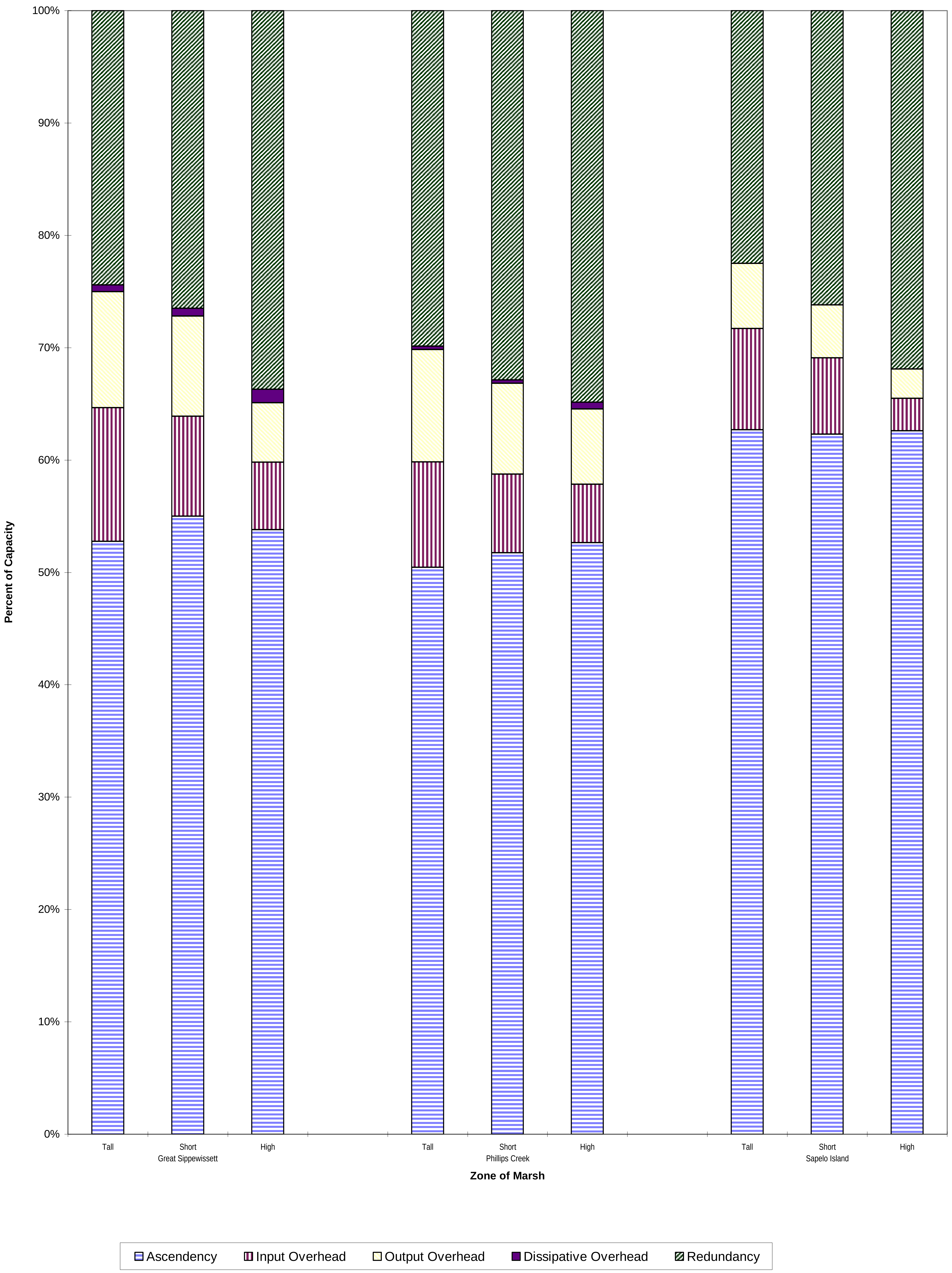
	Great Sippewissett			**Upper Phillips Creek**			**Sapelo Island**		
	Tall	**Short**	**High**	**Tall**	**Short**	**High**	**Tall**	**Short**	**High**
Capacity	1930.3	1576.4	1034.7	1247	1063.2	402.5	3841.4	2775.4	1624.3
Ascendency	1017.5	867.2	556.8	630.3	550.5	212.1	2410.1	1729.4	1016.7
Overhead	440.9	292.1	129	224.3	163.1	50.1	567.9	317.6	89.9
Redundancy	471.9	417.1	349	372.4	349.7	140.4	863.5	728.4	517.7
Internal Ascendency	647.3	601.8	399.8	407.3	407.2	161.3	1448.4	1124.6	852.6
Internal Redundancy	471.9	417.1	349	372.4	349.7	140.4	863.5	728.4	517.7

5.4.1 ***Relative Ascendency.*** Relative ascendency exhibited different patterns for each marsh (Figure 13). For Great Sippewissett, it was lowest in the Tall and highest in the Short. For Phillips Creek, it was lowest in the Tall and highest in the High. And for Sapelo Island, it was lowest in the Short and highest in the Tall. Therefore, there were no significant trends between marsh zones (p=0.717). The differences in relative ascendency between the marsh zones was very small. They ranged from 50.5% of capacity in Phillips Creek Tall to 62.5% in Sapelo Island Tall.

5.4.2 ***Overhead.*** Overhead associated with exogenous flows (inputs, outputs, and dissipations) consistently decreased moving across the marsh from Tall to High (Figure 13). Input overhead is consistent with this trend (p=0.05). Output overhead, which decreased from Tall to High, was also significantly different between marsh zones

Figure 13. System Level Indices Relative to Capacity

Figure 13. System Level Indices Relative to Capacity



(p=0.05). Dissipative overhead was a very small portion of capacity in each marsh zone, but it tended to increase across marsh zones.

5.4.3 ***Redundancy.*** Relative Redundancy, a part of total overhead, consistently increased moving across the marsh from Tall to High (Figure 13). This trend was significant (p=0.05). Redundancy ranged from 22.5% of capacity for Sapelo Island Tall to 34.9 % in Phillips Creek High marsh.

5.4.4 ***Internal Ascendency.*** Relative Internal Ascendency closely mirrored Relative Ascendency for each marsh (Figure 14). The patterns for each marsh were different. In Great Sippewissett, internal ascendency was highest in the Short marsh and lowest in the High marsh. In Upper Phillips Creek, it was highest in the Short marsh and lowest in Tall marsh. However, in Sapelo Island, it was lowest in the Short marsh and highest in the Tall. Therefore, no significant trends were found (p=0.717).

5.5 Total System Attributes

To evaluate how the marsh zones ranked with respect to maturity/stability indices, hierarchical cluster analysis was used. The variables used were FCI, APL, recycling associated with primary production (PPR), relative ascendency (RA), input overhead (IO), output overhead (OO), redundancy (Red), internal ascendency (IA), and mineralization/primary production (M/P) (Table 21). The meaning of each number was presented in Section 5.4.

Figure 14. Internal Ascendency and Redundancy

Figure 14. Internal Ascendancy/Redundancy

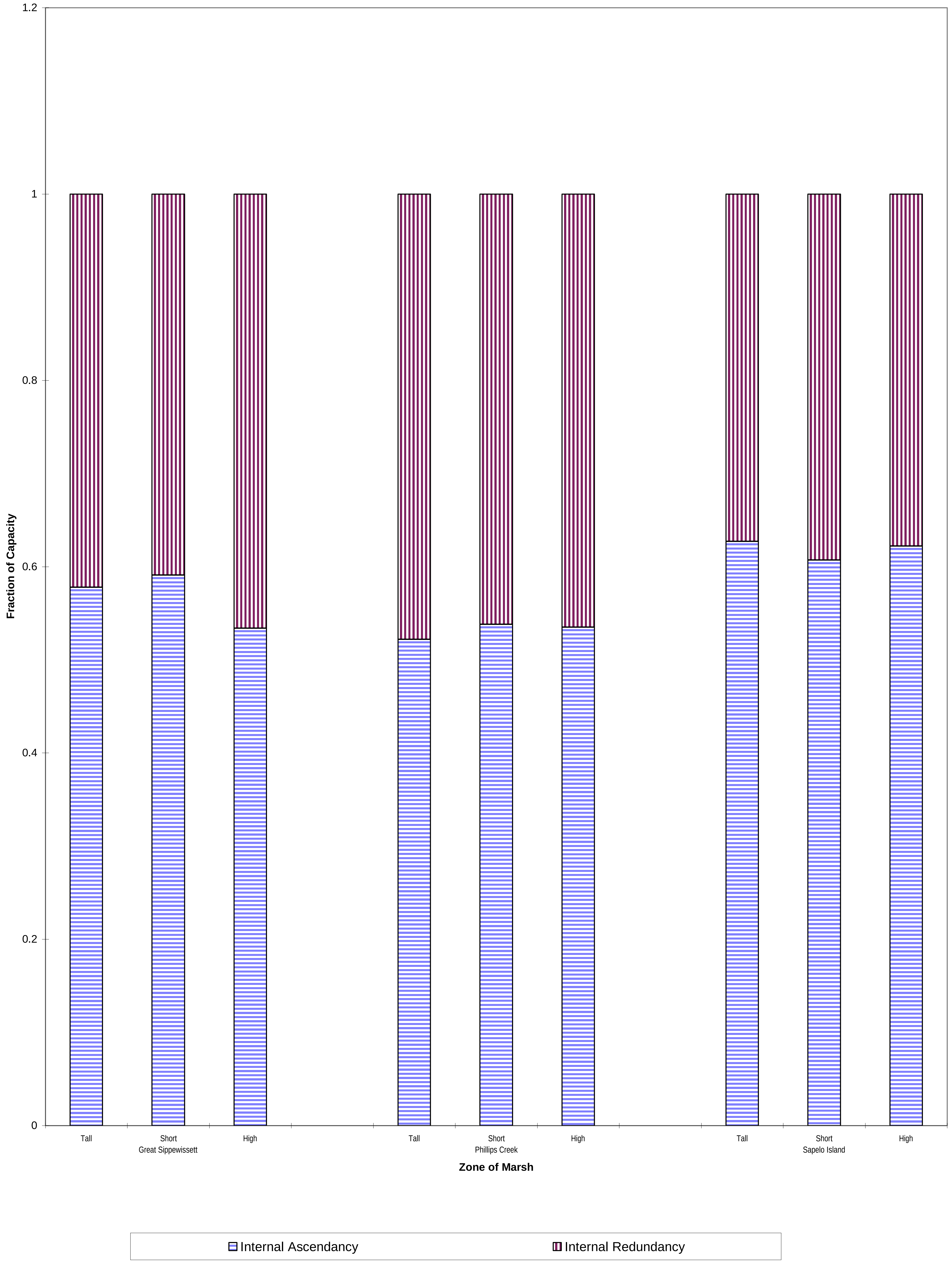


Table 21. Marsh Maturity/Stability Variables Used for Cluster Analysis and Ranking[1]. See text for variable names referred to by abbreviation in table.

	Great Sippewissett			Phillips Creek			Sapelo Island		
Variables	Tall	Short	High	Tall	Short	High	Tall	Short	High
FCI	29.7	36.5	47.1	36.1	50	53.2	40.8	41.5	80.1
APL	2.98	4.16	6.65	3.31	5.67	9.1	3.4	4.63	18
PPR	0.417	0.464	0.504	0.596	0.667	0.807	0.6	0.615	0.889
RA	0.527	0.55	0.538	0.505	0.518	0.527	0.627	0.623	0.626
IO	0.119	0.089	0.06	0.094	0.07	0.052	0.09	0.068	0.029
OO	0.103	0.089	0.053	0.1	0.081	0.067	0.058	0.047	0.026
Red	0.244	0.265	0.337	0.299	0.329	0.349	0.225	0.262	0.319
IA	0.578	0.591	0.534	0.522	0.538	0.535	0.627	0.607	0.622
M/P	0.902	1.12	1.03	1.18	1.12	0.736	1.79	2.07	1.51

[1] Units for numbers are as follows: FCI=%TST; APL=#compartments; PPR=fraction of compartment flow; RA, IO, OO, Red, IA=fraction of capacity; M/P=fraction of primary production

A correlation matrix was created to determine if the variables used to do a cluster analysis covaried (Table 22). Those variables with high positive correlation such as FCI and APL were removed one at a time to run a cluster analysis. New cluster analyses were run with a highly correlated variable removed from the analysis for each new run. It was discovered that the marsh zones did not change their cluster pattern using this technique. The data presented show the results of the full cluster analysis (Figure 15).

Generally, Tall and Short marsh zones clustered together, and High marshes clustered together (Figure 15). Phillips Creek Short marsh clustered with the High marshes. Sapelo Island High marsh was very different from all other marshes and clustered with none of the other marshes.

Figure 15. Cluster Analysis of System Level Attributes

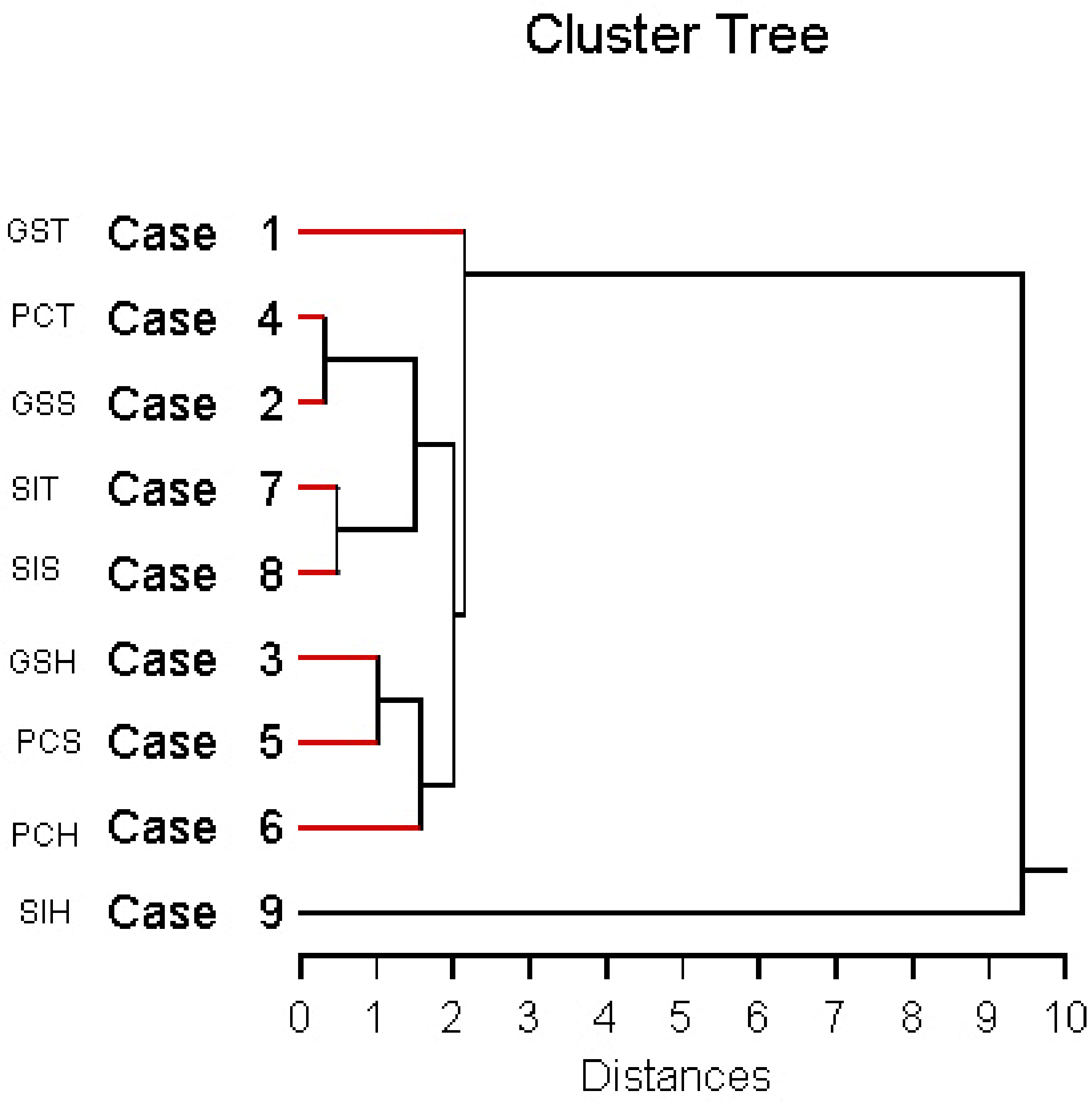

Cluster Tree
GST Case 1
PCT Case 4
GSS Case 2
SIT Case 7
SIS Case 8
GSH Case 3
PCS Case 5
PCH Case 6
SIH Case 9
0
1
2
3
4
5
6
7
8
9
10
Distances

Table 22. Correlation Matrix of System Attribute Variables (n=9)

	FCI	APL	PPR	RA	IO	OO	Red	IA	M/P
FCI	1.00	0.971	0.869	0.399	-0.912	-0.769	.569	0.213	0.111
APL		1.00	0.811	0.362	-0.859	-0.712	.536	0.23	0.019
PPR			1.00	0.323	-0.825	-0.625	.542	0.1	0.135
RA				1.00	-0.355	-0.772	-0.421	0.903	0.853
IO					1.00	0.827	-0.693	-0.062	-0.135
OO						1.00	-0.229	-0.493	-0.547
Red							1.00	-0.655	-0.505
IA								1.00	0.714
M/P									1.00

To further assess the level of maturity using different variables believed to be indicators of maturity, the marshes were also assigned a rank based on the above variables used for cluster analysis. Each marsh zone was ranked from least mature to most mature within a marsh using each variable as a stand-alone indicator of maturity. A marsh zone with a rank of 3 was the most mature, and 1 the least mature. For example, the variable FCI increased from Tall to High in all 3 marshes. It was assumed that the higher the FCI, the more mature the zone. Therefore, the Tall zone in each marsh received a ranking of 1 and the High zone a ranking of 3. Zone maturity was only compared within a marsh. The Short zone in Sapelo Island could receive a rank of 1 for a variable, while the same zone in Upper Phillips Creek received a 3 for the same variable. Variables such as redundancy, input overhead, and output overhead, were negatively correlated with maturity. Therefore, a marsh zone with a high redundancy was given a rank of 1.

When ranking with respect to maturity/stability indices above from lowest maturity to highest, it was found that the Tall marsh zones rank the least mature 70.4% of the time. The Short marsh zones ranked at intermediate maturity 70.4% of the time, and the High marsh zones ranked most mature 59.3% of the time (Table 23). Further, the mean rank followed the same pattern.

Table 23. Marsh Zone Rankings Based on Maturity/Stability Variables (See Table 21 for Variables)

	Mean Rank	% Time Rank Highest	% Time Rank Second	% Time Rank Lowest
Tall	1.48	18.5	11.1	70.4
Short	2.15	22.2	70.4	7.4
High	2.37	59.3	18.5	22.2

5.6 Reliability Factor

Each value used in each network was assigned a reliability factor (RF) as described in Section 4.4.1. The RF for each marsh zone was averaged to determine the reliability of the data used for each network (Table 24). Great Sippewissett had the highest level of reliability, while Upper Phillips Creek had the lowest. This was a reflection of the intensity of study on each marsh over the decades. The RFs were also weighted by flow to determine if the majority of flows were associated with higher RFs (Table 25). The weighted RFs show increased reliability of important flows in most cases. Only Great Sippewissett Short decreased upon weighting. To better understand how the RFs related to flow, the RFs were plotted against the percentage of numbers of flows that had a particular RF and against the percentage of TST for each RF (Figures 16-21). Each

Table 24. Average RF and Standard Deviation for Marsh Zones

	Tall	Short	High
Great Sippewissett	2.89±1.28	2.88±1.31	2.94±1.34
Upper Phillips Creek	2.07±1.73	2.12±1.73	1.67±1.77
Sapelo Island	2.25±1.78	2.22±1.77	2.25±1.79

Table 25. Flow Weighted Average RF for Marsh Zones

	Tall	Short	High
Great Sippewissett	3.06	2.75	3.02
Upper Phillips Creek	2.95	3.08	2.79
Sapelo Island	2.73	2.86	2.71

network contained a total of 60 flows. For Great Sippewissett, there was a general increase in percentage of number of flows associated with higher RFs (Figure 16). However, for Upper Phillips Creek and Sapelo Island, Figures 17 and 18 show that the data were generally either very reliable or were obtained by balancing the compartments inputs and outputs. When RFs were compared to the percentage of TST a better picture regarding reliability emerged (Figures 19-21). In all three marshes, the greatest percentage of TST was associated with RFs of 3 and 4. Sapelo Island had the greatest amount of flow associated with a RF of 0 of the 3 marshes. Over 20% of flows in Sapelo Island's Short and High zones were associated with a RF of 0. The rest of the marsh zones were less than 20%.

Figure 16. Great Sippewissett % of # of Flows per RF

Figure 16. Great Sippewissett % of # of Flows per RF

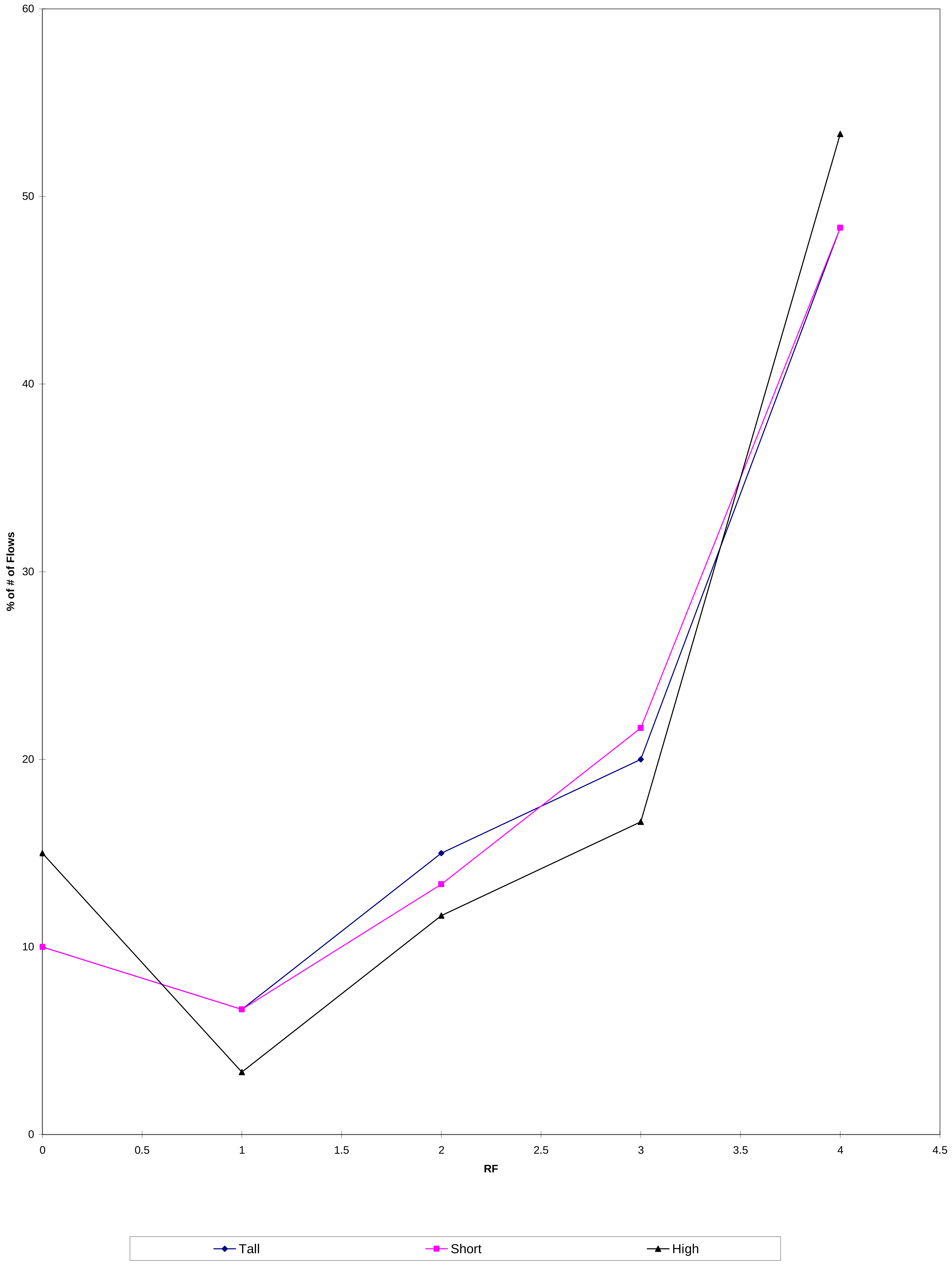


Figure 17. Upper Phillips Creek % of # of Flows per RF

Figure 17. Upper Phillips Creek % of # of Flows per RF

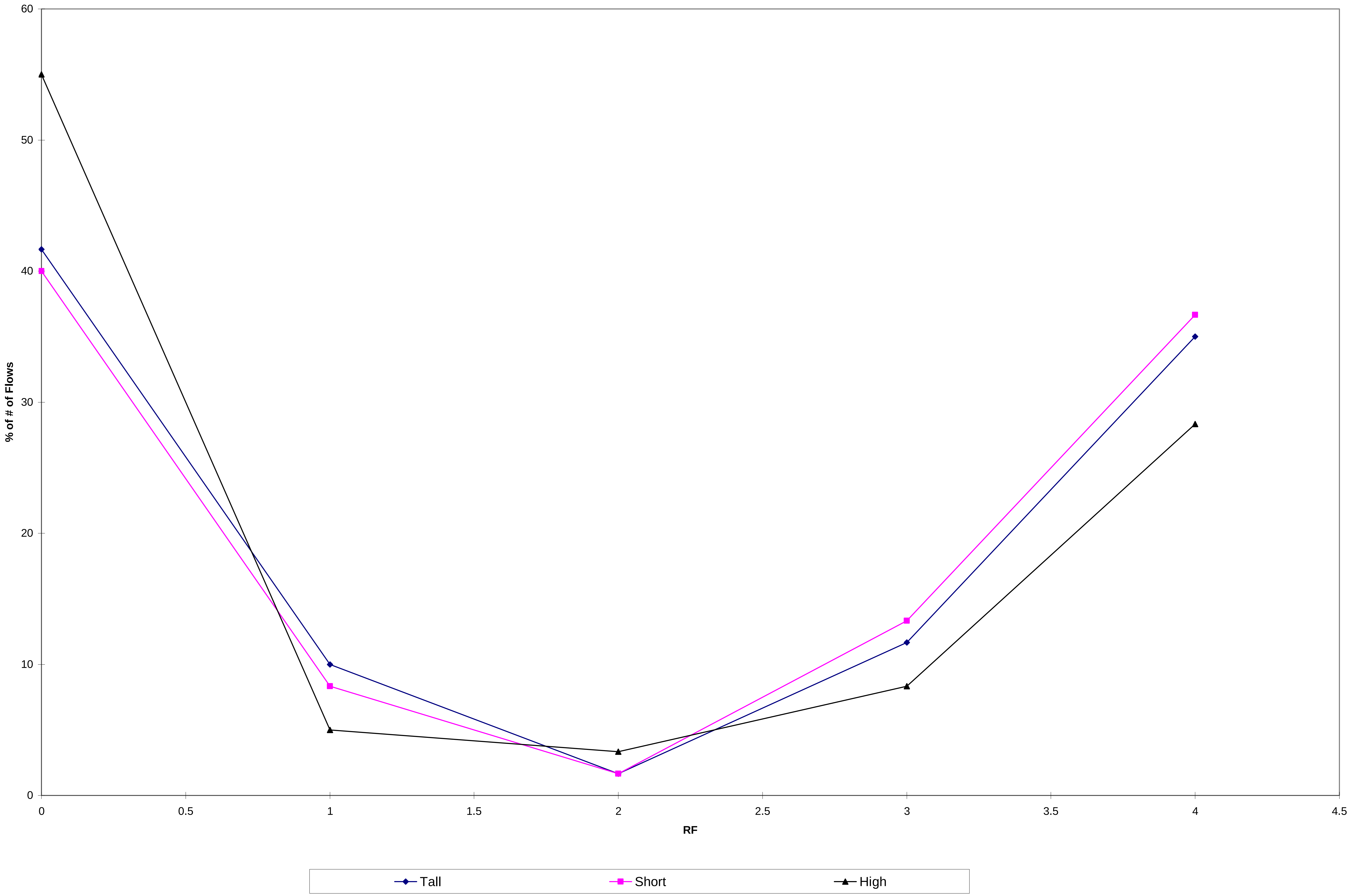


Figure 18. Sapelo Island % of # of Flows per RF

Figure 18. Sapelo Island % of # of Flows per RF

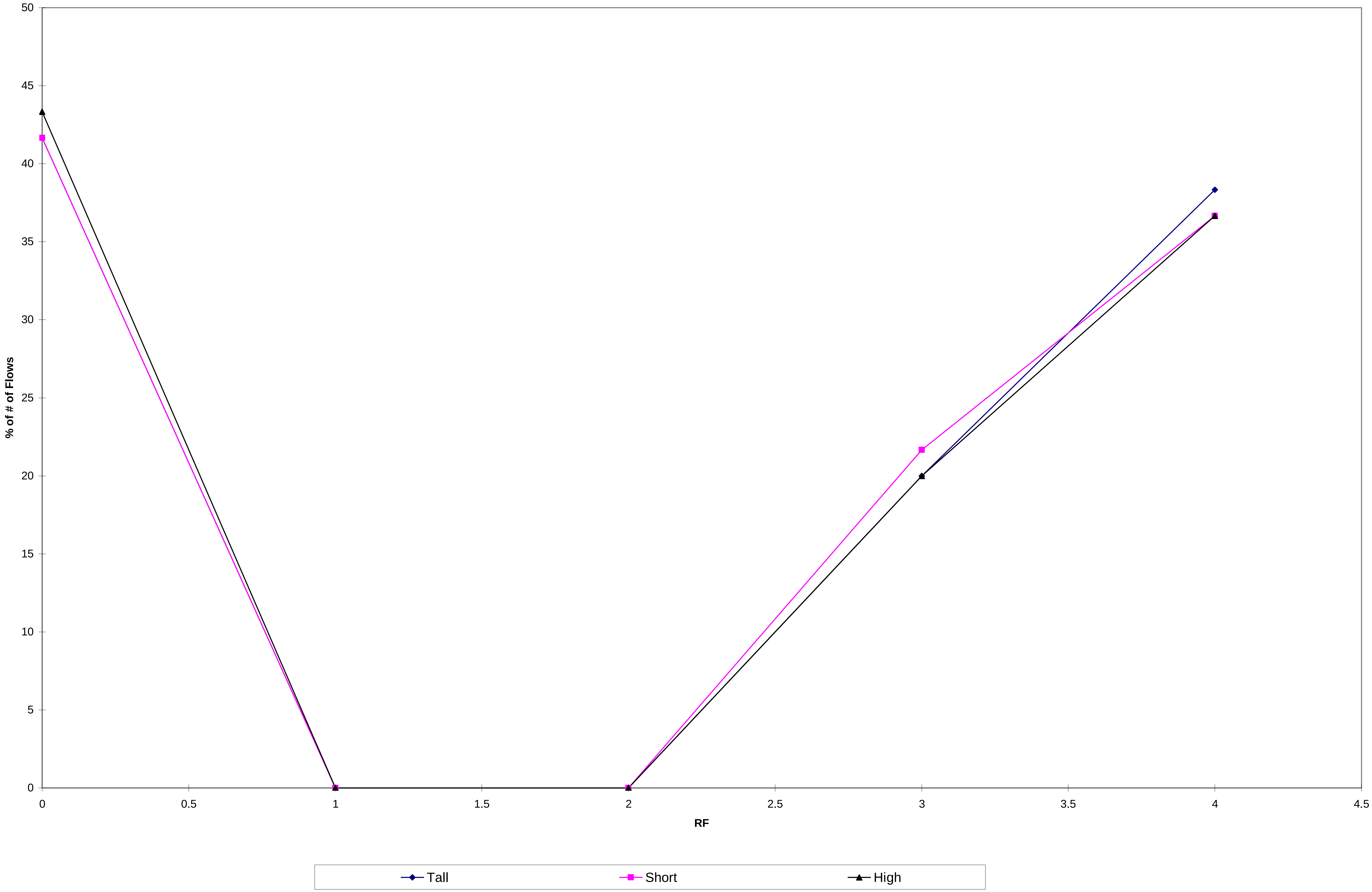


Figure 19. Great Sippewissett % TST per RF

Figure 19. Great Sippewissett % TST per RF

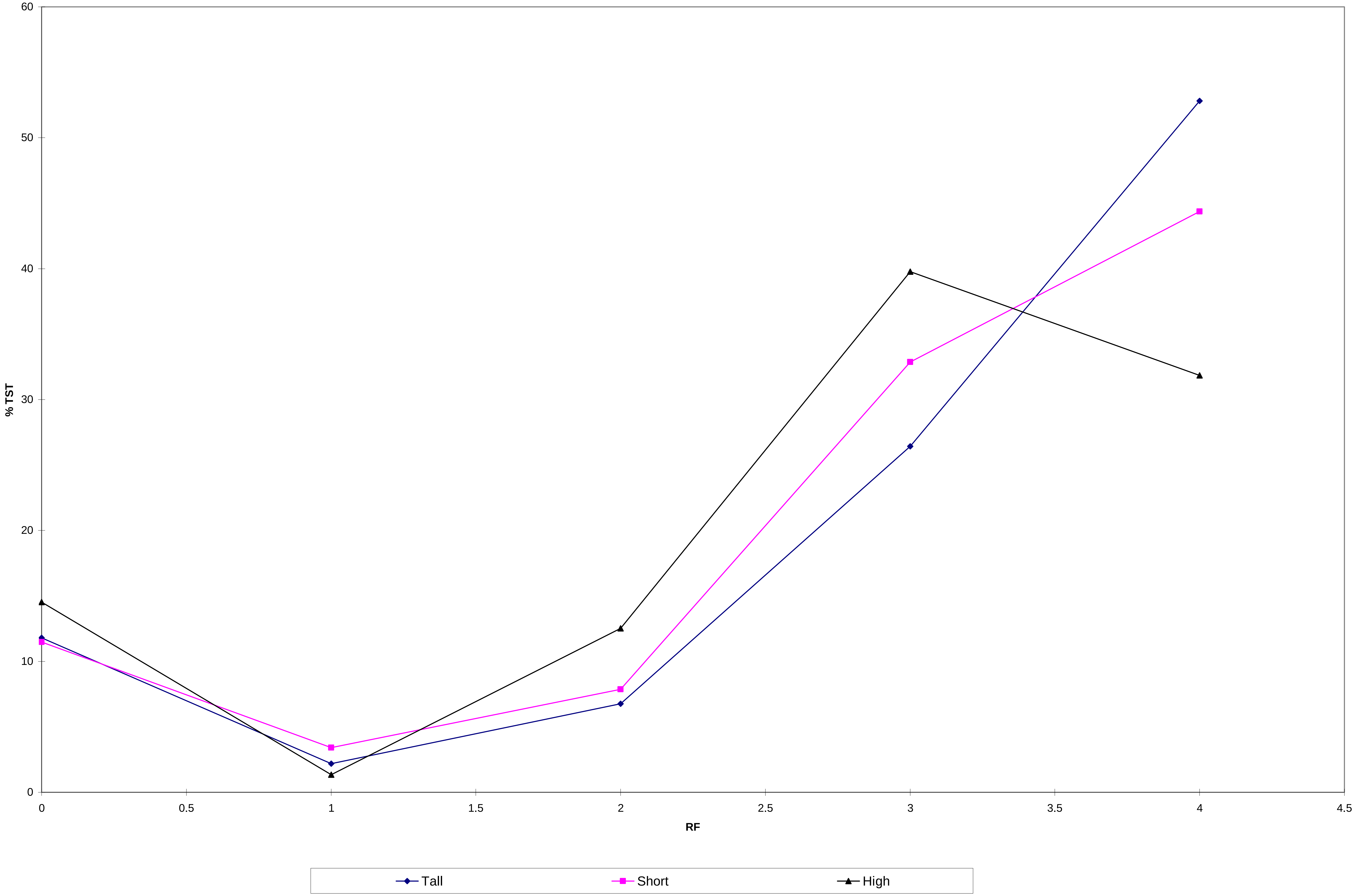


Figure 20. Upper Phillips Creek % TST per RF

Figure 20. Phillips Creek % TST per RF

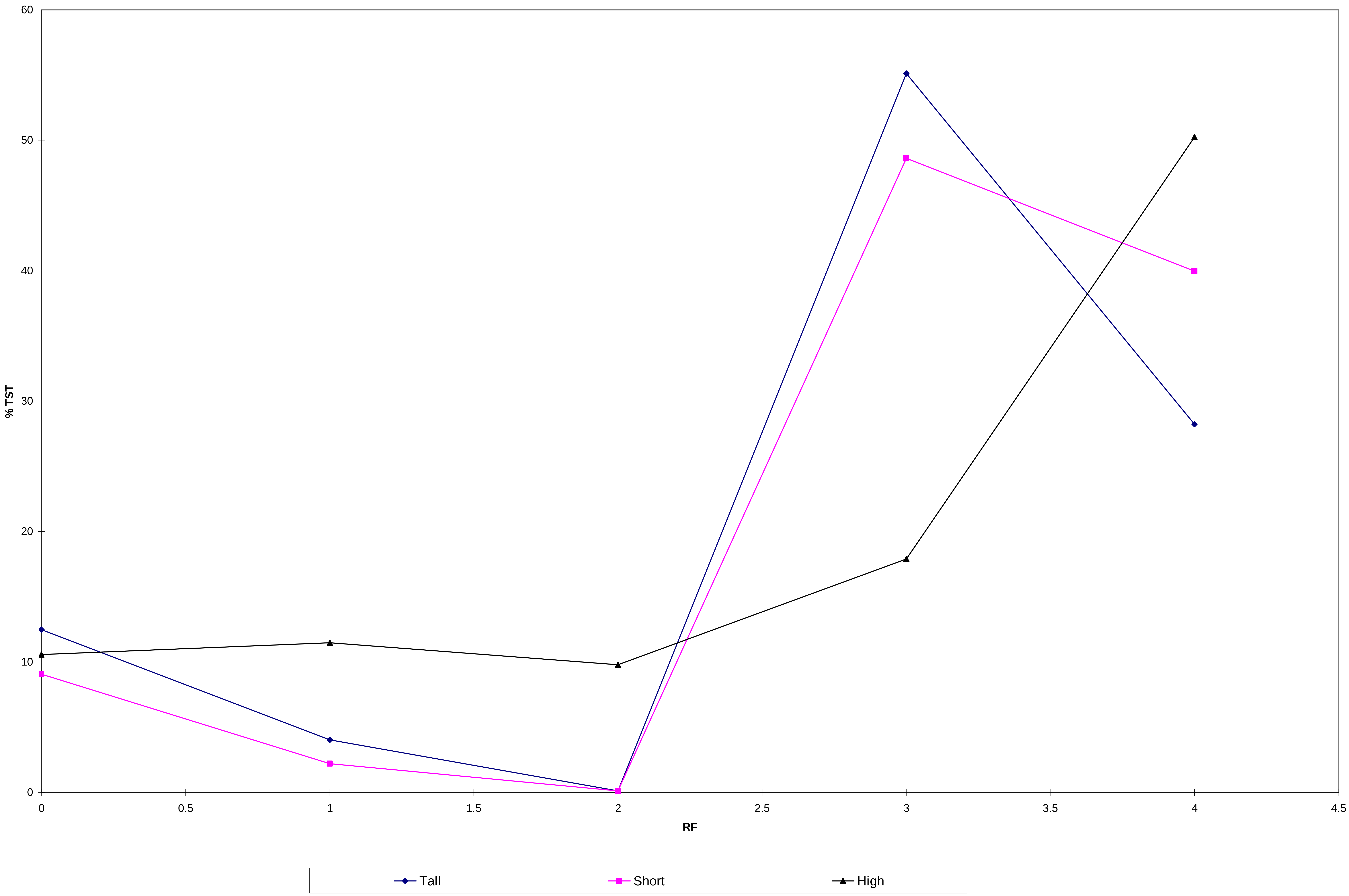
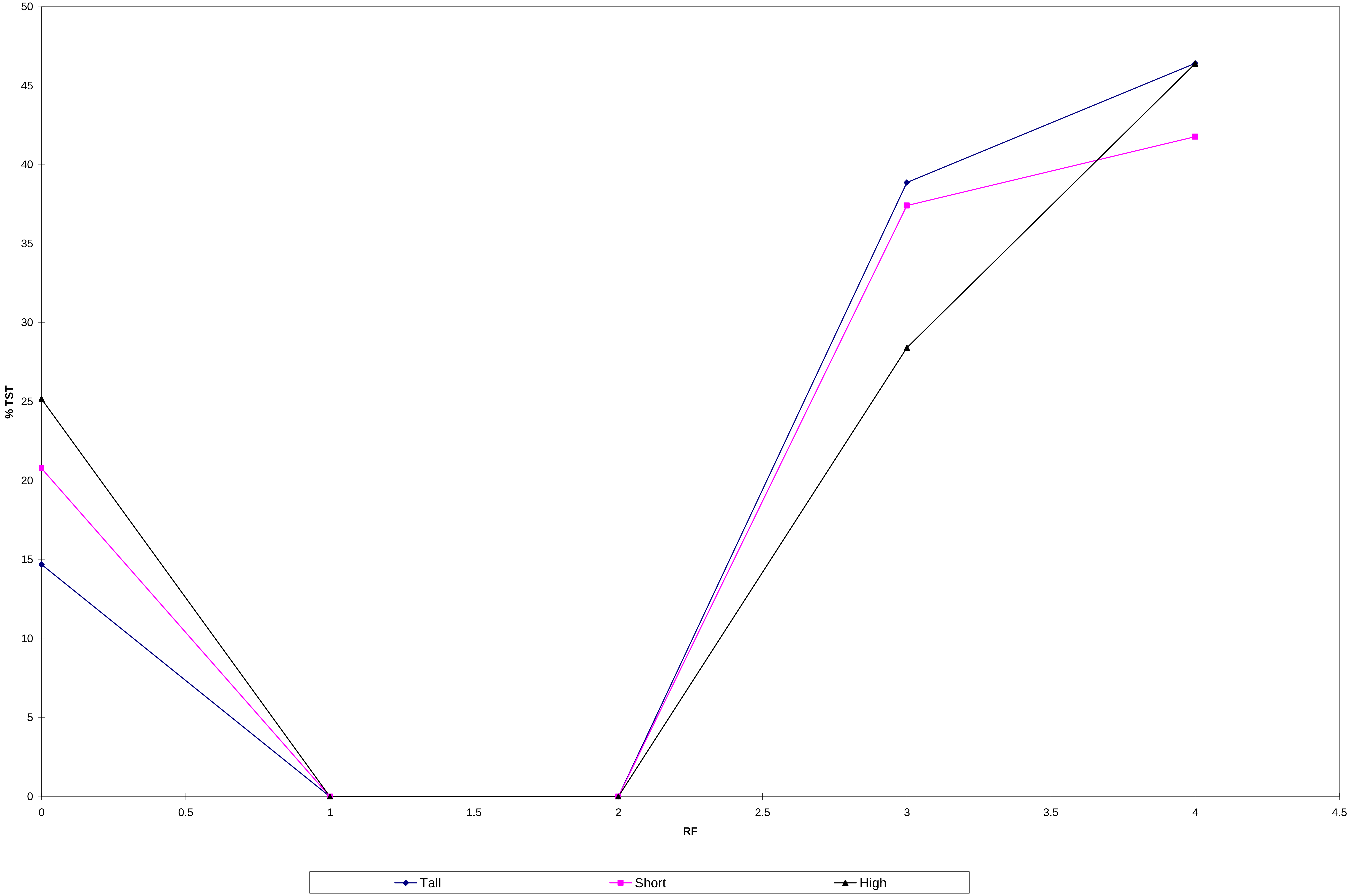


Figure 21. Sapelo Island % TST per RF

Figure 21. Sapelo Island % TST per RF



6.0 DISCUSSION

6.1 Differences in nitrogen cycling in marsh areas

Many scientists have found differences between marsh zones for particular nitrogen flows (Section 2.1.2 - 2.1.4). For example, Hanson (1977a) found that nitrogen fixation occurred at a higher rate in the Tall zone than the Short zone in Georgia. Many have studied above- and belowground primary production throughout marsh zones (Blum, 1993, Dai and Weigert, 1996; Gallagher and Plumley, 1979; Schubauer and Hopkinson 1984; Valiela et al., 1975; White and Howes, 1994a). The general conclusion is that aboveground production is higher in the Tall zone than the Short zone (Dai and Weigert, 1996; Gallagher and Plumley, 1979), but belowground production may be just the opposite (Valiela et al., 1976). High marsh production depends on the dominant plant species (Morris, 1980). There is also evidence that the mineralization rate is faster in the Tall zone than the Short zone due to tidal flushing (Howarth and Hobbie, 1982). Again, mineralization rates in the high marsh depend on the dominant plant species (Good et al., 1982). Denitrification is also believed to be highest in the Tall zone and lowest in the High zone associated with differences in tidal flushing (Kaplan et al., 1979). These individual processes within the nitrogen cycle show differences between marsh zones. Therefore, one can conclude the entire nitrogen cycle will be different among marsh zones. My contribution is in the evaluation of the integrated nitrogen cycle.

6.1.1 ***Export Routes of Various Imports.*** I found several patterns associated with the export of different nitrogen import pathways. However, the only statistically significant patterns were associated with precipitation and Tidal PN import. Burial and denitrification significantly increased in relative importance across the marsh from Tall to High when the import route was precipitation or Tidal PN. This does not conflict with Kaplan et al.'s (1979) findings that denitrification rates are faster in the Tall zone. They were measuring absolute rates. My findings consider % throughput within a marsh area. I also found that the tidal export of Tidal PN import significantly decreases in importance moving across the marsh from Tall to High. Patterns associated with precipitation are not surprising. Because of the decreased frequency of flooding in the high marsh zone, there is more opportunity for marsh surface interaction. However, in the Tall and Short zones, flooding is more frequent and there is greater opportunity for the precipitation to be flushed out by tide before there is contact with the marsh surface. Patterns related to Tidal PN may reflect the sedimentation/resuspension cycle. As the removal of tidal PN import becomes less important moving across the marsh, there may be more opportunity for particulates to settle out and become part of the marsh surface. In the Tall and Short zones, the flooding frequency reduces the relative amount of net sedimentation, decreasing the opportunity for significant marsh surface contact.

In contrast, tidal imports of NH_4^+, NOx, and DON did not show consistent patterns across marsh zones. Each marsh processed these nitrogen species very differently. NOx in Upper Phillips Creek and DON in Great Sippewissett and Sapelo Island were essentially flushed out of the marsh in the same manner. NOx was largely denitrified in Sapelo Island as a result of the high rate given by Whitney et al. (1981).

However, this rate is believed to be a potential rate rather than in situ (Whitney et al., 1981). NH_4^+ was transformed into PN in Sapelo Island before it was flushed out. There was not much information regarding DON, so the lack of significant patterns is not that surprising. The other 2 nitrogen species were very well studied for these marshes. Therefore, the lack of a pattern among marsh zones may be related to other aspects of the marsh such as geomorphology, climate, or methodology problems.

6.1.2 ***Total Contribution to Primary Production.*** When examining what nitrogen species contribute to primary production, patterns were found across marsh zones. All imports tended to increase their relative contribution to primary production moving across the marsh from Tall to High. However, there were only 2 imports that showed a significant trend, precipitation and Tidal PN. Between 16.7% (Sapelo Island Tall) and 89.1% (Upper Phillips Creek High) of precipitation went to primary production, the equivalent of 0.05-0.44g N/(m^2 x yr^1). The contribution of Tidal PN to primary production ranged from 8.75% (Sapelo Island Tall) to 69.8% (Upper Phillips Creek High), the equivalent of 0.20-6.68g N/(m^2 x yr^1). Tidal NH_4^+ showed an interesting trend of contributing least to primary production in the Short zone and most in the High zone, but this trend was not significant ($p=0.097$). It contributed from 4.0-48.9% of its throughput to primary production.

These trends may be related to the amount of interaction that each nitrogen species has with the marsh surface. As discussed above, precipitation and Tidal PN have more opportunity for marsh surface contact in the High marsh zone than in the Tall or Short zones. Thus, there is a greater probability in the high marsh that nitrogen originating from these sources will be taken up by the roots. The lack of a trend for Tidal DON is not surprising given the lack of knowledge of how it is processed in the marsh. The lack of a significant pattern for Tidal NOx and NH_4^+ may result from different geomorphologies or climate.

6.1.3 *Total Dependancy of Primary Production.* The amount of primary production's throughput that came from various sources was also examined. The only source of import that showed a significant trend across marsh zones was precipitation. It increased in importance moving across the marsh from Tall to High, but was a very small percentage of primary production's throughput (0.2-9.6%; 0.14-2.26g $N/(m^2 \times yr^1)$). Primary production was more dependent on the tidal imports, but showed no consistent pattern across marsh zones.

Tidal NH_4^+ showed very different patterns across marsh zones for each marsh. In Great Sippewissett, it contributed most to primary production in the Tall zone and least in the High zone. In Upper Phillips Creek, it contributed most to primary production in the Short zone and least in the Tall zone. And in Sapelo Island, it contributed most in the High marsh and least in the Short zone. In all cases except Sapelo Island High, primary production received less than 18% of its total throughput from tidal NH_4^+. Given that tidal NH_4^+ contributes less than 25% (except Sapelo Island High) of its throughput to primary production and that primary production gets less than 18% of its nitrogen from tidal NH_4^+, the pore NH_4^+ that the plants depend on must come from transformations of other nitrogen species.

Tidal NOx decreases in importance moving across the marsh from Tall to High in Great Sippewissett and Upper Phillips Creek. However, tidal NOx plays a larger role in Upper Phillips Creek than in Great Sippewissett. No pattern was apparent in Sapelo Island because of the relatively very small amount of nitrogen received by primary producers from tidal NOx. Likewise, primary production does not depend on tidal DON, and thus no patterns were apparent. Tidal PN is most important as a source of nitrogen in the Short zone in Great Sippewissett and Upper Phillips Creek, but least important in that zone in Sapelo Island. It ranged from 4.3% to 59.2% of primary production's throughput. Of all the tidal imports, tidal PN contributes most to pore NH_4^+, and pore NH_4^+ depends the most on tidal PN as a source of nitrogen from the tide. Thus, the sedimentation and mineralization processes are very important for making tidal imports available to primary producers.

The recycling of nitrogen within primary production, defined as the amount of nitrogen that originated in the root/rhizome compartment that returned to that compartment, showed a significant pattern across marsh zones. It increased in importance moving across the marsh from Tall to High. It accounted for between 41.7% and 88.9% of primary production's throughput. This also points to mineralization being a very important process for making nitrogen available to primary producers.

Though nitrogen fixation was not part of the statistical analysis, it is interesting to note that there were no patterns associated with primary production's dependence on nitrogen fixation. The dependency ranged from 4.7% in Upper Phillips Creek Tall zone, supporting Anderson et al.'s (1997b) approximation of 5%, to 79.5% in Sapelo Island Tall zone. Teal et al. (1979) estimated that nitrogen fixation was approximately a third of Great Sippewissett's primary production needs. I found a somewhat lower range of 13.9 % to 29.6% in Great Sippewissett marsh zones.

6.1.4 ***Groundwater.*** Groundwater was not subjected to statistical analysis because it is a negligible source of input for Sapelo Island and Upper Phillips Creek marshes. However, in Great Sippewissett, there were some interesting patterns. Groundwater import followed similar export routes as the other imports did. Tidal export decreased in importance moving across the marsh from Tall to High, and burial and denitrification increased in importance. A large portion of groundwater's throughput goes to primary production with the highest amount in the Short zone (70.2%) and the lowest in the Tall zone (68.3%). Primary production also depends heavily on groundwater for nitrogen. In each zone, more than 60% of primary production's nitrogen came from groundwater. Dependence was highest in the Short zone and lowest in the High zone. Valiela et al (1978) recognized groundwater as a major source of nutrients for primary producers and estimated that more nitrogen entered Great Sippewissett via groundwater than was needed for total primary production. Though my results do not support complete dependence on groundwater, primary production received more than 60% of its nitrogen from groundwater. It would be interesting to study other marshes with large amounts of groundwater import to determine if these patterns can be generalized.

6.1.5 ***Nitrogen Cycling Indices.*** FCI and APL are both used to measure the amount of total cycling within a system. FCI is a measure of the total amount of material in the system that is involved in cycling. APL is a measure of the average number of compartments a unit of material passes through before exiting the system. Both of these indicators significantly increased moving across the marsh from Tall to High. FCI ranged from 29.7% in Great Sippewissett Tall zone to 80.1% in Sapelo Island High zone. APL ranged from 2.9 in Great Sippewissett Tall zone to 18.0 in Sapelo Island High zone. My first hypothesis was that cycling would be highest in the High zone because of the reduced amount of tidal import but relatively high primary production. The results support my hypothesis that cycling will by highest in the High zone.

As a subset of FCI, I also looked at compartmental recycling, the amount of material that originates in a compartment, cycles through, and returns to that compartment. Recycling within the sediment compartments was significant. Pore NOx, NH_4^+, and PN all increased the amount of recycling within each compartment moving across the marsh from Tall to High. Of these, Pore NOx is probably the least important as recycling is lowest of these 3 compartments (Table 18). Recycling amounts were very similar between Pore NH_4^+ and Pore PN reflecting their role in the primary production/mineralization cycle. The recycling within the belowground plant biomass also significantly increased across the marsh. The trend for aboveground biomass recycling was not statistically significant ($p=0.097$). The other compartments did not have any significant trends across the marsh associated with recycling. Therefore, cycling appears to be closely linked to primary production, mineralization, and associated flows.

6.1.6 ***Mineralization.*** Mineralization is a very important part of total nitrogen cycling within the marsh. It provides the much needed Pore NH_4^+ for primary production. There is a trend for mineralization rate to be higher in the Tall zone than the Short. However, Blum (1993) did not find it to be significant. My second hypothesis was that relative mineralization (mineralization/TST) would be highest in the high marsh. When mineralization was divided by TST, primary production, or CT, there were no significant trends across marsh zones. Mineralization/TST tended to be highest in the High zone and lowest in the Tall zone, but the trend was not significant ($p=0.097$). Therefore, I reject my hypothesis.

6.2 Maturity and Stability

Maturity and stability were measured using indicators developed by Ulanowicz (1986) based on information theory. Developmental Capacity is the total size and complexity of a system’s flows. Ascendency is the amount of flow within that system that is organized and has been postulated to be an indicator of maturity. The difference between Capacity and Ascendency is called overhead. When Ascendency is divided by Capacity, it is called Relative Ascendency. Ulanowicz (1986) proposes relative ascendency is a good index to compare the maturity of different systems. When only internal flows are examined ascendency is referred to as internal ascendency and can be scaled by the internal development capacity to get the relative internal ascendency (Ulanowicz, 1986). This index can help determine the system’s reliance on exogenous flows when compared to relative ascendency (Baird and Ulanowicz, 1993).

Christensen (1995) did an extensive examination of different indicators of maturity as compared to E.P. Odum's 24 attributes of succession. He found that relative ascendency had a high correlation with other indicators of maturity. However, it was a negative correlation. He also found that total overhead had a very strong positive correlation with maturity. He concluded that indicators of stability were indicators of maturity (Christensen, 1995). However, I believe that Christensen's comparison of Ulanowicz's ascendency to Odum's maturity attributes may not be a fair comparison (Section 2.2.3).

The interpretation of maturity indicators also may be affected by the type of model used to evaluate a system. Foodweb models generally focus on carbon flow as a substitute for energy flow. Cycles involve only organic matter. Biogeochemical models focus more on primary production and microbial processes (Christian et al., 1996). Therefore indices that measure cycling such as the Finn Cycling Index (FCI) will have different interpretations for the different model types (Christian et al., 1996). Baird and Ulanowicz (1993) found in foodweb models that increased FCI was not an indicator of maturity but of stress. As the system becomes more stressed food chains shorten, causing material to cycle faster. However, in biogeochemical models, the foodweb is only a small part of the total model. Christian et al (1996) found that stress in the form of eutrophication was associated with a lower FCI. Dead organic matter also plays a different role in biogeochemical models than foodweb models. In biogeochemical models dead organic matter can be one of several nonliving compartments, whereas in foodwebs, dead organic matter is the only nonliving compartment.

6.2.1 ***Maturity Indices.*** I used relative ascendency as the indicator of maturity. I believe that it adequately captures Odum's (1969) attributes of a mature ecosystem. My third hypothesis was that relative ascendancy would be highest for the Short zone because under conditions of rising relative sea-level, this zone would experience a transition that would be the least extreme (Brinson et al., 1995). This zone would be the least perturbed by rising relative sea level, and therefore, be able to develop more efficient pathways for material such as nitrogen to flow. However, relative ascendency did not show any significant trends across marsh zones. Analysis does not support this hypothesis. Internal Ascendency, the organization of a system once exogenous flows are removed was also examined. Like relative ascendency, there were no significant patterns among marsh zones.

Overhead was divided into input, output, and redundancy, to evaluate trends across marsh zones. Both input and output overhead showed significant ($p=0.05$) trends decreasing across the marsh from Tall to High. This may be interpreted as decreasing stability moving across the marsh, increased susceptibility to perturbations, and increased opportunity for state change to occur. Since there is no significant trend associated with relative ascendency, it cannot be interpreted as a system increasing development at the expense of overhead. However, redundancy, overhead associated with internal flows, significantly increased across marsh zones from Tall to High ($p=0.05$). I propose that this reflects a decreased reliance on exogenous inputs and more reliance on internal cycling in the High zone.

6.2.2 ***Total System Attributes.*** Total system attributes attempt to capture the emergent properties of a system such as stability and maturity. Some have used these attributes to compare systems either over time or space (Forès and Christian, 1993; Forès et al., 1994; Baird et al., 1995; Christian et al., 1996; Christian et al., 1997). Sometimes indices have to be scaled to a relative level in order to make comparisons between systems, such as relative ascendency and FCI.

Using scaled maturity/stability indices, hierarchical cluster analyses showed that the Tall and Short zones tended to cluster together and that the High zones tended to cluster together (Table 21 and Figure 15). This supports Brinson et al.'s (1995) designation of the low marsh. The cluster pattern may be because of the similarity between the Tall and Short zones, both of which are dominated by *S. alterniflora* and received frequent tidal flooding, 100% and 50% versus 10% of all high tides covering the marsh surface.

When the marshes were ranked by the maturity/stability indices, there was a distinct pattern of the Tall zone ranking the lowest, Short zone second, and the High zone ranking highest in maturity. This did not follow either my prediction based on relative ascendency (Ulanowicz, 1986), or overhead (Christensen, 1995). It actually was just the opposite trend associated with overhead. Input and output overhead decreased across the marsh from Tall to High. Overhead decreases when either the magnitude of associated flows decreases or when these flows are partitioned more evenly (Ulanowicz, 1997). In this case, the magnitude of tidal imports and exports were significantly decreased moving across the marsh both in absolute and relative terms. Conversely to overhead, maturity based on ranking of maturity/stability indices increased across the marsh. Relative ascendency and overhead were some of the indices used for the ranking but there were 9 indices used for ranking, 4 of which (i.e., FCI, APL, primary production recycling, and mineralization/primary production) were unrelated to Ulanowicz's Ascendency hypothesis. Redundancy significantly increased ($p=0.05$) across the marsh from Tall to High. As discussed earlier, I propose that this reflects a decreased reliance on exogenous inputs and more reliance on internal cycling in the High zone, as both FCI and APL also significantly increase moving across the marsh from Tall to High. This may make the High marsh more stable and resistant to perturbations and state change. Christensen (1995) may have been correct in stating that indicators of stability are indicators of maturity, but the best indicator is not total overhead but instead is redundancy.

6.3 Comparisons Among Marshes

The original intent was NOT to make comparisons among the different marshes used in this study because there are several problems with comparing different marshes. The most important is the use of different methodologies to measure processes such as primary production, nitrification, mineralization and denitrification. Several different methods were used to estimate these rates resulting in different estimates (Table 3). For example, primary production is a major flow within the network and can significantly influence the analysis of nitrogen flow. It was measured by several different methods including Wiegert and Evans (1964) and regression (Dai and Wiegert, 1995). These methodologies result in different estimates of primary production (Dai and Wiegert, 1995). Therefore, it cannot be known for sure if the differences among marshes are real or artifacts of the methodology. There were also cases where data were not available for some marshes but were for others. Therefore, these factors must be kept in mind when making comparisons among marshes.

Among marsh patterns were examined for FCI, APL, and recycling associated with belowground plant biomass. There was a general but nonsignificant ($p=0.097$) pattern for recycling to be lowest in Great Sippewissett and highest in Sapelo Island. The rough estimates developed by Howarth and Hobbie (1982) for Great Sippewissett and Sapelo Island would suggest the opposite finding given that primary production and mineralization are major factors influencing the amount of recycling within a marsh zone. They estimated microbial heterotrophy for short *S. alterniflora* stands for both marshes. They found that microbial heterotrophy was much greater in Great Sippewissett (2590 g C x m^{-2} x yr^{-1}) than in Sapelo Island (870 g C x m^{-2} x yr^{-1}). They suggest this results from the greater belowground primary production in Great Sippewissett than Sapelo. However, I found that belowground primary production and mineralization rates were both higher for Sapelo Island than Great Sippewissett (Table 5.1 and Appendix A-F).

Mineralization/primary production tended to be highest in Sapelo Island and lowest in Great Sippewissett but not significantly ($p=0.097$). The mineralization rate was very different among marshes with the highest rate in Sapelo Island. This may be explained by climatic effects. However, Howarth and Hobbie (1982) found microbial heterotrophy to be higher in Great Sippewissett than Sapelo Island. Though these were rough estimates, they concluded that the inputs of carbon to the marsh soil were greater in Great Sippewissett than Sapelo Island (Howarth and Hobbie, 1982).

Relative ascendency showed a significant trend among marshes (p=0.05). It was lowest for Upper Phillips Creek and highest for Sapelo Island. Coincidentally, if maturity is defined as age, this pattern matches the ages of the marshes. Sapelo Island is the oldest marsh with an estimated age of 15,000 years (Hoyt, 1967). Great Sippewissett is approximately 2,000 years old (Valiela, 1983), and Upper Phillips Creek is the youngest at 200 years (Chambers et al., 1992). The trend among marshes for internal ascendency was similar to relative ascendency but was not significant (p=0.097).

Both relative input and output overhead tend to be highest in Great Sippewissett and lowest in Sapelo Island. However, only the input overhead trend was significant (p=0.05). Output overhead was nearly significant (p=0.097). This may be related to the diversity of imports. Great Sippewissett relies on 3 major imports (tide, groundwater, and nitrogen fixation) while Sapelo Island relies on 2 (tide and nitrogen fixation) and Upper Phillips Creek relies mainly on 1 import (tide). The more the diversity of imports the less information contained within the flows. However, when the Shannon Index of diversity was applied to the import flows, Sapelo Island showed the greatest diversity of flows (18.06), Great Sippewissett second (9.27), and Upper Phillips Creek least as expected (0.68).

There was also a significant trend associated with redundancy among marshes (p=0.05). Redundancy was highest in Upper Phillips Creek and lowest in Sapelo Island. This may be related to the developmental stage of the marsh. Relative ascendency, a measure of maturity, is lowest for Upper Phillips Creek and highest for Sapelo.

6.4 How Nitrogen Cycling May be Affected by Rising Relative Sea-Level

6.4.1 ***State Change Model.*** According to Brinson et al. (1995), marshes will respond to rising sea-level in a variety of ways. The proposed model is that a marsh zone will become the adjacent marsh zone moving toward the creek. Forest will become high marsh, high marsh will become low marsh, and low marsh will become subtidal. As these changes take place, the dominant plant species will change, and thus the amount and distribution of plant biomass will change. The type of soil structure will also change depending on which zone is considered (Brinson et al., 1995). And most obviously, the frequency of flooding will change. All of these factors affect how nitrogen cycles through a marsh zone.

6.4.2 ***Nitrogen cycling patterns across marsh zones.*** I found statistically significant nitrogen cycling patterns across marsh zones. Burial and denitrification increased in importance as export routes moving across the marsh from Tall to High when the import was precipitation or Tidal PN. The amount of recycling increased moving across the marsh from Tall to High. And maturity associated with nitrogen cycling, as measured by a ranking of maturity/stability indicators, increased moving across the marsh from Tall to High. These patterns should be affected by an increase in relative sea-level rise.

6.4.3 ***How a marsh's nitrogen cycle may respond to relative sea-level rise.*** As rising relative sea level transforms a high marsh zone to the adjacent low marsh zone as modeled by Brinson et al. (1995), the zone will probably experience a decrease in the importance of burial and denitrification as export routes, a decrease in recycling, and a decrease in maturity. But this does not mean that the total marsh is experiencing these patterns. If the marsh is migrating overland and maintaining its total area, there will be little change in its overall cycling characteristics. If the marsh is migrating overland and increasing its total area as is Upper Phillips Creek (Kastler, 1993), the marsh will be increasing cycling and maturity in an average squared meter if the High zone is the area increasing in size. If, as is the case in Great Sippewissett (Valiela, 1983) and Sapelo Island (Pomeroy and Wiegert, 1981), the marsh is migrating overland and prograding toward the sea, the overall change in the characteristic of the nitrogen cycle will depend on the rate at which each process occurs. If prograding occurs more rapidly than overland migration, the marsh will experience an overall decrease in nitrogen cycling and maturity in an average squared meter. If, however, the marsh is migrating overland faster than it is prograding, then there will be an increase in cycling and maturity. If the marsh is stalling at a steep slope, the marsh will cycle less nitrogen and decrease in maturity in an average squared meter. Depending on the steepness of the slope, the marsh may be replaced with open water.

In conclusion, the nitrogen cycle of salt marshes experiencing rising relative sea-level will change. The degree and direction of change will depend on the landscape setting of the marsh. Slope and degree of sediment supply will play key roles in determining how the nitrogen cycle of a salt marsh will be affected by rising sea level.

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APPENDIX A. GREAT SIPPEWISSETT ORIGINAL DATA.

Compartment	Original Data	Zone	Season	Source
Aboveground Biomass	400 g/m2/yr	High	Year	Valiela et al, 1975
Aboveground Biomass	300 g/m2	Short	Summer	Valiela et al, 1976
Aboveground Biomass	270 g/m2	Short	Summer	Valiela et al, 1976
Aboveground Biomass	2.3 g N/m2	Short	May	White & Howes, 1994c
Aboveground Biomass	2.7 g N/m2	Short	June	White & Howes, 1994c
Aboveground Biomass	3.4 g N/m2	Short	July	White & Howes, 1994c
Aboveground Biomass	4.5 g N/m2	Short	August	White & Howes, 1994c
Aboveground Biomass	4.0 g N/m2	Short	September	White & Howes, 1994c
Aboveground Biomass	3.2 g N/m2	Short	October	White & Howes, 1994c
Aboveground Biomass	750 g/m2/yr	Tall	Year	Valiela et al, 1975
Aboveground Biomass	350 g/m2/yr	Tall	Year	Valiela et al, 1975
Aboveground Biomass	1700 g/m2	Tall	Summer	Valiela et al, 1976
Aboveground Dead	14720 kg N	Total	August	Valiela & Teal,1979b
Aboveground Live	1107 kg N	Total	August	Valiela & Teal, 1979b
Aboveground Production	0.63 kg/m2/yr	High	Year	Valiela et al, 1975
Aboveground Production	423.7 g/m2/yr	Short	Year	Valiela et al, 1976
Aboveground Production	0.36 kg/m2/yr	Short	Year	Valiela et al, 1975
Aboveground Production	3.8 g N/m2/yr	Short	Year	White & Howes, 1994a
Aboveground Production	17 mol C/m2/yr	Short	Year	Howes et al, 1985
Aboveground Production	1210 kg N/yr	Short	Year	Leschine, 1979
Aboveground Production	2790 kg N/yr	Total	Year	Finn & Leschine, 1980
Aboveground Production	2790 kg N/yr	Total	Year	Finn & Leschine, 1980
Aboveground Production	51 kg N/d	Total	August	Valiela & Teal, 1979b
Animal	5000 kg N/yr	Total	Year	Valiela, 1983
Animals	9 kg N/yr	Total	Year	Valiela & Teal, 1979b
Animals	9 kg N/yr	Total	Year	Valiela & Teal, 1979b
Animals	1,700 kg	Total	Year	Valiela, 1983
Arthropods	1.15 kg N/d	Short	June 16-Sept 30	Jordan & Valiela, 1982
Belowground Biomass	23.0 g/m2/growing season	High	Growing Season	Valiela et al, 1976
Belowground Biomass	18.2 g/m2/growing season	High	Growing Season	Valiela et al, 1976
Belowground Biomass	23.2 g/m2/growing season	Short	Growing Season	Valiela et al, 1976
Belowground Biomass	58.9 g/m2/growing season	Short	Growing Season	Valiela et al, 1976
Belowground Biomass	970 dry mass g/m2	Short	Year	Howes et al, 1985
Belowground Dead	250 kg N	Total	August	Valiela & Teal, 1979b
Belowground Live	493 kg N	Total	August	Valiela & Teal, 1979b
Belowground Production	3,291.0 g/m2/yr	Short	Year	Valiela et al, 1976
Belowground Production	18.6-20.4 g N/m2/yr	Short	Year	White & Howes, 1994a
Belowground Production	3500 gC/m2/yr	Short	Year	Howes et al, 1985
Belowground Production	58.0-74.5 mol C/m2/yr	Short	Year	Howes et al, 1985
Belowground Production	929-1022 g C/m2/yr	Short	Year	White & Howes, 1994a
Belowground Production	3,921.7 g/m2/yr	Short	Year	Valiela et al, 1976
Benthic algae production	5.0 g N/m2/yr	Short	Year	White & Howes, 1994a
Benthic algae production	3.5 mol C/m2/yr	Short	Year	Howes et al, 1985
Biodeposition	450 kg N/yr	Short	Year	Leschine, 1979
Biodeposition	3154 kg N/yr	Total	Year	Valiela, 1983
Biodeposition	1265 kg N/yr	Total	Year	Finn & Leschine, 1980
Biodeposition	1265 kg N/yr	Total	Year	Finn & Leschine, 1980
Burial	1,310 kg N/yr	Short	Year	Jordan & Valiela, 1982
Burial	4.4 g N/m2/yr	Short	Year	White & Howes, 1994
Burial	7.4 mol C/m2/yr	Short	Year	Howes et al, 1985
Burial	3.2-4.6 g N/m2/yr	Short	Year	White & Howes, 1994b
Burial	3.7-4.1 g N/m2/yr	Short	Year	White & Howes, 1994a
Burial	25 kg N/yr	Short	Year	Leschine, 1979
Burial	2.7 g N/m2/yr	Total	Year	Valiela, 1983
Burial	25 kg N/yr	Total	Year	Valiela & Teal, 1979b
Burial	1,295 kg N/yr	Total	Year	Valiela, 1984
Burial	1,295 kg/yr	Vegetative	Year	Valiala & Teal, 1979a
Burial	5% of annual production		Year	Valiela et al, 1975
Decay	631.8 g biomass/m2	High	Year	Leschine, 1979
Decay	1 kg N/m2	High	Year	Leschine, 1979
Decay	4200 kg N/yr	Short	Year	Leschine, 1979
Decay	4 kg N/m2	Short	Year	Leschine, 1979
Decay	423.7 g biomass/m2	Short	Year	Leschine, 1979
Decay	0.4 g N/m2/yr	Short	Year	White & Howes, 1994c
Decay	10 kg N/d	Total	August	Valiela & Teal, 1979b
Decay	9440 kg N/yr	Total	Year	Finn & Leschine, 1980
Decay	9440 kg N/yr	Total	Year	Finn & Leschine, 1980

Decay	1,600 kg N/yr	Total	Year	Valiela, 1983
Decomposer	70% of aboveground prod	Total	Year	Valiela, 1983
Denitrification	66 kg N/yr	Algal Mat	Year	Kaplan et al, 1979
Denitrification	1,158 kg N/yr	Creek Bottom	Year	Kaplan et al, 1979
Denitrification	223 kg N/yr	High	Year	Kaplan et al, 1979
Denitrification	45 kg N/yr	Pannes	Year	Kaplan et al, 1979
Denitrification	25.2 mg N/m2/d	Short	May	White & Howes, 1994a
Denitrification	4.1-5.6 g N/m2/yr	Short	Year	White & Howes, 1994a
Denitrification	1,371 kg N/yr	Short	Year	Kaplan et al, 1979
Denitrification	2830 kg N/yr	Short	Year	Leschine, 1979
Denitrification	153 kg N/yr	Tall	Year	Kaplan et al, 1979
Denitrification	9 kg N/d	Total	Year	Valiela & Teal, 1979b
Denitrification	6,940 kg/yr	Total	Year	Valiala & Teal, 1979a
Denitrification	1,558 kg N/yr	Total	Year	Valiela & Teal, 1979b
Denitrification	6940 kg N/yr	Total	Year	Valiela, 1983
Denitrification	14.3 g N/m2/yr	Total	Year	Valiela, 1983
Denitrification	8250 kg N/yr	Total	Year	Finn & Leschine, 1980
Denitrification	6,940 kg N/yr	Total	Year	Valiela, 1984
DIN	12 kg/d	Total	August/September	Valiala & Teal, 1979a
DIN	0.05 kg N/d	Total	August	Valiela & Teal, 1979b
Excretion	420 kg N/yr	Short	Year	Leschine, 1979
Excretion	7130 kg N/yr	Total	Year	Valiela, 1983
Excretion	690 kg N/yr	Total	Year	Finn & Leschine, 1980
Excretion	690 kg N/yr	Total	Year	Finn & Leschine, 1980
Filtration	2650 kg N/yr	Short	Year	Leschine, 1979
Filtration	2530 kg N/yr	Total	Year	Finn & Leschine, 1980
Filtration	2530 kg N/yr	Total	Year	Finn & Leschine, 1980
Fish	2.33 kg N/d	Short	June 16-Sept 30	Jordan & Valiela, 1982
Grazers	10% of aboveground Prod	Total	Year	Valiela, 1983
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Grazers/Nekton	9.11 mussels/day	Short	Growing Season	Seed, 1980
Groundwater	2455 kg N/yr	Short	Year	Leschine, 1979
Groundwater	2,710 kg/yr	Total	Year	Valiala & Teal, 1979a
Groundwater	460 kg/yr	Total	Year	Valiala & Teal, 1979a
Groundwater	30 kg/yr	Total	Year	Valiala & Teal, 1979a
Groundwater	2,920 kg/yr	Total	Year	Valiala & Teal, 1979a
Groundwater	9 kg/d	Total	June/July	Valiala & Teal, 1979a
Groundwater	6,120 kg/yr	Total	Year	Valiala & Teal, 1979a
Groundwater	5,471 kg N/yr	Total	Year	Valiela & Teal, 1979b
Groundwater	2,495 kg N/yr	Total	Year	Valiela & Teal, 1979b
Groundwater	29 kg N/yr	Total	Year	Valiela & Teal, 1979b
Groundwater	492 kg N/yr	Total	Year	Valiela & Teal, 1979b
Groundwater	2,455 kg N/yr	Total	Year	Valiela & Teal, 1979b
Groundwater	12.6 g N/m2/yr	Total	Year	Valiela, 1983
Groundwater	2,921 kg N/yr	Total	Year	Valiela et al, 1978
Groundwater	31.2 kg N/yr	Total	Year	Valiela et al, 1978
Groundwater	458 kg N/yr	Total	Year	Valiela et al, 1978
Groundwater	2,713 kg N/yr	Total	Year	Valiela et al, 1978
Groundwater	6100 kg N/yr	Total	Year	Valiela et al, 1978
Groundwater	7180 kg N/yr	Total	Year	Finn & Leschine, 1980
Groundwater	15 kg N/yr	Total	Year	Finn & Leschine, 1980
Groundwater	530 kg N/yr	Total	Year	Finn & Leschine, 1980
Groundwater	2,921 kg N/yr	Total	Year	Kaplan et al, 1979
Groundwater	6,120 kg N/yr	Total	Year	Valiela, 1984
Leaching	0.4 kg N/d	High	June 16-Sept 30	Jordan & Valiela, 1982
Leaching	2.8 kg N/d	Short	June 16-Sept 30	Jordan & Valiela, 1982
Leaching	0.4 g N/m2/yr	Short	Year	White & Howes, 1994a
Leaching	73.5 mg N/m2/mo	Short	June	White & Howes, 1994a
Leaching	78.7 mg N/m2/mo	Short	July	White & Howes, 1994c
Leaching	70.6 mg N/m2/mo	Short	August	White & Howes, 1994c
Leaching	59.6 mg N/m2/mo	Short	September	White & Howes, 1994c
Leaching	128.9 mg N/m2/mo	Short	October	White & Howes, 1994c
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Leaching	0.4 g N/m2/yr	Short	Year	White & Howes, 1994c
Leaching	270 kg N/yr	Short	Year	Leschine, 1979
Leaching	7 kg N/d	Total	August	Valiela & Teal, 1979b
Leaching	1200 kg N/yr	Total	Year	Valiela, 1983
Leaching	2830 kg N/yr	Total	Year	Finn & Leschine, 1980
Leaching	630 kg N/yr	Total	Year	Finn & Leschine, 1980
Leaching	7 kg/d	Total	August	Valiala & Teal, 1979a

Litter	0-6.0 mol C/m2/yr	Short	Year	Howes et al, 1985
Litter	2200 kg N/yr	Total	Year	Finn & Leschine, 1980
Mineralization	14.9-16.3 g N/m2/yr	Short	Year	White & Howes, 1994a
Mineralization	700 kg/yr	Total	Year	Valiala & Teal, 1979a
Mineralization	700 kg N/yr	Total	Year	Valiela, 1983
Mineralization	3280 kg N/yr	Total	Year	Valiela, 1983
Mineralization	700 kg N/yr	Total	Year	Finn & Leschine, 1980
Mussel	2528 kg N/yr	Short	Year	Jordan & Valiela, 1982
Mussel	1264 kg N/yr	Short	Year	Jordan & Valiela, 1982
Mussel	691 kg N/yr	Short	Year	Jordan & Valiela, 1982
Mussel	261 kg N/yr	Short	Year	Jordan & Valiela, 1982
Mussel	7.49 kg N/d	Short	June 16-Sept 30	Jordan & Valiela, 1982
Mussel	2,530 kg N/yr	Short	Year	Jordan & Valiela, 1982
Mussel	1,260 kg N/yr	Short	Year	Jordan & Valiela, 1982
Mussel	165 kg N/yr	Total	Year	Finn & Leschine, 1980
Mussel	165 kg N/yr	Total	Year	Finn & Leschine, 1980
Mussel	1341 kg N		Year	Jordan & Valiela, 1982
Nitrification	0-10 kg N/d	Total	April-October	Kaplan et al, 1979
Nitrification	4740 kg N/yr	Total	Year	Valiela, 1983
Nitrification	9635 kg N/yr	Total	Year	Finn & Leschine, 1980
Nitrogen Fixation	14,140 g N/yr	Algal Mat	Year	Carpenter et al, 1978
Nitrogen Fixation	2.3 g N/m2/yr	Algal Mat	Year	Valiela, 1983
Nitrogen Fixation	71.90 ng N/cm2/h	Algal Mat	May	Van Raalte et al, 1974
Nitrogen Fixation	86.90 ng N/cm2/h	Algal Mat	May	Van Raalte et al, 1974
Nitrogen Fixation	44.30 ng N/cm2/h	Algal Mat	July	Van Raalte et al, 1974
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Nitrogen Fixation	33.56 ng N/cm2/h	Algal Mat	July	Van Raalte et al, 1974
Nitrogen Fixation	7.3 ng N/cm2/h	Algal Mat	July	Brenner et al, 1976
Nitrogen Fixation	155.7 ng N/cm2/h	Algal Mat	July	Brenner et al, 1976
Nitrogen Fixation	104 kg N/yr	Creek Bottom	Year	Kaplan et al, 1979
Nitrogen Fixation	1.9 ng N/cm2/h	High	March	Teal et al, 1979
Nitrogen Fixation	13.3 ng N/cm2/h	High	June	Teal et al, 1979
Nitrogen Fixation	28.2 ng N/cm2/h	High	July	Teal et al, 1979
Nitrogen Fixation	67.9 ng N/cm2/h	High	August	Teal et al, 1979
Nitrogen Fixation	18.7 ng N/cm2/h	High	September	Teal et al, 1979
Nitrogen Fixation	16.6 ng N/cm2/h	High	November	Teal et al, 1979
Nitrogen Fixation	10.3 ng N/cm2/h	High	November	Teal et al, 1979
Nitrogen Fixation	1.9 ng N/cm2/h	High	March	Teal et al, 1979
Nitrogen Fixation	18.1 ng N/cm2/h	High	June	Teal et al, 1979
Nitrogen Fixation	28.0 ng N/cm2/h	High	July	Teal et al, 1979
Nitrogen Fixation	70.5 ng N/cm2/h	High	August	Teal et al, 1979
Nitrogen Fixation	35.8 ng N/cm2/h	High	September	Teal et al, 1979
Nitrogen Fixation	19.4 ng N/cm2/h	High	November	Teal et al, 1979
Nitrogen Fixation	5.8 ng N/cm2/h	High	November	Teal et al, 1979
Nitrogen Fixation	114 kg N/yr	High	Year	Kaplan et al, 1979
Nitrogen Fixation	1.2 g N/m2/yr	High	Year	Valiela, 1983
Nitrogen Fixation	12.1 g N/m2/yr	High	Year	Valiela, 1983
Nitrogen Fixation	8,560 g N/yr	High	Year	Carpenter et al, 1978
Nitrogen Fixation	1.7 g N/m2/yr	Muddy Creek Bottom	Year	Valiela, 1983
Nitrogen Fixation	14,140 g N/yr	Pannes	Year	Carpenter et al, 1978
Nitrogen Fixation	880 g N/yr	Pink Sand	Year	Carpenter et al, 1978
Nitrogen Fixation	0.7 g N/m2/yr	Sandy Creek Bottom	Year	Valiela, 1983
Nitrogen Fixation	1270 kg N/yr	Short	Year	Leschine 1979
Nitrogen Fixation	0.8 g N/m2/yr	Short	Year	Valiela, 1983
Nitrogen Fixation	8.4 n N/m2/yr	Short	Year	Valiela, 1983
Nitrogen Fixation	1,096 kg N/yr	Short	Year	Kaplan et al, 1979
Nitrogen Fixation	2.3 ng N/cm2/h	Short	March	Teal et al, 1979
Nitrogen Fixation	27.7 ng N/cm2/h	Short	June	Teal et al, 1979
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Nitrogen Fixation	38.5 ng N/cm2/h	Short	July	Teal et al, 1979
Nitrogen Fixation	47.5 ng N/cm2/h	Short	August	Teal et al, 1979
Nitrogen Fixation	71.6 ng N/cm2/h	Short	September	Teal et al, 1979
Nitrogen Fixation	17.3 ng N/cm2/h	Short	November	Teal et al, 1979
Nitrogen Fixation	3.6 ng N/cm2/h	Short	November	Teal et al, 1979
Nitrogen Fixation	2.8 ng N/cm2/h	Short	March	Teal et al, 1979
Nitrogen Fixation	5.7 ng N/cm2/h	Short	June	Teal et al, 1979
Nitrogen Fixation	2.8 ng N/cm2/h	Short	July	Teal et al, 1979
Nitrogen Fixation	42.4 ng N/cm2/h	Short	August	Teal et al, 1979
Nitrogen Fixation	44.9 ng N/cm2/h	Short	September	Teal et al, 1979
Nitrogen Fixation	8.5 ng N/cm2/h	Short	November	Teal et al, 1979

Nitrogen Fixation	5.6 ng N/cm2/h	Short	November	Teal et al, 1979
Nitrogen Fixation	78,850 g N/yr	Short	Year	Carpenter et al, 1978
Nitrogen Fixation	31,130 g N/yr	Tall	Year	Carpenter et al, 1978
Nitrogen Fixation	63 kg N/yr	Tall	Year	Kaplan et al, 1979
Nitrogen Fixation	0.6 ng N/cm2/h	Tall	March	Teal et al, 1979
Nitrogen Fixation	2.2 ng N/cm2/h	Tall	June	Teal et al, 1979
Nitrogen Fixation	2.9 ng N/cm2/h	Tall	July	Teal et al, 1979
Nitrogen Fixation	7.5 ng N/cm2/h	Tall	August	Teal et al, 1979
Nitrogen Fixation	2.0 ng N/cm2/h	Tall	September	Teal et al, 1979
Nitrogen Fixation	0.7 ng N/cm2/h	Tall	November	Teal et al, 1979
Nitrogen Fixation	0.2 ng N/cm2/h	Tall	November	Teal et al, 1979
Nitrogen Fixation	1.2 ng N/cm2/h	Tall	March	Teal et al, 1979
Nitrogen Fixation	1.9 ng N/cm2/h	Tall	June	Teal et al, 1979
Nitrogen Fixation	2.8 ng N/cm2/h	Tall	July	Teal et al, 1979
Nitrogen Fixation	0.4 ng N/cm2/h	Tall	August	Teal et al, 1979
Nitrogen Fixation	2.0 ng N/cm2/h	Tall	September	Teal et al, 1979
Nitrogen Fixation	0.4 ng N/cm2/h	Tall	November	Teal et al, 1979
Nitrogen Fixation	0.2 ng N/cm2/h	Tall	November	Teal et al, 1979
Nitrogen Fixation	174 kg N/yr	Total	Year	Valiela & Teal, 1979b
Nitrogen Fixation	2,595 kg/yr	Total	Year	Valiala & Teal, 1979a
Nitrogen Fixation	3,280 kg/yr	Total	Year	Valiala & Teal, 1979a
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Nitrogen Fixation	297 kg/yr	Total	Year	Valiala & Teal, 1979a
Nitrogen Fixation	384 kg/yr	Total	Year	Valiala & Teal, 1979a
Nitrogen Fixation	145 kg N/yr	Total	Year	Valiela & Teal, 1979b
Nitrogen Fixation	1,273 kg N/yr	Total	Year	Valiela & Teal, 1979b
Nitrogen Fixation	8 kg N/d	Total	August	Valiela & Teal, 1979b
Nitrogen Fixation	3280 kg N/yr	Total	Year	Valiela, 1983
Nitrogen Fixation	145 kg N/yr	Total	Year	Valiela et al, 1978
Nitrogen Fixation	1,277 kg N/yr	Total	Year	Valiela et al, 1978
Nitrogen Fixation	2600 kg N/yr	Total	Year	Finn & Leschine, 1980
Nitrogen Fixation	3,280 kg N/yr	Total	Year	Valiela, 1984
Nitrogen Fixation	1,592 kg N/yr	Total	Year	Valiela & Teal, 1979b
Nitrogen Fixation	2600 kg N/yr	Total	Year	Finn & Leschine
Nitrogen Fixation	10-20 mg N/m2/d	Vegetative	Summer	Carpenter et al, 1978
Nitrogen Fixation	186 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	121 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	106.8 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	224.2 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	161.0 ng N/cm2/h	Vegetative	May	Van Raalte et al, 1974
Nitrogen Fixation	74.7 ng N/cm2/h	Vegetative	May	Van Raalte et al, 1974
Nitrogen Fixation	46.0 ng N/cm2/h	Vegetative	May	Van Raalte et al, 1974
Nitrogen Fixation	109.0 ng N/cm2/h	Vegetative	May	Van Raalte et al, 1974
Nitrogen Fixation	230.0 ng N/cm2/h	Vegetative	May	Van Raalte et al, 1974
Nitrogen Fixation	92.0 ng N/cm2/h	Vegetative	May	Van Raalte et al, 1974
Nitrogen Fixation	3.8 ng N/cm2/h	Vegetative	August	Van Raalte et al, 1974
Nitrogen Fixation	21.5 ng N/cm2/h	Vegetative	August	Van Raalte et al, 1974
Nitrogen Fixation	19.6 ng N/cm2/h	Vegetative	August	Van Raalte et al, 1974
Nitrogen Fixation	3.6 ng N/cm2/h	Vegetative	August	Van Raalte et al, 1974
Nitrogen Fixation	293.5 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	142.3 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	78.8 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	130.6 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Nitrogen Fixation	463.2 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Nitrogen Fixation	14.8 ng N/cm2/h	Vegetative	June	Van Raalte et al, 1974
Other	9 kg N/yr	Total	Year	Valiela, 1984
Other	26 kg N/yr	Total	Year	Valiela, 1984
Particulate N	9 kg/yr	Total	Year	Valiala & Teal, 1979a
Plant Uptake	155 kg N/yr	High	Year	Leschine, 1979
Plant Uptake	6990 kg N/yr	Short	Year	Leschine, 1979
Plant Uptake	1055 kg N/yr	Short	Year	Leschine, 1979
Plant Uptake	39 kg/d	Total	June/July	Valiala & Teal, 1979a
Plant Uptake	4000 kg N/yr	Total	Year	Valiela, 1983
Plant Uptake	4100 kg N/yr	Total	Year	Teal et al, 1979
Plant Uptake	4,100 kg N/yr	Total	Year	Valiela et al, 1978
Plant Uptake	16790 kg N/yr	Total	Year	Finn & Leschine, 1980
Plant Uptake	11200 kg N/yr	Total	Year	Finn & Leschine, 1980
Plant Uptake	5600 kg N/yr	Total	Year	Finn & Leschine, 1980
Plant Uptake	4,000 kg N/yr	Total	Year	Valiela, 1983

Plants	5,200 kg	Total	Year	Valiela, 1983
Pore DON	19200 kg N/yr	Total	Year	Finn & Leschine, 1980
Pore DON	18500 kg N/yr	Total	Year	Finn & Leschine, 1980
Precipitation	90 kg N/yr	Short	Year	Leschine, 1979
Precipitation	190 kg/yr	Total	Year	Valiala & Teal, 1979a
Precipitation	70 kg/yr	Total	Year	Valiala & Teal, 1979a
Precipitation	0.4 kg/yr	Total	Year	Valiala & Teal, 1979a
Precipitation	110 kg/yr	Total	Year	Valiala & Teal, 1979a
Precipitation	15 kg/yr	Total	Year	Valiala & Teal, 1979a
Precipitation	380 kg/yr	Total	Year	Valiala & Teal, 1979a
Precipitation	52 kg N/yr	Total	Year	Valiela & Teal, 1979b
Precipitation	0.2 kg N/yr	Total	Year	Valiela & Teal, 1979b
Precipitation	31 kg N/yr	Total	Year	Valiela & Teal, 1979b
Precipitation	89 kg N/yr	Total	Year	Valiela & Teal, 1979b
Precipitation	7 kg N/yr	Total	Year	Valiela & Teal, 1979b
Precipitation	0.5 kg N/d	Total	August	Valiela & Teal, 1979b
Precipitation	52 kg N/yr	Total	Year	Valiela et al, 1978
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Precipitation	0.2 kg N/yr	Total	Year	Valiela et al, 1978
Precipitation	31 kg N/yr	Total	Year	Valiela et al, 1978
Precipitation	89.2 kg N/yr	Total	Year	Valiela et al, 1978
Precipitation	6.5 kg N/yr	Total	Year	Valiela et al, 1978
Precipitation	178.9 kg N/yr	Total	Year	Valiela et al, 1978
Precipitation	380 kg N/yr	Total	Year	Valiela, 1984
Precipitation	179 kg N/yr	Total	Year	Valiela & Teal, 1979b
Resuspension	23,000 kg N/yr	Short	Year	Jordan & Valiela, 1982
Resuspension	1250 kg N/yr	Short	Year	Leschine, 1979
Resuspension	1270 kg N/yr	Short	Year	Leschine, 1979
Resuspension	60 mol/yr	Tall	Year	Hoews & Goehringer, 1994
Resuspension	760 mol/yr	Tall	Year	Howes &Doehringer, 1994
Resuspension	11945 kg N/yr	Total	Year	Finn & Leschine, 1980
Resuspension	20380 kg N/yr	Total	Year	Finn & Leschine, 1980
Sediment	19,100 kg N/yr	Short	Year	Jordan & Valiela, 1982
Sediment	40 % of uptake	Total	Year	Valiela, 1983
Sediment	46 kg N/d	Total	August	Valiela & Teal, 1979b
Sediment	15 kg N/d	Total	August	Valiela & Teal, 1979b
Sediment	10 kg N/d	Total	August	Valiela & Teal, 1979b
Sediment	116,800 kg	Total		Valiela & Teal, 1979a
Sediment	110,000 kg	Total	Year	Valiela, 1983
Sediment	49,000 kg N	Total	August	Valiela & Teal, 1979b
Sedimentation	490 kg N/yr	Short	Year	Leschine, 1979
Sedimentation	505 kg N/yr	Short	Year	Leschine, 1979
Sedimentation	19100 kg N/yr	Total	Year	Finn & Leschine, 1980
Sedimentation	19100 kg N/yr	Total	Year	Finn & Leschine, 1980
Shellfish	454/m2	Tall	Year	Leschine, 1979
Shellfish	0.7 kg N/d	Total	August	Valiela & Teal, 1979b
Shellfish	5 kg N/d	Total	August	Valiela & Teal, 1979b
Shellfish	10 kg N/d	Total	August	Valiela & Teal, 1979b
Shellfish	214 kg N	Total	August	Valiela & Teal, 1979b
Snails	0.23 kg N/d	Short	June 16-Sept 30	Jordan & Valiela, 1982
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Tidal Water	3 kg	Total	Year	Valiela, 1983
Tidal Water Exchange	16340 kg N/yr	Short	Year	Leschine, 1979
Tidal Water Exchange	18480 kg N/yr	Short	Year	Leschine, 1979
Tidal Water Exchange	6,760 kg N/yr	Short	Year	Jordan & Valiela, 1982
Tidal Water Exchange	8,170 kg N/yr	Short	Year	Jordan & Valiela, 1982
Tidal Water Exchange	2.0-3.2 g N/m2/yr	Short	Year	White & Howes, 1994c
Tidal Water Exchange	1.6 g N/m2/yr	Short	Year	White & Howes, 1994c
Tidal Water Exchange	1.1-1.2 g N/m2/yr	Short	Year	White & Howes, 1994c
Tidal Water Exchange	8 kg/d	Total	June/July	Valiala & Teal, 1979a
Tidal Water Exchange	16,300 kg/yr	Total	Year	Valiala & Teal, 1979a
Tidal Water Exchange	2,620 kg/yr	Total	Year	Valiala & Teal, 1979a
Tidal Water Exchange	150 kg/yr	Total	Year	Valiala & Teal, 1979a
Tidal Water Exchange	390 kg/yr	Total	Year	Valiala & Teal, 1979a
Tidal Water Exchange	6,740 kg/yr	Total	Year	Valiala & Teal, 1979a
Tidal Water Exchange	26,200 kg/yr	Total	Year	Valiala & Teal, 1979a
Tidal Water Exchange	26,252 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	386 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	154 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	2,623 kg N/yr	Total	Year	Valiela & Teal, 1979b

Tidal Water Exchange	16,346 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	6,743 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	2,623 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	386 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	154 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	16,346 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	26200 kg N/yr	Total	Year	Finn & Leschine, 1980
Tidal Water Exchange	2620 kg N/yr	Total	Year	Finn & Leschine, 1980
Tidal Water Exchange	6740 kg N/yr	Total	Year	Finn & Leschine, 1980
Tidal Water Exchange	4285 kg N/yr	Total	Year	Finn & Leschine, 1980
Tidal Water Exchange	26,200 kg N/yr	Total	Year	Valiela, 1984
Tidal Water Exchange	6,743 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	31,604 kg N/yr	Total	Year	Valiela & Teal, 1979b
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Tidal Water Exchange	1,215 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	166 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	3,539 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	18,479 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	8,205 kg N/yr	Total	Year	Valiela & Teal, 1979b
Tidal Water Exchange	4 kg N/d	Total	August	Valiela & Teal, 1979b
Tidal Water Exchange	4 kg N/d	Total	August	Valiela & Teal, 1979b
Tidal Water Exchange	3,539 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	1,215 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	166 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	18,479 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	8,205 kg N/yr	Total	Year	Valiela et al, 1978
Tidal Water Exchange	3540 kg N/yr	Total	Year	Finn & Leschine, 1980
Tidal Water Exchange	8200 kg N/yr	Total	Year	Finn & Leschine, 1980
Tidal Water Exchange	8320 kg N/yr	Total	Year	Finn & Leschine, 1980
Tidal Water Exchange	20% of aboveground production	Total	Year	Valiela et al, 1975
Tidal Water Exchange	31,600 kg N/yr	Total	Year	Valiela, 1984
Tidal Water Exchange	31600 kg N/yr	Total	Year	Finn & Leschine, 1980
Translocation	1.4 g N/m2/yr	Short	Year	White & Howes, 1994c
Volatilisation of NH3	10 kg N/yr	Short	Year	Leschine, 1979
Volatilisation of NH3	17 kg/yr	Total	Year	Valiala & Teal, 1979a
Volatilisation of NH3	8 kg N/yr	Total	Year	Valiela & Teal, 1979b

APPENDIX B. GREAT SIPPEWISSETT CONVERTED DATA.

RF=Reliability Factor

Compartment	Zone	Source	g N/m2/yr	RF	Comments
Aboveground Biomass	High	Valiela et al, 1975	6	3	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Biomass	Short	Valiela et al, 1976	4.5	3	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Biomass	Short	Valiela et al, 1976	4.05	3	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Biomass	Short	White & Howes, 1994c	2.3/may	4	
Aboveground Biomass	Short	White & Howes, 1994c	2.7/jun	4	
Aboveground Biomass	Short	White & Howes, 1994c	3.4/jul	4	
Aboveground Biomass	Short	White & Howes, 1994c	4.5/aug	4	
Aboveground Biomass	Short	White & Howes, 1994c	4.0/sep	4	
Aboveground Biomass	Short	White & Howes, 1994c	3.2/oct	4	
Aboveground Biomass	Tall	Valiela et al, 1975	11.25	3	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Biomass	Tall	Valiela et al, 1975	5.25	3	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Biomass	Tall	Valiela et al, 1976	25.5	3	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Dead	Total	Valiela & Teal,1979b	30.43	4	
Aboveground Live	Total	Valiela & Teal, 1979b	2.29	4	
Aboveground Production	High	Valiela et al, 1975	9.45	4	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Production	Short	Valiela et al, 1976	6.36	3	c 1.5 % N content of dry mass (Vince et al, 1981)
Aboveground Production	Short	Valiela et al, 1975	7.65	4	c 1.5% N content of dry mass (Vince et al, 1981)
Aboveground Production	Short	White & Howes, 1994a	3.8	4	
Aboveground Production	Short	Howes et al, 1985	4.76	1	C:N=50 (White & Howes, 1994c)
Aboveground Production	Short	Leschine, 1979	12.35	2	
Aboveground Production	Total	Finn & Leschine, 1980	5.77	4	
Aboveground Production	Total	Finn & Leschine, 1980	5.77	4	
Aboveground Production	Total	Valiela & Teal, 1979b	3.27/aug	4	
Animal	Total	Valiela, 1983	10.33	2	
Animals	Total	Valiela & Teal, 1979b	0.02	4	
Animals	Total	Valiela & Teal, 1979b	0.02	2	
Animals	Total	Valiela, 1983	3.51	2	
Arthropods	Short	Jordan & Valiela, 1982	.58/summer	2	
Belowground Biomass	High	Valiela et al, 1976	0.1	4	%N=.44, Hopkinson & Schubauer, 1984
Belowground Biomass	High	Valiela et al, 1976	0.08	4	%N=.44, Hopkinson & Schubauer, 1984
Belowground Biomass	Short	Valiela et al, 1976	0.1	4	%N=.44, Hopkinson & Schubauer, 1984
Belowground Biomass	Short	Valiela et al, 1976	0.26	4	%N=.44, Hopkinson & Schubauer, 1984
Belowground Biomass	Short	Howes et al, 1985	4.27	3	%N=.44, Hopkinson & Schubauer, 1984
Belowground Dead	Total	Valiela & Teal, 1979b	0.52	4	
Belowground Live	Total	Valiela & Teal, 1979b	1.02	4	
Belowground Production	Short	Valiela et al, 1976	14.48	3	%N=.44, Hopkinson & Schubauer, 1984
Belowground Production	Short	White & Howes, 1994a	18.6-20.4	4	
Belowground Production	Short	Howes et al, 1985	70	1	C/N=50, White & Howes, 1994c
Belowground Production	Short	Howes et al, 1985	13.93-17.89	1	C/N=50, White & Howes, 1994c
Belowground Production	Short	White & Howes, 1994a	18.58-20.44	3	C/N=50, White & Howes, 1994c
Belowground Production	Short	Valiela et al, 1976	58.83	3	c 1.5% N content of dry mass (Vince et al, 1981)
Benthic algae production	Short	White & Howes, 1994a	5	2	
Benthic algae production	Short	Howes et al, 1985	7.64	1	C/N=5.5, Valiela, 1983
Biodeposition	Short	Leschine, 1979	4.59	2	
Biodeposition	Total	Valiela, 1983	6.52	2	
Biodeposition	Total	Finn & Leschine, 1980	2.61	4	
Biodeposition	Total	Finn & Leschine, 1980	2.61	4	
Burial	Short	Jordan & Valiela, 1982	6.13	2	
Burial	Short	White & Howes, 1994	4.4	4	
Burial	Short	Howes et al, 1985	4.6	3	C/N=19.3, Valiela, 1983
Burial	Short	White & Howes, 1994b	3.2-4.6	2	
Burial	Short	White & Howes, 1994a	3.7-4.1	4	
Burial	Short	Leschine, 1979	0.26	2	
Burial	Total	Valiela, 1983	2.7	2	
Burial	Total	Valiela & Teal, 1979b	0.05	2	
Burial	Total	Valiela, 1984	2.68	4	
Burial	Vegetative	Valiala & Teal, 1979a	4.28	3	
Burial		Valiela et al, 1975	0.31	1	annual production from mean=6.22
Decay	High	Leschine, 1979	9.48	2	%N=1.5
Decay	High	Leschine, 1979	1000	2	
Decay	Short	Leschine, 1979	42.86	2	
Decay	Short	Leschine, 1979	4000	2	
Decay	Short	Leschine, 1979	6.36	2	%N=1.5
Decay	Short	White & Howes, 1994c	0.4	2	
Decay	Total	Valiela & Teal, 1979b	.64/August	4	
Decay	Total	Finn & Leschine, 1980	19.51	4	
Decay	Total	Finn & Leschine, 1980	19.51	4	

Decay	Total	Valiela, 1983	3.31	2	
Decomposer	Total	Valiela, 1983	4.35	1	aboveground from mean=6.22
Denitrification	Algal Mat	Kaplan et al, 1979	10.65	4	
Denitrification	Creek Bottom	Kaplan et al, 1979	24.58	4	
Denitrification	High	Kaplan et al, 1979	7.8	4	
Denitrification	Pannes	Kaplan et al, 1979	20.55	4	
Denitrification	Short	White & Howes, 1994a	.756/may	4	
Denitrification	Short	White & Howes, 1994a	4.1-5.6	4	
Denitrification	Short	Kaplan et al, 1979	6.85	4	
Denitrification	Short	Leschine, 1979	28.88	2	
Denitrification	Tall	Kaplan et al, 1979	20.32	4	
Denitrification	Total	Valiela & Teal, 1979b	0.58	4	
Denitrification	Total	Valiala & Teal, 1979a	14.34	4	
Denitrification	Total	Valiela & Teal, 1979b	3.22	4	
Denitrification	Total	Valiela, 1983	14.34	2	
Denitrification	Total	Valiela, 1983	14.3	2	
Denitrification	Total	Finn & Leschine, 1980	17.05	4	
Denitrification	Total	Valiela, 1984	14.34	4	
DIN	Total	Valiala & Teal, 1979a	1.51	4	
DIN	Total	Valiela & Teal, 1979b	0	4	
Excretion	Short	Leschine, 1979	4.29	2	
Excretion	Total	Valiela, 1983	14.74	2	
Excretion	Total	Finn & Leschine, 1980	1.43	4	
Excretion	Total	Finn & Leschine, 1980	1.43	4	
Filtration	Short	Leschine, 1979	27.04	2	
Filtration	Total	Finn & Leschine, 1980	5.23	4	
Filtration	Total	Finn & Leschine, 1980	5.23	4	
Fish	Short	Jordan & Valiela, 1982	1.17/summer	2	
Grazers	Total	Valiela, 1983	0.62	1	aboveground from mean=6.22
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Grazers/Nekton	Short	Seed, 1980		2	
Groundwater	Short	Leschine, 1979	25.05	2	
Groundwater	Total	Valiala & Teal, 1979a	5.6	4	
Groundwater	Total	Valiala & Teal, 1979a	0.95	4	
Groundwater	Total	Valiala & Teal, 1979a	0.06	4	
Groundwater	Total	Valiala & Teal, 1979a	6.04	4	
Groundwater	Total	Valiala & Teal, 1979a	0.02	4	
Groundwater	Total	Valiala & Teal, 1979a	12.65	4	
Groundwater	Total	Valiela & Teal, 1979b	11.31	4	
Groundwater	Total	Valiela & Teal, 1979b	5.16	4	
Groundwater	Total	Valiela & Teal, 1979b	0.06	4	
Groundwater	Total	Valiela & Teal, 1979b	1.02	4	
Groundwater	Total	Valiela & Teal, 1979b	5.07	4	
Groundwater	Total	Valiela, 1983	12.6	2	
Groundwater	Total	Valiela et al, 1978	6.04	4	
Groundwater	Total	Valiela et al, 1978	0.06	4	
Groundwater	Total	Valiela et al, 1978	0.95	4	
Groundwater	Total	Valiela et al, 1978	5.61	4	
Groundwater	Total	Valiela et al, 1978	12.61	4	
Groundwater	Total	Finn & Leschine, 1980	14.84	4	
Groundwater	Total	Finn & Leschine, 1980	0.03	4	
Groundwater	Total	Finn & Leschine, 1980	1.1	4	
Groundwater	Total	Kaplan et al, 1979	6.04	4	
Grounwater	Total	Valiela, 1984	12.65	4	
Leaching	High	Jordan & Valiela, 1982	1.5/summer	4	
Leaching	Short	Jordan & Valiela, 1982	1.4/summer	4	
Leaching	Short	White & Howes, 1994a	0.4	4	
Leaching	Short	White & Howes, 1994a	.0735/jun	4	
Leaching	Short	White & Howes, 1994c	.0787/jul	4	
Leaching	Short	White & Howes, 1994c	.0706/aug	4	
Leaching	Short	White & Howes, 1994c	.0596/sep	4	
Leaching	Short	White & Howes, 1994c	.1289/oct	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Leaching	Short	White & Howes, 1994c	0.4	4	
Leaching	Short	Leschine, 1979	2.76	2	
Leaching	Total	Valiela & Teal, 1979b	.45/aug	4	
Leaching	Total	Valiela, 1983	2.48	2	
Leaching	Total	Finn & Leschine, 1980	5.85	4	
Leaching	Total	Finn & Leschine, 1980	1.3	4	
Leaching	Total	Valiala & Teal, 1979a	.45/aug	4	

Litter	Short	Howes et al, 1985	0-3.6	1	C/N=20-60, Valiela, 1983
Litter	Total	Finn & Leschine, 1980	4.55	4	
Mineralization	Short	White & Howes, 1994a	14.9-16.3	4	
Mineralization	Total	Valiala & Teal, 1979a	1.45	4	
Mineralization	Total	Valiela, 1983	1.45	2	
Mineralization	Total	Valiela, 1983	6.78	2	
Mineralization	Total	Finn & Leschine, 1980	1.45	4	
Mussel	Short	Jordan & Valiela, 1982	11.84	4	
Mussel	Short	Jordan & Valiela, 1982	5.92	4	
Mussel	Short	Jordan & Valiela, 1982	3.24	4	
Mussel	Short	Jordan & Valiela, 1982	1.22	4	
Mussel	Short	Jordan & Valiela, 1982	3.75/summer	4	
Mussel	Short	Jordan & Valiela, 1982	11.84	4	
Mussel	Short	Jordan & Valiela, 1982	5.9	4	
Mussel	Total	Finn & Leschine, 1980	0.34	4	
Mussel	Total	Finn & Leschine, 1980	0.34	4	
Mussel		Jordan & Valiela, 1982	6.28	4	
Nitrification	Total	Kaplan et al, 1979	0-4.42/apr-oct	2	
Nitrification	Total	Valiela, 1983	9.8	2	
Nitrification	Total	Finn & Leschine, 1980	19.92	4	
Nitrogen Fixation	Algal Mat	Carpenter et al, 1978	2.28	4	
Nitrogen Fixation	Algal Mat	Valiela, 1983	2.3	2	
Nitrogen Fixation	Algal Mat	Van Raalte et al, 1974	.005/may	4	
Nitrogen Fixation	Algal Mat	Van Raalte et al, 1974	.006/may	4	
Nitrogen Fixation	Algal Mat	Van Raalte et al, 1974	.003/jul	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Nitrogen Fixation	Algal Mat	Van Raalte et al, 1974	.002/jul	4	
Nitrogen Fixation	Algal Mat	Brenner et al, 1976	.0005/jul	4	
Nitrogen Fixation	Algal Mat	Brenner et al, 1976	.012/jul	4	
Nitrogen Fixation	Creek Bottom	Kaplan et al, 1979	2.21	4	
Nitrogen Fixation	High	Teal et al, 1979	.0001/mar	4	
Nitrogen Fixation	High	Teal et al, 1979	.001/jun	4	
Nitrogen Fixation	High	Teal et al, 1979	.002/jul	4	
Nitrogen Fixation	High	Teal et al, 1979	.005/aug	4	
Nitrogen Fixation	High	Teal et al, 1979	.001/sep	4	
Nitrogen Fixation	High	Teal et al, 1979	.001/nov	4	
Nitrogen Fixation	High	Teal et al, 1979	.0008/nov	4	
Nitrogen Fixation	High	Teal et al, 1979	.0001/mar	4	
Nitrogen Fixation	High	Teal et al, 1979	.001/jun	4	
Nitrogen Fixation	High	Teal et al, 1979	.002/jul	4	
Nitrogen Fixation	High	Teal et al, 1979	.005/aug	4	
Nitrogen Fixation	High	Teal et al, 1979	.0026/sep	4	
Nitrogen Fixation	High	Teal et al, 1979	.001/nov	4	
Nitrogen Fixation	High	Teal et al, 1979	.0004/nov	4	
Nitrogen Fixation	High	Kaplan et al, 1979	3.99	4	
Nitrogen Fixation	High	Valiela, 1983	1.2	2	
Nitrogen Fixation	High	Valiela, 1983	12.1	2	
Nitrogen Fixation	High	Carpenter et al, 1978	0.3	4	
Nitrogen Fixation	Creek Bottom	Valiela, 1983	1.7	2	
Nitrogen Fixation	Pannes	Carpenter et al, 1978	6.43	4	
Nitrogen Fixation	Pink Sand	Carpenter et al, 1978	0.76	4	
Nitrogen Fixation	Creek Bottom	Valiela, 1983	0.7	2	
Nitrogen Fixation	Short	Leschine 1979	12.96	2	
Nitrogen Fixation	Short	Valiela, 1983	0.8	2	
Nitrogen Fixation	Short	Valiela, 1983	8.4	2	
Nitrogen Fixation	Short	Kaplan et al, 1979	5.48	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0002/mar	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0021/jun	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Nitrogen Fixation	Short	Teal et al, 1979	.0029/jul	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0035/aug	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0052/sep	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0013/nov	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0003/nov	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0002/mar	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0004/jun	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0002/jul	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0032/aug	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0032/sep	4	
Nitrogen Fixation	Short	Teal et al, 1979	.0006/nov	4	

Nitrogen Fixation	Short	Teal et al, 1979	.0004/nov	4	
Nitrogen Fixation	Short	Carpenter et al, 1978	0.39	4	
Nitrogen Fixation	Tall	Carpenter et al, 1978	0.35	4	
Nitrogen Fixation	Tall	Kaplan et al, 1979	8.38	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.00004/mar	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.0002/jun	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.0002/jul	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.0006/aug	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.0001/sep	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.00005/nov	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.00001/nov	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.00009/mar	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.0001/jun	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.0002/jul	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.00003/aug	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.0001/sep	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.00003/nov	4	
Nitrogen Fixation	Tall	Teal et al, 1979	.00001/nov	4	
Nitrogen Fixation	Total	Valiela & Teal, 1979b	0.36	4	
Nitrogen Fixation	Total	Valiala & Teal, 1979a	5.36	4	
Nitrogen Fixation	Total	Valiala & Teal, 1979a	6.78	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Nitrogen Fixation	Total	Valiala & Teal, 1979a	0.61	4	
Nitrogen Fixation	Total	Valiala & Teal, 1979a	0.79	4	
Nitrogen Fixation	Total	Valiela & Teal, 1979b	0.3	4	
Nitrogen Fixation	Total	Valiela & Teal, 1979b	2.63	4	
Nitrogen Fixation	Total	Valiela & Teal, 1979b	.51/aug	1	
Nitrogen Fixation	Total	Valiela, 1983	6.78	2	
Nitrogen Fixation	Total	Valiela et al, 1978	0.3	2	
Nitrogen Fixation	Total	Valiela et al, 1978	2.64	4	
Nitrogen Fixation	Total	Finn & Leschine, 1980	5.37	4	
Nitrogen Fixation	Total	Valiela, 1984	6.78	4	
Nitrogen Fixation	Total	Valiela & Teal, 1979b	3.29	4	
Nitrogen Fixation	Total	Finn & Leschine	5.37	4	
Nitrogen Fixation	Vegetative	Carpenter et al, 1978	1.23-2.46	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0138/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.009/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0079/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0167/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0116/may	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0054/may	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0033/may	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0078/may	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0166/may	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0066/may	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0003/aug	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0016/aug	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0015/aug	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0003/aug	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0218/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0106/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0059/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0097/jun	4	
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0345/jun	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Nitrogen Fixation	Vegetative	Van Raalte et al, 1974	.0011/jun	4	
Other	Total	Valiela, 1984	0.02	4	
Other	Total	Valiela, 1984	0.05	4	
Particulate N	Total	Valiala & Teal, 1979a	0.02	4	
Plant Uptake	High	Leschine, 1979	5.54	2	
Plant Uptake	Short	Leschine, 1979	71.33	2	
Plant Uptake	Short	Leschine, 1979	10.77	2	
Plant Uptake	Total	Valiala & Teal, 1979a	4.92/jun-jul	4	
Plant Uptake	Total	Valiela, 1983	8.27	2	
Plant Uptake	Total	Teal et al, 1979	8.47	2	
Plant Uptake	Total	Valiela et al, 1978	8.47	2	
Plant Uptake	Total	Finn & Leschine, 1980	34.7	4	
Plant Uptake	Total	Finn & Leschine, 1980	23.15	4	
Plant Uptake	Total	Finn & Leschine, 1980	11.58	4	
Plant Uptake	Total	Valiela, 1983	8.27	2	

Plants	Total	Valiela, 1983	10.75	2	
Pore DON	Total	Finn & Leschine, 1980	39.69	4	
Pore DON	Total	Finn & Leschine, 1980	38.24	4	
Precipitation	Short	Leschine, 1979	0.92	2	
Precipitation	Total	Valiala & Teal, 1979a	0.39	4	
Precipitation	Total	Valiala & Teal, 1979a	0.14	4	
Precipitation	Total	Valiala & Teal, 1979a	0	4	
Precipitation	Total	Valiala & Teal, 1979a	0.23	4	
Precipitation	Total	Valiala & Teal, 1979a	0.03	4	
Precipitation	Total	Valiala & Teal, 1979a	0.79	4	
Precipitation	Total	Valiela & Teal, 1979b	0.11	4	
Precipitation	Total	Valiela & Teal, 1979b	0	4	
Precipitation	Total	Valiela & Teal, 1979b	0.06	4	
Precipitation	Total	Valiela & Teal, 1979b	0.18	4	
Precipitation	Total	Valiela & Teal, 1979b	0.01	4	
Precipitation	Total	Valiela & Teal, 1979b	.03/aug	4	
Precipitation	Total	Valiela et al, 1978	0.11	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Precipitation	Total	Valiela et al, 1978	0	4	
Precipitation	Total	Valiela et al, 1978	0.06	4	
Precipitation	Total	Valiela et al, 1978	0.18	4	
Precipitation	Total	Valiela et al, 1978	0.01	4	
Precipitation	Total	Valiela et al, 1978	0.37	4	
Precipitation	Total	Valiela, 1984	0.79	4	
Precipitation	Total	Valiela & Teal, 1979b	0.37	4	
Resuspension	Short	Jordan & Valiela, 1982	107.68	2	
Resuspension	Short	Leschine, 1979	12.76	2	
Resuspension	Short	Leschine, 1979	12.96	2	
Resuspension	Tall	Hoews & Goehringer, 1994	0.28	1	
Resuspension	Tall	Howes &Doehringer, 1994	1.02	3	
Resuspension	Total	Finn & Leschine, 1980	24.69	4	
Resuspension	Total	Finn & Leschine, 1980	42.12	4	
Sediment	Short	Jordan & Valiela, 1982	89.42	2	
Sediment	Total	Valiela, 1983	5.88	1	uptake from mean=14.7
Sediment	Total	Valiela & Teal, 1979b	2.95/aug	4	
Sediment	Total	Valiela & Teal, 1979b	.96/aug	4	
sediment	Total	Valiela & Teal, 1979b	.64/aug	4	
Sediment	Total	Valiala & Teal, 1979a	241.42	4	
Sediment	Total	Valiela, 1983	227.37	2	
Sediment	Total	Valiela & Teal, 1979b	101.28	4	
Sedimentation	Short	Leschine, 1979	5	2	
Sedimentation	Short	Leschine, 1979	5.15	2	
Sedimentation	Total	Finn & Leschine, 1980	39.48	4	
Sedimentation	Total	Finn & Leschine, 1980	39.48	4	
Shellfish	Tall	Leschine, 1979		2	
Shellfish	Total	Valiela & Teal, 1979b	.04/aug	4	
Shellfish	Total	Valiela & Teal, 1979b	.32/aug	4	
Shellfish	Total	Valiela & Teal, 1979b	.64/aug	4	
Shellfish	Total	Valiela & Teal, 1979b	0.44	4	
Snails	Short	Jordan & Valiela, 1982	.12/summer	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Tidal Water	Total	Valiela, 1983	0.01	2	
Tidal Water Exchange	Short	Leschine, 1979	166.73	2	
Tidal Water Exchange	Short	Leschine, 1979	188.57	2	
Tidal Water Exchange	Short	Jordan & Valiela, 1982	31.65	2	
Tidal Water Exchange	Short	Jordan & Valiela, 1982	38.25	2	
Tidal Water Exchange	Short	White & Howes, 1994c	2.0-3.2	2	
Tidal Water Exchange	Short	White & Howes, 1994c	1.6	2	
Tidal Water Exchange	Short	White & Howes, 1994c	1.1-1.2	4	
Tidal Water Exchange	Total	Valiala & Teal, 1979a	1.01/jun-jul	4	
Tidal Water Exchange	Total	Valiala & Teal, 1979a	33.69	4	
Tidal Water Exchange	Total	Valiala & Teal, 1979a	5.42	4	
Tidal Water Exchange	Total	Valiala & Teal, 1979a	0.31	4	
Tidal Water Exchange	Total	Valiala & Teal, 1979a	0.8061	4	
Tidal Water Exchange	Total	Valiala & Teal, 1979a	13.93	4	
Tidal Water Exchange	Total	Valiala & Teal, 1979a	54.15	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	54.26	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	0.8	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	0.32	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	5.42	4	

Tidal Water Exchange	Total	Valiela & Teal, 1979b	33.79	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	13.94	4	
Tidal Water Exchange	Total	Valiela et al, 1978	5.42	4	
Tidal Water Exchange	Total	Valiela et al, 1978	0.8	4	
Tidal Water Exchange	Total	Valiela et al, 1978	0.32	4	
Tidal Water Exchange	Total	Valiela et al, 1978	33.79	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	54.15	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	5.42	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	13.93	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	8.86	4	
Tidal Water Exchange	Total	Valiela, 1984	54.15	4	
Tidal Water Exchange	Total	Valiela et al, 1978	13.94	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	65.32	4	
Compartment	**Zone**	**Source**	**g N/m2/yr**	**RF**	**Comments**
Tidal Water Exchange	Total	Valiela & Teal, 1979b	2.51	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	0.34	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	7.32	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	38.2	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	16.96	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	.26/aug	4	
Tidal Water Exchange	Total	Valiela & Teal, 1979b	.26/aug	4	
Tidal Water Exchange	Total	Valiela et al, 1978	7.32	4	
Tidal Water Exchange	Total	Valiela et al, 1978	2.51	4	
Tidal Water Exchange	Total	Valiela et al, 1978	0.34	4	
Tidal Water Exchange	Total	Valiela et al, 1978	38.2	4	
Tidal Water Exchange	Total	Valiela et al, 1978	16.96	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	7.32	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	16.95	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	17.2	4	
Tidal Water Exchange	Total	Valiela et al, 1975	1.24	1	Aboveground production from mean=6.22
Tidal Water Exchange	Total	Valiela, 1984	65.32	4	
Tidal Water Exchange	Total	Finn & Leschine, 1980	65.32	4	
Translocation	Short	White & Howes, 1994c	1.4	4	
Volatilisation of NH3	Short	Leschine, 1979	0.1	2	
Volatilisation of NH3	Total	Valiala & Teal, 1979a	0.04	2	
Volatilisation of NH3	Total	Valiela & Teal, 1979b	0.02	2	

Compartment	Zone	Source	g N/m2/yr	RF	Comments
Abovegound Biomass	High	Gallagher, 1975	9.12	3	%N=1.2, Gallagher, 1975
Abovegound Biomass	Short	Haines et al, 1977	3.14	4	
Abovegound Biomass	Short	Gross et al, 1991	10.94	3	%N=1.68, Kemp et al, 1990b
Abovegound Biomass	Short	Montague, 1982	1.22	3	%N=1.05, Hopkinsons & Shubauer, 1984
Abovegound Biomass	Short	Hopkinson & Schubauer, 1984	4.2	4	
Abovegound Biomass	Short	Whitney et al, 1981	4.7	4	Ecology of Salt Marsh
Abovegound Biomass	Short	Gallagher, 1975	3.77	3	%N=0.8, Gallagher, 1975
Abovegound Biomass	Short	Gallagher, 1975	2.79	3	%N=0.8, Gallagher, 1975
Abovegound Biomass	Tall	Haines et al, 1977	8.28	4	
Abovegound Biomass	Tall	Whitney et al, 1981	9.8	4	Ecology of Salt Marsh
Abovegound Biomass	Tall	Gallagher, 1975	7.87	3	%N=0.7, Gallagher, 1975
Abovegound Biomass	Total	Wiegert & Wetzel, 1979	3.55	3	C:N=38, Gallagher & Plumley, 1979
Abovegound Biomass	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Abovegound Biomass	Total	Chalmers, 1979	3.44	2	
Abovegound Biomass	Total	Schubauer & Hopkinson, 1984	9.37	3	%N=1.68, Vince et al, 1981
Aboveground Biomass	High	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Aboveground Biomass	High	Pomeroy et al, 1981		4	Ecology of Salt Marhs
Aboveground Biomass	Short	Pomeroy et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Short	Pomeroy et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Short	Pomeroy et al, 1981		4	Ecology of salt Marsh
Aboveground Biomass	Tall	Pomerory et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Tall	Pomerory et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Tall	Pomerory et al, 1981		4	Ecology of Salt marsh
Aboveground Dead	Short	Chalmers, 1979	0.87	3	%N=0.77, Hopkinson & Schubauer, 1984
Aboveground Dead	Short	Gross et al, 1991	3.53	3	%N=.77, Kemp et al, 1990b
Aboveground Dead	Short	Montague, 1982	1.42	3	%N=.77, Kemp et al, 1990b
Aboveground Production	High	Whitney et al, 1981	31.4	4	Ecology of Salt Marsh
Aboveground Production	High	Gallagher et al, 1980	30	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	33.6	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	30	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	18	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	26.4	3	%N=1.2, Gallagher, 1975
Aboveground Production	Short	Kemp et al, 1990b	13.4	4	
Aboveground Production	Short	Wiegert, 1979	39.16	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Short	Wiegert, 1979	41.39	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Short	Hopkinson & Schubaurer, 1984	33	4	
Aboveground Production	Short	Hason, 1977	3.47	3	%N=1.05, Hopkinson & Schubauer, 1984
Aboveground Production	Short	Haines et al, 1977	35.18	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Short	Whitney et al, 1981	18.6	4	Ecology of Salt Marsh
Aboveground Production	Short	Dai & Wiegert, 1996	29.78	3	C:N=50 White & Howes, 1994c
Aboveground Production	Short	Chalmers,1979	22.46	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Schubauer & Hopkinson, 1984	22.68	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Schubauer & Hopkinson, 1984	47.71	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	11.76	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	25.2	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	26.88	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	20.16	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	21.84	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Dai & Wiegert, 1996	64.58	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Tall	Wiegert, 1979	68.32	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Tall	Hanson, 1977	16.8	3	%N=1.05, Hopkinson & Schubauer, 1984
Aboveground Production	Tall	Haines et al, 1977	97.66	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Tall	Whitney et al, 1981	47.1	4	Ecology of Salt Marsh
Aboveground Production	Tall	Schubauer & Hopkinson, 1984	62.16	3	%N=1.68, Hopkinson & Schubauer, 1984
Aboveground Production	Tall	Gallagher et al, 1980	38.64	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	50.4	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	45.36	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	73.92	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	62.16	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Wiegert, 1986	65.79	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Total	Schubauer & Hopkinson 1984	47.71	3	%N=1.68, Vince et al, 1981
Aboveground Production	Total	Chalmers et al, 1985	26.46	3	%N=1.68, Vince et al, 1981
Aboveground Production	Total	Chalmers et al, 1985	41.45	2	C:N=38, Gallagher & Plumley, 1979
Aboveground Production		Hanson, 1983	13.4	4	
Aboveground Production		Hanson, 1983	21.7	4	
Algae Biomass	Total	Chalmers et al, 1985	23.27	3	C:N=5.5, Valiela, 1983
Algae Biomass	Total	Wiegert & Wetzel, 1979	0.18	4	C:N=5.5, Valiela, 183

Algae Production	Short	Wiegert, 1979	32.73	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	1.57/Jan-Feb	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	4.87/May-Jun	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	7.91/Jul-Aug	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	9.96/Sep-Oct	0	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	12.13/Nov-Dec	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	2.88/Mar-Apr	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	3.72/Jan-Feb	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	2.46/mar-apr	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	5.75/May-Jun	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	12.24/Jul-Aug	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	10.63/Sep-Oct	0	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	9.21/Nov-Dec	3	C:N=5.5, Valiela, 1983
Algae Production	Total	Chalmers et al, 1985	23.27	2	C:N=5.5, Valiela, 1983
Belowground Biomass	High	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Belowground Biomass	Short	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Belowground Biomass	Short	Hopkinson & Schubauer, 1984	3.3	4	
Belowground Biomass	Short	Gallagher, 1975	51.96	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Biomass	Short	Gross et al, 1991	3.66	3	%N=.44, Hopkinsons& schubauer, 1984
Belowground Biomass	Tall	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Belowground Biomass	Total	Wiegert & Wetzel, 1979	9	3	C:N=50, White & Howes, 1994c
Belowground Biomass	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Belowground Dead	Short	Gross et al, 1991	34.21	3	%N=1, Moran et al, 1989
Belowground Production	Short	Dai & Wiegert, 1996	7.94	3	C:N=50, White & Howes, 1994c
Belowground Production	Short	Schubauer & Hopkinson, 1984	8.89	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Short	Schubauer & Hopkinson, 1984	21.03	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Tall	Whitney et al, 1981	46.7	3	Ecology of Salt Marsh
Belowground Production	Tall	Schubauer & Hopkinson, 1984	9.28	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Tall	Dai & Wiegert, 1996	17.44	3	C:N=50 White & Howes, 1994c
Belowground Production	Total	Gallagher & Plumley, 1979	21.06	3	%C=38.1 C:N=38, Gallagher & Plumley, 1979
Belowground Production	Total	Schubauer & Hopkinson, 1984	21.03	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Total	Whitney et al, 1981	70	4	Ecology of Salt Marsh
Benthic Algae	Short	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Benthic Algae	Tall	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Benthic Algae	Total	Pomeroy et al 1981		4	Ecology of Salt Marsh
Benthic Algae	Total	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Benthic Algae	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Benthic algae production	Short	Wiegert, 1979	36.36	3	C:N=5.5, Valiela, 1983
Benthic algae production	Total	Haines et al, 1977	20	4	
Burial	Short	Wiegert, 1979	1.35	3	C:N=19.3, Valiela, 1983
Burial	Total	Wiegert, 1986	1.04	3	C:N=19.3, Valiela, 1983
Consumption	Short	Wiegert, 1979	0.82	3	C:N=38, Gallagher & Plumley, 1979
Consumption	Total	Barlocher et al, 1989		2	for Louisiana
Dead Biomass	Short	Haines et al, 1977	2.85	4	
Dead Biomass	Tall	Haines et al, 1977	6.79	4	
Dead Biomass	Total	Wiegert & Wetzel, 1979	1.49	3	C:N=87, White & Howes, 1994b
Death	Short	Hopkinson & Schubauer, 1984	14.4	4	
Decay	Short	Wiegert, 1979	1.82	3	C:N=38, White & Howes, 1994b
Decay	Short	Hopkinson & Schubauer, 1984	19.7	4	
Denitrification	Total	Haines et al, 1977	12	4	
Denitrification	Total	Whitney et al, 1981	65	4	Ecology of Salt Marsh
Denitrification	Total	Chalmers et al, 1976	7	4	
Denitrification		Sherr & Payne, 1979			
Detritus	Short	Alberts et al, 1992		4	
Detritus	Short	Haines et al, 1977	12	4	
Detritus	Short	Chalmers, 1979	10.5	3	%N=.77 Hopkinson & Schubauer, 1984
Detritus	Tall	Haines et al, 1977	21	4	
Excretion	Short	Montague, 1982	12.2	3	
Filter Feeders	High	Kuenzler, 1961	0.25	3	%N=10, Leschine, 1979
Filter Feeders	Short	Kuenzler, 1961	0.28	3	%N=10, Leschine, 1979
Filter Feeders	Tall	Kuenzler, 1961	3.15	3	%N=10, Leschine, 1979
Filter Feeders	Total	Kuenzler, 1961	0.04	3	%N=10, Leschine, 1979
Filter Feeders	Total	Kuenzler, 1961	0.12	3	%N=10, Leschine, 1979
Filter Feeders	Total	Kuenzler, 1961	0.08	3	%N=10, Leschine, 1979
Filtration	Short	Kemp et al, 1990a	1.27 /aug&sep	3	C:N=5.5 Valiela, 1983
Filtration	Short	Kemp et al, 1990a	1.37	3	C:N=5.5, Valiela, 1983
Filtration	Short	Kemp et al, 1990a	59.57	3	C:N=7, Valiela & Teal, 1979b
Grazer/Detritivore		Barlocher et al, 1989		2	

Grazers	Total	Wiegert & Wetzel, 1979	0.06	3	C:N=17, Valiela, 1983
Grazers/Nekton	Short	Kemp et al, 1990b	6.35	4	
Grazers/Nekton	Short	Kemp et al, 1990b	0.45	4	
Grazers/Nekton	Short	Kneib & Weeks, 1990		4	
Grazers/Nekton	Short	Kemp et al, 1990b	0.46	4	
Grazers/Nekton	Short	Newell et al, 1989		4	
Grazers/Nekton	Short	Fritz & Wiegert, 1991		4	
Grazers/Nekton	Short	Kneib, 1991		4	
Grazers/Nekton	Short	Pfeiffer & Wiegert, 1981		4	Ecology of Salt Marsh
Grazers/Nekton	Tall	Kneib & Weeks, 1990		4	
Grazers/Nekton	Tall	Pfeiffer & Wiegert, 1981		4	Ecology of Salt Marsh
Grazers/Nekton	Total	Dai & Wiegert, 1996		2	
Grazers/Nekton	Total	Smalley, 1960		3	
Grazers/Nekton	Total	Montague, 1982		4	
Grazers/Nekton	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Grazers/Nekton	Total	Smalley, 1960		3	
Leaching	Short	Hopkinson & Schubauer, 1984	0.7	4	
Litter	Total	Whitney et al, 1981	12 to 21	4	Ecology of Salt Marsh
Litter	Total	Weigert et al, 1981		4	Ecology of Salt Marsh
Mineralization	Total	Whitney et al, 1981	70	4	Ecology of Salt Marsh
Mussel	Short	Kemp et al, 1990a		4	
Nitrogen Fixation	High	Whitney et al, 1981	5	4	Ecology of Salt Marsh
Nitrogen Fixation	High	Whitney et al, 1981	4	4	Ecology of Salt Marsh
Nitrogen Fixation	Short	Hanson, 1983	13.1	4	
Nitrogen Fixation	Short	Haines et al, 1977	5.8	4	
Nitrogen Fixation	Short	Hanson, 1977	20-50	4	
Nitrogen Fixation	Short	Hanson, 1977	22.2-52.4	4	
Nitrogen Fixation	Short	Whitney et al, 1981	13	4	Ecology of Salt Marsh
Nitrogen Fixation	Short	Whitney et al, 1981	13.1	4	Ecology of Salt Marsh
Nitrogen Fixation	Tall	Hanson, 1983	39.7	4	
Nitrogen Fixation	Tall	Whitney et al, 1981	40	4	Ecology of Salt Marsh
Nitrogen Fixation	Tall	Whitney et al, 1981	39.7	4	Ecology of Salt Marsh
Nitrogen Fixation	Total	Hanson, 1983	2.92	4	
Nitrogen Fixation	Total	Hanson, 1983	53.29	4	
Nitrogen Fixation	Total	Haines, 1976	6	4	
Nitrogen Fixation	Total	Whitney et al, 1981	15	4	Ecology of Salt Marsh
Nitrogen Fixation	Total	Whitney et al, 1981	14.8	4	Ecology of Salt Marsh
Plant Uptake	Short	Hokinson & Schubauer, 1984	34.8	4	
Plant Uptake	Short	Haines et al, 1977	2.1	4	
Plant Uptake	Tall	Haines et al, 1977	10.7	4	
Plant Uptake	Total	Haies, 1976	11	4	
Plant Uptake	Total	Haines, 1976	22	4	
Pore NH4	Short	Chalmers et al, 1976	0.21	4	
Pore NH4	Tall	Chalmers et al, 1976	0.18	4	
Pore NH4	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Pore NH4	Total	Chalmers, 1979	0.19	2	
Pore NOx	Short	Chalmers et al, 1976	0.04	4	
Pore NOx	Tall	Chalmers et al, 1976	0.03	4	
Pore NOx	Total	Whitney et al, 1981	65	4	Ecology of Salt Marsh
Pore NOx	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Pore PN	High	Gallagher et al, 1980	13.9	4	
Pore PN	Short	Gallagher et al, 1980	9.9	4	
Pore PN	Short	Christian et al, 1981	727000	3	Ecology of Salt Marsh
Pore PN	Short	Chalmers et al, 1976	486.54	4	
Pore PN	Tall	Gallagher et al, 1980	21	4	
Pore PN	Tall	Christian et al, 1981	767000 g/m2	3	Ecology of Salt Marhs
Pore PN	Tall	Chalmers et al, 1976	485.8	4	
Pore PN	Total	Whitney et al, 1981	485	4	Ecology of Salt Marsh
Pore PN	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Pore PN	Total	Schubauer & Hopkinson, 1984	16.63	3	%N=0.44, Hopkinson & Schubauer, 1984
Precipitation	Total	Haines, 1976	0.07	4	TN=.3 g N/m2/year
Precipitation	Total	Haines, 1976	0.3	4	
Precipitation	Total	Haines, 1976	0.1	4	TN=.3 g N/m2/year
Precipitation	Total	Whitney et al, 1981	0.3	4	Ecology of Salt Marsh
Precipitation	Total	Whitney et al, 1981	0.3	4	Ecology of Salt Marsh
Precipitation	Total	Haines, 1976	0.13	4	TN=.3 g N/m2/year
Sediment	Short	Haines et al, 1977	493	4	
Sediment	Tall	Haines et al, 1977	463	4	

Sediment	Total	Gallagher & Plumley, 1979	98	4	
Sediment	Total	Wiegert & Wetzel, 1979	932.64	4	C:N=19.3, Valiela, 1983
Sediment DON	Total	Wiegert & Wetzel, 1979			
Sediment NH4	Short	Montague, 1982		4	
Sediment NH4	Short	Montague, 1982		4	
Sediment NH4	Short	Haines et al, 1977	0.255	4	
Sediment NH4	Tall	Haines et al, 1977	0.202	4	
Sediment NOx	Short	Haines et al, 1977	0.035	4	
Sediment NOx	Tall	Haines et al, 1977	0.033	4	
Sedimentation	Total	Whitney et al, 1981	3.3	4	Ecology of Salt Marsh
Standing Dead	High	Gallagher, 1975	7.27	3	%N=0.8, Gallagher, 1975
Standing Dead	Short	Gallagher, 1975	2.42	3	%N=0.7, Gallagher, 1975
Standing Dead	Tall	Gallagher, 1975	2.78	3	%N=0.7, Gallagher, 1975
Surface DON	Total	Chalmers et al, 1985	17.65	3	C:N=10.2, Hopkinson & Schubauer, 1084
Surface DON	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Surface NH4	Total	Whitney et al, 1981		4	Ecology of Salt Marhs
Surface PN	Total	Whitney et al, 1981	3.2	3	Ecology of Salt Marsh
Surface PN	Total	Chalmers et al, 1985	6.55	2	C:N=5.5, Valiela, 1983
Surface PN	Total	Chalmers et al, 1985	21.89	3	C:N=9.5, Valiela & Teal, 1979b
Surface PN	Total	Chalmers et al, 1985	5.27	3	C:N=5.5, Valiela, 1983
Surface PN	Total	Wiegert et al, 1981		3	Ecology of Salt Marsh
Surface PN	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Tidal DON	Total	Wiegert & Wetzel, 1979			
Tidal PN	Total	Wiegert & Wetzel, 1979	1.29	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Total	Wiegert, 1979	153.57	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Total	Wiegert, 1979	54.89	3	C:N=4.5 Valiela, 1983
Tidal Water Exchange	Total	Wiegert, 1979	111.71	3	C:N=7, Valeila & Teal, 1979b
Tidal Water Exchange	Total	Wiegert, 1979	30.45	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Total	Wiegert, 1986	85.43	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Total	Chalmers et al, 1985	191.13	3	C:N=5.5, Valiela, 1983
Tidal Water Exchange	Total	Chalmers et al, 1985	226.24	3	C:N=10.2, Hopkinson & Schubauer, 1984
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Montague, 1982		4	
Tidal Water Exhchange	Total	Whitney et al, 1981	46.6	4	Ecology of Salt Marsh
Tidal Water Exhchange	Total	Haines, 1976	3.1	4	
Tidal Water Exhchange	Total	Wiegert, 1986	9.41	3	C:N=17, Valiela, 1983
Tidal Water Exhchange	Total	Wiegert, 1979	13.97	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exhchange	Total	Chalmers et al, 1985	138.32	3	C:N=9.5, Valiela & Teal, 1979b
Tidal Water Exhchange	Total	Chalmers et al, 1985	283.41	3	C:N=10.2, Hopkinson & Schubauer, 1984
Translocation	Short	Newell et al, 1989		4	
Translocation	Short	Hopkinson & Schubauer, 1984	17.9	4	

Compartment	Original Data	Zone	Season	Source
Abovegound Biomass	760 g dw/m2	High	year	Gallagher, 1975
Abovegound Biomass	3.14 g N/m2/year	Short	year	Haines et al, 1977
Abovegound Biomass	651 g dry mass/m2	Short	Summer	Gross et al, 1991
Abovegound Biomass	116.4 g dry weight/m2	Short	Summer	Montague, 1982
Abovegound Biomass	4.2 g N/m2	Short	year	Hopkinson & Schubauer, 1984
Abovegound Biomass	4.7 g N/m2	Short	year	Whitney et al, 1981
Abovegound Biomass	471 g dw/m2	Short	year	Gallagher, 1975
Abovegound Biomass	349 g dw/m2	Short	year	Gallagher, 1975
Abovegound Biomass	8.28 g N/m2/year	Tall	year	Haines et al, 1977
Abovegound Biomass	9.8 g N/m2	Tall	year	Whitney et al, 1981
Abovegound Biomass	1124 g dw/m2	Tall	year	Gallagher, 1975
Abovegound Biomass	135 g C/m2	Total	year	Wiegert & Wetzel, 1979
Abovegound Biomass	135 g C/m2	Total	year	Wiegert et al, 1981
Abovegound Biomass	3.44 g N/m2	Total	year	Chalmers, 1979
Abovegound Biomass	557.96 g dw/m2/yr	Total	year	Schubauer & Hopkinson, 1984
Aboveground Biomass	1500 g dry wt/m2	High	year	Pomeroy et al, 1981
Aboveground Biomass	2200 g dry wt/m2	High	year	Pomeroy et al, 1981
Aboveground Biomass	2200 g dry wt/m2	Short	year	Pomeroy et al, 1981
Aboveground Biomass	1350 g dry wt/m2	Short	year	Pomeroy et al, 1981
Aboveground Biomass	400 g dry wt/m2	Short	year	Pomeroy et al, 1981
Aboveground Biomass	3300 g dry wt/m2	Tall	Annual	Pomerory et al, 1981
Aboveground Biomass	3700 g dry wt/m2	Tall	year	Pomerory et al, 1981
Aboveground Biomass	2000 g dry wt/m2	Tall	year	Pomerory et al, 1981
Aboveground Dead	113.6 g dw/m2/yr	Short	year	Chalmers, 1979
Aboveground Dead	459 g dry mass/m2	Short	Summer	Gross et al, 1991
Aboveground Dead	184.4 g dry weight/m2	Short	Summer	Montague, 1982
Aboveground Production	31.4 g N/m2	High	year	Whitney et al, 1981
Aboveground Production	2500 g dw/m2	High	year	Gallagher et al, 1980
Aboveground Production	2800 g dw/m2	High	year	Gallagher et al, 1980
Aboveground Production	2500 g dw/m2	High	year	Gallagher et al, 1980
Aboveground Production	1500 g dw/m2	High	year	Gallagher et al, 1980
Aboveground Production	2200 g dw/m2	High	year	Gallagher et al, 1980
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Aboveground Production	13.4 g N/m2/yr	Short	year	Kemp et al, 1990b
Aboveground Production	1488 g C/m2/yr	Short	year	Wiegert, 1979
Aboveground Production	1573 g C/m2/yr	Short	year	Wiegert, 1979
Aboveground Production	33.0 g N/m2/year	Short	year	Hopkinson & Schubaurer, 1984
Aboveground Production	330 g /m2/year	Short	year	Hason, 1977
Aboveground Production	1337 g/m2/year	Short	year	Haines et al, 1977
Aboveground Production	18.6 g N/m2	Short	year	Whitney et al, 1981
Aboveground Production	1489 g C/m2/yr	Short	year	Dai & Wiegert, 1996
Aboveground Production	1337 g dw/m2/yr	Short	year	Chalmers,1979
Aboveground Production	1350 g dw/m2/yr	Short	year	Schubauer & Hopkinson, 1984
Aboveground Production	2840 g dw/m2/yr	Short	year	Schubauer & Hopkinson, 1984
Aboveground Production	700 g dw/m2	Short	year	Gallagher et al, 1980
Aboveground Production	1500 g dw/m2	Short	year	Gallagher et al, 1980
Aboveground Production	1600 g dw/m2	Short	year	Gallagher et al, 1980
Aboveground Production	1200 g dw/m2	Short	year	Gallagher et al, 1980
Aboveground Production	1300 g dw/m2	Short	year	Gallagher et al, 1980
Aboveground Production	2454 g C/m2/yr	Tall	year	Dai & Wiegert, 1996
Aboveground Production	2596 g C/m2/yr	Tall	year	Wiegert, 1979
Aboveground Production	1600 g /m2/year	Tall	year	Hanson, 1977
Aboveground Production	3711 g/m2/year	Tall	year	Haines et al, 1977
Aboveground Production	47.1 g N/m2	Tall	year	Whitney et al, 1981
Aboveground Production	3700 g dw/m2/yr	Tall	year	Schubauer & Hopkinson, 1984
Aboveground Production	2300 g dw/m2	Tall	year	Gallagher et al, 1980
Aboveground Production	3000 g dw/m2	Tall	year	Gallagher et al, 1980
Aboveground Production	2700 g dw/m2	Tall	year	Gallagher et al, 1980
Aboveground Production	4400 g dw/m2	Tall	year	Gallagher et al, 1980
Aboveground Production	3700 g dw/m2	Tall	year	Gallagher et al, 1980
Aboveground Production	2500 g C/m2/year	Tall	year	Wiegert, 1986
Aboveground Production	2840 g dw/m2/yr	Total	year	Schubauer & Hopkinson 1984
Aboveground Production	1575 g C/m2/yr	Total	year	Chalmers et al, 1985
Aboveground Production	1575 g C/m2/yr	Total	year	Chalmers et al, 1985
Aboveground Production	13.4 g N/m2/year		year	Hanson, 1983
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Aboveground Production	21.7 g N/m2/year		year	Hanson, 1983
Algae Biomass	1 g C/m2	Total	year	Wiegert & Wetzel, 1979
Algal Production	180 g C/m2/yr	Short	year	Wiegert, 1979

Algal Production	146 mg C/m2/day	Short	Jan-Feb	Pomeroy, 1959
Algal Production	439 mg C/m2/day	Short	May-Jun	Pomeroy, 1959
Algal Production	702 mg C/m2/day	Short	Jul-Aug	Pomeroy, 1959
Algal Production	898 mg C/m2/day	Short	Sep-Oct	Pomeroy, 1959
Algal Production	1094 mg C/m2/day	Short	Nov-Dec	Pomeroy, 1959
Algal Production	260 mg C/m2/day	Short	Mar-Apr	Pomeroy, 1959
Algal Production	347 mg C/m2/day	Tall	Jan-Feb	Pomeroy, 1959
Algal Production	222 mg C/m2/day	Tall	March-April	Pomeroy, 1959
Algal Production	518 mg C/m2/day	Tall	May-June	Pomeroy, 1959
Algal Production	1086 mg C/m2/day	Tall	Jul-Aug	Pomeroy, 1959
Algal Production	958 mg C/m2/day	Tall	Sep-Oct	Pomeroy, 1959
Algal Production	830 mg C/m2/day	Tall	Nov-Dec	Pomeroy, 1959
Algal Production	128 g C/m2/yr	Total	year	Chalmers et al, 1985
Algal Production	128 g C/m2/yr	Total	year	Chalmers et al, 1985
Belowground Biomass	1340 g C/m2	High	year	Pomeroy et al, 1981
Belowground Biomass	700 g C/m2	Short	year	Pomeroy et al, 1981
Belowground Biomass	3.3 g N/m2	Short	year	Hopkinson & Schubauer, 1984
Belowground Biomass	11810 g dw/m2	Short	year	Gallagher, 1975
Belowground Biomass	831 g dry mass/m2	Short	Summer	Gross et al, 1991
Belowground Biomass	770 g C/m2	Tall	year	Pomeroy et al, 1981
Belowground Biomass	450 g C/m2	Total	year	Wiegert & Wetzel, 1979
Belowground Biomass	450 g C/m2	Total	year	Wiegert et al, 1981
Belowground Dead	3421 g dry weight/m2	Short	Summer	Gross et al, 1991
Belowground Production	397 g C/m2/yr	Short	year	Dai & Wiegert, 1996
Belowground Production	2020 g dw/m2/yr	Short	year	Schubauer & Hopkinson, 1984
Belowground Production	4780 g dw/m2/yr	Short	year	Schubauer & Hopkinson, 1984
Belowground Production	46.7 g N/m2	Tall	year	Whitney et al, 1981
Belowground Production	2110 g dw/m2/yr	Tall	year	Schubauer & Hopkinson, 1984
Belowground Production	872 g C/m2/yr	Tall	year	Dai & Wiegert, 1996
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Belowground Production	2100 g/m2/year	Total	year	Gallagher & Plumley, 1979
Belowground Production	4780 g dw/m2/yr	Total	year	Schubauer & Hopkinson, 1984
Belowground Production	70 g N/m2	Total	year	Whitney et al, 1981
Benthic algae	220 g C/m2	Total	year	Pomeroy et al 1981
Benthic algae	190 g C/m2	Total	year	Pomeroy et al, 1981
Benthic algae	1 g C/m2	Total	year	Wiegert et al, 1981
Benthic algae production	13 mg C/m2/hr	Short		Pomeroy et al, 1981
Benthic algae production	200 g C/m2/yr	Short	year	Wiegert, 1979
Benthic algae production	34 mg C/m2/hr	Tall		Pomeroy et al, 1981
Benthic algae production	20 g N/m2/year	Total	year	Haines et al, 1977
Burial	26 g C/m2/yr	Short	year	Wiegert, 1979
Burial	20 g C/m2/year	Total	year	Wiegert, 1986
Consumption	31 g C/m2/yr	Short	year	Wiegert, 1979
Consumption	12% annual S.a. prod	Total	year	Barlocher et al, 1989
Dead Biomass	2.85 g N/m2/year	Short	year	Haines et al, 1977
Dead Biomass	6.79 g N/m2/year	Tall	year	Haines et al, 1977
Dead Biomass	130 g C/m2	Total	year	Wiegert & Wetzel, 1979
Death	14.4 g N/m2/yr	Short	year	Hopkinson & Schubauer, 1984
Decay	69 g C/m2/yr	Short	year	Wiegert, 1979
Decay	19.7 g N/m2/yr	Short	year	Hopkinson & Schubauer, 1984
Denitrification	12 g N/m2/year	Total	year	Haines et al, 1977
Denitrification	65 g N/m2	Total	year	Whitney et al, 1981
Denitrification	7 g N/m2/yr	Total	year	Chalmers et al, 1976
Denitrification	31.7 ug/cm3/hour			Sherr & Payne, 1979
Detritus	60% of biomass	Short	year	Alberts et al, 1992
Detritus	12 g N/m2/year	Short	year	Haines et al, 1977
Detritus	113.6 g/m2/month	Short	year	Chalmers, 1979
Detritus	21 g N/m2/year	Tall	year	Haines et al, 1977
Excretion	3.6 mg NH4/g/d	Short	year	Montague, 1982
Filter Feeders	2.53 g dw/m2	High	year	Kuenzler, 1961
Filter Feeders	2.84 g dw/m2	Short	year	Kuenzler, 1961
Filter Feeders	31.48 g dw/m2	Tall	year	Kuenzler, 1961
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Filter Feeders	445 mg dw/m2	Total	year	Kuenzler, 1961
Filter Feeders	1200 mg dw/m2	Total	year	Kuenzler, 1961
Filter Feeders	820 mg dw/m2	Total	year	Kuenzler, 1961
Filtration	4766.3 ug C/m2/hr	Short	Aug and Sep	Kemp et al, 1990a
Filtration	7.52 g C/m2/yr	Short	year	Kemp et al, 1990a
Filtration	417 g POC/m2/yr	Short	year	Kemp et al, 1990a
Grazer/Detritivore	400 indiv/m2			Barlocher et al, 1989

Grazers	1 g C/m2	Total	year	Wiegert & Wetzel, 1979
Grazers/Nekton	6.35 g N/m2/yr	Short	year	Kemp et al, 1990b
Grazers/Nekton	.454 g N/m2/yr	Short	year	Kemp et al, 1990b
Grazers/Nekton	75 indiv/m2	Short	summer	Kneib & Weeks, 1990
Grazers/Nekton	.46 g N/m2	Short	year	Kemp et al, 1990b
Grazers/Nekton	243 indiv/m2	Short	December	Newell et al, 1989
Grazers/Nekton	.005 indiv/m2	Short	September	Fritz & Wiegert, 1991
Grazers/Nekton	1.71 indiv/m2	Short	year	Kneib, 1991
Grazers/Nekton	119.7 g dry wt/m2	Short	year	Pfeiffer & Wiegert, 1981
Grazers/Nekton	125 indiv/m2	Tall	Summer	Kneib & Weeks, 1990
Grazers/Nekton	197.7 g dry wt/m2	Tall	year	Pfeiffer & Wiegert, 1981
Grazers/Nekton	5% primary production	Total	year	Dai & Wiegert, 1996
Grazers/Nekton	12% of net production	Total	year	Smalley, 1960
Grazers/Nekton	50-700 indiv/m2	Total	year	Montague, 1982
Grazers/Nekton	1 g C/m2	Total	year	Wiegert et al, 1981
Grazers/Nekton	0.55 g dw/m2	Total	year	Smalley, 1960
Leaching	.7 g N/m2/yr	Short	year	Hopkinson & Schubauer, 1984
Litter	12 to 21 g N/m2	Total	year	Whitney et al, 1981
Litter	130 g C/m2	Total	year	Wiegert et al, 1981
Mineralization	70 g N/m2	Total	year	Whitney et al, 1981
Mussel	4.1 g shell-free dry weight/m2	Short		Kemp et al, 1990a
Nitrogen Fixation	5 g N/m2	High	year	Whitney et al, 1981
Nitrogen Fixation	4.0 g N/m2	High	year	Whitney et al, 1981
Nitrogen Fixation	13.1 g N/m2/year	Short	year	Hanson, 1983
Nitrogen Fixation	5.8 g N/m2/year	Short	year	Haines et al, 1977
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Nitrogen Fixation	20-50 g N/m2/year	Short	year	Hanson, 1977
Nitrogen Fixation	22.2-52.4 g N/m2/year	Short	year	Hanson, 1977
Nitrogen Fixation	13 g N/m2	Short	year	Whitney et al, 1981
Nitrogen Fixation	13.1 g N/m2	Short	year	Whitney et al, 1981
Nitrogen Fixation	39.7 g N/m2/year	Tall	year	Hanson, 1983
Nitrogen Fixation	40 g N/m2	Tall	year	Whitney et al, 1981
Nitrogen Fixation	39.7 g N/m2	Tall	year	Whitney et al, 1981
Nitrogen Fixation	8 mg N/m2/day	Total	year	Hanson, 1983
Nitrogen Fixation	146 mg N/m2/day	Total	year	Hanson, 1983
Nitrogen Fixation	6 g N/m2/year	Total	year	Haines, 1976
Nitrogen Fixation	15 g N/m2	Total	year	Whitney et al, 1981
Nitrogen Fixation	14.8 g N/m2	Total	year	Whitney et al, 1981
Plant Uptake	34.8 g N/m2/year	Short	year	Hokinson & Schubauer, 1984
Plant Uptake	2.1 g N/m2/year	Short	year	Haines et al, 1977
Plant Uptake	10.7 g N/m2/year	Tall	year	Haines et al, 1977
Plant Uptake	11 g N/m2/year	Total	year	Haines, 1976
Plant Uptake	22 g N/m2/year	Total	year	Haines, 1976
Pore NH4	.21 g N/m2	Short	year	Chalmers et al, 1976
Pore NH4	.18 g N/m2	Tall	year	Chalmers et al, 1976
Pore NH4	30 to 70 uM	Total	year	Whitney et al, 1981
Pore NH4	185.83 mg N/m2/yr	Total	year	Chalmers, 1979
Pore NOx	0.04 g N/m2	Short	year	Chalmers et al, 1976
Pore NOx	.03 g N/m2	Tall	year	Chalmers et al, 1976
Pore NOx	65 g N/m2	Total	year	Whitney et al, 1981
Pore NOx	7 to 13 uM	Total	year	Whitney et al, 1981
Pore PN	13.9 g N/m2/yr	High	year	Gallagher et al, 1980
Pore PN	9.9 g N/m2/yr	Short	year	Gallagher et al, 1980
Pore PN	7.27 mg N/cc	Short	February	Christian et al, 1981
Pore PN	486.54 g N/m2	Short	year	Chalmers et al, 1976
Pore PN	21 g N/m2/yr	Tall	year	Gallagher et al, 1980
Pore PN	7.67 mg N/cc	Tall	February	Christian et al, 1981
Pore PN	485.8 g N/m2	Tall	year	Chalmers et al, 1976
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Pore PN	485 g N/m2	Total	year	Whitney et al, 1981
Pore PN	18,200 g C/m2	Total	year	Wiegert et al, 1981
Pore PN	3,780 g dw/m2	Total	year	Schubauer & Hopkinson, 1984
Precipitation	22.3% of TN	Total	year	Haines, 1976
Precipitation	.3 g N/m2/year	Total	year	Haines, 1976
Precipitation	33.5% of TN	Total	year	Haines, 1976
Precipitation	0.3 g N/m2	Total	year	Whitney et al, 1981
Precipitation	0.3 g N/m2	Total	year	Whitney et al, 1981
Precipitation	44.2% of TN	Total	year	Haines, 1976
Sediment	493 g N/m2/year	Short	year	Haines et al, 1977
Sediment	463 g N/m2/year	Tall	year	Haines et al, 1977

Sediment	98 g N/m2	Total	year	Gallagher & Plumley, 1979
Sediment	18000 g C/m2	Total	year	Wiegert & Wetzel, 1979
Sediment DON	26 g C/m2	Total	year	Wiegert & Wetzel, 1979
Sediment NH4	6.3 umol N/l	Short	March	Montague, 1982
Sediment NH4	8.8 umol N/l	Short	September	Montague, 1982
Sediment NH4	.255 g N/m2/year	Short	year	Haines et al, 1977
Sediment NH4	.202 g N/m2/year	Tall	year	Haines et al, 1977
Sediment NOx	.035 g N/m2/year	Short	year	Haines et al, 1977
Sediment NOx	0.033 g N/m2/year	Tall	year	Haines et al, 1977
Sedimentation	3.3 g N/m2	Total	year	Whitney et al, 1981
Standing Dead	909 g dw/m2	High	year	Gallagher, 1975
Standing Dead	345 g dw/m2	Short	year	Gallagher, 1975
Standing Dead	397 g dw/m2	Tall	year	Gallagher, 1975
Surface DON	108 g C/m2/yr	Total	year	Chalmers et al, 1985
Surface DON	2-20 uM	Total	year	Whitney et al, 1981
Surface NH4	5 uM	Total	year	Whitney et al, 1981
Surface PN	3.2 g N/m2	Total	year	Whitney et al, 1981
Surface PN	36 g C/m2/yr	Total	year	Chalmers et al, 1985
Surface PN	208 g C/m2/yr	Total	year	Chalmers et al, 1985
Surface PN	29 g C/m2/yr	Total	year	Chalmers et al, 1985
Surface PN	5.6 g POC/m2	Total	year	Wiegert et al, 1981
Compartment	**Original Data**	**Zone**	**Season**	**Source**
Surface PN	.1-30 uM	Total	year	Whitney et al, 1981
Tidal DON	5.6 g C/m2	Total	year	Wiegert & Wetzel, 1979
Tidal PN	9 g C/m2	Total	year	Wiegert & Wetzel, 1979
Tidal Water Exchange	31.75 ug N/l	Short	year	Haines, 1979
Tidal Water Exchange	1.61 ug N/l	Short	year	Haines, 1979
Tidal Water Exchange	.44 ug N/l	Short	year	Haines, 1979
Tidal Water Exchange	19.09 ug N/l	Short	year	Haines, 1979
Tidal Water Exchange	29.8 ug N/l	Short	year	Haines, 1979
Tidal Water Exchange	1075 g C/m2/yr	Total	year	Wiegert, 1979
Tidal Water Exchange	247 g C/m2/yr	Total	year	Wiegert, 1979
Tidal Water Exchange	782 g C/m2/yr	Total	year	Wiegert, 1979
Tidal Water Exchange	213.16 g C/m2/yr	Total	year	Wiegert, 1979
Tidal Water Exchange	598 g C/m2/year	Total	year	Wiegert, 1986
Tidal Water Exchange	1051.2 g C/m2/yr	Total	year	Chalmers et al, 1985
Tidal Water Exchange	2715.6 g C/m2/yr	Total	year	Chalmers et al, 1985
Tidal Water Exhchange	2.75 ug N/l	Short	year	Haines, 1979
Tidal Water Exhchange	1.47 ug N/l	Short	year	Haines, 1979
Tidal Water Exhchange	.42 ug N/l	Short	year	Haines, 1979
Tidal Water Exhchange	11.69 ug N/l	Short	year	Haines, 1979
Tidal Water Exhchange	14.79 ug N/l	Short	year	Haines, 1979
Tidal Water Exhchange	2-3 umol N/l/tide	Short	year	Montague, 1982
Tidal Water Exhchange	46.6 g N/m2	Total	year	Whitney et al, 1981
Tidal Water Exhchange	3.1 g N/m2/year	Total	year	Haines, 1976
Tidal Water Exhchange	160 g C/m2/year	Total	year	Wiegert, 1986
Tidal Water Exhchange	97.82 g C/m2/yr	Total	year	Wiegert, 1979
Tidal Water Exhchange	1314 g C/m2/yr	Total	year	Chalmers et al, 1985
Tidal Water Exhchange	2890.8 g C/m2/yr	Total	year	Chalmers et al, 1985
Translocation	54% of N	Short	year	Newell et al, 1989
Translocation	17.9 g N/m2/year	Short	year	Hopkinson & Schubauer, 1984

Compartment	Zone	Source	g N/m2/yr	RF	Comments
Abovegound Biomass	High	Gallagher, 1975	9.12	3	%N=1.2, Gallagher, 1975
Abovegound Biomass	Short	Haines et al, 1977	3.14	4	
Abovegound Biomass	Short	Gross et al, 1991	10.94	3	%N=1.68, Kemp et al, 1990b
Abovegound Biomass	Short	Montague, 1982	1.22	3	%N=1.05, Hopkinsons & Shubauer, 1984
Abovegound Biomass	Short	Hopkinson & Schubauer, 1984	4.2	4	
Abovegound Biomass	Short	Whitney et al, 1981	4.7	4	Ecology of Salt Marsh
Abovegound Biomass	Short	Gallagher, 1975	3.77	3	%N=0.8, Gallagher, 1975
Abovegound Biomass	Short	Gallagher, 1975	2.79	3	%N=0.8, Gallagher, 1975
Abovegound Biomass	Tall	Haines et al, 1977	8.28	4	
Abovegound Biomass	Tall	Whitney et al, 1981	9.8	4	Ecology of Salt Marsh
Abovegound Biomass	Tall	Gallagher, 1975	7.87	3	%N=0.7, Gallagher, 1975
Abovegound Biomass	Total	Wiegert & Wetzel, 1979	3.55	3	C:N=38, Gallagher & Plumley, 1979
Abovegound Biomass	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Abovegound Biomass	Total	Chalmers, 1979	3.44	2	
Abovegound Biomass	Total	Schubauer & Hopkinson, 1984	9.37	3	%N=1.68, Vince et al, 1981
Aboveground Biomass	High	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Aboveground Biomass	High	Pomeroy et al, 1981		4	Ecology of Salt Marhs
Aboveground Biomass	Short	Pomeroy et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Short	Pomeroy et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Short	Pomeroy et al, 1981		4	Ecology of salt Marsh
Aboveground Biomass	Tall	Pomerory et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Tall	Pomerory et al, 1981		4	Ecology of Salt marsh
Aboveground Biomass	Tall	Pomerory et al, 1981		4	Ecology of Salt marsh
Aboveground Dead	Short	Chalmers, 1979	0.87	3	%N=0.77, Hopkinson & Schubauer, 1984
Aboveground Dead	Short	Gross et al, 1991	3.53	3	%N=.77, Kemp et al, 1990b
Aboveground Dead	Short	Montague, 1982	1.42	3	%N=.77, Kemp et al, 1990b
Aboveground Production	High	Whitney et al, 1981	31.4	4	Ecology of Salt Marsh
Aboveground Production	High	Gallagher et al, 1980	30	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	33.6	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	30	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	18	3	%N=1.2, Gallagher, 1975
Aboveground Production	High	Gallagher et al, 1980	26.4	3	%N=1.2, Gallagher, 1975
Aboveground Production	Short	Kemp et al, 1990b	13.4	4	
Aboveground Production	Short	Wiegert, 1979	39.16	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Short	Wiegert, 1979	41.39	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Short	Hopkinson & Schubaurer, 1984	33	4	
Aboveground Production	Short	Hason, 1977	3.47	3	%N=1.05, Hopkinson & Schubauer, 1984
Aboveground Production	Short	Haines et al, 1977	35.18	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Short	Whitney et al, 1981	18.6	4	Ecology of Salt Marsh
Aboveground Production	Short	Dai & Wiegert, 1996	29.78	3	C:N=50 White & Howes, 1994c
Aboveground Production	Short	Chalmers,1979	22.46	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Schubauer & Hopkinson, 1984	22.68	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Schubauer & Hopkinson, 1984	47.71	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	11.76	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	25.2	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	26.88	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	20.16	3	%N=1.68, Vince et al, 1981
Aboveground Production	Short	Gallagher et al, 1980	21.84	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Dai & Wiegert, 1996	64.58	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Tall	Wiegert, 1979	68.32	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Tall	Hanson, 1977	16.8	3	%N=1.05, Hopkinson & Schubauer, 1984
Aboveground Production	Tall	Haines et al, 1977	97.66	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Tall	Whitney et al, 1981	47.1	4	Ecology of Salt Marsh
Aboveground Production	Tall	Schubauer & Hopkinson, 1984	62.16	3	%N=1.68, Hopkinson & Schubauer, 1984
Aboveground Production	Tall	Gallagher et al, 1980	38.64	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	50.4	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	45.36	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	73.92	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Gallagher et al, 1980	62.16	3	%N=1.68, Vince et al, 1981
Aboveground Production	Tall	Wiegert, 1986	65.79	3	C:N=38, Gallagher & Plumley, 1979
Aboveground Production	Total	Schubauer & Hopkinson 1984	47.71	3	%N=1.68, Vince et al, 1981
Aboveground Production	Total	Chalmers et al, 1985	26.46	3	%N=1.68, Vince et al, 1981
Aboveground Production	Total	Chalmers et al, 1985	41.45	2	C:N=38, Gallagher & Plumley, 1979
Aboveground Production		Hanson, 1983	13.4	4	
Aboveground Production		Hanson, 1983	21.7	4	
Algae Biomass	Total	Chalmers et al, 1985	23.27	3	C:N=5.5, Valiela, 1983
Algae Biomass	Total	Wiegert & Wetzel, 1979	0.18	4	C:N=5.5, Valiela, 183

Algae Production	Short	Wiegert, 1979	32.73	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	1.57/Jan-Feb	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	4.87/May-Jun	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	7.91/Jul-Aug	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	9.96/Sep-Oct	0	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	12.13/Nov-Dec	3	C:N=5.5, Valiela, 1983
Algae Production	Short	Pomeroy, 1959	2.88/Mar-Apr	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	3.72/Jan-Feb	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	2.46/mar-apr	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	5.75/May-Jun	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	12.24/Jul-Aug	3	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	10.63/Sep-Oct	0	C:N=5.5, Valiela, 1983
Algae Production	Tall	Pomeroy, 1959	9.21/Nov-Dec	3	C:N=5.5, Valiela, 1983
Algae Production	Total	Chalmers et al, 1985	23.27	2	C:N=5.5, Valiela, 1983
Belowground Biomass	High	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Belowground Biomass	Short	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Belowground Biomass	Short	Hopkinson & Schubauer, 1984	3.3	4	
Belowground Biomass	Short	Gallagher, 1975	51.96	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Biomass	Short	Gross et al, 1991	3.66	3	%N=.44, Hopkinsons& schubauer, 1984
Belowground Biomass	Tall	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Belowground Biomass	Total	Wiegert & Wetzel, 1979	9	3	C:N=50, White & Howes, 1994c
Belowground Biomass	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Belowground Dead	Short	Gross et al, 1991	34.21	3	%N=1, Moran et al, 1989
Belowground Production	Short	Dai & Wiegert, 1996	7.94	3	C:N=50, White & Howes, 1994c
Belowground Production	Short	Schubauer & Hopkinson, 1984	8.89	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Short	Schubauer & Hopkinson, 1984	21.03	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Tall	Whitney et al, 1981	46.7	3	Ecology of Salt Marsh
Belowground Production	Tall	Schubauer & Hopkinson, 1984	9.28	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Tall	Dai & Wiegert, 1996	17.44	3	C:N=50 White & Howes, 1994c
Belowground Production	Total	Gallagher & Plumley, 1979	21.06	3	%C=38.1 C:N=38, Gallagher & Plumley, 1979
Belowground Production	Total	Schubauer & Hopkinson, 1984	21.03	3	%N=0.44, Hopkinson & Schubauer, 1984
Belowground Production	Total	Whitney et al, 1981	70	4	Ecology of Salt Marsh
Benthic Algae	Short	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Benthic Algae	Tall	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Benthic Algae	Total	Pomeroy et al 1981		4	Ecology of Salt Marsh
Benthic Algae	Total	Pomeroy et al, 1981		4	Ecology of Salt Marsh
Benthic Algae	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Benthic algae production	Short	Wiegert, 1979	36.36	3	C:N=5.5, Valiela, 1983
Benthic algae production	Total	Haines et al, 1977	20	4	
Burial	Short	Wiegert, 1979	1.35	3	C:N=19.3, Valiela, 1983
Burial	Total	Wiegert, 1986	1.04	3	C:N=19.3, Valiela, 1983
Consumption	Short	Wiegert, 1979	0.82	3	C:N=38, Gallagher & Plumley, 1979
Consumption	Total	Barlocher et al, 1989		2	for Louisiana
Dead Biomass	Short	Haines et al, 1977	2.85	4	
Dead Biomass	Tall	Haines et al, 1977	6.79	4	
Dead Biomass	Total	Wiegert & Wetzel, 1979	1.49	3	C:N=87, White & Howes, 1994b
Death	Short	Hopkinson & Schubauer, 1984	14.4	4	
Decay	Short	Wiegert, 1979	1.82	3	C:N=38, White & Howes, 1994b
Decay	Short	Hopkinson & Schubauer, 1984	19.7	4	
Denitrification	Total	Haines et al, 1977	12	4	
Denitrification	Total	Whitney et al, 1981	65	4	Ecology of Salt Marsh
Denitrification	Total	Chalmers et al, 1976	7	4	
Denitrification		Sherr & Payne, 1979			
Detritus	Short	Alberts et al, 1992		4	
Detritus	Short	Haines et al, 1977	12	4	
Detritus	Short	Chalmers, 1979	10.5	3	%N=.77 Hopkinson & Schubauer, 1984
Detritus	Tall	Haines et al, 1977	21	4	
Excretion	Short	Montague, 1982	12.2	3	
Filter Feeders	High	Kuenzler, 1961	0.25	3	%N=10, Leschine, 1979
Filter Feeders	Short	Kuenzler, 1961	0.28	3	%N=10, Leschine, 1979
Filter Feeders	Tall	Kuenzler, 1961	3.15	3	%N=10, Leschine, 1979
Filter Feeders	Total	Kuenzler, 1961	0.04	3	%N=10, Leschine, 1979
Filter Feeders	Total	Kuenzler, 1961	0.12	3	%N=10, Leschine, 1979
Filter Feeders	Total	Kuenzler, 1961	0.08	3	%N=10, Leschine, 1979
Filtration	Short	Kemp et al, 1990a	1.27 /aug&sep	3	C:N=5.5 Valiela, 1983
Filtration	Short	Kemp et al, 1990a	1.37	3	C:N=5.5, Valiela, 1983
Filtration	Short	Kemp et al, 1990a	59.57	3	C:N=7, Valiela & Teal, 1979b
Grazer/Detritivore		Barlocher et al, 1989		2	

Grazers	Total	Wiegert & Wetzel, 1979	0.06	3	C:N=17, Valiela, 1983
Grazers/Nekton	Short	Kemp et al, 1990b	6.35	4	
Grazers/Nekton	Short	Kemp et al, 1990b	0.45	4	
Grazers/Nekton	Short	Kneib & Weeks, 1990		4	
Grazers/Nekton	Short	Kemp et al, 1990b	0.46	4	
Grazers/Nekton	Short	Newell et al, 1989		4	
Grazers/Nekton	Short	Fritz & Wiegert, 1991		4	
Grazers/Nekton	Short	Kneib, 1991		4	
Grazers/Nekton	Short	Pfeiffer & Wiegert, 1981		4	Ecology of Salt Marsh
Grazers/Nekton	Tall	Kneib & Weeks, 1990		4	
Grazers/Nekton	Tall	Pfeiffer & Wiegert, 1981		4	Ecology of Salt Marsh
Grazers/Nekton	Total	Dai & Wiegert, 1996		2	
Grazers/Nekton	Total	Smalley, 1960		3	
Grazers/Nekton	Total	Montague, 1982		4	
Grazers/Nekton	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Grazers/Nekton	Total	Smalley, 1960		3	
Leaching	Short	Hopkinson & Schubauer, 1984	0.7	4	
Litter	Total	Whitney et al, 1981	12 to 21	4	Ecology of Salt Marsh
Litter	Total	Weigert et al, 1981		4	Ecology of Salt Marsh
Mineralization	Total	Whitney et al, 1981	70	4	Ecology of Salt Marsh
Mussel	Short	Kemp et al, 1990a		4	
Nitrogen Fixation	High	Whitney et al, 1981	5	4	Ecology of Salt Marsh
Nitrogen Fixation	High	Whitney et al, 1981	4	4	Ecology of Salt Marsh
Nitrogen Fixation	Short	Hanson, 1983	13.1	4	
Nitrogen Fixation	Short	Haines et al, 1977	5.8	4	
Nitrogen Fixation	Short	Hanson, 1977	20-50	4	
Nitrogen Fixation	Short	Hanson, 1977	22.2-52.4	4	
Nitrogen Fixation	Short	Whitney et al, 1981	13	4	Ecology of Salt Marsh
Nitrogen Fixation	Short	Whitney et al, 1981	13.1	4	Ecology of Salt Marsh
Nitrogen Fixation	Tall	Hanson, 1983	39.7	4	
Nitrogen Fixation	Tall	Whitney et al, 1981	40	4	Ecology of Salt Marsh
Nitrogen Fixation	Tall	Whitney et al, 1981	39.7	4	Ecology of Salt Marsh
Nitrogen Fixation	Total	Hanson, 1983	2.92	4	
Nitrogen Fixation	Total	Hanson, 1983	53.29	4	
Nitrogen Fixation	Total	Haines, 1976	6	4	
Nitrogen Fixation	Total	Whitney et al, 1981	15	4	Ecology of Salt Marsh
Nitrogen Fixation	Total	Whitney et al, 1981	14.8	4	Ecology of Salt Marsh
Plant Uptake	Short	Hokinson & Schubauer, 1984	34.8	4	
Plant Uptake	Short	Haines et al, 1977	2.1	4	
Plant Uptake	Tall	Haines et al, 1977	10.7	4	
Plant Uptake	Total	Haies, 1976	11	4	
Plant Uptake	Total	Haines, 1976	22	4	
Pore NH4	Short	Chalmers et al, 1976	0.21	4	
Pore NH4	Tall	Chalmers et al, 1976	0.18	4	
Pore NH4	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Pore NH4	Total	Chalmers, 1979	0.19	2	
Pore NOx	Short	Chalmers et al, 1976	0.04	4	
Pore NOx	Tall	Chalmers et al, 1976	0.03	4	
Pore NOx	Total	Whitney et al, 1981	65	4	Ecology of Salt Marsh
Pore NOx	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Pore PN	High	Gallagher et al, 1980	13.9	4	
Pore PN	Short	Gallagher et al, 1980	9.9	4	
Pore PN	Short	Christian et al, 1981	727000	3	Ecology of Salt Marsh
Pore PN	Short	Chalmers et al, 1976	486.54	4	
Pore PN	Tall	Gallagher et al, 1980	21	4	
Pore PN	Tall	Christian et al, 1981	767000 g/m2	3	Ecology of Salt Marhs
Pore PN	Tall	Chalmers et al, 1976	485.8	4	
Pore PN	Total	Whitney et al, 1981	485	4	Ecology of Salt Marsh
Pore PN	Total	Wiegert et al, 1981		4	Ecology of Salt Marsh
Pore PN	Total	Schubauer & Hopkinson, 1984	16.63	3	%N=0.44, Hopkinson & Schubauer, 1984
Precipitation	Total	Haines, 1976	0.07	4	TN=.3 g N/m2/year
Precipitation	Total	Haines, 1976	0.3	4	
Precipitation	Total	Haines, 1976	0.1	4	TN=.3 g N/m2/year
Precipitation	Total	Whitney et al, 1981	0.3	4	Ecology of Salt Marsh
Precipitation	Total	Whitney et al, 1981	0.3	4	Ecology of Salt Marsh
Precipitation	Total	Haines, 1976	0.13	4	TN=.3 g N/m2/year
Sediment	Short	Haines et al, 1977	493	4	
Sediment	Tall	Haines et al, 1977	463	4	

Sediment	Total	Gallagher & Plumley, 1979	98	4	
Sediment	Total	Wiegert & Wetzel, 1979	932.64	4	C:N=19.3, Valiela, 1983
Sediment DON	Total	Wiegert & Wetzel, 1979			
Sediment NH4	Short	Montague, 1982		4	
Sediment NH4	Short	Montague, 1982		4	
Sediment NH4	Short	Haines et al, 1977	0.255	4	
Sediment NH4	Tall	Haines et al, 1977	0.202	4	
Sediment NOx	Short	Haines et al, 1977	0.035	4	
Sediment NOx	Tall	Haines et al, 1977	0.033	4	
Sedimentation	Total	Whitney et al, 1981	3.3	4	Ecology of Salt Marsh
Standing Dead	High	Gallagher, 1975	7.27	3	%N=0.8, Gallagher, 1975
Standing Dead	Short	Gallagher, 1975	2.42	3	%N=0.7, Gallagher, 1975
Standing Dead	Tall	Gallagher, 1975	2.78	3	%N=0.7, Gallagher, 1975
Surface DON	Total	Chalmers et al, 1985	17.65	3	C:N=10.2, Hopkinson & Schubauer, 1084
Surface DON	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Surface NH4	Total	Whitney et al, 1981		4	Ecology of Salt Marhs
Surface PN	Total	Whitney et al, 1981	3.2	3	Ecology of Salt Marsh
Surface PN	Total	Chalmers et al, 1985	6.55	2	C:N=5.5, Valiela, 1983
Surface PN	Total	Chalmers et al, 1985	21.89	3	C:N=9.5, Valiela & Teal, 1979b
Surface PN	Total	Chalmers et al, 1985	5.27	3	C:N=5.5, Valiela, 1983
Surface PN	Total	Wiegert et al, 1981		3	Ecology of Salt Marsh
Surface PN	Total	Whitney et al, 1981		4	Ecology of Salt Marsh
Tidal DON	Total	Wiegert & Wetzel, 1979			
Tidal PN	Total	Wiegert & Wetzel, 1979	1.29	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Short	Haines, 1979		4	
Tidal Water Exchange	Total	Wiegert, 1979	153.57	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Total	Wiegert, 1979	54.89	3	C:N=4.5 Valiela, 1983
Tidal Water Exchange	Total	Wiegert, 1979	111.71	3	C:N=7, Valeila & Teal, 1979b
Tidal Water Exchange	Total	Wiegert, 1979	30.45	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Total	Wiegert, 1986	85.43	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exchange	Total	Chalmers et al, 1985	191.13	3	C:N=5.5, Valiela, 1983
Tidal Water Exchange	Total	Chalmers et al, 1985	226.24	3	C:N=10.2, Hopkinson & Schubauer, 1984
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Haines, 1979		4	
Tidal Water Exhchange	Short	Montague, 1982		4	
Tidal Water Exhchange	Total	Whitney et al, 1981	46.6	4	Ecology of Salt Marsh
Tidal Water Exhchange	Total	Haines, 1976	3.1	4	
Tidal Water Exhchange	Total	Wiegert, 1986	9.41	3	C:N=17, Valiela, 1983
Tidal Water Exhchange	Total	Wiegert, 1979	13.97	3	C:N=7, Valiela & Teal, 1979b
Tidal Water Exhchange	Total	Chalmers et al, 1985	138.32	3	C:N=9.5, Valiela & Teal, 1979b
Tidal Water Exhchange	Total	Chalmers et al, 1985	283.41	3	C:N=10.2, Hopkinson & Schubauer, 1984
Translocation	Short	Newell et al, 1989		4	
Translocation	Short	Hopkinson & Schubauer, 1984	17.9	4	

Compartment	Original Data	Zone	Season	Source
Aboveground Biomass	722.82 g/m2	High	Year	Tolley, 1996
Aboveground Biomass	27 g/m2	High	Year	Blum, 1997
Aboveground Biomass	60.72 g dw/m2	Short	Year	Blum, 1993
Aboveground Biomass	8 g/m2	Short	Year	Blum, 1997
Aboveground Biomass	35 g/m2	Tall	Year	Blum, 1997
Aboveground Biomass	156.34 g dw/m2	Tall	Year	Blum, 1993
Aboveground Production	800 g C/m2/yr	High	Year	Anderson et al, 1997a
Aboveground Production	846.9 g/m2/yr	High	Year	Tolley, 1996
Aboveground Production	14 g N/m2/yr	Short	Year	Anderson et al, 1997b
Aboveground Production	442.56 g dw/m2/yr	Short	Growing Season	this study
Aboveground Production	955.68 g dw/m2/yr	Tall	Growing Season	this study
Bacterial Uptake	2.74 g N/m2/yr	Short	Year	Neirkirk, 1996
Bacterial Uptake	315 umol/m2/tide	Short	Tidal Cycle	Chambers et al, 1992
Belowground Biomass	250 g/m2	High	Year	http://www.vcrlter.virginia.edu/elecvol
Belowground Biomass	0.79 g N/m2	Short	Year	this study
Belowground Biomass	900 g/m2	Short	Year	http://www.vcrlter.virginia.edu/elecvol
Belowground Biomass	0.1 g N/m2	Tall	Year	this study
Belowground Biomass	200 g/m2	Tall	Year	http://www.vcrlter.virginia.edu/elecvol
Belowground Dead	2.89 g N/m2	Short	Year	this study
Belowground Dead	1.35 g N/m2	Tall	Year	this study
Belowground Production	20.15 g N/m2/yr	High	Year	this study
Belowground Production	33 g N/m2/yr	Short	Year	Anderson et al, 1997b
Belowground Production	2140 g dw/m2/yr	Short	Year	Blum, 1993
Belowground Production	900 g AFDW/m2/yr	Short	Year	Blum & Christian, 1997
Belowground Production	680 g dw/m2/yr	Tall	Year	Blum, 1993
Benthic Algae	3.06 ug chl a/cm3	High	Year	Anderson et al, 1997a
Benthic Algae	10.12 mg/m2	Short	Year	Neikirk, 1996
Benthic Algae Production	5.0 g N/m2/yr	Short	Year	Anderson et al, 1997b
Benthic Filter Feeders	18.67/m2	Short	Year	this study
Benthic Filter Feeders	16/m2	Tall	Year	this study
Burial	4.0 g N/m2/yr	Short	Year	Anderson et al, 1997b
Decay	k=-0.254/yr (50% of decay at 2.7 years)	High	Year	Christian et al, 1990
Decay	66.3% remain of NPP	High	Year	Blum & Christian, 1997
Decay	7 g N/m2/yr	Short	Year	Anderson et al, 1997b
Decay	26 g N/m2/yr	Short	Year	Anderson et al, 1997b
Decay	76.9% of aboveground production	Short	Year	Blum, VCR/LTER Database
Decay	69.7% of belowground production	Short	Year	Blum, VCR/LTER Database
Decay	133.44 g dw/m2/yr	Short	Year	this study
Decay	69.15% remain of NPP	Short	Year	Blum & Christian, 1997
Decay	80.8 % of production	Tall	Year	Blum, VCR/LTER Database
Decay	68.4 % of belowground production	Tall	Year	Blum, VCR/LTER Database
Decay	479.47g dw/m2/yr	Tall	Year	this study
Decay	59.9% remain of production	Tall	Year	Blum & Christian, 1997
Denitrification	0.6 g N/m2/yr	Short	Year	Anderson et al, 1997b
Detritus formation	2.05 g N/m2/yr	High	Year	Buck, personal communication
Filter Feeding	16.04 g N/biomass/yr	Short	Year	this study
Filter Feeding	0.032 g N/biomass/yr	Short	Year	this study
Filter Feeding	11.79 g N/biomass/yr	Tall	Year	this study
Filter Feeding	0.032 g N/biomass/yr	Tall	Year	this study
Grazers	141.33/m2	Short	Year	this study
Grazers	8/m2	Short	Year	this study
Grazing	2% of NPP	High	Year	VCR 1998 All Scientist Meeting
Grazing	2% of NPP	Short	Year	VCR 1998 All Scientist Meeting
Grazing	2% of NPP	Tall	Year	VCR 1998 All Scientist Meeting
Leaching	0.96 g N/m2/yr	High	Year	this study
Leaching	0.62 g N/m2/yr	Short	Year	this study
Leaching	0.82 g N/m2/yr	Tall	Year	this study
Mineralization	13.27 g N/m2/yr	High	Year	Anderson et al, 1997a
Mineralization	1.14 mg N/m2/h	High	July	Anderson et al, 1997a
Mineralization	20.21 g N/m2/yr	Short	Year	Neirkirk, 1996
Mineralization	84 g N/m2/yr	Short	Year	Anderson et al, 1997b
Nitrification	7.09 g N/m2/yr	High	Year	Anderson et al, 1997a
Nitrification	0.9 mg N/m2/h	High	July	Anderson et al, 1997b
Nitrification	0.0 g N/m2/yr	High	Summer	Taylor, 1995
Nitrification	1.21 g N/m2/yr	Short	Year	Neirkirk, 1996
Nitrification	4.0 g N/m2/yr	Short	Year	Anderson et al, 1997b
Nitrogen Fixation	1.0 g N/m2/yr	Short	Year	Anderson et al, 1997b

Pore NH4	.11 g N/m2	High	Year	Anderson et al, 1997a
Pore NH4	4.62 uM	High	Year	Anderson et al, 1997a
Pore NH4	0.92 g N/m2	Short	Year	this study
Pore NH4	0.18 g N/m2	Tall	Year	this study
Pore NH4	32 uM	Tall	Year	http://www.vcrlter.virginia.edu/elecvol
Pore NOx	.11 g N/m2	High	Year	Taylor, 1995
Pore NOx	.02 g N/m2	High	Year	Anderson et al, 1997a
Pore NOx	1.01 uM	High	Year	Anderson et al, 1997a
Precipitation	0.25 g N/m2/yr	Total	Year	Anderson et al, 1997b
Precipitation	0.18 g N/m2/yr	Total	Year	Anderson et al, 1997b
Precipitation	0.31 g N/m2/yr	Total	Year	Keene & Galloway, 1997
Precipitation	0.15 g N/m2/yr	Total	Year	Keene & Galloway, 1997
Sediment release of NH4	846.6 umol/m2/tide	Short	Tidal Cycle	Chambers et al, 1992
Sediment release of NOx	6.31 g N/m2/yr	Short	Year	Neirkirk, 1996
Sediment uptake of NH4	0.41 g N/m2/yr	Short	Year	Neirkirk, 1996
Sedimentation	1.25 g N/m2/yr	Short	Year	Anderson et al, 1997b
Standing Dead	806.82 g/m2	High	Year	Tolley, 1996
Standing Dead	4.35 g N/m2/yr	High	Year	Buck, personal communication
Standing Dead	413.47 g dw/m2	Short	Year	this study
Standing Dead	652 g dw/m2	Tall	Year	this study
Surface PN	19.2 ug chl a/l	Short	Year	Neikirk, 1996
Tidal Water Exchange	3.4 umol/l	Tall	Year	VCR/LTER Database
Tidal Water Exchange	4.25 umol/l	Tall	Year	VCR/LTER Database
Tidal Water Exchange	2.98 umol/l	Tall	Year	VCR/LTER Database
Tidal Water Exchange	2.48 umol/l	Tall	Year	VCR/LTER Database
Translocation	7 g N/m2/yr	Short	Year	Anderson et al, 1997b

APPENDIX F. UPPER PHILLIPS CREEK CONVERTED DATA.

RF=Reliability Factor

Compartment	Zone	Source	g N/m2yr	RF	Comments
Aboveground Biomass	High	Tolley, 1996	11.35	3	%N=1.57 Vince et al, 1981
Aboveground Biomass	High	Blum, 1997	0.42	3	%N=1.57 Vince et al, 1981
Aboveground Biomass	Short	Blum, 1993	0.64	3	%N=1.05 Hopkinson & Schubauer, 1984
Aboveground Biomass	Short	Blum, 1997	0.13	3	%N=1.57 Vince et al, 1981
Aboveground Biomass	Tall	Blum, 1997	0.55	3	%N=1.57 Vince et al, 1981
Aboveground Biomass	Tall	Blum, 1993	1.64	3	%N=1.05 Hopkinson & Schubauer, 1984
Aboveground Production	High	Anderson et al, unpublished	16	4	C:N=50 White & Howes, 1994
Aboveground Production	High	Tolley, 1996	13.3	3	%N=1.57 Vince et al, 1981
Aboveground Production	Short	Anderson et al, 1998	14	4	
Aboveground Production	Short	this study	5.22	3	%N=1.18 this study
Aboveground Production	Tall	this study	17.58	3	%N=1.84 this study
Bacterial Uptake	Short	Neirkirk, 1996	2.74	2	
Bacterial Uptake	Short	Chambers et al, 1992	3.22	3	
Belowground Biomass	High	http://www.vcrlter.virginia.edu/elecvol	1.1	3	%N=0.44 Hopkinson & Schubauer, 1984
Belowground Biomass	Short	this study	0.79	3	
Belowground Biomass	Short	http://www.vcrlter.virginia.edu/elecvol	3.96	3	%N=0.44 Hopkinson & Schubauer, 1984
Belowground Biomass	Tall	this study	0.1	3	
Belowground Biomass	Tall	http://www.vcrlter.virginia.edu/elecvol	0.88	3	%N=0.44 Hopkinson & Schubauer, 1984
Belowground Dead	Short	this study	2.89	3	
Belowground Dead	Tall	this study	1.35	3	
Belowground Production	High	this study	20.15	1	Average SI & GS per unit biomass
Belowground Production	Short	Anderson et al, 1998	33	4	
Belowground Production	Short	Blum, 1993	9.42	3	%N=0.44 Hopkinson & Schubauer, 1984
Belowground Production	Short	Blum & Christian, 1997	3.96	3	%N=0.44 Hopkinson & Schubauer, 1984
Belowground Production	Tall	Blum, 1993	2.99	3	%N=0.44 Hopkinson & Schubauer, 1984
Benthic Algae	High	Anderson et al, 1996	0.18	3	chl a conversion Pickney 1994; C:N=5.5 Valiela, 1983
Benthic Algae	Short	Neikirk, 1996	5.88	3	chl a conversion Pickney 1994; C:N=5.5 Valiela, 1983
Benthic Algae Production	Short	Anderson et al, 1998	5	4	
Benthic filter feeders	Short	this study	0.26	3	1 mussel=0.0138 g N
Benthic filter feeders	Tall	this study	0.22	3	1 mussel=0.0138 g N
Burial	Short	Anderson et al, 1998	4	4	
Decay	High	Christian et al, 1990	1.09	4	For Cedar Island, NC
Compartment	**Zone**	**Source**	**g N/m2yr**	**RF**	**Comments**
Decay	High	Blum & Christian, 1997	6.79	1	NPP=20.15
Decay	Short	Anderson et al, 1998	7	4	
Decay	Short	Anderson et al, 1998	26	4	
Decay	Short	Blum, VCR/LTER Database	10.77	3	NPP=14 g N/m2/yr
Decay	Short	Blum, VCR/LTER Database	6.57	3	NPP=9.42 g N/m2/yr
Decay	Short	this study	1.27	3	%N=0.95 this study
Decay	Short	Blum & Christian, 1997	2.06	3	NPP=6.69
Decay	Tall	Blum, VCR/LTER Database	5.07	3	NPP=6.27 g N/m2/yr
Decay	Tall	Blum, VCR/LTER Database	2.05	3	NPP=2.99 g N/m2/yr
Decay	Tall	this study	3.07	3	%N=0.64 this study
Decay	Tall	Blum & Christian, 1997	1.2	3	NPP= 2.99
Denitrification	Short	Anderson et al, 1998	0.6	4	
Detritus formation	High	Buck, personal communication	2.05	3	%N=0.52 Hopkinson & Schubauer, 1984
Filter Feeding	Short	this study	4.13	1	biomass=0.26
Filter Feeding	Short	this study	0.01	1	biomass=0.26
Filter Feeding	Tall	this study	2.6	1	biomass=0.22
Filter Feeding	Tall	this study	0.01	1	biomass=0.22
Grazers	Short	this study		4	
Grazers	Short	this study	1.13	4	
Grazing	High	VCR 1998 All Scientist Meeting	0.27	2	used Tolley, 1996 data
Grazing	Short	VCR 1998 All Scientist Meeting	0.28	2	NPP=14 g N/m2/yr
Grazing	Tall	VCR 1998 All Scientist Meeting	0.35	2	NPP=17.58 g N/m2/yr
Leaching	High	this study	0.96	1	estimate from GS and SI
Leaching	Short	this study	0.62	1	estimate from GS and SI
Leaching	Tall	this study	0.82	1	estimate from GS and SI
Mineralization	High	Anderson et al, unpublished	13.27	4	
Mineralization	High	Anderson et al, 1997	9.99	4	
Mineralization	Short	Neirkirk, 1996	20.21	2	
Mineralization	Short	Anderson et al, 1998	84	4	
Nitrification	High	Anderson et al, unpublished	7.09	4	
Nitrification	High	Anderson et al, 1997	7.88	4	
Nitrification	High	Taylor, 1995	0	2	
Compartment	**Zone**	**Source**	**g N/m2yr**	**RF**	**Comments**
Nitrification	Short	Neirkirk, 1996	1.21	2	
Nitrification	Short	Anderson et al, 1998	4	4	
Nitrogen Fixation	Short	Anderson et al, 1998	1	4	

Pore NH4	High	Anderson et al, unpublished	0.11	4	
Pore NH4	High	Anderson et al, 1997	0.01	3	
Pore NH4	Short	this study	0.92	3	
Pore NH4	Tall	this study	0.18	3	
Pore NH4	Tall	http://www.vcrlter.virginia.edu/elecvol	0.04	3	
Pore NOx	High	Taylor, 1995	0.11	4	
Pore NOx	High	Anderson et al, unpublished	0.02	4	
Pore NOx	High	Anderson et al, 1997	0.01	3	
Precipitation	Total	Anderson et al, 1998	0.25	4	
Precipitation	Total	Anderson et al, 1998	0.18	4	
Precipitation	Total	Keene & Galloway, 1997	0.31	4	
Precipitation	Total	Keene & Galloway, 1997	0.15	4	
Sediment release of NH4	Short	Chambers et al, 1992	8.66	3	mean of given data
Sediment release of NOx	Short	Neirkirk, 1996	6.31	2	
Sediment uptake of NH4	Short	Neirkirk, 1996	0.41	2	
Sedimentation	Short	Anderson et al, 1998	1.25	4	
Standing Dead	High	Tolley, 1996	4.2	3	%N=0.52 Hopkinson & Schubauer, 1984
Standing Dead	High	Buck, personal communication	4.35	3	%N=0.52 Hopkinson & Schubauer, 1984
Standing Dead	Short	this study	3.93	3	%N=0.95 this study
Standing Dead	Tall	this study	4.17	3	%N=0.64 this study
Surface PN	Short	Neikirk, 1996	0.01	2	1 g C=2 g dw; C:N=5.5
Tidal Water Exchange	Tall	VCR/LTER Database	34.77	3	
Tidal Water Exchange	Tall	VCR/LTER Database	43.47	3	
Tidal Water Exchange	Tall	VCR/LTER Database	30.44	3	
Tidal Water Exchange	Tall	VCR/LTER Database	25.36	3	
Translocation	Short	Anderson et al, 1998	7	4	

APPENDIX G. BALANCED MODELS.

Standing Stock in g N x m^{-2}

Flows in g N x m^{-2} x yr^{-1}

The first column of numbers represents the averaged data obtained from literature. The balanced number column reflects the numbers used in the model after the model was balanced. The % difference represents the percentage the balanced number was changed from the original data inorder to balance the model.

The first column shows the flows from one compartment to another. For example, F1-2 is a flow from compartment 1 to compartment 2. F0-1 is an input to compartment 1, and F1-0 is an output from compartment 1.
F=flow
R=respiration