COMPETITIVE INTERACTIONS AND THE SPATIAL DISTRIBUTION OF CAREX LYNGBYEI AND SCIRPUS AMERICANUS IN A PACIFIC NORTHWEST BRACKISH TIDAL MARSH

by

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Scirpus Americanus In A Pacific Northwest Brackish Tidal Marsh

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Abstract

Zonal patterns of vegetation in brackish tidal marshes may be explained by Tilman's resource-ratio hypothesis, which proposes that spatial changes in plant dominance on nutrient gradients are controlled by resource competition for soil nitrogen and light. This hypothesis was evaluated by analyzing abiotic and biotic field data collected from a brackish tidal marsh on the Fraser River delta, British Columbia, and by performing manipulative experiments in the field and in common garden conditions.

The study site is dominated by two species which occupy distinct elevational domains in the upper intertidal zone. Elevations between -0.80 to 0.20 m (geodetic datum) are dominated by _Scirpus americanus_, while higher sites have communities dominated by _Carex lyngbyei_. Total soil nitrogen, standing crop, plant height, and shading of the soil surface were all found to be positively correlated to marsh platform elevation. These results suggest that _Scirpus americanus_ may be dominant in the low marsh because it is a better competitor for soil nitrogen. _Carex lyngbyei_ may be competitively dominant in the high marsh because its greater biomass and shoot height make it a superior competitor for light.

Shoot standing crops of both species increased significantly with increasing additions of nitrogen in field fertilization trials. Transplantation of both species at six different locations along the platform gradient revealed that both species are being competitively restricted in their spatial distribution by the presence of the other. Additional field experiments indicated that light competition is important in excluding Scirpus americanus from the high marsh Carex community, while below-ground competition by Scirpus americanus impedes Carex from establishing itself in low marsh sites.

Several results of this study, however, countered important predictions of the resource-ratio hypothesis causing the acceptance of an alternative hypothesis. Measurements of soil ammonium levels between communities suggested that the two species have equal abilities to consume limiting below-ground resources. The intensity of competition in the Scirpus community was found to be far weaker than predicted by the model. Biomass allocation patterns to shoot, rhizome, and root indicated that Carex lyngbyei should be a superior competitor for both above- and below-ground resources in the high marsh.

In conclusion, the zonal patterns of plant dominance observed at Brunswick Point are the result of evolutionary trade-offs caused by changes in soil nitrogen supply across the marsh platform. Soil nitrogen increases with elevation because tidal export of litter controls how much organic nitrogen is available for mineralization. Scirpus americanus dominates the nutrient-poor low marsh because it makes significant investment into the production of rhizomes which are used to conserve nitrogen losses from senescing tissues. This adaptation, however, comes with the cost of a lower investment into shoot and root tissues when compared to *Carex lyngbyei*, and results in a slower growth rate and smaller size in terms of biomass and shoot height. In the high marsh, the greater availability of soil nitrogen favors *Carex lyngbyei*, which invests this nutrient primarily to produce shoot and root tissues making this species a superior competitor for both above- and below-ground resources.

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CHAPTER 1

INTRODUCTION

1.1 Introduction

Tidal marshes are ideal communities for the investigation of theories concerning plant community dynamics and structure. These communities are quite simple systems, dominated by a few species which have the necessary adaptations to withstand the rigors of this environment (Chapman, 1974; Long and Mason, 1983). Common to most tidal marshes are zonal plant species patterns demarcated by elevation and inundation frequency thresholds on the marsh platform (Hinde, 1954; Adams, 1963; Nixon, 1982; Zedler, 1982; Vince and Snow, 1984; Lefor et al., 1987; Campbell and Bradfield, 1989; Bertness, 1991b; Pennings and Callaway, 1992).

A variety of factors can influence the distribution and abundance of plants in any community (Harper, 1977; Jefferies and Davy, 1979; Barbour et al., 1980; Crawley, 1986; Silvertown, 1987; Davy et al., 1988; Crawford, 1989). Most of the research work in tidal marsh habitats has focused on the way abiotic factors affect plant species distribution and abundance. For example, soil aeration (Mahall and Park, 1976c; Linthurst, 1979; Howes et al., 1981; Armstrong et al., 1985; Burdick and Mendelssohn, 1987), salinity (Cooper, 1982;

Dawe and White, 1982; 1986; Hutchinson, 1982; Snow and Vince, 1984; Ewing et al., 1989; Hellings and Gallagher, 1992; Pennings and Callaway, 1992), inundation frequency (Disraeli and Fonda, 1979; Dawe and White, 1982; 1986; Hutchinson, 1982; Hellings and Gallagher, 1992; Pennings and Callaway, 1992), disturbance (Bertness and Ellison, 1987; Ellison, 1987), soil drainage (Linthurst and Seneca, 1980; Mendelssohn and Seneca, 1980; Wiegert, Chalmers and Anderson, 1983), soil texture (Dawe and White, 1982; 1986), nutrient toxicity (Ingold and Havill, 1984; Mendelssohn and McKee, 1988; Koch and Mendelssohn, 1989) and nutrient limitation (Sullivan and Daiber, 1974; Valiela and Teal, 1974; Gallagher, 1975; Patrick and DeLaune, 1976; Mendelssohn, 1979b; Covin and Zedler, 1988) have all been suggested as important in controlling the distribution of plant species in tidal marsh habitats.

Other researchers have suggested that the elevational zonation of plant species on tidal marshes may be controlled to some degree by interspecific competition (Purer, 1942; Hinde, 1954; Pielou and Routledge, 1976; Zedler, 1977; Snow and Vince, 1984; Dawson and Bliss, 1987). Support for this hypothesis comes from a variety of observations and experimental tests. For example, observations of the upper and lower limits of species distribution have found contiguous distributional limits rather than random overlap in tidal marsh habitats (Pielou and Routledge, 1976; Zedler, 1977), while the results of transplant experiments have indicated that several species can survive outside their field limits (Stalter and Baston, 1969; Vince and Snow, 1984; Bertness and Ellison, 1987; Bertness, 1991a; 1991b; Pennings and Callaway, 1992). However, the strongest evidence for the occurrence of competition in these communities is derived from experimental studies that have manipulated the densities of competing species (Gray and Scott, 1977; Silander and Antonovics, 1982; Ellison, 1987; Covin and Zedler, 1988; Bertness, 1991a).

Several different models may explain plant zonation on tidal marshes. Figure 1.1 graphically displays these models, and compares them to a hypothetical observed tidal marsh field distribution pattern. In all of the models, the response of the plants along the elevation gradient is shown to be unimodal. Unimodal growth responses to abiotic gradients are quite common in natural vegetation (e.g., Whittaker, 1967; Grace and Wetzel, 1981; Pennings and Callaway, 1992), and are thus assumed to be common in tidal marsh plant communities.

The first model suggests that abiotic factors control the lower and upper limits of tidal marsh plant species (*Abiotic Model*). In this model, the observed field distribution mirrors the tolerance limits and growth response of the species to changing abiotic conditions along the marsh

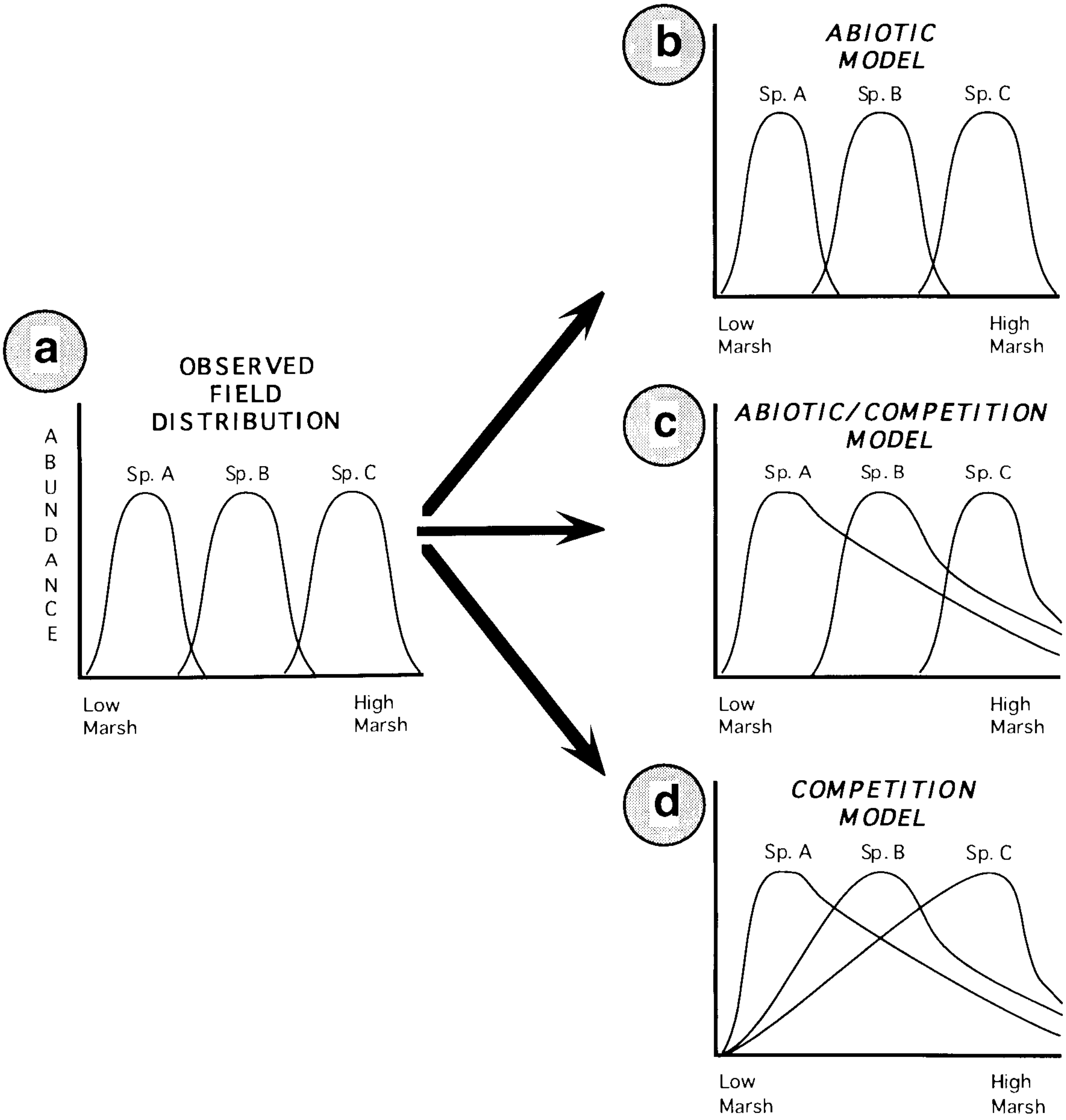

Figure 1.1. Explanatory models for elevational zonation of plants in tidal marshes. Graph "a" describes the observed abundance and field distribution of species A, B, and C. The model in graph "b" suggests that the observed abundance patterns are caused by a mirrored physiological response to abiotic factors. Model "c" proposes that abiotic factors control the lower limits of species distribution, while the upper limits are controlled by competition. Finally, model "d" indicates that for species B and C, both their upper and lower limits are set by competition.

platform. The second model suggests that the lower elevational limits of the dominant plants in tidal marshes is controlled by tolerances to harsh physical abiotic factors, while the upper limits are determined by competitive interactions (*Abiotic/Competition Model*). Competition is thought to be stronger in the upper limits of the plants' distributions because of a reduction in environmental stress (Pennings and Callaway, 1992). The findings of many researchers support this model for the explanation of tidal marsh plant zonation (Snow and Vince, 1984; Davy and Smith, 1985; Bertness and Ellison, 1987; Bertness, 1988; 1991a; 1991b). The final model proposes that the three dominant species are able to grow successfully across the entire marsh platform in the absence of the other species. It also suggests that competitive interactions exclude each species from the marginal regions of their possible field distribution and that the location of the border between species (Figure 1.1; A/B and B/C) is maintained by competition (*Competition Model*). Support for this model comes from the work of Pennings and Callaway (1992).

In summary, the first model suggests that the mechanism that controls the spatial pattern of plant species is physiological tolerance to abiotic factors. Physiological tolerance also controls the lower limits of the plants in the second model. In the latter two models, competition plays an important role in defining the position of the boundaries between the dominant plants. It is not clear, however, from these models which competitive "mechanism" leads to the spatial exclusion of the plant species involved.

Plant competition can be the result of mechanisms that involve the exploitation of limiting resources and/or physical interference via preemption of space (Tilman, 1982; Grace, 1987; Keddy, 1989). Most of the studies that claim to provide evidence for competition in tidal marsh plant communities incorporate techniques that only measure the "effects" of competition. There are, however, three exceptions in the research literature that do distinguish some of the competitive mechanisms that are responsible.

Covin and Zedler (1988) report that resource exploitation for soil nitrogen determined the competitive outcomes between Salicornia virginica and Spartina foliosa in a Californian salt marsh. Exploitation competition for limiting resources has also been reported in New England, where perennials out-competed the annual Salicornia europaea for light in disturbance-created patches in the low marsh (Ellison, 1987). Another study, in the same tidal marsh, suggested that interference by the dense root mats of Spartina patens inhibited the establishment of Spartina alterniflora in the high marsh community (Bertness and Ellison, 1987). Collectively, the results of these studies indicate that both exploitation and interference may play important roles in controlling tidal marsh plant population dynamics, local species patterns, and community structure.

The application of mechanistic approaches, that make use of individual-based theoretical models, to the investigation of problems dealing with community structure and dynamics is relatively new to ecology (Schoener, 1986). Recently, Tilman (1980; 1982; 1985; 1988; 1990a) has suggested that spatial and temporal patterns in some plant communities can be explained by a simple resource-based mechanistic model of plant competition. In this theory Tilman predicts: (1) that each species found in a plant community should be a superior competitor for a particular point along a soil nutrient: light gradient; and (2) that changes in the relative availability of these resources, either through time or space, should lead to changes in the composition of the community.

To date, support for Tilman's theory comes from general observations in several different community types (Tilman, 1982; 1988), and a number of descriptive and experimental studies in old-field habitats (Tilman, 1984; 1986a; 1987b; 1989; 1990b; Inouye et al., 1987; Tilman and Wedin, 1991a; 1991b; Wilson and Tilman, 1991; 1993). In general, these descriptive and experimental studies indicate that changes in species dominance in old-field plant communities are controlled primarily by the availability of soil nitrogen and by competition for this limiting soil resource and light.

Habitats low in soil nitrogen were found to be dominated, as theory predicted, by species that were superior competitors for soil nitrogen but poor competitors for light. In contrast, sites rich in soil nitrogen were dominated by species that were better competitors for light but poorer competitors for soil nitrogen. These studies also revealed, as suggested by theory, that changes in plant life history attributes would accompany changes in plant dominance. In nutrient-poor soils, the dominant plants were of smaller biomass and tended to allocate most of their photosynthate to the production of tissues used to gather the limiting soil resource. Species that were superior on nutrient-rich habitats were larger in biomass and were found to allocate a greater percentage of their fixed carbon into the production of tissues needed for the foraging of light.

To my knowledge there have been no published investigations of Tilman's ideas in tidal marsh communities, although Tilman (1986b) himself suggested that the existence of monospecific stands of Spartina alterniflora (a dominant species in marshes on the Atlantic coast) may result from its superior competitive ability for available soil nitrogen and light. By extension, elevational gradients of plant dominance in tidal marshes may be the result of changes in the spatial availability of soil nitrogen and competitive interactions involving this limiting soil resource and light. Soil nitrogen has frequently been shown to be the most limiting soil resource in tidal marsh plant communities (Sullivan and Daiber, 1974; Valiela and Teal, 1974; Gallagher, 1975; Patrick and DeLaune, 1976; Jefferies, 1977; Jefferies and Perkins, 1977; Mendelssohn, 1979b). Moreover, experimental manipulations in the field have revealed that this resource can control the competitive dominance of tidal marsh plant species (Covin and Zedler, 1988).

Spatial changes in plant competitive dominance on tidal marsh habitats may occur because the availability of soil nitrogen varies with elevation and inundation frequency of the tidal marsh platform. Tidal inundation influences the degree of aeration that occurs in the marsh soils, and aeration of the soil directly effects the cycling, storage and build-up of soil nitrogen (Ponnamperuma, 1984; Sprent, 1987). Anaerobic conditions decrease the rate of organic matter decomposition and suspend the conversion of organic nitrogen to inorganic nitrogen at the ammonium stage because these soil processes are primarily carried out by oxygen consuming organisms (Sprent, 1987). Inundation also influences the amount of organic and inorganic nitrogen that can accumulate in the marsh sediments. More frequent flooding increases the chance that tidal waters will carry away organic matter or inorganic ammonium (Valiela and Teal, 1974; 1979).

Figure 1.2 describes the resource-based competition hypothesis for tidal marsh plant zonation graphically for two

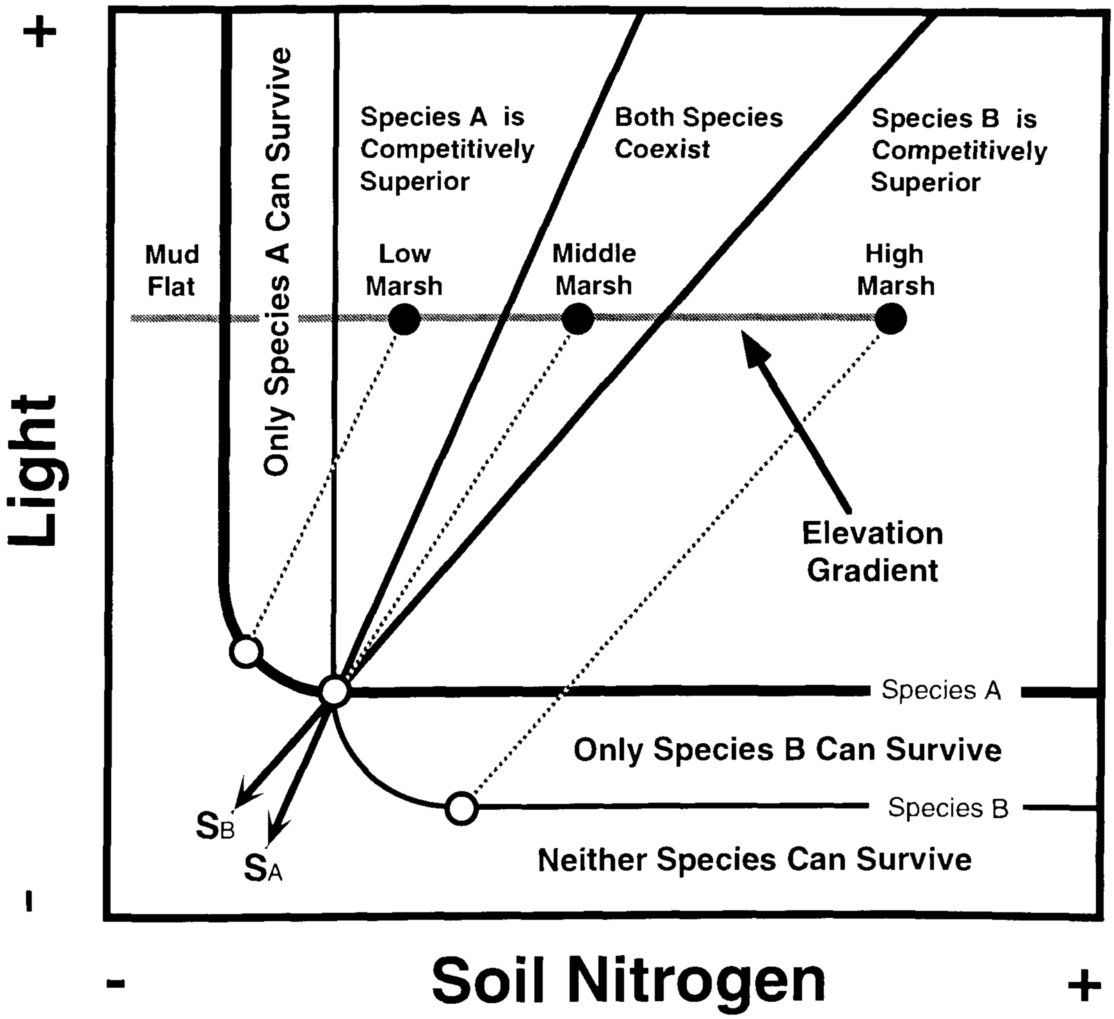

Figure 1.2. Hypothesized competition between two tidal marsh plants, Species A and B, for soil nitrogen and light (modified from Tilman, 1982). The zero net growth isoclines of both species (solid lines labeled species A and species B) delimit the necessary resource quantities required for survival and reproduction. The solid dots labeled "Low Marsh, Middle Marsh, and High Marsh" represent three hypothetical resource supply points along the habitat's elevation gradient before resource consumption. Consumption vectors for species A and B are shown with solid lines labeled SA and SB, respectively. Reduction of resource levels for each supply point by resource are illustrated with dotted lines. Open dots indicate the position of the supply points at equilibrium. The model suggests that species A has a lower requirement for nitrogen, and is predicted to competitively exclude species B from habitats where nitrogen is in short supply (Low Marsh). Species B has a lower requirement for light, and is predicted to displace species A in habitats where light is limiting to both species (High Marsh). The graph also shows that there are habitats where both species can coexist (Middle Marsh).

plant species with different requirements for soil nitrogen and light. The gray line on the illustration represents a gradient of nitrogen availability from the mid-tidal mud-flat, through the low marsh, to the high marsh zone. The black dots on the model represent resource supply points for three locations along this elevational gradient. The dotted lines from these points to the open dots located on the zero net growth isoclines of the two plant species trace resource consumption. The position of the isoclines of the two plants indicates that species A is a better competitor for soil nitrogen, and is predicted to out-compete species B in low marsh habitats where this resource is in short supply. Species B is predicted to be superior in habitats where soil nitrogen is in greater supply because it requires less light for survival. In the high marsh habitat, the greater availability of soil nitrogen would allow species B to accumulate more above-ground biomass than species A. Further, this greater accumulation of above-ground biomass by species B leads to the reduction of canopy light levels and the exclusion of species A by light reduction.

1.2 Objectives

The general objective of this study is to evaluate the application of Tilman's (1982; 1988) theories of plant competition and community structure to the zonal patterns of plant distribution found in tidal marshes. To test this hypothesis a brackish tidal marsh located at Brunswick Point, British Columbia was selected as a study site. A brackish tidal marsh was favored over a more saline marsh because the plants of this habitat are less influenced by the severe environmental effects of salinity and toxic cations (Odum, 1988). This consideration should simplify the interpretation of the results of measurements and experiments used in this study to test the suitability of Tilman's models to explain tidal marsh plant zonation.

The Brunswick Point marsh exhibits typical zonal patterns of plant distribution correlated with particular elevations on the intertidal platform. Moreover, the structure of the plant community found at Brunswick Point is common to many other brackish tidal marshes in the Pacific Northwest (Disraeli and Fonda, 1979; Hutchinson, 1982; 1988). In this marsh only two species tend to dominate, *Carex lyngbyei* in upper marsh sites and *Scirpus americanus* in the lower marsh sites (from now on referred to as high and low marsh).

According to the model developed in Figure 1.2 the spatial change in species dominance at the Brunswick Point tidal marsh is caused by an elevational gradient variation in soil nitrogen supply. *Scirpus americanus* dominates the low marsh because it is better adapted to compete for soil nitrogen when the supply of this resource is low. *Scirpus* *americanus* should also possesses certain life history attributes that are associated with its better below-ground competitive abilities (Tilman, 1982; 1988). These attributes would normally include small size, sensitivity to canopy light reduction, and greater biomass allocation to structures that aid in the efficient acquisition of soil nitrogen. On the other hand, *Carex lyngbyei* is dominant in the high marsh because it possesses attributes that make best use of higher levels of soil nitrogen. These attributes include larger size, greater photosynthetic efficiency, and greater biomass allocation to structures that aid in the acquisition of light. *Carex lyngbyei* cannot out-compete *Scirpus americanus* in the low marsh because it is less efficient at acquiring soil nitrogen. In the high marsh, greater soil nitrogen availability permits *Carex lyngbyei* to allocate more photosynthate to the production of above-ground tissues used to out-compete *Scirpus americanus* for light.

To test these ideas, descriptive and experimental methodologies were employed at Brunswick Point. These methods were intended to verify the predictions of the model developed here and to provide answers to the following more specific questions:

(1) Are the present distributional limits of *Scirpus americanus* and *Carex lyngbyei* controlled by abiotic factors, a combination of abiotic factors and competition, or just competition?

(2) Does the elevation gradient at Brunswick Point represent a gradient in the availability of soil nitrogen?

(3) Are the two dominant species limited in their growth by soil nitrogen, and could the efficient consumption of this resource by *Scirpus americanus* be responsible for the exclusion of *Carex lyngbyei* in the low marsh?

(4) Do light levels at the soil surface differ under the foliage of two dominant species, and could light reduction be responsible for the competitive exclusion of *Scirpus americanus* from the sites dominated by *Carex lyngbyei*?

(5) Are there any differences in life-history attributes between *Scirpus americanus* and *Carex lyngbyei* that would make them competitively superior in their particular habitats as predicted by Tilman (1982; 1988)?

CHAPTER 2

LITERATURE REVIEW

2.1 Definition of Interspecific Competition

Ecologists have recognized a number of different types of interactions that occur between populations of different species. These different interactions can be classified in simple terms according to the effect one species has on another species (Williamson, 1972; Abrams, 1987; Arthur and Mitchell, 1989). In this classification scheme, interspecific competition is defined as an interaction that has a negative effect on the equilibrium population size of both species.

Many verbal definitions have been proposed for interspecific competition (e.g., Harper , 1961; Milne, 1961; Miller, 1967; Pianka, 1981; Tilman, 1982; Begon, Harper, and Townsend, 1986; Arthur, 1987; Keddy, 1989; Grace and Tilman, 1990). The simplest of these are operational, concentrating on the phenomenological responses of the individuals to this interaction (Arthur, 1987). In this type of definition, competition is defined in terms of the direction of effect each species has on the other's population. The advantage of this type of definition is that it is verbally equivalent to the well-known Lotka-Volterra model of competition. Abrams (1987) has argued, however, that this type of definition of competition is ambiguous, because it fails to recognize a variety of interaction mechanisms that are not competitive in nature (e.g., Holt, 1977; Connell, 1990). To remedy this problem, Abrams (1987) suggests that interactions like competition should be described quantitatively in mathematical models.

Several definitions of plant competition exist that specifically emphasize the mechanisms by which this interaction operates in nature (Harper, 1961; Miller, 1967; Grime, 1979; Tilman, 1982; 1988; 1990a; Keddy, 1989). Keddy (1989: p. 2) defined competition as "the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability". The reference to resource limitation, as the mechanism by which one species affects another, makes this definition more precise than the operational definition. Further, this definition suggests that resource limitation can be the result of two somewhat distinct processes: exploitation and interference (Miller, 1967; Pianka, 1981; Keddy, 1989).

Competition by exploitation occurs between neighboring plant individuals when utilization of resources by the plants reduces the supply of these resources below some limiting threshold (Tilman, 1980; 1982; 1988; 1990a; Keddy, 1989). Resource exploitation, however, does not always cause the exclusion of a species from a community. The exclusion of one organism by another can only occur when one organism can survive below the limiting resource threshold of the other.

Competition by interference occurs when an individual directly prevents the physical establishment of another individual in its immediate vicinity (Keddy, 1989). Established plants can preempt the invasion and colonization of other individuals by way of dense root mats (Friedman, 1971; Bertness and Ellison, 1987), peat and litter accumulation (Werner, 1975; Grubb, 1977; Grime, 1979; Bertness, 1988), and mechanical abrasion (Putz et al., 1984; Rebertus, 1988). Interference can also result from the release of toxic allelopathic substances (Muller et al., 1968; Whittaker and Feeny, 1971; Rice 1974; 1979; Williamson, 1990).

As previously mentioned, the effects of certain species interactions can be mistakenly interpreted as being caused by competitive processes (Holt, 1977; 1984; Bender et al., 1984; Abrams, 1987; Connell, 1990; Louda, Keeler, and Holt, 1990). For example, using a simple mathematical model, Holt (1977; 1984) described a case where the effects of interspecific interactions involving predation or pathogenic attack may be apparently mistaken as competition. In addition, Connell (1990) has suggested that apparent competition can also arise from positive interactions among species.

2.2 Theoretical Models of Competition

Understanding how competition influences plant dynamics and community structure can be enhanced through simple models which employ mathematical equations for precision (Lotka, 1932; Tilman, 1982; 1988; 1990a). With these models we can examine the effect certain parameters have on species interactions through time. The following sections will describe Tilman's resource-based mechanistic model of plant competition.

2.2.1 Competition for One Resource

Tilman (1980; 1982) has proposed a mathematical model of two or more species competition which utilizes a resource-based mechanistic approach. This model differs from the traditional Lotka-Volterra model because it explicitly considers the precise mechanisms behind plant competitive interactions. The Lotka-Volterra model summarizes the effects of competitive interactions in a few descriptive parameters termed competition coefficients. The exact value of a competition coefficient depends on the type of resource, the consumption characteristics of the plant species, and the processes governing the supply of the resource to the plant (Tilman, 1982). In most studies, competition coefficients are estimated from the change in the population density of the competing species over a certain time period in controlled situations (Gause, 1932). Thus, the competition coefficients in the Lotka-Volterra model only describe the circumstance of the interaction, and do not directly measure the mechanisms responsible for competition. In Tilman's model, however, mathematical parameters describing resource consumption and supply are included in the competition equation allowing the researcher to better understand the exact mechanisms of species interaction.

Essentially, the resource-based mechanistic model of plant competition requires estimates of only two parameters. Under equilibrium conditions, the dynamics and long-term outcome of plant competition can be predicted, theoretically, from information describing the resource requirements of the interacting species and the supply rate of the resource (Tilman, 1982). Competitive displacement occurs when the limiting resource is depressed to a specific threshold level.

Mathematically mechanistic competition among several species for one resource can be described with a model based on the Monod (1950) equation. The Monod equation is used because it is a good approximation of the actual growth rate of many species (Tilman, 1982). When two or more species interact for one limiting resource as defined by the Monod equation, the competition model is written as follows:

$$dNi/Ni\ dt = riR\ /(R + ki) - mi\ ; \qquad i = 1,2,...,n$$

$$dR/dt = g(R) - \sum_{i=1}^{n} (dNi/dt + miNi)/hi \;;$$

where the subscript i refers to species-i, R is the quantity of the limiting resource, ri is the maximal growth rate ($dN/N\ dt$) asymptotically reached by species-i, ki the half saturation constant for species-i (or the resource availability at which growth reaches half of the maximal growth rate), mi is the mortality rate for species-i, hi is the number of individuals a unit of resource produces, Ni is the population size of species-i, and $g(R)$ controls the dynamics of resource renewal and depletion in the absence of species. This discussion, however, will use graphical models for the explanation of this theory. Further mathematical treatment of these ideas can be found in Tilman (1982).

The mechanistic model is best illustrated graphically by first considering the interaction of a single plant species with a single limiting resource (Figure 2.1(a)). In this graph a resource-dependent population curve and a line representing per capita mortality rate (m) are drawn for species A. The intersection point of these two curves determines the quantity of resource R* at which reproductive rate equals the mortality rate. If this species enters a habitat where the quantity of the limiting resource is greater than R*, its population density will increase until the level of the resource in the habitat is reduced to R*

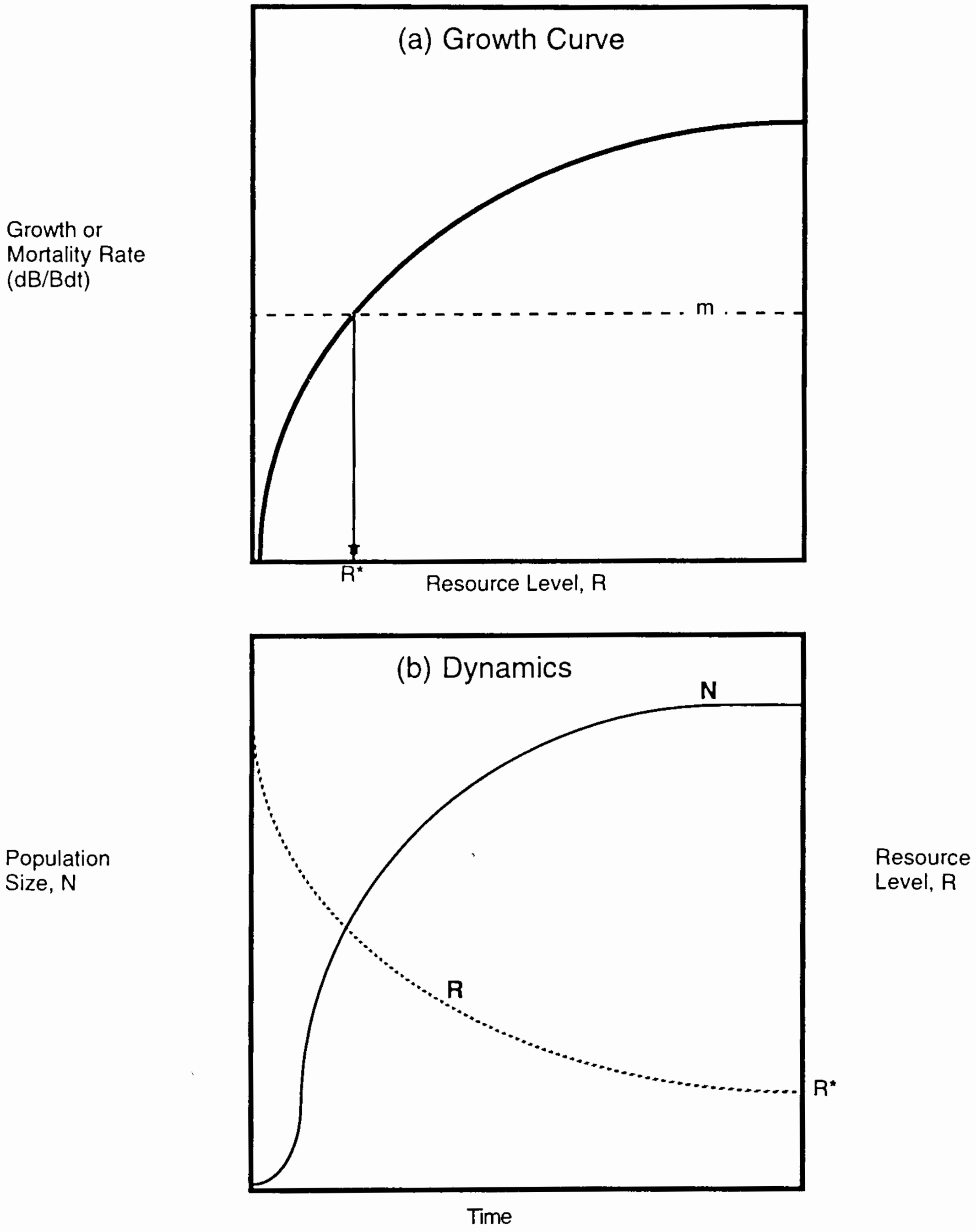

Figure 2.1. On graph (a) the solid curve illustrates the relationship between per capita growth rate and resource availability. The dashed line labeled m indicates the mortality rate experienced by the species. The intersection of these two lines is R*. R* describes the amount of resource R required by the species to maintain an equilibrium population. Graph (b) shows the population dynamics of the species under hypothetical conditions. The population reaches equilibrium population density when the resource level becomes R*. Modified from Tilman (1982).

(Figure 2.1(b)). This point represents a stable equilibrium, the state where the supply rate of the limiting resource equals the consumption rate.

Figure 2.2 presents a case of interspecific competition utilizing the resource-based mechanistic model (Tilman, 1982). In this figure, species A has a higher R* than species B (Figure 2.2(a)). If both species invade a habitat where the level of the limiting resource is higher than R^*_A, both species will increase in population density (Figure 2.2(b)). As the density of species A and B increases, the quantity of the limiting resource will decrease. When the resource is depressed to R^*_A, the population of species A will stop growing, while the population of species B will continue to increase. The continued increase in the population size of species B will cause the resource level to continue dropping until it reaches R^*_B. At this point there will be not enough resource available to support an equilibrium population of species A, and with time species A will be competitively displaced by species B.

The competitive exclusion of one species, when two or more species are competitively interacting for the same limiting resource, occurs when one of the species has a lower minimal resource requirement R* than the other species (O'Brien 1974; Tilman, 1976; Hsu et al., 1977; Armstrong and

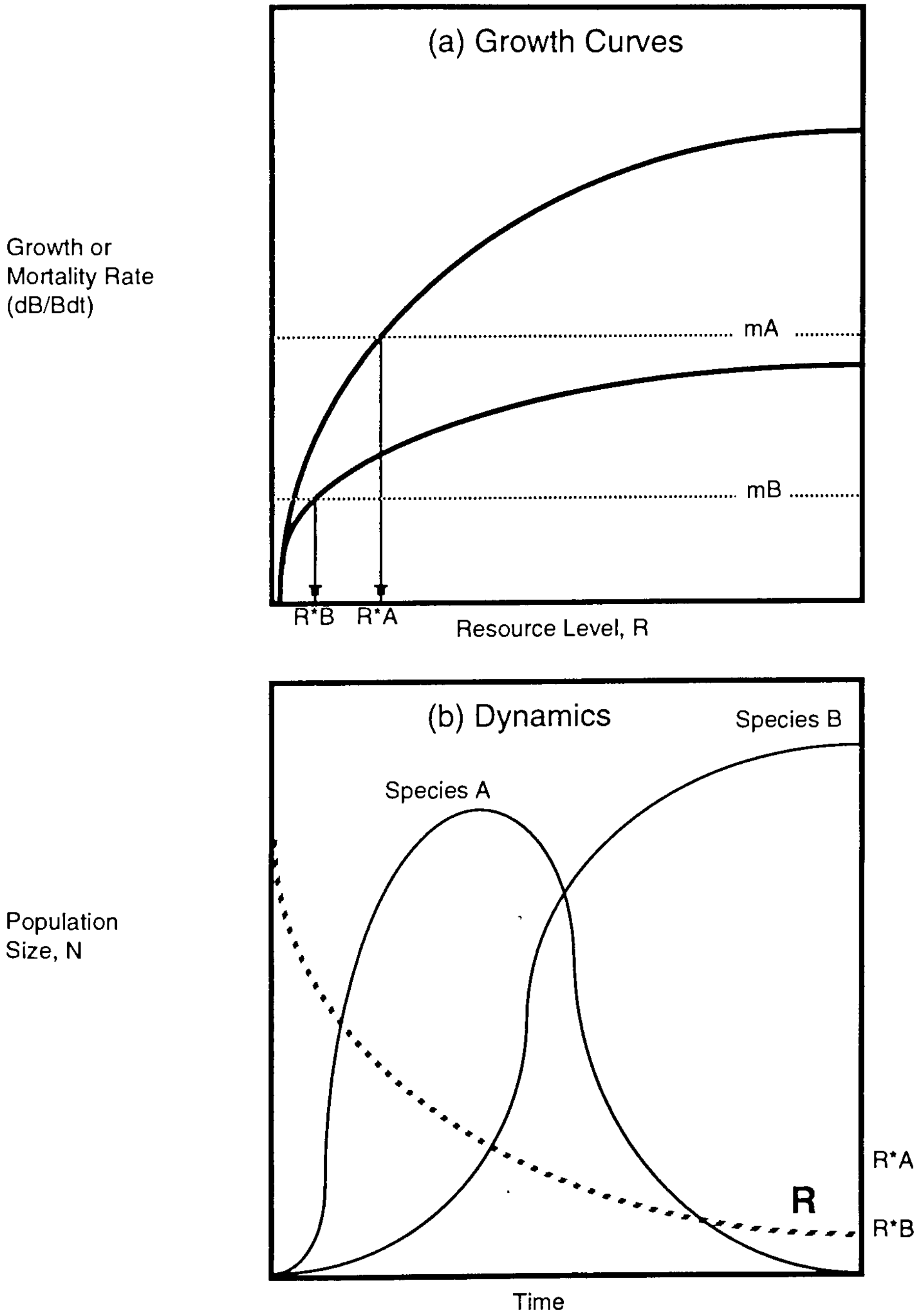

Figure 2.2. In graph (a), the resource dependent growth curves are drawn for species A and B. The lines labeled mA and mB illustrate the mortality rates for species A and B. The equilibrium resource requirement of these species are R*A and R*B. Graph (b) describes the dynamics of interspecific competition between these two species. The dashed line labeled R shows the reduction of the limiting resource with time. In this graph, species B excludes species A because R*B < R*A. Modified from Tilman (1982).

McGehee, 1980). If the species all have the same minimal resource requirement coexistence will occur.

2.2.2 Competition for Two or More Resources

The theoretical model just described for mechanistic plant competition can be extended for situations where two or more resources are consumed by two or more species (Tilman, 1980; 1982). This theoretical approach is an extension of the pioneering work of MacArthur (1972), Maguire (1973), Leon and Tumpson (1975), Petersen (1975), Taylor and Williams (1975) and Abrosov (1975). The extended model also describes how changes in the availability of just two resources can lead to changes in species dominance or result in two species being able to coexist. Application of this theory to natural plant communities suggests that along a quantity gradient of a limiting soil resource, changes in species dominance, plant biomass and height, and the availability of light at the soil surface will be observed (Tilman, 1982; 1986b; 1988). Plants that are superior competitors at a particular point along this soil nutrient gradient will also possess certain physiological and morphological adaptations necessary for competitive dominance (Tilman, 1988).

Tilman's model of competition for two or more resources can be described by the following differential equations (Pacala, 1989):

$$dNi/dt = Ni[fi(\mathbf{R}) - mi] \; ; \qquad i = 1,2,\ldots,Q$$

$$dRj/dt = gj(Rj) - \sum_{i=1}^{Q} Nifi(\mathbf{R})\, hij(\mathbf{R}) \; ; \qquad j = 1,2,\ldots,k$$

where Ni is the density of plant species-i, Rj is the mean concentration of resource j, $\mathbf{R}$ is the row vector (R1,...Rk), $fi(\mathbf{R})$ and mi are, respectively, the birth and death rates of species-i, $gj(Rj)$ governs the dynamics of resource renewal and depletion in the absence of plants, and $hij(\mathbf{R})$ gives the amount of resource j required to produce a new species-i plant. Once again, this discussion will use graphical models for the explanation of this theory. These ideas are more thoroughly addressed mathematically in Tilman (1980; 1982).

We begin by first considering the interaction of a single species on two limiting resources (Figure 2.3). On this graph the "zero net growth isocline" defines the dynamic population response of the species to the interactively essential resources X and Y (Tilman, 1982; 1988). The graphical placement of the two line segments that make up the isocline are determined by the R* levels for the two resources. At the zero net growth isocline the population's deaths and births balance each other out over time. In the area where resource quantities are greater than those of the zero net growth isocline, the population will increase in density until the resource levels are reduced, through

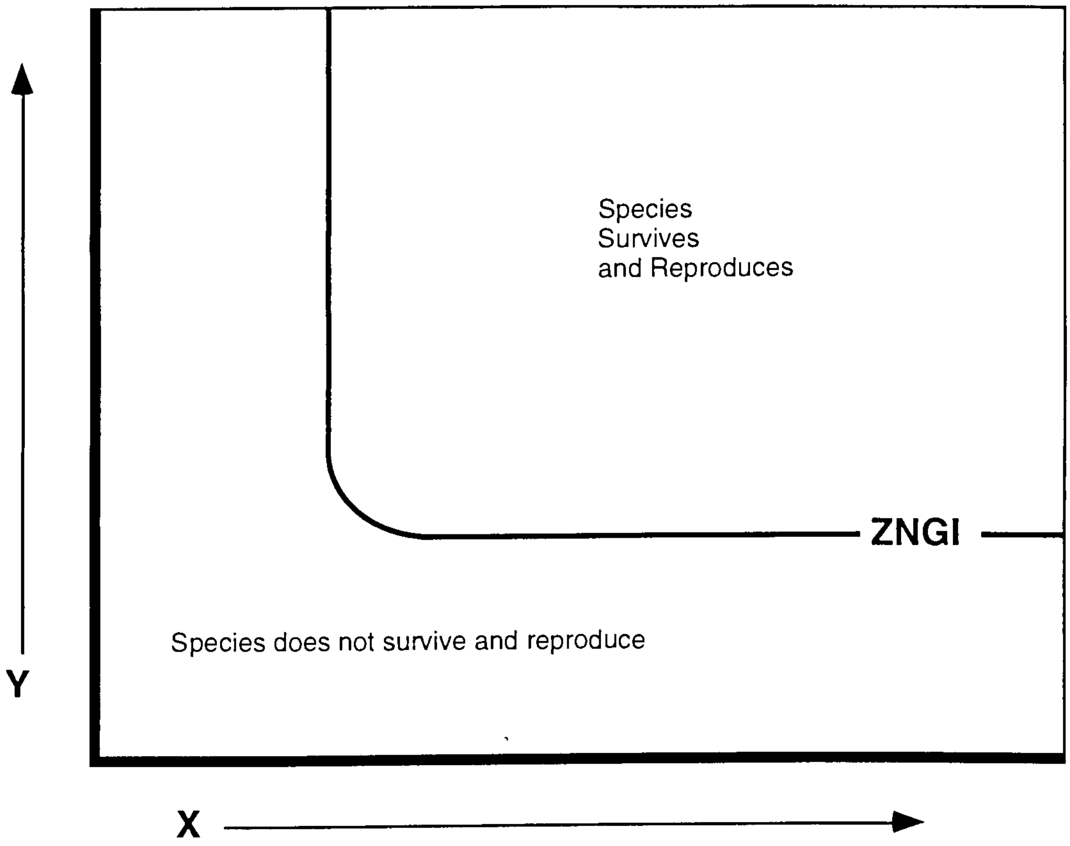

Figure 2.3. Graphical model showing the abundance of two resources (X and Y) and the zero net growth isocline (ZNGI) of a species. The ZNGI divides the hypothetical region where the species can survive and reproduce, and the region where it can not. The rounded corner on the isocline indicates that the two resources modeled in this graph are interactively essential and the plants have foraging plasticity (Tilman, 1988). Modified from Tilman (1982; 1988).

consumption, to a point located somewhere on the isocline. A population cannot exist in the area where resource quantities are lower than the zero net growth isocline because resource quantities are too low for survival.

Tilman (1980; 1982) suggests that the actual level of a resource in a habitat is controlled by consumption and supply (Figure 2.4). In all habitats resources are being constantly renewed to some abiotic level. This constant renewal can be represented hypothetically on Figure 2.4 as the "supply point". Any species, however, existing in this habitat will consume the resources it requires to maintain growth and reproduction. Resource consumption can be represented on the graph by consumption vectors, which describe the path that species-mediated resource depletion takes to the zero net growth isocline. If this species is removed the consumption vectors will become supply vectors until equilibrium is attained back at the supply point. The slope of the consumption vector is determined by the optimal ratio of resources X and Y the species requires for growth (Rapport, 1971; Tilman, 1982).

Superimposing the isoclines and consumption vectors of two species can produce four different competitive interactions. Each interaction has various outcomes determined by the placement of the supply point in graphical space. Figure 2.5 describes two of these interactions. In

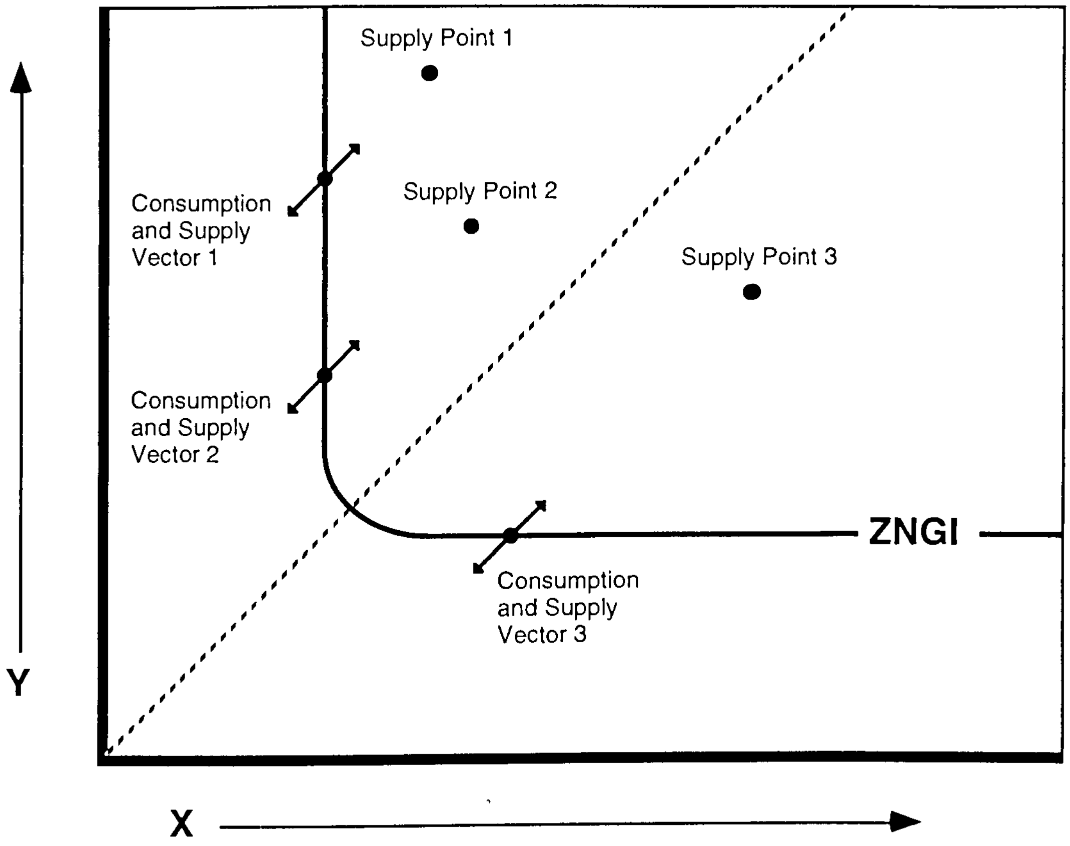

Figure 2.4. Graphic model describing the interaction of consumption and supply vectors on various supply points and the zero net growth isocline (ZNGI). The dashed line indicates the optimal consumption ratio of resources X and Y for this particular species. The three consumption and supply vectors show the hypothetical paths of resource reduction by species consumption. These vectors are parallel to the line representing the optimal consumption ratio. Modified from Tilman (1982; 1988).

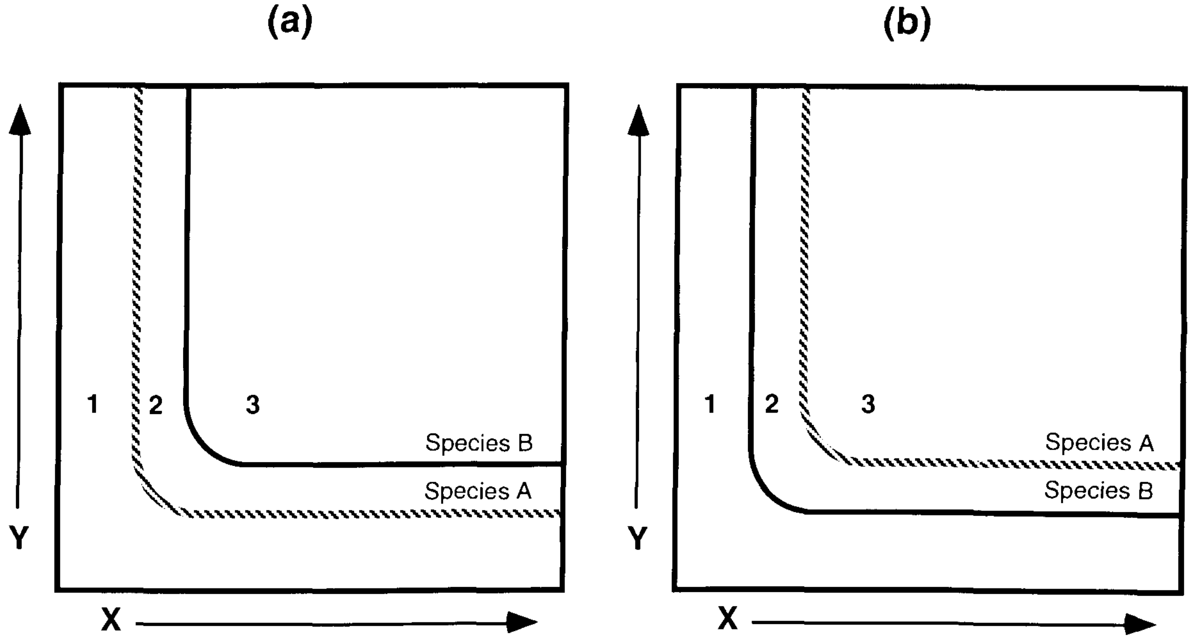

Figure 2.5. In graph (a), the zero net growth isocline (ZNGI) of species A is inside the ZNGI of species B. This condition will result in species A being able to survive successfully in lower quantities of the resources X and Y than species B. For a supply point in region 3, resource consumption will cause species A to reduce resource levels to a point below that required for the survival of species B. Species B can only survive in this region if it is allowed to grow by itself. A supply point in region 2 will have sufficient resources to only support species A. Both species A and B are unable to survive in region 1 because of scarcity of the necessary resources for growth. In graph (b), the positions of the two ZNGI are reversed from graph (a). Now species B is the dominant in region 3 in two species mixtures. In region 2 there are sufficient quantities of the two resources to allow only species B to survive. Finally, as in graph (a), neither species will be able to survive in region 1 because of insufficient resources. Modified from Tilman (1982; 1988).

graph (a) species A will competitively exclude species B in regions 2 and 3. This outcome is predicted because the zero net growth isocline of species B is outside that of species A. Thus, species A will be able to reduce the levels of resources X and Y to a level below that required for species B to survive. In region 1 neither species can exist because of insufficient resource quantities. Graph (b) illustrates a case where the zero net growth isocline of species B is now on the inside of species A. The competitive outcomes are, therefore, reversed, and species B is now the competitive winner in regions 2 and 3. In both of these cases the slope of the consumption vectors has no effect on the competitive outcome. Figure 2.6 describes a case of interspecific competition where coexistence is possible. Stable coexistence will only occur when each species consumes more of the resource which limits its own growth. This causes each species to inhibit its own growth more than it inhibits the growth of the other species (Tilman, 1980; 1982). In other words intraspecific competition is greater that interspecific competition for the two species. The condition just described can be identified on the graph by the relative placement of the consumption vectors (Figure 2.6).

In Figure 2.6, both species cannot exist in region 1 because resource quantities are below their zero net growth isoclines. A point in region 2 would only allow species A to exist, because resource quantities are too low for the

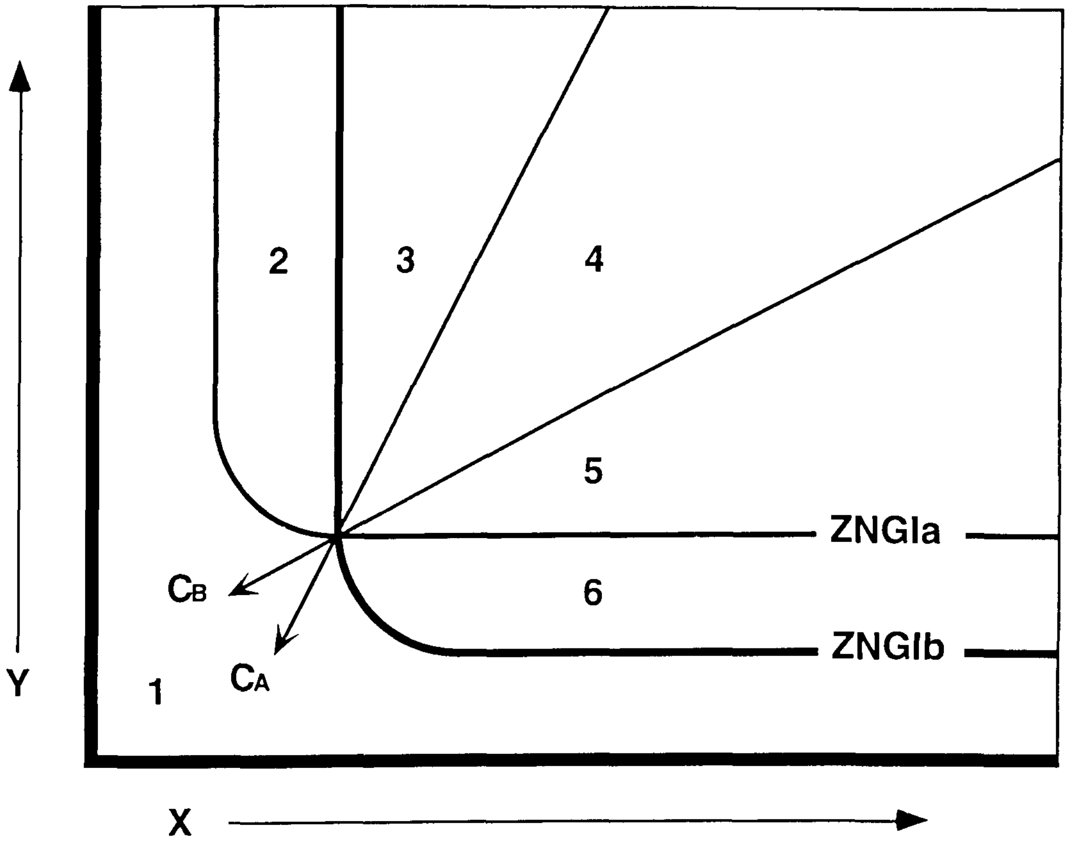

Figure 2.6. Zero net growth isoclines of species A (ZNGIa) and species B (ZNGIb) are described graphically in a situation where coexistence is possible. The placement of the isoclines indicate that species A is most limited by resource Y, while species B is most limited by resource X. Consumption vectors are illustrated for species A (CA) and B (CB). Both consumption vectors show that the two species consume more of the resource which most limits their growth and reproduction per unit time. For example, the consumption vector of species A (CA) is much steeper than that of species B (CB) suggesting that species A consumes more resource Y than species B. The overlapping zero net growth isoclines and consumption vectors of the two species produce six different regions of environment/species interaction. Supply points in region 1 result in neither species surviving. In region 2 species A can successfully reproduce and survive, but the level of resource X in this region is too low for species B. A supply point in region 3 results in species A excluding species B by reducing the level of resource X to the left of the isocline of species B. Supply points in 5 have the opposite outcome, and in this region species B is the competitive winner. In region 6 species B can reproduce and survive, but the level of resource Y in this region is too low for species A. Supply points in region 4 result in stable coexistence between the two species. See text for further discussion. Modified from Tilman (1982; 1988).

survival of species B (below species B's zero net growth isocline). Likewise, a supply point in region 6 would only allow species B to exist, because resource quantities are too low for the population of species A (below species A's zero net growth isocline). In region 3 both species are limited primarily by resource X. However, species A consumes proportionally more resource Y than resource X then species B. This condition causes any supply point in this region to be reduced parallel to the consumption vector C_A. Given time the supply point will equilibrate on species A's zero net growth isocline causing the competitive exclusion of species B. In region 5 both species are limited primarily by resource Y. Further, species B consumes proportionally more resource X than resource Y then species A. This condition causes any supply point in this region to be reduced parallel to the consumption vector C_B. With time the supply point will equilibrate on the zero net growth isocline of species B causing the competitive exclusion of species A. In region 4 both species coexist because the consumption of resources X and Y by species A and B equilibrates at the intersection of the two zero net growth isoclines.

A case where the equilibrium point is locally unstable is illustrated in Figure 2.7. Unstable equilibrium occurs when each species consumes more of the resource which most limits the growth of the other species. As a result each species inhibits the growth of the other species through

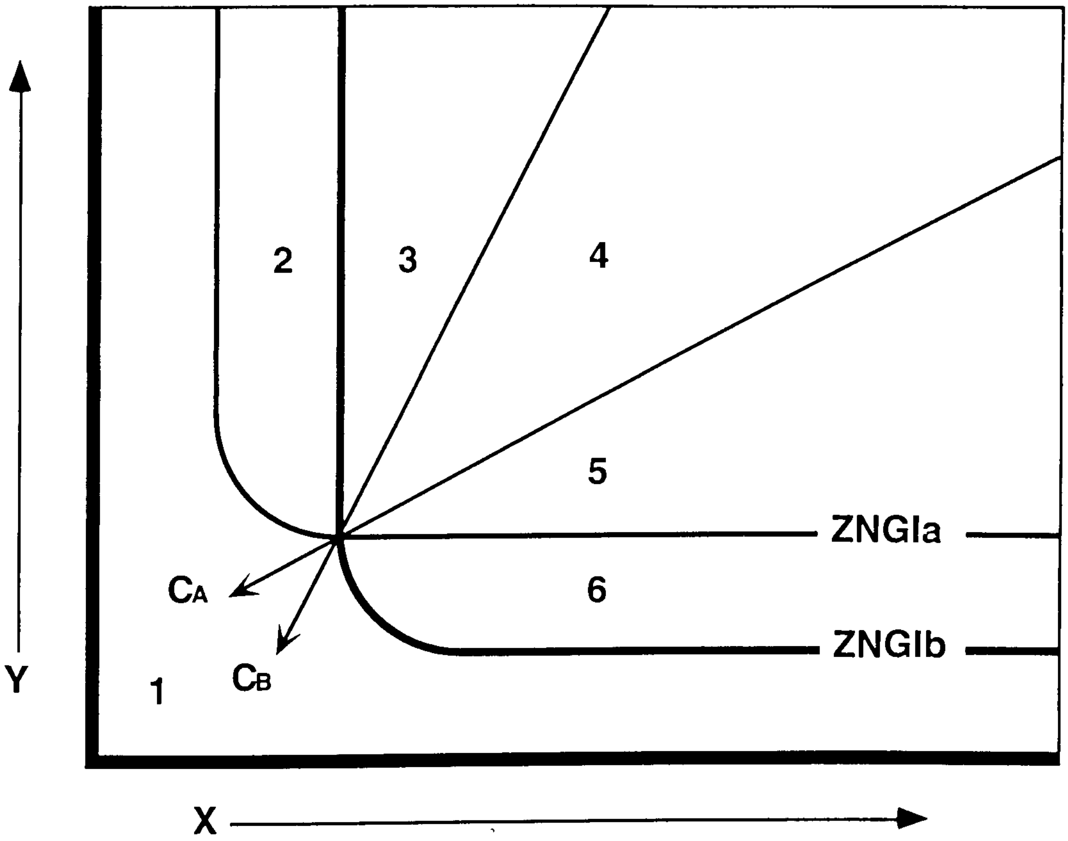

Figure 2.7. Zero net growth isoclines of species A (ZNGIa) and species B (ZNGIb) are described graphically in a unstable equilibrium situation. The position of the isoclines reveal that species A is most limited by resource Y, and species B is most limited by resource X. Consumption vectors are illustrated for species A (CA) and B (CB). These vectors indicate that each species consumes more of the resource which most limits the growth and reproduction of the other species. The position of the overlapping zero net growth isoclines and consumption vectors of the two species produce six different regions of environment/species interaction. Supply points in region 1, 2, 3, 5 and 6 have the same outcomes as described in the stable equilibrium case (Figure 2.6). Supply points in region 4 result in only one species surviving depending on its exact location. See text for further discussion. Modified from Tilman (1982; 1988).

consumption. Expressed in another way, interspecific competition is greater than intraspecific competition. This condition can be identified graphically by observing the placement of the consumption vectors of the two competing species (Figure 2.7).

Supply points located in regions 1, 2 and 6 of Figure 2.7 have the same outcome as in the stable equilibrium case in Figure 2.6. In region 3 both species are limited chiefly by resource X. However, species B consumes proportionally more resource Y than resource X then species A. This state causes any supply point located in this region to be reduced parallel to the consumption vector C_B. With time the supply point will equilibrate on species A's zero net growth isocline resulting in the competitive exclusion of species B. In region 5 both species are limited primarily by resource Y. Additionally, species A consumes proportionally more resource X than resource Y then species B. This situation causes any supply point in this region to be diminished parallel to the consumption vector C_A. Given enough time the supply point will equilibrate somewhere on the zero net growth isocline of species B inducing the competitive exclusion of species B. The outcome of a supply point located in region 4 is conditionally unstable because of the slope of the two consumption vectors. Thus, either species can win depending on the position of the supply point within this region.

When actual limiting resources like light and soil nitrogen, the two most limiting resources in the majority of terrestrial plant ecosystems (Harper, 1977; Tilman, 1988), are substituted for resources X and Y the theoretical outcomes just described can be modeled for natural plant communities (Tilman, 1988). Figure 2.8 describes four species each with different minimal requirements for light and soil nitrogen. Superimposing an environmental gradient of increasing soil nitrogen and constant potential light availability on this graph reveals that species dominance changes along this line. Theoretically, habitats that are low in soil nitrogen are dominated by species that are relatively better competitors for nitrogen than light. On the other end of this gradient, the dominant plant species will be better competitors for light rather than nitrogen. Resource consumption causes the reduction of both resources parallel to the optimal consumption vector as population densities increase. At equilibrium the availability of light will decrease with increasing supply of soil nitrogen.

Observations in natural and manipulated plant communities indicate that changes in species dominance do accompany increases in the supply of soil nitrogen (Tilman, 1984; 1987b). They also reveal that along this gradient there are general changes in the life history attributes of the plants (Tilman, 1986b; 1988). On nitrogen-poor soils, plants can maintain only a small total biomass. Further, to

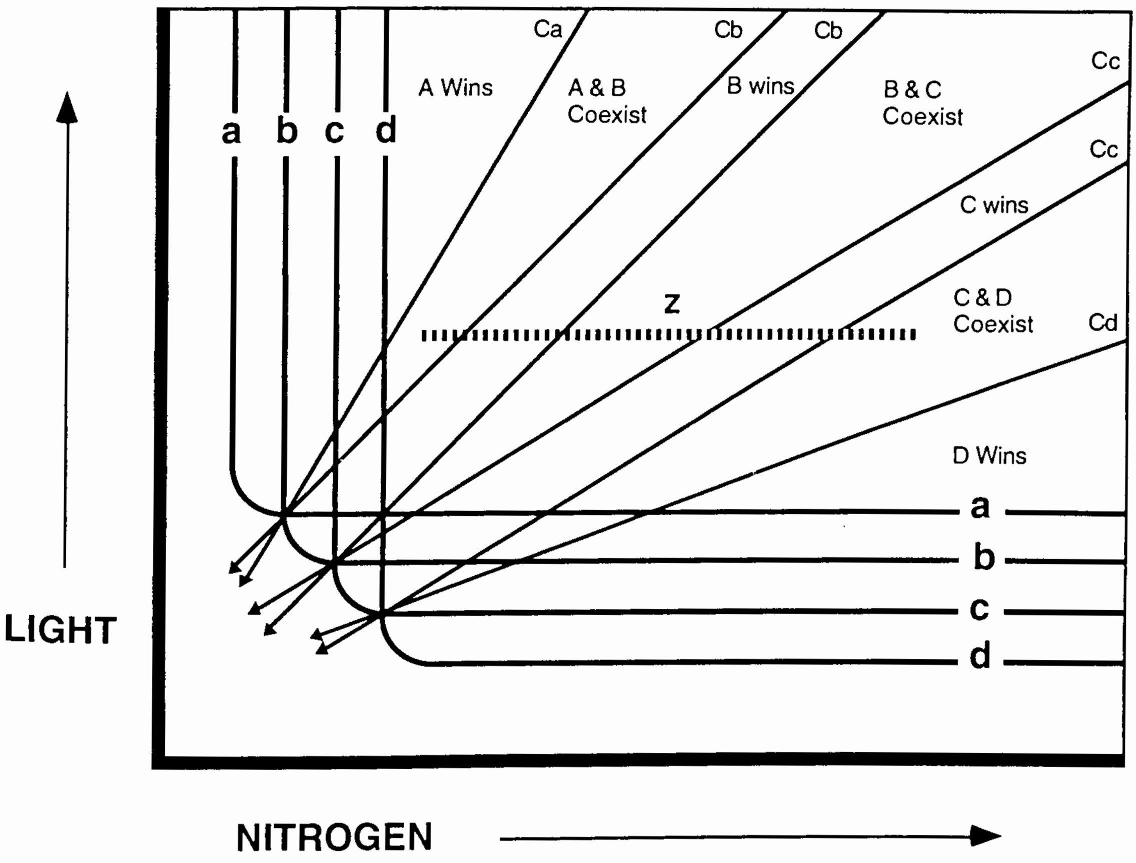

Figure 2.8. This resource diagram illustrates competition between four plant species (A, B, C, and D) for soil nitrogen and light in a stable equilibrium situation. The line "Z" represents a environmental gradient of increasing soil nitrogen and constant available light at initial gradient conditions. Zero net growth isoclines are identified for each species by lower case letters. Equilibrium points occur at the intersection of the four consumption vectors of the interacting species (Ca, Cb, Cc, and Cd). The location of these points indicate that the availability of light at equilibrium decreases with increasing initial soil nitrogen levels along the gradient. Competitive outcomes are also shown in the seven different regions of environment/species interaction.

be competitively superior these plants must allocate more growth to below-ground structures which aid in the acquisition of this limiting resource. Plants growing in nitrogen-rich soils maintain, relatively, a higher biomass. This increase in biomass also favors the greater production of above-ground structures and photosynthetic tissues. However, competitive superiority is now not primarily controlled by the plant's ability to acquire soil nitrogen. Instead, light becomes more limiting because the increase in foliage reduces the availability of this resource to overcrowded photosynthetically active leaves. To overcome this limitation, the plant that is a superior competitor in this habitat will allocate a greater proportion of its energy to a stem which lifts its leaf canopy above the competition.

In summary, the pattern of species replacement along a gradient of increasing soil nitrogen is dependent on the ability of species to compete for limiting soil and light resources. Habitats low in soil resources will be dominated with plants that are superior competitors for soil resources but poor competitors for light. These plants will be morphologically short in stature, small in size, and require only small quantities of soil nitrogen for survival. As the quantity of soil nitrogen increases along the gradient subsequent changes in species composition and morphology will also occur. Habitats high in soil resources will be dominated with plants that are superior competitors for light resources but poor competitors for soil resources. These species require more soil nitrogen to attain the greater height and biomass growth necessary for their survival. The dominance of these larger plants will also lower the level of light available to shorter plants growing beneath the canopy resulting in their competitive exclusion.

Tilman has derived a simple graphical model of plant competition that allows the prediction of the outcomes of consumer-resource interactions. The model only requires information on species resource preferences and consumption rates, and the resource supply rates of the habitat. Tilman's model differs from the model proposed by Lotka-Volterra in that it is resource-based and mechanistic. These two features allow the researcher to better understand the relationship between habitat resources and species interactions.

2.3 The Resource Ratio Hypothesis

The resource isocline approach of Tilman's competition theory is also capable of explaining the patchy pattern of species distribution commonly observed in natural vegetation (Tilman, 1982), and temporal changes in species abundance and composition during the course of succession (Tilman, 1985). Both of these situations are explained by modeling the habitat supply point as a series of points with various ratios of limiting resources that vary either spatially or temporally.

The theory presented so far has examined competition between two species for two limiting resources in which the outcome was predicted in a spatially homogeneous habitat (e.g., one given supply point). Field observations, however, indicate most natural habitats contain more than two species. These observations also reveal that habitats are more likely to be composed of a collection of heterogeneous patches of varying quantities of resources. We can explain these two situations, in relation to Tilman's competition model, by first considering the interaction of four species on two limiting resources (Figure 2.8). The isoclines and consumption vectors of the four plants indicate that each species requires different minimal quantities of the two resources to survive and reproduce. They also reveal that the competitive outcome of a particular supply point is determined by its exact location on the resource diagram. Figure 2.8 suggests that we can expect seven different possible competitive outcomes in this model.

Next, if we imagine a habitat as a collection of heterogeneous patches, each patch would have a supply point with a unique location on the resource diagram describing the ratio of resources available for consumption. The location of this point also determines which plants will be the winners and losers in species competition. Thus, for spatially heterogeneous habitats the supply point is not a single point on the resource diagram, but a resource supply region describing resource quantity variations across habitat space. Figure 2.9 describes a patchy habitat where four species competing for only two resources can coexist because of spatial heterogeneity of the limiting resources.

Long-term successional patterns observed in plant communities may also be the result of interspecific competition for limiting resources (Tilman, 1985). Tilman suggests the species composition at any stage of succession is strongly influenced by the position of the habitat supply point along the soil resource:light gradient (the resource ratio hypothesis of succession). In this model, succession begins with plants that are superior competitors for soil resources but poor competitors for light. These plants are morphologically short in stature, small in size, and require only small amounts of soil resource for survival. The supply point at this stage reflects a habitat which is low in soil resource, but high in the light resource. With time the level of soil resource increases allowing taller and larger species to become the dominant species of this community. These species require more soil resource but less light for survival, and can competitively exclude the shorter species through light reduction. The dominance of these larger species lowers the level of light available in the habitat. Thus, at this point in the succession the supply point of the

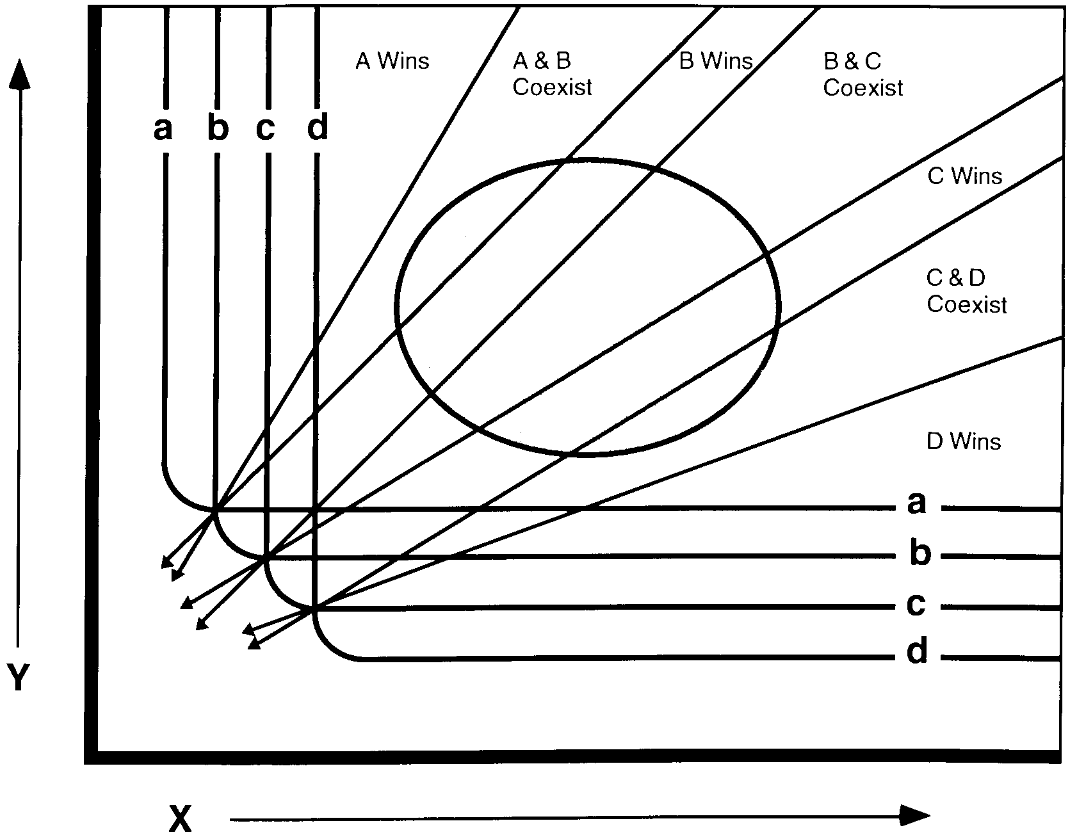

Figure 2.9. The following graph models interspecific competition in a habitat composed of a collection of heterogeneous patches. Spatial heterogeneity in the supply rates of the resources is illustrated by the "shaded" oval resource supply region. The situation modeled in this graph could allow all four species to coexist in this habitat.

habitat is high in soil resource, but low in the light resource. This entire sequence suggests that during succession the supply point of the habitat gradually changes from a resource ratio of low soil resource:high light to high soil resource:low light. In summary, the pattern of species replacement during succession is dependent on the increase in soil resources, and the ability of species to compete for soil and light resources.

Verification of the predictions presented in the resource ratio hypothesis of succession have come from descriptive and experimental studies in old-field habitats undergoing secondary succession (Tilman, 1986a; 1987a; 1990b; Inouye et al., 1987). Data from twenty-two abandoned old-fields of various ages indicated that nitrogen levels in the soil increase significantly with time (Inouye et al., 1987). Further, this increase in soil nitrogen was accompanied by a change in the species composition and a reduction in the availability of light at the soil surface. Generally, the change in dominant plants was from short, superior nitrogen competing species to taller, superior light competing species.

2.4 Plant Traits and Competitive Ability

Many plant ecologists have attempted to categorize which plant morphological and physiological attributes (plant traits) give one species a competitive advantage over another species (Gadgil and Solbrig, 1972; Grime, 1977; 1979; Chapin, 1980; Tilman, 1982; 1986b; 1988; 1990a; Berendse and Aerts, 1987; Chapin et al., 1987; Gaudet and Keddy, 1988; Berendse and Elberse, 1990b; Goldberg, 1990; Grace, 1990; Keddy, 1990; Goldberg and Landa, 1991; Berendse, Elberse and Geerts, 1992; Keddy, 1992; Aerts and van der Peijl, 1993). At present, there is no consensus on what factors determine which species will be a successful competitor under various habitat conditions (Grace, 1990; Goldberg, 1990). In this section, I will review the debate on this subject outlining some of the major theories and their predictions.

One of the first attempts to categorize the different strategies of organisms was based on the idea of r- and K-selection (MacArthur 1962; MacArthur and Wilson, 1967). In this theory, the basic traits of r- and K-strategists are the consequence of the proportional allocation of biomass and resources to reproductive and nonreproductive tissues and activities (Pianka, 1970; Gadgil and Solbrig, 1972). Allocation patterns are in turn controlled by the intensity of environmental disturbance. On this continuum, a r-strategist matures quickly, devotes a large fraction of their photosynthate to reproductive structures, and occupies repeatedly disturbed habitats. Further, the high rate of disturbance in the habitat of the r-strategists causes the population size of this species to be density-independent.

On the other hand, a K-strategist occupies equilibrium habitats, lives a long life, and allocates a small proportion of their biomass to reproduction. The population size of these species is density-dependent, and biotic interactions like competition play an important role in the regulation of their population size. Several researchers, however, have stated reservations concerning the general validity of the theory of r- and K-selection (Wilbur et al., 1974; Grubb, 1976; Moore, 1978; Grime, 1977; 1979).

Grime (1977; 1979) extended the plant strategy model based on r and K-strategies by introducing "stress" as another forcing mechanism on plant evolution. More specifically, Grime suggested that natural gradients of disturbance and stress limit the quantity of living plant material that can be present in any habitat. Accordingly, in environments where the intensity of stress and disturbance are low, competitive plants evolve and dominate. The characteristics or traits of these plants include a high maximum relative growth rate (RGR_{max}), the potential to produce a tall dense leaf canopy and a large root surface area, and the capacity for quick morphogenetic adjustments in the allocation of biomass to the production and spatial distribution of roots and shoots (Grime, 1979).

Under habitat conditions of low stress and high disturbance ruderals are dominant. Ruderals have an annual or short-lived perennial life-cycle that enables them to exploit the rapidly changing character of frequently disturbed habitats. Generally, they also have the capacity for high rates of biomass production with a large proportion of the biomass being allocated to seed production. A high number of seeds per plant are needed to ensure the germination of individuals in future disturbance created habitat gaps.

Finally, in habitats of high stress and low disturbance the dominant plants take on a stress-tolerating strategy. In these plants biomass production is constrained by a shortage or a surplus of certain environmental factors like water, light, heat, and mineral nutrients. To overcome deficiencies of these factors, plants with this strategy have a low maximum relative growth rate (RGR_{max}). Plants of the stress-tolerating strategy also possess specific morphological and physiological adaptations that allow them to persist in a stressful habitat. These traits can include an evergreen habit, long-lived organs, infrequent flowering, and low morphogenetic plasticity (Grime, 1979).

In summary, Grime's model can be reduced to the following two hypotheses: (1) that competition declines in importance and intensity in plant communities with increasing intensities of stress and disturbance and (2) that the different traits observed in plant species are associated with the evolution of discrete and predictable strategies for survival (Grime, 1988; Campbell and Grime, 1992). Certain empirical evidence for this model generally agrees with its conclusions (Grime, 1977; Shipley et al., 1989; Campbell and Grime, 1992). However, significant competitive effects can occur between species in unproductive habitats (Fowler, 1986; Chapin, McGraw and Shaver, 1989; McGraw and Chapin, 1989). As a result of these and other similar findings, researchers have suggested that declining soil fertility only alters the nature of competition from above- to below-ground (Newman, 1973; Tilman, 1988). In closing, the appropriateness of Grime's plant strategy model is still being debated.

As mentioned previously, several researchers have suggested that plants can compete in nutrient-stressed environments (Fowler, 1986; Chapin, McGraw and Shaver, 1989; McGraw and Chapin, 1989). Plants that survive and compete in these habitats should respond to nutrient stress in basically the same way. In general, this may include adaptations that either aid in capturing resources in short supply or adaptations that allow the plant to tolerate low resource availability (Chapin, 1980; Berendse and Aerts, 1987; Chapin et al., 1990; Chapin, 1991). In an intensive review of the literature, Chapin (1980; 1991) compared the traits of herbaceous crops from fertile habitats to similar wild plants from nutrient-poor habitats. His general findings are that plants from nutrient-poor habitats have the following attributes:

(1). Species from infertile environments tend to have a lower nutrient absorption rates per plant when compared to fertile crop species. This results in slow growth rates for these species even when they are provided with an optimal supply and balance of resources. Combined with this slow growth rate is a low capacity to extract needed resources.

(2). Root:shoot ratios tend to be higher in plants from infertile habitats. This may, however, be partially a phenotypic response to low nutrient availability.

(3). Many studies have shown that mycorrhizal associations are vital in nutrition of plants growing in infertile habitats. These associations reduce the energy expended by the plant to gather nutrients that are diffused slowly from the soil solution.

(4). Nutrient absorption in infertile habitats is often confined to times of sudden nutrient flush rather than steady-state availability during the growing season. To make best use of this phenomenon infertile plants are adapted to take up nutrients rapidly during cyclical nutrient flushes (e.g., spring increase in microbial activity, decomposition and mineralization of nitrogen).

Tilman's (1980; 1982) model of plant competition, reviewed earlier, suggests that the species with the minimum resource requirement (R*) will be the superior competitor in interspecific interactions under equilibrium conditions. This model also makes specific predictions regarding plant traits and competitive abilities on a primary level (Tilman, 1982). A recent extension of this basic theory to size-structured populations (Tilman, 1988) now examines the life histories and morphologies of higher plants and their competitive abilities in terms of photosynthate allocation to roots, stems, leaves, and seeds. This extension of Tilman's theories, however, makes different predictions than Grime (1979) and Chapin (1980; 1991) concerning growth rate and plant competitive superiority. Tilman (1988) believes that plants found in nutrient-poor habitats should have a relatively higher RGR_{max} when compared to species from nutrient-rich habitats. He makes this prediction, because his model suggests that nutrient-poor plant species make a greater investment in the production of roots which absorb soil nutrients. Greater absorption then leads to higher soil nutrient uptake and plant growth rates. Plants from nutrient -rich habitats are predicted to have a low RGR_{max} because much of their photosynthate is allocated to the production of structures for light foraging rather than soil nutrient foraging.

As in the case of Tilman's initial model (1982) of simple mechanistic competition for two resources, the revised hypothesis (1988) focuses on the universal need of land-based plants to forage for both below- and above-ground resources. It also suggests that a physical separation occurs between soil and light resources, and that this separation causes tradeoffs in photosynthate allocation patterns in the plant. Further, to obtain a higher proportion of one of these two resources a plant must allocate more photosynthate to the production of structures that can capture that resource. As a tradeoff, structures that are used to forage for the other resource suffer, and obtain proportionally less photosynthate for their construction and operation.

Comparison of the theories of Grime and Tilman indicates apparent discords in their predictions about what traits contribute to competitive superiority (Thompson, 1987; Tilman, 1987c; Thompson and Grime, 1988; Grace, 1990). Several papers have suggested that the re-defining of the competition terminology associated with these theories may correct for some of the discrepancies (Tilman, 1987c; Thompson, 1987; Thompson and Grime, 1988; Grace, 1990; Goldberg and Landa, 1991; Grace, 1993a). Thompson (1987) has suggested that the disagreements between the theories of Tilman and Grime arise from their different definitions of competition. Grime's (1977; 1979) model suggests that the species with the highest maximal growth rate will be the superior competitor because he defines competition as the ability of an *individual* to maximize resource capture. On the other hand, Tilman (1982; 1988) defines competition as the ability of a *population* to lower resource levels under equilibrium conditions, and thus proposes that the most superior species in a habitat will have the lowest R*.

The different definitions of plant competition are, however, only one of the contrasts between the theories of Tilman and Grime. The two authors also have divergent ideas about what evolutionary traits allow plants to be competitively superior in nutrient-rich and nutrient-poor habitats (Tilman, 1987c; Grace, 1990). Tilman (1982; 1988) suggests that nutrient-poor habitats are dominated by species that possess attributes that make them superior competitors for below-ground resources, while species in nutrient-rich habitats allocate more biomass to structures that enhance competition for light. In contrast, Grime (1979) proposes that productive habitats are dominated by plants that have evolved traits that make them superior competitors for both above- and below-ground resources. In unproductive habitats, evolution, according to Grime, has selected for non-competitive stress-tolerant plants who have reduced abilities to capture resources. These plants instead invest in strategies that allow them to tolerate low-resource quantities. At present the attempts of empirical studies to resolve this argument have been confusing as both theories are confirmed and refuted repeatedly (Tilman, 1984; 1986a; 1987b; 1991; Inouye et al., 1987; Aerts and Berendse, 1988; Shipley and Keddy, 1988; Campbell and Grime, 1989; 1992; Chapin, McGraw and Shaver, 1989; McGraw and Chapin, 1989; Aerts, 1990; Aerts et al., 1990; Gleeson and Tilman, 1990; Shipley and Peters, 1990; Tilman and Wedin, 1991a; 1991b;

Wilson and Tilman, 1991; 1993; Aerts, de Clauwe and Konings, 1992; Berendse, Elberse and Geerts, 1992; Turkington et al., 1993). Some of the confusion generated by the results of these studies may have occurred because: (1) several different measures of competition were used; (2) the experiments were run over variable time periods and habitat types; (3) only a limited number of species were examined; and (4) many different experimental designs were used. The results may also indicate that both Grime and Tilman have imperfect accounts of how plants compete.

Goldberg (1990) has suggested that the disparity between Tilman's and Grime's predictions is the result of both authors having an incomplete picture of how plant competition actually operates. She suggests that competition between plants can occur in two ways: in their competitive "effect" or ability to suppress other individuals (Grime's resource capture model) and in their competitive "response" or ability to avoid being suppressed (Tilman's R*) (Goldberg, 1990). Despite this identification of two types of competitive ability, most researchers studying plant competition have rarely taken this distinction into account (Tilman, 1984; 1986a; 1987b; 1991; Inouye et al., 1987; Shipley and Keddy, 1988; Campbell and Grime, 1989; 1992; Tilman and Wedin, 1991a; 1991b; Wilson and Tilman, 1991; 1993).

Recently, Goldberg and Landa (1991) investigated the role of competitive effect and response with seven herbaceous plants common in old fields. In a greenhouse experiment, an additive experimental design was used for all combinations of the plants as both target and neighbor species to test if there were uniform hierarchies in competitive effect and/or response and to determine if specific plant traits decided their hierarchical position. After five weeks of growth, consistent hierarchies were discovered for both competitive effect and response. As for traits, strong effect competitors were found to have larger maximum potential mass and a larger seed mass than response competitors when the plants were compared per-plant. Per-gram comparisons suggested that strong effect competitors had a higher maximum relative growth rate.

In the Netherlands, Berendse and Aerts (1987) and others (Aerts, 1990; Berendse and Elberse, 1990a; 1990b; Lambers and Poorter, 1992; Aerts and van der Peijl, 1993) have examined the role plant traits have in determining competitive superiority in species from habitats of contrasting fertility. They suggest, like Grime (1979) and Chapin (1980; 1991), that selection in nutrient-poor habitats is for plant attributes which reduce nutrient losses rather than to maximize the rate of nutrient acquisition. It is also suggested that plants from nutrient-rich habitats have evolved attributes that are negatively correlated to the attributes of plants dominant in nutrient-poor habitats (Poorter, 1990; Poorter and Remkes, 1990; Poorter et al., 1990; Poorter and Lambers, 1991; Lambers and Poorter, 1992). In short, these plants have adaptations that assist in the rapid capture of above- and below-ground resources resulting in a higher potential growth rate and a high nutrient loss rate from tissues (Lambers and Poorter, 1992).

The theory just described has been tested in a three-year field study of plant dominance in heathlands (Aerts and Berendse, 1988; Aerts and Berendse, 1988; 1989; Aerts, 1989; Aerts et al., 1990; Berendse and Elberse, 1990a; 1990b) and in a study that examined the success of Festuca rubra and Arrhenatherum elatius in a manipulated grassland ecosystem (Berendse and Elberse, 1990a; 1990b; Berendse, Elberse, and Geerts, 1992). The results of these studies did suggest that plants adapted to nutrient-poor habitats conserve nutrients better and have a poorer ability to capture above- and below-ground resources. The studies also suggest that the dominance of these species in nutrient-poor habitats is related to their ability to conserve captured below-ground resources. Fertilization of these nutrient-poor habitats resulted in the competitive exclusion of the resident species by plants that had a higher growth rate and a higher nutrient loss rate (Berendse and Elberse, 1990a; 1990b; Berendse, Elberse and Geerts, 1992). Competitive exclusion was the result of above- and below-ground competition. These results do not verify Tilman's (1988) prediction that plants adapt to nutrient-poor environments by allocating a higher proportion of their biomass to roots. They do, however, support the ideas of Grime (1979) and Chapin (1980).

Finally, many researchers have shown that the simple plant traits of height and biomass are significantly correlated to a plant's competitive ability (Clements, 1933; Goldsmith, 1978; Mitchley and Grubb, 1986; Wilson and Keddy, 1986; Gaudet and Keddy, 1988; Keddy and Shipley, 1989; Goldberg and Landa, 1991).

2.5 Factors Affecting the Distribution and Abundance of Tidal Marsh Plants

2.5.1 Physiological Tolerance

The community of plants that live in coastal marsh environments is exposed to a cycle of periodic inundation by water of varying degrees of salinity. In the extreme, these plants have to be adapted to survive stresses such as high soil solution salinities, mechanical injury by waves and flowing water, temperature shock of inundating waters, reductions in photoperiod, and soil waterlogging (Long and Mason, 1983; Crawford, 1989; Adam, 1990).

Research on the ecology of coastal marsh vegetation has primarily examined the role that soil salinity and tidal inundation have on plant distribution and abundance. The salinity of the pore water in tidal marsh soils can vary from fresh to values greatly exceeding that of sea water (Chapman, 1974; Odum, 1988). In some cases, hypersalinity and the development of salt pans may completely prevent the establishment of vegetation (Thom et al., 1975; Butler, et al., 1981).

Ecologists and physiologists have been studying the effects of salinity on plants for many years. From this research it is now possible to provide an overview of the various adaptations halophytes have made for survival (see Waisel, 1972; Reimold and Queen, 1974; Flowers et al., 1977; Greenway and Munns, 1980; Wainwright, 1980; Jefferies and Rudmik, 1984; Flowers, 1985; Osmond et al., 1987; Crawford, 1989; Adam, 1990). In general, the manner in which plants survive exposure to high amounts of salt varies with the way the salt enters vegetative tissues (Crawford, 1989). If the salt is deposited on the foliage and stems, plants tend to reduce uptake by exclusion and secretion processes. In conditions where the salt is located in the soil solution, plants tend to have adaptations that allow them to survive in osmotic equilibrium with these concentrations.

The maximum growth rate of tidal marsh plants under greenhouse or common garden conditions with experimentally varied salinity treatments varies with species, with most plants growing best in non-saline conditions (Cooper, 1982; Drake and Ungar, 1989; Ewing et al., 1989; Hellings and Gallagher, 1992). A few species, however, like Juncus gerardii and Salicornia europaea have been found to grow best in saline environments (Rozema and Blom, 1977; Cooper, 1982). These findings suggest that variation in growth response to salinity can be responsible for spatial variations in species dominance when soil salinity changes with the elevation of the tidal marsh platform (Mahall and Park, 1976b; Cooper, 1982; Earle and Kershaw, 1989).

Beare and Zedler (1987) have discovered that the salinity tolerance of Typha domingensis varies with life-cycle stage. Typha domingensis is commonly found growing in Californian tidal marshes with seasonally variable soil salinity. However, the seeds and seedlings of this species were found to be extremely sensitive to salt, while rhizomes tend to be salt tolerant. These findings may explain why invasion of Typha domingensis to new sites only occurs during prolonged periods of low soil salinity.

Anaerobic soil conditions impose two different types of stress on marsh plants (Ponnamperuma, 1984; Crawford, 1989). Firstly, flooding reduces the amount of oxygen found within the soil pores which is used for root and rhizome metabolism. Secondly, reducing conditions in the soil produce toxic products like ferrous and manganous ions, and sulphides. Plants growing in wetland soils avoid the effects of anaerobiosis by transporting oxygen from shoots where it is abundant to the roots, by switching to anaerobic metabolism or by developing roots in unsaturated soil horizons (Armstrong, 1978; Osmond et al., 1987; Crawford, 1989).

The most common adaptation that wetland plants possess to allow them to grow in waterlogged habitats is the presence of aerenchyma (Crawford, 1989; Adam, 1990). Aerenchyma connect the tissues of roots and rhizomes through a network of intercellular spaces to stomata located on above-ground organs. In non-wetland plants the volume of intercellular spaces is approximately 2-7 %, which is inadequate for oxygen diffusion to below-ground organs (Armstrong, 1978; 1979; 1982). In contrast, plants growing in anaerobic wetland conditions have up to 60% of their volume as pore space.

Anaerobic conditions in flooded soils also give rise to the formation of several reduced cations that are potentially toxic to plants. Sulphides have been shown to decrease plant yields in laboratory experiments and correlative field studies (King et al., 1982; DeLaune, Smith and Patrick, 1983; Ingold and Havill, 1984; Havill et al., 1985; Mendelssohn and McKee, 1988; Bradley and Dunn, 1989; Koch and Mendelssohn, 1989). Some species (e.g., Spartina cynosuroides and Salicornia europaea), however, have higher tolerances to sulphides than others (e.g., Spartina alterniflora, Atriplex patula, Festuca rubra, Puccinellia maritima, and Borrichia frutescens), which may explain the field distribution of these species in relation to sulphide concentration gradients (Ingold and Havill, 1984; Bradley and Dunn, 1989). Similar findings have also been documented for anaerobically-reduced forms of iron and manganese (Rozema, Luppes, and Broekman, 1985; Singer and Havill, 1985).

Of all the nutrients required by wetland plants nitrogen has been found to be the most limiting (Sullivan and Daiber, 1974; Valiela and Teal, 1974; Gallagher, 1975; Patrick and DeLaune, 1976; Jefferies, 1977; Jefferies and Perkins, 1977; Mendelssohn, 1979b; Covin and Zedler, 1988). Ammonium is the primary form of soil nitrogen consumed by wetland plants because anaerobic conditions inhibit nitrification (Ponnamperuma, 1984; Sprent, 1987). Several researchers, however, have noted that both hypoxia and sulphides may reduce plant growth by affecting ammonium uptake (King et al., 1982; DeLaune et al., 1983; Morris and Dacy, 1984; Mendelssohn and McKee, 1988; Bradley and Dunn, 1989; Koch and Mendelssohn, 1989). Bradley and Morris (1990) tested this hypothesis in a laboratory culture experiment where the effects of sulphide and oxygen concentration were examined on the ammonium uptake kinetics of _Spartina alterniflora_. Both factors were found to reduce nitrogen uptake significantly. Bradley and Morris (1990) also suggest that declines in plant growth due to salt stress may also be related to nitrogen uptake and plant metabolism. This hypothesis is based on the disclosure that salinity stress causes _Spartina alterniflora_ to accumulate nitrogen-containing osmotica (Cavalieri and Huang, 1981).

2.5.2 Disturbance

Pickett and White (1985) define disturbance as "... any discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." In tidal marshes, common disturbances include the removal of vegetation by grazers, wave erosion, extreme weather conditions, and the tidal deposition of floating materials (Beeftink, 1977; Bertness and Ellison, 1987; Ellison, 1987; Turner, 1987).

Theoretical models suggest that plants living in disturbed environments will develop evolutionary attributes that increase their fitness (Grime, 1977; 1979; Grubb, 1977). These attributes include a short life-cycle, high maximal growth rates, and the production of many small seeds (Grime, 1977; 1979). Verification of this theory for wetland and tidal marsh plants species is limited. Several studies have documented the existence of wetland plant species with life-history attributes that allow them to become the dominant species in newly created disturbance patches (Bertness and Ellison, 1987; Ellison, 1987; Shipley et al., 1989).

Annual species of Salicornia are common tidal wetland plant species that display typical ruderal characteristics. They are primarily found in disturbance created patches in the high marsh because of their ability to colonize these sites quickly (Ellison, 1987; Hartman, 1988). Patches are created in the high marsh when spring tides wash floating plant wrack up onto the marsh (Reidenbaugh and Banta, 1980; Hartman et al., 1983). The wrack destroys the plants below it, and with time the decomposition of the wrack and dead plants creates a patch of bare ground. The seeds of annual forms of Salicornia have a hairy coat that easily attaches to floating plant wrack allowing it to be the first colonizer in the patch (Ellison, 1987). After colonization and establishment Salicornia is quickly out-competed for light by perennials from neighboring patches that remained undisturbed (Ellison, 1987).

2.5.3 Herbivory

Herbivores can have a pronounced influence on many aspects of plant growth, survival and reproduction (Crawley, 1988). As a rule, herbivores tend to decrease the fitness and growth of a plant rather than killing it (Begon, Harper and Townsend, 1986; Crawley, 1988). In addition, several studies have indicated that the action of grazers can influence the structure of a plant community and its diversity (Scott et al., 1979; Dyer et al., 1982; Crawley, 1983; Huntly and Inouye, 1988; Naiman, 1988; Peart, 1989).

Vertebrates are usually the dominant herbivore on tidal marsh habitats (Adam, 1990). Of the vertebrates found grazing on these habitats, a small number of them are domestic livestock whose diet consists primarily of above-ground tissues (Jensen, 1985; Pehrsson, 1988; Turner, 1987; Adam, 1990). Livestock grazing has been found to significantly influence plant productivity and community composition (Ranwell, 1961; Gray, 1972; Reimold et al., 1975; Bakker, 1978; Turner, 1987; Pehrsson, 1988). In general, feeding by livestock tends to create the most preferred plant community composition for the continuation of grazing (Pehrsson, 1988; Adam, 1990), and heavy grazing by livestock can reduce above-ground productivity to significantly measurable levels (Reimold et al., 1975; Turner, 1987).

Waterfowl, particularly geese, tend to be the main natural grazer of tidal marsh plant communities. For example, grazing by Greater and Lesser Snow Geese (Jefferies, Jensen and Abraham, 1979; van der Bilt and Helming, 1978; Cargill and Jefferies, 1984b; Bazely and Jefferies, 1986; Giroux and Bedard, 1987; Boyd, 1988; Kerbes, Kotanen, and Jefferies, 1990) changes plant community structure and composition, and can significantly reduce plant productivity when grazing is heavy. Experimental enclosures at La Perouse Bay (Manitoba, Canada) contained 16 species of plants compared with 6 species in an adjacent control after five years of grazing by snow geese (Bazely and Jefferies, 1986). Grubbing by Greater

Snow Geese for the rhizomes of Scirpus americanus and Eleocharis spp., produced significant declines in their below-ground production when compared to ungrubbed sites (Giroux and Bedard, 1987).

Some researchers have suggested that certain levels of grazing can actually stimulate plant growth causing higher biomass in grazed areas (McNaughton, 1983; Cargill and Jefferies, 1984b; Bazely and Jefferies, 1985). For example, in a marsh dominated by Puccinellia phryganodes and Carex subspathacea, net above-ground primary productivity of ungrazed vegetation was found to be significantly less than areas grazed by the Lesser Snow Geese (Cargill and Jefferies, 1984b). Bazely and Jefferies (1985) suggested that the higher productivity observed in the grazed areas was caused by accelerated nitrogen cycling because of goose grazing. The production of faeces by the geese left the partially decomposed plant matter, containing organic nitrogen, in a form that was quickly mineralized and taken up by the plants (Ruess, Hik and Jefferies, 1989).

Much of our knowledge about insect herbivory in tidal marsh plant communities comes from descriptive observations. Only a few experimental studies have been conducted on insect defoliation of wetland plants, primarily because experimental enclosures are difficult to construct (Crawley, 1988). The descriptive accounts suggest that grazing by insects is usually uniform and has little effect on the standing crop

(Pfeiffer and Weigert, 1981; Foote, Kadlec and Campbell, 1988; Adam, 1990). However, there are a few reports of localized episodes of heavy defoliation where grazing has removed more than 40 % of the above-ground biomass (Parsons and de la Cruz, 1980; Ellison, 1987; Foote, Kadlec and Campbell, 1988).

2.5.4 Competition

This section presents the results of an intensive survey of the literature to find evidence of the operation of competition in tidal marsh habitats. The presentation of this survey will be organized according to the method used to infer competition. Species interactions of a competitive character in natural ecosystems can be demonstrated according to Giller (1984) in three ways: (1) by observing the negative and positive spatial distributions of species; (2) through observations of "natural" experiments in which the density of competitors are measured as they approach equilibrium, and (3) through addition and/or removal experiments in greenhouse and natural field conditions, where the equilibrium population density of the responding species is monitored. All of these techniques are based on the purely phenomenological Lotka-Volterra model of competition.

Tilman (1987a; 1988), however, suggests that an investigation of plant competition should focus on the mechanisms of species interaction rather than the phenomenon. Demonstration of the resource-based mechanistic model of plant competition would involve a multifaceted approach that summarizes experimental, observational and theoretical information (Tilman, 1988). Any evidence from the literature that can be used to test this model of competition will also be presented.

2.5.4.1 Tests of Spatial Pattern

The tests of spatial pattern and competition reviewed in this section involve the comparison of a species' fundamental niche with its realized niche. If partial competitive exclusion has taken place in the field, the fundamental niche will be reduced to a smaller realized niche (Pianka, 1981; Giller, 1984). One way to determine whether competitive exclusion controls community composition is to introduce species into habitats from which they are absent, and eliminate competitors from their immediate vicinity. If the species survives, grows and reproduces, we may infer that competitive exclusion caused its absence if it naturally has access to the site.

From research work in an Alaskan tidal marsh, Vince and Snow (1984) concluded that it was unlikely that tidal inundation was the causal agent responsible for zonal plant distribution. Rather, they suggested that plant zonation was mediated by the effects of other variables associated with inundation and interspecific competition. A reciprocal transplant of five dominant species indicated that all of these species survived and reproduced in zones outside their actual distribution over a two year experimental period (Snow and Vince, 1984). Similar results were also reported by Stalter and Batson (1969) and Bertness and Ellison (1987) from, respectively, South Carolina and New England salt marsh communities.

A comparison of niche breadths and niche overlaps in two emergent salt marsh communities discovered different intensities of competitive interactions (Russell, Flowers, and Hutchings, 1985). The two communities studied differed in their number of constituent species and in diversity. Mean niche overlaps were significantly smaller, and most species had lower niche breadths, on the marsh with more diverse vegetation. These results agree with Pianka's (1974) "niche overlap hypothesis", which suggests that maximum niche overlap should be smaller in intensely competitive situations with higher levels of diffuse competition.

Evidence for competitive interactions along a continuous gradient, such as the inundation gradient of a tidal marsh, may also be determined by a simple test which examines the location of the upper and lower limits of a species distribution (Pielou, 1975a; 1975b; 1977). In this test, competition is inferred when plant distributions are contiguous to each other rather than overlapping. Application of this test to fourteen salt marshes from five different areas indicated that the zonal boundaries of plant species may indeed be influenced by competition (Pielou and Routledge, 1976). Contiguous distributional limits have also been found using a similar technique in the vegetation patterns of a salt marsh on the Tijuana Estuary, California (Zedler, 1977).

Similar spatial patterns may, however, also arise from factors other than interspecific competition. The action of herbivores (Giroux and Bedard, 1987; Foote et al., 1988; Pehrsson, 1988) or disturbance (Sousa, 1984; Coffin and Lauenroth, 1988; Goldberg and Gross, 1988) may also cause a reduction in the potential distribution of a plant species.

2.5.4.2 Natural Experiments

Natural experiments can also provide evidence for interspecific competition between plant species. A natural experiment can be defined as any experiment where the researcher does not introduce the perturbation, but rather selects sites where the perturbation is already running or has run (Diamond, 1986). Examples of such natural experiments in the coastal wetlands of the Pacific Northwest include the following successful plant introductions: Cotula coronopifolia, Spartina alterniflora, Spartina anglica, Spartina patens, Spergularia marina, and Zostera japonica (Frenkel, 1987; Frenkel and Boss, 1988). The best studied of these introductions is that of Spartina patens on Cox Island, Oregon. Using aerial photographs, Frenkel and Boss (1988) determined that Spartina patens increased exponentially from three small patches with an area of 90 m^2 in 1939 to more than 90 patches with an area of 3000 m^2 in 1980. Most of the expansion of Spartina patens occurred by clonal growth. All of the areas of patch establishment were in a community dominated by Deschampsia caespitosa and Scirpus maritimus.

No measurements were made by Frenkel and Boss (1988) to document competitive exclusion of indigenous species with clonal expansion. Field observations, however, of the Spartina clones revealed they were primarily monotypic. It naturally follows from this observation that the expansion of each patch must have been at the expense of other species growing at the patch perimeter. The researchers anticipate that the Deschampsia caespitosa-Scirpus maritimus community will become a monotypic Spartina patens community with time as there is no re-establishment of the indigenous species within the Spartina clones.

2.5.4.3 Density Manipulative Experiments

The strongest evidence for the occurrence of plant competition in tidal marsh ecosystems has been from studies that have manipulated the densities of competing species. These studies generally utilize one of two different techniques. One technique involves the removal or addition of species to the community under field conditions. The other technique uses two-species mixture experiments to determine the outcome of growing two species together in controlled greenhouse or common garden conditions (de Wit, 1960; Harper, 1977).

Two-species mixture experiments have been used in two studies to examine competitive interactions in tidal marshes (Gray and Scott, 1977; Barbour, 1978). Gray and Scott (1977) grew Puccinellia maritima, Festuca rubra, and Agrostis stolonifera in pairs with various water levels, soil types and salinities. Puccinella was found to be more dominant than the other grasses at high salinities, while Agrostis was the dominant species in fresh water conditions. Puccinellia was also found to have a competitive advantage over Festuca at high water levels. These results were generally concurrent with the actual distribution of these species in field conditions.

Using a two-species mixture greenhouse experiment, Barbour (1978) examined the hypothesis that Jaumea carnosa was restricted to Californian salt marshes because it was a poor competitor with glycophytes on non-saline soils. In this study, Jaumea carnosa was grown with the glycophyte Lolium perenne in eight "de Wit" replacement series experiments each differing in salinity treatment. At low salinities *Jaumea*'s yield was depressed by 52% in the 50:50 mixture treatment with *Lolium perenne*. However, at high salinities competitive interaction between the two species was found to be insignificant. The results of this study suggest that intolerant halophytes such as *Jaumea* may be restricted in nature to salt marshes because they are poor competitors with glycophytes on non-saline soils.

In southern California, Covin and Zedler (1988) examined competition through species removal in plots either fertilized or unfertilized with urea. Under natural conditions, the low marsh of their study site was dominated by a mixture of *Spartina foliosa* and *Salicornia virginica*. Results from the fertilization experiment indicated that nitrogen was a limiting resource in the growth of *Spartina foliosa* in pure plots. In mixtures, fertilization had no apparent effect on *Spartina foliosa*, but did increase the growth of *Salicornia virginica*. The experimental removal of *Salicornia virginica* from mixed stands increased *Spartina foliosa* production, while the removal of *Spartina foliosa* did not effect the biomass production of *Salicornia virginica*. The authors concluded that the overall results indicate that *Salicornia virginica* is a superior competitor for nitrogen, and controls the growth of *Spartina foliosa* in both fertilized and unfertilized treatments.

In the Carpinteria salt marsh, located in southern California, Pennings and Callaway (1992) used field experiments to investigate the role of soil factors and plant competition in maintaining the monospecific zonation of *Salicornia virginica* (low marsh dominant) and *Arthrocnemum subterminalis* (high marsh dominant). On this marsh the standing biomass of both species was greatest at the elevation where the species border. Moving up-marsh of the border, *Arthrocnemum* size and vigor declines and soil salinity increases steadily with elevation until hypersalinity occurs causing a vegetation-free salt flat. Above the salt flat is a zone with a mixed-species community dominated by *Arthrocnemum*. Salinity conditions here are euryhaline. Seaward of the abrupt border of the two dominant species, *Salicornia* declines in biomass until a mudflat is reached at an elevation where flooding frequency is about 40%.

Two experiments were performed in this study over two growing seasons to investigate the relative importance of soil and biological factors in determining the zonation of *Salicornia* and *Arthrocnemum*. In the first experiment, growth rates and biomass of individuals were measured in the major marsh zones with neighbors present or experimentally removed. The second experiment involved transplanting both species into their own and the other species sites in treatments with neighbors removed or present. The results of the experiments indicated that both Salicornia and Arthrocnemum grew better in the zones either side of the border than in the low Salicornia zone or the high marsh mixed-species zone. Salicornia was found to be better adapted to tolerate higher levels of flooding found in the low Salicornia zone. Arthrocnemum seemed better able to tolerate high salinities, and therefore was dominant in the mixed-species zone.

In conclusion, this study suggests that plant competition was more important in the middle marsh zones where the effects of salinity and flooding are relatively minimal. In the lower elevations of the marsh platform, the physical effects of flooding exclude Arthrocnemum. At higher elevations in the mixed species zone, high salinities exclude Salicornia.

Studies on the Atlantic coast also suggest that competition is important in tidal marsh community structure (Silander and Antonovics, 1982; Bertness, 1988; 1991a; 1991b; Bertness and Ellison, 1987; Ellison, 1987). Silander and Antonovics (1982) investigated interspecific interactions in a North Carolina tidal salt marsh through perturbation experiments. In these experiments selected plants were removed from the community and the responses of the other species recorded. The removal of Spartina patens, in the high marsh, caused a significant increase in the abundance of Fimbristylis spadiceae, while the abundance of five other common species in this community remained the same. Likewise, the removal of Fimbristylis spadiceae from the same community resulted in the increase of just Spartina patens suggesting that the competition between these two species is symmetric. In contrast to the high marsh, the removal of Spartina patens in the low marsh had much less effect on Fimbristylis spadiceae's abundance.

In New England, Bertness and Ellison have completed several studies examining the factors responsible for the plant species patterns on a marsh at Rumstick Cove, Barrington, Rhode Island (Bertness and Ellison, 1987; Ellison, 1987; Bertness, 1991a; 1991b, 1992). This typical New England tidal marsh has a low marsh plant community dominated by a dense monoculture of Spartina alterniflora, that is inundated daily by tides (Nixon, 1982). The high marsh is flooded less frequently, and has two dominant species zones. On the seaward boundary, Spartina patens forms a monotypic zone, while the terrestrial boundary is dominated by a distinct band of Juncus gerardi. In addition to these three major vegetation zones, there are discrete patches found on the high marsh dominated by Salicornia europaea and Distichlis spicata.

Transplant experiments suggest that the distribution of the three dominant species does not conform to their potential distribution in the absence of other vegetation (Bertness and Ellison, 1987; Bertness, 1991a; Bertness, 1991b). Spartina alterniflora was found to be capable of vigorous growth across the entire marsh platform (Bertness and Ellison, 1987). Field experiments indicated that *Spartina alterniflora* is excluded from the upper marsh by the competitive interference of *Spartina patens* and *Juncus gerardi* roots mats (Bertness and Ellison, 1987; Bertness, 1988; 1991b; 1992).

Spartina patens was found to be restricted from the *S. alterniflora* zone by the extreme physical conditions created by increased tidal inundation (Bertness and Ellison, 1987; Bertness, 1991b). *Spartina patens* may be unsuited to survive in the low marsh because it lacks extensive aerenchyma tissues that aid in oxygenating roots in anoxic conditions (Anderson, 1973; Gleason, 1980). Extensive aerenchyma are, however, found in the tissues of *Spartina alterniflora* (Gleason, 1980). Transplants of *S. patens* in the low marsh died or grew poorly in the presence and absence of *S. alterniflora* neighbors (Bertness, 1991b). The results of these transplant experiments together with the physiological and morphological attributes of *S. patens* suggest that it is excluded from the *S. alterniflora* zone by abiotic factors rather than plant competition (Bertness, 1991b).

Plant competition, however, does seem important in controlling the distribution of *Spartina patens* in the zone dominated by *Juncus gerardi*. Both removal and transplant experiments indicated that *J. gerardi* competitively excludes *S. patens* from the terrestrial margins of the high marsh

(Bertness and Ellison, 1987; Bertness, 1991a). Juncus gerardi seems to be excluded from lower elevations by increased physical disturbance and flooding in the Spartina patens zone (Bertness and Ellison, 1987).

In the spring, large mats of dead Spartina alterniflora are deposited in the high marsh by the annual occurrence of spring high tides (Bertness and Ellison, 1987; Ellison, 1987). These mats often remain in place for several months, and by summer can cause the death of underlying vegetation. When the mats are removed, either by decomposition or another high tide, a vegetation-free patch is left open to plant colonization and establishment. The first species usually colonizing these patches are Salicornia europaea and Distichlis spicata (Bertness and Ellison, 1987; Ellison, 1987). However, as time passes these first colonizers are competitively displaced by Spartina patens and Juncus gerardi (Bertness and Ellison, 1987). Further work focusing just on Salicornia europaea discovered that the competitive displacement of this species by the dominant high marsh perennials was by way of light reduction (Ellison, 1987).

2.5.4.4 Mechanistic Evidence

As mentioned previously, Tilman (1986b) has suggested that the existence of monospecific stands of Spartina alterniflora may be the result of its ability to be the most superior competitor for the available soil nitrogen and light in that particular habitat. He also proposes that all other species, which are generally shorter that Spartina, are excluded because of the shade beneath Spartina's canopy. In the absence of direct evidence for the resource ratio model, three sorts of circumstantial evidence in favor of this model can be found: (i) soil nitrogen and light may be important limiting resources; (ii) tidal marsh productivity gradients are common: species replacement is associated with varying resource availability; and, (iii) functional linkages exist between soil nitrogen availability and plant productivity on tidal marsh platforms.

In tidal marsh ecosystems, as in most terrestrial ecosystems, nitrogen is the most important soil nutrient limiting plant growth and productivity (Valiela and Teal, 1974; Gallagher, 1975; Patrick and DeLaune, 1976; Chalmers, 1979; Mendelssohn, 1979b; Buresh, DeLaune and Patrick, 1980; Loveland and Ungar, 1983; Cargill and Jefferies, 1984a; Hopkinson and Schubauer, 1984; Covin and Zedler, 1988). Ellison (1987) found that the annual Salicornia europaea was restricted in distribution to recently disturbed patches in the high marsh, while undisturbed areas were usually well established with perennials like Spartina alterniflora. Using manipulative field experiments, Ellison concluded that Salicornia europaea could not invade undisturbed areas because the perennials reduced the availability of light to a level where Salicornia europaea could not survive. However, the young clonal ramets of the various perennial species could grow successfully in low light conditions.

Many researchers have noted correlations between elevation and plant productivity in tidal marsh habitats. In some cases productivity increases with marsh platform elevation (Vogl, 1966; Mahall and Park, 1976a; Disraeli and Fonda, 1979; Eilers, 1979; Vince and Snow, 1984). For example, Mahall and Park (1976a) studied a tidal marsh in California that consisted of a simple zonation of two monospecific communities that were separated at the mean high water mark. The species that occupied the zone above this mark, Salicornia virginica, attained between 550-960 g dry weight (dwt) m^{-2} of net above-ground production during the growing season. The other species, Spartina foliosa, occupied the lower zone, and had a net above-ground production of only 270-690 g dwt m^{-2}. On West Island, Nehalem Bay, Oregon, Eilers (1979) found a general linear increase in net production from 230 g dwt m^{-2} $year^{-1}$ in the low marsh to 2800 g dwt m^{-2} $year^{-1}$ in the high marsh.

Ponnamperuma (1984) and Sprent (1987) have suggested that the flooding of soils has a direct effect on the cycling and storage of soil nitrogen. More specifically, flooding produces anaerobic conditions in the soil that inhibit the aerobic respiration of soil organisms involved in the decomposition of organic matter to usable forms of nitrogen for plant uptake (Ponnamperuma, 1984). Several researchers (Valiela et al., 1978; Scudlark and Church, 1989; Chambers et al., 1992) have also found that ammonium release by mineralization in tidal marsh sediments is positively correlated with temperature. Tidal marsh habitats that are low in elevation should have lower quantities of available soil nitrogen than high marsh areas because of longer anaerobic conditions and lower sediment temperatures due to more prolonged flooding. In the high marsh, increased quantities of soil nitrogen will make this habitat more productive with the plants achieving greater biomass than their counterparts in the low marsh. Plants with a higher biomass, generally, are taller and have more and/or bigger leaves, thus making them efficient at intercepting incoming sunlight. These adaptations also make these plants good competitors for light (Tilman, 1988).

Not all tidal marshes, however, show a positive correlation between elevation and net primary production. Some marshes have their highest biomass located in the low marsh and/or along tidal channels (Zedler, 1977; Mendelssohn, 1979a; Niering and Warren, 1980; Gallagher and Kibby, 1981; Dawe and White, 1982; 1986). The suppression of plant productivity at higher elevations or away from tidal creeks may be due to high sediment salinities (Nestler, 1977; Rozema, 1979; Niering and Warren, 1980; Linthurst and Seneca, 1981; Pearcy and Ustin, 1984), and/or anoxia and toxic levels of soil sulphides (Linthurst, 1980; Mendelssohn and Seneca, 1980; Howes et al., 1981; King et al., 1982; DeLaune et al., 1983; Wiegert et al., 1983). Nevertheless, these findings do not invalidate the nitrogen/light gradient competition model, because high levels of salinity, soil sulphides, or low levels of soil aeration may also inhibit nitrogen uptake by plants (Mendelssohn, 1979a; Morris, 1980; Smart and Barko, 1980; Morris and Dacey, 1984).

Up to this point, this discussion has primarily been concerned with the role interspecific competition plays in community structure. However, competition between different genotypes of one species may result in habitat segregation within a species. Persistent genotypic differences have been observed in the tall and short growth forms of _Spartina alterniflora_ (Stalter and Batson, 1969; Gallagher et al., 1988). The tall form of this species usually grows along the levees of tidal creeks, while the short form grows further inland on the back marsh (Mendelssohn, 1979a; Wiegert, 1979). Measurements of environmental factors have shown that the habitats of the two growth forms differ in their soil salinity (Nestler, 1977; Linthurst and Seneca; 1981), sulphide concentration (Howes et al., 1981; King et al., 1982; DeLaune et al., 1983), and sediment aeration (Linthurst, 1980; Mendelssohn and Seneca, 1980; DeLaune et al., 1983). Further, these abiotic differences may reduce the availability of soil nitrogen for plant uptake in the habitat occupied by the short form (Morris, 1980; Smart and Barko, 1980; Morris and Dacey, 1984).

Experimental studies have shown Spartina alterniflora to be nutritionally limited by soil nitrogen (Valiela and Teal, 1974; Gallagher, 1975; Mendelssohn, 1979a; 1979b; Linthurst and Seneca; 1981). This limitation coupled with spatial variations in the availability of soil nitrogen and a limitation to light may have caused the directional selection of Spartina alterniflora ecotypes. Areas deficient in soil nitrogen for plant growth may have selected for ecotypes that have short height and low productivity because they require less of this nutrient for survival. These plants may also allocate more of their photosynthetic energy into the production of roots making them very efficient at obtaining soil nitrogen but poor at capturing light. On the other hand, sites that have a higher soil nitrogen availability may select for a form of Spartina alterniflora that allocates more of its energy to the production of leaves making it taller and more productive.

CHAPTER 3

STUDY SITE DESCRIPTION AND RESEARCH RATIONALE

3.1 The Study Site

The tidal marsh investigated in this study is located at the end of a peninsula known as Brunswick Point, which lies approximately 20 km south of Vancouver, British Columbia (Figure 3.1). The northern portion of this marsh is primarily influenced by freshwater from Canoe Pass, a small distributary of the Fraser River. Measurements of interstitial salinity at high and low marsh locations at this site by Moody (1978) indicated values of approximately 3 parts per thousand (ppt) throughout the growing season (April - August). Southern portions of this marsh receive less freshwater from Canoe Pass, and as a result had pore water salinities fluctuating around 5 ppt during the same time period (Moody, 1978).

The vegetation of this marsh exhibits the zonal patterns common to tidal marshes. Communities located in the northern part of the marsh are dominated by the perennials <u>Carex lyngbyei</u> Hornem., and <u>Scirpus</u> <u>americanus</u> Pers. (Figure 3.1). These two species are common in brackish marshes throughout the Pacific Northwest (Hutchinson, 1988), and usually occupy high and low marsh sites, respectively (Disraeli and Fonda, 1979; Hutchinson, 1982). Other common species in this marsh

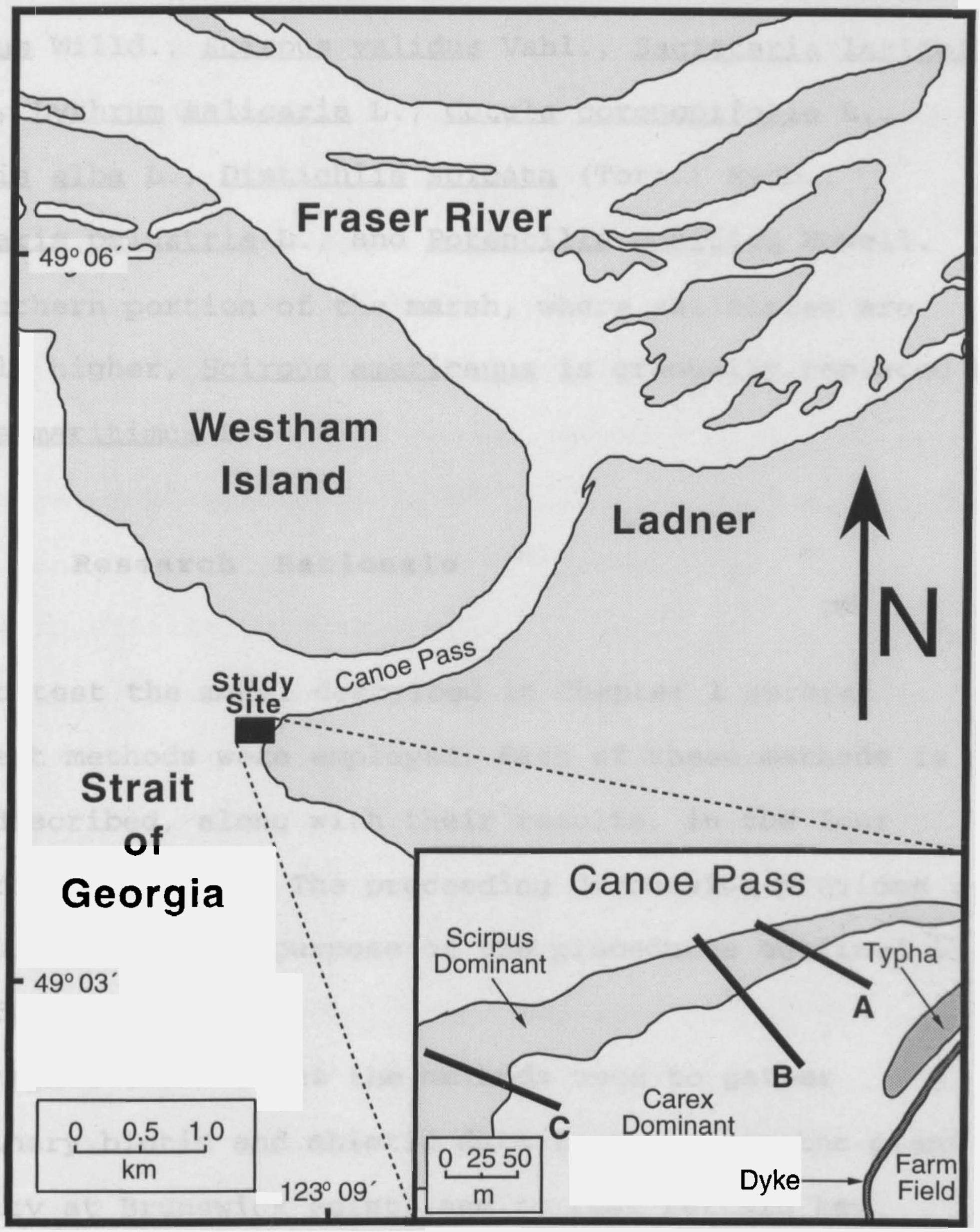

Figure 3.1. Location of the study site at Brunswick Point on the Fraser Estuary, British Columbia. Inset map displays the location of the sampling transects A, B and C. Distribution of dominant species on this map were determined from field survey.

include: *Triglochin maritimum* L., *Typha latifolia* L., *Juncus balticus* Willd., *Scirpus validus* Vahl., *Sagittaria latifolia* Willd., *Lythrum salicaria* L., *Cotula coronopifolia* L., *Agrostis alba* L., *Distichlis spicata* (Torr.) Rydb., *Eleocharis palustris* L., and *Potentilla pacifica* Howell. In the southern portion of the marsh, where salinities are slightly higher, *Scirpus americanus* is gradually replaced by *Scirpus maritimus* L.

3.2 Research Rationale

To test the model described in Chapter 1 several different methods were employed. Each of these methods is fully described, along with their results, in the four chapters that follow. The proceeding discussion provides a brief summary of the purpose of the procedures outlined in each of these chapters.

Chapter 4 describes the methods used to gather preliminary biotic and abiotic data to summarize the plant community at Brunswick Point, and to test certain key assumptions mentioned in Chapter 1. These assumptions suggest: (1) that platform elevation is positively correlated with plant productivity, soil nitrogen content, and plant shoot height; (2) that platform elevation is negatively correlated with light available beneath the plant canopy and tidal inundation frequency; (3) that the two dominant plant species, Scirpus americanus and Carex lyngbyei, occupy distinct zones on the marsh; and (4) that the availability of nitrate and/or ammonium is greater under Carex dominated sites.

The fertilization field experiments, described in Chapter 5, tested the hypothesis that nitrogen may be the limiting soil resource for both Scirpus americanus and Carex lyngbyei. After one growing season, measurements from both species recorded the response of above-ground biomass, shoot height, and available light at the soil surface, to the various fertilization treatments.

Chapter 6 describes the methods and results of four different transplantation experiments carried out at Brunswick Point. The first transplantation experiment was carried out to see if Scirpus americanus and Carex lyngbyei could grow beyond the range of elevations that they occupied at Brunswick Point. In the second experiment Scirpus americanus rhizomes were transplanted into upper marsh sites dominated by Carex lyngbyei in the spring of 1989. Once established, half of the experimental plots were treated by continually removing Carex lyngbyei shoots in the immediate neighborhood of the transplant during the growing season. In the other plots Carex lyngbyei grew alongside the Scirpus americanus transplants at normal field densities. Upon completion of the experiment, samples of above-ground biomass, shoot number and shoot height were taken from the transplants to examine the effect the treatments had on the *Scirpus* plants. The third experiment repeated the procedures of the second except that *Carex lyngbyei* rhizomes were now transplanted into the *Scirpus* community and sampling occurred after two growing seasons. The final experiment examined the growth of transplanted rhizomes of *Carex lyngbyei* under five different nutrient additions in the *Scirpus americanus* community. This experiment tested the hypothesis that additions of nitrogen fertilizer would increase the yield and shoot height of *Carex lyngbyei* individuals transplanted into resource-poor low marsh.

The experiments outlined in Chapter 7, examined the shoot growth and biomass allocation patterns of *Scirpus americanus* and *Carex lyngbyei* under various quantities of nitrogen and light in a common garden set up. The nitrogen common garden experiment specifically tested Tilman's (1988) predictions concerning biomass allocation and habitat productivity, and tried to determine each species' minimum nutrient needs. The light common garden experiment determined the sensitivity of the two species to reductions in light availability.

CHAPTER 4

BIOTIC AND ABIOTIC DESCRIPTION

4.1 Descriptive Field Measurements: 1988

During the spring of 1988, three sample transects were established in the northern portion of the Brunswick Point tidal marsh (Figure 3.1). These transects run through the two major vegetation zones, and parallel to the slope of the marsh platform. Along these transects 73 sample sites were systematically arranged and marked by stakes.

4.1.1 Species Biomass, Density and Height Measurements

Previous work in the Fraser Estuary has indicated that peak standing crop for the two dominant species, Scirpus americanus and Carex lyngbyei, occurs from July to early August (Kistritz et al., 1983; Boyd, 1988). As a result, measurements of above-ground biomass of all vascular species were made at each sample site during the period from July 10th to 24th, 1988. All biomass samples were collected from a 50 x 100 cm quadrat in which all plants were clipped to ground level. At the laboratory, living material was separated by species according to taxonomic nomenclature found in Hitchcock and Cronquist (1973). Once sorted, shoots were counted to determine density, washed of sediment, dried at 70°C for 72 h, and then weighed to 0.1 g.

Measurements of shoot height were determined for Scirpus americanus and Carex lyngbyei from the samples collected for biomass determination in transects A and B (Figure 3.1). Transect C was not sampled because of constraints in time and manpower. For each plot, heights were measured to the nearest 1.0 cm from 40 randomly selected shoots. If 40 plants were not available in the sample height was not determined.

4.1.2 Soil Measurements

At each of the 73 sample sites, a single soil sample of approximately 500 g was taken from the soil surface to a depth of 15 cm during the first week of August, 1988. Locations for each sample were randomly selected within a 50 x 100 cm quadrat placed in the unclipped region immediately down-marsh of the site stake. These samples were then air-dried in the laboratory, and sieved of all fractions > 2 mm to remove large roots and rhizomes. A subsample of approximately 20 g was taken from each soil sample for the determination of soil organic matter content by loss-on-ignition at 420°C for 1 1/2 h (McKeague, 1978). Another subsample of approximately 50 g was shipped to the Department of Soil Science, University of British Columbia, for the determination of extractable P, K, Ca, Mg, Na, Zn, Fe, Mn and total N. Total soil nitrogen was extracted from the samples by the macro-Kjeldahl method (Bremner, 1965a), and then measured on an Autoanalyzer II. All of the other nutrients were extracted using the Mehlich 3 procedure (Mehlich, 1984), and then ascertained with a Jarell/Ash Atomcomp/Series 2 ICAP.

4.1.3 Available Light Measurements

A few days prior to the destructive sampling of biomass from the three transects, 31 sample sites were randomly selected for the determination of available light at the soil surface. Available light was determined by taking paired measurements of solar radiation intensity above the vegetation and at the soil surface in each sample site using a Eppley pyranometer. This instrument measures short-wave radiation in the band from 0.3 to 3.0 μm (Oke, 1978). All measurements were taken on cloudless days within 2 h of solar noon. Of the 31 samples, 12 were located in the zone occupied by _Scirpus_ _americanus_, while the other 19 measurements were made in the community dominated by _Carex lyngbyei_. Available light at the soil surface was expressed as a percentage of the quantity of total incoming solar radiation measured above the plant canopy.

4.1.4 Elevation and Tidal Submergence

Elevation of the sample sites was measured with a dumpy level and stadial rod in early May, 1988. Geodetic conversion of these elevations was made by surveying back to municipal control benchmarks located on the dyke.

Percent time a particular elevation at the study site was submerged during the daylight hours (06:00 - 18:00 h) of the 1988, 1989, and 1990 growing seasons (April - August) were calculated by a computer program that uses a basic sine curve equation to simulate tidal fluctuations (Stock, 1972). This program computed submergence periods for specific platform heights, for each day, with predicted tide levels from Point Atkinson, British Columbia (Canadian Hydrographic Service, 1988; 1989; 1990), located 29 km north of the study site.

4.1.5 Data Analysis

Simple direct gradient analysis (Gauch, 1982) was employed to analyze the relationship between elevation and species abundance for each of the three transects sampled. Means and standard errors were calculated for species height, density and biomass data. To determine if plant height, available light, soil organic matter content, and soil nutrient status differed significantly between the two dominant plant community types either a Student's t-test or Mann-Whitney U-test was used. The nonparametric Mann-Whitney U-test was employed only if the data did not approach a normal distribution even after tranformations. The data were also examined for homogeneity of variance with Bartlett's test. If variances between data proved to be heteroscedastic transformations were used to correct this problem (Steel and Torrie, 1980).

Correlation analysis was used to examine the association between average shoot heights for Scirpus americanus and Carex lyngbyei with marsh elevation and soil nitrogen. Relationships between soil nutrients, available light, soil organic matter content, elevation and total above-ground plant biomass were also investigated with bivariate regression and correlation analysis. Data transformations were made only when necessary to meet the assumptions of bivariate regression (Steel and Torrie, 1980; Kleinbaum et al., 1987).

4.2 Descriptive Field Measurements: 1989

During the spring and summer of 1989 additional measurements of plant biomass and height, available light, and soil data were made in the field at regular monthly intervals (April 24, May 22, June 19, and July 20). The purpose of these measurements was to:

(1) examine the growth characteristics of the two species during the growing season;

(2) measure the change in available light at the soil surface during the growing season in *Scirpus americanus* and *Carex lyngbyei* stands; and

(3) measure the residual supply of nitrate and ammonium in the top 5 cm of the marsh sediment at sites where the two species grow.

For each of the sampling dates, the additional measurements were made from 40 equally-spaced sample sites located on a transect line that ran parallel to the slope of the marsh platform. All transects were located randomly within 25 meters of transect A of the 1988 field season (see Figure 3.1). Twenty of the sample sites were located in the *Scirpus*-dominated zone and the other 20 in the *Carex*-dominated zone. Areas in the high marsh dominated by *Juncus balticus* were not sampled.

4.2.1 Biomass, Height and Plant Canopy Measurements

Measurements of above-ground biomass of *Scirpus americanus* and *Carex lyngbyei* were made on the 4 sampling dates from 40 sample sites located on the randomly placed transect. All biomass samples were collected from 50 x 50 cm quadrats in which all species were clipped to ground level. At the laboratory, living material was separated by species according to taxonomic nomenclature found in Hitchcock and Cronquist (1973), washed of sediment, dried at 70°C for 72 h, and then weighed to 0.1 g.

Average plant canopy height measurements were made in each quadrat on each of the four sampling dates. Height of the canopy was determined with a 1 meter metal ruler or a stadial rod. All measurements were made to the nearest 5 cm, and the dominant species in the quadrat was recorded.

Shoot heights of _Carex_ _lyngbyei_ and _Scirpus_ _americanus_ were also measured in the narrow transition zone along the sampling transect. At the laboratory 60 random shoots (if less then 60 shoots were present then all shoots were measured) of each species were randomly selected from the plants harvested for biomass determination. Each shoot was measured to the nearest 1 cm.

4.2.2 Elevation and Soil Measurements

Elevation of the 40 sample sites was measured with a dumpy level and stadial rod for each transect within a few days of the four sampling dates. Geodetic conversion of these elevations were made by surveying back to municipal control benchmarks located on the dyke.

Approximately 50 g of soil was sampled from the center of each sample site to a depth of 5 cm for the determination of soil moisture content, extractable ammonium and extractable nitrate. Within 24 h of sampling, a 1 mol L^{-1} KCl solution (procedure follows Bremner, 1965b) was used to extract ammonium and nitrate from a subsample of approximately 10 g from each sample. Measurement of soil moisture content was made on the remaining portion of the sample for volumetric calculations of ammonium and nitrate levels in the soil. The measurement of soil moisture content for each sample was ascertained by the technique described in McKeague (1978). Upon completion of these procedures, the samples were then shipped within 24 h to the Department of Soil Science, University of British Columbia where extractable ammonium and nitrate levels were measured on an Autoanalyzer II.

4.2.3 Available Light Measurements

Available light at the soil surface was measured from each of the 40 sample sites on each transect just prior to the destructive sampling of plant above-ground biomass. Available light was determined, once again, by taking paired measurements of solar radiation intensity above the vegetation and at the soil surface in each sample site using a Eppley pyranometer. All measurements were taken on cloudless days within 2 h of solar noon.

4.2.4 Data Analysis

For each month, biomass, available light and plant canopy height data were plotted graphically to examine their relationship with elevation. The effects of sampling date and plant type on extractable soil nitrate and ammonium data were analyzed with a two-way ANOVA (Sokal and Rohlf, 1981). Differences in extractable soil nitrate and ammonium between species on each of the four sampling dates were determined by unpaired Student's t-tests (Sokal and Rohlf, 1981). Finally, in the plots where both species were present, height data of Scirpus americanus and Carex lyngbyei were analyzed with unpaired Student's t-tests to examine boundary dynamics (Sokal and Rohlf, 1981).

4.3 1988 Descriptive Field Measurement Results

4.3.1 Species Biomass, Density and Shoot Height

The plant community in the northern portion of the Brunswick Point marsh is composed of seven vascular plant species (Figures 4.1 and 4.2; Table 4.1). Of these species, Scirpus americanus and Carex lyngbyei are the dominants, each occupying distinct elevational zones on the marsh platform. Sites with elevations between -0.80 and 0.20 m (geodetic datum) were dominated by Scirpus americanus. Sagittaria

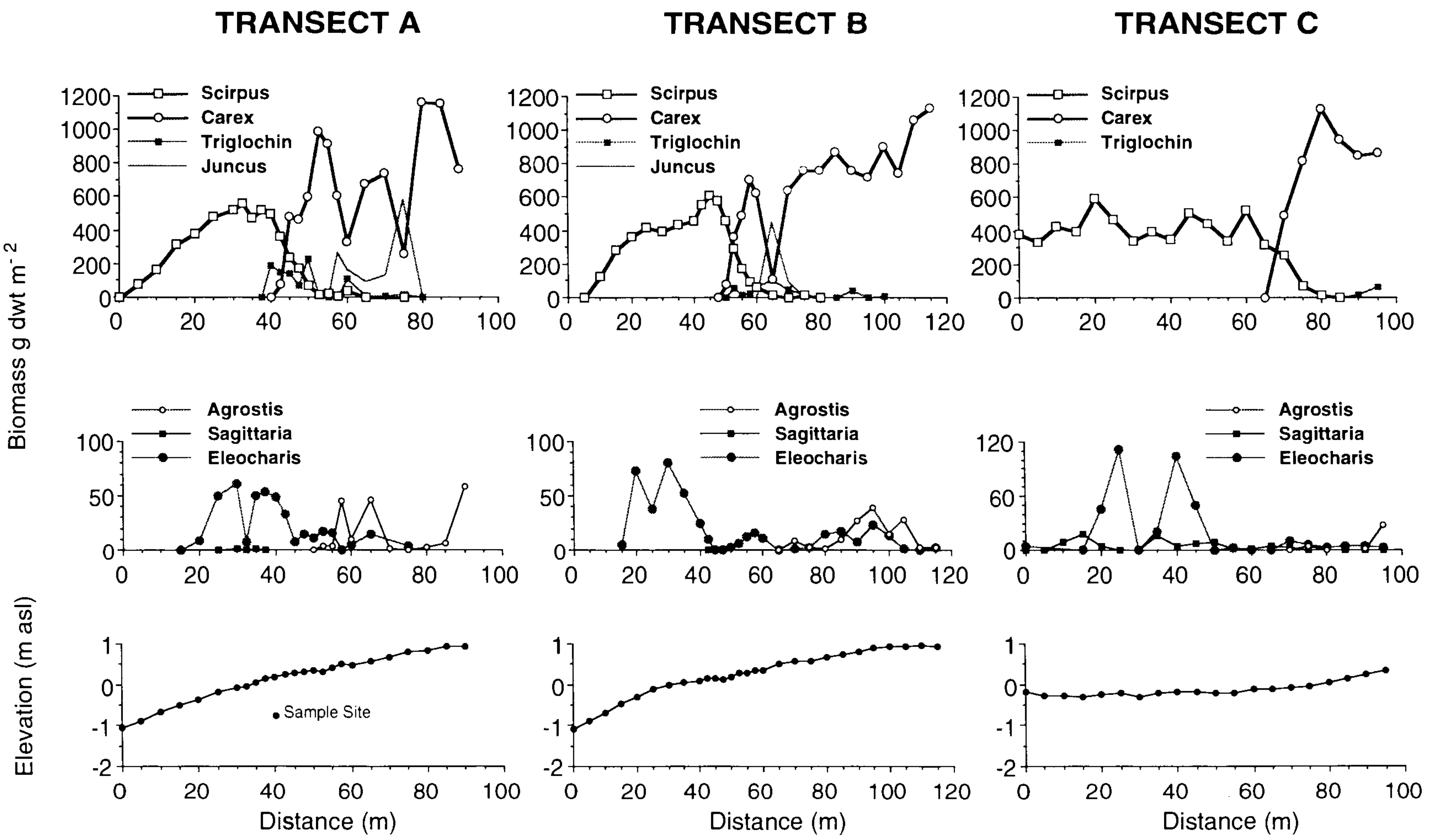

Figure 4.1. Above-ground plant biomass of dominant (upper graphs) and associated species (middle graphs) with elevation (lower graphs) on the three transects sampled at Brunswick Point.

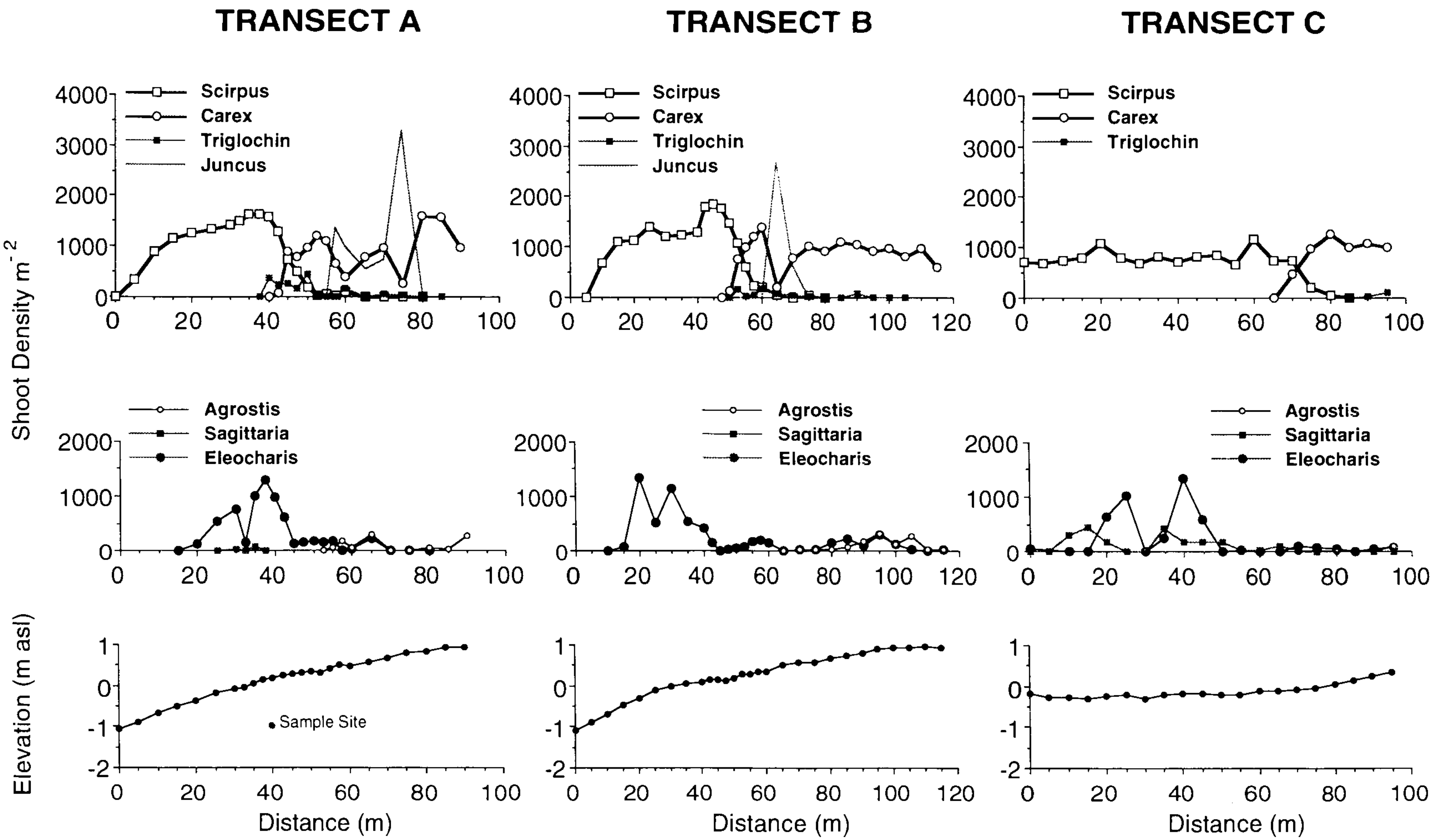

Figure 4.2. Plant shoot density of dominant (upper graphs) and associated species (middle graphs) with elevation (lower graphs) on the three transects sampled at Brunswick Point.

Table 4.1. Above-ground biomass and shoot density of plants recorded from the 73 plots sampled at Brunswick Point.

Species	Percent Frequency	Mean (± SE) **Biomass** (g dwt m^{-2})	Mean (± SE) **Density** (shoots m^{-2})
Scirpus americanus	76.7	294.3 ± 26.4	809 ± 74
Carex lyngbyei	49.3	698.9 ± 49.2	894 ± 60
Triglochin maritima	34.2	56.4 ± 12.9	104 ± 24
Eleocharis palustris	72.6	22.4 ± 3.6	310 ± 53
Sagittaria latifolia	24.7	4.5 ± 1.2	120 ± 33
Agrostis alba	28.8	16.4 ± 3.9	101 ± 22
Juncus balticus	11.0	226.1 ± 71.1	1295 ± 401

latifolia and *Eleocharis palustris* were also found growing in this zone. Their combined biomass, however, contributed only a small proportion to the total plant biomass in this low marsh community (Figure 4.1). Sites with an elevation greater than 0.20 m (high marsh) were usually dominated by *Carex lyngbyei* in a community that also included *Triglochin maritima*, *Juncus balticus*, and *Agrostis alba*. At a few of the higher elevation sites clonal patches of *Juncus balticus* attained considerable biomass and this species was the dominant plant in the local community.

Table 4.1 displays abundance and distribution data for these seven species. The most common species was *Scirpus americanus* which occupied 77 % of the quadrats sampled, with an average above-ground biomass in these quadrats of 294.3 g dwt m^{-2}. The second most common species was *Eleocharis palustris*, occupying 69 % of the quadrats with an average above-ground biomass of only 22.4 g dwt m^{-2}. *Carex lyngbyei* attained the highest average above-ground biomass, 698.9 g dwt m^{-2}, but was present in only 49 % of the quadrats. *Triglochin maritima*, *Agrostis alba* and *Sagittaria latifolia* were all found in approximately 1/3 of the sites sampled, and attained average above-ground biomass values of 56.4, 16.4 and 4.5 g dwt m^{-2}, respectively. The least common species was *Juncus balticus*. However, in the few sites it did occupy, it attained the third highest average above-ground biomass of

226.1 g dwt m^{-2}. These results are similar to those reported by Moody (1978) for this same area.

Carex lyngbyei shoots (89.5 ± 2.7 cm) were on average 13.8 cm taller than Scirpus americanus shoots (75.7 ± 1.7 cm). This difference is statistically significant according to an unpaired Student's t-test ($t = 4.307$, 54 df; $P < 0.0001$). At the overlap zone, Scirpus americanus was significantly taller than Carex lyngbyei in 4 out of 6 sample sites (Table 4.2). Moreover, observations in the field at this zone, over several years, suggested that Carex lyngbyei was slowly invading (approximately 0.3 m $year^{-1}$) the zone dominated by Scirpus americanus by rhizome advancement in some regions of the marsh.

4.3.2 Abiotic Differences Between Communities

Nitrogen, phosphorus and potassium are the soil nutrients required in the greatest quantity for plant growth (Russell, 1973; Jones, 1982). Of these three macronutrients, only the quantity of nitrogen was found to be significantly different in the rooting zone of the Scirpus americanus and Carex lyngbyei communities (Table 4.3). Total nitrogen was discovered to be twice as great in the Carex community. Quantities of three minor soil elements were also found to differ significantly between the Carex and Scirpus communities (Table 4.3). The concentration of calcium was

Table 4.2. Means (± SE) and sample sizes (n) of measured heights from Scirpus americanus and Carex lyngbyei individuals sampled in sites where both species coexist. Results of unpaired Student's t-tests comparing height data between the two species in each sample site are also shown. Differences that are significant have their associated probabilities listed for two-tailed comparisons, while results that are not significant are designated "n.s.".

	Scirpus americanus			Carex lyngbyei			
Sample Site	Mean	± SE	n	Mean	± SE	n	*P*
Transect A, Plot 13	86.7	3.2	40	69.8	3.0	40	<0.001
Transect A, Plot 14	81.6	3.7	40	70.9	3.5	40	<0.05
Transect B, Plot 14	81.3	4.2	40	65.8	2.3	40	<0.001
Transect B, Plot 15	78.8	3.6	40	75.1	2.0	40	n.s.
Transect B, Plot 16	85.6	2.6	40	78.6	2.4	40	[illegible]
Transect B, Plot 17	82.2	2.7	40	67.2	2.4	40	<0.0001

Table 4.3. Means (± SE) and sample sizes (n) of measured available light, soil organic matter content, and soil nutrient variables from Scirpus and Carex community sites at Brunswick Point marsh. Results of Student's t-tests or Mann-Whitney U-tests comparing data from the two different community types are also shown. Differences that are significant have their associated probabilites listed for two-tailed comparisons, while results that are not significant are designated "n.s.".

	Scirpus Community			Carex Community			
Variable	Mean	± SE	n	Mean	± SE	n	*P*
% Available Light [(1)]	43.78	4.91	12	4.81	0.53	19	<0.0001
Organic Matter (g kg^{-1})	34.2	0.6	36	54.3	2.6	32	<0.0001
N (g kg^{-1})	0.72	0.02	36	1.40	0.08	32	<0.0001
P (mg kg^{-1})	15.11	0.47	36	13.95	0.55	32	n.s.
K (mg kg^{-1})	221.36	13.39	36	234.23	14.49	32	n.s.
Ca (mg kg^{-1})	1198.22	23.94	36	1041.25	25.86	32	<0.0001
Mg (mg kg^{-1})	1188.24	19.67	36	1237.20	14.71	32	n.s.
Na (mg kg^{-1})	1007.74	21.47	36	1103.94	34.87	32	<0.05
Fe (mg kg^{-1})	583.34	10.67	36	563.16	8.92	32	n.s.
Zn (mg kg^{-1})	8.79	0.21	36	11.34	0.58	32	<0.001
Mn (mg kg^{-1})	39.05	2.26	36	38.97	3.26	32	n.s.

(1) Determined by taking paired measurements of solar radiation intensity above the vegetation canopy and at the soil surface.

discovered to be approximately 15 % greater in the *Scirpus* community sediments than in the *Carex* community. This small difference may be due to the greater abundance of mollusk shells in the low marsh sediments (personal observation). Nevertheless, calcium should have no limiting effect on plant growth along the elevational gradient because of its overall abundance (Jones, 1982). In the *Carex* community sediments, zinc and sodium were present in slightly greater quantities than in the *Scirpus* community. However, these minor differences in soil zinc and sodium content between the two plant communities are likely not great enough to affect plant growth (Jones, 1982).

Measurements in the two communities of percent soil organic matter and percent availability of light at the soil surface revealed significant differences (Table 4.3). Soil organic matter content was on average 60 % higher in the *Carex* community. As for percent available light at the soil surface, the leaves of the plants in the *Scirpus* community intercepted about 56 % of the light passing through their canopy. However, shading was much more intense in the *Carex* community where the plants blocked approximately 95 % of the incident radiation.

Average percent daily submergence for daylight hours during the 1988 growing season are presented in Table 4.4. As previously mentioned, *Scirpus americanus* is generally dominant in sites whose elevation was from -0.80 to 0.20 m.

Table 4.4. Mean percent daily submergence for the 12-h period from 06:00 - 18:00 h for selected months in 1988, 1989 and 1990 according to elevation.

1988

Elevation (m asl)	April	May	June	July	August	**Average**
-1.0	66.6	57.0	54.6	57.9	68.7	**61.0**
-0.8	62.1	52.0	49.0	53.6	64.8	**56.3**
-0.6	56.2	45.8	44.3	48.9	60.0	**51.1**
-0.4	50.7	41.1	38.2	43.4	55.0	**45.7**
-0.2	45.1	33.6	32.9	38.1	49.8	**39.9**
0.0	36.7	26.4	25.5	32.1	44.4	**33.0**
0.2	28.6	18.3	18.1	24.2	37.9	**25.4**
0.4	20.2	12.1	12.6	16.8	30.5	**18.4**
0.6	12.4	7.4	8.5	11.4	19.9	**11.9**
0.8	6.3	4.7	4.8	7.8	13.9	**7.5**
1.0	1.8	2.2	3.5	4.6	8.4	**4.1**

1989

Elevation (m asl)	April	May	June	July	August	**Average**
-1.0	67.0	59.1	55.6	58.7	67.2	**61.5**
-0.8	62.4	53.8	50.3	54.4	62.8	**56.7**
-0.6	58.0	47.3	44.6	49.3	57.8	**51.4**
-0.4	52.3	41.7	49.4	44.8	53.6	**46.4**
-0.2	45.9	34.7	34.5	39.4	49.2	**40.7**
0.0	38.9	27.0	27.5	33.5	43.3	**34.0**
0.2	27.8	19.1	20.4	26.0	37.4	**26.1**
0.4	17.9	12.8	13.7	19.0	29.2	**18.5**
0.6	10.2	7.5	9.1	13.3	20.1	**12.0**
0.8	6.0	4.6	6.2	8.6	14.0	**7.9**
1.0	2.8	2.0	3.5	6.0	8.8	**4.6**

1990

Elevation (m asl)	April	May	June	July	August	**Average**
-1.0	65.3	59.6	58.3	61.4	68.4	**62.6**
-0.8	60.6	53.2	52.9	57.5	64.8	**57.8**
-0.6	55.2	47.8	46.2	52.2	60.0	**52.3**
-0.4	50.3	41.9	40.8	47.7	54.8	**47.1**
-0.2	44.1	35.4	34.9	42.0	50.8	**41.4**
0.0	37.5	27.1	28.0	36.4	39.8	**35.0**
0.2	29.1	17.8	19.2	29.9	39.8	**27.2**
0.4	19.2	11.4	12.7	20.2	32.9	**19.3**
0.6	11.9	7.1	8.5	13.1	23.2	**12.8**
0.8	5.3	4.3	5.9	7.6	13.6	**7.3**
1.0	1.6	2.2	3.1	5.1	7.7	**3.9**

In terms of the submergence data averaged over the three year period, these sites are submerged during the inferred growing season (April - August) from 26.2 - 56.9 % of the time. Submergence periods for areas dominated by Carex lyngbyei were less than 26.2 % over this same time period.

4.3.3 Regression Analysis

Relationships between the abiotic and biotic variables measured in this study are presented in Table 4.5 and Figures 4.3 and 4.4. Of the 78 bivariate pairs analyzed in Table 4.5, 46 had significant associations ($P < 0.05$). Because of the nature of correlation analysis some of these associations may be due to chance alone, while others may be the result of common causes and/or direct influences (Sokal and Rohlf, 1981). Verification of causal connections between variables would require experimental manipulations. Nevertheless, there are several highly correlated relationships ($r^2 > 0.60$) that are quite meaningful to this study.

Total above-ground biomass was found to have a high positive correlation with elevation (Table 4.5). Biomass tends to increase linearly from around 100 g dwt m^{-2} at an elevation of -0.80 m to approximately 1000 g dwt m^{-2} at the highest elevations measured in this study (Figure 4.3). However, elevation is probably not the variable directly responsible for the changes in biomass. Total species aerial

Table 4.5. Bivariate regression correlation coefficients between soil nutrient, available light, soil organic matter content, elevation, and total above-ground plant biomass variables (n = 31 for all relationships involving the variable "% Available Light", n = 70 for all relationships involving the variable "Biomass", all others n = 73).

	Biomass	Elev.	O.M.	N	P	K	Ca	Mg	Na	Fe	Zn	Mn
Elev.	.834 ****											
Organic Matter ($g\ kg^{-1}$)	.770 ****	.906 ****										
N ($g\ kg^{-1}$)	.803 ****	.937 ****	.977 ****									
P ($mg\ kg^{-1}$)	-.191 n.s.	-.098 n.s.	-.159 n.s.	-.177 n.s.								
K ($mg\ kg^{-1}$)	.084 n.s.	.031 n.s.	.187 n.s.	.208 n.s.	.155 n.s.							
Ca ($mg\ kg^{-1}$)	-.431 ***	-.404 ***	-.276 *	-.296 *	.105 n.s.	.156 n.s.						
Mg ($mg\ kg^{-1}$)	.474 ****	.427 ***	.316 **	.419 ***	.087 n.s.	.141 n.s.	.121 n.s.					
Na ($mg\ kg^{-1}$)	.100 n.s.	.247 *	.274 *	.325 **	.068 n.s.	.265 *	.115 n.s.	.316 **				
Fe ($mg\ kg^{-1}$)	-.296 *	-.585 ****	-.380 ***	-.430 ****	-.218 n.s.	.130 n.s.	.342 **	-.322 **	-.086 n.s.			
Zn ($mg\ kg^{-1}$)	.458 ****	.400 ***	.299 *	.358 **	-.219 n.s.	.066 n.s.	-.252 *	.592 ****	.291 *	.074 n.s.		
Mn ($mg\ kg^{-1}$)	-.047 n.s.	-.024 n.s.	.201 n.s.	.098 n.s.	-.340 **	.053 n.s.	.278 *	-.295 *	-.195 n.s.	.340 **	-.261 *	
% Available Light	-.866 ****	-.848 ****	-.832 ****	-.838 ****	-.077 n.s.	-.015 n.s.	.426 *	-.466 **	-.402 *	.456 *	-.535 **	.304 n.s.

Note : n.s., not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$.

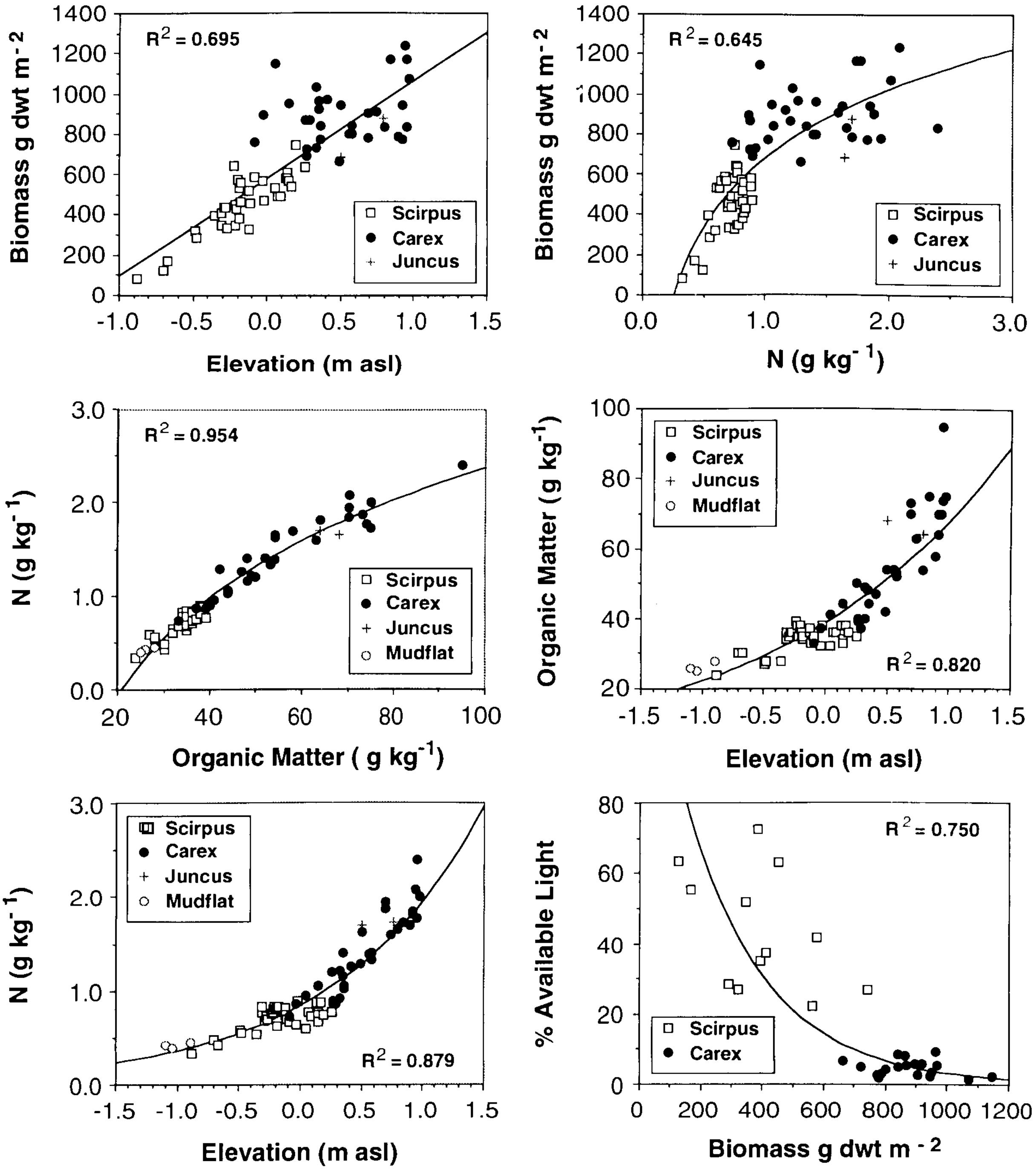

Figure 4.3. Scattergram plots of selected bivariate regressions from Table 4.4. Data point symbols indicate the dominant plant species in each sample site or the absence of any species (mudflat).

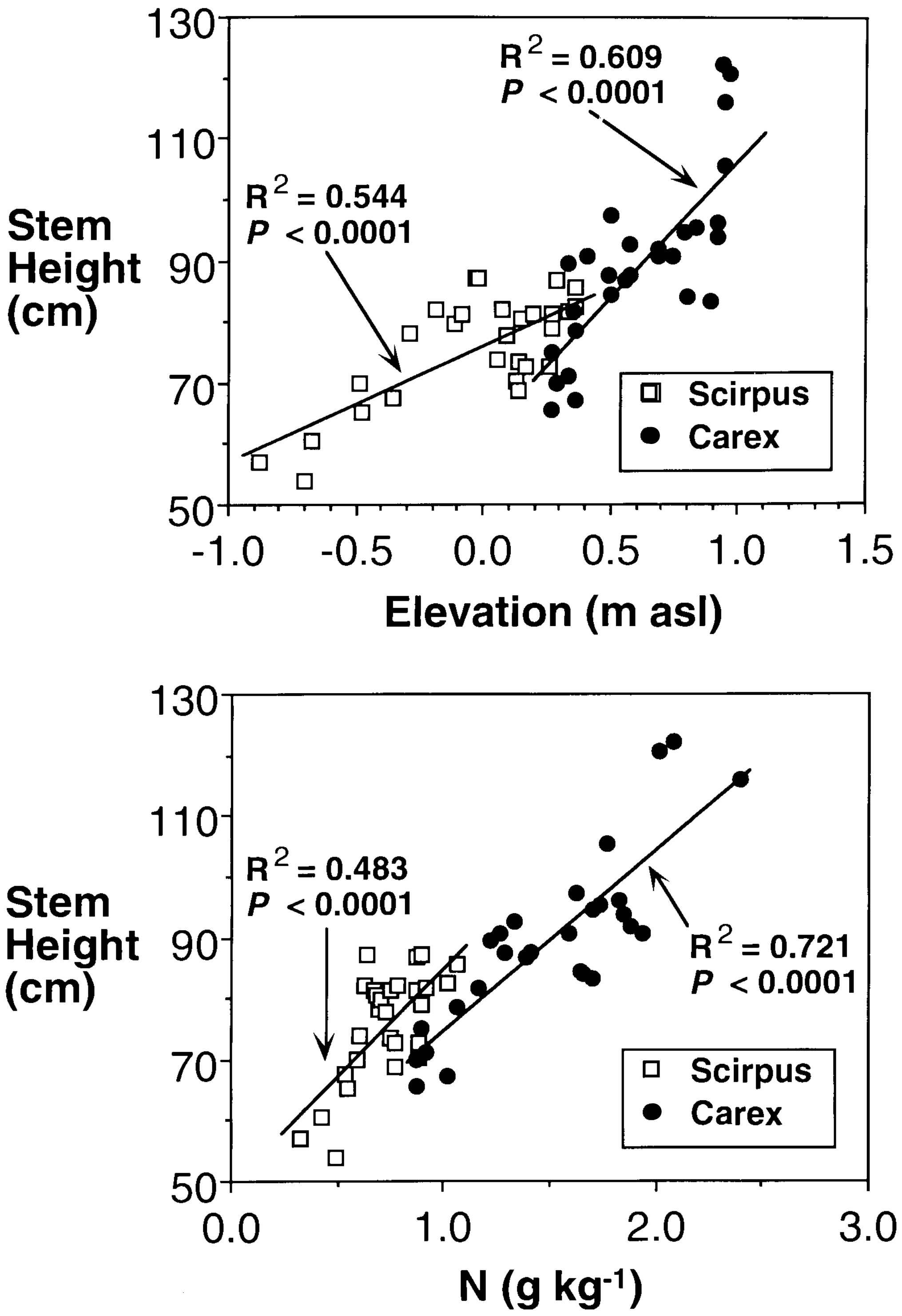

Figure 4.4. Scattergram plots of the relationship of Carex lyngbyei and Scirpus americanus shoot height with sample site elevation and total soil nitrogen (n = 28 for all four regressions).

biomass was also found to be highly correlated to total soil nitrogen (Table 4.5; Figure 4.3), and studies in tidal marsh communities have shown that soil nitrogen has a direct effect on biomass production (e.g., Valiela and Teal, 1974).

The highest correlation between the measured variables was between soil nitrogen and organic matter content (Table 4.5; Figure 4.3). This association is to be expected, because most of the nitrogen in tidal marsh sediments is found in organic combination (Aziz and Nedwell, 1979). High correlations were also found between platform elevation with organic matter content and total soil nitrogen (Table 4.5; Figure 4.3). Elevation probably influences the quantity of these two variables indirectly through other factors. Clearly, the amount of organic matter found in the sediments is directly related to above- and below-ground biomass production. In the high marsh, Carex lyngbyei produces more than twice as much above-ground biomass than the low marsh dominant Scirpus americanus (Table 4.1; Figure 4.1). Differences in the frequency of soil flooding can have a direct effect on the cycling and storage of nitrogen within soils (Ponnamperuma, 1984; Sprent, 1987; Craft et al., 1988). In particular, waterlogging stops the conversion of organic nitrogen to inorganic forms at the ammonium stage, and reduces the rate of organic matter decomposition. The frequency of marsh platform flooding can also influence the quantity of soil nitrogen and organic matter lost through physical export to the sea by tidal flushing (Valiela and Teal, 1974; 1979).

Percent available light at the soil surface was found to have high negative correlations with total above-ground biomass, elevation, soil organic matter and total soil nitrogen (Table 4.5). Of these four relationships, only the association between percent available light and biomass is conceivably directly functional (Figure 4.3). Increasing above-ground biomass probably reduces the light received at the soil surface by increasing the surface area in the plant canopy available for intercepting solar radiation. The other high correlations with available light are probably the result of common causes or direct relationships between these variables and total above-ground biomass (see Sokal and Rohlf, 1981, pp. 591-592).

Figure 4.4 describes the relationships between site elevation and soil nitrogen with measured shoot height of both Carex lyngbyei and Scirpus americanus. Elevation and soil nitrogen were found to have significant positive relationships with plant shoot height for both species. However, the association between shoot height and elevation is probably not causative, and may be the result of a common relationship with soil nitrogen. Verification of the causal connection between soil nitrogen and shoot height will be described later in Section 5.2.

4.4 1989 Descriptive Field Measurement Results

4.4.1 Biomass and Plant Canopy Analysis

Biomass, shoot height and plant canopy height measurements were made on May 22, June 19, and July 20, 1989. No measurements were made on April 24th because neither plant species had begun above-ground growth at this time. Figure 4.5 shows the growth of Scirpus americanus and Carex lyngbyei along a single transect running perpendicular to the elevation gradient of the marsh platform during the growing season. Observations in the field indicated that Carex lyngbyei began growth approximately 3 weeks before Scirpus americanus. By May 22, the average above-ground biomass of Carex lyngbyei (530.8 g dwt m^{-2}) along the sampled transect was approximately nine times greater than Scirpus americanus (59.8 g dwt m^{-2}). At the end of the growing season (approximately July 20) the relationship between above-ground biomass and elevation was similar to results obtained in 1988 field survey (see Figure 4.4).

Canopy height between the species also differed greatly along the transect (Figure 4.6). On May 22, Carex lyngbyei was on average 45 cm taller than Scirpus americanus. A similar height advantage also occurred on the June 19th sampling date. By July 20, the majority of the Scirpus plants lost their ability to stand upright and were lying flat,

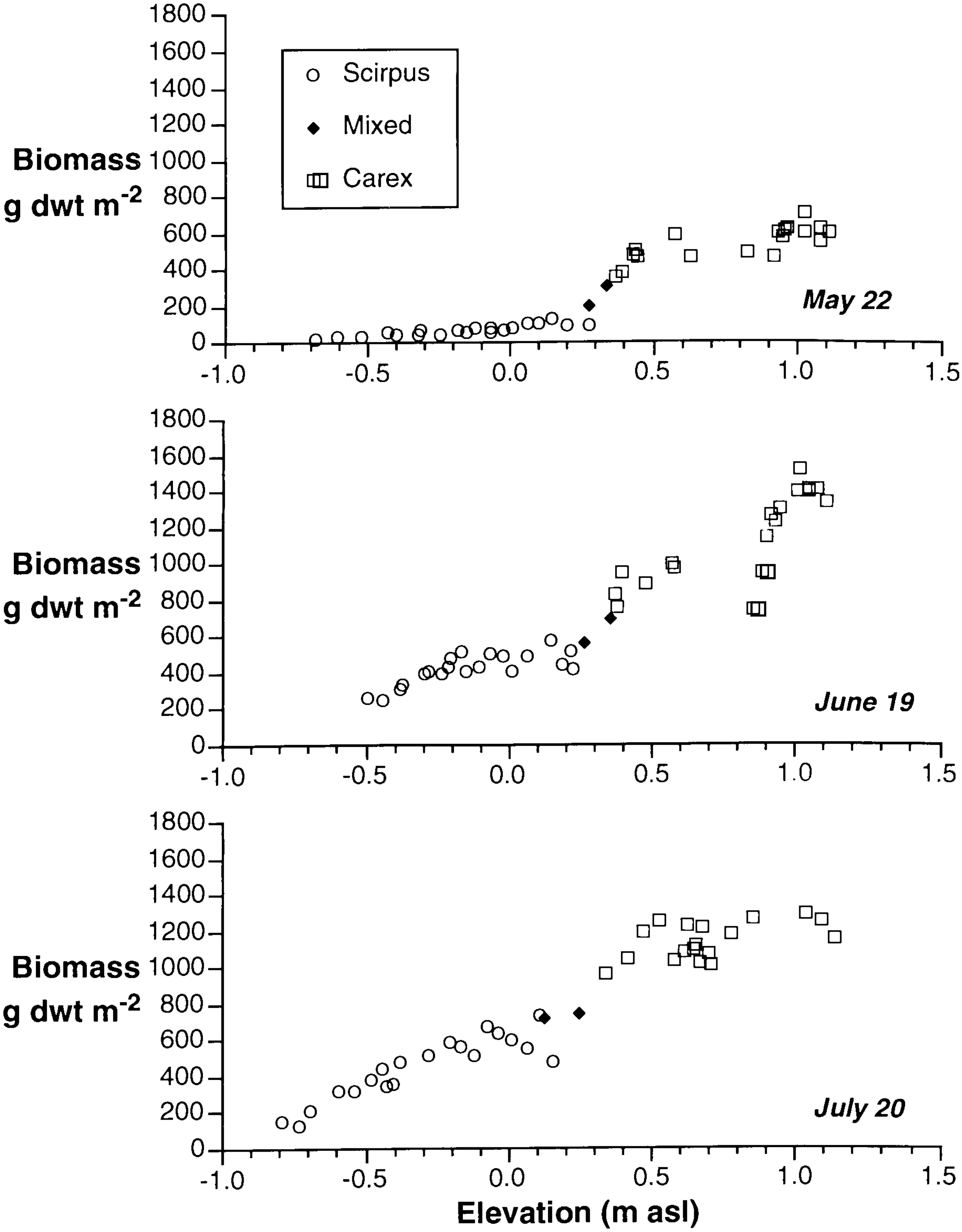

Figure 4.5. Above-ground biomass of Scirpus americanus and Carex lyngbyei sampled in the field along an elevational gradient on May 22, June 19, and July 20, 1989.

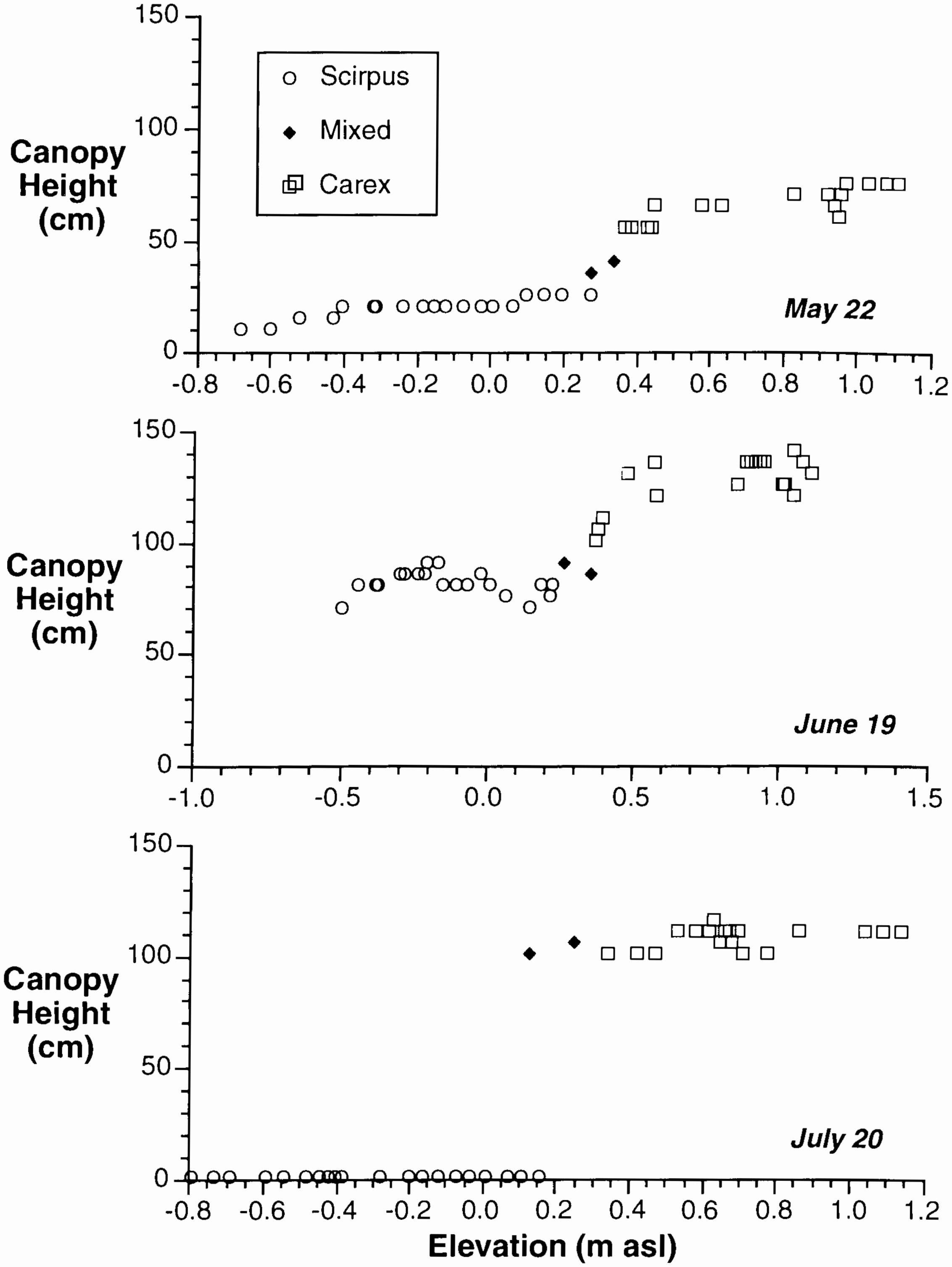

Figure 4.6. Canopy height of Scirpus americanus and Carex lyngbyei sampled in the field along an elevational gradient on May 22, June 19, and July 20, 1989.

while the height of the Carex lyngbyei canopy remained roughly the same as the previous month.

4.4.2 Available Light Analysis

Measurements of available light at the ground surface are presented in Figure 4.7 for May 22, June 19, and July 20th, 1989. Reduction in the availability of light beneath the Carex canopy began almost three weeks ahead of the Scirpus canopy. In May, an average of 97 % of the available light passed through the Scirpus canopy, while the Carex canopy reduced light levels at the ground surface to an average of 26 %. By June 19th, the availabilty of light at the soil surface in the Carex community was only 4 % on average. During that same sampling period, light levels in the Scirpus community were roughly 8 times greater with an average of 33 %. On July 20th, light levels in the Scirpus community increased to 100 %, because the plants of this community were now lying horizontally on the marsh platform. The Carex community, on the other hand, remained upright, and available light levels were similar to the previous sampling period.

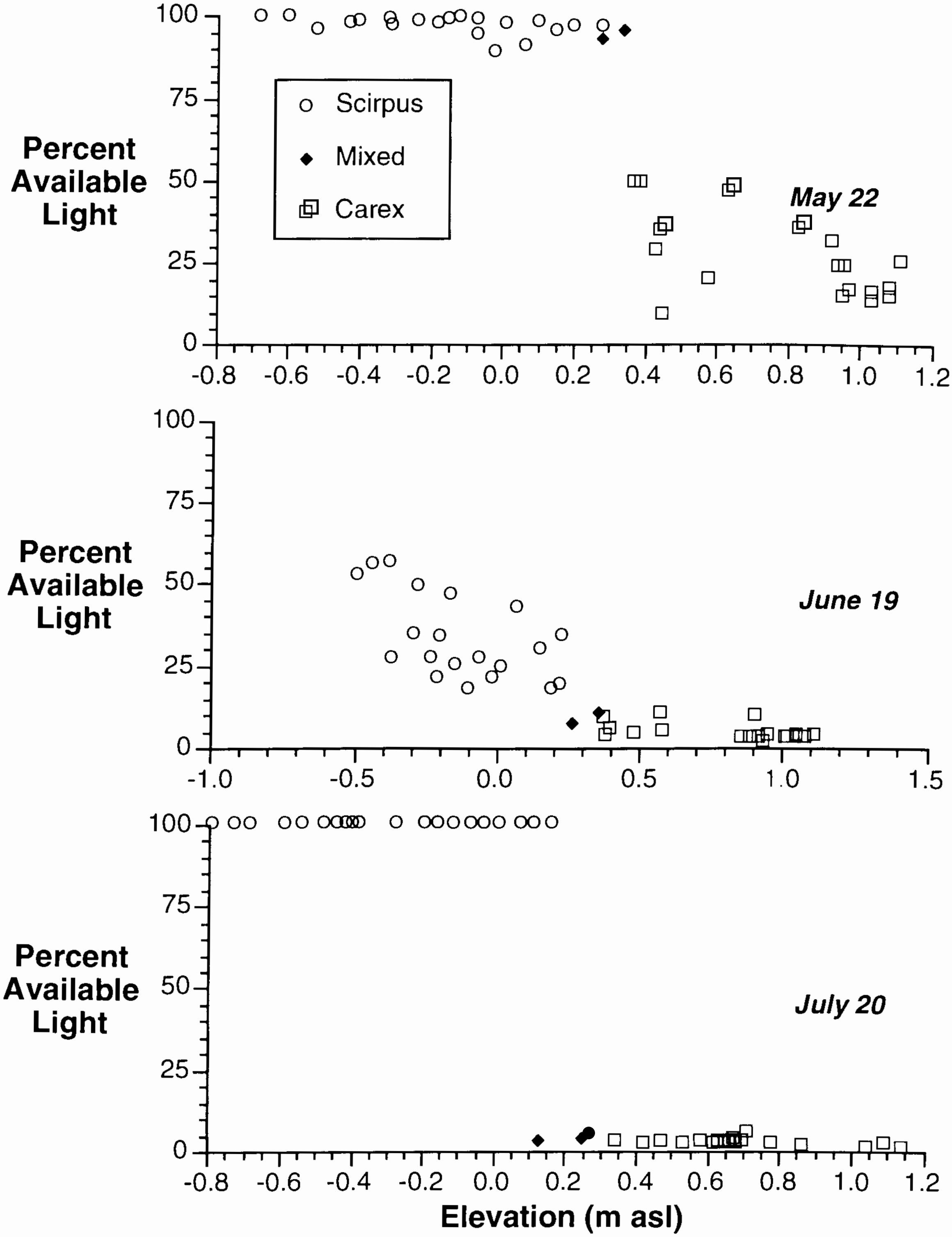

Figure 4.7. Percent available light found at the soil surface in field sites occupied by Scirpus americanus and Carex lyngbyei. Measurements were determined on May 22, June 19, and July 20, 1989.

4.4.3 Available Soil Nitrogen

No extractable nitrate was found in any of the soils sampled. Average extractable ammonium values in the soils of the two plant communities are given in Figure 4.8 for the four sampling dates. An initial analysis of the ammonium data with ANOVA indicated significant species (community) type and month of measurement effects (Table 4.6). Monthly effects were expected because mineralization of organic nitrogen by soil micro-organisms is controlled by temperature (Sprent, 1987). It follows then that April should have the lowest values and peak levels of ammonium should occur either in June or July. These results, however, were not attained. Instead, averaged monthly values for both communities indicated highest values in either April or May and lowest values in June. This deviation from the expected may be accounted for when plant consumption is also considered. Active consumption of the ammonium by the plants should reduce ambient levels in the soil to some minimal equilibrium level. Thus, greatest consumption should occur with maximum growth in June when mineralization is also high.

A closer examination of the soil ammonium values by month suggests that significant differences between the two community types only occurs in May (Table 4.7). During this sampling period, the Scirpus community had average ammonium

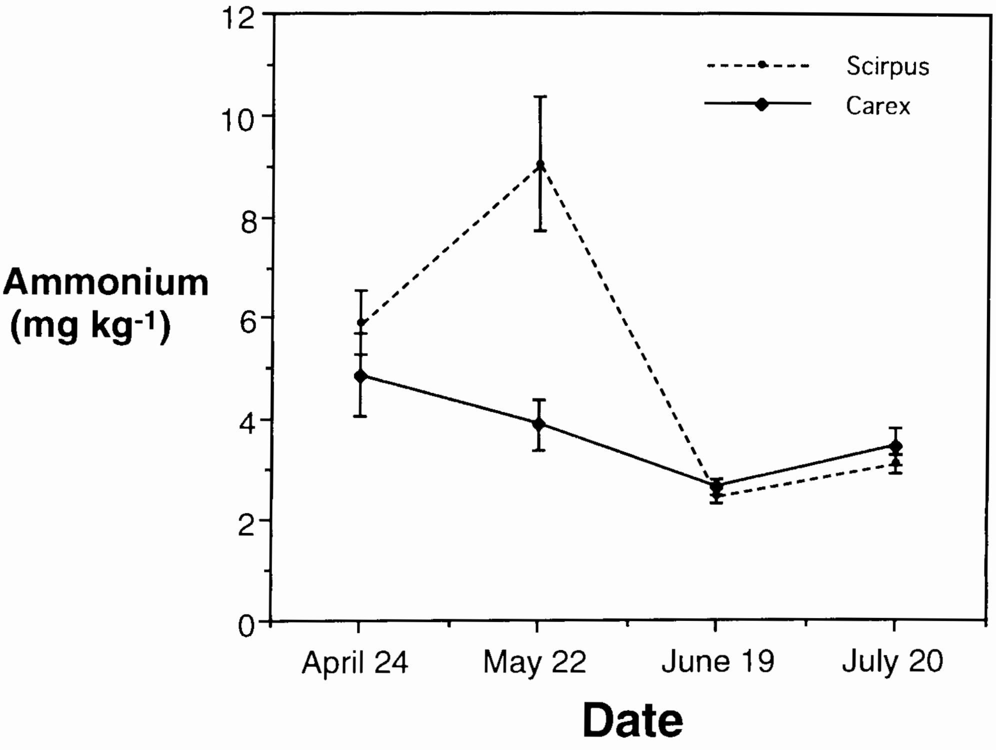

Figure 4.8. Mean (± SE) extractable soil ammonium found in <u>Scirpus</u> and <u>Carex</u> dominated sample sites for four dates during the growing season (n = 20 for each species and date). All soil samples were from the top 5 cm of the marsh sediment.

Table 4.6. Two-way ANOVA of extractable soil ammonium [log(x) transformation to homogenize variance] against species type and month of measurement.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Species	1	0.402	0.402	8.920	0.0033
Month	3	2.487	0.829	18.385	0.0001
Species **x** *Month*	3	0.855	0.285	6.319	0.0005
Error	152	6.855	0.045		
Total	159	10.599			

Table 4.7. Means (± SE) and sample sizes (n) of measured extractable soil ammonium from Scirpus and Carex community sites at Brunswick Point marsh on four sampling dates during the growing season. Results of Student's t-tests comparing data from the two different community types are also shown. Differences that are significant have their associated probabilites listed for two-tailed comparisons, while results that are not significant are designated "n.s.".

	Scirpus Community			Carex Community			
Month	Mean	± SE	n	Mean	± SE	n	*P*
April	5.91	0.63	20	4.88	0.53	20	n.s.
May*	9.04	1.31	20	3.89	0.49	20	<0.001
June	2.50	0.17	20	2.65	0.18	20	n.s.
July	3.10	0.20	20	3.45	0.36	20	n.s.

* Note : log(x) transformation was used to homogenize treatment variances.

values that were 2.3 times greater than the *Carex* community. This difference can possibly be explained by the fact that the *Carex* community had been growing for several weeks, and thus actively consuming soil nutrients from the rhizosphere. The *Scirpus* community, on the other hand, had just commenced above-ground growth.

4.4.4 Shoot Height Analysis

Table 4.8 displays mean shoot height data for quadrats where the two species coexisted. On May 22nd, *Carex lyngbyei* individuals were approximately 50 % taller than coexisting *Scirpus* plants in the transition zone. Mixed results were obtained from the three plots sampled on June 19th. On this sampling date, *Scirpus americanus* was significantly taller in the plot with the lowest elevation, no height difference between species occurred in the middle plot, and in the plot with the highest elevation *Carex lyngbyei* was taller. On the final sampling date, July 20th, *Scirpus americanus* was significantly taller in the plot with the lowest elevation. In the other two plots, no significant difference in species height was detected.

Table 4.8. Means (± SE) and sample sizes (n) of measured shoot heights from *Scirpus americanus* and *Carex lyngbyei* plants randomly sampled from quadrats in the transition zone on three dates during the 1989 growing season. Results of Student's t-tests comparing data from the two different species types are also shown. Differences that are significant have their associated probabilites listed for two-tailed comparisons, while results that are not significant are designated "n.s.".

		Scirpus americanus			*Carex lyngbyei*			
Date	**Plot #**	**Mean**	**± SE**	**n**	**Mean**	**± SE**	**n**	***P***
May 22	21	23.6	0.66	60	32.0	0.59	60	<0.0001
	22	26.3	0.92	60	38.2	0.76	60	<0.0001
June 19	21	70.4	2.01	60	61.1	1.47	60	<0.001
	22	75.7	2.18	60	73.1	1.97	60	n.s.
	23	88.1	2.74	46	95.6	2.37	60	<0.05
July 20	21	105.1	1.71	60	97.2	1.85	60	<0.01
	22	106.0	2.20	60	104.4	2.19	60	n.s.
	23	104.4	5.10	21	99.8	2.30	60	n.s.

CHAPTER 5

FERTILIZATION EXPERIMENT

5.1 Fertilization Experiment Methods

To test the hypothesis that soil nitrogen (or possibly phosphorus) is the limiting soil resource, fertilization experiments were established in the spring of 1989 in the zones dominated by Scirpus americanus and Carex lyngbyei. In the Carex zone five treatments were applied in 1.5 x 1.5 m plots surrounded by a 50 cm buffer zone in a 5 x 5 Latin square design to adjust for fertility differences in two directions (Box, Hunter and Hunter, 1978; Hicks, 1982). The Latin square was located between transects A and B (Figure 3.1) and spanned elevations from 0.70 to 0.90 m. Treatments consisted of a control (no fertilizer applied), 200 kg ha^{-1} N, 400 kg ha^{-1} N, 100 kg ha^{-1} P, and 200 kg ha^{-1} N + 100 kg ha^{-1} P. Nitrogen was applied with the commercial fertilizer urea (46-0-0), while phosphorus was applied as superphosphate fertilizer (0-45-0). Both fertilizers were applied to the plots in three equal quantities (33.3 % of the total application) at three different time periods. The fertilizers were first applied during the last week of March 1989. Subsequent applications were made five and eight weeks after the first. All fertilizers were placed 5 cm beneath the soil surface in equally spaced bands in each plot.

Adjacent (approximately 10 m south) to transect C another 5 x 5 Latin square treatment design was set up in the zone dominated by Scirpus americanus. The elevation of this experimental plot was between -0.15 and -0.25 m. Treatments and application dates for this experiment were identical to the experiment carried out in the Carex zone. However, the general topography of this area of the marsh is much flatter than the area where transects A and B are located. As a result many shallow water-filled hollows exist in this area on the marsh surface at low tide. Further, the presence of the numerous hollows in the Scirpus zone resulted in certain plots in the Latin square being established inside them. It was feared that the hollows were the result of goose grubbing and that the removal of Scirpus americanus rhizomes by the geese might influence the results of the experiment. Thus, to ensure the results of this fertilization experiment, a second set of plots were established in an area where the geese were known not to feed. This site was located near transects A and B in the Scirpus americanus community at an elevation from -0.10 to 0.20 m. The arrangement of this experiment was a simple randomized block design replicated five times with four treatments. This arrangement was picked over the Latin square design because of space limitations on the marsh platform. The treatments consisted of a control, 150 kg ha^{-1} N, 300 kg ha^{-1} N, and 450 kg ha^{-1} N. A Latin square design was not employed because the steeper platform slope in this area of the marsh provided less surface area for plot placement. All treatments plots were 2 x 2 m with a 1 m buffer zone around them. Fertilizers were once again placed 5 cm beneath the marsh surface, in bands, in three equal quantities at the same time periods as the previous fertilization experiments.

Plots in the Carex lyngbyei zone and Scirpus americanus zone (block design) were sampled for above ground biomass on June 13th and 14th, 1989 by clipping all plants at ground level in a 0.25 m^{-2} quadrat. Prior to the destructive sampling, percent available light at the soil surface was measured within 2 h of solar noon with an Eppley Pyranometer using the method described earlier. Because of time constraints, plots in the Scirpus americanus zone that were set up in a Latin square design were sampled only for above-ground biomass and shoot height on June 24, 1989. The average height of the plants sampled in all of the plots were determined by measuring 30 randomly selected plants to the nearest 1.0 cm in the laboratory. Analysis of the data collected was accomplished with ANOVA. Treatment comparisons were made with Tukey's honestly significant difference test. This test was chosen for analysis because of its simplicity and power (Einot and Gabriel, 1975; Underwood, 1981; Mize and Schultz, 1985; Day and Quinn, 1989). In all cases normality and variance equality were tested if the sample sizes were large enough. If the data had unequal variances, transformations were used for the correction of this problem (Steel and Torrie, 1980; Underwood, 1981; Day and Quinn, 1989).

5.2 Fertilization Experiment Results

Both above-ground biomass and shoot height of Carex lyngbyei in the field responded positively to the fertilizer treatments (Tables 5.1 and 5.3). In particular, the addition of nitrogen increased the above-ground biomass of Carex by more than 30 % and shoot height by approximately 21 % with the 200 kg ha^{-1} treatment (Tables 5.2 and 5.4). Applying nitrogen at 400 kg ha^{-1} did not significantly increase biomass production or shoot height compared to the 200 kg ha^{-1} treatment. The application of phosphorus alone did not significantly increase above-ground biomass and shoot height when compared to the control. Finally, the combination of 100 kg ha^{-1} of phosphorus with 200 kg ha^{-1} of nitrogen did not significantly increase yields compared to the same amount of nitrogen applied alone.

Increases in above-ground biomass produced concomitant decreases in light available at the soil surface in stands of Carex lyngbyei (Table 5.5). Significant decreases in available light were observed with the 200 kg ha^{-1} and 400 kg ha^{-1} nitrogen treatment, and the 200 kg ha^{-1} nitrogen + 100 kg ha^{-1} phosphorus treatment (Table 5.6). However, the

Table 5.1. Analysis of variance table of above-ground biomass for the *Carex lyngbyei* fertilization experiment.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Columns	4	24072.1	6018.03	0.8293	0.5316
Rows	4	45735.6	11433.90	1.5757	0.2436
Treatment	4	623408.0	158102.00	21.7870	< 0.0001
Error	12	87079.2	7256.60		
Total	24	789295.9			

Table 5.2. Mean above-ground biomass (± SE) of *Carex lyngbyei* for each fertilization treatment.

Treatment	**Biomass g dwt m^{-2}**
Control	886.32 (31.85)a
200 kg ha^{-1} N	1159.44 (65.37)b
400 kg ha^{-1} N	1232.40 (17.97)b
100 kg ha^{-1} P	853.52 (21.91)a
200 kg ha^{-1} N + 100 kg ha^{-1} P	1178.72 (41.87)b

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test ($P = 0.05$).

Table 5.3. Analysis of variance table of shoot height for the Carex lyngbyei fertilization experiment.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Columns	4	416.61	104.153	1.8254	0.1888
Rows	4	46.52	11.631	0.2038	0.9314
Treatment	4	2653.35	663.339	11.6260	0.0004
Error	12	684.70	57.059		
Total	24	3801.19			

Table 5.4. Mean shoot height (± SE) of Carex lyngbyei for each fertilization treatment.

Treatment	**Height cm**
Control	82.3 (5.9)a
200 kg ha^{-1} N	99.5 (2.0)b
400 kg ha^{-1} N	108.0 (1.8)b
100 kg ha^{-1} P	82.0 (3.4)a
200 kg ha^{-1} N + 100 kg ha^{-1} P	98.9 (1.9)b

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test ($P = 0.05$).

Table 5.5. Analysis of variance table of percent available light [ln(x) transformation to homogenize variance] for the Carex lyngbyei fertilization experiment.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Columns	4	0.183565	0.045891	4.6156	0.0173
Rows	4	0.095526	0.023882	2.4019	0.1076
Treatment	4	1.238860	0.309714	31.5000	< 0.0001
Error	12	0.119312	0.009943		
Total	24	1.637260			

Table 5.6. Back transformed mean percent available light values (± 95% confidence interval) at the soil surface for each fertilization treatment in the Carex lyngbyei zone.

Treatment	**% Available Light**
Control	6.6 (4.0, 10.8)a
200 kg ha^{-1} N	2.7 (1.7, 4.3)b
400 kg ha^{-1} N	1.6 (1.1, 2.7)c
100 kg ha^{-1} P	6.0 (4.8, 7.6)a
200 kg ha^{-1} N + 100 kg ha^{-1} P	2.8 (2.1, 3.7)b

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test (*P* = 0.05).

phosphorus/nitrogen combination in the latter treatment did not have an additional effect when compared to the 200 kg ha^{-1} nitrogen treatment. Similarly, phosphorus applied alone was not statistically different from the experimental control. In the Scirpus americanus fertilization treatments several plots in the Latin square experiment were poorly drained after tidal inundation and may have been grubbed by geese. Some of these plots produced extremely few Scirpus americanus shoots and low above-ground biomass, and were therefore excluded from the analysis. All of these plots were located in the last two "rows" of the experimental design. Analysis of this experiment (by ANOVA) was accomplished by excluding the restricting effect of the "columns" from the model. This effect corresponds to a direction perpendicular to the platform gradient.

Tables 5.7, 5.9, 5.11, and 5.13 present the analysis of the effects of the fertilization treatments on above-ground biomass and shoot height of Scirpus americanus in the Latin square and block experimental designs. Further analysis by multiple comparisons indicated that the addition of nitrogen increased the above-ground biomass of Scirpus by > 70 %, with no statistical difference between nitrogen application rates (Tables 5.8 and 5.12). Shoot height increased significantly (by 26 to 50 %) depending on the nitrogen application rate (Tables 5.10 and 5.14). Once again, the addition of phosphorus alone caused no significant increase in Scirpus

Table 5.7. Analysis of variance table of above-ground biomass for the Scirpus americanus fertilization experiment (Latin Square design).

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Rows	2	3988.76	1994.38	0.221	0.8063
Treatment	4	437410.03	109352.51	12.131	0.0017
Error	8	72112.47	9014.06		
Total	14	513511.26			

Table 5.8. Mean above-ground biomass (± SE) of Scirpus americanus for each fertilization treatment (Latin Square design).

Treatment	**Biomass g dwt m^{-2}**
Control	457.6 (37.1)a
200 kg ha^{-1} N	776.9 (63.8)b
400 kg ha^{-1} N	868.5 (68.6)b
100 kg ha^{-1} P	518.3 (23.7)a
200 kg ha^{-1} N + 100 kg ha^{-1} P	841.3 (44.5)b

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test ($P = 0.05$).

Table 5.9. Analysis of variance table of shoot height for the Scirpus americanus fertilization experiment (Latin Square design).

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Rows	2	32.624	16.312	1.245	0.3383
Treatment	4	2135.606	533.901	40.745	< 0.0001
Error	8	104.827	13.103		
Total	14	2273.057			

Table 5.10. Mean shoot height (± SE) of Scirpus americanus for each fertilization treatment (Latin Square design).

Treatment	**Height cm**
Control	77.0 (0.7)a
200 kg ha^{-1} N	97.6 (1.6)b
400 kg ha^{-1} N	104.6 (0.4)b
100 kg ha^{-1} P	77.9 (1.4)a
200 kg ha^{-1} N + 100 kg ha^{-1} P	101.8 (4.2)b

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test ($P = 0.05$).

Table 5.11. Analysis of variance table of above-ground biomass for the Scirpus americanus fertilization experiment.

Source	d.f.	Sum of Squares	Mean Square	F-ratio	Prob.
Blocks	4	110252.6	27463.1	3.4660	0.0421
Treatment	3	357285.8	119095.3	14.9740	0.0002
Error	12	95441.3	7953.4		
Total	19	562979.9			

Table 5.12. Mean above-ground biomass (± SE) of Scirpus americanus for each fertilization treatment.

Treatment	Biomass g dwt m^{-2}
Control	317.68 (21.18)a
150 kg ha^{-1} N	581.60 (63.32)b
300 kg ha^{-1} N	606.48 (56.82)b
450 kg ha^{-1} N	666.16 (50.97)b

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test ($P = 0.05$).

Table 5.13. Analysis of variance table of shoot height for the Scirpus americanus fertilization experiment.

Source	d.f.	Sum of Squares	Mean Square	F-ratio	Prob.
Blocks	4	41.158	10.289	0.697	0.6085
Treatment	3	1605.654	535.218	36.250	< 0.0001
Error	12	177.174	14.764		
Total	19	1823.986			

Table 5.14. Mean shoot height (± SE) of Scirpus americanus for each fertilization treatment.

Treatment	Height cm
Control	50.6 (5.9)a
150 kg ha^{-1} N	65.2 (2.0)b
300 kg ha^{-1} N	69.5 (1.8)bc
450 kg ha^{-1} P	74.7 (3.4)c

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test (*P* = 0.05).

Table 5.15. Analysis of variance table of percent available light [ln(x) transformation to homogenize variance] for the *Scirpus americanus* fertilization experiment.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Blocks	4	0.66823	0.01671	1.291	0.3276
Treatment	3	1.64996	0.54999	42.504	< 0.0001
Error	12	0.15528	0.01294		
Total	19	1.87206			

Table 5.16. Back transformed mean percent available light values (± 95% confidence interval) at the soil surface for each fertilization treatment in the *Scirpus americanus* zone.

Treatment	**% Available Light**
Control	32.4 (21.1, 49.7)a
150 kg ha^{-1} N	9.9 (6.6, 14.9)b
300 kg ha^{-1} N	6.7 (5.4, 8.2)c
450 kg ha^{-1} N	6.2 (4.9, 8.0)c

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test (*P* = 0.05).

americanus above-ground biomass or shoot height when compared to control treatments. Finally, the combination of 100 kg ha^{-1} of phosphorus with 200 kg ha^{-1} of nitrogen was not significantly different from the same amount of nitrogen applied alone.

The effect of fertilization on the amount of light available at the soil surface of stands of Scirpus americanus was only analyzed in block experimental design (Table 5.15). Significant decreases in available light of between 69 to 81 % were observed with the 150 kg ha^{-1}, 300 kg ha^{-1} and 450 kg ha^{-1} nitrogen treatments when compared to the control (Table 5.16).

CHAPTER 6

TRANSPLANTATION EXPERIMENTS

6.1 Field Distribution Experiment Methods

The purpose of this experiment was to determine whether the observed elevational ranges of Scirpus americanus and Carex lyngbyei are equivalent to their elevational distributions when grown alone. In this experiment, the two species were grown at six elevations across the range occupied by these species (- 0.51, - 0.02, 0.20, 0.39, 0.56, and 0.83 m asl). The three lowest sites were occupied by stands of Scirpus americanus, while the upper three occurred in the Carex lyngbyei zone.

The six experimental sites run parallel and approximately 10 m south of transect B (see Figure 3.1). Within each experimental plot 5 parallel rows of plastic pots were laid out on a line perpendicular to the slope of the marsh platform and buried flush with the surface of the marsh. All of the pots were placed into the marsh sediment during August and September of 1987. Each pot was 15 cm wide and 18 cm deep, and separated from other pots by a distance of approximately 10 cm. All pots were filled with soil collected from the mudflat located at the site (see Figure 3.1). The soil in the pots contained no living vascular plant material. During the period of settling in, the pots were constantly monitored for colonizing vascular plants, and any plants found colonizing were removed.

Scirpus americanus and Carex lyngbyei rhizomes were transplanted into the pots during the last week of March, 1989, using a golf course cup cutter to remove a soil core, complete with rhizomes with an approximate length of 17 cm and a radius of 5.2 cm. A similar core was removed from the pots in each plot, and then replaced by a randomly selected core containing either Carex lyngbyei or Scirpus americanus rhizomes. In total, 20 cores of each species were transplanted in each of the six experimental sites.

During the two growing seasons that this experiment ran, the region surrounding the pots (approximately 0.50 m radius from pot center) was removed of any vegetation by cutting the plants at the marsh surface. Harvesting of the two species in the 6 sites occurred on July 27, 1989 and July 13, 1990. On each of these dates, 10 pots at each site were clipped at ground level. The vegetation samples were then washed of sediment, dried at 70°C for 72 h, and then weighed to 0.1 g.

Means and standard errors were calculated from the 10 samples for each site and species. Samples were also subjected to one-way ANOVA to determine if site elevation had an effect on the growth of each species. Comparisons between treatment means were accomplished with Tukey's honestly significant difference test. This test was selected for analysis because of its simplicity and power (Einot and

Gabriel, 1975; Underwood, 1981; Mize and Schultz, 1985; Day and Quinn, 1989). In all cases normality and variance equality were tested if the sample sizes were large enough. If the data had unequal variances, transformations were used for the correction of this problem (Steel and Torrie, 1980; Underwood, 1981; Day and Quinn, 1989). If the transformations did not homogenize the variance of the data, a Welch's robust ANOVA was employed for analysis (Welch, 1951; Clinch and Keselman, 1982; Day and Quinn, 1989) followed by Games and Howell multiple comparison tests (Games and Howell, 1976; Day and Quinn, 1989).

6.2 *Scirpus americanus* Field Transplant Methods

An experiment was performed in which *Scirpus americanus* was transplanted into the high marsh areas dominated by *Carex lyngbyei* under two experimental treatments. The purpose of this experiment was to test the hypothesis that *Carex lyngbyei* competition excludes *Scirpus americanus* from the high marsh through light reduction. The two treatments consisted of the removal of all plants in a one meter square plot, and a control where all plants were left standing at field densities. Treatments were applied in the field near transect A at an elevation of between 0.55 to 0.90 m in a randomized paired design (Box, Hunter and Hunter, 1978), replicated 10 times, with treatments separated by a one meter buffer zone.

Each removal treatment received an application of the herbicide "Round-up" to all emerging plants in an area 75 x 75 cm in the center of the plots in late April. Two weeks after (May 5, 1989) the herbicide application a column of soil (10 x 10 cm and 30 cm deep) containing Scirpus americanus rhizomes was transplanted flush into the center of each plot. The removal plots were constantly monitored, and any plants found growing in the 75 x 75 cm area surrounding the Scirpus americanus rhizome transplants were removed by cutting them at ground level. After 84 days of growth in the experimental plots, all of the Scirpus americanus shoots in each 10 x 10 cm column were counted, measured for height, and then harvested at ground level for above-ground biomass determination (see Section 4.2.1 for methods). Analysis of the data collected in this experiment was accomplished with a paired Student's t-test.

6.3 Carex lyngbyei Field Transplant Methods

An experiment was performed in which Carex lyngbyei was transplanted into the low marsh area dominated by Scirpus americanus under two experimental treatments. The purpose of the experiment was to test the hypothesis that Scirpus americanus excludes Carex lyngbyei from the low marsh possibly through soil nitrogen competition. The two treatments consisted of the removal of all plants in a one meter square quadrat, and a control where all plants were left standing at natural densities. Treatments were applied in the field near transects A, B and C at an elevation of between 0.00 to 0.20 m in a randomized paired design (Box, Hunter and Hunter, 1978), replicated 10 times, with treatments separated by a one meter buffer zone.

On May 6, 1989, cores of soil (17 cm in length and 5.2 cm in radius) containing _Carex_ _lyngbyei_ rhizomes were removed from an elevation of between 0.55 to 0.90 m. The cores were then transplanted immediately into the center of each of the 20 experimental plots in the _Scirpus_ zone. After transplantation, the removal plots were constantly monitored, and any plants found growing in the 75 x 75 cm area surrounding the _Carex_ _lyngbyei_ rhizome transplants were removed by cutting them at ground level. After two growing seasons in the experimental plots all of the _Carex_ _lyngbyei_ shoots in each core were harvested at ground level on July 17, 1990. The shoots were then transported immediately to the laboratory where they were counted, measured for height by selecting 30 random shoots, and measured for dry biomass (see Section 4.2.1 for methods). The data were then analyzed with a paired Student's t-test.

6.4 Carex lyngbyei Field Transplant with Fertilization Methods

This experiment examined the growth of transplanted rhizomes of Carex lyngbyei which received five different nutrient additions in the Scirpus americanus zone. The experimental design was a 5 x 5 Latin square replicated twice with individual treatment cells measuring 1 meter square surrounded by 0.50 m buffer zone. Rhizome material was removed from the Carex lyngbyei zone (from an elevation from 0.70 to 0.90 m) from March 22nd to 25th 1989 with a golf course cup cutter. Four randomly selected rhizome cores were then immediately transplanted in each treatment cell equidistant from each other and the cell boundary.

The treatments of added nutrients consisted of a control (no fertilization), 200 kg ha^{-1} N, 400 kg ha^{-1} N, 100 kg ha^{-1} P, and 200 kg ha^{-1} N + 100 kg ha^{-1} P. Nitrogen was applied as commericial urea (46-0-0), and phosphorus was applied as commerical superphosphate fertilizer (0-45-0). Fertilizers were applied to the plots in three equal quantities (33.3 % of the total application) at three different time periods. The fertilizers were first applied during the last week of March 1989. Subsequent applications were made five and eight weeks after the first. All fertilizers were placed 5 cm beneath the soil surface in crisscrossing bands on either side of the rhizome cores.

On June 22, 1989 all above-ground biomass from the two healthiest core transplants was clipped at ground level for each treatment cell and immediately shipped to the laboratory. Only two cores were sampled out of the four transplanted because of time and labor constraints. At the laboratory all the Carex shoots for each treatment cell were then measured for height and an average height value was computed. On completion of the height measurements the plant material was then washed of sediment, dried at 70°C for 72 h, and then weighed to 0.1 g. Analysis of the height and above-ground biomass data was accomplished with ANOVA and multiple comparison tests (see Section 6.1 for complete statistical methods).

6.5 Field Distribution Experiment Results

Tables 6.1 and 6.2 present the results of analyzing the relationship of species above-ground biomass with site elevation for one and two growing seasons using ANOVA or Welch's robust ANOVA. Subsequent analysis, by way of multiple comparisons, revealed that significant differences in Scirpus americanus and Carex lyngbyei above-ground biomass occurred between transplants growing at different elevations (Tables 6.3 and 6.4). Graphically described, the seasonal accumulation of above-ground biomass for transplanted Scirpus americanus and Carex lyngbyei plants against elevation

Table 6.1. Analysis of variance tables of Scirpus americanus and Carex lyngbyei transplant above-ground biomass against site elevation in the distribution experiment. All plants were harvested July 27, 1989.

Scirpus americanus

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Site	5	434889.2	432402.3	6.486	< 0.0001
Error	54	724181.8	29617.4		
Total	59	1159071.0			

Carex lyngbyei

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Site	5	3263444.0	652688.8	3.796	0.0051
Error	54	9284836.4	171941.4		
Total	59	12548280.4			

Table 6.2. Analysis of variance table and Welch's ANOVA calculated parameters for Scirpus americanus and Carex lyngbyei transplant above-ground biomass against site elevation in the distribution experiment. All plants were harvested July 10, 1990.

Scirpus americanus

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Site	5	2162011.6	432402.3	14.600	< 0.0001
Error	54	1599341.8	29617.4		
Total	59	3761353.4			

Carex lyngbyei

Welch's ANOVA

A = 0.0006764, **B** = 0.0000002175
W = 52.560684, **df1** = 5, **df2** = 24.5413502
Significant, $P < 0.0001$

Table 6.3. Average (± SE) above-ground biomass values of Scirpus americanus and Carex lyngbyei for the six elevation treatments (n = 10) in the field distribution experiment. All plants were transplanted into experimental sites during the last week of March, 1989. Harvesting of plants took place on July 27, 1989. All statistical comparisons are intraspecific.

Site Elevation (m asl) [Species Zone]	Scirpus americanus Above-ground Biomass (g dwt m^{-2})	Carex lyngbyei Above-ground Biomass (g dwt m^{-2})
- 0.51 [Scirpus]	262.5a (31.9)	529.7v (103.8)
- 0.02 [Scirpus]	488.5b (42.9)	1165.4w (154.6)
0.20 [Transition]	383.8bc (36.8)	1070.1vwx (151.4)
0.39 [Carex]	353.2abcd (24.1)	1027.7vwxy (107.4)
0.56 [Carex]	381.4abcde (49.4)	1136.0wxyz (102.6)
0.83 [Carex]	229.6ade (28.5)	1241.9wxyz (153.3)

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test ($P = 0.05$).

Table 6.4. Average (± SE) above-ground biomass values of *Scirpus americanus* and *Carex lyngbyei* for the six elevation treatments (n = 10) in the field distribution experiment. All plants were transplanted into experimental sites during the last week of March, 1989. Harvesting of plants took place on July 10, 1990. All statistical comparisons are intraspecific.

Site Elevation (m asl) [Species Zone]	*Scirpus americanus* Above-ground Biomass (g dwt m^{-2})	*Carex lyngbyei* Above-ground Biomass (g dwt m^{-2})
- 0.51 [Scirpus]	201.3_{a} (46.0)	550.9_{v} (108.7)
- 0.02 [Scirpus]	593.3_{b} (44.4)	2332.0_{w} (298.3)
0.20 [Transition]	475.6_{bc} (56.6)	1944.7_{wx} (190.5)
0.39 [Carex]	230.7_{ad} (45.0)	1639.8_{xy} (64.4)
0.56 [Carex]	673.3_{bce} (86.4)	1391.4_{xyz} (114.3)
0.83 [Carex]	226.0_{ad} (31.5)	951.2_{vz} (65.2)

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test or a Games-Howell test if treatment variances were unequal ($P = 0.05$).

indicates that these two species can grow outside their natural distributions even after two growing seasons (Figures 6.1 and 6.2).

After one growing season, the above-ground biomass accumulation of Carex lyngbyei ranged from 1028 to 1242 g dwt m^{-2} in the 5 highest experimental sites (Table 6.3). In the lowest site, Carex biomass accumulation was approximately 530 g dwt m^{-2}, and was statistically different from only three of the transplant sites above it. After two growing seasons, greater variation in transplant biomass began to develop. Carex lyngbyei continued to grow at the lowest site (-0.51 m) even after two growing seasons. However, the accumulation of above-ground biomass at this site was now statistically similar only to the highest site in the experiment (Table 6.4). Maximum biomass after two seasons of growth was achieved at an elevation of -0.02 m, which is approximately 0.20 m below the lower boundary of the Carex community and approximately 1.0 m below sites of maximum accumulation in the field (see Figure 4.3). One explanation for these perplexing results may be related to the amount of plant resources allocated to the production of seeds. Field observations during the second growing season indicated that the transplants at the -0.02 m site were producing no seed heads, while transplants at the 0.20 m site produced a few seed heads. Moreover, transplants at experimental sites at 0.39, 0.56 and 0.83 m seemed to produce greater numbers of

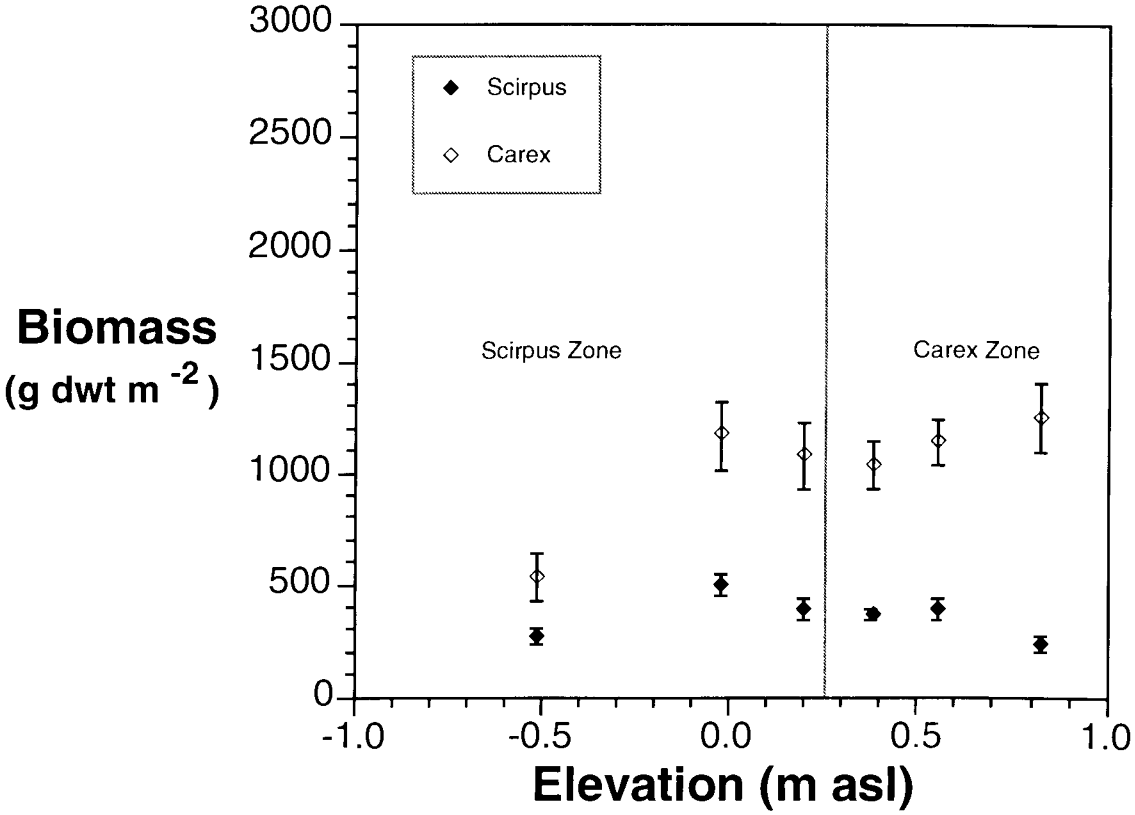

Figure 6.1. Above-ground biomass accumulation (± SE) of Scirpus americanus and Carex lyngbyei transplants after one growing season. Line at an elevation of approximately 0.25 m indicates the position of the species transition zone.

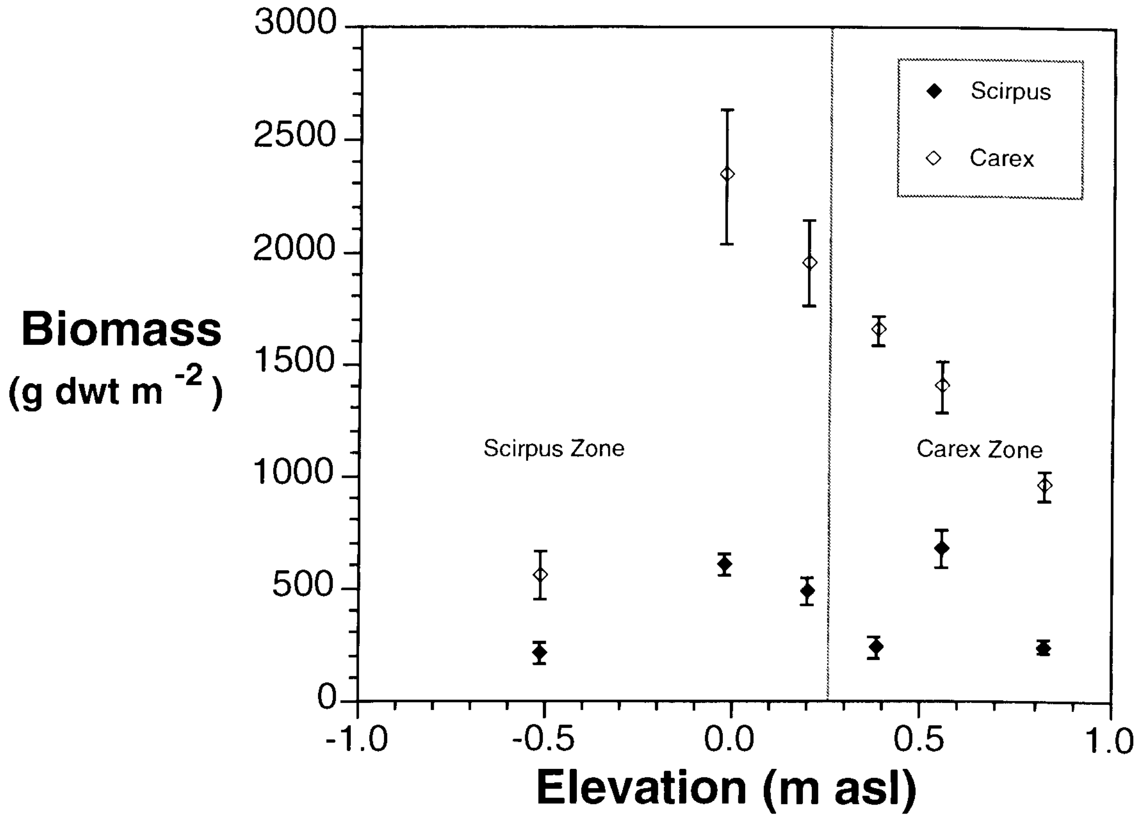

Figure 6.2. Above-ground biomass accumulation (± SE) of Scirpus americanus and Carex lyngbyei transplants after two growing seasons. Line at an elevation of approximately 0.25 m indicates the position of the species transition zone.

seed heads with elevation. Thus, the production of seed heads, which may be environmentally initiated, may reduce the amount of photosythate put into the production of stems and leaves, lowering overall above-ground biomass.

Scirpus americanus, after one growing season, achieved its lowest accumulation of above-ground biomass (approximately 250 g dwt m^{-2}) in sites with a site elevation of -0.51 and 0.83 m (Table 6.3). The other four sites had higher, but statistically similar, biomass values ranging from 350 - 490 g dwt m^{-2}. After two growing seasons, a more complex pattern developed (Table 6.4). Sites at an elevation of -0.51, 0.39, and 0.83 m accumulated above-ground biomass values between 475 - 675 g dwt m^{-2}, while the other three sites had lower biomass values ranging from 200 - 230 g dwt m^{-2}. The decline in Scirpus above-ground biomass production at 0.39 m may be due to the high concentration of soil sulfides (personal observation).

The lower productivity of both Scirpus americanus and Carex lyngbyei transplants in the lowest experimental site (-0.51 m) may be due to increased inundation and flooding. Several studies in tidal or similar aquatic environments have shown that prolonged flooding has an inhibitory effect on plant productivity (Jackson and Drew, 1984; Seliskar, 1988; 1990; Hellings and Gallagher, 1992). Finally, the decline in productivity of both species at the highest experimental site (0.83 m) may be an artifact of transplanting. Observations in the field, during June and July, indicated that the soil in the transplant pots was somewhat drier than the surrounding soil. Sites at this elevation are flooded only for short periods of time (see Table 4.4) and the presence of the pots may have impeded the movement of soil water.

6.6 *Scirpus americanus* Field Transplant Results

Table 6.5 shows the results of a Student's t-test analysis of *Scirpus americanus* above-ground biomass, average shoot height and shoot number for removal and control (*Carex* present) treatments. In the presence of *Carex lyngbyei*, *Scirpus* biomass and shoot number decreased significantly (by 75 and 77 %, respectively). The height of the few *Scirpus* shoots that continued to grow in the control plots increased by 62 %.

6.7 *Carex lyngbyei* Field Transplant Results

The results of a Student's t-test analysis of *Carex lyngbyei* above-ground biomass, average shoot height and shoot number for removal and control (*Scirpus* present) treatments are shown in Table 6.6. One of the replicates was lost when the experimental plots were destroyed by a drifting log. Nonetheless, after two seasons of growth with *Scirpus*

Table 6.5. Results of paired Student's t-tests comparing the means (± SE) of biomass, average shoot height, and shoot number of *Scirpus americanus* transplants for control and removal treatments in the *Carex lyngbyei* zone.

Variable	**Removal**	**Control**	**t-value**	**Prob.**
Biomass g dwt	7.29 (0.27)	1.80 (0.28)	16.904	< 0.0001
Average Shoot Height (cm)	57.0 (1.6)	92.4 (2.3)	14.116	< 0.0001
Shoot Number	28.3 (1.6)	6.4 (0.6)	13.744	< 0.0001

Note : For all variables treatment n = 10.

Table 6.6. Results of paired Student's t-tests comparing the means (± SE) of biomass, average shoot height, and shoot number of Carex lyngbyei transplants for control and removal treatments in the Scirpus americanus zone.

Variable	Removal	Control	t-value	Prob.
Biomass g dwt	34.2 (2.9)	23.8 (2.0)	4.459	0.0021
Average Shoot Height (cm)	70.3 (1.8)	72.1 (1.8)	0.752	0.4734
Shoot Number	63.7 (4.5)	44.2 (5.7)	3.695	0.0061

Note : For all variables treatment n = 9.

americanus, both Carex biomass and shoot number decreased significantly by 30 %. Carex shoot heights were, however, uniform across the treatments.

6.8 **Carex lyngbyei Field Transplants with Fertilization Results**

The effect of added nutrients to Carex plants transplanted into the Scirpus community were determined in this experiment by measuring above-ground biomass and average shoot height. For the variable above-ground biomass, ANOVA revealed significant treatment effects (Table 6.7). Subsequent analysis by multiple comparisons disclosed that above-ground biomass for the 200 and 400 kg ha^{-1} nitrogen and the 100 kg ha^{-1} phosphorus + 200 kg ha^{-1} nitrogen treatments were between 110 - 145 % greater than the control treatment (Table 6.8). No statistical differences were found between the various nitrogen treatments or between the control and the 100 kg/ha phosphorus treatment.

Fertilization also had a significant effect on the shoot height of Carex lyngbyei (Table 6.9). Individual treatment responses are described in Table 6.10. Shoot height increased approximately 40 % over the control with the application of either 200 kg ha^{-1} nitrogen, 400 kg ha^{-1} nitrogen or the nitrogen/phosphorus fertilizer combination. The application of phosphorus alone resulted in no increase in shoot height relative to the control.

Table 6.7. ANOVA table of above-ground biomass for the *Carex lyngbyei* transplant-fertilization experiment in the *Scirpus americanus* zone.

Source	d.f.	Sum of Squares	Mean Square	F-ratio	Prob.
Plots	1	51.633	51.633	3.448	0.0738
Rows Plot 1	4	174.716	43.679	2.917	0.0390
Columns Plot 1	4	124.234	31.059	2.074	0.1110
Rows Plot 2	4	138.570	34.643	2.313	0.0822
Columns Plot 2	4	9.339	2.335	0.156	0.9587
Treatment	4	664.794	166.198	11.097	<0.0001
Error	28	419.341	14.976		
Total	49	1582.627			

Table 6.8. Mean above-ground biomass (± SE) of *Carex lyngbyei* transplants for each fertilization treatment in the *Scirpus americanus* zone.

Treatment	Biomass g dwt
Control	6.12 (0.94)$_a$
200 kg ha^{-1} N	13.00 (1.84)$_b$
400 kg ha^{-1} N	15.00 (1.52)$_b$
100 kg ha^{-1} P	6.93 (0.90)$_a$
200 kg ha^{-1} N + 100 kg ha^{-1} P	13.47 (1.69)$_b$

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test (*P* = 0.05).

Table 6.9. ANOVA table of shoot height for the Carex lyngbyei transplant-fertilization experiment in the Scirpus americanus zone.

Source	d.f.	Sum of Squares	Mean Square	F-ratio	Prob.
Plots	1	156.369	156.369	8.191	0.0078
Rows Plot 1	4	34.372	8.593	0.450	0.7714
Columns Plot 1	4	102.441	25.610	1.342	0.2792
Rows Plot 2	4	224.436	56.109	2.939	0.0379
Columns Plot 2	4	57.292	14.323	0.750	0.5662
Treatment	4	5908.569	1477.142	77.376	<0.0001
Error	28	534.532	19.090		
Total	49	7108.011			

Table 6.10. Mean shoot height (± SE) of Carex lyngbyei transplants for each fertilization treatment in the Scirpus americanus zone.

Treatment	Height (cm)
Control	54.04 (1.01)a
200 kg ha^{-1} N	75.10 (1.77)b
400 kg ha^{-1} N	76.03 (1.53)b
100 kg ha^{-1} P	53.09 (1.29)a
200 kg ha^{-1} N + 100 kg ha^{-1} P	76.07 (2.05)b

Note: Means followed by the same letter are not significantly different by Tukey's honestly significant difference (HSD) test ($P = 0.05$).

CHAPTER 7

COMMON GARDEN EXPERIMENTS

7.1 Common Garden Nitrogen Experiment Methods

In a common garden located at Simon Fraser University, the two species were grown in pots that contained six different quantities of added fertilizer nitrogen. The purpose of this experiment was to measure the yield response of Scirpus americanus and Carex lyngbyei to various quantities of nitrogen. Response was determined by measuring plant height (soil surface to tip of the highest part of the plant), total biomass, and biomass allocated to root, rhizome, and shoots after 91 days of growth.

The soils for this experiment were a homogenized mixture of three parts fine commercial silica sand and one part sediment collected from the mudflats of Brunswick Point. Before the Brunswick Point sediment was added to the sand, it was air dried and then sieved through a 2 mm sieve to remove all but the finest plant parts. The nitrogen content of this mixture was not measured. However, measurement of total nitrogen in commercial fine silica sand (similar to what was used in this study) by Tilman (1986a) indicated levels less than 0.005 g kg^{-1}. Average measurement of total nitrogen in three mudflat soil samples in this study suggested levels of 0.42 g kg^{-1} ± 0.02 g kg^{-1} (Standard Error). Therefore, it is assumed that the level of total nitrogen in the mixture was approximately 0.1 g kg^{-1}.

The different nitrogen treatments were produced by adding various quantities of slow-release, microencapsulated NH_4NO_3 (Osmocote 40-0-0) fertilizer to the soil mixture. Treatments consisted of 100 (0.1 g kg^{-1}), 200 (0.2 g kg^{-1}), 300 (0.3 g kg^{-1}), 400 (0.4 g kg^{-1}), 500 (0.5 g kg^{-1}), 750 (0.75 g kg^{-1}) and 2000 (2.00 g kg^{-1}) mg of nitrogen added to each kg of dry soil. To guarantee that nitrogen would be the only limiting soil resource in this experiment, the soil mixture also received 3.0 g of P_2O_5 in the form of superphosphate (0-45-0), 3.0 g of muriate of potash (0-0-60), 1.0 g of reagent-grade $MgSO_4$, 6.0 g of reagent-grade $CaCO_3$ and 0.2 g of a commercial trace metal (Mn, Mo, Cu, Zn, Fe, and B) fertilizer per kg dry soil.

Because of ease of collection, individuals of both species were propagated from seed for the common garden experiments. Carex lyngbyei seeds were stratified under cold moist conditions and then germinated in a peat moss mixture at room temperature. Light was supplied by cool-white flouresent lamps located about 75 cm above the plants with a 16 h photoperiod. After two weeks of growth a single Carex seedling was randomly selected and transplanted into each pot. The seeds of Scirpus americanus would not germinate in numbers sufficient for this experiment even after stratification under cold, moist conditions. Therefore, rhizomes of Scirpus americanus were collected from the study site in mid-April, and then planted in a moist peat moss mixture. The rhizomes sprouted shoots after a few days at room temperatures under the same lighting conditions as the Carex seedlings. Shoots were removed from the rhizomes after one week's growth by cutting the rhizome 1 cm either side of the shoot base. The shoots of both species were transplanted into pots of undisclosed treatment rate to ensure randomness.

The young plants were transplanted into circular pots that measured 10 cm deep and 10 cm in diameter. A layer of paper towels was placed at the bottom of each pot to prevent the loss of soil from the holes at the base. For each species, treatments were replicated six times and each group of six replicates was placed in a separate 6 cm deep plastic tray that measured 52 x 26 cm. Within each tray, the six pots were evenly spaced to minimize light competition. Treatments for both species were placed outside in the common garden area on April 25, 1989, and were arranged in a completely randomized design to minimize location effects. Pots were watered at least three times a week, and a 3 cm reservoir of water was always kept in the tray.

Plants were measured for shoot height and then harvested for biomass on July 25, 1989. Height was measured from the soil base to the height of the tallest growing shoot. Upon collection plant biomass was promptly separated into shoots, rhizomes and roots, dried at 70° C for 72 h, and then weighed.

7.2 Common Garden Light Experiment Methods

In a common garden located at Simon Fraser University, the two species were grown in pots that were subjected to 4 different intensities of natural light. The objective of this experiment was to measure the yield response of Scirpus americanus and Carex lyngbyei to different levels of light. Yield response was determined, once again, by measuring plant height (soil surface to tip of the highest part of the plant), total biomass, and biomass allocated to root, rhizome, and shoots after 91 days of growth.

Soils in this experiment were identical to the "nitrogen" common garden experiment, with one exception. The amount of nitrogen (slow-release Osmocote) added to the soil was 2000 mg per kg of soil for all light treatments. The experimental apparatus consisted of four wooden box frames 120 x 120 x 120 cm in size constructed from 5 x 5 cm boards. To reduce light transmission 1, 2 and 3 layers of mosquito screen were attached to three of the frames on 5 sides. The 1, 2 and 3 layers of screening reduced light transmission to 53 %, 35 % and 15 % of the no-screen control as measured by an Eppley pyranometer.

Juvenile plants of *Scirpus americanus* and *Carex lyngbyei* were prepared for transplantation in exactly the same way as the nitrogen experiment. However, the plants used in the four light treatments were transplanted one day later into their pots on April 26, 1989, and eight replicates for each treatment were used. Replicates for each treatment and each species were then placed in separate 6 cm deep plastic trays that measured 52 x 26 cm. The eight pots for each treatment were evenly spaced apart in the plastic trays to minimize competition from foliage. The plastic trays, with their eight replicates each, were then put outside under their assigned treatment frame. All pots were watered at least three times a week, and a 3 cm reservoir of water was always kept in the tray.

The plants for the light experiment were measured for shoot height and then harvested for biomass on July 26, 1989 (100 % light treatment harvested July 25, 1989). Harvested biomass was immediately separated into shoots, rhizomes and roots in the laboratory, dried at 70° C for 72 h, and then weighed.

7.3 Data Analysis

Regression analysis was employed to examine plant response (dry weight of shoot, rhizome and root biomass) to nitrogen treatments. For all analyses, the data collected from the 100 % light transmission treatment in the light experiment were also added to give a 2000 mg treatment of nitrogen. Biomass response of shoot, rhizome and root components of Scirpus and Carex for the light experiment were analyzed with a two-way ANOVA (species and treatment were independent variables) and unplanned multiple comparison procedures (see Section 6.1 for complete statistical methods). Regression analysis was not used on the light experiment data because four treatments were found to be too few to accurately graph the nonlinear relationship between the X and Y variables.

Because of unavoidable cost contraints, both the light and nitrogen experiments suffer from pseudoreplication. Pseudoreplication is defined by Hurlbert (1984) as the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated or replicates are not statistically independent. In the nitrogen experiment, pseudoreplication arises because the replicates of each treatment and for each species shared the same water reservoir trays. This type of pseudoreplication is common in laboratory experiments and is sometimes referred to as *isolative segregration* (Hurlbert, 1984). Isolative segregration may result in false treatment effects caused by the differences in tray location or by the differential maintenance of the experimental trays. However, the effects of pseudoreplication in this experiment can be separated out if the replicates in each tray are averaged to produce one single treatment value. This separation was done by the computational methods in the regression analysis software which used the residuals from the regression line to estimate the error variance.

Pseudoreplication occurs in the common garden light experiment, once again, because of isolative segregation. Isolative segregration occurs in this experiment because the replicates of both species for each treatment were placed under a single shading frame, and because the replicates for each species and each treatment shared similar water reservoir trays. Moreover, the added confounding in this design caused by the shading frames made it impossible to separate out spurious treatment effects. As a result, the findings of this experiment should be interpreted with caution.

7.4 Common Garden Nitrogen Experiment Results

The relationships between shoot height, shoot biomass, rhizome biomass, root biomass and total biomass with the variable "nitrogen added" for both Scirpus americanus and Carex lyngbyei are displayed in Figures 7.1 to 7.5. All of these associations are positive and highly significant ($P < 0.005$). However, not all of the Carex lyngbyei plants survived at the lower nitrogen levels, and the regression

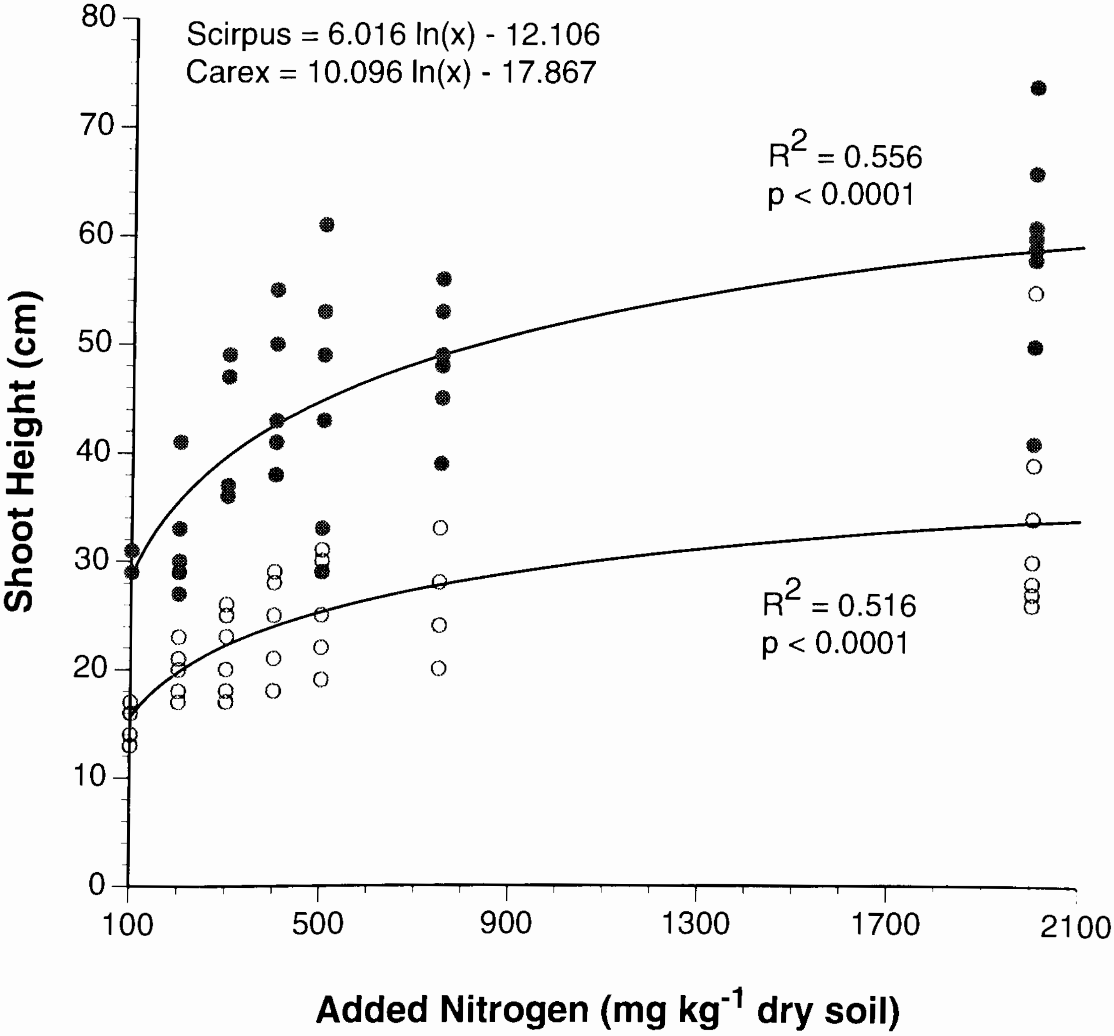

Figure 7.1. Relationship between shoot height and added soil nitrogen for Carex lyngbyei (●) and Scirpus americanus (○) plants grown under various resource levels in common garden conditions.

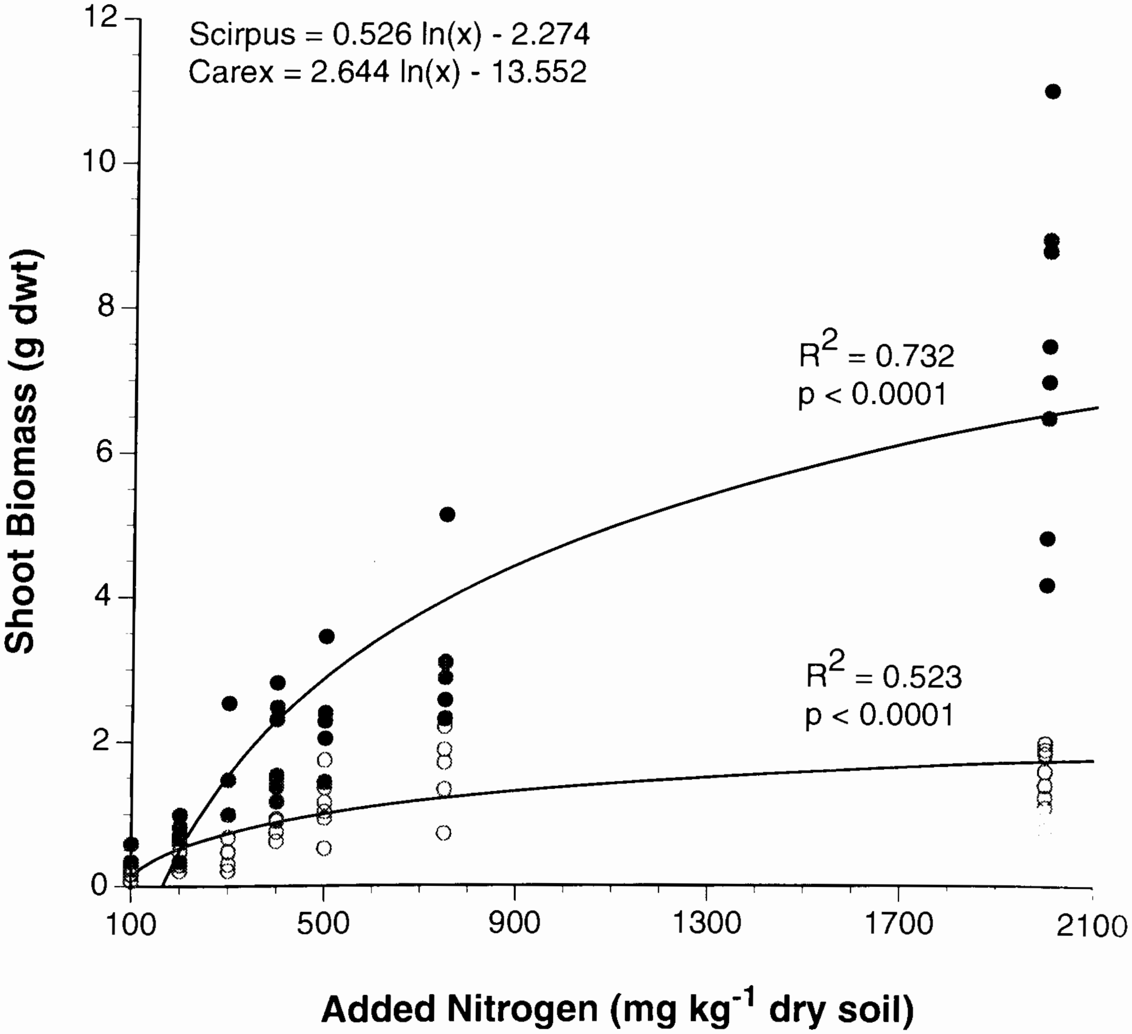

Figure 7.2. Relationship between shoot biomass and added soil nitrogen for Carex lyngbyei (●) and Scirpus americanus (○) plants grown under various resource levels in common garden conditions.

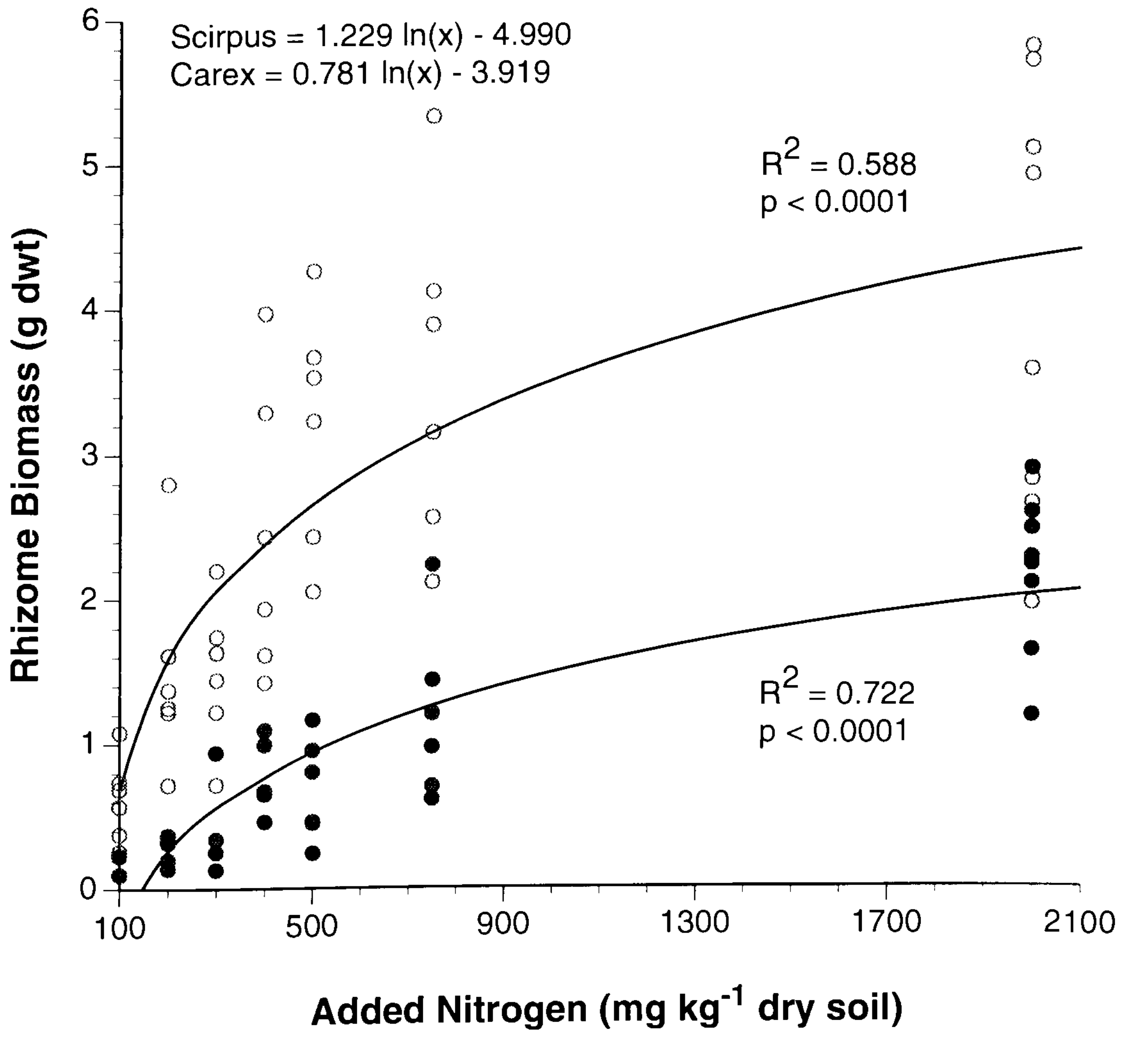

Figure 7.3. Relationship between rhizome biomass and added soil nitrogen for Carex lyngbyei (●) and Scirpus americanus (O) plants grown under various resource levels in common garden conditions.

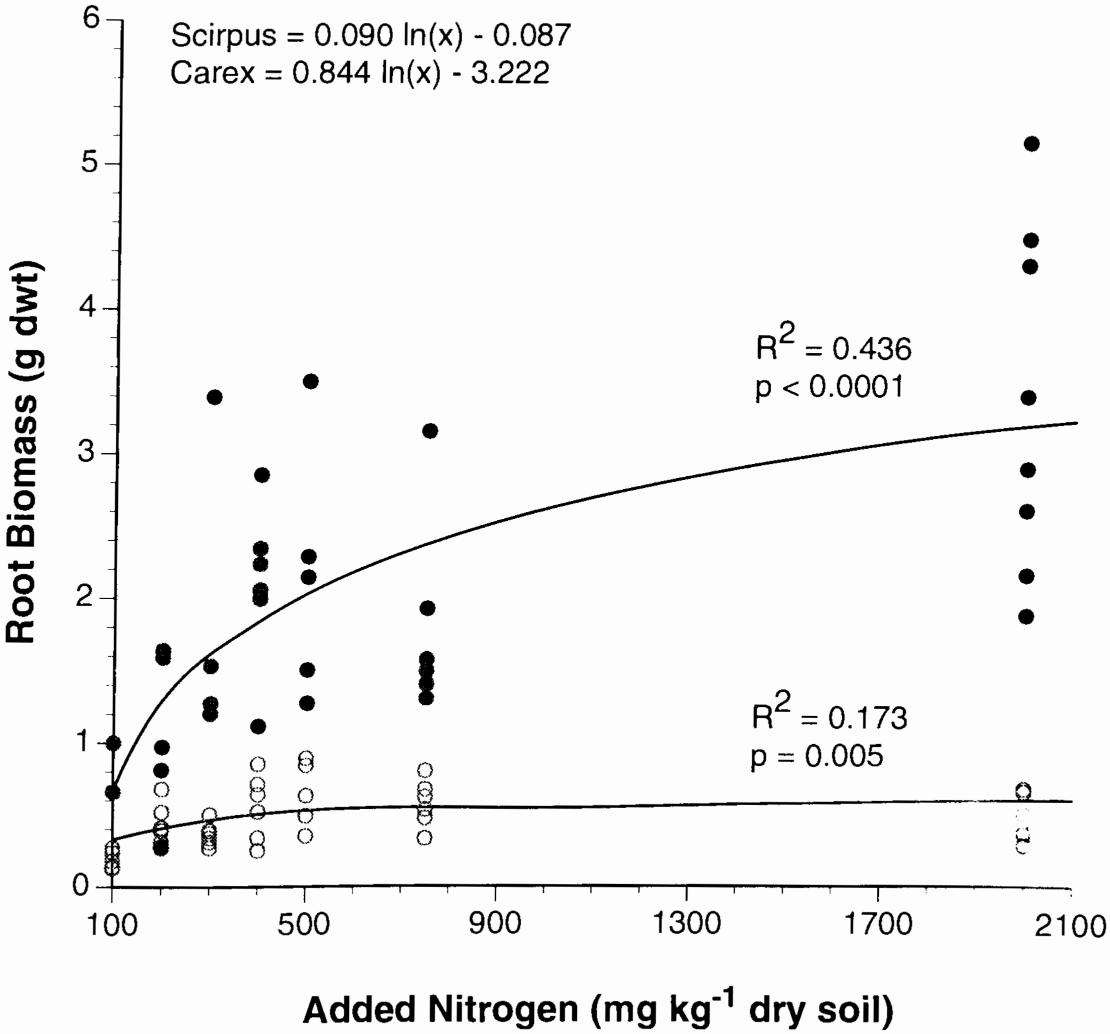

Figure 7.4. Relationship between root biomass and added soil nitrogen for Carex lyngbyei (●) and Scirpus americanus (○) plants grown under various resource levels in common garden conditions.

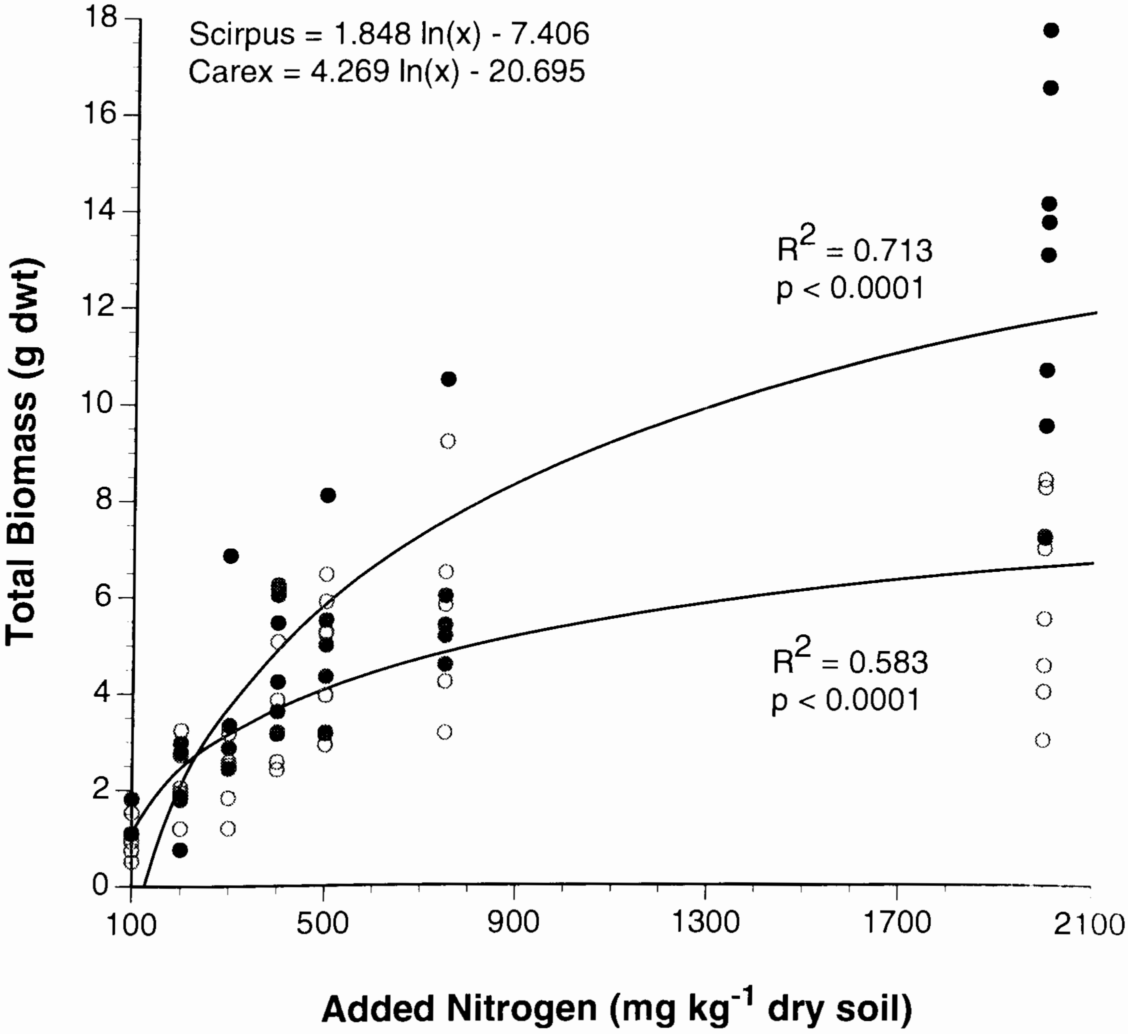

Figure 7.5. Relationship between total biomass and added soil nitrogen for Carex lyngbyei (●) and Scirpus americanus (O) plants grown under various resource levels in common garden conditions.

lines displayed are based only on those plants surviving. Only 2 of 6 plants survived the 100 mg treatment, while the 200 and 300 mg treatments had 5 and 4 plants surviving plants, respectively. Statistical comparison of the five pairs of regression lines found significant differences between their slopes, intercepts, and coincidence (Table 7.1). In general, the results of these analyses suggest that the two plant species have significantly different growth and biomass allocation characteristics across the experimental gradient of nutrient availability. Further, the slope of the regression lines for the variables shoot, root and total biomass suggest that the growth of *Scirpus americanus* is less limited by the quantity of nitrogen in the soil of treatments than *Carex lyngbyei*.

Carex lyngbyei was taller than *Scirpus americanus* at all nitrogen levels (Figure 7.1). At 2000 mg added nitrogen, *Carex lyngbyei* grew to an average shoot height of 58.9 cm, while *Scirpus americanus* attained a height of only 33.6 cm. For the other six treatment levels, *Carex* was approximately twice as tall as *Scirpus*.

Carex lyngbyei also accumulated more shoot and root biomass than *Scirpus americanus* (Figures 7.2 and 7.4). At the highest nitrogen level, *Carex*'s shoot and root biomass was 5 to 6 times as great, respectively, as the shoot and root biomass of *Scirpus americanus*. Both species had roughly similar total biomass accumulations for treatments 100 to 500

Table 7.1. Statistical comparison of the slopes, intercepts, and coincidence of the regression lines of Carex lyngbyei and Scirpus americanus for the nitrogen common garden experiment. Dependent variables for this comparison are listed in the table, while the independent variable in all cases examined is the amount of nitrogen added (See Figures 7.1 - 7.5).

Dependent Variable	Slopes are different	Lines are not coincident	Lines have different intercepts
Shoot Height	*	****	****
Root Biomass	****	****	****
Rhizome Biomass	*	****	****
Shoot Biomass	****	****	****
Total Biomass	****	****	****

Note: Significance values are; ****($P < 0.0001$), ***($P < 0.001$), **($P < 0.01$), or *($P < 0.05$).

mg N. However, at the highest nitrogen level (2000 mg) *Carex lyngbyei*'s total biomass was twice as great as *Scirpus americanus* (Figure 7.5). Finally, *Scirpus americanus* allocated 2 to 3 times more biomass to the production of rhizomes than *Carex lyngbyei* (Figure 7.3).

The proportion of biomass allocated to either shoots, rhizomes or roots as a function of nitrogen added to the soil is displayed in Figures 7.6 and 7.7 for *Scirpus americanus* and *Carex lyngbyei*, respectively. These graphs indicate that the two plants have different allocation patterns. More specifically, *Scirpus americanus* allocates approximately 60 - 68 % of its biomass to the production of rhizomes, 16 - 31 % to shoots, and 10 - 19 % to roots (Figure 7.6). Further, with increasing availability of soil nitrogen *Scirpus americanus* reduces the relative amount allocated to roots, and increases the amount allocated to shoots. *Carex lyngbyei* allocates most of its biomass to the production of shoots and roots (Figure 7.7). With increasing availability of soil nitrogen, *Carex* responded morphologically by allocating more biomass to the production of shoots. As the level of nitrogen was increased, the proportion of biomass allocated to shoots goes from about 32 % at 100 mg N to 57 % at 2000 mg N. On the other hand, the amount of biomass allocated to roots decreased from 57 % to 26 %. Finally, the amount of biomass allocated to rhizomes showed no real trend with increasing nitrogen availability.

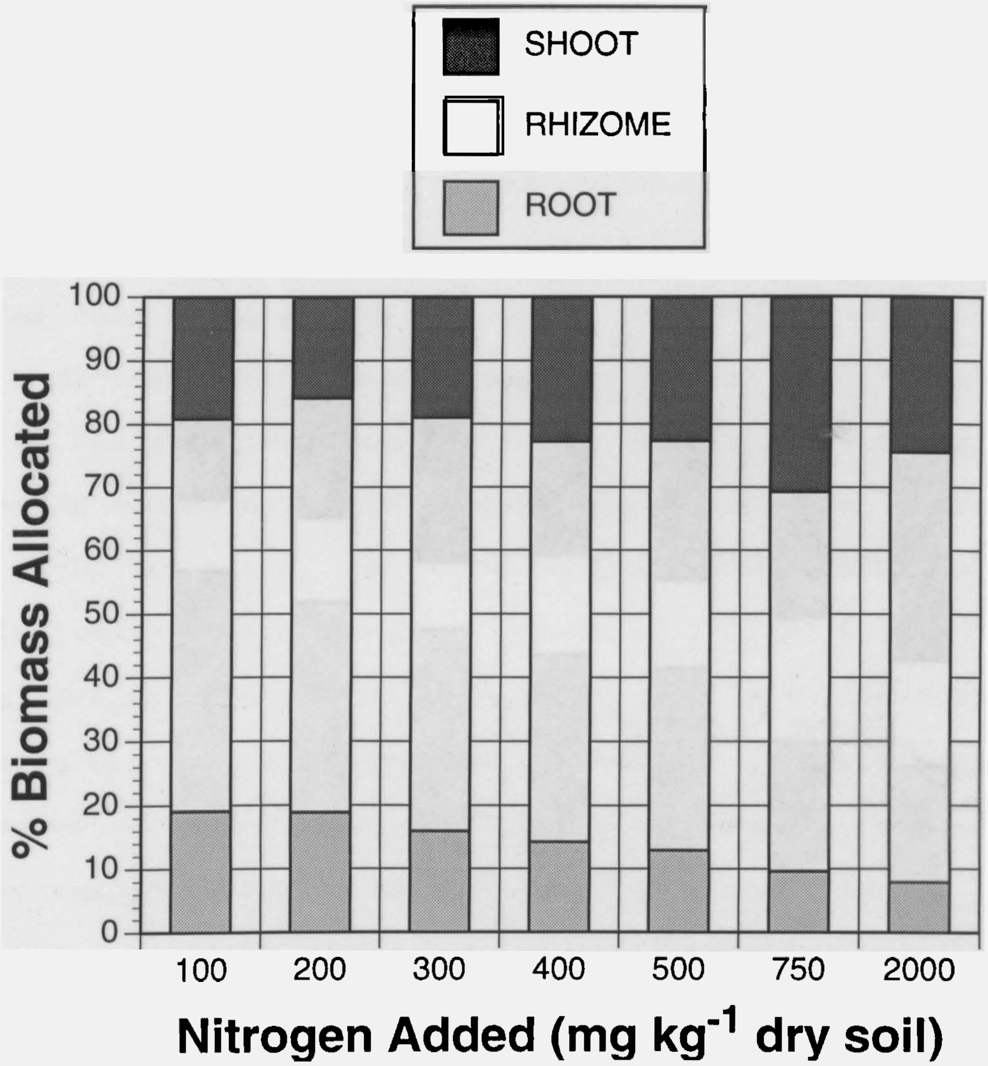

Figure 7.6. Biomass allocation patterns of Scirpus americanus plants grown under seven different levels of added soil nitrogen.

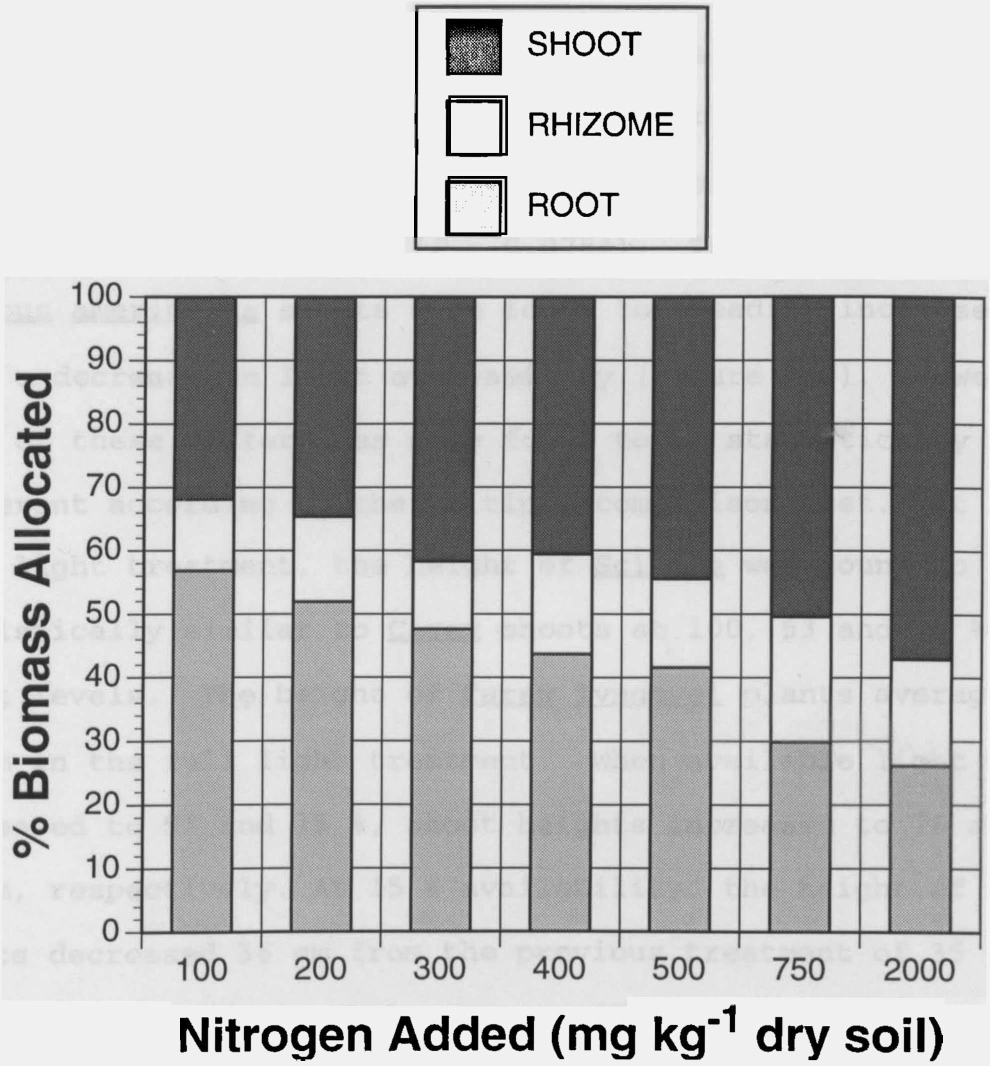

Figure 7.7. Biomass allocation patterns of Carex lyngbyei plants grown under seven different levels of added soil nitrogen.

7.5 Common Garden Light Experiment Results

Under varying levels of light intensity, Carex and Scirpus plants maintained significant differences in height between species, with average height for all treatments being 38 cm for Scirpus and 69 cm for Carex (Table 7.2). Results of the two-way ANOVA also indicated that significant treatment effects existed ($P = 0.0284$). The height of Scirpus americanus shoots were found to steadily increase with a decrease in light availability (Figure 7.8). However, none of these differences were found to be statistically different according to the multiple comparison test. At the 15 % light treatment, the height of Scirpus was found to be statistically similar to Carex shoots at 100, 53 and 15 % light levels. The height of Carex lyngbyei plants averaged 58 cm in the full light treatment. When available light was decreased to 53 and 35 %, shoot heights increased to 76 and 89 cm, respectively. At 15 % availability, the height of the shoots decreased 36 cm from the previous treatment of 35 %.

Table 7.3 displays the two-way ANOVA for shoot biomass. Highly significant ($P < 0.0001$) effects were found between species and treatments and their interaction. Scirpus americanus shoot biomass decreased steadily with each experimental reduction in light intensity (Figure 7.9). Of particular importance is the significant drop in Scirpus shoot biomass when percent available light was reduced from

Table 7.2. Analysis of variance table of shoot height [log(1+x) transformation to homogenize variance] for the common garden light experiment. Independent variables are species type, light treatment, and their interaction.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Species	1	0.989	0.989	56.258	< 0.0001
Treatment	3	0.171	0.057	3.249	0.0284
Species x Treatment	3	0.288	0.096	5.454	0.0023
Error	56	0.984	0.018		
Total	63	2.432			

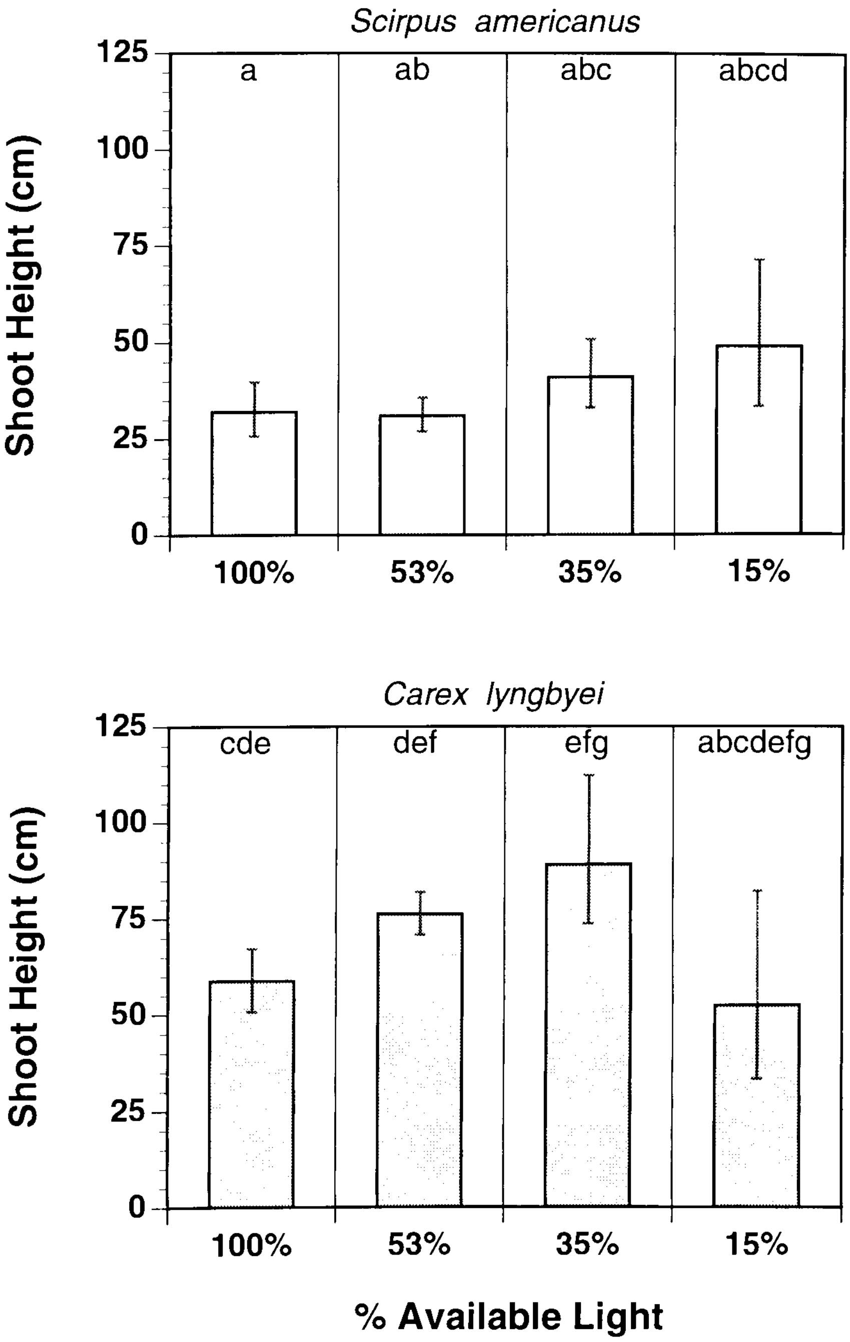

Figure 7.8. Mean shoot height (± 95% confidence interval) for Scirpus americanus and Carex lyngbyei after 91 days of growth under four light treatments in a common garden. Means with the same lowercase letters were not significantly different (*P* > 0.05) according to Tukey's HSD test.

Table 7.3. Analysis of variance table of shoot biomass [log(1+x) transformation to homogenize variance] for the common garden light experiment. Independent variables are species type, light treatment, and their interaction.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Species	1	3.080	3.080	212.932	< 0.0001
Treatment	3	1.932	0.644	44.512	< 0.0001
Species x Treatment	3	0.626	0.209	14.431	< 0.0001
Error	56	0.810	0.014		
Total	63	6.448			

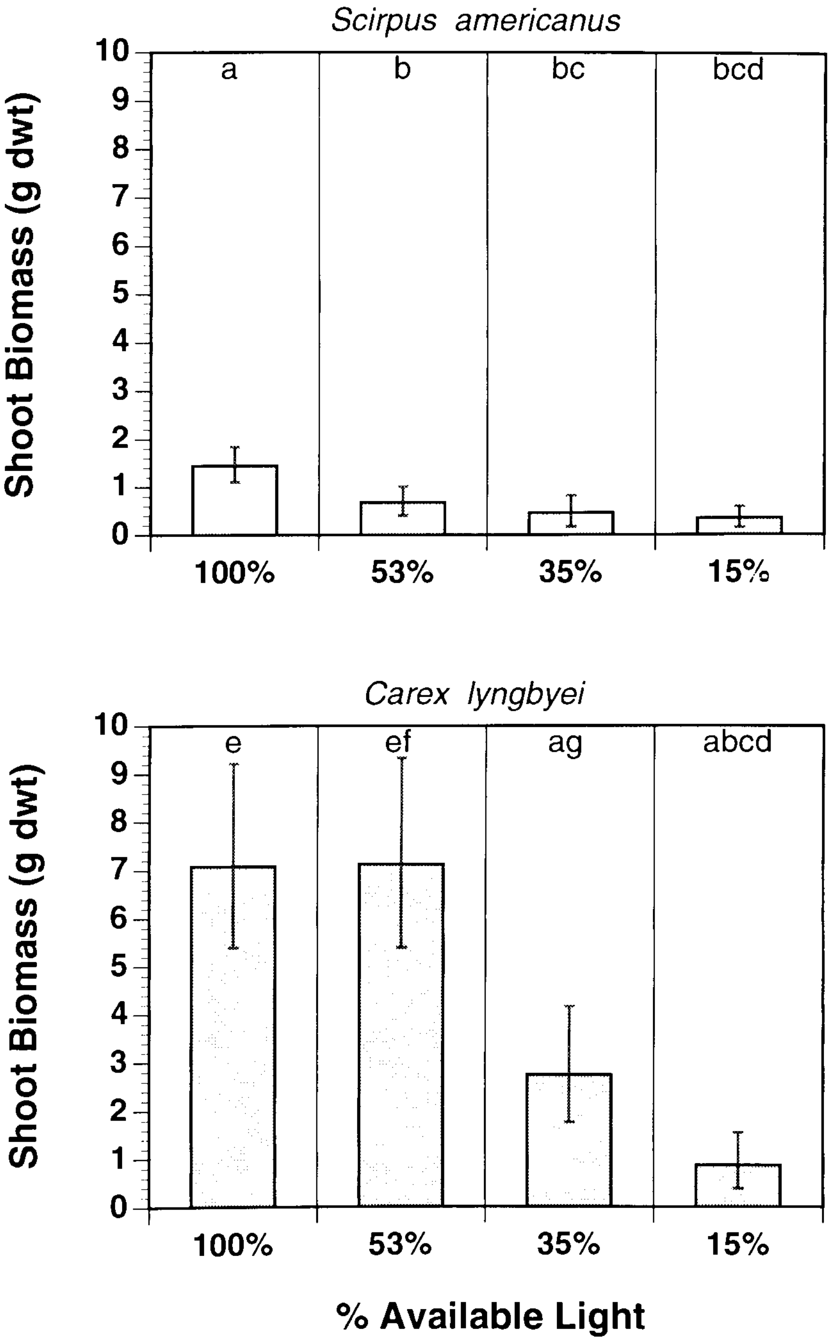

Figure 7.9. Mean shoot biomass (± 95% confidence interval) for Scirpus americanus and Carex lyngbyei after 91 days of growth under four light treatments in a common garden. Means with the same lowercase letters were not significantly different (*P* > 0.05) according to Tukey's HSD test.

100 to 53 %. A comparable drop was not exhibited by *Carex*. *Carex*'s shoot biomass remained nearly the same in the 100 and 53 % light treatments, and was almost 5 times greater than the shoot biomass of *Scirpus* at the 100 % light level. Shoot biomass of *Carex* at the 35 % light level was found to be similar to the biomass produced by *Scirpus* at full light intensity. Finally, both species had statistically similar biomass accumulations at the lowest light level.

Significant differences in rhizome biomass accumulation were found between species and light levels (Table 7.4). The interaction between the two independent variables was found not to be statistically important suggesting that the two species were experiencing similar effects to the experimental treatments. Figure 7.10 describes the change in rhizome biomass for the two species with light treatment. *Scirpus americanus* responded to the decrease in light availability with a steady decrease in rhizome biomass. No statistical difference in rhizome biomass was encountered between 100 and 53 % light treatments for *Carex*.

Root biomass and total biomass had similar effects to the independent variables according to ANOVA (Tables 7.5 and 7.6). Both variables also had significant interactions between species and light treatment effects. As in the other experiments, *Scirpus* experienced a decrease in root and total biomass with decreasing light availability (Figures 7.11 and 7.12). However, the multiple comparison test revealed no

Table 7.4. Analysis of variance table of rhizome biomass [log(1+x) transformation to homogenize variance] for the common garden light experiment. Independent variables are species type, light treatment, and their interaction.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Species	1	0.195	0.195	16.713	< 0.0001
Treatment	3	2.363	0.788	67.437	< 0.0001
Species x Treatment	3	0.050	0.017	1.437	0.2416
Error	56	0.654	0.012		
Total	63	3.262			

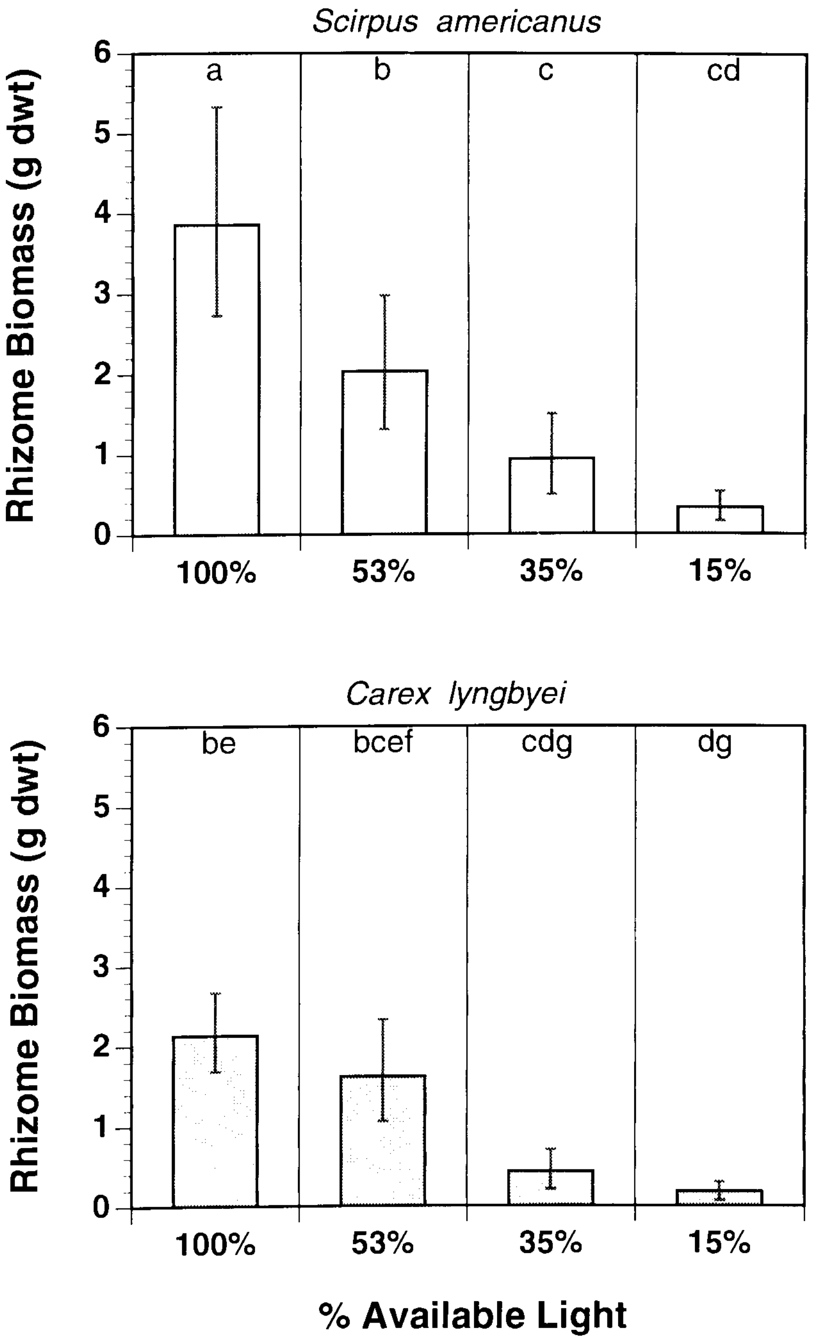

Figure 7.10. Mean rhizome biomass (± 95% confidence interval) for Scirpus americanus and Carex lyngbyei after 91 days of growth under four light treatments in a common garden. Means with the same lowercase letters were not significantly different ($P > 0.05$) according to Tukey's HSD test.

Table 7.5. Analysis of variance table of root biomass [log2(x) transformation to homogenize variance] for the common garden light experiment. Independent variables are species type, light treatment, and their interaction.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Species	1	85.468	85.468	130.356	< 0.0001
Treatment	3	173.351	57.784	88.133	< 0.0001
Species x Treatment	3	8.654	2.885	4.400	0.0075
Error	56	36.716	0.656		
Total	63	304.189			

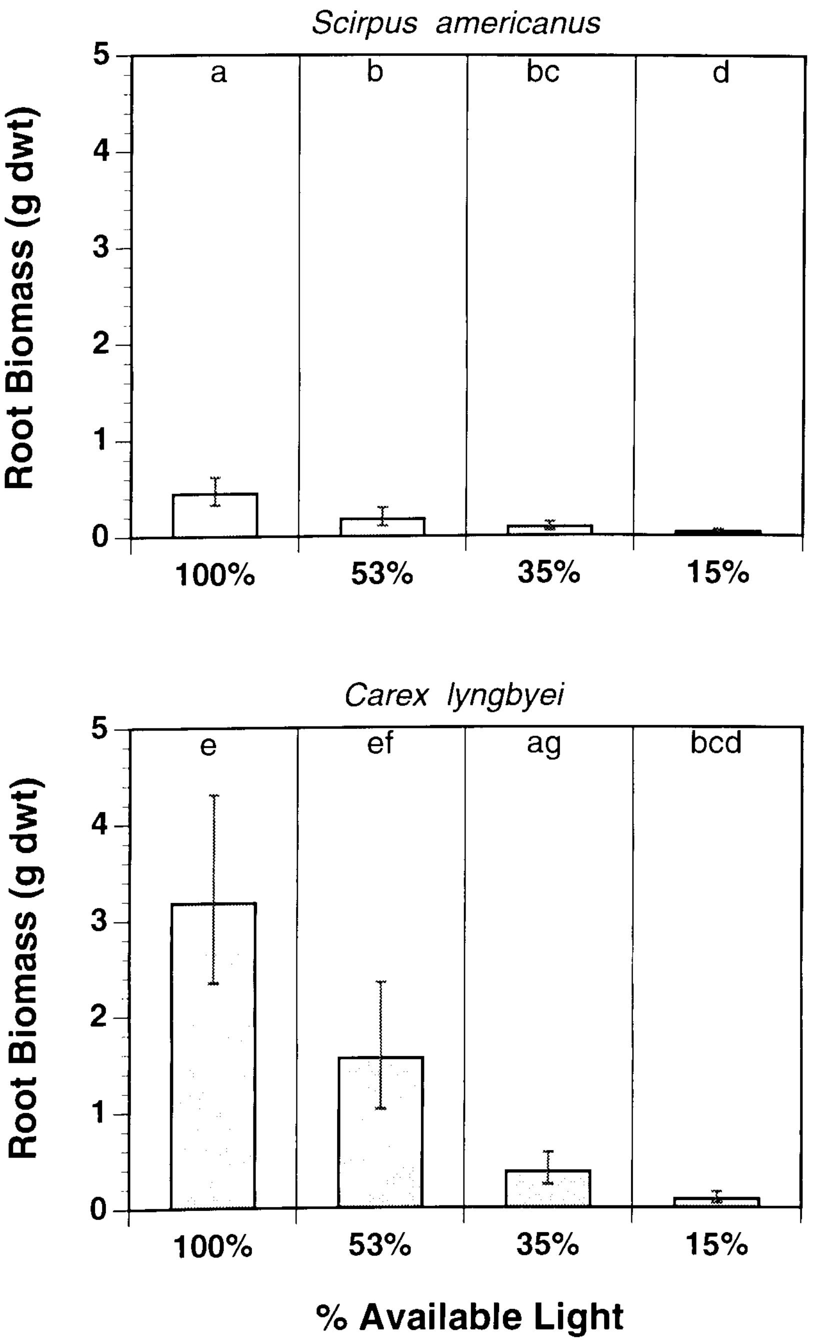

Figure 7.11. Mean root biomass (± 95% confidence interval) for Scirpus americanus and Carex lyngbyei after 91 days of growth under four light treatments in a common garden. Means with the same lowercase letters were not significantly different (*P* > 0.05) according to Tukey's HSD test.

Table 7.6. Analysis of variance table of total biomass [log(1+x) transformation to homogenize variance] for the common garden light experiment. Independent variables are species type, light treatment, and their interaction.

Source	**d.f.**	**Sum of Squares**	**Mean Square**	**F-ratio**	**Prob.**
Species	1	1.276	1.276	56.314	< 0.0001
Treatment	3	4.642	1.547	68.304	< 0.0001
Species x Treatment	3	0.278	0.093	4.090	0.0107
Error	56	1.268	0.023		
Total	63	7.464			

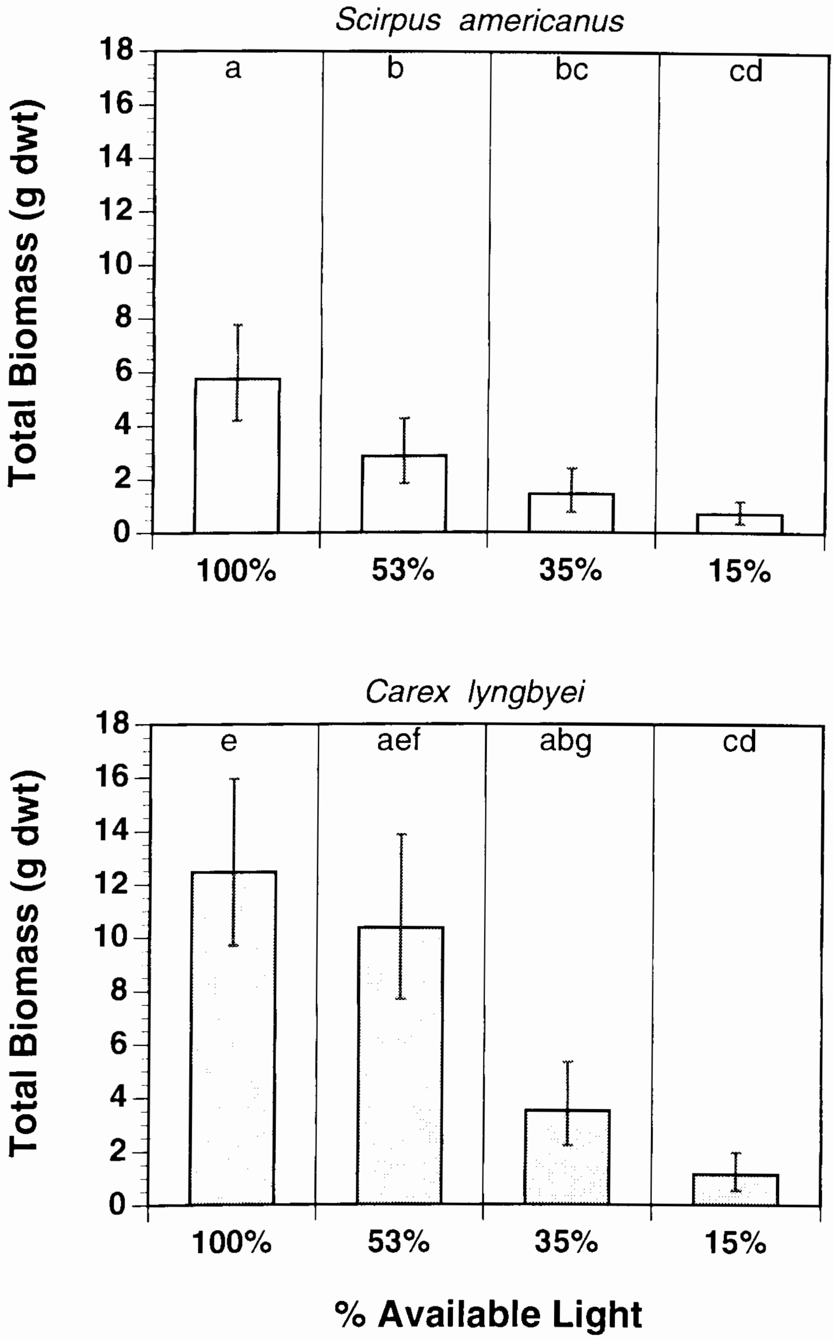

Figure 7.12. Mean total biomass (± 95% confidence interval) for Scirpus americanus and Carex lyngbyei after 91 days of growth under four light treatments in a common garden. Means with the same lowercase letters were not significantly different ($P > 0.05$) according to Tukey's HSD test.

difference in root and total biomass for Carex between 100 and 53 % light treatments. Beyond these cases, the two dependent variables displayed a general decline in value with decreasing light levels.

Figures 7.13 and 7.14 describe the proportion of biomass allocated to either shoots, rhizomes or roots under the four treatments of light intensity for Scirpus americanus and Carex lyngbyei, respectively. Both species responded to the decrease in light intensity by generally allocating relatively more biomass to the production of shoots. For Scirpus this increase in shoot biomass with light reduction was accompanied by a decrease in rhizome biomass only (Figure 7.13). The relative amount of root biomass seemed to remain constant under all four treatments. Carex lyngbyei adjusted its allocation patterns by allotting less biomass to the production of roots, while the relative amount of rhizome biomass remained fixed (Figure 7.14).

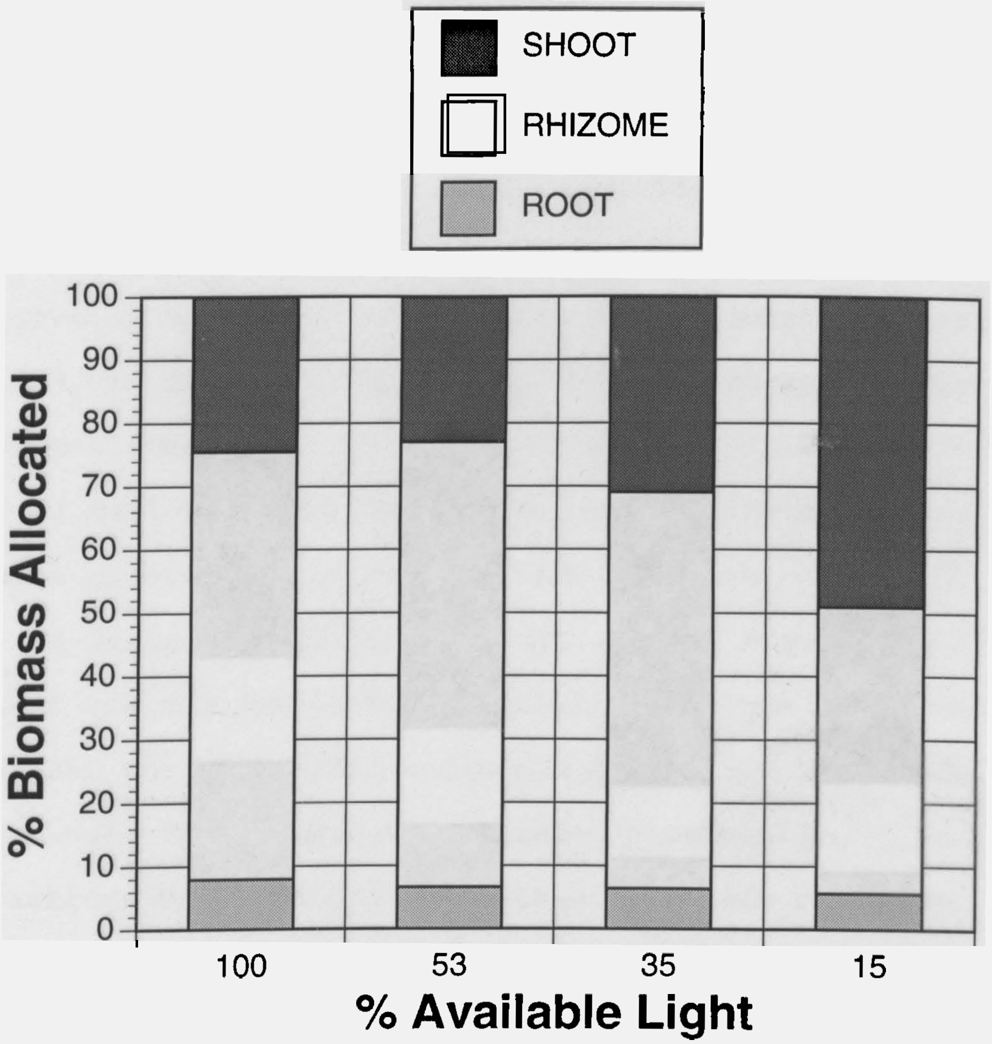

Figure 7.13. Biomass allocation patterns of <u>Scirpus americanus</u> plants grown under four different levels of available light. All plants were grown with 2000 mg of nitrogen (Osmocote - NH_4NO_3) added to each kg of dry soil.

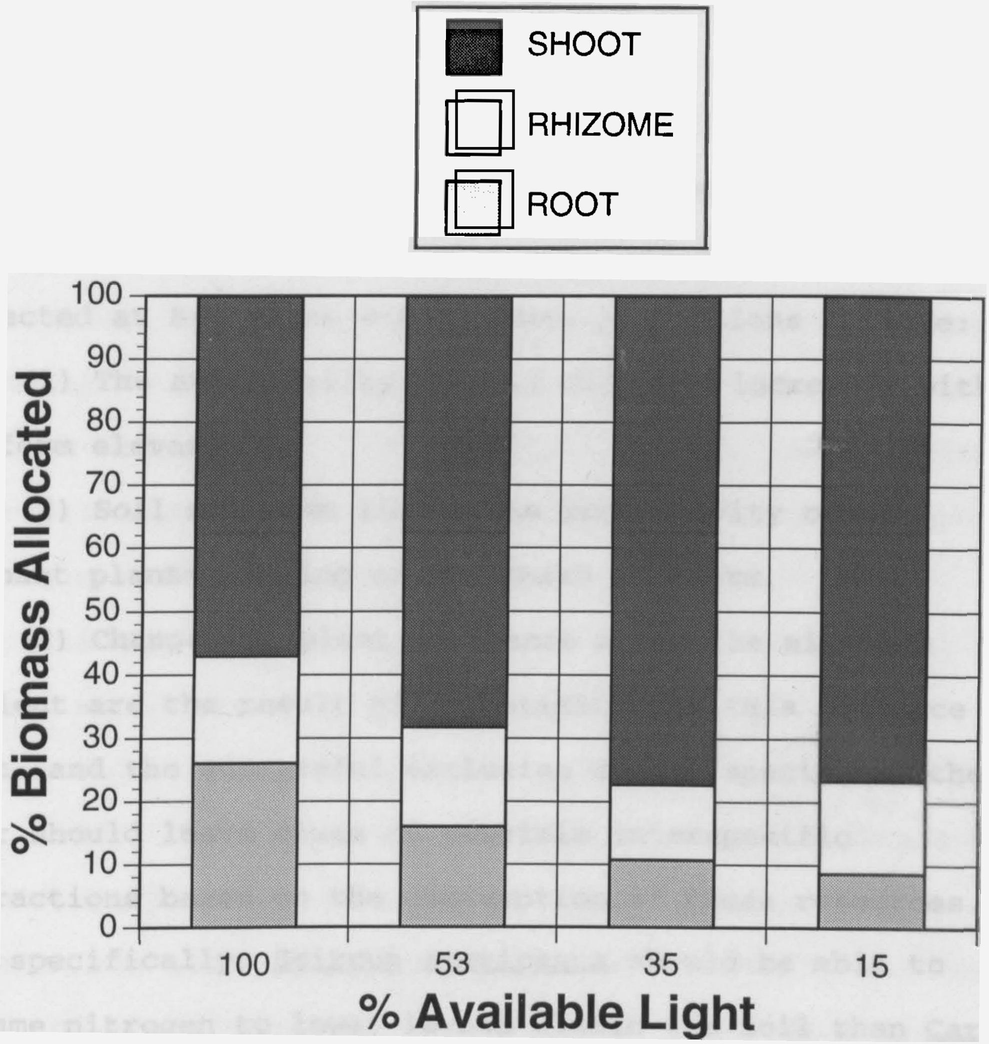

Figure 7.14. Biomass allocation patterns of *Carex lyngbyei* plants grown under four different levels of available light. All plants were grown with 2000 mg of nitrogen (Osmocote - NH_4NO_3) added to each kg of dry soil.

CHAPTER 8

DISCUSSION

8.1 Descriptive Field Measurements

Assessment of the model described in Figure 1.2 begins with the verification of certain predictions that can be fully or partly tested from the analyzed descriptive data collected at Brunswick Point. These predictions include:

(1) The availability of soil nitrogen increases with platform elevation.

(2) Soil nitrogen limits the productivity of the dominant plants growing on the marsh platform.

(3) Changes in plant dominance along the nitrogen gradient are the result of competition for this resource and light, and the successful exclusion of one species by the other should leave clues of possible interspecific interactions based on the consumption of these resources. More specifically, Scirpus americanus should be able to consume nitrogen to lower levels within the soil than Carex lyngbyei. Carex lyngbyei should, according to the model, reduce the availability of light beneath its canopy to levels much lower than those found underneath the canopy of Scirpus americanus.

Results of analyses of descriptive data collected in this study clearly indicates a separation of Scirpus *americanus* and *Carex lyngbyei* stands along a gradient of increasing elevation, total soil nitrogen and productivity at Brunswick Point tidal marsh (Figure 4.3). Variations in plant height and above-ground biomass of the two dominant species were found to be strongly correlated with elevation, soil organic matter and the supply of total soil nitrogen (Table 4.5; Figures 4.3 and 4.5). Tidal inundation is hypothesized to control the growth of *Scirpus americanus* and *Carex lyngbyei* by limiting the build-up of nitrogen in the marsh sediments. Inundation frequency limits the amount of total nitrogen found in the soil by regulating the rate of nitrogen mineralization and by controlling the rate of tidal export of organic matter and soluble forms of nitrogen.

Nitrogen flux characteristics of tidal freshwater marshes are probably similar to more saline systems (Stevenson et al., 1977; Simpson, Whigham, and Walker, 1978; Odum, 1988). Nitrogen primarily enters these ecosystems by way of precipitation, groundwater flow, and fixation by bacteria and algae (Valiela et al., 1978; Valiela and Teal, 1979). Of these sources, groundwater flow has been found to account for approximately 60 % of the net input of nitrogenous nutrients into a mature salt marsh ecosystem (Valiela and Teal, 1979). The amount of nitrogen fixed by rhizosphere bacteria has been discovered to be about 10 times greater (about 30 % of the net input) than that fixed by algae or non-rhizosphere bacteria (Valiela and Teal, 1979).

Precipitation inputs usually mirror the gains occurring from non-rhizosphere bacteria fixation. Losses of nitrogen are mainly through tidal exchanges and denitrification, and in general are in yearly balance with inputs (Valiela and Teal, 1979).

Tidal marshes can function as a sink or source of nitrogen depending upon a diversity of abiotic and biotic factors, and the time of the year (Odum, 1988). Additions and losses of nitrogen by the microbial processes of fixation and denitrification take place during the summer growing season (Valiela and Teal, 1979). During this period these two processes are normally in balance. Losses of nitrogenous nutrients by tidal export usually begins in mid-summer, when the plants have matured and begun senescence, and continues until late-winter (Valiela and Teal, 1979). Seasonal variation in nitrogen gains from precipitation and groundwater flow are comparatively less extreme and more seasonally uniform than the fluxes already discussed for the Great Sippewissett Marsh (Valiela and Teal, 1979). This consistency may, however, be a response to this area's particular climatology and hydrologic regime.

Examination of the temporal change in above-ground biomass and canopy height along the elevation gradient revealed that _Carex_ _lyngbyei_ begins its growth several weeks in advance of _Scirpus_ _americanus_. Further, during the growing season _Carex_ always maintained a height advantage over Scirpus according to monthly measurements during 1989 (Figure 4.6). This height advantage may be extremely important in regards to above-ground competition for light. Concurrent measurements of light availability at ground level suggest that light levels were consistently lower under the canopy of Carex during the entire growing season (Figure 4.7). These findings suggest that rhizomes of Scirpus trying to colonize up-marsh habitats dominated by Carex would have to contend with a lower availability of light because of the delayed emergence of shoots.

Measurements of available light at the soil surface show that Carex lyngbyei is more effective at intercepting light passing through its canopy (Table 4.3; Figures 4.4 and 4.7). Carex's greater capability at intercepting light may be attributed to morphological differences between the two species. Besides being taller, each Carex lyngbyei individual has between 4 – 8 blade-like leaves that come off a vertical stem at a 45 – 60° angle forming a thick canopy layer 50 – 120 cm above the ground surface. In contrast, Scirpus americanus has a single upright triangular culm, which acts as the main photosynthetic tissue providing light interception primarily on a vertical plane.

Coexistence of Scirpus americanus and Carex lyngbyei occurs only in a 10 to 15 m zone. In this zone, both species experience a drop in their above–ground biomass, possibly as a result of competition. At the transition zone, Carex maintained a height advantage only in May (Table 4.8). During the months of June and July this advantage became less evident as the height of Scirpus became equal to or slightly greater than Carex individuals. However, the height advantage of Scirpus during these months may be a response to light competition. Rhizomes of Scirpus may be allocating photosynthate to fewer shoots, making these shoots taller, to overcome light reduction by Carex individuals. Figure 4.2 indicates that the density of Scirpus shoots does drop dramatically in the transition zone.

Based on equilibrium models of nutrient consumption, the resource-ratio hypothesis would predict that the quantity of extractable soil nitrogen under the Scirpus community should be lower than under the Carex community (Tilman, 1982; 1988). During the 1989 field season, extractable ammonium was measured in both communities on four different sampling dates. On April 24, approximately a week before the onset of growth, measurements indicated that ammonium levels between the two communities were uniform. One month later, ammonium levels were more than twice as great in the Scirpus community, which is the opposite of model predictions. However, Scirpus had just begun above-ground growth, and may not have initiated active consumption of soil nitrogen. Individuals in the Carex community had been growing for more than three weeks, and therefore may have caused a lower level of ammonium in the soil rhizosphere because of more vigorous uptake. By June and July, vigorous above-ground growth was occurring in both communities, and the measured ammonium levels were found not to be significantly different between the communities. This result runs counter to a primary condition of the model in Figure 1.2, and suggests that the R*s for soil nitrogen may be similar for both *Carex lyngbyei* and *Scirpus americanus*. However, the model can be saved if these results are interpreted as concentration rather than consumption levels of ammonium. Further, it may be very difficult to detect differences in soil ammonium levels between the dominant species because either the field measurements were not accurate enough or the area of soil rhizosphere sampled does not represent the true consumptive equilibrium level of ammonium.

In summary, analyses of collected field data did not confirm all of the testable predictions of the hypothesis developed in Chapter 1. The prediction that nitrogen levels in the soil controlled plant productivity was only moderately confirmed by correlative analysis because the effect of other factors could not be ruled out. The measurement of ammonium levels in the communities dominated by *Scirpus americanus* and *Carex lyngbyei* suggests that the two species have equal abilities to consume below-ground resources. This discovery creates some doubt about the correctness of the central hypothesis of this study.

8.2 Manipulative Field Experiments

The results of the manipulative field experiments were carried out to evaluate the following predictions:

(1) Nitrogen is the soil resource limiting the growth of *Scirpus americanus* and *Carex lyngbyei*.

(2) The segregation of *Scirpus americanus* and *Carex lyngbyei* on the marsh platform is due to competition.

Both *Scirpus americanus* and *Carex lyngbyei* were found to be limited in above-ground biomass accumulation and shoot height by the availability of soil nitrogen. The limitation of these two species by soil nitrogen is not surprising. Many studies of tidal marsh plant communities have shown that the growth/yield of the dominant species occupying these habitats are limited by the availability of this soil resource (e.g., Valiela and Teal, 1974; Gallagher, 1975; Patrick and Delaune, 1976; Chalmers, 1979; Mendelssohn, 1979b; Buresh, Delaune and Patrick, 1980; Loveland and Ungar, 1983; Cargill and Jefferies, 1984a; Hopkinson and Schubauer, 1984; Covin and Zedler, 1988).

Nitrogen fertilization also influenced the amount of light passing through the canopies of both *Scirpus americanus* and *Carex lyngbyei*. The addition of nitrogen caused both species to increase their shoot biomass and height resulting in both species being able to intercept more incoming light. These results agree with the predictions of the model that suggest greater below-ground resource acquisition should lead to more effective light capture by the plant canopy. These findings also agree with other associated research testing this same aspect of Tilman's resource-ratio hypothesis (Tilman, 1984; Tilman and Wedin, 1991a).

The continued growth of *Scirpus americanus* and *Carex lyngbyei* at six transplant sites along the elevational gradient at Brunswick Point indicated that the potential and actual distribution patterns of these plants were not equivalent, rejecting the "Abiotic Model" discussed in Chapter 1 (also Figure 1.1). The results of this field transplant also suggest that the lower limit of *Scirpus americanus* may be set by abiotic factors, while the lower limit of *Carex lyngbyei* may be controlled by competition. This observation indicates the observed field distribution of these species cannot be explained by the "Abiotic/Competition Model". Several researchers (Snow and Vince, 1984; Davy and Smith, 1985; Bertness and Ellison, 1987; Bertness, 1988; 1991a; 1991b) have used this model to explain the zonal patterns of plant distribution at several typical salt marshes on the east coast of the United States and in Alaska. This model, however, has not been found to be universal. Pennings and Callaway (1992) have shown that competitive interactions at the border of two Californian marsh plants were not one sided but two sided.

Scirpus americanus individuals transplanted in the Carex zone performed poorly in the control treatment in terms of shoot density and above-ground biomass (Table 6.5). The average shoot height of the few surviving individuals was found to be greater than in the removal treatment. Interpretation of these results is, however, not entirely straightforward, and three possible explanations can be put forth: (1) the results indicate only below-ground competition; (2) the results indicate only above-ground competition; or (3) the results indicate both above- and below-ground competition. The first hypothesis can be rejected because the presence of Carex neighbors caused Scirpus shoot heights to increase by 62 %, while shoot density dropped by 77 %. These results suggest that Scirpus has re-allocated its biomass resources to produce fewer but taller shoots to penetrate the canopy of Carex. Absolute rejection or acceptance of the last two hypotheses is not possible because the experiment could not distinguish between the effects of Carex shoots alone and shoots and roots combined.

In the reciprocal experiment, Carex transplants suffered declines in above-ground biomass and shoot number when grown in the presence of Scirpus neighbors in the nutrient-poor low marsh (Table 6.6). There were, however, no effects on Carex shoot heights. These results suggest that the consumption of below-ground resource by Scirpus americanus basically limits the growth of Carex lyngbyei. The fact that Carex lyngbyei shoot heights changed little between treatments indicates that the shoots were not suffering from light reduction caused by the canopy of Scirpus americanus.

The results of Scirpus americanus and Carex lyngbyei field transplants were not absolutely concurrent with the theories of Tilman (1988). Tilman (1988) suggests that: (1) the intensity of above-ground competition should increase with habitat productivity while the intensity of below-ground competition should decrease with habitat productivity; and (2) total competitive intensity (the combination of above- and below-ground competition) should remain constant along this gradient. However, the intensity of the competition measured in the two experiments differed greatly and the results of the tranplant experiments suggested that competition was more intense in the nutrient-rich habitat. For example, reductions in biomass and shoot density were several times greater for Scirpus americanus individuals grown in the Carex community than vice-versa (Tables 6.5 and 6.6). This observation runs counter to Tilman (1988), however, it does support the predictions of Grime (1979) and others (Huston, 1979; Keddy, 1989). These researchers suggest that competitive intensity increases with plant biomass and site productivity.

The final experiment examined the effect that fertilization would have on Carex lyngbyei transplants grown in the *Scirpus americanus* zone. The results of the previous transplant experiment suggested that it was largely below-ground competition that reduced the vigor of *Carex lyngbyei* individuals transplanted into the *Scirpus* community. These findings together with the hypothesized competition model imply that interspecific interactions in the low marsh should primarily be for soil nitrogen. In nitrogen poor habitats, *Scirpus americanus* should out-compete *Carex lyngbyei* by being better adapted to forage for below-ground resources. However, if the levels of soil nitrogen in a nutrient-poor habitat are raised experimentally one would expect a competitive trade-off to occur. Under higher nitrogen levels *Carex lyngbyei* should become the dominant competitor because it can now allocate enough resources to the production of sufficient above-ground biomass to cause light reduction. The results of this experiment did illustrate that soil nitrogen additions would cause an increase in above-ground biomass and more importantly shoot height (Tables 6.8 and 6.10).

In summary, the results of the manipulative experiments do not offer unanimous support for the resource-ratio competition model developed in this thesis to explain the distribution of *Scirpus americanus* and *Carex lyngbyei* at Brunswick Point. The experiments do support the following predictions of the model: (1) the yields of the two species are indeed limited by soil nitrogen; (2) the potential distributions of the two species are reduced by competitive interactions; and (3) Scirpus americanus is excluded from Carex dominated communities primarily by light competition. The experiments also indicated that Carex lyngbyei was being excluded from the Scirpus community by way of below-ground competition. However, the intensity of this interaction was far weaker than predicted by the theories of Tilman (1988).

8.3 Common Garden Experiments

The common garden experiment involving the manipulation of soil nitrogen was carried out to test Tilman's predictions concerning biomass allocation and competitive superiority (Tilman, 1986b; 1988). According to Tilman's model, tradeoffs in above- and below-ground competition should be accompanied by changes in the pattern of plant biomass allocation to stems, leaves, and roots (Tilman, 1988). In this study both species allocate a sizable percentage of their biomass to the construction of rhizomes, a common tissue type found in many tidal marsh plants. Rhizomes are generally used by plants for asexual reproduction, resource acquisition, and anchorage, and can be specialized for the storage of translocated carbohydrates and nutrients (Grace and Wetzel, 1982; Biesboer, 1984; Hopkinson and Schubauer, 1984; Bernard, 1990; Chapin, Schulze, and Mooney, 1990; Karagatzides and Hutchinson, 1991; Raven, Evert, and Eichhorn, 1992; Grace, 1993b). However, Tilman (1986b; 1988) has not incorporated rhizomes into his model of resource competition and allocation of biomass production.

Carex lyngbyei allocates relatively more biomass to the production of shoots, has a greater total biomass, and is most limited in growth by soil nitrogen as predicted by Tilman's model (Tilman, 1986a, 1988). This is clearly demonstrated by the results of the regression analysis (Figures 7.2 and 7.5). The slopes of the regressions in Figure 7.2 suggest that *Carex lyngbyei* allocates progressively more biomass to shoots with each unit increment of soil nitrogen than *Scirpus americanus*. A greater allocation of biomass to shoots combined with its height advantage over *Scirpus americanus* (Figure 7.1) should make *Carex* a superior competitor for light. Similar relationships are also observed for total biomass. However, in these graphs the difference in slope trajectories is less (Figure 7.5).

Scirpus americanus allocates only a small percentage of its biomass to the production of roots when compared to *Carex lyngbyei* (Figure 7.6 and 7.7). At the lowest treatment (100 mg N/kg dry soil), *Carex lyngbyei*'s root biomass was twice as great as *Scirpus*, while at the highest application rate (2000 mg N/kg dry soil) the difference was 5.3 times higher (Figure 7.4). These findings suggest that *Carex* should be superior to *Scirpus* in the assimilation of soil nutrients because of its greater root biomass (Grime, 1979; Tilman, 1988). Further, visual inspection of the two species revealed that *Scirpus* *americanus* tends to have a "herring bone" root architecture typical of slow-growing species from nutrient-poor habitats, while *Carex lyngbyei* had a more dichotomous root architecture common to fast-growing species from nutrient-rich habitats (Fitter, 1987; Lambers and Poorter, 1992). These observations contradict the resource-ratio model that suggests *Scirpus americanus* should have a greater proportion of biomass allocated to the production of roots, because it is predicted to be the superior competitor for soil resources (Tilman, 1986b; 1988; and Figure 1.2).

Scirpus americanus allocates the majority of its photosynthate to the production of rhizomes (Figure 7.6) that are partially used as a sink to store translocated carbohydrates and nutrients when its shoots senesce in the late summer (Karagatzides and Hutchinson, 1991). This movement of nutrients from one tissue type to another may help *Scirpus* to minimize nutrient loss in an environment where nutrients are scarce. Similar adaptations have been reported for other plant species growing in nutrient-poor habitats (Chapin, 1980; 1991; Berendse and Aerts, 1987; Jefferies, Davy and Rudmik, 1988; Poorter, 1990; Poorter, Remkes and Lambers, 1990). According to the data displayed in Figure 7.6, *Scirpus americanus* allocated about 60 to 68 % of its biomass for the production of rhizomes. *Carex lyngbyei*, on the other hand, only allocated 11 to 20 % of its photosynthate to rhizomes (Figure 7.7).

Both species responded to the experimental increase in soil nitrogen by producing relatively more shoot and less root biomass, while allocation to rhizomes remained relatively fixed (Figures 7.6 and 7.7). However, these data also indicate that *Carex lyngbyei* is more flexible in its root:shoot ratio than *Scirpus americanus*. Fast-growing species from nutrient-rich environments tend to show more phenotypic plasticity in root:shoot ratio (Grime, 1979; Chapin, 1980; Lambers and Poorter, 1992). This allows fast growing plants to quickly fine tune the quantity and spatial distribution of above- and below-ground tissues as temporal changes in light and soil nutrient resources occur during the growing season (Grime, 1979).

Tilman's (1988) model also suggests that maximal relative growth rates should differ between the two species investigated in this study. More specifically, the model predicts that the maximal relative growth rate of a plant should be negatively correlated with the ratio of non-photosynthetic to photosynthetic tissues that it possesses (Tilman, 1988). In this study, maximal relative growth rates may be estimated from the yields of the two species in the nitrogen common garden experiment. On high fertility substrates (Figure 7.5) *Carex lyngbyei* grows approximately twice as fast as *Scirpus americanus*, which allocates relatively less biomass to the production of photosynthetic tissues (Figures 7.6 and 7.7). These results are in agreement with Tilman's (1988) model but also confirm the general idea that species adapted to low resource supply have a low growth rate (Chapin, 1980; Grime and Hunt, 1975; Grime, 1977; 1979; Aerts and Berendse, 1987; Chapin, Schulze, and Mooney, 1990; Lambers and Poorter, 1992).

In conclusion, the results of this experiment suggest that the morphology of *Scirpus americanus* and *Carex lyngbyei* controls their yield response to fertility manipulations. *Scirpus americanus* has a lower potential yield because it invests the majority of its photosynthate into the production of rhizomes. This is advantageous for survival in the nutrient-poor low marsh because it conserves nutrient loss from tissues. *Carex lyngbyei* has a greater potential yield because its allocation pattern promotes a high level of nutrient absorption and photosynthesis. This adaptation causes *Carex* to be competitively dominant in the nutrient-rich high marsh.

The last experiment in this study examined the effect light reduction would have on biomass accumulation and shoot height for both *Carex lyngbyei* and *Scirpus americanus* (Figures 7.9 to 7.12). Research examining the relationship between nitrogen and photosynthesis has shown that plants common to nutrient-rich habitats are able to grow more efficiently at reduced light availabilities (Field and Mooney, 1986). When light availability was decreased from 100 to 53 % only *Scirpus americanus* experienced significant declines in shoot, rhizome, root and total biomass tissues. Substantial declines in shoot, rhizome, root and total biomass for *Carex lyngbyei* occurred only when light levels were further reduced to ≤ 35 %. However, these declines were relatively greater than those experienced by *Scirpus*. The results of this experiment suggest that *Scirpus* is more sensitive to declines in light availability in the range from 100 - 53 %, which may concur with competitive dynamics in the field. When compared to actual field measurements of available light at the soil surface these values may seem high (Tables 4.3, 5.6 and 5.16; Figures 4.3 and 4.7). However, the field measurements are not measuring the availability of light in the canopy zone where photosynthesis is taking place.

Photosynthesis for *Scirpus americanus* is occurring on shoots that essentially intercept light on a vertical plane extending from the soil surface to the shoot tip. This peculiar geometry makes *Scirpus* extremely prone to shading from plant canopies whose leaf architecture is more horizontal and elevated. *Carex lyngbyei* has an architecture where the leaves are placed about 50 to 120 cm above the soil surface on a plane that is 45 - 60° from the horizontal. This change in leaf geometry results in a sudden increase in the level of shading along the marsh elevation gradient (see Figures 4.3 and 4.7). Combining these observations with the fact that the growth of *Scirpus americanus* is more sensitive to reductions in light availability (from 100 to 53 %) explains why the transition zone between the two species is so narrow.

In terms of biomass allocation, both species responded to the experimental reduction in light by producing relatively more shoot biomass (Figures 7.13 and 7.14). However, the two species differed in terms of which tissue type lost biomass due to the relative increase in shoot biomass. *Carex* compensated for its increase in shoot biomass by primarily decreasing the relative amount of biomass allocated to root production, while allocation to rhizomes remained relatively fixed. Increases in shoot biomass for *Scirpus* were counterbalanced by a relative decrease in biomass allocated to rhizomes, while relative allocation to roots remained constant. The presence of a higher percentage of storage tissues in *Scirpus* may provide support for rapid growth of above-ground tissues during times of increased light competition.

8.4 Nutrient Supply and Use Efficiency

The search for predictable patterns in the attributes of plant species that replace each other along nutrient gradients is one of the primary objectives of ecology (Grime, 1979; Chapin, 1980; Aerts and Berendse, 1987; Tilman, 1988; Aerts, 1990). At Brunswick Point only two species are dominant on a gradient of increasing soil nitrogen availability and elevation. In the nutrient-poor low marsh, *Scirpus americanus* dominates a community where plant productivity is low. Plants can adapt to nutrient-poor environments in essentially two ways: by maximizing the uptake of nutrients or by reducing the loss of nutrients (Grime, 1979; Chapin, 1980; Berendse and Aerts, 1987; Tilman, 1988; Berendse and Elberse, 1990a; 1990b; Berendse, Elberse, and Geerts, 1992). Tilman's models are based entirely on the assumption that plants survive in nutrient-poor environments by maximizing nutrient uptake from the soil (Tilman, 1986b; 1988). However, recent studies have revealed that some plants become competitively successful in nutrient-poor habitats by minimizing nutrient loss (Aerts, 1990; Berendse and Elberse, 1990; Berendse, Elberse and Geerts, 1992).

Figure 8.1 describes the dynamics of litter and organic matter and nitrogen cycling in the communities dominated by *Scirpus americanus* and *Carex lyngbyei*. The model suggests that the amount of soil organic matter available for mineralization is a function of two inputs: plant litter and consumers. Consumers supply a small amount of organic matter upon their death, shedding of tissues, and the defecation of digested plants or other consumers. Most of the organic matter that enters the soil system of the two communities comes from the decomposition of plant litter. Moreover, the amount of plant litter available for decomposition and

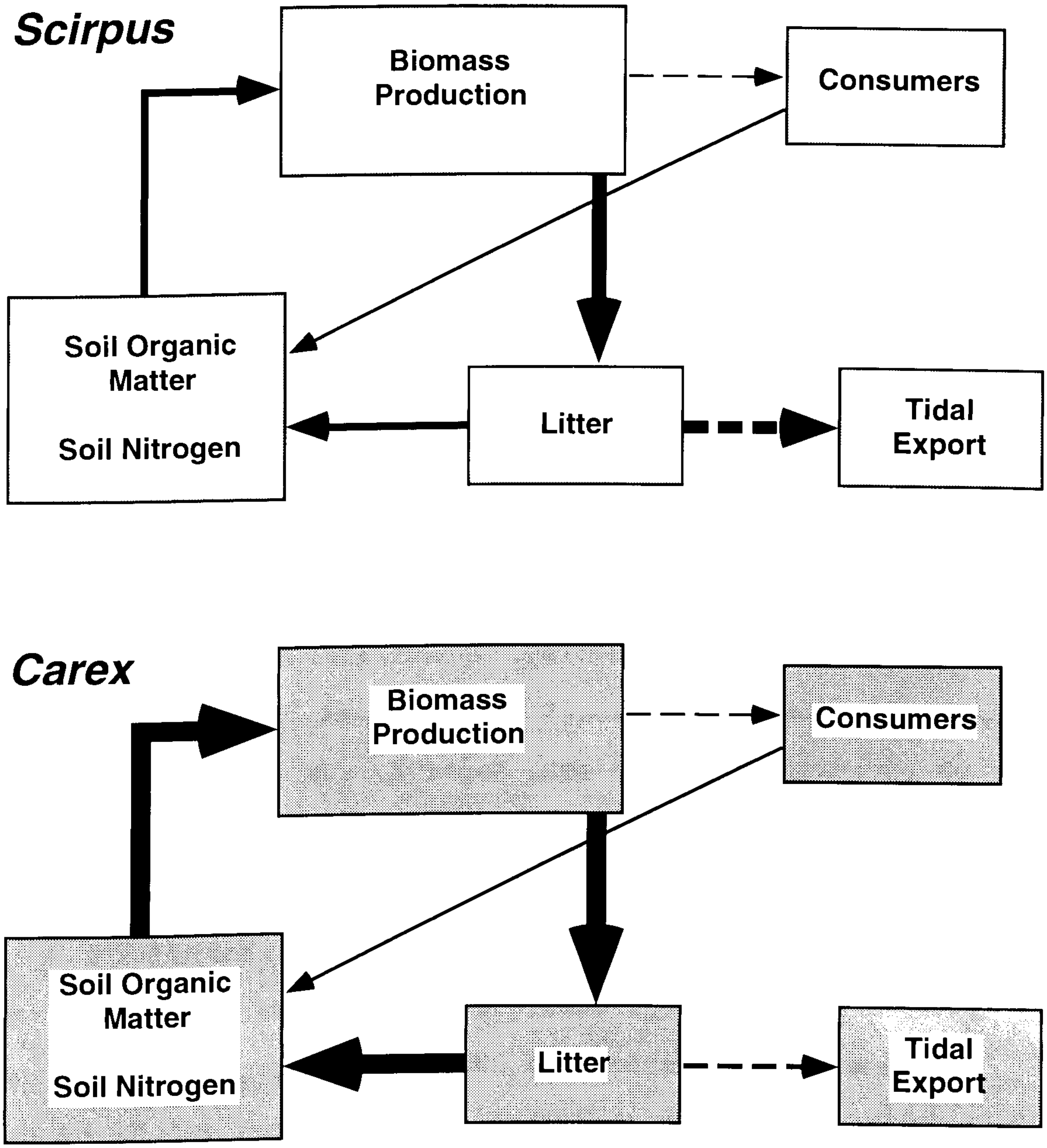

Figure 8.1. Model describing the cycling of organic matter and nitrogen in the communities of Scirpus americanus and Carex lyngbyei. The boxes describe the major sinks in this cycle. The arrows show the movement of organic matter and nitrogen from one sink to another, with arrow thickness representing relative quantities of transfer. Dashed arrows indicate the export of organic matter and nitrogen from the plant communities.

mineralization is controlled by the productivity of the plants growing on the soil and the amount of litter removed from the marsh surface by tidal flooding. In the Scirpus community, most of the above-ground biomass produced during the growing season is removed by inundating waters in the late summer and fall (personal observation). This removal of litter by tidal export is also responsible for the soils under Scirpus americanus having less organic matter and total nitrogen than soils under Carex lyngbyei individuals making these soils less productive (Figure 4.3 and Table 4.3). Removal of litter in the Carex community is far less because of its elevation, less frequent flooding, and more durable tissues (personal observation). Finally, the model in Figure 8.1 suggests that the "switch" from Scirpus americanus to Carex lyngbyei on the marsh platform may be a function of tidal export of litter.

Plants that lose a large percentage of their biomass during the period of non-growth must absorb more nutrients during the next growing season than plants that are more frugal of the nutrients that they have obtained (Berendse and Elberse, 1990). The results of this study suggest that Scirpus americanus is more successful in the nutrient-poor low marsh because it uses the nutrients it has procured frugally. This success is the result of its greater biomass allocation to the production of rhizomes that are used to store translocated nutrients at the end of the growing season. This adaptation, however, may make *Scirpus* less successful in the high marsh where soil nitrogen is in greater supply. The high marsh does not favor species that have a low growth rate, lower shoot height, and low allocation of biomass to the production of roots and shoots.

In the high marsh, the greater supply of soil nitrogen favors species that are less economical in terms of uptake, use and storage. *Carex lyngbyei* is dominant in the high marsh because it possesses specific attributes that allow it to successfully respond to this environment's greater soil nutrient supply by increasing its ability to acquire both above- and below-ground resources. These attributes include a high growth rate, greater shoot height, and a greater overall relative investment of biomass into root and photosynthetic tissues. At Brunswick Point, *Carex lyngbyei* invests only a small percentage of its biomass into the production of rhizomes because the high marsh is nutrient-rich. A high supply of soil nutrients does not favor the storage of nutrients because the cost of this storage may be expensive to the plant (Chapin, Schulze, and Mooney, 1990). *Carex lyngbyei* is not dominant in the low marsh because the attributes it possesses require a greater availability of soil nitrogen.

The zonal patterns of plant dominance observed at Brunswick Point are the result of evolutionary trade-offs caused by changes in soil nitrogen supply across the tidal marsh platform. *Carex lyngbyei* and *Scirpus americanus* have each evolved a particular collection of attributes that reflect the supply of below-ground resources in their tidal marsh habitats. *Scirpus americanus* dominates nutrient-poor sites at Brunswick Point because its significant investment into the production of rhizomes allows it to store translocated nutrients at the end of the growing season. This adaptation, however, comes at a cost of a lower investment into shoot and root tissue when compared to *Carex lyngbyei*, and results in a slower growth rate and smaller size in terms of biomass and shoot height. In the high marsh, the greater availability of soil nutrients favors *Carex lyngbyei* which invests these nutrients primarily to produce shoot and root tissues. This higher relative investment also leads to a faster growth rate and larger size in terms of biomass and shoot height.

CHAPTER 9

CONCLUSIONS

The existence of global, general patterns in tidal marsh plant communities suggests the existence of broad, general causative forces. In general, the distribution of plant species in any community are influenced by a variety of abiotic and biotic factors (Harper, 1977; Crawley, 1986; Crawford, 1989). This study tests the hypothesis that the spatial patterns of two dominant species observed in a brackish tidal marsh may be explained by exploitation competition for light and soil nitrogen.

Abiotic data collected from the study site at Brunswick Point indicate that the availability of soil nitrogen (the most limiting resource) and light beneath the plant canopy to be negatively correlated along an elevational gradient. Further, the segregation of the two species, *Scirpus americanus* and *Carex lyngbyei*, along this gradient invites an interpretation based on Tilman's resource-ratio hypothesis (Tilman, 1980; 1982; 1988). This interpretation suggests that the low marsh species, *Scirpus americanus*, is a superior competitor for soil nitrogen at low elevation sites. In high marsh sites where nitrogen is in greater supply, *Carex lyngbyei* is a superior competitor for light which becomes limiting to *Scirpus americanus* because of *Carex*'s high allocation of photosynthate to shoot production. However, measurement of the available ammonium in the *Scirpus* and *Carex* communities indicated that the two species have equal abilities to consume below-ground resources.

The results of the manipulative field experiments were supportive of the resource-ratio model. Fertilization of both species indicated that soil nitrogen was indeed the limiting factor to growth. Transplantation of *Carex lyngbyei* and *Scirpus americanus* at six sites across the elevation gradient indicated that their potential distributions were greater than their actual field distributions. Finally, transplantation experiments with several different treatment applications revealed that: (1) *Scirpus americanus* may be competitively excluded from the *Carex lyngbyei* dominated zone primarily by light reduction; (2) competition for soil nitrogen may be most important in the competitive exclusion of *Carex lyngbyei* from the *Scirpus americanus* zone; and (3) the intensity of these competitive interactions was far weaker in the *Scirpus* community. This final point, however, runs counter to the theories of Tilman (1988).

The results of the common garden experiments rejected important elements of the resource-ratio model. As predicted, *Carex lyngbyei* did allocate a greater relative percentage of biomass to the production of above-ground tissues confirming the hypothesis that it should be a better competitor for light than *Scirpus americanus*. However, *Scirpus americanus* did not allocate a greater relative percentage of biomass to the production of roots. Instead, *Scirpus americanus* was found to allocate most of its biomass into the production of rhizomes. *Scirpus* uses these rhizomes principally for vegetative reproduction and to store carbohydrates and nutrients that are translocated from its shoots at the end of the growing season. Translocation acts to conserve resources obtained by uptake during the growing season. Moreover, this adaptation may be responsible for its dominance in the nutrient-poor low marsh habitats, and may aid *Scirpus* in competitive situations by supplying stored resources for increased height growth when light becomes less available.

In summary, the common garden experiments suggested: (1) that *Scirpus* is more successful in the nutrient-poor low marsh because it is more frugal of the nutrients that it has secured for survival; (2) that *Scirpus* is more sensitive to reductions in light availability; (3) that *Carex* is adapted for rapid growth and extensive foraging for below- and above-ground resources; and (4) that *Carex* is less sensitive to declines in the availability of light.

The results of this study agree with studies in the Netherlands that have examined competition and nutrient availability in heathland and grassland plants (Aerts and Berendse, 1988; Aerts, 1990; Aerts, Berendse, de Caluwe, and Schmitz, 1990; Berendse and Elberse, 1990; Berendse, Elberse, and Geerts, 1992). Their studies have found that plant species growing in nutrient-poor habitats competitively exclude invaders from nutrient-rich habitats by possessing attributes that enable them to reduce their nutrient losses. These results, like the findings of this study, also do not confirm Tilman's (1988) hypotheses (1) that a genetically determined high proportional root biomass is one of the major adaptive strategies plants use to dominate in nutrient-poor habitats; and (2) that competition in nutrient-rich habitats is primarily for above-ground resources.

In conclusion, the theories of Tilman (1982; 1988) were used in this study to deductively evaluate the mechanisms that may be responsible for plant zonation in tidal marshes. The results of this study rejected this model, and now offer evidence for an alternative hypothesis. The continued testing of this hypothesis and its refinements will increase our understanding of how tidal marsh plant communities work.

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