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Growth and Herbivory of the Black Mangrove, *Avicennia germinans*, Along a Salinity Gradient

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Growth and Herbivory of the Black Mangrove, *Avicennia germinans,* Along a Salinity Gradient

by

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Abstract

Coastal communities will be most affected by global climate change and are important to study to understand current and future ecological processes. The current model for global climate change predicts a change in rainfall, which will alter the salinity of coastal systems. Given the presence of eutrophication in many coastal waters, it is important to understand the effects that this increase in nutrients, coupled with changes in salinity, will have on these communities. This study was conducted to understand the effect of salinity increase on the growth and herbivory of the black mangrove, *Avicennia germinans*, in the presence of increased nutrients. Explicitly, the effects of changing salinity (high, medium, and low) were coupled with fertilizer additions of nitrogen, phosphorus, both, or no fertilizer. Nutrient enrichment differentially affected the growth and herbivory of the plants between salinity zones. The medium salinity zone consistently produced the greatest increases in growth and herbivory. Added nutrients did not have an effect on growth in the low salinity zone. However, added nitrogen increased some growth variables in the medium salinity zone and added phosphorus increased some growth variables in the high salinity zone. Phosphorus also increased herbivory. The results point to diverse processes acting along the salinity gradient. There appears to be differential N- and P-limitation along the gradient. Additionally, the growth differences indicate abiotic and biotic limitations across the salinity gradient, with debilitating salinity acting in the high salinity zone and competition acting in the low salinity zone.

Chapter One: Introduction

Mangroves are located along the intertidal zone in the tropics and subtropics and cover some 17 million hectares worldwide. The mangrove forest ecosystem is one of the most productive in the world, although it has relatively low species richness and exhibits low spatial heterogeneity. Mangroves provide support for marine ecosystems, protection for inshore areas, and stability to the shoreline. Unlike many other plants, mangroves are able to tolerate a wide range of salinities, which makes their growth possible in a wide range of coastal zones.

Mangroves provide numerous ecosystem services. Their roots provide a hard substrate in a soft substrate environment giving many organisms such as sponges, bivalves, and algae a place to live (Ellison et. al. 1996). The space between the roots offers protection for many juvenile fish and prawns. Mangrove trees provide an important food source for many arthropod species such as insects and crabs, and mangrove leaf litter is an important food source for many species. This leaf litter is transformed into detritus which may be exported to other ecosystems, providing them with food and nutrients (Loneragan et. al. 1997; Davis et. al. 2003).

Humans also depend on mangroves for a variety of services. Mangroves provide wood for the production of timber, a site for catching commercially important fish, crustaceans, and mollusks, and shoreline protection from tropical storms (Duke et. al. 2007; Bosire et. al. 2008). Mangrove forests also provide income via tourism in many countries. A recent socioeconomic study on the benefits of the mangrove ecosystem to the village of Buswang, Philippines estimated services provided by mangroves generated an income of 564–2316 USD per hectare per year (Walton et. al. 2006).

Mangroves thrive in especially stressful environments. They can tolerate a wide range of salinities as well as nutrient-poor soils. Mangroves are able to deal with these conditions through salt-exclusionary devices and high nutrient resorption efficiency. Frequent studies on mangroves over the last several decades have focused on changes in ecological processes with nutrient enrichment (Feller et. al. 2007). The emphasis in many of these studies has been how nutrient enrichment effects mangrove growth and herbivore attack (Farnsworth & Ellison 1991).

Theoretically, the addition of fertilizer to a plant should stimulate its growth. Early studies in Florida on sites with and without bird rookeries, with the rookery site being the source of nitrogen fertilization, found an increase in the abundance of new branches, leaves, and reproductive elements in *Rhizophora mangle* at the nutrient enriched site (Onuf et.al. 1977). Later, Feller (1995) found that, at a study site in Belize, nitrogen enriched *Rhizophora mangle* trees exhibited growth rates similar to those of the control. However, when *R. mangle* trees at this site were phosphorus enriched, dramatic increases in shoot, leaf, and root growth were observed (Feller 1995).

Opposite results were obtained for similar nitrogen and phosphorus enrichment experiments in different locations (Feller et. al. 2003; Naidoo 2009). This fostered the notion that some mangrove forests are phosphorus-limited and some are nitrogen-limited (Feller 1995; Koch & Snedaker 1997; Feller et. al. 2007). In fact, sites can be both phosphorus and nitrogen limited with variations across tidal gradients (Boto & Wellington 1983; Feller et. al. 2003).

It is possible that the results of nutrient enrichment depend on salinity. Salinity affects plant growth. In general, increased salinity limits water uptake by plants. Therefore, plants growing in saline environments have lower leaf water potentials which leads to reduced stomatal conductance, intracellular CO_2 concentrations, and net photosynthesis (Lopez-Hoffman et. al.

2007). Mangrove performance decreases at more saline sites due to a greater energy demand to maintain physiological processes, with less energy available for growth and reproduction (Gongalves-AIvim et. al. 2001). Mangroves growing in high salinity have decreased growth rates, survival, and net photosynthesis. They also have higher root to shoot mass ratios than mangroves growing at low salinity (Lopez-Hoffman et. al. 2007). At higher salinity, leaves are smaller and more sclerophyllous (Gongalves-AIvim et. al. 2001). In addition to decreased water uptake, an increase in soil salinity can decrease nutrient availability (Bowdish & Stiling 1998; Feller et. al. 2003). As salinity increases, mangrove nutrient demand increases to be able to continue to operate salt-exclusionary mechanisms. Because salinity affects mangroves in these ways, there may be trade-offs between water-use efficiency and nutrient-use efficiency.

Herbivory can alter nutrient cycling patterns in mangrove systems (Feller 2002). By direct removal of leaf tissue, herbivores remove resources that were directed towards detrital pathways. In addition, the tissue removed by herbivores causes a decrease in the amount of nutrients available for resorption during senescence (Risley & Crossley 1988; Feller 2002).

Mangrove herbivory impacts individual plant growth and primary productivity. Root-boring isopods greatly reduce root growth rate (Perry 1988; Farnsworth & Ellison 1991; Ellison & Farnsworth 1993; Brooks & Bell 2001). Seedling growth rates are reduced by the invasion of herbivorous insects (Farnsworth & Ellison 1991, 1993; Feller 1995). However, cerambycid beetles excise mangrove branches creating light gaps in the canopy which allows for necessary light to encourage mangrove seedling growth (Ellison et. al. 1996). Loss of leaf tissue and branch removal results in a loss of total plant photosynthetic capacity (Lee 1991), and has also been shown to reduce mangrove reproductive output (Cannicci et. al. 2008).

Rates of herbivory on coastal plants have also been found to differ with salinity. Some mangrove studies have found an increase in gall density with an increase in salinity due to an increase in sclerophylly in vegetation growing in saline areas (Gongalves-AIvim et. al. 2001). Galling insects may be more protected in sclerophyllic vegetation (Price et. al. 1998). Alternatively, salt accumulation on mangrove leaves can deter other insects from settling, and some studies have found less herbivory on mangroves that occur in higher salinity sites (Jiminez 1984; Farnsworth & Ellison 1991).

Three major hypotheses have been established to understand how herbivory varies between plants. The plant stress hypothesis, proposed by White (1969), suggests that stressed plants are more susceptible to herbivore attack than their healthy counterparts. The buildup of amino acids in plant tissues is said to be the reason this pattern arises and densities of sap sucking insects can increase on stressed plants (White 1969). Additionally, stressed plants are less able to invest resources into making secondary chemicals to deter herbivore attack (Rhoades 1979). An opposing hypothesis, the resource availability hypothesis, proposed by Janzen (1974), suggests that stressed plants are more likely to have high concentrations of anti-herbivore compounds because leaf loss has a greater negative impact to plants growing in stressed, infertile conditions than in more benign, fertile areas. Therefore, plants located in stressful environments are less likely to be attacked by herbivores than those which inhabit a relatively stress-free environment. Lastly, the plant vigor hypothesis, proposed by Price (1991), predicts that vigorously growing plants will experience greater herbivore attack. By attacking the most robust, fast growing and nutrient rich plants, herbivores are ensuring successful, quicker larval development and better adult performance (Price 1991). These three hypotheses are not mutually exclusive. Herbivore attack rates may be greater in stressed plant populations, but

within an individual plant, herbivores may focus on those parts of the plant that are growing more vigorously (Goncalves-Alvim et. al. 2001). In support of the plant vigor hypothesis, the detrimental effects of salinity on plant growth have been shown to be reduced with an increase in nutrient availability (Feller 1995; Stiling & Moon 2005), with greater proportional increase of galling insects densities on high-salt plants than on low-salt plants with nutrient enrichment (Stiling & Moon 2005).

Here, we test whether the responses of mangroves, and their herbivores, to nutrient enrichment with nitrogen and phosphorus are altered by soil salinity and whether the plant stress or plant vigor hypothesis is best supported by the data. We predict that mangrove growth will increase in response to nutrient enrichment and will show the most marked increase with the highest level of salinity because stress will be alleviated the most. We expect that the plant vigor hypothesis will best explain herbivore dynamics in mangrove systems.

Plant species that are adapted to nutrient-limited soils, like mangroves, exhibit relatively lower growth rates, have greater concentrations of defensive compounds, and are not much attacked by herbivores (Janzen 1974). We predict that herbivory will increase in response to nutrient enrichment and this increase will be highest at the lowest level of salinity.

This research is particularly timely due to the current threat of global climate change and nutrient enrichment from coastal run-off. The current model for global climate change predicts a change in rainfall, which will alter the salinity of coastal systems (Karl & Trenberth 2003). Therefore, changes in growth and herbivory of mangroves subject to nutrient enrichment, monitored over a natural salinity gradient, may help us better understand and predict the future outcome of changes in nutrient levels and precipitation on mangrove systems.

Study Organism: *Avicennia germinans*

Avicennia germinans, the black mangrove, is an evergreen shrub that is prevalent in tropical and subtropical coastal areas. It is able to tolerate a wide range of salinities because of exclusion of salt through the roots, secretion of salt through leaf glands, and salt accumulation in the extracellular spaces in leaves (Goncalves-Alvim et. al. 2001). *A. germinans* has precocious leaf production, where if a branch is damaged several new shoots soon form. This differs from *Rhizophora mangle* in which leaf production is confined to the apical meristem (Cannicci et.al. 2008).

Study Site: Weedon Island Preserve

Weedon Island Preserve is located in St. Petersburg, Florida and covers 1280 ha along the west side of Tampa Bay. Tidal swamp comprises approximately 1056 ha of the preserve. This area contains an extensive amount of dredged mosquito ditches. This community consists of dense mangrove forests. Three species of mangroves can be found within the park; the red mangrove, *Rhizophora mangle*; the black mangrove, *Avicennia germinans*; and the white mangrove, *Laguncularia racemosa*. Typically, *R. mangle* is found closest to the water, *L. racemosa* is furthest from the water, and *A. germinans* inhabits the middle ground. However, at Weedon Island the mangrove species are fairly mixed without true delineation among the species (personal observation).

(http://www.weedonislandpreserve.org/pagesHTM/PDFs/WIPMngmtPlan.pdf)

Chapter Two: Methods

I measured growth and herbivory of 60 fertilized *Avicennia germinans* trees along a natural salinity gradient in Weedon Island Preserve for the duration of one growing season. Along this natural salinity gradient, there were three salinity levels, low, medium, and high, and within each of those three levels 20 trees were tagged for growth and herbivory measurements. Salinity measurements were recorded on a monthly basis from a porewater sample, at the base of each tree, using a refractometer. The average salinities in each of the salinity zones for the duration of the experiment are as follows: low, 34; medium, 55; high; 89. The averages reported here come from the last two months of salinity data collection, as the previous months' salinity data is not reliable due to issues with rainwater diluting the salinity for some measurements. The salinity data measurements for each month can be seen in Appendix 1. Trees were approximately 4m apart to ensure that the fertilizer did not affect adjacent trees (Feller 1995).

There were four treatments of nutrient enrichment: addition of nitrogen, addition of phosphorus, a combination of nitrogen and phosphorus, and a control in which fertilizer was absent. Nitrogen was added in the form of NH_4 (45:0:0) and phosphorus in the form of P_2O_5 (0:45:0). Fertilizer was applied in two 150g doses contained in six inch PVC piping with small holes drilled into the sides for gradual fertilizer release. Two holes were cored on either side of the mangrove that were 7cm in diameter and 30 cm deep to which the fertilizer tubes were placed. Once the fertilizer was in place, the hole was covered and marked. Control trees had holes cored, but no fertilizer was added, and the holes were filled in and marked. Upon completion of the study, the five branches from each tree were removed and brought back to the

lab. Two centimeter sections of the branches were removed and dried, and then burned to determine organic content.

Plant Growth

Growth measurements of the tagged trees were performed monthly. Five initially unbranched shoots were selected from each tree and marked with different colors of duct tape denoting each nutrient treatment. The leaves in the apical position of the shoot were marked with a black sharpie on the underside of the leaf to mark the starting point for growth measurements. The initial length of the shoot was measured and subsequent growth of those five initially unbranched shoots was measured on a monthly basis from the starting point defined by marked leaves. The number of new shoots and new leaves that arose from the initially unbranched shoot were recorded and marked. I also took pictures of two leaves from each shoot per tree to measure the change in area of those leaves over the course of one growing season. Plant growth at the shoot and leaf level has been found to be more sensitive to nutrient addition than overall tree height or the diameter at breast height (Feller 1995). The leaf area index was also measured on a monthly basis using the plumb bob method. The leaf area index was defined as the mean number of leaf contacts a weighted plumb line encounters when lowered five times at randomly selected points in the tree's canopy. This is an important measurement because several studies have found that rates of herbivory can be correlated with canopy cover.

Herbivory

Herbivory was measured as degree of leaf folivory. Two leaves, which showed no current signs of herbivory, from each initially unbranched shoot per tree, were marked to monitor leaf folivory for one growing season. Signs of herbivory included bites along the leaf margin, holes in the leaf, and trails/scrapes made by insects excavating tissue. This resulted in 10 leaves

per tree being examined and 600 total leaves to be monitored for folivory on a monthly basis for one growing season. Every month, digital images of these individual leaves were taken and used to determine the percent leaf area lost to herbivory. The area of the leaves and the area of the leaves lost to herbivory were analyzed using the image analysis software, Image J. Short term herbivory was measured in the form of monthly changes, but leaf life herbivory was determined by the amount of herbivory occurring on an individual leaf for the duration of the experiment. Additionally, a random selection of 10 leaves per tree were examined for signs of herbivory. These leaves were placed into one of two categories; leaves with or without herbivory.

To analyze treatment effects on branch length, organic content, and leaf lifetime an ANOVA was conducted, with N, P and salinity level as the main factors. Repeated measures ANOVA's were used to analyze the number of leaves, the number of new leaves, the number of new shoots, leaf area index, and both measures of herbivory, where month was the time effect. In addition an ANCOVA was conducted on the growth variables, with herbivory as the covariate, to determine if changes in growth were caused by herbivory, but the covariate was not significant.

Chapter Three: Results

Plant Growth

Salinity significantly affected the number of leaves ($F_{(2,48)}$=17.512, p=0.00000), new leaves ($F_{(2,48)}$=23.945, p<0.00000), and new shoots ($F_{(2,48)}$=8.027, p=0.001). The greatest number of leaves, new leaves, and new shoots was found in the medium salinity zone with lesser leaves, new leaves, and new shoots in the low and high salinity zones (Figure 1). Salinity also had a significant impact on the leaf area index (LAI) ($F_{(2,48)}$=9.167, p=0.004). Again, the LAI was highest in the medium salinity zone, followed by the low salinity zone, but was much lower in the high salinity zone (Figure 2). Finally, salinity had a significant effect on branch length ($F_{(2,48)}$=7.753, p=0.001). As before, branch lengths were greatest in the medium salinity zone, and lower in the high and low salinity zones (Figure 3).

The addition of phosphorus or nitrogen did not increase the number of leaves, new leaves, or new shoots, but the presence of nitrogen marginally increased branch length ($F_{(1,48)}$=3.135, p=0.08). There was a significant interaction between nitrogen and salinity on the number of leaves ($F_{(2,48)}$=3.755, p=0.03), with nitrogen only increasing the number of leaves in the medium salinity zone (Figure 4). The presence of nitrogen caused no increase in leaf number in either the low or high salinity zones. There was also a marginally significant interaction of nitrogen and salinity on branch length ($F_{(2,48)}$=2.774, p=0.07). In the medium salinity zone, the presence of nitrogen significantly increased branch length, whereas in the low and high salinity zones nitrogen did not have such an effect (Figure 5). Nitrogen had a marginally significant positive effect on leaf lifetime ($F_{(1,48)}$=3.910, p=0.05) (Figure 6) and organic content of branches

($F_{(1,48)}$=3.26, p=0.077) (Figure 7). There was a significant interaction of phosphorus and salinity on branch length ($F_{(2,48)}$=5.339, p=0.008). In the high salinity zone phosphorus increased branch length (Figure 8).

Finally, there was a significant three-way interaction of nitrogen, phosphorus, and salinity on the LAI ($F_{(2,48)}$=3.195, p=0.05). In the high salinity zone, the addition of nitrogen alone, and the coupled addition of nitrogen and phosphorus had a slight positive effect on the LAI. In the medium salinity zone, the LAI was greatest with the coupled presence of added nitrogen and phosphorus or the absence of them both. In the low salinity zone, the LAI was greatest with the presence of phosphorus or nitrogen alone (Figure 9).

Herbivory

Herbivory was measured in two separate ways. The first was by picking ten leaves, at random, per tree and determining whether or not they had any signs of herbivory. This yielded a frequency of leaves exhibiting signs of herbivory. The second was by taking pictures of two leaves per branch per tree and calculating the area of the leaf lost to herbivory using Image J software. The second measure of herbivory yielded no significant results.

There was a significant difference in the amount of herbivory with salinity ($F_{(2,48)}$=4.283, p=0.02). Herbivory was greatest in the medium salinity zone, and slightly less in the low salinity zone. Herbivory was extremely low in the high salinity zone (Figure 10). There was a significant increase in the frequency of herbivory with the addition of phosphorus ($F_{(1,48)}$=7.710, p=0.008), and a significant interaction between phosphorus and salinity on herbivory ($F_{(2,48)}$=3.297, p=0.046). Herbivory was greatest in the low and medium salinity zone with the presence of added phosphorus (Figure 11).

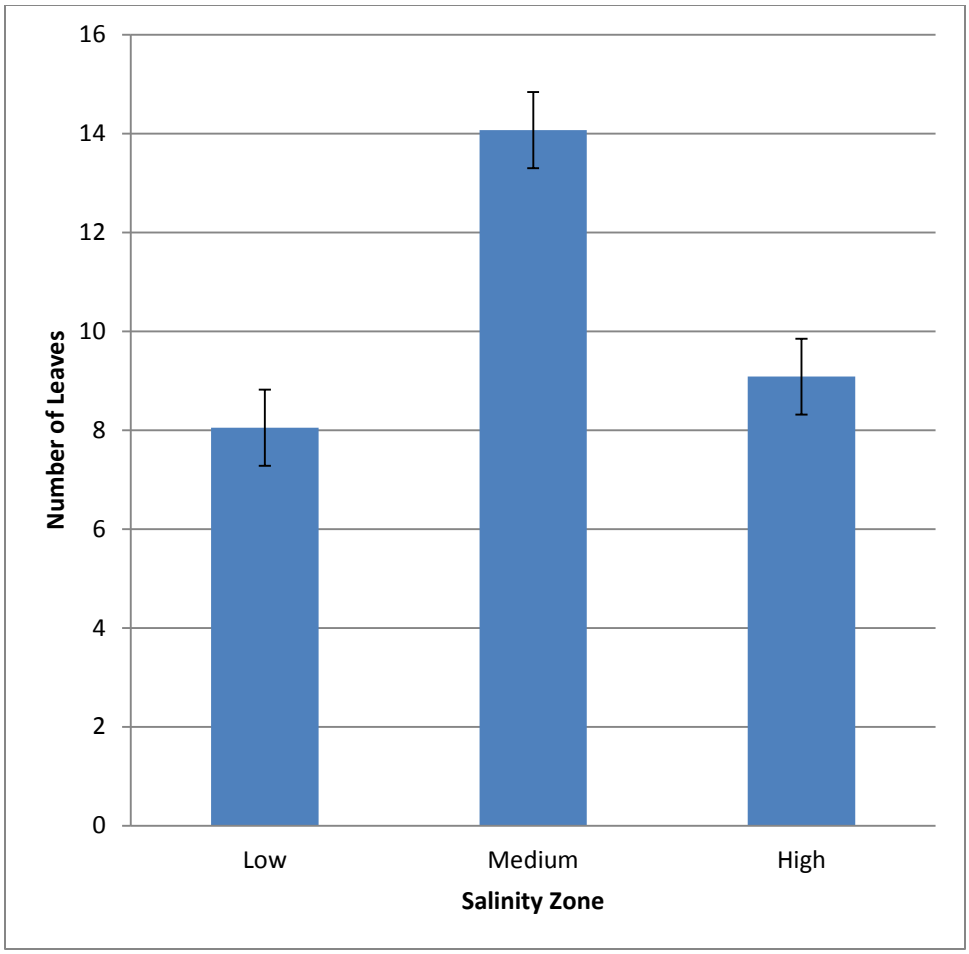

Figure 1. The effect of salinity on the number of mangrove leaves in different salinities. Similar relationships are present for the effect of salinity on the number of new leaves, new shoots, leaf area index, branch length, and frequency of herbivory. Vertical bars denote +/-standard errors.

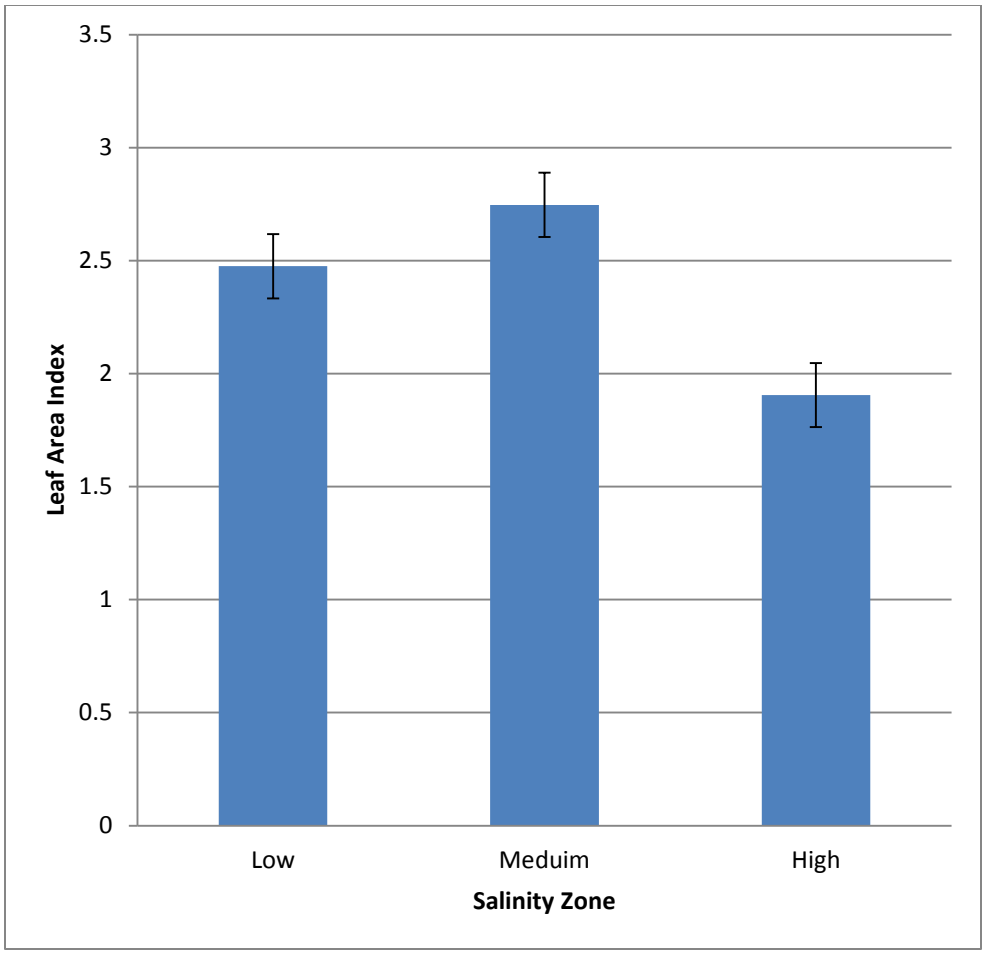

Figure 2. The effect of salinity on the leaf area index. Vertical bars denote +/- standard error.

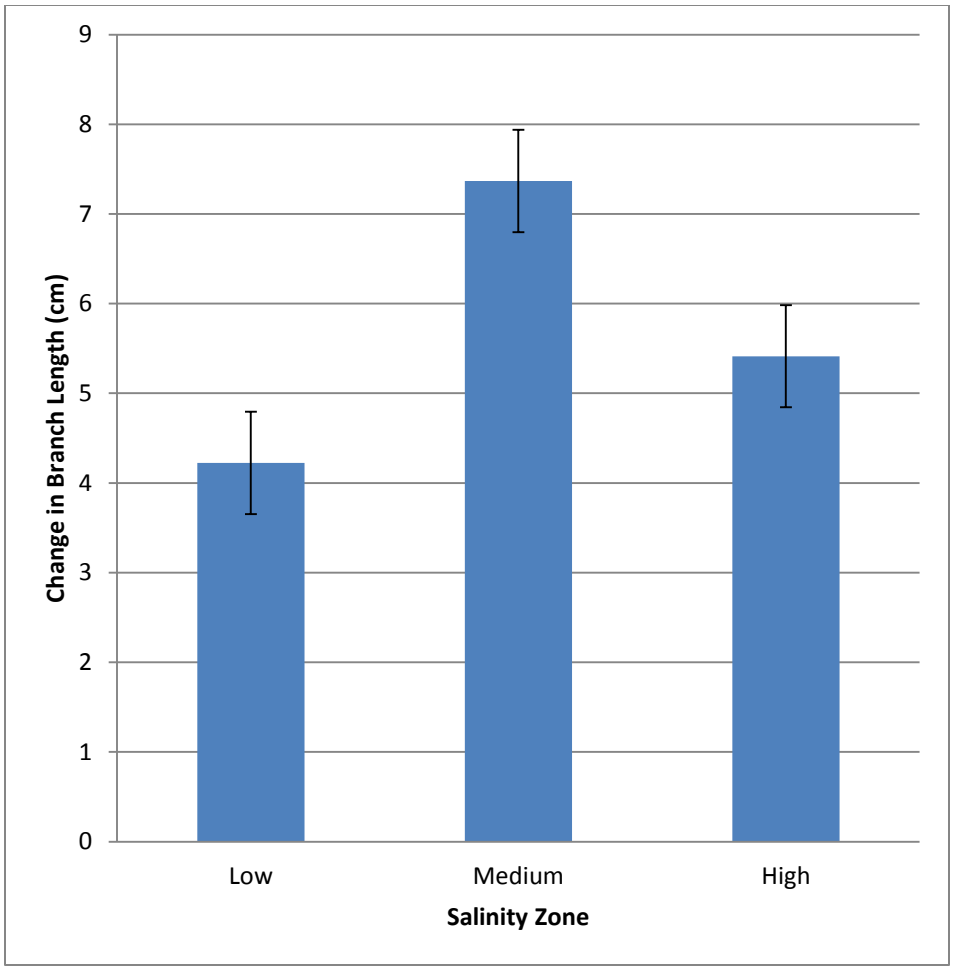

Figure 3. The effect of salinity on branch length. Vertical bars denote +/- standard error.

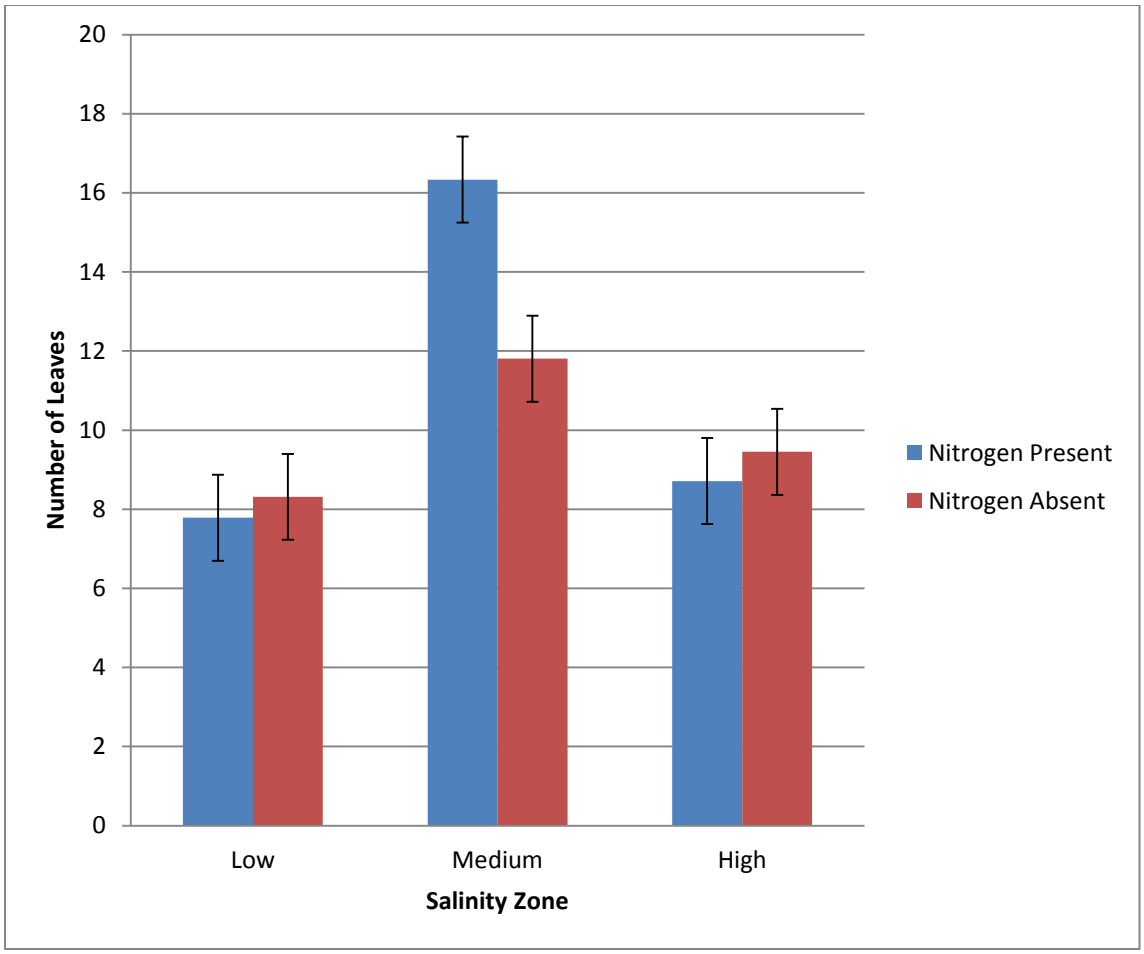

Figure 4. The effects of nitrogen and salinity on the number of leaves. Vertical bars denote +/- standard errors.

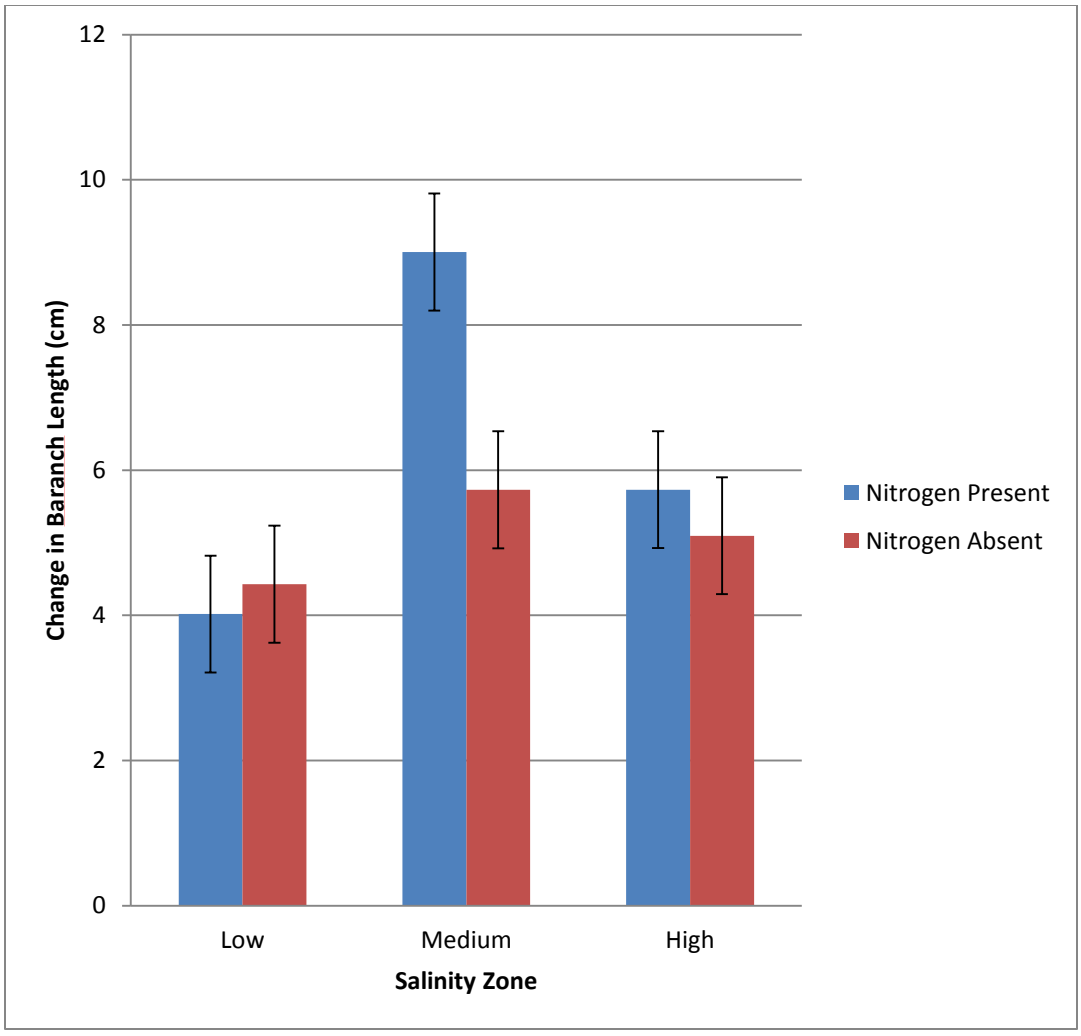

Figure 5. The interactive effect of the addition of nitrogen and salinity on branch length. Vertical bars denote +/- standard error.

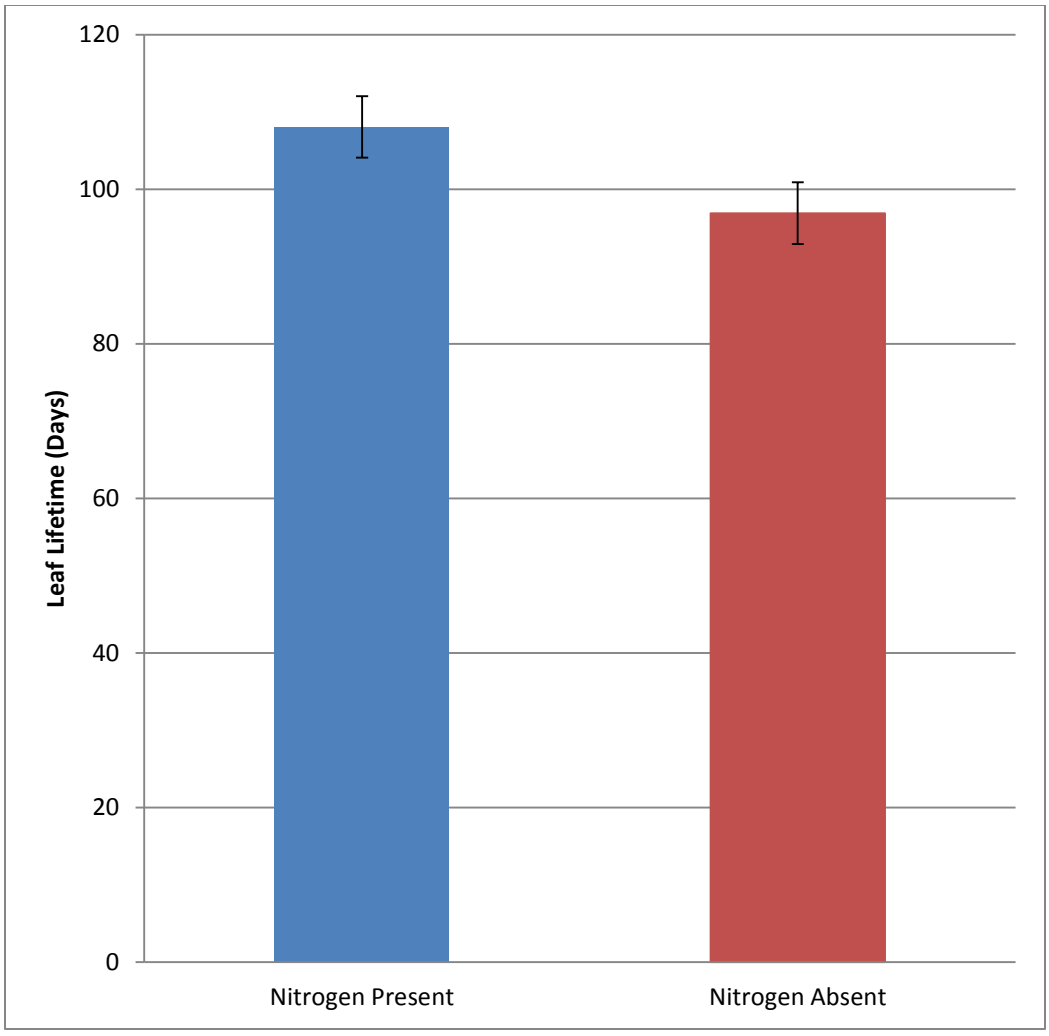

Figure 6. The effect of nitrogen on leaf lifetime. Vertical bars denote +/-standard errors.

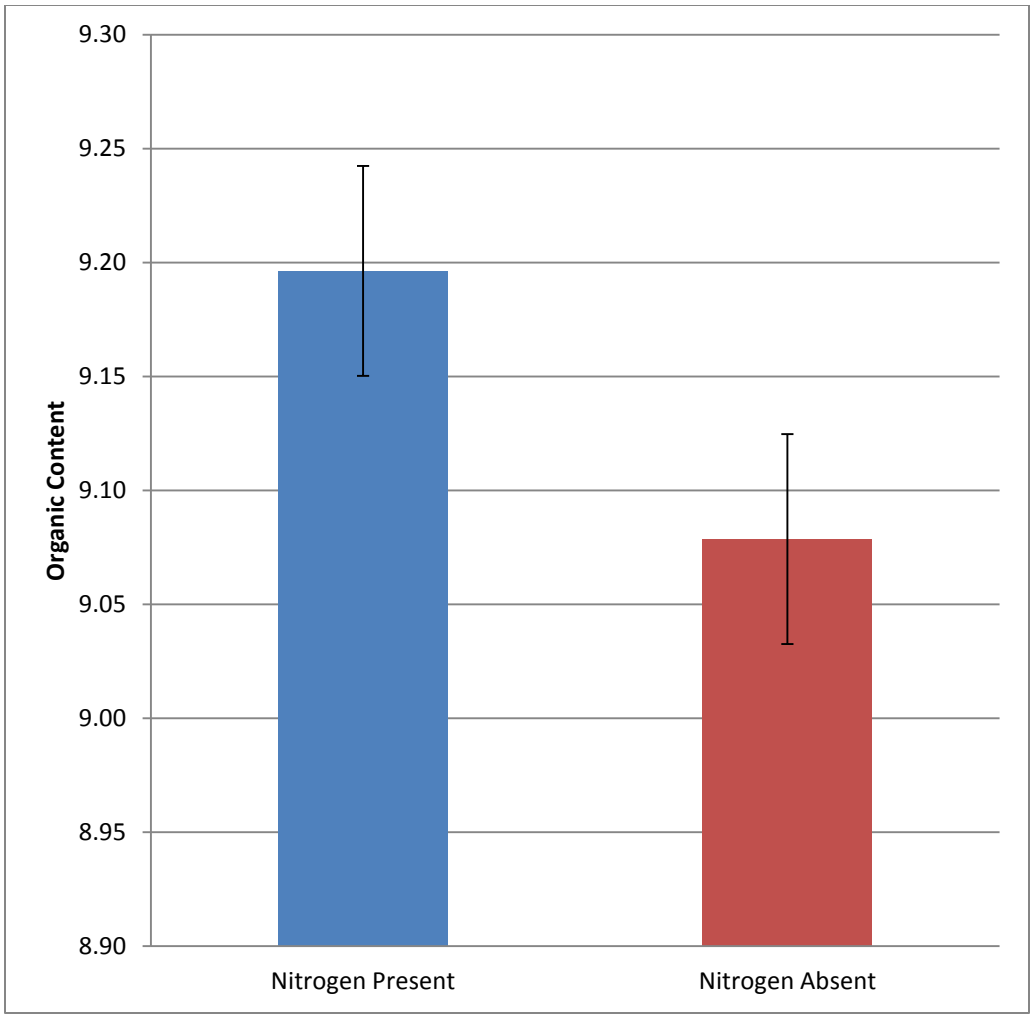

Figure 7. The effect of nitrogen on branch organic content. Vertical bars denote +/-standard errors.

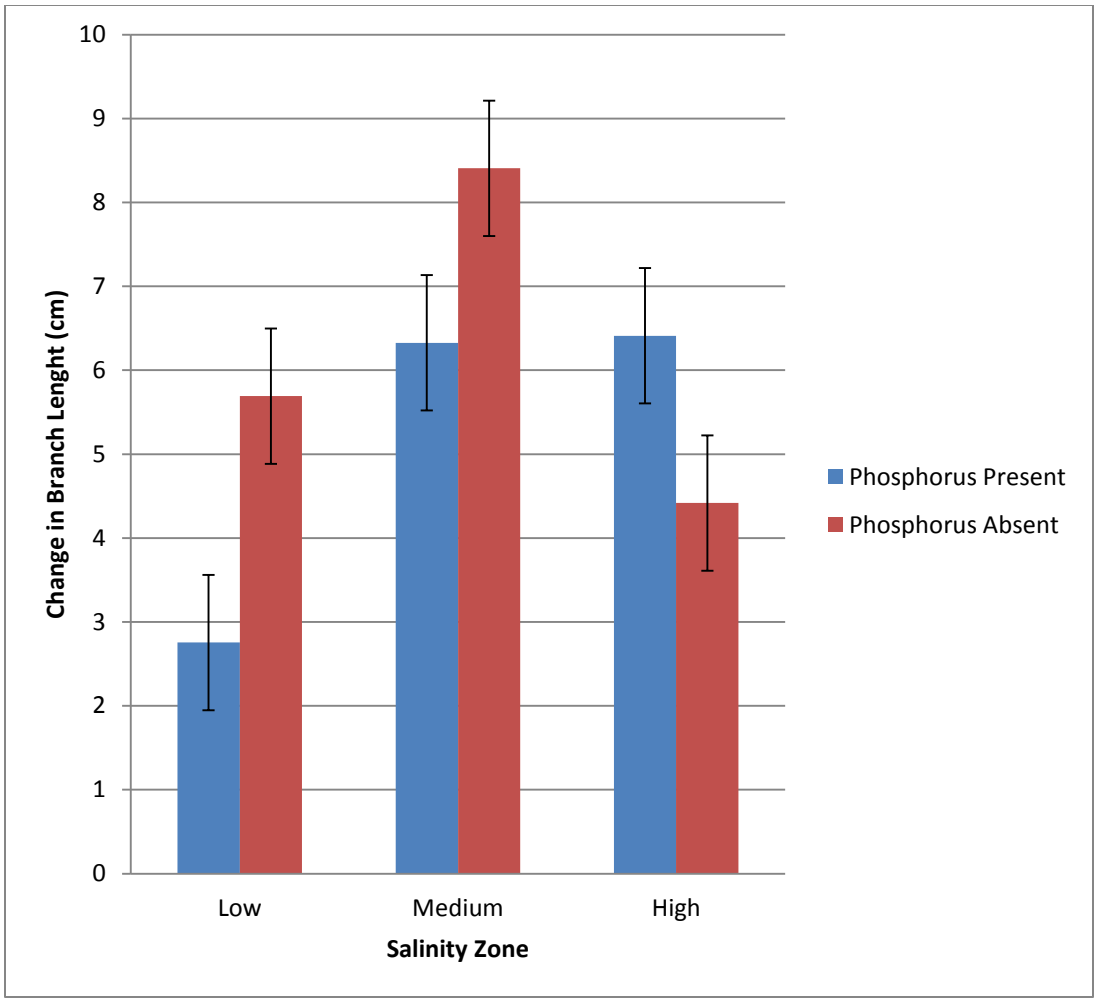

Figure 8. The effects of the addition of phosphorus and salinity on branch length. Vertical bars denote +/- standard error.

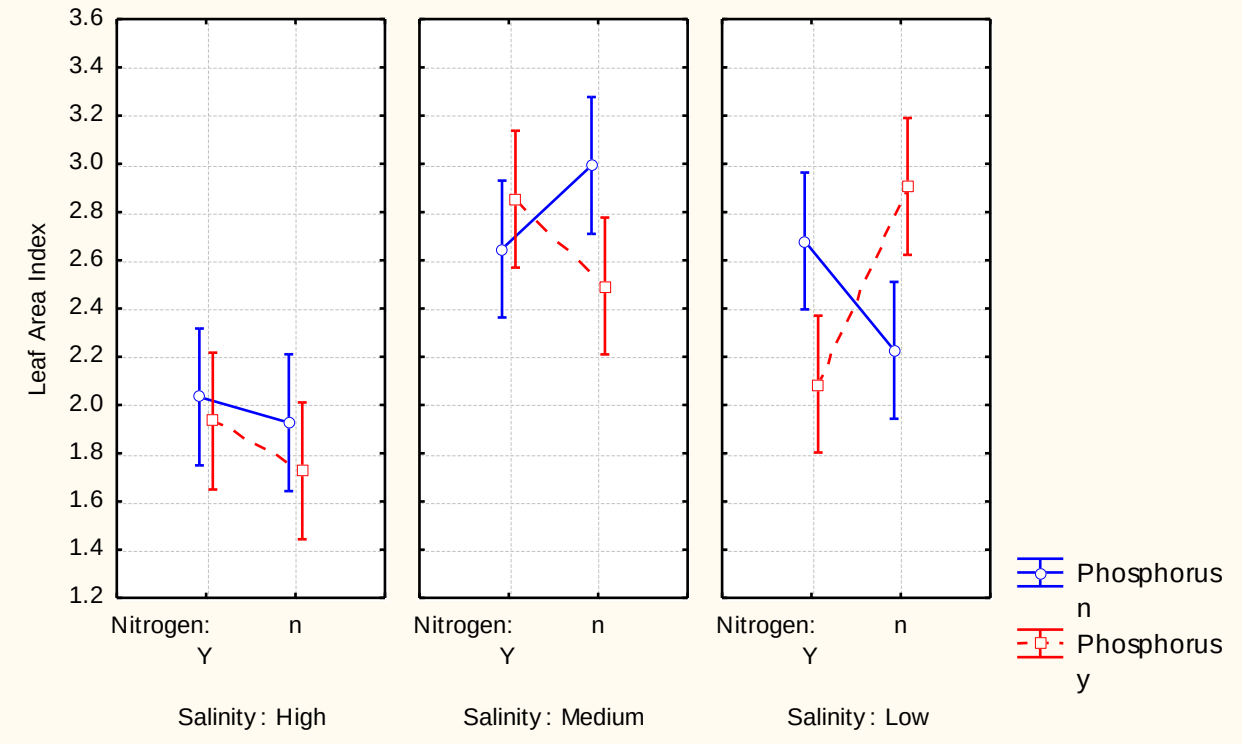

Figure 9. The effects of nitrogen and phosphorus and salinity on leaf area index. Vertical bars denote +/-standard errors.

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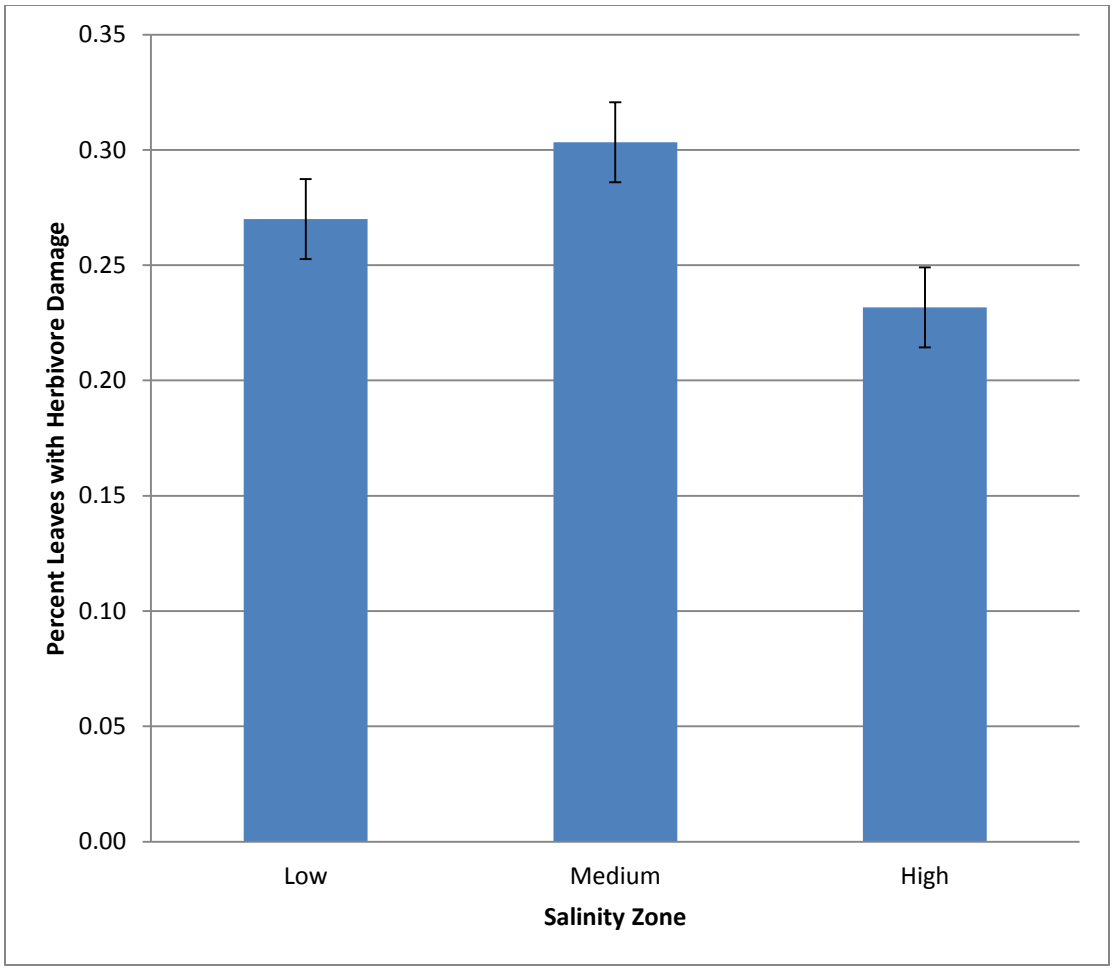

Figure 10. The effect of salinity on herbivory. Vertical bars denote +/-standard errors.

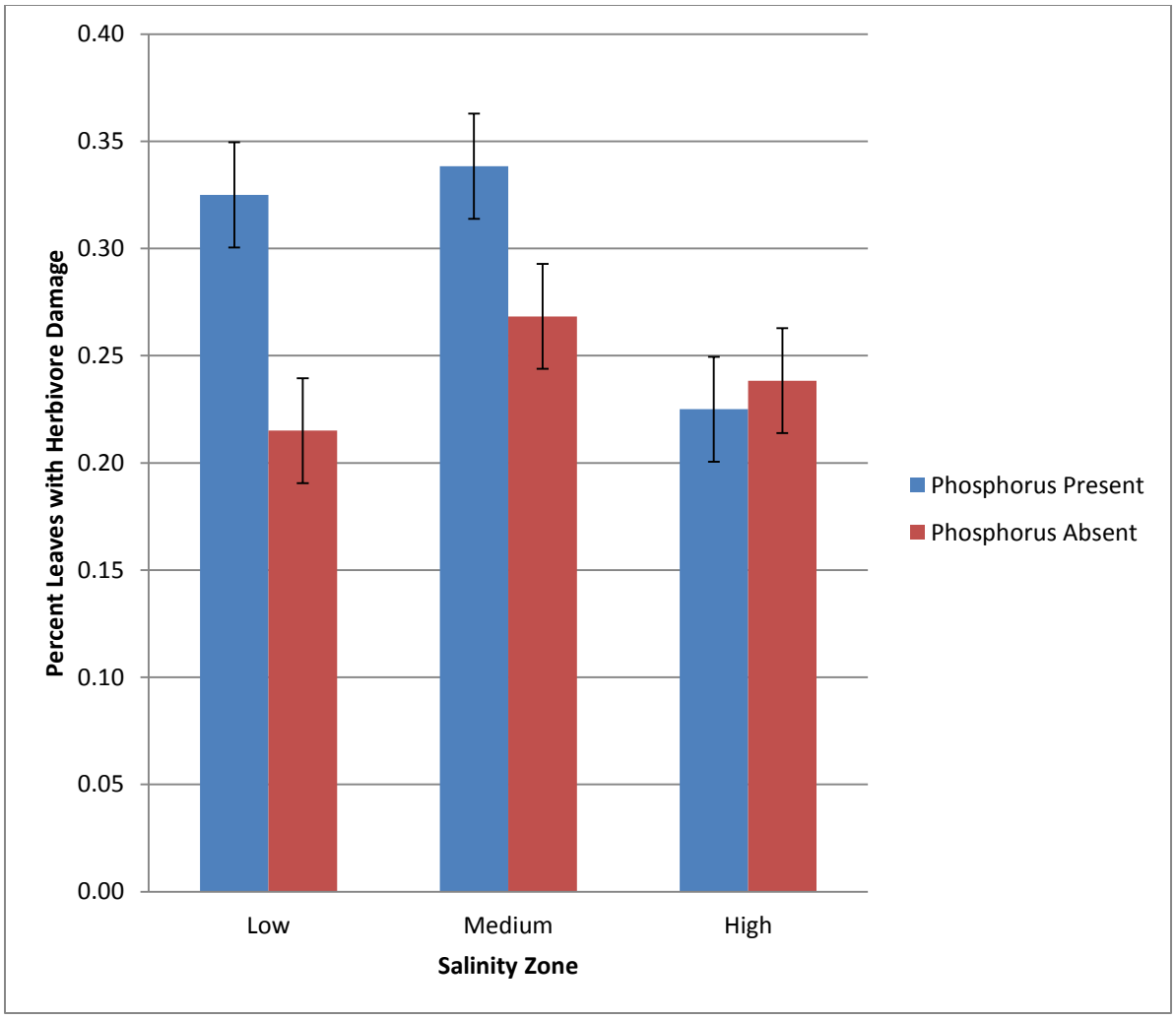

Figure 11. The effects of phosphorus and salinity on mangrove herbivory. Vertical bars denote +/-standard errors.

Chapter Four: Discussion

Plant Growth

Differences in the degree of leaf production, number of leaves, branch length, and leaf area index across the three salinity zones indicates that salinity strongly affects mangrove growth. Mangrove growth was consistently the greatest in the medium salinity zone. This is most likely due to a gradient of biotic and abiotic stresses occurring across the salinity gradient. Biotic stress is occurring in the low salinity zone in the form of competition with other plants, and abiotic stress is present in the high salinity zone in the form of very high salinities (Pennings & Callaway 1992, Pennings et. al. 2005). Therefore, the medium salinity zone may represent a middle ground where competition is low and salinity stress is tolerable, allowing for the greatest growth.

Competition for resources between plants can affect their growth. The low salinity zone had the greatest number and diversity of other plants compared to the other two salinity zones. In this zone, black mangrove trees were more widespread and interspersed with other vegetation (Table 1). This abundance of competing vegetation could limit uptake of added nutrients by black mangroves. Black mangroves have been found to be more efficient at water uptake than nutrient uptake when compared to the other mangrove species located in the same area (Lovelock & Feller 2003).

Recent studies have found that by reducing aboveground competition, mangrove seedling growth increased (Simpson et. al. 2013). Fertilized *Avicennia germinans* seedlings have been shown to increase leaf production in the absence of competing salt marsh vegetation (McKee &

Rooth 2008). Furthermore, with a decrease in competition, plant root biomass has been shown to decrease because of the decrease in competition for nutrients (Holl 1998). By alleviating competition for limited nutrients, mangrove seedlings are able to divest energy for root production and increase leaf production. Increasing leaf production allows for greater photosynthetic capabilities which can increase overall mangrove growth. Therefore, with this abundance and diversity of competing species in the low salinity zone, mangroves in this zone are not able to grow as extensively as mangroves in areas with less competition.

At the other environmental extreme, high salinity has a negative effect on water uptake by plants, which in turns leads to decreased rates of photosynthesis (Lopez-Hoffman et. al. 2007). In addition, at high salinities, mangroves have to devote more of their resources to physiological processes such as salt-exclusionary mechanisms (Gongalves-AIvim et. al. 2001). Therefore high salinity causes reduced mangrove growth.

Nutrient addition did not seem to increase mangrove growth in the low salinity zone. All of the growth variables showed either no change in growth or slight decreases in growth with the presence of nitrogen or phosphorus at the low salinity zone. Given that this zone is closest to the bay, nutrient availability could be already sufficient that this zone is not nutrient limited. Nitrogen limitation was most apparent in the medium salinity zone. Here, several of the growth variables showed greater increase with the addition of nitrogen. The number of leaves, branch length, and the number of new shoots all showed an increase in the medium salinity zone with the addition of nitrogen. In the high salinity zone the presence of phosphorus alone, and nitrogen and phosphorus together slightly increased mangrove growth. In summary, the results did not support my original hypothesis that nutrient addition would cause the greatest growth increases in the region of high salinity.

Herbivory

Three hypotheses were proposed to describe plant-herbivore interactions in mangrove ecosystems. The first is the plant stress hypothesis, in which herbivory would be greater on plants in stressed areas, such as high salinity, than in less stressed areas, such as low salinity, due to a decrease in secondary chemicals in plants in higher stressed areas (White 1969). The second is the resource availability hypothesis, which proposes that higher stressed plants will have greater anti-herbivore compounds because the loss of leaves would pose a greater detriment to those plants growing in less fertile soils than those in fertile soils (Janzen 1974). The third is the plant vigor hypothesis which suggests that herbivores should have greater attack rates on those plants growing the most vigorously (Price 1991). The plant vigor hypothesis seems to best explain the patterns of herbivory found in this study.

Herbivory was greatest in the medium salinity zone, where the greatest growth for these mangroves occurred. The high salinity zone has smaller, more sclerophyllous leaves which make them relatively unpalatable and harder to eat. Although the leaves may be palatable to herbivores in the low salinity zone, as shown by the increase in herbivory in the low salinity zone with the addition of phosphorus, there are more plant competitors in this area and the mangrove trees are more spread out, which may make it difficult for herbivores to locate mangrove trees. The plant vigor hypothesis was also supported by my herbivory studies on trees with added nutrients.

Herbivory was increased by added phosphorus, but only in the low and medium salinity zones. The mangroves in the high salinity zone did not show greater rates of herbivore attack even with the addition of nutrients to the system. This is most likely because at higher salinities

leaves tend to be smaller and more sclerophyllous (Gongalves-Alvim et. al. 2001) which makes them tougher to eat, even when nutrients are added. It is also possible that greater salt accumulation on leaves in the high salinity zone deterred insects from settling (Jiminez 1984). In summary, my results showed that changes in soil salinity and nutrient content, as would occur in a globally changed world, could substantially change both mangrove growth and herbivory, and ultimately change nutrient cycles in tropical and subtropical coastal systems.

Table 1. List of plant species in each salinity zone.

Low	**Medium**	**High**
Sesuvium portulacastrum	*Sesuvium portulacastrum*	*Sesuvium portulacastrum*
Monanthochloe littoralis	*Batis maritima*	*Batis maritima*
Batis maritima	*Laguncularia racemosa*	*Laguncularia racemosa*
Laguncularia racemosa	*Rhizophora mangle*	
Borrichia frutescens		
Rhizophora mangle		
Baccharis angustifolia		
Juncus roemerianus		

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Appendix 1: Table of Salinity Measurements Collected Monthly

Month	Salinity Zone	Nutrient Treatment	Salinity Measurement
July	Low	Nitrogen	25
July	Low	Nitrogen	26
July	Low	Nitrogen	19
July	Low	Nitrogen	27
July	Low	Nitrogen	30
July	Low	Phosphorus	17
July	Low	Phosphorus	18
July	Low	Phosphorus	28
July	Low	Phosphorus	29
July	Low	Phosphorus	26
July	Low	NitrogenxPhosphorus	25
July	Low	NitrogenxPhosphorus	24
July	Low	NitrogenxPhosphorus	19
July	Low	NitrogenxPhosphorus	17
July	Low	NitrogenxPhosphorus	23
July	Low	Control	30
July	Low	Control	16
July	Low	Control	18
July	Low	Control	29
July	Low	Control	24
July	Medium	Nitrogen	44
July	Medium	Nitrogen	36
July	Medium	Nitrogen	59
July	Medium	Nitrogen	56
July	Medium	Nitrogen	37
July	Medium	Phosphorus	45
July	Medium	Phosphorus	38
July	Medium	Phosphorus	49
July	Medium	Phosphorus	55
July	Medium	Phosphorus	57
July	Medium	NitrogenxPhosphorus	37
July	Medium	NitrogenxPhosphorus	36
July	Medium	NitrogenxPhosphorus	47

Appendix 1: (Continued)

July	Medium	NitrogenxPhosphorus	52
July	Medium	NitrogenxPhosphorus	54
July	Medium	Control	56
July	Medium	Control	39
July	Medium	Control	40
July	Medium	Control	58
July	Medium	Control	59
July	High	Nitrogen	88
July	High	Nitrogen	89
July	High	Nitrogen	100
July	High	Nitrogen	87
July	High	Nitrogen	92
July	High	Phosphorus	79
July	High	Phosphorus	94
July	High	Phosphorus	96
July	High	Phosphorus	85
July	High	Phosphorus	82
July	High	NitrogenxPhosphorus	84
July	High	NitrogenxPhosphorus	93
July	High	NitrogenxPhosphorus	91
July	High	NitrogenxPhosphorus	78
July	High	NitrogenxPhosphorus	86
July	High	Control	92
July	High	Control	89
July	High	Control	87
July	High	Control	85
July	High	Control	94
August	Low	Nitrogen	27
August	Low	Nitrogen	26
August	Low	Nitrogen	26
August	Low	Nitrogen	21
August	Low	Nitrogen	30
August	Low	Phosphorus	28
August	Low	Phosphorus	27
August	Low	Phosphorus	26

Appendix 1: (Continued)

August	Low	Phosphorus	23
August	Low	Phosphorus	28
August	Low	NitrogenxPhosphorus	26
August	Low	NitrogenxPhosphorus	27
August	Low	NitrogenxPhosphorus	26
August	Low	NitrogenxPhosphorus	23
August	Low	NitrogenxPhosphorus	27
August	Low	Control	27
August	Low	Control	28
August	Low	Control	27
August	Low	Control	22
August	Low	Control	28
August	Medium	Nitrogen	54
August	Medium	Nitrogen	70
August	Medium	Nitrogen	47
August	Medium	Nitrogen	54
August	Medium	Nitrogen	53
August	Medium	Phosphorus	64
August	Medium	Phosphorus	66
August	Medium	Phosphorus	50
August	Medium	Phosphorus	44
August	Medium	Phosphorus	56
August	Medium	NitrogenxPhosphorus	62
August	Medium	NitrogenxPhosphorus	55
August	Medium	NitrogenxPhosphorus	51
August	Medium	NitrogenxPhosphorus	49
August	Medium	NitrogenxPhosphorus	60
August	Medium	Control	64
August	Medium	Control	67
August	Medium	Control	65
August	Medium	Control	65
August	Medium	Control	54
August	High	Nitrogen	63
August	High	Nitrogen	67
August	High	Nitrogen	76

Appendix 1: (Continued)

August	High	Nitrogen	64
August	High	Nitrogen	56
August	High	Phosphorus	72
August	High	Phosphorus	67
August	High	Phosphorus	81
August	High	Phosphorus	60
August	High	Phosphorus	61
August	High	NitrogenxPhosphorus	68
August	High	NitrogenxPhosphorus	71
August	High	NitrogenxPhosphorus	70
August	High	NitrogenxPhosphorus	52
August	High	NitrogenxPhosphorus	71
August	High	Control	60
August	High	Control	79
August	High	Control	50
August	High	Control	35
August	High	Control	72
September	Low	Nitrogen	34
September	Low	Nitrogen	32
September	Low	Nitrogen	29
September	Low	Nitrogen	27
September	Low	Nitrogen	36
September	Low	Phosphorus	28
September	Low	Phosphorus	29
September	Low	Phosphorus	24
September	Low	Phosphorus	32
September	Low	Phosphorus	35
September	Low	NitrogenxPhosphorus	27
September	Low	NitrogenxPhosphorus	26
September	Low	NitrogenxPhosphorus	34
September	Low	NitrogenxPhosphorus	39
September	Low	NitrogenxPhosphorus	38
September	Low	Control	35
September	Low	Control	28
September	Low	Control	26

Appendix 1: (Continued)

September	Low	Control	29
September	Low	Control	37
September	Medium	Nitrogen	22
September	Medium	Nitrogen	54
September	Medium	Nitrogen	46
September	Medium	Nitrogen	33
September	Medium	Nitrogen	38
September	Medium	Phosphorus	29
September	Medium	Phosphorus	32
September	Medium	Phosphorus	52
September	Medium	Phosphorus	48
September	Medium	Phosphorus	33
September	Medium	NitrogenxPhosphorus	32
September	Medium	NitrogenxPhosphorus	31
September	Medium	NitrogenxPhosphorus	24
September	Medium	NitrogenxPhosphorus	59
September	Medium	NitrogenxPhosphorus	57
September	Medium	Control	34
September	Medium	Control	39
September	Medium	Control	46
September	Medium	Control	56
September	Medium	Control	25
September	High	Nitrogen	76
September	High	Nitrogen	84
September	High	Nitrogen	89
September	High	Nitrogen	90
September	High	Nitrogen	77
September	High	Phosphorus	75
September	High	Phosphorus	79
September	High	Phosphorus	82
September	High	Phosphorus	65
September	High	Phosphorus	78
September	High	NitrogenxPhosphorus	89
September	High	NitrogenxPhosphorus	92
September	High	NitrogenxPhosphorus	79

Appendix 1: (Continued)

September	High	NitrogenxPhosphorus	88
September	High	NitrogenxPhosphorus	86
September	High	Control	82
September	High	Control	91
September	High	Control	74
September	High	Control	84
September	High	Control	86
October	Low	Nitrogen	40
October	Low	Nitrogen	26
October	Low	Nitrogen	23
October	Low	Nitrogen	23
October	Low	Nitrogen	32
October	Low	Phosphorus	27
October	Low	Phosphorus	22
October	Low	Phosphorus	24
October	Low	Phosphorus	25
October	Low	Phosphorus	26
October	Low	NitrogenxPhosphorus	35
October	Low	NitrogenxPhosphorus	27
October	Low	NitrogenxPhosphorus	25
October	Low	NitrogenxPhosphorus	25
October	Low	NitrogenxPhosphorus	28
October	Low	Control	25
October	Low	Control	23
October	Low	Control	22
October	Low	Control	24
October	Low	Control	22
October	Medium	Nitrogen	20
October	Medium	Nitrogen	25
October	Medium	Nitrogen	20
October	Medium	Nitrogen	19
October	Medium	Nitrogen	50
October	Medium	Phosphorus	18
October	Medium	Phosphorus	60
October	Medium	Phosphorus	50

Appendix 1: (Continued)

October	Medium	Phosphorus	20
October	Medium	Phosphorus	42
October	Medium	NitrogenxPhosphorus	17
October	Medium	NitrogenxPhosphorus	21
October	Medium	NitrogenxPhosphorus	20
October	Medium	NitrogenxPhosphorus	26
October	Medium	NitrogenxPhosphorus	21
October	Medium	Control	21
October	Medium	Control	58
October	Medium	Control	26
October	Medium	Control	20
October	Medium	Control	50
October	High	Nitrogen	78
October	High	Nitrogen	68
October	High	Nitrogen	28
October	High	Nitrogen	63
October	High	Nitrogen	69
October	High	Phosphorus	78
October	High	Phosphorus	61
October	High	Phosphorus	61
October	High	Phosphorus	85
October	High	Phosphorus	60
October	High	NitrogenxPhosphorus	65
October	High	NitrogenxPhosphorus	70
October	High	NitrogenxPhosphorus	40
October	High	NitrogenxPhosphorus	76
October	High	NitrogenxPhosphorus	62
October	High	Control	75
October	High	Control	48
October	High	Control	38
October	High	Control	75
October	High	Control	58
November	Low	Nitrogen	26
November	Low	Nitrogen	36
November	Low	Nitrogen	40

Appendix 1: (Continued)

November	Low	Nitrogen	30
November	Low	Nitrogen	36
November	Low	Phosphorus	32
November	Low	Phosphorus	34
November	Low	Phosphorus	38
November	Low	Phosphorus	35
November	Low	Phosphorus	38
November	Low	NitrogenxPhosphorus	25
November	Low	NitrogenxPhosphorus	38
November	Low	NitrogenxPhosphorus	34
November	Low	NitrogenxPhosphorus	28
November	Low	NitrogenxPhosphorus	40
November	Low	Control	20
November	Low	Control	36
November	Low	Control	40
November	Low	Control	34
November	Low	Control	40
November	Medium	Nitrogen	53
November	Medium	Nitrogen	54
November	Medium	Nitrogen	53
November	Medium	Nitrogen	54
November	Medium	Nitrogen	51
November	Medium	Phosphorus	52
November	Medium	Phosphorus	50
November	Medium	Phosphorus	55
November	Medium	Phosphorus	46
November	Medium	Phosphorus	50
November	Medium	NitrogenxPhosphorus	52
November	Medium	NitrogenxPhosphorus	53
November	Medium	NitrogenxPhosphorus	51
November	Medium	NitrogenxPhosphorus	51
November	Medium	NitrogenxPhosphorus	53
November	Medium	Control	55
November	Medium	Control	56
November	Medium	Control	56

Appendix 1: (Continued)

November	Medium	Control	59
November	Medium	Control	55
November	High	Nitrogen	100
November	High	Nitrogen	95
November	High	Nitrogen	90
November	High	Nitrogen	80
November	High	Nitrogen	92
November	High	Phosphorus	90
November	High	Phosphorus	89
November	High	Phosphorus	90
November	High	Phosphorus	98
November	High	Phosphorus	89
November	High	NitrogenxPhosphorus	90
November	High	NitrogenxPhosphorus	87
November	High	NitrogenxPhosphorus	87
November	High	NitrogenxPhosphorus	90
November	High	NitrogenxPhosphorus	78
November	High	Control	87
November	High	Control	87
November	High	Control	92
November	High	Control	88
November	High	Control	65
December	Low	Nitrogen	34
December	Low	Nitrogen	36
December	Low	Nitrogen	40
December	Low	Nitrogen	36
December	Low	Nitrogen	30
December	Low	Phosphorus	30
December	Low	Phosphorus	31
December	Low	Phosphorus	38
December	Low	Phosphorus	36
December	Low	Phosphorus	30
December	Low	NitrogenxPhosphorus	25
December	Low	NitrogenxPhosphorus	34
December	Low	NitrogenxPhosphorus	32

Appendix 1: (Continued)

December	Low	NitrogenxPhosphorus	35
December	Low	NitrogenxPhosphorus	35
December	Low	Control	38
December	Low	Control	30
December	Low	Control	38
December	Low	Control	40
December	Low	Control	36
December	Medium	Nitrogen	58
December	Medium	Nitrogen	60
December	Medium	Nitrogen	58
December	Medium	Nitrogen	53
December	Medium	Nitrogen	57
December	Medium	Phosphorus	58
December	Medium	Phosphorus	55
December	Medium	Phosphorus	55
December	Medium	Phosphorus	51
December	Medium	Phosphorus	51
December	Medium	NitrogenxPhosphorus	58
December	Medium	NitrogenxPhosphorus	60
December	Medium	NitrogenxPhosphorus	53
December	Medium	NitrogenxPhosphorus	56
December	Medium	NitrogenxPhosphorus	54
December	Medium	Control	59
December	Medium	Control	57
December	Medium	Control	59
December	Medium	Control	53
December	Medium	Control	56
December	High	Nitrogen	102
December	High	Nitrogen	95
December	High	Nitrogen	91
December	High	Nitrogen	80
December	High	Nitrogen	81
December	High	Phosphorus	90
December	High	Phosphorus	92
December	High	Phosphorus	95

Appendix 1: (Continued)

December	High	Phosphorus	97
December	High	Phosphorus	87
December	High	NitrogenxPhosphorus	92
December	High	NitrogenxPhosphorus	91
December	High	NitrogenxPhosphorus	90
December	High	NitrogenxPhosphorus	93
December	High	NitrogenxPhosphorus	79
December	High	Control	88
December	High	Control	98
December	High	Control	92
December	High	Control	87
December	High	Control	73