was therefore consistent across treatments for each of the portions of the plant. Fine root percent carbon was less than half of either the aboveground tissue or the coarse roots (Fig. 19).

Percent nitrogen was highest in the aboveground portion of the plants used in the greenhouse study. Both treatment (p=0.0013) and plant part (p=0.0001) as well as the interaction (p=0.0313) were significant (Table 20). Two groups were found to occur in a post ANOVA analysis (Tukey Kramer multiple comparison test, p<0.05) (Fig. 20). The high percent nitrogen group consisted of the aboveground samples with the addition of the coarse root fraction of *Andropogon gerardii.* The other, lower concentration, group included all of the samples but the aboveground portion of *Andropogon gerardii.* Most

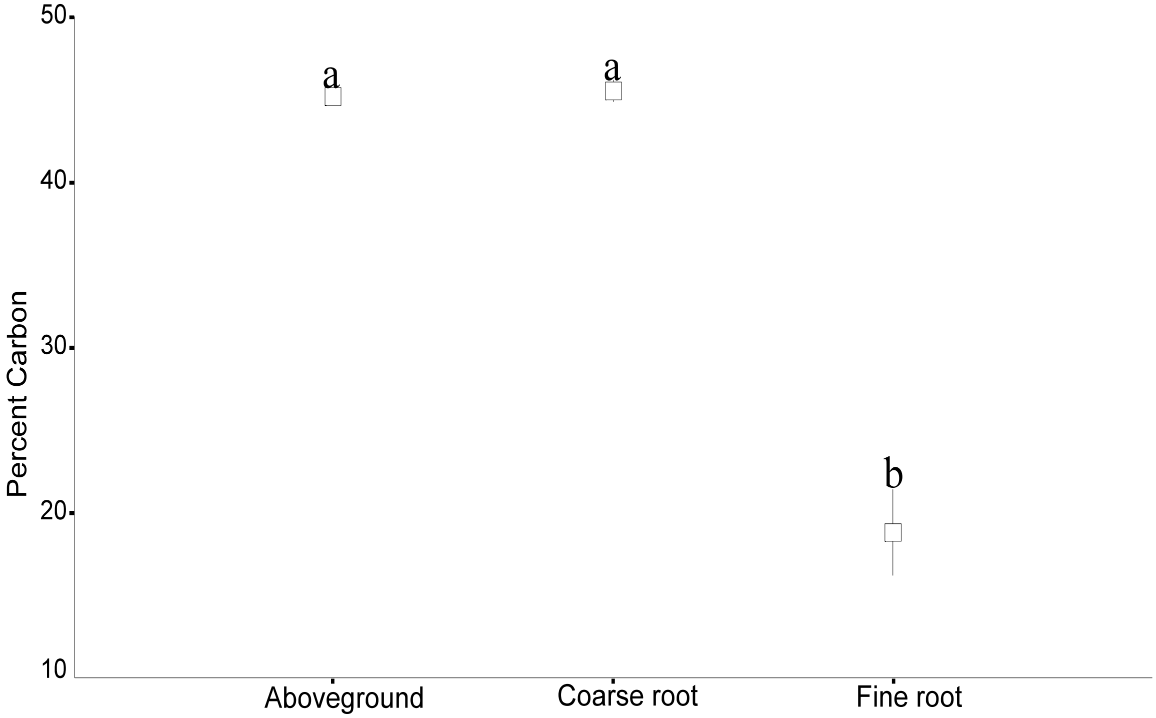

Figure 19. Mean percent C (% dry mass) by plant part. Bars with the same letter are not significantly different from each other (p<0.05).

Table 19. Percent carbon by treatment and plant part ANOVA.

Source	DF	SS	F value	Pr>F
Model	8	6923.45	24.60	0.0001
Plant Part	2	6641.31	94.40	0.0001
Treatment	2	75.30	1.07	0.3535
Plant Part*Treatment	4	55.75	0.04	0.8100
Error	36	1266.32		
Total	44	8189.77		

of the root fraction remained below one percent nitrogen. The general trend was for nitrogen concentration to decline from the aboveground to the coarse root to fine root. The interaction was significant because the coarse root fraction of *Andropogon gerardii* rose high and *Schizachyrium scoparium* as a whole declined in the sand.

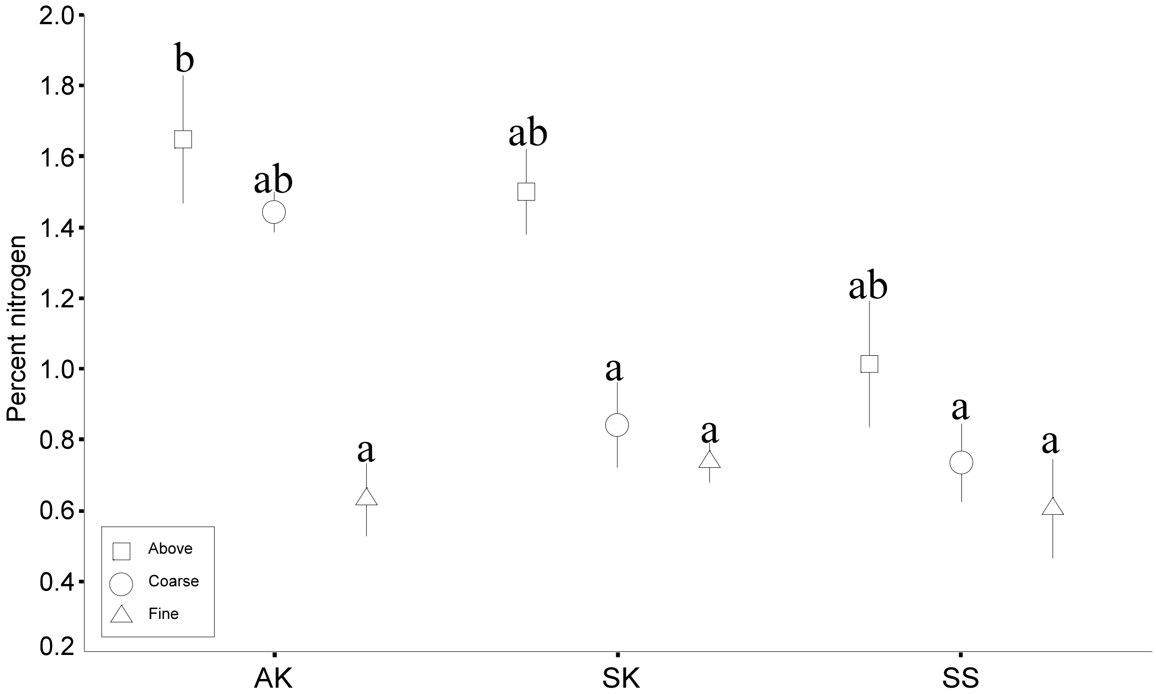

Figure 20. Percent nitrogen by treatment and plant part. AK= *Andropogon gerardii* in Konza Soil, SK = *Schizachyrium scoparium* in Konza soil, SS=*Schizachyrium scoparium* in barrier island sand. Bars with the same letter are not significantly different from each other ($p<0.05$).

Table 20. Percent nitrogen by treatment and plant part for greenhouse ANOVA.

Source	DF	SS	F value	Pr>F
Model	8	6.88	9.87	0.0001
Plant Part	2	4.10	23.52	0.0001
Treatment	2	1.40	8.01	0.0013
Plant Part*Treatment	4	1.04	2.99	0.0313
Error	36	3.13		
Total	44	10.01		

There were significant differences both between treatments (p=0.0002) and between plant parts (p=0.0001) with carbon to nitrogen ratio (Table 21). The interaction was not significant (p=0.0583). Plant parts were statistically separated into two groups with respect to carbon-nitrogen ratio (REGW, p<0.05). Coarse roots had a higher carbon nitrogen ratio than did either the fine roots or the aboveground tissue (Fig. 21). Each of the treatments was significantly different from each other (REGW, p<0.05). *Andropogon gerardii* in Konza Prairie soil had the lowest carbon-nitrogen ratio and *Schizachyrium scoparium* in sand had the highest carbon-nitrogen ratio (Fig. 22).

Table 21. Carbon nitrogen ratio by treatment and plant part ANOVA.

Source	DF	SS	F value	Pr>F
Model	8	8860.40	7.39	0.0001
Plant Part	2	6641.31	14.46	0.0001
Treatment	2	75.30	11.16	0.0002
Plant Part*Treatment	4	55.75	2.52	0.0583
Error	36	5393.11		
Total	44	143253.51		

Biomass was divided into aboveground and belowground portions rather than further dividing it into root fractions. Both the treatment and plant part main effects

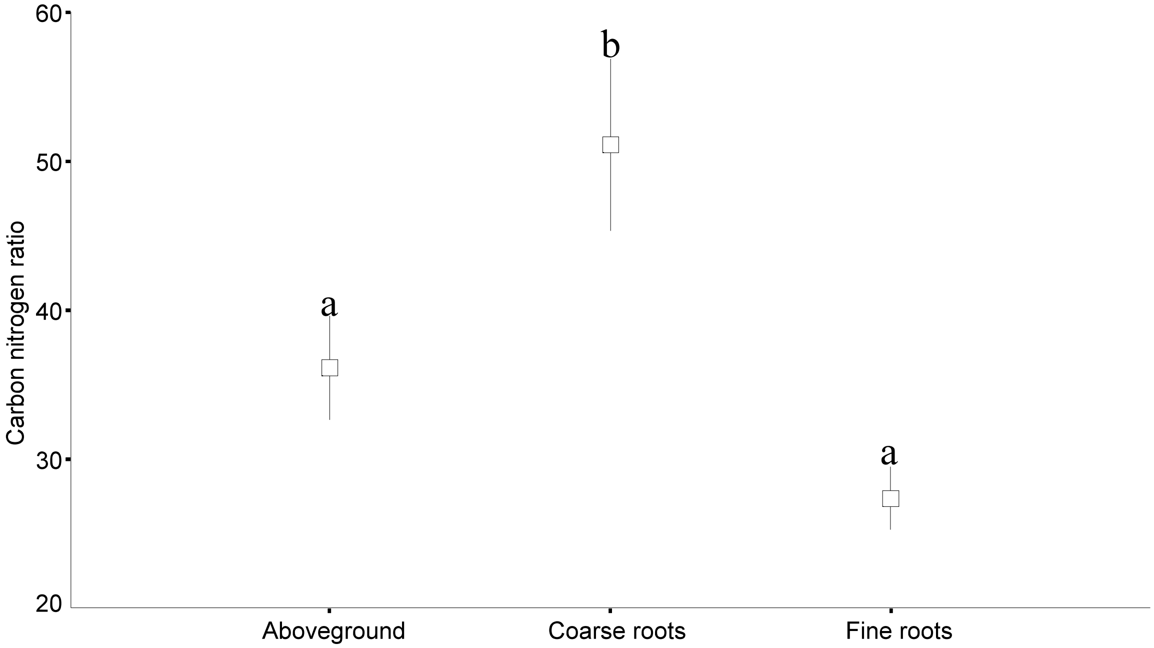

Figure 21. Mean carbon nitrogen ratio by plant part. Bars with the same letter are not significantly different from each other (p<0.05).

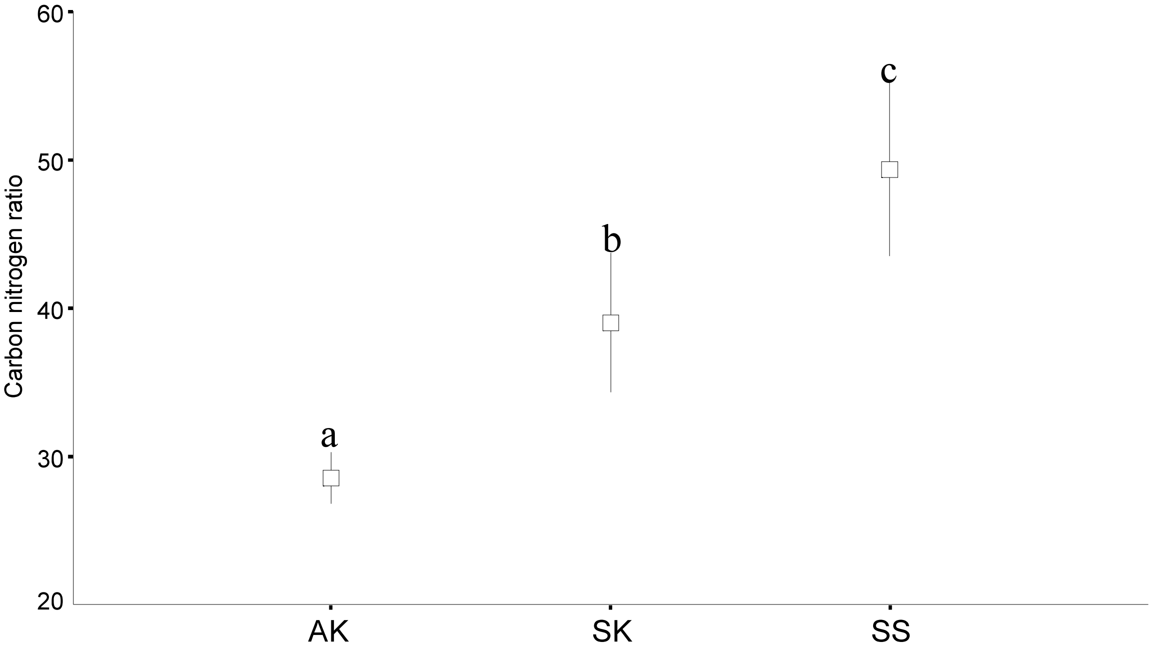

Figure 22. Mean C to N ratio by treatment. AK = *Andropogon gerardii* in Konza Soil, SK = *Schizachyrium scoparium* in Konza soil, SS = *Schizocarium scoparium* in sand. Bars with the same letter are not significantly different from each other (p<0.05).

were significant (p=0.0087, and p=0.0471 respectively); however, the interaction was not significant (p=0.9915) (Table 22). The belowground biomass was higher than the aboveground biomass by a ratio of nearly two to one (Fig. 23). Two groups formed within the treatment effect for biomass. The *Andropogon gerardii* grown in Konza Prairie soil and the *Schizachyrium scoparium* grown in Konza Prairie soil were significantly higher than the *Schizachyrium scoparium* grown in sand (Fig. 24). There was a factor of more than two to one between the *Schizachyrium scoparium* grown in sand and *Andropogon gerardii* grown in Konza Prairie soil. There were no significant differences with carbon change for the factors tested (Table 23). In general, the trends show decreasing aboveground growth and increasing belowground growth moving from

TABLE 22. Biomass by treatment and plant part ANOVA.

Source	DF	SS	F value	Pr>F
Model	5	3.53	3.12	0.0231
Plant Part	1	0.97	4.31	0.0471
Treatment	2	2.55	5.64	0.0087
Plant Part*Treatment	2	0.00	0.01	0.9915
Error	28	6.33		
Total	33	9.85		

TABLE 23. Change in carbon in greenhouse study ANOVA.

Source	DF	SS	F value	Pr>F
Model	5	4.6512e+00	1.73	0.1612
Treatment	2	4.6100e-06	0.00	1.000
Plant part	1	2.9365e-01	0.55	0.4665
Plant Part*Treatment	2	4.1735e+00	0.633.87	0.0327
Error	28	1.5084e+01		
Total	33	1.9735e+01		

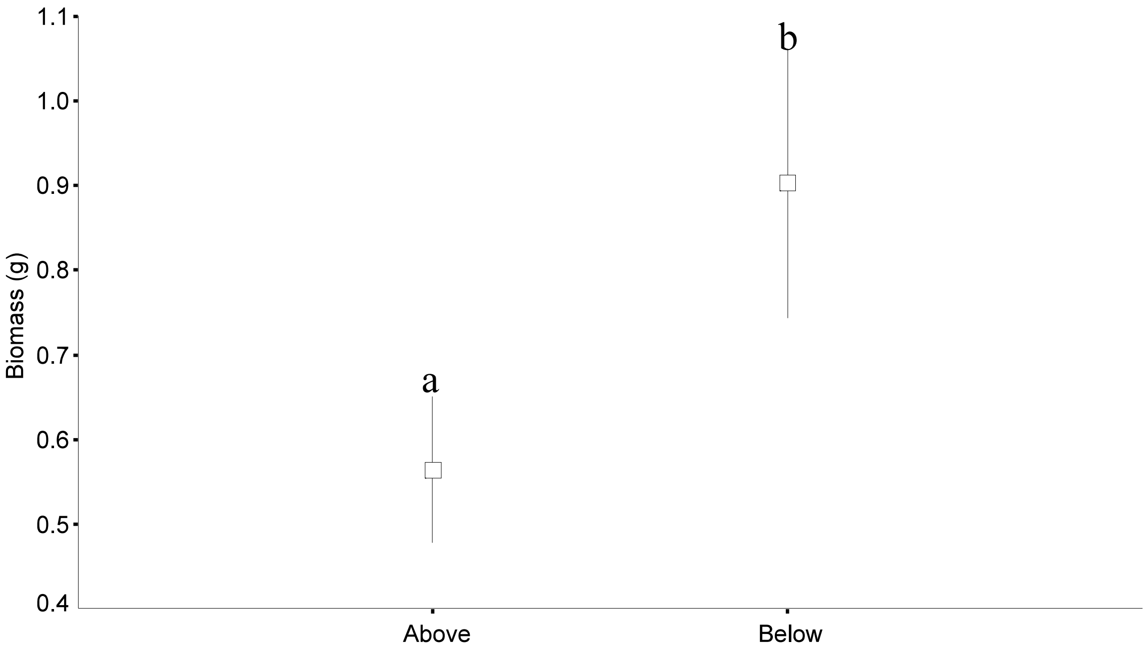

Figure 23. Mean biomass by plant part. Bars with the same letter are not significantly different from each other (p<0.05).

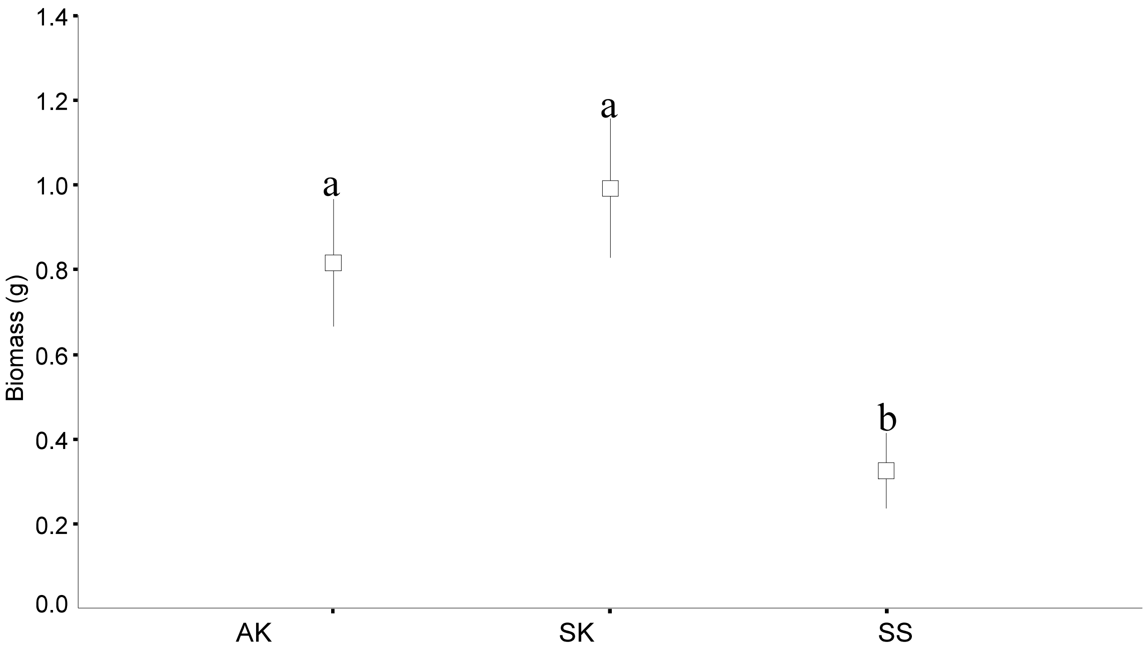

Figure 24. Mean biomass by treatment. AK= *Andropogon gerardii* in Konza Soil, SK = *Schizachyrium scoparium* in Konza soil, SS = *Schizocarium scoparium* in sand. Bars with the same letter are not significantly different from each other (p<0.05).

Andropogon gerardii grown in Konza Prairie soil to *Schizachyrium scoparium* grown in sand (Fig. 25).

There a significant interaction between plant parts and treatment for percent ^{14}C (p=0.0001) (Table 24). There was also a significant treatment effect (p=0.0001). Two groups emerged in the Tukey-Kramer multiple comparison test. The first high concentration group consists of the aboveground portion of the plants with the addition of both belowground fractions for *Schizachyrium scoparium* grown in sand (Fig. 26). The second lower concentration group contains *Schizachyrium scoparium* grown in sand, but also contains the roots for the other two treatments. Although not significantly higher with this test, the root portion of *Schizachyrium scoparium* grown in sand is much higher than that found in the other treatments. This increase resulted in a decline in the carbon staying within the aboveground tissue.

There were no significant differences in exchange ratios when belowground carbon demand was measured as change in carbon over the duration of the experiment (Table 25). The *Schizachyrium scoparium* grown in sand treatment was the only group with a negative exchange ratio (Fig. 27). When that group was removed from the analysis, the analysis was still insignificant; however, the exchange ratio went to a much more reasonable 19.8.

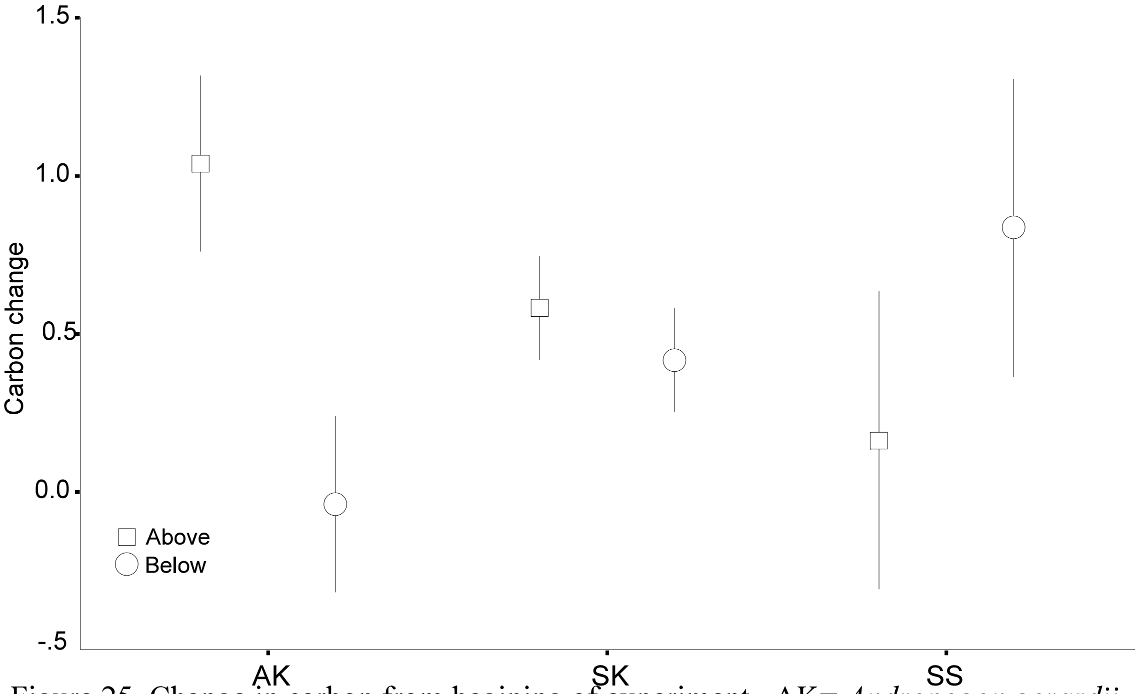

Figure 25. Change in carbon from begining of experiment. AK= *Andropogon gerardii* in Konza Soil, SK = *Schizachyrium scoparium* in Konza soil, *Schizocarium scoparium* in barrier island sand.

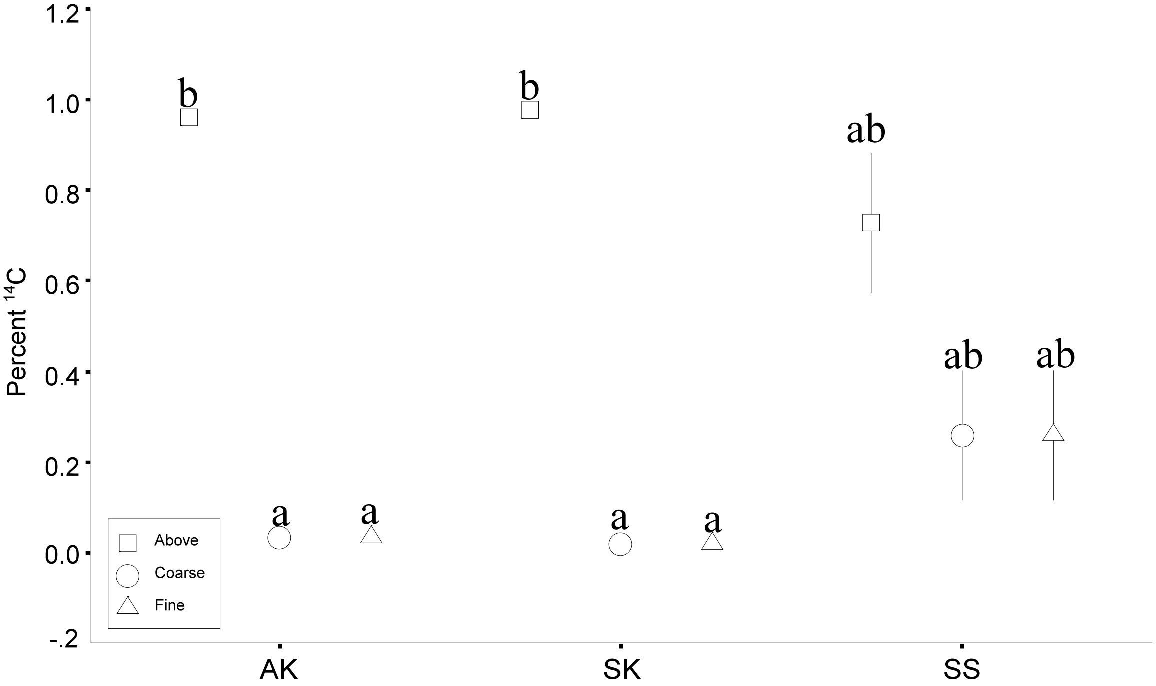

Figure 26. Mean percent ^{14}C by treatment and part. AK= *Andropogon gerardii* in Konza Soil, SK = *Schizachyrium scoparium* in Konza soil, SS = *Schizocarium scoparium* in sand. Bars with same letter are not significantly diffferent from each other ($p<0.05$).

TABLE 24. ^{14}C by treatment and plant part ANOVA.

Source	DF	SS	MS	F value	Pr>F
Model	8	6.86	0.86	29.24	0.000
Plant Part	2	5.32	2.66	90.70	0.000
Treatment	2	0.08	0.04	1.33	0.276
Plant Part*Treatment	4	0.71	0.18	6.09	0.001
Error	36	1.06	0.03		
Total	44	7.92	0.18		

TABLE 25. Change in belowground C: aboveground N exchange ratio ANOVA.

Source	DF	SS	MS	F value	Pr>F
Model	2	6.4371e+03	3.2185e+03	0.6078	0.5583
Error	14	7.4141e+04	5.2958e+03		
Total	16	8.0578e+04			

When percent of ^{14}C belowground was used to determine exchange ratios, there was a significant effect with treatment (Table 26). *Schizachyrium scoparium* grown in sand was a level of magnitude above the two treatments grown in Konza Prairie soil (Fig 28). This means that approximately ten times more carbon is sent belowground to recover the same amount of nitrogen in sand than the same plant would use in Konza Prairie soil.

TABLE 26. Belowground ^{14}C :aboveground N exchange ratio ANOVA.

Source	DF	SS	MS	F value	Pr>F
Model	2	6.0063e+06	3.0031e+06	7.4034	0.0080
Error	12	4.8677e+06	4.0564e+05		
Total	14	1.0874e+07			

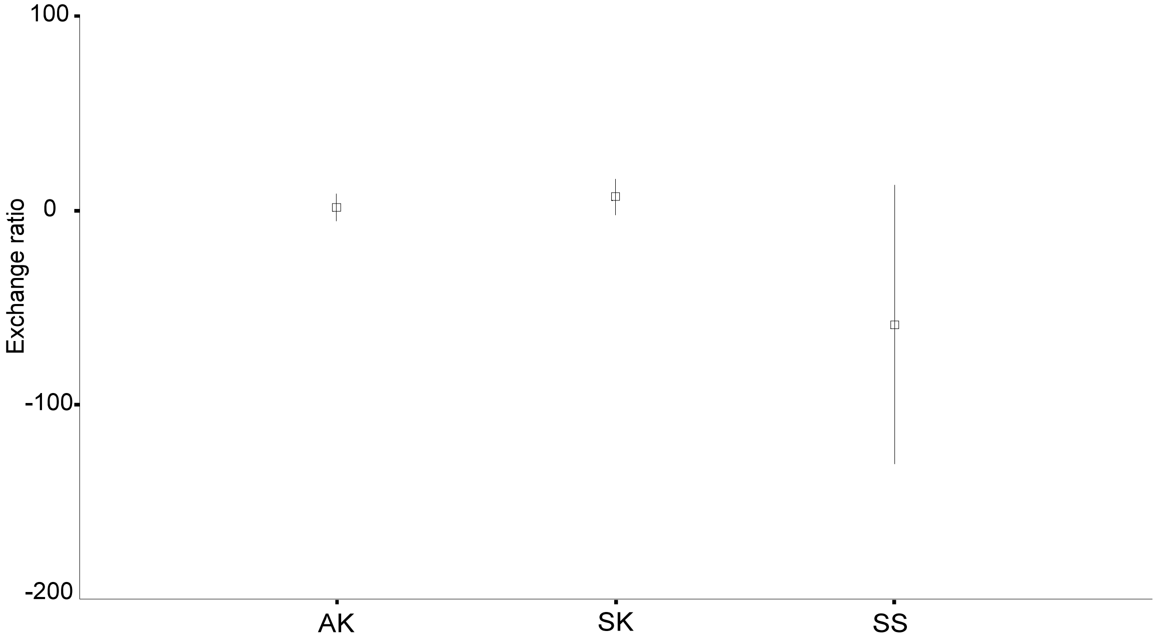

Figure 27. Mean exchange ratio calculated with change in carbon by treatment. AK= *Andropogon gerardii* in Konza Soil, SK = *Schizachyrium scoparium* in Konza soil, *Schizocarium scoparium* in barrier island sand.

Minirhizotron Root Length Density and Root Dynamics

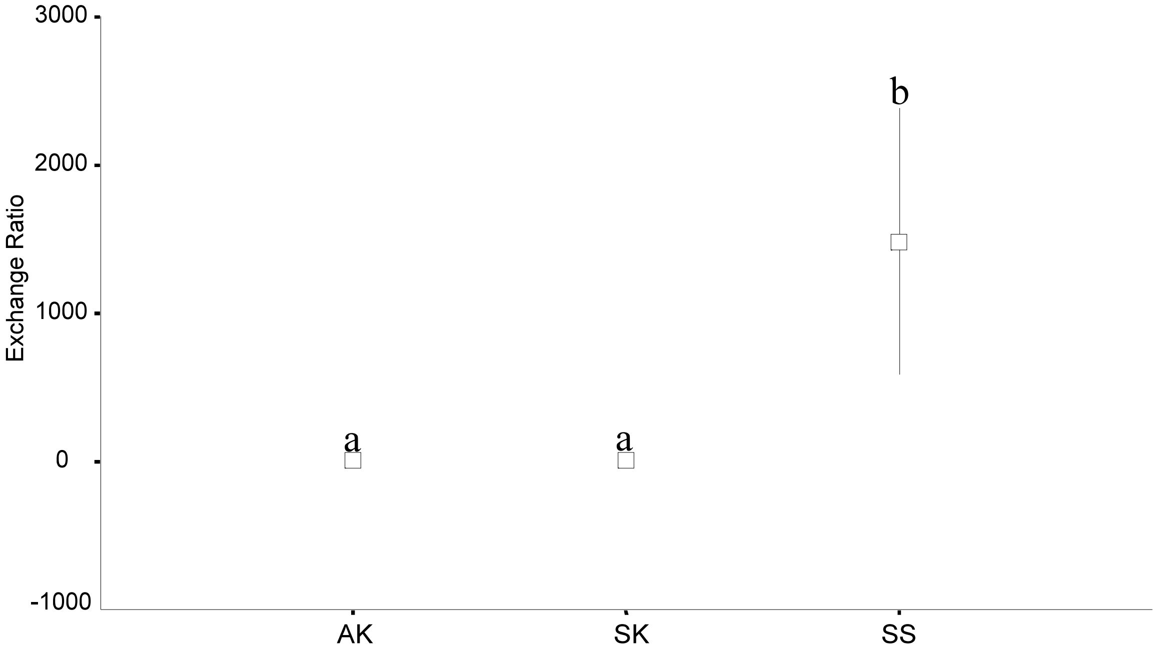

Figure 28. ^{14}C nitrogen exchange ratios for greenhouse study. AK= *Andropogon gerardii* in Konza Soil, SK = *Schizachyrium scoparium* in Konza soil, Schizocarium scoparium in barrier island sand. Bars with the same letter are not significantly different from each other.

For all parameters tested with the minirhizotron data, the difference between the treated and untreated side of each tube was tested rather than the variable itself. The analyses are regressions in which the treatment level (nitrogen enrichment) is used as a continuous independent variable. There were three levels of nitrogen enrichment including a blank in which deionized water was used. The other two levels were approximately 10 and 100 times the level of nitrate and ammonium found in the soil. A regression was run for each of the ecosystems independently.

There were no significant differences in either of the sites between treatments for any of the variables tested. None of the regressions were significant and the y-intercept was not significantly different from zero. This means that the differences from any of the groups were not significantly different from zero. Because the regressions were not significant, the treatments did not have a significant effect on any of the dependent variables tested.

Tests for differences in RLD with nitrogen enrichment for both Hog Island and Konza Prairie can be seen in Table 27 (Fig. 29). The R^2s were very low (0.08 to 0.05) and none of them were significant at the $p<0.05$ level. In addition, neither the intercept nor nitrogen enrichment were significant additions to the model. The nitrogen enrichment therefore had no effect on RLD for either site. The mean RLD from the surface to 50 cm depth was 7.18 (±5.00) for Hog Island and 14.15 (±7.91) for Konza Prairie (Fig. 29).

In addition to testing for differences with nitrogen level, the mortality of specific cohorts was compared between the last two sample dates. As mentioned in the methods

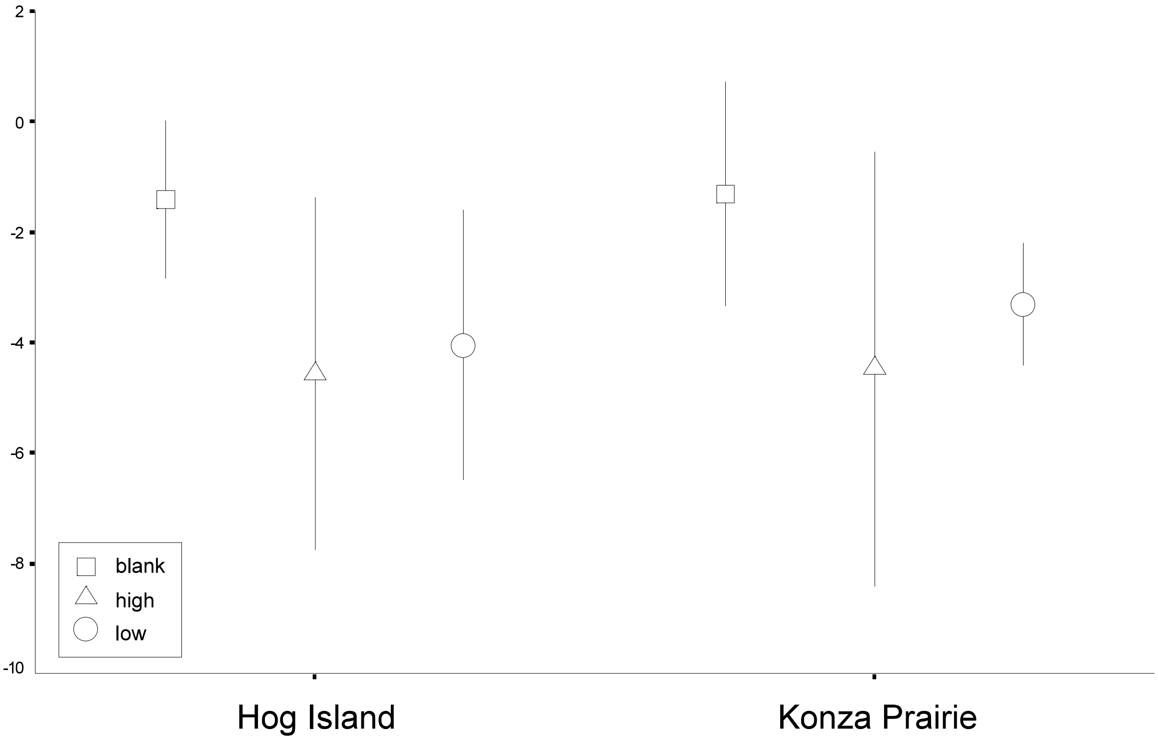

Figure 29. Mean difference in RLD with microsite enrichment.

TABLE 27. Hog Island regression models for growth and RLD.

					p-values of betas	
Site	variable	F	p-value	R2	intercept	enrichment
Hg	Growth	1.6709	0.2252	0.3784	0.6107	0.2252
Ks	Growth	1.3531	0.2717	0.3452	0.8703	0.2717
Hg	RLD	0.8959	0.3662	0.2868	0.4316	0.3662
Ks	RLD	0.7965	0.3931	0.2716	0.5391	0.3931

section, because both initiation date and nitrogen enrichment were independent variables, a series of models were tested. The models included both the main effects model (nitrogen addition and cohort) and the interaction of the two main effects. None of the regressions were significant (Fig 30, Table 28, 29). The R^2s ranged from 0.03 to 0.04. None of the variables, including the y-intercept, significantly improved the models.

Therefore, the differences in mortality between the treated and untreated sides of the minirhizotron tube were not significantly different from zero and neither initiation date nor nitrogen enrichment significantly influenced mortality. Mortality was 5.33 (±5.00) for Hog Island and 9.71(±5.98) for Konza Prairie (Fig. 30).

There were no significant differences in root growth with nitrogen addition in either Konza Prairie or Hog Island. The R^2s ranged from 0.08 to 0.14 and the regressions were not significant (Table 27, Fig. 31). In addition, as with RLD, neither the intercept nor nitrogen level significantly added to the regression models. This means that both the treatment level had no significant effect and the differences between the two sides of the minirhizotron tubes were not significantly different from zero. The growth rate for Hog Island was 3.67 (±3.71) and 10.82 (±5.52) for Konza Prairie.

TABLE 28. Konza regression models for mortality.

F	p-value	R2	intercept	init	enrichment	enrichment*init
0.302	0.5881	0.0142	0.119		0.588	
0.596	0.4486	0.0276	0.808	0.4486		
0.413	0.6671	0.0397	0.3681	0.4748	0.6216	
0.262	0.8515	0.0398	0.4973	0.6459	0.7697	0.9621

TABLE 29. Hog Island regression models for mortality.

F	p-value	R2	intercept	init	enrichment	enrichment*init
0.007	0.9320	0.0004	0.1179		0.9320	
0.535	0.4728	0.0248	0.1662	0.4728		
0.263	0.7715	0.0248	0.3664	0.4799	0.9007	
0.186	0.9048	0.0285	0.3957	0.8168	0.9291	0.8149

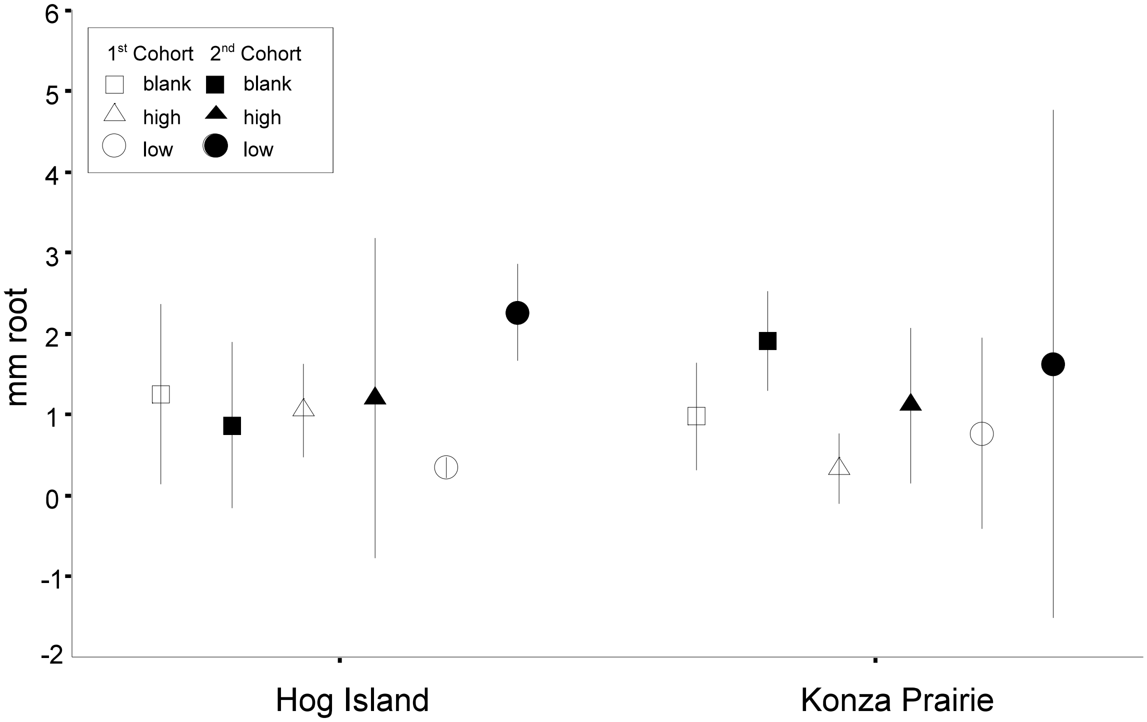

Figure 30. Mean difference in mortality with microsite enrichment. Open markers are from the first cohort. Solid markers are from the second cohort.

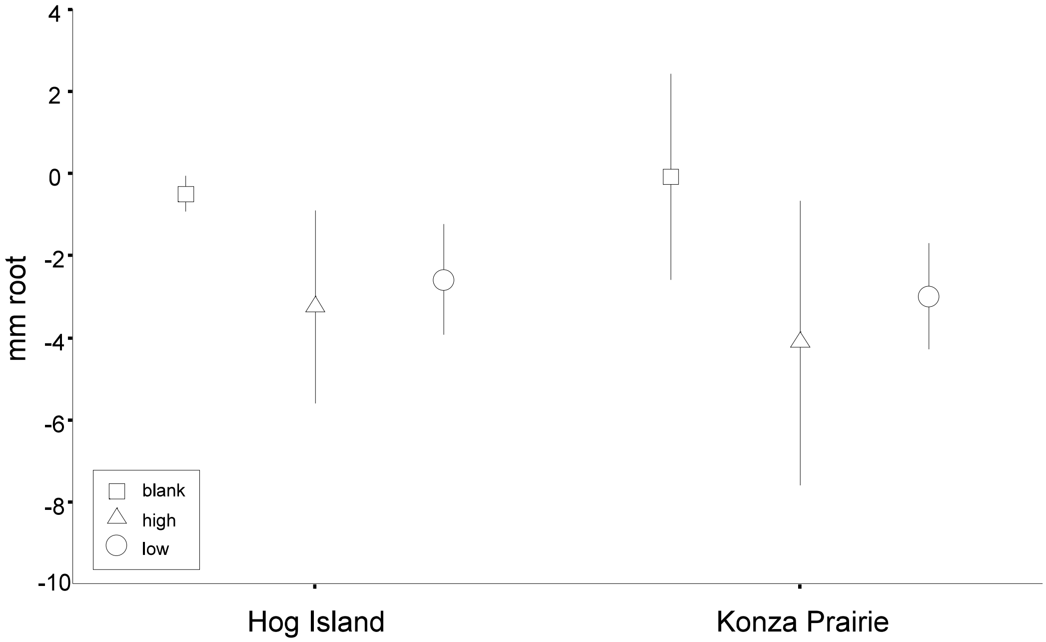

Figure 31. Mean difference in growth with microsite enrichment.

DISCUSSION

Most of the results of this study met expectations; however, there were some surprises. Overall, the plants that were adapted to nutrient rich conditions had higher nitrogen costs than those from the nutrient poor site. The field data, however, indicated a higher nitrogen cost for the roots than the shoots. There was no evidence of storage in either the field or the greenhouse, although there were strong relationships with carbon, nitrogen, and width and age of individual roots. The RP plant responded in a plastic manner to differing nutrient conditions. There was no difference in the carbon allocation over the period of the greenhouse experiment. There were, however, significant and dramatic changes when the allocation pattern with ^{14}C was analyzed. Although there was a larger proportion of biomass belowground in the field for the RP plant, when dominants from the two sites were analyzed, there was no significant difference in root:shoot ratios. Finally, there was not a significant response to the nutrient enrichment experiment.

Costs of Roots and Foliage

Contrary to predictions, field carbon:nitrogen ratios for roots were lower than the C:N ratio of the aboveground tissue. However, the carbon:nitrogen ratio was lower at Konza Prairie than at Hog Island. Because there was no significant difference in percent carbon between the parts of the plant, the differences are largely due to the differences in percent nitrogen. Although others have found a higher nitrogen content in leaves than in roots of plants (Tilman and Wedin 1991*b*, Schenk et al. 1995, Silsbury 1987), the nitrogen levels found within both the sites were similar to levels found previously (Conn and Day 1996, Stevenson and Day 1996, Conn and Day 1993, Seastedt and Knapp 1993).

Several studies have taken place on the same dune complex on Hog Island that was used in this study. In a study along the chronosequence of Hog Island, Conn and Day (1996) found belowground live root nitrogen levels of 0.70 (±0.02) and Stevenson and Day (1996) found fine root biomass %N to be 1.34 percent, bracketing the levels found in this study. Conn and Day (1993) also found that there was no significant difference in nitrogen content between live root size classes or between depths from 0-40 cm in 10 cm increments in the dune system. The Konza Prairie nitrogen levels were also within the range reported by previous researchers (Seastedt and Knapp 1993). Seastedt and Knapp (1993) also found that foliage nitrogen levels declined after a high in mid summer and increased belowground until the fall.

This study found that relatively more nitrogen than carbon is required for construction of roots than shoots. There was also a higher nitrogen cost at Konza than at Hog Island. Differences in C:N ratio were largely based upon the nitrogen content of the tissue because there were no significant differences in percent carbon. The difference in nitrogen level between the two systems suggests two possible explanations. First, as nitrogen levels increase, the level of nitrogen in foliage and roots increases (Glimskar and Ericsson 1999, Leith et al. 1999, Louahlia et al. 1999, Tilman and Wedin 1991*b*, Sage and Pearcy 1987, Bassirirad et al. 1999, del Arco et al. 1991, Leith et al. 1999, Chapin 1980). Tilman and Wedin (1991*b*) worked with both *A. gerardii* and *S. scoparium* although the lowest nutrient levels were higher than those on Hog Island. The second equally plausible explanation is that the plants on Hog Island naturally have a higher C:N ratio. The results from the grasses tested in the greenhouse study support the second explanation. *S. scoparium* had a higher C:N ratio than *A. gerardii* when grown in the high nutrient soil. The higher C:N ratio should allow a plant to survive at a lower nitrogen availability level. This is because the nitrogen can be used more conservatively throughout the plant. In addition, the nitrogen may be more effectively used in the nutrient poor environment. This would allow photosynthesis and root construction to occur in nutrient depauperate conditions prohibitive to other species.

In the greenhouse study, the nitrogen levels were higher within the foliage than in either the coarse or fine roots. This appears to contradict the results from the field work. However, Seastedt and Knapp (1993) found that nitrogen content in foliage declines after a peak in mid-summer while root nitrogen increases to a peak in fall. It may be that in the season of this study the foliar nitrogen declined below that of the roots in the field. Both sites were either in a sustained dry period or were recovering from a sustained dry period. The plants in the field may have started to senesce early.

The lower nitrogen levels for the aboveground biomass for the *S. scoparium* grown in sand may be indicative of the result of drought stress on nitrogen content. Sand is less able to retain water and therefore induces water stress in plants sooner, given the same level of watering and period of drying. The plants in sand, therefore, would be the first to show the effects of this stress.

Carbon and Nitrogen Storage

Chapin et al (1990) defined storage as ‘resources that build up in the plant and can be mobilized in the future to support biosynthesis’. A narrower definition was given by Staswick (1994), which further restricted the definition of storage compounds exclude those compounds used for plant metabolism. Compounds excluded from storage in either of these definitions include structural carbon such as lignin and cellulose, because these compounds cannot be broken down and translocated to other portions of the plant. The primary compounds used for carbon storage in plants are polysaccharides and sugars (Heilmaier and Monson 1994, Chapin et al. 1990). Nitrogen can be stored as nitrate, amino acids and proteins (Staswick 1994, Chapin et al. 1990, Millard 1988). Ideally, compounds would be segregated and compounds assigned to storage compounds, metabolically active compounds and storage compounds. An imprecise alternative is to determine the concentration of carbon and nitrogen within tissue and assume that concentrations above a baseline carbon or nitrogen level (representing the structural and metabolically active compounds) are storage. Because rhizomes usually are considered the belowground location for carbon and nitrogen storage (Chapin 1980), one would have expected the highest concentration within the course root fraction. There was not a larger proportion of carbon in the roots in the field studies.

In the greenhouse experiment, the coarse root fraction did have a higher proportion of carbon than the fine root fraction. However, the proportion of carbon in the coarse roots was not significantly greater than the aboveground proportion of carbon. One would have expected that if the carbon in the coarse roots were stored carbon, there would be a significantly higher proportion in *S. scoparium* grown in the nutrient rich soil. There was not a significant difference between treatments and there was not a significant interaction between treatments and plant part.

S. scoparium is adapted to low nutrient conditions (RP plant) and should therefore be inclined toward luxury consumption and storage (Chapin 1980, Grime 1974, 1977). There was no difference in percent carbon in the coarse roots of *S. scoparium* regardless of soil nutrient status. There was also no difference between the RR plant (*A. gerardii*) and *S. scoparium*. This seems to indicate that there may be structural similarities common to these grasses as the roots increase in width.

The C mm^{-1} root appears to contrast with the percent carbon data. As roots get older and wider, the absolute carbon content increases while the proportional carbon content remains stable. Because there is a strong relationship between carbon per mm, width and age, and no change of percent carbon, biomass must be correlated to percent carbon.

As the biomass of a given segment of root increases, the carbon increases proportionally. As roots age, they get both wider and heavier. This implies that as roots get older and wider they incorporate more mineral material in proportion to the carbon. The static carbon content also implies that the structural material of the roots is similar throughout age classes and widths of roots.

The morphology and development of roots significantly impact their carbon and nitrogen content. In contrast to roots of other groups, graminoids, as monocots, do not have secondary growth. After elongation, roots do not increase in width (Heilmaier and Monson 1994, Chapin et al. 1990, Millard 1988). While carbon is used extensively for the construction of plant cells, nitrogen is primarily a component of amino acids, proteins, and nucleic acids although a small portion do exist in lipids (Chapin et al. 1986). Amino acids and proteins are the most significant pool of nitrogen in the cell (Chapin et al. 1986). Nitrogen content is therefore correlated to protein content in cells.

The mitotically active tip produces many small cells as well as hormones to control growth. This results in a large cell surface to volume ratio for a given section of root near the root apex (Gandar 1980, Baluska et al. 1995). Protein content is also highest near the root tip (Silk and Erickson 1980), probably due to construction activity and hormone production. The cell membranes would likely also contain many proteins per unit area as the cells exchange growth signals.

As one moves back from the tip, there is a shift in cell function and therefore a shift in the proteins found within the cells. The cells elongate and are responsible for nutrient (Silk et al. 1986) and water uptake (Frensch et al. 1996, Silk et al. 1986). Uptake of anions such as nitrate, requires active transport, often across multiple membranes and conversion to usable forms (van der Werf et al. 1994). The cell is still expanding and therefore still requires proteins responsible for construction (Silk and Erickson 1980). The root construction and nutrient uptake increases protein content; however, this is balanced by the reduction in hormonal output.

The older portions of the root are primarily responsible for transport of nutrients and water to the upper reaches of the plant and carbohydrates to the lower portion of the plant. The metabolic activity of this portion of the root system should decline considerably from areas nearer the tip. Older roots are less likely to be sites for water uptake and uptake of cations due to suberization (Perumalla and Peterson 1986). They also are less likely to be growing. One would therefore expect fewer proteins in the cell membrane used for uptake, fewer proteins used in nutrient uptake and conversion and fewer proteins used to control construction of the cell.

There was a decrease in nitrogen of individual roots with width and age on Hog Island. Konza Prairie had an insignificant decline in nitrogen of individual roots with age and width, as was seen by the selection of the ANCOVA model and the negative slope of the regressions. In contrast, ng nitrogen per mm of individual roots increased with width for both Konza Prairie and Hog Island. On Hog Island, there was also a significant age effect. ng Nitrogen per mm increased with width for the oldest roots while the youngest roots showed little change (Fig. 18). The regression was relatively weak. If storage were to occur, nitrogen would increase in older and wider roots. Although nitrogen increased per mm of root, there was a decrease in nitrogen when considered on a percentage basis. This suggests that there was not significant storage of nitrogen in the roots. Nitrogen content may have increased per mm because the mass increases and there is a minimal requirement of amino acids per unit mass of root. As roots age, because there are fewer needs for proteins, there is likely to be a lower proportion of nitrogen in the root.

In the greenhouse experiment, the coarse and fine root nitrogen content of *S. scoparium* were not significantly different from each other. In addition, there was no significant difference between the two treatments for the roots. There was a significant difference in percent nitrogen between *A. gerardii* and *S. scoparium* roots. This is contrary to the theory that plants adapted to nutrient poor sites are more inclined to exhibit luxury consumption (Chapin 1980, Grime 1974, 1977).

The most important difference between the plants used in the greenhouse study was in percent nitrogen. Both the live and dead portions of *Andropogon gerardii* had higher concentrations of nitrogen. The difference between the plants may, therefore, be the RP plant tended to use nitrogen more sparingly than the RR plant. The low nutrient conditions of the sand may not have provided the RR plant with enough nitrogen to successfully generate tissue and when the stress of the simulated drought occurred, the plant was unable to survive because it had no reserves. This indicates that although

Schizachyrium scoparium does not store nitrogen or carbon, the plant is able to survive in low nutrient conditions by shifting its carbon belowground in a plastic manner while maintaining its nitrogen level in a conservative manner regardless of the nitrogen level. The conservation of nitrogen in the live tissue seems to allow for additional growth in a depauperate environment.

Exchange Ratios

The response of the plants in the greenhouse experiment seems to provide evidence for Grimes' hypotheses (Grime 1977 and Bloom et al. 1985) that RP plants are no more efficient at acquiring nitrogen than RR plants, but do not support Grimes hypothesis (Grime 1977) that plants adapted to RP plants do not respond in a plastic manner to changes in their environment. The exchange rate of nitrogen and carbon for *Andropogon gerardii* and *Schizachyrium scoparium* grown in high nutrient conditions was not significantly different. However, it was different from that of *Schizachyrium scoparium* grown in a low nutrient environment. This was due to the dramatic shift in carbon to the belowground portion of the plant which made the nitrogen more expensive. This would seem to indicate that even though this perennial species is one of the dominants in a low nutrient environment, and therefore, would most likely be placed into Grimes' stress tolerant category, it showed a flexible response to nutrient addition. In addition, Bloom's hypotheses (Bloom et al. 1985) on the efficiency of plants suggest that RR plants would be more efficient at using their resources than RP plants. Both plants had an equal return in nitrogen for the carbon sent belowground in the nutrient rich environment. It should be noted that the RR plants did not survive in the nutrient poor soil. This indicates that the plant was ill adapted to the environment or at least not as well adapted as the RP plants.

Carbon Allocation

Although there was not a significant difference between treatments in carbon partitioning when it was measured as change in carbon, there were significant differences with partitioning when ^{14}C was analyzed. What this means is that over the course of the experiment, there was no net increase between treatments. However, there was a difference in the way the plants were partitioning carbon at the end of the experiment. The leaves of the plants had the largest proportion of the ^{14}C for all treatments. This is to be expected because this is the portion of the plant that is taking in the labeled carbon dioxide and fixing it as sugar. A pilot study, performed in the greenhouse, with the same species found that with half the ^{14}C dosage, carbon was sent to the roots over a similar time period. Both species partitioned the carbon similarly in the Konza Prairie soil with a relatively equal proportion going to both the coarse and fine roots. When *S. scoparium* was grown in low nutrient sand, however, there was an increase in the carbon sent belowground. This should result in increased root production because carbon storage is not likely to be occurring. There is a lot of evidence ranging from observational studies (Tilman and Wedin 1991, Chapin 1986 ,1980, Chapin et al. 1990) to theoretical work (Grime 1974, 1977, Tilman and Wedin 1991*a*, *b*, Caldwell 1979) which suggests that root to shoot ratios increase in nutrient poor environments. The contribution of carbon belowground suggests that although there are no significant differences between treatments in root:shoot ratios, the carbon allocation from the time of the ^{14}C pulse to the end of the experiment would increase the root:shoot ratio.

The biomass data from the field shows that although there was a significant difference between the above and belowground portions of the plant for Konza Prairie, there were not significant differences for Hog Island. The high root biomass resulted in an above:belowground biomass ratio near 1:1 for Hog Island and near 6:1 for Konza Prairie. This is consistent with the root:shoot ratios discussed above. One would expect a larger percentage of biomass to be aboveground than belowground in a nutrient rich environment. However, the root dynamics in Konza Prairie result in a higher root turnover for that site. Konza Prairie had higher root mortality and birth rates. This results in a higher allocation per unit biomass. At the time of the study, mortality and birth of roots were not significantly different. The system was, therefore, in steady state with respect to root dynamics.

Response to Microsite Enrichment

There was not a significant response to any of the microsite enrichments. Although previous work has shown responses to microsite enrichment of both water and nutrients (Cui and Cladwell 1996,1998, Fransen et al. 1998), there is some evidence that a priming period is required before a response can be recorded. Caldwell et al. (1996) found that there was not a significant response in root length density when a 45 mM NH_4NO_3, 20 mM KH_2PO_4 solution was added in a single burst adjacent to desert shrubs. Earlier work at the same site found that when a more substantial pulse was added there was a response (Eisenstat and Caldwell 1988). Eisenstat and Caldwell (1988) found that there was a two to four fold response to the nutrient solution. Pregitzer et al. (1993)

found a similar response in a beach maple forest with nutrient solution, but there was no response to simple water addition. A pot study of *Lollium perenne* by Hodge et al. (1999) also found responses to both pulses and patches of labeled ^{15}N and ^{13}C. The only change in root dynamics was a change in root births. One might therefore conclude that had the nutrient level lasted longer, been stronger or been pulsed, there might have been a significant response in root births resulting in increased root length density. Additional tubes may also have reduced variance and produced significant differences. Unfortunately, the cost associated with producing an extended exposure level, adding tubes, or pulsing on a remote location rendered this possibility beyond the ability of this study. In short, the plants in neither of the systems were able to respond quickly enough to take advantage of the nutrients added to each system.

CONCLUSION

Measurements of individual roots may be crucial to determining accurate levels of nitrogen and carbon turnover. There have been attempts to calibrate rhizotron data with core data to determine nitrogen and carbon turnover rates (Burke and Raynal 1994, Hayes and Seastedt 1987). These studies, however, do not account for root width or age. As has been seen, root age and width are both significant factors when determining nitrogen and carbon per mm. Dramatically different results may be obtained when one calibrates nitrogen or carbon turnover with the width and age correction. Unfortunately, width is a more important predictor for nitrogen and carbon than age. Width is the least precise measurement made with minirhizotrons (Weber and Day, unpublished data). Although width can be used to divide roots into broad size categories, the data presented in this paper indicated that at least carbon per mm has significant differences with root width and the content changes along a well predicted continuum. Calibration of minirhizotrons should therefore include both soil cores for RLD data and individual roots for biomass, carbon and nitrogen content. This should provide a more accurate approximation of turnover.

This study also indicates that what is important for survival as a perennial grass in a nutrient poor environment is the ability to continue to photosynthesize in low nutrient conditions. Perhaps RP plants adapted, similar to xerophytic plants (Orians and Solbrig, 1977), are able to function over a wider range of nutrient levels and therefore can continue to operate when the RR plants can no longer operate. The functional life of the leaf and root are therefore extended beyond the level found in a mesotrophic plant. In contrast to Tillman's R* hypothesis (Tilman and Wedin 1991*a*, *b*) in which plants competitively remove nutrients in low nutrient environments so that other plants do not have access, the RP plants used in this study were simply able to survive at lower nutrient levels. This would tend to support Grimes' (1977) hypothesis of stress tolerant species. However, the species tested did not store nutrients. The RP grasses were simply able to survive and function in low nutrient environments through an adaptive physiology.

RP grasses may be able to compete with RR grasses by surviving during stressful periods. There was no storage of nitrogen or carbon in the RP plants. In fact, if anything, the RR plants were storing nitrogen in the nutrient rich environment. Both plants also maintained similar nitrogen exchange ratios in the high nutrient soil. The RP plant was able to dramatically shift its carbon allocation belowground in the low nutrient environment. This is different than the hypotheses of Grime (1974, 1977) in which a stress tolerant species has a less plastic response. The RR plants may, in fact, be less flexible in their allocation than the RP plant. The RP plant may conserve rather than store a limiting resource. Stress, in the form of drought, pushed RR plants below a key threshold and they perished.

Several issues have proven to be important in the study of these systems. First, roots must be primed in order to have a response to a pulse of nitrogen. Second, there is a continuum of nitrogen and carbon content with respect to the width and age of roots. This continuum may prove significant when determining fluxes of nitrogen and carbon in systems with minirhizotrons.

The most dramatic and significant difference in the greenhouse experiment was the change in the cost of nitrogen acquisition and ^{14}C partitioning for *S. scoparium*. This plastic response, combined with the lack of nutrient and carbon storage implies that these plants have a dramatic and physiological response to low nutrient conditions.

Most theories of competition and survival strategies assume a relatively even and predictable distribution of resources within a given environment. Tilman's R* hypothesis (Tilman and Wedin 1991*a*, *b*) assumes a slow even decline in resources which eventually drops below the threshold of less capable competitors. Grimes plant strategy theory (Grime 1977, 1974) assumes that plants adapt to nutrient poor environments through increased storage, but he inadequately discussed the importance of catastrophic stresses. Seastedt came closer to approximating the unevenness of resource distribution by stressing the importance of taking advantage of temporary optimal conditions in the transient maxima hypothesis (Seastedt 1988, Blair 1997). However, although taking advantage of the best environmental conditions may be most critical in resource rich environments, surviving the worst possible conditions may be most important in the most marginal environments. In these environments, there often are no reserves available. When a catastrophic loss of resource occurs, such as drought or grazing, the organism must have a physiology that permits survival, not by stored reserves, but by continued growth regardless of reserves in these limiting conditions.

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Responsible for literature search database containing over 1400 copies of citations for major literature review of wastewater pathogens, aggregation of data for tables and charts, production of graphs. Wrote grants and papers.

Database Designer/ Manager, Web Designer: *Norfolk Department of Public Health 12/99-7/00*
Responsible for design and management of a database for EMPACT beach monitoring project and design of web page for beach data. Also developed databases which converted information from paper-based systems to databases which allowed quick retrieval of data for required standard reports and charts.

Research Assistant (statistician): *Old Dominion University, Dept. of Biology* 8/99-1/00, 8/98-5/99
Designed new data entry system for Chesapeake Bay monitoring Program Phytoplankton lab. Retrieved data for graph production from long term data set. Analyzed data from *Pfiesteria piscicida* monitoring project and produced reports on data.

Adjunct Faculty: *Tidewater Community College, Portsmouth Va. 1/98-5/98*
Responsible for lecture and lab of general biology class.

Teaching Assistant: *Old Dominion University, Dept. of Biology 9/1997 - 12/1997*
Botany - Responsible for development, presentation and grading of Botany labs.
General Ecology - Assist Professor with class in field, participate in lab development.

Research Assistant (root research): *Old Dominion University, Dept. of Biology 1/1992 - 8/1997*
Responsible for initial setup and maintenance of minirhizotron equipment; perform field work and analysis of images; write protocols for minirhizotron operation and digital image analysis; maintain computer equipment. Assisted with experimental design. Work included both nutrient study on eastern shore of Virginia and CO_2 enrichment study at Merrit Island (Kennedy Space Center) Presented work at conferences and workshops.

SELECTED PUBLICATIONS AND PRESENTATIONS:

Authored 3 published papers, authored or coauthored 10 presentations at professional meetings, co-authored 2 technical reports

Weber, E.P. and H. G. Marshall. 1999. Water quality relationships to concentrations of Pfiesteria-like organisms in Virginia estuaries for 1998. Virginia Journal of Science. **50** (4): 365-380.

Weber, E.P. and F.P. Day. 1996. The effect of nitrogen fertilization on the phenology of roots in a barrier island sand dune community. Plant and Soil. **182**(1):139-148.

Day, F.P., E.P. Weber, C.R. Hinkle, and B.G. Drake. 1996. Effects of elevated CO2 on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. Global Change Biology. **2**:101-106.