Plant and Soil **182:** 139–148, 1996.

The effect of nitrogen fertilization on the phenology of roots in a barrier island sand dune community

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Received 12 September 1995. Accepted in revised form 21 March 1996

Key words: fine roots, minirhizotron, mortality, nitrogen fertilization, phenology, root cohorts

Abstract

Little work has been done on the phenology of root growth and senescence largely due to methodological difficulties. The application of minirhizotron technology has enabled the tracking of individual roots through an entire growing season. As a result, direct measures of mortality, root growth, and an analysis of cohorts can be obtained. This study examined the belowground response of vegetation in a nutrient limited system to nitrogen addition. Small plots on a 36 year old dune on Hog Island, a barrier island in the Virginia Coast Reserve Long Term Ecological Research Site, were fertilized with nitrogen. Minirhizotron tubes were installed in each fertilized and control plot. Each tube was sampled monthly for nine months, March through October of 1992. Root length density increased throughout the growing season with the greatest root length density in the top 20 cm of the soil profile. The fertilized plots had greater root length densities (14.1 mm cm^{-2}) than the unfertilized plots (2.9 mm cm^{-2}). There was no significant depth×treatment interaction. Root mortality did not significantly change with fertilization. The largest loss of roots for a cohort occurred within the first month. The dune grassland community did not respond to fertilization with large changes in root distribution or increases in mortality in this study.

Introduction

Little work has been done to explore the root distribution patterns that plants use to survive in nutrient-limited ecosystems. Previous research on roots has focused mainly on root/shoot biomass ratios (Bloom et al., 1985; Mooney and Winner, 1991, Orians and Solbrig, 1977; Thornley, 1969); however, little work has been done on the distribution of roots within the soil matrix particularly in natural systems. Current models rely upon root length rather than biomass to determine nutrient and water uptake rates (Baldwin et al., 1972, Cowan, 1965; Cushman, 1979; Gardner, 1960) and at least one study found a grass species to have twice the mass per unit length of root of another closely related grass (Caldwell and Richards, 1986).

Research which has observed root length density in natural systems has included observation of differences between competing species (Caldwell et al., 1981; Richards, 1984), differences between two similar hardwood forests (Hendrick and Pregitzer, 1993a,b) and the response to localized microsites of nutrients (Eisenstat and Caldwell, 1988; Pregitzer et al., 1993). The belowground response of a nutrient limited system, in terms of root length density, to mass fertilization has not been observed. Barrier islands provide a particularly good environment to observe nutrient-limited root distribution responses. The sandy soil of the islands makes root observation relatively easy and the low nitrogen status of the soil makes nitrogen availability easy to manipulate.

Because roots are an expensive portion of the plant to grow and maintain(Bloom et al., 1985; Caldwell, 1979), plants must optimize root distribution patterns to efficiently manage resources. Harris and Wilson (1970) found that four grasses showed different strategies of root deployment and that the strategy's effectiveness was directly related to the severity of stress placed upon the plant. The position of roots within the soil matrix should, therefore, reflect the optimization

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strategies plants use to perform root functions efficiently.

This study's goal was to determine what patterns could be observed in root distribution with a mass fertilization regime. Altering the most limiting mineral resource (nitrogen) should elicit the strongest response from the roots. Rapid expansion of root length density, large root mortality, and a shortening of root lifespan in response to nitrogen addition are all energetically expensive responses while conservative expansion of root length density, little root mortality and extention of root lifespan would indicate a more energetically frugal strategy. This was tested by examining root responses with minirhizotrons placed in nitrogen fertilized and reference plots.

Materials and methods

Site description

The study site is located on Hog Island, a barrier island off the eastern coast of the Delmarva Peninsula on the Virginia Coast Reserve (VCR) Long-Term Ecological Research (LTER) Site.

On north Hog Island accretion has produced distinct dune complexes as well as a foredune area. From the Atlantic Ocean to the bayside of the island, a chronosequence of dunes has been aged from 6 to 124 years old (Hayden et al., 1991). The present study was located on the stable 36 year old dune ridge.

The plant community on this dune complex is dominated by the perennial grasses *Ammophila breviligulata* Fernald, *Spartina patens* Muhl. and *Panicum amarum* Ell.(>85% perennial grasses by stem count >75% by cover class). The community is on a well-drained sand dune with surrounding wet areas. To the east is a freshwater marsh of *Spartina patens*. To the west are wax myrtle (*Myrica cerifera* L.) thickets.

Monthly rainfall and temperature data for 1992 ranged from maxima of 216 mm rainfall (August) and 25.1 °C mean temperature (July) to minima of 5.7 mm rainfall (December) and 0 °C mean temperature (December) (Krovitz and Porter, pers. commun.).

The soil of the study site is a Newhan-Corrolan complex (Dueser et al., 1976). This soil complex is characterized by an excessively drained typic thermic udipsamment (Newhan) in the higher elevations and the well drained aquic thermic udipsamment (Corrolan) in the lower elevations. The sandy soil provides few nutrients, and low nutrient and water retention (Dueser et al., 1976). All plots were placed within the Newhan series. A previous study on Hog Island (Day, 1993) found the fertilization regime used in the present study increased the soil solution nitrate from 0.29 (±0.06) mg L^{-1} to 29.28 (±5.93) mg L^{-1} and the ammonium from 0.08 (±0.01) mg L^{-1} to 19.86 (±6.83) mg L^{-1} at a depth of 15 cm. Based on monthly samples, the periodic application of fertilizer maintained these higher levels of nitrogen in the soil throughout the duration of the study.

Minirhizotrons

Minirhizotrons, clear tubes in which video tape recordings of roots are made, have been used at a variety of sites including a hardwood forest (Hendrick and Pregitzer, 1992, 1993a,b), agricultural systems (Hansson and Andren, 1987) and a simulated tropical forest (Körner and Arnone, 1991). Minirhizotrons were used to observe root dynamics in the present study because their non-destructive nature allowed direct measurement of mortality and root longevity.

The minirhizotron tubes were 2 m long, clear, 5.08 cm inner diameter butyrate tubes with 0.65 cm thick walls. Etched frames along the side of the minirhizotron tube allowed the minirhizotron camera to consistently orient on the same area of soil in repeated samplings. To prevent light from penetrating the minirhizotron tubes, the top of each tube was painted to just below the soil surface with a flat black paint. In addition, the top of the tube was wrapped with electrical tape to provide a light-tight fitting with a PVC cap.

Each tube was inserted into the soil at a 45° angle to the ground. Holes were augured to a depth which would allow observation through approximately 80 frames or 1 m of observable tube. The tubes were installed February 15-29, 1992.

Once the tubes had been in place for two to three weeks, the first readings were taken. Observations were made with the video camera system described by Hendrick and Pregitzer (1992). In the laboratory, a Targa +16 video board (Truevision) and ROOTS software (ver 8-22-89, Michigan State University Remote Sensing Laboratory) were used to manually digitize the video images.

Because black roots were shown to produce new live roots, color was not useful for determining root death in this study. All visible roots were assumed to be alive. Each root was placed into a cohort based on its first appearance. The cohort group provided the basis for survivorship calculations.

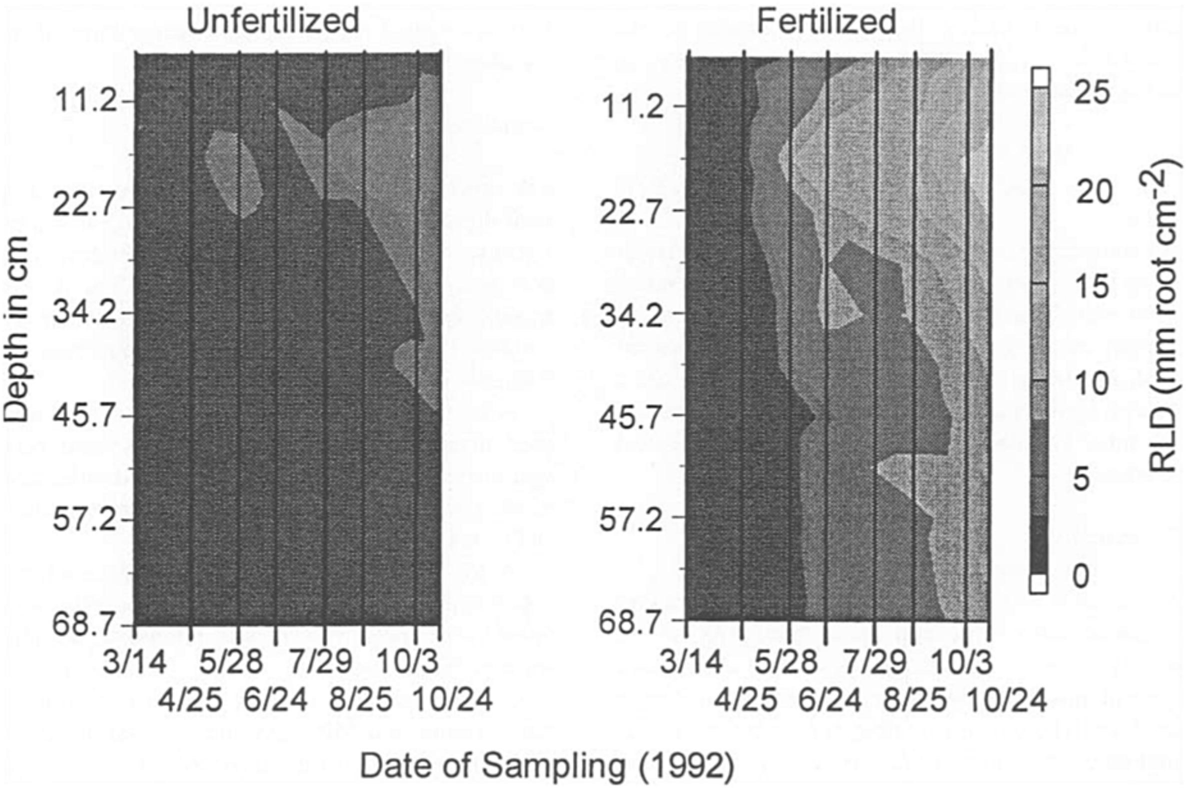

Figure 1. Contour plot of root length density by both depth and date for fertilized and unfertilized plots.

Experimental design

Eight 3×3 m plots were selected within the study site. The plots were representative of the dune ecosystem and were spaced a minimum of six meters apart to allow for independent treatment of the plots. Four plots were randomly assigned to nitrogen fertilization treatment and four plots were left as untreated controls. One of the control plots was dropped by the end of the study because it was strongly influenced by the adjacent *Myrica* thicket and *Myrica* roots. Fertilized plots received three applications of fertilizer during the year (March 14, June 10, and October 3 of 1992). Each application consisted of fifteen g N m^{-2} with a 70%-30% mix of coated temperature-release urea to uncoated urea. The site was monitored on an approximately monthly basis from March through October of 1992. Inclement weather and logistical problems prevented strict monthly sampling. Four minirhizotron tubes were placed in each plot, one meter from the adjacent sides, each tube perpendicular to one of the sides. Etched frames faced towards the center of the plot to reduce any possible edge effects.

Root length density

Root length density (RLD) has traditionally been a measure of root length per volume of soil. This paper uses root length density as a measure of the root length per area viewed along a minirhizotron tube. This is common usage of the term in the literature with this technology (Hendrick and Pregitzer, 1993a,b; Vos and Groenwold, 1987). Root length density (RLD) was calculated by summing all of the root lengths for a given area of the tube and dividing that quantity by the area of the tube observed. Root length density was calculated for each date and depth combinatian of each tube for analysis.

Mortality

To calculate root mortality, the root length was compared between sample n and sample n+1. If a root was not observed at time n+1 the root was assumed to have decomposed. The mortality was therefore 1.00 or 100%. If the root was longer at time n+1 than at time n, in other words the root grew between time n and n+1;

there was no mortality. If a root was smaller at n+1 than at n, a simple calculation was made to determine the fractional mortality (Eq. 1).

$$(\text{root length } n - \text{root length } n+1)/\text{root length } n = \text{mortality} \quad (1)$$

This measure was related to Hendrick and Pregitzer's (1992) mortality measure but because it was figured on an individual root basis, with root extension eliminated from the calculation, true mortality was actually measured. Mortality was calculated on a per frame basis and averaged for each depth and date combination of each tube. These means were then used for statistical analyses.

Cohort analysis

To determine root life expectancy, roots were placed into cohorts, or groups, based upon when the roots were initially observed. Percent change was calculated from time n to time n+1 for each cohort. The percent change was then divided by the number of days between sampling dates to control for different intervals between sampling dates. Root number density rather than root length density was used. This eliminated skewing the data in favor of longer roots.

Not all of the data were used for the statistical analyses. The reasoning for the removal process follows. It was believed that the largest percent change would occur between the first and second month of any cohort. Three consecutive percent changes were felt to be the minimum to ensure that the changes observed were not transitory. Four months of data were, therefore, determined to be the minimum number of sampling dates within any cohort. The first, second, third, fourth, and fifth cohorts had enough sampled dates to meet the minimum criteria to be chosen for this analysis. The first two cohorts were eliminated from the analysis because they contained too many missing values (percent change could not be calculated if there were no roots observed within a cohort). Therefore, only the third, fourth, and fifth cohorts were used in the analysis.

Because interest was focused upon the longevity of the roots, the analysis used root age. Root age was given by the number of dates since the roots were first observed, as discussed above. There were three root age categories for the percent change: one, two, and three. Root age one represented the percentage change interval from time one to time two. Root age two represented the percentage change interval from time two to time three and so forth.

Statistical analyses

The depths were pooled into three roughly 20 cm vertical depth classes (0-22 cm, 22-46 cm, 46-68 cm). Because depth classes were not independent, depth was analyzed as a repeated measure. The ANOVA model, therefore, had plots nested within treatments and both time and depth class as repeated measures for both root length density and mortality.

A nested, crossed, repeated measures model was used to analyze the cohort data. Plots were nested within treatments as was done with the other measures. However, cohorts were crossed with treatment and root age was a repeated measure.

A log transformation was used to normalize the root length density data. Because the analysis was an unbalanced design (plot 2 was removed), a sum of squares IV was used

An arcsine transformation was used to normalize the mortality data. Missing values reduced the degrees of freedom so that it was not possible to calculate the error term for the ANOVA. Because there were more missing values in the first few months of sampling, the first three turnover intervals were removed from the analysis to allow the calculation of the error term.

Because there was no a priori reason to believe that our data had othogonally spherical components, and tests for orthogonal sphericity are sensitive to non-normality (Crowder and Hand, 1990), all tests used the Greenhouse Geiser adjusted F.

Results

Root length density

The results showed three main effects and two interactions to be significant for root length density (Table 1). Figure 1 shows a plot of root length density for all unpooled depths and dates for both the fertilized and unfertilized treatments. The pattern of root length density with depth can be seen in both treatments with the greatest root length density occurring at 15 cm.

Both depth×date ($F=4.40$, $p<0.01$) and date × treatment ($F=10.51$, $p<0.01$) interactions were significant. Both the fertilized and unfertilized plots increased in root length density over time; however, the fertilized plots increased in root length density over time at

Table 1. Nested doubly repeated measures analysis of variance examining the effect of fertilizer on root length density over time and across three depth classes. DF–Degrees of freedom, SS–sums of squares, F Value–calculated F value, Adj Pr > F–Greenhouse-Geisser adjusted F value

Source of variation	DF	Type IV SS	Mean square	F-value	Pr>F
Treat[a]	1	343.763	343.763	43.16	0.0001
Plot(Treat)[a]	5	125.385	25.077	3.15	0.0282
Error	21	167.246	7.964		
Depth[a]	2	310.933	155.467	30.71	0.001
Depth x Treat	2	1.433	0.716	0.14	0.8680
Depth x Plot(Treat)	10	56.187	5.619	1.11	0.3776
Error(depth)[b]	42	212.626	5.063		
Date[a]	7	1043.13	149.019	69.18	0.0001
Date x Treat[a]	7	158.404	22.629	10.51	0.0001
Date x Plot(Treat)	35	118.880	3.397	1.58	0.0529
Error(Date)[c]	147	316.646	2.154		
Depth x Date[a]	14	70.265	5.019	4.40	0.0001
Depth x Date x Treat	14	11.357	0.811	0.71	0.6688
Depth x Date x Plot(Treat)	70	112.903	1.613	1.42	0.0757
Error(Depth x Date)[d]	294	334.983	1.139		

[a] Significant at the $p<0.05$ level.
[b] Greenhouse-Geieser Epsilon = 0.9977.
[c] Greenhouse Geisser Epsilon = 0.7607.
[d] Greenhouse Geisser Epsilon = 1.0664.

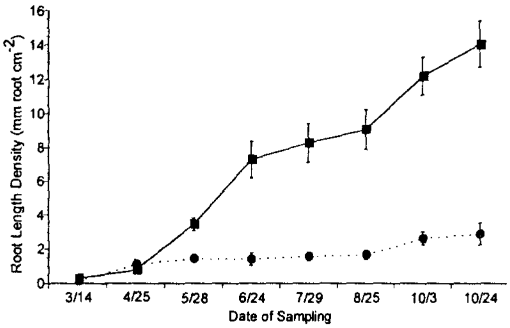

Figure 2. Root length density for fertilized plots (□) and unfertilized plots (●) from March 14, 1992 to October 24, 1992. Means and standard errors calculated from mean of plots, with root length density from entire tubes used to calculate plot means.

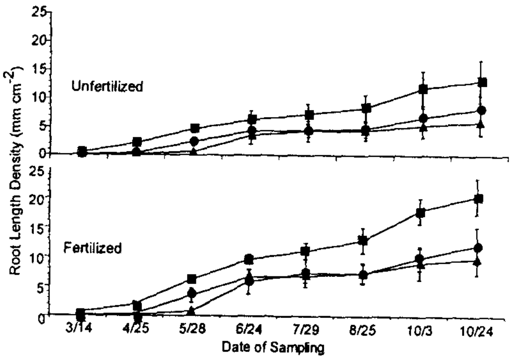

Figure 3. Root length density (RLD) for 0-20 cm depth (□), 20-40 cm depth (●), and 40-60 cm depth (△) for both fertilized and unfertilized plots. Means and standard errors calculated from mean of plots.

a faster rate (Fig. 2). Root length density was greater in the fertilized treatment (root length density =14.1 mm cm^{-2}, on 10/24/92) than in the unfertilized treatment (root length density =2.9 mm cm^{-2}, on 10/24/92) at the end of the study.

The depth×date interaction was somewhat less clear (Fig. 3). The 0-20 cm depth class showed a faster increase with time than the two deeper depth classes. The 20-40 cm and 40-60 cm depth classes were not different from each other. The 0-20 cm depth class had the greatest root length density.

Table 2. Nested doubly repeated measures analysis of variance examining the effect of fertilizer on turnover over time and across three depth classes. DF – Degrees of freedom, SS – sums of squares, F Value – calculated F value. SS and Mean square in ten thousandths

Source of variation	DF	Type IV SS	Mean square	F value	Adj Pr>F
Treat	1	0.061	0.061	0.05	0.8377
Plot(Treat)	3	0.131	0.044	0.03	0.9910
Error	5	6.618	1.323		
Depth	2	2.304	1.152	2.37	0.1609
Depth x Treat	2	4.613	2.306	4.74	0.0510
Depth x Plot(Treat)	6	1.686	0.281	0.56	0.7410
Error(depth)[b]	10	4.864	0.487		
Date[a]	3	1.271	0.424	10.75	0.0015
Date x Treat	3	0.120	0.040	1.02	0.4045
Date x Plot(Treat)	9	0.010	0.011	0.27	0.9578
Error(Date)[c]	15	0.059	0.039		
Depth x Date	6	1.170	0.028	1.04	0.3922
Depth x Date x Treat	6	0.295	0.049	1.81	0.2100
Depth x Date x Plot(Treat)	18	0.585	0.033	1.19	0.3808
Error(Depth x Date)[d]	30	0.817	0.027		

[a] Significant at the $p<0.05$ level.
[b] Greenhouse-Geisser Epsilon = 0.7800.
[c] Greenhouse Geisser Epsilon = 0.8029.
[d] Greenhouse Geisser Epsilon = 0.3582.

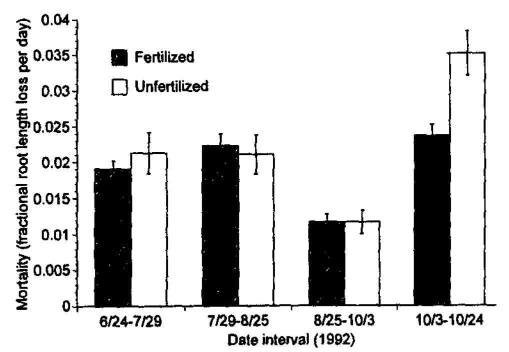

Figure 4. Mortality for date intervals of fertilized and unfertilized plots. Means and standard errors calculated from mean of plots with root length density from entire tubes used to calculate plot means.

Mortality

There were no significant differences between the fertilized and unfertilized plots (Table 2). Any tendencies between the fertilized and unfertilized plots favored higher mortality in the unfertilized plots (Fig. 4) which was in the opposite direction that current theory would suggest. Date was the only significant effect (F=10.75, $p<0.05$) (Fig. 4). The highest mortality was in the 10/3-10/24 interval and the lowest mortality was in the 8/25-10/3 interval.

Cohort analysis

Figure 5 shows the cohort root number density by date. The patterns and relative values of root numbers in different cohorts were similar to those of root length density for the plots seen in Figure 2. There was an increase in root number density throughout the growing season for both the fertilized and unfertilized plots. Examination of the individual cohorts revealed that cohorts show their largest decline from their first appearance to their second appearance.

The May and July cohorts showed similar patterns with root age (Fig. 6). The results for cohort analysis found one interaction to be significant (Table 3), cohort x root age (F=1082.21, $p>0.0001$) as well as the cohort and root age main effects (cohort F=1645.06, $p>0.0001$; root age F=949.72, $p>0.0001$). Root num-

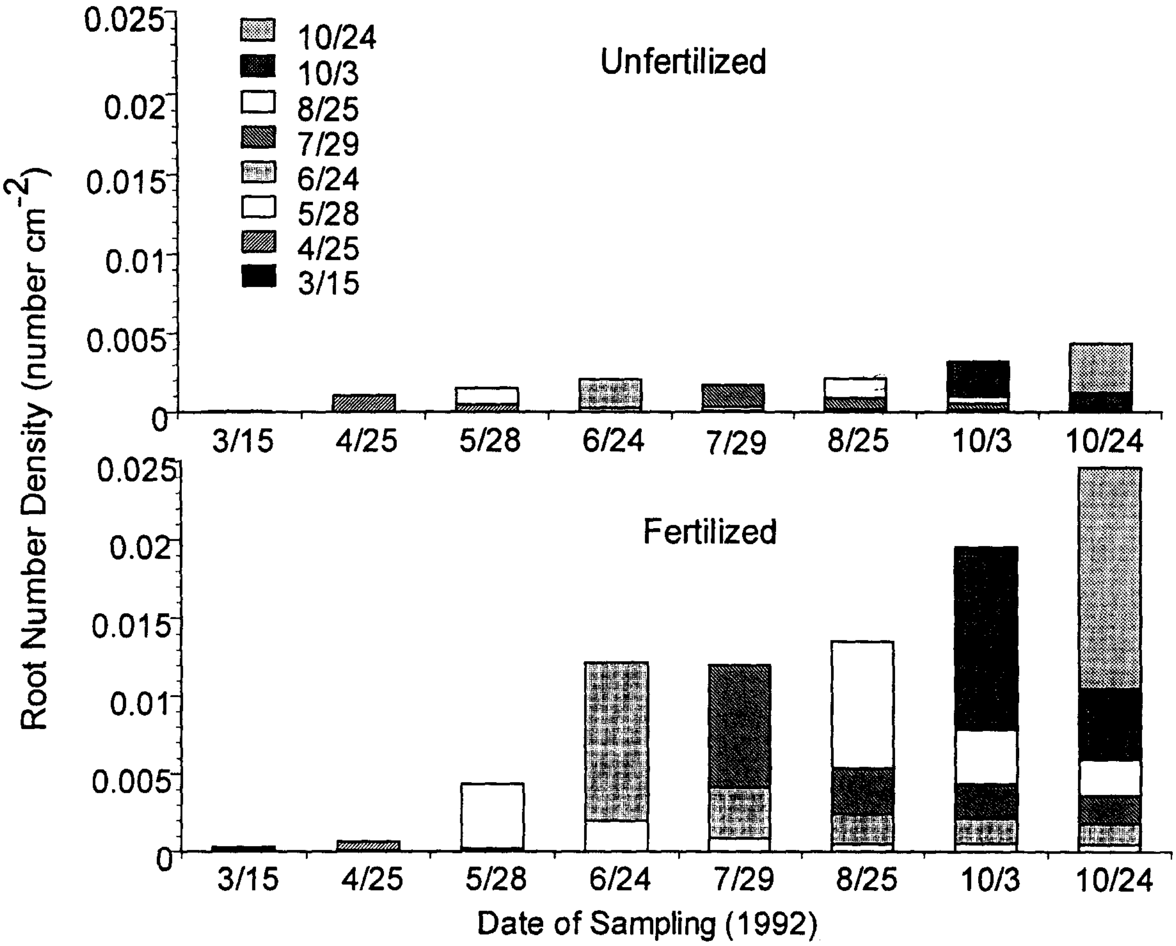

Figure 5. Cohort data by date for fertilized and unfertilized plots. Each pattern represents a cohort. Each column represents a sample date.

Table 3. Nested crossed repeated measures analysis of variance examining the effect of fertilizer on cohorts across three root age classes. DF – Degrees of freedom, SS – sums of squares, F Value – calculated F value

Source of variation	DF	Type IV SS	Mean square	F value	Adj Pr> F
Treat	1	0.00002	0.00002	0.03	0.8620
Plot(Treat)	5	0.131	0.0008	1.16	0.3433
Cohort	2	2.306	1.153	1645.06	0.0001
Treat x Cohort	2	0.0002	0.0001	0.16	0.8509
Error	49	0.034	0.0007		
Root age[a]	2	1.919	0.960	949.72	0.0001
Root age x Treat	2	0.0008	0.0004	0.40	0.5447
Root age x Plot(treat)	10	0.015	0.002	1.44	0.2097
Root age x cohort[a]	4	4.374	1.094	1082.21	0.0001
Root age x Treat x Cohort	4	0.001	0.0003	0.28	0.7723
Error(Root age)[b]	98	0.099	0.001		

[a] Significant at the $p<0.05$ level.

[b] Greenhouse-Geisser Epsilon = 0.5406.

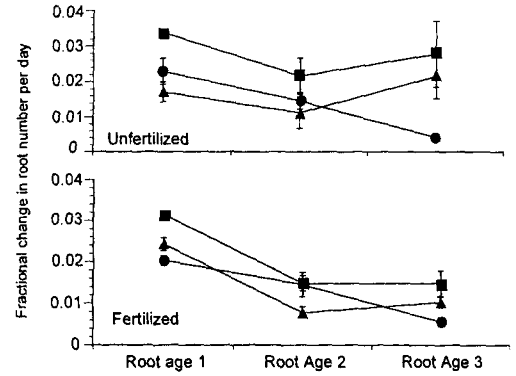

Figure 6. Cohort analysis percent change per day by root age category and cohort for both fertilized and unfertilized plots. (May cohort(□)), June cohort (●), July cohort (△)). Means and standard errors calculated from mean of plots with root length density from entire tubes used to calculate plot means.

ber density change was greatest for category one. Cohorts therefore lost most of their roots between the first and second time they were observed. The influence of the June cohort made the cohort×root age interaction significant. The last observation of the June cohort had a smaller daily percent change than the second root age category. The other cohorts both showed either a slight increase in root mortality rate or equal root mortality rate in the third root age category.

Discussion

Root length density

The nitrogen fertilization affected root length density of entire root systems. That is, there were no proportionally greater increases in root length density specific to depth class within the soil profile of the fertilized plots. Both aboveground and belowground biomass increased in a previous study that used the same fertilization regime at the same site used in the present study (Day, 1993). Regardless of the resource availability of the site, there is a large compendium of evidence that plants respond to fertilization through increased root mass. Tilman and Wedin (1991) found an increase in root biomass correlated with increasing nitrogen status for five perennial grass species. In addition, Wilson and Tilman (1991) found increasing root biomass with increased nitrogen supply in a study of competition along a nitrogen gradient.

The dune ecosystem had considerably smaller root length densities than other systems. Hendrick and Pregitzer (1992) found densities between 15-45 mm cm^{-2} in a northern hardwood forest. Atkinson and Fogel (1991) also found greater values (46 - 180 mm cm^{-2}) along a rhizotron in a northern hardwood forest with the plants adjacent to the rhizotron being *Prunus pumila* and *Pteridium aquilinum*. This fits with Gleason and Tilman's finding that root densities increase in later successional stages (Gleason and Tilman, 1991).

Mortality

There was no significant change in mortality in the fertilized compared to the unfertilized plots. This finding contrasts with the findings of Aber et al. (1985) who found increased turnover with nitrogen. Chapin (1980), Grime and Campbell (1991) and Sharpe and Rykiel (1991) suggested that stress tolerant plant roots are more likely to be used for nutrient storage. The fastest mortality rate was 0.035 fractional loss or 3.5 percent loss per day which is similar to that found by Hayes and Seastedt (1987) in a tall grass prairie. The mortality rate is considerably faster than that found by Hendrick and Pregitzer (1993b) in a northern hardwood forest (0.41 and 0.21 percent loss per day). The faster mortality rates are expected in a grassland when compared to a woody root system.

The changes observed in mortality by date were directly correlated to the number of days between sampling. Consequently, these changes may be the result of our sampling regime rather than a true measure of mortality. Because we sampled only once a month, it may be that there is an initial mortality that occurs in a shorter time period than the sampling interval, as a result the mortality rate may be an underestimate. Although no conclusions on mortality by date can be made in this study, the tests remove the effect of date on the other mortality factors tested. A more frequent sampling regime was cost-prohibitive in this study; however, future research should be done to determine the optimal sampling intervals for mortality rates in this system.

Cohort analysis

The initial large mortality followed by two slower mortalities for each cohort shows a differential shedding of roots dependent upon the age of the roots. Young roots are therefore more likely to senesce than older roots in this system. Caldwell (1979) suggested that short lived roots may better be able to uptake nutrient and water than longer lived roots. Although short lived roots were observed in this study, the fertilization treatment did not affect the occurence of ephemeral roots. No explanation is obvious for the decline in mortality for the June cohort.

Conclusion

The dune grassland community did not respond to the mass fertilization with large changes in root distribution or increases in mortality in this study. There were overall increases in root length density with fertilization; however, the pattern of root distribution remained the same. There was no significant increase in mortality as may be expected with an increase in nitrogen status. Although shortlived roots were observed in this system, they did not increase with fertilization. The lack of change in root deployment pattern and mortality rate and the lack of an increase in short lived roots with fertilization seem to imply that this community responds in a frugal manner to mass nitrogen inputs.

Acknowledgements

This project was supported by National Science Foundation grant BSR-9007899 and University of Virginia Subcontract 5-26024. We consulted with Mark Butler and J P Morgan on statistics. Chris Conn, Pat Dow, Irene Weber and Cindy Caplen assisted in the field. We also acknowledge Randy Carlson and Jimmy Spitler for operating the boats which took us to the island. This paper was prepared from a master's thesis completed by the first author at Old Dominion University.

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Section editor: G R Stewart