NUTRIENT FORAGING IN TEN SOUTHEAST COASTAL PLAIN PLANT SPECIES

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ABSTRACT

Plant root system response to nutrient heterogeneity was tested in ten plant species of varying life form and successional status. All plants tested are native to the South Carolina coastal plain. Morphological responses of the root system (scale, precision and discrimination) and overall plant response (sensitivity) to increasing nutrient heterogeneity were tested. Ten individuals of each species were placed into four treatments which had varying nutrient distribution but the same overall nutrient addition. Plants were harvested when roots reached pot edge. I observed high variation in scale (mass and extent of a root system), precision (the ability to proliferate roots in nutrient patches) and sensitivity (growth benefits gained as nutrient heterogeneity increases; measured as total biomass). No significant discrimination responses were observed, although greatest mean root density occurred at intermediate fertility levels for all species. I tested the hypothesis that scale and precision would be negatively correlated, and I did not observe this relationship in these plant species. However, in herbaceous species scale and precision were positively correlated. Sensitivity was not closely related to precision indicating that proliferating roots in fertile patches does not always yield growth benefits in heterogeneous soils. Further, some sensitive species had very low precision suggesting that other characteristics lead to positive growth response in heterogeneous environments. Plasticity of root uptake rates and demography of roots are proposed as two other mechanisms which may play important roles in plant sensitivity responses. Scale was negatively correlated to sensitivity for herbaceous plants suggesting that plants that monopolize the most soil space are not able to gain benefits from nutrient patches within the soil matrix. There was no trend observed to suggest that plant life form was correlated with precision or sensitivity. However, scale was greater in herbs than in woody plants, possibly because the two life forms develop at different times.

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Chapter 1: Introduction

Soil nutrients and water vary in both space and time (Nye & Tinker 1977; Fitter & Hay 1987; Fitter 1994). Soil resource heterogeneity can occur at many scales, including those detectable at the level of individual plants (Jackson & Caldwell 1993). Consequently, ecologists have paid much attention to natural heterogeneity in soil resource availability and the response of plants to such variation (Hooke, Burke & Laurenroth 1991; Gross, Pregitzer & Burton 1995; Humphry & Pyke 1997).

The term "foraging" has been used to describe the process by which root systems grow in the soil and thus capture nutrients (Bray 1958). Presumably, plasticity can increase the efficiency of resource foraging. One of the most common plastic responses is the proliferation of roots in bands of high fertilizer density (Passioura & Wetselaar 1972; Granato & Raper 1989). Historically, most studies of root response to fertilizer patches have examined agricultural species known to have particularly high growth rates and large demand for nutrients (Drew 1975; Fitter 1994; Robinson 1994). More recently, plant root foraging responses in natural communities have been studied to determine if they influence competitive interactions and succession (Crick & Grime 1987; Campbell, Grime & Mackey 1991; Jackson & Caldwell 1989; Mou, Mitchell & Jones 1997).

Three plastic responses which may be important to below-ground resource foraging are scale, precision, and discrimination. All three of these deal with morphology of root systems with respect to nutrient location. Scale (monopolizing nutrient capture by the development of an extensive root system) and precision (the tendency to proliferate roots in resource rich patches) were negatively correlated for eight herbaceous plant species native to Great Britain (Campbell, Grime & Mackey 1991). Discrimination (the ability to identify and proliferate roots in patches of higher nutrient concentrations when there is variation among patches) to our knowledge has not yet been explicitly tested, although Jackson and Caldwell (1989) observed that some species vary in root proliferation depending on patch concentration.

A fourth plastic trait, sensitivity, focuses on total biomass responses to different levels of heterogeneity. A sensitive plant displays increased biomass as the same amount of nutrients becomes more patchily distributed throughout the soil matrix. Sensitivity has been demonstrated experimentally for at least one clonal plant species; however, if enriched nutrient patches became too small, the plant responded as if the entire area was homogeneously poor (Birch & Hutchings 1994; Wijesinghe & Hutchings 1997). I believe that understanding sensitivity may be essential for predicting whether or not plants gain fitness benefits from increased allocation of roots in fertile patches.
Knowledge of the nutrient foraging patterns and individual species responses may be a key to understanding their competitive ability and dominance during various stages of succession. Species with the most extensive root systems (highest scale) are superior competitors in homogeneous conditions (Campbell et al. 1991). However, studies have not yet examined outcomes of competitive interactions in heterogeneous environments. Furthermore, it is not yet clear if consistent patterns of plasticity or resource foraging

strategies are associated with specific types of plants (e.g., early vs late successional species, herbaceous vs woody species). In an environment where nutrient distribution is heterogeneous, species which are highly sensitive to nutrient heterogeneity may have competitive advantages over those that are not (Grime 1987).

During a successional sequence it is possible that the advantages of precise foraging will change. Initially, growth will not depend on precise foraging due to low competitor density and high resource availability. However, as succession proceeds and space becomes more partitioned, greater benefits may be afforded to plants that are precise foragers.

Campbell et al. (1991) found a negative correlation between scale and precision in eight plant species. This observed correlation suggests a strategic trade-off between these two traits. However, the eight species were all herbaceous and were not from the same community. Investigations of root foraging using species from the same community will provide greater insight into within-community interactions. Furthermore, an understanding of the fitness benefits associated with foraging strategies is essential. An important assumption, based on the proposed trade-off between scale and precision is that by increasing precision, plants gain fitness in heterogeneous soil environments (Grime et al. 1991). This assumption has not yet been tested in heterogeneous soils.

The objective of this study was to quantify root system plasticity to various levels of soil heterogeneity using ten species from the same community. Scale, precision, discrimination, and sensitivity were measured and analyzed to answer the following questions: (1) Do these co-occurring species differ in root foraging behavior? (2) Are root foraging traits correlated? (3) Does increased root proliferation within nutrient patches confer growth benefits on species? (4) Is foraging ability related to life form?

Chapter 2: Methods

EXPERIMENTAL SETUP

A potted plant study was undertaken during the 1997 growing season in glass houses located at Virginia Tech, Blacksburg, Virginia, USA. The ten plant species used in this study are native to warm temperate forests of the coastal plain of South Carolina (Table 1; Radford, Ahles, & Bell 1968, Tucker 1996). I chose three annuals, three perennial herbs, and four woody plants to test for correlations between foraging ability and life form. In the fall and winter of 1996-1997 seeds were gathered from pine forests of different successional stages at the Savannah River Site, Aiken and Barnwell Counties, South Carolina, USA. Seeds were germinated on wet filter paper in a growth chamber, and then planted into a nutrient rich soil upon the emergence of cotyledons.

Plants were allowed to grow until large enough (2-4 cm tall) to survive transplant (one plant per pot) into 30 cm diameter by 28 cm deep pots filled with construction grade sand. I chose sand because it is naturally low in nutrient content, and the soils where the seeds were collected have sandy epipedons. Before transplanting, plant roots were gently rinsed with tap water to remove soil. Each plant was supplied with a small amount of fertilizer solution (30 ml of Peter's General Purpose Fertilizer: 200 ppm N, 87 P, 166 K) to promote seedling establishment. Five grams of native soil was added to provide access to indigenous microbes. Plants were misted for 30 seconds twice daily for two weeks and then once daily in the early morning for the rest of the study.

The study consisted of two experiments each with two treatments (total of four treatments). The same amount of nutrients were added to all treatments, but nutrient distribution varied among treatments. A general purpose slow release greenhouse fertilizer was used (6 g of 15-10-10 (N-P-K) plus minors, Grace-Sierra Horticultural Products). This quantity of fertilizer provided N mineralization rates similar to those in natural coastal plain pine forests. The fertilizer released nutrients slowly over the course of the experiment, therefore nutrients were not applied in pluses as is often the case in the natural environment. In the first experiment, fertilizer was broadcast evenly over the surface of the pot (homogeneous treatment = H) or all of the fertilizer was concentrated on the surface of just one quarter of the pot (quarter treatment = Q) following a method outlined by Mou et al. (1997). A finer scale of heterogeneity was applied in the second experiment. Fertilizer was added to three plugs (diameter 2.5 cm, depth 15 cm) of sand equally spaced from one another and from the plant. In the plugs equal treatment (PE) each plug had the same amount of fertilizer and in the plugs unequal treatment (PU) each plug had a different amount of fertilizer (differences between levels was a factor of four). The first experiment was used to assess precision, and the second to assess discrimination. Scale was measured using results from the first experiment as well as overall averages from all four treatments. Total biomass from all four treatments was used to detect sensitivity to different levels of nutrient heterogeneity. I perceive the heterogeneity of the treatments to increase along the gradient H < Q < PE < PU. The H

Table 1. Co-occurring species from South Carolina used in study.

Species	Successional status*	Life form
Chamaecrista nictitans (L.) Moench	1	annual
Erigeron canadensis L.	1	annual
Hypericum gentianoides L.	1	annual
Desmodium strictum (Pursh) DC.	2-3	perennial herb
Solidago nemoralis Aiton.	2-3	perennial herb
Diospyros virginiana L.	5-15	deciduous tree
Liquidambar styraciflua L.	5-100	deciduous tree
Pinus taeda L.	5-100	evergreen tree
Elephantopus tomentosus L.	>30	perennial herb
Euonymus americanus L.	>30	deciduous shrub

*years during secondary succession when species is most abundant, based on field observations

and Q treatments were a coarser scale of heterogeneity (large patches relative to pot size) compared to the PE and PU treatments. Ten replicates were planted per treatment for each species. Pots were laid out in a completely randomized design.

HARVEST

Plants were harvested when roots reached pot edge (determined by periodic harvest of extra plants). At this time the plants' roots systems had filled the pot both horizontally and vertically. To harvest, above-ground portions were removed and then roots from each nutrient patch within the pot were collected. In the homogeneous treatment, the below-ground portion was harvested in quarters for comparison with the quarterly treatment. Roots were separated from the sand by washing over a 2 mm mesh screen and then divided into three sections: the central or "tap root" which did not belong to any quarter, coarse roots (>1 mm diameter), and fine roots. The tap root was not present for all species, and in these cases the roots were separated into only two groups. Stem length and leaf area (using a LI-COR 3100 area meter) were measured. For *C. nictitans* and *P. taeda* leaf area was determined for a subsample of leaves and whole plant leaf areas were estimated by calculating a weight to leaf area ratio which was multiplied by the mass of the leaves collected. Following processing, all plant parts were dried to a constant mass at 60° C and weighed.

ION EXCHANGE TEST

Ion exchange membranes were used to ensure that fertilization patches remained at a higher fertility than the non-fertilized regions (Subler 1996; Abrams & Jarrell 1992). I tested for nitrate since it is the most mobile soil nutrient. Membranes were placed at two depths (9 cm and 18 cm) in each of seven quarterly fertilized pots with no plants in them. Four locations were tested: patch center, the boundry between the patch and the non-fertilized region, and 2.5 cm and 5 cm into the non-fertilized region. Pots were misted once in early morning to mimic the treatment of the pots with plants. Membranes were left in the pot for ten days, removed from the soil, and then extracted with 0.5 M NaCl. Extracts were analyzed using QuikChem AE flow injection analyzer (Lachat Instruments). The Lachat QuikChem method 12-107-04-1B (Nitrate in 2M KCl Soil extracts) was used with 0.5M NaCl for the carrier and standard diluent.

DATA ANALYSIS

Nitrate concentrations for the ion exchange membranes were log transformed to correct for heteroscadistic variance and then analyzed using two factor ANOVA, with location and depth of membranes as the main effects.

Three parameters were used to estimate scale: density, specific root length (SRL) and estimated total fine root length. Density of the root system was calculated by dividing the total mass of fine roots in the homogeneous treatment by the total volume of the pot. To determine SRL, at least fifteen samples of fresh roots (approximately 0.01-0.05 g dry mass) were randomly selected and the lengths were estimated using the grid method (adapted from Böhm 1979). Root samples were taken from soil of various fertility levels. The roots were then dried and weighed to estimate cm roots/g dry root mass. Total fine root length was estimated by multiplying the SRL by the average fine root dry mass per pot for each species. Because the root samples measured for length were taken from all treatments, the total fine root length was determined using the average dry mass for all treatments combined. Results for each measure of scale were compared using one way ANOVA with species as the main effect.

Precision was tested by comparing the relative fine root mass difference (RFRMD) between two randomly selected quarters from the H treatment to the RFRMD between the fertilized and opposite quarters in the Q treatment. RFRMD is calculated by dividing the fine root dry mass difference between two quarters by the total pot fine root dry mass (Mou et al. 1997). Division by the total pot fine root dry mass makes this a relative measure by correcting for differences in plant size. Differences in RFRMD were analyzed using two way ANOVA with treatment and species as main effects.

Plants that are able to discriminate between patch fertility levels were expected to exhibit more root biomass variability among plugs in the PU treatment than in the PE treatment. I tested for this by a homogeneity of variance F-test. The variable we tested was percent of the total root system in each plug.

To test for sensitivity I made four comparisons of total biomass: H vs Q, PE vs PU, H vs Q vs PE vs PU, and H+QU vs PE+PU. The fourth comparison is one of coarse versus fine scale heterogeneity, because in the H and Q treatments, patch size was large while in the PE and PU treatments, patch size was considerably smaller. Comparisons were made by two way ANOVA in which species and treatment were the main effects.

Pearson's correlation coefficients were calculated to test for the strength of the relationships among different morphological responses and between morphological responses and sensitivity. All statistical analyses were conducted using SAS (SAS 1996). To account for an unbalanced data set (Table 2) the mixed procedure (PROC mixed) was used in the analysis of scale, precision, and sensitivity, and species were dropped from analysis in cases when $n<5$ for any treatment being compared. Least-squares means were used for post hoc tests (SAS 1996).

Chapter 3: Results

Analysis of the ion exchange extracts revealed significant location ($p=0.0001$) effects, however depth and interaction effects were not significant ($p>0.05$). Nutrients leached downward, but there was little lateral movement in the soil (Fig. 1).

Poor germination or mortality lessened the number of replicates for some treatments in some species (Table 2). Thus, in some analyses, less than the full compliment of ten species could be analyzed.

All three measures of scale revealed significant species differences ($p<0.05$) which were as great as one order of magnitude(Table 3). Density and root length were highly correlated since they are both derived from the actual dry mass of roots (Tables 4&5).

Patchy nutrient availability caused a shift in root mass allocation in some species but not in others. Significant treatment (H vs Q), species, and interaction effects in RFRMD were detected (Table 6). In all cases the RFRMD in the H treatment was not different from zero indicating that root systems developed symmetrically ($p>0.05$). In the Q treatment, seven species had an RFRMD which was statistically different from zero, and of these the four with the greatest RFRMD were also statistically different from the homogeneous pots (Fig. 2). The RFRMD in quarterly fertilized pots was used as an index of precision (Table 7).

Evidence of discrimination was weak. The mean percentage of roots in the PE and PU plugs varied between 1% and 8% of the total pot root dry mass depending on species (Fig. 3). Significant heterogeneity of variance (PE vs PU) was detected in only one species, *Pinus taeda* ($p <0.05$). Variance was higher in the PU treatment due to one large observation at the lowest fertility level which caused this point to be higher than expected and to display a high standard deviation (Fig. 3). In the other six species, the range of mean values for the percent of the root system in plugs was greater for PU than for PE (data not shown) which suggests that some discrimination may have occurred. No index of discrimination was calculated.

Many species showed a slight increase in the percent of roots located in the plugs between the low and intermediate levels and a large decrease between the intermediate and high levels of fertility in the PU treatment (Fig. 3). To examine this relationship further, I plotted root density for all fertilizer densities used in both experiments (Fig. 4). In order to correct for the fact that the patches were different sizes, all values were divided by the volume of soil in the patch. For all eight species examined in this way, maximum root density occurred at an intermediate fertility level (Fig. 4). Some species differences were apparent. Two species had maximum rooting densities at around 8 g of fertilizer/dm^3 soil, while three others had maximum rooting densities at less than 2 g/dm^3 (Fig. 4).

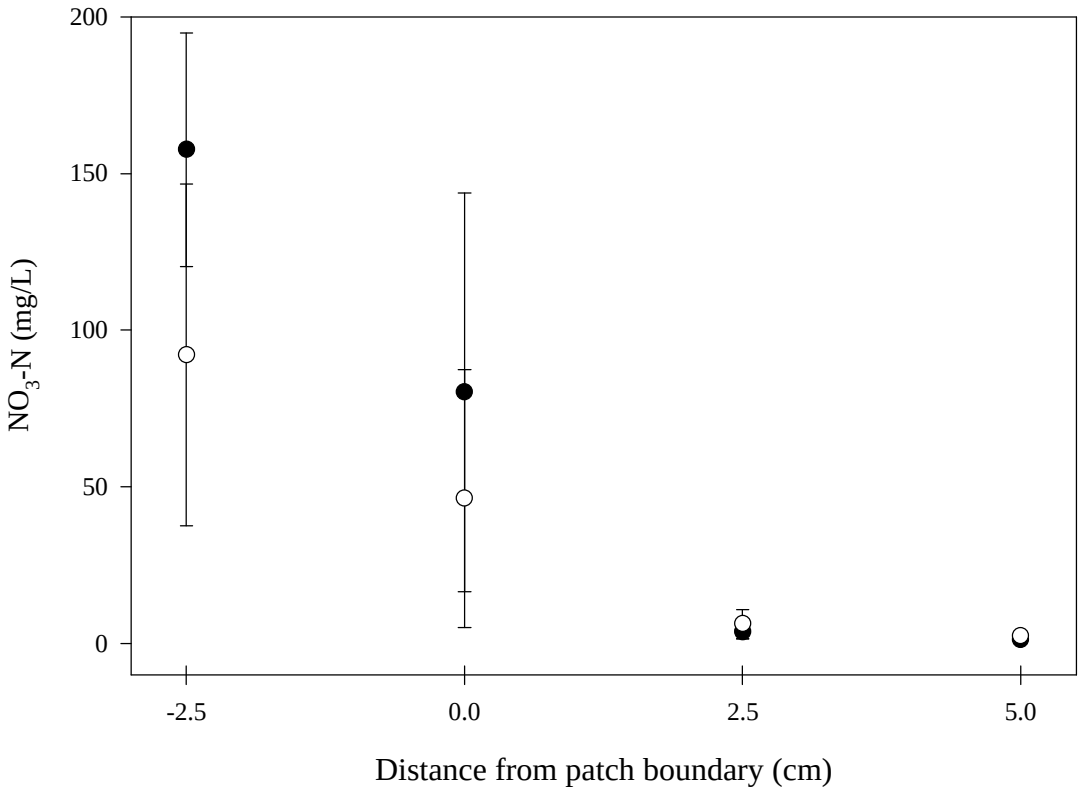

Figure 1. Nitrate concentrations at different depths and locations (negative values are within patches) in a quarterly treatment pot. Values obtained after a 10 day incubation of ion exchange membranes in seven pots. Mean ± standard deviation shown.

Table 2: Number of individuals harvested for each species, by treatment.

	SPECIES									
	Cn	Ds	Dv	Ea	Ec	Et	Hg	Ls	Pt	Sn
Experiment 1										
Homogeneous	10	9	10	12	10	10	10	10	11	8
Quarterly	10	9	9	5	10	10	7	9	10	9
Experiment 2										
Plugs Equal	10	9		4	9	10	7	8	10	9
Plugs Unequal	9	9		3	9	10		6	8	10

Species symbols are as follows: Cn- *Chamaecrista nictitans,* Ds- *Desmodium strictum,* Dv- *Diospyros virginiana,* Ea- *Euonymus americanus,* Ec- *Erigeron canadensis,* Et- *Elephantopus tomentosus,* Hg- *Hypericum gentianoides,* Ls-*Liquidambar styraciflua,* Pt- *Pinus taeda,* Sn- *Solidago nemoralis.*

Table 3: Means of three measures of scale ± standard error. In each column, numbers with the same letters are not significantly different ($p>0.05$). Multiple comparisons were completed using least-squares means with Tukey adjustment (SAS 1996).

	Density (g dry mass/dm^3 soil)	SRL (m roots/g dry mass)	Total fine root length (m)
S. nemoralis	0.116±0.030 [a]	392±66 [a]	504±54 [a]
C. nictitans	0.087±0.009 [a,b]	483±49 [a]	491±33 [a]
H. gentianoides	0.069±0.015 [a,b,c]	478±45 [a]	470±56 [a]
E. canadensis	0.057±0.008 [b,c,d]	411±44 [a]	393±29 [a]
D. virginiana	0.034±0.010 [c,d]	92±6 [b]	39±8 [b]
E. tomentosus	0.027±0.005 [c,d]	564±41 [a]	177±16 [b]
L. styraciflua	0.024±0.004 [c,d]	184±10 [b]	64±7 [b]
D. strictum	0.022±0.007 [c,d]	470±24 [a]	182±19 [b]
E. americanus	0.017±0.004 [d]	88±6 [b]	26±5 [b]
P. taeda	0.016±0.003 [d]	65±13 [b]	16±2 [b]

Table 4. Pearson's correlation coefficients for foraging characters for all species combined (n=10). Comparisons were between the indices calculated for each trait by species. P-values for the correlations are after the coefficients. See text for details on the calculation of indices.

	Density (scale)	SRL (scale)	Root length (scale)	Q RFRMD (precision)
SRL	0.47 (0.16)			
Root length	0.91 (<0.01)	0.73 (0.02)		
Q RFRMD	0.39 (0.27)	0.17 (0.64)	0.40 (0.25)	
Sensitivity	-0.38 (0.31)	0.21 (0.59)	-0.14 (0.73)	-0.11 (0.78)

Table 5. Pearson's correlation coefficients for foraging characters for herbaceous species only (n=6). Comparisons were between the indices calculated for each trait by species. P-values for the correlations are after the coefficients. See text for details about how the indices were calculated.

	SRL	Root length	Q RFRMD	Sensitivity
Density (scale)	-0.62 (0.18)	0.92 (0.01)	0.58 (0.23)	-0.78 (0.06)
SRL (scale)		-0.59 (0.21)	0.01 (0.99)	0.16 (0.16)
Root length (scale)			0.76 (0.08)	-0.55 (0.25)
Q RFRMD (precision)				-0.44 (0.38)

Table 6. ANOVA of the relative fine root mass differences in the homogeneous and quarterly treatments. See text for details on the calculation of RFRMD.

Source	d.f.	MS	*P*
Species (A)	9	0.14	0.0159
Treatment (B)	1	2.42	0.0001
AB	9	0.13	0.0282
Error	169	0.06	

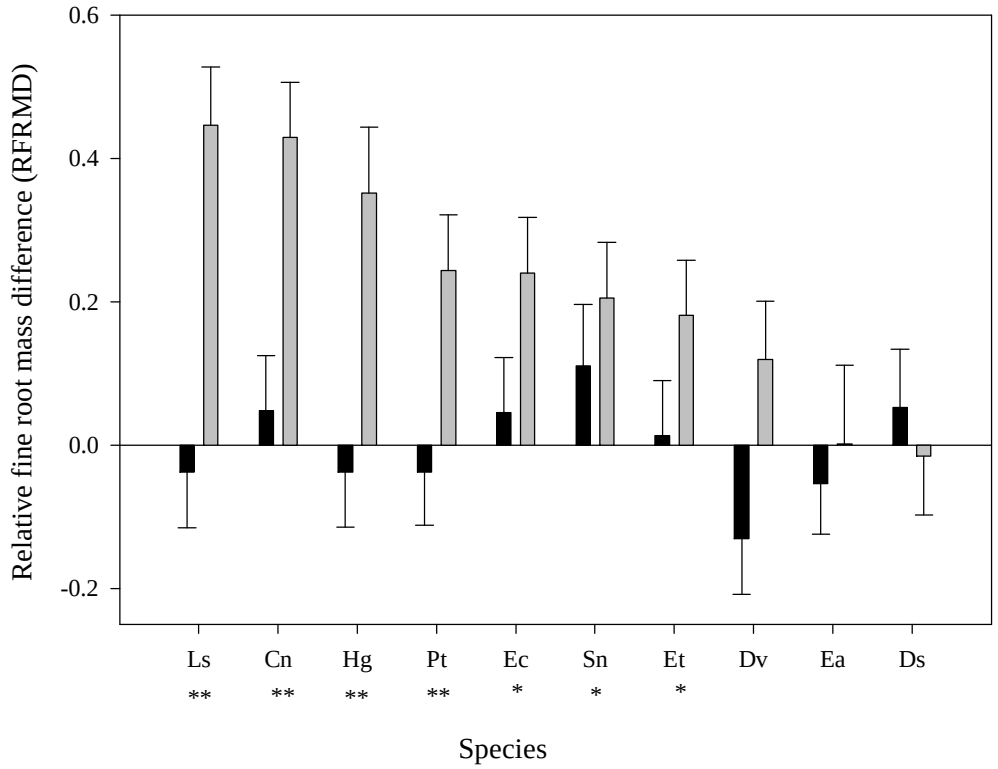

Figure 2. Homogenous and quarterly relative fine root mass (RFRMD) values. In all cases the H RFRMD was not different form zero ($p>0.05$). ** Q RFRMD is significantly different from zero and from the H RFRMD ($p<0.05$). * Q RFRMD is different from zero but no treatment effects are detected ($p<0.05$). Bars are least-squares means ± the standard error of the mean. Species symbols are as in Table 2. See text for details concerning calculation of RFRMD.

Table 7. Relative fine root mass differences (RFRMD) from the Q treatment for all ten species. These values were used in the correlation analysis as a index of precision.

Species	Relative fine root mass difference (Q treatment)
L. styraciflua	0.45
C. nictitans	0.43
H. gentianoides	0.35
P. taeda	0.24
E. canadensis	0.24
S. nemoralis	0.20
E. tomentosus	0.18
D. virginiana	0.12
E. americanus	0.00
D. strictum	-0.02

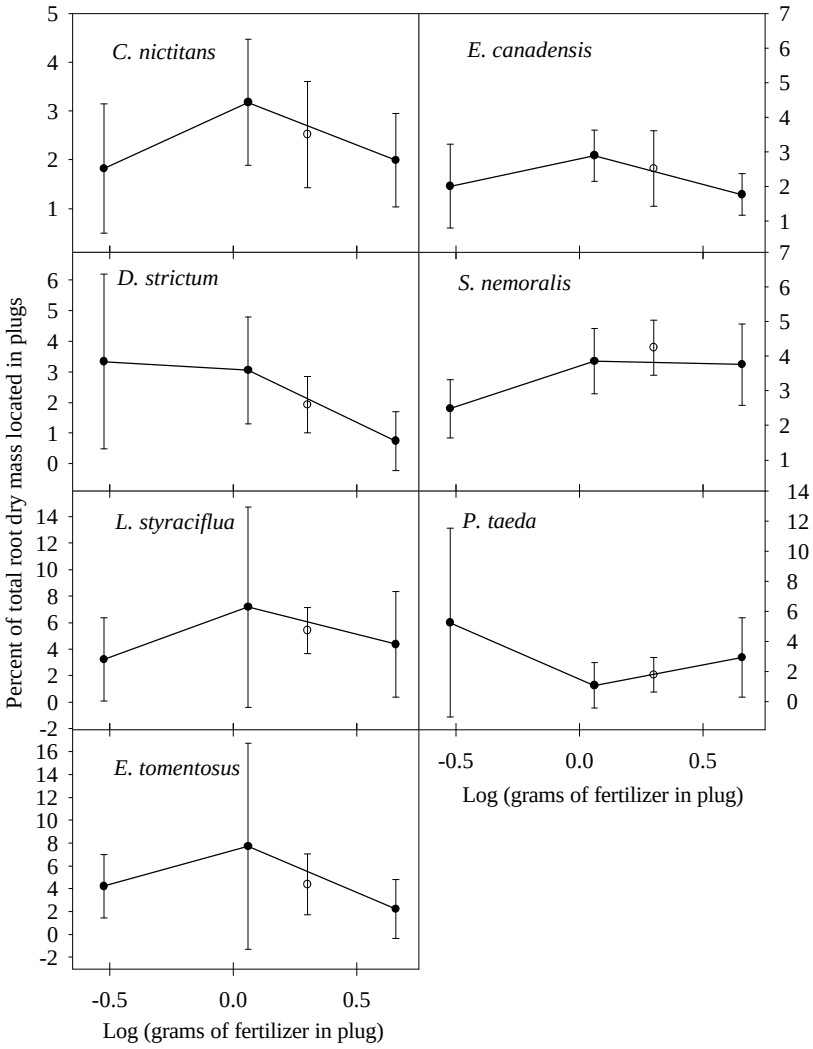

Figure 3. Percent of root system found in individual plugs in the plugs equal (o) and plugs unequal treatments (●). The plugs equal observations are an average of all plugs of equal fertility (three per pot) for each species (n=24-30). The plugs unequal observations are an average of each fertility level in the PU treatment (n=8-10). Bars are ± standard deviation.

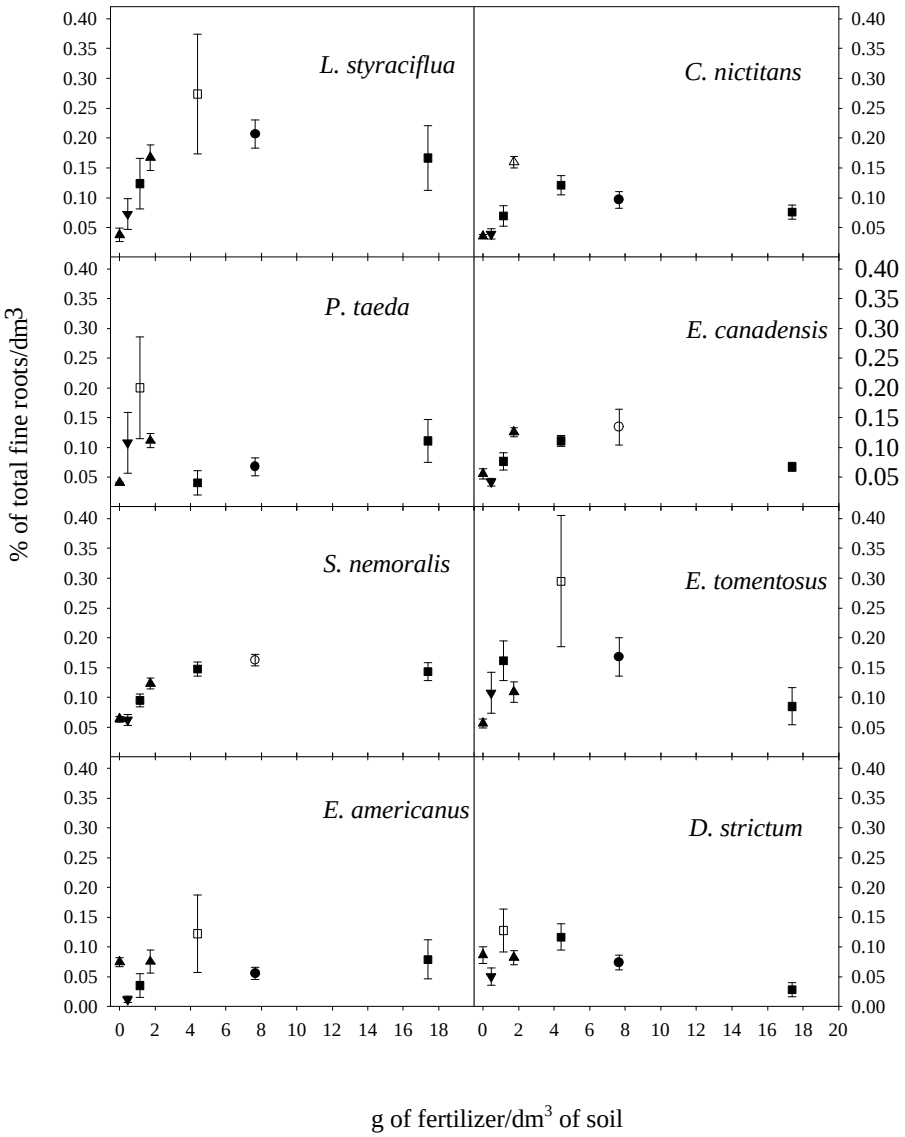

Figure 4. Density of roots in a patch plotted versus density of fertilizer in a patch. Symbols represent densities calculated from different treatments: homogeneous (inverted triangle), quarterly (upright triangle), plugs equal (circle), and plugs unequal (square). Maximum rooting density is shown as an open symbol.

Comparisons of H vs Q, PE vs PU, and H vs Q vs PE vs PU revealed no significant differences in biomass within any species ($p>0.05$). However, when the data were grouped together to consider very coarse nutrient heterogeneity (H and Q treatments) versus finer scale heterogeneity (PE and PU treatments) significant species, treatment and species x treatment effects were detected (Table 8). Four species had significantly more biomass in the finer scale treatment ($p<0.05$; Fig. 5). A sensitivity index was calculated for each species by dividing the difference between the average biomass of the plants from the coarse treatments and the biomass of the plants from the fine treatments by the fine treatment biomass. Sensitivity scores ranged from 0.54 to -0.19, with the greater numbers representing larger positive response to increased heterogeneity (Table 9). The species with negative scores had a lower average biomass when exposed to finer scale heterogeneity.

Scale and precision were not related as hypothesized. When all traits of species were compared, the only strong correlations ($r>0.50$) detected were between different measures of scale (Table 4). Correlations which excluded woody species revealed other strong relationships; for example, a positive relationship between one measure of scale (fine root length) and precision and a negative relationship between scale (both density and root length) and sensitivity (Table 5). There is also a slightly negative relationship between precision and sensitivity if woody species are excluded from the analysis. The strongest correlations between each successfully measured type of plasticity (scale, precision, and sensitivity) are plotted in Figure 6.

Table 8. ANOVA of the biomass of plants in coarse (H&Q) and fine (PE&PU) heterogeneity treatments.

Source	d.f.	MS	*P*
Species (A)	8	253	0.0001
Treatment (B)	1	104	0.0001
AB	8	25	0.0006
Error	308	7	

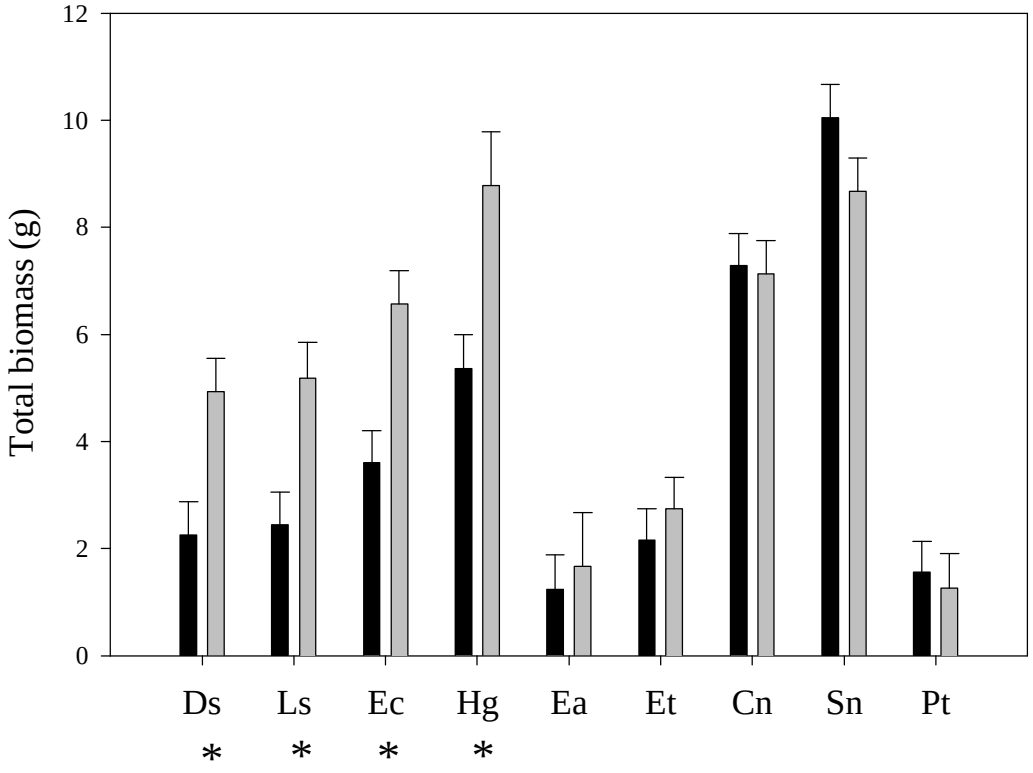

Figure 5. Total plant biomass in pots with fine scale (PE & PU) versus coarse scale (H & Q) heterogeneity (least-squares mean ± s.e.m.). Results were similar if PE & PU were compared to Q alone. * Significant treatment differences ($p<0.05$). Species symbols are as in Table 2.

Table 9. Species sensitivity scores. Score is a comparison of biomass for plants which grew in fine versus coarse heterogeneity regimes. A larger score is a positive response to a finer scale of heterogeneity. See text for description of how the score was calculated.

Species	Sensitivity Scores
D. strictum	0.54
L. styraciflua	0.53
E. canadensis	0.45
H. gentianoides	0.39
E. americanus	0.26
E. tomentosus	0.21
C. nictitans	-0.02
S. nemoralis	-0.16
P. taeda	-0.23

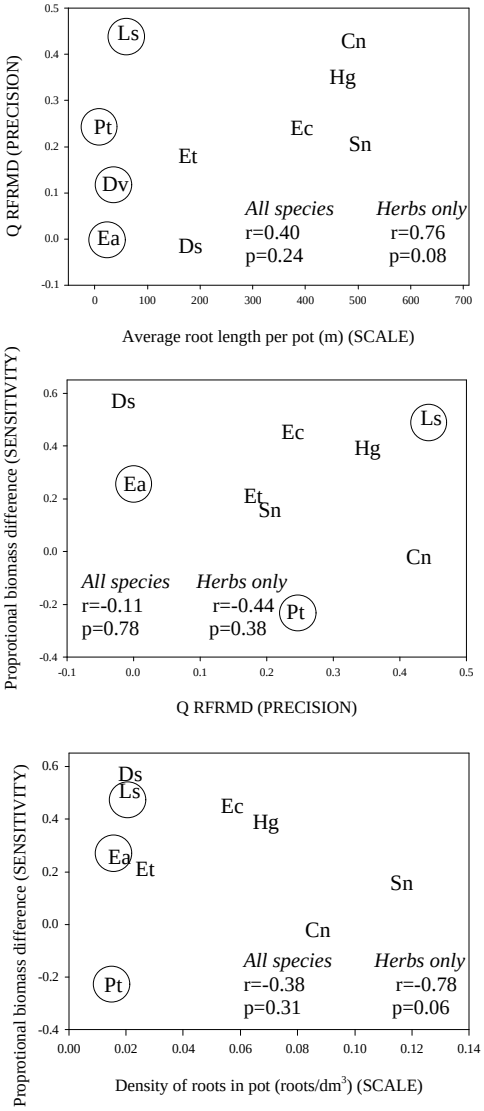

Figure 6. Relationships between scale, precision, and sensitivity. Scale chosen for plots had greatest correlation with other factor. Correlation coefficients are Pearson's. Woody species are denoted by circles. Symbols are as in Table 2.

Chapter 4: Discussion

The ten plant species tested in this study exhibited a wide range of morphological root plasticity and a large degree of variation in expression of growth benefits obtained at different levels of heterogeneity. These findings and those of others clearly show that plant root responses to nutrient heterogeneity in soils are complex (Crick & Grime 1977; Hutchings 1988; Jackson & Caldwell 1989; Campbell et al. 1991; Gleeson & Fry 1997; Mou et al. 1997).

I found significant differences in the scale, precision, and sensitivity of the species tested (Figs 2 & 5, Tables 3 & 5). Previous studies have reported differences for scale and precision, although techniques used to measure these characteristics are not always the same. In Campbell et al. (1991), scale for eight species was equated to biomass of the plants growing in a competitive environment. In my study, plants were grown in isolation and thus I only indirectly assessed competitive ability if one assumes that larger plants are more likely to be strong competitors. Campbell et al. (1991) also tested the precision of the same eight species and observed increases in root allocation to fertile patches in a range of 65% to 95% of total new growth. Their measurement of precision also differed in key ways from the current: nutrients were applied for two weeks only, and they were applied to two quarters of the pot. Further, plants were harvested at the same time, regardless of what percent of the pots were filled by the plants. Their measurements of precision may have been confounded by the different rates at which the plants grew. In a study more similar to mine, Mou et al. (1997) measured the relative fine root mass for *L. styraciflua* and *P. taeda* using the same homogenous and quarterly treatments I used, but with more fertilizer. They found RFRMD values for a quarterly fertilized pot that were similar to the values found in my study: around 0.50 for *L. styraciflua* and 0.25 for *P. taeda* versus 0.44 and 0.24, respectively in my study.

To my knowledge, no other study has clearly tested the response of multiple species to changing degrees of heterogeneity. However, the effects of spatial scale of nutrient heterogeneity on total growth were measured for *Glechoma hederacea*, a clonal herb, and this single species was able to successfully forage in large patches (25 cm x 50 cm) but responded to soils with small patches (12.5 cm x 12.5 cm, and smaller) as if they were homogeneously poor (Wijesinghe & Hutchings 1997). The surface area of the patch size when the plant could no longer detect nutrients is smaller than the size of the quarterly patch in my study.

I was unable to detect differences in discrimination among species. Discrimination responses may not have been discovered because the highest fertility level was too high, creating a situation which inhibited root proliferation. Most species in this experiment reached a peak rooting density at an intermediate fertilizer density after which proliferation dropped off as fertilizer density continued to increase (Fig. 4). These findings suggest that roots do indeed discriminate among patches of varying richness and that there is and optimum fertility level for stimulating root proliferation.

My data do not support the hypothesis that scale and precision are negatively correlated. When all species were compared, no measure of scale was negatively correlated with precision (Table 4). Furthermore, when just herbaceous plants were compared, relatively strong, positive relationships between scale and precision were detected (Table 4, Fig. 5). These correlations all lack power because they compare a limited number of species (n=10 overall, n=6 herbs), nonetheless they are interesting considering that Campbell et al. (1991) reported a negative relationship between scale and precision. The contrast in findings between my experiment and that of Campbell et al. (1991) suggests that relationships between root foraging traits may not be general across plant communities, or that the difference in methods used to measure scale and precision influence results dramatically. Additional studies are needed to resolve these issues.

The obvious advantage associated with the ability to proliferate roots in a nutrient-rich patch would be increased surface area for absorption in fertile soil. Grime (1977) predicted that plants which exhibit higher precision will therefore have a competitive advantage in heterogeneous environments. Sensitivity is a measure of whether or not a plant grows larger or faster as nutrient heterogeneity increases. As such, it may be an indicator of whether or not plant competitive ability (for space and presumably resources) would increase with as heterogeneity increases. With this in mind, and following Grime's prediction, I expected to find a positive relationship between sensitivity and precision, but no such effect was detected at the fertility levels of this experiment (Table 4, Fig. 6). The species with the highest and lowest precision rankings (*L. styraciflua* and *D. strictum*, respectively) were the two most sensitive species. However, *C. nictitans* and *P. taeda*, two other species for which homogeneous and quarterly RFRMD values were significantly different, had the two lowest sensitivity values, and furthermore the *P. taeda* value was negative. Fransen, de Kroon & Berendse (in press) found that nitrogen acquisition by plants is sometimes enhanced in heterogeneous environments, but they concluded that the enhancement was not related to root proliferation. These findings call into question the benefit that species obtain from the investment of carbon to proliferate roots in nutrient rich patches. In addition, it suggests that other mechanisms result in high sensitivity to nutrient heterogeneity.

One mechanism which may result in the ability to gain benefits from nutrient patches without increased root proliferation is plasticity in root uptake kinetics. Jackson, Manwaring, & Caldwell (1990) found that roots that were growing in nutrient patches increased their phosphate uptake rates up to 82% more than the uptake rates of roots growing outside patches for three plant species. In addition, Caldwell (1994) reported evidence that some plants are able to increase phosphate uptake from enriched patches without significantly increasing rooting density in patches.

Plasticity in root demography (births and deaths) is another possible explanation for increased sensitivity where there is no evidence of increased root biomass in patches. The effect of increased nutrient supply on root demography may depend largely on the nature of the nutrient addition: whether it is a homogenous or heterogeneous supply (Eissenstat

& Yanai 1997). Therefore, studies of root demographic response to nutrient heterogeneity are of interest. A field and a greenhouse study both provide evidence that some plants respond to nutrient patches with demographic plasticity (Gross, Peters & Pregitzer 1993; Pregitzer, Hendrick, & Fogel 1993), although the responses reported are not uniform. The field study reports an overall community response of increased root longevity in enriched patches compared to roots in control patches (Gross et al. 1993). However, the greenhouse study of four herbaceous species found a decreased life-span for the roots growing in enriched patches species (Pregitzer et al. 1993). Together, these suggest that plasticity in root demography is also a complex response, and by measuring only total root biomass in nutrient patches we are missing an important plastic response manifested by increased or decreased births and deaths of fine roots.

Although strong correlation between precision and sensitivity were not observed, a strong negative correlation between scale and sensitivity for herbaceous plants was detected (Table 4, Fig. 6). Herbaceous plants with high scale were less able to gain benefits from nutrient patches in soils. Perhaps for plants which exhibit high scale the key to success is to dominate the soil space as opposed to the ability to make use of the patches within the soil matrix.

In as much as these species also represent a successional sequence it appears that there is no relationship between successional status and sensitivity or precision (Table 10). The two species with the highest precision represent both an early successional herb and a tree species which is often abundant in a late successional forest. This comparison is confounded, of course, by the fact that for the species used in this study, life form and successional status co-vary.

Although they ranged widely in precision, as a group, woody plants exhibited the lowest scale. Thus, life form may be a fair predictor of a root system's scale, but not precision. For woody plants which have a lower growth rate compared to many herbs, it is likely that a longer experiment and larger pots would reveal greater variability in scale.

My data provide strong evidence that current theories about foraging behavior and trade-offs among certain traits need more testing and perhaps some rethinking. I believe that understanding the ability of roots to respond to nutrient patches will still prove helpful in making predictions about competitive interactions between individual species; however, it may be difficult to group species according to their root foraging abilities due to an apparent lack of correlations between root foraging traits and plant groups (herbs, woody species; early and late successional species). Further, more work needs to be done before we are able to suggest what traits lead to increased fitness in heterogeneous environments. In this study I assessed morphological root system responses only, and noted no clear pattern between them and growth benefits as heterogeneity increased. Perhaps if studies examine demographic and physiological plasticity in addition to root system morphology, clearer patterns between plant response to heterogeneity and fitness benefits will emerge.

Table 10. Rank correlations of foraging traits with successional status. (n=10 species, p-values given after correlation coefficients.) Each species was given a successional ranking (increases with year of dominance) and a ranking for each trait. The species with the highest value for a trait was ranked 1.

TRAIT	r (*P*-value)
DENSITY	0.58 (0.07)
SRL	0.41 (0.24)
FINE ROOT LENGTH	0.75 (0.01)
PRECISION	0.33 (0.34)
SENSITIVITY	0.15 (0.69)

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Appendix A.

Column headings for the appendices containing raw data from study:

CODE	TRT	MEANING	UNITS
LM	all	leaf mass*	grams
LAI	all	leaf area index	centimeters^2
#L	all	number of leaves	
SM	all	stem mass	grams
SL	all	stem length	centimeters
#B	all	number of branches	
PLUG	H	mass of one plug removed from a pot in the homogeneous treatment	grams
QUAF	H	mass of fine roots (<1 mm diameter) from a randomly selected quarter (quarter A)	grams
QUAC	H	mass of coarse roots (>1 mm diameter) from quarter A	grams
QUBF	H	mass of fine roots removed from the quarter opposite of QUA	grams
QUBC	H	mass of coarse roots removed from the quarter opposite of QUA	grams
RESTF	H	mass of roots that were not included in the plug, QUA or QUB.	grams
RESTC	H	mass of coarse roots that were not included in the plug, QUA or QUB.	grams
TAP	all	mass of the tap root	grams
FF	Q	mass of fine roots located in the fertilized quarter	grams
FC	Q	mass of coarse roots located in the fertilized quarter	grams
BAF	Q	mass of fine roots located in a quarter directly next to the fertilized quarter (buffer quarter A)	grams
BAC	Q	mass of coarse roots in buffer quarter	grams
BBF	Q	mass of fine roots in buffer quarter B	grams
BBC	Q	mass of coarse roots in buffer quarter B	grams
OF	Q	mass of fine roots in the quarter opposite the	grams
OC	Q	mass of coarse roots in the quarter opposite the fertilized quarter	grams
PF	PE & PU	mass of all fine roots in the pot (except those removed in plugs)	grams
PC	PE & PU	mass of all coarse roots in the pot (except those removed in plugs)	grams
A,B,C	PE	mass of roots removed from three plugs which had the same amount of fertilizer	grams
0.3	PU	mass of roots removed from plug which had 0.3 g	grams

		of fertilizer	
1.15	PU	mass of roots removed from plug which had 1.15 g of fertilizer	grams
4.55	PU	mass of roots removed from plug which had 4.55 g of fertilizer	grams

* all masses recorded are dry masses (plant material dried to 60° C)

Appendix B.

Raw data for *Chamaecrista nictitans*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
1.56	395	208	0.72	223	35	0.001	0.059	0.000	0.091	0.000	0.288	0.000	0.000
4.87	1235	408	2.85	501	71	0.027	0.691	0.182	0.211	0.000	0.623	0.241	0.000
4.81	1220	239	2.13	361	32	0.016	0.191	0.000	0.442	0.000	0.491	0.306	0.000
4.57	1158	323	2.31	516	48	0.010	0.205	0.000	0.671	0.162	0.557	0.021	0.000
3.80	963	496	3.53	724	68	0.018	0.489	0.000	0.100	0.000	0.327	0.053	0.000
4.70	1190	256	2.22	329	26	0.000	0.431	0.000	0.547	0.292	0.607	0.000	0.000
4.11	1042	318	2.52	468	40	0.026	0.278	0.000	0.312	0.144	0.929	0.103	0.000
4.64	1175	367	2.46	591	54	0.007	0.378	0.000	0.286	0.000	0.649	0.000	0.000
3.24	821	295	1.55	387	47	0.017	0.296	0.000	0.214	0.000	0.584	0.151	0.000
2.31	585	228	1.24	337	39	0.006	0.390	0.000	0.092	0.000	0.439	0.097	0.000

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
0.63	160	65	0.272	82	10	0.081	0.000	0.020	0.000	0.021	0.000	0.026	0.000	0.000
6.52	1653	447	3.052	751	79	1.319	0.239	0.213	0.000	0.101	0.000	0.128	0.000	0.000
6.21	1575	634	3.649	1011	93	0.959	0.323	0.147	0.000	0.148	0.000	0.113	0.000	0.000
4.87	1233	268	1.889	365	42	0.421	0.231	0.116	0.000	0.237	0.000	0.136	0.000	0.000
1.64	417	116	0.587	139	23	0.220	0.082	0.078	0.000	0.033	0.000	0.048	0.000	0.000
3.98	1007	341	1.882	457	60	0.570	0.000	0.169	0.129	0.215	0.020	0.105	0.000	0.000
3.24	822	266	1.674	410	43	0.485	0.073	0.220	0.000	0.107	0.000	0.085	0.000	0.000
3.41	865	296	1.714	419	44	0.332	0.207	0.190	0.000	0.092	0.000	0.115	0.000	0.000
4.34	1101	145	2.324	410	30	0.619	0.180	0.502	0.000	0.175	0.000	0.211	0.000	0.000
5.07	1284	366	3.259	682	61	0.773	0.066	0.188	0.000	0.282	0.068	0.191	0.000	0.000

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
3.21	812	320	1.38	398	47	0.743	0.271	0.023	0.011	0.010	0.000
5.96	1510	498	3.29	628	68	1.109	0.092	0.048	0.042	0.042	0.000
2.76	701	306	1.1	325	39	0.719	0.000	0.013	0.019	0.008	0.000
5.14	1302	509	2.63	681	68	1.013	0.000	0.078	0.040	0.042	0.000
8.08	2047	475	4.71	905	85	1.548	0.320	0.063	0.052	0.062	0.000
4.46	1130	354	2.69	379	34	0.957	0.136	0.014	0.012	0.015	0.000
3.42	868	284	1.99	492	50	0.891	0.153	0.018	0.018	0.010	0.000
4.20	1065	353	2.65	544	50	1.047	0.095	0.011	0.037	0.042	0.000
1.32	334	138	0.62	170	21	0.245	0.028	0.007	0.002	0.007	0.000
5.00	1267	477	2.56	607	70	1.515	0.143	.	0.041	0.065	0.000

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
1.05	266	119	0.54	135	21	0.184	0.012	0.006	0.004	0.003	0.000
3.38	857	383	1.82	404	47	0.759	0.000	0.031	0.031	0.010	0.000
2.21	560	268	1.06	337	40	0.536	0.116	0.007	0.019	0.012	0.000
7.28	1846	535	3.98	891	83	1.390	0.318	0.017	0.041	0.065	0.000
3.44	872	288	1.6	536	56	0.729	0.109	0.008	0.015	0.015	0.000
3.89	987	223	1.6	309	25	0.970	0.163	0.042	0.032	0.013	0.000
2.27	575	219	1.03	253	27	0.556	0.000	0.002	0.011	0.014	0.000
5.75	1456	508	3.17	668	67	1.142	0.079	0.010	0.044	0.023	0.000
4.19	1061	322	1.98	473	48	0.715	0.108	0.011	0.048	0.012	0.000

Appendix C.

Raw data for *Desmodium strictum*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
1.28	307	138	0.48	150	10	0.007	0.088	0.043	0.136	0.000	0.171	0.201	0.058
0.26	53	36	0.06	9	1	0.000	0.012	0.000	0.005	0.017	0.023	0.015	0.000
0.83	153	51	0.21	43	3	0.002	0.103	0.052	0.016	0.000	0.098	0.101	0.086
1.80	346	105	0.6	112	5	0.003	0.059	0.216	0.229	0.000	0.189	0.108	0.182
1.13	272	87	0.43	99	6	0.003	0.094	0.017	0.051	0.000	0.155	0.141	0.090
2.91	520	117	0.73	139	9	0.007	0.084	0.000	0.121	0.027	0.079	0.088	0.093
0.82	175	87	0.22	51	6	0.010	0.094	0.123	0.072	0.000	0.095	0.000	0.127
1.67	380	108	0.63	99	5	0.008	0.099	0.000	0.225	0.060	0.145	0.095	0.303
0.30	51	38	0.07	14	2	0.000	0.127	0.000	0.018	0.000	0.055	0.000	0.044

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
1.82	438	132	1.040	145	9	0.127	0.275	0.092	0.043	0.098	0.110	0.108	0.055	0.000
3.52	804	243	1.515	303	17	0.188	0.233	0.046	0.060	0.140	0.447	0.104	0.000	0.269
1.62	360	113	0.473	100	7	0.126	0.196	0.058	0.036	0.080	0.000	0.034	0.000	0.120
1.40	303	103	0.506	91	6	0.114	0.118	0.035	0.000	0.104	0.036	0.083	0.075	0.097
0.18	31	22	0.036	8	1	0.010	0.032	0.018	0.020	0.005	0.013	0.028	0.000	0.000
0.29	60	27	0.064	12	1	0.010	0.000	0.012	0.000	0.019	0.000	0.045	0.009	0.061
0.71	144	57	0.219	40	4	0.033	0.004	0.048	0.017	0.092	0.034	0.054	0.018	0.056
1.25	509	120	0.497	89	6	0.088	0.000	0.064	0.000	0.083	0.000	0.199	0.253	0.069
0.78	501	73	0.160	24	5	0.095	0.000	0.044	0.000	0.028	0.106	0.036	0.029	0.033

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
9.41	1515	393	2.97	394	19	0.971	1.138	0.038	0.013	0.044	0.273
1.56	327	104	0.38	76	11	0.268	0.177	0.021	0.003	0.009	0.032
3.42	900	192	1.26	195	14	0.418	0.496	0.008	0.014	0.006	0.149
1.40	289	115	0.39	84	12	0.152	0.145	0.000	0.004	0.001	0.070
0.40	76	42	0.07	17	4	0.038	0.030	0.000	0.001	0.000	0.013
2.80	593	153	1.1	173	9	0.590	0.446	0.023	0.008	0.015	0.137
4.80	934	289	1.91	284	13	0.718	0.497	0.009	0.008	0.007	0.306
1.72	408	133	0.53	84	13	0.253	0.294	0.008	0.002	0.004	0.090

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
3.64	751	216	1.12	187	9	0.478	1.634	0.010	0.002	0.009	0.334
3.62	687	207	0.8	158	9	0.665	0.271	0.011	0.018	0.003	0.233
1.62	339	141	0.59	103	12	0.327	0.226	0.012	0.002	0.001	0.197
3.54	175	180	1.23	173	7	0.812	0.837	0.010	0.048	0.012	0.176
3.75	892	180	1.3	213	9	0.458	0.638	0.007	0.008	0.015	0.201
4.30	886	288	1.33	173	18	0.878	0.355	0.015	0.024	0.004	0.194
1.35	229	93	0.31	72	8	0.215	0.075	0.014	0.010	0.000	0.049
1.66	313	99	0.6	79	7	0.285	0.115	0.008	0.015	0.001	0.220
0.95	215	81	0.29	45	6	0.243	0.146	0.027	0.003	0.000	0.096
2.58	430	114	0.71	96	5	0.376	0.284	0.010	0.018	0.002	0.079

Appendix D.

Raw data for *Diospyros virginiana* . Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
2.20	405	16	0.45	15	1	0.000	0.248	0.209	0.022	0.000	0.204	0.000	0.399
1.45	271	20	0.3	16	1	0.000	0.037	0.000	0.103	0.019	0.175	0.023	0.215
1.21	234	24	0.29	15	1	0.000	0.028	0.004	0.146	0.231	0.107	0.000	0.326
5.22	980	20	1.76	28	1	0.000	0.187	0.085	0.695	0.093	0.820	2.115	0.820
2.14	415	19	0.49	18	1	0.000	0.117	0.048	0.257	0.131	0.163	0.025	0.326
2.26	499	28	0.53	27	2	0.000	0.111	0.050	0.247	0.181	0.163	0.077	0.243
1.15	212	18	0.24	14	1	0.000	0.034	0.011	0.101	0.000	0.117	0.055	0.026
0.87	140	13	0.23	11	1	0.000	0.017	0.000	0.026	0.032	0.117	0.021	0.164
0.89	196	19	0.2	14	1	0.000	0.067	0.000	0.025	0.003	0.071	0.007	0.061
0.82	153	13	0.33	12	1	0.000	0.037	0.004	0.111	0.000	0.128	0.162	0.264

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
3.31	612	19	0.787	19	1	0.387	0.621	0.199	0.073	0.045	0.012	0.084	0.132	1.220
3.51	634	25	0.778	22	1	0.239	0.011	0.045	0.006	0.027	0.004	0.298	0.124	0.649
1.76	321	17	0.400	16	1	0.050	0.000	0.139	0.025	0.068	0.027	0.104	0.020	0.232
0.51	92	14	0.220	11	1	0.030	0.003	0.100	0.003	0.002	0.000	0.076	0.082	0.425
0.95	177	15	0.217	12	1	0.229	0.000	0.056	0.016	0.065	0.000	0.024	0.011	0.247
1.44	328	19	0.361	18	1	0.052	0.000	0.073	0.006	0.027	0.004	0.154	0.000	0.175
0.22	46	14	0.066	10	1	0.022	0.014	0.002	0.000	0.006	0.000	0.003	0.000	0.000
1.18	167	14	0.247	10	1	0.246	0.062	0.057	0.027	0.130	0.014	0.141	0.092	0.508
0.77	139	16	0.227	13	1	0.034	0.000	0.009	0.000	0.079	0.043	0.014	0.002	0.239

Appendix E.

Raw data for *Euonymus americanus*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
0.22	27	17	0.09	14	1	0.000	0.034	0.000	0.011	0.000	0.090	0.000	0.029
0.37	27	25	0.15	12	1	0.000	0.015	0.000	0.048	0.000	0.073	0.000	0.047
0.10	9	17	0.04	6	1	0.000	0.011	0.000	0.016	0.000	0.035	0.000	0.022
0.42	50	28	0.34	28	3	0.001	0.074	0.000	0.137	0.000	0.064	0.000	0.033
0.91	144	48	0.39	30	1	0.004	0.044	0.000	0.060	0.000	0.202	0.000	0.067
0.46	54	35	0.29	27	2	0.000	0.020	0.000	0.061	0.000	0.189	0.000	0.075
0.16	17	27	0.04	9	2	0.000	0.001	0.000	0.007	0.000	0.025	0.000	0.012
0.14	13	18	0.06	12	4	0.000	0.024	0.000	0.025	0.000	0.078	0.000	0.029
0.64	94	41	0.34	27	2	0.000	0.078	0.000	0.071	0.000	0.125	0.000	0.056
0.63	72	31	0.39	28	2	0.005	0.057	0.000	0.201	0.000	0.169	0.000	0.198
0.26	23	27	0.2	17	3	0.000	0.102	0.000	0.022	0.000	0.091	0.000	0.055
1.53	219	68	0.93	61	2	0.006	0.107	0.000	0.060	0.000	0.486	0.000	0.170

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
0.27	39	30	0.009	12	1	0.009	0.000	0.021	0.000	0.020	0.000	0.027	0.000	0.024
1.07	166	41	0.551	33	1	0.176	0.000	0.074	0.000	0.125	0.000	0.112	0.000	0.088
0.47	47	30	0.164	13	1	0.028	0.000	0.148	0.000	0.014	0.000	0.050	0.000	0.069
1.91	268	48	1.176	40	1	0.264	0.000	0.252	0.000	0.284	0.000	0.235	0.000	0.202
0.20	29	21	0.094	18	2	0.028	0.000	0.007	0.000	0.010	0.000	0.017	0.000	0.025

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
2.37	175	48	0.59	23	1	0.289	0.000	0.002	0.013	0.003	0.000
0.31	56	19	0.11	15	1	0.155	0.000	0.002	0.006	0.000	0.000
0.30	41	33	0.13	15	1	0.115	0.000	0.000	0.000	0.005	0.000
0.21	17	25	0.09	12	3	0.128	0.000	0.002	0.001	0.000	0.000

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
1.35	230	50	0.69	40	1	0.588	0.000	0.012	0.038	0.013	0.000
1.93	313	58	1.14	60	3	0.877	0.000	0.009	0.035	0.006	0.000
0.09	8	12	0.04	8	3	0.064	0.000	0.000	0.000	0.002	0.000

Appendix F.

Raw data for *Erigeron canadensis*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
0.56	94	.	0.1	1	1	0.003	0.161	0.085	0.055	0.000	0.119	0.000	0.000
1.17	259	.	0.3	11	5	0.001	0.101	0.000	0.186	0.000	0.244	0.043	0.000
2.31	395	.	0.39	9	1	0.006	0.251	0.127	0.187	0.057	0.260	0.083	0.000
4.97	896	.	2.93	163	10	0.026	0.477	0.029	0.349	0.000	0.635	0.193	0.521
2.81	552	.	0.45	4	1	0.010	0.155	0.000	0.351	0.117	0.436	0.267	0.000
2.52	394	.	0.31	6	3	0.018	0.371	0.000	0.442	0.053	0.325	0.112	0.107
1.06	237	.	0.13	1	1	0.004	0.221	0.014	0.080	0.000	0.203	0.000	0.119
0.97	123	.	0.13	2	1	0.009	0.142	0.000	0.078	0.000	0.229	0.000	0.078
1.60	310	.	0.17	4	2	0.006	0.174	0.000	0.274	0.000	0.310	0.000	0.265
2.99	699	.	0.47	34	7	0.013	0.306	0.000	0.208	0.000	0.443	0.070	0.320

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
1.60	250	.	0.175	1	1	0.321	0.026	0.174	0.000	0.057	0.000	0.112	0.000	0.224
3.04	620	.	0.344	6	4	0.512	0.070	0.192	0.069	0.182	0.034	0.186	0.000	0.057
2.68	491	.	0.592	32	6	0.427	0.048	0.127	0.077	0.128	0.000	0.081	0.000	0.000
2.38	392	.	0.359	2	2	0.358	0.000	0.150	0.000	0.225	0.000	0.219	0.000	0.077
1.02	190	.	0.194	1	1	0.182	0.023	0.050	0.000	0.204	0.000	0.069	0.000	0.079
1.21	297	.	0.232	3	2	0.139	0.011	0.061	0.000	0.055	0.000	0.136	0.000	0.048
2.94	558	.	0.313	2	2	0.536	0.201	0.371	0.000	0.176	0.000	0.156	0.000	0.000
3.23	585	.	0.321	7	5	0.364	0.077	0.211	0.078	0.194	0.021	0.148	0.000	0.148
1.67	356	.	0.353	40	9	0.279	0.000	0.083	0.000	0.086	0.053	0.053	0.000	0.315
2.76	560	.	0.295	3	3	0.287	0.072	0.135	0.000	0.121	0.000	0.320	0.082	0.077

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
5.86	1312	.	1.7	64	9	1.456	0.205	0.083	0.051	0.075	0.340
5.02	922	.	0.68	7	2	1.142	0.179	0.051	0.013	0.028	0.449
2.88	740	.	1.18	134	27	0.542	0.085	0.021	0.013	0.043	0.163
1.73	344	.	0.44	15	7	0.812	0.193	0.005	0.006	0.006	0.137
5.07	1230	.	1.31	36	7	0.992	0.150	0.061	0.022	0.036	0.352
3.37	530	.	0.5	3	1	0.812	0.193	0.016	0.009	0.012	0.228
6.94	1341	.	1.72	66	14	1.927	0.607	0.087	0.091	0.045	0.405
4.88	1035	.	0.74	7	3	1.339	0.277	0.043	0.060	0.023	0.116
3.18	617	.	0.87	92	20	0.258	0.103	0.032	0.049	0.013	0.089

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
5.01	1206	.	1.77	125	14	0.979	0.352	0.012	0.034	0.020	0.157
3.37	621	.	0.5	2	1	1.199	0.307	0.032	0.024	0.013	0.000
5.27	922	.	0.85	25	4	1.358	0.141	0.011	0.050	0.031	0.801
3.56	644	.	0.52	2	1	1.343	0.181	0.029	0.041	0.028	0.300
4.65	764	.	0.74	4	2	1.715	0.000	0.023	0.051	0.018	0.357
2.33	394	.	0.19	4	1	0.743	0.159	0.039	0.025	0.012	0.279
4.31	855	.	1.06	51	7	1.109	0.260	0.016	0.027	0.035	0.246
2.97	550	.	0.68	51	8	0.788	0.059	0.014	0.037	0.016	0.296
2.51	404	.	0.8	60	6	0.464	0.186	0.013	0.011	0.008	0.190

Appendix G.

Raw data for *Elephantopus tomentosus*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
1.34	292	15	0.09	1	1	0.010	0.080	0.025	0.048	0.000	0.078	0.141	0.000
3.41	729	15	0.23	4	1	0.025	0.117	0.131	0.377	0.043	0.204	0.094	0.000
0.90	192	12	0.08	1	1	0.000	0.090	0.023	0.011	0.000	0.065	0.027	0.000
0.29	51	4	0.02	1	1	0.012	0.002	0.000	0.084	0.000	0.048	0.000	0.000
2.04	379	15	0.14	1	1	0.005	0.260	0.110	0.206	0.000	0.201	0.000	0.000
0.27	47	4	0.02	1	1	0.000	0.043	0.000	0.038	0.038	0.018	0.000	0.000
3.74	824	31	0.27	2	1	0.023	0.136	0.058	0.236	0.005	0.269	0.000	0.000
2.05	398	13	0.07	1	1	0.002	0.124	0.000	0.085	0.060	0.045	0.040	0.000
2.40	639	24	0.21	3	1	0.004	0.159	0.000	0.033	0.007	0.167	0.022	0.000
2.80	497	20	0.21	4	1	0.022	0.058	0.069	0.077	0.017	0.212	0.216	0.000

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
3.20	652	20	0.337	4	1	0.189	0.049	0.190	0.042	0.068	0.032	0.193	0.122	0.000
1.60	291	11	0.074	1	1	0.294	0.026	0.125	0.000	0.091	0.046	0.030	0.028	0.000
0.43	67	11	0.062	1	1	0.011	0.000	0.015	0.000	0.023	0.000	0.014	0.000	0.000
1.49	334	13	0.081	1	1	0.092	0.000	0.026	0.044	0.085	0.035	0.049	0.034	0.000
0.98	157	12	0.077	1	1	0.034	0.000	0.131	0.000	0.092	0.000	0.021	0.000	0.000
1.27	258	12	0.138	1	1	0.147	0.000	0.042	0.008	0.020	0.021	0.048	0.049	0.000
1.82	385	17	0.077	2	1	0.254	0.000	0.064	0.044	0.046	0.000	0.060	0.038	0.000
0.75	101	7	0.089	1	1	0.039	0.000	0.042	0.000	0.098	0.000	0.059	0.000	0.000
0.37	53	4	0.041	1	1	0.091	0.030	0.015	0.000	0.017	0.053	0.049	0.000	0.000
1.09	267	11	0.090	1	1	0.108	0.033	0.034	0.021	0.067	0.000	0.065	0.022	0.000

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
2.86	507	20	0.21	2	1	0.180	0.125	0.017	0.009	0.017	0.000
2.04	384	13	0.15	2	1	0.128	0.105	0.019	0.000	0.001	0.000
2.18	390	27	0.11	1	1	0.334	0.000	0.002	0.009	0.005	0.000
3.32	385	18	0.19	1	1	0.252	0.082	0.010	0.022	0.005	0.000
2.60	663	18	0.15	2	1	0.264	0.089	0.011	0.013	0.004	0.000
3.31	691	21	0.15	1	1	0.359	0.185	0.028	0.031	0.017	0.000
2.56	549	20	0.13	1	1	0.228	0.096	0.006	0.016	0.012	0.000
0.32	57	6	0.01	1	1	0.071	0.000	0.000	0.000	0.000	0.000
1.54	283	17	0.14	1	1	0.219	0.066	0.001	0.008	0.019	0.000
3.18	678	21	0.17	1	1	0.228	0.207	0.015	0.019	0.062	0.000

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
1.90	339	11	0.15	2	1	0.291	0.084	0.006	0.005	0.004	0.000
1.10	192	15	0.04	1	1	0.131	0.083	0.005	0.005	0.000	0.000
2.21	425	17	0.19	2	1	0.222	0.069	0.008	0.009	0.002	0.000
4.25	1015	24	0.32	5	1	0.601	0.110	0.039	0.037	0.018	0.000
2.21	360	17	0.13	1	1	0.152	0.167	0.020	0.035	0.017	0.000
2.76	593	18	0.2	3	1	0.344	0.045	0.009	0.158	0.012	0.000
1.85	419	14	0.13	2	1	0.224	0.051	0.013	0.021	0.001	0.000
2.21	411	14	0.1	1	1	0.340	0.073	0.008	0.022	0.005	0.000
1.25	220	10	0.09	1	1	0.196	0.131	0.003	0.006	0.013	0.000
0.84	117	7	0.07	1	1	0.140	0.000	0.014	0.001	0.000	0.000

Appendix H.

Raw data for *Hypericum gentianoides*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
9.74	.	.	.	.	.	0.000	0.400	0.000	0.582	0.172	0.941	0.031	0.000
4.72	.	.	.	.	.	0.000	0.212	0.000	0.203	0.041	0.346	0.000	0.000
2.61	.	.	.	.	.	0.000	0.110	0.031	0.122	0.000	0.223	0.000	0.000
0.92	.	.	.	.	.	0.000	0.626	0.351	0.527	0.000	0.813	0.056	0.000
5.09	.	.	.	.	.	0.000	0.165	0.072	0.466	0.069	0.498	0.000	0.000
3.99	.	.	.	.	.	0.000	0.228	0.000	0.412	0.156	0.456	0.000	0.000
9.92	.	.	.	.	.	0.000	0.057	0.000	0.046	0.000	0.097	0.000	0.000
3.67	.	.	.	.	.	0.000	0.382	0.000	0.148	0.000	0.349	0.000	0.000
5.37	.	.	.	.	.	0.000	0.218	0.000	0.502	0.228	0.306	0.000	0.000
0.24	.	.	.	.	.	0.000	0.011	0.000	0.007	0.000	0.033	0.000	0.000

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
0.17	.	.	.	.	.	0.017	0.000	0.002	0.000	0.011	0.000	0.004	0.000	0.000
4.35	.	.	.	.	.	0.643	0.177	0.203	0.000	0.125	0.000	0.085	0.000	0.000
5.90	.	.	.	.	.	0.924	0.135	0.183	0.000	0.189	0.000	0.179	0.000	0.000
5.19	.	.	.	.	.	0.266	0.000	0.274	0.157	0.221	0.000	0.280	0.038	0.000
3.76	.	.	.	.	.	0.452	0.277	0.145	0.000	0.063	0.000	0.097	0.000	0.000
4.47	.	.	.	.	.	0.346	0.000	0.122	0.180	0.140	0.000	0.115	0.000	0.000
4.01	.	.	.	.	.	0.247	0.030	0.093	0.000	0.065	0.000	0.109	0.000	0.000

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
9.11	.	.	.	.	.	1.818	0.000	0.031	0.049	0.017	0.000
5.72	.	.	.	.	.	0.786	0.134	0.016	0.027	0.013	0.000
5.80	.	.	.	.	.	0.571	0.068	0.028	0.017	0.033	0.000
10.56	.	.	.	.	.	1.874	0.250	0.039	0.035	0.058	0.000
7.74	.	.	.	.	.	0.953	0.115	0.027	0.028	0.041	0.000
4.86	.	.	.	.	.	0.637	0.000	0.002	0.014	0.012	0.000
8.29	.	.	.	.	.	1.265	0.311	0.028	0.038	0.033	0.000

Appendix I.

Raw data for *Liquidambar styraciflua*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
1.70	451	24	0.81	34	4	0.010	0.052	0.012	0.059	0.240	0.230	0.194	0.129
2.32	564	33	1.04	46	7	0.009	0.006	0.000	0.228	0.168	0.157	0.091	0.298
1.08	202	13	0.3	13	1	0.007	0.009	0.036	0.155	0.000	0.100	0.175	0.079
1.49	384	25	0.51	28	4	0.003	0.151	0.000	0.040	0.000	0.115	0.087	0.216
4.20	937	55	1.6	74	7	0.004	0.254	0.038	0.216	0.085	0.243	0.144	0.621
0.30	53	7	0.23	9	1	0.000	0.071	0.000	0.030	0.052	0.048	0.155	0.000
3.41	827	59	1.6	101	10	0.010	0.143	0.175	0.067	0.077	0.099	0.000	0.355
0.93	224	16	0.22	12	1	0.016	0.062	0.042	0.027	0.035	0.128	0.000	0.087
0.43	42	9	0.08	6	1	0.000	0.019	0.000	0.002	0.000	0.039	0.038	0.000
0.43	98	11	0.16	9	1	0.000	0.001	0.000	0.089	0.053	0.051	0.000	0.000

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
0.11	23	3	0.061	6	1	0.055	0.000	0.000	0.000	0.002	0.000	0.001	0.000	0.000
0.69	118	14	0.179	10	1	0.127	0.011	0.002	0.000	0.036	0.000	0.003	0.000	0.022
0.13	33	9	0.016	4	1	0.004	0.025	0.002	0.000	0.006	0.000	0.005	0.000	0.000
0.10	18	4	0.055	6	1	0.022	0.000	0.002	0.000	0.001	0.000	0.002	0.000	0.000
0.62	129	12	0.149	9	1	0.066	0.080	0.015	0.000	0.026	0.000	0.009	0.000	0.000
2.21	406	28	0.498	16	1	0.162	0.057	0.088	0.089	0.046	0.028	0.012	0.000	0.216
2.48	501	51	1.051	54	6	0.228	0.103	0.037	0.054	0.181	0.000	0.065	0.018	0.220
3.31	678	46	1.087	48	6	0.178	0.058	0.036	0.000	0.043	0.025	0.082	0.157	0.404
0.81	188	11	0.224	12	1	0.051	0.048	0.015	0.000	0.033	0.000	0.039	0.000	0.065

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
3.57	891	55	1.4	56	8	0.379	0.274	0.085	0.003	0.003	0.488
6.90	1791	92	2.61	118	13	0.705	0.582	0.041	0.069	0.023	0.935
3.51	740	53	0.94	27	4	0.636	0.321	0.015	0.034	0.006	0.315
1.93	407	32	0.57	18	3	0.300	0.183	0.013	0.016	0.007	0.245
3.06	525	42	1.15	58	7	0.331	0.224	0.006	0.081	0.011	0.254
1.38	270	43	0.41	12	1	0.208	0.242	0.013	0.010	0.009	0.000
2.30	465	44	0.69	19	2	0.218	0.090	0.006	0.002	0.045	0.250
5.35	1293	67	2.67	103	10	0.648	0.478	0.053	0.060	0.055	1.655

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
3.48	691	46	1.13	31	4	0.611	0.316	0.019	0.043	0.016	0.411
2.04	497	36	1.08	62	8	0.278	0.187	0.013	0.015	0.040	0.209
2.06	457	31	0.78	21	1	0.515	0.279	0.008	0.007	0.056	0.488
1.80	476	28	0.93	37	3	0.232	0.190	0.008	0.019	0.009	0.251
1.74	355	32	0.7	16	1	0.239	0.265	0.000	0.080	0.001	0.000
2.65	568	57	0.81	54	8	0.354	0.203	0.043	0.011	0.006	0.310
1.98	359	38	0.57	17	1	0.313	0.083	0.012	0.028	0.010	0.202
3.26	641	37	1.32	48	6	0.471	0.401	0.006	0.016	0.017	0.253

Appendix J.

Raw data for *Pinus taeda*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
0.37	18	.	0.1	13	2	0.002	0.007	0.000	0.008	0.000	0.061	0.000	0.072
0.25	13	.	0.07	11	3	0.000	0.006	0.000	0.001	0.000	0.062	0.000	0.034
1.99	115	.	0.42	41	5	0.002	0.093	0.000	0.088	0.000	0.008	0.000	0.182
1.12	65	.	0.3	33	4	0.000	0.098	0.000	0.088	0.000	0.140	0.000	0.095
1.57	84	.	0.56	56	6	0.017	0.177	0.000	0.049	0.000	0.230	0.000	0.085
1.11	59	.	0.4	41	6	0.014	0.040	0.000	0.053	0.000	0.158	0.000	0.069
0.27	13	.	0.07	8	1	0.010	0.027	0.000	0.011	0.000	0.017	0.000	0.027
1.30	73	.	0.4	43	5	0.000	0.087	0.000	0.081	0.000	0.086	0.000	0.088
1.07	59	.	0.13	32	6	0.001	0.059	0.000	0.118	0.000	0.092	0.000	0.090
0.86	45	.	0.25	23	3	0.010	0.003	0.000	0.123	0.000	0.163	0.000	0.000
0.15	8	.	0.04	9	1	0.000	0.015	0.000	0.041	0.000	0.008	0.000	0.015

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
1.19	69	.	0.405	28	3	0.080	0.000	0.053	0.000	0.110	0.000	0.027	0.000	0.064
0.62	33	.	0.139	17	5	0.073	0.000	0.007	0.000	0.049	0.000	0.002	0.000	0.032
1.61	90	.	0.368	31	5	0.139	0.000	0.101	0.000	0.085	0.000	0.065	0.000	0.091
1.16	64	.	0.294	28	5	0.074	0.000	0.052	0.000	0.041	0.000	0.018	0.000	0.139
1.71	101	.	0.370	33	4	0.172	0.000	0.299	0.000	0.045	0.000	0.017	0.000	0.084
1.92	107	.	0.573	45	6	0.293	0.000	0.077	0.000	0.111	0.000	0.073	0.000	0.070
0.40	21	.	0.114	16	3	0.017	0.000	0.003	0.000	0.049	0.000	0.038	0.000	0.036
0.54	30	.	0.122	15	4	0.083	0.000	0.030	0.000	0.016	0.000	0.040	0.000	0.036
0.79	42	.	0.307	21	2	0.072	0.000	0.081	0.000	0.055	0.000	0.064	0.000	0.057

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
0.45	25	.	0.12	16	3	0.144	0.000	0.000	0.001	0.009	0.038
0.81	43	.	0.25	30	6	0.155	0.000	0.010	0.007	0.000	0.053
0.52	25	.	0.2	21	3	0.175	0.000	0.004	0.000	0.000	0.057
0.76	42	.	0.21	20	3	0.319	0.000	0.009	0.008	0.005	0.000
1.38	77	.	0.46	40	5	0.310	0.000	0.001	0.000	0.005	0.121
0.71	38	.	0.2	18	3	0.281	0.000	0.014	0.007	0.001	0.062
0.35	18	.	0.1	10	3	.	0.000	0.001	0.061	0.000	0.000
1.30	74	.	0.38	27	4	0.428	0.000	0.006	0.000	0.013	0.000
0.32	47	.	0.1	12	3	0.131	0.000	0.000	0.000	0.014	0.027
0.05	2	.	0.02	5	1	0.052	0.000	0.000	0.000	0.000	0.000

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
0.68	36	.	0.25	24	5	0.260	0.000	0.013	0.001	0.005	0.065
0.41	25	.	0.11	9	1	0.112	0.000	0.004	0.000	0.009	0.050
1.41	80	.	0.29	23	4	0.351	0.000	0.006	0.004	0.005	0.076
1.04	59	.	0.28	31	5	0.220	0.000	0.011	0.003	0.017	0.069
1.11	62	.	0.3	29	5	0.503	0.000	0.006	0.025	0.018	0.098
1.04	57	.	0.26	26	5	0.271	0.000	0.002	0.004	0.002	0.076
0.58	29	.	0.17	17	6	0.119	0.000	0.030	0.000	0.000	0.058
0.24	12	.	0.07	10	2	0.073	0.000	0.005	0.000	0.002	0.027

Appendix K.

Raw data for *Solidago nemoralis*. Column headings are listed in Appendix A.

Homogeneous treatment

LM	LAI	#L	SM	SL	#B	PLUG	QUAF	QUAC	QUBF	QUBC	RESTF	RESTC	TAP
0.43	51	21	0.02	1	1	0.001	0.110	0.011	0.022	0.000	0.022	0.000	0.000
0.92	109	29	0.03	2	4	0.004	0.134	0.043	0.045	0.000	0.021	0.000	0.000
4.73	546	151	0.16	16	14	0.005	0.225	0.095	0.266	0.000	0.236	0.007	0.000
12.09	1606	304	1.25	84	13	0.065	0.730	0.000	1.158	0.262	1.037	0.000	0.000
8.22	1048	323	0.4	93	14	0.031	0.423	0.000	0.536	0.000	1.040	0.000	0.000
10.57	1480	274	0.51	16	13	0.039	0.469	0.113	0.393	0.047	0.672	0.000	0.000
8.66	1162	153	0.64	26	16	0.067	0.870	0.000	0.614	0.211	1.529	0.120	0.000
10.55	1441	161	0.48	16	11	0.029	0.551	0.000	0.548	0.006	0.954	0.256	0.000

Quarterly treatment

LM	LAI	#L	SM	SL	#B	FF	FC	BAF	BAC	BBF	BBC	OF	OC	TAP
2.70	446	157	0.096	8	8	0.116	0.000	0.017	0.000	0.025	0.000	0.026	0.000	0.000
10.00	1440	274	1.342	112	18	0.710	0.000	0.609	0.242	0.380	0.000	0.336	0.029	0.000
6.84	897	192	0.280	17	15	0.412	0.000	0.118	0.000	0.256	0.000	0.266	0.000	0.000
7.50	.	172	0.283	14	12	0.246	0.000	0.127	0.084	0.122	0.000	0.231	0.077	0.000
4.39	632	154	0.198	5	4	0.349	0.128	0.106	0.000	0.118	0.000	0.147	0.000	0.000
11.00	1474	326	2.091	144	15	1.263	0.135	0.428	0.000	0.458	0.000	0.705	0.231	0.000
11.52	.	462	2.189	137	12	0.624	0.063	0.264	0.000	0.530	0.215	0.385	0.000	0.000
12.06	.	206	0.712	34	13	0.879	0.000	0.491	0.000	0.455	0.000	0.652	0.124	0.000
8.37	1230	244	0.808	43	8	0.742	0.040	0.144	0.047	0.293	0.000	0.223	0.120	0.000

Plugs equal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	A	B	C	TAP
10.39	1038	232	0.63	29	8	0.905	0.166	0.040	0.023	0.033	0.000
0.91	116	75	0.01	1	2	0.156	0.000	0.006	0.009	0.002	0.000
13.31	1545	284	0.38	18	12	1.629	0.465	0.098	0.051	0.106	0.000
9.93	1400	348	0.3	13	12	0.889	0.000	0.054	0.026	0.056	0.000
3.83	535	129	0.15	9	9	0.523	0.083	0.036	0.021	0.036	0.000
11.87	.	303	0.91	42	15	1.978	0.215	0.069	0.100	0.095	0.000
9.54	1261	308	0.63	17	14	1.708	0.121	0.088	0.056	0.077	0.000
8.40	1278	196	0.27	16	15	0.929	0.075	0.066	0.054	0.064	0.000
8.67	1329	203	0.69	43	11	1.172	0.101	0.061	0.066	0.062	0.000

Plugs unequal treatment

LM	LAI	#L	SM	SL	#B	PF	PC	0.300	1.150	4.550	TAP
7.14	1323	264	0.27	15	12	1.244	0.000	0.015	0.062	0.071	0.000
6.05	779	215	0.15	9	10	0.880	0.093	0.026	0.038	0.033	0.000
1.81	273	66	0.04	3	3	0.128	0.000	0.004	0.008	0.007	0.000
6.52	.	234	0.29	20	15	0.781	0.089	0.022	0.027	0.047	0.000
3.34	535	151	0.09	5	7	0.272	0.036	0.013	0.016	0.010	0.000
9.29	1366	187	0.41	22	15	0.867	0.159	0.027	0.031	0.029	0.000
1.47	122	86	0.05	3	6	0.411	0.000	0.010	0.011	0.012	0.000
9.31	1281	356	1.35	103	12	1.041	0.158	0.031	0.047	0.023	0.000
6.66	1000	163	0.42	22	16	0.921	0.204	0.019	0.032	0.046	0.000

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Master's Thesis: Resource Foraging in Ten Plant Species from the South Carolina Coastal Plain: Scale, Precision, Discrimination, and Sensitivity. Currently in progress.

An Investigation into the Feeding and Post-Feeding Diuresis of Male Corn Earworm Moths. Senior Honors Project, Mount Saint Mary's College, 1996.

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