

Correlations between soil nutrient availability and fine-root biomass at two spatial scales in forested wetlands with contrasting hydrological regimes

Matthew A. Neatrour, Robert H. Jones, and Stephen W. Golladay

Abstract: We investigated the relationship between soil nutrients and fine-root biomass at broad (among ecosystem types) and fine (within a 20 m × 20 m plot) spatial scales in forested wetlands of the southeastern United States. We selected three replicates each of high-fertility floodplain swamps, low-fertility depressional swamps, and intermediate-fertility river swamp sloughs and measured soil nutrient availability (NO₃-N, NH₄-N, and PO₄-P) and fine-root biomass. At one replicate of each wetland type, a dense network of sampling points was used to measure variability (variance and coefficient of variation) of soil nutrients and fine-root biomass. At the broad scale, fine-root biomass was lower in floodplain swamps than in either river swamp sloughs or depressional swamps. Also, multiple linear regression and Spearman's rank correlations indicated a negative relationship between soil nutrient availability and fine-root biomass. Fine-scale correlates between soil nutrient availability and fine-root biomass were generally weak. Fine-scale variability of NO₃-N and NH₄-N was greatest in the floodplain swamps, but nutrients were not spatially patchy at any of the sampled sites. We conclude that soil nutrient availability may control fine-root biomass at the broad scale, but it is unclear if the same is true at fine spatial scales.

Résumé : Les auteurs ont étudié la relation entre les nutriments du sol et la biomasse de racines fines à petite (entre les types d'écosystèmes) et grande (à l'intérieur de parcelles de 20 m × 20 m) échelles dans les terres humides boisées du sud-est des États-Unis. Pour chaque situation : marécages très fertiles situés dans la plaine inondable, marécages peu fertiles situés dans une dépression et marécages intermédiaires situés dans un faux chenal de rivière, ils ont sélectionné trois répétitions et mesuré la disponibilité des nutriments du sol (N-NO₃, N-NH₄ et P-PO₄) et la biomasse de racines fines. Ils ont eu recours à un réseau dense de points d'échantillonnage pour mesurer la variation (variance et coefficient de variation) des nutriments du sol et de la biomasse des racines fines dans une répétition de chaque type de marécages. À petite échelle, la biomasse de racines fines était plus faible dans les marécages situés dans la plaine inondable que dans les marécages situés dans un faux chenal de rivière ou dans une dépression. Également, la régression linéaire multiple et les corrélations de rang de Spearman indiquaient qu'il y avait une relation négative entre la disponibilité des nutriments du sol et la biomasse de racines fines. À grande échelle, les corrélations entre la disponibilité des nutriments du sol et la biomasse de racines fines étaient généralement faibles. La variation à grande échelle de N-NO₃ et N-NH₄ était la plus importante dans les marécages situés dans la plaine inondable mais les nutriments n'étaient pas spatialement répartis de façon irrégulière dans aucun des sites échantillonnés. Les auteurs concluent que la disponibilité des nutriments du sol pourrait contrôler la biomasse de racines fines à petite échelle mais il n'est pas clair que cela soit également vrai à grande échelle.

[Traduit par la Rédaction]

Introduction

Belowground net primary production, which may be as much as 50% or more of total net primary production (Keyes and Grier 1981; Vogt et al. 1986; Megonigal and Day 1988;

Powell and Day 1991; Megonigal et al. 1997), can show rather large variation from one ecosystem to the next. It is unclear if this variation is driven by factors that operate at large, whole-ecosystem scales or by the cumulative influence of factors that operate at fine spatial scales within ecosystems. By studies in which sampling is done at multiple spatial scales, it may be possible to determine the relative importance of factors structured at broad versus fine spatial scales.

At the whole-ecosystem scale it is well known that the proportion of total plant biomass that occurs below ground is strongly influenced by the availability of mineral nutrients. Empirical studies have shown a negative relationship between fine-root biomass and ecosystem fertility (Keyes and Grier 1981; Aber et al. 1985; Nadelhoffer et al. 1985; Vogt et al. 1987), and fertilization of nutrient-poor forests may reduce ecosystem root biomass (Gower and Vitousek 1989). In

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fertile ecosystems, trees apportion relatively little of their total C resources to root production, but the opposite may occur within infertile ecosystems, presumably because more roots are needed to facilitate adequate nutrient uptake (Chapin 1980; Nadelhoffer 2000). Alternatively, rapid fine-root turnover in fertile ecosystems may lead to higher root production even though fine-root biomass decreases with increasing fertility (Nadelhoffer et al. 1985; Nadelhoffer and Raich 1992; Hendricks et al. 1993; Nadelhoffer 2000; but see Burton et al. 2000).

Within ecosystems, the fine-scale spatial and temporal distributions of nutrients also influence fine-root biomass. Soil nutrients often vary substantially at scales less than 1 m (Jackson and Caldwell 1993a 1993b; Bell et al. 1993; Ehrenfeld et al. 1997). In response to this variability, many plants selectively increase root biomass within nutrient-rich patches in order to forage efficiently for nutrients (Robinson 1994; Hodge 2004). Therefore, soil nutrient availability and fine-root biomass are likely to be positively correlated within ecosystems. However, most studies linking nutrient patchiness and fine roots have been conducted in greenhouse or garden-plot conditions. Few such studies have examined natural forest ecosystems (but see Mordelet et al. 1996).

Soil nutrients have not only direct effects on root responses, but also indirect effects by influencing the distribution of plant species and the evolution of root responses within species. Furthermore, nutrient levels at broad scales may influence evolutionary responses of plants to fine-scale nutrient patterns. For example, it has been predicted that fast-growing species in high-fertility ecosystems will show high levels of morphological plasticity (i.e., root proliferation into nutrient-rich patches) to compensate for the high nutrient demand of the individual plant and its competitors (Grime 1994). On the other hand, slow-growing species common in low-fertility ecosystems are thought to have long-lived root systems that respond to fine-scale nutrient patches through physiological plasticity (i.e., an increase in nutrient uptake per unit root length) (Grime 1994; Hutchings and de Kroon 1994). The results of empirical studies have supported these predictions (Crick and Grime 1987; Hutchings and de Kroon 1994; Fransen et al. 1998, 1999). However, recent evidence suggests that differences in root foraging between fast- and slow-growing species may be due simply to differences in relative growth rates among plant species rather than to evolutionary specialization (Aanderud et al. 2003).

In forested wetlands of the Gulf Coastal Plain of the United States, there are distinctly different hydrologic patterns that influence ecosystem fertility. Nonalluvial wetlands receive most of their nutrient inputs from precipitation alone and are nutrient-poor. In contrast, alluvial wetlands periodically receive nutrient subsidies from river-flooding and are nutrient-rich. Hydroperiods of both types of wetlands generally begin in early spring (March) and extend to early to mid summer (June–July). Therefore, when soils are no longer saturated, these wetlands are good systems to test hypotheses about how fine roots respond to fertility among and within ecosystems. Although the effects of ecosystem-scale fertility on aboveground net primary production in wetlands are well known (Brinson et al. 1981; Brown 1981; Mitsch and Rust 1984; Megonigal et al. 1997), effects below ground are not.

In this study we investigated the relationship between soil nutrients and fine-root biomass in forested wetland ecosystems at two spatial scales: broad (among ecosystem types) and fine (within a 20 m × 20 m plot). At the broad scale we compared root biomass among three different wetland ecosystem types (depressional swamps, river swamp sloughs, and floodplain swamps) that vary in their hydrologic regimes. Depressional swamps are nonalluvial systems, whereas river swamp sloughs and floodplain swamps are alluvial systems. However, river swamp sloughs backfill during overbank flow and potentially receive fewer nutrient subsidies than floodplain swamps. We hypothesized that fine-root biomass is negatively related to broad-scale fertility and therefore predicted that root biomass would follow the pattern depressional swamp > river swamp slough > floodplain swamp. At the fine scale we measured patterns in root biomass and nutrient availability at sampling points within a 20 m × 20 m plot in each wetland. We also quantified the spatial variability of soil nutrients and fine-root biomass within these plots. We hypothesized that fine-root biomass is positively correlated with fine-scale fertility, and that the strength of correlations is also positively related to broad-scale fertility. Therefore, we predicted that the strength of the correlation between fine-scale fertility and fine-root biomass would follow the pattern floodplain swamp > river swamp slough > depressional swamp.

Materials and methods

Study sites

We identified three geographically distinct depressional swamps (D) and three river swamp sloughs (S) within Ichauway ecological reserve, which is managed by the Joseph W. Jones Ecological Research Center, Baker County, Georgia, USA. Three floodplain swamps (F) were located in the Chickasawatchee Wildlife Management Area, Baker and Calhoun counties, Georgia, USA. Wetlands at Ichauway have experienced almost no human disturbance since the 1930s (Watt and Golladay 1999) save for the removal of most large baldcypress (*Taxodium distichum* (L.) Rich.) in floodplain swamps during the first half of the 20th century.

Mean annual temperature is 19 °C and annual precipitation during the study year was 87 cm, which was 34% below normal (National Climatic Data Center, Asheville, North Carolina). Soils of floodplain swamps and river swamp sloughs are classified as Typic Fluvaquents of the Muckalle series. Soils of the depressional swamps consist of an organic-rich surface horizon and are classified as Histic Humaquents. Discharge of the Chickasawatchee Creek at Elmodel, Georgia, which was near our floodplain swamp sites, was ~45% below normal during the study year (US Geological Survey). Permanent staff gauges in river swamp sloughs and depressional swamps indicated that the sloughs had no standing water by early summer and all depressional swamps were dry by late summer (S.W. Golladay, unpublished data). However, the gauges were originally installed in the area at the lowest elevation in each wetland. Soils were not saturated at any of our sites when we sampled soil nutrients and roots in August 2001.

Study design

We randomly selected a 20 m × 20 m (0.04 ha) plot within each site in July 2001. Each plot was divided into 2 m × 2 m grid cells and consisted of 121 grid intersections. At two sites per wetland type we randomly selected 20 grid intersections to use as sampling points. At one representative site per wetland type (D1, S1, and F1) we sampled 80 systematically located points to gain precise estimates of fine-scale variability in nutrients and fine roots.

Field measurements

We identified and measured the diameter at 1.4 m (DBH) for all trees ≥ 2 cm DBH within each plot. DBH was measured above the butt swell for large *T. distichum*, *Taxodium ascendens* Brongn., *Nyssa aquatica* L., and *Nyssa sylvatica* var. *biflora* (Walt.) Sarg. We calculated basal area and tree density from these measurements.

We measured indices of soil N (NH₄-N and NO₃-N) and P (PO₄-P) availability at each sampling point within plots using ion-exchange membranes (Ionics Inc., Watertown, Massachusetts) (Qian et al. 1992; Cain et al. 1999). These nutrients were selected a priori because they generally limit productivity in forested wetlands within the southeastern United States (Lockaby and Conner 1999). Soil NH₄-N availability was sampled with cation-exchange membranes (type CR67-HMR) and NO₃-N and PO₄-P availabilities were sampled with anion-exchange membranes (type AR204-SZRA for NO₃ and type 204-UZR-456 for PO₄). We cut membranes into 2 cm × 4.5 cm sections and charged them with 0.5 mol/L NaHCO₃. On 14–16 August 2001, three membranes (i.e., one of each type) were vertically inserted into the top 10 cm of surface horizon at each sampling point spaced 2–4 cm apart. Membranes were incubated in situ for 48 h and refrigerated at 4 °C until extraction. Membrane-bound NO₃-N and NH₄-N were extracted with 40 mL of 2.0 mol/L KCl and PO₄-P was extracted with 40 mL of 0.5 mol/L HCl. Extracts were analyzed for NO₃-N, NH₄-N, or PO₄-P using an auto-analyzer (Lachat Quickchem AE, Lachat Instruments, Milwaukee, Wisconsin).

On 16–22 August 2001 we collected a 7.62 cm diameter × 30 cm deep soil core at each sampling point to measure root biomass. Cores were removed with a cylindrical steel tube that was constructed of well casing and pounded into the soil with a sledgehammer. Soil cores were immediately refrigerated at 4 °C and roots were extracted from each core within 3 weeks of sampling by washing the samples with a hydro-pneumatic root elutriator (Gillison's Variety Fabrication, Benzonia, Michigan) over a 1 mm mesh sieve. Live fine roots (<2 mm diameter) were removed from each sample and dried at 70 °C to a constant mass. Dead roots were discarded.

Statistical analyses

At the broad scale, the 80 sampling points at sites D1, S1, and F1 were not independent because the spatial arrangement of sampling points was originally designed to determine autocorrelation. Therefore, we randomly selected 20 of the 80 points to calculate site means, with the condition that each point had to be at least 2 m from an adjacent sampling point. When we repeated this procedure with different random samples of 20 points, relative rankings among sites did not

change. We used MANOVA to test for differences in soil fertility among wetland types with NO₃-N, NH₄-N, and PO₄-P as dependent variables, using the GLM procedure of SAS version 8 (SAS Institute Inc., Cary, North Carolina). We performed univariate ANOVAs to determine which variables were significant. Alpha for each univariate test was adjusted using a sequential Bonferroni technique to avoid inflation of the Type I error rate (Holm 1979).

We used three techniques to test our first hypothesis that root biomass is correlated with broad-scale fertility. First, we performed a univariate ANOVA to test whether fine-root biomass varied among wetland types. Second, we used multiple regression analysis with NO₃-N, NH₄-N, and PO₄-P as independent variables and fine-root biomass as the dependent variable. We selected the regression model with the lowest mean square error as the “best” model using stepwise, forward, and backward regression techniques. Third, we ran Spearman's rank correlations between nutrients and fine roots by combining the different types of nutrients into a nutrient index (en sensu Jackson and Caldwell 1993a). The nutrient index was created by ranking site means for each nutrient from 1 to 9 and then summing the ranks for each site. We feel that this technique is a robust measure of relative fertility among sites that can reveal relationships not detected by multiple regression analysis, which may suffer from complicated nonlinear correlations among nutrients that violate assumptions of independence. Nutrient (NO₃-N, NH₄-N, and PO₄-P) and fine root biomass values were log-transformed to meet assumptions of normality. All data in the tables and figures are back-transformed.

At the fine scale, we used Spearman's rank correlations to determine correlations between soil fertility and fine roots within each 20 m × 20 m plot at each site. We ran separate correlations for each nutrient (NO₃-N, NH₄-N, and PO₄-P) for each site and calculated correlations between a nutrient index and fine-root biomass. The nutrient index for each site was similar to that created for comparisons among sites, except that we separately ranked soil nutrients (NO₃-N, NH₄-N, and PO₄-P) for each sampling point within a site. A sequential Bonferroni technique was used to adjust α for the four correlations calculated at each site. We incorporated all 80 sampling points for sites D1, S1, and F1 for each correlation. We also assessed the fine-scale variability of nutrients and fine roots (i.e., “global” variability of Lister et al. 2000 and Guo et al. 2004), using the variance and coefficient of variation (CV), with the UNIVARIATE procedure of SAS version 8. We did not include sites with 20 sampling points because these sites had far less precise estimates of mean and variance and were not comparable to sites with 80 sampling points.

Results

Forest structure

Basal area for the nine sites measured during our study ranged from 37.6 to 126.7 m²/ha but did not vary significantly among wetland types (ANOVA, $p > 0.05$; Table 1). *Taxodium ascendens* and *N. biflora* were dominant at depressional swamps. River swamp sloughs were dominated by *T. distichum* at all sites, *N. aquatica* L. at S2, and *Planera aquatica* J.F. Gmel. at S1 and S3. *Nyssa aquatica* was domi-

Table 1. Basal area (m²/ha) of tree species (DBH >2 cm) at the nine study sites, based on diameter at 1.4 m (DBH) or above the butt swell measured in one 20 m × 20 m plot per site.

| | Wetland type | | | | | | | | | | | |
|--|--------------------|------|------|------|--------------------|-------|------|------|------------------|------|------|------|
| | Depressional swamp | | | | River swamp slough | | | | Floodplain swamp | | | |
| | D1 | D2 | D3 | Mean | S1 | S2 | S3 | Mean | F1 | F2 | F3 | Mean |
| <i>Nyssa sylvatica</i> var. <i>biflora</i> | 56.8 | 30.9 | 41.3 | 43.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Taxodium ascendens</i> | 15.0 | 48.5 | 26.0 | 29.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Taxodium distichum</i> | 0.0 | 0.0 | 0.0 | 0.0 | 19.4 | 48.6 | 15.3 | 27.8 | 4.2 | 0.0 | 6.6 | 3.6 |
| <i>Planera aquatica</i> | 0.0 | 0.0 | 0.0 | 0.0 | 14.3 | 0.0 | 27.6 | 14.0 | 1.6 | 2.4 | 0.0 | 1.3 |
| <i>Nyssa aquatica</i> | 0.0 | 0.0 | 0.0 | 0.0 | 3.8 | 75.0 | 0.0 | 26.3 | 25.9 | 75.7 | 61.4 | 54.3 |
| <i>Quercus laurifolia</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.5 | 3.7 | 5.2 | 0.0 | 3.0 |
| <i>Fraxinus pennsylvanica</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 12.6 | 3.6 | 0.0 | 5.4 |
| <i>Quercus lyrata</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.3 | 0.4 | 0.0 | 1.9 |
| Others | 1.1 | 0.3 | 0.6 | 0.7 | 0.0 | 1.6 | 7.7 | 3.1 | 3.3 | 1.0 | 0.3 | 1.5 |
| Total | 72.9 | 79.7 | 67.9 | 73.5 | 37.6 | 126.7 | 50.6 | 71.6 | 56.6 | 88.4 | 68.3 | 71.1 |

Note: D, depressional swamp; S, river swamp slough; F, floodplain swamp.

Fig. 1. Soil nutrient availability (A) and fine-root biomass (B) in three types of wetland: depressional swamps (D), river swamp sloughs (S), and floodplain swamps (F). A different letter above the bar indicates a significant difference among wetland types. Error bars show +1 SE.

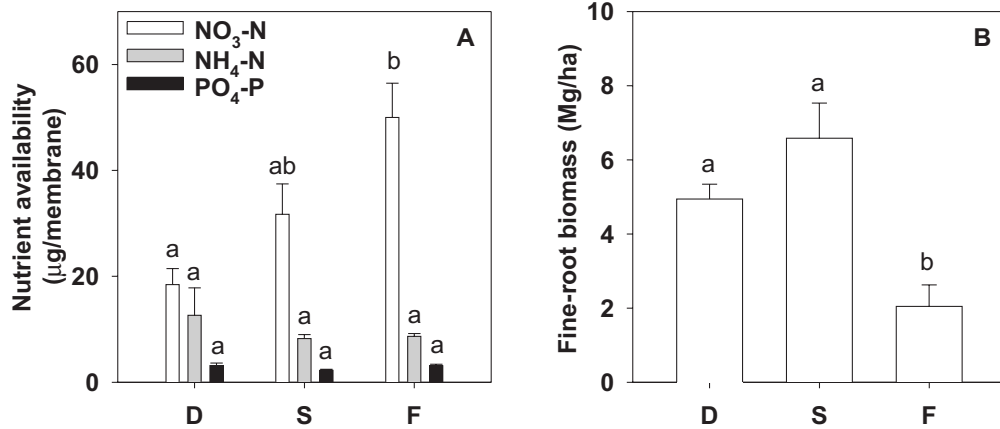
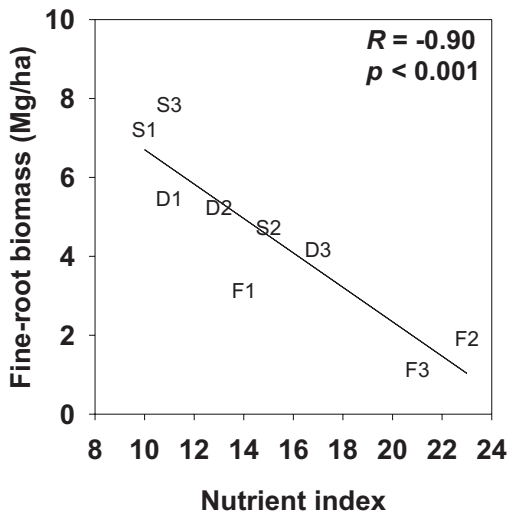


Fig. 2. Relationship between nutrient index and fine-root biomass based on Spearman’s rank correlation. Individual sites are indicated. For a description of wetland types see Fig. 1. The nutrient index was obtained by ranking site means for each nutrient among all sites and summing the ranks.



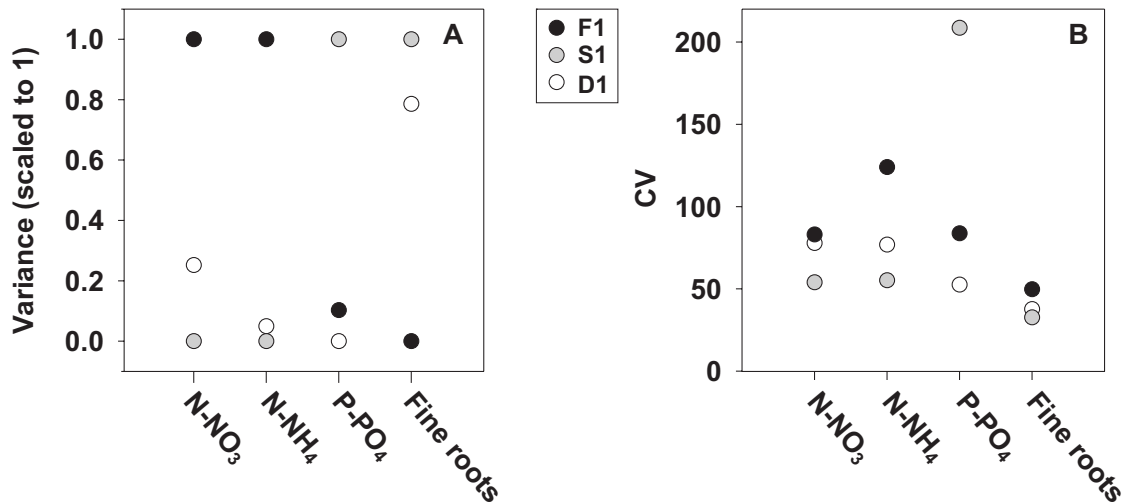
nant at floodplain swamps, with *Fraxinus pennsylvanica* Marsh., *T. distichum*, and to a lesser extent, *Quercus laurifolia* Michx. as codominants.

Broad-scale fertility and fine-root biomass

Indices of soil nutrient availability varied among wetland types (MANOVA, Wilks’ λ, $F_{[6,8]} = 3.67, p < 0.05$; Fig. 1). However, this variation was due to differences in mean NO₃-N availability among wetland types (ANOVA, $F_{[2,6]} = 10.78, p < 0.01$). Mean NO₃-N was ~2.5× greater in floodplain swamps than in depressional swamps ($p < 0.01$); availability in river swamp sloughs was intermediate. Wetland types did not vary in soil NH₄-N (ANOVA, $F_{[2,6]} = 0.40, p > 0.60$) or PO₄-P (ANOVA, $F_{[2,6]} = 2.73, p > 0.10$) availability.

Fine-root biomass was ~2.5–3× lower in floodplain swamps than in depressional swamps or river swamp sloughs (ANOVA, $F_{[2,6]} = 2.73, p < 0.05$; Fig. 1). There was no difference in fine-root biomass between river swamp sloughs and depressional swamps. However, the multiple regression model with NO₃-N, NH₄-N, and PO₄-P as independent variables explained 98% of the variation in fine-root biomass among sites and was highly significant ($p < 0.001$, data not shown). In addition, when the three soil nutrients (NO₃-N, NH₄-N, and PO₄-P)

Fig. 3. Variability of $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, and fine-root biomass at sites D1, S1, and F1. For a description of wetland types see Fig. 1. (A) Variance scaled to 1. (B) Coefficient of variation (CV).



were combined into a nutrient index, there was a negative correlation between the nutrient index and fine-root biomass (Spearman's rank correlation, $R = -0.90$, $p < 0.05$; Fig. 2).

Fine-scale fertility and fine-root biomass

None of the Spearman's rank correlations between fine-root biomass and soil nutrients ($\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$) or total nutrient index were significant ($p > 0.05$, data not shown). Variance of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ was greatest at F1 followed by D1 and S1 (Fig. 3). Variance of $\text{PO}_4\text{-P}$, in contrast, was highest at S1 and lowest at D1. CVs of nutrients among sites showed similar patterns to variances of nutrients except that the magnitude of difference among sites was much lower for CVs. Overall, CV of fine-root biomass was much lower than CVs of nutrients for each site. In addition, variance of fine-root biomass and estimated CVs showed conflicting patterns. Variance of fine-root biomass was greatest at S1 and lowest at F1, whereas CV of fine-root biomass was greatest at F1 and lowest at S1. This was most likely due to large differences in mean fine-root biomass among the sites, fine-root biomass being relatively low at F1 and relatively high at S1.

Discussion

Broad-scale fertility and fine-root biomass

Soil $\text{NO}_3\text{-N}$ availability was greatest in the floodplain swamps and lowest in the depressional swamps, but soil $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ did not vary among wetland types. This was not surprising because $\text{NO}_3\text{-N}$ is generally more mobile than $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ and is therefore more readily transported to floodplains during overbank flow. Groundwater from the Floridan aquifer in the Dougherty Plain of southwestern Georgia, which ranges from 20 to 5000 $\mu\text{g/L}$ $\text{NO}_3\text{-N}$, may also provide $\text{NO}_3\text{-N}$ inputs to floodplain swamps (S.P. Opsahl, Joseph W. Jones Ecological Research Center, Newton, Georgia, personal communication). In addition, a 10-week column incubation for three of the nine sites (D1, S1, and F1) in 2002 showed that N-mineralization rates were greatest in the floodplain swamp and lowest in the depressional swamp (M.A. Neatrour, unpublished data). Since soils were not saturated at the time of

sampling, much of the N may have been converted to $\text{NO}_3\text{-N}$ from $\text{NH}_4\text{-N}$. However, at the same sites as ours, Craft and Casey (2000) found that soil N accumulation did not differ. P accumulation was greater in the river swamp sloughs than in the depressional swamps. But high accumulations do not necessarily equate with greater availability. Soil N and P in depressional swamps, which include our sites, were largely in recalcitrant organic forms (Craft and Chiang 2002).

Our hypothesis that fine-root biomass is negatively correlated with broad-scale fertility was largely supported by results generated from multiple regression analysis and correlations with our nutrient index. These data are consistent with those from other studies of forest ecosystems (Keyes and Grier 1981; Aber et al. 1985; Nadelhoffer et al. 1985; Vogt et al. 1987). We also found that fine-root biomass was lowest in the floodplain swamps but did not follow the expected pattern (depressional swamps > river swamp sloughs > floodplain swamps) because values for depressional swamps and river swamp sloughs did not differ. However, river swamp sloughs dried more quickly than depressional swamps during the study year, and the latter sites had the greatest fine-root biomass. More C may have been allocated to fine roots to facilitate water uptake during drought conditions rather than in response to soil nutrient availability. Megonigal and Day (1992) showed that *T. distichum* saplings grown in periodically flooded mesocosms had higher root to shoot ratios and deeper root systems than those in continuously flooded mesocosms, presumably to access water and nutrients 50–60 cm below the soil surface. Furthermore, extended periods of inundation may reduce both fine-root biomass and production (Baker et al. 2001; Burke and Chambers 2003). Alternatively, the drier soils may have slowed root turnover rates at river swamp sloughs, leading to a relatively greater fine-root standing crop. Fluctuations in the water table in the rooting zone can cause changes between anoxic and well-oxidized conditions and increase root turnover (Keeley 1979; Hook 1984; Kozłowski 1984; Jones et al. 1996). However, we observed that the rooting zone at our plots within these sites was well-oxidized during the study year. If the depressional swamps and flood-

plain swamps only were considered, $\text{NO}_3\text{-N}$ availability was greater in the floodplain swamps than in the depressional swamps, and fine-root biomass was greater in the depressional swamps than in the floodplain swamps. These data suggest that soil nutrient availability at the broad scale may be an important factor affecting fine-root biomass in our systems.

Fine-scale fertility and fine-root biomass

Our data did not support the hypothesis that nutrients and fine roots are positively correlated at the fine spatial scale; correlations within sites were weak or nonexistent. Other studies, however, have demonstrated strong correlations between fine-root biomass and nutrient-rich microsites (St. John et al. 1983; Fahey and Hughes 1994; Mordelet et al. 1996). Mou et al. (1995) suggested that this correlation may be nutrient-specific, because they found a positive correlation between root density and soil P and K but not soil N.

We propose three possible reasons why fine-root biomass and soil nutrient availability were either unrelated or poorly correlated. First, stresses associated with soil anoxia may prevent efficient root foraging for nutrients in wetlands. Hence, forested-wetland species may be selectively placing roots in oxygen-rich patches rather than nutrient-rich patches to avoid stresses to root systems from soil anoxia. Jones et al. (1996) found that fine-root biomass was greater in higher (oxygen-rich) areas than in lower (oxygen-poor) areas, although the opposite pattern was found with net primary production of fine roots. However, we feel that stresses to root systems due to soil anoxia were low because our study sites were not saturated when roots and nutrients were measured. Furthermore, tree species in wetlands generally have adaptations to soil anoxia (e.g., water roots, aerenchyma) that allow root growth in flooded conditions.

Second, our use of ion-exchange membranes to sample soil nutrient availability may have not captured long-term nutrient patterns. Nutrients vary temporally as well as spatially (Ehrenfeld et al. 1997; Guo et al. 2004). We measured nutrient availability only once toward the end of the growing season. It is quite possible that nutrient conditions were different earlier in the growing season. Variation in fine-root life-span (Matamala et al. 2003; Trumbore and Gaudinski 2003) further reduces the ability to relate one-time measures of nutrient availability to one-time measures of fine-root standing crop. In addition, fine-root biomass may be relatively high in areas that have only recently become depleted. There is often local depletion of nutrients and water immediately adjacent to fine roots (Fitter and Hay 1987), and van Vuuren et al. (1996) found that fine-root proliferation into N-rich patches can continue even after nearly all of the N is gone.

Third, nutrients may not have been distributed into discrete patches that are relevant to the root systems of individual plants. Variance and CVs of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ were greatest in the floodplain swamp (F1) but greater in the depressional swamp (D1) than in the river swamp slough (S1). Except for $\text{PO}_4\text{-P}$ at S1, nutrient CVs were generally much lower than those reported for other forest ecosystems (Lister et al. 2000; Gallardo 2003), suggesting that overall variability was relatively low at our sites. In addition, geo-statistical (Robertson and Gross 1994; Guo et al. 2004) and trend surface analyses (Davis 1986) showed that D1, S1, and F1 exhibited large-scale trends in soil nutrient availability across

each site rather than across fine-scale patches. These large-scale trends in soil nutrients at our sites may have been related to the direction of flooding. Gallardo (2003) showed that differences in the distance from a pond caused large-scale differences in some soil properties across their plot in a floodplain forest in northwestern Spain.

Nutrients may not have been patchy at the fine scale because our sites were generally mature or maturing forests where roots may have fully exploited soil nutrients, resulting in relatively uniform depletion. In fact, the CV of fine roots at our sites was <50% and was always lower than nutrient variability (Fig. 3). Guo et al. (2004) found that the development of vegetation greatly decreased nutrient variability in pine forests of the southeastern United States that had been recently clear-cut or girdled.

In summary, we found that fine-root biomass was related to soil fertility at the broad scale but not at the fine scale. Our study shows that the relationship between soil fertility and fine-root biomass can vary across spatial scales. Therefore, spatial scale must be considered when investigating patterns in fertility and fine-root biomass.

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