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Transient nature of rhizosphere carbon elucidated by supercritical freon-22 extraction and ^{13}C NMR analysis

Felipe G. Sanchez[a,*], Maurice M. Bursey[b]

[a]*USDA Forest Service, P.O. Box 12254, Research Triangle Park, NC 27709, USA*
[b]*Department of Chemistry, University of North Carolina, Chapel Hill, NC 27599-3290, USA*

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Abstract

The region immediately adjacent to established roots of mature trees has been termed the "reoccurring rhizosphere" and it has been hypothesized that organic matter input from fine root turnover, root exudates and sloughing may result in a build up of the soil carbon in this region. The "reoccurring rhizosphere" for first-, second- and third-order roots of select loblolly pines (*Pinus taeda* L.) were examined on sandy, loamy sand and sandy loam soils. A significant carbon build up next to the root orders was confirmed for the sandy and loamy sand soils. The carbon build up was substantial (55% increase) next to the first-order roots of the sandy soil. However, the sandy loam soil did not display a significant amount of carbon build up next to the root orders. Extraction of the soil samples with supercritical freon-22 showed that the additional carbon in the "reoccurring rhizosphere" was highly soluble. Approximately 60% of the total soil carbon was extracted from the sandy and loamy sand soils, while approximately 40% was extracted from the sandy loam soil. A qualitative comparison of the extracts by liquid state ^{13}C nuclear magnetic resonance showed that the "reoccurring rhizosphere" region had a higher relative proportion of labile materials (i.e. carbohydrates, proteins, etc.) than the bulk soil. This information coupled with the high solubility in supercritical freon-22 suggests that the carbon build up in the "reoccurring rhizosphere" region of loblolly pines may be transient in nature.

Keywords: Roots; Soil organic matter; Rhizosphere; Nuclear magnetic resonance; Carbon

1. Introduction

In the South, the combination of deforestation and annual tillage of forest soils has reduced soil carbon by as much as 50% or more (Giddens and Garman, 1941). Restoring degraded soil and enhancing inherently poor soil can lead to increased productivity and carbon sequestration in forest systems. Afforestation of agricultural lands may have large positive effects on soil carbon pools. Some long-term studies have estimated that forest developing on abandoned agricultural lands increased soil carbon at a rate of 0.07-2.16 Mg/ha per year (Van Lear et al., 1995; Richter et al., 1995, 1999). The observed differences in the rates of carbon accumulation may be due to differences in the soil properties that stabilize carbon, such as clay and silt content (Hassink, 1995; Hassink and Whitmore, 1997). Model simulations have indicated that addition and incorporation of organic matter into the soil may restore and enhance soil systems by increasing sustainable levels of productivity and increasing both short- and long-term carbon sequestration by forest

* Corresponding author. Tel.: +1-919-549-4043; fax: +1-919-549-4047.
E-mail address: fsanchez@fs.fed.us (F.G. Sanchez)

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systems (Buford et al., 1999; Buford and Stokes, 2000). In a study conducted in North Carolina on the Lower Coastal Plain, soil carbon concentration consistently rose after 1.5 years for soils where forest slash was mulched and incorporated into the soil during site preparation (52 Mg C/g soil) as compared to pre-treatment values (24 Mg C/g soil) and control treatment values (31 Mg C/g soil) (Sanchez et al., 2000). It is uncertain how long the observed increases in soil carbon will persist or if other sources of belowground carbon (i.e. roots) will result in similar observations. However, Gresham (2002) reported that soil organic matter (SOM) levels had increased on an Atlantic Coastal site 10 years after harvesting and re-establishment of a second rotation loblolly pine forest. A meta-analysis on the effects of harvesting practices on soil carbon and nitrogen pools was done by Johnson and Curtis (2001) where they identified instances where there was substantial soil carbon increases after a harvest. These studies did not involve incorporation of forest slash thus root and forest floor inputs had to be the primary source of carbon.

Individual trees establish a long-lived network of primary, secondary and tertiary roots. Transient crops of fine roots that turnover each year are attached to this root system. Additionally, carbon from root exudates and sloughing is concentrated in this region. Therefore, an increased SOM concentration can be expected to build up next to these permanent roots. A pilot study identified a 35% increase in the amount of total soil carbon found laterally within 3.0 cm of a permanent secondary root system (Ruark, unpublished data). The samples were collected on a first rotation 40-year-old loblolly pine (*Pinus taeda* L.) stand growing on an abandoned farm site at the Department of Energy, Savannah River Institute (DOE-SRI) in Aiken, South Carolina. This increase was found at a depth of 10 cm in the Ap horizon, where previous agricultural practices probably left a homogeneous plow horizon. Ruark and Blake (1991) termed this area the "reoccurring rhizosphere" and considered the increased SOM concentration a result of fine root turnover throughout the length of the rotation. Inferential evidence for this hypothesis came from the large spatial variation observed in soil properties influenced by roots, such as total SOM and total soil nitrogen, in contrast to a relatively uniform property like soil texture. Organic matter from the forest floor is predominantly input as organic acid leachate from the foliage of a single dominant tree species. This leachate should influence the underlying mineral soil uniformly and it is less likely to heighten spatial variability. The large spatial variability in total SOM that occur in first generation pine stands within the previously homogenized Ap layer indicates that the variability was induced by plant root activity rather than organic matter input (Ruark and Zarnoch, 1992).

The annual net primary productivity (NPP) of biomass in a forest ecosystem is strongly linked to the productive potential of a site and the climate conditions that prevail in a given year. In forest ecosystems, SOM consists of a large array of components with the major input coming from fine roots of vegetation (Vogt et al., 1986). Estimates of the net annual carbon budget of a tree relegated to root growth and maintenance are disputed but range from 20 to 65% (Persson, 1979). Any changes in the amount of carbon allocated to the root system will coincidently affect the amount of fine root material entering the SOM pool, thus, changing the soil environment. The extent to which maximum NPP is achieved in a given year depends on climatic variations, which also induce alteration of SOM decomposition rates. This is particularly true for those of the highly labile SOM fractions that directly control nutrient cycling (Ruark, 1993). The cycling rates of essential nutrients are more closely related to forest productivity than the total amount of SOM (Cole and Rapp, 1981). This relationship is consistently reflected in equations for predicting nitrogen fertilization responses and nitrogen uptake, where variations in the factors regulating SOM decomposition rates (i.e. C/N ratios, moisture and temperature), is included (Edmonds and Hsiang, 1987; Binkley and Hart, 1989).

The objectives of this study are to determine if a "reoccurring rhizosphere" region exists for soils of different textural classes located on the DOE-SRI complex. If a "reoccurring rhizosphere" is detected, it is the goal of this study to assess the relative degeneracy of the additional organic matter. Sanchez and Ruark (1995) developed a method for extracting weakly bound (i.e. labile) SOM using supercritical freon-22 as a solvent. By extracting the SOM with supercritical freon-22, determining whether the increase in total SOM near permanent roots is attributable to increases in the labile SOM pool should be possible. The carbon chemical composition of the extracted material will be determined by ^{13}C nuclear magnetic resonance

(^{13}C NMR) to obtain further insight as to the potential degeneracy of the carbon extracted from the "reoccurring rhizosphere".

2. Site description

The study was conducted at the DOE-SRI complex located in the Upper Coastal Plain outside of Aiken, South Carolina. The site receives an average of 12 14 mm of annual precipitation with 3% as snow. Of the total annual precipitation, 54% occurs during April through September. Mean daily temperatures range from 11.7 to 24.1°C with an average of 17.9°C. The soils in this study were in the Lakeland (thermic, coated Typic Quartzipsamment), Fuquay (loamy, siliceous, thermic Typic Arenic Plinthic Paleudult) and Orangeburg (fine-loamy, siliceous, thermic Typic Paleudult) series. These soils represent the available moisture and texture gradient at the DOE-SRI complex. The stands were occupied by first generation, 40-year-old loblolly pine stands planted on abandoned farm land when the DOE-SRI complex was established.

3. Materials and methods

The "reoccurring rhizosphere" region was examined for loblolly pines on each of the three soil series types. Main lateral roots were followed out from the base of four randomly selected dominant trees in each stand to find four first-order pine roots at each tree. At each of these first-order roots, second- and third-order roots were located. A total of 144 roots were located for the study (three soil types x four trees x four replications per tree x three root orders). From within the Ap horizon, 6.0 cm^3 soil samples were systematically collected with a 0.8 cm diameter soil sampling tube. All three root orders were sampled at 1.5 cm intervals laterally for a distance up to 12.0 cm from each root and at a consistent soil depth of 12.0 cm. This was done at two positions along each root order to reduce sampling variability (Fig. 1). Samples were taken on average at a distance of 0.7 m from the main stem, lessening the possibility of organic input from stemflow. The samples were air dried and passed through a 2 mm mesh sieve. Samples at each

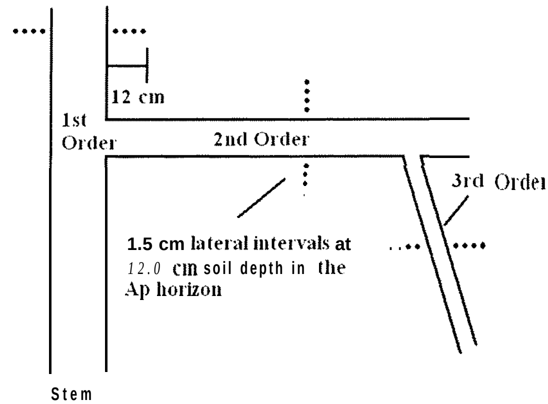

Fig. 1. Sampling scheme for collecting soil samples from the three loblolly pine root orders.

position along the root order were composited into 3.0 cm distance intervals and thoroughly mixed. At the laboratory, the soil samples were air dried and passed through a 2 mm mesh sieve. Subsamples were analyzed for total C and N content on a Carlo Erba NA 1.500 N/C/S analyzer' (Fisons Instruments, Danvers, MA).

Soil subsamples were extracted with supercritical freon-22 to determine if and where gradients related to the lateral distance from roots exist and which of the SOM fractions display the gradients. Sanchez and Ruark (1995) provide a complete description of the extraction procedure. Briefly, 5 g subsamples were shaken overnight with 1N HCl and washed with deionized water and air-dried. The subsample was placed in a 2.5 ml extraction vessel and 250 μl of trimethylimidazole (TMSI) was added. The additive (TMSI) is a strong, non-selective silylating reagent that disrupts the polar and ionic bonds in the soil and thus facilitates extraction. Each sample was extracted for 20 min with supercritical freon-22 at 40.53 MPa and 1 10°C. Three extractions were done for each sample to obtain complete extraction. All the extractions were done on a Suprex MPS 225 supercritical fluid extractor/chromatograph (Suprex Corp., Pittsburgh, PA). Carbon and nitrogen content of the extracted soil was determined on a Carlo Erba N/C/S analyzer and the amount extracted was calculated

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from the difference in carbon content in each soil sample before and after extraction.

The carbon chemistry of the extracted material was determined through liquid state ^{13}C NMR analysis. However, before the ^{13}C NMR analysis, the solubility of the extract was tested in a variety of conventional NMR solvents including methanol, acetone, water, carbon tetrachloride, chloroform and dimethylformamide. All extracts were only marginally soluble in these solvents. It was hypothesized that the extract could be brought into an aqueous solution by adding a surfactant. A cationic perfluorinated surfactant (catalog number S-637, Chem Service, West Chester, PA) was chosen for this experiment, because it was anticipated that the ^{13}C NMR signals originating from the surfactant would be shifted downfield and not interfere with the ^{13}C NMR spectrum of the extracts. All extracts were almost totally dissolved in 1% (v/v) solution of this perfluorinated surfactant in deuterium oxide. The extract was completely dissolved when the solution was heated to 50°C. To ensure that the sample would remain in solution, all the spectra were obtained at 50°C. To obtain a qualitative comparison of the extracted materials, the extracts were analyzed by liquid state ^{13}C NMR on a General Electric GN Omega NMR instrument (GE NMR Instruments, Fremont, CA). The spectra were obtained at 500 MHz and an operating frequency of 125.76 MHz with continuous broadband proton decoupling. The pulse length was set at 900 and a line broadening of 1 Hz was applied for each spectrum. Chemical shifts were reported relative to trimethylsilane that was used as an external standard.

Statistical analysis was done using SAS statistical software (SAS Institute, Cary, NC). Analysis of variance was used to examine the effects of soil series type on carbon concentration means for the different root orders. Additionally, a paired comparison t-test (dependent t-test) was used to compare the carbon means for the different sampling distances for a given root order and soil type.

4. Results and discussion

4. 1. Carbon concentrations

Table 1 shows the mean carbon concentrations, before extraction, next to the three root orders for the

Table 1
Soil carbon concentrations at the O-3.0 and 3.0-12.0 cm distances from first-, second- and third-order roots for Lakeland, Fuquay and Orangeburg soils

Soil series	Root order	Distance (cm)	N	Mean[a] (mg C/g soil)	S.E. (mg C/g soil)
Lakeland	1	0.0–3.0	8	11.3 (0.08)	2.0
		3.0–12.0	24	7.3	0.4
	2	0.0–3.0	8	11.1 (0.07)	0.5
		3.0–12.0	24	9.7	0.5
	3	0.0–3.0	8	11.4 (0.39)	0.8
		3.0–12.0	24	10.5	0.6
Fuquay	1	0.0–3.0	8	5.0 (0.22)	0.5
		3.0–12.0	24	4.3	0.2
	2	0.0-3.0	8	5.0 (0.02)	0.1
		3.0-12.0	24	4.6	<0.1
	3	0.0–3.0	8	4.4 (0.06)	0.2
		3.0-I 2.0	24	5.0	0.3
Orangeburg	1	0.0-3.0	8	5.2 (0.49)	0.3
		3.0-I 2.0	24	5.5	0.3
	2	0.0–3.0	8	6.6 (0.17)	0.7
		3.0–12.0	24	5.5	0.4
	3	0.0-3.0	8	5.1 (0.36)	0.4
		3.0–12.0	24	5.6	0.3

[a] For a given soil series and root order, means differ statistically at the significance levels shown in parenthesis

Lakeland, Fuquay and Orangeburg soils. The most pronounced difference occurred in the Lakeland soil. The carbon concentration at a distance <3.0 cm from the primary root increased 54.8% compared with the carbon concentration at a distance >3.0 cm. A modest, yet statistically significant at the $P > 0.1$ level, carbon build up (14.4%) was noted along the secondary root. The 8.6% increase for this area in the tertiary root is not significant. The observations for the Fuquay soil were similar to but of smaller magnitude than those of the Lakeland soil. There was a non-significant 16.3% and a significant 8.7% increase in soil carbon concentration in the area within 3.0 cm from the primary and secondary roots, respectively, as compared to the area >3.0 cm from the roots. An interesting drop in carbon (12%) occurred at a distance <3.0 cm from the tertiary root in the Fuquay soil. This observation was unexpected but consistent for each replication and significant at the $P > 0.1$ level. The source of this discrepancy is unclear as are its potential implications to the soil environment. In the Orangeburg soil, carbon concentration in the area <3.0 cm from the roots did not differ significantly from that in the area >3.0. This observation was consistent for the three root orders.

The observed differences for the three soil types may be partly due to differences in the propensity for lateral water movement and thus potential for lateral diffusion of SOM. Hydrologic soil groups are used to estimate runoff from precipitation. There are four hydrologic soil groups (Groups A through D) with water runoff potential being the lowest for soils from Group A and highest for soils from Group D. The Lakeland soils at the DOE-SRI complex are classified in Group A (low runoff potential) while the Fuquay and Orangeburg soils are in Group B (moderate runoff potential) (USDA — Soil Conservation Service, 1990). Additionally, the permeability of the Orangeburg soil (approximately 100 mm/h) is lower than the permeability of the Lakeland and Fuquay soils (both are >152 mm/h). As a result, lateral diffusion of SOM would be expected to be greatest on the Orangeburg soils and may account for the lack of significance for the soil carbon concentration values at different distances from the roots. The lesser build up of carbon adjacent to the roots on the Fuquay soils as compared to the Lakeland soils may also be partially due to lateral diffusion. The Lakeland and Fuquay soils at DOE-SRI are texturally similar and have the same permeability values. However, the Fuquay soil is more compact with a higher bulk density (1.65 Mg/m^3) as compared to the Lakeland (1.50 Mg/m^3) and Orangeburg (1.45 Mg/m^3) soils (USDA — Soil Conservation Service, 1990). The differences in bulk density, coupled with the difference in runoff potential, may be sufficient to allow for greater lateral diffusion and thus a smaller build up of soil carbon on the Fuquay soils as compared to the Lakeland soils.

4.2. SOM extraction

Sanchez and Ruark (1995) devised a method for the extraction of the labile SOM pool. This procedure uses supercritical freon-22 as a solvent, coupled with chemical derivatization with TMSI, to disrupt polar and ionic bonds in the soil and thus dissolve weakly bound (i.e. labile) SOM. Freon-22 has a strong dipole moment (1.42 D) and solvates a variety of compounds through dipole-dipole interactions. The SOM extracts obtained with this method were reported to be composed of low molecular weight materials (<900 Da) that had significant polar character (Sanchez and Ruark, 1995; Sanchez, 1996). It is anticipated that SOM compounds with these properties (small and polar) would be highly susceptible to microbial degradation.

Extraction efficiencies were similar for the Lakeland and Fuquay soils, while lower for the Orangeburg soil (Table 2). These results are expected since the Lakeland and Fuquay soils are texturally similar in the Ap horizon while the Orangeburg soil has higher clay content in the Ap horizon (USDA — Soil Conservation Service, 1990). Organic matter stabilization by

Table 2
Percentage the total carbon extracted from soil samples collected from the rhizosphere region of Loblolly pines located on Lakeland, Fuquay and Orangeburg soils

Soil series	Percent extracted[a]	S.E.	N
Lakeland	57.14a	1.27	96
Fuquay	56.85a	0.79	96
Orangeburg	40.20b	1.01	96

[a] Percent extracted was determined for each soil sample collected adjacent to the roots by taking the difference in the carbon concentration before and after extraction with supercritical freon-22 divided by the carbon concentration of the unextracted soil sample. N is the number of samples analyzed.

Table 3
Soil carbon levels next to first-, second- and third-order roots, after extraction with supercriticnl freon-22, for the Lakeland, Fuquay and Orangeburg soils

Soil series	Root order	Distance (cm)	N	Mean[a] (mg C/g soil)	S.E. (mg C/g soil)
Lakeland	1	0.0-3.0	8	3.7 (0.35)	0.4
		3.0–1 2.0	24	3.3	0.1
	2	0.0–3.0	8	4.3 (0.24)	0.4
		3.0-I 2.0	24	3.9	0.5
	3	0.0–3.0	x	4.3 (0.82)	0.2
		3.0–1 2.0	24	4.3	0.2
Fuquay	1	0.0-3.0	8	I .9 (0.87)	0.2
		3.0–1 2.0	24	1.9	0.1
	2	0.0–3.0	8	2.1 (0.45)	0.1
		3.0–12.0	24	2.0	0.1
	3	0.0–3.0	8	1.8 (0.09)	0.1
		3.0-l 2.0	24	2.0	0.1
Orangeburg	1	0.0-3.0	X	3.3 (0.87)	0.1
		3.0-I 2.0	24	3.3	0.1
	2	0.0-3.0	8	3.4 (0.65)	0.3
		3.0-l 2.0	24	3.2	0.1
	3	0.0–3.0	8	3.0 (0.49)	0.1
		3.0-I 2.0	24	3.1	0.1

[a] For a given soil series and root order, means differ statistically at the significance levels shown in parenthesis.

clays has been hypothesized (Jenkinson, 1977; Oades, 1989) and could lower extraction efficiencies. Table 3 shows no statistically significant difference in carbon concentration between the "reoccurring rhizosphere" area (i.e. <3.0 cm from the root) and the bulk soil (i.e. >3.0 cm from the root) after supercritical freon-22 extraction for each soils type and root order. This observation demonstrates that the additional carbon in the "reoccurring rhizosphere" area is being incorporated into the supercritical freon-22 extractable pool. As previously noted, the SOM extracted with supercritical freon-22 may represent the labile component of the SOM pool. Generally, the C/N ratio of a substrate is an indicator of its quality and degeneracy (McColl and Powers. 1998). For all the soils, the extracted material had a lower C/N ratio than the unextracted soil (Table 4) indicating that the extracted material was of high quality and thus susceptible to microbial degradation. This suggests that root activity over 40 years resulted in a build up of transient labile carbon. Consequently, root inputs (i.e. sloughing, exudates and products of fine root turnover) into the SOM pool will probably not result in long-term carbon sequestration but could potentially play an important role in short-term nutrient cycling.

4.3. NMR analysis

Soil extracts are complex mixtures of compounds and their NMR spectra usually show overlapping signals, making identification of individual compounds difficult. However, compound chemical classes can be identified by the signal intensities for a range of chemical shifts characteristic of given compound classes (Schnitzer, 1991). For example, in a ^{13}C NMR spectrum the chemical shift region of 106-158 ppm is investigated to detect the presence of aromatics and

Table 4
Carbon/nitrogen ratios for soil samples collected adjacent to first-, second- and third-order roots from the Lakeland, Fuquay and Orangeburg soils and the supercritical freon-22 soluble extracts obtained from these same soil samples

Soil series	Sample	C/N ratio	S.E.
Lakeland	Soil	37.43	2.07
	Extract	14.62	1.14
Fuquay	Soil	32.62	1.33
	Extract	24.26	0.23
Orangeburg	Soil	37.08	8.28
	Extract	18.43	0.37

phenolics in the sample. Identification of the different carbon compound classes and their relative contribution to the spectrum allows for an assessment of the carbon chemical composition of the mixture. Fig. 2 provides a qualitative comparison of the spectrum from the surfactant blank and extracts from the "reoccurring rhizosphere" and the bulk soil. The spectra were obtained with minima1 line broadening (1 Hz) to identify small molecules (Preston and Blackwell, 1985; Gressel et al., 1996; Preston, 1996). Small molecules in the spectrum may typify the building blocks of the larger humic substances as some of these molecules condense to form larger molecules while others may be by-products of depolymerization reactions. The spectra of the soil extracts in Fig. 2 shows the presence of several different carbon compound classes and there are several carbon compounds that are present in both spectra, however, the significance of the spectra comes from the relative contributions of the different carbon compound classes to their respective spectrum. Labile materials, such as peptides, amino acids and proteins (41-60 ppm) and carbohydrates (61-105 ppm) make up most of the total "reoccurring rhizosphere" extract as compared with the bulk soil extract. Similarly, relatively more stable compounds, such as aliphatics (O-40 ppm) and aromatics and phenolics (106–158 ppm), make up most of the total bulk soil extract as compared with the "reoccurring rhizosphere" extract. These results are consistent with the observations from the supercritical freon-22 extraction suggesting that the additional organic matter in the "reoccurring rhizosphere" is labile and thus transient in nature.

5. Conclusions

Evidence supporting the "reoccurring rhizosphere" theory hypothesized by Ruark and Blake (1991) has been presented. Increases in carbon concentrations in the "reoccurring rhizosphere" region (<3.0 cm from the root) as compared to the bulk soil (>3.0 cm from the root) were seen for the majority of the root orders in the Lakeland and Fuquay soils. On the Orangeburg soil, no significant difference in soil carbon concentration was seen in the "reoccurring rhizosphere" as compared with the bulk soil. The lack of a significant difference in carbon concentration with distance from

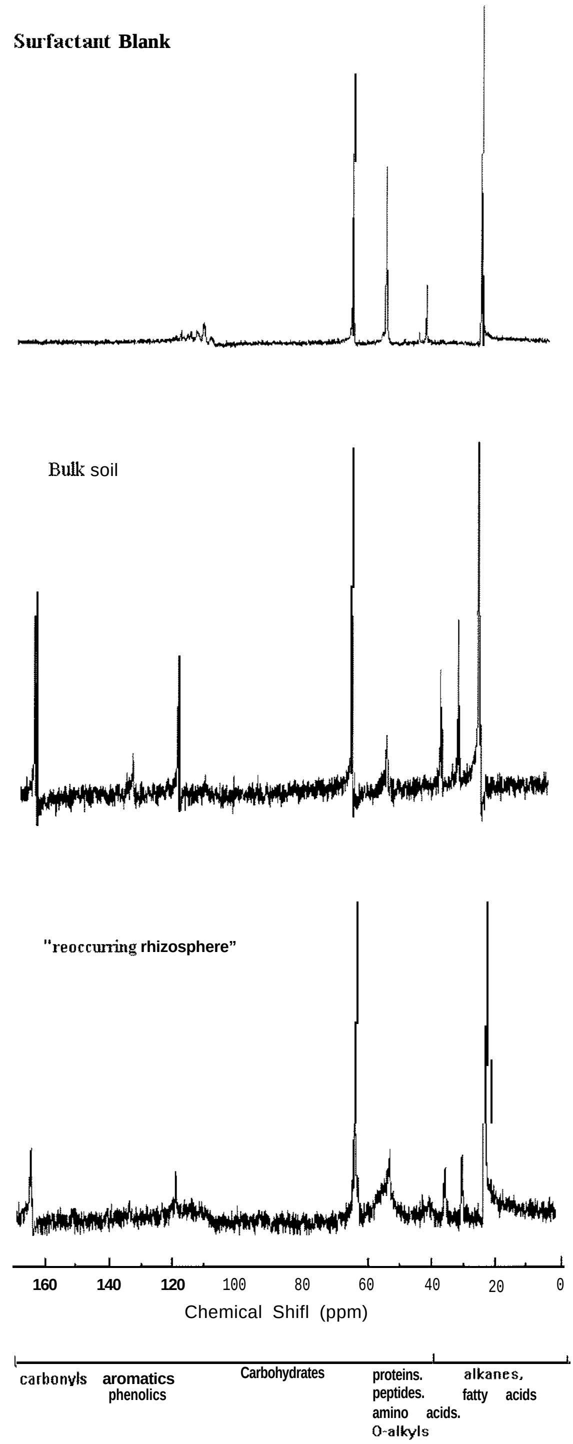

Fig. 2. ^{13}C NMR spectra of the surfactant blank and the extracts collected from soil samples from the bulk soil and the "reoccurring rhizosphere" of a Fuquay soil.

the roots in the Orangeburg soils may be due to a greater propensity for lateral diffusion of SOM as compared with the Lakeland and Fuquay soils. The existence of a "reoccurring rhizosphere" suggests that loblolly pine fine root material builds up to provide a favorable microenvironment beside roots. This favorable microenvironment may allow for increased nutrient and water supplies for tree roots and the associated microbes through a build up of organic matter.

This study has shown that the organic matter originating from roots will be incorporated into a supercritical freon-22 extractable pool and thus potentially the labile component of the SOM pool. It is unclear if the magnitude of the increases represents an upper equilibrium level on these soil types or even if the increased levels fluctuate greatly from year to year. The proportion of the increases associated with the labile pool may be related to nutrient cycling in proximity to fine roots, which has strong implications on the nutrient cycling dynamics of the tree. Although root exudates and sloughing provide significant sources of carbon in the "reoccurring rhizosphere" region, organic matter originating from fine root turnover probably makes up most of the material entering the soil. In addition to the fact that the additional organic matter in the "reoccurring rhizosphere" was soluble in supercritical freon-22 suggesting that it is labile material, the spectral data from the ^{13}C NMR analysis indicates that the additional organic matter in this region has a higher relative amount of labile compounds (i.e. peptides, amino acids, proteins and carbohydrates) as compared with the bulk soil which had more stable compounds (i.e. aliphatics, aromatics and phenolics). These observations indicate that root inputs into the SOM pool will not result in long-term carbon sequestration. Other organic soil amendments, such as forest slash and biosolids, with a different substrate quality (i.e. C/N ratio, lignin/N ratio) than roots may result in a longer residence time in the soil. Model predictions (Buford et al., 1999; Buford and Stokes, 2000) and the early results of field studies incorporating organic matter into the soil (Sanchez et al., 2000) suggest that the potential exists to sequester carbon in forest soils. It is also possible that larger, established roots will have a longer residence time in the soil (Van Lear et al., 1995; Gresham, 2002; Johnson and Curtis, 2001). However, this study demonstrates that the carbon inputs from root exudates and sloughing and fine root turnover primarily results in enhancing the SOM labile carbon pool which may be important for creating a favorable microenvironment (i.e. better water retention, higher nutrient levels) adjacent to established root systems.

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