Root contributions to long-term storage of soil organic carbon: theories, mechanisms and gaps

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Abstract
The depth to which plants locate their roots has important but yet poorly understood implications with regard to the profile distribution and dynamics of soil organic carbon (SOC). We compared the profile distribution of fine root biomass (FRB) with depth distribution of SOC, based on data recalculated from published literature. Mechanisms through which roots might contribute to long-term storage of SOC were reviewed. There was general agreement across previous studies that over 60% of SOC were in the top 0.3 m of soil, where FRB was concentrated. However, studies in which depth distribution of SOC was simultaneously compared to profile distribution of RB were not readily available, suggesting that this area of research has received limited attention. There is a paucity of empirical evidence to lend support to theorised mechanisms through which roots stabilise SOC. The relationship between profile distribution of roots and depth distribution of SOC must be evaluated on-site for defined landuses. A standardised format for presenting results must be developed and agreed upon to ease interpretation of the results. National Soil Science Societies may have a significant role in this process and this 19th World Congress of Soil Science will be an opportune assembly for dialogue.

Key Words
Carbon sequestration, climate change, landuse systems, rooting depth, soil aggregate stability.

Introduction
Plant roots differ in their capacity to explore the soil volume depending on the geographical location, botanical composition of the vegetation, and prevailing environmental factors (Canadell *et al.* 1996; Casper and Jackson 1997; Schenk and Jackson 2002). The relative importance of these differences and their implications for SOC sequestration belowground, are a subject of interest. It is feared that climate change could induce sweeping changes in the botanical composition of plant communities, especially where differences in rooting among plants already exist (Schenk and Jackson 2002). The impact of these changes on the storage and dynamics of C belowground are not well understood. We hypothesise that if roots are an important SOC input and also contribute to SOC stabilisation, then the depth distribution of SOC should follow the same pattern as that of roots. This paper reviewed existing literatures on FRB and SOC, and discussed gaps and potential for future research.

Materials and methods
To test our hypothesis that the depth distribution of SOC follows the same pattern as that of roots, we reviewed literature on the profile distribution of fine roots (FRs) and SOC. Preference was given to published literature with means along with their standard errors and sample sizes, which allowed us to recalculate the values for FRB and SOC by depth (in g/m^2). Where it was necessary to combine data, for instance for fine roots which had been split into two size classes (0 – 1 and 1 – 2 mm) for each given depth of sampling into one size class, new standard errors for the combined means were calculated following the approach outlined by Utts and Heckard (2007). For studies where matching the depth segments was not possible, symbols were appended to the mean values and their standard errors (both for FRB and SOC). The source(s) of data used to recalculate the values for these parameters are denoted by symbols in the first columns of tables 1 and 2.

Results and discussion
Profile distribution of fine root biomass for selected landuse systems
The profile distribution of FRB for defined landuses or plant species presented (Table 1), indicated that depth distribution of FRB varied with landuse but generally, over 60% of all live root biomass occurred above 0.1 m depth. Interestingly, the pattern of distribution of dead root biomass with depth (data not presented) was more related to that of FRB. Kirsi and Sisko (1999) explained that although fine roots account for only 15 – 20% of root biomass in forests, their growth and maintenance can account for as much as 76% of the total

net primary production. Rooting depth and profile distribution may be used to indicate potential to locate and sequester SOC in subsurface horizons (Rasse *et al.* 2005; Denef and Six 2006*)*, because during their growth, roots punch through moist soil deforming and repacking it (Hinsinger *et al.* 2009), while depositing C along their way (Hirth *et al.* 2005).

Table 1. Profile distribution of fine root biomass of selected landuse systems.

	Fine root (≤ 2 mm) biomass g/m^2 by soil depth (m)					
Landuse	0.0 – 0.2	0.2 – 0.4	0.4 – 0.6	0.6 – 0.8	0.8 – 1.0	> 1.0
YFS (14 – 16 yr)[†]	308±48.76	161±13.34	283±138.62	25±8.6		
TFS (26 – 29 yr)[†]	286 ±110.45	226±92.48	139±98.49	103±30.89		
OFS (114 – 121 yr)[†]	262±62.13	317±25.02	218±46.32	24±5.83		
Scots pine[††]	61.7±4.13	32.8±3.02	12.5±2.00			
Festuca grassland[†††]	925±199**	645±94**	301±77**	114±30**	91± 59**	67.5± >18**
Stipa grassland[†††]	297±58**	174±18**	73±10**	79±15**	98± 48**	51±>8**
Desert[†††]	216±49**	84±29**	17±5**	3±1**	0±0**	5±>2**
[a]Temp grasslands[‡]	980	238	126	42	14	
Tropic grassland[‡]	798	336	126	84	42	
Crops[‡]	93	18	15	6	4.5	
Native pasture[‡‡]	90±5.67^	22±6^	10±3.2^	10±2.8^	8±4.6^	36±>5.1^
Sown pasture[‡‡]	134±6.0^	10±1.4^	8±3.4^	6±2.2^	6±3.4^	10.6±8.2^
Native Vertosol[‡‡]	97±11.55^	38±8.2^	18±8.0^	8±3.8^		
Native Chromosol[‡‡]	107±28.21^	10±4.2^	10±3.8^	4±2.2^	6±2.78^	

Data recalculated from [†]Park *et al.* (2007), depths: 0 – 0.1, 0.1 – 0.3, 0.3 – C horizon and C horizon, respectively. YFS, TFS and OFS stand for young, transitional and old forest stands, respectively; [††]Vanguelova *et al.* (2005), depths: 0.0 – 0.15, 0.15 – 0.45 and 0.45 – 0.6, respectively; [†††]Schulz *et al.* (1996), data from an aridity gradient in Patagonia, **depths: 0.0 – 0.1, 0.11 – 0.3, 0.31 – 0.5, 0.51 – 0.75, 0.76 – 1.0 and > 1.0 m; [‡]Jackson *et al.* (1996) (FRB) and Jobbagy and Jackson (2000) (percentage distribution of the biomass by depth); [‡‡]Lodge and Murphy (2006), ^depths: 0.0 – 0.05, 0.05 – 0.1, 0.1 – 0.3, 0.3 – 0.5, 0.5 – 0.7, 0.7 – 0.9, 0.9 – 1.1, >1.1 m. Since the biomass of 0.0 – 0.05 and 0.05 – 0.1-m depth was pooled together, it also necessitated computing the respective combined standard errors following the same procedure in Utts and Heckard (2007).

Depth distribution of soil organic carbon

The distribution of SOC by profile depth for defined landuses or biomes (Table 2) shows that SOC tends to be concentrated in the topsoil where the highest FRB is located. We found a broad similarity between SOC distribution by depth and that of FRB. This relationship is supported by a number of conceptual models which seem to indicate that roots are not only the principal source of SOC but that root-OC is more stable in the soil than shoot-OC. Tisdall and Oades (1982) proposed a hierarchical model of soil aggregate development in which roots are the dominant structures holding together aggregates at the highest and most complex level of organisation. Gale *et al*. (2000) demonstrated how small soil macroaggregates and large microaggregates, held together by root-particulate organic matter (RPOM), could withstand slaking more than aggregates devoid of RPOM, a key factor in the stabilisation of SOC. Watteau *et al*. (2006) advanced the models of Tisdall and Oades (1982) and Gale *et al*. (2000) and observed that decay and water uptake could occur simultaneously in the "coarse" roots of maize (*Zea mays* L.). They also observed how silt- and clay-sized aggregates were drawn, along with water, toward central cylinders of decomposing coarse roots for distances of up to 15 µm, a process they postulated could initiate the formation of soil aggregates. Moreover, many fine roots were colonised by bacteria, whose decomposition upon death resulted in granulofibrillar residues which formed associations with silt and clay minerals. Therefore, roots are not just simple structures holding preformed aggregates together but roots act as centres for the formation of aggregates and nucleation of SOC in such aggregates (Watteau *et al.* 2006). Methodological advances that are being made in root studies with regard to their exploration and modification of the soil matrix should shed more light on their roles that have continued to elude rhizosphere scientists.

There is a dearth of published literature in which the depth distribution of SOC was simultaneously compared with profile distribution of FRB and FR morphological properties. Moreover, the existing literatures reported results in various non-standradised units, making it difficult to make comparisons across landuses and biomes. In some cases results from one study were presented in different sections in various journals, instead of in a consolidated article in a single journal publication. In some literature, crucial information was not declared, including sample sizes used, soil bulk density data where OC was given as %, which made it difficult to express SOC per-area-basis. Still in other literature, data on FRB and SOC was concealed in graphs, percentages, or never presented at all. The depths of measurement of the parameters also varied tremendously, as shown in the Tables 1 and 2.

Table 2. Profile distribution of soil organic carbon (SOC) in selected landuse systems or biomes.

	SOC g/m^2 by depth (m)					
Landuse	0.0 – 0.1	0.1 – 0.2	0.2 – 0.3	0.3 – 0.5	0.5 – 0.8	0.8 – 1.0
Eucalyptus forest[††]	5100	3600	2700	4500	4200	2800
Grassland[††]	4700	3000	2300	3600	1600	900
Native pasture[‡]	900		220*	100*	360*	360*
Sown pasture[‡]	1340		100*	80*	240*	30*
[a]Native Chromosol[‡]	1070		100*	100*	160*	20
Native pasture[G]	240		1990**	14.6**		13.1**
Pine plantation[G]	17.4		16.4**	1330**		1020**
Rice-berseem[‡‡]		3050[d]	2350[d]	1700[d]		
[b]KBS – LTER, MI[†††]		2140[d d]		520[d d]	260[d d]	
[c]Hoytville, OH[†††]		3560[d d]		1720[d d]	860[d d]	
[d]Placerville, CA[†††]		3620[d d]	3060[d d]		1460[d d]	
Temperate forests[†]		4830^	2150^	1270^	830^	630^
Tropical forests[†]		8370^	4790^	3590^	2720^	2280^
[e]Temp grasslands[†]		4310^	2420^	1580^	1260^	950^
[f]Tropic grasslands[†]		7130^	4550^	3560^	2570^	1980^
Boreal forest[†]		5600^	2800^	1460^	780^	560^
Deserts[†]		3700^	2460^	2020^	1680^	1460^
Crops[†]		6440^	3610^	2360^	1880^	1410^
Tundra[†]		4560^	3310^	2170^	800^	570^

The data used to compute SOC stocks were derived from: [†]Jobaggy and Jackson (2000) and Jackson *et al*. (1996), [††]Chen *et al*. (2005), [†††]Paul *et al*. (2006), [‡]Lodge and Murphy (2006), [‡‡]Majumda *et al*. (2008), [G]Guo *et al*. (2008). The depths of SOC values with symbols were different from those in the row just below the title "SOC Mg/ha by depth (m)" such that: *0.1 – 0.3, 0.3 – 0.5, 0.5 – 0.9 and 0.9 – > 1.1; **0.1 – 0.3, 0.3 – 0.6, 0.6 – 1.0; [d]0.0 – 0.2, 0.2 – 0.4 and 0.4 – 0.6; [d d]0.0 – 0.2, 0.25 – 0.5 and 0.5 – 1.0; ^0.0 – 0.2, 0.2 – 0.4, 0.4 – 0.6, 0.6 – 0.8 and 0.8 – 1.0 m. The SOC values for the terrestrial biomes denoted by ^are in Pg (1 Pg = 10^{15} g) recalculated from the data in[†], and all the rest in Mg/ha Abbreviations: [a]Native pasture on Chromosol, [b]Kellog Biological Research Station – Long-term Ecological Research, MI (Michigan State, USA), [c]Hoytville, OH (Ohio State, USA), [d]Placerville, CA (Canada, USA), [e]Temperate grasslands, [f]Tropical grassland.

Conclusion and research imperatives

There appears to be a relationship between the profile distribution of fine roots and depth distribution of SOC. However, simultaneous site- and landuse-specific studies comparing the depth distribution of roots and that of SOC are needed to generate empirical data to ascertain this relationship. Existing theories underpin roots for their dual role in the formation and stabilisation of soil aggregates on the one hand and the nucleation of SOC in such aggregates potentially for long-term storage belowground on the other hand. A standard procedure for data collection, interval depths of sampling, units of measurement and presentation format is needed to enable comparison of relationship between FRB and SOC under different systems. It is proposed that the type and minimum amount of data which should accompany future communications on depth distribution of FRs and SOC submitted for publication should be established to allow for consistency in presentation and interpretation of results without violating statistical principles and intellectual property issues.

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