



## Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation

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### Abstract

Understanding the origin of the carbon (C) stabilised in soils is crucial in order to devise management practices that will foster C accumulation in soils. The relative contributions to soil C pools of roots vs. shoots is one aspect that has been mostly overlooked, although it appears a key factor that drives the fate of plant tissue C either as mineralized CO<sub>2</sub> or as stabilized soil organic matter (SOM). Available studies on the subject consistently indicate that root C has a longer residence time in soil than shoot C. From the few studies with complete datasets, we estimated that the mean residence time in soils of root-derived C is 2.4 times that of shoot-derived C. Our analyses indicate that this value is biased neither by an underestimation of root contributions, as exudation was considered in the analysis, nor by a priming effect of shoot litter on SOM. Here, we discuss the main SOM stabilisation mechanisms with respect to their ability to specifically protect root-derived SOM. Comparing *in situ* and incubation experiments suggests that the higher chemical recalcitrance of root tissues as compared to that of shoots is responsible for only a small portion, i.e. about one fourth, of the difference in mean residence time in soils of root-derived vs. shoot-derived C. This suggests that SOM protection mechanisms other than chemical recalcitrance are also enhanced by root activities: (1) physico-chemical protection, especially in deeper horizons, (2) micrometer-scale physical protection through mycorrhiza and root-hair activities, and (3) chemical interactions with metal ions. The impact of environmental conditions within deeper soil layers on root C stabilisation appear difficult to assess, but is likely, if anything, to further increase the ratio between the mean residence time of root vs. shoot C in soils. Future advances are expected from isotopic studies conducted at the molecular level, which will help unravel the fate of individual shoot and root compounds, such as cutins and suberins, throughout soil profiles.

### Introduction

Plant root contributions to the accumulation of soil organic matter (SOM) need to be better evaluated in order to devise agricultural management practices that maximize carbon storage throughout the entire depth of the root-zone soil profile. Carbon storage in soils is particularly important because soils are the largest reservoir of organic carbon in terrestrial ecosystems, containing three times more carbon than the vegetation that they support (Post et al., 1982). As such, they represent a potential sink for the anthropogenic emissions of carbon dioxide that threaten the stability of the world's climate. Numerous studies are now focussing

on management practices that could increase the sequestration of C in soils (Follett, 2001; Janzen et al., 1998). Nevertheless, our understanding of the key factors that determine long C storage in soils remains limited (Neff et al., 2002). The relative contributions to soil C pools of roots versus shoots is one aspect that has been mostly overlooked, although it appears a key factor that drives the fate of plant-tissue C either as mineralized CO<sub>2</sub> or as stabilized SOM. In the present article, we will summarize research on the relative effects of above- and below-ground plant materials on C storage in soils, and present the state-of-the-art techniques that hold the greatest promises to further this field of research.

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Historically, the question of sustaining soil carbon levels has been addressed in terms of the amount and quality of above-ground crop residues that needs to be returned to the soil annually (e.g., Larson et al., 1972; Rasmussen et al., 1980). This control of soil C stocks through crop residue management has led to a greater emphasis on the transformation of above-ground plant fresh tissues and composts in soils than on that of plant roots. Nevertheless, early studies suggested that the relative contribution of plant roots to soil organic C stocks is larger than that of plant shoots (Broadbent and Nakashima, 1974). Long-term residue management studies suggest that above ground material has a limited impact on SOM levels as compared to that of root systems. Campbell et al. (1991) reported that 30 years of wheat (*Triticum aestivum*) straw restitution to soils did not modify the carbon content of these soils. Clapp et al. (2000) observed that 13 years of maize (*Zea mays* L.) shoot restitution in a non-fertilized conventionally tilled system decreased maize contribution to soil organic carbon (SOC) stocks from 9.1 Mg ha<sup>-1</sup> for roots alone to 8.7 Mg ha<sup>-1</sup> for roots plus shoots. Results from a 30-year maize experiment indicate that restitution of maize stalks vs. removal for silage had no impact on SOC contents (Reicosky et al., 2002). Although some studies have observed a significant contribution of crop shoot residues to SOC content (Barber, 1979; Hooker et al., 1982), this contribution was comparatively smaller than that of roots (Barber, 1979). Little impact of shoot residues on SOC was also observed in long-term residue burning studies (Moss and Cotterill, 1985; Nuttal et al., 1986 in Prasad and Power, 1991; Pikul and Allmaras, 1986; Rasmussen et al., 1980). A simulation study has suggested that maize root systems contributed 1.8 times more C to soils than the corresponding above-ground biomass (Molina et al., 2001). Results from all these studies raise the question of how more resistant is root-derived C as compared to shoot-derived C, and what are the mechanisms at play that specifically protect root C from being mineralized?

#### Quantitative evidences of the specific preservation of root C in soils

For the few available studies with complete datasets, we computed a relative contribution factor of roots vs. shoots to SOC, expressed as the ratio: (root-derived soil C/total root C input)/(shoot-derived soil C/total

shoot-C input). For example, if after  $n$  months or years of cultivation 40% of the estimated total root C input was retrieved as soil C and 20% of the total shoot-C input was retrieved as soil C, the corresponding relative contribution factor is equal to 2.0, i.e. 40/20. This factor expresses the relative residence time in soils of equivalent quantities of root-derived vs. shoot-derived carbon.

In the following analyses, as reflected in Table 1, we will separate two types of studies based on whether the roots were grown *in situ* or known amounts of roots (and shoots) were placed into soils at the beginning of the experiment. Hereafter, we will call the first set of experiments '*in situ* root growth' and the second set 'incubations'. Two types of incubation studies have to be considered: (1) free mixing of plant residues into soil, and (2) litter-bag experiments. Litter-bag results have to be interpreted with caution because they do not necessarily account for all the carbon present in the initial plant residue sample, some being potentially transferred to the surrounding soil. Nevertheless, we will see that they yield results for the parameters considered in this study very similar to those from experiments where residues are directly mixed into soils.

All *in situ* root growth experiments are based on contrasted treatments with and without shoot restitution to research plots. They diverge in the methods used to evaluate: (1) SOC quantities of root and shoot origins, and (2) fresh root-C inputs into the soil system. In the studies of Table 1, quantities of freshly deposited SOC in shoot-restitution and shoot-removal plots were determined either through comparison with bare fallow controls (Barber, 1979; Rasse, this study) or through <sup>13</sup>C signature changes in C3/C4 successions (Balesdent and Balabane, 1996; Bolinder et al., 1999; Clapp et al., 2000) and *in situ* labelled plots (Puget and Drinkwater, 2001). Fresh root C inputs into soils were estimated by Puget and Drinkwater (2001) through a  $\delta^{13}\text{C}$  measurement of the whole soil, i.e. soil + living roots, prior to killing the hairy vetch stand and letting the roots decompose *in situ*. This technique, which accounts for all types of root-C inputs to the soil, could be applied in this case because of the short duration of the experiment. All other studies of Table 1 used measured root biomass. Barber and Martin (1976) and Barber (1979) suggest that root exudation, turnover and cell sloughing represent an annual input of fresh root C into cropped soils equivalent to that of the measurable root biomass. Therefore, we used 200% of the measured root biomass C as an

Table 1. Relative contribution factor of roots vs. shoots to total SOC = (root-derived soil C/total root C input)/(shoot derived soil C/total shoot C input). Total SOC includes particulate organic matter from plant debris and finer texture pools of soil C

Method & crop type	Duration (months)	Relative contribution	Evaluation methods		References
			Total root C input	Tissue-derived soil C	
I. Root systems grown <i>in situ</i>					
Maize	132	1.50	200% Root biomass	Bare fallow control	Barber (1979)
Maize	48	1.75	200% Root biomass	Natural abundance <sup>13</sup> C	Balesdent and Balabane (1996)
Maize	180	1.70	200% Root biomass	Natural abundance <sup>13</sup> C	Bolinder et al. (1999)
Maize	152	3.30 <sup>a</sup>	200% Root biomass	Natural abundance <sup>13</sup> C	Clapp et al. (2000)
Hairy vetch ( <i>Vcia Villosa</i> )	5	3.70	Root biomass + <sup>13</sup> C SOC	<sup>13</sup> C labelling	Puget and Drinkwater (2001)
Alfalfa	24	2.70	200% Root biomass	Bare fallow control	Rasse (unpublished data)
average	90	2.40			
II. Incubation: shoot and root material mixed into soils					
Barley ( <i>Hordeum vulgare</i> )	60	1.33	Measured input	<sup>13</sup> C labelling	Broadbent and Nakashima (1974)
<i>Medicago</i> sp.	1	1.22	Measured input	<sup>14</sup> C labelling	Amato et al. (1984)
<i>Medicago</i> sp.	24	1.45	Measured input	<sup>14</sup> C labelling	Amato et al. (1984)
<i>Miscanthus giganteus</i>	20	1.26	Measured input	No-input control	Beuch et al. (2000)
Clover ( <i>Trifolium repens</i> )	3	1.30	Measured input	No-input control	de Neergaard et al. (2002)
Ryegrass	3	1.24	Measured input	No-input control	de Neergaard et al. (2002)
Average	18	1.30			
III. Incubation: litter-bag experiments					
<i>Fagus sylvatica</i>	36	1.55	Measured input	Total C in bag	Scheu and Schauerermann (1994)
<i>Festuca vivipara</i>	2	1.5	Measured input	Total C in bag	Robinson et al. (1997)
<i>Festuca vivipara</i>	13	2.1	Measured input	Total C in bag	Robinson et al. (1997)
<i>Poa liguralis</i>	21	0.94	Measured input	Total C in bag	Moretto et al. (2001)
<i>Stipa clarazii</i>	21	0.86	Measured input	Total C in bag	Moretto et al. (2001)
<i>Stipa tenuissima</i>	21	0.77	Measured input	Total C in bag	Moretto et al. (2001)
<i>Lepidium lasiocarpum</i>	3	1.33	Measured input	Total C in bag	Parker et al. (1984)
Average	17	1.29			

<sup>a</sup>average value of no-till and chisel-plough systems.

estimate of the total input of fresh root C into soils. We conducted similar calculations to that of Barber (1979) on the data extracted from Balesdent and Balabane (1996), Clapp et al. (2000) and Rasse (unpublished data). This doubling of the root biomass effectively reduces by half the estimated lifetime of root carbon into soils as compared to that of shoots, and therefore produces conservative estimates of the relative contribution factor of roots vs. shoots to SOC.

Incubation experiments are conducted with precisely measured amounts of roots and shoots and therefore do not require any hypothesis on non-root-biomass contributions. In the experiments where residues are directly mixed into soils, the final contribution to SOC was measured by differential CO<sub>2</sub> loss between the incubated sample and a control (Beuch et al., 2000; de Neergaard et al., 2002) or through

the use of <sup>13</sup>C (Broadbent and Nakashima, 1974) or <sup>14</sup>C labelled material (Amato et al., 1984). In the litter-bag experiments, the final amount of organic material present in the litter bag is directly determined. The fairly short duration of most incubation experiments suggests that they mostly evaluate the relative decomposition of roots vs. shoots, i.e. the contribution of particulate organic matter (POM) to SOC, and not so much the contribution of their constitutive carbon to more stable SOM pools. Incubation experiments measure essentially the relative chemical recalcitrance of root- vs. shoot-tissue, as will be discussed later in this review.

The *in situ* root growth experiments indicate that the relative root contribution to SOC has an average value 2.4 times that of shoot, with a minimum of 1.5 and a maximum of 3.7 (Table 1). The relative contribu-

tions to the soil organic C pool of root vs. shoot tissues appears consistently greater than 1.0 and remarkably high (Table 1), which confirms the dominant role of root C in soils as suggested by several authors (Boone, 1994; Milchunas et al., 1985; Norby and Cotrufo, 1998). Several long-term studies in wheat and maize systems reported no detectable shoot restitution effect on SOC contents (Campbell et al., 1991; Clapp et al., 2000; Reicosky et al., 2002), which supports the finding that the mean residence time in soils of root-derived C is longer than that of shoot-derived C. These data have not been included in Table 1 because it would correspond to an infinite value for the relative contribution of roots vs. shoots to SOC. In addition, our estimated value corroborates the report by Six et al. (2002b) that the absolute contribution of roots to the total particulate organic matter occluded within soil aggregates ranges between 1.2 and 6.1 times that of shoots.

Incubation studies yield a relative contribution factor of roots vs. shoots to SOC of 1.3 (Table 1). This value appeared quite consistent among studies, and between free-soil mixing and litter-bag experiments. Incubation studies do not consider all the SOM stabilisation mechanisms that favour the selective preservation of root-derived C in soils, such as the physical and physico-chemical protections that we will discuss later in this review (Figure 1). This potentially explains why this 1.3 factor is lower than the 2.4 factor derived from the six *in situ* root growth studies. A regression analysis conducted throughout all the data presented in Table 1 indicated no significant correlation between the duration of the experiment and the relative contribution factor of roots vs. shoots to total SOC ( $r^2 = 0.06$ ). The *in situ* root growth data (Table 1), together with the supporting evidences from the incubation studies (Table 1) and the numerous other studies cited in this section, leave little doubt that root C has a longer residence time in soils than shoot carbon does. This raises the question of the mechanisms that specifically protect root C from mineralization in soils.

## Mechanisms

Before analysing the explanatory mechanisms for the specific preservation of root C in soils, we have to consider the alternate hypothesis that such a specific preservation does not exist and results instead either from an underestimation of root C flux to soil or from a dominant priming effect of shoot tissues on SOM

mineralization. The first explanation, i.e. measurement artefact, implies that the phenomenon is not there at all. The second explanation implies that root and shoot tissues have specific effects on SOC but that the accumulated C is not preferentially that of root origin.

### *Is there an underestimation of root C flux to soil?*

Underestimation of root C flux to soil could potentially bias estimates of total root C contributions. Such an artefact can be generated by the large uncertainty on C contributions from root exudation and root cell sloughing. For this reason, we used the conservative estimate that root biomass on the one hand and root exudation and root cell sloughing on the other hand contributed equally to SOC stocks, as suggested by Barber and Martin (1976) and Barber (1979). The original data of Balesdent and Balabane (1996), which did not consider root exudation, yield a root/shoot relative contribution factor of 3.5. We doubled their estimated root contribution to take into account root exudation and turnover, which reduced the relative root contribution to SOC to 1.75 (Table 1). The same correction for root exudation was applied to the data of Barber (1979), as presented in his paper, and to our own estimates for alfalfa (*Medicago sativa*) root contributions (Table 1). This contribution of root exudation is likely to be overestimated. Balesdent and Balabane (1996) observed that the distribution of newly added C was identical for the root and shoot treatments throughout a range of particle size distributions. They argued that if root exudation was a major contributor to soil C, the finer fractions would have been more enriched in the root treatment as compared to the shoot treatment, which was not the case. It remains difficult to assess the estimate of Barber and Martin (1976) and Barber (1979) that the contribution of rhizodeposition to SOC equals that of root biomass. Although some older studies suggest that this contribution might even be higher (Smucker, 1984), more recent studies suggest that the estimate of Barber (1979) is likely an upper value (Hütsch et al., 2002; Xu and Juma, 1994). These elements indicate that the relative contributions to SOC of roots vs. shoots that we computed in Table 1 are more likely underestimated than overestimated.

Additional evidences clearly demonstrate that the larger relative contributions of roots vs. shoots to SOC are not an artefact induced by underestimation of root-C flux. The results presented by Puget and Drinkwater (2001), i.e. root/shoot relative contribution factor of 3.7, were obtained on the basis of the total root con-

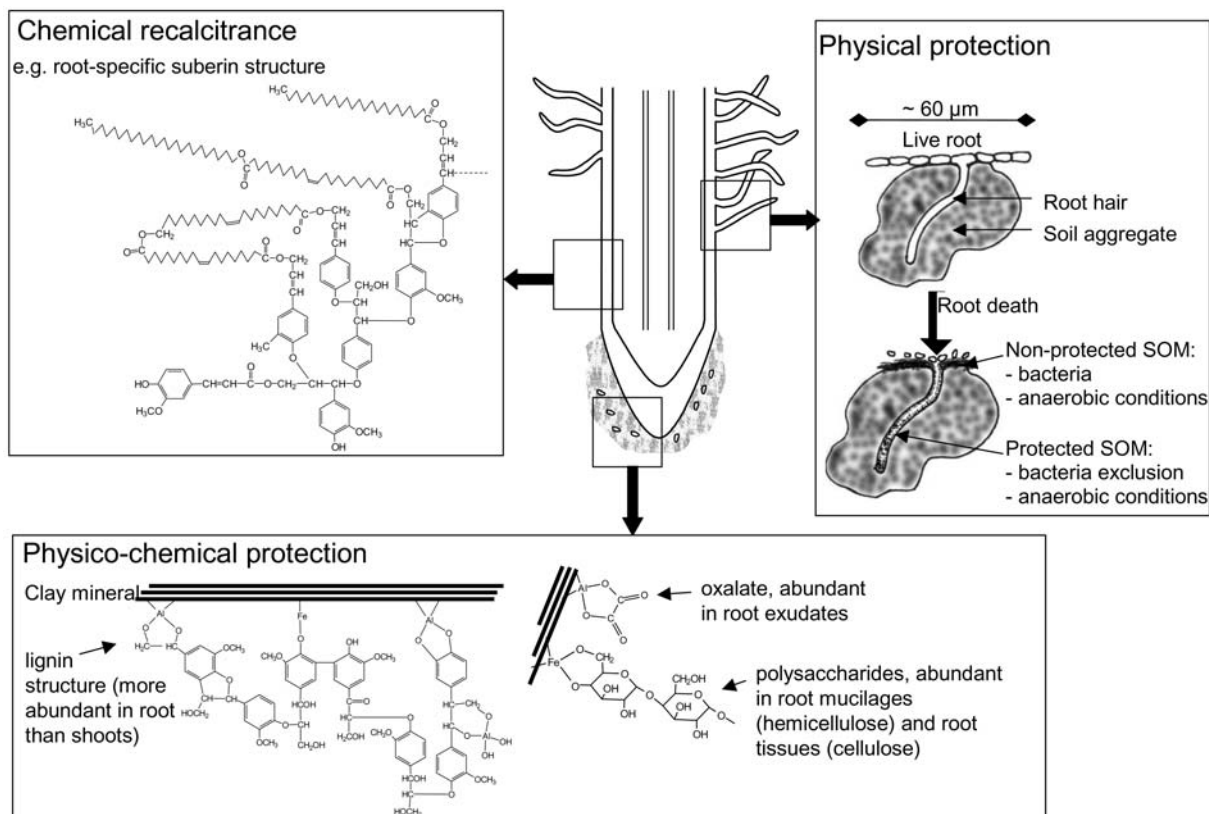


Figure 1. Schematic representation of the main processes resulting in the specific protection of root C in soils

tribution to SOC, which was estimated through  $^{13}\text{C}$  measurements of the whole soil organic matter. In their study the direct root biomass-C contribution was only 60% of the total root C contribution to soil, which implies that they would have obtained a relative contribution factor in excess of 5 based on root biomass alone. At last, incubation studies, where known amounts of root and shoot material are incorporated to soil, also indicate a preferential preservation of root C in soils (Table 1).

#### *Priming effect due to rhizodeposition and incorporation of shoot-derived plant litter*

Priming effect of plant residue on SOC mineralization has been reported in numerous studies for more than half a century, as reported in the literature reviews of Kuzyakov et al. (2000) and Fontaine et al. (2003). Rhizodeposition of root exudates can lead to C accumulation or C consumption (Kuzyakov et al., 2001). Soluble root exudates are labile compounds, which are preferentially decomposed and represent a carbon source for soil microbial biomass (Merckx

et al., 1985). The liberation of these substances into the rhizosphere can change the decomposition rate of soil organic matter and is referred to as priming effect (Kuzyakov et al., 2002). Several long-term studies have reported that SOC contents remained unchanged or were decreased by the addition of shoot residues to cropped soils as compared to the root contribution alone (Campbell et al., 1991; Clapp et al., 2000; Reicosky et al., 2002; Soon, 1998). In a two-year alfalfa experiment, SOC contents of Bt horizons of a bare fallow soil were decreased, although not significantly so, by the application of  $12 \text{ Mg ha}^{-1}$  of alfalfa shoot mulch (Rasse et al., 1999). Such results imply a priming effect of shoot-derived substances on the degradation of soil organic matter.

For the priming effect to be an explanatory mechanism of preferential root C preservation in soils, SOC mineralization must be more enhanced by shoot than root compounds. Although early studies have suggested that the presence of active root systems in soils could actually reduce the rate of SOM mineralization (Reid and Goss, 1982; Reid and Goss, 1983 in Cheng

et al., 2003; Sparling et al., 1982), more recent evidences point to a positive priming effect of living roots (Cheng et al., 2003; Fu and Cheng, 2002; Helal and Sauerbeck, 1986; Liljeroth et al., 1994;). At least one study indicates that root priming effect is of lesser magnitude than that of shoots (Kuzakov et al., 1999). Nevertheless, one study is certainly not enough to conclude given the great variability of priming effect responses to experimental conditions such as soil type, climate and plant species (Kuzakov et al., 2000).

Most importantly, differential priming effect does not explain the majority of the results presented in Table 1. The studies based on isotopic techniques traced the fate of newly added C independently from the mineralization of the old SOC (Balesdent and Balabane, 1996; Clapp et al., 2000; Puget and Drinkwater, 2001), which excludes the possibility that these results were influenced by differential priming effects on the old SOC. The same is true for the results of the incubation studies presented in Table 1. In summary, neither the underestimation of root C flux to soil nor a preferential shoot priming effect on SOM mineralization explains the higher relative contribution to SOC of roots vs. shoots as presented in Table 1. This raises the question of the mechanisms that preferentially preserve root C in soils. These mechanisms are represented in Figure 1.

#### *Chemical recalcitrance*

Chemical recalcitrance of plant litter material is generally attributed to the aromatic compound lignin (Tegelaar et al., 1989). Lignin is a polyphenolic molecule that has ether and C-C bonds. Microbial decomposition of this structure requires strong oxidation agents and only a limited number of soil microorganisms, namely the white-rot fungi, are able to completely mineralise lignin (Hammel, 1997). Biodegradability of plant litter material is often characterized through biochemical fractionation, such as the method of Goering and Van Soest (1970). This method leads to the quantification of a series of organic molecule fractions displaying decreasing biodegradability: acid soluble compounds, cellulose and lignin. The so-called lignin fraction obtained with this method actually includes other recalcitrant constituents such as tannins, cutins and suberins. Within a given species, the lignin content of roots obtained by the method of Goering and Van Soest (1970) is on average more than double than that of shoots (Table 2). Fernandez et al. (2003) investigating the chemical composition of roots and shoots of

ryegrass (*Lolium perenne*), *Pinus pinaster* and *Cocos nucifera* also observed that roots were more lignified than the aerial parts of the same species. Root and shoot lignins appear of similar molecular structure (Weichert, 1981), which suggests that the quantity of lignin itself is the main potential driver of differential degradation between roots and shoots. The lignin to N ratio has been proposed as a better indicator of chemical recalcitrance than lignin content alone and used extensively to distinguish plant residues that are difficult to degrade, i.e. high lignin/N ratio, from those that are more easily biodegraded, i.e. low lignin/N ratio (Moore et al., 1999; Parton et al., 1987; Paus-tian et al., 1992; Tietema and Wessel, 1992). The lignin/N ratio of root tissues approaches on average three times that of shoot tissues (Table 2).

In addition to lignin and N contents, other chemical composition traits of roots can potentially increase their chemical recalcitrance relative to that of shoots. Low phosphorus (P) content in the roots of tropical grass species has been suggested to control their rate of decomposition (Gijsman et al., 1997). Roots, as compared to shoots, have less readily decomposable soluble compounds (Beuch et al., 2000; Mary, 1987). Studies have suggested that condensed tannins play an important role in plant residue turnover, because they are selectively preserved upon microbial decay (Tegelaar et al., 1989). Tannins, along with lignins, are polyphenols involved in conferring rigidity to woody materials. They are the most abundant constituents of plants after cellulose, hemicellulose and lignins (Kögel-Knabner, 2002). Tannins, like lignin and other polyphenols, are resistant to biodegradation (Kraus et al., 2003 and references therein). The higher content of tannin-like substances in the roots of cereals may contribute to their slow late of decomposition (Waid, 1974).

Cutins and suberins are among the most recalcitrant plant molecular structures in soils (Tegelaar et al., 1989). Cutin is a polyester-like biopolymer that constitutes an integral part of the protective covering layer of above-ground vascular-plant tissues (Walton, 1990). Suberin is an analogous biopolyester, containing polyphenolic and polyaliphatic domains, that is mostly found in root tissues but is also present in the above-ground organs of woody species that undergo secondary thickening (Bernards, 2002). Therefore, while cutin is a shoot-specific compound, suberin is a good tracer of root activities only in ecosystems dominated by non-woody species. Both cutin and suberin polymers have a high potential for preservation within

Table 2. Lignin and lignin to N ratio of shoot and root tissues. Lignin quantification was conducted according to the method of Goering and Van Soest (1970)

Species	Lignin(%)			Lignin/N			Reference
	Roots (1)	Shoots (2)	Ratio (1)/(2)	Roots (3)	Shoots (4)	Ratio (3)/(4)	
<i>Chenopodium</i>	3.4	0.8	4.3	3.5	0.2	17.5	Gupta and Singh (1981)
<i>Desmostachya</i>	8.2	6.9	1.2	14.6	9.5	1.5	Gupta and Singh (1981)
<i>Dichanthium</i>	4.7	1.7	2.8	7.0	2.2	3.2	Gupta and Singh (1981)
<i>Sesbania</i>	2.1	1.6	1.3	1.5	1.4	1.1	Gupta and Singh (1981)
Hairy vetch	17.0	5.2	3.3	6.1	1.2	5.1	Puget and Drinkwater (2001)
<i>Leucaena</i>	8.0	2.0	4.0	3.8	0.7	5.4	Vanlauwe et al. (1996)
<i>Dactyladenia</i>	26.0	13.0	2.0	24.8	8.9	2.8	Vanlauwe et al. (1996)
<i>Flemingia</i>	4.6	3.0	1.5	1.1	1.8	0.6	Vanlauwe et al. (1996)
Rye grass	14.5	6.2	2.3	14.5	5.3	2.7	de Neergaard et al. (2002)
Clover	18.5	7.5	2.5	8.2	3.3	2.5	de Neergaard et al. (2002)
<i>Poa liguralis</i>	13.0	3.9	3.3	11.0	2.4	4.6	Moretto et al. (2001)
<i>Stipa clarazii</i>	16.0	4.9	3.3	12.0	2.7	4.4	Moretti et al. (2001)
<i>Stipa tenuisima</i>	19.0	7.9	2.4	17.0	8.7	2.0	Moretto et al. (2001)
Maize	9.5	6.6	1.4	–	–	–	Dignac et al. (2004)
Wheat	12.3	8.6	1.4	–	–	–	Dignac et al. (2004)
Average	11.8	5.3	2.2	9.6	3.7	2.6	

the mineral soil (Kögel-Knabner et al., 1989). Cutin and suberin, although being both polymers of hydroxycarboxylic acids, show some distinct differences in chemical composition (de Leeuw and Largeau, 1993). Therefore, these two molecules have a potential as biomarkers for the study of the contribution of root and shoot-derived litter to the organic matter of mineral soil. Recently, in grassland as well as forest soils, suberin was found to be a major contributor to the soil organic matter (Bull et al., 2000; Nierop et al., 2003).

Higher chemical resistance of root vs. shoot molecular structures implies that, all conditions being equal, molecular structures of root tissues are transformed at a slower rate in soil than their above-ground counterparts. Measuring this effect implies that root and shoot tissues are subjected to equal conditions in soils. Incubation studies meet this requirement, while field studies compound multiple effects on plant tissue decomposition. Incubation studies suggest that the mineralization rate of root tissues is intrinsically lower than that of shoot tissues, which points to a specific chemical resistance of root tissues as compared to that of shoot (Table 1). However, the experiments with free mixing of plant residues into soils do not demonstrate as such that untransformed plant molecules from roots are more resistant to chemical transformations as compared to those of shoots. Chemical recalcitrance can

not be inferred from the relative amounts of SOC generated by equal amounts of roots vs. shoots because the degradation rate of a molecular structure is not necessarily linked to the residence time of its constitutive C in soils, as recently pointed out by Gleixner et al. (2001). In other words, root tissues could decompose as fast as shoot tissues in soils but their transformation products would have longer residence time in soils. Litter bag experiments that compare final to initial litter tissue C can give us a better estimate of the chemical recalcitrance, with the caveat that most molecular structures remaining in the litter bag at the end of the experiment have not been transformed through microbial processes. The litter-bag experiments also indicate that, in general, root tissues are more chemically recalcitrant than shoot tissues (Table 1). Results from litter-bag experiments are consistent with those from experiments based on free mixing of plant residues into soils (Table 1), which suggests that both methods highlight a similar mechanism, i.e. the relative chemical recalcitrance of root- vs. shoot-derived molecular structures. Even when root residues have been ground prior to incubation, they are biodegraded more slowly than ground leaves (Waid, 1974). The relative contribution factor of roots vs. shoots obtained in incubation studies are well below those from the field studies, which have a median

value of 2.4. This comparison suggests that chemical recalcitrance explains about one fourth (+30% vs. +140%) of the longer turnover time of root-derived C in soils as compared to that of shoots.

*Physico-chemical protection through the interaction with minerals*

Close interaction of root tissues with the soil minerals has been suggested to be the main soil-specific protection pathway for root C (Balesdent and Balabane, 1996; Oades, 1995). Nevertheless, if such a direct contact promoted SOM stabilisation by itself then it would be logical that ploughing would increase the stabilisation of above-ground residue through increased contact with soil particles. Such is not the case, as most studies report that litter decomposition rates are increased by incorporation into surface soils (Hamadi et al., 2000). In a control  $^{14}\text{C}$  recovery experiment, Kisselle et al. (2001) observed a faster turnover of litter-derived C when incorporated into the soil. Stemmer et al. (1999) also report that the incorporation of cm-size shoot material to soil increases the rate of decomposition, although they suggest that this might not affect the final proportion of stabilised C. In addition, the dominant effect of ploughing on SOM dynamics is not stabilisation through increased contact between plant residues and soil particles. Indeed, ploughing either decreases the long-term storage of SOM in soils (Chan et al., 2002; Clapp et al., 2000; Doran, 1980; Franzluebbers et al., 1994; Sainju et al., 2002) or has no significant effect, especially when the entire depth of the soil profile is considered (Angers et al., 1995; Angers et al., 1997; Balesdent et al., 2000; Deen and Kataki, 2003). Therefore, the litter-turnover studies, supported by observation from ploughing experiments, indicate that closeness of contact between plant tissues and soil minerals does not necessarily imply increased preservation and stabilisation in soils. This implies that roots possess specific activities beyond their simple location within the soil proper that stimulates the interaction between root compounds and soil minerals. A recent review by Farrar et al. (2003) showed that roots interact with mineral soil in a manifold manner. The root cap is most important for release of compounds at the root-soil interface; root growth being the main factor determining carbon flow to the rhizosphere. There are two types of material deposited by roots: (1) water-soluble exudates such as sugars, amino acids and organic acids and (2) water-insoluble materials such as cell walls, sloughed-off

materials, and other root debris and mucilage (Brimecombe et al., 2001). Quantitatively, root exudation represents 7–8% of the total photosynthetic carbon (Farrar et al., 2003).

Plant roots produce organic acids varying in chain length with lactate acetate, oxalate, malate, citrate being the primary anion components. These molecules are generally considered as labile compounds that are mineralized within a few hours following release by roots (Chabbi et al., 2001; Grayston et al., 1996). Nevertheless, it is often ignored that due to their negative charge, these substances may become rapidly and readily sorbed to the mineral phase through cation bonding (Jones, 1998). For citrate, it was demonstrated that interaction with clay minerals and Fe oxides inhibits their degradation (Jones and Edwards, 1998). Di- and tri-carboxylic acids were found to be readily adsorbed to the solid phase, particularly in subsoil horizons containing abundant Fe and Al oxyhydroxides (van Hees et al., 2003). Fe oxides are effective sorbants of soluble organic matter (Kaiser and Zech, 1998). These soil minerals possess most of the available surface area in mineral soils (Kaiser and Guggenberger, 2000). Available surface area seems to govern the stabilisation of organic compounds (Saggar et al., 1996; Torn et al., 1997). Sorption of root-derived organic acids to the mineral phase may be more effective in subsoils with low contents of organic matter because mineral surfaces are not yet saturated with organic matter. Therefore, root-released compounds appear to have a selective advantage for stabilisation through binding on the mineral phase, especially so in deep soil horizons.

Extracellular polysaccharides from root mucilages are intrinsically labile compounds that play a major role as binding agents in soil aggregation (Oades, 1984). Due to their high content in hydroxy groups, they are very reactive and can form strong complexes with minerals and with other organic molecules. Early work reviewed by Oades (1978) showed that root mucilage is sorbed to clay material and stabilises microaggregates. As the root tip is continuously moving through soil pores, mucilage is distributed over mineral surfaces, which may result in intimate interactions. Root-derived insoluble carbon was found to be incorporated quicker into the soil microbial biomass than soil organic matter (Liang et al., 2002). These inputs of organic matter from root exudates and sloughing result in higher SOM concentration in rhizosphere than in bulk soil (Chiu et al., 2002; Sanchez and Bursey, 2002).



*Physical protection from microbial decomposers through aggregation*

The organic material released by roots plays a major role in the interaction between root, microorganisms and the mineral soil: roots improve aggregation by enmeshing soil particles together and by increasing microbial biomass which produces polymers that act as binding agents (Jastrow et al., 1998; Tisdali and Oades, 1979). The availability of organic carbon for microbial decomposition is limited when it is found inside soil aggregates (Golchin et al., 1994). The roots of *Arachis grabiata* and perennial weeds were found to improve aggregation in the subsurface horizons (Sainju et al., 2003), rather than increasing the C and N pools within the aggregates. Studies suggest that root carbon contributes more than shoot carbon to the formation of stable aggregates (Gale et al., 2000; Puget and Drinkwater, 2001), although the opposite was also observed when the shoot-C input largely exceeded that of roots (Rasse et al., 2000). The existence of stable macroaggregates in soil is very important for the stabilisation of SOM, because the formation of stable microaggregates is fostered within macroaggregates.

The increased aggregate stability may be attributed to the production of rhizosphere polysaccharides (Reid and Goss, 1981; Traoré et al., 2000) and/or fungal hyphae associated with the plant roots (Haynes and Beare, 1997; Tisdall and Oades, 1979; Tisdall et al., 1997). Apart from the chemical composition of mucilage (Watt et al., 1993), the soil water regime was shown to determine the formation and stability of soil adhering to the root surface (Watt et al., 1994). The tensile strength of aggregates adjacent to roots was shown to increase by intense and periodic drying of the soil resulting from evapotranspiration (Horn and Dexter, 1989). Using root mucilage analogues, Czarnes et al. (2000) demonstrated in a controlled study with wet and dry cycles that the stabilisation of soil structure around the root is due to interactive effects, such as increase of the bonding strength and diminution of the wetting rate.

The size of some root components and the scale of root activities appear particularly relevant to the specific physical protection of root-derived material as compared to that of shoots. Root hairs, which are appendages of root epidermal cells, are from 5 to 17  $\mu\text{m}$  across and from 80 to 1500  $\mu\text{m}$  long, depending on the species (Wulfsohn and Nyengaard, 1999). Figure 2 illustrates how grass roots produce abundant root

hairs, about 10  $\mu\text{m}$  across, which penetrate soil aggregates. Some plant families, such as the *Epacridaceae*, possess extremely fine roots of diameter approaching 50  $\mu\text{m}$  (Allaway and Ashford, 1996; Briggs and Ashford, 2001). In addition, most plant species transfer photosynthetically-fixed organic compounds to mycorrhizal fungi. These fungal hyphae are just a few micrometers across and seem to intensively exploit soil zones (Dodd et al., 2000). Properties of mycorrhizal fungi have been suggested to largely control the stabilisation of root-derived C in soils (Langley and Hungate, 2003). The most active components of root systems and associated mycorrhiza are ranging from a few to a few tens of micrometers across. This scale is especially relevant to physical protection of soil organic matter, which results from two main mechanisms: (1) the inaccessibility of fine pores to microbial decomposers and (2) the anoxic conditions prevailing in these fine pores (Six et al., 2002a) (Figure 1). Although microaggregates are generally defined as smaller than 250  $\mu\text{m}$ , the most stable ones are comprised within the 2–20  $\mu\text{m}$  fraction (Krull et al., 2003). Bacteria are not able to penetrate soil pores smaller than 3  $\mu\text{m}$  (Kilbertus, 1980). Pore size of about 10  $\mu\text{m}$  defines the boundary between free drainage water and capillary water (Kirkham and Powers, 1972). This implies that anoxic conditions are much more likely to prevail in soil pores of diameter smaller than 10  $\mu\text{m}$ . Through root hairs, mycorrhiza, and also fine roots to a lesser extent, root systems contribute a direct input of particulate organic matter at a scale corresponding to that of the physically protected carbon.

Here, we defend the hypothesis that numerous root activities happen at the 10- $\mu\text{m}$  scale where physical protection readily occurs, while incorporated shoot material undergoes a long decomposition process from the centimetric to the 10- $\mu\text{m}$  scale before reaching physically protected sites. In addition, interactive effects on decomposition rates between particle size and chemical composition, as suggested by Bending and Turner (1999), might further explain the protection of root C in soils.

*Protection by metal ions*

An explanation for lower decomposability of root-derived organic matter as compared to that of shoot origin may be the preferential incorporation into root litter material of metal ions such as Al and Fe. This selective preservation mechanism concerns mostly acid forest soils, where iron and aluminium are the most

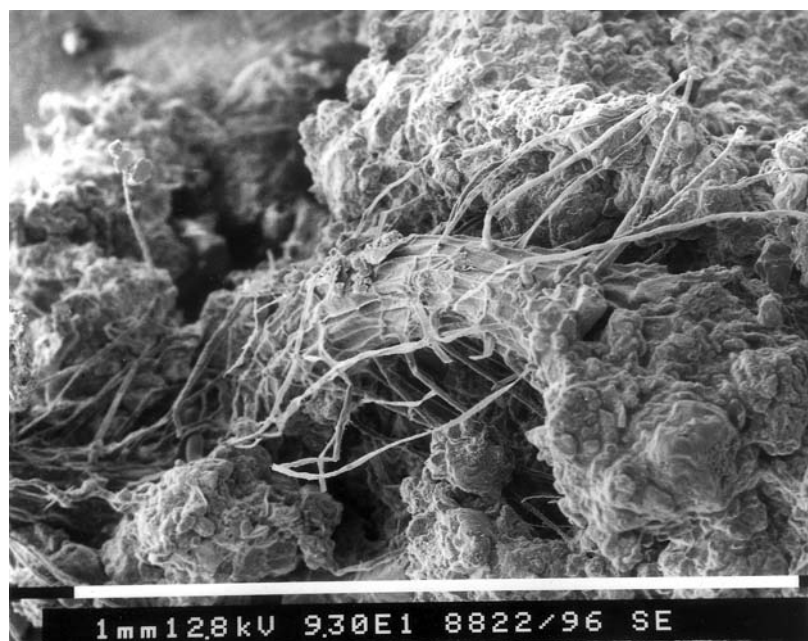


Figure 2. Scanning electron micrograph of a rye-grass root with root hair penetrating through soil aggregates (picture courtesy of Claire Chenu).

abundant metal ions in the soil solution. Aluminium has been recognized as a potential inhibitor of microbial degradation (Kinraide and Sweeney, 2003) especially if directly bound to organic matter (Fransson et al., 2003). Root enrichment in Al may occur in natural forest soils under coniferous trees, a vegetation leading to acidification of the surface soil. In a laboratory experiment with *Pinus* seedlings grown in Al enriched solution, root concentrations in Al were increased relative to those measured in shoots (Heim et al., 2003). In addition, X-ray microanalyses have shown that high levels of Al can be found in the root cortical apoplast of *Picea abies* growing in acid soil (Jentschke et al., 2001). In coniferous forest, a double effect may lead to preferential stabilisation of root carbon. Recalcitrant shoot-derived organic debris are not incorporated into the mineral soil – they accumulate on the forest floor leading to acidification and mobilisation of Al in the mineral soil. In turn, Al may be incorporated into the roots, thereby preventing their biodegradation.

In acid soils, there is also a high potential for iron release into the soil solution after acidic weathering of minerals. Acidic weathering may take place through the release of root exudates. The organic material in the rhizosphere may in turn interact with Fe, which promotes the formation of Fe oxides like ferrihydrite and organo-mineral complexes (Violante et al., 2003).

Similarly to the effect of Al and Fe in acidic soils, heavy metals such as Pb, Cu and Ni present in contaminated sites might selectively protect root organic matter. Indeed, several studies have demonstrated that plant growing on contaminated soils accumulated much larger quantities of heavy metal in their root tissues than in their shoots (Dahmani-Muller et al., 2000; De Vos et al., 1991; Derome and Nieminen, 1998). Nevertheless, this possible effect remains of limited significance to the global turnover of carbon in soils given the limited land area covered by such contaminated soils. This solely refers to the decrease of the plant residue decomposition because of the incorporation of heavy metals into plant tissue as being mainly connected with their toxicity for microorganisms.

Consequently, incorporation of metal ions into organic compounds appears as a likely mechanism for the selective preservation of root-derived SOM in acidic soils. This comes in addition to the very important role of polyvalent cations such as Mn, Ca and Mg for the stabilisation of SOM independent of its origin (Baldock and Skjemstad, 2000). The magnitude of the specific effect of metals on the stabilisation of root- vs. shoot-derived SOM remains difficult to evaluate. We suggest that more work is needed to examine organic matter origin and composition and the incorporation of metals in order to elucidate the importance of this sta-

bilisation mechanism for root-derived organic matter in soils.

#### *Reduced decomposition in deeper soil layers*

Environmental conditions prevailing in the deep soil profile have long been suggested detrimental to the decomposition of plant tissues (Weaver et al., 1935 in Gill and Burke, 2002). In subsoil horizons, the amount and activity of soil microorganisms was found to be minimal, with fungi being absent from the deep soil (Taylor et al., 2002). Pregitzer et al. (1998) suggested that larger and woodier root structures in deeper soil layers combined with low nutrient concentrations explain the lower decomposability. Nevertheless, although some studies report reduced decomposition rates with soil depth (Gill and Burke, 2002; Gill et al., 1999) others found no significant effect (Weaver, 1947) or observed increased decomposition rates with depth (Rovira and Vallejo, 2002). Even assuming that the overall effect is a reduced decomposition rate with soil depth, this reduction in decomposition rate could not account for the larger than expected accumulation of C in deep soil profiles (Gill and Burke, 2002; Paul et al., 1997; Van Dam et al., 1997). Therefore, the potential change of root litter decomposition rate with depth is probably ecosystem specific and might not play a substantial role in specifically preserving root carbon.

The specific preservation of soil C with depth is likely to stem from the physico-chemical protection of root carbon through interactions with soil minerals, according to the mechanisms described earlier in this article. Physico-chemical protection is thought to play an especially important role below the A horizon (Eusterhues et al., 2003). Jobbagy and Jackson (2000) found a correlation between the vertical organic carbon distribution and the clay content suggesting that in deep soil the organic matter may be associated in high proportions with the clay size fraction. Recently, evidence was provided that with increasing stabilisation of organic carbon in subsoils under forest, higher amounts of carbon are associated in the clay fractions. Chemical analyses suggested that (1) aliphatic compounds and (2) low molecular weight organic acids are present in close association with the mineral phase (Rumpel et al., 2004). Both components could be root-derived.

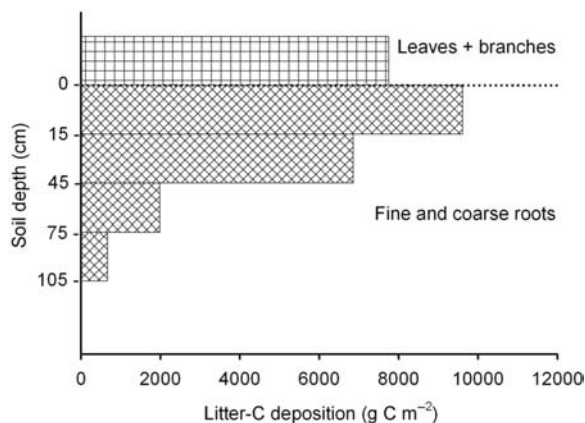


Figure 3. Simulated production of litter carbon over the lifespan of a 90-year old beech forest in Vielsalm (Belgium). Stemwood removal from the forest plot was simulated at harvests.

#### **Implications for C storage throughout the soil profile**

Dominant contribution of root-derived material to stable SOM requires not only that the residence time of root C in soils is longer than that of shoots but also that the amounts of root C incorporated into the soil profile through root turnover processes represent a substantial portion of the total C input to soils. A dominant contribution of root vs. shoot C to soils is certainly true in cropped systems where little above-ground residues are returned to soils, such as silage corn production systems for example. This dominant root contribution is not limited to crop systems. We used the TRAP mechanistic model (Rasse et al., 2001) to assess the total root and shoot-C litter production in temperate forests. This result indicates that during 66 years of Scots pine growth in Belgium more root C was returned to soils through root growth and turnover than the combined contributions of leaf, branch and stem litter (Rasse et al., 2001). A similar simulation conducted for 90 years of beech growth indicated that substantially more litter C was generated by root turnover than by above-ground leaf and branch litter, when stems were removed at harvest as under normal management practices (Figure 3). In grassland ecosystems, Gill et al. (2002) report that above- and below-ground productivity values are about equal. With equal to larger quantitative C contributions and longer-lived C in soils than shoots, roots potentially contributed most of the organic C currently stored in soils of most ecosystems. The preponderant contribution of root systems to soil C pools is likely to increase

with soil depth. Limited transport of shoot-derived organic material by soil faunal activity, implies a high contribution of root litter to SOM of subsoils (Fisher et al., 1994). This hypothesis was supported by the work of Nierop (1998) studying the composition of organic matter in B horizons, who found that a substantial proportion of the soil organic matter is derived from suberin, which is the protective layer of plant roots.

We have presented so far numerous evidences supporting the hypothesis that soil C is mostly composed of root C and increasingly so with soil depth. Nevertheless, implications in terms of carbon storage are not trivial. Root growth and distribution in soils explain little of the vertical distribution of soil C stocks and ages. No correlation was found between the vertical organic carbon distribution in the mineral soil and vegetation type (Jobbagy and Jackson, 2000), although some studies suggest that the vertical distribution pattern of carbon differs after a vegetation change (e.g. Fisher et al., 1994; Parfitt et al., 1997), which may be related to different rooting intensity of the plants. A large increase in  $^{14}\text{C}$  age with soil depth up to several thousand years was observed in several studies (Paul et al., 1997; Rumpel et al., 2002; Scharpenseel et al., 1989). Mean root age increases with soil depth (Gaudinski et al., 2001), but the maximum age of fine roots is in the range of 20 years (Gaudinski et al., 2000, 2001), which does not explain the very old age recorded for organic carbon found in subsoils. In surface-soil horizon, soil tillage practices and residence time of residue appear to have strong interactions with the proportion of root vs. shoot C stabilised in soils (Table 1 of this study; Six et al., 2002b; Wander and Yang, 2000). Currently, these poorly understood processes of C cycling in soils are hindering our ability to connect root-C inputs to the accumulation of stable SOM.

We believe that our understanding of plant tissue specific contributions to SOM will increasingly benefit from organic geochemistry methods of gas chromatography coupled to mass spectrometry (GC-MS) that allow for the identification of specific molecular structures in soils. Indeed, plant compounds of root origin have recently been traced through the identification of suberin structures (Bull et al., 2000; Nierop et al., 2003). These organic geochemistry techniques can now be coupled to compound-specific  $^{13}\text{C}$  isotopic signature measurements to quantify the lifespan of plant-derived molecular structures in soils where a vegetation change from C3 to C4 plants occurred

(Dignac et al., 2004). Such measurements are conducted by coupling a GC to an isotope ratio mass spectrometer via a combustion interface (GC-C-IRMS). Although few plant molecular structures appear entirely specific of either root or shoot tissues, coupled investigations of molecular structures by GC-MS and of their  $^{13}\text{C}$  isotopic signatures by GC-C-IRMS hold great promise for unravelling the distribution and fate of root compounds in soils.

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